LEAF WATER POTENTIAL AND TRANSPIRATION RATE AS AFFECTED BY SOIL MOISTURE REGIMES AND EVAPORATIVE DEMANDS OF THE ATMOSPHERE

by D. P. Gupta, *Deputy Director of Soil Conservation, Agriculture Department, Jammu, J. & K., and* M. B. Russell, *Department of Soil Physics, Jawaharlal Nehru Agricultural University, Jabalpur, M.P.*

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Determinations made on the leaf water potential in sunflower plant, by the 'dye' method throughout a drying cycle under varying evaporative conditions, showed that both soil moisture regimes and evaporative demands markedly influenced the leaf water potential. It was primarily controlled by the evaporative conditions, when soil moisture content was below 0.3 bar soil suction and by the soil moisture alone when the soil suction was above 3.0 bars. But in between these two limits the influence of the two environmental factors overlapped and the leaf water potential was found to be a function of both of them.

The leaf water potential value obtained when the soil moisture is not limiting is considered as potential value. The results indicated that a potential value of —13.7 bars characteristic of high evaporative demands was attained at a much lower soil water content corresponding to 3.0 bar soil suction when the evaporative demand was low.

The transpiration rate also followed changes in the leaf water potential. At leaf water potential value above —19.0 bar the transpiration rate increased with increasing evaporative demands. As the leaf water potential fell below —19.0 bars, the transpiration rate decreased and tended to remain about constant below —21.0 bars, at all evaporative demands.

Introduction

Factors affecting the internal water status of plants have been reviewed by a number of workers (cf. Fischer & Hagan (1965); Gardner (1965); Knipling (1967) and Slatyer (1963). The general conclusion from these reviews is that water potential in a non-transpiring plant approaches the water potential in the soil, but with the on-set of transpiration a gradient in water potential develops from the soil, to and through the plant and out into the external atmosphere. The level below that of the soil water potential to which the plant water potential falls during the day depends on the magnitude and duration of the lag of absorption behind transpiration. Transpiration is governed by the atmospheric factors determined by the evaporative demand. Absorption is governed partly by the soil factors including water content and unsaturated conductivity.

Soil moisture is being used extensively as an indicator of plant water status but researchers in soil-plant relationships are increasingly recognizing the limitation of soil moisture measurement alone as a means of accurately expressing the constantly changing internal moisture relations of plants (Hagan *et al.* 1959; Knipling 1967; Namken 1964).

According to Gardner (1960), over most of the water use range between upper and lower limits of availability the uptake of water by the plants is governed by the external factors but as the lower limits of availability are approached it becomes limited by the water flow rate of the soil-plant system.

Namken (1964) attributed 88 per cent of the variation in relative turgidity of cotton leaves to changes in soil moisture content, ambient temperature and open pan evaporation. Jana and Ghildyal (1967) found that plant tissues in rice remained highly hydrated only under flooded conditions and that tissue water content decreased when the soil moisture content was reduced below saturation. Under low evaporative demand, tissues remained rather highly hydrated, but as evaporative demand increased even under flooded conditions the tissue hydration decreased from 80 per cent to 74 per cent. Thus it is clear that the water status of plants depends on a combination of soil and atmospheric factors.

Water potential has been identified as the most useful term to express the free energy status of water in the soil-plant-atmosphere system (Taylor & Slatyer 1961). However, few measurements have been reported of changes of water potential of leaves in response to gradually varying environmental moisture stresses. The more sophisticated techniques that have been developed for direct measurement of leaf water potential involve very elaborate and costly equipment. Other techniques of measuring plant water status e.g., relative water content, relative stomatal opening, transpiration rate, etc., undoubtedly correlate with leaf water potential, but do not directly measure it. A simple inexpensive technique of determining leaf water potential developed by Shardakov (1948) and described by Knipling (1967) was modified and used to study the effect of changing soil moisture content under different evaporative demands on the leaf water potential of plants grown in an open pot house during the period of February to April 1971.

Materials and Methods

Soil and plant : Sunflower (*Helianthus annuus* L.) was used as a test plant in this study. Eight to ten plants of a Russian variety-strain No. EC 68415 were grown in 15 cm diameter tin cans 20 cm deep containing 4 kg of a sandy soil. The moisture characteristic of the soil, presented in Fig. 1 reveals that, of the water held in the soil between soil suctions of 1/3 bar and 15 bars more than half is held at suction values greater than 1 bar and about 40 per cent is held at suction values greater than 2 bars.

Soil moisture regimes : The soil moisture values were determined by daily weighing the pots with an accuracy of ± 5 gm between 7 and 8 a.m. The weight of the plants was small in comparison with the total soil weight and was ignored in calculations of soil moisture percentage. The soil moisture content (SMC) was expressed as the average percentage on a dry weight basis of the entire soil volume in each pot. As the soil surface was covered with glasswool, moisture gradients in the soil column were assumed to be small because of the negligible surface loss of water due to evaporation. It was further assumed that in each pot the roots thoroughly permeated the soil and uniformly depleted the entire volume of soil.

The soil in each pot was maintained at field capacity by daily watering until the plants reached the 6 leaf stage. Additions of water were then discontinued and the SMC was allowed to fall progressively to the permanent wilting percentage over a period of 8–10 days. By discontinuence of watering of different sets of pots at intervals of 2 or 3 days, pots with SMC values ranging from saturation to permanent wilting percentage were simultaneously available at several times during each experiment. This timing was so arranged that on each day during a drying cycle there were a number of pots having different SMC.

Evaporative demands : During the period of February to April atmospheric conditions in the pot house between 11 a.m. to 1 p.m. provided high evaporation rates. These were compared with high humidity conditions which gave much lower evaporation rates that were created during the same time period in a humid chamber. Each day during the drying cycle the plants were subjected for 3 to 4 hr to the differential evaporative conditions. During this period their transpiration rates were determined just prior to sampling of leaves for leaf water potential (LWP) measurements. Since the average hourly rate of change of SMC of the entire soil volume was small, it was assumed that the average SMC values calculated from weighings made at 7 to 8 a.m. were valid measures of the SMC during the period later in the same day when the LWP and transpiration rate measurements were made. During each 3 to 4 hr measurement period the evaporation demand (ED) was measured in each of the test chambers with small atmometers designed and fabricated for this study. These consisted of small cigarette-sized porous ceramic cylindrical tubes fitted to glass specimen tubes in a manner such that a water column was in contact with the evaporating surface of the porous tube. A set of 3 atmometers was placed in each test chamber and averaged to give the relative ED that existed therein during the daily measurement period. Among the many EDs measured during the course of an experiment no two values were identical. The curves, regression equations, and single and multiple correlation coefficients used to analyze the data were obtained from the pairs of values of LWP, TR, ED and SMC measured on each pot during the 3–4 hr test period each day during the drying cycles. Although the discussion uses SMC as the criterion of the moisture regime in the root zone these can be translated into SMS using the moisture characteristic curve in Fig. 1 and the doubly indexed abscissa in Figs. 3 and 4. For discussion purposes the EDs were divided into two groups although it is recognized that the individual daily ED values constituted a range of values within each of these two arbitrarily defined groups. Those in the low group viz., below 20 mg/cm^2/hr were classed as low ED and the group ranging from 40 to 110 mg/cm^2/hr as the high ED.

Sampling and leaf water potential measurements : The Shardakov (1948) 'dye' method as described by Knipling (1967) was used with some modifications to determine LWP. Minimal exchanges of water between the leaf tissue and test solution are detectable if the solution to leaf tissue ratio is reduced to the minimum. This was accomplished by reducing the test solution volume to only 0.5 ml in a 72 $\times$ 12 mm test tube and increasing the size of the leaf tissue to a 25 $\times$ 10 mm rectangle. The leaf sample was wrapped to one end of a 8 mm glass rod and immersed in the test solution. This caused the entire leaf tissue surface to come in contact with the test solution and reduced to less than two hr the time required to obtain detectable osmotic exchange. Mannitol was used to prepare a series of graded solutions having 1.0 bar water potential increments. All measurements of LWP were made at room temperature which was in the 30–35°C range. Variations in ambient temperature were assumed to have negligible effects on LWP determinations since both the test sample and the reference solution were always at the same temperature.

Leaf sampling was restricted to top-most newly matured leaves because Longenecker and Lyerly (1969) showed that at any given time newly matured top leaves and petioles to be the most reliable indicators of the moisture status of cotton plants. Two leaves, one from each of two plants in a pot and preferably facing the same direction, were used for single determination. Although it took only two to three min to collect and prepare the leaf sample and to insert it into the solution, the process was conducted inside a humid chamber to minimise dehydration of the leaf samples.

Transpiration rate : Since the surface evaporation from the pots was minimal. the losses in soil moisture were attributed solely to transpiration. Daily loss in weight gave total transpiration/pot/day. Total leaf area per pot was also calculated at the time of pot weighing and was used to calculate the transpiration rate per unit of leaf area. The surface area of leaves of different sizes was determined graphically at the beginning of the experiment. These values multiplied by the number of leaves of each size present at the time of TR determination gave an estimate of the total leaf area per pot.

Results and Discussion

The data on LWP as a function of SMC at two levels of ED are presented in Fig. 2. The data were summarized by four linear smooth curves through the regression lines representing the dependence of LWP on SMC in the high and low parts of the moisture range and under conditions of high and low ED. It is of interest to note that the start of more rapid decline in LWP occurred at a SMC of 11 per cent when ED of the atmosphere was high whereas with a low ED it occurred at a much lower SMC of about 8 per cent.

When the ED was high LWP did not respond to changes in SMC in the 11 to 30 per cent range where SMS was < 0.5 bars whereas at low ED the LWP was independent of SMC over the 8 to 30 per cent SMC range where SMS was < 1.5 bars. In the 3 to 11 per cent and 3 to 8 per cent SMC ranges for the high and low ED conditions respectively, there was a high positive correlation between LWP and SMC with the LWP decreasing rapidly with decreasing SMC.

If the mean LWP observed when the soil moisture was not a limiting factor is considered to be its potential value, these observations suggest that at high ED the LWP fell below its potential value at about 0.3 bar soil suction whereas when ED was low, a similar decline did not occur until the SMC fell to about 1.5 bar soil suction. Moreover, under conditions of low ED the potential value of —13.6 bars, characteristic of high ED, was not reached until SMC was reduced to about 7 per cent corresponding to a SMS of 3 bars. This behaviour is of great practical significance and shows the usefulness of LWP as a criterion for determining the need for irrigating a crop.

In the high soil moisture range the LWP differed significantly at the two EDs being 2 to 3 bars lower at high ED than under low ED conditions. In the low soil

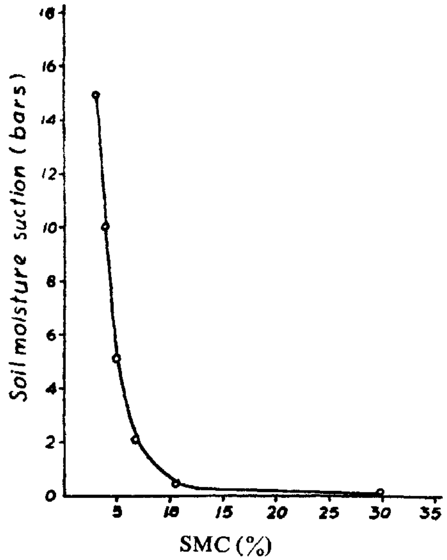


FIG. 1. Soil moisture characteristic curve.

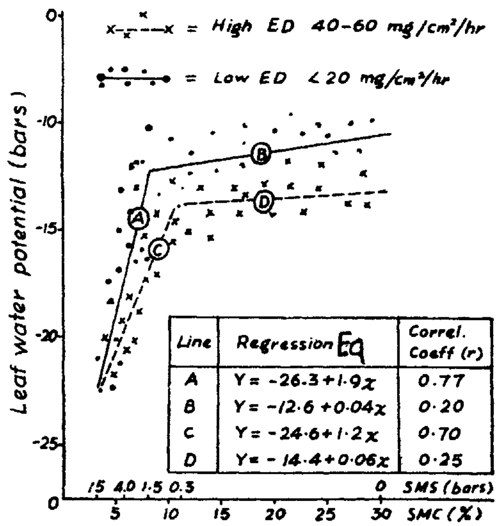
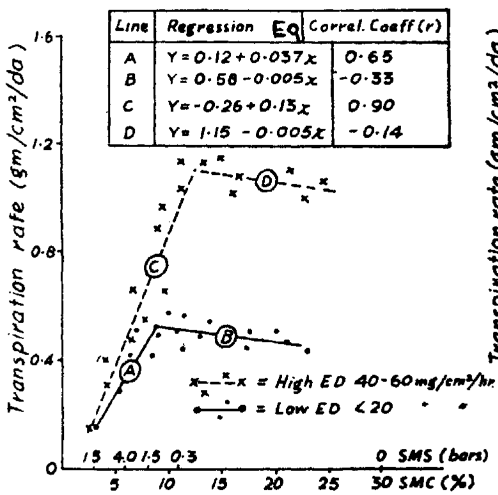


FIG 2. Leaf water potential as affected by soil moisture and evaporative demand



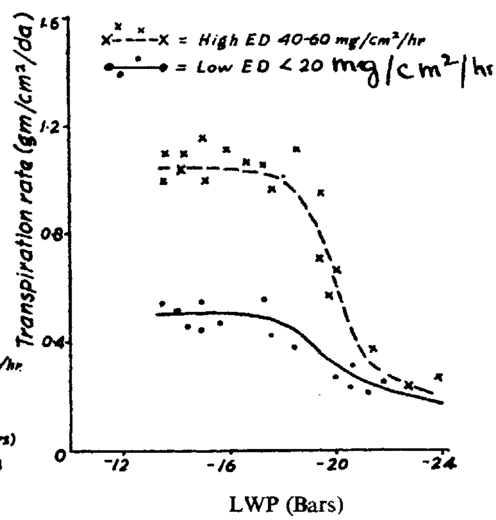


FIG. 3. Transpiration rate as affected by soil moisture and evaporative demand.

FIG. 4. Transpiration rate as affected by leaf water potential.

moisture range, the LWP at the two EDs did not differ significantly. A study of Fig. 2 indicates that this relation should hold good only upto about 6–7 per cent soil moisture. Above 6 per cent soil moisture the difference in LWP at two EDs is more than 2 bars. This suggests that above 6 per cent SMC corresponding to SMS < 4.0 bars the LWP was not dependent on SMC or SMS alone but was influenced by both the soil moisture conditions in the root zone and the evaporative demand of the atmosphere.

Below 6 per cent SMC there was no difference in effects of the different levels of ED on LWP, which therefore, must have been solely a function of SMC and its associated SMS. Similar observations have also been reported by Gardner (1960).

That the LWP was related to SMC and ED is shown by the highly significant multiple correlation coefficient R = 0.73. By comparison of the standard partial regression coefficients of $b_1' = 0.72$ and $b_2' = 0.16$, it was concluded that SMC had a 4.5 times greater influence on LWP than did the ED, at least over the respective ranges of these variables encountered in these experiments. Namken (1964) showed that soil moisture alone accounted for 7 per cent of the variation in relative turgidity in cotton, whereas ambient temperature and pan evaporation accounted for only 43 per cent of the variations.

As shown in Fig. 3, SMC and ED also affected the transpiration rate (TR). Within the ranges encountered during the experiment the TR at low ED fell below its potential rate at about 9 per cent SMC corresponding to SMS $\cong$ 1 bar, but at high ED the fall occurred at SMC of about 12 per cent or at SMS of about 0.3 bar. The potential TR was only 0.5 gm/cm²/da at low ED, but it more than doubled to 1.07 gm/cm²/da when the ED increased. At a SMC of 4–3 per cent corresponding to SMS of 15 bars, the TR for both ED conditions approached the same value of 0.15 to 0.2 gm/cm²/da. These results are in agreement with those reported by other investigators.

The observations noted above and the statistical analysis indicate that TR correlated with SMC and ED in a manner similar to that of LWP. At all values of ED, the SMC at which the TR fell below its potential rate corresponded rather well to those at which the LWP values began to decline from their potential values. This suggests that there was some relationship between the TR and LWP. Fig. 4 shows that above about —19 bars of LWP, the TR was independent of LWP but was dependent on ED. When LWP decreased below about —19 bars TR decreased rapidly when the ED was high and more gradually under conditions of lower ED. Under both high and low ED conditions the TR decreased to a low value of about 0.2 gm/cm²/da when the LWP fell below —22 to —24 bars. It is presumed that the rapid drop in TR in the —19 to —22 bar LWP range was caused by closing of the stomata and that the low TR at LWP< —24 bars represented cuticular transpiration.

The data summarized in Fig. 3 and 4 support the concept that over a considerable SMC range, where SMS is < 0.3 to 1.5 bars, TR is solely determined by the atmospheric ED and that adjustments of LWP are sufficient so that they maintain a moisture flow rate from the soil to the transpiring leaf large enough to prevent stomatal closure although a net loss of moisture from the plant tissues occurs as indicated by the progressive decrease of LWP. While the plant is in this LWP range the TR is independent of LWP and is controlled by ED alone. However in the LWP range of —19 to —22 bars the TR is strongly dependent on LWP because of the effect of the latter on stomatal closure. After the stomata are closed at LWP of —22 to —24 bars the TR is again independent of further reduction in LWP. This general interpretation of the data is in agreement with results reported by Ehlig and Gardner (1964) and by Gardner and Nieman (1964).

SUMMARY

Leaf water potential in sunflower was determined by the 'dye' method to study its behaviour under different evaporative demands throughout a drying cycle.

The results showed that in sunflower the leaf water potential was markedly influenced by both the soil moisture and atmospheric evaporative conditions. It was primarily controlled by the evaporative conditions when soil moisture was below 0.3 bar soil suction and by the soil moisture alone when the soil suction was above 3.0 bars. Between these two limits the influence of the two environmental factors overlapped and the leaf water potential was found to be a function of both the soil moisture and atmospheric conditions.

The leaf water potential obtained when the soil moisture is not limiting is considered as its potential value. The data indicated that at high evaporative demand the potential value was —13.7 bars but when the evaporative demand was low the potential LWP value was attained at a much lower soil water content corresponding to 3.0 bar soil suction.

The transpiration rate was independent of changes in the leaf water potential above —19 bars, although the transpiration rate increased with increasing evaporative demands. As the leaf water potential fell below —19.0 bars the transpiration rate under both high and low evaporative demand conditions decreased and tended to remain about constant below —22 to —24 bars.

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