

Understanding the Hydraulics of Porous Pipes: Tradeoffs Between Water Uptake and Root Length Utilization

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ABSTRACT

The water uptake region in roots is several hundred times longer than the root diameter. The distributed nature of the uptake zone requires that the hydraulic design of roots be understood by analogy to flow through a “porous pipe.” Here we present results of an analytical and experimental investigation that allowed an in-depth analysis of root hydraulic properties. Measurements on nodal maize roots confirm the nonlinear distribution of water uptake predicted by the porous pipe model. The major de-

sign parameter governing the distribution of water uptake along a porous pipe is the ratio between its axial and radial hydraulic resistance. However, total flow is proportional to the pipe’s overall resistance. These results suggest the existence of a tradeoff between the effective utilization of root length and the total capacity for water uptake.

Key words: Roots; Hydraulics; Maize; Porous pipe model

INTRODUCTION

The hydraulic properties of roots are best understood in light of their indeterminate growth (Caldwell 1976). Unlike leaves that are anatomically fixed at maturity, the region of active water uptake in roots is constantly renewed throughout the plant’s life span (Eissenstat and Yanai 1997; Esau 1977; Torrey and Clarkson 1975; Hsiao and Xu 2000). We generally think of roots in terms of their

ability to absorb materials, yet much of root development results in the isolation of the root vasculature from the soil. This process of root sealing begins with the development of an endodermal layer with an intact Casparian strip, which serves to isolate the apoplast of the stele from that of the cortex (Peterson and Enstone 1996; Peterson and others 1993; Haussling and others 1988). The subsequent deposition of cellulosic walls internal to the suberin lamellae further increases the resistance to apoplastic water movement (Peterson and Enstone 1996; Van Fleet 1961). Finally, as secondary growth is initiated, the root is further isolated by the development of a cork cambium from the endodermal and pericycle cell layers. Thus, root maturation results in water uptake being largely restricted to the

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unsuberized region near the root tip (Kramer and Boyer 1995). From a functional point of view, it might be argued that it is counterproductive to limit water uptake to a small portion of the root system. Because the principal function of roots is the absorption of water and soluble nutrients from the soil, why should roots cut themselves off from their external environment? Specifically, why should a root ever reduce its absorbing surface area? This is not a trivial question: the unsuberized portion of the root apex may constitute as little as 1% of the total root surface area in forest trees (Kramer and Bullock 1966).

Uptake of water requires that roots behave as porous pipes. In a porous pipe two resistances act in series, the first as water moves across the porous wall of the pipe and the second as the water flows through the length of the pipe itself (Munson–McGee 2002). A common scenario is when water is supplied to one end of the porous tube, which then leaks water along its length. If the walls of the pipe are highly permeable, then the length over which the pipe can actually deliver water to the surrounding medium will be limited. Similarly, when water is sucked from the end of porous tube, high radial permeability will limit the effective length of the tube from which water is absorbed. The simplest analogy to this situation is to think of a plastic drinking straw. When inserted into a martini (watch out for the olive!) it provides a pathway to pull liquid from the bottom of the glass. However, if small holes are made along the length of the straw, less and less liquid will be drawn from the bottom of the glass, despite the fact that the axial conductivity of the straw and the total driving force are unchanged. This explains the requirement for roots to limit their radial permeability as they mature. A root that failed to seal itself from the environment would have limited ability to absorb water from near its tip. The profile of water absorption along a root is determined by the relative magnitudes of the radial and axial resistances (Landsberg and Fowkes 1978). However, the capacity of a root to absorb water depends upon the combined axial and radial resistances.

In this article we use a combination of analytical and experimental methods to quantify the tradeoffs between water uptake and utilization of root length. Our goal is to incorporate both the cylindrical geometry and “porous” nature of the root in our description of root hydraulic properties. Although a number of studies have considered directly the hydraulic design of roots (Frensch and Steudle 1989; Landsberg and Fowkes 1978; Passioura 1984; Steudle 1995; Steudle and others 1993), their in-

terpretation is complicated by the fact that the measured hydraulic parameters are referenced to the external dimensions of the root. In this article we provide a uniform basis for characterizing the hydraulic design of roots as determined by the dimensionless ratio of longitudinal to radial resistance.

MATERIAL AND METHODS

Plant Material

Maize (*Zea mays* L., var B73XM017) was grown in 2-L pots containing a commercially available soil mixed with a slow release fertilizer. The plants were watered regularly. Greenhouse temperatures were approximately 26°C day/20°C night. Supplemental lighting was used to ensure that photosynthetic photon flux density (PPFD) was at least 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 h per day. After about 2 months, plants were transplanted to 1-gallon containers (20 cm deep) during which time the growth of new nodal roots was stimulated by removing approximately 50% of the existing roots.

Branchless, healthy roots, 15–25 cm in length, were carefully extracted from the loose soil mix and immediately transferred to the root pressure chamber (described below). A total of 13 (for good luck) roots were sampled, each from a different plant. All roots used in this study initiated above the soil level, resulting in marked epidermal suberization of the aerial (2–5 cm) portion of the root (Enstone and Peterson 1998). In this article we refer to the portion of the root in the soil as the “unsuberized zone” to distinguish it from the suberized aerial section. In some instance the above-ground region was sufficiently long to include the suberized section in the measurements.

The vascular development in maize has been well characterized (Esau 1977; Peterson and Steudle 1993). Protoxylem extends fairly close to the root tip (1–2 cm); however, the conductivity of these elements is low resulting in significant hydraulic isolation of the root tip (Peterson and Steudle 1993). Early metaxylem elements are the next to mature at 2–4 cm from the root tip, with the number of functional early metaxylem vessels reported to remain constant between 4 and 20 cm from the root tip (Frensch and Steudle 1989). The root lengths used in this study are unlikely to have had any functional late metaxylem elements, as these are reported to mature 20–40 cm from the root tip (St. Aubin and others 1986).

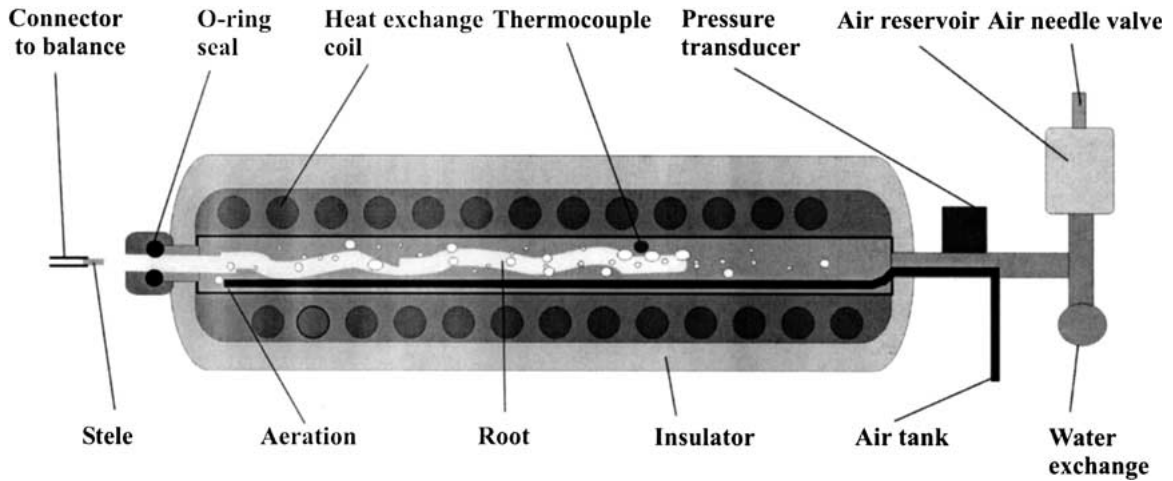


Figure 1. Drawing of the apparatus used to measure water flow through excised roots. An O-ring compressed by a screw cap seals the root into a pressure chamber. Tubing directs the xylem fluid expressed from the root onto an electronic balance (not shown). Compressed air bubbles go through the chamber to provide oxygen to the root as well as to pressurize the chamber. A refrigerated water bath (not shown) pumps fluid through a heat exchange coil in the chamber to control temperature.

Hydraulic Measurements

Root hydraulic properties were measured by pressurizing the solution surrounding the root apical zone and measuring the rate of sap exudation from the xylem as a function of the combined osmotic and hydrostatic driving gradient. Excised root apices approximately 20 cm long were placed, root tip inward, into a 0.8-cm-diameter stainless-steel chamber and sealed approximately 1 cm from the cut end of the root using a compression fitting consisting of a tightly wrapped layer of parafilm, rubber gasket, and O-ring (Figure 1). The stainless-steel chamber was filled with a dilute nutrient solution and pressurized. A set of solenoid valves maintained the pressure in the chamber such that a small volume of air leaked continuously through the bathing solution. Water flow from the cut end of the root was measured by directing the outflow onto a balance (Sartorius BP211D, ± 0.01 mg) using a flexible tube. This tubing was attached directly to the root stele approximately 5 mm outside of the steel chamber, eliminating the possibility that leakage across the cortex through the pressure seal could influence the flow measurements.

Flow through the root was measured over a series of decreasing hydrostatic pressures (0.4, 0.2, and 0.1 MPa). A solenoid was used to change the pressure automatically every 7 min (a time determined to be adequate for flow stabilization) while a computer continuously recorded flow rate and applied hydrostatic pressure (Omega PX236-GV100). Exudate from the open end of the root was collected prior to

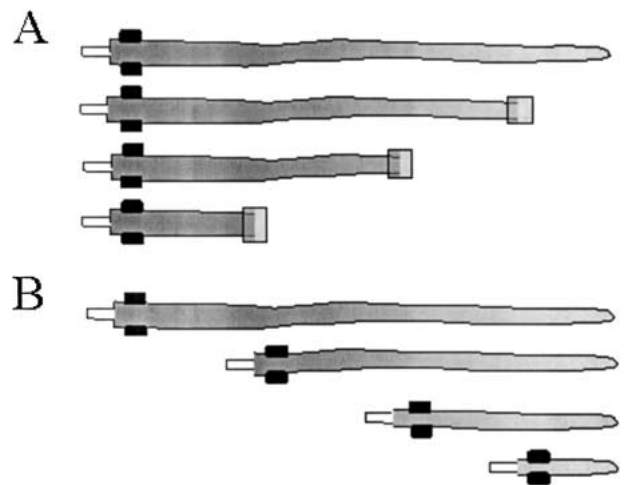


Figure 2. Schematic of two approaches used to measure water absorption as a function of length within the unsuberized zone: (A) distal successive cuts, (B) proximal successive cuts.

and immediately following the series of applied hydrostatic pressures and its osmotic potential measured using a vapor pressure osmometer (We-scors 5520, ± 0.02 MPa). The bulk osmotic potential of nutrient solution from the root chamber was also determined. The total driving gradient across the root (hydrostatic + osmotic pressure differences) was used to calculate root hydraulic properties. A linear relation between total driving force and flow was found within the range of applied pressures (data not shown). All flow data were normalized to

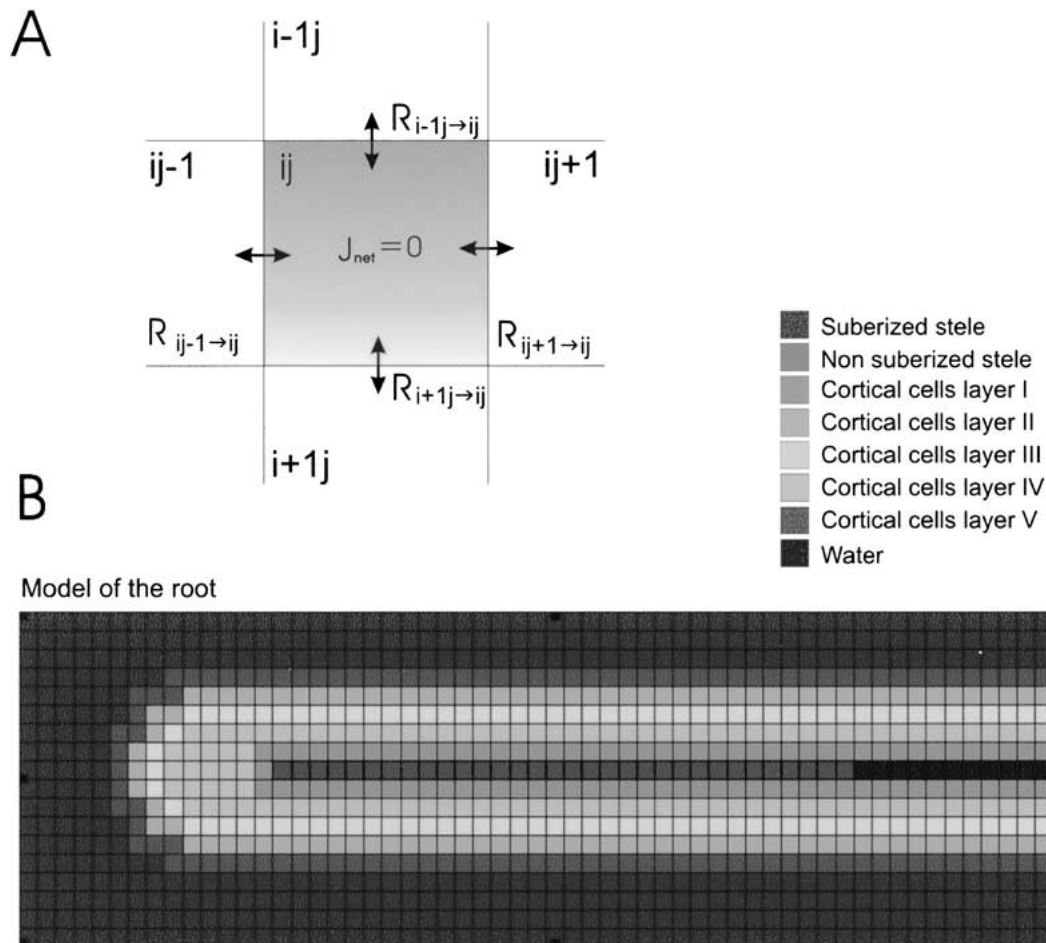


Figure 3. Graphical presentation of the model used to evaluate the relation between axial and radial hydraulic resistance. (**A**) Single element with water exchange through all four sides, (**B**) whole-root model, colors represent identity of individual elements.

a common driving force of 0.38 MPa, an arbitrarily chosen value from the range of applied pressures.

Following this initial measurement of the entire excised root, two types of manipulations were used to assess the distribution of water entry points along the length of the unsuberized zone. In the first type, segments (3–6 cm long) were successively cut from the root, beginning with the root tip and proceeding toward the basal end (Figure 2A). This allowed us to determine the contribution of each successively removed portion of the root to the initial rate of water uptake by the intact whole root. After each segment was removed, the cut end was sealed using a rubber tube filled with epoxy (5 Minute Epoxy, ITW Devcon, Danvers, MA) and the flux from the remaining portion of the root was remeasured as a function of applied pressure. On average, 4–6 segments were removed from each root. Water absorption through each region of the root was calculated as the initial flow rate (entire root) minus

flow determined for the same root with the apical portion removed. A total of seven roots were measured.

The second approach addressed the ability of different regions of the root to absorb water. Following an initial measurement of water flow, the root was removed from the steel tube, and a 3–6-cm section cut from the basal end (Figure 2B). The shortened root tip was then resealed into the pressure chamber and the flow rate was remeasured as a function of applied pressure. This was repeated until the root tip was less than 6 cm. The driving force (pressure plus osmotic potential difference across the root) was determined as described above. A total of six roots were measured.

Model

Root water uptake was simulated using a model that allowed us to specify the radial and the longitudinal

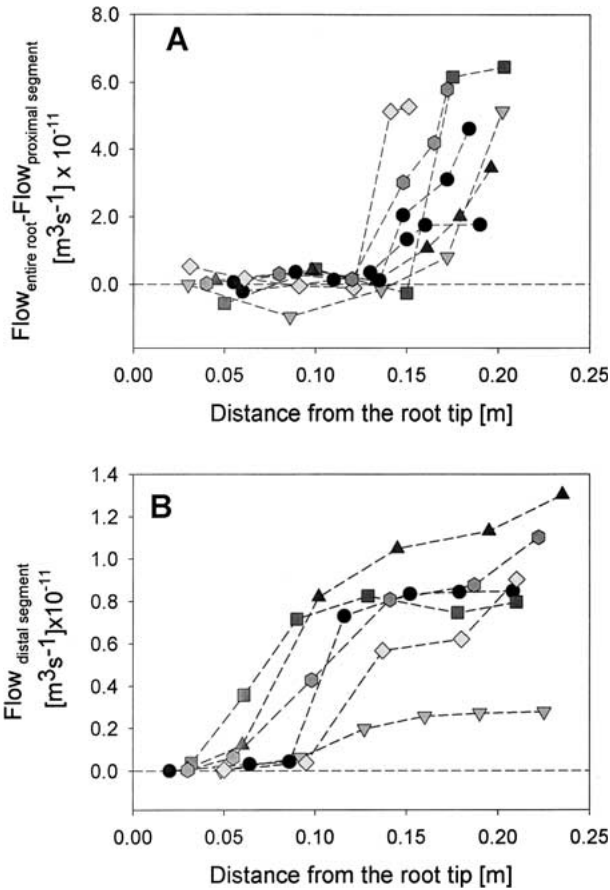


Figure 4. Mass flow rate of water (J_z) based on successive removal of root segments from the basal (A) and apical (B) ends of the unsuberized zone. In panel (A), flow from the basal root section is calculated as the difference between initial flow from intact root minus flow from the proximal end with sealed cut end (see Figure 2). Each line (marked by different symbols) represents different roots from different plants.

resistance as a function of distance from the tip. In this model the root and its immediate surroundings are represented by the two-dimensional matrix D :

$$D = \begin{bmatrix} a_{11} & a_{12} & \dots & a_{1m} \\ a_{21} & a_{22} & \dots & a_{21} \\ \dots & \dots & \dots & \dots \\ a_{n1} & a_{n1} & \dots & a_{nm} \end{bmatrix} \quad (1)$$

where each element a_{ij} encodes the identity of a specific portion of the root, that is, suberized stele, nonsuberized stele, layers of cortical tissue, and surrounding medium (Figure 3). The model includes major attributes of root tissues and their surroundings: (1) suberized stele where no exchange between stele and cortex is allowed (that is, endodermis fully suberized), (2) nonsuberized stele where exchange with the cortex is allowed at a

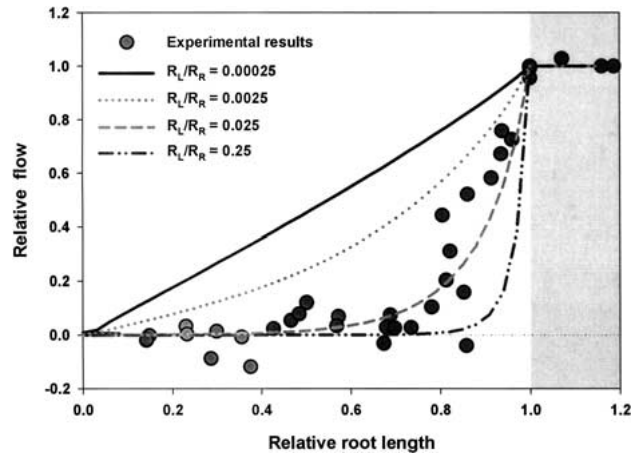


Figure 5. Water uptake along the root. Length is percent of unsuberized root length and water uptake is percent of total root water uptake. Shaded area represents the suberized portion of the root. Lines represent modeled water uptake for different ratios between longitudinal and radial resistance.

user-specified hydraulic resistance, (3) several layers of cortical cells (in this case five), (4) the external region surrounding the root, also divided into spatially explicit elements. All of the model runs presented in this article included the following assumptions. Longitudinal resistance in the stele is constant, based on observations that the number and dimensions of early metaxylem vessels within the unsuberized zone of maize do not change (Frensch and Steudle 1989). The hydraulic resistance between the cortex and the stele within the unsuberized region is constant along the length of the root. The hydraulic properties of cortical tissues are uniform; the cylindrical geometry of the root was incorporated by inversely relating resistance between consecutive layers to the distance from the stele. Each element surrounding the root was connected to an unlimited source of water such that there was no depletion of water around the root (that is, the root was immersed in a water bath).

Flow is generated in the model by imposing a pressure gradient between the external region surrounding the root and the portion of the stele furthest from the root tip. The model calculates the pressure within each element of the root based on the hydraulic resistances (for example, $R_{i-1j} \rightarrow ij$) between elements of the matrix D . For a steady-state condition, we assume that there is no change in net volume of each element (a_{ij}) of matrix D , that is, the sum of flows in and out from surrounding elements equals 0 ($J_{ij \text{ net}} = 0$). Each element of the root is allowed to exchange water only with the four adjacent, in-plane elements. Elements of the external

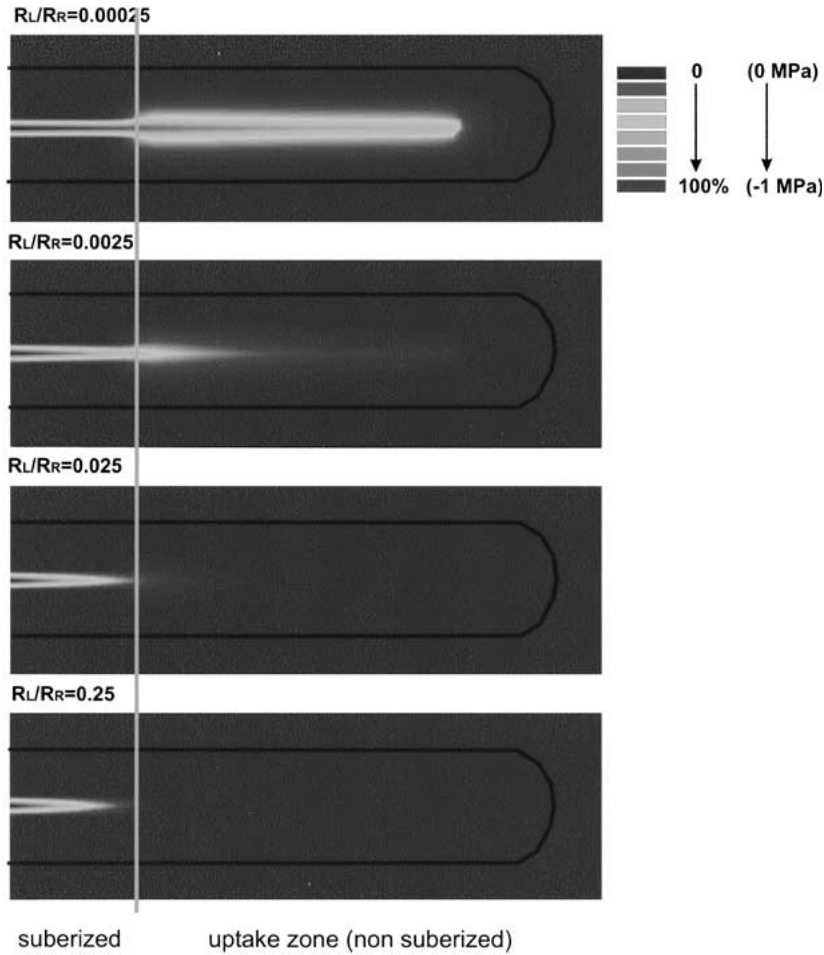


Figure 6. Modeled distribution of pressures within roots with different ratios of axial to radial resistance (axial resistance held constant). Black outline represents the root shape used in model.

medium have, in addition, the ability to exchange water with an additional, in this case infinite, source of water held at a constant pressure (P_{out}). The hydraulic resistance of this pathway is $R_{out \rightarrow ij}$. The general form of the mass flow across each element is

$$\frac{1}{R_{i-1j \rightarrow ij}} \Delta P_{i-1j \rightarrow ij} + \frac{1}{R_{i+1j \rightarrow ij}} \Delta P_{i+1j \rightarrow ij} + \frac{1}{R_{ij-1 \rightarrow ij}} \Delta P_{ij-1 \rightarrow ij} + K \frac{1}{R_{ij+1 \rightarrow ij}} \Delta P_{ij+1 \rightarrow ij} + \frac{1}{R_{out \rightarrow ij}} \Delta P_{out \rightarrow ij} = 0 \quad (2)$$

We can rewrite the above equation as:

$$\frac{1}{R_{i-1j \rightarrow ij}} P_{i-1} + \frac{1}{R_{i+1j \rightarrow ij}} P_{i+1} + \frac{1}{R_{ij-1 \rightarrow ij}} P_{ij-1} + \frac{1}{R_{ij+1 \rightarrow ij}} P_{ij+1} - \dots \left(\frac{1}{R_{i-1j \rightarrow ij}} + \frac{1}{R_{i+1j \rightarrow ij}} + \frac{1}{R_{ij-1 \rightarrow ij}} + \frac{1}{R_{ij+1 \rightarrow ij}} + \frac{1}{R_{out \rightarrow ij}} \right) P_{ij} = - \frac{1}{R_{out \rightarrow ij}} P_{out} \quad (3)$$

which allows us to create a complete set of simultaneous linear equations used to determine the

pressure in each element of the matrix D . To solve this set of simultaneous linear equations, we used a direct method in which we created a coefficient matrix A based on the user-specified hydraulic resistances and a right-hand-side vector b :

$$Ax = b \quad (4)$$

where x is the vector of pressures in each element of the matrix D and b is the vector describing the exchange between external elements and the out-of-plane infinite source (MatLab 5.0, Math Works, Natick, MA).

The axial hydraulic resistance R_L defined as equal to the hydraulic resistance between stele elements in longitudinal direction, while the radial resistance R_R is calculated as sum of the interelement radial resistances between the stele and the exterior of the root (Figure 3).

RESULTS

Maximum measured flow rates ranged from 2.3×10^{-11} to $1.3 \times 10^{-10} \text{ m}^3 \text{ s}^{-1}$ at a common driving

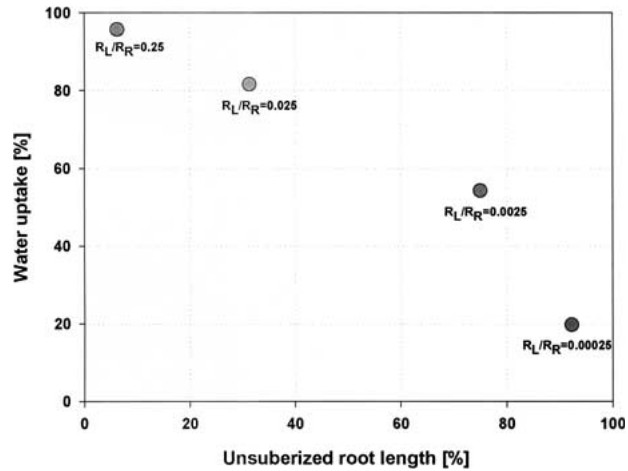


Figure 7. Tradeoff between root length utilization of and water uptake for different ratios of axial to radial resistance (axial resistance is held constant). Unsuberized root length is the percentage of the root length that delivers 90% of total water uptake. Water uptake is the percentage of maximum water uptake, where 100% is the flow through a root cut at the suberized/unsuberized boundary.

force of 0.38 MPa. Whole-root resistance ranged from 2.9×10^9 to 1.7×10^{10} MPa s m^{-3} , a span of 4.7-fold. Standardizing whole-root resistance by the surface area of the unsuberized region resulted in specific resistance values that ranged from 1.5×10^6 to 3.5×10^7 MPa s m^{-1} , a span of 22-fold. This increase in variation (4.7-fold versus 22-fold) suggests that root surface area is not an appropriate “standardization” factor in analyzing the hydraulic design of roots. Another way to look at these data is that root hydraulic resistance may not scale with root external dimensions.

Our first experiment, involving successive removal of apical segments, indicated that when water availability was unlimited (that is, under hydroponic conditions) flow from the apical 10–15 cm of the root was indistinguishable from the flow through the whole excised root (Figure 4A). Thus, approximately 70% of the unsuberized region contributed very little to root total water uptake. Water uptake occurred primarily in the first few centimeters of the basally located unsuberized zone, while the apical part was hydraulically isolated.

The second experiment involved the successive removal of basal sections while measuring flow through the remaining apical part of the root. Removal of several centimeters of the proximal end of the root had no or relatively little effect on water uptake through the remaining part of the root until more than 50% of the unsuberized root length had been removed (Figure 4B). Further cuts led to a

drop in uptake, suggesting an increase in root hydraulic resistance. Root apices less than 3–5 cm in length produced no measurable uptake under the pressures applied here. This suggests that 50% of the unsuberized root length (basal section) was not limited by radial hydraulic resistance and that around 70% of the unsuberized root length is hydraulically active (that is, it can absorb water).

Evidence that the hydraulic properties of the root were essentially constant along the basal half of the unsuberized zone (Figure 4B) indicates that the nonlinear shape of the water uptake profile along the root length (Figure 4A) can be attributed to the fact that the root behaves as a “leaky pipe.” By comparing modeled flows as a function of root length for a variety of hydraulic designs (Figure 5), we determined that the ratio of the axial to radial resistance of the maize roots used in this study was approximately 0.025 (that is, radial resistance was 40 times higher than the axial resistance). Deviation from this ratio leads to significant changes in the distribution of water uptake along the root (Figure 5). When the ratio was large, that is, the root was very leaky, water uptake was concentrated in a very short region at the base of the unsuberized zone. When the ratio was small, water absorption was essentially uniform along the entire length of the unsuberized zone such that the entire unsuberized portion of the root with developed xylem was involved in water uptake.

DISCUSSION

We have found that almost the entire unsuberized portion of the root (excluding the immature tip) is hydraulically active in the sense that it is capable of absorbing water. This is in agreement with studies of dye uptake (Haussling and others 1988; Varney and others 1993; Peterson and others 1993) as well as hydraulic measurements (Steudle and others 1987; Frensch and Steudle 1989; Melchior and Steudle 1993). However, our results show that only 30% of the root length is needed to deliver 90% of the total root water uptake. This finding can be explained only if the root has a “porous” structure. The ratio of axial to radial resistance consistent with this distribution of water uptake along the root was approximately 0.025. A similar ratio of resistances in maize roots was formerly reported by Frensch and Steudle (1989).

The effect of varying the ratio of axial to radial resistance on the distribution of pressures illustrates how a high R_L/R_R results in the hydraulic isolation of the root apex (Figure 6). This contrasts with the

situation when R_L/R_R is low, in which the pressure gradient within the xylem extends a long way into the unsuberized portion of the root (Figure 6). Thus, the relevant linear dimension of the root depends upon its intrinsic hydraulic parameters. The model results also demonstrate how the cylindrical geometry of the root leads to a nonlinear distribution of pressures across the root cortex. The drop in hydrostatic pressure across the outer layer of the cortex, regardless of R_L/R_R , was small compared with the inner layers (Figure 6). Thus, for a root composed of a uniform material (as in our model), the inner portions of the root play the dominant role in restricting the radial movement of water.

Although the ratio of axial to radial resistance is sufficient for describing profiles of water uptake, focusing only on the ratio of resistances neglects the fact that uptake depends on the total resistance (axial plus radial). We can use our model to explore potential tradeoffs between root length utilization and water uptake capacity. In this case, we hold R_L constant and examine how water uptake changes in relation to root length utilization. A decrease in the ratio of axial to radial resistance (by increasing R_R) results in a more uniform use of the root length but leads to a significant drop in water uptake (Figure 7). On the other hand, an increase of the ratio of axial to radial resistance (by reducing R_R) leads to the significant increase in water uptake (lower total resistance) but a reduction in the utilized root length. Thus, for a fixed longitudinal resistance, a tradeoff exists between total water uptake and effective utilization of root length for water absorption. This tradeoff might be additionally influenced by the resistance of the soil–root interface, since the interface between root and soil can be considered as an additional component of the radial resistance (Stirzaker and Passioura 1996). In particular, under dry conditions we expect a more linear distribution of uptake along the root.

A number of authors have reported water uptake by mature, woody portions of roots (Kramer and Bullock 1966; Van Rees and Comerford 1990; MacFall and others 1991). The analysis presented here demonstrates how permeability of basal regions of the root effectively short-circuits uptake by more apical regions. Thus, water uptake by mature regions is likely to represent damage to the root from the outside, or the penetration of the root exterior by the growth of lateral roots, rather than a region of active uptake.

Appreciation of the porous nature of the root apex leads to a number of interesting developmental issues involving root growth, root maturation, and the uptake of nutrients and water. Growth

(elongation) results in the production of the unsuberized, hydraulically active zone, while root maturation reduces the extent of the uptake zone (Van Fleet 1961; Haussling and others 1988; Peterson and Enstone 1996). Thus, the length of the unsuberized portion of a root represents the balance between root elongation and root maturation. How these two processes are coupled and how they control changes in the length of the unsuberized zone is unknown. A longer unsuberized zone in the root would add little to total water uptake and would lead to hydraulic isolation of the apical part. Such isolation of the root tip could be important for providing an adequate carbohydrate supply to the meristem (Bringhurst and others 2001; Bret–Harte and Silk 1994), since both the water potential gradients and thus mass flow into the root tip would be small. On the other hand, a shorter, unsuberized zone may limit a plant's capacity for water uptake in dry soil. The functional importance of unsuberized root length leads us to propose the existence of a developmental feedback that links growth and root maturation to the soil environment.

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