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Relative Importance of Soil Resistance and Plant Resistance in Root Water Absorption

D. C. Reicosky and J. T. Ritchie

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ABSTRACT

Soil water potentials, leaf water potentials, and transpiration rates of sweet corn (*Zea mays* L.), growing in a greenhouse, and grain sorghum (*Sorghum bicolor* L.), growing in a field, were determined to evaluate the magnitude of the combined soil and plant resistances to water flow in the plant system. Using a theoretical analysis of water absorption by roots, soil resistance was estimated. Plant resistance was inferred by the difference between the measured combined resistances and the estimated soil resistance. A wide range of soil hydraulic conductivity values for the plant rooting media which included nutrient solutions, peat-vermiculite-sand mixture, and a sand and clay soil maintained at various water potentials provided variations in calculated soil resistances. Our results showed that when root density was not unusually low, plant resistance to water transport was much larger than soil resistance, until the threshold soil hydraulic conductivity reached about 10^{-6} to 10^{-7} cm/day. This conductivity usually occurred at about −1 and −8 bars for the sandy and clay soils, respectively. These findings emphasize the need to consider plant resistance in water-uptake calculations when using equations that evaluate water potential gradients along the water flow path.

Additional Index Words: **leaf water potential, relative water content, root resistance, water uptake, stomatal resistance, transpiration, soil water potential.**

WATER UPTAKE by plant roots is a major component of the water balance of field soils. When one attempts to physically evaluate water flow in soil with a root water sink term, he should recognize the importance of the soil and plant properties. The significance of the resistance of water flow in the whole plant system, i.e. from the root surface to the evaporation sites in the leaves, has often been neglected in calculating water uptake by plant roots (Gardner, 1964; Whisler et al., 1968; Nimah and Hanks, 1973). Even though the calculated uptake patterns agreed reasonably well with experimental data, compensating errors probably masked the true nature of water uptake and could detract from a complete understanding of the soil-plant system. Some scientists (Kramer, 1938; Boyer, 1971) have recognized the significance of plant resistance to water flow but no one has incorporated this resistance into water uptake models.

Recent papers by Newman (1969a, b), Hansen (1974a, b), Boyer (1971), Miller et al. (1971), and Taylor and Klepper (1975) have shown the relative importance of plant and soil resistance. All concluded that plant resistance was large when the soil water content was near "field capacity" and root densities were typical of field values. Newman (1969a) presented evidence that mathematical models of Gardner (1960) and Cowan (1965), which predicted water flow to individual roots, overemphasized the importance of soil resistance by assuming lower than usual root densities. Newman used the same model with higher root densities (obtained from several literature sources) and calculated that soil resistance would remain smaller than plant resistance until the soil hydraulic conductivity reached a critical threshold of about 10^{-7} cm/day. For the soil he evaluated, the critical threshold conductivity corresponded to a matric potential of < -15 bars.

The location of the resistance to flow of water within the plant vascular system is not well understood. Kramer (1938) showed evidence that roots were the main source of resistance. Removal of sunflower (*Helianthus annus* L.) plant root eliminated the root resistance presumably offered by the cortex and resulted in very rapid inflow of water during the first 2 min after cutting. Barrs and Klepper (1968) using plant resistances calculated from leaf water potential and transpiration data, identified the roots as the site of major resistance to water flow in the plant. However, Begg and Turner (1970) measured water potential gradients in field grown tobacco (*Nicotiana tabacum* L.) and from their results suggested that root resistance was less than the resistance between the stem and the leaf.

There is greater uncertainty about the location of the resistance to water flow in the root system. Newman (1972) suggested that the resistance is located in the Casparian strip in the endodermis. Other possible locations of the resistance may be in the cytoplasm and plasmodesmata between the cells, the cell walls of the cortical tissue, or the walls of the xylem vessels.

Our purpose was to evaluate the relative importance of soil and plant resistances and their influence on leaf water potential and transpiration over a range of measured soil hydraulic conductivities and matric potentials commonly encountered in a Varina sandy loam and a Houston Black clay.

THEORY

The pathway of water movement can be expressed as resistances in series (Van den Honert, 1948) using the equation

$$T = \frac{\Psi_s - \Psi_r}{R_s} = \frac{\Psi_r - \Psi_l}{R_p} \qquad [1]$$

where T is the transpiration rate; Ψ_s, Ψ_r and Ψ_l are the water potential in the soil matrix, at the root surface, and in plant leaves, respectively; and R_s and R_p are resistances of the soil and plant pathway. For freely evaporating plant surfaces, transpiration is controlled by the atmospheric demand in the vicinity of the leaves. When the soil water deficit becomes sufficiently large and limits physiological processes, R_s and R_p can influence Ψ_l so that tran-

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[2]Soil Scientists, Southern Region, USDA-ARS, Florence, SC 29501, and Temple, TX 76501, respectively.

spiration is reduced through the stomatal mechanism. For plants growing in soil, evaluating R_p and R_s is complicated by our inability to measure Ψ_r during water uptake by roots. Equation [1] can be rewritten as

$$T = (\Psi_s - \Psi_l)/(R_p + R_s) \quad [2]$$

and then the combined soil and plant resistance can be evaluated. Our interest, however, is in the magnitude of the separate resistances.

Gardner (1960) derived a formula for determining the difference in the soil matric potential between the root surface and the soil at a distance away from the root. The root was assumed to be a uniform cylinder of radius r (cm) withdrawing water at steady state q_r (cm^3/cm root/day). The water was assumed to be taken up only from a distance c (cm), which is half the distance to another root, assuming uniform rooting, or $c = (\pi L_z)^{-1/2}$, where L_z is the root density (cm root/cm^3 soil). Assuming negligible osmotic potential, Gardner's formula is

$$\Psi_r - \Psi_s = \frac{q_r}{4\pi K} \ln(c^2/r^2) \quad [3]$$

where K is the soil hydraulic conductivity (cm/day). When we express T from Eq. [1] as a flux per unit ground area (cm/day) and we assume horizontal and vertical uniformity of roots growing to depth d (cm), and that all roots are equally effective in water absorption, then

$$q_r = T/L_z d \quad [4]$$

substituting Eq. [4] into Eq. [3] and assuming $c = (\pi L_z)^{-1/2}$, R_s from Eq. [1] becomes

$$R_s = \frac{\ln(1/r^2 \pi L_z)}{4\pi K L_z d} \quad [5]$$

when r, L_z, K, and d from Eq. [5] and T and Ψ_s from Eq. [2] are known, then

$$R_p = \frac{\Psi_s - \Psi_l}{T} - R_s. \quad [6]$$

METHODS AND MATERIALS

Two experiments were conducted independently at Florence, South Carolina, and Temple, Texas. The work at Florence, South Carolina, was an extension of previous work (Reicosky et al., 1975) and will be referred to as the greenhouse study. The Temple, Texas, experiment will be referred to as the field study.

Greenhouse Study

In the greenhouse study, sweet corn (*Zea mays* L. var. Silver Queen) was grown in 9-liter containers, some containing aerated half-strength Hoagland's solution and others a Varina sandy loam topsoil. Treatments consisted of two soil water levels and the solution culture. Both soil treatments were maintained near −0.1 bar as measured with tensiometers, until 5 days before measurement of plant water status. One series of plants was not rewatered at this time and the average matric potential, as determined with precalibrated soil moisture blocks, was −2 bars. The second treatment was frequently irrigated and maintained near a matric potential of −0.1 bar. The air temperature was controlled between 22 and 27°C. The solution culture was changed weekly. Plants were measured just after tasseling but before pollination on 4 Dec. 1972, when the plants were 53 days old. Plants were grown in a configuration similar to field plants with adequate border area, and each plant occupied 1,200 cm^2. All measurements were made on plants growing inside the border area.

Leaf water potentials were measured on the distal 30 cm of the leaf fully exposed to sunlight using the pressure chamber technique of Scholander et al. (1965). Part of the leaf tissue was cut away to permit insertion of the midrib into the pressure gland mounted on the chamber. Pressure was applied at the rate of approximately 0.4 bar/sec and the reading completed within 2 min after cutting the leaf.

The portion of the leaf cut away for potential measurements was used for relative water content determinations using techniques described by Barrs and Weatherley (1962). The tissue was sliced into about 1-cm^2 sections. After its fresh weight had been determined, the leaf tissue was floated on distilled water for 4 hours under laboratory light, then damp dried between layers of absorbent tissue, and its turgid weight determined. Its dry weight was determined after drying the leaf tissue for 24 hours at 70°C and the relative water content calculated. The leaf water potential and the relative water content data were smoothed using a 1-2-3-2-1 weighted running average technique (Jackson et al., 1973).

Stomatal resistance was measured using a calibrated porometer on the midportion of the uppermost, fully developed leaves. Since stomates on abaxial surface were most responsive to environmental variation, only data from this surface are presented.

Solar radiation was measured with an Eppley pyranometer mounted on top of the greenhouse with the output recorded on a strip chart recorder. Greenhouse air temperature was monitored with a hygrothermograph.

Field Study

During the 1973 growing season, two soil water treatments were imposed on the Houston Black clay soil. A wet treatment was frequently irrigated to maintain the soil matric potential in the root zone above −0.2 bar. In the second treatment, soil water was depleted under natural water use. In order to obtain a higher hydraulic conductivity under wet conditions than possible in the clay soil, a potting mixture was used for growth of some plants. The potting mixture consisted of equal parts of peat moss, vermiculite, and washed sand contained in a large steel cylinder (2.1 m in diameter and 1.4 m deep). The potting mixture was irrigated at the same frequency as the wet soil treatment. The cylinder containing the mixture was placed in the field next to the irrigated soil treatment with the top flush with the soil surface. The potting mixture was originally watered with a nutrient solution and kept adequately fertilized during growth of the sorghum. Hydraulic conductivity of the upper 30 cm of the clay soil 1 day after irrigation was approximately 0.007 cm/day and for the potting mixture about 0.05 cm/day. Hydraulic conductivity for the potting mixture was determined by the one-step method. For the field soil, conductivity was estimated from previously determined hydraulic properties (Ritchie et al., 1972).

The data were collected on 3 August from grain sorghum (*Sorghum bicolor* L.) planted in rows spaced 61 cm apart at a population of 190,000 plants/ha. Half-hourly evaporation rates were measured on the nonirrigated treatment with a weighing lysimeter. Net radiation and temperature over the nonirrigated canopy were recorded every half hour and used to calculate maximum evapotranspiration using the equilibrium evaporation equation of Priestly and Taylor (1972), calibrated from Temple evapotranspiration data. Other details regarding the field site, lysimeter installation for measuring evaporation are described elsewhere (Ritchie, 1971).

On 3 August, the sorghum plants had just passed the maximum vegetative stage of growth and were beginning to bloom. Leaf area index values averaged about 4 on all three plots. The sky was cloudless from sunrise until about 1100 hours and was intermittently cloudy thereafter. Solar radiation totaled 568 g cal/cm^2 for the day. Maximum temperature was 33°C, minimum temperature was 23°C, daily wind run was 115 km, and mean vapor pressure was 24 mbars.

The water content of the root zone in the nonirrigated treatment was measured on 1 and 6 August by the neutron scattering method for soil depths below 25 cm and by gravimetric sampling at 5-cm depth intervals for the surface of 20 cm. Root water absorption was calculated for the 5-day period from change in water content

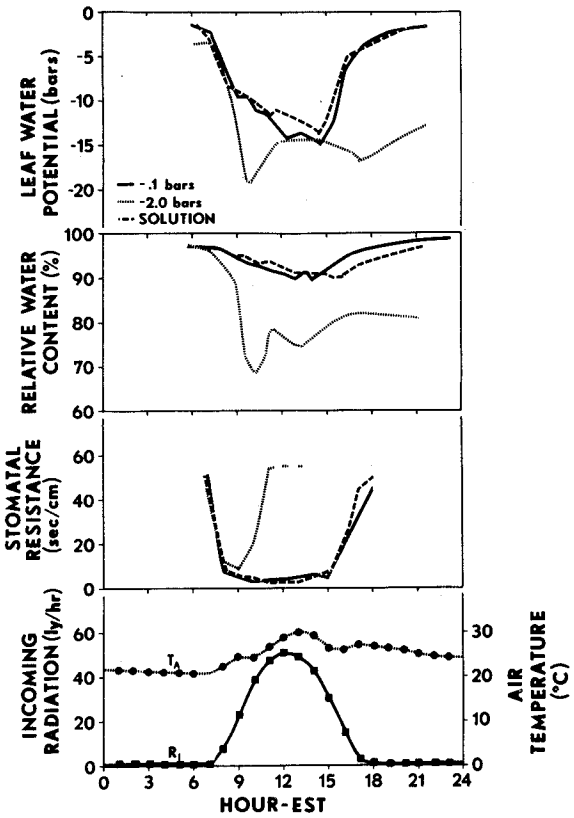

Fig. 1—Diurnal pattern of corn leaf water potential, stomatal resistances, solar radiation, and air temperature for the greenhouse study.

at each depth, making the necessary corrections for soil water flux at each depth.

Techniques and methods used for measuring leaf diffusion resistance and leaf water potential were essentially the same as those used for the greenhouse study, except the leaf diffusion values represent a harmonic mean of the adaxial and abaxial values.

RESULTS AND DISCUSSION

The results of the greenhouse study are summarized in Fig. 1. Leaf water potential, relative water content, stomatal resistance, solar radiation, and air temperature are plotted as a function of time for 4 Dec. 1972. The incoming radiation (R_I) is typical of a clear day and totaled 290 g cal/cm^2.

The diurnal patterns of leaf water potential and relative water content were essentially the same for plants growing in soil at -0.1 bar matric potential and those growing in Hoagland's solution. Because soil resistance is not present, the diurnal changes in leaf water potential of solution grown plants must be due to plant resistance. The similarity of leaf water potentials in the two treatments suggests that soil resistance also was unimportant, when compared to plant resistance, at -0.1 bar matric potential. Hydraulic conductivity of the Varina soil was about 0.1 cm/day at this matric potential.

The diurnal patterns of leaf water potential and relative water content for the plants at -2.0 bars matric potential substantially differed from those of the other two treatments. The leaf water potential was about -4 bars at sunrise and dropped to a minimum of about -19 bars. Since the plant resistance should have been about the same in all

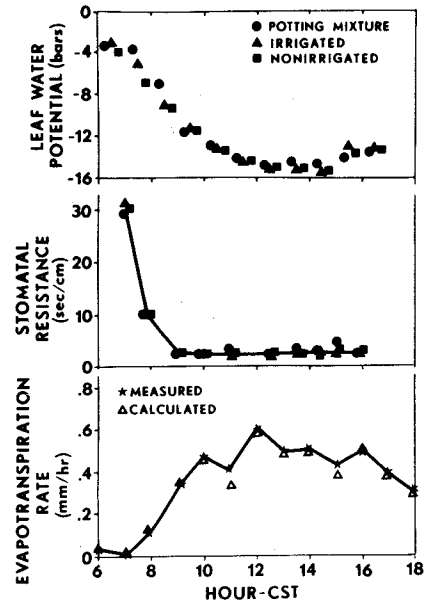

Fig. 2—Diurnal pattern of sorghum leaf water potential, stomatal resistance, and measured and calculated evapotranspiration for the field study.

three treatments, soil resistance must have been appreciable at -2 bars soil matric potential, which corresponds to a hydraulic conductivity of approximately 1×10^{-7} cm/day.

Water potential of the plants growing in the moist soil and in the solution culture recovered rapidly at sunset. The rapid increase in leaf water potential at 1600 hours was due to the shadow of an adjacent building moving across the plants. The dry treatment plants were severely desiccated and did not rehydrate from sunset to 2200 hours.

The stomatal resistance data show the expected trend, with the stomates opening rapidly after sunrise and closing rapidly after sunset for both the wet soil and in the solution treatments with the largest difference in the dry treatment. The stomates partially opened just after sunrise but since the transpiration demand plus the low soil water content (low hydraulic conductivity) caused stomatal closure under the high radiation load, they remained closed throughout the day.

Figure 2 summarizes the diurnal pattern of leaf water potential, stomatal resistance, and measured and calculated evapotranspiration for the field study. These leaf water potential and resistance values represent an average of four measurements made in a short time interval. Like in the greenhouse study, the leaf water potentials went through a diurnal change for all soil water treatments and ranged from approximately -3 bars near sunrise to -15 bars near solar noon. The close relationship between diurnal patterns of leaf water potential and actual evapotranspiration for the irrigated treatment is evident. The measured evapotranspiration rates agreed reasonably well with maximum evapotranspiration rates calculated with the calibrated Priestley-Taylor (1972) equation. The similarity in the average stomatal resistance, leaf water potential, and leaf area index for plants grown in the nonirrigated, irrigated, and potting mixture treatments suggest the measured evapotranspiration for the nonirrigated treatment should resemble that for the two irrigated treatments.

For 3 August, soil matric potential for the two irrigated

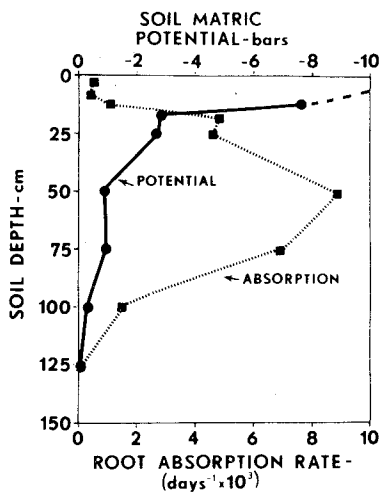

Fig. 3—Soil matric potential and root absorption rate for the nonirrigated sorghum treatment in the field study.

treatments was between −0.05 and −0.25 bar throughout the root zone. Matric potentials for the nonirrigated treatment are shown on the upper scale in Fig. 3. Root absorption rates for the nonirrigated treatment are shown on the lower scale of Fig. 3.

Approximation of the Soil and Plant Resistances

Using Eq. [5] and [6], we attempted to calculate reasonable values of soil (R_s) and plant (R_p) resistances for the greenhouse and field studies. Because we did not measure root density or total root length directly in either experiment, we calculated R_s values for each experiment by choosing two root densities an order of magnitude apart that should theoretically bracket root densities of the experiment as indicated from root densities in the literature. For the greenhouse plants, we chose root densities of 3 and 30 cm/cm^3, representing 2.4×10^4 and 2.4×10^5 cm total root length in 9 liters of soil or solution. These values agreed with published data for some container-grown corn plants (Downery and Mitchell, 1971; Taylor and Klepper, 1973). We assumed R_s was zero for the solution-grown plants.

For the field study, root density values of 0.3 and 3 were used in calculating R_s and we assumed an "effective" soil rooting depth of 100 cm. We chose the 100-cm depth because of the absorption pattern (plotted in Fig. 3) and from photographs of exposed sorghum root systems for this soil (Burnett and Tackett, 1968).

We made two sets of R_s calculations for the dry field soil because of our uncertainties about water uptake with a highly variable matric potential in the root zone. For one set of calculations we took a value of Ψ_s as −1 bar, throughout the root zone. We found this value by weighing the measured Ψ_s in proportion to measured water uptake. For the other calculations, only half the total root system was assumed effective in taking up water, representing an approximate depth increment of 25-75 cm. At this depth, Ψ_s averaged approximately −0.75 bar. Hydraulic conductivities used in all calculations of the Houston Black clay soil are taken from Ritchie et al. (1972).

Transpiration rates (T) for the greenhouse study were not measured directly, but were assumed to be equal to 60% of the solar radiation equivalent of latent heat flux. For the wet soil, we assumed a midday T rate of 1.2 cm/day. For the dry greenhouse soil T was assumed to be 0.6 cm/day at 0930 hours when the Ψ_l value was minimum (−19 bars) and stomata began to close (Fig. 1). In all the field plants T was approximately 1.32 cm/day at midday. Values of Ψ_l were taken as −15 bars for all calculations of R_p except for the dry greenhouse soil which was −19 bars. We approximated root radius (r) as 0.015 cm for all cases.

Table 1 summarizes the results from the calculations of R_s and R_p as well as some parameters used in the calculations. Evident from Table 1 is that R_s was extremely small as compared with R_p for all of the wet soils, usually about 5 orders of magnitude smaller. The greenhouse dry soil treatment was the only calculation with an R_s value > 2% of the R_p. The R_s calculation for the greenhouse dry soil treatment with the low root density produced an unrealistic negative R_p value, which indicated some error in one or more assumptions. The higher assumed root density calculation resulted in soil and plant resistances of similar magnitude. The stomatal resistance values in Fig. 1 show the plant response to the soil water deficit through the stomatal mechanism. The only significant field R_s values were those with assumed low rooting density. Changing the uptake pattern to half the root system made no significant difference in the R_s values because K in the wetter zone doubled over the weighted value for the 100-cm profile. If these calculations bracket a typical field situation, from these findings we can possibly generalize that for normal rooting densities R_s is small compared with R_p. The critical K value as reported here appears to lie between 10^{-4} and 10^{-7} cm/day. However in the field study, the root system was exposed to a wide range of K values and showed little absorption (Fig. 3) in the upper 15 cm where K was $< 10^{-6}$ cm/day. Below the 15-cm depth, both absorption and K increased. In the greenhouse study, where essentially all of the roots were exposed to a more uniform soil water status, R_s was significant when K was $\approx 10^{-7}$ cm/day. Thus based on the absorption pattern in the field and on the calculated R_s in the greenhouse study, the critical K value at which R_s becomes appreciable is about 10^{-6} to 10^{-7} cm/day. For the soils in our study, this threshold conductivity is at about −1 and −8 bars for the sandy and clay soils, respectively.

The critical K values, when R_s becomes appreciable, as we have concluded from this study and from Newman's (1969a) analysis for reasonable field root densities seem to agree well. Our data differs with Newman's data and similar data of Hansen (1974a, b) in Ψ_s value at which K is approximately 10^{-6} cm/day. Their evidence indicated Ψ_s near or below −15 bars when $K \approx 10^{-6}$ cm/day, while our evidence and that of Taylor and Klepper (1971, 1975) indicated the critical Ψ_s was between −1 and −10 bars. This difference may be due to the difference in techniques for determining K in relatively dry soils, rather than from true differences in K versus Ψ_s relations. This difference indicates the need for accurately measuring the K versus Ψ_s relationship as compared with making empirical extrapolations from measurement only in the wet soil range. A method proposed by Gardner (1962) to measure soil-water diffusivity during drying of soil cores, when coupled with field evaluation of water content versus Ψ_s relations, seemed to

Table 1—Calculations of soil and plant resistances (R_s and R_p), and values of rooting density (L_z), soil hydraulic conductivity (K), and soil matric potential (Ψ_s) used in the calculations for the greenhouse and field studies.

Experiment	L_z	K	Ψ_s	R_s	R_p
	cm/cm^3	cm/day	cm	day	
		Greenhouse			
Solution	3	Large	0	0.0	12787
	30	Large	0	0.0	12787
Soil "wet"	3	0.1	102	0.2	12702
	30	0.1	102	0.02	12702
Soil "dry"	3	10^{-7}	2,046	22.0×10^4	-19.0×10^4
	30	10^{-7}	2,046	1.6×10^4	12985
		Field			
Pot mixture "wet"	0.3	5×10^{-2}	204	0.4	11470
	3.0	5×10^{-2}	204	0.03	11470
Soil "wet"	0.3	7×10^{-3}	102	3.2	11545
	3.0	7×10^{-3}	102	0.2	11548
Soil "dry"	0.3	10^{-4}	1,023	224.0	10626
	3.0	10^{-4}	1,023	16.0	10834
Soil "dry"†	0.3	2×10^{-4}	767	224.0	10820
	3.0	2×10^{-4}	767	16.0	11028

† Half of root system assumed effective in uptake.

work well for evaluating K for Houston Black clay (Ritchie et al., 1972).

The implications of this study to the relationship between T and "available" soil water is of interest. Plants adapted to field conditions (which usually means that soil water deficits do not occur rapidly because of a large rooting volume) can be considered as 'freely evaporating" until the critical threshold soil resistance value is reached. Thereafter, T can be expected to decrease, with the amount of decrease dependent on the potential evaporation and the extent of soil water deficit. Using the Temple lysimeter clay soil as an example, the water content for a bulk density of 1.3 g/cm^3 at "field capacity" (about -0.05 bar) is 46% by volume (Ritchie et al., 1972). The water content at -8 bars (where $K \approx 10^{-6}$ cm/day) is about 30%. At -15 bars the water content is about 24%. Thus, about 73% of the total available water in the root zone should be "freely" available to plants. Ritchie (1973) summarized water extraction data for cotton, sorghum and corn and found that about 78% of the total extractable water in the lysimeter soil was freely available before transpiration was reduced. An almost identical argument can be made for alfalfa and sorghum crops at Phoenix, Arizona, growing on a clay loam soil from soil properties and evaporation data as reported by van Bavel et al. (1968) and van Bavel (1967). The critical soil matric potential when evaporation began to decrease was about -4 bars in the alfalfa study (1967).

This work emphasizes the need to consider the role of the plant when evaluating root water absorption. More precise work is needed however, in understanding the source of the large resistance to water flow caused by the whole plant, and particularly, its root system.

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