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Influence of Soil Water Stress on Evaporation, Root Absorption, and Internal Water Status of Cotton[1]

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ABSTRACT

Diurnal variations in leaf water potential, diffusion resistance, relative water content, stem diameter, leaf temperature, and energy balance components were measured in cotton (*Gossypium hirsutum* L. var. Lankart 57) during drought stress under field conditions. A plot of leaf water potential against either relative water content or stem diameter during the 24-hour period yielded a closed hysteresis loop. The relation between cell hydration and evaporation is discussed.

Despite low soil water potential in the main root zone, significant plant evaporation rates were maintained. Root absorption rates as a function of soil depth were calculated from water content profiles measured with a neutron probe. The maximal root absorption rate of 3.5×10^{-3} day^{-1} occurred at the 75-centimeter depth, well below the main root zone.

Stomatal resistance of individual leaves during the daylight hours remained nearly constant at 2.5 seconds centimeter^{-1} even though leaf water potentials approached −30 bars. A growth chamber study indicated stomatal closure occurred at potentials near −16 bars. Possible implications of high soil water stress in relation to stomatal function and growth are discussed. Based on an energy balance method, the actual to potential plant evapotranspiration ratio was 0.43 for the 24-hour period, indicating partial stomatal closure. A surface resistance, r_s, of 4.0 seconds centimeter^{-1} was calculated for the incomplete canopy with the use of the energy balance data. Alternatively, a canopy resistance of 1.3 seconds centimeter^{-1} was attained from a relationship between leaf area and stomatal resistance of individual leaves. If the soil resistance was assumed to be very large and the canopy resistance was weighted for the fractional ground cover of the crop, the calculated surface resistance was 4.3 seconds centimeter^{-1}. Under these conditions, the two independent estimates of r_s were in essential agreement.

Significant enhancement of our understanding of the response of internal plant water status to changes in the evaporative demand, in the water potential in the root environment, and in illumination have been made by theoretical analysis and by experiments under controlled conditions, but parallel studies with plants growing in a natural environment are relatively rare. Because of a prolonged drought in central Texas, the 1969 summer growing season provided an opportunity for field study of the water status of cotton under high soil water stress. Accordingly, diurnal variations in plant and soil water status and evaporation rate during drought stress were measured for purposes of comparison with theoretical predictions and with results from experiments under controlled conditions.

Field studies by Weatherley (32) and Slatyer (23) have shown that plant water status is directly influenced by evaporative demand until a critical soil water potential is reached. The transpiration rates presented in these studies were inferred from a technique with the use of excised leaves and cannot be interpreted in absolute quantities. Recent field studies with precision weighable lysimeters have clarified the relation between environmental factors and absolute transpiration rates, but simultaneous measurements of plant water status were not included (1, 19, 20, 27, 28).

When soil water is not limiting and prior to the establishment of a complete crop canopy, transpiration rates relative to the evaporation potential are approximately proportional to the square root of the LAI[2] for cotton and sorghum at the location of this study (20). After an effectively complete cover develops and so long as the stomates remain fully open, the transpiration rate is determined by the available energy (28). As the soil water potential decreases and water becomes limiting, actual evapotranspiration rates eventually fall below the potential rate. This increased resistance to transpiration is probably caused by a reduction in stomatal aperture although other mechanisms have been proposed (9, 14). Reductions in stomatal apertures of leaves are induced by changes in the internal plant water balance (12, 14, 24), but concrete relationships between the degree of stomatal opening, transpiration rates, and plant water status are not well defined, especially under stress conditions.

Daily fluctuations in the plant water balance appear to be nearly constant as long as the daily energy flux remains reasonably constant and soil water is not limiting (12). When these conditions are met, the same plant water potential or relative water content is achieved overnight. As water becomes limiting, the magnitude of the daily fluctuation increases and eventually the soil and plant water potentials decrease. When soil water potential falls below some critical level, a combination of both soil and atmospheric conditions controls the plant water status (6, 8, 18, 23, 32). Under greenhouse conditions,

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[2] Abbreviations: LAI: leaf area index; RWC: relative water content; SD: stem diameter.

De Roo (3) failed to find a simple quantitative relation between soil and plant water potentials. The situation of plants growing under field conditions is still more complex because the soil water potential in the root zone is seldom uniform with depth.

MATERIALS AND METHODS

General. The experiments were conducted at Temple, Texas, on Houston black clay soil during 1969. The data were collected on July 17 and 18 on cotton (*Gossypium hirsutum* L. var. Lankart 57) planted in rows spaced 0.92 m apart. The average plant height and leaf area were about 35 cm and 980 cm^2, respectively, providing a LAI of 1.9 and about 30% ground cover. Rainfall during June and July was 1.9 and 0.08 cm, respectively. Further details of early season rainfall and site conditions have been presented elsewhere (19, 20).

Environmental Measurements. Evapotranspiration rates were measured with an energy balance technique according to the equation:

$$LE = (R_n - S)/(1 + B) \qquad (1)$$

where LE is the latent heat flux, R_n is the net radiation flux, S is the soil heat flux, and B is the Bowen ratio. B is defined as:

$$B = \gamma(\Delta T/\Delta e) \qquad (2)$$

where γ is the psychrometric constant, ΔT is the temperature difference, and Δe is the vapor pressure difference between two heights above the canopy. Further details on the method are given by Tanner (26). R_n was measured with a Fritschen type net radiometer (5), and S was measured with commercial heat flux plates buried about 3 cm below the soil surface. Temperature and vapor pressure gradients over a 65-cm interval above the crop canopy were measured with diodes and lithium chloride dew cells as described elsewhere (19, 20). Soil water content profiles were determined with a neutron probe throughout the growing season, and matric potentials were estimated from the known water retention curves (unpublished data).

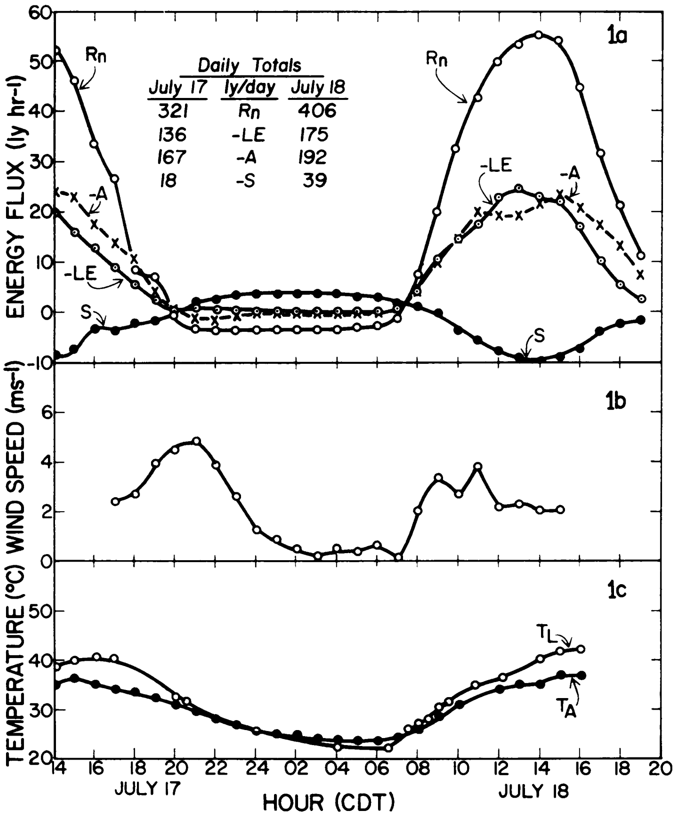

FIG. 1. Simultaneous changes in energy balance components (a), wind speed (b), and leaf and air temperature (c) throughout the period studied. ly: Langley.

Plant Measurements. Stomatal resistance, leaf water potential, relative leaf water content, and leaf temperature were measured on the uppermost, fully expanded leaves completely exposed to full sunlight. Stomatal resistances were measured on the upper surface with a modified resistance meter of the type described by Van Bavel *et al.* (29). The measuring cup was attached to a region of the leaf between the principal veins and was immediately removed after the measurement was taken. Leaf water potentials were determined in the field by a pressure chamber technique (22). This technique has proven satisfactory for cotton studies (11). Leaves were excised with a razor blade near the base of the petiole and inserted rapidly into the pressure chamber. Pressure from a tank of compressed nitrogen was applied at the rate of 0.2 to 0.3 bar sec^{-1}. The final reading was obtained within 60 to 90 sec after removal from the plant. Leaf discs (2.2 cm in diameter) were collected in the field and transported in closed weighing bottles to the laboratory for relative water content determinations (31). Triplicate samples of 10 discs each taken from 10 different plants were collected at each sampling time. The discs were floated on distilled water for 22 to 24 hr under laboratory light conditions. Excess moisture was removed by blotting before weighing to determine the turgid weight. Dry weights were obtained after oven drying at 70 C for 48 hr. Stem diameters were measured with a linear variable differential transducer as described by Namken *et al.* (16). The sensor, contained in a Plexiglas holder and attached to an iron stake for support, was attached to the main stem of the plant about 10 cm above the soil surface. Temperatures of individual leaves were measured with a Barnes model PRT-10 infrared radiometer.

RESULTS AND DISCUSSION

The magnitude of components of the energy balance during the test period are illustrated in Figure 1. Conditions during these observations could be considered typical for the dates and location. Net radiation fluxes near 1.0 Langley min^{-1} were reached on both days. The daily energy requirement for evaporation was approximately 45% of the total available. During daylight hours, derived values of the sensible heat flux (A) were negative, indicating that the entire surface including the crop canopy was losing energy to the air and leaf temperature (T_L) was greater than air temperature (T_A). Measured values of T_L and T_A are shown in the lower portion of Figure 1. Leaf temperature ranged from 6 C above to 1.5 C below air temperature. Overnight, (A) became positive indicating the surface was extracting heat from the air.

The plant-water status for the same period, expressed as leaf water potential (ψ_l) and RWC, is presented in Figure 2, a and b. As water vapor is lost by transpiration, a water potential gradient is established within the plant such that the size of this gradient reflects the balance between environmental demand and the rate of water extraction from the soil. Because the resistances to water movement within the plant and soil are finite, both ψ_l and RWC decrease during periods of increasing R_n and recover as R_n is reduced. The data presented in Figure 2 illustrate this diurnal pattern.

Maximal ψ_l of about −10 bars was observed just before sunrise on both days. The sharp reduction in ψ_l is probably associated with increasing light intensity, an observation which is consistent with the known effect of light on stomatal open-

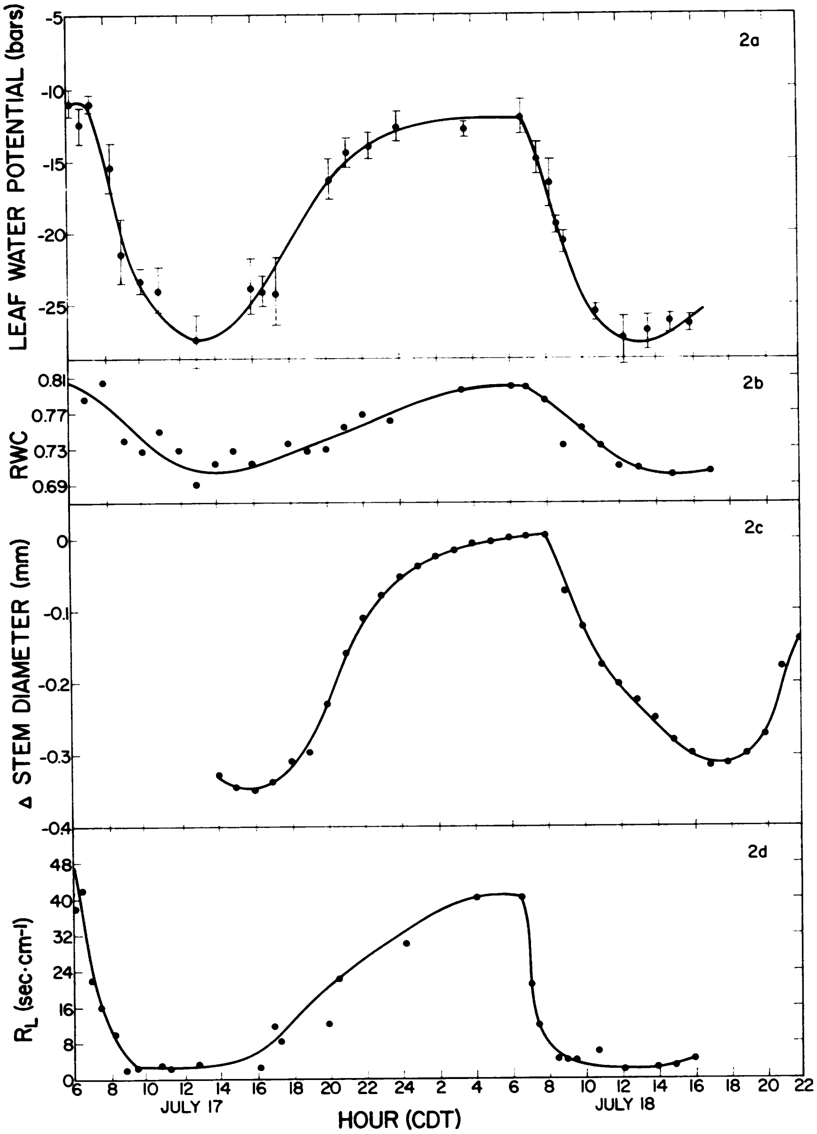

FIG. 2. Simultaneous changes in leaf water potential (a), relative water content (b), stem diameter (c), and stomatal resistance (d) throughout the period studied.

ing (4, 13). Minimal ψ_l of about −26 bars was reached between 1300 and 1400 hr, corresponding with maximal solar and net radiation. As the radiation load decreased in the afternoon hours, ψ_l increased rapidly, reaching a maximum about midnight. No further change was observed between midnight and sunrise, indicating that ψ_l was probably in equilibrium with the soil water potential surrounding the roots.

Although our data suggest that the effective soil water potential in the root zone was about −10 bars, plant water potential data provide no information concerning the soil water potential profile. The distribution of soil matric potential with depth is shown in Figure 3. Matric potentials were greater than −0.2 bars at 75 cm and below and decreased rapidly toward the surface. Water transmission characteristics of this soil have been evaluated, and the approximate hydraulic conductivity at −10 bars of soil matric potential is 10^{-6} cm day^{-1} (unpublished data). This potential falls within the range where rhizosphere resistance may limit the over-all transfer of water from the soil to the root surface (17), leading to reduced plant water potentials. The water potential data indicate that the majority of the root system was localized in the upper 25 cm of the profile, although actual root distribution was not determined. Limited root distribution studies at this site have shown cotton to have a tap root system with strong lateral branching only in the upper few inches of the soil profile (unpublished results, Blackland Conservation Research Center).

Ogata *et al.* (18) have shown that the rate of water absorption by roots, r_z, at depth z is given by:

$$r_z = (\delta\theta/\delta t) - (\delta v/\delta z) \quad (3)$$

where θ is the fractional volumetric soil water content at depth z, t is time in days, and v is the flux of water in the soil at z. During the growing season changes in θ with time at 25-cm depth increments were measured with the neutron scattering technique. The $\delta\theta/\delta t$ term for the various depths was estimated for July 18 from a graph of the θ *versus* t curves. The flux, v_z, was calculated from the product of the hydraulic gradient and the hydraulic conductivity at the various depths and $\delta v/\delta z$ was determined graphically. This latter term was negligible at all except the 125- to 150-cm depths when compared to the $\delta\theta/\delta t$ term. The calculated values of water ab-

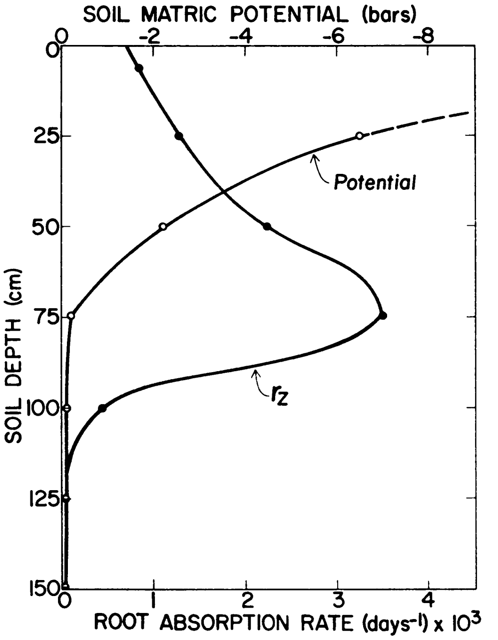

FIG. 3. Distribution of soil matric potential and root absorption rate (r_z) with soil depth.

sorption by the roots are given in Figure 3. Although the root absorption rate (r_z) was greatest near the 75-cm depth, the maximal value of 3.5×10^{-3} day^{-1} was quite low when compared with values reported for well watered soils (21, 30). Since the soil matric potential at 75 cm was about −0.2 bars, the low extraction rate also suggests low root density or high root impedance to water transport at this depth. Gardner (7) found a discrepancy between observed and calculated root distribution patterns based on soil water content changes and concluded that although there were more roots actually present at the lower depths than calculated, they were small and may have offered considerable impedance to water transport. Gardner's data support a previous hypothesis by Ogata *et al.* (18) that the impedance of roots to water transport can be an important factor determining the plant water status and the shifting nature of soil water extraction patterns.

The plant water potentials observed during this period may also be used as a qualitative indicator of the growth status of the crop. A previous study has shown that expansive growth of cotton seedlings is suspended at plant water potentials lower than −8 bars (11), which is in esssential agreement with values presented by Boyer (2) for corn, soybean, and sunflower. Since the plant water potential observed in this study did not rise above −10 bars, vegetative growth should have been inhibited. This conclusion is supported by seasonal data reported elsewhere which demonstrate that leaf area index and stem diameter were constant and the rate of dry matter accumulation was zero during this period (10, 20).

Leaf RWC is an estimate of water content rather than water potential. Relative water content ranged from 81 to 70% on both days. Concomitant with the daily fluctuation in RWC was a change in SD as shown in Figure 2c. The response of both RWC and SD to changes in R_n lagged behind changes in leaf water potential. After sunrise, leaf water potential fell much more rapidly than either RWC or SD. Similar observations have been reported by Namken *et al.* (16). Recovery to maximal potential was complete by 2400 hr, but maximal values of RWC and SD were not reached until sunrise. An interesting relationship between diurnal changes in leaf water potential and water content may be constructed from these data. With data from the smooth curves presented in Figure 2, a and b, a plot of RWC *versus* ψ_l yields a closed hysteresis loop (Fig. 4). Similar results are obtained for a plot of SD *versus* ψ_l.

The hystereis curves arising from these data are similar to dynamic water characteristic curves for nonswelling soils and wood (24). The desorption portion of the curve corresponding to the period of increasing net radiation was nearly linear throughout the range of −10 to −26 bars. The absorption curve also was nearly linear during the late afternoon hours of July 17 but changed to strongly curvilinear at sunset (2000 hr). Differences of 7 bars between absorption and desorption portions of the curve were observed at RWC near 76%. Similarly, RWC differences of 5% were observed at potentials near

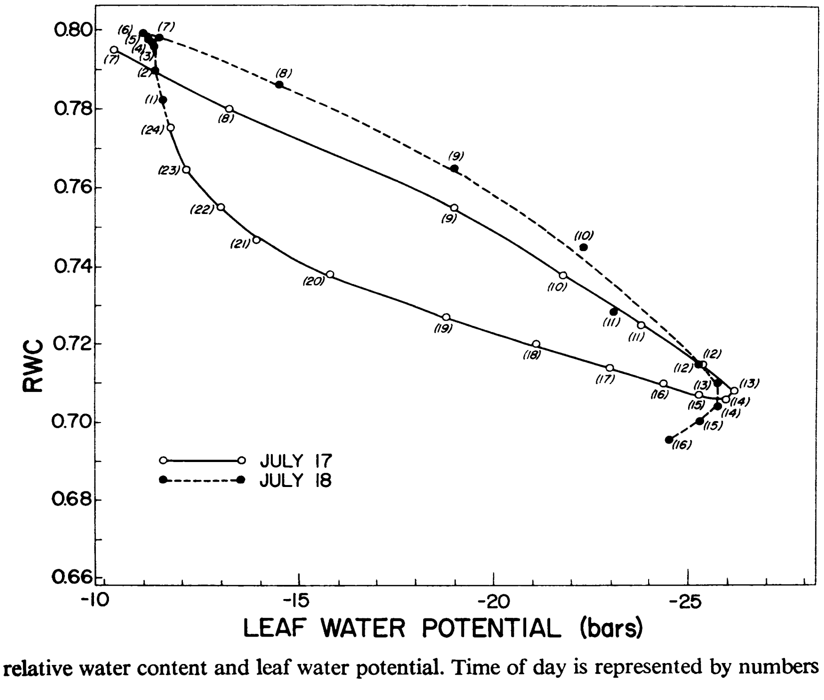

FIG. 4. Relation between relative water content and leaf water potential. Time of day is represented by numbers adjacent to each datum point.

−13 bars. The hysteresis curve may result from unequal resistances to water flow to evaporation sites compared with flow into cells of the leaf mesophyll. Under conditions of limiting water supply, the small amount of water absorbed by the leaf would be partitioned in proportion to resistances encountered in each flow path. Thus, as long as there is an appreciable evaporative demand, water may not be available for rehydration of the mesophyll cells. As the evaporative demand decreases during the afternoon hours, less water is lost by transpiration and the remainder is available for cell rehydration. After sunset, the resistance in the transpiration flow path is increased due to stomatal closure (Fig. 2d) and nearly all the water would be available for cell hydration.

The effect of light (sunrise) on stomatal opening under these conditions is demonstrated in Figure 2d. Stomatal resistance (R_L) fell from 40 to 2.5 sec cm^{-1} within 2 hr after sunrise and remained near the minimum between 0900 and 1700 hr on both days. Increases in R_L during the late afternoon hours on July 17 may be attributed to reduced light intensities due to increasingly cloudy skies.

Stomatal resistances between 2 and 3 sec cm^{-1} are approximately two and one-half times greater than commonly cited values for cotton and other species with maximally open stomata. In the present study, complete stomatal closure at leaf water potentials approaching −30 bars was not indicated. This result conflicts with data presented by Kanamasu and Tanner (12) and Boyer (2). Both reports indicate rapid increases in stomatal resistance at leaf water potentials of −8 to −12 bars for several species.

For comparative purposes, a growth chamber experiment was conducted with cotton in which stomatal resistance was determined during a drying cycle. Greenhouse-grown plants were placed in the growth chamber and maintained under well watered conditions for several days prior to sampling. The plants were approximately 75 cm tall and had 10 to 12 leaves. These results, along with the data from the field study (Fig. 2d) taken between 0830 and 1600, are presented in Figure 5.

The response of greenhouse-grown cotton plants to increasing water deficit was similar to that of corn, sunflower, soybeans, and snap beans (2, 12). Stomatal resistance increased sharply when leaf water potentials decreased to −16 bars, indicating stomatal closure. However, the stomatal resistance of the field-grown plants remained low even at leaf water potentials of −27 bars. These results indicate a possible modification of stomatal response to water stress caused by prolonged exposure to drought conditions in the field. Whether the stomata of these field-grown plants have lost the ability to close in response to water deficit, or whether the threshold deficit required for closure has been extended due to internal changes caused by prolonged exposure to severe water deficits, cannot be determined, although the latter explanation seems more likely. Wilting was not observed in field-grown plants but did occur in the upper leaves of greenhouse-grown plants at leaf water potentials near −15 bars.

The extent of stomatal control of evaporation during this period may be determined using published relationships. The relative contributions of soil evaporation (E_s) and plant transpiration (E_p) to the potential evapotranspiration (E_o) have been evaluated in the Temple location for row crops with incomplete canopies (20). When available soil water in the root zone was nonlimiting, E_p was approximately equal to E_o only after the plant canopy developed a critical LAI. Before development of an effective complete canopy, LAI and E_p/E_o were related according to the equation:

$$E_p/E_o = -0.21 + 0.70\ (\mathrm{LAI})^{1/2};\ 0.1 \leq \mathrm{LAI} \leq 2.7 \tag{4}$$

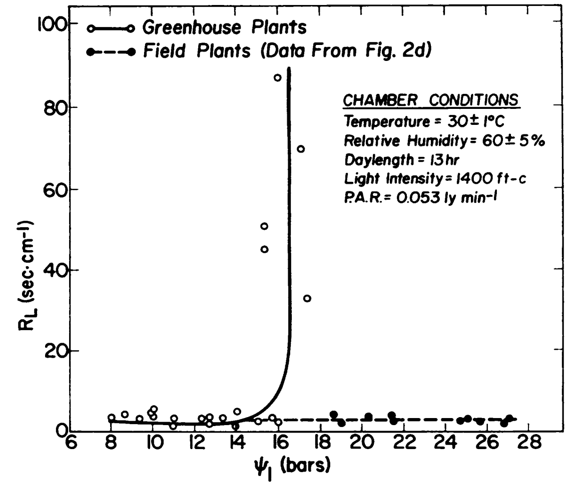

FIG. 5. Relation between stomatal resistance (R_L) and leaf water potential (ψ_l) for cotton plants in a growth chamber and plants grown under high soil water stress in the field. ly: Langley.

Applying this relationship to the current situation where LAI is 1.9 results in a plant evaporation rate of 0.76 of the potential rate. Measured evaporation rates derived from energy balance data for this period were 0.33 of the approximate potential evaporation. Assuming soil evaporation to be small, this analysis results in an actual to potential plant transpiration ratio of 0.43, indicative of stomatal regulation of evaporation.

An alternate evaluation may be made using the relationship presented by Monteith (15):

$$\frac{LE}{H} = \frac{(\Delta/\gamma) + r_i/r_a}{(\Delta/\gamma) + \frac{r_s + r_a}{r_a}} \tag{5}$$

where LE is latent heat flux, H is the net radiation flux (R_n) minus the soil heat flux (S), Δ is the slope of the saturation vapor pressure *versus* temperature curve, γ is the psychrometric constant, r_i is the "isothermal diffusion resistance," r_a is the aerodynamic diffusion resistance, and r_s is the surface diffusion resistance. With mean daytime values of air temperature (32 C), vapor pressure (25 millibars), and net radiation, equation 5 may be evaluated to obtain $r_s = 4.0$ sec cm^{-1}, where $r_a = 0.26$ sec cm^{-1} and $r_i = 1.3$ sec cm^{-1}. The surface resistance represents the sum of plant and soil resistances, weighted for the total surface area occupied by each and evaluated from data taken some distance above the crop. However, to reconcile the measured stomatal resistance with an independent estimate of the surface resistance, both canopy and soil resistances must be estimated. The canopy resistance (r_c) may be estimated from the relation suggested by Szeicz and Long (25):

$$r_c = R_L/\mathrm{LAI}_{\mathrm{eff}} \tag{6}$$

where the average daytime R_L was near 2.5 sec cm^{-1} (Fig. 2d), and $\mathrm{LAI}_{\mathrm{eff}}$ was assumed to be equal to the measured LAI of 1.9, giving a canopy resistance of 1.3 sec cm^{-1}. The soil resistance is further assumed to be very large in comparison to r_c, since the top several centimeters of the surface were quite dry. Both canopy and soil resistance must be weighted in proportion to the surface area occupied by each. During this period, the crop occupied about 30% of the total surface area; thus the reciprocal of the surface resistance may be represented by:

$$\frac{1}{r_s} = \frac{1}{r_c}\cdot(A_{\mathrm{crop}}) + \frac{1}{r_{\mathrm{soil}}}\cdot(A_{\mathrm{soil}}) \tag{7}$$

where A_{crop} and A_{soil} represent the fractional ground cover of the crop (0.30) and soil (0.70), respectively. Since r_{soil} must have been very large, the righthand term becomes insignificant, and equation 7 yields $r_s = 4.3$ sec cm^{-1}, which is well within the limits of experimental error implied in equation 5.

This study serves to illustrate how a cotton crop may continue to extract water from the soil and transpire during periods of prolonged drought. In spite of the low soil water potential in the main root zone, a significant plant evaporation rate was maintained. Plant evaporation was sustained by water extraction from layers of soil below the main root zone. Continued extraction was made possible by the failure of the stomata to close completely in response to low leaf water potentials. The sensitivity of cotton stomata to decreasing leaf water potential in the field was less than reported for other species or for greenhouse cotton. The actual plant evaporation rate and the associated surface resistance were adequately described by stomatal resistance values from individual leaves when the proportion of the surface occupied by the crop was known.

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