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# The effect of root shrinkage on soil water inflow

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### **SUMMARY**

As a soil dries, the roots growing in it may shrink and retain only partial contact with the soil. The steady-state model described here calculates the effect of root shrinkage on the water inflow across soils and roots with various hydraulic conductivities. Relative to standard conditions, typical of a secondary root in a loam at field capacity, the water inflow was very sensitive to the root radius, the root shrinkage, the root hydraulic conductivity and the water potential in the bulk soil and at the root endodermis. The inflow was insensitive to the density of rooting, and to the soil hydraulic conductivity except in dry sandy soil where this was lower than the root hydraulic conductivity. Loss of full contact can decrease the inflow by a factor of up to about three. In very dry conditions, vapour transfer across the air gap between the root and soil surfaces can contribute usefully to the total water inflow.

# 1. INTRODUCTION

It has long been known that a plant's rate of transpiration decreases as the supporting soil dries. Philip (1957) and Gardner (1960) were the first to examine whether this was caused by slow flow of water to the roots as the soil's hydraulic conductivity decreased, inducing stomatal closure. They calculated that resistance to flow across the soil should be small until the soil water potential had fallen to less than about  $-500 \,\mathrm{J\,kg^{-1}}$  ( $-5\,\mathrm{bar}$ ), whereas the rate of transpiration decreased at much higher water potentials of about  $-50\,\mathrm{J\,kg^{-1}}$ . Despite this, Gardner & Ehlig (1962, 1963) felt that the increase in total resistance over the whole soil-plant pathway was associated with a change in the soil resistance. Since there was insufficient evidence that a substantial resistance to water flow developed inside the plant when the root surfaces were at a low water potential, many workers concluded that there must be a contact resistance between the root surface and the soil (Taylor & Klepper 1975; Herkelrath et al. 1977a,b; Faiz & Weatherly 1977, 1978).

Huck et al. (1970) provided a clue to the nature of this resistance when they observed considerable diurnal variation in the diameter of cotton roots. Cole & Alston (1974) found that wheat roots shrank markedly on drying beyond  $-500\,\mathrm{J\,kg^{-1}}$  water potential, losing 60% of their original diameter by  $-1000 \,\mathrm{J\,kg^{-1}}$ . Al Najafi (1990) determined the diameter of the nodal roots of maize over a wide range of water potentials. At 250 J kg<sup>-1</sup> below the potential of the fully turgid roots, their diameter shrank by 10% and reached a shrinkage limit of 42% at  $1500\,\mathrm{J\,kg^{-1}}$  below the initial potential. Only the cortex contracted, the stele diameter remaining constant. From these observations Nye

(1992) calculated that main roots (1 mm diameter) would lose full contact with the soil at a water potential of  $-20\,\mathrm{J\,kg^{-1}}$ , secondary roots (0.1 mm diameter) at  $-70\,\mathrm{J\,kg^{-1}}$ , and root hairs (0.01 mm diameter) at  $-230\,\mathrm{J\,kg^{-1}}$ .

Fairly direct evidence that root shrinkage led to loss of full contact with the soil was obtained by Faiz & Weatherley (1982). They compared the leaf water potential of sunflowers growing in pots filled either with nutrient solution or with soil so moist that soil resistance could be discounted. The leaf water potential was up to  $600\,\mathrm{J\,kg^{-1}}$  lower in the soil grown plants. This difference was, however, largely removed if the soil pots were agitated, or if the soil was enclosed in a plastic bag that was then squeezed: clear evidence that good contact between root and soil had been restored. By assuming that as the soil dried the surface area of the root in contact with the soil decreased, Herkelrath et al. (1977b) were able to reconcile observed rates of transpiration with theoretical calculations. Tinker (1976) considered that as a root shrank it was likely to retain contact with the soil around part of its periphery because of surface tension forces. He used an electrical analogue to show that such partial contact was unlikely to alter soil water potential gradients greatly except at high rates of inflow. He suggested that root hairs and mucilage might bridge the gap. However, at the water potentials at which contact is lost it seems unlikely that the mucilage observed on the surface of roots in moist soils will remain hydrated. Cowan & Milthorpe (1968) and Nobel & Cui (1992) have also calculated that transport through the vapour phase might make a small contribution to water flow across large pores or gaps. Dalton (1989) confirmed this possibility experimentally. He determined the proportion of heavy water transported across the root-soil interface

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in liquid and vapour form, based on the idea that the vapour component will deplete a larger proportion of the lighter H<sub>2</sub>O, so enriching the fraction of D<sub>2</sub>O in the soil. His results indicated that, in water-stressed tomato plants, there was a very small component of vapour absorption by the roots.

Much of the difficulty in reaching a conclusion about the importance of soil resistance has arisen because of the wide differences in hydraulic conductivity between soils of different texture and water content, and differences in the size of the roots and their rate of inflow. This paper aims to quantify the effects of root shrinkage for a wide range of conditions. It presents a detailed model of the movement of water from the bulk soil across the soil-root interface and the cortex as far as the endodermis. It thus provides a submodel that can be incorporated in the many whole-plant transpiration models that have been proposed, as well as a standard by which more approximate treatments of this part of the whole transpiration pathway may be judged. For simplicity, a low salt concentration in the soil solution is assumed to avoid complications that may arise from osmotic effects near the root surface (Dalton et al. 1975).

As a root grows through moist soil, in most places it will maintain contact all round its perimeter. In other places it will cross large pores, or follow old root channels or worm holes, keeping contact at only one or two points around its perimeter. Contact all round the perimeter will be more important in homogeneous soils with aggregates no larger than the root diameter, whereas partial contact may predominate in coarsely aggregated soil (Nye & Tinker 1976, p. 163). This paper deals with homogeneous soils in which the diameter of the roots is larger than that of the soil pores.

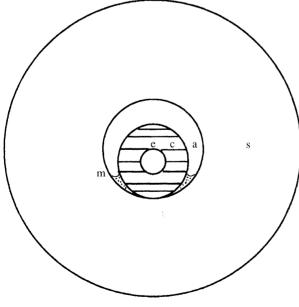


Figure 1. Contact between shrunken root and soil; s, soil; a, air gap; m, contact meniscus; c, cortex; e, endodermis.

# 2. A MODEL OF WATER INFLOW FROM THE SOIL TO ROOT ENDODERMIS

Figure 1 shows the system to be modelled. As the soil dries and the water potential in the cortex decreases, the root shrinks and loses contact with the soil over part of its circumference. The greater the shrinkage, the smaller is the contact angle  $\theta$ , shown in figure 2. It is assumed that the soil does not shrink and that partial contact will be maintained by surface tension forces. The model calculates the steady rate of water inflow from the radial zone supplying water to the root in the bulk soil to the root endodermis, given the water potentials of the bulk soil and of the root endodermis, the hydraulic conductivities of the soil and root, the size and shrinkage of the root, and the density of rooting.

Because the root lies to one side of its channel, the flow of water through both soil and root is not radially symmetrical, so the calculation requires twodimensional polar coordinates. The potentials across the root cortex, at the contact surface and across the soil, are, of course, unknown and the problem is to find them. To do so, trial values of these water potentials are introduced. An iteration procedure is used to adjust them until a steady state is attained and the inflows across the soil and the root are equal. At the contact surface, the shrinkage and the contact angle, which depend on the contact potential, are adjusted in the course of the iteration.

# (a) The theoretical basis of the model

(i) List of the main symbols

distance across air gap (m) δ

 $\phi$ soil water matrix flux potential (J m<sup>-3</sup> s)

surface tension (J m<sup>-2</sup>)  $\gamma$ 

 $\theta$ angle at soil cylinder centre (radians)

 $\theta'$ angle at root centre (radians)

 $\theta_{\mathrm{c}}$ angle at contact meniscus (radians)

 $\rho_{\mathrm{w}}$ density of water  $(kg m^{-3})$ 

ψ water potential (J kg<sup>-1</sup>)

 $\psi_{\rm e}$ soil pore entry water potential (J kg<sup>-1</sup>)

 $\psi_{i}$ water potential at the root-soil contact  $(J kg^{-1})$ 

 $\psi_{\rm o}$ water potential at the outside soil boundary  $(J\,kg^{-1})$ 

water potential at the root endodermis  $(J kg^{-1})$  $\psi_{\mathrm{endo}}$ 

dimensionless distance to meniscus centre

flux of water vapour  $(kg m^{-2} s^{-1})$ 

 $f_{\rm v}$ water flux (kg m<sup>-2</sup> s<sup>-1</sup>)  $f_{\mathbf{w}}$  I

a

water inflow across soil  $(kg m^{-1} s^{-1})$ 

I'water inflow across root  $(kg m^{-1} s^{-1})$ 

water inflow across air gap  $(kg m^{-1} s^{-1})$  $I_{\rm gap}$ 

hydraulic conductivity  $(kg m^{-3} s) (l J kg^{-1} =$ 1 m<sup>2</sup> s<sup>-2</sup>; hence the S.I. unit of hydraulic conductivity, defined by equation (11), has

units  $kg m^{-3} s$ 

 $k_{\rm c}$ hydraulic conductivity of root cortex

 $(kg m^{-3} s)$ 

hydraulic conductivity of saturated soil

 $(kg m^{-3} s)$ 

 $L_{\rm v}$  length of root per unit volume of soil (m<sup>-2</sup>) soil texture index

r radial distance from centre of soil cylinder (m)

r' radial distance from centre of root (m)

 $r'_{\text{endo}}$  root endodermis radius (m)

 $r'_{\rm o}$  root radius (m)

 $r_i$  inner radius of soil cylinder (m)

r<sub>o</sub> outer radius of soil cylinder (m)

root shrinkage

 $s_{\rm m}$  maximum root shrinkage

Sa proportion of sand (sand + silt + clay = 1.0; ratio silt to clay = 2.0)

t time (s)

x distance (m)

(ii) The relation between the contact angle and the contact potential

The first step is to find the width of the elongated meniscus between the soil and root cylinders. In figure 2, O is the centre of the soil and unshrunken root cylinder, O' is the centre of the shrunken root cylinder, and A, A' mark the edges of the contact meniscus with the soil and root, so that AA' is the width of the meniscus; B is its centre;  $\angle$ OAC and  $\angle$ O'A'C are assumed to be 90°, i.e. perfect wetting is assumed.

Construct the perpendicular BD. Let OA = 1 and AB = A'B' = a. The shrinkage OO'/OA = s. Then:

$$O'A' = 1 - s, (1)$$

$$BD = [(1 - s) + a] \sin \theta', \tag{2}$$

and BD = 
$$(1 - a) \sin \theta$$
, (3)

and BD = 
$$s/(\cot \theta - \cot \theta')$$
. (4)

Eliminating BD between equations (2) and (3),

$$a = \left[\sin \theta - (1 - s)\sin \theta'\right] / (\sin \theta + \sin \theta'). \tag{5}$$

Eliminating BD between equations (3) and (4),

$$(1 - a)\sin\theta(\cot\theta - \cot\theta') = s. \tag{6}$$

Eliminating a between equations (5) and (6) and simplifying,

$$(2-s)[\sin(\theta-\theta')]/(\sin\theta+\sin\theta')+s=0. \tag{7}$$

Equation (7) can be solved iteratively to express  $\theta$  in

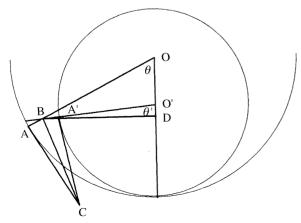


Figure 2. Geometry of the contact meniscus (see text).

terms of  $\theta'$ , and vice versa, for any given value of s. Now the meniscus width when OA = 1 is given by

$$AA' = 2a\cos\left[(\theta' - \theta)/2\right],\tag{8}$$

and equation (5) expresses a in terms of  $\theta$ ,  $\theta'$ . Hence AA' can be found in terms of either  $\theta$  or  $\theta'$  (see equation (7)) for any given value of s.

The width of the meniscus for a root of any unshrunken radius may now be related to the contact potential  $\psi_i$ . Consider unit length of meniscus along the axis of a root of unshrunken radius  $r_i$ . The surface tension forces normal to this length and acting in the direction CA and CA' are balanced by the force resulting from the (negative) contact potential. Now  $\angle OBO' = \angle BAA' + \angle BA'A = \theta - \theta'$ ; and  $\angle BAA' = \angle BAA'$ , because BC bisects  $\angle ACA'$ . Further,  $\angle BAA' = \angle ACB$ . Therefore  $\angle ACB = (\theta - \theta')/2$ . Hence, balancing the forces,

$$2\gamma \cos\left[(\theta' - \theta)/2\right] = -\psi_i \rho_w AA' r_i \tag{9}$$

Substituting the value of AA' from equation (8) in equation (9) and simplifying,

$$\psi_{\rm i} = -\gamma/(\rho_{\rm w} a r_{\rm i}). \tag{10}$$

Since a can be found in terms of  $\theta$  and  $\theta'$  by equation (5), and  $\theta$  can be related to  $\theta'$  by the solution of equation (7), then  $\psi_i$  can be related to  $\theta$ , albeit not explicitly.

(iii) The relation between the soil inflow and the contact potential

The treatment in this section follows that described by Campbell (1985, chapter 6). Water flux is given by Darcy's equation

$$f_{\rm w} = -k(\psi) \,\mathrm{d}\psi/\mathrm{d}x,\tag{11}$$

where k is the hydraulic conductivity and  $\psi$  is the soil water potential. Now for a wide range of soils,

$$k(\psi) = k_{\text{sat}}(\psi_{\text{e}}/\psi)^n, \tag{12}$$

where  $\psi_e$  is the air entry potential, which depends on soil texture, and the index n and  $k_{\rm sat}$  also depend on texture; n can vary from 3.5 in a sandy soil to 2.1 in a clay soil. Since  $\psi$  ranges from about  $-10\,\mathrm{J\,kg^{-1}}$  in moist soil to  $-1500\,\mathrm{J\,kg^{-1}}$  in dry soil at the wilting point the model must cater for a wide variation in hydraulic conductivity over a small radial distance from the root. This greatly complicates the finite difference solution of equation (11), although for our conditions it may be simplified by an integral transform due to Gardner (1958). Define the 'matric flux potential'  $\phi$  by

$$\phi = \int_{-\infty}^{\psi} k \, \mathrm{d}\psi. \tag{13}$$

If equation (12) is assumed then for  $\psi \leq \psi_c$ ,  $\phi = k\psi/(1-n)$ , where  $\phi$  is always positive and ranges from zero in very dry soil to  $\phi_c$  in saturated soil. Differentiating equation (13) and substituting in equation (11) gives

$$f_{\rm w} = -\mathrm{d}\phi/\mathrm{d}x. \tag{14}$$

Thus the matric flux potential can be regarded as the

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driving force for water movement without the complication of the variable coefficient k.

The steady-state movement of water from the bulk soil to the soil-root contact zone with the geometry of figure 1 may be fully described by solving the two-dimensional Laplace equation in polar coordinates (Smith 1978):

$$\partial^2 \phi / \partial r^2 + (\partial \phi / \partial r) / r + (\partial^2 \phi / \partial \theta^2) / r^2 = 0, \tag{15}$$

with appropriate boundary conditions which will now be defined.

Outer boundary,  $r = r_0$ .

If the length of root per unit volume of soil is  $L_v$ , then the average radius of the cylinder of soil exploited by a single root is  $r_o = 1/(\pi L_v)^{1/2}$ . At this boundary  $\psi = \psi_0$  and  $\phi = \phi_0$ .

Inner boundary  $r = r_i$ .

At this boundary the water flux will normally be confined to the contact zone, although in dry soil there is the possibility of some transfer of water vapour across the air gap (see later). Consequently,  $\psi$  and  $\phi$  will vary with  $\theta$  with a discontinuity at the edge of the contact zone,  $\theta_c$ .

The formal boundary conditions are therefore:

$$r = r_{\rm o}; \quad 0 < \theta < \pi; \quad \partial \phi / \partial r = 0; \quad \phi = \phi_{\rm o}; \quad \psi = \psi_{\rm o};$$
  
 $r = r_{\rm i}; \quad 0 < \theta < \pi; \quad \phi = \phi_{\rm i}; \quad \psi = \psi_{\rm i};$   
 $r = r_{\rm i}; \quad \theta_{\rm c} < \theta < \pi; \quad \partial \phi / \partial r = 0 \text{ (if no vapour transfer)};$ 

$$r_{\rm o} > r > r_{\rm i}; \quad \theta = 0; \quad \partial \phi / \partial \theta = 0;$$
 
$$\theta = \pi; \quad \partial \phi / \partial \theta = 0.$$

The total inflow of water across the soil is given by

$$I = 2 \int_{0}^{\pi} r(\mathrm{d}\phi/\mathrm{d}r) \,\mathrm{d}\theta. \tag{16}$$

The matric flux potential can be related to the water potential by substituting the value of k, determined from equation (12), in equation (13) and integrating:

$$\phi = k\psi/(1-n). \tag{17}$$

The assumption that the water inflow across the soil will rapidly reach a steady state for given potentials at  $r_{\rm o}$  and  $r_{\rm endo}$  is valid as long as  $r_{\rm i} \ll (2D_{\rm w}t)^{1/2}$ , where the soil water diffusivity,  $D_{\rm w}$ , is  $k\,{\rm d}\psi/{\rm d}w$ , where w is the soil water content (Cowan 1965).

(iv) The relation between inflow across the root cortex and the contact potential

The details of the pathways followed by water in traversing the root cortex, hypodermis and epidermis remain contentious (Passioura 1988; Oertli 1991), so for the purposes of this model the hydraulic conductivity within the root cortex including the hypodermis and epidermis is assumed to be constant. The two-dimensional Laplace equation in cylindrical polar coordinates is

$$\partial^2 \psi / \partial r^2 + (\partial \psi / \partial r) / r + (\partial^2 \psi / \partial \theta'^2) / r^2 = 0. \tag{18}$$

The boundary conditions are as follows:

$$\begin{split} r' &= r'_{\rm o}; \quad 0 < \theta' < \theta'_{\rm c}; \qquad \phi = \phi'_{\rm s}; \\ r' &= r'_{\rm o}; \quad \theta'_{\rm c} < \theta' < \pi; \qquad \partial \psi / \partial r = 0 \text{ (if no vapour transfer),} \end{split}$$

$$r' = r_{\rm endo}; \quad 0 < \theta' < \pi; \quad \psi = \psi_{\rm endo}$$
  $r_{\rm o} > r' > r_{\rm endo}; \quad \theta = 0; \quad \partial \psi / \partial \theta' = 0$   $\theta = \pi; \quad \partial \psi / \partial \theta' = 0.$ 

On the evidence of Al Najafi's (1990) work on maize nodal roots,  $r_{\rm endo}$  is assumed to be constant as  $\psi$  varies.

The total inflow across the cortex is given by

$$I' = 2 \int_{0}^{\pi} k_{\rm c} r(\partial \psi / \partial r) \, \mathrm{d}\theta'. \tag{19}$$

The assumption of a constant hydraulic conductivity across the root cortex is an idealization, since it may vary with the rate of transpiration (Slatyer 1967), and the relative influence of the endodermal and cortical cells is uncertain. Further, the fairly uniform structure of the cortex may be disrupted by formation of aerenchyma when the root suffers water stress (Al-Najafi 1990) and the pathways of water movement remain doubtful (Clarkson 1993).

# (b) Movement as vapour across the air gap

Cowan & Milthorpe (1968) have derived an expression for the isothermal flux of water vapour across an air gap that allows for the retarding effect of the reverse flow of heat from the condensation site to the evaporation site. This thermal effect reduces the diffusive conductivity of the humid air by a factor of  $1/(1 + \epsilon D/K)$ , where D and K are the molecular diffusion coefficients in air of water vapour and heat, respectively, and  $\epsilon$  is the rate of increase of the latent heat content of saturated air with increase of sensible heat content. At  $20^{\circ}$ C, D/K = 1.18 and  $\epsilon = 2.1$ , making the factor 0.29. The flux of water in the vapour form is given by

$$f_{\rm v} = -k_{\rm v} \,\mathrm{d}\psi/\mathrm{d}x,$$

where the hydraulic conductivity of the vapour, ignoring thermal effects,  $k_{\rm v}=3.18\times 10^{-12}\,{\rm kg\,s\,m^{-3}}$  at 20°C (Campbell 1985, equation 9.7). Allowing for thermal effects, the effective conductivity equals  $0.92\times 10^{-12}\,{\rm kg\,s\,m^{-3}}$  at 20°C.

The inflow across the air gap can be calculated from the difference between the adjacent water potentials in soil and root and the distance between them,  $\delta$ , each term being a function of  $\theta$ :

$$I_{
m gap} = 2 k_{
m v} \int\limits_{ heta c}^{\pi} r_{
m i} (\psi_{
m r} - \psi_{
m r}'^{i}) / \delta \, {
m d} heta.$$

# 3. THE COMPUTER PROGRAM

The soil zone in figure 2 was divided radially into

seven intervals of width increasing successively by a factor of 1.26. It was also divided into 15 segments whose angle increased successively by a factor of 1.46. The angle of the first and smallest segment was  $\pi/200$  radians. The root zone was divided radially into seven equally spaced intervals, and into 15 segments whose angles corresponded to those of the soil zone according to equation (7).

The Gauss-Seidel iterative method (Smith 1978, p. 229) was used to solve equations (15) and (18). At the root-soil boundary the equation required to update the contact potential is nonlinear because it involves the soil hydraulic conductivity, which itself depends on the contact potential. The bisection algorithm (Vandergraft 1983, p. 268) was used to solve it. It was also necessary to update in turn the root shrinkage, the root radial nodal intervals, the root nodal angular intervals, and the size of the air gap between soil and root. After the first 20 iterations these quantities changed only slowly, and it was sufficient to update them at intervals of 50 iterations. A total of between 500 and 1000 iterations was usually required before satisfactory convergence was achieved. A single run with given input parameters took about 30 min on an Acorn Archimedes desktop computer (rated at 4 million instructions per second

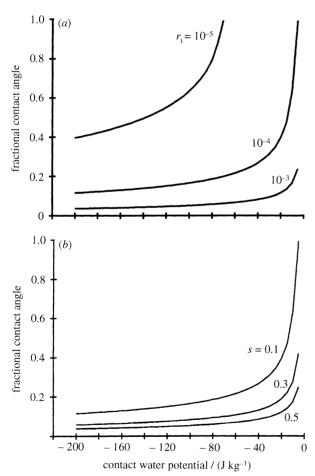


Figure 3. (a) The relation between the fractional contact angle and the contact water potential for roots of different radii (in metres) and shrinkage of 0.1. (b) The relation between the fractional contact angle and the contact water potential for a root of unshrunken radius  $10^{-4}\,\mathrm{m}$  and different degrees of shrinkage.

(MIPS)). The program in Basic V is available on request.

### 4. RESULTS

# (a) Contact angle effects

Figure 3a shows the relation between the fractional contact angle,  $\theta/\pi$ , and the water potential at the contact meniscus, for roots that have shrunk by 10%. The root radii are typical of a primary root, a secondary root, and a root hair. As the contact potential decreased, the fractional contact angle decreased rapidly as soon as full contact was lost. Coarser roots lost full contact at higher water potentials than finer ones since, in the coarser roots, the same contact meniscus width is attained at a smaller contact angle. Figure 3b shows the effect of shrinkage on a secondary root of radius  $10^{-4}$  m. As would be expected, at a given contact potential, increased shrinkage decreased the fractional contact angle.

Figure 4 shows the effect of the contact angle on the flow across the soil in isolation (with no flow across the

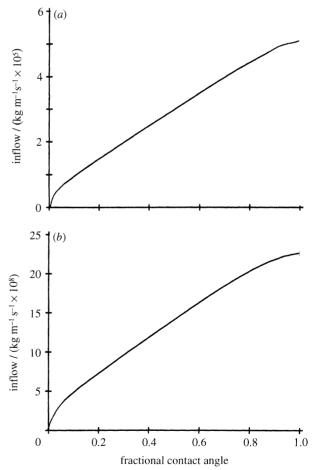


Figure 4. (a) The effect of the contact angle on the inflow across a soil between constant potentials at the outer radius and contact radius  $(r_{\rm o}=10^{-3}\,{\rm m},\ r_{\rm i}=0.4\times10^{-3}\,{\rm m},\ \psi_{\rm o}=-10\,{\rm J\,kg^{-1}},\ \psi_{\rm i}=-100\,{\rm J\,kg^{-1}}).$  (b) The effect of the contact angle on the inflow across the cortex of a root with constant potentials at the contact and the endodermis  $(r_{\rm o}'=10^{-4}\,{\rm m},\ r_{\rm endo}'=0.33\times10^{-4}\,{\rm m},\ \psi_{\rm i}=-100\,{\rm J\,kg^{-1}},\ \psi_{\rm endo}=-500\,{\rm J\,kg^{-1}}).$ 

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part of the inner soil boundary where the radial angle exceeds the contact angle) (figure 4a), and the root in isolation (figure 4b). Figure 4a shows that, for given water potentials at  $r_0$  and  $r_i$  – and therefore a constant range of soil hydraulic conductivity - increased shrinkage, leading to a decreased fractional contact angle, reduced the inflow, although not proportionately; as the fractional contact angle approached zero the inflow approached zero asymptotically. Figure 4b shows a similar effect of contact angle on flow across the root cortex for given water potentials at  $r_i'$  and  $r'_{\text{endo}}$ . To the extent that the resistance across the root cortex lies in the endodermis, the effect of the contact angle on the root inflow should decrease.

Lines of equal water potential in the soil and in the root cortex are shown in figure 5a,b. In figure 5a the very steep potential gradients near the contact zone are apparent. Figure 5b is an enlarged view of the root, which is shown as a filled circle in figure 5a. The potential decreases rapidly away from the contact, and it will be noted that the potential in most of the cortex is less than  $-1400 \,\mathrm{J\,kg^{-1}}$ .

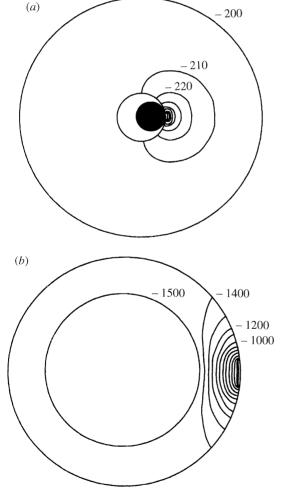


Figure 5. (a) Lines of equal water potential in a soil in contact with a shrunken root. Fractional contact angle with soil = 0.04; interval between lines =  $10 \,\mathrm{J\,kg^{-1}}$ ; contact potential =  $-290 \,\mathrm{J\,kg^{-1}}$ . (b) Lines of equal water potential in the root in contact with the siol in (a). Fractional contact angle with the root = 0.068; interval between lines =  $100 \text{ J kg}^{-1}$ .

### (b) Sensitivity to parameter values

Figure 6 is a sensitivity diagram showing the effects of changes in important parameters, varied singly, on the inflow of water to a shrunken secondary root in a standard root-soil combination. The values of these parameters in the standard were as follows.  $r_{\rm i}=10^{-4}\,{\rm m}; \;\; r_{\rm endo}=0.4\times 10^{-4}\,{\rm m}; \;\; r_{\rm o}=5\times 10^{-4}\,{\rm m}; \;\; s=0.00059\psi-0.207\times 10^{-6}\psi^2, \;\; {\rm where} \;\; \psi \;\; {\rm is} \;\; {\rm the} \;\; {\rm volume-averaged} \;\; {\rm roots} \;\; {\rm (Al \; Najafi \; 1990)}; \; {\rm this \;\; formula} \;\; {\rm the} \;\; {\rm volume \; averaged} \;\; {\rm roots} \;\; {\rm (Al \; Najafi \; 1990)}; \; {\rm this \;\; formula} \;\; {\rm the} \;\; {\rm volume \; averaged} \;\; {\rm volume$ gives a maximum value of s = 0.42 at  $\psi =$  $-1500 \,\mathrm{J\,kg^{-1}}$ );  $k_c = 10^{-10} \,\mathrm{kg\,m^{-3}}\,\mathrm{s}$ . From data summarized by Newman (1974), Steudle (1989) and de Willigen & Van Noordwijk (1987), the hydraulic conductivity of roots from their surface to the xylem is in the range  $(0.3-20) \times 10^{-10} \,\mathrm{kg} \,\mathrm{m}^{-3} \,\mathrm{s}$   $(1 \,\mathrm{kg} \,\mathrm{m}^{-3} \,\mathrm{s} \equiv$  $\begin{array}{ll} 10^3\,\mathrm{cm^2\,s^{-1}\,bar^{-1}}); & \psi_\mathrm{endo} = -1000\,\mathrm{J\,kg^{-1}}; & \psi_\mathrm{o} = \\ -100\,\mathrm{J\,kg^{-1}}. & \mathrm{Regarding\ soil\ texture,\ the\ ratio\ of} \end{array}$ (2.0-0.05 mm): silt (0.05-0.002 mm): clay  $(< 0.002 \,\mathrm{mm}) = 0.4 : 0.4 : 0.2$ . For a soil of this texture, n (equation (12)) = 2.44, and  $k_{\text{sat}} = 2.29 \times$  $10^{-4} \text{ kg m}^{-3} \text{ s.}$ 

In the standard run the water potential at the contact was 110 J kg<sup>-1</sup>, which is closer to  $\psi_0$  than to  $\psi_{\rm endo}$ , showing that the main resistance lay in the root. As can be seen from figure 5b, the water potential in most of the cortical tissue is close to the water potential at the endodermis, which is  $-1000 \,\mathrm{J\,kg^{-1}}$ in the standard root. Consequently, the root shrinkage was 0.36, and for this shrinkage the fractional contact angle was 0.069. Varying the parameters had the following effects.

# (i) Root radius

Increasing  $r_i$  alters three factors. It increases the

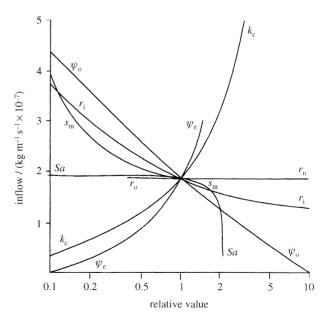


Figure 6. Sensitivity of inflow to controlling root and soil parameters. The values of the parameters in the standard root and soil were as follows:  $r_{\rm i} = 10^{-4} \, {\rm m}$ ;  $r_{\rm endo}' = 0.4 \times 10^{-4} \, {\rm m}$ ;  $r_{\rm o} = 5 \times 10^{-4} \, {\rm m}$ ;  $s_{\rm m} = 0.41$ ;  $\psi_{\rm endo} = -1000 \, {\rm J \, kg^{-1}}$ ;  $\psi_{\rm o} = -100 \, {\rm J \, kg^{-1}}$ ;  $k_{\rm c} = 10^{-10} \, {\rm kg \, m^{-3}} \, {\rm s}$ ; Sa = 0.4 (constant silt/ clay = 2).

Table 1. Effect of vapour transfer across air gap

water potential $(\psi_{\rm o})$ in bulk soil/J kg $^{-1}$	fractional contact angle	inflow $(kg m^{-1} s^{-1}) \times 10^{-7}$			
		without vapour transfer	with vapour transfer	increase	increase (%)
-50	0.101	2.25	2.37	0.12	5.1
-100	0.069	1.72	1.86	0.14	7.5
-200	0.046	1.20	1.35	0.15	11
-500	0.027	0.42	0.51	0.09	17

Values of all parameters except  $\psi_0$  are the same as for the standard root and soil.

perimeter and thus the surface available for uptake; it increases the path length between the root surface and the endodermis; and it decreases the fractional contact angle. The first two factors have opposite effects on the inflow and should cancel, but the decreasing fractional contact angle causes a steep decrease in the inflow in conditions when the main resistance is in the cortex (including the endodermis), as in the standard run.

# (ii) Rooting density

A change in  $r_0$  had little effect on the inflow, since the main resistance lay in the cortex, and the main contribution to the soil resistance was very close to the root surface where the hydraulic conductivity tended to decline sharply.

# (iii) Hydraulic conductivity of the cortex

Increasing the hydraulic conductivity of the cortex greatly increased the inflow, since under the standard conditions this was the main resistance.

# (iv) Soil texture

Increasing the hydraulic conductivity of the soil by decreasing its proportion of sand had little effect, since the main resistance was in the cortex. However, when the proportion of sand was increased to more than 0.8, while keeping the ratio of silt to clay constant at 2.0, the hydraulic conductivity of the soil decreased rapidly because of the increase in the value of the index n in equation (12). Eventually the soil resistance dominated the inflow, which declined steeply.

# (v) Effect of the root's capacity to shrink

The measure of a root's capacity to shrink at any given water potential is  $s_m$ . The value of  $s_m$  for the standard root is set at 1.0 in figure 6. If, at a given potential, a root shrinks by half as much as the standard root at the same potential, its  $s_{\rm m}$  value would be 0.5. The variation of inflow with  $s_m$  shows the effect of the air gap. If the root was able to shrink by only one tenth as much as the standard root, the inflow would have increased by a factor of 1.88 because the fractional contact angle would have increased from 0.069 to 0.31. If the root did not shrink at all (fractional contact angle = 1), the inflow would have increased by a factor of 3.17. Thus the

consequence of root shrinkage was to reduce the inflow under the standard conditions by a factor of about three.

# (c) Contribution of vapour transfer

Table 1 shows the effect of assuming that no water can cross the air gap as vapour. Vapour transfer increased the inflow by a small absolute amount, which, in dry soil with a low total inflow, would have been a useful contribution.

### 5. DISCUSSION

This treatment has been confined to roots that have forced their way through moist homogeneous soil, so that initially they are 'in contact with' the soil all round their perimeter, in the sense that the root-soil interface is representative of the range of pore sizes found in an average cross-section through the soil. Consequently, the soil hydraulic conductivity should not show any discontinuity until the actual root surface is reached. When the soil dries and the root shrinks the model assumes that the root will retain some contact with the soil by surface tension, and will not lose contact entirely. How far this model is true of roots in moist soil in general is uncertain. Sanders (1971), from visual observation of apple tree roots growing down a glass-fronted soil section, concluded that over 50% of the roots did not make good contact. Undoubtedly the proportion will vary with the soil and the type and age of the roots. The effects of the range of possible contact geometries when the initial contact is imperfect, due to worm holes, cracks and suchlike, and the extent to which root hairs or mycorrhizas can compensate, remain to be explored.

Except in dry sandy soil, the main resistance to water inflow lies in the root tissues. The model assumes the hydraulic conductivity of the root cortex, including the hypodermis and endodermis, is uniform. When quantitative data about the conductivities of different parts of the root become available, the model could be extended to include it fairly easily.

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