Water Transport in an Unsaturated Medium to Roots with Differing Local Geometries

C. L. Petrie,* Z. J. Kabala, A. E. Hall, and J. Simunek

ABSTRACT

Pearl millet [*Pennisetum glaucum* (L.) R. Br.: syn. *P. americanum* (L.) Leeke] develops substantially lower predawn leaf water potentials than cowpea [*Vigna unguiculata* (L.) Walp.] under conditions of soil dehydration, but overall root length densities are greater in millet than in cowpea. The hypothesis was tested that, due to differences in root geometry and root length density, root systems of millet become less efficient in water uptake than those of cowpea as soil dries. Plants were grown in an artificial medium in pots or 1.15-m tubes in a greenhouse and subjected to soil drying. Root geometries, root length densities, and water potentials of cowpea and millet were measured as the rooting medium dried. Distribution of roots was quantified by calculating a clumping ratio (total root length density divided by the root length density in the region surrounding individual root segment axes) at several depths within the profile. Overall root length densities were higher in millet than in cowpea, and root distributions differed. Millet roots were clumped locally along the root axis and globally within the profile, with the highest root length densities at the surface. Cowpea root lengths were one-half as dense as millet along the root axis and distributed fairly uniformly throughout the profile. These data were used in two-dimensional modeling of horizontal water transport from soil to branched segments of root axes of cowpea and millet to test the hypothesis. Simulations in which millet water potential became substantially lower than cowpea, and millet root length was twice as great as cowpea, predicted little difference in cumulative water flow to the roots of millet or cowpea during soil dehydration. This prediction is consistent with observations. Simulated water velocity vector fields indicated that millet's dense and clumped local root geometry became less efficient in water uptake under soil water deficits than cowpea's less dense and more evenly distributed root geometry because water uptake by millet was mainly at the root tips; in contrast, most of the root length of cowpea contributed to water uptake. Simulations conducted with millet root axes having different root length densities indicated that the low efficiency of millet in water uptake was due to the combined effects of local clumping and high root length density. When input parameters for roots and soil were varied, conclusions from the simulations remained the same.

UNDER CONDITIONS of progressive soil dehydration, pearl millet developed lower predawn leaf water potentials than cowpea, even when the plants were grown together in the same pot (Petrie and Hall, 1992a). Total resistance to water movement became greater in millet than in cowpea as the soil dried, but predawn water potential of roots (Ψ_R) was approximately the same as the water potential of leaves (Ψ_L) in both cowpea and millet, indicating that the difference between the total resistances was not within the plants (Petrie and Hall, 1992c). Application of a mannitol solution eliminated the differential effects of the resistance in that Ψ_L, in both plants, came into an approximate equilibrium at predawn with the osmotic potential of the solution (Petrie and Hall, 1992c). Consequently, the higher resistance to water flow in millet than cowpea under dry soil conditions may have been in the region of soil surrounding the roots.

Lower root length densities result in a longer average path length for water movement to roots and that longer path length is expected to increase the resistance to water flow in the soil (Newman, 1969). Overall root length density, however, was at least twice as great in millet as in cowpea (Petrie and Hall, 1992b). Predawn Ψ_L was lower for millet than for cowpea even when millet roots grew deeper than cowpea (Petrie and Hall, 1992b). When plants are grown primarily

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on stored soil water, greater rooting depth and root length density can be detrimental if they cause plants to use water too quickly (Ludlow and Muchow, 1988), but millet did not use more water than cowpea by the time when differences in predawn Ψ_L developed (Petrie and Hall, 1992b). Apparently there is no obvious explanation for the higher resistance to water movement in the soil surrounding the roots of millet compared with cowpea.

Computer simulation models have been used to study water uptake by roots and to evaluate the magnitude of resistances to water movement in the soil and in roots (Molz, 1981b). Root models are typically microscopic or macroscopic (Molz, 1981a). The microscopic model generally evaluates radial water transport to a single root cylinder of infinite length, while the macroscopic model examines the root system as a whole without considering effects of individual roots (Hillel et al., 1975, 1976). In macroscopic models, roots are assumed to be distributed uniformly over the entire soil profile, or root length densities that differ between layers are assumed to be uniformly distributed within each soil layer (Taylor and Klepper, 1978). Models can be static or can include root growth (Hillel and Talpaz, 1976). Steady state and transient flow have been modeled using analytic and iterative numerical methods, and numbers of dimensions modeled and input parameters have varied (Philip, 1966; Molz, 1981a,b). In macroscopic models, root water uptake is simulated with a root extraction function, and the forms chosen for this function vary. Molz (1981b) has noted that some of the controversy concerning the magnitudes of root and soil resistances may have resulted from different assumptions used in defining the extraction function. Application of the extraction function in a model results in spatial averaging, which ignores effects of water depletion around individual roots, but Hillel et al. (1975) found that a much lower plant water potential is required to maintain water flux into a plant when the model includes water uptake by individual roots. They stated that the neglect of flow patterns around individual roots is a major flaw in macroscopic models. A computerized tomography scan of the single root of a seedling showed experimentally that a water content gradient formed around the root as transpiration proceeded, and soil resistance in the sand–clay soil mix used in that study became important even when bulk soil water potential was high (Hainsworth and Aylmore, 1986, 1989).

Microscopic computer simulation models have been used to evaluate water transport to single, unbranched root segments, but most root axes have branches. Differences in root branching patterns can produce different geometries, which may affect root function by changing the shape of the root–soil interface and the space-filling properties of roots. Root geometry has been described and related to root growth and function with an approach from topology (Fitter, 1985, 1986). The two contrasting root geometries considered in this approach were the herringbone system, which has short, closely spaced primary laterals emanating from the axis, and the dichotomous system, which has secondary branches spaced at greater intervals (Fitter, 1986). Grass root systems were found to be more herring-

bone-like than legume root systems (Fitter, 1987). The herringbone system was hypothesized to be the most expensive in terms of root mass but more effective in soil exploration than the dichotomous system (Fitter, 1987). The effects of prolonged drought were not tested in experiments or simulations, however (Fitter, 1986, 1987). We are not aware of any computer simulations of water uptake by root systems with contrasting geometries under conditions of progressive soil dehydration.

The root geometries of cowpea (a legume) and millet (a grass) appear to differ. Millet has primary root branches that are generally short and densely distributed along the axis, similar to the herringbone system. Cowpea root branches are longer and less dense along the axis, similar to the dichotomous system. Preliminary studies indicated that millet root branches may be clumped along the root axis, while cowpea roots are spaced more widely and seem to be more uniformly distributed along the axis. A clumped distribution of branches along a root axis could cause localized drying of small regions of soil, encasing a substantial portion of the root surface in dry soil and increasing the apparent soil resistance to water flow to the axis. Such a root could be very efficient if water is applied frequently but becomes progressively less effective in water uptake when plants are subjected to prolonged soil dehydration.

The observed differences in cowpea and millet root axis geometry and root length density in the region surrounding the axis are on a local scale, a scale often considered unimportant because of its variability. Some aspects of root axis geometry, however, may be under genetic control and largely fixed for each species. If each segment of root axis is a module that is similar to other root segments, water transport to each local module may represent a pattern that is repeated at different locations in the root system. A more complete understanding of the local pattern could provide an improved understanding of water transport to the entire root system.

Water movement to branched root segments is three-dimensional. Even in a two-dimensional model, however, convergence of the numerical solution to a water transport problem requires a fine mesh and small time steps, particularly when steep water potential gradients develop. Many hours of computer time are required to solve the equations in each iteration of each time step. The number of equations solved in a three-dimensional model is orders of magnitude greater. Models require careful interpretation, and adjustments, such as time scaling, may be necessary in two-dimensional representations of three-dimensional problems. An advantage in two-dimensional modeling, however, is that a greater number of models can be studied economically, so that parameters of the problem can be varied individually and in combination, and their effects can be studied more closely.

The primary objectives of this study were to: (i) quantify differences in geometry and root length density of millet and cowpea roots, and (ii) model two-dimensional horizontal water flow to roots under drying conditions to determine whether the differences in root geometry and root length density could be responsible

for the lower predawn water potentials observed in millet than in cowpea.

MATERIALS AND METHODS

Experiments

Cowpea and millet were grown in a greenhouse in tubes 1.15 m long and 0.2 m in diam. filled with a 50:50 (v/v) mixture of Turface Plus (AIMCOR, Applied Industrial Materials Corp., Deerfield, IL) and a fine silica sand (maximum particle diameter of 2.5 × 10^4 or 60 mesh). Plants were subjected to progressive dehydration of the rooting medium (dry treatment) as described by Petrie and Hall (1992b); duration of the dry treatment was between 12 and 35 d. Samples of rooting medium were collected at 10 different depths from five tubes each of cowpea and millet at three different times after initiation of the dry treatment by inserting a coring tool horizontally through holes predrilled in the tubes (Petrie and Hall, 1992b). Roots were separated from the medium with a sieve and stored for later measurement (Petrie and Hall, 1992b).

Five root axes were selected at random from each sample of roots, placed on a glass plate, and photocopied; 1-cm axis segments were marked and axis root length densities within 0.5 cm on each side of the axis were measured (Petrie, 1992). In addition, total root length density was calculated for each depth at which roots were detected. The entire root sample was used to determine total root length by a modification of the Newman line intersect method (Tennant, 1975).

Although predawn Ψ_L was lower in millet than in cowpea as soil dried, values of predawn Ψ_L and Ψ_R were approximately the same within individual plants (Petrie and Hall, 1992c). Therefore, values of Ψ_R used in the simulations were assumed to be equivalent to values of predawn Ψ_L measured on cowpea and millet. Five replicate pots consisting of one cowpea and one millet plant growing together in a 25-L pot of Turface Plus–sand mix in a greenhouse were subjected to a dry treatment, and predawn measurements of Ψ_L were made with psychrometers on four different days after initiation of the dry treatment (Petrie and Hall, 1992a). A second-degree polynomial was fitted by the least squares method to the predawn Ψ_L values for cowpea and for millet, curve-fitting equations were derived, and a smooth curve of water potential over time was developed for each species.

Computer Simulation Model

Assuming that water flow in the vapor phase is insignificant, transient water flow in an unsaturated porous medium is described by the Richards equation (Richards, 1931), which is ordinarily solved by numerical means. The computer program used to simulate water transport in these models was the SWMII-ST program, an earlier version of SWMS-2D developed by Simunek et al. (1992). The program combined a Galerkin-type finite element approach for spatial discretization with a finite difference method for temporal discretization to solve a modified form of the Richards equation,

$$C\frac{\partial h}{\partial t} = \frac{\partial}{\partial x_i}\left[K(K_{ij}^A\frac{\partial h}{\partial x_j} + K_z^A)\right] - S,$$

where C is the soil water capacity function (m^{-1}), h is soil pressure head (m), K is hydraulic conductivity $(m\ s^{-1})$, S is a sink term for uptake by roots (s^{-1}), x_i are spatial coordinates (m), t is time (s), and K^A is a dimensionless tensor that describes conductivity anisotropy (Simunek et al., 1992). Since horizontal water transport was simulated in these studies, the vertical component of conductivity anisotropy,

K_z^A, was set to zero. The sink term, S, represents either a uniform or a nonuniform spatial distribution of the water uptake rate across a root zone of arbitrary shape. Since in our studies we wanted to evaluate water transport to individual roots with nonuniform distributions, S was set to zero and a different method (described below) was devised to simulate nonuniform uptake.

The expressions of van Genuchten (1980) were used to describe the unsaturated soil hydraulic properties:

$$\theta(h) = \begin{cases} \theta_r + (\theta_s - \theta_r)/(1 + |\alpha h|^n)^m & h < 0 \\ \theta_s & h \geq 0 \end{cases}$$

where

$$K(h) = \begin{cases} K_s K_r(h) & h < 0 \\ K_s & h \geq 0 \end{cases}$$

$$K_r = S_e^{1/2}[1 - (1 - S_e^{1/m})^m]^2$$

and

$$S_e = (\theta - \theta_r)/(\theta_s - \theta_r),$$

where θ is volumetric water content, θ_r is residual moisture content, θ_s is saturated water content, K_s is saturated hydraulic conductivity $(m\ s^{-1})$, α and n are parameters of the retention curve, and S_e is the degree of saturation. For these simulations, the soil hydraulic parameters for the A horizon of a grass field described in Simunek et al. (1992) were assumed representative of a soil that effectively supported plant growth. Values of the soil parameters were: $\theta_r = 0.001$, $\theta_s = 0.399$, $\alpha = 1.74\ m^{-1}$, $n = 1.3757$, $K_s = 3.33 \times 10^{-6}\ m\ s^{-1}$, and $m = 1 - (1/n)$, $n > 1$. Two sets of simulations were conducted to test the effect of differences in hydraulic conductivity on water transport to the roots. For the first set of simulations, K_s was reduced to $1.67 \times 10^{-6}\ m\ s^{-1}$, and for another set of simulations K_s was $3.33 \times 10^{-6}\ m\ s^{-1}$.

Representative, symmetrical, branched root segment axes were described for cowpea and millet using observations of roots and experimental measurements. Each root segment was compressed along the axis into a two-dimensional model. Each root axis became a point, and horizontal water flow to the axis point and root branches was simulated. Experimental measurements (presented below) indicated that millet overall root length density was twice as great as cowpea, and millet lateral roots were observed to be generally shorter and more densely distributed along the root axes than cowpea lateral roots. The root geometry used in the millet model, therefore, was locally clumped, with 16 short branches, each 0.25 cm long, radiating from the point representing the root axis. The root geometry used for the cowpea model had four longer branches, each 0.5 cm in length. Total root length densities in the two-dimensional models were 4 cm cm^{-2} for millet and 2 cm cm^{-2} for cowpea (Fig. 1a and 1b). Each simplified, branched root segment axis was assumed to be contained within a 1-cm^2 pot with a no-flow boundary (no water flowing in or out of the region except out of roots), no macropores, and no thermal gradients.

Values of Ψ_R assumed for cowpea and millet were obtained by fitting a second-degree polynomial to Ψ_L values measured experimentally. These Ψ_R values were input into the model at prescribed times, and differences in water content distribution and water velocity that resulted from the differences in root geometry were calculated and plotted. The Ψ_R values for cowpea and millet were based on predawn Ψ_L measurements taken during a 12-d period. In the root models, root length densities measured within a 1-
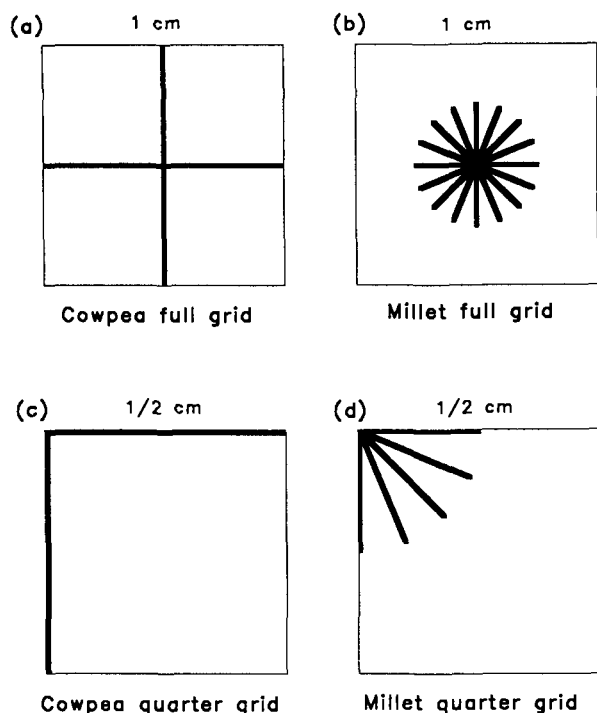
Fig. 1. Models for local water transport to a root axis with a geometry with a smaller root length density (2 cm cm^{-2}) that is not clumped (cowpea) and to a root axis with a geometry with a greater root length density (4 cm cm^{-2}) that is clumped (millet). Grids used in computer simulation: (a) cowpea full grid (1 cm^2), (b) millet full grid, (c) cowpea quarter grid (1/4 cm^2) and (d) millet quarter grid.

cm^3 soil volume were compressed into a 1-cm^2 area, so that much less water was available to roots in the 1-cm^2 simulations than would have been available within a 1-cm^3 rooting volume. Time was scaled, therefore, so that 1 d of real time was equivalent to 1 h of computer simulated time. Symmetry was assumed in the model, and water movement to only one quadrant of the 1-cm^2 area containing the cowpea and millet root axes was simulated (see Fig. 1c and d).

The sink term in the Richards equation solved by the SWMII-ST program assumes that the potential transpiration demand by plants is distributed across a two-dimensional root zone. Since the purpose of these simulations was to evaluate the effect of nonuniform local root distribution, the sink term was set to zero, boundary nodes corresponding to the two-dimensional geometric pattern of root branches within the mesh were designated as root nodes, and the program was modified to read changes in Ψ at the root nodes at the appropriate times (Dirichlet boundary conditions). One corner node represented the root axis, 10 root nodes were allocated to each 0.25 cm of root branch, and root nodes were spaced as evenly as possible along the line on a the grid that represented the root branch. By the property of symmetry, the root lengths on the perimeter of the mesh take up equal amounts of water from each side of the quadrant perimeter, and only five root nodes for every 0.25 cm of root length were spaced along the perimeter. The total number of root nodes, including the root axis, was 21 for cowpea and 41 for millet. All root nodes within the grid were at the same Ψ_R at any given time. The SWMII-ST program was modified to calculate cumulative and instantaneous flow to all root boundary nodes in the interior and on the perimeter. Output files were created for plotting water content distribution and water velocity vector fields using NCAR Graphics programs (University Corporation for Atmospheric Research, 1989).

To test the convergence of the numerical model, the program was run for coarse meshes of 441 evenly spaced nodes (21 by 21 grid) and for fine meshes of 1681 evenly spaced nodes (41 by 41 grid) for the cowpea and millet root geometries. Initial time steps of 0.6 s were used, with a dynamic adjustment via a multiplier of 1.3 when the number of iterations required for convergence was less than or equal to three. Water content, cumulative flow, and instantaneous flow were determined for cowpea and millet. Results were similar for coarse and fine meshes, implying convergence. Approximately 3 h of computer time on a SUNSPARK workstation (Sun Microsystems, Mountain View, CA) were required to run the computer program on each of the fine meshes; <1 h was required to run the program on the coarse mesh.

The basic millet model was varied by removing two root branches from the quarter grid (equivalent to eight branches removed from the full millet grid) to separate effects of root density from root geometry. The same number of root nodes as cowpea (21) was therefore arranged in the clumped, short-branched geometry of millet to establish a low-density millet model. The program was run on the grid for low-density millet using the Ψ_R values for both millet and cowpea so that the effects of differences in root geometry and root length density could be determined alone and in combination with differences in Ψ_R.

Since root length densities at the soil surface are generally at least four times as great in millet as in cowpea (Petrie and Hall, 1992b), a high-density millet root model containing 82 root nodes (double-axis millet) was created by adding a second one-quarter root axis to the lower right corner of the one-quarter millet grid shown in Fig. 1d. The program was run on the grid for double-axis millet with both the millet and cowpea Ψ_R values.

Computer simulations of water transport to each root geometry and root length density were run; values for total amount of water within the profile, outflow, mean head, water content at each node, and velocity vectors in the x and y directions were printed for the first 0, 600, and 900 s, and every 1 h thereafter until 12 h of simulated time were completed. Mass balances were calculated and found to account for at least 92% of the water in simulations using the coarse meshes and at least 96% for the fine meshes, indicating that computational and rounding errors were small. Changes with time in head, average water content, and cumulative flow to root nodes were plotted for cowpea root geometry run with the cowpea Ψ_R values, and for millet root geometry run with the millet Ψ_R values.

Water content output data generated at each node was used to plot water content distribution around cowpea, millet, low-density millet, and double-axis millet root geometries. Contour intervals of 0.005 (corresponding to 0.005 m^2 m^{-2} water content) were established for all contour plots. Water velocity vector fields were generated from velocity vector data at each node, and a lower limit of velocity was set at 8.33 × 10^{-10} m s^{-1} for easier comparison of root models.

RESULTS AND DISCUSSION

Experiments

Root length densities were measured to quantify root clumping. Axis root length density within a 0.5-cm radius immediately surrounding root segment axes was twice as great in millet as in cowpea (3.5 × 10^4 m m^{-3} for millet and 1.7 × 10^4 m m^{-3} for cowpea in Fig. 2). In cowpea, total root length densities were consistently lower than densities measured in the region surrounding individual root axes (Fig. 2). In contrast, millet total root length densities at the surface were significantly higher than the root length densities along the axes, but no significant differences were detected at lower depths. A dimensionless ratio of

total root length density to axis root length density (clumping ratio) was calculated to quantify global clumping of roots within the profile (Table 1). A clumping ratio of 1.0 indicates that approximately one root axis is contained within each 1 cm³ of soil, a ratio < 1.0 means that each root axis has access to a soil volume greater than 1 cm³, and a ratio > 1.0 indicates that more than one root axis is contained within each 1-cm³ volume.

Clumping ratios in cowpea were < 1.0 throughout the profile and were similar at all levels by Day 35 of the dry treatment (Table 1), indicating uniform root distribution on a global scale. In millet, the average clumping ratio at 0.1-m depth was 2.07 (indicating that approximately two millet axes were contained within each 1-cm³ volume at the surface), and millet clumping ratios decreased with depth (Table 1). Root distribution in millet, therefore, was clumped globally, from the top to the bottom of the rooting profile, as well as locally along the root axis. In a homogeneous rooting medium, a greater soil volume and a larger quantity of stored soil water are potentially available to each root when clumping ratios are lower.

Computer Simulation Models

Root Models

The root clumping values derived from experiments were used to develop representative root axis models for use in water transport simulations. For the millet-type geometry, three models were evaluated: (i) a 1-cm² model containing one millet axis and branches (41 root nodes) representing root distributions at lower depths; (ii) a 1-cm² model containing two millet axes and branches (82 root nodes) representing the greater degree of root clumping at the surface; and (iii) a low-density millet geometry (21 root nodes) that compared the effects on water transport of the differences in root geometry between cowpea and millet at the same root length density. For cowpea, a single model consisting of 21 root nodes was developed, since root length density in the region surrounding the root axis did not vary in cowpea and clumping ratios were relatively constant throughout the profile, indicating a relatively constant number of root axes per soil volume.

For these models, it was assumed that roots do not grow in each 1-cm² pot as soil dries. Root growth can increase the efficiency of water uptake, but root segments that have developed branches may not continue to grow, and overall rooting densities can decrease as soil dries (Klepper et al., 1973). In millet and other cereals, root growth may stop at anthesis (Gregory and Squire, 1979). When root growth ceases, water uptake depends on soil conductance of water to root surfaces (Klute and Peters, 1969), and the water potential gradient between the root and soil that drives water movement can be largely dissipated within 5 or 6 mm from the root surface (Cowan, 1965; Hainsworth and Aylmore, 1986). In a drying soil, a high root length density around the root axis can increase the rate of local soil dehydration and slow the rate of water uptake. Local root length density, and the spatial arrangement of that density, will determine the size and shape of the root–soil interface and affect water transport to the root.
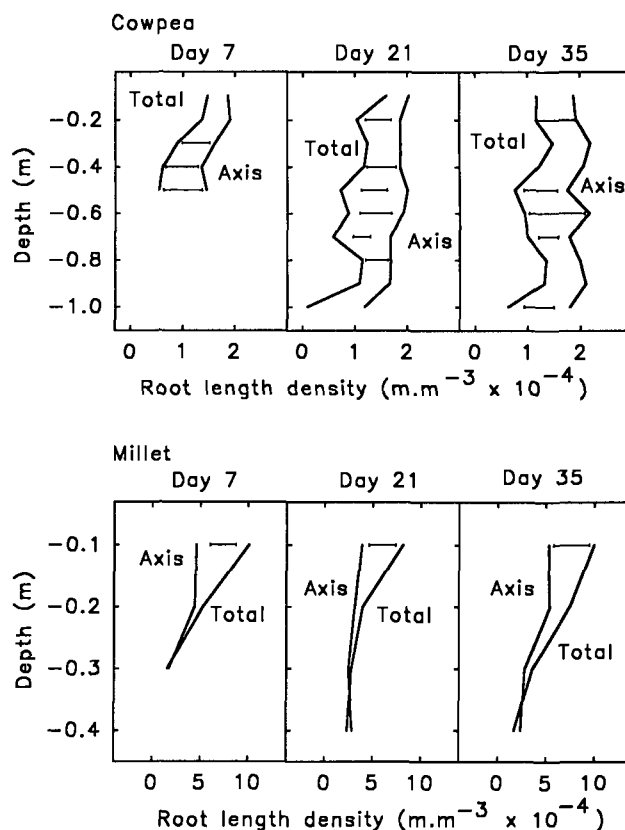

Fig. 2. Root length density in the total soil volume (total) and within a 0.5-cm radius around the root axis (axis) in cowpea and millet grown under a drying treatment in separate polyvinyl chloride tubes containing a Turface Plus–sand mixture (experiment planted 25 Aug. 1990). Five replicates destructively sampled on Days 7, 21, and 35 after initiation of dry treatment. Error bars indicate least significant differences at the 0.05 level [LSD(0.05)].

Initial Simulations

In the first set of computer simulations, water transport to root axes with cowpea root geometry (21 root

Table 1. Clumping ratios (dimensionless ratios of total root length density to root length density within a 0.5-cm radius around root axes) in tube depths containing roots. Dry treatment cowpea and millet were planted 25 Aug. 1990 in separate tubes containing a Turface Plus–sand mixture. Measurements were based on five replicates destructively sampled 7, 21, and 35 d after initiation of the dry treatment.

| | Clumping ratio | | | | | |
| | Day 7 | | Day 21 | | Day 35 | |
Depth	Cowpea	Millet	Cowpea	Millet	Cowpea	Millet
m						
0.1	0.79	2.21	0.79	2.11	0.63	1.89
0.2	0.71	1.20	0.55	1.27	0.60	1.37
0.3	0.55	0.90	0.66	1.12	0.67	1.29
0.4	0.45		0.63	0.83	0.58	0.71
0.5	0.37		0.36		0.43	
0.6			0.46		0.43	
0.7			0.35		0.56	
0.8			0.68		0.68	
0.9			0.65		0.62	
1.0			0.07		0.61	
Mean	0.57	1.44	0.52	1.33	0.55	1.32
SD	±0.18	±0.69	±0.21	±0.55	±0.11	±0.48

nodes) and millet root geometry (41 root nodes) was evaluated. The water potential values obtained experimentally declined from 0 to -0.8 MPa in cowpea and from 0 to -1.9 MPa in millet. Mean cumulative flow to root nodes was predicted to be similar for cowpea and millet ($\approx 1\%$ higher for millet) in the simulations, comparable to results obtained in greenhouse experiments with cowpea and millet grown in pots (Petrie and Hall, 1992b).

Throughout the simulation for cowpea, water content was lower in the region around the roots than in the regions furthest from the roots, and overall water content in the profile progressively decreased (Petrie, 1992). The change in water content contours between 4 and 12 h of simulated water transport indicated that a steeper water content gradient had developed between the region of soil around the root and the outer grid edges (Petrie, 1992; Fig. 3). Early in the simulation, water movement to the entire cowpea root length was $>8.33 \times 10^{-10}$ m s^{-1}, but water movement was slower in the region furthest from the root and in the region where the cowpea root branches joined the axis (Petrie, 1992). As the simulation continued, the rate of water movement to most of the root length was $> 8.33 \times 10^{-10}$ m s^{-1}, indicating that most of the root was involved in water uptake, but the area of slower water movement in the region farthest from the root became larger. By the 12th hour of simulation, the length of root involved in water uptake (Fig. 4) decreased slightly compared with the earlier simulations (Petrie, 1992).

For millet, water content contours by the 12th hour of simulation indicated that a larger zone of dry soil surrounded the root surface than for cowpea (Fig. 5). As the simulation progressed, the water content gradient from the soil region around the roots to the outer edges of the grid became steeper and water movement to refill the root zone became slower (Petrie, 1992).

The rate of water movement was greatest at the root tips during the entire simulation (Petrie, 1992) and, by the 12th hour of simulated water transport, only the outer portion of the root zone, representing the root tips, was exhibiting substantial water uptake (Fig. 6).

Effects of Varying Water Potential and Root Length Density

The effect on a water transport of the plant Ψ differences that developed between cowpea and millet was tested with simulations using values of Ψ_R for both cowpea and millet. Patterns of water content distribution and water velocity vectors were the same, but the gradient of water content from the region surrounding the root to the outer edge of the profile was steeper, and the water content in the region immediately surrounding the root was lower when the lower Ψ_R values based on measurements of millet were used with either cowpea or millet root models (Petrie, 1992). Water uptake in millet, however, still occurred primarily at the root tips (Petrie, 1992).

When water transport was simulated to a root axis with a root length density equal to that of cowpea but with a millet-type geometry (low-density millet), water content contours indicated that a smaller area of very dry soil surrounded the root branches (Fig. 7), and that water movement was faster in a larger area of the root zone (Fig. 8), than in millet with a higher root length density (Fig. 5 and 6). Patterns of results and differences between cowpea and millet were similar when the program was run on the same models using the cowpea Ψ_R values (Petrie, 1992). With both root length densities, the millet root geometry was less efficient than the cowpea root geometry, in that more
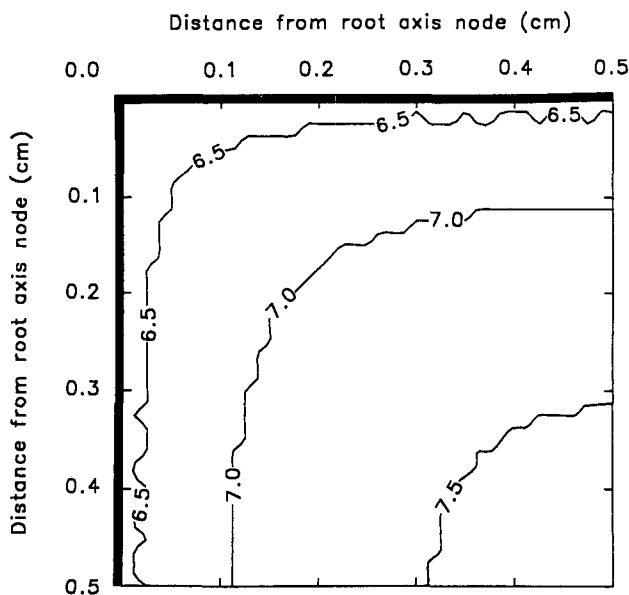

Fig. 3. Water content distribution ($\times$ 10^2) after 12 h of computer-simulated water transport to a root axis with cowpea geometry and cowpea water potential values. Bold lines indicate roots.
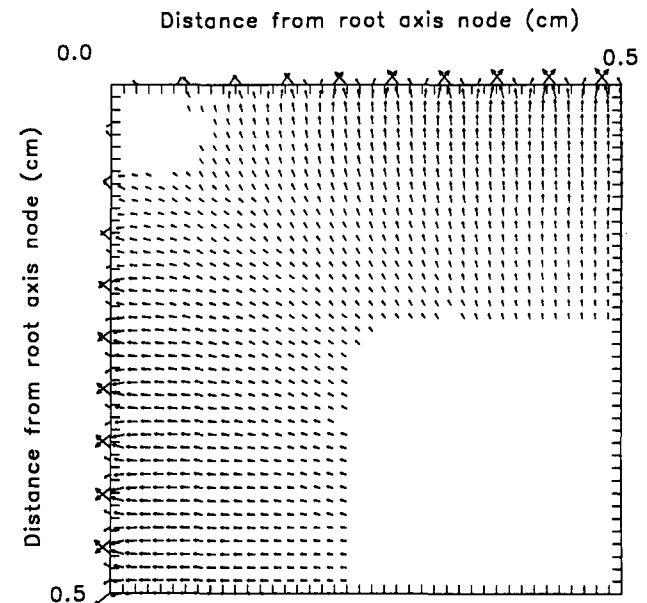

Fig. 4. Water velocity vectors $\geq 8.33 \times 10^{-10}$ m s^{-1} after 12 h of computer-simulated water transport to a root axis with cowpea geometry and cowpea water potential values. Maximum and minimum velocities were 3.50×10^{-9} and 3.00×10^{-11} m s^{-1}.
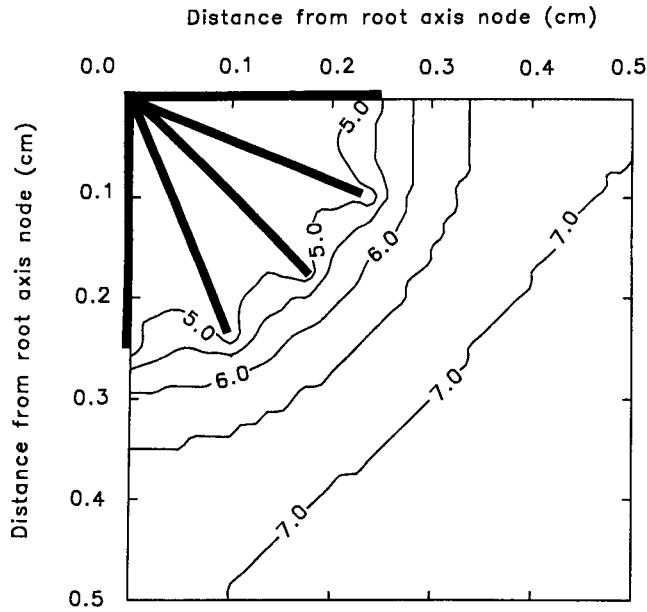
Fig. 5. Water content distribution (× 10²) after 12 h of computer-simulated water transport to a root axis with millet geometry and millet water potential values. Bold lines indicate roots.
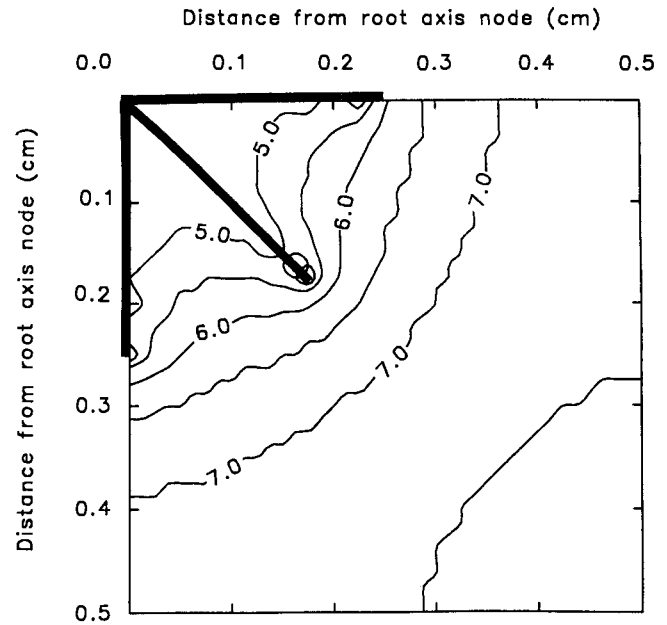

Fig. 7. Water content distribution (× 10²) after 12 h of computer-simulated water transport to a root axis with low root length density millet geometry and millet water potential values. Bold lines indicate roots. Overlapping circles represent on artifact of the method of representing root branches by root nodes in a simulation with sharp changes in water potential.
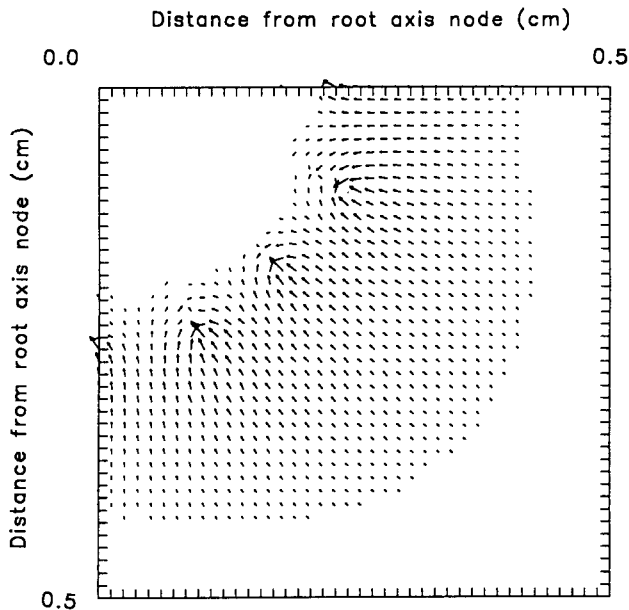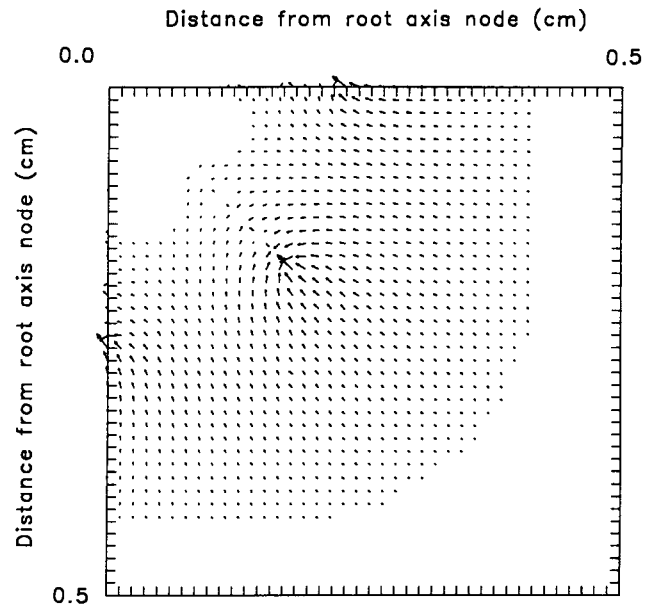

Fig. 6. Water velocity vectors ≥8.33 × 10⁻¹⁰ m s⁻¹ after 12 h of computer-simulated water transport to a root axis with millet geometry and millet water potential values. Maximum and minimum velocities were 7.17 × 10⁻⁹ and 5.00 × 10⁻¹⁵ m s⁻¹.

Fig. 8. Water velocity vectors ≥8.33 × 10⁻¹⁰ m s⁻¹ after 12 h of computer-simulated water transport to a root axis with a low root length density millet geometry and millet water potential values. Maximum and minimum velocities were 1.10 × 10⁻⁸ and 6.33 × 10⁻¹² m s⁻¹.

of the root length of millet than of cowpea was surrounded by a region of soil in which water movement was very slow. Higher root length densities caused millet roots to be even less efficient.

Clumping ratios for millet (Table 1) indicated that at least two millet root axes were present in each 1-cm³ soil volume at the surface. When water transport was simulated using the double-axis millet model, water

content contours indicated that drier soil surrounded the roots than for simulations run with the single-axis millet model (Petrie, 1992). Velocity vector fields indicated that regions of slow water movement had developed between the root axes and between the root

tips on each axis, most of the root length was encased in a region in which water movement was slow, and water uptake occurred mainly at the outer edge of the root region representing the root tips (Fig. 9). Results were similar when the model was run using the cowpea Ψ_R values (Petrie, 1992).

By the eighth hour of computer simulated water transport, millet Ψ was ≈ 0.3 MPa lower than cowpea in the initial simulations. Mean cumulative water uptake was about the same, however, for the cowpea root geometry (21 root nodes), millet root geometry (41 root nodes), and low-density millet root geometry (21 root nodes), and water uptake was only $\approx 1\%$ greater for the double-axis millet root geometry (82 root nodes). When the same Ψ_R values based on measurements of millet were used for the cowpea and millet geometries, water uptake throughout the simulation was ≈ 1.5 to 2% greater for cowpea than for all of the millet geometries, even though cowpea had one-half the root length density of millet and one-quarter that of the double-axis millet. A substantial increase in root length density, therefore, does not necessarily increase water uptake under conditions of soil dehydration.

Effect of Varying Hydraulic Conductivity

An additional set of simulations was conducted in which the initial hydraulic conductivity of the rooting medium was increased from $K_s = 1.67 \times 10^{-6}$ m s^{-1} to $K_s = 3.33 \times 10^{-6}$ m s^{-1}. These simulations were conducted for cowpea, millet, cowpea root geometry with millet Ψ_R values, and millet root geometry with cowpea Ψ_R values. Results were similar to simulations using the lower hydraulic conductivity, but overall water depletion was greater when hydraulic conductivity was higher (Petrie, 1992).

Discussion

According to the two-dimensional simulations, the millet root system was much less efficient than the cowpea root system due to the development of dry zones surrounding the roots that permitted little water uptake except at the root tips of millet. It is necessary to consider, however, whether the same phenomenon would occur in the real world, which is three-dimensional. There are technical constraints to conducting simulations in three dimensions. The computer time required to run a three-dimensional model would be substantially greater than for a two-dimensional model. The increase in simulated time from 12 h to 12 d, together with the increased number of equations solved at each iteration (>265 000 equations in the three-dimensional model compared with 1681 in the two-dimensional quarter grid) would require a supercomputer. Consequently we can only speculate about the effects of an additional dimension. In the two-dimensional simulations for cowpea, the 90° angle formed by the joining of branch roots to the axis created a small region of slower water movement, and water uptake at the root surfaces near that angle became less efficient as soil dried. Many such angles would be present in a three-dimensional model of a millet root axis and would cause many zones of less efficient water uptake. In contrast, a three-dimensional cowpea
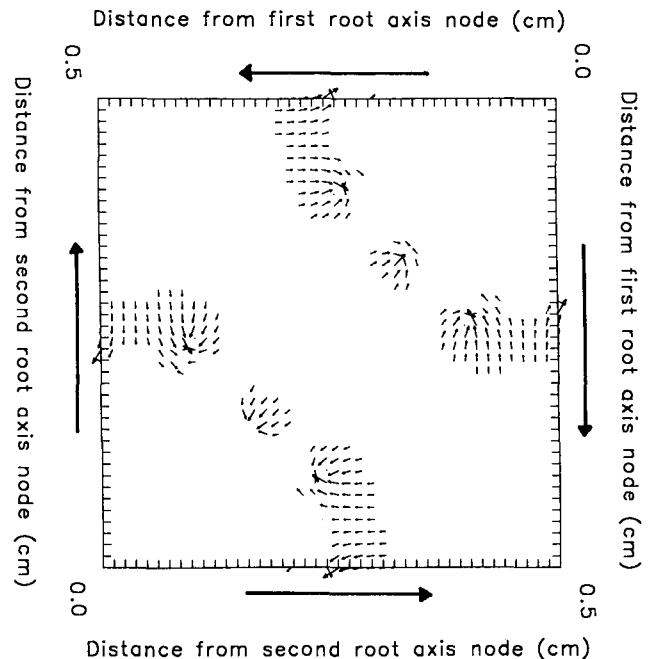

Fig. 9. Water velocity vectors $\geq 8.33 \times 10^{-10}$ m s^{-1} after 12 h of computer-simulated water transport in a profile with two root axes with millet geometry and millet water potential values. Maximum and minimum velocities were 2.67×10^{-9} and 5.00×10^{-15} m s^{-1}.

model would have fewer branch angles than millet, and a greater volume of stored soil moisture would be available to the root surfaces near those angles.

The root geometry and the high root length densities of millet are not unique. Hamblin and Tennant (1987) and Richards (1991) have also reported higher root length densities in cereals than in legumes grown under the same conditions. The reasons for the high root length densities and clumping in cereal roots are unclear. They may be evolutionary inefficiencies that have not been bred out of modern crops (Richards, 1991), ensurance against damage to part of the root system (Hamblin and Tennant, 1987), or a means for exploiting light rainfalls before water is lost from the soil surface through evaporation (Taylor, 1983). High rooting densities at the surface may also allow plants to exploit immobile nutrients such as P, or mobile nutrients such as N before they are lost through leaching.

The modeling approach used in these studies was modular; each root axis and its local branching pattern represented a pattern similar to that in other portions of the root system. The models predicted that the root geometry of millet became progressively less efficient than cowpea as soil dried, even when input parameters used in simulations were altered. In simulations that were conducted using the lower values of Ψ_R derived from experimental data on millet, the amount of water taken up by both cowpea and millet was only slightly greater than in simulations conducted using Ψ_R values for cowpea. For the cowpea root geometry, water moved with similar velocities across virtually all of the root surface. For the millet root geometry, water movement became very slow in most of the root region except for the root tips. At higher local root length

densities, an even greater proportion of the millet root surface was encased in dry soil in which water movement was slow. Water uptake was not necessarily greater with higher root length densities, even when the investment in root structure was two to four times as great.

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