Concurrent Comparisons of Stomatal Behavior, Water Status, and Evaporation of Maize in Soil at High or Low Water Potential

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ABSTRACT

Concurrent measurements of evaporation, leaf conductance, irradiance, leaf water potential, and osmotic potential of maize (Zea mays L. cv. Pa602A) in soil at either high or low soil water potential were compared at several hours on two consecutive days in July. Hourly evaporation, measured on two weighing lysimeters, was similar until 1000 hours Eastern Standard Time, but thereafter evaporation from the maize in the dry soil was always less than that in the wet soil; before noon it was 62% and by midafternoon, only 35% of that in the wet soil. The leaf water potential, measured with a pressure chamber, was between -1.2 and -2.5 bars and between -6.8 and -8 bars at sunrise (about 0530 hours Eastern Standard Time) in the plants in the wet and dry soil, respectively, but decreased quickly to between -8 and -13 bars in the plants in the wet soil and to less than -15 bars in the plants in the dry soil by 1100 to 1230 hours Eastern Standard Time. At this time, the leaf conductance of all leaves was less than 0.1 cm sec⁻¹ in the maize in the dry soil, whereas the conductance was 0.3 to 0.4 cm sec⁻¹ in the leaves near the top of the canopy in the wet soil. The osmotic potential, measured with a vapor pressure osmometer, also decreased during the morning but to a smaller degree than leaf water potential, so that by 1100 to 1230 hours Eastern Standard Time the leaf turgor potential was 1 to 2 bars in all plants. Thereafter, leaf turgor potential increased, particularly in the plants in soil at a high water potential, whereas leaf water potential continued to decrease even in the maize leaves with partly closed stomata. Evidently maize can have values of leaf conductance differing 3- to 4-fold at the same leaf turgor potential, which suggests that stomata do not respond primarily to bulk leaf turgor potential. Evidence for some osmotic adjustment in the plants at low soil water potential is presented. Although the degree of stomatal closure in the maize in dry soil did not prevent further development of stress, it did decrease evaporation in proportion to the decrease in canopy conductance.

The role of stomata in the regulation of $E'$ by a crop or leaf canopy is now well recognized (20-22). However, the mechanisms through which moisture stress induces stomatal closure, and hence regulation of $E$, have been less widely studied. In two previous papers, the stomatal behavior and water status of maize, sorghum, and tobacco were followed in plants growing in either soil at high (17) or low (15) water potential. At high soil water potential, $\psi$ varied diurnally over a considerable range, but the bulk leaf turgor never reached zero and the stomatal resistance was largely determined by the irradiance incident upon the leaf (14, 17); by contrast, at low soil water potential the stomata in the upper leaves closed early in the morning as the potential in the leaf decreased and the bulk leaf turgor approached a zero potential (15). The latter study also showed that the $\psi$ at which the stomata closed varied markedly with species, being highest in tobacco, intermediate in maize, and lowest in sorghum.

Other recent studies, however, have demonstrated that the critical water potential for stomatal closure is not unique for any given species, but varies with stage of development (6), growth conditions (8), position in the canopy (15), and previous stress history (10). Also, the development of plant water stress is influenced by aerial environment as well as the soil water status. Thus the development of stress and stomatal behavior in a species at high and low soil water potentials, using the data presented in the previous studies, is not a rigorous comparison since the data at the two soil potentials were obtained on different dates and even in different years.

In the present study, the stomatal behavior, plant water stress and $E$ of maize in soil at low and high water potentials have been compared over the same period of time and under the same meteorological conditions on plants at the same stage of development. The direct comparison of stomatal behavior and development of plant water stress of plants in moist and dry soil enabled the role of leaf turgor on stomatal behavior to be assessed and the concurrent measurement of $E$ enabled the role of stomatal conductance on $E$ to be evaluated.

MATERIALS AND METHODS

The study was conducted from 1100 hr on one day to 1400 hr the following day on two consecutive days in July, in a 0.5 ha field of maize (Zea mays L., cv. Pa602A) at the Lockwood Farm, Mt. Carmel, Connecticut. The maize was sown in mid-May to give a final plant population of 71,000 plant/ha. At the time of this study the crop was 1.5 m tall, had a LAI of 4.2, and the tassels were just emerging. The meteorological conditions at the Mt. Carmel Meteorological Station, 400 m from the experimental site, are given in Table I. Rainfall totalled only 40 mm in the previous 44 days, but the crop showed no signs of wilting except in small areas of shallow soil.

Each hour, except between 2100 and 0700 hr EST, the $E$
by the maize was measured with a pair of weighing lysimeters (12) briefly described by Waggoner et al. (23). The lysimeters were drums 85 cm deep and 56 cm in diameter, filled with soil 28 months previously and containing two maize plants; the LAI of the plants in each lysimeter was 4.1 and 4.3. The lysimeters were located 20 m from the northern edge and 150 m from the southern edge of the maize plot; with the wind in the southeast quadrant (Table I), the fetch was 70 m. Measurements began the day after wilting was first observed in the dry lysimeter. The other lysimeter had been maintained near field capacity by frequent watering. Before plants in the dry lysimeter showed any signs of wilting, and again after subsequent watering, $E$ from both lysimeters was compared and found to be similar. During the experiment the soil surface of both lysimeters was covered with a film of black plastic to eliminate differences in $E$ from the soil.

In addition to the hourly measurements of $E$, the stomatal conductance, irradiance, $\psi$, and $\pi$ were measured concurrently at five or six heights in the leaf canopy. The stomatal conductance and irradiance were measured on the two plants in each lysimeter; the samples for the measurement of $\psi$ and $\pi$ were taken from plants grown under identical conditions in drums buried in the ground 6.7 m and 13.3 m south of the lysimeters. Measurements of stomatal conductance on these plants were sufficiently similar to those in the lysimeters at all times of the day to give confidence in the procedure. The order in which the plants in the wet and dry soil were sampled was randomized.

The stomatal conductance of the horizontal portion of a leaf was measured with a ventilated diffusion porometer (19). The adaxial and abaxial stomatal conductances were measured separately on adjacent portions of the leaf, and the $k_i$ was calculated assuming that the two leaf surfaces acted as parallel conductors. The mean $k_i$ was calculated by summing the mean values of $k_i$ of the pair of leaves at the five heights in the canopy.

Immediately after the completion of the measurements of $k_i$, the irradiance incident upon the adaxial epidermis, in the region of conductance measurements, was obtained with a model 756 Weston Sunshine Illumination Meter (Weston Instrument Co., Newark, N.J.). The meter was calibrated in energy units with an Eppley pyranometer (Eppley Laboratory, Inc., Newport, R.I.); the calibration was obtained on several days with the illumination meter and pyranometer situated above the crop.

The leaf water potentials were measured on half a leaf placed in a pressure chamber (18), a modification of that described by Scholander et al. (13) which provides reasonable estimates of $\psi$ in maize (4).

The osmotic potentials were measured with a Model 302B Hewlett Packard (Avondale, Pa.) vapor pressure osmometer. Leaf samples from the opposite half of the leaf used for the measurement of $\psi$ were sealed into a test tube and quickly frozen in Dry Ice. The frozen samples were returned to the laboratory and then allowed to thaw before the cell constituents were expressed from the leaf and quickly transferred to the osmometer.

The $\psi$ and $\pi$, concurrently sampled and measured on the same leaf, were used to determine the bulk $P$ from the equation:

$$\psi = \pi + P$$

(1)

Matric potential was assumed to be zero.

The leaf area of the plants in the lysimeters was measured nondestructively using the formula (11):

$$\text{Leaf area} = \text{length} \times \text{maximum width} \times 0.75$$

(2)

The leaf area of the crop was similarly obtained from four randomly chosen plants.

RESULTS

Because the rates of $E$ were similar between 1100 hr and 1400 hr on the two days, the data for this period are combined and presented diurnally from midnight to midnight. Early morning dew and light cloud kept $E$ low and equal on the two lysimeters until 1000 hr EST (Fig. 1). Thereafter, the rates of $E$ diverged: for plants in wet soil, $E$ continued to rise until midafternoon and then decreased rapidly until sunset (1900 hr EST); for plants in dry soil, $E$ remained relatively constant between 1000 and 1600 hr and then decreased. Thus, just before noon the $E$ from the plants in the dry soil was 62% of that in the wet soil, but by midafternoon it was only 35%. Over the 24 hr period, $E$ was only 2 mm in the dry soil compared with 5 mm in the wet soil.

Concurrent measurements of $k_i$, $\psi$, $\pi$, and $P$ are presented in Figure 2. Because the vertical profiles of irradiance were similar at similar times of day to those observed previously in maize (17), they are omitted from Figure 2. For leaves at the top of the canopy the irradiance increased from zero at sunrise to

![Fig. 1. Hourly evaporation from maize at either high (wet) or low (dry) soil water potential. For meteorological conditions see Table I.](https://academic.oup.com/plphys/article-lookup/10.1093/pl Physiol/55.5.932)
Fig. 2. Vertical profiles of leaf conductance, leaf water potential, leaf osmotic potential, and leaf turgor potential in a maize crop at either high (●) or low (○) soil water potential at four times of day (EST).

The mean \( \pi \) at sunrise was \(-9.6\) bars and \(-13.4\) bars for plants in the wet and dry soil, respectively. In all plants, \( \pi \) decreased during the day to minimum values in the early afternoon. Because \( \pi \) did not decrease as rapidly nor to the same degree as \( \psi \), by late morning (1100 to 1230 hr EST) \( P \) of all leaves was between 1 and 2 bars. Of particular note in the fact that at this time \( P \) of plants in the wet soil was lower than that of plants in the dry soil except in one leaf at the base of canopy, and even by early afternoon, when \( \psi \) and \( \pi \) reached their minimum values, the mean \( P \) of all leaves of plants in the dry soil were only marginally lower than those in the wet soil. However, because the recovery of \( P \) was quicker in the plants in wet soil than those in dry soil, by 1700 to 1830 hr EST, the mean \( P \) of plants in the wet soil was 4.9 bars whereas it was only 1.3 bars in the plants in the dry soil.

The changes in \( \psi \) and \( \pi \) between the time intervals in Figure 2, as a mean of five levels in the canopy, are given in Table II. The change in \( \psi \) between the maximum values near sunrise (0500 to 0630 hr EST) to the minimum values in the early afternoon (1300 to 1430 hr EST) was greater in the plants in dry soil than in wet soil. The change in \( \psi \) was twice as great in the plants in dry soil than in those in wet soil between late morning (1100 to 1230 hr EST) and early afternoon (1300 to 1430 hr EST) when \( k \), was less than 0.15 cm sec\(^{-1}\). As indicated above, the mean change in \( \pi \) from the maximum values near sunrise (0500 to 0630 hr EST) to minimum values in the early afternoon (1300 to 1430 hr EST) was not as great as the change in \( \psi \), but there was a considerable diurnal change of 6.6 bars and 4.5 bars in the plants in the soil at low and high water potential, respectively.

Differences in the diurnal change of \( \psi \) and \( \pi \) are reflected in the diurnal change in \( P \). The relation between \( P \) and \( \psi \) for leaves at intermediate heights in the canopy in both the soil at high and low potentials is shown in Figure 3a. The leaves at the top and base of the canopy are omitted because it was shown previously that these differed from leaves at intermediate heights (15). The regressions, fitted as previously (15), indicate that the \( P \) and, hence \( \pi \), was greater at an equivalent \( \psi \) in the leaves of plants in dry soil than in those in wet soil. As the figure and correlation coefficients indicate, however, there was considerable variation in the regressions. This was in part because leaves at three intermediate levels in the canopy were used, and the \( P \) at equivalent \( \psi \) was progressively smaller at progressively lower levels in the canopy (Fig. 3a).

<table>
<thead>
<tr>
<th>Time Interval</th>
<th>( \Delta \psi )</th>
<th>( \Delta \pi )</th>
</tr>
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<tbody>
<tr>
<td>0500-0630 to 1100-1230</td>
<td>-8.3</td>
<td>-8.3</td>
</tr>
<tr>
<td>1100-1230 to 1300-1430</td>
<td>-1.6</td>
<td>-0.8</td>
</tr>
<tr>
<td>1300-1430 to 1700-1830</td>
<td>+1.5</td>
<td>+2.4</td>
</tr>
<tr>
<td>1700-1830 to 0500-0630</td>
<td>+8.4</td>
<td>+6.7</td>
</tr>
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Table II. Changes in Leaf Water Potential (\( \Delta \psi \)) and Osmotic Potential (\( \Delta \pi \)) in Maize Growing in Either Dry or Wet Soil. Values are the means of the leaves at five or six heights in the canopy.
source of variation, however, is shown in Figure 3b where the values for one set of leaves at the same height in the canopy for the wet and dry soils are shown from near sunrise to late afternoon. As can be seen from this figure, $P$ decreased markedly as $\psi$ decreased in the morning so that by late morning $P$ was between 1 and 2 bars in the plants at both low and high soil water potentials: this rate of decrease in $P$ with decreasing $\psi$ was similar for leaves at other heights in the plants in both the wet and dry soil. However, thereafter $P$ increased even though there was a further decrease in $\psi$. The increase in $P$ between late morning (1100 to 1230 hr EST) and late afternoon (1700 to 1830 hr EST), during which time $\psi$ varied by less than 2.5 bars, was greater in the plants in wet soil than those in dry soil.

The influence of $k_\nu$ on $E$ is assessed in Figure 4. For plants in both wet and dry soil, $E$ increased linearly with $k_\nu$. In the wet soil $E$ and $k_\nu$ varied linearly over a considerable range. In the dry soil, the range over which $E$ and $k_\nu$ varied was smaller than that in the wet soil, but the correlation was the same, within the scatter of the points, as that for the wet soil.

**DISCUSSION**

The concurrent comparisons of stomatal behavior, water status, and evaporation of maize at either high or low soil water potential, but under similar meteorological conditions and at the same stage of development, has demonstrated that closure of stomata as a result of internal plant stress has a direct effect upon the rate of evaporation of the crop, that bulk leaf turgor does not regulate stomatal behavior, and that the degree of stomatal closure observed in this study does not prevent the development of further stress in the plant. Furthermore, evidence is provided that some osmotic adjustment in response to stress may occur in maize.

The abrupt increase in stomatal resistance, or decrease in $k_\nu$, as the plant water status fell below a critical value, was shown in a previous paper (15). The influence of this decrease in $k_\nu$ on the evaporation has been clearly shown in this study. The $E$ by the plants in the dry soil began to fall below that in the wet soil when $\psi$ fell below -15 bars and $k_\nu$ decreased (Figs. 1 and 2). The close correlation between mean $k_\nu$ and the hourly mean of $E$ in plants in the dry soil as well as those in the wet soil (Fig. 4), measured under the same meteorological conditions, indicates that $E$ is directly under stomatal control and is reduced in proportion to the mean stomatal closure of the leaves in the canopy. The closure of stomata in response to low soil moisture and plant water stress has been well documented under field conditions (1, 3, 5), but few comparisons have been made under exactly the same meteorological conditions or with plants at the same physiological stage of development, since observations have usually been made on different days in a drying or wetting cycle.

The regulation of $E$ by stomata is well recognized and is considered to be a means of controlling or preventing the development of further stress. However, it is clear from Figure 2 that the stomata in leaves at the top of the canopy only partly closed and this did not completely prevent further $E$ (Fig. 1), nor did it prevent the further development of stress as indicated by the decrease in $\psi$ between the late morning and early afternoon observations (Table II). This suggests that maize may be poorly adapted to drought conditions. On the other hand, some osmotic adjustment occurs during the same late-morning to early-afternoon interval in which $k_\nu$ is low (Table II), thus increasing $P$ (Fig. 3b). Some of the decrease in $P$ as $\psi$ decreased presumably results from the concentration of solutes in the cell as water is extracted, but the observation that $P$ increased to a greater degree in the plants at high rather than low soil
water potential suggests that at least some of the decrease in \( \pi \) may arise from photosynthesis and sugar accumulation in the leaf. Moreover, the greater \( P \) at equivalent \( \psi \) in maize in dry rather than wet soil indicates that an osmotic adjustment of approximately 2 bars had been caused by the decreasing soil and leaf water potential as stress developed (Fig. 3a). Clearly any decrease in the \( \pi \) as stress develops confers an advantage on the species during drought.

It has been pointed out elsewhere that although there is not a unique, critical \( \psi \) for stomatal closure for a particular species, presumably because of adjustments in \( \pi \) during the development of stress, stomatal closure occurred at values of \( P \) between 0 and 2 bars in all species (16). This suggests a unique \( P \) for stomatal closure in all species at all stages of growth. However, the present study indicates that this is clearly not the case because at the same \( P \), the \( k \), of the leaves near the top of the canopy was 0.1 cm sec\(^{-1}\) and 0.3 cm sec\(^{-1}\) in the plants at low and high soil water potentials, respectively (Fig. 2). This emphasizes that stomata do not respond to changes in bulk leaf turgor, but to differences in turgor between the guard cells and neighboring cells in the epidermis. A similar conclusion can be drawn from the observations, that first, \( k \), does not change over a considerable range of \( P \) (15), and second, abaxial stomata close at greater values of \( \psi \) and \( P \) than adaxial stomata (7, 9).

Finally, the profiles of \( k \), \( \psi \), \( \pi \), and \( P \) that were observed in the plants in wet and dry soil (Fig. 2) were similar to those observed previously in maize at either low (15) or high (17) soil water potential. However, in the present study, \( k \), in plants from the wet and dry soils varied markedly at the same \( P \), whereas this was not noted in the previous studies. Furthermore, in the present case, the stomata of the well-irradiated maize leaves were nearly closed at values of \( \psi \) less than -15 bars, whereas in the previous studies, stomatal closure did not occur until the values of \( \psi \) fell below -16 to -17 bars (15). Inasmuch as controlled environment studies have indicated that wheat stomata close at lower values of \( \psi \) as the crop ages (6), this variance may simply reflect the fact that the studies of maize were conducted at different physiological stages. The present study was conducted when the tassels were just emerging, whereas the previous studies were conducted when the plants were fully developed and the ear was filling. Thus the three studies complement one another and demonstrate that stomatal behavior and water status in different seasons may be compared if comparisons are also made in the same environment and with plants of the same physiological age.

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LITERATURE CITED