

Availability of Soil Water to Plants as Affected by Soil Moisture Content and Meteorological Conditions¹

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SYNOPSIS. Actual transpiration decreased with decreasing soil moisture content and increasing potential transpiration. Average soil suction in the root zone when the actual transpiration rate fell below the potential rate varied from 12 bars when the potential transpiration rate was 1.4 mm. per day to 0.3 bar when the potential rate was 6 to 7 mm. per day.

MUCH attention has been given to the problem of predicting rates of water use from crops under conditions where soil water supply is not limiting. For a homogeneous, actively growing crop it is usual to call this water use the potential transpiration rate. The potential transpiration rate is primarily determined by weather factors. Less attention has been given to the question: What happens when soil water supply limits transpiration, i.e., at what soil moisture content does the actual transpiration rate fall below the potential rate, and can this be predicted for any given soil-plant-weather combination? This paper presents the results of experiments in which this question was studied.

GENERAL CONSIDERATIONS

The problem has been considered from a dynamic viewpoint by Philip (8) and Gardner (2). The reader is referred to these two papers for a detailed theoretical treatment of transpiration as a dynamic process. Water moves through the soil to the plant root and from the root to the transpiring leaves along pressure gradients, gradients of suction (negative pressure) in the soil, and gradients of diffusion pressure deficit, DPD, in the plant. By analogy with the flow of heat into an infinitely long cylinder, Gardner has obtained the solution of the differential equation describing the flow of water through the soil to the root in the course of transpiration. His solution of the flow equation reveals that the suction gradient between root and soil necessary to maintain a given rate of water uptake by the root, i.e., a given transpiration rate, is proportional to the rate of water uptake or the potential transpiration rate and inversely proportional to the capillary conductivity of the soil.

The capillary conductivities of soils decrease rapidly with increasing soil suction. Consequently, as the soil dries, large suction gradients develop between the root and the soil around it. In the case of passive absorption, water movement through the plant arises from a gradient in DPD between the transpiring leaves and the roots. This DPD gradient is assumed to be proportional to the transpiration rate (13). Thus, to maintain transpiration in a drying soil

where the capillary conductivity is decreasing and the suction at the plant root is increasing correspondingly, the DPD in the leaves must continually rise so that the necessary DPD gradient between leaf and root is still present. The rise in DPD in the leaves is accompanied by a decrease in turgor pressure resulting in closing of the stomata and dehydration of the leaves. Consequently, the permeability of the plant to water flow decreases and the transpiration rate must decline.

Likewise, an increase in the potential transpiration rate will hasten the rise in the DPD of the leaves leading to a more rapid fall in turgor and permeability of the plant with decreasing soil moisture supply.

Thus, we expect transpiration rates to decline with decreasing soil moisture content and we expect that this decline will be evident at higher and higher soil moisture contents as the potential transpiration rate increases. The particular soil moisture content at which the decline in transpiration occurs will also depend on the soil properties. In soils in which most of the water is held at low suction, the decline should not be evident until most of the "available" soil water has been extracted. In soils in which suction increases rapidly as soil moisture content decreases, the decline in transpiration should be noticeable at comparatively high soil moisture contents. The reader is referred to Gardner (2) for an illustration of the differences between soil types.

Since the decrease in permeability of the plant and the consequent decrease in transpiration result from turgor-induced changes such as closing of the stomata and dehydration of the leaves, one expects that the soil moisture content at which transpiration rate decreases should be coincident with the soil moisture content at which the plant wilts. That is, the wilting point will also be expected to vary with soil moisture properties and with the potential transpiration rate.

The foregoing discussion has been concerned with some of the dynamic aspects of water availability to plants. The remainder of the paper presents observations made by the authors in experiments to verify, at least qualitatively, these theoretical predictions concerning the effects of variations in soil water supply and the potential transpiration rate on actual transpiration and the wilting point.

EXPERIMENTAL PROCEDURE

Transpiration rates and growth rates of corn plants were examined in detail during a 5-week period commencing just prior to tasseling. In order to impose soil moisture treatments and achieve reasonable uniformity of soil moisture throughout the root zone, it was necessary to restrict the volume of soil available to the roots. This was accomplished by raising the plants in containers filled with soil. The 20-gallon containers were 18 inches in diameter and 24 inches in depth. They were set in the field with their tops level with the ground surface at a spacing of 40 inches from center to center. A 4-plant hill of corn was raised in each container. Field-grown corn, also in 40-inch hills, was raised on all sides. There were 136 containers.

The soil with which the experiment was performed is a **Colo** silty clay loam. Field capacity for this soil is 36% by volume and the soil moisture content corresponding to a suction of 15 bars is 22% by volume. The moisture characteristics are shown in **Figure**

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1. Reference to this figure will disclose that of the water held in the soil between field capacity and the 15-bar percentage, more than half is held at suction values greater than 1 bar and almost 40% is held at suction values greater than 2 bars.

When the containers were filled, an access pipe for the probe of a neutron moisture meter was inserted in each container. An outlet was provided in the bottom of each container to allow for drainage of excess water.

After the plants had emerged, the soil surface was covered with black plastic film to prevent surface evaporation. Losses in soil moisture could then be attributed to transpiration. As the plants grew, watering was accomplished by pumping known amounts of water from a large storage tank at the experimental site into each container. Until the treatments involving variation in the soil moisture regime were imposed, the soil in all containers was maintained as close as possible to field capacity by application of water at appropriate intervals.

During the period in which transpiration rates were measured, soil moisture readings were made daily between the hours of 1600 and 1800. The size of the containers was such that the sphere of measurement of the neutron meter was just contained within the walls of the container when the soil was at its driest.

The moisture contents reported in later sections are averages for the effective root depth of the plants in the containers, which was 21 inches. The roots permeated the soil in the containers thoroughly except for a small zone of about 1 inch at the bottom. Since the root zone was restricted, the rates of water use could be determined with much more precision than would have been possible in the field where plants extract water at varying rates from different positions of the profile. The water in the containers was depleted from the various depths at a uniform rate; gradients in soil moisture content from top to bottom were small. In view of these facts it is felt that the average soil moisture contents quoted for the root zone of the plants are meaningful and provide a basis for experimental interpretation of the analyses of Philip and Gardner referred to in the introductory section.

Soil moisture treatments consisted of the depletion of soil moisture content at regular intervals during some 5 weeks of the growing season to values corresponding to soil suctions of 2.5, 5, and 15 bars. Depletion of soil moisture was accomplished by withholding irrigation. Control treatments in which soil suction was

not allowed to exceed 0.5 bar were also maintained. There were 18 treatments comprising 7 controls and 11 variable soil moisture treatments. The basic design was replicated eight times. Full details of the treatments imposed are given by Denmead (1).⁴ The treatments were so arranged that on each day during the 5-week period there were a number of containers at different soil moisture contents ranging from field capacity to the 15-bar percentage. In this way, the combined effects of daily variations in weather conditions and variations in soil moisture supply on transpiration rate could be studied.

RESULTS AND DISCUSSION

Actual transpiration rate vs. potential—For convenience, we can regard the transpiration rate at field capacity as representing the potential transpiration rate. The actual transpiration rates at different soil moisture contents on 3 of the days in the experiment are shown in Figure 2. The days shown represent high, moderate, and low potential

⁴Denmead, O. T. 1961. Availability of soil water to plants. Unpub. Ph.D. thesis, Iowa State University, Ames, Iowa.

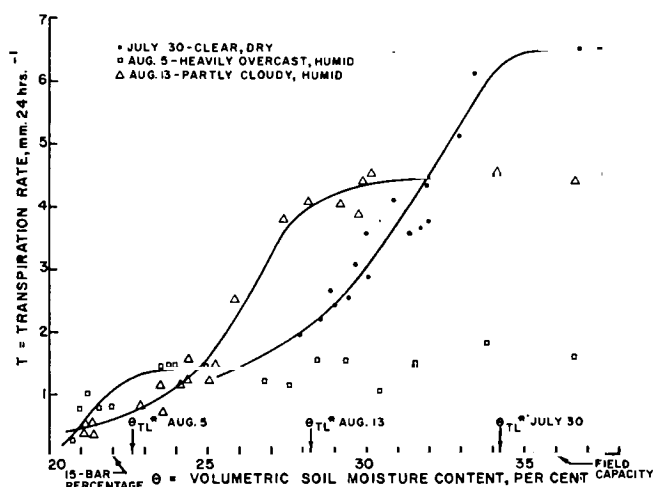


Figure 2—Actual transpiration rate as a function of soil moisture content.

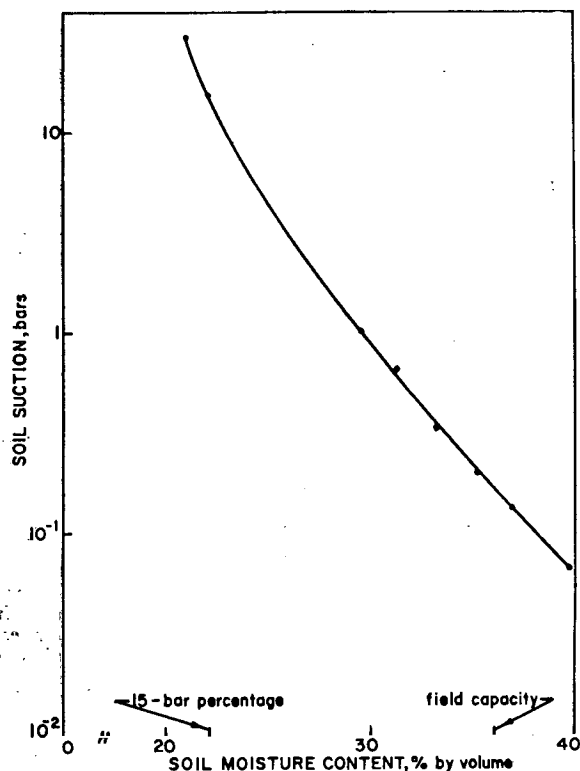


Figure 1—Relation between soil suction and volumetric soil moisture content for Colo silty clay loam.

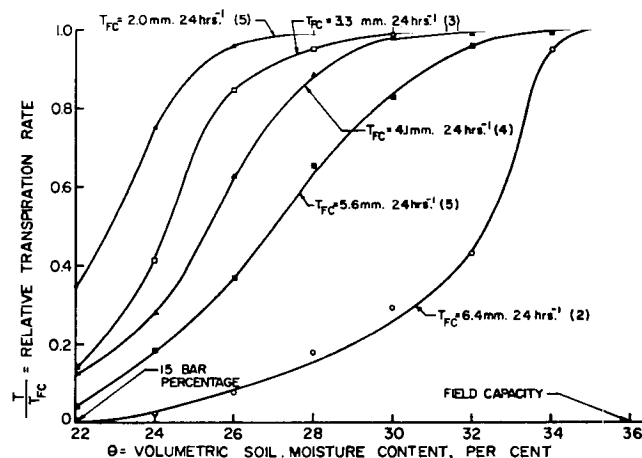


Figure 3—Relative transpiration rate as a function of soil moisture content for different potential transpiration conditions. The curves represent days on which the transpiration rates at field capacity had the value shown in the body of the figure. The numbers in parentheses refer to the number of days of observation represented by each curve.

transpiration rates. The transpiration rate at field capacity (the potential transpiration rate) was determined primarily by meteorological conditions as shown in a later section. On all days the actual transpiration rate decreased as soil moisture content decreased. The decline in transpiration rate occurred at higher soil moisture contents as the potential rate increased.

Among the many days examined, days similar to each other in meteorological conditions and the potential transpiration rate were encountered. These days were grouped according to the value of the potential transpiration rate; then the mean relative transpiration rate (actual/potential) was calculated for each group for selected values of soil moisture content. The relative transpiration rate is shown as a function of soil moisture content for a range of potential transpiration rates in Figure 3. The same trends as were observed in Figure 2 are again evident. The data in these figures illustrate the importance of knowing the particular meteorological conditions (which in turn determine the potential transpiration rate) under which results have been obtained when considering reports on the availability of soil water to plants. Under conditions leading to a high potential transpiration rate, the actual transpiration rate may be considerably less than the potential rate even though soil moisture supply might be considered adequate. Under conditions leading to a low potential transpiration rate, the actual transpiration rate will equal the potential rate down to very low soil moisture contents.

Figure 4 depicts relative transpiration rate as a function of the average soil suction in the root zone for a range of potential transpiration rates. For the most extreme conditions encountered in the experiment, when the potential transpiration rate was 6.4 mm. per day, the actual transpiration rate fell significantly below the potential rate when the average soil suction was only about 0.3 bar. For moderate potential transpiration rates of 3 to 4 mm. per day, the potential transpiration rate could be maintained until the average soil suction was about 2 bars. When the potential transpiration rate was only 1.4 mm. per day, this rate was maintained until the average soil suction was as much as 12 bars.

Comparison with reported observations—In Figure 5, four proposals for the variation in relative transpiration rate with variation in soil moisture content are shown. Veihmeyer and Hendrickson's (14) thesis represented by curve A is essentially for equal availability of soil water almost to the 15-bar percentage. The data presented in Figure 3 for low potential transpiration rates and those presented by Gardner (2) for a sandy soil in which most of the soil water is held at low suction indicate that such a thesis is indeed tenable.

Pierce's (9) proposal, curve B, is based on records obtained from a weighing lysimeter over several weeks. During this time, environmental conditions would be expected to vary widely. His curve agrees well with those obtained under the "usual" weather conditions of a moderate potential transpiration rate pertaining in the experiments described here.

Thornthwaite and Mathers' (12) proposal for a linear relation between relative transpiration rate and "available" soil water, curve C, is based on observations made at O'Neill, Nebraska, in the Great Plains study of 1953 (4). The soil was a sandy loam. The observations were made under very dry atmospheric conditions with high radiation intensities. It is seen that curve C, or, better, curve D which

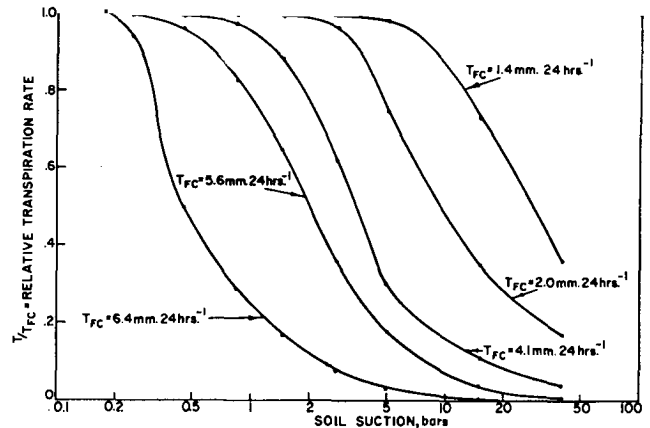


Figure 4—Relative transpiration rate as a function of soil suction for different potential transpiration conditions. The curves represent days on which the transpiration rates at field capacity had the values shown in the body of the figure.

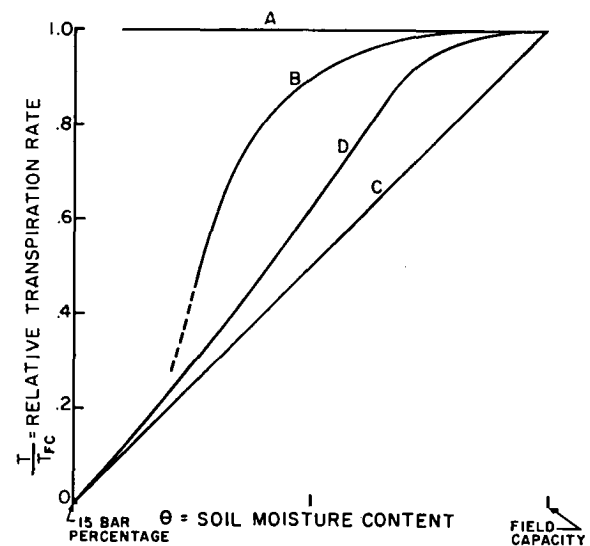


Figure 5—Various proposals for the relationship between relative transpiration rate and soil moisture content. See text for explanation of curves.

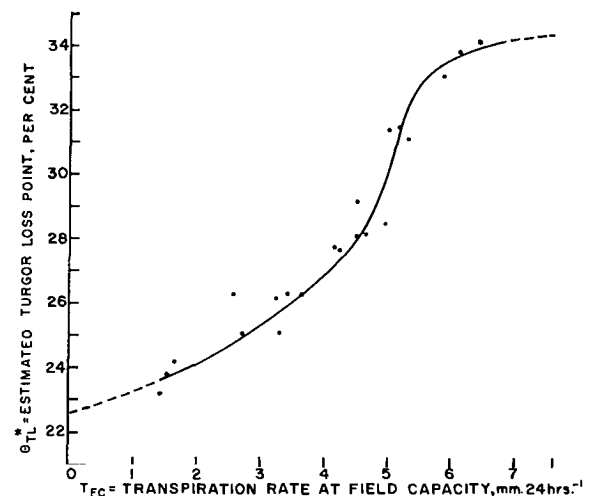


Figure 6—Variation in the estimated turgor loss point with variation in potential transpiration rate.

is redrawn from the original O'Neill data, agrees well with a curve obtained for a high potential transpiration rate in the present experiment.

It should be mentioned here that the decline in relative transpiration rate with increasing soil suction has been observed by many workers investigating rates of water use by crops. Reports of such observations include those of Makkink and Van Heemst (6), Slatyer (11), Hagan et al. (3), Lemon et al. (5), Scholte Ubing (10) and Bahrani and Taylor (1).

Wilting in relation to soil moisture content and meteorological conditions—It was pointed out in the introductory section of this paper that the soil moisture content at which the transpiration rate fell below the potential rate should be coincident with the wilting point. This soil moisture content, referred to here as the turgor loss point, was estimated for each of the 25 days of observation from the graphs of actual transpiration rate v. soil moisture content which were similar to those shown in Figure 2. For example, the estimated turgor loss point was 34.2% on July 30, 28.2% on August 13, and 22.6% on August 5. The relationship between these estimated turgor loss points and the potential transpiration rate is shown in Figure 6. The turgor loss point increased rapidly from 23% soil moisture when the potential transpiration rate was 1.4 mm. per day to 34% when the potential transpiration rate exceeded 6 mm. per day.

The turgor loss points estimated from the transpiration curves agreed well with visual observations of the incidence of wilting taking during the experiment. Observations on many days confirmed the fact that plants growing at soil moisture contents greater than the estimated turgor loss point appeared to be maintaining full turgor while plants growing at lower soil moisture contents showed greyish discoloration with some curling, particularly in the top leaves. It was also observed that, whereas on days when the potential transpiration rate was high, plants growing at soil moisture contents less than the estimated turgor loss point were wilting, the same plants on a succeeding day with a lower potential transpiration rate would show no signs of wilting as long as the soil moisture content was greater than the estimated turgor loss point.

Measurements of dry matter accumulation were made in one section of the experiment on plants which had been

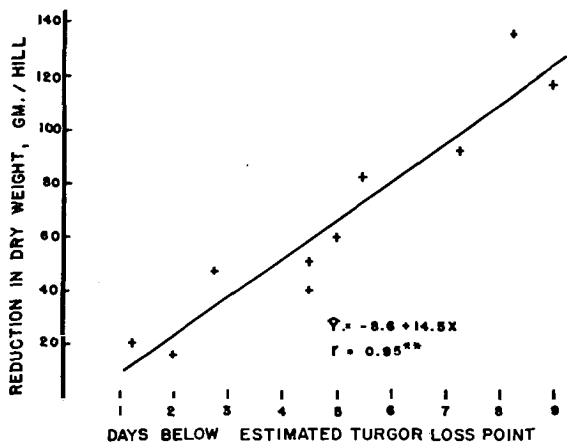


Figure 7—Reduction in dry weight of plants subjected to various periods of soil moisture stress as a function of the number of days in the stress period on which soil moisture content was less than the estimated turgor loss point.

subjected to various periods and intensities of soil moisture stress. The total number of days on which soil moisture content was less than the estimated turgor loss point was determined for each treatment along with the reduction in dry weight below that of the control plants. In Figure 7 the relationship between the period of soil moisture stress and the reduction in dry weight is depicted.

The fitted regression line in Figure 7 is linear and passes close to the origin; the intercept is not significantly different from zero. The slope of the regression line, 14.5 g. per hill per day is close to the mean growth rate of the control plants, viz., 13.9 g. per hill per day. This evidence suggests that once the soil moisture content is less than the turgor

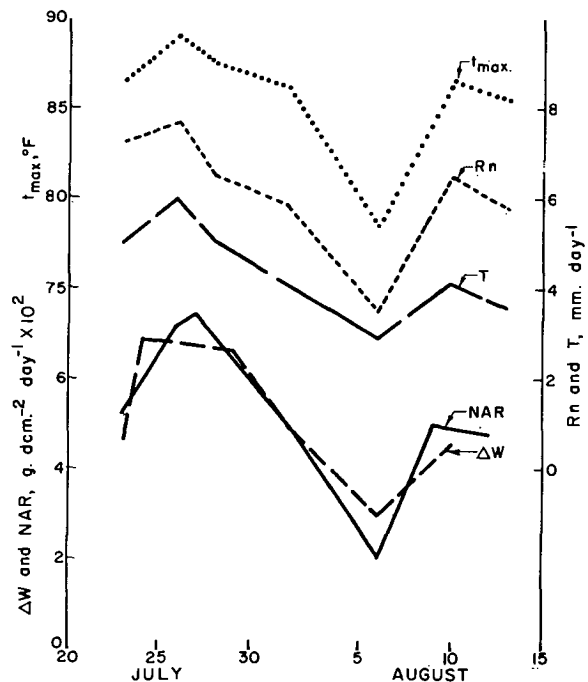


Figure 8—Net assimilation rate, NAR, reduction in rate of dry matter production, ΔW , average net radiation, R_n , average transpiration rate, T , and average daily maximum temperature, t_{max} for different periods in the experiment.

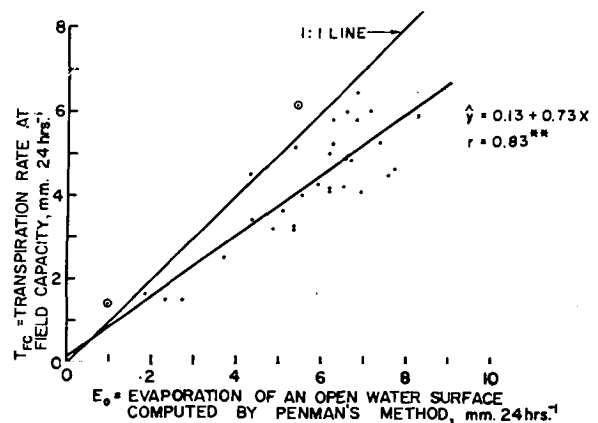


Figure 9—Relation between daily transpiration rate at field capacity and the estimated evaporation of an open water surface computed by the method of Penman (7).

loss point, the plant virtually ceases to assimilate carbon dioxide.

To compare the slope of the regression line in Figure 7 with the mean growth rate of the control plants is to oversimplify the situation, since the control plants were not gaining weight at a constant rate throughout the experiment. To show the variation in the growth rate of the control plants and the coincident variation in the effect of moisture stress on dry matter accumulation, Figure 8 is presented. In this figure the net assimilation rate, NAR, of the control plants is shown as a function of time for the duration of the experiment, along with the average reduction in dry weight per day, ΔW , measured over periods in which the soil moisture content was less than the turgor loss point. NAR is a measure of the rate of dry matter production of a plant. It is the rate of increase of dry weight per unit leaf area. Thus,

$$\text{NAR} = \frac{1}{\bar{A}} \left(\frac{W_2 - W_1}{t_2 - t_1} \right)$$

when \bar{A} is the mean leaf area of the plant between times t_2 and t_1 and W_2 and W_1 are the dry weights of the plant at times t_2 and t_1 . NAR is here expressed in units of g. dry matter per dm.² leaf area per day $\times 10^2$. ΔW is calculated on the same basis, i.e.,

$$\Delta W = \frac{1}{\bar{A}} \left(\frac{W_2 - W_1}{t_2 - t_1} \right)$$

when \bar{A} is the mean leaf area of the treated plants during time t_2 to t_1 , which is the number of days for which soil moisture content was less than the estimated turgor loss point, W_2 is the weight of the control plants at time t_2 , while W_{2t} is the weight of the treated plants at time t_2 . Neglecting respiratory losses, if assimilation were to cease and soil moisture content was less than the turgor loss point, then W_{2t} should equal W_1 and the ΔW measured over a period of soil moisture stress should equal the NAR over that period.

The quantitative agreement between NAR and ΔW is good. From Figures 7 and 8 it is evident that the turgor loss point is a significant soil moisture constant in soil-plant-water relationships, apparently representing the lower limit of availability of soil water for dry matter accumulation.

It is also evident from Figure 8 that a quantitative evaluation of the effects of soil moisture stress on plant production requires some knowledge of the variation in NAR. NAR itself is influenced by weather conditions and for this reason the average net radiation, R_n , and the maximum temperature, t_{\max} , have also been plotted in the figure. Slow growth in the first week of August was associated with a period of cool, cloudy weather. The dependence of NAR on the radiation intensity is evident.

Transpiration rate in relation to meteorological conditions—The dependence of the potential transpiration rate on weather conditions has been mentioned several times in previous paragraphs. For completeness, the average transpiration rate at field capacity, T , is shown as a function of time in Figure 8 where the average net radiation is also shown. The relationship between the daily measurements of transpiration rate at field capacity and the evaporation of an open water surface computed from observations of net radiation, temperature, humidity, and wind velocity at

the experimental site by Penman's (7) method is shown in Figure 9.

SUMMARY

Dynamic aspects of the availability of soil water to plants are discussed briefly. It is pointed out that as the soil dries, the actual transpiration rate should fall below the potential rate and that this decline in relative transpiration rate should occur at higher and higher soil moisture contents as the potential transpiration rate increases. Since the decline in relative transpiration rate results from a loss of turgor in the plant, the soil moisture content at which plants wilt should also increase as the potential transpiration rate increases.

Transpiration rates from corn plants grown in containers in the field were determined under varying conditions of soil water supply and varying potential transpiration rates. For moderate potential transpiration rates (3 to 4 mm. per day), the actual transpiration rate fell below the potential rate when the average soil suction in the root zone was about 2 bars. When the potential transpiration rates were as high as 6 to 7 mm. per day, this decline in relative transpiration rate occurred at about 0.3 bar. When the potential transpiration rate was only 1.4 mm. per day, the relative transpiration did not decline until about 12 bars.

The soil moisture content at which the decline in relative transpiration rate occurred, referred to as the turgor loss point, varied from a volumetric soil moisture content of 23% when the potential rate was 1.4 mm. per day to 34% when the potential transpiration rate exceeded 6 mm. per day. Measurements of dry matter production suggested that once the soil moisture content was less than the turgor loss point, the plants virtually ceased to assimilate.

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