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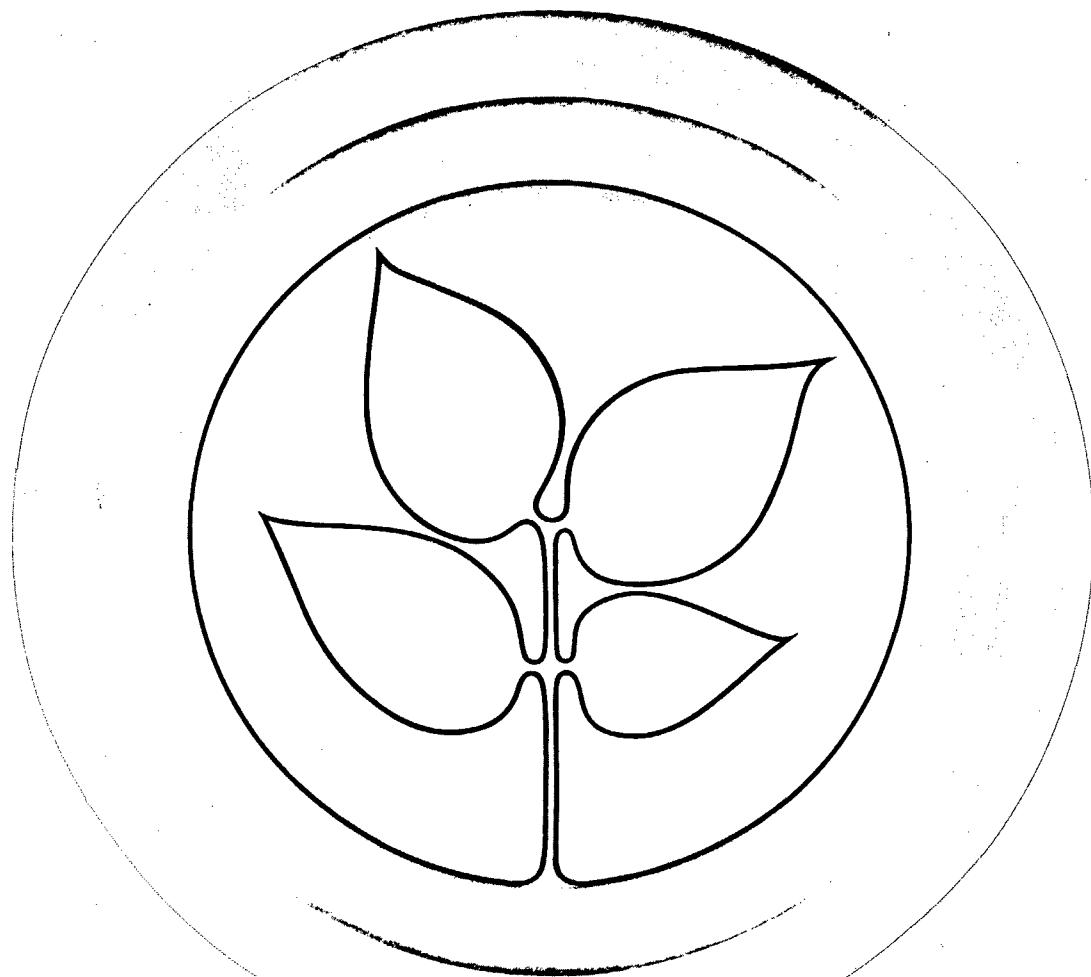
Plant response to climatic factors

Proceedings of the Uppsala Symposium

Réponse des plantes aux facteurs climatiques

Actes du colloque d'Uppsala

Unesco



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Réponse des plantes aux facteurs climatiques

Proceedings of the Uppsala symposium

Edited by R. O. Slatyer

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Foreword

Avant-propos

A symposium on Plant Response to Climatic Factors was held in Sweden, from 15 to 20 September 1970. It was organized by Unesco in co-operation with the Swedish Government, and in consultation with FAO and WMO. It took place at the Agricultural College of Sweden at Uppsala, where the Department of Plant Husbandry provided the local arrangements. Professor E. Åberg was chairman of the local organizing committee and president of the symposium. Dr U. Wünsche was secretary of the organizing committee.

The purpose of the meeting was to stimulate research in environmental biology, particularly the area dealing with the physical and biological basis of agroclimatology, with a view to improving present knowledge of the way in which primary climatic factors influence plant responses and of the way in which this knowledge can be applied to practical agroclimatological problems. It was also intended to bring together biologists concerned with environmental physiology and environmental scientists concerned with environmental physics and agroclimatology. The role of phytotrons as research tools in environmental biology was recognized.

The interest of the scientific community in these questions was demonstrated by the participation of more than 130 specialists from 25 countries. The opening address of the symposium was given by H. E. Mr I. Bengtsson, Minister of Agriculture of Sweden. It was followed by addresses by L. Hjelm, Rector of the Agricultural College of Sweden at Uppsala, by Michel Batisse, Director, Natural Resources Research Division of Unesco, and by Professor E. Åberg.

The programme was divided into two parts: the first dealt with basic physiological responses of plants to light, temperature and water; the second with the evaluation of these factors in agroclimatology. Special emphasis was put on cereals and other economic crop plants.

Organisé en collaboration avec le gouvernement suédois et en consultation avec la FAO et l'OMM, le colloque de l'Unesco sur la réponse des plantes aux facteurs climatiques s'est tenu à l'Institut agronomique de Suède (Uppsala) du 15 au 20 septembre 1970. Le comité local d'organisation avait pour secrétaire le docteur U. Wünsche et pour président le professeur E. Åberg. Ce dernier a été désigné comme président du colloque.

L'objet de cette réunion scientifique était de stimuler les recherches sur la biologie de l'environnement, notamment sur les bases physiques et biologiques de l'agroclimatologie, afin de mieux connaître le mécanisme par lequel les facteurs climatiques primaires influent sur la réponse des plantes et les moyens d'appliquer cette connaissance aux problèmes pratiques d'agroclimatologie. Il s'agissait en outre de mettre en contact des biologistes s'intéressant à la physiologie du milieu et des spécialistes de la physique et de l'agroclimatologie du milieu. Le rôle des phytotrons comme instruments de recherche sur la biologie de l'environnement a été reconnu.

L'intérêt que porte le monde scientifique à ces questions a été mis en évidence par le nombre important de spécialistes qui ont participé au colloque: plus de 130, appartenant à 25 pays. Le colloque a été ouvert par un discours de S. Exc. M. I. Bengtsson, ministre de l'agriculture de Suède, et par des allocution de M. L. J. Hjelm, recteur de l'Institut agronomique de Suède (Uppsala), de M. Michel Batisse, directeur de la Division des recherches relatives aux ressources naturelles (Unesco), et du professeur E. Åberg.

Le professeur E. Ackerberg, de l'Association suédoise pour les semences, a prononcé l'allocution de clôture.

Le programme comprenait deux parties: la première concernait les réponses physiologiques fondamentales des plantes à la lumière, à la température et à l'eau; la seconde, l'évaluation de ces facteurs en agroclimato-

The first part of the programme consisted of three major sections:

The effect of light on plant growth, development and yield.

The effect of temperature on plant growth, development and yield.

The effect of internal water status on plant growth, development and yield.

The second part of the programme consisted of two major sections, each having two subdivisions. There were:

Estimation of the radiation and thermal microenvironment from meteorological and plant parameters.

Development of simplified agroclimatic procedures for assessing temperature effects.

Estimation of internal crop water status from meteorological and plant parameters.

Development of simplified agroclimatic procedures for assessing effects of water supply.

In each section a key review paper was commissioned and, in addition, contributed papers were invited from participants.

Altogether some sixty papers were contributed and most of them appear in this volume. The authors have had the opportunity of reviewing their papers in the light of discussions at the symposium. It has, therefore, been decided not to reproduce the discussions. The points of view expressed are those of the authors and are not necessarily endorsed by Unesco.

Taking an overall view of the conference, several conclusions can be drawn. In the first place, it appears that the upsurge of activity in modelling such processes as crop photosynthesis and crop transpiration, which has taken place over the past few years, has had two important results. One is that it has highlighted research problems in plant physiology and environmental physics, and active study of many of these problems is now under way. The other is that there has been an application of these models and the associated techniques to the development of simple, but realistic, practical procedures which can be used in agroclimatology.

Secondly, there now appears to be considerable interest among plant physiologists in using phytotrons to provide environmental control for studies at the cellular and tissue level, as well as at the whole plant level. This reflects increasing awareness of the contribution that phytotrons can make as biological research tools. Such studies should furnish quantitative information of great value in providing a biochemical and physiological interpretation of environmental effects on plant responses.

Another desirable outcome of the meeting was the degree of communication which was possible between biological and environmental scientists, a phenomenon which was rather unusual even a few years ago. In addition, there appeared to be a high degree of communication between the physicists and the physiologists concerned with leaf and plant physics and crop micro-

logic. On s'est occupé particulièrement des céréales et d'autres cultures d'intérêt économique.

La première partie du programme comportait trois sections:

Effet de la lumière sur la croissance, le développement et le rendement des plantes.

Effet de la température sur la croissance, le développement et le rendement des plantes.

Effet de l'état hydrique interne des plantes sur leur croissance, leur développement et leur rendement.

La seconde partie du programme était divisée en deux sections, comprenant chacune deux subdivisions, à savoir:

Estimation du rayonnement et du micro-environnement thermique d'après les paramètres météorologiques et les paramètres des végétaux.

Mise au point de techniques agroclimatiques simplifiées pour évaluer les effets de la température sur le développement des cultures.

Estimation de l'état hydrique interne des plantes cultivées d'après les paramètres météorologiques et végétaux.

Méthodes agroclimatiques simplifiées pour évaluer l'effet de l'approvisionnement en eau.

Pour chaque section, on avait demandé un rapport de synthèse, et les participants avaient en outre été invités à présenter des communications.

Au total, une soixantaine de communications furent présentées. La plupart figurent dans le présent volume. Comme les auteurs ont eu l'occasion de revoir leurs communications à la lumière des débats du colloque, il a été décidé de ne pas reproduire les débats. Les points de vue exprimés sont, bien entendu, ceux des auteurs et n'engagent pas nécessairement l'Unesco.

De l'ensemble des débats on peut tirer plusieurs conclusions. D'abord, il semble que, ces dernières années, le développement rapide des activités tendant à établir des modèles de processus tels que la photosynthèse et la transpiration des cultures ait eu deux résultats importants: le premier est d'avoir mis en lumière des problèmes de recherches sur la physiologie végétale et la physique du milieu, dont beaucoup sont activement étudiés à l'heure actuelle; le second est que ces modèles et les techniques qui leur sont associées ont été appliqués à la mise au point de méthodes simples et pratiques, utilisables en agroclimatologie.

En second lieu, les spécialistes de la physiologie des plantes paraissent actuellement porter un intérêt considérable aux phytotrons, grâce auxquels il est possible d'obtenir un milieu artificiel pour faire des études au niveau de la cellule et des tissus ou de la plante dans son ensemble. Cela montre qu'ils prennent de plus en plus conscience du rôle des phytotrons dans la recherche biologique. Ces études devraient permettre de recueillir de précieux renseignements quantitatifs en apportant une interprétation biochimique et physiologique des effets du milieu sur la réponse des plantes.

Le colloque a eu un autre résultat heureux: il a permis aux biologistes et aux spécialistes de l'environnement

meteorology, and the agroclimatologists and meteorologists concerned with the practical use of crop-environment information. The use of important parameters which couple plants to their environment, such as diffusive resistance to gas exchange, and leaf and surface temperature, has played an important part in providing a common language for these groups of scientists and should enable the development of increasingly effective procedures for agroclimatic analyses and surveys in the future.

Unesco wishes to thank the organizing committee and the Swedish authorities for having organized this symposium. The Organization also expresses its gratitude to Professor Slatyer, who kindly agreed to edit the papers for publication.

de communiquer largement entre eux, ce qui naguère ne se produisait que rarement. En outre, il a donné lieu à de nombreux échanges de vues entre, d'une part, les physiciens et les physiologistes qui s'intéressent à la physique des feuilles et des plantes et à la micrométéorologie des cultures et, d'autre part, les agroclimatologues et les météorologues qui s'intéressent à l'utilisation pratique des renseignements sur l'environnement des cultures. L'emploi d'importants paramètres reliant les plantes à leur milieu — comme la résistance de diffusion aux échanges gazeux et la température de la feuille et de la surface végétale — a joué un rôle majeur en ce qu'il a permis à ces groupes de spécialistes de parler un même langage; il devrait favoriser dans l'avenir la mise au point de méthodes de plus en plus efficaces pour les analyses et les études agroclimatiques.

L'Unesco tient à remercier le comité d'organisation et les autorités suédoises pour l'organisation de ce colloque. Elle exprime sa gratitude au professeur Slatyer, qui a accepté d'assurer la mise au point rédactionnelle des communications en vue de leur publication.

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Introductory address: Climates and plants in world production of food

E. Åberg
Department of Plant Husbandry,
Agricultural College of Sweden,
Uppsala (Sweden)

When I studied the papers that have been submitted to this symposium I observed both the great variation in the subjects treated and the many angles from which the problems of plant response to climatic factors have been studied. These observations have made clear the great need for continued and new investigations in the field. One almost gets the feeling that plant scientists working with theoretical or practical problems in this field, or in both of them, have not only woken up to the importance of learning more about the problems of the response of plants to climatic factors; they have become fascinated by the findings of their investigations.

Furthermore, the preparations for this symposium have made me aware of the large number of scientists seriously working on the relationships between climates and plants. I have also noted—and this is most interesting and, I think, indicative of future development—that there is a considerable number of young people becoming interested in studying this field. A follow-up to their studies will, in many cases, undoubtedly be an engagement in scientific investigations in different sections concerning the interaction between climates and plants.

Faced with this situation, one may ask the question: Why do we have this development? One answer is natural. Instruments and other equipment for making more efficient studies of climatic influences and of plant responses to climatic factors have been rapidly developed during the last decades. Factors and reactions that could not be investigated a few years ago can now be readily studied or are within reach for study. This leads to new results, new interpretations. It stimulates new efforts. Computer techniques become more and more used not only for meteorological recordings and analyses, but also for gearing plant growth and analysis of plant developments into channels that make studies of the relationships between plants and climates more effective than before. Investigations with this aim are seriously

planned and carefully followed up. They are, in their nature, advanced and will, in all probability, become much more advanced in the foreseeable future. Still, they are not speculative in the same sense as certain reports in the literature which suggest methods for changing the climate in order to improve world food production. I think of methods like the one put forward by Vester (1970), namely that satellites circling around the world should be used for reflecting the sunrays in order to multiply food production.

My intention in the statements made so far is to focus your interest on current and possible investigations for which new instruments and improved techniques mean so much. Many investigations of this type will be discussed in the next few days. They will unveil ideas about future developments and cause debates. No doubt agreements, disagreements and vivid discussions as to the best approaches to future progress in this field will be registered during this week of discussions. I judge this rather theoretical part of the field of plant response to climatic factors so open to change and so interesting, that I expect a development of the kind I have outlined. I know that this part is so important for the future progress in the whole area of plant-climatic relations that I find it urgent that the discussions will be both intensive and constructive. Such a statement may lead someone to believe that other sections of our discussions on plant response to climatic factors are less important. This is far from the truth. They are just as important, but they may include more practical aspects and the planning and fulfilling of the investigations in these sections must observe this.

I have raised the question as to why such a great number of people, especially young people, are becoming interested in this type of study. I mentioned the rapid development in the field of instruments and other equipment as one explanation and I elaborated on that explanation. What then are the other explanations for

the increasing interest? I can see several, but I can think of two worth mentioning. They are the existing awareness of the milieu around us and the need for improving agricultural production in developing countries. They have a strong influence on the general developments in the world today and a definite bearing on the question I have indicated in the title of this paper, i.e. the question of climates and plants in world production of food.

Thus, the second explanation of the interest in plant response to climatic conditions that I like to consider is the existing awareness of the milieu and its influence on our way of living. In the whole world today there is a desire to put developments that influence the environment (i.e. the milieu for plants, animals and human beings) on the right course. Undesirable developments should be stopped. This is a question of much wider aspects than the theme for this symposium, but parts of it will be included in our discussions. Such parts are those dealing with changes in plant stands, plant development, yields and quality of yields that are influenced by climatic factors. These may then be macroclimatic or microclimatic. I will give a few examples.

Climatic influence on evenness and development of the stands of cereals is first of all due to water. Seeding time of cereals in relation to the dividing line between the rainy and dry periods in the tropics has a remarkable effect on the evenness and thickness of the stands obtained. This effect remains during the whole growing period and has a definite influence on both quantity and quality of the yield. Weather conditions immediately after the seeding of spring cereals in temperate zones, for example in the area of Sweden where this symposium is being held, have a striking effect on the composition of the stands. Again the main factor is water. The cereal stands often become uneven due to lack of water for germination and early development. This year we have had a very striking effect in this direction. The unevenness not only causes great losses in quantity of yields, but also considerable problems due to poor quality, which is easily noticeable through a large amount of green or poorly developed kernels in the harvested products. Both in the tropics and in the temperate zones one can partly correct this situation by choosing different crops and different varieties within the crops. But even if this is possible, the problem as a whole cannot be solved by these measures. There is a need for intensified studies of plant environments in relation to climates and to treatments of the soils in order to find means of getting a better milieu for the germinating seeds and the seedlings. And this means getting a better milieu also for the growing and ripening plant.

In fact, as a result of uneven germination and retarded seedling development, big differences in α -amylase activity in wheat can be recorded at harvest time both in kernels from neighbouring plants in the same field and in kernels from different ears on the same plant. This is a follow-up effect of uneven germination and emer-

gence. But there are big differences in α -amylase activity also between kernels from the top and the bottom of the same ear, as shown by experiments at the micro-climatic station in the Department of Plant Husbandry at this college. From the data so far available, there is reason to believe that the various differences in α -amylase activity that can be obtained in a wheat field are dependent on the humidity and temperature gradients in the stand, as well as on differences in ripening stages between different plants, tillers and parts of the ear. Thus, it can be stated that water, as a part of the milieu around the plants, has a very striking effect on characters of the plants and their products and this is the case independent of the locality in the world. But it is not the only influential climatic factor to be observed in the discussion on the milieu; light and temperature are also very influential. The reaction of plants to macroclimates is too well known to be taken up in this introductory talk, but the influence of microclimates should be observed; it no doubt will be an essential topic in this week's discussion. Rademacher (1950) discussed the light conditions in stands of cultivated plants with regard to both the appearance of weeds and the ability of weeds to compete with cultivated plants. He emphasized the differences between crops and varieties of crops with regard to light absorption and shading ability, but also the differences in light absorption in the same crop or the same variety of a crop, due to variations in the cultivation methods applied. In a doctor's thesis from the Department of Plant Husbandry at the Agricultural College of Sweden, which will be publicly defended next month, Kornher (1970) stressed that light energy is often a limiting factor for growth and production. He discussed the possibilities of making use of the available light and concluded that they are dependent on the distribution of the light in the stands. Among other things, Kornher has studied the interaction between the light conditions in stands of cereals used as nurse crops for grasses and clovers and the growth of the undersown species of grasses and clovers. He has found that, for example, meadow fescue was able to compensate for part of the light intensity reduction in dense oat stands by elongation. The meadow fescue plants grew taller. But he could also show that red clover during the same light intensity conditions could not compensate in this way. Instead the net assimilation rate and relative growth rate of the clover plants was considerably reduced.

As you are almost at the 60th latitude north I would like to mention one or two examples from this area to illustrate the effect of temperature in marginal areas. Low temperatures may kill overwintering crops such as winter rape (Torsell, 1959), but are usually not the most common reason for the winterkilling of wheat and rye. This means that frozen ground under the snow cover is usually not the most serious reason for winter damages in the stands of wheat and rye. More dangerous is a combination of temperature and humidity at the soil surface. As has been shown by Larsson in 1961

and in later work, not yet published, conducted at the Department of Plant Husbandry at this college, the combination of temperature and humidity factors promote the development of fungi attacking plants of wheat and rye. This combination is more easily obtained under a dense stand of wheat and rye than under a thin stand of these crops.

Naturally, at the marginal areas on the northern latitudes, the effect of low temperatures without the interference of fungi is also a most important one. It is of interest especially in spring-sown crops, as the lack of tolerance to low temperatures in certain of these crops limits their use under northern conditions. This is the case for crops that otherwise would be very valuable contributors to the production in these areas, for example, maize and soya beans. Low temperatures in the spring and the fall have, in our regions, so far prevented their use on an agricultural scale. Investigations in the Department of Plant Husbandry here in Uppsala have shown that low temperatures, especially during the early parts of the growing season, cause uneven stands of maize. Varietal differences in reaction to low temperatures exist. Studies that are partly published (Åberg, 1965), partly under preparation for publication, show that breeding work with the aim of obtaining maize varieties better adapted to environmental conditions in northern regions is needed. The improvement should aim at a better cold tolerance during the early part of the growing season. Similar results have been obtained for soya beans. Holmberg (1968) has, in his breeding work, succeeded in developing daylength-neutral types and is now concentrating on types that are also cold-tolerant.

The examples on the influence of water, light and temperature in stands of cultivated plants and on the competition in these stands have been chosen with the idea of bringing to your attention the great influence of climatic factors under natural conditions, i.e. under conditions where no artificial interference has occurred. However, if we are to consider the influence of climates on plants and plant environments in intensified agriculture, we cannot neglect the use of chemicals of different types, their effect under various climatic conditions and the meaning of this for the discussion of the milieu for the plants. The use of herbicides in a stand of cultivated plants may be chosen as an example in this particular field. However, it is not the techniques in connexion with the use of herbicides that should be brought up for discussion, it is the climatic factors of importance for the breakdown of herbicides applied to plants and soils. Water is again an important climatic factor; temperature is another one. At a moisture content of the soil equal to 40–60 per cent of the water holding capacity, the optimum conditions for a rapid microbial breakdown of herbicides are found. The optimum temperatures range between 25° and 30° C. Investigations with the herbicide picloram, which is very resistant to breakdown in the soil, were carried

out at the Department of Plant Husbandry at this college. Results from the investigations that have not yet been published show that the amount of the herbicide broken down in the soil was 14 times larger at a temperature of 25° C than at a temperature of 5° C (Ebbersten, personal communication). In the experiments, conditions other than temperature were constant. The data show the decisive importance of climatic factors such as precipitation and temperature on the persistence in the soils of this herbicide. Similar results have been obtained with other herbicides.

I think it is quite clear from what I have stated so far that when we discuss the increasing interest in climates and their influence on plants from an agricultural point of view, we should be aware that this increasing interest has a good backing in the world-wide efforts to change the milieu that influences the lives of plants, animals and human beings. Actually the climates, especially the microclimates, are in many situations decisive for crop development. If we are aware of this, it is not difficult to bring into the discussion the third explanation for the increasing interest in the interaction between climates and plants. In the developed countries of the world there are great activities for helping the developing countries increase agricultural production. I limit myself in this case to the activities in the field of crop production. If we engage ourselves in this field, we will soon realize that many of the results from our own countries that we like to fall back on when starting field experiments or when trying to advise people in the developing countries, cannot be used for this purpose until they have been carefully checked under the local conditions in the areas where they are to be applied. Climatic factors are then a very important part of the pattern needed for a successful contribution. We must then seriously ask ourselves: Do we have enough climatic data and do we have enough experience of the variation in these data to act in such a manner that we can take the responsibility for our actions? Sometimes we do. Often we do not. Thus we have a wide-open field for future developments and contributions in the field of plant response to climatic factors when we engage ourselves in improvement work in developing countries. Especially as we are anxious to introduce into these countries new species of cultivated plants and new varieties of old ones. In our enthusiasm for getting involved in the problems on plant response to climatic factors in the developed countries, we should not forget the importance of the problems in this field in the developing countries and to start work on them in those countries.

I can sum up in a few words. Improvement of instruments and measuring techniques have, in recent years, focused the attention on possible contributions by investigations on the interaction between climates and plants. The world's need for a better environment for crops and for a better milieu in general has, together with the need for an increased food production in the

developing countries, favoured investigations in the field of climates and plants. It is our obligation to continue these investigations and use them advantageously in guiding crop production towards the very important achievement: more and better food.

I would like to end by saying how happy I am that this symposium on plant response to climatic factors can take place at the Agricultural College of Sweden just at a stage in the development when so much is at stake with regard to the contribution of plants to world production of food.

Résumé

Discours d'ouverture. Climats et plantes : conséquences pour la production mondiale de denrées alimentaires (E. Åberg)

Ce colloque a lieu à un moment où il est plus nécessaire que jamais de mieux connaître les problèmes posés par les réactions des plantes aux facteurs climatiques. Les recherches faites à ce sujet ces dernières années ont éveillé l'intérêt de très nombreux spécialistes. Pourquoi? La première explication est que les appareils et autres équipements que nécessite l'étude des influences du climat et des réactions des plantes se sont rapidement perfectionnés au cours des dernières décennies. Ces perfectionnements ne stimulent pas seulement les recherches entreprises sur les réactions des plantes aux facteurs climatiques; ils préparent en outre le terrain pour de futures recherches, théoriques aussi bien que pratiques.

Parmi les autres explications auxquelles on peut songer, deux méritent d'être mentionnées particulièrement: la prise de conscience actuelle à l'égard du milieu qui nous environne; la nécessité d'améliorer la production agricole dans les pays en voie de développement. Ces deux dernières explications jouent un grand rôle dans l'ensemble des progrès réalisés actuellement et ont une incidence très nette sur le problème posé dans le titre du présent document.

Dans le monde entier, on éprouve aujourd'hui le désir d'orienter judicieusement les progrès qui influent sur l'environnement, c'est-à-dire sur le milieu où vivent les végétaux, les animaux et les êtres humains. Les évolutions nuisibles à cet égard devraient être arrêtées. Il s'agit là d'une question qui débouche sur des domaines bien plus vastes que le thème de ce colloque. Ces domaines sont ceux qui ont trait aux changements des peuplements végétaux, aux progrès en matière de végétaux, aux rendements et à la qualité des rendements, où le

climat joue un rôle. Il peut s'agir d'un macroclimat ou d'un microclimat, comme le montrent les recherches sur l'influence qu'exercent l'eau, la lumière et la température sur les peuplements de plantes cultivées. Il y a également intérêt à étudier l'emploi qu'on fait des diverses catégories de produits chimiques, l'effet de ces produits chimiques dans telles ou telles conditions et la conclusion à en dégager pour l'étude du milieu où vivent les plantes.

Si des facteurs comme ceux qui viennent d'être énumérés ont éveillé l'intérêt dans les pays développés, il importe de bien comprendre qu'ils méritent tout autant d'intérêt — sinon davantage — dans les pays en voie de développement. Les facteurs climatiques sont très importants à cet égard; mais très souvent on ne les connaît pas aussi bien qu'il le faudrait. Ici s'ouvre donc un très vaste domaine pour les recherches et les travaux futurs en matière de réponse des plantes aux facteurs climatiques, une fois que les efforts en vue d'améliorer les plantes dans les pays en voie de développement commenceront vraiment à porter leurs fruits.

Des améliorations remarquables de l'appareillage ainsi que des techniques de mesure ont été constatées ces dernières années. Elles ont attiré l'attention sur les contributions que des chercheurs pourraient apporter à la connaissance de l'interaction des climats et des plantes. Le besoin qui se fait sentir dans le monde entier d'un meilleur environnement pour les cultures et d'un meilleur milieu en général, et la nécessité d'accroître la production des denrées alimentaires dans les pays en voie de développement ont favorisé les recherches sur les climats et les plantes. Notre devoir est de poursuivre ces recherches et d'en tirer parti pour orienter la production agricole vers ce résultat très important: accroître et améliorer la production des denrées alimentaires.

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I The effect of light
on plant growth,
development and
yield

I Effet de la lumière
sur la croissance,
le développement
et le rendement
des plantes

The effect of light on plant growth, development and yield

L. T. Evans
CSIRO, Division of Plant Industry,
Canberra, A.C.T. (Australia)

Solar radiation, trapped by chlorophyll in the processes of photosynthesis, provides the substance of plant growth and crop yield. Absorbed by other pigments, it controls the partitioning of that substance among the various plant organs through the processes of photomorphogenesis, and the reproductive cycle through the processes of photoperiodism. The relation between crop yield and radiation can, therefore, be extremely complex, and is by no means dominated by the effects on photosynthesis.

SPECTRAL DEPENDENCE

Many substances in plants absorb radiation at certain wavelengths, but only a few undergo photochemical transformations which result in specific biological responses. Water, for example, has a high absorbancy at many wavebands in the infra-red region of the spectrum; the energy absorbed by leaves at these wavelengths is not used photochemically, and must be dissipated by re-radiation at longer wavelengths, by convection, or by transpiration of water. However, much of the solar radiation in these bands is absorbed before it reaches the vegetation by atmospheric water and CO₂, thereby greatly reducing the heat load on the plants. Similarly, the ultra-violet (UV) wavebands, most strongly absorbed by nucleic acids and proteins, are largely eliminated by atmospheric ozone. The longer wavelength (300–400 nm) UV is absorbed by the chlorophylls, supporting some photosynthesis, and by the phototropic pigment. It can also, like blue light, cause the photoreactivation of nucleic acids inactivated by exposure to short-wave UV radiation. However, these effects hardly account for the reported stimulations of growth by small amounts of UV added to visible radiation (Lockhart and Brod-fürher, 1961).

Absorption by leaves is strong in the visible region of the spectrum, particularly in the red and blue bands. In the green it is lower and more variable, ranging from 50 to 90 per cent depending on the thickness and past history of the leaves (Bjorkman, 1968; Gates *et al.*, 1965). Of the incident radiation not absorbed by the leaves, about half is reflected and the other half transmitted. Reflection is greater than transmission in thick or glossy leaves, and greatly exceeds transmission at low angles of incidence.

ACTION SPECTRA

The action spectrum for a light dependent process, showing the relative effectiveness of radiation of different wavelengths, is of value in indicating the nature of the receptor pigment, but can differ considerably from the absorption spectrum. The concentration of the pigment, for example, can affect the relative absorption at various wavelengths; the more chlorophyll there is in plant cells, the higher is the absorption of green light relative to that of wavelengths at the absorption maxima (Bjorkman, 1968; Kirk and Reade, 1970), a fact which partly accounts for the relative effectiveness of green light in photosynthesis by leaves (Fig. 1(a)). Other pigments may act as screens; for example, carotenoids absorb strongly in the blue region near the absorption maxima of the chlorophylls, thereby lowering the relative effectiveness of blue light in photosynthesis. However, some of the energy absorbed by the carotenoids is transferred to chlorophyll by inductive resonance. Because there are many organelles of dimensions comparable with the wavelengths of visible light, refraction and scattering may further reduce the relative effectiveness of the shorter wavelengths. On the other hand, this is increased in action spectra presented on a quantum basis, since the energy of a quantum is inversely proportional to the wavelength.

plants, the action spectrum is the classical Beltsville one, with maximum effect at 660 nm for brief exposures to light. With longer exposures the optimum proportion of Pfr is lower (Lane *et al.*, 1965) and the action maximum shifts to 700 nm or even longer wavelengths (Borthwick *et al.*, 1969).

HIGH ENERGY REACTION

A consequence of the initial overemphasis on the low energy switching action of phytochrome was that photomorphogenic responses to long exposures of high energy light were thought to be controlled by a "high energy reaction" mediated by a pigment other than phytochrome. Action spectra varied considerably (e.g. Fig. 1(c)), but peak effectiveness was usually found in the blue and far-red regions. There has been extended discussion as to whether phytochrome or a separate blue-far-red pigment is involved, but it now appears that many features of the high energy reaction can probably be explained in terms of phytochrome action. Hartmann's (1966) model is based on the decay of phytochrome following conversion to the Pfr form, a spectrophotometrically detectable process which may not, however, apply to the physiologically active phytochrome in green tissues. Another recent model is that of Borthwick *et al.* (1969). Hartmann considers that not only action in the red-far-red region of the spectrum, but also the pronounced action in the blue region, can be explained in terms of phytochrome. However, comparison of the response to blue wavelengths in Figure 1(c) with the action spectra for phytochrome in Figure 1(b) suggests that another pigment may be involved. In fact, the action spectrum for *Petunia* in the blue region of Figure 1(c), and that given by Hartmann (1967), bear marked resemblances to that for phototropism in Figure 1(d).

PHOTOTROPISM

The controlling pigment for phototropism is still uncertain. Carotenoid absorption spectra match the action spectra closely in the blue region, but not at 370 nm, while flavins match it at 370 nm, but not as well in the blue region. Perhaps both are involved, one—presumably the more abundant carotenoid—acting as a screen to generate a marked gradient in the tissue at wavelengths strongly absorbed by the other, the receptor pigment.

Blue light, apart from its dominant role in phototropism and the high energy reaction of photomorphogenesis, also has pronounced effects on the following phenomena: (a) the stimulation of respiration (Kowallik and Gaffron, 1966; Kowallik and Kowallik, 1969; Poskuta, 1968; Voskresenskaya, 1961); (b) protoplasmic viscosity and streaming (Virgin, 1954); (c) stomatal opening (Heath *et al.*, 1965; Raschke, 1967); (d) protein synthesis (e.g. Payer and Mohr, 1969).

To what extent these are related responses mediated by one pigment is unknown, but the effects on protoplasmic viscosity may participate in phototropic curvature (Curry, 1969).

PHOTOMORPHOGENESIS

In established plants, the intensity and spectral composition of light influence morphogenesis not only through phytochrome and the high energy reaction, but also through photosynthesis. In seedlings, on the other hand, growth may be wholly supported by endosperm or cotyledonary reserves for more than a week and the role of photoreactions other than photosynthesis can be analysed more clearly. Grown in darkness, dicotyledonous seedlings show marked elongation of the hypocotyl, while the cotyledons and leaves remain small and folded. The adaptive value of this etiolation response is clear, the use of reserves for axis elongation maximizing the likelihood that the seedlings will reach the light. Once in the light, hypocotyl growth is reduced, the plumular hook opens, the cotyledons and leaves expand, plastids develop and pigments are formed, maximizing the interception of light for photosynthesis. Thus the essence of photomorphogenesis is control of the partitioning of reserves or assimilates among leaves, stems and roots.

In older plants, dependent on photosynthesis for growth, the effects of light are more complex. A lower light intensity, while tending to increase stem elongation by etiolation, may also reduce it due to lack of assimilates. In barley sown at a range of densities, for example, shading caused by high densities increased elongation in the first formed internodes but reduced that in the later ones, presumably as the supply of assimilates became more limiting (Kirby and Faris, 1970). Leaf length changed in a similar manner; in fact, this component of monocotyledonous leaf growth often appears to respond to light in the same way as does stem growth. The higher the light intensity the shorter, but broader and thicker, were wheat leaf blades (Friend *et al.*, 1962). Since length changed proportionally more than breadth, the area of individual leaves was greatest in low intensity light, but leaf area per plant may increase with increased light intensity up to full sunlight because of increased tillering.

The rates of initiation, emergence and expansion of wheat leaves increased to some extent with increase in light intensity, but the additional assimilate at higher intensities was mostly invested in increased tillering and root growth (Friend, 1965), a pattern of response common among the gramineae (Evans *et al.*, 1964). The increased tillering at high intensities is due to a higher proportion of tiller primordia developing into independent shoots, not to any increase in their initiation, and is an important component of the ability of the small-grained cereals to take advantage of additional radiation. Longer days

have two, opposed, effects on tillering; they tend to increase it because of the increase in total radiation and assimilate supply (Aspinall and Paleg, 1964), but to decrease it, in long-day cereals at least, due to earlier inflorescence initiation and increased apical dominance.

Branching in many dicotyledons does not increase with increase in radiation as noticeably as does tillering in most gramineae, perhaps because many dicot leaves can increase in area with increase in intensity up to about half daylight (Newton, 1963) or to even higher intensities when nutrients are not limiting (Milthorpe and Newton, 1963), with the consequence that additional leaf growth utilizes much of the additional assimilate.

Root growth in most plants is very much affected by the radiation environment, the root/shoot ratio being greatly reduced in low light intensities (Brouwer, 1962; Evans *et al.*, 1964). This response is rapid (Richardson, 1953), and the deeper roots are those most affected (Welbank *et al.*, 1968). The effect is clearly an indirect one, through the supply of assimilates, since exposure to light may inhibit the growth of roots, as it can that of tubers (Tsuno and Fujise, 1965). However, since shoot growth in turn depends on the uptake of water and nutrients by roots, and possibly on growth substances such as cytokinins and gibberellins exported by them, a mechanism exists for ensuring the roots of a minimum supply of assimilate, in that the growth of leaves may otherwise be limited by that of roots.

PHOTOSYNTHESIS AND LIGHT: SINGLE LEAVES

The relationship between light intensity and photosynthesis by single leaves is of central importance in determining crop photosynthesis. Several empirical expressions for the relation have been developed, based on diffusion resistance analogues of the general form

$$P = F + R = \frac{c_a - c_c}{r_a + r_s + r_m + r_x}$$

where P = the rate of gross photosynthesis, per unit leaf area; F = the rate of net photosynthesis, per unit leaf area; R = the rate of respiration, per unit leaf area; c_a = the concentration of CO_2 in the air; c_c = the concentration of CO_2 at the carboxylating surface; r_a = the diffusion resistance for CO_2 transfer in the boundary layer; r_s = the diffusion resistance for CO_2 transfer through stomata and cuticle; r_m = the diffusion resistance for CO_2 transfer through the mesophyll; and r_x = the carboxylation resistance.

The use of such expressions has been of real value in the analysis of differences between species and of the effect of environmental conditions, but there are many problems with such analyses.

LIGHT AND RESPIRATION

First, there is considerable uncertainty as to how respiration is affected in the light. In plants with Calvin cycle photosynthesis, CO_2 efflux can be shown, by various means, to increase in light more or less proportionally to photosynthesis at moderate temperatures but more markedly at high temperatures (Hofstra and Hesketh, 1969; Jolliffe and Tregunna, 1968). In air, the rate of this "photorespiration" may be several times higher than the dark respiration rate, but at low oxygen concentrations it is inhibited and photosynthesis enhanced. The enhancement has been used to estimate the magnitude of photorespiration, but cyclic electron flow in photosynthesis may also be inhibited by atmospheric oxygen levels (Heber, 1969). In plants with the C_4 -dicarboxylic acid pathway of photosynthesis, this light-dependent decarboxylation appears to be almost absent, but attempts to find Calvin cycle plants without it have failed (Cannell *et al.*, 1969). Its role is unclear, but since it is not evident in tropical gramineae, and since Calvin cycle plants can grow at low oxygen concentrations, this light-dependent decarboxylation is apparently not required for growth and differentiation and probably should not be referred to as respiration. However, the loss of CO_2 by this process is of such magnitude that it is difficult to believe it arises simply from back reactions controlling the rate of photosynthesis, and it may play a role in terpenoid or protein synthesis in chloroplasts (Shah and Rogers, 1969).

Since the tropical gramineae can grow in continuous light, yet have no "photorespiration", true respiration can hardly be completely inhibited in light as is sometimes assumed. Marsh *et al.* (1965) and Anderson and Fuller (1967) found light to have no effect on the turnover of the tricarboxylic acid cycle. Reduced respiratory turnover during photosynthesis has been found with many chloroplast preparations (see Reid, 1970), presumably because of competition for ADP between photophosphorylation and glycolytic phosphorylation. However, this may be counterbalanced in leaves by increased cytoplasmic consumption of ATP in syntheses stimulated either by photosynthetic supply of substrate or by other photoreactions, such as the effects of blue light on protein synthesis and cytoplasmic streaming cited above. In this connexion it is notable that respiration appears to be stimulated in blue light.

RESISTANCE ANALYSES

There are, therefore, uncertainties of considerable magnitude in quantifying the effects of light on the term R in the equation above. These also affect the assumptions about c_c , which can hardly be a unique value in view of the diverse geometry of carboxylating surfaces in relation to CO_2 derived from both air and respiration. Of the sequential resistance terms, r_s is strongly dependent on the light environment. This effect

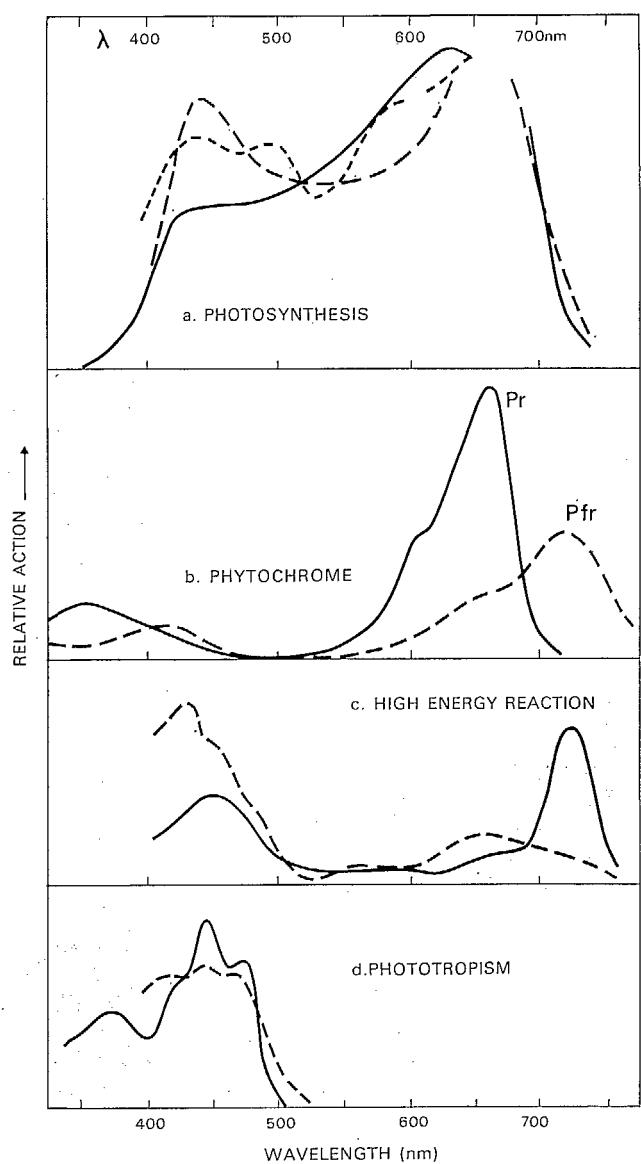


FIG. 1. Action spectra.

- Photosynthesis under equal incident energy by leaves of wheat (---: Hoover, 1937. —: unpublished data of K. J. McCree) and maize (----: Bulley *et al.*, 1969).
- Phytochrome transformations *in vitro* (Butler *et al.*, 1964).
- High energy reaction of photomorphogenesis in the plumar hook opening of lettuce (—: Mohr and Noblé, 1960), and suppression of hypocotyl growth in *Petunia* (----: Evans *et al.*, 1965).
- Phototropism in *Avena* seedlings (—: Curry, 1969. ----: Shropshire and Withrow, 1958).

PHOTOSYNTHESIS

Action spectra can vary considerably, depending on the conditions of growth, as may be seen by comparing the two curves for photosynthesis in wheat in Figure 1(a). Given such variation, there is no good evidence, at the moment, that blue light is relatively more effective for photosynthesis in maize and other non-Festucoid gramineae with the C₄-dicarboxylic acid pathway than it is in Calvin cycle plants like wheat. It has been suggested that "photorespiration" is most marked in blue light, in which case plants like maize which lack photorespiratory loss of CO₂ would use blue light more effectively in photosynthesis. However, Bulley *et al.* (1969) found no change in the action spectrum for photosynthesis by radish leaves when the oxygen concentration was reduced to 2 per cent to inhibit photorespiration.

Whereas plants in nature are exposed to a range of wavelengths, action spectra are usually determined under monochromatic light, and the results can be misleading if there is synergism between certain wavelengths. The Emerson effect in photosynthesis, by which far-red light can greatly enhance photosynthesis in the presence of red light, although of little effect on its own, is a case in point.

Phytochrome, a protein pigment with a biliene chromophore, occurs in plants at a far lower concentration than chlorophyll, but controls a wide spectrum of photomorphogenic responses: germination and dormancy, leaf growth and unfolding, stem and root growth, plastid differentiation, anthocyanin synthesis, flower induction, and the response to many rhythmic phenomena. Exposed to far-red light, the pigment is converted, through a series of intermediates, to the red absorbing Pr form. Exposed to red light the Pr form is transformed back, through several intermediates, to the far-red absorbing Pfr form. This is believed to be the biologically active form, but action by Pr, or even by some of the short-lived intermediates, is not rigorously excluded. The action spectra given in Figure 1(b) are for the photochemical transformations in solutions of the pigment *in vitro* in which, because of the reversible reaction, certain features are clearer than in the biological action spectra (e.g. Hendricks and Borthwick, 1963). Note, for example, that the Pfr form shows considerable absorption in the red region of the spectrum, with the result that, even at photostationary equilibrium in red light, not more than 80 per cent of the phytochrome is in the Pfr form. In far-red light, on the other hand, at least 1 to 2 per cent is in the Pfr form.

Following the discovery of photoreversibility in 1952, the many red-far-red reversal experiments with short exposures to light tended to over-emphasize the all-or-nothing switch action of phytochrome. More recently, emphasis has been placed on the quantitative nature of phytochrome action, in which the optimum level of Pfr, and the action spectrum, depends on the duration of action. For the promotion of flowering in long day

TABLE 1. Some estimates of resistance to CO₂ exchange by leaves (sec cm⁻¹)

Species	r_a	r_s	r_m	r_x	Reference
<i>Phaseolus vulgaris</i>	0.5	0.6–2.2	4.5–9.1	0.06–0.6	Chartier <i>et al.</i> , 1970
<i>Phaseolus vulgaris</i>	1.4	1.4	5.2		Gale and Poljakoff-Mayber, 1968
<i>Glycine max</i>	—	1.6–3.2	1.6–2.0		Dornhoff and Shibles, 1970
<i>Glycine max</i>	1.1	2.7	5.5		El-Sharkawy and Hesketh, 1965
<i>Hibiscus tiliaceus</i>	1.1	1.9	7.3		El-Sharkawy and Hesketh, 1965
<i>Avena sativa</i>	1.1	1.7	4.1		El-Sharkawy and Hesketh, 1965
<i>Zea mays</i>	1.1	1.5	1.0		El-Sharkawy and Hesketh, 1965
<i>Zea mays</i>	—	2.4	0.4–0.9		Gifford, 1970
<i>Panicum maximum</i>	0.9	1.9	1.0		Ludlow, 1970
<i>Sorghum album</i>	0.9	3.3	0.8		Ludlow, 1970
<i>Glycine javanica</i>	1.1	1.7	4.5		Ludlow, 1970

has usually been ascribed almost wholly to the control of intercellular space CO₂ concentration by photosynthetic rate, but Gifford (1970) has presented evidence that a CO₂-independent, light-dependent mechanism may also have a controlling influence in maize. As noted above, blue light is most effective in this reaction.

Meidner (1969) has already pointed out the unsatisfactory nature of the term mesophyll resistance, which may include gaseous diffusion in the intercellular spaces—dependent on cell packing and likely to differ considerably between the upper and lower surfaces, as does r_s —the entry of CO₂ into the cell wall pores, its solution and transport to the chloroplasts by diffusion and by protoplasmic streaming, and entry into the chloroplasts. A term of such heterogeneity is of limited value in analysis, but the entries in Table 1 give some idea of the relative magnitudes of the resistances to CO₂ exchange in leaves with open stomata. With closed stomata, r_s may rise to 35–40 sec cm⁻¹ (Gaastra, 1963), but with open stomata the mesophyll tends to provide greater resistance to CO₂ diffusion, except in the tropical gramineae, and effects on r_m can have a considerable influence on photosynthetic rate (Chartier *et al.*, 1970).

We may now consider some of the factors influencing the relationship between leaf photosynthetic rate and light intensity.

SPECIES AND VARIETAL DIFFERENCES

The major difference is that between species with the Calvin cycle and those with the C₄-dicarboxylic acid pathway (Hatch *et al.*, 1967; Johnson and Hatch, 1968). This latter pathway, most common among the tropical gramineae, but found also in species from some dicotyledonous families, is characterized by a less marked light saturation of photosynthetic rate (Hesketh, 1963; Hesketh and Moss, 1963; cf. wheat and maize leaves in Fig. 2). A major cause of the higher maximum rates in the tropical gramineae appears to be the absence of light-dependent decarboxylation, but higher affinity

for CO₂ by the carboxylating enzymes, higher enzyme capacity, and greater assimilatory recapture of respiration CO₂, may all contribute. Also associated with the dicarboxylic acid pathway are the occurrence of dimorphic chloroplasts and a characteristic leaf anatomy, a lower CO₂ compensation point, higher optimum temperatures for photosynthesis and growth, higher maximum growth rates, and more rapid and complete translocation of assimilates from the leaves (Hofstra and Hesketh, 1969; Hofstra and Nelson, 1969).

Considerable differences in photosynthetic rate at high light intensities exist among Calvin cycle plants. Some, the primitive wheats for example, may have rates at least as high as those of maize or sugar cane (Evans and Dunstone, 1970); most are comparable with the wheat leaves in Figure 2(a), but some reach light saturation at even lower intensities. Differences in stomatal distribution, in the surface/volume ratio and packing of mesophyll cells, and in chlorophyll and enzyme contents, affecting r_s , r_m and r_x , undoubtedly contribute to these differences (El-Sharkawy and Hesketh, 1965).

Varieties within a species may also differ considerably in their photosynthetic rate at higher light intensities, as in maize (Duncan and Hesketh, 1968; Heichel and Musgrave, 1969), sugar cane (Irvine, 1967), *Phaseolus* (Izhar and Wallace, 1967), soybeans (Curtis *et al.*, 1969; Dornhoff and Shibles, 1970; Dreger *et al.*, 1969) and *Lolium* (Wilson and Cooper, 1969a). However, plant to plant variation in photosynthetic rate can be high, and differences in environmental history and age can readily confound those differences between varieties. The differences between maize varieties in their photosynthetic rates are strongly dependent on the environment in which they are grown (Gifford, 1970), most of the inter- and intravarietal variation being due to variation in r_s . In *Lolium perenne*, however, differences between ten genotypes in their photosynthetic rate at light saturation were not related to stomatal characteristics, but were negatively correlated with mesophyll cell size (Wilson and Cooper, 1969a).

Among races of *Dactylis glomerata*, large varietal differences in photosynthetic rate were associated with differences in carboxyldismutase activity (Treharne and Eagles, 1969); r_x would have to be much higher than the uppermost entry in Table 1 suggests for this to account for the differences in photosynthetic rate.

ENVIRONMENTAL HISTORY

The conditions under which leaves develop may have a considerable influence on their light/photosynthesis function. The status of many nutrients can, of course, affect photosynthetic rate: nitrogen level, for example, can affect both mesophyll and stomatal resistance (Ryle and Hesketh, 1969), and potassium status may have pronounced effects on stomatal response (Fischer and Hsiao, 1968).

In *Lolium perenne*, higher photosynthetic rates were associated with growth at higher light intensities and lower temperatures; brighter light resulted in increased stomatal size (Wilson and Cooper, 1969c), whereas lower temperatures did not appear to affect stomatal or mesophyll dimensions, and may have influenced r_x (Wilson and Cooper, 1969b). In other plants, however, r_m can be influenced by light intensity during growth (Hesketh, 1968).

EFFECTS OF AGE AND DEMAND

The photosynthetic rate of individual leaves may be profoundly affected by their own age and by that of the plant, through effects on demand and on leaf rank. In *Lolium* the earlier formed leaves have smaller mesophyll cells and higher photosynthetic rates per unit leaf area (Wilson and Cooper, 1969d). Similarly, in many cereals the last formed (flag) leaf blade may be smaller and have smaller cells and a higher photosynthetic rate, than those below it.

For most leaves, their highest photosynthetic rate is reached when the blade is fully expanded, and may be maintained for only a short time, the subsequent fall being dependent on canopy structure and the demand for assimilates. In flag leaves of wheat the rate may fall soon after leaf appearance, associated with low demand at the time of anthesis, but may then rise substantially as grain growth becomes rapid and demand increases (Evans and Rawson, 1970). Comparable rises at time of increased demand have been found in potatoes at the beginning of tuber growth (Gifford and Moorby, 1967), in maize during grain growth (Ermilov, 1963) and in soybeans at pod filling (Dornhoff and Shibles, 1970).

Many experiments have shown that photosynthetic rate can be varied by changing the demand for assimilates (King *et al.*, 1967; Neales and Incoll, 1968). Removal or inhibition of tubers, ears, pods or fruit can cause a rapid fall in photosynthetic rate of the leaves supplying them if alternative sinks are not available, or it can be raised when the leaf surface is reduced by

defoliation or disease. There is still debate as to whether these effects are mediated by assimilate levels or via effects of hormones. The latter are unlikely where the effects can be simulated by the application of sugars (e.g. Grob and Rufener, 1969).

TIME OF DAY

Even under constant light conditions diurnal cycles in the rate of photosynthesis may be apparent due to diurnal rhythms in stomatal opening ability (e.g. in wheat, Meidner and Mansfield, 1965). These rhythms, mediated by phytochrome, vary with growing conditions, and can cause stomata to close well before darkness. Other factors affecting photosynthetic rate may also vary diurnally, resulting in quite complex seasonal changes. In sugar cane, for example, photosynthesis was highest at the beginning of the day in summer, followed by a mid-day depression, whereas in winter it was highest in the early afternoon (Kortschak and Forbes, 1969).

EFFECTS OF FLUCTUATING LIGHT

With the movement of clouds, and of leaves in the wind, there can be rapid changes in the illumination of leaves, with periodicities which vary from one crop to another (Norman and Tanner, 1969). Brief intermissions, of a second or less, from high light intensities can increase photosynthetic efficiency when the enzymatic reactions are limiting. Longer intervals in low light, of the order of minutes, may on the other hand reduce photosynthetic efficiency because stomata tend to close more rapidly than they open. Both enhancement with rapid changes in intensity and depression with slower changes have been found (Evans, 1963; Ino, 1969; McCree and Loomis, 1969). McCree and Loomis suggest that their net effect under natural conditions will be slight.

PHOTOSYNTHESIS AND LIGHT: PLANT COMMUNITIES

Energy incident on a crop is absorbed by leaves at all levels, the lower ones receiving only that reflected or transmitted by the upper ones, together with light flecks not intercepted by them. Consequently, photosynthesis by the crop as a whole is much less subject to light saturation than is that by single leaves, as may be seen from Figure 2.

Photosynthesis by the wheat community (Fig. 2(a)) in the favourable environment of an artificially lit cabinet reached an efficiency approaching the maximum that could be expected. In the field crop comparable rates were reached, with little evidence of light saturation, on 15 October, a day of high ambient CO₂ level. On 16 October, however, a day of lower CO₂ levels and wind speeds, there was marked light saturation of photosynthesis by the crop, similar to that for single

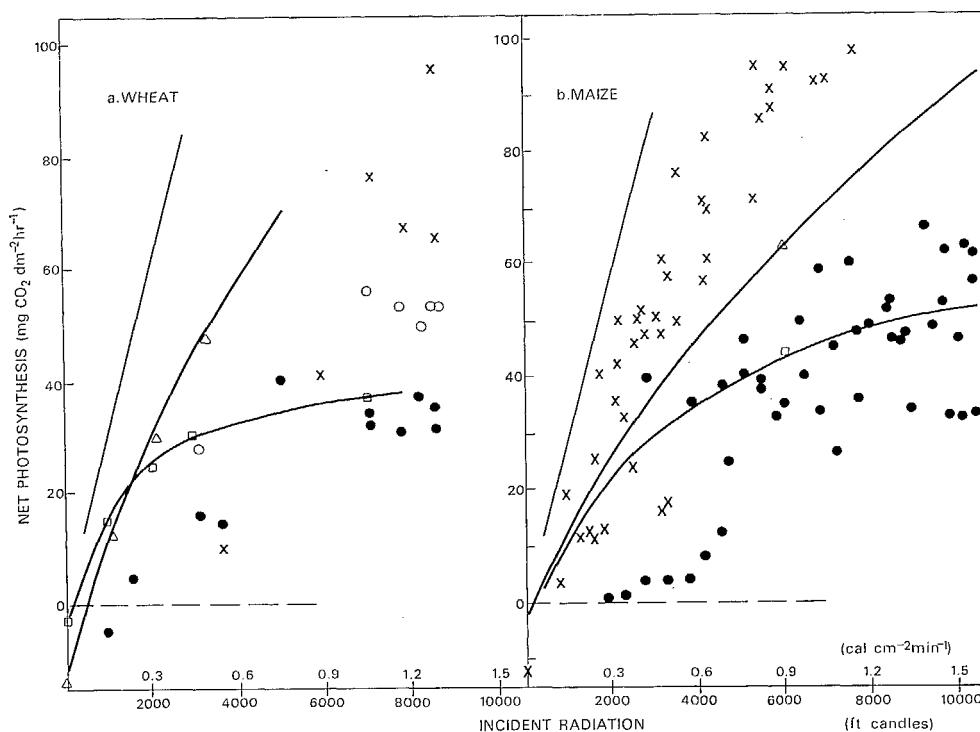


FIG. 2. Relationship between photosynthesis and incident radiation for single leaves and plant communities.

(a) *Wheat*. —□—: single leaves (Evans and Dunstone, 1970); —△—: crop in artificially lit cabinet (King and Evans, 1967). Field crop (LAI 3.2, data of Denmead, 1970): ○ = 14 October; × = 15 October; ● = 16 October.

(b) *Maize*. —□—: single leaves (Hesketh, 1963). —△—: field crop, enclosed (Baker and Musgrave, 1964). Field crop, open (Lemon, 1967 and unpublished data): × = 26 July; ● = 27 July.

The sloping lines to the left of each figure indicate the maximum efficiency for 8 quantum photosynthesis, assuming 26 per cent loss by reflection and absorption by inert tissue.

leaves. The low photosynthesis by the crop at low intensities was probably due to the fact that these measurements were made at the beginning or end of the day, with low sun angle and rapidly changing conditions.

In the maize crop (Fig. 2(b)) the curvature of the graph due to light saturation was less than in wheat, as one would expect from the single leaf curves. In the enclosed crop, under forced ventilation, the relationship between photosynthesis and incident radiation was similar on the two days. In the open crop there was marked light saturation on 27 July, a day of little wind, whereas on the more turbulent 26 July photosynthesis by the open crop considerably exceeded that by the enclosed crop. For both wheat and maize, therefore, pronounced light saturation of crop photosynthesis can occur under conditions limiting the supply of CO₂ to the stomata.

The relationship between photosynthesis by a plant community and the incident light is also influenced by the leaf area index (LAI), this relation in turn depending on the geometry of light penetration and the respiratory losses.

Light penetration into a canopy of leaves is strongly influenced by their size and shape, inclination and azimuthal orientation, vertical separation and horizontal arrangement, and absorption by structures other than leaves (Anderson and Denmead, 1969; Loomis and Williams, 1969; Monteith, 1969). These characters differ considerably not only between species and varieties, but also with stage of development of a community. The optimum geometry, in terms of light distribution for maximum crop photosynthesis, has been extensively discussed; it varies with climatic conditions—such as sun angle and the proportions of direct and diffuse light—and with stage of development. But there are other factors which may also have an important bearing on

optimum crop geometry. Leaf distribution influences crop ventilation, and Isobe's (1967) analysis suggests that crop structures optimal for light penetration may be poorest for CO_2 renewal. Leaf distribution also influences the microclimate of the sink organs. Moreover the shape of the photosynthetic profile in relation to the position of these organs may be more important than the sum total of photosynthesis.

In wheat and barley, for example, the ears are at the top of the canopy and are active in photosynthesis, and they and the uppermost leaves are the main sources of assimilate for grain-filling. Thus, increased penetration of light to the lower canopy may have little effect on the carbohydrate economy of the ear and could even be disadvantageous if it delayed senescence and the mobilization of nitrogenous and other compounds from the lower leaves. In maize, on the other hand, leaves in the middle of the canopy contribute much to grain filling (Allison and Watson, 1966; Eastin, 1969; Pendleton and Hammond, 1969), and greater penetration of light is desirable. With root and tuber crops, photosynthesis by the lower leaves may be particularly important. In crops such as peas, where a fruit is borne in each axil, each fruit is most dependent for assimilates on the leaf subtending it (see Wardlaw, 1968), and the light profile must not be too attenuated with depth in the canopy. Moreover, there may be specific vascular connexions between certain leaves and certain parts of the sink organ, as with sunflower inflorescences (Prokofyev and Sobolev, 1957) and sugar beet roots (Belikov and Kostetsky, 1964). Thus, the determination of optimum crop geometry for maximum photosynthesis may involve much more than light penetration.

CROP RESPIRATION

The magnitude of crop respiration plays an important role in determining the relationships between light intensity, LAI and crop photosynthesis. Early models (e.g. Davidson and Philip, 1958) assumed that respiration was proportional to leaf area, and since light interception and gross photosynthesis approached an asymptote with increasing LAI, net photosynthesis was optimal at an intermediate LAI. However, lower, older leaves do not import assimilates from upper ones (Wardlaw, 1968), and rapidly adapt to shaded conditions with a lower respiration rate (Ludwig *et al.*, 1965; McCree and Troughton, 1966). As a result, the respiratory rate of the crop community tends to be proportional to the rate of gross photosynthesis, and net photosynthesis is to be asymptotic with increasing LAI. Respiration is thought to be tightly coupled under most conditions; thus, it can probably be partitioned, as McCree (1970) has suggested, into a maintenance term (for protein turnover, translocation, etc.) and a growth and storage term for new syntheses. The efficiency of these latter processes varies from 50 to 65 per cent for new tissue (Cooper and McDonald, 1970) up to about 80 per cent

for starch storage (Evans and Rawson, 1970) and even higher for sugar accumulation. The maintenance term is more or less proportional to accumulated plant weight (McCree suggests 1.5 per cent of total dry weight per day) and, therefore, becomes substantial towards the end of the life cycle, when the respiratory loss of CO_2 by plant communities is commonly 40–60 per cent or more of daily photosynthesis (King and Evans, 1967; Monteith, 1966; Thomas and Hill, 1949).

REPRODUCTIVE DEVELOPMENT

For many crops it is the fruits and seeds which are harvested by man, and high yields require the development of a reproductive storage capacity sufficient to maintain photosynthesis at high rates. In the case of other crops, such as sugar cane, beet, tobacco and lettuce, high economic yields are obtained only when reproductive development is delayed or prevented. Control of reproduction is, therefore, a key factor in agriculture. Of the components of the light environment, daylength is the dominant one in this context, and control is most effectively operated at the first steps in the reproductive process, the induction of flowering. However, later steps in the process, such as the differentiation of flowers or the setting of fruit, may also be very sensitive to daylength, as may the induction of dormancy, tuberization and bulbing in some plants, and other partitioning phenomena such as tillering in the cereals.

The pigment phytochrome plays a key role in mediating the day-length response in all plants and it appears likely that induction in both long-day and short-day plants requires the participation both of processes favoured by high, and of processes favoured by low Pfr levels. Whichever is more limiting must coincide with or follow the diurnal period of photosynthesis or mobilization of reserves, and it is this requirement that determines the photoperiodic responses of plants (Evans, 1971). Because the responses are mediated by phytochrome, both low-intensity light and short-light interruptions may have profound effects, particularly with short-day plants. Light from street lamps, oil flares and moth traps has been shown to interfere with their flowering. Even bright moonlight could do so were it not for other adaptive reactions, such as the folding of leaves (Bünning and Moser, 1969a, b). Brief light interruptions are used to control flowering of sugar cane in Hawaii, and of many horticultural plants.

Among wild plants, daylength control of flowering, together with juvenility and the response to vernalization, plays an important adaptive role in confining flowering to the periods most favourable to it, and many wild plants are strongly photoperiodic. For example, Katayama (1964) found a marked relationship between latitude of origin and critical dark-period length in fifteen species and 285 strains of *Oryza*, with a decrease

of 2.6 minutes for each degree increase in latitude. There were two exceptions. Strains from Assam had a shorter critical dark period than expected from their latitude, presumably associated with the lower temperatures at the higher altitudes of their origin, and strains of *Oryza longiglumis* from New Guinea had a longer critical dark period than expected, presumably associated with the dense shade of their natural habitat.

Among cultivated plants it has sometimes been necessary to modify these responses in the direction of daylength-indifference. For example, cultivation in higher latitudes has required selection for a less stringent requirement for short days for the initiation of tuberization in potatoes, and of flowering in corn, sorghum and soybeans. In fact, indifference to daylength has been suggested as a general objective in breeding programmes for some widely distributed crops. However, many modern varieties remain very sensitive to daylength, such as some tropical rices (Dore, 1959; Njoku, 1959), and response to daylength by crops can play an important adaptive role.

Most obviously, response to daylength is of value in delaying flowering in crops such as sugar beet, sugar cane, tobacco or pasture grasses, in which reproductive development is deleterious to yield. A requirement for long days can be of value in delaying inflorescence initiation until the risk of frost injury to embryonic ears has passed. Varieties of wheat and barley from higher latitudes are particularly responsive to day length (see Kirby, 1969), possibly for this reason. In lower latitude environments, such as Israel and Australia, adaptation is more complex. Initiation must be delayed until after the frosts, but must then be rapid enough to ensure that the ripening ear is not caught by drought and high temperatures. The range of daylength is small, but there must be considerable sensitivity within it. The number of days required for induction, and the rate of change in daylength, can be important in this context, and also in determining the timing of inflorescence growth relative to that of the stem.

Depending on the nature of the response to increasing induction, which in turn depends on inflorescence structure and position, a photoperiodic requirement can play an important role in maximizing yield components. In crops with determinate inflorescences, such as wheat, exposure to longer days hastens inception of the terminal spikelet relative to that of the lateral ones, and thereby reduces spikelet number and potential grain yield per ear (Rawson, 1970). Thus, in selecting for yield, plant breeders may have unconsciously selected for photoperiodic responses which result in some delay in inflorescence initiation.

LIGHT AND YIELD

The effects of light on yield can be separated into those during early vegetative growth and differentiation of the storage organs on the one hand, and those which

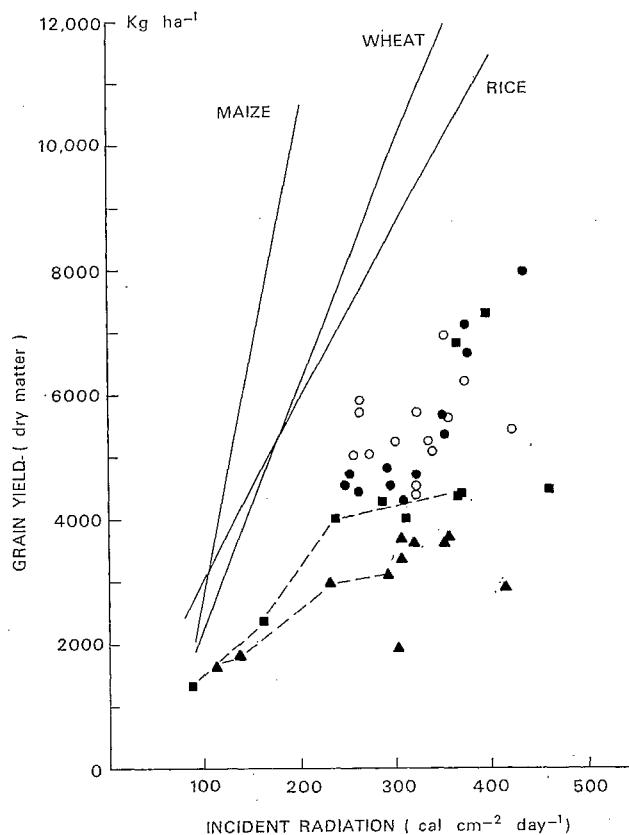


FIG. 3. Relationships between grain yield and incident radiation during the period of grain filling.

- *Indica* rice, variety IR8, grown in the Philippines from serial plantings 1968/69 (data of de Datta and Zarate, 1969).
- *Japonica* rice, grown at various sites in Japan during 1968. (Japan I.B.P., 1970).
- Winter wheat, grown in England over several years (data of Welbank *et al.*, 1968 and unpublished data).
- ▲ Spring wheat.

Broken lines link treatments subjected to degrees of shade in one year. The solid lines give estimates of the potential yield of maize, wheat and rice, based on assumptions described in the text.

follow and determine the extent to which they are filled on the other. Photosynthesis is the dominant process in this latter stage. Assimilates stored earlier in the life of the plant usually contribute little to the growth of seed, fruit and tuber, which depends mainly on concurrent photosynthesis. Nevertheless, the early light environment may have profound effects on yield through effects on characters which determine the potential storage capacity and the timing of the development cycle in relation to the seasonal changes of radiation. Photomorphogenic and photoperiodic reactions are dominant in this context, but photosynthesis can also be important

at this earlier stage through effects of assimilate supply on the numbers of ears, spikelets or florets which develop in cereals, for example.

A crucial question for plant breeders and agro-climatologists is whether storage capacity, as determined by morphogenic effects of radiation early in the season, is more limiting to yield than is photosynthesis during the filling period. Figure 3 shows the relationship between grain yield of rice and wheat and the incident radiation during the grain-filling period. With both spring and winter wheat, the data published by Welbank *et al.* (1968) suggest that yield was limited by incident radiation only at very low levels, and tended to become asymptotic at higher radiation. Either the capacity to store assimilates was limiting at higher radiation levels, or associated features such as higher temperatures or greater water stress adversely affected yield. It is interesting, therefore, that unpublished data from their more recent experiments with other varieties reveal greater yield responses to higher radiation, comparable with those found for *japonica* rice in Japan and for a high yielding variety of *indica* rice in the Philippines. With the latter, supplied with abundant water and nutrients, yield increased with increasing radiation during grain-filling, the correlation coefficient between them being 0.713 (de Datta and Zarate, 1969). However, other seasonal differences were confounded with those in radiation. In the case of the Japanese rice crops grown at a series of stations in 1968, the correlation between yield and radiation during grain-filling was only 0.179 (Japan IBP, 1970). Such data then, of which we need much more for high-yielding varieties grown under favourable conditions, give no clear answer as to whether photosynthetic or storage capacity most limits yield in these crops.

Another approach to this question is to estimate the maximum potential grain yields of these crops given their present photosynthetic characteristics. The solid lines in Figure 3 give such estimates for maize, wheat and rice, based on the following assumptions:

1. Of the incident radiation 45 per cent is active in photosynthesis (cf. Szeicz, 1966).
2. By reflection 16 per cent of it is lost (cf. Yocom *et al.*, 1964), and a further 10 per cent is absorbed by photosynthetically inert structures (cf. Loomis and Williams, 1963).
3. Eight quanta are required to reduce each molecule of CO_2 ; over the visible spectrum this is equivalent to an average conversion efficiency of 26 per cent.
4. The reduction in photosynthesis by crops due to light saturation was estimated from the curves for enclosed communities given in Figure 2: with 500 cal cm^{-2} day $^{-1}$, for example, it was taken as 12 per cent for maize, 36 per cent for wheat and rice. A far more satisfactory solution to this step in the estimation is now possible for individual crops, given more detailed data on canopy structure and the radiation environment.

5. A conversion factor of 3,500 cal g^{-1} of dry weight was taken.
 6. Respiration losses were estimated on the basis developed by McCree (1970); daily losses were taken as 1.5 per cent of accumulated dry weight (taken as 1 kg m^{-2}) plus 25 per cent of gross photosynthesis.
 7. Grain-filling was assumed to take 30 days for rice, 40 days for wheat, and 50 days for maize.
 8. During these periods 90 per cent of the net assimilate was translocated to the grain.
 9. Of plant material accumulated before anthesis (assumed to be 1 kg m^{-2}), 10 per cent could be mobilized to the grain in maize and wheat, 20 per cent in rice.
- The first six assumptions provide estimates of maximum crop growth rates; at 500 cal cm^{-2} day $^{-1}$, for example, these are 59 g m^{-2} day $^{-1}$ for maize and other plants with the C₄-dicarboxylic acid pathway, and 44 g m^{-2} day $^{-1}$ for Calvin cycle plants. The highest crop growth rates recorded at such a radiation level, namely 54 g m^{-2} day $^{-1}$ for *Pennisetum typhoides* (Begg, 1965) and 43.6 g m^{-2} day $^{-1}$ for *Festuca arundinacea* (Sheehy and Cooper, unpublished data) approach these estimates closely. This does not validate the assumptions made, but it does suggest that crop photosynthesis can approach the assumed efficiency, and that the gap between actual and potential grain yields in Figure 3 may, therefore, reflect insufficient storage capacity. However, there is too much uncertainty at this stage about many of the most important assumptions, such as the magnitude of respiration losses, to be confident of this conclusion. On the one hand Stoy (1966) concluded from his model that grain yield in wheat was probably limited by the supply of assimilates at a radiation level of about 400 cal cm^{-2} day $^{-1}$. Murata's (1965) model for rice, on the other hand, suggests that potential yields are far higher than those indicated by the solid line for rice in Figure 3, i.e. that storage capacity is severely limiting.

Other evidence which suggests that photosynthetic capacity does not limit grain yields at higher radiation levels is as follows:

Evolution in wheat has been accompanied by a progressive fall in photosynthetic rate of the flag leaves (Evans and Dunstone, 1970). Admittedly, leaf size has increased, but grain size has also increased proportionately, and in any case the photosynthetic rate per unit leaf area is the major determinant of assimilation by a closed canopy. Grain yields could hardly have risen in spite of so marked a fall in photosynthetic rate had the supply of assimilate been limiting. As noted above, differences in photosynthetic rate between varieties have been found in several crops, but in no case have these been shown to be consistently related to yield rankings (e.g. Watson *et al.*, 1963; Irvine, 1967; Dornhoff and Shibles, 1970).

Grain yields in wheat can be increased by treatments which increase only the storage capacity of the ear (Bingham, 1966; Rawson and Evans, 1970a). With rice, grain size is even less elastic than in the free-

threshing wheats, being enclosed by rigid glumes, and storage capacity can place rigid limits on yield (Murata, 1969).

Balance sheets of net photosynthesis by the various organs of high-yielding wheat varieties grown under controlled conditions, and of the need for assimilates for grain growth and respiration, reveal that photosynthesis can be more than sufficient to meet even the maximum demands for grain development (Evans and Rawson, 1970).

There are many instances in which treatments substantially reducing photosynthesis, such as shading or partial defoliation, have much smaller effects on grain growth and yield, e.g. in maize (Allison and Watson, 1966; Duncan *et al.*, 1965) and wheat (Asana *et al.*, 1969; Rawson and Evans, 1970b). One mechanism buffering grain yield against such stresses is the mobilization of more of the reserves accumulated during earlier growth, another is a rise in the photosynthetic rate of the remaining structures (King *et al.*, 1967; Rawson and Evans, 1970b). Both clearly indicate that grain growth was not being limited by the supply of assimilates. Among wheat varieties, buffering of yield against reduced photosynthesis was most marked

in the lower yielding ones. In those with potentially higher yields, the assimilates were more fully mobilized and there was less buffering against stress, as Finlay and Wilkinson (1963) found with barley varieties.

If grain yields are frequently not limited by the supply of assimilates, only rarely will there be a simple relation between yield and incident radiation during grain-filling. Morphogenic effects of light on the components of storage capacity can be as important as photosynthesis in determining yield, and are far more complex in their interactions, with the result that our ability to develop satisfactory models of the effects of radiation on yield remains severely limited.

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Résumé

Effet de la lumière sur la croissance, le développement et le rendement des végétaux (L. T. Evans)

L'auteur passe en revue les questions suivantes: manière dont la photosynthèse, le phototropisme et le phytochrome dépendent du spectre et réactions de haute énergie; la photomorphogenèse chez les dicotylédones comparée à la photomorphogenèse chez les monocotylédones; rapport entre la vitesse de photosynthèse de feuilles isolées et le rayonnement incident en fonction de l'espèce, de l'histoire du milieu, de l'âge, des besoins, de l'heure de la journée et des circonstances changeantes; effet de la lumière sur la respiration et ordre de grandeur de la respiration dans les communautés de plantes.

Bref examen du rapport entre la durée du jour et le développement reproductif; la durée du jour influe sur le rendement non seulement en agissant sur le moment de la floraison et le développement des fruits, compte

tenu du rayonnement saisonnier et du risque de gelée ou de sécheresse, mais aussi en déterminant plusieurs éléments du rendement.

La photosynthèse par les communautés de plantes, même chez les espèces à cycle de Calvin, peut ne manifester qu'une faible saturation de lumière si le vent est suffisant pour assurer le renouvellement de CO₂, et elle peut s'approcher de l'efficacité maximale théorique lorsque les conditions sont favorables. Des évaluations du rendement potentiel maximal à divers niveaux de rayonnement sont données pour le Blé et le Maïs. Le rendement effectif tend vers le rendement potentiel maximal aux faibles niveaux de rayonnement, mais il tombe bien au-dessous aux niveaux élevés. Plusieurs séries de constatations semblent indiquer que cette chute n'est pas due à une limitation par la capacité de photosynthèse des cultures.

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The energy balance of leaves¹

A. R. Aston, R. J. Millington, D. B. Peters
Agronomy Department, University of Illinois
Urbana, Ill. (United States of America)
United States Department of Agriculture and
Agronomy Department, University of Illinois
Urbana, Ill. (United States of America)

A general energy balance of a leaf may be written as:

$$\frac{\partial}{\partial t} \int_V C_v (T - T_o) dV = \int_A \bar{F} \cdot \bar{n} dA + \int_V S dV \quad (1)$$

where t = time (min); C_v = volumetric heat capacity of the leaf (cal cm⁻³ °C⁻¹); T = leaf temperature (°C); T_o = reference temperature (°C); V = leaf volume (cm³); A = leaf area (cm²); S = source term (cal cm⁻³ min⁻¹); \bar{n} = normal inward unit vector; $\bar{F} \cdot \bar{n}$ = normal component of net energy influx (cal cm⁻² min⁻¹). The net energy influx \bar{F} represents the energy fluxes due to solar and thermal radiation, convection, conduction and evaporation. The source term S represents the energy production and/or consumption associated with photosynthesis and the basic metabolism of the leaf.

Aston *et al.* (1969) incorporated into a growth chamber an infra-red radiative flux similar to that experienced under natural conditions, and in so doing gave another means of controlling leaf temperature.

The over-all energy balance of a vertical leaf in this plant chamber under conditions of forced convection was written as

$$Q = a_s S + R_{BB} + R_W + C + E [\text{ly min}^{-1}] \quad (2)$$

where Q = heat storage; $a_s S$ = absorbed shortwave radiation; R_{BB} and R_W = radiation exchange between leaf and sink plates and chamber walls, respectively; C = convective flux; and E = latent heat flux.

The convective transfer of heat H (cal min⁻¹) across the boundary layer of a flat plate (leaf) is written as

$$H = A h_c \Delta T \quad (3)$$

where h_c = transfer coefficient of convection (cal cm⁻² min⁻¹ °C⁻¹); A = area (cm²); and ΔT = temperature difference between the surrounding air and the plate.

The thermal transfer resistance r_h (min cm⁻¹) is defined according to Raschke (1960) as

$$H = A \frac{C_p \rho}{r_h} \Delta T \quad (4)$$

where C_p = heat capacity of air (cal gm⁻¹ °C⁻¹) and ρ = air density. The total sensible heat transfer from the leaf may be partitioned with respect to the two sides of the leaf. Using subscripts 1 and 2 for the first and second sides respectively

$$H_1 = A_1 h_c \Delta T_1 = A_1 \frac{C_p \rho}{r_{h1}} \Delta T_1 \quad (5)$$

and

$$H_2 = A_2 h_c \Delta T_2 = A_2 \frac{C_p \rho}{r_{h2}} \Delta T_2 \quad (6)$$

Assuming that the surface temperatures of both sides are equal ($T_{L1} = T_{L2}$), the leaf is orientated parallel to mean wind flow and $A_1 = A_2$ then the total heat flow (H_T) from the leaf is written as

$$H_T = H_1 + H_2 \\ = 2A h_c \Delta T = \left(\frac{1}{r_{h1}} + \frac{1}{r_{h2}} \right) A C_p \rho \Delta T \quad (7)$$

The convective flux C (ly min⁻¹) averaged over the total leaf surface (sides one and two) is obtained by dividing equation (7) throughout by $\int_A (dA_1 + dA_2) \approx 2A$ such that

$$C = h_c \Delta T \\ = \left(\frac{r_{h1} + r_{h2}}{2r_{h1} \cdot r_{h2}} \right) C_p \rho \Delta T \quad (8)$$

1. Contribution from the Illinois Agricultural Experiment Station and the Corn Belt Branch, Soil and Water Conservation Research Division, Agricultural Research Service, United States Department of Agriculture.

In the case where $r_{h1} = r_{h2}$ then

$$C = \frac{C_p \rho}{r_h} \Delta T \quad (9)$$

where r_h = thermal transfer resistance averaged over the total leaf surface area ($2A$).

The transfer of latent energy (LE) from an evaporating surface can be written as

$$LE = -A LH h_v \Delta \chi \quad (10)$$

where h_v = transfer coefficient of water vapour (cm sec^{-1}); A = area (cm^2); LH = latent heat of vaporization (cal g^{-1}); and $\Delta \chi$; = $\chi_e - \chi_o$ = vapour concentration difference between the leaf and the surrounding air. The transfer coefficient is equal to the diffusivity for water vapour in air divided by the effective boundary layer thickness, thus giving the units of cm sec^{-1} . The vapour transfer resistance r_v (sec cm^{-1}) is defined as the reciprocal of the transfer coefficient such that

$$LE = -ALH \frac{1}{r_v} \Delta \chi \quad (11)$$

The diffusion of water vapour from leaves has been considered in terms of a network of resistances (Gaastra, 1959; Milthorpe, 1962; Monteith, 1963).

The total water vapour transfer resistance (r_v) consists of an air resistance (r_a) connected to a parallel network of a cuticle resistance (r_c) and a stomatal resistance (r_s) such that

$$r_v = r_a + \frac{r_c r_s}{r_c + r_s} \quad (12)$$

As with convective transfer of sensible heat, the latent energy transfer (LE with units cal sec^{-1}) can be written for both sides 1 and 2 of a leaf

$$LE_1 = -A_1 LH h_v \Delta \chi_1 = -A_1 LH \frac{1}{r_{v1}} \Delta \chi_1 \quad (13)$$

and

$$LE_2 = -A_2 LH h_v \Delta \chi_2 = -A_2 LH \frac{1}{r_{v2}} \Delta \chi_2 \quad (14)$$

Assuming that the vapour concentrations at the two surfaces of the leaf are equal, then the total latent energy transfer is

$$\begin{aligned} LE_T &= LE_1 + LE_2 \\ &= -2A LH h_v \Delta \chi = -\left(\frac{1}{r_{v1}} + \frac{1}{r_{v2}}\right) LH \Delta \chi \quad (15) \end{aligned}$$

Equation (15) can be used to determine the latent heat flux (E with units ly min^{-1}) of a hypostomatous leaf and modified, when considering an amphistomatous leaf, to

$$E = -LH \frac{1}{r_v} \Delta \chi \quad (16)$$

where r_v = vapour transfer resistance related to the total leaf surface area ($2A$).

An important point to remember in the determination of leaf transfer resistances is the area basis on which the respective fluxes are calculated. A factor of $\times 2$ can be involved, depending on whether one or both sides of leaf are considered.

The vapour pressure at the evaporating surface of the leaf is usually taken to be the saturated vapour pressure (e_s) which, at equilibrium, is a function of the surface temperature (Gaastra, 1959; Powell, 1940; Slatyer and Bierhuizen, 1964). Considering a small volume element of moist air and assuming that water vapour behaves as an ideal gas, the vapour pressure (e) of water can be represented as

$$e = \frac{\chi}{M_v} R_u T \quad (17)$$

where X = density or concentration of water vapour (9 cm^{-3}); M_v = molecular weight of water (18 g mole^{-1}); R_u = universal gas constant ($8.31 \times 10^7 \text{ erg mole}^{-1} \text{ deg K}^{-1}$); and T = absolute temperature.

Substitution of the mixing ratio defined as

$$\text{Mixing ratio } \omega = \frac{\text{Mass of water vapour}}{\text{Mass of dry air}}$$

into equation (17) gives

$$\begin{aligned} \omega &= \frac{M_v}{M_d} \frac{e}{P_a - e} \\ &\approx 0.622 \frac{e}{P_a} \text{ assuming } e \ll P_a \quad (18) \end{aligned}$$

where M_v , M_d = molecular weights of water and dry air respectively; e = vapour pressure (mm Hg); and P_a = atmosphere pressure (mm Hg). It follows that

$$\Delta \chi \approx \frac{0.622 \rho \Delta e}{P_a} \quad (19)$$

where ρ = density of dry air.

The objectives of the present work were to examine the energy balance of artificial leaves under conditions of independently controlled radiative, sensible heat and latent heat exchange, to provide quantitative information on heat and mass transfer coefficients and to compare the latter with estimates presented in the literature.

MATERIALS AND METHODS

The experiments were conducted in a Plexiglas growth chamber in which wind speed, air temperature, humidity and visible and thermal radiant fluxes were regulated. The apparatus has been described elsewhere (Aston *et al.*, 1969). The leaf was placed in a vertical position between two large black surfaces approximately 20 cm square which acted as sinks for thermal radiation. The surfaces were isolated from the main air stream using 0.025 mm

Polyethylene such that they acted only as thermal sinks through long wave radiant exchange. Dry ice was placed behind the black body plates to give an effective surface temperature in the order of -50°C .

The artificial leaf was constructed with two pieces ($5 \times 5\text{ cm}$) green blotting paper separated by absorbent paper towel. It was sealed around the edges with epoxy cement and was wetted by capillarity from a constant head source. The dry and wet weights of the leaf were determined and the mass average heat capacity (C) was calculated using the following relationship:

$$C = \frac{M_W \cdot C_W + M_C \cdot C_C}{M_W + M_C} \quad (20)$$

where M_W , M_C = mass of water and dry material respectively and C_W , C_C = heat capacity of water and cellulose respectively. Two chromel-constantan thermocouples (0.05 mm) were incorporated into the green blotting paper leaf such that the couple junctions were positioned just below the evaporating surfaces.

RESULTS

The energy balance of the saturated green blotting paper leaf is presented in Figures 1 and 2. These diagrams show the effect of different humidity conditions (29 and 41 per cent) within the chamber. The black plates were at ambient temperature (25°C). At the lower humidity value (29 per cent) the leaf transpired initially at a rate of $4.65 \times 10^{-4}\text{ g H}_2\text{O cm}^{-2}\text{ min}^{-1}$, which cooled the leaf to a temperature 10.5°C below ambient, compared with an evaporation rate of $4.07 \times 10^{-4}\text{ g H}_2\text{O cm}^{-2}\text{ min}^{-1}$ and a leaf temperature 7.7°C below ambient at the higher relative humidity condition. These evaporation rates were averaged over the total surface area of the leaf

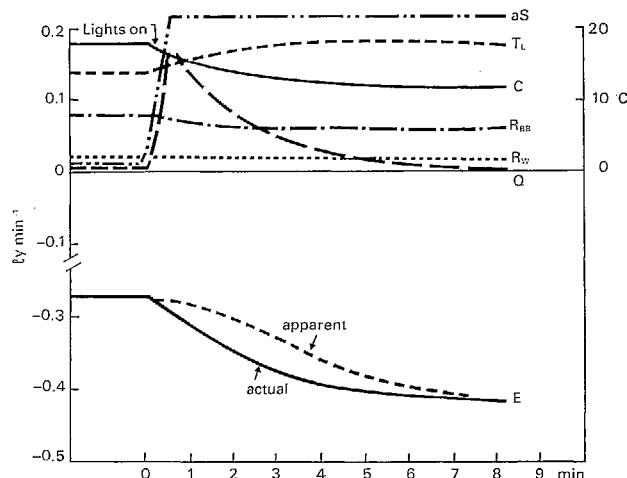


FIG. 1. The effect of visible radiation on the energy balance of the saturated paper "leaf". (Cold sink temperature \approx air temperature, relative humidity \approx 29 per cent.)

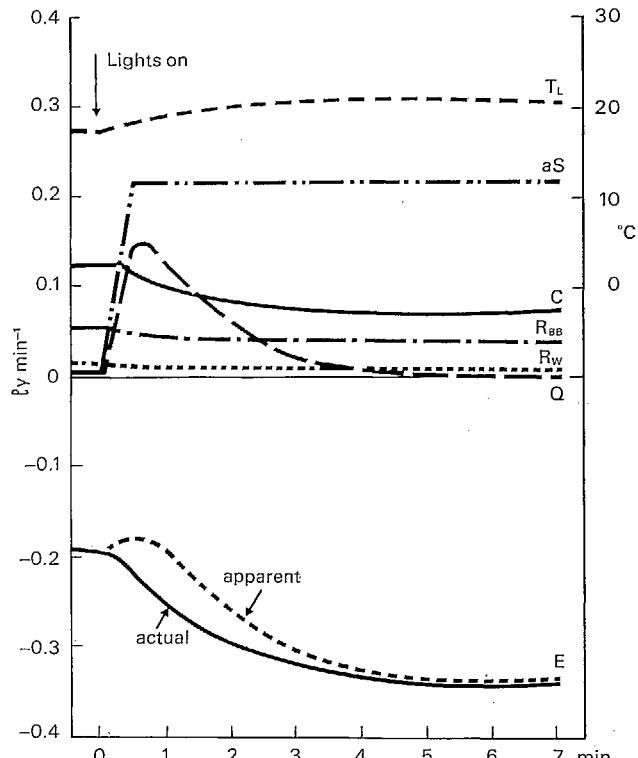


FIG. 2. The effect of visible radiation on the energy balance of the saturated paper "leaf". (Cold sink temperature \approx air temperature, relative humidity \approx 41 per cent.)

(2.4) and resulted in latent heat fluxes (E) of -0.270 and $-0.196\text{ ly min}^{-1}$ respectively. By convention, an energy flux away from the leaf is negative and a flux directed to the leaf is positive. At this initial steady state condition, both Q and $a_S = 0$; E was determined from load cell data and the convective flux was calculated using the relationship of Gates (1962)

$$C = 5.7 \times 10^{-3} \left(\frac{V}{L} \right)^{1/2} \Delta T \quad (21)$$

where V = windspeed (cm sec^{-1}); L = characteristic length (cm); and ΔT = temperature difference between the surrounding air and the leaf. Using equation (2) the net thermal radiant exchange (R_N) can be determined. Since

$$R_N = R_{BB} + R_W \quad (22)$$

Knowing the temperature distribution and a radiation interchange factor F_{BB} , the respective radiant exchanges were obtained using the following relationships

$$R_{BB} = F_{BB} \sigma (T_{BB}^4 - T_L^4) \quad (23)$$

$$R_W = (1 - F_{BB}) \sigma (T_W^4 - T_L^4) \quad (23a)$$

where T_{BB} , T_W , T_L = temperatures of sink plates, chamber walls and leaf, respectively. The factor F_{BB} is

a function of view angles, emissivities, internal reflection and areas within the chamber and is assumed to remain constant under the conditions of each of the experimental runs. At the new steady states achieved after the lights were turned on, leaf temperatures had increased to 18.1 and 20.8°C, and evaporation rates had increased to 7.15×10^{-4} and 5.78×10^{-4} g H₂O cm⁻² min⁻¹, resulting in latent heat loads of -0.415 and -0.335 ly min⁻¹ respectively for the low and high humidity environments. During this final steady state where the storage flux $Q = 0$, the absorbed shortwave flux was determined from equation (2) and was found equal to 0.215 ly min⁻¹. It was assumed that this shortwave flux remained constant and was the same for all experimental runs when the lights were on.

During the transient stage after the lights were turned on, $\alpha_s S$ was known, C , R_{BB} and R_W were calculated and E was determined from the time rate of change of the water pan weight and was also verified using equation (2). Under these transient conditions, however, the latent heat flux determined by weighing tended to underestimate the actual latent heat load. The extent of the underestimation apparently depends on the rate of evaporation at the leaf surface. To illustrate this, the actual evaporation, determined from equation (2), was compared with the apparent evaporation measured by

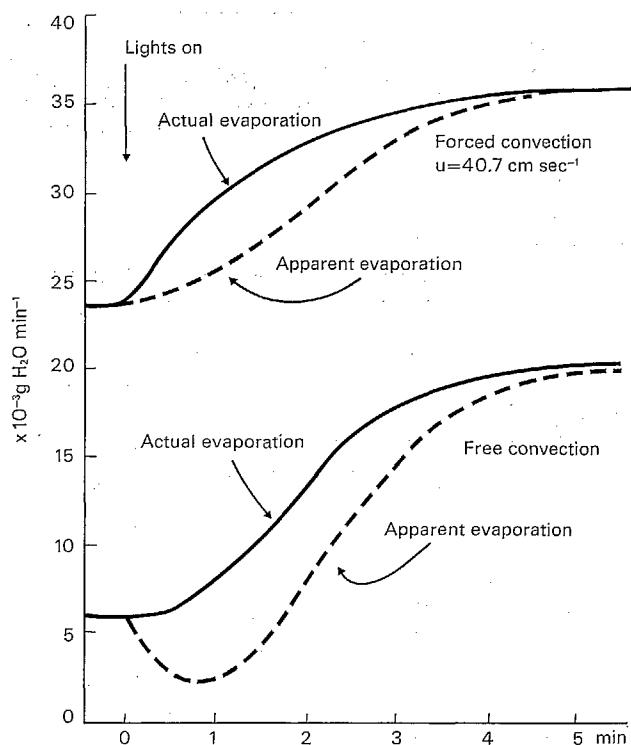


FIG. 3. The time course of actual and apparent evaporation from the saturated paper "leaf" under forced and free convective conditions.

the time rate of change of the pan weight for both forced and free convective conditions (Fig. 3). Under free convective conditions, with lower evaporation rates, the rate of change of apparent evaporation became negative immediately after the lights were turned on indicating desorption of the leaf water. This phenomenon can be explained by considering the blotting paper leaf as a porous medium. On the basis that surface tension radius of curvature was the principal water-holding mechanism (Wilkinson and Klute, 1962), an increase in leaf temperature would decrease the surface tension of the water in the pores, allowing water to drain from the artificial leaf.

Calculation of the vapour transfer resistance r_a during the initial steady state ($r_a = 0.86$ sec cm⁻¹) and use of this value in equation (16) gave further verification of the actual evaporation rates measured during the transient stage after the addition of the visible light load.

Windspeed inside the chamber was adjusted to give velocities within the range 20–80 ft min⁻¹. An energy balance was undertaken at the steady state at each windspeed and is represented in Figure 4. Relative humidity inside the chamber was maintained at 29 per cent. There was no visible light load. The convective flux (C) was calculated from equation (21), the thermal radiative exchanges (R_{BB} and R_W) were calculated using $F_{BB} = 0.8$ obtained from the previous experiments and the latent heat flux was determined from evaporation measurements and again verified using equation (2). Leaf temperature decreased slightly (1°C) as air speed was increased, giving rise to a slight increase in the long wave radiative exchange between the leaf and the black plates. By far the greatest change occurred in the calculated convective and measured latent heat exchanges and the magnitude of these two

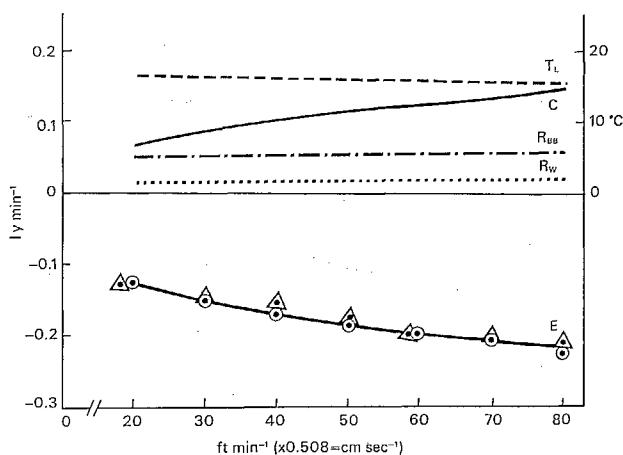


FIG. 4. The effect of windspeed on the energy balance of the saturated paper "leaf". (Cold sink temperature ≈ air temperature.)

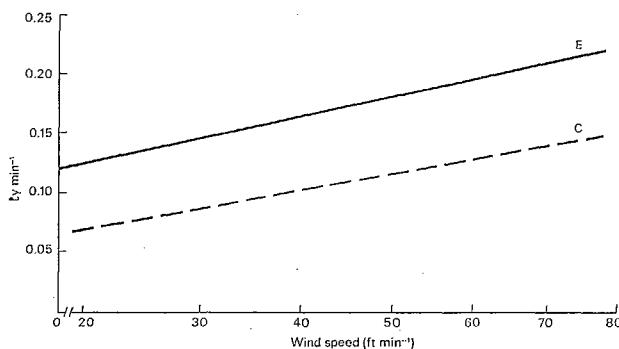


FIG. 5. The effect of windspeed on the latent heat and convective heat fluxes for the saturated paper leaf. (The data fit the relation, $y = b + mV^{1/2}$.)

fluxes were proportional to $(V)^{1/2}$ as shown in Figure 5. The thermal transfer resistance r_h (Gates 1962) was obtained from the calculated convective flux using equation (9) and the water vapour transfer resistance r_a (experimental) was determined from the experimental leaf water evaporation rates using equations (16) and (19). The effect of windspeed on these resistances is presented in Figure 6, with additional data from Thom (1968). Dry ice was placed behind one black plate and the effect of increased long wave radiative exchange on the leaf is shown in Figures 7 and 8. Leaf temperature was reduced to 9°C below ambient. The temperature gradient across the leaf was 2.2°C . Relative humidity in the chamber was 41 per cent and wind speed 80 ft min^{-1} . Lowering of the surface temperature of the second black plate increased the long wave radiative exchange to $-0.260 \text{ ly min}^{-1}$. This further reduced leaf temperature to 14.5°C below ambient with a gradient of 0.03°C across the leaf.

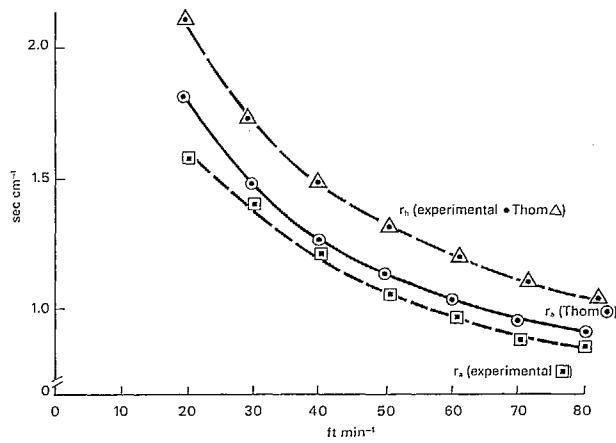


FIG. 6. The effect of windspeed on the thermal and vapour transfer resistances of the saturated paper "leaf". (Values calculated from equation (28) are shown thus: Δ and \bigcirc .)

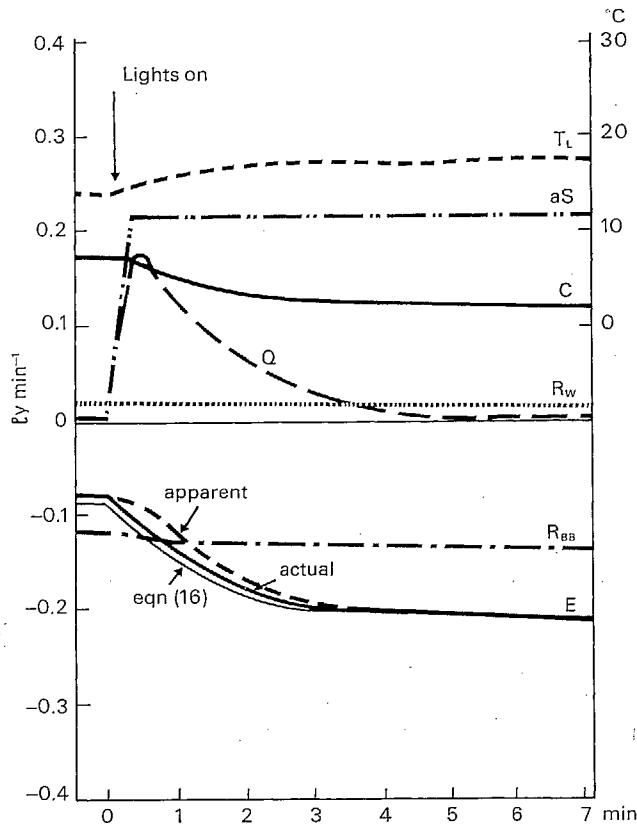


FIG. 7. The effect of visible radiation and thermal radiation on the energy balance of the saturated paper "leaf". (Left cold sink temperature $\approx -50^\circ\text{C}$, right cold sink temperature \approx air temperature.)

Addition of a visible light load increased leaf temperature to 17.8° and 15.2°C , which correspondingly increased the latent heat load to -0.21 and $-0.123 \text{ ly min}^{-1}$, as is shown in Figures 7 and 8 respectively.

The latent heat flux determined from load cell data was verified from equation (2) and calculated from equation (16); however, it is apparent that the latter method tended to overestimate the actual latent flux at leaf temperatures less than 15°C .

This result may indicate a temperature effect on the mass transfer coefficient.

DISCUSSION

A comparison of the heat transfer coefficients and resistances was made using relationships presented by Gates (1962), Raschke (1960) and Thom (1968). According to Gates (1962), for a plate parallel to the wind

$$h_c = 5.7 \times 10^{-3} \left(\frac{V}{L} \right)^{1/2} \quad (24)$$

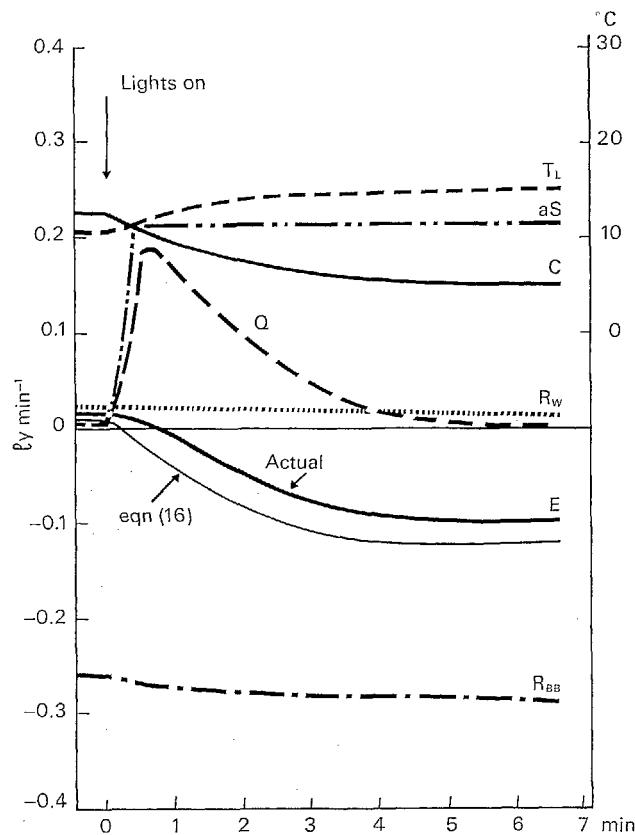


FIG. 8. The effect of visible radiation and thermal radiation on the energy balance of the saturated paper "leaf". (Left and right cold sink temperature $\approx -50^{\circ}\text{C}$.)

where h_c = convection coefficient ($\text{cal cm}^{-2} \text{ min}^{-1} ^{\circ}\text{C}^{-1}$); V = windspeed (cm sec^{-1}); L = characteristic length; and ΔT = temperature difference between the leaf and the air. This relation has been verified by Aston, Millington and Peters (1969) using a dry, copper, artificial leaf. The convective flux was averaged over the total leaf surface ($2A$).

Thom (1968) defines a dimensionless coefficient of sensible heat transfer (C_h) as

$$C_h = \frac{1}{\rho A C_p} \frac{H}{V \Delta T} \quad (25)$$

$$= 1.4 \left(\frac{VL}{v} \right)^{-\frac{1}{2}} \left(\frac{K}{v} \right)^{\frac{2}{3}}$$

where H = rate of heat transfer (cal sec^{-1}); ρ = air density; A = area; C_p = heat capacity of air ($\text{cal g}^{-1}^{\circ}\text{C}^{-1}$); V = windspeed (cm sec^{-1}); K = molecular diffusivity of heat ($\text{cm}^2 \text{ sec}^{-1}$); and v = kinematic viscosity ($\text{cm}^2 \text{ sec}^{-1}$).

Rearranging and writing a convective flux with units ly min^{-1} , averaged over the total leaf surface $2A$, equation (25) becomes

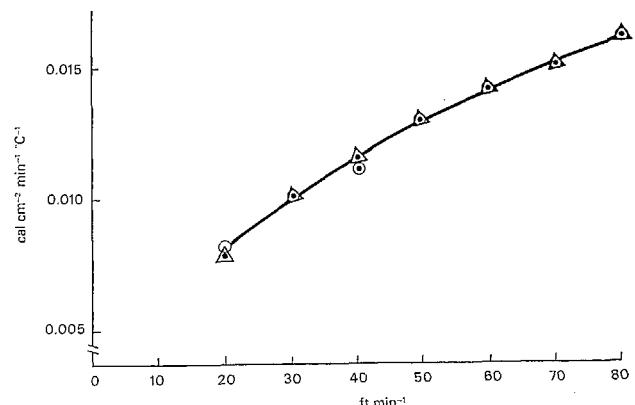


FIG. 9. The effect of windspeed on the convection coefficients of a vertical "leaf". (Values calculated from equations (24) and (27) are shown as Δ and \odot respectively.)

$$C = \frac{H}{2A} \quad (26)$$

$$= 42 \left(\frac{VL}{v} \right)^{-\frac{1}{2}} \left(\frac{K}{v} \right)^{\frac{2}{3}} \rho C_p V \Delta T$$

where C = convective flux (ly min^{-1}). Using the definition that the convection coefficient, with units $\text{cal cm}^{-2} \text{ min}^{-1} ^{\circ}\text{C}^{-1}$, is the convective flux divided by ΔT , the dimensional coefficient of equation (26) is

$$h_c = 42 \left(\frac{VL}{v} \right)^{-\frac{1}{2}} \left(\frac{K}{v} \right)^{\frac{2}{3}} \rho C_p V \quad (27)$$

The convection coefficients of equations (24) and (27), using the conditions of the preceding experiment, are calculated and plotted in Figure 9. It can be seen that the two coefficients are identical under the experimental conditions. It follows that there is similar agreement between thermal transfer resistances calculated using either equation (9) of Raschke (1960) or the following general equation defined by Thom (1968).

$$r_{ash} = 2 \times 1.84 \left(\frac{L}{V} \right)^{\frac{1}{2}} \left(\frac{D, K}{v} \right)^{-\frac{2}{3}} \quad (28)$$

where D = diffusivity of water vapour in air; r_a has units sec cm^{-1} . A factor of $\times 2$ is required to base the resistance on the total surface area, $2A$ (Figs. 6 and 10).

The process of heat and mass transfer from a leaf involves a transfer across a boundary layer or film at the leaf surface. The diffusivity of water vapour and kinematic viscosity of air are, therefore, evaluated at the mean temperature of the film with the assumption that there is a linear temperature gradient. The mean temperature (T_f) would be as follows

$$T_f = \frac{T_l + T_a}{2} \quad (29)$$

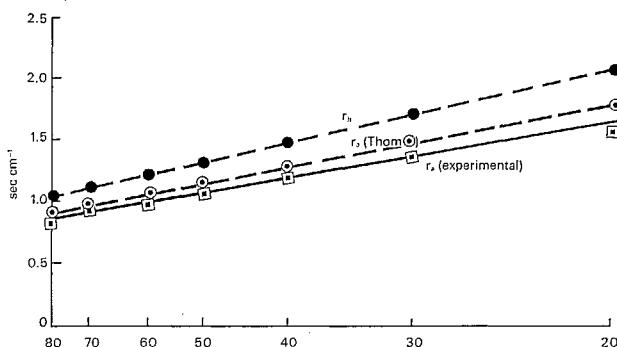


FIG. 10. The effect of windspeed on the thermal and vapour transfer resistance of the saturated paper "leaf". (The data fit the relation $y = b + mV^{-\frac{1}{2}}$. (Values calculated from equation (28) are shown thus \circ and \odot .)

where T_l = leaf temperature; and T_a = air temperature. The use of mean diffusivities and viscosities in equation (28) results in a transfer resistance averaged across the boundary air layers surrounding the leaf. This is in agreement with equation (24) in that the heat transfer coefficient (h_c) is also an averaged coefficient.

Since the evaporative heat flux is proportional to $V^{\frac{1}{2}}$, a result that has been shown by Slatyer and Bierhuizen (1964) with windspeeds as low as 0.6 cm sec^{-1} , it follows that the water vapour transfer resistance r_a is proportional to $V^{-\frac{1}{2}}$. The transfer resistance r_a calculated from equation (16) is compared in Figure 10 with r_a of equation (28). Equation (28) slightly overestimates r_a with a greater tendency for overestimation at the lower windspeeds.

It is apparent from Figures 6 and 10 that the transfer resistances of heat and water vapour are not identical within the windspeed range of 20 – 80 ft min^{-1} . The ratio of the heat transfer resistance calculated from Gate's equation (24) or Thom's equation (28) to the mass transfer resistance of equation (28) is 1.16, which corresponds numerically to $(D/K)^{\frac{1}{2}}$ where $D = 0.251 \text{ cm}^2 \text{ sec}^{-1}$ and $K = 0.21 \text{ cm}^2 \text{ sec}^{-1}$. According to Kusuda (1965) the ratio $r_h : r_a$ is equal to the reciprocal of the convective Lewis relation, $(D/K)^{\frac{1}{2}}$ for forced convection. He found in detailed experimental studies that $r_h : r_a$ may vary from 1.25 to 1.2, Slatyer and Bierhuizen (1964) have found experimentally that the ratio $r_h : r_a$ has an upper limit of about 1.2.

Within the windspeed range of these experiments, the ratio of the calculated thermal resistance to the

measured mass transfer resistance averaged 1.23 for the higher windspeeds and 1.31 at 20 ft min^{-1} . Thermal buoyancy effects were assumed unimportant and the estimates may be in error, especially at the lower windspeeds and large air-leaf temperature differences.

It is important to know the magnitude of the thermal radiation transfer when examining the energy fluxes and transfer coefficients associated with an evaporating surface when the surface temperature deviates from that of the surrounding areas that "view" the leaf. This is especially true when dealing with low windspeeds. For example, under the conditions used in the previous experiment, at a windspeed of 20 ft min^{-1} the long-wave radiative load approximately equals the convective flux and is 50 per cent of the latent heat load (Fig. 4).

The vapour transfer resistance defined by Thom (1968) overestimates the actual resistance, compared with the experimental results, by 6 per cent at a windspeed of 80 ft min^{-1} . The discrepancy is increased to 18 per cent with windspeeds as low as 20 ft min^{-1} . This is in agreement with Thom's (1968) conclusion that equation (28) would overestimate the transfer resistance for windspeeds less than 100 ft min^{-1} .

The effect of reduced leaf temperature due to increased long-wave radiant exchange appears to be an increase in the vapour transfer resistance. This can be explained partly by the temperature dependence of the diffusivity of water vapour and kinematic viscosity of air. More exact studies are required to completely characterize these effects.

CONCLUSIONS

The results and subsequent comparisons have shown, within the range of environmental conditions studied that there is reasonable agreement between the definitions and calculations of the thermal transfer coefficients and resistances by the methods of Gates (1962), Raschke (1960) and Thom (1968) as long as the area basis on which they are based includes both leaf surfaces.

Further detailed studies are required on the transfer of mass and energy to and from crop leaves. The highly productive leaves in the upper part of the plant canopy are subjected to varied atmospheric radiation and to ever-changing wind patterns. With the present system, independent control of the dominant environmental variables has been accomplished and has thereby promoted insight into the various processes involved.

Résumé

Bilan énergétique des feuilles (A. R. Aston, R. J. Millington et D. B. Peters)

On a fait une étude expérimentale du bilan énergétique de feuilles artificielles mouillées soumises à des échanges de chaleur latente et de chaleur sensible radiative contrôlés indépendamment. Des informations quantitatives sont fournies sur les coefficients de chaleur et de

masse, et les valeurs obtenues ont à peu près concordé avec les rapports indiqués dans les ouvrages spécialisés. Toutefois, les résultats ont montré que la chaleur calculée et les résistances au transfert de masse déterminé expérimentalement ne sont pas les mêmes, mais sont dans le rapport de 1,2/1,0 approximativement pour les vitesses de vent comprises entre 9 et 24 mètres/minute.

Mots clés : bilan énergétique des feuilles; rayonnement.

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Utilisation de pyranomètres linéaires dans l'étude des éléments du climat lumineux dans la végétation

C. Baldy, J.-C. Combres et R. Bonhomme
Station centrale de bioclimatologie
Centre national de recherches agronomiques
de l'Institut national de la recherche agronomique,
Versailles (France)

INTRODUCTION

La croissance des plantes est sous la dépendance directe du rayonnement d'origine solaire, et son étude implique l'analyse précise des rayonnements visible et infrarouge court. Un grand nombre de travaux sont actuellement effectués dans ce domaine, et une bibliographie de la question a été présentée par Chartier (1970). En ce qui concerne les mesures de rayonnement, l'analyse de leur extinction dans le couvert constitue un sujet très important; la connaissance des variations enregistrées à chaque niveau permet d'analyser les conditions précises de fonctionnement de chaque feuille à chaque instant, et donc la photosynthèse nette de l'ensemble végétal.

Les études actuellement entreprises tant sur le rayonnement photosynthétiquement utile (Norman *et al.*, 1969) que sur le rayonnement global (Chartier, 1970) et le rayonnement net (Impens et Lemeur, 1969) montrent que l'utilisation de la formule de Beer, généralement convenable, deviendrait insuffisante dans certains cas, quand le couvert devient hétérogène, par exemple.

Il est nécessaire d'entreprendre des mesures directes dans les différentes conditions réelles; mais cela impose aussi d'intégrer les fluctuations locales de telle façon que celles-ci soient analysables et permettent de déduire les lois générales. Ces conditions imposent un grand nombre de répétitions instantanées. Ces considérations nous ont conduit à étudier des pyranomètres de grandes dimensions, sensibles, et ayant une constante de temps aussi brève que possible, afin de pouvoir analyser tous les éléments du climat lumineux de courte longueur d'onde, d'origines ascendante ou descendante (direct et réfléchi), en intégrant les taches de soleil et parallèlement en ne mesurant que le rayonnement diffus ascendant et descendant à chaque niveau.

DESCRIPTION SOMMAIRE DU PYRANOMÈTRE LINÉAIRE INRA

Voilà déjà plus de dix ans que des tentatives sont faites pour obtenir des pyranomètres économiques, fiables et réellement utilisables dans les conditions naturelles (Monteith, 1959).

L'analyse critique de la fabrication a été faite par nous (Combres *et al.*, 1970), et l'appareil est utilisé largement dans toutes nos études, qui portent actuellement essentiellement sur le Blé et le Maïs, mais aussi sur le Pin sylvestre (*Pinus silvestris L.*). Une présentation technique des opérations de fabrication a été rédigée par J.-P. Le Buhan (1970).

Il s'agit d'un circuit imprimé en constantan, constitué d'une série de 75 créneaux. Par électrolyse coulométrique, on dépose sur ceux-ci, par moitié, un dépôt de cuivre parfaitement adhérent. Le métal déposé a ainsi des propriétés voisines de celles du métal massif.

Sur les thermocouples en série ainsi réalisés on dépose un revêtement aussi blanc que possible pour une moitié (source froide) et aussi noir que possible pour l'autre (source chaude). On a choisi pour cette dernière le noir "3M" recommandé par l'OMM.

Ces peintures doivent avoir de nombreuses qualités: résistance et invariance au vieillissement, matité aussi complète que possible, liant non photosensible, etc. La pile thermoélectrique ainsi réalisée est montée dans un tube en verre pyrex hermétiquement clos. Le montage est réalisé de telle façon que l'ensemble soit parfaitement réglable, afin d'obtenir une horizontalité parfaite. Un niveau à bulle est soudé à une extrémité de l'ensemble, de telle façon que, par construction, il soit parallèle au circuit. Un support réglable permet de parfaire l'horizontalité du montage.

Nous avons cherché à préciser les caractéristiques de l'appareil, et des tests ont été effectués par l'un de nous (J.-C. Combres) à l'Institut royal météorologique de

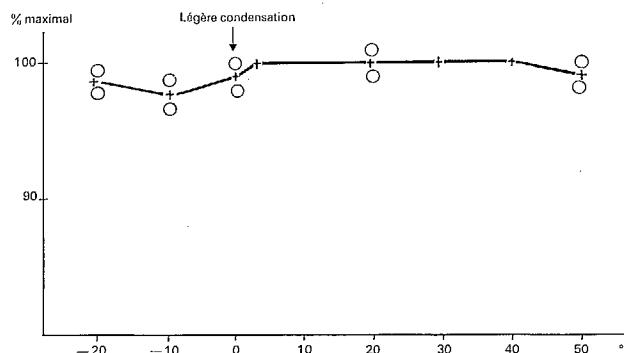


FIG. 1. Stabilité thermique des pyranomètres.

Belgique (Uccle), grâce à la grande bienveillance de son directeur, M. van Mieghem, et en particulier de M. Dogniaux, spécialiste éminent en la matière.

On a pu montrer qu'entre -20 et $+50$ °C l'appareil est insensible à la température (fig. 1). La position de la source, par contre, est importante, puisque ce pyranomètre linéaire n'a pas de centre de symétrie. Mais cette difficulté est moins sensible quand la source est située pratiquement à l'infini, ce qui est le cas du soleil: les mesures des facteurs de correction ont été effectuées; elles ont permis de montrer que l'influence de l'orientation est faible (voisine de 1%) en rayonnement diffus, par temps couvert de façon homogène.

Nous étalonnons ces piles par rapport au pyranomètre de Moll donnant $8,4 \text{ mV/cal cm}^{-2} \cdot \text{mm}^{-1}$. Les pyranomètres INRA varient faiblement entre eux quand leur résistance interne avoisine 13Ω (tableau 1) et qu'ils produisent un courant de $20 \text{ mV/cal cm}^{-2} \cdot \text{mm}^{-1}$ en moyenne, avec une fluctuation extrême inférieure à $\pm 4\%$. L'écart extrême entre la position azimutale la plus défavorable et la position azimutale la plus favorable, pour la pile présentant le plus grand écart, est inférieur à $\pm 4\%$.

Grâce aux améliorations obtenues lors du cuivrage, on est parvenu à une bonne isosensibilité de ces pyranomètres.

mètres et de chaque thermocouple les composant, ce qui linéarise bien la réponse de l'appareil sur toute sa surface. Le temps de réponse de ces piles est de 3,7 secondes, comparable donc à celui de la pile de Moll (4,5 s) (Combres *et al.*, 1970).

EXEMPLES D'UTILISATION DANS UN COUVERT DE MAÏS

Ces pyranomètres permettent en particulier de vérifier statistiquement l'applicabilité de la loi de Beer dans le cas d'une culture peu continue, comme le Maïs. On a étudié particulièrement l'importance à attribuer au rayonnement diffus dans le couvert, en occultant le soleil au moyen d'une plaque mobile. Les graphiques présentés ci-après (fig. 2, 3, 4a, 4b et 5) permettent d'illustrer certaines études déjà entamées et destinées à être reprises et améliorées.

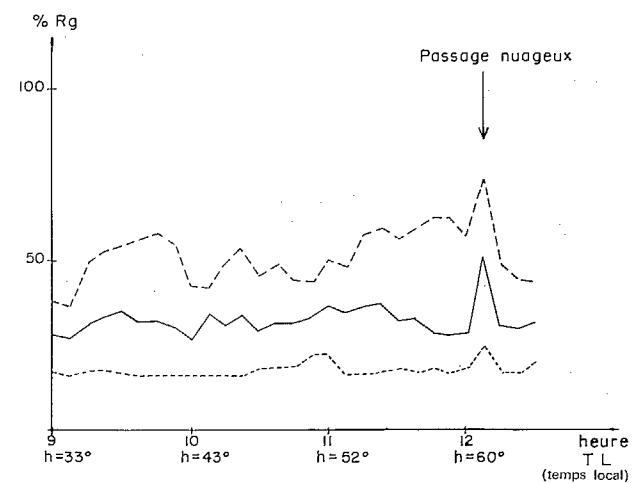


FIG. 2. Moyenne, enveloppe des maximums et minimums, pour 7 répétitions à 90 cm dans la végétation. Maïs, 28 juillet 1969 (h: hauteur du soleil).

TABLEAU 1. Testage des pyranomètres. Valeur moyenne en % du rayonnement mesuré au même instant par une pile de Moll pour les différentes positions azimutales (le pyranomètre étant réglé horizontalement) par ciel clair (juin 1970)

Pile n°	D 14	D 17	D 19	D 24	D 25	D 28	D 30	D 32	D 34	D 35
Résistance	13,1	13,1	13,0	13,1	12,9	12,9	13,3	13,1	13,1	13,3
% Moll	239	236	229	241	232	231	236	237	234	229

TABLEAU 2. Valeur de réponse du pyranomètre D 14 pour quelques positions en direction par rapport au soleil par ciel clair (juin 1970), en % de la pile de Moll

Direction	S-E	E	N-E	N	W	
% Moll	243	233	238	239	238	soit une moyenne de $238,6 \pm 4,2$

La figure 2 est destinée à montrer la fluctuation instantanée du rayonnement reçu dans la végétation à chaque instant: elle présente les moyennes, les maximums et les minimums du rayonnement global reçu à 90 cm dans le Maïs (rayonnement descendant). Sous un indice foliaire cumulé voisin de 2,0 (28 juillet 1970). Cela représente la moyenne de 7 répétitions; en se reportant à l'article de McCree et Loomis (1969), on doit pouvoir conclure que la valeur moyenne enregistrée doit

correspondre sur le plan de la photosynthèse à la moyenne des extrêmes. Il s'agit dans la présente représentation de la valeur du rayonnement en pourcentage du rayonnement global incident, celui-ci variant beaucoup au cours de la journée: à 12 h 30, un passage nuageux très important explique la pointe enregistrée. La courbe enveloppe des minimums correspond au rayonnement diffus seul à ce niveau, et l'intervalle entre la courbe minimale et la courbe maximale donne une estimation de l'énergie apportée par les taches de soleil (Bonhomme, 1970).

La figure 3 donne l'évolution de l'albédo au-dessus d'une culture de Maïs, huit jours après la floraison mâle, par journée claire; l'albédo est présenté en pourcentage du rayonnement global descendant. Il s'agit donc de la fraction réfléchie, mesurée à 1 m au-dessus du couvert. On passe d'une valeur proche de 40% pour une hauteur du soleil de 22° à une valeur de 20% pour 58°.

Les deux figures 4a et 4b caractérisent l'évolution du rayonnement global dans la végétation, c'est-à-dire l'extinction par le couvert. Les graphiques présentent trois résultats partiels, les 6 et 10 août, pour des valeurs peu élevées du rayonnement solaire. Les graphiques présentent l'extinction en fonction et du LAI (surface foliaire cumulée par niveau) et de la hauteur de la végétation, en coordonnées semi-logarithmiques. On constate une dérive systématique des données par ciel clair, au voisinage du sommet de la culture: on n'a pas

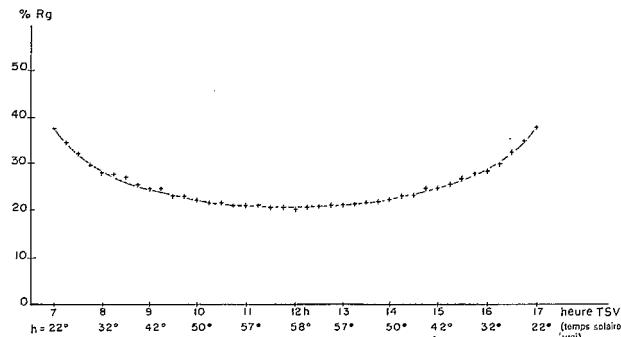


FIG. 3. Évolution de l'albédo au-dessus d'une culture de Maïs adulte.

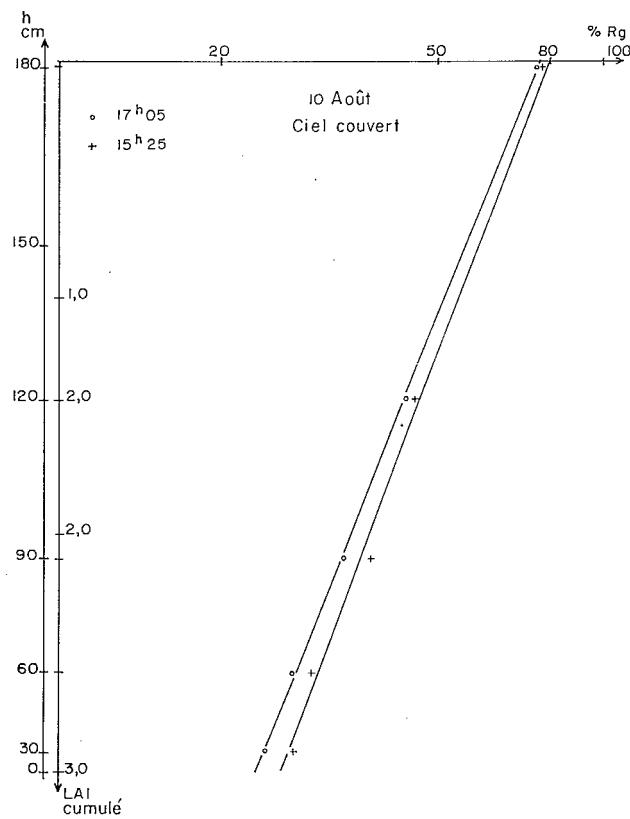


FIG. 4a. Évolution de l'extinction du rayonnement dans la végétation. Ciel ouvert.

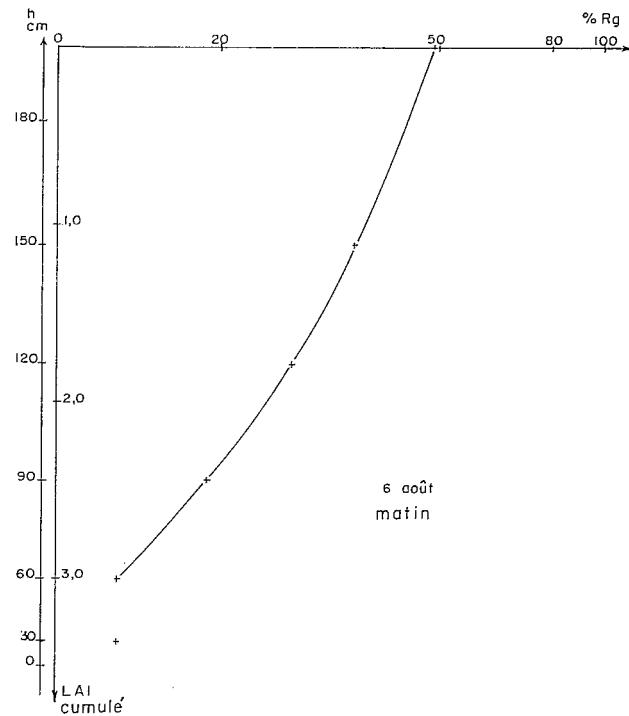


FIG. 4 b. Évolution de l'extinction du rayonnement dans la végétation. Ciel clair.

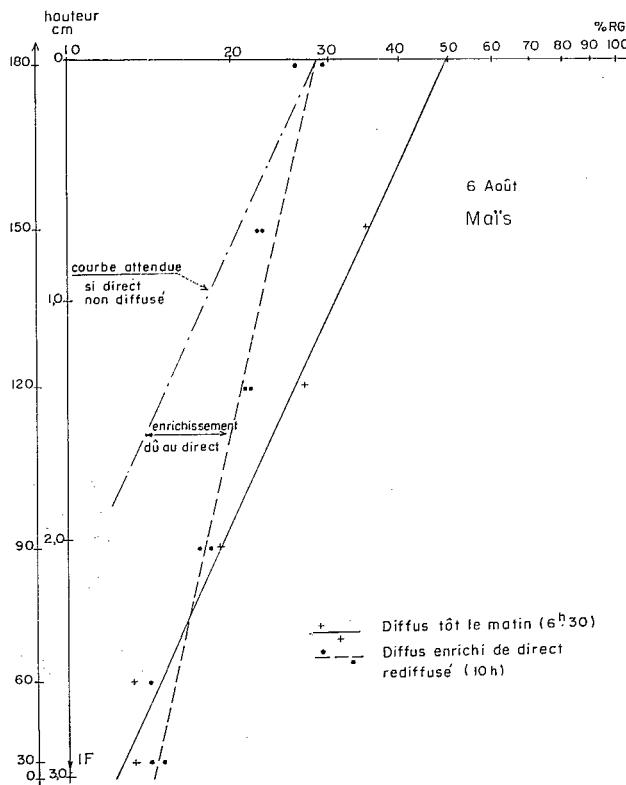


FIG. 5. Comparaison des rayonnements diffus tôt le matin (6 h 30) et à 10 heures.

tenu compte en effet du LAI des panicules mâles dans l'établissement du LAI total. Cela est particulièrement notable tôt le matin ou tard le soir, quand les panicules

ombrent au maximum les feuilles supérieures du Maïs. Par éclairage diffus dû à un ciel couvert, l'écart est beaucoup plus faible, et la loi se vérifie mieux.

La figure 5 présente, pour la même journée du 6 août, la comparaison des valeurs de rayonnement diffus tôt le matin (6 h 30) et à 10 heures. On constate un enrichissement en lumière dans le profil quand le soleil est plus haut; cela doit être dû au rayonnement direct rediffusé par les feuilles par ciel clair.

CONCLUSIONS ET PROSPECTIVES

Les résultats exposés ci-dessus ne sont encore que très partiels, et ils ont été obtenus avec un matériel encore expérimental, moins régulier et moins sensible que celui qu'on met actuellement au point.

Ces pyranomètres linéaires permettent donc des mesures systématiques, comportant un nombre suffisant de répétitions (Combres *et al.*, 1970) dans la végétation. La modicité de leur prix de revient, au moins quand leur fabrication est envisagée en nombre suffisant, doit permettre aux utilisateurs de multiplier les points de mesure, condition nécessaire à toute étude statistiquement valable.

Parallèlement à ce pyranomètre, qui fournit une réponse pratiquement constante entre 300 et 3 000 nm, nous préparons des piles identiques, mais comportant un filtre Wratten 88 A destiné à mesurer l'infrarouge seul et, par différence, la fraction visible résiduelle dans les profils végétaux: cette information est essentielle pour analyser la photosynthèse nette dans la végétation.

Summary

The use of linear pyranometers in the study of the components of the light climate in vegetation (C. Baldy, J.-C. Combres, R. Bonhomme)

The Department of Bioclimatology of the National Institute of Agronomic Research at Versailles (France) has developed a linear pyranometer based on a printed circuit. Thirty-five centimeters in length, it comprises 75 thermocouples in series and gives a practically stable

response for all directions on a horizontal plane: 20 mV/cal cm⁻² mn⁻¹ of total radiation of shortwaves received. Its development and performance are described here, and some examples of its use for ascending and descending radiation are given. The scientific possibilities which this appliance opens up for physical studies of the light climate of vegetation, as in other environments are touched on briefly.

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Influence of light intensity on growth and energy conversion in mass cultures of *Scenedesmus* sp.

J. C. Wesselius

Laboratory of Plant Physiological Research,
Agricultural University,
Wageningen (The Netherlands)

The conversion of solar energy was found to be highest in agricultural crops with a closed-crop surface. Under these conditions energy conversion reached values of 5–10 per cent (cf. Gaastraa, 1962; Alberda, 1962).

Kamel (1959) with barley and mangold, found energy conversion values of 10–12 per cent during a period of up to one month. In contrast with higher plants, algae can be maintained during longer periods on cell densities which completely absorb incident energy. Thus, Oorschot (1955), with *Chlorella* cultivated in small vessels, was able to obtain energy conversion values of 8 per cent. It is questionable, however, whether these data can be directly compared with results obtained using other types of culture vessels with larger surfaces, since the irradiated surface and volume were very small.

Maximal productivity in communities of terrestrial and water plants was discussed by Steemann-Nielsen (1957, 1960). He concluded that the productivity of terrestrial plants must be superior to that of water plants and algal mass cultures, due to the higher photosynthetic capacity of leaves in comparison with algae.

In order to compare growth rates and energy conversions in mass cultures with agricultural crops, we cultivated the algae in the open, under conditions which proved to be optimal in the laboratory.

We investigated the influence of light intensity and light distribution on the rate production and energy conversion in mass cultures of *Scenedesmus* sp.

MATERIALS AND METHODS

Scenedesmus sp. was cultivated in 50-litre tanks with lucite walls, made from domestic washing machines. The vessels were situated in the open, or were illuminated with Philips HPLR 400-watt mercury lamps in the laboratory. A gas mixture of 4–5 per cent CO₂ in compressed air was continuously bubbled through a suspen-

sion containing: KNO₃—10 mM; MgSO₄—2 mM; KH₂PO₄—1 mM; 1 ml A4; 0.1 ml B7 solution (cf. Arnon, 1938). The temperature of the culture was kept constant at 30° C.

Precultivation was carried out in two steps. *Scenedesmus* sp., cultivated on Beyerinck agar slants, was inoculated into 1-litre Erlenmeyer flasks containing 300 ml of the medium described above. The flasks were placed on a rocking table, at a constant room temperature of 23° C. Illumination from below heated the cultures up to 30° C. Light was provided continuously from 5 fluorescent tubes (Philips TLM 125-watt/33 RS). The light intensity at the bottom of the flasks was about 7×10^4 erg cm²/sec.

Air containing 4 per cent CO₂, filtered through cotton wool, was continuously bubbled through the suspension at a rate of 2.4–3.1 litres/hr.

Since the culture solution mentioned above was especially suitable for low-cell densities, growth was stopped after four days, when cell density reached 1–2 µl packed cell volume/ml. From this suspension, 5 ml was inoculated into a modified medium, adapted for cultivation without large pH shifts. The only modification in the composition already mentioned was an increase in the KH₂PO₄ concentration from 1 to 15 mM. Cells were harvested after three days at a final density of 5–7 µl/ml.

The incident energy on a horizontal plane (measured by the Physics Department) was used as a basis for the calculation of the energy conversion. A comparison with thermopile measurements collected at the place of the experiment showed that, on average, 75 per cent of the incident energy on an open field was received in the experimental situation. Reflection and absorption by the lucite material of the tanks amounted to 10 per cent of the incident energy.

Energy conversion was computed as $E = [(V \times \Delta P \times a) / (I \times a)] \times 100$ per cent, where ΔP =daily production in

g/l ; a = caloric value ($1\text{ g ash-free dry weight} = 5.05\text{ kcal}$); I = incident energy in $\text{kcal/m}^2/\text{day}$; A = area in m^2 ("apparent horizontal surface"), V = volume.

Incident energy over the vertical and horizontal surfaces was calculated from the total global radiation received on a horizontal plane. This was done by comparing light-limited growth rates in *Scenedesmus* sp. cultures receiving light on the complete surface and on the horizontal surface only. The production rates are then proportional to the apparent surfaces, expressed as a horizontal plane (= "apparent horizontal surface").

The results are presented in Table 1.

TABLE 1. Production values under conditions of light limitation in tanks. The screened tank had the side walls darkened up to the surface of the culture solution (horizontal illumination over 0.232 m^2)

Date	Production unscreened (g/vessel)	Production screened (g/vessel)	Ratio	"Apparent horizontal surface"
7-10 April	26.25	13.45	1.951	0.45
15-17 April				
19-23 April	45.60	28.50	1.595	0.37
9-11 May				
12-13 May	12.24	8.18	1.500	0.35
27-30 June	13.65	9.75	1.395	0.32

It can be observed that the "apparent horizontal surface" decreased when the days became longer, due to the higher elevation of the sun in summer. It was assumed that these estimates were representative for the average weather conditions during these particular times of the year. Depending on the day length, the appropriate "apparent horizontal surface" was used.

RESULTS

Highest energy conversions can be expected under conditions of light limitation. Net photosynthesis then depends on the amount of absorbed energy and respiration.

Growth over a couple of days was measured by diluting the culture to initial densities of 0.60, 0.95, and $1.50\text{ }\mu\text{l}$ packed cell volume/ml. Figure 1 shows that growth was linear and, therefore, depended on the incident energy. The energy conversion values calculated for the Figure 1 data are presented in Figure 2. The average efficiency decreased from 4.2 per cent at the lowest starting concentration, to 3 per cent at the highest starting concentration.

Since there was light limitation and complete light absorption, the differences are probably caused by respiration.

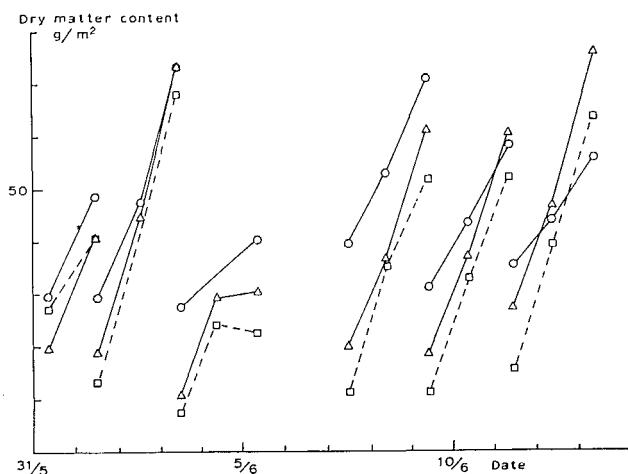


FIG. 1. Dry matter content of *Scenedesmus* sp. cultures. Normal nitrate medium, temperature 30° C . Average concentrations: $\circ-\circ$, $1.5\text{ }\mu\text{l/ml}$; $\triangle-\triangle$, $0.95\text{ }\mu\text{l/ml}$; $\square-\square$, $0.60\text{ }\mu\text{l/ml}$.

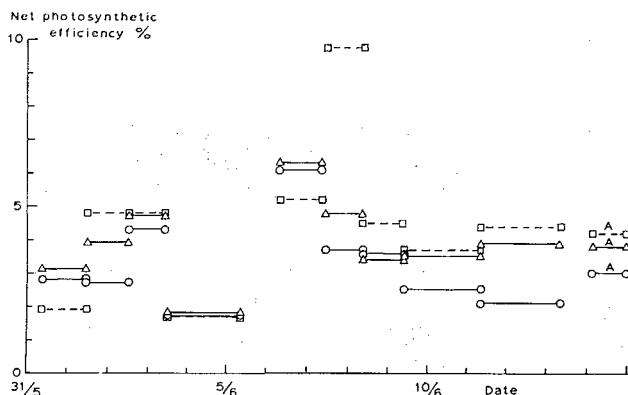


FIG. 2. Net photosynthetic efficiencies for *Scenedesmus* sp. Normal nitrate medium, temperature 30° C . Initial concentrations $\circ-\circ$, $1.5\text{ }\mu\text{l/ml}$; $\triangle-\triangle$, $0.95\text{ }\mu\text{l/ml}$; $\square-\square$, $0.60\text{ }\mu\text{l/ml}$. Energy conversion based on data collected for an open field. (A = average.)

In order to determine the growth rate as a function of the daily energy input, the cultures were diluted every day to a density of $0.50\text{ }\mu\text{l/ml}$. Data from experiments made in September, April and May are presented in Figure 3.

The correlation between incident radiation and production rate, as tested using Kendall's correlation test, was significant in Figures 3(a) and (b), and probably significant in Figure 3(c). This means that production was light limited.

The average energy conversions calculated for the experiments in Figure 3, and for other experiments with daily dilutions to initial concentrations of $1.0\text{ }\mu\text{l/ml}$, are presented in Table 2.

TABLE 2. Growth of *Scenedesmus* sp. in tanks in natural daylight. Normal culture medium temperature was maintained at 30° C. Cultures were diluted daily to the indicated density (packed cell volume/ml). Figures in brackets denote the duration of the experiments in days

Month	PAR ¹ (kcal/m ² /day) average	Efficiency (0.5 µl/ml)	PAR ¹ (kcal/m ² /day) average	Efficiency (1.0 µl/ml)
June 1963 ² (12)	2 492	4.2	2 492	3.8
June 1963 ² (8)	1 288	5.7	—	—
September 1964 (9)	1 334	4.5	1 051 (6)	4.2
April/May 1965 (9)	1 279	6.6	—	—
May 1965 (8)	1 971	4.0	1 658 (13)	3.0

1. Photosynthetically active radiation.

2. Earlier experiment, added for comparison only. The cultures were diluted to cell densities of 0.5–0.6 µl/ml over periods varying from 1–3 days.

The efficiencies of energy conversion at initial concentrations of 1.0 µl/ml were lower than those with cell densities of 0.5 µl/ml. This is attributed to respiration.

It would be interesting to see whether *Scenedesmus* sp. cultures could be saturated at lower initial cell densities. Daily production rates at an initial cell density of 0.25 µl/ml, plotted as a function of incident energy are presented in Figure 4.

One tank was diluted daily, while the other was inoculated with a cell sample kept at +5° C. The aim was to reduce the variability which might have occurred as a result of the dilution technique, i.e. changes in the physiological properties of the starting material. As can

be observed in Figure 4, the optimum growth rate was changed to somewhat lower values when the culture was diluted every day. In general, however, differences were not very large. Light saturation occurred at values of about 1,200 kcal/m²/day. The maximum energy conversion reached 7 per cent of the incident energy.

In general, cultures in tanks, with a depth of layer of 20 cm, are so thick that light intensity will not be sufficient to saturate photosynthesis in large parts of cultures. Therefore, variability in maximum photosynthetic rates will only be important in the top layers of the culture vessels. Respiration seems to be the crucial factor causing variability in maximum photosynthetic rates under light limited conditions.

We determined the energy conversion in cultures with media containing nitrate under light-limited conditions over the season February–November (Fig. 5). In the winter months incident energy was too low and too changeable to guarantee an undisturbed growing period. The scarce data collected in late fall and early spring are insufficient to give a clear idea of the energy conversion in winter. At best they may indicate that energy conversion is lower in winter than in summer.

The average net photosynthetic efficiency for 117 days was 4.35 per cent of the incident radiation.

These measurements were valid for an open field. Screening by the buildings reduced the possible maximum duration of sunshine to 10.5 hr.

A comparison of measurements at the location of the experiment and the data collected by the Physics Department showed that, on average, 75 per cent of the incident radiation on an open field was received at the location of the tanks. Furthermore, reflection and ab-

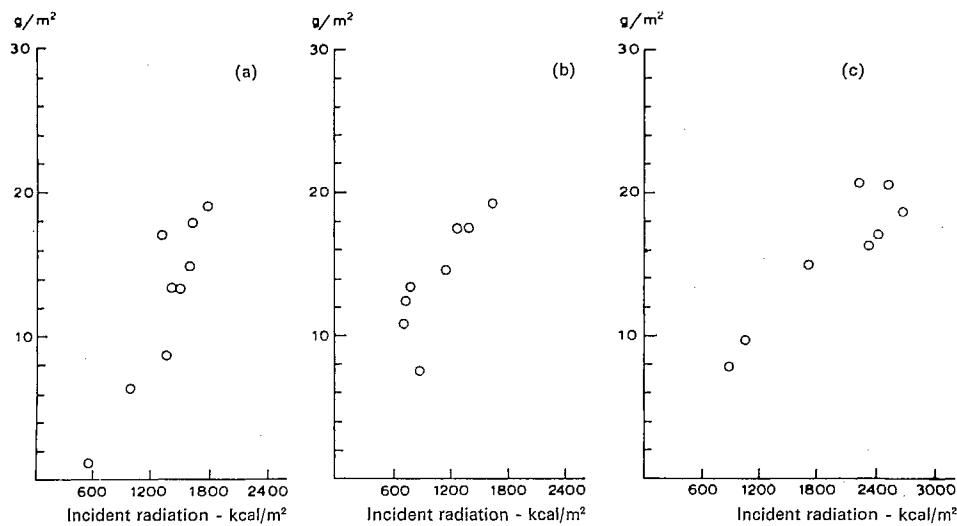


FIG. 3. Daily production rates for *Scenedesmus* sp. Daily dilutions to 0.50 µl/ml (packed cell volume/ml). Normal nitrate medium, temperature 30° C. (a) September 1964; (b) April–May 1965; (c) May 1965.

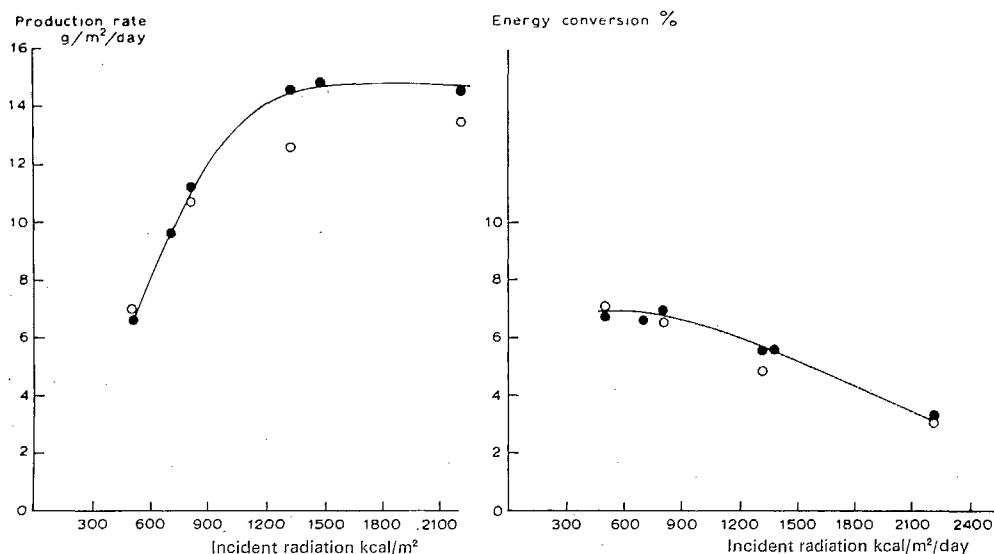


FIG. 4. Production rates for *Scenedesmus* sp. Daily dilutions to a density of 0.25 $\mu\text{l}/\text{ml}$. Normal nitrate medium, temperature 30° C. ●—●, cooled cells; ○—○, daily diluted cells.

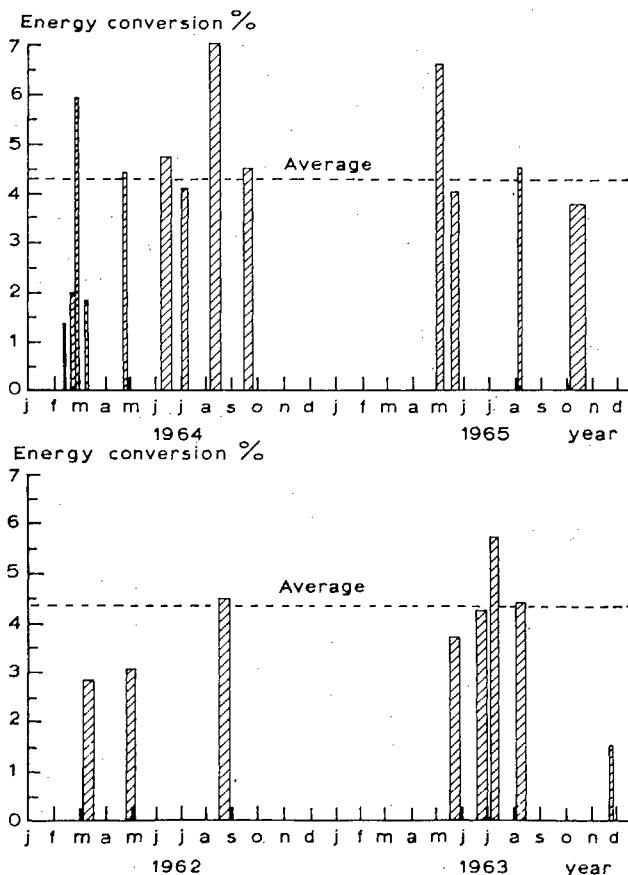


FIG. 5. Energy conversions for *Scenedesmus* sp. under conditions of light limitation. Normal nitrate medium, temperature 30° C. Energy conversion based on data collected in an open field. Letters refer to months.

sorption by the lucite wall amounted to 10 per cent. The average energy conversion, based on the incident radiation at the location of the experiment was, therefore, 6.45 per cent instead of 4.35 per cent. Using the same calculation, the maximum energy conversion in July and August amounted to 10.2 per cent.

The foregoing experiments demonstrated that energy conversion of algal cultures in tanks situated in the open was not better than in a conventional crop with a closed-leaf surface. The growth rate under light-limited conditions depends on the average energy received per cell and thus on the geometry of the culture vessel and the stirring velocity. The latter had a fixed value in the tanks which were used. A decrease in the depth of layer might influence the efficiency of stirring under otherwise unchanged conditions.

Each of two tanks were placed under one Philips HPLR 400-watt mercury lamp. They received light via the upper surface only. The energy supply on the surface of both tanks was the same. One tank received the normal volume of 50 litres and served as a control. The other tanks contained: 50, 40, 30, or 25 litres of a medium with the composition: urea, 10 mM; MgSO_4 , 2 mM; KH_2PO_4 , 1 mM; trace elements (cf. methods), 2 ml/l; Fe^{++} solution, 2 ml/l.

Growth rates, expressed as mg/day, were compared for each run, which lasted 2–4 days. Absolute growth rates were also expressed as percentage of the 50-litre vessel. The results are presented in Figure 6.

Although the energy flux unit surface remained the same, it is evident that the energy received per litre of suspension increased when the volume was decreased.

It can be seen that the growth rates increased roughly linearly with the energy received per litre of suspension;

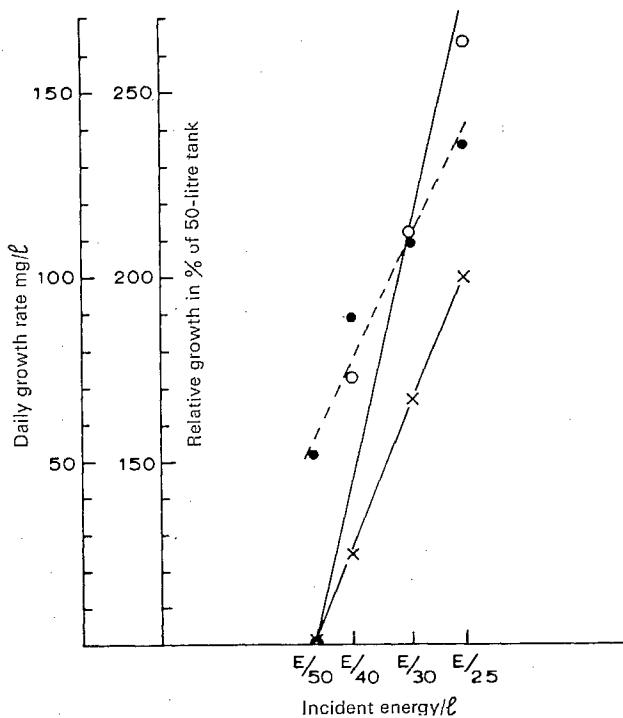


FIG. 6. Daily growth rates for *Scenedesmus sp.* with a different volume culture solution. Illumination with 2 HPLR 400-watt mercury lamps from above. Relative growth rates expressed as a percentage of the 50-litre tank. ●—●, daily growth rate (absolute); ×—×, relative growth rate as a percentage of the 50-litre tank (expected); ○—○, relative growth rate (calculated from daily growth rates).

that is, the culture as a whole behaved as under light limited culture conditions. The relative growth, as a percentage of that in the 50-litre tank, increased more

than expected when the depth of layer was decreased. This means that there was an increased energy conversion on the basis of incident light.

DISCUSSION

The energy conversion under light-limited conditions, based on the incident radiation received at the location of the experiment, reached values which were not lower than the optimal yields measured in the field (cf. Kamel, 1959; Alberda, 1962; Sibma, 1968). Nichiporovich and Malofeev (1965), with kale, investigated the effect of light intensity on the efficiency of photosynthesis at various plant densities. In all cases the energy conversion decreased with higher light intensities. An increase of plant density in the range $0.25\text{--}10 \text{ m}^2 \text{ leaf area/m}^2$ ground surface resulted in higher energy conversion values.

In the experiment to investigate the influence of cell density on energy conversion (Figs. 1 and 2), a decrease in efficiency was found at higher cell densities. It can be demonstrated that algae can be packed in much higher densities than the highest density reported by Nichiporovich and Malofeev (1965). Probably an increase of plant density is favourable up to a certain limit. At still higher plant densities, a decrease in efficiency will follow owing to self-shading and a relative increase in respiratory processes.

Steemann-Nielsen's (1957) statement, that water communities in general have lower production rates than terrestrial communities, is, therefore, only partly true. Although the primary productivity of the water community is lower than production in terrestrial communities, algal mass cultures may equal or even surpass the best production rates in agricultural crops. In particular, the ability to maintain high productivity over a long period reflects an advantage of algae.

Résumé

Influence de l'intensité lumineuse sur la croissance et la transformation d'énergie dans des cultures de grandes quantités de Scenedesmus sp. (J. C. Wesselius)

Scenedesmus sp. a été cultivé dans des machines à laver de 50 litres à parois transparentes, en plein air.

L'énergie solaire pénétrait par les surfaces horizontales et verticales. Nous avons exposé une méthode permettant de déterminer l'énergie incidente quand le rayonnement sur un plan horizontal est connu.

La conversion énergétique a été mesurée dans les cultures diluées tous les deux ou trois jours pour un volume cellulaire centrifugé déterminé. Des dilutions

pour des volumes cellulaires compris entre $0.6 \mu\text{l/ml}$ et $1.5 \mu\text{l/ml}$ produisirent une croissance limitée. Le rendement photosynthétique net a diminué quand, au commencement de l'expérience, le volume cellulaire centrifugé était augmenté.

L'auteur a étudié l'influence de l'apport quotidien d'énergie sur la croissance de cultures diluées tous les jours pour des volumes cellulaires centrifugés de $0.25 \mu\text{l/ml}$, $0.50 \mu\text{l/ml}$, $1.0 \mu\text{l/ml}$. La saturation de la photosynthèse a été possible dans des cultures diluées tous les jours jusqu'au seuil de $0.25 \mu\text{l/ml}$. Pour des densités cellulaires centrifugées supérieures au début de l'expérience, la conversion énergétique a diminué.

L'auteur a déterminé le rendement photosynthétique net en plein air de février à novembre pendant 117 jours en 4 ans. La conversion énergétique moyenne a été de 6,45%. Un maximum de 10,2% a été mesuré en juillet et en août.

La croissance s'est améliorée quand on a diminué la profondeur de la culture en suspension dans les machines éclairées par la lumière artificielle. La conversion énergétique a été améliorée, l'apport d'énergie par unité de volume ayant augmenté plus que prévu.

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The effects of photoperiod on growth and morphogenesis in maize (*Zea mays* L.): field trials in Colombia

C. A. Francis

Centro Internacional de Agricultura Tropical,
Cali (Colombia)

Among the climatic factors which influence plant adaptation, the photoperiod (or effective dark period) is one which most clearly distinguishes the conditions at different latitudes. The effects of day length are apparent in maize and other sensitive species when varieties are moved north or south from their zone of adaptation (Kiesselbach, 1950). Tropical maize varieties grown in higher latitudes react with an extended period of vegetative growth, producing taller plants with more leaves. In these genotypes, anthesis and fertilization may not occur early enough in the field in temperate regions to produce seed. Conversely, temperate zone hybrids grown near the equator mature more rapidly than in areas where they were developed, and in most conditions do not attain normal plant height, number of leaves, or yield. Temperature and other variables are confounded with photoperiod in most field studies, and effects of photoperiod alone on growth and development are difficult to describe.

Photoperiod sensitivity in maize has severely limited the exchange of germplasm among breeding programmes in different latitudes. The isolation of insensitive genotypes would allow the incorporation of this characteristic into diverse sources of maize from the tropics and into highly productive hybrids and other combinations in all latitudes. Studies were initiated in 1968 to find sources of photoperiod insensitivity and to evaluate several methods of testing in different latitudes. Results of the experiments in growth chambers (Francis *et al.*, 1969) and the first season in the field (Francis *et al.*, 1970) showed that a range in sensitivity was present in maize. Further work on isolation and results of growth measurements are presented here.

MATERIALS AND METHODS

An experimental area 40×50 m was equipped with 300 W floodlights along one side. These lights, 3 m

above the soil surface, produced a gradient in light intensity which decreased with distance from the light source. Light intensity ranged from 25 ft candles near the lights to less than 1 ft candle at the extreme edge of the field. Control clocks turned lights on at 1 a.m. to limit the dark period to about 7 h (17 h photoperiod). In the first experiment 48 hybrids, varieties, and mixtures were planted in rows perpendicular to the light source. Thus each genotype was exposed to a range of intensity of artificial light during the time when the lights were on. Dissections of plants and classification of growing points as vegetative or reproductive at two ages allowed an estimation of the date of differentiation of each genotype. In the second season, 24 genotypes were resown in 2-row plots following the design in the previous test. Plants of each genotype were dissected at weekly intervals, and the differentiation date was interpolated from these data. On each date, plant heights were measured to the tip of the longest leaf and growing point height was determined. Number of leaves visible and number fully expanded were counted. In the second season, a number of crosses were made between pairs of sensitive and insensitive genotypes.

RESULTS AND DISCUSSION

In the first field test most genotypes were sensitive to the differences in photoperiod to which they were exposed. Tassel differentiation occurred near the light source at least three weeks later than under normal daylength conditions at the end of the field farthest from the lights. Other genotypes, including a temperate-zone hybrid from Minnesota, were relatively insensitive to the additional hour of light; the average difference in the time to tassel differentiation between the two photoperiod conditions in these strains was only six days. Among the sensitive genotypes tested, the most pro-

TABLE 1. Days from emergence of plants to tassel differentiation in sensitive and insensitive genotypes of maize, second field experiment

Genotype	Metres from light source							Sensitivity difference ¹
	2	6	10	15	20	25	30	
<i>Sensitive</i>								
ICA V. 503	45	45	24	25	24	18	18	27
ICA H. 207	31	24	22	17	18	18	17	14
D. V. 351	36	36	22	22	23	22	18	18
D. H. 253	37	37	22	22	19	22	18	19
Mixture No. 4	45	45	33	31	30	23	24	21
Blanco Común	32	25	24	19	22	22	17	15
Mean of 12 sensitive genotypes ²	35.6a	32.9a	26.1b	23.7bc	22.5bc	20.9bc	18.8c	16.8
<i>Insensitive</i>								
U.S.A. 342	17	18	18	17	17	16	16	1
L. E. Synthetic	17	16	16	16	17	16	16	1
Trojan-DX-O ₂	17	17	16	13	13	12	13	4
Mean of 6 insensitive genotypes ²	19.5a	18.7a	17.7ab	16.2bc	16.0bc	15.5c	15.8c	3.7

1. Sensitivity difference in number of days between tassel differentiation in long and short days (2 and 30 m from artificial light source respectively).

2. Means followed by the same letter are not significantly different (5% level) using Duncan's Multiple Range Test.

nounced delay in reproductive development occurred near the light source where the intensity of artificial light was at least 8 ft candles. There was also a significant delay in tassel differentiation at intensities greater than 1-2 ft candles, although this was less pronounced than the three-week delay mentioned above.

The second field test was designed to determine the date of differentiation with more precision, and to check more critically the light intensities above which a significant delay would occur. Results from this test are shown in Table 1. Days to tassel differentiation in 6 sensitive and 3 insensitive genotypes are given for 7 distances from the light source. The mean difference for all sensitive genotypes was 17 days, compared with 22 days in the first test. The mean sensitivity difference in relatively insensitive genotypes was about 4 days, while this value was 6 days in the previous test. Relative sensitivity of individual genotypes was quite consistent in results from the two tests.

Although the means for sensitive genotypes suggest a quantitative delay in differentiation with increasing light intensity, each genotype showed a characteristic delay above a particular intensity. Plants of several sensitive genotypes were harvested at 1 m intervals in the critical regions to determine more precisely the distance and light intensity above which these characteristic delays occurred. As shown in Table 2, the critical distance from the light source for specific genotypes varied from 6-7 m (6 ft candles) for D.V. 351 to 9-10 m (4 ft candles) for ETO and others. There is apparently genetic variation in the critical light intensity needed under these conditions for a major delay in floral differentiation. There were also critical distances for the minor delay, as shown in the lower half of Table 2. The first two mixtures (No. 20 and No. 12) showed an abrupt change at 15-17 m (2 ft candles), while the mixture No. 4 showed this change at 21-23 m (1.3 ft candles). There is apparently a significant delay in the

TABLE 2. Days from emergence of plants to tassel differentiation in several sensitive genotypes of maize at frequent intervals of distance from the light source, second field experiment

Genotype	Metres from light source					Genotype	Metres from light source					
	6	7	8	9	10		15	17	19	21	23	25
D. V. 351	36	24	23	23	22	Mezcla No. 20	30	21	22	22	22	22
D. H. 253	37	37	23	23	22	Mezcla No. 12	32	24	24	22	22	22
ICA V. 503	45	45	45	45	24	Mezcla No. 11	30	30	30	21	21	22
Mezcla No. 10	30	30	29	29	24	ICA V. 503	25	24	24	17	18	18
ETO	33	33	33	33	23	Mezcla No. 4	31	30	30	29	23	23

TABLE 3. Mean plant heights and leaf numbers for 24 genotypes at 7 distances from light source; maize 4-weeks-old, second field experiment

	Metres from light source						
	2	6	10	15	20	25	30
Plant height (cm)	114	112	120	119	117	120	120
Leaves visible	13.6	14.0	14.0	14.2	14.0	14.2	14.3
Leaves expanded	8.9	9.1	9.1	9.0	9.0	9.0	9.1

field at intensities of at least 1–2 ft candles, with some genetic variability in the critical intensity above which a genotype will be delayed.

Rate of leaf emergence and development and growth in plant height were not affected by the different intensities of light used to extend the day nor by the extreme differences in photoperiod. In Table 3, the plant heights and leaf numbers at 4-weeks-old in the second experiment illustrate the uniformity in growth and development under these diverse conditions. Final leaf number and plant height are greater under long days. This is due to a longer period of vegetative development and later floral differentiation, and not to any difference in growth rate. Over a number of genotypes and conditions, growing point height is highly significantly and positively correlated with stage of tassel development. This confirms the reports of Hanway (1963) that tassel differentiation and the beginning of stem elongation occur simultaneously. However, exceptions to this pattern, such as insensitive genotypes which differentiate well before stem elongation begins and sensitive genotypes which display considerable elongation before floral

differentiation occurs, suggest that these events are not functionally interdependent. This confirms the suggestions of Arnold (1969).

CONCLUSIONS

Field screening with artificial lights was a successful method for identifying genotypes of maize insensitive to the effects of extended photoperiod. Results from two seasons were consistent for almost all materials in the tests. Two insensitive lines and one insensitive hybrid were identified, and these or others may be used to incorporate insensitivity into tropical races and synthetics of maize. Extreme differences in photoperiod do not change the growth or development rate, and the differences which are observed in the field in different locations must be dependent on temperature and other factors. An inheritance study on photoperiod sensitivity is in progress. In the field tests, two distinct delays in floral differentiation were observed at light intensities above two distinct levels. Further work is needed in this area.

The study of growth and development in maize and other cultivated crops will lead to a better understanding of adaptation. Although maize as a species is widely adapted, photoperiod sensitivity is one of the important factors which currently limits the range of adaptation of many individual genotypes. A practical application of this screening procedure to identify sources of insensitivity and the proposed use of this trait will make races of maize available for programmes in other latitudes. These studies indicate that the problem of photoperiod sensitivity can be overcome in maize, and all improvement programmes will benefit from the availability of lines with wider adaptability and of more sources of new germplasm.

Résumé

Les effets de la photopériode sur la croissance du Maïs (*Zea mays* L.) : essais sur le terrain en Colombie (C. A. Francis)

Une prolongation de la photopériode par des lumières artificielles dans des champs tropicaux a démontré que la plupart des génotypes tropicaux sont sensibles à la lumière diurne et a permis de distinguer entre les lignées de Maïs sensibles et les lignées non sensibles à cette lumière.

Pour prolonger la photopériode, on a fait varier d'une façon continue l'éclairage, de 270 à 10 lux; cette variation a révélé deux intensités critiques d'éclairage pour le Maïs. Aux intensités dépassant 54 lux et 15 lux, on observait des retards caractéristiques de la différenciation florale d'environ vingt jours et huit jours respecti-

tivement. Il y avait des variations génétiques aux intensités critiques de lumière pour un retard supérieur de la différenciation florale.

Des changements de photopériodes n'ont pas modifié les taux de croissance, la hauteur des plants ou le taux d'apparition des feuilles de façon significative avant la différenciation des organes mâles. L'allongement de la tige ne s'est pas effectué parallèlement à la différenciation des organes mâles. La transmissibilité de la sensibilité à la photopériode est présentement à l'étude. Cette méthode d'identification sur le terrain peut être utilisée pour déterminer le seuil critique d'éclairage pour diverses espèces de cultures et permettre ainsi la sélection et le développement de sources de matériel génétique utilisables par des centres d'amélioration situés à diverses latitudes.

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Determining the heat transfer coefficient of leaves

Zh. V. Stojanov
Forest Research Institute,
Sofia (Bulgaria)

In the equation of heat balance, the heat transfer coefficient is an important factor, as, for example, in the following form (Brown and Escombe, 1905):

$$R = 2K_i \cdot \Delta t + L \cdot E$$

where R = the radiation balance, cal/cm² min, K_i = heat transfer coefficient, cal/cm² min °C, Δt = leaf-air temperature difference, °C, L = latent heat of vaporization of water, 600 cal/g, E = transpiration, g/cm² min.

Usually one determines K_i from the foregoing formula in darkness, when $R = 0$ (Brown and Wilson, 1905). Apparently, it is better to determine K_i in the light, under the same conditions under which K_i is to be applied, simultaneously with the other physiological measurements, and not in a separate experiment. That is why two methods are proposed, which obviate the sudden shading of the leaf (Linacre, 1964, 1967; Kuperman and Bochkov, 1967) and also some additional measurements.

FIRST METHOD

The leaf is placed consecutively in air at two different degrees of humidity, under the same illumination and radiation balance. Then, at the one air humidity, $R = 2K_i \cdot \Delta t_1 + L \cdot E_1$, and at the other, $R = 2K_i \cdot \Delta t_2 + L \cdot E_2$, where Δt_1 , E_1 and Δt_2 , E_2 are respectively the leaf-air temperature difference and the transpiration at the two air humidities. Then, by equating the right hand sides of these equations, and after transformations the following formula is obtained:

$$K_i = \frac{L(E_2 - E_1)}{2(\Delta t_1 - \Delta t_2)}$$

This equation is valid if all the variables except the air humidity are constant and the difference between the two air humidities is not very great.

Using this formula, an experiment was conducted with a poplar twig, placed in a cup with water, the surface of the water being covered with paraffin oil to prevent gas exchange with the air.

The leaf-air temperature difference was measured with a copper-constantan thermopile, one junction of which was fastened to the underside of a leaf, by means of an adhesive band, and the other, shaded and in the free air, was at a distance of 1 cm from the leaf. The air temperature was measured by means of a mercury bulb thermometer, placed beside the free junction in the air. The cup containing the twig was placed in a 1-litre cuvette, through which air was driven by means of a pump, with a velocity of 2 litres/min. Air humidity was controlled by means of dry CaCl₂ or solutions of CaCl₂. The transpiration was measured psychrometrically (Stojanov and Antov, 1970), the psychrometer being included in the air stream beyond the outlet from the cuvette. Before and after the experiment was conducted, control measurements of air humidity were made, i.e. without a twig in the cuvette. The cuvette was illuminated with a luminescent lamp.

Under these conditions, by repeatedly passing air with 37 per cent relative humidity through the cuvette for 30 min, the value obtained for E_1 was 0.000260 g/cm² min and for Δt_1 was +1.6° C, and with air with 67 per cent relative humidity, E_2 was found to be 0.000142 g/cm² min, Δt_2 , +2.2° C, and K_i was equal to +0.059 cal/cm² min °C.

If several measurements of E and Δt are made using air with different degrees of relative humidity, then a value of K_i can be obtained from the above formula for heat balance, which would give a constant value for R , the radiation balance.

SECOND METHOD

The leaf is placed successively in two different light intensities, R_1 and R_2 . R_2 is achieved by means of a screen of semitransparent glass or paper. All other variables, including air humidity, are kept constant. At the two degrees of illumination:

$$R_1 = 2K_i \cdot \Delta t_1 + L \cdot E_1$$

and

$$R_2 = 2K_i \cdot \Delta t_2 + L \cdot E_2.$$

From these the following formula is obtained:

$$K_i = \frac{L \left(\frac{R_1}{R_2} \cdot E_2 - E_1 \right)}{2 \left(\Delta t_1 - \frac{R_1}{R_2} \cdot \Delta t_2 \right)}$$

Thus it is not necessary to know the absolute values of R_1 and R_2 , but only the ration R_1 / R_2 . This is fortunate since the radiation balance cannot be measured with sufficient accuracy. The ratio R_1 / R_2 can be obtained by placing beside the twig an albedometer (lux meter, or other suitable instrument). Then, because all the variables except the light intensity remain unchanged, the ratio R_1 / R_2 is approximately equal to

the ratio of the readings of the albedometer at the two light intensities.

Using this method, an experiment was conducted in which a horse chestnut composite leaf was enclosed in a polyethylene bag, through which air was driven by means of a pump. Beside the leaf a lux meter was placed, exposed to the same light conditions as the leaf. The leaf-air temperature difference and the transpiration were measured in the same way as described for the first method. The leaf was illuminated for 30 min with a luminescent lamp. At 6,000 lux light intensity, E_1 was 0.000134 g/cm² min and Δt_1 was +2.20° C, and at 2,200 lux light intensity, E_2 was 0.000101 g/cm² min and Δt_2 was +0.55° C. Since $R_1 / R_2 = 2.73$, the value obtained for K_i was +0.058 cal/cm² min ° C.

It is possible to use this method in the open air, without a polyethylene bag, by measuring the transpiration gravimetrically for detached twigs, placed in a cup of water with oil on the surface, a photometer, and other instruments.

The above values of K_i were obtained by tow methods under the same conditions. Using other experimental conditions (wind velocity, light intensity, infra-red radiation, etc.) values of K_i were obtained from 0.01 to 0.09.

Résumé

Détermination du coefficient de transfert de chaleur des feuilles (Z. V. Stojanov)

Deux méthodes pour la détermination du coefficient de transfert de chaleur de feuilles éclairées sont proposées.

Première méthode. On soumet la feuille successivement à deux degrés différents d'humidité de l'air. Si Δt_1 , E_1 et Δt_2 , E_2 sont respectivement les différences de température feuille-air et la transpiration dans les deux sortes d'humidité de l'air, et L la chaleur latente de l'évaporation, alors le coefficient de transfert de chaleur K_i est donné par la formule:

$$K_i = \frac{L (E_2 - E_1)}{2 (\Delta t_1 - \Delta t_2)}$$

Deuxième méthode. On soumet la feuille successivement à deux intensités lumineuses différentes, qu'on mesure

avec un luxmètre (ou un albédomètre, etc.) posé près de la feuille, dans les mêmes conditions lumineuses.

La formule suivante a été déduite:

$$K_i = \frac{L \left(\frac{R_1}{R_2} \cdot E_2 - E_1 \right)}{2 \left(\Delta t_1 - \frac{R_1}{R_2} \cdot \Delta t_2 \right)}$$

avec

K_i : coefficient de transfert de chaleur

L : chaleur latente de l'évaporation de l'eau

R_1 et R_2 : bilans radiatifs aux deux intensités de la lumière

E_1 et E_2 : transpiration aux deux intensités de la lumière

Δt_1 et Δt_2 : différences de température feuille-air aux deux intensités de la lumière.

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Illumination and stomatal resistance to transpiration in three field crops

N. C. Turner

Connecticut Agricultural Experiment Station,
New Haven, Connecticut 06504,
(United States of America)

Light, together with water, is a primary environmental factor determining stomatal behaviour. An extensive field study of the daily march of stomatal movement showed that stomata opened by day and closed by night in a wide range of species (Loftfield, 1921); Loftfield concluded that stomatal opening was correlated with the presence of light when conditions were favourable. More recently the effect of light on diffusion of water vapour through the stomata has been characterized for a number of species under the controlled conditions of the laboratory (Gaastra, 1959; Kuiper, 1961; Slatyer and Bierhuizen, 1964). Because of the paucity of field data, Waggoner and Reifsnyder (1968) used these observations in the development of a rational simulator of canopy evaporation. However, the stomatal response to illumination in the laboratory should be verified in the field. This paper reports the vertical profiles of stomatal resistance in three field crops, and compares the stomatal responses to illumination obtained from the field observations with those obtained under controlled laboratory conditions for two of the three crops.

VERTICAL PROFILES OF STOMATAL RESISTANCE, LEAF DENSITY AND ILLUMINATION IN THE FIELD

The light incident upon a leaf within a crop canopy will vary with time of day and depth in the canopy. However, other environmental variables, notably humidity, temperature, and concentration of carbon dioxide, all of which are known to affect stomata, will also vary with time of day and depth in the canopy. Furthermore, the physiological age and condition of the leaf may affect the stomatal behaviour. In a preliminary study conducted in a maize crop and two woodland species, it was observed that the vertical profiles of leaf resistance measured near midday could be explained, in the case

of the two well-watered forest canopies, largely in terms of illumination. However, an increase in stomatal resistance independent of light was observed in the lower, yellowing leaves of maize (Turner, 1969).

Diurnal changes in the vertical profiles of stomatal resistance, illumination and leaf water potential were followed in crops of maize, sorghum and tobacco on clear days during 1968 and 1969 (Turner and Begg, unpublished data). Stomatal resistances were measured with a ventilated diffusion porometer, calibrated in units of sec cm⁻¹ (Turner and Parlange, 1970). The resistance of each epidermis was measured separately and the two epidermes treated as parallel resistors to diffusion. Thus, the leaf resistance (r_l) is obtained from the sum of the reciprocals of the adaxial resistance (r_{ad}) and abaxial resistance (r_{ab}):

$$\frac{1}{r_l} = \frac{1}{r_{ad}} + \frac{1}{r_{ab}}$$

Leaf water potentials were measured with the pressure chamber described by Scholander *et al.* (1964) but, since they did not decrease enough to initiate stomatal closure, they are not reported here. Illumination was observed with a Weston sunshine illumination meter.

The mean stomatal resistances at three times of day are shown in Figure 1; intermediate profiles are omitted for clarity. Clearly, resistance increased with depth into the canopy in all three species in the middle of the day. Near noon the increase in resistance of tobacco only occurred in those leaves below 50 cm (Fig. 1(c)). This was also true of sorghum (Fig. 1(b)), but the latter was a short crop with its flag leaf at a mean height of 82 cm, whereas tobacco was a much taller crop with the uppermost leaf above 130 cm from the ground. In the maize, also a tall crop, the leaf resistance around midday began to increase in those leaves less than 100 cm from the ground (Fig. 1(a)). Four to five hours from noon, the stomatal resistance of the upper leaves had increased

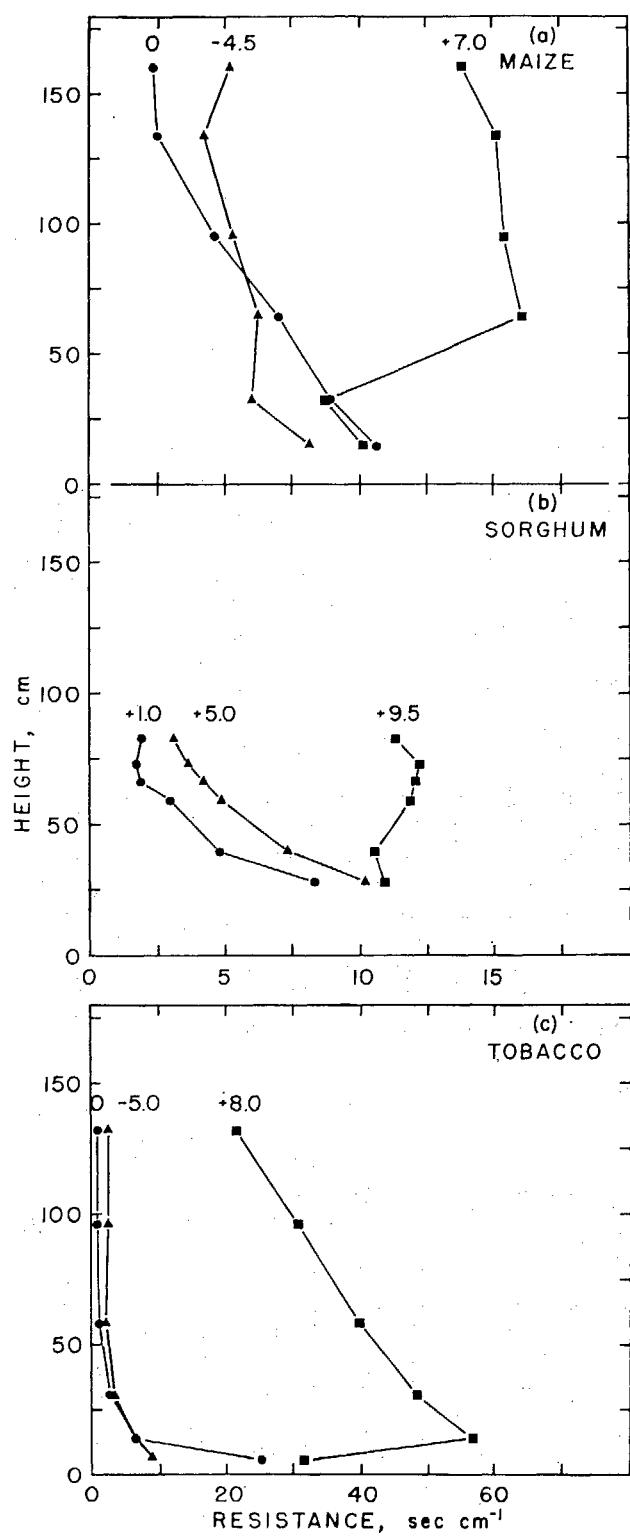


FIG. 1. Vertical profiles of leaf resistance at three times of day in (a) maize; (b) sorghum; and (c) tobacco. Times are calculated from noon, Eastern Standard Time (EST). Note that the scale of leaf resistance is changed in (c).

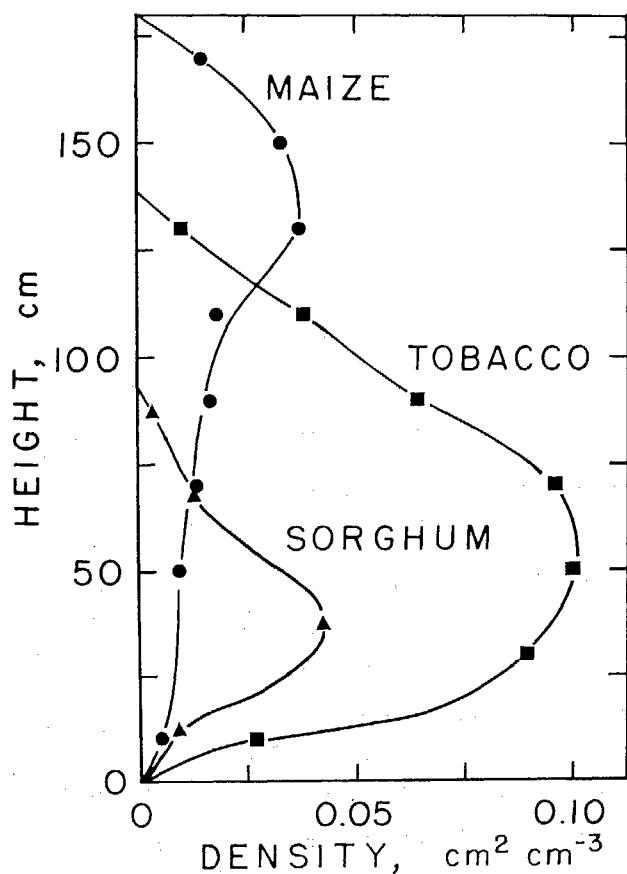


FIG. 2. Vertical profiles of leaf area density in maize, sorghum and tobacco.

in all three species and by 7 h from noon the resistances were equally large in all leaves.

The three crops differed in their total leaf area and leaf area distribution (Fig. 2). Maize, which was sampled just prior to tassel emergence, had a widely dispersed leaf area with the largest leaf density 150 cm above the ground; its leaf area index (LAI) was 3.2. The tobacco, which was flowering and had a much higher LAI of 8.5, had its densest leaf surface at 50 cm from the ground. The sorghum, also flowering, was a short crop with a low LAI of 1.7 and had its greatest density of leaves 40 cm above ground level. The effect of these different distributions of leaf area on the profiles of illumination can be seen from Figure 3. Thus, at midday, the upper leaves were well illuminated, but the illumination rapidly declined within the canopy, resulting in mean values of less than 3,000 ft candles in the lower leaves of all three species. Five hours from the noon vertical profiles still had the same general shape, but the difference in illumination between upper and lower leaves was smaller. Eight hours from noon all leaves were in darkness.

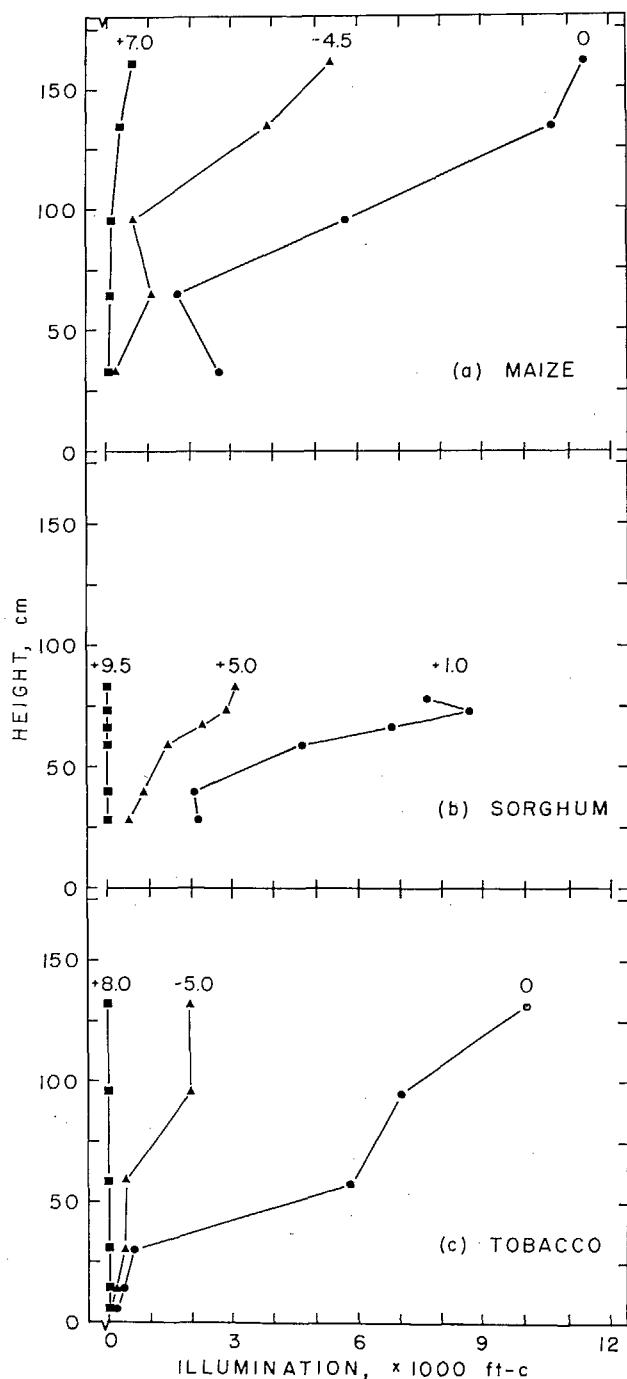


FIG. 3. Vertical profiles of illumination, incident upon the adaxial leaf surface, at three times of day in (a) maize; (b) sorghum; and (c) tobacco. Times are calculated from noon, EST.

STOMATAL RESPONSE TO ILLUMINATION IN THE FIELD

The individual observations used to determine the profiles of leaf resistance and light were replotted in Figure 4 to indicate the stomatal response to illumination. Since no differences in response between the adaxial and abaxial stomata could be distinguished in maize and sorghum, only the response of leaf resistance to illumination is presented (Figs. 4(a) and (b)). However, in the case of the tobacco, the adaxial resistance was always higher, this particularly being the case below 3,000 ft candles illumination (Fig. 4(c)).

In a previous study, senescence (i.e. visible yellowing) in the older, lower leaves of maize was shown to be partly responsible for the increased resistance in the lower canopy (Turner, 1969). Figure 4(a) shows that the lowest leaf had a high leaf resistance when well illuminated and the resistance did not change irrespective of the incident light level. Clearly, therefore, stomata in senescent maize leaves are non-functional. In the sorghum, the lower leaves quickly senesced and yellow leaves were scarce. Likewise, non-functional stomata were not observed. However, the stomatal resistances at corresponding illumination were, on average, somewhat greater in the lowermost leaves, i.e. those below leaf 9 (flag leaf = 1). Since the lowermost leaves of tobacco were never well illuminated, it was not possible to say from this study whether these leaves lost their ability to respond to light. However, in a subsequent study, on the same crop two weeks later, it was shown that, by removing surrounding plants in order to allow light to penetrate to the lower leaves, the stomata in those leaves below 13 from the top of the plant failed to open in high light (Turner and Incoll, 1971). Most of these lower leaves had high levels of chlorophyll, but were continuously shaded by the upper leaves.

If the older leaves are disregarded, it is evident that the hyperbolic stomatal response to illumination was very similar in maize and sorghum. The minimum leaf resistance (R) was the same in both species at 2 sec cm^{-1} and the illumination for $2R$ was approximately 4,000 ft candles. However, in tobacco the minimum leaf resistance was 1.0 sec cm^{-1} with the illumination at $2R$ being 1,500 ft candles, i.e. the tobacco stomata were wider open in dimmer light than the two grass species. As noted earlier, the adaxial and abaxial stomata responded differently; the minimum adaxial resistance was approximately 4 sec cm^{-1} whereas the minimum abaxial resistance was 1.5 sec cm^{-1} . The minimum resistances doubled at 3,000 ft candles and 1,500 ft candles, respectively, and the stomata closed at 2,000 ft candles in the adaxial epidermis and below 500 ft candles in the abaxial epidermis.

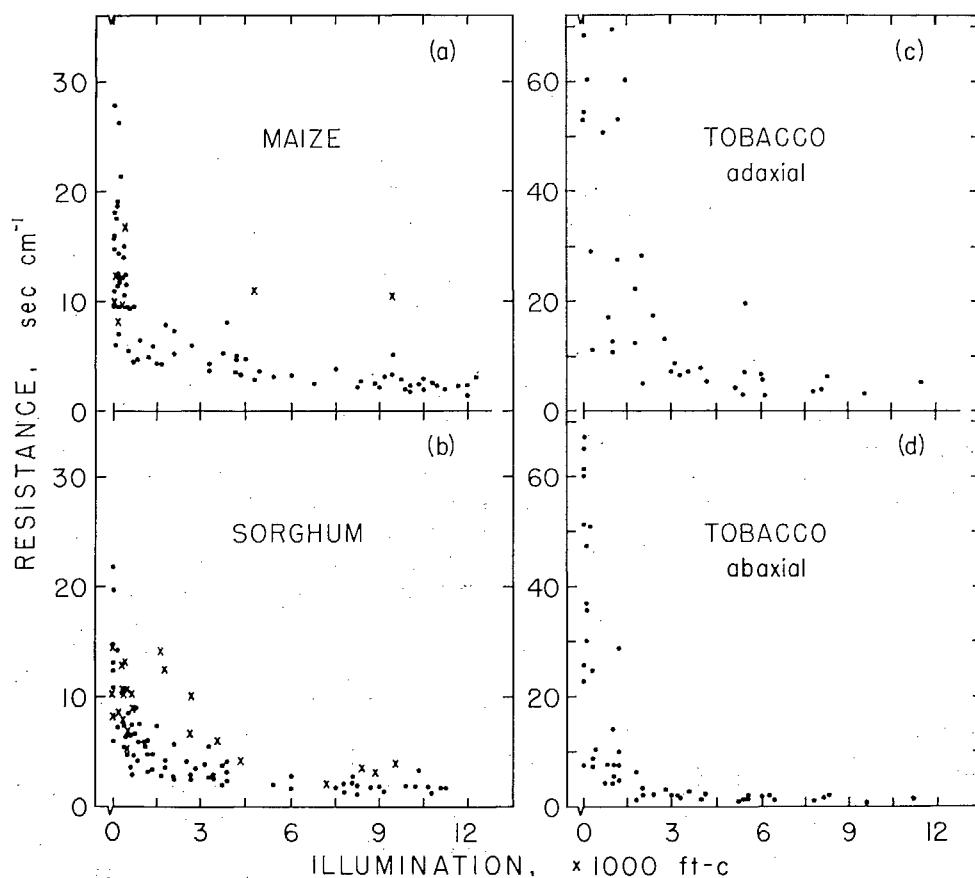


FIG. 4. The relationship between stomatal resistance and illumination for (a) maize; (b) sorghum; (c) adaxial tobacco epidermes; and (d) abaxial tobacco epidermes. The crosses in (a) and (b) refer to the oldest leaf sampled per plant. Resistances greater than 70 sec cm^{-1} were omitted.

STOMATAL RESPONSE TO ILLUMINATION IN A CONTROLLED ENVIRONMENT

The stomatal response to light was also determined for sorghum and tobacco while the other environmental factors were left constant. Young, fully-expanded leaves of both species were placed horizontally in a room maintained at $26.5 \pm 0.5^\circ \text{C}$, 60 ± 5 per cent relative humidity and illuminated at 5 levels from 10 ft candles to 8,900 ft candles. After 45 min for equilibration, the epidermal resistance to transpiration was measured with the ventilated diffusion porometer. Leaf resistance was calculated as previously.

The sorghum and tobacco both had a minimum leaf resistance of 2.5 sec cm^{-1} at maximum illumination, i.e. 8,900 and 7,600 ft candles, respectively, and both doubled this minimum resistance at about 4,000 ft candles. By inverting the leaves at the same illumination, it was shown that the two species differed in their light require-

ment to open the abaxial stomata (Turner, 1970). The adaxial stomata, which are normally exposed to bright light, closed at 2,000 ft candles in both sorghum and tobacco, whereas the abaxial stomata, normally in dim light, closed at approximately 1,000 ft candles in sorghum and 200 ft candles in tobacco.

CONCLUSIONS

The basic hyperbolic response of stomatal resistance to illumination obtained in the field compared favourably with that obtained for single leaves in the laboratory. This indicates that, in well-watered field crops, light is a primary determinant of stomatal resistance. Clearly, some of the variation evident in this study may result from diurnal or internal changes in the spectral composition of light, temperature, relative humidity, and level of carbon dioxide, none of which were measured in this study. However, some variability can also be ascribed

to our inability to accurately measure the illumination in the plane and over the area sampled for the measurement of leaf resistance.

The agreement between laboratory and field observations suggests that relationships determined in the laboratory are generally acceptable for crop simulator studies. Certainly, the introduction of laboratory measurements of the stomatal response to radiation improved the ability of a simulator of canopy evaporation to mimic changes observed in the field (Waggoner *et al.*, 1969), although introduction of the relationship did not greatly affect canopy photosynthesis (Waggoner, 1969).

However, the hyperbolic response of stomata to illumination did not apply in lower, yellowing maize leaves or in the lower tobacco leaves which were still green; the stomata were non-functional. Therefore, stomatal: light relationships obtained for single leaves under controlled conditions should be used with discretion. In most crops the area of senescing leaves will be small and can be safely ignored. However, in situations similar to the tobacco, in which a large proportion of the leaf area has non-functional stomata, or when a large proportion of the crop is senescing, consideration must be taken of the inability of the stomata to respond to light.

Résumé

Éclairement et résistance des stomates à la transpiration chez trois plantes de grande culture (N. C. Turner)

Résistances stomatales et flux lumineux sont mesurés à intervalles réguliers durant une journée complète dans des champs de Maïs, de Sorgho et de Tabac. Pendant le jour, les feuilles près du sol ont toujours une résistance supérieure à celle des feuilles situées plus haut. L'augmentation de résistance des feuilles près du sol est surtout due à la diminution de l'intensité lumineuse, quoique la sénescence tende aussi à augmenter la résistance des basses feuilles du Maïs, qui jaunit, et du Tabac. Les mesures des résistances stomatales et du flux lumineux prises au même instant sont utilisées pour comparer la réponse des stomates à la lumière pour les trois variétés de plantes. Le Maïs (feuilles vertes) et le Sorgho ont une résistance minimale comparable (R) de 2 s cm^{-1} , tandis que pour le Tabac cette valeur est seulement de 1 s cm^{-1} . Pour une résistance double du minimum ($2R$)

l'intensité lumineuse est de $43\,000 \text{ lumens m}^{-2}$ pour le Maïs et pour le Sorgho, et de $16\,000 \text{ lumens m}^{-2}$ pour le Tabac; donc les stomates du Tabac sont relativement plus ouverts à faible intensité lumineuse. Les stomates du Maïs et du Sorgho ont une réponse similaire pour les deux faces de leurs feuilles; au contraire, pour le Tabac, la résistance de la face supérieure est toujours plus importante que la résistance de la face inférieure. Par exemple, la résistance minimale de la face supérieure du Tabac est de 4 s cm^{-1} tandis que la résistance de la surface inférieure est de $1,5 \text{ s cm}^{-1}$; les résistances sont le double du minimum à $32\,000$ et $16\,000 \text{ lumens m}^{-2}$, respectivement. La réponse stomatale du Sorgho et du Tabac aux variations d'intensité lumineuse est aussi mesurée en laboratoire pour des conditions bien déterminées. Les résultats en laboratoire et sur le terrain concordent; cela indique que les stomates répondent surtout au flux lumineux lorsque la terre est suffisamment arrosée.

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Influence de la qualité de la lumière sur la croissance et la floraison

R. Jacques

Laboratoire du phytotron,
Centre national de la recherche scientifique,
91 Gif-sur-Yvette (France)

L'action la plus anciennement connue de la lumière sur la vie de la plante s'exerce par l'intermédiaire de la chlorophylle: c'est la photosynthèse. Quelques heures d'éclairement intense permettent une forte activité photosynthétique et assurent le minimum trophique indispensable à la vie de la plante: après ces quelques heures d'éclairement (dont le nombre est voisin de 8 à 10 pour le plus grand nombre d'espèces, en éclairement artificiel), un éclairement faible exerce une très grande influence sur la morphogenèse (notamment la germination, la croissance de la tige, la surface des feuilles et leur teneur en chlorophylle, la synthèse d'anthocyanes, la floraison, etc.) par l'intermédiaire du phytochrome.

Notre recherche va porter sur le rôle de cet éclairement faible sur l'élongation et la floraison.

En ce qui concerne l'élongation, plusieurs auteurs néerlandais (Wassink *et al.*, 1950; Stolwijk, 1952; Meijer, 1957) ont montré la grande efficacité de la lumière bleue (radiations de longueurs d'onde λ comprises entre 400 et 500 nm) et surtout du rouge sombre (λ proche de 700 nm), ce qui correspond à l'observation courante des symptômes d'étiollement en lumière incandescente. Ce spectre, retrouvé avec plus de précision par Mohr (1957), s'expliquait, d'après cet auteur, par un pigment (hypothétique) responsable de ce qu'il appelait la «réaction à haute énergie».

Or l'accroissement de nos connaissances en ce qui concerne le phytochrome incitait à reprendre cette étude avec des moyens techniques précis.

Après avoir démontré l'activité bleue et rouge sombre (R. Jacques, 1968) à la fois sur la stimulation de l'élongation d'entre-nœuds de tiges, sur la diminution de la synthèse de chlorophylle et sur l'inhibition de floraison d'une plante de jours courts, nous limiterons cette expérimentation à l'activité de la région rouge du spectre sur l'élongation et la floraison.

MATÉRIEL ET TECHNIQUES

On utilise une plante caulescente, au photopériodisme de jours courts (JC) (*Chenopodium polyspermum L.*), et deux plantes en rosette au photopériodisme de jours longs (JL) (*Blitum capitatum* et *virgatum*); ces trois plantes sont des Chénopodiacées.

Au phytotron, dans des conditions parfaitement réglées en éclairement (quantité, qualité et durée), en température et en humidité, les plantes reçoivent 9 heures d'éclairement trophique. A la fin de cette période, elles sont soumises à diverses radiations monochromatiques pendant une durée de 15 heures.

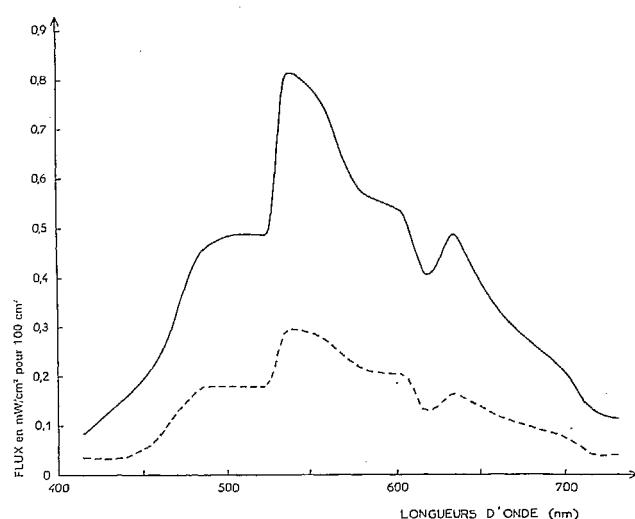


FIG. 1. Répartition du flux obtenu avec l'illuminateur spectral pour chaque longueur d'onde, à l'intensité minimale (---) et maximale (—) d'alimentation de la lampe.

Les diverses radiations monochromatiques sont fournies par un illuminateur spectral décrit, dans sa première version, en 1964 (Jacques *et al.*, 1964). Le remplacement de la source par une lampe à arc au xénon de plus forte puissance (4 000 W; lampe Osram X BO) nous permet maintenant d'obtenir sur une plage de 100 cm² (10 × 10 cm) des flux allant jusqu'à 0,8 mW · cm⁻² (fig. 1) avec une pureté spectrale pour chaque plage de 100 nm en moyenne. L'utilisation de filtres neutres et la possibilité de modifier à volonté les dimensions des plages spectrales permettent d'établir aisément des spectres d'action isoquantiques.

Ainsi, après les 9 heures d'éclairage en lumière blanche fournie au phytotron (éclairage artificiel mixte, fluorescent et incandescent; 115 000 ergs · cm⁻² s⁻¹), les plantes subissent, par cycle photopériodique de 24 heures, 15 heures d'irradiation supplémentaire de faible énergie (0,5 n Einstein · cm⁻² s⁻¹), et ce pendant un nombre variable de cycles.

RÉSULTATS

Élongation. Le spectre d'action obtenu (fig. 2) met en évidence une forte activité des radiations de $\lambda=710$ nm. Les radiations de longueurs d'onde supérieures ($\lambda=730$ nm, par exemple) sont moins actives. Le rouge clair est peu stimulant (dans nos conditions expérimentales, même la lumière du rouge clair exerce une stimulation de croissance, comparée à la croissance obtenue à l'obscurité).

Hartmann (1966) a montré que l'on pouvait calculer le pourcentage des deux formes du phytochrome dans du matériel éclairé par une ou plusieurs radiations monochromatiques. Bien que pour des feuilles vertes la présence de la chlorophylle notamment altère certainement un tel calcul, on peut le tenter; on constate (fig. 2) que l'activité de la lumière augmente quand la proportion du phytochrome actif (ou P_{RS}, c'est-à-dire forme du phytochrome absorbant dans le rouge sombre) par rapport au phytochrome total diminue, tout au moins jusqu'à une valeur de l'ordre de 7% où le maximum de croissance est atteint. Ensuite, lorsque le rapport $\frac{P_{RS}}{P_{total}}$ diminue encore, l'allongement est moins prononcé.

Floraison. Nous avions montré (R. Jacques, 1968) que les radiations bleues et rouge sombre, employées dans les mêmes conditions que celles définies ci-dessus, étaient efficaces pour inhiber la floraison du *Chenopodium polyspermum* L., plante de JC.

Le spectre d'action obtenu sur les 2 *Blitum* de JL met en évidence les points suivants:

Une espèce (*B. capitatum*), dont la floraison peut être provoquée en dyspériode de 9 heures par un apport de gibbérelline exogène, par exemple l'acide gibbérellique AG₃ (M. Jacques, 1968), fleurit préférentiellement à 718 nm; la zone d'efficacité va de 695 à 730 nm.

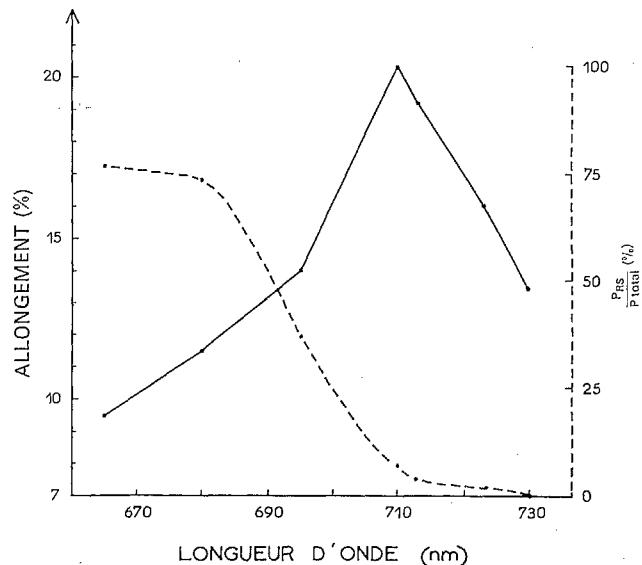


FIG. 2. Spectre d'action de l'élongation d'entre-nœuds de tige du *Chenopodium polyspermum* L. (—); comparaison avec la proportion de phytochrome actif (P_{RS}) (---).

L'autre espèce (*B. virgatum*), non induite à fleurir sous l'action de l'acide gibbérellique en conditions dyspériodiques de 9 heures, fleurit préférentiellement à 695 nm: par rapport à l'espèce précédente, le spectre d'action est donc décalé vers les plus courtes longueurs d'onde; les radiations de $\lambda > 720$ nm sont inactives.

Le rouge clair ($\lambda=660$ nm) est inefficace chez les deux espèces.

INTERPRÉTATION ET DISCUSSION

Les radiations qui maintiennent une proportion de phytochrome actif faible, mais constante, pendant un temps long (ce qui est le cas du rouge sombre et à un degré moindre du bleu) sont les plus efficaces pour stimuler la croissance.

La floraison de certaines plantes de jours longs peut avoir lieu préférentiellement aux mêmes longueurs d'onde que celles stimulant la croissance d'entre-nœuds, ce qui explique l'efficacité de la lumière incandescente et l'inefficacité de la lumière fluorescente. D'autres plantes, l'Épinard, la Betterave et la Jusquiaume (Borthwick *et al.*, 1969) ont un comportement identique. Pour d'autres plantes de jours longs, au contraire, le spectre d'action est décalé vers les plus courtes longueurs d'onde; le rôle du phytochrome dans l'induction florale est donc complexe.

Un décalage du spectre d'action est obtenu en irradiation bichromatique (rouge clair ou rouge sombre superposé aux radiations monochromatiques): le maximum d'activité se retrouve toujours pour le même pour-

centage, faible, de phytochrome actif. L'explication de cette corrélation existant entre une teneur faible en phytochrome actif et le maximum d'activité physiologique reste à trouver. Le mode d'action du phytochrome est également inconnu: tout au plus peut-on supposer que les radiations du rouge sombre favoriseraient la synthèse des gibberellines endogènes. En effet, il a été montré (Weinberg et Voeller, 1969) que la stimulation de la germination de spores de Fougères par la lumière s'accompagne d'une augmentation des gibberellines endogènes. De tels faits sont certainement possibles dans

les plantes vertes, bien que des recherches doivent être entreprises pour le démontrer.

Ainsi on peut conclure en insistant sur l'importance de connaître, lors de l'emploi d'un éclairage artificiel, sa composition spectrale exacte et tout particulièrement le rapport rouge clair / rouge sombre qui, principalement, détermine une certaine teneur en phytochrome actif. Pour chaque espèce, il est nécessaire d'entreprendre une analyse du type de celle qui vient d'être décrite, selon le résultat que l'on désire obtenir (stimulation ou inhibition de la croissance et de la floraison).

Summary

Influence of the quality of light on growth and blooming (R. Jacques)

The action of light through phytochrome on growth and blooming was analysed in a phytotron by means of monochromatic rays used singly or superimposed.

With artificial lighting the ratio of dark red light to pale red light was the determining factor in the morpho-

genesis of plants. For instance, a high ratio has a marked effect in increasing stem length and is essential for the blooming of certain long-day plants.

There is therefore a correlation between the maximum physiological response and the presence of a low proportion of active phytochrome. The explanation of this phenomenon has yet to be found.

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The relationship between light intensity and reproductive capacity

F. H. Whitehead
Botany Department
Imperial College
London (United Kingdom)

It is becoming increasingly clear that distribution, competition, survival, etc., can often be studied in terms of "compensating mechanisms". This expression was first used by me in a paper in 1962 (Whitehead, 1962). Today I would define it in rather more sophisticated terms than when first used. A compensating mechanism is where adaptive changes occur in morphology and anatomy in response to environmental factors. In physiological terms these cancel out the adverse environmental effect to an extent permitting an individual to survive. It is interesting to note that, using the method of growth analysis (proportionality of root, stems and leaves over the course of time), it can be seen that these modifications in anatomy and morphology arise because of a differential employment of assimilates. Despite the fact that individual survival takes place, the overall biological efficiency is reduced in the process of this type of adaptation. These compensating mechanisms have been found to be operative in response to the stimulus of many types of environmental factors, but only those in relation to light intensity will be considered here.

It has long been known that certain species of plants growing in the shade have larger, thinner leaves than the same species growing in the sun. For example, sun and shade leaves are terms one finds in the classical ecological literature. A more detailed study was made by Blackman and Rutter (1946), but this was limited in the sense that the parameters used and the types of analysis employed were restricted to those in general agricultural research. Some bias in those types of analysis has occurred because they were developed by physiologists concerned in agricultural research, and since their interest was in yield per plant, yield per unit area, etc., yield is usually employed in relation to some commercially important part of the plant, seeds, roots, stems, etc. Little attention was paid to overall developmental and comparative morphology.

Myerscough and Whitehead (1966, 1967) showed that for *Chamaenerion* and other species in light intensities of 100, 70 and 40 per cent daylight a compensating mechanism was functioning. The relatively greater extent of leaf material as a proportion of the total dry matter of the plant was such that, despite the lowered biochemical rate of photosynthesis, the same amount of carbon was accumulated over a period of time by plants grown at these three different light intensities. It was found that at later harvests there was no significant difference in dry weight per plant in the three treatments. Leaf area and leaf dry weight, however, was greatest at the lowest and least at the highest light intensity. It was also found that the plants in the 40 per cent light treatment lagged behind in total dry weight at the earlier harvests. Over a period of time it can be said that the plants at the three different daylight levels were equally efficient as photosynthetic carbon accumulators due to the operation of a compensating mechanism. This operates so that, as light intensity is reduced, with concomitant reduction of photosynthetic rate, an increased volume of photosynthetic tissue ensures that the same amount of carbon is fixed per unit of time.

In the same paper, the unit leaf rate, which can be calculated (Whitehead and Myerscough, 1962) and expressed as a rate, is examined. The term α is used for the index of this rate. α is simply calculated and shown in the papers already referred to as the rate of leaf area increase, divided by the rate of dry weight accumulation. In the discussion of this aspect of growth analysis, Briggs *et al.* (1920) have shown that it can vary between an index of 1, that is a linear function to a logarithmic function the index of which can be any quantity larger than 1, and up to some higher order which can be more than the cube. When the index is 1, that is when the increase of the unit leaf rate is a linear quantity, it means that all the products of photosynthesis are being apportioned in morphological development in the same

ratio and at the same rate as in the previous period. When the index is greater than 1, that is when logarithmic increase is occurring, it means that more assimilates are being produced than are required to maintain the former rate of development of leaf material. It follows that there is a surplus of material which may be used in extra root, stem, leaf or other organ production. At a later time, when flowering commences, it appears usual for this extra material to be diverted into formation of flowers, fruit and seeds. This is clearly shown by the correlation (correlation coefficient 0.98) between this surplus $\bar{W} (\alpha - 1)$ (calculated as that proportion of weight which is left over after the linear requirement of addition to the "photosynthetic entity" has been so employed) and the production of capsules of *Chamaenerion angustifolium* (Whitehead and Myerseough, 1962). If this is considered in the terms used by the economists in discussing their problems, it could be said that the investment in plant and machinery, that is the formation of photosynthetic material, was much greater in the lower daylight ranges, but the productivity, with this increased plant and machinery, was less than that of the full daylight plants. This is a case of a simple, correlation between adaptation to low light intensity and reduction in flowers, fruit and seeds.

In the same investigation, it was found that *Tussilago farfara* had a very well-developed compensating mechanism in relation to lowered light intensity, although its growth form and morphogenesis were different from those of *Chamaenerion*. Despite this difference of growth form, the same general conclusion of reduced reproductive capacity held good, though differently expressed. *Tussilago farfara* forms, in the current season's growth, a number of stolons which ramify just below the surface of the soil, usually to considerable distances (over 1 m). The number of stolons formed each year is governed by the same formula of $\bar{W} (\alpha - 1)$ as was the case of the capsules, seeds and flowers of *Chamaenerion*. These stolons form a resting bud in the autumn which flowers in the next season and later forms a rosette of leaves. It then produces, later in the season, a crop of stolons which repeat the process. It was found that the number of flowers was determined by the surplus weight of the previous year and also the number of vegetatively reproduced plants. The rate of spread of this species, both by seed and vegetatively, is thus controlled by the extent of adaptation to low light intensity. The number of stolons normal in a plant in full daylight averages about 8 or 9, whereas in 40 per cent daylight it is usually between 1 and 2.

This demonstrates the relationship between adaptation to low light intensity and the reduction of reproductive capacity. The situation is, however, more complicated than would appear from what has been said so far. It was mentioned that, in those species with a well-developed compensating mechanism, there was an increase in the material which was employed in leaf formation. The plant was proportionately more leafy in

the low light intensity replicates than in the full daylight replicates. This is most easily shown over a series of harvests grown at different daylight levels, by taking the total dry weight of each individual as a 100 per cent and the weight of leaf, root and stem then being calculated as a percentage of this whole. Over a period of time it is possible to see in all the treatments the changes in proportionality between these three main morphological categories independently of their overall performance (i.e. total dry weight). When this data for *Filipendula ulmaria* and *Iris pseudacorus* is plotted graphically, as in Whitehead and Faheemudin (in press), it was found that, as the level of light intensity decreased, a proportionately higher amount of assimilates was being devoted to the formation of leaves and leaf material. If, out of the total, a larger proportion of assimilates was being employed for leaf formation, it can only be at the expense of one or both of the other morphological categories. It was found in *Filipendula ulmaria* that there was little effect on the stem proportionality, but the extra leaf proportion was almost entirely at the expense of the root proportionality.

Regarded from the point of view of water relations, these plants are very much more at risk than the plants in full daylight because they are losing water from a bigger shoot system and possess a smaller root system to take up water replacing that which is lost. Normally this is not of a great importance because the water regime in shady conditions is such that there is less water stress in these habitats than in the fully exposed habitats. If the shading is removed the results can be fatal. It is best seen in the case of *Chamaenerion angustifolium* already referred to. This is a frequent component of the herb flora of the most completely shaded parts of beech woods where, in response to the lowered light intensity, the leaves may be as much as 4 cm or more across, compared with the 1 cm or so of the normal, unshaded, plant. The root system can be less than half that of the unshaded plants. If now some branches or a tree are removed, allowing full sunlight to fall on these plants, permanent wilting occurs in the course of 3 or 4 hr, even if the soil is saturated with water. In other words, despite the optimum conditions for water uptake, the root system is inadequate to take up enough water to balance that being lost by the shoot.

The effects on the postponing of flowering are also important. In the case of *Chamaenerion*, already described above, not only were fewer flowers produced, but also the commencement of flowering was delayed. The 40 per cent light intensity plants start to flower some 4 weeks after the full light plants.

Compensating mechanisms are not possessed to the same degree by all species, enabling an evaluation of the survival value of such a mechanism. *Datura stramonium* shows almost no increase in leaf area or volume with reduction of light intensity. When its performance was compared with that of *Chamaenerion*, it was found that the proportionate reduction in flowering and seed

production was much greater (by a factor of over $\times 4$) in *Datura*.

It would appear, therefore, that although adaptation to lowered light intensity by means of a compensating mechanism exacts a price in reduced reproductive capacity, it is not so great as that demanded from a species without such a compensating mechanism. It is not surprising to find that all species capable of competing in reduced light conditions appear to possess such compensating mechanisms, possession or otherwise of which can be used to classify species as "shade tolerant" or "shade intolerant" respectively.

A further possible significance of the possession of a compensating mechanism is that, regardless of the reduced reproductive capacity, some species may be enabled to persist through an unfavourable light regime until better conditions return. It would appear from my current research that *Iris pseudacorus* is a good example. It has been found possible to relate the annual rhizome increment to light conditions over the year. These rhizomes persist in the fen carrs in Britain so that light

regimes over the past 40–50 years can be assessed. In any one year the rhizome increment can be related to a total annual energy increment in relation to a range of canopy densities. The canopy over a period of time opens and closes as the willows and alders grow, mature, senesce and die. These studies show that the approximate time for the full cycle of open–closed–open canopy is in the region of 30–35 years. It was also found that, when the canopy is most closed and shade is deepest, no plants of any species can become established and most species are shaded out and die. *Iris*, however, although not flowering and showing no branching of its rhizome, produces leaves not much larger in diameter, but 3–4 times the length. It would seem clear that, in this case, it is the possession of so strongly developed a compensating mechanism that permits this species to persist through the adverse light regime.

Although this paper is concerned only with adaptation to low light intensity, it should be noted that compensating mechanisms in relation to other factors have been shown to exist.

Résumé

Relations entre l'intensité lumineuse et la capacité de reproduction (F. H. Whitehead)

L'auteur étudie l'existence de mécanismes de compensation réagissant à une réduction de l'intensité lumineuse. Il cite des exemples pour montrer que certaines espèces de végétaux peuvent mieux que d'autres accroître la proportion des tissus à activité photosynthétique aux dépens des racines et des tiges lorsque l'intensité lumineuse s'abaisse durablement. Il décrit des cas où il en résulte des gains égaux de carbone assi-

milé sur des périodes de quelques semaines pour 100%, 70% et 40% de lumière du jour. En compensation d'une intensité lumineuse moindre, le pouvoir de reproduction exprimé en nombre de fleurs, de fruits et de graines est réduit proportionnellement, comme l'indique la formule $W(\alpha - 1)$. Il est également démontré que le pouvoir de reproduction est réduit encore plus chez les espèces dont la capacité de compensation est médiocre.

Des constatations analogues ont été faites en ce qui concerne la reproduction végétative, la survie après pérennisation, les réserves alimentaires, etc.

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The effects of photoperiod and light intensity on the growth of some weeds of crop fields¹

K. P. Singh and B. Gopal
Department of Botany
Banaras Hindu University
Varanasi (India)

INTRODUCTION

The man-managed cropland ecosystem is not a single species ecosystem because a large number of weed species flourish within it.

Man makes continued efforts to keep them under control by mechanical weeding or use of chemicals for obtaining maximum yields from the crop species. The crop fields are continuously infested by various weed species at different stages of crop growth which compete with the crop plants for nutrients, water, light, etc. Thus, it is important to investigate the ecological requirements of weed species, along with those of the crop plants, to assess the stress upon the latter and to identify the vulnerable stages in the life-cycle of the weeds, especially in relation to the micro-climatic conditions within the cropland ecosystem. These may ultimately help in devising suitable control measures.

Crop plants exert considerable influence on the micro-climatic conditions. Depending upon the nature of the crop plants, the light penetration through the crop canopy gets modified in quantity as well as quality (Saeki, 1963; Monsi, 1968; Baumgartner, 1972). Since the classical work of Garner and Allard (1920) on the photoperiodic responses of tobacco, great advances have been made in the study of plant responses to varying light periods. The subject has been reviewed at length by Salisbury (1963). The effects of reduced light intensities on the growth and reproduction have been described for several plants (Evans and Hughes, 1961; Hughes and Evans, 1962; Lockhart, 1963; Kuroiwa *et al.*, 1964; Blackman, 1968; Whitehead, 1969). These studies have again revealed differences in responses of various plant species to different light intensities. The present communication reports the results of an investigation of growth response in relation to varying light intensities and light periods of four weed species namely, *Anagallis arvensis* L. var. *coerulea* (blue flowered),

Chenopodium album L., *Amaranthus spinosus* L. and *Portulaca oleracea* L.

PHENOLOGY

The phenology of the four species as observed in the field at and around Varanasi ($25^{\circ} 18' N$, $83^{\circ} 1' E$) is described below.

Anagallis arvensis and *Chenopodium album* are winter annuals growing extensively in irrigated cultivated fields (with crops like wheat, gram, pea, potato, etc.). The former species also grows in moist flower beds and along water channels. Both the species are observed to avoid highly shaded crops like sugar-cane, and are absent from relatively drier ruderal habitats and grasslands. The earliest seedlings appear in the field in late October (beginning of the cold season) and afterwards fresh crops of seedlings continue to appear until February. The flowers appear by the middle of December and later vegetative growth and flowering continue simultaneously until the end of March. The late seedlings, however, flower earlier and usually develop into stunted plants. The seeds are dispersed in April-May, at the time of crop harvesting, and remain in soil during the whole summer and rainy season.

Portulaca oleracea occurs almost throughout the year in moist habitats, with more profuse growth in summer and the rainy season. The species is composed of three varieties, which are chiefly distinguished by the leaf shape (Khoshoo and Singh, 1966). Of these, two wild varieties with obovate (OL) and narrowly obovate leaves (NL) have been investigated. The OL and NL

1. These studies form a part of the PL 480 research project entitled "Ecological studies of noxious weeds, common to India and America, which are becoming an increasing problem in the Upper Gangetic Plains".

varieties often grow intermixed in cultivated fields and gardens. The OL variety, however, grows in several other more biotically disturbed habitats, such as road sides, brick pavements, etc. This is because of its ability for induction of a wide range of modifications in the vegetative features and reproductive capacity, and its small seeds, which ripen even when the plants are uprooted. Furthermore, self-pollination and cleistogamic tendencies under adverse conditions are added advantages (Khoshoo and Singh, 1966). Both the varieties, especially the NL variety, prefer an open habitat and seem to avoid heavily shaded crops. Both varieties are annuals, exhibiting variations in the life-span of individual plants under different seasons (2–4 months). Flowering usually starts when the plants are about 1 month old and attain 10–12 leaves, provided moisture supply is not limited, and continues later together with vegetative growth.

Amaranthus spinosus is also an annual growing throughout the year. The plants grow in cultivated fields, on embankments and along water channels and, more profusely, in waste places (on garbage heaps) and in abandoned fields. Individuals of all stages of vegetative growth can be spotted at any time. The seeds germinate several times during a year, but flowering occurs either during early summer (March–early May) or early winter (September–October). The seedlings appearing in March–April, as well as those emerging in November–December, come to flowering in mid-May. Similarly, the seedlings which emerged during July–September flower in early October.

EXPERIMENTAL PROCEDURES

The results reported in this paper are based on experiments conducted on plants raised from seeds collected from the crop fields at Varanasi, except in the light intensity experiments on *Portulaca oleracea* and *Chenopodium album*, the seeds of which were collected from Etawah ($26^{\circ} 47' N$, $79^{\circ} 2' E$) and Kanpur ($24^{\circ} 28' N$, $80^{\circ} 24' E$) respectively. The seedlings were grown in earthen pots filled with a mixture of garden soil (sandy loam) and farmyard manure (3 : 1), and were watered periodically. The experiments on the four species were conducted at different times of the year and this has resulted in some minor differences in the light conditions used in the experiments.

VARIATIONS IN THE PHOTOPERIOD

In experiments on the effects of different photoperiods, the natural daylength was extended by using 300-W incandescent bulbs fitted with aluminium reflectors and held above the pots at a height of 1 m. The light arrangement provided an intensity of about 500 lux at the level of the plant surface. For shorter photoperiods, the daylength was cut short by covering the

plants with light-proof wooden boxes. There were 3–10 plants used for each treatment. In *C. album* and *Amaranthus spinosus*, 7 to 8-day-old seedlings and in *P. oleracea* 15-day-old seedlings were subjected to different photoperiodic treatments. In case of *Anagallis arvensis*, due to the occurrence of juvenile photoperiodicity (K. P. Singh, 1969), seed germination and seedling establishment was allowed under an 8-hr photoperiod and treatments were begun on 5-day-old seedlings.

VARIATIONS IN LIGHT INTENSITY

To study the influence of light intensity, bamboo sheds 1 m high were constructed and were covered on all sides with 1 to several layers of muslin cloth. The light intensity under the sheds was measured as percentage of that in the open sun with the help of a photometer. In *A. spinosus*, only 2 levels of light intensity were used—open sun and a tree shade (about 50 per cent that of full sunlight). In these experiments also 3–10 plants were used for each light intensity level. Seedlings, 7–8 days old, of *C. album* and *A. spinosus* were transferred to different sheds, whereas, at the time of transference, the seedlings of *A. arvensis* and *P. oleracea* were 15 and 3 days old respectively.

RESULTS

EFFECTS OF DIFFERENT PHOTOPERIODS

Anagallis arvensis. The data obtained after 30 and 45 days' growth (Table 1) show that no flowers are produced up to 10-hr photoperiod. In the 11-hr photoperiod, flowering is initiated to some extent, but more time is required for appearance of floral buds. As the photoperiod is increased above 12 hr a smaller number of days is required for floral initiation. Thus the species is a long-day plant with the critical photoperiod between 10 and 11 hr. In the first 30 days almost the same number of flowers are produced in plants subjected to

TABLE 1. Effect of photoperiod on flowering¹ and fruiting in *Anagallis arvensis*

Photoperiod (hr)	Number of flowers after		Number of capsules	Number of days required for floral initiation
	30 days	45 days		
8	0	0	0	—
9	0	0	0	—
10	0	0	0	—
11	4.3	8.0	1.6	24
12	10.6	10.0	11.0	15
13	10.0	10.2	9.0	14
14	9.7	18.2	8.1	9
15	12.4	17.4	10.0	9

1. Signifies that no flowering took place.

TABLE 2. Effect of photoperiod on growth and reproduction in *Amaranthus spinosus*

Character	Photoperiod (hr)							
	8	9	10	11	12	13	14	15
Root length (cm)	11.3	12.6	13.0	13.7	12.0	11.1	14.1	9.8
Shoot length (cm) excluding inflorescence	25.1	24.7	22.3	20.4	24.4	16.9	17.9	28.0
Inflorescence length (cm)	7.1	7.4	9.9	12.1	16.5	4.6	8.1	10.2
Root dry weight (g)	0.5	0.9	0.9	1.3	0.9	0.9	0.9	0.9
Shoot dry weight (g) including inflorescence	1.5	2.7	2.9	3.5	2.7	2.7	2.5	2.5
Number of days taken for floral initiation	37	36	35	27	27	36	35	32
Total seed weight per plant (mg)	86	87	205	420	578	38	84	108

TABLE 3. Effect of photoperiod on growth and flowering¹ in *Chenopodium album*

Character	Photoperiod (hr)							
	4	6	8	10	12	14	16	20
Shoot length (cm)	8.3	14.2	14.0	20.0	16.3	13.3	20.5	20.7
Number of branches	1	2	2	4	2	3	6	8
Leaf area (cm ²)	1.5	1.2	1.4	1.3	2.8	3.5	4.2	10.8
Total dry weight (g)	0.6	0.8	0.6	0.7	1.3	0.5	0.3	0.2
Days required for floral initiation	38	36	26	18	27	36	—	—

1. Signifies that no flowering took place.

12- or 15-hr photoperiods, but later longer photoperiods (14 hr and 15 hr) are more favourable. However, capsule formation, which occurs after 30 days, is not affected by daylength between 12 and 15 hr.

Amaranthus spinosus. After 45 days' growth (Table 2) it is observed that length and dry weight of the roots increase up to an 11-hr photoperiod and start decreasing thereafter. Similarly, the shoot dry weight also reaches maximum at an 11-hr photoperiod, but the shoot length (with or without inflorescence) did not show any definite trend. No appreciable difference was noted in the total shoot length between 8- and 11-hr photoperiods. The plants flower at all the photoperiods used in the experi-

ment. The floral initiation was earlier at 11- and 12-hr photoperiods and the maximum length of the inflorescence, and thus the number of flowers and seeds and seed weight, was obtained at the same photoperiod.

Chenopodium album. The data obtained on plants grown under different photoperiods for 45 days are presented in Table 3. The maximum shoot length and number of branches are attained with a 10-hr photoperiod, with another peak at 16- and 20-hr photoperiods. The leaf area increases regularly with the photoperiod under 20 hr, while maximum dry weight is obtained in plants grown under a 12-hr photoperiod. No flowering occurred in plants exposed to more than a 14-hr photoperiod.

TABLE 4. Effect of photoperiod on growth and flowering in *Portulaca oleracea*¹

Character	Variety	Photoperiod (hr)					
		4	6	8	10	12	16
Shoot length (cm)	OL	12.6	18.9	15.4	14.0	13.0	13.1
	NL	—	—	2.8	4.5	5.6	6.2
Number of branches	OL	2.0	8.1	10.0	9.5	13.5	5.6
	NL	—	—	3.5	4.7	5.4	5.6
Number of leaves	OL	16	56	48	55	61	35
	NL	—	—	17	52	53	62
Number of flowers	OL	2.6	20.6	26.1	36.6	48.1	23.5
	NL	—	—	4.0	14.2	10.2	10.4

1. 4- and 6-hr photoperiods were not used for the NL variety.

Thus the species may be called a short-day plant with a critical photoperiod between 14 and 16 hr. Further experimentation revealed that the critical photoperiod is 14.5 hr (Gupta, 1970). However, at photoperiods below 14 hr the plants exhibited a quantitative response, i.e. the floral initiation took only 18 days under a 10-hr photoperiod as against 36–38 days under 4–6 or 14-hr photoperiods.

Portulaca oleracea. The data (30 days' growth period) in Table 4 reveal that the 2 varieties of the species are day neutral, but exhibit some differences in their response to various photoperiods. The shoot length, and number of branches and leaves are almost the same at photoperiods between 6 and 16 hr in the OL variety, with somewhat higher values at 10- to 12-hr photoperiod, but in the NL variety these characters tend to increase with the longer photoperiods. Flowering is observed at all the photoperiods under study, but the maximum amount of flowering occurs at a 12-hr photoperiod in the OL variety and at a 10-hr photoperiod in the NL variety.

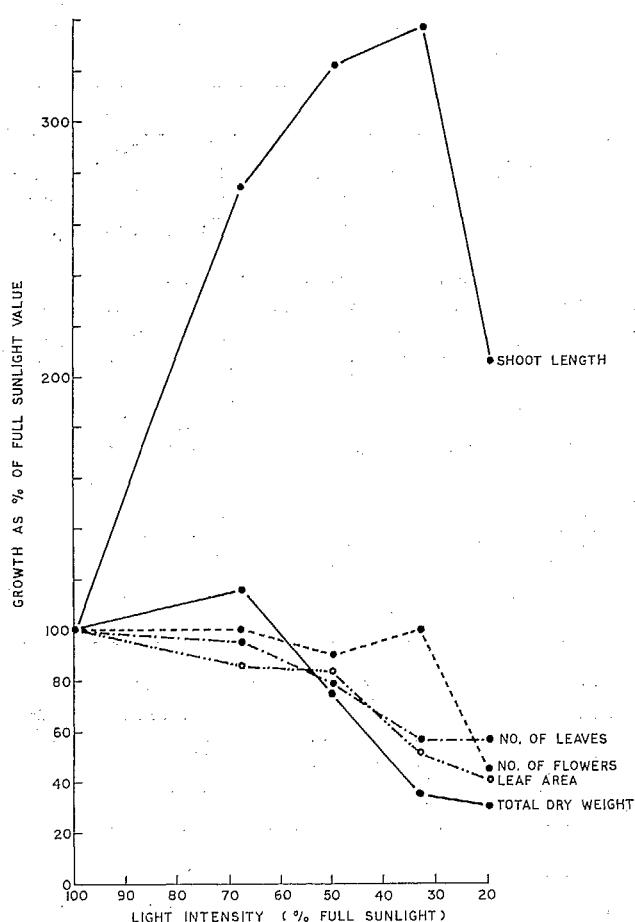


FIG. 1. Growth and flowering of *Anagallis arvensis* under reduced light intensities.

EFFECTS OF DIFFERENT LIGHT INTENSITIES

Anagallis arvensis. The total dry weight of the plant, which is at a maximum in 70 per cent sunlight, decreases consistently at lower light intensities. However, the number and area of leaves gradually decrease from the highest values at 100 per cent sunlight to the lowest at 20 per cent sunlight (Fig. 1). The shoot length is considerably increased with decreasing light intensity up to 33 per cent sunlight beyond which it decreases, but remains double that at 100 per cent sunlight intensity. A reduction of light intensity to one-third of full sunlight does not cause any appreciable difference in flower number.

Amaranthus spinosus. The plants grown at 50 per cent sunlight for 1 month show considerable reduction in growth (Fig. 2). The shoot length and the leaf area are reduced to only two-thirds of that in full sunlight, while the total dry-matter accumulation is more markedly affected and is only one-third of that in full sunlight. The most noteworthy effect of shading is the complete suppression of flowering and also the reduction of the characteristic spines to simple, short, hairy outgrowths. Thus the plant behaves as an obligate helio-phyte.

Chenopodium album. The data presented in Figure 3 for the plants grown at different light intensities for 42 days reveal that both vegetative and reproductive growth are promoted by a slight reduction in the light intensity from that of full sunlight. The shoot length, number of branches and leaves and individual leaf area (at the third internode) are all greatest at 70 per cent sunlight and decrease at full sunlight or at lower light intensities. The total dry-matter accumulation at 70 per cent sunlight is more than 3 times that at full sunlight, but is very much reduced at lower light intensity levels. Similarly, the number of inflorescences and total seed output per plant are also maximum at 70 per cent sunlight and are heavily reduced at 50 and 40 per cent sunlight. At 40 per cent sunlight the seeds fail to develop in most of the inflorescences.

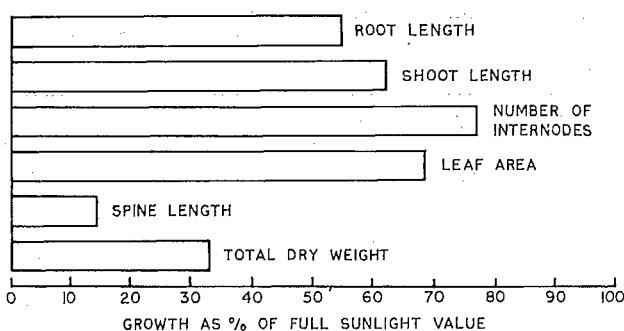


FIG. 2. Growth of *Amaranthus spinosus* in 50 per cent sunlight.

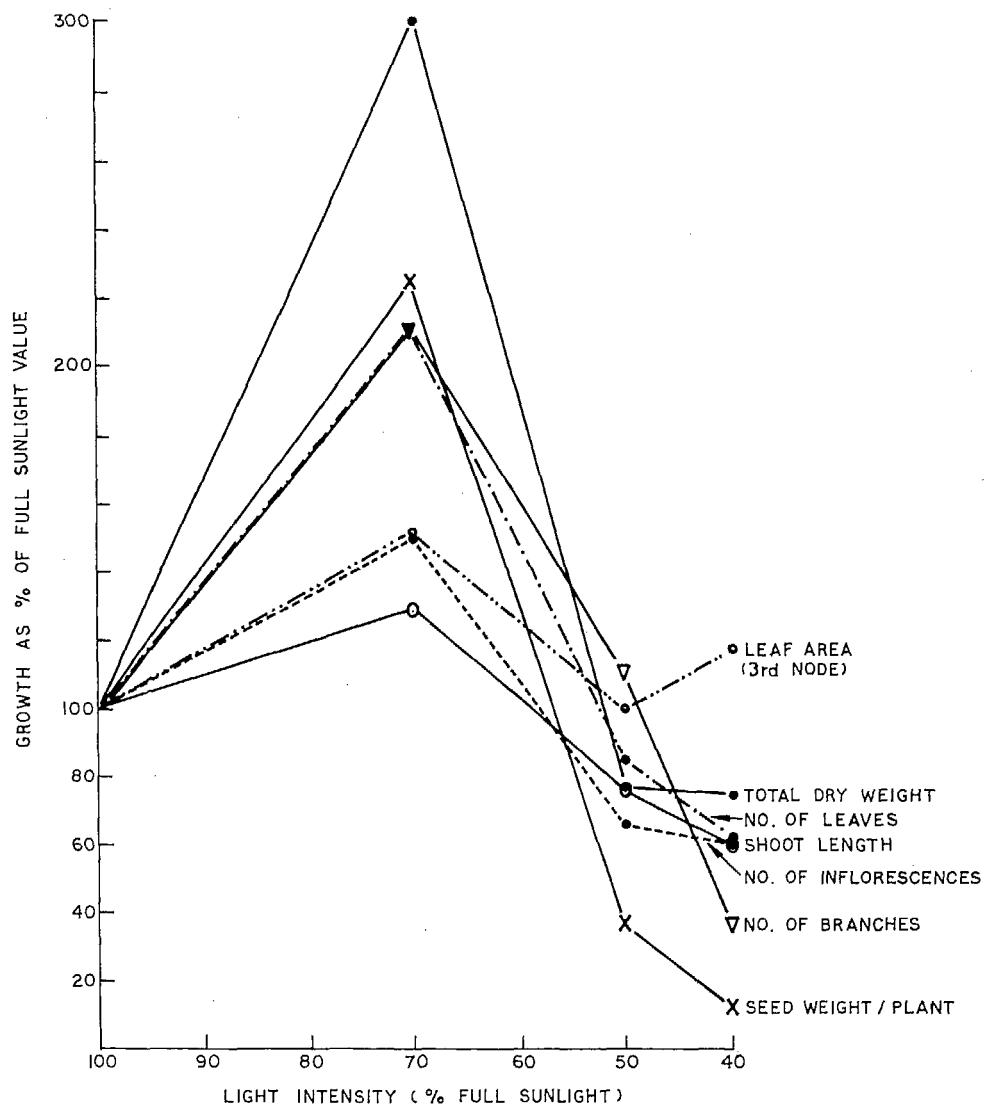


FIG. 3. Effect of variations in light intensity on growth and reproduction in *Chenopodium album*.

Portulaca oleracea. The two varieties reveal marked differences in their behaviour towards varying light intensities. Full sunlight is clearly best suited for the growth of the NL variety, which shows a considerable decrease in number of leaves, total dry matter accumulation and total number of flowers in response to decreasing light intensities (Figs. 4(a) and (b)). The OL variety on the other hand, shows highest values of leaf number, dry-matter accumulation and number of flowers at 70 per cent sunlight; these values being 1.5–2 times more than those at full sunlight. At lesser light intensities, however, all the values tend to decrease. Plants of both the varieties tend to grow erect under

reduced light intensities, with the result that maximum shoot height in the NL variety is obtained at 40 per cent sunlight and in the OL variety at 70 per cent sunlight. It is remarkable that seed production in the LN variety decreases sharply at 70 per cent sunlight and almost stops at 40–50 per cent light intensity, whereas the OL variety produces a slightly greater number at 70 per cent sunlight and very few seeds at 40 per cent sunlight. The number of seeds in each capsule of both the varieties was considerably reduced at lower light intensities, so that even in the OL variety the significant increase in flowering at 70 per cent sunlight is offset by the reduction in seed number.

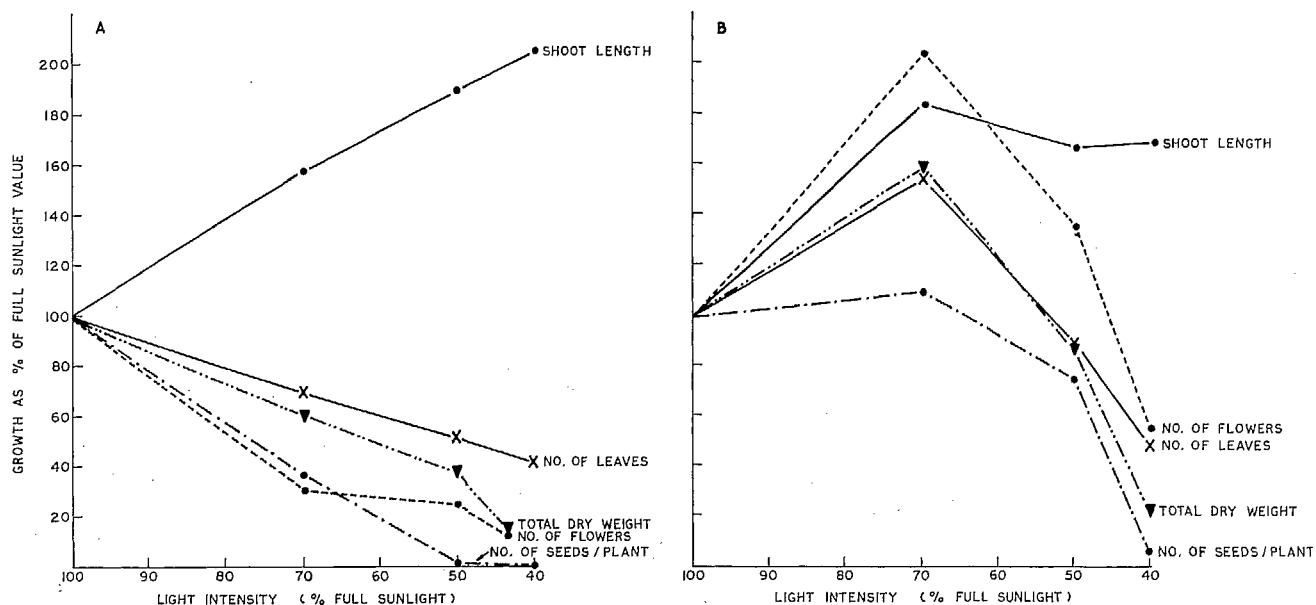


FIG. 4. Growth and flowering of NL (a) and OL (b) varieties of *Portulaca oleracea* under reduced light intensities.

DISCUSSION

EFFECTS OF PHOTOPERIODS

The present study on the 4 species, all inhabiting the crop fields, reveals differences in their photoperiodic requirements. The 2 weeds which are winter annuals are either long-day (*Anagallis arvensis*) or short-day (*Chenopodium album*) plants. On the other hand, the other 2 species, which occur almost throughout the year, are day neutral. Of the 4 species under consideration, *A. arvensis* has been extensively studied outside India for its flowering behaviour, especially in response to various photoperiods. Chouard (1950, 1957) was the first to report that this species is a qualitative long-day plant, and later Brulfert and Chouard (1961) showed that a single exposure to long day was sufficient to induce flowering. Later studies by Ballard and Grant-Lipp (1963, 1964) and Brulfert (1965) have shown that the red and blue flowered strains of the species (var. *foenicula* and var. *coerulea*) have a critical photoperiod between 12 and 12.5 hr at temperatures above 10° C (Ballard, 1969). The present study on the blue flowered variety shows that the Indian populations of the species have a critical photoperiod between 10 and 11 hr, while the mean daily temperature during the growth period is decidedly above 10° C. This leads us to assume that several ecological races exist within the species which differ also in their photoperiodic requirements. Population differentiation in relation to latitude of occurrence has already been demonstrated in the species by Misra *et al.* (1968).

C. album has been found, in the present study, to behave as a short-day plant with a critical photoperiod of 14.5 hr (Gupta, 1970), exhibiting a quantitative response with maximum flowering at a 10-hr photoperiod. These findings are contrary to those of Cumming (1959), who has shown that this species flowers up to a 20-hr photoperiod and even in continuous light, though it takes more time. Gupta (1970) has shown that flowering can be induced at photoperiods longer than 16 hr by interrupting the light period with a half-hour of darkness. He has also reported that repeated cycles of dark interruption promote flowering; this is in agreement with the conclusion of Schwabe (1961) that flowering is enhanced in short-day plants due to summation of the effects of favourable dark induction cycles. It may be noted that in a related species, *C. rubrum*, the various ecotypes flower earlier in short to intermediate photoperiods (Cumming, 1961, 1963, 1967, 1969). These differences in the photoperiodic responses of *C. album* may also be due to population variations.

Amaranthus spinosus is day neutral exhibiting a quantitative response with maximum flowering at a 12-hr photoperiod. It appears that daylength does not control the incidence of flowering in nature: instead temperature seems to be more important as both the flowering periods observed in nature (early summer and early winter) correspond to a mean daily temperature of 25–26° C, with a wide diurnal variation of 10–16° C. Another well-investigated species, *A. retroflexus* (McWilliams *et al.*, 1967), consists of several photoperiodic ecotypes which have, however, not been observed in *A. spinosus*. Pandeya and Adhyaru (1969) have reported

population variations in *A. spinosus* otherwise on the basis of seed size and seedling colour.

Portulaca oleracea, another day neutral plant, exhibits a quantitative response. Both the varieties show marked differences in their responses and it is noteworthy that the response of the NL variety is very similar to that of *P. smallii* investigated by Cotter and Platt (1959) inasmuch as that in both the flowering is maximum at a 10-hr photoperiod, while vegetative growth is best at a longer photoperiod.

EFFECTS OF LIGHT INTENSITY

The species under investigation show 2 kinds of growth responses in relation to varying light intensity. First, the NL variety of *P. oleracea* and *A. spinosus* both appear to be obligate heliophytes showing maximum growth in full sunlight and an almost proportionate decrease in growth at lower light intensities. Bakker (1960) has also reported a significant decrease in growth of seedlings of *Cirsium arvense* and *Tussilago farfara*, even at light intensities only slightly lower than full sunlight. In several bulbous species, Wassink (1969) found a linear decrease in total dry weight at reduced light intensities. It is interesting to note that prostrate plants of the NL variety of *P. oleracea* as well as *Eleusine indica*, another locally investigated heliophyte (J. S. Singh, 1969a), tend to become erect under shade, attaining maximum height at the lowest light intensity employed. A similar response of heliophytes (increase in height and decrease in total dry-matter production) has also been reported by Shirley (1936), Burkholder (1936) and Benedict (1941).

Second, the OL variety of *P. oleracea*, *A. arvensis* and *C. album* all grow best at 70 per cent sunlight, showing reduction at greater or lesser light intensities. It is possible that invariably more mesic conditions under partial shade (70 per cent sunlight) allow a better water balance in the plant resulting in a greater photosynthetic surface and, hence, greater dry-matter accumulation in *C. album* and the OL variety of *P. oleracea*. However, in *A. arvensis*, possibly increased photosynthetic efficiency compensates for slightly lesser photosynthetic area at 70 per cent sunlight, as has also been reported in *Stellaria media* (Sinha, 1968). Hughes and Evans (1962) reported that light intensities above 80 per cent and below 20 per cent have very adverse effects on vegetative growth of *Impatiens parviflora*. Likewise, Lockhart (1963) and J. S. Singh (1969b) also demonstrated an inhibitory effect of full solar radiation on growth of pinto beans and *Cassia tora* respectively.

The degree of flowering and seed production appears to depend in general on the extent of vegetative growth. Thus, the flowering and seeding response of all the species studied here can be broadly stated to be of 2

types. On the one hand, the heliophytes (*A. spinosus* and the NL variety of *P. oleracea*) show sharp suppression of flowering with the result that seed formation is almost completely stopped at about 50 per cent sunlight. Such a steep decline in seed production in the shade has also been reported by Bakker (1960) in *C. arvense* and *T. farfara*. On the other hand, species showing better vegetative growth at 70 per cent sunlight exhibit parallel reproductive growth too. Also the seed production per plant at lower light intensities is affected more adversely than the number of flowers per plant. This is largely due to failure of seed setting in a good proportion of flowers.

Generally the species which maintain themselves successfully at less than full sunlight have the compensatory capability of diverting assimilates from root to leaf production; the increased relative amount of leaf tending to compensate for the reduction in light intensity (Whitehead, 1969). In species showing suppression of growth by lowered light intensity (e.g. *Datura stramonianum*) there is little or no diversion of assimilates to compensate for lower energy increment (Whitehead, 1969). The former have a better chance of establishment in relatively shady crop fields. Indeed, *A. arvensis*, *C. album* and the OL variety of *P. oleracea* exhibit more luxuriant growth in between the thinly-grown crop plants than in open habitats. Thus, apart from the methods of weed control already in practice, a modification in the cropping system, producing greater crop foliage in the shortest time, may be advocated to control the recurrence of such weeds.

Our data suggest that, in the Upper Gangetic Plain, growth and reproduction of all the investigated weeds are affected more by the light régime in different habitats than the day length. In the Upper Gangetic Plains (approximately 25–30° N latitude), according to the calculations of Gorczynski (1945), on average the day-length at 28° N varies from 10.4 hr (December) to 13.9 hr (June). From the view point of their photoperiodic requirements, all the species are well adapted to flower in this range; the day neutrals flowering best at 10–12 hr, and the critical photoperiods of the long-day as well as short-day species (10–11 hr and 14.5 hr respectively) being well within the range.

ACKNOWLEDGEMENTS

We are greatly indebted to Prof. R. Misra (Varanasi) for his valuable suggestions, and to Dr S. R. Gupta (Jhansi) for allowing us to use some of his unpublished data on *Chenopodium album*. Grateful thanks are also due to the United States Department of Agriculture, Agriculture Research Service, for financial support under the PL 480 funds.

Résumé

Effets de la photopériode et de l'intensité lumineuse sur la croissance de certaines plantes adventices des champs cultivés (K. P. Singh et Brij Gopal)

L'envahissement des champs cultivés par diverses espèces de plantes adventices à différentes étapes de la croissance des cultures constitue un sérieux problème pour l'agriculture. Pour déterminer quelles sont les étapes vulnérables du cycle biologique de ces mauvaises herbes en relation avec les conditions lumineuses de la terre de culture, on a fait une étude des réactions de croissance de quatre mauvaises herbes communes, à savoir: *Anagallis arvensis*, *Chenopodium album*, *Amaranthus spinosus* et deux variétés sauvages (OL et NL) de *Portulaca oleracea*, à différentes photopériodes et intensités lumineuses. *A. arvensis* et *C. album* sont des plantes annuelles hivernales qui croissent surtout dans les champs de Blé, tandis que les deux autres espèces croissent toute l'année, généralement dans les lieux découverts entre les cultures ou dans les champs abandonnés.

On a observé que *A. arvensis* est une plante de jour long dont la photopériode critique est comprise entre 10 et 11 heures, et que *C. album* est une plante de jour court dont la photopériode critique est de 14,5 heures. Les deux autres mauvaises herbes sont indifférentes à la longueur du jour. Mais ces quatre mauvaises herbes présentent une réaction quantitative à la durée du jour

en ce sens que la croissance végétative maximale et la floraison, et la période la plus courte de mise à fleurs, sont observées pour une photopériode particulière.

On a constaté que l'intensité lumineuse est un facteur relativement important de la croissance végétative et reproductive. *A. spinosus* et la variété NL de *P. oleracea* sont des héliophytes obligatoires dont la meilleure croissance s'effectue en plein soleil. Lorsque la lumière solaire est réduite d'environ 50%, la croissance diminue sensiblement et la floraison et la montée en graines sont complètement arrêtées. D'autre part, chez les deux autres espèces et chez la variété OL de *P. oleracea*, la croissance maximale et la floraison sont atteintes à 70% du plein soleil. Si l'intensité lumineuse est réduite encore pour ne plus atteindre que 20 à 30% du plein soleil, l'effet inhibiteur est très sensible, notamment sur la production de graines.

Les auteurs concluent que ces quatre plantes adventices sont bien adaptées aux conditions lumineuses des plaines de la haute vallée du Gange pour ce qui concerne les besoins en photopériodes. Toutefois, l'intensité lumineuse joue un rôle important dans la vie de ces mauvaises herbes et il est possible qu'une modification du système de culture qui aurait pour effet d'accroître la couverture végétale dans le temps le plus court contribuerait à les neutraliser.

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II The effect of temperature on plant growth, development and yield

II Effet de la température sur la croissance, le développement et le rendement des plantes

The effect of temperature on plant growth, development and yield

J. F. Bierhuizen
Department of Horticulture,
Agricultural University,
Wageningen (Netherlands)

INTRODUCTION

Many physiological processes in higher plants proceed at temperatures between 0° and 40° C. Thus a wide temperature range for growth exists, although some crops are more adapted to relatively low, moderate or even high temperatures. Breeding has extended this range in the last decades. From an agronomic point of view, however, temperature is still of vital importance for plant growth, development and yield.

Provided the temperature requirement of a certain species is known, a choice of a favourable area can be made, since long term averages of annual and diurnal variation in temperature are often available throughout the world. Moreover, at sub-optimal temperatures, an increase in air temperature (glasshouse, plastic cover) can be realized, but such installations often require a high capital investment. The application of such techniques is only feasible when high capital returns are expected. Prevention of excessive air temperature and moderate changes in soil temperature are more often applied.

Because the effects of temperature on plant growth, development and yield are numerous, and a vast amount of literature has been published concerning them, only the agricultural application will be discussed here.

SOIL TEMPERATURE REQUIREMENTS FOR GERMINATION AND EMERGENCE

Some species germinate as soon as external conditions, such as temperature, water availability and oxygen concentration, are favourable. Sometimes inhibitors in the pulp of the seed prevent germination directly after harvest (tomato, cucumber), whereas often an after-ripening effect of some days to several months is necessary independently of the presence of inhibitors. Cold temperatures between 0 and 10° C, for some weeks to

several months have also been found necessary to break dormancy (apple, pear, peach). The effect of temperature on germination and emergence will be discussed, assuming that the above-mentioned prerequisites have been satisfied.

In the nineteenth century, great attention was paid to temperature effects on germination and plant growth. Sachs distinguished three cardinal points of vital activity: a minimum temperature below which no activity occurs, an optimum at which the highest activity occurs, and a maximum temperature above which the activity is zero again. Haberlandt, cited by Grafe (1914), gave cardinal temperature points for the germination of seeds of a large number of plants (Table 1). Pfeffer (1903) already realized that "the cardinal points can never be determined with more than approximate accuracy, since their position is related to the external conditions, the duration of exposure, the age of the plant and its previous treatment".

It is obvious, therefore, that numerous methods for evaluating the effect of temperature on germination and subsequent plant growth have been recommended in the past. An extensive review has been given by Klages (1942) on the advantages and disadvantages of the various temperature efficiency indices such as length of the growth period, heat unit and exponential and physiological indices. Although, in general, metabolic processes double their rate with an increase in temperature of 10° C (Q_{10}), growth expressed as germination or stem elongation often shows, within a certain range, a linear response between minimum and optimum temperature. A higher correlation will be obtained with the exponential index for a Q_{10} of 2.0 and with a heat unit index in the case of a linear response. In a small temperature range, however, both methods may give the same accuracy of prediction. Since the calculation of heat units is carried out more easily, the application of this index has drawn wide attention.

TABLE 1. The cardinal temperatures for the germination of some important agricultural crops (Haberlandt, cited by Grafe, 1917)

Plant	Cardinal temperature ($^{\circ}\text{C}$)			Number of days necessary for germination at different temperatures ($^{\circ}\text{C}$)			
	Minimum	Optimum	Maximum	4.3	10.2	15.7	19.0
Wheat	3- 4.5	25	30-32	6	3.0	2.0	1.7
Rye	1- 2	25	30	4	2.5	1.0	1.0
Barley	3- 4.5	20	28-30	6	3.0	2.0	1.7
Oats	4- 5	25	30	7	3.7	2.7	2.0
Maize	8-10	32-35	40-44	—	11.2	3.2	3.0
Rice	10-12	30-32	36-38	—	—	—	—
Grass	3- 4	26	30	—	6.5	3.2	3.0
Flax	2- 3	25	30	8	4.5	2.0	2.0
Tobacco	13-14	28	35	—	—	9.0	6.2
Hemp	1- 2	35	45	3	2.0	1.0	1.0
Sugar-beet	4- 5	25	28-30	22	9.0	3.7	3.7
Red clover	1	30	37	7.5	3.0	1.7	1.0
Lucerne	1	30	37	6	3.7	2.7	2.0
Peas	1- 2	30	35	5	3.0	1.7	1.7
Lentil	4- 5	30	36	6	4.0	2.0	1.7
Vetch	1- 2	30	35	6	5.0	2.0	2.0

A heat unit (S) in degree days is assumed to be a constant for a particular growth stage, and may be calculated by multiplying the ambient temperature (T) minus a minimum temperature (T_{\min}) in degrees centigrade by the period of emergence (t) in days or

$$S = (T - T_{\min}) \times t. \quad (1)$$

A plot between T and the reciprocal value of t should give a linear relationship from which the unknown values of S (the slope) and T_{\min} (the intercept) can be calculated according to

$$T = \frac{s}{t} + T_{\min} \quad (2)$$

At constant temperatures, in the laboratory, the above-mentioned equations can be readily used. However, diurnal thermoperiodicity seems to be of importance for germination as well (Koller *et al.*, 1962). Studies under field conditions, therefore, with varying sowing dates during the season may give a more direct practical application. In such experiments either an overall average temperature during the germination period can be calculated from which a minimum temperature can be subtracted ($T - T_{\min}$), or summations can be made of average daily temperatures minus a minimum temperature [$\Sigma(T - T_{\min})$]. These two methods of calculation might give a different heat unit when the average daily temperature is lower than T_{\min} .

Geslin (1944) carried out sowing experiments at constant temperatures in climate chambers and at diurnal temperature variations in the field. The heat unit was 40.6 degree days (Fig. 1, example I) for germination of wheat seeds in petri dishes between wet filter papers at constant temperatures. The heat unit for emergence, in

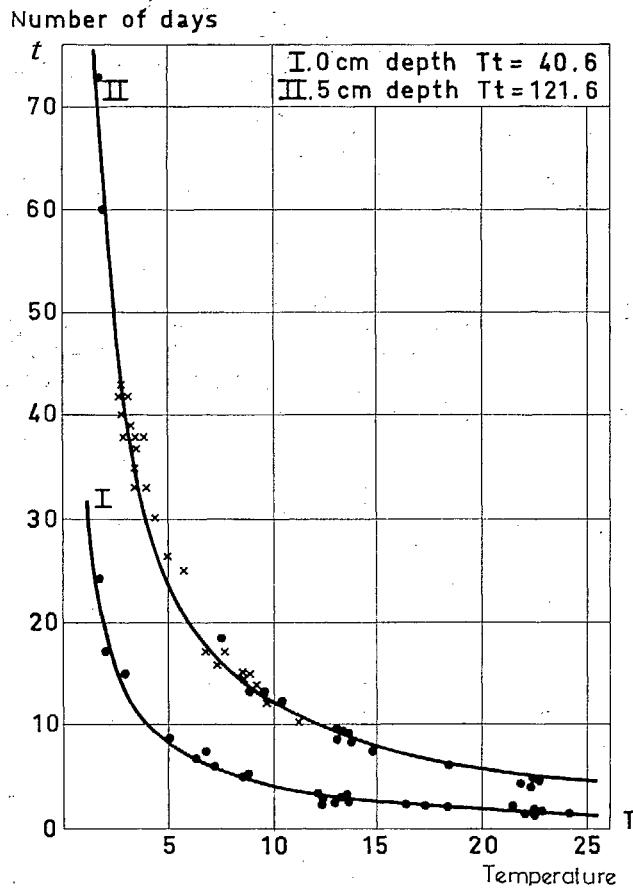


FIG. 1. The effect of soil temperature (T) on the duration in days (t) of emergence (I) and germination (II) (after Geslin, 1944).

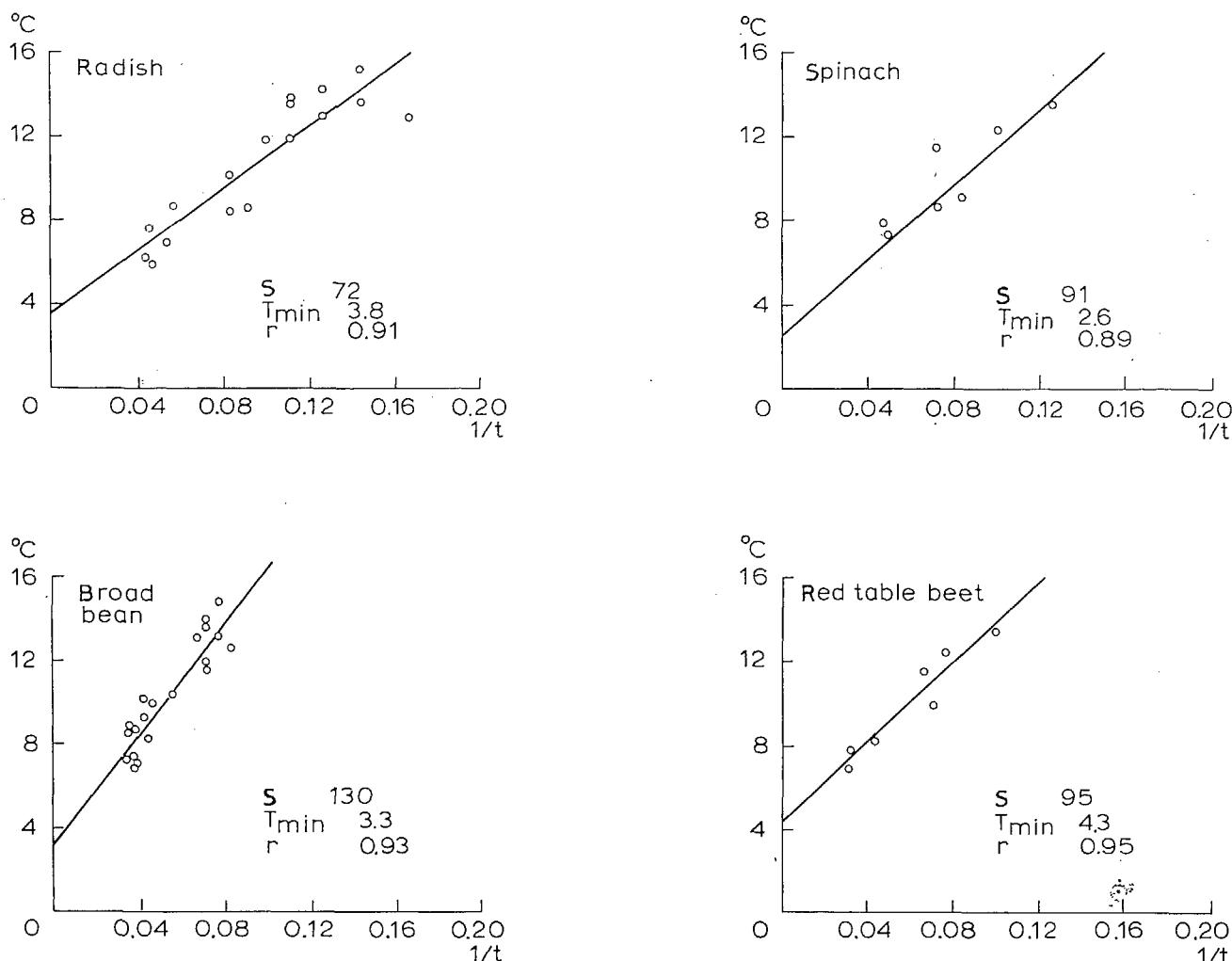


FIG. 2. The relationship between average soil temperature in $^{\circ}\text{C}$ and the reciprocal duration for 50 per cent emergence (days^{-1}) (S is the heat sum in degree days, T_{\min} the minimum temperature for emergence in $^{\circ}\text{C}$ and r the correlation coefficient, after Bierhuizen and Feddes, 1969).

which the temperature at the sowing depth of 5 cm was used, was 121.6 degree days (Fig. 1, example II). In the latter case the points in the figure represent constant temperature experiments between 0° and 24°C and oscillating temperatures in the field between 0° and 18°C . No significant differences were observed between laboratory and field data.

It is evident from the figure that a small increase in soil temperature near the minimum temperature results in a large decrease in time for emergence, whereas the time reduction is small at higher temperatures. A practical consequence is that early emergence can be achieved relatively cheaply with plastic cover, mulching, etc. A physical approach to heat transport and heat capacity of the soil is beyond the scope of this paper. It is obvious

that the heat unit for germination depends to a large extent on the depth measurement of the soil temperature, which varies widely in the top 10 cm soil layer. In the top layer the variation in soil moisture content is largely due to evaporation and rainfall, but soil moisture measurements at this depth are extremely difficult. Since germination depends also, to a great extent, on the prevailing moisture conditions in the immediate surroundings of the seed, it could affect the heat unit under too wet conditions (resulting in lack of oxygen) or too dry conditions (lack of moisture).

Sowing experiments were carried out in spring at various ground water levels and in various soil types, which involved different moisture and temperature levels (Bierhuizen and Feddes, 1969). In Figure 2, the

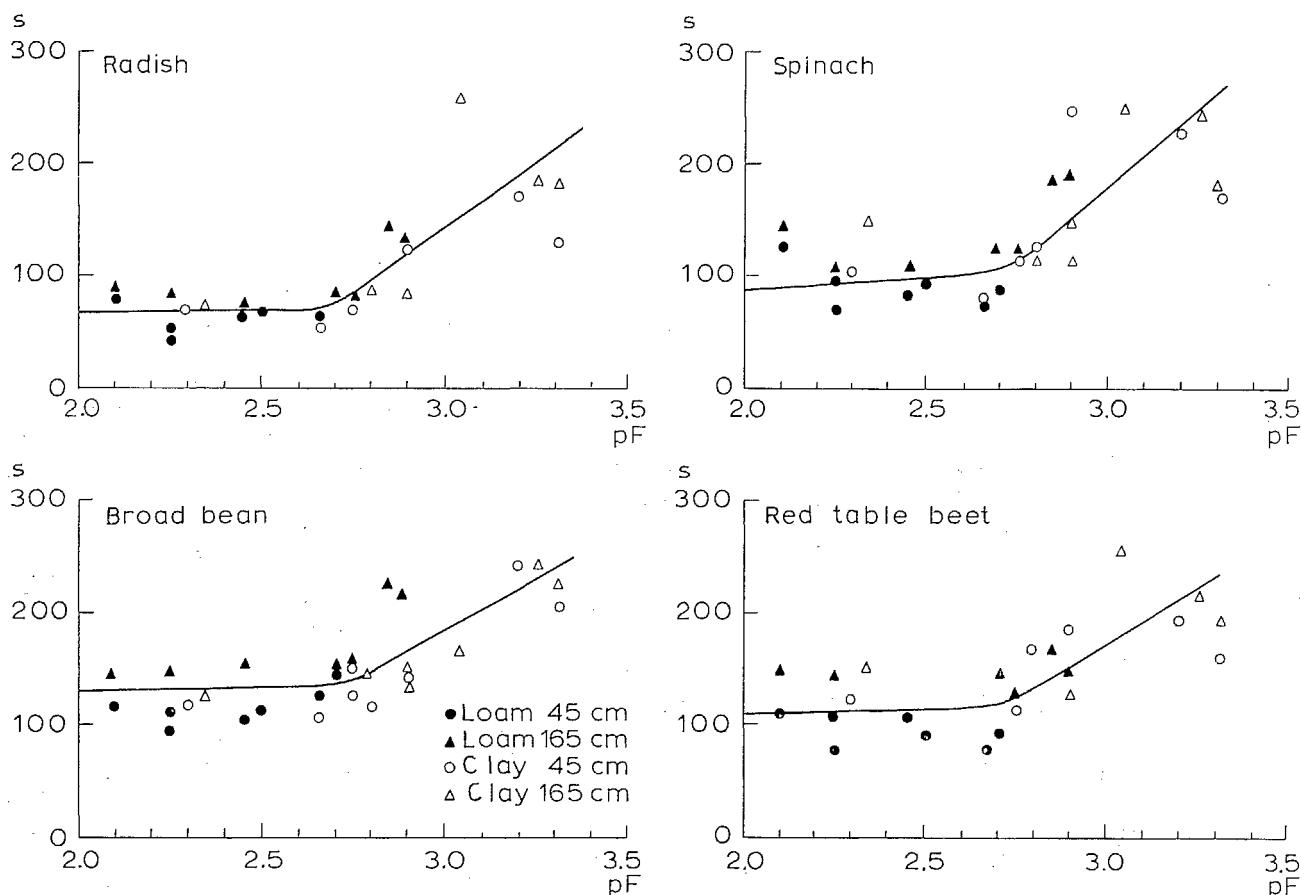


FIG. 3. The effect of soil moisture tension (pF) on heat sum (after Bierhuizen and Feddes, 1969).

calculated average temperature from measurements at the 3 cm sowing depth is represented versus the reciprocal of time for 50 per cent germination, for those treatments in which a favourable moisture condition was present. In this way, according to equation (2), a linear relationship was obtained from which the heat unit and the minimum temperature could be calculated. Thereafter, the heat unit of all treatments was calculated, according to equation (1), and plotted versus the average soil moisture tension in pF of the top layer for the first 5 days after sowing (Fig. 3). From this figure it is evident that the heat unit rises at pF values higher than 2.6. There also seems to be a tendency for a rise to occur in the heat unit below a pF of 2.0. In experiments at constant temperatures and soil moisture tensions, Feddes (1971) observed that below field capacity (pF 2.0) and above pF 2.7 the time required for emergence increased with increasing values of pF, whereas the percentage of final emergence was far less than 90–100 per cent (Fig. 4).

A low value of T_{\min} does not imply a low heat unit, as may be seen already from Figure 2. The heat unit

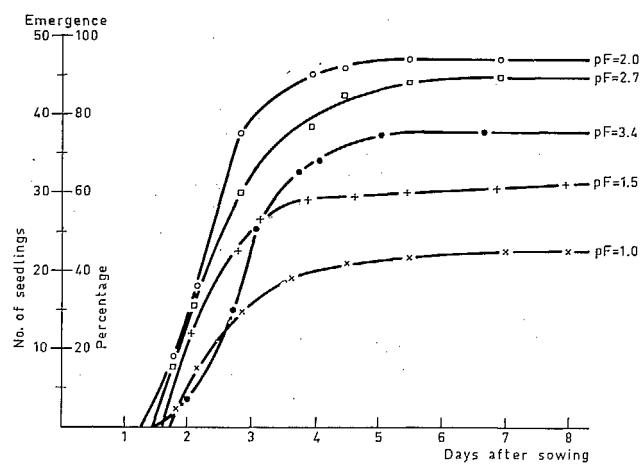


FIG. 4. The effect of soil moisture tension on germination (Feddes, 1971).

TABLE 2. Heat units of various agricultural crops for germination and emergence (after Tamm, 1933)

Plant	Heat unit	Plant	Heat unit
Spring rye	44	Peas	90
Winter rye	46	Oats	90
Winter wheat	47	Hemp	96
Spring wheat	52	Flax	98
White mustard	60	Red clover	99
Cole-seed	60	Horse beans	117
Hairy vetch	65	Lucerne	119
Lentil	67	Broad beans	127
Winter barley	70	White clover	134
Spring barley	75	Yellow lupins	139
Common vetch	80	Blue lupins	140
Crimson clover	83	Serradella	167

will largely depend on the permeability of the seed-coat to moisture and oxygen; the surface-volume ratio of the seed may be important as well. The variation in heat units for different species is shown in Table 2, after Tamm (1933).

In summary, one might conclude that the heat unit concept for germination can be applied under natural conditions. The calculated heat unit, however, depends to a large extent on the depth of soil temperature measurement and on the prevailing soil moisture conditions. Practical methods for increasing soil temperature in the range near T_{\min} result in much earlier emergence.

SOIL AND AIR TEMPERATURE REQUIREMENTS DURING THE VEGETATIVE AND GENERATIVE PHASES

Following germination, the soil temperature may still influence the development of the leaf area index (LAI = the leaf surface per unit soil surface) of the young seedling. Gradually, however, air temperature and other climatic factors, such as light, become of greater importance for the vegetative and the generative phases.

It should be kept in mind that, for each species, a favourable soil temperature should be maintained for water and ion uptake. It has been shown by Weatherley (1963) that the root resistance for water uptake depends on the metabolic activity of the root cells. At sub-optimal temperatures the water uptake increases in the order of 10 per cent $^{\circ}\text{C}$ increase in soil temperature. On the other hand, water transport in the xylem vessels and in the leaves increases only in the order of 1 per cent $^{\circ}\text{C}$ increase in temperature. The latter increase can be ascribed mainly to changes in viscosity. The range over which sub-optimal soil temperatures occur depends on the species and is low, for example, for lettuce ($4-10^{\circ}\text{C}$), moderate for tomato ($10-16^{\circ}\text{C}$), and high for cucumbers. In the latter case, wet straw bales are often applied in order to increase soil temperature.

The soil temperature during the day is often of greater importance than that during the night, since it is necessary to maintain a favourable internal crop-water status in the presence of a high evaporation rate during the day. In practice, the diurnal variation in soil temperature lags behind the diurnal evaporative demand. This aspect is of great importance when comparing field experiments with those in a phytotron. In the latter, day and night temperatures are applied to plants which are usually grown in small containers, in which the phase lag between soil temperature and air temperature is much smaller than in big containers or in the field. With cotton for example (Stern and Bierhuizen, unpublished data), the application of a sub-optimal night temperature resulted in a large reduction in yield when grown in a big container. No significant decrease was observed in a small container, however, due to the relatively higher soil temperature during the day.

The effect of air temperature will be discussed only in relation to some aspects of photosynthesis and respiration, dry and fresh weight production and the application of heat units.

Photosynthesis often shows a sub-optimal range, a fairly wide optimum, and a decrease above 35°C . In the sub-optimal range, a low temperature (e.g. lettuce), an average (e.g. tomato) or a high temperature (e.g. melon and cucumber) requirement exists (Fig. 5, after Klapwijk, 1969a). This diagram, of course, largely depends on the prevailing light conditions. Respiration doubles its rate with an increase in temperature of 10°C . Above 45°C , however, a sharp decline in respiration occurs due to damage of the respiratory mechanism (Fig. 6, after Klapwijk, 1969b).

Hence the net gain in dry weight production (photosynthesis minus respiration) varies with temperature, as does cell division, elongation and the formation of flowers (shown for tomatoes in Figure 6, after Klapwijk, 1969b). The highest net gain in dry weight occurs at a temperature of 20°C , whereas the rate of development is relatively slow, resulting in a heavy crop with large cells and a late development of trusses. At a high temperature the net gain in dry weight is smaller, but the development is more rapid, resulting in a light crop with an earlier formation of trusses. The total yield of

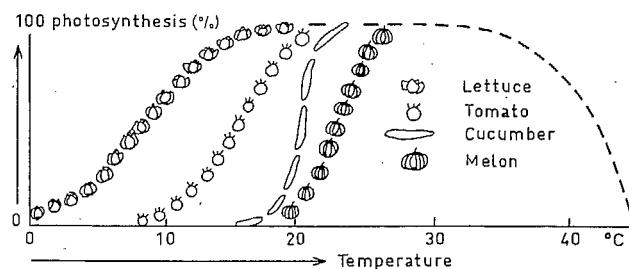


FIG. 5. The effect of temperature on photosynthesis (after Klapwijk, 1969a).

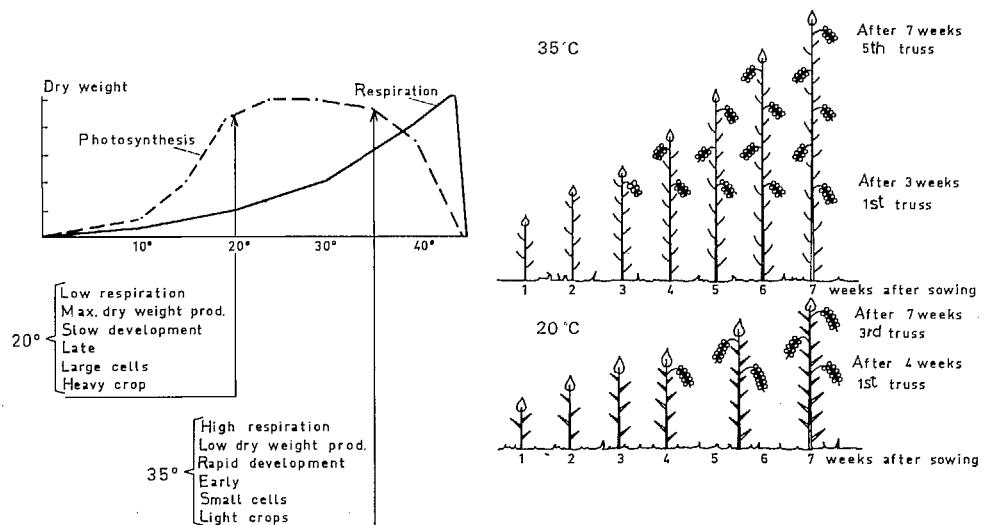


FIG. 6. The effect of temperature on dry weight production and earliness of tomatoes (after Klapwijk, 1969b).

tomatoes in the latter case might be lower, but a higher price due to the earliness of crop formation often favours the application of higher temperatures for tomatoes. During spring, when light intensities are increasing, step-wise increases in day and night temperatures are applied to tomatoes in glasshouses. Due to the increased daily amount of light energy, the net gain in dry weight increases, permitting faster development of the plant as a result of higher temperatures.

Three important factors in the above statements should be discussed, namely the leaf area index, source and sink relations and the ageing of the leaves.

With an increase in leaf area index, the lowest leaf in the canopy receives less light and may reach a (light) level at which photosynthesis is less than respiration. Davidson and Philip (1958) calculated the relationship between leaf area index and net gain of production and also showed that the optimal leaf area index shifts to higher values at higher light intensities. An increase in temperature, on the other hand, reduced the optimal leaf area index. For tomatoes defoliation from below is a normal practice and should be beneficial for dry matter production. However, the acceleration of fruit colouring and the reduction of diseases are important consequences of defoliation as well. Recent calculations have shown, however, that respiration depends also on the supply of assimilates, and canopies with a high and a low leaf area index will more or less respire the same total amount (de Wit *et al.*, 1969).

The demand for assimilates in a generative part is often fulfilled by a supply from the neighbouring leaves or those leaves which have a direct transport link. Removing the generative part or taking away the sink may result in a decrease of net photosynthesis of these leaves, as was observed with wheat (Evans, personal

communication). Net photosynthesis of coffee (a shade plant) is very low in comparison with that of other species. After a dark period, however, nearly the same net photosynthesis rates may occur. Because of the slow growth rate and the relatively large amount of starch in the leaves, it might be assumed that the sink is small, and will be rapidly saturated after illumination (Nunez *et al.*, 1968). It seems evident that the reduction in net photosynthesis at a constant light intensity after darkness is not due to stomatal closure, since transpiration does not alter. An increase in photorespiration must, therefore, occur resulting in a rise in the internal CO₂ concentration and a reduction in the CO₂ gradient for net photosynthesis. In such a case the effect of temperature is of particular importance. In Figure 7, the effect of temperature and light on net photosynthesis of 4 varieties of coffee is shown (after Nunez *et al.*, 1969). It is obvious that net photosynthesis is already saturated at a fairly low light intensity. At temperatures above 24°C this saturation level decreases by approximately 10 per cent per degree increase in temperature. The cultivar S 228-23 (Fig. 7) is better adapted to unfavourable temperatures. Growth rate also decreased above 24°C, whereas transpiration increased, resulting in a large increase in the transpiration coefficient. In practice, shade trees are applied in coffee cultures in order to reduce excessive temperatures.

Ageing of the leaves may be initiated and accelerated by too high temperatures. This will shorten the growth period for net dry weight production. Fortanier (1970) assumes that the senescence of tulip leaves is induced via the newly initiated bulbils. Air temperatures above approximately 20°C, however, greatly stimulate ageing processes. Thus a sea climate, such as exists in the Netherlands, having a smaller annual variation in tem-

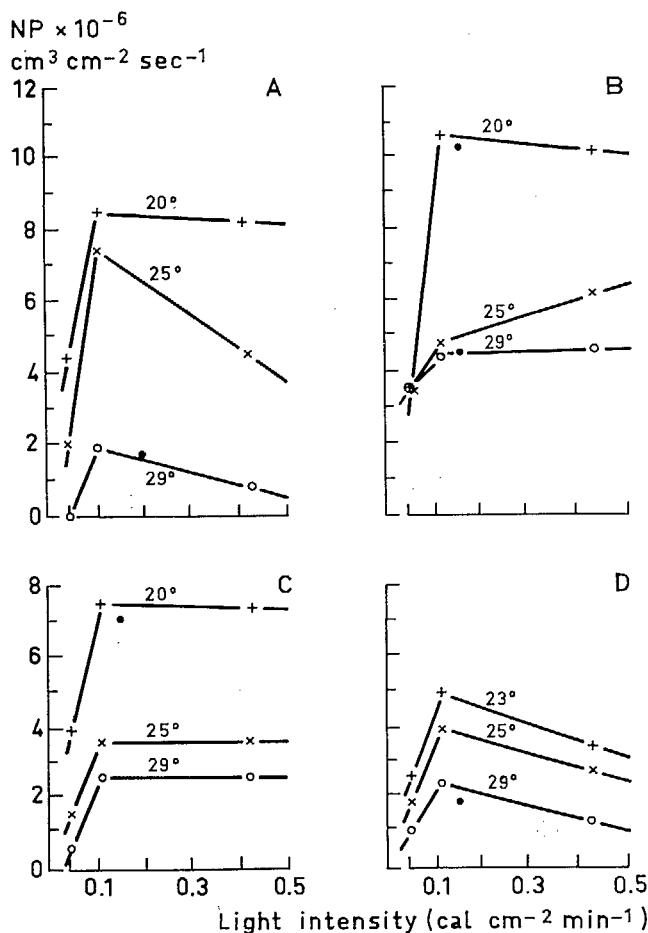


FIG. 7. The effect of light intensity and temperature ($^{\circ}$ C) on net photosynthesis (NP) in plants of *Coffea arabica* from a high altitude in the region of Gimma, Ethiopia (A), and from a selection S288-23, India (B), and in plants of *Coffea canephora* (*robusta*), from BP42 y 809 a selection obtained in Yangambi starting from Java material (C) and from a selection SA34 (D) from Java (after Nunez *et al.*, 1969).

perature, often exhibits a larger production of bulbs than a land climate. In practice, temperature and also other environmental factors may be unfavourable for some time during the growth season without influencing the yield to any great extent. However, in cases where an unfavourable condition leads to an irreversible process such as senescence, a large effect on production must be expected.

Apart from germination, heat units have also been used in predicting harvest time. This method is of special importance for crops used in canning and freezing industries in order to obtain a regular supply of the raw materials. Although a high degree of accuracy in predicting harvest dates is obtained within a certain area, heat units may vary consistently from one year to another and also during the season.

An important aspect in applying heat units is the question of whether temperature or light or any other environmental factor is the main limiting factor for growth and yield. In temperate zones the light intensity is often the main limiting factor for growth. In such a case an evaluation on the basis of total radiation should give a better result than on a basis of heat units. Since there is a high correlation between radiation and temperature, a heat unit may still give reasonable results. In spring, however, the heat unit is lower than in autumn, under conditions of total radiation which are otherwise similar. In comparing heat units and total radiation for spring and autumn crops in a glasshouse, it can be shown that yield and harvest are better estimated on the basis of total radiation (Fig. 8, after Bierhuizen and Feddes, 1969).

In a glasshouse, however, the temperature is higher and light intensity is lower than in the field. It may be expected that, under such conditions, temperature would become a less and light a more limiting factor for growth. For lettuce, however, under outdoor conditions in Finland (Suhonen, 1969) and south-west regions of the Federal Republic of Germany (Hartman, 1969), the seasonal variation in heat units may be ascribed also to variations in light intensity.

In summary, soil temperature is an important factor in the vegetative and generative phase of crop development. In this respect more attention should be drawn to the effect of soil temperature in comparing field and container experiments in the phytotron. An increase in air temperature, for example for tomatoes, accelerates the development (light crop) resulting in an earlier yield, whereas lower temperatures exhibit a heavy late crop, often with higher yields. Extreme air temperatures must be prevented in those cases where early senescence occurs or photorespiration is important. The heat unit index can be applied in predicting harvest, although calculation on the basis of total radiation is more advisable.

TEMPERATURE REQUIREMENTS FOR FLOWER FORMATION

In temperate regions a cold requirement (vernalization) is often necessary for the initiation or acceleration of flowering. It is well known, for instance, that winter cereals must be sown before the winter period in order to fruit within 12 months. Spring cereals, however, flower soon after spring and often cannot survive winter cold. According to Chouard (1960), the effect of vernalization depends on the following factors:

1. A minimum imbibition of water is necessary for occurrence of the low temperature vernalization process and at the same time imbibition should be low in order to hinder seedling growth.
2. The vernalization process cannot be initiated before a period of activation at higher temperatures.

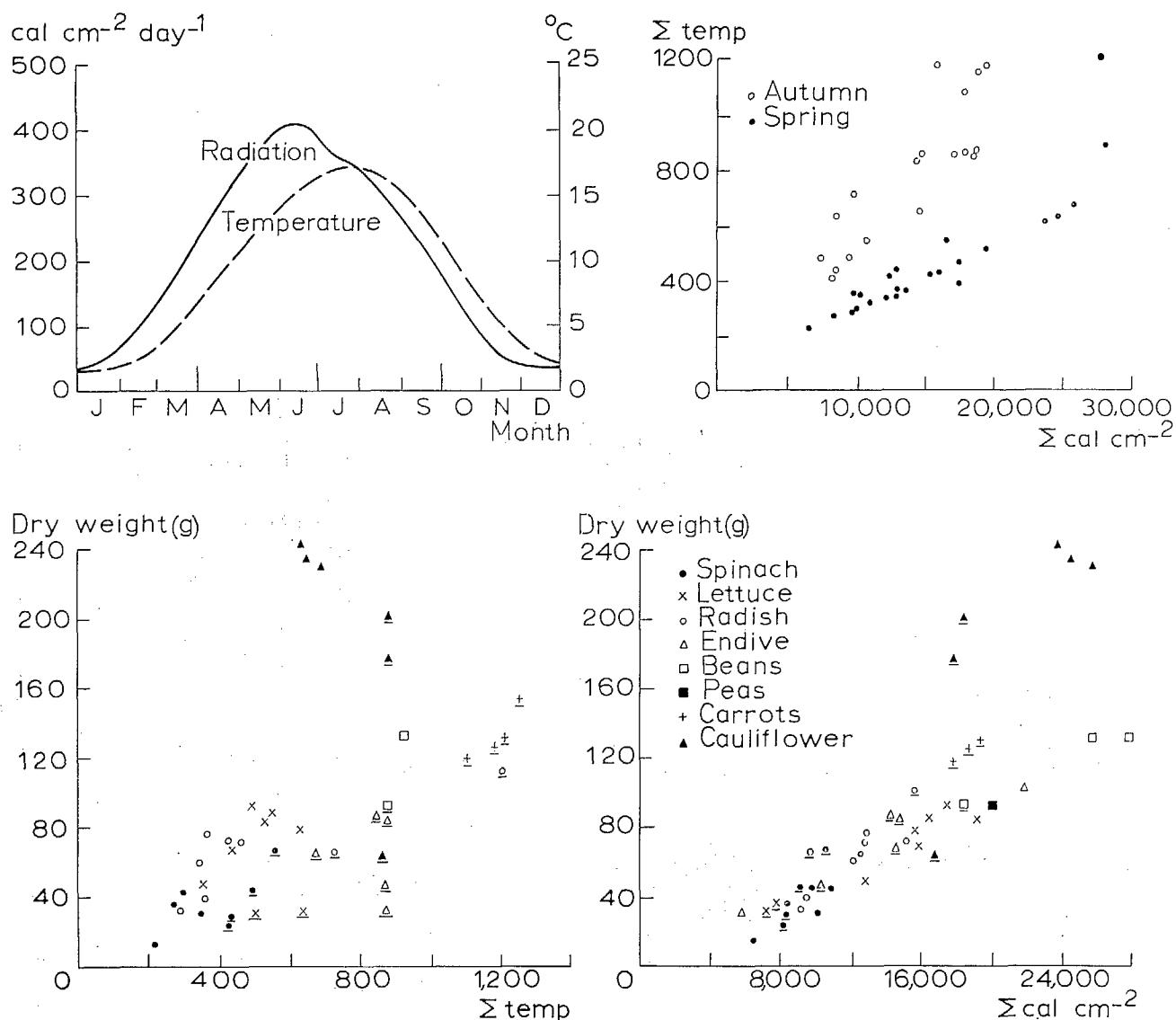


FIG. 8. The relationship between radiation and temperature and that between total radiation and heat unit for spring and autumn crops and the effect of heat unit and total radiation on dry matter production of spring and autumn crops (after Bierhuizen and Feddes, 1969).

3. The presence of air (oxygen) is necessary.
4. An appropriate duration and temperature of chilling is necessary. The optimum range of chilling usually varies between +1° and +7° C. The effect decreases from 0° to -4° and disappears completely below -6° C. It also decreases above +7° C and disappears completely between 12° C and 14° C. (See Fig. 9, after Hänsel, 1953.) Above 15°-17° C de-vernalizing effects of high temperatures become effective.

The cold requirement is necessary for winter annuals which are sown in the autumn and flower and fruit the

following year. Some spring sown species, however, also require some cold for the acceleration of flowering. Biennial species with a vegetative phase in the first year and a generative phase in the second year often require chilling (plant vernalization) to induce the latter phase. The cold requirement of monocotyledons and dicotyledons has been reviewed by Napp-Zinn (1961) and a physiological analysis on vernalization is given by Purvis (1961).

The mechanism of vernalization is not yet completely understood. It is known that most species which react

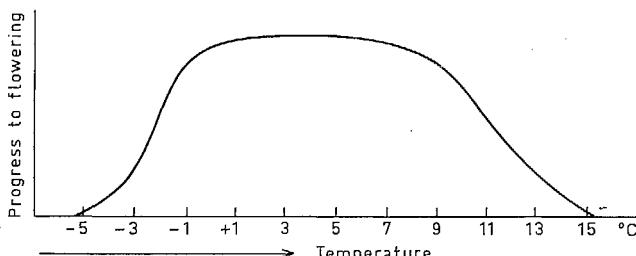


FIG. 9. The effect of temperature during vernalization on flowering response (after Hänsel, 1953).

to vernalization behave as "long day" plants. The relationship between vernalization and photoperiodicity is the more evident because in some cases (e.g. rye) a short day can substitute for chilling. Wellensiek and Doorenbos (1956) distinguished 4 groups of plants with regard to induction and occurrence of flowering: (a) no specific cold requirement is present (tobacco, tomato); (b) during realization a cold requirement is necessary (Brussel sprouts); (c) a cold requirement at any time is necessary for induction and moderate temperature for realization (wheat, endive, sugar-beet); (d) a juvenile period must precede a cold treatment for induction and a moderate temperature for realization (*Hyocyanus*). For the realization of flowering most species must also have reached a specified stage in development (e.g. number of leaves).

It should be mentioned here that some species (such as spinach and rice) are induced to flower by high temperatures. This phenomenon is less common than vernalization.

The most extensive studies on temperature requirements have been made with bulbous and tuberous plants, in which anatomical studies of the primordia have frequently been made simultaneously in the course

TABLE 3. Temperature treatments ($^{\circ}\text{C}$) and the length of each stage in weeks (w), for growth cycles of 12, 8 and 6 months, in tulips

Stage	12 months		8 months		6 months	
Heat treatments						
After ripening	4 w.	25°	3 w.	25°	1 w.	35°
Organ formation	4 w.	20°	3 w.	17°	3 w.	17°
Organ retardation	6 w.	17°	—	—	—	—
Cold treatment						
First rooting	6 w.	10°–5°	4 w.	9°	4 w.	5°
Termination dormancy	10 w.	5°–3°	4 w.	5°	5 w.	5°
Imposed dormancy	6 w.	3°–6°	—	—	—	—
Growth						
Leaf growth	6 w.	6°–11°	6 w.	12°	5 w.	18°
Bulb growth	6 w.	11°–15°	6 w.	15°	6 w.	15°
Senescence	4 w.	15°–17°	2 w.	24°	2 w.	24°

of the temperature treatments (Hartsema, 1961). Various stages in development have been distinguished for which different temperature optima exist (Table 3; after Fortanier, 1970).

From a practical point of view, one might conclude that, in temperate zones, the cold requirement is normally satisfied during winter. In cases where an artificial cold treatment is given (e.g. for seeds, bulbs, chicory roots), subsequent development often requires an artificial temperature, because growth is out of phase from the existing annual variation in temperature. Chilling is important for shortening the breeding cycle (Table 1), earliness of emergence and maintenance of year-round cultures (Wellensiek, 1962). In a recent publication (Wellensiek, 1970) a more extensive review of temperature and day-length requirements of vegetables is given.

Résumé

Effet de la température sur la croissance, le développement et le rendement des plantes (J. F. Bierhuizen)

L'auteur examine l'influence de la température sur la germination, le stade végétatif et génératif et la mise à fleur.

La température du sol influe fortement sur la germination et la levée (fig. 1). La température minimale et l'unité de chaleur nécessaire pour la levée dépendent de l'espèce (tableaux 1 et 2) et peuvent être calculées d'après l'équation n° 2 (fig. 2). La valeur calculée de l'unité de chaleur est fonction, d'une part, de la profondeur à laquelle les mesures de la température du sol ont été effectuées et, d'autre part, de l'humidité du sol (fig. 3 et 4).

Dans le stade végétatif et génératif, nous pouvons distinguer les plantes d'après leur besoin en température

pour la photosynthèse (fig. 5). Une température de l'air élevée, par exemple, provoque chez la Tomate une faible augmentation de la matière sèche, un développement rapide et une récolte relativement faible et précoce (fig. 6). Elle peut aussi accélérer la sénescence (Tulipe) et réduire la photosynthèse nette en cas de forte photo-respiration (fig. 7). Bien que la méthode employant l'unité de chaleur puisse être utilisée pour prévoir la date de la récolte, c'est plutôt la méthode fondée sur le rayonnement qui serait à conseiller (fig. 8).

Les besoins en température pour la mise à fleur et la floraison dépendent de l'espèce. Le tableau 3 présente pour les oignons de Tulipe un schéma détaillé des besoins en température aux différents stades de développement. La vernalisation fait généralement apparaître un optimum entre + 1 et + 7° C (fig. 9).

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The effect of temperature on the quality of hops

L. P. Smith
Meteorological Office
Bracknell (United Kingdom)

INTRODUCTION

This paper deals with the influence of mean air temperature between time of flowering and harvest on the quality of hops, as measured by α -acid content. The data on which the relationships are based have come from trials in the United Kingdom and several European centres.

TRIALS AT WYE, KENT (UNITED KINGDOM)

The first evidence of the influence of temperature was obtained in 1965 from the results of trials carried out at Wye during the years 1961–64 on 5 hop varieties, namely, S.978, S.1478, Fuggle, Northern Brewer and Hallertau. The α -acid content of all varieties was highly correlated with the mean July–August temperature. Taking the mean percentage of all 5 varieties; the results are shown in Table 1.

Thompson (1968) suggested that "the limited evidence available tends to indicate that mean air temperature in August in this country is the critical factor influencing the quality of hops". He quoted experiments carried out in France, which suggested that sunshine is important during development and ripening of the cones and

German research which claimed, however, that hot, dry sunny summers gave low α -acid values. He also quoted Burgess (1964), who thought that August mean air temperature was critical.

INTERNATIONAL TRIALS

The investigation was taken further with the aid of information from a series of international hop variety trials sponsored by the Hops Liaison Committee of the European Brewery Convention (Brown *et al.*, 1970).

These trials were conducted in 6 countries and included the varieties S.1478, Fuggle, Northern Brewer, Hallertau and Spalt. Meteorological and crop stage data were available and samples of the hops were analysed for α -acid in the same laboratory.

Occasionally the results were spoilt by the incidence of disease or storm damage, and the crop stages in Czechoslovakia were somewhat difficult to interpret as the number of days between full flower and harvest in that country was much less than elsewhere, suggesting that the interpretation of the earlier data needed to be modified.

A plot of α -acid content against the mean July–August temperatures revealed the existence of an optimum temperature. The results are shown in Figures 1–3, and can be summarized as follows:

The optimum temperature appeared to be between 16° and 17° C. The quality of S.1478 and Spalt appeared to decrease at a similar rate either side of the optimum. In Fuggle, Northern Brewer and, to a lesser extent, Hallertau, the decrease was far more evident on the cooler side; temperatures higher than the optimum had a less adverse effect.

Attention was also paid to the soil moisture status, inferred from potential transpiration and rainfall, but this revealed no consistent effect on quality.

TABLE 1. Influence of temperature on α -acid content of hops

Year	α -acid content (%)	Mean July-August temperature (°C)
1961	4.9	14.4
1962	5.3	15.4
1963	5.2	15.3
1964	6.7	16.7

● England ■ Czechoslovakia + Denmark
 ○ Belgium □ Federal Republic of Germany

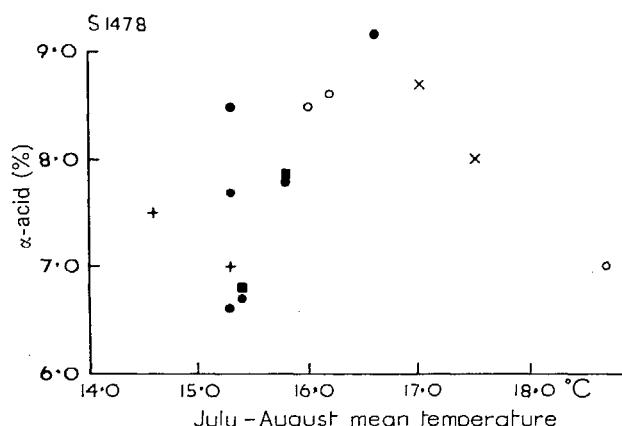
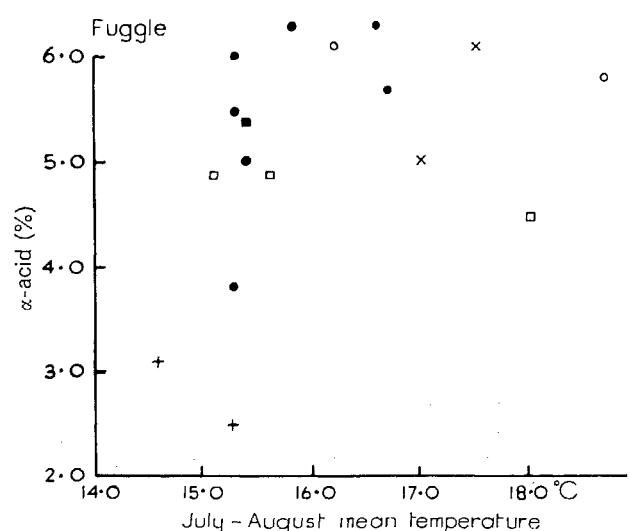


Fig. 1. Relationship between percentage of α -acid in hops and mean temperature (varieties S. 147 B and Fuggle).

From temperatures available for 10-day periods, a "temperature parameter" was chosen giving the average daily deviation from the following critical mean temperature values: S.1478, -16°C ; Spalt and Hallertau, -17°C ; Fuggle and Northern Brewer, -16.5°C .

The α -acid content was plotted against this temperature parameter.

The results are shown in Table 2 and illustrated in Figures 4 and 5. Taking into account the errors inherent in the sampling and analysis of the hops, and in the



sampling and observation of the temperatures, the relationship between quality and the temperature parameter seems acceptable at this stage.

In confirmation of the existence of an optimum temperature, it was found that in some 40 years of records of hops grown by Guinness Hop farms at Bodiam, Sussex (United Kingdom), the highest soft resin contents occurred in years when the mean July and August temperatures were near 61.5°F , (approximately 16.5°C).

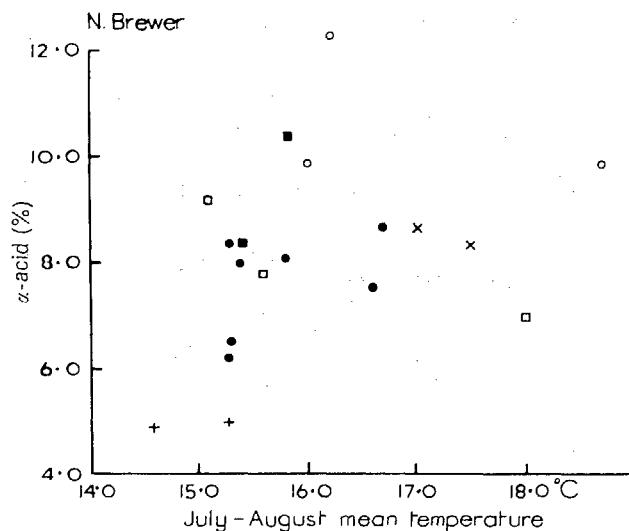
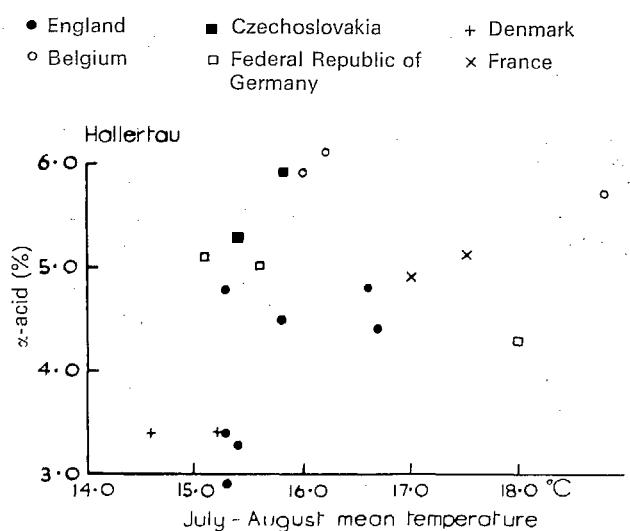


Fig. 2. Relationship between percentage of α -acid in hops and mean temperature (varieties Northern Brewer and Hallertau).



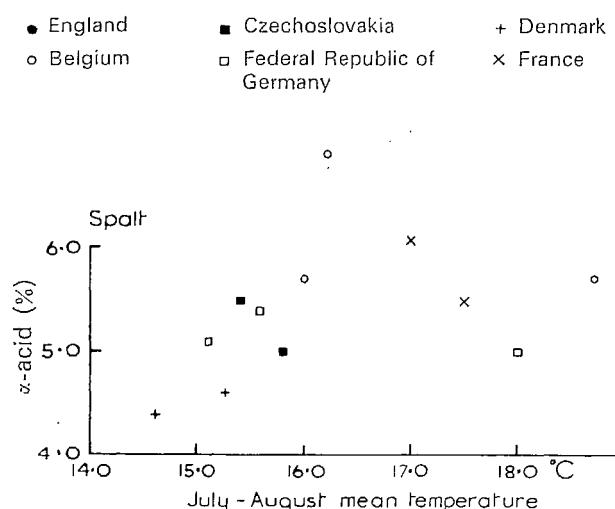
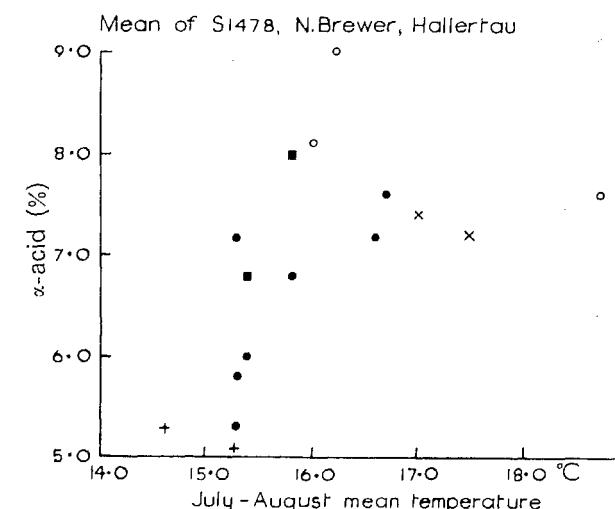


FIG. 3. Relationship between percentage of α -acid in hops and mean temperature (varieties Spalt and mean of three varieties).

RESULTS FROM COMMERCIAL SITES IN KENT

It was known that differences in quality existed within relatively small areas in Kent and these differences were not easily explainable in terms of cultural practices. A study of the siting of the various gardens indicated that height above sea-level might be a factor, which again suggests that ambient temperatures rather than incoming sunshine were likely to be the critical influence. Sunshine does vary with height, but not nearly as much as temperature. Examination of year-to-year



variations at any one site is complicated because sunshine and temperature are highly correlated in summer.

With the co-operation of the Hop Research Department at Wye and the Hops Marketing Board, an experiment was carried out in 1969 on Bullion hops at 8 hop gardens in Kent. Pairs of maximum and minimum thermometers were used in modified screens (the type used generally in frost liability experiments), and daily readings were taken together with observations of crop stages. The exposure of the thermometers was made as uniform as possible.

TABLE 2. Quality and temperature parameters (TP): international trials

	S. 1478		Spalt		Hallertau		Fuggle		Northern Brewer	
	α -acid (%)	TP								
1965										
Czechoslovakia	—	—	5.5	2.4	5.3	2.3	5.4	1.7	8.4	2.0
Denmark	7.5	1.9	4.4	3.2	3.4	2.8	3.1	2.7	4.9	2.7
England	7.8	1.7	—	—	4.5	1.8	—	—	8.1	1.9
France	8.0	1.6	5.5	1.0	5.1	0.9	6.1	1.2	8.4	1.4
Germany (Fed. Rep. of)	—	—	5.5	2.4	5.0	2.2	4.9	2.0	7.8	1.9
1966										
Czechoslovakia	7.8	1.5	5.0	1.9	—	—	—	—	—	—
Denmark	7.0	2.4	4.6	4.0	3.4	3.5	2.5	3.5	4.8	3.5
England	8.5	1.1	—	—	4.8	1.8	6.0	1.3	8.4	1.4
Germany (Fed. Rep. of)	—	—	5.5	1.4	5.1	1.4	4.9	1.2	9.2	1.1
1967										
Belgium	7.0	2.0	5.7	0.9	5.8	0.9	5.8	1.1	9.9	1.2
England	9.2	0.9	—	—	4.8	1.8	6.3	0.9	7.5	1.4
Germany (Fed. Rep. of)	—	—	5.0	1.9	4.3	1.9	4.5	1.9	7.0	2.1
Correlation	0.95		0.78		0.80		0.95		0.90	

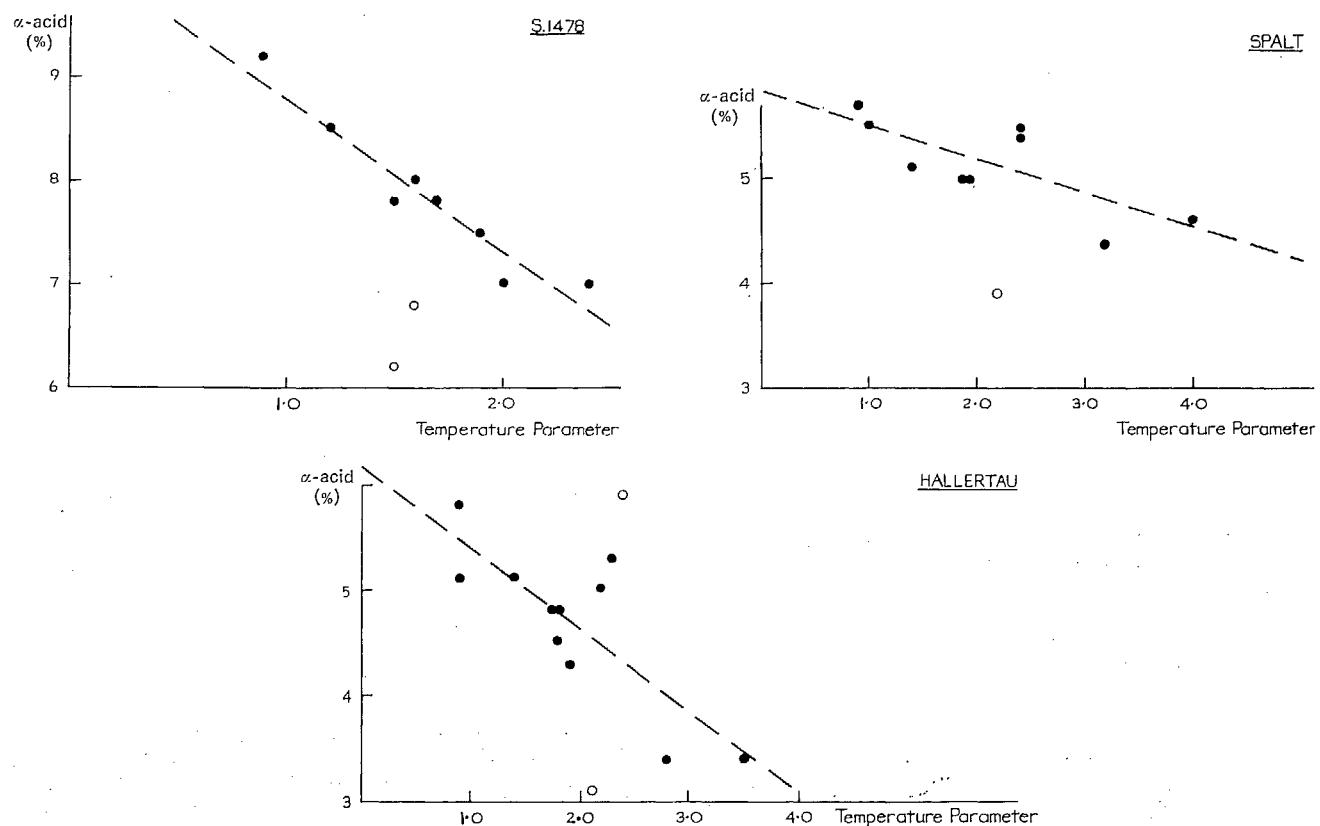


FIG. 4. Relationship between percentage of α -acid in hops and a temperature parameter (varieties S. 147 B, Spalt and Hallertau). O = unreliable data.

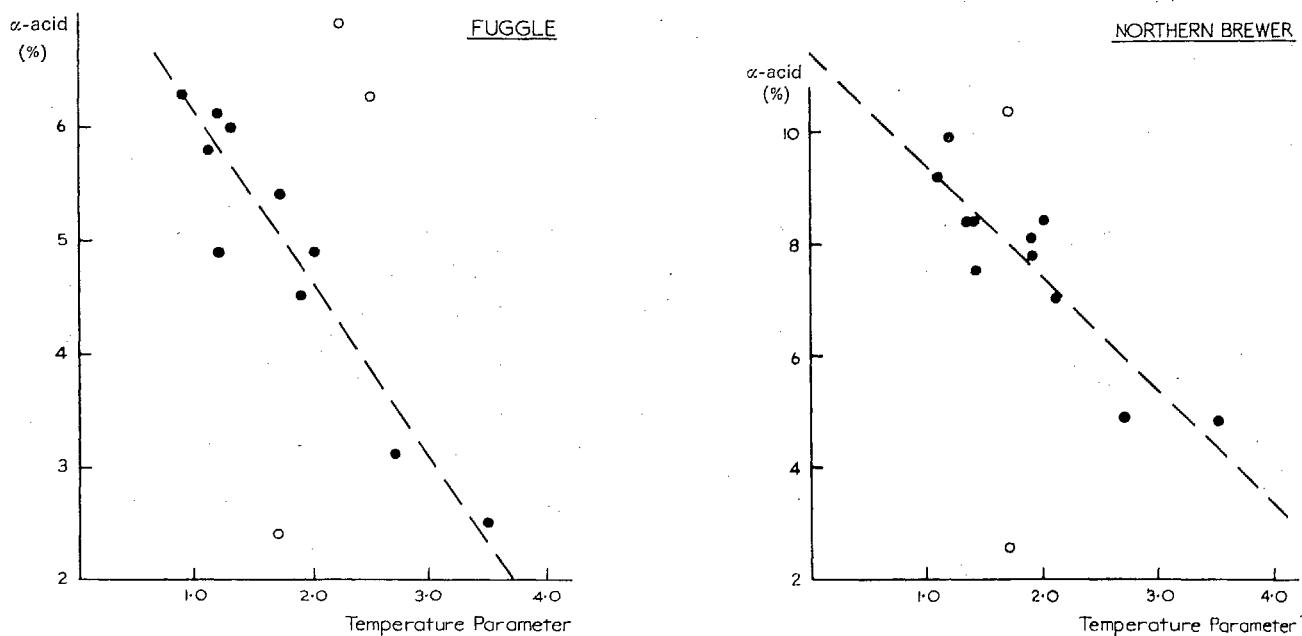


FIG. 5. Relationship between percentage of α -acid in hops and a temperature parameter (varieties Fuggle and Northern Brewer).

TABLE 3. Comparison of hops from different sites

Site	Critical period	Mean temperature (°C)	α -acid (%)	Day maximum at picking	Hop yield
D	17 July–12 September	16.75	8.9	26	17.4
C	16 July–11 September	16.95	8.1	24	19.4
G	17 July–17 September	17.37	7.0	21	20.2
A	16 July–4 September	17.37	6.2	20	18.4
H	22 July–20 September	17.41	6.3	21	19.9
J	20 July–15 September	17.55	4.5	18	16.3
I	17 July–19 September	17.64	6.3	21	18.7
B	13 July–12 September	17.93	6.9	26	24.5

July 1969 was much warmer than usual and, as a result, the mean temperatures from time of burr to picking date were above the proposed optimum. It was, therefore, encouraging to find that the best quality hops came from the site with the lowest mean temperature (see Table 3).

The correlation coefficient between α -acid and mean temperature is -0.69 , the departure from linearity being principally due to results from B (too high) and J (too low).

It might be significant that the yield at B is the highest, and that at J the lowest. The only apparent meteorological effect was the mean day maximum temperature on the first 2 days of picking. Hops at B were picked on, or just after, the 2 warmest days in September; those at J were associated with the coldest days. The correlation coefficient between α -acid and picking maxima is 0.84 , but further evidence is needed before this can be regarded as more than fortuitous.

BELGIAN TRIALS

To examine in greater detail the possible influence of weather at, or immediately prior to picking, use was made of the reports of trials issued by the Institut National Belge du Houblon (1968). These involved the sampling and analysis of hops picked at frequent intervals before and after full maturity (assumed to be the stage of maximum α -acid content). From the varieties under trial, Northern Brewer was selected for investigation as its quality variation was greatest. Daily weather data were not available from the site, but those reported from Uccle were used as a reliable reference station, although it was realized that Uccle temperatures were likely to be higher than those in the trial grounds.

Results were available for 11 years. Those in 1967 were discarded as the hops were badly affected by mould. Sampling dates varied from 14 August to 15 September; the dates of burr or full flower were not known.

TABLE 4. Quality and temperature factors: Belgian trials

Year	α -acid		Mean temperature to date of sampling (°C)		Mean maximum temperature, 2 days previous to sampling (°C)
	%	Date	from 1 July	from 16 July	
Above optimum					
1959	16.0	29 August	19.58	19.30	25.5
1964	16.0	18 August	18.35	19.30	26.0
Optimum					
1958	16.6	31 August	17.95	17.86	30.5
Below optimum					
1968	15.3	6 September	17.44	16.96	19.5
1961	14.8	13 September	17.05	16.80	20.5
1963	14.7	3 September	16.82	16.83	20.0
1960	14.6	5 September	16.54	16.88	20.5
1966	14.0	15 September	16.77	16.68	19.5
1965	13.8	31 August	16.53	16.84	20.5
1962	13.3	9 September	16.18	16.44	17.5
Disease affected year					
1967	13.8	31 August	18.53	18.51	20.0

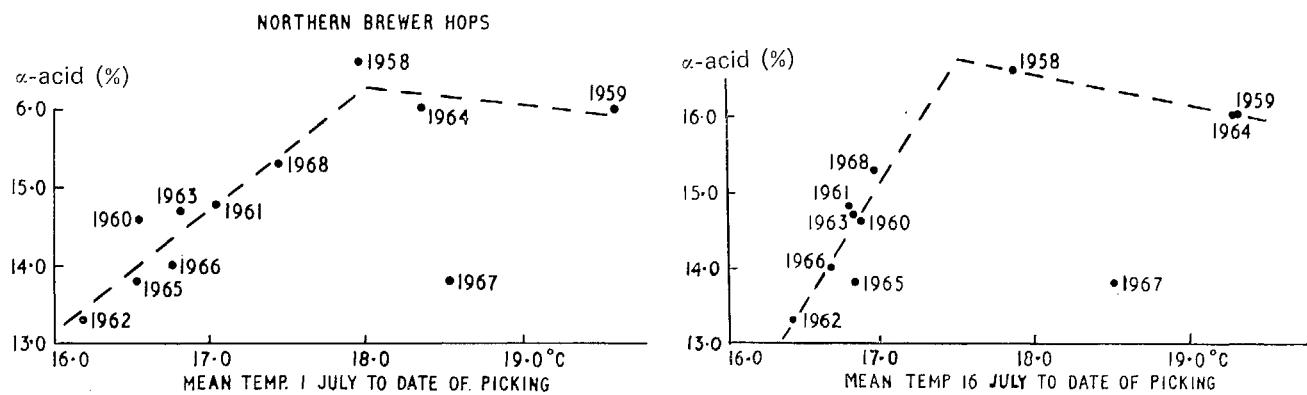


FIG. 6. Belgian trials, Northern Brewer hops. Relationship between optimum α -acid percentage and mean temperature over final growth stage.

Note: the crop was badly affected by disease in 1967.

To check the hypothesis that the mean air temperature during the time of cone development is important, this factor was calculated for the period from 1 July or 16 July to date of sampling of hops with the highest quality in each year, although it must be realized that the correct starting date (related to crop stage) must vary from year to year.

As will be seen from Table 4, illustrated in Figure 6, the same pattern emerges as had been deduced from the international trials. There was a definite optimum temperature and a rapid linear decrease in quality for temperatures below the optimum. The loss of quality of over 2 per cent α -acid which occurred in 1967 may have been caused by the attack of mould.

Table 4 also shows the mean maximum temperatures on the 2 days previous to sampling (which was generally done in the morning). Again the best qualities were picked after the warmest days—the worst quality was picked after the coolest days (Table 5, Figs 7 and 8).

CONCLUSIONS

Evidence from a number of trials for several varieties of hop in European countries appears to substantiate the hypothesis that the mean air temperature over the last 40–60 days before maturity exercises a strong influence on the α -acid content.

Further trials regarding the effect of weather immediately prior to picking are needed before any firm conclusion can be reached.

ACKNOWLEDGEMENTS

Thanks are due to the Hops Liaison Committee for providing international data for this investigation through J. F. Brown, of Arthur Guinness, Son & Co. (Dublin) Ltd, to D. R. Tristram, also of St Jame's Gate, Dublin, and Messrs Thompson, Neve and Farrar at Wye

TABLE 5. Variation of quality with date of picking (Belgium, 1964)

Date	Maximum temperature at Uccle 2 days previous to sampling ($^{\circ}\text{C}$)	α -acid (%)	Mean temperature ($^{\circ}\text{C}$) 1 July to sampling	Date	Maximum temperature at Uccle 2 days previous to sampling ($^{\circ}\text{C}$)	α -acid (%)	Mean temperature ($^{\circ}\text{C}$) 1 July to sampling
18 August	26.0	16.0	18.35	1 September	18.5	14.8	18.02
17 August	25.5	15.7	18.33	31 August	18.5	14.8	18.10
28 August	33.0	15.4	18.34	30 August	23.0	14.8	18.19
19 August	22.5	15.4	18.27	15 August	20.0	14.5	18.28
26 August	24.5	15.3	18.17	24 August	21.5	14.4	17.99
16 August	22.0	15.3	18.31	20 August	18.5	14.3	18.18
27 August	29.5	15.2	18.30	23 August	21.0	13.8	18.01
29 August	30.5	15.0	18.29	21 August	16.5	13.8	18.14
25 August	22.0	14.9	18.04	14 August	17.0	13.8	18.29
				22 August	21.0	13.7	18.01

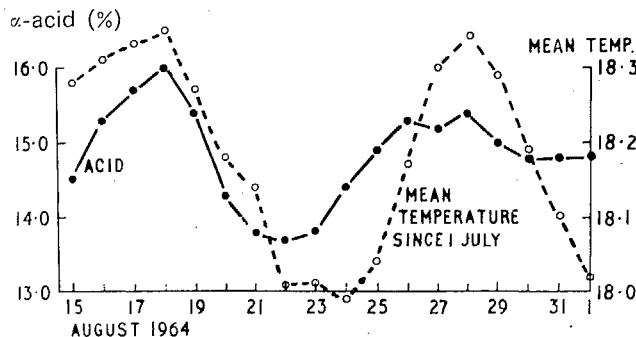
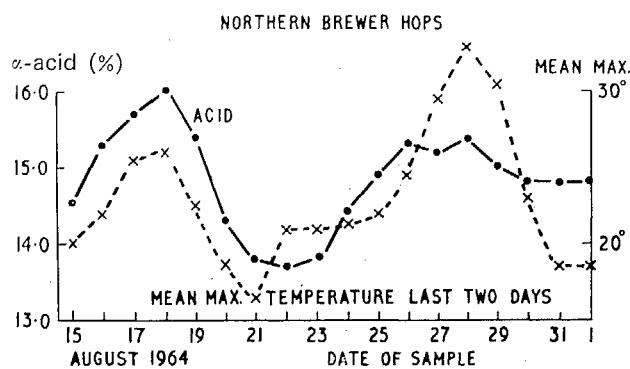


FIG. 7. Belgian trials, 1964, Northern Brewer hops. Variation of α -acid percentage with mean temperatures over final growth stage and with maximum temperatures on the two days prior to picking.

College for their help in providing other data and for their helpful advice and guidance.

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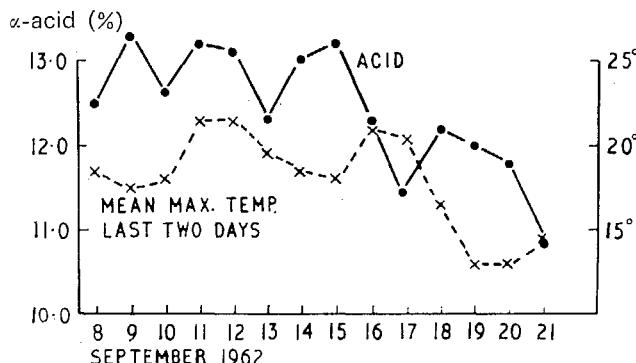
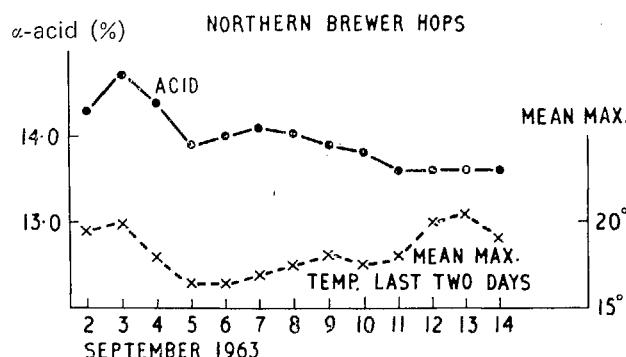


FIG. 8. Belgian trials, 1963 and 1962, Northern Brewer hops. Variation of α -acid percentage with maximum temperatures on the days prior to picking.

Résumé

La qualité du Houblon et la température de l'air
(L. P. Smith)

Des essais faits sur plusieurs années dans quelques pays européens indiquent que la température moyenne de l'air entre la floraison et la récolte a une grande influence

sur la qualité du Houblon mesurée par le contenu alpha-acide. Ce rapport s'exprime d'une façon linéaire de part et d'autre d'une température optimale qui peut varier selon la variété du Houblon. On pourrait aussi en déduire que les températures qui précèdent de près la récolte ont une influence sur la qualité.

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The effect of sulphydryl reagents on cell permeability

J. Levitt
University of Missouri, Columbia,
Missouri (United States of America)

According to a recent theory (Levitt, 1962) freezing injury is due to intermolecular disulphide bond (SS) formation between protein molecules, leading to protein aggregation and irreversible denaturation. For several reasons, it has been suggested (Levitt and Dear, 1970) that these changes are confined to the membrane proteins. Thus, when a plant develops freezing resistance during the 'hardening' process, the permeability of its cells increases. The same hardening process leads to a marked change in the protein sulphydryl (SH) groups. The purpose of this investigation was to find out whether or not there is a direct relationship between these two changes—i.e. does a change in the SH groups of the membrane proteins produce a change in cell permeability?

As in the earlier studies, permeability to urea was determined, using the deplasmolysis method. This method was long ago shown to give essentially results identical with those obtained by direct analysis of the cell sap for penetrating solute (Collander and Bärlund, 1933). Since the direct method is applicable only to large cells such as occur in some algae, the indirect deplasmolysis method must be used for the small cells of higher plants. Certain precautions must, however, be taken. The osmotic potential (or osmolality) of the cell was first determined plasmolytically (Levitt, 1964). The penetrating (non-toxic) solute was then applied in a concentration which was hypertonic, only by 2–4 atm., in order to prevent too severe a plasmolysis, which might conceivably affect permeability. This also permitted deplasmolysis to occur in a relatively short time (1–2 hr), both for convenience of measurement and in order to confine changes to a minimum. For greater accuracy and precision, the cells were preplasmolysed for a few minutes in a non-penetrating solute of the same osmotic potential as the subsequently applied penetrating solute. This assures a uniform cell surface for penetration, and leads to a well-rounded and, therefore,

easily observed protoplast during deplasmolysis. Using this technique, repeated measurements on the same leaf agreed within ± 10 per cent.

The SH reagents were first tested using a logarithmic series of concentrations. This permitted selection of the highest concentration usable without injury. Pronounced injury is detected by rupture of the cells and loss of pigment during subsequent deplasmolysis in solutions of the penetrating solute. Cytoplasmic swelling may also be detected as a result of less severe injury.

The procedure was, therefore, as follows. Freehand sections were made from the lower surface of the midrib of a leaf of red cabbage (*Brassica oleracea*, var. *capitata*) using only the basal 5 cm, and extending only 2–3 mm on either side of the midrib. When carefully prepared, such sections always included a portion of the one-cell-thick epidermis free from other adhering cells and, therefore, in close contact with the solution. These naturally pink cells clearly show the slightest trace of plasmolysis. They retain their colour when alive and lose it when killed. The sections were immediately immersed in a hypotonic, balanced solution (0.1 M 9:1 NaCl + CaCl₂). A standard number of these sections was then transferred to the same solution, this time containing the highest non-injurious partial concentration of the SH reagent to be tested. After a predetermined time in this solution, sections were then transferred to the hypertonic urea (0.45–0.75 M). In the case of the two thiols (β -mercaptoethanol, ME; dithiothreitol, DTT), the urea solutions contained the same partial concentration of the thiol as was used in the pretreatment solution, in order to maintain the reduced state. The other SH reagents were not included in the urea solutions. The sections were observed under the microscope from time to time until half the cells were deplasmolysed and the other half just incipiently plasmolysed. The time required to achieve this state was taken as the deplasmolysis time. Relative permeability

TABLE 1. Relative permeability of red cabbage epidermal cells to urea after treatment at 1-3° C with the given SH reagent¹

SH reagent	Concentration (molar)	Time in solution (hr)	Number of trials	Relative permeability
β-mercaptoethanol (ME)	10 ⁻²	1-24	11	0.97±0.15
dithiothreitol (DTT)	10 ⁻²	5-40	4	0.60±0.17
iodoacetamide (IA)	10 ⁻⁴	7-40	11	0.66±0.10
methylmercuric iodide (MMI)	10 ⁻⁵	9-24	8	0.59±0.15
N-ethylmaleimide (NEM)	10 ⁻⁵	12-18	3	0.50±0.10
p-chloromercuribenzoate (PCMB)	10 ⁻⁴	9-40	11	3.7 ±1.5

1. Urea concentration 0.45-0.75 M. Treatment solution 0.1 M 9:1 NaCl + CaCl₂ with or without (control) the given partial concentration of SH reagent.

Relative permeability = $\frac{\text{Time for deplasmolysis in urea after treatment}}{\text{Time for deplasmolysis in urea after control}}$

$\frac{\text{Treatment in control solution}}{\text{Time for deplasmolysis in urea after treatment for same time in solution with SH reagent}}$

is inversely proportional to deplasmolysis time. It was, therefore, calculated from the ratio of the deplasmolysis time of control sections (kept in 0.1 M 9:1 NaCl + CaCl₂) to the deplasmolysis time of the treated sections.

When the sections were treated at room temperature (22-25° C) for 1-3 hr, none of the SH reagents produced any change in cell permeability. A significant decrease in permeability was produced by 1 hr in methylmercuric iodide (MMI), when the concentration used (10⁻⁴ M) was high enough to injure the cells, producing a swelling and vacuolation of the cytoplasm at the ends of the cells. After 4-5 hr in the MMI solution, the cells lost their pigment and were, therefore, dead.

In order to prevent such injury, weaker solutions were used, and they were cooled to 1-3° C before immersing the sections in them. At this temperature, the rate of uptake of the reagents must be markedly decreased and, therefore, the treatment times were considerably increased. Table 1 shows that this treatment resulted in marked decreases in permeability with most of the reagents (DDT, IA, NEM, MMI), a marked increase with one (PCMB), and no effect with one (ME).

Although all the substances tried are SH reagents, they may conceivably produce their effects on per-

meability by reactions other than combination with SH groups. For this reason, and also in order to prove that it is not simply an injurious effect, the change must be proved reversible. An attempt was, therefore, made to reverse the effects by ME, which releases SH reagents, regenerating the SH groups, and which was shown to have no effect by itself on permeability. Table 2 shows that the effect is reversed by ME, both in the case of the decrease in permeability (IA, MMI), and in the case of the increase in permeability (PCMB). Surprisingly, the control, balanced solution without ME also permitted at least some reversal of the change in permeability, though it occurred much more slowly than in the presence of ME. This is not so obvious from the average values, which include shorter periods showing partial reversal, and longer periods permitting complete reversal. Presumably, this reversal is a spontaneous, metabolic effect.

Another effect of the SH reagents was also observed. Within a few hours, they brought the streaming of the cytoplasm to a stop. This, of course, proves that they penetrated. In at least some cases, this cessation of streaming was also reversible by treatment with ME.

Injury sometimes occurred if the sections were retained too long in the non-injurious solutions. Therefore, in later experiments, treatments of only 9-15 hr were used; less than 9 hr was insufficient for a consistent, measurable response. With these treatments, using the concentrations listed in Tables 1 and 2, there was no detectable difference from the controls, as determined by pigment retention, by appearance of protoplasm (except for cessation of streaming) and by ability to survive plasmolysis and deplasmolysis. The one exception was NEM, which developed 'cap plasmolysis' (i.e., swelling of the terminal cytoplasm layer). For this reason, tests with NEM were later abandoned.

In spite of the precautions taken to use concentrations of SH reagents which do not produce observable injury, it may be suggested that the permeability changes are simply the result of undetectable, but irreversible,

TABLE 2. Relative permeability of red cabbage epidermal cells to urea after treatment at 1-3° C with the given SH reagent and after following this treatment with either ME, or a control balanced solution

SH reagent	Relative permeability			
	Followed by:			
After 9-19 hr in SH reagent	5-24 hr in 10 ⁻² M ME	5-24 hr in 9:1 NaCl + CaCl ₂		
10 ⁻⁴ M IA	0.65±0.5 (5) ¹	1.15±0.15 (5)	0.85±0.15 (2)	
10 ⁻⁴ M PCMB	3.6 ±1.7 (8)	0.93±0.15 (7)	3.5 ±2.5 (6)	
10 ⁻⁴ M MMI	0.59±0.17 (6)	1.18±0.27 (6)	0.77±0.25 (3)	

1. Number in parentheses = number of trials.

injury. This explanation is improbable, since both increases and decreases in permeability were obtained. It was effectively disproved by showing that the changes are, indeed, reversible. The only logical explanation, therefore, is that the permeability changes are due to effects on membrane SH groups. Similar changes in permeability by applied SH reagents, have been obtained with red blood cells (Sutherland *et al.*, 1967). In further agreement with the above results, exposure of erythrocytes to doses of ionizing radiation greater than a few thousand rads results in an increased passive cation permeability (Sutherland and Pihl, 1968). This was accompanied by a loss of SH groups due to their oxidation to SS. Several of our present results support this relationship between SH groups and permeability:

1. All four tested SH reagents produced permeability changes.
2. These changes were reversed when the SH reagent was replaced by a small-molecule thiol, mercaptoethanol (Levitt and Scarth, 1936). The slower, spontaneous reversal in the absence of ME (and of SH reagent) is also in agreement with the above explanation, since living cells are known to have the enzymes and cofactors necessary for regenerating SH groups. Because of these substances, actively metabolizing human erythrocytes possess a mechanism permitting them to reduce membrane disulphides formed as a result of radiation damage (Sutherland and Pihl, 1968). It was possible to obtain this reduction, however, only at normal body temperature, not at temperatures close to 0° C. This is to be expected in the case of warm-blooded mammals not adapted to metabolize at low temperatures. Cabbage, on the other hand, can metabolize and even grow for indefinite periods at temperatures close to 0° C. It is not surprising, then, that it can perform metabolic processes at low temperatures which mammals can accomplish only at considerably higher temperatures.

The objection may be raised that the above results of Sutherland and Pihl are not comparable with my results since they measured cation permeability and I measured urea permeability. Stadelmann (1969), however, also obtained changes in cell permeability (both decreases and increases) due to radiation of onion cells, and he measured urea permeability.

This metabolic reversal of the attachment of side groups to protein SH may also provide the explanation for the temperature effect. At the low temperature (1–3° C) the metabolic reversal must occur very slowly, too slowly to prevent the tying up of a sufficient number of membrane SH groups to alter permeability. At the higher temperature (22–25° C) the metabolic processes would be accelerated much more than the cell permeability change. Therefore, perhaps the rate of metabolic removal of the side groups and regeneration of the membrane SH groups would equal the combined rates of penetration of the reagent through the membrane and

attachment to the membrane SH groups. The net effect would then be no change in permeability. There is, however, another possible explanation. Brandts (1967) has shown that proteins denature reversibly at low temperature. Perhaps denaturation unmasks membrane SH groups, which were previously protected from combination with the SH reagents.

It is not immediately apparent why the combination of chemical substances with membrane SH groups should alter membrane permeability. Any proposed explanation must, of course, be purely hypothetical until we attain a full understanding of membrane structure and the consequent mechanism of membrane permeability. Concepts of this mechanism have undergone considerable change in recent years. The old, lipid-sieve theory was first opposed by Davson and Danielli's (1943) concept of the membrane as a lipid layer sandwiched between two protein layers. More recent evidence (Green and MacLennan, 1969), however, opposes such a simple structure, and once again permits a concept of polar "pores" within an apolar lipid layer. The above results can be explained on the basis of such a membrane. If the pores are just large enough to permit the passage of small polar molecules, such as the urea used in this investigation, and if these pores are lined with protein side-groups, including SH groups, then it is easy to explain a decrease in permeability produced by SH reagents. Any reagent which combines with the SH groups within the pores, will partially block the pore, decreasing the number of molecules of penetrant that can pass through per unit time. Thiols would not be expected to alter the pore size if they are present in sufficiently high concentration to maintain the SH groups in the reduced state. ME (molecular weight 78), therefore, has no effect (by itself) on permeability. DTT, on the other hand, is a much larger molecule than ME, with a molecular weight of 154. Furthermore, it is capable of combining with two SH groups. Therefore, if one molecule of DTT combines with two SH groups within a pore, it may block it sufficiently to prevent the entrance of a second molecule which would otherwise reduce the mixed disulphide and regenerate the protein SH. ME, on the other hand, is small enough to penetrate even a partially blocked pore and to split off any group forming a mixed disulphide with the protein. This explanation is supported by the ability of ME to reverse the permeability change induced by the above SH reagents.

The one result that does not seem to fit the above picture is the increase in permeability induced by PCMB. This is all the more surprising in view of the decrease in permeability induced by the other Hg-containing reagent (MMI). PCMB, however, is a much larger molecule than MMI. It presumably must diffuse into the cell due to the apolar properties of the benzene ring, which permit it to dissolve in the lipid portion of the membrane rather than by passing through the polar "pores". It could then combine with protein SH groups

on the inner side of the membrane. It has been shown that when PCMB combines with SH groups of protein, this leads to a partial unfolding of the protein. Perhaps, in this way, the PCMB induces an enlargement of some of the protein "pores" in the membrane. This would also explain the observed increase in permeability due to intermolecular protein SS formation (Sutherland and Pihl, 1968). Such intermolecular SS bonding between proteins must either occur as a result of unfolding (and, therefore, of pore enlargement) or it must induce unfolding by producing strains in the protein molecule.

The SH groups which combine with the SH reagents cannot be at the outer surface of the membrane, since the permeability effect is observed only after several hours. Furthermore, the cessation of cytoplasmic streaming (which is a corroboration of Tazawa's (1968) earlier observation with PCMB) occurs several hours before the permeability effect. Thus the SH reagents must penetrate completely through the membrane before they produce their effect. This means that they must combine with SH groups on the inner side of the membrane before they can affect cell permeability. This conclusion is in agreement with Sutherland and Pihl (1968). They too obtained evidence that the SH groups which influence passive cation permeability are localized within the membrane and not on its external surface. This is to be expected, since the majority of the membrane SH groups are situated inside the diffusion barrier, and only 1-1.5 per cent occur outside it (van Steveninck *et al.*, 1965).

The lag between the time required for the streaming to cease and the time required for the change in permeability supports the "pore" concept. If the permeability effect were simply due to a combination with SH groups on the inner surface of the membrane, it should occur as rapidly as the effect on cytoplasmic streaming. If, however, the important SH groups are somewhat masked, as they would be if located within "pores", then the time-lag is understandable. The SH groups would also, presumably, have to be masked from molecules penetrating from the outside (otherwise the effect would precede the cessation of cytoplasmic streaming), but not from molecules which have already penetrated and are on their return journey outward. This arrangement would be a reasonable protective one, permitting the cell to change its own permeability from within, but tending to prevent any such change from without.

On the basis of the above results, it is conceivable that the permeability increase which occurs during the hardening of plants to freezing, is due to changes in the protein SH groups of the membrane. Unfortunately, however, it cannot be stated that a loss of SH always leads to an increase in permeability, since either an increase or a decrease can be obtained by tying up this group with different reagents.

ACKNOWLEDGEMENT

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Résumé

L'effet des réactifs sulfhydryles sur la perméabilité de la cellule (J. Levitt)

Les cellules épidermiques du Chou rouge se montrent moins perméables à l'urée après traitement à basse température (0-3 °C) par plusieurs réactifs sulfhydrylés, plus perméables après traitement par un de ces réactifs

(PCMB). Les deux modifications ont été inversées après immersion dans une solution d'un thiol (ME), ou après plusieurs heures sans contact avec le réactif SH. L'augmentation de la perméabilité qui accompagne l'augmentation de la résistance au gel peut donc être rattachée à l'action des sulfhydrylés qui a été mise en évidence.

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Photoperiod and temperature effects on a number of plant characters in several races of maize grown in the field

A. F. E. Palmer
The International Maize and Wheat Improvement Center (CIMMYT),
Mexico D. F. (Mexico)

Maize as a crop exhibits a very broad area of adaptation. It is grown over wide ranges of both latitude and altitude. However, individual varieties of maize generally exhibit adaptation to a narrow band of latitude or altitude. Good adaptation, in this sense, is considered to be the ability to grow normally and produce a yield of grain under the prevailing climatic conditions. Other important aspects of adaptation, such as resistance to insect and disease attacks, will not be considered in this paper.

Tropical maize varieties when grown at higher latitudes normally display tremendous vegetative growth, and grow much taller than in their area of best adaptation. Flowering is delayed and frequently does not occur before the growing season is over. If flowering does occur there is generally insufficient time for grain filling before the first killing frost. Similarly, when maize varieties from temperate areas are grown at tropical latitudes, a decrease in productivity is observed. The time needed to reach maturity is reduced and plant height is also decreased.

Movements of varieties that involve changes in altitude at the same latitude also generally cause maize varieties to exhibit poor adaptation in terms of maturity and productivity.

These effects, though well known, have not been adequately studied nor put on a quantitative basis. Also, the causes are generally thought of in terms of latitude and altitude instead of the underlying factors such as photoperiod, temperature and possibly other environmental factors.

These climatic responses have greatly restricted the area of adaptation of improved maize varieties and hybrids. Development of widely adapted, high-yielding varieties could do much to alleviate the world food problem. CIMMYT has as one of its goals the production of such widely adapted, high-yielding varieties. However, unless such varieties are to be developed purely

by chance, much more background information is needed on the adaptive responses of maize to its environment. The experiments reported here summarize the results of a preliminary attempt to pinpoint the important growth responses and environmental factors involved.

MATERIALS AND METHODS

Two varieties of each of seven Mexican races of maize were planted in Mexico at a number of dates throughout the year. The races and varieties used are shown in Table 1. Six of these races are well adapted to elevations between 1,000 and 1,800 m above sea level. The seventh race, Zapalote Chico, is adapted to lower elevations (Wellhausen *et al.*, 1952). A previous report suggests that Zapalote Chico may be photoperiod insensitive (Anderson, 1959). Two improved varieties were included each year as check varieties. In 1968 these varieties were Bolochó (an early maturing variety) and Puebla Group 1 (a late maturing variety). Puebla Group 1 was replaced by Cortazar (also late maturing) in 1969.

Plantings were made on 21 April, 21 May, and 21 June in 1968 and 1969 at Roque in the State of Guanajuato. Roque is situated 220 km north-west of Mexico City at an elevation of 1,750 m and latitude 20° 30' N. In

TABLE 1. Races and varieties studied under different dates of planting

Race	Variety
Celaya	Composite II, Guanajuato 2
Bolita	Oaxaca 174, Oaxaca 180
Maíz Dulce	Guanajuato 100, Jalisco 188
Cónico Norteño	Guanajuato 24, Querétaro 27
Tabloncillo	Nayarit 50, Nayarit 16
Zapalote Chico	Oaxaca 179, Chiapas 110
Pepitilla	Guerrero 221, K-128-A

TABLE 2. Sites, dates of planting, observed daylength at planting dates, and mean maximum and minimum temperatures during the 30 days following planting

Site	Number of planting ^a	Planting date	Observed ^{1,2} daylength	Mean temperatures for 30 days after planting (°C) ^a	
				Maximum	Minimum
Roque, Gto.	1	21 April	12 h 36 min	29.2	10.3
Roque, Gto.	2	21 May	12 h 57 min	30.0	12.6
Roque, Gto.	3	21 June	13 h 12 min	26.7	13.4
Tepalcingo, Mor.	4	1 October	11 h 31 min	32.5	15.0
Tepalcingo, Mor. 1968	5	1 November	11 h 04 min	30.4	12.2
Tlaltizapán, Mor. 1969					
Tepalcingo, Mor. 1968	6	1 December	10 h 43 min	29.2	10.5
Tlaltizapán, Mor. 1969					
Tlaltizapán, Mor.	7	21 December	10 h 41 min	30.1	8.8

1. Observed daylength is the period between the times when the sun's disc was half below the horizon in the morning and evening when observed from the site of planting
 2. Observed daylengths and mean temperatures are for 1 year only on plantings 4 and 7. For other planting dates the values are means of 2 years data.
 3. Used in Figures 1 to 6.

1968 plantings were also made on 1 October, 1 November, and 1 December at Tepalcingo in the State of Morelos. Tepalcingo is situated 100 km south of Mexico City at an elevation of 1,300 m and latitude 18° 35' N. In 1969, plantings were made on 1 November, 1 December, and 21 December at Tlaltizapán, Morelos. Tlaltizapán is also 100 km south of Mexico City at an elevation of 947 m and latitude 18° 43' N. Thus, the plantings in the State of Guanajuato were made under conditions of increasing daylength, and those in Morelos were made under decreasing daylengths. The sites used, dates of planting, daylengths at planting dates, and mean maximum and minimum temperatures during the 30 days following planting are presented in Table 2. Daylengths observed as described in the footnote to Table 2 will be shorter than the effective daylengths described by Francis (1970).

Two fertility levels of nitrogen (80 and 160 kg/ha) were used. Each variety was replicated twice in each fertility level at each planting date. Two-row plots were used in the first year and four-row plots in the second year. Twenty-eight plants were included in each row. Row spacing varied with the prevailing practices at each station, but plant population was maintained at 44,000 plants/ha in all plantings by altering the spacing between plants in the row. Irrigation and pest control procedures were carried out as necessary.

The following plant characteristics were observed on 10 competitive plants in each plot:

1. Days to flower (time from planting to 50 per cent plants silking).
2. Ear height (to node of attachment of the upper ear).
3. Grain dry weight per plant.
4. Stover dry weight per plant (all above-ground parts of the plant except grain).
5. Grain/stover ratio on dry weight basis.

Days to flower, ear height, and the grain/stover ratio were chosen as indicators of the response of the varieties to changes in daylength. The true photoperiodic effect is on flower initiation, but dissection of growing points for this observation was not possible in this experiment. Hence, days to flower was used as a measure of this photoperiodic effect. Ear height and the grain/stover ratios give some indication of the relative vegetative growth under the different photoperiods. The grain/stover ratio is a measure of plant efficiency that may serve as an indicator of stability to changing daylengths.

Corn stunt disease resulted in fewer than 10 competitive plants being available for grain and stover determinations in a few entries at Tepalcingo in 1968. This disease also caused the complete planting at Tlaltizapán on 1 October 1969 to be discarded. This explains the absence of data for this planting date and the inclusion of a planting on 21 December 1969 (see Table 2).

RESULTS AND DISCUSSION

For the purposes of this paper the data will be presented in the form of means for each of the 7 races and each of the 3 improved varieties. The traits measured showed no clear-cut response to nitrogen at the levels used. Hence, the nitrogen levels have been treated as replications. So, in Figures 1 to 6, each point is the mean taken over 2 replications, 2 varieties and 2 nitrogen levels for the 7 races, and the mean taken over 2 replications and 2 nitrogen levels for the 3 improved varieties. Also, for planting dates 4 and 7, the values are for 1 year's data, while for the other plantings the values are means of 2 years' data. The 2 varieties in each race reacted in a very similar manner for all the measured traits.

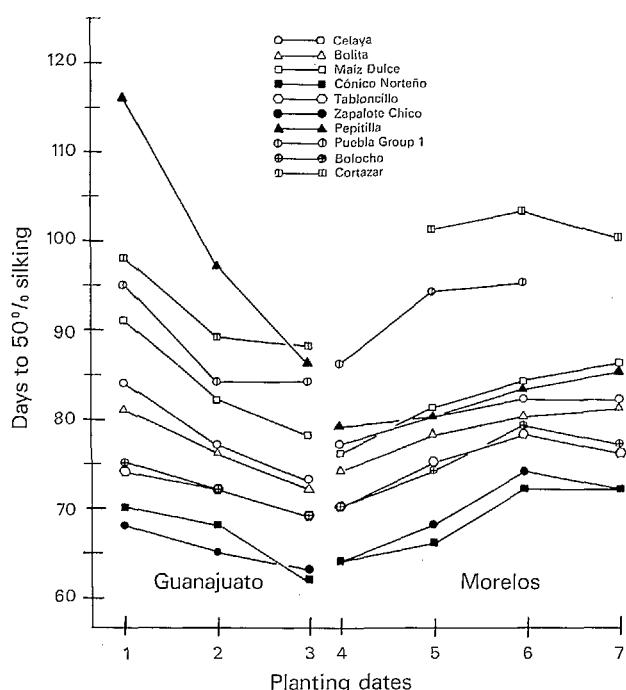


FIG. 1. Days from planting to flowering (50 % silking) for 7 Mexican races of maize and 3 improved varieties with 7 different planting dates. For planting dates see Table 2.

DAYS TO FLOWER

The data for days to flower at the different planting dates are presented in Figure 1. It is clearly evident from the figure that a wide range of maturity classes was included in the experiment. Also, a similar trend is observed for all the races and varieties. In the three plantings in Guanajuato the time from planting to flowering decreased as planting time was delayed, i.e. flowering was earliest under the longer photoperiod experienced by the 21 June planting. Likewise, the 21 May planting flowered earlier than the 21 April planting. This trend is true for all the materials in the test. The race Pepitilla showed the greatest change in days to flower when planted in Guanajuato, i.e. from 116 days when planted on 21 April to 86 days when planted on 21 June. The races Tabloncillo and Zapalote Chico and the variety Bolocho showed the most stability in this trait at these three planting dates.

In general, the differences were less pronounced in the Morelos plantings, but the trend was for a longer period to flower as the daylength at planting became shorter. In these plantings, the race Pepitilla flowered much earlier than in the plantings in Guanajuato and it was one of the most stable materials in this trait at the Morelos locations. By contrast, the variety Cortazar flowered later when planted in Morelos than when planted in Guanajuato. Each of the other materials in the

study showed a similar range in days to flower at the two locations. None of the materials showed great stability in the time from planting to flowering at all planting dates. However, the earlier materials appear to be more stable than the later varieties in this respect.

These data showing later flowering under shorter daylengths are inconsistent with the premise that maize is a short-day plant (Kiesselsbach, 1950), or a day-neutral plant (Rogers, 1950). However, the maximum difference in daylength at different plantings in this experiment was 2 h 31 min. Also, the maximum daylength at planting was 13 hr 12 min, which is still a photoperiodically short day for maize (Arnold, 1969; Francis *et al.*, 1970).

It thus appears, at these intermediate daylengths, that some other environmental factor was exerting an effect strong enough to override completely the effect of small changes in daylength. This other factor could be temperature. Mean maximum and minimum temperatures for the 30 days following each planting date are presented in Table 2. The changes observed in days to flower at different dates of planting follow closely those that would be expected from the changes in temperature. This is especially true with respect to the changes in minimum temperature. Lower minimum temperatures resulted in a longer period from planting

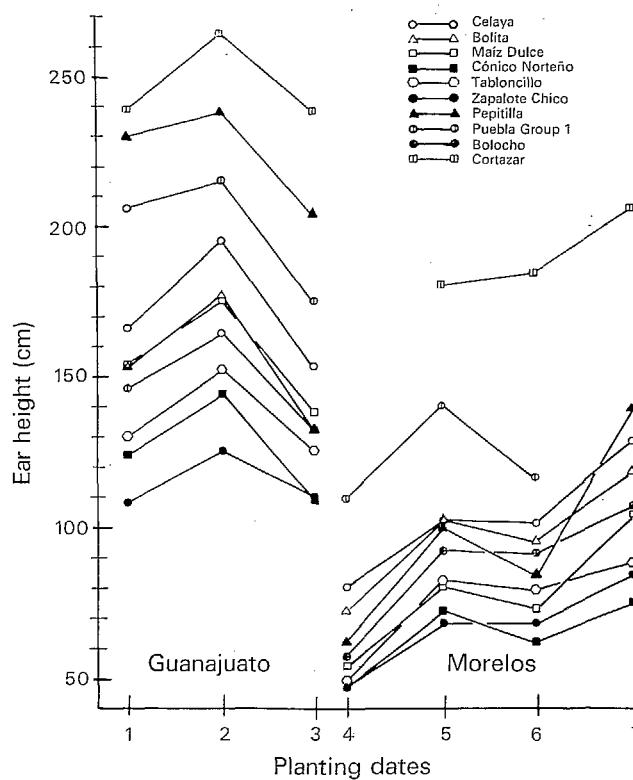


FIG. 2. Ear height of 7 Mexican races of maize and 3 improved varieties with 7 different planting dates. For planting dates see Table 2.

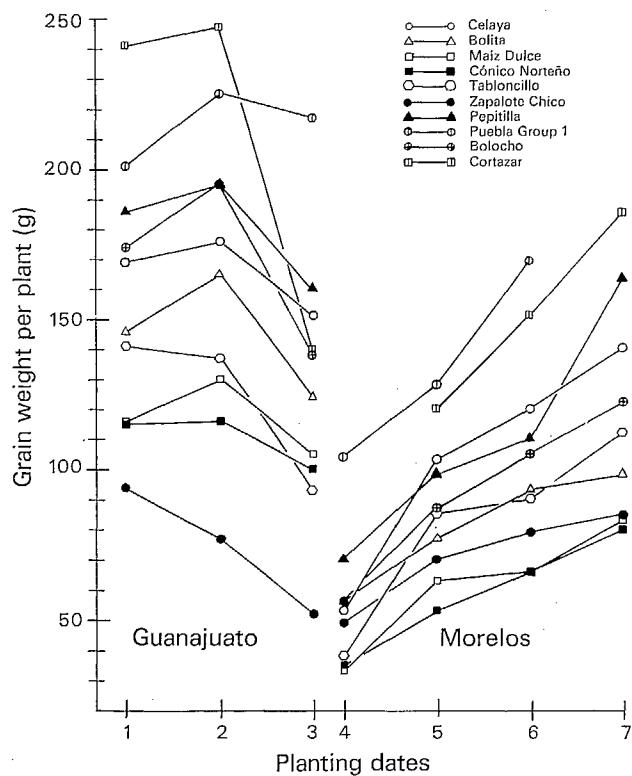


FIG. 3. Grain weight per plant of Mexican races of maize and 3 improved varieties with 7 planting dates. For planting dates see Table 2.

to flowering, and vice versa. This suggests that some type of heat unit system can be derived for predicting flowering, and perhaps maturity, of tropical maize varieties. The importance of interactions between photoperiod and temperature in controlling flowering in maize has previously been emphasized by Roberts and Struckmeyer (1938) and Duncan and Hesketh (1968).

EAR HEIGHT

Ear height data for the various planting dates are presented in Figure 2. Again, the materials used exhibited a wide range of plant height (as indicated by ear height). Also, all the materials used show a similar pattern of changes from one planting date to another. There is no clear effect of photoperiod on ear height. The effect of temperature on rate of development may also be affecting plant height. It is interesting to note that, without exception, all materials planted in Morelos were shorter than they were in any planting in Guanajuato. With the exception of the races Celaya, Bolita, and Pepitilla when planted in Morelos on 21 December, the shortest race when planted in Guanajuato (Zapalote Chico) was always taller than the other races in the Morelos plantings.

GRAIN WEIGHT PER PLANT

Data for this trait are presented in Figure 3. The materials included in this study display a wide range of grain weight per plant under the conditions of this experiment. At a population of 44,000 plants/ha, as used in this experiment, 100 g grain per plant is equivalent to a yield level of 4.4 metric tons of dry grain per hectare. Similar trends for each material are evident from Figure 3. In Guanajuato, the May planting generally yielded more grain than the April planting, while the June planting was inferior to either of the other two. In Morelos, grain weight per plant increased at each successive planting for all materials. It is not possible to pinpoint a direct relationship between photoperiod at planting, or temperatures following planting, and grain per plant. However, in general, the longer the time from planting to flowering the greater the plant height and the greater the grain weight per plant.

STOVER WEIGHT PER PLANT

Data for this trait are presented in Figure 4. The comments made above in terms of range of values and trends in grain weight per plant apply equally for stover weight per plant.

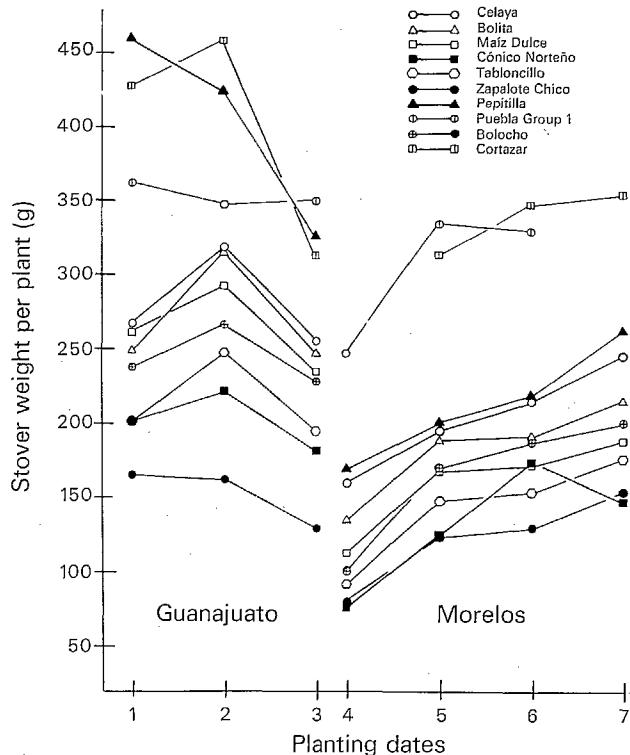


FIG. 4. Stover weight per plant of 7 Mexican races of maize and 3 improved varieties with 7 planting dates. For planting dates see Table 2.

GRAIN / STOVER RATIO

Data for this trait are presented in Figure 5. The values are derived from individual plant values of the grain/stover ratio, not from the mean values for grain and stover weights in Figures 3 and 4.

Despite the consistently similar responses of all materials in terms of grain weight per plant and stover weight per plant (Figs. 3 and 4), it is perhaps surprising to observe such variable responses in the grain/stover ratios of different varieties. This serves to illustrate the complexities in the interpretation of ratios of two variables. The grain/stover ratio, although some measure of plant efficiency, integrates many responses of the plant to its environment throughout the whole growth cycle. From Figure 5 it is obvious that the grain/stover ratio in this experiment is not a very meaningful indication of varietal response to photoperiod.

From Figure 5 it can be seen that the races Celaya, Maíz Dulce, Tabloncillo and Pepitilla were very plastic in their grain/stover ratios in Morelos. The grain/stover ratio increased greatly with successive plantings in Morelos. In the Guanajuato plantings, only Tabloncillo displayed this type of plasticity from one planting date to another. It is interesting to note that Zapalote Chico was fairly plastic in its grain/stover ratio in Guanajuato. It was also at the lower end of the scale of observed

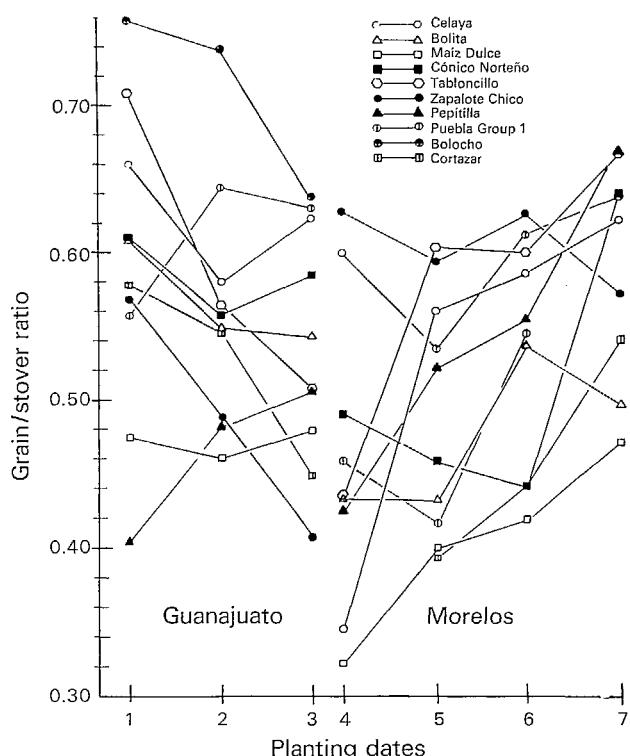


FIG. 5. Grain/stover ratio for 7 Mexican races of maize and 3 improved varieties with 7 planting dates. For planting dates see Table 2.

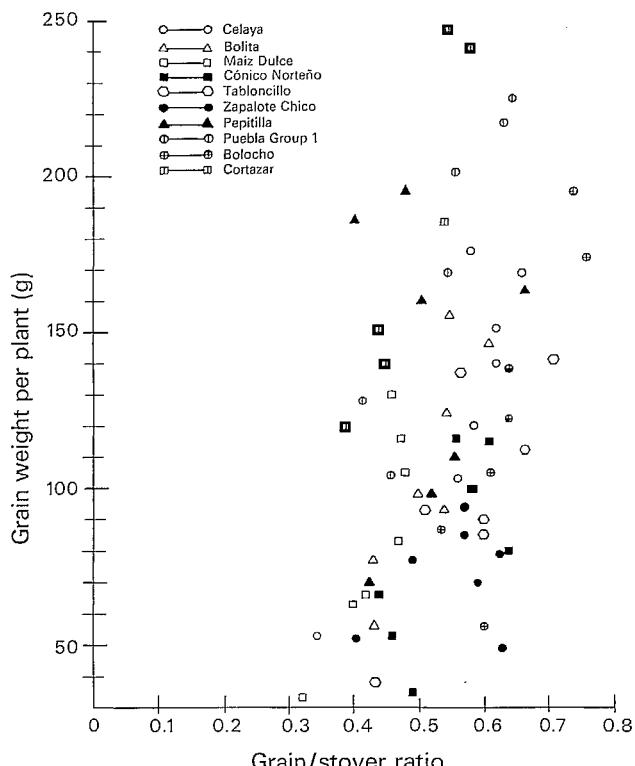


FIG. 6. Grain weight per plant from Figure 3 plotted against grain/stover ratio from Figure 5.

ratios. However, in Morelos it possessed the greatest stability in grain/stover ratio, and this at a high value for the ratio. The improved early variety Bolocho was also fairly stable at a high value for this trait in Morelos. It also displayed the highest grain/stover ratio in all three plantings in Guanajuato. The trend shown by Cónico Norteño in Morelos is probably a result of inadequate sampling at Tepalcingo in 1968. A high incidence of the corn stunt disease in this race reduced sample size at that location.

Grain weight per plant is plotted against the grain/stover ratio in Figure 6 to investigate the possibility of a relationship between these traits. At all levels of grain production for the materials and planting dates used in this study, the values for the grain/stover ratio fell in the range 0.3–0.8, with the majority in the range 0.4–0.7. Thus, there is no clear overall relationship between grain weight per plant and the grain/stover ratio, though some individual materials show a positive correlation between the two traits, e.g. Bolita, Tabloncillo, Puebla Group 1, Bolocho, and Cortazar.

From the preceding figures it is evident that the taller, later improved varieties (Puebla Group 1 and Cortazar) are high in grain production but do not show high grain/stover ratios. On the contrary, the shorter, early improved variety Bolocho, though lower in grain production, shows a consistently high grain/stover ratio. These

results were obtained at a population level of 44,000 plants/ha; undoubtedly, different relationships would exist at higher population levels.

CONCLUSIONS

The studies reported here serve to underline the complexity involved in studying adaptation of maize. Recent studies (Francis *et al.*, 1969, 1970) suggest that photoperiod-insensitive types of maize can be identified under a single temperature regime. Temperature changes are obviously involved in effects of altitude on the time to flowering of a maize variety. The present experiments

suggest that temperature may also be as important as photoperiod when latitude changes are involved. Production of a variety of maize that possesses the degree of temperature insensitivity (in terms of its effect on time to flowering) necessary for very wide adaptation may be neither possible nor desirable.

ACKNOWLEDGEMENT

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Résumé

Effets de la photopériode et de la température sur divers caractères de plusieurs sous-espèces de Maïs cultivées (A. F. E. Palmer)

On a planté les 21 avril, 21 mai et 21 juin, dans l'État de Guanajuato, Mexique ($20^{\circ} 30'$ latitude N), 7 sous-espèces de Maïs mexicain à raison de 2 variétés de chacune et 3 variétés améliorées. Les 1^{er} octobre, 1^{er} novembre, 1^{er} décembre et 21 décembre, on a effectué les mêmes plantations dans l'État de Morelos, Mexique ($18^{\circ} 40'$ latitude N). Ces opérations ont eu lieu dans les années 1968 et 1969. La durée maximale du jour au moment de la plantation était de 13 h 12 min (21 juin), et la durée minimale de 10 h 41 min (21 décembre). Une population de 44 000 plants par hectare a été utilisée. Le temps de mise à fleur (50% de bourgeons femelles), la taille de l'épi, le poids de grain sec par plant, le poids de tige sèche par plant (toutes les parties aériennes de la plante sauf le grain) ainsi que le rapport grain/tige ont été les caractères pris en considération pour mesurer l'effet de la photopériode.

La mise à fleur a été accélérée pour toutes les variétés dans les deux États susmentionnés lorsque diminuait la durée du jour au moment de la plantation. Cela, contrairement à toute attente, si le Maïs est une espèce de jour court ou indifférente à la durée du jour. Aucune des variétés soumises à l'expérience n'a fait preuve de sta-

bilité, en ce qui concerne le temps de mise à fleur pour toutes les dates de plantation. Cette réaction apparemment anormale à la photopériode était probablement imputable à une influence prédominante du facteur température. La différence maximale de la photopériode à l'époque de la plantation entre deux dates de plantation était de 2 h 31 min. De même, dans tous les cas, la durée d'exposition des plantes à la lumière pouvait probablement être qualifiée de « courte » pour le Maïs. Dans ces conditions, l'effet de la température (notamment du minimum nocturne) paraît l'avoir emporté complètement sur tout effet dû aux petites différences de photopériode. Les températures inférieures minimales dans les trente jours qui suivirent la plantation retardèrent la floraison de tous les génotypes. Cela semble indiquer qu'un certain type de régime thermique permettrait de prévoir la floraison du Maïs dans les régions tropicales. Des études préliminaires où l'on a utilisé la lumière artificielle pour allonger la durée de l'éclairage et des feuilles de matière plastique pour augmenter la température minimale du sol dans les débuts de la croissance confirment que la température peut avoir un effet supérieur à celui de la photopériode sur le temps de la mise à fleur.

Les autres caractères étudiés n'ont fait apparaître aucune réaction nette ni à la photopériode ni à la température.

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Environmentally conditioned effects of acute gamma irradiation on growing barley plants

T. Hermelin

Department of Genetics and
Plant Breeding,
Agricultural College of Sweden,
Uppsala (Sweden)

The ontogenesis of a plant is conditioned by an intrinsic mechanism regulated by the genetic make-up in co-operation with environmental factors at every stage throughout the life cycle. In higher plants the nature of such an interaction is very complex. In this report the effects of acute gamma irradiation of barley, and the dependence of these effects on environmental conditions, are considered.

MATERIALS AND METHODS

The experiments started in 1962 and 1963. Seeds of the 2-row barley variety Bonus were planted in plastic buckets at Bogesund, and the plants were exposed to the ^{137}Cs source (Ehrenberg, 1956, 1960). The material to be treated was divided into 4 (1962) or 5 (1963) series, each of them irradiated at different times of the day with a dose of 800 rad for 1 hr. Just prior to irradiation, the plants were cut back to carry only 1 tiller per plant. Emerging lateral shoots were repeatedly cut off until maturity. The series were numbered 801b-f and irradiated as follows: 801b, 00.00–01.00 hr; 801c, 06.02–07.02 hr; 801d, 12.04–13.04 hr; 801e, 18.06–19.06 hr; 801f, 13.35–14.35 the following day.

Each such set of treatments was repeated four times in both years. In 1962, 19, 21, 23 and 25 July, and in 1963, 27–28 and 30–31 July, 2–3 and 5–6 August. In all except 5 treatments, 50 tillers were irradiated and 200 (1962) or 100 (1963) tillers were included in the material as unirradiated controls. The non-irradiated controls were handled in exactly the same manner as the irradiated material.

Cytological examinations of some representative tillers revealed that meiosis occurred at the first date of irradiation in 1962 and at the second date in 1963 in the spikes investigated.

In both experimental years the records at the meteorological station Röskär, about 1.5 km from the gamma

field, were collected. In addition, in 1963 a thermo-hygrograph was placed close to the gamma source.

Most of the measurements performed are described elsewhere (Hermelin, 1967, 1970) and are, therefore, only briefly described below:

Auricle position = the height to the topmost visible auricle.

Spike position = the height to the top of the spike.

Survival = the percentage of harvested tillers out of those irradiated.

Number of spikelets per spike. (Spikelets smaller than 2/3 of fully developed ones are excluded.)

Fertility = the percentage of seed set of the number of developed spikelets per spike.

Germination = the percentage of emerged seedlings of seeds sown in the field.

The year of treatment is called γ_1 and the succeeding years γ_2 , γ_3 , etc. These designations are not to be confused with X_1 , X_2 , etc. used in seed treatments.

RESULTS AND DISCUSSION

The radiation effects of each treatment were considered as the difference between the amount of induced changes and the capacity to compensate for such injuries. Since the given dose and dose rate are constant for all material irradiated, differences between treatments must depend on the capacity of the plants to withstand the irradiation and this, in its turn, depends on the ontogenetic stage and the milieu conditions at the time of irradiation. In both years the tillers were in a very expansive phase of vegetative development, with about 30 cm of shoot growth in 1 week. During the same period, meiosis and haplophase occurred in most of the irradiated flowers. The statements about the ontogenetic stage based on some fixed spikes cannot, however, be valid throughout the material, since the development of the single flowers does not proceed synchronously within

TABLE 1. The survival (%) in γ_1 of acutely irradiated Bonus barley in 1962 and 1963; 50 tillers per treatment

Year	Date of irradiation	Series					
		801b	801c	801d	801e	801f	Mean
1962	19 July	72	78	92 ¹	86	—	86.7
1962	21 July	90	90 ¹	94	98	—	92.3
1962	23 July	98	94	96	86	—	95
1962	25 July	100	96	98	98	—	97
	Mean	90	89	94.5	92	—	92.3
1963	27-28 July	40	38	52	46	76	50.4
1963	30-31 July	8 ²	24	78	54	76	48.6
1963	2-3 August	78	88	96	100	100	92.4
1963	5-6 August	98 ³	93 ³	96	100	92	95.8
	Mean	55.3	59.6	80.5	75	86	71.5

1. 49 tillers irradiated.
2. 47 tillers irradiated.
3. 43 tillers irradiated.

the spike (Bonnett, 1935; Ekberg and Eriksson, 1965; Mansuri, 1969). Despite efforts, a homogeneous material at the time of irradiation was not completely achieved.

The milieu factors at the time of irradiation may influence the effects recorded. Since the irradiations were performed in an outdoor plant, such external factors as temperature and humidity could not be controlled. During the experiments of 1962, the amount of precipitation was 18.1 mm, compared with 2.2 mm in the 1963 experimental period. There were also differences between the days of irradiation (cf. Figs. 1(a) and 2(b)). The only environmental factor which could be controlled was the time for exposure, and discussion of this factor will be given particular emphasis in this paper.

SURVIVAL

The results presented in Table 1 show comparatively small effects of the irradiation in 1962. No differences between series are found for the 4 days of irradiation and the only significant difference between days of treatment is found in series 801b. In 1963 the material was significantly injured at 3 out of the 4 instances of irra-

diation. In this material, also, the most profound effects were registered for series 801b. The other series, listed in order of increasing tolerance, is 801c, 801e, 801d and 801f.

NUMBER OF SPIKELETS PER SPIKE

As seen in Table 2, the general trend in both experimental years is an increased spike size the later the material is irradiated. This tendency can be explained by the fact that the earlier the irradiation is performed, the less differentiated are the spikelets; when the glumes are more or less completely developed they are less susceptible to damage. In the 1962 material no reduction in spike size is found after irradiations on 25 July. For the 1963 material the same is true for series 801d, 801e and 801f irradiated on 2-3 and 5-6 August.

It is of special interest to see whether significant differences occur between series treated on the same day or on 2 consecutive days. In the 1962 material, a significant difference is only found after irradiations on 21 July, when series 801d gave more spikelets per spike than series 801b, 801c and 801e. If the 1963 material is arranged in order of increasing number of spikelets per spike, *t*-tests reveal the following relations (lines indicate non-significant differences):

27-28 July	801b	801c	801e	801d	801f
30-31 July	801b	801c	801d	801e	801f
2-3 August	801c	801b	801d	801e	801f
5-6 August	801b	801c	801f	801d	801e

In all four instances, an irradiation at midnight (series 801b) caused the most severe damages, followed by series 801c irradiated in the morning. In 3 days series 801f proved to be the most radioresistant, and in two instances this series gave more spikelets per spike than series 801d, which was exposed 1 day earlier. When treated on 5-6 August the reverse relationships appeared. This may be associated with the comparatively low temperature on 6 August. This theory will be further developed below.

TABLE 2. Number of spikelets per γ_1 -spike of acutely irradiated Bonus barley in 1962 and 1963; 24.6 ± 0.2 and 24.9 ± 0.3 spikelets per spike in the 1962 and 1963 control materials, respectively

Year	Date of irradiation	Series			
		801b	801c	801d	801e
1962	19 July	20.6 ± 0.5	21.6 ± 0.4	21.7 ± 0.4	20.9 ± 0.4
1962	21 July	21.4 ± 0.4	21.7 ± 0.5	22.9 ± 0.4	21.7 ± 0.3
1962	23 July	22.5 ± 0.4	23.3 ± 0.4	23.3 ± 0.3	23.3 ± 0.3
1962	25 July	24.9 ± 0.3	24.0 ± 0.4	24.4 ± 0.4	24.6 ± 0.4
1963	27-28 July	18.6 ± 0.9	19.7 ± 0.8	21.2 ± 0.7	20.4 ± 0.6
1963	30-31 July	16.5 ± 2.3	17.6 ± 1.0	19.6 ± 0.5	21.2 ± 0.6
1963	2-3 August	21.5 ± 0.5	21.0 ± 0.4	25.1 ± 0.2	25.5 ± 0.3
1963	5-6 August	20.4 ± 0.4	22.8 ± 0.6	25.4 ± 0.3	26.3 ± 0.2

VEGETATIVE DEVELOPMENT IN γ_1

The mean vegetative size of the tillers at irradiation, measured as auricle position, is shown diagrammatically in Figures 1 (b) and 2 (b) for the 1962 and 1963 materials, respectively, by filled bars. In the same figures the auricle and spike positions at harvest are also shown (hatched and open bars, respectively).

As for other radiation effects previously discussed, the material irradiated in 1962 shows smaller effects than the 1963 material. Nevertheless, in all series of the 1962 material, the spike positions are significantly lower than the control.

As for the 1962 material, the radiation effects decreased the later the material was treated in 1963. The irradiations on 30–31 July seem to yield the largest effects, a tendency already found for survival and the number of spikelets per spike (Tables 1 and 2). All treatments shown in Figure 2 (b) gave decreased spike positions compared with the control.

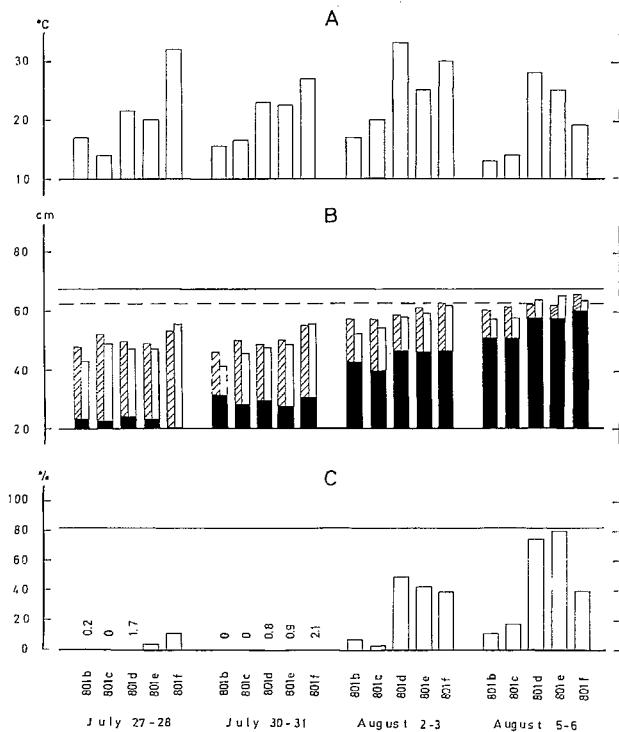


FIG. 1. Temperatures, vegetative development and fertility in γ_1 of acutely irradiated Bonus barley in 1962. (a) Temperature records at Röskär, 1.5 km from the gamma field. Temperature of series 801 b = minimum temperature of the day. (b) Vegetative development. Auricle positions at irradiation (filled bars), auricle positions at harvest (hatched bars) and spike positions at harvest (open bars). Horizontal broken and full lines indicate auricle and spike positions of the control, respectively. (c) Fertility in γ_1 . Horizontal line indicates the fertility of the control.

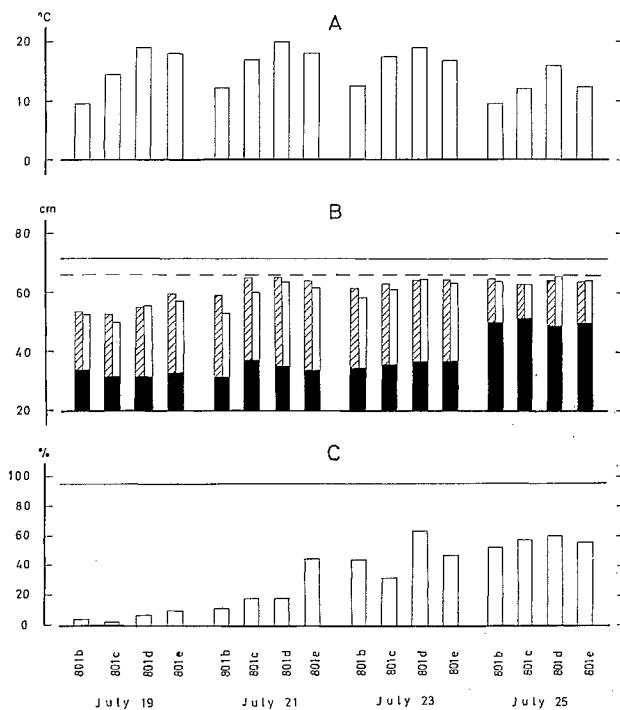


FIG. 2. Temperatures, vegetative development and fertility in γ_1 of acutely irradiated Bonus barley in 1963. (a) Temperature records from the thermohygrograph placed in the gamma field. (b) Vegetative development. The same symbols as in Figure 1 (b). (c) Fertility in γ_1 . Horizontal line indicates the fertility of the control.

In both years the irradiations caused considerable effects on shoot growth in series 801b and 801c, with irradiation at midnight appearing as the most injurious treatment. The irradiations at noon and in the afternoon of the same day seem to influence the final length of the tillers similarly. When the 2 series 801d and 801f are compared, the latter is less affected in 3 out of 4 instances.

Another approach is to study the relationship between auricle and spike positions at harvest. In both controls the spikes had emerged from the sheaths and the differences between the two characters are significant. In the irradiated material this happened only for series 801e irradiated on 5 August 1963. The tops of the spikes were still within the sheaths in many treatments. Of these cases 5 occurred in series 801b and 4 in series 801c.

FERTILITY

The decrease of seed set is a very sensitive criterion of radiation damage in the year of irradiation. The results are presented in Figures 1 (c) and 2 (c) for the 2 experimental years. In 1963 almost no kernels developed after irradiations on 27–28 and 30–31 July. In 1962 all dose treatments gave decreased fertilities compared with

TABLE 3. The correlation between the temperature at the time of acute irradiation of Bonus barley in 1962 and 1963 and the fertility in γ_1 , and the precipitation during the days of irradiation

Year	Date of irradiation	Correlation coefficients	Precipitation (mm)
1962	19 July	0.797	0.4
1962	21 July	0.367	—
1962	23 July	0.405	—
1962	25 July	0.991	3.6
1963	2–3 August	0.764 (0.887) ¹	—
1963	5–6 August	0.704 (0.975)	0.5 (6 August)

1. Correlation coefficients, given in parentheses, are based on the thermohygrograph records.

the control. The material irradiated on 25 July yielded significant differences between the series, a trait congruent with the vegetative development of the material. For the treatments in the remaining 3 days, the irradiations at midnight and in the morning again appear to be the most effective.

Large differences are evident between the series irradiated in 1963, and the 2 series 801b and 801c again showed the largest effects. Series 801d, 801e and 801f gave different patterns in the 2 sets of irradiation in August. In Figure 2 (a) the temperatures recorded by the thermohygrograph placed in the gamma field are shown. These records showed a difference of 3°C between the times for irradiation of series 801d on 2 August and series 801f on 3 August, respectively. The fertility difference between the 2 treatments is significant. On 5–6 August the difference in temperature between the 2 times of irradiation was even larger (9°C) and a larger difference in fertility was observed. If such a correlation between the temperature at the time of irradiation and the effects recorded in γ_1 is not merely due to chance, the relatively high sensitivity of series

801b and 801c to irradiation may be explained as a temperature effect. As seen in Table 3, a correlation between temperature at irradiation and fertility at harvest exists. The correlation is most close when the thermohygrograph records are considered. This is not surprising since these records describe the temperature in the gamma field better than data collected about 2 km away. The strong correlation for material irradiated on 25 July in 1962 can be explained by the cloudy and rainy weather on this day, which facilitates good agreement between temperature readings at Röskär and in the gamma field.

GERMINATION IN γ_2

The results in Table 4 must be evaluated with caution due to the facts that (a) the seeds sown constitute a non-random sample of the flowers irradiated in γ_1 , and (b) the conditions for germination throughout the experimental area are not homogeneous. With these restrictions in mind, some general conclusions may be drawn. The first concerns the decreased germinability the later the material is irradiated. This tendency is not unexpected since damages induced at "later" stages will tend to appear in γ_2 (Hermelin, 1970). The second general trend concerns the differences between the series. Series 801b and 801c again seem to be most affected. If the last dates of irradiation of both years (25 July and 5–6 August, respectively) are more closely examined, there is a marked correlation between temperature at irradiation and germination in γ_2 , with the coefficients 0.889 and 0.909 (thermohygrograph values), respectively.

CONCLUDING DISCUSSION

Ionizing radiations, like other kinds of abnormal treatment, have been proved to disturb the normal course of plant development and ontogenesis. The severity of this interference depends on the conditions at the time of treatment. The ontogenetic stage of the plants irra-

TABLE 4. Germination in γ_2 of acutely irradiated Bonus barley in 1962 and 1963. Germination of control materials 73 and 70.9 per cent, respectively

Year	Date of irradiation	801b		801c		Series 801d		801e		801f	
		Seeds planted	Germination (%)								
1962	19 July	26	(62)	12	50	58	79.3	71	60.6	—	—
1962	21 July	109	73.4	171	74.9	194	71.1	451	78.5	—	—
1962	23 July	456	65.4	326	50.6	693	77.8	434	68.4	—	—
1962	25 July	603	58.7	615	64.9	674	66.8	619	61.9	—	—
1963	27–28 July	1	(0)	—	—	10	(40)	3	(67)	36	(75)
1963	30–31 July	—	—	—	—	10	(60)	7	(14)	18	(67)
1963	2–3 August	65	50.8	27	(59)	529	57.7	513	55.9	457	62.1
1963	5–6 August	125	40.8	156	50.6	772	61.0	911	64.3	377	51.5

Note: Figures between brackets = germination figures for treatments with less than 50 seeds planted.

diated is one important factor. It has been shown in the present investigation that there are large differences in radiation effects, even between materials irradiated at different times within a short period of barley ontogenesis. Similar results have also been reported by Devreux and Scarascia Mugnozza (1964) in *Nicotiana tabacum*.

Besides ontogenetically conditioned radiation sensitivity, large differences between series irradiated at various times of the day were observed. One factor, the radiation dose, is kept constant and consequently one must assume that the primary effects must be similar for all series irradiated on the same day (series 801f in 1963 included). If this assumption is true, the observed differences between series must depend on varying abilities to repair and compensate for the induced damages. One way to test this hypothesis is to see if there is a diurnal periodicity which enhances or decreases radiation effects. Mäkinen (1963) found a diurnal mitotic activity in *Allium cepa*, roots, even when the material was illuminated continuously and the temperature was kept constant. If there were a diurnal periodicity, the differences in the effects between any 2 series irradiated on the same day would be similar for all instances of irradiation. This was not found, at least not when the 2 series 801d and 801f are studied (Tables 2 and 4, Fig. 2).

The second way to explain the reactions of different series to irradiation is to attempt to correlate the temperature and the magnitude of radiation effects; such a correlation seems strong (Table 3). It is known that a comparatively low temperature retards growth (Pope, 1943) and causes a prolonged mitotic cycle time (Evans

and Savage, 1959; López-Sáez *et al.*, 1969). As a consequence of this temperature-dependent cytological activity, the plant cells show an increased sensitivity to irradiation at lower temperatures (Sparrow and Evans, 1961). Furthermore, Caldecott (1961) showed that a pre- or post-treatment of barley seeds at 75° C decreased the radiation effects compared with seeds treated at a constant temperature of 20° C. Sparrow and Evans (1961) discussed the possible influence of a higher oxygen pressure at lower temperatures as a factor for increased radiosensitivity. However, in evaluating the ultimate effect of the treatment, one must consider not only the primary effects of the radiation, but also the capacity of the plant material for repair. Kiefer (1967) concluded that the restitution processes are slowed down by decreased culture temperatures. This decreased capacity to compensate for radiation damages may depend on a lower mobility of the chromosomes and, consequently, a decreased capacity for restitution. The results obtained in the present investigation indicate that differences between series exposed to gamma radiation the same day must primarily depend on the actual temperatures at the time of irradiation.

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Résumé

Effets d'une irradiation gamma intense sur des plants d'Orge en croissance, dans des conditions diverses d'environnement (T. Hermelin)

Des plants en croissance de la variété d'Orge à deux rangs Bonus ont été exposés à la source de rayons gamma ^{137}Cs à Bogesund (Suède). En 1962 et en 1963, on a soumis 4 séries différentes à la dose de 800 rad pendant une heure, le même jour, à minuit, dans la matinée, à midi et dans l'après-midi. En 1963, une série supplémentaire a été irradiée le lendemain à midi. Chaque suite de traitements a été répétée 4 fois chacune de ces deux années, les périodes d'expérimentation ayant atteint, au total, 7 jours en 1962 et 11 jours en 1963. Des examens cytologiques ont montré que les fleurs étaient en haplophase pendant les périodes expérimentales.

Les effets ci-après du rayonnement ont été mesurés sur le matériel étudié, qui a également fait l'objet de contrôles: survie, nombre d'épillets par épis, dévelop-

pement végétatif, fécondité et germination sur le terrain l'année suivante. On a constaté qu'il y avait des effets différents sur le matériel irradié des deux années, mais que les rapports entre les séries étaient congruents. L'intensité des effets du rayonnement différait selon le jour de l'irradiation, ce qui a été attribué essentiellement à des différences d'ordre génétique de la sensibilité au rayonnement. En comparant les traitements effectués le même jour, on a constaté que les irradiations faites à minuit et dans la matinée avaient eu le plus d'effet. On a trouvé de fortes corrélations entre la température au moment du traitement et la fécondité dans l'année de l'irradiation, ainsi qu'entre la température et la germination l'année suivante. Dans l'un et l'autre cas, les effets les plus intenses ont été obtenus à de basses températures, quel que fût le moment de la journée où le matériel avait été irradié. Les effets importants semblent dépendre d'une moindre aptitude à réparer les dégâts provoqués par le rayonnement.

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Bilan énergétique de la feuille. Application de l'étude des cinétiques de température à la détermination des résistances aux flux gazeux

S. de Parcevaux et A. Perrier,
avec la collaboration technique de J.-P. Le Buhan
Station centrale de bioclimatologie,
Institut national de recherches agronomiques,
Versailles (France)

INTRODUCTION

Les échanges gazeux de vapeur d'eau et de gaz carbonique entre les feuilles et l'air sont essentiels à la vie des plantes; c'est pourquoi de nombreuses recherches sont entreprises afin de mieux les définir. Dans cette voie, l'étude du bilan énergétique a retenu depuis quelques années l'attention d'un certain nombre de chercheurs. En fait, les feuilles constituent des surfaces d'échanges gazeux et énergétiques entre la plante et le milieu aérien environnant. D'un point de vue aérodynamique, l'écoulement de l'air est perturbé au niveau de ces surfaces, et il se crée une couche d'air à fort gradient de vitesse, vitesse qui s'annule au niveau de la paroi. Cette couche d'air est un obstacle aux échanges qui s'exprime souvent en terme de résistance (Bange, 1953; Raschke, 1958; Parcevaux, 1963; Linacre, 1966; Impens, 1966; Impens *et al.*, 1967) et, plus rarement, en longueur de diffusion ou épaisseur d'une couche limite équivalente à travers laquelle les échanges n'auraient lieu que par diffusion moléculaire (Bouchet, 1963; Parcevaux, 1964, 1966; Linacre, 1966; Perrier, 1968; Daudet et Perrier, 1968). Cette dernière notion n'est représentative des phénomènes physiques qu'au niveau strict de la surface.

Après quelques rappels commentés des notions fondamentales intervenant dans l'équation du bilan énergétique au niveau d'une feuille, les différentes manières d'exprimer les longueurs de diffusion ou les résistances dans le cas des feuilles dissymétriques seront précisées. Puis une étude de la cinétique de la température sous l'influence d'un flux de rayonnement additionnel conduira à la détermination des longueurs de diffusion dans les conditions naturelles et pour des feuilles symétriques; les résultats seront comparés à ceux obtenus par deux autres méthodes. Enfin, la dernière partie sera consacrée à une très brève esquisse de la généralisation de cette méthode au cas des feuilles dissymétriques.

RAPPELS ET COMMENTAIRES. ÉQUATION GÉNÉRALE DU BILAN ÉNERGÉTIQUE D'UNE FEUILLE

Alors que les échanges énergétiques se font d'une façon homogène par l'ensemble de la surface, la diffusion des gaz, pour sa grande majorité, emprunte la voie stomatique. Il apparaît ainsi une nouvelle résistance, ou longueur de diffusion, qui s'ajoute à la précédente. La première dépend essentiellement des conditions physiques (vent, rugosité, dimension); la deuxième est sous l'influence de la régulation stomatique liée à l'état physiologique du végétal.

Dans tous les cas où la diffusion moléculaire existe, on est en droit d'adopter la loi de Fick. En exprimant la densité de flux de vapeur d'eau en équivalent énergétique φ_L , et en considérant les phénomènes au niveau de la surface de la feuille, on peut écrire:

$$\varphi_L = -L D \frac{0,622}{R_a T} \frac{p(T_s) - p(T_r)}{\delta + \delta'} = -L \Lambda \frac{p(T_s) - p(T_r)}{\delta + \delta'} \quad [1]$$

L est la chaleur latente de vaporisation de l'eau; D , la diffusivité de la vapeur d'eau dans l'air; R_a , la constante des gaz relative à l'air sec; T , la température absolue; T_s , la température de surface; T_r , celle du point de rosée dans l'air ambiant; $p(T)$ est la pression de vapeur saturante; Λ défini par la relation [1] a la dimension d'un temps et peut être appelé temps de diffusion de la vapeur d'eau dans l'air (Daudet et Perrier, 1968); δ est l'épaisseur de la couche limite relative à la vapeur d'eau et δ' la longueur de diffusion équivalente à l'ensemble stomate et cuticule; δ' est nul pour une surface mouillée.

De même, la densité de flux de chaleur φ_s peut s'écrire:

$$\varphi_s = -a \rho C_p \frac{T_s - T_a}{\delta T} = -K \frac{T_s - T_a}{\delta T} \quad [2]$$

a est la diffusivité thermique; K désigne la conductivité thermique de l'air; C_p est la chaleur spécifique à pression constante; ρ la masse spécifique de l'air; T_a , la température de l'air; δ_T est l'épaisseur de la couche limite relative à la température.

Les résistances sont habituellement définies par le quotient d'un écart de « concentration » (grandeur x par unité de volume) à la densité de flux correspondante (grandeur x par mètre carré et par seconde). Ainsi, par rapport aux échanges de chaleur, on définit classiquement une résistance r_a [$\sim \Delta(\rho C_p T)/\varphi_s$], mais on définit de même par rapport aux échanges de masse ou de vapeur d'eau par exemple une résistance r'_a [$\sim \Delta(LC)/\varphi_s$] où C est la concentration de l'élément considéré. D'après [1] et [2], on aura:

$$r_a = \frac{\delta T}{a} \text{ et } r'_a = \frac{\delta}{D} \quad [3]$$

Ces deux relations sont équivalentes. Certains chercheurs (Linacre, 1966; Impens *et al.*, 1967) choisissent la première forme, d'autres la deuxième (Bange, 1953; Gates, 1968).

En régime purement turbulent, les deux paramètres r_a et r'_a tendent vers des valeurs voisines, mais en régime laminaire:

$$\frac{\delta T}{\delta} = (a/D)^{1/3}, \text{ d'après Brun, (1956)}$$

et:

$$\frac{r_a}{r'_a} = \frac{D}{a} \cdot \frac{\delta T}{\delta} = \frac{D}{a} \cdot \left(\frac{a}{D}\right)^{1/3} = \left(\frac{D}{a}\right)^{2/3} = f^{2/3} = 1,12 \quad [4]$$

Il est donc essentiel de préciser, lors d'une détermination, la définition choisie.

En introduisant la constante psychrométrique γ , définie selon Bernard (1969), et en appliquant la formule des accroissements finis à la différence des pressions de vapeur, les relations [1] et [2] peuvent s'écrire pour une face de la feuille:

$$\varphi L = -L \Lambda P' \frac{(T_s - T_r)}{\delta + \delta'} \quad [1']$$

$$\varphi_s = -L \Lambda \gamma \frac{T_s - T_a}{\delta} \quad [2']$$

A un instant donné, l'équation générale du bilan sera:

$$\varphi + \varphi_e + \varphi_s + \varphi_L - MC \frac{dT}{dt} = 0 \quad [5]$$

où φ représente la densité de flux de rayonnement incident absorbé, φ_e celle du rayonnement émis; MC est la masse en eau par unité de surface de feuille, et dT/dt la variation de température en fonction du temps.

Pour une feuille mince, le gradient interne de température est négligeable (Perrier, 1966, 1968; Bernard, 1968). Les températures T_s des deux faces sont donc les mêmes.

La densité de flux de rayonnement émis par les deux faces de la feuille est donnée par:

$$\varphi_e = -2\epsilon\sigma T_s \quad [6]$$

ϵ est l'émissivité de la feuille, σ la constante de Stefan-Boltzman, T_s la température de la feuille en °K.

IMPORTANCE DE LA SYMÉTRIE DES DEUX FACES DE LA FEUILLE

Habituellement, l'analyse des échanges au niveau d'une face introduit deux types de longueur de diffusion (l'une dans l'air δ , l'autre au niveau de la cuticule et des stomates δ'). L'extension de ce mode d'expression à l'ensemble de la feuille conduit à définir globalement deux valeurs dont la signification est plus complexe, et qui ne sont plus indépendantes. C'est la relation de dépendance entre ces différents termes qui est analysée ici en fonction de la dissymétrie des deux faces d'une feuille.

Dans le cas le plus général, si δ_i , δ_s , δ'_i , δ'_s sont les longueurs de diffusion relatives aux couches limites et à l'ensemble stomates-cuticule, des faces inférieures (indice i) et supérieures de la feuille (indice s), les équations [1] et [2] écrites pour la somme des deux faces deviennent:

$$\varphi_L = -L \Lambda P'(T_s - T_r) \left(\frac{1}{\delta_s + \delta'_s} + \frac{1}{\delta_i + \delta'_i} \right) \quad [1'']$$

$$\varphi_s = -L \Lambda \gamma (T_s - T_a) \left(\frac{1}{\delta_s} + \frac{1}{\delta_i} \right) \quad [2'']$$

On peut poser les trois relations [7], [8] et [9]:

$$\frac{2}{\delta} = \frac{1}{\delta_i} + \frac{1}{\delta_s} \quad [7]$$

[Expression permettant de traduire la valeur de la longueur de diffusion relative à l'air dans le cas d'une dissymétrie entre les deux faces de la feuille; une différence de rugosité ou de position par rapport à l'écoulement d'air entraîne une inégalité entre δ_i et δ_s ($\delta_i \neq \delta_s$); la dissymétrie est exprimée par la valeur de β ($\beta = \delta_i/\delta_s$.)]

$$\frac{2}{\delta'} = \frac{1}{\delta'_i} + \frac{1}{\delta'_s} \quad [8]$$

[Expression permettant de traduire la valeur moyenne de la longueur de diffusion relative à l'ensemble stomates-cuticule; une dissymétrie morphologique ou de régulation entre les deux faces de la feuille entraîne une inégalité entre δ'_i et δ'_s ; la dissymétrie est exprimée par la valeur d' α ($\alpha = \delta'_i/\delta'_s$.)]

$$\frac{2}{\delta + \delta'} = \frac{1}{\delta_s + \delta'_s} + \frac{1}{\delta_i + \delta'_i} \quad [9]$$

[Expression permettant de traduire globalement l'effet d'une double dissymétrie; dans ce cas, δ' dépend non

seulement des stomates et de la cuticule, mais aussi des couches limites des deux faces; δ et $\delta' + \delta''$ sont directement mesurables sans qu'il soit nécessaire de connaître leurs composantes; par contre, δ'' ne dépend que des stomates et de la cuticule, mais n'est pas mesurable lorsque δ'_i et δ'_s ne sont pas tous les deux connus.]

La dépendance de δ' avec les couches limites δ_s et δ_i n'est que rarement signalée (Raschke, 1958; Moreshet et al., 1968). Ces derniers ont comparé dans un certain nombre de cas les valeurs de δ' et δ'' en utilisant un calculateur.

Nous allons exposer ici un calcul général permettant d'analyser tous les cas de feuilles, quelle que soit la valeur relative des différentes longueurs de diffusion, sans toutefois dissocier la diffusion cuticulaire de celle des stomates. Il est en effet très difficile de séparer ces deux trajets qui sont soumis aux modifications mécaniques soit des stomates, soit des pores de la cuticule. La régulation stomatique est évidemment plus importante que la régulation cuticulaire, mais cette dernière n'est pas négligeable, et il est en conséquence souvent difficile de savoir si les stomates sont réellement totalement fermés ou encore très légèrement entrouverts.

En tenant compte des relations [7] et [9], il est possible d'écrire:

$$\frac{\delta'}{\delta} = 2 \frac{\delta'_i}{\delta'} \frac{2 \frac{\delta_i}{\delta_s} \cdot \frac{\delta'_i}{\delta} + \frac{\delta'_i}{\delta_s} + \left(\frac{\delta_i}{\delta_s}\right)^2}{2 \frac{\delta_i}{\delta_s} \left(1 + \frac{\delta'_i}{\delta_s}\right) \frac{\delta'_i}{\delta} + \frac{\delta'_i}{\delta_s} \left(1 + \frac{\delta_i}{\delta_s}\right)^2} \quad [10]$$

soit, en introduisant α et β et en posant $Y = \delta'/\delta$ et $X = \delta'_i/\delta$,

$$Y = 2X \frac{2\beta X + \alpha + \beta^2}{2\beta(1+\alpha)X + \alpha(1+\beta)} \quad [10']$$

Suivant les différentes valeurs d' α et de β , on peut tracer les courbes Y en fonction de X , c'est-à-dire donnant δ' en fonction de la longueur de diffusion cuticulo-stomatique de la face inférieure de la feuille, δ' représentant la valeur couramment donnée dans la littérature pour la résistance moyenne d'origine cuticulo-stomatique d'une feuille. La représentation serait identique si l'on avait choisi la longueur de diffusion cuticulo-stomatique de la face supérieure.

Pour les valeurs positives de X et Y , la dérivée première par rapport à X de l'équation [10'] est toujours positive: elle est donc constamment croissante; la dérivée seconde, toujours négative, s'annule pour $\alpha = \beta$, ce qui conduit alors à une relation linéaire entre X et Y (fig. 1). La pente à l'origine est donnée par:

$$Y'(X''=0) = 2 \frac{\alpha + \beta^2}{\alpha(1+\beta)^2} \quad [11]$$

L'équation de l'asymptote est:

$$Y = \frac{2X}{1+\alpha} + \frac{(\alpha-\beta)^2}{\beta(1+\alpha)^2} \quad [12]$$

La figure 1 représente la construction de quelques courbes $Y=f(X)$ dans le cas général et dans quelques cas particuliers pour $\alpha=0$, $\alpha=\beta$ et $\alpha \rightarrow \infty$. La figure 2 représente le faisceau de courbes obtenu pour cinq valeurs de α et trois valeurs de β .

La dissymétrie externe (présence de poils sur une face, orientation par rapport au vent...) ou écart du paramètre β vis-à-vis de l'unité, a moins d'influence que la dissymétrie dans la répartition des stomates traduite par les valeurs d' α . $\alpha \rightarrow \infty$ correspond par exemple à une feuille dont la face supérieure serait mouillée par suite de la présence de rosée, la face inférieure étant sèche. $\alpha=0$ correspond à une feuille dont la face supérieure serait très cutinisée et ne porterait pas de stoma (exemple: feuille d'Olivier).

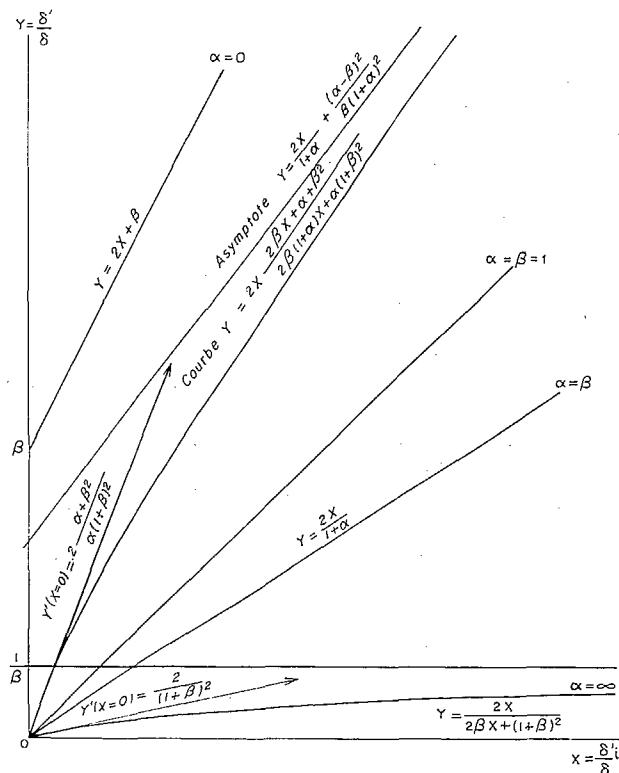


FIG. 1. Relation théorique donnant la variation de la longueur de diffusion moyenne d'une feuille δ' , valeur habituellement utilisée pour définir l'action de la cuticule et des stomates en fonction de la longueur de diffusion relative à la face inférieure pour un cas quelconque de dissymétrie α (biologie) et β (aérodynamisme). Quatre cas particuliers ont été également présentés:

- $\alpha = 0$ (face supérieure parfaitement imperméable);
- $\alpha = \beta = 1$ (symétrie aérodynamique et biologique parfaite);
- $\alpha = \beta$ (même dissymétrie pour l'aérodynamisme et la biologie);

$\alpha \rightarrow \infty$ (face supérieure parfaitement évaporante). Les écarts entre δ' et les valeurs réelles de δ' et δ'_s ($\delta'_s = \delta'_i/\alpha$) peuvent être considérables.

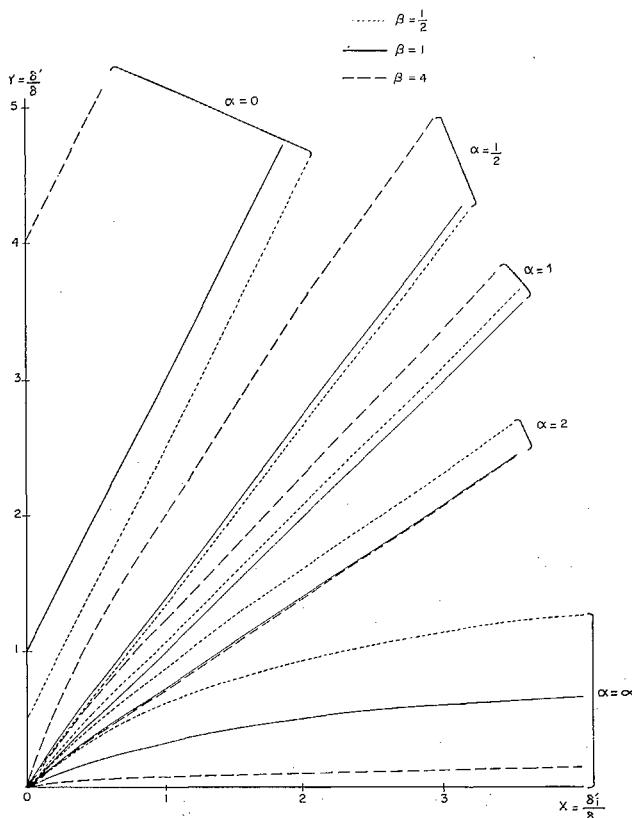


FIG. 2. Faisceau de courbes pour trois valeurs de dissymétrie aérodynamique ($\beta = \frac{1}{2}, 1$ et 4) et pour cinq valeurs de dissymétrie biologique ($\alpha = 0, \frac{1}{2}, 1, 2, \infty$) correspondant aux courbes théoriques présentées sur la figure 1.

Ainsi, pour une feuille donnée (α) et pour une valeur globale δ' déterminée de façon classique, il correspond des valeurs réelles de δ'_i et de δ'_s ($\delta'_s = \delta'_i/\alpha$) qui dépendent d'autant plus de β (dissymétrie aérodynamique) qu' α est différent de 1.

Inversement pour une valeur de δ'_i (par exemple, $\delta'_i = \delta$) et pour une dissymétrie aérodynamique donnée ($\beta = 1$), δ' variera de $0,3 \delta$ à 3δ suivant la valeur d' α ; cette variation sera plus grande pour $\beta > 1$ et plus faible pour $\beta < 1$.

Les figures 1 et 2 montrent bien l'erreur qu'on commet dans le cas où α et β sont différents de l'unité, en assimilant δ' à la longueur de diffusion cuticulo-stomatique moyenne de la feuille.

Cette erreur est classique lors du calcul de la longueur de diffusion (ou de la résistance) cuticulo-stomatique par la méthode du « rameau coupé » pour les feuilles dissymétriques. Dans ce cas, il est indispensable de pouvoir dissocier les caractéristiques de chacune des deux faces.

Grâce à la relation [8], il est possible de comparer, comme Moreshet *et al.* (1968), mais par le calcul direct, les valeurs de δ' et δ'' .

En reportant dans [10'] le rapport $\frac{\delta''}{\delta}$ obtenu d'après [8], il vient, en posant $Z = \delta'/\delta''$:

$$Z = \frac{X + \frac{\alpha + \beta^2}{2\alpha}}{X + \frac{\alpha}{1+\alpha} \cdot \frac{(1+\beta)^2}{2\beta}} = 1 + \frac{\frac{(\alpha - \beta)^2}{2\beta(1+\alpha)}}{X + \frac{\alpha}{1+\alpha} \cdot \frac{(1+\beta)^2}{2\beta}} \quad [13]$$

Comme précédemment, il serait possible de tracer les courbes donnant Z en fonction de X pour diverses valeurs des paramètres α et β . Le faisceau de courbes obtenues conduirait aux mêmes conclusions.

ÉTUDE DE LA CINÉTIQUE DE LA TEMPÉRATURE SOUS L'INFLUENCE D'UN FLUX DE RAYONNEMENT ADDITIONNEL. APPLICATION A LA DÉTERMINATION DES LONGUEURS DE DIFFUSION DANS LE CAS D'UNE FEUILLE A SYMÉTRIE DORSIVENTRALE

La symétrie bifaciale absolue est assez rare dans le règne végétal; elle se rencontre chez les Phyllodes (Acacia) et les Cladodes. Mais pour beaucoup de plantes, notamment les Graminées et en particulier le Maïs, il existe une symétrie bifaciale approximative, ce qui justifie l'étude de ce premier cas simplifié.

L'équation générale [5] du bilan s'écrit alors, compte tenu des relations [1'], [2'] et [6]:

$$\varphi - 2\varepsilon\sigma T_o + 2LA\gamma \frac{T_a - T_o}{\delta} - 2LA P'or \frac{T_o - T_r}{\delta + \delta'} - MC \frac{dT_o}{dt} = 0 \quad [14]$$

La température de la feuille T_o peut être déterminée grâce à un thermocouple convenablement introduit dans la feuille (Perrier, 1968) ou par radiométrie infrarouge, si l'émissivité est uniforme. Un psychromètre pourra donner les températures T_a et T_r . Pour la masse en eau de la feuille, certains chercheurs (Linacre, 1966) adoptent une valeur moyenne: il nous semble préférable de la déterminer à la fin de chaque série d'expériences. Pour cela, il faut séparer l'eau de la matière sèche, ce qui revient à écrire:

$$MC = M_s C_s + M_E C_E$$

M_s et M_E étant les masses de matière sèche et d'eau par unité de surface; C_s et C_E , les chaleurs massiques avec:

$$C_s = 0,3 \text{ cal. g}^{-1} = 1250 \text{ J. kg}^{-1}$$

$$C_E = 1 \text{ cal. g}^{-1} = 4180 \text{ J. kg}^{-1}$$

La première valeur est provisoire; des déterminations précises sur différents végétaux sont envisagées; δ et δ' sont les inconnues recherchées; φ est également une inconnue qui sera éliminée ultérieurement.

Un des avantages principaux de l'utilisation de l'équation [14] est de permettre la détermination des longueurs de diffusion des feuilles en place.

Impens (1966) a appliqué aux feuilles de Haricot placées dans les conditions naturelles, une équation analogue en supposant le régime isotherme établi. Dans ce cas, deux expériences sont nécessaires pour calculer δ et δ' (ou r_a et r_s); l'une est réalisée avec une feuille normale, l'autre avec une feuille recouverte d'un film autocollant imperméable à la vapeur d'eau (Impens, 1966) ou enduite d'un antitranspirant (Perrier, 1966; Hunt et Impens, 1968). Le rayonnement absorbé φ est admis identique dans les deux cas.

Linacre (1966) et Perrier (1966) ont simultanément et indépendamment publié deux études de la cinétique de la température d'une feuille soumise à une variation brusque du rayonnement incident. Dans les deux cas, les expériences ont été faites au laboratoire. Comme le soulignent ces auteurs, le temps, de l'ordre de la minute, nécessaire pour déterminer les caractéristiques de la cinétique de température est largement inférieur au temps de réaction d'ouverture ou de fermeture des stomates.

L'étude suivante constitue une synthèse des travaux d'Impens, de Linacre et de Perrier complétée par quelques apports originaux en vue de l'utilisation au champ. Les modifications quasi permanentes introduites par Impens sont remplacées par des conditions réversibles (mouillage d'une ou des deux faces, ventilation additionnelle). Une amélioration essentielle apportée par l'un des auteurs pour l'étude des cinétiques en conditions naturelles consiste à utiliser un spot lumineux focalisé (1 centimètre carré environ de surface), ce qui permet d'étudier non plus la cinétique de la température, mais celle de la différence des températures entre deux points voisins (2 à 4 centimètres) d'une même feuille. La mesure différentielle peut être directement obtenue grâce aux deux sondes d'un même thermocouple ou à l'aide d'un radiotermomètre spécialement équipé à cet effet. L'avantage de cette méthode différentielle est considérable, car elle supprime l'influence des fluctuations rapides du milieu ambiant (vent, rayonnement).

ÉTUDE THÉORIQUE

Reprenons l'équation [14] dans le cas d'un rayonnement additionnel $\Delta\varphi_1$:

$$\varphi + \Delta\varphi_1 - 2\varepsilon\sigma T'_1 + 2L\Lambda\gamma \frac{T_a - T_1}{\delta} - 2L\Lambda P'_{1r} \frac{T_1 - T_r}{\delta + \delta'} - MC \frac{dT_r}{dt} = 0 \quad [15]$$

Par soustraction des deux équations [14] et [15], il vient en posant: $\Delta T_{o1} = T_1 - T_o$ [16]

$$\begin{aligned} \Delta\varphi_1 - 2C\varepsilon\sigma T_o^3 \Delta T_{o1} - \frac{2L\Lambda\gamma}{\delta} \Delta T_{o1} - \frac{2L\Lambda P'_{o1}}{\delta + \delta'} \\ \Delta T_{o1} - MC \frac{d(\Delta T_{o1})}{dt} = 0 \end{aligned} \quad [17]$$

avec $C \simeq 4 + \frac{6\Delta T_{o1}}{T_o}$ et en pratique on prend en pre-

mière approximation $T_o^3 \sim T_a^3$ et pour le calcul de C , $T_o \sim T_a$ et $\Delta T_{o1} \sim \frac{(\Delta T_{o1})M}{2}$

En toute rigueur, la température initiale T_o peut être mesurée et utilisée dans le calcul du terme de flux émis.

Les variations simultanées de T_o et T_1 dues à un même facteur externe sont ainsi éliminées de la cinétiqe. L'avantage essentiel de la méthode différentielle réside dans ce phénomène.

Lorsque le régime permanent est atteint, le dernier terme de l'équation [17] est nul, d'où:

$$\delta' = \delta \left[\frac{\frac{P'_{o1}/\gamma}{(\Delta\gamma_1)/(\Delta T_{o1})M} - 2C\varepsilon\sigma T_a^3}{\frac{\delta}{2L\Lambda\gamma} - 1} - 1 \right] \quad [18]$$

Dans le cas d'une feuille mouillée sur les deux faces ($\delta=0$) et T_2 et T_3 étant les températures initiale et finale:

$$\delta = \frac{2L\Lambda(P'_{23} + \gamma)}{\frac{\Delta\varphi_2}{(\Delta T_{23})M} - 2C\varepsilon\sigma T_a^3} \quad [19]$$

en supposant les couches limites identiques sur la feuille mouillée et sèche, il devient possible de déterminer δ et δ' .

Dans le cas d'une feuille dont la transpiration serait bloquée par un film plastique ou un antitranspirant (Impens, 1966; Hunt et Impens, 1968), l'équation [17] donne, T_4 et T_5 étant les températures initiale et finale:

$$\delta = \frac{2L\Lambda\gamma}{\frac{\Delta\varphi_3}{(\Delta T_{45})M} - 2C\varepsilon\sigma T_a^3} \quad [20]$$

Les valeurs de δ calculées à partir des équations [19] et [20] doivent être identiques. En admettant que la présence d'eau, d'un film plastique ou d'un antitranspirant ne modifie pas l'albédo de la feuille, on a:

$$\Delta\varphi_1 = \Delta\varphi_2 = \Delta\varphi_3 \quad [21]$$

cette égalité peut être vérifiée par l'expérience. En effet, pour déterminer ces valeurs de $\Delta\varphi$, il faut étudier les phénomènes immédiatement avant et après l'allumage ou l'extinction du rayonnement additionnel. Avant l'allumage, le premier et le dernier membre de l'équation [17] sont nuls, car le système est en équilibre, c'est-à-dire:

$$(\Delta T_{o1})_t = 0 \left(2C\varepsilon\sigma T_a^3 + \frac{2L\Lambda\gamma}{\delta} + \frac{2L\Lambda P'_{o1}}{\delta + \delta'} \right) = 0 \quad [17']$$

Il est d'ailleurs fort probable, et l'expérience le montre, que, si les points de mesure ont été correctement choisis, l'écart $(\Delta T_{o1})_t=0$ est égal à zéro, et l'équation [17'] est identiquement nulle.

Une fraction de seconde après l'allumage (fraction suffisamment courte pour que l'écart (ΔT_{o1}) n'ait pas encore eu le temps de varier), l'équation [17] est valable et, en tenant compte de [17'], que ΔT_{o1} soit nul ou non il vient:

$$\Delta\varphi_1 = MC \left[\frac{d(\Delta T_{o1})}{dt} \right] t=0 \quad [22]$$

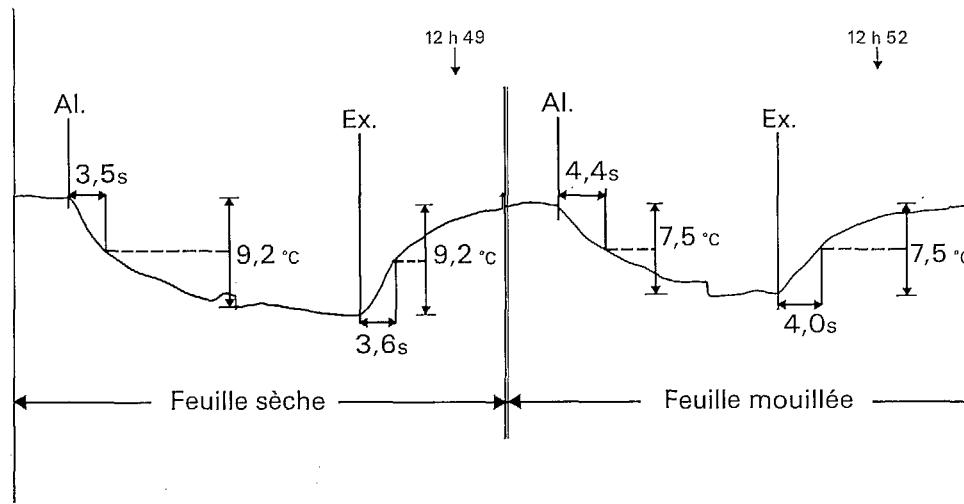


FIG. 3. Exemple de cinétique de réchauffement et de refroidissement pour une feuille sèche puis mouillée sur sa face inférieure ($\delta^*_i = 0$ et $\alpha = 0$). Al. = Allumage du flux additionnel; Ex. = Extinction du flux additionnel.

la pente à l'origine de la cinétique de réchauffement donne donc la valeur de $\Delta\gamma$.

A l'extinction (Perrier, 1968), la relation est identique, au signe près, la pente étant inversée.

Il est possible d'intégrer l'équation différentielle [17] en fonction du temps, en supposant les conditions aux limites suivantes:

$$(\Delta T_{o1})_{t=0} = 0$$

$$(\Delta T_{o1})_{t=\infty} = (\Delta T_{o1})_M$$

Dans ce cas, on obtient:

$$\log \left[1 - \frac{(\Delta T_{o1}) t}{(\Delta T_{o1}) M} \right] = - \frac{\Delta \varphi_1}{(\Delta T_{o1}) M} \cdot \frac{1}{MC} t \quad [23]$$

Cette théorie, confirmée par l'expression en conditions naturelles conduit à une variation exponentielle de l'écart de température lors de l'apport ou du retrait brutal d'un rayonnement additionnel $\Delta\varphi$ (fig. 3 et 4).

En considérant, comme Linacre (1966) la constante de temps, c'est-à-dire le temps $t \frac{1}{2}$ pour lequel $(\Delta T_{o1}) t = \frac{(\Delta T_{o1}) M}{2}$, on a:

$$\frac{\Delta \varphi_1}{(\Delta T_{o1}) M} = \frac{0,69 MC}{t \frac{1}{2}} \quad [24]$$

cette dernière technique de calcul est plus simple que celle représentée par l'équation [22], mais la façon la plus précise d'obtenir la pente à l'origine est, selon [23], de déterminer graphiquement la pente y' de la droite

donnant $\log \left[1 - \frac{(\Delta T_{o1}) t}{(\Delta T_{o1}) M} \right]$ en fonction du temps

(Perrier, 1966), on en déduit alors:

$$\frac{\Delta \varphi_1}{(\Delta T_{o1}) M} = - 2,30 y' MC \quad [25]$$

Connaissant ΔT_{o1} et MC , les relations [24] ou [25] permettent de déterminer $\Delta\varphi_1$. Dans le cas d'une feuille mouillée, MC ne peut être déterminée avec précision; cette difficulté disparaît en admettant la relation [21].

En tenant compte de [19], la relation [18] peut s'écrire:

$$\frac{\delta'}{\delta} = \frac{P'_{o1} / \gamma}{\left(\frac{P'_{23}}{\gamma} + 1 \right) \frac{\Delta \varphi_1 - 2 C \varepsilon \sigma T_a^3 (\Delta T_{o1}) M}{\Delta \varphi_2 - 2 C \varepsilon \sigma T_a^3 (\Delta T_{23}) M}} \quad [18']$$

$$\frac{(\Delta T_{23}) M}{(\Delta T_{o1}) M} - 1 \quad [18']$$

L'expérience montre que, notamment pour les feuilles de Mais:

$$\frac{\Delta \varphi_1 - 2 C \varepsilon \sigma T_a^3 (\Delta T_{o1}) M}{\Delta \varphi_2 - 2 C \varepsilon \sigma T_a^3 (\Delta T_{23}) M} \approx 0,95$$

et donc:

$$\frac{\delta'}{\delta} = \frac{P'_{o1} / \gamma}{0,95 \left(\frac{P'_{23}}{\gamma} + 1 \right) \frac{(\Delta T_{23})}{(\Delta T_{o1}) M} M - 1} \quad [18']$$

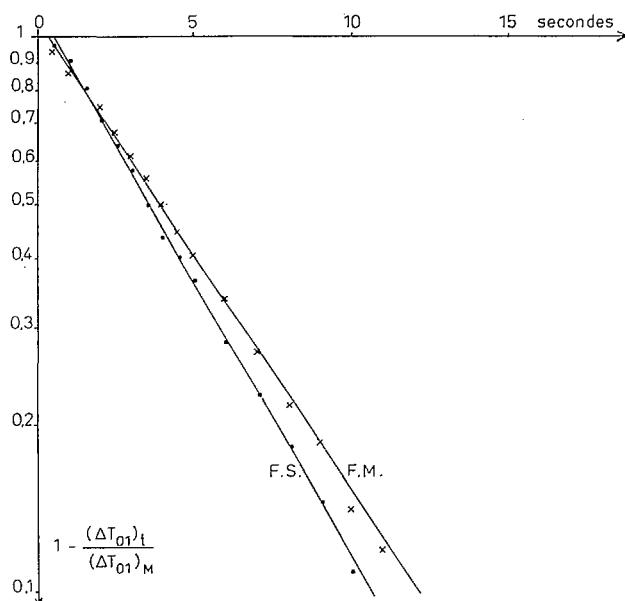


FIG. 4. Diagramme donnant en ordonnée logarithmique l'évolution du rapport $(\Delta T_{01})_M - (\Delta T_{01})_t$ en fonction du temps t

pour les deux cinétiques de refroidissement (extinction) présentées sur la figure 3 (feuille sèche, F.S. et feuille mouillée, F.M.). Le décalage de l'origine des temps provient d'une mauvaise appréciation du temps initial lors du dépouillement (erreur de 0,3 à 0,5 s).

Cette relation approchée est intéressante, car elle donne, sans avoir recours à la cinétique de la température ni à la détermination de la masse en eau MC , un ordre de grandeur du rapport des épaisseurs de diffusion ou, ce qui revient au même, des résistances dans la feuille et dans l'air.

En ce qui concerne l'équation [18], le résultat du calcul d'erreur n'étant pas très favorable, ce qui était à prévoir, il faut veiller à déterminer l'épaisseur δ de la couche limite dans l'air, la masse en eau MC de la feuille, et la pente à l'origine de la cinétique avec le maximum de précision. L'erreur sur δ' est en effet deux à trois fois supérieure à l'erreur sur chacun de ces termes.

RÉSULTATS

La figure 3 représente un exemple d'un enregistrement de l'écart de température ΔT obtenu sur une feuille de Maïs dans les conditions naturelles le 24 juillet 1969. La première partie de la courbe correspond à une feuille sèche et la deuxième à la même feuille partiellement

mouillée. La figure 4 donne la valeur de $\log [1 - \frac{(\Delta T_{01})_t}{(\Delta T_{01})_M}]$

en fonction du temps. Les droites obtenues permettent de déterminer la pente à l'origine des cinétiques de refroidissement. Cette feuille pesait $19 \text{ mg} \cdot \text{cm}^{-2}$.

Les résultats obtenus par cette technique ont été comparés (voir tableau, page suivante) à ceux obtenus par deux autres techniques.

En effet l'équation [1] appliquée au cas d'une feuille symétrique coupée et à celui d'une surface identique de papier buvard mouillé permet également de déterminer δ et δ' connaissant les températures de surface de la feuille et du papier buvard. Avec certaines précautions (Parcevaux, 1963, 1965), l'utilisation de cette équation donne des résultats valables, mais elle exige la destruction du matériel biologique, puisque la feuille doit être détachée de la plante pour permettre les pesées.

La deuxième technique a consisté à déterminer δ' grâce à l'emploi d'un poromètre à diffusion, mis au point par Djavanchir (1970) d'après le principe décrit par Wallihan (1964) et repris par Van Bavel *et al.* (1965). Les résultats de cette dernière technique ont permis d'apprécier le rapport $\frac{\delta'_1}{\delta'_s}$ et d'obtenir la valeur de δ' grâce à la relation [9].

Ces techniques ont été utilisées simultanément, mais sur des feuilles différentes d'une même culture de Maïs en conditions naturelles. Malgré cela, le tableau montre un accord acceptable entre les diverses valeurs expérimentales obtenues.

CAS D'UNE FEUILLE NON SYMÉTRIQUE

Dans ce cas, il faut déterminer les différentes longueurs de diffusion δ_i , δ_s , δ'_i et δ'_s relatives aux deux faces de la feuille. Le nombre d'inconnues étant plus grand, il est nécessaire de faire appel à d'autres conditions expérimentales: ventilation artificielle additionnelle combinée au mouillage de la face supérieure ou de la face inférieure de la feuille.

La théorie de ce cas général est élaborée, mais nous n'avons pas encore obtenu les résultats expérimentaux correspondants. En conséquence, il nous a paru préférable de ne pas alourdir davantage le texte de cet article.

CONCLUSION

Il se dégage de cette étude qu'il est indispensable de savoir à quel type de flux la résistance est relative. Dans le cas de comparaisons entre les différents résultats publiés, il convient évidemment de tenir compte des définitions utilisées.

Pour avoir un paramètre plus stable et plus représentatif des phénomènes réels, nous avons préféré utiliser les longueurs de conduction et de diffusion qui expriment dans une unité simple les épaisseurs des couches limites équivalentes. Tout a été ramené à la longueur de diffusion relative à la vapeur d'eau qui permet également de traduire le rôle de la cuticule et des stomates par une longueur fictive de diffusion. Les écarts entre les résistances relatives aux différents flux sont pratiquement

Résistances et longueurs de diffusion obtenues sur la troisième feuille à partir de l'épi mâle dans une culture de Maïs à La Minière, par pesée d'une portion de feuille (tr.), par l'étude du bilan énergétique (Cin.) et par porométrie de diffusion (Por.).

Feuille III		Résistance stomatique						R_a s. m. ⁻¹		δ m. 10 ⁻³		
		R _s s. m. ⁻¹			δ^* m. 10 ⁻³							
Date	Heure	tr.	Cin.	Por.	tr.	Cin.	Por.	Ev.	Cin.	Ev.	Cin.	
24-7-69	12 h 20-12 h 30	188	187	—	5,0	4,9	—	70	48	1,8	1,3	Vent fort
28-7-69	11 h 28-11 h 30	264	—	332	7,0	—	8,8	54	—	1,4	—	Vent modéré
	12 h 20-12 h 33	282	—	530	7,5	—	13,9	57	—	1,5	—	à fort
5-8-69	8 h 11- 8 h 55	—	388	305	—	10	7,7	—	101	—	2,6	Vent nul à faible
	9 h 20- 9 h 30	—	212	246	—	5,5	6,3	—	98	—	2,5	
	10 h 15-10 h 30	—	250	304	—	6,5	7,8	—	80	—	2,0	
	10 h 45	—	211	—	—	5,4	—	—	109	—	2,6	
	11 h 6-11 h 25	325	163	357	8,0	4,4	9,4	78	95	2,1	2,4	
	11 h 44-11 h 55	193	237	277	5,1	6,1	7,2	108	88	2,8	2,3	
	12 h 15-12 h 45	—	273	—	—	7,1	—	—	79	—	2,0	
	14 h 46-15 h 28	250	191	162	6,6	5,0	4,3	113	65	2,9	1,7	
	15 h 41-16 h 15	315	—	250	8,0	—	6,6	135	—	3,5	—	
	16 h 48-16 h 55	—	188	393	—	5,0	10,4	—	84	—	2,2	
	16 h 55-16 h 58	—	800	400	—	20,7	10,6	—	79	—	2,1	
	17 h 55	—	—	770	—	—	20	—	—	—	—	
	20 h 15	—	—	3 840	—	—	99	—	—	—	—	
10-9-69	15 h -15 h 25	322	460	—	8,2	11,7	—	54	54	1,35	1,35	Vent fort
	15 h 35-15 h 58	332	236	—	8,5	6,0	—	72	69	1,80	1,70	
	16 h 15	450	—	—	11,4	—	—	34	—	0,76	—	
	16 h 40-16 h 53	405	425	—	10,2	11,0	—	66	—	1,6	—	
	17 h 2-17 h 17	830	1 330	—	20,8	34	—	89	50	2,2	1,25	
	17 h 45-17 h 53	1 340	348	—	33,5	8,9	—	63	89	1,55	2,2	Vent modéré

réduits de moitié dans le cas de l'emploi des longueurs de conduction et de diffusion (5 à 10% au lieu de 10 à 20%).

Dans le cas des feuilles dissymétriques, il est nécessaire de déterminer les longueurs de diffusion ou les résistances, séparément pour les deux faces, si l'on veut pouvoir interpréter le rôle exact de la plante dans la diffusion gazeuse (transpiration, photosynthèse). Un paramètre global traduisant à la fois le végétal et le milieu ambiant, comme c'est le cas de la résistance habituellement nommée résistance stomatique, n'est pas suffisant. Une telle valeur n'est utilisable que si elle est complétée par au moins une des valeurs réelles relatives aux stomates et à la cuticule de l'une des faces.

L'étude du bilan énergétique de la feuille analysée par les cinétiques de réchauffement ou de refroidisse-

ment, dans les conditions naturelles, aux différents niveaux de la végétation, permet de déterminer les longueurs de diffusion ou les résistances aux flux gazeux sur les deux faces de la feuille. Dans le cas des feuilles symétriques, les techniques sont relativement simples à employer. Les résultats concordent d'une façon satisfaisante avec ceux obtenus par d'autres procédés.

Grâce à la radiométrie infrarouge, avec visée alternative de deux points voisins d'une feuille, il sera même possible d'effectuer ces déterminations sans toucher à l'organe végétal.

Les principaux avantages de cette technique sont les suivants: une grande rapidité et une faible perturbation aussi bien du milieu extérieur que de l'organe végétal lui-même. En contrepartie, cette technique est coûteuse et exige des calculs assez importants.

Summary

Flow energy balance of the leaf. Application of the study of the kinetics of temperature to the determination of resistances to gaseous fluxes (S. de Parcevaux and A. Perrier).

The determination of resistances at the level of the leaves under natural conditions with the least possible

disturbance is very useful in agronomy. For this purpose a method based on the analysis of the kinetics of heating and cooling, artificially induced (Figs 3 and 4), has been improved so that it can be used easily under natural conditions. It has been used on maize and compared with other methods (Table 1). Interpretation of such kinetics is based on a comparative study of the

energy flow at two neighbouring points in a leaf at first dry and then moistened. One of the points is subjected to a constant additional radiating flux (spot). Here the study is made not on the basis of the resistances, but on the basis of the diffusivities, which are more representative. Further, in the most probable case, that of a

dissymmetrical leaf (Figs 1 and 2), it shows the poor definition of stomatic resistance used until now, which led to an erroneous interpretation of the morphological and physiological role of the plant. (The error could be negligible or considerable according to the case.)

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Influence globale de la lumière, de la température et de l'humidité sur la photosynthèse et la respiration

Zh. V. Stojanov et R. J. Florov
Institut forestier
et École supérieure de sylviculture,
Sofia (Bulgarie)

Dans l'étude de l'influence des facteurs du milieu sur la croissance des plantes, on envisage en général séparément: l'influence de la lumière, l'influence de la température, l'influence de l'humidité, etc. Dans la présente communication, les auteurs démontrent qu'il existe une possibilité d'appréciation de l'influence globale de ces facteurs sur la photosynthèse et la respiration. C'est l'entropie de dissipation dans le feuillage des plantes. Cette méthode est exposée en détail dans la communication de Florov. Ici, les auteurs présentent l'application de cette méthode dans des investigations physiologiques sur la photosynthèse et la respiration. Les expériences ont été effectuées dans les directions suivantes: a) interdépendance entre l'entropie et la photosynthèse; b) coefficient d'utilisation de la photosynthèse brute.

Les expériences physiologiques ont été effectuées — dans un système fermé où l'air circule — avec des branchettes plongées dans un verre d'eau dont la surface a été recouverte de paraffine liquide, afin d'éliminer les différents échanges gazeux entre l'air et l'eau. On a mesuré la température des feuilles par thermocouple cuivre-constantan. Une des soudures a été fixée sur la surface inférieure de la feuille à l'aide d'une bande, alors que l'autre se trouvait à l'air libre à une distance de 1 centimètre.

La température de l'air a été mesurée à l'aide d'un thermomètre à mercure dont le réservoir se trouvait près de la soudure libre du thermocouple.

La transpiration a été mesurée par la méthode psychrométrique.

On a déterminé la photosynthèse (à la lumière) et la respiration (en obscurité) en mesurant la concentration de CO_2 de l'air circulant dans le système.

Cet air, avant d'entrer dans la cuvette, passait par un dispositif destiné à conditionner son humidité. Chaque expérience en air sec et en air humide durait trente minutes. Après chaque expérience, on ouvrait le système pendant dix minutes pour égaliser la concen-

tration de CO_2 dans le système avec celle de l'air libre.

Sur la base des données de la transpiration ($E \text{ g/cm}^2 \text{ mn}$), on a déterminé la chaleur consommée par la transpiration ($L.E.$, où $L \approx 600 \text{ cal/g}$). Le flux de chaleur P ($\text{cal/cm}^2 \text{ mn}$) a été déterminé par la différence de température feuille-air ΔT et le coefficient de l'échange de chaleur K_i ($\text{cal/cm}^2 \text{ mn } ^\circ\text{K}$) selon la formule $P=2K_i \cdot \Delta T$. Par ces données ont été déterminés le bilan de radiation $R = P+L.E.$ et la vitesse de l'entropie de dissipation σ_d selon la formule:

$$\sigma_d = P \frac{\Delta T}{T^2} + L.E. \frac{\Delta q}{T} \quad [1]$$

où Δq est la différence entre l'humidité spécifique de l'air au niveau des stomates et celle de l'air libre en g/g et T la température moyenne absolue feuille-air.

INTERDÉPENDANCE ENTRE L'ENTROPIE ET LA PHOTOSYNTHÈSE

Les expériences effectuées avec des branchettes de Tilleul (*Tilia grandifolia* L.) ont montré que la photosynthèse est plus élevée en air humide (85% humidité relative) qu'en air sec (45% humidité relative). Au contraire l'entropie de dissipation est plus faible en air humide qu'en air sec (tableau 1).

Il faut toujours comparer les résultats consécutifs en air sec et en air humide, parce que l'activité physiologique diminue avec la durée de l'expérience dans le climat de la cuvette.

On doit soit comparer les données moyennes de toutes les mesures qui sont: en air sec, la photosynthèse $0,000133 \text{ mg CO}_2/\text{cm}^2 \text{ mn}$, l'entropie de dissipation $\sigma_d = 0,00002295 \text{ J/cm}^2 \text{ mn } ^\circ\text{K}$; mais en air humide,

TABLEAU 1

Mesures consécutives de trente minutes	Photosynthèse mg CO ₂ /cm ² mn	Entropie de dissipation δ/cm ² min °K
Air sec	0,000208	0,00001594
Air humide	0,000281	0,00001052
Air sec	0,000148	0,00002730
Air humide	0,000163	0,00000830
Air sec	0,000044	0,00002560
Air humide	0,000148	0,00001097

la photosynthèse 0,000197 mg CO₂/cm² mn, et l'entropie de dissipation $-\sigma_d = 0,00000989 \text{ J/cm}^2 \text{ mn } ^\circ\text{K}$.

Ainsi l'entropie de dissipation et la photosynthèse ont une évolution contraire: en conditions favorables pour l'activité physiologique de la feuille, quand la photosynthèse est élevée, l'entropie de dissipation est basse, et au contraire, en conditions défavorables, la photosynthèse est basse, mais l'entropie de dissipation augmente. Par conséquent, l'entropie de dissipation est un indice sensible pour la réaction de la feuille vers la tension des conditions du milieu.

En outre, les données représentées montrent que l'entropie de dissipation est conjuguée avec la photosynthèse de la même façon que la respiration. Cela nous suggère qu'il faut chercher une liaison entre l'entropie et la respiration. Il serait possible de déceler une telle liaison si l'on pouvait déterminer le coefficient d'utilisation de la photosynthèse brute à l'aide de l'entropie de dissipation, au lieu de la respiration.

LE COEFFICIENT D'UTILISATION DE LA PHOTOSYNTHÈSE BRUTE DÉTERMINÉ PAR L'ENTROPIE DE DISSIPATION

Il est connu que la photosynthèse brute est égale à la somme de la photosynthèse nette et de la respiration pendant la photosynthèse. Le coefficient d'utilisation de la photosynthèse brute (CU) a été calculé en pourcentage du bilan de radiation R de la feuille:

$$\begin{aligned} CU\% &= \frac{\text{photosynthèse brute}}{R} \% \\ &= \frac{\text{photosynthèse nette} + \text{respiration}}{R} \% \end{aligned} \quad [2]$$

Pour déterminer la photorespiration, on mesure la respiration en obscurité immédiatement après la photosynthèse, en supposant qu'il existe sur l'intensité de la respiration une action postérieure à la période avec lumière. Beaucoup de chercheurs ont constaté que la respiration en obscurité dans de telles conditions est deux ou plusieurs fois plus élevée que s'il n'y a pas de période lumineuse et ils concluent que pendant la photosynthèse la respiration augmente.

Dans nos expériences, on faisait suivre chaque mesure de trente minutes de la photosynthèse d'une période obscure de trente minutes afin de déterminer la respiration et le coefficient d'utilisation selon la formule [2].

En outre, le coefficient d'utilisation de la photosynthèse brute a été déterminé par l'entropie de dissipation, conformément à la constatation que l'entropie est conjuguée avec la photosynthèse comme la respiration, selon la formule suivante:

$$CU\% = \frac{\text{photosynthèse nette} + T \cdot \sigma_d}{R} \% \quad [3]$$

où $T \cdot \sigma_d$ = chaleur de dissipation, qui doit exprimer quantitativement les pertes des assimilats pendant la respiration.

Dans le tableau 2 sont présentées les valeurs du CU calculées par les deux méthodes: la respiration en obscurité et par l'entropie de dissipation.

Les résultats du tableau 2 montrent que les valeurs de CU calculées par l'entropie sont plus élevées que celles calculées par la respiration. Pour le Peuplier, CU par l'entropie est 2,7 fois plus élevé que CU par la respiration; pour le Chêne 1,8 fois, etc. On peut expliquer ces différences grâce à la photorespiration, qui est plus élevée que la respiration en obscurité après la période lumineuse et grâce à l'entropie qui exprime quantitativement la photorespiration.

On démontre que l'entropie exprime la photorespiration par d'autres expériences sous différentes conditions de l'humidité de l'air et simultanément de la lumière. Ainsi des expériences avec le Tilleul montrent des valeurs égales du CU (1,4%), malgré les différentes valeurs de l'humidité de l'air (40 et 80%) et du bilan de la radiation (0,5769 et 0,3451 J/cm² mn).

En exprimant quantitativement la photorespiration, l'entropie de dissipation représente un indice global qui montre l'influence simultanée des trois facteurs essentiels du milieu sur la respiration, la photosynthèse et la croissance des plantes. Ayant à l'esprit qu'un tel indice n'existe pas en physiologie pour exprimer l'action commune des facteurs essentiels sur les phénomènes fondamentaux dans la plante, comme la respiration et la photosynthèse, on peut souligner l'importance de cet indice dans les recherches sur la réponse de la plante aux facteurs climatiques.

TABLEAU 2

Espèces	CU % par T. δ _d	CU % par la respiration
<i>Populus euramericana</i>	1,6	0,6
<i>Quercus robur</i>	0,9	0,5
<i>Fraxinus parvifolia</i>	1,2	0,3
<i>Ulmus montana</i>	0,9	0,6

Summary

The total effect of light, temperature and humidity on photosynthesis and respiration (Zh. V. Stojanov and R. J. Florov).

The authors demonstrate the possibility of estimating the global and simultaneous effect of the fundamental factors of the milieu—light, temperature and humidity—on photosynthesis and respiration on the basis of the dissipation entropy of the leaves. This paper gives the application of the method, presented in the paper by Florov, to physiological investigations of photosynthesis and respiration.

The dissipation entropy is combined with photosynthesis in the same manner as respiration. In fact,

the heat of dissipation $\sigma d. T$, where σ is dissipation entropy and T is the absolute temperature, expresses quantitatively the respiration in the light.

It is concluded that the dissipation entropy, expressing quantitatively the daylight respiration is a global index which represents the simultaneous effect of the three fundamental factors of the milieu on respiration and photosynthesis, ergo on the growth of the plants. The fact that, in physiology, there is no such index to express the global influence of the essential factors on such fundamental processes in the plant as respiration and photosynthesis underlines the importance of this index in investigations on the response of the plant to climatic factors.

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Comparative study of five genotypes of bulrush millet (*Pennisetum typhoides* Burm. S. & H.) under a range of photoperiods and temperatures

J. E. Begg and G. W. Burton

Division of Land Research, CSIRO,
Canberra, A.C.T. (Australia);

Crops Research Division, ARS, USDA, Coastal Plain
Experiment Station, Tifton, Ga (United States of America)

The high photosynthetic efficiency of bulrush millet (*Pennisetum typhoides* Burm. S. & H.) has contributed to the very high growth rates and high seasonal yields obtained under favourable conditions in a tropical savannah climate (Begg, 1965a, b; Norman and Begg, 1968). Since tropical grasses are capable of higher growth rates than temperate grasses at temperatures above 20° C (Cooper and Tainton, 1968), there is interest in developing new lines of these tropical species for forage production in warm temperate regions with summer rainfall. Some promising new lines of bulrush millet have recently been developed (Burton, 1965, 1966) and further hybridization and breeding would be facilitated if their response to temperature and photoperiod was more fully understood. The objective of this research was to measure the growth and development of a number of lines of bulrush millet under a range of temperatures and photoperiods appropriate to the summer growing season in tropical and warm temperate regions.

MATERIALS AND METHODS

The millets included in this study were the Tifton inbred lines 31, 23, 13, 13E (an early mutant produced by irradiating 13), together with the F₁ (13E × 13). Inbreds 31 and 13E may be considered "early", and inbreds 13 and 23 "midseason", based on days to anthesis from field sowings at Tifton (Burton, 1965, 1966). The seed was sown in a 1:1 mixture of perlite and vermiculite in 7-inch (17.8 cm) pots. For the germination-establishment period these were placed in a glasshouse with a day/night temperature of 33/28° C (the day temperature applied from 8.30 a.m. to 4.30 p.m.) and with a photoperiod of 16 hr. Sixteen days after sowing, when the seedlings had four to five fully emerged leaves, they were thinned to one per pot and transferred to naturally-lit phytotron B.T. cabinets (Morse and Evans, 1962)

for the temperature-photoperiod treatments. These consisted of the six possible combinations of two temperature regimes (day/night 36/28° C, 28/20° C), and three photoperiods, 12, 14 and 16 hr. All cabinets received 10 hr of daylight (6.30 a.m. to 4.30 p.m.) and before the shutters came down at 6.30 a.m. incandescent lamps provided low intensity light (25–50 ft candles at plant height) to make up the required photoperiod. There were five pots of each genotype × treatment combination and they were given modified Hoaglands solution at 8.30 a.m. and noon and water at 4.00 p.m. For each plant a record was kept of the number of leaves on the main stem, and the number of days from sowing to the appearance of (a) the first tiller (ligule of its first leaf visible), (b) the flag leaf (ligule visible), and (c) first anthesis on the main stem. At harvest, 10 days after first anthesis, plant height was measured and the plant was then subdivided into main stem, tillers and roots for oven-dry weight determination.

RESULTS

The effect of genotype on development and yield is shown in Table 1. In terms of time of flag leaf and anthesis, the inbreds may be listed from early to late as 13E, 31, 13 and 23. In terms of dry matter production and growth rate the later maturing inbreds were greatly superior. The hybrid between the normal inbred 13 and its early mutant showed partial dominance for days to anthesis, complete dominance for yield and heterosis for plant height.

The effects of photoperiod and temperature are shown in Table 2. The rate of development to flag leaf and anthesis was greatest at the shortest photoperiod, whereas the yield was higher at the 14 and 16 hr photoperiods. Rate of development to anthesis and leaf number was greater at the higher temperature, whereas dry matter yield was higher at the lower temperature.

TABLE 1. Genetic effects

Parameters	Genotypes					
	31	13E	13	F ₁ (13E × 13)	23	Standard error
Days to first tiller	20.7	19.1	16.8	18.7	19.3	0.3
Days to flag leaf	45.3	45.6	54.7	51.7	66.8	0.4
Days to first anthesis	59.1	56.1	65.9	62.4	80.9	0.4
Leaves on main stem	16.9	18.5	20.5	20.2	24.2	0.1
Total height (cm)	187.3	208.1	230.6	244.4	188.8	3.1
Number of tillers	3.9	5.3	5.7	6.2	4.8	0.3
Dry weight, main stem (g)	18.5	24.5	47.6	45.9	50.8	1.5
Dry weight, tillers (g)	18.4	25.3	73.4	74.0	73.6	3.8
Dry weight, roots (g)	7.9	8.6	16.9	17.7	31.3	1.4

TABLE 2. Environmental effects

Parameters	Photoperiod (hr)				Temperature day/night (°C)		
	12	14	16	Standard error	28/20	36/28	Standard error
Days to first tiller	19.0	19.0	18.7	0.2	19.0	18.8	0.2
Days to flag leaf	42.1	57.6	58.8	0.3	52.3	53.3	0.3
Days to first anthesis	52.4	69.6	72.7	0.3	66.2	63.5	0.3
Leaves on main stem	17.5	21.0	21.7	0.1	18.1	22.1	0.1
Total height (cm)	197.3	266.1	212.1	2.4	214.5	209.2	1.9
Number of tillers	4.6	5.1	5.9	0.2	5.5	4.9	0.2
Dry weight, main stem (g)	23.1	45.0	44.3	1.1	41.1	33.8	0.9
Dry weight, tillers (g)	29.3	63.9	65.6	2.9	61.7	44.1	2.4
Dry weight, roots (g)	5.4	21.4	22.7	1.0	17.2	15.8	0.9

The interactions between factors affecting time to anthesis are shown in Tables 3, 4 and 5. While none of the genotypes are obligate short day plants, they all flowered earlier under short days (Table 3). The difference between genotypes in time to anthesis was greatest at the 14 and 16 hr photoperiods (ranges of 33 and 37 days), while there was very little difference at 12 hr (range of 4 days). The F₁ hybrid flowered a little later

than the mean of the parents at the 14 hr photoperiod, showing a slight degree of dominance for lateness.

Most genotypes reached anthesis sooner at the higher temperature, the exception being 13E, and the variation between genotypes averaged over all photoperiods was greater at the lower temperature (Table 4). The effect of photoperiod was greater at the higher temperature and the temperature effect was greatest at 14 hr (Table 5).

TABLE 3. Days to first anthesis, genotype-photoperiod interaction

Genotype	Photoperiod (hr)			
	12	14	16	Mean
31	51.6	58.8	67.0	59.1
13E	51.6	56.0	60.7	56.1
13	51.7	74.7	71.2	65.9
F ₁ (13E × 13)	51.5	68.8	66.9	62.4
23	55.7	89.5	97.6	80.9
Mean	52.4	69.6	72.7	Interaction Standard error = 0.7

TABLE 4. Days to first anthesis, genotype-temperature interaction

Genotype	Temperature day/night (°C)		
	28/20	36/28	Mean
31	62.9	55.4	59.1
13E	53.7	58.5	56.1
13	68.7	63.0	65.9
F ₁ (13E × 13)	63.3	61.5	62.4
23	82.5	79.4	80.9
Mean	66.2	63.5	Interaction Standard error = 0.6

TABLE 5. Days to first anthesis, photoperiod-temperature interaction

Photoperiod (hr)	Temperature day/night (°C)		
	28/20	36/28	Mean
12	52.9	51.9	52.4
14	74.2	64.9	69.6
16	71.5	73.8	72.7
Mean	66.2	63.5	Interaction Standard error = 0.5

TABLE 6. Yield of top growth, genotype-photoperiod interaction (g/plant)

Genotype	Photoperiod (hr)			
	12	14	16	Mean
31	30.6	37.6	42.6	36.9
13E	47.2	48.0	54.2	49.8
13	67.1	139.8	156.1	121.0
F ₁ (13E×13)	69.7	152.3	137.5	119.9
23	47.4	167.3	158.7	124.4
Mean	52.4	108.9	109.9	Interaction Standard error = 8.2

TABLE 7. Yield of top growth, genotype-temperature interaction (g/plant)

Genotype	Temperature day/night (°C)		
	28/20	36/28	Mean
31	42.8	31.1	36.9
13E	40.9	58.8	49.8
13	132.3	109.7	121.0
F ₁ (13E×13)	132.9	106.8	119.9
23	165.5	83.4	124.4
Mean	102.9	78.0	Interaction Standard error = 6.7

TABLE 8. Yield of top growth, photoperiod-temperature interaction (g/plant)

Photoperiod (hr)	Temperature day/night (°C)		
	28/20	36/28	Mean
12	50.4	54.4	52.4
14	132.3	85.7	108.9
16	125.8	93.8	109.9
Mean	102.9	78.0	Interaction Standard error = 5.2

The range in the yield of top growth between genotypes was greatest at 14 and 16 hr photoperiods, with the yield of the early lines, 13E and 31, being about one third of the late lines (Table 6). The yield of the F₁

hybrid was the same as that of the late parent, showing complete dominance over its early mutant for yield.

Photoperiod had little effect on yield of the early lines 13E and 31; however, the yield of later lines was at least doubled by increasing the photoperiod from 12 to 14 hr or 16 hr (Table 6). With the increase in photoperiod, there was also an increase in the number of tillers and the number of leaves on the main stem (Table 2).

The range between genotypes in yield of top growth was greater at the lower temperature. Inbred 13E yielded 44 per cent more at the higher temperature, but all other genotypes yielded less (Table 7). Inbred 23 yielded only half as much at the higher temperature. The effect of photoperiod on yield was greater and the temperature effect on yield was greatest at 14 hr photoperiod (Table 8).

The highest yield, 231 g/plant, was recorded by the late inbred 23 at the 14 hr photoperiod and 28/20°C temperature regime. Allowing for its late maturity, this still represented the highest overall growth rate recorded, 2.2 g/day, which was also achieved by genotypes 13 and F₁ (13E×13) under the 28/20°C temperature regime and 16 and 14 hr photoperiods respectively. The overall growth rate of inbreds 23, 13 and the hybrid at the 12 hr photoperiod and 28/20°C temperature regime, was 0.7, 1.0 and 1.0 g/day respectively, i.e. less than half the rate at the 14 or 16 hr photoperiod.

DISCUSSION

The genotypes included in this study all behaved as facultative short day plants, i.e. they were capable of flowering under long days (16 hr photoperiod), but flowered much earlier under short days. The phytotron results were in good agreement with field data from Tifton, e.g. inbred 13 planted in the field in May, June, July and August reached anthesis in 74–85 days from sowing (Burton, 1965) and in the phytotron at 14 hr photoperiod in 68–81 days from sowing at the high and low temperature regime respectively. When planted in the greenhouse at Tifton in December–January with photoperiod less than 12 hr, inbred 13 reached anthesis in 54–58 days from planting—in the phytotron at 12 hr and 28/20°C temperature regime, it took 53 days.

Abnormal head development has been reported in Tift 23A (Burton, 1966) when primordia develop under a 16 hr day. In this study the rate of head development from flag leaf emergence to first anthesis was significantly slower at the 16 hr photoperiod in lines 23 and 31, with some heads aborting prior to emergence, while in lines 13E, 13 and the hybrid, head development was normal under all photoperiods.

For ease of utilization in a breeding programme it is desirable to have all genotypes in flower about the same time and as early as possible. Millet genotypes should be grown under short days (e.g. 12 hr photoperiod) and

a temperature regime of about 28/20° C to achieve early, uniform flowering. A suitable field site for such work would be near the equator.

There is some confusion in the literature on the effect of photoperiod on the growth of single plants. This can arise from the occurrence of flowering in some photoperiods and not in others, or from a failure to distinguish between total energy and true photoperiodic effects. The experimental procedure used to achieve a range of photoperiods in the phytotron kept the period of solar radiation for active photosynthesis constant at 10 hr. In three millet genotypes, plant growth increased under long photoperiods and was associated with an increase in tillering and leaf growth on the main stem. Watkins (1940) found that top, root and rhizome growth in *Bromus insencis* all increased with photoperiod, while

in *Festuca arundinacea*, Templeton *et al.* (1961) found that photoperiod had no net effect on growth, due to the greater tillering and root growth in short days offsetting greater leaf growth in long days.

Temperature can affect the growth response to day-length, thus Lovvorn (1945) found no effect of day-length on either top or root growth of four grasses grown at 27–32° C, but increases in both top and root growth with increase in daylength at 16–21° C. Similarly, in millet, the growth response to photoperiod was greater at the lower temperature regime, 28/20° C. The marked superiority of the later maturing inbreds (13 and 23) and the F₁ hybrid for dry matter production and growth rate under long days at the lower temperature regime is an indication of their suitability for the development of forage types for use in warm temperature regions.

Résumé

*Étude comparative de cinq génotypes de Millet à chandelle (*Pennisetum typhoides* Burm. S. et H.) soumis à une série de photopériodes et de températures* (John E. Begg et Glenn W. Burton)

La croissance et le développement de cinq génotypes de Millet à chandelle ont été comparés dans des conditions de milieu bien définies pour trois durées de jour (12, 14 et 16 heures) où la période d'éclairement pour la photosynthèse active a été maintenue constante à 10 heures, et pour deux régimes de température diurne/nocturne (36/28° et 28/20 °C). Les génotypes se sont comportés comme des plantes à jour court facultatives, fleurissant à toutes les photopériodes bien que beaucoup plus tôt tous les jours courts. Pour la photopériode de

12 heures, il y a eu un effet relativement faible du génotype ou de la température sur la date de l'anthèse. L'effet du génotype s'est manifesté le plus clairement pour les photopériodes longues (14 et 16 heures) au régime de température inférieur.

Bien que le rayonnement solaire reçu ait été le même dans tous les traitements et que les photopériodes aient été étendues au moyen d'une lumière à incandescence de faible intensité, le rendement a été au moins doublé pour trois génotypes soumis aux jours longs (14 et 16 heures). Avec l'accroissement de la photopériode, il y a eu également un accroissement du nombre des tiges et du nombre des feuilles sur la tige principale.

Ces résultats sont considérés sous l'angle de la mise au point de types fourragers destinés à être utilisés dans les régions tempérées chaudes.

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The effect of temperature on growth and dry weight distribution of populations of *Poa annua* L.

D. M. Calder
Botany School,
University of Melbourne (Australia)

INTRODUCTION

Poa annua is an allotetraploid grass of European origin now found widely distributed in temperate regions of the world and at high altitudes in the tropics (Hubbard, 1954). Its wide distribution and considerable ecological success in different environments makes it an ideal subject for a biosystematic study. The present contribution is concerned more specifically with the temperature responses of a series of populations collected from several different climatic regions and grown together under controlled conditions for analysis.

Attention has been drawn by Tutin (1957) to the large number of "races" of *P. annua*; several of these may be found growing together in one garden plot. Timm (1965) collected the species widely in Europe and recognized three main forms: (a) a procumbent vigorous type, rooting at the nodes and found chiefly in the Federal Republic of Germany and the German Democratic Republic; (b) a less vigorous, but also procumbent, form from northern Europe and alpine localities in the south; (c) a type forming erect bunches of tillers with poor leaf development, this form being more characteristic of the Mediterranean region. Our work (Ellis *et al.*, 1971) has revealed several races from Australia and these are genetically distinct, one being diploid (Ellis *et al.*, 1970).

A question of fundamental importance in this study concerns the genetic basis of the ecological success of *P. annua*. Is it because the species is phenotypically plastic or is it, as Tutin (1957) believes, ecologically successful because the species is an aggregate of many stable inbreeding populations, each having a separate hybrid origin or having developed from the original hybrid through a series of distinct mutations? If the latter is the case, the races comprising the *P. annua* complex resemble closely the microspecies of an apomictic aggregate and are comparable in genetic struc-

ture with the varieties of an inbreeding cereal such as wheat. Alternatively, the species may carry a high degree of heterozygosity, so that it is capable of rapid response to selection, with the formation of distinct ecotypes. The question of the genetic structure of *P. annua* remains unresolved because there has been no satisfactory study of its breeding system to date.

P. annua assumes economic significance in southern Australia on two counts. In lawns, such as bowling and golf greens, it grows well during the winter and spring but quickly dies out in summer, leaving large areas of bare ground. In pastures it provides winter and early spring grazing, but is neither as persistent nor as productive as other herbage grasses. Both these points regarding its seasonal growth pattern suggest that higher temperatures, water stress or both of these are factors responsible for the death of *P. annua*. Our view is that temperature sensitivity is a more likely primary cause and this view is strengthened by the observation that *P. annua* is rarely found in tropical climates.

EXPERIMENTAL METHODS

All experiments were carried out under conditions of controlled temperature, photoperiod and light quality, provided in artificially lit cabinets using equal numbers of Phillips "Warm White" and "Daylight" self-reflecting 40 watt fluorescent tubes. The light intensity at plant height ranged between 1,800 and 1,300 ft candles of visible light and the photoperiod was 12 hr. The cabinets were run at a constant 10°, 20° or 30° C.

Seed was germinated at 20° C on filter paper. When the first leaf was emerging through the coleoptile, the seedlings were transplanted into pots of sand which were watered regularly with a complete nutrient solution.

In harvesting, the whole plant was removed from the pot and the roots washed free of sand. Measurements

TABLE 1. Name and origin of *Poa annua* populations used in this study

Name and origin	Climate (after Koppen and Geiger, 1930)	Latitude	Number of plants in source population
Mauritius: from cultivated ground in Port Louis, Mauritius	Af	20° S	20
You Yang: grassland, You Yang State Forest Reserve, Victoria (Australia)	Csb	38° S	100+
South Australia: grazed pasture, Waite Research Institute, South Australia	Csb	35° S	10
Melbourne: park lawn, Melbourne (Australia)	Cbf	38° S	100+
Aberystwyth: single plant, Welsh Plant Breeding Station (United Kingdom)	Cbf	52° N	1
Alpine Wales: 1,000 ft inland from Aberystwyth (United Kingdom)	Cbf	52° N	20
Macquarie: coastal sward, Macquarie Island	Dc	54° S	100+
Polar: intersection of Arctic Highway and Polar Circle, Norway	Dcf	67° N	20
New Guinea 8,000: New Guinea Highlands 8,000 ft	H	6° S	20
New Guinea 12,000: New Guinea Highlands 12,000 ft	H	6° S	20

of leaf width and length were taken for leaves on the main axis. The plant was then divided into root, leaf blade and "sheath" (= sheath + stem = rest of plant) and these components dried at 100° C for 24 hr. After drying, the material was cooled over CaCl₂ and weighed to the nearest 0.001 mg. For each population, four plants were sampled at each harvest. There were six harvests at 10° C and 30° C and seven at 20° C.

From these data the following growth parameters were determined:

1. Relative growth rate (*R*) (Blackman, 1919).
2. Net assimilation rate (*E*) (Williams, 1946).
3. Leaf weight ratio (*L/W*) (Williams, 1946).
4. Distribution indices (Williams, 1960).
5. Growth indices (Calder and Nicholls, unpublished).

Aberystwyth and Mauritius grown at 20° C and 30° C were induced to flower prior to the completion of the harvesting schedule. Reproductive development results in a change in the pattern of dry weight distribution towards an increase in "sheath" growth, thus making between population comparisons with vegetative plants invalid. Consequently data on flowering plants have been excluded when determining growth parameters.

Some details of the origin of the populations selected for study are given in Table 1.

DRY WEIGHT ACCUMULATION

The dry weight determinations and relative growth rates are given in Tables 2 and 3 respectively. The data in Table 2 are mean harvest weights (mg) transformed to log_e. Polynominal regressions were fitted to all sets of data, but in no instance was there a significant improvement over the linear regression. Hence, all comparisons of treatments and populations are based on a linear relationship between weight and time as expressed by the regression coefficient.

At all temperatures the two populations from New Guinea (climate H) were amongst the heaviest plants by the end of the experimental periods and at 20° C and 30° C the two populations from the Mediterranean climates (Csb) were the lightest.

Populations from cold temperate climates (Cb and Dc), e.g. Alpine Wales, Macquarie, Polar and Aberystwyth, show a greater dry weight accumulation at 30° C than at 20° C. Mauritius, You Yang and South Australia (A and Csb) are more efficient at 20° C than at 30° C. At 10° C the most efficient plants are the New Guinea populations with South Australia, Polar and Alpine Wales doing least well (Table 2 and Figs 1 to 4).

Comparing relative growth rates (Table 3 and Fig. 5), all populations show an increase of *R* at 20° C compared with 10° C. Between 20° C and 30° C the population reaction to temperatures is more complex, with some falls and some rises. The overall trend is a very small reduction in *R* at 30° C, and this is most marked in the population from South Australia. In South Australia these plants are exposed to very high summer temperatures associated with severe moisture stress. The *R* of the population from Mauritius, contrary to the general trend and in particular to the trend of the other populations from warmer climates, increases quite significantly between 20° C and 30° C. This population is naturally exposed to high temperatures and rarely, if ever, suffers moisture stress. The other populations where *R* rises between 20° C and 30° C are Aberystwyth, Polar and Macquarie and it is likely that they are rarely exposed to temperatures of this order in their place of origin.

Contrary to what one might expect, populations from cold climates have the lower *R*'s at 10° C and at 20° C. If there is selective significance in this, it could be argued that selection has favoured genes for slow metabolic activity at low temperatures, the more active plants being prone to injury by extremes of cold.

In all populations the net assimilation rate (*E*) falls with time and in some this fall is considerable (Table 4). A fall in *E* is to be expected and is associated with a compensating rise in *L/W*. *E* is higher at 20° C and 30° C than at 10° C.

Figure 6 shows the range of *E* from first to last harvest at each temperature for each population, as well as the mean maximum and minimum values which are the initial and final values respectively.

The effect of temperature on growth and dry weight distribution of populations of *Poa annua* L.

TABLE 2. Dry weights ($\log_e \text{mg}$) for *Poa annua* populations grown under constant temperatures of 30° , 20° or 10° C in 12 hr photoperiods

Population name	Temperature (° C)	Harvest date (days from sowing)										
		15	20	25	28	29	34	35	37	42	44	49
Mauritius	30	0.146	0.664	1.600	—	2.246	3.231	—	—	—	—	—
	20	0.631	0.885	1.985	—	2.460	3.064	—	3.680	—	4.852	—
	10	-0.109	0.145	—	0.743	—	—	1.201	—	2.237	—	2.782
You Yang	30	-0.145	0.511	1.146	—	1.869	1.749	—	3.200	—	—	—
	20	0.236	0.628	1.616	—	2.217	3.315	—	3.038	—	4.382	—
	10	-0.239	-0.342	—	0.549	—	—	1.312	—	1.957	—	2.643
South Australia	30	-0.362	0.069	0.643	—	1.144	1.548	—	2.452	—	—	—
	20	-0.331	-0.336	0.540	—	1.241	1.972	—	2.899	—	3.797	—
	10	-0.317	-0.580	—	0.029	—	—	0.937	—	1.309	—	2.347
Melbourne	30	0.555	0.450	1.765	—	2.535	3.259	—	3.646	—	—	—
	20	0.440	1.004	1.931	—	2.314	3.182	—	3.843	—	4.969	—
	10	-0.437	0.216	—	0.611	—	—	1.418	—	2.185	—	2.809
Aberystwyth	30	0.171	0.759	1.911	—	2.412	3.136	—	—	—	—	—
	20	0.534	1.047	1.606	—	2.271	2.955	—	3.329	—	—	—
	10	-0.061	0.241	—	0.778	—	—	1.606	—	2.160	—	2.704
Alpine Wales	30	0.653	1.219	1.572	—	2.703	3.122	—	3.457	—	—	—
	20	0.177	0.877	1.637	—	2.285	2.977	—	3.120	—	4.306	—
	10	0.090	0.111	—	0.842	—	—	1.418	—	2.106	—	2.339
Macquarie	30	0.311	1.050	1.795	—	2.486	2.742	—	3.444	—	—	—
	20	0.389	0.795	1.528	—	2.166	2.773	—	2.811	—	3.788	—
	10	0.266	0.188	—	0.698	—	—	1.749	—	2.095	—	2.686
Polar	30	0.297	0.949	1.756	—	2.513	2.973	—	3.334	—	—	—
	20	0.479	0.864	1.681	—	2.090	2.399	—	3.190	—	4.463	—
	10	-0.056	0.182	—	0.748	—	—	1.263	—	1.905	—	2.343
New Guinea 8,000	30	0.800	1.183	2.161	—	2.622	3.519	—	3.780	—	—	—
	20	0.683	1.260	2.109	—	2.773	3.283	—	4.092	—	5.029	—
	10	0.363	0.397	—	1.258	—	—	1.756	—	2.346	—	3.191
New Guinea 12,000	30	0.336	1.146	2.001	—	2.686	3.326	—	3.769	—	—	—
	20	0.553	1.025	2.060	—	2.679	3.391	—	4.072	—	4.933	—
	10	-0.378	0.077	—	0.979	—	—	1.895	—	2.540	—	3.388

TABLE 3. Relative growth rates R (mg/mg/day) for *Poa annua* populations at 30° , 20° and 10° C

Population	30°	20°	10°
Mauritius	0.159	0.145	0.087
You Yang	0.134	0.145	0.091
South Australia	0.120	0.154	0.083
Melbourne	0.148	0.157	0.094
Aberystwyth	0.150	0.135	0.084
Alpine Wales	0.133	0.140	0.074
Macquarie	0.137	0.119	0.078
Polar	0.142	0.131	0.073
New Guinea 8,000	0.144	0.152	0.085
New Guinea 12,000	0.157	0.158	0.112

DRY WEIGHT DISTRIBUTION

From the above analysis it is evident that the populations studied show genetically controlled differences in growth which, in a broad sense, may be related to the climate in the place of origin. In other words, *P. annua* exhibits a range of climatic types and it seems likely that its ecological success is related to genetic variability rather than phenotypic plasticity.

Further analysis of these differences is possible by investigating more deeply the way in which the plant allocates its dry weight during growth. Dry weight distribution may vary among populations or in the one population grown under different conditions and may

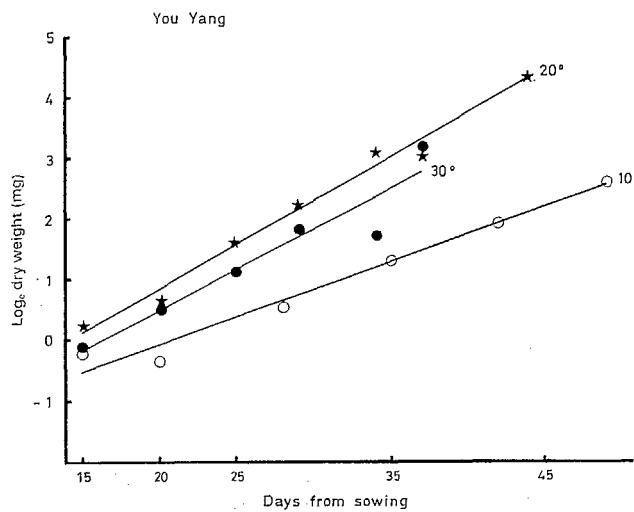


FIG. 1. You Yang. Relationship between dry weight and time for four populations of *P. annua* grown at 30°, 20° and 10° C.

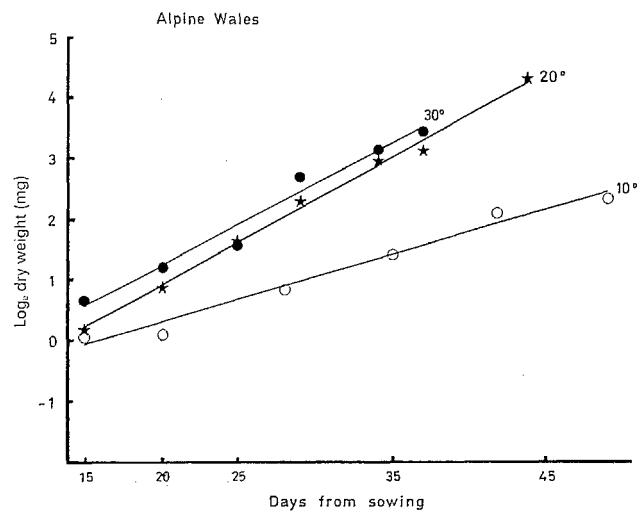


FIG. 2. Alpine Wales. Relationship between dry weight and time for four populations of *P. annua* grown at 30°, 20° and 10° C.

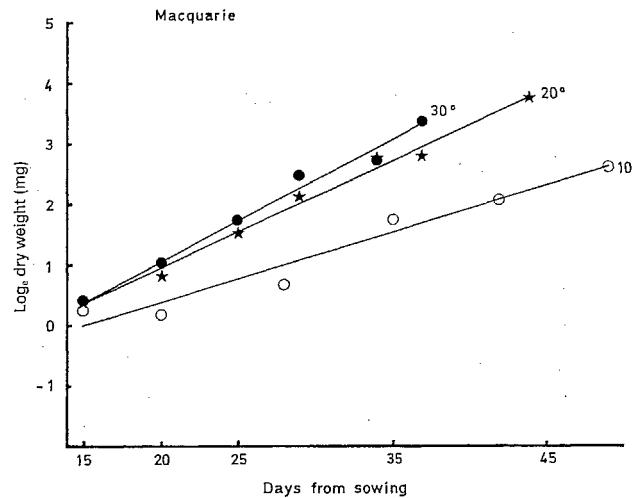


FIG. 3. Macquarie. Relationship between dry weight and time for four populations of *P. annua* grown at 30°, 20° and 10° C.

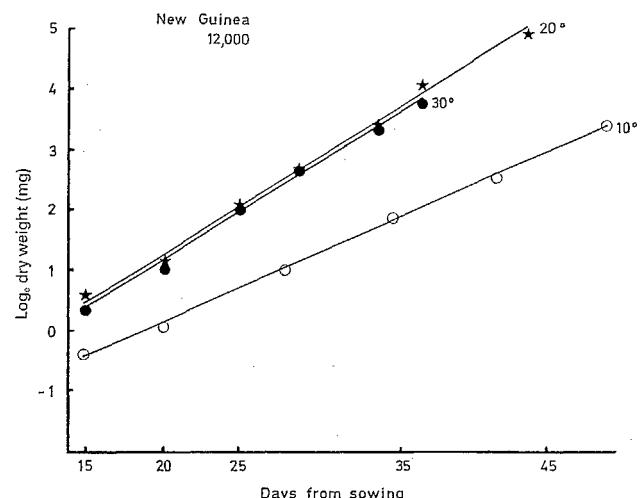


FIG. 4. New Guinea, 12,000. Relationship between dry weight and time for four populations of *P. annua* grown at 30°, 20° and 10° C.

offer further information relating to climatic adaptation.

An effective way of looking at dry weight distribution is to compare the relative growth rate of an organ based on dry weight with the relative growth rate of the whole plant in the following way: $(R_{\text{organ}}) / (R_{\text{plant}})$. This ratio might be called the growth index (Calder and Nicholls, unpublished). When the growth index is greater than one, then that component is growing more rapidly than the plant as a whole; when less than one, it is growing less rapidly.

Since the *P. annua* data support a linear relationship of dry weight with time, even for the component organs, it is obvious that each component investigated has a

single growth index, thus simplifying the between-population and between-temperature comparisons. This information is presented in Table 5.

For the ten contrasting populations studied, the two components of the shoot, i.e. the leaf and sheath, in general grow more rapidly than the whole plant while the root grows less rapidly (Fig. 7). On a population comparison, there are some interesting variations in these general trends. The populations from South Australia and Alpine Wales have the highest overall leaf distribution index, while the two New Guinea populations have the lowest. Root growth is proportionately less in Polar than in all others and highest in

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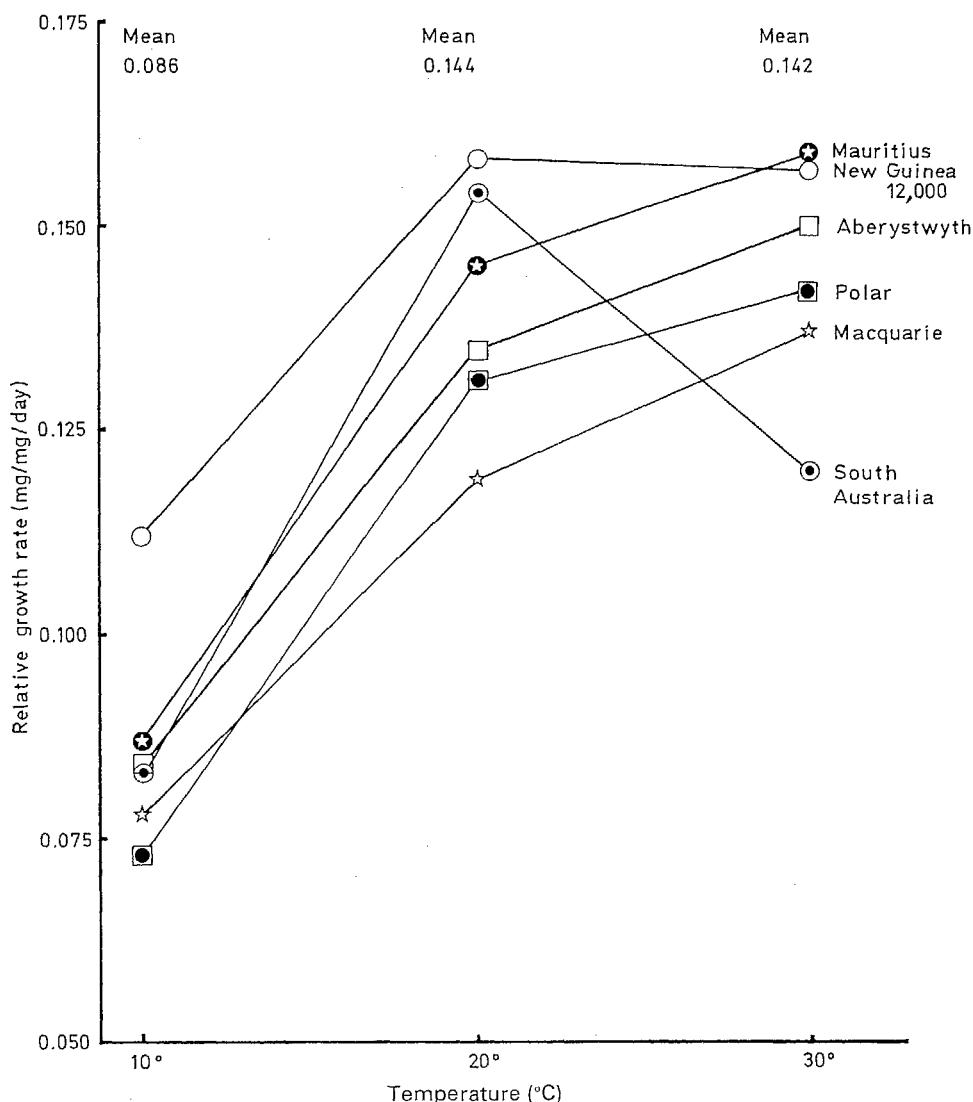


FIG. 5. Relative growth rates (mg/mg/day) of selected *P. annua* populations grown at 30°, 20° and 10° C.

TABLE 4. Net assimilation rates *E* (mg/mg/leaf/day) for *Poa annua* populations grown at 30°, 20° and 10° C.

Population	Temperature (°C)					
	30		20		10	
	Initial	Final	Initial	Final	Initial	Final
Mauritius	0.392	0.260	0.453	0.243	0.321	0.189
You Yang	0.413	0.237	0.509	0.249	0.386	0.185
South Australia	0.453	0.210	0.628	0.257	0.524	0.150
Melbourne	0.501	0.223	0.603	0.243	0.332	0.182
Aberystwyth	0.333	0.311	0.453	0.247	0.367	0.158
Alpine Wales	0.441	0.214	0.427	0.270	0.402	0.150
Macquarie	0.347	0.228	0.371	0.210	0.313	0.142
Polar	0.372	0.229	0.424	0.210	0.284	0.143
New Guinea 8,000	0.386	0.247	0.485	0.267	0.336	0.159
New Guinea 12,000	0.369	0.290	0.448	0.320	0.332	0.241

New Guinea 12,000. The higher sheath growth index in Aberystwyth probably reflects the early flowering characteristic of this population.

The high leaf indices for Alpine Wales and Macquarie at 30° C are associated with low root indices. In other words, in these populations at high temperatures, leaf production is proceeding at the expense of roots to a degree which must ultimately result in an imbalance which will make the plant more susceptible to water stress. In the natural environment of both these populations they are rarely, if ever, exposed to temperatures of this order, and then only for very short periods, and they probably never suffer water stress. In these circumstances selection has not operated against increasing leaf production with increasing temperature. At 10° C these populations are well below average in their

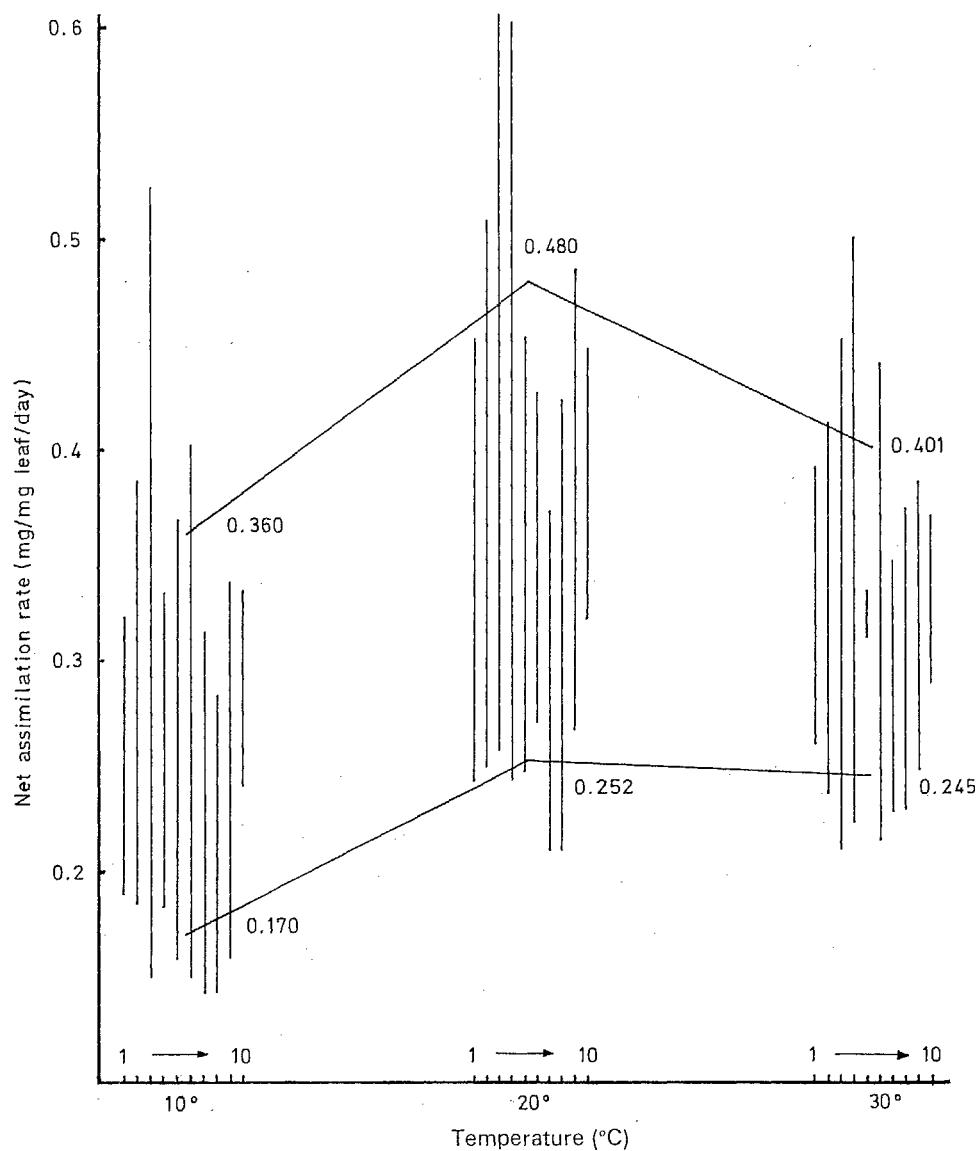


FIG. 6. Range of net assimilation rates (mg/mg/leaf/day) in all *P. annua* populations between initial (upper) and final (lower) harvests. Populations reading from left to right in each block as listed in Table 4.

TABLE 5. Growth indices of leaf, root and sheath for *Poa annua* plants grown at constant 30°, 20° and 10° C

Population	Leaf				Root				Sheath			
	30°	20°	10°	Mean	30°	20°	10°	Mean	30°	20°	10°	Mean
Mauritius	1.178	1.157	1.149	1.161	0.858	0.784	0.801	0.814	1.101	1.109	1.045	1.083
You Yang	1.191	1.171	1.234	1.199	0.754	0.814	0.765	0.778	1.208	1.084	1.123	1.138
South Australia	1.291	1.197	1.430	1.273	0.745	0.872	0.689	0.769	1.061	0.967	1.302	1.110
Melbourne	1.191	1.200	1.249	1.213	0.765	0.795	0.701	0.754	1.178	1.122	1.100	1.133
Aberystwyth	1.299	1.223	1.033	1.188	0.703	0.711	0.865	0.760	1.267	1.237	1.189	1.231
Alpine Wales	1.401	1.112	1.247	1.253	0.688	0.842	0.705	0.745	1.189	1.082	1.154	1.142
Macquarie	1.301	1.165	1.140	1.202	0.589	0.784	0.883	0.752	1.378	1.069	0.884	1.110
Polar	1.155	1.184	1.278	1.206	0.746	0.731	0.597	0.690	1.066	1.167	1.282	1.172
New Guinea 8,000	1.260	1.135	1.141	1.145	0.724	0.844	0.801	0.790	1.231	1.070	1.116	1.136
New Guinea 12,000	1.070	1.074	1.084	1.076	0.923	0.907	0.866	0.899	0.988	1.086	1.099	1.058
Mean	1.234	1.161	1.199	1.195	0.750	0.808	0.767	0.775	1.167	1.099	1.129	1.131

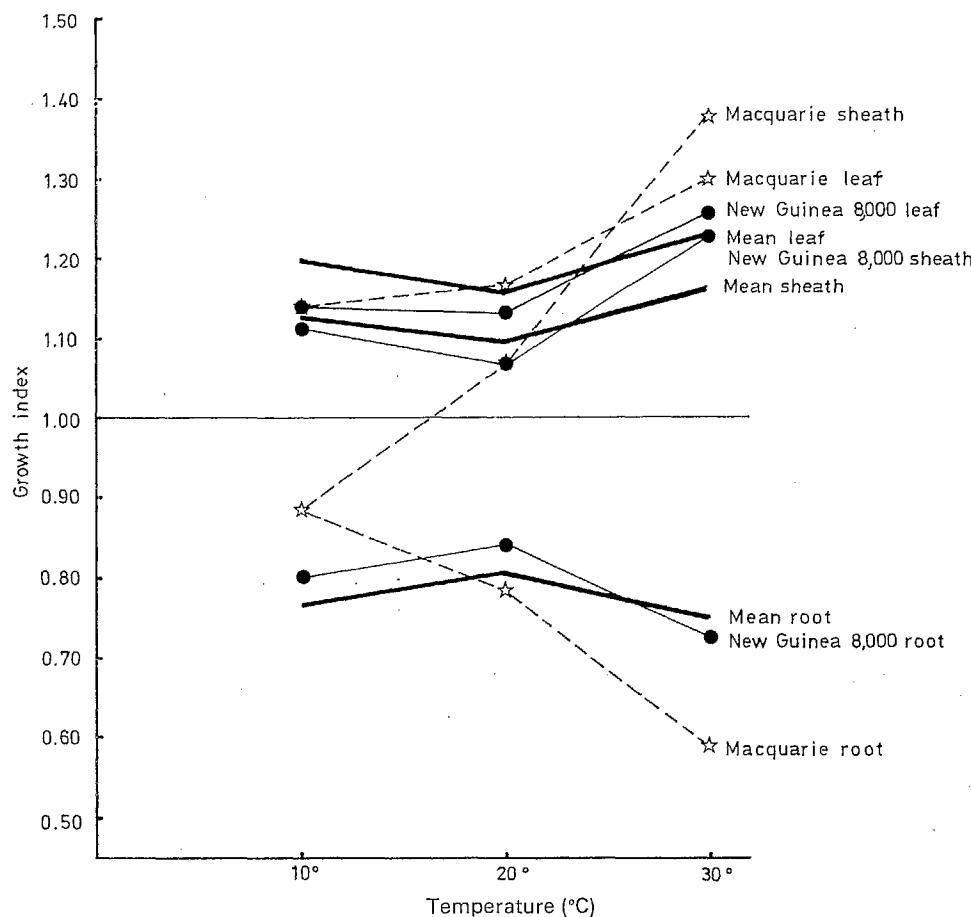


FIG. 7. Growth indices for leaf, root and sheath, mean for all populations as well as Macquarie and New Guinea 8,000.

leaf growth index and, significantly, both You Yang and South Australia are above average.

These results suggest that climatic adaptation can be achieved through genetic control of the relative growth of plant organs and, further, that within the genetic framework, environmental factors may cause changes in the growth indices.

CONCLUSIONS

These results show clearly that *P. annua* exhibits a degree of phenotypic plasticity when exposed to different temperature conditions. It is questionable if this plasticity is more highly developed in this species than in other plants of comparable ecological range. It is clear also that the populations studied show genetic discontinuity. In the absence of more precise information on the climates in the regions from which the particular populations were collected, it would appear that these populations do show growth responses which may impart an adaptive advantage in their natural environment. It is suggested, therefore, that the ecological success of

P. annua is not attributable to any one single feature of its physiology or genetic structure. It shows some phenotypic plasticity; it also shows the development of genetically distinct races. These races probably arise as a result of natural selection from a gene pool, although there is no evidence presented here which conclusively supports this view or disproves the possibility of the existence of many near-homozygous lines from which the environment selects the fittest.

With reference to the populations from Mediterranean climates in Australia, it is of interest to note that these show the greatest sensitivity to high temperature. A problem of *P. annua* in this part of the world is its tendency to die out in early summer after having established a dominant position in lawns and pastures during the winter. On the evidence presented here, selection appears to have acted to lower the capacity for growth at higher temperature. The interpretation of this response could, however, be put another way. Since summer droughts in these regions of Australia are sufficiently severe to kill all plants of *P. annua*, selection might well favour the plants capable of strong winter growth and prolific seed production during the

cooler months of winter and spring. It is plausible to suppose that plants selected for growth under cool conditions will not do well at high temperatures.

That high temperatures themselves are not the dominant selective force can be deduced from the fact that Mauritius does not demonstrate the same degree of inhibition. In this climate, plants are exposed to high temperatures, but they rarely experience water stress. The temperature responses of these warmer climate populations are worthy of more critical study.

A generalization which seems possible from these results is that populations adapted to either the high or the low temperature extremes of the *P. annua* range grow less well in the temperature most comparable to that of their climate of origin. Examples from warm climates have just been discussed and those from cold climates, e.g. Macquarie and Alpine Wales, add support. In these,

selection may have favoured those plants which tend towards dormancy at low temperatures. Such a response would allow plants to survive extremes of cold. It is probably no coincidence that the cold climate populations have a tendency towards perenniability, while the warm climate populations tend towards the annual habit.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge financial support from the Nuffield Foundation. The Australian Antarctic Division made facilities available for a visit to Macquarie Island as part of this project. Computer programming was undertaken by Mr A. O. Nicholls, whose help is gratefully acknowledged, and special thanks go to Miss M. Booth for her willing help.

Résumé

Effet de la température sur la croissance et la répartition du poids sec de populations de Poa annua L.
(D. M. Calder).

Poa annua est probablement originaire d'Europe, mais est maintenant largement répandue dans les climats tempérés chauds ou frais du monde entier. Dans les régions tropicales, on la trouve presque exclusivement à des altitudes élevées. La large tolérance de cette espèce aux conditions du milieu peut s'expliquer par une plasticité phénotypique exceptionnelle ou par une variabilité génétique, ou par ces deux causes à la fois. L'auteur analyse la croissance, mesurée de plusieurs façons, de dix populations indigènes ou naturalisées de *P. annua*, recueillies sous plusieurs climats et cultivées à des températures maintenues à 10, 20 et 30 °C.

Les résultats indiquent qu'il existe des différences génétiques entre ces populations et que chaque popu-

lation présente en outre un certain degré de plasticité phénotypique. La sélection naturelle dans les climats chauds et froids extrêmes a été modératrice et a favorisé les sujets dont la croissance est réduite aux températures voisines des extrêmes qu'ils subissent dans la nature; par exemple, comparés à tous les autres, les sujets originaires des climats chauds tendent à croître moins bien à 30 °C, et les sujets originaires des climats frais tendent à croître moins bien à 10 °C. Les populations diffèrent aussi par la croissance relative des parties composantes, c'est-à-dire la feuille, la racine et la gaine, et la température semble avoir un effet significatif sur chacun de ces caractères.

L'auteur, examinant la signification adaptative des différents types de répartition du poids sec, conclut que la régulation de la modification du poids sec peut être un mécanisme qui permet l'adaptation à des températures différentes.

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Vernalization and photoperiodism of common wheat as related to the general and specific adaptability of varieties

Z. Martinić
Faculty of Agriculture
Zagreb University (Yugoslavia)

INTRODUCTION

Vernalization requirement and photoperiodism are 2 decisive traits governing development rate of varieties of common wheat. A good variety, when introduced into a new region, may give poor yield if its generative development is delayed, because its vernalization requirement is not saturated or the day length is too short for its normal development. The same variety in another region may develop too early and suffer winter injuries, causing the stand and yield to be poor. On the other hand, poor yield might be the consequence of a very long natural photoperiod in a new region. When a variety reacts very strongly to the long photoperiod, the vegetation period of the variety will be hastened and accompanied by small heads and low seed set. Thus, appropriate vernalization requirement and response to photoperiod are important for good adaptability of varieties in a given region.

This belief is as old as the discovery of the dependence of vernalization requirement and photoperiodism of common wheat on the regions of origin of varieties. Because of this, introduction of new varieties for use directly and for breeding purposes was done first from the regions of similar latitudes with similar environmental conditions. However, this formerly dogmatic belief has recently been changing. New recombinations of traits such as vernalization requirement, winter hardness, response to photoperiod and vegetation period in some new varieties suggest that, at least for spring wheat, it is possible to achieve recombinations adapted to a wide range of environmental conditions.

In the history of modern agriculture there are enough examples for the statement to be made that lowering of response to photoperiod accompanies every marked progress in wheat breeding, especially in regions below 45° of latitude; such a case appeared in Italy 40–50 years ago (Martinić, 1966). The Mexican varieties with

almost universal adaptability have low response to photoperiod (Fig. 8) (Borlaug, 1965; Martinić, unpublished data). The new Yugoslav high-yielding varieties are less sensitive to day length than varieties previously grown in Yugoslavia (Figs 11 and 12). Some French, as well as U.S.S.R. varieties at Krasnodar Station (among which Bezostaja-1 now covers an area of about 10,000,000 ha), are of the low-responding type (Martinić, 1966 and unpublished data).

It is the opinion of a number of authors (Borlaug, 1965; Bell and Kirby, 1966; Pugsley, 1968), that the 2 comprehensively studied traits, vernalization and photoperiodism, which are often identified with winter hardiness and vegetation period, have to be more exploited in breeding of better, wider-adapted crop varieties.

PHENOTYPIC AND GENOTYPIC VARIABILITY OF VERNALIZATION REQUIREMENT

Phenotypic variation in vernalization requirement within the species *Triticum aestivum* spp. *vulgare* is a quantitative phenomenon. Some varieties do not respond at all to low temperature treatment in sprouted seeds. Such varieties as S-1 and Newthatch (Fig. 1) could be considered as true spring types. Some other varieties, classified in practice as spring types, could be identified as dual-purpose, intermediate, or very weak winter types. The time from emergence to heading is shortened by 5–6 days in variety Akakomugi, by 8–9 days in Fortunato, by 10–12 days in varieties Mara and Abbondanza (Fig. 2) and by as much as 30 days in variety Leone, when vernalized seeds are sown in late spring (Martinić, 1964, 1967). In the unvernalized controls, heading is delayed for a certain number of days, depending on the variety, but uniform heading occurs even

when sowing is in late spring. There are still other varieties which fail to head or suffer extremely delayed heading when unvernalized seeds are sown in late spring. These latter varieties differ in the duration of vernalization treatment required for uniform heading. The duration of low-temperature treatment required varies from 20–30 to more than 60 days, depending upon variety. For example, in the present study, varieties Minhardi and Fiorello (Fig. 3) needed 20–30 days of vernalization treatment for uniform heading. Libellula (Fig. 4) and San Pastore required 30–40 days; Cappele Desprez and U-1, about 40 days; Bankuty-1205 and Bezostaja-1, 40–50 days; Elia and Etoile de Choisy (Fig. 5), 50–60 days, and Heine VII (Fig. 6) needed more than 60 days of vernalization treatment for uniform heading, when sown in late spring near Zagreb (Martinić, 1964, 1967).

The genetic control of the phenomenon is rather simple, and in many cases there are 1, 2 or 3 gene pairs involved (Cooper, 1923; Hayes and Aamodt, 1927; Ausemus *et al.*, 1946; Schmalz, 1958; Tsunewaki and Jenkins, 1961; Vicent and Goujón, 1965; Le Grand, 1966; Pugsley, 1968; Martinić, 1969, unpublished data). Thus, the selection of the desired genotype in breeding programmes seems to be rather a simple procedure.

Nevertheless, the genetic background to vernalization requirement, as well as to many other physiological traits, with regard to number of loci involved (Knott, 1959; Morrison, 1960; Tsunewaki and Jenkins, 1961), and especially to the number of multiple alleles in them, must be expected to be much more complex than is at present believed. Pleiotropic effects, which strongly influence the criteria used for evaluation of the trait, obscure the phenomenon from the genetic standpoint.

PHENOTYPIC AND GENOTYPIC VARIABILITY IN RESPONSE TO PHOTOPERIOD

For a long time wheat was considered as a typical long-day plant. Nevertheless, in the course of various studies, it has become clear that there is considerable phenotypic variation in response to photoperiod within the species *Tr. aestivum* ssp. *vulgare* (Figs. 7–12); (Doroshenko and Razumov, 1929; Wienhues, 1961; Borlaug, 1965; van Dobben, 1965; Martinić, 1964, 1966). However, a surprising find in the present study was the fact that all the high-yielding varieties which were successfully introduced into Yugoslav agriculture in the last 10 years were far less sensitive to day length than varieties previously grown in this region (Figs 11 and 12). It was concluded that the dogmatic belief about adaptability and specific response to photoperiod, at least in this particular case, was not valid (Martinić, 1966).

The present investigation shows that photoperiodism, like vernalization requirement, is a quantitative phenomenon. Thus, it was possible to conclude (Martinić, 1964,

1966) that varieties showed delayed heading of 5–30 days when grown for 50 days in shortened photoperiod. In the same study, low-response varieties, in order to reach the heading stage, required from 11 to 158 hr less light when treated for 50 days with shortened photoperiod than when grown under the natural long-day conditions in Zagreb. On the contrary, traditional varieties, previously grown in Yugoslavia, and some other high-responding varieties, when grown under the same shortened photoperiod, needed from 78–275 hr of light more than when grown under the natural long-day conditions (Fig. 13) in May, June and July in Zagreb. No variety investigated in the present study, in photoperiods from 9 to 16 hr, could be considered as a true day-neutral type. The varieties nearest to such a type seem to be Elia and Etoile de Choisy (Fig. 13), but this particular point needs further investigation under controlled conditions. All low-response varieties, according to the present investigation, should be considered as low-response long-day types.

The genetic control of response to photoperiod has been studied less than vernalization requirement, especially in wheat. In earlier studies, it was investigated together with vegetation period, heading and maturity. As shown by Ausemus *et al.* (1967), heading and maturity are affected by genes found on every chromosome of the wheat plant. Borlaug, 1964 (after Pugsley, 1966), suggested a simple genetic control of the response to photoperiod of common wheat. Pugsley (1965) has shown that 1 major gene governs high response to photoperiod of variety Selkirk and 1 major and 1 minor or modifying gene in variety Thatcher. He further suggests that additional genes may be present. The study of the present author (Martinić, unpublished data) suggests that there are 2 complementary genes involved in 3 studied crosses (Newthatch × San Pastore, Newthatch × Etoile de Choisy, Newthatch × Abbondanza) and 3 complementary genes involved in the fourth cross (San Pastore × Bankuty 1205). The fifth cross (Newthatch × S-1) does not allow any suggestion about the number of pairs involved in the control of response to photoperiod to be made.

RELATIONSHIP BETWEEN VERNALIZATION REQUIREMENT, PHOTOPERIODISM AND SOME OTHER IMPORTANT TRAITS

The relationship between vernalization requirement, tillering capacity, height of the culm, number of leaves per culm, fertile and unfertile tillers per plant, as well as number of spikelets per head, is rather well known.

When development is delayed through lack of low-temperature treatment or short photoperiod, a variety generally tillers abundantly and may have, along with the prolonged life-cycle, more heads per plant, leaves per culm and spikelets per head, which are all ultimately reflected in the grain yield.

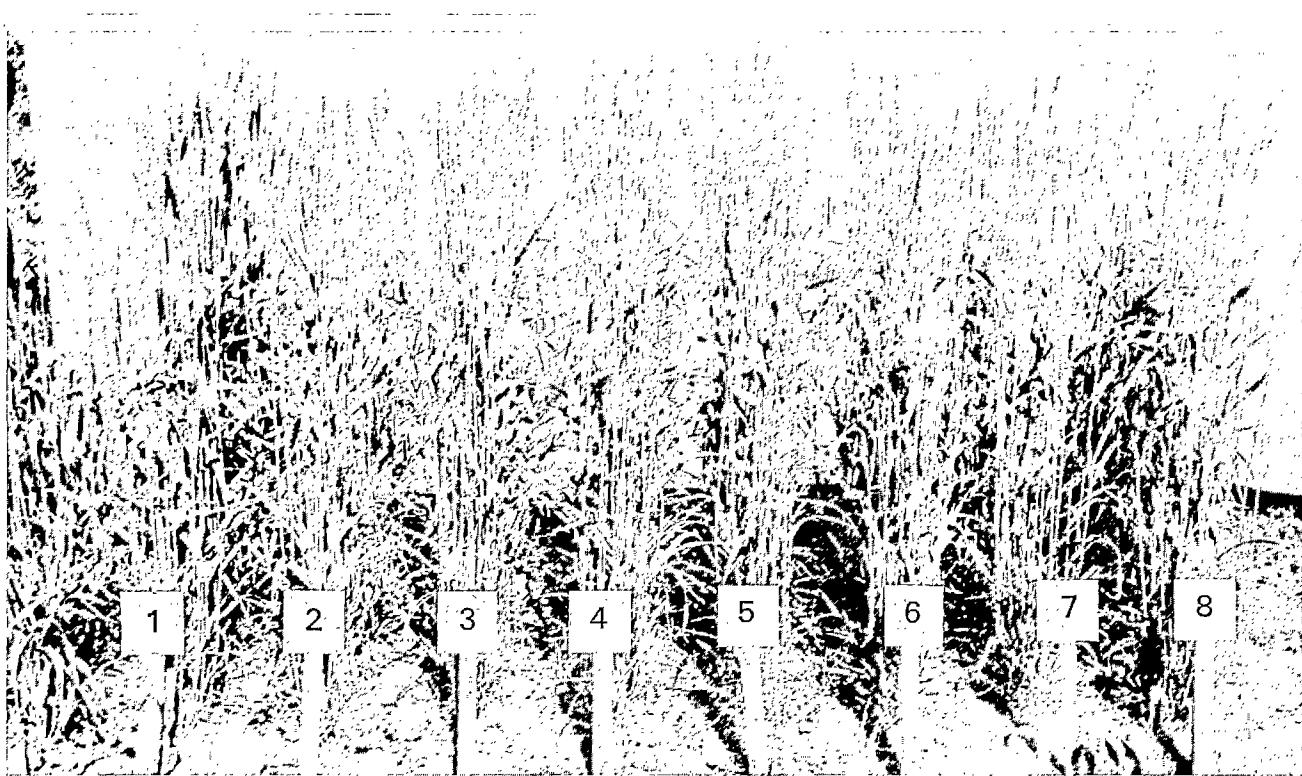


FIG. 1. Newthatch—true spring wheat, not responding to vernalization treatment. Sown 18 April 1963 with seeds vernalized (1), for 60 days (2), for 50 days (3), for 40 days (4), for 30 days (5), for 20 days (6), for 10 days (7), and unvernalized control (8). Development stage 61 days after emergence.



FIG. 2. Abbondanza—dual-purpose very weak winter type, delays heading for 10–12 days if sown in late spring with unvernalized seeds (8).



FIG. 3. Fiorello—true winter wheat, fails to head uniformly if vernalized for less than 30 days (5).



FIG. 4. Libellula—true winter wheat, fails to head uniformly if vernalized for less than 40 days (4).



FIG. 5. *Etoile de Choisy*—true winter wheat fails to head uniformly if vernalized for less than 50 days (3).



FIG. 6. *Heine VII*—true winter wheat, fails to head even when vernalized in sprouted seeds for 60 days (2).



FIG. 7. The appearance of plants at the beginning of treatment with shortened photoperiods.



FIG. 8. Mexican variety Pitic 62—low response to photoperiod, nearly true spring type. (1) Vernalized for 40 days and grown in shortened photoperiod (11.30 hr) for 50 days. (2) Vernalized for 40 days and grown in natural day length (13.45–15.45 hr). (3) Natural day length without vernalization treatment. (All samples taken on the same day.)

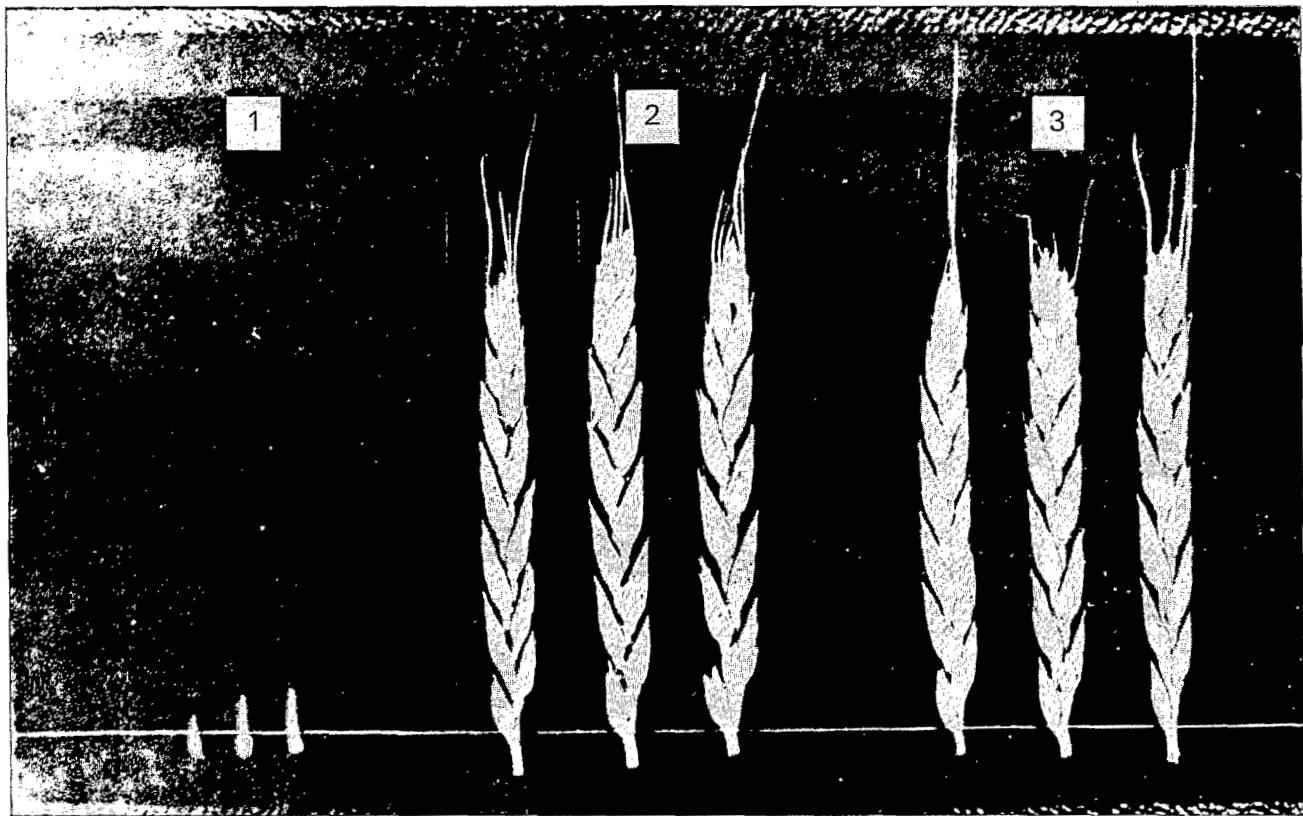


FIG. 9. Canadian variety Selkirk—high response to photoperiod, a true spring wheat. (1, 2 and 3 as in Fig. 8; all samples taken on the same day.)

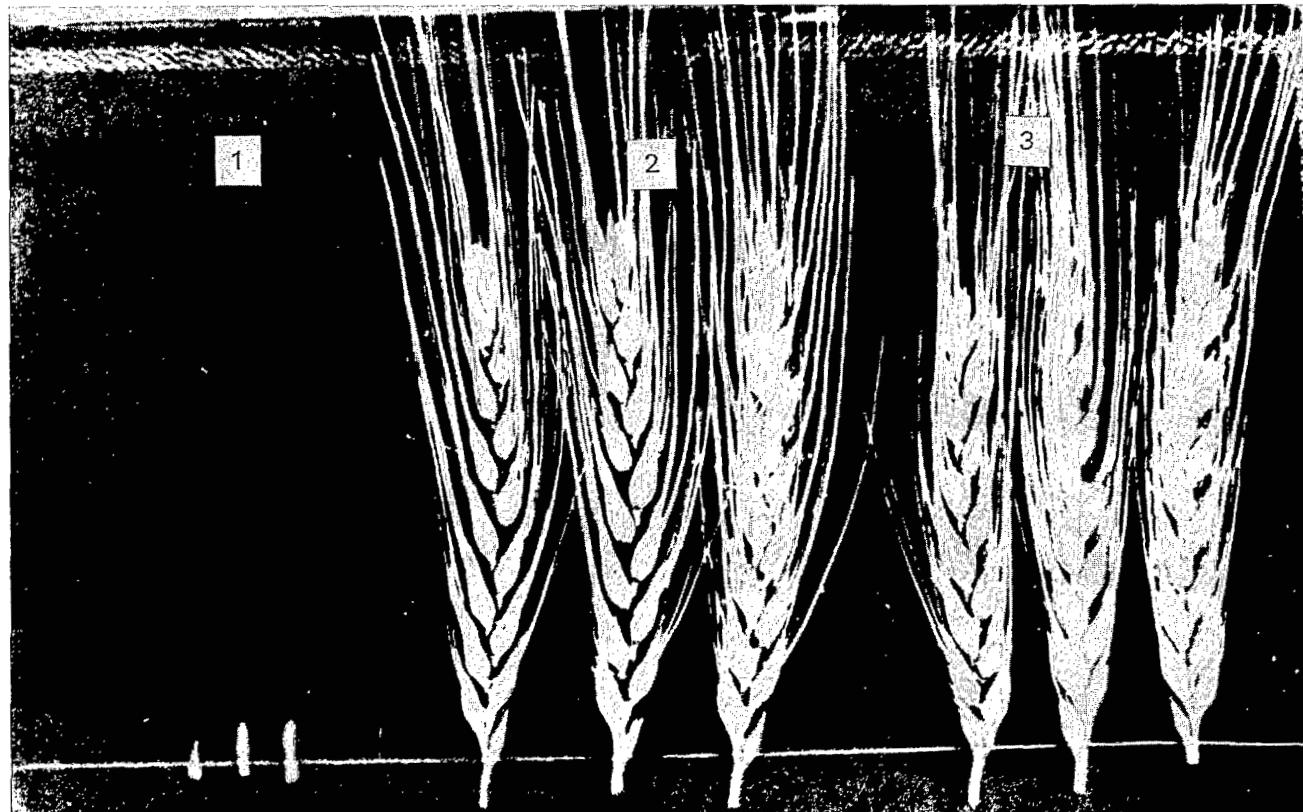


FIG. 10. Mexican variety Nadadores 63—high response to photoperiod, a true spring wheat. (1, 2 and 3 as in Fig. 8; all samples taken on the same day.)



FIG. 11. New Yugoslav variety Crvena Zvezda—low response to photoperiod, a true winter wheat. (1, 2 and 3 as in Fig. 8; all samples taken on the same day.)



Fig. 12. Yugoslav variety U-1, a winter wheat previously grown in this country—high response to photoperiod, winter type wheat (1-3.) Vernalized for 52 days and grown in different shortened photoperiods for 50 days. (4) Vernalized for 52 days and grown in natural long day (13.30-15.45 hr). (5) Unvernalized, grown in natural long day.

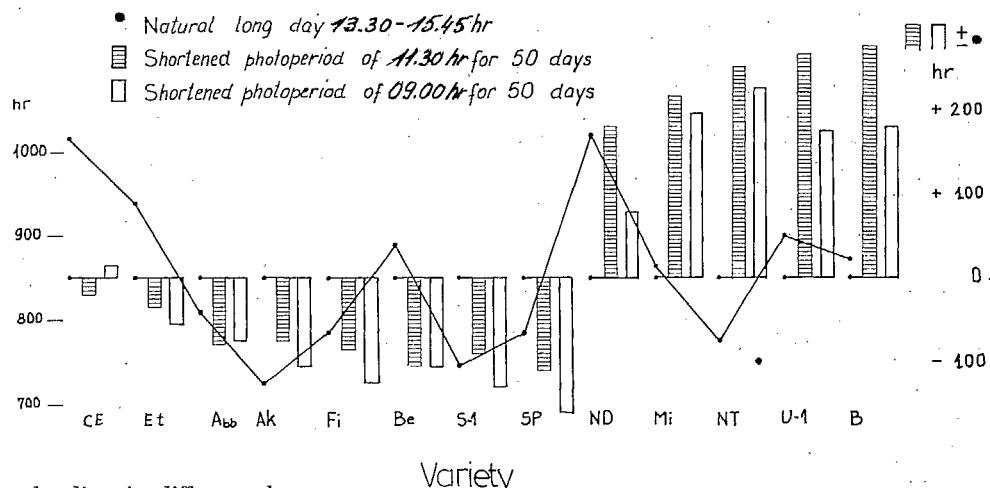


FIG. 13. Hours of daylight to heading in different photoperiods with different genotypes. Varieties with low response to photoperiod (CE, Elia; Et, Etoile de Choisy; Abb, Abbonanza; Ak, Akakomugy; Fi, Fiorello; B, Bezostaja-1; S-1; SP, San Pastore), when grown for 50 days in shortened photoperiod, required from 11 to 158 hr of daylight less to reach heading than when grown in natural long day. On the contrary, high response varieties (ND, Nord Desprez; Mi, Minhardi; NT, Newthatch; U-1; B, Bankuty 1205) required from 78 to 275 hr of daylight more when treated for 50 days with shortened photoperiod.

The only possible way of utilizing these associations in agricultural practice is, as Pugsley (1965) also suggests, through the use of the specific genes controlling the traits discussed (i.e. by the plant breeder).

The breakers of well known correlations between the wheat plant characteristics, such as winter hardiness and vegetation period, vernalization requirements and photoperiodism respectively have been known and utilized and resulted in development of widely adapted winter wheat varieties such as San Pastore (Italy), Etoile de Choisy (France) and Bezostaja-1 (U.S.S.R.).

It was shown by the author that there are varieties which, in spite of having quite the same low-temperature requirement, differ considerably in their time from emergency to heading when sown in the autumn (Martinić, 1964).

Still more unexpected was the discovery that some low-response varieties, along with high-response ones, have at least the same emergence to heading period, when sown in the autumn and grown under the same Yugoslav agroclimate (Martinić, 1964). From Winnipeg Research Station, Manitoba (Research Report, 1968), it was reported that Mexican variety Pitic 62, superior in yield by 24 per cent to variety Manitow in 17 tests in the Prairie Provinces of Canada, matured almost one week later than Manitow under Canadian growing conditions. However, Pitic 62 is a low-response type (Fig. 8) while Manitow responds strongly, like Selkirk (Fig. 9), to photoperiod (Martinić, 1969, unpublished data). This suggests that genes governing low response

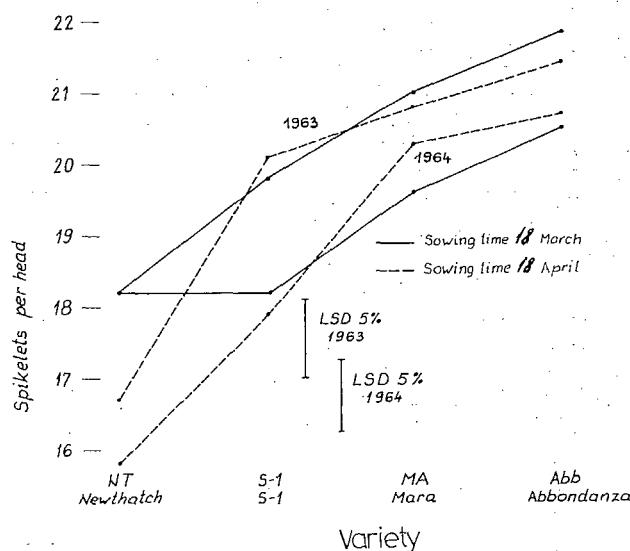


FIG. 14. Number of spikelets per head with 2 different spring sowing times. The significant reduction in number of spikelets per head with late sowing time was observed only in Newthatch, a variety with high response to photoperiod. The remaining 3 varieties, with low response to photoperiod, represent the correlation breakers of the "well known" connexion between seeding time and a number of spikelets per head. LSD = least significant difference.

to photoperiod should not necessarily be coupled with short vegetation period. This opens a new possibility for lengthening the initiation to heading period. Thus, correlation exceptions could be expected to be present among all the important characteristics influencing adaptability and economic yield of varieties (Fig. 14).

RELATIONSHIP BETWEEN VERNALIZATION REQUIREMENT, PHOTOPERIODISM AND GENERAL AND SPECIFIC ADAPTABILITY

There is no sense in discussing general or specific adaptability of varieties if their adaptability is not combined with superior yield.

With regard to vernalization requirement and photoperiodism, a generally adapted variety should be a true spring wheat with a low response to photoperiod or, better still, a day-length neutral type. As a matter of fact, such a variety is hypothetical because any one variety will not be adapted to some winter wheat areas, at least in early autumn sowing (Martinić, 1969). True winter types with a low response to photoperiod should be much better adapted to a wide range of winter wheat environments. (Martinić, 1968, 1969). Quite a great number of Italian, Krasnodar Station (U.S.S.R.) and new Yugoslav varieties and strains, as well as some French ones, belong to the latter type. To what extent this model type could be improved toward general adaptability to winter wheat environments is an open question. Nevertheless, it offers promising research leads into wide adaptability in winter wheat. It should be pointed out here that, at least in the same winter wheat areas, near-true spring types give yields year after year as high as or higher than winter ones, when sown in late autumn. In looking for specific adaptability, breeders have at their disposal a number of the genes which have been found to be responsible for both mechanisms and, undoubtedly, plenty of undetermined allelic or non-allelic genes with a wide range of effects. However, it seems that specific adaptability is still less important than often thought because no agricultural environment will be perfectly alike year after year (MacKey, 1966). Thus, it is realistic to expect that adaptability to a wide

range of environments helps a variety to have stable adaptability in the same agroclimate over a period of years.

DISCUSSION

The detailed study of varieties with superior yielding capacity under a wide range of environments (i.e. varieties tending to be generally adapted) and those adapted to one special environment is planned in the International Biological Programme (IBP) using spring wheat as a model plant (Finlay, personal communication). It is hoped that such a study will enable the construction of a hypothetical model which will help breeders in screening genotypes for adequate adaptability.

The evolution of genes governing photoperiodism in bred wheat followed perfectly the situation in wild species because, in the course of centuries of evolution, primitive agricultural practice was similar to the natural environment. Therefore, the theory about the dependence of response to photoperiod on regions of origin of varieties is very likely to be true. Man, using modern practices, is daily changing the agroclimate as a whole. Thus, many genes in a new "man-made environment" are becoming of second-rate significance and, as often shown, can be successfully replaced with alleles developed in other regions and acting better in a new situation.

The present study, like many others, could help in building an ideal, hypothetical model towards which the breeder should be aiming in his work. However, exploitation of the great genetic variability within early generations and the use of adequate screening procedures are still the best ways for real improvement of varieties, irrespective of whether wide or specific adaptability is sought.

Widely adapted genotypes will tend to be intermediate in many important characteristics (Finlay, 1968).

The balance between vegetative and generative development in true spring genotypes with low response to almost universal adaptability, seems to be realized through those compensating mechanisms which respond more flexibly than vernalization and photoperiodism to different agroclimatic conditions.

Résumé

Vernalisation et photopériodisme du Blé Triticum aestivum ssp. vulgare en relation avec l'adaptabilité générale et spécifique des variétés (Z. Martinić).

Cette communication porte sur la variabilité phénotypique et génétique des conditions de vernalisation et sur le photopériodisme du Blé tendre par rapport à

d'autres propriétés agronomiques importantes comme: la résistance au froid, la période végétative/épiaison/maturité, et le rendement des grains. De nombreuses exceptions aux corrélations existantes ne sont pas assez connues et exploitées des sélectionneurs qui recherchent des variétés de Blé d'hiver et de Blé de printemps très adaptables et d'un rendement élevé.

En ce qui concerne la relation entre les conditions de la vernalisation et l'adaptabilité générale, la variété qui pourrait être considérée comme généralement adaptable devrait être du type printanier. Cette variété semble être irréalisable, tout au moins pour les semaines automnales précoces dans de nombreuses régions de Blé d'hiver. Du point de vue du photopériodisme, la variété qui pourrait être considérée comme généralement ou largement adaptable devrait nécessairement être d'un type à faible réaction ou, mieux encore, d'un type neutre, qu'elle soit cultivée dans une région de Blé d'hiver ou de Blé de printemps.

Quant à l'adaptabilité spécifique, de nombreux allèles d'effet quantitatif majeur ou mineur sur l'expression phénotypique de deux caractères existant dans *Triticum vulgare* pourraient être mieux exploités dans de nombreux programmes au moyen du processus de sélection et d'essais adéquats de criblage.

La vernalisation et le photopériodisme ne sont nullement les seuls caractères qui influent sur l'adaptation et sur le rendement du grain. Il semble cependant que le photopériodisme joue un rôle plus direct en ce qui concerne le rendement stable et élevé des grains.

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Carbohydrate metabolism and photosynthesis of tropical grasses subjected to low temperatures

S. H. West

United States Department of Agriculture,
Agricultural Research Service, Crops Research Division,
and the Agronomy Department, University of Florida,
Gainesville, Florida (United States of America)

Extensive research effort has been expended on the comparison of the physiological characteristics of tropical and temperate plants. Much of this work involves grasses, where emphasis is on pathways of CO₂ assimilation, efficiency of photosynthesis, sub-cellular morphology, and presence or absence of pertinent enzymes. These two plant types differ in their adaptation to low temperature and the reasons for this difference are the subject of this report.

Wherever possible, tropical plants are selected for agricultural use because of their more efficient photosynthesis and greater growth potential. However, many tropical and semi-tropical areas of the world experience temperatures as low as 10° C at night. Unfortunately, most tropical plants become dormant after exposure to such low temperatures and this causes substantial economic losses. It is hoped that there may be enough variability in the wild-type plants to select for resistance to low temperature. This paper reports a search for the mechanism by which cool season dormancy in tropical grasses is mediated so that selection criteria may be established and screening procedures developed.

GROWTH RESPONSE

Digitaria decumbens was used for many of the low temperature studies because it is grown extensively for pasture and forage and is susceptible to low temperatures. Cuttings of the top three nodes of this grass were rooted, potted and grown for 4 weeks in 30° C days and 25° C nights. At this time the shoots were cut back to within 2 inches (5 cm) of the soil level. The plants were then placed in a range of growth chambers at different night temperatures and returned to the outside to a day temperature of approximately 30° C. After 4 weeks of these treatments, the plants from both temperature treatments were harvested at ground level

TABLE 1. Growth of *Digitaria decumbens* after 4 weeks in 10° 20°, or 30° C night and 30° C day temperatures. Data are average of 6 plants

Night temperature (° C)	Dry weight (g)	Standard deviation
10	18	0.29
20	29	0.46
30	38	0.27

and dry weights were determined. The low night temperature reduced the growth to less than half of that in plants exposed to 30° C nights (Table 1).

PHOTOSYNTHESIS DEPRESSION

Digitaria decumbens plants were grown in pots, as above, for 3 weeks at which time net photosynthesis rates were determined as described by Wolf *et al.* (1969). Initial photosynthetic rates were established and then the plants were subjected to 10° and 30° C night treatments. Photosynthesis of the same leaf used in the initial measurement was measured again after 1, 2 and 3 nights exposure. One night at 10° C was sufficient to reduce

TABLE 2. Photosynthesis rates at 30° C of entire tops of *Digitaria decumbens* subjected to varying numbers of nights at 10° C. Control plants were grown at 30° C day and night

Treatment	Percentage control
1 night at 10° C	60
2 nights at 10° C	59
3 nights at 10° C	61
3 nights at 10° C, then 3 nights at 30° C	85

the photosynthetic rate to 60 per cent of that in the 30° C control (Table 2). The rates in the low temperature plants remained depressed for the duration of the experiment.

The reason for the reduced photosynthesis rates at this point was unknown and was the subject and motivation of the following observations.

CHLOROPLAST SIZE

Siegenthaler and Packer (1965) showed that chloroplasts active in photosynthesis shrink in size because energy transfers lead to ATP synthesis and the translocation of ions out of the organelles. Their conclusions were based upon differences in the packing volume of chloroplasts in the presence of light and in darkness. Using their techniques, it has been shown (West, 1970) that chloroplasts from the 10° C temperature treated plants which were less active in growth, had a greater packing volume than those from the 30° C treated plants. In this work it was also noted that chloroplasts isolated from plants given 10° C treatments formed less cohesive pellets and that chlorophyll leakage was more extensive; these observations suggested chloroplast injury.

STARCH ACCUMULATION

During the packing volume experiments mentioned above, white pellets were deposited in the bottom of the centrifuge tubes in which the chloroplasts from plants grown in 10° C night temperature were isolated. Qualitative tests indicated that these white pellets were starch. Quantitative tests (Madsen, 1968) showed (Table 3) that the starch content of the chloroplasts from 10° C treated plants was 10 times that in the 30° C treatment. A single night of 30° C following 10° C night treatment reduced this accumulated starch to only 3 times that in the chloroplasts that had received only 30° C night treatment.

The chemical analyses were substantiated by electron micrographs of chloroplasts in which starch grains were clearly visible at the end of a day of photosynthesis (Hilliard and West, 1970). The starch grains disappeared if the plants received a night treatment at

TABLE 3. Accumulation of starch in chloroplasts from *Digitaria decumbens* subjected to different temperature regimes

Treatment	Starch content (mg/g fresh weight)
30° C night	0.6
1 night at 10° C	4.1
2 nights at 10° C	6.0
2 nights at 10° C plus 1 night at 30° C	1.6

TABLE 4. Fresh weight, chloroplast starch accumulation, and photosynthesis in *Pennisetum typhoides* after 2 weeks' growth in cold-night or cold-day treatments

Treatment	Fresh weight (g)	mg starch/g fresh weight	Percentage rates ¹
10° C day, 30° C night	9.19	5.14	100
30° C day, 10° C night	60.3	11.46	51
30° C day, 25° C night	—	—	98

1. Percentage of pre-treatment photosynthesis rates remaining after 3 days' exposure to the temperature treatments.

30° C, but remained if the plants were exposed to a 10° C night temperature. Extensive starch accumulation in mesophyll chloroplasts, such as that seen in *Digitaria decumbens*, has not been reported previously in other tropical grasses. Starch also accumulated in the bundle sheath chloroplasts.

TEMPERATURE-PHOTOPERIOD

The question of whether low temperature influences growth by directly affecting photosynthesis or by affecting the subsequent metabolism and use of the starch was investigated by varying the sequence of temperature treatments and light. One may conjecture that low temperatures during the light period would reduce growth by reducing photosynthesis. If the influence of low temperature was on photosynthesis, low day temperatures would be more detrimental to plants than low night temperatures.

Tests were conducted by placing pots of 4-week-old *Pennisetum typhoides*, a tropical millet, in two chambers having 12-hr photoperiods. One chamber had a 10° C day and a 30° C night, the other chamber had a 30° C day and 10° C night.

After 2 weeks of growth in these treatments, the fresh weight of warm day/cold night plants was 65 per cent of that of plants having cold days and warm nights (Table 4). Similar data have been collected by McCloud (personal communication) using this species, as well as *Digitaria decumbens*.

Starch analyses of the millet plants after 2 weeks of treatment indicated that the chloroplasts in the plants from the cold night treatments had accumulated twice as much starch as the plants from the cold day treatments (Table 4). This accumulation of starch appears to limit growth of at least these two tropical species through its reduction of photosynthesis.

Photosynthesis rates in single leaves of 4-week-old plants of tropical millet were determined before and after they were subjected to the various treatments shown in Table 4. The 30° C day/10° C night reduced the photosynthesis rate to 50 per cent of that obtained initially on the same leaves, whereas the rates were unchanged by the other two treatments (Table 4).

TABLE 5. Hill reaction potential and ^{33}P incorporation of chloroplasts isolated from 10° and 30° C treated *Digitaria decumbens* plants

Night temperature (° C)	Hill reaction absorption at 630 μ	^{33}P incorporation (cpm)
10	0.062	3 654
30	0.120	1 302

HILL REACTION

Injury to the chloroplast apparatus caused by the accumulation of starch may account for the reduced photosynthesis. One measure of injury may be made by observing the ability of the chloroplasts to perform the Hill reaction portion of photosynthesis. Chloroplasts were isolated by centrifugation of sucrose homogenates of leaves of *Digitaria decumbens* grown as described above. The plants were exposed to a 1-night treatment of 10° or 30° C in growth chambers. The ability of the isolated chloroplasts to perform the Hill reaction was measured by the methods and procedures of Moreland and Hill (1962). The ability of the chloroplasts to carry out this part of the photosynthetic process was reduced by the 10° C night treatment to one half that of the 30° C (Table 5). These data indicate some temporary impairment of the photochemical reaction of photosynthesis by the low temperature treatment.

INCORPORATION OF NUCLEIC ACID PRECURSORS

It was thought that chloroplasts injured by the low temperature treatment would synthesize nucleic acids and protein at a faster rate than non-injured chloroplasts in order to replace the photosynthetic potential. A measure of this rate would indicate the degree of injury. These assumptions were tested by incubating chloroplasts, isolated as above, with ^{33}P and with an aliquot of the respective supernatant resulting from the isolation centrifugation. Marked increases in the incorporation of ^{33}P , presumably into nucleic acids, were caused by the low temperature treatment (Table 5).

The study of the rate of nucleic acid synthesis or "turn-over" suggests that injury in the form of physical disruption has occurred. The increased synthesis of nucleic acid would be required to facilitate the increased chloroplast synthesis. Injury is also suggested by the

reduced ability of the chloroplasts to perform the Hill reaction and the discovery that a cold night reduces photosynthesis and growth more than a cold day.

ECOTYPE RESPONSE

Further evidence that the growth depression caused by low temperatures is associated with starch accumulation was obtained by comparing the starch accumulation levels of low temperature sensitive and resistant plants. Selections of *Eragrostis curvula* reported to have varying adaptation to low temperature (Farrington, personal communication) were subjected to 10° C nights and starch accumulation was followed. Selections that had temperature adaptation similar to that of *Digitaria decumbens* accumulated starch to a level similar to that of the *Digitaria* (Table 6). The selection that grew well in low night temperatures did not accumulate starch.

MECHANISM OF ACTION

The observations on starch accumulation in chloroplasts and photosynthetic activity of tropical plants subjected to 10° C night temperatures suggest the following mechanism by which photosynthesis and growth may be reduced by the temperature treatments. During a warm sunny day, chloroplasts accumulate starch grains. If the following night is warm, the starch is degraded, translocated and used by the plant. If the night is cold, the starch grains are still in the chloroplasts the following morning, when photosynthesis begins again and additional starch accumulates. As this accumulation continues, even at a slow rate, for several days, the physical integrity of the chloroplasts is impaired. This injury may require the synthesis of new photosynthetic units and this may account for the slow recovery of some of the tropical plants, such as *Digitaria decumbens*, in the spring.

TABLE 6. Starch content of chloroplasts from selections of *Eragrostis curvula* with varying winter growth potentials when subjected to temperature treatments

Temperatures for 3 nights (° C)	Growth in winter (mg starch/g fresh weight)		
	High	Intermediate	Low
10	1.71	4.35	3.78
30	2.30	2.13	1.82
Ratio of 10°/30° C	0.74	2.04	2.08

Résumé

Métabolisme des glucides et photosynthèse de Graminées tropicales soumises à de basses températures (S. H. West)

L'auteur a étudié le mécanisme par lequel de faibles températures (10°C) provoquent l'hibernation chez des plantes tropicales. Cette hibernation peut causer des graves pertes économiques. La croissance réduite, selon cette étude, se produit à de faibles températures et est liée à des taux réduits de la photosynthèse. Les analyses micrographiques, chimiques et électroniques indiquent que les basses températures nocturnes empêchent la dissipation des grains d'amidon qui s'accumulent dans les chloroplastes des plantes tropicales pendant les heures chaudes de la journée. La photosynthèse continue et de basses températures nocturnes ont provoqué une accumulation accrue de l'amidon dans les chloroplastes

jusqu'à ce que cet organite soit détérioré. Une preuve de ces lésions a été fournie par la réduction de l'aptitude des chloroplastes, chez des plants soumis à de basses températures, à mener à bien la partie de la photosynthèse correspondant à la réaction de Hill. Des études du renouvellement ou de la synthèse de l'acide nucléique ont également permis de conclure à des lésions. La constatation qu'un traitement jour chaud/nuit froide a réduit la croissance à 60% seulement de celle de plants soumis à un traitement jour froid/nuit chaude vient renforcer la conclusion selon laquelle la diminution de la croissance de végétaux tropicaux peut être causée par l'accumulation d'amidon dans les chloroplastes et les lésions qui s'y produisent en conséquence. Chez les végétaux qui croissent bien à de faibles températures, l'amidon ne s'accumule pas.

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Growth responses of maize plants to temperature

R. Brouwer¹, A. Kleinendorst² and J. Th. Locher²

1. Laboratory for Plant Physiological Research, Agricultural University, Wageningen (The Netherlands)

2. Institute of Biological and Chemical Research of Field Crops and Herbage (IBS), Wageningen (The Netherlands)

INTRODUCTION

Although almost all physiological processes are influenced by temperature, quantitative differences may occur (Went, 1957). In addition, some processes are more likely to determine growth rates than others. Over a number of years, the present authors collected data on maize which revealed a number of crucial determinants of the quantitative response of maize plants to temperature.

MATERIALS AND METHODS

Maize seedlings were grown on nutrient solution in climate rooms and glasshouse compartments which were kept at various constant temperatures. In most cases root temperatures were controlled and varied independently of the prevailing air temperatures. In some cases the temperature of the growing point of the shoot was varied independently of both air and root temperature; normally the temperature of this growing point up to the 8th leaf stage was the same as the root temperature and, due to stem elongation, gradually passed into the air temperature after that stage.

Growth rates were measured by frequent harvests at which fresh and dry weights, shoot/root ratios, leaf length, leaf width, leaf area per unit leaf weight, total root length and root surface per unit root weight were estimated. Short-term growth responses were measured by recording the rate of increase in leaf length.

Rate of development was estimated by counting the number of visible leaves, a leaf being included as soon as it emerged from the sheaths of the foregoing leaves.

In addition, in many cases, rates of photosynthesis and exudation rates of the root system during the hour after shoot excision were measured at harvest times.

RESULTS

RATE OF DEVELOPMENT

Temperature appeared to be a major factor in determining the rate of leaf appearance. Both light quality (daylight, fluorescent light, and light from high pressure mercury lamps) and light intensity (70,000–140,000 ergs $\text{cm}^{-2} \text{ sec}^{-1}$) were of minor importance. Even the nutrient supply, varying from one-quarter to twice Hoagland concentration, was much less effective (Figs 1 and 2) in altering the rate of leaf appearance. The rate of leaf

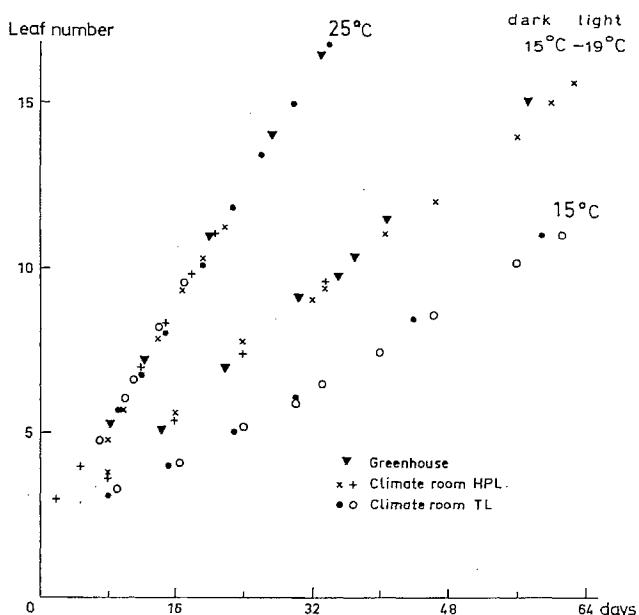


FIG. 1. Effect of temperature on the rate of leaf appearance under various light conditions.

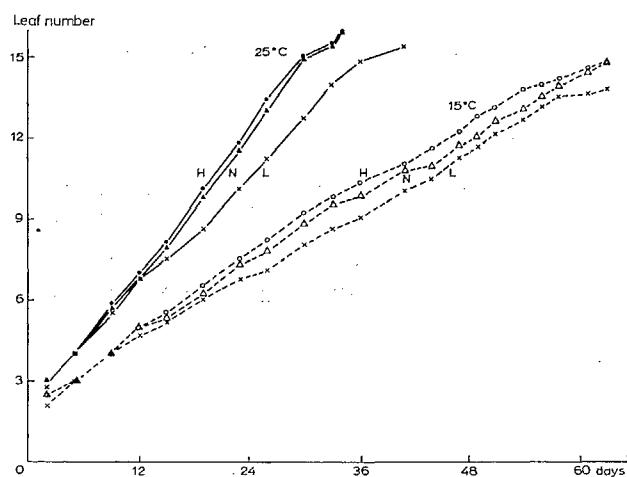


FIG. 2. Interaction between the effect of temperature and of nutrient concentration on the rate of leaf appearance. ($L = \frac{1}{4}$; $N = 1/1$ and $H = 2/1$ times concentration of normal Hoagland solution).

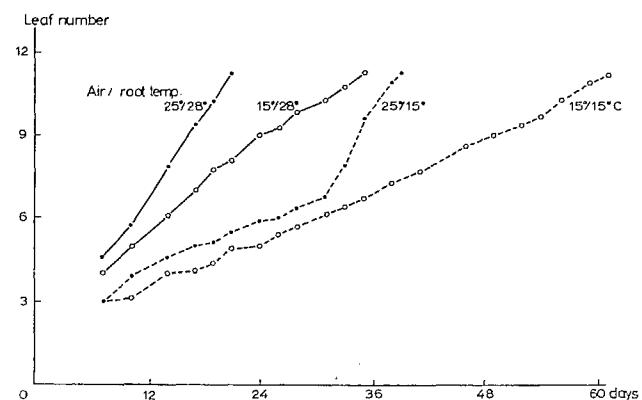


FIG. 3. Time course of leaf appearance at air temperatures of 15° C or 25° C combined with temperatures of the root environment of either 15° or 28° C.

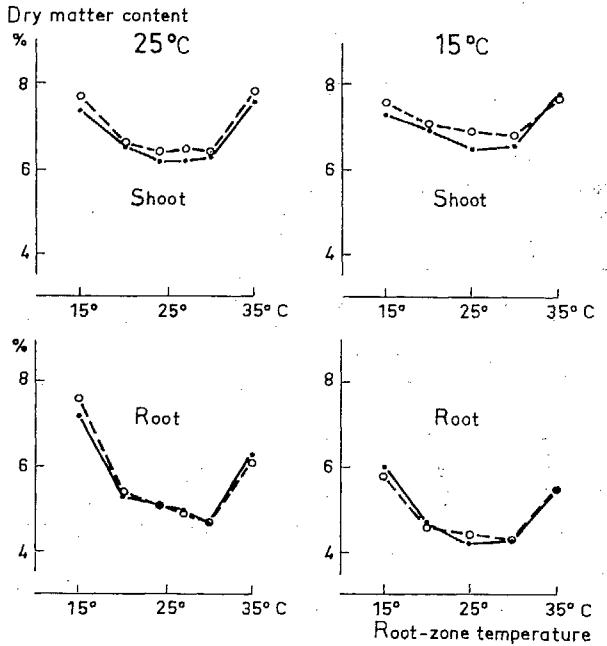
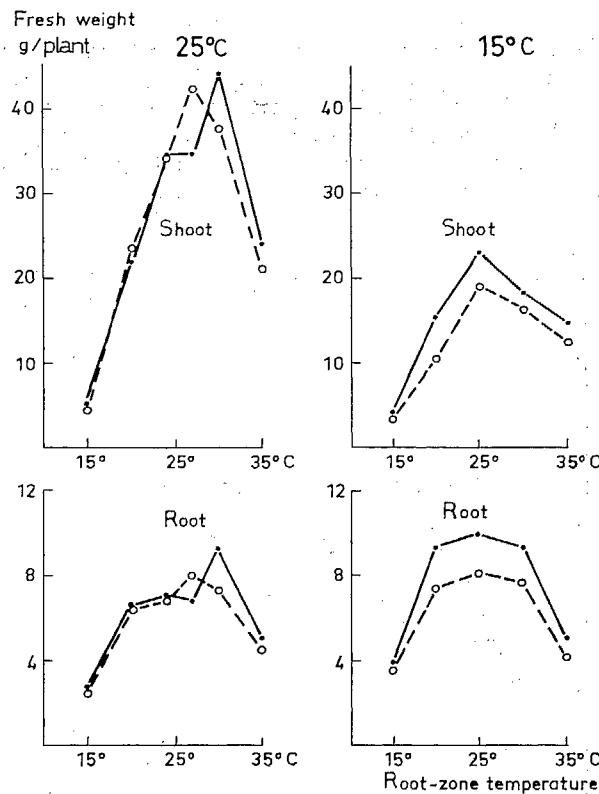


FIG. 4. Shoot weights, root weights, and dry matter content of 3-week-old maize plants grown at two air temperatures (15° and 25° C) combined with a series of root zone temperatures (15–35° C). (Continuous and broken lines refer to two different experiments.)

appearance was determined by the temperature of the growing point of the shoot. Figure 3 shows that the root temperature controlled this rate up to about the 8th leaf stage, while air temperature later gradually took over the control of this process when the growing point emerged from the root environment into the air. All further steps up to the development of the male and female inflorescences were completely controlled by the air temperature.

RATE OF GROWTH

With optimal nutrient supply, growth rate was affected by the ambient temperature under all light conditions. Increasing the temperature from 15°C to 25°C resulted in an increase in relative growth rate from 0.068 to 0.230 g g⁻¹ day⁻¹ in the glasshouse experiment and in the climate rooms (at +100,000 ergs cm⁻² sec⁻¹) from 0.074 to 0.210 g g⁻¹ day⁻¹, showing a Q_{10} of about 3.

Varying the root temperature from 15°C to 35°C affected growth rates at both air temperatures, but

air temperature still exerted a clear influence, mainly on shoot growth (Fig. 4). Root weight appeared to be less influenced by the air temperature, but if it was, it was always in the opposite direction to shoot growth. At 15°C air temperature, shoot growth was less at all root temperatures, but dry matter content (Fig. 4) and soluble carbohydrate content in shoots and roots were higher. This is assumed to be a direct cause of the slightly higher root weights over the whole range of root temperatures in combination with the air temperature of 15°C.

MORPHOLOGICAL ASPECTS

Due to small differences in the responses of growth and development rates to an increase in temperature from 15°C to 25°C plant weights at comparable stages of development were somewhat higher at the lower temperatures. Root temperature appeared to be as effective as overall temperature in this respect, particularly so far as the lower leaves were concerned (Fig. 5).

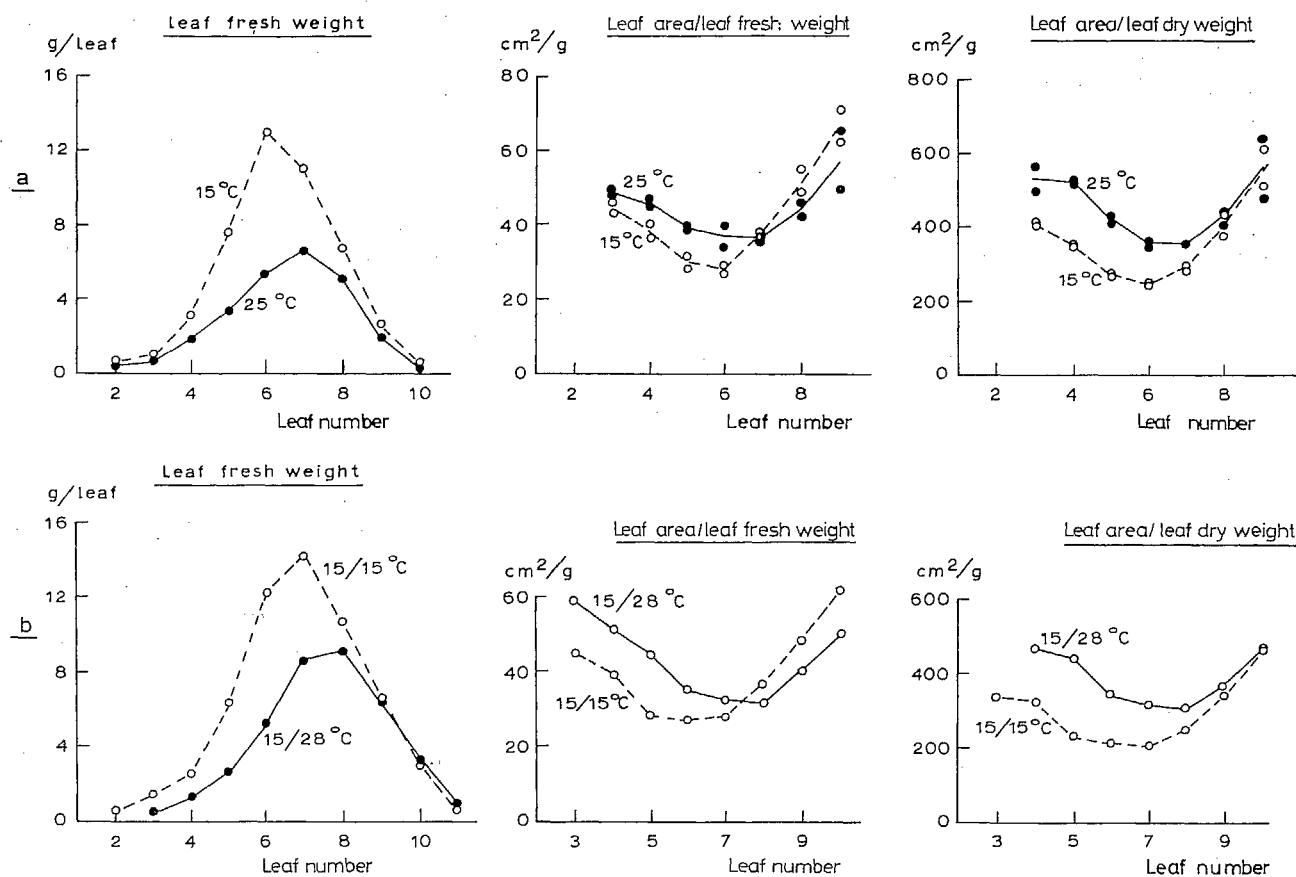


FIG. 5. Fresh weights and area/weight ratios of the subsequent leaves of maize plants: (a) grown at overall temperatures of 15°C or 25°C up to the 11th leaf stage; (b) grown at an air temperature of 15°C combined with a root zone temperature of 15°C or 28°C up to 12th leaf stage.

Leaf weights were higher at 15° C than at 25° C. With only minor differences in leaf length, this was achieved by a broadening of the leaves at 15° C. At the lower temperature, leaf area per unit leaf weight, both on a fresh and dry weight basis, was smaller. With leaf area on a plant weight basis, differences were still greater as a consequence of the relatively high root weights at 15° C.

The same tendency, reduction in the area: weight ratio at low temperatures, was also found for the root system. The higher the temperature, the finer the branching of the roots. This resulted at the 10th leaf stage in an average root length of 5,750 cm g⁻¹ of root dry weight at 15° C and 14,545 cm g⁻¹ of root dry weight at 25° C. From this the surface area was calculated and amounted to 1,150 cm² g⁻¹ at 15°C and 2,420 cm² g⁻¹ at 25° C.

THE EFFECT OF ROOT TEMPERATURE VERSUS GROWING POINT TEMPERATURE

Various experiments with beans and, partly, also with maize (Brouwer and Kleinendorst, 1967; Grobelaar, 1963) led to the assumption that root temperature effects were mediated by its effect on the water permeability of the root tissue, resulting in various levels of water stress in the growing regions of the shoot. However, since preliminary experiments showed that the ultimate effect of root temperature was less severe on older plants than on seedlings, the position of the growing point seemed to be important. Hence a number of experiments were performed in which root tempera-

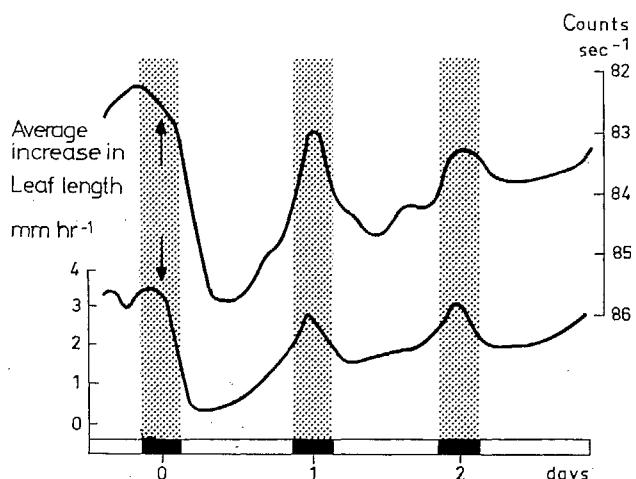


FIG. 7. Response of leaf growth rate and water content to a change in root temperature from 20° C to 5° C (start indicated by arrows).

tures and growing point temperatures were varied independently (see for details Kleinendorst and Brouwer, 1970). At the same time the water content of the leaves was estimated with a β -gauge. Figures 6 and 7 show that a lowering of either root temperature or shoot growing point temperature resulted in an immediate reduction in leaf elongation rate. Only in the case of lowering the root temperature, was this growth reduction accompanied by a reduction in water content of the leaf tissue (Fig. 7). It appeared that, in this treatment, a partial recovery of both the elongation rate and the leaf water content gradually occurred during the two to three days of the treatment. Simultaneously, the soluble sugar content of the tissue increased to rather high levels, indicating that the recovery resulted from an osmotic adjustment. The recovery was not found at the low temperature treatment of the growing point.

It is assumed, therefore, that the temperature of the root medium influences the growth of young seedlings mainly by its effect on the activities of the growing point and additionally causes an enhanced water stress. In older plants, the effect on the growing point gradually diminishes, and the only effect of temperature is the enhanced water stress, which is less severe in maize due to osmotic adjustment.

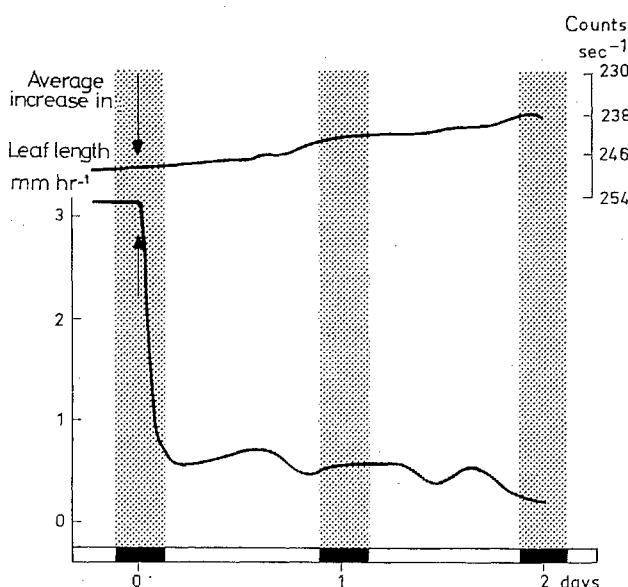


FIG. 6. Response of leaf growth rate and water content to a change in growing point temperature from 20° C to 5° C (start indicated by arrows).

DIRECT AND INDIRECT EFFECTS OF TEMPERATURE

The experiments described above indicated that the temperature of the growing points determined the rate of formation and growth of new organs. Under constant external conditions, this led to a higher degree of differentiation in situations where low growth rates were found, resulting in a higher dry matter content and a smaller surface area per unit of weight. This applied for both shoot and root tissues. It is clear that this, in

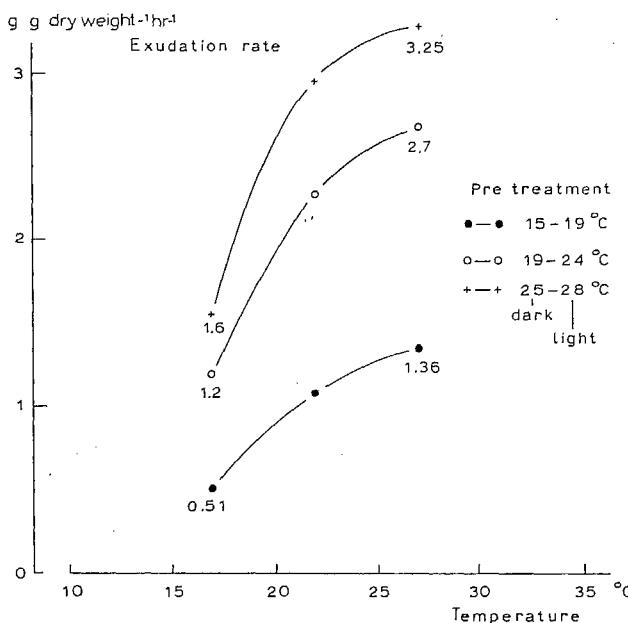


FIG. 8. The influence of temperature on the bleeding rate of excised root systems which were grown at different temperatures (pretreatment temperatures).

turn, may influence the relative intensity of various physiological processes depending on which basis (area or weight) the data obtained at various temperatures were compared.

So, for instance, the bleeding activity per gramme of root was weight determined not only by the temperature of the root medium during the measurement, but also by the temperature at which the root systems were grown. In Figure 8 the bleeding rate per gramme of root dry weight of three types of root systems is plotted against the temperature during the experiment. The direct temperature reaction, a more than twofold increase in the bleeding rate on increasing the temperature from 17°C to 27°C, was found irrespective of the temperature at which the roots were grown. The bleeding rate, however, appeared to be determined, to a large extent, by this temperature, being much higher in the case of the more finely branched roots grown at 25–28°C than for the thicker roots grown at a temperature of 15–19°C, with intermediate values for roots grown at 19–24°C. Hence, the ratio between the bleeding rate of roots grown at 25–28°C was 6 times the rate shown by roots grown at 15–19°C.

The same relationship holds for the rates of photosynthesis. In contrast with any other plant species, maize displays a clear temperature effect on photosynthesis per unit of leaf area at normal (0.03 per cent) carbon dioxide concentrations. In addition, this effect appears considerably enhanced when expressed on a leaf weight basis or on a plant weight basis. The latter is shown in Figure 9, where the photosynthesis versus light

intensity curves of maize plants grown at 25°C are compared with the same curves for plants grown at 15°C. On a leaf area basis, the 25°C curve is about twice as high as the 15°C curve. Due to differences in area/plant weight ratio, the differences were accentuated considerably when expressed on a plant weight basis.

CONCLUSIONS

Examination of the growth response of maize plants to temperature revealed that various processes, which in combination determine the growth rate, are not affected to the same degree. Considering photosynthesis as the basic process, it appeared that low temperatures reduced the rate of the energy conversion per unit leaf area, even at normal carbon dioxide concentration. However, growth rate was reduced still more, since less of the carbohydrate material produced was converted to assimilating tissue. Van Dobben (1962) emphasized the importance of this phenomenon and showed, for various plant species, that the relative growth rates at different temperatures were correlated with shoot/root ratios. Not only shoot/root ratios, but also specific leaf weight was affected, and in the overall growth response to temperature about 50 per cent of the effect could be ascribed to changes in morphology and the other 50 per cent to the direct effect of temperature on photosynthesis.

Looking at the physiological background of the morphological features, it appeared that, in all cases, low temperatures influenced area development more than differentiation. A check in the rate of area expansion, achieved by either a water stress due to low root

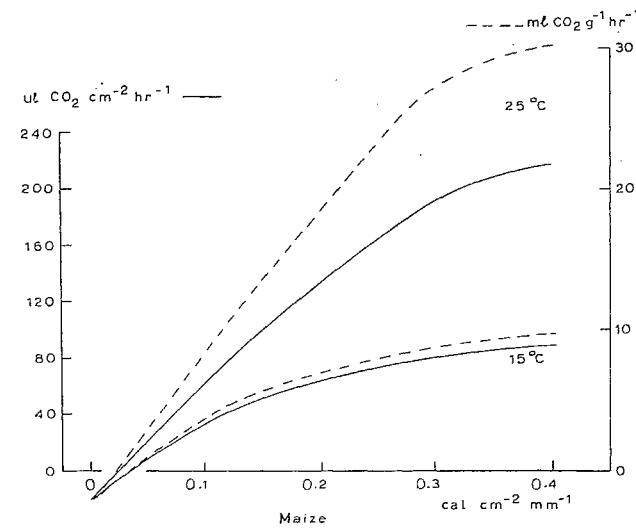


FIG. 9. The rates of carbon dioxide exchange at various light intensities measured with maize plants grown and photosynthesizing at 15°C or 25°C and expressed on leaf area basis (continuous lines) or on plant dry weight basis (dotted lines).

temperatures or just a low temperature of the growing region, resulted in accumulation of dry matter and a high concentration of soluble carbohydrates (Grobbelaar, 1963; Kleinendorst and Brouwer, 1970) enabling differentiation processes to go on almost undisturbed. According to Allsopp (1954), many differentiation pro-

cesses depend on the carbohydrate level. It is not yet known whether hormones are also involved. The present data indicate that, under favourable growing conditions, area growth and differentiation compete for the available carbohydrates, leading to high area: weight ratios both in roots and leaves.

Résumé

Croissance de plants de Maïs en fonction de la température (R. Brouwer, A. Kleinendorst et J. Th. Locher)

Des plants de Maïs ont été cultivés sur solution nutritive dans des salles climatisées ou dans des compartiments de serre maintenus à diverses températures constantes. La température de l'environnement des racines était indépendante de la température de l'air ambiant et, dans certains cas, la température du bourgeon terminal de la partie aérienne a varié indépendamment et de

la température de l'air, et de la température de la racine.

L'effet direct de la température sur les processus physiologiques comme la photosynthèse, l'absorption de l'eau et l'absorption des minéraux a été suivi de modifications de la morphologie des racines et des feuilles, de sorte que l'effet final sur la croissance a pu être attribué à raison d'environ 50% aux effets directs de la température sur le rythme des processus limitants et à raison d'environ 50% aux effets indirects par l'entremise des modifications des caractères morphologiques.

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III The effect of internal water status on plant growth, development and yield

III Effet de l'état hydrique interne des plantes sur leur croissance, leur développement et leur rendement

The effect of internal water status on plant growth, development and yield

R. O. Slatyer

Department of Environment Biology
Research School of Biological Sciences
Australian National University
Canberra (Australia)

The way in which water stress affects the growth, development and yield of crops has been a subject of great interest for many years. Despite this interest, however, and despite the importance of the phenomenon to agricultural production, a clear and quantitative understanding of water stress effects does not yet exist.

There are several reasons why this situation exists. In the first place, water stress affects almost all biophysical and biochemical processes, so the integrated effects on growth and development are extremely complicated. Second, plant-water status is a highly dynamic parameter, strongly influenced by conditions in the soil and atmospheric micro-environment, and also regulated, to different degrees in different situations and with different species, by physiological factors. It therefore constitutes a difficult parameter to control experimentally. Third, the field of activity is one in which researchers frequently start by examining a particular effect of water stress on a particular process, and then develop their work into a study of the process rather than of the effect. In this way, feedback from biochemistry and biophysics into physiology and agronomy is often rather restricted and tenuous.

The present paper reviews some of the basic relationships between water deficits and physiological processes, and then examines the effects of water deficits on morphogenesis, finally considering the specific effects on grain yield in cereals. It is based largely on an earlier review (Slatyer, 1969).

WATER DEFICITS AND PHYSIOLOGICAL PROCESSES

The effect of water stress on such key processes as nutrient uptake, carbohydrate and protein metabolism, and translocation of ions and metabolites, is intimately linked with the effects on development, since rate of

development affects, and is affected by, these other processes.

For example, root development affects the size and character of the absorbing system for mineral nutrients; shoot development has a direct feedback on the rate of carbohydrate and protein metabolism. The source strength represented by the size and activity of the photosynthetic system and the sink strength represented by tissue which requires carbohydrate, but which is not actively photosynthesizing, influences the rate of translocation.

However, two important areas of plant metabolism—those of nitrogen and carbon metabolism—are so basic to growth and development that they warrant separate consideration.

WATER DEFICITS, PROTEIN SYNTHESIS AND NITROGEN METABOLISM

In general there appears to be a reasonably clear dependence of the growth rate of developing tissues and organs on protein synthesis, and a close association between protein synthesis and RNA content, and between RNA and DNA levels (see, for example, Woodstock and Skoog, 1960, 1962; Williams and Rijven, 1965). Figure 1 (from Williams and Rijven, 1965) shows the nature of some of the associated phenomena for a developing wheat leaf, although these authors are very cautious in the degree to which they associate any pair of these parameters, or assign cause and effect relationships.

From the known effects of water stress on rate of development, it can be expected that there will be associated effects on many aspects of protein synthesis. Indeed, interruption of protein synthesis and proteolysis are generally observed when stress is imposed (Zholkevich and Koretskaya, 1959; Chen *et al.*, 1964; Shah and Loomis, 1965; Ben-Zioni *et al.*, 1967).

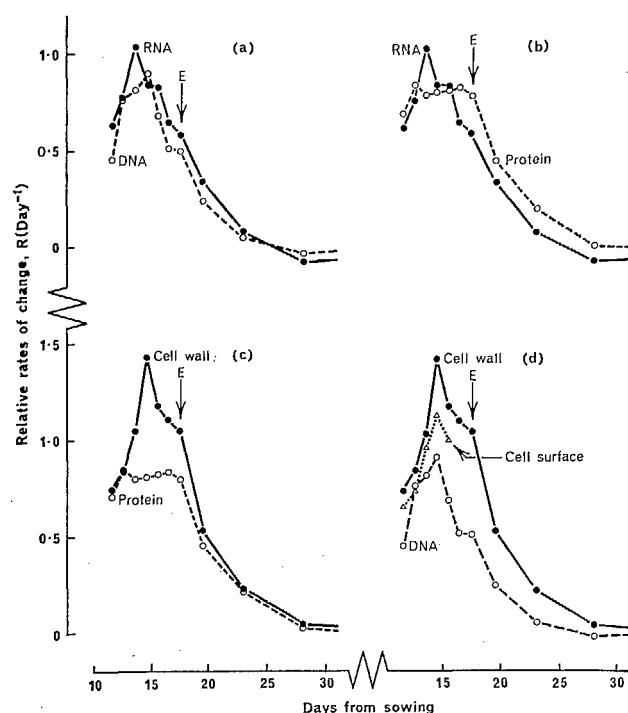


FIG. 1. Relative rates of change in various attributes of the fourth leaf of a wheat plant, from initiation to maturation. E is time of leaf emergence. (a) DNA and RNA, (b) RNA and protein nitrogen, (c) protein nitrogen and cell wall material, (d) DNA, cell wall material and cell surface (from Williams and Rijven, 1965).

Although few studies of the effects of water stress on nucleic acid metabolism have been made, the results form a fairly consistent pattern.

In the first place, Shah and Loomis (1965) found a tendency for the DNA content per cell, which remained relatively constant with age in expanding beet leaves, to be reduced by water stress only if severe wilting occurred and was protracted (Fig. 2). Gardner and Nieman (1964) showed a marked reduction of the rate of increase in DNA content of developing, and presumably actively dividing, cotyledonary leaves of radish, at slight stress levels, but also found that there was still some increase in DNA level when severe stress was imposed. Together these results appear to be consistent with a marked sensitivity of cell division to stress, but with cell breakdown occurring only in developed tissues and under severe and prolonged stress conditions.

An effect on RNA levels (Fig. 2) tends to occur at lower stress levels and the ratio of RNA in stressed to that in unstressed leaves appears to decline progressively. Shah and Loomis (1965) concluded that RNA synthesis was impaired by stress and also that some degradation occurred of the RNA which was already formed when stress was imposed. A similar conclusion was reached by Zholkevich and Koretskaya (1959) with

pumpkin roots. Gates and Bonner (1959) attributed the relative decline to enhanced degradation of RNA already formed, rather than to impeded synthesis, because evidence with ^{32}P -labelled RNA showed that, while total activity remained constant in the controls, there was a progressive loss of label in stressed plants. They considered that the continued synthesis provided a base from which growth could be rapidly resumed upon rewatering.

The slightly different responses observed by these various workers are probably related in some degree to the developmental stage of the tissues with which they worked. A similar comment can probably be applied to the rather inconclusive results obtained to date by different workers as to the effect of water stress on the nucleotide composition of RNA (see, for example, Kessler, 1961; Shah and Loomis, 1965; West 1966; Stutte and Todd, 1967).

Of more significance is the observation by several workers (West, 1966; Genkel *et al.*, 1967; Chen *et al.*, 1968; Hsiao, 1970; Nir *et al.*, 1970) that polysome formation is slowed and that polysome breakdown occurs during stress. This could be due to either a direct effect of stress on the polysomes themselves, or on the supply of messenger RNA which is needed for polysome aggregation. Nir *et al.* (1970) proposed that stress may directly affect DNA and inactivated messenger RNA synthesis, resulting in a decrease in the polysome population and hence in normal protein synthesis. Whether the effect is directly on the polysomes or not, it is noteworthy that only small levels of water stress are needed. With water potentials of the order of $\psi = -6$ bars, Hsiao (1970) observed a marked and rapid shift in the ratio of polysomes to monosomes in maize seedlings, which was reversible under his conditions. Where more severe stress is imposed, recovery is slowed or, in some cases, does not occur (Chen *et al.*, 1968).

Changes reported in uptake and redistribution of nitrogen and phosphorus (Gates, 1957) are consistent with the effects on nucleic acid and protein synthesis, suggesting that in expanding leaves the normal tendency to synthesize soluble nitrogen and phosphorus into more highly organized compounds was checked by water stress and that, especially in older leaves, hydrolytic breakdown processes tend to occur.

Furthermore, nitrate reductase activity is sharply reduced by water stress (Huffaker *et al.*, 1970), indicating an associated reduction in available substrate for amino acid formation.

The role of certain growth substances, particularly auxins, gibberellins and kinins, in retarding senescence, and the general similarity of many stress effects to processes associated with senescence, has provoked interest in the role of growth substances in water stress phenomena. With regard to protein synthesis, Richmond and Lang (1957) and Osborne (1965) have shown that the addition of cytokinins to the leaves of a number of annual plants has retarded chlorophyll degradation and

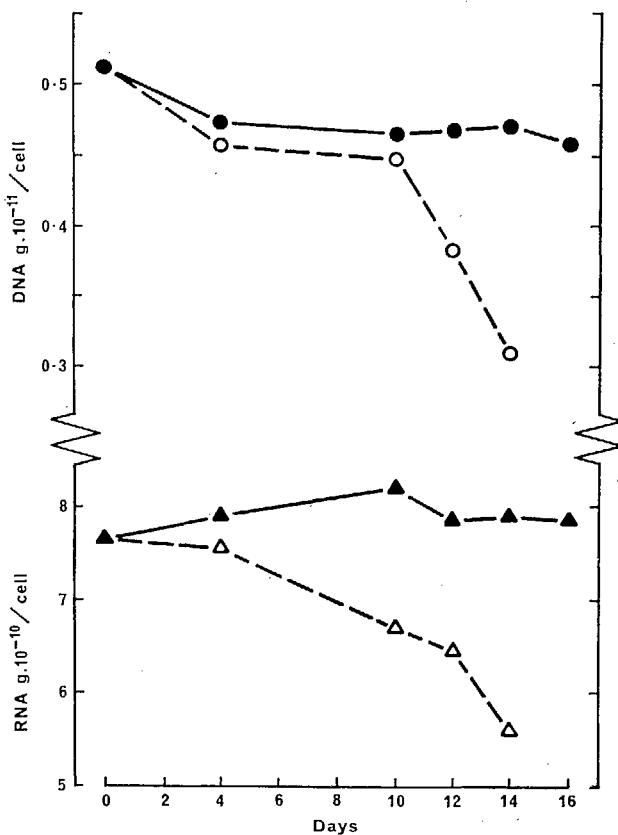


FIG. 2. DNA and RNA concentrations, expressed on a per cell basis, for stressed (----) and unstressed (—) sugar-beet leaves. The progressive onset of stress caused wilting of the leaves from about day 10 onwards (after Shah and Loomis, 1965).

has promoted amino acid incorporation and protein synthesis.

Recently Ben-Zioni *et al.* (1967) and Itai *et al.* (1968) have examined the role of root cytokinins in influencing protein synthesis in leaves. The former workers studied the effect of kinetin in the incorporation of L-leucine in stressed tobacco leaves. Even though the stress imposed was brief and mild (a water potential of about $\psi = -4$ bars), stressed tissues showed a marked reduction in ability to incorporate L-leucine into protein, the reduction being more pronounced in older than younger leaves. Stressed plants also had lower cytokinin levels in the root exudate than did control plants.

The addition of kinetin restored incorporation in stressed leaves to levels approximating that of the controls, although a higher applied kinetin concentration was required to achieve this effect, compared with levels in control plants. These workers are cautious in assigning a causal role for cytokinin level in protein synthesis, and point out that reductions in both cytokinin levels and protein synthesis could be merely reflections of disturbed metabolism. However, the known effects of kinins on rate of senescence suggest that cytokinin supply to the shoot is important in the maintenance of active protein synthesis, and also suggest that studies of root development and metabolism in relation to hormone balance may provide important insights into aspects of stress physiology.

A frequently observed effect of stress is the appearance of high levels of free amino acids, especially pro-

line, and amides (Chen *et al.*, 1964; Kemple and Macpherson, 1954; Mothes, 1956; Prusakova, 1960). In addition, Barnett and Naylor (1966) found that, although amino acids were continually synthesized during water stress in Bermuda grass, protein synthesis was inhibited and protein levels decreased. In their experiments water stress induced a marked increase in free proline, the ^{14}C level of which turned over very slowly. Stressed shoots accumulated much more proline newly synthesized from glutamic acid than did control shoots. It was suggested that the slow turnover of labelled proline may reflect an inhibition of proline catabolism.

There is no clear understanding of the significance of this rise in proline level. However, Barnett and Naylor (1966) suggested that free proline may act as a storage compound for both carbon and nitrogen during water stress, when both starch and protein synthesis are inhibited. Such a storage pool might be utilized for renewed growth upon rewetting.

Various inhibitors have also been observed to influence development. Among them CCC (2-chloroethyltrimethylammonium chloride) (see, for example, Humphries *et al.*, 1965) has created considerable interest and has been claimed to increase cereal yield under stress conditions. Humphries (1968) has reviewed the literature on this phenomenon and concluded that the primary effect of CCC is to increase root growth relative to shoot growth, thus delaying the onset of stress and reducing its severity. There may be a link between the role of CCC and that of cytokinin, since the effects of CCC on root

growth may influence the supply of kinins to the shoot, perhaps leading to stress tolerance.

Overall, it is clear that quite small water deficits can have a direct effect on nucleic acid metabolism and hence on protein synthesis. It seems likely that effects on amino-acid composition are indirect and that all these effects are largely reversible, as long as the stress is not too severe or too protracted. The role of root hormones in controlling protein synthesis is still obscure, but it may be more general, influencing overall morphogenesis, rather than directly affecting nucleic acid metabolism.

WATER DEFICITS, PHOTOSYNTHESIS AND CARBOHYDRATE METABOLISM

Carbohydrate metabolism can be affected in a number of ways by water deficits. There appear to be direct and indirect effects on photosynthesis, and on a number of intermediate components and processes.

In general, net photosynthesis is progressively reduced by water stress, and negative values may develop when stress is severe (El-Sharkawy and Hesketh, 1964; Slatyer, 1967). It is assumed that this response is mediated partly by a way of impeded CO_2 supply following stomatal closure and partly by a direct effect of dehydration on the photosynthetic system.

Recent studies (Troughton, 1969; Troughton and Slatyer, 1969; Boyer, 1970a; Slatyer, this volume) have provided evidence that the observed reduction in net photosynthesis with increasing stress can be completely attributed to stomatal closure until quite severe stress exists. The type of evidence obtained is shown in Figure 3, where the change in intracellular resistance caused by reductions in relative water content is plotted. Intracellular resistance is the slope of the curve relating CO_2 concentration (between the mesophyll cell wall surfaces and the chloroplasts) to CO_2 exchange. Any reduction in CO_2 exchange, per unit of CO_2 supplied, causes an increase in intracellular resistance. It can be seen from Figure 3 that there was no increase in intracellular resistance in the leaves of several species until relative water contents equivalent to permanent wilting. Direct effects of dehydration, then, appeared in the non-drought-sensitive species (cotton, maize), but more severe stress (corresponding to water potentials of the order of $\psi = -20$ to -30 bars) before direct effects on wheat and millet were found.

If progressive stomatal closure is the primary cause of the first stages of the photosynthetic response to water stress, there should be supporting evidence from other types of experiment which indicate that the photosynthetic apparatus, and the reactions associated with respiration, are relatively unaffected until severe water stress exists.

As far as the photosynthetic apparatus is concerned, the recent work of Santarius and colleagues (Santarius and Heber, 1967; Santarius and Ernst, 1967; Santarius,

1967) with isolated chloroplasts, and with leaf tissue segments, has provided evidence that such key processes in the photosynthetic reduction of CO_2 as ATP synthesis, the reduction of NADP and the reduction of phosphoglyceric acid (PGA), were unaffected until very severe stress existed. In the leaf segments this corresponded to relative water contents of less than 50 per cent (probably equivalent to water potentials below -25 bars). Although Santarius observed reductions in net photosynthesis, no attempt was made to control or assess stomatal effects or other aspects of the CO_2 supply system; the key results, therefore, are those just reported.

This work is supported by the studies of Huffaker *et al.* (1970), which showed that water deficits equivalent to about $\psi = -11$ to -12 bars, developing over a 4-day period, had relatively little effect on the primary carboxylating enzymes for photosynthesis in barley, even though leaf elongation ceased at about $\psi = -2$ to -3 bars.

Recent experiments by Troughton and Slatyer (1969) have also provided evidence of the tolerance of gross photosynthesis to water deficits. In experiments in which photorespiration was suppressed by oxygen-free air, no effect on the mesophyll resistance of cotton leaves was observed, even when relative water contents of 55 per cent were imposed (equivalent to water potentials of about $\psi = -50$ bars). Since respiration was suppressed, the experiment effectively demonstrated that gross photosynthesis was unaffected by stresses of this magnitude.

The effect of water deficits on respiration is somewhat obscure, partly because of the failure of many investigators to distinguish between dark respiration and photorespiration in those species in which the latter process is evident, partly because of the difficulties in measuring photorespiration, partly because of complications due to stomatal closure and partly because of possible differences in short-term and long-term effects.

With regard to dark respiration, most recent studies have indicated that it is relatively unaffected by water deficits, until at least moderate water stress exists, and that a reduction rather than an increase is likely to occur. With *Chlorella*, for example, Greenway and Hiller (1967) found that water potentials of $\psi = -10$ bars did not affect respiration over periods of about 2 hr, although reductions were observed when the water potential was reduced to $\psi = -20$ bars. In short-term (several minutes) experiments, even water potentials of this level did not affect the uptake of acetate-2- ^{14}C and also had little effect on the distribution or level of ^{14}C in the intermediates of the tricarboxylic acid (TCA) cycle, suggesting that there was no direct inhibition of respiratory pathways. In longer-term (up to 56 hr) experiments with beet leaves, referred to above, Santarius (1967) found that dark respiration was not reduced until extremely severe stress (water potentials probably below $\psi = -100$ bars), existed.

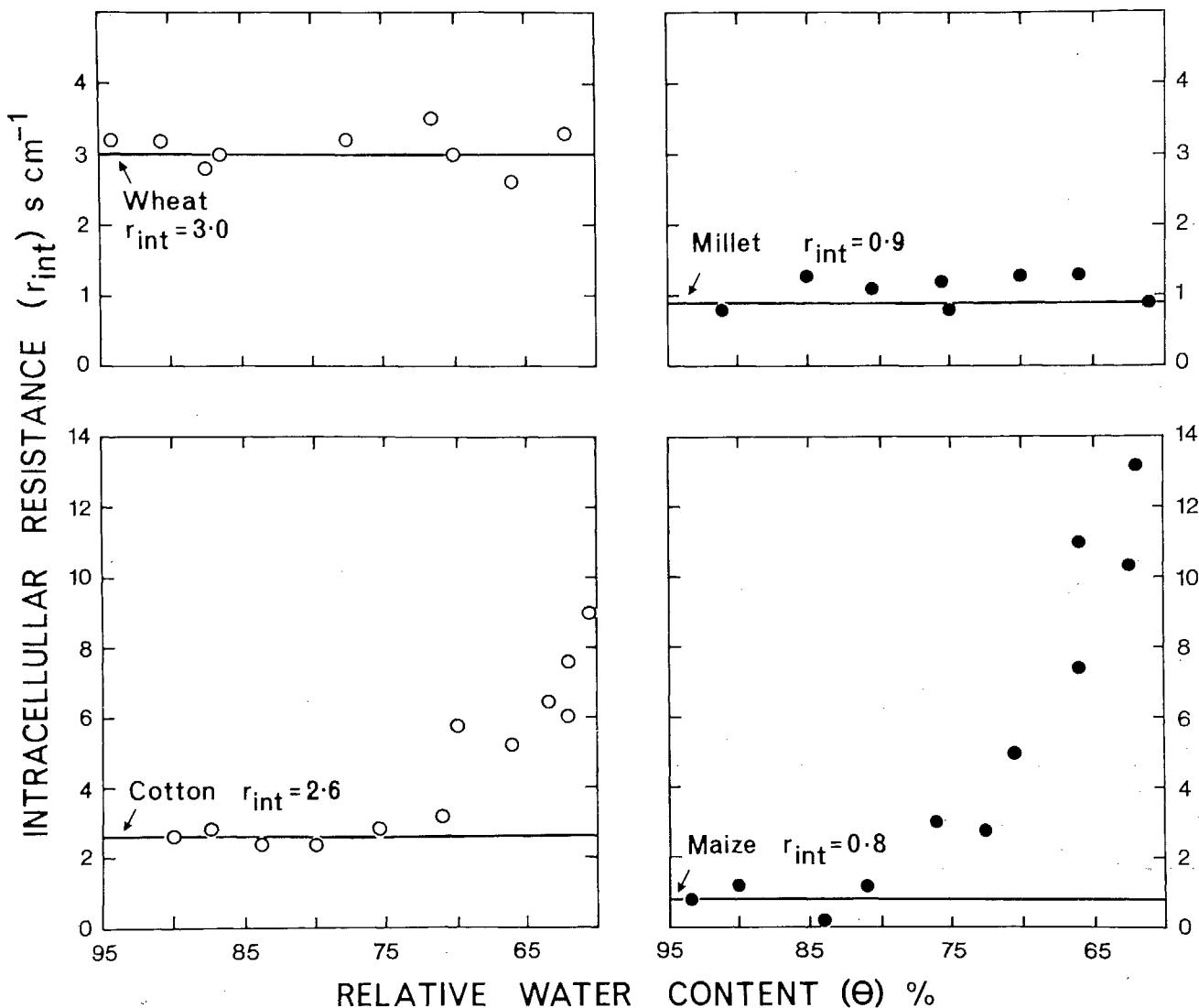


FIG. 3. Effect of relative water content on intracellular resistance of wheat, millet, cotton and maize leaves (after Slatyer, this volume).

More recently, Boyer (1970b) has found a progressive decrease in dark respiration of corn, soybean and sunflower shoots, as water stress was increased. About a 50 per cent reduction was observed as leaf water potential dropped from $\psi = -4$ to $\psi = -16$ bars, after which a relatively constant rate was noted. It is possible that stomatal resistance may have affected this pattern.

The effect of water stress on photorespiration is difficult to assess because photosynthesis is proceeding at the same time. One index of an effect is a change in the CO_2 compensation point and Meidner (1961, 1962) has measured increases in this parameter as stress was imposed in several species, suggesting that photorespiration increases even at moderate stress levels. By

comparison, Troughton and Slatyer (1969) did not observe a change in the CO_2 compensation point of cotton leaves under the stress conditions previously reported. A complicating factor in all respiration work is the marked dependence of dark respiration, and more particularly photorespiration, on temperature (Zelitch, 1967). Since stomatal closure generally induces an increase in leaf temperature, indirect effects of water stress on net photosynthesis through this means may outweigh direct effects of dehydration.

To summarize the preceding paragraphs, it can be stated that there is increasing evidence that stomatal closure, directly by impeding CO_2 supply and indirectly by increasing leaf temperature, is the mechanism by

which water stress first leads to reduced net photosynthesis under natural conditions. As stress becomes more severe and more protracted, direct effects will finally be observed, but more work remains to be done before this matter can be satisfactorily resolved.

Another factor which has been observed to influence photosynthesis is the availability of suitable sinks for assimilates. When utilization of assimilates is impeded, substantial reductions of net photosynthetic rate have been observed (see, for example, Burt, 1964; Nösberger and Humphries, 1965). Again, the response pattern can be expected to vary between species. In species which can store significant amounts of assimilate as starch in the leaves, any effect can be expected to be much less than in species in which there is little starch storage, such as wheat. In wheat, King *et al.* (1967) have shown dramatic and pronounced effects of sink size on photosynthesis under non-stressed conditions.

During water stress, it appears quite probable that assimilates may be accumulated at sites of photosynthesis, since expansion growth is probably restricted sooner, and to a greater degree, than photosynthesis. Wardlaw (1967, 1969) examined this phenomenon in wheat and perennial rye grass. He concluded that, although leaf photosynthesis was not affected until after growth rate had been reduced, there was no evidence of sink size directly affecting the rate of photosynthesis. However, he conceded that this interpretation could be revised, and that lack of suitable sinks could retard photosynthesis under appropriate conditions.

Wardlaw (1967, 1969) also examined the translocation mechanism in these experiments. As Table 1 shows, he found that the velocity of assimilate movement in the conducting system was not reduced, as long as adequate sink capacity existed, and he concluded that the conducting system was remarkably resistant to water stress. Although these results conflicted with the conclusions of some other workers (Zholkevich, *et. al.* 1958; Plaut and Reinhold, 1965; Hartt, 1967), which suggest a direct effect of stress on translocation, sink capacity may have been a factor in some of those experiments. The continued movement of assimilates from the green stems to the roots and buds in the perennial grass *Phalaris*

tuberosa, when the leaves had been shed during severe stress, indicates that the conducting tissue can be well maintained (McWilliam, 1968), even if the velocity of translocation is reduced.

Transport within the leaf does appear to be reduced by stress under some conditions. Although Plaut and Reinhold (1967) showed enhanced movement of ^{14}C applied to stressed bean leaves, Wardlaw's (1967) data and Hartt's (1967) experiments with sugar cane show a greater retention of photosynthetic assimilates, in wilted wheat leaves and a slower, but prolonged, movement of the assimilates out of the leaf. This result, however, may have been influenced by sink capacity because, in a subsequent experiment with perennial rye grass, Wardlaw (1969) was able to maintain rates of movement out of stressed leaves, as long as adjacent actively photosynthesizing leaves were removed.

One of the most commonly reported effects of water deficits on carbohydrate metabolism is an increase in sucrose levels and decrease in starch levels (see, for example, Iljin, 1957). These changes are frequently associated although there are reports of reduced polysaccharide levels not being accompanied by an increase in sugar content (Woodhams and Kozlowski, 1954).

Hiller and Greenway (1968) have recently examined more specific aspects of these phenomena in short-term experiments with *Chlorella*. Their primary results were generally similar to those just described, water deficits (equivalent to water potentials down to $\psi = -10$ bars) causing a marked increase in sucrose synthesis, as measured by incorporation of applied ^{14}C -glucose into sucrose, and an immediate and pronounced suppression of polysaccharide synthesis. They also observed reduced ^{14}C incorporation into methanol-soluble intermediates other than sucrose, which was more pronounced for sugar phosphates than for amino acids. Incorporation into uridine diphosphate glucose (UDPG) was depressed more than that into hexose monophosphates, especially when stress was not too severe. Generally similar reductions in sugar phosphate levels have been observed in stressed *Trifolium subterraneum* (Wilson and Huffaker, 1964), and in starch formation in stressed sunflower (Plaut and Ordin, 1964).

The question arises as to the relationship between the enhanced sucrose and reduced polysaccharide levels. Reduced starch levels have been attributed to factors such as reduced photosynthesis and increased hydrolysis as well as to decreased synthesis (see, for example, Mothes, 1956; Kozlowski, 1964). Although all these factors may operate, Hiller and Greenway (1968) found little evidence of hydrolysis, at least in the short-term response to stress; similar levels of ^{14}C activity in methanol-soluble compounds being observed in stressed and unstressed cells which had previously been supplied with ^{14}C -labelled bicarbonate in the light. They concluded that reduced starch formation was an indirect result of increased sucrose synthesis, rather than from a direct effect of water stress on starch synthesis.

TABLE 1. Effect of progressive water stress imposition in wheat during grain development on photosynthesis and velocity of translocation (after Wardlaw, 1967)

Days after water deprived	Photosynthesis (mg $\text{CO}_2 \text{dm}^{-2} \text{hr}^{-1}$)	Velocity of assimilate movement (cm hr^{-1})	
		Flag leaf sheath	Top internode
0	12.40	33	45
2	13.25	42	36
4	12.30	27	39
6 ¹	7.15	39	72

¹ Leaves wilted.

WATER DEFICITS AND PLANT DEVELOPMENT

The growth and development of a plant depends, in the simplest terms, on continuing cell division, on the progressive initiation of tissue and organ primordia, and on the differentiation and expansion of the component cells until the characteristic form of the plant is realized. Associated with this, basically genetically controlled, phenomenon is an interconnected web of metabolic events which involve the uptake of nutrients from soil and air, the synthesis of metabolites and structural materials and the transport of substances within the plant body.

Since all plant processes take place in what is effectively an aqueous medium, and since water is involved as a transporting agent or as a reactant in many of these processes, it is not surprising that reduced water uptake and dehydration can have deleterious effects on most physiological processes.

Both the initiation and differentiation of vegetative and reproductive primordia in the apical meristems, and the enlargement of the cells thus differentiated, are very sensitive to water stress.

The effect on primordial initiation appears to be superficially similar to that of dormancy, in the sense that initiation can be completely suspended without the potential for subsequent development being impaired, as long as the stress is not too severe or too protracted. Figure 4 (from Gates, 1968) provides a good illustration of this point, using apical development of lupin as experimental material. The virtual cessation of appearance of new primordia as soon as stress was imposed, followed by renewed development upon relief of stress, is a phenomenon that has frequently been referred to in water stress literature (see, for example, Gates, 1955a, 1968; Slatyer, 1967).

Cell division is also very sensitive to stress, but the observation that leaves of plants which have undergone periods of stress may contain a similar number of cells to unstressed controls (Petinov, 1965) suggests that the

capacity for resumed activity upon relief of stress may remain unimpaired. As distinct from the situation with primordial initiation, however, where complete suspension may occur, cell division may continue during stress, though at a much reduced rate, until quite severe conditions exist (Gardner and Nieman, 1964). This provides the opportunity for a relatively rapid resumption of growth when stress is removed.

The renewed development upon rewatering may proceed at a more rapid rate than in the controls, sometimes enabling stressed plants to "catch up". This phenomenon, evident in Figure 4, has also been demonstrated on a field scale. Morton and Watson (1948), for example, showed that a crop of sugar beet subjected to repeated cycles of water stress interspersed by irrigations developed, overall, at the same rate as the well irrigated controls. Even so, where stress is more severe or is protracted, the rate of development can be markedly reduced, delayed flowering and maturation frequently being observed (Salter and Goode, 1967). In addition, the character of both vegetative and floral development can be seriously affected.

Cell enlargement, the other essential component of growth, is also affected at very slight stress levels (Hsiao *et al.*, 1970). In fact, this is usually the first observable symptom of water deficits, and is a main cause of the stunting which is perhaps the most common sign of water stress under field conditions.

The main difference between the long-term effect of reduced rates of cell enlargement, and that of primordial initiation and cell division, is that cell enlargement is a plastic type of phenomenon, closely linked with the laying down of fairly rigid cell wall materials (Plaut and Ordin, 1964). In consequence, slower rates of enlargement are generally associated with smaller final cell size, so that "catching up", of the type referred to with regard to primordial initiation, is largely precluded.

In some species cell enlargement is so sensitive to water deficits that stem elongation or leaf enlargement can be inhibited by small diurnal water deficits that occur even with well watered plants on days of high radiation incidence (see, for example, Loomis, 1934). A more general response is one of a progressive decline in rates of cell enlargement as water deficits develop, with enlargement ceasing when turgor pressure levels are still at the level of several bars (Stransky and Wilson, 1964; Boyer 1968, 1970b).

Associated with these reduced rates of organ development and cell enlargement are many indirect effects on physiological processes, since nutrient inflow, and protein and carbohydrate synthesis and metabolism, are immediately affected by reduced developmental activity of cells and tissues. A key implication to final biological yield follows from the effect of reduction in cell expansion on total leaf area. This reduces the size of the photosynthesizing surface and can be expected to reduce crop growth rate unless leaf area is not limiting net assimilation rate.

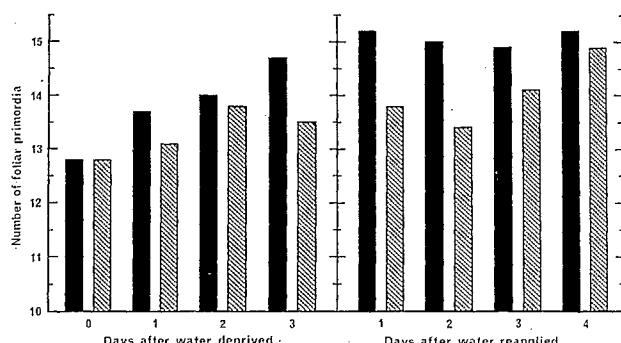


FIG. 4. Numbers of foliar primordia in lupin apices during water deprival and upon rewatering (shaded columns) compared with well watered controls (solid columns) (after Gates, 1968).

The effect of water stress on the continued development of tissues which are already mature, or approaching maturity, resembles that of hastened senescence. One of the earliest signs of stress is the migration of phosphorus from older leaves to the stems and meristematic tissue (Williams and Shapter, 1955; Gates, 1957). This is closely followed by the movement of nitrogen, suggesting progressive protein hydrolysis and breakdown of normal cell function. Furthermore, the stomata tend to remain closed and become non-functional (Slatyer and Bierhuizen, 1964).

Little is known of the effects of water deficits on root development. Although it is sometimes stated that root development is enhanced relative to shoot development during stress, there is little quantitative information on this point (Weaver, 1926; Troughton, 1962; Salim *et al.*, 1965).

Two types of effects can be expected, the first being a reduction in rates of meristematic activity and of root elongation directly associated with the level of internal water deficit; the second, an effect of suberization on the water and nutrient uptake properties of the root system as a whole.

Most research has shown a progressive reduction in rate of root elongation as water stress is imposed (Salim *et al.*, 1965; Newman, 1966) and, in some cases, root elongation ceases before shoot growth. In this regard Newman's (1966) work with flax shows a high dependence of rate of root extension on local soil water potential. Thus roots in relatively moist soil may continue to elongate, even though the plant as a whole is subject to severe internal water stress. In consequence, continued exploration of the soil mass by root systems might be expected until the root zone is reduced to the same general level of water potential.

The effect of water stress on suberization can be expected to vary depending on the local rates of root extension. In rapidly growing roots a non-suberized zone of 10–20 cm may occur in some species, constituting a highly active and extensive absorbing surface. As rates of root elongation are reduced, the rate of suberization exceeds the rate of elongation, and the non-suberized zone is reduced, until it is virtually eliminated in non-elongating roots. This phenomenon, common under conditions of severe water stress, substantially reduces the effective surface of the roots and their activity as absorbing organs.

In summary, it can be stated that the effect of stress on growth tends to be most pronounced in those tissues which are in rapid stages of development, a conclusion already reached by other workers (Williams and Shapter, 1955; Gates, 1968). Primordial initiation and cell enlargement are particularly susceptible. Although cell enlargement does not appear to compensate following the removal of stress, initiation does, as long as the stress has not been too severe. The developing tissues appear to enter a rejuvenating phase on relief of stress and relative growth rates of such plants may be more rapid

than those of controls (Gates, 1955a, 1955b; Williams and Shapter, 1955). This rapid growth is aided by the continued, slow cell division which has occurred, and by the availability of nutrients released from older tissues.

EFFECT OF WATER STRESS ON GRAIN YIELDS IN CEREALS

In focusing the general effects of water stress on growth and development on to the specific problem of grain formation and crop yield, there are 3 key stages to be considered. The first of these is the stage of floral initiation and inflorescence development, when the potential grain number is determined. The second is the stage of anthesis and fertilization, when the degree to which this potential is realized, is fixed. The third is the stage of grain filling, when grain weight progressively increases.

Although many aspects of yield development are common to all cereals, it is difficult to generalize widely as to the effects of water stress on grain yield, because of the considerable differences which do exist, in morphogenesis generally and reproductive development in particular, between various species. In the following discussion, data will be used to illustrate both similarities and differences in development patterns.

WATER STRESS AND INFLORESCENCE DEVELOPMENT

Dealing first with the development of the inflorescence, there is good evidence that even slight water stress can reduce the rate of appearance of floral primordia. Figure 5 (from Husain and Aspinall, 1970) shows that number of primordia is more sensitive to water stress than development of existing primordia. This is probably typical for most cereals. These studies suggest that if the stress is mild, and if the period of stress is

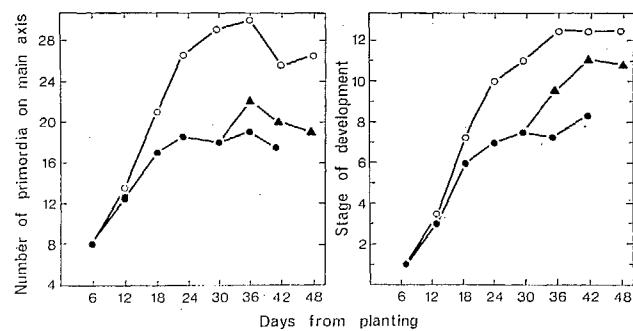


FIG. 5. Total number of primordia on main axis (left side) and stage of development (right side) of barley subjected to prolonged water stress. Plants watered throughout (○); not watered after day 0 (●); not watered between days 0 and 30 (▲) (after Husain and Aspinall, 1970).

relatively brief, rate of primordial initiation, upon relief of stress, is more rapid than in the controls and the total number of spikelets formed may be unaffected. On the other hand, if the stress is severe, or prolonged, total spikelet number may be substantially reduced.

Nicholls and May (1963) provided evidence that initiation of new primordia in the barley plant coincides with the appearance of stamen initials on the first formed spikelets. This is supported by the work of Williams (1966) on unstressed wheat plants. From their observations, Nicholls and May suggest that the number of spikelets per inflorescence is determined by the balance between the rate of primordial initiation relative to that of spikelet development. Since spikelet development appeared to be less affected by stress than primordial formation, it follows that prolonged stress at the stage of floral initiation could markedly reduce the potential number of grains per ear.

An example of this effect is given in Figure 6, where data from Nicholls and May (1963) are presented. The treatments consisted of a well watered control and two water stress treatments. All treatments were well watered until about 10 days after germination. The first stress treatment was then deprived of water until the soil water potential dropped to $\psi = -5$ bars when it was rewatered, the second water stress treatment remained deprived of water, but soil water potential did not drop below $\psi = -15$ bars.

Compared with the control plants, the rate of primordial formation in the plants deprived of water is seen to diverge almost immediately, so that the double ridges of the first spikelet primordia did not appear until several days after floral initiation commenced in the controls. (The total number of leaf primordia initiated was, however, the same in each treatment.) Rate of initiation of floral primordia became progressively slower in the stressed plants but, upon rewatering, the rate in the "mild" stress treatment increased rapidly so that, by the time of stamen initiation, total spikelet number was almost the same as in the controls. By comparison, in the "severe" stress treatment, total spikelet number was at a much lower level at the time when development of the spike was concluded.

Although this interpretation, if it could be generally applied, would provide a simple explanation of the effects of water stress on inflorescence development in cereals, the indeterminate character of the barley inflorescence may permit this type of response to a much greater degree than in species where the spike is determinate, and the rachis terminates in an apical spikelet. The explanation certainly appears inadequate to account for the developmental patterns observed in grain sorghum, for example. In experiments in which the timing and duration of stress were varied around the stage of floral initiation, but in which all treatments constituted "severe" stress (wilted for 1 week or more), Whiteman and Wilson (1965) found that the development of the sorghum inflorescence could be suspended

during stress, yet could be resumed on rewatering and result in a flowering head not significantly different from that of control plants.

Although sorghum is known to be a drought-tolerant crop, it seems probable that, as more data are collected, differences of a similar order may emerge between other common cereals. In corn, for example, Volodarski and Zinevich (1960) have claimed that a somewhat similar phenomenon occurs to that in sorghum, retardation of ear initiation during stress being completely reversible. Unfortunately, the degree of stress imposed was not well defined and, if mild, the reversible response would be expected. However, evidence from Robins and Domingo (1953) and Denmead and Shaw (1960) that corn in the vegetative stage is relatively tolerant to stress, suggests that the indeterminate nature of corn-ear development may lend itself to recovery of this type upon of relief stress.

The effect of water stress on the induction and transmission of the floral stimulus—that is, on the number of leaves formed prior to the commencement of floral initiation—has not been investigated in much detail in cereals. In general, there appears to be little evidence of pronounced shifts in the number of vegetative primordia prior to floral initiation. Nicholls and May (1963) showed that, in barley, stress imposed about 10 days before floral initiation did not effect the number of

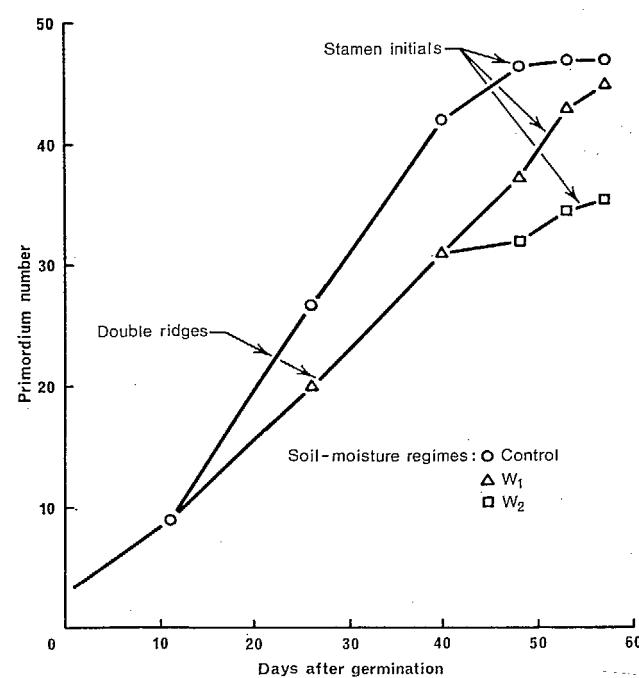


FIG. 6. Number of primordia formed in barley plants exposed to stress (W_1 , W_2) compared with well watered controls. In the intermediate treatment (W_1) the plants were rewatered when soil water potential dropped to -5 bars (after Nicholls and May, 1963).

vegetative primordia formed. Whiteman and Wilson (1965) showed that, with sorghum, as the date of onset approached the normal time of floral initiation, mean leaf number could be reduced by up to 3 leaves.

More recently, Aspinall and Husain (1970) have shown more pronounced effects in photoperiod-sensitive species. Severe osmotic stress, imposed during a brief 24-hr induction cycle, completely prevented flowering in *Lolium temulentum* and in other species. Stress during the period immediately following induction did not suppress induction unless defoliation was also imposed. These data suggest that there can be a stress induced suppression of induction itself, but that stress does not destroy the stimulus once formed. However, it appears to delay the translocation of the stimulus out of the leaf.

From the stage of spikelet initiation to fertilization of the ovules, a number of other processes, associated with the development of the inflorescence, are likely to be sensitive to water deficits and thus cause a reduction in the number of grains per ear, or even in the number of fertile ears. Such effects have been reported in most cereals, for example in barley (Aspinall *et al.*, 1964; Skazkin and Zavadskaya, 1957; Wells and Dubetz, 1966), oats (Paauw, 1949; Novikov, 1952, 1954; Skazkin and Lukomskaya, 1962), wheat (Chinoy, 1962; Single, 1964; Bingham, 1967) and corn (Robins and Domingo, 1953; Denmead and Shaw, 1960; Volodarski and Zinevich, 1960).

The effects have been attributed, in some cases, to specific interference with the sexual development of the spikelets, such as meiosis in the gametes (Skazkin and Leiman, 1952; Novikov, 1954; Skazkin and Zavadskaya, 1957; Bingham, 1967). However, the availability of mineral nutrients and carbohydrates during the pre-flowering phase also appears to influence spikelet development, floret fertility and grain set.

Examples of this phenomenon are provided by the work of Single (1964) and Davidson (1965) with wheat. Single imposed a series of nitrogen treatments on wheat grown in nutrient culture, which involved varying the nitrogen status from severely limiting to non-limiting conditions at various stages of development. Nitrogen deficiency prior to spikelet initiation had a predictable marked effect on spikelet number and, if the nutrient level was not increased during the later development of the inflorescence, the number of fertile florets per spikelet did not exceed 1. However, an increase in the nitrogen level, after spikelet initiation but before the appearance of the flag leaf, caused a marked increase in the number of fertile florets and hence on final grain number.

In Davidson's experiment the leaves of the experimental plants were clipped to maintain leaf area indices (LAIs) at levels of 3 and 1, compared with levels of up to 10 in control plants. The clipping treatments commenced after floral initiation, so did not affect the number of spikelets laid down, yet grain number per

spikelet was reduced from 1.57 in the controls to 0.88 and 0.76 in the 2 treatments, respectively.

Although water stress was not imposed in these studies, photosynthesis, and hence the supply of assimilates, was markedly reduced by the treatments which were imposed. In Single's work the supply of nitrogen to the developing inflorescence was probably also reduced, in which case additional direct effects on protein synthesis and cell development could have occurred. However, redistribution of other nitrogen in the plant may have partly offset this effect.

These results clearly indicate the importance of stress on the progressive development of the inflorescence prior to anthesis. In wheat, of course, the potential for variable floret numbers provides an opportunity for compensatory effects if stress is removed. This may also apply to oats, but would not apply to crops such as rye, barley or maize in which floret number is fixed (Bonnett, 1966). On the other hand, although compensation may not occur, relief of stress in many species during the stage of inflorescence development may permit final grain number to approach the potential represented by the number of spikelets initiated.

A frequently observed effect of water stress in the pre-flowering stage is a delay in date of flowering. In sorghum, as has already been mentioned, the delay is closely related to the period of stress, but in other crops the relationship is less obvious. In wheat Chinoy (1960) showed that a period of 7 days' wilting delayed anthesis by 8–18 days for 8 varieties tested when applied at the pre-flowering stage. In this species, therefore, as compared with sorghum, post-stress development was less rapid than in control plants.

WATER STRESS AND FERTILIZATION

Stress at anthesis can markedly reduce fertilization and grain-set in most cereals. Perhaps the most sensitive crop, at this stage, appears to be corn (Robins and Domingo, 1953; Denmead and Shaw, 1960), reductions of over 50 per cent in yield being caused by relatively brief periods of wilting (see Table 2).

TABLE 2. Effect of water regime on grain yield in corn (after Robins and Domingo, 1953)

Treatment	Yield (bushels/acre)	Shelling %
Irrigated at anthesis, plus 3 subsequent irrigations	138.3	82.9
Irrigated at anthesis, plus 2 subsequent irrigations	132.9	81.9
Irrigated at anthesis, no subsequent irrigation	95.0	82.7
Wilted at anthesis, plus 2 subsequent irrigations	79.1	76.7
Wilted at anthesis, plus 1 subsequent irrigation	66.7	77.6

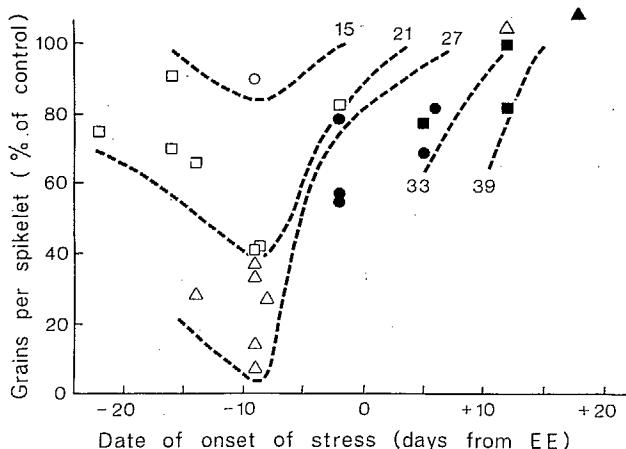


FIG. 7. Response of grains per spikelet to various degrees of plant water stress at various stages of development. The broken lines are lines of equal stress, the number indicating the maximum xylem tension which was imposed (after Fischer, this volume).

Since water stress frequently is associated with arid atmospheric conditions, it is sometimes suggested that stress at this stage acts by way of dehydration of pollen grains. However, it also seems probable that germination of the pollen, or growth of the pollen tube from the stigma to the ovules, may be impaired.

From the work of Robins and Domingo (1953) with corn, it appears that the latter explanation was the correct one in their experiments, since adequate amounts of pollen were available from well watered plants adjacent to stressed ones. It seems likely that, if the styles are wilted, the germination of the pollen or the growth of the pollen tube from the stigma to the ovules may be interfered with. This could be expected to be more pronounced in corn than in other cereals.

The relative sensitivity of different species to stress at the pre-flowering and flowering stages appears to vary somewhat, but comparable stress treatments have seldom been imposed and internal water deficits have seldom been measured, so detailed comparisons are impossible.

Recent work by Fischer (this volume) provides information on the effect of stresses imposed up to 3 weeks before and after ear emergence on yield development in wheat. For a given degree of water stress, grain yield was reduced most when the stress developed about 10 days before ear emergence, because of pronounced effects on the number of grains formed per spikelet. His data are summarized in Figures 7 and 8. The direct effect of degree of stress during this period in grain number per spikelet is also presented.

Species which flower over an extended period, usually because of the progressive flowering of tillers which develop after the main stem, are somewhat protected from isolated periods of stress. Some compensation also

occurs if stress early in the vegetative period, which may interfere with spikelet development on the main stem, serves to promote tiller development. Although tillers may not have as many spikelets as a non-stressed main stem, the total number of grains per plant may be relatively little affected by a stress which severely reduces main stem grain number (see, for example, Aspinall *et al.*, 1964).

WATER STRESS AND GRAIN FILLING

The third component of grain yield—weight per grain—is influenced both by pre-flowering and post-flowering conditions. In almost all cases, however, the post-flowering stage is the more important.

Yield development requires the accumulation of photosynthate in the grain. The 2 sources for these assimilates are photosynthesis in the ear itself and translocation from elsewhere in the plant. Although photosynthate accumulated prior to anthesis contributes to grain filling, and in some cases may provide a significant proportion of grain yield, by far the greatest contribution is usually from photosynthesis after anthesis by the ear, leaves and stem (see, for example, Porter *et al.*, 1950; Thorne, 1963; Carr and Wardlaw, 1965; Allison and Watson, 1966). Figure 9 (from Asana, 1966) demonstrates this point in relation to wheat, showing that virtually all the increase in dry weight after anthesis is associated with grain filling. Clearly water stress, by reducing photosynthesis at this time, can lead to large yield decrements.

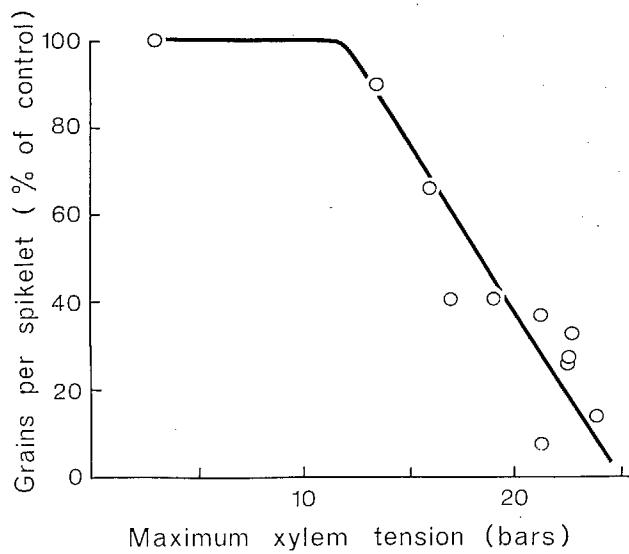


FIG. 8. Effect of plant water stress (expressed as xylem tension) on number of grains per spikelet, for stress treatments commencing between 15 and 5 days before ear emergence (EE) (after Fischer, this volume).

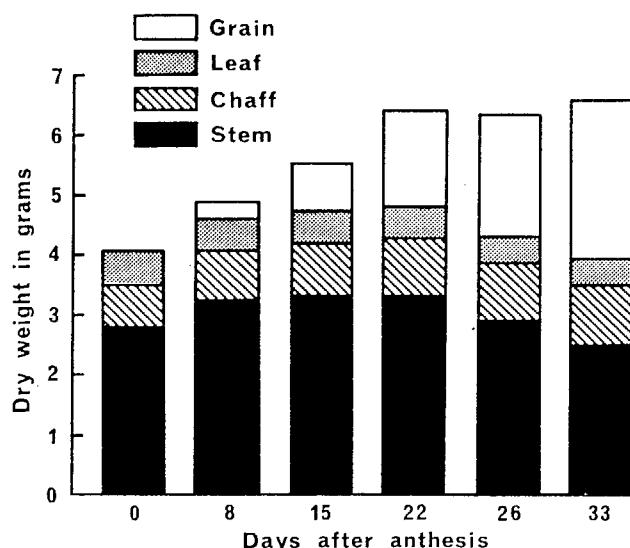


FIG. 9. Dry weight components of the tops of wheat plants from anthesis to maturity (after Asana, 1966).

Although Wardlaw (1967, 1969) has shown fairly conclusively that there is little effect of water stress on translocation of assimilates in the conducting tissue itself, he has pointed out that translocation out of the leaves is slowed and prolonged by water stress. This phenomenon, combined with evidence that water stress hastens rather than slows maturation, and with the direct effect of stress on photosynthesis in the ear as well as in the leaves, contributes to lower grain weight in stressed plants.

Because grain filling is a relatively rapid process, because most of the increase in plant weight after anthesis involves grain development, and because it is a terminal process, it follows that the reduced photosynthesis at any point of the post-anthesis stage may have effects on grain weight which may not be compensated for by activity at other stages of grain filling (Aspinall, 1965; Fischer, this volume).

On the other hand, there is also evidence that there may be an upper limit to grain size and rate of grain filling in any one phenotype and that, in non-stressed plants, surplus photosynthate may be available. The

work of Buttrose and May (1959) in which grain removal in barley did not lead to increased weight of the remaining grains is consistent with this view. It follows that a reduction in photosynthesis, caused by water stress, may not lead to reduced grain weight until any surplus photosynthate is eliminated. In this connection Asana and Basu (1963) showed that, for wheat, reduced photosynthesis caused by stress early in the grain filling stage could be compensated for by enhanced translocation from the stem. They considered that, because of hastened senescence of leaves of stressed plants, stress occurring later in the grain filling stage could not be compensated for in this manner.

Prolonged stress throughout grain filling, even at moderate levels, almost invariably reduces grain weight (Salter and Goode, 1967). Fischer and Kohn (1966) have shown that wheat yield tends to be inversely correlated with the stress-induced rate of senescence of photosynthetic tissue after flowering. In some situations an enhanced gradient of grain weight from the base to the tip of the ear develops (Aspinall, 1965).

The relative importance of photosynthesis in the ear, the flag leaf, and elsewhere in grain filling does not appear to be a major factor in interpreting yield decrements under water stress conditions, even though it has been a subject of controversy for some time. There are, of course, important differences between species associated partly with crop morphology. For example, the role of ear photosynthesis is greater in wheat than in corn (Allison and Watson, 1966). In the presence of water stress, there is likely to be more rapid senescence of older leaves, which would lead to a flow of assimilates from them towards the ear, but would eliminate their continued role in supplying assimilates. Consequently the role of continued ear and flag leaf photosynthesis would become relatively greater.

In conclusion, it is apparent that, although maximum yield is likely to be obtained only if adequate water status is maintained throughout the life of cereal crops, mild or relatively brief stress can usually be compensated for by subsequent development under favourable conditions. In this regard, the stage of inflorescence development appears to be the most adaptable, although this is truer in some crops than in others. Anthesis is probably the least adaptable, since it is such a brief, yet important, stage in the development of crop yield.

Résumé

Effet de l'état hydrique interne des plantes, sur leur croissance, leur développement et leur rendement
(R. O. Slatyer)

Les effets des déficits hydriques sur la croissance, le développement et le rendement sont étudiés en fonction

tout d'abord de l'apparition des déficits internes, puis de divers processus physiologiques et de la morphogenèse, enfin, du rendement en grain, dans le cas particulier des céréales.

Étant donné la grande diversité des formes de réaction selon les espèces, l'auteur ne fait que deux généralisa-

tions concernant les effets du déficit hydrique sur le rendement des céréales. La première est que, dans la plupart des cultures, la croissance et le développement ne s'effectuent intégralement, et le rendement n'est maximal, que lorsqu'un état hydrique élevé est maintenu pendant tout le cycle végétatif.

La seconde est que les effets nuisibles des déficits hydriques sont généralement le plus accusés dans les tissus et les organes qui se trouvent en voie de croissance et de développement particulièrement rapides.

Des recherches récentes ont mis en évidence deux aspects importants des effets des déficits hydriques.

Premièrement, des déficits hydriques même accusés ne semblent pas, tout au moins lorsqu'ils sont de courte durée, affecter directement le mécanisme de la photosynthèse. Au contraire, la quasi-totalité des diminutions de la photosynthèse peuvent être attribuées à la fermeture des stomates, qui empêche le CO₂ de parvenir aux chloroplastes. Dans le second cas, il s'agit de rapport entre le rendement en grain et la déshydratation à différents stades de la croissance. Dans un milieu artificiel on peut aujourd'hui beaucoup mieux chiffrer l'effet de la déshydratation au moment de la mise à fleur, de la floraison et de l'épiaison.

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Variations in transpiration, net CO₂ assimilation and leaf water potential of pepper plants produced by changes in the root and top environment

B. E. Janes
Plant Science Department
University of Connecticut
Storrs, Conn. (United States of America)

INTRODUCTION

The importance of stomatal, mesophyll and cuticular resistances and their relationship to the movement of CO₂ from the ambient air to the photochemical site within the leaf have recently been discussed in some detail by Barrs (1968), Troughton and Slatyer (1969) and Holmgren *et al.* (1965). These authors concluded that there was a much greater variation in stomatal resistance than in mesophyll resistance. In contrast to earlier evidence (Gaastra, 1959; Willis and Balasubramaniam, 1968; Slatyer and Bierhuizen, 1964; Gale *et al.*, 1966) there was little change in mesophyll resistance over a wide range in leaf water potential. Barrs (1968) considered mesophyll resistance to be small. Meidner (1969) questioned this and suggested that the mesophyll resistance is appreciable, but is much less variable than stomatal resistance.

There is some evidence that the cuticle may be more permeable to water than to CO₂. Barrs (1968) indicated that the cuticle of pepper leaves had a low permeability to both water and CO₂, with the permeability to CO₂ being somewhat less than that to water.

The CO₂ compensation point has been used as an indication of the photosynthetic efficiency of different species and genera of plants (Moss *et al.*, 1969; Heichel and Musgrave, 1969). Those plants which have little or no photorespiration have a low CO₂ compensation point. Plants with an appreciable photorespiration, such as peppers, have a high compensation point. Meidner (1967) showed that there was an increase in compensation point from 0 to 25.8 µl CO₂ l⁻¹ of air with an increase from low to high water stress in maize plants.

Much of the information dealing with the effect of stress on transpiration and photosynthesis has been obtained on single leaves, usually but not always attached to an intact plant. The data presented here were obtained using whole plants and compare the

magnitude of response of uniform plants to several environmental variables both singly and in combination. The data were obtained during the course of research planned primarily to obtain information on the effect of the environment on the forces and resistances to movement of water through plants (Janes, 1970). With additional instrumentation it was possible to obtain information on net CO₂ assimilation. These data permitted interesting comparisons to be made of resistance to gaseous diffusion into and out of the leaves and the relationships between transpiration, net CO₂ assimilation and plant stress could be studied.

MATERIALS AND METHODS

Pepper plants (*Capsicum annuum* L. var. California Wonder) were grown in aerated Hoagland's nutrient solution in an environment controlled as follows: temperature 26° C, relative humidity 60–70 per cent, illuminated for 18 hr day⁻¹ with fluorescent and quartz iodine lights giving radiant energy of 1.05×10^5 ergs cm⁻² sec⁻¹ at plant height. The treatments were imposed on the plants when they were 4–5 weeks old and had a leaf area of 2–4 dm² for 1 surface. The rate of transpiration, net CO₂ assimilation (NA) and relative water content (RWC) of leaves were measured in a small chamber in which the temperature, relative humidity and CO₂ concentration of recirculated air were controlled and measured. The equipment and operations are described by Janes (1970).

The data reported here were obtained from 2 different sets of experiments. In the first, the response of pepper plants to the following treatments was noted: high light, 1.5×10^5 ergs cm⁻² sec⁻¹; low light, 3.5×10^4 ergs cm⁻² sec⁻¹; 3 levels of CO₂, 50, 268 and 730 µl CO₂ l⁻¹ of air; nutrient solution osmotic potentials (OP) of -0.5, -5.0 and -7.5 bars. The relative humidity was maintained

at 40 per cent for most of the measurements. Data were also obtained from 1 group of plants subjected to varying osmotic potentials, 2 light intensities and 70 per cent relative humidity at $268 \mu\text{l CO}_2 \text{ l}^{-1}$ of air.

In the second set of experiments, changes in transpiration, net CO_2 assimilation and water potential of pepper plants growing in solutions of -0.5 and -5.0 bars OP and subjected to varying root temperatures were measured. Plants of the desired size were placed in the measuring system and allowed to come to equilibrium with the root temperature maintained at 23–25°C. When the plants were at a steady state, the rates of transpiration and net assimilation were noted and the roots cooled rapidly to the desired level. The measurements were made with air having $268 \mu\text{l CO}_2 \text{ l}^{-1}$ of air and relative humidity of 40 per cent. Plants were subjected to either high or low light as indicated above.

At termination of the experiment the relative water content of the leaves was determined. The leaf water potential (ψ_L) was estimated from the previously determined relationship between ψ_L and RWC.

The techniques used to alter OP of the nutrient solution using polyethylene glycol (PEG 400) and sequence of imposing treatments are described by Janes (1970).

RESULTS

LIGHT INTENSITY, CO_2 LEVEL AND OP OF NUTRIENT SOLUTION

The changes in transpiration, net assimilation and ψ_L for pepper plants subjected to 3 levels of CO_2 , 3 levels of OP in the nutrient solution and 2 light levels are shown in Figures 1 and 2. The rate of transpiration of pepper plants subjected to either high or low light intensity was reduced by a decrease in the OP of the nutrient solution and an increase in CO_2 content of air. Changing the light intensity from low to high increased the rate of transpiration of all plants, with the relationship between CO_2 concentration and OP unchanged. The most dramatic changes in NA were associated with a change in CO_2 concentration of the ambient air from 50 to $730 \mu\text{l CO}_2 \text{ l}^{-1}$ of air. The increase was approximately sixfold for plants in high light and threefold for plants in low light. In high light a decrease in OP of the nutrient solution resulted in a decrease in NA. In general, the changes in NA and transpiration were parallel in plants at high light (Figure 1). The 1 marked exception was noted in plants with $268 \mu\text{l CO}_2 \text{ l}^{-1}$ of air and 70 per cent

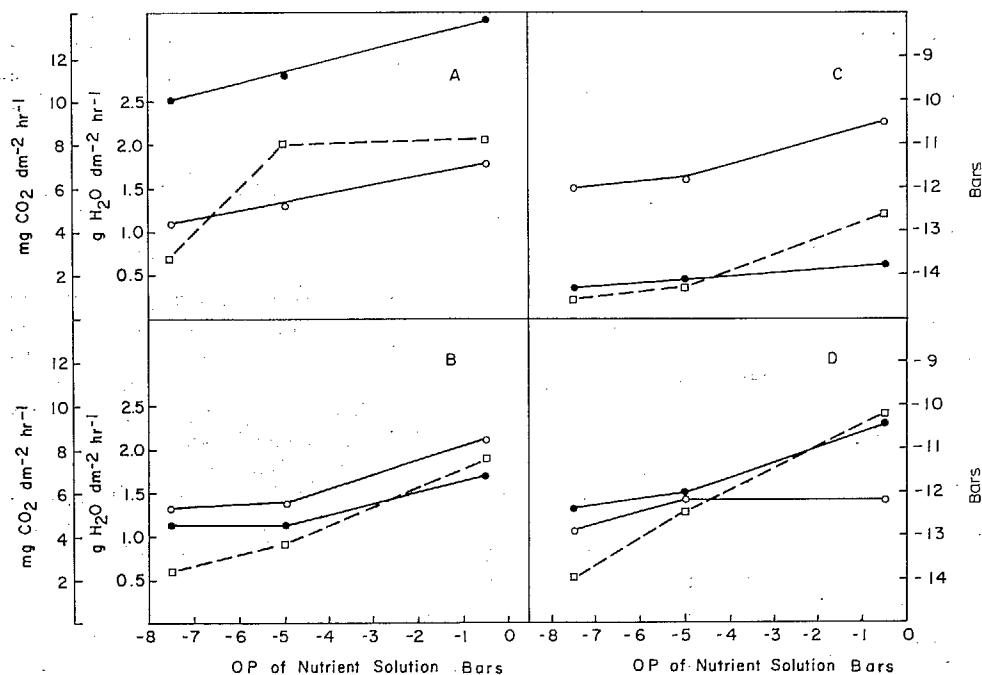


FIG. 1. Effect of OP of nutrient solution, CO_2 concentration and relative humidity of air on transpiration, net CO_2 assimilation and water potential of pepper plants. High light intensity, $1.5 \times 10^5 \text{ ergs cm}^{-2} \text{ sec}^{-1}$; (A) $760 \mu\text{l CO}_2$, (B) and (A) $268 \mu\text{l CO}_2$, (C) $50 \mu\text{l CO}_2$; (A), (B), (C) 40 per cent relative humidity; (D) 70 per cent relative humidity; \square — \square , ψ_L ; \bullet — \bullet , net CO_2 assimilation; \circ — \circ , transpiration.

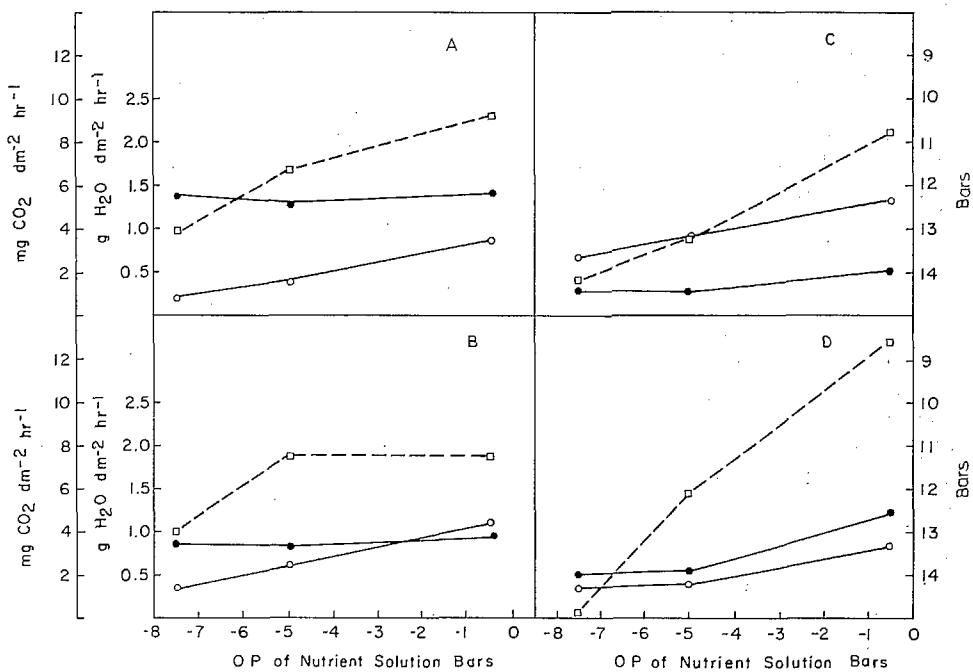


FIG. 2. Effect of OP of the nutrient solution, CO_2 concentration and relative humidity of air on transpiration, net CO_2 assimilation and water potential of pepper plants. Low light intensity, $3.0 \times 10^4 \text{ ergs cm}^{-2} \text{ sec}^{-1}$. (A) 760 $\mu\text{l CO}_2$, (B) and (D) 268 $\mu\text{l CO}_2$, (C) 50 $\mu\text{l CO}_2$; (A), (B), (C) 40 per cent relative humidity; (D) 70 per cent relative humidity. \square — \square , Ψ_L ; ●—●, CO_2 assimilation; ○—○, transpiration.

relative humidity. The changes in ψ_L and NA were similar. There was some indication that a change from -5.0 bars to -7.5 bars OP resulted in a greater decrease in ψ_L than in NA.

At low light intensities (Fig. 2), changing the OP from -0.5 to -5.0 to -7.5 bars reduced the rate of transpiration with little or no change in the rate of NA. The maximum rate of NA for the plants at 730 and 268 $\mu\text{l CO}_2 \text{ l}^{-1}$ of air was approximately 6 and 4 $\text{mg dm}^{-2} \text{ hr}^{-1}$ respectively. Under these conditions the increase in stomatal resistance evidenced by a decrease in transpiration did not appear sufficient to alter the slow rate of diffusion of CO_2 necessary to utilize completely the limited amount of energy available.

There was little change in transpiration, but a large change in NA with a change in the OP of the nutrient solution of the plants at high light, 268 $\mu\text{l CO}_2 \text{ l}^{-1}$ of air and 70 per cent relative humidity. In this situation the rate of transpiration was limited by the evaporative demand and not by closing of stomates. Thus, the rate of CO_2 diffusion in plants at -0.5 bar OP was not influenced by stomatal opening allowing for a maximum NA at a low rate of transpiration. There was a small decrease in NA of plants in an atmosphere with 50 $\mu\text{l CO}_2 \text{ l}^{-1}$ of air as the OP was reduced (Fig. 2). There was

a reduction in NA of plants at 70 per cent relative humidity and 268 $\mu\text{l CO}_2 \text{ l}^{-1}$ of air as the OP was reduced from -0.5 to -5.0 bars.

In low light, the relationship between ψ_L and transpiration was evident, but not as clear as in high light. This lack of correlation resulted from the fact that water moved from roots to the top of plants as a result of water potential difference between the nutrient solution and ψ_L and not leaf water potential (Janes, 1970). There was no relationship between ψ_L and NA in low light.

These data indicate that light intensity, CO_2 concentration and OP of the nutrient solution all influence stomatal opening and thus the rate of diffusion of gases into and out of a leaf. These 3 factors appear to operate independently of each other, with only minor interaction between them.

ROOT TEMPERATURE

The effect of cooling the roots of plants growing in nutrient solution of -0.5 and -5.0 bars OP is illustrated in Figures 3 and 4. During the 17 hr of the experiments the plants were continuously exposed to the low-light intensity. Each figure represents values for a single representative plant. With the onset of cooling the roots

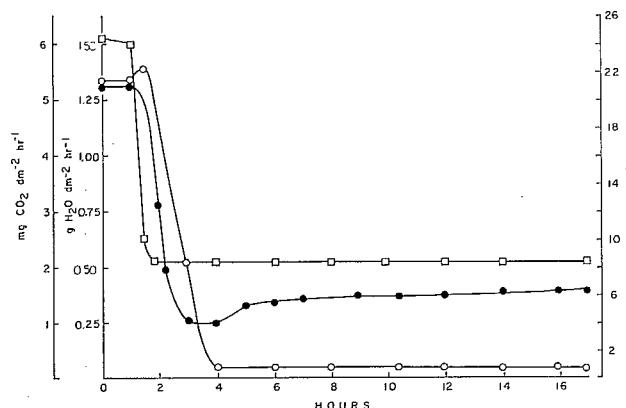


FIG. 3. Effect of rapid cooling of roots on NA and transpiration of a pepper plant growing in nutrient solution of -0.5 bars OP. \circ — \circ , transpiration; \bullet — \bullet , NA; \square — \square , root temperature.

of plants in -0.5 bars solutions, there was a brief period of increased transpiration followed by a rapid decrease to a steady state depending on the temperature of the roots (Fig. 3). The time responses of CO_2 measurements were such that any rapid change in NA at the start of

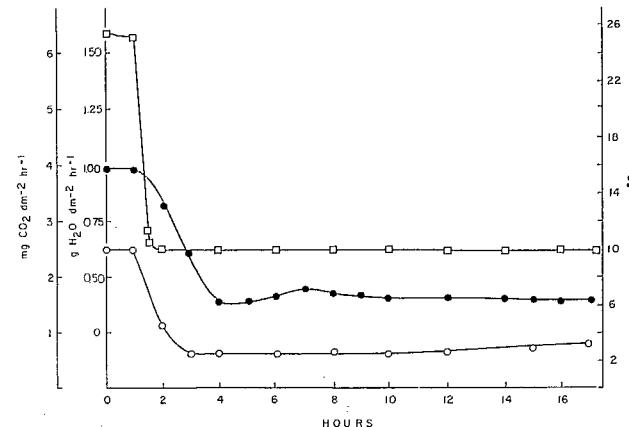


FIG. 4. Effect of rapid cooling of roots on NA and transpiration of a pepper plant growing in nutrient solution of -5.0 bars OP. \circ — \circ , transpiration; \bullet — \bullet , NA; \square — \square , root temperature.

cooling could not be detected. NA reached a minimum value 2–3 hr after the start of cooling, followed by a gradual increase in rate. The value at end of 17 hr was approximately $1 \text{ mg dm}^{-2} \text{ hr}^{-1}$ higher than the lowest value reached. The plant in -5.0 bars solution did not

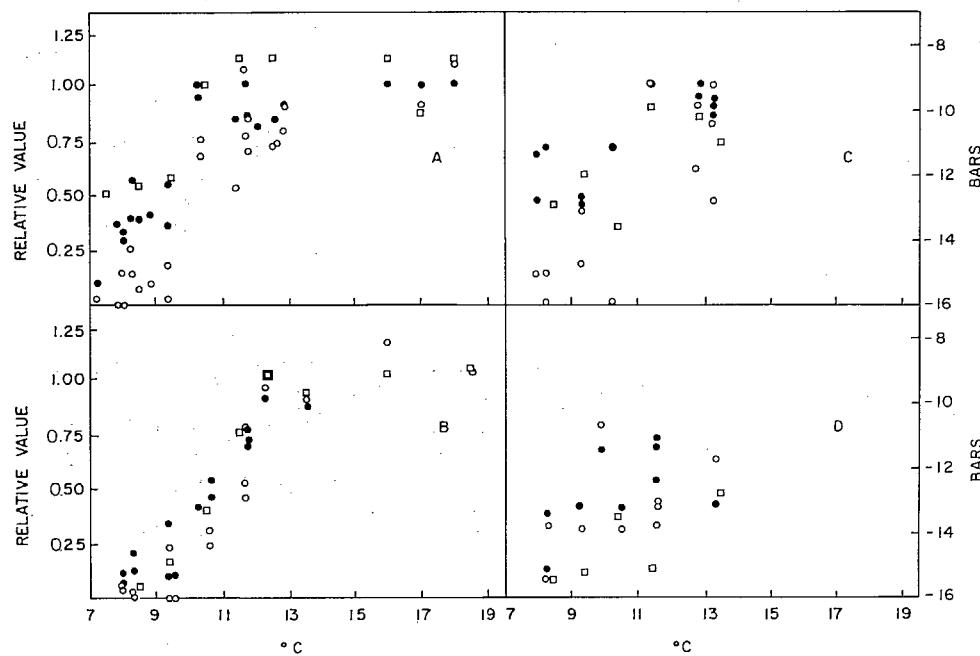


FIG. 5. Effect of root temperature on transpiration, NA and water potential of leaves of pepper plants. (A), plants at low light and -0.5 bars OP; (B), plants at high light and -0.5 bars OP; (C), plants at low light and -5.0 bars OP; (D) plants at high light and -5.0 bars OP. \circ — \circ , transpiration; \bullet — \bullet , NA; \square — \square , water potential.

TABLE 1. Effect of light intensity, OP and transpiration of nutrient solution on transpiration and NA

Solution OP (bars)	Light	Number of plants	Transpiration (g H ₂ O dm ⁻² hr ⁻¹)	Assimilation (mg CO ₂ dm ⁻² hr ⁻¹)
First experiment 268 µl CO ₂ l ⁻¹ of air 40 per cent relative humidity				
-0.5	low	5	1.10	3.82
-0.5	high	5	2.11	6.70
-0.5	low	5	0.63	3.40
-5.0	high	5	1.38	4.40
Root temperature 23°–25°C				
-0.5	low	22	1.30	5.30
-0.5	high	17	2.27	13.81
-5.0	low	17	0.53	3.91
-5.0	high	9	0.91	8.10
Root temperature 2 hr 7°–10°C				
-0.5	low	10	0.18	1.98
-0.5	high	7	0.06	1.70
-5.0	low	5	0.18	2.26
-5.0	high	3	0.23	2.86

show an increase in transpiration at start of cooling (Fig. 4). There was some indication of cycling in rate of NA during the cooling period.

The effects of root temperatures in the range 7–19°C are shown in Figure 5. These were short-term experiments, the plants being harvested when they reached the lowest value for transpiration, approximately 2 hr after start of cooling. The values for transpiration and NA for individual plants with cooled roots are presented as the relative value of rates of the same plant before cooling (root temperature 23–25°C). Water potential values are average of plants within each 1° range of root temperature. The average values of transpiration and net assimilation of plants with roots at 23–25°C and at 7–10°C are given in Table 1.

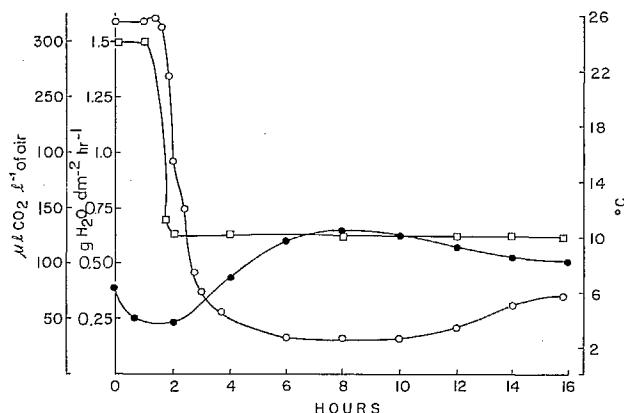


FIG. 6. Relation between transpiration and compensation point of a pepper plant, with roots cooled. O—○, transpiration; ●—●, compensation point; □—□, root temperature.

Reducing the root temperature from 24–16°C had no apparent effect on NA or transpiration. A reduction in temperature from 16–13°C resulted in some increase in resistance to water flow and a decrease in NA, but little change in ψ_L . Further cooling of the roots had a dramatic effect on the plants. Transpiration and NA were markedly reduced (Table 1, Fig. 5). The relative reduction was greater in the plants in -0.5 bars solution than in plants of -5.0 bars solution.

As an indication of the effect of stress on the assimilation mechanism, changes in compensation point with decreasing temperature were noted. The plants were placed in the measuring system at low light, CO₂ supply cut-off and changes in CO₂ concentration of the air monitored for a period of 14–17 hr of continuous light as root temperature was reduced to 10°C and maintained at that level.

As the roots were cooled to 10°C, the compensation point gradually increased to a value of approximately 130 µl CO₂ l⁻¹ of air after 7 hr and then dropping to near 100 µl CO₂ l⁻¹ of air after 15 hr (Fig. 6). The plants were growing in -0.5 bars solution. Plants in -5.0 bars solution responded in a similar manner.

DISCUSSION

The rate of NA is dependent on CO₂ concentration, light intensity, resistance to CO₂ movement into the leaf, leaf temperature and the physiological condition of the plant associated with the genetic make-up and environment during growth. The marked difference in NA without a similar difference in transpiration recorded for the 2 different groups of plants (Table 1) would indicate a physiological difference in the plants. This difference in NA was not altered by short-term changes in environment associated with the imposed treatments. The only obvious sources of variation between the 2 groups of plants were associated with different batches of seed and a fluctuation in the environment, most likely light intensity, during growth.

The information presented is primarily of interest in relation to the resistance to the diffusion of CO₂ as it moves through the stomates and/or cuticle and the mesophyll cell walls to the photochemical sites within the chloroplasts of the leaves. There was agreement with the evidence presented by Troughton and Slatyer (1969), Barrs (1968) and Holmgren *et al.* (1965) indicating that when light was not a limiting factor the diffusion of both CO₂ and water vapour was controlled by stomatal movement.

Cooling of the roots resulted in an increased resistance to the flow of water, thus reducing the supply to the leaves. The reduced supply of water to leaves resulted in a decrease in ψ_L of the leaves and a reduction in the rates of transpiration and NA. The changes in transpiration and NA were parallel, indicating that the same mechanism was controlling both processes. This control

was undoubtedly in the stomates. As pointed out by Barrs (1968), this parallel response indicates that the mesophyll resistance remained relatively constant over a wide range of leaf water potentials. In the present experiments, the response produced by a decrease in osmotic potential was similar to the response produced by dehydration resulting from cooling of the roots. This was further evidence that the mesophyll resistance was not altered by change in ψ_L .

The variation in compensation point has been related to the efficiency of the photosynthetic process (Moss *et al.*, 1969; Heichel and Musgrave, 1969). This is a useful factor in a comparison of plants with differing genetic composition. The variation in compensation point with root cooling reported here may also indicate that, under

conditions of high water stress, there is an inhibition of the photosynthetic process. However, this seems to be contradicted by the fact that the compensation point was not affected by the change in OP of the nutrient solution from -0.5 to -5.0 bars, or that the rate of NA was not affected by considerable change in ψ_L .

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Résumé

Variations produites dans la transpiration, l'assimilation nette de CO₂ et le potentiel d'eau de la feuille des Poivriers par des modifications apportées au milieu des racines et des sommités (B. E. Janes)

Le régime de la transpiration et de l'assimilation nette de CO₂ et le potentiel d'eau de la feuille des Poivriers ont été évalués dans une petite salle dans laquelle la température, l'humidité relative et la concentration de CO₂ de l'air recirculé étaient contrôlées et mesurées. Les données rapportées ont été obtenues en notant la réaction de deux séries de plantes aux changements du milieu. Dans la première série d'expériences, toutes les combinaisons des traitements suivants ont été utilisées: haute lumière $1,5 \times 10^5$ ergs cm⁻² s⁻¹; basse lumière $3,5 \times 10^4$ ergs cm⁻² s⁻¹; trois niveaux de CO₂: 50, 268 et 730 µl CO₂ par litre d'air, des potentiels osmotiques de solution nutritionnelle de -0,5, -5,0, -7,5 et -9,5 bars. Dans la deuxième série d'expériences, la température des racines dans la solution nutritionnelle avec soit -0,5, soit -5,0 bars de potentiel osmotique, a été variée de 7 à 25°C et soumise à une lumière soit haute, soit basse. L'effet de la température des racines sur le point de compensation de CO₂ a été évalué en retenant le CO₂ des plantes soumises continuellement à la lumière, avec la température des racines contrôlée comme on le souhaitait.

Un changement dans le potentiel osmotique de la solution nutritionnelle de -0,5 à -7,5 bars a réduit tant la transpiration que l'assimilation nette de CO₂ à la lumière haute. A la lumière basse, il s'est produit une diminution dans la transpiration, mais nul changement dans l'assimilation nette de CO₂ avec une réduction du potentiel osmotique de la solution nutritionnelle. La lumière ne limitant pas, les changements dans la transpiration et l'assimilation nette étaient parallèles entre des degrés très éloignés de tension de l'eau de la plante. La lumière limitant, les changements dans la transpiration et l'assimilation nette n'ont été parallèles que lorsque la fermeture des stomates réduisait la diffusion de CO₂ de telle façon que la concentration de CO₂ dans les chloroplastes et non la lumière était l'élément limitateur.

Le point de compensation de CO₂, approximativement 50 µl CO₂ par litre d'air, n'a été affecté par aucun des traitements qui ne fermaient pas complètement les stomates. En refroidissant les racines à 10° ou moins, on provoquait la fermeture complète des stomates, et le point de compensation a été porté à un maximum de 130 µl CO₂ par litre d'air. On estime que la hausse du point de compensation a été le résultat d'une résistance beaucoup plus haute à la diffusion de CO₂ dans la cuticule et non dans les stomates.

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Le potentiel hydrique et la résistance à la diffusion dans les stomates indicateurs de l'état hydrique de la plante

A. Berger

Centre national de la recherche scientifique
Centre d'études phytosociologiques
et écologiques
Montpellier (France)

INTRODUCTION

La tâche de l'agroclimatologue confronté avec des problèmes pratiques d'irrigation ou avec des problèmes de recherche fondamentale sur une meilleure efficience de l'eau peut être facilitée par la connaissance exacte de l'état hydrique du végétal.

Le schéma classique de la circulation de l'eau à travers la plante depuis le sol jusqu'à l'atmosphère permet de voir rapidement que l'état hydrique du végétal est la réponse intégrée de celui-ci à un certain nombre de facteurs climatiques distincts (évapotranspiration potentielle, état hydrique du sol, etc.). Cette réponse peut être mesurée par diverses techniques directes ou indirectes dont la mesure du potentiel hydrique et l'état de l'appareil stomatique sont les principales.

Chacun des paramètres ainsi envisagés peut avoir une signification différente dont la connaissance exacte doit permettre une prévision correcte de la réponse des plantes aux stress hydriques.

LA CIRCULATION ET L'ÉTAT DE L'EAU DANS LA PLANTE

L'eau circule dans le système sol-plante-atmosphère sous l'action de différences de potentiel hydrique et ce dans le sens d'une diminution du potentiel, depuis le sol vers les racines, puis à travers celles-ci et le long de la vascularisation jusqu'aux feuilles et enfin vers l'atmosphère. Les résistances à la circulation de l'eau dans toutes les parties de ce système ont des valeurs différentes. Cela tient à ce que dans certaines zones la circulation de l'eau est un phénomène d'écoulement visqueux (sol, vascularisation), dans d'autres zones un phénomène de diffusion à l'état liquide ou vapeur (racines, épiderme). Des valeurs respectives de ces résistances et du gradient du potentiel hydrique entre le sol et l'atmosphère dépendra l'équilibre

hydrique de la plante. Si pour des raisons externes au végétal l'entrée de l'eau dans la plante est inférieure à la sortie, le bilan est déséquilibré et un déficit hydrique apparaît. Cela peut arriver soit parce que le potentiel de l'eau dans le sol diminue, soit parce que la demande évaporatoire du climat devient trop élevée.

Van den Honert (1948) propose d'assimiler la circulation de l'eau dans le système sol-plante-atmosphère à un processus en chaîne. Cette proposition n'est valable que lorsque le système fonctionne en régime permanent et en conditions isothermes. Dans ces conditions on peut appliquer au système une loi analogue à la loi d'Ohm et qui relie le débit de l'eau au niveau d'une résistance à la différence de potentiel aux bornes de celle-ci. En appliquant cette loi au passage de l'eau du sol vers la plante, puis de la plante vers l'atmosphère van den Honert montre que la résistance la plus élevée, dans les conditions de régime permanent, se situe entre la plante et l'atmosphère. Cette résistance est située dans les couches qui séparent la surface des cellules du mésophylle de l'atmosphère et est schématiquement décomposée en deux parties. La première, essentiellement soumise à l'influence du végétal par l'intermédiaire du fonctionnement de l'appareil stomatique, permet une certaine régulation des pertes hydriques à travers l'épiderme des feuilles (r_{ep}). La seconde, soumise aux conditions externes, essentiellement aux turbulences au niveau de la feuille, règle la diffusion de la vapeur d'eau depuis la surface de la feuille jusqu'à l'atmosphère libre (r_a).

L'expérience montre cependant que le régime permanent est une chose peu courante, et l'existence journalière de déficits hydriques chez les végétaux indique que dans de nombreuses conditions la résistance à l'entrée de l'eau dans la plante est plus élevée que la résistance à la sortie. En outre, assimiler le système sol-plante-atmosphère uniquement à une série de résistances constitue un schéma simple mais incomplet. Des travaux récents (Hallaire, 1964) sur la circulation dans le sol

et sur la circulation de l'eau dans la plante (Weatherley, 1963) ont montré que ces deux systèmes sont constitués de voies privilégiées de circulation de l'eau à faible résistance — gros capillaire et racines dans un cas et vascularisation et membranes cellulaires dans l'autre — séparés de zones de stockage par des résistances à la circulation élevées. Ces zones de stockage sont dans le sol la masse du sol séparant les racines, dans la plante les cellules séparées par le cytoplasme de la voie principale de circulation et une zone de stockage dans cette voie principale elle-même.

Les relations que laisse prévoir le schéma de van den Honert entre les débits et les potentiels ne sont que rarement observées par l'expérience et uniquement dans les conditions où les effets capacitifs du sol et de la plante sont négligeables. Dès que ces effets deviennent importants, ces relations sont modifiées de façon extrêmement sensible (Berger, 1969).

L'application des schémas proposés par Hallaire et Weatherley entraîne deux conséquences qui demandent encore des vérifications expérimentales. Dans le sol, la notion de potentiel hydrique mesurée à partir de l'humidité globale de la masse du sol doit être remplacée par la notion de potentiel efficace ou potentiel à la surface des racines. Ces deux potentiels peuvent être très différents, suivant la densité de l'enracinement et les propriétés physiques du sol. Dans la plante, un problème de même nature se présente. Les mesures du potentiel hydrique des tissus végétaux portent toujours sur des fragments qui sont, nous l'avons vu, un système complexe composé de voies principales et de zones de stockage séparées par des résistances. Lors de l'évolution rapide du déficit hydrique dans un tel système, des gradients de potentiel apparaissent entre les différents constituants du tissu et il est probable que la valeur mesurée n'est qu'une valeur moyenne pour l'ensemble. Il serait beaucoup plus intéressant de connaître les valeurs exactes du potentiel soit au niveau de la voie principale de circulation, soit au niveau des zones de stockage que sont les cellules suivant qu'on traite un problème de circulation générale de l'eau ou un problème d'influence du stress hydrique sur des fonctions physiologiques ayant leur siège dans les cellules. Ce point sera repris lors de la discussion de la validité et de l'intérêt des mesures de potentiel hydrique et de résistance à la diffusion dans les stomates pour caractériser l'état hydrique des plantes.

CARACTÉRISATION DIRECTE DE L'ÉTAT HYDRIQUE DU VÉGÉTAL

Un certain nombre de caractéristiques permettent de décrire l'état hydrique du végétal. Elles peuvent être groupées en deux grandes catégories, dont l'une fait appel à la mesure de la quantité d'eau contenue dans les organes végétaux et l'autre à la mesure de son état énergétique.

MESURE DE LA TENEUR EN EAU

La teneur en eau est le plus simple et le plus immédiat des paramètres permettant de mesurer l'état hydrique. Sa mesure est rapide et introduit peu de perturbations dans l'échantillon. Il est cependant difficile de comparer les résultats obtenus pour différentes espèces, différents organes et pour une même espèce à différentes périodes. La teneur en eau est en général exprimée soit en pourcentage du poids sec, soit en pourcentage du poids frais. Or, au cours de la journée, le poids sec des organes varie par accumulation ou migration de substances, de sorte qu'on ne peut pas toujours utiliser le poids sec comme base. Exprimées sur la base du poids frais, les variations de teneur en eau sont alors estompées.

De nombreux auteurs se sont donc dirigés vers le calcul de la teneur en eau exprimée en pourcentage de la teneur en maximum que peut contenir l'organe prélevé. Ainsi sont apparues les notions dérivées les unes des autres de « turgescence relative » TR (*relative turgidity, RT*), de « déficit de saturation hydrique » DSH (*relative saturation deficit, RSD*) et de « *relative water content* » (RWC).

La difficulté pour la mesure du DSH réside dans la resaturation correcte de l'échantillon. Une période de resaturation trop brève aboutit à une resaturation partielle, une période trop longue donne une valeur trop élevée, car les phénomènes de croissance des tissus entraînent une absorption supplémentaire. Diverses techniques ont été proposées pour remédier à ces difficultés. Le choix d'échantillons de petite taille permet d'avoir une période de resaturation de courte durée, le blocage de la croissance par des inhibiteurs chimiques ou par le froid permet d'éviter l'effet parasite de la croissance cellulaire. Une étude de la cinétique de l'absorption de l'eau par le tissu autorise une correction correspondant à l'effet de la croissance (Oatsky, 1960, 1963).

La mesure indirecte de la teneur en eau a été tentée par diverses techniques, absorption de rayonnement β , mesure des variations d'épaisseur des feuilles, de taille des fruits, de diamètre des tiges (Holmes et Shrim, 1969). Cette dernière technique semble très commode à utiliser pour établir une corrélation entre l'état hydrique de la plante et les facteurs externes, et cela sans perturber le végétal étudié.

MESURE DU POTENTIEL DE L'EAU

Pour décrire la circulation de l'eau dans le système sol-plante-atmosphère, la teneur en eau ou toute caractéristique dérivée sont inutilisables, car on n'obtient ainsi aucun renseignement sur l'état énergétique de l'eau. De plus, la comparaison des résultats ne peut être possible que si tous les auteurs utilisent la même notion et expriment les valeurs obtenues de la même manière. La notion de potentiel hydrique s'est depuis quelques années imposée à tous les chercheurs travaillant dans le

domaine de la circulation de l'eau, soit dans le sol, soit dans la plante.

Le potentiel hydrique dans un milieu correspond à la différence de potentiel chimique de l'eau dans le système et de l'eau pure libre, et est symbolisé par la lettre grecque ψ . Le potentiel de l'eau pure étant égal à 0, le potentiel hydrique d'un milieu est en général exprimé par un nombre négatif.

Dans un milieu complexe comme un tissu végétal, le potentiel hydrique peut se décomposer en un certain nombre de termes correspondant chacun à des phénomènes particuliers. Le potentiel osmotique (Π) dû à la présence de solutés dans la cellule, essentiellement dans la vacuole, le potentiel hydrostatique ou potentiel de turgescence (P) développé dans la cellule en réponse au potentiel osmotique et à la déformation élastique des parois cellulaires, le potentiel matriciel (τ) dû aux forces d'inhibition des colloïdes et aux forces capillaires dans les parois cellulaires.

L'expression suivante permet de relier ces différents termes,

$$\psi = \Pi + \tau + P$$

et l'on peut synthétiser ces différentes notions de manière dynamique dans le diagramme de Hofler.

Il existe une relation plus ou moins complexe entre ces différents potentiels et la teneur en eau ou le DSH des tissus végétaux. Cette relation est cependant variable suivant l'âge, les conditions de développement et l'origine spécifique des tissus. Il y a dans les tissus des changements de composition chimique au niveau des vacuoles ou des propriétés élastiques des cellules qui rendent difficile la détermination d'une relation unique qui permettrait de calculer les potentiels à partir des teneurs en eau. La mesure directe des potentiels semble dans beaucoup de cas préférable au calcul à partir d'une telle relation.

Le potentiel hydrique global

La mesure du potentiel peut se faire par différentes méthodes. Certaines sont basées sur la présence ou l'absence d'échanges d'eau entre des solutions et le matériel, d'autres portent sur la mesure directe du potentiel.

L'absence d'échange d'eau entre une certaine solution et le matériel indique l'égalité entre le potentiel osmotique de la solution et le potentiel hydrique du matériel végétal. Les échanges sont repérés soit par des mesures de poids ou de taille sur le matériel, soit par des mesures des propriétés de la solution telles que l'indice de réfraction ou la densité. Les échanges d'eau se font soit à l'état liquide, soit à l'état gazeux. La méthode nécessite un grand nombre de solutions de potentiel osmotique croissant, dans lesquelles on place les échantillons, surtout si l'on ne connaît pas la gamme des potentiels hydriques atteints par les tissus.

Les échanges à l'état liquide sont rapides, mais présentent une série d'inconvénients. Il peut y avoir une sortie de substances du tissu vers la solution, ce qui

peut modifier leur concentration. Le soluté créant le potentiel osmotique des solutions doit être choisi de telle façon qu'il ne pénètre pas dans les tissus. Il semble donc préférable de remplacer le sucre et le mannitol, souvent utilisés, par du carbowax dialysé. Parfois un échange non osmotique entre l'eau de l'espace libre que constituent la vascularisation et la paroi cellulosa et la solution aboutit à modifier la concentration de la solution externe et peut-être même celle de la solution en contact direct avec le protoplasme (Gaff et Carr, 1964). Lemée et Laisnée (1951), puis Lemée et Gonzalez (1965) proposent, pour éviter cela, de rincer au préalable l'échantillon pendant une heure, puis de le placer dans une nouvelle solution pendant six heures avant de faire la mesure. Ces précautions sont peut-être suffisantes pour éliminer l'effet de dilution, mais le problème se pose alors de savoir si cette méthode ne mesure pas uniquement le potentiel du protoplasme au lieu du potentiel total du tissu, puisque tout l'espace libre envahi par la solution externe n'intervient plus dans la mesure.

Le schéma général que nous avons décrit au début de cet exposé donne à penser que le potentiel hydrique dans l'espace libre sera, dans certaines circonstances, différent du potentiel dans la cellule elle-même, au niveau de la vacuole ou du cytoplasme. Nous avons également signalé que le potentiel dans l'espace libre est celui qui provoque la circulation de l'eau à travers la plante alors que le potentiel cellulaire joue un rôle important sur un certain nombre de fonctions physiologiques. Ces considérations seront de la plus grande importance lorsque nous discuterons la signification physiologique de tous les paramètres permettant de décrire l'état hydrique du végétal.

Lorsque la mesure porte sur la taille ou sur le poids des échantillons, l'infiltration de la solution dans les espaces intercellulaires ou intracellulaires pour les cellules plasmolysées fait qu'on n'atteint pas le point d'équilibre recherché (Ashby et Wolf, 1947; Slatyer, 1958).

Les échanges d'eau entre l'échantillon et la solution peuvent se faire à l'état de vapeur. Dans ces conditions, le volume de liquide utilisé peut être plus élevé et ne peut être contaminé par l'échantillon. La mesure permettant de déterminer le point d'équilibre entre l'échantillon et une certaine solution se fait sur l'échantillon lui-même. Il s'agit, en général, d'enregistrer des variations de poids de celui-ci. Les échanges à l'état de vapeur sont plus lents qu'à l'état liquide. La saturation de la couche d'air qui sépare l'échantillon de la solution est rapide. Cependant, la sorption et la désorption de l'eau par les tissus est plus lente (surtout la sorption, qui n'est jamais complète). Pendant tout le temps que dure l'échange, le poids sec diminue par respiration et le résultat est de ce fait légèrement entaché d'erreur. Il faut donc trouver un temps d'équilibre juste suffisamment long pour que les échanges aient lieu sans que la perte de poids soit importante; huit à dix heures sont cependant nécessaires.

La mesure directe de l'humidité relative dans l'atmosphère surmontant l'échantillon placé dans une chambre close permet de connaître le potentiel hydrique de celui-ci. Il existe, en effet, entre les deux une relation simple.

$$\psi = \frac{RT}{M} \ln \frac{P}{P_o}$$

relation dans laquelle ψ est le potentiel hydrique, T la température absolue, R la constante des gaz parfaits, M la masse moléculaire de l'eau, p la tension de vapeur dans l'air à la température T et P_o la tension de vapeur saturante à la même température T .

La mesure est faite soit par psychromètre thermo-électrique à effet Peltier (Spanner, 1951) ou à goutte pendante (Richards et Ogata, 1958), soit à partir de la vitesse d'évaporation d'une goutte pendante (Macklon et Weatherley, 1965).

Le temps d'équilibre est beaucoup plus court que dans la méthode précédente — trois à six heures, suivant le potentiel du tissu étudié. Toutes ces méthodes demandent des conditions de température constantes, aussi bien pour éviter dans la chambre des gradients de potentiel hydrique d'origine thermique que pour permettre des lectures correctes dans le cas des méthodes thermo-électriques.

Une source d'erreur commune à toutes les méthodes à échange en phase vapeur est la difficulté de mesurer des potentiels très forts (supérieurs à -2 ou -3 bars). En effet, sur ces tissus, la croissance en volume des cellules continue et a pour conséquence de diminuer le potentiel des tissus. C'est ainsi que Tinklin et Weatherley (1966) observent qu'il est difficile de mesurer un potentiel égal à 0 lorsque la transpiration est nulle, et ceci en culture hydroponique de potentiel nul. Cela doit dépendre de l'âge physiologique des tissus; personnellement, nous obtenons des valeurs proches de 0 pour des tissus d'*Helianthus annuus* L. et de *Quercus ilex* L. prélevés sur des feuilles adultes et amenés à saturation avant la mesure. L'existence éventuelle d'une telle difficulté doit être vérifiée dans chaque cas particulier.

Nous allons citer ici deux méthodes qui ont l'avantage, par rapport aux précédentes, d'être plus rapides et de ne nécessiter qu'un matériel qui peut être transporté sur le terrain. Dans la méthode de la chambre en pression qui a été développée par Scholander et ses collaborateurs (1965), un rameau ou une feuille est placé dans une chambre, la tige ou le pétiole sortant à travers un bouchon étanche à l'extérieur de la chambre. La pression atmosphérique dans la chambre est augmentée progressivement et la mesure consiste à repérer à partir de quelle pression la sève sort du bois. La valeur ainsi trouvée correspond à la tension qu'il y avait dans la vascularisation au moment du prélèvement du rameau. Pour la connaissance exacte du potentiel hydrique dans la vascularisation, il faut ajouter à la valeur ainsi trouvée le potentiel osmotique du suc extrait. Ce potentiel osmotique est en général très faible. Cary et Fisher (1969) proposent une méthode de connaissance du potentiel hydrique

que des tissus foliaires par mesure de l'abaissement du point de congélation des tissus par rapport à celui de l'eau. Ils présentent un appareil comportant un générateur de froid à effet Peltier qui refroidit une chambre dans laquelle est placé l'échantillon coincé entre deux thermistances montées en pont. L'appareil est étalonné au préalable par des solutions de potentiel osmotique connu. La méthode a été comparée aux psychromètres thermo-électriques et semble donner satisfaction, compte tenu qu'elle présente l'avantage d'être simple et très rapide.

Le potentiel osmotique

Le potentiel osmotique (Π) de la cellule a souvent été utilisé pour caractériser l'état hydrique des végétaux. Certains auteurs pensent même qu'il est plus significatif que le potentiel hydrique total. Ainsi Walter (1931, 1966) affirme que le degré d'imbibition et d'hydratation du protoplasme dépend plus de π que de ψ . Les méthodes de mesure du potentiel osmotique sont basées soit sur la mesure directe de sucs extraits des tissus, soit sur des mesures indirectes sur le tissu intact.

La mesure directe du potentiel osmotique du suc extrait se fait soit par cryoscopie, soit par tonométrie thermo-électrique. Les résultats ainsi obtenus sont assez comparables quelle que soit la méthode. Les plus grandes difficultés lors de la détermination de Π sur des jus résident dans l'extraction. L'extraction sous pression sur des tissus vivants risque le plus souvent de se solder par un échec, car le cytoplasme des cellules se comporte comme une membrane semi-perméable et ne laisse passer, tant qu'il est vivant, que de l'eau distillée. Il est conseillé de tuer le cytoplasme par le froid, ce qui permet en outre de fixer le tissu et d'empêcher toute réaction qui romprait l'équilibre biochimique du suc. La dilution du suc vacuolaire par l'eau qui imbibé les parois cellulaires ou le protoplasme ne joue, d'après de nombreux auteurs, qu'un rôle négligeable.

La plupart des méthodes de mesure indirecte du potentiel osmotique sont basées sur un fait, qui est évident lorsqu'on examine le diagramme théorique de Hofler. Au cours de la déshydratation des cellules, lorsque le point de plasmolyse commençante ou limite est atteint, le potentiel hydrique égale le potentiel osmotique du suc vacuolaire, et le potentiel de turgescence des tissus devient égal à 0. La plus ancienne technique consiste à placer des échantillons de tissus dans des solutions de potentiel osmotique décroissant et à noter, par observation microscopique, à partir de quelle solution apparaît la plasmolyse (Crafts, Currier et Stocking, 1949). Une variante de cette technique consiste à mesurer l'espace libre apparent (*apparent free space*, AFS) des tissus placés dans les différentes solutions. Quand les cellules commencent à se plasmolysent, l'AFS augmente brusquement (Bernstein et Nieman, 1960). Il est également possible de repérer la plasmolyse commençante en suivant un indice du potentiel de turgescence

tel que la déformation de l'échantillon (Tazawa, 1957) ou la fréquence de résonance de l'échantillon soumis à vibration forcée — celle-ci variant avec la turgescence du tissu (Virgin, 1955). Cette fréquence, qui diminue lorsque Π des solutions décroît, reste stable à partir d'une certaine valeur considérée comme égale à Π dans le suc vacuolaire à la plasmolyse commençante. Les valeurs ainsi obtenues correspondent toutes au potentiel osmotique à la plasmolyse commençante; lorsque cela est possible, une correction de volume permet de connaître le potentiel osmotique au moment du prélèvement des tissus.

Comme pour les mesures de potentiel hydrique en milieu liquide, le choix du soluté est extrêmement important, et le carbowax dialysé s'avère être le meilleur matériel.

Le potentiel de turgescence

Le potentiel de turgescence (P) est également un des paramètres plus ou moins sensibles, suivant les types de tissu à l'état hydrique du végétal. Certains auteurs (Oertli, 1966, 1968) considèrent que le potentiel de turgescence est le paramètre le plus important de l'eau dans la plante, tout en admettant que certaines réactions de celle-ci dépendent directement du potentiel hydrique total.

Nous venons déjà de voir dans les paragraphes précédents des méthodes de mesure de P . Il faut y ajouter les mesures manométriques directes de Buttery et Boatman (1964). Une méthode indirecte et très pratique consiste à mesurer le potentiel hydrique global du tissu, à tuer celui-ci par le froid de façon à supprimer le potentiel de turgescence et à faire une deuxième mesure qui correspond alors à $\Pi + \tau$. Par différence, on peut calculer P . Ce procédé ne peut être utilisé que pour des méthodes où les échanges se font à l'état de vapeur. Le psychromètre thermo-électrique est très pratique pour réaliser une telle mesure de P . Il est évident que les erreurs faites sur ψ et $\Pi + \tau$ s'ajoutent et que la détermination de P est ainsi moins précise. Il a parfois été trouvé par cette méthode des valeurs de P négatives, en général sur des sclérophylles et xérophytes diverses. Nous-mêmes l'avons rencontré chez *Quercus ilex* L., dans l'après-midi entre 13 et 17 h, mais la valeur négative trouvée est tellement faible (1 à 2 bars) qu'il semble peut-être plus plausible d'interpréter cela comme une turgescence nulle.

CARACTÉRISATION INDIRECTE DE L'ÉTAT HYDRIQUE DU VÉGÉTAL PAR LE DEGRÉ D'OUVERTURE DES STOMATES

Nous avons vu dans la section «La circulation et l'état de l'eau dans la plante», p. 201-202, qu'une des résistances les plus élevées se situait au niveau de l'épiderme (r_{ep}). Cette résistance offre la particularité d'être variable dans le temps dans de grandes proportions et d'agir à

la fois sur le flux de vapeur d'eau et sur celui de CO_2 . Elle est constituée de deux résistances en parallèle, une résistance cuticulaire relativement constante et une résistance stomatique très variable. Les variations de la résistance à la diffusion dans les ostioles stomatiques sont soumises à un certain nombre de paramètres internes et externes au végétal — état hydrique, température foliaire, teneur en CO_2 , niveau lumineux, etc. Les deux plus importants sont le rayonnement absorbé par les feuilles et l'état hydrique de celles-ci.

ÉTAT HYDRIQUE

Lorsque le déficit hydrique apparaît dans les feuilles, on observe en général une fermeture des stomates qui agit sur les pertes hydriques. Lorsque le bilan hydrique s'améliore, si les autres conditions restent constantes, les stomates s'ouvrent et la résistance à la diffusion diminue. C'est ainsi que par un jeu d'ouverture et de fermeture peut s'établir une régulation des pertes hydriques du végétal, et que le degré d'ouverture des stomates peut constituer un indice de l'état hydrique de la plante. D'autres paramètres interviennent cependant et il faut connaître leur rôle pour interpréter correctement les résultats.

ACTION DE LA LUMIÈRE

La lumière, si toutes les autres conditions sont favorables, provoque une ouverture de l'appareil stomatique et une diminution de la résistance à la diffusion. Pour les végétaux développés dans des conditions naturelles, la résistance minimale est atteinte lorsque le rayonnement global est égal ou supérieur à $1/4$ ou $1/3$ du rayonnement global maximal. On observe parfois une augmentation de la résistance épidermique lorsque le rayonnement augmente au-delà de ces valeurs. Il ne semble pas que ce soit une action directe du rayonnement, mais, plus vraisemblablement, une action indirecte par l'intermédiaire de la déshydratation des feuilles. Nous avons personnellement observé que l'appareil stomatique ne réagit pas de la même façon, à des niveaux lumineux identiques, suivant qu'il s'agit du matin ou de l'après-midi. Cela est vraisemblablement le résultat d'une interaction hydrophotique, interaction qui se signale également par l'apparition d'oscillations cycliques de la résistance épidermique lorsque le niveau lumineux est constant (Cox, 1968).

AUTRES FACTEURS

La réactivité des stomates à ces principaux facteurs n'est pas la même suivant l'âge physiologique des feuilles; Solarova (1965) montre, en effet, que les déficits hydriques correspondant au maximum d'ouverture et à la fermeture totale dépendent de celui-ci. Kanemasu et Tanner (1969) signalent également que chez le Haricot l'épiderme inférieur réagit différemment de l'épiderme supérieur aussi bien à la lumière qu'au stress hydrique.

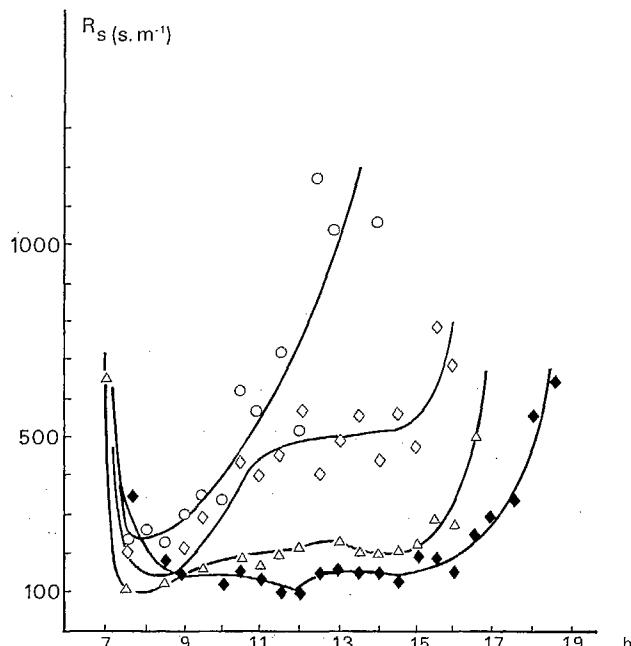


FIG. 1. Courbes journalières de la résistance à la diffusion de la vapeur d'eau dans les stomates de feuilles de Tournesol (R_s). Chaque courbe correspond à un état hydrique différent.

Il faut également signaler à ce propos le fait que la relation entre le DSH et l'ouverture des stomates n'est pas unique, les très faibles déficits ayant tendance à bloquer l'appareil stomatique.

Souvent l'appareil stomatique n'est sensible au stress hydrique que lorsque le potentiel hydrique ainsi atteint est très faible. C'est ainsi que Kanemasu et Tanner (1969) donnent les chiffres de -8 et -12 bars. Nous même avons observé sur Tournesol des valeurs seuil de -12 bars. Il faut enfin savoir que souvent le développement antérieur d'un stress hydrique intense modifie la réaction des stomates à tel point qu'il leur faut plusieurs jours après l'irrigation pour récupérer une réactivité normale.

Il ressort de tous ces faits que la relation entre le degré d'ouverture des stomates et l'état hydrique de la plante, quoique très nette, est cependant soumise à l'influence de nombreux facteurs internes et externes. Lorsqu'on cherche à caractériser l'état hydrique du végétal par le degré d'ouverture des stomates, il faut donc se placer dans des conditions aussi standards que possible, notamment sur des feuilles ayant le même âge physiologique et toujours dans les mêmes régions de la feuille. Étant donné l'aspect dynamique du développement du stress hydrique dans la plante au cours de la journée, il faut choisir la période où celui-ci est le plus intense et répéter tous les jours les mesures durant cette période.

Les investigations dans ce domaine pourraient se diriger vers la recherche de stades dans le développe-

ment des feuilles, où les stomates sont particulièrement réactifs au stress hydrique. Les stades ainsi définis seraient utilisés pour tester l'état hydrique de la culture.

RÉSULTATS EXPÉIMENTAUX CONCERNANT LA RELATION ENTRE LE DEGRÉ D'OUVERTURE DES STOMATES, LE POTENTIEL HYDRIQUE DES FEUILLES ET LE RAYONNEMENT GLOBAL

Les résultats que nous présentons ici ont été obtenus sur une culture en plein champ d'*Helianthus annuus* var. INRA 65.01. Afin de nous affranchir des différences de réactivité de l'appareil stomatique suivant l'âge et la zone de la feuille, nous avons opéré sur des feuilles de même âge et dans leur partie centrale. Les feuilles de la strate supérieure étaient placées horizontalement de façon à recevoir la lumière solaire directe toute la journée.

La résistance à la diffusion a été calculée par la méthode proposée par Impens (1966) et déjà utilisée par nous (Berger, 1969). Le potentiel hydrique des tissus a été mesuré sur des tissus foliaires prélevés immédiatement après la période de mesure de la résistance à la diffusion, avec des psychromètres thermo-électriques. Les données relatives au rayonnement global ont été obtenues avec un pyranomètre Eppley.

Sur la figure 1 sont portées un certain nombre de courbes journalières de la résistance à la diffusion de la vapeur d'eau, et ce suivant différents niveaux de stress hydriques. La première remarque qui s'impose est que les courbes ne sont pas symétriques par rapport à 12 h 45 comme le sont les courbes de rayonnement correspondantes. Cela indique nettement l'influence du stress hydrique grandissant au cours de la journée et est illustré de manière décisive par la figure 2. Cette figure correspond à une plante bien irriguée; le potentiel hydrique ne descend jamais en dessous de -200 J.kg⁻¹. La relation entre la résistance et le rayonnement global n'est cependant pas unique et l'on peut, sur le graphique, séparer deux trajets nettement différents pour le matin et l'après-midi (les points correspondent au matin, les croix à l'après-midi). Il faut noter également que le plateau de résistance minimale n'est atteint que pour un rayonnement global de 600 W.m⁻².

La figure 3 nous montre la même relation pour une plante moins bien alimentée en eau et dont le potentiel hydrique atteint un minimum de 600 J.kg⁻¹. Ici les deux trajets du matin et de l'après-midi sont beaucoup plus nettement séparés, surtout lorsque le rayonnement global est inférieur à 500 W.m⁻². Le minimum de résistance est atteint pour un rayonnement global de 300 W.m⁻². Le fait que celui-ci, dans le cas précédent, n'est atteint que pour 600 W.m⁻² est la manifestation d'un blocage hydro-passif des stomates.

Les figures 4 et 5 correspondent à des degrés plus élevés de sécheresse, puisque les potentiels hydriques les plus faibles sont de -1 300 J.kg⁻¹ et de -1 600 J.kg⁻¹. Les courbes sont alors fortement déformées et

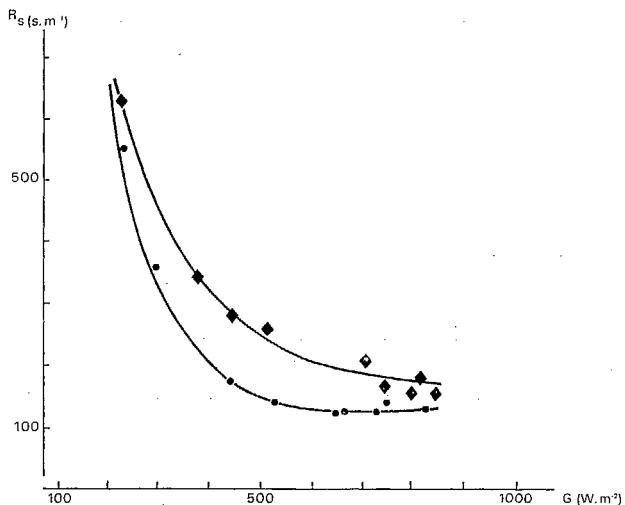


Figure 2

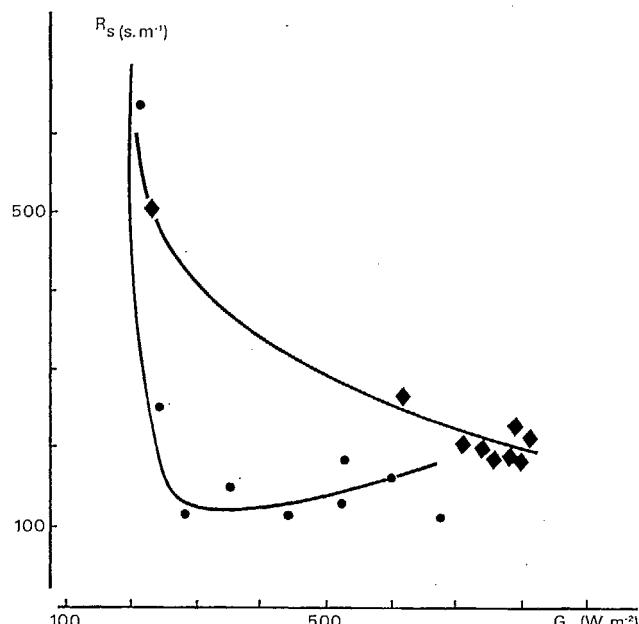


Figure 3

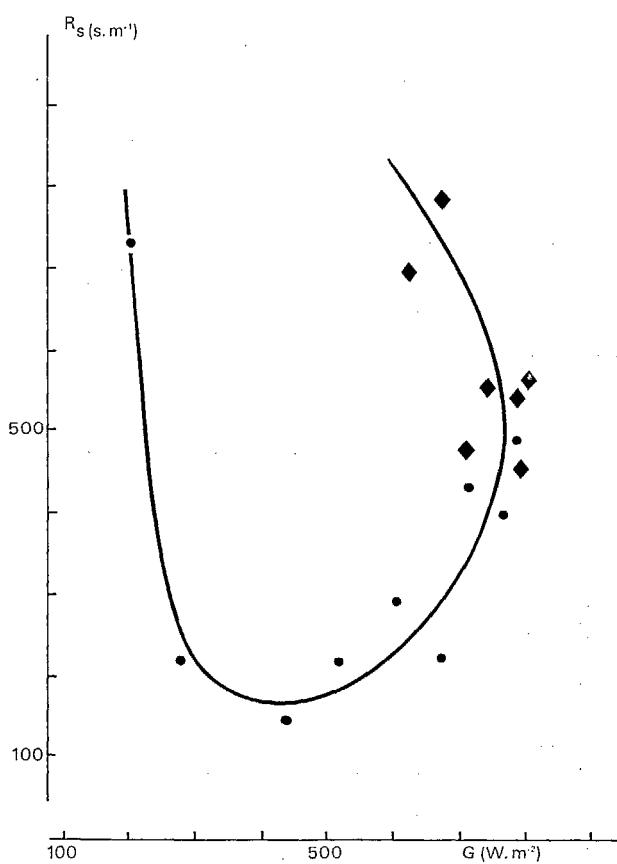


Figure 4

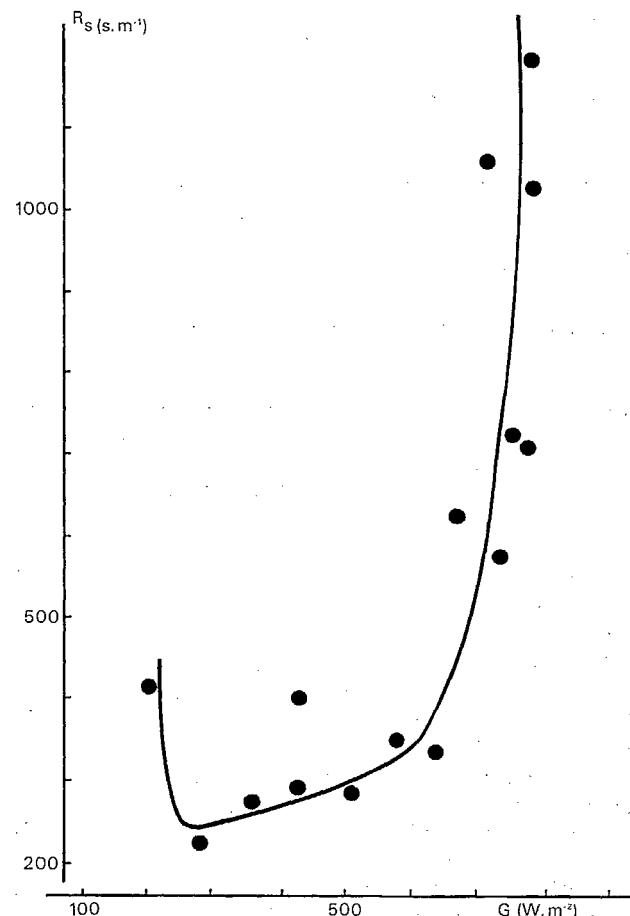


Figure 5

FIG. 2, 3, 4 et 5. Relation entre la résistance à la diffusion (R_s) et le rayonnement global reçu (G). Lorsqu'on passe de la figure 2 à la figure 5, le stress hydrique est de plus en plus élevé. Les points correspondent aux données de la matinée, les losanges à celles de l'après-midi.

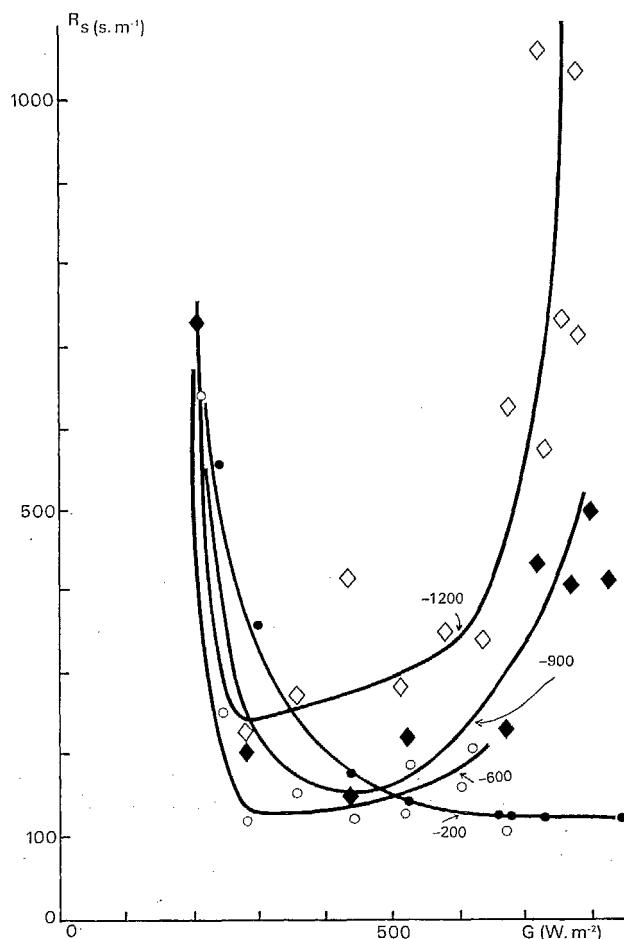


FIG. 6. Cette figure regroupe sur un même graphique des données relatives à la matinée, comparables aux précédentes. Les chiffres sur les courbes donnent la valeur du potentiel hydrique lorsque le rayonnement global atteint 600 W.m⁻².

ne correspondent plus aux courbes théoriques généralement avancées. Sur la figure 5, seules les valeurs du matin sont représentées; l'après-midi, la résistance atteint des valeurs de l'ordre de 3 000 s.m⁻¹, ce qui correspond à la fermeture totale des stomates.

La figure 6 essaie de résumer l'évolution de la relation résistance en fonction du rayonnement global lorsque le potentiel hydrique des feuilles varie. Une idée de l'ordre de grandeur de ce potentiel est donnée par la valeur de celui-ci lorsque le rayonnement global atteint 600 W.m⁻². Les résultats présentés ici se rapportent aux matinées seulement.

Pour essayer de séparer l'influence du potentiel hydrique et celle du rayonnement, nous avons tracé (fig. 7) la relation entre la résistance et le potentiel hydrique, et ce durant la période de la matinée où le rayonnement global est compris entre 500 et 800 W.m⁻². Dans ces conditions, le rayonnement est relativement stable et n'a plus qu'une très faible influence sur la résistance.

Jusqu'à une valeur de -800 J.kg⁻¹, la résistance est stable; à partir de ce seuil, elle commence à augmenter pour prendre, au-delà de -1 200 J.kg⁻¹, des valeurs très élevées.

Les relations entre la résistance et le rayonnement global (fig. 2) et entre la résistance et le potentiel hydrique (fig. 7) obtenues dans des conditions quasi stables paraissent simples. Les autres figures montrent cependant qu'un modèle réaliste doit tenir compte du fait que, dans les conditions naturelles, le rayonnement et le stress varient simultanément et qu'ainsi les relations deviennent plus complexes.

On a proposé de décrire l'influence du rayonnement par une relation hyperbolique de la forme:

$$R_s = A + \frac{B}{G}$$

R_s = résistance à la diffusion dans les stomates
 G = rayonnement
 A et B = constantes

et d'introduire l'influence du stress hydrique par différentes valeurs de A qui seraient fonction du potentiel hydrique des feuilles. Cette façon de voir aboutit à une famille de courbes du type de celle proposée par Shawcroft et Lemon. Il reste actuellement à trouver la loi de variation de A en fonction de ψ .

L'ensemble des observations que nous avons faites nous ont permis de tracer une telle famille de courbes. Le nombre de points est encore limité mais permet déjà de prévoir l'allure des phénomènes et l'importance relative du rayonnement et du potentiel hydrique sur le degré d'ouverture des stomates (fig. 8).

Si l'on excepte le cas particulier de la courbe correspondant au fort potentiel hydrique, où le blocage hydro-passif joue un rôle important, la différence essentielle semble tenir à la valeur du palier de saturation.

Il faut noter, comme l'ont déjà signalé certains auteurs, qu'entre 0 et -500 J.kg⁻¹ l'influence du potentiel hydrique sur la résistance à la diffusion de la vapeur d'eau est faible, et que par conséquent la mesure du degré d'ouverture des stomates sur des feuilles adultes est un test peu sensible pour les forts potentiels.

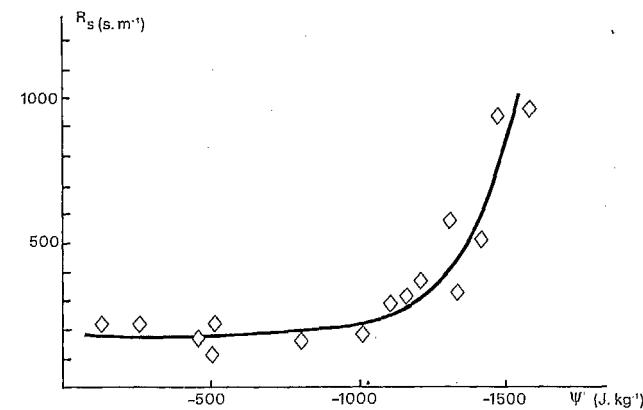


FIG. 7. Relation entre la résistance à la diffusion (R_s) et le potentiel hydrique (ψ).

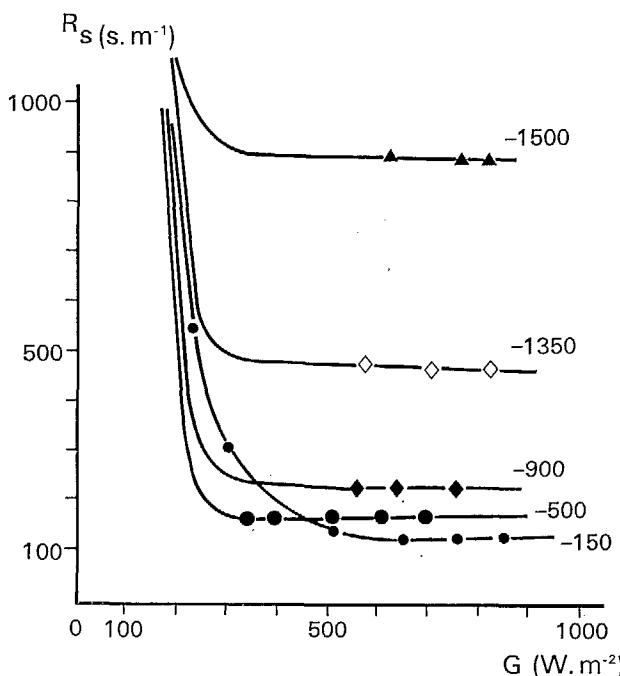


FIG. 8. Famille de courbes donnant la relation entre la résistance à la diffusion et le rayonnement global pour diverses valeurs du potentiel hydrique dans les feuilles.

MÉTHODES DE MESURE DU DEGRÉ D'OUVERTURE DES STOMATES

Observation directe

La méthode la plus courante est celle qui consiste à prélever un fragment d'épiderme et à le fixer par l'alcool éthylique ou le dioxane. Le fragment fixé est alors observé au microscope, celui-ci permettant de mesurer la taille des ostioles. Cette technique se trouve limitée à un nombre restreint d'espèces (pour lesquelles elle donne de bons résultats), car il est difficile chez de nombreuses espèces de prélever l'épiderme seul et d'assurer une fixation correcte (Shmueli, 1953, 1967).

Observation d'empreintes épidermiques

Ces difficultés peuvent être levées en utilisant pour la mesure l'empreinte de l'épiderme prise avec un caoutchouc, une résine ou une matière plastique synthétiques. Cette technique est cependant inutilisable chez les espèces à pilosité importante. Pour les taxa à ostioles larges, les résultats sont satisfaisants; si les ostioles sont longs et étroits, la résine ne moule que leur partie externe lorsqu'ils sont proches de la fermeture (Solarova, 1956; Johnson et Brun, 1966), or nous savons que c'est dans cette zone des faibles ouvertures que les stomates sont les plus efficaces sur la transpiration (Ting et Loomis, 1963).

Ces deux techniques, bien que très simples, sont d'un maniement difficile, car il faut mesurer un grand nombre de stomates pour obtenir une valeur moyenne caractérisant valablement la surface foliaire étudiée. Il existe des techniques plus rapides, qui intègrent la réponse d'une certaine surface de l'épiderme et qui sont utilisables sur le terrain bien que technologiquement plus compliquées.

La méthode d'infiltration

Elle est basée sur la façon dont pénètre à travers l'épiderme une goutte de liquide lipophile placée à sa surface. La pénétration provoque sous l'épiderme une zone sombre qui s'observe facilement à l'œil nu. Le déroulement du phénomène dépend à la fois de la taille des ostioles, de la viscosité du liquide et de la tension superficielle entre la cuticule et le liquide.

Les plus anciens procédés consistaient à utiliser des mélanges différents de deux substances telles que l'alcool isobutylique et l'éthylène-glycol. La mesure consistait à appliquer une goutte de chaque mélange et à repérer lequel pénètre dans la feuille (Oppenheimer, 1951).

Une technique plus simple n'utilise qu'un seul mélange; la mesure porte alors sur le temps nécessaire pour observer un certain degré d'infiltration (Shmueli, 1953). De nombreux auteurs (Shmueli, 1953; Dale, 1961; Rees, 1961) ont pu étalonner cette méthode soit en degré d'ouverture des ostioles, soit en résistance à la diffusion. Elle a été utilisée en irrigation pour déterminer le moment de l'arrosage, mais ses possibilités pratiques semblent limitées, car elle demande un opérateur expérimenté et habile, si l'on veut obtenir de bons résultats.

Les méthodes porométriques

Les physiologistes s'intéressent au fonctionnement de l'appareil stomatique ont mis au point de nombreux appareils qui permettent de mesurer la perméabilité de l'épiderme foliaire. Pendant longtemps ces techniques ont été trop délicates pour être utilisées hors du laboratoire. Depuis quelques années, cependant, sont apparus des types de poromètre suffisamment simples, robustes et portables pour être utilisés sur le terrain. Deux grands types sont à distinguer suivant le principe de fonctionnement: le poromètre à écoulement d'air, inspiré de l'appareil original d'Alvim (1965) et le poromètre à diffusion, ayant pour origine l'appareil proposé par Wallihan (1964).

Le poromètre à écoulement d'air n'indique que la résistance à l'écoulement visqueux de l'air à travers la feuille et non la résistance à la diffusion à travers l'épiderme.

Le poromètre à diffusion permet de mesurer la résistance à la diffusion des deux faces de la feuille séparément. Cela constitue un avantage sérieux dans la mesure où, pour définir l'état hydrique à partir de l'ouverture des stomates, on a intérêt à s'adresser à des zones des feuilles particulièrement sensibles au déficit hydrique.

C'est ainsi que Shimshi (1964) et Kanemasu et Tanner (1969) ont observé que les stomates de la face supérieure répondent les premiers à la naissance d'un déficit hydrique. L'appareil de Wallihan a été amélioré par Van Bavel et ses collaborateurs, qui proposent une méthode d'étalonnage et une correction de température, et par divers autres auteurs. Cet appareil en est arrivé à un stade de perfectionnement qui donne à penser qu'il peut être très utile dans tous les travaux d'écologie et d'agroclimatologie concernant l'état hydrique des végétaux.

RÉPONSE DES VÉGÉTAUX AUX STRESS HYDRIQUES INTERNES

L'utilisation de paramètres internes tels que le potentiel hydrique ou la résistance à la diffusion à travers l'épiderme pour déterminer l'état hydrique des végétaux et pour guider le déroulement des irrigations nécessite la connaissance des réponses des végétaux au stress hydrique. On dispose actuellement de peu de renseignements utilisables sur l'influence de l'état hydrique. Pour une grande part, cela est dû au fait que cet état est essentiellement dynamique et que les techniques permettant de mesurer correctement le potentiel hydrique sont encore peu souples, demandent beaucoup de temps et sont par conséquent peu utilisées. Nous allons ici résumer les connaissances actuelles sur quelques points particuliers tels que croissance cellulaire, photosynthèse, respiration, synthèse de la chlorophylle.

La croissance foliaire est contrôlée par trois processus différents : initiation des primordias, division cellulaire, croissance cellulaire. Les stress hydriques ralentissent, puis stoppent ces processus, mais ceux-ci reprennent après irrigation. La division cellulaire reprend même à un taux supérieur, ce qui permet un certain rattrapage. La croissance cellulaire, qui est sensible à un faible stress, peut reprendre après irrigation, mais du fait de la rigidité cellulaire le rattrapage n'est pas total. Boyer (1968) a montré que la croissance cellulaire a été affectée lorsque le potentiel hydrique atteint -2 bars chez le Tournesol et cesse complètement entre -3,5 et -4 bars. Étant donné la pression osmotique observée, égale à -10 bars, la turgescence minimale nécessaire pour l'accroissement cellulaire est de l'ordre de 6,5 bars. Un stress hydrique relativement faible peut donc agir en diminuant la surface foliaire par rapport à un témoin irrigué et, dans la mesure où la surface foliaire est un facteur limitant de la photosynthèse, agir en définitive sur la production finale de la culture.

Le déficit hydrique agit également sur le métabolisme général du carbone. Les effets globaux du DSH sur la photosynthèse et la respiration sont bien connus (Brix, 1962). D'une manière générale, la photosynthèse et la respiration nocturne diminuent lorsque le potentiel hydrique diminue. Pour ce qui est des phénomènes de photorespiration, les faits sont moins nets. Meidner (1961, 1962) constate une augmentation avec le stress

hydrique, et ce dès les faibles déficits; Troughton et Slatyer (1969) ne l'observent pas.

Au sujet de la photosynthèse nette, un problème fondamental est celui de savoir si la photosynthèse nette est affectée uniquement par l'intermédiaire du degré d'ouverture des stomates ou bien par d'autres processus physiologiques. Troughton (1969) aborde ce problème expérimentalement, sur du Coton, en mesurant simultanément la résistance à la diffusion du CO₂ à travers l'épiderme et la résistance à la diffusion au niveau du mésophylle, et ce en fonction du DSH. Les résultats de cette étude montrent que le degré d'ouverture des stomates affecte, avant tout autre processus, la photosynthèse nette lorsqu'un déficit hydrique s'installe dans la plante. Idso (1968), à l'issue d'une étude théorique, déclare que la photosynthèse est vraisemblablement affectée avant tout autre processus tel que le degré d'ouverture des stomates ou la transpiration. Il pense que les résultats expérimentaux obtenus jusqu'à maintenant l'ont été dans des conditions expérimentales très différentes des conditions de culture. Il n'apporte cependant pas les preuves expérimentales de son assertion.

Ce point est pourtant essentiel pour les problèmes d'irrigation, car suivant que le degré d'ouverture des stomates sera le premier facteur à agir ou non sur la photosynthèse, lors de l'installation d'un déficit hydrique, la mesure de ce degré d'ouverture aura une signification plus ou moins grande dans la prévision rationnelle des dates d'irrigation.

Virgin (1965) signale également que la formation de la chlorophylle est fortement sensible au déficit hydrique, dès les faibles déficits — ce qui peut également affecter la photosynthèse nette.

D'une manière générale, nous voyons que la mesure directe de l'état énergétique de l'eau dans la plante, sous ces divers aspects, serait un test plus sensible que la mesure indirecte constituée par le degré d'ouverture des stomates. En effet, beaucoup de fonctions physiologiques sont perturbées dès les faibles déficits, avant toute réaction stomatique. Pour le cas particulier de la photosynthèse nette, le problème reste encore de savoir si celle-ci et le degré d'ouverture des stomates sont étroitement liés ou si la photosynthèse est perturbée avant le degré d'ouverture des stomates.

CONCLUSION

Les paramètres choisis — teneur en eau, potentiel hydrique global, potentiel osmotique du suc vacuolaire, potentiel de turgescence et degré d'ouverture des stomates — sont des indicateurs diversement valables de l'état hydrique des plantes. Il serait souhaitable que la mesure de la teneur en eau soit remplacée par la mesure du potentiel hydrique afin de disposer d'un dénominateur commun à toutes les études physiologiques et agroclimatologiques. Le potentiel hydrique serait déjà un bien meilleur indicateur de l'état hydrique, bien qu'il

ne corresponde qu'au résultat global de l'interaction de divers facteurs, tels que π ou P , qui ont vraisemblablement une incidence plus directe sur les paramètres physiologiques. Il est probable que le potentiel de turgescence est le paramètre le plus intéressant pour beaucoup de fonctions, notamment pour la croissance cellulaire, pour le degré d'ouverture des stomates et pour les réactions biochimiques au niveau du protoplasme (Oerthli, 1966, 1968). Il faut toutefois penser, en agroclimatologie, à ne pas trop compliquer les notions et les techniques au point de les rendre peu applicables dans la réalité. Par

contre, les recherches fondamentales concernant la circulation de l'eau dans la plante, le développement du stress hydrique et la réponse des végétaux devraient faire appel à ces différents paramètres lorsque cela est souhaitable.

Le degré d'ouverture des stomates est un test indirect de l'état hydrique et qui parfois est peu sensible aux faibles déficits. Le choix de zones foliaires particulièrement réactives doit pouvoir permettre d'améliorer la sensibilité de la méthode dans la prévision des dates d'irrigation et lui donner une signification spécifique à chaque stade de la végétation.

Summary

Water potential and stomatal diffusive resistance as indicators of plant water status

The soil-plant-atmosphere model of water circulation in plants and the distribution of potentials in this system indicate that the water state in plants depends on a number of physical conditions of the soil, atmospheric conditions, and plant conditions.

The plant response integrates all these conditions, and as soon as one of them becomes unfavourable to

plant water balance, some physiological stresses are induced.

Factors are suggested for plant water status evaluation, with the principal purposes of timing irrigation and improving research on plant response to water stress. These factors are water potential and stomatal aperture. Methods for measuring them are proposed and discussed in terms of present knowledge about plant response to water stress.

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Influence de la sécheresse sur la photosynthèse et la croissance du Cotonnier

J. B. Vieira da Silva

directeur de recherches à l'Office de la recherche scientifique et technique outre-mer
Paris (France)

INTRODUCTION

Les connaissances sur l'influence de la sécheresse sur la photosynthèse et la respiration ont été partiellement passées en revue par Stocker (1960). Les conclusions des différents auteurs sont parfois contradictoires (Gaastra, 1963), ce qui n'est pas étonnant, car la photosynthèse mesurée par l'échange de CO₂ est l'aboutissement de plusieurs phénomènes, depuis les réactions photochimiques jusqu'aux résistances diffusives, en passant par le cycle de fixation du carbone, le transfert plus ou moins important de produits élaborés et la respiration. Chacun de ces phénomènes peut être affecté par la sécheresse d'une façon ou d'une autre, et l'importance relative de ces effets peut se traduire par des modifications de l'échange de CO₂ dans un sens ou dans un autre. En outre, l'abscission des feuilles comme résultat de l'action de la sécheresse a des conséquences immédiates sur la photosynthèse totale de la plante, et la réduction de la surface foliaire due au ralentissement de la croissance diminue aussi les possibilités d'assimilation.

Chez le Cotonnier, Saad (1954 a, b) a étudié le taux photosynthétique de *Gossypium barbadense* et a vérifié qu'il était maximal entre 8 et 10 heures du matin, et il indique que la fermeture des stomates ne serait pas la cause de la diminution ultérieure, en s'appuyant sur le fait que la face adaxiale, bien que n'ayant que la moitié du nombre des stomates de la face abaxiale, a une intensité photosynthétique réduite seulement de 20% par rapport à cette dernière: il pense que la diminution de la photosynthèse est due à la diminution de l'hydratation de la feuille.

Cependant, El-Sharkawy et Hesbeth (1964) ont trouvé que c'était la fermeture des stomates qui contrôlait la photosynthèse dans *G. hirsutum* cultivar (*Deltapine smoothleaf*) et que la surface stomaticque risquait même d'être limitative pour des intensités lumineuses élevées. Ils ont vérifié aussi que l'augmentation de température

diminuait le rendement photosynthétique de plantes ayant les stomates ouverts, sans que la transpiration soit diminuée.

Les travaux d'El-Sharkawy *et al.* (1965) ont montré que le taux d'assimilation était semblable dans 26 espèces et variétés de *Gossypium* étudiées, et que les différences rencontrées dans l'assimilation totale étaient dues à un développement plus rapide de la surface foliaire lié à un poids de graine plus élevé et par conséquent à des cotylédons plus grands. Muramoto *et al.* (1965) ont obtenu les mêmes résultats avec des variétés cultivées.

Lemaeva (1957) considère que la sécheresse provoque d'abord une diminution de la photosynthèse liée à une intensification de la respiration; ensuite, lorsque la respiration diminue, on enregistre un accroissement de la production photosynthétique, qui dépasse le niveau initial. Stocker (1948) avait appelé ces deux phases: phase de réaction et phase de restitution.

Cependant, les travaux récents de Boyer (1965) indiquent que la photosynthèse est surtout dépendante du potentiel hydrique (DPD ou force de succion), tandis que la respiration paraît être liée au potentiel osmotique ou peut-être au potentiel de pression.

L'influence des facteurs du milieu sur la photosynthèse du Cotonnier a été étudiée par Bierhuizen et Slatyer (1964) en relation avec les résistances externes et internes. Comparant des antitranspirants, Slatyer et Bierhuizen (1964 a, b) ont vérifié que l'acétate de phénylemercure était le seul qui, à des doses faibles, diminuait la transpiration par fermeture des stomates sans diminuer la photosynthèse dans la même proportion, ce qui augmentait l'efficacité de l'eau utilisée par la plante. L'effet de la sécheresse atmosphérique a été étudié par Bierhuizen et Slatyer (1965).

La photosynthèse apparente diminue régulièrement avec l'augmentation de la température de la feuille du Cotonnier (Baker, 1965; Ludwig *et al.*, 1965) et Troughton et Cowan (1968) ont vérifié que la photosynthèse

croît avec la transpiration pour des températures inférieures à 40 °C, diminuant ensuite pour s'annuler à 51 °C. L'influence de l'hydratation sur les échanges gazeux a été étudiée par Troughton (1969).

Le transport de CO₂ de l'air vers les chloroplastes est soumis à une série de résistances. Par analogie avec la loi d'Ohm pour le flux électrique, nous pouvons admettre que la photosynthèse nette, en conditions de lumière saturante et CO₂ limitant (P en cm³ CO₂ cm⁻² sec⁻¹) est donnée par

$$P = \frac{[\text{CO}_2] \text{ air} - [\text{CO}_2] \text{ chloroplastes}}{R_a + R_s + R_{mes}}$$

où [CO₂] air et [CO₂] chloroplastes représentent respectivement la concentration de CO₂ dans l'air et au voisinage des chloroplastes; R_a représente la résistance à la diffusion dans la couche limite, R_s la résistance stomatique (la résistance cuticulaire pour le CO₂ est si grande que, étant en parallèle avec la résistance stomatique, elle peut être négligée) et R_{mes} la résistance au transfert de CO₂ dans le mésophylle.

Dans le cas considéré par la plupart des auteurs, la limitation de la photosynthèse en lumière saturante est due au processus de diffusion, et il se trouve donc que CO₂ chloroplastes est nulle et que l'expression antérieure se simplifie (Gaastra, 1959):

$$P = \frac{[\text{CO}_2] \text{ air}}{\sum R}$$

En réalité, il s'agit d'une situation limite, car la concentration de CO₂ au niveau des chloroplastes risque de ne pas être nulle dans plusieurs circonstances.

En outre, si R_a et R_s sont des résistances bien définies, R_{mes} est une résistance qui englobe plusieurs phénomènes. Nous pensons pouvoir la diviser dans les composantes suivantes:

R_m : Résistance proprement dite à la diffusion de CO₂ dans le mésophylle.

R_e : Résistance à l'excitation, ce qui englobe non une vraie résistance mais la vitesse de production de produits phosphorylés et du pouvoir réducteur nécessaires à la fixation de CO₂.

R_c : Résistance à la carboxylation. Cette résistance peut être due soit au fonctionnement des enzymes responsables par la fixation de CO₂, soit à un possible effet de l'accumulation des produits de la photosynthèse sur le processus de carboxylation.

R_r : Résistance due à la photorespiration. Il s'agit d'une fausse résistance, plutôt d'une compétition au niveau du chloroplaste entre le CO₂ de l'air et le CO₂ produit par la photorespiration, l'absorption de ce dernier diminuant en même temps celle du premier.

L'effet des résistances diffusives dans la couche limite et au niveau des stomates a déjà été étudié par les auteurs cités dans l'introduction. Il suffit de rappeler ici les résultats obtenus par nous (Vieira da Silva, 1967), qui montrent des différences entre espèces de Cotonnier quant à l'hydratation relative qui correspond au point de fermeture des stomates. Ces différences se traduisent

par des périodes plus ou moins longues de résistance stomatique faible, ce qui peut avoir pour conséquence, tout autre fait étant constant, une assimilation de CO₂ pendant une période aussi plus ou moins longue.

Il faut souligner que la résistance stomatique, contrôlée par la fermeture de ces organes, diminue généralement plus la diffusion de la vapeur d'eau que celle de CO₂ (Zelitch, 1967). En effet, les réductions de transpiration observées par Shimshi (1969) sur des Cotonniers cultivés en plein champ n'étaient pas accompagnées par des réductions de photosynthèse. En outre, Troughton et Cowan (1968) avaient observé, chez des Cotonniers présentant une transpiration cyclique et en conditions de température élevée, une diminution et même une annulation de l'absorption de CO₂, pour des transpirations toujours croissantes. Cela montre l'intérêt des études sur les phénomènes habituellement groupés sous le terme générique de résistance du mésophylle.

INFLUENCE DE LA SÉCHERESSE SUR LES RÉACTIONS PHOTOCHEMIIQUES

L'effet de la sécheresse sur les réactions photochimiques est encore mal connu. Tandis que Todd et Basler (1965), en ce qui concerne le Blé, n'ont pas trouvé d'influence de la sécheresse sur la réaction de Hill, Nir et Poljakoff-Mayber (1967), Santarius et Ernst (1967), Santarius et Heber (1967) et Santarius (1967, 1969) ont vérifié que la dessiccation diminuait non seulement la réaction de Hill, mais aussi la photophosphorylation.

Il a été montré dans des travaux antérieurs (Vieira da Silva, 1968a, b, 1969, 1970b; Vieira da Silva et Poisson, 1969) que la sécheresse peut libérer des hydrolases contenues dans les structures cellulaires, les enzymes passant ainsi dans la phase soluble, et contribuer aussi à l'augmentation de leur activité totale. L'effet néfaste de certaines hydrolases sur l'appareil photosynthétique a déjà été observé par Bamberger et Park (1966) et par Constantopoulos et Kenyon (1968).

Les réducteurs de croissance diminuent l'activité d'une des hydrolases, la ribonucléase (Brook *et al.*, 1967; Vieira da Silva, 1970a) et retardent la sénescence des tissus végétaux (Halevy *et al.*, 1966), augmentant la résistance des plantes à la sécheresse (Halevy et Kessler, 1963; Plaut et Halevy, 1966; Vieira da Silva, 1970a).

Ces considérations nous ont conduit à étudier l'effet de la sécheresse provoquée par un choc osmotique sur la réaction de Hill et la photophosphorylation cyclique de chloroplastes du Cotonnier et à vérifier l'action du chlorure de (2-chloroéthyl) triméthylammonium (CCC) en présence du traitement osmotique.

MÉTHODE EXPÉIMENTALE

Traitement osmotique et chimique

Le traitement a consisté à ajouter du CCC à raison de 250 mg par plante dans la solution nutritive de Hoagland

servant à cultiver des Cotonniers (*G. hirsutum* variété HAR 444.2 et *G. thurberi*) âgés de 3 mois. Deux semaines après l'addition de CCC, 4 plantes subissaient un traitement osmotique de -20 J. mole^{-1} par addition de polyéthylène glycol 600 (PEG 600) à la solution nutritive, et 4 autres plantes continuaient à recevoir la solution normale. Ce même traitement était appliqué à 8 plantes n'ayant pas reçu de CCC.

Réaction de Hill

De la quatrième feuille à partir de l'apex, un échantillon de 3,5 g est prélevé 24 heures et 48 heures après le début du traitement osmotique et broyé à 5°C , avec un peu de sable, dans un mortier refroidi, en présence de 100 ml d'un mélange contenant: tampon Tris, 0,05 M de pH 7,8; saccharose, 0,4 M; NaCl, 0,01 M; cystéine, 5 mM; 2-mercaptopropanoïde, 5 mM; acide ascorbique, 0,5 mM; carbowax 4000, 0,6%; polyvinylpyrrolidone (PVP), 0,2% et serum albumine de bœuf (SAB), 0,2%. Le broyat est ensuite filtré sur deux couches de gaze et les débris enlevés par une centrifugation à $200 \times g$ pendant 2 minutes. Les chloroplastes sont ensuite séparés par centrifugation à $1000 \times g$ pendant 10 minutes, lavés et remis en suspension dans un milieu contenant du tampon Tris, 0,05 M de pH 7,8, du NaCl 0,01 M, du saccharose, 0,4 M, du PVP, 0,2% et du SAB, 0,2%.

La réaction de Hill est mesurée à l'aide de ferrocyanure de potassium dans un volume de 3 ml contenant: Tris-HCl de pH 7,8, 40 μ moles; NaCl, 70 μ moles; $MgCl_2$, 12 μ moles; NaK phosphate de pH 7,8, 12 μ moles; $K_3Fe(CN)_6$, 1,5 μ mole. La suspension de chloroplastes utilisée contenait 50 μg de chlorophylle, déterminée par la méthode d'Arnon (1949). La réaction se poursuit dans un bain thermostaté à 20°C , sous une illumination de 50 000 lux, pendant 5 minutes, et est arrêtée par l'addition de 0,3 ml d'acide trichloroacétique à 30%. Après centrifugation, le ferrocyanure de potassium est dosé dans le surnageant avec l'O-phénanthroline, selon la méthode d'Avron et Shavit (1963).

Photophosphorylation cyclique

Aucun traitement au CCC n'a été effectué dans ces expériences. Le broyage et la séparation des chloroplastes furent réalisés dans les mêmes conditions que pour la réaction de Hill, sauf que le milieu de broyage comprenait de l'acide ascorbique à la concentration de 0,02 M. Le mélange réactionnel contenait (dans 3 ml): Tris-HCl de pH 7,8, 45 μ moles; NaCl, 60 μ moles; $MgCl_2$, 12 μ moles; NaK phosphate de pH 7,8, 12 μ moles; ADP, 12 μ moles; phénazine méthosulfate, 0,09 μ mole et une suspension de chloroplastes correspondant à 30 μg de chlorophylle. Au mélange était ajoutée une quantité de ^{32}P suffisante pour permettre de compter entre $5,10^4$ et $5,10^5$ c.p.m. dans les 3 ml.

Les conditions d'illumination étaient les mêmes que pour la réaction de Hill, mais l'incubation se faisait

TABLEAU 1. Influence d'un traitement osmotique (-20 J. mole^{-1}) et du CCC (250 mg par plante) sur la réaction de Hill dans deux espèces de Cotonnier (en μ moles de ferrocyanure par mg de chlorophylle et par heure)

Cotonnier	Période après le traitement osmotique			
	24 heures		48 heures	
	<i>G. hirsutum</i>	<i>G. thurberi</i>	<i>G. hirsutum</i>	<i>G. thurberi</i>
Témoin				
Traitement osmotique	208,6	223,6	28,8	54,8
Solution normale	312,5	255,5	134,4	243,3
CCC				
Traitement osmotique	200,2	185,6	88,8	135,4
Solution normale	334,0	193,5	165,4	268,4

pendant 15 minutes à 20°C et la réaction était alors arrêtée par l'addition de 0,3 ml d'acide trichloroacétique à 20%. Après centrifugation, l'ATP formé était séparé et déterminé par la modification d'Avron (1960), de la technique de Nielsen et Lehninger (1955).

RÉSULTATS ET DISCUSSION

Les valeurs de l'activité Hill obtenues après 24 heures de traitement osmotique sont plus faibles pour *G. hirsutum* que pour *G. thurberi* (tableau 1, fig. 1). Après 48 heures, les pourcentages de réduction sont identiques pour les deux espèces: les pieds traités au CCC montrent l'intensité de la réaction de Hill à un niveau plus élevé

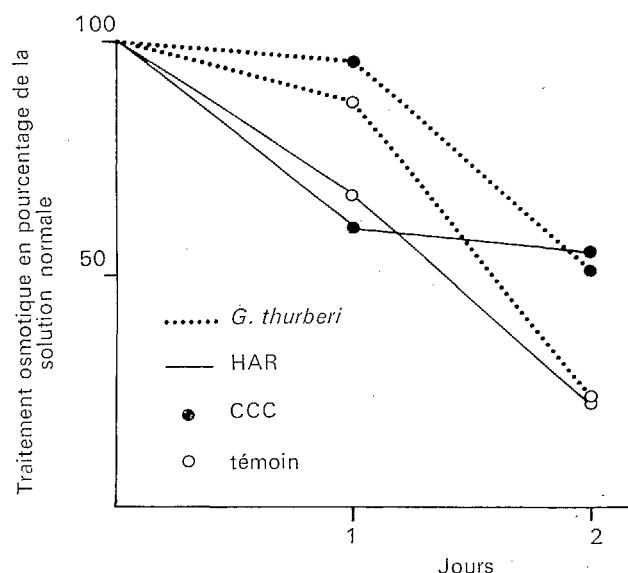


FIG. 1. Réduction de la réaction de Hill. Traitement osmotique (-20 J. mole^{-1}) en pourcentage des valeurs des plantes cultivées dans une solution nutritive normale. En abscisse, nombre de jours après l'initiation du traitement osmotique.

TABLEAU 2. Influence d'un traitement osmotique (-20 J. mole $^{-1}$) sur la photophosphorylation cyclique chez *G. thurberi* (48 heures après le traitement)

	Série I		Série II	
	A ^a	B ^b	A ^a	B ^b
Traitement osmotique	175,0	57,8	110,9	40,6
Témoin	302,8	100,0	273,3	100,0

^a, μ moles ATP par mg de chlorophylle et par heure.
^b, Poucentage du témoin.

que celui des témoins, pour lesquels les valeurs n'atteignent que 20% de l'activité normale. Ces résultats confirment que, pour le Cotonnier, la sécheresse, indépendamment de son action sur la photosynthèse, peut aussi, par la fermeture des stomates, affecter la réaction de Hill.

L'action du CCC, qui se traduit ici par une conservation de la réaction de Hill en conditions de sécheresse, est peut-être liée à son rôle dans le contrôle de la synthèse de l'acide gibberellique endogène (Barnes *et al.*, 1969), celui-ci pouvant être impliqué dans la régulation de l'activité hydrolytique pour beaucoup de tissus végétaux (Filner *et al.*, 1969).

Le traitement osmotique provoque également une dépression de la photophosphorylation cyclique (tableau 2). Cela confirme les résultats des auteurs précédemment cités, qui avaient trouvé aussi une diminution de la photophosphorylation avec la dessiccation. A l'appui de ces données, Heber (1967) a montré que la déshydratation par le gel détériore les membranes chloroplastiques et décuple la photophosphorylation.

INFLUENCE DE LA SÉCHERESSE SUR LA RÉSISTANCE A LA CARBOXYLATION

Dans un travail antérieur (Vieira da Silva, 1970b), nous avions montré que la fraction chloroplastique des feuilles de *G. thurberi* se vide en grande partie de ses protéines sous l'action de la sécheresse. Cette fraction contient, chez les plantes témoins, 68% des protéines de la cellule, mais seulement 35 et 22% dans des conditions de sécheresse croissante. Une partie considérable des protéines solubles des chloroplastes est constituée par la fraction I (Wildman et Bonner, 1947). Cette fraction présente une activité ribulosediphosphate carboxylase [EC 4.1.1.39] (Ridley *et al.*, 1967); ces auteurs ont aussi vérifié que la fraction I était plus facilement libérée des chloroplastes que la fraction II. Il paraît donc probable que cette perte d'une partie de l'équipement enzymatique sous l'action de la sécheresse soit néfaste au rendement de la carboxylation, par perte totale ou partielle des enzymes nécessaires. En outre, l'hypothèse émise par Boussingault (1868), selon laquelle « l'accumulation des produits de l'assimilation dans une feuille illuminée peut être responsable de la réduction du taux de photosynthèse nette dans cette feuille », a reçu depuis confirmation par les expériences de plusieurs auteurs (voir

Neales et Incoll, 1968), même si l'on rencontre dans certains ouvrages des résultats qui paraissent contradictoires.

Nos expériences sur le Cotonnier (Vieira da Silva, 1968c) ont montré une accumulation des sucres solubles dans les feuilles avec la sécheresse. Les études faites en utilisant le saccharose ^{14}C (Konan, 1970) indiquent de plus que la sécheresse du milieu racinaire et surtout la sécheresse de l'air ont une importance considérable dans l'exportation des glucides des feuilles.

Il peut se concevoir qu'un des effets de la sécheresse sur la résistance dite diffusive du mésophylle est celui qui résulte de l'accumulation de glucides dans les feuilles.

Toutefois, les effets de périodes courtes de sécheresse sont évidemment très différents: Troughton et Slatyer (1969) ont pu ainsi vérifier que la diffusion de CO_2 dans la phase liquide n'était pas affectée dans ce cas, ce qui indiquait une résistance du mésophylle constante. L'importance des effets biochimiques ne devient sensible que si la sécheresse se prolonge.

INFLUENCE DE LA SÉCHERESSE SUR LA PHOTORESPIRATION

L'action de la photorespiration sur le résultat net de la photosynthèse est très grande (Lake, 1967a, b; Zelitch, 1967). Troughton et Slatyer (1969) ont montré que le Cotonnier est une des plantes qui présentent cette intensification de la respiration à la lumière. Dans ces conditions, l'augmentation de température de la feuille due à la fermeture hydroactive des stomates et à la diminution de la transpiration, déjà observée par Eaton et Belden (1929) et par Pallas et Harris (1964), et confirmée sur des plants de Cotonnier en transpiration cyclique par Ehrler *et al.* (1965) peut avoir comme conséquence une diminution considérable de la photosynthèse.

INFLUENCE DE LA SÉCHERESSE SUR LA TENEUR EN CHLOROPHYLLE

Un dernier aspect de l'influence de la sécheresse sur la photosynthèse est celui étudié par Virgin (1965), qui a vérifié que même des déficits hydriques très réduits diminuaient le taux de formation de protochlorophylle et que cette inhibition était réversible.

INFLUENCE DE LA SÉCHERESSE SUR LA CROISSANCE

Une expérience a porté sur cinq variétés de *G. hirsutum* et sur le *G. anomalum*. Les plantes, cultivées dans des pots contenant 700 g de terre sèche, ont été soumises, à partir d'un mois d'âge, à cinq cycles de dessèchement du sol, ou arrosées tous les jours jusqu'à la capacité au champ.

TABLEAU 3. Influence de cinq cycles d'assèchement du sol sur les caractéristiques de six variétés de Cotonnier

Cotonnier	Pourcentage de croissance en hauteur par jour		Pourcentage d'hydratation relative (3 ^e feuille)	Poids de matière sèche	Surface foliaire totale	Poids de matière sèche (3 ^e feuille)	Nombre de feuilles produites		Rapport partie aérienne / racines
	1 ^{re} période	2 ^e période					en g	en dm ²	
en mg									
<i>G. anomalam</i>									
Témoin	5,72	6,57	92,0	5,78	8,09	172	3,50	6,50	4,71
Sécheresse	3,52	3,24	59,4	1,49	2,29	74	1,25	4,20	5,57
<i>G. hirsutum</i>									
Allen									
Témoin	3,32	1,83	80,2	7,87	5,85	318	4,50	3,20	4,31
Sécheresse	0,73	1,37	54,8	2,31	2,33	165	0,25	3,50	4,34
HAR 444.2									
Témoin	4,15	1,31	85,0	6,87	5,10	267	3,50	2,50	4,48
Sécheresse	1,36	1,47	50,4	2,28	2,26	130	0,00	4,50	4,62
ATH 555.7									
Témoin	3,18	1,94	84,0	7,85	6,31	378	2,00	6,50	3,77
Sécheresse	0,83	1,24	55,5	2,21	1,82	161	0,00	3,00	4,14
Race <i>punctatum</i>									
Témoin	3,69	3,95	85,4	8,00	8,26	354	3,25	4,50	3,85
Sécheresse	0,83	1,71	52,8	1,91	2,26	140	0,25	4,00	3,60
BJA									
Témoin	4,12	1,67	85,8	7,70	5,96	362	2,25	4,00	4,08
Sécheresse	0,98	2,12	58,4	2,16	2,28	219	0,50	2,00	3,76
P.P.D.S.									
P = 0,05	± 1,08	± 0,91	± 8,1	± 1,82	± 2,30	± 59			
P = 0,01	± 1,46	± 1,23	± 10,9	± 2,45	± 3,11	± 80			
P = 0,001	± 1,93	± 1,64	± 14,5	± 3,25	± 4,12	± 106			

Le taux moyen de croissance (*TC*) en hauteur (*h*), donné par l'expression:

$$TC = \frac{h_2 - h_1}{h_1 (t_2 - t_1)} \times 100$$

a été calculé pour toutes les plantes, d'abord entre le deuxième et le troisième cycle d'assèchement (10 jours) et ensuite entre le troisième et le cinquième cycle (18 jours). Le nombre de feuilles produites pendant ces deux périodes a été enregistré. A la récolte, trois jours après le cinquième cycle, ont été également déterminés: la matière sèche de la troisième feuille utilisée pour l'estimation de l'hydratation relative (Hewlett et Kramer, 1963), la surface foliaire totale mesurée par une méthode photométrique [Bonzon, 1964] (corrigée des feuilles récoltées pour analyse); la matière sèche totale par plante; le rapport en matière sèche entre partie aérienne et partie souterraine.

Les résultats (tableau 3) montrent un effet considérable de la sécheresse sur le taux de croissance en hauteur pendant la première période mesurée en ce qui concerne les variétés de l'espèce sensible *G. hirsutum*; par contre, *G. anomalam*, résistant, présente une réduction beaucoup moins importante. Pendant la deuxième période, les plantes sensibles montrent une reprise de croissance due à l'adaptation (*hardening*) sous l'effet de l'assèchement et leur TCR est de même ordre de grandeur que celui des témoins. Il faut noter cependant que, la fructification

étant plus précoce chez ces derniers, la croissance en hauteur est de ce fait ralentie. La race *punctatum*, qui a une floraison plus tardive, ne montre pas ce ralentissement de croissance chez les plantes arrosées. Le même phénomène d'adaptation se retrouve dans le nombre de feuilles produites pendant la première et la deuxième période mesurées.

La sécheresse diminue considérablement la surface de la troisième feuille et la surface foliaire totale, aussi bien chez l'espèce résistante que chez les variétés sensibles, et diminue aussi le poids sec total de la plante. Cependant, le rapport partie aérienne / partie souterraine ne

TABLEAU 4. Nombre de feuilles produites par plante et pourcentage d'abscission foliaire

Plante	Nombre de feuilles produites		Pourcentage d'abscission	
	Témoin	Sécheresse	Témoin	Sécheresse
<i>G. anomalam</i>	23,00	18,00	22,8	45,8
<i>G. hirsutum</i>				
Allen	18,75	12,50	21,3	42,0
HAR 444.2	17,75	13,75	19,7	43,6
ATH 555.7	17,00	10,75	17,6	41,9
Race <i>punctatum</i>	16,75	13,00	20,9	34,6
BJA	16,00	10,00	23,4	42,5

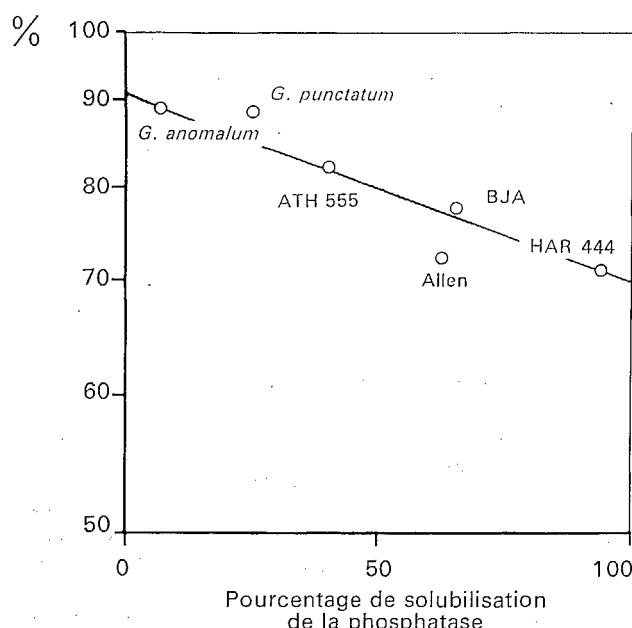


FIG. 2. Influence de la sécheresse sur la production de matière sèche par unité de surface foliaire. Corrélation avec la solubilisation de la phosphatase acide (en abscisse). En ordonnée, le rapport matière sèche / surface foliaire des « traitements secs » en pourcentage du même rapport chez les témoins.

paraît pas être sensiblement affecté par la sécheresse, dans les conditions de l'expérience (les plantes étant cultivées en pots de dimensions assez réduites de 800 ml de capacité).

Si l'on considère le nombre total de feuilles produites et le pourcentage d'abscission, on note (tableau 4) que la sécheresse diminue dans tous les cas le nombre total de feuilles produites et double le pourcentage d'abscission foliaire.

L'influence de la sécheresse sur le rendement en matière sèche, par rapport à la surface foliaire, est différente suivant les variétés. La réduction de la production de matière sèche par rapport à la surface foliaire, sous l'effet de la sécheresse, décroît avec l'augmentation de la solubilisation de la phosphatase acide, mesurée dans les mêmes pieds (fig. 2). Cela n'est dû ni à une meilleure conservation de l'eau, car toutes les espèces ont été amenées, dans chaque cycle, à un flétrissement total et à une hydratation également réduite (tableau 3), ni à une différence dans le taux d'abscission foliaire, puisque celui-ci est sensiblement toujours le même (tableau 4).

La solubilisation des enzymes hydrolytiques, ici la phosphatase acide, serait donc responsable de la moindre efficacité photosynthétique chez les plantes sensibles: cette hypothèse est conforme aux expériences déjà citées de Bamberger et Park (1966) et de Constantopoulos et Kenyon (1968).

Summary

Influence of drought on the photosynthesis and growth of the cotton plant (J. B. Vieira da Silva)

Drought influences photosynthesis not only through stomata closure but also through biochemical reactions. Drought depresses the Hill reaction and cyclic photo-

phosphorylation in the cotton plant. CCC protects treated plants against Hill reaction depression.

Drought-induced liberation of hydrolytic enzymes could explain the observed reduction of photosynthetic efficiency.

Drought reduces height growth, leaf size and number of leaves, and doubles the leaf abscission percentage.

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Internal water status and plant response in relation to the external water régime

W. R. Gardner
Soils Department,
University of Wisconsin
Madison (United States of America)

The qualitative effects of water stress upon plant response are reasonably well known. Quantitative relationships between soil water potential, plant water potential, evapotranspiration, and growth rate have been difficult to derive because of the many physical and biological processes involved. Improvements in instrumental techniques during the past few years, particularly the development of better means of measuring the plant water potential and the stomatal resistance, now permit us to bridge the gap between environmental factors and plant response, in so far as plant water relations are concerned, in at least a semi-quantitative manner, and to delineate the problems yet to be resolved.

It is well beyond the scope of this paper to review the extensive, but pertinent, literature on soil-plant-water relationships. It is the purpose here to discuss the interaction between the plant and its environment in a semi-quantitative way, drawing upon only a few data to illustrate the points. Idso (1968), in his treatment of the relationship between transpiration and photosynthesis, essentially eliminates the stomates from consideration and appears to argue (from a consideration of the water potential gradients) for an almost complete decoupling between transpiration and photosynthesis. It is my feeling that the experimental evidence is now convincingly in favour of a very intimate coupling between transpiration and photosynthesis through stomatal control of gaseous exchange between the plant leaf and the surrounding atmosphere. The approach is rather straightforward. It requires that one be able to relate the plant-leaf water potential to the soil-water potential and the transpiration rate and the stomatal resistance or conductance to the leaf-water potential. It is the objective of this paper to show how this might be done, drawing principally upon the data of my colleagues, since such data are most readily available.

RELATIONSHIP BETWEEN TRANSPERSION RATE AND LEAF WATER POTENTIAL

Water transport from the soil to the plant leaf appears to be a largely passive process that depends upon the water potential gradient between the soil and the leaf. Figure 1 shows a typical relationship between the relative flux through the plant and the difference in potential between the solution surrounding the plant roots and the potential in the leaves. These particular data are for beans in a growth chamber (Millar, personal communication, 1970) with the roots in culture solutions with various osmotic potentials due to added salts, and in soils with matric potentials down to -5 bars. The ordinate is expressed on a relative basis since we are uncertain as to how best to express it.

This nonlinear type of relationship for flux through plant roots is very similar to many reported in the literature. A number of explanations for this non-linearity have been offered, but I believe that it is probably a natural consequence of the semi-permeable nature of the root membranes. This problem is being studied and analysed further, since it has important implications with respect to water uptake patterns and the interaction between ion and water uptake. What is of interest here is that, as the flux through the plant increases, the water potential in the leaves must drop correspondingly until a value for the potential difference between the leaf and the water external to the plant root is about -4 bars. Beyond this point, further increases in flux result in only modest increases in the potential drop across the plant. Many of the data in the literature, as well as our recent measurements on onions (Millar, personal communication, 1970), indicate an even more curvilinear relationship.

The relationship between the flux through the plant and the potential evapotranspiration is rather complex

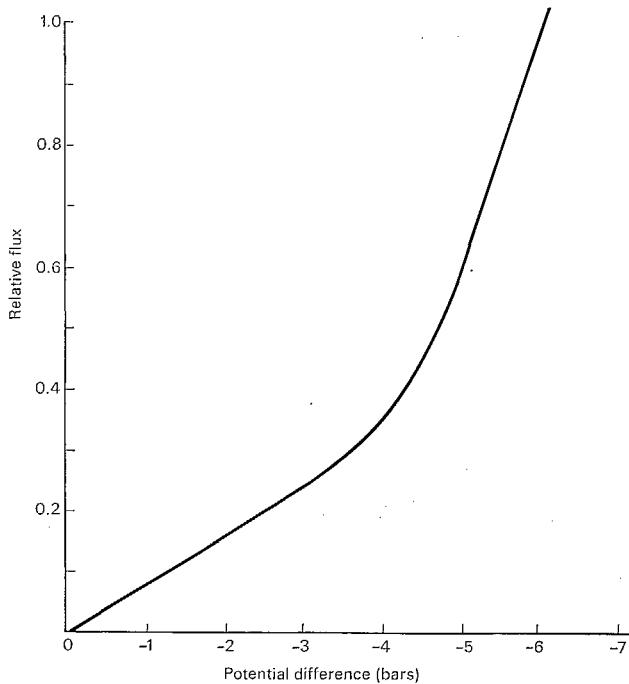


FIG. 1. Relative flux through a bean plant as a function of the water potential difference between the solution surrounding the roots and that in the leaves.

and will not be discussed here. However, if the stomatal resistance is known, the relationship can be calculated from meteorological measurements (Black *et al.*, 1970). It should be pointed out that as the soil water potential decreases, the maximum relative flux possible is reduced by stomatal closure and at soil water potentials below about -3 bars, the flux does not go above the linear portion of the expression curve, for the bean plants in question. At very low values of the soil-water potential, the transpiration rate is controlled by the capillary conductivity of the soil (Lang and Gardner, 1970). The exact shape of curves such as that shown in Figure 1 depends upon the root to top ratio and the various factors that affect root permeability.

INTERNAL WATER STATUS OF THE PLANT

There are consistent relationships between the leaf water potential and other aspects of the internal water status of plant leaves. These have been considered in some detail by Gardner and Ehlig (1965), including the effect of saline substrates (Ehlig, *et al.* 1968).

Figure 2 shows the turgor pressure as a function of total leaf water potential for beans, derived from data given by Kanemasu and Tanner (1969). (It was assumed that the osmotic potential was -10 bars when the total potential was zero.) At water potentials below about

-8 bars it is difficult to estimate the turgor potential with any precision. It is important to note the marked reduction in turgor potential in the range from zero to -6 or -7 bars total potential. With even modest transpiration rates, the potential drop across the plant is 5 or 6 bars, so that the turgor potential is substantially below its maximum value, even when the soil water potential is near zero.

We have observed that, in a large number of cases under greenhouse conditions, the plant leaf water potential during the day tends to remain at a rather constant amount below the soil water potential, regardless of the value of the latter. This, however, is not invariably the case. Figures 1 and 2 taken together show that, when the soil water potential surrounding the plant roots is no lower than about -1 bar, the turgor pressure of the plant leaves depends more strongly upon the transpiration rate than upon the soil water potential. Furthermore, in this range of soil water potentials, it is not expected that the potential at the root-soil interface is substantially lower than the average soil water potential, except in special cases (Gardner, 1960). Thus, the internal water status of a plant leaf appears to depend more upon the transpiration rate than upon the soil water potential.

RELATIONSHIP OF LEAF WATER STATUS TO STOMATAL RESPONSE

The mechanisms controlling stomatal behaviour are very complex and it will be necessary here to neglect all but the effect of water stress when light and other factors such as nutrition are not limiting. Figure 3

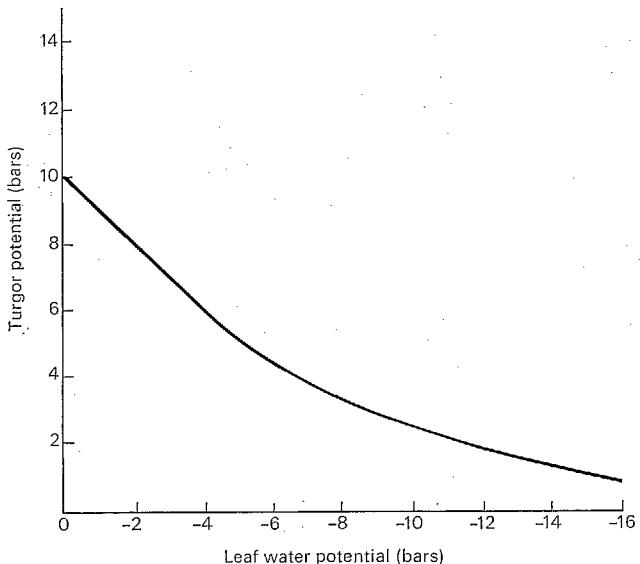


FIG. 2. Relationship between total leaf water potential and turgor potential for beans.

shows the data on stomatal conductance ($= 1/\text{resistance}$) given by Kanemasu and Tanner (1969) plotted as a function of leaf turgor potential. In this case I have plotted the reciprocal of the resistance, or conductance, since I think this is preferable conceptually. The actual data fall remarkably nearly on a straight line, both for the abaxial and adaxial stomates. At very low values of the conductance, the cuticular conductance may also be contributing importantly to the flux and this is included in the stomatal conductance.

This relationship between turgor potential and stomatal conductance is not expected to be unique. It is here that light, CO_2 , nutrition, temperature and the many other factors which affect plant growth should be expected to have an influence. Since water is potentially a problem for all higher plants, survival and optimal growth require that stomatal conductance be very sensitive to all factors influencing plant growth. Whether plants do, in fact, control water loss and CO_2 uptake optimally under all conditions is really the important question.

Figure 3 illustrates a very good correlation between stomatal conductance and turgor potential. Since the turgor potential is, in turn, influenced profoundly by the transpiration rate, there appears to be a very direct coupling between stomatal conductance and transpiration. As the soil water potential decreases below -1 bar, there is also a direct relationship between stomatal conductance and soil water potential. A direct relationship between turgor potential and stomatal conductance is to be expected since the stomates operate in the context of the surrounding cells. However, there appears to be no *a priori* reason to expect this relationship to be linear. The data of Ehlig *et al.* (1968) show this relationship to be relatively independent of the salinity level for pepper.

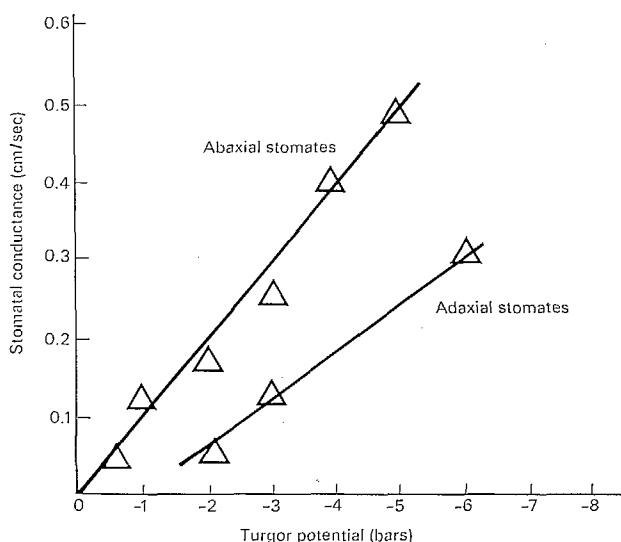


FIG. 3. Stomatal conductance as a function of leaf turgor potential for beans, obtained under field conditions (Kanemasu and Tanner, 1969).

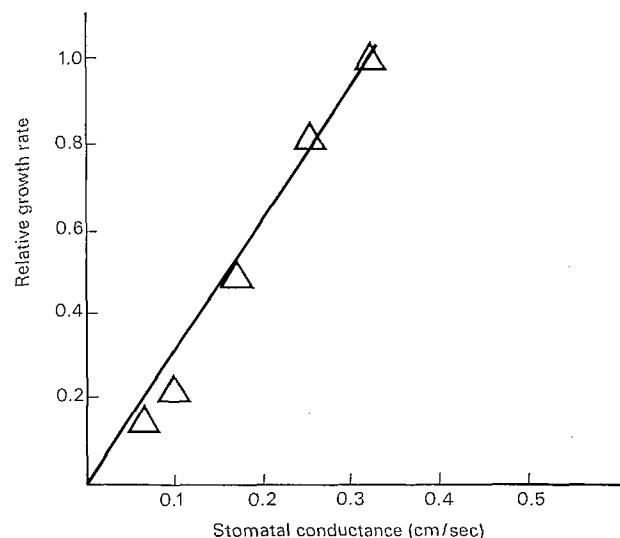


FIG. 4. Relative growth rate as a function of stomatal conductance for beans in a growth chamber (Kanemasu and Tanner, 1969).

RELATIONSHIP BETWEEN STOMATAL CONDUCTANCE AND GROWTH RATE

Figure 4 shows the relationship between growth rate and stomatal conductance for beans, again taken from the paper by Kanemasu and Tanner (1969). Within the precision of the data, the experimental points fall upon a straight line passing through the origin. At high values of stomatal conductance, for example, the relative growth rate tends to level out at a maximum value. This is due, in part, to neglect of the mesophyll resistance and boundary layer resistance, which become important when stomatal resistance is low. Curves of this type suggest that the growth of the plant is regulated through the stomatal apparatus, whatever the mechanism that determines the stomatal conductance.

RELATIONSHIP OF PLANT GROWTH TO ENVIRONMENTAL FACTORS

From curves such as those in Figures 1–4 one can now relate plant growth to the external water régime when other factors such as light, CO_2 and nutrients, are constant, and the picture is not complicated by disease. Figure 5 shows the relative growth rate plotted as a function of leaf water potential. Values of the potential near zero are difficult to obtain in the light and at low light intensities this will be the limiting factor. Thus, the interaction between light and stomatal behaviour under water stress is yet to be determined. The curve in Figure 5 is similar in shape to those obtained by Gardner and Nieman (1964) for growth of detached

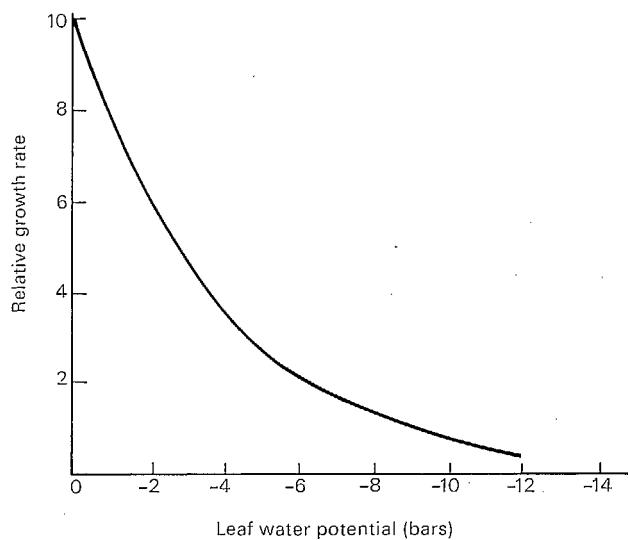


FIG. 5. Relative growth rate as a function of leaf water potential in a growth chamber (Kanemasu and Tanner, 1969). The adaxial stomata remained closed during the experiment.

radish cotyledons incubated with substrates containing different concentrations of mannitol. It is tempting to speculate that the turgor pressure also directly regulates cell division and cell enlargement so as to render the cell number and cell size compatible with the rate of assimilation. Some attention is being given to this idea, since plants in which the stress is not relieved at night might exhibit an apparent increase in mesophyll resistance, in contrast to the experiments of Troughton (1969) in which mesophyll resistance of stressed cotton plants was independent of leaf water content over a wide range of water contents.

Figure 6 shows the stomatal conductance as a function of relative transpiration rate calculated using the data from Figures 1-5. The family of curves represents different values of water potential just outside the plant root. The relationship between this potential and the average soil water potential depends upon the extent of the root system, the transpiration rate and the capillary conductivity of the soil.

An important conclusion to be drawn from Figure 6 is that, when the soil water potential is in the range zero to -1 bar, the stomatal conductance is more profoundly influenced by the transpiration rate than by the soil water potential. As the transpiration rate increases, the stomatal conductance decreases and, if the stomates are limiting CO_2 uptake, the growth rate decreases. The partitioning of evapotranspiration between transpiration from the leaves and evaporation from the soil surface becomes a matter of more than academic interest. In the field experiments reported by Kanemasu and Tanner (1969) the evaporation from the soil surface was about 40 per cent of the total evapotranspiration (Black *et al.*, 1970). Covering the soil surface to reduce

evaporation could result in a reduction in plant growth if the latent heat which was formerly used in evaporation was sufficiently well distributed throughout the canopy so as to increase the transpiration through the plants. This reduction becomes relatively less important as the transpiration rate increases.

As the soil water potential decreases below about -1 bar, it appears to become more important than atmospheric factors which influence the transpiration rate. When the plant wilts sufficiently to reduce the transpiration rate, the range of transpiration rates which result from exposure to variations in potential evapotranspiration is reduced. In the experiments from which these data were obtained, the relative transpiration did not exceed about 0.2 for the -10 bars curve and about -0.1 for the -3 bars curve. Even when the plants are badly wilted, one would expect the transpiration rate to have an effect upon plant growth, since it is related to the extent to which the stomates open in the light.

Many important features of stomatal behaviour have not been discussed here. To reiterate, Figure 3 should not give a single curve, but families of curves showing stomatal conductance as a function of leaf turgor pressure as influenced by other factors. These would include light, nutrition, temperature, aeration status of the roots, CO_2 level and any other factor that influences stomatal behaviour. One known effect is that, after being subjected to stress, the stomates do not open as wide after turgor is restored as they did before loss of turgor until after a period of one or two days. Whatever additional

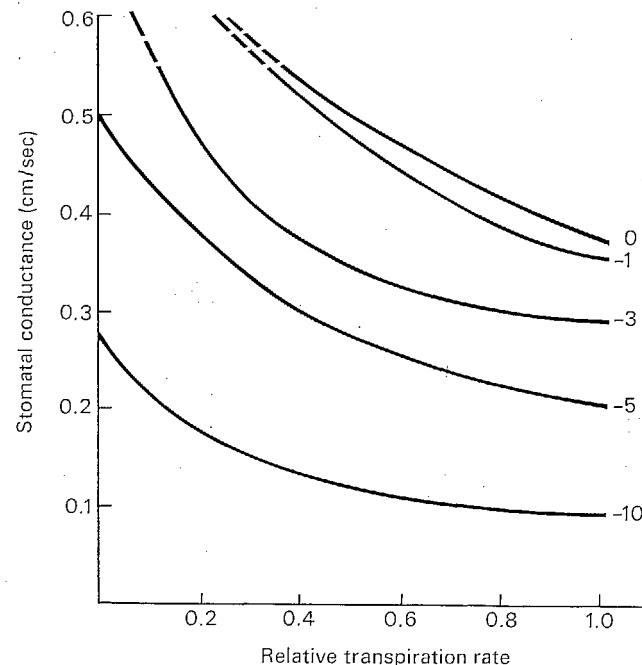


FIG. 6. Stomatal conductance as a function of relative transpiration rate. The different curves represent different values of the water potential outside the plants roots.

factors are involved, it appears quite likely that relationships between stomatal conductance and turgor potential and between turgor potential and transpiration can be found so that one can estimate quantitatively the influence of the external water régime upon plant response. It also appears that, through the stomates, the transpiration rate and the growth rate are coupled in an important way. This may not detract from some of Idso's (1968) conclusions about irrigation scheduling, but it does make an important difference when one considers ways in which to enhance plant growth or increase water use efficiency. In evaluating the water factor in agroclimatatology, the stomatal resistance would seem to be the most useful single measurement. Measurements of plant and soil water potential and estimates of leaf turgor are also highly desirable.

It is now possible to make measurements of the water potential of plant leaves and the rate of transpiration from the plant with a view to predicting the influence of environmental factors, including the soil water potential, on plant leaf water potential. If a relationship between leaf water potential and stomatal conductance can be established, it is then possible to predict the effect of environmental factors upon plant growth when water is limiting. The stomatal conductance appears to depend directly upon the turgor pressure in the leaves, but the influence of other factors such as light, temperature and nutrition on this relationship is not fully known. Environmental factors appear to have an important influence on the plant water status, even though the plant is transpiring at the potential rate, and soil water may not be limiting.

Résumé

État hydrique interne et réaction sous l'effet du régime hydrique externe des végétaux (W. R. Gardner)

Il est maintenant possible de mesurer le potentiel hydrique des feuilles et le taux de transpiration de la plante afin de prévoir l'influence des facteurs du milieu, notamment du potentiel hydrique du sol, sur le potentiel hydrique des feuilles. Si l'on peut établir un rapport entre le potentiel hydrique des feuilles et la conductance des stomates, il devient possible de prévoir l'effet des

facteurs du milieu sur la croissance des plantes lorsque l'eau est un facteur limitant. La conductance des stomates paraît dépendre directement de la pression de turgescence dans les feuilles, mais on ne sait pas exactement comment d'autres facteurs tels que la lumière, la température et la nutrition influent sur ce rapport. Les facteurs du milieu semblent exercer une influence importante sur l'état hydrique de la plante, même si l'eau du sol n'est pas un facteur limitant et si la plante transpire au taux potentiel.

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Role of endogenous metabolic water in plants under conditions of water deficit

B. B. Vartapetian

K. A. Timiriazev Institute of Plant Physiology,
Academy of Sciences of the U.S.S.R.
Moscow (U.S.S.R.)

The molecular oxygen taken up from the atmosphere during respiration is used in the cell mainly as an acceptor of the hydrogen of the organic compound being oxidized. This hypothesis, advanced by Palladin (1912) and Wieland (1912), has received direct experimental confirmation only recently, by the use of labelled oxygen O_2^{18} Hübner *et al.*, 1962; Vartapetian, 1970; Vartapetian and Kursanov, (1955).

It has now become clear that molecular oxygen may be utilized not only to oxidize the hydrogen of the respiratory substrate, with the formation of endogenous water, but also for a direct oxygenation of carbon atoms of the compound being oxidized (Hayaishi, 1964; Mason, 1965). However, the contribution of the latter method of oxidation is small. The available evidence indicates that the dominant path of aerobic oxidation of organic substances in the cell is not through direct incorporation of atmospheric molecular oxygen into the substrate, but through its use as the acceptor of hydrogen. Endogenous water is thus the end product of oxygen metabolism of the cell.

In this connexion the question arises as to whether endogenous water may be of any serious importance in the water balance of plants and animals; in other words, whether the deficit of exogenous water may be made up, to certain extent, by the endogenously formed water. Such a possibility would be particularly important for organisms in arid areas.

EXPERIMENTAL

It should be noted that direct experimental evidence concerning the role of endogenous water in the water balance of plants or animals is still rather scanty. Only certain experimental and theoretical approaches in this field will be considered below.

Labelled oxygen has offered certain opportunities for observing the formation of endogenous water (Vartape-

tian, 1970). The first experiments with heavy oxygen were carried out on animals. Since the same procedure was later applied to study endogenous water in plants, a short account will be given of these experiments with the silkworm *Bombyx mori*.

At the pupal and imago stages, i.e. when they cease to ingest food and water, silk-worms were placed in chambers isolated from the external atmosphere. The only source of oxygen for respiration was the gaseous O_2^{18} supplied to the chamber. During respiration, gaseous O_2^{18} was used in the cells to form H_2O^{18} , as was established by subjecting the water from the insect body to mass spectrometric analysis. The longer the insects stayed in the gaseous O_2^{18} atmosphere, the higher was O^{18} concentration in the body water. It was possible to calculate the proportion of endogenous water in the insect body knowing the O^{18} concentration in the molecular oxygen and in the body water. These calculations showed that, by the end of silkworm life, the main bulk of body water was of an endogenous metabolic origin.

Turning now to a consideration of the possible role of endogenous water in plants, it should be noted that succulents are of special interest in this respect since they are well adapted to dwelling under arid conditions. Cactus plants are known to be capable of persisting without water for months and still maintaining their tissues in a relatively well hydrated state. Therefore, it was reasonable to assume that this peculiarity of succulents is due, at least partly, to their ability to make up for the loss of intracellular water by the endogenous water formed from atmospheric oxygen.

However, our experiments with the cactus *Cereus hexagonus*, using a procedure similar to that just described for *Bombyx mori*, have shown that during respiration this plant synthesizes only an insignificant amount of endogenous water from the external oxygen. After 20 days of exposure to the O^{18} -containing atmosphere (3.50 atom per cent excess), the O^{18} -content in

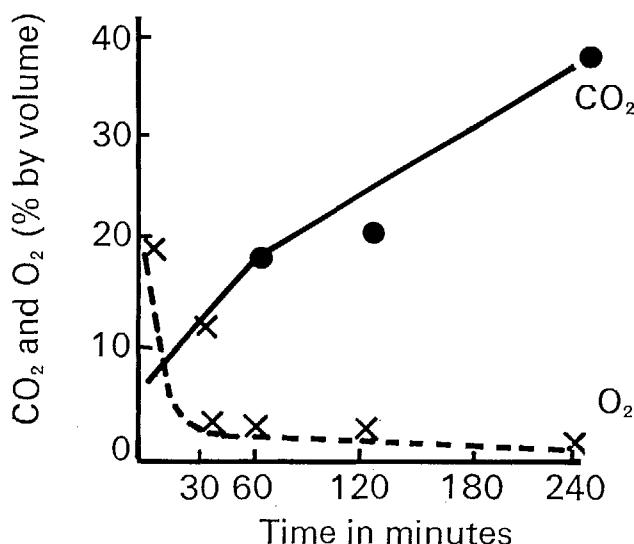


FIG. 1. Change in the internal gas composition of green tomato fruits under conditions excluding gaseous exchange with the external atmosphere. (In darkness.)

the intracellular water was only 0.06 atom per cent excess. This low level could be partly due to the poor permeability of the integument and succulent structure of the cactus, which prevented excessive loss of water and at the same time hampered the penetration of external gases, including molecular oxygen, inside the tissues. As a result, external oxygen must be relatively poorly utilized in metabolism. Moreover, unlike the tissues of *Bombyx mori*, succulent tissues do not accumulate fats or other reduced compounds which could serve as a rich source of hydrogen atoms for the formation of endogenous water during the reduction of atmospheric oxygen. It is known that during the night succulents accumulate, in significant quantities, only organic acids (Bennet-Clark, 1949; Ranson and Thomas, 1960). In the daytime tissues of succulents are enriched with carbohydrates through photosynthesis. However, the fact that it is difficult for the external oxygen to get inside the cactus plant, or for the photosynthetic oxygen and carbon dioxide to get out of it, must favour the establishment in the cactus body of an internal oxygen cycle resulting in the formation of endogenous water through reduction of both photosynthetic oxygen and respiratory carbon dioxide.

The foregoing considerations regarding the mechanism of endogenous water formation in cactus tissues have received a solid substantiation in experiments with immature green tomato fruits in light and darkness. While green tomato fruits are, of course, very different from cactus stems physiologically, they have much in common with them in anatomical, morphological and biochemical respects. For that reason, knowledge of the gaseous exchange in green tomato fruits may provide insight into the events occurring in other succulent

tissues, including the cactus. Also, tomato fruits are much more convenient to use in experiments. The results obtained are considered below.

In order to obtain an idea of the rate of oxygen uptake by fruit tissues, a series of experiments was undertaken in which the access of external air to the fruits was precluded by plastering the site of attachment of the fruit stem, as well as a small area on the fruit top with modelling clay. Such fruits were stored in darkness at 20–25° C for 0.5, 1 or 3 hr, after which the internal atmosphere was evacuated and the CO₂ and O₂ contents were determined in it.

The results are shown diagrammatically in Figure 1, from which it is seen that in darkness the oxygen store in the tomato fruit, following its isolation from the external atmosphere, falls steeply, thus indicating considerable activity of aerobic processes occurring therein. Within 30 min of the interruption of the air supply to the internal tissues, the oxygen store was almost totally depleted, so that the cells passed over to the anaerobic type of respiration.

In order to ascertain whether the green cells of tomato fruits are able to regulate the gaseous régime of their tissues, a second series of experiments was carried out, which differed from the first series only in that the fruits were kept in the light (about 7,000 lux).

It was found that, in the light, the oxygen content sharply increased in green succulent fruits (Fig. 2). As the chlorophyll content per gram fresh weight in tomato fruits is only 0.24–0.30 per cent of its content per gram of leaves, it may be concluded that the photochemical apparatus of tomato fruits operates under great stress.

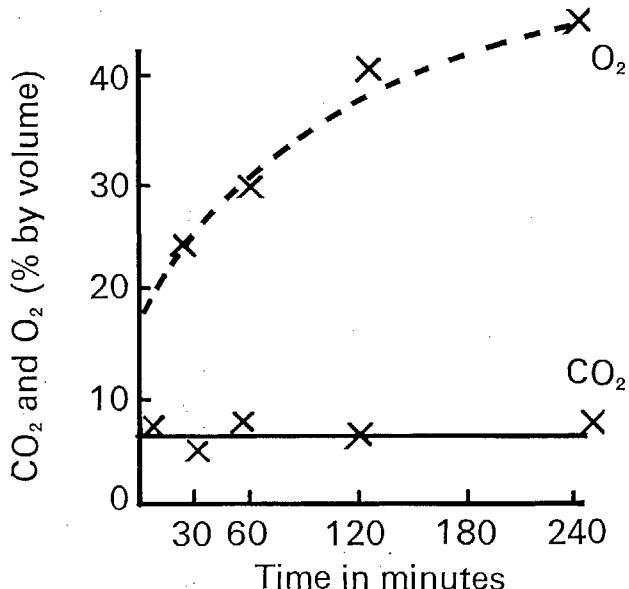


FIG. 2. Change in the internal gas composition of green tomato fruits under conditions excluding gaseous exchange with the external atmosphere. (In light.)

Thus, the photosynthesis of green succulent tomato fruits proved to be sufficient to appreciably affect the gaseous regimen in internal tissues, which in turn may be an important factor in metabolic regulation.

Green tomato fruits are characterized by a high intensity of aerobic processes, so that when air cannot gain access inside, almost all the oxygen store in the internal atmosphere is used up within 30 min.

By studying green tomato fruits one may get an idea of the gaseous exchange in other plants which are poorly adapted to carry out photosynthesis using external carbon dioxide. Indeed, our experiments with green tomato fruits have convincingly shown that the presence of chlorophyll in succulent fruits enables them to supply their tissues with oxygen for prolonged periods without oxygen inflow from the outside, owing to the photo-reduction of respiratory carbon dioxide as well as of the carbon dioxide formed during the breakdown of photolabile products. Clearly, the above mechanism of respiration-photosynthesis interaction can hardly be of any great significance in the water balance of green tomato fruits, in which the main roles of this process are the re-utilization of carbon, removal of excess carbon dioxide, and provision of aerobic conditions for the tissues.

As far as the succulents growing under conditions of water deficit are concerned, endogenous water acquires particular importance together with tissue aeration and carbon re-utilization. The oxygen cycle, which is established in their tissues owing to the interaction of photosynthesis, respiration and organic acid metabolism, results in the re-utilization of intracellular water. The proportion of endogenous water arising in the cells of succulents as a result of biochemical reactions may constitute a sizable part of the total water store in the tissues.

Bearing in mind, on the one hand, the results of the above experiments with cactus plants using O^{18} and, on the other, the peculiarities of gaseous exchange in green succulent tomato fruits, as well as taking into account the anatomical and physiological features of succulents, a closer look at the molecular transformations occurring in cactus cells is required so as to gain an insight into the mechanisms by which cactus cells continuously synthesize water in the course of metabolism.

The anatomical and morphological characteristics of cactus plants are well suited to prevent them from excessive water losses. At the same time, these characteristics must prevent the "leakage" from their tissues of the oxygen formed during day hours through photosynthesis, as well as the respiratory carbon dioxide accumulated at night. As regards carbon dioxide, its loss is not only prevented mechanically, but is also made up for biochemically, as a result of enzymatic reactions of carboxylation with the formation of organic acids.

Under these circumstances, an internal oxygen cycle is established in cactus tissues so that the water lost

by the plant during metabolism is later regenerated in the course of biochemical processes. Indeed, in the daytime, the intracellular water is decomposed in the course of photosynthesis in the outer chlorophyll-bearing tissues. The resulting organic substances and oxygen are transported to the inner parts devoid of chlorophyll, where water is regenerated in the process of respiration from the hydrogen of the organic substrates and from the oxygen evolved during photosynthesis. However, water is not only synthesized in the cell during respiration, but is also partly decomposed, because water oxygen is attached to the carbon of the respiration substrate to form respiratory carbon dioxide. The oxygen atom in the molecule of respiratory carbon dioxide arises from water.

The respiratory carbon dioxide is, in turn, transported from the inner to the outer tissues, where water is again generated through photosynthesis from the oxygen, contained in the respiratory CO_2 , which previously (during water decomposition) was attached to the carbon of the respiratory substrate. The cycle is then repeated: the water lost by cells during photosynthesis is again formed as a result of respiration, while the water decomposed during respiration is regenerated in the course of photosynthesis.

When the ambient temperature is high, a common occurrence in those areas where cactus plants are found, the intra-tissue temperature rises steeply, due to a low level of transpiration of the plant. Observations have shown that cactus plants tolerate well temperatures up to 65° C, whereas wheat plants die when exposed to 49° C for 10 min (Henkel, 1965). The respiratory rate of cactus cells under these conditions must likewise rise sharply. This gives some idea of the extent of water regeneration during metabolism in the cactus.

At night, when no photosynthesis occurs, water is formed through respiration from the previously accumulated photosynthetic oxygen. Concurrently, other water molecules in the cell are decomposed and their oxygen atoms form part of the respiratory carbon dioxide. Respiratory carbon dioxide is stored as a result of carboxylation reactions and incorporated into the organic acids which at night accumulate in large amounts in succulents. During the day, carbon dioxide is decarboxylated from the organic acids and becomes involved in photosynthetic reactions as a result of which one oxygen atom of the carbon dioxide is again incorporated into water. Thus, that part of the cellular water which has been used up during the night in the process of respiration, is regenerated in the course of photosynthesis during the day.

Figure 3 sums up schematically the mechanism of oxygen re-utilization whereby water is continuously (day and night) regenerated in succulent tissues. The proposed scheme shows the mechanism of re-utilization of endogenous oxygen. However, this does not rule out the possibility of participation of exogenous carbon dioxide and oxygen in these processes (e.g., of carbon

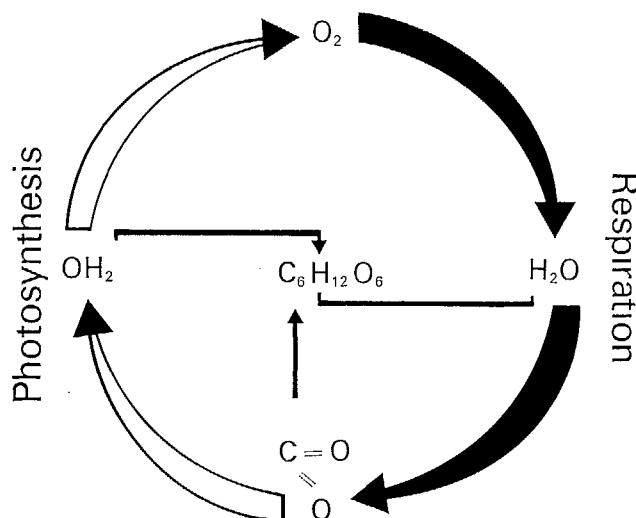


FIG. 3. Scheme to show oxygen re-utilization in succulents.

dioxide and oxygen from the atmosphere or of carbon dioxide supplied from the soil by roots).

Tentative calculations have shown that, within several weeks of being deprived of external water, cactus tissues contain no traces of the water supplied originally to them through the root system, and all of the water found in the plant must be of a metabolic origin.

It would be very interesting to ascertain the role of endogenous water in the water balance of non-succulent plants, particularly of crops. Although the evidence obtained thus far is still too scanty to make any definite conclusions on this point, several papers have recently

appeared which are especially devoted to a discussion of this question (Gordon, 1969; Henkel *et al.*, 1967; Vartapetian, 1970). In this connexion it should be noted that many investigators have observed a noticeable enhancement of respiratory processes during plant wilting. Thus, in sugar beet plants, a loss of 30 per cent of the water from the leaves more than doubles the respiratory rate (Rubin, 1963). On the other hand, it has been reported that, when tissues lose water during drought, the uncoupling of oxidation and phosphorylation processes results in reduced efficiency of the utilization of energy liberated during respiration (Zholkevich, 1963). From the point of view developed in this paper, this phenomenon (stimulation of respiration without a corresponding accumulation of liberated energy) may also be regarded as an adaptation by means of which the plant enhances the formation of endogenous water at a critical period.

The validity of this view has been tested recently in experiments by Henkel *et al.* (1967), who have found the intensification of respiration occurring during foliage wilting is accompanied by a reduced coupling of oxidation and phosphorylation. The metabolic water formed during this process constitutes a sizable proportion of the total water store of leaf cells and may appreciably increase the amount of water available to protoplasmic colloids during drought.

Analysing the results of his experiments designed to elucidate the role of endogenous water in wheat during drought, Gordon (1969) was inclined to think that the water formed in wheat plants during respiration may play a great part in mitochondrial swelling and contraction.

Further studies will be performed to elucidate this poorly known aspect of plant physiology.

Résumé

Rôle de l'eau métabolique endogène dans les plantes en état de déficit hydrique (B. B. Vartapetian)

L'auteur examine dans cette communication certains moyens expérimentaux et théoriques d'aborder l'étude du rôle que joue l'eau endogène dans l'équilibre hydrique de divers organismes.

L'utilisation de l'isotope lourd de l'oxygène, O_2^{18} , a permis de faire des observations directes de la formation et de l'accumulation d'eau métabolique H_2O^{18} chez des animaux et des végétaux. Il est démontré que, dans certains organismes, l'eau endogène peut constituer une part appréciable du stock d'eau total du corps.

Une analyse particulièrement détaillée est faite du mécanisme par lequel l'eau endogène se forme dans les plantes succulentes en état de déficit hydrique prolongé. L'auteur montre que, disposant d'un appareil photo-

chimique capable d'utiliser très efficacement la chlorophylle, les végétaux succulents photoréduisent rapidement le gaz carbonique respiratoire, malgré la masse relativement grande des tissus et une teneur relativement faible en chlorophylle. Dans des conditions de déficit hydrique aboutissant à un isolement relatif des tissus succulents à l'égard du milieu extérieur, il s'établit dans la plante succulente un cycle d'oxygène interne sur la base de processus biochimiques rigides (photosynthèse, respiration); ce cycle a pour effet une régénération continue de l'eau utilisée précédemment au cours du métabolisme cellulaire.

L'auteur examine en outre le rôle que joue l'eau endogène dans la reconstitution du stock hydrique de plantes non succulentes en état de déficit hydrique. Il conclut que l'eau endogène peut jouer un certain rôle dans le bilan hydrique de divers organismes.

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The effect of water stress at various stages of development on yield processes in wheat

R. A. Fischer

International Maize and Wheat Improvement Center
(CIMMYT), Mexico, D.F.

INTRODUCTION

Evidence has accumulated that grain yield of cereals is particularly sensitive to water stress at a certain stage of the plant's development. This evidence has recently been summarized by Salter and Goode (1967). The stage of development generally, but not always, implicated as being the "most sensitive" is that covering approximately the last 15 days before anthesis, and the yield component or parameter most affected is the number of grains per inflorescence or ear (Aspinall *et al.*, 1964; Bingham, 1966; Hutcheon and Rennie, 1960; Paauw, 1949; Skazkin and Lukomskaya, 1963; Wells and Dubetz, 1966). Although some workers have accurately defined and reproduced the soil stress cycles used, it cannot be assumed that the levels of plant water stress which arise at the various stages of development within the same experiment are equal. Plant water stress is only controlled by soil water stress, but also by resistances in the soil-plant-atmosphere catenary and particularly by the potential evaporative power determined by the atmospheric environment (Cowan, 1965). Working in a carefully controlled constant environment, as did Hutcheon and Rennie (1960), does not completely overcome this problem, since there is no allowance for the changes in plant resistances, especially the decrease in resistance to water loss from the system resulting from the increase in transpiring surface of the plants as they grow. In few of the above experiments was the level of plant water stress measured. Therefore it is difficult to assess the magnitude of the possible interaction between stage of development and degree of stress.

Because of the failure of the published work to define unequivocally the stages of development which are more, or less, sensitive to water stress (i.e. plant water stress) and because it is more logical to attempt to understand the responses of yield and yield parameters by relating them to plant water stress levels, the study reported

here was undertaken. Wheat plants were subjected to single, defined periods of water stress lasting only from 1 to 4 days and plant water stress was measured by several methods. Treatments were restricted to the period about 3 weeks either side of ear emergence (EE).

METHODS

All three experiments reported here were carried out with a single Australian wheat variety, Gabo, grown in containers, filled with 2,000 g of oven-dried soil of a silty nature. At about 4 weeks after sowing, the soil surface was covered with 100 g of alkathene chips in order to retard surface evaporation. Nutrients were added at sowing and further additions of nitrogen were made in order to eliminate the possibility of complications due to the soil drying treatments releasing nitrogen (Joffe and Small, 1964).

Plants grew at all times in controlled environment cabinets in the CSIRO Phytotron at Canberra. A photoperiod of 16 hr was used in experiment 2 and 14 hr in the other experiments (light intensity of 8 to 12 mW cm⁻², 0.4–0.7 µm, provided by cool white fluorescent tubes and incandescent lamps). In all experiments, the day and night temperatures were controlled at 21° C and 16° C respectively. Relative humidity was uncontrolled in experiment 1 and was about 80 per cent. In the other experiments, it was controlled at 60 per cent (day), 50 per cent (night), but during the periods of water stress, in order to control potential transpiration rates, the day time relative humidity was raised to between 75 and 85 per cent, the exact level depending on the stage of development. Under such conditions the variety Gabo reached EE in 64–69 days.

At 3 weeks after sowing, 7 similar plants were selected in each container; all tillers were removed each week. At 7 weeks after sowing, just before water stress treat-

ments began, all leaves other than the uppermost 4 on each shoot were removed. At EE, these were reduced to the uppermost 3 leaves. In order to enforce self-pollination in treatments with stress at or before EE and in appropriate control treatments, all ears were covered with glassine bags for a period of 1 week after EE.

EXPERIMENTAL TREATMENTS

Normally all plants received abundant water, being watered regularly to maintain soil water potential higher than -0.8 bar. Plant water stress was induced as a result of withholding water. Water stress was applied only in the period 3 weeks either side of EE. Water stress treatments at various stages of development within the same experiment were made equal on 3 bases.

1. The potential transpiration rate per container (i.e. water loss per day without stress) was adjusted to a value which was the same for all stages of development. This was done by alteration of the cabinet relative humidity.
2. The containers began to dry out such that the soil water potential at the end of the photoperiod on day zero of the drying cycle was always the same, this value being approximately -2 bars.

3. The duration of the period without water was held constant to within 2 hr, being 3 or 4 days, depending on the experiment. Rewatering was always carried out close to the middle of the photoperiod.

This technique is, therefore, one of holding constant the initial boundary conditions and the termination time of the soil drying cycle.

In all experiments such stresses of the same duration were applied at each of the stages of development examined. In later experiments additional treatments examined responses to the degree, duration and speed of onset of stress at a given stage of development. In all cases, each water stress treatment involved only one drying cycle. Appropriate control treatments, well watered at all times, were run in each experiment.

Later experiments also included heavy shading treatments and defoliation treatments, applied to some control containers and designed to simulate the effects of water stress. Shading treatments involved holding well watered plants for several days at sufficiently low light intensities to prevent net CO₂ fixation.

Results are presented as treatment means, being the average obtained from the two, three and four replicates adopted in experiments 1, 2 and 3 respectively. They are plotted as response surfaces and curves in which

TABLE 1. Water stress treatments and effects on terminal soil and plant water status

Experiment	Treatment	Day of onset of stress ¹	Duration of stress (days)	Potential transpiration (g/pot)	At rewetting		
					Soil water (% grav) ²	Xylen tension (bars)	Leaf relative water content (percentage) ³
1	D1	-16	4	100	—	17.3	64.6
	D2	-9	4	105		19.1	57.6
	D3	-2	4	105		29.4	†
	D4	+5	4	105		32.8	††
	D5	+12	4	108		36.9	††
	D6	+18	4	109		40.4	††
2	B1	-14	2	134	4.65 3.96 4.08 4.47 3.86 3.77 4.23 3.61	16.0	72.0
	D1	-14	4	134		22.6	53.0
	D2	-8	4	150		22.6	48.8
	B3	-2	2	148		19.4	60.8
	D3	-2	4	148		30.5	†
	D4	+5	4	131		36.3	†
	B5	+12	2	135		26.5	59.8
	D5	+12	4	135		38.7	††
3	C0	-22	3	135	4.32 4.32 4.86 4.29 4.02 3.82 3.90 3.79	19.1	57.3
	C1	-16	3	134		18.2	58.6
	A2	-9	1	143		13.5	78.5
	B2	-9	2	143		17.1	63.5
	C2	-9	3	143		21.3	53.8
	D2	-9	4	143		23.8	†
	C3	-2	3	142		27.8	49.5
	C4	+6	3	131		32.6	††

1. Date, in days from EE, of day zero of stress cycle.

2. g water per 100 g soil.

3. †=partial death of leaf lamina; ††=complete death of leaf lamina.

each treatment of each experiment is represented as a point.

MEASUREMENTS

1. Just before rewatering, and at all times in experiment 1, plant water stress was measured by two methods. The first involved determination of the relative water content of the uppermost fully expanded leaf and, after EE, of the ear itself. The basic technique used has been described by Barrs and Weatherley (1962).

In the second, a pressure cell similar to that described by Scholander *et al.* (1966), Boyer (1967) and Roo (1969) was used to determine xylem tension. Before EE, the shoot was cut off 5 cm below the uppermost stem node and after EE the ear was similarly cut 5 cm below its base. Xylem tension was determined at these cut surfaces.

In addition, soil water content was determined directly by core sampling of the container immediately before rewatering. In experiment 3 some estimates of stomatal aperture were made using a viscous air flow resistance porometer similar to that used by Fischer *et al.* (1970). Photosynthetic area changes through the stress cycle were measured. Photosynthetic area includes all green parts (lamina, sheath, peduncle, ear) and was assessed on the same basis as described by Fischer and Kohn (1966).

2. After the stress period, changes in photosynthetic area were followed until maturity. At maturity all remaining shoots were harvested individually for the determination of the numerical yield components and the dry weight of parts.

RESULTS

PLANT WATER STATUS

Table 1 summarizes the major water stress treatments of all experiments, showing also the soil and plant water stress reached at rewatering of each treatment. The symbols for treatments employ a capital letter to denote the number of days stress and a number to denote the approximate stage of development when the stress arose.

It is seen that the potential transpiration rate was held reasonably constant within each experiment. Nevertheless, Table 1 shows a large effect of stage of development on the terminal plant water stress for stress treatments of the same initial boundary conditions and of the same duration. Results for experiment 1 are further illustrated in Figure 1. Both leaf relative water content and xylem tension show this dependence on developmental stage. On the other hand, ear relative water content shows a reverse response, but this simply reflects a change in the water potential-relative water content relationship for whole ears as the grains grow. For this reason ear relative water content is of dubious value as an indicator of plant water stress.

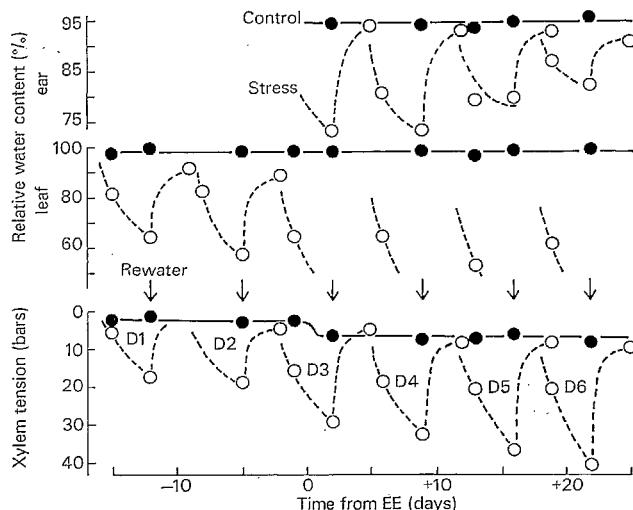


FIG. 1. Plant water status for the stress treatments and for control plants. Experiment 1.

The trend of increasing terminal plant water stress with age is seen to be accompanied by a decline in the terminal soil water content in all experiments (Table 1). Whether this effect explains entirely the response in plant water stress is examined in Figure 2. These results suggest that there was no interaction between stage of development and the relationship of relative water content of leaves to soil water status. Examination of the xylem tension values, after allowing for gradients in water stress in the plant between the middle stem (measured before EE) and the upper peduncle (measured after EE), confirm this contention. It appears, therefore, that the lower water status in the plants stressed at a later stage of development is due to more severe soil drying. The explanation of this effect is probably that

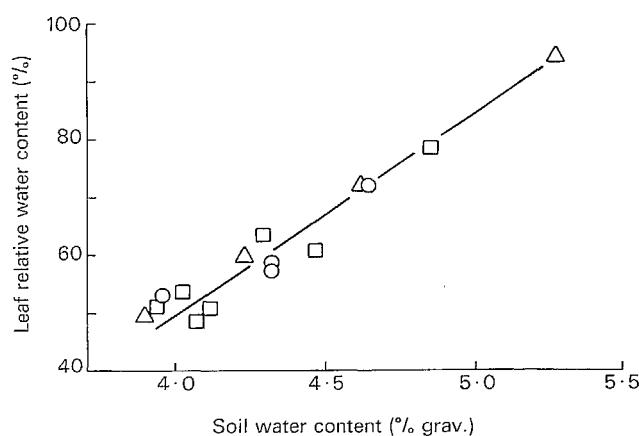


FIG. 2. Relationship of leaf relative water content to soil water content. All experiments, measurements separated on the basis: before EE — 9 days (○), EE — 9 days to EE (□), after EE (△).

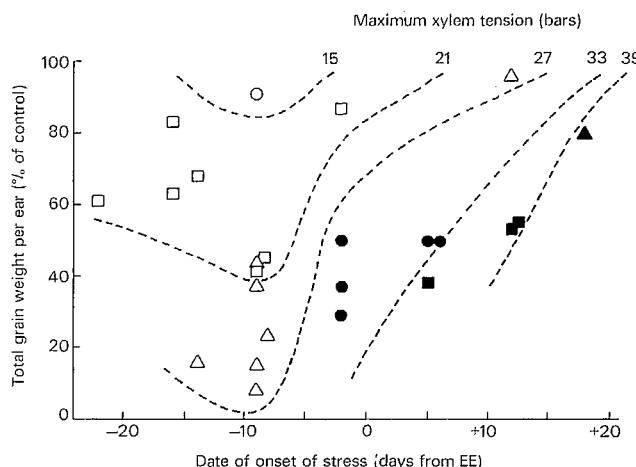


FIG. 3. Response of grain yield per ear to various degrees of plant water stress at various stages of development. All experiments, including some treatments not shown in Table 1; symbols refer to the designated ranges of maximum xylem tension (see text).

stomatal closure is less sensitive to plant water stress in older plants. Estimates of stomatal aperture, obtained with the porometer in the third experiment, but not presented here, support this idea. Since the soil containers were small and completely explored by the plant root systems, it is unlikely that changes in rooting with age were of significance.

GRAIN YIELD AND YIELD PARAMETERS

Some early severe water stress treatments prevented a few shoots from producing ears. This effect is not considered here, where results and discussion are restricted to the responses in grain yield of those ears which emerged.

Because similar periods without water caused different degrees of plant water stress at different stages of development, grain yield results reflect the interaction of these two factors. To show this, results are presented graphically such that each treatment is plotted in the abscissa dimension according to the date of onset of stress, and in the ordinate dimension according to the grain yield per ear as a percentage of control grain yield for the experiment (Fig. 3). Different symbols are used to indicate the maximum degree of plant water stress (the maximum xylem tension) attained in each treatment. Thus iso-stress lines for plant water stress can be plotted, dividing the various symbol classes.

Figure 3 shows that grain yield was most sensitive to a given degree of plant water stress at a stage about 10 days before EE. The sensitivity to stress decreases markedly at later stages of development; as one would expect, grain yield is largely unaffected by any stress commencing later than 20 days after EE. Sensitivity to stress also decreases towards earlier stages of development.

TABLE 2. Yield parameters

Grain weight per ear:

1. Source size (a) photosynthetic area at EE
(b) active life of photosynthetic tissue after EE
(c) efficiency of photosynthetic tissue
2. Sink size (a) rachis nodes per ear
(b) spikelets per rachis node
(c) grains per spikelet
3. Outcome (a) source sink ratio
(b) grain growth response

The breakdown of grain yield into yield parameters is shown in Table 2. All the parameters listed under either source or sink size are probably to the first approximation independent of one another and may, therefore, show specific effects of water stress without the possibility of confounding effects due to internal competition as, for example, is the case with mean grain weight.

Source size is represented by the product of the three source parameters listed and estimates the potential supply of assimilate available for accumulation in the developing grains. This assumes that the major part of grain carbon comes from photosynthesis after EE (Birecka and Dakic-Wlodkowska, 1966). Sink size, similarly, is here considered to be the product of the three sink parameters or simply the number of grains per ear. Mean grain weight, and hence grain yield, is determined ultimately by the source to sink ratio and by certain characteristics inherent in the growing grain.

Table 3 summarizes the responses of relevant yield parameters to main treatments. The photosynthetic area duration per shoot (PAD) integrates the effects of the first two parameters listed under source size in Table 2. It is the integral of the area under the photosynthetic area curve between the period EE to EE + 36 days, but excluding actual periods of shading or stress. The 36-day limit was set since dry weight accumulation

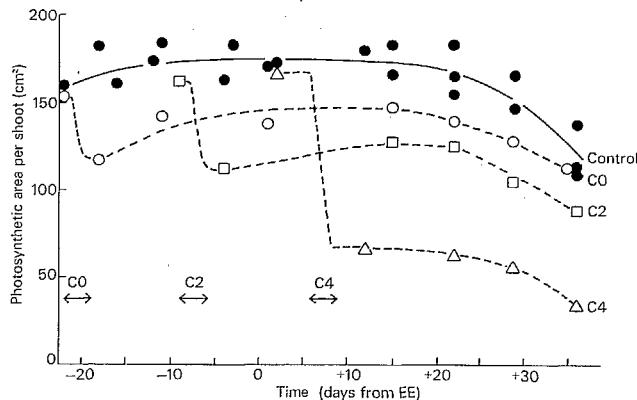


FIG. 4. Effect of water stress at various stages on the time course of photosynthetic area per shoot. Experiment 3, see Table 1 for details.

TABLE 3. Yield and yield parameters for all main treatments of all experiments

Treatment ¹	Date of onset of treatment ²	As a percentage of control ⁴					
		Grain weight per ear	PAD per shoot ³	Spikelets per ear	Grains per spikelet	Grains per ear	Weight per grain
Experiment 1							
Control		(1.44 g)		(19.6)	(1.82)	(35.5)	(40.3 mg)
D1	-16	83		90	91	79	105
D2	-9	41		94	41	40	96
D3	-2	29		96	57	54	61
D4	+5	50		100	69	69	73
D5	+12	53		108	82	83	70
D6	+18	80		100	109	104	74
Experiment 2							
Control		(1.66 g)	(4,800 days cm ²)	(18.7)	(2.20)	(40.3)	(40.8 mg)
B1	-14	68	109	97	66	67	102
D1	-14	16	83	68	28	16	100
P1	-14	89	114	93	88	85	105
D2	-8	23	84	81	27	20	118
B3	-2	90	89	99	83	85	105
D3	-2	37	49	100	55	55	81
P3	-2	96	—	98	96	98	100
D4	+5	38	39	100	78	78	50
P4	+5	97	—	106	91	100	98
B5	+12	96	85	103	105	109	92
D5	+12	53	54	97	100	100	53
P5	+12	93	—	95	100	98	96
Experiment 3							
Control		(1.69 g)	(5,930 days cm ²)	(18.7)	(2.30)	(43.4)	(38.2 mg)
CO	-22	61	82	93	75	69	90
PO	-22	89	98	98	90	88	103
C1	-16	63	89	98	70	67	101
A2	-9	91	100	102	90	90	104
B2	-9	45	92	101	41	40	114
C2	-9	43	68	97	37	37	109
D2	-9	15	46	90	14	11	118
P2	-9	70	102	104	56	58	126
3C	-2	50	51	102	79	78	65
C4	+6	50	45	103	82	83	62
P4	+6	97	87	102	92	92	108

1. Shading treatments designated by P were imposed for 4 and 3 days respectively in experiments 2 and 3. Light intensities during shading were 1 mW cm⁻², 0.4–0.7 µm, in experiment 2 and <0.5 mW cm⁻², 0.4–0.7 µm, in experiment 3.

2. Days from EE.

3. PAD = photosynthetic area duration from EE to EE + 36 days.

4. Actual values for controls shown within brackets.

in grains probably ceases after this date. The efficiency or potential for photosynthesis per unit area of green tissue over the post-EE period was not measured. It is assumed to be largely unaffected by prior treatment, such that source size is best estimated by PAD as defined.

The number of rachis nodes, or potential spikelets, per ear is not shown in Table 3 since it was unaffected by any treatment and averaged 19.4 over all experiments. Spikelets were only counted if they were considered large enough to contain complete florets (i.e. spikelets longer than about 0.5 cm from base to tip of the sterile

glume). Grains were only counted if they weighed more than 1 mg at maturity.

1. Source size. The major effect in all experiments was stimulated senescence of green parts during the actual period of water stress (Fig. 4). The magnitude of this effect relative to the initial green area was closely related to the degree of stress and this relationship was independent of the stage of development (Fig. 5). Water stress did not appear to stimulate senescence of green tissue after rewetting (Fig. 4); in fact, in some treatments, final senescence was retarded by early water stress, especially where the sink size was

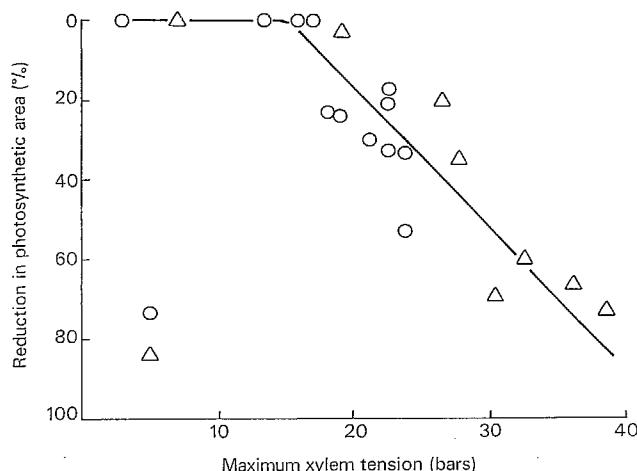


FIG. 5. Effect of degree of water stress on the reduction in photosynthetic area per shoot during the stress cycle, expressed as a percentage of the photosynthetic area present immediately prior to stress. Experiments 2 and 3; O — stress before EE — 2 days, Δ — stress after this date.

reduced markedly by this stress. Other effects of water stress on photosynthetic area, such as leaf and stem extension, were relatively small in these experiments. Variation in photosynthetic area at EE (not shown in Table 3) and in PAD between treatments is, therefore, adequately explained on the basis of the response shown in Figure 5 and the stage of development at which the stress arose.

2. Sink size. Moderate water stress up until about 5 days before EE reduced, to a limited extent, spikelet development at potential spikelet positions on the rachis. Suppression of spikelet development by water stress occurred almost exclusively at the base of the ear rather than the top. In contrast to water stress, shading treatments in this period had little or no effect on spikelets per ear.

Grains per spikelet were reduced drastically by moderate water stress during the period 15 to 5 days before EE (Figs. 6 and 7). The sensitivity to stress rapidly decreased after this period, although severe stress did reduce grains per spikelet up to 10 days after anthesis. Five of the six shading treatments of Table 3 imposed between EE - 22 and EE + 5 caused small reductions in grains per spikelet, averaging 8 per cent, while with the sixth, P2 of experiment 3 commencing at EE - 9 days, the reduction was 44 per cent.

3. Weight per grain. Source sink ratio (i.e. PAD divided by grains per ear) has been proposed as a major determinant of grain size (Table 2). This ratio can be calculated from the data of Table 3. It is evident that, generally, pre-EE water stress increased the source sink ratio whereas post-EE stress had an opposite effect. In any one experiment, weight per grain is

positively related to the source sink ratio, approaching asymptotically an upper limit (Fig. 8). This limit presumably represents the inherent maximum capacity of the grain to utilize assimilate, given an unlimited supply. Since stress treatments follow, to the first approximation at least, the same relationship as control treatments in Figure 8, it is suggested that stress, or the after-effect of stress, did not alter substantially either the capacity of the grains to grow, given a certain assimilate supply, or the capacity of the green tissues to photosynthesize given a certain rate of withdrawal of assimilate.

DISCUSSION

PLANT WATER STATUS

The results show that plants exposed to a soil drying cycle for a given number of days under carefully controlled conditions may reach different levels of plant water stress depending on their stage of development. This possibility has been neglected in most experiments aiming to investigate the water stress sensitivity of the plant at various stages of development.

Measurement of plant water status is also important for another reason. It became apparent in all experiments that, during the soil drying cycle, there were large differences (8 to 20 bars), in the photoperiod and the dark period, between water potential of the plant top (estimated by xylem tension in the plant) and that of the bulk soil. Plant water potential was always lower, presumably because water uptake lagged continually behind water loss, indicating large resistances to water transport in the soil-plant system in these experiments. Thus soil water potential or water content may not be a good estimator of plant water potential during soil drying cycles. This has, of course, been shown theoret-

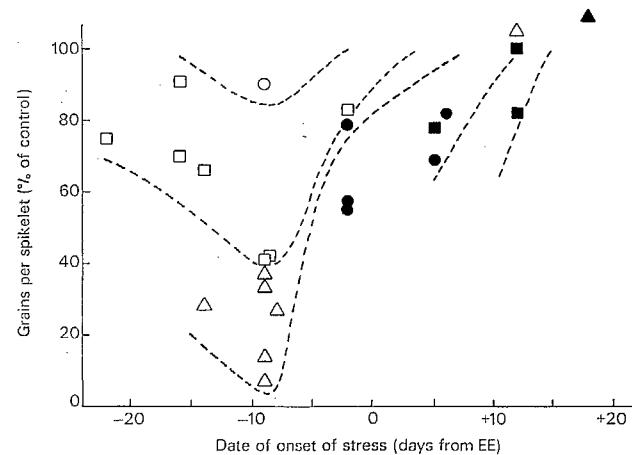


FIG. 6. Response of grains per spikelet to various degrees of plant water stress at various stages of development. All experiments (see Fig. 3).

cally (Cowan, 1965), but has also been neglected in most water stress experiments.

In applying these results to the field situation, there appears to be no reason why, in theory, the effect of stage of development would not be qualitatively the same unless, with age, extension of the volume of the root zone downwards or increased root density were sufficient to compensate for the suspected developmental changes in stomatal responsiveness. Should multiple stress cycles occur, stomatal responsiveness may change markedly (Pasternak, personal communication). Also, because soil volumes are larger, soil-plant resistances may be smaller, plant water potential may be closer to soil water potential and overnight recovery of plant water status may be more marked.

GRAIN YIELD AND YIELD PARAMETERS

The results presented here confirm those of workers mentioned earlier dealing with the sensitivity of yield in cereals to water stress. The measurement of plant water stress, however, provided a more quantitative basis than previously available for interpreting the interactions with stage of development. The approach to grain yield, namely that of dividing yield into several relatively independent underlying processes, provides a simple framework within which to examine the treatment effects.

Thus water stress at all stages reduced, in a consistent manner, the photosynthetic area relative to that existing at the time of onset of stress. Similar effects for wheat have been observed by Asana *et al.* (1958) and Fischer and Kohn (1966). Because stress periods were short and there is relatively little new photosynthetic tissue formed in wheat plants after flag leaf emergence (EE — 15 days),

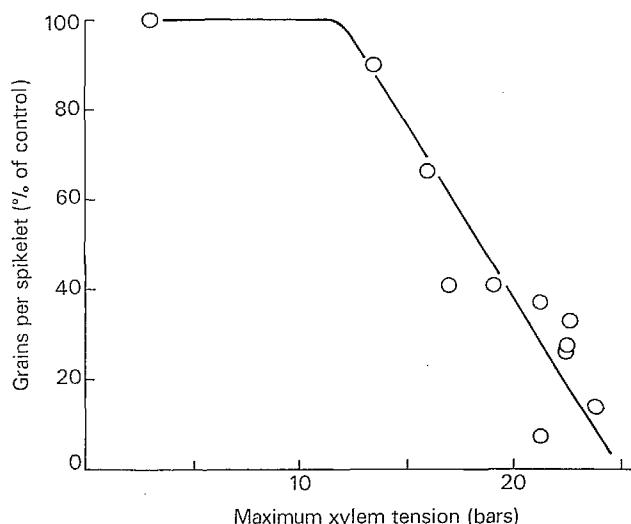


FIG. 7. Grains per spikelet versus plant water stress for stress treatments commencing in the period EE — 15 to EE — 5 days. All experiments.

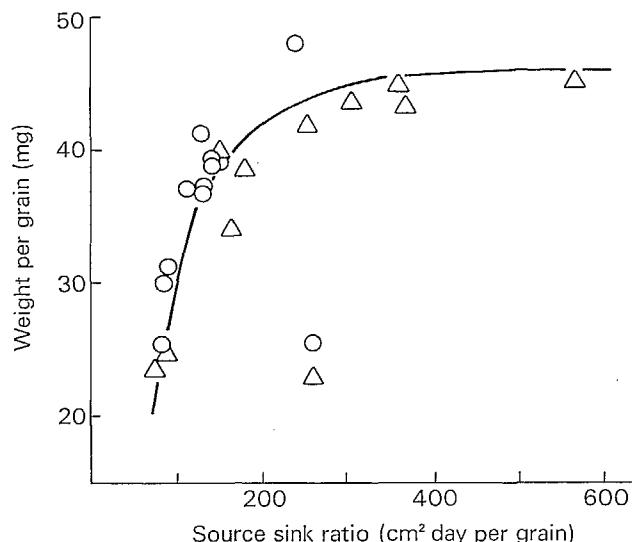


FIG. 8. The effect on grain size (weight per grain) of variation in source sink ratio (PAD divided by grain numbers, see text). Experiment 3; O — control, defoliated and shaded treatments, Δ — water stress treatments.

the above response appears to represent the major effect of stress on the source of carbohydrate for grain filling.

Changes in sink size, as defined by grain number per ear, were dominated by water stress effects on grains per spikelet over the period 15 to 5 days before EE. This period corresponded to that of rapid elongation of the ear, anthers and carpels. Such an effect of stress has been tentatively associated with the occurrence of meiosis in the pollen mother cells (Bingham, 1966; Skazkin and Lukomskaya, 1962). This also appears to be a feasible explanation for the results presented here, since plants stressed at this stage of development were often observed to produce abnormal anthers, while having normal female parts, and to be male sterile. More work needs to be done to relate the occurrence of greatest stress sensitivity to the cytological state of the anthers at the time. That this occurrence might be coincident with the so-called coenocytic stage of anther development (Heslop-Harrison, 1966) is a very interesting possibility.

The not insignificant sensitivity of grains per spikelet to shading confirms that carbohydrate supply to the developing florets and the young grains can also exert an influence. Part, if not all, of the effects on grains per spikelet of water stress at or after EE may be explained by an interruption in the supply of carbohydrate to the ear. Wardlaw (1970) has found that moderate shading for 10 days immediately after anthesis reduced grain number markedly in wheat.

The two major causal parameters in the grain yield response to the water stresses applied are summarized in Figure 9. Photosynthetic area is seen to be much less sensitive to stress than number of grains per spikelet,

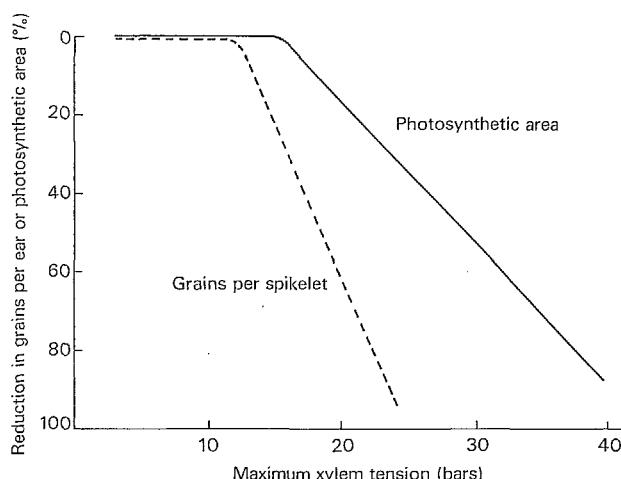


FIG. 9. Major yield parameters and their response to plant water stress. The response of grains per spikelet comes from data restricted to stresses commencing in the period EE — 15 to EE — 5 days (see Fig. 7), while the photosynthetic area response is derived from results at all stages of development tested (see Fig. 5).

which was significantly reduced by stresses not affecting leaf senescence. The former largely determined the source size for the post-EE period and the latter the sink size. That the interaction of source and sink in determining final grain size was encompassed in a single relationship (Fig. 8) was perhaps fortuitous considering the factors ignored in this relationship. These include possible after-effects of stress on photosynthetic rates (Ashton, 1956) and on the capacity of grains to grow

(Aspinall, 1965). Nevertheless, the approach appears to be sound enough to warrant further use and it does give the type of asymptotic response of grain size to increased supply of photosynthate which was suggested by the results of a grain thinning experiment by Bingham (1967).

In applying the above information on plant responses to water stress to the field situation, one is particularly limited by the problem of an appropriate single parameter which adequately describes the water stress experienced by the plant during a drying cycle. As well as the maximum degree of stress, which formed the stress indicator in this study, there is evidence that the duration of stress may be important. Also the part of the plant on which plant water stress is measured should be related to the plant response with which one is concerned. In this respect, xylem tension measured on the stem of the plant may provide a more useful indicator of plant water stress than relative water content of leaves, especially when stress effects on the developing ear may dominate the overall yield response.

ACKNOWLEDGEMENTS

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Résumé

Effet de la contrainte hydrique à diverses étapes du développement sur le rendement du Blé (R. A. Fischer)

Des plants de Blé (var. *Gabo*) cultivés dans des bacs remplis de terre en milieu contrôlé ont été soumis au dessèchement du sol pendant des périodes déterminées, dans chaque cas durant un à quatre jours. Des traitements de la contrainte ont été appliqués à diverses étapes de la période, trois semaines de part et d'autre de l'épiaison. La teneur relative en eau des feuilles et les tensions du xylème ont été mesurées immédiatement avant la réhydratation.

Bien que les conditions initiales, aux limites des cycles de dessèchement du sol, aient été maintenues constantes (taux de transpiration potentielle par bac et teneur du sol en eau), les plants ont d'autant plus desséché le sol qu'ils se développaient, ce qui a provoqué une aggravation de leur contrainte hydrique terminale pour des cycles de dessèchement d'égale durée. Cet effet s'expli-

quait très probablement par une diminution de la sensibilité des stomates à la contrainte hydrique de la plante à mesure que celle-ci vieillissait.

Pour un degré donné de contrainte hydrique maximale de la plante, la production de grain a été le plus réduite lorsque la contrainte a augmenté dix jours environ avant l'épiaison. Dans l'ensemble, les variations de la production de grain en fonction de la contrainte hydrique ont été liées au changement quantitatif de la source et du récepteur des substances assimilées dans la période postérieure à l'épiaison. La source était déterminée en grande partie par les effets de la contrainte hydrique de la plante, indépendamment du stade de développement, sur la sénescence du tissu de photosynthèse au cours de la période effective de contrainte. Le récepteur, qui correspondait surtout au nombre de grains par épillet, était lui-même influencé de façon frappante par le degré de contrainte hydrique de la plante s'élargissant au cours de la période comprise entre quinze et cinq jours avant l'épiaison.

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Changes in internal water status and the gas exchange of leaves in response to ambient evaporative demand

M. J. Aston

Botany Department, School of General Studies,
Australian National University
Canberra (Australia)

INTRODUCTION

Considerable work has been carried out on the various responses of plants to increasing soil moisture deficits. Of particular interest is the gaseous exchange between the leaf and the atmosphere because of the connection of carbon dioxide exchange and photosynthesis with growth, and of transpiration with the water economy of the plant. Such work has been adequately reviewed by Vaadia *et al.* (1961). In this work, decreased carbon dioxide supply and water loss due to decreases in the diffusive capacity of the stomata, are usually cited as the most common effects of increasing soil moisture deficits on gaseous exchange. Stomata close as the result of lowered plant turgor due to low water supply. In most studies provisions have not been made for rigorous environmental control and, although there were indications that the evaporating power of the air was important, insufficient conclusions could be drawn.

Kramer (1959) has indicated that the internal water status of plants is affected by both supply and loss of water. Work on corn by Denmead and Shaw (1962) has shown that transpiration is affected by evaporative demand as well as the level of soil water. Other workers have found that the internal water status of plants, and subsequently transpiration and growth, are affected by evaporative demand even when the roots are adequately supplied with water (Aston, 1963, 1967; Brouwer, 1956; Satoo, 1948). Field observations are commonly made in which growth and production appear to be reduced in adequately watered soils in areas where evaporation is high. Reports of reductions in gaseous transfer from leaves due to water deficits resulting from cold roots are not uncommon.

The aim of the present experiments is to further define and study the problem. Thus carbon dioxide exchange and transpiration have been studied under conditions where the roots were adequately supplied with water and where the evaporative demand was varied.

METHODS

Experiments were carried out on 8-week-old sunflower (*Helianthus annuus* cultivar Advance) and dwarf brown beauty bean (*Phaseolus vulgaris*) plants grown in a fine sandy clay loam under glasshouse conditions. Experiments were carried out in a Plexiglas plant chamber in which the environment was fully controlled. Within the chamber one leaf was enclosed in a smaller chamber in which the environment was also controlled. This arrangement allowed ambient conditions around the whole plant to be varied while measurements were made simultaneously on the whole plant and, under more precisely controlled conditions, on the single leaf. Radiation levels around 0.9 langleys min⁻¹ were supplied with iodine quartz lights above a flowing water filter. Ambient temperatures of 20–25° C were maintained and air in the chambers was stirred at velocities around 45 cm sec⁻¹. Evaporative demand was varied by changing the ambient humidity over the range 20–90 per cent at 25° C. Soil temperature was kept at 20° C. Transpiration was measured with a differential psychrometer (Slatyer and Bierhuizen, 1964a) and carbon dioxide levels were measured with a Grubb Parsons SB2 infra-red gas analyser on differential mode. Relative turgor was measured using a β-ray gauge calibrated against tin foil discs and standard measurements of relative turgor. Leaf temperatures were measured with 40 gauge copper–constantan thermocouples, pressed against the underside of the leaves. Resistances were calculated according to Ohm's law concepts (Bierhuizen and Slatyer, 1964; Slatyer and Bierhuizen, 1964b).

RESULTS

All values relevant to sunflower are expressed on the basis of the total area of the upper and lower surfaces because the leaves are amphistomatous. Bean leaves

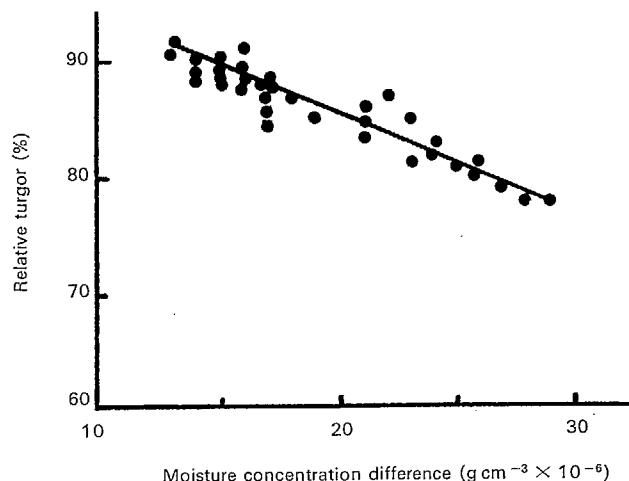


FIG. 1. Relative turgor of sunflower in relation to moisture concentration difference between leaf and air.

are hypostomatus and values are expressed on the area of one side of the leaf only. The various components of resistance were not separated and total resistance includes the parallel resistance to diffusion of the cuticle and the resistance of the surrounding air boundary layer (1.0 sec cm^{-1} for wet blotting paper of the same shape and exposure).

The values of moisture concentration difference between the leaf and the atmosphere, although related to atmospheric humidity, were not always the same for plants exposed to the same conditions. Because water loss is more closely related to these values than to actual ambient values, all data are expressed as a function of the moisture concentration difference between leaf and air.

In both plants relative turgor was found to decrease with increasing moisture concentration difference be-

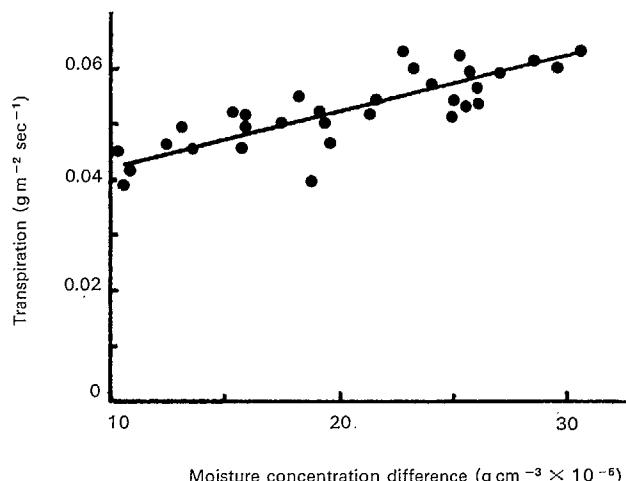


FIG. 3. Transpiration of sunflower in relation to moisture concentration difference between leaf and air.

tween the leaf and air (Figs 1 and 2), even though the roots were adequately supplied with water in the soil. Turgor values varied in the range 92–68 per cent for beans and 91–78 per cent for sunflower, with moisture concentration differences varying between 10 and $29 \times 10^{-6} \text{ g water cm}^{-3}$ of air. The bean plant exhibited wilting symptoms around a relative turgor of 70 per cent. The relationship between relative turgor and leaf-air moisture concentration difference appeared to be linear for the sunflower, while that for the bean was curvilinear.

Interspecific differences in relative turgor response were further exhibited in that both plants, while reacting to the loss of turgor and apparently closing their stomata, behaved in different ways. The sunflower plants showed a linear increase in transpiration (Fig. 3) while

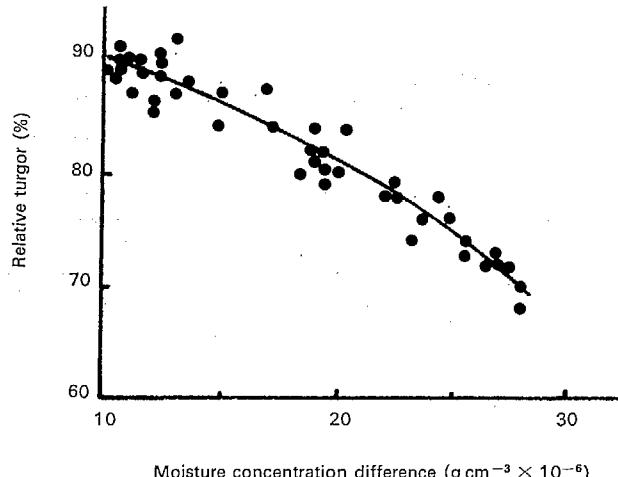


FIG. 2. Relative turgor of beans in relation to moisture concentration difference between leaf and air.

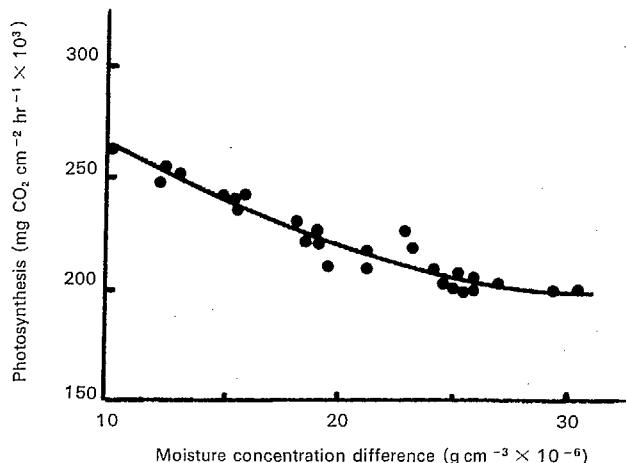


FIG. 4. Photosynthesis of sunflower in relation to moisture concentration difference between leaf and air.

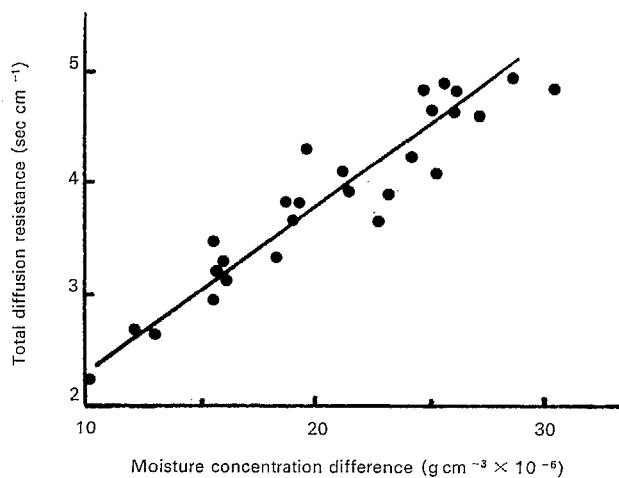


FIG. 5. Total resistance to diffusion of sunflower in relation to moisture concentration difference.

photosynthesis declined (Fig. 4) in a manner which was difficult to interpret as linear or curvilinear. These changes are associated with a linear increase in total resistance to gaseous diffusion with increasing evaporative demand (Fig. 5). On the other hand, both transpiration (Fig. 6) and photosynthesis (Fig. 7) of the beans showed a curvilinear decline with increasing evaporative demand, these changes being associated with a curvilinear increase in total resistance to diffusion (Fig. 8).

During the experiments, further differences between the two species were evident in the transient behaviour of the plants as the ambient humidity was changed. Ambient humidity was decreased, in a stepwise manner, with the change being effected within 5 min. In response, the transpiration value of sunflower shifted directly up

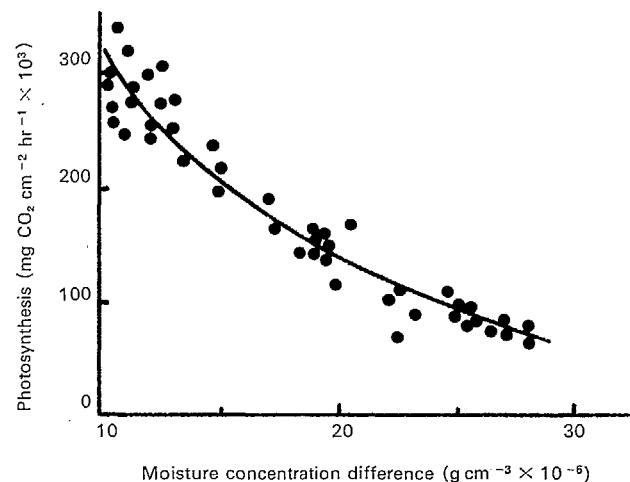


FIG. 7. Photosynthesis of beans in relation to moisture concentration difference between leaf and air.

and the photosynthesis value down to new levels and remained there. Transpiration of the bean plants jumped to a level higher than the original value as the evaporative demand was increased, but fell within 2–3 min to a lower steady state level. Photosynthesis declined at the same time as transpiration declined.

DISCUSSION

These results verify the often observed phenomenon that plants may be subjected to water stress even though there is adequate soil water. This type of result is common where water uptake is restricted by low temperatures, but in this case the phenomenon has occurred at normal root temperatures. Because of its relationship

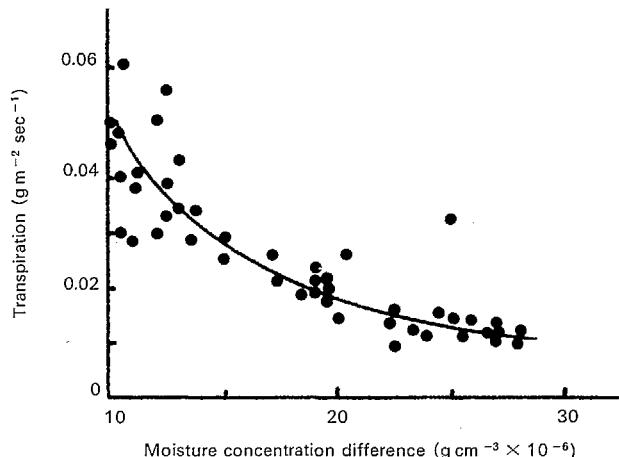


FIG. 6. Transpiration of beans in relation to moisture concentration difference between leaf and air.

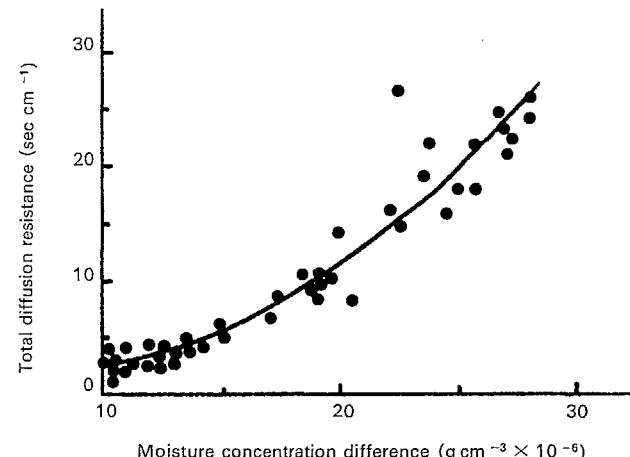


FIG. 8. Total diffusion resistance of beans in relation to moisture concentration difference between leaf and air.

with evaporative demand, it is obvious that the loss of turgor results from an excess of water loss over absorption. Although the plants used were grown in the glasshouse and were not "hardened" before use, it is expected that the results will differ little from those of plants grown under natural conditions. One reason for this expectation is that the glasshouses were located in a dry climate and did not contain many plants, thus high humidity was not obtained. The conditions of evaporative demand which were obtained were similar to those to which a plant might be exposed in the field. However, it is possible that conditions surrounding the experimental plant could be more severe than under field conditions because of its isolation from a crop with consequence of a "clothes-line effect".

In both species, losses of turgor resulted in increased resistances to gaseous diffusion interpreted as stomatal closure. Previous experiments (Aston, 1963, 1967; Slatyer and Bierhuizen, 1964*a*, *b*) have indicated that neither resistance to diffusion through the surrounding boundary layer nor cuticular diffusion resistance vary with ambient humidity. Thus the changes in total resistance to water vapour diffusion may be interpreted as being due to stomatal closure.

In sunflower, the resultant reductions in gaseous diffusion were not sufficient to overcome the natural increase in transpiration due to increased gradients. However, the stomata closed and, consequently, photosynthesis was significantly reduced. Beans are apparently more sensitive plants and, besides reaching lower turgor levels and showing visible signs of wilting, they exhibited much greater reductions in gaseous diffusion. In this case both transpiration and photosynthesis were reduced, even at

high ambient moisture concentration levels. In both plants reductions due to increases in stomatal resistance were less for photosynthesis than for transpiration, an obvious result of the contribution of an additional resistance, the mesophyll resistance, to the total resistance in the case of photosynthesis.

It is interesting to note that each subsequent reduction in ambient humidity further reduced turgor, even at values around 70 per cent relative turgor, indicating that the stomata were apparently still open.

The occurrence of reduced gas exchange at high humidity levels raises the question of data validity and of survival of plants under field conditions. As mentioned previously, it is possible that with a "hardening" pre-treatment beans would not have been as sensitive to evaporative demand.

In conclusion, it is obvious that water stress may develop in plants subjected to high evaporative demand, even though soil water supply is adequate. As a result of such water stress, photosynthesis is reduced and one would expect that growth would also be reduced as a consequence. The reaction of plants appears to differ with the species. While, in the present experiments, evaporative demand has been imposed by lowering ambient humidity, it is likely that high radiation levels and wind might impose similar effects, as indicated by the work of Brouwer (1956) and Satoo (1948). The implication for plants growing in arid climates is such that, even under irrigation, water stress may occur because of climatic conditions; an effect that may be difficult to overcome, except possibly with the aid of a transpiration depressant.

Résumé

Modifications de l'état hydrique interne et échanges gazeux des feuilles sous l'effet de la demande évaporatoire ambiante (M. J. Aston)

Des expériences en milieu contrôlé ont été faites avec des Haricots et des Tournesols pour déterminer l'effet d'une forte demande évaporatrice sur l'état hydrique de la plante et sur la diffusion gazeuse de plantes suffisamment approvisionnées en eau. La demande évaporatoire a été créée en faisant varier l'humidité ambiante entre 20 et 90% à 25 °C.

Dans ces deux végétaux, on a observé des diminutions importantes de la turgescence, suivies d'une augmenta-

tion de la résistance des stomates. Les Haricots se sont révélés plus sensibles que les Tournesols: la diminution de la turgescence et de la diffusion gazeuse y a été plus forte. La réduction de la diffusion de vapeur d'eau chez le Tournesol n'a pas été suffisante pour compenser les accroissements résultant d'une humidité réduite. Néanmoins, des réductions de transpiration chez le Haricot se sont produites chaque fois que l'humidité a diminué. La photosynthèse a diminué à mesure qu'augmentait la demande évaporatoire.

Ces résultats signifient que, sur le terrain, la contrainte hydrique et la croissance réduite peuvent se produire lorsque l'humidité du sol est suffisante.

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Controlled environment studies of the effects of variable atmospheric water stress on photosynthesis, transpiration and water status of *Zea mays* L. and other species

H. D. Barrs
CSIRO Division of Irrigation Research
Griffith, N. S.W. (Australia)

Builders of models of the movement of water through plants (Gradmann, 1928; Honert, 1948; Cowan, 1965) have recognized the existence of 2 principal types of components, driving forces and resistances to flow. Capacitance is probably also important, but is usually ignored since, as in the present study, only steady-state conditions are considered. A basic assumption of these models is that resistance to flow of water in the liquid phase from the roots through the stems to the evaporating sites in the leaves (the surfaces of the mesophyll cells) is constant. This is analogous to the postulate that such movement of water obeys an Ohm's law type of relationship, i.e. current = driving force/resistance, or that any increase in current (transpiration rate) must be matched by a proportionate increase in the driving force (water potential gradient).

Whether such an assumption is warranted has been queried from time to time (Rawlins, 1963; Heath, 1967), and there is in fact a certain amount of experimental evidence which suggests that it may not be wholly correct (Brewig, 1939; Brouwer, 1953, 1954; Macklon and Weatherley, 1965; Tinklin and Weatherley, 1966). Such experimental evidence consists essentially of comparisons of steady-state measurements of the water potential gradient accompanying various levels of flow rate. The work of Weatherley and associates cited above illustrates this approach well. However, there is some doubt as to the accuracy of their estimates of leaf water potential (Barrs and Kramer, 1969), and they confined their attention to 1 species. The problem has, therefore, been reinvestigated in the work reported here, in which the behaviour of a number of species has been compared. The work has been supplemented by simultaneous measurements of net carbon dioxide uptake to see whether any alteration of plant water status which may occur when transpiration rate is varied (by altering atmospheric relative humidity) is accompanied by a change in net photosynthetic rate.

MATERIALS AND METHODS

Plants of maize (*Zea mays* L. cv. N.E.H. 1151), sunflower (*Helianthus annuus* L. cv. Large Grey), cotton (*Gossypium barbadense* L. cv. Pima - S2), pepper (*Capsicum frutescens* L. cv. Californian Wonder) and tomato (*Lycopersicon esculentum* L. cv. Rheinlands Ruhm) were grown in the greenhouse in Hoagland's No. 2 nutrient solution, modified by the replacement of ferric citrate with a chelated form of iron ('Sequestrene 138') giving 10 ppm iron. The same variety of tomato plant, together with a wilty mutant ("*sitiens*") which has a faulty stomatal apparatus such that the stomates show little or no closing tendency (Tal, 1966), was grown in another greenhouse fitted with a mist propagator which maintained a high humidity around the plants and wetted their leaves with a fine spray about once a minute. These conditions were necessary for the successful growth of the wilty mutant.

When about 6-8 weeks old, individual plants were transferred to a CSIRO LBH growth cabinet (Morse and Evans, 1962) in which temperature, humidity and light intensity were controlled. In addition, carbon dioxide concentration was kept approximately constant by ducting the air intake of the cabinet to the outside of the building. A single, attached leaf, or part thereof trimmed where necessary, was enclosed in an assimilation chamber (Lang *et al.*, 1969) and ventilated with the conditioned cabinet air. The transpiration rate of this leaf was measured with an improved differential psychrometer (Barrs and Klepper, 1968) and its photosynthetic rate, with an Onera 80 infra-red carbon-dioxide gas analyser (Barrs, 1968). The temperature of the leaf was monitored with a specially mounted and insulated bead thermistor pressed against the underside of the leaf (Harris and Barrs, 1970). The water potential of this leaf was estimated by taking samples from nearby similar leaves and using Peltier-cooled thermocouple

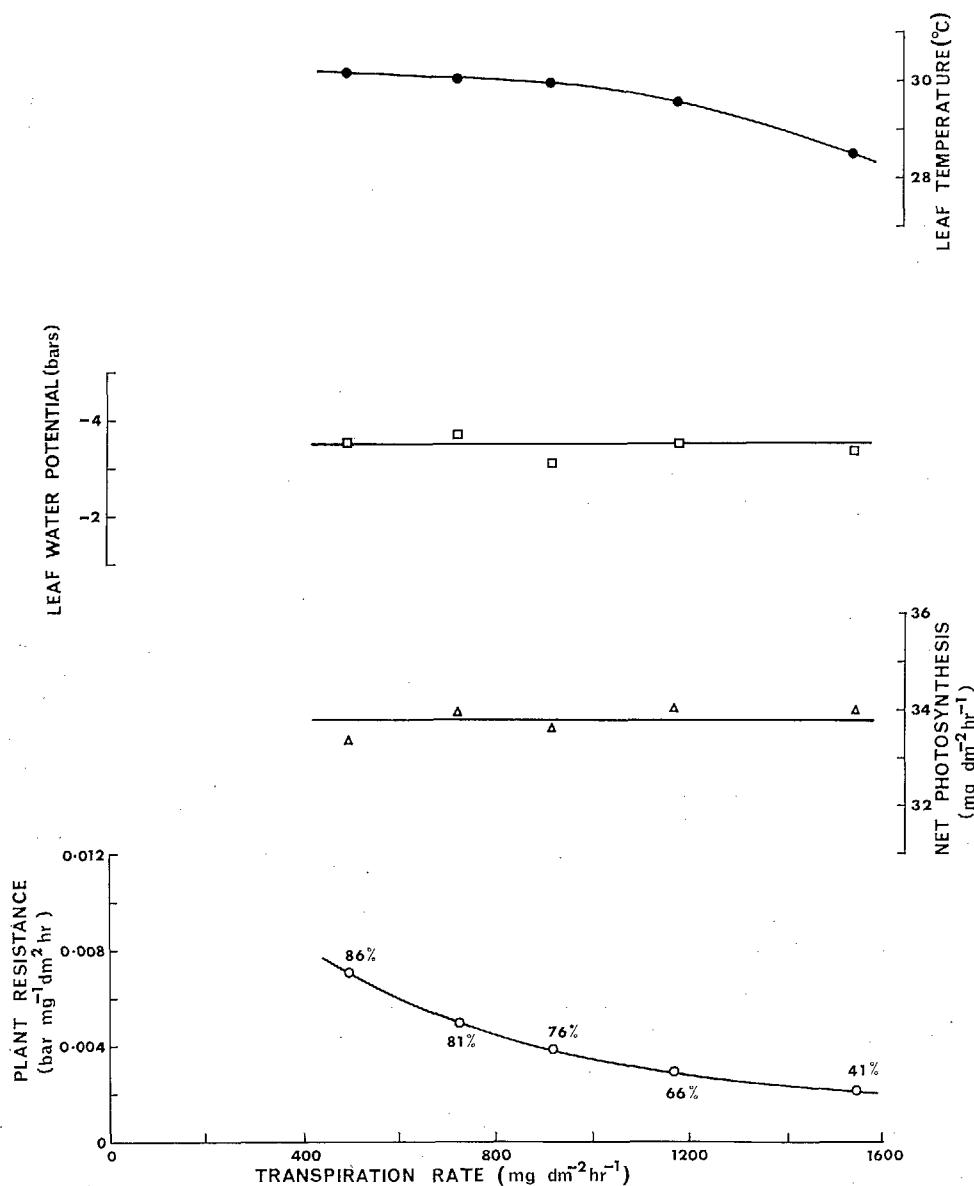


FIG. 1. Relationships between maize leaf temperature, leaf water potential, resistance to water flow and transpiration rate as affected by step-wise changes in relative humidity at 30° C.

psychrometers (Barrs, 1965); except in the case of cotton where the pressure chamber was preferred (Barrs and Klepper, 1968). This indirect approach was necessary because of the destructive nature of available techniques for measuring leaf water potential. However, it gives satisfactory estimates of the water potential of the leaf in the assimilation chamber (Barrs and Klepper, 1968). The leaf in the assimilation chamber received light at an intensity of 0.24 cal cm⁻² min⁻¹ measured with a Kipp

solarimeter. Following Gardner and Niemann (1964), the effective water potential of the nutrient solution was assumed to be zero (its actual water potential was -0.6 bar). Resistance to flow in the liquid phase through the plant was, therefore, calculated by dividing leaf water potential (bars) by transpiration rate (mg dm⁻² hr⁻¹), giving the water potential difference in bars required to move 1 mg of water/dm² of leaf surface per hour through the plant.

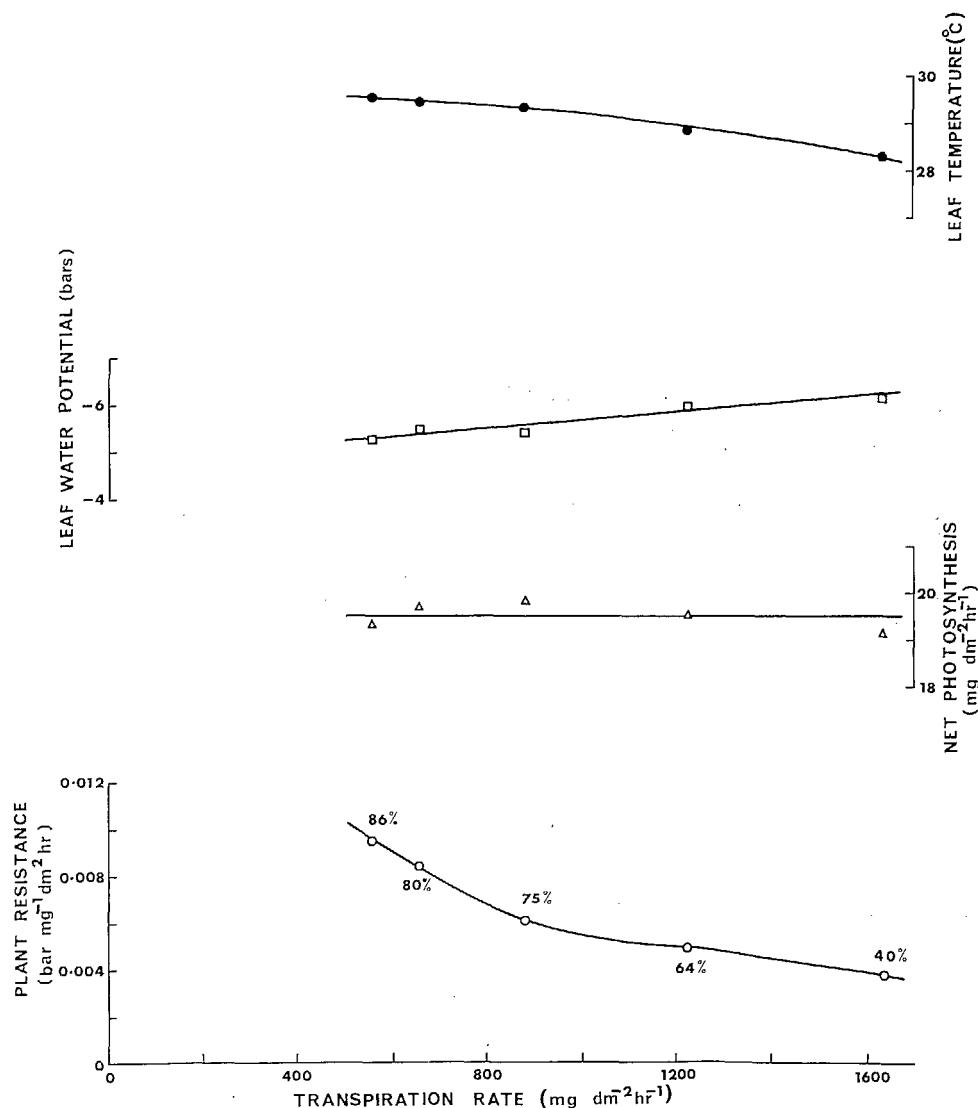


FIG. 2. Relationships between tomato leaf temperature, leaf water potential, resistance to water flow and transpiration rates as affected by step-wise changes in relative humidity at 30° C.

RESULTS AND DISCUSSION

Figure 1 shows the behaviour of a maize plant as the relative humidity around it was lowered step-wise from 86 to 41 per cent at a constant air temperature of 30° C. The most striking observation was the constancy of leaf water potential, approximately -3.5 bars, despite the fact that transpiration rate increased more than 300 per cent. This suggests that the water status of the leaf was completely unaffected by the drastic increase in the aerial evaporative demand. Provided these measurements are valid, it is apparent that there was a trebling

of the liquid water flux, with no increase in the driving force (leaf water potential). This could only be brought about by a concomitant reduction in the resistance to liquid flow rate through the plant. Such an effect is illustrated by the computed resistance curve, which is shown to decline progressively as the transpiration rate increases. In fact, resistance seemed to decline in such a way as to maintain leaf water potential constant. Care is, therefore, needed in applying an Ohm's law analogue to the movement of liquid water through the maize plant, since there seems to be no relationship, at least under these experimental conditions, between leaf

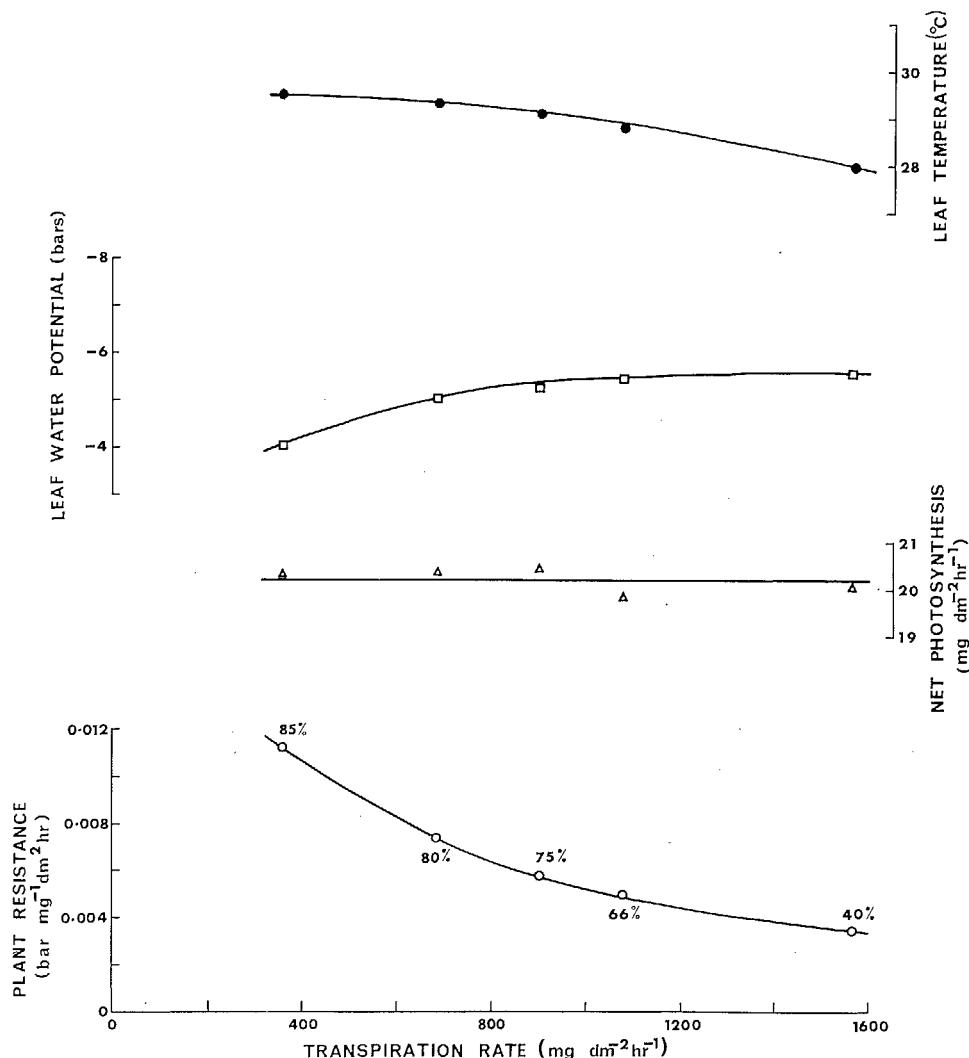


FIG. 3. Relationships between tomato leaf temperature, leaf water potential, resistance to water flow and transpiration rate as affected by step-wise changes in relative humidity at 30° C. This plant was grown in continuous high humidity under a mist propagator.

water potential and rate of flow. Rather, the relationship that does appear to be followed is:

$$\text{plant liquid phase resistance} = \frac{\text{a constant}}{\text{flow rate}} \quad (1)$$

The leaf temperature data show that leaf temperature declined somewhat as transpiration increased. This may be expected to affect transpiration rates, causing them to be a little lower (especially at the lower humidities) than would have been the case had leaf temperature remained constant, because of the associated decline in the magnitude of the saturation vapour pressure within the leaf. This, in turn, will be reflected in the calculated

resistance curve, which perhaps would have fallen to a slightly lower value than shown. However, the main conclusion of the argument as summarized in equation (1) would not have been affected. The net photosynthesis rate remained constant throughout the experiment and, therefore, was not affected by the transition from high to low relative humidity. Generally, similar results were obtained for sunflower.

Results for tomato are shown in Figure 2. The most important difference between this and the two preceding experiments was the failure of leaf water potential to remain constant; instead there was a trend for water potential to decline as relative humidity was lowered.

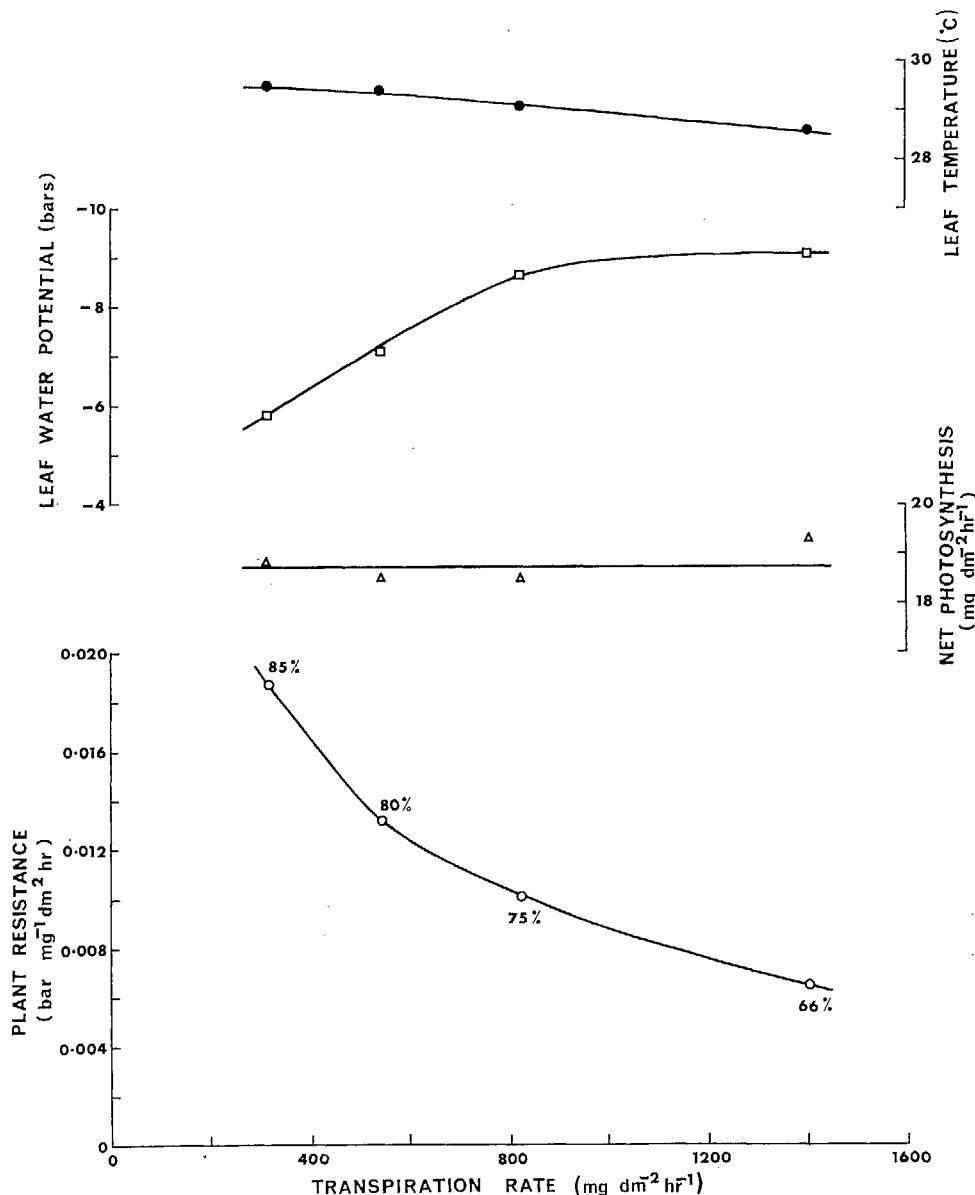


FIG. 4. Relationships between "wilt mutant" tomato leaf temperature, leaf water potential, resistance to flow and transpiration rate as affected by step-wise changes in relative humidity at 30° C. This plant was grown in continuous high humidity under a mist propagator.

In this species there was then, in contrast to maize and sunflower, a tendency towards an Ohm's law type of behaviour, i.e. for the driving force to increase with the increase in flow rate. However, the effect was small and, as the resistance curve shows, a considerable reduction of resistance occurred as flow rates increased; this was undoubtedly important in preventing leaf water potential from falling to even lower values. Despite the slight increase in leaf water stress, there was no obvious

depression of net photosynthetic rate. As with maize, leaf temperature declined with increase in transpiration rate, although the effect was slightly smaller. Transpiration rates may have been depressed slightly in consequence, as noted previously, especially at the lower humidities.

Figure 3 shows results for a second tomato plant which was raised in a greenhouse fitted with a mist propagator and, therefore, continually exposed to a high humidity

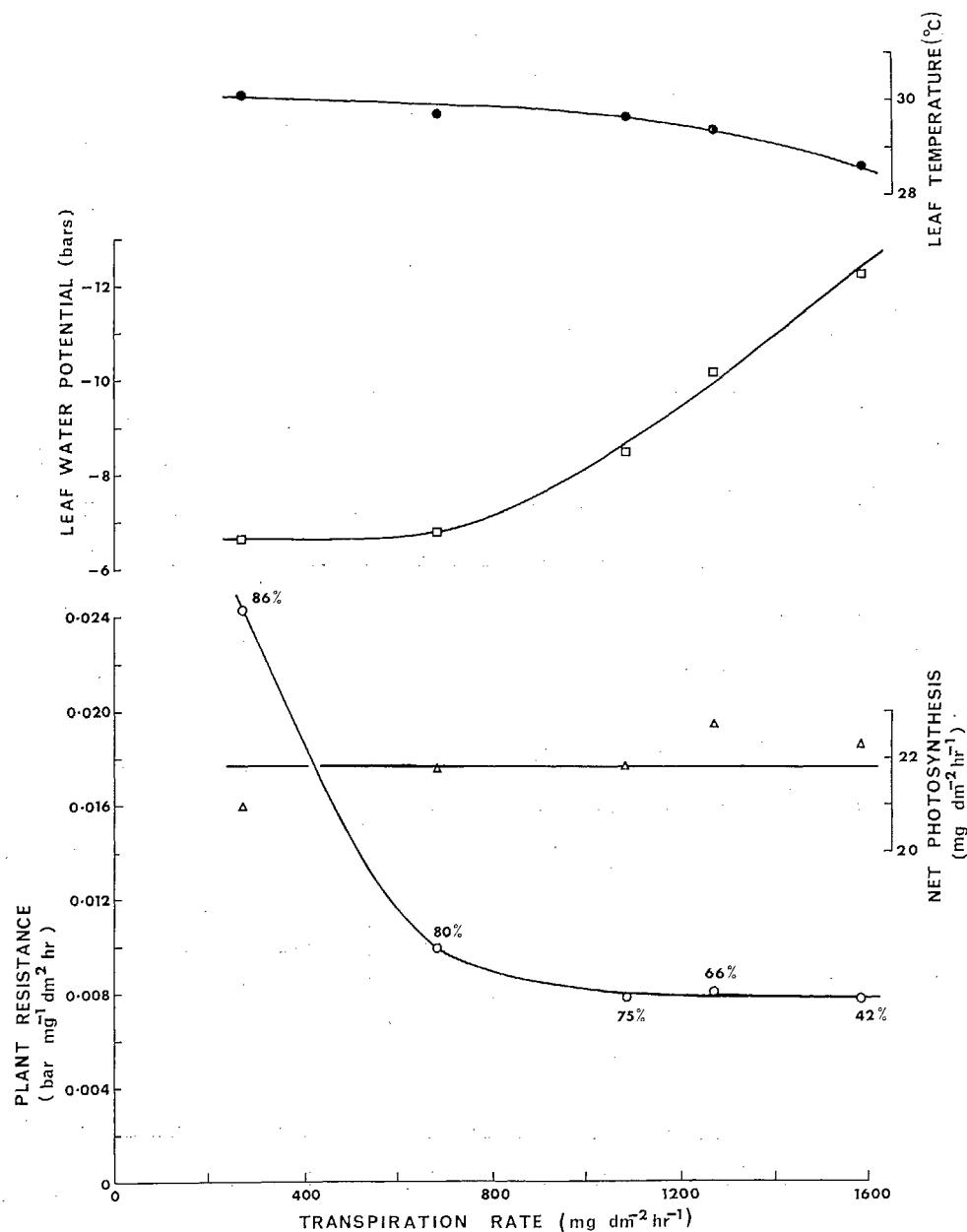


FIG. 5. Relationships between cotton leaf temperature, leaf water potential resistance to flow and transpiration rate as affected by step-wise changes in relative humidity at 30° C.

throughout its growth. This plant served as a control for an experiment (to be described immediately after this one) with the wilty mutant *sitiens*. It was thought of interest to compare the performance of the 2 normal tomato plants, since the one grown in the mist propagator had not, until the experiment, ever experienced high transpiration rates. Despite this, as Figure 3 shows, the plant grown in the mist propagator responded like the plant grown in the standard greenhouse as humidity

was lowered. Again there was a definite, though small, tendency for leaf water potential to fall, but the overall level of leaf water potential was, if anything, slightly higher than in the preceding experiment, even though transpiration rates were very comparable throughout. Hence this plant experienced no more water stress than the normal greenhouse plant. This is borne out by the continued constancy and same general level of its photosynthetic rate. The two resistance curves are similar

and support the general, perhaps rather surprising, conclusion that growth under high humidity in no way impaired the ability of the tomato plant to withstand the effects of rather sudden exposure to low humidity.

The previous experiment served as a control for a similar experiment with the wilty mutant tomato *sitiens* which was also (and, in this case, necessarily) grown under a mist propagator. As Figure 4 shows, the range of humidities to which the mutant could be exposed was restricted, since irreversible dehydration occurred at 40 per cent relative humidity. The plant provides several interesting points of comparison with the normal parent (compare with Fig. 3). Leaf water potentials were generally lower in the mutant. This could perhaps be expected at the lowest humidity tested (66 per cent), where abnormally wide stomatal apertures may have caused the abnormally high transpiration rate observed. However, the low water potential at the highest humidity (85 per cent), where the transpiration rate was very similar to that of the control, cannot be explained as easily in this way. An alternative explanation which fits all the data is that the mutant offers a higher resistance to flow of liquid water than does the normal parent over the whole range of conditions tested. This suggests that the "wiltiness" observed in the mutant may, in part, be due to abnormally high resistance to liquid flow, as well as to the very imperfect stomatal control of transpiration already demonstrated (Tal, 1966). The leaf water potential data suggest that, initially at least, as humidity is lowered, the mutant more nearly follows an Ohm's law analogue. Despite the (for tomato) fairly high water stress finally encountered, there was no tendency for net photosynthetic rate to fall.

The next species investigated was cotton (Fig. 5). The plant was interesting since its behaviour at the lowest humidities was the closest approximation to an Ohm's law analogue found. This is apparent from the steep, virtually linear fall of leaf water potential as relative humidity was lowered below 75 per cent and also from the virtual constancy of resistance to liquid flow at humidities below this value. However, initially, there was considerable departure from an Ohm's law analogue

and a very considerable lowering of resistance when humidity was changed from 86 to 80 per cent. Despite the considerable final water stress (-12.3 bars), there was no overall trend for any reduction in net photosynthesis. Generally similar results were obtained for pepper.

GENERAL DISCUSSION

A comparison of all the species studied shows that there is considerable variation in their behaviour and that there is no overall pattern analogous to an Ohm's law relationship. Indeed, a complete departure from such a relationship is shown for maize and sunflower, where flow rates may vary widely without apparent change in leaf water potential. These two species, therefore, behaved similarly to castor bean (Macklon and Weatherley, 1965) over a similar range of humidities. Later work (Tinklin and Weatherley, 1966) showed castor bean leaf water potential did in fact rise at very high humidities (100 per cent and values only just below this). Such high humidities could not be attained in the LBH cabinet available, hence this possibility could not be examined for the species studied in this paper. If such behaviour is general, then resistance may not continue to rise as sharply as extrapolation of the resistance curves at higher humidities would suggest and the prediction (Janes, 1970) that resistance (in pepper) approaches infinity at very low flow rates may not be entirely correct. Whilst maize and sunflower exhibited constancy of leaf water potential as humidity was lowered, the remaining species examined may, perhaps, be arranged in a series showing increasing approximation to Ohm's law behaviour *viz.* normal tomato, pepper, mutant tomato, cotton.

One feature which was common to all the species studied was the occurrence of a decline in resistance to flow as flow rate increased, although the extent and importance of this varied from species to species. This is illustrated in Table 1, where leaf water potentials have been calculated assuming that an Ohm's law relation-

TABLE 1. Comparison of observed (ψ obs.) and calculated (ψ calc.) leaf water potentials in bars. ψ calculated was obtained by multiplying the initial (highest) resistance to flow by the appropriate transpiration rate. The difference between the potentials measure the magnitude of stress avoidance due to reduction of flow resistance (see text)

Maize ¹		Sunflower ¹		Cotton ¹		Normal tomato ¹		Normal tomato ²		Mutant tomato ^{2,3}		Pepper ¹	
ψ obs.	ψ calc.	ψ obs.	ψ calc.	ψ obs.	ψ calc.	ψ obs.	ψ calc.	ψ obs.	ψ calc.	ψ obs.	ψ calc.	ψ obs.	ψ calc.
-3.5	—	-5.6	—	-6.6	—	-5.3	—	-4.0	—	-5.8	—	-3.5	—
-3.7	-5.1	-5.8	-18.6	-6.8	-16.8	-5.5	-6.2	-5.0	-7.7	-7.1	-10.0	-4.2	-7.1
-3.1	-6.5	-5.4	-30.4	-8.5	-26.7	-5.4	-8.4	-5.2	-10.2	-8.7	-15.6	-4.5	-5.3
-3.5	-8.3	-5.0	-33.6	-10.2	-31.2	-6.0	-11.7	-5.5	-12.1	-9.1	-26.2	-3.3	-9.7
-3.4	-11.0	-5.2	-39.7	-12.3	-38.9	-6.2	-15.6	-5.6	-17.6	—	—	-6.4	-12.5

1. Grown in standard greenhouse. 2. Grown in greenhouse under mist propagator.

3. Wilty mutant, see text.

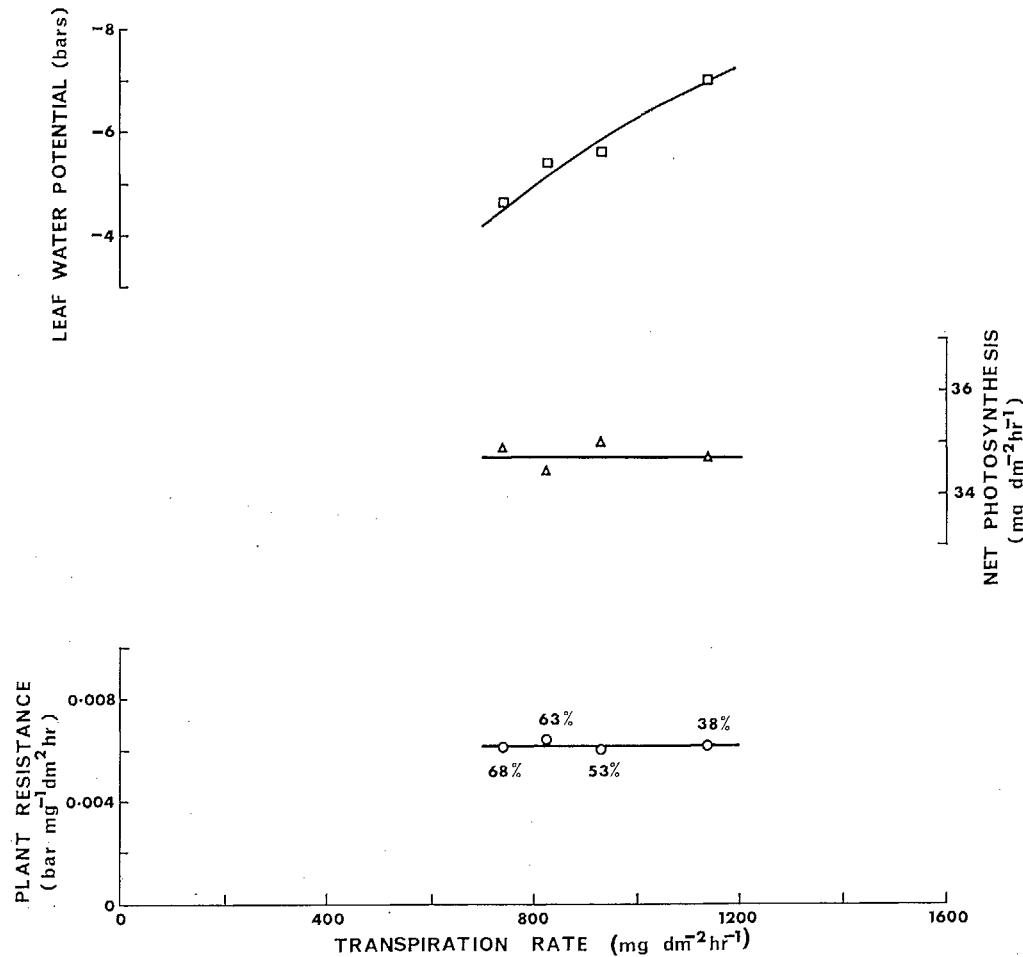


FIG. 6. Relationships between maize leaf water potential, resistance to flow and transpiration rate as affected by step-wise changes in relative humidity at 22° C.

ship does hold, and that resistance remained constant at the highest value observed. Comparison of potentials calculated in this way with those actually observed affords a measure of the importance of the rate of fall of resistance with fall in humidity in preventing leaf water potentials from falling to excessively low values. Such reduction in resistance was least important in maize (Table 1). This was probably because the absolute level of resistance at the highest humidity was already the lowest observed in the species examined. On the other hand, sunflower, which resembled maize in maintaining a constant leaf water potential, had the highest initial resistance to flow and, therefore, showed the largest decline in resistance as flow rate increased. Despite this, sunflower was not able to maintain as low a resistance as maize; this is why the constant level of leaf water potential in sunflower was somewhat lower than that in maize (-5.4 and -3.5 bars, respectively).

The importance of this ability to lower resistance to flow in sunflower is seen from Table 1, which shows that the final leaf water potential would otherwise have fallen to as low as -39.7 bars, a condition of extreme water stress, especially when compared with the low final stress of -5.2 bars actually observed. It should be borne in mind that this experiment was carried out at 22° C, rather than the standard 30° C used for the other experiments, and it is possible that a small part of the high resistance to flow observed in sunflower could have been due to this use of a lower temperature.

The most intriguing question that the present results raise is just how and where the reductions in plant resistance to flow which have been shown to occur are brought about. Tinklin and Weatherley (1966) demonstrated that the largest resistance to liquid flow occurs in the root system of the castor bean plant. If this is universally true, then it is possible that the effect is

principally brought about by a reduction in resistance to flow through the roots. Barrs and Klepper (1968) have shown that resistance to flow through roots may be increased by transferring plants grown in nutrient solution to distilled water for several days. It was, therefore, of interest to see how far such pretreatment would modify the response of a maize plant to step-wise decrements of relative humidity.

A preliminary result is shown in Figure 6. Comparison with Figure 1 shows 2 important major differences. Firstly, plant resistance remained constant, and secondly, presumably as a consequence, leaf water potential decreased linearly with increase in transpiration. It seems, then, that the pretreatment converted maize from being a plant to which an Ohm's law analogue was completely inapplicable, to one to which such an analogue was completely applicable. It is tempting to suggest that this was due to loss of the ability of the root to lower its resistance with increase in flow rate. Certainly resistance to flow was considerably higher than in the normal plant at comparable transpiration rates. However, more work is necessary to place this speculation on a sound experimental basis.

A further difficulty is that this experiment was carried out at 22° C instead of 30° C and plant resistance to liquid flow may have been modified by the lower temperature, although this is unlikely to be the entire explanation of the result. That the leaves were functioning normally is shown by the rate of net photosynthesis, which was in fact slightly higher than that of the untreated maize plant. Despite the decline in leaf water potential of the pretreated plant (to -7 bars at the lowest humidity), there was no evidence of any accompanying decline in net photosynthesis.

A further point of enquiry is whether the ability to reduce resistance to flow as transpiration rate increases serves any useful purpose. In the case of plants rooted in nutrient solution this does seem to be the case in view of the calculations of stress avoidance achieved

by this means which are shown in Table 1. However, the situation with plants rooted in soil is not so clear. If, as Tinklin and Weatherley (1968) maintain, there is considerable drying of wet soil immediately adjacent to roots as a result of moderately rapid transpiration, or, as they put it, there is a dominant rhizosphere resistance to the flow of water through the plant-soil system, then no amount of reduction in plant resistance to liquid flow will avail the plant. If, however, as Newman (1969) maintains, the rhizosphere resistance only becomes appreciable when the soil is near or beyond the wilting point, then the possibility remains that this apparently widespread ability to decrease resistance to flow is an important means by which plant may combat aerial water stress.

A final feature of all the experiments was the observation that net photosynthetic rate was not reduced as relative humidity was lowered. This is perhaps understandable for the maize and sunflower plants (Figs 1 and 2), where leaf water potentials remained constant, and it seems reasonable to suggest that stomatal apertures may, therefore, have remained similarly largely unaffected. Such constancy of stomatal aperture has, in fact, been demonstrated for castor bean (Tinklin and Weatherley, 1966) under similar conditions. As already noted, this species resembled sunflower and maize in maintaining leaf water potential constant in the face of reductions in relative humidity. The constancy of net photosynthesis in the other species examined here is perhaps surprising; apparently stomatal apertures must have remained constant, or nearly so, in these also. Presumably this was because the final levels of water stress reached were insufficient to cause any significant stomatal closure. This is perhaps reasonable for pepper (-6.4 bars) and normal tomato (-5.6 and -6.1 bars), but is unexpected for cotton, where the final leaf water potential fell as low as -12.3 bars. It may be that the critical level of leaf water potential for the onset of stomatal closure is abnormally low in this species.

Résumé

Étude en milieu contrôlé des effets des variations de l'humidité atmosphérique sur la photosynthèse, la transpiration et l'état hydrique de Zea mays L. et d'autres espèces (H. D. Barrs)

Lorsqu'on a soumis un plant de Maïs, qui poussait dans une solution nutritive, à des réductions progressives de l'humidité relative dans un environnement contrôlé, on a trouvé que le potentiel hydrique des feuilles se maintenait à une valeur constante élevée malgré la forte augmentation de la transpiration qui l'accompagnait. Ce fait a conduit à supposer que la résistance au flux de l'eau liquide à travers la plante a dû baisser en même

temps qu'augmentait la transpiration afin que se maintienne la constance observée du potentiel hydrique des feuilles. On a comparé le comportement du Tournesol, de la Tomate, du Poivrier et du Cotonnier dans des conditions identiques. Seul le Tournesol a montré un potentiel hydrique constant. Dans les autres espèces, le potentiel hydrique a baissé avec l'humidité relative. La baisse était faible pour la Tomate, un peu plus grande pour le Poivrier et maximale pour le Cotonnier. Un mutant flétri de Tomate a montré également une grande baisse du potentiel hydrique des feuilles.

Toutes les plantes ont accusé une baisse de la résistance du flux liquide avec l'augmentation de la transpi-

ration. La grandeur de cet effet a varié d'une espèce à l'autre. Elle était surtout élevée pour le Tournesol et le Cotonnier, qui auraient autrement souffert du manque de l'eau à des faibles taux d'humidité, et petite pour le Maïs, remarquable, en général, par sa faible résistance au flux liquide. Les résultats ont donc montré que, dans aucune plante, le mouvement de l'eau n'a obéi en simple analogie à la loi d'Ohm du mouvement de l'eau; toutes les plantes se sont écartées d'un tel modèle jusqu'à un certain point. Cependant, un plant de Maïs qu'on a transféré pendant plusieurs jours d'une solution nutritive dans de l'eau distillée a, par la suite, obéi de près à ce modèle (c'est-à-dire que l'augmentation de la transpiration était accompagnée d'une augmentation proportionnelle du potentiel hydrique des feuilles, alors que la résistance au flux liquide restait constante). Cette réaction était compatible avec le fait que les changements

de résistance au flux liquide s'effectuent principalement dans les racines.

Toutes les plantes ont montré une absence de liaison entre l'activité photosynthétique et le niveau de l'humidité atmosphérique. Cela suggère que l'ouverture des stomates était, la plupart du temps, indépendante de l'humidité relative et qu'il se manifestait une baisse modérée du potentiel hydrique des feuilles. On a considéré comme importantes les réductions indiquées ci-dessus de la résistance au flux liquide, responsable de ces réactions. La comparaison de l'efficience de l'usage de l'eau a montré que le Maïs est extrêmement efficace parce que son activité photosynthétique nette était plus haute que celle des autres espèces. La Tomate a été l'espèce la moins efficace à cause du taux relativement bas de photosynthèse et de sa transpiration élevée.

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Aeration of roots in relation to molecular oxygen transport in plants

B. B. Vartapetian

K. A. Timiriazev Institute of Plant Physiology
Academy of Sciences of the U.S.S.R.
Moscow (U.S.S.R.)

The anatomical and morphological characteristics of higher plants facilitate gaseous exchange of their tissues with the external atmosphere. For this reason the aerobic type of metabolism is usually readily maintained in plant cells. Not infrequently, however, it proves very difficult for atmospheric oxygen to gain access to the plant or some part of it. Such a situation may arise, for instance, in roots under natural conditions or as a result of human intervention. This causes sizeable losses to farming for, being organs of mineral nutrition for the plant, roots need a constant inflow of molecular oxygen from the outside if their normal metabolism and function are to be maintained.

A danger of anaerobiosis arises, for example, in fields subjected to regular flooding for irrigation purposes. As a result, stores of oxygen are rapidly depleted because of the respiration of the roots themselves and of soil microorganisms. Large amounts of carbon dioxide, methane and other gases accumulate, thus making oxygen respiration even more difficult. With flooding, anaerobic conditions may persist not only while the air spaces remain filled with water, but also some time thereafter, particularly in poorly structured soils which become more compact and form a surface crust which is relatively difficult for the air to penetrate. The extensive and increasing use of irrigation in many countries makes it necessary to pay increasing attention to the problem of oxygen regimen of roots of various agricultural crops.

In northern regions, winter and perennial crops sometimes also experience a marked root hypoxia because of the formation, in winter months, of a continuous ice crust on the soil surface through which very little oxygen and carbon dioxide can diffuse. Certain difficulties as regards oxygen supply from the atmosphere must also be experienced by plants growing on marshy or very densely packed soils. Finally, anaerobiosis can occur in the root zone of plants grown without soil on nutrient solutions (hydroponics). This method has been increas-

ingly practised in recent years not only for experimental, but also for practical purposes.

Whatever the cause of anaerobiosis, the 2 essential factors are the gas composition of the medium in the root zone and the actual root resistance to anaerobiosis, i.e. the ability of the roots to continue growth and assimilation of nutrients when the oxygen content is minimal.

In view of the above, the possibility of maintaining a normal oxygen regimen in root tissues by transporting molecular oxygen from above-ground green organs to roots of the plant is of special interest not only from theoretical considerations but also from its great practical importance, intimately associated with the practices of cultivation of agricultural plants on hard and marshy soils and with the practical aspects of irrigation and hydroponics.

Clearly, a solution to these problems would promote the use of correct farming practices for irrigated crops, e.g. it would permit the determination of the maximum permissible duration of flooding and indicate any need for the surface crust to be removed by hoeing, etc.

There are conflicting data in the literature concerning the possibility of atmospheric oxygen transport to the roots through above-ground organs and the response of roots of various plants to anaerobiosis (Brown, 1947; Evans and Ebert, 1960; Soldatenkov and Chirkova, 1963; Kursanov, 1966; Jensen and Kirkham, 1963; Durell, 1941; Erickson, 1946; Dubinina, 1961). Moreover, these data are often derived from indirect observations.

In order to clarify the problem, polarographic techniques have been used in an attempt to detect intra-tissue oxygen transport in various plant species, considering this process as a possible means of satisfying the oxygen requirements of roots in an anaerobic environment. Concurrently, with the aid of electron microscopy, the changes occurring in the cell ultrathin

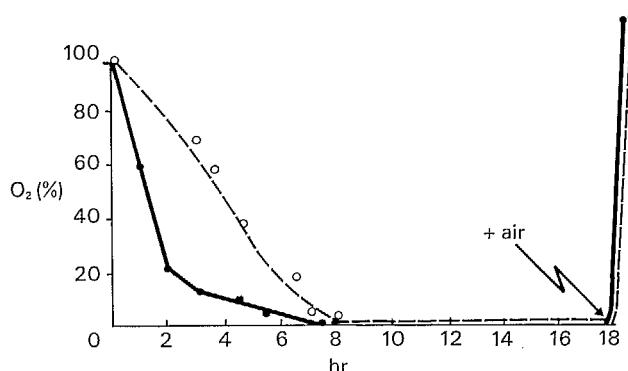


FIG. 1. Time-course of oxygen uptake by roots of 30-day-old plants of *Cucurbito pepo*. Solid line represents readings of the electrode placed inside the root. Dotted line shows readings of the electrode in the solution.

structure under the effect of anaerobiosis have been studied. Bean, tomato, pumpkin and rice plants have been used in these experiments. This paper is concerned solely with the results of studies on pumpkin (*Cucurbito pepo*) and rice (*Oryza sativa*) plants, which may be considered to represent 2 plant types which react in opposite fashions to oxygen deficiency.

To study the possibility of oxygen transport from the above-ground parts, plant roots were placed in a nutrient solution (3 l), and platinum electrodes were used to measure oxygen in the rhizosphere. One of the electrodes measured the oxygen content in the solution and the other, in the tissues of the root itself.

Figure 1 presents results of experiments with 30-day-old pumpkin. The ordinate here, as in Figures 3-5, represents the relative oxygen content in the solution, the oxygen content after a 30-min bubbling of oxygen through the solution being taken as 100 per cent, and that after a 30-min bubbling of gaseous nitrogen as O₂. The abscissa represents the time in hours that had elapsed since the immersion of roots into the aerated solution.

It will be seen from Figure 1 that oxygen was continuously declining in the rhizosphere from the moment the roots were placed into the solution, so that after 8 hr all of the oxygen had been used up and no signs of its being supplied from the above-ground organs were observed. It was only after a repeated bubbling of air through the solution that the O₂ content was found to rise steeply.

Of immediate practical interest are the results of observations of adult (50-day-old) pumpkin plants whose roots were placed in 3-l pots. To register oxygen in the rhizosphere, one platinum electrode was placed inside the root mass, another was fixed at the outer root surface, and a third remained in the solution some distance away from the roots. As soon as 30 min after cessation of aeration, practically all the oxygen inside the root mass had been used up, although some 80 per cent

of the initial amount of oxygen still remained in the solution (Fig. 2). It can also be seen from Figure 2 that a short-term bubbling of air through this solution promptly restored the oxygen concentration.

This pattern was even more strikingly demonstrated in experiments on oxygen uptake by roots of adult pumpkin plants placed in a 6-l vegetative pot (Fig. 3). A different picture was observed if the solution was continuously agitated. In this case the differences in oxygen content between the various parts of the rhizosphere disappeared almost completely.

Thus, in stationary nutrient solutions, interruptions of root aeration lasting more than 30-60 min must lead to an appreciable depression of aerobic metabolism of root cells in those plants in which oxygen transport from the above-ground parts is slight. At the same time, the results show well how far removed are the degrees of root aeration generally adopted when growing plants on nutrient solutions from the optimal values of oxygen supply to the roots. This circumstance should be borne in mind when growing plants on nutrient solutions and in developing optimum oxygen regimens in hydroponics.

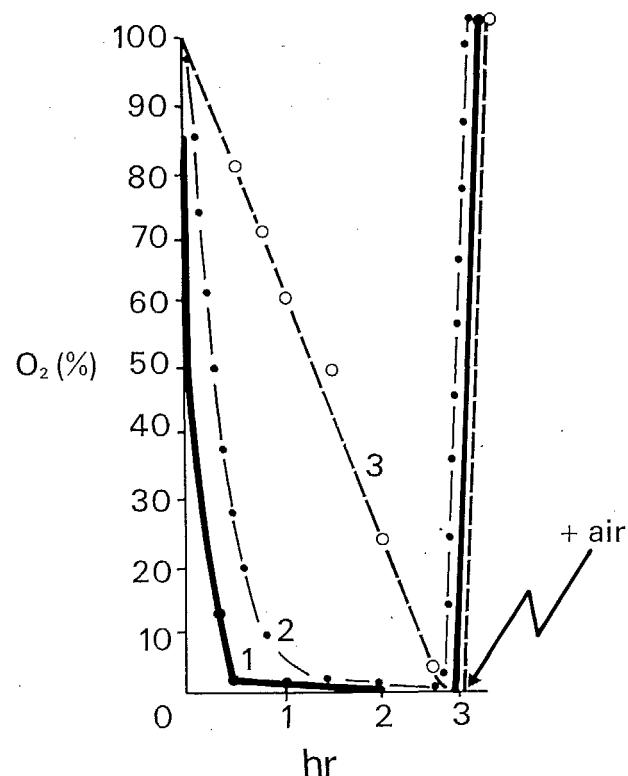


FIG. 2. Distributional pattern of oxygen in the rhizosphere of *Cucurbito pepo*.

1. Electrode placed inside the root mass.
2. Electrode placed in the solution in immediate proximity of roots.
3. Electrode placed in the solution some distance away from roots.

Returning now to the possibility of oxygen transport in the plant itself, it should be noted that, using direct oxygen measurements, we have failed to detect any oxygen transport in the roots and in the surrounding solution in pumpkin plants. Nevertheless, the above evidence does not rule out the possibility of other means of O_2 transport in plant tissues. Thus, it may be supposed that oxygen is actively transported, being incorporated into some labile compounds not registered polarographically. Also, one of the reasons for our failure to detect oxygen could be the fact that it moves in the plant from above downwards at a high speed but in such low concentrations that it is not detectable polarographically. However, if the contribution of this means of oxygen transport is sufficient to meet, even only partly, the respiratory requirements of the roots, then one should observe enhanced O_2 uptake by the roots from the nutrient solution.

To test the validity of this assumption, the above-ground parts were removed from 1 of 2 plants of the same age and size, and the roots were placed in the nutrient solution. The kinetics of O_2 uptake by the isolated roots from the solution was measured polarographically. In parallel experiments, similar measurements were made of oxygen absorption by roots of the second plant with the above-ground organs retained. As can be seen from Figure 4, removal of the above-

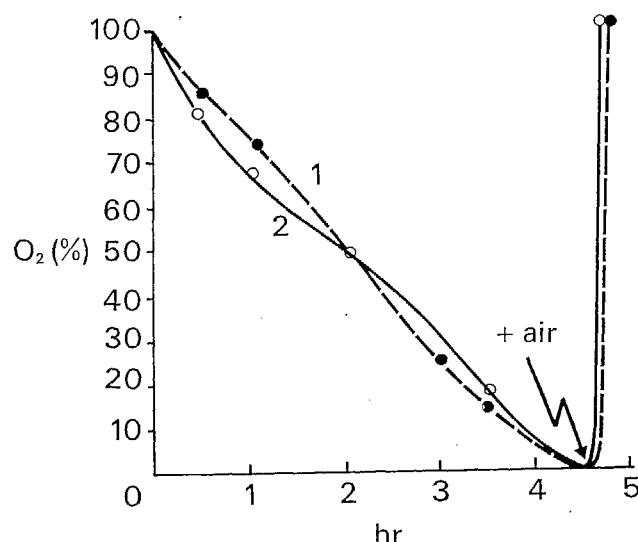


FIG. 4. Time-course of oxygen uptake by isolated roots (1) and attached roots (2).

ground parts had no substantial effect on the time-course of oxygen uptake by the plant.

These results strongly suggest that, in the overall oxygen balance of the roots of the plants studied, the proportion of oxygen supplied from the above-ground parts was insignificant. However, the above results have not yet provided sufficient grounds for excluding completely the possibility of some, if only slight, oxygen transport to the roots which might be substantial from the physiological point of view. For that reason, attempts have been made to explore this possibility by studying the ultrastructure of root cells under conditions when the direct oxygen access to the rhizosphere from the external atmosphere was excluded.

These experiments were staged with 45-day-old pumpkin plants, using the following 3 treatments: (a) the Knop solution, into which the roots were immersed, was continuously aerated by bubbling air through it; (b) oxygen-free nitrogen was continuously bubbled through an identical solution; and (c) the solution with roots was not aerated, so that a strong oxygen deficiency developed and carbon dioxide accumulated within several hours. To rule out the possibility of the plants being poisoned with carbon dioxide, the solution was renewed every 4–6 hr under conditions of continuing anaerobiosis, with removal of oxygen by preliminary bubbling of nitrogen through the solution. In the anaerobic treatments, the surface of the nutrient solution was carefully isolated from the ambient air. Solution temperature was maintained at about 27°C.

After 24 hr, the tips of the pumpkin roots in all the 3 treatments were fixed, and ultrathin sections of the meristems were examined under the electron microscope (Fig. 5).

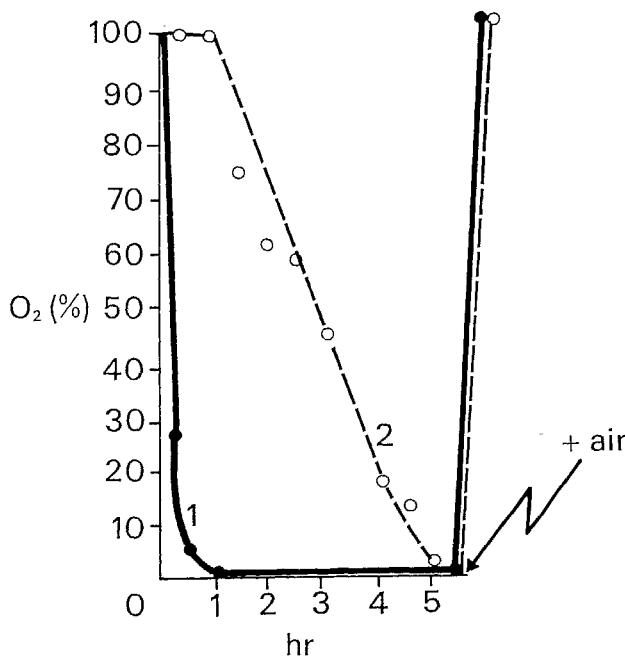


FIG. 3. Distributional pattern of oxygen in the rhizosphere of *Cucurbito pepo*.

1. Electrode placed inside the root mass.
2. Electrode placed in the solution some distance away from roots.

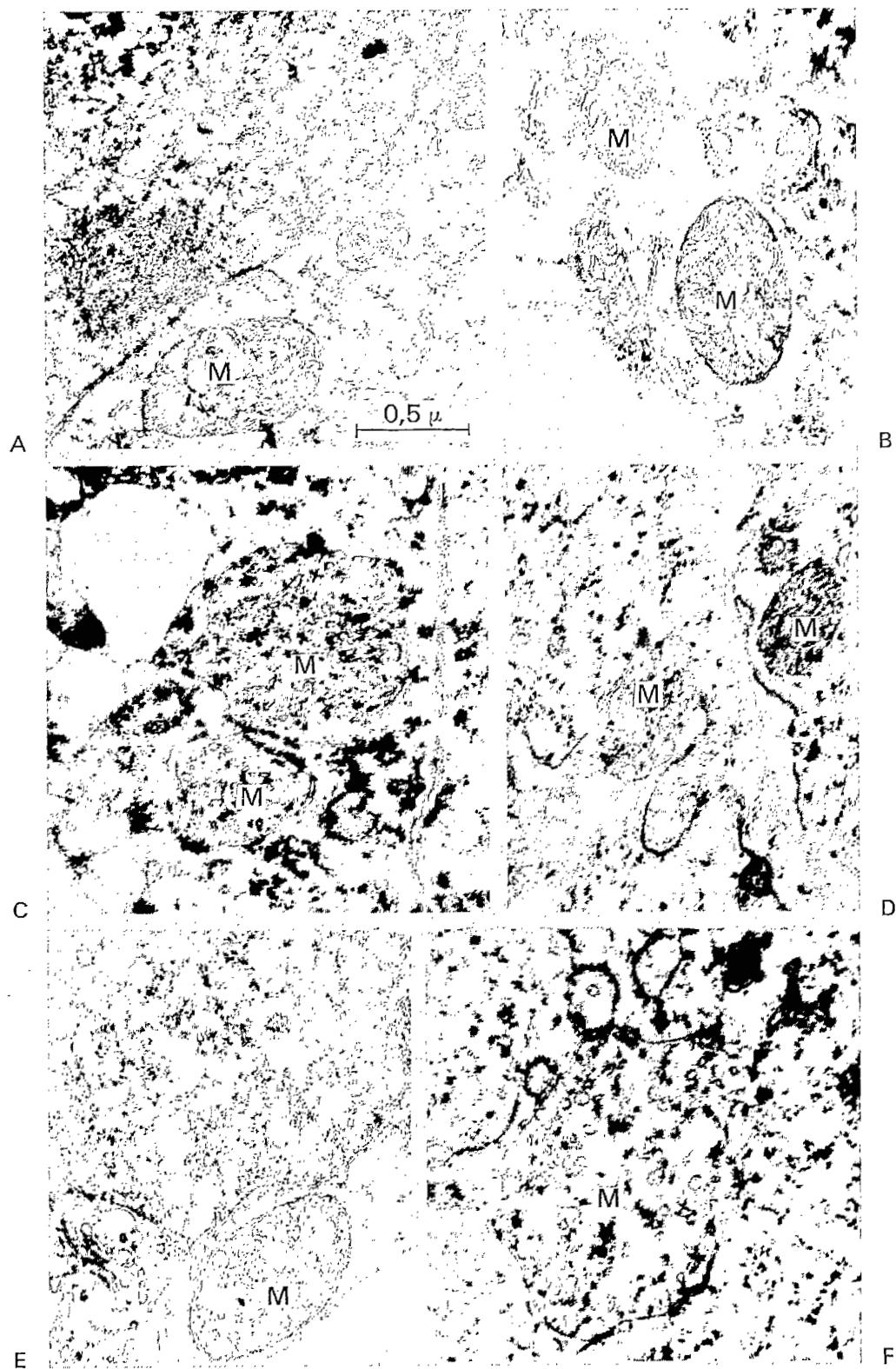


FIG. 5. (A) after bubbling with air for 50 hr; (B) after no aeration for 24 hr; (C) and (D) after no aeration for 50 hr; (E) after bubbling with nitrogen for 24 hr; (F) after bubbling with nitrogen for 50 hr. M = Mitochondria.

It was found that the mitochondria of the pumpkin roots exposed for 24 and 50 hr to an aerated medium had an ultrastructure typical of normal cells of many plants (Fig. 5 (A)).

In the cells of those roots placed for 24 hr in nutrient solution without bubbling or bubbled with nitrogen for 24 hr, there were no substantial changes in mitochondrial ultrastructure (Figs 5 (B) and (C)).

Marked ultrastructural changes occurred only after the 50-hr bubbling with nitrogen and following 50-hr of exposure to a medium in which oxygen was gradually

depleted. Two main types of lesion were found in the mitochondria (Figs 5 (C) and (F)).

In the first case, mitochondria swelled and considerably increased in size. The outer membrane of the mitochondria moved away from the inner membrane, and it was only in some small areas that their normal parallel arrangement could still be observed. As a result, a sharp increase occurred, not only of the inner mitochondrial compartment, but also of the inter-membrane space. The mitochondrial matrix clarified and only a few electron-dense granules remained in it. Some

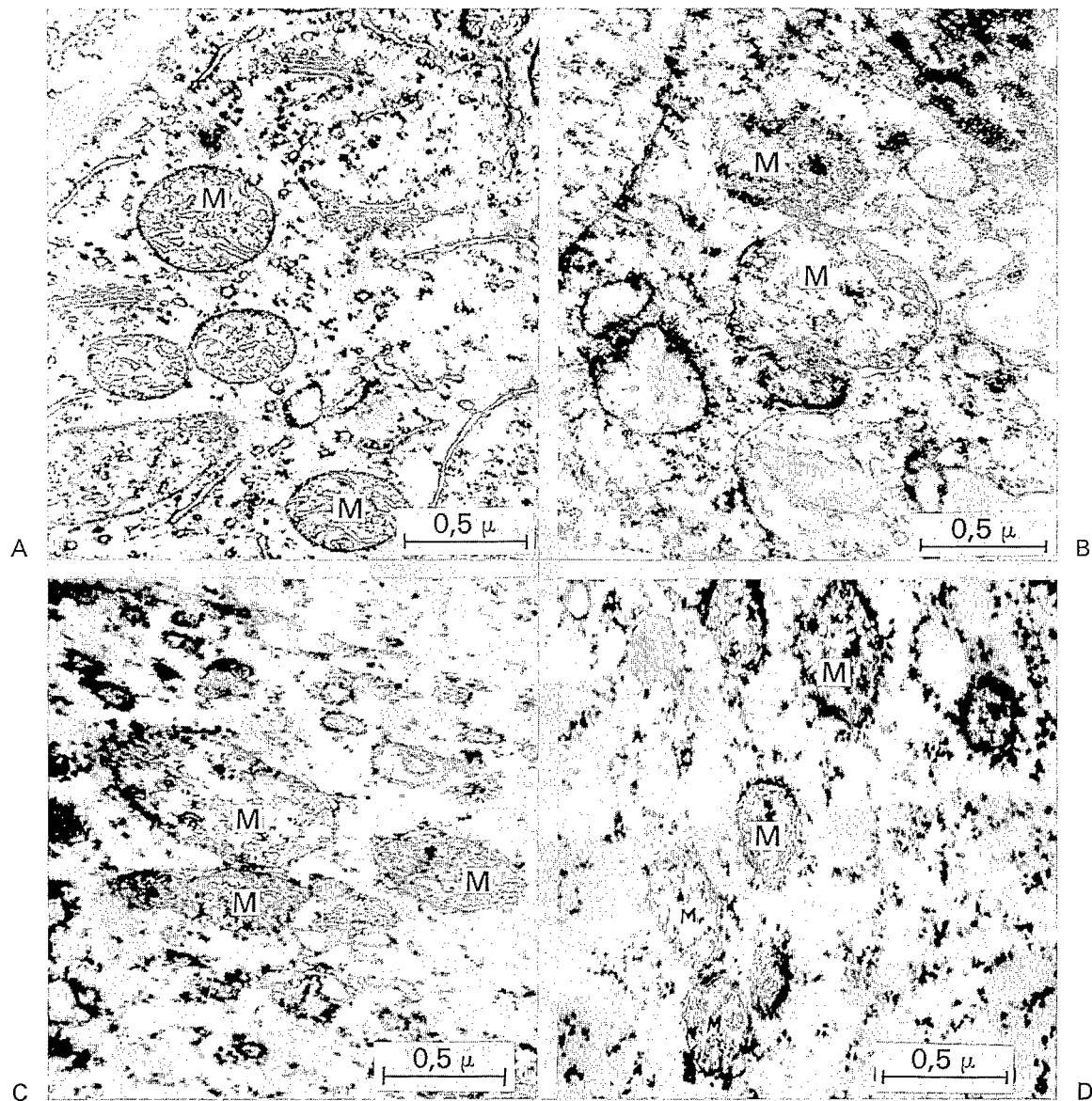


FIG. 6. Mitochondrial ultrastructure in cells of separated rice roots during anaerobiosis: (A) after bubbling with air for 24 hr; (B) after bubbling with nitrogen for 1 hr; (C) after bubbling with nitrogen for 24 hr; (D) after bubbling with nitrogen for 24 hr followed by bubbling with air for 48 hr. M = mitochondria.

cristae appeared as elongated tubules and some as round vesicles (Figs 5 (C) and (F)).

Another type of change in the mitochondrial ultrastructure, which was sometimes seen in the same cells, consisted in a strongly increased compactness of the mitochondria, their entire inner compartment being filled by compact granules and some vesicles, remnants of destroyed cristae. The outer membrane was seen to have moved away from the inner membrane at certain places (Fig. 5 (D)).

Apparently, the condition of the mitochondrial ultrastructure after 50 hr of anaerobiosis corresponded to that state when mitochondria are irreversibly damaged.

Together with changes in mitochondrial ultrastructure, oxygen deficiency led to destructive changes of other cellular organelles. The protoplasm clarified, the number of free ribosomes decreased sharply, and the cisternae of the endoplasmic reticulum swelled. After 50 hr of anaerobiosis, cell nuclei decreased in size and the nuclear envelope was fragmented into small pieces which were vesicles shaped in cross-section. The main part of the nucleus became optically empty at places and some compact granules appeared.

Thus our experiments suggest that, under the above conditions, the gaseous exchange between roots and above-ground parts could not maintain normal aerobic metabolism in the cells of the root meristem.

A different response to root anaerobiosis was displayed by rice plants. Experiments have demonstrated that, unlike the pumpkin, tomato, bean and other plants, the cell ultrastructure of root meristem in rice does not experience any appreciable signs of damage during long-term isolation of the rhizosphere from the external atmosphere. There may be 2 alternative explanations for the great resistance of rice root cell ultrastructure. Either it is accounted for by the biological characteristics of rice, which is cultivated under conditions of flooding and, consequently, of oxygen deficiency in the soil and may be adapted to retain normal cellular structure and function even in the prolonged absence of oxygen; or the cell resistance of rice (and probably some other water plants) to anaerobiosis is only apparent rather than actual and is accounted for by the fact that the oxygen coming from the above-ground organs is able to maintain aerobic conditions even when the possibility of gaseous exchange of the rhizosphere with the ambient atmosphere is completely excluded.

To decide which of the alternatives is correct, experiments were staged in which the possibility of oxygen supply from the above-ground parts was ruled out by removing them and subjecting the detached roots to anaerobic conditions by placing them in a moist chamber bubbled with nitrogen. Electron microscopic examination of such roots (Fig. 6) revealed that rice root cells

are highly sensitive to oxygen deficit. As seen from Figure 6 (B), as early as after 7 hr of anaerobiosis, the cell ultrastructure appeared grossly impaired. In other experiments, destructive changes in cellular organelles were observed in rice roots after only 4–5 hr of exposure to nitrogen atmosphere.

Some of the mitochondria increased in size and became irregularly shaped. In the swollen mitochondria the matrix was clarified and cristae decreased in number. However, other mitochondria had a compact matrix in which remnants of cristae were difficult to discern (Fig. 6 (C)).

When, after 24 hr of anaerobiosis, the separated roots were placed into water through which air was bubbled, the damaged cells not only failed to recover, but even showed increasing signs of organelle damage and breakdown (Fig. 6 (D)). The observed picture corresponded to an extreme degree of cell damage.

Therefore, the root cells of rice, which flourishes in soils practically devoid of oxygen, appear to tolerate anaerobiosis even more poorly than the root cells of ordinary crops cultivated on soils which are far better aerated. The "resistance" of rice root cells to anaerobiosis is most likely due to the fact that, as they obtain oxygen from the above-ground parts, the rice root cells are only slightly dependent on the oxygen content in the environment.

This is well illustrated by results of our polarographic studies of oxygen transport in rice plants. In these experiments the roots of 30-day-old rice plants were placed in water into which a platinum electrode was introduced. Another platinum electrode was placed directly into the roots several centimetres above the tip of the root meristem. The water surface was covered by a layer of vaseline to isolate the rhizosphere from the external atmosphere. Despite this, oxygen levels remained rather high for a long time, both in the root tissues and the water. When oxygen-free nitrogen was later bubbled through the water, all the dissolved oxygen was removed from the water, while the oxygen content in the root tissues remained rather high, apparently due to a constant inflow of molecular oxygen from the above-ground organs. When bubbling was stopped, oxygen reappeared in the solution in progressively increasing amounts.

Since no oxygen could directly reach the rhizosphere from the external atmosphere in the above experiments, it is logical to conclude that oxygen could appear only as a result of its transport from the above-ground parts, via the tissues of the plant itself. This was confirmed in the same experiments following removal of the above-ground parts when oxygen was gradually, but completely, eliminated from the rhizosphere.

Résumé

L'aération des racines en relation avec le transport d'oxygène moléculaire chez les plantes (B. B. Vartapetian)

Les racines des plantes se trouvent fréquemment dans des conditions où il est difficile à l'oxygène du sol ou de la solution nutritive de leur parvenir, ce qui entraîne inévitablement des troubles du métabolisme et la perturbation de l'ultrastructure ainsi que l'inhibition de la fonction des racines, si le manque d'oxygène extérieur n'est pas compensé par le transfert de O_2 à l'intérieur de la plante elle-même à partir de ses organes verts aériens.

L'auteur de la présente communication expose les résultats de ses recherches, en envisageant ce problème sous son aspect physiologique.

Il montre que, chez certains végétaux (la Courge), le transfert de O_2 des parties aériennes vertes aux racines ne peut établir à lui seul les conditions aérobie normales dans les racines. Pendant l'anaérobiose, les racines de ces plantes éprouvent des troubles de leur métabolisme et, si l'anoxie dure plus de cinquante heures, subissent des modifications profondes de leur structure cellulaire fine, notamment dans les mitochondries.

Chez d'autres végétaux (par exemple, le Riz), du fait de l'existence de conduits aériens dans les tissus de leurs tiges et racines, la pauvreté du sol en oxygène peut être compensée par un apport d'oxygène en provenance des parties aériennes. Chez le Riz, cette source d'oxygène est si grande que de l'oxygène transféré peut même se dégager des racines vers l'atmosphère. De ce fait, les racines de ces végétaux ne souffrent pas d'anoxie en milieu anaérobiose. Par contre, ces racines ne présentent pas de résistance à l'anaérobiose, car, si leur alimentation en O_2 par l'intermédiaire des parties aériennes est interrompue, leurs cellules manifestent les mêmes signes de désorganisation que celles des plantes du premier groupe (comme la Courge).

L'application de la technique polarographique a permis à l'auteur de déterminer la répartition de l'oxygène dans la solution nutritive et de mesurer le taux d'absorption de O_2 par des plantes cultivées dans des solutions nutritives.

L'auteur conclut que l'alimentation des plantes en oxygène mérite de retenir autant l'attention que la fumure des sols.

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Transpiration resistance in leaves of maize grown in humid and dry air

B. Slavík

Institute of Experimental Botany
Czechoslovak Academy of Sciences
Prague (Czechoslovakia)

The influence of air humidity on growth of plants has often been underestimated (e.g. Went, 1957) as it is only one of the factors determining the negative component of the plant water balance. Even with sufficient water supply, low air humidity is one of the causes of daily water deficit and it is possible that they may have a permanent and irreversible influence on the structure of leaf surfaces which in turn may influence the internal factors affecting transpiration. The following experiments were planned in order to explore this phenomenon.

MATERIAL AND METHODS

Maize (*Zea mays* L.) ev. Pioneer was cultivated in a mixture of vermiculite and coarse sand (1:1) using about 4-l carton containers, with watering twice a day, once with deionized water and once with full nutrient solution, to ensure ample soil water. The plants were placed on tracks in phytotron chambers ($214 \times 278 \times 219$ cm) with inner air volume of 7.520 m^3 . The 2 variants were grown throughout in either 40 ± 5 per cent or 85 ± 5 per cent relative air humidity, respectively, during the 12-hr-day and 40 ± 5 per cent and nearly 100 per cent relative air humidity, respectively, during the night. The air temperature was 28°C and the night-air temperature 20°C . Irradiation was by fluorescent tubes providing about 3,500 ft candles at the top of the plants. All the measurements described were performed using plants 28 and 44 days old.

Transpiration resistance was measured using a Kauffmann (1967) type transpiration porometer, similar to that suggested by Slatyer (1966) and described by Byrne *et al.* (1970). The porometer cup is ventilated, the air dried before each measurement by silica gel. The time necessary for a change of the air humidity in the ventilated inner volume of the porometer from 31.5 per cent to 33.75 per cent relative humidity at 28°C air temper-

ature was measured. The orifice of the porometer was 0.64 cm^2 .

Determinations of stomatal density and size were made by direct replica methods. Transpiration rates of total plants were determined by measuring the rate of increase of air humidity from 44 to 49 per cent at 28°C in a closed phytotron chamber, of the same dimension and irradiation as described with additional ventilation ($r_a = 0.37 \text{ sec cm}^{-1}$). In each case a "stand" of 12 plants on a track was measured. Transpiration rates were calculated per unit area of green leaves.

RESULTS AND DISCUSSION

In order to obtain representative data, the influence of the leaf insertion level on transpiration resistance was first determined. The median insertion leaves (the sixth, seventh and eighth leaves) were measured and the results are given in Table 1. A rather surprising minimum value of resistance was obtained in the seventh leaf, accompanied by a corresponding maximum value of stomatal density. More detailed studies have shown that this was due to interference in the ontogenetic development of the individual leaves. The size of the stomata increased slowly with increase in insertion height of the leaf. In spite of these insertional differences, the leaves used for measurement were sufficiently homogeneous to yield results which could be treated statistically and compared.

In Figure 1 a comparison of the daily course of transpiration resistance of abaxial surfaces of the sixth to the eighth leaves in both variants is shown. In plants grown in dry air, the transpiration resistances in the morning averaged about $1.6\text{--}1.7 \text{ sec cm}^{-1}$. A gradual increase was then observed, so that after 7–10 hr of light period, the average values were $4.2\text{--}4.5 \text{ sec cm}^{-1}$.

TABLE I. Average transpiration resistance with opened stomata in comparison with stomata density and size in the sixth, seventh and eighth leaves of the test plants

	Dry-air plants			Humid-air plants		
	Transpiration resistance (sec cm ⁻¹)	Stomata number per 1 mm ² abaxial surface	Average length of the stomata (μm)	Transpiration resistance (sec cm ⁻¹)	Stomata number per 1 mm ² abaxial surface	Average length of the stomata (μm)
6th leaf	2.4	85.5	37.3	0.98	85.5	44.1
7th leaf	1.9	90.8	46.8	0.94	87.5	49.2
8th leaf	2.35	77.5	48.4	1.04	75.0	51.5

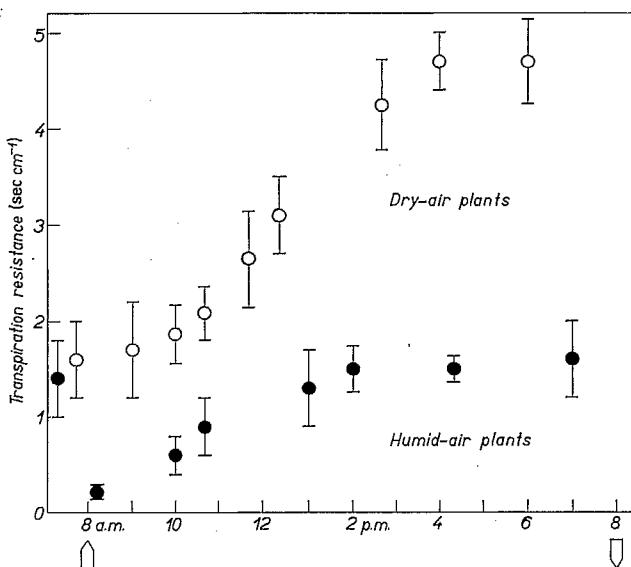


FIG. 1. Daily course of average transpiration resistance values of plants grown in dry or in humid air. Abaxial surfaces of the sixth, seventh and eighth leaf were used. O = lights-on and lights-off times. (Each point is the mean of at least 20 determinations.)

In plants grown in humid air, the comparable resistance values were always found to be lower. After a dark period value of about 1.5 sec cm^{-1} , transpiration resistance dropped to an average of 0.22 sec cm^{-1} in the morning and mean values around 1.5 sec cm^{-1} were found in the afternoon. The afternoon values, with more or less hydroactively closed stomata, corresponded to the premorning values, with photoactively closed stomata. Thus it is probable that they represent cuticular resistance in both cases. On average, the dry air plants had transpiration resistance levels 3 times higher than those of the humid air plants.

Transpiration rates (Fig. 2) were measured in a set of 12 plants, including both humid-air plants and dry-air plants, in dry-air conditions. The plants were maintained during the remainder of the day period in dry air and humid air, respectively, the humid-air plants not being transferred to the measuring dry-air chamber until immediately before each measuring series (time point A in Fig. 2).

Transpiration rates in plants grown in humid air were about 50 per cent higher than in plants grown in dry air, but decreased very rapidly after the transfer to dry air due to increasing water deficit and hence hydroactive closure of the stomata. There was almost no difference in the initial transpiration rate values (at point A) between the morning and afternoon determinations, due to the normal diurnal course of transpiration resistance in humid-air conditions, where the plants were always kept until the beginning of the transpiration measurement at point A.

By comparison, initial transpiration rates of plants grown in dry air were lower in the afternoon, but decreased very slowly during each transpiration measurement. This decrease corresponded to the normal diurnal course of transpiration rates in dry air conditions.

The results permit the following conclusions to be drawn: the transpiration rates in plants grown in humid air were higher and the transpiration resistances were lower than in plants grown in dry air, when measurements of both groups of plants were made under dry-air conditions. This difference seems to be due to (a) lower cuticular resistance in humid-air plants, as may be seen from the comparison of dark-period values (assuming photoactive closure was complete) and afternoon values (assuming hydroactive closure was complete) in humid-air plants in dry-air conditions, and (b) to a small degree, a slightly greater average size of stomata in the leaves measured, while the average stomatal density was not much different, even slightly lower (Table 1).

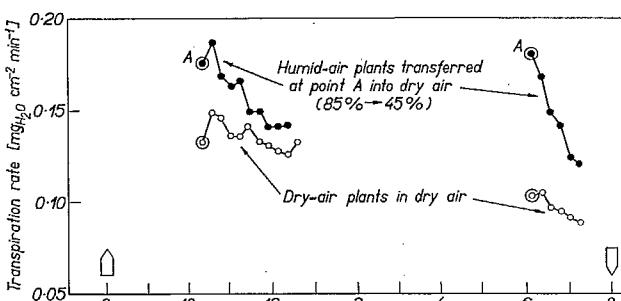


FIG. 2. Examples of daily changes of transpiration rates (in 44–49 per cent relative air humidity at 28°C) of plants grown in dry or in humid air. O = lights-on and lights-off times.

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Résumé

Résistance à la transpiration de feuilles de Maïs cultivé en atmosphère humide et en atmosphère sèche (B. Slavik)

On a trouvé que la résistance à la transpiration r_l [$s \text{ cm}^{-1}$] des faces dorsales de feuilles de Maïs (*Zea mays L.*), mesurée au moyen d'un poromètre de transpiration ventilé, était plus élevée de manière significative pour des plants cultivés en atmosphère sèche [$40 \pm 5\%$ hum. rel. à 28°C pendant la période lumineuse de 12 heures et 20°C pendant la période d'obscurité] que pour des plants cultivés en atmosphère humide [$85 \pm 5\%$ hum. rel. à 28°C pendant la période lumineuse de 12 heures et $95 \pm 100\%$ hum. rel. à 20°C pendant la période d'obscurité]; dans les deux cas, une humidité abondante était fournie par le substrat. Ces différences sont dues manifestement à des différences de la résistance cuticulaire (r_c), qui était trois fois plus grande chez les plants cultivés en atmosphère sèche. Les différences du nombre moyen des stomates (un peu plus grand chez les plants cultivés en atmosphère sèche) ou de leur taille légèrement plus grande chez les plants cultivés en atmosphère humide peuvent ne pas expliquer les différences moyennes ci-dessus de r_l . Les résultats de la mesure de la transpiration corroborent ces conclusions.

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Effects of short periods of water stress on leaf photosynthesis

R. O. Slatyer

Department of Environmental Biology
Research School of Biological Sciences
Australian National University
Canberra (Australia)

INTRODUCTION

Water stress is perhaps the most widespread cause of yield decrements in agricultural crops. Much research, particularly in subhumid and arid regions, has been devoted to its study and to the amelioration of stress effects by various cultural procedures. Frequently, the most successful procedures have been those which have attempted to fit the phenological characteristics of the crop species into the agroclimatic characteristics of the region in which the crops are to be grown. If plant breeding is used to improve varietal selection for particular environments, the matching of genotype, ecotype and environment should be even more effective.

In such work, the plant breeder relies, in part, upon the physiologist to provide him with meaningful and realistic selection parameters. Considerable interest has, therefore, been focused on the degree to which metabolism and morphogenesis in various species and varieties is affected by water stress (see, for example, Crafts, 1968; Gates, 1968; Slatyer, 1969; Kramer, 1969).

In this regard a basic parameter is the effect of water stress on photosynthesis itself. For many years it has been recognized that water stress can affect photosynthesis either by a direct effect of dehydration on the photosynthetic apparatus or by an indirect effect by way of stomatal closure, which impedes CO_2 entry. In general, as stress is imposed, there is a progressive decrease in photosynthesis and an associated decrease in transpiration (see, for example, Brix, 1962; Slatyer, 1967). This association indicates that stomatal closure is closely linked with the decrement in photosynthesis, but does not necessarily imply a causal relationship.

In consequence, efforts have been made to separate the indirect effect of stomatal closure from the direct dehydration effects, generally by examining the effects of water stress on photosynthesis at constant or known stomatal resistance values. With this approach, several

workers (Shimshi, 1963; Baker and Musgrave, 1964; Whiteman and Koller, 1964; Gale *et al.*, 1966) have found evidence of a direct dehydration effect. More recently, however, Troughton (1969) and Troughton and Slatyer (1969) have examined the effect of water stress on the intrinsic photosynthetic capacity of cotton leaves, as reflected in the intra-cellular "resistance" to CO_2 transport. From these studies they concluded that there were no direct effects of water stress on the photosynthetic apparatus until the plants were desiccated beyond the permanent wilting percentages. In other words, all the decline in photosynthesis was attributable to stomatal closure. The present experiments extend these studies to several other species.

METHODS

GENERAL

Plants of cotton (c.v. Deltapine smooth leaf), wheat (c.v. Gabo), maize (c.v. Golden Bantam), bulrush millet (c.v. Katherine Pearl), *Atriplex hastata* and *A. spongiosa* were grown in water culture or soil in a temperature-controlled greenhouse.

When well established, water-stress treatments were induced by discontinuing watering, in the case of the soil-grown plants, or by progressively reducing the temperature of the culture solution. As water stress developed, measurements of net photosynthesis, transpiration and the related gas exchange parameters were determined in a leaf chamber of the type described by Jarvis and Slatyer (1966).

Individual attached leaves were set up in the inner compartment of the chamber, the environment of which was rigorously controlled at desired gas concentrations, air transfer rates, air and leaf temperature, and radiation flux density. The light source was a Xenon arc which provided a saturating radiation flux density of 460 W m^{-2}

(in the 400–700 nm wave band) for measurement purposes. The remainder of the plant obtained general illumination from the same light source at flux densities of about 200–500 W m⁻². Room temperature was maintained at 23° C and excess heating of the leaves not enclosed in the chamber was prevented by ventilation with a small fan.

Leaf temperature was measured with a copper-constantan thermocouple threaded through a side vein of a leaf. Transpiration was determined from measurements made with differential psychrometers (Slatyer and Bierhuizen, 1964). CO₂ exchange was measured with a URAS gas analyser calibrated with Wösthoff gas mixing pumps. Capillaries and micromanometers were used to measure the flow rates of air and the output from all sensors was displayed on an integrating digital voltmeter.

Desired gas concentrations of high stability were obtained by storing mixed air, nitrogen and CO₂, as appropriate, in large (~3,000 l) PVC balloons. Additional lower CO₂ concentrations were obtained by partial removal of CO₂ on-line from various mixtures prior to reaching the leaf chamber.

DETERMINATION OF GAS EXCHANGE PARAMETERS

The key parameters required for the present study were leaf (stomatal) diffusive resistance to CO₂ transfer (r_l),

and intracellular resistance (r_{int}). The former is a measure of the permeability of the gas phase pathway from the surface of the photosynthesizing cells to the natural surface of the leaf. Its primary variable component is due to changes in stomatal aperture and it therefore effectively monitors stomatal diffusive resistance. The latter parameter is a measure of the intrinsic photosynthetic efficiency of the leaf, i.e. it determines the rate of CO₂ exchange between the cell wall surface and the effective carboxylation/decarboxylation surface within the photosynthesizing cells. It is not a true resistance in the same sense as r_l .

The significance of these parameters can be appreciated from the following: The equation for transpiration, E , (g cm⁻² sec⁻¹) is generally written in the form

$$E = \frac{c'_w - c'_a}{r'_a + r'_l} = k \frac{e'_w - e'_a}{r'_a + r'_l} \quad (1)$$

where c'_w and c'_a (g cm⁻³) are, respectively, the water vapour concentration at the surfaces of the mesophyll cell walls and in the bulk air, e'_w and e'_a are the corresponding vapour pressures and k is a conversion factor. The value of k is $2.89 \times 10^{-4}/T$, where e is in mm Hg and T is the temperature in degrees Kelvin. r'_a (sec cm⁻¹) is the diffusive resistance to water vapour transfer across the boundary layer which sheathes the leaf and r'_l is the diffusive resistance in the leaf to water vapour

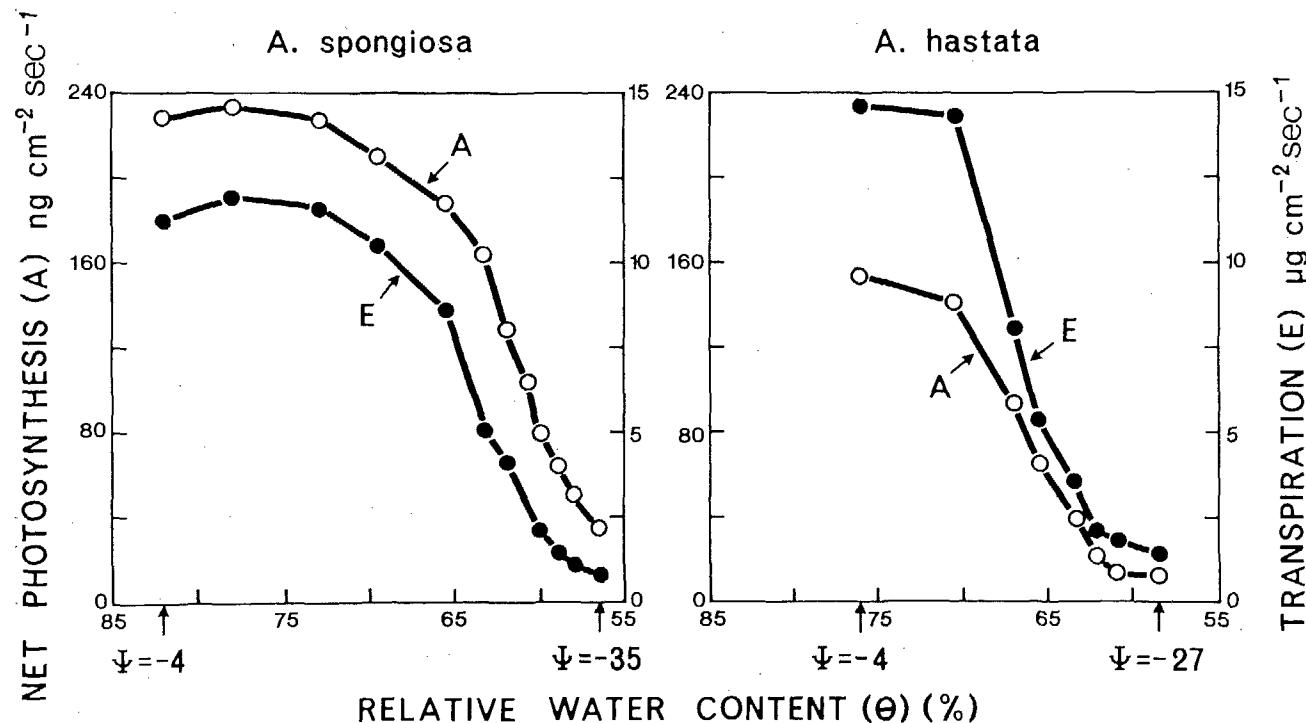


Fig. 1. Effect of decreasing relative leaf water content on rates of net photosynthesis (○—○) and transpiration (●—●) in *Atriplex spongiosa* and *A. hastata*. Leaf water potential (Ψ) values are in bars.

transfer. Strictly speaking, r'_l refers to the sum of the cuticular and stomatal diffusive resistances (see, for example, Slatyer, 1967), so when the stomata are closed r'_l represents cuticular resistance alone. Under open stomata conditions, the cuticular resistance is so high relative to stomatal resistance the r'_l effectively represents stomatal resistance alone. For these experiments it is convenient to use the net leaf resistance rather than to partition r'_l into stomatal and cuticular components.

Since c'_w is assumed to be the saturation vapour concentration at the leaf temperature, $(r'_a + r'_l)$ was obtained from measurements of transpiration rate, leaf temperature and ambient vapour pressure. The level of r'_a was made constant, and relatively small, by standardized ventilation procedures. For each species its value was found using a piece of wet blotting paper ($r'_l = 0$), instead of a real leaf. For any set of measurements of $(r'_a + r'_l)$, r'_l was then obtained by subtraction of r'_a .

The equation for photosynthesis, F , ($\text{g cm}^{-2} \text{ sec}^{-1}$) is generally written in the form

$$F = \frac{c_a - c_{int}}{r_a + r_l + r_{int}} = \frac{c_a - c_w}{r_a + r_l} = \frac{c_w - c_{int}}{r_{int}} \quad (2)$$

where c_{int} is the effective intracellular CO_2 concentration (g cm^{-3}) and the other symbols refer to CO_2 concentrations and resistances in the same way that they are used for water vapour in equation (1). r_a and r_l are related to r'_a and r'_l by the ratio of the diffusion coefficients of CO_2 and water vapour in air (≈ 1.56).

The first term on the right-hand side of equation (2) represents the total CO_2 pathway from the bulk air to the effective carboxylation/decarboxylation surface within the mesophyll cells, the second term describes the extra-cellular gaseous component of the CO_2 pathway, and the third term the intra-cellular component. Therefore, r_{int} represents an equivalent resistance, including not only a "resistance" to liquid phase diffusion inside the cell but "resistance" associated with the photosynthetic processes themselves.

All these parameters can be obtained from sets of measurements relating F to c_a , collected simultaneously with measurements of the water vapour parameters just discussed. It is necessary to make the measurements under conditions of CO_2 limitation and light saturation.

Estimates of c_w are then made from the values of F , c_a and $(r_a + r_l)$ using the second term on the right-hand side of equation (2), rewritten in the form

$$c_w = c_a - F(r_a + r_l) \quad (3)$$

Since c_{int} is assumed to be constant (and equal to the CO_2 compensation point (Γ) under CO_2 limiting conditions), r_{int} can then be obtained from the third term of equation (2), or from the slope of the curve relating F to c_w .

In practice, therefore, a simple test as to whether or not water stress is affecting net photosynthesis by way of stomatal closure alone, or by interference with the photosynthetic apparatus, can be made by obtaining

an $F(c_w)$ curve for a non-stressed plant and then determining the degree to which water stress affects this relationship. Values of r_{int} for stressed and non-stressed plants can be calculated from the $F(c_w)$ curve and the values compared.

RESULTS

In Figure 1 typical data relating rates of net photosynthesis (A) and transpiration (E) to decreasing relative water content (θ) are presented for *Atriplex hastata* and *A. spongiosa*. The range of θ values represents a range of leaf water potentials from approximately -4 bars to -27 bars in the case of *A. hastata* and from -4 bars

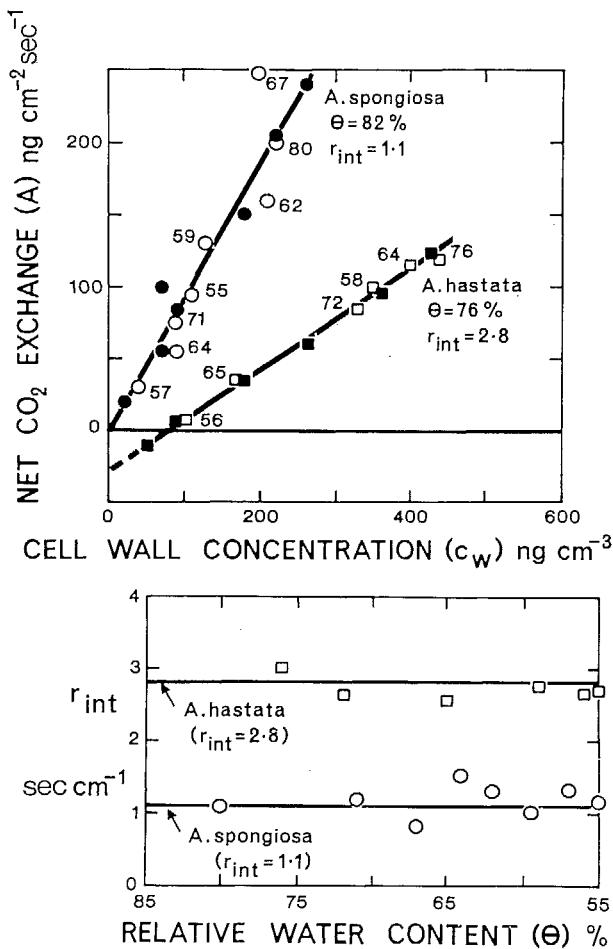


FIG. 2. Upper: CO_2 response curves for *Atriplex spongiosa* and *A. hastata* under non-stress (●) and stress (○) conditions. The line is a curve of best fit through the non-stressed points; the slope of the curve is the intracellular resistance, r_{int} . The figures against each hollow point indicate the θ value at which the point was obtained. Lower: Values of r_{int} plotted against θ , using the data from the upper part of the figure. The horizontal lines give the r_{int} values obtained for non-stress conditions.

to -35 bars in *A. spongiosa*. Permanent wilting occurs at about -15 and -20 bars, respectively, in these species. (The relatively low θ values for water potentials of only -4 bars are due to the salt content of these halophytic species.) Generally similar curves were obtained for the other species examined. It can be appreciated that, associated with the progressive decline in transpiration, was a substantial and progressive increase in stomatal diffusive resistance to both water vapour and CO_2 transfer.

The degree to which this decline can be attributed to a direct effect of dehydration on the photosynthetic apparatus, as distinct from the indirect effect of stomatal closure in impeding the supply of CO_2 to the photosynthesizing cells, can be interpreted from Figure 2. In the upper part of the figure, CO_2 response curves for both species used in Figure 1 (but from different experiments) are plotted, the line being drawn through the solid points which were obtained under non-stressed conditions. The hollow points refer to values obtained as stress was progressively imposed, the numbers referring to the actual level of relative water content for each point.

It can be seen that the stressed points still fall on the basic, non-stress, line even for relative water contents as low as $\theta = 55$ per cent. The r_{int} values calculated from each point ($r_{int} = (c_w - \Gamma)/A$) are also plotted in the lower part of Figure 2, confirming the absence of any trend towards an increase of r_{int} with increasing dehydration. (The horizontal line refers to the non-stress level of r_{int}). In consequence, all of the decline in net photosynthesis observed in Figure 1 can be attributed to stomatal closure.

In Figure 3, r_{int} values for wheat, cotton, millet and maize, obtained by the same procedure, are also plotted against relative water content. The non-stress levels of r_{int} (respectively 3.0 , 2.6 , 0.9 and 0.8 sec cm^{-1}) are shown by the horizontal line on each diagram. The most severe stress levels obtained for wheat were $\theta = 62$ per cent, $\psi = -28$ bars; cotton, $\theta = 60.5$ per cent, $\psi = -25$ bars; millet, $\theta = 61$ per cent, $\psi = -30$ bars; and maize, $\theta = 62$ per cent, $\psi = -26$ bars. In all species permanent wilting appears at θ values between 75 and 80 per cent.

It is apparent that, in wheat and millet, the pattern observed in the 2 *Atriplex* species was repeated, no

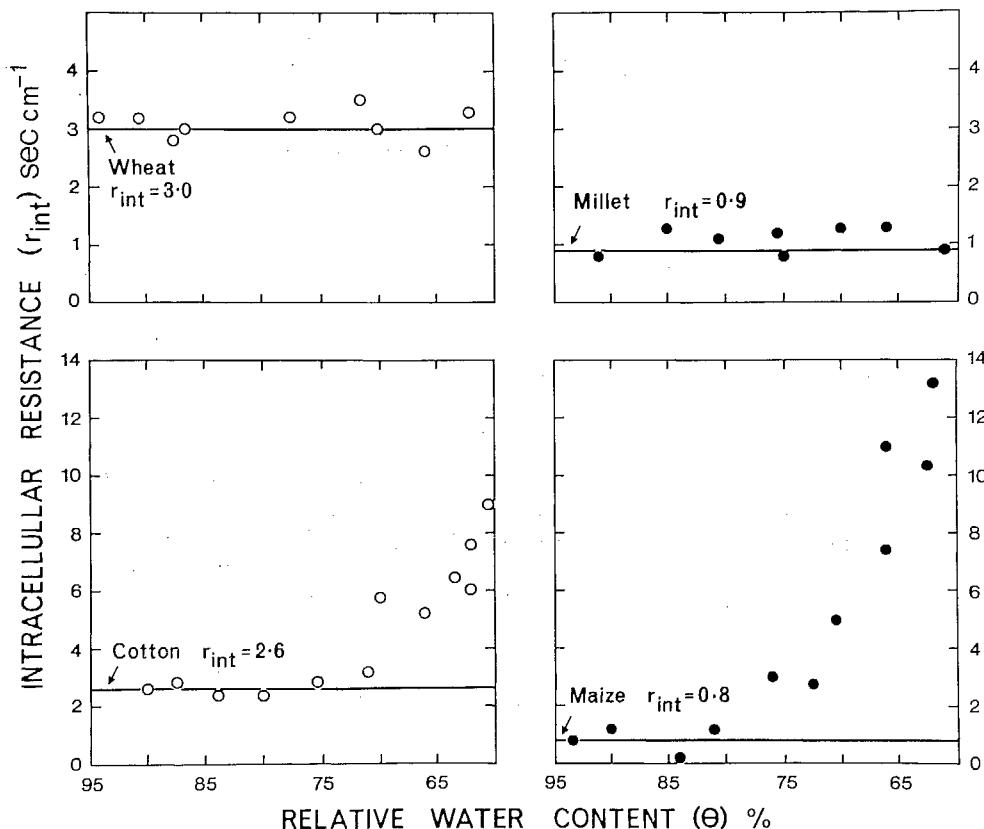


FIG. 3. Values of r_{int} for cotton, wheat, millet and maize, plotted against relative water content. The horizontal lines give the r_{int} values obtained for non-stress conditions.

evidence being obtained of an increase in r_{int} over the range of stress levels tested. In the relatively drought sensitive species, cotton and maize, a similar situation existed until stress levels slightly beyond those necessary to cause permanent wilting occurred. Beyond this stage r_{int} values began to increase, indicating a direct effect of dehydration on photosynthetic apparatus.

DISCUSSION

The results presented here provide clear evidence that, for short periods of water stress, there appears to be no effect of stress on the photosynthetic apparatus itself (expressed in terms of r_{int}), until stresses more than those required to induce permanent wilting were imposed. Until that stage was reached, all the decline in net photosynthesis could be attributed to impeded CO_2 supply caused by stomatal closure. Even at water potentials beyond the wilting percentage, only 2 relatively drought sensitive species showed evidence for a direct physiological effect of stress, even though severe stresses were imposed, to levels equivalent to leaf water potentials of about -25 to -30 bars. Since these stresses caused substantial and progressive reductions in net photosynthesis, it follows that until r_{int} increased, all the decreases in net photosynthesis were caused by stomatal closure.

In placing these results in ecological and agronomic perspective, it is readily conceded that, at some stage of stress imposition and persistence, there will be direct

lesions in the photosynthetic apparatus, as well as indirect ones associated with impedance of other metabolic or morphogenetic processes. Also, while these data provide a measure of the effect of water stress on carboxylation efficiency at low CO_2 levels, they do not provide evidence at high CO_2 levels. However, as far as they can be extrapolated, the present results suggest that such stresses will have to be either more severe or more prolonged than those imposed here.

It should also be pointed out that, under normal conditions, stomatal closure is associated with a rise in leaf temperature, which may lead to increased respiration rates and hence depressed rates of net photosynthesis and enhanced CO_2 compensation points and r_{int} values. In the present experiments leaf temperature was deliberately controlled so that only direct effects would have been observed.

In view of the recent interest in species exhibiting " C_4 " metabolism (in which the primary carboxylation products are C_4 dicarboxylic acids (Hatch and Slack 1970)), it is noteworthy that the C_4 species used in this study (*Atriplex spongiosa*, maize and millet) showed no characteristic response pattern in r_{int} or r_l as stress was imposed. However, the relatively low r_{int} values of these species, together with their very low CO_2 compensation points, are apparent from Figure 3. Their very low CO_2 compensation points suggest that they may not exhibit a reduction in net photosynthesis, and an increase in r_{int} , if leaf temperature were to rise with stomatal closure, as has just been suggested as a possible indirect response under natural conditions.

Résumé

Effets de courtes périodes de contrainte hydrique sur la photosynthèse foliaire (R. O. Slatyer)

Plusieurs espèces de plantes cultivées (Cotonnier, Blé, Maïs, Millet) et deux espèces de plantes indigènes *Atriplex spongiosa* et *Atriplex hastata* ont été soumises à de courtes périodes de contrainte hydrique de divers degrés d'intensité.

Sous la contrainte hydrique, une diminution progressive de la photosynthèse nette a été observée chez toutes les espèces. Mais, jusqu'à ce que le stade de flétrissement permanent ait été atteint, cette décroissance a pu être

attribuée entièrement, chez toutes les espèces examinées, à l'effet de la fermeture des stomates sur l'approvisionnement en CO_2 ; aucun effet direct de la déshydratation sur l'appareil de photosynthèse lui-même n'a pu être décelé. Ce comportement s'est maintenu même sous les contraintes extrêmes (équivalant à des potentiels hydriques de l'ordre de -35 bars), chez toutes les espèces sauf les deux plus sensibles: le Maïs et le Cotonnier. Dans ces deux espèces, un effet direct sur l'appareil de photosynthèse, se manifestant par un accroissement de la résistance (intracellulaire) du mésophylle au transport de CO_2 , a pu être observé à partir de potentiels hydriques d'environ -15 bars.

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Particularités adaptatives de la Moutarde blanche, *Sinapis alba* L., à la sécheresse

N. Vartanian
maître assistant,
Laboratoire d'écologie végétale, Faculté des sciences
91 Orsay (France)

La Moutarde blanche, *Sinapis alba* L., annuelle spontanée des champs, au printemps dans les régions tempérées, est aussi une plante de culture facile, grâce à son cycle biologique rapide, sa rusticité et ses faibles exigences nutritionnelles qui lui permettent de s'accommoder de tous les terrains. On l'utilise ainsi comme engrais vert ou culture dérobée. Elle se présente comme une mésophyte, pouvant néanmoins supporter de larges variations dans l'alimentation en eau.

Au cours d'une étude expérimentale écophysiologique portant sur la croissance et la morphogenèse du système racinaire de *Sinapis alba* en relation avec le bilan hydrique dans la plante, nous avons pu observer un certain nombre de faits qui rappellent le comportement de plantes adaptées au milieu sec.

CROISSANCE DU PIVOT

Le système racinaire de *Sinapis alba*, typiquement pivotant, présente une grande sensibilité au facteur hydrique, qui se traduit par une forte plasticité morphologique: dans la marge d'eau utile, entre le point de flétrissement permanent et la capacité de rétention, le développement du pivot est prépondérant par rapport aux ramifications latérales, et nous avons tenté d'analyser les variations de sa vitesse de croissance en fonction de l'interaction des facteurs hydrique, édaphique et atmosphérique.

MATÉRIEL ET TECHNIQUES

On utilise des germinations de *Sinapis alba*, âgées de 24 heures, dont la radicule possède quelques millimètres de longueur.

Les cultures sont effectuées dans des tubes de verre mesurant 30 ou 50 cm de long, pour un diamètre de 3,5 cm, et contenant respectivement 500 ou 800 g de

terre. Ces tubes sont placés dans des portoirs en bois clos (où les racines seront ainsi à l'abri de la lumière), inclinés légèrement (12°) par rapport à la verticale (afin que la croissance du pivot puisse être toujours suivie le long de la paroi de verre) (fig. 1).

Le substrat utilisé est un sable très faiblement calcaire, neutre ($\text{pH } 6,9$), pauvre en éléments nutritifs, à texture grossière, dont la réserve d'eau utilisable, entre le point de flétrissement permanent ($\text{pf } 4,2$, humidité 1,8%) et la capacité de rétention ($\text{pf } 2$, humidité 5,6%) est d'environ 3,8%. La porosité de ce sable est assez élevée (aux alentours de 45%), de sorte que l'aération n'est jamais limitante dans la gamme d'humidité choisie. Ce sable est stérilisé et amené à l'humidité voulue avant d'être introduit dans les tubes. Ceux-ci sont ensuite fermés avec du parafilm, qui limite les pertes d'eau par évaporation.

Une germination de *Sinapis alba* est repiquée, à travers le parafilm, sur le bord de chaque tube. Nous avons vérifié au préalable que la croissance du pivot n'était pas modifiée par l'inclinaison des tubes ni par la proximité de la paroi de verre, par comparaison avec des plantes dont la racine croissait au milieu du sol de tubes maintenus verticaux.

Les expériences, d'une durée de 15 jours, se déroulent en conditions expérimentales rigoureusement contrôlées: lumière ($15 \cdot 10^4 \text{ ergs s}^{-1} \text{ cm}^{-2}$, pendant 16 heures par jour), température constante (22 ou 24 °C) et humidité atmosphérique (50 ou 70% d'humidité relative) au phytotron de Gif-sur-Yvette. L'humidité atmosphérique saturante était obtenue en entourant les parties aériennes des plantes d'un sachet en polyéthylène, à travers lequel on a vérifié que la diffusion du gaz carbonique était suffisante pour que la photosynthèse puisse s'effectuer normalement. L'évaporation d'un coton maintenu humide assurait la saturation de l'atmosphère des sachets dont le degré hygrométrique était vérifié à l'aide d'un psychromètre à thermistances.

Au fur et à mesure que la jeune plantule se développe, le sol s'assèche, sous l'effet de la transpiration, et un gradient vertical de potentiel hydrique, croissant à partir de la surface, s'établit dans les tubes. Mais la croissance du pivot progresse dans tous les cas plus vite que le front d'assèchement, de sorte que la zone d'elongation sensible à la variation d'humidité du sol, et localisée aux quelques millimètres à l'arrière de l'apex méristématique, se trouve toujours, au cours de la croissance, à l'humidité initiale.

RÉSULTATS

La figure 2 traduit l'effet conjugué des humidités édaphique et atmosphérique sur la vitesse de croissance du pivot.

Influence de l'humidité du sol

Quelle que soit l'humidité atmosphérique, on observe un optimum ou une zone optimale de croissance du pivot. La croissance est faible aux potentiels trop bas (humidité insuffisante) et se ralentit également aux humidités élevées en faveur des racines latérales.

Des observations analogues ont été faites par Ronnike (1957) sur le Lupin, Kausch (1955) sur la Fève, et Walter (1963) sur le Pois, qui trouvaient un optimum de croissance de la racine principale pour un potentiel hydrique de -7 atmosphères, alors que la croissance des racines latérales comme celle des parties aériennes était au contraire maximale aux humidités plus élevées.

Nous avons constaté, en outre (Vartanian, 1967), que cet optimum de croissance de la racine principale dépendait étroitement de l'humidité atmosphérique.

Influence de l'humidité atmosphérique

Lorsque l'humidité atmosphérique augmente et que par conséquent la demande évaporative diminue, l'optimum de croissance du pivot est décalé vers les faibles humidités du sol, le fait le plus remarquable étant l'obtention de l'optimum pour des valeurs d'humidité du sol proches du point de flétrissement permanent, en atmosphère saturée [fig. 2] (2,2%, potentiel hydrique = 12,6 J. mole⁻¹).

Dans les conditions d'humidité atmosphérique extrêmes (sèche ou saturée), il existe d'ailleurs une large zone optimale, dans le premier cas parce que la forte demande

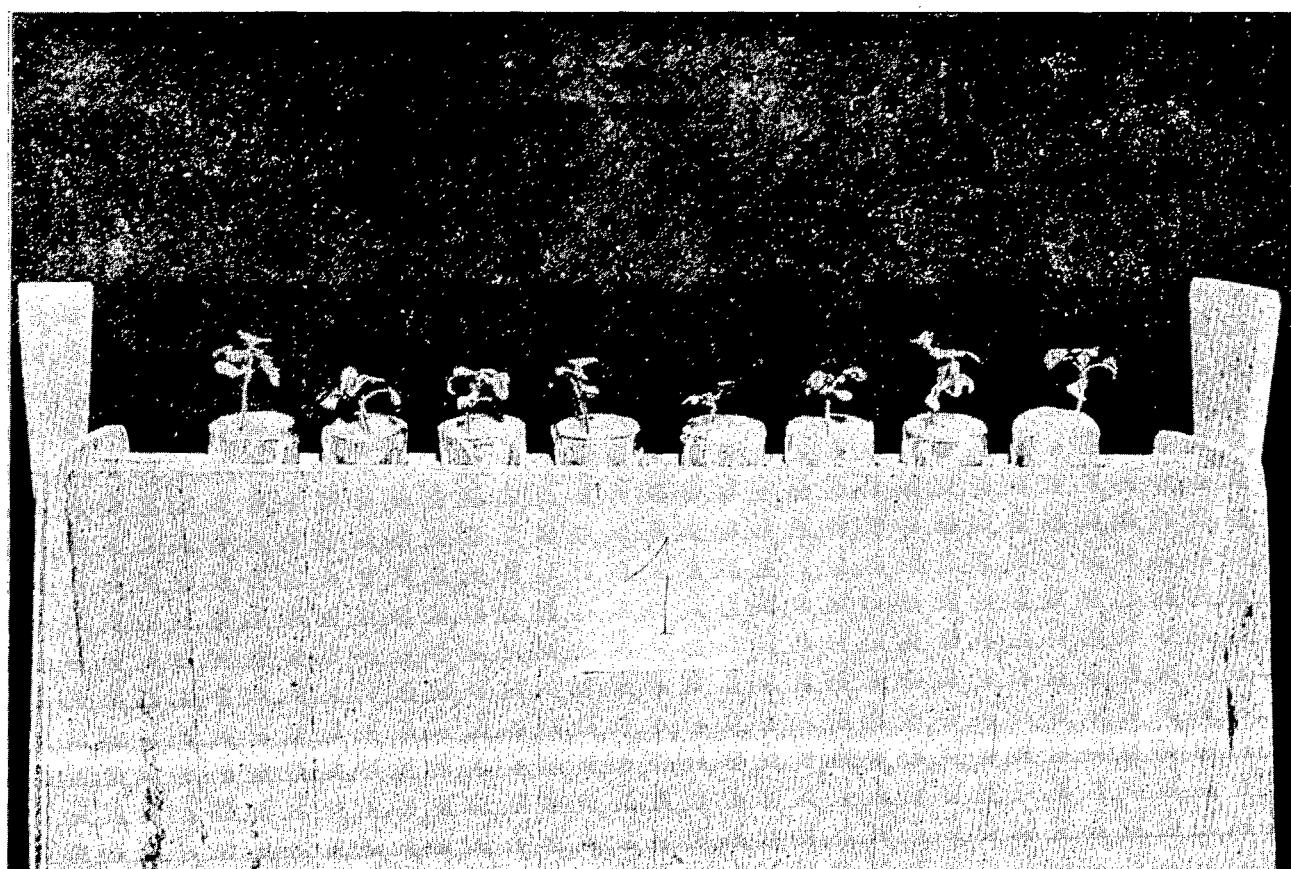


FIG. 1. Cultures de *Sinapis alba* en tubes de verre.

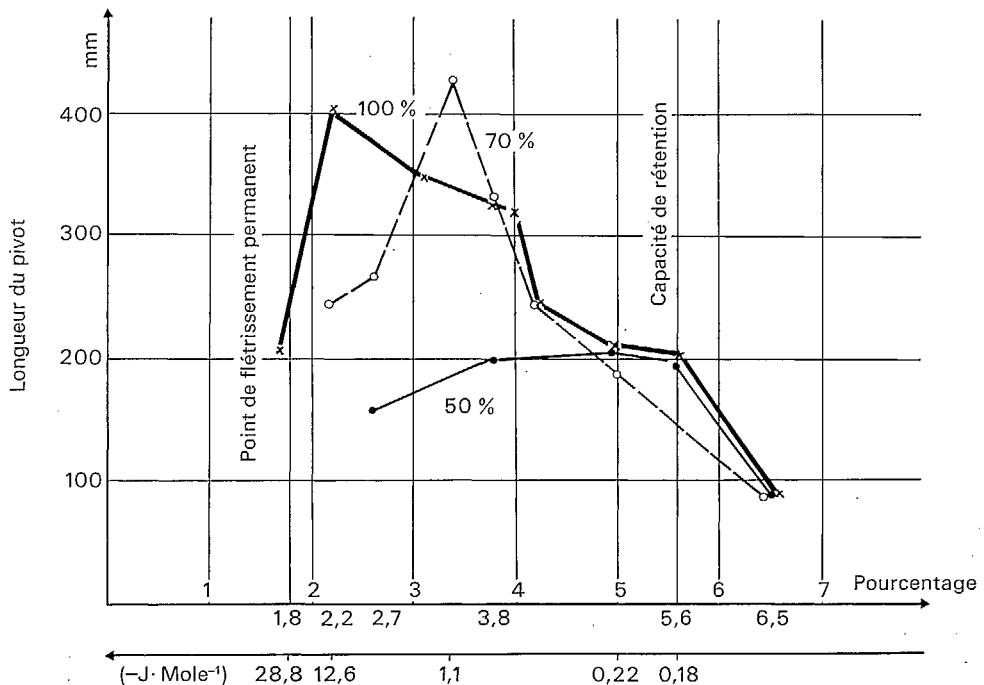


FIG. 2. Longueur de la racine principale de *Sinapis alba* âgée de 15 jours, en fonction de l'humidité du sol, à 3 niveaux d'humidité atmosphérique.

évaporative est limitante quelle que soit l'humidité du sol, dans le second cas parce que l'humidité atmosphérique étant très favorable, la variation d'humidité du sol s'avère, dans une large gamme, peu importante (variation tamponnée).

Au contraire, à 70% d'humidité, la sensibilité du pivot à l'humidité du sol est très grande et l'optimum étroitement localisé. Nous avons pu interpréter ces observations comme la conséquence, sur la vitesse de croissance du pivot, des gradients de potentiel hydrique induits dans la plante par les variations simultanées d'humidité atmosphérique et édaphique, et plus précisément la croissance du pivot a été reliée au potentiel hydrique de la racine même (Vartanian, 1969).

Signalons que la vitesse de croissance du pivot est constante dans la zone optimale, alors qu'elle se ralentit plus ou moins précocement dans les zones d'humidité infra- et supra-optimales.

La Moutarde blanche, *Sinapis alba*, paraît ainsi posséder la possibilité, dans certaines conditions d'humidité édaphique et atmosphérique, d'émettre un pivot à croissance rapide (3 cm par jour) susceptible de s'enfoncer profondément dans le sol: au bout de trois semaines de culture en sol sec et atmosphère saturée, la vitesse de croissance du pivot n'offre encore aucun signe de ralentissement, alors que le pivot mesure déjà 60 cm de long et que les parties aériennes atteignent à peine une hauteur de 3 cm.

D'une part, la présence d'un pivot profond en sol sec est un caractère fréquent chez les plantes des régions arides ou semi-arides, auquel de nombreux auteurs (Oppenheimer, 1961; Walter, 1963; Kausch, 1960) ont attribué le sens d'une adaptation à la sécheresse. Walter (1963) indique qu'en raison de la compétition dans les régions arides on trouve surtout des espèces dont la croissance rapide (verticale ou horizontale d'ailleurs) est fixée génétiquement. Une vitesse de croissance rapide du pivot aux dépens des racines latérales et des parties aériennes paraît effectivement avantager considérablement ces plantes. Beaucoup d'exemples sont rapportés par Oppenheimer (1961), Killian et Lemée (1956), Birand (1962), d'espèces appartenant à des familles très diverses, dont le rapport entre la longueur de la partie aérienne et celle de la partie souterraine varie de 1/10 jusqu'à 1/300, et dont la vitesse de croissance de la radicule peut atteindre plusieurs centimètres par jour.

D'autre part, l'effet stimulant de l'humidité atmosphérique élevée sur la vitesse de croissance du pivot avait déjà été remarqué par Breazeale *et al.* (1953) et relié à une éventualité d'absorption d'eau par les feuilles.

ABSORPTION D'EAU PAR LES FEUILLES ET TRANSFERT AUX RACINES

L'absorption d'eau atmosphérique liquide ou sous forme de vapeur par les parties aériennes des plantes est un

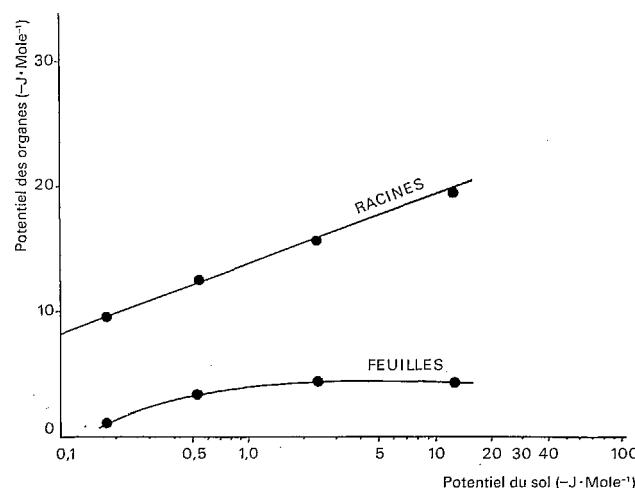


FIG. 3. Variation du potentiel hydrique des feuilles et des racines de *Sinapis alba*, en fonction du potentiel hydrique du sol, en atmosphère saturée d'humidité.

phénomène connu depuis longtemps et que plusieurs auteurs ont nettement mis en évidence (Breazeale, McGeorge et Breazeale, 1950; Haines, 1952; Stone, Went et Young, 1950; Meidner, 1954) et dont l'intérêt écophysiologique et même agronomique souvent discuté (Stone, 1957a, b; Went et Duvdevani, 1953; Duvdevani, 1957; Kraaijenga, 1963), très controversé (Monteith, 1963; Slatyer, 1960), a cependant été reconnu comme non négligeable chez des espèces de régions arides qui doivent supporter de longues périodes de sécheresse et peuvent utiliser les moindres condensations d'humidité atmosphérique sans lesquelles elles ne pourraient survivre (Waisel, 1958, 1960; Bhatt et Lahiri, 1964).

Outre la possibilité d'absorption d'eau par les feuilles, de nombreux travaux ont de plus montré qu'un transfert pouvait s'effectuer vers les racines, selon un flux inversé (Slatyer, 1960; Müller-Stoll, 1963; Vaadia et Waisel, 1963).

INVERSION DU GRADIENT DE POTENTIEL HYDRIQUE CHEZ LE «*SINAPIS ALBA*» EN ATMOSPHÈRE SATURÉE D'HUMIDITÉ

Techniques

Les plantes cultivées dans les conditions expérimentales précédemment exposées sont récoltées âgées de 15 jours et le potentiel hydrique des feuilles et des racines est mesuré par la méthode de Shardakov (1953). Cette méthode souvent critiquée nous a cependant donné d'excellents résultats, conformes de plus à ceux fournis par les méthodes d'équilibre de tension vapeur et des thermocouples psychrométriques (Rhaïem, 1969). Les mesures sont effectuées 3 heures après le début de la photopériode.

Résultats

Les résultats sont traduits par la courbe de la figure 3, où chaque point représente le potentiel hydrique moyen d'une vingtaine de feuilles ou de racines prélevées sur des plantes différentes, ayant poussé dans la même condition hydrique. On constate que le potentiel hydrique des feuilles se maintient constant autour de la valeur $-4,5 \text{ J. mole}^{-1}$ indépendamment de la diminution du potentiel hydrique du sol, alors que le potentiel hydrique racinaire diminue comme une fonction logarithmique de celui du sol, fait que nous avions déjà mis en évidence dans d'autres conditions de demande évaporative (Vartanian et Vieira da Silva, 1968a). Ce qui entraîne l'apparition dans la plante d'un gradient inversé de potentiel hydrique dont la valeur absolue augmente avec la diminution de potentiel hydrique édaphique et racinaire (fig. 4). La valeur élevée du potentiel maintenue dans les feuilles ne peut se concevoir sans faire intervenir une absorption d'eau atmosphérique par les feuilles de *Sinapis alba* placées en atmosphère saturée, au cours de

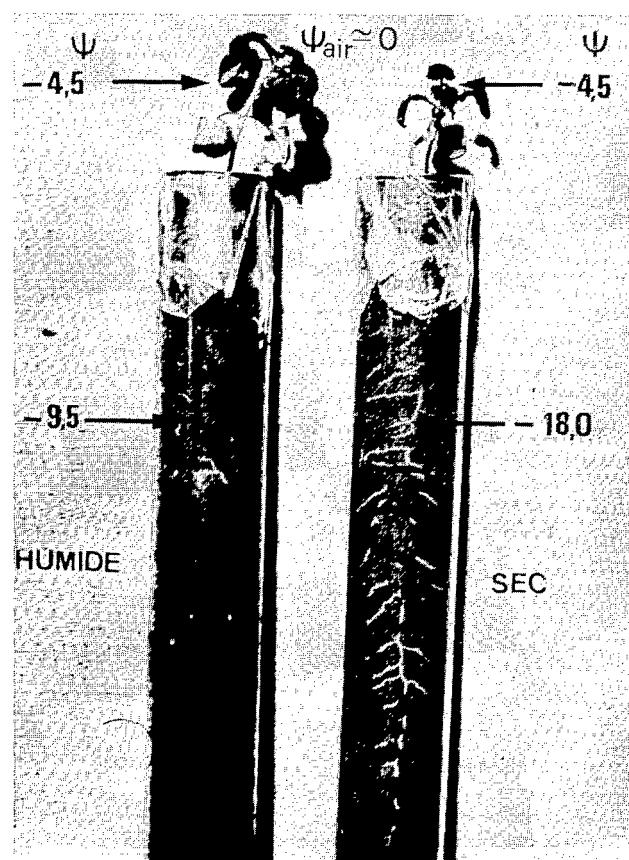


FIG. 4. Gradient inversé de potentiel hydrique dans la plante (en $J \cdot mole^{-1}$) en atmosphère saturée. A gauche, culture en sol humide; à droite, culture en sol sec. Les chiffres indiquent la valeur du potentiel hydrique au niveau des feuilles et des racines.

la nyctipériode, qui annule leur déficit hydrique. Nous avons montré (Vartanian et Vieira da Silva, 1968b) que cette absorption nocturne alternait avec une faible transpiration diurne due à l'échauffement des feuilles dont la température devient supérieure à celle de l'air au cours de la photopériode, les deux phénomènes n'étant pas incompatibles comme l'avaient déjà souligné plusieurs auteurs (Breazeale, McGeorge et Breazeale, 1950; Stone, Went et Young, 1950). De plus, des mesures du gradient dans la plante après des périodes nocturnes allant de 2 à 5 jours nous ont permis de constater qu'en l'absence de toute transpiration un très net transfert aux racines pouvait s'effectuer. Des modèles théoriques indiquant le sens du flux d'eau dans le système sol-plante-atmosphère ont d'ailleurs été proposés pour interpréter ces résultats à partir des données expérimentales.

CONSÉQUENCES POUR LA CROISSANCE RACINAIRE

L'existence d'un gradient inversé de potentiel hydrique chez *Sinapis alba*, en sol sec et atmosphère saturée, permet d'interpréter assez vraisemblablement la croissance rapide du pivot dans ces conditions.

Vieira da Silva (1968) a montré que chez le Cotonnier soumis à un stress hydrique les glucides solubles s'accumulaient dans les feuilles en raison d'un ralentissement du transfert aux racines. Par contre, lorsque les parties aériennes des plantes sont placées en atmosphère saturée, il constate, avec l'emploi de saccharose ^{14}C , une migration accélérée des glucides des feuilles vers les racines, qu'il attribue à l'existence d'un gradient inversé de potentiel hydrique établi dans la plante et déterminant un flux passif d'eau des feuilles aux racines. Ainsi les glucides non utilisés par les parties aériennes (on sait qu'en conditions de sécheresse du sol l'utilisation des produits de la photosynthèse est ralentie) seraient totalement disponibles pour la croissance racinaire si leur transfert est rendu possible par un flux inversé.

D'autre part, plusieurs auteurs, dont Pallas (1958), Clor, Craft et Yamaguchi (1962), Cordes (1966), ont mis en évidence une accélération du transfert de substances de croissance (AIA et 2-4 D, marqués au ^{14}C) appliquées sur les feuilles, vers les racines en atmosphère humide. Cordes a ainsi observé que la vitesse de transfert de l'AIA marqué était doublée quand l'humidité atmosphérique relative passait de 50 à 70% ou plus. Selon cet auteur, en atmosphère humide, le xylème serait une voie de transfert basipète disponible, en raison du ralentissement du flux transpiratoire acropète normal.

L'influence de l'humidité atmosphérique sur le transfert éventuel d'un facteur de croissance endogène susceptible de stimuler la croissance du pivot chez *Sinapis alba* nous est suggérée par les expériences suivantes:

Des germinations de Moutarde âgées de 24 heures sont repiquées en atmosphère saturée et sol sec ou humide. Dans le premier cas, le pivot poussera vite et

profondément, dans le deuxième cas, très lentement. Dans la culture en sol sec, si l'on arrose le sol vingt-quatre heures après le repiquage, le pivot va croître aussi lentement que si la plante avait poussé dès le départ en sol humide. Au contraire, si le sol est arrosé sur toute la hauteur du tube, trois jours après l'implantation en sol sec, le pivot garde son rythme de croissance rapide jusqu'au bout de l'expérience, bien qu'il soit maintenant en sol complètement humide.

Il semble donc que le pivot soit très sensible à la sécheresse du sol dans les premières heures qui suivent son implantation, et que le sol sec induise, dès le départ, une vitesse de croissance rapide du pivot. Ensuite, l'induction étant réalisée, la stimulation de croissance qui en découle s'exprime quelle que soit alors l'humidité du sol. Ces expériences sont réalisées en atmosphère saturée, où l'effet du stimulus induit par le sol sec peut s'exprimer grâce au gradient inversé de potentiel hydrique créé par ces conditions.

FORMATION D'UNE STRUCTURE RACINAIRE XÉROMORPHIQUE

CONDITIONS EXPÉRIMENTALES

Effet d'un assèchement progressif: initiation d'une structure xéromorphique

Les cultures de *Sinapis alba* sont effectuées au phytotron selon les techniques déjà décrites.

Le sol humide au départ (à la capacité de rétention, par exemple) s'assèche sous l'effet de la transpiration, en atmosphère sèche (50% d'humidité relative, température 24 °C). Au bout d'une dizaine de jours, on observe sur les racines latérales d'ordre 1, émises par le pivot en progression basipète, la présence d'ébauches de racines d'ordre 2. (En sol humide, les racines latérales d'ordre 2 apparaissent normalement plus tard, vers le quinzième jour.) Des ébauches semblables existent aussi sur le pivot. Elles sont toutes localisées dans la partie proximale de la racine (fig. 5). Dans cette région, le sol est déjà considérablement asséché, le potentiel hydrique a baissé de 21 J. mole $^{-1}$. Le potentiel hydrique racinaire au moment de l'apparition des ébauches se situe autour de -2.0 J. mole $^{-1}$. Une liaison très étroite a été remarquée entre l'apparition de ces ébauches racinaires et le niveau de potentiel hydrique dans la racine même, indépendamment des potentiels hydriques édaphique et atmosphérique (Vartanian, 1971a).

Évolution de cette structure

Si l'assèchement continue, on n'observe aucune évolution: les rudiments restent à l'état d'ébauches racinaires. Ils prennent un aspect renflé à la base, qui fait penser à une tubérisation mais ne s'allongent pas. Les plantes



FIG. 5. Système racinaire de *Sinapis alba* âgé de 1 mois montrant le pivot, les racines latérales d'ordre 1 et les ébauches d'ordre 2 tubérisées. X 10.

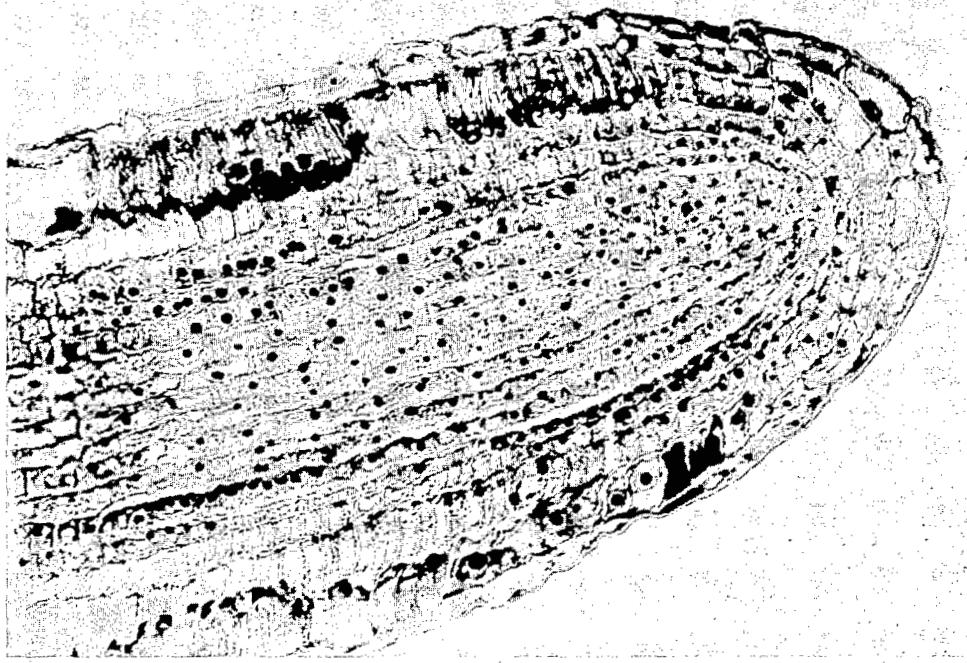


FIG. 6. Section longitudinale axiale d'ébauche âgée de 15 jours, montrant la croissance radiale des cellules corticales méristématiques.

Fixation Navaschine. Coloration hématoxyline-éosine. $\times 370$.

peuvent persister ainsi pendant 2 mois, avec une allure complètement desséchée.

Par contre, lorsque les plantes sont replacées en atmosphère saturée, quelques jours après l'apparition des ébauches, celles-ci montrent un début d'allongement. Ce fait semble constituer une preuve supplémentaire de l'absorption d'eau par les feuilles et de son transfert aux racines sous l'effet d'un gradient inversé de potentiel hydrique qui s'établit lorsque la plante, croissant en sol sec, est placée en atmosphère saturée.

Au bout de 2 mois, alors que les feuilles sont complètement fanées, il suffit de réhydrater le sol jusqu'à la capacité de rétention pour que la croissance reprenne au niveau des méristèmes caulinaires et racinaires: les ébauches de racines d'ordre 2 s'allongent, se couvrent de poils absorbants, perdent leur aspect renflé et peuvent même se ramifier pour donner un nouveau système racinaire fonctionnel permettant à la plante un développement complet jusqu'à la floraison. Alors que toutes les autres parties du système racinaire sont lignifiées, ces ébauches constituent donc des points de survie, permettant à la plante d'attendre, en vie ralenti, que les conditions d'humidité redeviennent favorables.

CARACTÈRES DES ÉBAUCHES RACINAIRES

Caractères morphologiques

La figure 5 montre que ces ébauches racinaires sont deux fois plus larges ($\approx 200 \mu$) que les racines latérales qui les portent. Leur longueur n'excède pas un millimètre pour les plus âgées. Elles sont dépourvues de poils absorbants et présentent souvent un aspect irrégulier qui peut être l'indice d'une disharmonie de croissance entre la zone corticale et la stèle.

Caractères histologiques

Des sections longitudinales axiales réalisées dans ces ébauches selon les techniques classiques de microscopie photonique, colorées au vert de méthyle pyronine (après fixation au FAA) ou à l'hématoxyline-éosine (après fixation au mélange de Navaschine) nous ont permis d'effectuer un certain nombre d'observations.

Structure de racine

Sur ces ébauches, les différents territoires histologiques d'une racine (coiffe, méristème sub-apical, écorce, cylindre central) sont aisément reconnaissables.

Modifications structurales particulières et leur évolution

La coiffe est peu développée, elle possède au plus quatre assises cellulaires, dans les ébauches âgées. L'assise pilifère ne forme jamais de poils absorbants. Les trois assises cellulaires de l'écorce, caractéristiques d'une racine primaire de *Sinapis alba*, ne subissent pratiquement pas d'évolution au cours du vieillissement des ébauches. Mais, dès le stade jeune, elles présentent une particularité remarquable (fig. 6): une très notable croissance radiale (qui multiplie par cinq la largeur des cellules) dans la zone méristématique, ce qui traduit une accélération de la différenciation. De plus, dans la zone de différenciation, les cellules corticales sont hypertrophiées (fig. 7), et dans les ébauches âgées elles présentent une accumulation considérable de grains d'amidon (fig. 8). Croissance radiale des cellules corticales méristématiques et hypertrophie des cellules corticales différencierées sont responsables de la largeur des ébauches comparée à celle des racines latérales.

Au niveau de la stèle centrale, la zone d'elongation maximale, réduite à 60 μ dans une ébauche jeune, s'accroît très peu avec l'âge des ébauches (250 μ dans une ébauche âgée). L'accélération de la différenciation observée dans l'écorce se manifeste encore ici dans la précocité de formation du xylème qui apparaît à 200 μ

de l'apex dans une ébauche jeune, à 400 μ dans une ébauche âgée. Malgré l'absence d'évolution dans la plupart des territoires histologiques, la différenciation du xylème continue (dans une ébauche âgée de deux mois et demi, il n'y a plus de protoxylème mais seulement du métaxylème).

Discussion

Causalité physiologique. De ces observations, nous pouvons donc retenir que les ébauches sont bien des racines, qui ne s'allongent pas et se tubérisent. En effet, sous l'action d'une inhibition d'origine externe ou interne, si la croissance par elongation est suspendue, la croissance radiale est stimulée et l'organe se tubérisé (Courdroux, 1966). Une ébauche de tubérisation a même été observée ainsi par Stein et Forrester (1964) sur des racines de Maïs et de Pois dont l'elongation était momentanément inhibée par trempage dans l'eau lourde. La présence d'amidon accuse encore le caractère de racines tubérisées des ébauches de *Sinapis alba* obtenues en conditions d'assèchement. Cette accumulation d'amidon, apparue progressivement sous l'action du stress hydrique, pourrait bien résulter d'un endurcissement de la plante correspondant à la « phase de restitution » de Stocker. De nombreux travaux cités par Stocker

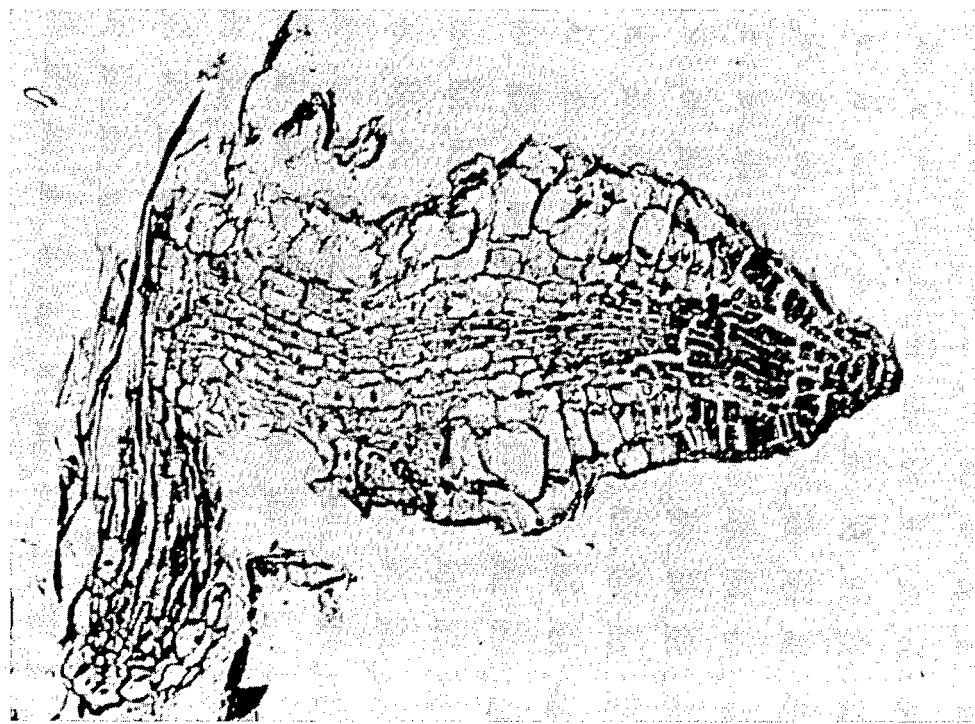


FIG. 7. Section longitudinale axiale d'une ébauche âgée de 2 mois. On remarque l'absence quasi totale d'elongation et l'hypertrophie des cellules corticales différencierées.

Fixation FAA. Coloration vert de méthyle pyronine. $\times 160$.

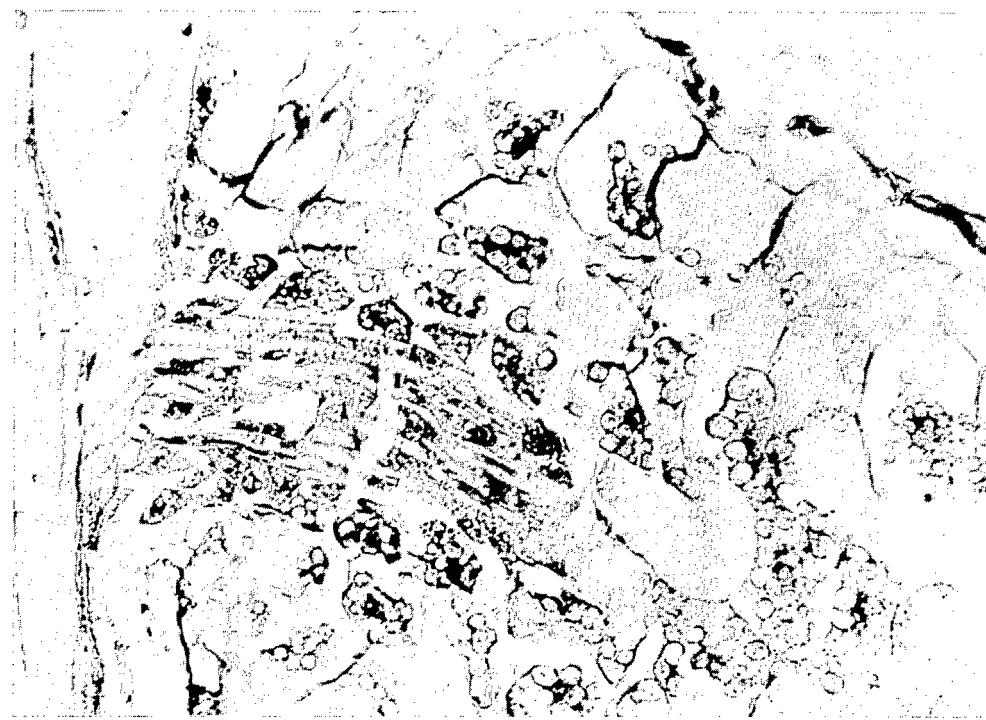


FIG. 8. Section longitudinale axiale de la base d'une ébauche âgée de 2 mois et demi montrant le raccordement des vaisseaux du métraxylème à ceux de la racine parentale, l'hypertrophie des cellules du parenchyme cortical, et l'abondance des grains d'amidon.

Fixation Navaschine. Coloration hématoxyline-éosine. $\times 640$.

(1961) ont montré que l'amidon hydrolysé dans les tissus végétaux dès l'installation du déficit hydrique (phase de réaction) était ensuite synthétisé à nouveau, cette synthèse correspondant à l'adaptation de la plante aux conditions difficiles. Il est bien connu, d'autre part, que les manifestations xéromorphiques s'accompagnent d'une augmentation de la teneur en glucides (Allsopp, 1965; Killian et Lemée, 1956; Iljin, 1929).

Les caractères histologiques relevés dans les ébauches — accélération de la différenciation liée à un ralentissement de l'élongation cellulaire, croissance radiale, puis hypertrophique des cellules corticales — sont, de plus, des signes indéniables de l'action de substances de croissance. Torrey (1953) a bien observé sur le Pois que l'AIA à une concentration qui inhibait l'élongation racinaire, accélérerait la différenciation des éléments du xylème et stimulait la croissance radiale des cellules corticales. Avec l'emploi de substances chimiques de croissance telles le 2-4-D, plusieurs auteurs, dont Wilde (1951) et Hammer (1941), ont obtenu sur le Haricot ou la Tomate une stimulation de la rhizogénèse, accompagnée d'une inhibition d'élongation des racines produites, d'une accélération de la différenciation du xylème et de la croissance radiale des cellules corticales. Il semblerait que les ébau-

ches de racines observées chez *Sinapis alba* soient dues à des modifications d'équilibre entre régulateurs de croissance sous l'action d'une forte carence hydrique installée progressivement.

Signification biologique. La conséquence immédiate de l'existence de ces ébauches est de conférer à la plante une forme de résistance à la sécheresse lui permettant d'attendre un retour aux conditions d'humidité favorables pour reprendre sa croissance. Selon la définition de Maximov appliquée à tout caractère engendré chez la plante par le milieu sec, une telle structure peut être qualifiée de xéromorphe.

Cela rappelle les observations de Wilcox (1968) et de Stone (1965) sur les racines courtes, dormantes, *short dormant roots, white-bead like roots* de *Pinus resinosa, ponderosa, lambertiana*, présentes en quantité notable dans les horizons supérieurs complètement secs du sol, où elles peuvent rester vivantes jusqu'à ce que les conditions hydriques s'améliorent. Cependant, ces racines décrites par Wilcox (1964) ont une structure tout à fait différente, elles ne présentent aucun signe de tubérisation et possèdent des assises de dormance, relevant d'un processus de métacutisation.

La transformation de racines tubérisées en racines absorbantes fonctionnelles paraît tout à fait remarquable chez une plante annuelle telle que *Sinapis alba* dont les racines sont éphémères. Un tel phénomène se rencontre parfois chez une plante vivace (*Ficaria*, décrite par Courdoux, 1966).

En dehors des rudiments de racines, décrits par Cannon (1911) chez quelques annuelles désertiques qui correspondent à des racines de deuxième poussée ne se développant que dans de bonnes conditions d'humidité, la présence de racines tubérisées ne paraît pas avoir été signalée chez une plante annuelle.

Cette structure xéromorphique du système racinaire de *Sinapis alba* semblerait correspondre à un phénomène de vieillissement anticipé, puisqu'elle correspond à l'initiation des racines latérales d'ordre 2 précocement stimulée sous la forme d'ébauches. Oppenheimer (1961) rapporte que l'apparition des xéromorphoses a souvent été interprétée comme le résultat d'un vieillissement accéléré sous l'action de l'assèchement. Vieira da Silva (1970) a montré que la carence hydrique accélérerait la sénescence des feuilles de Cotonnier en déclenchant pré-maturément la tendance à l'hydrolyse dans les tissus.

CONCLUSION

Sous l'action du milieu sec, diverses adaptations ont été mises en évidence chez *Sinapis alba*, notamment la stimulation de croissance du pivot en sol sec et atmosphère saturée, et l'initiation accélérée de racines latérales qui restent courtes et tubérisent, mais sont susceptibles de reprendre leur croissance lorsque les conditions hydriques s'améliorent.

Quelques xéromorphoses plus classiques avaient déjà été observées sur cette plante au niveau des parties aériennes, telle l'augmentation du nombre de stomates, du nombre de vaisseaux dans les pétioles, ou de la densité de nervation foliaire (Rippel, 1919; Lundkvist, 1955) sans qu'on ait pu cependant leur accorder une signification adaptative quelconque.

Cet ensemble de réactions à la sécheresse qui s'expriment aussi bien sur les plans anatomique et morphologique que physiologique montre chez *Sinapis alba* une large potentialité adaptative.

Summary

Adaptive characteristics of white mustard Sinapis alba L. to drought (N. Vartanian)

White mustard, *Sinapis alba* L., grown under experimental control conditions of edaphic or atmospheric drought, exhibits certain adaptive characteristics: accelerated growth of the tap-root in dry soil and saturated atmosphere; appearance of xeromorphosis at the root system level, resulting from progressive drying and a reduction in root water potential. The rapid growth of the tap-root in dry soil and saturated atmosphere is

interpreted as the effect of a transfer of trophic or growth promoting substances to the roots by means of the water potential inverse gradient which is set up in the plant under these conditions.

The xeromorphic structure of the root system is presumably induced by an imbalance between growth regulators, produced by the acute lack of water. This structure enables the plant to resist drought by virtue of its tuberous and dormant roots which act as a retention factor during unfavourable humidity conditions.

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Experimental evidence for the effect of barometric pressure on photosynthesis and transpiration

J. Gale

Department of Botany, Hebrew University
Jerusalem (Israel)

Theoretical aspects of the possible effect of barometric pressure on photosynthesis and transpiration were studied in this laboratory (papers in preparation). It was argued that, contrary to expectation (Decker, 1947; Mooney *et al.*, 1966; Tranquillini, 1964), the availability of CO₂ for photosynthesis should not be much reduced by low barometric pressure, despite the concomitant reduced concentration of CO₂ in the air (mass per volume). This, essentially, is due to an increase of the CO₂-in-air diffusion coefficient compensating for the reduced CO₂ concentration. It was also predicted that the photosynthesis of plants which have high efficiencies of photosynthesis and low mesophyll resistance to the uptake of CO₂, should be less affected by low barometric pressure than plants having high values of mesophyll resistance. Such differences in efficiency have been related to the presence, in plants of low efficiency, of the Calvin cycle of CO₂ fixation and photorespiration and to the presence of the C₄ carbon fixation pathway and absence of photorespiration in plants with high photosynthetic efficiency (Bull., 1969).

Calculations showed that the escaping tendency of water should be considerably increased by even small reductions in barometric pressure. As in this case, the increase of the coefficient of diffusion of water vapour in air, at reduced pressures, would add to the effect of the reduced air-moisture density, consequently when water and energy (radian or advective) are readily available, transpiration of plants growing at even moderate elevations should be considerably greater than that of plants at low elevations.

The effect of pressure on evaporation has been noted by earlier authors (Crafts *et al.*, 1949). However, although a few of the terms in some of the well known semi-empirical equations of evapotranspiration potential are pressure dependent (e.g. Monteith, 1965), most emphasis has been placed on the supply of radiant energy. Under Mediterranean-type climatic conditions, large

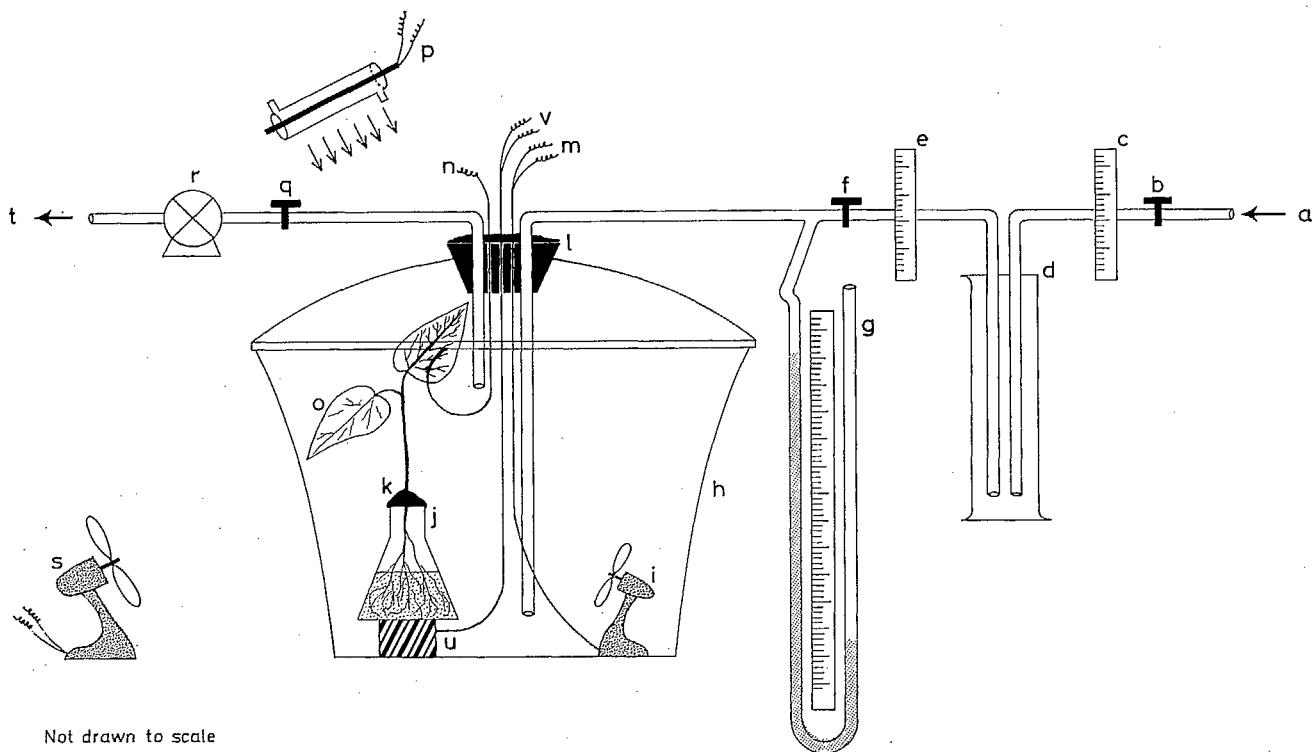
amounts of advective energy are often available to plants, and presently available equations for estimating evapotranspiration do not cope with such situations.

The present paper presents evidence, obtained in the laboratory under isothermal conditions, which supports the predictions discussed above.

MATERIALS AND METHODS

Carbon dioxide uptake and transpiration were measured in an open flow system. An infra-red gas analyser was used for detecting CO₂ and lithium chloride hygrometers for sensing humidity. Air of constant temperature (25° C) was supplied to the chamber. The air contained 200 µl/l CO₂ and water vapour at a level of 50 per cent relative humidity at 25° C. The plant chamber consisted of a dessicator jar of 25 cm diameter. The plants were placed in water, in an Erlenmeyer flask within the jar and the neck of the flask was sealed around the plant with plasticine. Illumination was with a water-jacketed 1,500 W Sylvania quartz-line lamp which gave approximately 0.4 cal cm⁻² min⁻¹ within the jar at the height of the leaves. A constant flow of air (measured at room pressure) and different, controlled barometric pressures within the chamber were obtained with the system shown in Figure 1.

Air was drawn through the plant chamber by the suction pump (r) at a constant flow rate, controlled by the valve (q) and measured by the flowmeter (e). Air was supplied under a small pressure head at (a); the rate of flow was measured at (c), where it was maintained at a level about 50 per cent higher than that at which it was taken up by the system; the surplus air overflowed from (d). Air pressure within the chamber was controlled by the valve (f). Changes in airflow due to closure of valve (f) were offset by adjustments of valve (q). Pressure in the chamber was measured with the



Not drawn to scale

FIG. 1. Open flow gas system for measuring transpiration and photosynthesis under conditions of reduced barometric pressure. (a) air supply at controlled temperature, CO_2 and humidity content; (b) flow valve—for controlling flow in (c); (c) flowmeter (flow controlled to about 1.5 l min^{-1}); (d) cylinder height 45 cm; (e) flowmeter (flow controlled to exactly 1 l min^{-1}); (f) (q) flow valves for controlling flow in (e) and pressure in chamber; (g) mercury manometer—height 60 cm; (h) plant chamber consisting of dessicator jar—diameter 25 cm; (i) fan within jar; (j) Erlenmeyer flask; (k) plasticine seal; (l) vacuum sealing around tubes and leads which pass through rubber stopper in top of dessicator jar; (m) electric lead to fan; (n) thermocouple pressing on underside of leaf for monitoring leaf temperature; (o) plant leaf or model (see text); (p) water jacketed Sylvania quartz-line lamp—1,500 W; (q) flow restricting valve [see (f)]; (r) membrane pump, with capacity of 250 mmHg suction at 1 l min^{-1} ; (s) fan for cooling chamber; (t) air exhaust leading to hygrometer and infra-red gas analyser; (u) magnetic stirrer (used only for NaOH model); (v) electric lead to magnetic stirrer.

manometer (g), the value so obtained being subtracted from barometric pressure, to give absolute pressure. The elevation of the laboratory at Jerusalem is 800 m and barometric pressure varies around 693 mmHg. While the plant in this system is held at varying pressures, the measuring devices (flowmeters, hygrometer and infra-red gas analyser) operate at room pressure. Leaf temperatures were measured with a thermocouple (n), pressed to the underside of the leaf. From these temperatures and from transpiration and vapour gradients, stomatal resistances were calculated by the usual

procedures (Gaastra, 1959). Absolute values of stomatal resistances so calculated were not very accurate due to the irregular orientation of the leaves to the light and to the asymmetry of the bean leaves (Gale, 1968). However, changes in stomatal resistances could easily be detected.

In order to test the physical principles involved in the effect of pressure on evaporation and CO_2 uptake, the system was first tested on a model. The model consisted of a 38 cm^2 petri dish covered and sealed with filter paper, then 10 ml of 1 N NaOH solution was injected

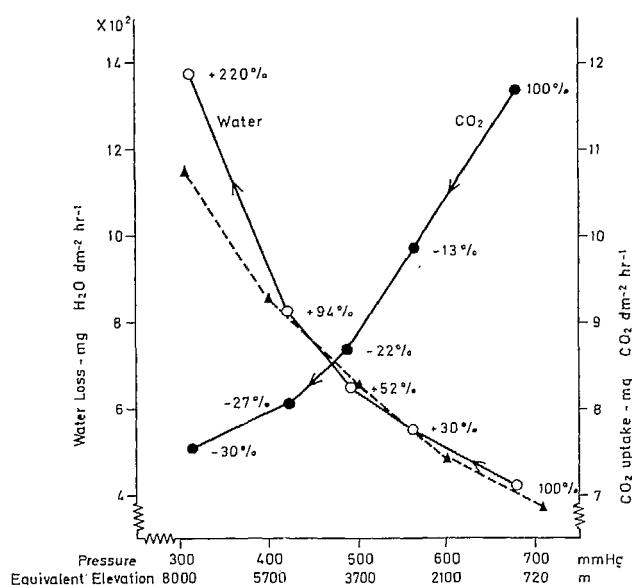


FIG. 2. Effect of barometric pressure on the water loss and CO_2 uptake of a model. <, Course of experiment; O—O, Experimental; ▲—▲, Predicted.

through the filter paper immediately prior to the experiment. This model was expected to evaporate water and to absorb CO_2 in a manner analogous to that occurring in the diffusion pathways of transpiration and photosynthesis. The resistance through the filter paper is parallel to stomatal resistance and the resistance over the paper to boundary layer resistance.

Bean (*Phaseolus vulgaris*) was chosen as a plant having low photosynthetic efficiency and relatively high mesophyll resistance to CO_2 uptake. Entire seedlings at the 2 juvenile leaf stage were used. The roots were in tap water.

Maize (*Zea mays*) was chosen because of its high photosynthetic efficiency and low mesophyll resistance. Single leaves approximately 5 cm wide were cut off from 2-month-old seedlings and placed in water in the Erlenmeyer flask (Fig. 1 (j)). The leaves were cut short to leave an exposed section of 35–40 cm^2 .

Moist paper models of the same size and shape as the Petri dish model and the bean or maize leaves were used to estimate boundary layer resistances, as described by Gaastra (1959).

Experiments were generally begun at room pressure, and measurements of transpiration and leaf temperature were made for calculation of initial stomatal resistance. Pressure was then reduced in stages. At least 45 min were allowed at each stage for the plant and system to come into equilibrium before new measurements of photosynthesis and transpiration were made. At the end of the experiment air pressure was returned to normal and stomatal resistance was again calculated. A few check experiments were run, starting from low and

ascending to high pressure. The results were essentially the same as in the experiments run in the reverse direction.

From 4 to 6 runs of each type of experiment (model, bean and maize) were made.

RESULTS

The results were very uniform within each type of experiment. They could not, however, be pooled as there were variations of stomatal movement, in the course of the experiments, which modified the results. A representative result of each type of experiment is presented below.

The results of an experiment carried out with the Petri dish model are given in Figure 2, which shows that with each decline in air pressure, water loss from the model increased. The rate of water loss at 300 mmHg was 320 per cent of that at 690 mmHg. The escaping tendency shown in the figure has been calculated for pressures of 700–300 mmHg from the boundary and "stomatal" resistances. These were measured at 690 mmHg and, consequently, the predicted and measured values coincide at this pressure. The close agreement between the predicted escaping tendency and the measured water loss indicates that a sufficient supply of energy was available to support this rate (see "Discussion"). The disparity at low pressure is unexplained, but may have been caused by drying of the filter paper and widening of its pores.

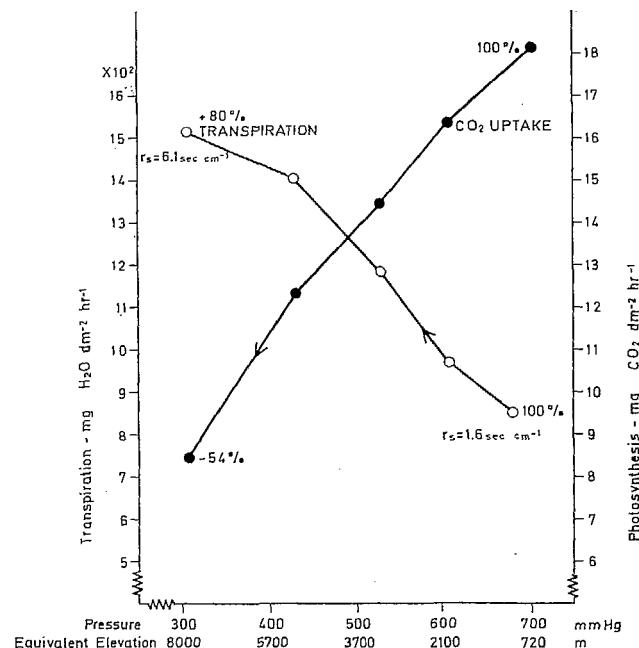


FIG. 3. Effect of barometric pressure on the transpiration and photosynthesis of a bean plant. <, Course of experiment.

The curve for CO_2 uptake shows that the percentage reduction of CO_2 uptake was considerably less (~30 per cent) than the drop in barometric pressure (~50 per cent). However, the reduction of CO_2 uptake was greater than anticipated for a model lacking internal resistance to CO_2 uptake (r_m) and is more in agreement with that expected for a model showing resistance to CO_2 uptake in the liquid phase. This may have been caused by the formation of carbonates at the surface of the solution and to inadequate stirring. As we do not know the value of the resistance of the NaOH solution to CO_2 uptake, nor whether this resistance was constant, a predicted curve could not be calculated.

Photosynthesis declines and transpiration increases with each fall in barometric pressure in the experiment with the bean plant shown in Figure 3. However, the increase in transpiration was less and the decrease in photosynthesis was greater than expected. This was no doubt caused in part by the increase of stomatal resistance from 1.6 at the start of the experiment to 6.1 sec cm^{-1} at 300 mmHg.

The results of the experiment with maize, shown in Figure 4, show that the rise in transpiration with the fall in air pressure, was much greater than in the bean plant (Fig. 3). It was equal to that obtained with the model (Fig. 2). It should be noted that there was hardly any change in stomatal resistance. Photosynthesis was, however, little affected and fell only 6 per cent for a 56 per cent drop in pressure. The small fluctuation which occurred between 690 and 550 mmHg may have been caused by changes in stomatal aperture.

In the above experiments there was the constant complication of stomatal closure during the course of

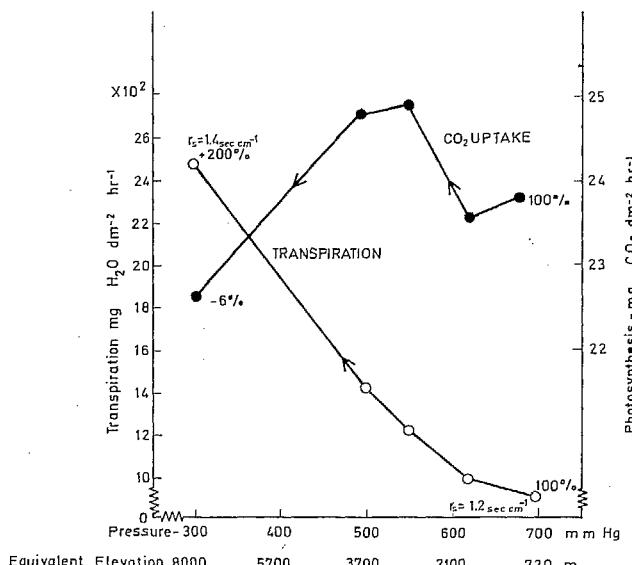


FIG. 4. Effect of barometric pressure on the transpiration and photosynthesis of a maize plant leaf. <, Course of experiment.

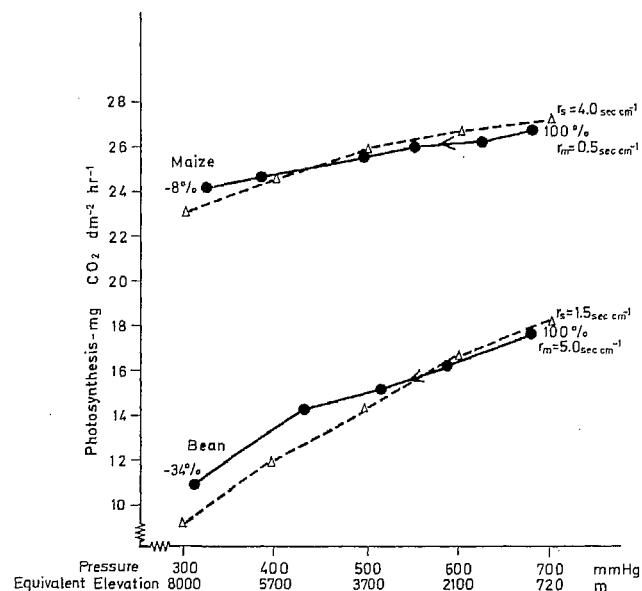


FIG. 5. Effect of barometric pressure on the photosynthesis of maize and bean plants under humid air conditions. <, Course of experiment; △---△, Predicted; ●—●, Experimental. Press. 65 p.

the experiment, especially with the bean leaves. This was probably caused by loss of turgor due to the high rates of transpiration at low barometric pressures. In order to overcome this difficulty in the evaluation of the effect of pressure on photosynthesis, the experiments were run with moist air (relative humidity 80 per cent at 25° C). In these experiments transpiration was not measured. The results of 2 such experiments, 1 with maize and 1 with bean plants, are shown in Figure 5.

In these experiments photosynthesis, transpiration and leaf temperatures were first measured at normal pressure (693 mmHg) and with incoming air at 50 per cent relative humidity at 25° C for calculation of stomatal (r_s) and mesophyll (r_m) resistances to CO_2 . Only then was the incoming air humidity raised to 80 per cent for the rest of the experiment (actual humidity in the chamber was even higher due to transpiration). The initial values of r_s and r_m were used to calculate the effect of falling barometric pressure on photosynthesis from theory.

Predicted and actual values of photosynthesis showed good agreement (Fig. 5). For a total drop of 56 per cent in pressure the photosynthesis of the bean plant fell to 66 per cent of its original value, while that of the maize leaf fell to only 92 per cent of the initial values. In 6 such experiments with maize and 8 with beans, photosynthesis in bean fell by 31.2 ± 2.4 per cent and in maize by 9.9 ± 4 per cent for a drop in pressure of from 690 to 310 mmHg.

DISCUSSION

The experiments carried out with the model (Fig. 2) and with the plants (Figs 3 and 4) show that barometric pressure can have a large effect on evaporation and transpiration. The effect of barometric pressure is on the escaping tendency of the water (Gale, in preparation). Ultimately the rate predicted by the escaping tendency equation will not be maintained unless there is an adequate supply of energy and water. In these experiments incoming radiation was at the rate of 0.4 cal $\text{cm}^{-2} \text{ min}^{-1}$. Assuming that 80 per cent of this energy could be used for transpiration and that approximately 600 calories are required to evaporate 1 g of water at 25°C , then this is sufficient energy to evaporate 3.2 g water $\text{dm}^{-2} \text{ hr}^{-1}$. This is more than the maximum transpiration rate attained in these experiments — 2.5 g $\text{dm}^{-2} \text{ hr}^{-1}$ (maize at 300 mmHg; Fig. 4).

The increase of transpiration with falling pressure in the bean experiment (Fig. 3) is considerably less than that of the model (Fig. 2) or the maize plant (Fig. 4). It was suggested above that this could be explained by the closure of the stomata in the course of the experiment. This may be taken as an example of lack of water limiting transpiration in the presence of a high escaping tendency and an adequate supply of energy. Although the bean roots were in water, the leaves were evidently losing water at a rate greater than the roots could supply it.

The above experiments show that, although photosynthesis of plants with low photosynthetic efficiencies decreases with falling barometric pressure, it does so to a lesser degree than the fall in pressure. Photosynthesis of plants with low mesophyll resistance to CO_2 uptake is only slightly affected by large changes in barometric pressure.

These experiments were carried out under approximately isothermal conditions and relatively low barometric pressures (to 300 mmHg) were attained. This was done in order to evaluate the physical principle involved. However, a pressure of 300 mmHg is only reached, under natural conditions, at an elevation of about 8,000 m. At this height temperatures would normally be too low for plant growth. However, from the data given above, it can be seen that, under isothermal conditions and when energy is available, transpiration may be increased as much as 30 per cent for a drop in pressure equivalent to a rise in elevation from sea level to about 1,000 m.

In the hills of Mediterranean-type regions almost isothermal conditions often prevail in the summer season, up to heights of 1,000 m and above. Furthermore, energy for increased rates of transpiration is often available both from high levels of radiation (Ashbel, 1950) and from the advective heat carried in hot dry winds (Katznelson, 1956). On the other hand, the decreased availability of CO_2 for photosynthesis at such relatively low elevations would be only a minor factor in plant growth.

Résumé

Données expérimentales pour l'étude de l'influence qu'exerce la pression atmosphérique sur la photosynthèse et la transpiration (J. Gale)

L'auteur présente les résultats d'expériences sur l'influence de la pression barométrique sur la photosynthèse et la transpiration. Une basse pression réduit moins la photosynthèse que la baisse de la pression et la chute concomitante de la teneur de l'air en gaz carbonique (masse de CO_2 /volume d'air). Il est démontré que l'effet de la basse pression sur le CO_2 disponible pour la photo-

synthèse varie avec les caractères physiologiques de la plante, et qu'il est particulièrement minime chez les plantes ayant une faible résistance du mésophylle à la fixation de CO_2 .

Une pression atmosphérique réduite augmente considérablement la tendance des molécules d'eau à s'échapper. Lorsque l'approvisionnement en eau et en énergie est suffisant, il peut en résulter une très grande augmentation de la transpiration, ce qui peut avoir une importance écologique considérable dans les régions montagneuses de climat méditerranéen.

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L'enceinte climatisée en tant qu'outil permettant de relier les recherches de laboratoire et de terrain

F. E. Eckardt

Section d'écophysiologie du CEPE
CNRS, Montpellier (France)

La production primaire et la quantité de biomasse végétale immobilisée par un écosystème donné dépendent non seulement du rendement de la photosynthèse, mais aussi de la manière par laquelle les produits de la photosynthèse sont utilisés, soit pour édifier des organes chlorophylliens capables d'intercepter et de transformer l'énergie rayonnante du soleil, soit pour former des organes de stockage ou de défense, consommateurs seulement d'énergie. Le jeu conjugué des trois processus, photosynthèse, respiration et répartition des photosynthétats, détermine ainsi pour une part essentielle le montant des entrants et sortants en énergie de l'écosystème ainsi que la biomasse pouvant être maintenue dans les conditions du milieu naturel.

Par l'étude parallèle des échanges de carbone entre la surface de la couverture végétale et la basse atmosphère d'un côté, et du mode d'utilisation de ce carbone pour édifier le végétal de l'autre, on peut faire ressortir certains aspects caractéristiques dans le comportement des divers écosystèmes malgré des différences d'espèce, de climat, d'histoire, etc. (fig. 1). Ce n'est toutefois qu'avec l'introduction de modèles mathématiques de simulation, statiques ou dynamiques, qu'il est devenu possible, par une méthode adéquate, de révéler les propriétés liées à la qualité de système auto-adaptatif de l'écosystème, de faire apparaître la signification des divers caractères structuraux ou fonctionnels dans l'ensemble (Curry et Chen, 1970; Sauvezon, 1970; de Wit, 1965, 1969) [fig. 2]. Pour évaluer le rôle dans le fonctionnement de l'écosystème de certaines caractéristiques tels l'indice foliaire ou la loi donnant la photosynthèse en fonction de l'éclairement, il faut connaître la dépendance de la production en carbone, par exemple, de ces caractéristiques. La variation de l'indice foliaire ou de la loi-réponse mentionnée, étant impossible à réaliser *in vivo*, qu'il faut effectuer l'expérimentation à l'ordinateur.

De grandes difficultés existent cependant pour obtenir de l'information sur des sous-systèmes convenables sous

forme de données physiologiques de base ou pour tester le modèle. La biosphère s'est développée en tant que totalité, si bien que les divers rapports de cause à effet qui constituent le fondement de son fonctionnement en dernière analyse sont étroitement interconnectés. A titre d'exemple, la respiration n'augmente pas proportionnellement avec la biomasse sur pied, mais plutôt avec la photosynthèse. Pareillement, la photosynthèse apparente n'augmente pas continuellement avec l'indice foliaire mais tend asymptotiquement vers une valeur limite (Evans, 1970).

LES AVANTAGES DE LA MÉTHODE DES ENCEINTES

Il est donc souvent bien trop ambitieux de vouloir déduire le fonctionnement de tout un écosystème à partir de quelques données sur son comportement physiologique en fonction des facteurs mésologiques obtenus au laboratoire par l'étude de plantes en pots. En pareilles circonstances, les modes de distribution des photosynthétats dans la croissance, de même que la photosynthèse et la respiration, peuvent différer considérablement de ceux observés sur le terrain, en particulier chez des plantes habituellement exposées à des conditions édaphiques sévères, difficiles ou impossibles à reproduire au laboratoire. Le saut est trop grand. Il faut relier la méthodologie de laboratoire (fig. 3) avec celle du terrain (fig. 4a, b; 5a, b; 6, 7) de manière à pouvoir décrocher par paliers la plante ou l'organe végétal de son milieu naturel. Il faut pouvoir suivre son comportement lorsque progressivement elle sera exposée à des conditions contrôlées semblables à celles du laboratoire, afin de mettre en évidence des différences de comportement expliquables par exemple par la rupture de rythmes biologiques ou par des changements d'alimentation en eau et en éléments nutritifs des organes étudiés. Il faut égale-

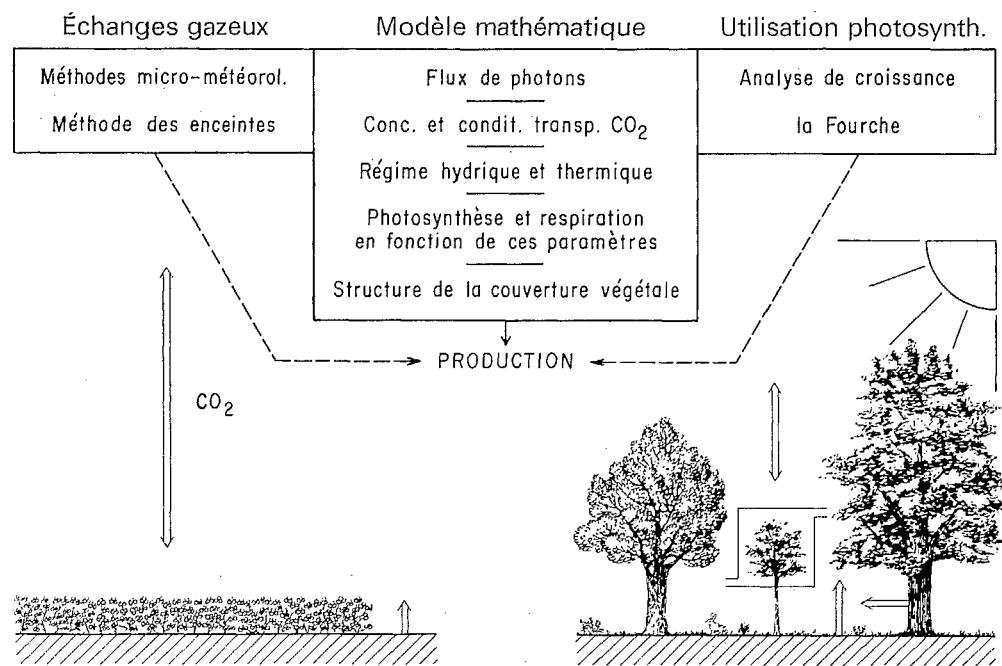


FIG. 1. Comparaison entre deux types d'écosystème.

- a) La jeune culture (à gauche): la presque totalité du CO₂ alimentant les organes chlorophylléens provient de la basse atmosphère; une fraction importante du carbone fixé est utilisée pour former des organes chlorophylléens.
- b) La vieille forêt (à droite): il y a d'autres sources de CO₂ que la basse atmosphère; une fraction importante du carbone fixé est utilisée pour former des organes ne participant pas à la photosynthèse. La distribution différente des produits de la photosynthèse amène des différences du point de vue de la photosynthèse, de la respiration et de la biomasse sur pied.
- c) En haut: méthodes permettant l'évaluation de diverses composantes de la production primaire.

ment pouvoir tenir compte des différences de dimensions des systèmes étudiés au laboratoire et sur le terrain.

A cet égard, l'enceinte climatisée s'avère d'une grande utilité en permettant d'établir un pont entre les recherches de terrain et les recherches de laboratoire. Elle permet notamment: a) de subdiviser l'écosystème en compartiments de dimensions convenables; b) de rendre réglables à volonté divers facteurs mésologiques de manière à passer progressivement aux conditions de laboratoire; c) de faire varier ces facteurs au-delà de leurs domaines de variation habituels pour faciliter l'établissement des rapports de causalité entre le comportement physiologique et le facteur varié; d) de suivre l'évolution du comportement physiologique résultant de changements provoqués intentionnellement dans la structure du feuillage ou dans les conditions d'environnement, afin d'étudier à la fois la réponse instantanée et la réponse à long terme, de nature adaptative; e) de tester le modèle par paliers sur des sous-systèmes de plus en plus complexes

placés dans des conditions se rapprochant progressivement de celles du milieu naturel.

La méthode des enceintes se situe ainsi entre les méthodes micrométéorologiques et celles de laboratoire, les premières renseignant sur le comportement des plantes dans les conditions naturelles, les secondes sur leur comportement dans des conditions contrôlées au moyen de plantes soit fraîchement transférées du terrain, soit cultivées au laboratoire. En transférant des plantes du terrain, on peut suivre leur adaptation aux nouveaux rythmes mésologiques; en utilisant des plantes cultivées au laboratoire, on peut connaître le comportement des plantes qui se sont développées dans des conditions autres que celles de l'écosystème dans lequel elles poussent normalement.

L'emploi à bon escient de l'enceinte climatisée exige cependant une connaissance à la fois pratique et technique de son fonctionnement, afin de pouvoir juger de la validité des résultats des mesures dans les diverses

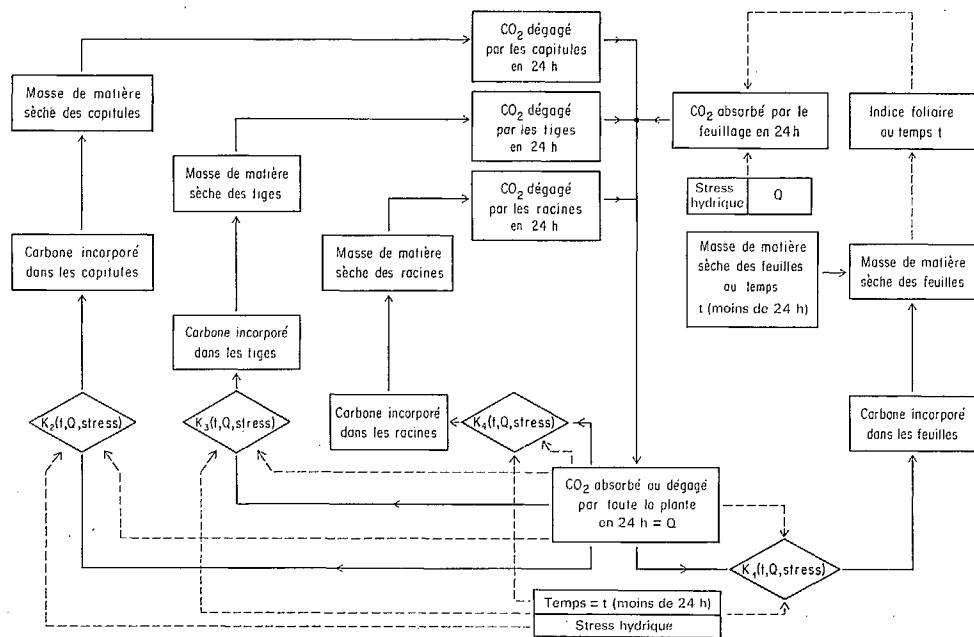


FIG. 2. Diagramme de fonctionnement d'un écosystème au niveau de la production primaire. Ce schéma montre comment le carbone provenant du CO_2 de l'air entraîne, suivant la manière dont il est distribué dans la plante, une augmentation non seulement de la biomasse — ce qui accroît la respiration — mais également, lorsque des tissus chlorophylléens sont formés, de sa capacité d'intercepter l'énergie rayonnante du soleil et, du fait de la photosynthèse, d'incorporer du carbone. Connais-
sant les lois de distribution des produits de la photosynthèse, on peut donc prévoir le changement de biomasse et de capacité de photosynthèse qu'entraîne une certaine incorporation photo-
synthétique de carbone.

conditions d'utilisation. Il convient en particulier de spécifier au départ que le problème du climat de l'enceinte — *das Kuvettenproblem* des auteurs de langue allemande — est toujours loin d'être résolu. Le climat ou, mieux, « le temps » dans une enceinte climatisée, quel que soit le degré de perfectionnement du système de climatisation utilisé, reste toujours différent de celui de l'extérieur. Un effort en vue de reproduire exactement le temps extérieur serait d'ailleurs difficile à justifier, l'un des principaux avantages de l'enceinte étant précisément de simplifier le milieu naturel afin de permettre l'étude du comportement des plantes sous l'effet d'un nombre réduit de facteurs essentiels, que ces facteurs soient réglés de manière à suivre les variations extérieures ou soient réglés à volonté comme au laboratoire.

Pour établir le lien entre mesures du terrain et de laboratoire, il importe de bien connaître, compte tenu du principe de fonctionnement de l'enceinte, les divers facteurs non réglables susceptibles d'influencer le comportement physiologique des plantes étudiées et de préciser les méthodes permettant de réduire les erreurs

qu'ils peuvent introduire dans les résultats. Le présent article a pour objectif de résumer, par des exemples extraits de travaux en voie de publication, l'expérience acquise à cet égard à Montpellier.

DIFFICULTÉS INHÉRENTES A LA MÉTHODE ET PRÉCAUTIONS A PRENDRE

La méthode des enceintes appliquée à l'étude du comportement des plantes dans les conditions naturelles consiste dans le principe à mesurer les quantités de CO_2 , d'eau et d'énergie qu'il faut fournir à l'enceinte ou évacuer de celle-ci pour rétablir à leurs valeurs normales non seulement les échanges gazeux, mais aussi l'élimination de la chaleur à partir des feuilles par re-rayonnement, convection et évaporation. La reproduction exacte des conditions naturelles est irréalisable, les conditions radiatives, la structure fine de l'atmosphère, le bilan hydrique, l'amplitude et la période des fluctuations des paramètres en jeu se trouvant le plus souvent modifiés. A ces difficultés

s'ajoutent celles de mesurer des dégagements de CO₂ et d'installer l'enceinte de manière à obtenir des résultats représentatifs de tout l'écosystème.

Appliquée à l'étude de plantes dans des conditions différentes de celles du milieu extérieur, la méthode reste la même à ceci près que les signaux fournis par les sondes prélevant les conditions extérieures sont remplacés par des signaux réglables à volonté. La variation de l'éclairage est toutefois réalisée au moyen de miroirs ou d'écrans. Utilisée ainsi, l'enceinte provoque l'apparition de gradients anormaux au sein de l'écosystème dont les effets sont souvent difficiles à évaluer.

CONDITIONS RADIATIVES

Dans la conception de l'enceinte, un grand soin doit être pris pour éviter des changements trop grands des échanges radiatifs entre la plante et le milieu extérieur. Il convient de tenir compte des propriétés optiques des maté-

riaux ainsi que de la géométrie de l'enceinte. Pour des enceintes destinées à l'étude des échanges gazeux de rameaux au sommet ou à l'intérieur de la couverture végétale, la forme cylindrique est souvent préférable. Lorsque les génératrices du cylindre sont orientées parallèlement à l'axe polaire, l'absorption et la diffusion du rayonnement solaire restent lors de la journée indépendantes de l'azimuth et de la distance zénithale du soleil (fig. 7).

Quelles que soient les propriétés optiques des parois de l'enceinte, elles provoquent toujours une réduction de l'éclairage et un accroissement du rapport du rayonnement diffus au rayonnement global. En présence d'un feuillage, les effets de l'absorption et de la diffusion se compensent partiellement et peuvent s'annuler, en certaines circonstances comme le montre plus loin l'exemple des Tournesols. L'application du modèle de Wit (1965) semble constituer un moyen valable d'évaluer ces effets (fig. 8a, b).

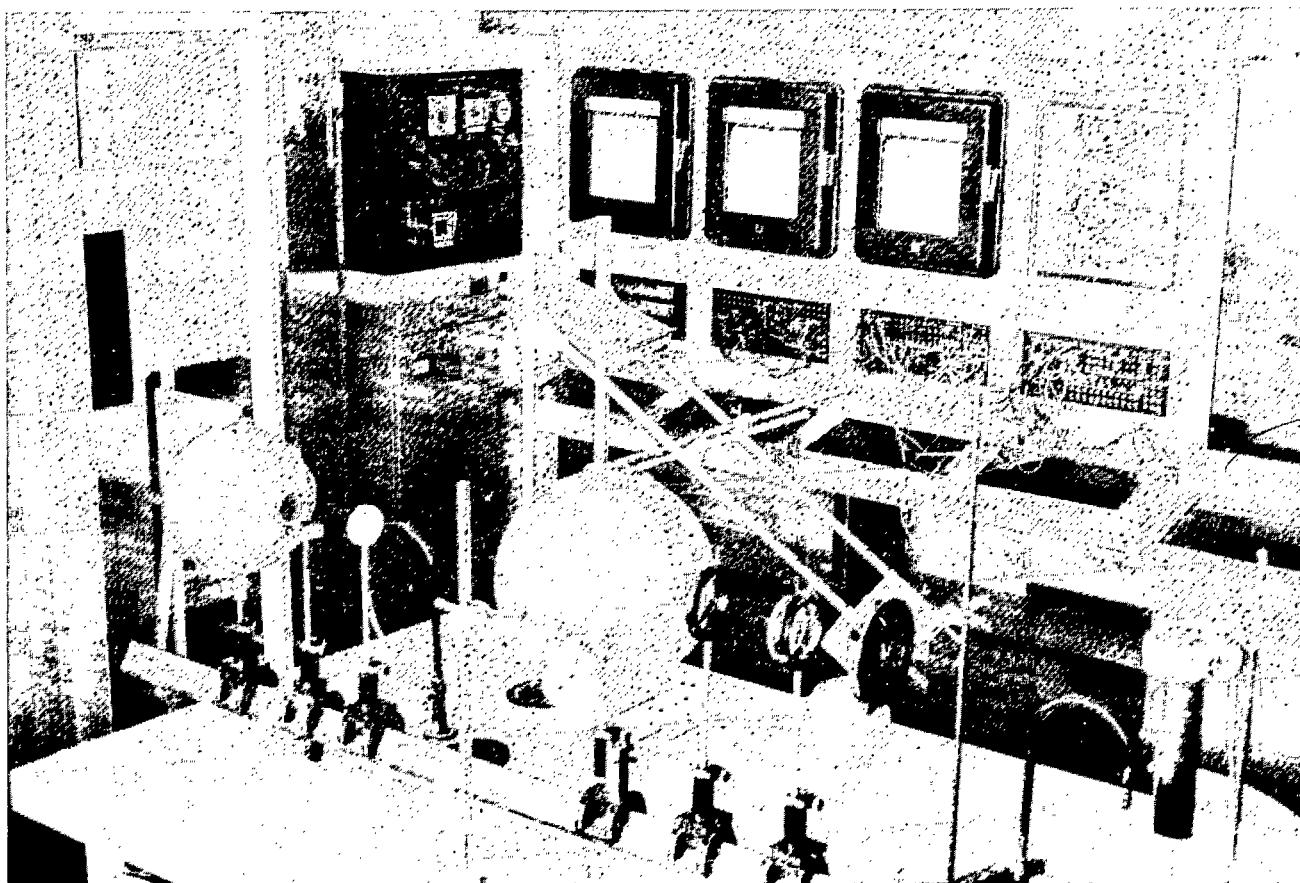


FIG. 3. Laboratoire équipé pour la mesure des échanges gazeux. Au fond, à gauche: salle climatisée éclairée par une lampe au xénon. Au fond à droite: ensemble de régulation permettant le contrôle indépendant et automatique de la température, de la teneur en CO₂ et en vapeur d'eau de l'air et de l'éclairage.

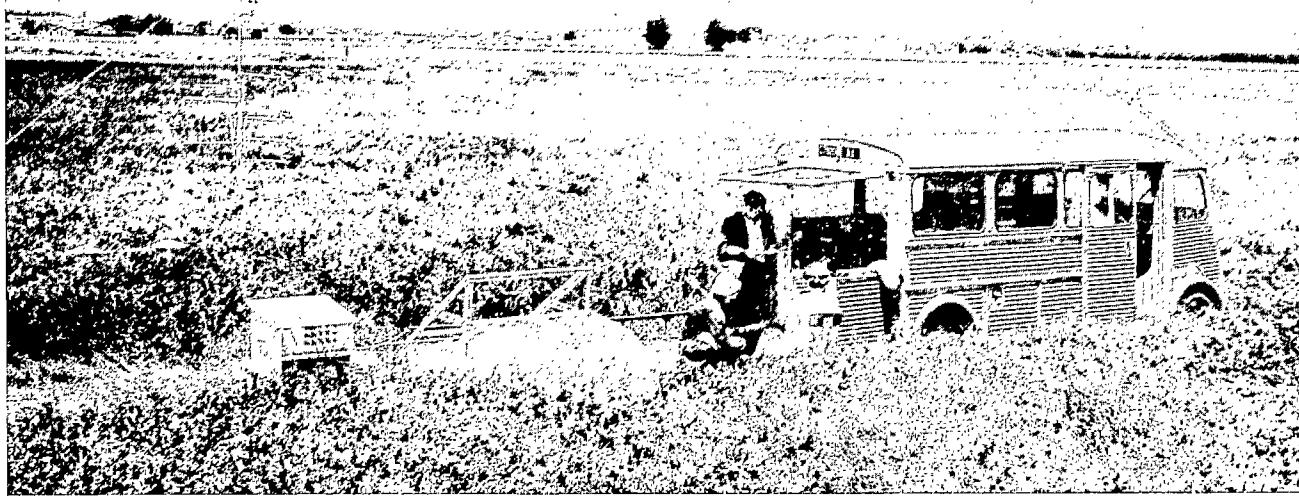


FIG. 4. a) Ensemble de dispositifs utilisés pour l'étude des échanges gazeux d'un champ de *Medicago sativa*. Premier plan: enceinte climatisée et laboratoire mobile. Arrière-plan: mât équipé de sondes micrométéorologiques.

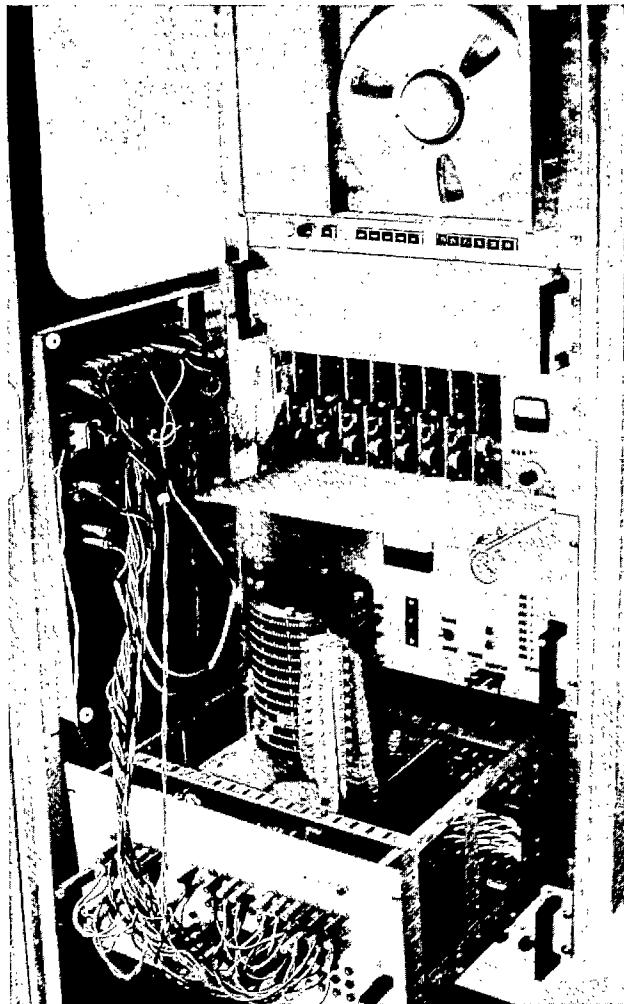


Fig. 4. b) Intérieur du laboratoire mobile: programmeur et enregistreur magnétique.



FIG. 5. a) Ensemble de dispositifs utilisés pour la mesure des échanges gazeux de *Salicornia fruticosa*. Enceinte climatisée et laboratoire mobile.



Fig. 5. b) Détail de la surface expérimentale. Fermée, l'enceinte recouvre 1 m² de sol.



FIG. 6. Enceinte climatisée pour l'étude des échanges gazeux. Contrôle automatique de la température et des teneurs en CO_2 et en vapeur d'eau de l'air. Installés dans une culture d'*Helianthus annuus*.

STRUCTURE DE L'ATMOSPHÈRE

Quoique le principe de l'enceinte soit essentiellement celui de la soufflerie climatisée en circuit fermé (Eckardt, 1966), la variation de l'état de turbulence de l'air et à plus forte raison celle de la structure fine de l'atmosphère ne peuvent se faire que dans des limites restreintes. D'une part, il est difficilement concevable de créer comme à l'extérieur des « coups de vent », d'autre part, la circulation de l'air dans l'enceinte ne doit pas descendre au-dessous d'un certain seuil à partir duquel la climatisation devient impossible.

Pour créer malgré ces difficultés des conditions dans l'enceinte proches de celles du milieu naturel, il reste la possibilité d'installer des sondes de mesure de la température et de l'humidité extérieure à un niveau tel, dans la couverture végétale, que le vent a déjà influencé la valeur de ces grandeurs. Grâce à ce procédé, il a été possible d'obtenir des résultats de mesures d'évaporation

à partir d'une culture de Luzerne presque identiques à ceux réalisés par la méthode du bilan de quantité de mouvement. Il n'en reste pas moins que le procédé est peu défendable du point de vue théorique, aucun critère ne permettant d'indiquer l'emplacement le plus favorable des sondes (fig. 4a, b).

L'installation de diffuseurs dans l'enceinte est généralement nécessaire, à moins que l'air ne passe par des fentes le conduisant parallèlement aux parois de l'enceinte à l'entrée et à la sortie de celle-ci (fig. 9).

RÉGIME HYDRIQUE

Lorsque la végétation souffre d'un manque d'eau, le degré d'ouverture des stomates, et donc les échanges gazeux, est déterminé par un équilibre délicat, lui-même subordonné aux conditions des milieux extérieur et intérieur des plantes. Même de très faibles modifications du microclimat provoquées par l'enceinte peuvent par con-

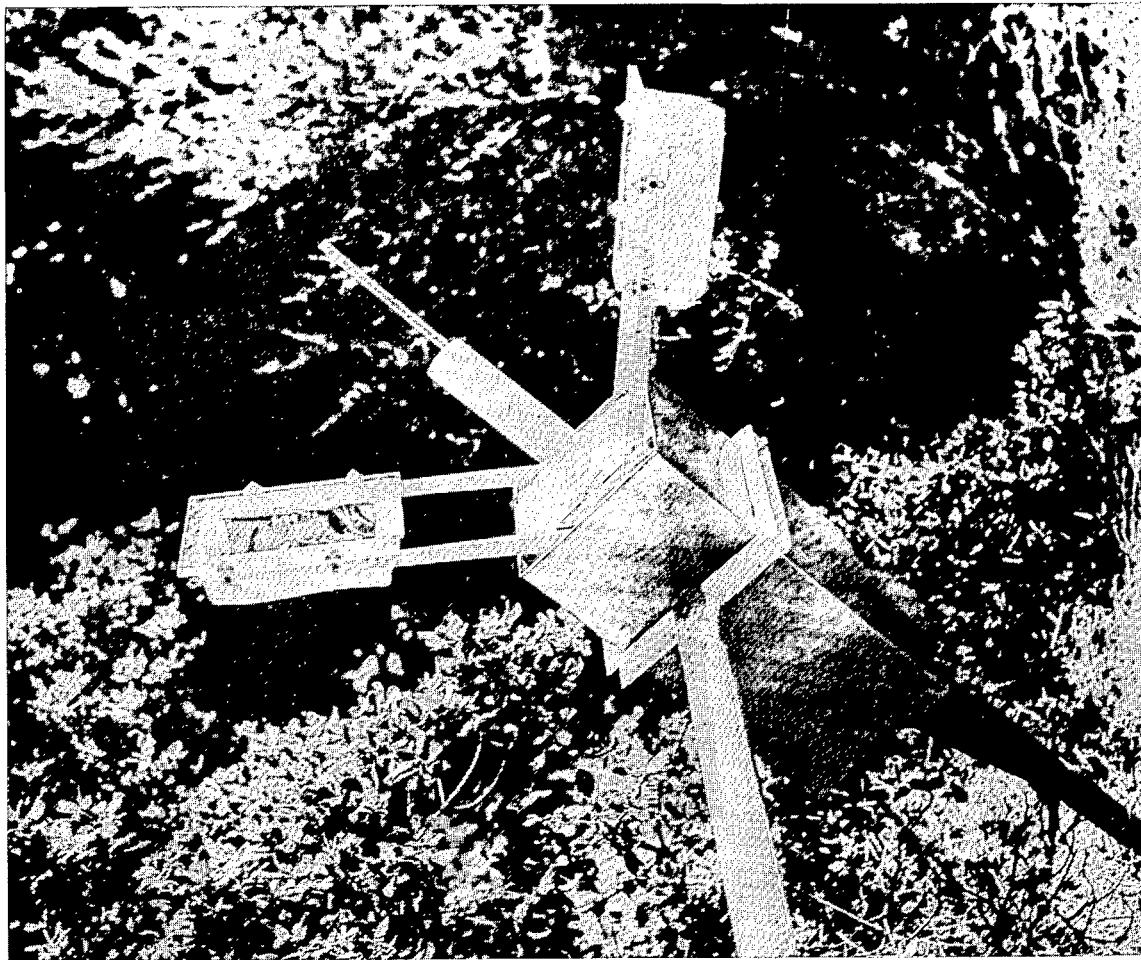


FIG. 7. Enceinte climatisée pour mesures des échanges gazeux au niveau de la couronne des arbres. En alternant ouverture et fermeture de l'enceinte, on peut obtenir un enregistrement du type indiqué dans la figure 11.

séquent changer radicalement le comportement de la plante. La dépression de l'absorption de CO_2 de l'après-midi, notamment, peut se présenter sous une forme très différente de celle de la réalité (fig. 10).

Pour parer à l'éventualité d'erreurs résultant de l'action de l'enceinte sur les stomates, on peut l'ouvrir et la fermer périodiquement et comparer les taux des échanges gazeux à la fin d'une période de fermeture et au début de la suivante. Si les deux taux diffèrent, l'enceinte a provoqué un changement de climat trop prononcé (fig. 7; 11a, b). En pareilles circonstances, il est nécessaire que les systèmes de régulation puissent conserver en mémoire leurs positions pendant la durée de l'ouverture, afin d'éviter de brusques changements de climat dans l'enceinte lors des fermetures.

En outre, l'ouverture et la fermeture périodiques de l'enceinte présentent l'avantage de réduire l'effet cumu-

latif des différences de climat existant entre l'intérieur et l'extérieur de l'enceinte. En l'absence de stress hydriques, il semble toutefois possible d'obtenir un comportement physiologique dans une enceinte proche de celui observé à l'extérieur, même si elle est fermée en permanence. Au cours d'expériences effectuées à Montpellier, le développement dans une enceinte maintenue fermée de quatre pieds de Tournesol, régulièrement arrosés, restait pratiquement le même qu'à l'extérieur, depuis leur sortie du sol, avec un indice foliaire de 1,9 en fin de croissance contre 1,8 en moyenne pour le reste de la culture (fig. 6, 12a, b).

AMPLITUDE ET PÉRIODE DE FLUCTUATIONS

Tous les systèmes de régulation qui comportent des retards importants entre le début de la perturbation

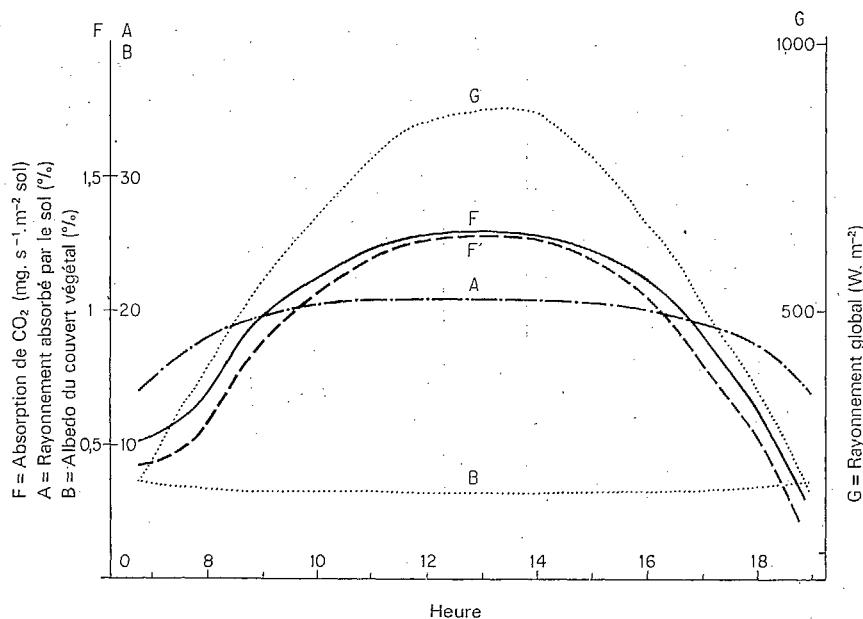


FIG. 8. a) Absorption de CO_2 par mètre carré de culture d'*Helianthus annuus* calculée d'après le modèle de Wit. Les courbes F et F' donnent respectivement la photosynthèse à l'extérieur et à l'intérieur de l'enceinte, la différence étant due à l'absorption, à la réflexion et à la diffusion de la lumière par les parois de l'enceinte.

et la naissance du signal de correction restent sujets à des fluctuations ou des « pompages » considérables. De tels retards sont particulièrement importants pour une régulation de la teneur en CO_2 en présence de variations brusques de la photosynthèse, qui se produisent, par exemple, lorsque le soleil est caché par un nuage. La réduction de la photosynthèse ne se répercute pas immédiatement sur la concentration en CO_2 dans l'air au niveau de l'analyseur différentiel utilisé, soit en raison de la résistance de l'air entre les tissus photosynthétiquement actifs et le tube d'absorption de l'air, soit en raison de l'effet tampon exercé par la végétation et, éventuellement, par le sol. Il faut aussi ajouter le retard dû à l'inertie de la vanne proportionnelle réglant l'injection de CO_2 pur.

Le système de régulation qui convient le mieux à un tel cas est la régulation par action proportionnelle discontinue: la vitesse d'ouverture ou de fermeture de la vanne d'admission de CO_2 pur est proportionnelle à l'écart entre les valeurs suivie et suiveuse, mais la régulation n'est utilisée que pour corriger périodiquement le degré d'ouverture de la vanne, la période séparant les corrections étant de même ordre de grandeur que le retard dans le système. Il est à noter que le retard dû à la distance entre l'enceinte et l'analyseur est négligeable devant les autres retards mentionnés, l'air circulant à grande vitesse en circuit fermé entre les deux. Pour évaluer les échanges gazeux instantanés il est généralement nécessaire d'enregistrer l'amplitude du pompage, puis au dépouillement, de corriger les résultats

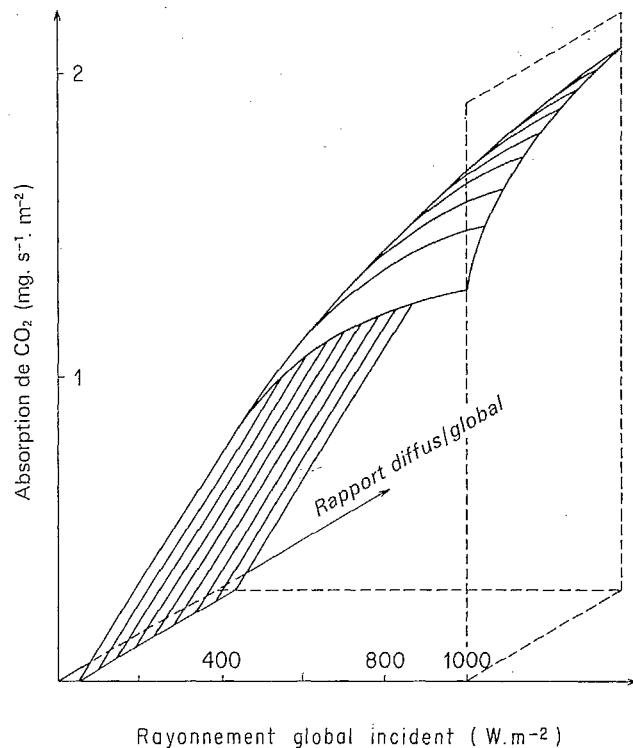
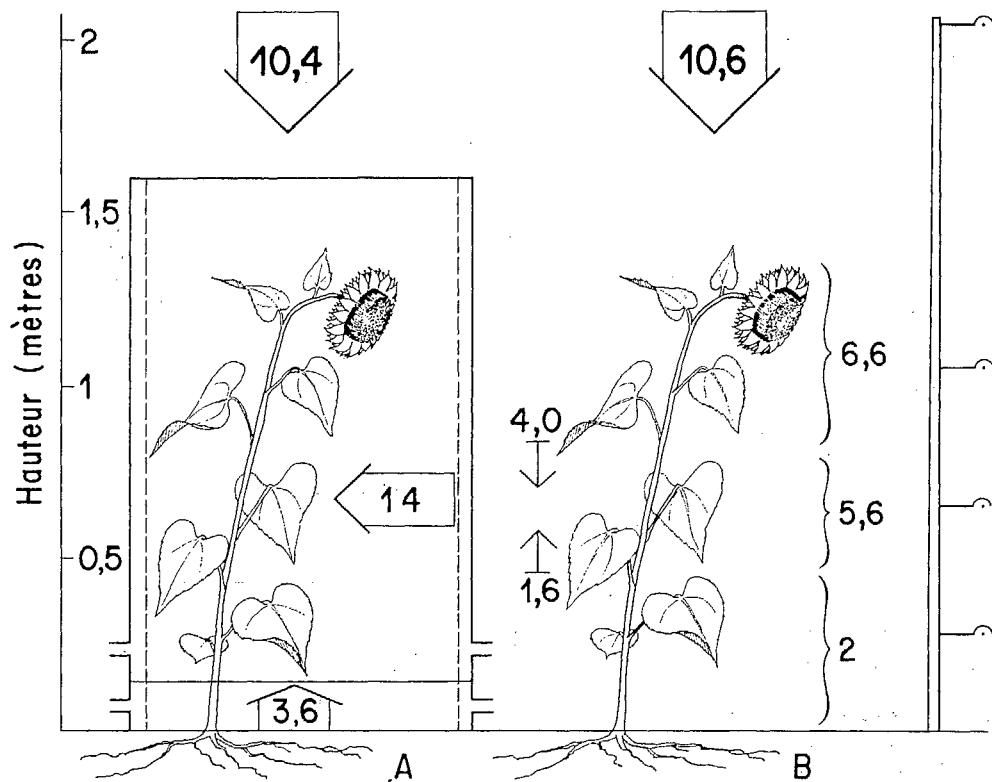


Fig. 8. b) Abaques de courbes permettant de corriger l'effet sur la photosynthèse de la réduction du rayonnement global incident et de l'augmentation du rapport rayonnement diffus/global dans l'enceinte.

Grammes de carbone entrant dans l'écosystème par mètre carré pendant la période diurne de la journée



Grammes de carbone entrant dans l'écosystème par mètre carré pendant la période diurne de la journée

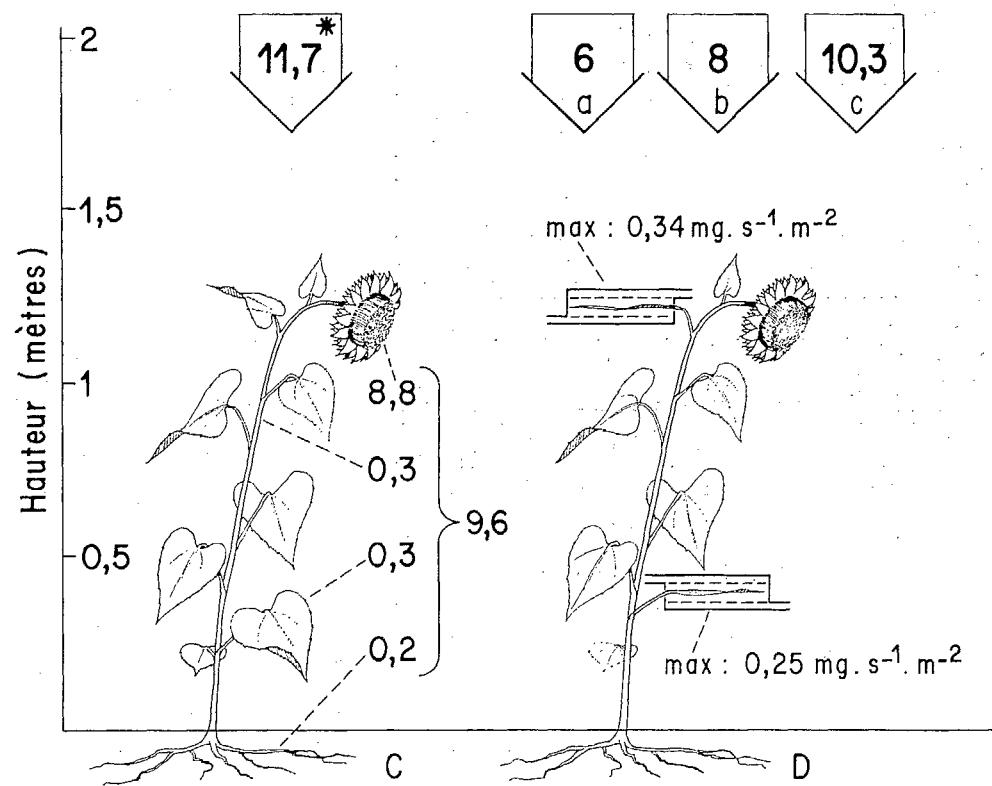


FIG. 9

tats au moyen d'un programme de calcul mis au point à cet effet.

Les fluctuations provoquées par le système de régulation de CO_2 sont d'ailleurs une source d'erreurs telle qu'il semble parfois plus favorable d'utiliser des enceintes en circuit ouvert, quitte à faire varier la vitesse de renouvellement de l'air en fonction de la photosynthèse, de manière à éviter des variations trop importantes dans la concentration en CO_2 . Pour des petites enceintes, les fluctuations naturelles de la teneur en CO_2 de l'air extérieur, dont le rôle physiologique est d'ailleurs assez mal connu, se retrouvent dans l'enceinte, bien qu'atténues. Dans les grandes enceintes recouvrant un feuillage important, le contrôle de la teneur en CO_2 par injection de ce gaz est toutefois souhaitable, l'absence de proportionnalité entre la concentration en CO_2 et la photosynthèse chez les feuilles peu éclairées empêchant une correction des résultats après coup.

←

FIG. 9. Entrants en carbone par m^2 d'écosystème — une culture d'*Helianthus annuus* — à partir de la basse atmosphère, de 6 à 20 heures, déterminés au moyen de quatre méthodes.

A. La méthode des enceintes utilisant une enceinte d'un volume de $1,7 \text{ m}^3$ recouvrant quatre plantes, la régulation de la teneur en CO_2 étant réalisée par action intégrale discontinue. La valeur 14 correspond à celle effectivement mesurée. Dans les conditions de rayonnement existant à l'extérieur de l'enceinte, cette valeur devrait être supérieure — de 7% environ — si l'on tient compte des différences des conditions de rayonnement; cependant l'indice foliaire plus élevé sous l'enceinte (1,9) par rapport à la moyenne du champ (1,8) compense sensiblement cet effet des parois de l'enceinte.

B. La méthode du bilan énergétique appliquée à l'intérieur de la couverture végétale. Le flux ascendant de $1,6 \text{ g} \cdot \text{m}^{-2}$ à $0,5 \text{ m}$ concourt à confirmer le dégagement de CO_2 important du sol. Les valeurs indiquées en accolades sont les quantités de carbone absorbées par chacune des strates.

C. L'analyse de croissance: La valeur 11,7 est obtenue en additionnant le carbone incorporé dans la plante en 24 heures à celui dégagé la nuit par les organes aériens ($2,1 \text{ g} \cdot \text{m}^{-2}$); à cette valeur devrait être ajoutée la respiration nocturne des racines et retranchée la respiration diurne des micro-organismes du sol; toutefois, ces deux valeurs se compensent partiellement.

D. Le modèle mathématique de de Wit, en déduisant du carbone absorbé par le feuillage, le carbone dégagé pendant le jour par respiration à partir du sol ($3,6 \text{ g} \cdot \text{m}^{-2}$) et des tiges et capitules ($0,8 \text{ g} \cdot \text{m}^{-2}$). Les valeurs 6, 8 et 10,3 sont obtenues en utilisant dans le modèle trois valeurs différentes pour la pente à l'origine de la courbe exprimant les échanges gazeux en fonction de l'éclairement pour la feuille; cette relation a été déterminée au moyen de petites chambres réfrigérées à l'eau avec circulation d'air en circuit ouvert, respectivement: a) au laboratoire en salle climatisée, b) sur le terrain en faisant varier l'éclairement par un jeu d'écrans à un moment donné de la journée, c) sur le terrain à partir des évolutions journalières de l'absorption de CO_2 et du rayonnement global. Les valeurs maximales de l'absorption instantanée de carbone sont données pour une feuille supérieure et une feuille située à 40 cm du sol.

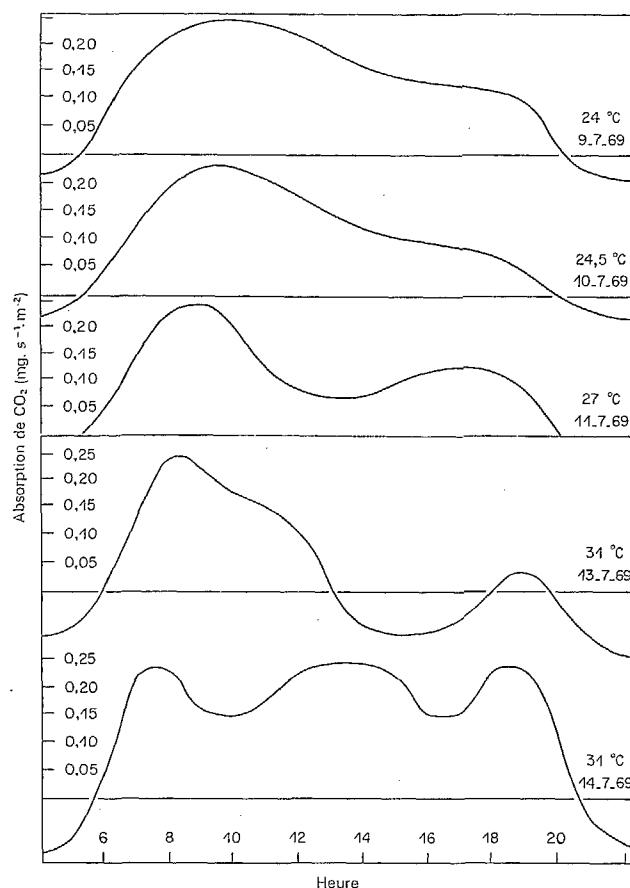
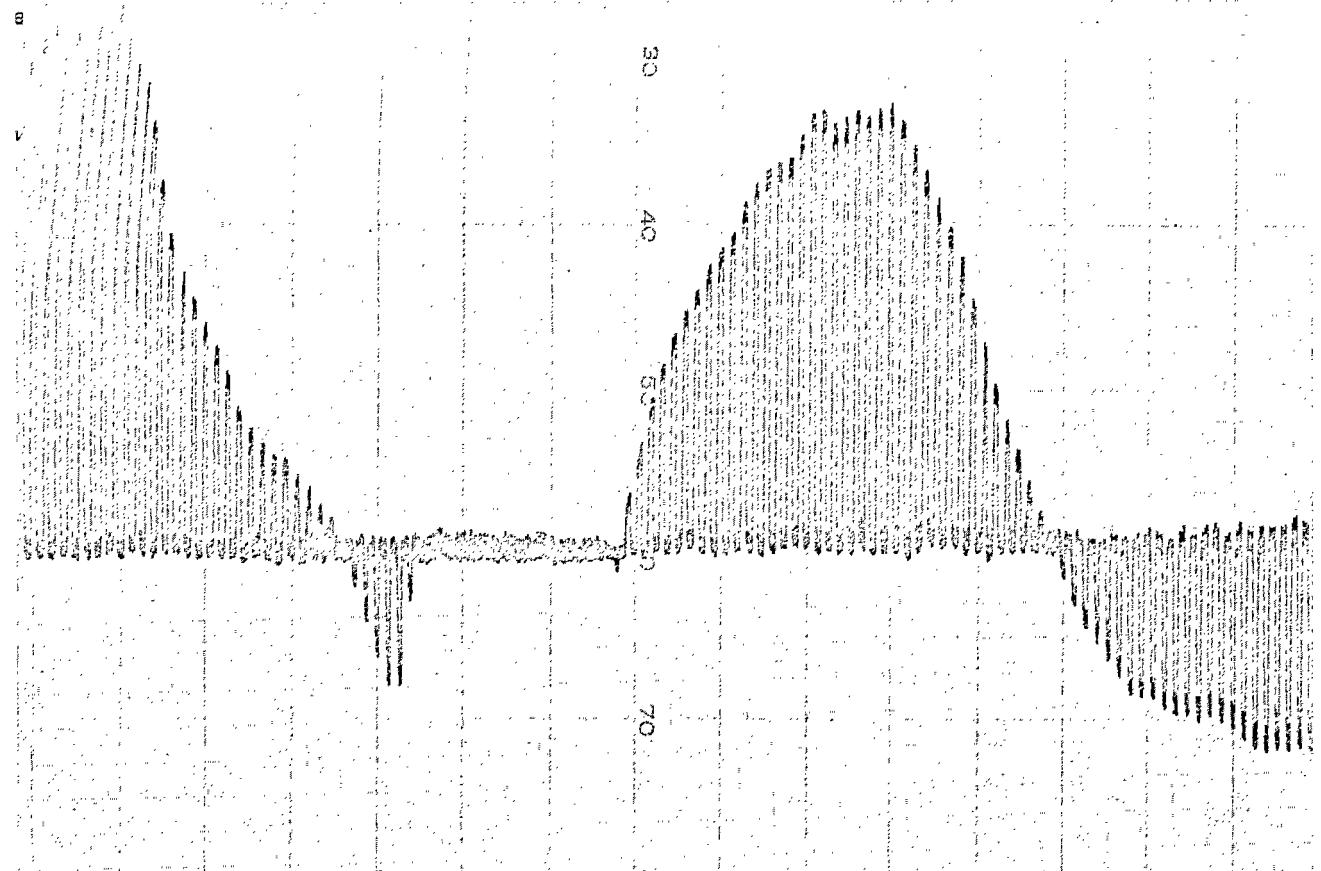


FIG. 10. Échanges gazeux de *Quercus ilex* L. pendant la période de dessèchement du sol. L'accentuation de la dépression de l'après-midi allant de pair avec l'accroissement de la température laisse supposer un rapport de causalité direct. Une augmentation volontaire de l'humidité de l'air dans l'enceinte — effectuée pour le dernier graphique le 14 juillet 1969 — fait cependant disparaître la dépression vespérale démontrant le rôle important du bilan hydrique dans le comportement de la plante.

DÉGAGEMENTS DE CO_2

Un problème important se pose en présence de dégagements de CO_2 par la végétation ou par le sol, l'évacuation de ce gaz étant difficile dans les conditions du terrain. Ici, de nouveau, il est possible de tirer profit de la possibilité d'ouvrir et de fermer l'enceinte. Après la fermeture de l'enceinte la concentration en CO_2 s'accroît suivant une loi assimilable à une exponentielle. Connaissez la pente de cette courbe à l'instant de la fermeture et le volume de l'enceinte, le dégagement instantané de CO_2 se calcule facilement (Borderie et Sauvezon, 1971). Dans ces calculs, il importe en outre de tenir compte des fuites de l'enceinte qui doivent être déterminées en la vidant de son contenu végétal et en l'isolant du sol.

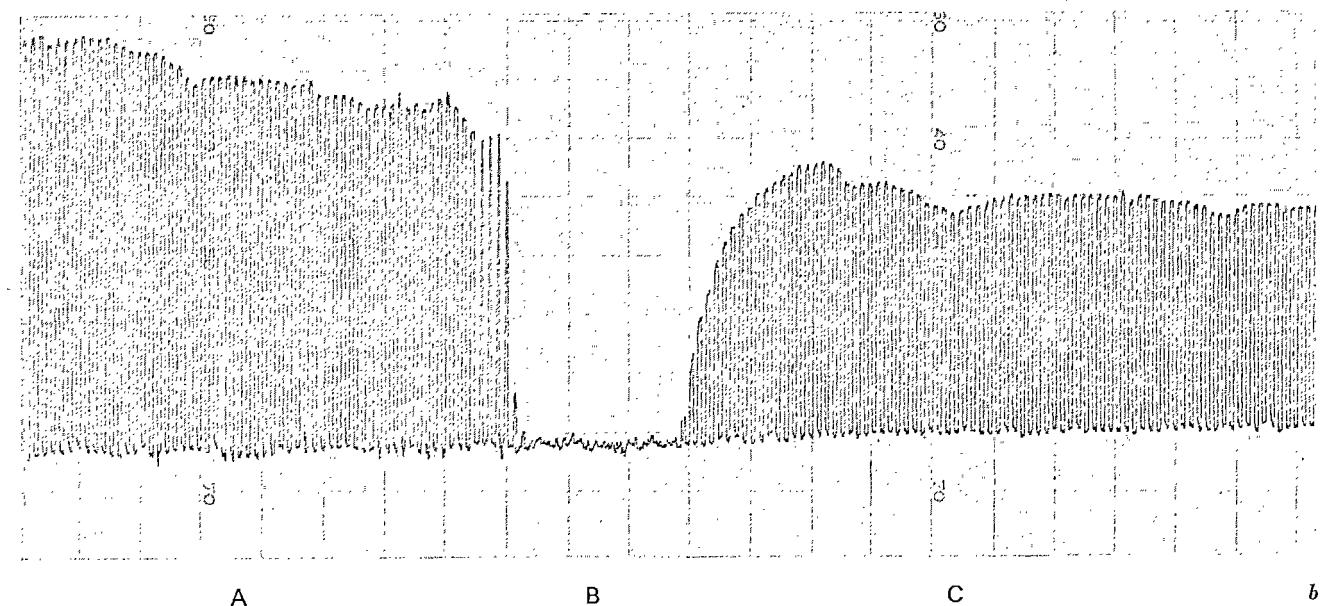


A

B

C

a



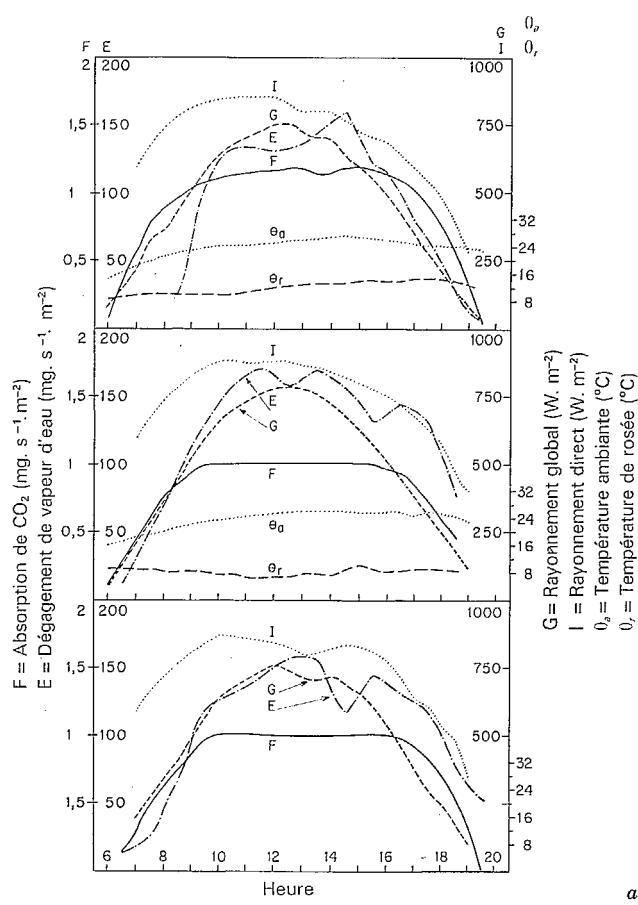
A

B

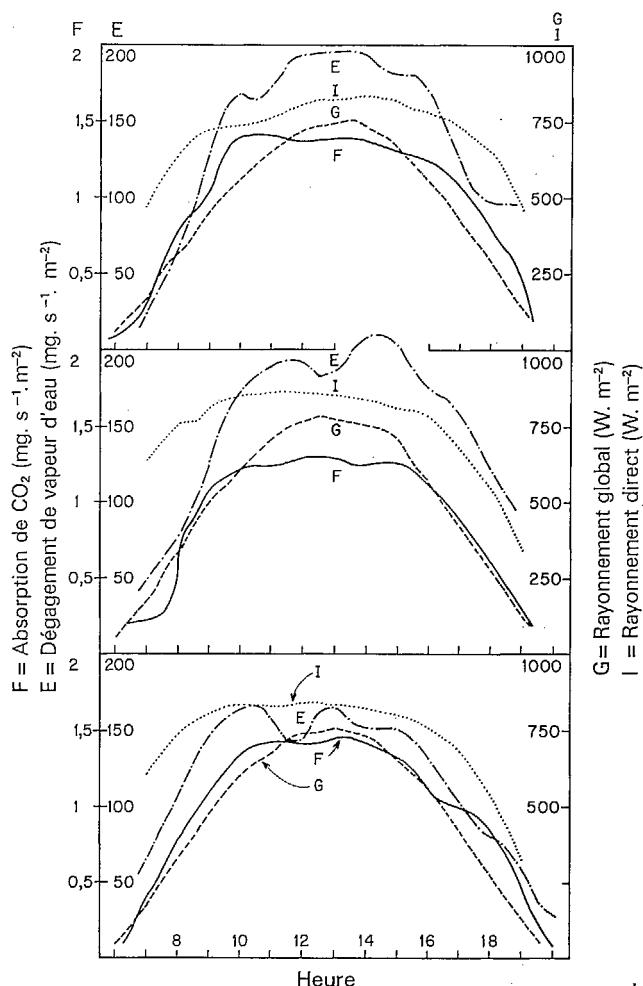
C

b

FIG. 11. Échanges gazeux de *Quercus ilex*. Absorption de CO₂ avant: A, pendant: B et après: C l'ouverture de l'enceinte.
 a) Humidité et température dans l'enceinte identiques à l'intérieur et à l'extérieur de l'enceinte.
 b) Même situation mais température dans l'enceinte élevée de 6 °C par rapport à l'extérieur.



a



b

FIG. 12. Absorption de CO_2 par une culture d'*Helianthus annuus* pour deux indices foliaires déterminés par la méthode des enceintes (voir figure 6).

- a) Indice foliaire = 1,2.
- b) Indice foliaire = 1,8.

Une cause d'erreur difficile à éviter est liée à la dépendance de la photosynthèse de la teneur en CO_2 de l'air.

Grâce à ce procédé, il a été possible de constater des dégagements de CO_2 au cours de l'après-midi dans un champ de Luzerne lors du dessèchement du sol, constatations confirmées ailleurs par des mesures parallèles effectuées par la méthode du bilan de quantité de mouvement (Saugier, 1970) [fig. 4].

Par le même procédé, il a été possible d'évaluer les échanges gazeux de touffes d'âges différents de *Salicornia fruticosa* pendant l'été, et de mettre en évidence l'accroissement du rapport respiration de maintenance / photosynthèse chez les plus âgés. La végétation étudiée, depuis longtemps protégée dans la réserve zoologique et botanique de Camargue, ressemble à maints égards à des forêts vierges en miniature chez lesquelles les

arbres les plus âgés, à productivité nette trop faible, cèdent le pas aux arbres plus jeunes dotés d'une productivité nette supérieure (fig. 5).

INSTALLATION DE L'ENCEINTE

L'installation d'une enceinte nécessite bien souvent une étude préalable de la structure de la couverture végétale ou du climat radiatif, afin d'assurer une bonne représentativité des données acquises (Eckardt, Méthy et Sauvezon, 1969). Ce problème de représentativité des sous-systèmes choisis constitue encore une difficulté essentielle de la méthode des enceintes (fig. 1).

A ce problème se greffe celui d'éviter des modifications du milieu extérieur de l'enceinte par le matériel installé. Il est essentiel en particulier de ne pas provoquer de

changements dans le transport d'assimilats entre l'organe étudié et les autres parties de la plante soit en ralentissant ou en accélérant des phénomènes de sénescence, soit en modifiant les conditions d'utilisation ou de stockage de ces éléments. En séparant le sol de la partie aérienne de l'écosystème, par exemple au moyen de feuilles de plastique attachées autour de tiges, ou de matériaux imperméables au CO₂ coulés sur le substrat édaphique, une modification des conditions mésologiques des racines est toujours à craindre.

COMPARAISON AVEC D'AUTRES MÉTHODES

En prenant les précautions qui conviennent, les résultats obtenus par la méthode des enceintes se comparent cependant dans certains cas favorablement avec ceux obtenus par d'autres méthodes. Lors d'une étude du comportement physiologique d'un champ de Tournesols, les entrants en carbone dans l'écosystème à partir de la basse atmosphère pendant la journée furent évalués respectivement par quatre méthodes :

1. La méthode des enceintes, en utilisant une enceinte d'un volume de 1,7 m³ recouvrant quatres plantes, la régulation de la teneur en CO₂ étant réalisée par action proportionnelle discontinue.
2. La méthode du bilan énergétique appliquée à l'intérieur de la couverture végétale de manière à permettre l'évaluation du flux vertical de CO₂ en fonction de la hauteur.
3. L'analyse de croissance, en additionnant le carbone incorporé dans les inflorescences, tiges, feuilles et racines à celui dégagé la nuit par respiration.
4. Le modèle de de Wit en déduisant du carbone absorbé par le feuillage, le carbone dégagé par respiration à partir des tiges, des inflorescences et du sol. La relation donnant l'absorption de CO₂ par la feuille considérée individuellement, en fonction de l'éclairement, était déterminée au moyen de petites chambres simples réfrigérées à l'eau avec circulation d'air en circuit ouvert, et respectivement : a) au laboratoire en salle

climatisée, b) sur le terrain en faisant varier l'éclairage par un jeu d'écrans à un moment donné de la journée, c) sur le terrain à partir des évolutions journalières de l'absorption de CO₂ et du rayonnement global.

La confrontation des méthodes démontre la bonne concordance des résultats (fig. 10) et met en évidence l'importance considérable des conditions d'obtention de la courbe donnant l'absorption de CO₂ en fonction de l'éclairage (Eckardt, Heim, Méthy, Saugier et Sauvezon, 1970).

CONCLUSIONS

Il est clair, d'après ce qui précède, que des mesures de terrain au moyen d'enceintes climatisées impliquent un matériel important et dispendieux comprenant notamment un laboratoire mobile équipé d'un matériel d'automatisation et d'enregistrement perfectionné.

La question se pose donc de savoir si, compte tenu de ses nombreux inconvénients, la méthode des enceintes est suffisamment utile pour justifier les crédits investis. A cet égard, il convient de remarquer que pour l'étude de beaucoup de phénomènes physiologiques dans des écosystèmes naturels elle semble actuellement irremplaçable. D'un autre côté, il conviendrait probablement de reconsidérer la question des enceintes dans le contexte des phytotrons. Les problèmes à étudier et les techniques utilisées sont en grande partie communs. Dans l'avenir, pour des raisons économiques et pratiques, il serait probablement favorable de concevoir certains types d'enceintes comme des chambres climatisées mobiles, normalement installées dans le phytotron, mais transportables sur le terrain lorsque cela est nécessaire.

Dans ce cas, une des objections le plus souvent faites à l'encontre des phytotrons, à savoir qu'ils ne permettent l'étude du comportement des plantes que dans des conditions trop éloignées de celles du terrain, se trouverait éliminée pour une grande part.

Summary

The controlled-environment cuvette as a tool for linking laboratory and field research (F. E. Eckardt)

Energy input into the ecosystem, and energy expenditures involved in maintaining biomass required for interception and transformation of radiant energy from the sun are closely related to the way substances elaborated in photosynthesis are partitioned among the various plant organs. Particular structural and functional features characterizing various ecosystems are therefore to a considerable extent attributable to the way photo-

synthesis, respiration and the partitioning mechanism work together as an integrated self-adjusting system.

Dynamic simulation modelling techniques are available for studying properties of such systems, but considerable difficulties exist in obtaining information on adequate subsystems both in the form of basic physiological data and for testing of the model. In general, it is too ambitious to derive the functioning of a whole ecosystem from a few response patterns studied in the laboratory on plants grown in pots. Under such circumstances, the distribution of photosynthates, as well as

photosynthesis and respiration, can be considerably different from that observed in the field, in particular in plants normally exposed to severe soil conditions impossible to reproduce in the laboratory.

For this reason, it is often extremely difficult to apply data obtained in the laboratory for solving precise practical problems in agriculture. The complexity of the natural environment is too great in comparison to that of the environment created in the laboratory. One of the primary tasks of bio-climatology and eco-physiology is therefore to establish a link between these two levels of study.

To this end, research has been carried out in Montpellier with a view to defining a methodology bridging the gap between field and laboratory research. The input of carbon into an ecosystem, a *Helianthus annuus* crop, from the lower atmosphere during the day was estimated by means of four methods: (a) The cuvette method, using 1.7 m³ cuvettes with periodically discontinuous action control of CO₂ concentration; (b) The energy balance method, applied within the plant cover so as to permit evaluation of vertical CO₂ flux as a function of height; (c) Growth analysis, by adding up carbon incorporated in the inflorescences, stems, leaves and roots and carbon released by respiration during the night; (d) The de Wit model, by subtracting carbon given off through respiration by stem, inflorescences and soil from carbon taken up by the foliage, the carbon uptake by individual leaves as a function of irradiance being determined by means of open-circuit leaf chambers respectively (i) in the laboratory in growth cabinet, (ii) in the field by varying irradiance at a given moment by a set of screens, and (iii) in the field from the day curves of CO₂ absorption and global radiation.

There was a good agreement of results, the most deviating values being obtained by using in the model curves expressing CO₂ absorption as a function of irradiance, or certain characteristics of these, acquired in the laboratory and, to a lesser extent, by using curves acquired in the field with the aid of screens.

Experiments show the advantage of using jointly controlled-environment cuvettes or enclosures and mathematical models. The controlled-environment cuvettes make it possible (a) to subdivide the ecosystem into compartments of convenient dimensions, (b) to make various environmental factors readily controllable, so as to create, progressively, conditions similar

to those of the laboratory, (c) to vary these factors beyond their normal range of variation, so as to facilitate the assessment of causal relationships between the physiological behaviour and the factor varied, (d) to follow the changes in physiological behaviour resulting from voluntarily induced modifications of foliage geometry or of environmental conditions, so as to enable the study not only of short-term physiological reactions but also of long-term reactions of adaptive character, (e) to test the model step-wise, using sub-systems of increasing complexity under conditions progressively closer to those of the natural environment. The models, for their part, enable the evaluation of errors referable to the cuvette due for example to modifications of the ratio between diffused and global radiation and, by using them as simulators, the assessment of the true role in primary production of various structural and functional elements of the ecosystem, thus facilitating the selection of priorities for research.

In designing the cuvette, the importance of (a) securing identical transmission and diffusion of radiation at all altitudes and azimuths of the sun through adequate geometry, (b) preventing cumulative effects of change in microclimate by periodical opening of the cuvette, and (c) not altering conditions to which sink organs for assimilates are normally exposed, is stressed. Detailed study of the structure of the plant cover as well as of the radiation climate prior to installation of the cuvette is in most cases required.

Examples are given showing the possibility of evaluating effects of change in irradiance and diffuse to global radiation ratio by mathematical modeling, of simulating effects of wind by proper installation of external sensors, of monitoring effects of change in the water regime of the plant by observing its behaviour during periodical opening and closing of the cuvette, of correcting errors due to "hunting" in the control system by recording of deviations between the value of the controlled quantity and the value of the same quantity measured outside the cuvette, of measuring CO₂ given off in respiration by recording the increase in concentration of this gas during the first minutes following the closing of the cuvette. Afternoon depression in CO₂ absorption due to the water stress is illustrated by measurements on *Quercus Ilex* and negative absorption by measurements in a *Medicago sativa* crop as well, as in *Salicornia fruticosa* stands with different canopy structure.

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IV Estimation of the temperature factor in agroclimatology

IV Estimation du facteur température en agroclimatologie

Estimation of the radiation and thermal micro-environment from meteorological and plant parameters

A. Baumgartner

Institute of Meteorology, Munich
(Federal Republic of Germany)

INTRODUCTION

In the foregoing sections of the symposium the manner in which the physical parameters of the environment, such as radiation or temperature, affect the process of plant production have been discussed. It is the task of this paper to describe the radiation and thermal field in the vicinity of the plant bodies in terms of meteorological and plant parameters. Also, the inter-relations between the distribution of the physical properties of the atmosphere within the stand and the properties of the plants will be outlined. Finally the sources or sinks of production and transpiration due to the distribution of radiation and temperature in the stand space are evaluated.

RADIATION

GENERAL REMARKS

Radiation is a form of electromagnetic energy transport. In the following discussion, only wave-lengths (λ) between 280 nm and approximately 100 μm which are characteristic for the range of solar and terrestrial radiation are considered. The radiation between 280 nm and 3 μm , originating from the sun, is defined as short wave radiation; that of 3 μm to 100 μm caused by emission from terrestrial bodies, is termed long wave, infra-red, thermal or terrestrial radiation. As is well known, the wave-lengths from 400–760 nm are visible for the human eye, which is most sensitive to green light.

As seen from the review by Hofmann in Table 1 only 4 per cent of the radiation energy from the sun belongs to the ultra-violet region (280–400 nm) but 45–70 per cent of the total solar radiation is in the range of the infra-red region ($> 0.8 \mu\text{m} < 6.8 \mu\text{m}$) and not visible. The ratio of the energy in defined spectral ranges to the

total energy of solar radiation is relatively constant, therefore measurements of parts of the total sun spectra are proportional to other parts of the sun spectra. This is an important fact for radiation measurements in plant production studies.

The intensity and quality of the long wave radiation depends on the surface temperature θ_o ($^{\circ}\text{K}$) of the emitting bodies. The energy (E) which is radiated from surface unit into the half sphere is defined by the law of Stefan and Boltzmann:

$$E = \varepsilon\sigma\theta_o^4$$

The factor $\delta = 0.826 \times 10^{-10} \text{ cal cm}^{-2} \text{ min}^{-1} \text{ deg K}^{-4}$ is a constant and ε is the emissivity, which is of the order 0.95–0.99 for plant bodies. The terrestrial radiators have temperatures in the order of $273^{\circ} \pm 40^{\circ}\text{K}$. The maximum of the thermal radiation is between 9 and 12 μm , but 50 per cent of the energy is between 4–35 μm . The intensities, dependent on the surface temperatures, θ_o ($^{\circ}\text{C}$), are shown in Table 2 using the data of Baur (1970). The emission of plant bodies at average temperatures is approximately of the order of $1/4$ to $1/3$ of the so-called solar constant, which is $2 \text{ cal cm}^{-2} \text{ min}^{-1}$.

For practical purposes it is useful to distinguish the following radiation fluxes quantitatively and qualitatively.

(a) short wave fluxes

I	= direct radiation from sun
D	= diffuse radiation = scattered sky radiation
R_s	= reflected radiation = $r_s (I + D)$
$I + D$	= global radiation, r_s = reflectivity,
$100 \times r_s$	= reflection or albedo. With an absorptivity,
a_s	= $1 - r_s$, the surfaces absorb the following net radiation in the short wave range:

$$Q_s = I + D - R_s = a_s (I + D).$$

TABLE I. Partition of extraterrestrial sun radiation
(After Hofmann, 1965)

	λ (μ)	Energetic portion (%)	Photometric portion (%)	Sensitivity of human eye (%)
Ultra-violet A	0.28	0.5		
Ultra-violet B	0.32	1.0		
Ultra-violet C	0.40	6.5		
Violet	0.44	5.2	0.4	1.0
Ultra-blue	0.48	6.4	3.4	8.3
Ice-blue	0.49	1.5	2.0	20.8
Sea-green	0.54	7.5	32.3	66.8
Leaf-green	0.57	4.4	27.8	98.2
Yellow	0.59	2.9	15.2	81.4
Orange	0.61	2.8	10.2	56.8
Red	0.76	17.1	8.7	8.0
Infra-red A	1.4	32.3		
Infra-red B	3.0	10.7		
Infra-red C	6.8	1.2		

The short wave net radiation, Q_s , is regarded as positive during daytime, however at night $Q_s = 0$.

(b) long wave fluxes

- E = emission from terrestrial surfaces
- A = emission from atmospheric constituents
- R_1 = reflected radiation = $r_1 \cdot A$.

With an absorptivity $a_1 = 1 - r_1$, the net long wave radiation is defined by:

$$Q_1 = A - E - r_1 A = a_1 A - E.$$

Generally E exceeds A , hence Q_1 generally has negative values.

(c) net radiation

from (a) with (b); the surplus or loss of energy by the radiation exchanges or the net radiation of surfaces

$$Q = Q_s + Q_1 = a_s (I + D) + a_1 A - E.$$

It may be seen from these definitions that the radiation climate relating to plants has many aspects, which cannot be outlined in all phases in a short review paper. Therefore some key ideas are outlined in the following treatment of the theme.

OPTICAL PROPERTIES OF PLANT BODIES

As in the case of the human eye, which perceives only the wave-lengths 400–760 nm, the different spectral ranges have their specific importance for the balance of matter and energy in plants. For photosynthesis, only the wave-lengths between 450 and 650 nm are of special interest, but all radiation quantities take part in the heat balance. For an understanding of the production

processes and the driving function of radiation exchanges for plant life processes, qualitative as well as quantitative analyses of the radiation fluxes are urgently required. For example, the water vapour transfer in transpiration, the carbon dioxide uptake, or the nutrient transports are directly correlated with the quantity of net radiation.

The energy transfer by radiation is related to plant bodies in different ways.

Spectral absorption

Due to their chemical components or their physical structure, plants absorb selectively in discrete wavelengths and utilize radiation in the chemical process of photosynthesis. The contribution of the constituents of plant matter may be seen in Figure 1 which is based on the results of Sauberer and Härtel (1959) and of Dirmhirn (1964).

Ultra-violet radiation is first absorbed by the anthocyanins, flavones and tannins and in small amounts also by carotenoids. Light will be scattered by the celluloses and absorbed by the orange-red carotenes, yellow xanthophylls, dark green chlorophyll a and light green chlorophyll b. The maximum chlorophyll absorption is in the blue (450 nm) and in the red (650 nm) regions.

At the border of visibility of the human eye for red light, plants also lose their absorptivity, which increases again in the infra-red range, especially in the absorption bands for water (1.45 and 1.95 μm), depending on the water content of the plant bodies. Radiation of wave-length greater than 650 nm also influences the photochemical activity; however, it is of less importance for the optical differentiation of plants.

In the infra-red spectral range greater than 3 μm , plants (especially the water in them) absorb almost completely. The emissivity coefficient for leaves are in the range 0.96 to 0.995, as deduced by Idso *et al.* (1969). Plant bodies may, therefore, be considered as "black bodies" for infra-red or thermal radiation.

Spectral reflection

Plants reflect radiation with spectral characteristics corresponding to the properties of the plant constituents and transmit distinct wave-lengths of light. Assuming

TABLE 2. Specific thermal radiation ($\text{cal cm}^{-2} \text{min}^{-1}$)
(After Baur, 1970)

0_0 ($^{\circ}\text{C}$)	E	0_0 ($^{\circ}\text{C}$)	E
-10	0.396	30	0.698
0	0.460	40	0.794
10	0.531	50	0.901
20	0.610		

a radiation load on plant surfaces of Q_o , then reflection (R) and transmission (T) are related to absorption (A) by the law of energy conservation:

$$Q_o = A + R + T = 100 \text{ per cent.}$$

Compared with the absorption, the sum of $(R + T)$ is relatively small. The partial transparency of plant bodies, like needles and leaves, results in the fact that R is composed of the surface reflection, R_o , and T_u . The term T_u represents radiation scattered within the plant bodies then reflected back to the surface. The transmission is due to reflection within the plant bodies, hence reflection and transmission have similar spectral distributions, as shown in Figure 2. The representation is based mainly on Sauberer and Härtel (1959) and Dirmhirn (1964), in accordance with similar results of Seybold (1934), Seybold and Weissweiler (1942) or of Alexeyev (1963) and others.

Reflection and transmission have maxima in the green light as well as in the infra-red A and B. The impression of the green colour of plants depends on the high reflectivity, the relatively high intensity of solar radiation and the great sensitivity of the human eye for green light. The reflectivity and the transparency are expressed in near infra-red UR-A. The cartography of vegetative earth surfaces by films with high sensitivity in the infra-red region is based on the individual behaviour of plants in that spectral range. The strong infra-red reflection of plant surfaces is often also an important means for protection of plant life against damage due to overheating, especially in high mountain plants, as the energetic part of solar radiation is predominantly in the infra-red region.

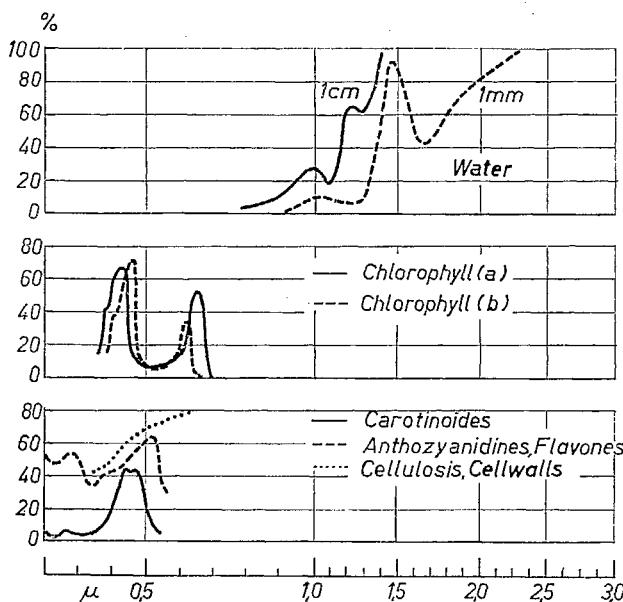


FIG. 1. Spectral absorption of plant constituents, relative units.
(After Sauberer and Härtel, 1959, and Dirmhirn, 1964.)

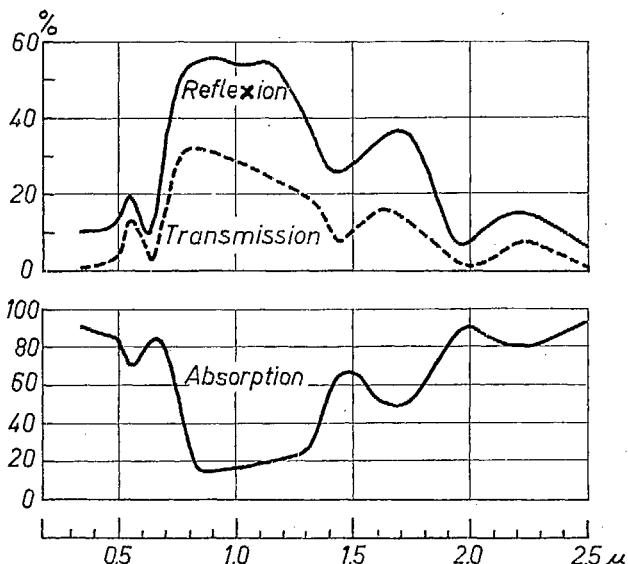


FIG. 2. Spectral distribution of reflection, absorption and transmission for plant leaves. (After Sauberer and Härtel, 1959, and Dirmhirn, 1964.)

The values given in Table 3 by Egle (1937), Seybold and Weissweiler (1942) and Sauberer and Härtel (1959) may be regarded as averages for reflection, transmission and absorption of green leaves.

As a rule one may postulate that approximately 75 per cent of the incident radiation will be absorbed, 15 per cent reflected and 10 per cent transmitted. "Shade" leaves are more transparent than "sun" leaves.

TRANSMISSION OF RADIATION IN PLANT STANDS

The radiation fluxes provided by sun and sky to plant stands may penetrate into the stand space directly to distinct layers and partially to the earth's surface, producing sunflecks there. The main part, however, will be absorbed or transmitted by multiple reflections,

TABLE 3. Spectral radiation components of green leaves
(After Egle, 1937; Sauberer and Härtel, 1959;
Seybold and Weissweiler, 1942)

$\lambda (\mu)$	Reflection (%)	Transmission (%)	Absorption (%)
0.34	9	0	91
0.44	11	2	87
0.51	14	10	76
0.58	14	10	76
0.64	13	9	78
1	45	50	5
2.4	7	28	65

TABLE 4. Spectral variation of radiation after transmission through plant leaves (After Sauberer and Härtel, 1959)

λ	0.55	0.70	0.95 μ
1 leaf	0.14	0.20	0.42
2 leaves	0.020	0.04	0.18
3 leaves	0.0028	0.008	0.075
4 leaves	0.004	0.0016	0.032

transmissions or emissions from layer to layer and diminished by each process. By spectral transmissions also qualitative changes in the radiation field are caused.

Wave-length transformations

For the quality of the radiation in the different layers, it is important that reflections and transmissions result in similar wave-length transformations. With each reflection and transmission, red and infra-red radiation increases relative to the other wave-lengths. Sauberer and Härtel (1959) estimated the variation in radiation after penetration through several plant leaves (see Table 4).

Towards the interior of the stand, a relatively intensive decrease of light in the chlorophyll-absorption bands at 450 and 650 nm and a relatively small decrease of green light at 550 nm and of infra-red radiation at 800 nm can be observed. Dirmhirn (1964) found that, under the canopy of deciduous trees on clear days, infra-red radiation forms the main component of radiation and on cloudy days the main component is green light.

Generally, the incoming radiation in stands is a mixture of spectral distribution comprising direct and unfiltered radiation of sun and sky and the indirect, already transformed, irradiations in the stand space. This is illustrated in Figure 3.

On thinning of stands, the photometric part for assimilation increases. This also happens as a result of the decrease in the chlorophyll content towards fall and on defoliation after the vegetation period. Within coniferous plant stands, where transmission in the needles does not occur, there are less modifications of the spectral distributions than in deciduous forests. This has been shown by many authors e.g. Knuchel (1914), Seybold (1934) Federer and Tanner (1966) or Vézina

and Boulter (1966) whose data for clear days are listed in Table 5.

The integral transmission to the earth's surface is 13.3 per cent in pines and 15.6 per cent in maple. However, on cloudy days it is 34.4 per cent in maple. The transmission in plant stands is more intensive for scattered radiation than for the direct sun radiation.

Vertical profile of short wave, visible radiation

With regard to the quantitative distribution of radiation in the vertical profile in stand space, the plant material acts like filters. Baumgartner (1955) has shown, in a linear diagram, that two basic types of profiles can be distinguished if the height above ground is normalized to the stand height, $H = 1.0$. The individual height is expressed as the ratio, Z/H . The distribution of the absorbing plant mass determines the shape of the profiles. Idso and de Wit (1970) differentiated four types of stands related to the leaf inclinations, namely planophile, erectophile, plagiophile and tremophile canopies. If the absorbers are mainly in the upper parts of the stand, as in forests, then the light profile is convex; if they are situated in the lower part, as in grassland, then the profiles are concave. With the growth of a stand the matter distribution and the structure are changing. As shown by Stern and Donald (1962) for grass/clover swards also the shape of the vertical light profiles is changing synchronously.

For filters like plant canopies, the Lambert-Bouguers absorption law can be applied to some extent in the form:

$$I_\lambda = I_{o,\lambda} \exp(-k_\lambda d).$$

I_λ and $I_{o,\lambda}$ are the light intensity within and above the canopies. $I_{o,\lambda}$ is the relative illumination (per cent), k is an extinction coefficient and d represents the distance from the upper level of the canopy to the earth's surface. The absorption law, however, can only describe the relations correctly if the absorbers (plant substance) are distributed evenly in the vertical direction. This is normally not the case, therefore k_λ is variable and equal to a function of (Z/H) . The filter characteristics are determined from density and structure of the leaves, needles, shoots, twigs, etc. The distribution of the surfaces of plant material is approximately represented by the leaf area index (LAI, F). Monsi and Saeki (1953), followed by Isobe (1962), Kuroiwa and Monsi (1963), and Saeki (1963), introduced the LAI in Lambert-Bouguers law instead of d . They found that the logarithm of the relative illumination decreases linearly with the LAI, i.e.:

$$I_\lambda = I_{o,\lambda} \exp(-k_\lambda F).$$

In Figure 4, an example is given for isotropic distribution of the incident light and for leaf angles $\alpha = 0^\circ$ and 60° respectively, to the horizon. Distributions for extinction coefficients are shown with $k = 0.5$, 1.0 and 1.5 for

TABLE 5. Spectral composition of radiation above and under forest canopies (After Vézina and Boulter, 1966)

λ	344 ultra-violet	444 blue	528 green	645 red	737 infra-red	nm
Sun	10	25	25	22	18	100 %
Pine	18	23	21	14	24	100 %
Maple	8	12	18	10	51	100 %

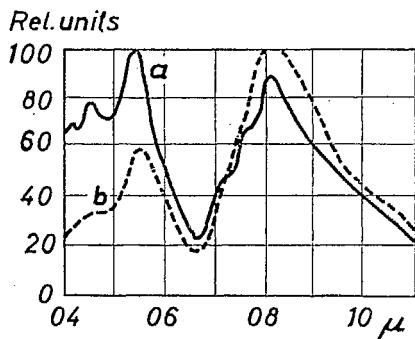


FIG. 3. Spectral distribution of global radiation within stands. a: cloudless sky, b: overcast sky. Relative units. (After Dirmhirn, 1964.)

horizontal leaves. Three leaf layers are already sufficient to decrease the light intensity down to the critical illumination of 5 per cent of I_o , which is a minimum for positive net photosynthesis.

Horie and Udagawa (1969) have extended the formula and considered the influence of the leaf angles by introducing a frequency distribution function:

$$\xi_{ij} = F_{ij}/\sum_j F_{ij} \quad F_{ij} = F_{ij}/F_j,$$

where F_{ij} denotes LAI with inclination of the i -th class in the j canopy layer and F_j is the total LAI in the j layer. Six classes of leaf inclination angles with the range of $\pi/12$ are assumed. ξ_{ij} represents the probability density of LAI with inclination angle in the i -th layer. With downward cumulative LAI of F within the canopy, the distribution of direct solar radiation is given by:

$$I_d(F) = I_{d,o} \exp(-\bar{K} \cdot F),$$

where $\bar{K} = \sum_j K_j F_j / \sum_j F_j$. Similar equations give, apply or hold for diffuse sky radiation. The role of scattered radiation becomes very important for the photosynthesis of a community with relatively horizontal foliage.

For calculations of the radiation intensity at the earth's surface under canopies, geometrical parameters of stands have been taken into account e.g. for forests, the diameter of openings, the age of stand, the number of stems, the stem diameter, the diameter integral, the stemcircle area, the screening degree, etc. The correlations of such parameters with the relative illuminations are of a high degree, and as Brechtel (1962) has shown, of the order of 0.8. Light measurements, therefore, can be used to estimate the LAI as well as for evaluation of stand density.

Vertical profile of long wave radiation

The distribution of long wave radiation is determined by the stand structure and density, the thermal radiation of the atmosphere (A), the emission of the earth's surface (E_s) and the emission of plant surfaces (E_p).

Lemon *et al.* (1963) and Saito (1964) have shown that Beer's law can also be applied approximately for long wave radiation profiles.

Owing to the dependence of the emission on the surface temperatures, the long wave radiation is determined, in the first place, by the temperature distribution within the stand. Long wave radiation is transmitted in the canopy in stepwise transformation from plant body to plant body. By the emissions and absorptions, the temperatures of the plant bodies are made equal to the temperatures in the environment. The radiation transmission can, therefore, be evaluated from the temperature distribution within the stand. The more dense the canopy is, the lower the partition of A and E_s .

The absorption coefficient for long wave radiation, E_s , penetrating the canopy, can be evaluated from the projections of the plant bodies. An example is given in Table 6 by Lorenz and Baumgartner (1970) for a 30 m high spruce stand. The values for the effective radiation surface indicate that long wave emission of a dense canopy is determined, in the first instance, by the upper layer of the plant stand. Figure 5 by Saito (1964) shows the same results. The temperature of the upper parts of the canopy determines the energy losses.

NET RADIATION OF SINGLE LEAVES

The radiation exchange of a single leaf depends on the type and form of the plant body, on the degree of exposure to sun and environment, the location within

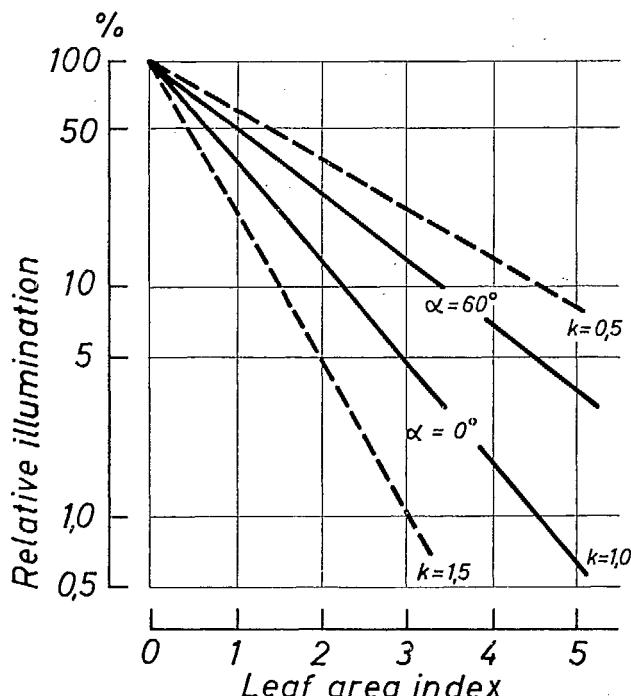


FIG. 4. Vertical profiles of relative illumination in plant canopies. (After Saeki, 1963.)

TABLE 6. Extinction and emission of the canopy of a spruce stand (After Lorenz and Baumgartner, 1970)

Layer (m)	Needle surface (%)	Extinction coefficient (m^{-1})	Effective radiation surface (%)	Surface temperature ($^{\circ}\text{C}$)
26.6–29.0	7.1	0.068	19.6	26.0
24.2–26.6	28.9	0.277	40.8	25.9
21.8–24.2	44.5	0.427	22.7	24.9
19.4–21.8	13.9	0.133	5.1	23.8
17.0–19.4	5.6	0.054	1.8	22.8
Soil surface			10.0	18.3

the canopy, etc. Also, plant bodies are comparable with geometrically defined surfaces only as a first approximation.

For a horizontal leaf, the radiation exchange is given by the sum of the net radiation at the upper leaf surface, Q_o , and at the lower leaf surface, Q_u :

$$Q_o = I + D - R_{s,o} + A - E_o + T_o - R_1 + Z_o$$

$$Q_u = a_s r_s (I + D) - R_{s,u} - T_u + Z_u - R_{z,u}$$

R_o and $R_{s,u}$, respectively, and E_o and $E_{s,u}$, respectively, are the short or long wave reflections or emissions; T_o and T_u are the transmissions and are quantitatively relatively small; Z_o is the long wave radiation from surrounding leaves. The volume element of an isolated leaf has a greater net radiation during the daytime than the area unit of leaf surface or of the earth's surface. The difference is approximately 10 per cent. During the night, this difference disappears, as E_o and Z are then of equal value. The upper leaf surfaces naturally contribute more to the net radiation gain during the day than the lower surfaces.

The relative position of plant material plays a big role in the energy conservation. A vertical leaf has a smaller net radiation loss than a horizontal one during

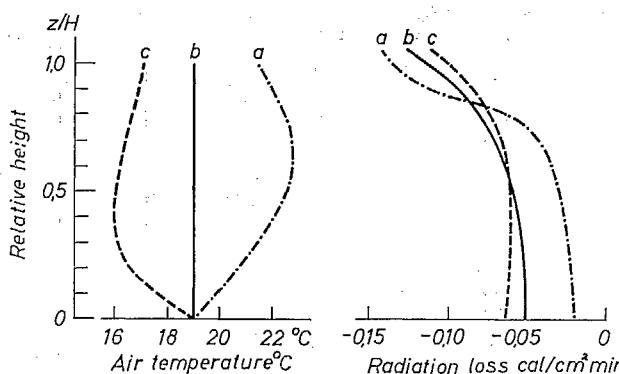


FIG. 5. Long wave radiation loss of a rice field, dependent on air temperature profiles. (After Saito, 1964.)

TABLE 7. Ratios of radiation absorption

Needles of:	F_s/F	F_l/F
Fir	0.32	0.94
Spruce	0.34	0.88
Pine	0.29	0.85

the night, as the emission from the environment is normally higher than the emission from the atmosphere. During the night, spheres lose only $\frac{3}{4}$ of the energy in comparison with horizontal, flat bodies. The effective surface of plant bodies is different; Tibbals *et al.* (1964) have shown that for absorption of solar radiation or of terrestrial radiation, the effective surfaces (F_s , F_l) are related to the whole surface F by the ratios as shown in Table 7.

For a single cylinder in a horizontal position, $F_s/F = 1/\pi = 0.318$, but, for randomly distributed cylinders, the value decreases to 0.203. For sky radiation, Gates (1965 b) assumed $\frac{1}{2} F$ as the effective surface. He formulated the radiation balance of a plant body in a general form, as:

$$Q = a_s(I + D) \cdot F_s + F_s r_s a_s(I + D \cdot F_s/2 + a_1(A + Z) \cdot F_l/2 - \varepsilon \delta T^4 \cdot F_l).$$

For a_s , Gates used the values shown in Table 8.

In general, plant bodies of small size have a higher net radiation than bodies of greater size. Due to the more intensive heat transfer, they are cooler and emit less intensively than more extended bodies.

NET RADIATION DISTRIBUTION IN CANOPIES

Figure 6 shows the field of net radiation for a spruce stand during a clear summer day.

The most intensive radiation energy transformations occur in the upper levels of the canopy. This layer is also the active level in the biological respect. It is identical to the layer of maximal source strength for transpiration as well as for photosynthesis.

The net radiation at the earth's surface under canopies depends on the density of the stands as illustrated in Figure 7. In naturally closed canopies, only 5–10 per cent of the net radiation at the top of the canopy is present; in open stands, 40 or 50 per cent. Due to the physical

TABLE 8. Values of a_s (After Gates, 1965b)

	For direct sun	For sky radiation
Leaf	0.5–0.6	0.6–0.7
Succulents	0.6–0.8	0.66–0.76
Needles	0.88	0.88

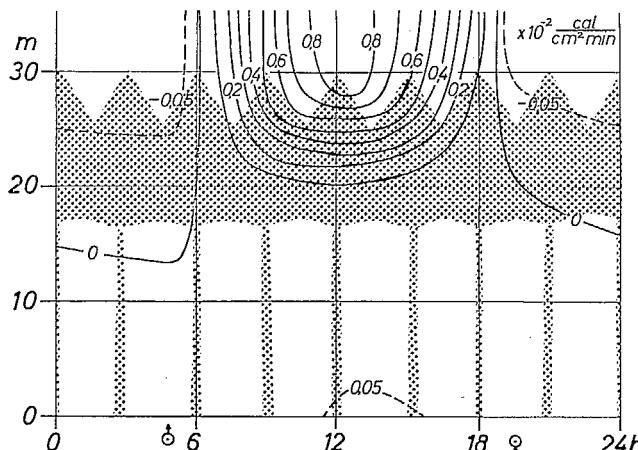


FIG. 6. Distribution of net radiation within a spruce stand during a clear day. (After Baumgartner, 1962.)

parameters for reflection and emission, the various plant stands have different energy gains as observed by Allen *et al.* (1963), Denmead *et al.* (1962) and Stanhill *et al.* (1966). Net radiation differs up to 30 per cent. Forests have higher radiation incomes than crops, arable lands or grasslands. For this reason they are more intensive water consumers than other plant stands.

THERMAL ENVIRONMENT

GENERAL REMARKS

The thermal environment is determined by heat supply and transformations. The heat exchanges are defined by the law of energy conservation. For surfaces or for a volume of stand space, this may be expressed by:

$$Q = B + H + V + K + \dots,$$

where Q = net radiation; B = body heat of soil layers, plant mass and of air layers within stand space; H = sensible heat of air; V = latent heat and K = conversion of radiation in photosynthesis.

In this respect, temperature is an expression of the energetic behaviour, and temperature changes are caused by energy exchanges. For an understanding of the

TABLE 9. Heat capacity of plant mass and air inside stands (After Baumgartner, 1970)

	Dry matter (g cm ⁻²)	Plant (cal cm ⁻² ground)	Air (°C)
Grass, crops	0.2-0.5	0.4	0.02
Bushes	1.0-2.0	1.2	0.04
Mature forests	5-10	6	0.9

thermal responses and of the thermal environment of plants, the heat capacity, the sensible heat transfer processes and the latent heat conversions have to be discussed.

HEAT CAPACITY AND RESPONSES OF PLANT BODIES TO HEAT TRANSFER

Estimations of the heat capacity of the plant masses give the values shown in Table 9.

The heat supply of a whole stand is very small in relation to the energy load of the solar radiation. For example, at noon a mature forest can be warmed by 1° within a few minutes. The heat capacity of three needles is of the order of 20 mcal deg C⁻¹, and that of a leaf, 50 mcal cm⁻² deg C⁻¹ and corresponds to the sensible heat transfer which occurs within a few minutes or less. The molecular heat transfer through organic substances has a velocity of about 2 cm hr⁻¹. Thus, the heat load on changing radiation intensity on days with cloudy sky may be absorbed by the assimilating or transpiring organs in a short time. The short term fluctuations in temperature in natural environments have their effect in the production apparatus and processes.

SENSIBLE HEAT TRANSFER

It has been shown already that the storage capacity of the radiation heat load in the plant bodies is limited and that the transfer of heat into the plants is slow. Also, the molecular heat transfer into the surrounding air, which is approximately at the rate of 4 mcal cm⁻²

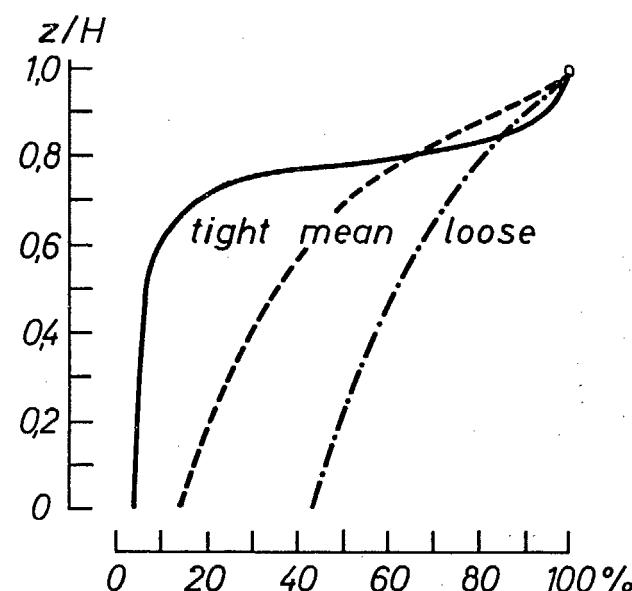


FIG. 7. Vertical distribution of net radiation in plant stands, depending on density of stand. (After Baumgartner, 1963.)

TABLE 10 Temperature differences $\Delta\theta = \theta_o - \theta_a$ at the boundary layers of *Tropaeolum maius* (After Berger-Landefeldt, 1958)

Distance from leaf surface (mm)	Upper side (°C)	Lower side (°C)
1	6.6	4.2
2	4.4	3.5
3	3.0	2.8
5	1.8	2.3
10	0.6	0.1
20	0.1	0.0
50	0	0

$\text{min}^{-1} \text{deg}^{-1}$ and 5–10 times smaller than the molecular heat transfer in the solid plant bodies, cannot prevent overheating at the surfaces. Fortunately, other processes are much more effective, namely, the latent heat loss, the free convection and the forced convection by turbulent heat transfer.

Free convection

The heat storage within the laminar boundary layer and in the transition zone with the air generally forms an unstable temperature distribution. By fine structure measurements of the temperature field in the vicinity of dry and wet leaves, Berger-Landefeldt (1958) estimated the depth (d) of the laminar layer of large leaves to be in the order of millimetres; the transition zone from surface temperature (θ_o) to air temperature (θ_a), may be as much as centimetres. On a sunny day he observed the temperature profiles listed in Table 10 for a transpiring leaf of *Tropaeolum maius*.

Corresponding to the archimedian principle, air bubbles leave the boundary layer and transport energy at the rate

$$L_c = \alpha_c \cdot F \cdot \Delta\theta,$$

where α_c is the transfer coefficient for free convection, F is a number related to the size and form of the body, and $\Delta\theta = \theta_o - \theta_a$. Gates *et al.* (1965) estimated the free convection for a leaf of diameter D to be

$$L_c = 0.006 \cdot \frac{(\Delta\theta)^{1/4}}{D}.$$

For a pine twig, Gates *et al.* (1965) found that α_c has the value

$$\alpha_c = 0.011 + 36 \times 10^{-3} (\Delta\theta)^{0.3} \text{ cal}^{-1} \text{ cm}^{-2} \text{ min}^{-1} \text{ deg}^{-1}.$$

The transfer characteristics can be expressed by aerodynamic dimensions like the Nusselt, Grasshof or Reynolds number. Warm air convection has been recorded by Gates *et al.* (1963) with schlierenphotography. Hsu (1963) found that the rate of free convection at the upper surface of a horizontal leaf is twice that at the lower surface.

Forced convection

In a similar way, the forced convection by the vertical component of air flow is formulated by:

$$L_f = \alpha_f (\theta_o - \theta_a).$$

The heat transfer coefficient, α_f , in $\text{mcal cm}^{-2} \text{ min}^{-1} \text{ deg}^{-1}$, depends not only on the flow velocity and turbulence, but also on the geometry of the plant surfaces. The ratio $1/\alpha_f$ defines the diffusion resistance of the boundary layer between plant and air for the heat transfer.

The heat transfer coefficient, α_f , for a plate with tangential flow has been expressed by Eckert (1949) as a function of the depth of the laminar layer and the molecular heat transmission coefficient, $\lambda\alpha$:

$$\alpha_f = \frac{3 \cdot \lambda\alpha}{2 \cdot d}$$

It is inversely proportional to the horizontal dimension d . This means that the heat transfer is greatest at the edges of the leaves and lowest in the centres. This statement is also in agreement with the heat transfer equation for a plate in the form:

$$\alpha_f = 55 \cdot (v/D)^{1/2} \text{ mcal}^{-1} \text{ cm}^{-2} \text{ min}^{-1} \text{ deg}^{-1}$$

where v = wind velocity and D is the distance from the upwind edge. Raschke (1956) estimated the heat transfer across an oval leaf with diameter D as:

$$\alpha_f \sim 0.7 \cdot D^{-0.3} \cdot v^{1/2}.$$

The rate of heat transfer depends on the angle between the leaf surface and the direction of air flow. Vertical

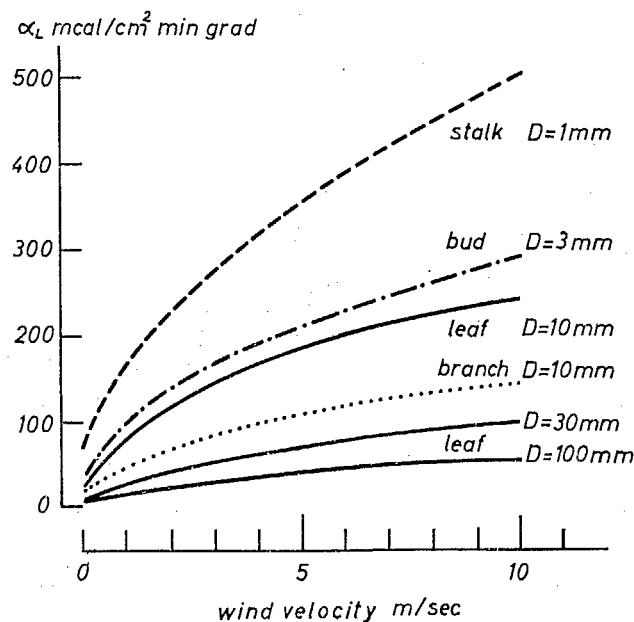


FIG. 8. Heat transfer coefficients of various plant bodies as a function of size and wind speed.

leaves have twice the heat transfer at the upwind than the downwind side.

The heat transfer is very different for the individual plant parts, not only according to the size, but also with the shape and form of the plant bodies. The behaviour of different plant parts is shown in Figure 8. In general, one may state that heat transfer decreases with the size of the plant body and increases with the degree of sub-division of the plant body.

Heat transfer is a self-regulating system, as it tends to decrease the temperature difference (s) ($\Delta\theta$) and the depth (d) of the boundary layer. Classical examples of this have been given by Raschke (1956), who illustrated the distribution of temperature and heat transfer on a leaf of *Canna indica*. The study of heat transfer phenomena is not only a problem of biophysics, it is also one of the keys for understanding the transfer of water vapour and carbon dioxide. There is a high correlation between the heat transfer and the carbon dioxide fixation. It is evident that the shape of the assimilating and transpiring organs plays a role in determining the rate of photosynthesis since, under natural conditions, it has an influence on the turbulent diffusion of the carbon dioxide potential in the surrounding air.

LATENT HEAT TRANSFER

As in the case of sensible heat transfer, one may describe the vapour transfer from the surfaces of a plant to the air in the environment by:

$$W = h (q_o - q_a),$$

where W is the rate of water vapour transfer, q_o is the specific water vapour content at the temperature θ_o , at the plant surface, and q_a is the specific water vapour content in the air. The water vapour transfer coefficient can be related to the heat transfer coefficient by:

$$h = \alpha/C_p$$

where C_p is the specific heat of air ($0.24 \text{ cal g}^{-1} \text{ deg}^{-1}$). The latent heat is then determined by the introduction of the enthalpy for evaporation ($r \approx 600 \text{ cal g}^{-1}$ of water):

$$V = rW = rh (q_o - q_a).$$

Using the water vapour pressure e in place of q , the heat for transpiration is given by:

$$V = r \cdot \frac{0.623}{b} \cdot \frac{\alpha}{C_p} \cdot (e_o - e_a).$$

It is easy to see that the heat transferred by evaporation is proportional to the transfer factor h . Thus a small leaf evaporates more water per unit area than a large leaf. In general, latent heat transfer is more energetically effective than sensible heat transfer, and high transpiration rate is the best protection against overheating. Under a given radiation load, the overheating depends on the ratio of sensible heat transfer to or from a transpiring surface to the latent heat use. Linacre (1967) in Australia

found an equilibrium of θ_o and θ_a at $\theta_a = 31^\circ \text{ C}$. θ_o is greater than θ_a for air temperatures smaller than 31° C . Farmer (1969) observed that $\theta_o > \theta_a$, if leaves of cottonwood evaporated less than $4 \times 10^{-6} \text{ g}$ of water $\text{cm}^{-2} \text{ s}$.

HEAT AND MOMENTUM TRANSFER INSIDE STANDS

Two factors of dominant importance for the heat transfer and the thermal environment inside stands are the decrease in radiation heat load on plants and the decrease in wind velocity towards the earth's surface. Both can be directly related to stand parameters.

The wind profile above the stand is formulated by the well known, so-called logarithmic wind profile:

$$u(z) = u^* / k \cdot \ln \frac{z-d}{z_0}$$

when u^* = mixing velocity; $k = 0.4$, the Karman constant; z = the height above the earth's surface; d = the zero plane displacement; and z_0 = the roughness parameter. The roughness parameter is a characteristic for the different vegetation surfaces, e.g. its values are approximately 0.5 for lawn, 2 for grassland, 10 for field crops, 200 cm for forests. The increase means that with the increase in height of the vegetation cover, the turbulence and the vertical mixing inside the stand increase.

The wind profile within the stands can also be expressed by stand parameters. Saito (1962) found that the shearing stress τ depends on the volumetric leaf area index, F^1 , for leaves and stems together, in the form:

$$\tau = \rho(1-F^1) \cdot a \cdot u^2$$

and increases with the square of the wind velocity. ρ = air density and a is a function of du/dz . The vertical profile of the diffusion coefficient, $K(Z)$, which is of importance e.g. in evaluating the heat, momentum, or the carbon dioxide transfers within stands, is given by:

$$K(Z) = \frac{Q_z - B_z}{C_p \cdot \rho \frac{d\theta}{dz} + r \cdot \frac{da}{dz}}$$

It can be estimated from the explicit energy balance in the different layers of the stand (see Begg *et al.* (1964), Uchijima and Wright, 1964; Uchijima (1969) and Uchijima *et al.* (1970); and others). An example is given in Figure 9 for a forest stand.

The coefficient of diffusivity, $K(Z) = A/\rho$, decreases towards the earth's surface, as do the wind velocity and the shearing stress. Therefore, the high carbon dioxide content in the stand cannot be used for photosynthesis, unlike the smaller carbon dioxide content from the atmosphere above the stand. The contribution of soil carbon dioxide is only $1/3$ of the assimilated carbon dioxide coming from the air above the canopies.

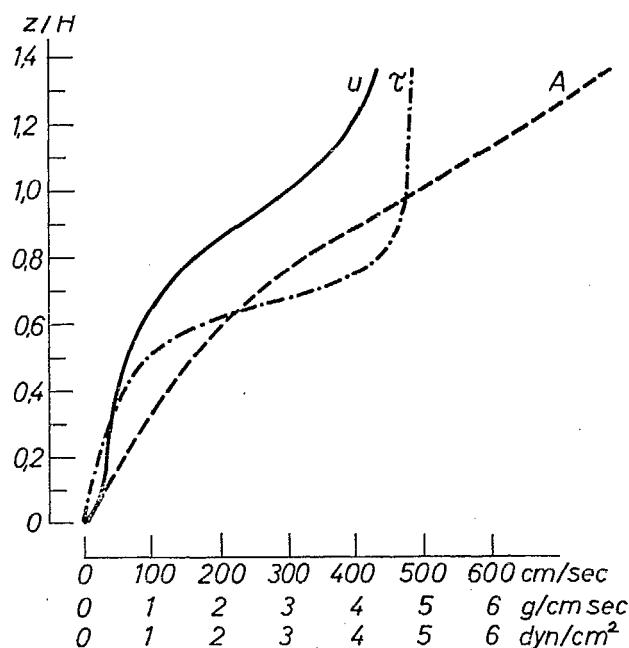


FIG. 9. Vertical profiles of wind speed (u), turbulent exchange coefficient (A) and of shearing stress (τ) within plant stands.

One aspect to be mentioned here is that the composition of the turbulent flow in the stand is different from the flow above the canopy. Spectral determinations of the turbulence in a larch stand by Allen *et al.* (1963, 1968) have shown that, inside the stand, an increase of larger turbulent elements is to be observed. This means that the exchange mechanism is different from that in the air of the upper levels of the stands.

VERTICAL TEMPERATURE DISTRIBUTION WITHIN STANDS

The vertical temperature distribution within stands is governed mainly by the heat supplied by the conversion of radiation in the canopy and by the scattering of the heat due to the vertical air exchanges. In naturally closed stands, the temperature maximum will be situated primarily in the upper light canopy; in less dense stands there can be a secondary maximum at the earth's surface. For the production process it is important that the temperature differences within the whole stand space are only of the order of degrees. The main temperature dependent process is respiration which, in principle, increases exponentially with temperature. The vertical profile of temperature within the stand space varies the respiration intensity only by a few per cent. This is in contrast to the effect on photosynthesis by a reduction of photosynthetic radiation to $1/10$ of that above the canopy. The temperature dependent evaporation component also has its maximal potential in the layer near the temperature maximum.

MODELLING THE PHYSICAL ENVIRONMENT IN STANDS; SOURCE POWER OF PLANT PROCESSES

The physical properties, related to the stand parameters, outlined in this paper have been used to establish models for the simulation of the environment in plant stands and to apply these for evaluating production itself.

ENERGY BALANCE MODEL FOR LEAF TEMPERATURE AND TRANSPERSION

A number of authors, e.g. Bernard (1965), Curry (1969), Gates (1965a), Impens (1965), Knoerr and Gay (1965), Raschke (1956), Saito (1962) and Uchijima and Wright (1964, 1969, 1970) have used the energy balance terms for simulations of the behaviour of transpiring or non-transpiring plants. The main problem is to find the relationships between transfers and resistances of boundary layer and plant organs. An example is given in Figure 10 to demonstrate the use of these models.

For a given absorbed isolation on the ordinate, the dotted line on the abscissa indicates the rise in temperature which would occur at the plant surface if the plant transferred its heat load by emission only. From

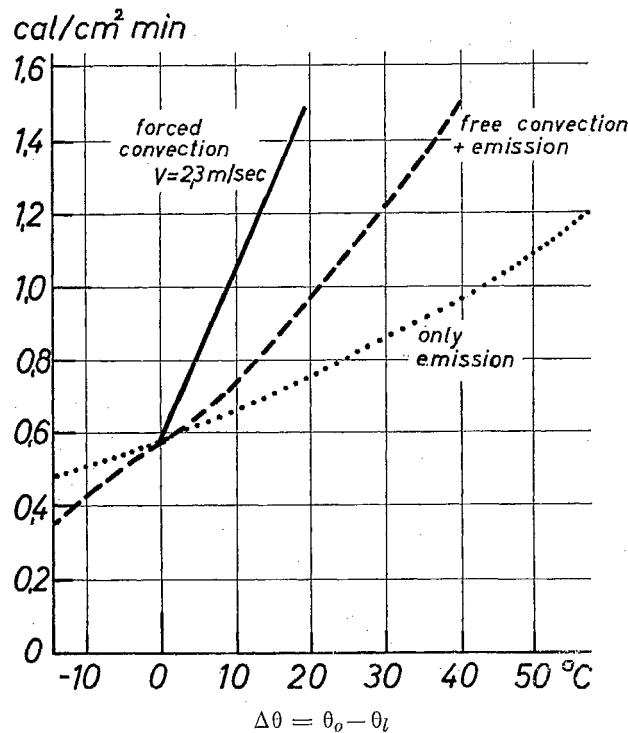


FIG. 10. Energy balance model of a leaf surface. Overheating ($\Delta\theta$) is given in terms of net radiation for only emission or for emission + free convection or for emission + free convection + forced convection. (After Gates, 1965.)

the dashed line, the increase in temperature can be seen if free convection occurs also. From the full line, the temperature differences $\Delta\theta = \theta_o - \theta_a$ in forced convection can be seen. Under given conditions, transpiration can also be estimated from this type of diagram, if one has a knowledge of the actual surface temperature.

MODELS OF THE MICROCLIMATE AND FLUXES IN STANDS

Another type of theoretical approach to the micro-environment is that of using the energy balance for individual layers of the stand. The resistances or the conductivities for the vertical flow of air and water vapour or carbon dioxide have to be introduced into the equations. For steady state conditions, the net radiation values above and under the canopy are given and the vertical profile of net radiation is expressed in terms of the leaf area index $F(Z)$ (see Cowan, 1968; Denmead, 1964; Menzhulin, 1970; Philip, 1964; Uchijima and Wright, 1964; Waggoner *et al.* 1969).

AERODYNAMIC APPROACHES FOR ESTIMATING CARBON DIOXIDE ASSIMILATION

Similar to the heat, momentum and water vapour fluxes, due to gradients in the concentrations of carbon

dioxide, the carbon dioxide flux, F_c , can also be estimated by using the diffusion approach, for example, in the form:

$$F_c = D_c \text{ grad } D = k^2 \cdot \rho \cdot \frac{(u_2 - u_1) \cdot (C_1 - C_2)}{l u \left(\frac{Z_z - d^2}{Z_o} \right)}$$

where $k = 0.4$, ρ = air density; u_1 and u_2 are wind velocities; C_1 and C_2 are the carbon dioxide concentrations at heights Z_1 and Z_2 ; d is the zero plane displacement, and Z_o is the roughness parameter. Satisfactory results are published by Monteith (1963), Inoue (1965), Uchijima (1969) and Baumgartner (1969).

MODELS FOR ESTIMATING THE SOURCE STRENGTH FOR PHOTOSYNTHESIS

Using the natural distribution of the physical environment in the stand, in terms of radiation, temperature and diffusivity conditions, as well as the response characteristics and resistances of plant bodies, one is able to transform micrometeorological distributions into productivity distributions. Such an example is given by Baumgartner (1969). Further studies with field laboratories are needed to get the response characteristics under natural conditions.

Résumé

Estimation du rayonnement et du micro-environnement thermique d'après les paramètres météorologiques et les paramètres des végétaux (A. Baumgartner)

Partant de la terminologie du rayonnement, l'auteur donne tout d'abord un aperçu des propriétés optiques des organismes végétaux et de la transformation du rayonnement dans les peuplements végétaux. La qualité du rayonnement dans les peuplements végétaux est un mélange de rayonnement direct et de rayonnement filtré. L'auteur exprime les profils verticaux du rayonnement visible en fonction de l'indice de la surface foliaire. Il introduit dans la loi de Beers l'angle d'inclinaison des feuilles. Les profils du rayonnement à grande longueur d'onde peuvent être décrits de la même façon, mais en n'utilisant que les projections dépassantes des organismes végétaux. Le rayonnement net d'une feuille considérée isolément peut être évalué à l'aide de la surface effective. Dans le profil vertical, le rayonnement

net atteint son maximum dans les strates supérieures de la voûte. Sur le terrain, l'énergie maximale qui produit la transpiration et l'assimilation est à peu près identique à celle du rayonnement net.

Dans la seconde partie, l'auteur étudie l'environnement thermique en fonction du bilan calorique. La capacité et le transfert thermiques dans les organismes végétaux, le transfert de chaleur sensible par convection libre et convection forcée sont mis en relation avec les paramètres des végétaux. Le transfert de chaleur latente est analogue au transfert de chaleur sensible. D'après la répartition verticale des caractéristiques du rayonnement et du transport, on peut déterminer le champ de la température verticale dans les peuplements végétaux.

La troisième partie est consacrée à des applications consistant à utiliser les paramètres physiques et biologiques pour établir des modèles du microclimat et pour évaluer les énergies qui produisent l'assimilation, la respiration et la transpiration dans les différentes strates des peuplements végétaux.

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Development of simplified agroclimatic procedures for assessing temperature effects on crop development

G. W. Robertson

Research Station, Canada Department of Agriculture,
Swift Current, Sask. (Canada)

INTRODUCTION

It is well known that temperature determines, to a large extent, the types of crops which can be grown in a given region. Classical climatologists used temperature as one of two main characteristics for classifying the climates of the world. In their classifications both Koppen and Trewartha used temperature as the factor for the basis of the main climatic divisions (Trewartha, 1968). Thornthwaite (1948) proposed a climatic classification based on two temperature-derived factors, "thermal efficiency" and "summer concentration of thermal efficiency", along with a moisture factor. These classifications were of interest to ecologists because, in a broad sense, the world distribution of native plants and cultivated crops paralleled the climatic zones.

In the temperate zone the time of tree budding, when grass turns green, and of planting annual crops is determined largely by the temperature in the early spring. Ecologists speak of heat-loving and cool-loving plants: these are inherited characteristics established during evolution in their climatic zones of origin. Yet, in spite of the apparent influence which temperature has on the geographical distribution of plants and their cycle of reproduction, very little progress has been made towards developing rational methods which have universal application for processing meteorological and climatological temperature data to explain how plants may be expected to react under given environmental conditions.

The problem of understanding the effect of temperature on plants differs greatly from that of making use of meteorological temperature data for explaining the growth and development of plants. The plant physiologist, the nutritionalist and the biochemist have studied the former problem from many aspects, particularly under controlled conditions. Agrometeorologists, ecologists and horticulturalists have used techniques relative

to the latter. However, few really good controlled field experiments have been undertaken to develop models for explaining how temperature affects the rate of progress of plants towards maturity.

The first problem, i.e. the physiological effect of temperature on plants, has been reviewed by Dr Bierhuizen (this volume). This review will deal primarily with the response of plants to meteorological or climatological temperatures, particularly with regard to development.

A critical review of the various systems and techniques for relating crop development to temperature was prepared by Wang (1960). In that review, he covered much of the earlier published research. Consequently, this review will concentrate on pertinent developments in the past decade. This paper will not be a critical review, but simply an outline of historic developments to show how crop/weather development models evolved and led finally to the development of the biometeorological time scale (BMTS) of the author (Robertson, 1968) and how it can be applied to a practical large scale cereal zonation problem (Williams, 1969).

EVOLUTION OF MODELS

The earliest attempts to use atmospheric temperature data to explain the variations in the response of plants in different climatic zones was done by Réaumur, the inventor of the thermometer scale bearing his name. His work and its impact up to recent times have been reviewed by many authors such as Thornthwaite *et al.* (1954), Holmes and Robertson (1959), Wang (1960) and Robertson (1968).

The technique used by Réaumur is worthy of brief review here because it is still used almost in its original form by many ecologists, horticulturalists and vegetable canning companies. Essentially the scheme assumes that

TABLE 1. Phenology of Marquis wheat in a number of North American areas (After Nuttonson, 1957)

	Latitude	Date of seeding	Date ripe	From emergence to ripe			Average length of day multiplied by degree-days
				Days	Degree-days	Average length of day (hr)	
Fairbanks, Alas.	64°	3 June	29 August	78	2 054°	19.0	39 026
Beaverlodge, Alta.	55°	27 April	24 August	102	2 296°	16.7	38 343
Saskatoon, Sask.	52°	3 May	2 August	89	2 375°	16.4	38 950
Indian Head, Sask.	51°	7 May	13 August	86	2 394°	16.4	39 262
Portage la Prairie, Manitoba	50°	7 May	13 August	78	2 398°	16.0	38 368
Winnipeg, Manitoba	50°	13 May	14 August	77	2 448°	16.0	39 168
Havre, Mont.	49°	23 April	31 July	85	2 454°	15.7	38 528
Dickinson, N.D.	48°	20 April	31 July	89	2 540°	15.4	39 116
Alliance, Nebr.	42°	31 March	9 July	97	2 793°	14.7	41 057
Lincoln, Nebr.	41°	1 April	9 July	86	2 816°	14.5	40 832
Tlalnepantla, Mex.	19°	1 December	7 May	148	3 711°	11.7	43 419
Mean				92	2 571°		39 643
Standard deviation				16	366°		1 454
Coefficient of variation (per cent)				17.4	14.2		3.7

a given variety of a plant requires the same summation (k) of daily mean temperature (T_m) from planting (P) to maturity (M), regardless of the temperature. Réaumur used a thermometer scale with zero at the freezing point of ice and he considered only the positive temperatures.

Today we would express the concept by an equation such as

$$\frac{M}{P} T_m = k \quad (1)$$

where

$$T_m = 0/T_m < 0$$

or, more generally, when the threshold of growth (or development) is not zero but rather, a :

$$\frac{M}{P} (T_m - a) = k \quad (2)$$

where

$$(T_m - a) = 0/T_m < a.$$

This scheme developed very slowly and a century later Boussingault (1837) calculated the total quantity of "heat" required to ripen grain by essentially the same method. He called the product of the mean daily temperature above 0° C for the period and the length of the period in question "degree-days".

Some 40 years later, Tisserand (1875) modified Réaumur's and Boussingault's hypothesis that the rate of development varied with time and temperature. He adopted the rule that work done by the plant could be represented by the product of the mean temperature and the number of hours of daylight between sunrise and sunset. Thus Tisserand disregarded the dark hours just as his predecessors disregarded temperatures below the freezing point of water.

Nearly another half century passed before Garner and Allard (1920) observed and described the phenomenon of photoperiodism: the effect of the relative length of day and night on the rate of development of floral and leaf buds.

Nearly 30 years then elapsed before Nuttonson (1948) showed that, for certain varieties of wheat, flax, eggplants and peas, the number of degree-days from emergence to maturity multiplied by the average daylength was more constant from station to station than was the number of degree-days alone. This photothermal concept could be expressed mathematically as

$$\frac{M}{P} \Sigma (T_m - a) = K \quad (3)$$

where

$$(T_m - a) = 0/T_m < a$$

L is the average daylength during the phenological period, K is the photothermal constant.

The advantage of the photothermal constant, K , over the degree-day constant, k , is well illustrated (Table 1) by data from Nuttonson (1957).

The heat unit or degree-day concept has been used quite extensively by commercial canners to schedule the fraction of a crop maturing at any one time in order that their cannery would not be swamped by all fields reaching maturity at the same time. The procedure followed for using degree-days for such planning purposes was reviewed and discussed by Holmes and Robertson (1959). The concept is still very much in vogue today; witness the recent issue of tables for the rapid calculation of degree-days (Williams and MacKay, 1970). Their method is a modification of methods suggested by Lindsey and Newman (1956) and Arnold (1960). It takes into consideration the problem of calcu-

lating degree-days on days when the minimum is below the threshold temperature but the maximum is above.

Thorntwaite and Mather (1954) proposed a unique system for relating plant development to climatic data. They assumed that transpiration, growth and development are all proportional to one another and are all affected by temperature in the same way. Using this assumption, they defined the development index in terms of the amount of water needed for potential evapotranspiration as calculated by Thorntwaite's (1948) formula. This formula is a complex function of the mean daily and the mean monthly air temperatures multiplied by a daylength factor. For a given location or climatic region the potential evapotranspiration is found to be a nearly linear function of temperature (above 0° C) multiplied by a daylength factor. Thus their development index is very nearly the same as Nuttall's concept of photothermal units. A study of the relationship between mean air temperature and potential evapotranspiration was made by Pelton *et al.* (1960). They observed a close relationship between these two factors, but pointed out that this is not the result of a causative effect, but because of a common control by net radiation.

The concepts of long and short day plants and critical values of daylength and nightlength were known since Garner and Allard's work on photoperiodism in 1920. It appears, however, that the idea of using a lower critical value for photoperiod or for night length in a developmental equation was first suggested by Robertson in 1953. He reported a developmental equation based only on daylength of the form

$$\sum_{E}^H (L - b) = K_L \quad (4)$$

where

L is the length of photoperiod,

b is the critical photoperiod,

K_L is a photoperiod summation constant for the phenological period from emergence (E) to heading (H).

$$(L - b) = 0/L < b.$$

Six plantings of Redman wheat (a long day cereal) and of crown proso millet (a short day cereal) were made at two-weekly intervals throughout the summer of 1952 at Ottawa, latitude 45° 24' N. The daylength variation from planting to planting was sufficient to cause marked differences in development rate of the two crops.

It was found that the equation for development for the Redman wheat was

$$\sum_{E}^H (L - 10.7) = 194 \quad (5)$$

and for crown proso millet was

$$\sum_{E}^H (D - 5.7) = 151. \quad (6)$$

Wheat, being a long day plant, was found to have a threshold photoperiod of 10.7 hr of daylight for the period from emergence to heading. On the other hand, millet, a short day plant or a long night plant, required a dark period greater than the threshold of 5.7 hr of darkness. These results appeared to be consistent with known reactions of these two crops to photoperiod.

The fact that plants do not respond to temperature in a linear manner has been known ever since Lehenbauer (1914) demonstrated, with reference to the root growth of maize, the principle of cardinal points: i.e. that plants have lower and upper critical limits and an optimum value of temperature for growth and development. Ferguson (1958) suggested a unique method for relating development to hourly day-time temperatures as well as taking into account a non-linear response. He expressed his relationship by means of the following equation

$$a_1 \Sigma (T - a) + a_2 \Sigma (T - a)^2 + a_3 \Sigma (T - a)^3 + \dots = 1 \quad (7)$$

T is the hourly day-time temperature.

$$(T - a) = 0/T < a$$

a is the threshold temperature

a_1, a_2, \dots are regression constants.

Summations were taken over the period from seeding to maturity. Instead of assuming that the total summation was a constant to be determined, he set the expression equal to the stochastic value 1. The example he cites, using garden peas, considered only daylight temperature. His phenological data were from only one station and the photoperiod, which would have been subject to negligible variation from year to year, was assumed to be above the lower critical threshold at all times.

Biochemical reactions within plant cells are different in the day from those at night. During the day, photosynthesis, translocation and respiration take place, while at night photosynthesis ceases and translocation is reduced. It was not too surprising when Went (1956) showed that some plants have a different response to night temperature than to day temperature. He found that tomatoes, in order to set fruit, required a definite night-time temperature which was much lower than the day-time requirement.

This fact was later incorporated into an equation by Brown and Chapman (1960) for estimating the development rate of soybean. Their "soybean development units", or SDUs, were based on the number of hours of darkness (sunset to sunrise) as a quadratic function of the average temperature, \bar{T} , for the period. In general their equation could be expressed as:

$$Y = a_1 \bar{T} + a_2 \bar{T}^2 + a_0 \quad (8)$$

where Y is the average rate of development (reciprocal of the total number of night hours in the phenological period). They found that the values of the regression coefficients were dependent on the soil water status for the phenological period from planting to flowering.

After flowering the relationship appeared to be linear and not dependent on the soil water status. Their relationships were used for preparing soybean zonation maps in the Great Lakes Region (Brown and Chapman, 1961).

Further use of curvilinear temperature relationships for determining development was described by Franquin (1968). He related the number of fruits to a quadratic function of temperature, but found that the number of nodes was a linear function of temperature. He also distinguished between "thermic" relationships in the case of non-photoperiodic species and "conditionally thermic" relationships for photoperiodic species, since such relationships hold only for specific photoperiods. He also made a further distinction between plants with axial flowering (cotton, groundnuts) and ones with terminal inflorescence (sorghum).

Livingston (1916) used the idea of Lehenbauer (1914) to develop what he called a physiological index, since it was based on actual physiological measurements on maize. However, as Livingston pointed out, the technique had several shortcomings and the idea did not seem to be widely accepted at the time.

Recently, another attempt to use a physiological index for zonation purposes was reported by Utaaker (1968). He used the concept of the respiration equivalent (*RE*), which was introduced by Dahl and Mork (1959). They argued that heat does not supply directly the energy for growth in the plant. The energy needed for the different growth processes, apart from the photochemical process of photosynthesis, is chemical-energy released through respiration. Provided the plant is kept at full turgor, the respiration is mainly controlled by temperature. It increases with increasing temperature and reaches its maximum at temperatures of about 45–50°C (different for different plant species) then declines rapidly with increasing temperature. It is assumed that growth is proportional to respiration above a certain basal value. When hourly and bi-hourly observations of temperature are available, it is possible to evaluate a temperature-growth index (*RE*) from the temperature-respiration relationship. This index is evaluated by counting the number of hours (N_i) within certain temperature intervals, multiplying this number by the relative respiration (Re_i) at the appropriate temperature level and then accumulating all the products, i.e.:

$$RE = \sum_{i=1}^n Re_i N_i \quad (9)$$

where n is the number of temperature classes. Utaaker claims that this index is clearly akin to the heat-sum, and that it may be regarded as a "corrected" heat-sum. There appears to be no distinction between growth and development in this concept. The index is used to prepare maps showing a meso-scale study of the growth climate.

Primault (1968) described a biometeorological index for determining the possibility of extending the corn-growing area in Switzerland. His index is of the form

$$\Sigma T_a + s \Sigma S + p \Sigma P_{30} = I \quad (10)$$

where

T_a is mean daily temperature,

S is the duration of sunshine,

P_{30} is the 24-hr precipitation (the maximum is set at 30mm per day),

s and p are regression coefficients to be evaluated by regression methods,

I is the index limit.

This equation has been used along with long-term weather records for determining the probability of maturing corn at various locations in the country.

All techniques discussed so far have used air temperature as measured in a meteorological screen or shelter, the assumption being that this is sufficiently representative of the effective crop temperature. Robertson (1953) proposed a method for calculating effective crop temperature from standard meteorological factors. His equation was of the form

$$T_p = T_a + k \frac{Q_N - Q_E}{1 + 0.01 \bar{W}} \quad (11)$$

where

T_p is the effective daily crop (or plant) temperature,

T_a is the average daily air temperature,

Q_N is the daily radiation balance (net radiation),

Q_E is the heat equivalent of the daily evapotranspiration rate of the crop,

\bar{W} is the average daily wind speed.

The coefficient k is a crop constant depending on crop density and height, among other things, and can be determined by regression analysis. For the crop of millet in question, $k = 0.18$. For conditions during one season in Ottawa it was calculated that the effective crop temperature averaged 2.5°C greater than ambient air temperature, while on individual days it ranged from 1°C lower to 5°C higher than ambient air temperature. It appears that such allowances for differences between effective crop temperature and ambient air temperature have not been given consideration in crop development/weather relationship models until quite recently.

It was over a decade later before Newman *et al.* (1967) expanded on this idea. Their approach was not to consider temperature, but what they called net radiant heat load on the vegetative surface. This consisted of calculating the excess of actual heat flux on the vegetative surface above a base flux of 0.524 cal cm⁻² min⁻¹ corresponding to a base temperature of 10°C.

The actual heat flux was computed from microclimatic observations within the grove (orange). Observations consisted of air temperature, wind, and black-globe temperatures taken bi-hourly. The results, applied to the development of oranges, were found to be superior to the accumulation of degree-days above a threshold of 12.8°C, but limited to temperatures below 35°C.

TABLE 2. The development of spring wheat in Canada; temperature and photoperiod: 5-year averages, 1953-57 (After Ripley, 1959)

Factor	Harrow	Ottawa	Normandin	Swift Current	Lacombe	Beaver Lodge	Fort Vermilion	Fort Simpson
Latitude (N.)	42° 02'	45° 24'	48° 51'	50° 16'	52° 28'	55° 11'	58° 23'	61° 52'
Planting date	18 April	16 May	28 May	16 May	16 May	12 May	18 May	20 May
Planting to emergence:								
Days	10	6	10	10	10	11	10	10
Maximum (° C)	16.1	20.6	20.0	18.3	17.8	17.8	18.9	17.2
Minimum (° C)	5.0	7.8	7.2	5.6	3.9	4.4	3.3	4.4
Emergence to heading:								
Days	50	45	42	51	54	60	40	40
Maximum (° C)	21.7	22.8	22.2	22.2	21.1	19.4	20.6	21.7
Minimum (° C)	10.6	11.7	9.4	8.9	7.8	6.7	7.2	9.4
Photoperiod (hr)	14.7	15.5	16.1	16.3	16.6	17.2	18.1	19.5
Heading to maturity:								
Days	31	29	54	41	59	54	48	38
Maximum (° C)	26.7	26.7	20.6	25.6	21.7	20.6	21.7	22.8
Minimum (° C)	15.6	14.4	9.4	10.6	7.8	7.2	8.9	10.0
Photoperiod (hr)	15.1	15.1	14.3	15.0	14.8	15.5	16.5	17.6

Obviously the situation regarding crop development/weather models appears to be fluid, if not confused. The trend is towards relationships which appear to be more sound from a physiological point of view, i.e. they use curvilinear relationships, physiological indices, and attempts to include expressions for night-time temperature, photoperiod, and radiation balance. There appears to be ample room, however, for the development of a model that includes the desirable features of all these factors and which would be universal in application. This is the aim of the research which will be discussed in the remainder of this paper.

THE CANADIAN PROBLEM AND EXPERIMENT

During the decade or more following the end of the Second World War, the Canadian wheat industry underwent several changes. Some 9 million hectares of virgin land were available for new farmers in northern parts of Alberta and British Columbia. New varieties of wheat, which were more drought and rust resistant than the older ones, were being developed. Farmers were using new agronomic techniques, including pesticides and fertilizers. The agronomic research work being undertaken on wheat and other cereals was complemented by research by plant physiologists and agrometeorologists, who conducted experiments both in controlled environmental rooms (Friend, 1961) and in the field (Ripley, 1959). Since the geographic range over which wheat can be grown in Canada extends from about 42° N in southern Ontario to about 62° N in Northwestern Canada, variations in photoperiod and temperature played no small role in breeding, selection and testing of these new varieties. These environmental

influences on rate of development appeared to be almost unpredictable and certainly the effects on lengths of the period from seedling emergence to heading and from heading to maturity at various locations were most perplexing (Table 2). Studies in controlled environmental rooms led to a better understanding of the effects of temperature and photoperiod on tillering, spikelet and primordia initiation and general overall development (Friend *et al.*, 1963).

These laboratory experiments were complemented by field studies, such as produced the data for Table 2 (Carder, 1957; Ripley, 1959). The main purpose of these field studies was not so much to learn why wheat responds to temperature and photoperiod, but to be able to evaluate and estimate what influence environmental conditions, including temperature and photoperiod, have on the development and growth of wheat. To obtain data for such studies required establishing agrometeorological observing sites and plots at some eight Agricultural Research Stations across Canada. These were selected primarily because of the diversity of climate and of the interest and enthusiasm shown by local staff for the project.

The meteorological observations were taken near (within a few metres of) the crops. These observations were of the macrometeorological nature in that sites had full exposure to sun and wind. No attempt was made to measure the environment inside the crop on a routine basis, although special microclimatic studies were made from time to time (Cordukes and Robertson, 1963; Baier, 1969). Factors observed included maximum and minimum air temperature, grass minimum temperature, dew point temperature, rainfall, bright sunshine, wind at 2 m, and evaporation by means of the black porous disc atmometer (Robertson and Holmes, 1958). The crops included two varieties of wheat, oats, barley,

millet, corn and flax. Besides final yield of grain and straw, heights were measured at certain phenological stages and the dates of phenological stages noted. Data from this project have formed the basis for several studies (Baier and Robertson, 1965, 1967, 1968; Robertson, 1968).

The project was carried out from 1953 to 1957, when some of the crops and varieties were changed. It was then carried on for a second 5-year period from 1958 to 1962. One crop, Marquis wheat, was used over the whole 10-year period. Professor Pascale in Buenos Aires also co-operated in this study. He gathered data on Marquis wheat and meteorological observations for 5 years. At Buenos Aires and at a few stations in Canada, it was possible to make more than one planting per year. Thus there were three sets of data as follows:

1. Regression data 1953–57 consisting of 56 station-year plantings.
 2. Test data 1958–62 consisting of 42 station-year plantings.
 3. Buenos Aires data 1961–65 consisting of 14 plantings.
- During early investigations of the influence of temperature on the rate of wheat development, it soon became apparent that the degree-day concept of Réaumur would not explain the effect of temperature on rate of development from emergence to heading of Marquis wheat in the diverse climatic conditions experienced over the wide latitudinal range experienced in Canada. This conclusion was arrived at using the degree-day or heat-unit equation (2) in its linear form

$$\frac{1}{N} = k_1 (\bar{T}_m - b_o) \quad (12)$$

where

- N is the number of days from date of crop emergence (E) to date of heading (H),
- $1/N$ is the average daily rate of development from date of emergence to date of heading,
- \bar{T}_m is the average of the mean daily temperatures (T_m) for the period in question for $T_m > b_o$,
- b_o is the threshold temperature for development,
- k_1 is the average daily rate of development per degree above the threshold temperature, b_o .

It follows that k_1 is the reciprocal of k in equation (2). A simple comparison by correlation and regression of the average daily mean temperatures (\bar{T}_m) during the period in question and the reciprocal of the duration of the period indicated the degree of fit (Fig. 1). For the eight Canadian stations used in this study there was obviously no relationship.

A comparison of the degree-day equation (2) and the photothermal equation (3) for estimating age in days from planting to maturity provided interesting results. The regression data consisted of 44 station-year-crops which reached maturity in the first 5-year period, 1953–57. These data were used to determine the average summation constants in both the degree-day equation (1,059 C-degree-days) and the photothermal equation

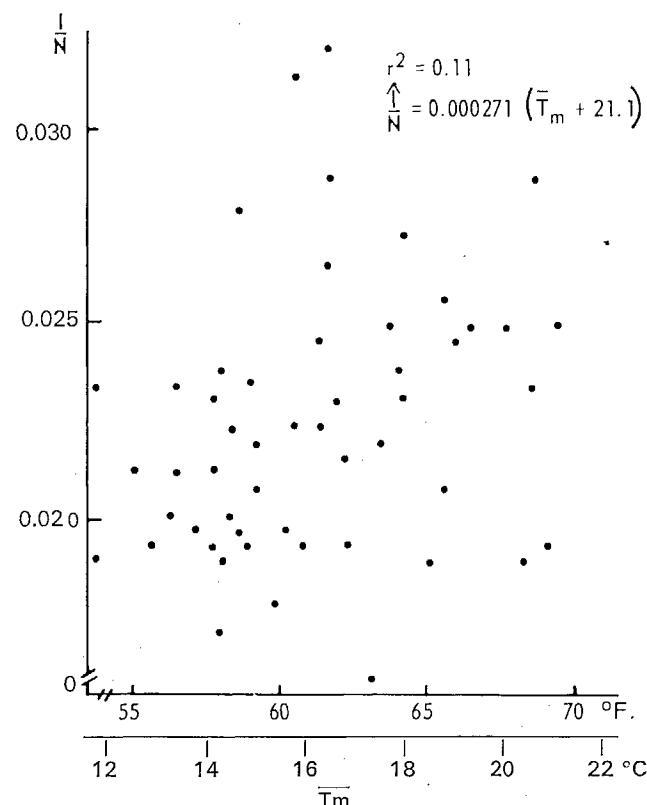


FIG. 1. Scatter diagram of the reciprocal of span (N) for period crop emergence to heading against mean temperature (\bar{T}_m) for the same period using regression data 1953–57, showing inability of simple heat-unit equation to account for influence of temperature on development. (Robertson, 1968.)

(17,051 C-degree-day hr). In both equations a threshold temperature of 4.4°C was used.

The bias in the estimated age of all crops was calculated as the average of the estimated age of all the crops at maturity minus the average of all actual ages (Table 3). For the regression data this bias was zero; i.e., the equations were made to fit the data, on average. Both equations show a bias of about –4 days for the test data of 1958–62, probably indicating that the data might be in error by this much. However, the bias for Buenos Aires data of 1961–65 is 41 days for the degree-day equation and –20 days for the photothermal equation, indicating that neither equation is fully effective for this purpose, although the photothermal equation is better than the degree-day one.

The bias compares the relative value of the two equations for estimating purposes on a group or set of data. To determine the relative usefulness of each equation for estimating age of individual crops, the root mean square error (RMSE) is a suitable statistic. Although there was no bias in the regression data as a whole, the estimate of each crop age for the 44 cases did include errors. The RMSE for the regression data

TABLE 3. Comparison of the degree-day technique and the photothermal technique for estimating the number of days from planting to maturity for Marquis wheat in Canada and Buenos Aires (unit is day)

	Bias			Root mean square error		
	Reg.	Test	B.A.	Reg.	Test	B.A.
Degree-day	0.0	-4.0	-41	11.8	14.4	14.2
Photothermal	0.0	-4.2	-20	9.7	14.4	7.4
Number of cases	44	41	14	44	41	14

1. Reg. = Canadian regression data 1953-57; Test = Canadian test data 1958-62;
B.A. = Buenos Aires data 1961-65.

was 11.8 days for the degree-day estimates (Table 3). The photothermal estimates were slightly better, with an RMSE of 9.7 days. For the test data both techniques gave the same RMSE. There was, however, considerable difference in favour of the photothermal equation (14.2 compared with 7.4 days) for the Buenos Aires data.

Although these simple tests indicated that the photothermal equation is superior for estimating purposes, particularly on the basis of results for the Buenos Aires crops, the results are not altogether satisfactory, making it desirable to look further into the form of the equations and the fundamental concepts on which they were based.

THE BIOMETEOROLOGICAL TIME SCALE

After testing many hypotheses and equations, it was finally concluded that a good model for relating the length of time for a crop to reach maturity to its thermal and photoperiod environment should have the following minimal physiological characteristics:

1. The mathematical form of the relationship should be such that it represents, as far as possible, the true response of the plant (or crop) to its environment. The coefficients in such an equation should be characteristic of the development period of the species and variety in question and should be independent of the climatic zone or region in which the crop is grown. Such coefficients would, therefore, be genetic characteristics of the plant.
2. The form of the expression for each environmental factor should be such that it considers the three cardinal points: the lower critical limit, the optimum, and the upper critical limit (Hildreth *et al.*, 1941). This applies not only to temperature, but to photoperiod as well.
3. Since these cardinal points may change with changing growth and development activities of the plant, the characteristic coefficients in a mathematical model should change with the life cycle of the crop, which should be divided into shorter spans each of which consists of a homogeneous growth and development process.

4. The operator joining various environmental factors or functions should be of a form compatible with the physiological process within the plant, i.e. environmental factors should be combined (e.g. multiplied or added) with each other on as short a time basis as is practical before accumulating from one time interval to another.

5. Day and night factors should be treated separately, since growth and development processes may differ during the light period and the dark period (Went, 1956).

These criteria may be summed up in an equation of the form (Robertson, 1968)

$$r = \frac{dM}{dt} = F_1(L) \cdot F_2(T) \quad (13)$$

where

r is the average rate of maturity per unit of time, t ,

M is the degree of maturity,

$F_1(L)$ designates some curvilinear function of photoperiod,

$F_2(T)$ designates some curvilinear function of day and night temperature.

Integration of equation (13) over time leads to an expression for the degree of maturity or development (M) over a phenological period from one phenological stage, S_1 to another, S_2

$$\int_{S_1}^{S_2} r dt = M = \int_{S_1}^{S_2} F_1(L) \cdot F_2(T) dt. \quad (14)$$

Since M cannot be observed numerically, it was appropriately set to the stochastic value of one (Ferguson, 1958) for each specific phenological period. Thus equation (14) becomes

$$\int_{S_1}^{S_2} F_1(L) \cdot F_2(T) dt = 1. \quad (15)$$

It should be noted that the function of temperature is multiplied by the function of daylength. Thus, if either one of these functions is zero, the whole expression becomes zero for that particular time interval. In other words, the crop would not develop during such an interval.

As it is usually desirable to relate crop development to ordinary, readily available meteorological (or climatological) observations; these were used in the final mathematical equation derived from equation (15). The duration of time from sunrise to sunset was used as photoperiod, daily maximum air temperature as representing the day-time crop temperature and daily minimum air temperature as representing the night-time crop temperature. Daily values were considered the shortest practical interval. Quadratic equations were used for $F_1(L)$ and $F_2(T)$ as this type of equation is the simplest which permits the characterization of the 3 cardinal points.

TABLE 4. Final regression coefficients in the triquadratic equation determined from 1953-57 regression data (Basis ° C)

Coefficient	Period (see text)				
	PE	EJ	JH	HS	SR
a_0		8.41	10.93	10.94	24.38
a_1	$V_1 = 1$	1.005	0.926	1.389	-1.140
a_2		0.0	-0.0603	-0.0819	0.0
b_0	6.87	-4.64	5.92	5.66	3.15
b_1	0.0195	-0.00632	0.000532	0.000442	0.000121
b_2	-0.000723	0.000163	0.0	0.0	0.0
d_1	0.0175	0.000660	0.000710	0.0000560	0.000620
d_2	-0.000735	-0.0000139	0.0	0.0	0.0

The final form of the practical expression for which all coefficients could be evaluated was:

$$1 = \frac{S_2}{S_1} \left[\left\{ a_1 (L - a_0) + a^2 (L - a_0)^2 \right\} \cdot \left\{ b_1 (T_1 - b_0) + b_2 (T_1 - b_0)^2 + c_1 (T_2 - b_0) + c_2 (T_2 - b_0)^2 \right\} \right] \quad (16)$$

where

L is the daily photoperiod,

T_1 is the daily maximum temperature,

T_2 is the daily minimum temperature,

a_0, a_1, a_2, b_0 , etc. are coefficients to be evaluated.

The integration or summation is to be carried out daily from one phenological stage, S_1 , to another, S_2 .

For identification and discussion purposes this equation has been called the triquadratic model.

For simplicity it can be expressed as

$$1 = \frac{S_2}{S_1} V_1 (V_2 + V_3). \quad (17)$$

This equation must be algebraically manipulated in order to evaluate the coefficients by regression analysis using observed field data. Equations (16) and (17) can be expressed in two forms.

$$\begin{aligned} \frac{1}{\Sigma V_1} &= P_0 + P_1 \frac{\Sigma (V_1 T_1)}{\Sigma V_1} + P_2 \frac{\Sigma (V_1 T_1^2)}{\Sigma V_1} + P_3 \\ &\quad \frac{\Sigma (V_1 T_2)}{\Sigma V_1} + P_4 \frac{\Sigma (V_1 T_2^2)}{\Sigma V_1} \end{aligned} \quad (18)$$

or

$$\begin{aligned} \frac{1}{\Sigma (V_2 + V_3)} &= q_0 + q_1 \frac{\Sigma (V_2 + V_3) L}{\Sigma (V_2 + V_3)} + q_2 \\ &\quad \frac{\Sigma (V_2 + V_3) L^2}{\Sigma (V_2 + V_3)} \end{aligned} \quad (19)$$

where the coefficients, p 's and q 's, are functions of the a 's, b 's and c 's in equation (16). Summation in each case is carried out for daily values over the phenological

period in question. The values of the p 's and q 's can be evaluated by regression analysis since equations (18) and (19) are linear partial regression equations. However, as there are two equations and two sets of coefficients, these must be evaluated by an alternating iterative technique which requires electronic data processing procedures.

For a cereal crop, it was assumed that five phenological periods would provide sufficiently homogeneous physiological periods for regression purposes. These periods were: planting to emergence (PE); emergence to jointing (EJ); jointing to heading (JH); heading to soft dough (HS); and soft dough to ripe (SR).

The final regression coefficients (Table 4) and the characteristic response curves (Fig. 2) show features of Marquis wheat which have been observed under controlled environmental conditions. The lower critical limits for temperature and photoperiod and the optimum values where curvilinear responses are indicated have been verified to within experimental limits (Friend, 1961; Friend *et al.*, 1963). Even the low threshold temperature of -4.7°C has recently been given credence by research on the cold tolerance of wheat in controlled environments (Roberts and Grant, 1968); Robertson, 1970).

Some of the characteristic response curves (Fig. 2) are missing, others are linear. During the period PE, when the seed was in the ground, there was no response to photoperiod. This was indicated by statistically non-significant coefficients for this curve. In some cases the actual temperatures or photoperiods under which crops were grown did not reach the optimum or maximum cardinal values and, therefore, the response curves turned out to be straight lines.

One very obvious conclusion is that the crop's response to temperature and photoperiod does vary markedly from period to period.

For a more complete discussion of the results the reader is referred to the original paper (Robertson, 1968).

To make use of these relationships, the coefficients were used in the equation

$$\begin{array}{cccccc} \tilde{E} & \tilde{J} & \tilde{H} & \tilde{S} & \tilde{R} \\ \Sigma w_1 & + \Sigma w_2 & + \Sigma w_3 & + \Sigma w_4 & + \Sigma w_5 = 5 \\ P & E & J & H & S \end{array} \quad (20)$$

where

$w_1 = V_1(V_2 + V_3)$ for each phenological period.

In other words, the equation is used in much the same way as the degree-day equation (2) in that the numerical value of $V_1(V_2 + V_3)$ for each day, using appropriate coefficients for period PE, is summed from date of planting to the date when the sum = 1 which is the estimated date of emergence, \tilde{E} . Then, using appropriate coefficients for the next period, EJ, the process is repeated, and so forth to date of maturity or ripeness when the sum equals 5.

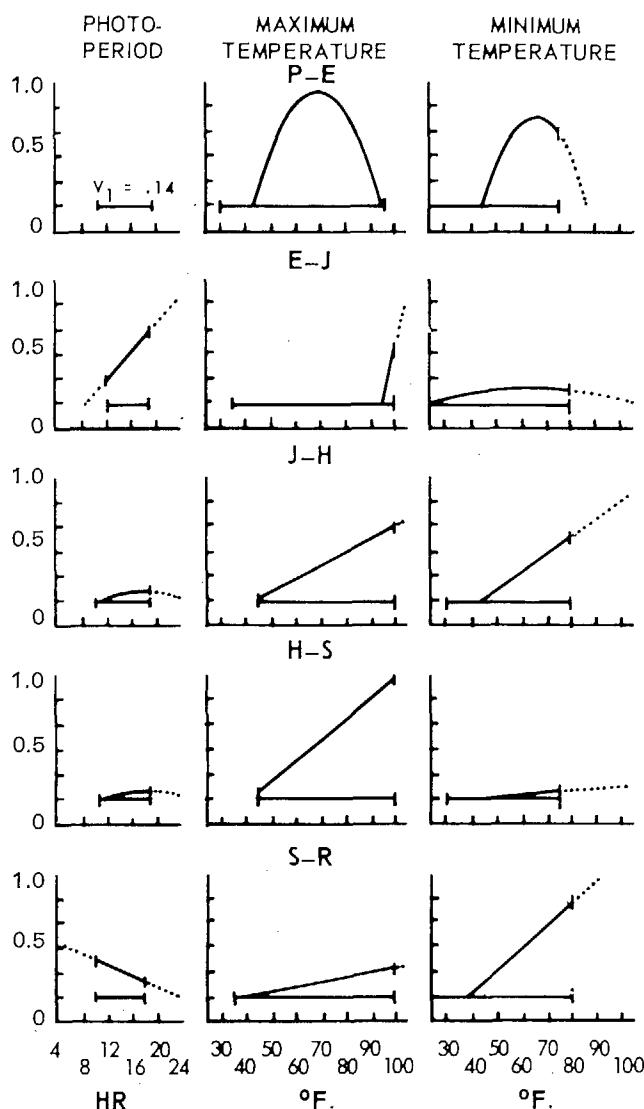


FIG. 2. Characteristic of daily-rate-of-development response curves for Marquis wheat based on the regression coefficients of Table 4 (the dotted portions of the curves are beyond the range of observed data). The ordinates are relative values of the daily contribution of the three environmental factors to the daily rate of development. For explanation of *P*, *E*, etc. see text. (Robertson, 1968.)

Development curves can be plotted using the daily summation data illustrating the progress of the crop towards maturity (Fig. 3). When used in this manner, the equation gives what has been called a "biometeorological time scale" (BMTS) in which zero (0) represents planting date, 1-emergence, 2-jointing, 3-heading, 4-soft dough and 5-ripe. The relative ability of the three models to predict the progress of Marquis wheat toward maturity at Buenos Aires is well illustrated in Figure 3.

As mentioned earlier, three sets of data were available. The Canadian 1953-57 data was used to determine all coefficients (Table 4, Fig. 2). The Canadian 1958-67 data and the Buenos Aires data were used to verify the results. Several statistical comparisons were made to show the relative ability of the degree-day equation, model 2; the photothermal equation, model 3; and the triquadratic equation, model 4 as estimators of the age, after emergence, of various phenological stages. A fourth equation, model 1, was also used as a check. This consisted simply of assuming that all periods required a fixed number of days for development corresponding to the average number of days as determined for the regression data, 1953-57 (Table 5). Mathematically this can be represented as

$$\frac{S_2}{\sum} \frac{1}{N} = 1$$

where *N* is the average span from phenological stage *S*₁ to stage *S*₂. This has been called Model 1 for comparison purposes (Table 6) and gives the worst possible systematic estimate of the age (after planting) at any stage. The bias (Table 6) indicates how well each model fits all cases combined in each set of data. At Buenos Aires, the average age at ripeness differed greatly from that in Canada (bias = 54 days). Neither the degree-day equation or the photothermal equation would estimate this, although the triquadratic equation did.

Actually, individual crop ages at the ripe stage ranged from 60 days at Ottawa for a crop planted 27 May 1955 to 199 days at Buenos Aires for a crop planted 14 June 1963. The RMSE for this average age model (Model 1, Table 7) is quite large for all phenological stages and

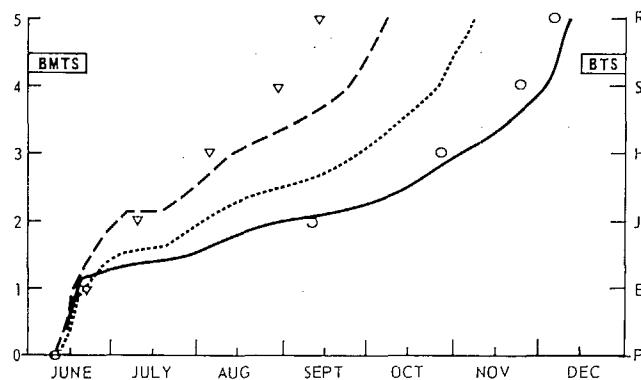


FIG. 3. The accumulated development of Marquis wheat at Buenos Aires, 1965. BMTS is the biometeorological time scale and BTS is the actual biological time scale (for explanation of *P*, *E*, *J*, etc., see text). (Robertson, 1968.)

○ ○ ○ observed stage dates.

▽ ▽ ▽ average stage dates for 1953-57 Canadian data.

..... degree-day technique.

— — — photothermal technique.

— triquadratic model.

TABLE 5. Average age (after planting) of Marquis wheat at different stages

	Stage				
	Emergence	Jointing	Heading	Soft dough	Ripe
Age (days)	9	29	55	80	95

data sources indicate that this characteristic is not homogeneous for crops from various regions and, therefore, not genetic in origin. For most data sources and phenological stages the RMSE of the age decreases from Model 1 to Model 4, indicating the superiority of the triquadratic model.

It can be concluded from this that the thesis that crops require a fixed amount of heat (accumulated degree-days) or photothermal units is not correct and that the values of those so-called summation constants are not genetic characteristics of the crop. On the other hand, the values of the coefficients in the triquadratic model (Table 4) and the resulting response curves (Fig. 2) appear to be characteristic of the specific crop variety under consideration and are, in all probability, of genetic origin. There is, however, room for improvement as indicated by the RMSE for the triquadratic model (Table 7). Reasons for the errors still remaining may be due to:

1. Incorrect model, particularly for the shape of the response curves.
2. Inability of maximum and minimum air temperatures to represent actual crop temperatures.
3. Varying fertility and soil water levels from crop to crop.

TABLE 6. Bias in averages of the estimated ages at phenological stages for various models and data sources (unit is day)

Phenological stage	Data source	Model			
		1	2	3	4
Emergence	Regression	0.2	0.1	0.1	0
	Test	0.9	0.4	0.5	-0.8
	Buenos Aires	-3.6	-2.6	0.9	-3.9
Jointing	Regression	0.1	-0.1	0.1	-0.1
	Test	-1.2	1.1	1.4	-0.4
	Buenos Aires	-47	-41	-23	-12
Heading	Regression	0.2	-0.1	0.0	-0.1
	Test	1.0	3.0	2.9	1.0
	Buenos Aires	-55	-40	-17	+2
Soft dough	Regression	-0.1	+0.3	-0.1	-0.1
	Test	-1.5	0.0	-0.9	-1.2
	Buenos Aires	-60	-43	-22	+2
Ripe	Regression	0.0	0.0	0.0	0.0
	Test	-6.2	-4.0	-4.2	-7.5
	Buenos Aires	-54	-41	-20	0.0

4. Incorrect photoperiod and the influence of light intensity on photoperiodic response.
5. Inability to define and measure phenological stages precisely.

A PRACTICAL APPLICATION OF THE BIOMETEOROLOGICAL TIME SCALE

During the preparation of soil data for the Canada Land Inventory (during the latter half of the past decade) a problem of land use interpretation arose. Climatic data are quite necessary for such interpretations and some production experience is essential. One can look at the soils in the remoter areas of Northwestern Canada, but crop production data, and particularly climatological data, are very sparse. According to Ouellet (1969), there are 218 long term climatological stations in the three Prairie Provinces of Canada, but only 25 per cent of these are north of latitude $53^{\circ} 20'$ and only 46 in all of the territory north of 60° . Yet this is the region where some 9 million hectares of virgin land are available.

About this time several important researches were completed which provided the background for the preparation of a wheat zonation map for Western and Northwestern Canada (Williams, 1969). Hopkins (1968) showed that the distribution of normal (30 year average) air temperature over the great plains of Western Canada could be related to longitude, latitude and altitude. He developed a regression equation involving first and second powers of these three factors for estimating the normal maximum and minimum air temperatures for any month at any point on the great plains. Williams and Sharp (1967), working closely with Hopkins, developed techniques and computer programmes for esti-

TABLE 7. Root mean square error (RMSE) between actual age at various phenological stages and that estimated by different models (unit is day)

Phenological stage	Data source	Model			
		1	2	3	4
Emergence	Regression	3.5	3.1	3.3	2.5
	Test	5.7	3.8	3.9	4.8
	Buenos Aires	3.8	2.1	2.3	2.2
Jointing	Regression	6.6	7.3	6.1	4.5
	Test	7.5	7.4	6.5	5.3
	Buenos Aires	18.0	15.9	9.3	6.6
Heading	Regression	8.4	10.8	8.7	4.4
	Test	8.1	6.8	5.1	4.0
	Buenos Aires	23.5	16.2	8.4	4.9
Soft dough	Regression	12.5	13.0	10.4	8.1
	Test	11.1	9.8	7.2	8.1
	Buenos Aires	24.7	12.6	6.4	4.2
Ripe	Regression	15.6	11.8	9.7	8.8
	Test	12.1	14.4	14.4	6.8
	Buenos Aires	26.9	14.2	7.9	5.4

TABLE 8. Number of stations with first autumn freeze on or before date with indicated normal minimum temperature for a given risk (Williams, 1969)

Normal minimum temperature (° C)	Earliest	Percentage risk														Normal minimum temperature (° F)			
		10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	Latest	
<0.56																	5	<33.0	
0.56-1.06																	1	5	33.0-33.9
1.11-1.61																	4	34.0-34.9	
1.67-2.17																	1	8	35.0-35.9
2.22-2.72																	2	8	36.0-36.9
2.78-3.28																	1	7	37.0-37.9
3.33-3.83																	2	5	38.0-38.9
3.89-4.39																	7	6	39.0-39.9
4.44-4.94																	8	5	40.0-40.9
5.00-5.50																	9	4	41.0-41.9
5.56-6.06																	6	3	42.0-42.9
6.11-6.61																	1	1	43.0-43.9
6.67-7.17	1	2	1	2	8	8	6	1											44.0-44.9
7.22-7.72	1	2	6	11	8	1													45.0-45.9
7.78-8.28	1	6	8	3															46.0-46.9
8.33-8.83	1	6	2																47.0-47.9
8.89-9.39	4	2																	48.0-48.9
9.44-9.94	6	1																	49.0-49.9
≥10.00	5																		<50.0

mating normal daily maximum and minimum temperatures from Hopkins' regression formula. Using these estimates of temperature, Williams (1969) developed a technique using the BMTS of Robertson (1968) to estimate the date of maturity of wheat at some 1,200 grid points covering the Canadian Great Plains. These dates were related to the normal minimum temperature to be expected at that time and these in turn, were related to freezing temperature probabilities prepared by Coligado *et al.* (1968) using a technique developed by Robertson and Russelo (1968) (Table 8). The final map (Fig. 4) shows the detail which such a technique will give. The results were verified by local experience wherever it existed; otherwise by the opinions of experienced agronomists and soils experts. Over the central and southern parts of the Canadian Great Plains, the agreement of the estimated zones with the actual zones of wheat producing areas (Fig. 5) gave credence to the usefulness of the whole technique and helped verify the validity and usefulness of the BMTS.

The technique and results gave a rational explanation of the effect on rate of wheat development caused by the confounding problem of changing photoperiod, temperature and elevation as one moves westward across the southern great plains of Canada and northward through Alberta and into the Northwest Territories (Fig. 6).

Another practical use of the BMTS might be to provide a continuous function of crop development to which to relate soil water. In a recent piece of research

(Baier and Robertson, 1967), soil water during various periods of wheat development was calculated by means of the versatile soil water budget (Baier and Robertson, 1965). In that study, calculated soil water was related to various observed phenological periods. Where such observations are lacking, the periods could be computed by means of the BMTS technique. Such research is currently under way at the Agrometeorology Section of the Canada Department of Agriculture in Ottawa, where attempts are being made to relate crop yields to soil water, total global energy and temperature during specific short intervals on the BMTS.

FUTURE DEVELOPMENTS

In the study of the influence of day and night temperatures and photoperiod on crop development, Marquis wheat was the only crop which has been analysed in depth. Preliminary analyses of oats, barley, millet (a short day crop) and a second variety of wheat have been made. The results are most encouraging and indicate that the triquadratic model will apply equally well to other cereals whether long day or short day plants. Analyses of data for other cereals should be completed. It would be interesting to test the technique on crops other than cereals, particularly those with axial flowering habit such as cotton and groundnut.

As pointed out earlier, and as indicated by the RMSE in Table 7, there is still ample room for improvement in

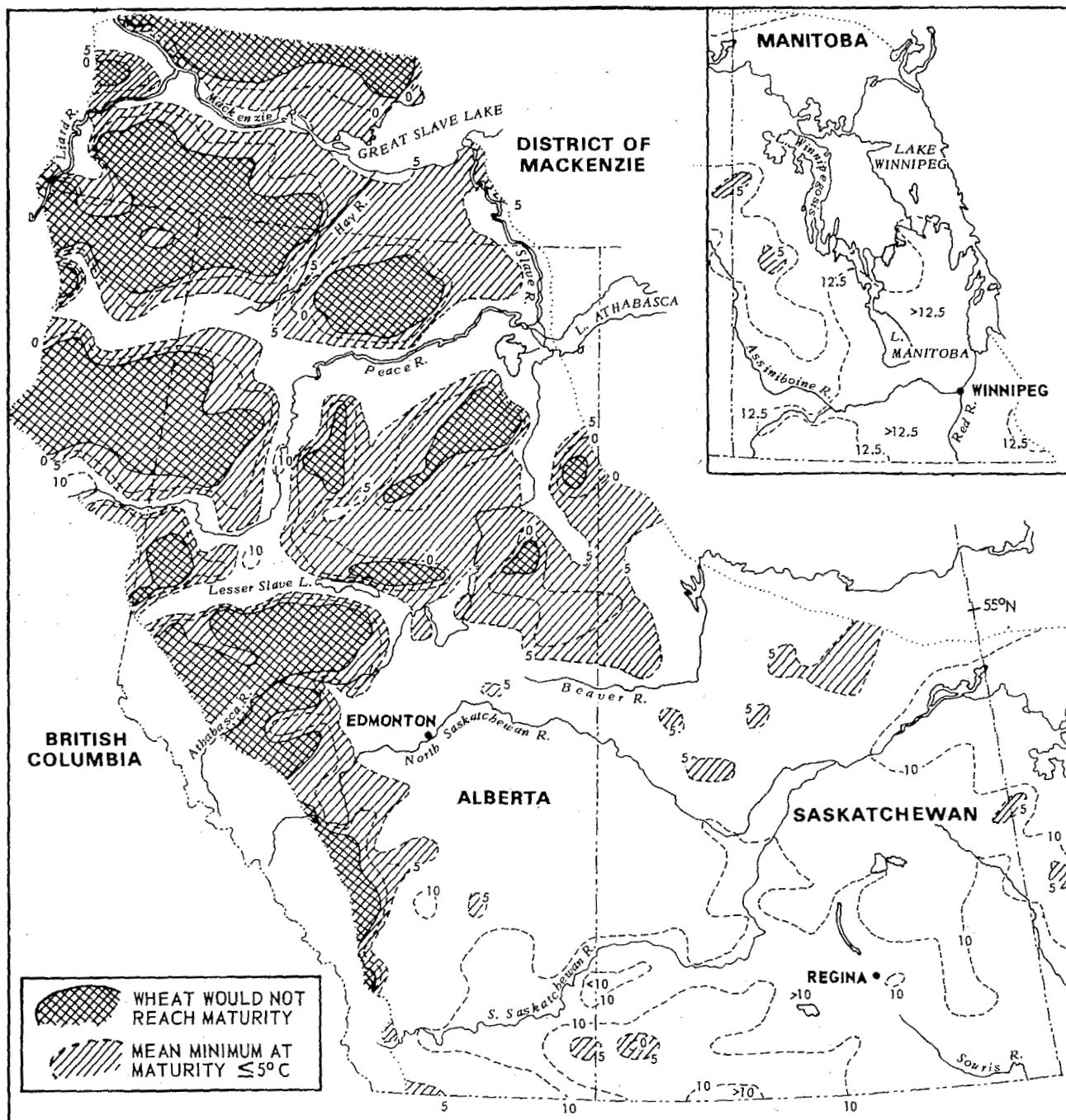


Fig. 4. Zonation of the Canadian Great plains for spring wheat. Dashed lines join points with equal normal minimum daily temperature at maturity and solid lines outline areas where wheat would theoretically not mature. (Williams, 1969.)

estimating various phenological dates from environmental factors. The ultimate is a mathematical model which would involve near instantaneous values of the environment, thus getting away from crude, once-a-day

measurements of maximum and minimum temperatures. On the other hand, any model that is to be practical must make use of readily available meteorological or climatological factors. These are quite limited. Why not

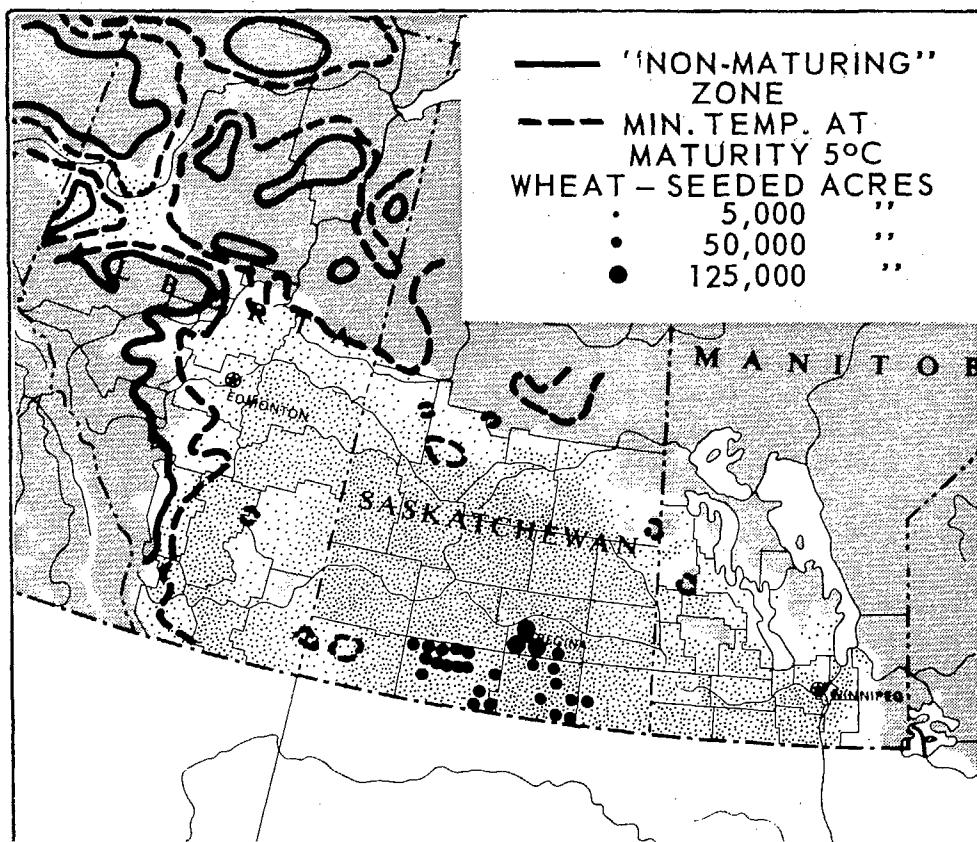


FIG. 5. The boundary of Canadian Prairie wheat-producing areas determined by means of the BMTS and the Williams/Hopkins temperature interpolation formula compared with actual seeded land areas. Each small dot represents 2,023 seeded hectares (5,000 acres) based on the 1961 census. Solid lines correspond to outline of cross-hatched area on Figure 4 and dashed lines to the 5°C isotherm. (Williams, 1969.)

estimate hourly temperatures from daily maximum and minimum values?

Some method should be used for estimating the effective crop temperature from existing environmental factors. Some years ago it was shown (Robertson, 1953) that the effective crop temperature could be crudely estimated from temperature, wind, sunshine and vapour pressure data; see equation (11). Recent studies of the heat balance of individual leaves may be useful in this regard (Linacre, 1964, 1967). Such consideration may not be necessary where the temperature is near the optimum for the crop. Where it is near either the lower or upper critical limit, however, one degree difference can make a large contribution to the development rate of the crop.

Another factor which is overlooked, but which is well known by plant physiologists, is the effect of low light intensities on the rate of crop development (Friend *et al.*, 1963). What effect does the weak light intensity during the long twilight periods in northern

latitudes or during periods of dense cloud have on the rate of crop development? Can this be incorporated logically into a crop development/weather model?

It appears that the intensity of solar energy affects the rate of crop development through two processes: (a) by contributing to the effective crop temperature (Robertson, 1953); and (b) by contributing to the photoperiodic response of the plants which is essentially a photochemical response (Friend *et al.*, 1963). Since the intensity of solar energy and air temperature are related (Linacre, 1969; Walter, 1969) the true effect of solar energy on the rate of crop development will be confounded and, therefore, difficult to rationalize, unless great care is taken in the design of an appropriate mathematical model.

It should be emphasized here, that in a study such as this, which involves regression analysis, it is most important to have crop observations from areas covering a wide range of environmental conditions including

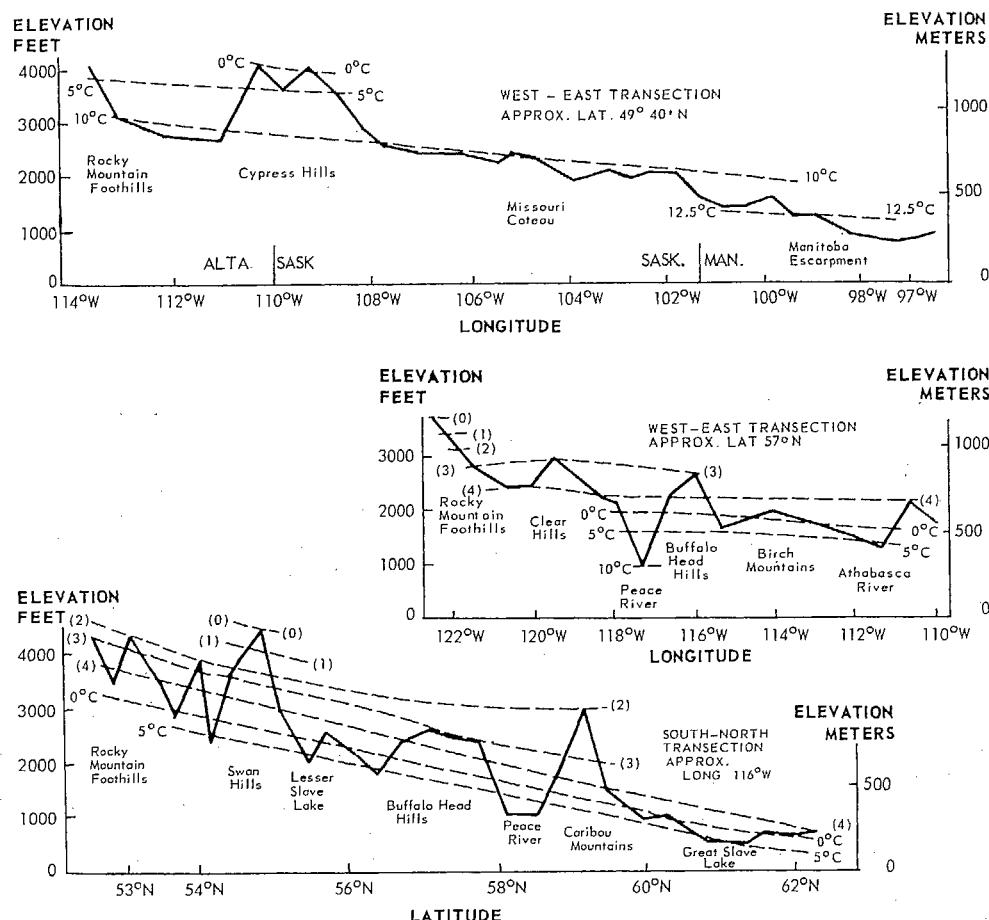


FIG. 6. Transections showing changes in wheat zonation going eastward along two parallels of latitude, and northward along a meridian of longitude. Solid lines show approximate topography. Dashed lines join points of equal phenological stage passed (bracketed figures), or of equal minimum temperature at maturity. (Williams, 1969.)

conditions near the critical limits. Some studies have been made in areas where the environment is near optimum and no crop response/environment relationship could be detected. Erroneous conclusions concerning the reliability of the data, of the factors observed and of the sensibility of the crop to specific factors may be drawn from such studies (Dermine and Klinck, 1966).

One thing lacking in the Canadian studies in order to carry on detailed analysis is reliable crop data from unusual climatic combinations of temperature and photoperiod which are not found in Canada. Data are needed from areas of high temperature and short photoperiod (in the tropics); from areas of low temperature and long photoperiod (northwestern Europe); and from areas with low temperature and short photoperiod (high plateaux in the tropics). The object is to try to gather phenological data under as a wide a range

of natural temperature and photoperiod and of combinations of these two factors as possible. There are three methods of achieving environmental variability for this purpose:

1. Grow the crops in different climatic zones.
2. Plant at different times of the year in one climatic zone.
3. Grow the crops over a succession of years.

The first method will give the greatest variability in the environmental factors. Great care must be taken, however, to assure equal fertility of soils at different stations. Careful management of a project involving several stations is obviously necessary.

The second method has certain advantages in so far as uniformity of soil and soil fertility is concerned. The range of variability of photoperiod and temperature is somewhat limited. Furthermore, only those stations

with long frost-free periods can achieve multiple dates of planting. Management at a single station is relatively simple.

The third method produces only small variation in the environment. At high latitudes the temperature regime may vary from year to year, but the photoperiod will be constant unless the date of seeding is varied. At low latitudes annual variations will be minimal. The greatest advantage of continuing the gathering of data at one site for several years is to conform results and to increase the experience of technical staff in managing crops for observational purposes and in making the observations.

These studies on crop development in relation to their environment must have special data obtained from well-managed crops. The seed source must be controlled to assure continuing genetic purity of a variety during the trials. The fertility level of the soil must be uniformly high at all stations. Insects and diseases must be carefully controlled. Lastly, the crop observations must be precise.

Then there is the problem of undertaking and completing the analyses of data. The very nature of the analyses demands that all observations be collected at a central point, checked and then subjected collectively to analyses and investigations of various types which require electronic data processing procedures.

Finally, the relationships or equations must be put to practical use. This is an area of research in itself. Where the problem is one of detailed zonation, scarcity of observations is usually a problem. Interpolation formulae for completing a square grid system such as was used by Hopkins (1968) and Williams (1969) can be improved upon, particularly in more hilly and mountainous areas than experienced in the Canadian Great Plains. Consideration should be given to the influence of slope and aspect as well as distance from water in addition to the three factors of latitude, longitude and elevation considered by Hopkins (Solomon *et al.*, 1968).

Research on such techniques may require observations and surveys on topoclimatology similar to those undertaken by van Eimern (1968).

A green revolution, particularly in subtropical and tropical countries, started at the close of the last decade. This revolution will continue throughout the present decade. With the introduction of high yielding dwarf varieties of wheat and rice, the replacement of rice by corn and sorghum in many areas and the attempt to introduce barley where it has never been heard of before; all are going to bring about tremendous changes in the agricultural and cultural patterns of many countries. These changes will extend even to those countries which may not be directly involved in the green revolution. For example, the Canadian farmer today faces a serious problem of over-production of wheat. Surplus grain apparently cannot be disposed of because of lack of world demand, partly due to the increase in rice and wheat production brought on by the green revolution. Thus Canadian farmers must consider turning to other cereal crops (McGinnis, 1970) which may have development cycles unlike those of well-known wheat varieties. It has been found that high-yielding rice varieties will yield still higher if grown with irrigation during the dry season when solar energy is high (De Datta and Zarate, 1970). This is a radical departure from the usual procedure of growing rice during the wet season. The need for a crop BMTS is well illustrated by Cochemé and Franquin (1967) in their study of the agroclimatology of the semiarid area south of the Sahara in West Africa. They attempted to use the development cycle of various crops such as corn, millet, soybean and cotton to fit the crop to the existing moisture cycle for maximum growth and yield.

All of these crop changes, new crop introductions and agroclimatic surveys aimed at the practical problem of increasing world food production could benefit greatly by a better knowledge of the BMTS of crops and better techniques for applying this knowledge.

Résumé

Mise au point de techniques agroclimatiques simplifiées pour évaluer les effets de la température sur le développement des cultures (G. W. Robertson)

L'évolution des rapports mathématiques pour exprimer l'influence de la température sur le développement des cultures est retracée de 1735 à nos jours. Cette évolution a abouti à une équation triquadratique tenant compte des températures diurne et nocturne et de la photo-

période pour calculer une échelle temporelle biométéorologique pour une culture céréalière. Cette équation est étudiée de façon assez approfondie. Son application à un problème pratique de zonation céréalière à grande échelle est ébauchée. Les insuffisances de ce système sont signalées; aussi est-il proposé pour l'avenir d'entreprendre des recherches sur la construction de modèles en faisant appel à la coopération internationale en vue de rassembler les données concernant les cultures.

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Some results of sowing time tests with spring wheat

A. Mäde

Martin-Luther University, Section Plant Production,
Halle (German Democratic Republic)

The knowledge about the response of agricultural plants to weather, especially the relationships between weather and yield, is a basis of agricultural climatology and agricultural meteorology has practical value in advising farmers or agricultural authorities. In the past, the majority of workers used statistical methods. Today the aim is to develop models for plant growth and yield. In this situation the efficiency of these two procedures should be compared.

One problem is that there have been too few field tests with adequate observations. Normally, meteorological data may be available, but biological data which allow a division in phenological terms are seldom available.

This paper considers the use of sowing time experiments in agroclimatic studies.

METHODS

In the years 1963 and 1965, tests were carried out with spring wheat. Sowing was started at the first possible day in spring and repeated at intervals of five days. Each sowing grew under different meteorological conditions. The calculations were stopped with approximately the tenth sowing.

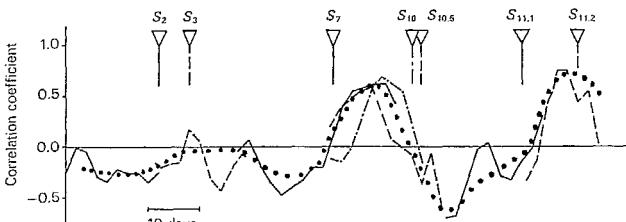


FIG. 1. Trendline of correlation between grainweight and sunshine, 1963-65.

The meteorological data were taken from a climatological station close to the test area. The stages of growth were observed according to the Feekes Scale.

RESULTS

The following stages, describing the development of the wheat, for each sowing were noted:

the day of sowing :	stage 0	: (S_0)
during tillering :	stage 2	: ($S_{2, 3}$ or 4 leaves)
	stage 3	: (S_3 , tillers formed)
during stem extension :	stage 7	: (S_7 , second node visible)
	stage 10	: (S_{10} , ear in "boot")
during heading :	stage 10.5	: ($S_{10.5}$, flowering)
during ripening :	stage 11.1	: ($S_{11.1}$, milk ripeness)
	stage 11.2	: ($S_{11.2}$, wax ripeness).

Each sowing started with 1,000 grains. Factors describing the yield were:

E_1 the number of emerged grains
 E_2 the number of stems

E_3 the number of harvested ears
 E_7 the weight of grains (air-dried).

Yield factors, related to the number of emerged grains, were correlated with precipitation (number of days with 3.0 mm rain or more), sunshine (in number of hours per day) and daily variation of air temperature (sum of the daily data during the interval under study).

The stages S_2 , S_3 , S_7 , S_{10} , $S_{10.5}$ and $S_{11.2}$ were taken as zero points for the phenological time-scale.

Correlation coefficients were first computed for overlapping five-day intervals. The results of these computations show periods in which there is a significant

influence of meteorological factors on the yield parameters.

Figure 1 illustrates the trend of correlation between grain weight and sunshine for twenty sowings in the years 1963 and 1965. The abscissa shows the time and the "S_i" gives the mean time of their approach during the growing season. The ordinate gives the correlation coefficient of Bravais. The marking of the correlation lines for the different stages corresponds to that of the time marks in the figure.

With the help of these correlation coefficients for overlapping five-day intervals, a trendline can be determined, which is dotted in Figure 1.

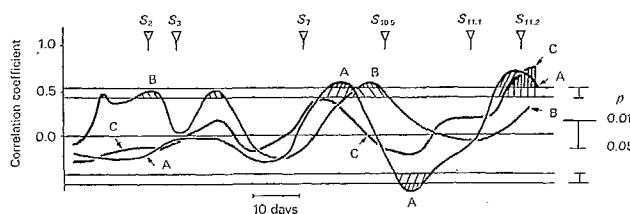


FIG. 2. Correlation between sunshine and grainweight (A), number of stems (B) and number of harvested ears (C). The limits of significance (p) are given on the right.

Figure 2 contains correlation coefficients between the meteorological factor "sunshine" and the biological components "grain weight" (line A), "number of stems" (B) and "number of harvested ears" (C).

The relationship between sunshine and "grain weight" is significantly positive (the limits of significance are at the right side of the figure) between the stages S₇ and S_{10.5}; that is, during the stalk-shooting and during the period of wax ripeness. It is significantly negative a short time after the flowering of the wheat. Regarding line B, there is an influence on the number of stems in the stages after the emergence of the grains and at the end of the stem extension. Line C gives no significant correlation during the growing season, but a short time before harvesting there is a significant influence of sunshine on the number of harvested ears.

Figure 3 gives another interpretation. It shows the influence of sunshine (A), precipitation (B) and daily variation of air temperature (C) on the weight of grains.

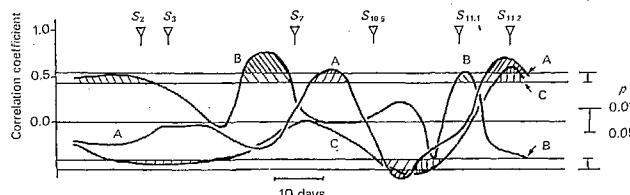


FIG. 3. Correlation between the dry weight of grains and sunshine (A), the number of days with precipitation (B) and the daily variation of air temperature (C). The limits of significance (p) are given on the right.

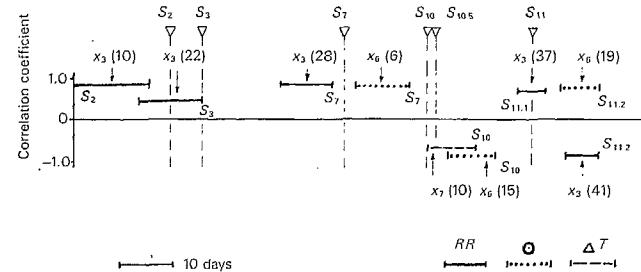


FIG. 4. Periods with significant correlation between grain-weight (y_6) and three meteorological factors: RR: precipitation; dotted line: sunshine; ΔT : daily variation of air temperature.

The figure shows a significant positive correlation with the precipitation in the period of emergence, in the period before the stem extension and during the stage milk ripeness. The daily variation of air temperature has a significant negative correlation during the first stages of the development of wheat and after flowering.

Figure 4 gives the result of a computation based on Figure 3, but with periods longer than five days. The abscissa is the time-axis. The ordinate shows the correlation coefficients. The different lines represent the amount of the maximal correlations. The length of these lines marks the periods of greatest efficiency. Nearly the whole growing season is covered with significantly positive or negative correlations between the grain weight (y_6) and the three meteorological factors-precipitation (x_3 full lines in Fig. 4), sunshine (x_6 , dotted lines) and daily variation of the temperature (x_7 , broken lines). The S_i characterize the phenological stages used as zero points. The number of the correlation coefficient is given with the index (aa) in the term $x_i(aa)$.

Further computations were made for the number of stems (y_1) and number of harvested ears (y_2). The knowledge of the periods with significant correlations

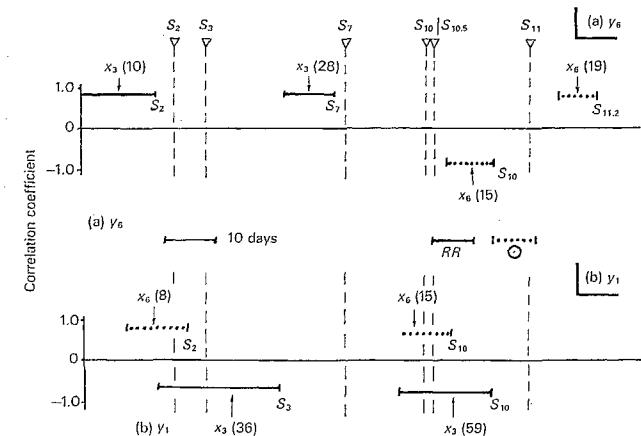


FIG. 5. Periods with significant correlation used for multiple linear regressions.

suggests a regression between the y_i and x_i (aa) would be meaningful. Accordingly, a multiple linear regression was used and gave the following results.

Relative to y_6 , there are two equations with a high coefficient of determination (B):

$$y_6 = 0.4522 + 0.0295 x_3(10) - 0.0038 x_6(15) + 0.0034 x_6(19) \quad (1)$$

$B = 0.94$

$$y_6 = 0.4342 + 0.0309 x_3(28) - 0.0035 x_6(15) + 0.0038 x_6(19). \quad (2)$$

$B = 0.93$

The different terms provide an error of less than 1 per cent for equation 1 and nearly 1 per cent for equation 2. Figure 5 (a) gives the position of the periods used and their biological zero points.

Both equations show the important influence of sunshine on the yields of grains. If the sunshine increases by one hour per day, there will be a change of the hours of sunshine during the periods $x_6(15)$ and $x_6(19)$ of approximately 15 per cent and a predicted change of the yield of approximately 6 per cent. The same influence caused by precipitation would require a change of days with rain from 30 to 45 per cent of the mean.

Another regression was computed for y_1 (number of stems). The periods used are given in Figure 5 (b).

The equation is

$$y_1 = 1.1482 - 0.0499 x_3(36) - 0.0753 x_3(59) + 0.0044 x_6(8) + 0.0035 x_6(15) \quad (3)$$

$B = 0.093.$

A t -test gives an error of less than 1 per cent for the three variables.

Résumé

Résultats d'essais d'ensemencement de Blé de printemps à différents moments (A. Mäde)

L'auteur analyse quelques résultats donnés par deux essais d'ensemencement de Blé de printemps effectués sur la base d'intervalle phénologiques. Il signale que la réaction des plantes à un facteur météorologique donné est différente suivant que l'on considère le déve-

loppement du nombre des tiges, ou celui du nombre des épis ou le poids sec des grains. En ce qui concerne le poids sec des grains, l'auteur explique l'influence des précipitations, de la durée de l'éclairement et de la variation quotidienne de la température. Il semble en conséquence difficile de décrire la corrélation entre la croissance et le rendement des plantes et un indice composé de plusieurs éléments météorologiques.

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Effects of spatial leaf distribution on penetration and interception of direct radiation

R. Lemeur

Laboratory of Plant Ecology, Faculty of Agricultural Sciences, University of Ghent (Belgium)

INTRODUCTION

Recently attempts have been made to construct mathematical models describing the radiation régime in plant communities. Special attention has been focused on the correlation between light penetration and photosynthetic activity in an attempt to predict daily growth rates of several crops. Although such models should be used with extreme care, and applied only in situations where the theoretical assumptions are valid, mathematical models are particularly useful when the effect of changes in single parameter on the behaviour of a whole system has to be studied. The following discussion should be interpreted in this way.

Most treatments of light penetration in canopies assume a random foliage distribution in space (Monsi and Saeki, 1953; Warren Wilson, 1965; Anderson, 1966; Anderson and Denmead, 1969; Duncan *et al.*, 1967; Cowan, 1968; etc.). Therefore, each leaf has the same probability of being found at an arbitrarily chosen site in the plant community. This limiting condition excludes all statistical affinity (preferential leaf sites in the neighbourhood of stems), and requires a disperse leaf display in space.

In order to obtain a complete characterization of the foliage display, additional information on leaf inclination and leaf azimuth must be provided. Most theories are limited to hypothetical situations of constant leaf angle and a non-preferential azimuth. However, reality is approached only when both a leaf-angle distribution and an azimuthal dependence appropriate to the crop studied are taken into account. Until now, the effect of spatial leaf orientation was included only in the model of Ross and Nilson (1966), introducing a leaf normal distribution function. Apart from language difficulties (it was presented in Russian), comparison with Western terminology and generally accepted hypotheses is difficult.

Starting from a different base and accepting random distribution of leaf area in space, this theory adapts existing models (see references above) to an arbitrarily chosen spatial orientation function. The technique reveals a close correspondence between experimentally measured and theoretically predicted data.

ASSUMPTIONS AND DEFINITIONS

A simple model of a plant community is postulated as a frame for further developments. The basic description of the radiation régime represents a synthesis of actual modelling:

- (a) Leaves are simulated by thin, black planes randomly dispersed in space;
- (b) There is a constant leaf inclination (α) in relation to the horizon;
- (c) Leaves are assumed to have no preferred azimuthal direction.

The independent variables are: leaf inclination (α), solar elevation (β) and downward cumulative leaf area index (f).

The similarity of a light ray and a needle passing through the foliage has been frequently used in radiation models. As a result of random leaf display, the zero term of the Poisson distribution indicates the probability of no interception. Related to leaf area index (f) and to an extinction coefficient (μ), this probability is expressed as a penetration function $P(f)$:

$$P(f) = \exp(-\mu f). \quad (1)$$

$P(f)$ can be equated with the projection of gaps in the foliage. Projected onto a horizontal plane, equation (1) indicates the "horizontal sunlit area". "Gap frequency" denotes the relative amount of projection onto a plane perpendicular to the direction of penetration (β). The relative flux density of direct radiation is equivalent to

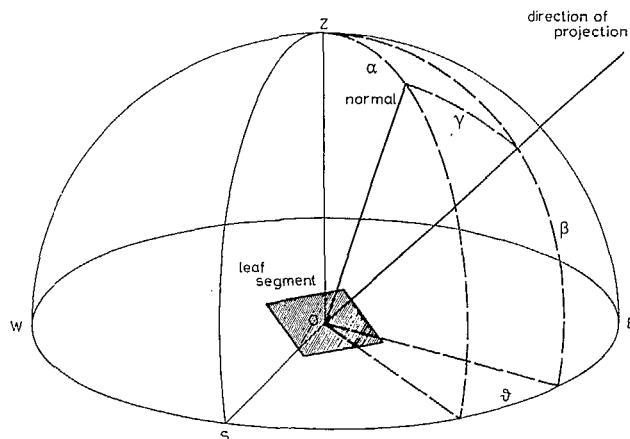


FIG. 1. A leaf segment defined in a spherical system of coordinates.

either the horizontal sunlit area or the gap frequency, according to the radiation measure being referenced to a horizontal or perpendicular plane respectively.

For a given solar elevation (β), the flux density impinging on an inclined leaf surface depends on the azimuth difference (θ) between leaf and sun. For black leaves (radiation absorbed = amount intercepted), the difference of the penetration function between two depths (f) and ($f + \Delta f$) per unit leaf area index, i.e. $[P(f) - P(f + \Delta f)] / \Delta f$, tends to the radiation intercepted at depth (f) when $\Delta f \rightarrow 0$. Disregarding the sign, the interception function $I(f)$ is found as the derivative of the penetration function. Hence,

$$I(f) = -\frac{\partial P}{\partial f} = \mu \exp(-\mu f). \quad (2)$$

Although expression (2) has to be related to the mean flux density per unit leaf area index, it remains valid on a unit leaf area basis.

The total sunlit leaf area (measured in units leaf area) is proportional to the horizontal sunlit area at each depth in the canopy. Integration of the penetration function between $(0, f)$ gives the sunlit leaf area index f^* :

$$f^* = \frac{1}{\mu} [1 - \exp(-\mu f)]. \quad (3)$$

In terms of the Poisson distribution, the expression between the square brackets represents the probability of a ray intercepting at least one time. The inverse extinction coefficient converts from horizontal projected leaf area to leaf area.

The effect of leaf angle and solar elevation on penetration and interception is introduced through the extinction coefficient (μ). This mean value of the Poisson distribution represents the mean number of interceptions in a layer of unit leaf area index. In the random-type model μ is equated to:

$$\mu = P_{\alpha\beta} / \sin \beta, \quad (4)$$

where $P_{\alpha\beta}$ stands for the ratio between the mean projection of a leaf on a plane normal to the sunrays and the actual area of the leaf. Division by $\sin \beta$ corrects for the increasing path length through the foliage with more oblique angles of penetration (β).

Reeve (1960) has presented a calculation procedure to obtain integrated values of $P_{\alpha\beta}$ for each arbitrarily chosen combination of α and β . On the other hand, $P_{\alpha\beta}$ represents also the mean value of $\cos \gamma$, γ being the angle between the direction of penetration and the normal on the leaf segment (see Fig. 1). The mean value is averaged over all the azimuth differences $(0, 2\pi)$ between sun and leaf segment. In a spherical system of co-ordinates the cosine law gives:

$$\cos \gamma = \cos \alpha \sin \beta + \sin \alpha \cos \beta \cos \theta. \quad (5)$$

Reeve's expressions adapted to the chosen system of co-ordinates are:

$$\left. \begin{aligned} P_{\alpha\beta} &= \overline{\cos \gamma} = \cos \alpha \sin \beta, \text{ when } \alpha < \beta \\ \text{and } P_{\alpha\beta} &= \overline{\cos \gamma} = \frac{2}{\pi} \sin \alpha \cos \beta \sin \theta_0 + [(2\theta_0/\pi) - 1] \\ &\quad \cos \alpha \sin \beta \end{aligned} \right\} \quad (6)$$

when $\alpha \geq \beta$

and where $\theta_0 = \pm \text{Arc cos}(-\cot \alpha \tan \beta)$.

The radiation régime in our hypothetical plant community is completely defined in the system of expressions (1), (2), (3), (4) and (6). As far as the restrictions (a), (b) and (c) hold, this approach has been successful.

DEVELOPMENT OF AN INTEGRATED EXTINCTION COEFFICIENT WITH RESPECT TO A SPATIAL ORIENTATION FUNCTION

When leaf inclination (α) and leaf azimuth (θ) vary between $(0, \pi/2)$ and $(0, 2\pi)$ respectively, a spatial distribution function is needed to characterize the foliage display. Such distributions are conveniently represented by the probability that a leaf segment has an inclination within $(\alpha, \alpha + d\alpha)$ and an azimuth within $(\theta, \theta + d\theta)$:

$$g(\alpha, \theta) d\alpha d\theta \quad (7)$$

where $g(\alpha, \theta)$ stands for a probability density function. Hence the cumulative frequency of occurrence of inclination and azimuth respectively within $(0, \alpha_0)$ and $(0, \theta_0)$ is:

$$G(\alpha_0, \theta_0) = \int_0^{\alpha_0} \int_0^{\theta_0} g(\alpha, \theta) d\theta d\alpha. \quad (8)$$

The condition $G(\pi/2, 2\pi) = 1$ being fulfilled, $g(\alpha, \theta)$ is normalized. When the dependence of $g(\alpha, \theta)$ upon α is the same for all values of θ , then:

$$g(\alpha, \theta) = g'(\alpha) \cdot g''(\theta) \quad (9)$$

because the random values of α and θ are mutually independent.

In order to obtain an appropriate extinction coefficient in situations where a spatial distribution exists, equation (4) must be weighted with respect to the probability of occurrence of each inclination and azimuth. Hence the ratio $P_{\alpha\beta}$ is to be modified as follows:

$$P_{\alpha\beta} = \int_0^{\pi/2} \int_0^{2\pi} g(\alpha') \cdot g''(\theta) \cos \gamma d\theta d\alpha. \quad (10)$$

Sometimes the complexity of the probability density function will introduce integration difficulties. However, in some particular cases, $g(\alpha, \theta)$ can be simplified, by applying approximation techniques in the following way:

(I). A constant inclination (α_0) of foliage is postulated and the leaf azimuth is random. Then:

$$\left. \begin{aligned} g'(\alpha) &= C_1 \delta(\alpha - \alpha_0) \\ \text{and } g''(\theta) &= C_2. \end{aligned} \right\} \quad (11)$$

$\delta(\alpha - \alpha_0)$ represents the Dirac delta function, which is reduced to 0 when $\alpha \neq \alpha_0$ and to 1 when $\alpha = \alpha_0$. To allow normalization, the constants C_1 and C_2 are equated to 1 and to $1/2\pi$ respectively.

From equations (10) and (11) we obtain:

$$P_{\alpha\beta} = \frac{1}{2\pi} \int_0^{2\pi} \cos \gamma d\theta \quad (12)$$

where $\cos \gamma$ stands for equation (5). Expression (12) calculates the mean value of $\cos \gamma$ and is equivalent with (6). Hence, the original expressions of Reeve (1960) are re-established.

(II). A leaf angle distribution function is postulated. The leaf azimuth is still distributed at random. Then:

$$\left. \begin{aligned} g'(\alpha) &= f(\alpha) \\ \text{and } g''(\theta) &= 1/2\pi. \end{aligned} \right\} \quad (13)$$

Wit (1965) distinguishes four types of canopies. In planophile and erectophile canopies horizontal and vertical leaves, respectively, are predominant. The leaves in plagiophile and extremophile canopies occur most and least frequently, respectively, at some oblique inclination. Such distribution functions are represented in Figure 2. Appropriate equations were determined, and identified with $f(\alpha)$:

$$f_1(\alpha) = \frac{3\alpha^2}{k^3} - \frac{6\alpha}{k^2} + \frac{3}{k} \quad (\text{planophile canopy}) \quad (14)$$

$$f_2(\alpha) = \frac{3\alpha^2}{k^3} \quad (\text{erectophile canopy}) \quad (15)$$

$$f_3(\alpha) = \frac{12\alpha^2}{k^3} - \frac{12\alpha}{k^2} + \frac{3}{k} \quad (\text{extremophile canopy}). \quad (16)$$

The plagiophile leaf distribution function has been empirically determined from horizontal translation and recombination of the symmetrical parts of equation (16). The constant (k) in the nominator equals 90 when α is expressed in degrees.

To avoid complex integration procedures, the range $(0, \pi/2)$ has been subdivided into twelve successive intervals of 7.5° , so that integration with respect to α could be replaced by a summation of terms:

$$P_{\alpha\beta} = \frac{1}{2\pi} \sum_{j=1}^{12} \int_{\pi/24(j-1)}^{\pi/24j} \int_0^{2\pi} f(\alpha) \cos \gamma d\theta d\alpha. \quad (17)$$

Appealing to the mean value theorem of integrals, equation (17) can be written as:

$$P_{\alpha\beta} = \sum_{j=1}^{12} p(\alpha j, \beta) \int_{\pi/24(j-1)}^{\pi/24j} f(\alpha) d\alpha \quad (18)$$

$$\text{or } P_{\alpha\beta} = \sum_{j=1}^{12} p(\alpha j, \beta) [F(\alpha)] \frac{\pi/24 f}{\pi/24(j-1)} \quad (19)$$

where αj stands for the mid-point between the integration limits $(\pi/24)(j-1)$ and $(\pi/24)j$, β for solar elevation, and $p(\alpha j, \beta)$ for the ratio derived in (I), where leaf inclination was constant. The expression between the square brackets denotes the difference of the cumulative frequency distribution between the inclinations $(\pi/24)(j-1)$ and $(\pi/24)j$.

TABLE I. $p_{\alpha\beta}$ ratios corresponding to the leaf angle distribution functions of Figure 2.

Solar elevation β	Planophile	Erectophile	Extremophile	Plagiophile
15°	0.320	0.550	0.432	0.443
30°	0.475	0.517	0.513	0.469
45°	0.634	0.471	0.568	0.525
60°	0.767	0.421	0.591	0.601
75°	0.853	0.380	0.589	0.662
90°	0.883	0.364	0.583	0.685

Table 1 summarizes the $P_{\alpha\beta}$ ratios corresponding to planophile, erectophile, extremophile and plagiophile canopies. Their respective leaf angle distribution functions are illustrated in Figure 2. Substitution of expression (19) into (4) gives the weighted extinction coefficient (μ) appropriate to the chosen leaf angle distribution function. The dependence of μ on solar elevation is shown in Figure 3 and compared with the initial extinction coefficients corresponding to fixed leaf inclination. (III). The foliage has a constant inclination (α_0), but the leaves have a definite affinity to certain azimuthal directions. Such azimuthal dependence was observed by Ross and Nilson (1967), and Loomis and Williams (1969). To their experimental figures, a second-degree equation in polar co-ordinates of an ellipse is identified with the

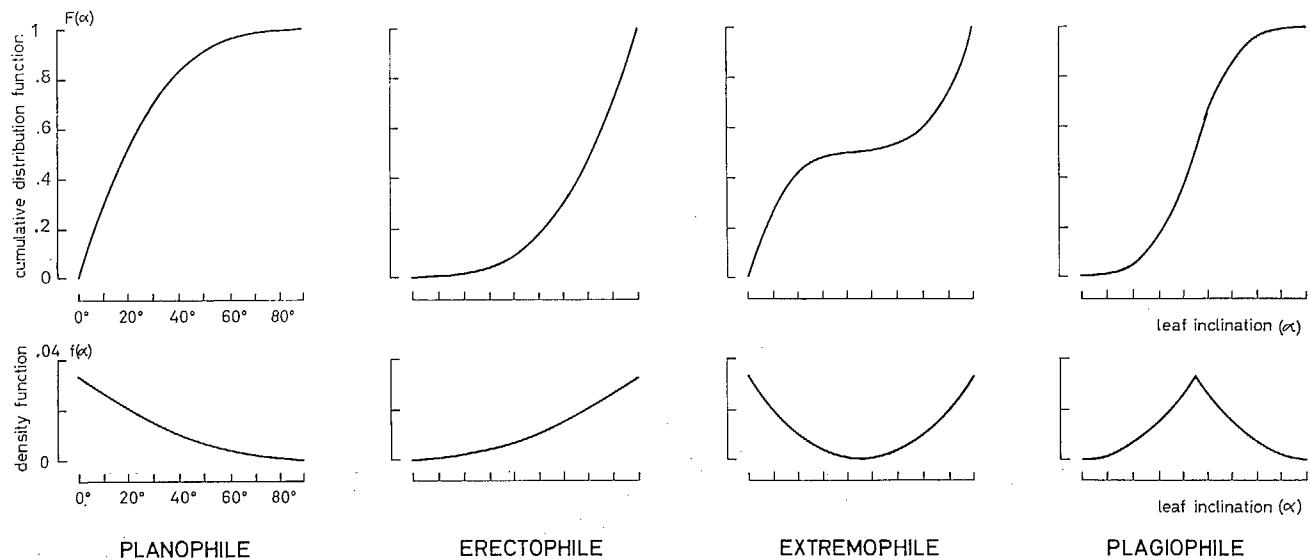


FIG. 2. Cumulative leaf angle distribution functions and corresponding density functions of the four types of canopies.

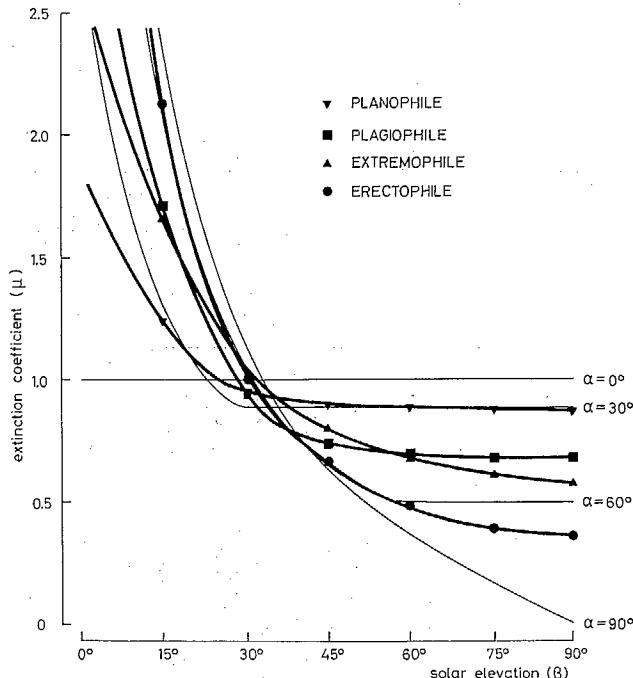


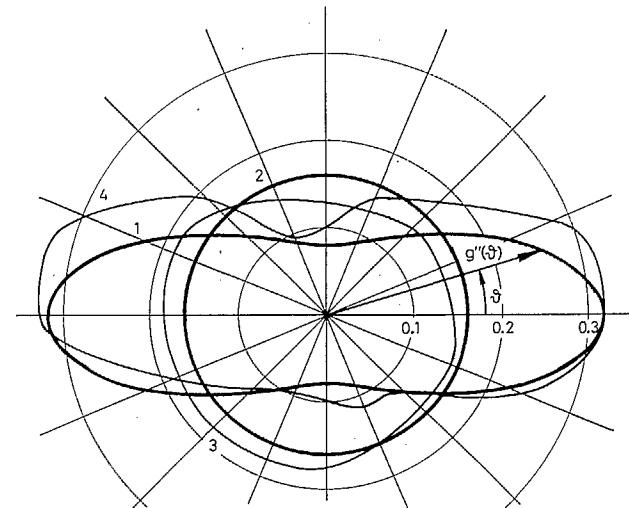
FIG. 3. The extinction coefficient as a function of solar elevation. Heavy lines correspond to the leaf angle distributions of Figure 2.

azimuthal distribution function $g''(\theta)$ (see Fig. 4). Again, the system of probability density functions is limited to:

$$\begin{aligned} g'(\alpha) &= \delta(\alpha - \alpha_0) \\ \text{and } g''(0) &= a^2 b^2 / (a^2 \sin^2 \theta + b^2 \cos^2 \theta) \end{aligned} \quad (20)$$

where $g''(0)$ represents the square of the radius vector

FIG. 4. Theoretical and observed azimuthal density functions. No units being specified in the paper of Loomis and Williams, their data for corn are relative to curve 1.



- Azimuthal density functions:
1. $g''(0) = ab/2\pi(a^2\sin^2\theta + b^2\cos^2\theta)$
 2. $g''(0) = 1/2\pi$ (random)
 3. ROSS AND NILSON (corn)
 4. LOOMIS AND WILLIAMS (corn)

of an ellipse with centre at the origin and semi-axis a and b . The smallest axis (i.e. b) is perpendicular to the sunrays when $b < a$. Hence the leaf area is pointed to the azimuthal direction of the sun with the largest probability. When $b > a$, the direction of maximum probability is perpendicular to the solar azimuth. With other solar orientations relative to the ellipse, the vectorial

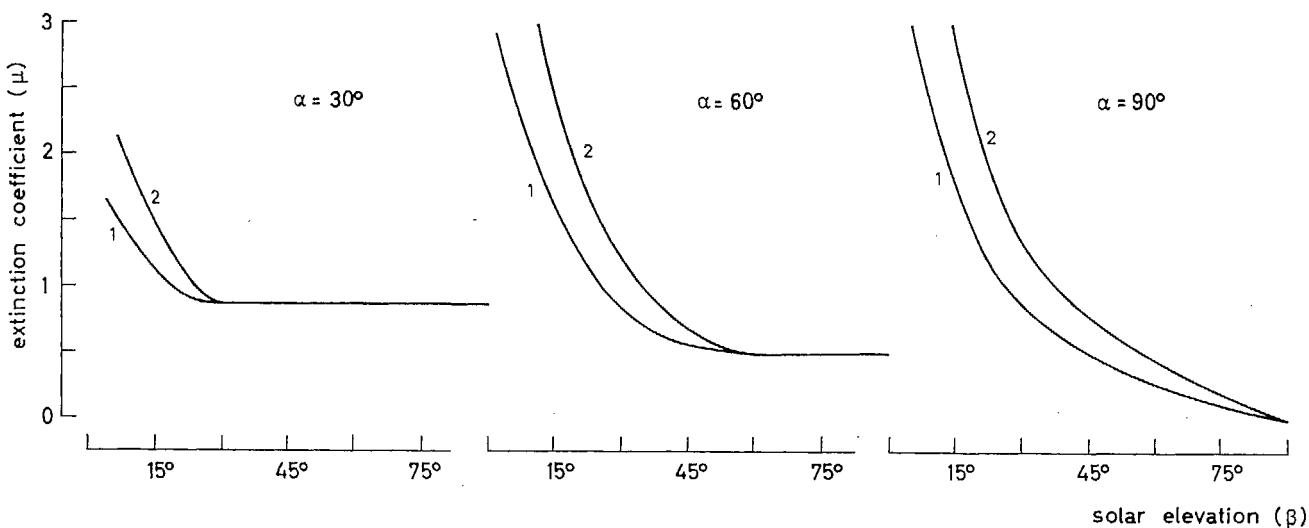


FIG. 5. Minimum (1) and maximum (2) extinction coefficients corresponding to directions of maximum probability respectively perpendicular to or parallel with the solar azimuth. The dependence on solar elevation is represented for different leaf inclinations and for the azimuthal density function of Figure 4, curve 1.

angle θ of $g''(\theta)$ and the variable θ in expression (5) are not identical and the polar equation $g''(\theta)$ no longer holds. Therefore, this treatment is limited to the two situations mentioned above, in which extreme values are expected.

Substitution of the system (20) into expression (10) gives the appropriate value of the ratio $P_{\alpha\beta}$. As long as the radiation load is impinging on the upperside of the leaf segment only, $\cos \gamma$ is always positive and integration results in $\cos \alpha \sin \beta$, a value also found for random azimuth when $\alpha < \beta$ (see equations (6) and case I). When $\alpha \geq \beta$, $P_{\alpha\beta}$ must be equated to:

$$P_{\alpha\beta} = A \left(1 + \frac{2}{\pi} \operatorname{arc tg} (a/b \operatorname{tg} \theta_0) \right) + B \left(\frac{2a}{\pi b m} \operatorname{arc tg} (m \sin \theta_0) \right) \quad (21)$$

when $a > b$,

$$\text{and to } P_{\alpha\beta} = A \left(1 + \frac{2}{\pi} \operatorname{arc tg} (a/b \operatorname{tg} \theta_0) \right) + B \frac{a}{\pi b n} \log \frac{1 + n \sin \theta_0}{1 - n \sin \theta_0} \quad (22)$$

when $a < b$.

where $m = (a^2/b^2 - 1)^{1/2}$,

$n = (1 - a^2/b^2)^{1/2}$,

$\theta_0 = \operatorname{Arc cos} (-\operatorname{cotg} \alpha \operatorname{tg} \beta)$,

$A = \cos \alpha \sin \beta$,

and $B = \sin \alpha \cos \beta$.

Expressions (21) and (22) permit calculation of the ratio $P_{\alpha\beta}$, which corresponds to the chosen azimuthal

distribution of Figure 4. Therefore, values must be attributed to the constants a and b , depending on the square root of the ratio of maximum and minimum probability density. At the same time $g''(0)$ should be normalized or $2\pi ab = 1$. Hence, a second relationship between the variables is established so that calculation of both values a and b is made possible.

Values of $P_{\alpha\beta}$ for different solar elevations (β) and different leaf inclinations (α) are listed in Table 2. The maximum-minimum ratio of the probability density is 4. This means the azimuthal direction of maximum probability coincides with or is perpendicular to the solar

TABLE 2. Maximum and minimum $P_{\alpha\beta}$ ratios corresponding to the azimuthal distribution function of Figure 4, curve 1

Solar elevation (β)	Leaf inclination (α)						
	0°	15°	30°	45°	60°	75°	90°
15°	0.259	0.250	0.389	0.534	0.647	0.719	0.744
			0.295	0.361	0.418	0.455	0.468
30°	0.500	0.483	0.433	0.507	0.591	0.647	0.667
				0.413	0.414	0.418	0.419
45°	0.707	0.683	0.612	0.500	0.507	0.534	0.544
					0.413	0.361	0.342
60°	0.866	0.837	0.750	0.612	0.433	0.389	0.385
						0.295	0.242
75°	0.966	0.933	0.837	0.683	0.483	0.250	0.199
							0.125
90°	1.000	0.966	0.866	0.707	0.500	0.259	0

azimuth when $a = 2b$ and $a = b/2$, respectively. Taking account of equation (4), appropriate extinction coefficients were derived from Table 2. Their dependence on solar elevation is illustrated in Figure 5 for different leaf inclinations.

(IV). The spatial orientation of leaves is determined both by a leaf angle and an azimuthal distribution function. When the leaf angle and the azimuthal are mutually independent, computation techniques explained in sections (II) and (III) can be used to obtain the appropriate $P_{\alpha\beta}$. On the contrary, any relationship between (α) and (θ) results in a double integration of extreme complexity.

This procedure has been applied to corn as an illustrative example. The leaf angle distribution function of maize has been measured in the past. The experimental figures could be distinguished into two types. A special type of erectophile foliage was reported by Wit (1965), Stewart (1968), and Loomis and Williams (1969), while Ross and Nilson (1967) found that the frequency of leaf angles was proportional to $\cos \alpha$. The relative frequency being the same as the relative frequency of occurrence of the surface elements of a sphere, they introduced the spherical or uniform distribution function. However, we restricted ourselves to a mean profile of the first type (see Fig. 6).

Appropriate values of this cumulative leaf angle distribution function were used in expression (19). Accepting an azimuthal dependence such as studied in case III,

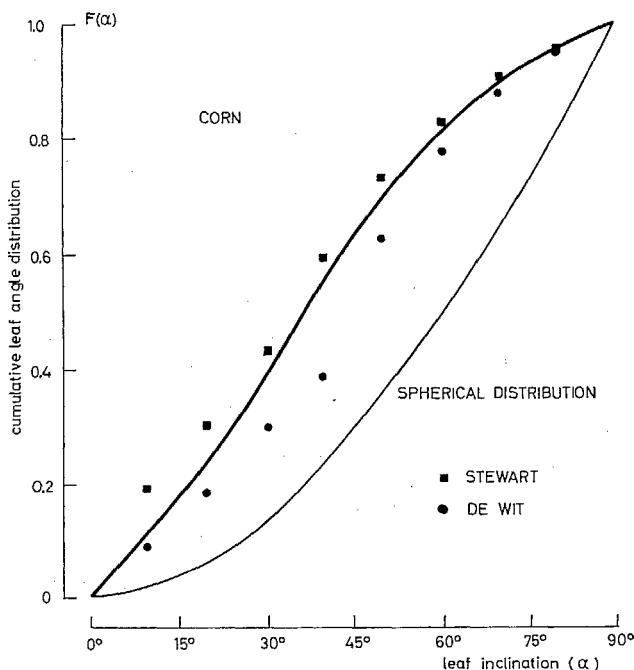


FIG. 6. Mean cumulative leaf angle distribution of corn, as used in our calculation procedure of the integrated extinction coefficient.

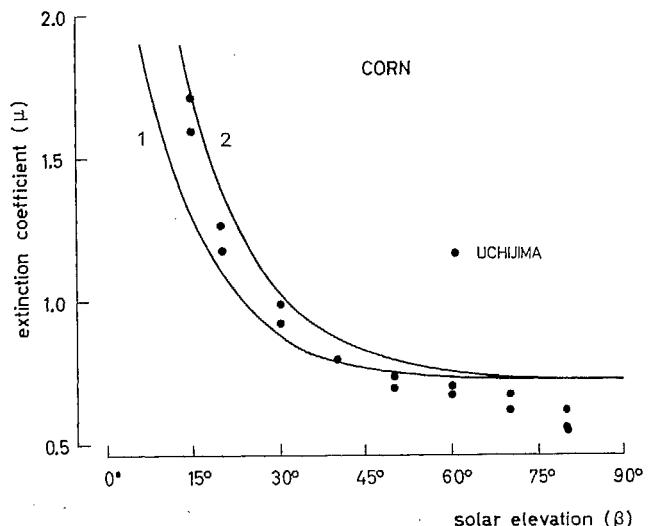


FIG. 7. Minimum (1) and maximum (2) extinction coefficients of corn represented as a function of solar elevation and compared to the experimental figure of Uchijima *et al.* (1968). Curves (1) and (2) correspond to direction of maximum probability perpendicular to or parallel with the solar azimuth, respectively.

the $P_{\alpha\beta}$ ratios of Table 2 were substituted as $p(\alpha j, \beta)$ values. From equations (19) and (4) an integrated extinction coefficient of corn was obtained. The relationship with solar elevation is represented in Figure 7 and compared with the experimental figures of Uchijima *et al.* (1968).

The daily course of the radiation régime within a stand of corn was calculated from the system (1), (2) and (3), using the integrated extinction coefficient. The same expressions were evaluated, using an extinction coefficient appropriate to a fixed foliage inclination of 45°. The differences between the respective results are illustrated in Figure 8.

COMMENTS AND CONCLUSIONS

The principal aim of this work has been to improve existing models describing direct radiation distribution within plant stands. Former models claimed a constant extinction coefficient when leaf inclination was smaller than solar elevation. Only vertical leaves implied a dependence within the complete range of solar elevations. Our technique permits gradual transition between the extreme situations of horizontal and vertical leaves. Figure 3 illustrates the smoothing effect of leaf angle distribution functions on the relationship between extinction coefficient and solar elevation. Consequently marked differences of penetration, interception and sunlit leaf area as predicted with constant leaf inclination during the daily course of the sun, will be lowered. This confirms the old theory that each plant stand acts as

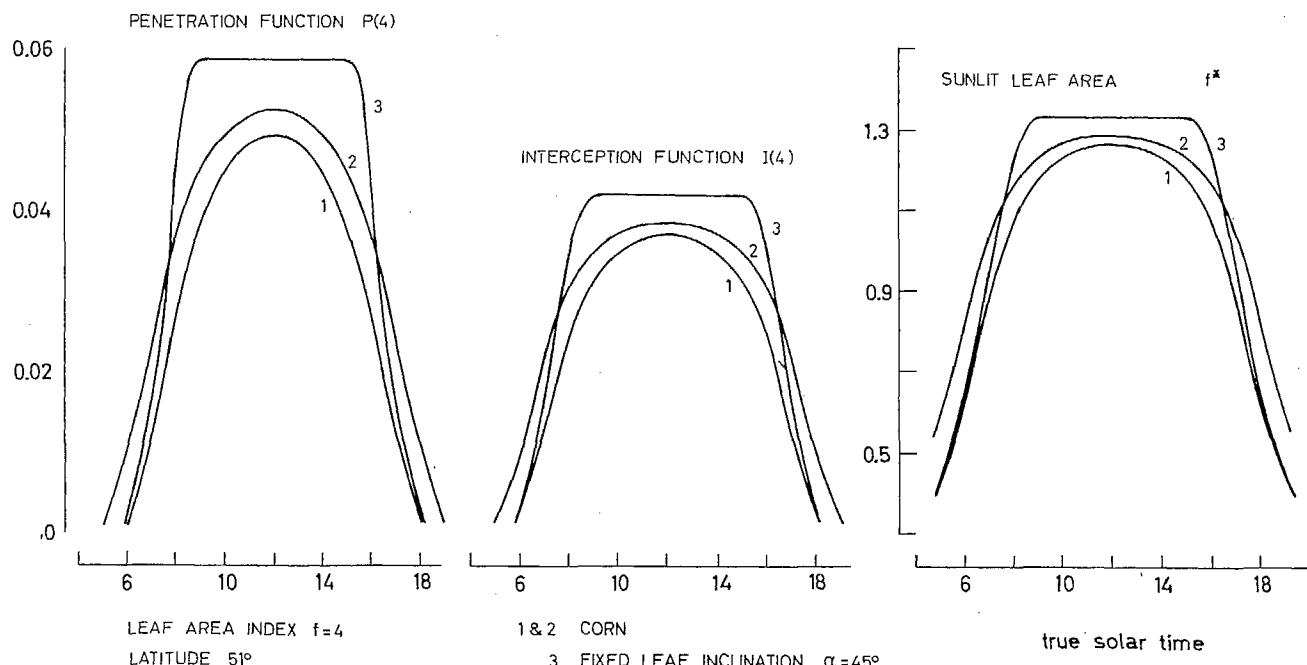


FIG. 8. Daily course of the characteristic functions describing the radiation régime in a corn canopy. Curves (1) and (2) correspond to the appropriate extinction coefficients of Figure 7. Curve (3) results from an extinction coefficient of fixed leaf inclination $\alpha = 45^\circ$.

an integrating medium with respect to meteorological and physical parameters.

The notable feature of Figure 5 is the fact that our azimuthal leaf distribution does not alter the extinction coefficient when $\alpha < \beta$. Due to the symmetry of the distribution function, increased contributions of large projections to $P_{\alpha\beta}$ in directions of high probability, are balanced by an equal amount of small projections of leaves with a phase difference π . However, for $\alpha > \beta$ expressions (21) and (22) predict maximum and minimum values corresponding to an increased azimuthal probability which is, respectively, parallel with or perpendicular to the solar azimuth. The discrepancy between maximum and minimum extinction coefficient increases with more erectophile canopies and lower solar elevation. The same conclusions apply to the penetration function, the interception function and the sunlit leaf area.

Another inherent feature of our azimuthal dependence is the effect on the relative frequency of occurrence of radiation intensities impinging on inclined leaf planes. In earlier models with fixed leaf inclination, each flux density occurred with the same probability as a result of azimuthal randomness. With our model, however, the relative frequency of occurrence must be equated with the postulated azimuthal probability density. Furthermore, when a leaf angle distribution function $g'(\alpha)$ is included, the former frequency distribution has

to be multiplied by the probability density $g'(\alpha)$. Hence, one should be careful to relate the photosynthetic activity of a plant community to the mean flux density, as expressed through the interception function. Impens and Lemeur (1970) pointed out that, in such a situation, the use of mean values instead of the frequency distribution could introduce appreciable error.

Figure 7 illustrates the good fit between Uchijima's experimental extinction coefficients, which were derived from a measured leaf normal distribution function, and our predicted theoretical values. Although his method refers to a "mean effective leaf area function", introduced by Ross and Nilson (1966), a parallelism between our expressions and the Russian model could be drawn.

Figure 8 summarizes the effects of the spatial orientation of maize leaves both on penetration and interception of direct radiation, and on sunlit leaf area index. Each set of curves represents the daily course of the corresponding functions $P(f)$, $I(f)$ and f^* at a depth $f=4$ in the canopy. The dependence on solar elevation was calculated for our experimental field (latitude: 51°N) and is appropriate to 1 July. Compared with the same functions for a fixed leaf inclination of 45° , all values are lowered with high and medium solar elevations (i.e. between 9 a.m. and 3 p.m.). This results from a preponderance of small leaf inclinations in our postulated distribution function of maize. Though the contribution

of leaf inclinations $\alpha < 45^\circ$ is small, a marked dependence on higher solar elevations should be noticed.

At the same time maximum and minimum values are evaluated. They correspond with azimuthal directions

of preferential leaf orientation, respectively, normal to or parallel with solar azimuth. As expected, the discrepancy increases with lower solar elevations.

Résumé

Les effets de la distribution spatiale des feuilles sur la pénétration et l'interception du rayonnement solaire direct (R. Lemeur)

Supposant un couvert végétal homogène, l'auteur a développé une description mathématique de l'orientation spatiale des feuilles. Des fonctions, exprimant la distribution des inclinaisons et la distribution des azimuts lui ont permis d'établir un coefficient d'extinction intégré qui caractérise la pénétration et l'interception du rayonnement solaire direct.

Il démontre que: a) dans le cas d'une inclinaison constante des feuilles, les valeurs extrêmes des coefficients

d'extinction en fonction des différentes hauteurs du soleil sont diminuées par l'introduction d'une distribution angulaire; b) pour une inclinaison constante et en acceptant une distribution azimuthale et elliptique, le coefficient intégré se dédouble en valeurs maximales et minimales quand le soleil frappe la face inférieure des feuilles.

Un modèle antérieur pour la description du microclimat lumineux a été adopté aux caractéristiques spatiales du Maïs. Cette technique mathématique révèle une meilleure correspondance entre les résultats expérimentaux et les valeurs théoriques.

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Daytime distribution of energy sinks and sources and transfer processes within a sunflower canopy

I. I. Impens

Laboratory of Plant Ecology, Faculty of Agricultural Sciences, University of Ghent (Belgium)

INTRODUCTION AND THEORY

The rigid coupling between micrometeorological, crop and plant parameters has been studied on a field plot of sunflowers. The measurement of plant community activity, and the response of sunflower plants to their physical environment, has been attempted by the energy balance approach. Reference may be made to Cowan and Milthorpe (1968), Denmead (1964), Lemon (1967, 1968), Monteith (1968), Philip (1964), Uchijima (1962) and others for more detailed discussions of the technique. Only a brief statement of the working formulae is presented for clarity.

The energy budget at some horizontal plane (z) in the canopy may be represented by the equation (neglecting the relatively small air and crop heat storage components):

$$Rn(z) - S = - LK\chi(z) \frac{\partial\chi}{\partial z} - C_p \rho_a K_H(z) \frac{\partial T}{\partial z} + \lambda K_C(z) \frac{\partial C}{\partial z} \quad (1)$$

$$\left. \begin{array}{rcl} \text{with } LK\chi(z) \frac{\partial\chi}{\partial z} & = & LE(z) \\ C_p \rho_a K_H(z) \frac{\partial T}{\partial z} & = & H(z) \\ \lambda K_C(z) \frac{\partial C}{\partial z} & = & \lambda P(z) \end{array} \right\} \quad (2)$$

where: Rn , LE , H , λP and S are the flux densities of net radiation, latent heat, sensible heat, photochemical energy (equivalent of CO_2 flux) and the soil-sensible heat storage term ($\text{cal cm}^{-2} \text{min}^{-1}$), $K\chi$ – K_H – K_C the turbulent transfer coefficients for water vapour, sensible heat and CO_2 respectively ($\text{cm}^2 \text{sec}^{-1}$). L is the latent heat of evaporation of water (580 cal g^{-1}), C_p is the specific heat of air at constant pressure (0.24 cal g^{-1}), ρ_a is the density of air ($0.00118 \text{ g cm}^{-3}$), λ is the thermal

conversion factor for fixation of CO_2 ($2,500 \text{ cal g CO}_2^{-1}$), χ is the absolute humidity of the air (g cm^{-3}), T is the temperature of the air ($^\circ \text{C}$) and C the CO_2 concentration of the air (g cm^{-3}).

The sign convention adopted is that negative fluxes are considered upward. Making use of the similarity assumption, the energy balance equation (1) leads to an expression for the combined vertical turbulent transfer coefficient:

$$K(z) = \frac{Rn(z) - S}{-L \frac{\partial\chi}{\partial z} - C_p \rho_a \frac{\partial T}{\partial z} + \lambda \frac{\partial C}{\partial z}} \quad (3)$$

The necessary measurements include vertical profiles of net radiation, water vapour, air temperature, CO_2 and sensible heat storage in the soil. From these and from equations (1), (2), and (3), flux profiles of the entity in question can be constructed by successive heat budget analyses at several levels within the canopy. Taking the derivative [$\partial(\)/\partial z$] of the flux density profile with respect to height, flux divergence or source and sink intensity, distribution can be calculated either on a unit volume basis or, when leaf area density distribution is known, on a unit leaf area basis.

MATERIALS AND METHODS

The sunflowers had been sown in NW-SE-oriented rows on our experimental field at Melle ($51^\circ 3' \text{N}$). Although continuous investigations were made for nearly two months, the data presented here were collected on 6 August 1969. At the day of observation the crop was vegetatively fully developed with an average height of 220 cm and a leaf area index of 3.62.

Measurements of Rn , χ , T and C were made at 265 cm and 230 cm from the ground above the top of the crop and at five levels within the foliage: 180, 140,

TABLE 1. Hourly mean values of incident global radiation, net radiation, air temperature, absolute humidity and wind speed at the uppermost measuring level (265 cm) and of soil sensible heat storage: 6 August 1969

Hours	6.3	8.3	10.3	12.3–13.3	15.3	17.3	19.3
R_i (cal $\text{cm}^{-2} \text{min}^{-1}$)	0.035	0.372	0.758	1.016	0.920	0.276	0.053
R_n (cal $\text{cm}^{-2} \text{min}^{-1}$)	0.022	0.256	0.527	0.695	0.605	0.184	0.035
T ($^{\circ}\text{C}$)	16.90	19.60	21.50	23.24	23.60	22.50	19.84
χ (g m^{-3})	14.46	14.55	13.80	11.20	8.81	9.00	10.37
U (cm sec^{-1})	126	196	266	273	298	280	182
S (cal $\text{cm}^{-2} \text{min}^{-1}$)	-0.004	0.007	0.015	0.026	0.020	0.001	-0.008

100, 60 and 20 cm from the ground. The 265 cm level served as the reference level.

Net radiation values were calculated by averaging the readings of three instruments mounted at some distance from each other. For measurements of air temperature, humidity and CO_2 concentration, air intakes were located on an instrument mast at the appropriate levels. Each intake consisted of an insulated Perspex tube which housed the thermocouple junctions, with parallel horizontal baffles connected to the upper end. The design prevented radiative heating errors, provided good horizontal spatial average and minimized atmospheric disturbances in the sampling area. Four-junction thermopiles were used to measure temperature gradient between adjacent levels. The top inlet also provided an air reference temperature.

The bulked air from each intake was drawn simultaneously by hose to the laboratory, at a distance

of ± 20 m from the measuring site. Here subsamples of air were diverted to differential H_2O and CO_2 infra-red gas analysers and differences in concentration between the reference level and the lower levels analysed in sequence. Absolute water vapour concentration could be measured by referencing the 265 cm air to air passed through a temperature-controlled water bath.

Soil sensible heat storage was measured with ten heat flow discs wired in series and placed 0.5 cm below the surface of the soil. In addition to these necessary microclimatic measurements, incident (above and below the canopy) and reflected global radiation were measured, as well as wind speed.

Leaf temperature-air temperature differences were measured at each of four heights with 4-junctions 36-gauge copper-constantan thermopiles. Each of 4 leaf junctions was inserted in a small vein of a different leaf at a given height and referenced to air junctions

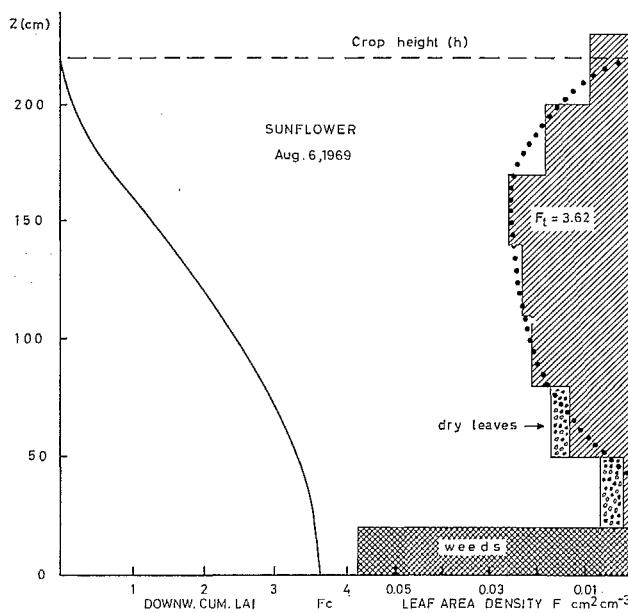


FIG. 1. Leaf area density profile and downward cumulative leaf area distribution (downw. cum. LAI) in the sunflower crop.

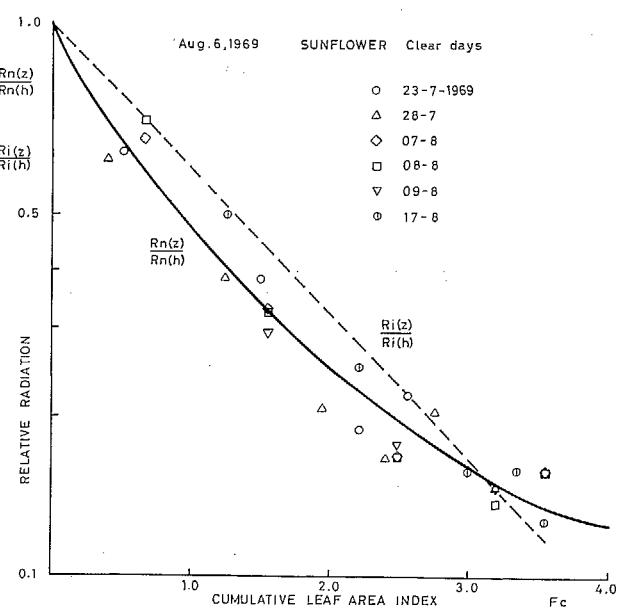


FIG. 2. Daytime radiation transmission versus downward cumulative leaf area index. Data points refer to R_n values. The relationship between short wave radiation transmission and F_c is represented by the dashed line.

Daytime distribution of energy sinks and sources and transfer processes within a sunflower canopy

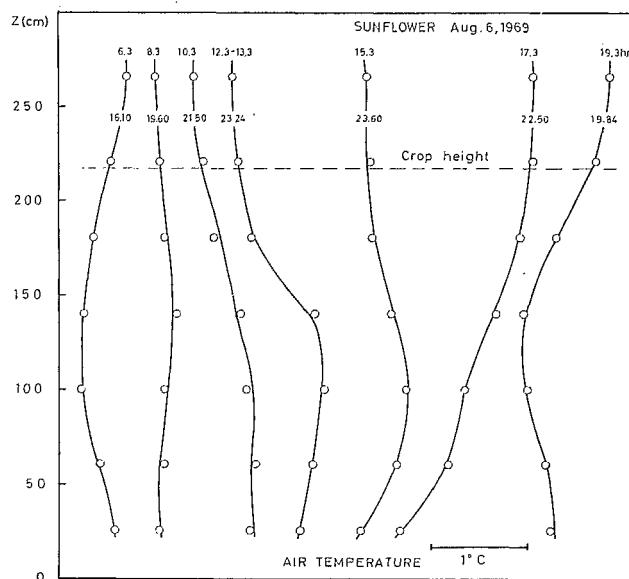


FIG. 3. Daytime temperature profiles within and above the sunflower crop for one-hour periods around the time as indicated.

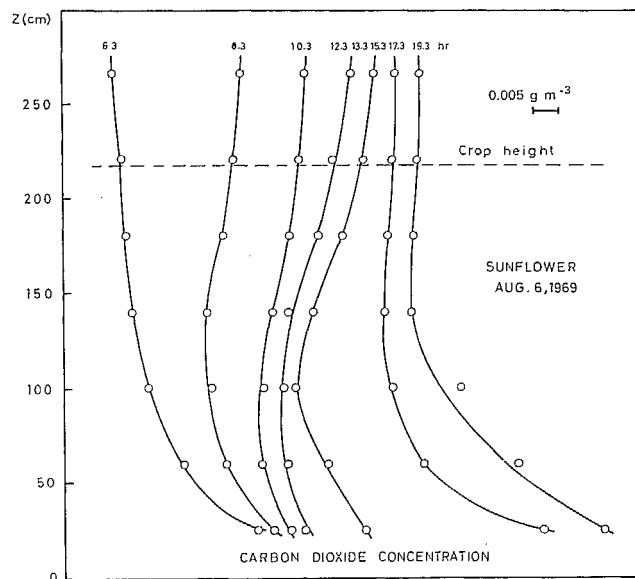


FIG. 5. Daytime CO_2 concentration profiles within and above the sunflower crop for one-hour periods around the time as indicated.

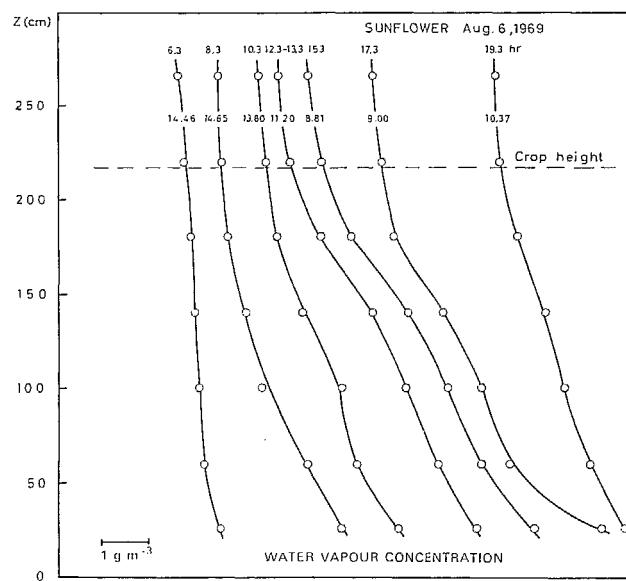


FIG. 4. Daytime water vapour concentration profiles within and above the sunflower crop for one-hour periods around the time as indicated.

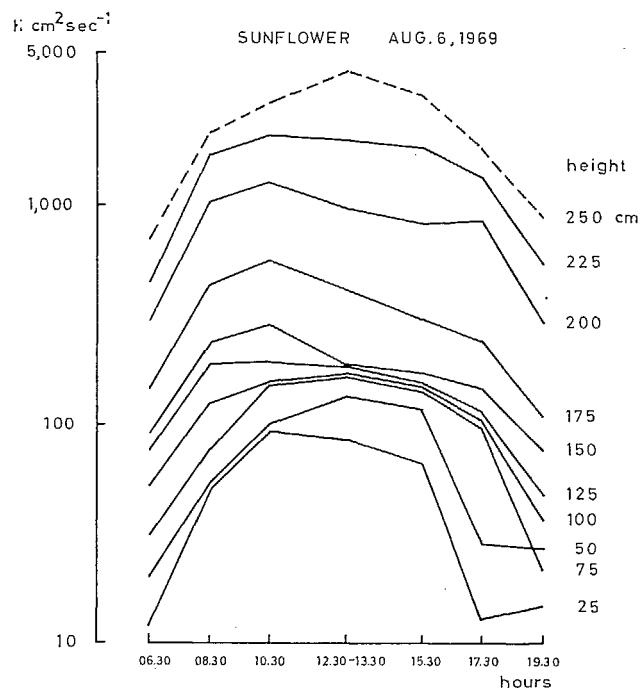


FIG. 6. Diurnal variation of the computed turbulent transfer coefficient at various heights within the crop.

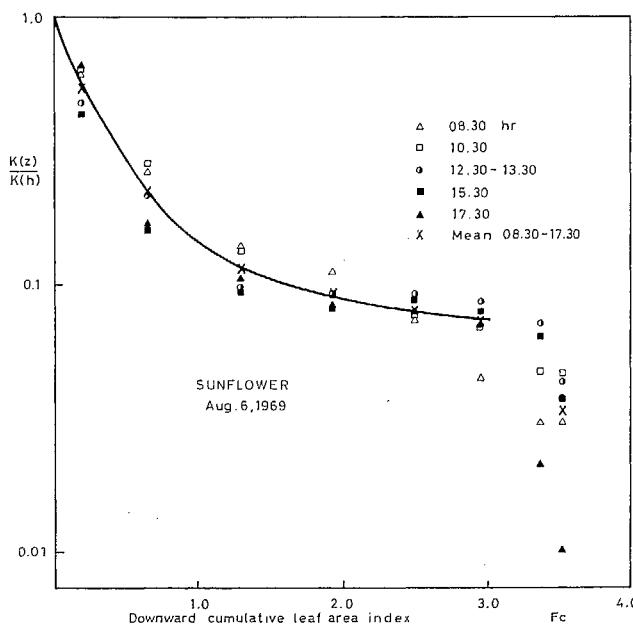


FIG. 7. The ratio of the turbulent transfer coefficient at height z to that at the top of the crop plotted as a function of downward cumulative leaf area index for five observation periods.

positioned a few centimetres below the leaves which served as a shade. All the signals were recorded on a digital data acquisition system. A complete measurement of each set of profiles took about 12 min. Our hourly data represent an average of five consecutive readings. The sampling site had a fetch of 45 m to the south-east, direction of prevailing winds.

EXPERIMENTAL RESULTS AND DISCUSSION

A summary of some important microclimatic parameters is presented in Table 1.

The leaf area density F ($\text{cm}^2 \text{cm}^{-3}$), and the downward cumulative leaf area index distribution, $F_c = \int_z^h F dz$, in the sunflower crop are presented in Figure 1. Due to an insufficient pre-emergence herbicide treatment, the soil surface was covered with weeds. Extinction of net radiation showed only a slight diurnal trend on clear days with minimum values around noon: this agrees with earlier findings (Impens and Lemeur, 1969). Daytime ratios (9 a.m. to 5 p.m.) of transmitted to incident net radiation plotted as a function of F_c gave an equation of the form:

$$Rn(z) / Rn(h) = \exp(-\alpha_1 F_c + \alpha_2 F_c^2) \quad (4)$$

with extinction coefficient constants of net radiation $\alpha_1 = 0.822$ and $\alpha_2 = 0.074$ (Fig. 2). The relationship

between short wave radiation extinction and F_c could be described by a simple exponential equation:

$$Ri(z) / Ri(h) = \exp(-\beta F_c). \quad (5)$$

with $\beta = 0.58$ for clear days and $= 0.54$ for overcast days.

Figures 3, 4 and 5 show the hourly mean vertical profile data of temperature, absolute humidity and CO_2 concentration for selected periods throughout the day. In order to calculate the gradients, the smoothed profiles were differentiated by taking slopes at each 25 cm height interval. From these gradients and the distribution of Rn with height, turbulent exchange coefficients ($K(z)$) were calculated, solving equation (3). The diurnal variation of the turbulent transfer coefficient at various heights is shown in Figure 6. The results span a total range of almost four orders of magnitude, but stay within one order of magnitude for a given level. The lowest $K(z)$ values at the bottom of the canopy are still two orders of magnitude greater than molecular diffusion coefficients. (For comparison, representative molecular diffusion values for common gases in air are $0.1-0.3 \text{ cm}^2 \text{ sec}^{-1}$.) The curve drawn in Figure 7 shows the relative decrease of the turbulent exchange coefficient with depth in the canopy as a function of accumulated leaf area index. The distribution is best fitted by a cubic exponential equation. The strong attenuation of $K(z)$ in the lowest levels of the canopy is largely due to the occurrence of weeds acting as a second vegetative cover. In the upper eight-tenths of the crop, the normalized distribution can be approximated by the equation:

$$K(z) = K(h) \exp(-\gamma_1 F_c + \gamma_2 F_c^2). \quad (6)$$

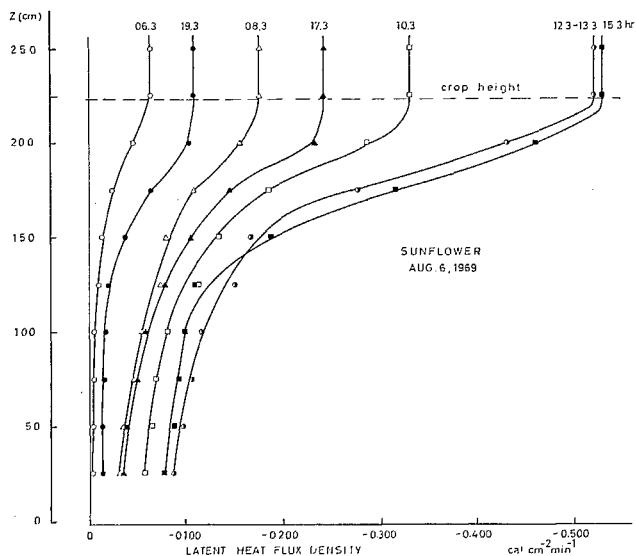


FIG. 8. Vertical profiles of latent heat flux density in sunflower as indicated by hour at the top of each profile. Negative values signify upward flux (vaporization).

Daytime distribution of energy sinks and sources and transfer processes within a sunflower canopy

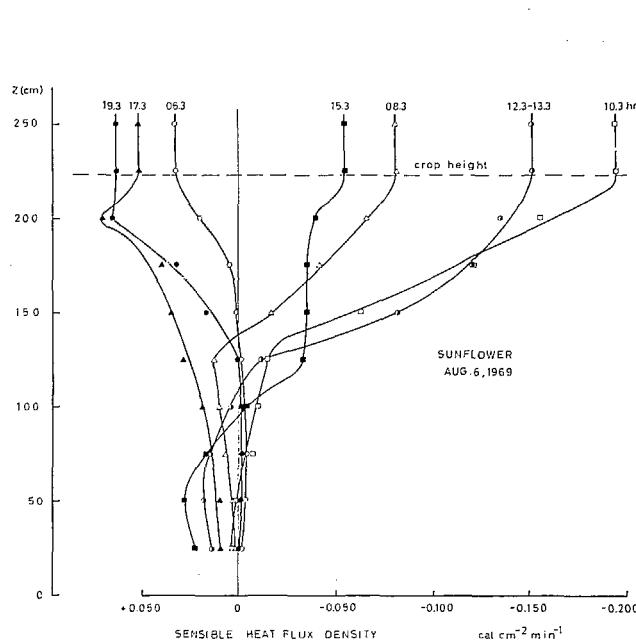


FIG. 9. Vertical profiles of sensible heat flux density in sunflower as indicated by hour at the top of each profile. Negative values signify upward flux.

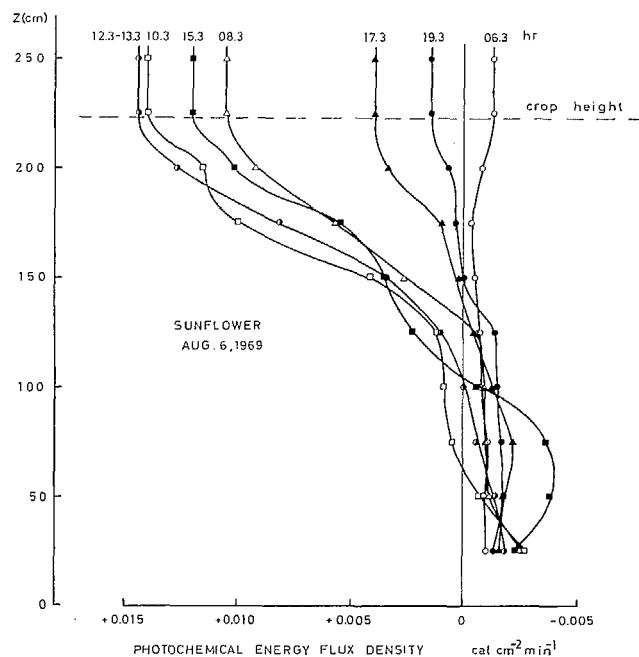


FIG. 10. Vertical profiles of photochemical energy flux density in sunflower as indicated by hour at the top of each profile. Negative values signify upward flux (respiration).

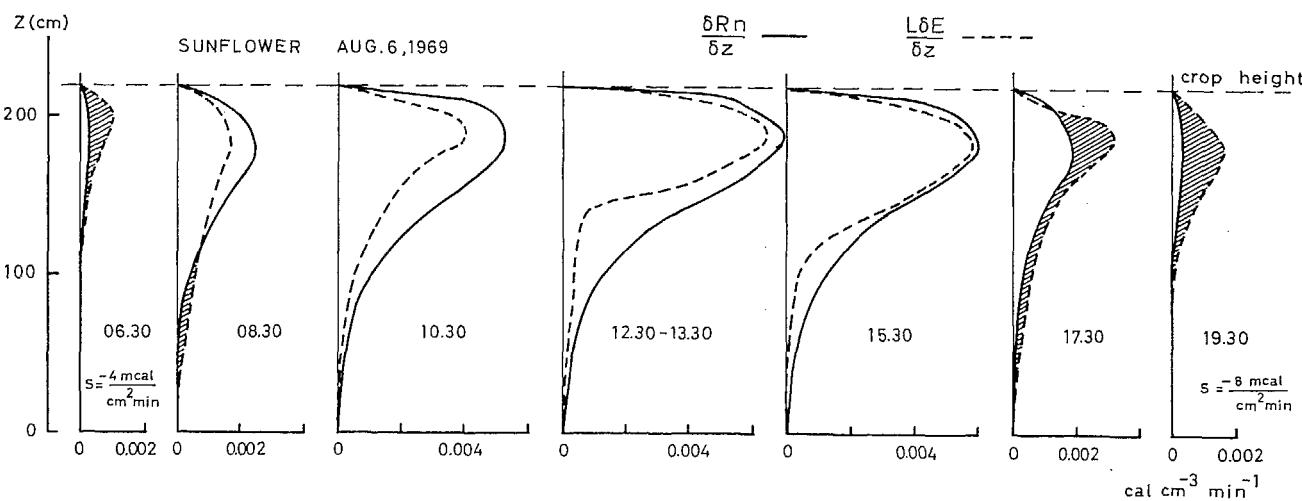


FIG. 11. Sink intensity distribution of net radiation and source intensity distribution of latent heat ($\text{cal cm}^{-3} \text{min}^{-1}$) on a plant canopy volume basis for the indicated time in a sunflower crop. The horizontal distance between the net radiation and the latent heat curves gives the source strength ($\delta R_n/\delta z - \delta L_E/\delta z$) or the sink strength distribution of sensible heat.

TABLE 2. Percentage of net radiation absorbed in crop canopy layers used for transpiration: $L\Delta E/\Delta Rn \times 10^2$

Height (cm)	Time (hr)							[06.30-19.30]
	06.30	08.30	10.30	12.30-13.30	15.30	17.30	19.30	
150-225	348	62	60	83	90	110	295	86
100-175	205	60	55	55	78	133	305	73
50-125	195	150	69	61	31	198	225	78
[50-225]	315	66	60	72	85	130	320	83

γ_1 and γ_2 were determined to be 2.64 and 0.61 respectively; $K(h + 0.1h) \approx 1.56K(h)$.

Using the appropriate form of equation (2), flux densities were calculated in 25 cm steps. The constructed flux profiles are shown in Figures 8, 9 and 10. Inspection of Figure 10 reveals that, even at the bottom of the crop, the leaves were above the light compensation point from early morning until mid-afternoon. From 15.30 hr on, the light compensation level in the canopy (or the zone where there was neither a decrease nor increase in the upward CO_2 flux) moved upwards.

For practical reasons, finite difference ratios have been used to obtain source-sink strength distribution in the canopy instead of the differentiation procedure. Denmead (1966) and Uchijima *et al.* (1970) have shown that finite difference ratios approximate closely the

average gradients for a crop layer between two plants, provided the vertical distance apart is kept reasonably small. So, $\Delta(\)/\Delta z$ can be used interchangeably with $\partial(\)/\partial z$. Figure 11 compares the sink strength for net radiation and the source strength for latent heat on a plant canopy volume basis. At 06.30 hr the evaporative flux through the full depth of the canopy exceeded the available energy and there was a net influx of sensible heat from the atmosphere. At 08.30 hr transfer of sensible heat from the upper to the lower layers served to maintain transpiration rate in excess of the available radiant energy. By noon the zone of maximum sensible heat loss had moved from the upper half of the canopy to the centre of the crop, where a layer of warm air had developed (see also Fig. 3 and Table 2). With the exception of the upper level, all layers were gaining

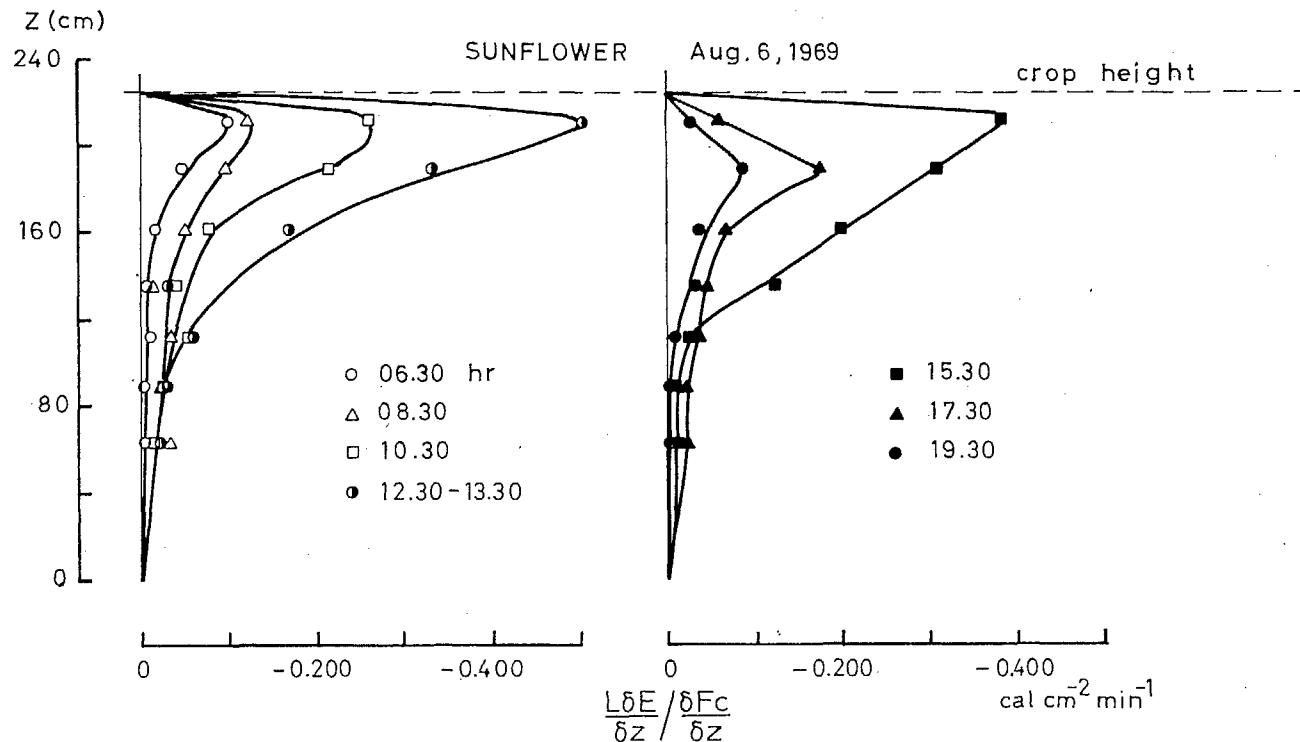


FIG. 12. Source intensity distribution of latent heat on a leaf area basis ($L\delta E/\delta F_c/\delta z$) at indicated periods in the sunflower canopy.

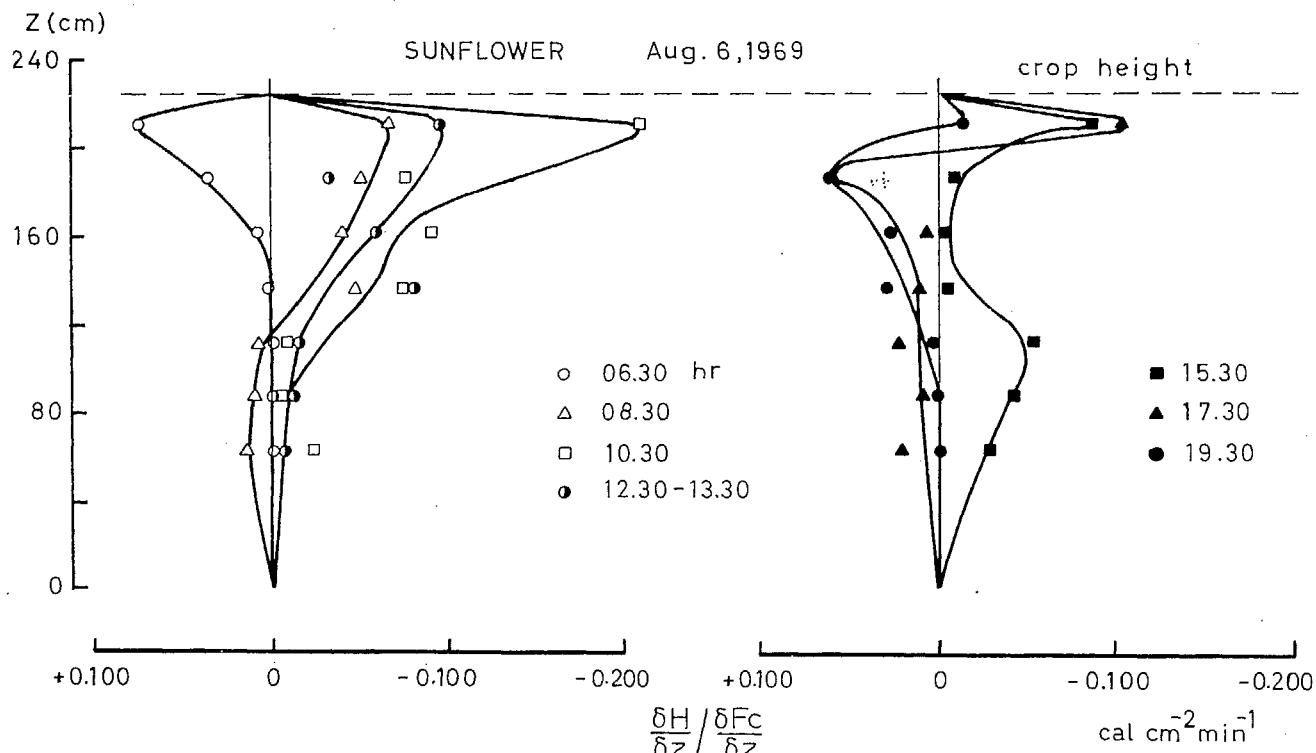


FIG. 13. Source and sink intensity distribution of sensible heat on a leaf area basis ($\delta H/\delta z/\delta F_c/\delta z$) at indicated periods in the sunflower canopy. Negative values mean heat loss, positive, heat gain by convective transfer.

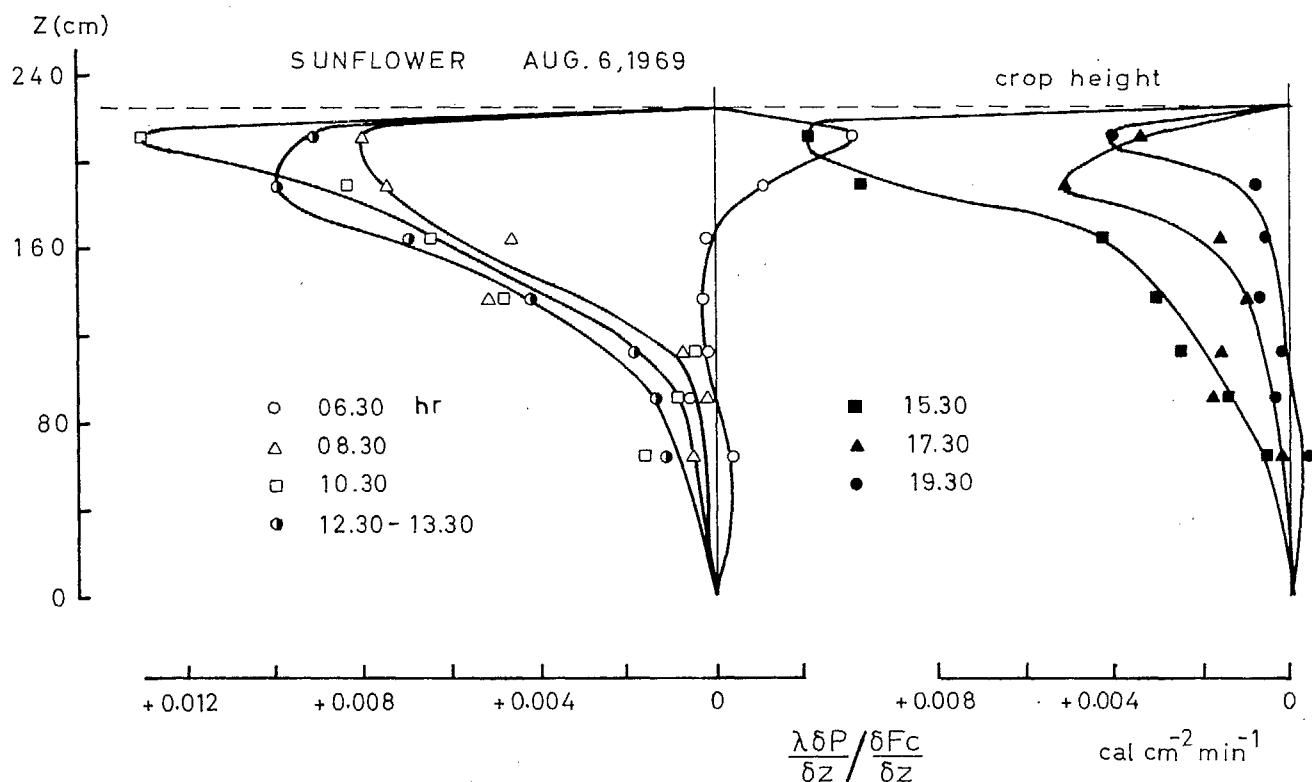


FIG. 14. Source and sink intensity distribution of photochemical energy on a leaf area basis ($\lambda \delta P/\delta z/\delta F_c/\delta z$) at indicated periods in the sunflower canopy. Negative values signify respiration and positive values photosynthesis.

TABLE 3. Water use efficiency or energy equivalent of photosynthesis/transpiration $\lambda P/LE$, within the crop

Height (cm)	Time (hr)					
	08.30	10.30	12.30-13.30	15.30	17.30	[08.30-17.30]
150-225	7.9	5.0	3.1	2.9	3.6	3.7
100-175	12.1	6.3	5.1	3.1	2.8	4.8
50-125	1.8	1.8	5.0	10.1	5.1	4.3
[50-225]	8.3	5.2	3.8	3.2	3.1	

adverted sensible heat from the air at 17.30 hr. At 19.30 hr transpiration rate was maintained almost entirely by a net gain of sensible heat from the atmosphere.

The percentage of net absorbed radiation used for transpiration was calculated for each layer within the crop. The $L\Delta E/\Delta Rn$ ratios were relatively constant with height in the canopy, but showed a pronounced daytime trend. Table 2 shows the height variation of the $L\Delta E/\Delta Rn$ ratio for different times of day.

A trend toward higher values of the $L\Delta E/\Delta Rn$ ratio at the beginning and end of the day was also found by Begg *et al.* (1964) for bulrush millet and by Brown and Covey (1966) for corn. These latter authors, however, found that around midday the percentage of net absorbed radiation used for transpiration increased with depth in the crop.

The vertical source-sink intensity distributions of latent heat, sensible heat and photochemical energy on a leaf area basis ($\partial(\)/\partial z / \partial Fc/\partial z$) for different times of day are given in Figures 12, 13 and 14. Latent heat and photochemical energy profiles show diurnal and height dependent changes in phase with and related to radiation distribution.

Figure 12 shows a decrease in transpiration of the upper leaves in the late afternoon. This could be attributed to unfavourable water relationships in the uppermost leaves. In the decade preceding the time of the study only 2.5 mm rain were recorded.

Light response, or photosynthesis in photochemical energy equivalence per unit of absorbed short-wave radiation (300-3,000 nm), $\lambda\Delta P/(1-r)\Delta R_i$, decreased with depth in the canopy, with a maximum efficiency somewhat below the top layer (r is the reflection coefficient for short-wave radiation). Efficiency decreased from 08.30 hr to 15.30 hr and increased again near late afternoon. Mean daytime efficiency ratios were 3.4 (150-225 cm), 2.5 (100-175 cm) and 1.7 (50-125 cm). Mean leaf efficiency of the canopy (50-225 cm) in terms of absorbed short wave radiation was -1.5 (respiration), 4.4, 2.8, 2.5, 2.4, 3.7 and 4.4 respectively at 06.30, 08.30, 10.30, 12.30-13.30, 15.30, 17.30 and 19.30 hr. As a consequence, leaf water use efficiency, or the ratio of the rate of CO_2 exchange to the rate of H_2O exchange expressed on an energy equivalence basis, decreased as the day proceeded. Values of $\lambda P/LE$ for different plant layers and different times of day are presented in Table 3.

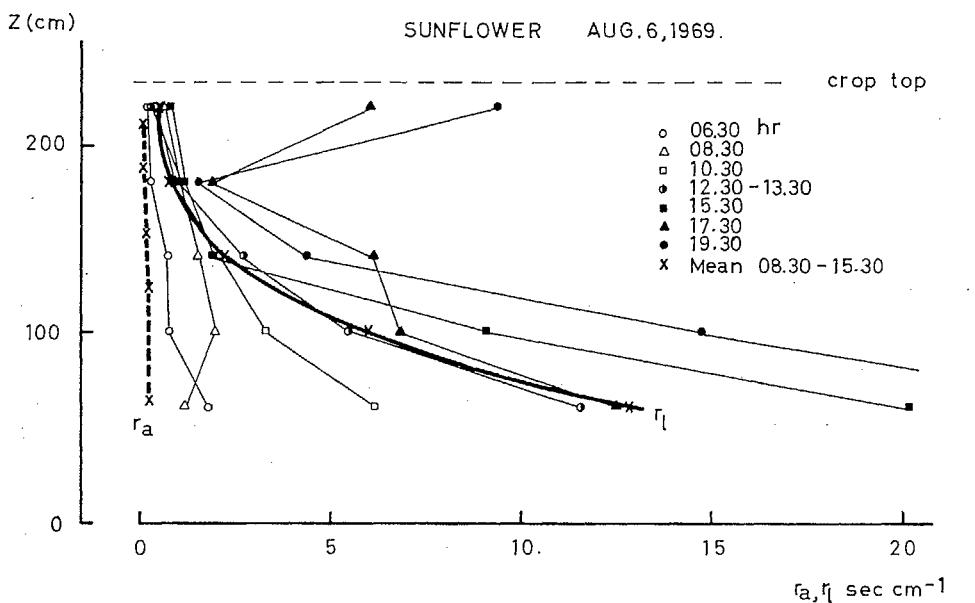


FIG. 15. Total water vapour [internal (r_s) + external boundary layer (r_ω)] resistance per unit leaf area with height in crop at different times of day.

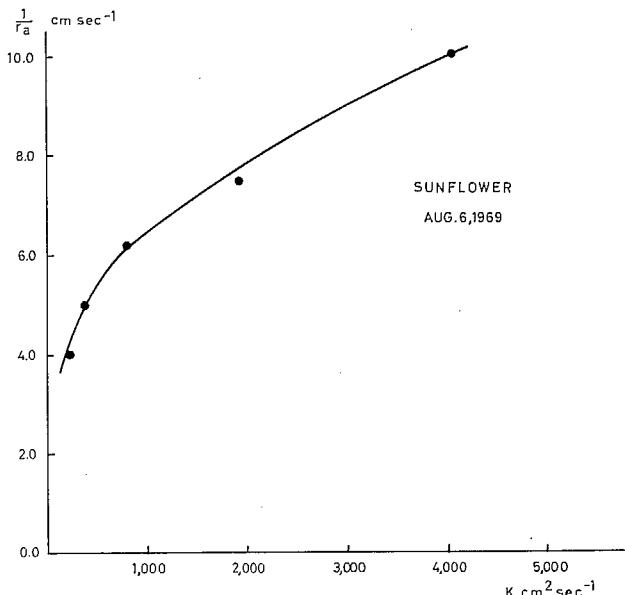


FIG. 16. Relationship between vertical turbulent transfer coefficient and leaf boundary air layer diffusivity within the sunflower canopy. Mean 08.30–15.30 hr values.

The leaf to air transfer coefficients were calculated from the relationships,

$$r_l = \frac{L}{L - \frac{\partial E}{\partial z} / \frac{\partial Fc}{\partial z}} \chi_l^o - \chi_l \quad (7)$$

$$\text{and } r_a = \frac{C_p \rho_a}{\partial H / \partial z} T_l - T \quad (8)$$

where r_l (sec cm^{-1}) is the total (external boundary layer + internal) leaf resistance to water vapour transfer, r_a is the external leaf boundary layer resistance and χ_l^o (g cm^{-3}) is the saturation concentration of water vapour at leaf temperature T_l . Boundary layer resistances for water vapour and heat are assumed equal. The r_l values show a general increase with depth in the canopy and with time of day (Fig. 15). There is a reduction in stomatal aperture at the upper leaves at 17.30 hr and 19.30 hr. r_a is almost negligible compared with r_l , especially in the lower eight-tenths of the canopy. This agrees with earlier experiments and with results obtained by other researchers (Impens *et al.*, 1966; Uchijima, 1966). The relationship between the

bulk air turbulent diffusivity and the leaf boundary layer diffusivity within the sunflower canopy is given in Figure 16. Boundary layer diffusivity ($1/r_a$) and total leaf diffusivity ($1/r_l$) decreased both exponentially with depth in the canopy as a function of downward cumulative leaf area index (Fig. 17):

$$r_a(h) / r_a(z) = \exp(-0.32 Fc) \quad (9)$$

$$\text{and } r_l(h) / r_l(z) = \exp(-0.92 Fc). \quad (10)$$

Extinction of $1/r_a$ is low when compared with the decrease of the turbulent transfer coefficient with depth in the canopy. From the comparison of the attenuation characteristics of K and $1/r_a$, one must conclude that the boundary layer around the sunflower leaves was essentially laminar (Hunt *et al.* 1968; Uchijima, 1966). On the other hand, computed boundary air layer resistances are smaller than predicted from classical boundary layer formulae. Measuring leaf temperatures, however, is difficult and a large relative error is likely to occur.

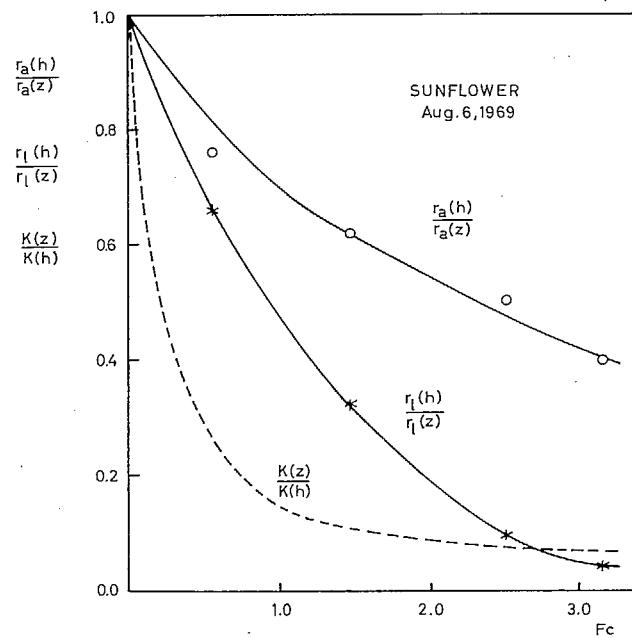


FIG. 17. Normalized profiles of external boundary air layer diffusivity r_a^{-1} , and of total leaf diffusivity, r_l^{-1} , representing the mean of all profiles taken during the 08.30–15.30 hr period. For comparison the turbulent transfer coefficient profile has also been presented.

Résumé

Répartition et dissipation à différents moments de la journée de l'énergie radiative absorbée et processus de transfert dans un couvert de Tournesol (I. I. Impens)

Pour rechercher la répartition et la dissipation de l'énergie radiative absorbée dans un couvert de Tournesol bien développé, nous avons appliqué la technique du bilan énergétique aux valeurs, à différents niveaux, du rayonnement net, des températures des feuilles et de l'air, de l'humidité absolue et de la concentration en gaz carbonique. Le flux de chaleur dans le sol a également été mesuré, ainsi que le rayonnement incident, réfléchi et transmis, et la vitesse du vent au-dessus de la végétation. Pour estimer les flux verticaux de la vapeur d'eau, de la chaleur et du gaz carbonique dans les couches d'air occupées par cette végétation, à différents moments de la journée, l'auteur a calculé la distribution du coefficient de transfert turbulent. Les profils de densité de flux ont été modifiés pour trouver la distribution, à l'unité de surface foliaire, des zones de perte et de gain. L'auteur a pu déterminer une baisse exponentielle du rayonnement net aussi bien que du coefficient de transfert turbulent, avec l'indice foliaire

cumulatif et un déplacement du tiers supérieur au tiers inférieur du couvert, de la zone de la plus grande perte de chaleur sensible depuis le milieu de la matinée jusque tôt dans l'après-midi. Tôt dans la matinée et tard dans l'après-midi, la transpiration dépassait la valeur correspondant au rayonnement net absorbé par l'épaisseur totale du couvert et était amplement maintenue par un apport net de chaleur sensible de l'atmosphère. De la pointe du jour au milieu de l'après-midi toutes les couches foliaires restaient au-dessus du point de compensation. L'efficience photosynthétique de la lumière culminait près du début et près de la fin de la journée, mais diminuait avec la profondeur du couvert. L'efficience de l'eau absorbée diminuait au cours des heures.

La résistance totale (interne et externe) de la feuille au transfert d'eau par diffusion et la résistance de la couche limite augmentaient toutes les deux de façon exponentielle avec l'indice foliaire cumulatif.

r_e augmentait aussi au cours de la journée et dépassait de beaucoup la valeur de r_a , surtout dans la moitié inférieure de la végétation. L'extinction de r_a^{-1} était faible comparée à la baisse du coefficient de transfert turbulent dans la profondeur du couvert.

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Analyse de la surface des taches de soleil, de l'indice foliaire et de l'inclinaison moyenne des feuilles à l'aide de photographies hémisphériques

R. Bonhomme

Station de bioclimatologie,
Institut national de recherches agronomiques,
Centre de recherches agronomiques des Antilles
et de la Guyane
Petit-Bourg, Guadeloupe (France)

Depuis la description par Hill (1924) d'un objectif photographique ayant un angle de visée de 180°, de nombreux auteurs ont utilisé des dispositifs de photographie hémisphérique pour estimer l'insolation ou l'énergie solaire reçue dans des constructions, sous des forêts, ou quelquefois sous des cultures (Beckett, 1934; Riblet, 1951; Susuki et Satoo, 1954; Tonne, 1958; Coombe et Evans, 1960; Clark, 1961; Brown, 1962; Anderson, 1964).

Nous nous proposons de montrer l'intérêt de cette technique pour la mesure de la pénétration du rayonnement solaire direct dans une culture. Nous montrerons aussi comment, et à quelles conditions, ces photographies hémisphériques peuvent être utilisées pour l'évaluation de l'indice foliaire en place d'une part et, d'autre part, de l'inclinaison moyenne des feuilles du couvert végétal. Quelques résultats obtenus sur des cultures de hauteur et de port différents seront discutés pour estimer la précision de la méthode.

TECHNIQUE DES PHOTOGRAPHIES HÉMISPHÉRIQUES

L'appareil utilisé est un Nikon F équipé d'un *fish-eye* (1:5,6; 7,5 mm de focale) dont l'angle de visée est de 180°. Cet appareil est placé horizontalement dans la culture, dirigé vers le haut, et donne ainsi une photographie hémisphérique de l'ensemble de la voûte végétale située au-dessus de lui. Les dispositifs de retardement ou de commande à distance de l'obturateur permettent à l'opérateur de se placer hors du champ de visée.

Afin d'accroître le contraste entre les feuilles et le ciel, pour faciliter un dépouillement ultérieur, nous nous attachons à: *a*) choisir pour opérer une aube, un crépuscule ou une journée à ennuagagement total pour éviter les taches de lumière dues au soleil lui-même ou à des surfaces réfléchissantes: tiges, pétiolées; *b*) utiliser un film

très sensible et un révélateur accentuant les contrastes; *c*) faire des tirages sur papier dur.

Lorsque ces photographies sont tirées sur papier, il est nécessaire d'inclure dans le tirage une partie des deux rangées de perforations de la bande négative (fig. 1). En effet, le repérage précis du centre de la photographie (0) s'effectue en traçant un axe longitudinal correspondant au milieu du négatif et un axe transversal à égale distance des perforations proches du centre.

Les points de la voûte végétale relatifs à une hauteur de visée *h* sont situés sur la circonférence d'un cercle de centre 0: la correspondance approximativement linéaire entre *h* en degrés et la distance à 0 sur la surface sensible est donnée par le constructeur de l'objectif. Il est alors facile de tracer les cercles concentriques représentant les lignes d'isohauteur de visée pour *h* variant, par exemple, de 10 en 10°.

MESURE DES SURFACES DE TACHES DE SOLEIL

Dans les couches supérieures d'un couvert végétal, une grande partie de l'énergie solaire captée est due au rayonnement solaire direct. Pour toute étude de photosynthèse d'une culture ou de microclimat lumineux dans celle-ci, il importe donc de connaître la pénétration des rayons solaires directs.

Il est possible de caractériser ce rayonnement solaire direct par la mesure, à un niveau et pour une hauteur du soleil donnés, de la surface relative des taches de soleil par unité de surface de sol: *s_h*. La connaissance de *s_h* permet de calculer, dans la végétation, l'énergie solaire directe: *S · s_h*, où *S* est le rayonnement solaire direct mesuré sur un plan horizontal au-dessus de la culture. Nous utiliserons ultérieurement les valeurs de *s_h* pour différentes valeurs de *h*, afin d'en déduire la géométrie (indice foliaire, inclinaison moyenne des feuilles) du couvert végétal étudié.

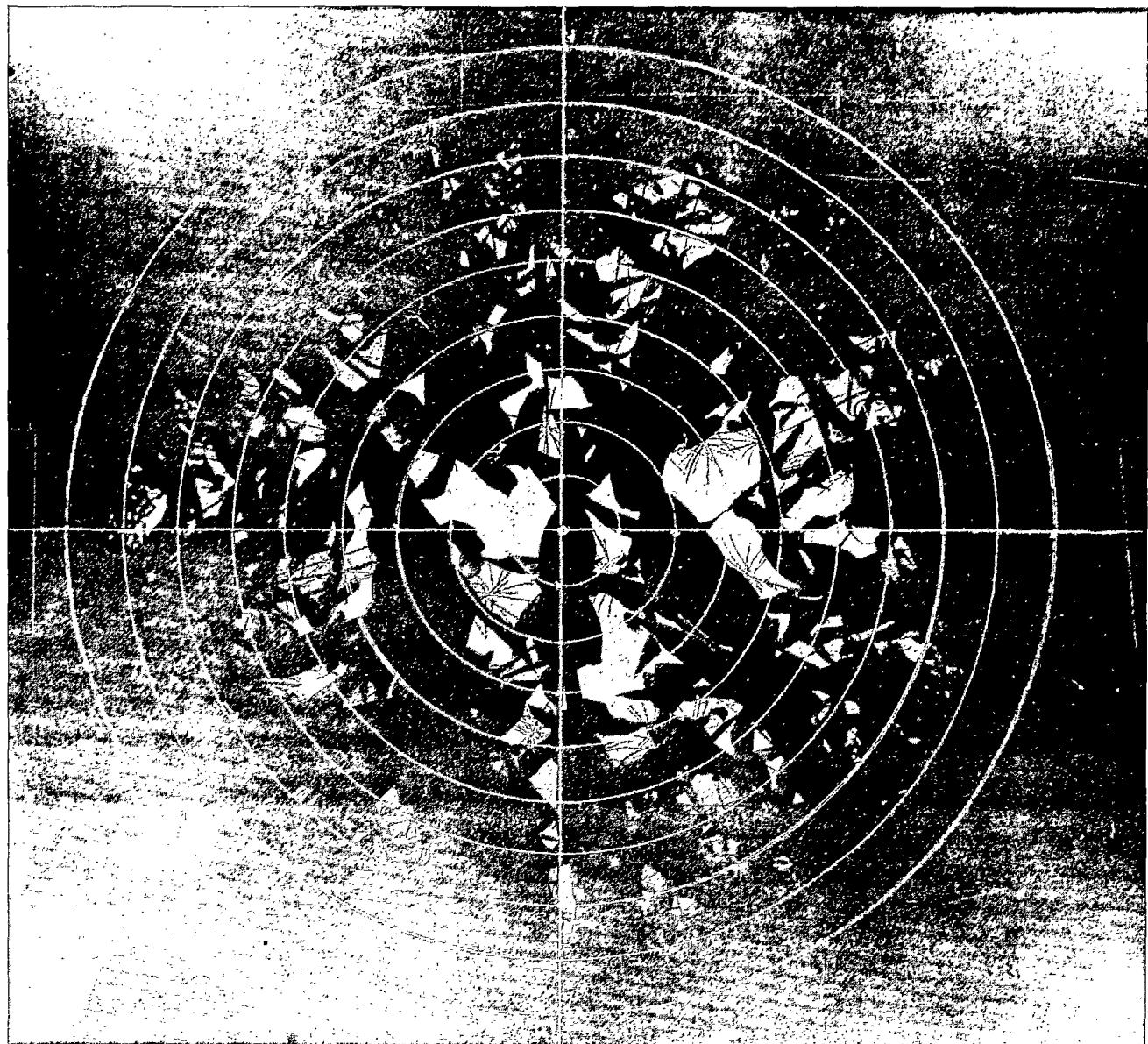


FIG. 1. Photographie hémisphérique prise sous une culture de Maïs. Axes de centrage et cercles d'isohauteur de visée h .

PRINCIPE DE LA MESURE

Comme l'indique la figure 2, partie gauche, pour une hauteur h il y a seulement deux rayons vecteurs du rayonnement solaire direct (XA et XB) incidents en X le matin et le soir. Il serait donc nécessaire de faire un grand nombre de photographies en des points différents; il viendrait:

$$s_h = \frac{n_A + n_B}{2n_X}$$

où: n_A est le nombre de points X tels que A se détache sur le ciel; n_B le nombre de points X tels que B se détache sur le ciel; n_X le nombre total de points X , donc de clichés.

Aussi faisons-nous l'hypothèse que, pour un point donné dans la végétation, la probabilité de voir le ciel à travers le feuillage est la même, pour une hauteur donnée, dans toutes les directions (nord, sud, est, ouest). Cette hypothèse doit être vérifiée sur plusieurs clichés pris à un niveau en effectuant, selon une des méthodes décrites dans le paragraphe suivant, un dépouillement

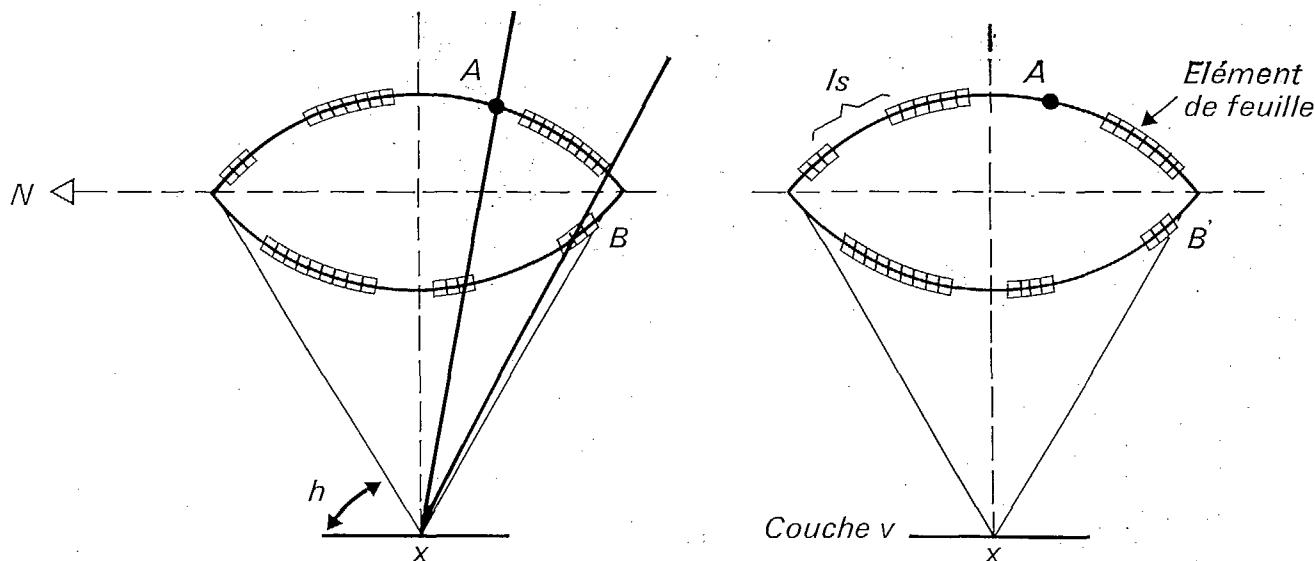


FIG. 2. Mesure de la surface des taches de soleil.

par quadrant. Si cette vérification se révèle exacte, la figure 2, partie droite, montre qu'on peut utiliser toute la longueur du cercle et non plus seulement les points A et B. Il vient alors:

$$s_h = \frac{l_s}{2\pi R}$$

où l_s est la longueur de l'arc de cercle se détachant sur le ciel; R le rayon du cercle.

Nous considérerons par la suite que le couvert végétal répond à cette hypothèse simplificatrice et que la mesure de s_h porte sur des cercles concentriques.

RÉALISATION PRATIQUE

Deux problèmes essentiels se posent pour la réalisation pratique de cette technique: a) avoir, à un niveau dans une culture, un nombre assez important de points de mesure pour tenir compte de l'hétérogénéité du couvert végétal; b) assurer un dépouillement assez précis des photographies avec des méthodes suffisamment rapides.

Le choix du nombre de clichés, à un niveau, est sous la dépendance de plusieurs facteurs dont, en particulier: l'hétérogénéité horizontale (effet des rangs), l'indice foliaire, la taille, les dimensions des feuilles de la culture, mais aussi la hauteur de visée h et la précision désirée sur s_h . Il en résulte que, pour chaque plan de mesure, il est nécessaire d'effectuer de nombreuses photographies et de calculer le nombre minimal nécessaire pour avoir, pour une certaine valeur de h , une précision sur s_h égale ou supérieure à un certain seuil. Le tableau 1 montre que, pour une culture de petite taille (Patate douce: *Ipomea batatas*), il est nécessaire d'avoir un nombre de clichés plus important que dans le cas d'un couvert végétal plus élevé (*Zea mays*). De plus, la précision sur

s_h varie avec h et est maximale pour des hauteurs de visée de 30 à 60°.

Le dépouillement est effectué, par exemple, par classes de hauteur de 10°. A partir des clichés agrandis sur papier, nous pouvons: a) soit tracer des cercles concentriques correspondant aux centres des classes de hauteur et faire sur chacun le rapport entre la longueur se détachant sur le ciel et le périmètre; b) soit, de façon plus précise, planimétrer (directement ou par pesée) dans chaque couronne circulaire la surface des zones de ciel et rapporter cette valeur à la surface de la couronne.

Nous envisageons également de procéder à une automatisation du dépouillement par des lecteurs photoélectriques se déplaçant sur les cercles concentriques correspondants à des hauteurs de visée connues.

TABLEAU 1. Valeurs de s_h mesurées (intervalle de confiance) de 95%

Hauteur du soleil h	<i>Ipomea batatas</i>	<i>Zea mays</i>
5°	0,003 - 0,006	
15°	0,023 - 0,036	0,001 - 0,005
25°	0,054 - 0,081	0,013 - 0,023
35°	0,077 - 0,113	0,047 - 0,071
45°	0,103 - 0,155	0,080 - 0,150
55°	0,142 - 0,209	0,138 - 0,142
65°	0,102 - 0,244	0,152 - 0,216
75°	0,064 - 0,359	0,200 - 0,254
85°	0,020 - 0,395	0,130 - 0,270
Nombre de photographies	30	16
Indice foliaire	2,8	2,9
Hauteur en mètres	0,40	2,10

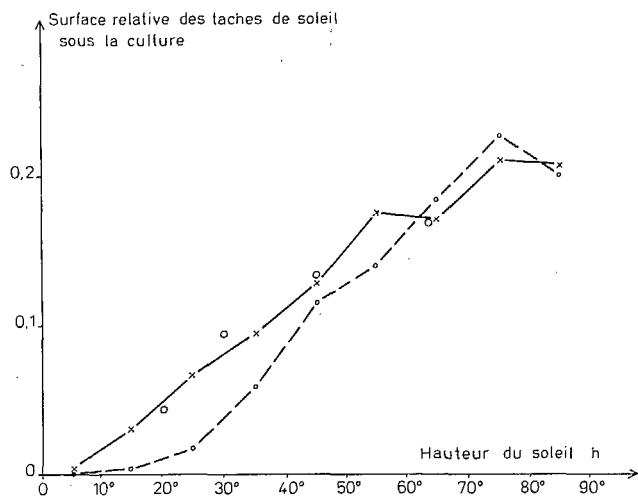


FIG. 3. Surface relative des taches de soleil sous la culture en fonction de h .

○ Méthode des fibres optiques	Culture de Patate
×—× Photographies hémisphériques	
—○— Photographies hémisphériques.	Culture de Maïs, f: 2,9

DISCUSSION DE QUELQUES RÉSULTATS

Il est possible de comparer les valeurs de s_h obtenues à l'aide de photographies hémisphériques à celles résultant d'autres méthodes de mesure. Nous avons décrit, d'autre part (Horie, 1966; Bonhomme, 1970), une technique qui consiste à placer de nombreux repères et à compter, à distance par l'emploi de fibres optiques, la proportion de repères ensoleillés pour une hauteur de soleil h et un niveau donnés. La figure 3 montre le bon accord entre les résultats des deux méthodes de détermination de la surface relative des taches de soleil: elle met aussi en évidence l'évolution différente de s_h en fonction de h selon la culture considérée.

MESURE DE L'INDICE FOLIAIRE EN PLACE

La plupart des méthodes de mesure de l'indice foliaire sont destructives; seules des techniques d'estimation (corrélations surface-dimensions linéaires, comparaison à des feuilles standard ou à des formes géométriques simples) permettent de déterminer l'indice foliaire sans trop perturber la culture. Ces dernières méthodes sont longues à mettre en œuvre (sommation des surfaces de chaque feuille) et nécessitent une délimitation précise des surfaces de mesure dans la végétation. Dans le cas d'une végétation de grande taille, la plupart des techniques sont irréalisables: cas des forêts...

Nous utilisons une méthode qui, moyennant quelques hypothèses sur la structure du couvert végétal, permet, à partir des surfaces des taches de soleil, le calcul de l'indice foliaire total ou par niveau.

La mesure de l'indice foliaire en place à partir de photographies hémisphériques n'est possible que si, en plus de l'hypothèse nécessaire pour la mesure de s_h , le couvert végétal est tel que: a) le sol est totalement et régulièrement couvert par la culture; b) l'azimut des feuilles, par rapport au soleil, peut prendre toutes les valeurs avec la même probabilité; c) la probabilité de présence d'une feuille en un point donné d'une couche ne dépend pas de la position de ce dernier, qu'il soit à l'ombre ou au soleil.

Ces conditions sont réalisées pour certaines cultures couvrant bien le sol dans la mesure où celles-ci ne présentent pas de rangs ou de phénomènes de phototropisme marqués. Il faut signaler aussi que les valeurs d'indice foliaire obtenues tiennent compte des surfaces foliaires, mais aussi de la section verticale des tiges ou des inflorescences qui font obstacle à la pénétration du rayonnement solaire direct et sont donc prises en compte dans la mesure des s_h .

La méthode décrite dans cet article est voisine de celle de Warren Wilson (1963), qui utilise les fréquences de contact feuille-aiguille par différentes inclinaisons de cette dernière. Dans la méthode présentée nous considérons au contraire la fréquence des rayons lumineux qui traversent sans interception la culture pour différentes hauteurs de pénétration.

CAS D'UNE CULTURE DONT LES FEUILLES ONT LA MÊME INCLINAISON

Étant donné les hypothèses faites sur la structure du couvert végétal, Chartier (1966) montre que, sous une couche de feuilles d'épaisseur Δf suffisamment faible pour qu'il n'y ait pas superposition par rapport aux rayons solaires, la surface relative des taches de soleil s_h est:

$$s_h = 1 - \Delta f \cdot K(i, h)$$

où: $K(i, h)$ est une fonction qui varie avec i et h selon les indications de la figure 4, i représentant l'inclinaison des feuilles sur un plan horizontal et h , la hauteur du soleil.

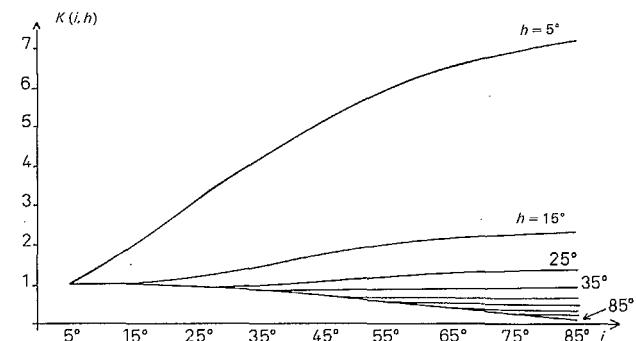


FIG. 4. Variations de la fonction $K(i, h)$ en fonction de i pour différentes valeurs de h .

Sous la *n*ème couche de feuillage, nous avons (les feuilles étant réparties uniformément dans chaque couche):

$$s_h(n) = [1 - \Delta f \cdot K(i, h)]^n$$

de même:

$$s_h(n+1) = [1 - \Delta f \cdot K(i, h)]^n [1 - \Delta f \cdot K(i, h)]$$

Donc:

$$\Delta s_h(n+1) - s_h(n) = -s_h(n) \times \Delta f \cdot K(i, h)$$

et sous une culture d'indice foliaire f :

$$s_h = e^{-K(i, h)f}$$

Nous constatons, sur la figure 4, que les valeurs de $K(i, h)$ varient peu en fonction de i pour $h = 35^\circ$; la figure 5 montre que $1,12 K(i, h = 35^\circ)$ reste voisin de 1 avec comme valeurs extrêmes 0,90 et 1,10. Pour $h = 35^\circ$, s_h va donc varier essentiellement en fonction de f et être assez indépendant de i ; nous allons pouvoir ainsi évaluer f connaissant $s_h = 35^\circ$; nous avons en effet:

$$\begin{aligned} 1,12 \cdot 2,3 \log_{10} s_{35^\circ} &= -(0,9 \text{ à } 1,1)f \\ 2,576 \log_{10} s_{35^\circ} &= -(0,9 \text{ à } 1,1)f \end{aligned} \quad [1]$$

De façon analogue, nous pouvons combiner les s_h obtenus pour deux hauteurs de visée:

$$\begin{aligned} 0,65 K_{25^\circ} + 0,40 K_{65^\circ} &= 0,95 \text{ à } 1,05 \\ 0,30 K_{15^\circ} + 0,70 K_{55^\circ} &= 0,98 \text{ à } 1,02 \end{aligned}$$

Il en résulte que l'indice foliaire peut être calculé aussi à partir des relations:

$$1,495 \log_{10} s_{25^\circ} + 0,92 \log_{10} s_{65^\circ} = (0,95 \text{ à } 1,05)f \quad [2]$$

$$0,690 \log_{10} s_{15^\circ} + 1,61 \log_{10} s_{55^\circ} = -(0,98 \text{ à } 1,02)f \quad [3]$$

CAS D'UNE CULTURE A INCLINAISON VARIABLE

Considérons maintenant un couvert végétal répondant aux hypothèses précédentes, ayant une proportion de surface foliaire égale à P_1 pour l'inclinaison i_1 , P_2 pour i_2 ... ($P_1 + P_2 + \dots = 1$). Nous allons limiter nos calculs à trois classes (de centres 15° , 45° , 75°), car nos résultats expérimentaux portent sur de tels cas, mais il est facile de généraliser la méthode de calcul à 9 classes d'inclinaison, par exemple.

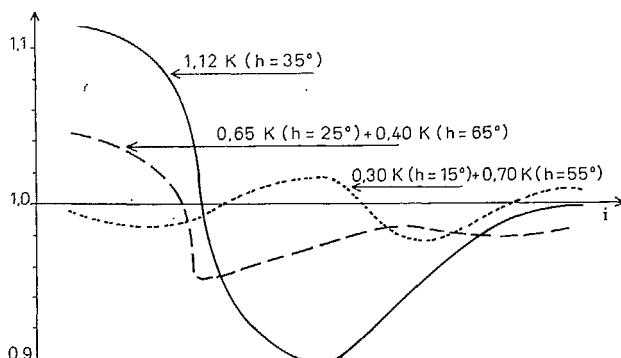


FIG. 5. Valeurs de différentes fonctions de $K(i, h)$ en fonction de i .

TABLEAU 2. Indice foliaire cumulé (valeurs moyenne et extrême)

	Indice foliaire calculé	Indice foliaire mesuré
<i>Patate douce (30 photographies)</i>		
1	2,2 — 3,1 (2,6)	Feuilles + pétioles
2	2,1 — 3,0 (2,5)	2,5 — 0,30
3	2,0 — 2,5 (2,3)	
4	1,5 — 2,1 (1,7)	
<i>Mais (16 photographies par niveau)</i>		
Niveau 0,30 m	1 2,7 — 3,8 (3,1) 2 2,9 — 3,8 (3,3) 3 2,9 — 3,5 (3,1) 4 2,7 — 3,5 (3,0)	Feuilles + tiges + épis 2,67 — 3,15 (2,90)
Niveau 0,60 m	1 2,0 — 2,8 (2,4) 2 2,2 — 2,7 (2,4) 3 2,2 — 2,6 (2,4) 4 1,9 — 2,5 (2,4)	2,26 — 2,70 (2,54)
Niveau 0,90 m	1 1,7 — 2,4 (2,0) 2 1,6 — 2,1 (1,8) 3 1,7 — 2,0 (1,8) 4 1,7 — 1,9 (1,8)	1,76 — 2,08 (1,97)
Niveau 1,20 m	1 0,8 — 1,2 (1,0) 2 0,9 — 1,3 (1,1) 3 1,1 — 1,4 (1,3) 4 1,0 — 1,3 (1,2)	1,28 — 1,51 (1,37)

De façon analogue au cas précédent, sous la *n*ème couche, pour une hauteur h , en supposant $K(i, h)$ constant dans chaque classe, nous avons:

$$s_h(n) = [1 - p_1 \Delta f \cdot K(i_1, h) - p_2 \Delta f \cdot K(i_2, h) - p_3 \Delta f \cdot K(i_3, h)]^n$$

Donc:

$$s_h = e^{-f [p_1 K(i_1, h) + p_2 K(i_2, h) + p_3 K(i_3, h)]}$$

Si $h = 35^\circ$, $K(i, h = 35^\circ)$ est constant; d'où:

$$s_h = e^{-f K(i, h = 35^\circ)} (p_1 + p_2 + p_3) = e^{-f K(i, h = 35^\circ)}$$

et le calcul est identique au cas précédent.

Si nous considérons trois hauteurs de visée, 15° , 45° , 75° , nous pouvons écrire:

$$\begin{aligned} -2,3 \log_{10} s_{15^\circ} &= p_1 f K(i_1, h_1) + p_2 f K(i_2, h_1) + p_3 f K(i_3, h_1) \\ -2,3 \log_{10} s_{45^\circ} &= p_1 f K(i_1, h_2) + p_2 f K(i_2, h_2) + p_3 f K(i_3, h_2) \\ -2,3 \log_{10} s_{75^\circ} &= p_1 f K(i_1, h_3) + p_2 f K(i_2, h_3) + p_3 f K(i_3, h_3) \end{aligned}$$

et résoudre ce système d'équations pour en déduire $p_1 f$, $p_2 f$ et $p_3 f$. Par exemple:

$$p_1 f = \frac{\begin{vmatrix} \log_{10} s_{15^\circ} & K(i_2, h_1) & K(i_3, h_1) \\ \log_{10} s_{45^\circ} & K(i_2, h_2) & K(i_3, h_2) \\ \log_{10} s_{75^\circ} & K(i_2, h_3) & K(i_3, h_3) \end{vmatrix}}{\begin{vmatrix} K(i_1, h_1) & K(i_2, h_1) & K(i_3, h_1) \\ K(i_1, h_2) & K(i_2, h_2) & K(i_3, h_2) \\ K(i_1, h_3) & K(i_2, h_3) & K(i_3, h_3) \end{vmatrix}}$$

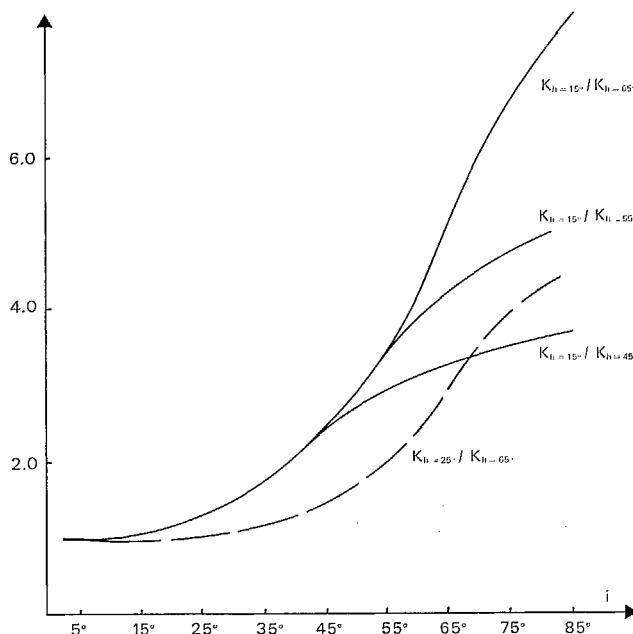


FIG. 6. Valeurs de différentes fonctions des rapports $K(i, h)$ pour la détermination graphique de l'inclinaison moyenne des feuilles.

La relation $p_1 f + p_2 f + p_3 f = f$ permet de calculer f . Si nous prenons les valeurs de $K(i, h)$ données par la figure 4, nous obtenons par résolution :

$$p_1 f = -1,61 \log_{10} s_{15^\circ} + 6,98 \log_{10} s_{45^\circ} - 3,07 \log_{10} s_{75^\circ}$$

$$p_2 f = 2,23 \log_{10} s_{15^\circ} - 12,0 \log_{10} s_{45^\circ} - 9,78 \log_{10} s_{75^\circ}$$

$$p_3 f = 6,24 \log_{10} s_{45^\circ} - 6,24 \log_{10} s_{75^\circ}$$

et

$$f = 0,62 \log_{10} s_{15^\circ} + 1,21 \log_{10} s_{45^\circ} + 0,47 \log_{10} s_{75^\circ} \quad [4]$$

Nous avons donc une méthode de détermination de f qui fait intervenir les valeurs s_h obtenues pour trois hauteurs h .

RÉSULTATS EXPÉRIMENTAUX

Afin de tester la validité des hypothèses nécessaires aux calculs précédents, nous avons choisi deux cultures très différentes pour effectuer des vérifications expérimentales : Patate douce (*Ipomea batatas*) et Maïs (*Zea mays*). L'indice foliaire est mesuré par planimétrage direct des feuilles sur des zones de la culture voisines du lieu d'obtention des clichés. Dans chaque détermination par le calcul nous avons tenu compte de l'erreur relative aux s_h (en prenant un intervalle de confiance de 95%) mais aussi des coefficients extrêmes possibles des différentes formules.

Nous avons indiqué, dans le tableau 2, les intervalles d'indice foliaire calculés par les quatre formules, en assimilant les cultures soit à un couvert d'inclinaison constante (1, 2, 3), soit à un couvert à inclinaison variable (4). Ces différentes formules donnent des valeurs compara-

bles entre elles et qui sont du même ordre que les valeurs mesurées; il faut noter cependant les faibles valeurs obtenues par le calcul (ou les fortes valeurs mesurées) dans le cas de la Patate douce.

MESURE DE L'INCLINAISON MOYENNE DES FEUILLES D'UNE CULTURE

Si nous supposons que le couvert végétal a des feuilles dont l'inclinaison est constante, les relations

$$s_h = e^{-K(i, h)} f$$

vont nous donner, connaissant s_h et f (calculé par les méthodes précédentes), une valeur de $K(i, h)$ pour chaque hauteur de visée. Nous pouvons ainsi calculer neuf valeurs de i ; toutefois, les erreurs sur les mesures de s_h ainsi que sur le f calculé font que les intervalles estimés pour i sont souvent très importants.

Nous utilisons donc pour calculer l'inclinaison moyenne une méthode ne nécessitant pas la connaissance préalable de f . Si nous faisons les rapports de $\log s_h$ pour diverses hauteurs, ceux-ci sont indépendants de f ; si nous choisissons des hauteurs très différentes, nous avons là une méthode assez précise de détermination de i . La figure 6 indique les variations de $K(i, h=15^\circ)/K(i, h=45^\circ)$, $K(i, h=15^\circ)/K(i, h=55^\circ)$; $K(i, h=15^\circ)/K(i, h=65^\circ)$, $K(i, h=25^\circ)/K(i, h=65^\circ)$ en fonction de i et permet une détermination graphique de i à partir du calcul de $\log s_{15^\circ}/\log s_{45^\circ} = K(i, h=15^\circ)/K(i, h=45^\circ)$, etc.

TABLEAU 3. Inclinaison moyenne entre le sommet et le niveau considéré

	Inclinaison moyenne calculée (4 méthodes de détermination graphique)	Inclinaison moyenne mesurée (rapporteur)
<i>Patate (30 photographies)</i>		
Niveau 0	28°—40° (33) 34—44 (39) 28—47 (39) 31—55 (46)	37
<i>Maïs (16 photographies par niveau)</i>		
Niveau 0,30 m	40—77 (50) 47—56 (51) 48—62 (54) 54—64 (59)	43
Niveau 0,60 m	45—60 (52) 47—57 (51) 50—59 (55) 51—59 (56)	44
Niveau 0,90 m	52—64 (56) 47—61 (54) 55—64 (59) 55—68 (60)	45
Niveau 1,20 m	45—77 (57) 47—62 (54) 55—64 (59) 55—67 (60)	47

Dans le cas d'une culture dont l'inclinaison des feuilles est variable, les termes p_1f , p_2f ... représentant la part d'indice foliaire se trouvant à l'inclinaison i_1 , i_2 ... s'évaluent facilement en fonction de $\log s_{h_1}$, $\log s_{h_2}$... L'indice foliaire f étant calculé ailleurs, il est possible d'estimer p_1 , p_2 ... Toutefois, nous n'avons pu obtenir une précision suffisante sur s_{h_1} , s_{h_2} ... pour que cette estimation soit acceptable; dans les résultats expérimentaux qui suivent nous n'avons donc pas procédé à une détermination des probabilités d'inclinaison des feuilles.

Le tableau 3 nous donne les inclinaisons moyennes calculées et mesurées (à l'aide d'un rapporteur) pour chaque culture. Si les valeurs obtenues pour *Ipomea batatas* sont acceptables, par contre les calculs portant sur *Zea mays* donnent une valeur assez différente et toujours supérieure aux mesures. Nous pouvons expliquer en partie ce résultat: *Ipomea batatas* se rapproche beaucoup d'une culture à inclinaison constante (si l'on ne tient pas compte des pétioles), ce qui n'est pas le cas de la culture de *Zea mays* considérée. Ces difficultés

pourront sans doute être levées lorsque, par un nombre de photos plus important, nous effectuerons des calculs d'inclinaison sur des couverts végétaux à inclinaison variable.

CONCLUSION

Cette technique des photos hémisphériques permet une mesure facile des taches de soleil et peut donc à ce titre rendre de grands services pour l'étude de la pénétration du rayonnement solaire direct. De plus, elle donne des indications intéressantes sur la géométrie, particulièrement l'indice foliaire, du couvert végétal étudié. D'autre part, l'existence de ces clichés fournit des données particulièrement objectives et complètes sur la culture considérée. Une amélioration de la précision devrait en faire une technique extrêmement utile pour des études sur cultures assez élevées aussi bien qu'en forêt (études de photosynthèse, de turbulence...).

Summary

Analysis of the area of sun-spots, the leaf index and average tilt of leaves by means of hemispheric photographs
(R. Bonhomme)

Using a camera equipped with a "fish-eye" and placed horizontally in the crop and directed upwards, one can obtain photographs of the whole plant arch. On examination, the hemispheric photographs obtained in this way reveal the proportion of direct solar energy transmitted at the level measured. The quantity is calculated on the basis of the relative area of sun-spots, s_h that is, the area of sun-spots per unit of soil area at a given level for a solar altitude h . If the plant cover under study meets certain criteria with regard to its homo-

geneity (good soil cover, absence of rows, etc.), it is found that for a focus of a height of 35 degrees the s_h values depend largely upon the leaf index and very little on the tilt of the leaves. From this we have worked out a method of calculating the leaf index f (formula 1). By combining the s_h values for particular heights h , one can also calculate the f , sometimes with greater accuracy (formulae 2, 3 and 4). It is also possible by calculating the \log_{10} relationships of certain s_h values to obtain an expression which varies only in terms of i and gives, by graphic determination, a value for the average tilt of the leaves of the crop. Experimental findings obtained with two very different crops <*Ipomea batatas* and *Zea mays*>—are discussed.

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Row-crop microclimate

R. J. Luxmoore, R. J. Millington and D. B. Peters
Agronomy Department, University of Illinois, Urbana
(United States of America)

INTRODUCTION

In analysis of the relationships between plants and their environment, the scale of study has shown continuing refinement with time. Earliest ecological studies showed correlations between the major climatic regions and the vegetation forms of whole continents. Today, relationships between single leaves and their boundary layer or the pathway from the chloroplast to the environment reflect the intensive nature of contemporary studies. Intermediate between these extremes is the analysis of plant-environment interaction with row-sown crops. Although the practice of ploughing, sowing and cultivating crops in rows dates almost from the introduction of the most primitive agricultural implements, the physical or physiological basis of benefits or deficiencies of particular crop configurations, in terms of crop production, are not well understood.

Let us consider a crop in which all plants and elements of the plants are randomly distributed within the crop height. There is random variation within the age, physiological activity and size, orientation, elevation and so on of the plant parts. Provided the crop area is large, it appears intuitively that flow and redistribution of energy and matter could be treated in a one-dimensional manner provided air flow over the crop was laminar.

When the air movement is turbulent and characterized by random velocities in the x , y and z directions, then even in the isotropic crop there will be a mosaic of crop-environment subsystems within which flow will be independent of quadrant and three-dimensional. However, interchange between adjacent elements in a horizontal plane could cancel out and a one-dimensional analysis could suffice at a sufficiently macroscopic level.

When crop elements are non-randomly dispersed in any horizontal plane, then both the movement of the sun and the wind, either laminarized or turbulent,

dictates that analysis must be at least two-dimensional. However, so far there has been little attempt to pursue these problems other than in windbreak studies, wind tunnel models and some work on the effect of turbulent pressure pulses on the exchange of soil gases.

It is proposed here to present some data and discussion of radiation, mass and momentum exchange in row-sown soybeans. The objective is to draw attention to some of the problems encountered and, where possible, to suggest means of attacking the problems in a way which should lead to better understanding of the crop-environment relationships.

RADIATION

Growth analysis and light interception studies have shown that, as the leaf area index (LAI) of a soybean crop increases, both light interception and crop dry weight increase (Shibles and Weber, 1965). Further, a large proportion of incident energy is dissipated in the outer leaf zone of the soybean canopy and particularly in the uppermost part of the crop (Shaw and Weber, 1967).

The Bouguer-Lambert law of light extinction has been applied to soybean canopies in studies of Singh *et al.* (1968) and Sakamoto and Shaw (1967). In the latter case an extinction coefficient of about 0.4 was obtained. Shaw and Weber (1967) showed that both light penetration and dry matter accumulation increased when the soybean canopy was slightly lodged. Leaf arrangement as well as LAI is important in the light relationships of a crop. The present work was undertaken to examine the influence of soybean canopy structure on some radiant energy relations (Luxmoore *et al.*, 1970).

The Amsoy cultivar of soybean (*Glycine max L.*) was grown during the summer (May-September) of 1969

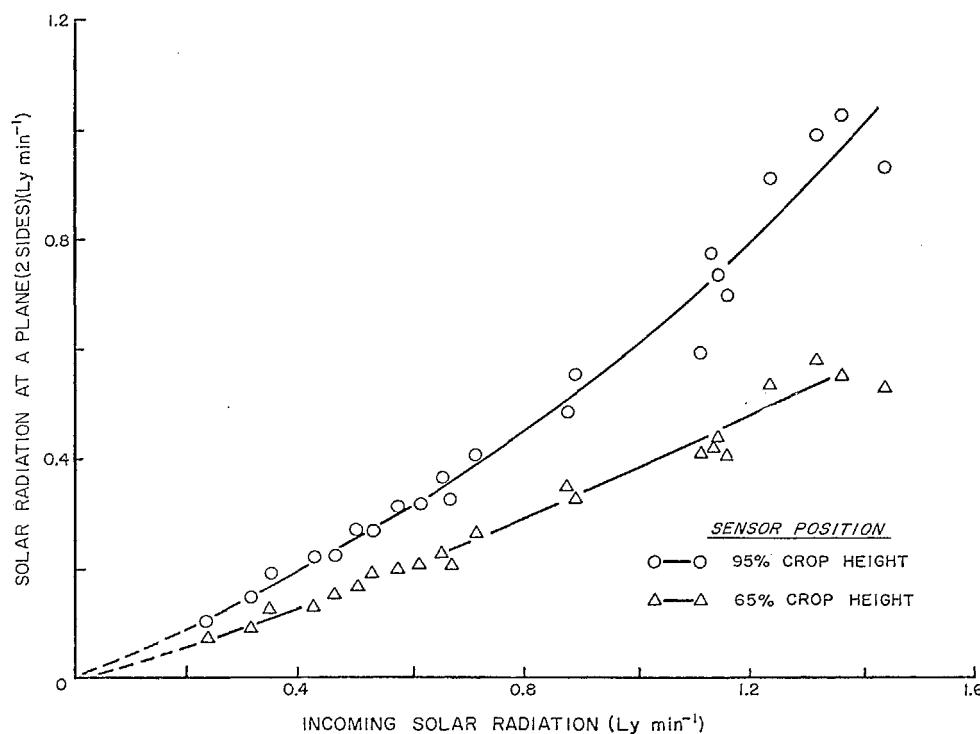


FIG. 1. Solar radiation (310–2750 nm waveband) received on the upper and lower surfaces of a plane at two positions in a soybean canopy as a function of incoming solar radiation above the crop on the 57th day from planting. Crop height, 86 cm.

at Urbana, Illinois in north-south rows, spaced 76 cm apart. The planting density was about 25 plants per metre of row.

Measurements of canopy outline were made during the latter half of the season and leaf area of the crop was determined, in 20-cm height increments, using an optical planimeter.

Incoming solar and net radiation were monitored above the crop with an Eppley pyranometer and a miniature net radiometer (Fritsch, 1961), respectively. Tube solarimeters additively measured the radiation flux received on a strip (76 cm long and 2 cm wide) for both upper (A) and lower (B) surfaces. Some were fitted with Schott glass RG8 filters which excluded radiation with a wave-length less than 700 nm. A solarimeter of each type and two net radiometers were placed above the crop and at four heights in the middle of the canopy along the row axis.

The row-planted soybean canopy used in this study has, in cross-section, a peripheral layer of leaves supported by an inner structure of stems and petioles. The canopy outline shows dominant temporal change in the uppermost leaf zone and this is associated with a change in cumulative LAI.

As the flux density of incoming solar energy increased (e.g. during the morning), the energy (A + B) received

by a solarimeter (310–2750 nm waveband) at a particular plane within the canopy increased. Figure 1 shows data obtained at 57 days from planting. The relationship deviates from linearity, indicating that the canopy is not composed of randomly disposed horizontal leaves, and that changes in sun angle and/or leaf inclination with change in the incoming radiation flux are important in determining the energy distribution within the canopy. A more striking departure from linearity was obtained for the relationship between visible radiation (310–700 nm waveband) received at a plane within the crop and the incoming visible energy above the crop (Fig. 2). Periods of high radiation are associated with sun elevation near the zenith and, during these times, changes in leaf inclination, due to water stress, result in a more open canopy. Further, the penetration of reflected radiation into the canopy is increased at low angles of incidence of incoming energy to leaves.

For each position within the canopy, the radiation flux received from the upper hemisphere (A) was calculated by taking half of the sum of the solarimeter (A + B) and net radiometer (A – B) measurements. Since the wave-length sensitivities of solarimeters and radiometers are different, incoming radiation (A) is slightly overestimated. Figure 3 shows the solar radiation received from the upper hemisphere as a percentage

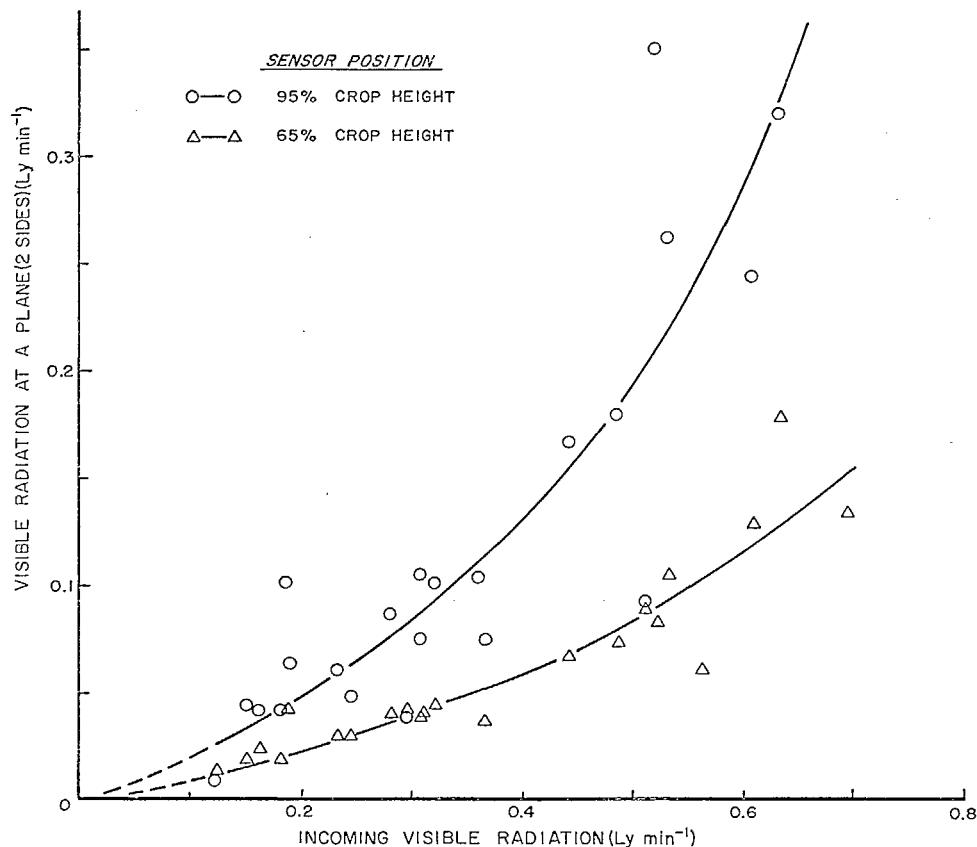


FIG. 2. Visible radiation (310–700 nm waveband) received on the upper and lower surfaces of a plane at two positions in a soybean canopy as a function of incoming visible radiation above the crop on the 57th day from planting. Crop height, 86 cm.

of the total radiation $[(A \cdot 100) / (A + B)]$ as a function of relative height within the canopy. From 65 to 85 per cent of the radiation received in the plane of the solarimeters came from the upper hemisphere, the remainder being reflected radiation sensed by the lower surface. The proportion of reflected energy is slightly larger for the middle layers of the canopy.

The extinction coefficient (k) for each layer of leaves was obtained from the Bouguer-Lambert relation

$$k = \frac{\ln \left(\frac{A_u}{A_l} \right)}{\text{LAI}}$$

where A_u and A_l are the solar radiation fluxes at the upper and lower boundaries of a canopy layer having a given LAI. Mean values of k calculated from about fifteen observations taken during a day. A large variation in k with position in the canopy was found (Fig. 4). The maximum extinction coefficient occurred in the uppermost leaf layer ($k < 1.4$). In the middle layers, k reached a minimal value (0.35–0.82), then increased

again in the lowest leaf zone. Since leaf arrangement has less influence on k under diffuse light conditions, the increase in k in the lowest leaf layer may be due to an increased proportion of diffuse radiation lower in the canopy. Values of extinction coefficients reported by Sakamoto and Shaw (1967) are similar to those found in the present data at 50–80 per cent of crop height.

The large variation in k with position in the canopy indicates that the assumption of a homogenous medium, on which the Bouguer-Lambert law is based, cannot be simply applied to these data. The spatial variation in the extinction coefficient is due primarily to dissimilarities in orientation between upper and lower leaves, and in their positions in relation to both the sun and the sensors. Lower in the canopy, leaves are more or less vertical, whereas the upper leaves tend to be horizontal, except under water stress. At 40–80 per cent of crop height, the attenuation of energy between two sensors within the crop is chiefly due to stems and petioles; however, in the calculation, it is attributed to the large amount of leaf located in the peripheral zone of the canopy.

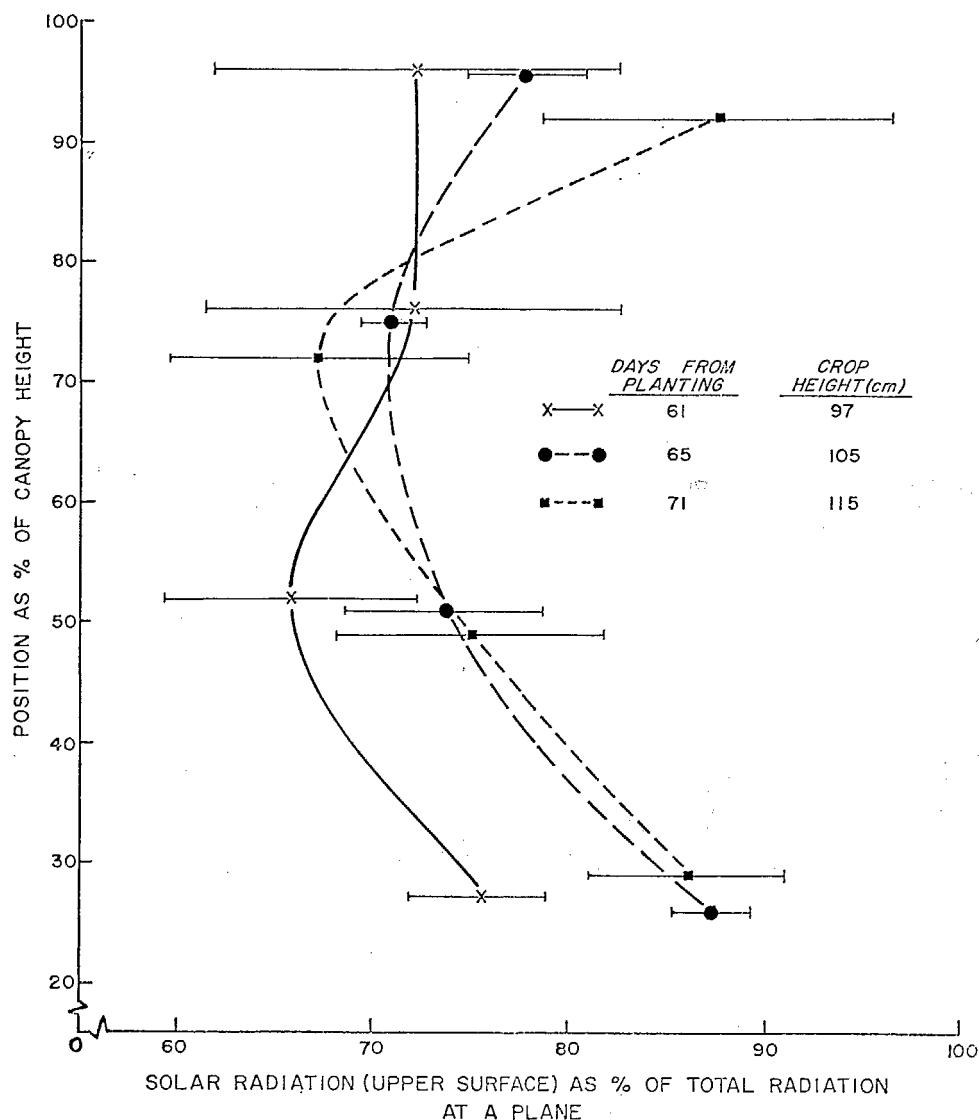


FIG. 3. Relationship between solar radiation received on the upper surface of a plane as a percentage of the total energy at the plane and relative location in the canopy obtained at three times during the season. Mean positive and negative standard deviation shown.

In an analysis of a model canopy composed of leaves with a constant angle of inclination, randomly distributed and with no preferred orientation, Anderson (1966) showed that, unless the leaves are horizontal, the value of k varies with changing sun angle. Since mean values of k were calculated from a series of measurements taken during a full day, sun angle effects were averaged and are confounded in the value of k . Thus, any change in k with position in the canopy may be associated with concomitant change in leaf position and inclination; Anderson (1966) has shown that the canopy

extinction coefficient is influenced by change in leaf inclination.

It is, therefore, seen that the Bouguer-Lambert law does not fit our results. Several models that have been proposed in recent years (Loomis and Williams, 1969) for the relationship between leaf, light intensity and crop photosynthesis assume a canopy of leaves that are randomly distributed for any particular layer in the crop. These models cannot be applied to the soybean row-crop. A general model is required, accounting for variation in canopy geometry in three dimensions. In

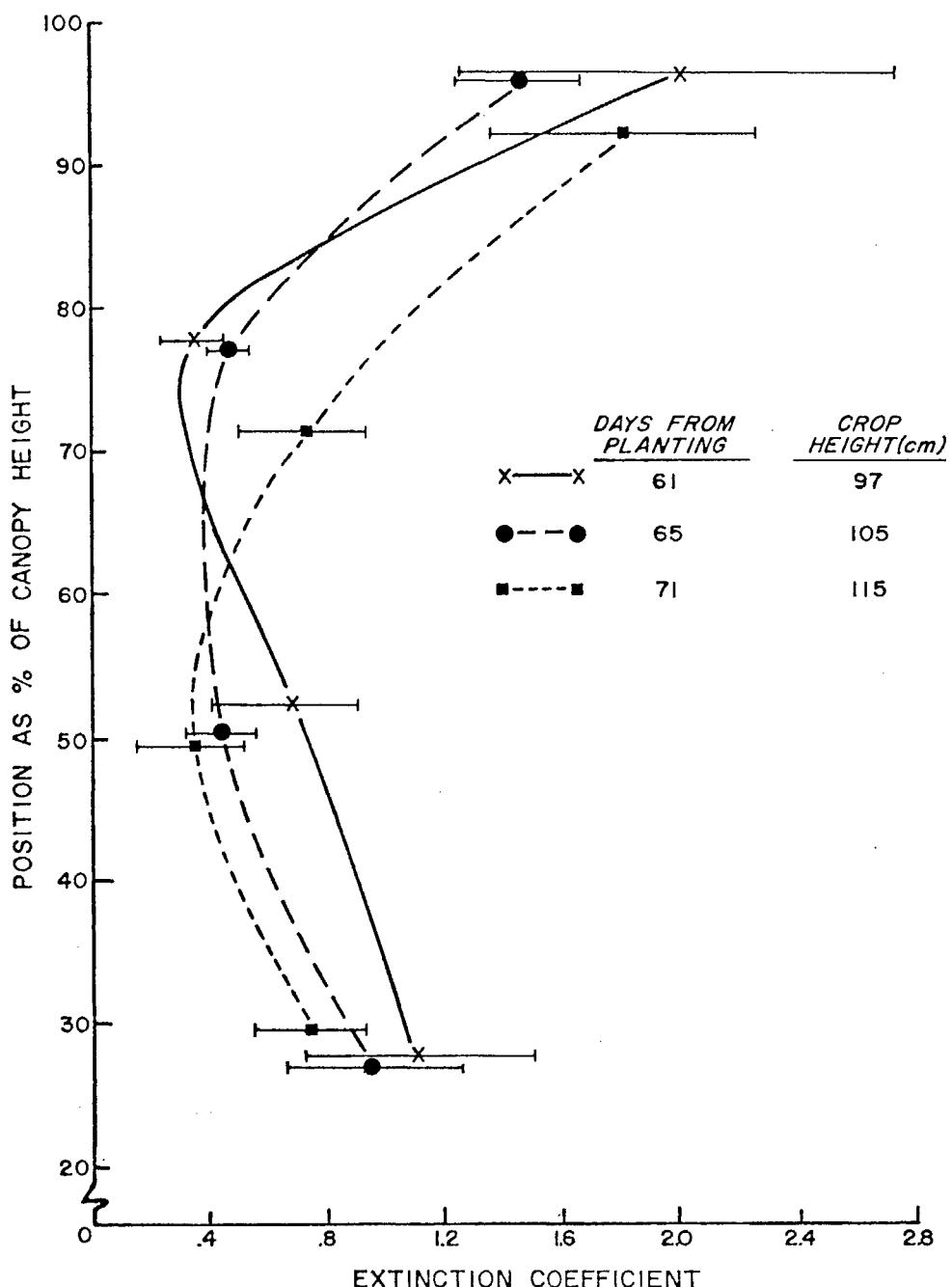


FIG. 4. Relationship between extinction coefficient of solar radiation and relative location in the canopy obtained at three times during the season. Mean positive and negative standard deviation shown.

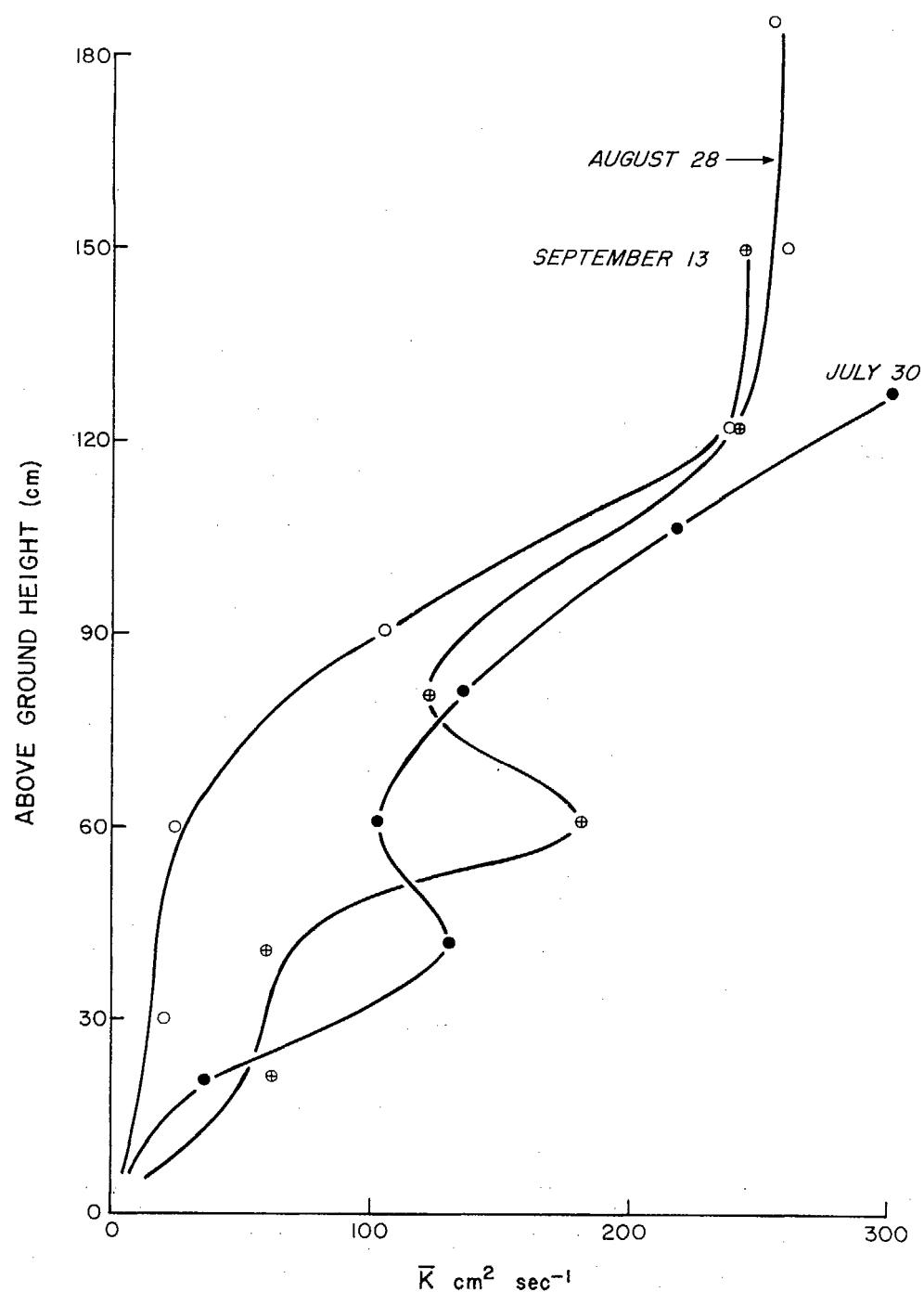


FIG. 5. Profiles of \bar{K} , the exchange coefficient in soybeans.

the case of a soybean crop, measurement of the position, size, shape, inclination and orientation of each leaflet for a length of row, together with measurement of direct and diffuse radiation above the crop, would enable the energy flux density at each leaflet to be calculated, provided the leaf reflectance and transmission properties were known.

MASS TRANSFER

Transfer of water vapour can be regarded as an energy exchange phenomenon, but both evapotranspiration and photosynthesis are coupled mass and energy exchange phenomena. Moreover, the end measure required is a rate of mass transfer, the mass of carbon dioxide taken up or the mass of water lost per unit time. For these reasons and because of present limitations of meteorological measures of velocity and momentum transfer to predict mass transfer, it was proposed to examine the use of controlled mass transfer phenomena in the field to predict mass transfer to and from a crop.

Roberts (1923) provides several solutions to point source problems, including examples where the properties of the medium are anisotropic. In the simple case, the isotropic medium, for combined convection and "diffusion",

$$\frac{\partial C}{\partial t} = - \left(u \frac{\partial C}{\partial x} + v \frac{\partial C}{\partial y} + w \frac{\partial C}{\partial z} \right) + \bar{K} \nabla^2 C$$

where C is the concentration of material in the medium; u , v and w are the component velocities in the x , y and z directions and \bar{K} , the exchange coefficient or eddy diffusivity, which is assumed to exhibit neither velocity nor spatial variation.

For a point source of strength $Q \text{ g sec}^{-1}$ the concentration distribution is given by

$$C(r, \theta) = \frac{Q}{4 \pi \bar{K} r} \exp \left(-\frac{ur}{2\bar{K}} (1 - \cos \theta) \right)$$

where u is the time-averaged velocity along the x (horizontal axis), and v and w , the time-averaged velocities along the transverse (horizontal) and vertical axes respectively, are zero. Considering only the horizontal xy plane at $z = 0$, then θ is the angle between the x axis and the radius joining the point (r, θ) and the origin.

The major criticism of the Fickian approach to dispersion of artificial sources in the atmosphere has centred around the observed dependence of \bar{K} on distance from the source. This finding is not surprising when estimates of \bar{K} are based on concentration distributions over length scales where, in fact, K (or the tensor (\bar{K})) is varying significantly. In addition, methods of analysis of concentration data have required a measure of u , a time-averaged wind velocity which itself can be a function of the period of averaging. The

method followed was selected for two reasons: firstly, by sampling very close to the source and in the same horizontal plane, effects due to spatial variation in u and \bar{K} would be minimized; secondly, by sampling at two radial distances from the source, either some account of the components of \bar{K} might be obtained or the use of ratio or difference methods of data treatment might assist in analysis by obviating the need for values of u in the computation. Propane gas was used as a controlled source and by measuring concentrations only several centimetres from the source, estimates of \bar{K} were obtained.

In Figure 5 (Millington and Peters, 1969) the profiles of \bar{K} obtained on three occasions are shown. Each estimate of \bar{K} is the mean of four to six values. Analysis of variance of two days' data showed no effect of time on the estimates of \bar{K} at each height and the least significant difference between heights on 28 August was $29 \text{ cm}^2 \text{ sec}^{-1}$ and for 13 September was $30 \text{ cm}^2 \text{ sec}^{-1}$. No analysis was made of the 30 July data, which are assumed to have variance comparable with that from the other two days.

The profile of 30 July was obtained when the bean rows were quite distinct and the canopy had not closed over. The profile on 28 August was obtained in the crop at maximum growth with a closed canopy. The 13 September profile was obtained after leaf fall. The striking feature of the results is the bulge in the first and last profiles at 40 and 60 cm respectively. This bulge occurs beneath the main crown of leaves in the canopy of the young crop and beneath the crown of dried petioles and pods in the senescent crop. It is clear that the "alleyway" between the rows provides a path for considerable air movement beneath the bulk of the foliage or petioles and fruit. These two profiles contrast sharply with that obtained in the closed canopy at maximum leaf area. Here there is no evidence of appreciable air movement deep in the canopy comparable with that in the open stands.

In a second trial, two source-sample units were sited within rows and two between rows. No significant effect of time was found, but there were significant differences between sites and between duplicates. The coefficient of variability of estimates of \bar{K} based on eight observations was 3.5 per cent of the grand mean ($\bar{K}_{\text{Average}} = 60 \text{ cm}^2 \text{ sec}^{-1}$). The use of the tracer gas technique permitted evaluation of mass transfer coefficients within a soybean crop. In open row situations, the transfer coefficient did not decline in a monotonic manner with depth below the upper surface of the crop, but exhibited a local maximum and minimum. This spatial pattern of variation of the transfer coefficient coupled with the high variance of the mean wind velocity within the canopy is illustrative of the problems of source, sink and flux estimations within the canopy.

These first studies were performed with point sources and the average concentrations at radial distances of 1.5 to 30 cm from the source were measured on gas

TABLE I. The comparison of the mode to the mean velocity with the standard deviation and turbulent intensity of each; also, the skewness and kurtosis with the 5 per cent significance level of each as a function of height (S = significant; NS = not significant.)

Height (cm)	Mode		Mean		Skewness	Significance level	Kurtosis	Significance level
	Velocity (cm sec ⁻¹)	Turbulent intensity	Velocity (cm sec ⁻¹)	Turbulent intensity				
420	470 ± 123	0.26	402 ± 102	0.26	0.12	NS	2.50	S
340	375 ± 94	0.25	353 ± 91	0.26	0.28	NS	3.04	S
260	260 ± 103	0.40	306 ± 92	0.30	0.30	NS	3.32	S
180	221 ± 101	0.46	257 ± 95	0.37	0.16	NS	2.25	S
140	135 ± 132	0.98	215 ± 105	0.49	0.32	NS	2.20	S
120	60 ± 65	1.08	94 ± 54	0.58	1.49	S	5.26	S
90	61 ± 30	0.50	68 ± 30	0.44	1.87	S	7.13	S
75	51 ± 14	0.28	45 ± 13	0.29	-0.01	NS	3.26	S
60	48 ± 16	0.34	41 ± 14	0.35	0.58	S	4.59	S
45	49 ± 15	0.31	40 ± 12	0.31	-0.09	NS	2.45	S
30	40 ± 16	0.40	32 ± 14	0.44	0.01	NS	2.14	S
15	41 ± 16	0.39	36 ± 15	0.42	-0.08	NS	2.44	S

samples from aspirated rings or sweeping-point collectors. The data fitted the relation

$$Q \propto r^2 \bar{u} \bar{C} + r^2 \bar{K} \frac{d\bar{C}}{dr}$$

and regression analysis showed that 99 per cent of the variance of Q/r^2 could be accounted for. However, the estimate of \bar{u} obtained in the analysis was about 10–50 per cent of \bar{u} measured by heated thermocouple anemometry.

These data and the regression analysis suggest that the mean concentration sensed in the $x-y$ plane at $z=0$ is that of a waving plume and that the period of the fluctuations in the orientation of the plume axis are very short compared with the 30 min time averaging period.

The term containing \bar{u} is small within the crop and the earlier analysis of data based on

$$Q = 4\pi r^2 \bar{K} \frac{d\bar{C}}{dr}$$

remains essentially valid.

Further studies have been made of concentration distributions about "infinite" vertical and horizontal line sources concurrently with point sources. The sources and collectors were mounted on wind vanes above the crop and gas concentrations were measured along the downwind axis. From these studies it was found that the crosswind and vertical mass exchange coefficients were similar in magnitude. To derive the downwind coefficient a measure of \bar{u} is necessary and for equality of the K_x , K_y and K_z components, that is the downwind, crosswind and vertical exchange coefficients, the required value of \bar{u} was about 25 per cent of that observed with heated thermocouple anemometers.

Within the closed canopy it is probable that the component exchange coefficients are of similar magnitude and that derivation of source terms, layer by layer, in a linear flow model can be undertaken. However, in

the crop with distinct, separate rows there is variation in \bar{K} in two dimensions and it remains to be shown that the component coefficients are, in fact, similar in magnitude.

MOMENTUM

The erratic unstable nature of the turbulent boundary layer in the lower atmosphere is highly influenced by the roughness of the row crop. This complication distorts the frequency distribution (Perrier, Luxmoore, Peters, Millington, 1970; Uchijima and Wright, 1964) of the velocity, requiring an intensive examination of temporal and spatial variations of wind structure. The difficulty of selecting specific time and space increments for turbulent analysis has been noted (Hinze, 1959; Perrier, Millington, Peters, Luxmoore, 1970; Sutton, 1953) but, in general, the evaluation of phenomenological parameters of wind are based upon the assumption of a *normal* frequency distribution. The problem cannot be resolved for all conditions alike because of changes in the turbulent structure of the boundary layer caused by roughness effects, variable synoptic wind velocity, gustiness, interaction with buoyancy forces, etc. Another difficulty arises as to the type, shape and electrical characteristics of the wind sensor, as well as the characteristics of the read-out device of a particular anemometer system, i.e. each system inherently observes a particular turbulent structure dependent on its peculiar sensitivity and configuration.

Horizontal wind was measured within and above the crop surface of a 0.8 hectare soybean field. The soybeans were 110 cm tall, with a LAI of 4. The soybeans were planted in north-south rows 76.2 cm apart, at a density of 121,410 plants per hectare.

The vertical profiles of horizontal wind speed were measured with heated-thermocouple anemometers at

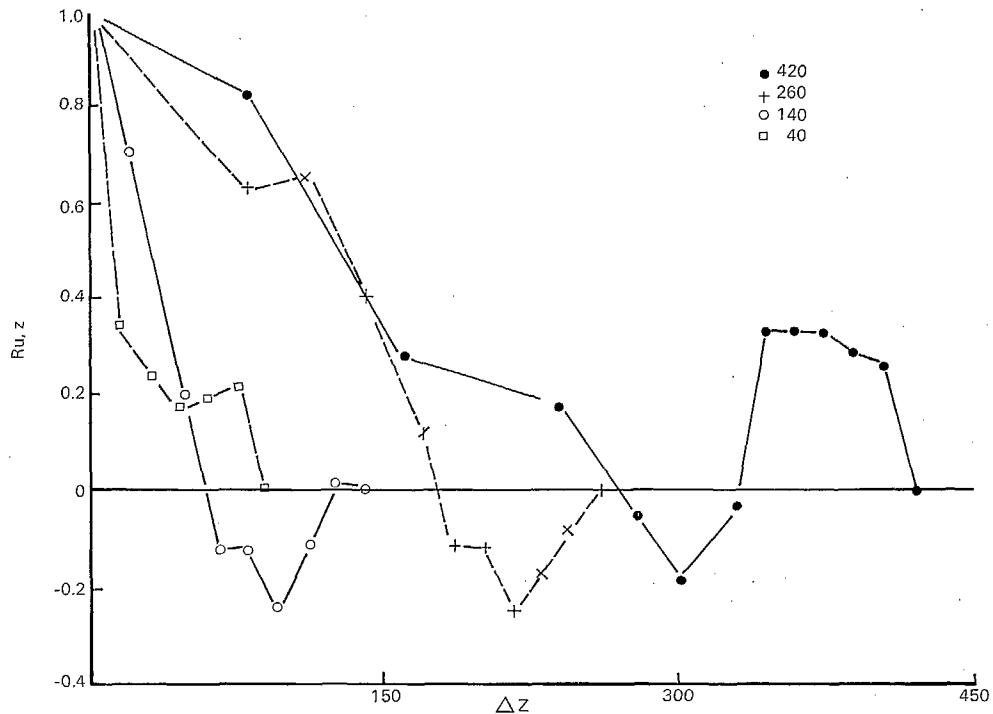


FIG. 6. Spatial (Eulerian) correlation coefficients $R_{u,z}$ of the velocity fluctuations in the turbulent boundary layer for four heights above the soybean canopy.

heights of 15, 30, 45, 60, 75, 90, 120, 140, 180, 260, 340 and 420 cm above ground on two single-poled towers in close proximity between crop rows. The anemometers were calibrated in a small subsonic wind tunnel which had a 4 : 1 nozzle reduction and a test chamber volume of $11 \times 21 \times 51 \text{ cm}^3$. The turbulent intensity of the mean velocity within the test section (coefficient of variation) was 1.50 per cent at a velocity of 400 cm sec^{-1} when measured by a hotwire anemometer system. The reference velocities for calibration procedures were measured by a pitot tube in connexion with a slanting manometer, as well as the hotwire anemometer system. The heated-thermocouple anemometers were all zeroed at 10.00 millivolts and a data acquisition system was used as the read-out device. The anemometer calibrations were functionally related to the following expressions, within the given limits:

$$U = \exp(A_1 + A_2 \sqrt{v}) \quad 89.4 \leq U \leq 894.1$$

$$U = B_1 + B_2 \ln v \quad 0 < U < 89.4$$

where U is the wind velocity in cm sec^{-1} , v is the voltage output and A and B are the appropriate constants for each anemometer.

The heated-thermocouple anemometers sense all air movement in the horizontal plane, whereas velocity is

normally a vector term whose direction must be specified. To meet the requirements for analysing the logarithmic profile equation of the above canopy data, it was assumed that the value obtained from the heated-thermocouple anemometers represented only a one-dimensional horizontal wind. Further, it was assumed that the synoptic wind direction specified the direction of the wind data above the crop canopy which was from west to east, i.e. perpendicular to the row crop.

A comparison of the experimentally obtained wind structural parameters is shown in Table 1 as a function of the above-ground height. None of the mean velocities at each specified time increment tested exhibited a normal distribution; all showed varying degrees of skewness and kurtosis as demonstrated by Snedecor's (1950) T -test.

For the case presented in Table 1, the magnitude of the standard deviation tends to increase with height, whereas the turbulent intensity maximizes near the height of the crop (110 cm) and remains somewhat stable above and below this region. In general, the turbulent intensity is lower above the plant canopy than below (Perrier *et al.* 1970 *a* and *b*; Uchijima and Wright, 1964) but various patterns of the turbulent intensity with height are achieved by the magnitude of the synoptic wind, shape and elasticity of the crop

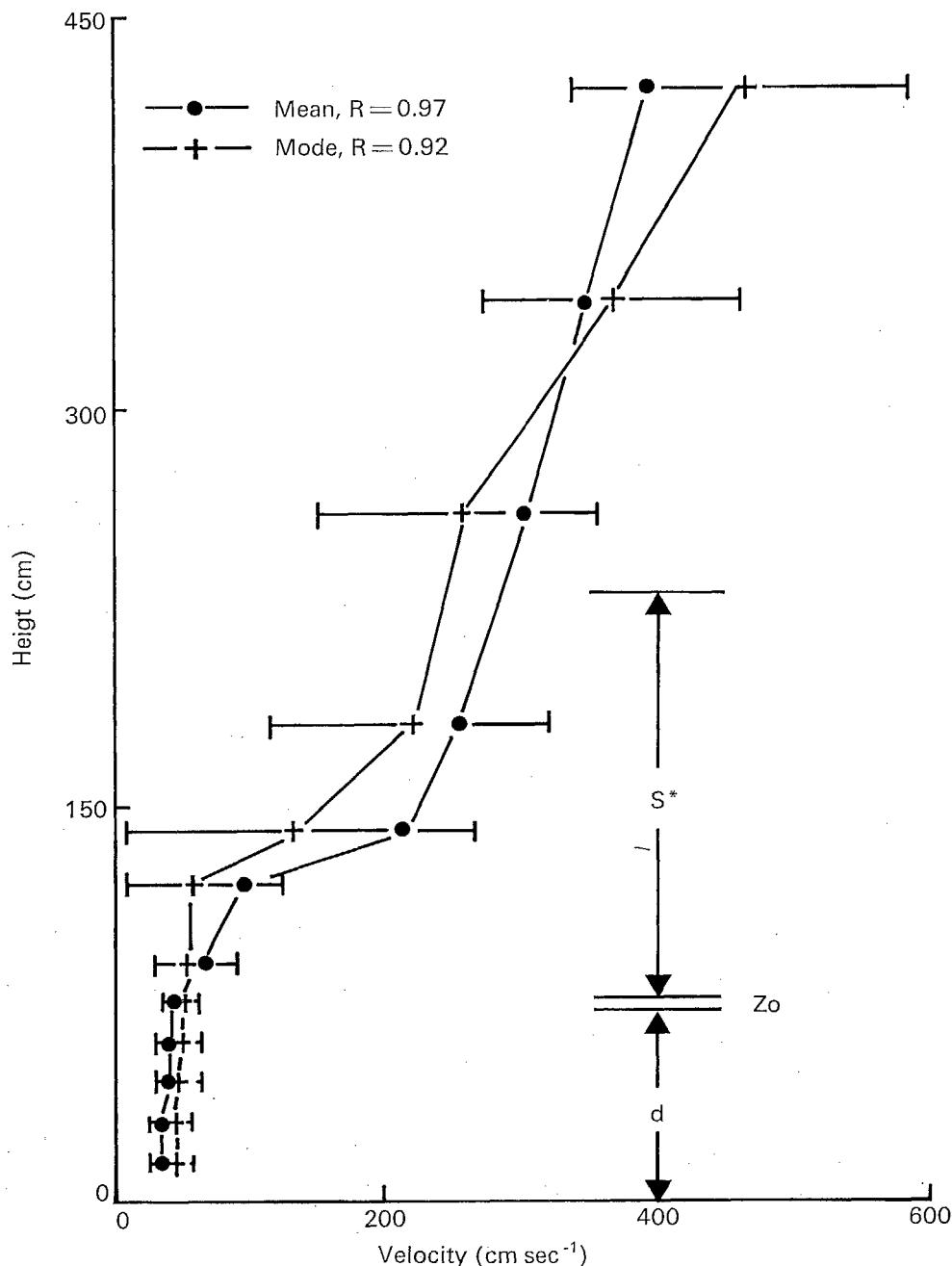


FIG. 7. Wind movement profile for mean and mode with the standard deviation about the mode, where δ^* is the boundary layer displacement height, Z_o is the roughness length and d is the displacement heights in and above the plant air layer for soybean canopies (log-law correlation coefficients are added).

surface, as well as external factors such as gustiness; thus only a general trend exists for all increments of time. These high values of turbulent intensity clearly indicate the change in scale of turbulence from above to within the soybean canopy.

A quantitative relationship of the temporal structure of turbulence can be obtained by observing the velocity fluctuations at a given time period, but at different locations. This relation is termed the Eulerian correlation coefficient $R_{u,z}$ as described by Schlichting (1968) and is shown in Figure 6 as a function of the change in height at four given heights. When the correlation coefficient becomes negative, the velocity at that difference in height is changing dipolar to the wind at the fixed elevation (either 420, 260, 140 or 90 cm). The soybean canopy was at 110 cm above the soil surface and the correlation coefficients referenced from the 90 cm height did not become negative (although the values are quite low), which suggests that at this instance of time and space the anemometers were measuring within the same bundle of turbulent air. This does not imply that these data are static, on the contrary, Perrier, Luxmoore, Peters and Millington (1970) have shown that each time increment gives rise to a separate set of data which contains similar sets of structural characteristics. These data give rise to the concept of at least a two-dimensional cavity type flow field existing within the soybean canopy.

As the heated-thermocouple anemometers are not measuring a vector directed wind, but a random movement in the horizontal plane (Perrier, Millington, Peters, Luxmoore, 1970; Perrier, Luxmoore, Peters, Millington, 1970), they do not meet the requirements for analysing the phenomenological turbulence models based on the one-dimensional analysis employing Prandtl's mixing length hypothesis and von Karman's similarity hypothesis. However, the assumptions are made that the wind structure within the boundary layer above the crop canopy is homogenous and, further, that all synoptic flow is considered perpendicular to the direction of the crop rows. Thus, as the concept of a non-normal frequency distribution of velocity exists, Figure 7 exemplifies a "typical" wind profile relation for computation of the log-law relation based on the above assumptions.

This analysis demonstrates that velocity distributions within and above a soybean canopy show varying degrees of skewness and kurtosis and that analysis employing mean velocities is in question unless the frequency distribution is normal. The form of the

relationship of the Eulerian correlation coefficient, as well as the magnitude of the turbulent intensity, demonstrates that air movement is not simply related to the wind above the canopy, thus accentuating the effects of two-dimensional cavity flow.

CONCLUSION

When plant-environment interaction is to be assessed at some height above an extensive plant community, methods already evolved can provide the framework for study. Within the crop canopy, however, even when its structure is more or less isotropic, the process of momentum dissipation is more complex than the customary models can account for. This has been shown with our studies on both mass exchange coefficients and momentum transfer.

In row-sown crops and in spaced plant communities, for example orchards, the relations between crop and environment are even more complex.

It is at present proposed to continue with the kinds of studies outlined here. Our objectives are firstly to account for the radiation environment within soybeans, and secondly, to assess the meteorological and crop characteristics contributing to variation in mass and momentum transfer within the crop. The geometry of the canopy and its optical properties will provide a basis for the first. However, sensible heat flux and latent heat flux and their relationship to gradients in net radiation depend not only on the physiological status and geometry of the plants, but on momentum transfer within the canopy. Exchange of carbon dioxide exhibits a similar dependence on crop and environmental characteristics.

To model the crop performance in relation to the macro-environment above requires knowledge of the subsystems of the whole and, moreover, finding the means whereby the subsystems are interlocked. Some parts of the whole offer fewer difficulties. The profiles or surfaces of visible radiation within the crop can be modelled fairly readily. However, analysis of the coupled energy-mass transfer processes, so markedly dependent on air movement within the crop, can only be taken further by a fuller understanding of the process of momentum dissipation. The very high intensity of turbulence and the apparently almost omni-directional nature of the air movement in the crop pose problems outside the scope of the usual treatments of fluid dynamics.

Résumé

Le microclimat des cultures en rangées (R. J. Luxmoore, R. J. Millington et D. B. Peters)

Étude de quelques aspects des problèmes que posent les rapports plante-milieu dans des cultures semées en rangées. La répartition du rayonnement à l'intérieur de la culture montre l'importance de l'anisotropie de la

répartition des feuilles dans les rangées. Les coefficients de transfert de masse varient horizontalement et avec la hauteur, et la diminution avec la hauteur n'est pas monotone. L'intensité turbulente dans le volume de la culture est élevée et le processus de dissipation de la quantité de mouvement n'est pas expliqué par les modèles micrométéorologiques habituels.

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A comparison of simple climatological parameters for estimating phasic development of wheat in Western Australia

E. A. Fitzpatrick

Department of Agronomy, Institute of Agriculture,
University of Western Australia, Nedlands (Australia)

INTRODUCTION

It is well established that many annual crops have varying sensitivity to temperature and moisture conditions throughout their life span. Therefore, to achieve an agronomically useful interpretation of climatic data from a succession of years, it is often necessary to delimit, in retrospect, specific phases of crop development without the aid of direct phenological information.

If varieties of "spring" wheat are planted in southern and eastern Australia at various times over the late autumn to mid-winter period, substantial differences in the pattern of phasic development occur. Such differences in developmental rate are not effectively expressed simply as a function of planting times because recognition is not given to between-season differences in prevailing levels of temperature, radiation and day length during the period of crop development. Reliable estimates of year to year variation in phasic development are needed if changes in available soil water are to be simulated realistically from evaporation and rainfall data (Fitzpatrick and Nix, 1969). Also, it has been shown that an improved assessment of the effects of water stress on grain yield can be obtained through explicit reference to conditions of estimated available soil water and potential evaporation at, and immediately following, time of flowering (Nix and Fitzpatrick, 1969). These findings are closely in accord with results of much field and laboratory experimental work to assess the effect of water stress on yields of cereal crops (Salter and Goode, 1967).

To meet a need for estimating the time for wheat to reach flowering stage, research was undertaken within the Agronomy Department of the University of Western Australia to compare the effectiveness of a number of alternative parameters that might be used to delimit this important variable. With a view to the sparse climatic data available for most stations within the

wheat-producing areas of Western Australia, special attention was directed to simple parameters, involving single or combined elements.

Before assessing the limited phenological data available from within the Western Australian wheat belt, data obtained from planting of wheat at the Western Australia Institute of Agriculture field station at Shenton Park, a suburb 5 km west of Perth, were examined.

With stronger marine influences, Perth (latitude $31^{\circ} 37'$, longitude $115^{\circ} 51'$, elevation 61 m) has a lower daily and annual temperature range than most parts of the Western Australian wheat belt. Although the local environment is not truly representative in this respect, it was none the less of advantage initially to compare several possible "predictors" of the phasic development at this local site. Here phenologic data for a larger number of varieties and for a wider spread of planting dates were available, and a wider range of meteorological elements could be considered.

The purpose of this paper is to report results of this initial comparison of alternative simple parameters from climatic data for estimating phasic development of wheat grown at the Shenton Park site.

PHENOLOGICAL AND METEOROLOGICAL DATA

The unpublished phenological data used in this study were collected by Singh (1970) as a part of an experimental programme to assess variation in the development, growth and yield attributes of a range of genotypes exhibiting differential response to vernalization and photoperiod. Although plantings were made at mid-month over a complete year between May 1966 and April 1967, only those data for plantings between April and September are used in this study. Phenologic

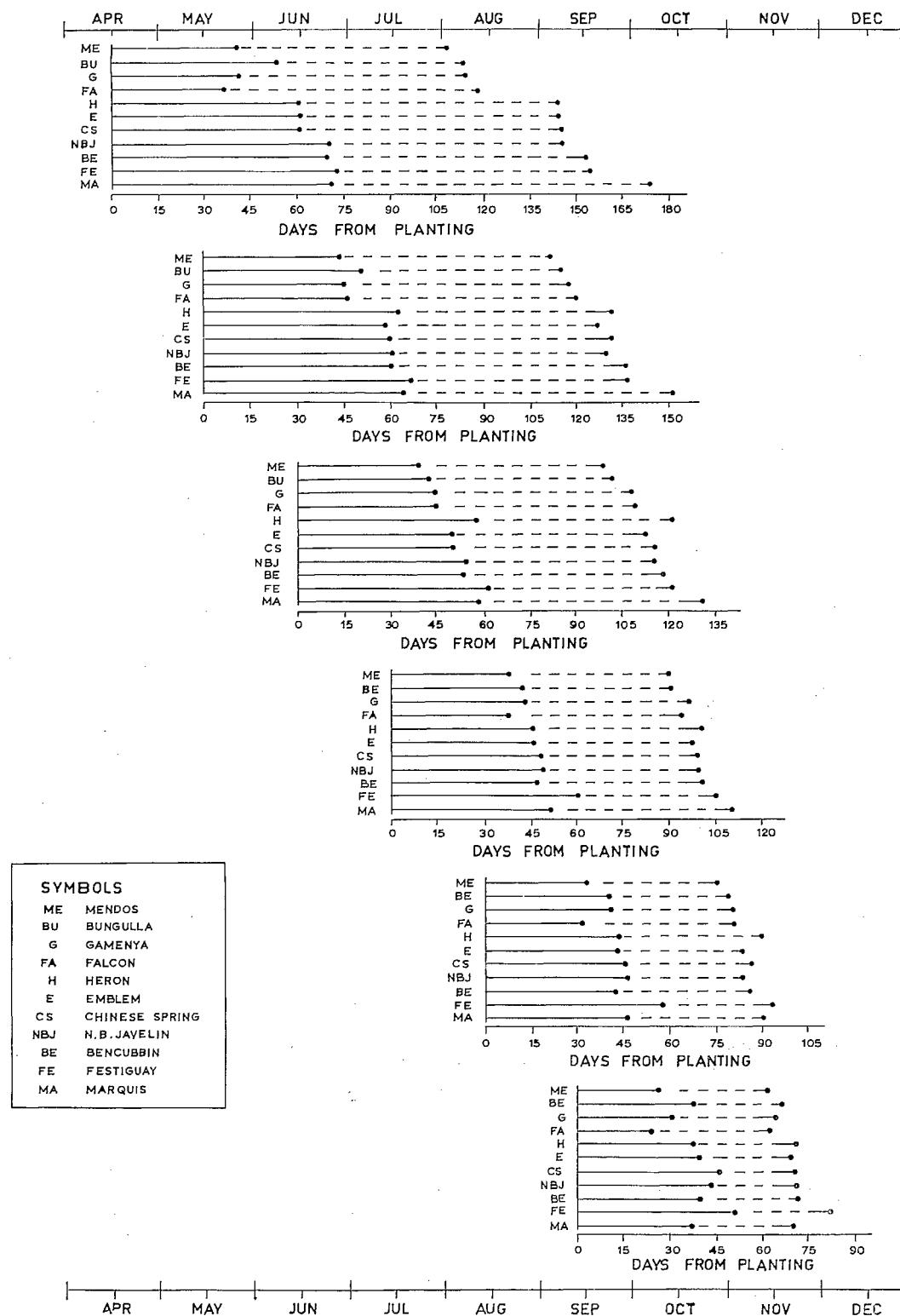


FIG. 1. Showing time span from planting to floral initiation (solid line) and to flowering (broken line) for eleven varieties of wheat planted at mid-month, April to September, at Shenton Park, Western Australia.

TABLE 1. Monthly climatic data for July and November of 1966¹

Element	July 1966	November 1966
Total rainfall	181 mm	7 mm
Total evaporation (Class A pan)	59 mm	225 mm
Mean maximum screen temperature	17.2° C	24.3° C
Extreme screen maximum temperature	21.7° C	34.8° C
Mean minimum screen temperature	9.6° C	14.8° C
Extreme screen minimum temperature	6.1° C	9.4° C
Mean dew point at 0900 hr	8.3° C	11.1° C
Mean global solar radiation	232 cal cm ⁻² day ⁻¹	633 cal cm ⁻² day ⁻¹
Mean duration of sunshine	5.3 hr	9.9 hr
Photoperiod (at mid-month)	10.23 hr	13.75 hr

1. All data are for the Bureau of Meteorology station in Perth, except that for global solar radiation, which is for Perth Airport (Guildford).

data for plantings before April and after July are not representative of normal agronomic practice within this Mediterranean environment. However, the August and September plantings were included to give an extended range of temperature, radiation, and day length conditions, to which all varieties were exposed.

Data indicating the time span from planting to flowering were available for all varieties. Date of flowering was assessed as the *average* date of flowering on the *primary* tiller.

Over the experimental period, supplemental irrigation was applied, as needed, to prevent water stress. Timing of these applications ranged from daily during the dry summer months, to a complete discontinuance during the rainy winter period.

Figure 1 shows graphically the time span to floral initiation and to flowering for mid-month plantings of eleven varieties between April and September. It is clearly seen that, although individual varieties display some distinctive patterns in the time to initiation and to flowering, there is a general shortening of these spans for eleven varieties with progressively later plantings. Also, it appears that separate varieties assume a fairly consistent sequential position in their phasic development under the prevailing environmental conditions within the time limits of the data used here.

Table 1 gives selected monthly climatic data for July and November 1966 and illustrates the range of environmental conditions over the period that these data were collected.

For this analysis and subsequent discussion, it is convenient to group the eleven varieties into *rapid*,

intermediate, and *slow* developing classes according to the time from planting to flowering for the April 1967 planting. This grouping is given in Table 2, with the observed time span to the two stages for April and September plantings.

Daily maximum and minimum screen temperatures were observed at the experimental site, as well as rainfall. Other temperature data, including observations from wet and dry bulb thermometers in a Stevenson screen and soil temperature under a bare surface, were available from the Regional Office of the Bureau of Meteorology in the City of Perth. Daily receipts of global solar radiation, as measured by a Robitzsch bimetallic actinograph, were available from the Bureau of Meteorology station at Perth Airport (Guildford), approximately 16 km east of the experimental site.

METHODS

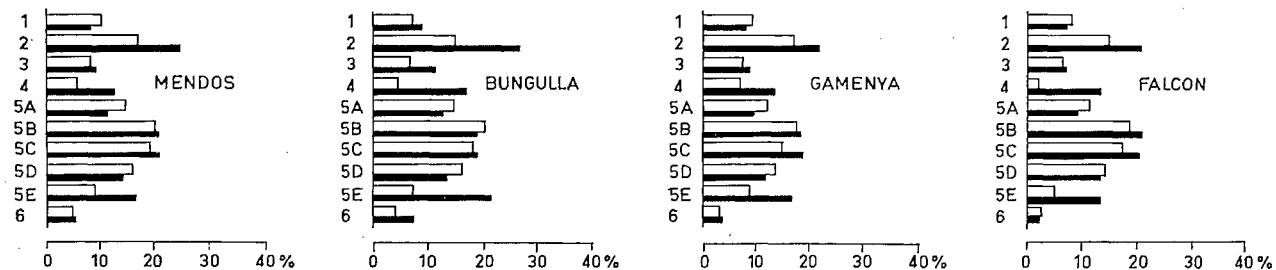
Temperature, radiation and photoperiod are all positively correlated within the phenologically defined periods from successive planting dates. It is not the purpose of this study to explore the specific responses of particular genotypes to one or the other of these elements.

As already noted, the varieties used here have varying degrees of response to vernalization, thus further complicating the specific pattern of development of individual genotypes from a causal viewpoint. The aim here is rather to assess the overall "predictive" value of simple parameters which, by their generalized nature, inevitably reflect something of several significant causal factors.

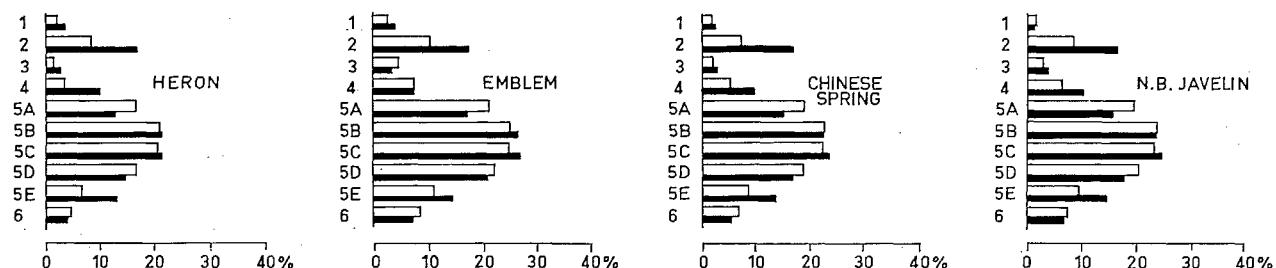
TABLE 2. Classification of 11 wheat varieties according to time span from April planting to flowering, and showing time in days from planting to initiation and to flowering for April and September plantings

Class and variety	Planting to initiation		Planting to flowering	
	April	September	April	September
<i>Rapid developing</i>				
Mendos	40	26	110	61
Bungulla	53	37	113	66
Gamenya	40	29	117	64
Falcon	36	24	118	62
<i>Intermediate developing</i>				
Heron	61	37	144	70
Emblem	61	38	144	68
Chinese Spring	61	45	145	70
N. B. Javelin	70	42	145	70
<i>Slow developing</i>				
Bencubbin	68	39	153	71
Festiguay	72	50	154	81
Marquis	70	37	174	70

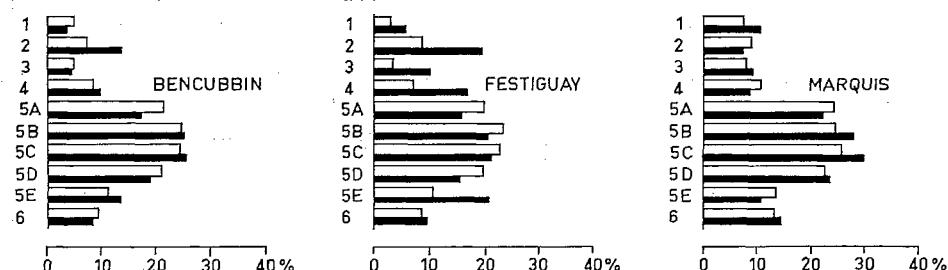
RAPID DEVELOPING VARIETIES



INTERMEDIATE DEVELOPING VARIETIES



SLOW DEVELOPING VARIETIES



SYMBOLS	
1	GLOBAL SOLAR RADIATION
2	NET RADIATION
3	ESTIMATED EVAPORATION
4	PAN EVAPORATION
5A	MAX. SOIL TEMPERATURE
5B	MAX. AIR TEMPERATURE
5C	MEAN AIR TEMPERATURE
5D	PHOTOTHERMAL UNITS
5E	ENERGY DEGREE UNITS
6	DEVELOPMENTAL UNITS

FIG. 2. Comparison of coefficients of variation of ten climatological parameters for the interval, planting to flowering, for eleven varieties of wheat planted monthly between April and September at Shenton Park, Western Australia. Open bars show coefficients determined for April-July plantings; solid bars for April-September plantings.

The parameters used are given below:

Item	Observed or derived parameter
1	Global solar radiation
2	Net radiation
3	Estimated evaporation (Australian sunken tank)
4	Pan evaporation (U.S. Class A)
5A	Maximum soil temperature at 25 mm minus 10°C
5B	Maximum screen temperature minus 10°C
5C	Mean screen temperature minus 4.5°C
5D	Photothermal unit
5E	Energy degree unit
6	Developmental unit.

Data for Item 2, the net radiation, were not available as observations, but were estimated from item 1 using a semiempirical relationship given by Penman (1948). It could not be ascertained whether the albedo of 0.24 assumed here, or the values of empirical constants as used by Penman, were the most appropriate for the environmental conditions at the experimental site (Fitzpatrick and Stern, 1965).

Item 3 is an estimate of evaporation based upon an empirical relationship found between observed evaporation from the former Australian standard sunken tank evaporimeter and a vapour pressure deficit term formulated from maximum temperature, dew point and photoperiod (Fitzpatrick, 1963). The independent variable in this case closely resembles the saturation

deficit and is obtained from maximum screen temperature weighted for day length, and dew point.

Observed Class A pan evaporation was included on the expectation that this element would be highly correlated with the prevailing temperature and radiation levels over any given phase of development.

Items 5A to 5E are all variants of a method long in use and variously described as the "temperature summation", "heat unit" or "reminder index" system, a critical review of which has been given by Wang (1967). These are wholly, or partially, determined from the summation of daily temperature rises above some base temperature, appropriate to the species. Following common practice, a base of 4.5° C, considered generally appropriate for temperate species, was used for determining Item 5C. Items 5A and 5B are similar to 5C, but using the maximum temperature 25 mm below a bare soil surface, and the maximum temperature at screen height, respectively, instead of mean screen temperature. A base of 10° C was used with these maximum temperatures. A number of workers in the U.S.S.R. (Molga, 1962) have used this base with maximum temperature.

Item 5D, the photothermal unit, is the parameter used by Nuttonson (1948). This value is determined as the product of photoperiod and the number of degrees that mean temperature rises above the threshold appropriate to the species, that is, as the product of photoperiod and item 5C as described above.

Item 5E, the energy degree unit, a parameter described by Wang (1967), is conceptually closely related to Nuttonson's photothermal unit. In this case the multiplier used to adjust degree-days (item 5C) is the global solar radiation rather than photoperiod. As used here, it is the product of items 1 and 5C.

Within humid and marine climates minimum temperature and dew point are generally highly correlated (Gentilli, 1955). In consideration of plant development, the minimum temperature rather than dew point would be expected to be the most directly relevant variable. Item 6 was thus introduced as a parameter identical with the estimated evaporation (item 3) except that minimum temperature (t_{min}) has been substituted for dew point (d) in calculating the vapour pressure deficit term ($e_0 - e_{min}$ instead of $e_0 - e_d$). This parameter gives expression to maximum temperature (t_{max}), photoperiod (N), and minimum temperature (t_{min}) since $\theta = f(t_{max}, N)$. The variable, $e_0 - e_{min}$, closely resembles $e_{max} - e_{min}$ as used by Halstead (1951) as a practical basis for estimating potential evapotranspiration.

The means and coefficients of variation were determined separately for plantings within two overlapping periods: (a) April to July inclusive, and (b) April to September inclusive. As previously noted, the April-July limits are more truly representative and can be considered as the maximum range of planting dates that could, in practice, be used within the wheat belt with existing cultivars.

RESULTS AND DISCUSSION

COMPARISON OF COEFFICIENTS OF VARIATION

Planting to flowering interval

Figure 2 shows the comparison of coefficients of variation for the selected parameters based on their summation from time of planting to flowering. Large differences in the coefficients of variation for various parameters are evident. A high degree of consistency in the relative levels of the coefficients is evident over all varieties. It is of interest that (a) day degrees calculated from the maximum soil temperature at 25 mm depth at the Perth station give, without exception, lower coefficients than their counterpart based on the screen maximum temperature at the experimental site, and (b) coefficients for observed pan evaporation are markedly reduced by comparison with other parameters when considering the longer time span, planting to flowering.

The coefficients of variation for global solar radiation, estimated evaporation and developmental units are, in almost all cases, less than 10 per cent for both the April-July and April-September plantings. The coefficient of variation for global solar radiation is for all varieties, substantially lower than that for estimated net radiation, and is almost without exception lower than that for energy degree units.

The results in Figure 2 suggest that the developmental rate of wheat in this environment must be more closely in phase with the receipt of global solar radiation and closely related elements (e.g. maximum soil temperature and pan evaporation) than with the mean ambient air temperature as determined at screen height.

Comparison of errors

Figure 2 provides a basis for assessing the quasi-constancy of various parameters, but does not show either the magnitude of errors that result from their summation or the extent to which errors may be seasonally biased (non-random) with successive plantings.

Table 3 shows the errors in days that result from adopting the mean value of the summations for items 1, 5C, 5E, 3 and 6 over the planting to flowering period. Large biased errors occur with parameters that are wholly or in part derived from temperature summation. For energy degree units, the errors in estimated days to flowering are generally higher than those obtained solely from global solar radiation summation between planting and flowering. By inference from Figure 2, it can safely be accepted that errors in estimated flowering date using photothermal units would be generally intermediate between those for items 3C and 3E, as shown in Table 3.

Table 4 shows that the simple summation of mean daily temperatures above 4.5° C gives an error larger

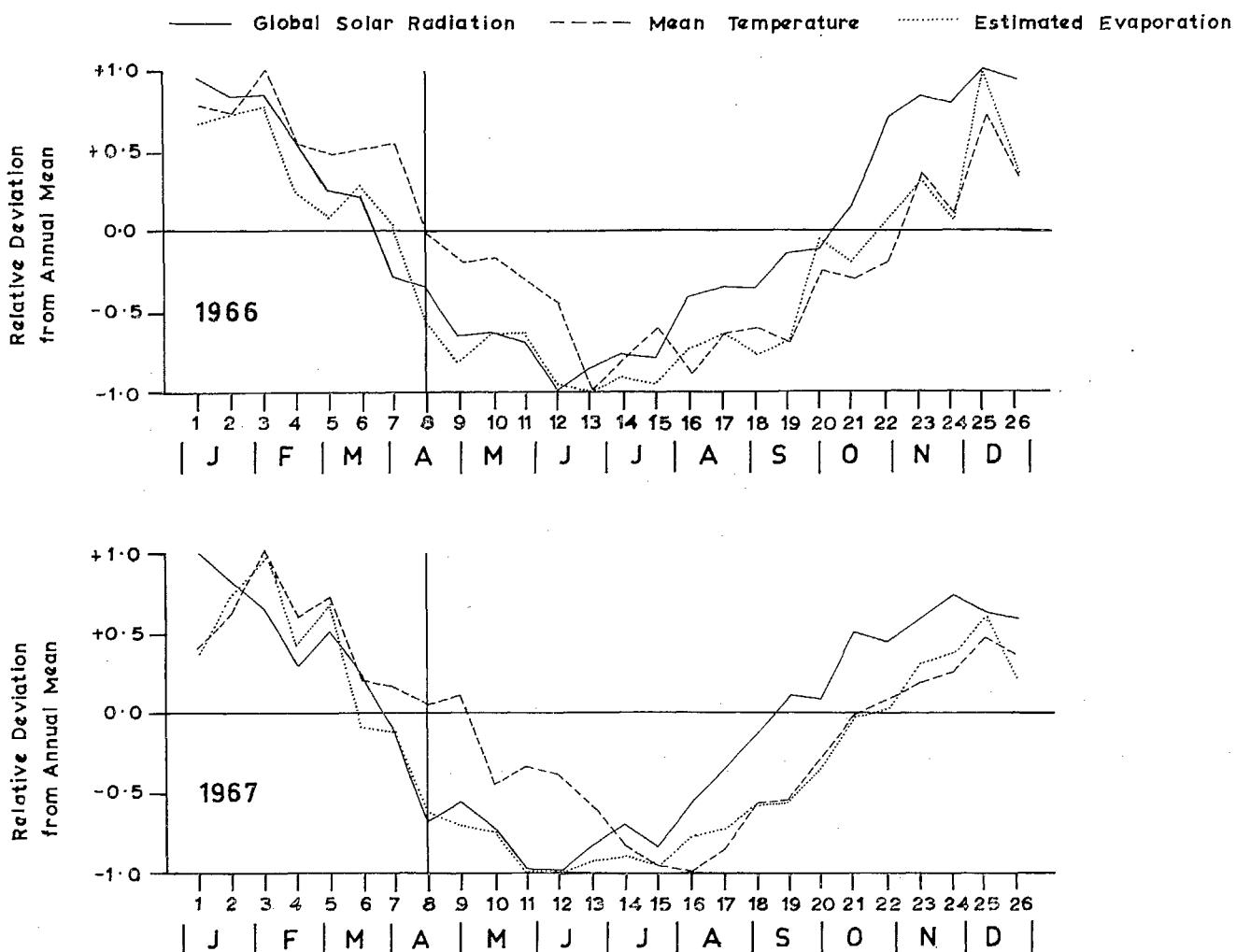


FIG. 3. Seasonal trends of global solar radiation, mean screen temperature, and estimated evaporation during 1966 and 1967 at Perth, Western Australia. All plotted values are fortnightly means scaled such that the highest, lowest, and mean of each element are represented as +1.0, -1.0 and zero, respectively.

than those obtained from an assumed constant rate of development between planting and flowering. Energy degree units gives a relative mean error substantially less than that for simple temperature summation, but for most varieties this is greater than that obtained simply by summing the global solar radiation between planting and flowering.

Using estimated evaporation to delimit time of flowering of the eleven varieties, the mean errors are between 14 and 56 per cent of the mean error obtained from an assumed constant mean time to flowering for each of the four plantings. The corresponding range of the relative error for developmental units is 19 to 38 per cent. These results for estimated evaporation and developmental units support earlier findings from

similar, but less extensive, studies of climatic aspects of phasic development of two day-neutral varieties of wheat in Queensland (Fitzpatrick and Nix, 1969), and suggest that either of these parameters may provide an empirical basis for estimating the time span to flowering over a wide range of environments within Australia.

These results, which show predictive advantages when explicit reference to daily maximum and minimum temperatures are made, are generally in agreement with findings of other workers (Lindsey and Newman, 1956; Wang and Broyson, 1956; Robertson, 1968).

Although the errors obtained using items 3 and 6 are evidently somewhat biased (Table 3), and in some cases larger than those from summation of global solar

TABLE 3. Errors in predicted intervals between planting and flowering of eleven varieties of wheat using summations of four parameters starting at mid-month plantings, April to July inclusive. All values expressed to the nearest day. Negative values indicate predicted date before observed flowering, positive values, after observed flowering

Wheat varieties	Global solar radiation				Mean daily temperature (4.5° C base)				Energy degree units (4.5° C base)				Estimated evaporation				Developmental units			
	April	May	June	July	April	May	June	July	April	May	June	July	April	May	June	July	April	May	June	July
<i>Rapid developing varieties</i>																				
Mendos	+13	+1	-3	-4	-30	-3	+14	+12	-5	+3	+8	-6	+5	-4	+6	-4	+1	-4	+5	-1
Bungulla	+10	-3	-0	-5	-30	-4	+12	+13	-5	+2	+7	-5	+4	-5	+5	-2	0	-5	+5	0
Gamerya	+12	+1	-2	-6	-29	-1	+9	+11	0	+6	+3	-5	+5	-2	+1	-4	+2	-1	+1	-2
Falcon	+12	-2	-2	-3	-29	-4	+9	+14	-1	+3	+2	-3	+4	-4	+1	-1	+2	-4	+1	0
<i>Intermediate developing varieties</i>																				
Heron	0	0	-3	+1	-36	+1	+9	+19	-7	+7	+1	0	-3	+1	-1	+3	-6	+2	0	+4
Emblem	-4	+2	+1	0	-44	+1	+14	+14	-13	+7	+6	0	-8	+2	+2	+2	-12	+2	+4	+3
Chinese Spring	-2	-1	+2	+1	-39	-1	+14	+18	-10	+6	+6	0	-5	0	+4	+3	-9	0	+5	+4
N. B. Javelin	-3	0	0	+1	-40	0	+13	+19	-11	+7	+5	0	-6	+1	+3	+3	-10	+1	+4	+5
<i>Slow developing varieties</i>																				
Beneubbin	-7	-1	+2	+3	-43	-1	+14	+21	-13	+4	+6	+2	-11	0	+4	-2	-12	+1	+5	+6
Festiguay	-5	+1	+2	+1	-40	+1	+14	+18	-12	+5	+5	-1	-9	+1	+3	+2	-11	+2	+4	+5
Marquis	-12	0	+3	+3	-43	-2	+11	+21	-18	+4	+6	+3	-12	-2	+4	+8	-17	0	+5	+10
Mean absolute error	7.3	1.1	1.8	2.6	36.6	1.7	12.1	16.4	8.6	4.9	5.0	2.3	6.6	2.0	3.1	3.1	7.4	2.0	3.6	3.6
Error range April to July	-12 to +13				-44 to +21				-18 to +8				-12 to +8				-17 to +10			

TABLE 4. Ratio of mean error in estimated time to flowering to mean error, assuming that the mean time span to this stage applied for each of four plantings, April to July

Wheat varieties	Planting to flowering				
	Global solar radiation	Mean daily temperature	Energy degree units	Estimated evaporation	Developmental units
<i>Rapid developing varieties</i>					
Mendos	0.62	1.74	0.65	0.56	0.32
Bungulla	0.50	1.64	0.53	0.44	0.28
Gamenya	0.66	1.56	0.44	0.38	0.19
Falcon	0.54	1.60	0.26	0.29	0.20
<i>Intermediate developing varieties</i>					
Heron	0.07	1.16	0.27	0.14	0.21
Emblem	0.11	1.20	0.43	0.23	0.34
Chinese Spring	0.10	1.14	0.35	0.19	0.29
N. B. Javelin	0.06	1.16	0.37	0.21	0.32
<i>Slow developing varieties</i>					
Bencubbin	0.18	1.11	0.35	0.24	0.34
Festiguay	0.13	1.09	0.34	0.22	0.33
Marquis	0.21	0.91	0.36	0.31	0.38

radiation, these parameters have the advantage of requiring only temperature data available for a network of stations within the Western Australian wheat belt, whereas virtually no radiation data exist for the whole of this area.

The comparatively small errors for estimated evaporation, developmental units and global solar radiation prompts consideration of seasonal trends of the various parameters. Figure 3 shows the trend of fortnightly means of global solar radiation, mean screen temperature and estimated evaporation, scaled so that the highest and lowest values of each parameter have values of +1.0 and -1.0 respectively, and with the zero reference corresponding to the annual mean. The trends clearly reveal the familiar large lag of air temperature behind global solar radiation characteristic of regions under strong marine influence.

It has earlier been shown that simple temperature summation gives a marked underestimation of the time span to flowering for early plantings, and overestimation for late plantings. The pattern of these errors, when considered in relation to the seasonal trends of global solar radiation and mean screen temperature (Fig. 3), suggests that seasonal changes in the micro-environment to which crops respond in their phasic development are more closely in phase with the régime of global solar radiation than of ambient air temperature at screen height for this macro-environment.

Figure 3 shows that the régime of estimated evaporation follows closely that of radiation to mid-winter, and thereafter follows the mean temperature trend. Plotting developmental units against the estimated evaporation showed that these parameters were not only highly correlated, as is to be expected, but also that there was no discernible phase difference between the two. Thus, through the weightings of daily maximum and minimum temperature obtained from the vapour pressure/temperature relationship, a seasonal régime more closely in accord with that of global solar radiation — and apparently also that of the photothermal micro-environment of the crop — is obtained.

CONCLUSION

It has been shown that daily temperature data can be simply transformed to give a more realistic expression of trends in phasic development than is obtained by temperature summations either with or without adjustment for daylength. No attempt has been made in this study to optimize this transformation.

Considering the form of the vapour pressure deficit relationship, it seems likely that the time span to flowering would be overestimated if mean temperatures were persistently high and accompanied by a narrow range between maximum temperature and dew point, or minimum temperature in the case of developmental units. However, such conditions rarely occur in the climatic environment of the wheat belt.

It seems highly probable that a single, simple exponential function could be used in place of the saturation vapour pressure/temperature relationship to effect an optimal transform.

As an aid to interpretation of existing climatic records, these simple and direct relationships appear promising for estimating time to flowering of a range of cultivars. Evidence from this study suggests that no empirical constants for individual varieties need be invoked other than the mean value of the summation of these parameters as determined from existing phenologic data. The applicability of these parameters under the climatic conditions throughout the wheat belt is being investigated.

ACKNOWLEDGEMENTS

The author greatly appreciates the assistance of Mr. B. B. Singh for use of unpublished phenologic data, and of Mr. W. Martinick, who carried out much of the initial data analysis. Programming and computational assistance of Mrs. M. Walton is gratefully acknowledged. These studies were supported by financial assistance from the Rural Credits Development Fund.

Résumé

Comparaison de paramètres climatologiques simples en Australie-Occidentale (E. A. Fitzpatrick)

L'auteur compare, en utilisant des données phénologiques et météorologiques des environs de Perth, en Australie-Occidentale, dix paramètres climatologiques pour évaluer leur efficacité comme moyens de prévision des phases du développement de onze variétés de Blé mises en terre d'avril à septembre. Ces variétés présentaient des réactions caractéristiques à la vernalisation et à la durée du jour; mais pour la période examinée on a constaté un raccourcissement généralement compatible du temps nécessaire pour la mise à fleur et pour la floraison. Pour la variété au développement le plus rapide, le temps qui s'écoule entre la mise en terre et la floraison est ramené de 110 à 89 jours entre les mises en terre d'avril et de septembre. Pour la variété au développement le plus lent, ce délai est raccourci de 174 à 109 jours.

Des dix paramètres considérés, ceux qui reposaient en totalité ou en partie sur de simples additions de températures sous abri ont donné les erreurs les plus grandes en temps estimatifs pour la mise à fleur et la floraison. Il y a eu des erreurs relativement faibles avec les additions du rayonnement solaire global et de deux paramètres où la température journalière maximale sous abri, le point de rosée ou la température minimale sont combinés en utilisant le rapport tension de saturation / température pour donner un coefficient de pondération différent à ces éléments. Il est apparu que les paramètres fondés sur la température journalière sous abri ainsi transformée sont plus étroitement en phase avec la tendance saisonnière du rayonnement solaire global qu'avec la température atmosphérique moyenne, laquelle marque dans ce milieu un retard considérable par rapport aux énergies solaires incidentes reçues.

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A topographic parameter for evaluation of minimum temperature distribution on clear calm mornings

A. Hočević
Biotechnical Faculty,
University of Ljubljana (Yugoslavia)

In hilly areas a peculiar minimum temperature distribution may be found on clear calm mornings (Schnelle, 1963). It is characterized by such expressions as "Thermal belt", "Warmer Hangzone", "Cold air pocket", "Kaltluftsee" and so on. Temperatures are generally higher on the slopes than at the bottoms of valleys and basins. This phenomenon has been known for centuries and farmers have been using this knowledge by planting temperature-sensitive plants on the slopes. This is the other reason, besides the insolation, that orchards and vineyards are found on the slopes in a hilly country.

This knowledge is only qualitative and it is highly desirable to obtain some quantitative measure for evaluation of minimum temperature distribution as well. Lacking quantitative measurements, an attempt will be made to define such a parameter in this study.

From the theoretical work of Brunt, Groen and Phillips (in Sutton, 1953), one can see that the minimum temperature of the horizontal plane following a clear calm night, which should be close to minimum air temperature, is a function of net radiation, length of the night and thermal properties of the soil and the air. On a slope, the determination of minimum air temperature has additional parameters, the main one being located along the slope.

Therefore, one can start with the known equation, which gives the local change of air temperature as a function of heat flux, vertical and horizontal advection of heat.

$$\frac{\partial T}{\partial t} = \frac{1}{C_p} \frac{\partial Q}{\partial t} - (\bar{\gamma}a - \bar{\gamma})w - \nabla_h T \cdot \vec{v}_h \quad (1)$$

where $\partial T/\partial t$ is the local change of air temperature; C_p , specific heat at constant pressure; $\partial Q/\partial t$, heat flux; $\bar{\gamma}a$, dry adiabatic lapse rate; $\bar{\gamma}$, lapse rate; w , vertical wind velocity; $\nabla_h T$, horizontal temperature gradient and \vec{v}_h , horizontal wind velocity.

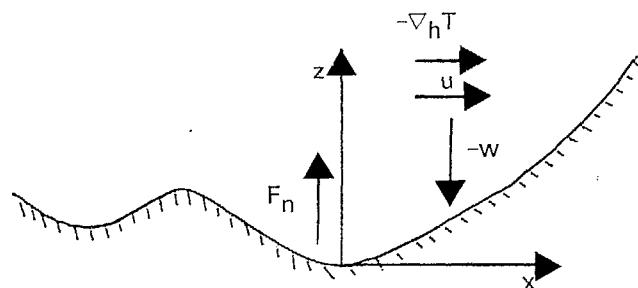


FIG. 1. Meteorological parameters in an air drainage basin.

Let us apply this equation two-dimensionally to the slope in a clear calm night (Fig. 1). In the co-ordinate system used, the right-hand terms have the following qualitative values: the first one can be identified as the net radiation and is negative during the night; its quantitative evaluation can be found elsewhere (e.g. Haltiner-Martin, 1957). The vertical advection term is positive, because of drainage. Vertical wind velocity is negative and lapse rate is smaller than dry adiabatic lapse rate. The horizontal advection term is positive, because the horizontal temperature gradient is negative toward the slope; temperature over the valley is higher than on the surface of the slope, and the horizontal wind velocity in this case (component u) is positive. At night on the slope only the radiation term contributes to the cooling.

From equation (1), one can find the vertical temperature gradient of local change of air temperature along the slope as

$$\frac{\partial^2 T}{\partial z \partial t} = \frac{1}{C_p} \frac{\partial}{\partial z} \left(\frac{\partial Q}{\partial t} \right) - \frac{\partial}{\partial z} \left[(\bar{\gamma}a - \bar{\gamma}) w \right] - \frac{\partial}{\partial z} (\nabla_h T \cdot \vec{v}_h). \quad (2)$$

Expressions $\partial Q/\partial t$, $(\bar{\gamma}a - \bar{\gamma})w$ and $\nabla_h T \cdot \vec{v}_h$, as functions of z and t , are generally not known. Therefore, it seems reasonable to assume a linear relationship at the first

approximation. At the bottom of the air drainage basin (at the end of the slope) the net radiation exists, but neither vertical nor horizontal advection. So one can write

$$\frac{\partial_2 T}{\partial z \partial t} = \frac{1}{C_p} \frac{\partial}{\partial z} (F_n + C_p k_1 z) + \frac{\partial}{\partial z} (k_2 z) + \frac{\partial}{\partial z} (k_3 z). \quad (3)$$

Integration of equation (3) with respect to z and t gives:

$$T(z, t_r) = \frac{1}{C_p} \int_{t_s}^{t_r} F_n dt + \int_{t_s}^{t_r} k_1 z dt + \int_{t_s}^{t_r} k_2 z dt + \int_{t_s}^{t_r} k_3 z dt + T(z, t_s) \quad (4)$$

where t_s and t_r are times at sunset and sunrise and F_n is the net radiation. k_1 , k_2 and k_3 are constants which depend on the length of the night and on the inclination, roughness and thermal properties of the slope. With the assumption that they are independent of time, equation (4) can be written as

$$T(z, t_r) = \frac{1}{4} \int_{t_s}^{t_r} F_n dt + Kz + T(z, t_s) \quad (5)$$

where $\int_{t_s}^{t_r} F_n dt$ is the net heat lost by radiation during the night, K is a coefficient and z is the relative height above the bottom of the air drainage basin. The coefficient K is given by:

$$K = \int_{t_s}^{t_r} (k_1 + k_2 + k_3) dt \quad (6)$$

and represents the minimum vertical temperature gradient along the slope.

Equation (5) gives the minimum temperature distribution as a function of net heat lost by radiation during the night, temperature distribution in the evening and height above the bottom of the air drainage basin. Assuming that temperatures are uniform in the evening, the minimum temperature along the slope is only a function of net heat loss and height above the bottom of the air drainage basin. From equation (5) one can also see that the minimum temperatures will be the same in different air drainage basins if no differences in heat loss exist.

In equation (5), the second right-hand term, which determines local differences, deserves special attention. Lacking a theory for defining quantitatively the coefficient K , one can obtain it through knowing the minimum temperature distribution in the relief. With such empirical knowledge, equation (5) can be used for a rough prediction of minimum temperature distribution in the relief. Coefficient K is, of course, not universal, but depends on the relief from which it was derived.

Empirical evaluation of coefficient K was made for the rolling country of Central County, Pennsylvania, United States of America. Temperature measurements were made, using a thermistor thermometer mounted on the fender of a car, on clear calm mornings before sunrise, when the temperature is close to the value of minimum temperature. The relative heights of the observation points were obtained in the following way. From a topographic map (1: 25,000), the air drainage basins and their bottoms were located using the borders of water-sheds and taking into account narrow ditches, through which the cold air could not flow. Knowing the absolute heights of observation points, the relative heights used in the defined co-ordinate system were easily obtained.

The data were collected on two traverses in Nittany Valley in spring, 1968. On the traverse with 58 observation points, 18 runs were made, not always in really clear and calm conditions. Data were collected on the traverse with 28 observation points on 13 mornings with these conditions fully met. In 8 out of 18 runs on the first traverse and 8 out of 13 runs on the second, the correlation coefficients between minimum temperature and relative height were higher than 0.70. In some runs the correlation coefficient was as high as 0.94. The mean vertical minimum temperature gradient along the slope—coefficient K in equation (5)—was found to be $6.2 \pm 1.8^\circ \text{C}/100 \text{ m}$.

These results can be compared with the measurements of minimum temperatures in hilly country of Slovenia, Yugoslavia. Their evaluation shows a temperature gradient of $4.4^\circ \text{C}/100 \text{ m}$. This value of K is less than the one previously mentioned, possibly because the nights were not completely clear and calm, the length of the night was shorter in June and the net radiation was smaller (Petkovšek *et al.*, 1969).

Results obtained from observations at different locations indicate that, in the case where observations in the relief are lacking, the relative height of the observation point above the bottom of the air drainage basin can be a rough but useful parameter for evaluation of minimum temperature distribution, whereas the net heat loss by radiation, and the evening temperature, determine the lowest minimum temperature.

Résumé

Paramètre topographique pour l'évaluation de la répartition de la température minimale au cours des matinées calmes et claires (A. Hočvar)

L'auteur démontre que l'altitude relative du point d'observation au-dessus du fond de bassin de drainage aérien est un paramètre utile pour une évaluation quan-

titative sommaire de la répartition de la température minimale dans un relief dispersé. Cette constatation a été déduite, après certaines simplifications, de l'équation qui donne la modification locale de la température atmosphérique; certaines mesures effectuées aux États-Unis d'Amérique et en Yougoslavie en ont apporté la preuve.

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Net radiation estimated from global solar radiation

E. A. Fitzpatrick and W. R. Stern
Institute of Agriculture,
University of Western Australia, Nedlands (Australia)

INTRODUCTION

Within an agricultural region a close network of net radiation stations is seldom practicable, and there is a need for developing methods by which net radiation may be estimated from other meteorological data. For regional agroclimatic studies, it is desirable that estimates of net radiation conform as closely as possible to representative soil and moisture conditions, and to the agronomic practices prevailing in the region. For this reason, simple and direct methods are needed that will allow extrapolation of such estimates within a region with reasonable confidence.

Semi-empirical methods based on physical considerations have been used most widely for estimating net radiation. These rely strongly upon the Stefan-Boltzmann relationship expressing thermal radiative flux as a function of the fourth power of absolute temperature. Empirical adjustments are used to accommodate varying conditions of cloudiness and/or vapour pressure (Angström, 1916; Brunt, 1932, 1939; Penman 1948). Recently, the problem has been re-examined by Linacre (1968, 1969), who develops a number of simplified formulae from an entirely temperature-dependent relationship for the atmospheric counter radiation under clear sky conditions (Swinbank, 1963).

Practical difficulties with physically-based methods include differentials between surface and atmospheric temperatures, and the form of the adjustment for cloudiness. More recently, the justification for using vapour pressure as a further empirical adjustment has been questioned (Swinbank, 1963).

The basis for an entirely empirical approach is found in the high correlations between totals of net radiation and global solar radiation documented by many workers (e.g. Shaw, 1956; Monteith, 1965; Stanhill *et al.*, 1966; Davies, 1967; Fritsch, 1967; Field, 1967). Many workers have either noted considerable variation in the

relationship between net and global solar radiation for differing weather conditions and vegetation, or imply a highly variable relationship by confining their investigations to days with clear skies.

Considering the uncertainty in empirical adjustments in physically based formulae, it seemed worth while to analyse available radiation data to explore possibilities for developing *simple* empirical relationships requiring only measured or estimated global solar radiation.

SOURCES OF DATA AND METHODS

In this study daily (24 hr) data were analysed in a deliberate effort to avoid any loss of evidence contained within the original data in respect of the effect of variable cloudiness on net radiation. It was not expected that daily estimates would satisfy the accuracy normally needed where daily net radiation is required for experimental purposes.

The primary data used are the measured net and global solar radiation from Kimberley Research Station at Kununurra, Western Australia (latitude $15^{\circ} 42' S$, longitude $128^{\circ} 36' E$) and from the C. W. Thornthwaite Laboratory of Climatology at Centerton, New Jersey, United States of America (latitude $39^{\circ} 30' N$, longitude $75^{\circ} 10' W$). The Kimberley site is representative of a tropical, dry-monsoonal environment; Centerton represents a mid-latitude, humid continental environment. Since our interest was specifically in estimating net radiation over periods allowing active plant growth, only the data from March to October for Centerton are used in this study.

At the Kimberley site, net radiation was measured between October 1961 and October 1962 above a well-watered cotton crop using CSIRO net radiometers (Funk 1959); global solar radiation was measured with a recording Kipp solarimeter (Radiation Commission of IAM, 1968).

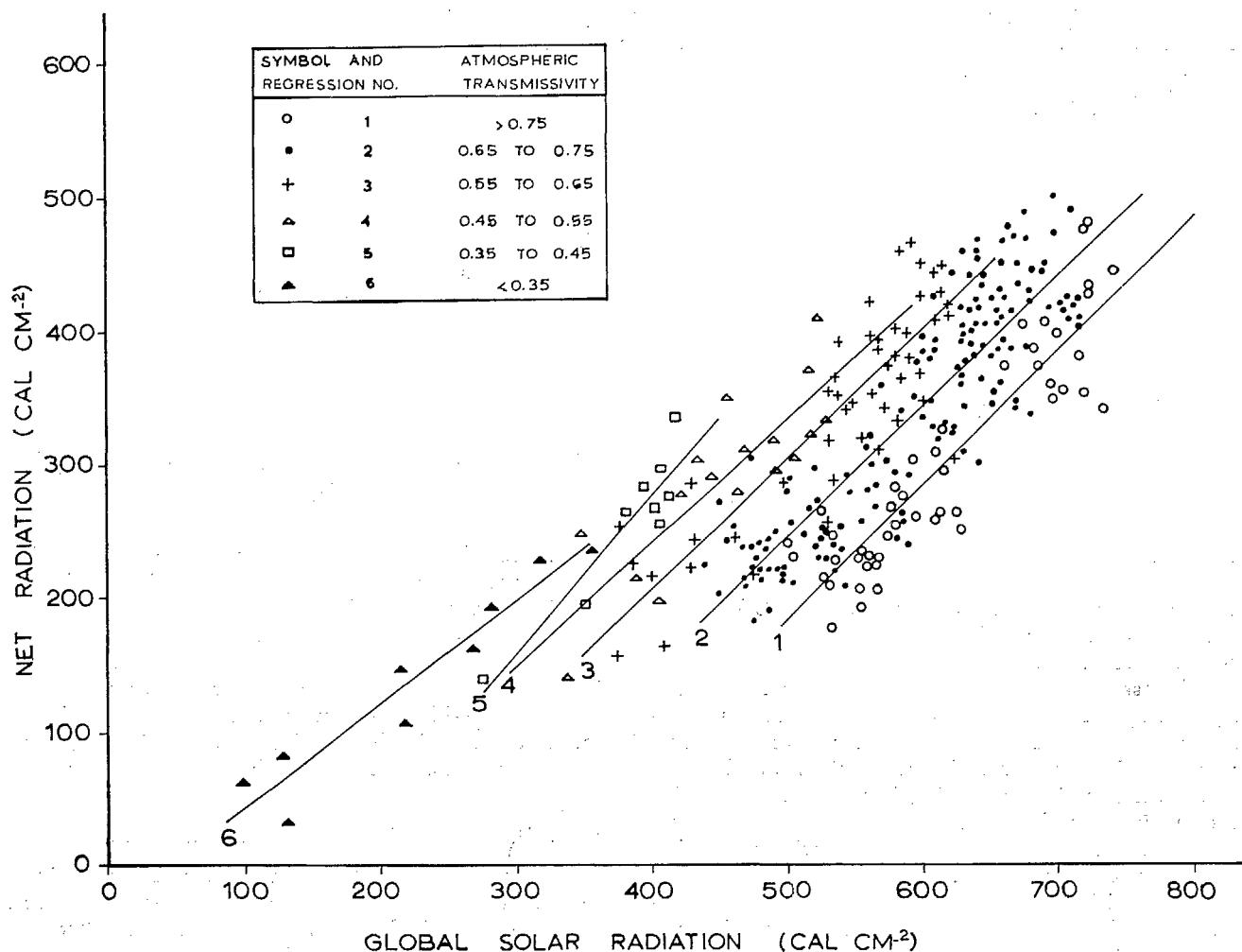


FIG. 1. The relationship between daily net radiation over irrigated cotton and global solar radiation for Kimberley Research Station in northern Western Australia, with the data classified according to level of atmospheric transmissivity.

TABLE 1. Correlation-regression parameters from analysis of measured daily net (Q_n) and global solar radiation (Q_t) at Kimberley Research Station, Western Australia, for six classes of atmospheric transmissivity (Q_t/Q_e)

Regression number	Atmospheric transmissivity Q_t/Q_e	Number of days N	Regression constant with standard error (s.e.) $Q_n = a + b Q_t$		Means		Correlation coefficient r	Adjusted intercept ¹ a'
			$a + s.e.$	$b + s.e.$	Q_t	Q_n		
1	over 0.75	49	-323.4 ± 41.7	1.01 ± 0.07	616.0	300.3	0.90	-297.2
2	0.65 to 0.75	173	-247.6 ± 23.3	0.98 ± 0.04	594.6	335.8	0.89	-241.0
3	0.55 to 0.65	51	-180.9 ± 44.9	0.97 ± 0.08	542.6	344.7	0.85	-181.6
4	0.45 to 0.55	18	-124.8 ± 63.1	0.91 ± 0.14	460.0	294.8	0.84	-151.4
5	0.35 to 0.45	9	-193.6 ± 59.1	1.17 ± 0.15	383.3	255.6	0.93	-116.2
6	less than 0.35	9	-35.1 ± 18.2	0.77 ± 0.07	225.3	139.2	0.95	-79.8

1. Adjusted intercept, a' , is the value of the intercept term of the linear regression equation, assuming that the mean value of b over all classes of atmospheric transmissivity is used with regression line passing through the means of Q_t and Q_n .

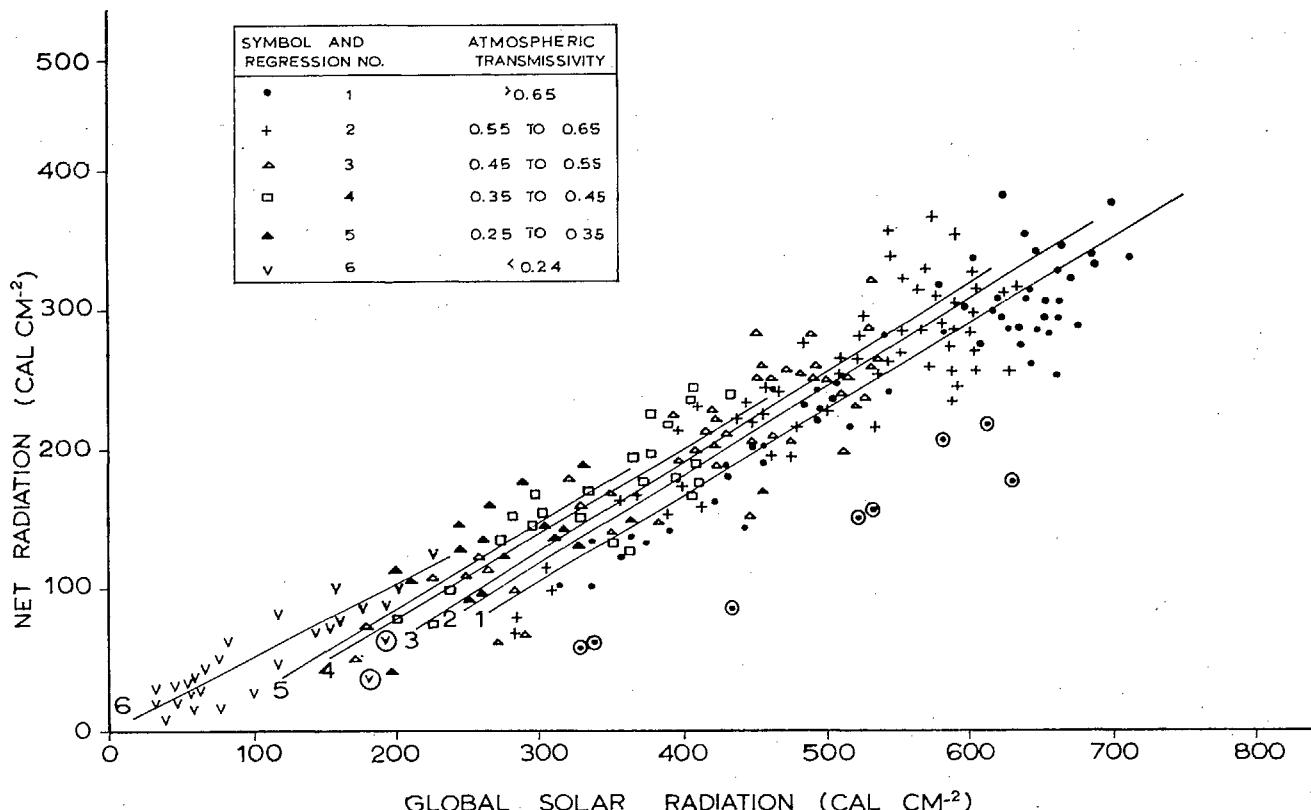


FIG. 2. The relationship between daily net radiation over non-irrigated grass and global solar radiation for Centerton, New Jersey, with the data classified according to level of atmospheric transmissivity. Encircled symbols are for ten days with atypical net radiation régime not included in regression analysis.

For Centerton, published daily radiation data between June 1966 and July 1967 were used (Mather, 1967). At this site net radiation was measured over non-irrigated grass with a C. W. Thornthwaite Associates net radiometer system, and global solar radiation with an Eppley pyrheliometer.

The ratio of the daily global solar radiation to extraterrestrial radiation was determined. This ratio is referred to here as the *atmospheric transmissivity* (Huschke, 1959).

The daily radiation data for each station were classified according to the value of atmospheric transmissivity. The most overcast days were represented by a class with atmospheric transmissivity equal to, or less than, 0.35 for Kimberley, and equal to, or less than, 0.25 for Centerton. The days with least cloud and lowest atmospheric turbidity had values exceeding 0.75 at both stations.

Separate correlation-regression analyses were made for each class of atmospheric transmissivity at each station. These analyses revealed a consistent pattern of the relationship between net radiation, global solar

radiation and atmospheric transmissivity that would allow further generalization.

Symbols used in this paper are given below.

Q_n	= daily (24 hr) net radiation (cal cm^{-2})
Q_t	= daily global solar radiation (cal cm^{-2})
Q_e	= daily extraterrestrial radiation (cal cm^{-2})
Q_t/Q_e	= atmospheric transmissivity (non-dimensional)
n	= daylength (hr)
n/N	= relative duration of sunshine (non-dimensional)
T	= mean air temperature (screen height) ($^{\circ}\text{K}$)
t	= mean air temperature (screen height) ($^{\circ}\text{C}$)
e	= vapour pressure (mm Hg)
σ	= Stefan-Boltzman constant
α	= albedo coefficient
a and b	= empirical constants.

RESULTS

RELATIONSHIPS DERIVED FROM THESE DATA

Figure 1 shows the relationship between measured net radiation and global solar radiation at Kimberley

TABLE 2. Correlation-regression parameters from analysis of measured daily net (Q_n) and global solar radiation (Q_t) at Centerton, New Jersey, for six classes of atmospheric transmissivity (Q_t/Q_e)

Regression number	Atmospheric transmissivity Q_t/Q_e	Number of days N	Regression constant with standard error (s.e.)		Means		Correlation coefficient r	Adjusted intercept ¹ a'
			$a + s.e.$	$b + s.e.$	Q_t	Q_n		
1	over 0.65	58	-75.8 ± 17.6	0.60 ± 0.03	557.1	257.6	0.87	-71.1
2	0.55 to 0.65	60	-62.0 ± 24.4	0.61 ± 0.05	512.7	252.3	0.86	-50.2
3	0.45 to 0.55	48	-65.7 ± 24.3	0.63 ± 0.05	436.9	211.2	0.85	-46.5
4	0.35 to 0.45	25	-39.8 ± 26.2	0.61 ± 0.07	341.2	167.8	0.72	-33.7
5	0.25 to 0.35	21	-33.2 ± 27.6	0.60 ± 0.11	256.8	122.2	0.78	-29.3
6	less than 0.25	27	-3.09 ± 4.9	0.49 ± 0.04	98.2	50.8	0.90	-7.2

1. Adjusted intercept, a' , is the value of the intercept term of the linear regression equation, assuming that the mean value of b over all classes of atmospheric transmissivity is used with regression line passing through the means of Q_t and Q_n .

Research Station for the 309 days with available data. Although there is considerable scatter, clearly much of this is associated with differing levels of atmospheric transmissivity. Parameters for the fitted regression lines are given in Table 1.

Similarly, Figure 2 shows the daily net and global radiation data for 249 days at Centerton. Again the scatter is large. In plotting the data it was found that on ten days in Figure 2, the net radiation was considerably below that of other days having generally the same levels of global solar radiation, within the same class of atmospheric transmissivity. Examination of hourly meteorological data from Philadelphia (48 km north of Centerton) on these days revealed that, on all these occasions, marked changes in cloudiness in late afternoon and evening had occurred, thus causing an atypical radiational régime. In applying the correlation-regression analyses, the data for these ten days were not included. Parameters obtained from these analyses are given in Table 2.

It is evident from the regression lines of Figures 1 and 2, and from the regression coefficients given in Tables 1 and 2, that, relative to the differences in the intercept term, slope differences between classes are small. Except for the class with lowest atmospheric transmissivity at each station (regression 6), the individual slopes do not differ from the mean of the slopes for the remaining classes by more than twice the standard error. For regression 6, the individual slopes do differ significantly from the mean slope at $P = 0.05$, but only marginally so.

The mean of the slopes of the regressions (b in Tables 1 and 2) are 0.97 for Kimberley and 0.59 for Centerton. Applying these slopes at the centroid of each of the six regressions for each station, a set of adjusted linear regressions was obtained.

The adjusted intercept term, a' , can be related to the level of atmospheric transmissivity. In Figure 3, values of a' are plotted against the mean of the daily atmospheric transmissivities within each class. For Centerton, the relationship is linear. For the Kimberley

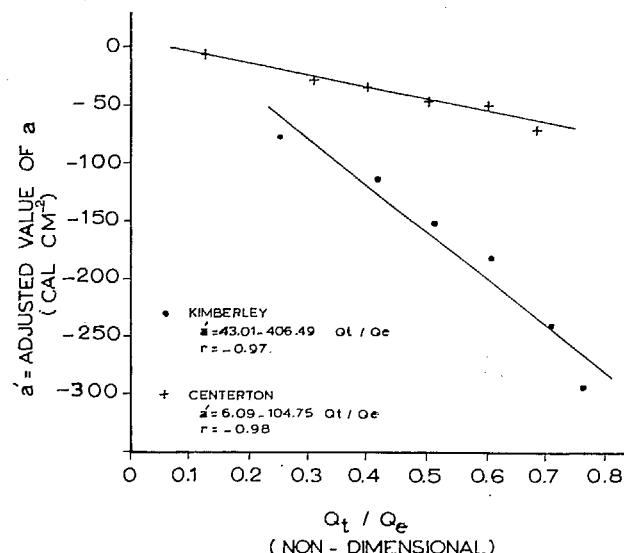


FIG. 3. The relationship between the adjusted intercept term of six regression equations (a' in Tables 1 and 2) and the mean daily atmospheric transmissivity for the six specified classes for Kimberley and Centerton.

data, there is evidence of curvilinearity, but, considering possibilities of errors from a number of factors influencing net radiation, a linear trend was regarded as adequate.

Prediction equations expressing the net radiation as a function of global solar radiation and atmospheric transmissivity were obtained using the mean slopes and the regressions in Figure 3. These are, for Kimberley,

$$Q_n = 0.97Q_t - 406.49(Q_t/Q_e) + 43.01 \quad (1)$$

and for Centerton,

$$Q_n = 0.59Q_t - 104.75(Q_t/Q_e) + 6.09. \quad (2)$$

The albedo measured above the cotton crop at Kimberley was 0.18 (Fitzpatrick and Stern, 1965). This compares with an estimated value of 0.22 over grass at Centerton (Field, 1967). This probably accounts, in part,

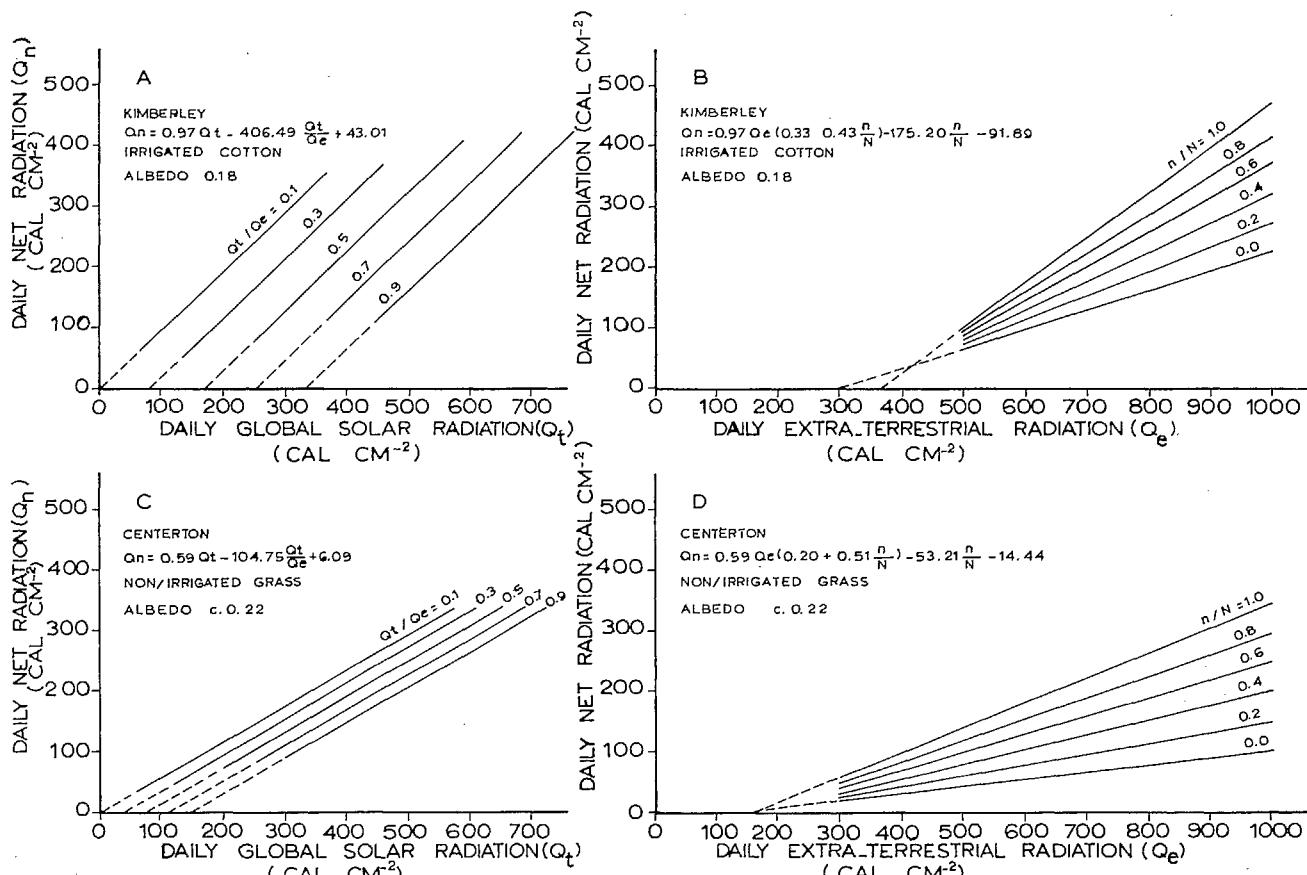


FIG. 4. (A) Graph of equation (1) for Kimberley. (B) Graph of equation (7) for Kimberley. (C) Graph of equation (2) for Centerton. (D) Graph of equation (8) for Centerton.

for the difference in slope between the two sites; temperature relations are also likely causes.

Several relationships for expressing atmospheric transmissivity as a function of the ratio of measured duration of sunshine (n) to daylength (N) were obtained from Kimberley daily solar radiation and sunshine data (Fitzpatrick and Stern, 1965). The simplest of these was a linear relationship,

$$Q_t/Q_e = 0.33 + 0.43(n/N) \quad (3)$$

from which

$$Q_t = Q_e[0.33 + 0.43(n/N)]. \quad (4)$$

Using the same linear form, relationships were derived from the global solar radiation for Centerton, and sunshine data for Philadelphia. These are:

$$Q_t/Q_e = 0.20 + 0.51(n/N) \quad (5)$$

and

$$Q_t = Q_e[0.20 + 0.51(n/N)]. \quad (6)$$

By substitution, the following equations were obtained, and these require only measured sunshine duration, daylength, and extraterrestrial radiation.

For Kimberley Research Station,

$$Q_n = 0.97 Q_e [0.33 + 0.43(n/N)] - 175.20(n/N) - 91.89 \quad (7)$$

and for Centerton,

$$Q_n = 0.59 Q_e [0.20 + 0.51(n/N)] - 53.21(n/N) - 14.44. \quad (8)$$

It was expected that equations 7 and 8 would give less reliable estimates of net radiation than equations (1) and (2). However, where global solar radiation has not been measured, but sunshine data are available, equations of this form may be used for some purposes.

Equations (1), (2), (7) and (8) are shown graphically in Figure 4.

COMPARISON WITH OTHER ESTIMATION FORMULAE

It was of general interest to compare estimates obtained from formulae derived by regression analysis of these data with those from several alternative semi-empirical, physically based methods.

TABLE 3. Correlation parameters from analysis of measured and estimated daily net radiation (Q_n) using alternative empirical and physically based formulae with data from Kimberley Research Station, Western Australia

Functional relationship	Test ¹	Elements used				Correlation coefficient (r)	Coefficient of determination (r^2)	Standard error of estimate (cal cm $^{-2}$)
		Global solar radiation	Temperature	Vapour pressure	Sunshine			
<i>Empirical:</i>								
Equation (14)	D	+				0.79	0.63	54.6
Equation (1)	D	+				0.91	0.82	37.0
Equation (7)	D				+	0.87	0.76	42.6
<i>Empirically adjusted physically based:</i>								
Equation (9) (Penman)	D	+	+	+	+	0.93	0.87	30.8
Equation (10) (Swinbank)	P	+	+	+		0.93	0.87	31.6
Equation (11) (Linacre 1)	I	+	+	+		0.92	0.84	35.0
Equation (12) (Linacre 2)	P		+		+	0.82	0.67	50.6

1. D indicates constants in relationship wholly dependent upon the data used. P indicates constants in part independent of the data. I indicates all constants independent of the data.

Daily radiation data from other sites were not available, and thus an altogether independent comparison of errors in estimated daily net radiation from alternative methods has not been possible to date.

Using Kimberley data, the authors have previously (Fitzpatrick and Stern, 1965) assessed errors in estimated net radiation within separate seasons from two formulae developed from relationships given by Penman (1948) and Swinbank (1963) respectively.

$$Q_n = Q_t(1-\alpha) - \sigma T^4(0.352 - 0.049\sqrt{e_d})[0.3 + 0.7(n/N)] \quad (9)$$

and

$$Q_n = Q_t(1-\alpha) - \sigma T^4(1.0 - 0.936 \times 10^{-5}T^2)[0.155 + (n/N)]. \quad (10)$$

The constants used in Penman's original equation were found to produce large, seasonally biased errors, whereas the constants in equation (9) are optimal for Kimberley and give unbiased estimates of net radiation at this location. The value of 0.155 in equation (10) was determined empirically from our data.

Estimates of daily net radiation were also obtained from two formulae derived from relationships given by Linacre (1969). These are:

$$Q_n = 1440.0[6.94 \times 10^{-4}Q_t(1.0 - \alpha) - 0.0016(100.0 - t)f] \quad (11)$$

$$\text{and } Q_n = 1440.0[6.94 \times 10^{-4}Q_e(1.0 - \alpha) \times [a + b(n/N)] - 0.0016(100.0 - t)f] \quad (12)$$

$$\text{where } f = 0.2 + 0.8(n/N). \quad (13)$$

Table 3 shows the elements used with the alternative formulae, and the values of r , r^2 and standard error of estimate from correlation-regression analysis of observed and estimated daily net radiation. The measured value of 0.18 was used for the albedo coefficient in equations (9-12). Although some of the fitted regressions departed

significantly from a 1:1 relationship, the bias involved in this respect was small. Table 3 also includes a correlation-regression analysis of daily measured net and global solar radiation. The derived regression equation,

$$Q_n = 0.66Q_t - 52.47 \quad (14)$$

represents the simplest available form of empirical prediction.

Similarly, estimates of daily net radiation for Centerton were obtained by these same procedures and were compared with measured net radiation. Results are given in Table 4.

For Centerton the original constants adopted by Penman (1948) were used:

$$Q_n = Q_t(1.0 - \alpha) - \sigma T^4(0.56 - 0.09\sqrt{e_d})[0.1 + 0.9(n/N)]. \quad (15)$$

Linacre's formula, equation (12), was used with values of a and b taken as 0.20 and 0.51 respectively [from equation (5)]. Albedo was taken to be 0.22, the value estimated by Field (1967) in an original description of net radiation at this site.

The derived regression equation relating measured daily net radiation and global solar radiation is

$$Q_n = 0.50Q_t - 7.05. \quad (16)$$

As for the Kimberley analyses, regressions fitted by least squares to estimated and observed net radiation did, in some cases, differ significantly from a 1:1 relationship. This was not unexpected, since empirical constants derived elsewhere were involved. However, the bias in this respect was small, and in all cases there was a scatter of points above and below the 1:1 relationship. In making this comparison of estimates, the atypical days previously excluded from the sample in the derivation of equations (1) and (7) were included for all methods.

TABLE 4. Correlation parameters from analysis of measured and estimated daily net radiation (Q_n) using alternative empirical and physically based formulae with data from Centerton, New Jersey

Functional relationship	Test ¹	Elements used				Correlation coefficient (r)	Coefficient of determination (r^2)	Standard error of estimate (cal cm^{-2})
		Global solar radiation	Temperature	Vapour pressure	Sunshine			
<i>Empirical:</i>								
Equation (16)	D	+				0.93	0.86	32.4
Equation (2)	D	+				0.94	0.88	30.0
Equation (8)	D				+	0.87	0.76	42.8
<i>Empirically adjusted physically based:</i>								
Equation (15) (Penman) ²	I	+	+	+	+	0.89	0.78	40.7
Equation (10) (Swinbank) ²	I	+	+			0.92	0.84	34.7
Equation (11) (Linacre 1)	I	+	+			0.93	0.86	32.9
Equation (12) (Linacre 2)	P		+		+	0.76	0.58	57.1

1. D indicates constants in relationship wholly dependent upon the data used. P indicates constants in part independent of the data. I indicates all constants independent of the data.

2. Actual values of n/N not available for Centerton data. The inverse functional value of n/N based on equation (7) was used when applying equations (15) and (10).

DISCUSSION

Clearly, from Tables 3 and 4, a large proportion of the total variance in net radiation (r^2) is accounted for using a simple linear relationship between net and global solar radiation: equations (14) and (16). In fact, at Centerton (Table 4), the application of a direct relationship of this kind gives a standard error of estimate which is no larger than that obtained with equations (10), (11) and (15) which use additional meteorological data, and are developed initially from physical considerations. On the other hand, for the tropical location (Table 3), a considerably larger proportion of total variance of net radiation is accounted for with the three physically-based equations.

For Kimberley an additional 20 per cent of variance is accounted for through the addition of the atmospheric transmissivity term within the empirical relationship [equation (1)], and the standard error of estimate is reduced from 55 to 37 cal cm^{-2} . The value of r^2 is lower than for equations (9) to (11), but not more than an additional 5 per cent of the variance can be explained by using these equations which require further meteorological data; the standard error of estimate is reduced by no more than 7 cal cm^{-2} .

For Centerton, the proportional reduction of error through introduction of atmospheric transmissivity within the empirical relationship is considerably smaller than at the tropical site. Equation (2), based on global solar radiation and atmospheric transmissivity, gives a smaller error than any other method.

These results, based on data from two dissimilar environments, suggest that, where estimates of net radiation are required for a particular agro-ecological region, it is distinctly advantageous to include the atmos-

pheric transmissivity as an additional term, especially as no further observational data are required.

As was expected, errors in the estimated net radiation from equations (7) and (8), based only upon sunshine data, are considerably higher than those from equations (1) and (2), respectively. Similarly, equation (12) gives a much larger error than equation (11).

It is notable that equation (9) with constants obtained from Kimberley data, gives a considerably lower error than equation (15) applied at Centerton. This clearly illustrates the need for cautious preliminary testing of the appropriateness of empirical constants with relationships established under dissimilar environmental conditions.

It is of interest that equation (10), which is developed from Swinbank's original analysis and from Kimberley Research Station data, gives a smaller error at Centerton than does equation (15), which includes the vapour pressure term according to Brunt (1939). The constants that have been used in equations (10) and (15) were not derived from these data; therefore the application of these equations constitutes an entirely independent test.

The error resulting from equations (1) and (2) developed in this study is roughly comparable with that from equation (11). As applied here for daily periods, Linacre's equation (11) is wholly independent of these data, and the high correlations at both sites support the validity of his procedures.

It will be noted that equations (1) and (2) are of such a form that the two coefficients and the constant term might readily be evaluated by multiple regression analysis, with global solar radiation and atmospheric transmissivity as the determining variables.

If simultaneous records of net and global solar radiation are available at some representative regional centre within an area of generally similar temperature régime,

simple relationships such as equations (1) and (2) may be useful for obtaining estimates of net radiation with accuracy adequate for regional agroclimatic assessments. Nomograms, as in Figure 4, provide a simple practical means of appraising rapidly within a region the approximate levels of net radiation characteristic of the crop, soil, and moisture conditions at the regional centre.

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Résumé

Évaluation du rayonnement net d'après le rayonnement solaire global (E. A. Fitzpatrick et W. R. Stern)

Le rayonnement solaire global et net quotidien d'un emplacement situé dans la partie tropicale du nord-ouest de l'Australie et le rayonnement d'un emplacement situé à latitude moyenne dans la partie orientale des États-Unis d'Amérique ont été analysés pour évaluer l'utilité de formules empiriques simples en vue d'estimer le rayonnement net (Q_n). Ces données ont permis d'obtenir une relation ne nécessitant que le rayonnement solaire global mesuré (Q_t) et la transmissivité de l'atmosphère, déterminée comme étant le rapport entre le rayonnement solaire global au rayonnement extraterrestre (Q_e). Cette relation est de la forme :

$$Q_n = aQ_t - \frac{bQ_t}{Q_e} + c$$

où a , b et c sont des constantes empiriques exprimant les conditions de la végétation, du sol et de l'humidité d'une région particulière.

En utilisant la transmissivité de l'atmosphère avec le rayonnement solaire global, l'erreur d'estimation du

rayonnement net a été moindre qu'en utilisant une relation linéaire plus simple fondée uniquement sur le rayonnement solaire global. L'inclusion de la transmissivité de l'atmosphère a réduit davantage l'erreur d'estimation dans l'emplacement tropical que dans l'emplacement situé à une latitude moyenne.

L'erreur de la relation empirique ci-dessus a été comparée à l'erreur de plusieurs formules à base physique auxquelles sont apportés des correctifs empiriques pour la nébulosité et/ou la tension de vapeur d'eau, et nécessitant des données météorologiques supplémentaires. La relation ci-dessus a donné une erreur moindre à l'emplacement situé à latitude moyenne, mais une erreur légèrement plus grande à l'emplacement situé sous une latitude tropicale.

Ces analyses suggèrent que, à condition de disposer de mesures précises du rayonnement net à une station de référence, les formules empiriques simples ne nécessitant pas de données autres que le rayonnement solaire global mesuré ou estimé pourraient être utilisées pour évaluer le rayonnement net avec une précision suffisante pour des études agroclimatiques interprétatives.

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The radiation régime of a spruce forest

J. J. Landsberg, P. G. Jarvis and M. B. Slater
Department of Botany, University of Aberdeen
(United Kingdom)

INTRODUCTION

The radiation régime above and within various field crops has received considerable attention in recent years, but there are comparatively few data available from forests.

In the Fetteresso forest in north-east Scotland, near Aberdeen, (latitude 56° N, longitude 2° W) all the components of the energy balance of a stand of Sitka spruce (*Picea sitchensis* (Bong) Carr.) are being measured, together with carbon dioxide concentration at a number of levels. Parallel measurements of various aspects of tree response to climate are being made. In this paper some of the radiation data collected in the summer of 1969 are presented. These data cover the period June to September, during which time the noon elevation of the sun varies from about 58° to 45° (List, 1963).

The site is on a 7 per cent north-east facing slope. There are about 4,000 trees/ha in the experimental area, the average height being about 10 m. The trees have been "brashed" (pruned clean) from ground level to a height of about 3 m. Live foliage elements first occur at a height of about 4.5 m. The ground is covered by a layer of litter, giving way, at 5 to 10 cm depth, to a peaty soil over clay. The litter layer is always damp.

The amount of incident energy absorbed by a plant stand determines the potential rates of photosynthesis and water use by the stand. The amount, and spectral composition, of radiant energy penetrating into the depths of the stand limits the photosynthetic potential of the foliage layers, while the fluxes of water vapour and heat at any given level are determined by the energy available at that level and the manner in which it is partitioned, as well as by the degree of turbulence pertaining at any given time.

Monsi and Saeki (1953) suggested that the attenuation of light in plant stands may be described by an expression analogous to Beer's (or the Bouguer-Lambert) law,

and it has been shown (e.g. Begg *et al.*, 1964; Impens and Lemeur, 1969) that the extinction of net radiation can be similarly described. The relationship, for plant stands, is defined by

$$\begin{aligned} R_n(z) / R_n(h) &= \exp \left(-k \int_z^h L_z \cdot dz \right) \\ &= \exp (-kL) \end{aligned} \quad (1)$$

where h refers to the height of the canopy top and z to any height above the ground. $L = \int_z^h L_z \cdot dz$, thus defined, is the area of foliage per unit area (leaf area index), and L_z is the area per unit volume (leaf area density). By definition, the extinction coefficient, k , is the slope of the line relating $\ln[R_n(z)/R_n(h)]$ to cumulative leaf area index. The integration $\int_z^h L_z \cdot dz$ is always carried out through the vertical interval.

Equation (1) is only strictly valid for light passing through a homogeneous medium. For a beam of direct radiation incident on the surface of a homogeneous medium at an angle β to the surface, the mean irradiance at a point in the medium would be expected to be proportional to the path length through the medium. For a plant stand, as the sun approaches the horizon, the path length of the direct rays through the foliage increases, with an increased chance of interception, and absorption, by the foliage. Hence the extinction coefficient, k as derived above, would be expected to increase as β decreases. If k varies in proportion to the path length, it follows from simple trigonometric considerations that k should vary as $\text{cosec } \beta$.

In a detailed theoretical analysis of light penetration into stands Anderson (1966) showed that, for direct short-wave radiation, the extinction coefficient (K) could be defined in terms of leaf shadow area (L_β) on a plane perpendicular to the direct beam, and leaf area index (L), by the expression

$$K = L_\beta / (L \sin \beta). \quad (2)$$

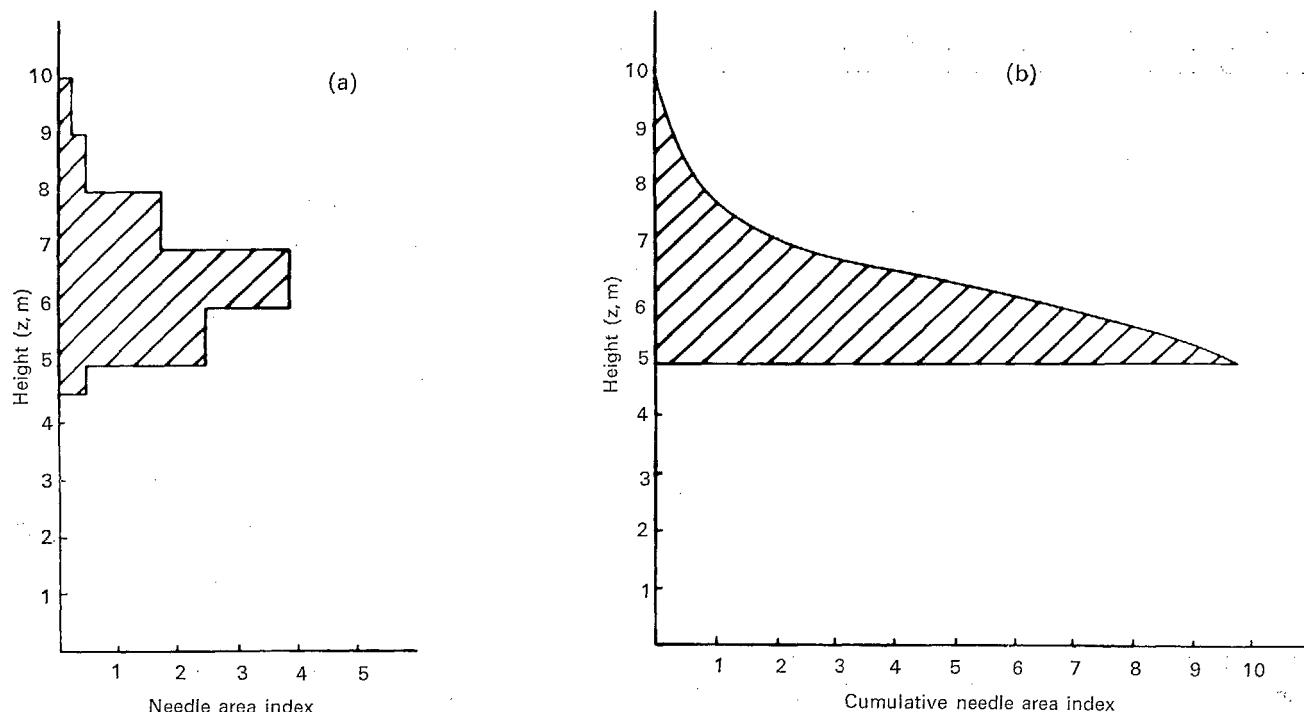


FIG. 1. (a) Needle area index in 1 m layers for a spruce stand in the Fetteresso Forest; (b) Needle area index cumulated from the top downwards for the spruce stand.

Monteith (1969) developed this approach to give an expression for the fraction of light transmitted through n layers of leaf area index L . Taking the transmittance of spruce needles as zero (see Gates *et al.* 1965) this can be written as

$$R_n(z) / R_n(h) = \exp [L \ln (1 - \cos \theta \operatorname{cosec} \beta / n) n] \quad (3)$$

where θ is the mean angle between a plane normal to the incident beam and the mean leaf angle, averaged over azimuth angles from 0° to 360° . The term $\cos \theta \operatorname{cosec} \beta$ is equivalent to $L_\beta / (L \sin \beta)$ in equation (2). For random foliage equation (3) tends to the limit

$$\begin{aligned} R_n(z) / R_n(h) &= \exp [-L \cos \theta \operatorname{cosec} \beta] \\ &= \exp (-KL) \end{aligned} \quad (4)$$

where $K = \cos \theta \operatorname{cosec} \beta$. The above expressions were derived for short-wave radiation, but are used here as the basis for the analyses of profiles of net radiation, although it is unlikely that any realistic definition of $\cos \theta$ is possible for foliage of the type considered here.

MEASUREMENTS

DETERMINATION OF NEEDLE AREA

As part of a study of nutrient uptake and cycling by Sitka spruce, Dr H. Miller of the Macaulay Institute

of Soil Research, Aberdeen, has used a stratified sampling procedure, based on tree size classes, to select 16 trees from the area near the micrometeorological masts. These trees have been cut down and the distribution of foliage, according to age and position in the canopy, has been defined. The relative contribution which each size class makes to the total population has been obtained from mensuration data provided by the Forestry Commission. Dr Miller has kindly made available to us his data on foliage dry weight distribution, and provided us with subsamples of the foliage, on which we measured the projected (plan) needle areas on a photo-electric planimeter of the type described by Marshall (1968), and estimated the relationship between needle dry weight and needle area. This ratio varies with age. Vertical profiles of needle area index (Fig. 1) have been constructed from these data. The curve of cumulative leaf area index shown in Figure 1b has been used in the evaluation of radiation attenuation in the plant stand (discussed later).

RADIATION MEASUREMENTS

Two Moll-Gorczyński (Kipp and Zonen) solarimeters were mounted, parallel to the slope, on the top of a 15 m mast. One of these, fitted with a clear glass dome, measured total (direct plus diffuse) incoming short-wave radiation, Q , between wave-lengths of about 0.3

to $3\text{ }\mu\text{m}$. The other, fitted with a Schott RG 8 filter, measured only radiation of wave-length greater than about $0.7\text{ }\mu\text{m}$ (Q_i). The difference ($Q - Q_i$) is P , the amount of photosynthetically useful radiation.

The downward (Q_h) and upward (Q_r) fluxes of short-wave radiation were measured by two Monteith solarimeters (Lintronic), with ground-glass domes, mounted horizontally, back to back, separated by a 45 cm diameter white aluminium disc, about 4 m above the canopy. The albedo, or reflectance, of the underlying surface is given by $Q_h/Q_r = \alpha$.

Net radiation (R_n) sensors (Swissteco) were mounted on arms on a neighbouring mast. The mast is a 30 cm equilateral triangle, and the radiometers were at least 1 m from it. It was calculated that the influence of the mast, in terms of the proportion of the radiometer's field of vision which it occupied, was negligible. A ventilated Funk radiometer with hemispherical polythene covers was exposed about 4 m above the canopy. One metre long, linear net radiometers were used at the canopy top and inside the plant-air layer where two instruments in series were used in the region of greatest foliage concentration. In May 1969, all instruments were cross calibrated and checked against the Funk radiometer.

The distribution of foliage, in relation to the size of the instruments, poses a sampling problem which may not have been completely overcome. The output of each sensor (or pair of sensors) was automatically recorded by a data-logger every 10 min, and averaged over periods of 1 hr during processing. This gives a degree of integration in both space and time which should ensure that the results are reasonably representative of this type of plant stand.

Seventy-six hours data, from eight days, are analysed in this paper. The days were 5 and 6 June, 21, 22 and 25 July, and 18, 19 and 27 August 1969. The first two were bright and clear, the second two dull and misty, the fifth bright and clear and the last three were cloudy with sunny intervals.

RESULTS

PROPORTION OF PHOTOSYNTHETICALLY USEFUL RADIATION

Mean hourly values of the ratio P/Q were averaged over each of the eight days measurements considered here. Hourly means between 0.42 and 0.69 were recorded. The daily averages varied from 0.45 on a clear, dry day, to 0.57 on a damp, misty day, with an over-all mean value of 0.53. When all the available hourly values were plotted against time, on a single graph, there was considerable scatter, but when the values for each hour were averaged, a smooth curve could be drawn through the points (Fig. 2).

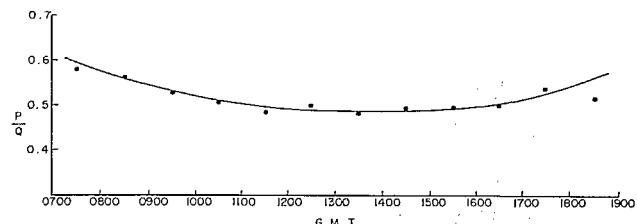


FIG. 2. The variation in the ratio of photosynthetically useful radiation (P) to total incoming shortwave radiation (Q) with time of day. The points are averages of observations on different days.

ALBEDO

The albedo (α) (mean hourly values) was effectively constant for both sunny and overcast days. Values recorded in the morning before 09.00 hr, and evening after 16.00 hr were sometimes slightly higher than those during the middle of the day, but these differences were not consistent. A more interesting phenomenon was a marked increase in albedo on two misty days, when mean values of 0.180 and 0.173 were obtained. An over-all mean value of 0.155, including these high values, was obtained from all the measurements.

RELATIONSHIP BETWEEN NET AND TOTAL SHORT-WAVE RADIATION

In Figure 3, 76 hourly means of R_n and Q (mW cm^{-2}) have been plotted against one another. The equation describing the best fitting line is

$$R_n = 0.87Q - 2.71 \text{ mW cm}^{-2}. \quad (5)$$

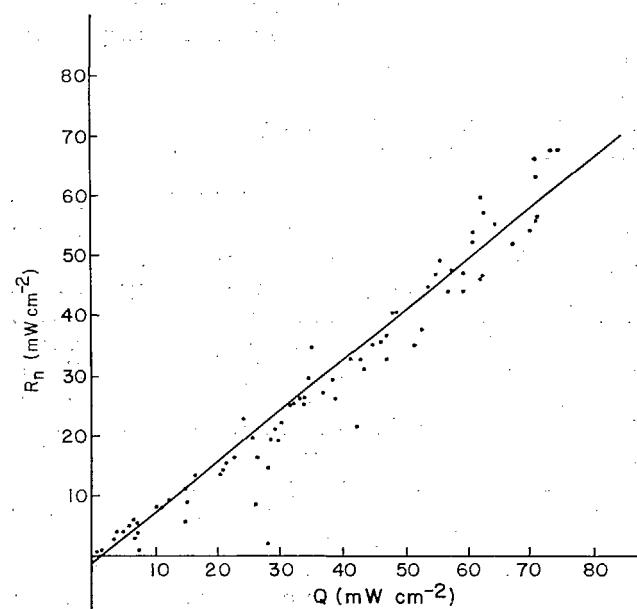


FIG. 3. Net radiation (R_n) as a function of total incoming short-wave radiation (Q).

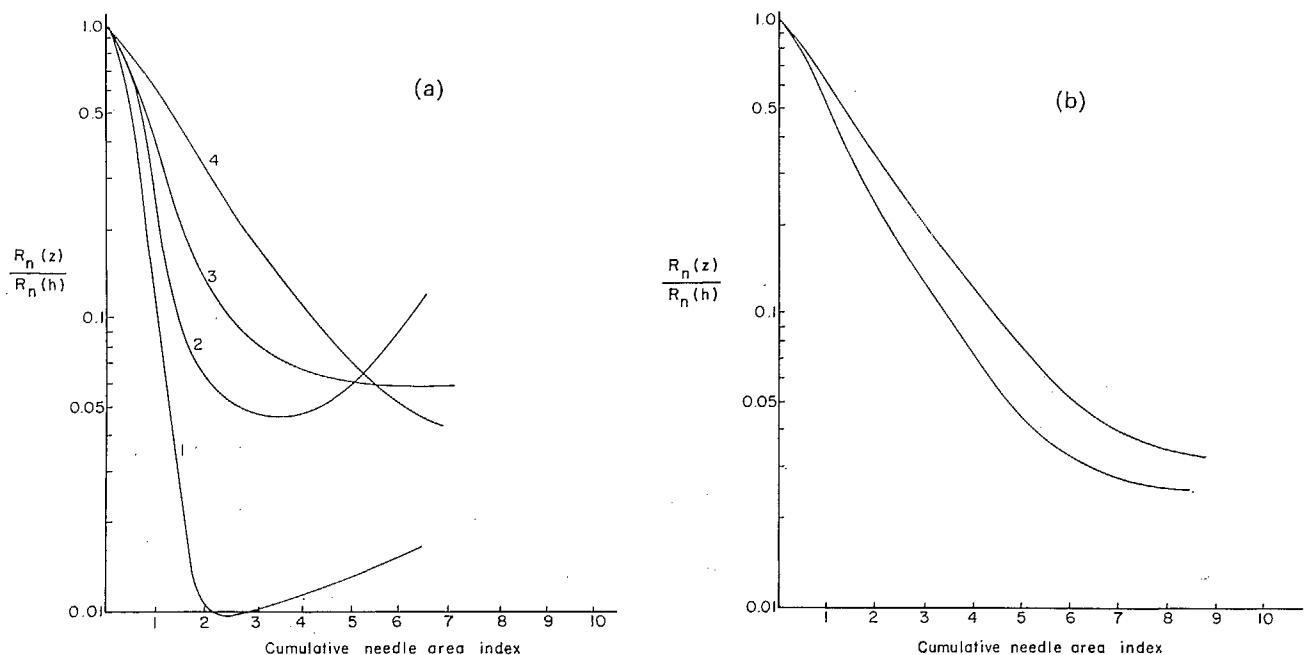


FIG. 4. Attenuation of radiation in the plant stand: (a) Representative curves of $\ln[R_n(z)/R_n(h)]$ plotted against cumulative needle area index, for different times on a sunny day; (b) The limits of the variation in $\ln[R_n(z)/R_n(h)]$, plotted against cumulative needle area index, on an overcast day.

The regression accounted for 96 per cent of the variation in R_n (hence the correlation coefficient was $\sqrt{0.96} \approx 0.98$). An equally good fit (accounting for 97 per cent of the variation in R_n) was obtained with a quadratic regression. The curvature was very slight, and could be ascribed largely to the non-linearity of the points near the origin.

ATTENUATION OF RADIATION IN THE PLANT STAND

Mean hourly values of the ratio $R_n(z)/R_n(h)$ at a number of levels inside the canopy have been plotted, on a logarithmic scale, against cumulative needle area index for a clear day (Fig. 4a) and an overcast day (Fig. 4b). For clarity only four mean curves have been plotted in Figure 4a. These curves show clearly that the rate of attenuation of net radiation varied with time of day. A feature of the curves at low sun angles is the apparent increase in R_n in the lower levels of the forest. When β is comparatively large, the curves become more or less linear. The two curves in Figure 4b, for the overcast day, when all the radiation was in the diffuse form, span the limit of variation observed. There was no evidence of any consistent trend in the rate of attenuation, but all the curves are non-linear and follow the quadratic form, described by Impens and Lemeur (1969), in the lower part of the canopy.

Using equation (1), extinction coefficients were derived from the hourly data represented by the curves in Figure 4a, using only the linear portions. The values obtained are given in Table 1.

The mean value of k derived from the curves represented in Figure 4b was 0.58. Taking $k = 0.6$, the point where $R_n(z)/R_n(h) = 0.05$, conventionally taken as the point of complete extinction, is at $L \approx 5$ for this plant stand.

The values of k , given above, are plotted against β and $\text{cosec } \beta$ in Figure 5a and b. Two curves are obtained in each case, depending on whether the rays of the sun are shining against the slope ($\beta > \beta'$, where β' is the angle to the horizontal made by a beam of direct solar radiation) or in the direction of the slope ($\beta < \beta'$).

DISCUSSION

It is generally accepted that the ratio P/Q can vary widely. Gaastra (1958) assumed a value of 0.40 and Wit (1965) used 0.50. The range 0.42–0.69 reported here is very similar to that given by McCree (1969) in his comments on Monteith's (1969) paper and by Gaastra (1968). The high values on damp, misty days are to be expected, in view of the strong absorption of infra-red radiation by water vapour in the atmosphere. Similarly, higher values may be expected in the morning

TABLE I.

GMT	07.00– -08.00	08.00– -09.00	09.00– -10.00	10.00– -11.00	11.00– -12.00	12.00– -13.00	13.00– -14.00	14.00– -15.00	15.00– -16.00	16.00– -17.00	17.00– -18.00
β^1	37	42	47	52	53	51	46	41	32	29	17
k	3.08	1.62	1.20	0.80	0.65	0.55	0.67	0.90	1.16	1.62	2.56

1. β was corrected for the slope and azimuth of the land by the formula given by both Gates (1965) and Sellers (1965). Because of the north-easterly slope of the site (azimuth = -145° from south) β is maximum at about 11.30 hr.

and evening when the radiation path length is longer. The effect of these variations on photosynthesis is currently being tested in a model of canopy photosynthesis.

The albedo of coniferous forests usually appears to vary between about 0.10 and 0.15 (Rutter, 1968), with some published observations outside these limits; Barry and Chambers (1966) measured values up to 0.20 and Federer (1968) gave values varying between 0.13 and 0.19 for white pine (*Pinus strobus*). The value of 0.155 presented here is, therefore, of the same order as other values for coniferous communities. The lack of variation in albedo through the day, in contrast to the marked diurnal variation in the albedo of field crops (Monteith and Szeicz, 1961), can be attributed to the very rough canopy, which in no way approaches a plane surface. The high reflectance observed on damp days almost certainly results from the presence of free water droplets on and between the needles.

In view of the low albedo of the forest, the slope of equation (5), defining the relationship between R_n and Q , is of the order to be expected for this surface. Studies bearing on this relationship have been based on various time periods (see Linacre, 1968). For comparison with the results presented here, the data of Fritsch (1967), who calculated linear regressions of R_n on Q from hourly values, are considered. Pooling data from six field crops, Fritsch obtained an equation with a slope of 0.734, which is considerably lower than that of equation (5), and the intercept ($0.118 \text{ cal cm}^{-2} \text{ min}^{-1}$, as against $0.039 \text{ cal cm}^{-2} \text{ min}^{-1}$) was considerably higher. This indicates a lower thermal flux from the forest surface, suggesting that it is relatively cooler than the crop surfaces. Idso *et al.* (1969), assessing Fritsch's results in relation to equations based on daily totals, showed that the use of hourly means resulted in more reliable equations than might be obtained from daily totals, since the relatively small proportion of negative net radiation on long days, compared with that on short days, may bias the slopes of equations based on daily data.

Equation (5) can be integrated to make estimates of total daily net radiation over the requisite daylight period, although this may be dangerous until a greater volume of detailed data are available on the variation

in thermal radiation régime of the forest with time of day and weather conditions.

The upward tendency displayed by the curves in Figure 3, in the lower part of the canopy, almost certainly results from the increasing magnitude of the downward long-wave radiation flux with increasing depth into the canopy. This is probably also the reason for the quadratic extinction coefficients defined by Impens and Lemeur (1969). Air temperature measurements indicated a very warm layer in that part of the canopy, between 7 m and 8 m above the ground, where the foliage was most dense. For example, on a clear bright day, with

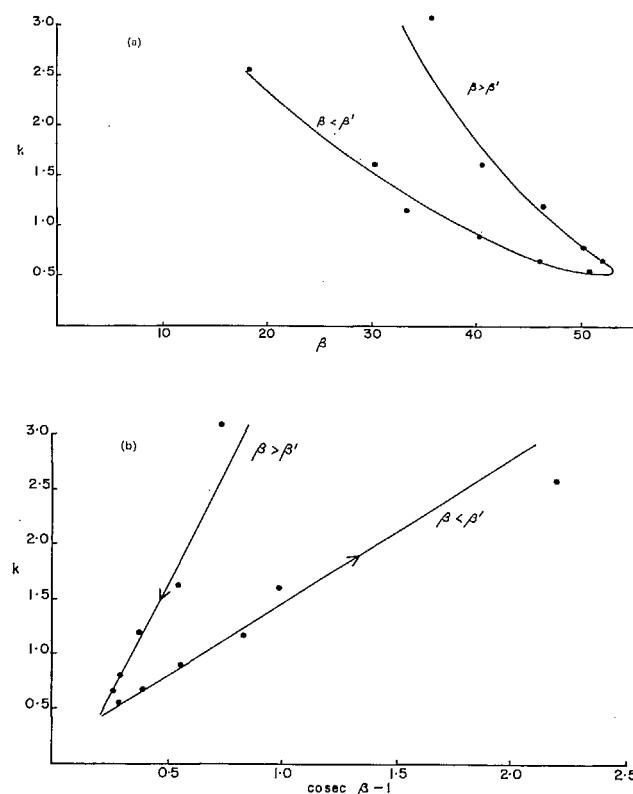


FIG. 5. (a) The extinction coefficient (k) as a function of sun elevation (β); (b) k as a function of $\text{cosec } \beta$.

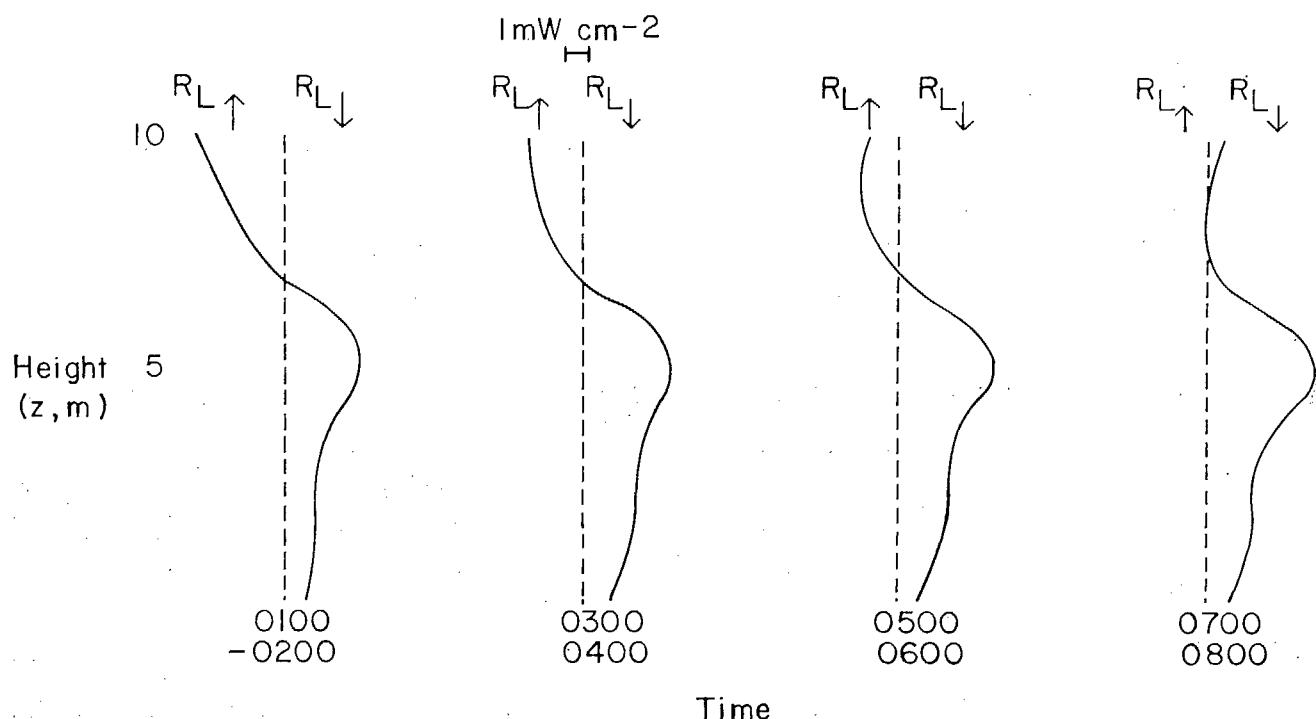


FIG. 6. Profiles of net radiation inside the spruce canopy for alternative hours from 01.00 to 08.00. Note the magnitude of the downward flux, and the gradual decrease in the magnitude of the upward flux as sky radiation increases with the approach of the day.

a windspeed at $h + 5$ m of about 5 m sec^{-1} , average temperatures inside the canopy for the period 11.52 to 13.12 hr were: $z = 0.5 \text{ m}$, 16.1°C ; $z = 8 \text{ m}$, 19.7°C ; $z = h$ (10 m), 18.1°C ; $z = 13.5 \text{ m}$, 17.2°C . (The differences between these values can be much greater on a still day.) If the foliage temperature is approximately equal to the ambient temperature, these data indicate a net upward flux from the warm layer to the top of the canopy of about 1 mW cm^{-2} , and a net downward flux to the ground, of about 2 mW cm^{-2} .

Saito (1964) has given equations for the calculation of net long-wave radiation within plant communities which could be used to describe the situation more precisely.

The warm layer usually persists through the night. As an example of the effects of this, some profiles of net radiation during the latter part of a night, the first half of which was misty, are presented in Figure 6. The mist and cloud cleared at about midnight. These night-time profiles illustrate clearly the downward flux of long-wave radiation from the warm layer which causes the curvilinear profiles of net radiation during the day.

Certain characteristics of the canopy with regard to the interception of radiation can be derived from Figure 5. In the first place, the linear relationships between k and $\text{cosec } \beta$ verify the dependence of the

extinction of radiation on β specified by the theoretically derived equation (4). The equations for the two lines are:

$$k = -0.51 + 4.1 (\text{cosec } \beta - 1) \quad (\beta > \beta') \quad (6a)$$

$$k = 0.16 + 1.3 (\text{cosec } \beta - 1). \quad (\beta < \beta') \quad (6b)$$

These two distinct relationships indicate an interaction between the structure of the canopy, the slope of the ground and the incident direct beam solar radiation. The greater sensitivity of k to small changes in β in the morning than in the afternoon can be attributed to the influence of the slight slope to the north-east on the penetration of radiation into the canopy, probably largely between the spire-shaped crowns. A small increase in β has a much larger effect on penetration in the morning, when the sun's rays are directed against the slope ($\beta > \beta'$), than in the afternoon, when they are in the direction of the slope ($\beta < \beta'$). At any value of β , k is smaller in the afternoon than in the morning. Since the crowns of the trees show no obvious azimuth effects in canopy structure, this azimuth effect on k suggests that penetration of radiation into the canopy is less dependent on the angle made by the direct beam with the surface of the canopy than on the angle it makes with the crowns of the trees.

For leaves arranged homogeneously and isotropically, the rate of extinction of radiation would be expected to

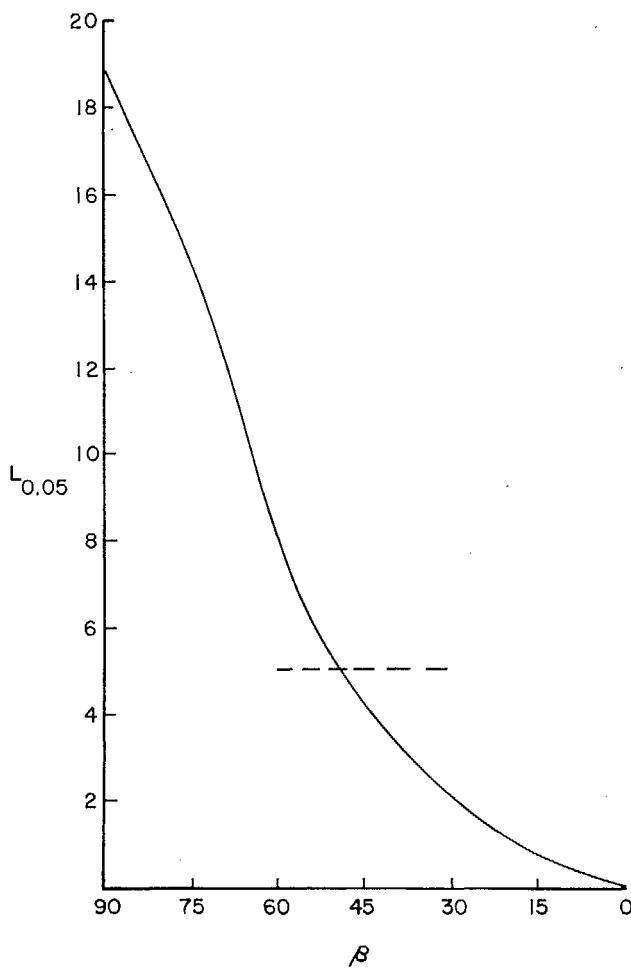


FIG. 7. The leaf area index at which 95 per cent of Q is absorbed ($L_{0.05}$) at different sun elevations. The dotted line shows the lack of dependence of $L_{0.05}$ on β on an overcast day.

be proportional to $\text{cosec } \beta$, i.e. $dk/d(\text{cosec } \beta)$ would be unity. Since the slope of equation (6b) approximates unity when $\beta < \beta'$, the canopy, under these conditions, is behaving as a homogenous medium. The intercept of equation (6b) on the ordinate ($k = 0.16$) gives the value of the extinction coefficient at $\beta = 90^\circ$, which could be taken as an extinction coefficient (K_0) characteristic of the canopy. The appropriate extinction coefficient [$K(\beta)$] for direct radiation incident at any angle β would then be derived from equation (6b) as

$$K(\beta) = K_0 + 1.3 (\text{cosec } \beta - 1). \quad (7)$$

For broad flat leaves, randomly arranged, K_0 lies between unity, for horizontal foliage (irrespective of the magnitude of β) and zero, for vertical foliage (Anderson, 1966). Thus it is a useful descriptive parameter embracing both the arrangement and inclination of leaves. This concept cannot be pursued too far in our particular case, because of the "hysteresis loop" in our k values and also because it does not seem justified, at present,

to apply analyses developed for broad leaves to conifer foliage in greater detail. However, if equations similar to (7) can be established for other crops, it could be useful for comparative purposes.

The value of k derived for diffuse radiation (0.58) is similar to those listed by Monteith (1969) for crops with foliage of intermediate inclination (alfalfa, beans, bulrush millet, rice) and this suggests that the effective foliage units in the spruce canopy are the twigs rather than the individual needles. These units are not uniformly distributed. They are clumped, with large gaps between individual branches. The ratio [gap area (no foliage) / unit ground area] exceeds 0.8 throughout the canopy, therefore the clumps of twigs carry a dense mass of needles of about five times the average leaf area index for the whole layer. It may, therefore, be more useful to evaluate the extinction of radiation in a spruce canopy in terms of a model which takes into account separately the interception of radiation by "leaves", or clumps of foliage, and the transmission of radiation unimpeded through gaps (e.g. Monteith, 1969; Kira *et al.* 1969). An estimate of sunspot frequency could then be derived—an important factor in calculating potential photosynthesis.

The use of such a model requires careful evaluation of canopy structure in terms of foliage units of defined density and transmission characteristics, and of the gaps between them. In addition, in conifer canopies, such a model must also take into account the predominantly diffuse character of radiation transmitted through the foliage, resulting from the penumbras of the small needles. We have collected data on canopy structure for such a model, which we hope to present soon.

The leaf area index which accounts for absorption of 95 per cent of the incident radiation is often taken to indicate the maximum leaf area index which the canopy can economically support. In diffuse radiation this leaf area index is about 5; its variation with β in direct radiation is shown in Figure 7. The k values from which the curve was calculated were derived from equation (6b). Since the leaf area index of the spruce canopy is about 10, and since β only approaches 60° in the middle of June, it would appear that the stand is in need of thinning—for our conditions a leaf area index of about 5 would probably be optimum. However, this conclusion may be modified in the light of actual diffuse irradiance, sunfleck frequency and leaf photosynthesis/irradiance relationships now being assessed in a model.

ACKNOWLEDGEMENTS

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Résumé

Le régime de rayonnement d'une forêt de Sapins (J. J. Landsberg, P. G. Jarvis et M. B. Slater)

On a mesuré dans une forêt de Sapins (*Picea sitchensis* (Bong) Carr.) du nord-est de l'Écosse, pendant l'été de 1969, le rayonnement incident de courte longeur d'onde (Q), le rayonnement incident utilisé par l'activité photosynthétique (P), la réflexion (α) dans les courtes longueurs d'onde qui se produit au-dessus des arbres, et le rayonnement net (R_n) à différentes hauteurs dans le feuillage.

Le rapport P/Q variait entre 0,36 et 0,65; sa valeur moyenne était 0,46. L'albédo (α) était le plus élevé lorsque le temps était humide; il ne montrait aucune

variation journalière et sa valeur moyenne était 0,155. La relation entre R_n et Q était définie par l'équation

$$R_n = 0,87Q - 2,71 \text{ mW cm}^{-2}$$

Par temps couvert, le coefficient d'extinction de R_n vers l'intérieur de la voûte était indépendant de l'heure de la journée, avec une valeur moyenne de 0,58. Par temps ensoleillé, il était en rapport avec la hauteur du soleil (β), mais il présentait ce qui peut être décrit comme une boucle d'hysteresis, selon que la faible pente était orientée vers le soleil ou parallèlement à lui. Les deux bras de la boucle étaient en rapport linéaire avec la cosec β , mais les pentes de ces rapports étaient très différentes.

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Climatic and geographical relations of *Syringa vulgaris* L. and their agricultural applications

J. M. Caprio

Agricultural Experiment Station, Montana State University,
Bozeman, Montana (United States of America)

Annual variations in the spring weather of temperate regions play an important role in the production of perennial deciduous tree crops. Much potential fruit crop is frequently lost in some areas due to the occurrence of a severe freeze at a time when the plant is at the critical bloom stage. While it is a common observation that the time of bloom of a given crop at a given place varies from year to year, the relationship between the meteorological environment and these time-variations of bloom date is not known precisely. An understanding of the causes of the annual variation in the time of bloom would help in planning remedial measures in the problem mentioned above, as well as in other aspects of agricultural production.

In this study, an attempt is made to elucidate the relationship between the environment and time-variations in bloom dates through an analysis of phenological information on *Syringa vulgaris* L.

EXPERIMENTAL

Information on mean "begin bloom" date of this perennial woody shrub for the period 1957-66 were determined for a large number of locations throughout western United States (Caprio, 1966). Mean monthly maximum and minimum temperatures for the ten-year period 1951-60 were available for 360 locations where phenological data on the purple common lilac were also recorded (United States Department of Commerce, 1965). It was assumed that the monthly mean values represented the mean temperature of the middle of each month. A polynomial expressing temperature as a function of time was fitted through the seven known points of temperature from January through July, by regression analysis. Thus, the mean maximum temperature at any point in time for a given station is expressed as:

$$T_{\max} = a + bt + ct^2 + dt^3$$

in which T_{\max} is mean maximum temperature on any date t (1 March is considered as date number one).

Similarly, the mean minimum temperature at any point in time for a given station is expressed as:

$$T_{\min} = e + ft + gt^2 + ht^3.$$

The coefficients, a, b, c , and d thus describe the temperature distribution for maximum temperature and the coefficients e, f, g and h describe the temperature distribution for minimum temperature.

In order to determine whether lilac "begin bloom" date is related to temperature distribution, bloom dates for the 360 stations were expressed as a function of these eight coefficients by regression analysis. The results of the analysis are given in Tables 1 to 4. Table 1 gives the results of the regression of "begin bloom" date on the eight temperature coefficients for the 360 stations throughout the Western Region.

The relationship, as indicated by the F-test, is highly significant. The square of the multiple correlation coefficient indicates that 93 per cent of the variance of the dependent variable is accounted for by the regression. The standard error of estimate is 5.8 days. The t-tests indicated a highly significant relation between the "begin bloom" date and the temperature coefficients a, b and e . The remaining temperature coefficients do not contribute significantly to the relationship.

The t-tests in this analysis suggest that date of bloom is more dependent on minimum temperature than on maximum temperature. While only the zero-time temperature intercept is significant for maximum temperature, as indicated by the t-test for e , both the zero-time intercept (a) and the linear coefficient (b) for minimum temperature are significant.

Table 2 gives the results of the regression of "begin bloom" date on latitude, elevation and the eight temperature coefficients for the 360 stations throughout the Western Region.

TABLE 1. Lilac "begin bloom" date as a function of eight temperature coefficients for data from throughout the Western Region

Variable	Mean	Regression coefficient	<i>t</i>
<i>a</i>	+23.73	-1.730	-16.83
<i>b</i>	+0.1643	-110.3	-8.07
<i>c</i>	+0.1437 (10^{-2})	-3013	-1.19
<i>d</i>	-0.7708 (10^{-5})	-0.2041 (10^6)	-0.58
<i>e</i>	+48.14	-1.338	-16.31
<i>f</i>	+0.2354	-17.59	-1.32
<i>g</i>	+0.1364 (10^{-2})	+1624	+0.71
<i>h</i>	-0.7225 (10^{-5})	-0.1206 (10^6)	+0.42
<i>y</i>	63.25 (Dependent)		
Source of variation		D.F.	S.S. M.S. F
Attributable to regression		8	148396 18549.4 551.87
Deviation from regression		351	11797.6 33.6122
Total (<i>N</i> = 360)		359	160193
<i>R</i> ²	= 0.9264		
S.E.	= 5.798		

Note: D.F. = degrees of freedom
S.S. = sum of squares
M.S. = mean square
F = ratio of mean squares

*R*² = square of the multiple correlation coefficient
S.E. = standard error
t = Student's *t*

TABLE 2. Lilac "begin bloom" date as a function of latitude, elevation and eight temperature coefficients throughout the Western Region

Variable	Mean	Regression coefficient	<i>t</i>
Region			
Latitude	+41.62	+1.939	+7.94
Elevation	+3564	+0.4429 (10^{-2})	+9.75
<i>a</i>	+23.73	-1.143	-9.67
<i>b</i>	+0.1643	-106.3	-8.70
<i>c</i>	+0.1437 (10^{-2})	-0.1106 (10^5)	-4.60
<i>d</i>	-0.7708 (10^{-5})	-0.1442 (10^7)	-4.19
<i>e</i>	+48.14	-0.5082	-3.54
<i>f</i>	+0.2354	-10.68	-0.90
<i>g</i>	+0.1364 (10^{-2})	+4255	+2.00
<i>h</i>	-0.7225 (10^{-5})	+0.3559 (10^6)	+1.38
<i>y</i>	+63.25 (Dependent)		
Source of variation		D.F.	S.S. M.S. F
Attributable to regression		10	150927 15092.7 568.44
Deviation from regression		349	9266.38 26.5512
Total (<i>N</i> = 360)		359	160193
<i>R</i> ²	= 0.9422		
S.E.	= 5.153		

See note in Table 1.

TABLE 3. Lilac "begin bloom" date as a function of eight temperature coefficients for Idaho, Montana and Wyoming

Variable	Mean	Regression coefficient			
<i>a</i>	+16.79	-2.197	-9.98		
<i>b</i>	+0.2091	-170.4	-9.78		
<i>c</i>	+0.1752 (10^{-2})	-0.1133 (10^6)	-3.00		
<i>d</i>	-0.1065 (10^{-4})	-0.9114 (10^6)	-1.52		
<i>e</i>	+40.65	-1.135	-6.76		
<i>f</i>	+0.2632	-26.18	-0.88		
<i>g</i>	+0.1683 (10^{-2})	+2566	+0.50		
<i>h</i>	-0.8843 (10^{-5})	+0.5834 (10^6)	+0.74		
<i>y</i>	+79.70 (Dependent)				
Source of variation		D.F.	S.S.	M.S.	F
Attributable to regression		8	14731.5	1841.44	107.27
Deviation from regression		113	1939.89		
Total (<i>N</i> = 122)		121	16671.4	17.1672	
<i>R</i> ²	= 0.8836				
S.E.	= 4.143				

See note in Table 1.

TABLE 4. Lilac "begin bloom" date as a function of latitude, elevation and eight temperature coefficients for Idaho, Montana and Wyoming

Variable	Mean	Regression coefficient	<i>t</i>		
Latitude	+44.76	+0.9156	+1.76		
Elevation	+4039	+0.2211 (10^{-2})	+2.36		
<i>a</i>	+16.79	-1.854	-6.71		
<i>b</i>	+0.2091	-160.3	-8.65		
<i>c</i>	+0.1752 (10^{-2})	-0.1249 (10^5)	-3.24		
<i>d</i>	-0.1065 (10^{-4})	-0.1259 (10^7)	-1.97		
<i>e</i>	+40.65	-0.8079	-3.12		
<i>f</i>	+0.2632	+5.546	+0.16		
<i>g</i>	+0.1683 (10^{-2})	+5513	+1.01		
<i>h</i>	-0.8843 (10^{-5})	+0.9202 (10^6)	+1.14		
<i>y</i>	+79.70 (Dependent)				
Source of variation		D.F.	S.S.	M.S.	F
Attributable to regression		10	14826.0	1482.60	89.18
Deviation from regression		111	1845.37	16.6250	
Total (<i>N</i> = 122)		121	16671.4		
<i>R</i> ²	= 0.8893				
S.E.	= 4.077				

See note in Table 1

Again, the total relationship is highly significant, as indicated by the F-test. Ninety-four per cent of the variance of bloom date is accounted for by the regression. The standard error of estimate is 5.2 days. Both latitude and elevation, as well as the temperature coefficients *a*, *b*, *c*, *d* and *e*, are highly significant. The regression coefficient for latitude indicates that bloom occurs 1.9 days later for each degree of latitude. Each 100 ft (30.5 m) of elevation is associated with a 0.44-day later bloom date. Since temperature coefficients are also

independent variables in this equation, the effects of the geographical co-ordinates on bloom dates are not as large as when only geographical co-ordinates are considered as independent variables. This is because temperature decreases with increasing latitude and increasing elevation and the date of bloom occurs at a later date in colder climates.

Since data from throughout the Western Region includes information from areas where delayed foliation is known to occur because of inadequate winter chilling,

similar analyses were conducted for an area in the north-eastern part of the region consisting of the states of Idaho, Montana and Wyoming. Table 3 gives the results of the regression of "begin bloom" date on the eight temperature coefficients for the 122 stations in this area for which both temperature and phenological information were available.

The relationship again proved to be highly significant, as indicated by the F-test. Eighty-eight per cent of the variability of bloom date is accounted for by the regression. The standard error of estimate is 4.1 days. The t-tests indicate a highly significant correlation between the dependent variable and the temperature coefficients a , b , c and e . Thus, while three minimum temperature coefficients (a , b and c) are significant, only one maximum temperature coefficient (e) is significant. The higher t values for the minimum temperature coefficients again suggest that date of "begin bloom" is more dependent on minimum temperatures than on maximum temperatures.

Table 4 gives the results of the regression of "begin bloom" date on latitude, elevation and the eight temperature coefficients for the 122 stations in Idaho, Montana and Wyoming.

The relationship is highly significant, as indicated by the F value of 89.18. Eighty-nine per cent of the variability of "begin bloom" date is accounted for by the

regression. The standard error of estimate is 4.1 days. In contrast with the analysis of the whole region, neither latitude nor elevation was shown to be highly significant by the t -test. Elevation, however, is significant at the 5 per cent level. The t -tests indicate a highly significant correlation between the dependent variable and the temperature coefficients a , b , c and e . The high t values for minimum temperature coefficients in this analysis again substantiate the results of all three of the previous regressions, which suggest that "begin bloom" date is more dependent on minimum temperatures than on maximum temperatures.

CONCLUSIONS

The results of this study, which suggest that minimum temperatures play a dominant role in determining the date of bloom, may have important agricultural implications. If the normal time sequence of minimum temperatures does play a dominant role in determining the time of bloom of deciduous fruit crops, it would appear that heat-unit systems which do not make a distinction between minimum and maximum temperature effects would have only limited application. The results of this study appear to suggest the possibility that the time of bloom could be partially affected by such factors as preconditioning and soil temperature.

Résumé

Relations climatiques et géographiques des dates de floraison de Syringa vulgaris L. et leurs applications en agriculture (J. M. Caprio)

Les analyses de régression entre les dates moyennes du commencement de la floraison de *Syringa vulgaris* L. et les coefficients polynômes, exprimant la variation diachronique des températures journalières normales maximale et minimale en 360 stations, indiquent une relation très étroite entre la date de floraison et la température dans toute la région ouest des États-Unis; 90 % environ de la variance des dates de floraison s'expliquent par les coefficients de température. Les analyses de régression suggèrent que la série diachronique normale de la température minimale peut avoir plus d'influence sur

la date moyenne du commencement de la floraison que la série diachronique normale de la température maximale. En utilisant les données des stations des onze États de l'Ouest, la latitude et l'altitude sont apparues très significatives quand ces variables étaient incluses dans la régression avec les huit coefficients de température. Toutefois, ni la latitude ni l'altitude n'étaient très significatives pour la même régression quand seules étaient utilisées les données des États septentrionaux de l'Idaho, du Montana et du Wyoming. Le degré d'association élevé entre la date moyenne de la floraison et la série diachronique normale de la température minimale peut être partiellement en rapport avec les effets de facteurs tels que le préconditionnement et la température du sol.

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Un index bioclimatique complexe pour l'accumulation de la biomasse végétale

R. J. Florov

École supérieure de sylviculture, Sofia (Bulgarie)

L'assimilation des organismes vivants à des systèmes ouverts faite par L. Bertalaufy a créé de nouvelles conditions favorables à l'application en biologie des principes physiques.

Une particularité caractéristique des organismes vivants en tant que systèmes ouverts est l'autorégulation, qui leur permet de conserver un état stationnaire quand la production d'entropie (l'entropie de dissipation) a des valeurs minimes pour des conditions données du milieu.

Les plantes sont des systèmes ouverts vivants qui assurent pour eux-mêmes un état stationnaire adéquat pendant la période de végétation par le moyen de l'homéostase de l'appareil stomatal leur permettant de maintenir une transpiration sans obstacle et une température basse du feuillage. En de telles conditions, notamment, l'entropie de dissipation a des valeurs minimes.

D'après les recherches des dernières années, l'entropie de dissipation acquiert une signification très importante dans la biologie. Ayant en vue l'analogie de Branson, Patten conclut que l'entropie peut être regardée comme très étroitement liée avec la respiration. Cette conception est acceptée aussi par Galoux (1964). Les deux auteurs déterminent l'entropie en mesurant la respiration.

Nous déterminons l'entropie de dissipation directement sur la base de la thermodynamique des phénomènes stationnaires irréversibles par comparaison avec la respiration.

Pour déterminer l'entropie de dissipation du feuillage des plantes, nous partons des travaux de Denbigh (1954) et Veinik (1965), à la base desquels se trouve la théorie d'Onsager. Ce qui est remarquable dans cette théorie est la liaison entre l'entropie de dissipation et les forces et vitesses thermodynamiques comme elles ont été dénommées par Onsager. Ce sont des gradients de température, le potentiel chimique, etc., et les flux: flux de chaleur, de matière, etc. A partir de ces données et sur

la base de notre interprétation du potentiel chimique entre le feuillage et l'air ambiant comme pression de la vapeur d'eau, nous avons déduit la formule suivante pour la vitesse de l'entropie de dissipation dans le feuillage des plantes:

$$\sigma_d = P \frac{\Delta T}{T^2} + L.E \frac{\Delta^2 q}{T} \quad [1]$$

où:

σ_d = vitesse de l'entropie de dissipation en cal/cm² mn °K;
 P = flux de chaleur feuille - air en cal/cm² mn;
 ΔT = différence de température feuille - air;
 T = température absolue moyenne feuille - air;
 $L.E$ = chaleur consommée par la transpiration en cal/cm² mn;
 Δq = différence entre l'humidité spécifique de l'air au niveau des stomates et l'humidité spécifique de l'air ambiant en g/g.

En outre, une analogie a été déterminée entre le canal d'information avec bruit selon Channon (1963) et la plante, où l'entropie conditionnelle H_y/x de Channon représente en effet l'entropie de dissipation σ_d et la plante est représentée comme bilan d'entropies

$$\sigma_{in} = \sigma_{ex} + \sigma_d \quad [2]$$

où

σ_{in} représente la négentropie de la radiation solaire assimilée pendant la photosynthèse brute;
 σ_{ex} la négentropie de la biomasse accumulée;
 σ_d l'entropie de dissipation.

En multipliant [2] par T , on obtient:

$$T\sigma_{in} = T\sigma_{ex} + T\sigma_d \quad [3]$$

en cal/cm² mn, où

$T\sigma_{in}$ représente la photosynthèse brute;

$T\sigma_{ex}$ la biomasse accumulée;

$T\sigma_d$ la perte des assimilats pendant la respiration.

Numéro	Localité	Altitude	Coefficient d'utilisation de la photosynthèse brute	Production moyenne annuelle à cent ans, tiges et branches		Différence (mesurée - calculée)
				m	%	
				m³/ha	m³/ha	m³/ha
1. <i>Pinus sylvestris</i> L.						
1	Joundola	1 390	0,997	6,50	6,16	-0,34
2	Joundola	1 380	0,969	8,23	8,53	0,30
3	Joundola	1 380	0,995	8,00	7,70	-0,30
4	Joundola	1 380	0,910	8,70	10,20	1,50
5	Joundola	1 580	0,837	8,00	10,60	2,60
6	Joundola	1 520	1,000	5,70	5,31	-0,39
7	Joundola	1 440	0,993	11,90	11,70	-0,20
8	Joundola	1 460	0,949	7,30	8,00	0,70
9	Joundola	1 500	0,982	6,50	6,50	0,00
10	Joundola	1 360	0,947	9,40	10,13	0,73
11	Joundola	1 330	1,060	6,50	4,90	-1,60
12	Joundola	1 300	0,925	7,30	8,50	1,20
13	Joundola	1 320	0,980	9,63	9,70	0,07
14	Joundola	1 520	0,982	11,90	11,90	0,00
15	Joundola	1 450	0,995	11,90	11,70	-0,20
16	Mouglia	1 350	0,893	11,0	13,26	2,26
17	Mouglia	1 750	0,997	6,50	6,80	0,30
18	Mouglia	1 700	1,030	6,50	5,77	-0,73
19	Mouglia	1 700	0,940	6,50	7,45	0,95
20	Jablanitza	420	1,010	8,70	8,00	-0,70
21	Jablanitza	420	0,931	10,10	11,40	0,30
22	Plachkovtzi	500	0,963	8,70	9,20	0,50
23	Kazanlak	380	1,050	7,30	5,27	-2,03
			<u>0,970</u>			<u>9,9</u>
2. <i>Picea excelsa</i> L.						
1	Joundola	1 510	1,172	17,10	17,10	0,00
2	Chepelare	1 380	1,204	17,10	16,30	-0,80
3	Chepelare	1 450	1,171	17,10	17,47	0,37
4	Chepelare	1 500	1,207	15,30	14,40	-0,90
5	Chepelare	1 200	1,184	17,10	16,75	-0,35
6	Ambaritza	680	1,211	21,50	20,30	-1,20
7	Choumen	230	1,150	17,10	17,71	0,62
8	Mouglia	1 600	1,172	13,60	13,60	0,00
9	Mouglia	1 700	1,196	8,50	7,90	-0,60
10	Mouglia	1 750	1,112	12,20	13,56	1,36
11	Predeal (Roumanie)	1 000	1,185	17,10	16,80	0,30
12	Poiana Mare (Roumanie)	1 000	1,185	17,10	16,80	0,30
			<u>1,180</u>			<u>4,0</u>
3. <i>Abies alba</i> L.						
1	Joundola	1 510	1,25	19,40	19,40	0,00
2	Mouglia	1 430	1,23	7,50	8,06	0,56
3	Mouglia	1 450	1,27	10,40	9,60	-0,80
4	Mouglia	1 200	1,22	13,90	14,90	1,00
5	Mouglia	1 500	1,26	7,50	7,20	-0,30
			<u>1,25</u>			<u>4,0</u>
						<u>5,3</u>

Sur la base des équations [1] et [3], des données ont été analysées dans des conditions naturelles de peuplements purs de *Pinus sylvestris* L., *Picea excelsa* L. et *Abies alba* L. La valeur annuelle moyenne de l'entropie de dissipation σ_d pendant la période de végétation a été déterminée en employant le bilan thermique du feuillage comme surface active des peuplements ou, plus précisément, la méthode de Boudyko (1956). L'accumulation de la biomasse végétale $T_{\sigma_{ex}}$ a été déterminée par des méthodes de dendrométrie sur le terrain. La somme de $T_{\sigma_{ex}}$ et T_{σ_d} , selon l'hypothèse, doit être égale à la photosynthèse brute. Si cela est vrai, la valeur du coefficient d'utilisation de la photosynthèse brute déterminée par la photosynthèse brute $T_{\sigma_{in}}$, divisée par la radiation solaire incidente moins la radiation reflétée par le feuillage, doit être une quantité constante, indépendamment des variations climatiques et de l'humidité du sol. Les résultats présentés dans les parties 1, 2 et 3 du tableau de la p. 424 montrent une assez bonne stabilité des valeurs du coefficient d'utilisation de la photosynthèse brute aux différentes conditions des stations forestières naturelles et les indices statistiques révèlent une probabilité suffisante.

En conséquence, l'entropie de dissipation dans le feuillage des plantes exprime quantitativement la perte des assimilats pendant la respiration. Cette perte augmente avec la diminution de l'humidité du sol.

La deuxième argumentation de l'hypothèse a été faite par le calcul de la productivité potentielle des stations naturelles forestières avec la formule suivante:

$$T_{\sigma_{ex}} = (Q + q)_n(1 - \alpha) \cdot 0,01 Cu - T_{\sigma_d} \quad [4]$$

où

$(Q + q)_n(1 - \alpha)$ représente la radiation solaire incidente moins la radiation reflétée par le feuillage;

n la nébulosité;

α l'albédo;

Cu est le coefficient d'utilisation de la photosynthèse brute en pourcentage.

Dans ce cas, le coefficient d'utilisation de la photosynthèse brute a été déterminé une seule fois dans des conditions optimales d'humidité du sol: 0,982 % pour *P. sylvestris*, 1,172 % pour *P. excelsa* et 1,25 % pour *A. alba*. Les résultats présentés dans les parties 1, 2 et 3 de tableau ci-contre, montrent une différence entre la productivité calculée et la productivité réelle (mesurée) de 10 % pour *P. sylvestris* et 5 % pour *P. excelsa* et *A. alba*.

En conclusion:

1. L'entropie de dissipation déterminée sur la base de la thermodynamique des phénomènes stationnaires irréversibles exprime quantitativement la perte des assimilats pendant la respiration;
2. On détermine l'entropie de dissipation dans le feuillage des plantes à l'aide de la différence de température feuille-air, la différence entre la pression des vapeurs d'eau au niveau des stomates et la pression des vapeurs d'eau dans l'air libre, le flux de chaleur feuille-air et la transpiration;
3. Les équations [1], [3] et [4] peuvent être utilisées comme base d'un système technique de régulation des paramètres du milieu pour obtenir une production maximale de biomasse végétale et pour calculer la vitesse de cette production dans des conditions naturelles ou artificielles.

Summary

A complex bioclimatic index for accumulation of vegetal biomass (R. J. Florov)

The entropy of dissipation, determined on the basis of the thermodynamics of the steady state, expresses quantitatively the losses of assimilates during respiration.

The author determines the dissipation entropy in the leaf system of plants by means of the leaf-air tempera-

ture difference, the difference between the water-vapour pressure at the leaf stomata level and in free air, the heat flux between the leaf and the air; and by means of the transpiration.

The proposed equations might be utilized as a basis of a technical system for regulating the environmental parameters to obtain a maximum production of vegetal biomass and to calculate the rate of production under natural and artificial conditions.

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A model of temperatures, transpiration rates and photosynthesis of sunlit and shaded leaves in vegetation canopies

P. C. Miller

Department of Biology,
Center for Regional Environmental Studies,
San Diego, California (United States of America)

INTRODUCTION

The physical and biological processes affecting primary production are many, and because of the complexity, the primary production process has been analysed with quantitative models to clarify significant parameters and underlying physiological processes. Previous models (Monsi and Saeki, 1953; Davidson and Philip, 1958; Monteith, 1965; Wit, 1965; Duncan *et al.*, 1967) have included constant respiration rates. They have not included the effects of evaporation on water stress, water stress on leaf resistance, and leaf resistance on primary production. Leaf and air temperatures have not been considered. These deficiencies may not be important in estimating the production of agricultural crops in temperate areas where reasonable primary production values are known and water is not severely limiting, but a more refined analysis is appropriate for plants in high temperatures or under water stress.

DESCRIPTION OF THE MODEL

The model uses the following as input data defining the environment: the daily courses of the solar zenith angle, total diffuse solar radiation, infra-red radiation from the sky, wind velocity, air temperature and humidity above the canopy; ground temperature below the canopy; and vertical profiles of air temperature and humidity in the canopy. The canopy is defined with data on: vertical distributions of leaf area index, leaf slope and leaf widths; the maximum and minimum leaf resistances; the leaf clustering factor; the extinction coefficients defining the photosynthesis-light and respiration-temperature curves. The model calculates profiles of the mean leaf temperatures for sunlit and

shaded leaves hourly as an intermediate variable. Since the temperature of the leaves depends on the infra-red radiation from other leaves, the leaf temperature profile is calculated with successive corrections of the radiation profile until the leaf temperature and radiation profiles do not change. The programme then calculates the energy budget and rates of transpiration, respiration and gross and net photosynthesis for sunlit and shaded leaves. Hourly, at each level, the total water loss and gross and net photosynthesis are calculated from weighted averages of sunlit and shaded leaves. After calculating, one-day summary tables of hourly transpiration and gross and net photosynthesis for each level are produced with totals for each level, each hour, and the 24-hr day.

The model is based on a heat transfer equation for a single leaf (Gates, 1962, 1965) modified to include a term to calculate processes of energy exchange for an average leaf of any orientation. The basic equation states that the absorbed energy from solar and infra-red radiation and convection is lost by infra-red radiation, convection and transpiration. Thus:

$$S_{abs} + IR_{abs} = IR \pm C + \lambda E. \quad (1)$$

S_{abs} and IR_{abs} are the absorbed solar and infra-red radiation; IR is the infra-red radiation lost from the leaf; C is the convective exchange which can be to or from the leaf, depending upon the temperatures of the leaf and air, and λE is the transpirational loss. The units are cal $cm^{-2} min^{-1}$.

In the expanded equation (Miller, 1967) leaf orientation is assumed to affect the energy absorbed from the direct solar beam, but not to affect the energy exchanged by infra-red radiation, convection, transpiration and diffuse and reflected solar radiation. Assuming that the leaves are oriented equally in all compass directions, and that leaves in a stratum do not shade each other, the energy budget of an average leaf in a given stratum in the canopy is:

$$\begin{aligned} & \frac{1}{2} [a_1 K S_d + (\% \text{ sky}) a_2 S_s + a_3 S_r] + \\ & + \frac{\epsilon}{2} [(\% \text{ sky}) I R_s + (1 - \% \text{ sky}) I R_{L+1} + I R_{up}] \quad (2) \\ & = \epsilon \sigma (T_1 = 273)^4 + 5.85 \times 10^{-3} (V)^{1/2} (W)^{-1/2} \\ & \quad (T_1 - T_a) + \lambda (\rho \omega_1 - \rho \omega_a) (r_1 + r_a)^{-1} \end{aligned}$$

where a is the absorbance of the leaf to solar radiation; S_d is the direct solar radiation beam measured on the horizontal in $\text{cal cm}^{-2} \text{ min}^{-1}$; S_s is the diffuse solar radiation from the sky; S_r is reflected solar radiation from below; ϵ is the emittance of the leaf; $I R$ is the infra-red radiation, subscripted s for sky radiation, $L + 1$ for radiation from leaves in the level above the level of interest, and up for the upward flux; σ is the Stefan-Boltzman constant; T_1 is the leaf temperature in $^{\circ}\text{C}$; V is the wind velocity in cm sec^{-1} ; $\rho \omega$ is the vapour density of the leaf, subscript 1, for the air, subscript a in g cm^{-3} ; r_1 and r_a are the resistances to water loss of the leaf and leaf boundary layer in min cm^{-1} . Equation (2) can be solved for leaf temperature and transpiration iteratively or by direct solution using approximations. Under cloudy conditions, S_d is zero.

K is the ratio of the area of the shadow cast by an inverted cone on to a horizontal surface to the area of the sides of the cone and is calculated from (Miller, 1969):

$$\text{when } \alpha \leq \beta; K = \cos \alpha \quad (3a)$$

$$\begin{aligned} \text{and when } \alpha < \beta; K = & (\cos \alpha) / 2 + (\sin \alpha) / (\pi \tan \beta) \\ & + (\cos \alpha / \pi) (20 - \sin 20) \quad (3b) \end{aligned}$$

where $\theta = \arctan(\cot \alpha \tan \beta)$; α is the leaf inclination from the horizontal, and the solar altitude. "% sky" is the percentage of the sky hemisphere "seen" by a leaf at α level and is calculated from:

$$(\% \text{ sky})_L = [\sum (1 - c K_i) F_{\varphi_i}] L \quad (4)$$

where K_i is the extinction coefficient for radiation passing through the canopy with an angle of incidence i , calculated with equation (3); c is a leaf clustering factor; φ_i is the percentage of total sky radiation received on a horizontal surface from a band with a mean inclination i (Anderson, 1966; Duncan *et al.*, 1967; Wit, 1965); and F is the leaf area index above the level.

Photosynthesis is calculated from two equations for individual leaves, one relating photosynthesis to absorbed solar radiation (Monteith, 1965) and the other relating photosynthesis to leaf resistance (Gaastra, 1963).

$$P_g = [a_p + b_p / S_{abs}]^{-1} \quad (5a)$$

$$P_g = ([\text{CO}_2]_{\text{air}} - [\text{CO}_2]_{\text{leaf}}) (1.72 r_1 + r_a + r_{me})^{-1}. \quad (5b)$$

Photosynthesis is calculated by both equations (5a) and (5b) and the smaller photosynthetic rate is chosen, permitting photosynthesis to be both light and resistance limited. Respiration is calculated as:

$$R = R_0 Q_{10}^{0.1(T-T_0)}. \quad (6)$$

Net photosynthesis is calculated as gross photosynthesis minus respiration.

Leaf resistance to water loss (r_1) is related to leaf water deficit (WD) and absorbed solar radiation by two equations:

$$r_1 = r_{1\min} - \text{WD} / (10.75 - 40.0 \text{ WD}) \quad (7a)$$

$$r_1 = r_{1\min} + 0.002 / (0.001 + S_{abs}). \quad (7b)$$

Leaf water deficit is calculated as the difference between water uptake and water loss over a period of time added to the previous water deficit. With equation (7a) leaf resistances remain low until a water deficit of 20 per cent develops, then increase abruptly so that a deficit of 25 per cent is not exceeded. Leaf resistance is calculated by equations 7a and 7b, and the larger of the two resistances is chosen to allow stomates to be opened and to be closed by leaf water deficit. The assumption is made that leaves are in the sun and shade at random, no particular leaf being in the sun for more than 5 min at a time. The leaf resistances and water deficits are averages for all leaves in the canopy at a level.

Within the canopy, direct solar radiation decreases, depending upon the vertical distribution of leaf area, leaf inclination, and solar altitude; and the downward stream of infra-red radiation commonly increases. The percentage of leaves at a level which are sunlit is given by:

$$(\% \text{ sun})_L = (1 - K) F_L. \quad (8)$$

K is calculated by equation (3), and F_L is the leaf area index above the level.

VALIDATION

METHODS

Microclimate, stand structures, leaf temperatures and leaf resistances were measured in low uniform red mangrove (*Rhizophora mangle* Roxb.) stands located in Florida, south of Miami, at approximately longitude $80^{\circ} 3' \text{ W}$, latitude $25^{\circ} 4' \text{ N}$. In 1968, profiles of radiation, air temperature, humidity and wind were measured hourly through a 44-hr period on 20 and 21 June on a 24-point multipoint recorder and a portable potentiometer. Additional measurements of radiation were made through the daylight hours on 23 June, to measure direct and diffuse solar radiation. Leaf temperatures were measured through the 44-hr period. Leaf resistances of red and white mangroves and buttonwood were measured through the day, while microclimatic measurements were being taken in different sites where three or all four of the mangrove species occurred together. In January, profiles of five components of radiation, air temperature, humidity and wind were measured at six levels and nineteen leaf temperatures were measured at three levels ten times every 15 min on a Vidar data-acquisition system.

Solar and infra-red radiation were measured as discussed by Miller (1967). Air temperatures and humidities were measured with aspirated psychrometers;

ground temperatures with thermocouples near the surface of the ground or water; and leaf temperatures with thermocouples imbedded in the leaves. Wind was measured with three cup anemometers and with five heated thermocouple anemometers in June and with a Thornthwaite cup anemometer system in January.

Leaf resistances were measured bi-hourly or hourly at the top, middle, and bottom of the canopy. Leaf resistances were measured similarly to Bavel *et al.* (1967) in 1968 and similarly to Kanemasu *et al.* (1969) at the other times. Values for a_p and b_p in equation (5a) were estimated from Golley *et al.* (1962), assuming a correspondence of 7,000 ft candles per 1 cal $\text{cm}^{-2} \text{min}^{-1}$ solar radiation (List, 1963). Fitting equation (5a) to their mean photosynthesis values gave a value of 2.4 for a_p and fitting the equation to their maximum values gave a value of 1.38. A value of 0.03, which is comparable to Monteith (1965), allowing for use of absorbed rather than incident solar radiation, was calculated for b_p . The values for a_p and cell resistance must correspond with the measured leaf resistance. Since leaf resistances of 0.05 and a_p value of 1.38 were the lowest values measured, these values were used in the calculations and cell resistance of 0.22 was assumed.

Golley *et al.* (1962) gave average night respiration rates of 0.0898 g organic matter $\text{m}^{-2} \text{hr}^{-1}$ for sun leaves; 0.0930 g organic matter $\text{m}^{-2} \text{hr}^{-1}$ for seedling leaves; in the simulations, R_0 was set equal to 0.91 g organic matter $\text{m}^{-2} \text{hr}^{-1}$, T_0 equal to 23°C and Q_{10} arbitrarily set equal to 2.0.

RESULTS

The mean temperatures of sunlit and shaded leaves at different levels in the canopy were predicted within 1.0°C of the observed mean leaf temperatures with a variety of environmental conditions. The calculated upward infra-red measurements within the canopy were 0.02 cal $\text{cm}^{-2} \text{min}^{-1}$ of the observed.

The qualitative pattern of increased leaf resistances occurring earlier in the day at the top of the canopy than at the bottom occurred in both the measurements and calculations for June. The January measurements indicated no increase in leaf resistance due to water deficit and the model calculated none. The same rate of water uptake was used in all calculations.

Evapotranspiration rates from the canopy and substrate, calculated hourly with the June data using the heat balance-Bowen ratio method, were about 0.67 cm day $^{-1}$. The pan evaporation for two South Florida Weather Bureau stations in June was 0.53 and 0.58 cm day $^{-1}$ (Weather Bureau, 1950). Transpiration rates, calculated for an individual leaf and multiplied by the leaf area index, gave a transpirational loss from the canopy of 0.15 cm day $^{-1}$. Transpirational loss from the canopy calculated with the model was about 0.12 cm day $^{-1}$, which was less than that calculated

from the individual leaf method because leaf resistances in the model were higher. Transpirational water loss was about 22 per cent of the total water loss, which is similar to that for some irrigated crops, and accounts for much of the discrepancy between the mangrove evapotranspiration and the pan evaporation.

Primary production calculated with the model was comparable to Golley *et al.* (1962). Golley's estimates correspond with 5.9 g organic matter $\text{m}^{-2} \text{day}^{-1}$ for net photosynthesis of a stand with a leaf area index of 2.6, and the model calculated 5.6. Gross photosynthesis per unit leaf area was greater in the model because a lower a_p value was used, but respiration was also higher, probably because it was allowed to increase with temperature. An estimate of mean daily photosynthesis in June and January for each level in the canopy, weighted according to the probability of receiving different total solar radiation amounts in each month, gave an average annual production of 2.7 g organic matter $\text{m}^{-2} \text{day}^{-1}$. The mean net photosynthesis at the bottom level was negative in both June and January. The total leaf area used in the simulation was 2.67, whereas the leaf area indices measured in four stands ranged from 2.21 to 2.52. The leaf area index used in the simulation may have been above an "optimum" leaf area index, and extra leaf area, which would be parasitic according to the model, should be lost. The leaf area index used for the lowest level was 0.20 and the loss of this leaf area would give a leaf area for the stand similar to the observed. Acclimation of the photosynthetic or respiratory processes due to shading was not included in the simulations, and would have increased the productive leaf area index above the "optimum". The second lowest level showed a positive net production in June and a negative net production in January with an annual mean of -0.003 g organic matter $\text{m}^{-2} \text{day}^{-1}$. Levels above this had positive production rates in both June and January.

INFLUENCE OF CANOPY ARCHITECTURE ON PRODUCTION AND TRANSPERSION

The influence of properties of the vegetation canopy on production and transpiration was ascertained by defining a standard day (Table 1) and canopy (Table 2) and varying one property at a time over a reasonable range of values. The model used hourly values in the calculations, but only values for every other hour are shown. Some of the conclusions will apply to any canopy, but some applications must be made cautiously due to the various interactions between parameters.

The daily courses of the vertical distributions of leaf temperatures, leaf resistances, leaf water deficits, transpiration, net photosynthesis and transpiration efficiency in the canopy were calculated for the standard day (Fig. 1) and one in which there is no direct solar radiation (Fig. 2).

TABLE 1. Values for the daily courses of environmental variables used to define the standard day

	02.00	04.00	06.00	08.00	10.00	Hour, solar time						
						12.00	14.00	16.00	18.00	20.00	22.00	24.00
Solar altitude (degrees)	0	0	10	35	63	89	63	35	10	0	0	0
S_{total} (cal $\text{cm}^{-2} \text{min}^{-1}$)	0	0	0.01	0.50	0.99	1.16	1.12	0.81	0.18	0	0	0
S_{diff} (cal $\text{cm}^{-2} \text{min}^{-1}$)	0	0	0.01	0.07	0.16	0.20	0.19	0.12	0.02	0	0	0
IR_{sky} (cal $\text{cm}^{-2} \text{min}^{-1}$)	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60
Wind (cm sec^{-1})	60.0	60.0	80.0	125.0	175.0	225.0	225.0	175.0	100.0	60.0	60.0	60.0
Air temperature ($^{\circ}\text{C}$)	23.0	23.0	23.0	27.5	29.0	30.0	30.0	30.0	28.0	25.5	23.0	23.0
Humidity ($10^{-6} \text{ g cm}^{-3}$)	20.2	20.0	20.0	20.5	19.5	20.5	20.5	20.5	20.0	20.0	20.0	20.0
Ground temperature ($^{\circ}\text{C}$)	25.6	25.1	24.1	24.3	24.2	25.0	25.8	26.7	26.6	26.5	26.4	26.4

The sun rises at about 06.00 hr and the temperatures of sunlit and shaded leaves begin to differ, although both are below air temperature. By 08.00 hr the temperature of sunlit and shaded leaves differ further; sunlit leaves within the canopy are hotter than sunlit leaves at the top of the canopy, and shaded leaves within the canopy are cooler than shaded leaves at the top of the canopy. By 10.00 hr the temperatures of sunlit leaves are similar throughout the canopy, although temperatures of sunlit leaves at level 5 are lower than the other sunlit leaves because of low leaf resistances and high transpiration rates. Temperatures of shaded leaves are above air temperature at the top of the canopy, and below air temperature at and beneath level 5. By 12.00 and 14.00 hr a similar pattern has occurred, except that the level of minimum sunlit leaf temperature has dropped to level 4, due to stomatal closure and decreased transpiration at level 5. At 18.00 hr temperatures of sunlit leaves are above and shaded leaves below air temperature. At night there is no difference between the temperatures of leaves which were either sunlit or shaded during the day.

Leaf resistances are maximal at night because there is no absorbed solar radiation. By 18.00 hr leaf resistances at all levels are relatively low, but by 10.00 hr leaf resistances at the top have increased because of

high leaf water deficits. As water deficits develop at lower levels, leaf resistances increase deeper in the canopy.

Leaf water deficits are assumed to equal zero before the sun rises. As stomates open and transpiration begins, a water deficit develops in leaves at the top of the canopy first because leaves at the top are sunlit and transpire at the sunlit rate longer than leaves within the canopy.

Transpiration at night is negligible because of high leaf resistances and almost saturated air. At 06.00 and 18.00 hr, transpiration is higher at the top than within the canopy because of lower leaf resistances and higher wind speeds. By 10.00 hr transpiration decreases, and temperatures of shaded leaves at the top of the canopy rise above air temperature. The level at which the highest transpiration rates occur decreases through the day as stomatal closure occurs at levels near the top of the canopy. At all times of the day sunlit leaves transpire more than shaded leaves.

The vertical profiles of net photosynthesis follow the vertical profiles of transpiration since both were often limited by leaf resistances to the diffusion of gases. Net photosynthesis is negative at night since respiration exceeds photosynthesis. Net photosynthesis rates of sunlit and shaded leaves are similar because the higher photosynthesis of sunlit leaves occur with higher

TABLE 2. Values defining the standard canopy used to estimate the influence of canopy parameters on physiological responses. F is the leaf area index in the stratum

Height interval	F	Leaf density (mg fresh weight cm^{-2} leaf surface)	Width (cm)	Leaf slope (degrees)	Albedo (%)	Absorbance (%)	r_1 max (min cm^{-1})	r_1 min (min cm^{-1})	a_p ($\text{gm}^{-1} \text{m}^2 \text{hr}$)	b_p (cal cm^{-2} min^{-1})	
1.75	2.00	0.015	50	4.0	60	0.18	0.60	2.00	0.05	1.38	0.030
1.50	1.75	0.060	66	4.0	54	0.18	0.60	2.00	0.05	1.38	0.030
1.25	1.50	0.405	60	4.0	48	0.18	0.60	2.00	0.05	1.38	0.030
1.00	1.25	0.560	57	4.0	42	0.18	0.60	2.00	0.05	1.38	0.030
0.75	1.00	0.655	54	4.0	36	0.18	0.60	2.00	0.05	1.38	0.030
0.50	0.75	0.515	52	4.0	30	0.18	0.60	2.00	0.05	1.38	0.030
0.25	0.50	0.260	48	4.0	24	0.18	0.60	2.00	0.05	1.38	0.030
0.00	0.25	0.200	29	4.0	18	0.18	0.60	2.00	0.05	1.38	0.030

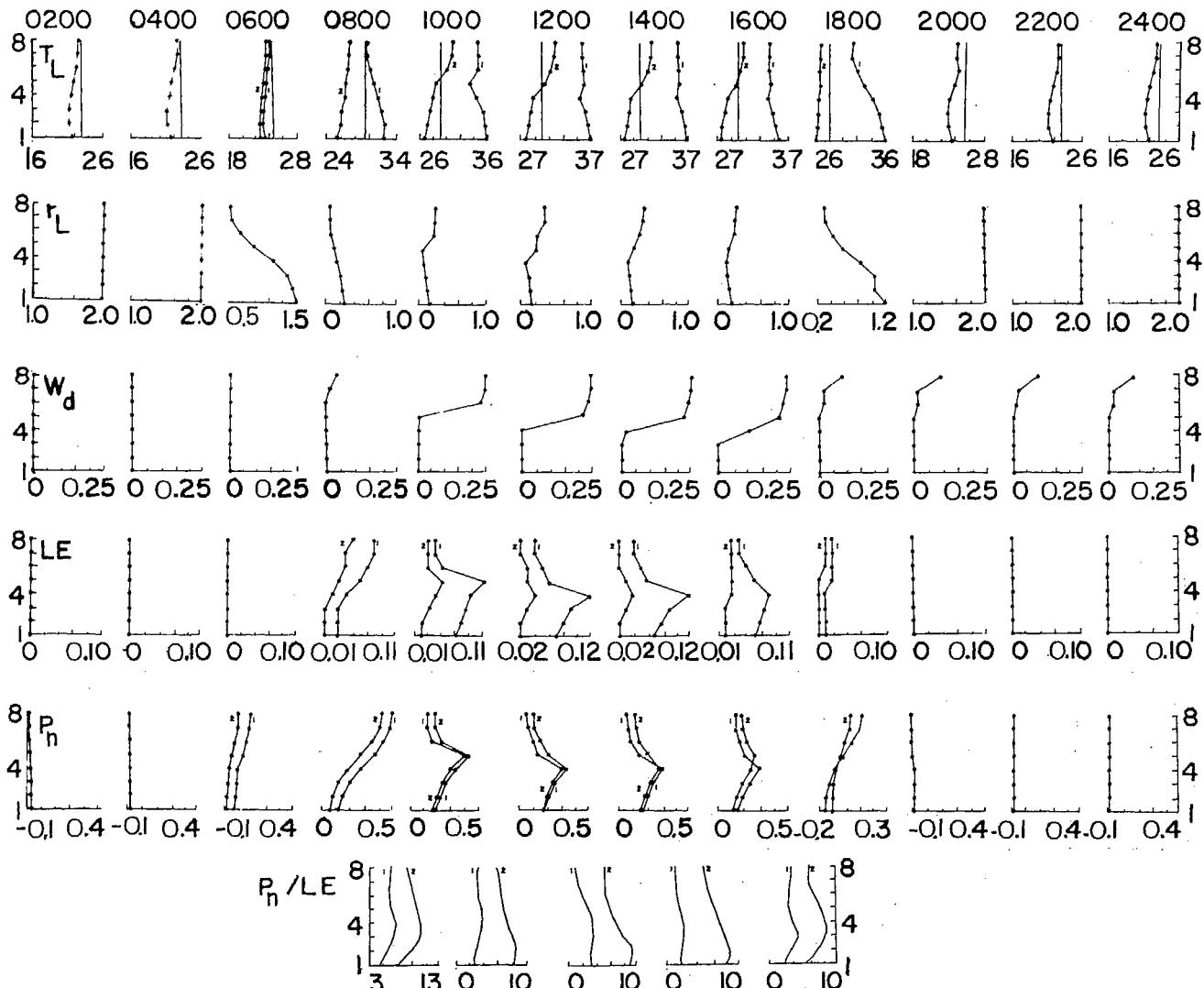


FIG. 1. Daily courses of profiles of temperature (T_L), leaf resistance (r_L), water deficit (W_d), transpiration (LE), net photosynthesis (P_n) and transpiration efficiency (P_n/LE) of sunlit and shaded leaves on a clear day with total radiation of 697 cal cm^{-2} day⁻¹ and high solar altitudes. Air temperatures used as input data are shown by the vertical line in the leaf temperature graphs. Units for leaf temperature are °C; leaf resistance, min cm^{-1} ; water deficit, percentage; transpiration, $\text{cal cm}^{-2} \text{min}^{-1}$; net photosynthesis, $\text{g dry organic matter m}^{-2} \text{hr}^{-1}$; and transpiration efficiency, $(\text{g organic matter m}^{-2} \text{hr}^{-1})/(\text{cal cm}^{-2} \text{min}^{-1})$, which equals 10.25 $\text{g dry organic matter produced per g water lost}$.

respiration rates of the sunlit leaves. Net photosynthesis of sunlit leaves is usually higher than that of shaded leaves, but by 09.00 hr leaf resistances limit photosynthesis of both sunlit and shaded leaves at the top of the canopy, and the higher respiration rates of the sunlit leaves reduce the net photosynthesis to below that of shaded leaves. Within the canopy, leaf resistances are lower, gross photosynthesis is higher, and the net photosynthesis of sunlit leaves is slightly higher than that of shaded leaves.

The transpiration efficiency is the organic matter produced per unit of water lost. Shaded leaves have

higher transpiration efficiencies than sunlit leaves throughout the canopy, and both sunlit and shaded leaves have higher efficiencies within the canopy, than at the top. As solar altitude increases, the highest transpiration efficiencies occur lower in the canopy. The highest transpiration efficiencies occur lower in the canopy than the highest net photosynthesis rates throughout the day.

On a completely overcast day (Fig. 2), there is no differentiation between sunlit and shaded leaves, since there is no direct solar beam. Leaf temperatures were below air temperatures throughout the day and decreased

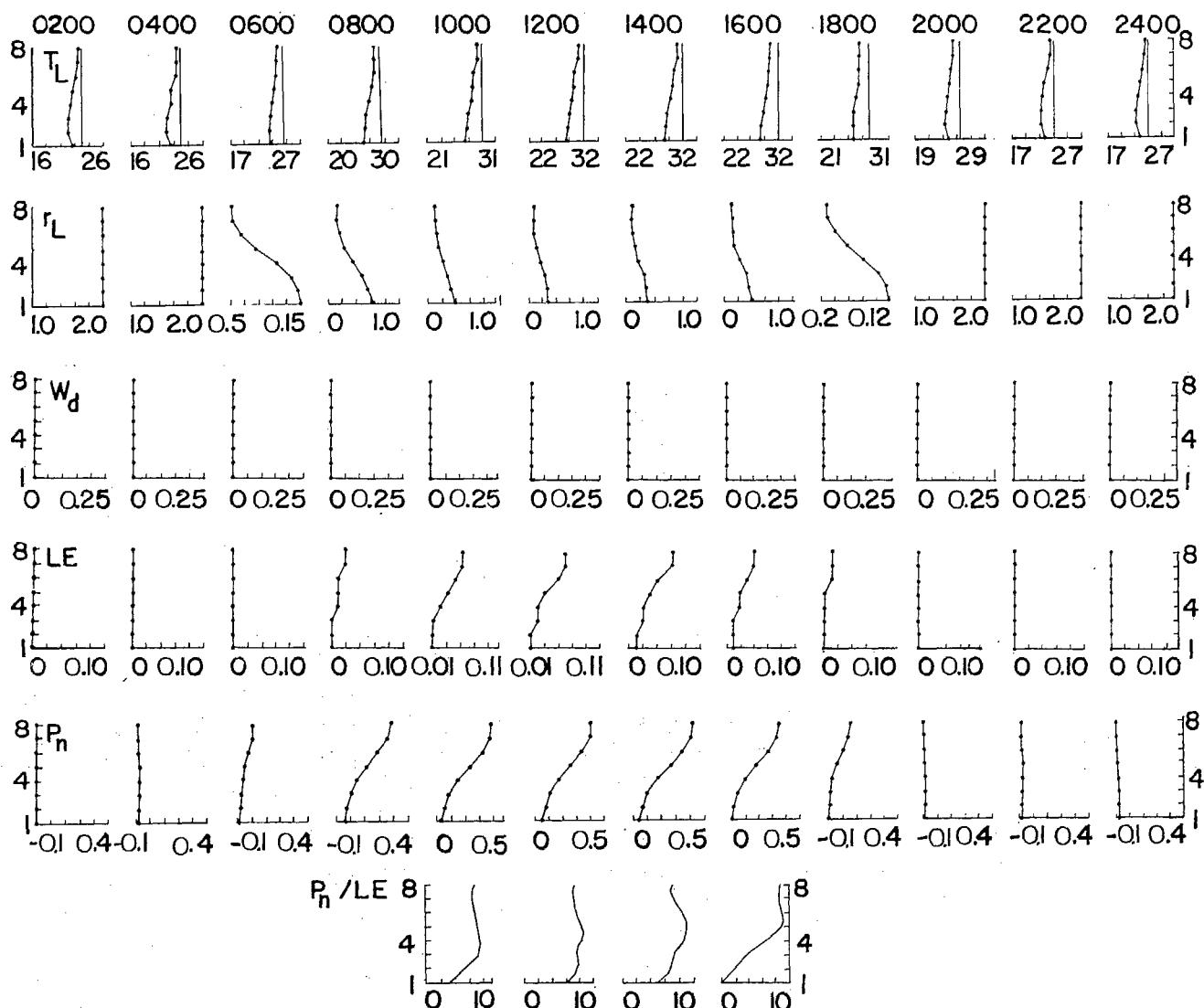


FIG. 2. Daily course of profiles of temperature (T_L), leaf resistance (r_L), water deficit (W_d), transpiration (LE), net photosynthesis (P_n) and transpiration efficiencies (P_n/LE) of sunlit and shaded leaves on an overcast day with $90 \text{ cal cm}^{-2} \text{ day}^{-1}$ total solar radiation. Units are the same as in Figure 1.

with depth in the canopy. A leaf water deficit never developed and leaf resistances were limited by absorbed solar radiation. Thus, leaf resistances were low at the top of the canopy and increased within the canopy. Transpiration and net photosynthesis were higher at the top and transpiration efficiencies were higher within the canopy, but at a higher level than in Figure 1.

The influences of leaf width, leaf absorption and " a_p " values [equation (5a)] on the daily maximum and minimum leaf temperatures, transpiration, net photosynthesis and transpiration efficiency were analysed. As leaf width increased, maximum leaf temperatures increased and minimum leaf temperatures decreased. Daily transpiration decreased and transpiration effi-

ciency first increased and then decreased after a leaf width of about 3 cm was obtained. The calculations indicate that narrow leaves are desirable for maximum production if water is unlimited, but that leaves 3–4 cm wide are desirable if water is limited.

As leaf absorbance increased, maximum leaf temperatures, transpiration, net photosynthesis, and transpiration efficiency increased. Minimum leaf temperatures remained constant. The calculations indicated that it is advantageous to have relatively high absorbance, 0.6 being a common high value (Birkebak and Birkebak, 1964).

The " a_p " parameter in equation (5a) is related to the minimum leaf resistance; as " a_p " increased, the minimum

leaf resistance is also increased. Thus, as a_p increased maximum leaf temperature increased and transpiration, net photosynthesis and the transpiration efficiency decreased. The calculations indicated that it is advantageous to have low a_p and minimum leaf resistances for maximum production and efficient water utilization.

The total leaf area index and leaf inclination interact to influence the physiological processes. Total leaf area index was varied by varying the total leaf area while maintaining a constant fraction of the total in each level. As leaves became more steeply inclined, maximum leaf temperatures decreased and minimum leaf temperatures increased.

Calculations showed that total daily evaporation increased with leaf inclination, because more solar radiation penetrated through the canopy, increasing the percentage of sunlit leaves at levels within the canopy. As the leaf area index increased, maximum leaf temperatures increased and minimum leaf temperatures decreased. Total evaporation tends to increase with leaf area index because there is more evaporating surface. However, with nearly horizontal leaves, evaporation decreases with increasing leaf area index above about 4.

With steeply inclined leaves, gross photosynthesis continued to increase up to a leaf area index of 8; but with more horizontally inclined leaves, maximum gross photosynthesis occurred with lower leaf area indices. With low leaf inclinations, gross photosynthesis decreased with high leaf area indices because water deficits developed rapidly and leaf resistances rose. Net photosynthesis increased with leaf inclination at all leaf area

indices. As leaf area index increases, net photosynthesis continues to increase with steeply inclined leaves; but as leaves are more horizontally inclined, a maximum net photosynthesis occurs with lower leaf area indices.

Transpiration efficiency also increases with leaf inclination at all leaf area indices. With high leaf inclinations, transpiration efficiency increases with leaf area index; but with low leaf inclinations, a maximum transpiration efficiency occurs.

Maximum production of well-watered stands should be obtained with steeply inclined leaves, high leaf area indices, low minimum leaf resistances and a_p values, high leaf absorbances, and narrow leaf widths. As water becomes limiting, maximum production can be obtained with steeply inclined leaves, high but slightly reduced leaf area indices, low minimum leaf resistances, high leaf absorbances and broader leaves. If, in addition, leaves are less steeply inclined, leaf area indices should be reduced to maximize production.

More data on canopy properties and production rates are needed to further substantiate and refine these relationships.

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Résumé

Modèle des températures, des taux de transpiration et de la photosynthèse de feuilles au soleil et de feuilles à l'ombre dans les voûtes foliaires (P. C. Miller)

Un modèle de production primaire et de transpiration des voûtes foliaires a été élaboré à partir du budget thermique de feuilles considérées isolément. Ce modèle comprend: a) les influences du rayonnement solaire et du rayonnement infrarouge, du vent, de la température de l'atmosphère, et de l'humidité sur les températures, la transpiration et la photosynthèse de feuilles au soleil et de feuilles à l'ombre; b) les interrelations entre la température des feuilles, la transpiration, le déficit hydrique des feuilles, la résistance des feuilles, l'évaporation et la photosynthèse brute. Il est actuellement mis au point et essayé dans une forêt de mangrove rouge de la Floride du Sud, aux États-Unis d'Amérique; mais il peut être appliqué en toutes régions. Les essais préliminaires ont confirmé le modèle. L'influence relative de diverses voûtes foliaires et propriétés de l'environnement a été évaluée au moyen d'expériences de simulation. Les courbes quotidiennes calculées des températures de

feuilles au soleil et de feuilles à l'ombre, la résistance des feuilles, le déficit hydrique, les taux de transpiration et de photosynthèse nette, et l'efficacité de la transpiration (pour deux journées hypothétiques différentes) sont donnés. D'autres calculs indiquent que les feuilles étroites sont souhaitables pour la production maximale si l'eau est fournie en quantité illimitée, mais que des feuilles de 3 à 4 cm de largeur sont souhaitables si l'eau est limitée. Nous avons vu aussi qu'il est avantageux d'avoir un a_p faible et des résistances foliaires minimales pour une production maximale et une utilisation efficace de l'eau, quelle que soit la limitation de l'approvisionnement en eau. Les échanges par convection dans la voûte foliaire ont diminué brusquement lorsque l'indice de surface foliaire a dépassé 2. Si l'eau n'est pas un facteur limitant, la production maximale est observée lorsque les feuilles sont fortement inclinées et que l'indice de surface foliaire est compris entre 6 et 8. Si l'eau est un facteur limitant, la production maximale peut se constater lorsque les feuilles sont inclinées un peu moins fortement.

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Agrometeorological factors influencing spring wheat yield and grain quality in the Union of Soviet Socialist Republics

N. N. Jakovlev
Vavilov's Institute of Plant Industry,
Leningrad (U.S.S.R.)

The U.S.S.R. is the largest wheat-growing region in the world. At present the total wheat production in the U.S.S.R. accounts for more than 28 per cent of the total world wheat production. Spring wheat is important, among others, and in the U.S.S.R. an area of more than 48 million hectares is cultivated.

GEOGRAPHICAL CORRELATIONS

With regard to the influence of climatic factors upon spring wheat yield, the following geographical correlations may be stated, according to the data from many years' trials at the State crop testing station.

In regions where the period of heading to maturity lasts 40–45 days at a mean air temperature of 14–16°C, the average spring wheat yields for many years are within the limits 1,800–1,900 kg/ha at the crop testing stations in the European part of the U.S.S.R. and 2,000–2,400 kg/ha in Siberian taiga and subtaiga zones.

In regions with a mean air temperature of 17–19°C, in a period of wheat production lasting 33–35 days, the average yield is reduced to 1,400–1,800 kg/ha.

In regions with a mean air temperature of 20–23°C, where the period of heading to maturity lasts 29–32 days and less, the average yields of spring wheat are reduced to 1,100–1,400 kg/ha.

During the period of heading to maturity with a mean air temperature of 20°C, the maximum temperatures on some days, which reach 30–35°C or more, have detrimental effects on plants. Hence, in the years with a yield of 80 per cent of the long term average, the temperature in the period of heading to wax ripeness in most cases is 20°C.

In 70–85 per cent of cases, droughts coincided with temperatures above 20°C in the period of heading to maturity.

Dividing the period heading to maturity into parts of various duration and comparing them with average yields, it may be stated that, according to data from 760 trials at the crop testing stations in 1962–1968, under conditions not limiting growth, the yield capacity increases with continuation of the period heading to wax ripeness. Thus, if the period is of 51 days' duration, the yield capacity reaches 2,500–2,600 kg/ha on average; if 30 days or less, it is reduced to 1,300 kg/ha.

The duration of these periods is related to temperature; the higher the temperature, the shorter the intervals between phases. This relationship is expressed with the correlation coefficient 0.78 ± 0.13 (within the limits of 14–23°C).

A period of 24–25 days from heading to wax ripeness for spring wheat is considered to be the minimum for good yields. To the south-east and in middle Asia in some years it is reduced to 21 days.

Low wheat yields (1,100 kg/ha or less) are often produced if the period from seedling emergence to wax ripeness equals 76 days (on average); of these, 44 days fall in the period from seedling to heading and 32 days in the period from heading to ripeness.

High yields (3,000 kg/ha or more) are produced at the crop testing stations if the period from emergence to wax ripeness is about 95 days, 50 days falling in the period from emergence to heading, and 45 from heading to wax ripeness.

In the northern regions of U.S.S.R. although the heading to maturity period is of sufficient duration, a yield reduction is noted because of its coincidence with unfavourable conditions (low temperature, frosts, abundant rains).

Grouping the yield capacity data according to the period from seedling emergence to heading, the same regularity is revealed as for the heading to wax ripeness period.

Spring wheat yield capacity increases in accordance with the increase in duration of the period from emer-

gence to heading. If this period is of 46 days' duration, the yield is 2,200–2,500 kg/ha (on average), if 40 days or less, it is reduced to 1,500–1,600 kg/ha.

Although the correlation coefficient between the duration of the period emergence to heading and mean air temperature is less than for the period heading to wax ripeness, it is still 0.62 ± 0.11 .

The longer the period from emergence to heading and from heading to wax ripeness, the higher the wheat yield, as long as these periods do not coincide with low (10°C or less) or high temperature during ripening or with shortage or excess of water. Under these conditions the late maturing varieties are of higher yield capacity than moderate and early maturing spring wheat varieties. This does not apply to the south-east, where the medium maturing varieties ripen before drought, but the ripening period of the late maturing varieties coincides with droughts; therefore, under these conditions, the late maturing varieties are not high yielding.

Taking these observations into consideration, the variety distribution in the U.S.S.R. is accomplished by taking advantage of different meteorological conditions as they apply to various periods of plant growth.

EFFECT OF MOISTURE AND TEMPERATURE

Moisture and temperature also influence spring wheat yield. The quantity of rainfall is very closely correlated with temperature. During abundant rainfall, the temperature is usually reduced, the air humidity is high and wheat development is delayed. In years with little rainfall, the picture is quite the opposite.

Moisture shortage often occurs during high temperatures in the region of stations where the quantity of rainfall during the period mentioned is 25–60 mm on average (far east excluded), but in other regions the quantity of rainfall is more than 70–100 mm.

To the south-east in 30–50 per cent of the years, the period from heading to wax ripeness may be very dry, and there is only sufficient moisture in 25–35 per cent of years.

Although in the second period spring wheat is under the influence of meteorological and temperature conditions, the most important period for moisture uptake is the first; i.e. seedling to heading or, more precisely, seedling to flowering. Under severe drought conditions with very low rainfall (13–18 mm), the yield is reduced to 50 per cent or less. Under drought conditions with 28–35 mm of rain, the yield is reduced to 20 per cent or less. In an analysis of the importance of moisture, it was stated that in North Kazakhstan in years favourable for high yields (viz. 120 per cent of the average of many yearly yields), the average quantity of rain falling on any one day in the period of tillering to heading was 1.3–4.2 mm, and in unfavourable years 0.0–0.9 mm. In the years with bad harvests, the very low moisture

level is characteristic of the whole plant growth period. Years giving high yields of spring wheat are usually characterized by increased rains in May–July (175–185 mm) and comparatively low temperatures in July (20°C or less).

In many trials, the relationship between yield and meteorological conditions was associated with different periods of plant development: from seedling to wax ripeness, from tillering to heading, from heading to wax ripeness, etc. But there have been no investigations analysing the meteorological conditions at the stage from stooling to milky ripeness. In our opinion, the conditions during this period have the greatest influence on yield formation.

In the period from stooling to heading, the flower number in the spike is determined, and in the period from flowering to milky ripeness, the number of grains in the spike and the number of spikelets are determined. In the phase of stooling, the increase in dry matter begins and reaches its maximum at the stage of milky ripeness, then ceases. The greatest consumption of soil moisture is in the period from stooling to milky ripeness. At the stooling stage, some differences in vegetative growth exist between varieties. This is why the relationship between yield capacity and meteorological conditions should be studied during this period of growth.

THE HYDROTHERMAL COEFFICIENT

The most precise method of evaluating environmental conditions is accomplished by means of the hydrothermal coefficient (i.e. the ratio of quantity of rainfall to the sum of active air temperatures, divided by 10).

Having the data for soil moisture content in a 50 cm layer for the period seedling to emergence, and the hydrothermal coefficients (htc) for the period of stooling to milky ripeness, it was possible to state that, according to the results of 4,293 trials at testing stations with different soil types:

1. The spring wheat yields are different on different soil types, but at one and the same humidity level, the yields are lower on the sod-podzolic soils.
2. On the grey forest soils, southern and black chestnut chernozems having the same moisture index, the yields are nearly identical.
3. If the htc is less than 0.3 at the period of stooling to milky ripeness, the wheat yields from different soil types are nearly identical, depending more on the initial soil water supply. Thus, if the soil moisture at the seedling period is less than 50 mm, the yields are about 480–540 kg/ha, and if the soil moisture is more than 50 mm, the yields are about 690–890 kg/ha.
4. At an htc of 0.4–0.7 and an initial supply of available soil water of 50 mm in the 50 cm soil layer, the yields increase according to soil type up to 900–

- 1050 kg/ha; and at an htc of 1.4–1.8 and the same soil water supply in the period of seedling emergence, the yields increase up to 1,310–1,490 kg/ha.
5. The highest wheat yields under conditions of adequate moisture are registered on common, typical and calcareous chernozems. On these soils there is a greater dependence of yielding capacity upon moisture. Slightly lower yields occur on leached podzolized chernozems.
 6. The highest average wheat yields (1,910–2,380 kg/ha) at an htc of 1.1–1.3 are produced on sod-podzolic, grey forest soils and on leached and podzolized chernozems. On common, typical and calcareous chernozems and on southern, black chestnut chernozems, the yields are higher when the htc is 1.4–1.8.
 7. When the htc is 1.9–2.3 or more at the stage of stooling to milky ripeness and the initial available soil water supply is more than 70 mm in a 50 cm soil layer, a marked yield reduction occurs on the sod-podzolic and grey forest soils. Very often, under these conditions, the plants are lodged. Because of this the area under the variety Saratovskaja 29 in the forest-steppe zone of Siberia is not being expanded.

For analysis of the reaction of various varieties to different levels of moisture content, an experiment was carried out with seven highly drought resistant varieties. From the results of the investigations, it was concluded that the varieties differed essentially in their yield capacity according to soil moisture supply and index of moisture in the period of stooling to milky ripeness.

However, under the conditions of soil water shortage (less than 50 mm in a 50 cm soil layer) and htc 0.5 or lower in the period of stooling to milky ripeness, the difference in yielding capacity between varieties is comparatively negligible, varying from 560–700 kg/ha. But when the soil moisture supply is 50–70 mm in the period of seedling emergence to milky ripeness these differences are more evident. We distinguish between the following high yielding varieties: Bezenchukskaja 98, Saratovskaja 38, Zavolzhskaja, Saratovskaja 210, Saratovskaja 29, and Red Star. These varieties outyield the moderately resistant variety Lutescens 62.

At the same htc, but with available soil water at a value of 70 mm and more at the beginning of the vegetative period, the above-mentioned varieties may be divided into two groups: (a) Saratovskaja 210, Zavolzhskaja, Bezenchukskaja 98, Saratovskaja 29—the highest yielding varieties; (b) Red Star, Erytrospermum 841, Albidum 43 and Saratovskaja 38—lower yielding varieties, but they all outyield Lutescens 62.

Under improved humidity conditions, the drought-resistant varieties Erytrospermum 841 and Albidum 43 are inferior to other varieties. However, the variety Erytrospermum should be produced in the territories with frequent droughts, especially on the light chestnut soils and sierozems in semidesert and desert regions of Kazakhstan.

At an htc of 0.9–1.1 and soil water content of 50–70 mm and higher, the difference between yields of various varieties increases. The most productive varieties are: Saratovskaja 210, Saratovskaja 29, Saratovskaja 38, Bezenchukskaja 98; inferior to them are: Erytrospermum 841, Albidum 43, Lutescens 62.

The temperature is of no lesser importance in the reaction of varieties to moisture. So, at a mean temperature of 22° C and above in the period of flowering to milky ripeness at an available soil water content of 30–70 mm in 0.3 m soil layer, the spring wheat yield of the variety Saratovskaja 29, according to the data from 46 trials, is 1,730 kg/ha, and at a temperature of 16–18° C, according to data from 54 trials, is 2,200 kg/ha.

High temperature (above 20° C) with abundant rainfall (more than 100 mm) in the period of heading to maturing favours rust development, but low temperature limits disease development.

Micrometeorological data on peculiarities of spring wheat varieties are used for determining the correct geographical variety distribution in the U.S.S.R.

GRAIN QUALITY

Investigations on wheat grain quality are important also. Grain development is closely connected with agricultural techniques and biological peculiarities of the varieties, as well as agrometeorological and climatic factors. This is well illustrated by the experiments carried out in 1966. The seeds from various places and years of reproduction were sown in Pushkin (near Leningrad). The following spring wheat varieties were used: Cezium 111, Lutescens 758, Saratovskaja 29, the seeds of which were produced in fourteen different towns during 1957–61.

Comparing technological qualities of wheat grain from Pushkin with other localities, it was stated that in 62 per cent of cases the seed quality was reduced, in 18 per cent it was increased and in 20 per cent it showed no change. Changes in quality of different varieties depended more upon environmental conditions than on biological peculiarities.

The main index of physico-chemical and baking properties of wheat is protein content. The grain quality changes according to protein content and other characteristics. In the group with a protein content of less than 14 per cent, the physico-chemical and baking indices were lower than in groups with a protein content of above 14 per cent.

The relationship between protein content and gluten in the variety Saratovskaja 29 (according to 241 tests) is expressed with a correlation coefficient of 0.88 ± 0.03 . Grouping the data, the relationship between physico-chemical and baking qualities of the grain may be revealed. So, if the spring wheat variety Saratovskaja 29 has gluten content of less than 30 per cent, the baking strength is 430 ergs. If the gluten content is 30.1–40.0

per cent, the baking strength is 551.1, and if the gluten content is 40.1 per cent or more, the baking strength is 561.7 ergs.

From 100 flour grains of the variety Saratovskaja 29 with a gluten content of less than 30 per cent, under the conditions found in western Siberia, the average bread volume is 592.5 ml, and with gluten content of 30 per cent or more, 614.5 ml. The general grain glassiness changes respectively from 57.0 and 60.6 per cent.

Investigations carried out for many years at the State testing stations revealed that the difference in protein content between varieties grown under the same environmental conditions is no more than 1.3 per cent. In some years, according to the weather conditions, the average suspended protein content in the market wheat grain fluctuates in the different regions as follows: north-western, central, Byelorussian and Baltic republics, from 9.5 to 13.5 per cent; central chernozem zones, from 12 to 15.5 per cent; north Kazakhstan, from 12 to 17.5 per cent; western Siberia, from 14 to 19 per cent; far east, from 11 to 16 per cent; Krasnoyarsk, from 12.39 to 23.25 per cent.

For determining the conditions which influence the protein content in grain and raw gluten content in 70 per cent wheat flour, the materials of the Central Laboratories of the State testing stations were used to evaluate different varieties for the period 1953-66. These materials were grouped in order of increasing available moisture content in the 50 cm soil layer in the period

of seedling emergence, and in order of moisture indices in the period of stooling to milky ripeness.

A satisfactory 14 per cent protein content is produced when the moisture index is no more than 1.1-1.2 and the sum of the active temperatures is no less than 1,820° C. The best grain quality is produced when the temperature sum is 2,000° C and htc is no more than 1.0.

The growing of hard wheat used for producing high quality macaroni, vermicelli and grainy flour is of great importance for our country. In 1968 an area of 5.8 million hectares was under hard wheat.

The quality of the hard wheat grain, as well as the soft wheat grain, is much influenced by temperature and moisture. There are regular changes in wheat macaroni qualities according to various moisture indices in different temperature zones. According to data from 559 experiments, it was stated that the best grain glassiness, the highest raw gluten content and the best macaroni qualities are produced when the moisture index is 1.0 or less in zones with temperature totals of 2,000° C or more. That is why hard wheat is produced very successfully in those regions where the mean sum of temperatures during many years is not lower than 2,000° C (i.e. mean temperatures are higher than 10° C) and htc is not more than 1.0.

The influence of agrometeorological conditions on grain formation must be investigated in the near future, with the aim of obtaining the highest content of amino acids.

Résumé

Facteurs agrométéorologiques qui influent sur le rendement du Blé de printemps et la qualité de ce grain en URSS (N. N. Jakovlev)

Les analyses qui ont été faites pendant de nombreuses années dans les stations d'expérimentation agricole de l'URSS montrent, par comparaison avec les données météorologiques, que les rendements du Blé de printemps sont maximaux lorsque la température atmosphérique moyenne est de 14-16 °C au moment de l'épiaison-maturité; ils sont moindres lorsque la température est de 17-19 °C, et ils sont les plus faibles lorsqu'elle est de 20-23 °C.

On obtient un rendement supérieur à 30 q/ha lorsque l'intervalle entre la germination et l'épiaison est de cinquante jours, et, entre l'épiaison et la maturité, de quarante-cinq jours. Si les précipitations sont de 39-42 mm au cours de la période germination-épiaison, le rendement peut diminuer de 20 % et si les précipitations sont de 13-18 mm, de 50 %. Si l'on possède des données sur la teneur en eau disponible dans les 50 premiers centimètres de sol au cours de la période de

l'apparition de jeunes plants, et si l'on connaît les coefficients hydrothermiques pendant la période tallage-maturité de l'albumen, on peut indiquer comment varie le rendement du Blé de printemps sur le territoire de l'URSS d'après 4 293 expériences faites dans les stations de recherche sur différents types de sols.

Il a été constaté qu'on obtient les rendements les plus élevés lorsque l'eau disponible dans les 50 premiers centimètres du sol est supérieure à 90 mm et lorsque le coefficient hydrothermal est de 1,1 à 1,3 sur des chernozems motteux podzoliques, forestiers gris, lessivés ou podzolisés, et lorsque le coefficient est compris entre 1,4 et 1,8 sur des chernozems communs, typiques et calcaires et sur des chernozems méridionaux noirs ou châtaigniers.

Pour une réduction initiale de l'eau du sol (moins de 50 mm) dans cette couche de sol et un coefficient hydrothermal inférieur à 0,3 au cours de la période tallage-maturité de l'albumen, les rendements sur divers types de sols diminuent considérablement, tandis que disparaît toute différence entre les quantités obtenues. Dans ces conditions, la différence entre les

rendements des variétés n'a guère de signification, mais elle s'accroît lorsque l'humidité s'améliore. Quand l'eau du sol est supérieure à 70 mm et le coefficient hydrothermique compris entre 1,9 et 2,3 ou plus, le rendement diminue aussi.

La meilleure qualité du grain donné par le Blé de printemps (protéines, gluten, glaçage, force boulangère, volume du pain) est obtenue lorsque la somme des températures atmosphériques est de 2 000° (au-dessus

de 10°), pour un coefficient hydrothermique ne dépassant pas 1. On estime que les meilleurs sols sont les chernozems quand ces conditions sont réunies. L'excès d'humidité et une température atmosphérique moindre (inférieure à 14-15 °C) au cours de la maturation de l'albumen diminuent la qualité du grain.

L'étude agroclimatique des particularités des variétés de Blé de printemps en URSS contribue à une répartition géographique plus rationnelle de ces variétés.

Towards realistic simulation of the natural plant climate¹

C. H. M. van Bavel

Department of Soil and Crop Sciences and

Institute of Life Science,

Texas A. and M. University (United States of America)

INTRODUCTION

Our aim is to understand the effects of natural variation in environmental factors and to predict plant response under outdoor conditions. Nevertheless, we will find ourselves compelled to conduct studies that are controlled with regard to the entire environment, in order to (a) establish effects of single parameters and (b) verify models that predict multifactor effects.

As Gaastraa (1969), for example, noted earlier, it is not necessary to duplicate the magnitude and the variation of the environmental factors as found outside. However, it is very necessary to elicit vital responses from the plants comparable with those occurring in nature, for example, transpiration rates, photosynthesis and respiration rates, leaf expansion rates, development rates, stomatal action, root proliferation and activity, and so on. Also, though single leaf and single plant studies will always be important, the essential data will have to be obtained from plant communities in which the characteristic self-shading, humidity build-up, CO₂ depletion and canopy temperature distribution can be simulated. Finally, and with special reference to agricultural crops, it is necessary that plants can be grown to maturity so that yield data may be obtained.

Without intent to criticize any specific installation, we may safely state that all known growth chambers or phytotrons suffer from some or all of the following deficiencies with regard to the general criteria given above:

1. Light levels are too low, compared with natural conditions, seldom exceeding 150 W/m² photosynthetically active radiance (PAR = 0.4–0.7 micron waveband). A sharp fall of radiance with distance from the lights is common.
2. Total radiant energy load is usually even lower, by comparison, seldom in excess of 200 W/m².

3. Air speed is usually small, less than 0.2 m/sec, and random.
4. Measurement and control of CO₂ is absent.
5. Dimensions are insufficient to allow small stands of plants to grow to maturity.
6. Responsiveness of the systems for control of air temperature and humidity is often poor, because the time constants of the sensors of the control mechanisms and of the heat sinks and sources, are much too large, of the order of several minutes.

WHAT ARE REALISTIC GOALS AND METHODS IN PLANT CLIMATE SIMULATION AND CONTROL?

From a design point of view a logical sequence of goals can be noted in the diagram shown in Figure 1. The selection of a goal regarding lighting is an independent input and ought to precede all other options. The next independent choices are those of the dew-point range and air speed. All following specifications must take the previous two into account. In the following, we discuss goals and techniques for each major parameter to be simulated.

ILLUMINATION AND IRRADIANCE

The goal here is to maintain radiant flux density levels at the leaves that result in rates of photosynthesis and leaf temperatures comparable with the natural environment. Because of the "light saturation" effect, well known for individual leaves, it has been assumed that "saturation" light levels would suffice for simulation. This is false because of the generally non-normal orientation of leaves and, more so, because of mutual shading

1. Research in part supported by the University's Nuplex Program.

TABLE 1. Typical PAR and TSR flux densities obtainable with four different lamp types, derived from actual installations or designs

Type	Commercial type ¹	Lamp density (kW/m ²)	Irradiance		Illuminance (klux)	Cooling (kW/m ²)
			PAR ² (W/m ²)	TSR ² (W/m ²)		
Fluorescent	CW/VHO 215 W	1.6	130	150	32	1.4
High pressure mercury	HPL-33 400 W	5.8	400	840	127	5.0
High pressure sodium	Lucalox 400 W	3.6	450	900	167	2.7
Metal halide	Metalarc (in reflector) 400 W	2.4	425	850	137	1.6

1. Brand names of commercial lamps are given as representative examples, not to indicate preference.

2. Below a barrier of 0.9 transmittance in the 0.4-2.0 micron waveband.

in stands. The photosynthetically active irradiance by natural light can be as high as 500 W/m² (0.7 cal/cm² min) without "saturating" a fully developed canopy, as recently shown for soybeans by Egli *et al.*; (1970). The corresponding total short-wave radiation (less than 2 microns) is about twice the PAR.

Flourescent lamps can provide only about one-quarter of the maximum natural PAR. Arc lamps have a much greater output, are smaller, and allow denser packing. Also, they have more realistic ratios of PAR to total short-wave radiation (TSR). In Table 1, the characteristics of four common lamp types are given when used in a luminous ceiling of an artificial plant environment.

Table 1 suggests that, using lamp types now commercially available, realistic PAR levels can be obtained. For the arc-type lamps, reflectors are available that direct light downwards with efficiencies of 70 per cent or more. The advantage of doing so is apparent from the data for metal halide lamps. Not only is the PAR level 3.3 times greater than that for fluorescent lamps, but the cooling requirement for the removal of excess heat in the lamp compartment is not much greater.

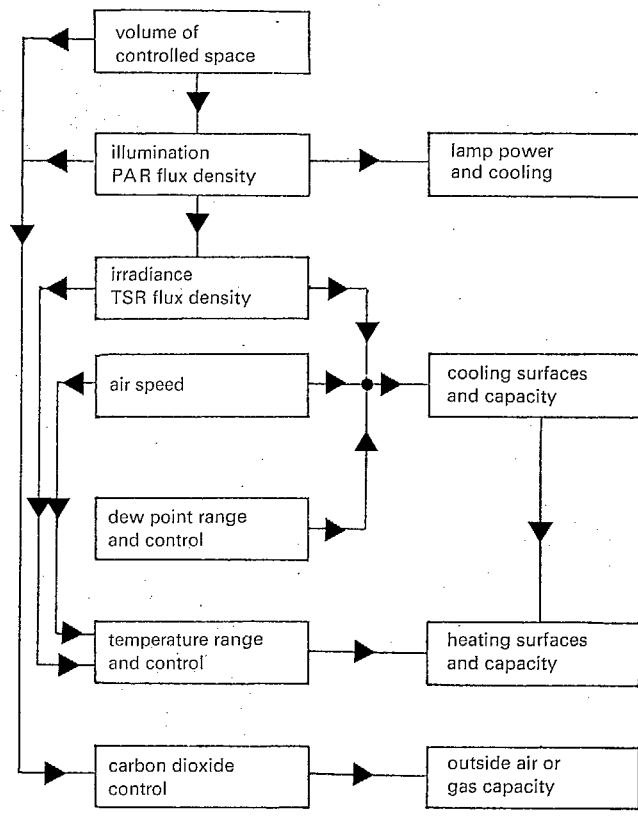
The data of Table 1 are illustrative only and will vary with individual brands and the age of the lamps. With the sodium vapour and metal halide lamps, greater lamp densities can be achieved than shown.

Since, with even the most efficient lamps, more than 65 per cent of the lamp power is turned into sensible heat, it is mandatory that a light barrier made from glass or clear plastic be used. In some lamps this may also be desirable to exclude ultra-violet radiation (less than 0.3 micron wave-length). Airtight sealing of the plant chamber will also be easier with a transparent ceiling.

AIR CIRCULATION

Gaastra (1969) made a plea for greater air speeds in climate rooms. His argument is that in the usual becalmed environment, transpiration rates are likely to be erratic and abnormally low, because of the high

resistance of the leaf boundary layer. To this we can add that the semi-closed conditions of stomata at light levels below 150 W/m² PAR (see Ehrler and van Bavel, 1968) aggravates the problem even further in the conventional artificial environment.



SPECIFICATIONS

COMPONENTS

FIG. 1. Flow chart of objectives and ensuing technical specifications in environmental simulation design. PAR = photosynthetically active radiance; TSR = total short wave radiance.

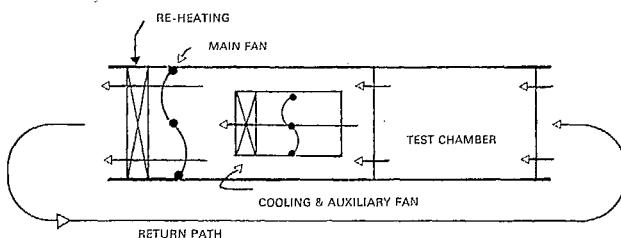


FIG. 2. Schematic arrangement of VARES (variable air ratio environment simulator). The speeds of the two fans can be varied independently.

In order to achieve boundary layer resistances of less than 0.25 sec/cm—a value suggested by the calculations of Gaastra—a leaf of dimension 4 by 4 cm must be ventilated on its edge by air with a velocity of about 0.5 m/sec (1.8 km/hr). This simple calculation (see Monteith, 1964) suggests that realistic simulation requires unidirectional, horizontal air flow of 1 m/sec and more. To achieve high rates of transpiration and associated depressions of leaf water potential and leaf water content, air speeds up to 5 m/sec (18 km/hr) may be desirable. The model calculations of Gaastra (1969), Gates (1968), and others demonstrate also that, at low air speeds and high radiation levels, unrealistic differences between air and leaf temperature result and it is likely that the leaf temperatures will vary greatly among themselves under such conditions.

In order to simulate natural conditions, air flow must be horizontal. In dense plant arrangements in a chamber this will result in the typical stagnation of the air in the canopy that is found outside. It would seem impossible to simulate natural wind profiles by simple means, but so far there is no known reason for wanting to do so.

For experimental purposes it is further desirable that the air-speed be variable and as high as 5 m/sec, as noted above. This may interfere with the efficient and constant operation of the cooling coils, in that high air speeds increase the sensible heat ratio, whereas the principal purpose of the coil is to extract latent heat. We propose here a novel approach, which will be used in a chamber with a floor area of 5 m², now under construction at Texas A. and M. University. In it the air circulation through the cooling coil and through the system as a whole are independently variable. This variable air ratio environmental simulation (VARES) principle is illustrated in Figure 2. A computer programme to give the optimum air speed ratio for a given set or range of conditions is under development.

HUMIDITY AND TEMPERATURE CONTROL

Control of air humidity has probably been the least satisfactory and most frustrating aspect of climate simulation. The problems are due to (a) unjustified

preference for specifying the conditions in terms of relative humidity, rather than of absolute humidity or dew-point, (b) attempts to control humidity with a wet bulb device, (c) lack of appreciation for the technical problem of controlling the dew-point below 0° C and (d) imposition of unwarranted requirements as to accuracy of control upon chamber designers and suppliers.

Humidity control in the plant environment has as its purpose the regulation of transpiration, or, more generally, the state of hydration of plant parts and tissues. This, in turn, is determined directly by the absolute humidity, more commonly measured as vapour pressure or as a dew-point value. This factor, then, must be controlled and the system capability must be expressed in the attainable range and control accuracy of vapour pressure or dew-point.

During the growing season of many crop plants, the absolute humidity changes are not profound, representing mostly alternating masses of polar and tropical, or continental and marine air. During the period March to November the mean dew-point in the United States at screen level varies from -3° C to 20° C, exclusive of

TABLE 2. Increase in evaporation rate from a well-watered canopy resulting from a dew-point decrease of 1° C. The conditions are given as (1) the radiant balance of the surface, (2) the ambient air temperature and (3) air speed, and the (4) dew-point. Calculations are based on a drag coefficient of 0.006

Conditions	Evaporation rate per m ²	Increase
“Cold desert”:		
1. 700 W/m ²		
2. 5° C	0.533 kg/hr	3 per cent
3. 5 m/sec		
4. DP 3° C		
“Hot desert”:		
1. 700 W/m ²		
2. 35° C	1.445 kg/hr	1 per cent
3. 5 m/sec		
4. DP 10° C		
“Tropics”:		
1. 700 W/m ²		
2. 30° C	0.866 kg/hr	<1 per cent
3. 1 m/sec		
4. DP 20° C		
“Temperate”:		
1. 400 W/m ²		
2. 20° C	0.554 kg/hr	5 per cent
3. 5 m/sec		
4. DP 15° C		

higher elevations. Even in the low deserts of Arizona and California, June dew-points are around 5°C.

Thus, we propose that, for many purposes, dew-point control from 1°C to 20°C shall suffice, simplifying the designing task greatly by avoiding values below freezing. In order to assess the required accuracy, it should be remembered that the energy balance principle that governs water use by vegetation outside, is equally applicable in a growth chamber. The combination formula as given by Penman and others (see van Bavel, 1966) suggests that control of evaporation by leaves to 5 per cent of its absolute value, requires typically no more than a 25 per cent control of the absolute humidity. Even at a dew-point of 1°C, a control accuracy of 1°C is, therefore, quite acceptable, and easily manageable. This proposition is illustrated in Table 2 in which the increase in evaporation that results from a 1°C decrease in dew-point in four selected environmental situations is calculated.

Having made the point that dew-point or absolute humidity control is rational and not demanding in range nor accuracy, as long as it can be above 0°C, the remaining question is how to best accomplish it.

Since the wet bulb temperature is an ambiguous indication of humidity, it makes a poor control element. A dewcel, so-called (see Tanner and Suomi, 1956, for example) can be used. In our experience a much simpler approach is to control the temperature of the condensing element in the air conditioning apparatus. The fact that plants lose water continually in large amounts makes this possible and this option has been overlooked by designers of plant chambers.

With a well-designed coil for cooling and dehumidification, the temperature of the air leaving the coil is very close to the dew-point. Thus, a thermometer of any desirable nature (thermocouple, resistance wire, thermistor, diode, or liquid expansion) can be used to set the dew-point by regulating the flow of coolant through the coil.

In our experience, dew-point control of 0.2°C is not at all difficult, provided the control system has the requisite sensitivity and response time. Both items are featured by standard industrial control elements.

Air temperature control, as long as it is separated entirely from humidity control, is straight-forward and consists of controllable reheating of the air after it leaves the dehumidification element. Air temperature control to the nearest 0.5°C or better should not present any problem with standard industrial components.

In summary, a rational approach to adequate control of humidity and temperature can be based upon the recognition of one's true objectives and the fact that plants impose a relatively large latent heat load upon the system. Proper insulation will tend to make this latent-to-sensible heat load ratio even higher. Thus the appropriate method is to lower the air temperature to the desired dew-point and to reheat it to the desired temperature. In Figure 3 data are given that illustrate

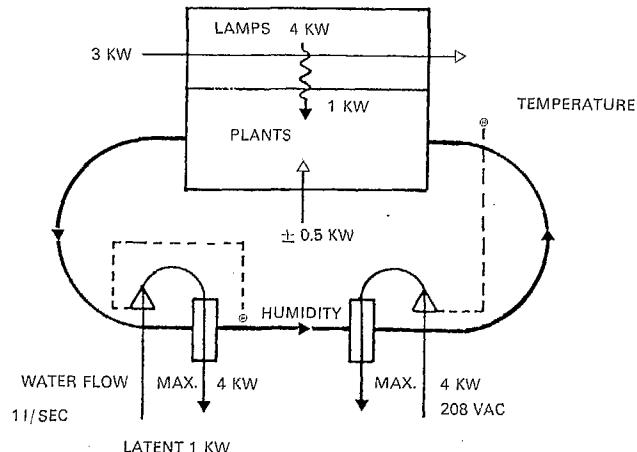


FIG. 3. Performance characteristics of a 1 m² pilot model environmental simulator for plant production experiments. Dotted line shows control connexion to valves.

total volume	3.7 m ³
plant chamber	0.60 × 0.60 × 1.80 m = 0.65 m ³
air speed	1.2 m/sec = .43 m ³ /sec
lighting	10 lucalox at 400 W = 3.6 kW/m ²
barrier	3 mm lucite
radiant load	1 kW, 420 W/m ² PAR
cooling	chilled water coil + automatic mixing valve
heating	nichrome wire heater + SCR power controller
temperature	5°–40°C ± 0.3°C
dewpoint	3°–35°C ± 0.2°C, or (ambient – 10) whichever is more
carbon dioxide	100–2000 ppm
response time	about 0.1°C/sec.

the capabilities of an existing climate chamber based on the principles discussed here. Superficially, such a system is wasteful of energy and, often, engineers and suppliers try to overcome this by cycling or alternating heating and cooling. In terms of performance these economies are false.

CARBON DIOXIDE CONCENTRATION

In the first analysis, plants and plant stands tend to respond linearly to ambient CO₂ levels (see for, example, Baker, 1965; Egli *et al.*, 1970). One would think that the recording and control of such a variable would be a standard feature of plant environments, but this is not the case. Usually a certain amount of "fresh" air is led into the plant space, and it is assumed that this will do. In the first place, the "fresh" air may be quite variable in CO₂ content, particularly if large buildings or parking lots are near to the intake. Variation between 300 and 350 ppm is common. The air inside buildings is even more subject to variation.

We submit that a serious study of the effect of environment upon plant function must provide a record of the CO₂ level. Once this is done, control can be provided with little additional effort. For continuous operation, a compensation technique as suggested, for example, by Koller and Samish (1964), is suitable also for large chambers. Carbon dioxide gas in either pure or diluted form is admitted to the chamber so as to keep the level constant as measured by an infra-red gas analyser. During periods of darkness the CO₂ will build up to a level where the evolution rate equals the leakage rate of the chamber. Since respiration is not considered sensitive to CO₂ level, this appears to be without objection.

For the system described in Figure 3, a typical CO₂ fixation rate is 25 cm³/min, or 7 ppm CO₂/min. Such a change is easily detectable and can be counteracted by an intermittent CO₂ flow rate of, for example, 100 cm³/min. To achieve a minimum depression of 10 ppm by means of "fresh" air introduction, one would require 2.5 m³/min, almost an entire air change every minute and 10 per cent of the entire circulation. The problem thus raised for temperature and humidity control is obvious.

In terms of control accuracy, absolute infra-red gas analysers can be calibrated in the 300 ppm range with an accuracy of about 1 ppm (see Bate *et al.*, 1969), and

control action can be obtained with deviations from set point less than 3 ppm without undue complications. Such specifications are well in excess of requirements of the usual ecological experiments.

CONCLUSION

The usefulness of artificial environments for ecologically oriented research on plant behaviour can be greatly improved over current practices by (a) increasing maximum irradiance to approximately 500 W/m² PAR and 1000 W/m² TSR, (b) controlling the level of ambient CO₂, (c) increasing the air flow up to 5 m/sec and making it horizontal and variable, and (d) by controlling the absolute humidity.

We have shown that the above goals can be achieved by (a) using modern arc lamps, separated from the plant compartment by a transparent barrier, (b) designing the plant chamber as a closed, recirculating system with CO₂ injection, (c) separating the air flow over the conditioning surfaces from that through the plant chamber, making the latter independently variable, and (d) by setting realistic goals for range and accuracy of control for the absolute humidity, rather than relative humidity, and achieving them by controlling the temperature of the condensing coil.

Résumé

Vers une simulation réaliste du climat naturel de la plante
(C. H. M. van Bavel)

Un milieu artificiel permettant de simuler de façon réaliste les conditions en plein air est un moyen indispensable de mettre au point des méthodes précises pour la prévision du comportement des végétaux. Actuellement, cette technique est trop rudimentaire, notamment en ce qui concerne l'éclairage à des niveaux suffisamment élevés, la simulation du flux naturel d'air,

la régulation de la teneur en gaz carbonique et la détermination correcte et le contrôle de l'état hygrométrique. Il faudrait que, sur ces quatre points, on puisse utiliser de façon simple des appareils généralement disponibles sur le marché pour l'éclairage, l'analyse des gaz et la climatisation, en vue d'atteindre des objectifs rationnels en ce qui concerne le degré d'intensité, la précision de la régulation et la vitesse de la réaction. L'auteur fournit des données sur la performance d'un modèle pilote construit selon les principes indiqués.

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**V Estimation of the
water factor
in agroclimatology**

**V Estimation du
facteur eau
en agroclimatologie**

Estimation of internal crop water status from meteorological and plant parameters

R. W. Shawcroft, E. R. Lemon

Soil and Water Conservation Research Division,
Agricultural Research Service, United States Department
of Agriculture, Ithaca, New York (United States of America)

and D. W. Stewart

Canadian Department of Agriculture, Swift Current,
Saskatchewan (Canada)

(In co-operation with the New York State College of
Agriculture, Cornell University, Ithaca, New York.)

Crop water status can be expressed directly in terms of the water potential of plant material or indirectly in terms of the partitioning of energy received by the crop. The water status of a crop must be evaluated to develop crop, soil, and water management techniques that can be applied to practical agroclimatological problems. Any estimate of crop water status should consider the plant response to environmental conditions and characterization of these conditions. Plant and meteorological parameters that can be evaluated in agronomic crops form a basis for arriving at estimates of the crop water status. Therefore, the objective of this paper will be to review some of the meteorological tools and techniques and to consider how they can be combined with certain plant parameters for arriving at estimates of crop water status. The emphasis will be on indirect expression of the water status rather than a detailed approach to measuring water relations of plant tissue. The review will include research using meteorological techniques, research using plant parameter measurements, and combinations of the two approaches. Some aspects of micrometeorological modelling will be discussed.

METEOROLOGICAL APPROACH

Meteorologists have used an approach for evaluating the water status of plant communities based on the balance of energy at plant and soil surfaces. The approach considers the radiation exchange at the earth's surface, and the airflow processes controlling the exchange of mass and momentum at the earth's surface. From the diurnal cycle of aerodynamic exchange processes and the energy balance, the source and sink intensity of latent heat flux, sensible heat flux, and photochemical energy flux have been assessed. The patterns of the flux components during the day illustrate the coupling between the meteorological elements and physiological functions of the plant.

Since the partitioning of the energy received by a crop depends on the water status of the crop, the evapotranspiration rate of a crop is an indirect measure of the crop water status. The measurement of evapotranspiration as a meteorological element has received considerable attention (for reviews see Jensen, 1966; Hagan *et al.*, 1967). Evapotranspiration is measured on several scales—from seasonal estimates based on empirical methods to short time periods by energy balance methods or precision lysimetry. Tanner (1967) discusses some of the measuring techniques and comments on the advantages of micrometeorological methods. When applicable, micrometeorological methods can measure evapotranspiration over very short time periods (a few minutes), can provide flux measurements of entities other than evapotranspiration (CO_2 , heat), and can provide additional information (temperature, humidity) that can be related to short-term physiological response.

Begg *et al.* (1964) studied the diurnal energy exchange as well as the relative plant water content, stomatal aperture, and photosynthetic activity of a crop of bulrush millet. The study included measurements of leaf area, total dry matter production, and soil water. The soil water level at the time of this study was approaching the wilting stage. The decrease in transpiration and the increase in sensible heat flux corresponded to stomatal closure during the middle of the day and demonstrated the coupling between climatic elements and plant response. As the radiation intensity decreased in the afternoon, transpiration actually increased as a result of additional energy being extracted from the air and increasing transpiration from lower layers in the crop. This study demonstrates the value of an integrated plant physiological-micrometeorological approach, and how this becomes more useful as a tool that can be used for prediction of responses than any of the observations would have been separately.

Brown and Covey (1966) used an energy balance approach to evaluate the fluxes of sensible heat and latent heat by layers in a fully grown corn crop. They found the transpiration rate of the crop to be related to three micrometeorological parameters, net radiation, saturation-water vapour pressure deficit of air, and a leaf-to-air transfer coefficient; and two plant parameters: leaf wetness and leaf area density. They defined a "leaf wetness" parameter as a "lumped" factor for the plant transpiration regulatory processes. This parameter is related, in a physiological sense, to the stomatal resistance to vapour loss and to the resistance of movement of water within the plant. The calculated values of the wetness parameter through the day agreed with the expected patterns of stomatal behaviour. No direct measurements of plant water status or stomatal aperture were made, but the water status of the crop was implied from the analysis of the energy balance measurements.

PLANT PARAMETERS

The types of plant parameters that can be used to evaluate the water status of a crop under field conditions have been referred to briefly, i.e., leaf area, leaf water potential, and stomatal aperture. Very little reference has been made to direct measurement of water status of the plant tissue in the field. A detailed review of the various techniques will not be made, since several recent works are available (Slatyer, 1967; Slatyer and Shmueli, 1967; Barrs, 1968).

The direct measurement of internal water status of crops growing in the field remains a difficult task. The development of thermocouple psychrometers capable of measuring the water potential of intact leaves in the field is still being perfected (Hoffman and Herkelrath, 1968; Rawlins *et al.*, 1968; Calissendorff and Gardner, 1969). Until the design problems are overcome, indirect measures of the water potential of the crop will still be used (Barrs, 1968).

Kramer (1969) contends that the only reliable method of evaluating plant water stress is by direct measurement on experimental plants. This is particularly important if we are to study the mechanisms of operation of water stress. However, the correlation between indirect measures of water status and the crop response can be useful in developing management practices for dealing with agroclimatic problems.

Certain plant responses have been implied from meteorological analyses. Shinn and Lemon (1968) evaluated plant water status directly in conjunction with measurement of evapotranspiration by meteorological techniques over a corn (*Zea mays*) field. The variation in leaf water potential at different heights in a corn crop was studied during a period of increasing soil water tension. The upper leaves exhibited a bimodal fluctuation in the water potential, whereas the lower leaves exhibited a more constant water potential

through the day. There was no evidence that evapotranspiration decreased, even though plants showed visible signs of wilting. A similar bimodal trend could be expected in stomatal closure. Since evapotranspiration for the crop was not bimodal, it was concluded (a) that stomatal closure was ineffective in reducing transpiration, or (b) that the transpiration decrease from the upper leaves due to stomatal closure was compensated by the evapotranspiration from the lower leaves where potentials apparently did not reach values to induce stomatal closure. Stomatal aperture was not measured in their study.

The work reported by Shinn and Lemon (1968) in corn is contrasted, in general, to the work reported by Begg *et al.* (1964). The latter work showed advective energy transport increased transpiration from the lower leaves, and also how stomata responded to a more negative water potential in the upper leaves to reduce transpiration. The results from the corn field, in a more humid area where advection was less likely, suggest that stomata were ineffective in reducing transpiration, if in fact, they did close at all in response to the more negative water potentials. The continued increase in transpiration suggests that stomata may be insensitive to decreases in water potential until some critical water potential is reached. If this is so, the critical water potential is likely to be different for different crop species. In the case of the bulrush millet, the stomatal closure indicated that the critical water potential in the upper leaves was reached. The issue is not settled since stomatal aperture was not measured in the corn field study.

Stomatal aperture has been implied as a plant parameter that can be used to evaluate the response of plants to changes in plant water status. Complete reviews of the mechanism of stomatal action are available (Heath, 1959; Ketellapper, 1963; Meidner and Mansfield, 1968; Zelitch, 1969). Based on these reviews, it can be concluded that the predominant environmental factors influencing stomatal behaviour are light intensity, CO_2 concentration of the air surrounding the leaf, leaf water status, and temperature. Separating the mechanisms by which each factor operates becomes very difficult because the influence of one factor often consists of interaction with another.

Slatyer (1969) concluded that the direct impedance of the CO_2 supply and the resulting increase in leaf temperature, upon stomatal closure, may be the primary mechanism by which water stress leads to reduce net photosynthesis under natural conditions. Assuming that stomata act as the first order influence on photosynthesis and transpiration, stomatal aperture can be used as a parameter for evaluating the crop water status.

Quantitative measurements of this plant parameter will, therefore, enhance the usefulness of various models involving the microclimate of the crop. The separation of light intensity and water potential effects on stomatal diffusion resistance is a logical step for evaluating the effect of water stress in various models.

The development of a porometer for field use has made possible more quantitative and rapid measurements of stomatal diffusion.

Subsequent field studies (Ehrler and Bavel, 1967; Turner, 1969; Burrows, 1969; Hurd, 1969) appear to substantiate the concept that, under most field conditions, light intensity and leaf water potential are the primary factors influencing stomatal movement. Hyperbolic relationships between stomatal resistance and light intensity have been developed under controlled conditions where water stress was unlikely (Gaastra, 1959; Kuiper, 1961; Ehrler and Bavel, 1968; Turner, 1969).

To consider the effects of decreasing water potential, the relationship of leaf resistance and leaf water potential must be known. The critical water potential concept as discussed by Slatyer (1967) and by Barrs (1968) should be evaluated in depth. The critical water potential is defined here as the water potential that the leaf tissue must reach before stomatal resistance begins to rise. Kanemasu and Tanner (1969) have examined this concept in snap beans (*Phaseolus vulgaris* L.) and found the critical water potential for the abaxial surface to be -11 bars and for the adaxial surface to be -8 bars. Ehlig and Gardner (1964) found stomata did not begin to close until leaf water potentials of -5 to -12 bars were obtained, depending on species. Dale (1961) found that the critical relative water content (RWC) of cotton was 85 per cent RWC, or about -12 bars. If one considers the diurnal change of leaf water potential, stomata may be viewed as an on-off switch for transpiration depending on the critical potential.

MODELLING APPROACH

The examples cited in this review show how meteorological techniques and measured plant parameters have been used to evaluate the partitioning of energy received by the crop and indirectly to evaluate the crop water status. One objective of this work is to be able to predict the crop water status and to use this prediction in application of soil and water management practices. To achieve this objective it is necessary to combine the approaches in some systematic way. The mathematical model tries to do this by fitting all the available information that can be described mathematically into a system of equations for simulation of processes in the plant community. Obviously all interactions are not known to the extent that they can easily be included in the model. Certain assumptions must be made until information from experimental work delineates the interactions.

Microclimate models are used to calculate the exchange of energy within and above the plant community and to calculate the vertical profiles of humidity, temperature, wind, and radiation in the canopy. Several models of this type, with variations as to the emphasis and assumptions, have been developed (Philip, 1964;

Denmead, 1964; Cowan, 1968; Waggoner and Reifsnyder, 1968; Waggoner *et al.*, 1969). One of the main differences in the models has been the way the leaf properties have been included. Leaf resistance was first assumed to be uniform in the canopy (Philip, 1964) and then, as the response to light and the effectiveness of leaf wetness were demonstrated (Brown and Covey, 1966), the effects of changing the minimum resistance in the canopy were used in the simulation of the crop climate (Waggoner and Reifsnyder, 1968). Cowan (1968) used a combination of the energy balance model for calculating fluxes and the momentum balance model for determining the ventilation characteristics of the canopy. He included a variable leaf resistance as an input to his model.

These models deal only with the exchange of sensible and latent heat, and further refinements are necessary for including photosynthesis and respiration of the plant community. One approach is to combine the microclimatic models with radiation models. Radiation models define the photosynthetically active light régime in the canopy and consider the direct and diffuse light, leaf angle distribution, light scattering and solar elevation (Wit, 1965; Duncan *et al.*, 1967).

A third type of model that is necessary for complete simulation is a model for leaf assimilation and respiration of CO₂. Waggoner (1969a) describes such a model and includes the relationship of stomatal resistance to concentration of CO₂ inside the stomatal cavity and to light intensity. In another paper, Waggoner (1969b) summarizes how the photosynthesis-respiration models can be coupled with microclimatic models to act as a crop simulator and predict profiles of temperature, vapour pressure, and CO₂.

The complete plant community models can be used to test the response of the plants to a variety of factors. In attempting to evaluate the water factor, the response of the plants to changes in water status must be included in these models. It must be reiterated that estimation of the internal crop water status from meteorological and plant parameters, as discussed thus far, is not designed to predict what the plant water potential might be under a certain set of conditions; but, rather, it is designed to predict certain plant processes that are an integration of all the factors that are interacting, including the internal crop water status. Such processes as evapotranspiration and photosynthesis of plant communities are used in this sense as indirect measures of the internal water status of the crop.

The next section of this paper will be concerned with relevant studies with which we have been closely associated. A plant community model will be used to simulate plant processes. Included in the model will be a submodel evaluating the stomatal response to changing plant water status. Results are compared with flux measurements determined by the energy balance method.

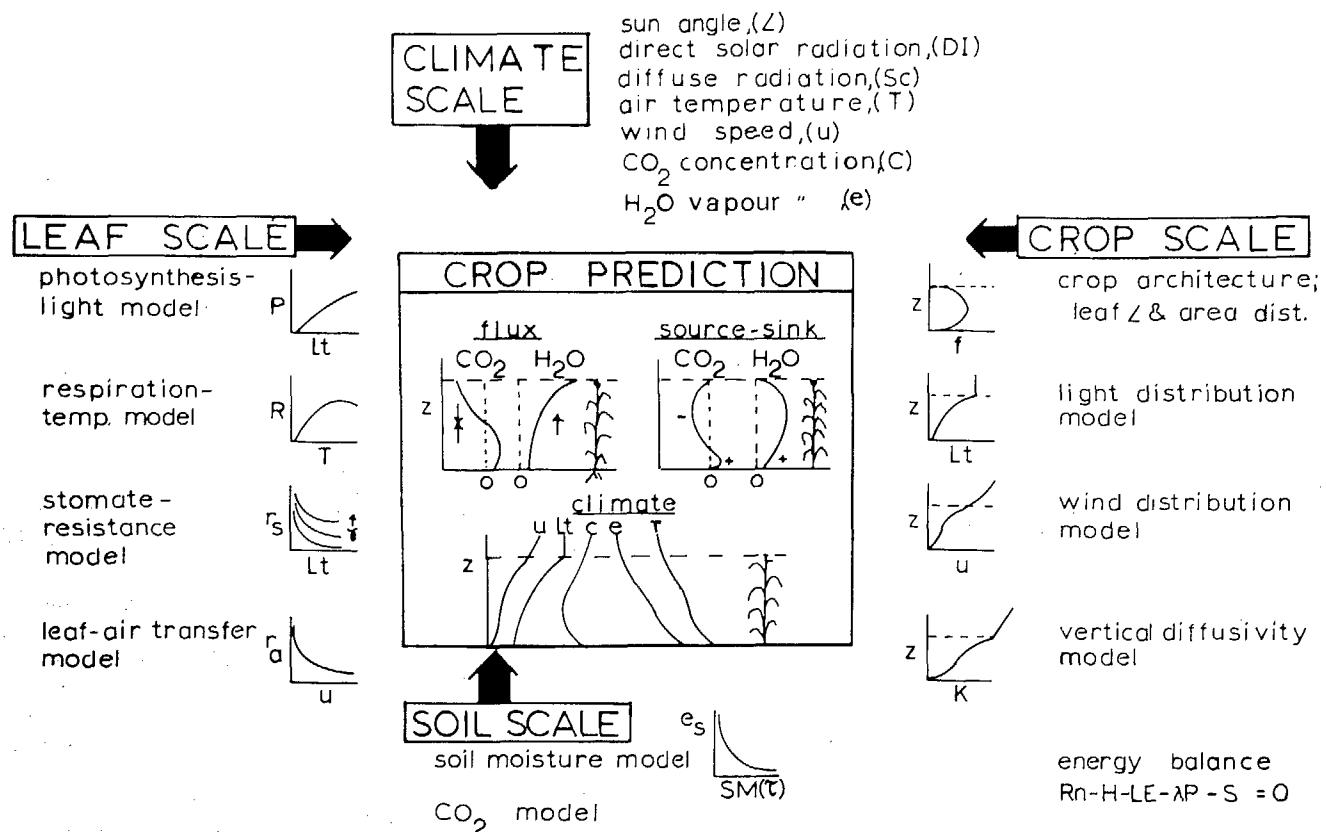


FIG. 1. Schematic representation of soil-plant-atmosphere model (SPAM) showing the sub-model inputs and predicted crop climate.

COMBINATION OF METEOROLOGICAL AND PLANT PARAMETERS

The plant community model (Stewart, 1970) and the stomatal-water stress model (Shawcroft, 1970) were developed and tested concurrently with energy balance measurements and other microclimatic measurements as part of the Microclimate Investigations Project at Ithaca, New York.

Stewart (1970) compiled a model that includes characteristics of all the models discussed. The soil-plant-atmosphere model (SPAM) is represented schematically in Figure 1. The model consists of a series of sub-models of the climate, crop, leaf, and soil scale. These are combined in a computer programme that, by means of numerical analysis and iterative techniques, calculates the climate in the crop, the flux of various components into or from the crop canopy, and the source-sink intensity of various components. The radiation model considers the leaf area density, leaf angle, solar angle, and light scattering in the canopy and is an improvement in that no extinction coefficients need

to be assumed for penetration of visible and net radiation. The model calculates the various crop climate elements using measured values at a reference height above the crop. The model was tested by comparison with measurements in the crop canopy. The calculated profiles of CO_2 and water vapour agreed quite closely with the measured profiles. The largest difference occurred near the ground where the calculated temperatures were as much as 0.5° lower than the measured temperatures. In Stewart's preliminary testing of the model, sensible heat flux was underestimated and latent heat flux was overestimated, when compared with similar components measured by the energy balance technique. The calculated values were sensitive to changes in stomatal resistance, and to temperature and vapour pressure at the immediate soil surface. The stomatal resistance-water stress sub-model was included as a means of simulating the effects of water stress.

Field data collected during 1967 and 1968 enabled the leaf resistance-light intensity relationships of Figure 2 to be constructed. The measured resistance values plotted in Figure 2 are from intact leaves at various positions in the canopy and at various times of the day

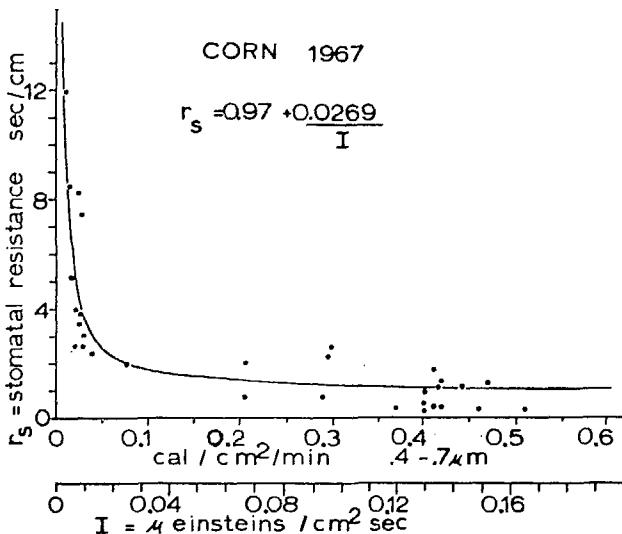


FIG. 2. Light intensity-stomatal resistance relationship for unthinned stand.

on cloud-free days. Relative water contents (RCW) of leaves on the same days were above 94 per cent.

A hyperbolic equation was fitted to the data points in order to obtain a mathematical expression of the relationship. The general equation for this relationship is:

$$r_s = \gamma_0 + \frac{\beta_0}{I} \quad (1)$$

where γ_0 and β_0 are constants having the units of sec/cm and $\mu\text{einsteins}/\text{cm}^3$ and I is the light flux density in $\mu\text{einsteins}/\text{cm}^2 \text{ sec}$. The values of γ_0 and β_0 , as determined from the regression analysis, were calculated to be 0.97 and 0.0269. The shape of the curve agrees well with similar measurements on beans by Kuiper (1961) and on corn by Turner (1969) and by Ehrler and Bavel (1968). The absolute values of the resistances and light at which resistance increases rapidly also compare well with the same points as reported in the work cited. The main feature of this relationship is that, over a large range of light intensity up to full sunlight, the leaf resistance changes very little. Assuming this same relationship holds for all active leaves in the canopy, light intensities at lower layers in the canopy would have to be at low levels to cause stomatal closure.

The relationship shown in Figure 2 was used to calculate the leaf resistances at lower depths in the canopy. The calculated values were slightly higher than the measured resistances. The light intensity value used was a mean value and it is likely the leaf was actually seeing some instantaneous value of higher intensity. This relationship (equation 1) is concluded to be a reasonable approximation of the response of stomata under field conditions to changes in light intensity and under conditions free from water deficits. It is subsequently to be used in the development of a model that includes the influence of water deficits.

From the field data, two generalizations can be made. Firstly, stomata of corn open in accordance with the well-known response to increasing light intensity in the morning hours. The aperture continues to increase until some maximum aperture is obtained. This maximum aperture (or minimum resistance) is related to the degree of water stress prevailing for any particular day, with the minimum resistance decreasing as stress decreases. Secondly, decreasing (more negative) water potential has little effect on stomata until some critical water potential is reached. Once this critical potential is reached, resistance values increase sharply, even though there is an improvement in the water balance of the plant. The overriding influence of the water potential over the light response can occur even under relatively adequate soil water conditions.

STOMATAL MODEL

Assuming no water stress conditions, the light intensity-leaf resistance relationship given in equation (1) can be considered as the "ideal" no-stress case. Consider γ_0 and β_0 constants for the ideal case. In order to have r_s remain finite at some very low light intensity, i.e. $I \rightarrow 0$, a minimum light intensity, I_0 , is introduced that corresponds to some maximum, finite resistance r_c . This resistance is taken to be constant and can be considered as the cuticular resistance or some maximum resistance when the stomata are closed. Expressing this similarly to equation (3) gives:

$$r_c = \gamma_0 + \frac{\beta_0}{I_0} \simeq r_s \quad (2)$$

with r_c as a constant and γ_0 and β_0 as constants, I_0 can be calculated. From equation (1), the minimum r_s for the day, r_{min} , approaches γ_0 at high light intensities. Following the suggestion from experimental measurements, imposing a water stress condition will cause the minimum resistance, r_{min} , to increase. One can think of a family of curves of the general shape as the ideal case, but with changing γ as water stress increases. A schematic representation of this is given in Figure 3. Then for some stress condition, i.e. RWC decreasing:

$$r_c = \gamma + \frac{\beta_0}{I} \quad (3)$$

$$r_s = \gamma + \frac{\beta_0}{I + I_0}. \quad (4)$$

Note that I_0 is added to I in equation (4) to maintain r_s at some finite value (r_c) when I becomes zero. The water stress influence is introduced by considering $\gamma = f$ (water stress).

Stewart (1970) included equation (4) in the plant community model as a means of estimating the stomatal resistance at various levels in the canopy once the light flux densities at leaf surfaces of different leaf

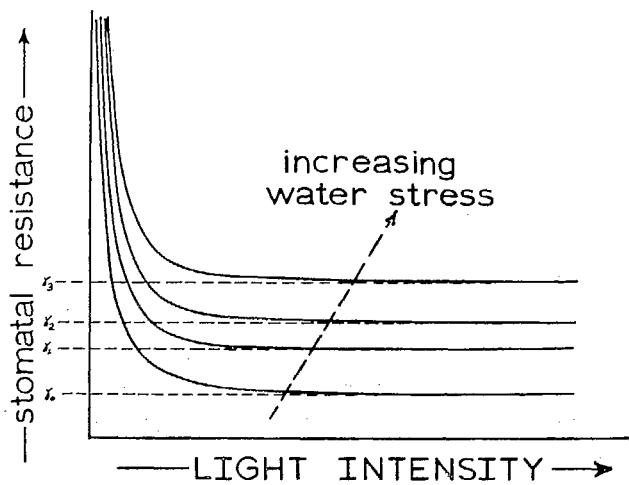


FIG. 3. Schematic representation of light intensity-water stress interaction on stomatal response.

angles were calculated. The model takes various reference parameters that are mean values measured over one-half-hour periods as inputs and calculates profiles and energy flux values for this half hour. In order to vary the stomatal resistance in the computer model, the value of γ for each half hour must be included as an input. The γ value can be approximated from the minimum stomatal resistance, since, from equation (1), r_{min} approaches γ at high light intensities. For example, r_{min} equals 1.08 sec/cm if I is taken at mid-day value of 0.23 μ einstein/cm² sec with a γ of 0.97. The appropriate γ can be estimated from measured resistances. The γ value for any half-hour period sets limits on the minimum resistance value. The vertical distribution of the resistances in the canopy will be determined by the same light intensity-resistance relationship and will depend on the calculated light attenuation in the canopy. If several half-hour periods throughout the day are chosen for testing, the γ value may change according to the measured resistance values. For example, the ideal "no-stress" case would imply that the γ would be the same for all periods through the day and would be the minimum γ value, i.e. γ_0 .

PLANT COMMUNITY MODEL TESTING

The approach used for testing the model was to select, for a given day, five half-hour periods beginning at 08.00, 10.00, 12.00, 14.00, and 16.00 hr. The reference input data for three periods were obtained from measurements in the field for corresponding time periods.

There is a need for an independent check of the model. The measurements necessary for applying the energy balance technique described by Lemon (1967) were made. A modification of this technique using the Bowen

ratio was used to determine the total flux from the canopy. The Bowen ratio, $B = k\Delta T/\Delta e$, (where k is the psychrometer constant and ΔT and Δe are the differences in temperature and absolute humidity over the same height interval), was determined by plotting measured values of T against e and taking the slope of this line. The slope of the $T-e$ curve can be used to determine B above the crop, since the flux above the crop is constant and T and e are linearly correlated. Once the Bowen ratio is known, the total flux components can be calculated using the energy balance relationship and the assumption that the diffusivities of heat, water vapour, and CO_2 are equal (Fritsch, 1966). The energy balance flux values are used as a standard for comparison with the model.

The model is a system of equations that describes the turbulent transport of heat, momentum, and mass from some reference height above the crop surface to the individual leaf surfaces. There are two boundaries to the system (the reference height and the soil surface) and conditions at both boundaries must be known or defined. In this model, the soil surface is defined in terms of the heat flux into the soil, which is measured directly using heat flux plates near the surface, and the surface soil water tension, which can be estimated from soil water tension measurements at various depths in the soil. The model uses these two surface soil inputs to determine the effective vapour pressure at the soil surface and the soil temperature and, subsequently, the flux of latent and sensible heat from the soil surface. The difficulty of predicting a mean or effective surface soil water tension is apparent if the relationship between soil water tension and percentage soil water is examined. For the soil in Ellis Hollow, the soil water characteristic curves show that the soil water potential changes from -50 bars at 6 per cent water by volume to less than -10,000 bars at 3.5 per cent. The soil at the immediate surface was in the percentage range where the soil water tension changes drastically. The large soil water tensions used as inputs in the model should not be confused with the effective soil water tension in the root zone which will be in the range for plant growth.

Two surface soil water tensions were assumed as inputs to the model: -600 bars as the "wet" surface and -8,000 bars as the "dry" surface. The -600 bars tension results in a vapour pressure of 20.5 millibars at 25° C and 63.7 millibars at 45° C. The -8,000 bars tension corresponds to an extremely dry surface with vapour pressure values of 0.1 millibars at 25° C and 0.4 millibars at 45° C surface temperature. The surface soil in the experimental field contains over 50 per cent by volume of large flat stones. Although the -8,000 bars tension leads to low vapour pressure values, it is not unrealistic when the high percentage of the surface consisting of the dry, flat, stones is considered.

As a systematic approach to the testing the approximate minimum stomatal resistant ($\gamma \approx r_{min}$) was first assumed constant throughout the day. The results of

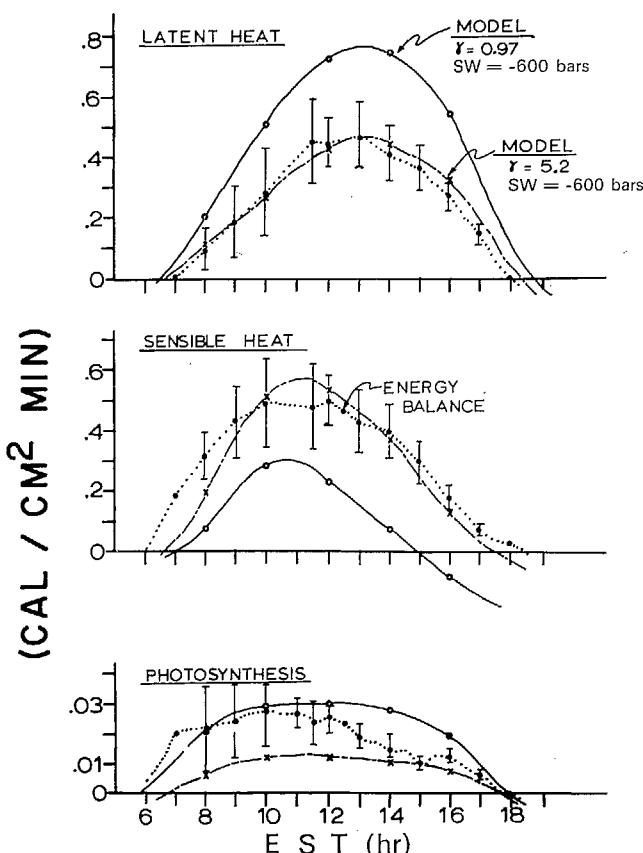


FIG. 4. Latent heat, sensible heat, and photochemical energy flux determined by the energy balance method and calculated by the model with two values of minimum stomatal resistance, $\gamma = 0.97$ and $\gamma = 5.2$, each taken as constant values through the day. Surface soil water tension (SW) held constant at -600 bars for each value of γ . (Corn, unthinned, 18 Aug. 1968.)

the model testing with $\gamma = 0.97$ sec/cm and with $\gamma = 5.2$ sec/cm are shown in Figure 4. The surface soil water potential (SW) was held constant at -600 bars. The latent heat, sensible heat, and photochemical energy flux calculated by the model were compared with the flux values determined by the energy balance technique.

The γ value of 0.97 sec/cm, taken at each hour through the day, simulates a condition where stomata are at their maximum opening throughout the day. With this condition the latent heat flux calculated by the model was much larger than the energy balance method, and the sensible heat flux was much less. The photochemical energy flux as determined by the energy balance method shows an increase in the morning hours, but declines sharply in the afternoon. The model, with $\gamma = 0.97$ sec/cm, calculates photosynthesis values that were close to the energy balance values in the morning, but overestimated photosynthesis in the afternoon. When γ was increased to 5.2 sec/cm, the latent and

sensible heat flux values calculated by the model agreed more closely with the energy balance method. However, the calculated photosynthesis with $\gamma = 5.2$ sec/cm was considerably below the energy balance value except at points late in the afternoon.

Although the calculated sensible heat and latent heat flux values with $\gamma = 5.2$ sec/cm agreed closely with the energy balance method, the energy balance photosynthesis indicated that stomata were open in the morning, corresponding more closely to the no-stress case of $\gamma = 0.97$ sec/cm. This suggested that some factor other than stomata was involved.

The surface soil water tension is another variable in the model. The results of changing the surface soil water tension are shown in Figure 5, where two soil water tensions were tested with $\gamma = 0.97$ sec/cm. The calculated flux values with $\gamma = 0.97$ sec/cm and SW = $-8,000$ bars were in closer agreement with the energy balance than with $\gamma = 0.97$ sec/cm and SW = -600 bars. There was still an overestimation of latent heat

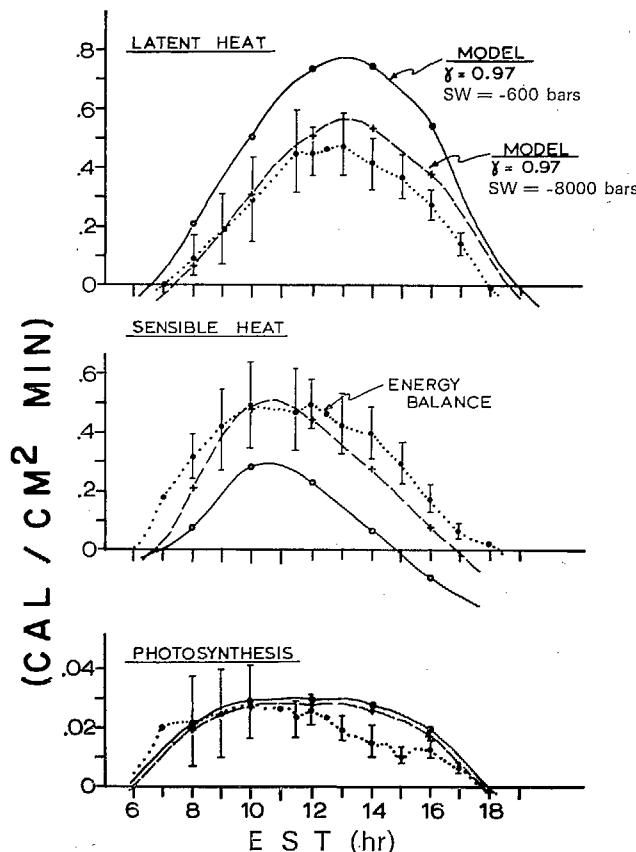


FIG. 5. Latent heat, sensible heat, and photochemical energy flux determined by the energy balance method and calculated by the model with two values of surface soil water tension (SW), -600 bars and $-8,000$ bars, each with a constant minimum stomatal resistance ($\gamma = 0.97$) through the day. (Corn, unthinned, 18 August 1968.)

TABLE 1. Total flux values obtained in a corn field, Ellis Hollow, New York, 18 August 1968. Values are cal/cm²/day, for the period between 07.00 and 19.00 hr. SW = surface soil water tension in bars. γ = approximate minimum stomatal resistance in sec/cm

	Model			Energy balance
	$\gamma=0.97$ SW = -600	$\gamma=5.2$ SW = -600	$\gamma=0.97$ SW = -8000	
Latent heat	340	196	227	182
Sensible heat	44	202	170	216
Photosynthesis	15	6	14	11

flux and photosynthesis and an underestimation of sensible heat flux by the model, as compared with the energy balance method in the afternoon hours. The results of the model testing with input parameters held constant through the day are summarized in Tables 1 and 2, where the integrated daily total flux values are shown.

Obviously there is some combination of stomatal resistance and surface soil water tension that predicts values close to those of the energy balance. There is no point in adjusting the two input parameters unless there is some criterion for evaluating their change during the day. Surface soil water tensions were the most difficult to evaluate, and the values used as input parameters are assumed values. However, the change of stomatal resistance has been measured, and the values of γ corresponding to measured resistances were used as inputs to the model along with an assumed value of surface soil water tension which was also taken to be constant throughout the day. An example of the results is shown in Figure 6.

The latent heat and sensible heat flux values are nearly identical in the morning. However the model

TABLE 2. Summary of total flux values as determined by model and energy balance techniques for period between 06.00 and 19.00 hr, 18 August 1968. Values are in units of cal/cm² day; γ determined from measured stomatal resistances

Net radiation above crop	421
Latent heat flux	
Energy balance	184
Model	142
Sensible heat flux	
Energy balance	216
Model	253
Photosynthesis	
Energy balance	11.2
Model	10.9

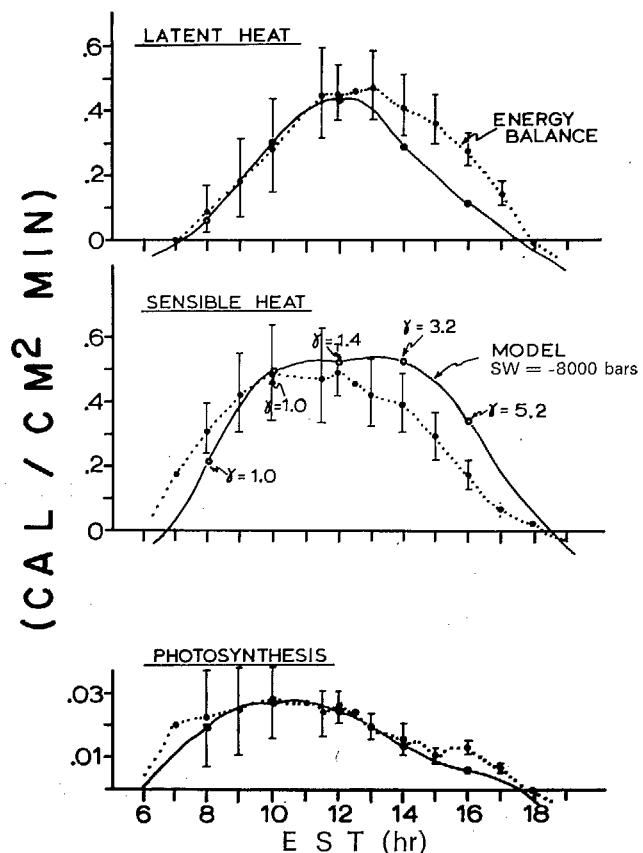


FIG. 6. Comparison of energy balance and calculated flux values using γ values determined from measured resistances. (Corn, unthinned, 18 August 1968.)

overpredicts sensible heat and underpredicts latent heat flux in the afternoon. Using a γ value determined from the measured resistances in the model had the general result of predicting more sensible heat flux and less latent heat flux than determined by the energy balance method. This general result indicated that the effective stomatal resistance might be less than determined by an average of several individual leaf measurements. A shift in the resistance values used in the model to a slightly lower value would result in calculated values in closer agreement with the energy balance method.

Diurnal change in effective surface soil water tension and effective surface vapour pressure may be more significant than changes in stomatal resistance in accounting for the differences between the model and the energy balance values. The effective surface water tension could change throughout the day as the soil dries. Even if the soil water tension does not change appreciably during the day, the effective vapour pressure will still increase as the surface temperature increases. The latent heat flux values calculated by the model are generally less than the energy balance values, suggesting that the actual, effective, surface

vapour pressure was higher than determined by the model from the assumed input values. A soil water tension intermediate between the -600 and -8,000 bars value would result in a calculated latent heat flux in closer agreement with the energy balance values. The calculated photosynthetic energy flux, using measured stomatal resistances, were in much closer agreement with the energy balance values than where the resistances were held constant through the day. The same result would be likely to occur using a variable surface soil water tension through the day.

CONCLUSIONS

Since the objective of this paper has been to estimate the crop water status from plant and meteorological parameters, we need to examine how the model has been used in meeting our objectives. The sub-model for stomatal response to water deficits was developed from field measurements of stomatal resistance and relative water content. These field measurements do not give direct information about other plant processes, i.e., photosynthesis and transpiration. The energy balance method evaluates the meteorology of the crop, and shows how the energy received by the crop is being utilized. Certainly some simple correlations between a few parameters can be made, but as more parameters are measured and the interactions observed, the information gained from these correlations becomes difficult to interpret. The model is useful because it simulated the plant response to a variety of input parameters. The reasonable agreement between the model and the energy balance lends credence to the correctness of the sub-models, and makes the sub-models, by themselves, more useful as tools for predicting the crop water status. For example, if the model calculates a low photosynthesis, low latent heat flux, and high sensible heat

flux, when the reference level meteorological data for a given time period and a certain stomatal resistance are used as inputs, it would suggest that the leaf water potential had reached the critical point for inducing stomatal closure.

Evaluating the stomatal resistance of the crop will give an indication as to the water status of the crop. However, the probability that stomata do not begin to close until some critical water potential is reached makes the use of stomatal resistance as the sole measure of water status questionable unless the critical water potential for different crops has been determined. The basic relationships between stomatal resistance and the critical water potential need to be examined in greater detail and for more crop species. The question of changing sensitivity of stomata within a single species as a result of alternate dry and wet periods also becomes important if the information is to be used to plan practical management techniques.

The modelling approach has been discussed as an example of how the plant parameters and meteorological parameters can be combined in a systematic way to evaluate the plant response to a change of a large number of factors simultaneously. The model can be manipulated to arrive at "answers", but this is a dangerous procedure. The value of the exercise lies in the fact that it forces us to systematize our approach and helps identify areas where more precise information is needed. For example, the model showed the need for more information on the effective vapour pressure and effective water tension at the soil surface. The model evaluates the crop water status in terms of the over-all plant processes of photosynthesis, latent heat flux, and sensible heat flux, rather than a direct assessment of the plant water potential.

The models will be refined to include additional factors. There is still a need for precise measurement of the plant and meteorological parameters to test and improve the models.

Résumé

Estimation de l'état hydrique interne des plantes cultivées d'après les paramètres météorologiques et végétaux (R. W. Shawcroft, E. R. Lemon et D. W. Stewart)

L'état hydrique des plantes cultivées peut être estimé indirectement en mesurant la répartition de l'énergie reçue par une culture au moyen de techniques météorologiques et aussi en mesurant certains paramètres végétaux comme le potentiel hydrique foliaire, la teneur hydrique relative et l'ouverture stomatale. L'auteur examine un moyen permettant de combiner ces deux techniques à l'aide d'un modèle de communauté végétale. Un modèle simplifié de réaction stomatale aux

déficits en eau sert à introduire des données dans le modèle plus grand pour le calcul du flux d'énergie sensible, latente et photochimique de la culture. Le modèle stomatal a été mis au point à partir de mesures de la résistance stomatale et de la teneur hydrique relative effectuées dans un champ de Maïs (*Zea mays*). Les essais de ce modèle en utilisant des résistances mesurées comme entrées ont donné un accord étroit entre les composants calculés et les composants mesurés du bilan énergétique. La combinaison des paramètres météorologiques et végétaux en un modèle a l'avantage de systématiser l'étude et elle précise les secteurs où il faudrait davantage d'informations de base.

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Simplified agroclimatic procedures for assessing the effect of water supply¹

G. Stanhill

The Volcani Institute of Agricultural Research,
Bet Dagan (Israel)

The subject of this paper is particularly well suited to the framework of an historical review, for it is one that has figured prominently in the development of the scientific method, no doubt because of the close connexion between the supply of water and food in the early centres of civilization. As new techniques of measurement and analysis were developed in both meteorology and agriculture, they were almost immediately utilized in the assessment of the effects of water supply on agricultural productivity.

Viewed historically, we can distinguish several approaches. The first, and still most widely available, climatic index of water supply is rainfall, considered either as a seasonal total or at particular stages of crop development. Almost simultaneously, drought indices, based on the absence or deficiency of rain, were computed and correlated with crop yield. Drought indices merge, almost imperceptibly, into water balance procedures in which water supplied by rain or irrigation is balanced against the atmospheric demand for water assessed by climatological methods. Some thirty years ago, soil water storage concepts were introduced into calculations of the water balance and computed values of soil water status are now the most widely used agroclimatic parameter for assessing the effect of water supply.

At the beginning of the present century there was much interest in the direct use of values of water loss from crop surfaces as an index of crop yield and growth, and there has recently been a revival of interest in this approach in a more sophisticated form. Climatically computed values of potential evapotranspiration have also been used to assess climatically limited, potential crop yields.

RAINFALL AS AN INDEX OF WATER SUPPLY

The first published description of rainfall measurements from India dates back to 400 B.C. and contains the following reference to the agroclimatic use of such data: "According as the rainfall is more or less, the superintendent shall sow the seed which require either more or less water" (Kautilya, 321-291 B.C.).

Reviewing the relationships at the turn of this century, Abbe (1905) concluded that "in a dry climate the harvests are to an extraordinary degree dependent on rainfall, on the other hand in moist climates crops are diminished by extremely large quantities of rain".

This point is illustrated in Figure 1, where the relationship between total seasonal rainfall and wheat yield are shown for two contrasting climatic regions. The data of Geslin and Bouchet (1966) suggest an inverse relationship between seasonal rainfall and yield in the moist Paris basin region, maximum yields occurring during years of below normal rainfall. By contrast, data from an arid region of Israel (Lomas and Shashoua, *in press*) suggest a more linear relationship, maximum yields being associated with maximum rainfall.

Obviously, different models of the rainfall-yield relationship are likely to be appropriate in different climatic regions. Considering the simplest case first, of rainfall-yield relationships in arid zones, and taking the wheat crop as an example, a number of workers have shown linear regressions to be a satisfactory model for relating total seasonal rainfall to yield.

Probably the most extensive such investigation was that of Cole (1938), who related the yield of spring wheat to crop season precipitation (1 January to 31 July) at nineteen sites in the semi-arid Great Plains area of the United States of America during the thirty-year period 1906-35. At the different sites, annual variation in

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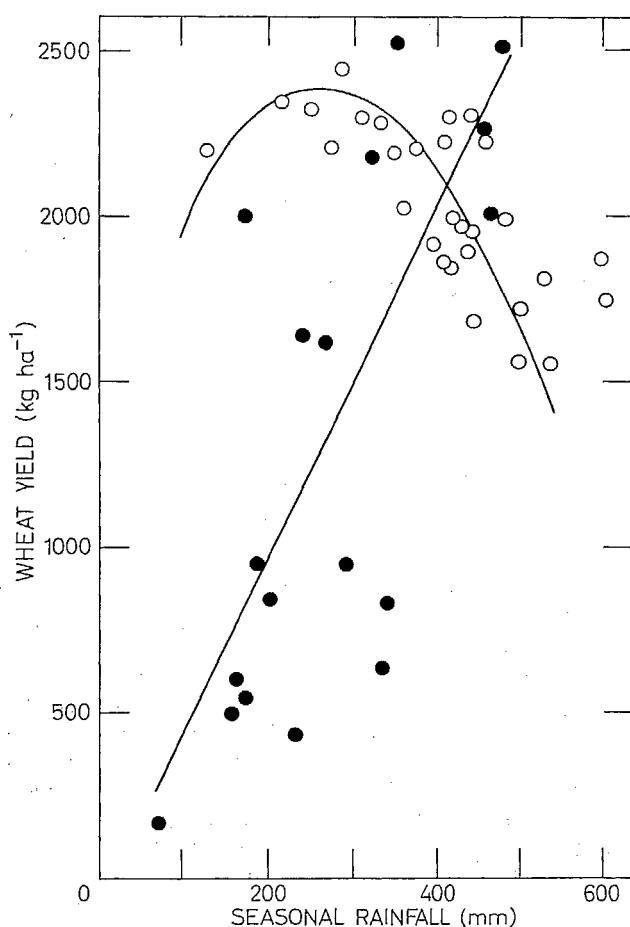


FIG. 1. Relationships between wheat yields and total seasonal rainfall in an arid (Israel) and a humid (France) region.

- Paris basin, France, 1900–36 (after Geslin and Bouchet, 1966).
- Mishmar HaNegev, Israel, 1948–68 (after Lomas and Shashoua, in press).

precipitation accounted for between 36 and 80 per cent of the annual variation in yield. When 272 station-years' data were grouped together in a common regression for the main wheat-growing area of the region, 54 per cent of the variation in yield could be ascribed to variation in precipitation. When the data were further grouped, by relating the mean yield of all the sites to the mean precipitation for all 30 years, 77 per cent of the annual yield variation was accounted for. The constants of the regression equations for individual sites varied considerably, slopes ranging from a maximum of $8.40 \text{ kg ha}^{-1}, \text{mm}^{-1}$, to a minimum of 4.27 , while values of the intercepts ranged from -1450 to -530 kg ha^{-1} .

Pengra (1952) used the same model to relate average county yields of three cereal crops in thirteen districts of South Dakota to rainfall during and preceding the crop season (1 April to 31 July, and 1 September to

31 March, respectively). Averaging the correlations for spring wheat in all the counties, the annual variations in rainfall during both periods accounted for 37 per cent of the yield variation.

Staple and Lehane (1954b) obtained the same degree of correlation with twelve years of wheat yield data from seven experimental sites in Saskatchewan on the Canadian Prairies. In this case, the data on rainfall during a two-year period were used, in order to include precipitation during the fallow year which preceded the crop season.

It is clear that the correlations obtained at individual sites are too low for practical applications. However, both Cole (1938) and Pengra (1952) showed that, by grouping data from individual sites into areal means, almost 80 per cent of the yield variation could be accounted for; the latter investigator found an equally high correlation between pre-season rainfall (1 September to 31 March) and yield. Cole's study shows that even this degree of correlation is insufficient for accurate yield prediction: in the thirty-year period studied, the average error of rain-based yield estimates was 21 per cent of the mean.

The current rapid increases in yield due to agro-technical advances—wheat yields increased by 5 per cent per year in the Great Plains of U.S.A. during the 1950–59 decade (Thompson, 1964)—further reduce the predictive value of weather-based yield estimates, for the statistical relationships are likely to be obsolete by the time they have been reliably established.

Nevertheless, statistical methods can be useful in analysing retrospectively the reasons for changes in crop yields (Thompson, 1963, 1964) and also in predicting the probable distribution pattern of relative yields to be expected for a given distribution pattern of interannual rainfall. The variability of yields is a factor of considerable importance in land use planning.

An excellent example of such an application is provided by Perrin de Brichambaut and Wallen's (1963) agroclimatological study of the Near East. Values of the interannual variability of seasonal and monthly rainfall were used to assess the possibilities of dryland farming throughout the region. Because of areal differences in rainfall variability, the threshold limit for dryland farming (defined as an area where crop failures due to insufficient rain would not occur more than twice in ten years) did not correspond to a single value of annual rainfall, but varied from 180 to 230 mm yr^{-1} .

Simple linear regression models are also very widely employed in hydrology to relate the water yield of a catchment area to its annual rainfall. A number of refinements have been used in addition to annual rainfall. These include an allowance for the time lag between rainfall and runoff from the catchment, an intensity term such as the ratio of rainfall total to number of rain days, and a distribution term to describe the interannual distribution of the rain. In a 30-year study

of river flow in the 68 km² Steenbras catchment in South Africa, Harvey and Whitmore (1960) showed that these four rainfall terms accounted for 97 per cent of the variance in river flow during 80 per cent of the period. For the entire period, the average discrepancy between actual and predicted runoff was 7.5 per cent.

In semi-arid and arid zones, simple linear relationships are often sufficiently accurate to be useful in assessing the effect of different systems of land use management on water yield. Shachori and Michaeli (1965) have reviewed the literature and analysed the results of a large number of experiments where the effect of woody perennial vegetation on water yield was contrasted with that of a grass or bare soil cover. Figure 2, taken from their data, shows the mean results from twenty-three paired catchment studies analysed in a linear regression model.

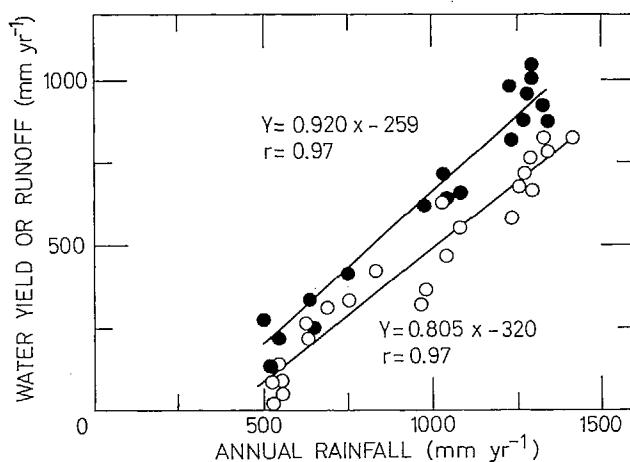


FIG. 2. Relationships between annual water yield and rainfall for two cover types; each point represents the result of a paired experimental investigation (after Shachori and Michaeli, 1965).

- Grass or bare ground cover.
- Forest, woodland or maquis scrub ground cover.

The threshold rainfall values (at which runoff is zero) suggested by their equations are 400 and 280 mm yr⁻¹ for the woody and herbaceous vegetation, respectively. The authors refer to ecological studies in the eastern Mediterranean littoral, showing that these are the annual rainfall values found on the borders delimiting the natural habitat of these two vegetation types.

The different slopes of their equations suggest that the difference in the water yield, and evapotranspiration of the two cover types, increases with rainfall. Such relationships are of considerable agroclimatic, as well as hydrological, significance and their explanation offers a challenge to plant physiologists and ecologists.

The above investigation utilized areal in place of annual variation to study the relationship between rainfall and yield. Walter (1963) provides another

example of this approach: The annual dry matter yield of ungrazed grassland was shown to be a linear function of rainfall over a 50–500 mm range obtained by taking a transect inland from the sea in an arid part of south-west Africa. The temperature and vegetation type are stated to remain more or less constant over the region studied. The results are reproduced in Figure 3.

In more humid climates, where rainfall is not the only or necessarily the most important yield-determining factor, the relationships are more complex than those hitherto discussed, and more complex methods of analysis are needed.

One widely used approach has been to include a number of other climatic variables with rainfall in multiple curvilinear regression models. Ramamurti and Banerjee (1966), for example, combined total seasonal rainfall with five other climatic variables in three different combinations which were correlated with fourteen years' wheat yield data from Dharwar, India. The highest proportion of yield variation explained by any of the three regressions was 86 per cent; the standard error of this estimate was 30 per cent of the mean yield. Another combination of climatic elements estimated the yield with a standard error of 17 per cent.

Thompson (1963, 1964) used the same technique to distinguish between the effects of weather and technology on the increases in agricultural yields in the United States. A refinement used by Thompson (1963) in his study of maize and soybean yields in five Corn Belt States was the division of rainfall into four periods and the inclusion of terms to allow for interactions

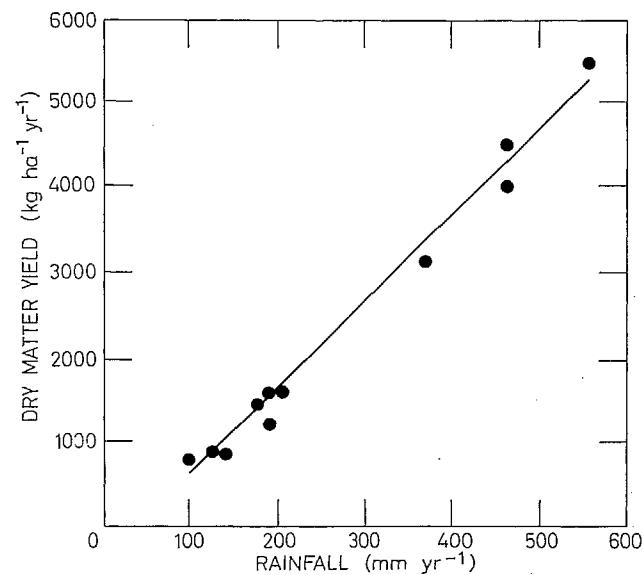


FIG. 3. Relationship between annual dry matter yield of ungrazed grassland and annual rainfall; each point represents a sampling point in a transect across a region of increasing aridity in south-west Africa (after Walter, 1963).

between rainfall and mean air temperature, the other climatic variable examined. In each of the ten equations reported, at least 94 per cent of the yield variation was accounted for by weather variations and technology (i.e. due to year of measurement), and the relationships were all highly significant.

The division of total seasonal rainfall into shorter periods also improves the predictive ability of linear regression models. Thus Staple and Lehane (1954b) found that, when total rainfall was divided into growing season and the presowing, conservation period, a simple multiple linear regression explained 62 per cent of the wheat yield variation at an experimental station in southern Saskatchewan, compared with 36 per cent when the single value of total rainfall was used. A comparison of the slopes in the multiple equation showed that rain falling during the growing season was five times as effective in increasing yield as that falling during the preceding fallow period.

Subsequent investigations of wheat production from the entire Canadian prairie area has shown that division of the growing season into shorter, monthly periods leads to a further increase in the accuracy of yield prediction. Thus Williams (1969) has shown that the total annual wheat production in this region can be predicted from rainfall data, with an average deviation of only 13 per cent.

The effect of rainfall variation during periods even shorter than one month has also been widely studied. One simple technique is to correlate rainfall amounts during short time intervals with final yields obtained from a long series of observations, the aim being to find the critical physiological stage for yield formation. Figure 4, taken from Mäde (1968), illustrates the results that can be obtained by this technique: thirty-nine years of rainfall data were correlated with the yield of winter rye grown at the phenological gardens at Halle in the German Democratic Republic. An earlier example of the use of this method of analysis has been reported by Klages (1942) for the maize crop. Another approach, developed by Azzi (1956) is based on the analysis of rainfall and yields during years with very good and poor harvests, rejecting years with intermediate yields. For each phenological period of crop growth, four cardinal levels of rainfall are established by selecting the level above which only very good harvests were obtained, the level below which only poor harvests were recorded and an intermediate level separating half of the good harvests in the intermediate zone between the upper and lower rainfall levels. The fourth level, that of excess rainfall, is that above which only poor yields are obtained.

Azzi has proposed the use of the intermediate level, termed the drought equivalent, and that of excess rainfall, to select the optimum crops and varieties for districts with different rainfall régimes.

A more widely used and quantitative method of analysis was developed by Fisher (1924) to examine the

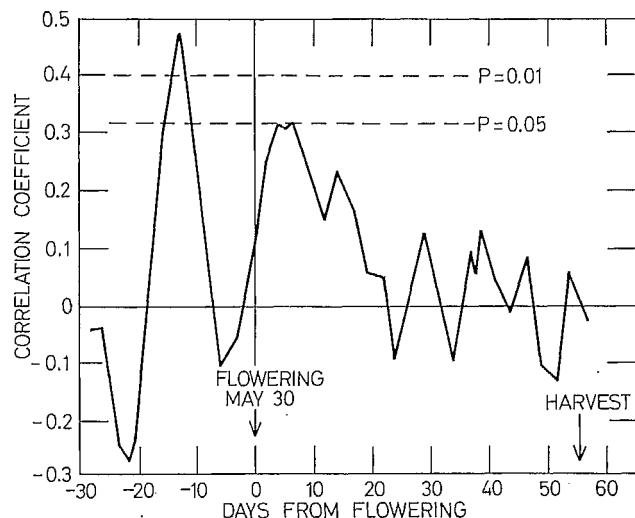


FIG. 4. Correlation between rainfall at different phenological periods and yield of winter rye at Halle, 1900-39 (after Mäde, 1968).

effect of weather conditions on the yields of the classical Rothamsted wheat fertilizer experiments, started in 1843 and continuing to the present day.

Fisher analysed the effect of the seasonal distribution of rainfall during sixty years on the wheat yield from 13 plots, each of which received a different manurial or fertilizer treatment. The rainfall of each year, which was divided into 61 periods of 6 days, was fitted with a fifth-degree polynomial on time.

The next stage in the analysis was to relate yield to the corresponding coefficients of the polynomial in a linear multiple regression equation including trend variables to allow for slow changes in yield due to non-weather causes. This equation gives the yield to be expected in any year for which the rainfall distribution is known, and thus allows estimation of the effect on final yield of a unit change in rainfall during any particular period. Similarly, the average effect of supplementary irrigation or artificial rainfall applied at any particular date can be evaluated. An example of the results obtained by this method at two very different sites is given in Figure 5.

Fisher's analysis showed that, at Rothamsted, rainfall distribution variations accounted for, on average, one-third of the variation in yield. However, the importance of rainfall variations varied considerably on the different plots. Thus, on the highest-yielding plot which received annual applications of farmyard manure, over 40 per cent of the yield variance could be explained by variation in rainfall, whereas on the equally high-yielding plot receiving 146 kg nitrogen $\text{ha}^{-1} \text{yr}^{-1}$ in chemical fertilizers, only 23 per cent of the yield variation could be accounted for. A similarly small percentage was found with the lowest-yielding, unfertilized plot.

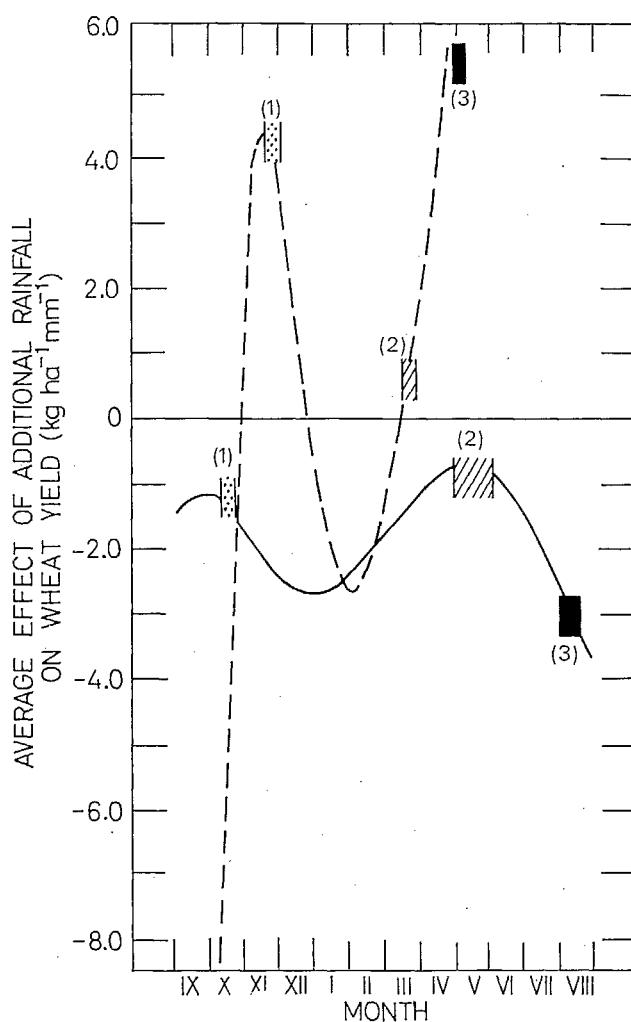


FIG. 5. Average effect of additional rainfall at different times on wheat yield as calculated by Fisher's method in an arid (Israel) and a humid (United Kingdom) region.

— Rothamsted, England, Farmyard manure plot yields (after Russell and Watson, 1940).

-- Mishmar HaNegev, Israel, Average settlement yields (after Lomas and Shashoua, in press).

(1) Sowing stage.

(2) Flowering stage.

(3) Harvest stage.

However, certain features were common to the response curves on all the plots: the average effect of additional rainfall was to depress the yield for all the fertilizer treatments. In general, the yield reduction was least when additional rain fell in early winter and at tillering stage, in early spring. The greatest yield reduction was when rainfall was above normal during mid-winter and during the preharvest period in mid-summer.

Buck (1961), in another analysis of this same experimental data, showed that the rainfall effects are attributable mainly to the total amount of rainfall

irrespective of its distribution; inclusion of rainfall distribution variates did not significantly reduce the variance on any of the plots. Buck included data on air temperature and hours of bright sunshine in his analysis, neither of which terms significantly accounted for any variance in yield, although the calculated effect of the latter term was much greater in size than the former.

The practical application of Fisher's results and those obtained by applying his method of analysis to two other series of wheat fertilizer experiments in England has been brought out by Russell and Watson (1940) in their discussion of the influence of the distribution and total amount of rainfall on the effectiveness of various fertilizer treatments applied to different soil types under different systems of cultivation. Russell (1950) also discusses the use of Fisher's method to investigate the effect of rainfall distribution on the quality of the grain harvested. He shows that the relationship is sufficiently close in the case of the nitrogen content of the barley crop in England to allow a reasonable forecast to be made two months before harvest.

A number of investigations using this method of analysis have been reported for wheat crops growing under more arid conditions. Hopkins (1935) studied the effect of rainfall distribution on the yield of three varieties of spring wheat grown under two different systems of cultivation at seven sites in western Canada. Although the regression coefficients were positive for all but the sowing and harvest period, the proportion of yield variation accounted for by rainfall was somewhat less than in England.

By contrast, Gangopadhyaya and Sarker's (1965) analysis of some Indian measurements showed that, on the average, 75 per cent of the total variation in wheat yields from five crop weather observatories could be accounted for by variation in rainfall distribution. Lomas and Shashoua (in press) analysed two series of wheat yield data from an arid zone of Israel and found that 61 and 79 per cent, respectively, of the yield variance could be accounted for by variance in rainfall distribution. However, 52 and 66 per cent, respectively, of the variance was accounted for by a simple linear regression of yield on total seasonal rainfall and, as at Rothamsted, the improvement by including rainfall distribution within the season was not significant.

Fisher's method has been applied to a number of other crops in addition to wheat. These include barley in England (Wishart and Mackenzie, 1930); maize at nine stations in seven of the central states of the United States (Davis and Harrell, 1941), and in Illinois (Runge and Odell, 1958); cotton in India (Kalamakar and Satakopan, 1960); and sugar cane in India (Acharya *et al.*, 1960).

A direct test of Fisher's method of calculating the effect of additional water supply on crop yield is possible by comparing such results with those obtained from a series of irrigation experiments carried out at

the same site. For example, the results of Lomas and Shashoua's analysis of the rainfall and wheat yield relationship in southern Israel (see Fig. 5) can be compared with Shimshi's conclusion drawn from a six-year series of wheat irrigation experiments conducted on the same soil type only 10 km distant.

Shimshi (1969) found that the highest marginal response to additional water was obtained from early irrigation applied immediately after sowing, even in relatively rainy years and even in years with early rains. The response ranged from $4 \text{ kg ha}^{-1} \text{ mm}^{-1}$ in a rainy year to $24-25 \text{ kg ha}^{-1} \text{ mm}^{-1}$ in a dry year. Early irrigation ensured early development, enabling the crop to enter the cold mid-winter in a robust and well-developed stage and to take advantage of the late winter rains.

The efficiency of later irrigations varied according to the pattern of rainfall. When applied during a dry spell at the end of winter, a late irrigation was almost as effective as an early one, provided that subsequent heavy rainfall did not render it unnecessary. No special sensitivity to drought was found at the booting or heading stage. The general conclusion from the six years of experiments was that water deficiency during the early stages causes damage which is only partly reversible by a subsequently favourable moisture régime.

Although there is some measure of general agreement between Shimshi's experimental conclusions and those to be drawn from Lomas and Shashoua's statistical analysis of rain and yield data, the comparison brings out a number of important weaknesses in the statistical approach: (a) Serial interactions are ignored, although it is clear that, for example, the effect on yield of additional water supply in the beginning of an above-average rainfall season will be much less than in a below-average season. (b) The statistical approach assumes a linear relationship between rainfall excess or deficit and yield at all growth stages. Clearly this cannot be so over an unlimited range of deviations and even over a limited range there is experimental evidence against a linear relationship. (c) Unless other weather parameters are included in the analysis, the effect of any such deviations correlated with rainfall will be attributed to the latter. (d) The length of rainfall period chosen for analysis may be critical for certain crops and patterns of rainfall distribution. Despite these limitations, the results obtained by Fisher's method may be useful to plant physiologists in concentrating their attention on the stages of crop development when yield is especially sensitive to the effect of changes in the water supply.

DROUGHT AS AN INDEX OF THE EFFECTS OF WATER SUPPLY

At its simplest, drought may be defined as the absence of rainfall and thus provides an even more readily available index of water supply than rainfall. No doubt

for this reason the early literature contains many references to drought indices being used to assess the effect of water supply on crops. The main drawback to their use is the difficulty in adequately defining the beginning and end of a drought, and this was recognized at an early stage. The Babylonian Talmud, concluded in the fifth century, contains extensive discussion on these points (Malter, 1967). The severity of drought was then categorized by the length in the delay of the start of the rainy season after its customary date. Thus, if the first rains were delayed 30 days, "distinguished individuals began to fast", while if no rain had fallen by 40 days, "the court orders a three-day communal fast".

The discussion continues: "How much rain must fall in order that the congregation may stop fasting? There must be rain enough to penetrate the cavity made by the plough; this is the opinion of R. Meir; R. Judah said, if the soil is dry it is enough if the rain penetrates to the depth of a hand-breadth, in moderately soft soil the penetration of two hand-breadths is required, and in tilled, loose, ground three hand-breadths."

A review of the more recent, statistical methods used to define drought from rainfall observations is provided by Maher (1968) and illustrated by examples drawn from the computer analysis of long-term rainfall series from Australia. The review also discusses methods available for specifying the persistence of runs of dry months and dry years and for examining the spatial association of rainfall series so that the areal extent of droughts can be examined.

These two aspects of drought are of major importance in arid zone agriculture based on livestock grazing of rain-fed pasture. In such cases, decisions on livestock density should be based not only on long-term average values of rainfall and the probability of droughts of given intensities and durations, but also on the likelihood of periodic fluctuations in the persistence of dry spells and their areal extent.

This application of drought indices implies that the relationship between rainfall, or its absence, and yield is known. Alternatively, drought indices could be used to assess the effect of drought. One approach would be to compare, over a long period, the yearly values of various drought indices with some independent, quantitative assessment of drought damage, or agricultural production. The index showing the highest correlation could then be selected as the most valid. The difficulty of this approach is that of obtaining a sufficiently long series of quantitative assessments of drought damage under a comparable system of agricultural production.

A semi-quantitative study of this nature has been made by Everist and Moule (1952) with special reference to the economic effects of drought on pastures and sheep husbandry in the semi-arid parts of Queensland, Australia.

An alternative experimental technique for determining the effect of drought at specific growth stages on crop yields would be to use mobile rain shelters of

the type employed in irrigation research in humid areas. Salter *et al.* (1961) have discussed the various experimental techniques which can be employed.

So far, the procedures described for assessing the effect of rain or drought on yield have assumed that the effect of water supply is independent of the atmospheric demand. This is clearly not so, and most drought indices include a climatic measure of the atmospheric demand for water (at one time termed "evaporability" and now more usually referred to as "potential evapo-transpiration") as well as rainfall.

The most widely used parameter has been air temperature, no doubt because it is also the most generally available. A number of different combinations of air temperature and rainfall form the basis of the main systems of climatic classification. In most of these, total rainfall provides the numerator of the index, and some function of mean air temperature—which may be simple or highly complex—provides the denominator. Burgos (1968) has reviewed the different systems with special attention to their agroclimatic use in assessing productivity. His conclusion is that it is very difficult to apply such indices to specific problems, although they may be very useful for general studies in agricultural geography.

Budyko (1956) has also described the various climatological indices based on the water balance approach. A full account is given of a number of once widely used methods which utilize the saturation vapour pressure deficit of the air as the measure of evaporability.

In the same reference, Budyko also describes a more recent energy-balance index termed the "radiational index of dryness". This is a dimensionless ratio: the surface radiation balance divided by the latent heat equivalent of precipitation. This index has been widely used in the U.S.S.R. to study, on a continental and global scale, the influence of climate on the distribution of the major plant and soil associations.

On a more local, agricultural scale, Uchijima (1962) has used the radiational index of dryness to provide an agroclimatological classification of Japan in relation to paddy rice cultivation. This author prefers the radiation balance approach to previous agroclimatic systems of cultivation based on air temperature because of its sounder physical basis. This, it is claimed, enables the index to be used to make a quantitative evaluation of dry matter production, supplementary irrigation, total water requirements, and earliest dates for transplantation. Presumably this claim refers to regional studies, for no evidence is presented to show that this particular index is any more applicable to detailed studies at a specific site than any of the previously used indices.

SOIL WATER STATUS AS AN INDEX OF THE EFFECT OF WATER SUPPLY

Previously discussed results (e.g. Russell and Watson, 1940) have shown that crop response to water supply depends to a very considerable extent on the type of soil on which the crop is grown, and on the soil treatment. It is, therefore, reasonable to suppose that, for use at specific sites, agroclimatic methods of assessing the effect of water supply would be much improved by including a soil water balance term. Alternatively, by including data on the local soil water characteristics, it should be possible to compute the soil water status at a particular site by agroclimatic methods.

Reiss (1939) appears to have been the first to suggest this second approach. He balanced estimates of evapotranspiration, calculated as a fraction of the measured water loss from a Piche evaporimeter, against measurements of rainfall and irrigation. Predicting the use of such methods for irrigation control, Reiss concluded his paper "we are able to know at each moment the water balance of the soil and can therefore prevent plants wilting by irrigation before they show any external signs of water shortage".

Slatyer (1968) has recently reviewed the use of soil water balance relationships in agroclimatology and, therefore, in this paper attention will be confined to their application in assessing yield response, concentrating on two approaches: those developed in the U.S.S.R. and the United Kingdom.

The first field application of a meteorological method to assess soil water balance appears to have taken place in the U.S.S.R. some twenty-five years ago. Verigo and Razumova (1963) have provided a full description of the method with many examples of the results obtained. Changes in the available soil water content at different depth levels are computed from meteorological measurements by empirical multiple linear regression equations derived from many thousands of field measurements of soil water content, mean air temperature and precipitation made throughout the U.S.S.R. Relationships were computed for the main growth stages of each important crop for the main soil-climate zones in which the crop was grown.

The general form of the regression is:

$$\Delta W = aT + bP + cW - d$$

where ΔW is the variation in available soil water content for a given soil depth over a 10-day period (mm)

T is the mean air temperature for the same period ($^{\circ}\text{C}$)

P is the total precipitation for the same period (mm)

W is the initial available soil water content for the period (mm)

a, b, c and d are fitted constants.

Correlation coefficients for this equation are reported to fluctuate between 0.7 and 0.9, in most cases exceeding 0.8. Widespread tests have shown that soil water content estimated by this method rarely differs from the measured values by more than 20 per cent.

Yields were then correlated with the amounts of water loss during different growth periods, as calculated from the above equation, in a further series of multiple linear regression equations. For example, the equation developed for predicting the yield of spring wheat in the northern steppe region of Kazakhstan was:

$$Y = 1.7 E_1 + 12.7 E_2 + 14.7 E_3 - 740, r = 0.88$$

where Y is the yield (kg ha^{-1})

E_1 is the total water loss during the sowing to shooting stage,

E_2 refers to water loss during the shooting to flowering stage,

and E_3 to the flowering to waxy ripeness stage (all in mm).

Obviously, the two later growth stages are the most important and, with little loss of accuracy ($r = 0.83$), the equation was simplified by combining these growth stages and replacing the water loss during the first stage by the initial available water content of the top metre at time of shooting.

Other agricultural uses of meteorologically based estimates of soil water content are described by Verigo and Razumova (1963). These include estimation of the dates when different soil cultivation practices become possible before freezing and after thawing; estimation of water requirements and yields of irrigated crops and the mapping of the average soil water content at various critical stages of crop development in the different soil-climate zones of the U.S.S.R. Probability tables have also been drawn up to show the likelihood of the soil water content reaching critical levels in different regions at different dates.

The second, somewhat less empirical, method of calculating soil water status climatologically was developed by Penman in the United Kingdom (Penman, 1949, 1952, 1962). It has been very widely used for a number of agricultural purposes, apart from exploring yield-soil water relationships. In Penman's method, measured values of precipitation and irrigation are balanced against values of potential evapotranspiration. These latter values can be estimated from climatological measurements by Penman's combined energy balance and aerodynamic equation or by some simpler, more empirical, climatological equation. Alternatively, potential water loss can be calculated as a function of the measured water loss from one of the many types of evaporimeters in use. The various methods of calculation and measurement available have recently been reviewed (Stanhill *et al.*, 1968).

In Penman's approach, soil water status is parameterized by the soil moisture deficit, the current

negative value of the cumulative soil water balance. This is equivalent to the volume of water necessary to restore the soil to its maximum stable water-holding capacity, generally known as field capacity. If the water supply exceeds the potential loss, the difference is ascribed to drainage or run-off. Calculations during periods when the soil moisture deficit is zero are of hydrological and pedological interest and may also be important for the calculation of salt or nutrient leaching from agricultural soils.

Water surpluses are non-cumulative, i.e. field capacity is assumed to be a single, stable value, but as soon as potential loss exceeds supply a soil moisture deficit begins to accumulate. Obviously this cannot increase indefinitely. In Penman's scheme (1949), water loss continues at the potential rate until the "root reservoir" is exhausted, at which point the soil moisture deficit is termed the "root constant", a value dependent on soil, crop and rainfall characteristics whose specification "will be almost entirely guesswork". After this point is reached, further water loss follows the pattern established for a drying bare soil, i.e., another 25 mm is lost at the potential rate, after which it drops abruptly to 8 per cent of the potential rate. Alternatively, the root reservoir approach may be replaced by the available water content of the root zone if its depth and soil characteristics are known (Salter and Williams, 1967).

Apart from difficulties in defining and estimating potential evapotranspiration (Stanhill, 1965) and in measuring rainfall and irrigation, there are a number of additional sources of error in the soil moisture deficit approach.

Firstly, on fine-textured soils, field capacity is not a constant value and the maximum water-holding capacity may vary significantly during the year according to soil temperature, viscosity effects, and rates of soil wetting and drying. Second, the actual rate of evapotranspiration is often reduced to a value considerably below the potential rate before all of the available soil water in the root zone is exhausted. The characteristic drying curve depends on both soil (the water potential release curve) and climate (the rate of potential evapotranspiration) characteristics. Baier (1969) has reviewed a number of models that have been suggested and states that a season's measurements are necessary to decide which is most applicable for a given set of crop-site characteristics. Third, the soil moisture deficit does not uniquely define soil water status, as the effect of a given deficit is likely to vary, depending on whether the soil is drying or becoming wetter. During a drying cycle, the volume of available water remaining in the root zone is probably rather evenly distributed at a relatively high negative water potential and is, therefore, relatively unavailable for transpiration and growth. In a wetting cycle, the same volume of available water will be concentrated in the upper, wetted zone at a low water potential. Lastly, if soil moisture deficit calculations are started during a period when loss exceeds

supply, the initial datum point must be directly measured.

Soil moisture deficits have been related to yields in at least four different models. The simplest one relates yields to the average or total soil moisture deficit occurring during different growing seasons. This approach has been used very successfully in an analysis of sugar cane production in Hawaii (Chang, 1963). Deficits were calculated on a daily basis by balancing rainfall against Class A pan evaporation, which had been found to equal potential evapotranspiration from sugar cane. Water loss was assumed to continue at the potential rate until the total available water content of the root zone was exhausted. Analysis of ten years of results from six fields on a plantation in northern Hawaii showed highly significant negative correlations for four of the fields, with an average slope of $-36.8 \text{ kg cane ha}^{-1} \text{ mm}^{-1}$ soil moisture deficit for the five non-irrigated fields. This response slope was used to evaluate the profitability of installing an irrigation scheme to cover the entire plantation. Extrapolation of the regression line to zero deficit was used to compute the potential yield under full irrigation. The value obtained, 40 per cent more than the average yield of non-irrigated fields, agreed with the yield obtained from the irrigated field during the wettest season.

Smith (1966) successfully correlated meteorological estimates of mean soil water deficit with the yield of copra, another tropical plantation crop, measured over nineteen years on a 320 ha coconut plantation in Trinidad. Fifty-six per cent of the yield variance could be explained by variance in the mean deficit during the twelve months preceding harvest and the correlation increased with the period considered so that 61 and 66 per cent of yield variance was accounted for by the mean soil water deficit during the twenty-four and twenty-nine months' period before harvest. Correlations with rainfall for the same three periods accounted for much less of the yield variance; 10, 19 and 41 per cent respectively.

Yields have also been related to maximum, rather than average soil moisture deficits. An example of this approach is shown in Figure 6, where the five-year average yields of turnips and swedes in forty-one English counties have been related to the long-term average maximum soil moisture deficit during the six summer months. The negative relationship was highly significant and accounted for 57 per cent of the areal variation in yield. However, the use of maximum in place of average deficit only marginally improved the correlation (r^2 average = 52 per cent).

Maximum values of soil moisture deficits are widely used in irrigation practice and experimentation, with water being applied whenever climatologically determined values of soil moisture deficit are reached. Penman (1952, 1962) has also investigated the effect on yield of irrigation treatments in which the maximum permitted deficit was varied during the growth season to

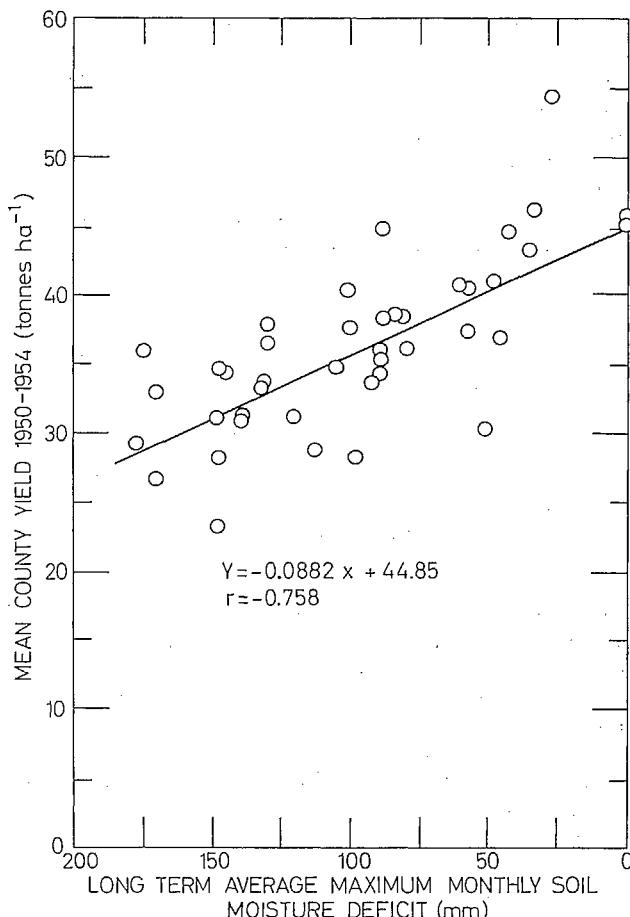


FIG. 6. Relationship between average yield of turnips and swedes in forty-one English counties and the average maximum soil moisture deficit (after Stanhill, 1956).

determine which, if any, crop stages are especially sensitive to water deficit.

Soil moisture deficits occurring during specific stages of crop development can also be related to yield analytically, using the same techniques as described for rainfall indices. For example, analysis of the county yields and soil moisture deficits in England previously referred to showed that areal variations in mean monthly soil moisture deficits during the six summer months (April to September) explained 3, 48, 56, 56, 57 and 52 per cent, respectively, of the areal variation in turnip yield. The short-term response of the same crop to soil moisture deficits in the four mid-summer months was also analysed by Fisher's technique. The results showed considerable differences in the yield response to reductions in the soil moisture deficit. This varied from an increase of 86 kg ha^{-1} per mm deficit reduction during both June and July, to a decrease of $124 \text{ kg ha}^{-1} \text{ mm}^{-1}$ during both August and September.

Another soil moisture deficit index which can be used to assess yield effects is the number of days during which the soil moisture deficit is below a given critical level. The critical level can be determined directly from irrigation experiments or analytically, by selecting the value which gives the most linear relationship to yield.

Rickard (1960) used permanent wilting percentage in the root zone as the critical level and correlated the number of days below this point (referred to as drought days) with seasonal production of pasture and lucerne crops in New Zealand. Four series of production records were used, with correlation coefficients of -0.95, -0.92, -0.91 and -0.58.

Hutchinson *et al.* (1958) used a soil moisture deficit equal to or greater than 13 mm for a three-week period to define the onset of a "water strain" period for the development of rainfed cotton crops in Africa. The number of weeks from planting to the onset of water strain was then related to yield in a multiple linear regression model which included rainfall subsequent to the water strain period and date of planting. The three factors accounted for 62 per cent of the tenfold variation in annual yields, with the water strain index contribution equalling the sum of the two other factors.

In very arid regions a different approach to soil moisture budgeting may be more appropriate, substituting a positive available water content index for the negative soil moisture deficit. The balance would be zero at the beginning of the rainy season and return to this value after the last rains, when all of the available soil water had been exhausted. The number of days that the available soil water content was above a minimum level could then be used as an index for plant growth. Hillel and Tadmor (1962) have used this approach to compare the various habitats available to natural vegetation in the Negev desert of southern Israel.

Bassett (1964) used a similar approach to study the annual variation in the timber growth of a southern pine forest in Arkansas. Growth days were defined as those during which the calculated soil water content in the top 30 cm exceeded a previously determined critical limit. Linear regression between the number of such days per year and timber increment were highly significant, accounting for 97 per cent of the annual growth differences.

Climatological estimates of soil water status have recently been used to provide the starting point for complex models used to study the optimum strategy for resource management. Goodall (1970) has outlined one such model describing the growth of a sheep flock grazing on a semi-arid pasture. The current available soil water content is estimated from rainfall and air temperature measurements and, expressed as a fraction of the possible available soil water, used to compute the relative growth rate of the different species of a semi-shrub pasture community with a series of complex empirical equations. Another set of equations is then used to relate the weight increment of the grazing sheep

to that of the pasture. The whole model is designed for a series of computer experiments to study the effect of changes in environmental conditions and management practice on the productivity of the sheep flocks.

Apart from the practical uses made of soil water balance calculations at individual sites, it should be noted that such estimates are provided routinely on a nationwide scale in a number of countries. The scheme used in the United Kingdom has been fully described in a recent technical bulletin which contains long-term average values (Smith, 1967). In the United States maps of a "crop moisture index" are published weekly; Palmer (1968) has given details of the methods used.

The ability of soil water indices to predict wheat yields has been compared with that of rainfall indices by Baier and Robertson (1968). Yields measured at eight Canadian sites during five seasons were correlated with rainfall totals and the meteorologically calculated soil water status at different depths in the root zone, each season consisting of five months or five crop development periods. An elaborate statistical analysis of the results is presented, but the only aspect considered here will be the comparison of the variation in actual yields explained by rainfall or soil water. Soil water status at the most significant of the depth zones accounted for 70 per cent of yield variation, compared with 17 per cent explicable by variations in total rainfall. By including estimates of soil water status at more than one depth zone in the regression, over 80 per cent of the yield variation could be explained, and such estimates had an average coefficient of variation of 21 per cent. The authors explain the very low correlation of yield with rainfall by the fact that rain was excessive at some of the sites.

EVAPOTRANSPIRATION AS AN INDEX OF THE EFFECT OF WATER SUPPLY

Indices based on soil water status integrate the soil characteristics of the site under study with the climatic elements of water supply and demand. They do not, however, directly include plant characteristics, which represent the segment of the soil-plant-atmosphere water continuum most closely related to the physiological processes governing yield formation. Evapotranspiration provides an agroclimatic index which does include the effect of plant factors, and it has been widely used to assess the effect of water supply on both growth and yield.

When the soil-plant complex imposes no resistance to water transport, then, by definition, actual evapotranspiration equals its climatically limited potential rate. As rates of both potential evapotranspiration and photosynthesis are primarily dependent on the radiative energy flux from the sun (de Wit, 1958), a close relationship is to be expected between rates of dry matter accumulation and evapotranspiration under potential

conditions. If evapotranspiration proceeds at a rate below its potential, then the relationship between the actual and potential loss is a function of the internal, crop resistance to water loss (Monteith, 1965), the most important component of which is normally stomatal resistance. As this also represents an important element in the series of resistances to carbon dioxide flux and hence dry matter production, it is reasonable to expect a close relationship between the ratios of actual to potential evapotranspiration and actual to potential dry matter production.

ACTUAL EVAPOTRANSPIRATION

The close relationship between transpiration and dry matter increment has been known to plant physiologists for over 200 years. The ratio between the two rates, known as the transpiration or water use efficiency ratio, was intensively studied by crop physiologists at the beginning of this century, usually by means of successive harvests from container-grown crop plants. For this reason their absolute results are of limited interest. de Wit (1958) re-analysed some of these data and showed that much of the site-to-site and year-to-year differences in the slope of the dry weight to transpiration relationships could be removed when transpiration was expressed as a ratio of open water surface evaporation or potential transpiration. A method of irrigation control was proposed based on the use of crop constants derived from simple pot experiments.

Many of the results of the early investigations were also used by Arkley (1963) in his study of the effect of changing soil and climatic conditions on the relationship between plant growth and transpiration.

The early American field investigations of the relationship between crop yield and evapotranspiration have been discussed by Klages (1942); in nearly all cases simple linear regressions were adequate. Verigo and Razumova (1963) report similar relationships found in field measurements from various zones of the U.S.S.R. On the Canadian prairies, Staple and Lehane (1954b) found that, with a simple linear regression, 69 per cent of the variation in yields of wheat crops grown during twelve years at seven stations in southern Saskatchewan, could be accounted for by variations in the total seasonal evapotranspiration. A curvilinear relationship, fitted by a quadratic equation, accounted for 75 per cent of the yield variation. Analysis of thirty-one years of measurements at one of the stations, Swift Current (Staple and Lehane, 1954a), showed even higher correlations: evapotranspiration accounting for 77 per cent of the wheat yield variation in the simple linear regression and 89 per cent in the quadratic, curvilinear relationship.

In both of the investigations a comparison can be made with the results obtained by rainfall-yield relationships. In the first investigation, 36 per cent of the

yield variation was accounted for by a simple linear regression on total precipitation and 62 per cent by a multiple regression which included the fallow and crop season precipitation separately. At Swift Current, 56 per cent of the wheat yield variation was accounted for by variations in the rainfall during the growing season.

A later study (Williams, 1969) of the total wheat production on the Canadian prairies during sixteen years also allows a comparison of the accuracy of estimates based on evapotranspiration with those based on precipitation to be made. Complex multiple linear regressions were used, including monthly values of both potential evapotranspiration and precipitation, or of precipitation alone. The average deviation of the yield estimates was only 7 per cent in the first case, but 13 per cent in the latter case.

Penman (1962) used climatologically computed values of evapotranspiration as a growth index in his analysis of the results of a series of irrigation experiments at Woburn in southern England. The index consists of total potential evapotranspiration during the period that soil moisture deficit was above empirically selected values of the root constant (the values selected varying with soil treatment and crop). Accumulated values of dry matter production of grass were linearly related to accumulated actual evapotranspiration over a period of six years, with only slight deviations during the winter. The slope of the relationship was used to assess yield response to both water and nitrogen application, photosynthetic efficiency, and the start of the growth season.

The grass crop is particularly well-suited to this type of analysis, as yield is almost equivalent to the total net dry matter production and frequent harvests enable the large seasonal variation in this growth index to be utilized.

Smith (1960) also found a linear relationship between the average annual yields of meadow hay in England and meteoerologically computed values of evapotranspiration, assuming a critical soil moisture deficit of 50 mm. A seventeen-year period was used for the analysis and allowance was made for yield improvements during this period by including the year of measurement in the multiple linear regression model. The country was divided into four main areas and, although the constants varied considerably between the areas, the mean percentage errors of estimate were all less than 4 per cent. When all areas were grouped together, the error in annual estimates of total meadow hay production in England averaged 2.1 per cent and the correlation coefficient between estimated and actual values was 0.95.

Laycock (1964) has adapted the same model in an analysis of annual tea yields from a plantation in Malawi. The tea plantation forms an almost complete leaf canopy whose young shoots are harvested periodically and which is almost completely removed periodically by heavy pruning. Experimentally determined reduction factors

were used to adjust for the reduction in evapotranspiration caused by this pruning. Tests of linearity suggested that the critical soil moisture deficit was zero; actual evapotranspiration was, therefore, taken to equal rainfall or adjusted potential evapotranspiration, whichever value was lower.

Within a single season there was no clear relationship between yield and evapotranspiration, but simple linear regressions of annual yield on adjusted evapotranspiration accounted for 84 and 94 per cent of the yield variation measured in two series of field measurements.

Penman's model has also been applied to the yields of annual crops, with varying success. At Woburn, Penman (1962) found that the same model used to describe dry matter production of grass could be applied successfully to early and main crop potato crops. It was somewhat less successful when applied to yields of sugar beet and spring beans. No relationship whatsoever was found between yields of spring barley and spring wheat and estimates of actual evapotranspiration.

A re-analysis of the winter wheat yields from the classical fertilizer experiment at Rothamsted yielded the same negative results (Buck, 1961). By contrast, Buck found that a multiple linear regression equation, including estimates of total seasonal evapotranspiration, year of harvest (to allow for time trends) and an index of virus yellows incidence, explained 78 per cent of the variation in the average annual yield of sugar beet harvested in England and Wales during a fifteen-year period. Analysis of variance showed that evapotranspiration alone accounted for 53 per cent of yield variance. Total seasonal rainfall variance explained 25 per cent of yield variance, and rainfall for each of the six months of the growing season explained 30 per cent in an analysis of the type introduced by Fisher. Inclusion of March rainfall, when excesses can delay sowing and leach nitrogen, allowed 40 per cent of the variation in sugar beet yields to be explained by reference to rainfall variation.

The same investigation analysed the complex relationship between potato yield and evapotranspiration in two districts of England. Simple correlations with seasonal evapotranspiration accounted for 26 and 15 per cent of yield variance, with seasonal rainfall totals showing zero correlations in both districts. However, when a potato blight damage index was included in multiple linear regressions, evapotranspiration accounted for 18 and 50 per cent of yield differences, while rainfall accounted for 30 per cent in one district and 0 in the other.

This example shows the limitations of the purely statistical and empirical approach. High correlations between the weather parameters and disease incidence almost completely obscured the direct effect of weather on yield. Although beyond the scope of this review, it may be noted that a number of the agroclimatic indices of water supply discussed have also been successfully used to assess the incidence of, and damage caused by,

pests and diseases of agricultural crops and livestock and the optimum timing of control measures.

Agroclimatic indices, in particular estimated actual evapotranspiration, have also been used to compute the effect of water supply on yield-determining growth processes. For example, Hutchinson *et al.* (1958) used their previously mentioned water stress index to describe the effect of rainfall deficiencies on cotton leaf area development, a major yield determinant.

Hearn (1969) has used estimates of actual evapotranspiration in a complex physiological model of the growth and yield formation of cotton crops growing in the desert environment of southern Arabia. In two years highly significant linear relationships were found between estimated evapotranspiration and the final dry weights of cotton crops which differed as to variety, irrigation treatment and sowing date. The final plant dry weight was itself linearly related to seed cotton yield. The slopes of the dry weight to evapotranspiration relationships were similar in both years, but nearly 30 per cent less than the slope computed for the potential photosynthesis to potential transpiration relationship. This difference was attributed to an observed reduction of photosynthetic efficiency with age.

RATIO OF ACTUAL TO POTENTIAL EVAPOTRANSPIRATION

A number of investigators have used this ratio very successfully to assess yield response to water status. Fitzpatrick and Nix (1969) used weekly measurements of rainfall and estimates of open water surface evaporation in a sub-humid to semi-arid region of central Queensland, Australia, to compute soil water status. These values were then used along with phenological data to estimate actual evapotranspiration rates from crops of cotton, grain sorghum and wheat. In another paper (Nix and Fitzpatrick, 1969), the same authors related the ratio of estimated actual to potential evapotranspiration at different growth stages to the yields of wheat and sorghum crops measured during a long series of varietal trials at several sites in Queensland. The growth stage showing the highest correlation with yield was anthesis for two varieties of both sorghum and wheat. A number of simpler agroclimatic indices were also correlated with crop yield and the results, reproduced in Table 1, show the superiority of the actual to potential evapotranspiration ratio. However, even better results were obtained by another index of crop water stress. This "stress index" consisted of the estimated available water at the beginning of the critical flowering stage divided by the mean potential evapotranspiration rate during the critical period.

The relationship between stress index and the yields of five varieties of sorghum was found to be linear, but a curvilinear relationship provided a better fit to the wheat yield data. Fitted quadratic equations accounted

TABLE 1. Correlations between grain yields and various water supply indices. Biloela, Queensland (After Nix and Fitzpatrick, 1969)

Water supply index	WHEAT, variety Gobo			SORGHUM, variety Wheatland		
	Mean	Standard deviation	r^2	Mean	Standard deviation	r^2
<i>Rainfall, mm</i>						
Total crop season	170	72	0.14	347	100	0.01
Sowing to heading stage	97	51	0.20	195	66	0.04
Available soil water at sowing	144	28	0.31 ¹	133	32	0.21
2 + 3	241	55	0.49 ²	328	78	0.09
<i>Actual evapotranspiration, mm</i>						
Total crop season	239	26	0.38 ²	409	71	0.01
Sowing to heading stage	139	16	0.41 ²	247	47	0.07
<i>Actual to potential evapotranspiration, ratio</i>						
At critical period	—	—	0.49 ²	—	—	0.36 ²
<i>Stress index at critical period, weeks</i>						
Using long-term mean weekly potential			0.56 ³			0.60 ²
Using specific weekly potential			0.69 ³			0.76 ²

1. Significant at $P = 0.05$.
 2. Significant at $P = 0.01$.
 3. Significant at $P = 0.001$.

for between 60 and 83 per cent of the yield variation in four wheat varieties, a common regression explaining 60 per cent of the yield differences.

A quadratic equation also fitted the relationship between wheat yields and the stress index when data from five Queensland centres were analysed. Regressions at individual sites accounted for between 60 and 71 per cent of yield variation and a combined regression for 66 per cent. A significant improvement in the correlation was obtained by computing the value of the stress index from evapotranspiration estimates made for specific weeks in place of long-term average values for the same dates.

Fitzpatrick and Nix (1970) incorporated the ratio of actual to potential evapotranspiration as the Moisture Index in a multifactor Growth Index used to assess relative dry matter yields from pasture crops in Australia. The other two climatic indices, incorporated multiplacatively, were a Light Index, a complex function of the ratio of global to extra-terrestrial solar radiation, and a Thermal Index, calculated from mean air temperature, using separate growth curves for each of the three main types of Australian pasture crops.

Weekly values of this agroclimatic growth index were calculated for 277 Australian sites and the agronomic implications of the annual pattern of dry matter production were discussed for a number of representative stations.

The actual to potential evapotranspiration ratio has been used, somewhat less empirically, to assess sugar cane yields in Hawaii (Chang *et al.*, 1963). The measured relationship between yield and meteorologically estimated soil moisture deficit at four plantations was generalized in the following quadratic equation:

$$Ya/Yp = ax^2 + bX + c$$

where Ya/Yp is the ratio of actual to potential yield
 X is the ratio of actual to potential evapotranspiration
 and a, b and c are empirically fitted constants.

The equation was valid for values of X greater than 0.73 and when the soil moisture deficit did not exceed 0.27 of potential evapotranspiration. Potential yield was derived from the experimental data by extrapolating the yield response curve to zero soil moisture deficit. As such data are not generally available, potential yield was expressed as an empirical function of potential evapotranspiration in the working equation, both values being primarily dependent on solar radiation. The working equation was tested with water use and yield data from 21 fields in two sugar cane plantations in Hawaii. The average deviation between estimated and actual yields was only 7 per cent.

Relationships of the above type closely resemble those derived by Mitscherlich from the "Law of diminishing returns", which states that when all growth factors save one are maintained constant, yield increases due to successive equal increments of the variable factor diminish progressively. This law, as expressed by Mitscherlich's equation:

$$\ln(Yp - Ya)/Yp = -cW$$

where W is the level of the variable factor
 c is a constant
 and Ya and Yp retain their previous meanings,

was used more than fifty years ago to relate yields to soil water status (Mitscherlich and Floes, 1913). The

results are of limited use as they were obtained in pot experiments with irrigation treatments based on an inadequate understanding of the physics of soil water movement. The equation, however, might still prove to be a useful basis for analysis if used with improved soil water indices.

A different theoretical approach to water-yield relationships is now being developed which also utilizes the ratio of actual to potential evapotranspiration. Full details would be inappropriate to a review of simplified agroclimatic procedures, but briefly, the ratio is used to calculate the internal or stomatal resistance of the entire crop canopy to water vapour diffusion on a unit soil area basis (Monteith, 1965). Functional relationships are next established between crop resistance and the various climatic, plant and soil parameters, including soil water status, known to be of importance.

After calculating the external boundary layer resistance of the crop from its aerodynamic properties and

wind speed (Monteith, 1965), the internal and external crop resistances are corrected for the calculation of carbon dioxide flux. Such calculations can proceed in two ways. If estimates of the mesophyll resistance to carbon dioxide transport and fixation are available, then carbon dioxide flux, and hence dry matter production, can be computed by Fick's law, assuming carbon dioxide concentration in the chloroplasts to be zero. Alternatively, if measurements of dry matter production, and hence, carbon dioxide flux, are available, then mesophyll resistance can be computed.

With values of the boundary, stomatal and mesophyll resistances and their relationships to plant, soil and climatic factors known, it should be possible to compute the dry matter production and evapotranspiration under various environmental conditions. Szeicz and Long (1969) used this approach to assess the response of a grass-clover crop in Denmark to increasing soil water stress and Stanhill (in press) has similarly calculated the response of an orange plantation in Israel.

Résumé

Méthodes agroclimatiques simplifiées pour évaluer l'effet de l'approvisionnement en eau (G. Stanhill)

L'auteur passe en revue un certain nombre de méthodes agroclimatiques simplifiées qui ont été utilisées pour évaluer l'effet de l'approvisionnement en eau sur le rendement de cultures, notamment le Blé.

La question est abordée sous l'angle historique, avec rappel des divers indices d'approvisionnement en eau et modèles de rendement dans l'ordre de complexité croissante. La plupart des recherches considérées visaient à expliquer la variation annuelle du rendement en un même site ou secteur; dans certains cas, les rapports aréolaire ont été étudiés; et, récemment, l'effet de l'approvisionnement en eau sur le développement du rendement au cours d'une même saison de croissance a été examiné.

En région aride, où la demande d'eau dépasse l'offre et constitue le facteur déterminant du rendement, les plus simples des indices de l'approvisionnement en eau et des modèles du rendement se sont révélés efficaces. Ainsi, on a pu expliquer jusqu'à 80 % de la variation annuelle du rendement de cultures de Blé par des régres-

sions linéaires simples sur la hauteur de pluie saisonnière totale. En région humide, où l'offre d'eau dépasse la demande et ne constitue plus le facteur limitant, des résultats presque aussi concluants ont été obtenus, mais pour une gamme très réduite de cultures ne comprenant pas le Blé. Le rendement des plantes de pâturage, qui est pratiquement équivalent à leur accroissement en matière sèche, a fait apparaître une corrélation linéaire élevée avec les évaluations climatologiques de l'évapotranspiration effective.

Par contre, les essais de mise en corrélation d'indices très complexes d'approvisionnement du sol en eau avec le rendement du Blé et d'autres cultures annuelles se sont généralement révélés peu concluants dans les régions humides. Dans ces cas, les progrès futurs devront probablement être attendus de la mise au point de modèles physiologiques rationnels qui permettront d'évaluer l'effet de tous les facteurs importants du milieu, y compris l'approvisionnement en eau, plutôt que du perfectionnement d'indices d'approvisionnement en eau devant être utilisés empiriquement dans des modèles purement statistiques de la relation du rendement.

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Bilan hydrique de l'assolement Blé-jachère et évaporation d'un sol nu, en région semi-aride

A. Perrier

Station centrale de bioclimatologie,
Centre national de recherches agronomiques,
Versailles (France)

Le but de cette analyse est de définir, dans les conditions particulières des Hauts Plateaux algériens et dans le cadre des techniques traditionnellement utilisées pour le travail de cet assolement, quel gain quantitatif réel la jachère entraîne et quels sont les facteurs caractéristiques d'un sol nu sur lesquels il est possible d'intervenir afin de permettre une amélioration des réserves hydriques de la jachère.

ANALYSE EXPÉRIMENTALE DU BILAN HYDRIQUE

L'analyse fine d'un bilan hydrique peut se faire soit par une analyse des flux, pluie et évaporation (méthode du bilan d'énergie ou aérodynamique) (Tanner et Fuchs, 1968), soit par l'analyse des variations de l'humidité du sol dans les conditions naturelles — méthode gravimétrique, méthode des sondes ou méthode neutronique (Barrada et Decroux, 1965). C'est l'analyse de l'humidité pondérale du sol par la méthode gravimétrique (soit H , exprimé en kg d'eau par kg de sol sec) qui a été retenue pour servir de point de départ à notre investigation; elle permet de suivre, en fonction de la profondeur et du temps, et de façon simple (minimum d'équipement), les variations d'humidité et les zones de réserve exploitable pour les plantes. La précision des déterminations dépend essentiellement de la bonne localisation des échantillons prélevés — surtout au voisinage de la surface (prélèvement manuel) — du nombre de prélèvements en fonction de la profondeur et de leur répétition dans l'espace, et enfin de la fréquence des analyses au cours du temps. A cet effet, quatre parcelles en assolement Blé-jachère (région de Sétif, Hauts Plateaux) ont été suivies sur une période d'un an en réalisant des prélèvements hebdomadaires à 13 niveaux (voir tableau 1) et avec un minimum de trois répétitions par parcelle.

MÉTHODE D'ANALYSE DES DONNÉES EXPÉRIMENTALES

A partir des profils hydriques, il est possible d'élaborer trois types de résultats qui concernent: les variations d'humidité du sol (vitesse de réhumectation et de dessèchement des différentes zones du sol); les zones de réserves facilement utilisables par la plante et leur évolution; enfin, si la précision est suffisante, l'évolution quantitative des réserves du sol ou du déficit et, compte tenu des pluies, l'évolution de l'évapotranspiration réelle.

Évolution de l'humidité

Cette évolution est représentée sur la figure 1 pour une parcelle en Blé et une en jachère au moyen de courbes d'isohumidité. Ces courbes présentent l'avantage de tenir compte en chaque point de l'ensemble des valeurs voisines (profils précédent et suivant, et couche sous-jacente et sus-jacente) et d'être par conséquent le résultat d'une pondération des erreurs expérimentales liées à chaque valeur d'humidité.

A partir de ces courbes, il est possible localement d'appliquer l'équation de diffusion ($\partial H / \partial t = D \partial^2 H / \partial z^2$) et d'en déduire approximativement une valeur de D (Wyllie et Gardner, 1958):

$$D = \frac{10^{-4}}{\Delta t / (\Delta H_1 - \Delta H_2)} \text{ m}^2 \text{ j}^{-1}$$

Δt , temps en jours pour avoir une augmentation d'humidité de 0,01 à la profondeur z
 ΔH_1 et ΔH_2 , écarts d'humidité mesurés par rapport à la profondeur z considérée (pour une épaisseur donnée de 0,1 mètre de part et d'autre de ce point)

$$\Delta H_1 = H_{(z-0,1)} - H_{(z)}$$

$$\Delta H_2 = H_{(z)} - H_{(z+0,1)}$$

TABLEAU I

Z	0-5	5-10	10-15	15-20	20-35	35-50	50-70	70-90	90-110	110-130	130-150	150-170	170-190	
$H_{ci} \times 100$	$25,5 \pm 0,6$	$25,5 \pm 0,6$	$26 \pm 0,3$	$26 \pm 0,5$	$25,6 \pm 0,5$	$25,5 \pm 0,8$	$27,3 \pm 0,6$	$21,9 \pm 0,8$	$18,7 \pm 1,2$	$17,0 \pm 1,2$	$14,9 \pm 0,5$	$18 \pm 0,5$	$17,7 \pm 1,5$	
$H_{fi} \times 100$	$18,7 \pm 0,7$	$18,4 \pm 0,8$	$18,1 \pm 0,6$	$18,0 \pm 0,6$	$17,6 \pm 0,8$	$18,3 \pm 1,1$	$14,6 \pm 1,0$	$11,5 \pm 1,0$	$12,7 \pm 1,1$	$14,6 \pm 0,6$	$12,8 \pm 0,8$	$13,6 \pm 0,8$	$13,5 \pm 0,7$	
$\rho_i (Hc) \text{ kg m}^{-3}$	1 150	1 150	1 200	1 200	1 150	1 300	1 350	1 350	1 450	1 450	1 550	1 500	1 450	
rum_i mm	3,92	4,20	4,70	4,80	18,80	14,00	34,60	28,10	17,40	7,00	6,50	10,20	12,20	
$\Sigma rum_i = RUM = 160 \text{ mm}$														

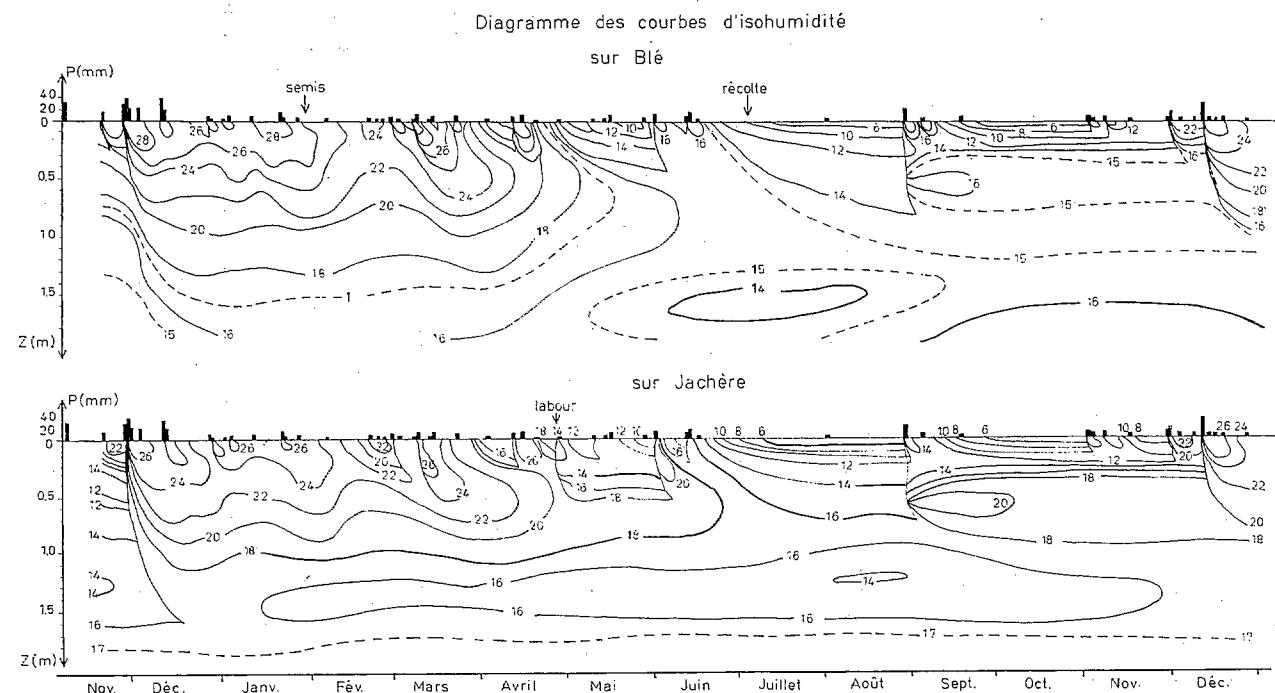


FIG. 1. Évolution des courbes moyennes d'isohumidité de deux parcelles en assolement Blé-jachère dans la région de Sétif (Algérie). P, pluie journalière en millimètres; Z, profondeur explorée en millimètres.

La valeur calculée de D en période de réhumectation est voisine de $1,2 \text{ à } 1,5 \text{ } 10^{-2} \text{ m}^2 \text{ j}^{-1}$ entre 0,5 et 1 mètre de profondeur; en période de dessèchement, elle atteint $0,2 \text{ à } 0,5 \text{ } 10^{-2} \text{ m}^2 \text{ j}^{-1}$ dans les 50 premiers centimètres.

Ainsi, pour une variation relative de 30 % de l'humidité, qui passe de 0,25 à 0,16, la diffusivité diminue d'un quart environ. Ce résultat est classique, mais il joue un rôle déterminant dans la formation du mulch (II, 4) (Gardner, 1961). En effet, la densité de flux $\varphi_L (\varphi_L = D \delta (\rho H) / \delta z \text{ en kg m}^{-2} \text{ j}^{-1}, \text{ ou mm j}^{-1})$ entraîne, pour des gradients moyens $\delta H / \delta z$ d'environ $0,2 \text{ m}^{-1}$, une densité de flux de masse de $1,3 \text{ mm j}^{-1}$ au maximum ($D \sim 0,5 \text{ } 10^{-2}$ et $\rho \sim 1300 \text{ kg m}^{-3}$). Cette part assurée par la diffusion est faible devant l'évaporation potentielle ($1,5 \text{ à } 10 \text{ mm j}^{-1}$).

Réhumectation (voir fig. 1, novembre-janvier). La réhumectation est rapide avec les fortes pluies de fin d'automne ou de début d'hiver et se prolonge tout l'hiver (faible évaporation, pluies fréquentes).

Le front ou profondeur maximale atteint par telle ou telle courbe d'isohumidité progresse de façon sensiblement identique (6 cm j^{-1}) pour les deux parcelles (fig. 1, Blé et jachère). Cependant, une même courbe d'isohumidité pénètre plus profondément dans le cas du Blé (parcelle plus humide au départ, car précédemment en jachère) [Feodoroff, 1965]. Ainsi, par exemple, la courbe 18 % descend à 1,10 mètre sur la sole en jachère et à 1,35 mètre sur la sole en Blé. Ce résultat et l'évolution parabolique des courbes d'isohumidité dans la première phase de réhumectation correspondent assez bien à la solution classique d'un choc hydrique (Carslaw et Jaeger, 1950; Sherwood, 1936), qui entraîne pour une courbe d'isohumidité une progression en $a\sqrt{t}$, a étant d'autant plus petit que l'humidité moyenne de départ est plus faible.

Dessèchement (voir fig. 1, mars-avril). Le dessèchement s'installe de façon progressive (mars-avril) dès que l'évaporation atteint $2 \text{ à } 3 \text{ mm j}^{-1}$, les pluies devenant peu abondantes et moins fréquentes. Le dessèchement se traduit par la pénétration d'allure également parabolique des courbes d'isohumidité. Dès que l'humidité de la surface est suffisamment faible, soit une humidité voisine de celle en équilibre avec l'humidité de l'air (dessèchement maximal), l'évaporation est considérablement réduite et un régime stable tend à s'établir (courbes d'isohumidité pratiquement horizontales pendant la période de septembre à octobre pour la parcelle en Blé et de juillet à septembre pour la jachère).

Ce frein ou effet du mulch naturel n'apparaît sur la jachère que début juillet, car les pluies d'avril, mai, juin, réhumectant le mulch qui s'installe, permettent une reprise de l'évaporation et un dessèchement un peu plus important du sol (voir Action des fortes pluies, p. 482).

Sur la parcelle en Blé, l'assèchement du sol en profondeur par les racines se poursuit jusqu'en août, malgré, à cette date, une couche superficielle très sèche. Cette

action du système racinaire semble se faire sentir même après la récolte (début juillet), ce qui traduirait un effet des chaumes sur l'évaporation (Charles, 1961).

Évolution des zones de réserve

Compte tenu des variations importantes des caractéristiques physiques des différentes couches de sol (horizons pédologiques), le rôle vis-à-vis de la plante des différentes zones de même humidité est assez variable.

Pour mieux préciser ce rôle, il a été défini pour chaque profondeur une réserve utilisable rum_i qui conduit à une réserve utilisable totale pour l'ensemble du sol

$$(190 \text{ cm}) \text{ RUM} \left(\text{RUM} = \sum_{i=1}^{i=13} rum_i \right).$$

Cette réserve utilisable a été définie arbitrairement comme étant la quantité d'eau cédée par une couche de sol qui passerait de l'humidité H_c en équilibre avec une pression d'une atmosphère à l'humidité H_f en équilibre avec une pression de seize atmosphères (point de flétrissement permanent).

$$rum_i = \rho_i(H_i) \cdot (H_{ci} - H_{fi}) \cdot \Delta z_i$$

Δz_i épaisseur de la couche considérée en mètres

$\rho_i(H_i)$ densité apparente de la couche en kg m^{-3}

rum_i réserve utile en kg m^{-2} d'eau ou en mm d'eau.

En fonction du temps, la schématisation de la réserve réelle ru_i à chaque niveau peut s'exprimer simplement en fraction de la réserve utilisable:

$$(ru_i / rum_i) \cdot 100 = 100 \cdot \rho_i(H_i) \cdot (H_i - H_{fi}) / \rho_i(H_{ci}) \cdot (H_{ci} - H_{fi})$$

Il a ainsi été possible de tracer les zones de même gamme de pourcentages de la réserve utilisable (fig. 2), définissant, avec plus de précision que les humidités, le rôle du sol dans l'alimentation hydrique de la culture.

Le tableau 1 donne un exemple de valeurs de H_{ci} , H_{fi} , ρ_i , rum_i et RUM pour une des parcelles.

Pour la parcelle en Blé, les zones de réserve supérieure à 50 % diminuent progressivement dès la fin de mars pour disparaître presque totalement du profil (fin juin); sur jachère, par contre, en dehors du labour, qui provoque un dessèchement brutal de 60 cm de sol, cette disparition de la zone de réserve supérieure à 50 % n'apparaît définitivement en surface qu'au début de juin et ne descend pas au-dessous de 70 cm. Aussi, dès les premières pluies de novembre ou décembre, les réserves de la jachère à chaque niveau se trouvent rapidement reconstituées à plus de 50 %; elles permettent un semis précoce et un meilleur développement, en particulier du système racinaire, favorable à la croissance au cours de la période printanière où le déficit est toujours marqué. En effet, dès le début de mai, les 10 à 20 premiers centimètres sont pratiquement au voisinage du flétrissement permanent; les faibles réserves disponibles sont alors relativement profondes et ne sont exploitables que si le sol permet un développement racinaire en profondeur.

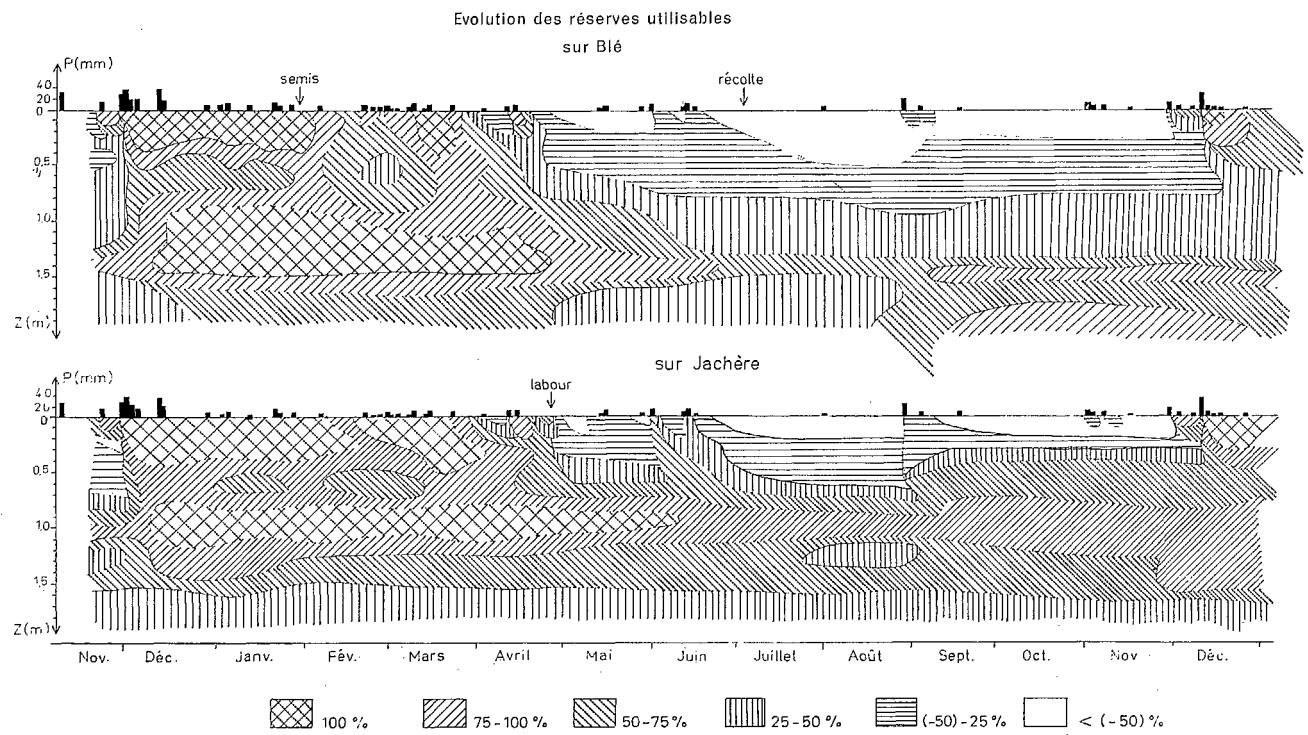


FIG. 2. Évolution des zones de même pourcentage, X, de la réserve utilisable pour les deux parcelles de la figure 1. $X = \frac{100\rho_i(H_i)}{\rho_i(H_{ci})} \cdot \frac{(H_{ci} - H_{fi})}{(H_i - H_{fi})}$. Six zones ont été tracées: $X > 100\%$; $75\% < X < 100\%$; $50\% < X < 75\%$; $25\% < X < 50\%$; $-50\% < X < 25\%$; $X < -50\%$.

Évolution quantitative des réserves

Les réserves totales à un instant donné R ou utiles RU peuvent se chiffrer simplement par les relations suivantes:

$$R = \sum_{i=1}^{i=13} \rho_i(H_i) \cdot H_i \cdot \Delta z_i$$

ou $RU = \sum_{i=1}^{i=13} \rho_i(H_i) \cdot [H_i - H_{fi}] \cdot \Delta z_i$

Pour ce calcul, il est plus précis d'utiliser les valeurs moyennes d'humidité de chaque couche, fournies non par les profils expérimentaux hebdomadaires, mais par le graphique général (fig. 1) pour les journées choisies arbitrairement.

De tels calculs conduisent à la représentation de l'évolution moyenne de ces réserves (R ou RU) [fig. 3] tout au long de l'année et pour les parcelles en jachère et en Blé (les calculs ont été réalisés tous les neuf à quinze jours afin d'encadrer les zones de pluies et de déterminer les humidités moyennes de chaque profondeur à un moment où l'évolution hydrique est plus faible; il est ainsi possible d'éviter les erreurs considérables dues à l'imprécision de l'humidité à un niveau donné en zone de forte réhumectation).

Cette variation des réserves permet aussi de traduire l'évapotranspiration réelle, compte tenu des pluies et dans l'hypothèse d'un ruissellement, d'un drainage ou d'une alimentation profonde négligeables (fig. 4).

ANALYSE DES RÉSULTATS

Ces différentes représentations des variations hydriques de parcelles identiques placées soit en jachère, soit en Blé, permettent de chiffrer sous l'angle hydrique le rôle exact de la jachère, et de traduire l'importance de certains facteurs tels que le labour, les pluies, etc.

Économie d'eau

La résultante globale de l'effet de la jachère sous l'angle hydrique, dans les conditions particulières de l'expérience, a été un gain de 60 mm d'eau (ΔR en fin de saison, fig. 3; ou ETR (Blé) — ETR (jachère), fig. 4). Ce gain global est important, puisqu'il représente 35 à 40 % de la réserve utilisable (RUM).

Le tableau 2 donne, pour quatre parcelles, les résultats obtenus.

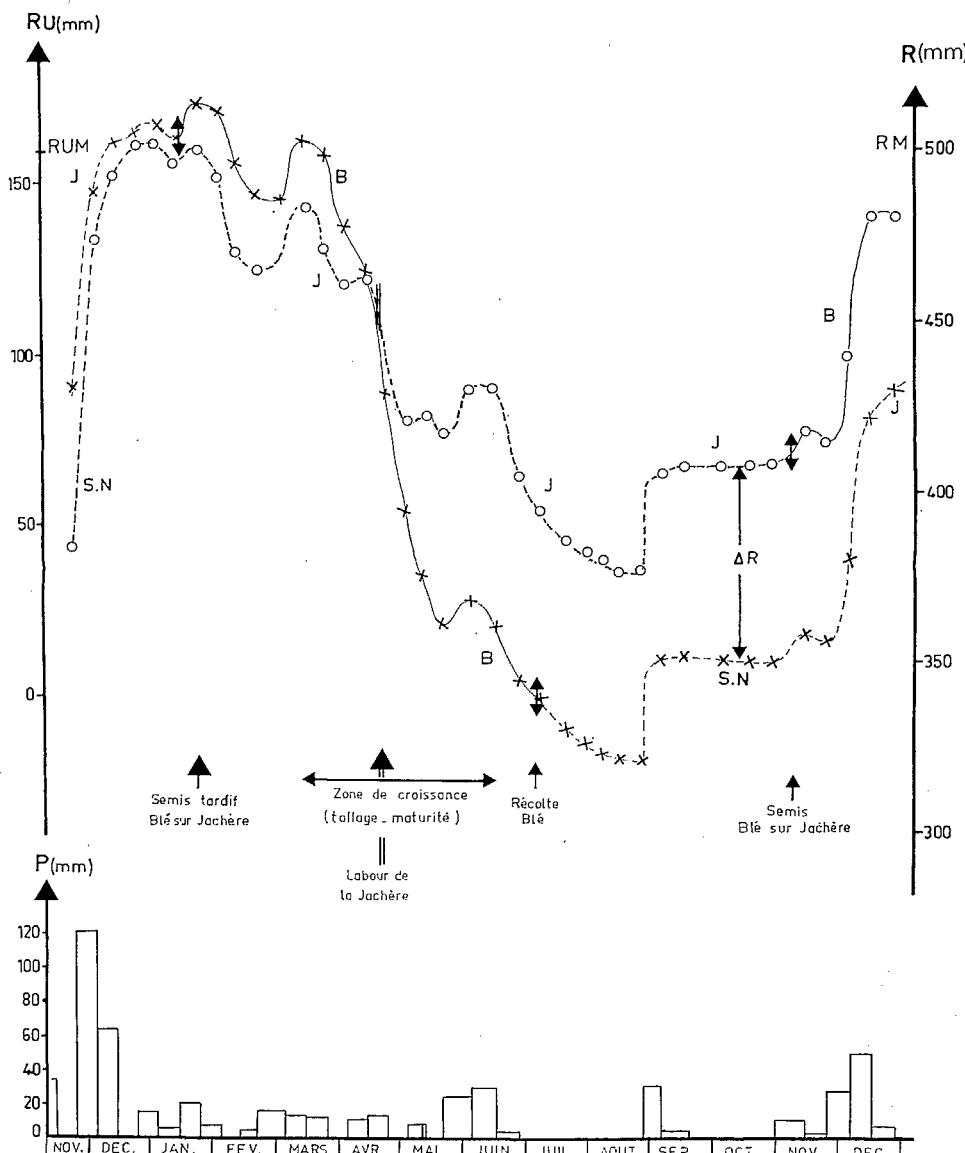


Fig. 3. Graphique général traduisant l'état des réserves pour la parcelle en Blé (X) et la parcelle en jachère (O) [année 1967-1968]. P, pluie en millimètres; RU, réserve utilisable en millimètres; RUM, réserve utilisable totale en millimètres; R, ré-

serve totale en millimètres; ΔR , gain hydrique de la jachère; J, période en jachère; S.N., période en sol nu après la récolte avant l'année en jachère (trait en pointillé); B, période en Blé (trait plein).

TABLEAU 2

Parcelle	Réserves en mm (RU)	
	24-XI-67	27-XI-68
1	66 (fin jachère)	84 (fin Blé)
2	115 (fin jachère)	90 (fin Blé)
3	27 (fin Blé)	141 (fin jachère)
4	58 (fin Blé)	147 (fin jachère)
Gain moyen (jachère-Blé)	43 mm	57 mm

Ces résultats moyens confirment le fait généralement admis que la jachère permet une économie voisine de $\frac{1}{4}$ des pluies (Buckman et Brady, 1960).

Cependant, dans les conditions pédoclimatiques de l'expérience, la pluviométrie hivernale est généralement suffisante pour réalimenter en grande partie les réserves du sol, et la différence de réserve ou gain de la jachère (60 mm) tend à s'estomper en fin d'hiver (20 à 40 mm). L'intérêt de la jachère considérée ici (végétation spontanée jusqu'au labour de printemps) n'est donc pas évident; l'utilisation d'un engrais vert ou d'une culture

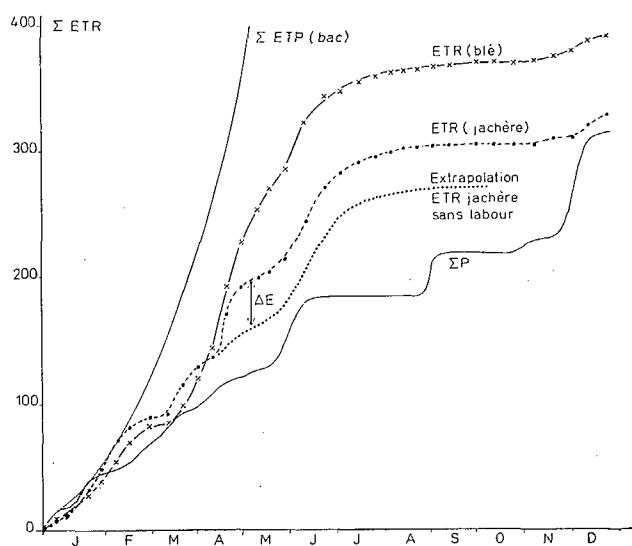


FIG. 4. Évolution cumulée des pluies et de l'évapotranspiration. P, somme des pluies en millimètres; ETR (jachère), évapotranspiration cumulée de la jachère en millimètres; ETR (Blé), évapotranspiration cumulée de la parcelle en Blé en millimètres; ETP (bac), évaporation potentielle cumulée en millimètres, mesurée au bac d'évaporation sur les parcelles; ΔE , perte probable due au labour.

d'hiver qui n'accroîtrait pas le déficit hydrique pourrait être favorable.

Comparaison des évapotranspirations réelles sur Blé et jachère

Sur sol nu bien humide, avec des réserves importantes, ETR suit pratiquement l'évaporation potentielle; c'est le cas des mois de janvier et de février malgré leur sécheresse importante ($ETP = 105 \text{ mm}$; $ETR (\text{jachère}) = 85 \text{ mm}$; $ETR (\text{Blé}) = 75 \text{ mm}$). Par contre, avec les évaporations importantes de mars et d'avril, le dessèchement rapide de la surface apparaît et diminue considérablement l'ETR sur jachère. Du 15 mars au 15 mai, période de pleine croissance de la végétation: $ETP = 280 \text{ mm}$, $ETR (\text{Blé}) = 170 \text{ mm}$, $ETR (\text{jachère}) = 90 \text{ mm}$, ce qui correspond à des évaporations moyennes de $4,7$, $2,8$ et $1,5 \text{ mm j}^{-1}$. Il est intéressant de constater qu'en faisant abstraction de l'action desséchante du labour (fig. 4, courbe en pointillé), le frein à l'évaporation se poursuivant, l'ETR (jachère) de cette période ne représenterait plus que $1,0 \text{ mm j}^{-1}$ au lieu de $1,5 \text{ mm}$, ce qui souligne l'action efficace de la jachère.

Pour l'ensemble de la phase de croissance du Blé (15 mars - 15 juin), les évaporations moyennes sont de $5,7$ (ETP), $2,6$ (Blé), $1,2 \text{ mm}$ ($\text{jachère sans labour}$); la parcelle en Blé représente alors une évaporation réelle égale à la moitié de l'évaporation potentielle, ce qui place la plante dans des conditions hydriques peu

favorables. Cette évaporation est pourtant deux fois plus importante que celle de la jachère. Après cette période de dessèchement important, l'ETR (jachère) devient pratiquement nulle de juillet aux premières pluies (novembre).

Action du labour de printemps

Sous l'angle hydrique, le labour de 25-30 cm de profondeur se traduit par le dessèchement des 60 premiers centimètres de sol (fig. 1) et par une perte d'eau moins 30 mm (ΔE , fig. 4); une telle perte réduit pratiquement d'un tiers l'économie d'eau de la jachère, qui passe ainsi de 90 à 60 mm . L'effet hydrique du labour en fin de période des pluies et en forte évaporation potentielle est néfaste.

Action des fortes pluies

Les fortes pluies observées à la mi-janvier, au début mars et surtout fin mai-début juin, entraînent une réhumectation qui permet une reprise intense de l'évaporation surtout sur jachère. En effet, alors que l'évaporation de la jachère aurait dû tomber à une valeur faible ($0,3 \text{ mm j}^{-1}$, pendant les pluies de fin mai - début juin), elle remonte à 3 mm j^{-1} , provoquant une évaporation totale voisine de 70 mm pour 50 mm de pluie tombée (fig. 3 et 4), ce qui correspond à une reprise de l'action desséchante de 20 mm environ.

Par contre, la pluie d'orage de fin août fut particulièrement bénéfique, car la présence de larges fentes de retrait (3 cm de largeur, 50 à 60 cm de profondeur) et l'intensité de la pluie permirent une accumulation totale en profondeur des 30 mm tombés sans réhumectation importante de la surface. Cette pluie, contrairement aux précédentes et malgré les très fortes évaporations potentielles (10 mm j^{-1} et plus), fut entièrement stockée (fig. 1 et 3).

Formation d'un mulch

La formation d'une épaisseur suffisante de sol sec conduit à réduire presque totalement l'évaporation (août à octobre, fig. 4); en réalité ce frein considérable n'intervint que lorsque l'épaisseur de terre sèche atteignit environ 60 cm (terre sèche dont l'humidité est très inférieure à la capacité au champ).

Tous les travaux culturaux superficiels qui visent à réduire cette épaisseur et à maintenir une plus grande réserve sont, sous l'angle hydrique, d'un grand intérêt (voir p. 483 et suivantes).

CONCLUSION

La méthode gravimétrique employée avec des précautions suffisantes et un nombre d'échantillons important (profondeur, répétitions, fréquences) peut conduire,

à partir des courbes moyennes d'isohumidité, à une interprétation chiffrée assez précise de l'évolution des réserves et de l'évapotranspiration.

Dans le cas particulier étudié ci-dessus, l'économie d'eau de la jachère dont les effets viennent d'être analysés (60 mm ou 1/3 RUM) peut être améliorée par :

La suppression du labour de printemps, remplacé par un labour d'automne ou d'hiver pour augmenter les possibilités d'emmagasinement et diminuer les pertes par ruissellement. En effet, pour la période de forte réhumectation (novembre-décembre), les pertes sont de 30 % environ, dont 20 % sont imputables au ruissellement (Energoprojekt, Belgrade, 1956).

La pratique des façons superficielles qui devrait permettre le désherbage et la formation d'une couche de terre sèche, dont l'épaisseur, la granulométrie et la densité constituaient un frein efficace, sans oublier l'apport possible de substances particulières (Nerpin, Pakshina et Boudarenko, 1968).

ANALYSE DE L'ÉVAPORATION D'UN SOL NU EN FONCTION DU MULCH

Il est important de définir la façon dont les caractéristiques physiques d'un mulch interagissent pour réduire l'évaporation.

BILAN ÉNERGÉTIQUE AU NIVEAU D'UN MULCH EN RÉGIME PERMANENT

Soit un mulch d'épaisseur ξ dont l'humidité est telle qu'en chaque point l'humidité du sol est en équilibre avec la pression partielle de vapeur d'eau qui diffuse en ce point. En régime permanent le mulch ne participe donc pas à l'évaporation, qui se produit alors à une profondeur ξ .

Le bilan d'énergie à la surface du mulch dépend du rayonnement net φ_R , du flux de chaleur sensible φ_S et du flux de conduction φ_C :

$$\varphi_R + \varphi_S + \varphi_C = 0 \quad [1]$$

A la base du mulch, là où se produit l'évaporation φ_L , le régime permanent entraîne

$$\varphi_C + \varphi_L = 0 \quad [2]$$

Si T_a , T_s et T_i sont les températures respectives de l'air, de la surface du mulch et de la surface évaporante, et T_r et T_{rs} , les températures du point de rosée de l'air et de l'air à la surface du sol (Daudet et Perrier, 1968),

$$\varphi_S = -\lambda_a \cdot (T_s - T_a) \cdot \delta_T \quad [3]$$

$$\varphi_C = -\lambda_s (T_s - T_i) \xi^{-1} \quad [4]$$

$$\varphi_L = -L\Lambda_o \Delta (T_i - T_{rs}) (\alpha \xi)^{-1} \text{ (à travers le mulch)} \quad [5]$$

$$\varphi_L = L\Lambda \Delta (T_{rs} - T_r) \delta_F^{-1} \text{ (dans l'air libre)} \quad [6]$$

avec L , chaleur latente de vaporisation de l'eau; λ_a , conductivité calorifique de l'air; λ_s , conductivité calorifi-

que du mulch; Λ_o et Λ , temps de diffusion dans le mulch et l'air libre (produit de la diffusivité vapeur D_o ou D par le rapport M/RT ; M , masse moléculaire de l'eau; R , constante du gaz parfait; T , température en °K); Δ , dérivée de la tension de vapeur saturante; α , un coefficient traduisant l'effet de porosité et de tortuosité; δ_F , épaisseur de diffusion ou couche limite équivalente correspondante et δ_T , couche limite équivalente thermique.

En introduisant dans l'expression de φ_S la constante psychrométrique γ et l'épaisseur de diffusion δ_F , on a :

$$\varphi_S = -L\Lambda \gamma (T_s - T_a) \delta_F^{-1} \quad [3 bis]$$

Pour des conditions extérieures données, φ_R , T_a , T_r , δ_F , il est possible de définir une évaporation potentielle φ_L et la température de surface correspondante T_{so} , correspondant l'une et l'autre à un sol humide en surface $\varphi_{Lo} = \Delta [\varphi_R + L\Lambda \gamma (T_a - T_r) \delta_F^{-1}] (\Delta + \gamma)^{-1}$.

On pourra alors calculer, en fonction des paramètres du mulch (soit Λ_o , α , λ_s et ξ), les grandeurs φ_L , T_s et T_i ; soit,

$$\text{si } x = [\Lambda (\Lambda_o / \alpha)^{-1} + L\Lambda \Delta \lambda_s] \xi \delta_F^{-1} \quad [7]$$

$$\frac{\varphi_L}{\varphi_{Lo}} = \frac{1}{1 + x \gamma / (\Delta + \gamma)} \text{ (fonction décroissante de } x) \quad [8]$$

$$\frac{T_s - T_r}{T_{rs} - T_r} = \frac{1 + x}{1 + x \gamma / (\Delta + \gamma)} \text{ de } x \text{ ou de } \xi \text{ du mulch} \quad [9]$$

$$\frac{T_i - T_r}{T_{so} - T_r} = \frac{1 + x / (1 + L\Lambda \Lambda_o / \alpha \lambda_s)}{1 + x \gamma / (\Delta + \gamma)} \text{ de } x \text{ ou de } \xi \text{ du mulch si } L\gamma \Lambda_o / \alpha \lambda_s < 1 \quad [10]$$

ANALYSE DE L'EFFICACITÉ D'UN MULCH

Ainsi la réduction de l'évaporation par un mulch ou son efficacité φ_L/φ_{Lo} (relation 8) décroît de façon hyperbolique avec x ; la décroissance étant d'autant moins rapide que Δ est plus grand (température moyenne plus élevée) [fig. 5, courbe n° 1]. Corrélativement, la température de surface du mulch T_s croît en fonction de x (relation 9). En revanche, contrairement à ce qui est généralement invoqué comme raison de l'action du mulch, c'est-à-dire une baisse de la température T_i de la surface évaporante, la température au niveau de cette surface T_i ou $(T_i - T_r)$ croît dans les conditions naturelles en fonction de x , la condition restrictive (relation 10) étant pratiquement toujours réalisée.

Paramètres intervenant sur l'efficacité

L'efficacité du mulch (rapport φ_L/φ_{Lo}) dépend de trois paramètres propres au mulch — sa perméabilité (Λ_o/α), sa conductivité (λ_s), son épaisseur (ξ) — et d'un paramètre propre au milieu extérieur et caractérisant l'intensité des échanges convectifs, c'est-à-dire l'épaisseur de diffusion δ_F .

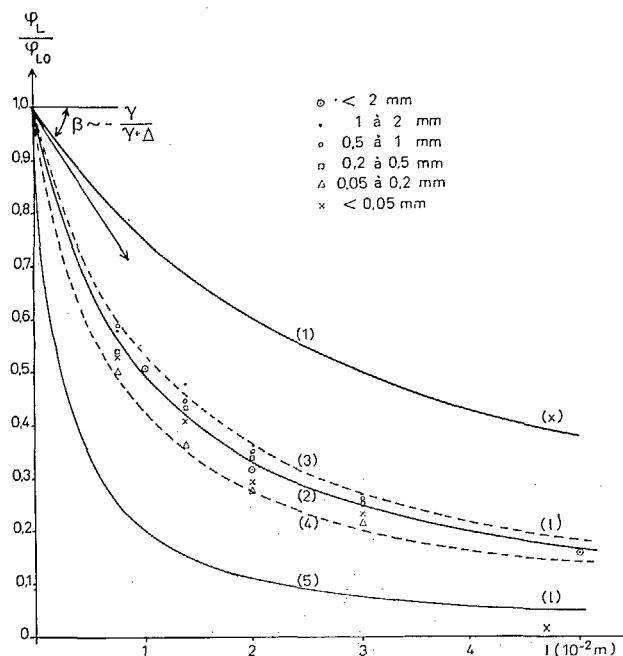


FIG. 5. Relation théorique et expérimentale traduisant l'efficacité Φ_L/Φ_{L0} du mulch en fonction de x ou de $\xi=l$ (relation 7). Courbe n° 1, courbe théorique (relation 8) en fonction de x ; courbe n° 2, courbe expérimentale pour une terre complètement tamisée à 2 mm (agrégats < 2 mm) en fonction de l'épaisseur du mulch ($\xi=l$); courbe n° 3, courbe expérimentale extrême obtenue au laboratoire pour une terre ne comprenant que de gros agrégats ($l < 2$ mm); courbe n° 4, courbe expérimentale extrême pour une terre plus fine ($0,05 < \text{agrégats} < 0,2$ mm); courbe n° 5, courbe théorique correspondant à la courbe expérimentale n° 2 en tenant compte de la variation du paramètre δ_F beaucoup plus petit dans les conditions naturelles que dans les conditions de laboratoire.

Le rôle de l'épaisseur ξ a été souligné, puisque x (variation ci-dessus) est proportionnel à ξ et joue dans le même sens.

Rôle de la porosité

La porosité ε du mulch intervient, d'une part, sur la perméabilité, en première approximation $\Lambda/(\Lambda_0/\alpha) = 1/\varepsilon$ (Carman, 1956) et, d'autre part, sur la conductivité calorifique λ_s , qui croît lorsque ε décroît (de Vries, 1963). La porosité joue donc de façon inverse sur la perméabilité et la conductivité, mais, dans l'expression de x , le terme lié à la conductivité, $L\Lambda\Delta/\lambda_s$ est d'un ordre de grandeur inférieur au terme lié à la diffusion [10 à 20 % de $\Lambda/(\Lambda_0/\alpha)$]. Il est donc pratiquement préférable de diminuer la porosité afin d'augmenter au maximum l'efficacité, soit la valeur de x pour ξ et δ_F donnés.

Rôle de l'épaisseur de diffusion

En effet, un mulch déterminé (Λ_0/α , λ_s et ξ donnés) n'aura pas la même efficacité suivant la valeur de δ_F

(relations 7 et 8). L'efficacité du mulch augmente toujours (décroissance du rapport Φ_L/Φ_{L0}) lorsque les conditions d'échange extérieures deviennent plus favorables (décroissance de δ_F). Mais, si l'efficacité augmente toujours avec la décroissance de δ_F , l'intensité de l'évaporation Φ_L ne décroît réellement que si (d'après la relation 8 avec Φ_{L0} remplacée par sa valeur):

$$[\Lambda / (\Lambda_0/\alpha) + L\Lambda\Delta/\lambda_s] \xi > L\Lambda (\Delta + \gamma) \quad [11]$$

$$(T_a - T_r) \Phi_{R^{-1}} = \delta_{FC}$$

Ainsi, si nous appelons δ_{FC} l'épaisseur critique de diffusion qui ne dépend que des conditions extérieures (Daudet et Perrier, 1968), Φ_L décroît quand les échanges augmentent (δ_F diminuant) si les caractéristiques du mulch (Λ_0/α , λ_s et ξ) satisfont à la relation 11. Cette diminution réelle de l'évaporation se produit lorsque l'épaisseur équivalente $[\Lambda / (\Lambda_0/\alpha) + L\Lambda\Delta/\lambda_s] \xi$, qui traduit le frein réel opposé par le mulch, devient supérieure à l'épaisseur critique de diffusion δ_{FC} .

RÉSULTATS EXPÉIMENTAUX

Les efficacités de diverses épaisseurs de mulch ont été analysées en conditions contrôlées sur une même terre répartie par tamisage en fonction de sa granulométrie (fig. 5).

La décroissance hyperbolique en fonction de l'épaisseur x du mulch (relation 8) se vérifie parfaitement et, comme on pouvait s'y attendre, l'efficacité de la terre complète correspond à une efficacité moyenne des diverses granulométries employées (courbe n° 2, fig. 5).

Enfin l'efficacité augmente lorsque la granulométrie moyenne diminue (courbes nos 3 et 4, fig. 5) à l'exception de la granulométrie la plus fine ($< 0,05$ mm); cette dernière présente en effet une porosité plus grande, ce qui entraîne une efficacité moindre du mulch (tableau 3).

Le rôle de δ_F ayant été souligné ci-dessus, rappelons que l'efficacité réelle serait beaucoup plus forte pour ce type de terre (courbe n° 5, fig. 5) dans les conditions naturelles (δ_F faibles) que dans les conditions d'expériences (δ_F élevé). Un mulch de 5 cm avec une terre parfaitement sèche et une granulométrie 2 mm conduiraient à une réduction de 95% de l'évaporation; ce résultat, dans les conditions de la jachère étudiée ci-dessus, conduit malgré tout à une évaporation réelle non négligeable de 15 mm par mois (1/10 de la réserve RUM). En effet, pour les mois d'été, l'évaporation potentielle est approximativement

TABLEAU 3

Granulométrie (dimension des agrégats)	1-2 mm	0,5-1 mm	0,2-0,5 mm	0,05-0,2 mm	0,05 mm
Porosité ε mesurée	0,49	0,44	0,36	0,31	0,48
Conductivité λ_s estimée	0,21	0,24	0,31	0,38	0,22
$\Lambda/(\Lambda_0/\alpha) + L\Lambda\Delta/\lambda_s$	2,52	2,69	3,10	3,48	2,54

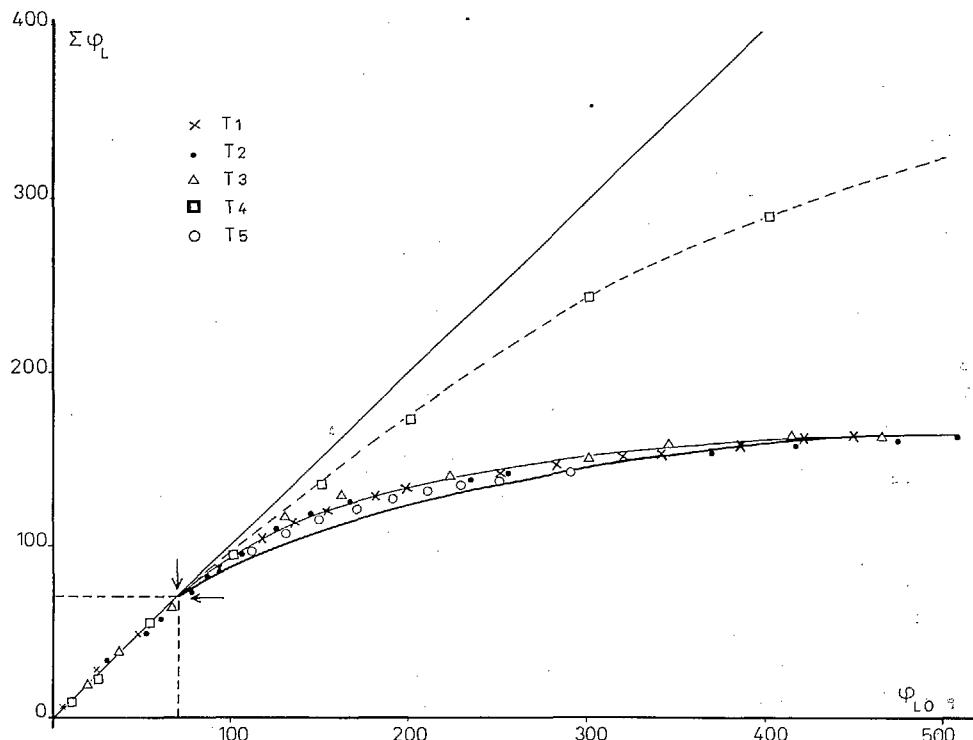


FIG. 6. Évolution de l'évaporation cumulée en fonction de l'évaporation potentielle pour un sol saturé soumis à différentes évaporations. Trait plein: courbe théorique calculée à partir de la relation 14 (évolution théorique d'un mulch) dans les conditions particulières de l'expérience.

de 10 mm j⁻¹. Une évaporation négligeable (quelques millimètres par mois) nécessiterait, dans ces conditions, une épaisseur de mulch de 20 à 25 cm, et c'est pratiquement ce qui se produit naturellement fin juillet (fig. 1 et 4).

Un mulch efficace consisterait en 10 à 20 cm de sol finement pulvérisé et tassé, capable de réduire au maximum la porosité; mais le coût d'un tel travail en fin de saison des pluies se justifie-t-il économiquement?

Si, généralement, les façons superficielles ne sont pas économiquement recommandées, c'est souvent parce que le traitement du sol est insuffisant (mauvaise pulvérisation du sol, d'où une porosité trop grande).

ÉVAPORATION D'UN SOL NU

En zone semi-aride, avec des évaporations potentielles considérables, il y a formation naturelle plus ou moins partielle d'un mulch qui tend à se stabiliser (régime permanent atteint pendant la période de juillet à novembre, fig. 1). La progression de ce mulch correspond au dessèchement progressif du sol vers la profondeur et, si la contribution de la diffusion liquide est alors considérée comme négligeable dans l'évaporation qui

n'est alimentée que par le dessèchement du sol, on peut écrire:

$$\varphi_L \cdot dt = L\rho (H_o - H_e) d\xi \quad [12]$$

ρ , densité apparente du sol; H_o , humidité du sol au départ sur tout le profil; H_e , humidité du sol en équilibre avec l'air supposé constant; $d\xi$, progression du mulch en fonction du temps dt . On en déduit:

$$\xi(t) = [1/L\rho (H_o - H_e)] \cdot \int_0^t \varphi_L(t) dt \quad [13]$$

soit en tenant compte des relations 7 et 8,

$$\Sigma \varphi_L = \sqrt{a^2 + 2a \Sigma \varphi_{Lo} - a} \quad [14]$$

avec

$$a = \frac{\delta_F \rho (H_o - H_e)}{(\Lambda / (\Lambda_o / \alpha) + L \Lambda \Delta / \lambda_s)}$$

$$\Sigma \varphi_L = \int_0^t \varphi_L(t) dt \text{ et } \Sigma \varphi_{Lo} = \int_0^t \varphi_{Lo}(t) dt$$

L'évaporation cumulée suit, dans ces conditions et en première approximation, une loi parabolique en fonction du temps ou de l'évaporation potentielle cumulée $\Sigma \varphi_{Lo}$ (fig. 5). Cette évolution n'apparaît qu'au bout d'un

certain temps pendant lequel la diffusion liquide assure le débit $\varphi_L = \varphi_{Lo}$ (Feodoroff et Rafi, 1962). Puis la décroissance de φ_L par rapport à φ_{Lo} est d'autant plus grande que a est plus petit, c'est-à-dire que: la réserve hydrique $\rho(H_e - H_o)$ est faible au départ; les conditions d'échanges sont favorables (δ_F petit); la perméabilité A_0/α et la conductivité λ_s sont petites.

En réalité, il y a distorsion par rapport à ce schéma théorique puisque, à chaque instant, le dessèchement à la base du mulch est limité par la diffusion liquide. Compte tenu des conditions expérimentales, il est possible de tracer (trait plein, fig. 6) la courbe théorique répondant à la relation 14. L'écart entre les courbes expérimentales et la courbe théorique traduit l'apport par diffusion liquide (Hallaire, 1960; Nguyen Minh, 1966). Dans les quatre cas où une évaporation potentielle intense a été provoquée artificiellement (5,2 à 6,1 mm j⁻¹), il y a formation d'un mulch qui joue un rôle déterminant, les apports par diffusion ne provoquant qu'une distorsion faible et d'autant plus faible que l'évapotranspiration potentielle est plus forte. On retrouve une confirmation expérimentale dans certains travaux (Vernet, 1964). Par contre, avec une évaporation faible (1,4 mm j⁻¹) et une réserve au départ à peu près triple (courbe en pointillé, fig. 5), l'écart par rapport au schéma précédent est considérable, et la diffusion joue un rôle prépondérant, doublant la valeur de

l'évaporation théorique prévue en l'absence d'un apport important par diffusion (Gardner et Fireman, 1958),

C'est la formation naturelle de ce mulch qui, dans les conditions semi-arides, entraîne une économie d'eau non négligeable qui serait entièrement consommée par évaporation si l'évaporation potentielle, plus faible, permettait une bonne diffusion pendant toute la phase de dessèchement. La valeur de la diffusivité des sols permet, corrélativement à celle de l'évaporation potentielle, une formation plus ou moins rapide de ce mulch; ainsi les terres à faible diffusivité favorisent l'apparition du mulch.

Il est non moins certain que l'évolution normale d'un mulch naturel (évolution parabolique) conduit malgré tout à une évaporation cumulée non négligeable qui ne peut être réduite que par la formation rapide d'un mulch artificiel, plus efficace car entièrement sec et moins conducteur que le mulch naturel.

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Summary

Water balance of wheat/fallow rotation and evaporation of a bare soil under semi-arid conditions (A. Perrier)

The most accurate analysis possible of the water balance of wheat/fallow rotation was carried out on the Algerian high plateaux by the gravimetric method. The object was to analyse the climatic, edaphic and cultural factors involved in water consumption and gain. As long as certain precautions are taken, this method provides sufficiently accurate figures of the usable reserves and actual consumption of water to make it

possible to determine the quantitative role of these factors.

The natural formation of a mulch is the determining factor in the influence of fallow on the water balance and one of the factors which can be directly controlled. A theoretical analysis of the energy balance of the mulch was therefore made. By this means the main parameters of its effectiveness can be defined and its natural evolution can be predicted. On the basis of this information the advisability of planting with good effect can be considered.

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A water balance recorder for hydroclimatic and agroclimatic measurement of precipitation and evaporation

O. Klausius

6101 Seehheim/Bergstrasse (Federal Republic of Germany)

The development of simplified agroclimatic procedures for assessing effects of water supply, especially of water deficits in soil and plant cover, has to respect the natural conditions of precipitation and evaporation, changing permanently from day to day and from hour to hour. Certainly, the measurement of soil water content has been greatly facilitated by the development of the neutron scattering method. Nevertheless, its application needs separate neutron moisture probes for the upper soil to a depth of 30 cm and the sub-surface soil below it; furthermore it needs a man. Thus this method is limited in application to distinct times and places and generally it is unsuitable for a permanent continuous measurement of water income and loss from and to the air by precipitation and evaporation. Under these presuppositions it will be necessary to have approximate methods for precalculating or assessing the soil water balance between the different times of each single soil moisture measurement.

One way to solve this problem might be the use of so-called evaporation formulae based upon meteorological data usually available by chance from stations nearby or more or less further away. Another way is to develop and use instruments recording precipitation and evaporation directly in the field under the same agroclimatic conditions as they are required. We have developed and tested such an instrument—we call it a water balance recorder. It will be described here, together with its theory and examples of application in the field. This instrument is under Federal German patent application and is made by Siegfried Bosch, 78 Freiburg, Waldkircher Strasse 49 (Federal Republic of Germany).

CONSTRUCTION TASK

The task was to construct a continuously recording instrument sensitive to both rainfall and evaporation,

measuring their difference in the sense of positive or negative water balance. It was, therefore, necessary to find an evaporation sensor comparable quantitatively with a precipitation sensor, and then to combine both elements in a recording unit, where they compensate each other in their amounts of water turnover from and to the atmosphere, so that the hydroclimatic water balance will be recorded directly.

THEORY

The measurement of precipitation is (outside of snow and dew problems, which may be neglected here) not very problematical. Against the background of approved rain-gauge constructions, special theories are unnecessary. There is only the problem of the right dimensions for the collecting hole in its relationship to the dimensions of the evaporation sensor and to those of the recording unit.

On the contrary, the measurement of evaporation needs theoretical consideration. In the ideal case of hydroclimatic theory, the evaporating body should form a plane water surface of true air temperature without hysteresis effects. This might be realized by a small, thin water container with compensation for the evaporation-cooling effect by electrical heating. Among the different evaporation bodies described, we found that the Piche filter disc satisfied at least a great part of these conditions; the body, is small, thin, and free from hysteresis effects, as it is used for instantaneous evaporation measurements in eco-physiological transpiration studies often and successfully. Although the temperature of the Piche filter disc is not the true air temperature, it corresponds to the psychrometer difference; it works at the temperature of the wet-bulb thermometer of a ventilated psychrometer, even when exposed to ventilations of only a few decimetres per second, as shown in

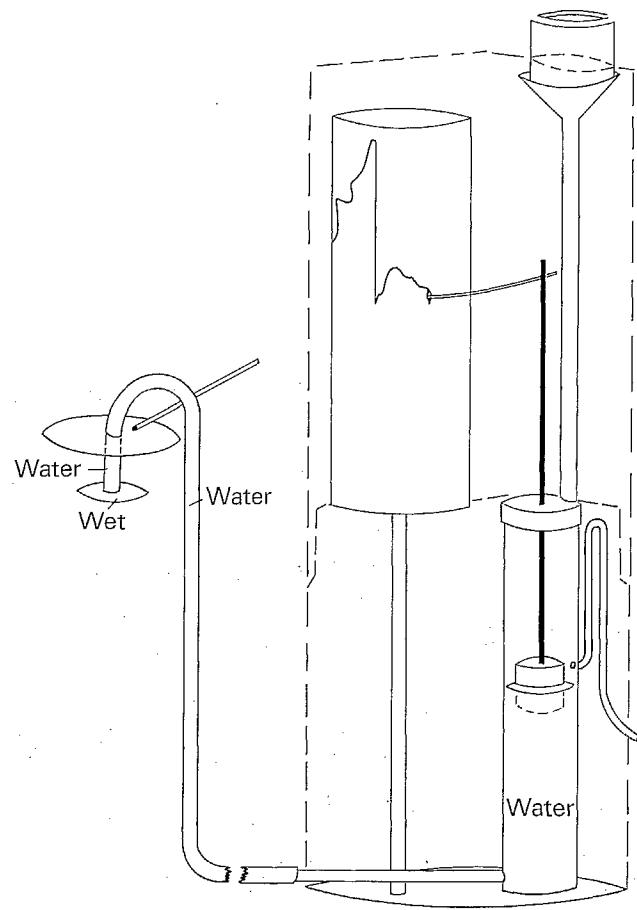


FIG. 1. Principle of the water balance recorder (construction Klausing).

very detailed studies (Schmid, 1933) with 5 cm discs. This behaviour of the filter disc follows from its small mass and its thinness, and it is related to the correct deflection of unventilated thermo-needle psychrometers.

Now the psychrometer difference with respect to the wet-bulb temperature is well-defined, and is energetically intermediate between the full energy flow from the air at its true temperature to the filter disc on the one hand, and the complete loss of energy consumption by vaporization at the dew-point temperature on the other. That is why a distinct psychrometer difference, once reached under conditions of minimum ventilation, cannot be changed by more ventilation, even though evaporation from the wet bulb may be significantly increased.

This energetically intermediate working temperature of the Piche filter disc means that it vaporizes half the amount of water compared with the ideal water surface artificially heated to the true air temperature. Thus a Piche filter disc wetted on both sides vaporizes exactly

that amount of water that would be expected from an open water surface of the same dimensions at the true air temperature. In another paper (Klausing, 1965) I have already shown that the small part of the filter surface screened off by the Piche tube causes an almost negligible reduction of evaporation, compensated for completely by an additional evaporation due to the "edge effect".

CONSTRUCTION

On this theoretical basis our water balance recorder has been constructed. Figure 1 shows the instrument working on the same principle as that of a rainfall recorder (pluviograph) and a Piche-atmograph (Klausing, 1957, 1965). A rain gauge hole with an aperture diameter of 5 cm collects the incoming rainfall and leads the rainwater into a cylindrical float receptacle. This cylinder has an inside diameter of 5 cm. The narrow siphon is for automatic emptying of the upper part of the receptacle after large amounts of rainfall down to a lower start level. At the lowest point of the water cylinder there a flexible tube is fixed, leading the water to the Piche evaporation body hanging under a Plexiglas roof (a disc of acrylic glass), protected against uptake of rainwater. In its lower part the receptacle, therefore, has the function of a water container, feeding the filter disc. For hydroclimatic measurements a 5 cm filter sheet is used. In the water container is a floating gauge. The water in the float receptacle rises during rainfall and falls during evaporation. The up-and-down movement of the float is transcribed by a directly attached recording arm on the recording chart, which is fixed onto the watch-drum. The transcription ratio is 1:1; 1 mm of recording height corresponds to 1 mm water depth of rainfall or evaporation.

A rising graph line denotes a preponderance of rainfall and, therefore, a positive water balance, whereas a falling graph denotes evaporation preponderance with negative water balance. A uniform or oscillating horizontal graph indicates a constant or equalized water balance. The recording watchdrum turns one full rotation per week. The water balance recorder, therefore, provides a continuous record throughout a period of seven days. The hydroclimatic water balance resulting from comparison of the amount of rainfall with that of the maximum potential evaporation is transcribed.

The water container is so dimensioned that the supply of water at the start level will last for one week, even under high intensity of evaporation, for instance in the Tropics. Of course, it is not possible to work with the instrument at temperatures below 0° C, but a connexion to a plug for a built-in bulb with cable and a transformer (mains 220 volts a.c., instrument 6 volts) can prevent troubles during slight night frosts in spring and autumn.

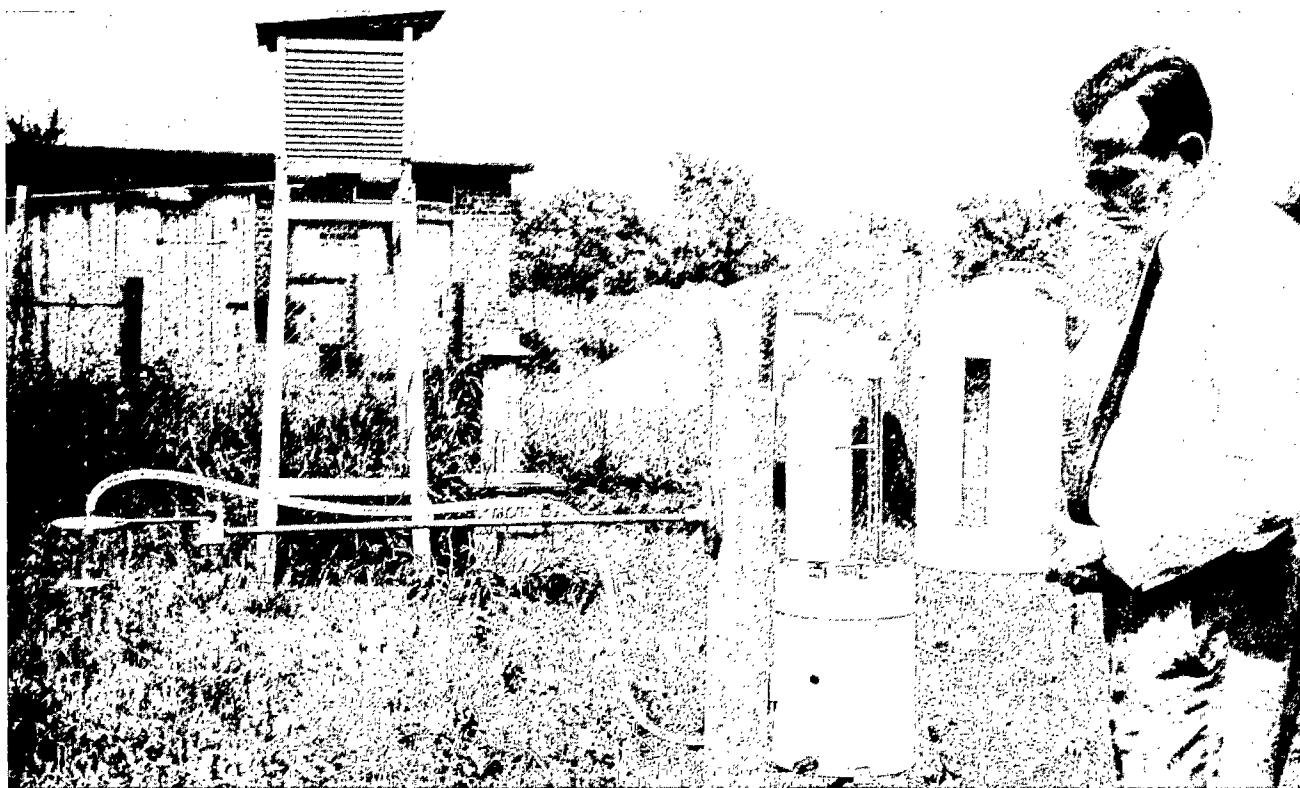


FIG. 2. The water balance recorder (construction Klausing). Above, open; below, closed.



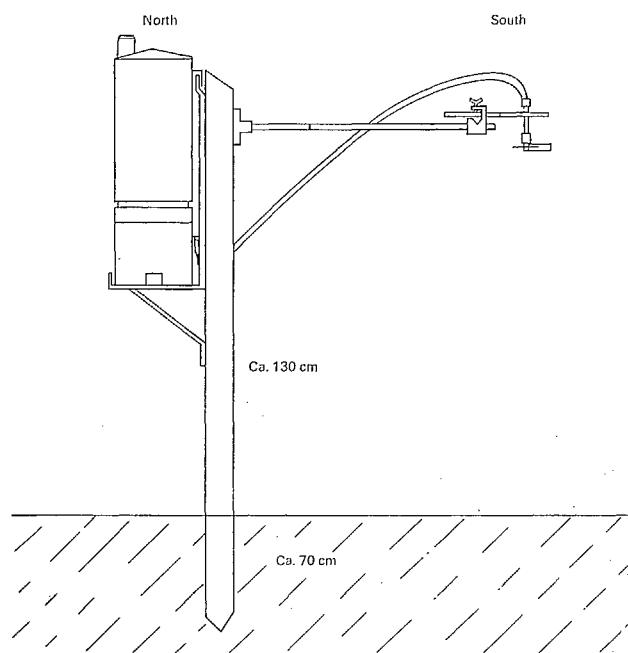


FIG. 3. Scheme for installing the water balance recorder in the field.

APPLICATION IN AGROCLIMATICS

As shown in Figure 2, the water balance recorder needs only a post for installation and can thus be used easily everywhere in the field. It may be placed directly in cultivated land (Fig. 3).

Two typical recording curves from the southern part of the Federal Republic of Germany demonstrate two contrasting types (negative and positive) of hydroclimatic water balance during two weeks in summer 1969 impressively (Fig. 4(a)(b)). What is the agroclimatic value of such recording curves? Firstly, they give general information about the hydroclimatic water conditions for plant cover and soil at the stations where they are recorded. Secondly, comparing recording curves from different stands may show the differences in hydroclimatic conditions of life for the cultivated plants resulting from rainfall and air tendency to evaporate. Of course, the instrument cannot detect plant transpiration and it cannot take into account soil evaporation as it has only one wet leaf without stomata and does not know whether the soil is wet or dry! But its measurement is more than merely a qualitative or relative one. It indicates the water balance under the conditions of rainfall and maximum potential evaporation, i.e. under conditions which may be realized, for example, by flood-irrigated rice fields or by open surfaces in the tropics. This indication is given by the good agreement of 5 cm Piche evaporation to tropical water levels (Klausing, 1957).

In the tropics of El Salvador I found the following averages of evaporation in closely neighbouring stations:

Station	Lake Station Chamnico water-gauge	Land Station San Andres 5 cm Piche
Evaporation measured by:		
April 1956 (dry season)	12.5 mm/day	12.3 mm/day
October 1956 (rainy season)	5.2 mm/day	5.3 mm/day

The reason for this good agreement is that in tropical waters the average water temperature is very close to the average temperature of the air, as conditioned by low annual oscillation of both. In other climates with larger annual changes of temperature, the evaporation from lakes and other open water surfaces is much lower than that of the Piche disc in our recorder. On the daily change of temperature in both media (water and air) is

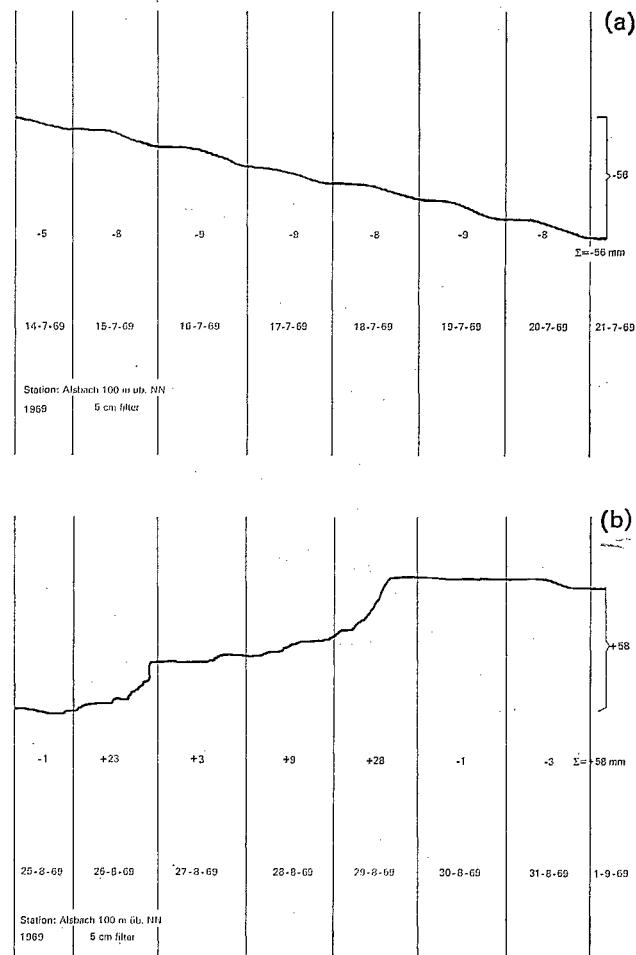


FIG. 4. Water balance recorder diagrams. (a) showing typical dry season curves; (b) showing typical wet season curves.

TABLE 1. The agroclimatic water balance in Braunschweig-Völkenrode in a summer period 1969

Day	Method:	Water balance in mm/day			
		1	2	3	4
28.7	-4	-6	-6	-5	
29.7	-7	-8	-8	-6	
30.7	-4	-4	-4	-5	
31.7	-6	-6	-7	-5	
1.8	-9	-10	-6	-5	
2.8	-10	-10	-8	-5	
3.8	-5	-6	-6	-5	
4.8	+3	+1	+1	-2	
5.8	-4	-6	-7	-5	
6.8	-5	-5	-5	-5	
7.8	-5	-6	-4	-4	
8.8	-5	-6	-6	-4	
9.8	-9	-9	-6	-4	
10.8	-8	-8	-6	-4	
Sum	-78	-89	-78	-64	

Methods:

1. Water balance recorder (construction Klausing) with 3 cm filter
2. Rain gauge and ceramic evaporimeter (Czeratzki's pattern)
3. From meteorological data (according to Haude formula)
4. From meteorological data (according to Thornthwaite-Pfau formula).

superimposed a different annual course and a different phase retardation caused by different hysteresis effects. These circumstances generally produce a lower natural evaporation from cooler water surfaces or wet soils than indicated by the water balance recorder with 5 cm Piche equipment. In these cases reduction factors would have to be used for determining natural evaporation from waters and wet soils.

Furthermore, the agroclimatic objects are generally not water levels and wet, bare soils, but rather cultivated lands with mostly superficially dry soils and more or less developed plant covers. Only exceptionally are they wetted, and the rate of evapotranspiration or the agroclimatic water balance is of more interest as are drier soil and weather.

For these agroclimatically interesting objects and vaporizing agricultural land surfaces, even perhaps for different plant species and their different phases of growth, single distinct reduction factors should be determined and used for determining their plant and soil water balance on the basis of the indications given by the water balance recorder. This will be the task of the user. It is only a question of experience to know what coefficient to use when and in which phases of plant growth to determine the water balance progression successfully.

For general information this procedure is no real problem, but it seems to be complicated and laborious. The purpose of this symposium is not to recommend

TABLE 2. Water balance at Alsbach Water Research Station (1–6 June 1970)

Object	Method	Amount (mm)
Hydroclimatic	Water balance recorder with 5 cm filter	-59
Bare soil (sand)	Weighing lysimeters	-12... -14
Grassland (grown)	Weighing lysimeters	-22... -27
Open water surface	1 m ³ /1 m ² water basin freely exposed	-26
Gooseberry shrubs	Non-weighing lysimeters + neutron probe	-28
Plum trees	Energy balance	-29
Agroclimatic	Water balance recorder with 3 cm filter	-25

complicated methods, but rather to point out simplified agroclimatic procedures for assessing effects of water supply. From this point of view I am much indebted to my colleague Mr Eberhard Siegert (Agrometeorological Station, 3301 Braunschweig-Völkenrode, Federal Republic of Germany), who kindly tested the water balance recorder at his station last year. Under his conditions the use of a 3 cm filter disc instead of the 5 cm sheet gave him a true picture of what we can call a general agroclimatic water balance. For the period 28 July to 10 August 1969 he sent me data set out in Table 1 (Siegert, personal communication, 1969).

For a fortnight the four methods do not differ more than ± 12.5 mm, or less than 1 mm/day on average—a very good result. Siegert's example shows that it is possible to put the agroclimatic coefficient for reducing the maximum potential evaporation as given by 5 cm filters into the water balance recorder by reduction of the filter diameter—a very simple but ingenious operation. For the whole summer period (11 May to 31 October 1969) the comparison of the four different methods shows a satisfying correlation (Fig. 5).

TABLE 3

	Precipitation (mm)	Evaporation (mm)	Water balance (mm)
Bare soil		320.1	+75.7
Grassland	395.8	431.9	-36.1
Gooseberry plantation		454.3	-58.5
Plum orchard		471.1	-75.3
Average	395.8	419.3	-23.5
Water balance recorder with 3 cm filter disc	403	427	-24

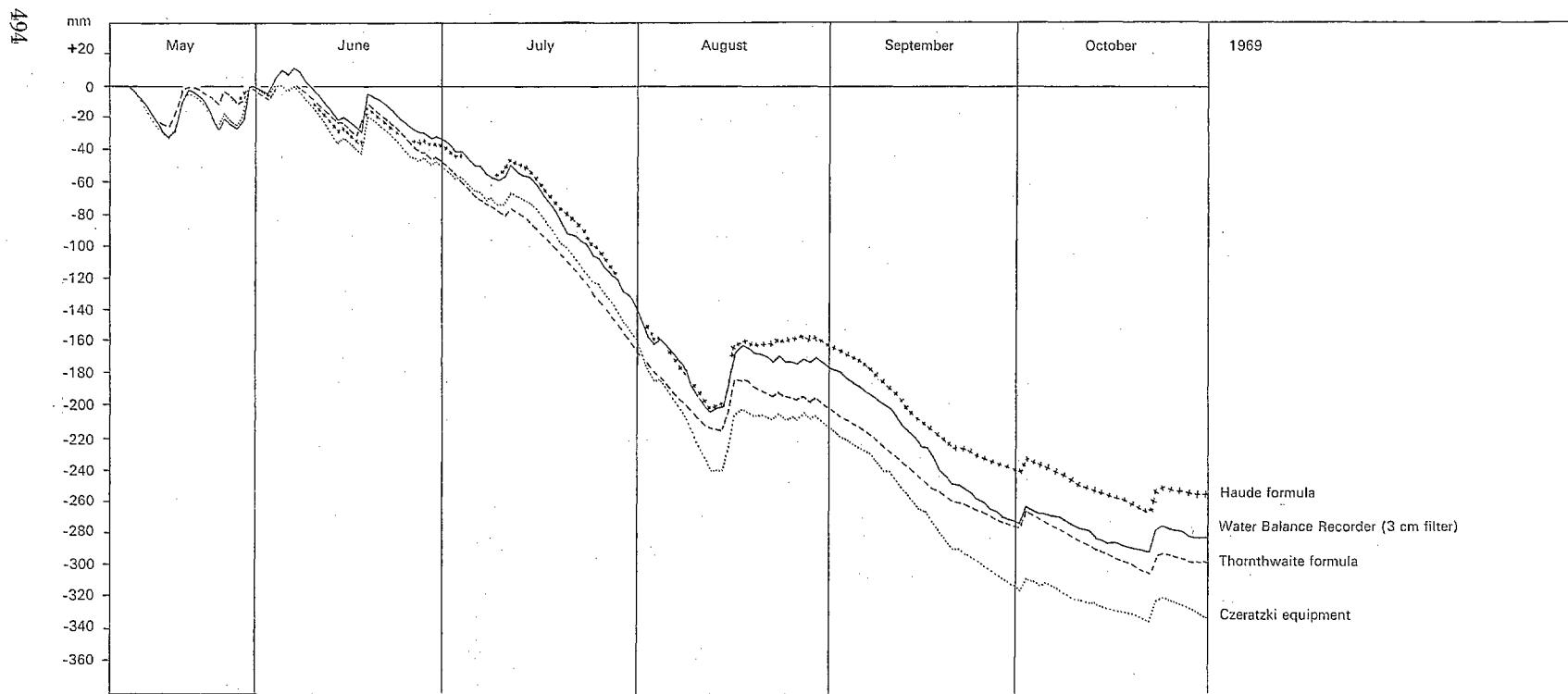


FIG. 5. Comparison of agroclimatic water balance curves during summer 1969.

The four agroclimatic methods tested by Siegert have to be compared with respect to their economy of man-hours. From this point of view, the indirect methods using formulae based upon observations at meteorological stations need their full equipment and an additional mathematical expense, which might be reduced only by a computer. Using a simple rain gauge and evaporimeter at least daily observations will be necessary involving time spent reaching distant stands. The water balance recorder combines the simplicity of the basic equipment with a minimum amount of work. It has to be checked only once a week and does not require any mathematical work, merely looking at the chart, which can be seen through the window of the outer housing at any time.

A comparison of the balance given by the water balance recorder with the real water balance of distinct objects in agriculture is desirable. With respect to this question I give the following example (Table 2) from my own experimental station in Alsbach.

The radiation potential for the same period calculated from the difference between precipitation and radiation equivalent for evaporation corresponded to a value of 60 mm potential water loss for a black surface.

This example shows clearly the aptitude of the water balance recorder especially for agroclimatic measurements. For the summer period (1 May to 31 October 1970) the following values were found (Table 3).

Résumé

Enregistreur du bilan hydrique pour la mesure hydroclimatique et agroclimatique des précipitations et de l'évaporation (O. Klausing)

L'hydrobilangraphe enregistre de façon continue pendant sept jours de suite le bilan hydroclimatique, c'est-à-dire la résultante entre la hauteur d'eau de pluie et la hauteur d'évaporation. L'appareil fonctionne sur le principe du pluviographe et de l'évaporographe. Pendant les pluies, le niveau de l'eau monte dans le réservoir à flotteur, tandis qu'il descend au cours de l'évaporation. Le mouvement de montée et de descente du flotteur est transmis par un levier à plume monté directement sur ce flotteur et enregistré ainsi sur le papier diagramme fixé sur le tambour de l'appareil. Le rapport des bras de levier est égal à 1:1. L'enregistrement fournit une image expressive du comportement hydroclimatique et permet une interprétation quantitative simple et facile

du bilan hydroclimatique. L'instrument considéré étant un enregistreur à inscription directe, on parvient à mesurer le bilan hydroclimatique chaque jour et chaque semaine en le relevant sur le papier diagramme, dont une hauteur d'enregistrement de 1 mm correspond à une hauteur de pluie ou d'évaporation égale à 1 mm. Une courbe ascendante indique un surplus des pluies, donc un bilan hydroclimatique positif, tandis qu'une courbe descendante signifie une évaporation supérieure ou un bilan hydroclimatique négatif. Une courbe horizontale du niveau caractérise un bilan hydroclimatique équilibré. L'enregistrement peut s'interpréter toutes les heures. L'appareil ne peut fonctionner aux températures inférieures à -5°C . L'hydrobilangraphe peut être utilisé aussi pour la mesure agroclimatique du bilan potentiel de l'eau édaphique (pluie moins l'évaporation de l'eau édaphique). A cette fin, l'appareil peut être utilisé avec des filtres-disques de 3 cm de diamètre. Théorie et exemples d'utilisation.

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Water relations, measured as electrical resistance of leaves, and its relation to plant growth and production

K. Kreeb and R. Abdelall

Abteilung für Ökophysiologie und Vegetationskunde,
University of Hohenheim, Stuttgart
(Federal Republic of Germany)

INTRODUCTION

Water relations of plants may be characterized by various physiological data. Walter (1931) pointed out that one has to consider a certain "state of water" (hydrature) of the protoplasm, because it is that part of the cell in which life processes are located. Fundamental details on these questions have been already given by Walter and Kreeb (1970) (see also Weatherley, 1965). Hydrature can be defined as the relative activity of water in a certain system expressed as a percentage.

Because the hydrature of the protoplasm (hy_{pp}) cannot be determined directly, we may use the "osmotic potential" (π^* , "potential osmotic pressure") of the vacuolar sap as an indirect indicator value (see the thermodynamic model of the cell given by Kreeb and Borchard, 1967). Because the methods used for determining π^* are destructive, Kreeb (1966) suggested the use of the electrical resistance of leaves (R_B) for evaluating hy_{pp} (see also Walter and Kreeb, 1970). With this method continuous measurements, even on intact leaves, are possible. Kreeb and Bogner (1967) and Abdelall (1971) have shown that with xerophytic plants, e.g., *Eucalyptus blakelyi* and *Quercus ilex*, a good correlation exists between π^* and R_B (regression coefficient is almost 10); but with mesophytic plants, e.g., *Gossypium barbadense*, *Sorghum vulgare* and *Zea mays*, this correlation is not so good, but still meaningful (regression coefficient is less than 5).

The purpose of our experiments was to investigate the correlation between R_B and growth and production, which is expected on the basis earlier of results of many authors.

MATERIALS AND METHODS

Pot plants of *Eucalyptus blakelyi*, 6 months old, and young plants of *Sorghum vulgare* and *Gossypium barba-*

dense, raised in the glasshouse, were subjected to different water treatments. Except for "optimum water supply" (control), we prepared four treatments (each having five replications), which were applied each time that an electrical resistance of a vertically exposed soil-nylon-block (constructed after Farbrother and Harrison, 1957) reached a certain predetermined value. Treatment II can be considered as fairly moist, treatments III-V as increasingly drier.

Usually the following parameters were measured every other day:

1. R_B (see Kreeb, 1966; Walter and Kreeb, 1970);
2. The leaf temperatures, with miniature size thermistors (Kreeb, 1964), needed for temperature correction of R_B values (the temperature dependence of the R_B values of the leaves of the species used has been determined in a climatic chamber);
3. Growth as height of plants or leaf area increments (see Stickler *et al.*, 1961; Ashley *et al.*, 1963);
4. At the end of the investigation period, fresh and dry weights (103° C) were determined.

All the data have been statistically evaluated.

RESULTS

EUCALYPTUS BLAKELYI

Figure 1 represents the course of R_B values during the investigation period. It shows fluctuations, as also found with π^* curves. R_B increases with decreasing irrigation quantities as well as with increasing irrigation intervals, depending on parallel soil moisture measurements which were controlled with electrical resistance of nylon blocks. Although the method of R_B determination must be considered primarily as a relative one, even absolute values in kilohms show a fairly good relationship to treatments.

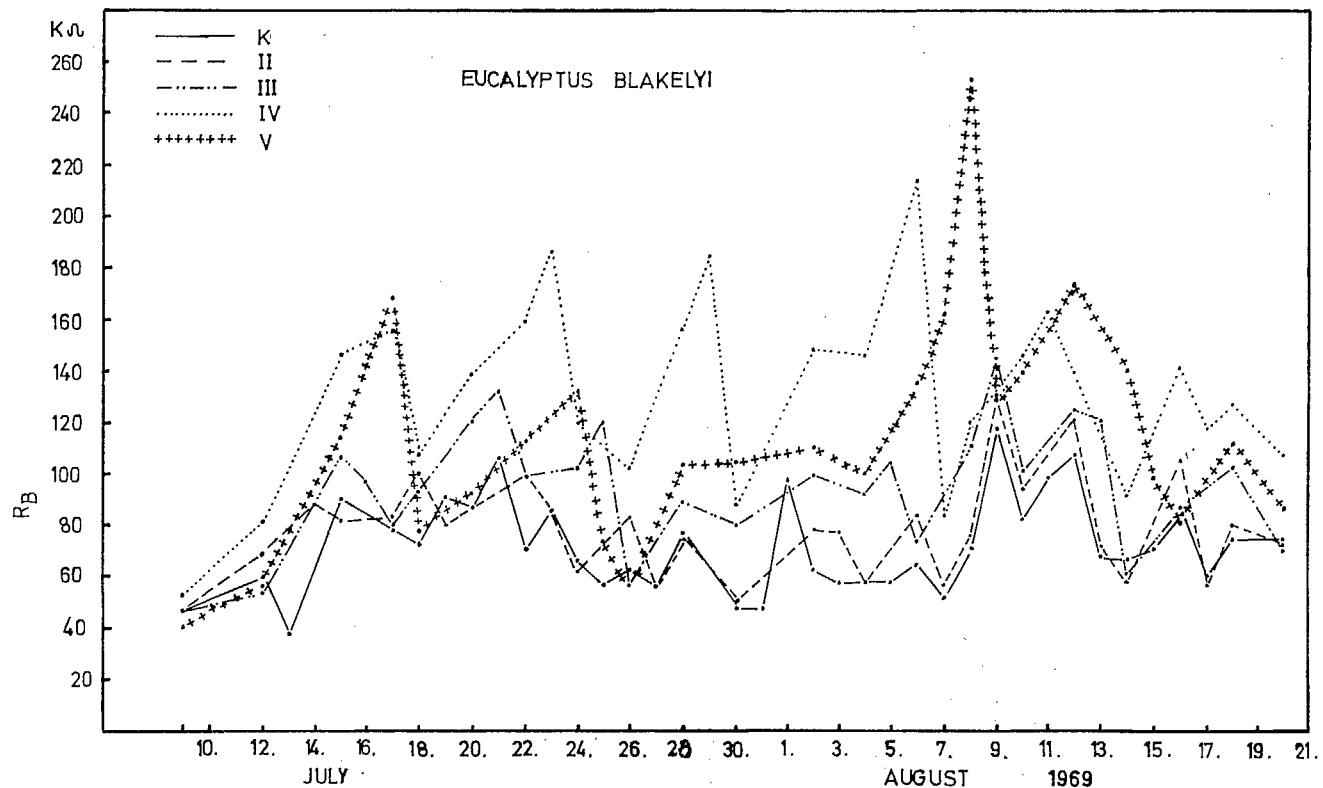


FIG. 1. Effect of water régimes on electrical resistance of *Eucalyptus* leaves (R_B) during the experimental period. (K = control.)

TABLE 1. Fresh (F) and dry (D) weights of *Eucalyptus blakelyi* shoots after 43 days of treatment in g (mean of 5) and as a percentage of the control

Treatments	F		D	
	g	%	g	%
I, control (K)	23.4	100	7.1	100
II	11.9	50	4.2	59
III	10.1	43	3.7	51
IV	6.7	28	2.6	36
V	6.0	25	2.4	34

The mean size of *Eucalyptus blakelyi* plants, determined on various dates, is given in Figure 2(a). It can be seen that, during the investigation period, differences between water régimes increased significantly. For both growth height and leaf area (Fig. 2(b)), the depression in growth is much greater between the control and treatment I than between any two others. It seems that this effect is in accordance with yield curves, dependent on π^* , given by Kreeb (1963). Similar effects have also been found with regard to fresh and dry weight measurements (see Table 1).

The correlation between R_B and production has been calculated with $N = 25$ (all plants of an experiment) and $N = 5$ (means of each treatment). Table 2 shows that correlation coefficients (r) are highly significant in almost all cases.

GOSSYPIUM BARBADENSE

R_B curves with this species are also well differentiated, although fluctuations are smaller than with *Eucalyptus* (Fig. 3). Differences in height are, as expected, not

TABLE 2. Correlation coefficients (*Eucalyptus blakelyi*) for production dependence on R_B values

Production (weight)	$N = 25$	$N = 5$
Fresh shoot	-0.61 ³	-0.82 ¹
Dry shoot	-0.62 ³	-0.85 ¹
Fresh leaves	-0.60 ³	-0.80 ¹
Dry leaves	-0.61 ³	-0.83 ¹
Dry roots	-0.54 ²	-0.77

Significant: 1. at 5 per cent; 2. at 1 per cent; 3. at 0.1 per cent level.

TABLE 3. Fresh (F) and dry (D) weights of *Gossypium barbadense* shoots after 48 days of treatment in g (mean of each treatment) and as a percentage of the control

Treatments	F		D	
	g	%	g	%
I, control (K)	15.0	100	4.5	100
II	9.3	62	3.1	68
III	8.7	58	2.8	63
IV	8.3	55	2.7	60
V	8.0	53	2.6	58

TABLE 4. Correlation coefficients (*Gossypium barbadense*) for production dependence on R_B values

Production (weight)	N = 25	N = 5
Fresh shoot	-0.68 ³	-0.84 ¹
Dry shoot	-0.61 ³	-0.86 ¹
Fresh leaves	-0.72 ³	-0.83 ¹
Dry leaves	-0.72 ³	-0.85 ¹
Dry roots	-0.64 ³	-0.92 ²

Significant: 1. at 5 per cent; 2. at 1 per cent; 3. at 0.1 per cent level.

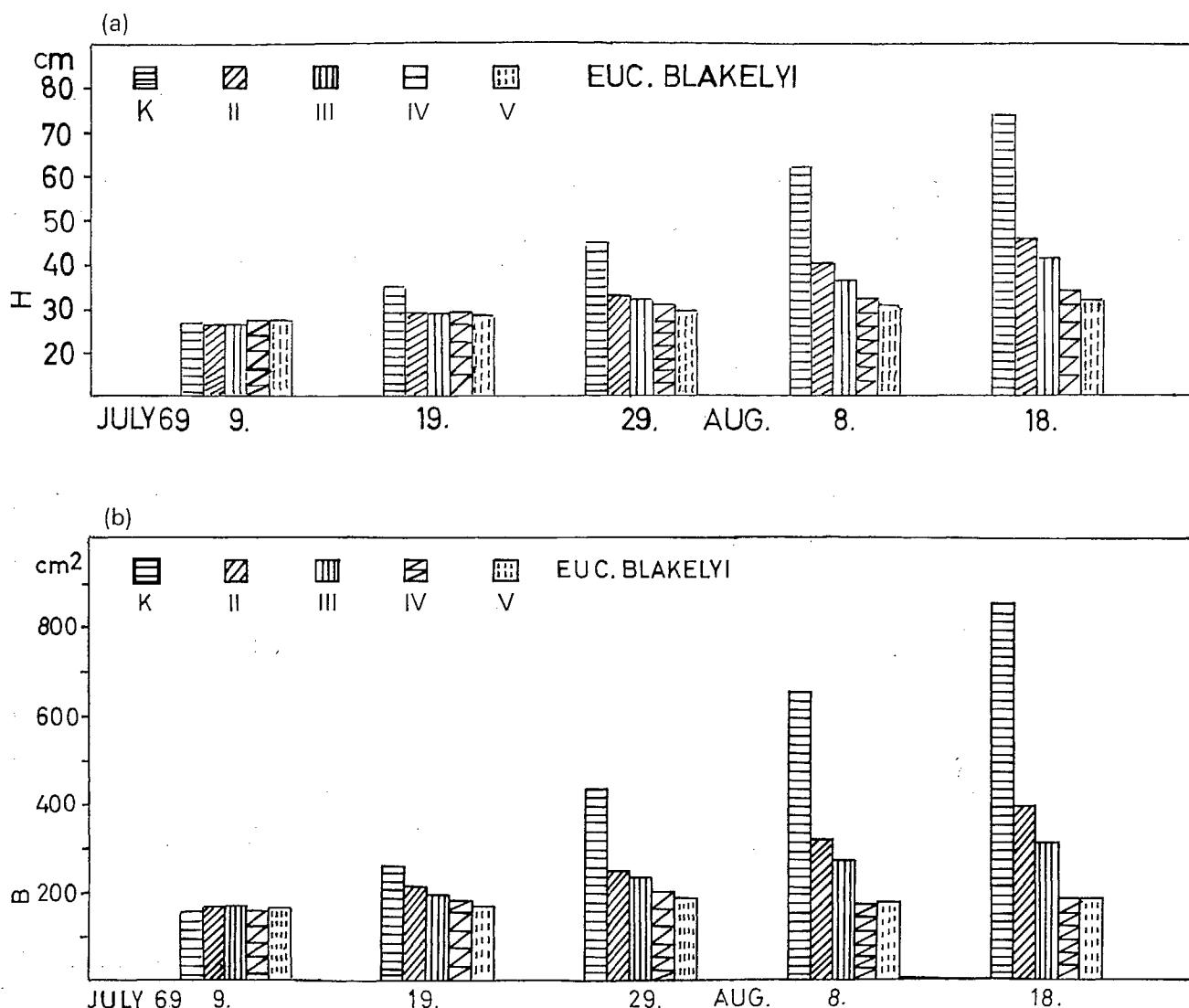


FIG. 2. *Eucalyptus* plants as affected by water régimes. (K = control.) (a) Growth height (H); (b) leaf area (B).

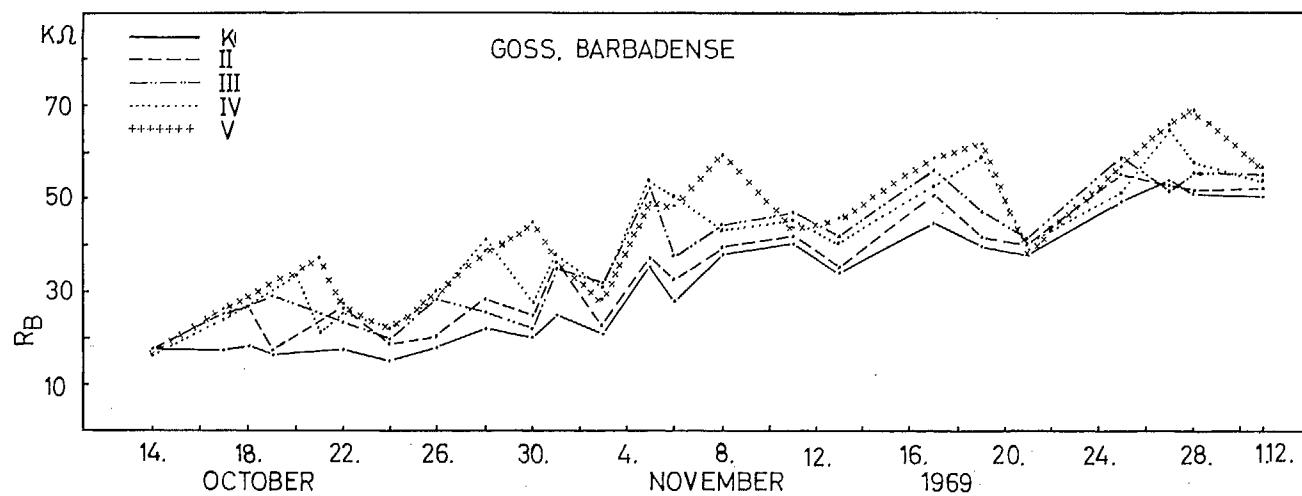


FIG. 3. Effect of water régimes on electrical resistance of *Gossypium barbadense* leaves (R_B) during the experimental period. (K = control.)

significant, but leaf area increments were significantly different, as compared with control (Fig. 4). The fresh and dry weights and statistical data are given in Tables 3 and 4.

SORGHUM VULGARE

R_B curves are given in Figure 5, showing clear response to the water treatments. Even with this mesophytic species of the grass family, the correlations between R_B

values and mean increase in height and production (shoot dry weight) are highly significant (Figs. 6 and 7). These facts show that R_B is, at least for many species, a good indicator of hy_{pp} .

Because all results have been obtained from mean values, we wanted to check whether the dependence between growth and R_B values is real. Therefore we measured in some treatments growth, represented by height measurements, and R_B values simultaneously. The effects of increasing dry conditions and after-

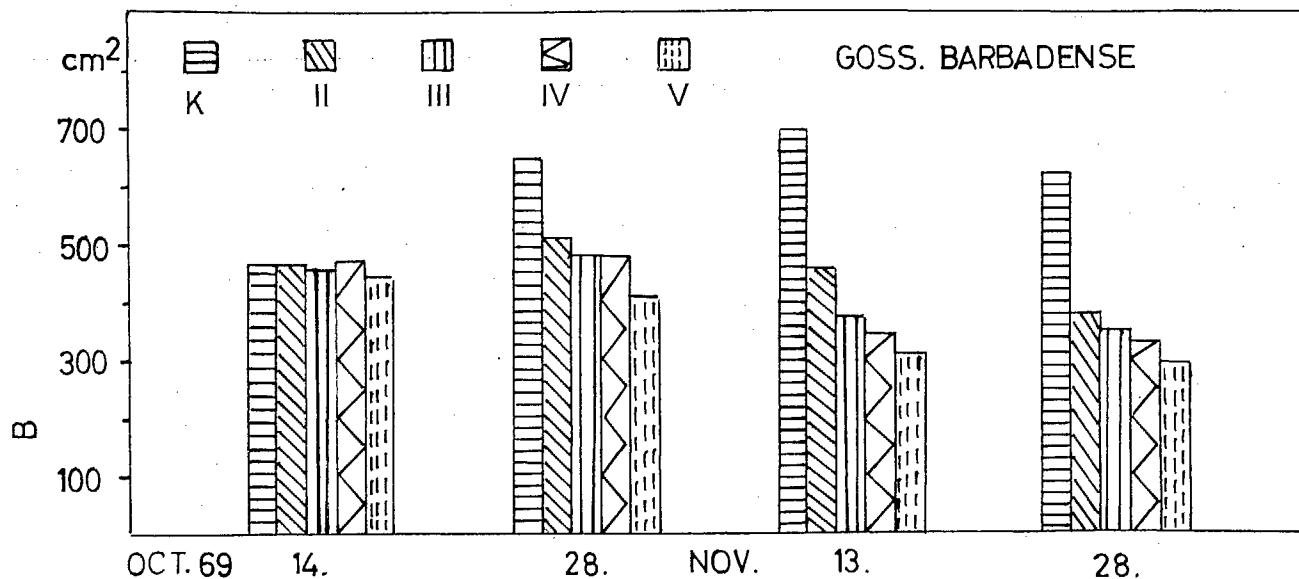


FIG. 4. Leaf area (B) of *Gossypium barbadense* as affected by water régimes. (K = control.)

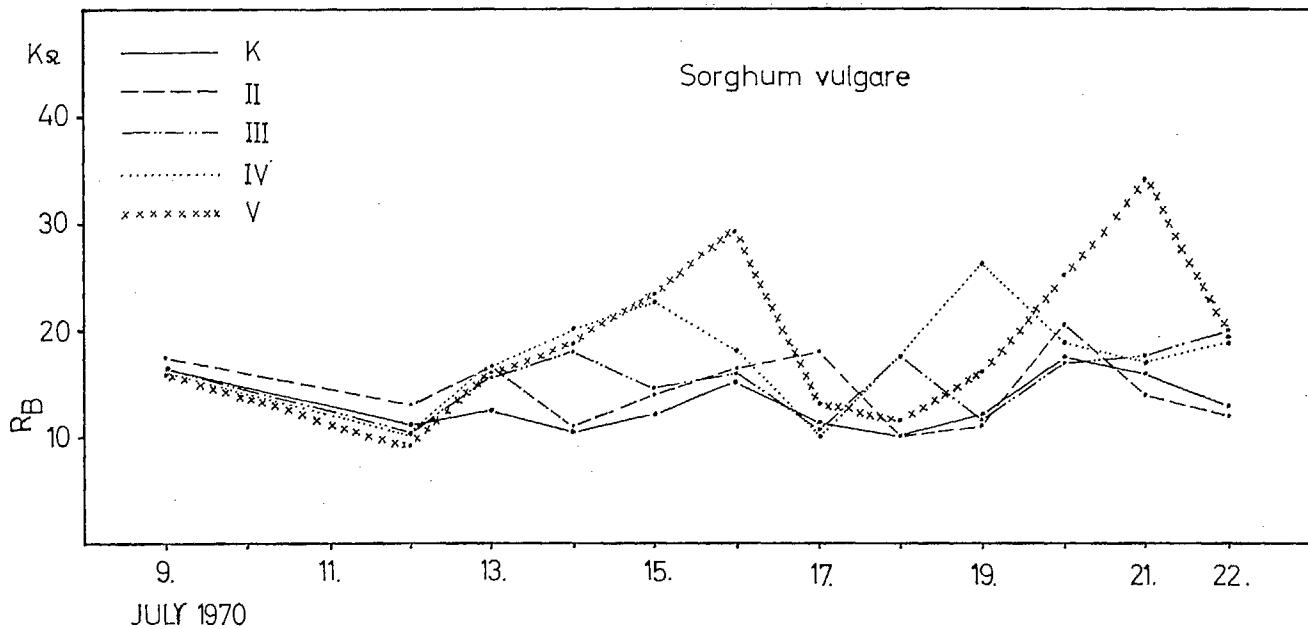


FIG. 5. Effect of water régimes on electrical resistance of *Sorghum vulgare* leaves (R_B) during the experimental period. (K = control.)

irrigation effects at the plants are obvious (Fig. 8), especially in treatments III-V. The curves of growth and R_B are nearly symmetrical. High R_B values, meaning drought conditions, are accompanied by retarded increase in height of plants. Irrigation after drought leads to a decrease of the R_B value and, therefore, an increase in height.

DISCUSSION

The experiments have shown that the electrical resistance of leaves (R_B) represents the hydrature of the protoplasm (hy_{pp}). Significant correlations between R_B and growth and production have been found in all test

species. Thus, it may be stressed that the electrical resistance method, apart from being a non-destructive method, may be employed as a technique of recording hy_{pp} . But the values measured (kilohms) have still to be taken as relative values, meaning that only changes of R_B over a minimum value (saturation) are evident. By comparing many single leaves of the same water status, there are differences in absolute R_B values found. Therefore, only mean values or relative changes are representative. Relative changes are more distinct with xerophytic than with mesophytic leaves. There might be mesophytic plants which show no change of R_B at all after their water content changes. These fundamental questions, which must be answered for a causal understanding of the electrical resistance phenomenon in leaves, are now being studied.

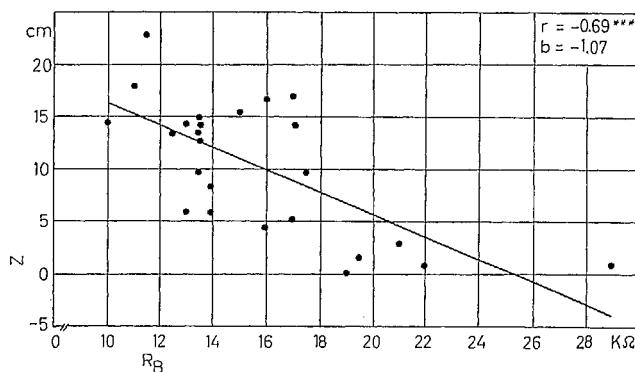


FIG. 6. Correlation between electrical resistance of leaves (R_B) and growth rate (Z) of *Sorghum vulgare*.

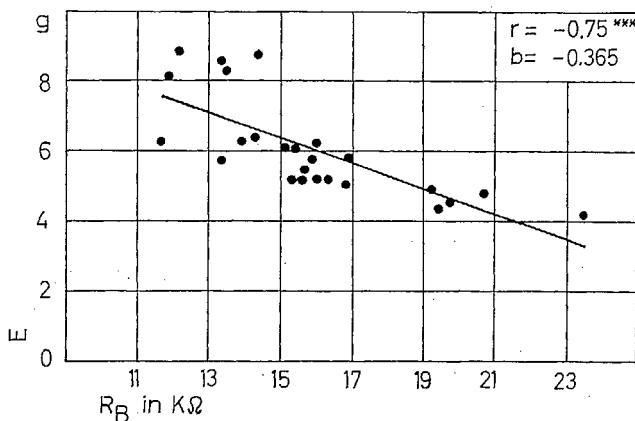


FIG. 7. Correlation between electrical resistance of leaves (R_B) and production (dry weight of shoots, E) of *Sorghum vulgare* (r and b = correlation and regression coefficients respectively).

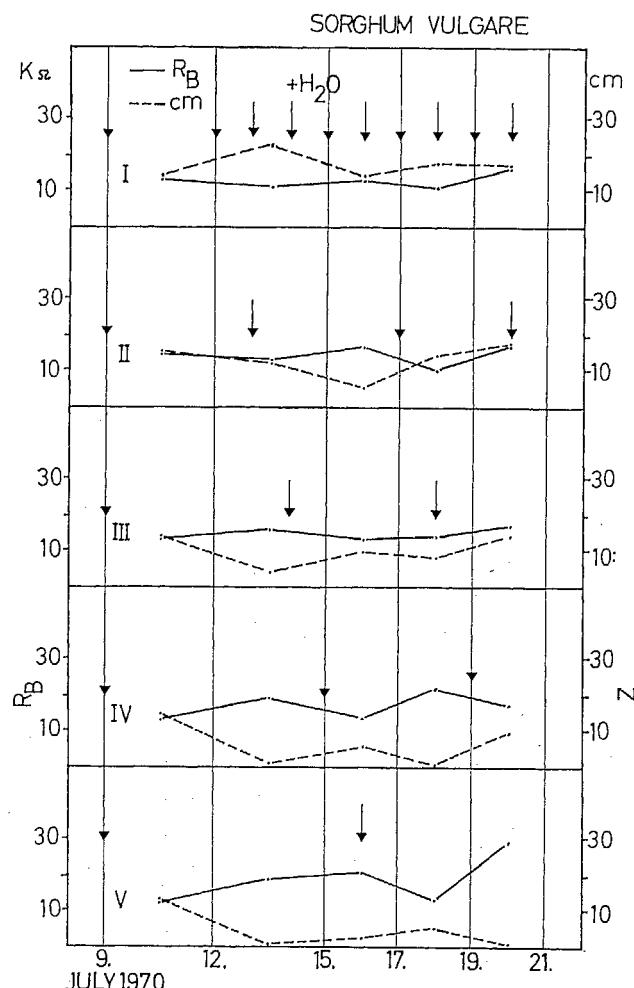


FIG. 8. Electrical resistance of *Sorghum vulgare* leaves (R_B) and height of plants (Z) as affected by water régimes (mean of five replications).

Résumé

Les échanges hydriques mesurés par la résistance électrique des feuilles, et la corrélation avec la croissance et la production (K. Kreeb et R. Abdelall)

L'hydratation du protoplasme, définie thermodynamiquement, peut être mesurée par la pression osmotique potentielle de la vacuole (méthode destructrice).

La résistance électrique d'une feuille, qui peut être enregistrée, fait apparaître une bonne corrélation avec

les changements de la pression osmotique potentielle pendant les périodes sèches. Du point de vue écologique, cette méthode semble convenir à cause de son dispositif non destructeur.

Il existe une corrélation significative entre les valeurs R_B (moyennes pour la période de recherches) et les augmentations de la surface foliaire, la hauteur et la production de matière fraîche et de matière sèche,

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Relative significance of soil and plant evaporation in estimating evapotranspiration

O. T. Denmead

Division of Plant Industry, CSIRO,
Canberra (Australia)

Evapotranspiration denotes the sum total of evaporation from soil and transpiration from foliage. This paper is concerned with estimating the relative amounts of each component, and the extent of their interdependence.

An analysis of evaporation from bare soil has been given by Philip (1957). If the soil is wet enough, its evaporation rate will be equivalent to that from a saturated surface exposed to the same atmospheric conditions; but as the soil dries, its evaporation rate will be either that from a saturated surface or a rate determined entirely by the soil properties, whichever is the less.

Associated with these changes in soil evaporation rate will be changes in the amount and, perhaps, the direction of sensible heat exchange at the soil surface. In crops, it has been observed that a wet, freely evaporating soil can constitute a strong sink for sensible heat exchange with the canopy; and its evaporation rate then exceeds the supply of available radiant energy (net radiation less soil heat flux)—e.g., Brown and Covey (1966), Denmead (1968) and Figure 1 of this paper. As the soil surface dries, it becomes a source rather than a sink for sensible heat exchange and this can produce significant modifications to the canopy microclimate—the return of sensible rather than latent heat making for a hotter, drier atmosphere about the foliage (Denmead, 1968). Thus the moisture status of the soil surface can be expected to influence the potential transpiration rate. The extent of this influence is examined in later sections.

A complete treatment of the problem would seek to predict the course of soil evaporation and evapotranspiration as the surface changed from fully wet to completely dry. However, this would be a much more complicated task than can be dealt with here. Such an analysis would require prediction of the changing distribution of water throughout the soil profile, knowledge

of the root distribution and the hydraulic properties of the soil, and calculation of the rates of water movement to the soil surface and the roots. Here, only two soil moisture states are considered: one in which the soil surface is wet and able to evaporate as a saturated surface, and one in which the soil near the surface is so dry that no evaporation occurs.

THE GENERAL APPROACH

The analysis of energy exchange is via the energy balance. Sharing of the net radiation at the soil surface, R_s , is described by

$$R_s = H_s + LE_s + G \quad (1)$$

where H_s is the flux density of sensible heat exchange between the surface and the air, L is the latent heat of vaporization of water, E_s is the soil evaporation rate, and G is the flux density of heat in the soil.

As shown by Philip (1957), and developed in a slightly different manner in this paper, the magnitudes of the terms on the right-hand side of equation (1) depend on the equilibrium temperature obtained by the soil surface. This paper is concerned with the determination of the surface temperature from relatively simple observations of the weather above plant stands, and knowledge of the structure of the canopy and the moisture and thermal properties of the soil. From this follows an examination of the effects of surface temperature on energy exchange at the soil surface, on the canopy microclimate and on the consequent exchanges of heat and water vapour at foliage surfaces.

ENERGY EXCHANGE IN THE CANOPY

In the air. The statements below summarize the analyses of Philip (1964) and Denmead (1968) for the steady-state,

simultaneous transfer of heat and water vapour in a horizontally homogeneous canopy. The same general approach has been followed by Waggoner and Reifsnyder (1968), Cowan (1968) and Waggoner *et al.* (1969).

At any level z in the canopy,

$$R_z = H_z + LE_z + G \quad (2)$$

where R is the average net radiation and H and E are the vertical flux densities of sensible heat and water vapour. H and E are defined by the transfer equations:

$$H_z = -\rho c_p K_z dT/dz; \quad (3)$$

$$LE_z = -\rho L K_z dq/dz; \quad (4)$$

where ρ is the density of air, c_p is the specific heat of air at constant pressure, K is a height-dependent turbulent transfer coefficient (assumed equal for heat and water vapour), T is the temperature of the air, and q is its specific humidity.

The equivalent temperature θ is defined by:

$$\theta = T + Lq/c_p. \quad (5)$$

Combination of equations (2), (3), (4), and (5) leads to

$$R_z - G = -\rho c_p K_z d\theta/dz. \quad (6)$$

Thus, if we know that $T = T_*$, $q = q_*$ at a reference level z_* (conveniently, the top of the canopy), equation (6) can be integrated:

$$\theta_z = \theta_* - \int_{z_*}^z \frac{R_z - G}{\rho c_p K_z} dz. \quad (7)$$

The integration requires description of R and K by appropriate functional forms. In later sections, we employ:

$$R_z = R_* \exp [-\gamma A (1 - z/z_*)], \quad z < z_*; \quad (8)$$

$$K_z = K_* \exp [-0.96 A (1 - z/z_*)], \quad z < z_*. \quad (9)$$

In equations (8) and (9), R_* and K_* are the values of R and K at $z = z_*$, and A is the total leaf area index (LAI) of the canopy. In equation (8), the attenuation of R in the canopy has been assumed to approximate that of short-wave radiation. The parameter γ is an extinction coefficient determined by the foliage angle and solar altitude, and given explicitly by Anderson (1966). The value of 0.96 in equation (9) is an average of several published values (e.g., Brown and Covey, 1966; Uchijima and Wright, 1964) and unpublished observations by the author.

At leaf surfaces. For convenience in discussion, the foliage of the canopy is assumed to consist of leaves only.

Position in the canopy can be specified both in terms of height, z and LAI cumulated from the ground, a .

The local leaf exchange rates are described by

$$dH/da = H_l = \rho c_p [(T_l - T)/r_a]; \quad (10)$$

$$L dE/da = LE_l = \rho L [(q_{sat}(T_l) - q)/(r_a + r_l)]. \quad (11)$$

In equations (10) and (11), H_l and LE_l are the rates of exchange of sensible and latent heat between the leaves and the air around them per unit area of leaf surface, T_l is the mean leaf temperature at position a , $q_{sat}(T_l)$ is the corresponding saturation specific humidity, r_a (the reciprocal of a transfer coefficient) is an apparent resistance to transfer of heat and water vapour between the leaf surface and the surrounding air, and r_l is a resistance to the diffusion of water vapour through the stomata and cuticle of the leaf. Following Philip (1964) and Uchijima (1966), r_a has been taken to be inversely proportional to K . Specifically, in later developments,

$$1/r_a = 0.01 K.$$

Linking exchanges in the air and at leaf surfaces. From equations (2), (5), (10) and (11), the foliage surface temperature can be related to the local air temperature by

$$\frac{T_l}{r_a} + \frac{L}{c_p} \left[\frac{q_{sat}(T_l)}{r_a + r_s} \right] = \frac{1}{\rho c_p} \frac{dR}{da} + \frac{T}{r_a} + \frac{\theta - T}{r_a + r_s}. \quad (12)$$

A second relationship between T_l and T is obtained by differentiating equation (3) with respect to a :

$$\frac{d}{dz} \left[K_z \frac{dT}{dz} \right] + \left[\frac{T_l - T}{r_a} \right] \frac{da}{dz} = 0. \quad (13)$$

Equations (12) and (13) can be solved simultaneously by numerical methods, with the help of equation (7), to yield the profiles of T and T_l . The conditions on the solution are

$$\left. \begin{aligned} T &= T_*, \quad z = z_*; \\ \lim_{a \rightarrow 0} (-\rho c_p K dt/dZ) &= H_s. \end{aligned} \right\} \quad (14)$$

Calculation of H_s and G is discussed in the next section.

Once T and T_l are known, it is a simple matter to infer q and $q_{sat}(T_l)$. From these, H_l , E_l , H and E follow.

ENERGY EXCHANGE AT THE SOIL SURFACE

Soil heat flux. In solving equation (1) for the components of the energy balance at the soil surface, it is necessary to relate soil heat flux, G , to surface temperature, T_s . de Vries (1958) gives a solution for the soil heat flux as a function of the surface temperature when the latter is a prescribed function of time. However, it seems more in keeping with observation (e.g., Monteith, 1958; Penman and Long, 1960), to describe the time dependence of the heat flux by the positive part of a sine curve during the daylight hours and a constant negative heat flux overnight. Following Brunt (1932), the relation between

the heat flux and the surface temperature of the soil is then:

$$\left. \begin{aligned} G &= -(T_s - T_m) (\lambda C \omega)^{1/2} (1 + \pi \sin \omega t) / 2f(t); \\ f(t) &= \frac{\pi}{4} \cos \left(\omega t + \frac{\pi}{4} \right) - \frac{1}{3/2} \cos \left(2\omega t - \frac{\pi}{4} \right) - \\ &\dots - \frac{1}{(4n^2 - 1)(2n)^{1/2}} \cos \left(2n\omega t - \frac{\pi}{4} \right). \end{aligned} \right\} \quad (15)$$

In equation (15), T_m is the mean temperature of the soil surface over 24 hr, λ is the soil thermal conductivity, C is the volumetric heat capacity of the soil, ω is the radial frequency, and t is time. λ and C are assumed constant with depth, and it is assumed also that there is no net change in heat storage over 24 hr. This transient model of the soil heat flux has been adopted in later sections of the paper.

Surface temperature and the surface energy balance. As a convenience in computation, the foliage has been assumed to extend from a height of 2 cm to z_* . Thus,

$$\begin{aligned} a &= 0, z = z \\ a &= A, z = z_*. \end{aligned}$$

R_s , H_s and E_s are assumed constant with height between the soil surface and 2 cm. In this region, K is assumed to increase linearly with height from a value of $0.25 \text{ cm}^2/\text{sec}$ (the molecular diffusivity for water vapour in still air) to its value at 2 cm. Then, from equation (7)

$$R_s = h(\theta_s - \theta_2) + G \quad (16)$$

where the surface transfer coefficient, h , is given by

$$h = \rho c_p \int_0^2 K_z^{-1} dz.$$

Surface wet. In this case,

$$\theta_s = T_s + Lq_{\text{sat}}(T_s)/c_p.$$

Since both G and θ_{*s} are known functions of T_s , and θ_2 is known from equation (7), (16) has the form

$$R_s = g(T_s)$$

which can be solved directly for T_s by a simple iterative procedure. With T_s known, G follows from equation (15), H_s is given by

$$H_s = h(T_s - T_2),$$

and E_s will follow by difference in equation (1). However, although θ_2 is known at this stage of the calculation, T_2 is not. It is obtained by solving the differential equation (13) with the new condition

$$\lim_{a \rightarrow 0} (-\rho c_p K dT/dz) = h(T_s - T_2). \quad (14a)$$

H_s and E_s follow.

Surface dry. Since E_s is zero, the surface energy balance equation becomes

$$R_s = h(T_s - T_2) + G. \quad (17)$$

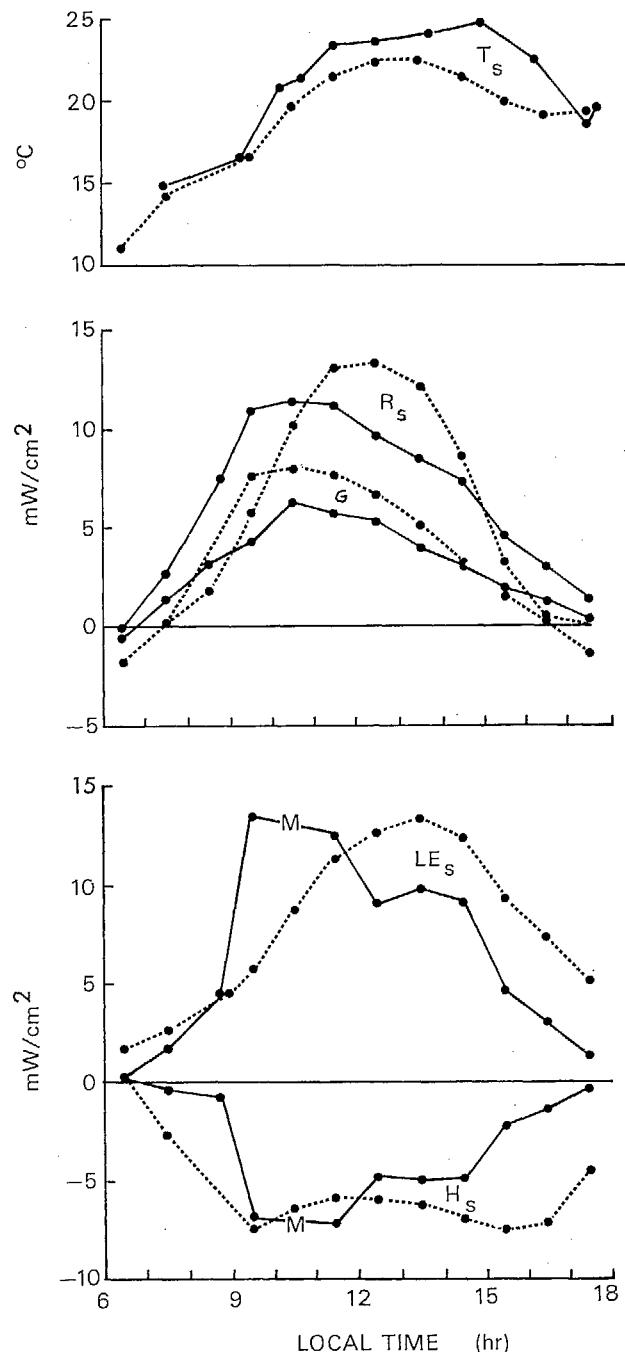


FIG. 1. Measurements (solid lines) and predictions (dashed lines) of soil surface temperature (T_s) and net radiation (R_s), soil heat flux (G), latent heat of evaporation (LE_s), and sensible heat flux (H_s) at the soil surface beneath a wheat crop of LAI 3.2.

T_s is obtained by solving equation (13) with condition equation (14a) by iterating on T_s until equation (17) is satisfied. With T_s and T_2 known, G and H_s follow.

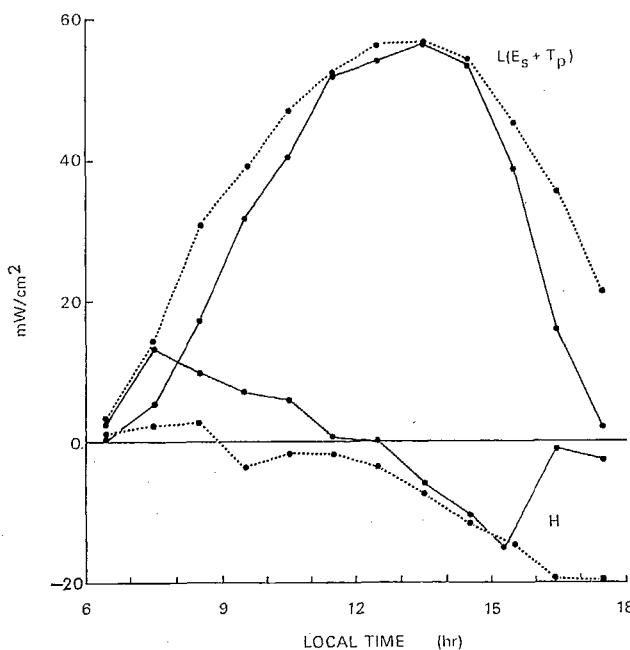


FIG. 2. Measurements (solid lines) and predictions (dashed lines) of evapotranspiration [$L(E_s + T_p)$] and sensible heat exchange (H) of the wheat crop of Figure 1.

TESTING THE MODEL

Predictions of the model have been tested against data obtained in an irrigated wheat crop at Deniliquin, New South Wales (Australia), latitude 35°S (Denmead, unpublished data, 1968). The wheat had a LAI of 3.2 and was 81 cm tall. In applying the model analysis to the field situation, the following input data were assumed:

Time of year: 16 October.
 Leaf angle: 60° uniformly.
 R_* , q_* , T_* : As measured.
 K_* : 400 cm²/sec.
 Leaf area distribution: $da/dz = \text{constant} = 0.04 \text{ cm}^{-1}$.
 Leaf resistance: $r_l = 1.5 [1 + (z_* - z)/75] \text{ sec/cm}$.

(These data correspond to the field measurements during the mid-day hours.)
 T_m : 16.4 °C.
 λ and C : As measured at a volumetric soil moisture content of 0.4.

Figure 1 compares measurements and predictions of soil surface temperature and the components of the energy balance at the soil surface on 16 October. Space does not permit a detailed discussion, but it can be claimed that agreement is generally good. The main features of

the field situation are predicted by the model, particularly the high gain of sensible heat with the consequence that soil evaporation is almost twice the supply of available radiant energy, $R_s - G$.

Figure 2 shows comparisons of the evapotranspiration and sensible heat exchange of the whole crop. Agreement is very good during the mid-day hours, but the model overestimates evapotranspiration at other times. This appears to be mainly attributable to the assumption of unchanging leaf resistances throughout the day. Supplementary measurements in the field showed that, in fact, leaf resistances decreased from high values in the morning to minimum values about mid-day (those assumed in the model), and then increased after 15.00 hr.

Some finer details of the analysis are shown in Figures 3 and 4. In Figure 3, measured and predicted profiles of temperature, specific humidity and cumulative evaporation through the canopy are shown for the period between 11.00 and 12.00 hr. The comparison in Figure 4 is perhaps the most sensitive test of the correctness of the description of exchange processes at leaf surfaces. It shows differences between leaf and air temperature at four levels in the canopy at various times between 10.00 and 16.00 hr. For this period, the model appears to predict the source-sink distributions for heat and water vapour with an acceptable accuracy.

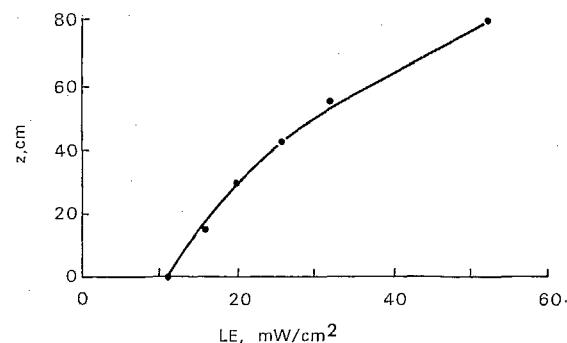
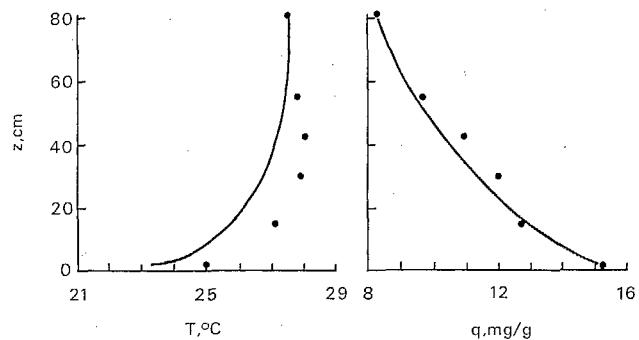


FIG. 3. Measurements (points) and predictions (lines) of air temperature, specific humidity and latent heat flux in the wheat crop of Figure 1.

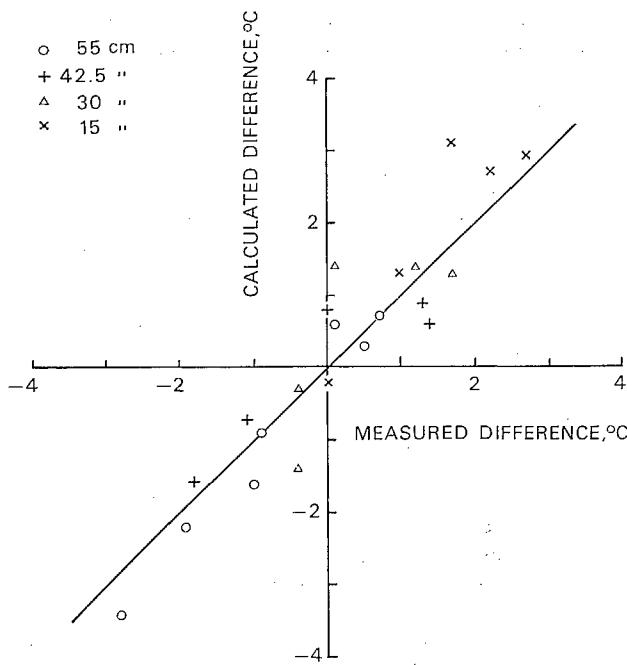


FIG. 4. Comparison of measured and predicted differences in temperature between leaves and surrounding air at four heights in the wheat crop of Figure 1.

EFFECTS OF SOIL MOISTURE STATUS AND CANOPY STRUCTURE ON EVAPOTRANSPIRATION

INTERDEPENDENCE OF TRANSPiration AND SOIL EVAPORATION

As suggested in the introduction, the moisture status of the soil surface can be expected to influence the canopy microclimate. This is illustrated in Figure 5, which shows calculations of temperature and humidity at mid-day in model crops with LAI of 3 when the surface is wet and dry. The input data are the same as for the comparisons with the field observations in the previous section, except that in the dry case, the values of λ and C have been reduced to correspond to a volumetric soil moisture content of 0.05. The contrasts between the two situations are large and require little comment.

Of more interest are the source strengths for heat and water vapour shown in Figure 6. The large differences in canopy microclimate have only a minor effect on energy partitioning: transpiration is almost independent of soil conditions.

RELATIVE MAGNITUDES OF SOIL EVAPORATION AND TRANSPIRATION

We distinguish between evaporation from the soil, E_s , and the total transpiration from the leaves, T_p . These

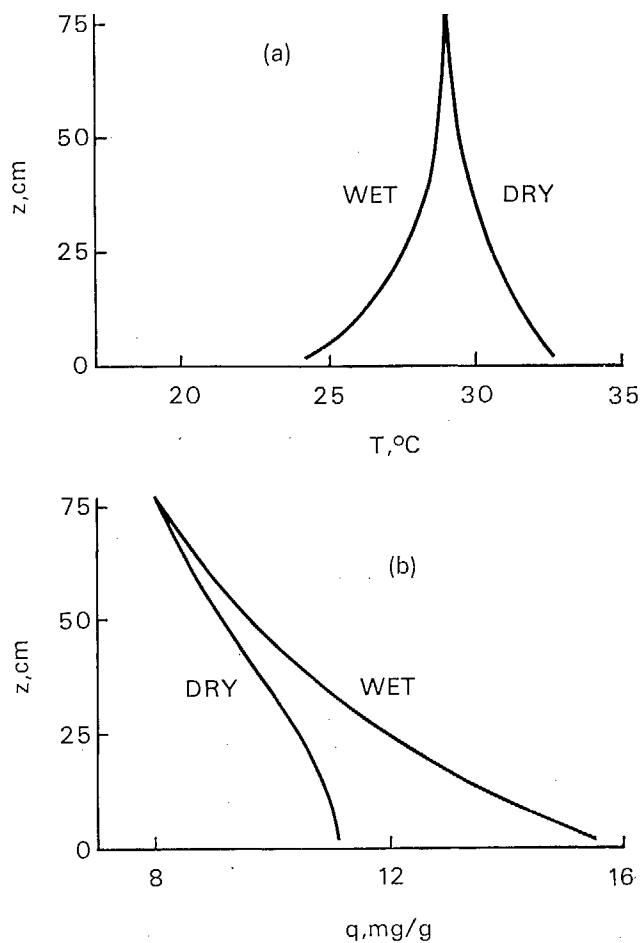


FIG. 5. Calculated profiles of (a) air temperature (T) and (b) specific humidity (q) in model crop with an LAI of 3 when soil surface is wet and dry.

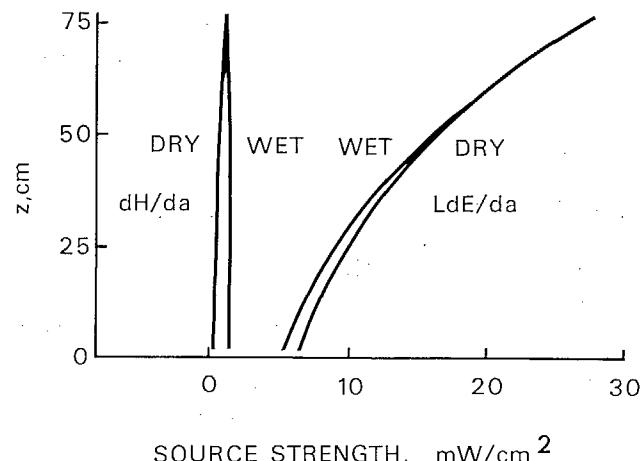


FIG. 6. Source strengths of sensible heat (dH/da) and latent heat ($L dE/da$) for the situations of Figure 5.

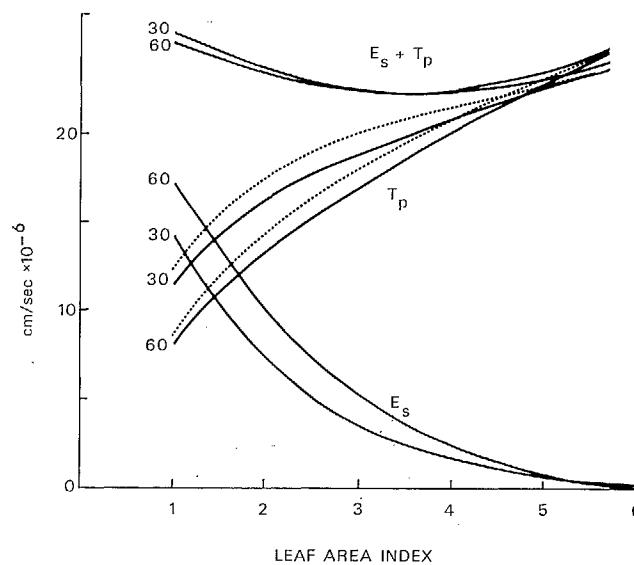


FIG. 7. Soil evaporation (E_s), total transpiration (T_p) and evapotranspiration ($E_s + T_p$) as functions of LAI for soil surface wet (solid lines) and dry (dashed lines) for two leaf angles, 30° and 60° .

are shown, along with evapotranspiration, in Figure 7 as functions of LAI at mid-day on our example day, for canopies with leaf angles of 30° and 60° . When the soil is wet, E_s becomes negligible in both cases at an LAI of 6, but for LAIs between 1 and 3, it can be large relative to transpiration.

The differences in E_s and T_p between a 30° and a 60° canopy result from differences in the interception of radiation by the foliage. When the soil surface is wet, this has virtually no effect on evapotranspiration, but when the surface is dry, a situation of some practical

importance occurs. Then the only water loss is by transpiration—the dashed lines in Figure 7—and appreciable differences exist at the smaller LAIs. For instance, transpiration from a 30° canopy is 43 per cent more than from a 60° canopy at an LAI of 1, 22 per cent more at an LAI of 2, and 11 per cent more at an LAI of 3.

CONCLUSIONS

From the view point of simplifying the estimation of evapotranspiration, the main contribution of the present paper is to show that the two components, soil evaporation and transpiration, can be regarded as virtually independent and, therefore, additive. In this sense, the work can be regarded as an attempt to quantify Penman's (1956) concept of a complete crop cover.

When the soil surface is wet, evapotranspiration does not appear to be very different from Penman's potential evapotranspiration. When the soil surface is dry, however, evapotranspiration from the common agricultural crops (with LAI of, say, 1 to 4) can be considerably less—to judge by the results here, by as much as 60 per cent at an LAI of 1 down to 10 per cent at an LAI of 4. In view of the additive nature of E_s and T_p , it may be sufficient in these cases to deduct amounts of this order from the potential evapotranspiration. Refinements could include an allowance for leaf angle and the soil thermal properties, but these are probably unnecessary for many practical applications.

Several problems still remain, for instance, accounting for soil moisture states intermediate between the wet and dry cases considered here, and prediction of the distribution of leaf resistances in the canopy. Obviously the complete model of evapotranspiration will be a very complicated one.

Résumé

Importance relative de l'évaporation du sol et de la plante pour évaluer l'évapotranspiration (O. T. Denmead)

Étude des quantités relatives des composantes de l'évapotranspiration — évaporation du sol et transpiration de la plante — ainsi que de leur degré d'interdépendance.

L'auteur présente une analyse d'un modèle d'évapotranspiration reposant sur le bilan énergétique. Il cherche tout d'abord à prévoir la température de la surface du sol à partir d'observations relativement simples du climat qui règne au-dessus des peuplements végétaux, ainsi que de données sur la structure de la voûte foliée

et sur les propriétés hygrométriques et thermiques du sol. Il examine alors les effets de la température de la surface sur l'échange énergétique à la surface du sol, sur le microclimat de la voûte foliée et sur les échanges de chaleur et de vapeur d'eau qui en résultent à la surface des feuilles.

Il apporte une attention particulière à la confrontation du modèle avec les observations sur le terrain. Le modèle paraît reproduire convenablement les caractéristiques principales de la situation réelle.

L'analyse porte sur les effets de l'état hydrique du sol et de la structure de la voûte foliée sur l'évapotranspiration. En ce qui concerne les cultures ordinaires,

l'évapotranspiration du sol paraît être un élément important des pertes d'eau totales. La principale conclusion est que l'évaporation du sol et la transpiration peuvent être considérées comme pratiquement indépen-

dantes l'une de l'autre et comme pouvant par conséquent s'additionner. Cela permet des simplifications dans l'évaluation de l'évapotranspiration effective lorsque la surface du sol s'assèche.

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The effect of light and water potential on dry matter production of field crops

P. E. Rijtema

Institute for Land and Water Management Research,
Wageningen (Netherlands)

INTRODUCTION

For analysis of the production of field crops it is desirable to know maximum and actual production per unit of soil surface. Since dry matter production is mainly the result of net photosynthesis, the production of compounds other than carbohydrates can be ignored quantitatively. The photosynthetic rate depends on the formative development of the plant, as this determines to what extent and during which period of the year the crop is able to convert solar energy into photosynthetic products.

Although for practical purposes the total dry matter production of a field crop is of much more interest than the daily production rate, it is necessary to analyse the influence of environmental factors in terms of this rate since factors such as crop height, soil cover and water potential vary in a complex way throughout the growing season.

The present paper gives a method of calculating the actual daily production rate, as well as the total production as determined by the light conditions, crop development and water potential conditions in the various stages of growth. Moreover, a discussion will be given of the direct and the indirect effects of water potential conditions in the various stages of growth, and of the way in which these effects can be taken into account in a production function.

THE EFFECT OF LIGHT ON PRODUCTION

The production of dry matter of crops is a result of net photosynthesis. This photosynthetic process consists of several steps, such as the use of energy for the reduction of CO_2 , a diffusion process for the transport of CO_2 to the chloroplasts and a series of biochemical processes.

These partial processes are affected in different ways by external conditions and each of them may limit the dry matter production in the field.

When calculating dry matter production from agro-climatological data, it is useful to regard light energy as the main factor in such a production model, as this factor can be determined with the greatest ease and accuracy under field conditions. The other partial processes involved with photosynthesis then have to be used as correction factors.

The estimation of photosynthesis of leaf canopies, as given by Wit (1965) will be used as a basic term in the production function. Wit's approach is mainly based on solar radiation and leaf distribution. For a set of standard crop conditions, he calculated the daily photosynthetic rate for very clear days, as well as for overcast ones, assuming that the light intensity on overcast days is 0.2 times the corresponding value (H_c) on very clear days. The light energy is expressed in $\text{cal cm}^{-2} \text{ day}^{-1}$ for the light range from 400 to 700 nm. The daily photosynthetic rate under Wit's standard conditions is given in Table I.

The daily production rate during each period can be calculated as proposed by Wit's, using:

$$P = F \cdot P_o + (1-F) P_c \quad (1)$$

where P is the production in $\text{kg carbohydrate day}^{-1} \text{ ha}^{-1}$; P_o the production on overcast days; P_c the production on very clear days; F the fraction of time that the sky is clouded. The value of F is obtained from $(H_c - H_a) / (0.8H_c)^{-1}$, where H_c is the mean radiation on clear days and H_a is the actual mean value equalling $0.5H_{sh}$. H_{sh} is the global radiation in $\text{cal cm}^{-2} \text{ day}^{-1}$.

The production calculated in this way must be considered as the potential production (P_{pot}) of a standard crop as defined by Wit (1965). The actual crop conditions will generally deviate from these standard crop conditions. Part of these deviations will be due to differences

TABLE 1. The daily totals of light (wavelengths 400–700 nm) on very clear days (H_c) in cal cm⁻² day⁻¹, the photosynthetic rates on very clear days (P_c) and on overcast days (P_o) in kg carbohydrate ha⁻¹ day⁻¹ for a standard crop. $r_a = 0.5 \text{ sec cm}^{-1}$ (After de Wit, 1965)

North latitude	15 Jan.	15 Feb.	15 March	15 Apr.	15 May	15 June	15 July	15 Aug.	15 Sept.	15 Oct.	15 Nov.	15 Dec.
0°												
H_c	343	360	369	364	349	337	342	357	368	365	349	337
P_c	413	424	429	426	417	410	413	422	429	427	418	410
P_o	219	226	230	228	221	216	218	225	230	228	222	216
10°												
H_c	299	332	359	375	377	374	375	377	369	345	311	291
P_c	376	401	422	437	440	440	440	439	431	411	385	370
P_o	197	212	225	234	236	235	236	235	230	218	203	193
20°												
H_c	249	293	337	375	394	400	399	386	357	313	264	238
P_c	334	371	407	439	460	468	465	451	425	387	348	325
P_o	170	193	215	235	246	250	249	242	226	203	178	164
30°												
H_c	191	245	303	363	400	417	411	384	333	270	210	179
P_c	281	333	385	437	471	489	483	456	412	356	299	269
P_o	137	168	200	232	251	261	258	243	216	182	148	130
40°												
H_c	131	190	260	339	396	422	413	369	298	220	151	118
P_c	219	283	353	427	480	506	497	455	390	314	241	204
P_o	99	137	178	223	253	268	263	239	200	155	112	91
50°												
H_c	73	131	207	304	380	418	405	344	254	163	92	61
P_c	147	223	310	409	484	522	509	448	358	260	173	130
P_o	60	100	150	207	251	273	265	230	178	121	73	51
60°												
H_c	22	72	149	260	356	408	389	309	201	103	37	14
P_c	66	151	254	383	487	544	523	436	316	195	94	49
P_o	19	60	114	187	245	276	265	216	148	82	31	11
70°												
H_c	0	20	89	209	331	408	380	269	142	45	2	0
P_c	0	65	185	350	506	612	575	427	262	114	7	0
P_o	0	16	74	158	241	291	273	200	112	38	1	0
80°												
H_c	0	0	28	162	334	424	393	248	81	3	0	0
P_c	0	0	94	333	571	663	632	474	195	11	0	0
P_o	0	0	24	133	257	318	297	196	69	2	0	0
90°												
H_c	0	0	0	154	339	428	397	252	40	0	0	0
P_c	0	0	0	371	588	677	646	497	167	0	0	0
P_o	0	0	0	131	269	319	302	215	35	0	0	0

in the various resistances in the diffusion pathway. Rijtema and Endrödi (1970), giving a further analysis of the data presented by de Wit, concluded that, for the standard crop conditions, the sum of the resistances equals 4.9. In order to correct for differences in the resistances in the diffusion pathway, the production rate of the standard crop is multiplied by the ratio of the resistances of the standard crop to the sum of the resistances of the actual crop, as given in equation 2:

$$P = \frac{4.9}{r_a + r_s + r_m} \cdot P_{\text{pot}} \quad (2)$$

where P is the production rate of the actual crop, r_a the exchange resistance between the bulk air and the effective surface canopy in sec cm⁻¹ r_s is the diffusion resistance of the crop in sec cm⁻¹ and r_m the mesophyll resistance of the crop in sec cm⁻¹.

This production function only holds for full cover crops. Partial soil cover results in a waste of light available for photosynthesis. The effect of partial soil

cover can be eliminated by multiplying the production rate of a full cover crop by the fraction of the surface area covered by the plants (Rijtema and Endrödi, 1970), giving the following expression:

$$P = \frac{4.9}{r_a + r_s + r_m} S_c P_{\text{pot}} \quad (3)$$

where S_c is the fraction of soil cover.

The losses due to respiration have not yet been taken into account in the calculated value of the production. It has been shown (Rijtema and Endrödi, 1970) that the assumption that the respiration rate is proportional to the production rate gives reasonable results. This decrease in production can be given by an efficiency factor, α , giving as the final expression for the production function:

$$P = \alpha \frac{4.9}{r_a + r_s + r_m} S_c P_{\text{pot}}. \quad (4)$$

Sibma (1968), analysing production data of ten different crops, concluded that, under the climatological conditions in the Netherlands, the various species have a very similar mean production rate of about 200–250 kg dry matter $\text{ha}^{-1} \text{day}^{-1}$ from the time the soil is completely covered by a green crop surface under optimum conditions of water supply. Compared with the results of the production rates calculated using equation 4, it is found that the efficiency factor α is about 0.6–0.7.

The production rate decreases markedly near maturation. A first approach to quantify this phenomenon has been given by Rijtema and Endrödi (1970) for a potato crop, relating the value of the mesophyll resistance, as well as the efficiency factor to the number of dead leaves. The effect of the increasing number of dead leaves on the value of the surface resistance has also been taken into account (Endrödi and Rijtema, 1969).

THE EFFECT OF WATER POTENTIAL ON PRODUCTION

It is necessary to distinguish between two phenomena when discussing the effect of water potential on the production rate. The first one is the "active" water uptake by the plant due to a potential gradient between soil moisture suction and osmotic pressure in the plant. The second phenomenon deals with the "passive" water uptake for transpiration.

The "active" water uptake restores the water content of the plant during the night. This process is very important for the growth of stems and leaves by cell elongation. The reduction in elongation starts at low soil moisture suction (pF) values as is shown in Figure 1.

As the value of the external transport resistance (r_a) depends on crop height, it will be clear that reduction in elongation affects this resistance. Data of Szeicz *et al.* (1969) for potatoes and Slabbers (1969) for sunflower, alfalfa, sugarbeet and wheat give values for r_a similar to those derived from the data given by Rijtema (1965) for a grass cover. Thus, for different agricultural crops,

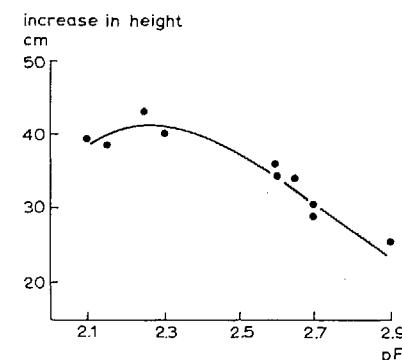


FIG. 1. The relationship between the increase in height of broad beans and soil moisture suction (pF) during the period from 15 May to 6 June.

the data of r_a , given in Table 2 in relation to crop height and wind velocity, can be used.

Apart from the effect of cell elongation on the value of r_a , a second factor in relation to soil cover is of importance. In Figure 2 the relationship between crop height and soil cover is given for two crops. When a period of drought occurs during early stages of growth without a full soil cover, it results in a lower soil cover percentage during part of the growing season. Figure 3 shows the effect of a period of drought of 14 days on crop height and soil cover of a non-irrigated potato crop in comparison with an irrigated one. The period of drought affected both crop height and soil cover for 60 days, although sufficient precipitation was received after that period of drought for crop height to resume a rapid rate of increase. It is clear from the results presented in Figure 3 that, when the period of drought starts at a later date in the growing season, the duration of its effect is reduced.

Though the effect of stem and leaf elongation on the daily production rate can be adequately described in

TABLE 2. Values of r_a (sec cm^{-1}) in relation to crop height (cm) and wind velocity in (m sec^{-1}) at 2 m height

Wind velocity	Crop height									
	0	2	5	10	20	30	40	50	70	90
0.5	7.06	5.52	2.70	1.72	1.27	1.14	1.04	0.96	0.90	0.85
1.0	4.00	3.13	1.53	0.97	0.72	0.64	0.59	0.54	0.51	0.48
1.5	2.97	2.32	1.14	0.72	0.54	0.48	0.44	0.40	0.37	0.35
2.0	2.48	1.94	0.95	0.60	0.44	0.40	0.37	0.34	0.32	0.30
2.5	2.08	1.62	0.80	0.51	0.37	0.33	0.30	0.28	0.26	0.25
3.0	1.81	1.41	0.69	0.44	0.32	0.29	0.27	0.25	0.23	0.22
4.0	1.47	1.15	0.56	0.36	0.27	0.24	0.22	0.20	0.18	0.18
5.0	1.24	0.97	0.48	0.30	0.23	0.20	0.18	0.17	0.15	0.15
6.0	1.08	0.85	0.42	0.26	0.20	0.18	0.16	0.15	0.13	0.13
7.0	0.97	0.76	0.37	0.23	0.18	0.16	0.14	0.13	0.12	0.11

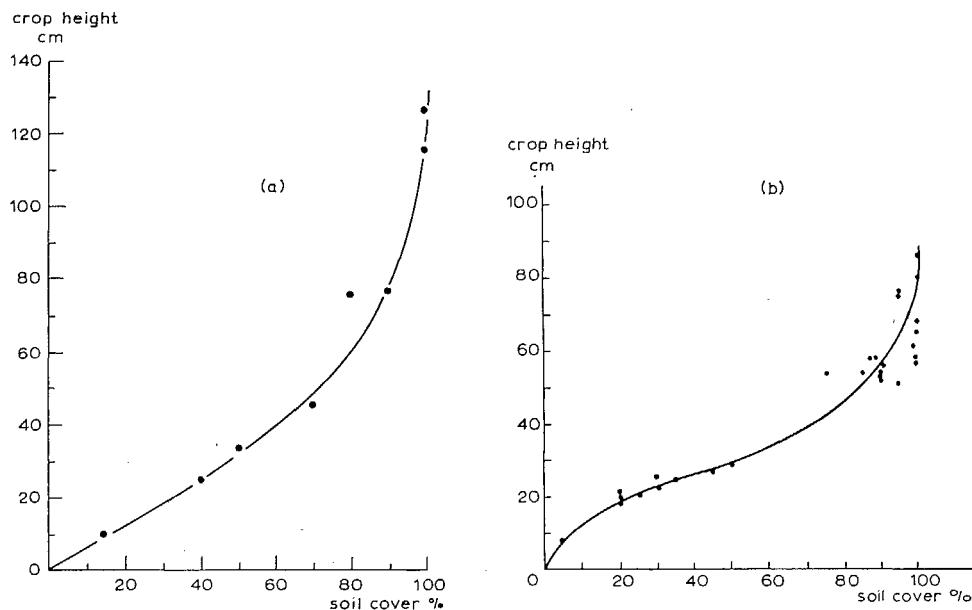


FIG. 2. The relationship between crop height and percentage of soil cover: (a) spring wheat; (b) potatoes.

terms of external transport resistance and soil cover, a third aspect must be mentioned. The production function gives the production rate of total dry matter, but not the distribution of dry matter over the various parts of the plant. Particularly during the heading of cereals, a reduced elongation rate can be critical for the distribution of dry matter produced after heading into grain and straw. Data of Vos and Toussaint (1966) show that, with an equal amount of available water during growth, the grain-straw ratio varied markedly between 0.42 and 0.84, depending on the values of soil water potential during heading, whereas the total dry matter production did not change very much.

The "passive" water uptake for transpiration can be regarded as a continuous flow of water by potential gradients from the ground-water level, through the soil and roots of the plants to the leaves, where it is transformed by solar energy into water vapour. As vaporization occurs in the sub-stomatal cavities, the suction must be the greatest in the leaves, since they constitute the final stage of the liquid pathway. Even when soil water appears to be freely available, the transpiration demand can be so high during the day that temporarily high suctions develop which cause a closing of the stomata resulting in an increase of the crop surface resistance, r_s .

Rijtema (1965, 1966) gives the surface resistance for transpiration as a sum of partial resistances due to soil cover (r^c_s), light intensity (r^l_s) and suction in the leaves (r^ψ_s). For the production function given above, only the last two factors have to be considered, as the effect of soil cover has already been taken into account. The relationship between the light dependent term (r^l_s) and the mean radiation intensity during the day is given in Table 3.

Rijtema (1965) showed that the suction dependent surface resistance term (r^ψ_s) can be given by the general equation:

$$r^\psi_s = f \left[E_T^{\text{pot}} (R_{pl} + b/k) + \psi \right] \quad (5)$$

where E_T^{pot} is the potential transpiration rate, R_{pl} the transport resistance of the crop for liquid flow, b a geometry factor of the root system, k the capillary conductivity of the soil at mean suction ψ in the effective root zone of the crop. Values of R_{pl} and b for grass and cereals are given by Rijtema (1965, 1968) and for potatoes by Endrödi and Rijtema (1969). It appears, from these investigations, that the value of r^ψ_s can vary from 0 to 6.0 sec cm⁻¹.

As the production function deals with CO₂ diffusion and not with water vapour diffusion, the sum of r^l_s and

TABLE 3. Values of the light dependent resistance (r^l_s) and mean radiation intensity during the day

Radiation intensity (cal cm ⁻² min ⁻¹)	0.10	0.15	0.20	0.25	0.30	0.38	>0.38
r^l_s , (sec cm ⁻¹)	3.17	2.32	2.31	1.02	0.55	0.0	0.0

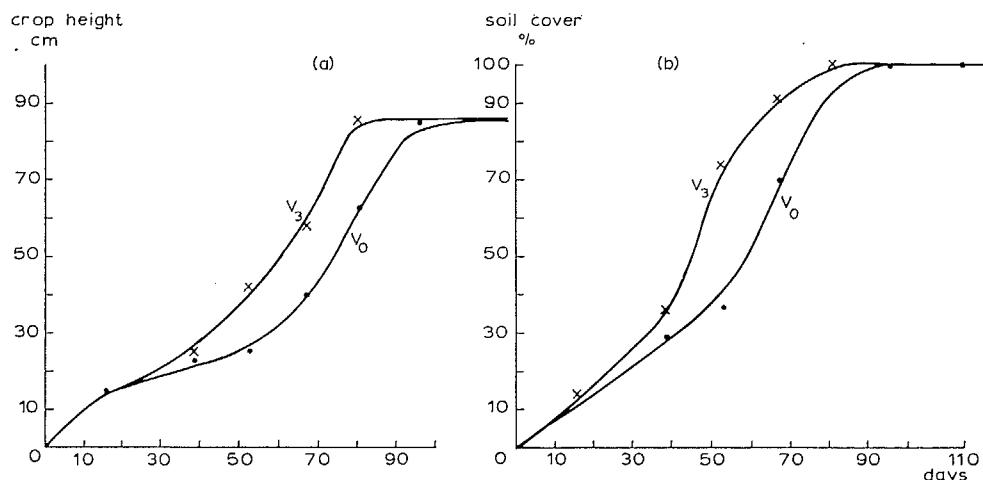


FIG. 3. The relationship between crop development and time for a non-irrigated field (v_0) and a frequently irrigated one (v_3). A period of drought was present from 30 to 44 days after the start of the growing season: (a) change in crop height with time; (b) change in soil cover percentage with time.

r_s^ψ must be multiplied by $(D_{H_2O}) (D_{CO_2})^{-1}$, which is the ratio of the diffusion coefficients of water vapour and of CO_2 . So r_s in the production function can be calculated as:

$$r_s = (D_{H_2O}) (D_{CO_2})^{-1} (r_s^l + r_s^\psi). \quad (6)$$

Equation 6 describes the combined effects of evaporative demand of the atmosphere, the internal crop resistance for water transport and the soil conditions on the increase in surface resistance due to stomatal closure. It can be used in the production function to evaluate the effect of these factors on the production rate.

DISCUSSION

For standard crop conditions, with r_a equal to 0.5 sec cm^{-1} , the total resistance equals 4.9 sec cm^{-1} , resulting in a value of 4.4 sec cm^{-1} for $(r_s + r_m)$. It has been shown in a previous paper (Rijtema, 1965) that the surface resistance for transpiration of some full cover crops under conditions of high light intensity and optimum water supply is almost zero. As the diffusion coefficients of H_2O and CO_2 differ considerably, it does not necessarily follow that for these crops, under the optimum conditions, the surface resistance for CO_2 also equals zero. When the production calculated for the standard crop conditions is considered as the potential one, it must follow that the given value of 4.4 sec cm^{-1} represents a minimum value of the sum of r_s and r_m . In the remaining discussion this value will be regarded as r_m , but it must be kept in mind that it also includes the minimum value of the surface resistance.

The reduction in stem and leaf elongation affects the value of the external resistance r_a , due to a reduced increase in crop height with time. The values of r_a in the range of normal wind velocities and crop heights vary from 0.6 to 0.3 sec cm^{-1} . The effect of this variation in the value of r_a on the daily production rate is very

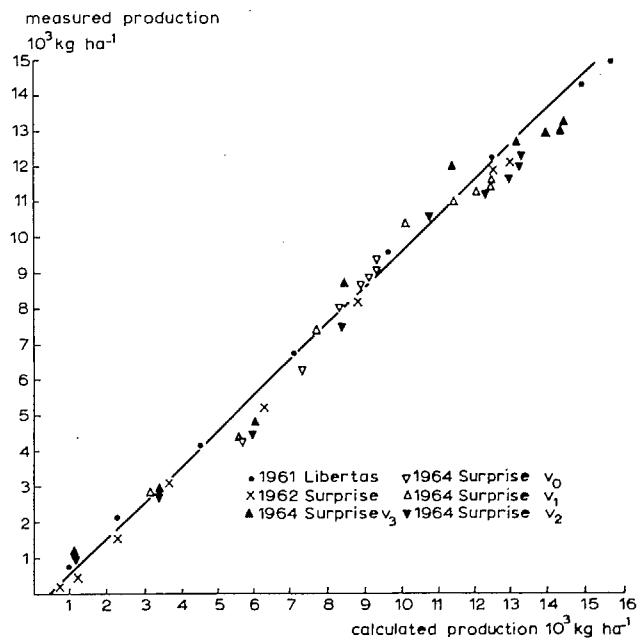


FIG. 4. The relationship between the calculated dry matter production of a potato crop and the actual data obtained from periodical harvests.

small, resulting in a production rate relative to the standard crop of 0.98 and 1.04 respectively. This result also shows that the production function is not very sensitive to small errors in the determination of r_a .

The reduction in stem and leaf elongation also affects the soil cover fraction during growth. As the soil cover fraction is a linear factor in the production function it influences the daily production rate considerably. The duration of the effect of reduced elongation not only depends on the length of the period of drought, but also on the time within the growing season when this drought period starts, as well as on the time required after this period to reach a full cover.

The effect of extreme water potentials in the crop causing stomatal closure is described by equation 5. The decrease in the daily production rate due to this effect depends entirely on the various factors described in this equation, but it results in a variation in the relative production rate of from 1.0 under optimum water supply conditions to 0.4 under severe stress conditions.

Some experimental evidence has suggested that high leaf temperatures increase the physiological ageing of the crop; as a result maturation starts at an earlier date,

resulting in a shortening of the growing season. High water potentials, which cause an increase in surface resistance, result also in higher leaf temperatures and an earlier maturation of the crop. The effect of maturation is described in the production function by an increase in r_s and r_m and a decrease in the efficiency factor α .

A comparison between calculated and measured dry matter production of potatoes is given in Figure 4. The measured data were obtained from periodic harvests in irrigation experiments. The data of 1961 and 1962 refer to frequently irrigated fields, whereas the data of 1964 refer to fields with irrigation after 15 per cent (v_1), 50 per cent (v_2), or 25 per cent (v_3) moisture extraction and a field without irrigation (v_0). Reduction in transpiration caused a wide variation in the value of r_s . Moreover, the distribution of crop height and soil cover, as well as the distribution of the percentage of dead leaves at the end of the growing season, differed considerably over the growing period.

There is good agreement between the dry matter production as determined by periodic harvests and the data calculated with equation 4, indicating that a reasonable estimation of dry matter production can be obtained using the given production function.

Résumé

Effets de la lumière et du potentiel hydrique sur la production de matière sèche des plantes de grande culture (P. E. Rijtema)

L'auteur propose une fonction pour le calcul de la production de matière sèche des plantes de grande culture aux différents stades de leur développement en utilisant une modification de la méthode suggérée par de Wit (1965).

Il tient compte de l'influence des divers aspects du développement de la plante, comme sa hauteur, la couverture du sol et la maturation, ainsi que des effets directs et indirects du degré d'humidité sur la production journalière.

La méthode proposée peut servir à évaluer la réduction de la production de matière sèche sous l'effet de la sécheresse à différents moments de la saison végétative.

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A quantitative account of the influence of solar radiation, water and nitrogen supply on the photosynthesis of wheat communities in the field

D. W. Puckridge

Waite Agricultural Research Institute,
Glen Osmond (Australia)

INTRODUCTION

The field assimilation chamber has proved to be a useful tool for the measurement of photosynthesis of crop communities. Using data obtained with one of these in a study of the growth of two wheat cultivars sown at three densities, Puckridge and Ratkowsky (1970) used a simple mathematical model for predicting CO₂ uptake. Predicted values of CO₂ uptake for any specified leaf area index (LAI) and solar radiation gave good agreement with CO₂ uptake measured with the assimilation chamber in the period from 6 weeks before anthesis until leaf senescence was complete.

In an attempt to determine the general application of the model, this work was followed by an examination of the effects of water and fertilizer nitrogen on the growth and photosynthesis of wheat crops sown at a seeding rate of 90 kg/ha.

METHODS

Two cultivars of wheat, Gabo and Pitic 62, were sown on 20 June 1969, in 11-row drill strips with 18 cm between the rows, at a seeding rate of 90 kg/ha. There were four cultural treatments; natural rainfall, or natural rainfall plus supplementary irrigation, in combination with 0 or 90 kg/ha of fertilizer nitrogen. The nitrogen was given in two applications, each of 45 kg/ha, on 10 July and 14 August.

Photosynthesis measurements were made on part of each drill strip; the remainder was used for assessing other plant characteristics. Samples were cut at two weekly intervals for the determination of LAI, dry weight, and tiller and ear production.

Changes in photosynthesis were determined by the measurement of CO₂ uptake in two field assimilation chambers of the type described by Puckridge (1969).

Each chamber included seven rows of the crop and covered an area of 2.79 m². Early in the morning the assimilation chambers were placed over the plots and were sealed by setting the bottom edges of the chamber into a narrow water-filled channel borne on a sheet metal frame that was pressed into the ground. Throughout the day the CO₂ concentration of the air in the chambers was monitored, and CO₂ added as necessary to maintain the concentration within ± 10 ppm of the mean atmospheric concentration of 305 ppm.

The amount added to each chamber was recorded for 15 min intervals. Short-wave solar radiation within the chamber was recorded using a Kipp solarimeter and the mean radiation calculated for the same 15 min periods.

Air temperature within the assimilation chambers was held constant throughout the day. The temperatures used were based on the mean monthly ambient temperatures and were increased monthly from 12 °C in August to 20 °C in November. Photosynthesis measurements were interrupted at noon for measurement of dark respiration: the CO₂ supply was cut off and the concentration in the chamber allowed to decrease to 50 ppm below ambient, a light-proof cover was then put over the chamber, and the rate of CO₂ increase measured as the concentration passed the ambient level.

Rainfall in relation to the time of sowing, 20 June, and the commencement of irrigation, 20 August, was as follows:

1 April to 19 June	176 mm
20 June to 19 August	141 mm
20 August to 30 September	87 mm
October	2 mm
November	24 mm
Total for growing season	430 mm

Irrigation water was applied to the appropriate treatments at 12 mm per week for 11 weeks from 20 August

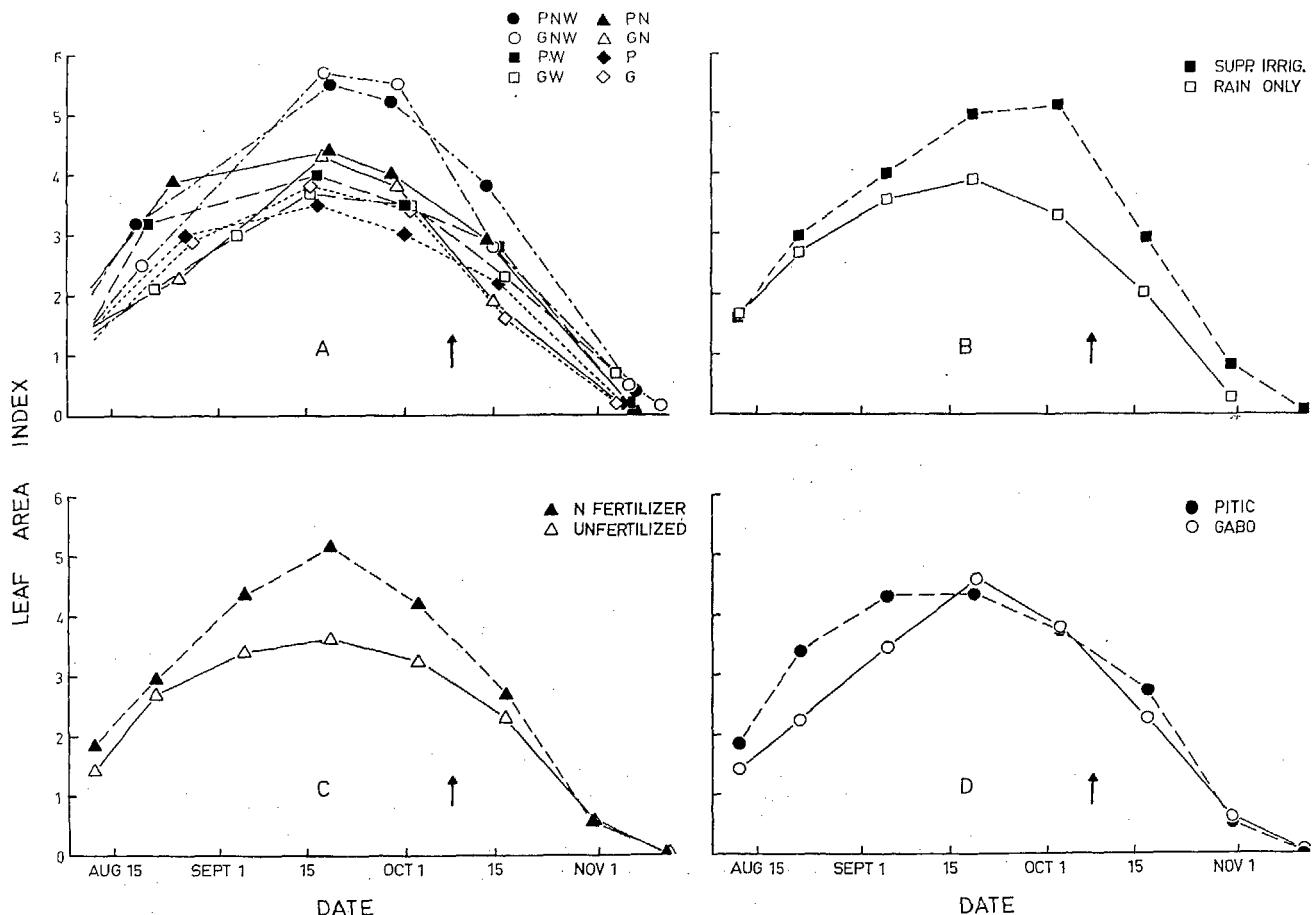


FIG. 1. Changes in LAI with time.
A. Individual treatment combinations. P = Pitic, G = Gabo, N = nitrogen fertilizer, W = supplementary irrigation.
B. Main effects of water (SUPP. IRRIG. = supplementary irrigation).
C. Main effects of nitrogen.
D. Main effects of cultivar.
Arrows show mean date of anthesis.

to 11 November. The mean date of anthesis was 8 October and the plants were fully mature by 25 November.

RESULTS

The results are presented for the individual treatment combinations and, for the main effects of water, nitrogen and cultivar.

LEAF AREA INDEX

Figure 1A shows the pattern of leaf area development for the individual treatment combinations. LAI included both the leaf laminae and the projected area (length ×

diameter) of the green parts of the stems. The points shown in this graph were calculated for individual plots on the day of their respective CO_2 uptake measurements by interpolating from the two-weekly harvest data. Maximum LAI was attained by the plots with both supplementary water and nitrogen (PNW and GNW), and the lowest values occurred on the unsupplemented plots (P and G).

The weekly harvest data were combined to give the two-weekly means presented in graphs B and C. Supplementary water increased both the maximum LAI attained and extended the period in which green leaf was present (Fig. 1B), whereas fertilizer increased only the maximum LAI (Fig. 1C). Pitic had a greater LAI than Gabo before flag leaf emergence (Fig. 1D), but thereafter there were no differences between varieties,

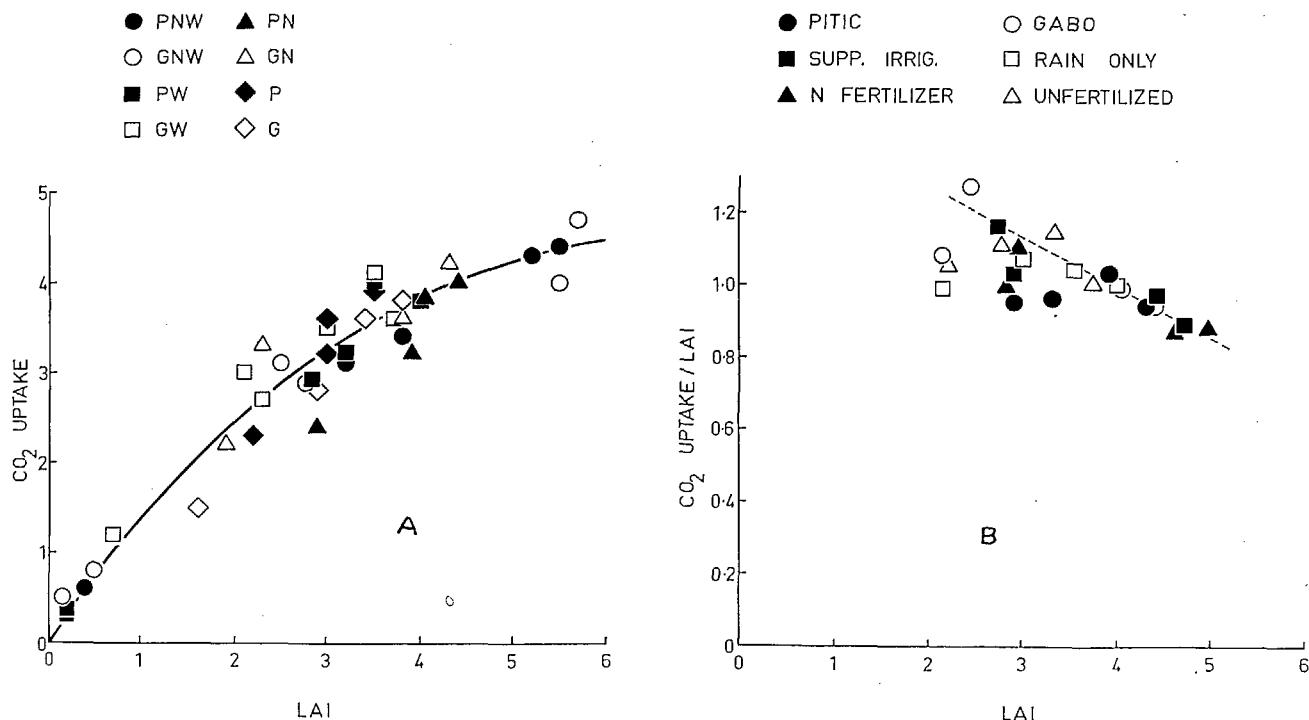


FIG. 2. A. The effect of LAI on CO_2 uptake, using a standard radiation of $0.6 \text{ cal/cm}^2/\text{min}$. Points are for all treatment combinations and all dates of measurement. (PNW, GNW, etc., as in Figure 1A.)
B. The effect of LAI on CO_2 uptake/LAI for the main effects of water, nitrogen or cultivar. Radiation $0.6 \text{ cal/cm}^2/\text{min}$. (SUPP. IRRIG. = supplementary irrigation.)

CARBON DIOXIDE UPTAKE

Both CO_2 uptake and solar radiation were expressed as means for 30 min periods throughout the day and curves were fitted to the data for CO_2 uptake versus solar radiation.

In order to make a comparison between treatments and different dates of measurement, a standard solar radiation of $0.6 \text{ cal/cm}^2/\text{min}$ was chosen and the CO_2 uptake at this radiation was taken from the smoothed curves. These values are shown in Figure 2A plotted against LAI for all dates and treatment combinations. There was a curvilinear relationship between LAI and CO_2 uptake which appeared to be independent of treatment or age of the plant. All treatments could be fitted by the single curve.

The effect of LAI on the CO_2 uptake per unit of LAI is given in Figure 2B for the main effects of water, nitrogen and cultivar. There was a marked trend of diminishing CO_2 uptake/LAI with increasing LAI for all measurements made up to 2 October, six days before anthesis. This trend is shown by the dotted line, dis-

regarding the six low points between LAI 2 and 3. The divergence shown for LAI values between 2 and 3 results from the points obtained from the 14–17 October measurements. These occurred after a very dry period, in which no rain fell between 25 September and 17 October. In the same period radiation averaged $555 \text{ cal/cm}^2/\text{day}$ compared with an eleven-year mean for September and October of 352 and $476 \text{ cal/cm}^2/\text{day}$ respectively. Photosynthesis at this time may have been affected by water stress to a greater degree than leaf senescence, even in the irrigated plots where the divergence from the earlier trend was least. Some difficulty was met in the visual estimation of the proportion of the leaf and stem which was photosynthetically active, and in the calculation of LAI from samples taken from areas other than that part of the crop used for photosynthesis measurements. An overestimate of LAI would decrease the ratio, but the curves in Figure 1A indicate that the estimates of LAI were consistent. After 17 October there was no complete set of treatment combinations, so the main effects are not shown for low LAI values.

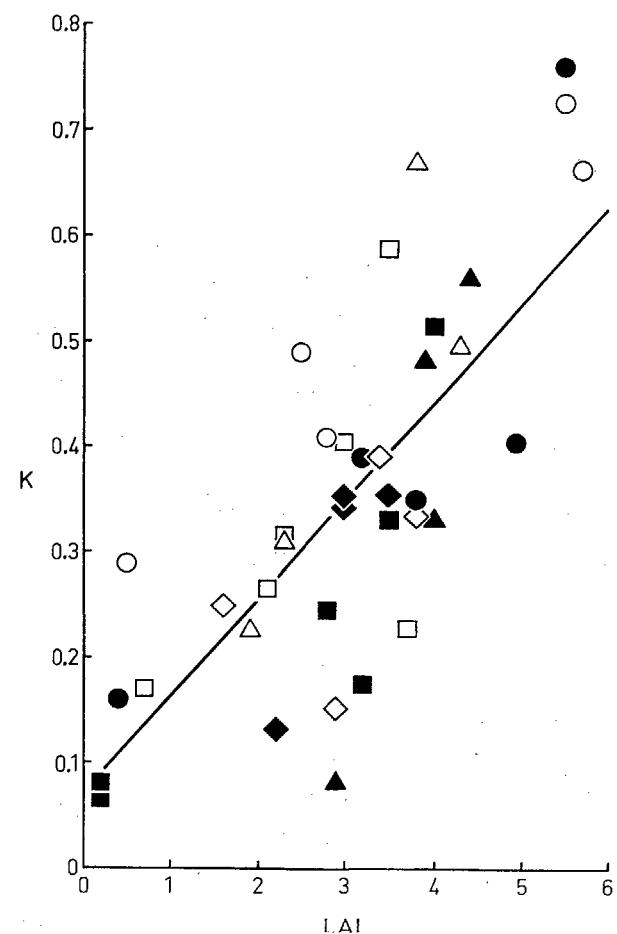
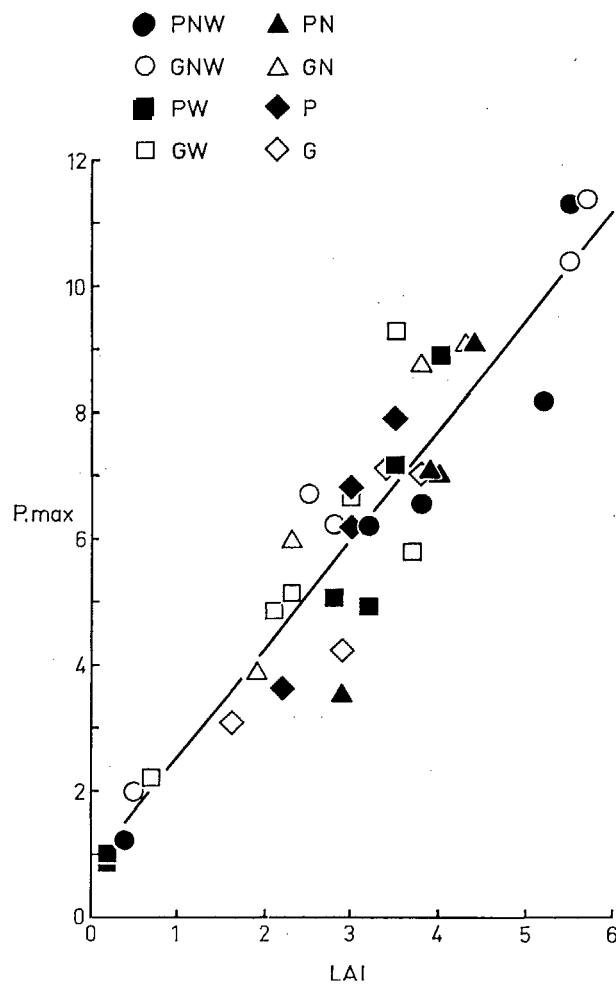


FIG. 3. The parameters P_{\max} (asymptotic rate of photosynthesis) and K (radiation intensity at $P_{\max}/2$) plotted against LAI. Predictions of photosynthesis used these regression lines. (PNW, GNW, etc. as in Figure 1A.)

ANALYSIS OF RADIATION-PHOTOSYNTHESIS CURVES

The data for all curves of CO_2 uptake versus radiation were examined to determine whether they would fit the mathematical model previously used to evaluate the effects of density (Puckridge and Ratkowsky, 1970). In this approach, the photosynthesis function for single leaves (Wit, 1965; Duncan *et al.*, 1967)

$$P = \frac{P_{\max} \cdot I}{I + K} - R \quad (1)$$

where I is the solar radiation, R is the dark respiration, and P is the net CO_2 uptake, was used as an approximation for the behaviour of the whole canopy. This equation has the mathematical form of a rectangular hyperbola, and was fitted to the CO_2 uptake and solar radiation data of the day's photosynthesis measurements for each plot. From the hyperbolae, values were

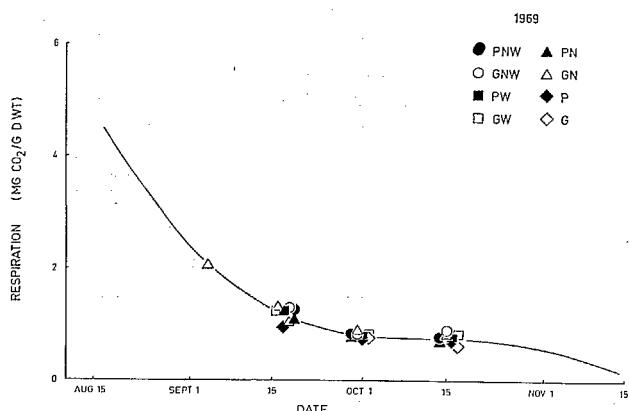


FIG. 4. Changes in dark respiration per unit dry weight (DWT). Extrapolations based on curve obtained in the previous season. (PNW, GNW, etc., as in Figure 1A.)

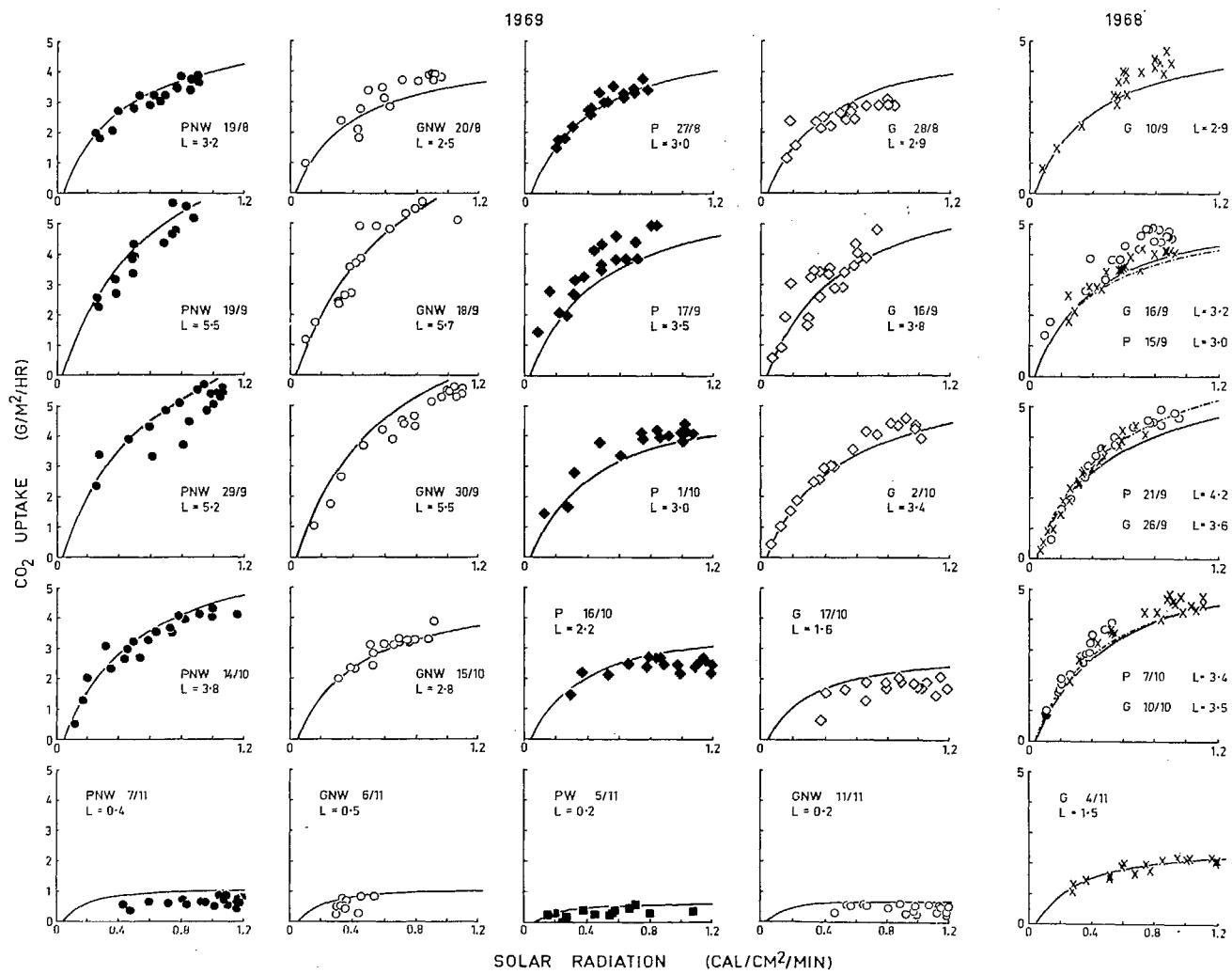


FIG. 5. Comparison of predicted curves with measured CO_2 uptake (points for 30 min means) for all NW and control treatments and dates in 1969, and for eight plots in 1968. All predictions were based on the same regression lines of P_{\max} and K and used measured values only for LAI (L) and respiration. (PNW, GNW, etc., as in Figure 1A.)

obtained for P_{\max} (the asymptotic rate of photosynthesis) and K (radiation intensity at $P_{\max}/2$). The parameters P_{\max} and K were then plotted against LAI as shown in Figure 3.

Initially the regressions were calculated for each cultivar independently, but they were not significantly different and the data were then pooled to give the lines shown in Figure 3.

Predicted values of CO_2 uptake for the daily range of solar radiation were then obtained for each plot using the following procedure:

1. For a given LAI, values of P_{\max} and K were read from the lines of best fit in Figure 3.

2. Respiration was calculated from the curve in Figure 4 and the dry weight curve of the particular treatment combination. (Respiration was not measured on all occasions and the extrapolations in Figure 4 were based on the curve obtained in the previous season.)

3. CO_2 uptake was calculated using equation (1). The predictions are shown as curves in Figure 5. Each curve may be compared with observed values of CO_2 uptake (30 min means) shown as the points on the graphs. The first four columns show measurements made in 1969 for treatments with both water and nitrogen and treatments with neither. Similar results were obtained for the other treatment combinations. There

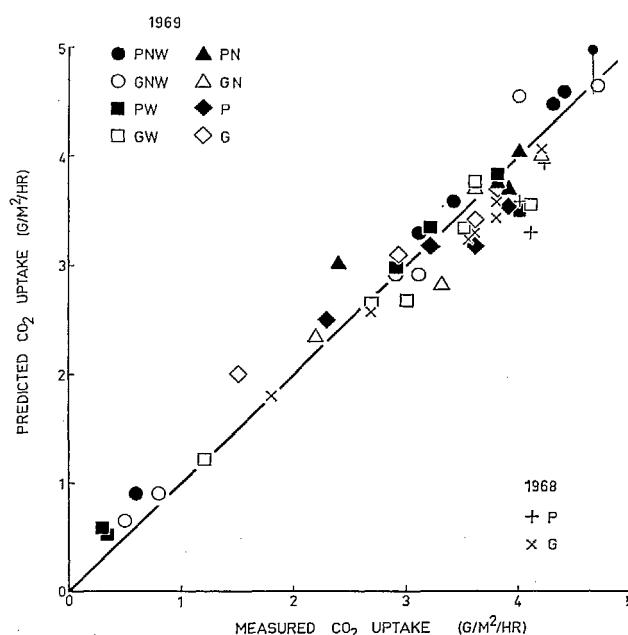


Fig. 6. Comparison of predicted and measured values of CO_2 uptake at a solar radiation of 0.6 cal/cm 2 /min. All treatment combinations and dates of measurement for both seasons. (PNW, GNW, etc., as in Figure 1A.)

was good agreement between predicted and observed CO_2 uptake for the whole period of measurement from mid-August, 7 weeks before anthesis, until early November, when the plants were nearing maturity and the LAI was almost too small to measure.

The last column of Figure 5 shows predictions for eight plots at this seeding rate on which photosynthesis was measured in the 1968 season. The points are the half-hourly measured values of CO_2 uptake and the predicted curves were based on P_{\max} and K values from 1969 (Fig. 3), using only LAI and respiration from 1968. The agreement between predicted and observed values shows that the crop behaved similarly in the two seasons and that the data from one season could be used to predict photosynthesis in another season.

A comparison of predicted and observed CO_2 uptake for all plots for which measurements were available in both seasons is given in Figure 6. The basis of comparison is CO_2 uptake at a radiation level of 0.6 cal/cm 2 /min. Measured CO_2 uptake was taken from the curves fitted to the original data. The line is drawn through zero with a slope of one, and there is no indication that any treatment combination departed from the general relationship.

DRY MATTER AND GRAIN PRODUCTION

There were no marked differences in dry matter production before 3 October, when the mean dry weight

for all treatments was 770 g/m 2 . Thereafter, there was an increasing difference between the irrigated plots, which reached a mean maximum of 1,100 g/m 2 , and the non-irrigated plots, where the mean maximum was 930 g/m 2 . On 16 October, plots with nitrogen had more dry matter than those without nitrogen, and Pitic was greater than Gabo, but the differences did not persist to the final harvest.

The highest grain yields were obtained from the plots with supplementary irrigation, and the addition of nitrogen had little effect on the yields of these plots. However, for the plots with natural rainfall only, the addition of nitrogen reduced the yield of grain. Yields as a mean of the two cultivars were:

Irrigation and nitrogen	358 g/m 2
Irrigation only	370 "
Nitrogen only	260 "
Control	301 "

The grain yields for the main effects are given in Table 1, together with the leaf area duration (LAD) for both the whole period after 12 August, and for the period from anthesis to maturity. The comparison of grain production and LAD for the effect of water or cultivar showed that grain production was more closely related to LAD for the whole period, than to LAD after anthesis. However, the effect of nitrogen was to give an inverse relationship between grain production and LAD.

DISCUSSION

The results of this experiment and the one in the previous season (Puckridge and Ratkowsky, 1970) have shown that the main determinant of photosynthesis in the period from six weeks before anthesis to maturity is the area of the green surfaces of the plant. These green surfaces included the leaf laminae and the projected area of the green parts of the stem, but excluded the ear surfaces. The asymptotic curve of photo-

TABLE 1. Comparison of grain yield and integrated LAI (LAD) for the main effects of water, nitrogen and cultivar. LAD given as relative areas under the LAI curves

	Grain yield		LAD	
	g/m 2	Relative	12 August-maturity	Post-anthesis
Supplementary irrigation	364	100	100	100
Natural rainfall	281	77	77	57
N fertilizer	309	85	99	84
Unfertilized	336	92	76	71
Pitic	336	92	93	81
Gabo	309	85	82	74
Mean	322			

synthesis against LAI for a standard level of radiation of 0.6 cal/cm²/min indicated that photosynthesis during the period was independent of age or treatment and it was possible to fit all data with the same basic parameters, P_{max} and K , and to use these in a simple model for the prediction of photosynthesis. Once the basic parameters were obtained, the only measured values necessary for prediction of photosynthesis of a plant community were the LAI and the respiration. An adequate measure of respiration was obtained from a generalized curve of dark respiration/dry weight and of dry weight/m². It may be possible to further refine the model so that measurements of respiration are not necessary.

There were no obvious effects of the type of radiation (diffuse or direct sunlight), and the fit of the predicted and observed results has been good enough to suggest that the greatest source of error could be the estimation of LAI by sampling from other sections of the drill strips. The plots on which photosynthesis measurements were made were not harvested until the completion of the experiment. Grain yield showed a stronger relationship to LAD for the whole period of the experiment than for the period after anthesis. The effect of water in this environment was to increase the LAD in the latter part

of the season and relative grain yields were the same as relative LAD for the whole season. However, for the comparison of treatments with or without nitrogen, grain yields were independent of photosynthesis and a reverse relationship to LAD was found, with the greatest reduction in yield occurring in the non-irrigated plots. Under Australian conditions this depression in yield is known as "haying off" and may be expressed as failure of tillers to produce ears, as ear sterility or as pinched grain (Taylor, 1965). There are also indications that applied nitrogen may cause adverse physiological changes for grain production in the wheat plant besides the effects on photosynthesis (Fischer and Kohn, 1966; Swartz and White, 1966). It is, therefore, apparent that while total community photosynthesis can be measured or predicted with considerable accuracy, further studies are needed on the partition of photosynthesis and the distribution of photosynthate.

ACKNOWLEDGEMENTS

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Résumé

Étude quantitative de l'influence du rayonnement solaire et de l'approvisionnement en eau et en azote sur la photosynthèse de champs de Blé (D. W. Puckridge)

L'auteur traite des effets de l'approvisionnement en eau et en azote et de leur interaction sur la photosynthèse de champs de Blé dans un environnement du type méditerranéen. Il étudie à cet effet deux cultivars et compare l'indice cumulé de la surface foliaire, la matière sèche et la production de grain. Ceux-ci ont été examinés

en fonction de l'activité photosynthétique saisonnière et diurne mesurée par l'absorption du gaz carbonique.

Pour une grande partie de la saison de croissance, il a établi une relation entre l'indice cumulé de la surface foliaire et l'absorption du gaz carbonique; il a pu ainsi élaborer un modèle mathématique qui permet de prévoir les taux de photosynthèse pour toutes les combinaisons de l'indice cumulé de la surface foliaire et du niveau du rayonnement solaire.

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A field method for determining soil water availability to crops

R. H. Sedgley, K. A. Seaton and W. R. Stern

Department of Agronomy,
Institute of Agriculture, University of Western Australia,
Nedlands (Australia)

INTRODUCTION

The physical basis of soil water availability to plants is fairly well understood and is documented by Slatyer (1967). Since Philip (1957) first formulated a mathematical model of soil water availability, there has been considerable development and refinement of the theory (Cowan, 1965; Gardner, 1960). The assumptions and limitations inherent in these models are discussed in depth by Philip (1966).

Even though these models have been developed, there has been little progress in relating these concepts to the characterization of soil water availability in the field. Denmead and Shaw (1960), Gardner and Nieman (1964) and Rawlins *et al.* (1968) give experimental approaches in this direction. Rose and Stern (1965) describe a method for calculating, from field data, the withdrawal of water from soil by roots as a function of depth; such data are complementary to field measurements of the availability of soil water.

The main factors controlling the availability of water to a crop, and hence the water status of the crop, are: the soil water diffusivity (D), which is the ratio of the hydraulic conductivity (k_s) to the specific water capacity $(d\theta)/(d\psi_{soil})^1$ of the soil; the root density-depth distribution; root diameter; plant resistances to water movement R_p ; the leaf water potential ψ_w at which pronounced stomatal closure occurs (termed the critical potential; Cowan, 1965) and the potential evaporation rate from the crop (E_o).

This paper sets out to reconcile the body of theory referred to above with the needs of *ad hoc* investigations, and to provide a basis for understanding the limits of water extraction by crops in the field. The demonstration by Boyer (1969) of equilibrium curves for leaf water potential (ψ_{leaf}) in non-transpiring plants has been used as a starting point to develop such a procedure. On the basis of these equilibrium curves, Boyer

developed a model that enabled him to estimate resistances in various parts of a plant from measurements of leaf water potential. A similar method is proposed here for characterizing the availability of soil water to cereals, in terms of the soil resistance to water uptake by a crop.

BASIS FOR THE METHOD

A first order decay reaction was used to describe the progress of leaf water potential to equilibrium and this is exponential in form. From this, an expression for resistance (R) to water flow in the soil-plant continuum was derived, assuming that the resistance to free-energy transfer in the continuum was proportional to water transfer over the same path and that the constant of proportionality was unity (see Boyer, 1969).

R was regarded as a measure of the resistance to flow of water between the leaves and the soil, and could be expressed as the sum of component resistances in series, i.e. R_s , a soil resistance, and R_p , a plant resistance:

$$R = R_s + R_p. \quad (1)$$

Stomatal resistance is not included, because flow beyond the leaf into the atmosphere is not being considered. As ψ_{soil} varies, R_p is assumed to remain constant; this may not necessarily hold under all conditions. In wet soil, when $R_s \approx 0$, then $R \approx R_p$; as the soil dries, R increases and the soil resistance R_s is obtained by difference

$$R_s = R - R_p. \quad (2)$$

R_s is thus seen to be a function of the soil water potential, ψ_{soil} .

1. θ represents the soil volumetric water content and ψ_{soil} , the soil water potential as measured with a tensiometer.

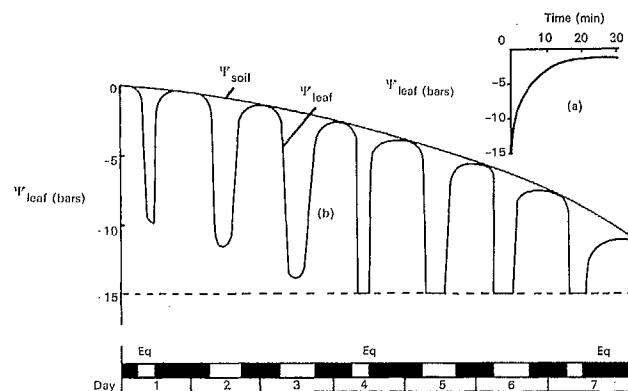


FIG. 1. Schematic representation of changes in leaf water potential (ψ_{leaf}) during a drying period. (a) After Boyer (1969), corresponding to equilibration period on day 1 (see also Figure 2); (b) After Slatyer (1957). Eq = equilibration.

The equation for calculating R_s was derived in the following way, starting with the differential equation describing the progress of leaf water potential to equilibrium:

$$d\psi_{leaf}/dt = -k \psi_{leaf} \quad (3)$$

where t = time (sec)

ψ_{leaf} = leaf water potential (cm)

k = proportionality constant (sec^{-1})

Integrating with respect to time:

$$\psi = \psi_0 e^{-kt} \quad (4)$$

where ψ_0 is the leaf water potential at $t = 0$.

The leaf water potential at $t = t_{1/2}$, the half time to reach static equilibrium is

$$\psi_{t_{1/2}} = \psi_{eq} + \psi_0 \quad (5)$$

where $\psi_{eq} = \psi_{leaf}$ at static equilibrium. It is assumed that $\psi_{eq} = \psi_{soil}$ where ψ_{soil} is the bulk soil water potential as measured by a tensiometer or similar instrument.

Substituting equation (5) into equation (4)

$$k = \ln \frac{2\psi_0}{\psi_{soil} + \psi_0} / t_{1/2} \quad (6)$$

and the resistance $R = 1/k$

$$= t_{1/2} / \ln \frac{2\psi_0}{\psi_{soil} + \psi_0}. \quad (7)$$

The procedure, therefore, involved equilibration when the soil was wet in order to estimate R_p and thereafter at intervals as the soil dried out. This is shown schematically in Figure 1. The calculation of R_s , the quantity required, is obtained from determinations of ψ_0 and ψ_{soil} , together with sufficient intermediate points for calculation of a half time.

Boyer's leaf model was not used for estimating resistances; instead, a model in which the path length was implicit in the resistance term was preferred, as in the general expression for steady state flow through the soil-plant continuum, of the form given by Slatyer (1967):

$$q = dV/dt = (\psi_1 - \psi_2) r_{1,2} = (\psi_2 - \psi_3) r_{2,3} = \text{etc.} \quad (8)$$

where q is the flow rate of water, V the volume flow of water across area A in time t , ψ is the water potential, r is the resistance.

Subscripts refer to segments of the continuum. Unfortunately it is not yet possible to use this equation for estimating $r_{1,2}$ where it is equivalent to R_s .

EXPERIMENTAL

Resistances were estimated for 6-week-old plants of the winter wheat variety Mexican growing in a lysimeter of 30 cm diameter and depth 45 cm, in which there was uniform root penetration and a density of the order of 4.0 cm cm^{-3} of soil. The transpiring plants progressively dried the soil from near saturation to near wilting point in an LBH growth cabinet (Morse and Evans, 1962). Equilibration of leaf and soil water potentials was allowed to occur initially after wetting, and then at several stages as drying occurred.

The procedure at each equilibration was to determine ψ_{leaf} , switch off lights in the growth cabinet to minimize transpiration, and subsequently at intervals to determine ψ_{leaf} on leaves withdrawn from the cabinet.

Leaf water potentials were determined by the pressure cell method developed by Scholander *et al.* (1965). This

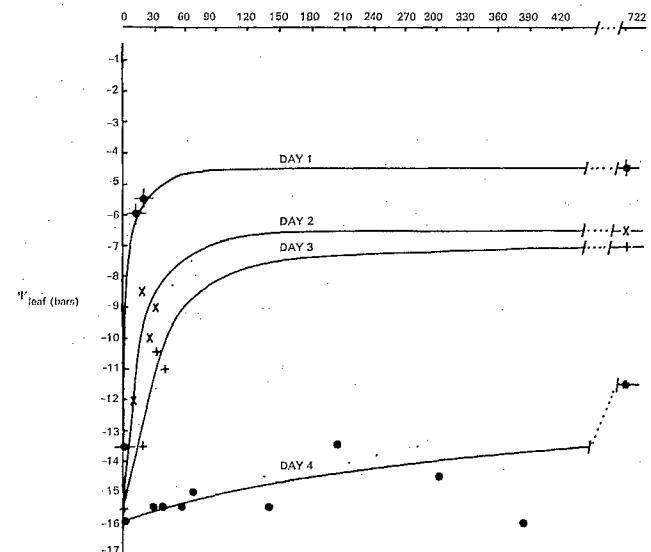


FIG. 2. Leaf water potential (ψ_{leaf}) as a function of time during an equilibration period.

TABLE 1. Plant resistance (R_p) and soil resistance (R_s) as a function of soil water potential (ψ_{soil})

Initial ψ_o (bars)	Equilibrium $\psi_{eq} = \psi_{off}$ (bars)	Half-time for equilibration $t_{1/2}$ (min)	Resistance			Soil hydraulic conductivity k_s (cm sec $^{-1}$)
			Soil-plant R (min)	Plant R_p (min)	Soil R_s (min)	
-13.5	-4.5	3	7.4	7.4	≈ 0	—
-15.0	-6.5	15	45.0	7.4	37.6	1.3×10^{-4}
-15.5	-7.0	30	93.6	7.4	86.2	5.8×10^{-5}
-16.0	-11.5	380	2 507.4	7.4	2 500.0	2.0×10^{-6}

had the advantage over current psychrometer techniques in that it was simple to operate and could be used in the field. Leaf water potentials were corrected for xylem osmotic potential as suggested by Boyer (1967), and these were determined with a vapour pressure osmometer.

Application of the pressure cell for determining leaf water potentials on leaf laminae has not previously been reported. Provided due care was taken, a satisfactory gas-tight seal between the rolled-up wheat leaf and the rubber pressure seal could be obtained, without crushing the xylem elements. Measurements in which there was a suggestion of constriction of the xylem elements were rejected. The fact that samples were obtained from different plants appeared to be the main source of variability.

RESULTS

Figure 2 shows the data for four equilibration periods. Taking into account the variability experienced, the data conformed well enough with the assumption of an exponential change in leaf water potential during the equilibration. The initial and final leaf water potentials, ψ_o and ψ_{eq} , and $t_{1/2}$ provided a means of calculating the soil resistance R_s according to equation (7). These results are shown in Table 1.

On the assumption made previously, that R_p is independent of ψ_{soil} , Table 1 shows the large increase in soil resistance, R_s , as the soil water potential, ψ_{soil} , fell below -6 bars. The relationship between ψ_{soil} and R_s is exponential and for comparatively small decreases in ψ_{soil} below -6 bars, there was a steep increase in R_s . In terms of the theory outlined, this was interpreted as a decrease in soil water availability. The nature of the function $R_s(\psi_{soil})$ is consistent with its dependence on the soil hydraulic conductivity, the order of magnitude of which is also shown in Table 1. R_s is taken to be inversely proportional to the hydraulic conductivity. Thus

$$R_s = B/k_s \quad (9)$$

where B is a geometric factor with dimensions of length (cm). We regard B as an effective path length that is

dependent on root density and the geometry of the soil-root system, and is analogous to A/L used by Gardner (1968). As a first-order approximation, B was taken as half the mean distance separating roots and this could be calculated from root density.

DISCUSSION

The method outlined here for characterizing soil water availability by means of a soil resistance, which is a function of the soil water potential, is consistent with the theory of soil water uptake by plants. Such a method, which does not call for elaborate apparatus and requires only simple procedures, offers encouraging prospects for use in the field. It has most direct application in a situation where roots are uniformly distributed through the soil profile, as was the case in this experimental study. In a stratified soil with a non-uniform root distribution, the soil resistance may be interpreted as an integrated resistance for the profile occupied by roots. Similarly, ψ_{soil} represents the integrated soil water potential (Taylor, 1953).

This availability parameter (R_s) must also be related to the supply function (E_w), an evaporation parameter enunciated by Cowan (1965); but this needs to be investigated.

The parameter R_s combines the effects of the soil hydraulic conductivity and a path length factor arising from the soil-root geometry and root distribution. It will, therefore, vary between soil types because of differences in hydraulic conductivity and/or differences in root distribution. Within a soil type with a stable hydraulic conductivity, variations in the resistance function will arise from variation in root development and distribution. These will depend on cultural treatments such as time of sowing, cultivation, fertilizer application, seasonal conditions such as temperature, excess rainfall leading to waterlogging, and on genotype. The soil resistance function may be useful in assessing the importance of these factors on the occurrence of crop water deficits during critical periods in the crop's development.

Résumé

Méthode pratique pour déterminer l'eau du sol accessible aux cultures (R. H. Sedgley, K. A. Seaton et W. R. Stern)

Une méthode agroclimatologique est présentée pour évaluer la résistance du sol, dont dépend l'accessibilité de l'eau du sol aux cultures sur le terrain. Cette méthode repose sur une mesure de la montée du potentiel hydrique lorsqu'une feuille retrouve, après un état de contrainte, un état d'équilibre entre l'eau du sol et l'eau de la plante. La formule ci-après a été établie:

$$R = t_{1/2}/\log 2\psi_o/\psi_{sol} + \psi_o$$

dans laquelle: R = résistance au transfert d'énergie libre dans le continuum sol-plante; $R = R_p + R_s$, où R_p est la résistance de la plante (à l'exclusion de la résistance stomatale) et R_s est la résistance du sol;

$t_{1/2}$ = la moitié du temps nécessaire pour que se rétablisse le potentiel hydrique de la feuille;

ψ_o = le potentiel hydrique initial de la feuille;

ψ_{sol} = le potentiel hydrique du sol, considéré comme étant égal au potentiel hydrique final de la feuille à l'état d'équilibre.

En sol saturé, R_s est négligeable et $R = R_p$. Quand le sol se dessèche, la valeur de R augmente et la plus grande partie en est attribuée au développement de R_s , qui est considéré comme étant fonction du potentiel hydrique du sol.

Hypothèses supplémentaires: la résistance de la plante n'est pas fonction du potentiel hydrique du sol; les résistances au transfert d'énergie libre sont proportionnelles aux résistances au transfert d'eau: le potentiel hydrique de la feuille se met en équilibre avec l'eau du sol suivant une courbe exponentielle avec le temps.

Les potentiels hydriques des feuilles de Blé ont été calculés par la méthode de la bombe à pression. Les résistances estimatives du sol ont varié de façon exponentielle jusqu'à 2500 minutes (potentiel hydrique du sol de -11,5 bars). Ce comportement est en accord avec la théorie physique qui considère la résistance du sol comme combinant les effets de la conductivité hydraulique du sol et de la géométrie racines-sol.

L'application de la résistance du sol, R_s , comme paramètre d'accessibilité de l'eau du sol est examinée.

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The effect of rainfall on wheat yields in an arid region

J. Lomas and Y. Shashoua
Division of Agricultural Meteorology,
Israel Meteorological Service,
Bet Dagan (Israel)

INTRODUCTION

The cultivation of wheat in arid regions is an economically risky undertaking, mainly because of fluctuating rainfall distribution. Yet wheat remains a relatively drought-resistant crop, although it has a theoretically high water demand per unit of dry matter produced (Peterson, 1965). Wheat is grown in the southern part of Israel, where the mean annual rainfall is approximately 200–250 mm, and it has been suggested by Brown and Cocheme (1969) that a successful crop can be obtained in Kenya on as little as 150 mm. A means of assessing the effect of rainfall on wheat production is of considerable interest to agricultural planners and may permit crop yield "forecasting" in arid regions, while the wheat crop is still in the field.

Fisher (1924) developed a special statistical technique for examining the effect of rainfall on the yield of wheat. The same method of analysis was applied by Gangopadhyaya and Sarker (1965). Kalamakar and Satakapan (1940) examined the influence of rainfall on cotton yield, and Acharya *et al.* (1960) on sugar cane yields. Williams and Robertson (1965) used regression techniques to analyse wheat production in relation to precipitation and, more recently, Williams (1969) extended this study by including potential evapotranspiration in the multiple regression. This study is an attempt to establish rainfall-crop yield relationships of wheat for an arid region.

METHODS

During the three growing seasons of 1965/66 to 1967/68, 28 wheat yield samples of the Florence variety were taken from 12 communal settlements. The settlements were situated in the north-western part of the arid Negev in the vicinity of Beer Sheva (latitude 13° 14' N,

longitude 34° 47' E, 270 m elevation). The sampling method consisted of taking 8 random replicates of 1 m² of wheat in the field, cutting the crop and threshing the wheat at the Hazerah seed company. The wheat yield was subsequently weighed and the weight of 1,000 grains established. Standard meteorological rain gauges from which rainfall data were obtained, were available at or near each sampling plot. Data for 18 years of wheat yields were also obtained from the communal settlement of Mishmar Hanegev (latitude 31° 22' N, longitude 34° 43' E, 200 m elevation), where a standard meteorological station was maintained. The data obtained gave the average yield of marketed wheat including all wheat varieties during a given year. Fisher's (1924) method was used for the analysis of the data.

Assuming a linear relationship between wheat yields and rainfall distribution, the following equation can be written:

$$Y = C + \sum_{i=1}^n a_i r_i \quad (1)$$

where Y = yield of wheat in kg/1,000 m²

C = a constant

$a_1 a_2 \dots a_n$ = the regression coefficients

$r_1 r_2 \dots r_n$ = quantity of rainfall in mm per 2 weeks.

The above equation can also be rewritten in the following way:

$$Y = C + a' \bar{r} + \sum_{i=1}^n \beta_i r_i = \beta_i r_i \quad (2)$$

where $\sum_{i=1}^n \beta_i = 0$ and $\bar{r} = \sum r_i/n$ is the average rainfall in mm per 2-week period.

The effect of rainfall distribution is given by the β_i coefficients while the effect of the annual amount of

rainfall is given by the a' coefficient. Thus a wheat-rainfall response curve can be obtained throughout the growing season of the crop. The rainfall distribution for periods of 2 weeks at each sampling place is expressed by an orthogonal polynomial of the fifth degree

$$r_{ij} = \bar{r}_j + \rho_{1j} T_{i1} + \dots + \rho_{5j} T_{i5} \quad (3)$$

where r_{ij}

= the quantity of rainfall during period i at sampling place j ;

\bar{r}_j = the mean quantity of rainfall for periods of 2 weeks during the season, at sampling place j ;

ρ = the coefficients of the regression

T'_{is} = the orthogonal polynomials function of time with the following two properties:

$$\sum_{i=1}^n T_{ir} T_{is} = 0$$

$$\sum_{i=1}^n T_{ir}^2 = \lambda_r \text{ and } \sum_{i=1}^n T_{ir} = 0.$$

The \bar{r}_j the ρ_j coefficients are denoted as the rainfall constants.

The series of the rainfall constants are then correlated with the corresponding yields of wheat.

$$Y = C + a'\bar{r} + \alpha_1\rho_1 + \alpha_2\rho_2 + \dots + \alpha_5\rho_5. \quad (4)$$

Finally the coefficient of the response curves is obtained by

$$\beta_i = \frac{\alpha_1 T_{i1}}{\lambda_1} + \frac{\alpha_2 T_{i2}}{\lambda_2} + \dots + \frac{\alpha_5 T_{i5}}{\lambda_5}. \quad (5)$$

During the 3-year sampling period, agrotechnical methods were uniformly applied throughout the area. This was certainly not the case for the 18-year growing period at the agricultural settlement, Mishmar Hanegev. During that time wheat varieties changed, rotations were improved, fertilizer treatments increased, weeds were controlled and the crop mechanized. All improvements contributed to an increase in wheat yields irrespective of rainfall. In the statistical analysis it was, therefore, necessary to account for agrotechnical progress.

Assuming, therefore, that agrotechnical progress is proportional to time and total annual rainfall, the following equation was used in the analysis of the data:

$$Y = C + a'\bar{r} + \alpha_1\rho_1 + \dots + \alpha_5\rho_5 + btX + b'(tX)^2 \quad (6)$$

where Y = is the yield in kg/1,000 m²

C, a' = constants

\bar{r} = the average rainfall in mm per 2-week period; ρ_1, \dots, ρ_5 = rainfall constants; $\alpha_1, \dots, \alpha_5$ = regression constants of yield on rainfall constants

t = time variable taking the value 1 for the first year, value 2 for second year, etc.

X = total rainfall

b, b' = regression constants of agrotechnical progress.

The statistical analysis was carried out as previously outlined. Data on wheat yields were extracted from the records of the communal settlement which provided values for the average yield from approximately 120 hectares of wheat grown annually. The rainfall season commenced in October and ceased during April, including 15 rainfall periods. The wheat crop was planted during the month of November/December and harvested during the month of May. Thus the 15 rainfall periods commenced 1 month, or so, before planting. The 2-weekly rainfall periods are presented in numerical order as follows: 1–14 October = rainfall period 1; 15–28 October = rainfall period 2; 29 October–11 November = rainfall period 3; 12–25 November = rainfall period 4; 26 November–9 December = rainfall period 5; 10–23 December = rainfall period 6; 24 December–6 January = rainfall period 7; 7–20 January = rainfall period 8; 21 January–3 February = rainfall period 9; 4–17 February = rainfall period 10; 18 February–2 March = rainfall period 11; 3–16 March = rainfall period 12; 17–30 March = rainfall period 13; 1–14 April = rainfall period 14; 15–27 April = rainfall period 15.

RESULTS

During the 3-year sampling period, rainfall varied considerably in the northern Negev. During the first year the total annual rainfall at Beer Sheva reached 249 mm, indicating a relatively rainy winter season. The second year's total rainfall averaged 220 mm, while during the last year near-drought conditions prevailed with only 163 mm measured. The actual rainfall at the 28 sampling places during the same period varied to a much greater extent, ranging from 141 mm during 1968/69 to 487 mm during 1967/68. Thus, a relatively wide range of annual rainfall was included in the sample. The same can be said of wheat yields which ranged from 47 kg/1,000 m² during 1968/69 to 361 kg/1,000 m² during 1967/68.

The rainfall data for the regional station at Beer Sheva during the sampling period and the mean rainfall and its coefficient of variation for the 18-year period at Mishmar Hanegev are given in Table 1.

From Table 1, it can be seen that variable rainfall conditions occurred during the sampling period.

A summary of the wheat yields harvested at the sampling plots and at Mishmar Hanegev is presented in Table 2.

Simple linear regressions between the total annual rainfall and the yield of wheat gave fairly good results ($r = 0.721$ significant at 1 per cent level, standard error of estimate 65 kg/1,000 m²). Multiple correlations improved the results slightly, although not significantly so. During analysis, it was found that the matrix of the rainfall constants was near singularity due to the high intercorrelation between the variables of the distribution constants. The following eigenvalues of the matrix were

TABLE 1. Rainfall (mm) at the regional station Beer Sheva (1966/67-68/69) and at Mishmar Hanegev (1948/49-67/68)

Station		Periods													Total	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Beer Sheva																
1966/67	11.5	0.0	34.2	0.0	6.7	50.9	0.5	15.5	39.6	11.0	13.9	17.6	38.3	0.4	0.2	240.3
1967/68	5.6	0.0	0.4	37.2	13.5	11.7	10.7	39.8	60.5	6.3	2.9	0.0	6.9	0.0	25.0	230.5
1968/69	0.0	1.2	7.3	3.7	47.2	1.2	6.3	9.3	30.0	1.6	0.0	2.4	38.1	9.0	5.2	162.5
Mishmar Hanegev (1948/49-67/68)	2.3	2.8	6.3	16.1	23.1	32.5	17.0	39.7	27.5	21.3	30.7	15.9	19.2	7.2	4.2	266
Coefficient of variation	235	257	156	144	178	117	99	142	72	86	88	155	109	156	205	39

TABLE 2. Mean wheat yields (kg/1,000 m²), their standard deviation and coefficient of variation at the sampled plots and at Mishmar Hanegev

Item	Sampled plots			Mishmar Hanegev
	1966/67	1967/68	1968/69	1948/49-67/68
Mean yield (kg/1,000 m ²)	202.4	200.8	155.0	120.1
Standard deviation	84.9	100.5	72.5	79.2
Coefficient of variation	42	50	47	66
	5	12	11	18

obtained: $U_1 = 2.7$; $U_2 = 1.5$; $U_3 = 1.2$; $U_4 = 0.4$; $U_5 = 0.1$; $U_6 = 0.1$.

The largest correlation coefficient between the variable \bar{r} and ρ_2 was -0.826 and that between ρ_2 and ρ_3 was -0.602 ; ρ_2 and ρ_3 were, therefore, discarded. The following multiple regression was obtained:

$$Y = 25.5 + 5.934\bar{r} - 37.46\rho_1 + 1725\rho_4 - 5476\rho_5 \quad (7)$$

$$r = 0.783$$

standard error of estimate = 62 kg/1,000 m².

The inclusion of ρ_2 and ρ_3 gave a slightly better correlation coefficient ($r = 0.805$), but a higher standard error. The average effect of 1 mm rainfall during the growing period on wheat yields was an increase of 0.393 kg/1,000 m², not taking into account the effect of rainfall distribution.

The a_i coefficients and the β_i coefficients are given in Table 3. Using the β_i coefficients, a response curve was drawn (Fig. 1(a)) showing the expected average effect on yield (kg/1,000 m²) due to an additional 1 mm of rain above the mean values at any point of time. From this figure it can be seen that, assuming a constant average rainfall, additional rainfall prior to sowing and during the period of germination and initial growth is

TABLE 3. The a_i coefficients (equation 1) and the β_i coefficients (equation 5) of the response curve. (Sampled plots.)

Rainfall period	a_i	β_i	Average rainfall (mm)
1	2.118	1.722	7.1
2	0.491	0.096	2.7
3	0.325	-0.070	6.1
4	0.720	0.324	49.8
5	1.119	0.724	39.6
6	1.248	0.853	27.4
7	1.045	0.649	12.7
8	0.597	0.202	47.4
9	0.078	-0.318	56.6
10	-0.323	-0.719	8.3
11	-0.461	-0.857	9.8
12	-0.305	-0.700	4.8
13	0.002	-0.394	28.6
14	0.071	-0.325	8.4
15	-0.792	-1.188	16.4

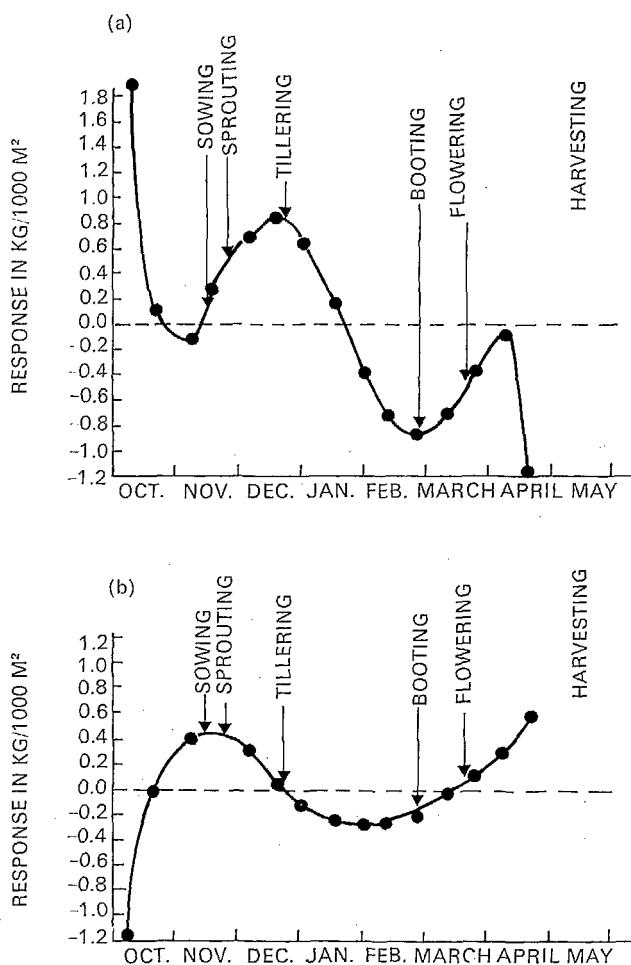


FIG. 1. The response curves at (a) 28 sampling plots (1966/67-68/69) and (b) at Mishmar Hanegev (1948/49-67/68).

beneficial to the crop. Additional rainfall above the average during mid-winter (end of January and February) at the end of the growing season (March and April) affects the crop adversely.

This sampling method had the advantage of uniform agrotechnical practices and sampling techniques. All the sample sites were in a relatively small geographical area and the wheat crop was, therefore, exposed to near identical synoptic situations. Keeping those considerations in mind, data were also analysed for Mishmar Hanegev, for which a long period of rainfall and wheat data were available. Such data were very useful in so far as they showed no apparent correlation between the rainfall of any one particular year and another. During the years sampled rainfall varied considerably, as can be expected in an arid region. The lowest annual rainfall recorded was 80.8 mm (1959/60), while in the雨iest year (1964/65), 490.3 mm were measured. It seems, therefore, that a fair range of rainfall conditions was experienced.

The yield of wheat ranged from 18 kg/1,000 m² during the lowest rainfall year (1959/60) and up to 255 kg/1,000 m² during the rainiest year (1964/65), also indicating an extreme range in crop yields. Linear regression between the total annual rainfall and the yield of wheat gave good results ($r = 0.815$, significant at the 1 per cent level). Multiple correlation techniques adjusted for agrotechnical progress improved these results ($r = 0.888$, significant at the 1 per cent level), but not significantly so. Agrotechnical progress was accounted for by bTX and $b'(tX)^2$ as part of the whole equation (6). The results of the analysis showed that no significant difference was obtained by the inclusion of the term $b'(tX)^2$ and this term was, therefore, omitted from the equation. During the analysis it was found that the matrices of the rainfall constants were singular, yielding: $U_1 = 3.70$; $U_2 = 1.30$; $U_3 = 0.80$; $U_4 = 0.60$; $U_5 = 0.40$; $U_6 = 0.20$; $U_7 = 0.0$.

The largest correlation coefficient between the variable \bar{r} , and ρ_2 was -0.811 and ρ_2 was, therefore, discarded. The following multiple regression was obtained.

$$Y = -13.1 + 5.619\bar{r} + 8.350\rho_1 + 249.3\rho_3 - 1928\rho_4 + 954.0\rho_5 + 0.01297t X \quad (8)$$

$$r = 0.888$$

standard error of estimate = 46 kg/1,000 m².

The average effect of 1 mm of rainfall during the period was an increase in the yield of 0.373 kg/1,000 m², not taking into account the effect of rainfall distribution.

The inclusion of ρ_2 , the discarded variable, gave a slightly better coefficient ($r = 0.895$), but higher standard errors for the coefficients. The a_i coefficients and the β_i coefficients are given in Table 5.

Using the β_i coefficient, a response curve was drawn (Fig. 1(b)) showing the expected average effect on yield (kg/1,000 m²) due to an additional 1 mm of rain above the

TABLE 4. The a_i coefficients (equation 1) and β_i coefficients (equation 5) of the response curve. (Mishmar Hanegev.)

Rainfall period	a_i	β_i	Average rainfall (mm)
1	-0.793	-1.167	2.3
2	0.345	-0.030	2.8
3	0.792	0.417	6.3
4	0.883	0.458	16.1
5	0.674	0.299	23.1
6	0.457	0.083	32.5
7	0.268	-0.106	17.1
8	0.149	-0.225	39.7
9	0.111	-0.264	27.5
10	0.142	-0.232	21.3
11	0.224	-0.151	30.7
12	0.336	-0.038	15.9
13	0.475	0.101	19.2
14	0.660	0.285	7.2
15	0.945	0.571	4.2

mean values at any point of time. From this figure it can be seen that, assuming a constant average rainfall, additional rainfall during the first part of the growing season is of considerable importance whilst, during the second part of the growing season and especially during the months of January and February it affects the yield adversely. On the other hand, at the beginning of the rainfall season, additional rainfall seems detrimental to yields. At the end of the growing season the response curve shows considerable increases in yield for additional rainfall. It should be remembered, however, that the actual amounts of rainfall at the extremes of the rainfall season are rather small.

Annual rainfall does not seem to affect wheat quality, as expressed by the weight of 1,000 grains, to any great extent. During the sampling period the mean weight of 1,000 grains was 41.0 g and the coefficient of variation only 14 per cent. The correlation between annual rainfall and grain weight was very low ($r = 0.139$).

DISCUSSION

The area investigated lies in the north-western part of the arid Negev with an average annual rainfall of 204 mm. The fluctuations in rainfall are, however, considerable and during the period of investigation nearly twice that amount (490 mm) was recorded in 1964/65 and less than half that amount (81 mm) in 1959/60.

The coefficient of variation of the total annual rainfall was 39 per cent, but for 2-weekly periods it ranged from 72–257 per cent. (see Table 1). This was most noticeable at the beginning and the end of the rainy season. In the arid region, with a potential evaporation demand of 6.6 mm/day during October (USWB class A' pan mean values for 5 years) and 8.0 mm/day during April, rainfall during those months is seldom likely to be effective.

Rainfall during the rest of the wheat-growing season seems more certain, although the actual amounts are relatively small.

This is a low rainfall area for the growing of wheat, but it seems that, given average and well-distributed rainfall, a successful crop can be grown. Staple and Lehane (1954) showed that, under Canadian conditions, a wheat crop could be obtained with a total evapotranspiration of —141 mm, which may "require" an annual rainfall of 200–250 mm. In Australia, wheat is extensively grown in areas with an annual rainfall of 250–375 mm (Watt, 1948), while in the United States of America an annual rainfall of 425–625 mm is adequate to produce good crop yields if rainfall is skilfully conserved (Finnell, 1948).

Under such low rainfall conditions, it seems that every additional amount of rainfall may be of critical importance. It is for this reason that good correlations can

be obtained between annual rainfall and wheat yields in arid regions. In the Southern High Plains of Texas, variations in rainfall during the growing season (October–June) accounted for 55–66 per cent of the variability of wheat yields (Army, 1959). This was also the case in Israel, where rainfall accounted for some 77 per cent of the variance in yields (Lomas, 1968). In Canada, on the other hand, best results were obtained when rainfall during June–July was correlated with wheat yields; 51 per cent of the variation in yield could be accounted for by the variation in rainfall, while pre-season rainfall could account for only some 22 per cent (Sallans, 1948). This may be due to the fact that other limiting factors were also involved, such as temperature, disease or insect damage (Sallans, 1948). In northern Negev, total annual rainfall could be used to explain 52–66 per cent of yield variance. These results may suggest that, in low-rainfall areas where wheat is grown on freely draining soil, fairly good results can be obtained by correlating wheat yields with annual rainfall and that this relationship is linear (Fig. 2).

In spite of the relatively wide fluctuations in annual rainfall, which ranged from 140 mm to 480 mm during the sampling period, the weight of 1,000 grains seems independent of rainfall. Apparently, under drought conditions, grain number per ear and the number of ears per plant are mainly affected (Asana, 1958). Under some conditions of drought, during the first 4 weeks after dehiscence, the yellowing of the leaves and stems was hastened, the rate of increase of grain weight was unaffected, the grain number was reduced and the 1,000 grain weight increased (Asana and Mari, 1958). Thus a reduction in rainfall may result in a smaller number of fruit-bearing plants and also a reduction in the size of the wheat heads. Apparently it does not affect the weight of wheat grains, but only their number.

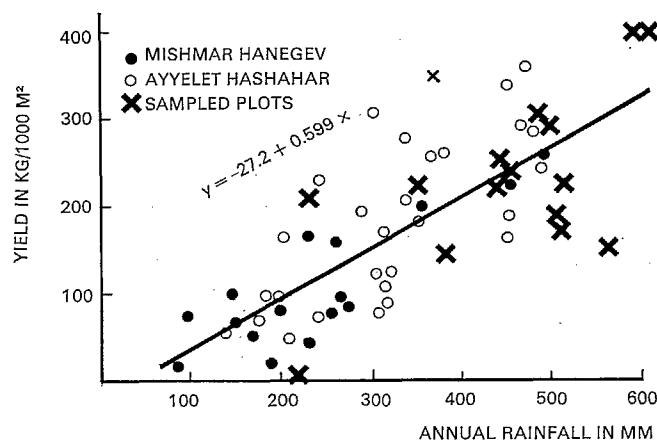


FIG. 2. Relationship between annual rainfall and the yield of wheat in a semi-arid region. $r = 0.154$, significant at the 1 per cent level; $r = 60$; standard error estimate = 66 kg/1,000 m².

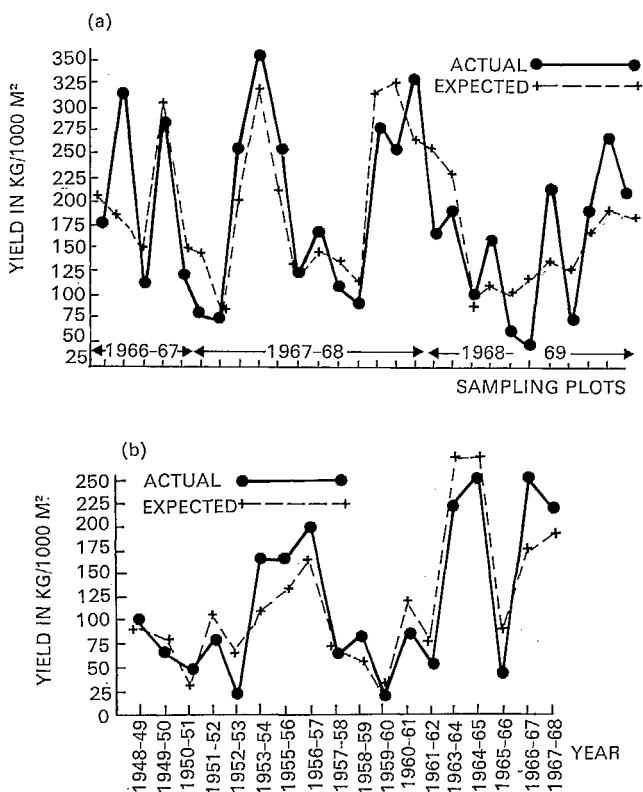


FIG. 3. Actual and calculated yields at (a) 28 sampling plots (1966/67-68/69) and (b) at Mishmar Hanegev (1948/49-67/68).

The effect of rainfall distribution was first investigated by Fisher (1924). In the Broadbalk wheat experiment, total rainfall and its distribution accounted for only 40 per cent of the variation of wheat yields on some of the plots. In a much later analysis by Buck (1961) using the same data, the total amount of rain and its distribution accounted for 12–33 per cent of the variance in yield, depending on the plot. The rainfall effects are mainly attributable to the total amount of rain falling in the year, irrespective of its distribution. Using the same method, Gangopadhyaya and Sarker (1965) could account for 75 per cent of the total variation in yield and our own results show that in northern Negev annual rainfall and its distribution can account for 61–79 per cent of wheat yield variance. It seems, therefore, that this method of analysis considerably improves the relationship between rainfall and the yield of wheat under arid conditions. A comparison between actual yields and expected (calculated) yields is presented in Figure 3. The rainfall distribution curves obtained show fairly general agreement except at the ends of the rainfall season.

Additional rainfall prior to sowing (mean sowing date 10–20 November) seems advantageous at the sampled plots (Fig. 1(a)), but detrimental at Mishmar Hanegev

(Fig. 1(b)). Rainfall early in the season is generally assumed to be beneficial, enabling field operations to be carried out easily and contributing to the preparation of a uniformly textured and weed-free seed bed. On the other hand, it may also be that above-average rainfall during the month of October may be associated with below-average rainfall in the subsequent months of November, December and January (Krown, 1966) and thus affect the yield of wheat in a negative way. Thus, in the final analysis, the effect of pre-sowing rainfall on wheat yields will mainly depend on the rainfall amounts and their distribution from the time the crop has been planted (10–20 November) to the tillering stage (25 December) when rainfall variability is 113–178 per cent (see Table 1). Rainfall above the average during this period has most beneficial effects. This can easily be understood when considering that, although in the early stages of growth (2–4 weeks) the actual rate of water consumption is small (Venkataraman, 1956), the shallowness of the root system makes the wheat crop most dependent on rainfall.

During this first month of growth, 75 per cent of the water absorbed by the crop comes from the 0–30 cm soil layer (Chavez and Laird, 1959). During the months of January and February the wheat crop makes hardly any growth, while rainfall is at a maximum and coefficients of variation are at a minimum 72–142 per cent (see Table 1). Thus additional rainfall during this period is of no importance, and may even be harmful to crop yield.

Similar effects were also observed in the dry climate of the Toulouse region, where increase in winter rainfall depressed yields considerably (Malterre and Fioramonti, 1957). Excessive rainfall during a period when the wheat crop makes little or no growth may deplete soil nitrogen without adding to the soil moisture reserves. As growth commences in the spring months and the booting stage is reached (25–28 February), soil moisture seems adequate, but by the time the wheat crop flowers (15–20 March), when evapotranspiration may be at its maximum (Muzick *et al.*, 1963), additional rainfall above the mean values seems to be advantageous once again.

Under Mediterranean-climate conditions, therefore, it seems that the most critical rainfall period is from the date of sowing to tillering. An addition of say 50 mm of irrigation will, on average, increase wheat yields by some 40–60 kg/1,000 m² (see Table 5), making the growing of wheat in this arid region very much less risky and considerably increasing the usefulness of natural rainfall.

Irrigation experiments carried out in this area (Shimshi, in: Yaron *et al.*, 1969) confirm the results obtained from the statistical analysis, that early irrigation is usually the most efficient, resulting in the highest marginal response in yield. Shimshi (in: Yaron *et al.*, 1969) points out that, even in rainy years, irrigation timed at this stage will increase yield by 0.4 kg/1,000 m²/mm, but during dry years the response will be 2.4–2.5 kg/

1,000 m²/mm. This would increase yields by 20–125 kg/1,000 m² for an irrigation application of 50 mm. These figures agree extremely well with the mean increase of 40–60 kg/1,000 m² for an additional irrigation of 50 mm, as calculated from our own response curve.

Since, at the present prices of wheat and water, the

"break-even" point seems to be 0.3 kg/1,000 m²/mm, and the mean response to 50 mm of additional irrigation is 0.8–1.2 kg/1,000 m²/mm, it seems that additional irrigation during the early stages of wheat growth in the arid northern Negev is an economic proposition.

Résumé

Effet des précipitations sur les rendements du Blé dans une région aride (J. Lomas et Y. Shashoua)

Le rapport entre les précipitations annuelles et les rendements d'un Blé non irrigué dans une région aride (200 mm environ) semble linéaire. Des corrélations simples expliquent de 52 % à 66 % environ de la variation totale du rendement. Le poids du grain récolté ne semble pas influencé par la hauteur de pluie annuelle.

La technique de Fisher explique, compte tenu de la répartition des pluies, 61 % à 79 % de la variation totale du rendement. Les courbes de réaction à la répartition des pluies indiquent que, dans les conditions climatiques locales, une hauteur de pluie supplémentaire pendant la première partie de la saison de croissance serait très avantageuse et augmenterait les rendements du Blé. Le Blé devrait, si possible, être irrigué pendant cette partie de la saison de croissance; une irrigation équivalant à une tranche d'eau de 50 mm pourrait, en moyenne, accroître les rendements de 40 à 60 kg par 1 000 m².

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Measured and modelled effects of microclimate modification on evapotranspiration by irrigated crops in a region of strong sensible heat advection

N. J. Rosenberg and K. W. Brown
University of Nebraska, Lincoln, Nebraska
(United States of America)

The Great Plains extend from about the 95th meridian to the foothills of the Rocky Mountains and from northern Texas to the Canadian Prairie Provinces. This vast region of even topography is one of the most important for food and fibre production in North America. The region is open to incursions of maritime-tropical and continental-polar air masses. Maritime-polar air masses, greatly modified by passage over the western mountain ranges, also dominate the more westerly portion of the plains region at times. Continental-tropical air masses are also experienced, particularly during spring and early summer.

Most of the annual precipitation occurs during the growing season when extended periods of high temperature may also be experienced, often in combination with strong winds and low humidity.

The Great Plains is, then, a region in which the variety, variability and intensity of weather events makes the study of plant response to climatic factors particularly important in developing the technologies needed for stability and maximization of crop production.

The state of Nebraska is centrally located in the Great Plains. Because of its immense and accessible underground water resource, estimated as sufficient to cover the entire state with more than 10 m of water, irrigation developments are proceeding rapidly. Nebraska is now the third largest state in irrigated acreage in the nation, with prospects of unimpeded growth for some decades ahead. This rapid growth in irrigation and the opportunities it affords to overcome climatically imposed stresses on crop production motivated development of research programmes in agricultural meteorology in the early 1960s. The primary objectives of the programme are these:

To characterize the climate of the state with respect to normal and extreme climatic conditions related to crop production.

To increase water use efficiency (crop produced/unit of water consumed) by providing techniques for microclimatic amelioration.

To determine the quantities of water required to produce good quality crops under irrigation and to develop means to predict this demand.

AN ADVECTIVE CLIMATE

The main research location is an installation for study of evapotranspiration and water use efficiency established in 1966 in eastern Nebraska at Mead (latitude 41° 09' N., longitude 96° 30' W., elevation 347 m). The field is in an area of level to undulating terrain with good fetch.

Other studies, cited below, on the effects of wind-breaks on growth of irrigated crops have been conducted at Scottsbluff, in the irrigated North Platte Valley of western Nebraska (latitude 40° 47' N., longitude 103° 41' W., elevation 1,225 m).

Tanner and Lemon (1962) have suggested that evapotranspiration in humid regions does not normally exceed the energy available as net radiation. In more arid regions, Fritsch and Bavel (1963) have shown that evapotranspiration may exceed the net radiation considerably when advection of sensible heat occurs. Irrigated "oases" in arid regions are subject to the influence of locally generated sensible heat advection. An evaluation of the magnitude of both local and large-scale advective sources of sensible heat advection in our region, which is neither humid nor arid, was the first task.

Figure 1 relates total daily evaporation from bare soil or evapotranspiration from a broadcast crop (alfalfa) or row crop (soybeans), measured lysimetrically at Mead, to the net radiation balance on the same days. Most data points show ratios greater than unity, indicating that

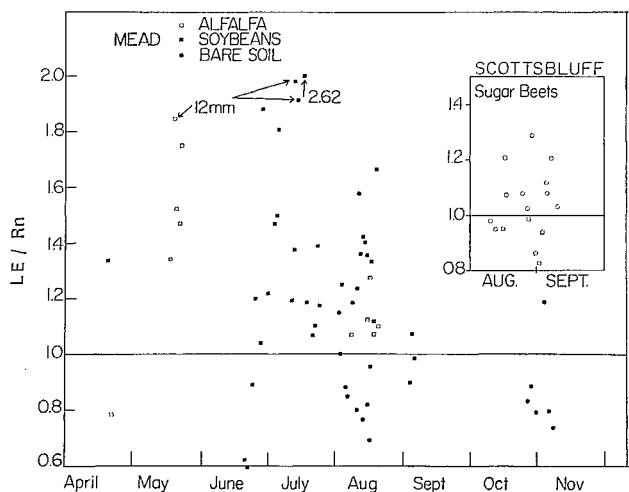


FIG. 1. Daily values of latent heat flux/net radiation (LE/R_n), measured lysimetrically at Mead, and by Energy Balance-Bowen Ratio at Scottsbluff, Nebraska. Bare soil and sugar beets, 1966; alfalfa, 1967; soybeans, 1969.

sensible heat advection supplies significant amounts of energy to drive the evaporative process. Points falling below the line are related to unusual plant stress (e.g., on 22 April—refers to alfalfa after a night of frost), immature plants not fully covering dry soil (20–21 June—soybeans) or to dry surface and depleted water supply in bare soil. Certain items of the data are indicative of local advection and others of regional advective effects (Rosenberg, 1969a, 1969b). It should be noted that days on which extreme water use occurs (~ 12 mm) are often, but not always, those in which the advective contribution of energy is proportionally greatest.

Data based on Energy Balance-Bowen Ratio estimates of water use in a sugar beet field at Scottsbluff, Nebraska (Fig. 1) show both the frequency and relative contribution of energy by advection in late summer (Brown, 1969).

A MODEL OF WATER USE

We wished to evaluate the range and extent of plant water use in a region where soil water supply is variable, where a wide range of crops is grown, where ambient conditions vary greatly in time and space and where advective sources of sensible heat are significant in the total energy balance on the field and regional scale. To do this by detailed field plot research only did not appear feasible. Some means of extrapolating findings from the experimental fields was required. A model which considers plant as well as climatic variables was derived to predict latent heat flux (LE) from field crops and the influence of various treatments and techniques

of microclimatic amelioration on LE . The model will be recognized as a variant of those proposed previously by Gates (1968), Linacre (1964), Monteith (1965), Raschke (1960) and others for single leaves. If a field crop behaves similarly, it may be characterized by the energy balance by substituting values of air resistance and crop resistance for the air and stomatal resistance of an individual leaf. The derivation will not be repeated here.

The "resistance model" (complete list of symbols given in Appendix)

$$LE = \frac{\left[f \left(\frac{(R_n - LE) r_a}{C_p \rho} + T_a \right) - e_a \right] \frac{Mw/Ma}{P} L_\rho}{r_a + r_c}$$

provides an estimate of evaporative flux from leaf surfaces if the net radiation (R_n), air temperature (T_a) and vapour pressure (e_a), and air (r_a) and crop resistances (r_c) are known. An iterative procedure was developed to solve the equation, starting with a first estimate provided by:

$$LE = \frac{Mw/Ma [L_\rho [\Delta (T_l - T_a) + \delta]]}{P (r_a + r_c)}.$$

The iteration continues until succeeding calculations of LE agree to within 1 per cent. Figures 2–4 show LE as

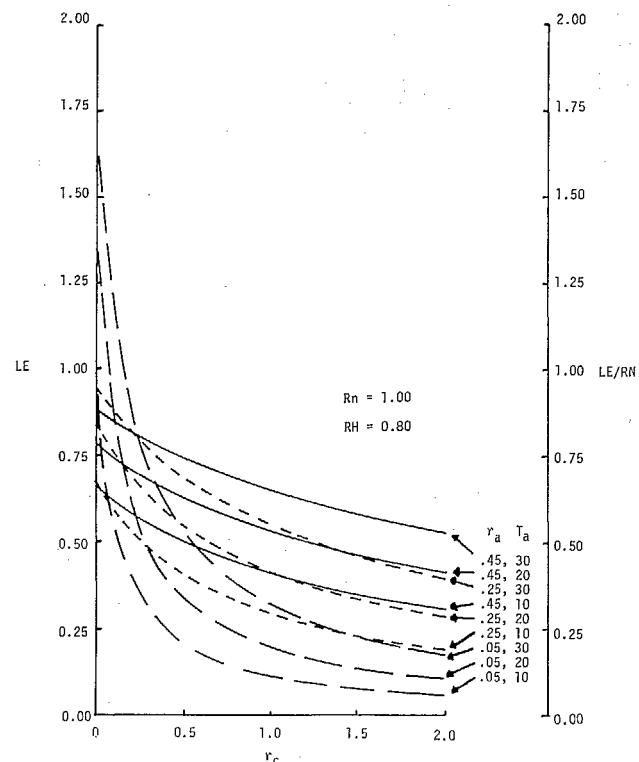


FIG. 2. LE ($\text{cal cm}^{-2} \text{min}^{-1}$) as a function of fixed R_n ($\text{cal cm}^{-2} \text{min}^{-1}$) and relative humidity (RH) over a range of crop canopy resistance, r_c (sec cm^{-1}), air resistance, r_a (sec cm^{-1}) and air temperature, T_a ($^{\circ}\text{C}$).

a function of r_c , T_a , and r_a as the model for fixed conditions of R_n and e_a .

Air temperature and humidity are measurable in the field.

Such data, for preparation of "climatological" estimates of LE with the model, can be obtained from records maintained by many national weather services at first order stations. Net radiation, too, is measurable in the field or may be estimated using climatological records of solar radiation as Linacre (1968), Stanhill *et al.* (1966) and others have proposed.

There is a growing physiological and agrometeorological literature giving data on r_s . Gaastra (1959) presented information for a number of crops under controlled conditions. Milthorpe and Penman (1967) have developed computational methods and Bavel *et al.* (1965), Kanamasu *et al.* (1969) and Waggoner (1965) have developed instrumental methods of estimating stomatal resistance. Brown and Rosenberg (1970a) and Hales (1970) have given data on sugar beet and alfalfa stomatal resistance under field conditions. Although more data, particularly on the diurnal activity of stomata, are needed, those available may be combined with leaf area index (LAI) to calculate crop resistance. Monteith (1965) also summarizes values of r_c for various crops.

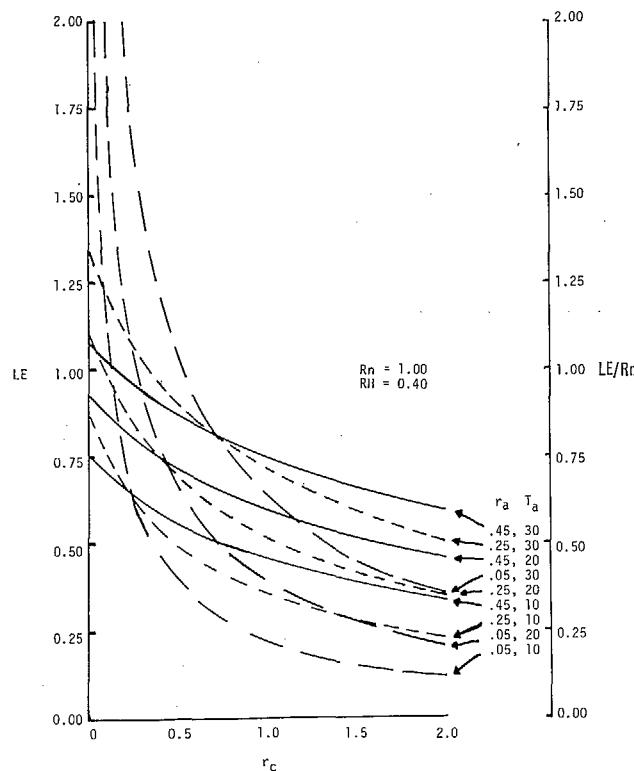


FIG. 3. LE ($\text{cal cm}^{-2} \text{min}^{-1}$) as a function of fixed R_n ($\text{cal cm}^{-2} \text{min}^{-1}$) and relative humidity (RH) over a range of crop canopy resistance, r_c (sec min^{-1}), air resistance, r_a (sec cm^{-1}) and air temperature, T_a ($^{\circ}\text{C}$).

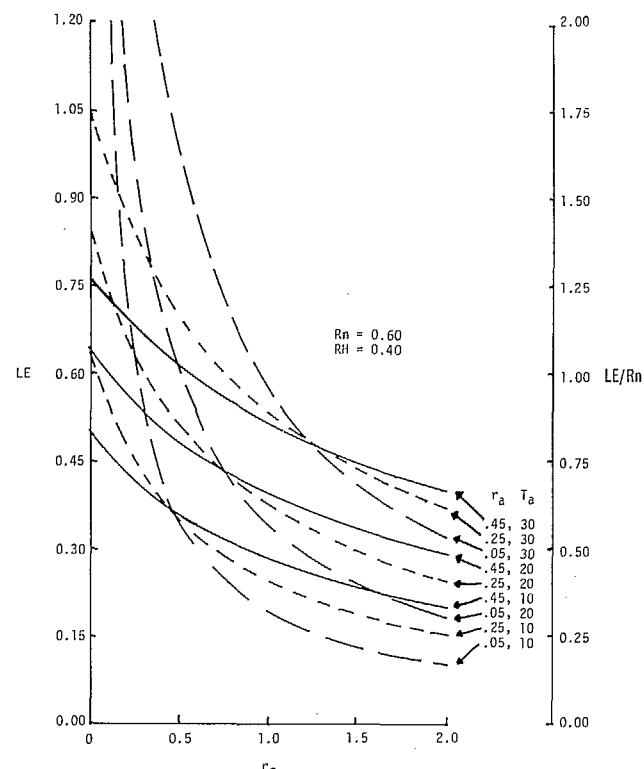


FIG. 4. LE ($\text{cal cm}^{-2} \text{min}^{-1}$) as a function of fixed R_n ($\text{cal cm}^{-2} \text{min}^{-1}$) and relative humidity (RH) over a range of crop canopy resistance, r_c (sec min^{-1}), air resistance, r_a (sec cm^{-1}) and air temperature, T_a ($^{\circ}\text{C}$).

r_a can be computed from aerodynamic parameters as Monteith (1963, 1965) has done. Alternatively, it can be calculated if surface temperature and sensible heat flux are determined. An increasing literature of detailed field experimentation may make generalized estimates of r_a as a function of wind speed and crop structural characteristics possible.

Leaf systems are complex. To make use of such a model as is shown here requires detailed knowledge of r_c and r_a as variable functions of the plant's physiology and geometry as well as of the externally imposed stresses and treatments. Limitations inherent in use of the model are discussed in detail by Brown (1969). Thus far it has been used to evaluate the effects of various microclimate or plant-surface modifications on LE with interesting results, detailed below.

EFFECTS ON EVAPOTRANSPIRATION INDICATED BY MODEL

GENERAL

Figures 2-4 show that LE is inversely proportional to r_c in all circumstances. The dependence of LE on r_c is

greatest when r_a , e_a (in terms of relative humidity, RH) and R_n are low. The relationship between LE and r_s is less sensitive to air temperature than to the other microclimate parameters. Together, these figures suggest that stomatal control of LE is greatest under cloudy conditions, or the low radiation intensity of early morning and late afternoon, or when the leaf is shaded rather than in sunlight. Increasing windspeed (decreasing r_a) results in a greater stomatal control of evapotranspiration. With r_c set to zero, the figures predict free-water evaporation under the specified conditions.

WINDBREAKS

Table 1 illustrates the changes in evapotranspiration rate predicted by the resistance model, considering changes in microclimate and plant response which have been measured in shelter in a number of Nebraska studies. Changes observed consistently in dry bean (Rosenberg, 1966a), snap bean (Rosenberg *et al.*, 1967) and sugar beet crops (Brown and Rosenberg, 1970; Rosenberg, 1966b) sheltered with snow fence or with tall growing corn, include increased daytime air temperature, increased day and night vapour pressure, reduced windspeed and increased r_a , wider stomatal aperture (and therefore reduced r_s and r_c) and more turgid leaves. No important influence on net radiation has been observed.

Part A of Table 1 illustrates how these changes affect LE at a fixed net radiation of 1 cal $\text{cm}^{-2} \text{min}^{-1}$

when applied one at a time. The most profound effects are predicted when temperature and humidity are increased. When all observed changes are used in the model, a negligible effect on water use is predicted. This is, in fact, what we have found in the studies of shelter effect cited above and in Brown and Rosenberg (1971).

Part B of Table 1 predicts the effect of shelter on evapotranspiration under varying types of weather situations. The greatest water-saving effects occur in shelter under conditions of sensible heat advection ($LE/R_n > 1$). The effect of a shelter on the water economy is also significant in cloudy weather. The effect of increased windspeed is not great, except when r_c is very small. The predictions are consistent with observation (Brown and Rosenberg, 1971).

A further test of the resistance model is shown in Figures 5(a) and 5(b). Data represent conditions over irrigated and sheltered sugar beets. Hourly net radiation is shown on the two days represented. Estimates of LE were made with the resistance model and by means of the Energy Balance-Bowen Ratio method (Fritsch, 1965). Agreement between data points is good on the non-advection day (11 August) and also under conditions of sensible heat advection after about 12.00 h on 15 August.

ANTITRANSPIRANTS

Antitranspirants have been suggested as a potentially useful means of modifying water use by plants (Gale

TABLE 1. Resistance model estimates of windbreak influence on evapotranspiration rate

		R_n (cal $\text{cm}^{-2} \text{min}^{-1}$)	r_c (sec cm^{-1})	r_a (sec cm^{-1})	T_a (°C)	e_a (millibars)	LE (cal $\text{cm}^{-2} \text{min}^{-1}$)	Change in LE From open Shelter/Exposed (%)
<i>Part A</i>								
	Open	1.00	2.0	0.10	23.0	18.0	0.89	—
Change from open	r_c	1.00	1.5	0.10	23.0	18.0	0.97	+9
	r_a	1.00	2.0	0.20	23.0	18.0	0.84	-6
	T_a	1.00	2.0	0.10	25.0	18.0	1.03	+16
	e_a	1.00	2.0	0.10	23.0	22.0	0.74	-16
	Shelter	1.00	1.5	0.20	25.0	22.0	0.88	-1
<i>Part B</i>								
Cloudiness	Open		2.0	0.10	23.0	18.0	0.65	-27
	Shelter	0.50	1.5	0.20	25.0	22.0	0.55	-38
-15								
Increased crop resistance	Open	1.00	3.0	0.10	23.0	18.0	0.77	-14
	Shelter		2.5	0.20	25.0	22.0	0.74	-17
-4								
Increased wind	Open	1.00	2.0	0.05	23.0	18.0	0.96	+8
	Shelter		1.5	0.15	25.0	22.0	0.91	+2
-5								
Increased air temperature	Open	1.00	2.0	0.10	33.0	18.0	1.62	+82
	Shelter		1.5	0.20	35.0	22.0	1.35	+52
-17								
Increased aridity	Open	1.00	2.0	0.10	23.0	8.0	1.30	+46
	Shelter		1.5	0.20	25.0	12.0	1.11	+25
-15								

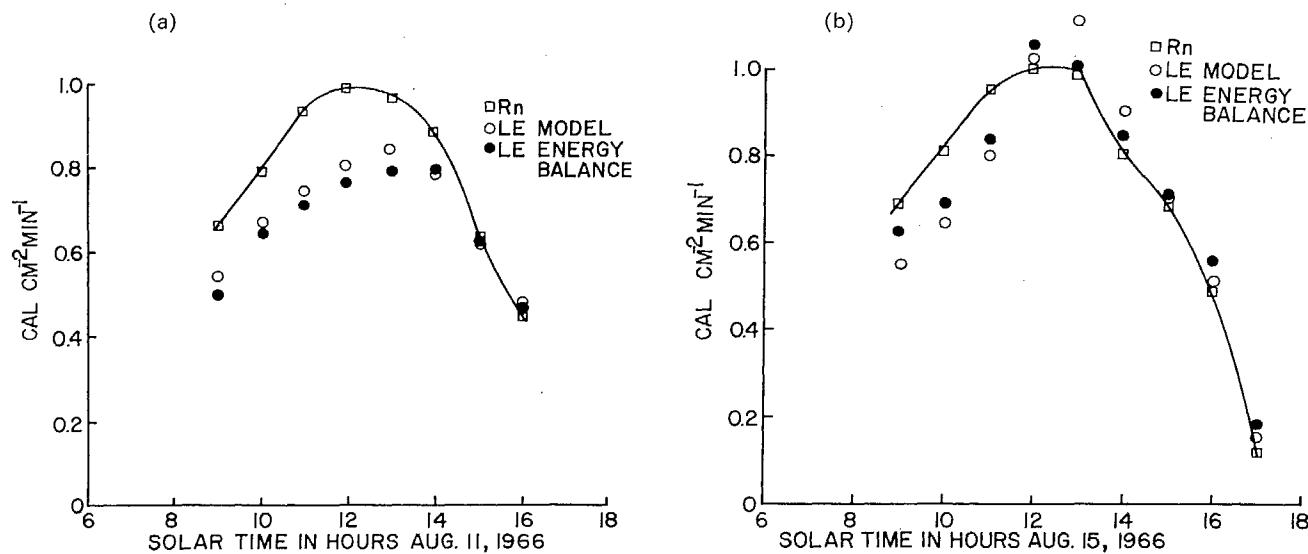


FIG. 5. (a) Hourly net radiation over sugar beets at Scottsbluff, Nebraska, 11 August 1966, and a comparison of LE estimated by the Energy Balance-Bowen Ratio method and by the resistance-model. (b) Same for 15 August 1966.

and Hagen, 1966; Zelitch and Waggoner, 1962). The materials may be classified as "film-formers" and "stomate-closers". Both types of materials should increase the stomatal resistance to vapour flow. The data of Hales (1970) and Monteith (1965) suggest that increases in r_s greater than 33 per cent may be obtained on individual leaves. However, because of the difficulty of achieving uniform treatment of an entire crop, a

33 per cent increase in r_c was used to calculate LE given in Table 2. Under a net radiation of 1 cal $\text{cm}^{-2} \text{min}^{-1}$ and in cool, windy and dry air (Set 1), a 13 per cent reduction of evapotranspiration rate of a treated crop is predicted. The following five sets illustrate the influence of decreased windiness, increased temperature, increased vapour pressure and combinations of these under the same net radiation. Two further examples are given

TABLE 2. Resistance model estimates of the influence of an antitranspirant material on evapotranspiration rate

Set	R_n (cal $\text{cm}^{-2} \text{min}^{-1}$)	r_c (sec cm^{-1})	r_a (sec cm^{-1})	T_a (°C)	e_a (millibars)	LE (cal $\text{cm}^{-2} \text{min}^{-1}$)	Change in LE	
							Antitranspirant/Untreated (%)	
1	1.0	1.5	0.10	10	10	0.53	-13	
	1.0	2.0	0.10	10	10	0.46		
2	1.0	1.5	0.40	10	10	0.62	-2	
	1.0	2.0	0.40	10	10	0.61		
3	1.0	1.5	0.10	30	10	1.84	-9	
	1.0	2.0	0.10	30	10	1.68		
4	1.0	1.5	0.40	30	10	1.10	-3	
	1.0	2.0	0.40	30	10	1.07		
5	1.0	1.5	0.10	30	30	1.06	-7	
	1.0	2.0	0.10	30	30	0.99		
6	1.0	1.5	0.40	30	30	0.89	-2	
	1.0	2.0	0.40	30	30	0.87		
7	0.50	1.5	0.10	10	10	0.32	-13	
	0.50	2.0	0.10	10	10	0.28		
8	0.50	1.5	0.40	30	30	0.51	-2	
	0.50	2.0	0.40	30	30	0.50		

under low net radiation, such as might occur in cloudy weather or the beginning and end of the daylight period. Water savings are proportionately greatest when LE flux is low. During periods of strong sensible heat delivery, as in Set 3, a 10 per cent water saving is predicted. During hot, dry, but calm periods the effect is small.

Since, among others (Davenport, 1967; Waggoner *et al.*, 1964), we have found the influence of PMA-antitranspirant in the field to be transitory, its usefulness is doubtful. Hales (1970) observed no significant difference in water use by alfalfa treated with 10^{-5} M PMA at Mead, Nebraska, during an eleven-day run in 1968. A short period did occur at midday on 4 July (two days after treatment), when stomatal resistance was increased from about 1.5 to 2.0 sec cm $^{-1}$.

SUMMARY AND CONCLUSIONS

A model has been elaborated and graphical solutions prepared to estimate evapotranspiration by crops growing in climatic circumstances typical of the American Great Plains. The model considers the effects of sensible heat advection which our studies have shown to be a major determinant of the quantity of energy available at the evaporating surface. The model requires knowledge of the net radiation, air temperature and vapour pressure—all easily measured or estimated from clima-

tological records—and of the stomatal (crop) resistance and air resistance—for which more information, gathered in local field experiments, is needed.

The model predicts, with acceptable accuracy, the influence of a windbreak on LE and gives good agreement with Energy Balance-Bowen Ratio calculations based on field measurements. The model, too, predicts that antitranspirants will have little effect on water use by field-grown crops in the climatic circumstances of the eastern Great Plains, a prediction in agreement with limited observations on our part.

The model, considering as it does both atmospheric and plant factors, one of which (r_c) reflects soil moisture conditions, appears sensitive enough to detect differences in water use caused by agronomic treatment. The model should be useful for predicting differences in actual water use between distinct regions, as well.

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APPENDIX: LIST OF SYMBOLS

C_p	= specific heat of air at constant pressure
E	= water vapour flux
L	= heat of vaporization of water
LE	= latent heat flux
Ma	= molecular weight of air
Mw	= molecular weight of water
P	= atmospheric pressure
R_n	= net radiation
T	= temperature
e	= water vapour pressure
$f()$	= functional notation
r_a	= resistance to diffusion of water vapour and sensible heat in air external to the leaf

r_s, r_c = stomatal resistance and crop resistance (per unit leaf area, per unit ground area) to diffusion of water vapour

Δ = $\frac{des}{dt}$, slope of the saturation water vapour pressure curve

δ = saturation vapour pressure deficit

ρ = air density

Subscripts

a	= air
l	= leaf

Résumé

Effets mesurés et calculés sur modèle d'une modification du microclimat sur l'évapotranspiration de cultures irriguées dans une région de forte advection de la chaleur sensible (N. J. Rosenberg et K. W. Brown)

La région centrale des grandes plaines de l'Amérique du Nord est soumise au vent et sujette à de fréquentes et fortes élévations de température. Il en résulte que les récoltes, même quand elles sont bien irriguées, souffrent d'un déficit temporaire d'eau.

Un modèle d'évapotranspiration, fonction de la température et de l'humidité de l'air, du rayonnement net

et des résistances à la diffusion dues à la couche d'air près des feuilles et par les stomates a été mis au point.

Une solution numérique au modèle et des exemples graphiques sont fournis. Les prévisions de l'influence des brise-vent sur l'évapotranspiration concordent avec les résultats des mesures effectuées au cours d'une série d'expériences dans une région semi-aride de l'ouest du Nebraska. Le modèle permet de prévoir également un effet très limité de l'emploi d'un antitranspirant. Cette prévision concorde également avec les résultats des mesures effectuées dans le climat plus humide de l'est du Nebraska.

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Evaluation of evapotranspiration models for prediction of soil moisture storage under a *Prosopis cineraria* community and estimation of potential evaporation

A. Krishnan

Central Arid Zone Research Institute, Jodhpur (India)

R. S. Kushwaha

Department of Mathematics, Jodhpur University,
Jodhpur (India)

INTRODUCTION

Several methods are available for the prediction of evaporation from climatological factors. Many of them use the Dalton type of relationship with wind speed and saturation deficit values as major factors (Deacon and Swinbank, 1958; Herbeck, 1962; Kohler, 1954; Rohwer, 1931). Several empirical formulae have been derived, based on temperature with allowance for day length and/or humidity factors (Blaney and Criddle, 1950; Hargreaves, 1956; Lowry and Johnson, 1942; Thornthwaite, 1948). More stress on the radiation factor is given in the studies of Jensen and Haise (1963), Linacre (1964) and Wilcox (1963).

The work of Penman (1948, 1956) became a land mark in such types of investigations. He combined the aerodynamic and energy balance approaches and took into account a comprehensive range of factors. His method was criticized by many scientists, especially with regard to estimation of net radiation and omission of soil heat flow (Makkink, 1957; Tanner and Pelton, 1960). A few improved combination models have also been suggested (Bavel, 1966; Slatyer and McIlroy, 1961).

There is considerable controversy as to the relative transpiration rates of plants in the soil moisture range from field capacity to the permanent wilting percentage. Some have reported equal availability in the entire range (Van Bavel, 1955; Lowry, 1959; Veihmeyer, 1956), while others found linear relationships between relative transpiration rate and available soil water (Denmead and Shaw, 1962; Slatyer, 1962; Thornthwaite and Mather, 1955). Some others have noticed an exponential relationship (Lemon, 1956). Differences in the ratios of actual to potential evapotranspiration during different growth phases of vegetation have also been reported by many scientists (Denmead and Shaw, 1959; Gangopadhyaya *et al.*, 1969; Jensen and Haise, 1963; Prasher and Singh, 1963; Shaw, 1963; Slatyer, 1955, 1956).

Thus any model for evaluating evapotranspiration by soil moisture budgeting should have two parts, one relating the ratio of actual to potential evapotranspiration in terms of stage of growth of vegetation and another depicting changes occurring in this ratio by the depletion of available soil moisture storage. Examples of such models are provided by Fitzpatrick *et al.* (1967) and Slatyer (1966).

The object of this paper is, therefore, to evolve evapotranspiration models for the *prosopis cineraria* community in the Jodhpur region of India, in order to predict soil moisture storage at any time within the growing season of the community. A critical examination of Penman's method, as applicable to Jodhpur conditions, is also presented. Equations for predicting evaporation on a five-day mean basis from individual climatic factors are also given.

CLIMATE, SOIL TYPE AND VEGETATION OF THE REGION

The Jodhpur region falls in the arid zone with Thornthwaite moisture index-45. The climate is strongly seasonal and the year can be divided into four distinct seasons: winter (December to February), hot-weather period (March to June); monsoon (July to September); and post-monsoon (October and November). The normal annual rainfall is 366.0 mm, of which 327.6 mm occurs in the monsoon season, constituting 89 per cent of total precipitation. The coldest month of the year is January, with mean maximum and minimum temperatures of 25 °C and 9 °C respectively. Occurrence of frost is rare. The mean maximum temperature during the hottest month (May) is 41–42 °C. Temperatures during the monsoon are moderate, with minimum diurnal variations. Under the hot arid climatic conditions evaporation losses are high. The mean annual evaporation as

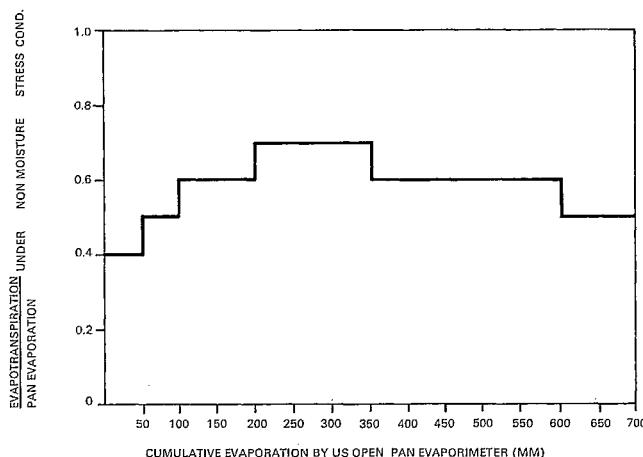


FIG. 1. Evapotranspiration model—Part A for native vegetation in Jodhpur.

measured by United States open pan evaporimeter is 2,640 mm. The highest evaporation of 440 mm per month is recorded during May. Monsoon evaporation is of the order of 180–200 mm per month, while winter evaporation is 100–120 mm per month.

The soil at the experimental site is sand to 15 cm depth (clay content: 6 per cent) and sand to loamy sand downwards to 200 cm depth (average clay content: 8 per cent). Below this is a thick layer of Kanker, which is an accumulation of calcium carbonate concretion material and the pebbles of palaeozoic rocks. The soil texture is quite uniform and unaggregated to a depth of 200 cm with a nearly constant bulk density of 1.5 g/cm³.

The site of the experiment is the Central Research farm of the Central Arid Zone Research Institute, Jodhpur. The plot for determining the water balance in the *Prosopis cineraria* community has an area of 1,228 m². Among the grasses, dominant species are: *Dactyloctenium sibiricum*, *Eleusine compressa*, *Cenchrus biflorus*, *Cenchrus setigerus*, *Panicum antidotale*, *Aristida adscensionis*, *Cyperus rotundus*. These plants represent the general native vegetation of the region. The detailed water balance of this community has been discussed by Krishnan *et al.* (1968).

MATERIALS AND METHODS

Soil moisture content was determined by a gravimetric method, from three locations in the experimental site. Supplementary observations by the neutron moderation method were also made.

A graphical integration method was used to determine the mean water contents in different layers of the soil for various ten-day periods. The daily evaporation values were measured by a standard United States open pan evaporimeter with a wire mesh cover. The total

solar and sky radiation required in Penman's equations was measured with a Kipp solarimeter. The sunshine data required for computing the effective long-wave radiation in Penman's formula were recorded with a Campbell-Stokes sunshine recorder. The mean wind speed was recorded by a cup counter anemometer and was averaged over twenty-four hours.

RESULTS AND DISCUSSION

EVAPOTRANSPIRATION MODELS FOR THE *Prosopis cineraria* COMMUNITY

Figure 1 gives Part A of the model which predicts the pattern of evapotranspiration as a function of cumulative evaporation by United States open pan evaporimeter from the time of soil water recharge (viz. from first effective rainfall) under non-moisture stress conditions. It is seen that the ratio of actual to potential evapotranspiration increases from 0.40 directly after soil moisture recharge to a maximum of 0.70, corresponding to 200–300 mm of cumulative evaporation, and then declines to a steady value of 0.50. Thus, even the maximum evapotranspiration under arid zone conditions is only a fraction of the potential rate due to restricted plant growth.

Part B of the model (Fig. 2) predicts the pattern of decline in evapotranspiration as total water storage declines. Although Cowan (1965) and Denmead and Shaw (1962) stated that this pattern would be influenced by the potential evapotranspiration rate, as well as by soil and plant characteristics, field measurements in the

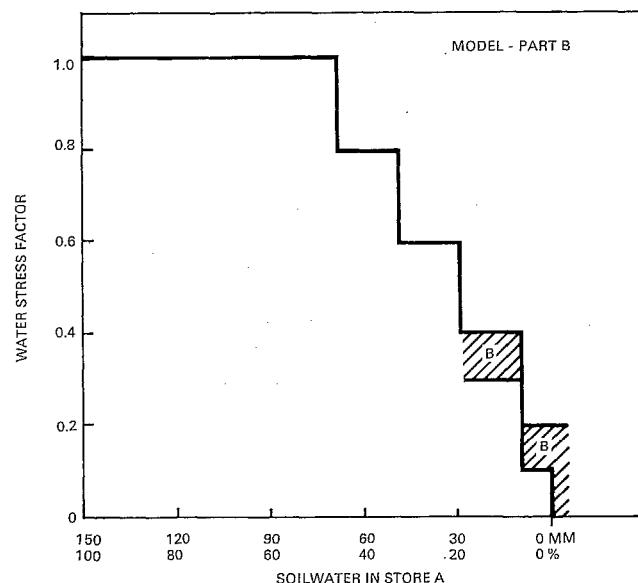


FIG. 2. Evapotranspiration model—Part B for native vegetation in Jodhpur.

Jodhpur region, as well as in Central Australian deserts, showed little influence of factors other than that of soil water (Fitzpatrick *et al.*, 1967).

For the Jodhpur region, the available water content of the soil is approximately 0.75 cm of water per cm of soil depth. Effective rooting depth of the vegetation community under study can be taken as 2 m below the surface, beyond which the Kanker pan occurs. Thus there is a soil water storage capacity of 150 mm in the range from field capacity to wilting percentage. But the water extraction in these communities does not cease when the wilting percentage is reached, but continues until a fairly consistent minimum value is reached which represents an additional survival storage capacity of 0.030 cm of water per cm of soil depth. The soil storage of available water and the survival storage are referred to as Store A and Store B respectively in this study. Thus the maximum values of these storages are 150 mm and 60 mm respectively and the total (Store A + Store B) is 210 mm.

It is seen from the proposed model (Fig. 2) that with the native vegetation in Jodhpur, the water stress factor becomes less than unity when Store A becomes less than 70 mm (47 per cent of available water capacity). Thus, including the survival storage (Store B), it is seen that, so long as the total moisture is above 130 mm, the pattern of extraction from the soil storage by evapotranspiration would depend on the stage of growth of the vegetation. When the total moisture storage is less than 130 mm, the evapotranspiration rate relative to free water evaporation obtained by Part A of the model must also be multiplied by the water stress factor presented in Part B of the model.

After Store A is reduced to less than 30 mm, withdrawals are made in the proposed model from both the stores as per following proportions:

- (a) Extraction from Store B/Extraction from Store A = $\frac{1}{4}$, for values of Store A between 10 and 30 mm;
- (b) Extraction from Store B/Extraction from Store A = 1, for values of store A less than 10 mm.

The proportion of extraction from Store B is indicated by shaded areas in Figure 2.

The step functions presented in Figures 1 and 2 were obtained after repeated trials with a few years' data. Finally, only those values which gave maximum fit with the observed data were chosen.

The accumulated evaporation recorded by United States open pan evaporimeter presented as the absicca in Part A of the model (Fig. 1), affords a practical and realistic integration of factors affecting growth, leaf area expansion, and evapotranspiration.

Run-off was measured in the experimental plot by constructing run-off tanks at the experimental site. In the absence of such measured run-off data, effective rainfall has to be estimated from the rainfall versus run-off relationship for the locality concerned.

During recharging the soil water storage, the effective rainfall is partitioned in the ratio 3:1 into Store A and

TABLE 1. Comparison of the actual moisture storage with predicted values

Dates	Soil moisture storage (mm) up to 2 m	
	Actually measured	Predicted by Figures 1 and 2
16 July 1965	43.3	48.9
4 August 1965	133.1	111.9
19 August 1965	102.4	56.7
2 September 1965	106.1	101.7
18 September 1965	82.5	63.0
6 October 1965	50.3	48.9
8 July 1966	54.0	70.3
5 August 1966	130.1	150.7
18 August 1966	139.9	138.9
2 September 1966	83.3	82.0
30 September 1966	59.3	63.3
15 October 1966	52.1	49.5
15 July 1967	57.7	57.3
29 July 1967	132.7	132.6
14 August 1967	141.4	142.3
26 August 1967	147.0	146.5
6 September 1967	114.0	123.2

Store B respectively, until Store B reaches its maximum value. Thereafter all the recharge is added to Store A. This procedure, as well as the relative extraction procedure from Store A and Store B, are similar to those suggested by Fitzpatrick *et al.* (1967).

Comparison of predicted values from the model and observed values of soil moisture

Daily predicted soil moisture storage was worked out from the model for 1965–67 from the date of the first effective rainfall to the end of October. Table 1 compares the predicted moisture storage from the model with measured soil moisture storages when these data were available.

From Table 1, it can be seen that the evapotranspiration model gives a reasonable prediction of soil moisture under the *Prosopis cineraria* community in Jodhpur for most of the periods considered. In 1964 (not shown in the table), when there were hot desiccating winds and high evaporative conditions, and in years in which there were abnormally long growing seasons, a different model had to be used at the commencement of the season.

COMPARISON OF POTENTIAL EVAPORATION FROM PENMAN'S METHOD AND OBSERVED EVAPORATION FROM UNITED STATES OPEN PAN EVAPORIMETER

Figure 3 shows the five-day means of evaporation actually recorded by United States open pan evaporimeter and the corresponding values of potential evaporation computed by the method of Penman (1948),

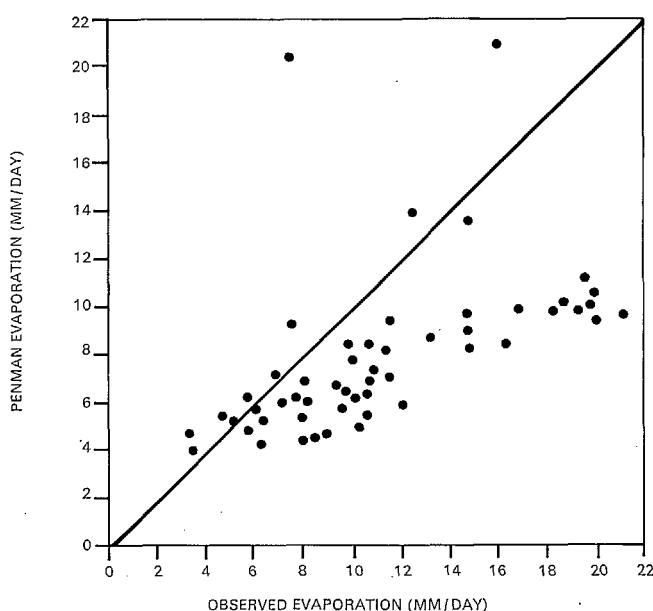


FIG. 3. Comparison of observed evaporation and potential evaporation by Penman's method.

1956). The ideal case where both methods give the same result, represented by the straight line $y=x$, is also indicated in the same figure. Five-day means presented in the figure correspond to the growing season of the vegetation covering the period 30 July to 6 November 1963 and 10 May to 30 October 1964.

It is seen that Penman's method underestimates evaporation considerably. All five-day means of pan evaporation are higher than the corresponding means of evaporation predicted by Penman's method, except for small values of pan evaporation corresponding to the presence of active monsoon conditions over Jodhpur. Some of the values of Penman evaporation are less than half of the pan evaporation values. Underestimation of potential evapotranspiration by Penman's method has also been reported by Abdel Azeez *et al.* (1964), Bathkal and Dastane (1968), Sharma and Dastane (1968), Smith (1964), Tanner and Pelton (1960), and Thompson and Boyce (1967).

On further examination of the aerodynamic and energy balance terms of Penman evaporation, it is noticed that under Jodhpur conditions the aerodynamic term is very much greater than the energy balance term. But, in general, the magnitude of the former term in Penman's equation is one fourth of that of the latter term. Hence the actual value of the Penman evaporation exceeds the energy balance term only very slightly.

In order to derive an improved weighting for the aerodynamic and energy balance terms, the following multiple regression equation was fitted to the observed evaporation by United States open pan evaporimeter in relation to these terms.

$$Y = 1.1295 X_1 + 0.6096 X_2 - 3.2243$$

where X_1 is the energy balance term, X_2 the aerodynamic term and Y is the evaporation, all expressed in mm/day. The multiple correlation coefficient is 0.9823, indicating that 97 per cent of the variance in the dependent variable has been explained by both the terms. Thus it can be seen from the above equation that the relative ratio of the energy balance to the aerodynamic term according to the observed values of evaporation should be 1.13: 0.61 and the higher value given in Penman's formula for the energy balance term (of the order of from three to four times that of aerodynamic term) does not give a true picture under arid zone conditions. Figure 4 gives the five-day means of the observed evaporation and the predicted evaporation predicted from the equation given above.

MULTIPLE REGRESSION OF EVAPORATION WITH INDIVIDUAL CLIMATOLOGICAL FACTORS

Multiple regressions relating evaporation to individual climatological factors have also been studied. The following factors are considered:

X_1 —Total solar radiation in cal/cm²/day¹.

X_2 —Net radiation computed by Penman's formula in cal/cm²/day¹.

X_3 —Saturation deficit at maximum temperature in mm of mercury.

X_4 —Mean daily wind speed in km/h.

X_5 —Saturation deficit at mean air temperature in mm of mercury.

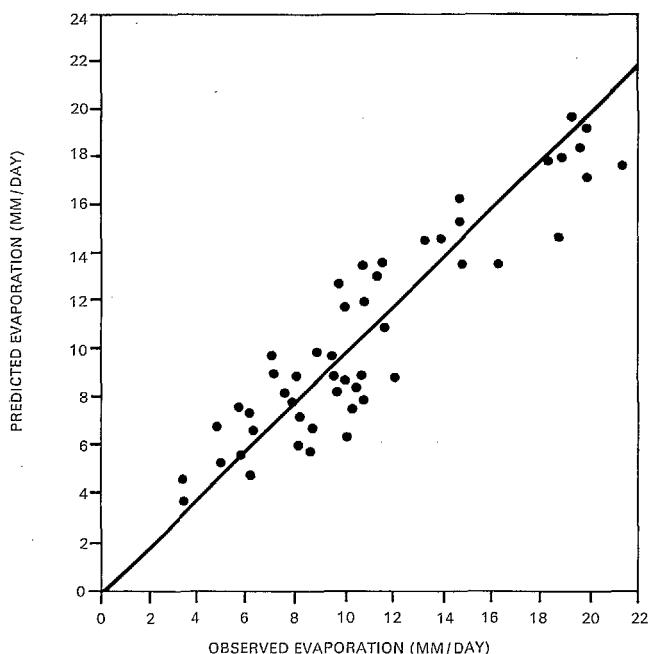


FIG. 4. Comparison of observed evaporation and predicted evaporation with new weighting given to energy balance and aerodynamic terms.

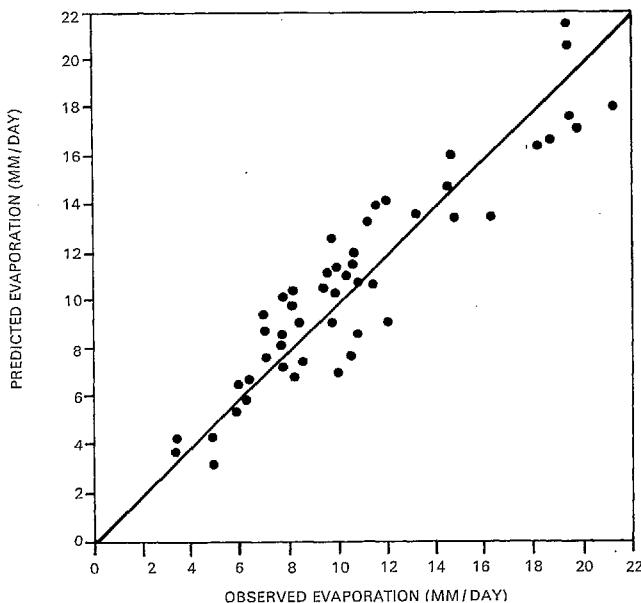


FIG. 5. Comparison of observed evaporation and predicted evaporation with a combination of factors.

The correlation coefficients of evaporation (Y) in mm/day with the factors X_1 to X_5 are 0.6988, 0.5139, 0.6921, 0.6274 and 0.4829 respectively. Since X_1 and X_2 as well as X_3 and X_4 are interdependent factors, only the one giving the higher correlation is taken for multiple regression analysis in each case. Accordingly, the interrelation of total radiation (X_1), saturation deficit at maximum temperature (X_3) and wind speed (X_4) was attempted.

Apart from multiple regression with all the three factors, investigation of the regression with two factors at a time would also be useful in determining the

advantage of successive addition of independent variables in the explanation of variance in Y . These data, applying to the combinations from X_1 to X_3 , are as follows:

$$\begin{array}{ll} R_{13} = 0.7659 & R^2 13 = 0.5867 \\ R_{14} = 0.8577 & R^2 14 = 0.7357 \\ R_{34} = 0.9111 & R^2 34 = 0.8300 \\ R_{134} = 0.9372 & R^2 134 = 0.8782 \end{array}$$

The actual regression equation with all the three variables is as follows:

$$Y = 0.0122 X_1 + 0.2559 X_3 + 0.5677 X_4 - 9.0657$$

The square of the correlation coefficient presented above, known as the coefficient of determination, measures the percentage of variance in Y determined by the various combinations of X .

In spite of the fact that the total radiation as a single factor has the maximum correlation coefficient with evaporation (0.6988), by considering pairs of factors, the best combination which has maximum association with the dependent variable is the combination of saturation deficit at maximum temperature and wind speed, which explains 83 per cent of variance in Y . With the inclusion of total radiation to this pair, only 5 per cent more of the variance is explained. The total radiation alone explains 49 per cent of variance. Together with wind speed this explains 74 per cent, and with saturation deficit, 88 per cent. Analysis of variance indicates that the regression of evaporation with the three factors X_1 , X_3 and X_4 taken either singly, in pairs, or all together, is significant in all cases.

Figure 5 shows, for this combination of factors, the points representing five-day means of observed evaporation and the corresponding evaporation estimated by the multiple regression equation. The line $y = x$, representing the ideal case where both are equal, is also indicated in the figure. The closeness of fit of the scattered points to this straight line is evident.

Résumé

*Évaluation de modèles d'évapotranspiration pour la prévision de l'humidité accumulée dans le sol, sous une communauté de *Prosopis cineraria* et estimation de l'évaporation potentielle* (A. Krishnan et R. S. Kushwaha)

Les auteurs proposent un modèle d'évapotranspiration pour la prévision de l'humidité accumulée dans le sol sous une communauté de *Prosopis cineraria* à Jodhpur (Inde). Pour la valeur potentielle nécessaire au modèle, on a pris l'évaporation mesurée au moyen d'un évapomètre sur bac à ciel ouvert d'un type courant aux États-Unis d'Amérique. Dans le climat de zone aride qui règne à Jodhpur, le rapport entre l'évapotranspira-

tion effective et sa valeur potentielle passe de 0,40 immédiatement après la réhumidification du sol à un maximum de 0,70, puis diminue jusqu'à une valeur constante de 0,50. Tant que l'humidité totale accumulée est supérieure à 130 mm, la valeur de l'évapotranspiration par rapport à l'évaporation d'une nappe d'eau libre donnée par la partie A du modèle dépend du stade de croissance de la végétation; lorsqu'elle est inférieure à 130 mm, il faut également tenir compte du facteur de contrainte hydrique présenté dans la partie B du modèle. On constate que ces rapports traduisent bien la réalité pour la plupart des années, sauf celles où la saison de croissance est anormalement longue ou précoce,

lorsque souffle un vent brûlant et desséchant et que l'évaporation est forte.

L'évaporation potentielle calculée par la méthode de Penman est sensiblement inférieure à l'évaporation enregistrée au moyen de l'évaporomètre sur bac à ciel ouvert de type américain. Dans le climat de Jodhpur, le terme « aérodynamique » est très supérieur au terme « bilan énergétique » pendant la saison de croissance de la végétation. Une équation de régression multiple de l'évaporation, en relation avec ces termes, peut s'exprimer comme suit: $Y = 1,1295 X_1 + 0,6096 X_2 - 3,2243$, avec un coefficient de corrélation multiple de 0,98, montrant que la pondération supérieure donnée dans la

formule de Penman au terme du bilan énergétique de l'ordre de 3 à 4 fois celle du terme aérodynamique ne donne pas une idée fidèle des conditions en zone aride.

Bien qu'à lui seul le rayonnement solaire et céleste total ait le coefficient de corrélation maximal avec les évaporations observées, les deux facteurs qui offrent ensemble l'association maximale sont: le déficit de saturation à l'époque où la température est maximale et la vitesse du vent. Ces deux facteurs expliquent 83 % de la variance du paramètre qui en dépend. La somme du rayonnement total mesuré n'explique que 5 % de cette variance.

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Water régime of plants under the extreme conditions of high-mountain deserts of Pamirs

V. M. Sveshnikova
Botanical Institute,
U.S.S.R. Academy of Sciences, Leningrad (U.S.S.R.)

The adaptation of plants to the extreme dryness of soils and air occurs in many ways. The most important of these are the adaptive changes in the character of the water régime, which play an essential role in the adaptation to the desert conditions, together with the biochemical and physico-chemical properties of cells.

In the course of these investigations carried out in the Pamirs, the author endeavoured to understand the character of the water régime in plants under conditions of extremely low soil water supply and of extreme air dryness (Sveshnikova, 1962a). For this purpose the water régime was studied both in closely related species and in those belonging to different ecological groups. By means of the investigation and comparison of a number of parameters of the water régime carried out during several vegetative seasons, correct ideas of the state of the water balance of the plants, its relationship to the environmental conditions and the mechanisms of its regulation could be obtained. The consumption of water by the vegetation was also determined.

The investigations were carried out at an altitude of 3,860 m in the vicinity of the Pamirs Biological Research Station of the Institute of Botany of the Academy of Sciences of the Tajik S.S.R. The material for these studies included the dominant species of the prevalent primitive desert-plant aggregations (*Eurotia ceratoides*, *Artemisia rhodantha*) and of the locally spread primitive meadow aggregations (*Hordeum turkestanicum*, *Potentilla multifida*, *Astragalus chadjanensis*, *Kabresia capilliformis*).

The detailed characterization of the environmental factors, such as the amount of precipitation, its distribution in time and the character of its fall, the seasonal and annual dynamics of the soil moisture, the processes of condensation in the soils of the high-mountain deserts, the evaporation from the soil surface, the thermal régime of the soil, as well as the régime of the air humidity and the air temperature, is given by Sveshni-

kova (1962a). Therefore only a concise account is given here.

Since the extremely small total precipitation is received very intermittently, the accumulation of available moisture in the soils down to 1 m depth is practically impossible. The depth of penetration of the precipitation into the soil is insignificant (generally 5–30 cm, rarely to 70 cm). Thus low moisture values prevail throughout the soil and sub-soil.

Apart from the very small amount of precipitation, the general character of the soil moisture régime is also determined by the intense processes of evaporation and condensation both on the surface and in all the soil layers. The intensity of condensation was shown to be very high under the conditions of Pamirs (0.07–0.63 mm at a depth of 1 m and 0.05–0.37 mm on the soil surface during one night). Thus, due to condensation, the soils and sub-soils receive supplementary moisture in addition to precipitation (31.7 and 15.0 mm due to condensation in the superficial soil layer and in deeper layers respectively). However, the moisture supply for the plants proved to be lower in the Pamirs than in many other desert regions.

Extremely low humidity (40–60 per cent during the morning hours and 7–13 per cent in the afternoon) of the air layers close to the ground, where the main phytomass of the above-ground parts of plants is situated, results in the extremely high rate of potential evaporation.

All this complex of environmental factors affects drastically the most important physiological processes in the plants. Here the survival of plants depends largely on their capacity for adaptive transformation of the course and the rate of physiological processes during each day and throughout the entire vegetative season (Oppenheimer, 1951; Sveshnikova, 1962a).

Thus measurements of the water content in the leaves throughout the vegetative season help to reveal the

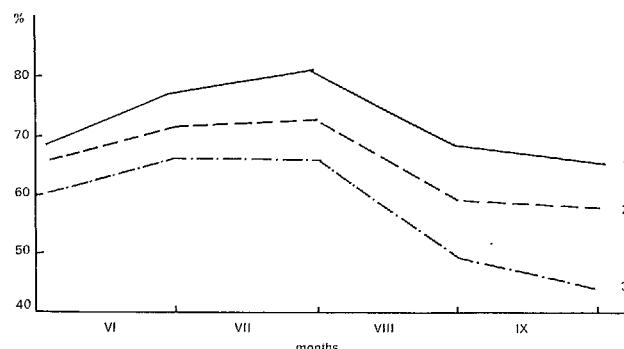


FIG. 1. The dynamics of the water content (in per cent of fresh weight) in the leaves of high-mountain desert plants during the vegetative season. Numbers refer to different species.

dynamics of accumulation and loss of water. The fluctuations of the total leaf water content in the leaves in the main species of primitive plant aggregations of high-mountain deserts of the world, such as *Eurotia ceratoides* (L.) C.A.M., *Artemisia rhodantha* Rupr., *Stipa glareosa* Smirn., are relatively gradual, compared with the abrupt fluctuations in the plants of hot deserts (Klimoshkina, 1948; Shreve, 1914; Vasilyev, 1931, and certain other authors). Also, unlike the plants of hot deserts, the water content in the leaves does not decrease from spring to summer but, on the contrary, increases (Fig. 1). The highest water content in the leaves is usually observed in July, but sometimes it is recorded in August, depending on the time of rainfall. A considerable decrease in the water content of the leaves takes place

at the end of July; it is associated with the preparation of the plants for winter (Sveshnikova, 1956a). A rather abrupt decrease in the water content of leaves takes place by the beginning of autumn; this decrease is associated with the ageing of leaves and the exhaustion of the moisture reserves in the soil. In meadow plants the level of the water content in leaves remains almost constant throughout the vegetative season (Fig. 2). In desert species the water content of leaves is subject to fluctuations, the range of which is much wider than in meadow plants (20–22 per cent v. 5–9 per cent).

The water reserve in the leaves of desert plants remains quite constant during the day. This is one of the characteristic features peculiar to the plants of different desert regions of the world, e.g. the Kara-Kumy Desert (Kokina, 1935), Arizona (Shreve, 1914), Israel (Shmueli, 1948), Kazakhstan (Klimoshkina, 1948) and Pamirs (Sveshnikova, 1962a). The value of the water deficit was determined as the difference between the water content in fully saturated leaves in a moist chamber and that under natural conditions. This difference is indicative of the value of the maximal deficit. It reached 35–50 per cent and proved to be about the same in the plants of hot deserts in plains and in those of high-mountain deserts. The value of the water deficit estimated from the ratio of the minimal water content in the leaves in the day to the maximum content early in the morning regarded conventionally as the 100 per cent saturation (Krasnoselskja-Maksimova, 1917), proved to be 3–13 per cent for the plants of high-mountain deserts; this value is very similar to the corresponding value for tundra plants.

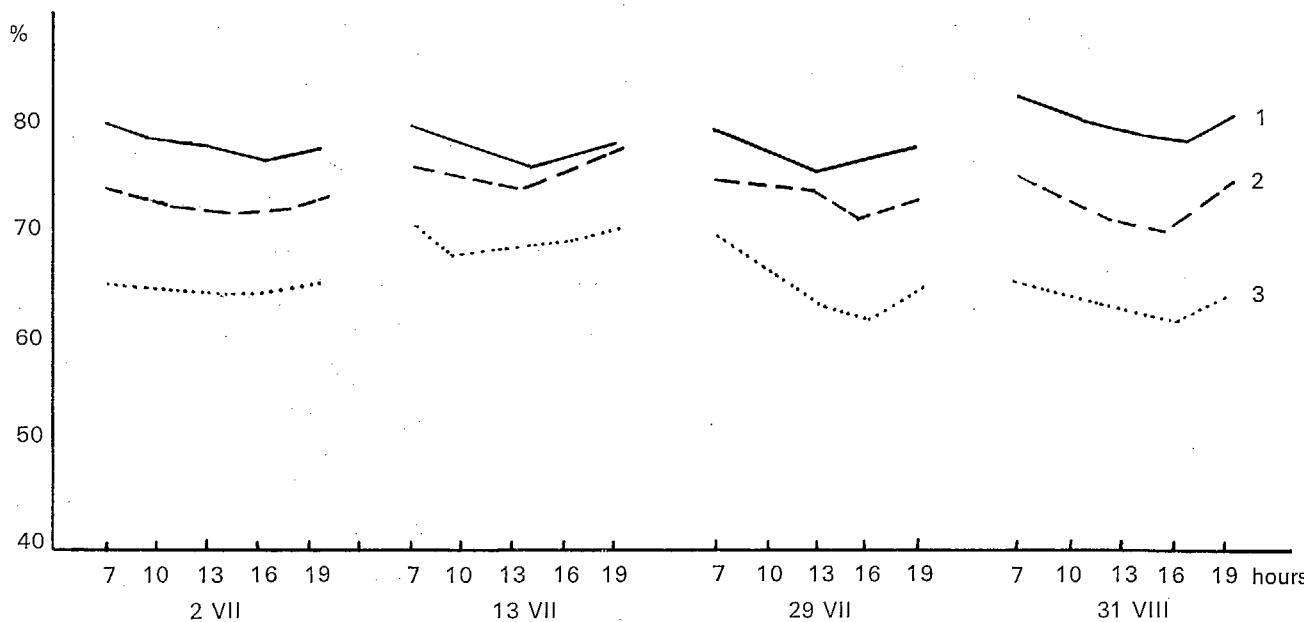


FIG. 2. The dynamics of the water content of the leaves of meadow plants during the day and during the vegetative season. Numbers refer to different species.

For the investigation of the water expenditure by desert plants it is important to determine not only the rate of the loss of the water reserve, but also the extreme limit of dehydration that the plants studied are able to endure.

It was shown, by the determination of the rate of water expenditure by detached shoots of plants, that the reserve of free water in different species inhabiting high-mountain deserts can be spent completely during 30–150 min. The smallest loss of water (up to 3–4 per cent of the initial weight) was observed in desert plants, e.g. in *Zygophyllum rosowii* Byd. But meadow plants, such as *Astragalus chadjanensis* Franch. and other species are least resistant to water loss, which can be equivalent to 16 per cent of the initial weight.

The most adverse conditions for the survival of plants in Pamirs are observed in winter owing to the absence of the snow cover during a large part of the season and to the extremely low temperatures, attaining -48°C at the soil surface.

In the course of the analysis of the seasonal variations of the water content in overwintering parts of plants (Sveshnikova, 1956a), the greatest loss of water was recorded during the months with the lowest temperatures of the air and soil. At this time the water content in the roots of *Eurotia ceratoides* and *Artemisia rhodantha* falls to one-half its value in summer, and to only one-third in *Stipa glareosa*. It is remarkable that the preparation of plants for overwintering begins as early as July. At this time the water content in overwintering organs falls rather abruptly, despite the fact that the water-temperature régime of the soil and air is still favourable for the absorption of water by roots. The decrease in the water content of plant roots lasts from July until the beginning of January.

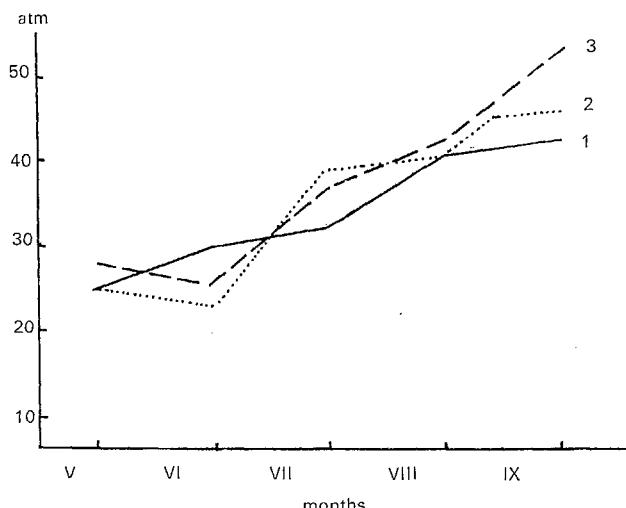


FIG. 3. The changes of the values of the osmotic pressure in the leaves of the high-mountain desert plants during the vegetative season. Numbers refer to different species.

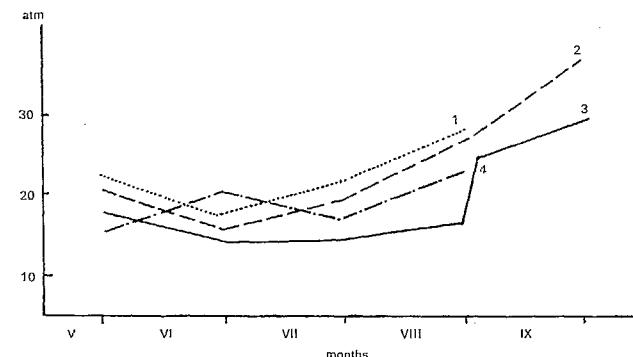


FIG. 4. The changes of the osmotic pressure values in the leaves of high-mountain meadow plants during the vegetative season. Numbers refer to a different species.

No evaluation of the effect of low temperatures and water deficiency on the water régime of plants is possible unless the osmotic pressure is measured. The average values of this characteristic in the 115 species studied were 20–25 atm. (42 per cent), 15–20 atm. (34 per cent) and 10–15 atm. (24 per cent) (Sveshnikova, 1956).

The maximal values of the cell sap concentration are most interesting from the standpoint of the ecological characterization of plant species. They are observed at the time of the greatest stress of the main environmental factors, such as the water deficiency in the soil, severe night frosts, etc.

The effect of autumn night frosts on the changes in the osmotic pressure in the daytime is not immediate. When night frosts first occur, the cell sap concentration is low, while the daytime maximum osmotic pressure is attained before the temperature maximum. On subsequent days, when temperatures become still lower, the osmotic pressure increases markedly, as does its diurnal variation (Sveshnikova, 1944).

In the desert and the meadow plants of Pamirs the osmotic pressure gradually increases during the vegetative season (Figs 3 and 4). In the middle of the summer a decrease in the osmotic pressure occurs, possibly due to the fall of precipitation. A rapid increase in the cell sap concentration in leaves is observed in autumn. It is caused by the steady fall in temperature which stimulates the formation of osmotically active products (Zalenskiy, 1955).

In the course of studying the interrelations between the plants and the environment in arid regions, special attention should be paid to the dependence of the osmotic pressure in plants on the provision of habitats with water (Birand, 1955; Hauck, 1929; Keller, 1952; Shmueli, 1948, and many other authors). The view became firmly established that, among the factors affecting the osmotic pressure, soil moisture was most important. Under the conditions of the Pamirs, the concentration of the cell sap within the same species can vary consid-

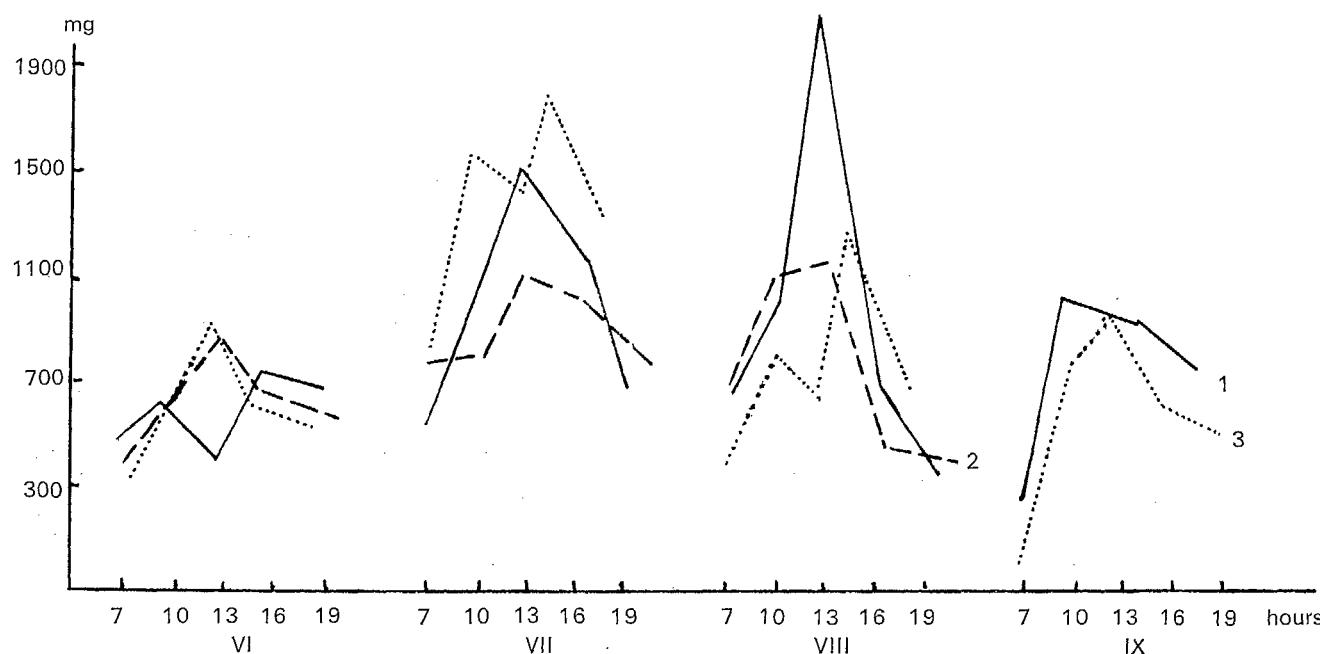


FIG. 5. The dynamics of the diurnal changes in the transpiration rate (in mg per g of fresh weight per hr) in high-mountain desert plants during the vegetative season. Numbers refer to different species.

erably (up to ± 16 atm. deviation from the mean, the average deviation being ± 7 – 10 atm.), depending on the water content in the soil.

Under conditions of natural water supply, the diurnal variations in the osmotic pressure in the leaves of plants are characterized by a maximum about noon. Under conditions of optimal water supply (artificial watering), the characteristic feature is a relatively low concentration of the cell sap, the maximum osmotic pressure occurring in the afternoon.

As was shown by a study of the process of transpiration, which is most closely associated with the changes in the environmental conditions (Sveshnikova, 1962), the rises and falls in the water loss curve during the day are very conspicuous in desert plant species, particularly in summer (Fig. 5). Different ecological types of plants (*Eurotia ceratoides*, *Christolea crassifolia* Cambess., *Artemisia pamirica* C. Winkl., *Astragalus chadjanensis*) differ from one another in the course of the variations in the transpiration rate during the day, the onset of the daytime maximum being recorded between 12.00 h and 13.00 h in desert plants and at 16.00 h in meadow plants.

In the plants of the Pamirs under the conditions of natural soil water supply, the rate of transpiration rises gradually during almost all the summer and decreases only in the first half of the autumn.

Under the conditions of high-mountain deserts, where abrupt and considerable changes in temperature occur (the average range of diurnal temperature variations is

25 – 30° C) (Sveshnikova, 1962a), it was considered to be important to determine the dependence of the changes in the transpiration rate on temperature. It was established by these studies that, at negative temperatures (up to -10° C), transpiration is observed only in desert edificator species, while in meadow species no transpiration is observed at temperatures below -2° C. Within the temperature interval from -1° to $+5^\circ$ C, the rate of water loss begins to increase and attains its maximum value in desert species between 20 – 25° C. In meadow plants the transpiration rate increases significantly at $+25$ – $+27^\circ$ C. The dependence of transpiration on temperature is particularly conspicuous in the autumn, when the ranges in the diurnal variations of the transpiration rate become much wider owing to the abrupt and considerable change in the temperature.

The mean values of the transpiration rate (in mg per g of fresh weight per hour) in high-mountain desert species range from 280 to 830 at different times of the day. The highest transpiration rate (1,000–2,500) was observed in meadow species, while the lowest was recorded in desert species with semisucculent leaves, such as *Zygophyllum rosowii* and *Christolea crassifolia*.

These losses by transpiration expressed in terms of water loss per hectare are very small because of the insignificantly small above-ground mass.

The capacity to maintain more or less active vital functions and the equilibrium of the water balance in such a conspicuously arid environment, is apparently

determined by the plasticity of several physiological processes, by the development and distribution of the root systems, by the capacity of a complete or partial leaf shedding at critical moments or of replacing large leaves by small ones, etc. (Evenari, 1953; Oppenheimer, 1960; Stocker, 1929; Sveshnikova and Zalenskiy, 1956).

A tentative classification of the plants studied with respect to the type of regulation of their water budget is as follows:

For the desert species of dwarf shrubs, such as *Eurotia ceratoides* and *Artemisia rhodantha*, the daily expenditure of water calculated for all the transpiring phytomass proved to be very economical, the water reserve being renewed only 7 times a day. In cases of such an economical water expenditure, the water balance is characterized by active reorganization at the time of the onset of unfavourable conditions. The capacity of leaves to withstand dehydration proved to be very pronounced in these plants. The equilibrium of the main elements of the water régime combined with the relatively high transpiration rate was possible owing to the small number of leaves and the resulting high root-shoot ratio (up to 300), the location of the root systems in the zone of the intense condensation, the capacity of developing a high osmotic pressure and, possibly, the capacity of hygroscopic absorption of the atmospheric water vapour in the night inherent in the superterranean organs. The course of development of plants is also indicative of a relatively successfully balanced water budget. The growth of the superterranean phytomass proceeded throughout the vegetative season. Unlike many plants of hot deserts, no shedding of leaves for the reduction of the surface for transpiration was ever observed in these plants of high-mountain deserts.

For the cespitose grasses, the characteristic feature is the lower water content in the leaves as compared with other species. The wide variations in osmotic pressure during the day and during the vegetative season, the withering of a part of the leaves (beginning from the middle of the summer), and the limited development of the reproductive organs, were all features indicative of the stress in the water balance in *Stipa glareosa*. Apparently this stress was caused, not only by the arid climate, but also by the location of the root system in the rapidly drying soil horizons. The main features of the water régime of dwarf desert shrubs with a semisucculent type of leaf as *Zygophyllum rosowii* and *Christolea crassifolia* were the low transpiration rate and cell sap concentration and the stable high water content in the leaves. Another characteristic feature was the very small range of variations in the main indicators of the water régime throughout the vegetative season. The range in variation of the transpiration rate during the day was very small because of the extremely short time of opening

of the stomata during each day. Because of the low transpiration rate and the large water reserve in leaves and roots, the equilibrium of the water balance was so stable that these species, particularly *Christolea crassifolia*, were capable of developing a relatively luxuriant above-ground phytomass. Another factor favourable for the vigorous growth of the shoots was the development of a large root system in those soil horizons where condensation was most intense.

The cushion plants, *Acantholimon diapenoides* Boiss. and *Gypsophila capituliflora* Rupr., had a uniform water régime, the characteristic features of which were the constant small water deficit, small transpiration rate and only slight changes in the cell sap concentration, both diurnal and during the vegetative season (Sveshnikova, 1962a). The stability of the water budget of these species was apparently due to the well-developed root system, the considerable water reserve in the roots and the more favourable water régime in the soils.

Dwarf shrubs of the type of *Artemisia pamirica* C. Winkl., *Astragalus borodini* and *Dragocephalum heterophyllum* Benth., inhabiting dry stream beds under conditions of a relatively sufficient water supply, were characterized by a high rate of transpiration, a high water content in leaves, and low values of the osmotic pressure. These features of the water relations probably restrict the distribution of these species of plants.

Meadow plants, *Astragalus chadjanensis*, *Potentilla multifida* L., *Polygonum viviparum* L. and *Hordeum turkestanicum* Nevski, had a very high rate of transpiration, a high water content of the leaves throughout the period of development and a permanently low concentration of cell sap. Under the conditions of good water supply, the resistance to water loss was very poor owing to a high transpiration rate and an insufficiently well-developed root system. This slight plasticity of the water régime and the consequent high requirement of water limit the distribution of the meadow plant in the Pamirs.

As can be seen from the above generalizations, the life forms of plants constituting the main primitive plant aggregations in the desert areas of Pamirs have adopted various ways of regulating water balance. This is achieved both by different combinations of the main characteristics of the water relations and by the ratio of the below- and above-ground plant masses. The survival of plants under the desert conditions is, to a great extent, dependent on their capacity to regulate both the course and the intensity of the main physiological processes, in particular of the water relations during the day and during the vegetative season. There are only a few plant species capable of balancing their water budget efficiently enough to become adapted to the unfavourable conditions of high-mountain deserts.

Résumé

Régime hydrique des plantes dans le climat très rigoureux des déserts de haute montagne du Pamir (V. M. Sveshnikova)

Dans les déserts de haute montagne du Pamir, on a étudié pendant plusieurs années le régime hydrique des plantes qui s'y trouvent soumises à des conditions d'alimentation en eau du sol très insuffisantes et à une extrême sécheresse de l'atmosphère.

Les caractéristiques suivantes ont été étudiées: transpiration et pression osmotique; déficit en saturation, réserve d'eau des feuilles et vitesse de sa disparition; faculté pour les parties aériennes des plantes d'absorber la vapeur d'eau de l'atmosphère; eau consommée par la couverture végétale. On a obtenu des données sur la valeur et la dynamique des caractéristiques ci-dessus au cours de la journée et pendant la saison végétative, ainsi que sur le rythme du travail des stomates, la répar-

tition des systèmes radiculaires et la corrélation entre leur dimension et celle de la partie aérienne des plantes; enfin sur le régime hygrométrique des sols.

Les résultats obtenus ont permis de classer les diverses formes de vie végétale, qui constituent les principales agrégations primitives de plantes, d'après le mode de régulation de leur budget hydrique. Dans le climat des déserts de haute montagne, la vie des plantes dépend avant tout de la souplesse avec laquelle les processus physiologiques les plus importants, en particulier le régime hydrique, peuvent s'adapter aux différents rythmes d'activité pendant la journée et durant la saison végétative. Un petit nombre seulement d'espèces végétales se sont adaptées au climat très rigoureux des déserts de haute montagne; il s'agit de plantes capables de maintenir efficacement en équilibre leur régime hydrique et d'autres fonctions physiologiques d'une importance vitale.

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Concluding address: The value of climatic studies in modern agriculture

Erik Åkerberg
The Swedish Seed Association, Svalöv (Sweden)

Old documents often talk about the vegetable kingdom and its dependence on the world around. The embryo of a new approach which has gradually developed to our modern science broke through with Aristotle. In papers written by Theofrastos, who lived 300 years before Christ, the relationship between plant and habitat was clearly described. One of his works gives a detailed description of the dependence of the plants on environment, a description which in many cases is a precursor of our modern ecological research.

Thousands of years of accumulated knowledge about our cultivated plants and their characteristics have led to an adaptation and evolution of crop husbandry in order to utilize, in the best way, environment, climate, soil and so on. This is clearly illustrated by the extension of cultivated plants in the world in relation to different ecological conditions. We find the same thing when studying crop husbandry in individual countries or smaller regions. Crop husbandry in England is an interesting example of close adaptation to the changing environments which occur in that country, with herbage plants as dominating crops in the west and cash crop holdings mainly in the east. However, this may not hide the fact that the human exploitation of the natural resources of the earth has, at many places, taken place without considering the ecological requirements carefully enough. I am here thinking of the important regions which have been subjected to soil and wind erosion.

It is often emphasized that the world population is suffering from lack of food. A further increase in food production is urgent, including the production of some special nutrients like protein. If this is to be possible we have to increase our knowledge about the demands of plants on the environment and further adapt our plant material to environments suitable for cultivation. This means that increased attention must be paid to ecological research work in our future agricultural

scientific research. We must get a more complete knowledge about the specific demands of our cultivated plants on the environment and, not least, the climatic conditions. Our knowledge about these questions has, however, considerably increased during the last years, caused, among other things, by the supply of more modern and effective equipment and technology.

Experimental ecology has a particular value for research on cultivated plants. The study of natural adaptation has been considerably intensified from the moment when Professor Göte Turesson began his ecotype studies and ahead to modern works carried out by Dr Jens Clausen, Dr W. Hiesey and others. Their studies are a very important background for modern plant breeding and modern crop husbandry, both in order to illustrate the selection effect through the natural environment and to get new and valuable gene material in plant breeding work.

A primary condition for meaningful work in the field of experimental ecology is a sound knowledge of those environmental factors which influence crop development, crop production and product quality. Secondly, we need knowledge about the physiological background to increased production. Of the environmental factors, only climatic ones will be discussed here. The examples to which I will refer in this very brief survey and which shall serve as a background for my considerations are mainly taken from Swedish studies.

The word "climate" combines factors like radiation, temperature, water supply and so on. We can speak about macroclimate, which means the climate within larger or smaller regions. We have also the conception of local climate, which regards the climatic factors within more limited regions, and finally we have the micro- or bioclimate that describes the climatic factors which form around living plants.

The macroclimate in Sweden is characterized by great differences in temperature from the northern to the

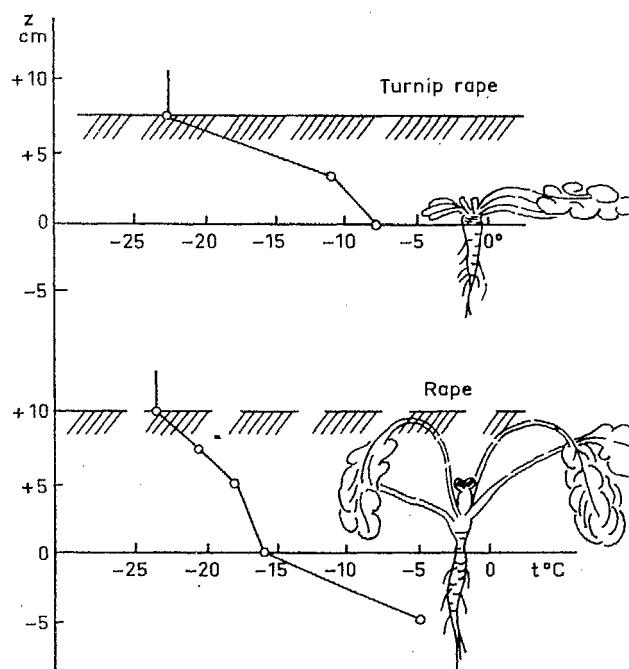


FIG. 1. Vertical temperature distribution in stands of rape and turnip rape at minimum temperature, Mosjö, 14 December 1955.

southern part of the country during the winter months. The mid-summer climate is not so variable. The average temperature for the month of July is thus about the same all over the country, and is favourable for crop husbandry, of course mainly in the northern regions. Variations in the local climate are often found in regions with large topographical differences or with more extreme climate. The nordic countries, also within limited regions, show the importance of such variations.

The influence of the bioclimate has been studied in winter rape and winter turnip rape by Dr Bengt Torsell in his work on over-wintering problems in these two species. The two crops have rather different growth habits in the vegetative stage, mostly to the disadvantage of rape. On one occasion, during a cold winter day with some snow cover, Dr Torsell measured the temperature in the growing point of rape and turnip rape and found a difference of as much as 10°C (see Fig. 1). A good knowledge of the bioclimate is often necessary to understand and explain the reaction of the plants as influenced by the climate.

Today we have a much better opportunity of evaluating all the components which constitute different types of climate, but more attention should be paid to climatic research, not least in order to give a basis for crop husbandry and for a suitable adaptation of plant material to prevailing climates. In this connexion, it is important to follow trends in the climate, as such trends may have a decisive influence on crop husbandry. As an example of a trend in climate, the average temperature for the

two months of July and August in Svalöv, southern Sweden, during the period 1921–65 are shown in Figure 2. This average temperature is characterized by a clear increase up to the 1940s and then followed by a decrease to 1965. The differences in average temperature during this period is as much as 2°C , which has had a serious effect on the ripening process of the cereals. The 1950s and the first part of the 1960s were characterized by delayed maturity and deterioration of the quality of some crops.

In modern agriculture there is also a great need for reliable weather forecasts, especially at harvest time. Weather forecasts by radio and television are used widely in Swedish agriculture. But, in addition, there is in some regions local information for special purposes. As already mentioned, during the 1950s, Sweden had unfavourable harvest conditions which seriously damaged bread grain quality. Sprouting, as a result of increased α -amylase formation, could often be found. To prevent such damages it was of importance to give farmers daily, local weather forecasts and also to inform them of changes in the average enzyme activity. This has resulted in an improvement of the quality of bread grains, as the farmers start the harvest before the drop in quality is too big (see Fig. 3).

A corresponding example can be given from the growing of peas for canning. For this crop the heat unit system is used to predict the harvest time. This system was put into practice after intensive studies by Dr Lennart Ottosson. There is a clear relationship between the sum of heat units and the flower and pod formation in different pea varieties, as is shown in Table 1. This

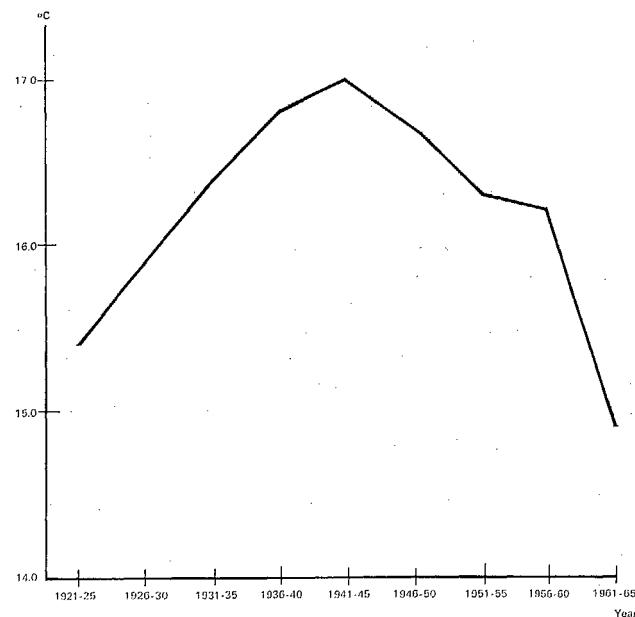


FIG. 2. Daily average temperature in Svalöv during July–August.

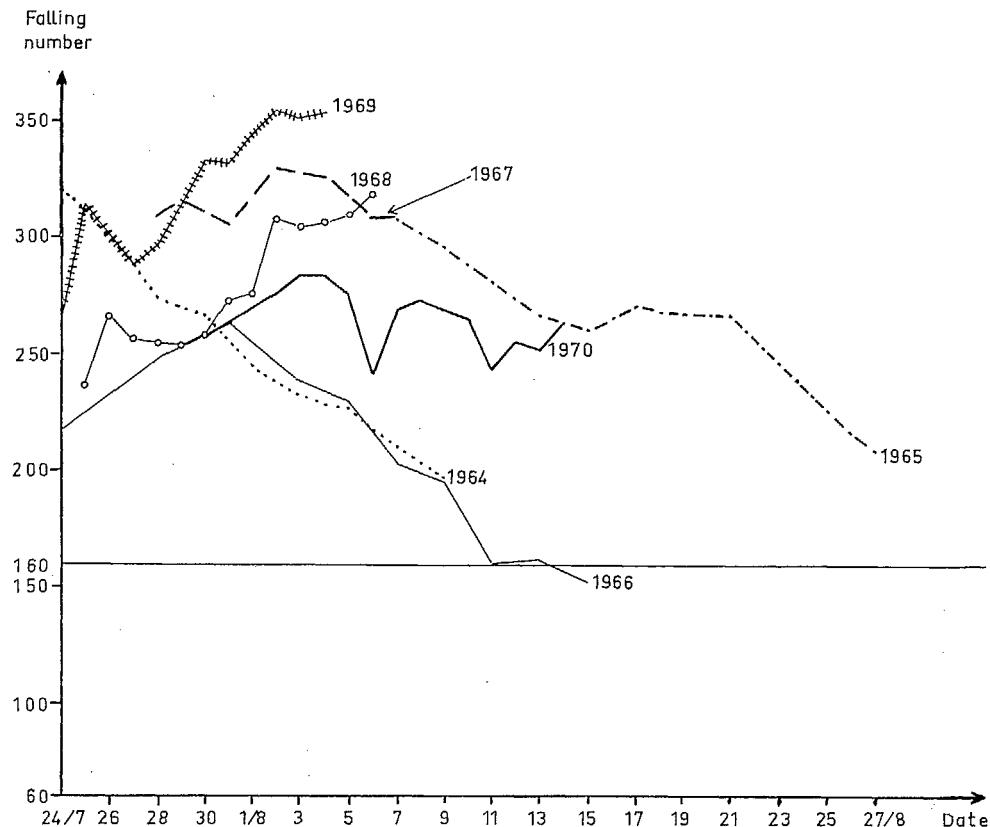


FIG. 3. Development of falling number in rye, Kungs II, during ripening. Mean values from the years 1964–70. The falling number is a measure of the α -amylase activity. The lower limit for the acceptance of rye as bread grain is 160 (9 g of flour, 25 ml of water).

relationship makes possible a careful planning of the growing of peas for canning and the time for the harvest of different pea varieties.

When regarding the interactions between climate and plant growth from an agricultural point of view, we sooner or later have to ask the question: What physiological properties of the plant material have to be considered in detail in our efforts to achieve a high level of productivity as well as a good quality of the harvested products? This question has to be put in relation to processes within the plants which are of special importance for the growth and development of the latter, both as single specimens and when growing in dense communities. These growth-limiting processes may be classified as primary and secondary ones in the sense that primary processes are those which are directly involved in the synthesis of organic matter and in the distribution and final storage of this matter within the plants, whereas secondary processes affect these activities only in an indirect manner, e.g. by counteracting an external stress. It must be emphasized, however,

that this does not mean that these latter processes are of secondary importance, on the contrary they may often limit plant productivity in a very decisive way and thus deserve our most careful attention.

Among the primary processes, those which are connected with the trapping of the energy from the sun and the further transformation of this energy into chemical compounds are of outstanding importance for determining the productivity of a plant community. The process of photosynthesis holds a key position in this sequence of events and its efficiency, together with the size and duration of the photosynthetically active surface, actually sets the upper limit of how much dry matter can theoretically be produced under the prevailing external conditions. Since part of the produced matter is lost during a plant's lifetime via respiration, this latter process, too, exerts a decisive influence on the magnitude of the ultimate dry matter production of a plant community.

The study of the two basic processes, photosynthesis and respiration, and how they respond to different

TABLE I. Peas for canning. Comparison between heat unit sums expected and observed

Variety	Node in flower	Heat unit sum expected	Heat unit sum observed
Alaska	10th	630	606
Surprise	10th	630	664
Kelvedon Wonder	11th	670	679
Pride	13th	750	745
Wrinkled peas F ₅	13th	750	755
Wrinkled peas F ₆	14th	790	780
Profusion	15th	830	817
Lincoln	15th	830	804

climatic factors, is thus of vital importance for the further development of agriculture, since it allows predictions of potential production levels in various climatic regions to be made. This will enable agronomists and plant breeders to set up productivity standards which they may use as aims and reference points in their particular efforts to increase the yielding ability of the cultivated plants.

However, it is not in the farmer's interest simply to produce a large amount of dry matter, this matter must have such a chemical composition as to satisfy the demands of the consumer and it must be stored in the right places within the plants, i.e. those parts which are to be harvested. Therefore the formation of assimilates, as well as their distribution, transformation, and final storage at different sites within the plants, are subjects which are of considerable interest to all those working with different aspects of crop productivity. Comparatively little is known about possible climatic effects on these particular processes and there is a strong need for intensified research work in this important field. As an example of such an attempt it should be mentioned that in Sweden a number of workers from different branches of biological and agricultural sciences are making a joint effort to investigate the influence of various climatic factors, such as temperature, day-length, etc., on the phenotypic expression of a specific genetic character causing an unusually high lysine content in the grain proteins of barley. Since this highly valuable character, which seems to be due to the effect of a single, recessive gene, has been found in a material originating from Ethiopia, it is of very great practical interest to find out how it expresses in other climatic environments and also to see, whether its response to the external conditions is changed if the gene is transferred to plants with a differing genotypic make-up. For investigations of this kind, growth chambers and phytotrons have proved to be indispensable analytical tools.

Another problem of great theoretical and practical importance concerns the induction of flowering in various plants. This induction is often strongly correlated

with certain climatic conditions, particularly day length and temperature, and in many cases the extension of a crop to new growth areas may be seriously hindered by a lack of adaptation of the flowering process to the climatic conditions in these areas. Thus an increased knowledge of the physiology of flower formation, and particularly of its dependence on different climatic factors, is highly desirable and, as a matter of fact, this field has also been rather extensively investigated during recent years. That the practical consequences of an improvement of the plant material in this respect may be enormous is best illustrated by the great success the new, photoperiodically insensitive, semi-dwarf wheat varieties have had in a great number of countries with widely varying climatic conditions.

With respect to production-determining processes of a secondary character, these often relate to the response of the plants to external stresses of one kind or another. At least three major kinds of such stresses can be distinguished: temperature stresses, water stresses, and nutrient stresses. Of these, only the two first ones are due to climatic influences and have thus been considered during this symposium. From an agricultural point of view the ability of the cultivated plants to survive, more or less, sudden adverse changes in climatic conditions is an absolute necessity. However, it is equally important that they can do so without losing their production capacity to a great extent, since a serious decrease in yield will result. Plant breeders and other research people in the field of agronomy, therefore, pay much attention to this particular aspect of stress physiology and the production of new varieties with an increased resistance to climatic stresses of various kinds is one way to secure a high and consistent production level, even under less favourable external conditions.

When plant breeding started in Sweden some eighty years ago, one of the first objectives was to improve the winter-hardiness of the autumn-sown wheat varieties which were introduced from countries with a milder climate. Ever since then the problem of resistance to low temperatures has continued to be one of high priority and many investigations, both on fundamental and applied aspects, have been carried out in Sweden, as well as in other countries. Despite the now classic works of Åkerman, Tumanov, Levitt and others on the basic processes underlying the development of cold resistance in overwintering plants, this phenomenon is still by no means fully understood and much work remains to be done. Also, with regard to other aspects of winter-hardiness, much more information is needed. In this connexion I would like to mention the investigations of Dr Bengt Torssell and Dr Rune Larsson and others at Ultuna, which have contributed considerably to a better understanding of the different mechanisms by which autumn-sown crops may escape the strains of a hard winter and still retain a relatively unaffected production capacity.

With respect to resistance to high temperatures, many fewer investigations have been made than on cold resistance. One reason may be that damage due to overheating is less frequent, another that it is often difficult to separate heat and drought effects, at least when considering the reactions of field grown crops. Clearly more basic information is needed on this problem.

Last, but not least, on this list of climatically induced stresses is the drought problem. In many parts of the world deficiency of water is the principal limiting factor in crop production and it is of vital importance in these regions both to find ways to increase the amount of available water by means of irrigation and other technical devices, and to improve the water economy of the plant material itself. This can be done by breeding more drought-resistant varieties. In addition, the possibility of reducing water consumption by applying chemical antitranspirants to the plants has received much attention during recent years. An effective weed control and a proper soil management may also reduce the water losses considerably and thus contribute to increased crop production. In order to evaluate the merits and drawbacks of these different approaches it is essential to have as complete information as possible regarding the interactions between plant and soil on the one hand and relevant climatic factors on the other. Again much has been done already, but the number of questions increases rather than decreases and there is an urgent need for much more precise information than is available at the moment. In this connexion it may also be pertinent to refer to the great importance of the use and misuse of the world's water resources has for our own health and comfort.

As already mentioned, the connexion between climate and plant development ought also to be judged in relation to genetic variation and the adaptability which occurs in different cultivated plants. The study of the natural selection, the occurrence of ecotypes and so on gives us very good information. Many examples could be given to illustrate the effect of natural selection, but only one shall be quoted here, taken from a paper by

TABLE 2. Growth at low temperature of climatic races of *Lolium perenne*

Climatic races <i>Lolium perenne</i>	Relative leaf expansion at 5°C (%)	Relative leaf expansion in December (%)	Survival at -5°C (%)	Mean temperature of winter months (°C)
Algiers	26.6	28.0	0	10
New Zealand	13.8	14.8	20	6
Oregon	12.4	13.9	13	4.5
Irish	12.2	12.8	47	6
Devon	11.1	13.2	36	6.5
Melle	9.5	13.7	57	1.5
Pajbjerg	7.6	11.0	73	0
Russian	7.7	9.7	92	-4

TABLE 3. Potato, chemical composition of tubers

	56-66° N. Field conditions	14-24 h Growth chamber
Dry matter	2-4% lower 66° N.	Similar
Crude protein	No tendency	Higher 14 h
Sugar	Higher 66° N.	Higher 24 h
Chlorogenic acid	Similar	Similar
Tyrosine	Higher 56° N.	Similar

Dr J. P. Cooper. Dr Cooper has studied different ecotypes of *Lolium perenne* and found in this study considerable differences in the leaf development at low temperature among these ecotypes (Table 2). The types which had a good leaf development at a fairly low temperature have also shown low survival at a temperature of -5 °C. For the plant breeder it is of great importance to carry out the testing of the breeding material in such a way that satisfactory information is obtained about the reaction to the climatic environment of new varieties. New means are hereby at his disposal. In certain cases we can use pure laboratory trials. The phytotron is, for many purposes, a valuable tool. We must know, however, that these new means do not fully reflect field conditions. Field trials must necessarily be carried out for the final calculation of reliability of different varieties as well as of different cultivation methods.

Dr Magnhild Umaerus has made penetrating studies of the reaction of different potato varieties, grown in a growth chamber and under field conditions, with day length as varying factor. In Table 3 some of the differences he found are shown. The table demonstrates very well that some characters are influenced in different ways in field studies at varying day length than in a growth chamber. Among such characters are dry matter, protein and tyrosine content of the tubers. The reason for this difference may be the fact that the field conditions are more complex and more difficult to define than the conditions in the growth chamber. The complex nature in the field has been demonstrated in all the studies of the relationship between yield from a cultivated plant and climatic factors. It is also important that the ecology of cultivated plants, and plant-soil problems, are studied at a micro-climate station, not least for studies of the bioclimate.

What I have said above is intended to emphasize the need for increased research into cultivated plant ecology in order to clarify further the conditions needed for increasing the world's supply of food. As already mentioned, this is a very important matter for the whole world. What possibilities exist for a more intensive utilization of the climate in order to obtain an increase in production? No one can give a correct answer, but it does not seem impossible that studies of growth and production with mathematic models based on collected climatological and physiological data can at least pro-

vide part of this information. Modern computers are able to analyse a great number of parameters. We must also remember the possibility we have to utilize solar energy still better.

Finally—and this is one of the intentions of this paper—I wish to stress the great value of this conference and I hope that it will result in intensified international

co-operation concerning the important problem for modern agriculture: better knowledge about the response of cultivated plants to climatic factors.

The physiological view points of this paper have been obtained from Dr Volkmar Stoy. His valuable contribution is highly appreciated.

Résumé

*Valeur des études climatiques pour l'agriculture moderne
Discours de clôture.
(E. Åkerberg)*

Les connaissances accumulées sur nos plantes cultivées et sur leurs caractères au cours de milliers d'années d'observations ont permis une adaptation ou une mise au point des modes de culture de façon à utiliser au mieux le milieu, le climat, le sol, etc. C'est ce qu'illustre clairement l'extension des plantes cultivées dans le monde en relation avec différentes régions écologiques. Et nous faisons les mêmes constatations lorsque nous étudions les modes de culture à l'échelle de pays particuliers ou de régions plus petites. Cela ne saurait toutefois dissimuler le fait que l'exploitation des ressources naturelles de la terre par l'homme a eu lieu dans de nombreux endroits sans qu'il soit suffisamment tenu compte des exigences de l'écologie. Je songe ici aux immenses étendues qui, par suite de mesures prises par l'homme, ont souffert de l'érosion du sol et de l'érosion éolienne.

On entend souvent dire aujourd'hui que la population du globe souffre d'une pénurie de produits alimentaires. Il est donc urgent d'en accroître encore davantage la production, et notamment la production de certaines substances nutritives particulières comme les protéines. Pour que cela soit possible, nous devons accroître nos connaissances sur les besoins spécifiques des plantes cultivées en ce qui concerne le milieu, et notamment le climat; en outre, nous devons adapter notre matériel végétal aux milieux de culture possibles. Cela signifie, en bref, que les recherches écologiques doivent prendre une importance et un développement accrus dans nos futures recherches agronomiques.

L'écologie expérimentale donne une base très importante aux recherches sur les plantes cultivées. Pour entreprendre des études sur l'écologie expérimentale, il faut d'abord que nous ayons une connaissance précise et sûre des facteurs du milieu qui influent sur le développement des végétaux, sur leur rendement et sur la qualité des produits obtenus, et aussi que nous connaissons les conditions physiologiques d'un accroissement de la production. Parmi les facteurs du milieu, nous n'examinerons ici que les facteurs climatiques.

Le mot climat englobe des facteurs comme le rayonnement, la température, les apports d'eau, etc. Nous pouvons parler de macroclimat quand il s'agit du climat d'une région plus ou moins grande. On peut parler aussi de climat local, lorsqu'il s'agit des facteurs climatiques d'une région plus limitée; enfin, nous avons le micro-climat ou bioclimat, c'est-à-dire les facteurs climatiques qui constituent le milieu environnant les plantes. Nous avons aujourd'hui de bien meilleures possibilités de juger et d'évaluer tous les éléments qui constituent les différents types de climat. De façon générale, il convient d'apporter une attention accrue aux recherches climatiques, notamment pour fournir une base encore meilleure à la mise au point de modes de cultures et à une adaptation satisfaisante du matériel végétal au climat environnant. A cet égard, il importe de suivre toutes les tendances du climat, car ces tendances peuvent influer de façon décisive sur le mode de culture et sur les rendements des cultures. Dans l'agriculture moderne, on a également un grand besoin de prévisions météorologiques, surtout au moment des récoltes, pourvu que ces prévisions soient fiables.

Quels sont les caractères physiologiques que nous devons étudier particulièrement pour obtenir une productivité suffisante et une qualité satisfaisante? Cette question peut être considérée en relation avec les processus végétatifs dont dépend le développement des végétaux: on distinguera les processus « primaires » et les processus « secondaires ». Parmi les premiers figurent la photosynthèse, la respiration, la croissance, la répartition et la mise en réserve des assimilats, la transition de la phase végétative à la phase reproductive; parmi les processus secondaires, on peut citer les apports d'eau, les apports de substance minérale, les contraintes thermiques, etc. C'est à l'interaction de ces processus avec les facteurs climatiques qu'il faut apporter une attention de plus en plus grande.

Le lien entre le climat et le développement de la plante doit également être considéré en fonction de la variation génétique et de l'adaptabilité dont font preuve nos plantes cultivées. L'étude de la sélection naturelle et la présence d'écotypes nous donnent ici de très bonnes informations de base. Pour le sélectionneur, il est particulièrement important d'expérimenter le matériel végé-

tal sélectionné afin d'obtenir des renseignements satisfaisants sur la réaction des variétés nouvelles au milieu climatique. On dispose donc, de ce fait, de moyens nouveaux. Dans certains cas, nous pouvons recourir aux essais en laboratoire seulement. Le phytotron est à de nombreux égards un instrument utile. Mais il nous faut savoir que ces moyens nouveaux ne reflètent qu'imparfaitement les conditions sur le terrain. Il est indispensable d'effectuer des essais sur le terrain pour calculer finalement la fiabilité des différentes espèces ainsi que des différentes méthodes de culture.

Ce que nous venons de dire devrait confirmer la nécessité de multiplier les recherches sur l'écologie des plantes cultivées, afin de connaître mieux encore les conditions que doit remplir la production dans le monde entier de produits alimentaires végétaux. Il s'agit, nous l'avons vu, d'une question très importante pour l'ensemble de la planète. Quelles possibilités existe-t-il d'une utilisation plus intensive du climat pour réaliser un gain de

production? Il ne semble pas impossible que des études de croissance et de production au moyen de modèles mathématiques fondés sur un ensemble de données climatologiques et physiologiques puissent fournir une information de ce genre. Les machines modernes de traitement des données peuvent analyser un grand nombre de paramètres. Nous ne pouvons pas non plus oublier la possibilité qui nous est offerte de mieux utiliser encore l'énergie solaire, qui n'intervient aujourd'hui que dans une très faible mesure dans la production de substances organiques par les végétaux.

Enfin — et telle était mon intention en rédigeant le présent article — je voudrais souligner l'utilité de cette conférence et j'espère qu'il en résultera une intensification de la coopération internationale concernant l'important problème de l'agriculture moderne: à savoir une meilleure connaissance de la réponse des plantes cultivées aux facteurs climatiques.

List of participants / Liste des participants

- ÅBERG E., Department of Plant Husbandry, Agricultural College of Sweden, S-750 07 Uppsala (Sweden/Suède).
- ÅKERBERG E., Swedish Seed Association, S-26800, Svalöv (Sweden/Suède).
- AL-ANI, T. A., Institute for Applied Research on Natural Resources, Abu-Ghraib, Baghdad (Iraq/Irak).
- ALMGARD, G., Department of Genetics and Plant Breeding, Agricultural College of Sweden, S-75007 Uppsala (Sweden/Suède).
- ANDERSSON, L. Agricultural College of Sweden, S-75007 Uppsala (Sweden/Suède).
- ASLYNG, H. C., Hydrotechnical Laboratory, The Royal Veterinary and Agricultural University, Bülowsgade 23, 1870 Copenhagen V (Denmark/Danemark).
- ASTON, M., Botany Department, School of General Studies, Australian National University, Box 4, Canberra 2600 ACT (Australia/Australie).
- BAADSHAUG, O. H., Norwegian Agricultural Research Board, NLH, Box 47, 1432 Vollebekk, Lyngveien 14 C, A s (Norway/Norvège).
- BARRS, H. D., Division of Irrigation Research, CSIRO, Griffith, N.S.W. 2680 (Australia/Australie).
- BAUMGARTNER, A., Meteorologisches Institut, 8 München, Amalienstrasse 52 (Federal Republic of Germany/République fédérale d'Allemagne).
- BERGER, A., Centre national de la recherche scientifique, B.P. 1018, Montpellier (France).
- BERGGREN, R., Swedish Institute of Meteorology and Hydrology, Box 34006, Stockholm (Sweden/Suède).
- BIERHUIZEN, J. F., Agricultural University, Department of Horticulture Haagsteeg, P.O. Box 30, Wageningen (Netherlands/Pays-Bas).
- BILDERLING, N. de, Centre national de la recherche scientifique, Phytotron, 91 Gif-sur-Yvette (France).
- BLONDON, F. Centre national de la recherche scientifique, 91 Gif-sur-Yvette (France).
- BONHOMME, Institut national de la recherche agronomique, CRAAG, Domaine Dyclos, Petit-Bourg, Guadeloupe (France).
- BOYER, Y. Centre national de la recherche scientifique, Laboratoire de physiologie végétale, 1, rue Victor-Cousin, 75005 Paris (France).
- BRAG, H., Department of Plant Physiology, Sölvegatan 35, Lund (Sweden/Suède).
- BROUWER, R., Laboratory for Plant Physiological Research, Gen. 11, Foulkesweg 72, Wageningen (Netherlands/Pays-Bas).
- BRUN, W. A., Department of Agronomy and Plant Genetics, University of Minnesota, St Paul, Minnesota 55101 (United States of America/États-Unis d'Amérique).
- CALDER, M., Botany School, University of Melbourne, Parkville, Victoria 3052 (Australia/Australie).
- CAPRIO, J. M., Plant and Soil Science Department, Montana State University, Bozeman, Montana 59715 (United States of America/États-Unis d'Amérique).
- CHOUARD, P., directeur du Phytotron, Centre national de la recherche scientifique, 91 Gif-sur-Yvette (France).
- CHRISTERSSON, L., Institute of Plant Physiology, University of Lund, Lund (Sweden/Suède).
- DENMEAD, O. T., CSIRO, Division of Plant Industry, P.O. Box 109, Canberra City, A.C.T. 2601 (Australia/Australie).
- DUDA, M., Czechoslovak Academy of Sciences, Botanical Institute, Dubravská cesta 26, Bratislava (Czechoslovakia/Tchécoslovaquie).
- ECKARDT, F. E., Centre national de la recherche scientifique, B.P. 1018, 34 Montpellier (France).
- ELOWSON, S., Royal College of Forestry, 10405 Stockholm (Sweden/Suède).
- ERLANDSON, G., University of Lund, Department of Plant Physiology, Sölvegatan 35, Lund (Sweden/Suède).
- EVANS, L. T., CSIRO, P.O. Box 109, Canberra ACT 2601 (Australia/Australie).
- FALK, S., Institute of Plant Physiology, University of Gothenburg, S-41319 Göteborg (Sweden/Suède).
- FITZPATRICK, E. A., Department of Agronomy, University of Western Australia, Nedlands, Western Australia 6009 (Australia/Australie).
- FLOROV, École supérieure forestière, Sofia 56 (Bulgaria/Bulgarie).
- FORS, L., Department of Plant Ecology, University of Lund, O Vallgatan 14, 22361 Lund (Sweden/Suède).
- FRANÇOIS, J., Laboratoire d'écologie végétale, Faculté des sciences agronomiques de l'État, B-5800 Gembloux (Belgium/Belgique).

List of participants / Liste des participants

- FRANQUIN, P., Office de la recherche scientifique et technique outre-mer, 70, route d'Aulnay, 93 Bondy (France).
- GALE, J., Hebrew University of Jerusalem, Department of Botany, Jerusalem (Israel/Israël).
- GARDNER, W. R., Soils Department, University of Wisconsin, Madison, Wisconsin 53706 (United States of America/États-Unis d'Amérique).
- GOPAL, B., Banaras Hindu University, Department of Botany, Varanasi-5 (India/Inde).
- GÖTLIND, G., Department of Plant Physiology, Uppsala University, Skolg. 21, 75221 Uppsala (Sweden/Suède).
- HELDAL, B., Agricultural College of Norway, 1432 Vollebekk (Norway/Norvège).
- HELLKVIST, J., Department of Physiological Botany, University of Uppsala, Box 540, 75121 Uppsala (Sweden/Suède).
- HELLQUIST, S., The Phytotron of the Royal College of Forestry, S-10405 Stockholm 50 (Sweden/Suède).
- HERMELIN, T., Agricultural College of Sweden, Department of Genetics and Plant Breeding, S-75007 Uppsala 7 (Sweden/Suède).
- HOČEVAR, A., Biotechnical Faculty, University of Ljubljana, Krekov trg 1, Ljubljana (Yugoslavia/Yougoslavie).
- HULTEN, H., Royal College of Forestry, 10405 Stockholm 50 (Sweden/Suède).
- HYLMO, B., Nordreco AB, Bjuv S (Sweden/Suède).
- IMPENS, I., University of Ghent, Faculty of Agricultural Sciences, Laboratory of Plant Ecology, Coupure Links 533, 9000 Ghent (Belgium/Belgique).
- INGELÖC, T., Royal College of Forestry, S-10405 Stockholm 50 (Sweden/Suède).
- INGESTAD, I., Royal College of Forestry, S-10405 Stockholm 50 (Sweden/Suède).
- JACQUES, R., sous-directeur du Phytotron, Centre national de la recherche scientifique, 91 Gif-sur-Yvette (France).
- JAKOVLEV, N. N., Vavilov's Institute of Plant Industry, Lenigrad (U.S.S.R./URSS).
- JANES, B. E., University of Connecticut, Storrs, Connecticut 06268 (United States of America/États-Unis d'Amérique).
- JARVIS, P., University of Aberdeen, Department of Botany, St Machar Drive, Aberdeen AB92UD (United Kingdom/Royaume-Uni).
- JONASSEN, G., State Experiment Station Landvik, 4890 Grimstad (Norway/Norvège).
- KENT, A. J., Mars Ltd., Slough, Bucks (United Kingdom/Royaume-Uni).
- KJER, G., Hansen Hydroteknisk Laboratorium, Büllowsvej 23, Copenhagen (Denmark/Danemark).
- KLAUSING, O., Hess. Landesamt für Gewässerkunde, 6101 Seeheim/Bergstrasse, Waldstr. 3 (Federal Republic of Germany/République fédérale d'Allemagne).
- KORNHER, A., Sunnerstavägen 19B, 75251 Uppsala (Sweden/Suède).
- KRAMER, P. J., Duke University, Department of Botany, Durham, N.C. (United States of America/États-Unis d'Amérique).
- KREEB, K., University Stuttgart-Hohenheim, 7 Stuttgart-Hohenheim, Kirchnerstr. 5 (Federal Republic of Germany/République fédérale d'Allemagne).
- KRISHNAN, A., Climatologist, Central Arid Zone Research Institute, Jodhpur (India/Inde).
- KRISTENSEN, K. J., Royal Veterinary Agricultural University, Hydrotechnical Laboratory, Höjbakkegaard, 2630 Taastrup, Copenhagen (Denmark/Danemark).
- KVIFTE, G., Agricultural College of Norway, 1432 Vollebekk (Norway/Norvège).
- KYLIN, A., Department of Botany, University of Stockholm, S-10405 Stockholm (Sweden/Suède).
- LANDSBERG, J. J., University of Aberdeen, Department of Botany, Aberdeen AB 9 2UD (United Kingdom/Royaume-Uni).
- LEAF, E. L., Grassland Research Institute, Hurley, Maidenhead, Berks. (United Kingdom/Royaume-Uni).
- LEHTONEN, P., Institute of Reforestation, Royal College of Forestry, 10405 Stockholm (Sweden/Suède).
- LEMEUR, R., University of Ghent, Faculty of Agricultural Sciences, Laboratory of Plant Ecology, Coupure Links 235, Ghent (Belgium/Belgique).
- LEVITT, J., Department of Botany, Tucker Hall, University of Missouri, Columbia, Mo. (United States of America/États-Unis d'Amérique).
- LEXANDER, K., Department of Plant Physiology, University of Lund, Lund (Sweden/Suède).
- LOMAS, J., Meteorological Service, P.O. Box 25, Bet-Dagan (Israel/Israël).
- LUNDQVIST, J., Department of Plant Biology, University of Uppsala, Box 559, 75122 Uppsala 1 (Sweden/Suède).
- MÄDE, A., Martin-Luther Universität, Section Plant-Production, Grosse Steinstrasse 81, DDR 402 Halle (Saale) (German Democratic Republic/République démocratique allemande).
- MARTINIC, Z., Faculty of Agriculture, Zagreb University, P.O. Box 95, Zagreb (Yugoslavia/Yougoslavie).
- MATTSON, L., Agricultural College of Sweden, Department of Genetics and Plant Breeding, S-75007 Uppsala (Sweden/Suède).
- MELLART, E. A. R., Agricultural University, Laboratory of Physics and Meteorology, Wageningen (Netherlands/Pays-Bas).
- MILLINGTON, R. J., United States Department of Agriculture, Soil and Water Conservation Research Department and University of Illinois, S-212 Turner Hall, University of Illinois, Urbana, Illinois 61801 (United States of America/États-Unis d'Amérique).
- MOUSSEAU, M., Centre national de la recherche scientifique, 91 Gif-sur-Yvette (France).
- NORDENSKIOLD, H., Department of Genetics and Plant Breeding, Agricultural College of Sweden, S-75007 Uppsala (Sweden/Suède).
- NORDIN, A., University of Lund, Sölvegatan 35, Lund (Sweden/Suède).
- NYSTRÖM, S., Department of Plant Husbandry, Agricultural College of Sweden, S-75007 Uppsala (Sweden/Suède).
- ODIN, H., Royal Forestry College, 10405 Stockholm (Sweden/Suède).
- OHLENDORF, H., Department of Genetics and Plant Breeding, S-75007 Uppsala (Sweden/Suède).
- OKALI, D., Department of Botany, University of Ghana, Legon, Accra (Ghana).
- OLVANG, H., Agricultural College of Sweden, S-75007 Uppsala (Sweden/Suède).
- PALMER, A. F. E., International Maize and Wheat Improvement Center, Londres 40, Apdo. Postal 6-641, Mexico 6, D.F. (Mexico/Mexique).
- PARCEVAUX, S. de, Institut national de la recherche agronomique, Station centrale de bioclimatologie, route de Saint-Cyr, 78 Versailles (France).

- PEACOCK, J. M., Grassland Research Institute, Hurley, Maidenhead, Berks. (United Kingdom/Royaume-Uni).
- PERRIER, A., Institut national de la recherche agronomique, route de Saint-Cyr, 78 Versailles (France).
- PERTTU, K., Department of Reforestation, 10405 Stockholm 50 (Sweden/Suède).
- PUCKRIDGE, D. W., Waite Agricultural Research Institute, University of Adelaide, Glen Osmond, South Australia (Australia/Australie).
- RASCHKE, K., MSU/AEC Plant Research Laboratory, Michigan State University, East Lansing, Michigan 48823 (United States of America/États-Unis d'Amérique).
- ROBERTSON, G. W., Research Station, Canadian Department of Agriculture, P.O. Box 1030, Swift Current, Sask. (Canada).
- RODSKJER, N., Agricultural College of Sweden, Laduwägen 13, S-75247 Uppsala (Sweden/Suède).
- ROOK, D. A., New Zealand Forest Service, Forest Research Service, Private Bag, Rotorna (New Zealand/Nouvelle-Zélande).
- ROSENBERG, N. J., Agricultural Climatology, University of Nebraska, Lincoln, Nebraska 68503 (United States of America/États-Unis d'Amérique).
- RIJTEMA, P. E., Institute for Land and Water Management Research, P.O. Box 35, Wageningen (Netherlands/Pays-Bas).
- RUFELT, H., Institute of Physiological Botany, University of Uppsala, Kohagsv. 2, S-75252 Uppsala (Sweden/Suède).
- SCHNEIDER, T., Laboratory of Physics and Meteorology, Agricultural University, Wageningen (Netherlands/Pays-Bas).
- SHAWCROFT, R. W., United States Department of Agriculture, Agriculture Research Service, Central Great Plains Field Station, Box K, Akron, Colo. (United States of America/États-Unis d'Amérique).
- SIREN, G., Royal College of Forestry, Institute of Reforestation, 10405 Stockholm (Sweden/Suède).
- SKAAR, E., Department of Geophysics, University of Bergen, Geof. Institute, AVD.B., Bergen (Norway/Norvège).
- SKJELVAG, A. O., Norwegian Agricultural Research Board, Agricultural College of Norway, 1432 Vollebekk (Norway/Norvège).
- SLAVIK, B., Czechoslovak Academy of Sciences, Institute of Experimental Botany, Flemingovo 2, Prague 6 (Czechoslovakia/Tchécoslovaquie).
- STANHILL, G., Volcani Institute of Agricultural Research, P.O. Box 15, Rehovot (Israel/Israël).
- STERN, W. R., Agronomy Department, University of Western Australia, Nedlands, Western Australia 6009 (Australia/Australie).
- STICTER, C. J., Laboratory of Physics and Meteorology, Agricultural University, Duivendaal 2, Wageningen (Netherlands/Pays-Bas).
- STOY, C. V., Swedish Seed Association, S-26800 Svalöv (Sweden/Suède).
- TAERUM, R., Botanical Institute, 1432 Vollebekk (Norway/Norvège).
- TARSIA, N., ENCC, Centro Sperimentazione Agricola e Forestale, P.O.B. 9079, 00100 Roma (Italy/Italie).
- TURNER, N. C., Connecticut Agricultural Experiment Station, P.O. Box 1106, New Haven, Connecticut 06504 (United States of America/États-Unis d'Amérique).
- TUVESSON, M., Department of Plant Husbandry, Agricultural College of Sweden, S-75007 Uppsala (Sweden/Suède).
- UMAERUS, M., Swedish Seed Association, S-26800 Svalöv (Sweden/Suède).
- VAN BABEL, C. H. M., Texas A and M University, 427 Biological Sciences, College Station, Texas 77843 (United States of America/États-Unis d'Amérique).
- VAN DER VALK, G., Bulb Crop Research Center, Heerweg 345, Lisse (Netherlands/Pays-Bas).
- VARTANIAN, N., Faculté des sciences, Écologie végétale, 91 Orsay (France).
- VARTAPETIAN, B., Institute of Plant Physiology, Academy of Sciences of the U.S.S.R., Leninsky prospekt 33, Moscow (U.S.S.R./URSS).
- VERI, G., Laboratorio di Radiobiochimica ed Ecofisiologia vegetali, Via dei Primate Sportivi 21, C.N.R. Rome (Italy/Italie).
- VIEIRA DA SILVA, J. B., Office de la recherche scientifique et technique outre-mer, 24, rue Bayard, 75008 Paris (France).
- WADSWORTH, R. M., University of Reading, Botany Department, University of Reading, London Road, Reading RG1 5AQ (United Kingdom/Royaume-Uni).
- WASSINK, E. C., Agricultural University, Laboratory of Plant Physiological Research, Gen. Foulkesweg 72, Wageningen (Netherlands/Pays-Bas).
- WEILLE, G. A. de, Royal Netherlands Meteorological Institute, De Bilt (Netherlands/Pays-Bas).
- WELANDER, M., Department of Plant Physiology, University of Lund, Sölvegatan 35, Lund (Sweden/Suède).
- WESSELIUS, J., Laboratory of Plant Physiological Research, Agricultural University, Wageningen (Netherlands/Pays-Bas).
- WEST, S. H., United States Department of Agriculture and University of Florida, Agronomy Department, University of Florida, Gainesville, Florida 32601 (United States of America/États-Unis d'Amérique).
- WHITEHEAD, F. H., Imperial College, Department of Botany, London S.W. 7 (United Kingdom/Royaume-Uni).
- WÜNSCHE, U., Department of Plant Husbandry, Agricultural College of Sweden, S-75007 Uppsala 7 (Sweden/Suède).
- ZOBERI, M. H., University of Ife, Institute of Physiological Botany, Ile-Ife (Nigeria/Nigéria).

INTERNATIONAL ORGANIZATIONS / ORGANISATIONS INTERNATIONALES

COCHEMÉ, J., Sous-division de l'écologie végétale et des ressources génétiques, Division de la production végétale et de la production des plantes, FAO, via delle Terme di Caracalla, Rome (Italy/Italie).

RIJKS, D. A., OERS/PNUD/FAO, B.P. 154, Dakar (Senegal/Sénégal).

SMITH, L. P., WMO, Meteorological Office, Bracknell (United Kingdom/Royaume-Uni).

UNESCO SECRETARIAT / SECRÉTARIAT DE L'UNESCO

BATISSE, M., Director, Natural Resources Research Division,
SCE, Unesco, Place de Fontenoy, 75700 Paris (France).

FOURNIER, F., Consultant, Natural Resources Research Division,
SCE, Unesco, Place de Fontenoy, 75700 Paris (France).

SLATYER, R. O., Consultant, Natural Resources Research Division,
SCE, Unesco, Place de Fontenoy, 75700 Paris (France).