Growth and Development of Chickpeas under Progressive Moisture Stress

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INTRODUCTION

Most studies on the effects of moisture stress on crop plants have been concerned with the effects of intermittent droughts. Such stresses can occur under field conditions in climates or seasons characterized by irregular and intermittent rainfall, for example the monsoon (kharif) season in India. However there are other situations in which crops are grown during seasons with little or no rainfall, and with no supplemental irrigation, where they depend on the moisture that is present in the soil at the beginning of the cropping season; this moisture in the soil is progressively depleted during the growth of the crop. Such is the situation, for example, in the winter rainfall areas of the West Asian and North African regions where in the summer the growth and development of crops depend on the moisture accumulated in the soil during the winter, and in India where winter (rabi) crops depend on the moisture stored in the soil during the preceding monsoon season. Crops taken during the winter season make up about 35% of the total foodgrain production in India and about 60% of the total production of pulses (Malone, 1974). In India, crops taken during this season include wheat, sorghum, chickpeas, and safflower and in the winter rainfall areas of the West Asian and North African regions, wheat, barley, and chickpeas.

This paper deals with chickpeas (Cicer arietinum L.) grown in the winter season in India. (About 87% of the total world acreage of chickpeas is in the Indian subcontinent: 78% in India, 9% in Pakistan (van der Maesen, 1972).) However, many of the physiological problems may be similar for summer-grown chickpeas in West Asia, North Africa, and elsewhere, and also for other crops that are grown under comparable conditions.

The winter growing season in the Indian subcontinent is succeeded by the hot dry summer season during which crops cannot generally be grown except under irrigation. The transition from the winter to summer seasons is quite rapid. As the night and day temperatures begin to rise the relative humidities both in the night- and daytime fall. Daily open-pan evaporation increases from 4 mm or below to more than 8 mm within a few weeks. This period of transition occurs earlier in Peninsular India (late January–February) than in the Indo-Gangetic plain of Northern India (mid-March–April), and consequently the winter growing season is longer in the North than the South.

Because the winter cropping season is not "open-ended," crops of too long a duration or which are planted too late in the season undergo a "forced maturation" as the summer season begins; this has an adverse effect on the yield. In these circumstances one of the most important physiological characteristics in winter crops such as chick-peas is an appropriate growth-duration, and one of the most important agronomic factors affecting yield is the time of planting.

In the shorter growing season of Peninsular India short-duration cultivars generally give higher yields; longer duration cultivars do better in North India, where the longer growing season permits greater overall levels of yield to be achieved. These general principles are widely known and recognized by plant breeders.

A further important aspect of the winter growing season in the Indian subcontinent is that winter crops are generally sown after the cessation of the monsoon rains; the seeds are sown in soil that is drying out.

In India the average yields of chickpeas obtained by farmers are often only about one-quarter or less than a quarter of those that can be achieved under nonirrigated conditions in experiment stations within the same region with similar cultivars. In many parts of India one of the most important reasons for the low yields seems to be that the plant stands in farmers' fields are poor owing to the failure of many of the seeds to germinate because of inadequate moisture in the seedbed.

Agronomic approaches to this problem include improved seed drills, higher seed rates, and earlier sowings. However in the major chickpea-growing area of Northwestern India, where the monsoon rains generally end in September, although earlier sowings result in better germination of chickpeas, all the limited range of cultivars that have been tested so far are harmed by the high temperatures prevailing at that time (average maximum temperatures around 35 °C) (S. M. Virmani, personal communication, based on research carried out by the All India Coordinated Dryland Project Centre at Hissar, Haryana, India). For this reason plantings must be delayed until the temperatures decline by late September and October, when the moisture conditions in the seedbed are less favorable for germination.

In relation to stand establishment in such conditions, the selection, or development by breeding, of cultivars tolerant to higher temperature in the seedling stage might enable earlier sowings to be made. This is feasible in fields that have been fallow during the monsoon season where there is no need to wait for the harvest of a monsoon crop.

A further physiological character that could be very useful in achieving better plant stands in situations where chickpeas are sown after the cessation of the rains would be an improved ability to germinate under conditions of limited soil moisture. In some preliminary investigations we have found that there are considerable varietal differences for this character.

On an experiment station with irrigation facilities good stands can be assured by means of irrigation. But irrigation cannot be the answer to this problem in many of the regions where chickpeas are grown by farmers who are unable to irrigate the crop. As and when irrigation and other improved facilities become available to farmers, their general tendency is to replace chickpeas by more remunerative crops, such as high-yielding cultivars of wheat. In North India between 1960 and 1970 for these reasons, the area under chickpeas declined by over 30% (van der Maesen, 1972). Most of the effort directed toward the improvement of chickpeas must be carried out on the assumption that the crop will usually receive little or no irrigation under farmers' conditions.

In this paper we describe some of our observations on growth and development of unirrigated chickpeas at Hyderabad, where there is an 80% probability, that is, a probability that in 8 of 10 years, there will be no rainfall between November and February, during the chickpea growing season. In Northwestern India there are generally some winter rains between January and March, but at New Delhi, for example, at the 80% probability level the total rainfall in this period is 4.1 mm and at the 60% probability level 22.3 mm; the annual average rainfall is 715 mm (data from Anon., 1971). This illustrates that, even in those regions of India where there is a high probability of some rainfall during the chickpea growing season, the amounts of rainfall are generally small and the great majority of the water requirements of the crop must be met from moisture already present in the soil.

MATERIALS AND METHODS

The experiments reported here were carried out at the ICRISAT farm (Hyderabad) on vertisols (deep black cotton soil) which had been left fallow during the monsoon season. The soil (pH 7.5) was low in available nitrogen and phosphate. Single superphosphate at the rate of 45 kg P₂O₅/ha and zinc (45 kg ZnSO₄/ha) were added and incorporated at the beginning of the monsoon season. The plants

were sown on 1 October 1974 by hand at a spacing of 30×10 cm in replicated plots (plot size: 6×8 m). Two seeds were sown per hill and plants were thinned in the early seedling stage to give a uniform stand. For growth analysis samples consisting of five plants per plot were separated into their component parts (rachis, pinnae, stems, pedicels and peduncles, flowers, pods, nodules, and extractable roots). Leaf area of the pinnae was measured with a Hayashi-Denkoh Automatic Area Meter, model AAM-7.

The development of the root system of plants in the same plots as those from which samples were taken for growth analysis was studied by taking soil cores with a mechanical soil auger (tube diameter 76 mm). The cores were centered on the stumps of plants which were cut off immediately beforehand. Three replicates were taken on each occasion from each plot. Nearby cores were taken with a smaller auger (tube diameter 1 cm) for the gravimetric determination of soil moistures (two replicates per plot). The cores were divided at 15-cm intervals representing 15-cm increments in depth. For root and nodule counts the soil samples were soaked in water overnight and then washed thoroughly in running water in a sieve. The numbers and lengths of the root fragments and of nodules were recorded. The nodules were dried in an oven at 80 °C to constant dry weight for dry weight determinations. These operations were carried out by the ICRISAT Farming Systems Section under the supervision of Dr. Sardar Singh.

A trial to investigate the effects of shading during the reproductive phase was carried out with a late cultivar, cv. F-502, planted on 11 November 1975. Flowering began on 17 January 1976 and the shading treatments began soon afterward, on 22 January and were continued until the time of harvest (15 March 1976). The shades consisted of white cotton cloth, purchased locally, of three thicknesses which intercepted 50, 75, and 80% of the photosynthetically active radiation at noon (measured with a quantum photometer sensitive to light in the 400-700 m_{\mu} range: Lambda Instruments Corporation). The cloth was fixed approximately 30 cm above the plant canopy, supported by bamboo stakes. The sides were left open and there was a free circulation of air beneath the shades. Maximum temperatures beneath the shades were slightly lower (1-2°C) than those in nonshaded plots, and minimum temperatures slightly (1-2°C) higher. Within each of the three replicates the four treatments (nonshaded control, 50, 75, 80% shade) were randomized. The size of the shaded and control plots was 2.0×1.8 m.

In order to investigate the effects of row-spacing on the growth

and development of the plants, "fan" plantings were made with 4 mlong rows diverging from a central point to a row-to-row spacing of 1 m at the periphery. The plant-to-plant spacing within the rows was 10 cm.

RESULTS

Growth and Development

The pattern of accumulation and distribution of dry matter and of development of leaf area and of pods is illustrated by the data for two cultivars of Indian origin ('desi' cultivars), shown in Figures 1 and 2. Cv. JG-62 is an early cultivar of appropriate duration for cultivation in the relatively short growing season at Hyderabad; cv. T-3 is a medium-late cultivar developed in North India. In cv. JG-62 the leaf area continued to increase and there was also a net increase in stem weight until about halfway through the reproductive phase. However in cv. T-3 there was little net gain in weight of these vegetative structures after flowering, and the leaf area began to decline early in the reproductive phase. In both cultivars there was no net gain in pod number per plant after the leaf area index (LAI) started to decline rapidly.

The decline in LAI and leaf dry weight per plant (Figures 1 and 2) took place because of the senescence and abscission of leaves. In both 1974-1975 and 1975-1976 when we compared a number of different cultivars we found that the range of time in which the onset of the decline in LAI began was much narrower (about 70 to 80 days after sowing) than the range of time to the beginning of flowering (37 to 72 days after sowing); this decline began earlier in the reproductive phase of the late cultivars than the early ones, in a pattern similar to that illustrated in Figures 1 and 2.

The pattern of root growth of these plants is illustrated in Figure 3. As the soil in the surface zones dried out there was little or no net development of roots in these zones, but deeper down, where the water content of the soil was higher, roots development continued almost until the end of the reproductive phase. With time the growth of roots took place in progressively deeper zones of the soil, down to 120 cm. The percentage of the total root system in the deeper zones increased until about 50% of the total length of roots were found below 60 cm (Figure 4).

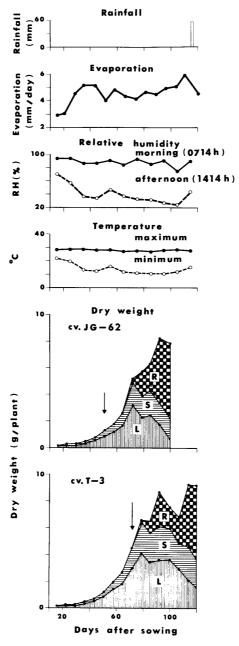


Figure 1. Changes in total dry matter and distribution of dry matter in leaves (L), stems (S), and reproductive structures (R) of chickpea cvs JG-62 and T-3 throughout the growing season with data on rainfall, evaporation, relatively humidity, and temperature during the same period. The times at which flowering began in 50% of the plants are indicated by arrows.

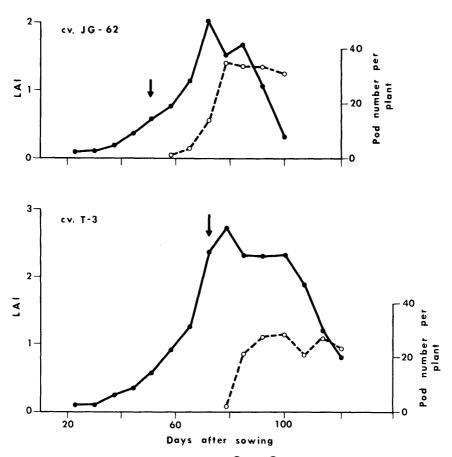


Figure 2. Changes in leaf area index (\bigcirc — \bigcirc) and pod number per plant (\bigcirc --- \bigcirc) during the growing season of chickpea cvs. JG-62 and T-3.

Practically all the nodules were found in the 0 to 15 cm zone; occasionally some were present in the 15 to 30 cm zone, but these never accounted for more than 10% of the total nodule mass. The change in the dry weight of nodules per plant with time is shown in Figure 5. Although there were large sampling errors involved in the collection of nodules, a general pattern of increase during the vegetative phase and decline during the later part of the reproductive phase can be seen. In cv. JG-62 the nodule mass continued to increase for at least 1 week after flowering began and in some other cultivars we have observed increases for up to 3 weeks after flowering.

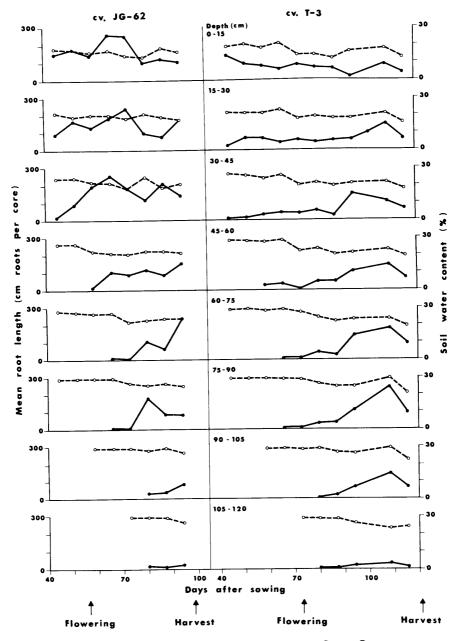


Figure 3. Changes with time in the lengths of roots (\bigcirc — \bigcirc) of chickpea cvs. JG-62 and T-3 and moisture content (\bigcirc --- \bigcirc) at different depths of the soil.

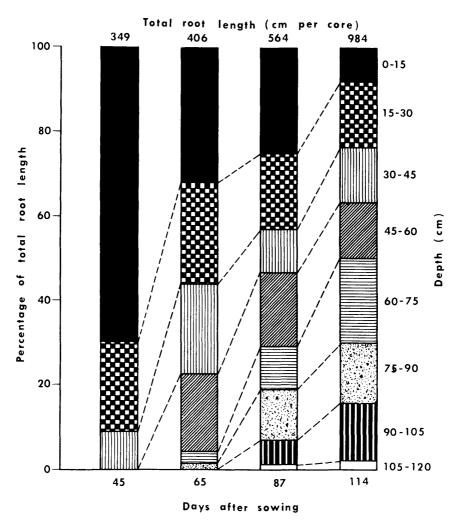


Figure 4. Percentage of the total root length of chickpeas cv. T-3 at different depths at four stages of growth.

Effects of Flower Removal

When pod development is prevented by the repeated removal of flowers from the plants, the senescence of the plants is delayed and they remain green and continue growing after control plants have matured and dried. The root development of such plants in the deeper

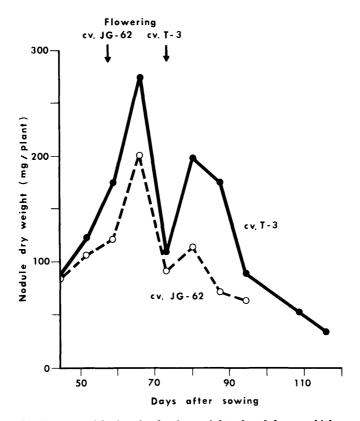


Figure 5. Changes with time in the dry weight of nodules on chickpeas cvs. JG-62 and T-3.

zones of the soil is greater than in controls, and the nodules continue developing, rather than regressing as they do during the pod-filling period in the controls. For example in cv. T-3 in control plants the mass of the nodules declined to less than 50 mg/plant by the time of harvest (Figure 5), while plants from which flowers had been recovered had a nodule mass of 400 mg/plant at that time. But although senescence can be delayed by preventing pod development, it cannot be prevented indefinitely; as the temperatures rise and the relative humidities fall at the end of the winter season, even these podless plants show increasing signs of stress. They shed all but their youngest leaves and their nodules regress.

Effects of Soil Moisture

Irrigation of chickpeas during the reproductive phase generally leads to increased yields, unless the soil moisture content is already quite high before the irrigation treatment. Not surprisingly, the effects of irrigation are pronounced on soils with a low water-holding capacity in which the profile dries out more rapidly in the dry winter season. In an alfisol (shallow red soil) we have observed four- to tenfold increases in yield and dry matter production with irrigation. In such experiments the lack of moisture results in an earlier senescence and maturation of the plants.

What is probably an analogous phenomenon can be seen very clearly in the border rows of chickpea plots as the crop matures. For some time after the plants within the plots dry up and mature, the border rows remain green. The prolongation of flowering, pod filling, and growth in the border rows is most probably explicable in terms of the access of their roots to a larger volume of moist soil.

Similarly, when chickpeas are planted in a "fan" design, with rows diverging from a central point, the plants that are most crowded at the center mature first, while those at the periphery have a more protracted growing, flowering, and podding period and remain green longer.

In such "fan" plantings the total dry matter and yield per plant generally increase with the distance between the rows but this is not simply because of the longer growth period and later maturation of the more spaced plants. Even at an earlier stage the wider-spaced plants are bigger, indicating that there is competition between the rows (Figure 6). However, this competition takes place even when there is no overlap of canopies or mutual shading between the rows. This indicates that the plant-to-plant competition is not above ground, for light, but below ground, most probably for water.

In such fan plantings plants of different cultivars (of similar duration groups) differ in their ability to respond by increasing their growth and yield as the distance between the rows increases. These varietal differences in "plasticity" in response to spacing most probably depend on varietal differences in the extent and activity of the root system. We have not found any relationship between plant plasticity judged by this criterion and the morphology of the shoot system, that is, the architecture of the plant canopy.

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Figure 6. "Fan" plantings of chickpeas at Hyderabad 99 days after sowing. CV. F3-WFx384-1-MF is in the foreground.

competition for water by the root system. LAIs are generally low (Figure 2), rarely exceeding 2 or 3, and therefore mutual shading within the canopy is unlikely to be of much importance, especially at the high levels of photosynthetically active radiation (about 1700 to 2000 μ eisteins/m-sec) which generally prevail during the winter season.

However, under conditions in which water (and soil nutrients) are not limiting and under favorable climatic conditions, higher LAIs are achieved. Then the main factor in plant-to-plant competition may be competition for light. This may be the case in North India, for example, when chickpeas are grown on soils with a high water-holding capacity which has been given a heavy presowing irrigation. We have carried out experiments under such conditions at Hissar (Haryana) and found that in "fan" plantings similar to those made at Hyderabad, there was little evidence of interrow competition after the rows diverged beyond the region in which there was mutual shading between the rows. But this sort of situation is not typical of the soil moisture regimes under which chickpeas are generally grown by farmers in India.

Effects of Shading

We have carried out experiments in which chickpeas were shaded by cloth shades fixed above the field-plots at the time flowering began; the shading continued until the plants matured.

The most striking effects of these shading treatments during the reproductive phase was a delay in the senescence of the lower leaves and of the plants as a whole. This delay was greater the thicker the shade. For example, in cv. F-502 3 weeks after shading began, the nonshaded controls had lost an average of 39 leaves per plant, and those under shades intercepting 50, 75, and 80% of the light had lost 24, 17, and 15 leaves, respectively. The shaded plants remained green and growth and pod development continued even after the nonshaded controls had matured and dried up.

The total dry weight at harvest, yield, and yield components of shaded and nonshaded plants of cv. F-502 are shown in Table 1. There was an increase (significant at the 5% level) in the total dry weight, yield, and pod number of the plants under the 50% shades compared with the controls. The 75 and 80% shading treatments tended to reduce these, but the reductions were not statistically significant. As the intensity of shading increased the average seed number per pod declined and 100 seed weight increased.

These results were obtained with plants of a late cultivar planted late, which were probably under considerable moisture stress during the reproductive phase. The following year (1975-1976) we carried

TABLE 1

Effects of shading throughout the reproductive period on yield and yield components of cv. F-502 (Hyderabad, winter season 1975–1976).

	Yield (kg/ha)	Total dry weight (kg/ha)	Harvest index	Pods/m ²	Seeds/ pod	100 Seed weight (g)
Control	660	1389	47.3	424	1.11	14.2
50% shade	834	1655	51.0	526	1.08	14.6
75% shade	613	1230	49.7	381	1.07	15.2
80% shade	650	1304	49.7	386	1.07	15.6
LSD (5%)	165.0	363.3	4.45 (n.s.)	99.4	0.038	0.860
CV%	12.0	13.0	4.5	11.6	1.8	2.9

out further shading trials with early and medium duration cultivars planted earlier. Again we found that the plants under the 50% shades produced rather more total dry weight and a higher yield than the controls, but the yield and the total dry weight were reduced by 80% shades (N. P. Saxena and A. R. Sheldrake, unpublished results).

DISCUSSION AND CONCLUSIONS

The decline in LAI was the first visible symptom of the phase of senescence and maturation of the plants. The fact that the decline in LAI occurred much earlier in the reproductive phase of late cultivars such as T-3 than in early cultivars such as JG-62 indicates that it was not simply related to the phenological stage of the plants, but also influenced by the environmental conditions. This decline took place at a time when there was little change in the maximum or minimum temperature. There was, however, a progressive decline in the relative humidity in the afternoons (Figure 1), and a progressive depletion of the soil moisture from the upper zones of the soil (Figure 3). This suggests that moisture stress was one of the main reasons for the timing of the onset of the phase of senescence. The same conclusion is suggested by the accelerated senescence and maturation of plants grown under unirrigated conditions on a red soil of low water-holding capacity and also the delay of senescence and maturation under irrigated conditions, or in wide-spaced plants or plants in border rows which have access to greater reserves of soil moisture. In general, the same reasons probably account for the prolongation of the growth of chickpeas and the later onset of senescence and maturation under North Indian conditions where temperatures remain lower for a longer time, and the relative humidities higher. In all these cases the delay in senescence and maturation of the plants is associated with more growth and higher yields.

The delayed senescence and maturation of the shaded plants is unlikely to be explicable in terms of differences in air temperature, which were small; moreover the free circulation of air under the shades probably prevented the relative humidity from rising much above that in the control plots. The lack of a reduction in yield by the 50% shades is not so surprising in view of the light intensity and the low leaf area index (less than 2); under such shading the light intensities may still have been near-saturating for photosynthesis. However, the delay in senescence in the shaded plants, and the significantly increased yields indicate that the shading reduced

the stress or stresses which were accelerating the senescence process. The most probable explanation could be given in terms of the reduction in radiation load on the leaves. The resultant reduction in the rate of transpiration might have lessened the degree of moisture stress and/or the reduced heating of the leaves might have resulted in less heat stress. We think that this reduction in heat stress is of considerable importance. Shading trials carried out recently with and without irrigation has shown that the effects of 50% shading are just as pronounced when the plants are irrigated and thus presumably under less moisture stress (N. P. Saxena and A. R. Sheldrake, unpublished results). Furthermore, similar shading trials with pigeonpeas (Cajanus cajan) grown during the winter season under similar conditions to chickpeas have not given comparable results: Senescence and maturation were only slightly delayed and there was no increase in the yields of the shaded plants (A. Narayanan and A. R. Sheldrake, unpublished results). Chickpeas are known to be sensitive to high temperatures and cannot be grown successfully in the hot season in India even if well irrigated, whereas pigeonpeas are much more heat tolerant.

The heat stress to which chickpea leaves may be exposed as a result of the absorption of radiant energy during the winter season presumably occurs when evaporative cooling takes place too slowly to prevent a rise in temperature of the leaves. We have found by measuring the relative water content (Slatyer, 1967) of chickpea leaves throughout the day that the leaves lose water after about 8 a.m., but that this water loss ceases soon after midday; during the afternoon the relative water content increases again. This indicates that the stomata are closed during the afternoon and that transpiration, and hence evaporative cooling of the leaves, is taking place at a low rate. Under such conditions the leaves would be expected to heat up. We hope to begin more detailed studies of these parameters soon.

The onset of the senescent phase of the plants is thus related both to the time of onset of flowering and pod development (earlier in early cultivars) and to the environmental conditions. We do not know whether flowering itself by altering the internal balances of hormones, and so on, initiates the process of senescence as it seems to in some annual plants (Leopold et al., 1959), but there is no doubt that the senescence of the plants is accelerated by the development of pods.

The decline in LAI is part of a vicious spiral of senescence, in which developing pods compete for photoassimilates and nutrients with the vegetative growing meristems and young developing leaves in the shoots and with nodules and roots below ground. During the

pod-filling phase, the nodules regress (Figure 5) and net nitrogen uptake into the plant ceases (N. P. Saxena and A. R. Sheldrake, unpublished results). Meanwhile the roots continue to grow in the deeper zones of the soil (Figures 3 and 4), but it seems probable that the activity and development of the root system is reduced progressively as a result both of declining assimilate supplies from the dwindling leaf area and also of increasing competition from the developing pods. Restrictions on the growth and activity of the roots must result in a reduced water supply to the leaves, more moisture stress, and a further acceleration of leaf senescence. Meanwhile, under field conditions, the relative humidities fell in the daytime, and later also after dark, leading to increased evaporation.

While the yield of seeds depends both on the total dry matter accumulated by the plants and the proportion of dry matter partitioned into the seeds, it seems to be the case in chickpea, at least under Hyderabad conditions, that the rate of accumulation of dry matter depends on pod development itself. We have found that, in plants where the pod development has been reduced, delayed, or prevented, the total dry matter accumulated by the plants is reduced substantially (N. P. Saxena and A. R. Sheldrake, unpublished results). This may be an example of the regulation of photosynthetic "source activity" by "sink demand" (Evans, 1975).

These qualitative conclusions vaguely indicate something of the complexity of the quantitative interactions within the plants and between the plants and their aerial and underground environments. We know so little about any of these factors in chickpeas that we cannot even think of building a quantitative predictive model.

At present, probably the most useful thing we can do as physiologists interested in increasing the economic yields of chickpeas is to help to work out empirical screening methods by means of which cultivars or plants in breeders' segregating populations that possess desirable heritable characters can be identified. In the introduction to this paper we mentioned two such characters for which screening techniques might be useful: One is the ability of seeds to germinate under conditions of low water potentials in soil; another is the ability of plants to perform well after early plantings when the temperatures are high.

In relation to the ability of the plants to grow and yield well under conditions of progressive moisture stress, in the first place the selection of cultivars of an appropriate maturity group may be the most important and the easiest type of selection to carry out. It is, indeed, already carried out by plant breeders themselves. For detecting the different abilities of genetically different plants within a given maturity group to yield as well as possible under conditions of moisture stress the simplest and most reliable method would be to grow them under such conditions in the field and to measure the yield. The problems would be firstly to know the sorts of soil and environmental conditions in which the plants would be grown by farmers in different regions and secondly to decide how to devise screening procedures on the experiment station which would give an indication of the performance of the plants under these conditions. Details such as the soil type, time of planting, control of the initial water content of the soils, whether to irrigate, under what sort of conditions the non-moisture-stressed "controls" (if any) should be grown, and so on, all must be worked out.

It would be easier for us, as physiologists, if some one else worked out all these empirical details and then presented us with "droughtresistant" and "non-drought-resistant" cultivars. We could then confine ourselves to investigating differences between them. But it does not look as if any one else is going to work out the details of such empirical screening procedures, or even decide what sorts of screening procedures should be developed. So we will have to do it ourselves, even if it is only for the purely selfish reason that, without screening methods, we cannot begin to test predictions about the importance under field conditions of quantitative characteristics such as rates of CO₂ assimilation, heat tolerance of isolated tissues. osmotic pressures, water potentials, stomatal apertures and resistances, levels of abscisic acid. Without either a simple technique for comparing the yield of different cultivars in the field under reasonably definable conditions of moisture stress, or a technique using controlled environments which has been shown to agree with performance of plants in the field, we cannot test the importance of varietal differences in any one of these quantitative characters, and still less can we test predictions about the performance of plants that might be produced by deliberate breeding for combinations of these characters.

In general, probably the cheapest, simplest, and most reliable screening techniques we can work out for predicting field performance would be techniques that involve measuring field performance itself. In relation to screening for performance under moisture stress, or heat stress, such work would be possible in the field only if the moisture and temperature conditions were fairly predictable. Furthermore we would know what sorts of screening procedures to carry out only if the growing conditions in the chickpea-producing regions were reasonably well definable.

Fortunately the growing conditions are much more definable and predictable in the case of chickpeas and other crops that are grown in a dry season than they are for crops dependent on intermittent and irregular rainfall during rainy seasons. The amount of moisture available to chickpeas and other crops grown under similar conditions can be fairly well defined at the beginning of the growing season and depends on the soil type and the amount of moisture already stored in it. At a given location, the temperatures, evaporation, and relative humidities throughout the growing season follow a fairly predictable pattern. All these factors should make the work of agro-climatologists, physiologists, agronomists, and breeders working on such crops easier, and also more interesting because of the better prospects for understanding and prediction.

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