Comparative Resistance of the Soil and the Plant to Water Transport[1]

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ABSTRACT

The resistances to liquid water transport in the soil and plant were determined directly and simultaneously from measurements of soil, root, and leaf water potentials and the flux of water through the soil-plant system to the sites of evaporation in the leaf. For soybean (Merr.) transporting water at a steady rate, water potential differences between soil and root were smaller than between root and leaf over the range of soil water potentials from −0.2 to −11 bars. As soil water was depleted, water flow through the soil and plant decreased to one-tenth the maximum rate, but both the soil resistance and plant resistance increased. The plant resistance remained larger than the soil resistance over the entire range of soil water availability. Previous suggestions that the soil is the major resistance have ignored the increase in plant resistance and/or assumed root densities that were too low.

The supply of water to plants has major consequences for growth. During rapid growth, large amounts must be extracted from the soil and moved through the frictional resistances of the soil-plant system. As water is depleted in the soil, the forces for extraction increase and the frictional resistances become larger, causing growth-inhibiting water potentials to develop in the plant. The forces required for extraction of water from the soil are reasonably understood, but the frictional resistances to water movement are less clear. Some studies suggest that the soil represents the largest resistance as water becomes decreasingly available (9, 12, 13, 30), but others suggest that the plant is the largest resistance (1, 14, 19, 22, 24–27, 29). The interpretation of these studies is difficult because each involved approximations of one or more of the resistances in the soil-plant system. No experiments are available in which both soil and plant resistances are measured directly and simultaneously. The work presented here was undertaken to supply some of these measurements over a wide range of water availability.

THEORY

A simple mass budget can characterize the liquid water moving to any plant part if the small amount used as a reactant in metabolism is ignored:

$$A + T = H + G \tag{1}$$

where A and T are the fluxes for absorption and water loss, and H and G are the fluxes for water storage representing reversible changes in hydration and irreversible growth, respectively. The flux for absorption is usually positive, whereas that for water loss is negative. Each flux is defined either on the basis of unit area (*e.g.* for leaves, $cm^3 s^{-1} cm^{-2}$ of projected area or $cm s^{-1}$) or for the entire quantity of tissue ($cm^3 s^{-1} plant^{-1}$).

If tissue water potential is constant, H is zero. If at the same time, tissue water potential is too low to permit rapid growth, G is zero and $A = -T$. In practice, different T are obtained according to the external conditions and, by holding T and tissue water potential constant in each condition, water transport through the system can be studied without the complicating effects of changes in H within the plant. Furthermore, by working at large A, tissue water potentials are generally low enough to prevent rapid growth. Then the resistance (R) to water flow can be defined by $-T = A = \Delta\psi/R$, where $\Delta\psi$ is the difference in potential (bars) between the water source and the tissue.

For water transport through the plant, the resistances of the soil and plant are in series and it is possible to represent each resistance separately according to:

$$A = -(\psi_l - \psi_o)/(R_{os} + R_{sl}) = -(\psi_s - \psi_o)/R_{os}$$
$$= -(\psi_l - \psi_s)/R_{sl} \tag{2}$$

where R_{os} and R_{sl} are the frictional resistances of the soil and plant (bar s cm^{-1} or bar s plant cm^{-3}, depending on the units of A) and o, s, and l represent the soil, root surface, and leaf mesophyll, respectively.

The evaluation of Equation 2 is complicated by the fact that solutes have relatively little effect on water movement through the soil but a large effect on water movement through the plant. Thus, measurements of potential in the soil should not include solutes. Operationally, however, the water potential (which contains a solute component) can be used to evaluate Equation 2 if the solute content of the soil is negligibly small. In that case, ψ_o primarily consists of the matric component of the water potential and should accurately reflect the force involved in water movement through the soil, while, at the same time, ψ_s and ψ_l include all the forces acting on water in the root and leaf.

A potentially more difficult problem is the measurement of ψ_s. Although measurements of the water potential of the root surface have been attempted (11, 28), current methods of measuring water potential probably indicate an average for the sample. Therefore, the water potential of the root no longer represents ψ_s but ψ_i, which is an average ψ equal to the water potential somewhere between the root surface and the root xylem when water is flowing through the soil-plant system. Changes in ψ_i should reflect changes in ψ_s under steady conditions (the exact relationship will be given

below). Equation 2 then must be modified to:

$$A = -(\psi_i - \psi_o)/R_{oi} = -(\psi_l - \psi_i)/R_{il} \qquad (3)$$

where R_{oi} is the resistance of the soil plus root external to i and R_{il} is the resistance of the plant internal to i. Since the soil resistance is solely contained in R_{oi}, R_{oi} shall be called the soil resistance even though a certain amount of the root resistance is present as well. Similarly, since R_{il} consists solely of the frictional resistances of the plant, R_{il} shall be called the plant resistance, even though a certain amount of root resistance is included.

In the following experiments, soil and plant resistances were obtained from equation 3 using measurements of ψ and A under conditions where $A = -T$.

MATERIALS AND METHODS

Plants and Growth Conditions. Soybean (*Glycine max* L. Merr. cv Wayne) seeds were germinated 4 days in Vermiculite and the seedlings were transplanted to a mixture of sterile silt loam soil-Perlite-peat (70:15:15) in plastic pots with 15 cm top diameter. During transplanting, seedlings were inoculated with a commercial preparation of *Rhizobium* and a suspension of the spores of the endomycorrhizal fungus (*Glomus fasciculatus*) known to colonize soybean roots in the field. Plants were grown in a controlled environment chamber (day/night temperature, 30/20 C; day/night RH, approximately 40/90%; daytime irradiance, 210 w m^{-2}; photoperiod, 14 h). Plants were watered once with 400 ml phosphate-free nutrient solution (12 mM KCl, 4 mM MgSO$_4$, 5 mM CaCl$_2$, 0.33 mM FeSO$_4$, and 5 mM KNO$_3$) at transplantation and received water whenever the soil surface appeared dry thereafter. Phosphate was deleted from the nutrient medium because it inhibits mycorrhizal growth.

Transpiration and Water Potentials. Experimental plants 32 to 36 days old were watered thoroughly and permitted to drain. Then the pot was placed on a wire support in a plastic bag that was sealed around the stem (Fig. 1). A small tube was included with the stem for aeration of the roots. Early experiments with plants in clay pots gave variable soil and root water potentials due to contact of the pot with condensate in the plastic bag. The use of plastic pots supported by a grid (Fig. 1) overcame this problem. After a period of water use by the plant (2 h to 3 days), the

aeration port was sealed and transpiration was measured by weight loss of the pot-soil-plant system. To avoid endogenous rhythms, all measurements of transpiration were made in the growth environment between the 2nd and 6th h of the photoperiod. Transpiration was considered steady when the rate changed by 5% or less/h (usually after 3 to 4 h). Previous work (5–7) showed that leaf water potentials also became constant after 3 to 4 h in similar plants.

After steady transpiration occurred, water potentials of leaves, roots, and soil were measured. A leaf was washed and permitted to dry 3 to 4 h before the experiment was begun. Two discs were rapidly removed from a trifoliolate leaf for replicate measurements of ψ_l (Fig. 1A). Sampling was done in the same controlled environment in which transpiration had been measured.

After sampling for ψ_l, the plant was detopped and transferred to a humid chamber, the pot was removed from the soil mass, and two samples of soil were rapidly obtained from 3 to 5 mm below the lateral surface for measurements of outer ψ_o. The soil mass then was opened and two samples of soil were removed from the center for measurement of inner ψ_o (Fig. 1A).

Immediately after sampling the soil, two primary roots were removed from near the base of the shoot (Fig. 1B), the soil particles were shaken away, the nodules were removed, and a secondary root (4 to 6 cm) was detached from each primary root and inserted in the thermocouple chamber for replicate measurements of ψ_i (Fig. 1C).

All measurements were made by isopiestic technique (8) in thermocouple chambers 2 cm high and 2 cm in diameter coated with melted and resolidified petrolatum (3). Determinations were corrected for heat of respiration (2).

Characterization of Root System. The root systems of representative plants were gently washed from the soil and root lengths and diameters were determined. Root lengths were estimated by the method of Newman (23), modified by counting the number of root intersections with a regularly spaced grid rather than randomly placed lines. Tests indicated this method gave root lengths within 6% of the actual lengths. Root diameters were measured with a hand-held micrometer or with a light microscope containing an ocular micrometer and were divided into three diameter classes designated primary (originating from the root-shoot transition region), secondary (originating from primary roots), and tertiary (originating from secondary roots) (Fig. 1C). The roots were also checked for the presence of mycorrhizal hyphae under the light microscope.

RESULTS

Replicate measurements of ψ_o, ψ_i, and ψ_l usually showed differences of 0.8 bar or less (Fig. 2), except for one instance with soil (1.0 bar difference, Fig. 2A) and one instance with roots (2.4 bar difference, Fig. 2B). The soil dried out uniformly and ψ_o^{outer} was within 0.8 bar of ψ_o^{inner} (Fig. 3A). In addition, ψ_i did not vary more than ±0.2 bar along the longitudinal axis of the root except for one case that differed by 1.1 bar (Fig. 3B). However, ψ_l often differed when samples were obtained from lower and upper leaves
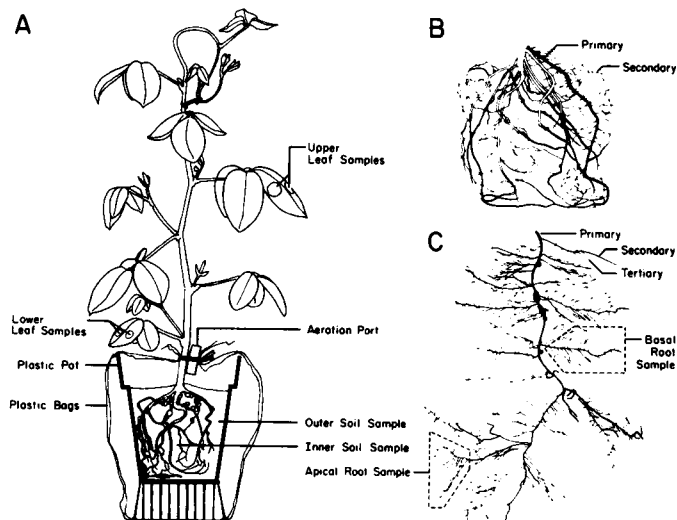

FIG. 1. Soybean plant showing (A) position of leaf and soil samples for water potential, (B) position of primary root (darkened) from which root samples were obtained, and (C) details of root branching and position of root samples for water potential. Drawing is of plant used in one of the experiments.
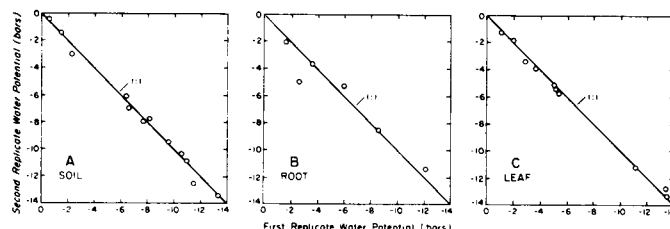

FIG. 2. Reproducibility of replicate water potential measurements from (A) soil, (B) roots, and (C) leaves during steady transpiration. Each point is a single determination.
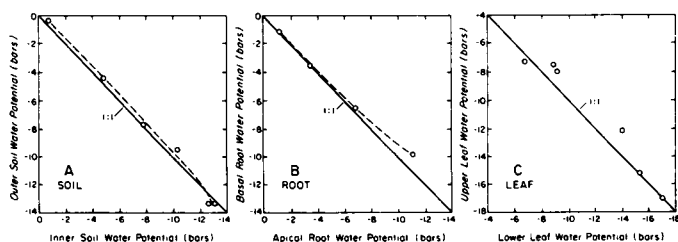
FIG. 3. Effect of sample position on water potential measurements in the soil-plant system during steady transpiration. A, inner and outer soil position; B, basal and apical root position along primary root axis; and C, upper and lower leaf position along stem. Positions for samples are as shown in Figure 1. Each point is a single determination.

Table I. *Soil, Root, and Leaf Water Potentials in a Soybean Plant Having Zero Transpiration*

The plant was exposed to a dark, humid atmosphere for 18 h prior to sampling for water potentials.

Replicate	Water Potential		
	Soil	Root	Leaf
	bars		
1	−2.3	−3.6	−2.9
2	−3.0	−3.6	−3.4

of the same plant (Fig. 3C). Consequently, water potentials were measured in defined locations in the soil-plant system for all experiments: inner soil, basal root, and upper leaf.

To test whether the method of measuring these water potentials gave comparable results, a plant was placed in a dark humid chamber for 18 h. During this time, transpiration was undetectable and ψ_o, ψ_i, and ψ_l should have equalized. Table I shows that ψ_o, ψ_i, and ψ_l were similar after this equilibration. There was no sign of root exudation in the samples during the measurement of ψ_i. Thus, measurements of soil, root, and leaf water potentials were considered equivalent and could be compared.

To measure the resistances to water transport in the soil and the plant, transpiration was allowed to occur under steady conditions in the growth room until the rate had been constant for at least 1 h. Under these conditions, water potentials of the leaves are essentially constant (5-7). The water potentials varied between −0.2 and −11 bars in the soil, −1 and −13 bars in the roots, and −4.5 and −16 bars in the leaves, depending on the length of time since the plant was last watered (Fig. 4). In moist soil, transpiration was rapid (Fig. 4, B and C), the water potential difference between root and soil was about 1 bar, and that between leaf and root was about 2.5 bars (Fig. 4A). If the soil was permitted to dehydrate somewhat before steady transpiration was re-established, all water potentials decreased in parallel with each other: ψ_i remained about 2 bars below ψ_o, and ψ_l remained about 3 bars below ψ_i (Fig. 4A). Steady transpiration initially increased as the soil dried but then decreased (Fig. 4 B, C). When the soil had dehydrated to a ψ_o of −11 bars, ψ_i had decreased to −13 bars and ψ_l was −15.5 bars. It was not possible to obtain reliable measurements of ψ_i below −13 bars. However, ψ_i this low were associated with transpiration that had decreased to one-tenth of the maximum. Therefore, the measurements spanned most of the significant changes in water flow that could be induced by low water potentials.

The soil had an osmotic potential (measured in water draining from the pots) of about −0.1 bar, which could be neglected when calculating soil resistances (see "Theory"). Also, since T and ψ were constant and ψ was generally too low to permit rapid growth (4, 17), the conditions for Equation 3 were satisfied. The exception was for roots at ψ_i above −5 bars (Fig. 4A), where growth could have caused ψ_i to be somewhat lower than in nongrowing roots
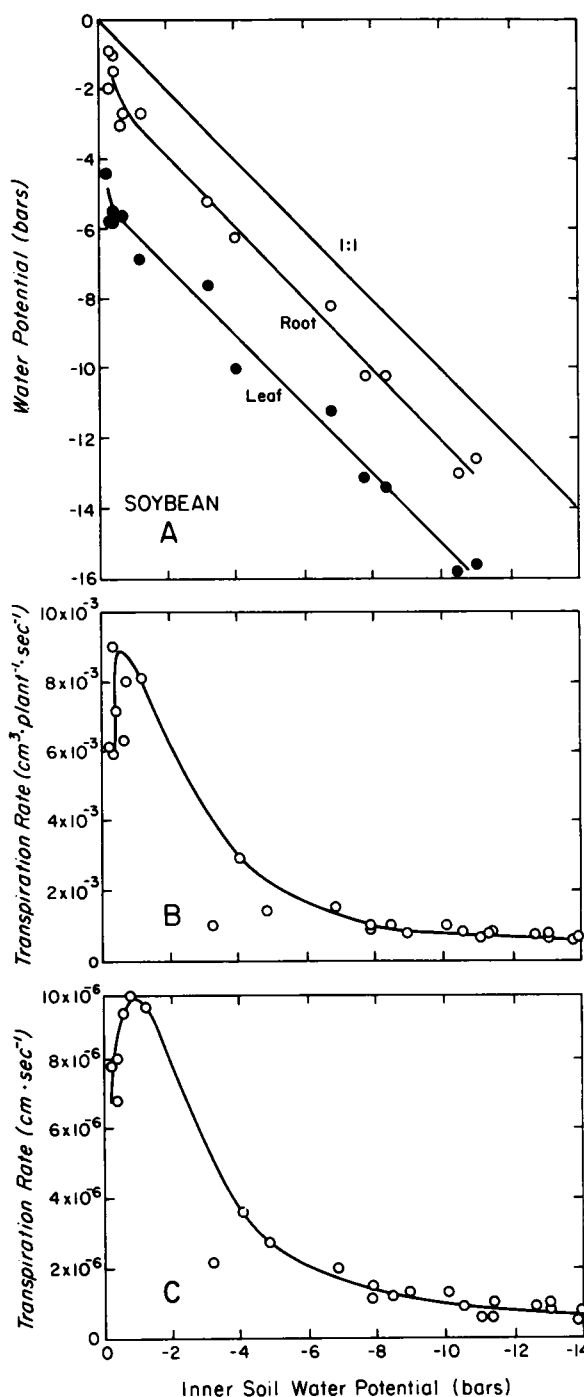

FIG. 4. Water potentials of soil, roots, and leaves, and rates of transpiration in soybean plants at a range of soil water potentials. A, water potentials of inner soil, basal roots, and upper leaves (see Fig. 1); B, rates of transpiration/plant; and C, rates of transpirations/unit projected leaf area. Each water potential is the average of two replicates. At each soil water potential, a different soil-plant system was used and transpiration and soil, root, and leaf water potentials were measured in each one when leaf water potential and transpiration were steady.

(7, 17) and the soil resistance to be similarly somewhat larger. Soil resistance was nevertheless smaller than the plant resistance (calculated from Equation 3 using the data of Fig. 4) regardless of the water status of the soil-plant system (Fig. 5) and whether the resistances were calculated on a unit leaf (Fig. 4B) or plant (Fig. 4C) basis. Both resistances increased as the soil dried (Fig. 5A). At ψ_o of −11 bars, the soil and plant resistances were 14 and 12
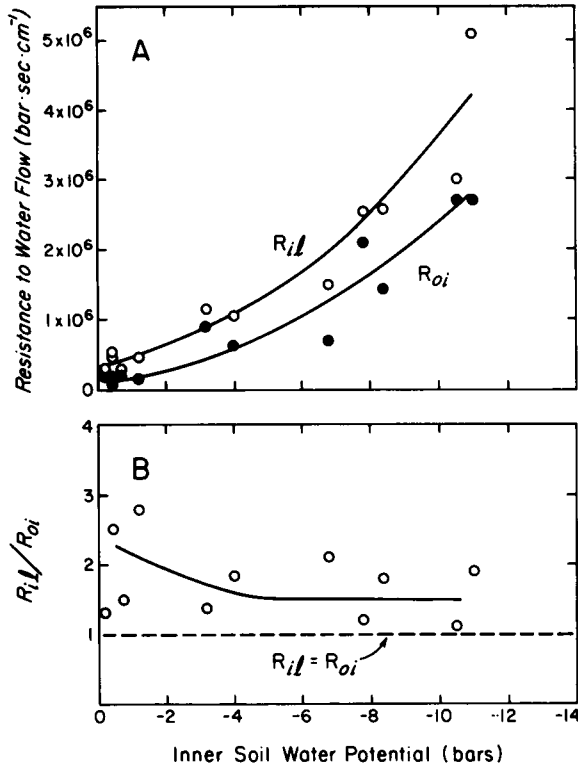
FIG. 5. Resistance to water flow of the soil-plant system at various soil water potentials. A, resistance between the soil and an intermediate position on the radial path into the root (R_{oi}) and resistance between this intermediate root position and the leaves (R_{il}); B, ratio of R_{il}/R_{oi}.

DISCUSSION

The resistance of moist soil contributes little to the resistance of the soil-plant system because of the small forces necessary to move water through the largely water-filled soil pores (1, 5, 12–15, 19, 22, 24–27). As the soil dries, however, its resistance increases. This has led some investigators (9, 12, 13, 30) to conclude that the resistance of the soil eventually becomes the largest resistance in the soil-plant system. The resistance of the plant was often assumed constant regardless of the water potential (9, 13, 27). The study presented here shows that this was not the case. Plant resistance also increased and, as a consequence, remained larger than the soil resistance over the entire range of water potentials studied.

The two approximations made in the work presented here were conservative ones that would only strengthen this conclusion. First, although it was not possible to measure the water potential of the root surface, such a measurement would have increased the calculated plant resistance and decreased the soil resistance. Second, although some growth probably occurred in the roots in moist soil, the cessation of growth would have caused root water potentials to be less negative, and the calculated plant resistance would again be increased and soil resistance decreased.

What then caused the increase in plant resistance? Since the measurements in the plant were of average water potentials of roots and leaves, the increase must have occurred in the root interior, the vascular system, or the leaf. Previous work has shown that resistance to water movement in the vascular tissue increases when plants dehydrate, presumably as a result of increased tension on water in the xylem vessels (6, 21). The change in resistance is most dramatic in those vessels with large diameters (6) and appears to result from the cavitation of the water columns (21). Cavitation has been observed at leaf water potentials of −8 bars in castor bean (20) and increased vascular resistances have been observed in sunflower at leaf water potentials below −9 bars (6). In the work presented here, increases in plant resistance were observed below a leaf water potential of −8 bars.

Changes in resistance also may have occurred in the roots. Kramer (18) demonstrated increases in the resistance to water flow through roots after plants were subjected to a period of low soil water potentials, probably from root suberization and losses in viability. Problems with root viability might explain our inability to measure root water potentials below −13 bars, since the psychrometer failed to achieve a stable reading, as if the tissue were losing viability.

At the same time that the plant resistance increased, the soil resistance increased, perhaps because of the well known losses in water conductivity of drying soils. However, since the outer portion of the root system was included in the soil resistance, changes at the soil-root interface would also affect this resistance. Several

times the corresponding resistances in the wettest soil, respectively.

The roots of a representative plant (Fig. 1) were measured and totaled 161 m, exclusive of root hairs and mycorrhizal hyphae (Table II). There were 16 primary roots. The tertiary roots had a diameter of 0.14 to 0.31 mm, accounted for 75% of the total root length, and were heavily infected with mycorrhizae. The root density was 9.78 cm cm^{-3} of soil and 91.3 cm cm^{-2} of soil surface (top surface) in a soil volume of 1650 cm^3. The total surface area of the roots (exclusive of root hairs and hyphae) was 1,600 cm^2, which compared to a total (upper and lower) leaf surface of 1,200 to 1,800 cm^2.

Based on these dimensions, the maximum rate of water uptake/unit length of root was 1.9×10^{-3} cm^3 cm^{-1} root h^{-1} and the maximum entry velocity/unit surface of root was 1.9×10^{-2} cm h^{-1} (Table II).

Table II. *Root Characteristics of a Soybean Plant*

Roots were classified as in Figure 1.

Root Type	Measurement							
	Number	Length		Density		Mean diameter	Surface area	Maximum rate water uptake	Maximum entry velocity
		Total	Average	Root length/ cm^3 soil	Root length/ cm^2 upper soil surface				
		cm		*cm*		*cm*	*cm^2*	*cm^3 cm^{-1} root h^{-1}*	*cm h^{-1}*
Primary	16	384	24.0	0.23	2.2	0.104	121		
Secondary	854	3,760	4.40	2.28	21.3	0.0513	606		
Tertiary	11,800	12,000	1.02	7.27	67.9	0.0231	870		
Total	12,600	16,100	1.28	9.78	91.3	0.0316	1,597	1.9×10^{-3}	1.9×10^{-2}

investigators (15, 22, 27) found alterations in soil-root resistance to water transport that could only be explained by an increase in resistance at the soil-root interface. Decreases in soil-root contact could have contributed to this increased resistance. Losses in soil-root contact have been observed in water-deficient roots, primarily due to root shrinkage (16).

The involvement of events at the soil-root interface in the soil resistance made it important to estimate how much of the root tissue was included in R_{oi}. It was assumed that the root radial tissue was uniform and in the form of a solid cylinder with steady water flow occurring radially. Application then could be made of the equation governing the steady state water potential distribution between the epidermis and xylem of a root. This equation may be written as (22):

$$\frac{d^2\psi}{dr^2} + \frac{1}{r}\frac{d\psi}{dr} = 0 \tag{4}$$

where r is a radial coordinate measured from the center of the root outward. If Equation 4 is solved according to Crank (10), with water potential specified at the root surface ($r = r_s$) and at the xylem ($r = r_x$), one obtains:

$$\psi(r) = \frac{\psi_x \, ln(r_s/r) + \psi_s ln(r/r_x)}{ln(r_s/r_x)} \tag{5}$$

where ψ_x and ψ_s are the water potentials at the xylem and root surface, respectively. A similar equation would apply if the endodermis were the inner boundary since the xylem and endodermis were within 1 to 3 cells of each other in soybean (judged from cross-sections).

The tertiary roots of soybean had r_s/r_x of about 6 (r_x varied because of the shape of the xylem tissue, so an average was used). Figure 6 shows that the radial distribution of ψ (calculated from
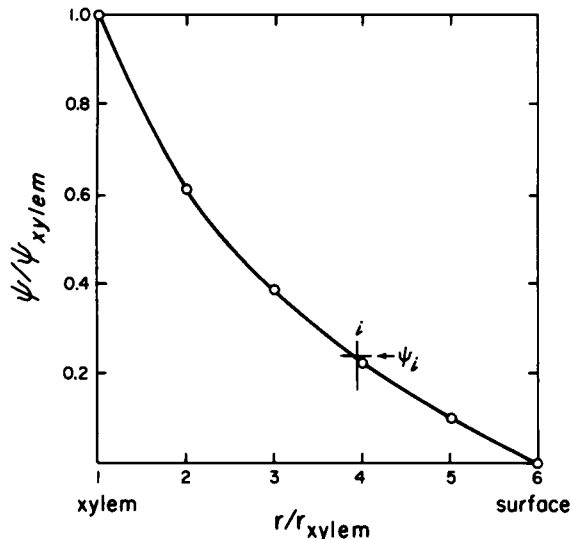

FIG. 6. Water potentials calculated at different positions between the xylem and root surface of a tertiary soybean root when steady water movement is occurring through the root. The root surface is assumed to be in moist soil having a water potential of zero. The abscissa shows the position (r) between the xylem and root surface expressed in multiples of the xylem radius. The ordinate shows the water potential (ψ) expressed as a fraction of the water potential of the xylem. The water potential (ψ_i) is the average water potential indicated by the thermocouple psychrometer and i is the position of ψ_i in the radial gradient. This water potential is calculated from the radial gradient according to Equation 6. Accordingly, ψ_i is 0.58 of the distance from the xylem to the root surface and 0.24 of the water potential of the xylem. The root tissue external to i is part of the "soil resistance" (R_{oi}) and the root tissue internal to i is part of the "plant resistance" (R_{il}).

Equation 5) for an intact tertiary root in moist soil (ψ at epidermis = 0) is steepest at the xylem because the small xylem radius is associated with a faster water flux than at the epidermis under steady conditions. When the root is excised for a measurement of root water potential, steady flow stops and there is internal equilibration of the ψ gradients. The psychrometer should then display a volume average water potential ($\bar{\psi}$) according to:

$$\bar{\psi} = \frac{1}{(r_s^2 - r_x^2)\pi} \int_x^x 2\pi r \psi dr \tag{6}$$

This integral, when evaluated by the trapezoidal rule using the ψ gradient of Figure 6, gives $\bar{\psi} = 0.24 \, \psi_x$. Therefore, the volume averaged water potential of the root is equivalent to the water potential 0.58 of the distance from r_x to r_s when the root is intact (Fig. 6), and this represents the location of ψ_i. As a consequence, R_{il} must have included the inner 41% of the root volume (pericycle, endodermis, and part of cortex), as well as the upper parts of the plant. Conversely, R_{oi} must have included the outer 59% of the root volume, as well as the soil.

The bulk of the root system consisted of tertiary roots that no doubt controlled most of the resistance of the root system. If it had been possible to assess the amount of mycorrhizal hyphae and root hairs, the tertiary roots and their associated structures would have accounted for still more of the root system. Even so, the density of the total root system (91.3 cm cm^{-2} of soil surface) was intermediate among reported values (24). These densities are much greater than those assumed by Cowan (9) and, together with his assumption of constant plant resistance, probably account for the disagreement between his prediction of a dominant soil resistance and our finding of a dominant plant resistance in drying soils. A similar conclusion applies to the work of Gardner and Ehlig (13), who also assumed a constant plant resistance.

The large root densities in the present experiment were associated with a maximum root water uptake of only 1.9×10^{-3} cm^3 cm^{-1} root h^{-1}. From this value, the model of Gardner (12) would have predicted a water potential difference of about 0.5 bar between the soil and root surface at ψ_o of -10 bars. In the work presented here, differences of this magnitude were negligible compared to those in the plant (about 5 bars; see Fig. 4). This implies that the plant resistance should have dominated the flow system rather than the reverse (12).

The only possible conclusion is that, at least for young plants, the plant resistance is the largest resistance in the soil-plant system over the entire range of soil water availability likely to be important. This implies that alterations in water transport characteristics of the plant could have a major influence on leaf water status and, in turn, plant growth in both moist and dry soil.

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