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A model for water uptake by plant roots

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Abstract

We present a model for water uptake by plant roots from unsaturated soil. The model includes the simultaneous flow of water inside the root network and in the soil. It is constructed by considering first the water uptake by a single root, and then using the parameterized results thereby obtained to build a model for water uptake by the developing root network. We focus our model on annual plants, in particular the model will be applicable to commercial monocultures like maize, wheat, etc. The model is solved numerically, and the results are compared with approximate analytic solutions. The model predicts that as a result of water uptake by plant roots, dry and wet zones will develop in the soil. The wet zone is located near the surface of the soil and the depth of it is determined by a balance between rainfall and the rate of water uptake. The dry zone develops directly beneath the wet zone because the influence of the rainfall at the soil surface does not reach this region, due to the nonlinear nature of the water flow in the partially saturated soil. We develop approximate analytic expressions for the depth of the wet zone and discuss briefly its ecological significance for the plant. Using this model we also address the question of where water uptake sites are concentrated in the root system. The model indicates that the regions near the base of the root system (i.e. close to the ground surface) and near the root tips will take up more water than the middle region of the root system, again due to the highly nonlinear nature of water flow in the soil.

Keywords: Water movement; Soil; Plant water uptake; Mathematical model

1. Introduction

An adequate supply of water is one of the most important resources required for plant growth and function. Due to the undoubted importance of water conditions for plant growth, much effort has been expended on trying to quantify the amount of water a plant requires. In normal circumstances, the amount of water within a plant is set by a balance between the water uptake through the roots and the rate of transpiration through the leaves. If the water saturation, i.e. the volume of water per unit volume of soil, is below a level termed the 'permanent wilting point', then uptake ceases, and the plant will wilt (Tinker and Nye, 2000, p. 27). If however the rainfall is very high then the plant roots can become waterlogged. If waterlogging persists for long periods of time then the roots can start rotting and the plant will eventually die.

Clearly, the rate of water uptake by plants and the factors which control this, are of fundamental interest from an agricultural point of view. In addition it seems inevitable that the onset of global warming will lead to greately altered patterns of rainfall. Therefore, understanding how different plant species will be affected by different rainfall conditions is necessary to help to predict the changes in ecosystems due to global warming. Whilst much can be learned from empirical studies, developing our theoretical understanding of water uptake by plants is surely to be desired. This is even more true in an age when genetic modification gives us some hope of "engineering" plants to suit particular rainfall patterns.

The problem of modelling water uptake by plant roots has previously been dealt with by numerous authors (for example, Davis, 1940; Gardner, 1964; Landsberg and Fowkes, 1978; Rowse et al., 1978; Molz, 1981; Iwata et al., 1988; Lafolie et al., 1991; Bruckler et al., 1991; Chen and Lieth, 1992; Clausnitzer and Hopmans, 1994; Nye, 1994; Thornley, 1996; Bengough, 1997; Doussan et al., 1998a; Wu et al., 1999) using two alternative approaches. One approach, of which Doussan et al. (1998b) is the most recent development, is to model water flow inside the root branching structure,

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assuming that the soil is and remains fully saturated. The other approach, of which Clausnitzer and Hopmans (1994) is the most recent representative, calculates the changes in soil moisture conditions assuming that the pressure inside the root branching structure is constant and uniform. There have been no models that link the flow inside the root branching structure to the flow in the soil. In this paper we consider simultaneous flow inside the roots and in the soil, and model the water uptake by the developing root system. We focus our attention on annual plants, such as maize, important to agriculture. We consider the development of the root system to be pre-determined and not dependent on soil moisture conditions. Although this is a simplification, we set out in the discussion section how this assumption could be relaxed once more data concerning this subject becomes available.

In this paper we will assume that the soil is homogenous. Thus, we are neglecting the soil cracking and the fluid channels that might have formed in the soil as a result of climate change or organisms, such as worms cohabiting the soil with plants. Clearly, the model set out in this paper will be closer to the conditions in carefully controlled laboratory pot experiments. We will also only calculate the variations in the soil moisture conditions as a function of soil depth, thus neglecting the horizontal variation in water transport. We believe this assumption to be applicable for a situation of field crop, i.e. the situation where the root length density does not vary horizontally a great deal. Additional mathematical justifications for this assumption are given in the text and in appendices. The assumption about vertical variation in soil moisture conditions can be relaxed if the practical experimental situation requires it. One can indeed build a full three-dimensional model. This paper should be viewed as introducing the mathematical methodology for dealing with branched root system water uptake and techniques for calculating simultaneous water movement in the soil and inside the root system. However, as this paper is already long, we have chosen to limit ourselves to the one-dimensional model only.

Our model in this paper consists of coupled partial differential equations: one for root internal pressure and one for the soil water saturation. We will derive analytical and numerical approximations for the solution to this problem.

2. Water movement in unsaturated soil

In describing soil water movement at the macroscale, we conceive of the root system as being homogeneous at the microscale, so that we can define quantities such as root density and water uptake per unit soil volume. The equation for conservation of water in the soil is thus

$$\phi \frac{\partial S}{\partial t} + \nabla \cdot \mathbf{u} = -F_w, \qquad (2.1)$$

where ϕ is the (constant) porosity of the soil, S is the relative water saturation in the soil ($S = \phi_l/\phi$, where ϕ_l is the volumetric water fraction), $\mathbf{u}$ is the volume flux of water and F_w is the uptake of water by plant roots (volume per unit time per unit volume of soil).

The volume flux of water is given by Darcy's law, i.e.

$$\mathbf{u} = -\frac{k}{\mu}[\nabla p - \rho g \hat{\mathbf{k}}], \qquad (2.2)$$

where k is the soil permeability, μ is the viscosity of water, p is the water pressure in the soil, ρ is the density of water and g is the gravitational acceleration, and $\hat{\mathbf{k}}$ is the unit vector downwards. A reasonable representation of the soil permeability in terms of relative water saturation is given by the following formula of Van Genuchten (1980):

$$k = k_s K(S) = k_s S^{1/2}[1 - (1 - S^{1/m})^m]^2, \quad 0 < m < 1, \qquad (2.3)$$

where k_s is the water permeability in fully saturated soil, $K(S)$ is the experimentally determined function showing the reduction in water mobility in the soil due to the reduction in relative saturation. It originates from the fact that as the relative water saturation decreases, the capillary and surface tension forces will become more important resulting in lower mobility of water in the system (Van Genuchten, 1980).

Similarly the water pressure in the soil pores can also be linked to the relative water saturation via the suction characteristic (Van Genuchten, 1980; see also Fig. 1), i.e.

$$p_a - p = p_c f(S), \quad f(S) = (S^{-1/m} - 1)^{1-m}, \qquad (2.4)$$

where p_a is atmospheric pressure, and p_c is a characteristic suction pressure determined from experimental data. It is common to take $p_a = 0$ (i.e. measure *gauge* pressures relative to atmospheric pressure), and we shall follow this practice. Parameter m is experimentally determined for different soils (Van Genuchten, 1980).

The mass conservation equation together with Darcy's law is generally known as Richards equation for water flow in the soil. When written in terms of relative water saturation only, it is given by

$$\phi \frac{\partial S}{\partial t} = \nabla \cdot [D_0 D(S) \nabla S - K_s K(S) \hat{\mathbf{k}}] - F_w, \qquad (2.5)$$

where the water diffusivity in the soil is $D_0 D(S) = (k/\mu)|\partial p/\partial S|$, and

$$D_0 = \frac{p_c k_s}{\mu}\left(\frac{1-m}{m}\right),$$
$$D(S) = S^{1/2-1/m}[(1 - S^{1/m})^{-m} + (1 - S^{1/m})^m - 2]. \qquad (2.6)$$

In the term for conduction of water due to gravity, the (saturated) hydraulic conductivity K_s is given by

$$K_s = \frac{\rho g k_s}{\mu}. \tag{2.7}$$

Table 1 gives values of the parameters D_0, p_c and m for various different soil types, and Table 2 gives other parameters used here and later in the model. Fig. 1 shows typical forms for the relative permeability, suction and diffusivity as a function of S.

2.1. Boundary condition at the surface of the soil

The boundary condition at the soil surface describes the amount of water flowing into the soil due to rainfall or watering. Thus, we take the boundary condition at the surface of the soil to be given by

$$-D_0 D(S)\frac{\partial S}{\partial z} + K_s K(S) = q_s \quad \text{at } z = 0, \tag{2.8}$$

where q_s is the volume flux of water per unit soil surface area per unit time, i.e. rate of rainfall.

If the rainfall is very large (larger than the saturated hydraulic conductivity), then surface ponding will occur, and the above boundary condition is replaced by

$$S = 1 \quad \text{at } z = 0, \tag{2.9}$$

which in turn implies that the water movement from the surface will be determined by the pressure condition via Darcy's law (Celia et al., 1990).

In this article we will not discuss surface ponding problems and thus only deal with the boundary condition given by Eq. (2.8).

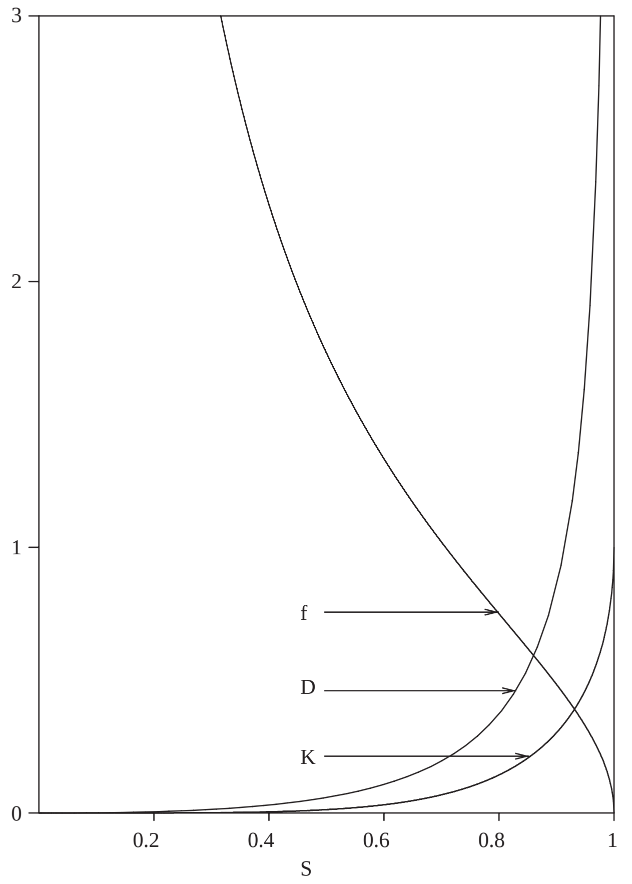

Fig. 1. Graphs of the saturation (S) dependence of hydraulic conductivity (K), suction characteristic (f), and soil water diffusivity (D) given by (2.3), (2.4) and (2.6), respectively, when $m = 0.5$.

2.2. Boundary condition at the base of the soil layer

The boundary condition at the base of the soil will generally depend on the site considered. If the water table is supposed to be at a fixed level $z = l_w$, then we should prescribe $S = 1$ at $z = l_w$. This is the case of efficient drainage, and may be appropriate in agriculture. On the other hand, it is more appropriate for soil

Table 2
Miscellaneous typical parameter values

Parameter	Definition	Value
ρ	Density of water	2.6×10^3 kg m^{-3}
g	Gravitational acceleration	9.8 m s^{-2}
q_s	Volume flux of water per unit soil surface area	1 m yr^{-1}
$2\pi a k_r$	Overall radial conductivity of water per unit length of root	7.85×10^{-10} m^2 s^{-1} MPa^{-1}
$\lvert P\rvert$	Absolute value of pressure at the base of the root	1 MPa
a	Root radius	5×10^{-4} m
L_1	Max. length of 1st order root	8 cm
L	Max. length of zero order root	50 cm
l_a	Length of apical non-branching zone	15 cm
l_n	Interbranch distance	0.7 cm
$\cos\beta$	Cosine of the branching angle between zero and 1st order roots	0.5

Table 1
Values for soil parameters (Van Genuchten, 1980)

Parameter	ϕ	D_0 ($\times 10^{-6}$ m^2 s^{-1})	K_s (cm day^{-1})	p_c ($\times 10^5$ Pa)	m	m
Hygiene Sandstone	0.250	0.67	108.0	0.124	0.90	10.5
Touchet Silt Loam G.E.3	0.469	4.37	303.0	0.196	0.86	7.09
Silt Loam G.E.3	0.396	0.50	4.96	0.232	0.51	2.06
Guelph Loam (drying)	0.520	1.17	31.6	0.085	0.51	2.03
Guelph Loam (wetting)	0.434	—	—	0.049	0.64	2.76
Beit Netofa Clay	0.446	0.14	0.082	0.645	0.15	1.17

overlying an aquitard, and also in laboratory pot experiments, to prescribe zero water flux at the base. We make the latter choice here, and thus prescribe

$$-D_0 D(S)\frac{\partial S}{\partial z} + K_s K(S) = 0 \quad \text{at } z = l_w. \tag{2.10}$$

Clearly, the depth of aquitard depends on the specific geological site considered and it can vary considerably. In this paper we take l_w to be order of 1 m, as this would be appropriate for analysing data from pot experiments in a container of ≈ 1 m deep (Gardner, 1964).

It is clear that the choice of the boundary condition will quantitatively influence the outcome of the model and thus when using this model for interpreting specific physical situations in the field care should be taken to define the right one. However, we believe that our choice of zero flux boundary condition will not give qualitatively different results from the full saturation boundary condition in the case where the full saturation level is deep in the soil. The results of course change when the level of full saturation is very near the soil surface. The extreme example of this is waterlogged soil leading to root death.

3. Water uptake by a single cylindrical root

In the first part of this section we describe the model for the water flow within the single cylindrical root. The second part of this section will deal with estimating the water saturation profile around a single cylindrical root. We concentrate our analysis on the differences between roots of different sizes so as to be able to extend our modelling in the following section to the root branching structure scale.

3.1. Water pressure inside the single cylindrical root

Water flows from the roots to the leaves and shoots along the xylem tubes located in the central part of the root (see Fig. 2). Xylem vessels are tube-like structures formed of non-living cells which provide mechanical support to the roots and stems, and transport the water and nutrient ions. In the case of agricultural plants like maize and beans, the xylem tubes can be divided into three different size categories: protoxylem, early metaxylem and late metaxylem tubes (Steudle and Peterson, 1998). Protoxylem tubes have the smallest radius, but they are open for most of the root length.[1] Early metaxylem tubes are larger in radius than protoxylem tubes, but they are open and functional only after a short distance from the tip of the root. Late metaxylem tubes are the largest in radius and they are thought to be open and functional only at a distance from the root tip equal to the apical non-branching zone. The exact size of xylem tubes is strongly dependent on the root branch order. In Table 3 we present morphological data on xylem tubes of maize plant based on articles by Frensch and Steudle (1989), Weerathaworn et al. (1992), and Varney et al. (1991).

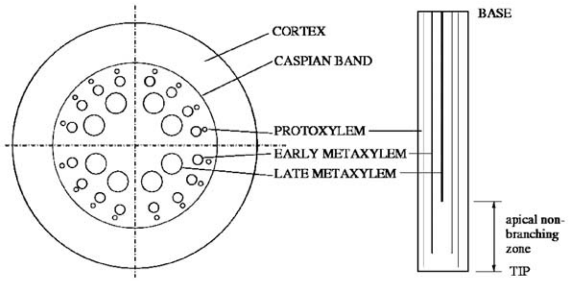

Fig. 2. Root cross-sectional structure with all three types of xylems, after Steudle and Peterson (1998).

Water flow along the xylem tubes has been shown to be very well characterized by Poiseuille law for water flow in a cylindrical tube (Frensch and Steudle, 1989). Thus, we take the axial flux of water (downwards) inside the root to be given by the sum of all the fluxes in each open and functional xylem tube, i.e. we take

$$q_z = -k_z\left[\frac{p_r}{z} - \rho g\right], \tag{3.1}$$

where p_r is the root fluid pressure inside the xylem tubes, z is the position along the root, and the quantity

$$k_z = \sum_i \frac{\pi n_i R_i^4}{8\mu} \tag{3.2}$$

is known in the soil science literature as the root axial conductivity; R_i is the radius of the xylem vessel, n_i is the number of open functional xylem vessels with radius R_i per cross section of the root, and i is an index for different radius categories. The units of q_z are m^3 s^{-1}, and those of k_z are m^4 Pa^{-1} s^{-1}. The form of k_z has been successfully validated for various different root classes (see Table 3). We note that since, in the maize zero order roots, the late metaxylems are not open near the apical non-branching zone, then the axial conductivity in this zone is much lower than in the main branching region and in basal non-branching zone, i.e. $k_{z,0}[E] < k_{z,0}[E+L]$ (see Table 3).

Water movement from the soil across the root cortex (see Fig. 2) to the xylem tubes is much less well understood. In general, water is thought to move inside the root cortical tissues along at least two separate pathways: the apoplasmic and symplasmic pathways (Steudle and Peterson, 1998). In the case of the apoplasmic (sometimes also known as the passive) pathway, water flows between the cells in response to a pressure gradient between the xylem vessels and soil. In the case of the symplasmic pathway the water moves inside the cell and water movement from cell to cell

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[1] By open xylem tube we mean open mature xylem tube that can carry water flow.

Table 3
Properties of xylem elements of zero and first order roots

Order i	$d = 2a$ (μm)	d_E (μm)	n_E	d_L (μm)	n_L	$k_{z,i}$ $[E]$ ($\mathrm{m^4\ s^{-1}\ MPa^{-1}}$)	$k_{z,i}$ $[E+L]$ ($\mathrm{m^4\ s^{-1}\ MPa^{-1}}$)	Ref.
0	1000	27.4	16.2	92.3	6.6	1.875×10^{-10}	1.198×10^{-8}	(a), (b)
1	200	5	3	—	—	4.6×10^{-14}	4.6×10^{-14}	(c)

a is the radius of the root, i.e. $d = 2a$ is the diameter of the root, d_E is the diameter of early metaxylem elements, n_E is the number of early metaxylem elements per cross-sectional area, d_L is the diameter of late metaxylem elements, n_L is the number of late metaxylem elements per cross-sectional area, $k_{z,i}$ $[E]$ is the hydraulic conductivity calculated using Poiseuille's law, assuming that only early metaxylem elements are functioning, and $k_{z,i}$ $[E+L]$ is the hydraulic conductivity calculated assuming that early and late metaxylem elements are all functioning. References are: (a) Frensch and Steudle (1989), (b) Weerathaworn et al. (1992) and (c) Varney et al. (1991).

occurs via apoplast, plasmodesmata or cytoplasm. The symplasmic pathway requires membrane transport proteins to move water from extracellular space into the cells and because of that this pathway is often called the active pathway.

It has been very difficult to quantify the relative importance of one pathway over the other, and therefore most theoretical work has been concerned with determining the parameter for water diffusivity in the cortical tissues applicable for passive pathway. The most commonly used model has been the circuit analog model (Molz, 1981). Using this model Molz determined the diffusivity of water in the root cortical tissues to be $D = 1.26 \times 10^{-6}\ \mathrm{m^2\ s^{-1}}$. Various authors have also measured the radial fluxes of water through root cortical tissues (North and Nobel, 1996) and those measurements have been found consistent with the cortical tissue water diffusivity calculations. In this paper we will consider only the passive pathway of the water for the following reasons. The inclusion of the active pathway would require us to introduce the chemical potentials inside the plant roots. These potentials primarily rise because of the nutrient uptake by the plant roots. However, in the current paper we will not introduce the nutrient uptake and its interplay with water uptake into our model as we believe we can obtain valuable knowledge about the plant-soil continuum by studying the passive pathway, i.e. pressure driven pathway, only. This is in agreement with a view held by Steudle and Peterson (1998). They find that the water movement through the root system is primarily passive, i.e. water passes through roots without plant actively dedicating its resources into transporting it. This is in comparison to nutrient uptake that is generally thought to be an active process. Steudle and Peterson (1998) also note that even though different pathways of water movement through the root system might be important in different regions of the root system, the overall radial hydraulic conductivity of the root tissues might not necessarily be altered as the down-regulation of one of the pathways is compensated by the up-regulation of the other. Thus, even though we acknowledge that the nutrient uptake and resulting osmotic pressure inside the root system can be important for the water uptake by plant roots we will neglect this in the current paper. The combined models for simultaneous water and nutrient uptake will be presented in a further publication.

Considering the passive radial water pathway only we take the radial flux of water q_r to be given by (Landsberg and Fowkes, 1978)

$$q_r = k_r(p - p_r), \tag{3.3}$$

where k_r is the root radial water conductivity parameter; the units of q_r are $\mathrm{m\ s^{-1}}$, so those of k_r are $\mathrm{m\ Pa^{-1}\ s^{-1}}$. One can generally assume that the thickness of root cortex tissues is proportional to the radius of the root a. This argument is based on the root water diffusivity model discussed in Molz (1981). Based on this the flux of water across the cortex is inversely proportional to Δa, the thickness of the cortex. Thus, we assume in this paper that the thickness of root cortex Δa is the main component determining the root radial water conductivity k_r and that Δa is proportional to the root radius a. This implies that $2\pi a k_r$ is constant for roots of different radius.

In the literature we can find several reports that deal with the variations in root radial conductivity with root age, environmental conditions in the soil, etc. (Steudle and Peterson, 1998; Javot and Maurel, 2002; Henzler et al., 1999; Jackson et al., 2000). These studies are primarily performed to consider a single water pathway level. However, even though one pathway might be inhibited depending on root age, etc., the other pathways are thought to be able to compensate this loss and thus the overall radial hydraulic conductivity of the plant root might not change considerably (Steudle and Peterson, 1998). We acknowledge that such variations in root radial conductivity might be important for micro-scale water movements in the soil and inside the roots, however we will neglect such variations in this paper as inclusion of such effects is likely to make only a small quantitative difference to the results since the variation in overall radial conductivity is small (Steudle and Peterson, 1998), i.e. much less than three orders of magnitude in comparison to the axial conductivity. However, we will discuss in the conclusion section of this paper how the spatial variations in root radial hydraulic conductivity could be incorporated into the model presented in this paper so that with a detailed quantitative data of the spatial dependence of the hydraulic conductivity, the model could still be used.

The conservation of incompressible water inside a single cylindrical plant root is given by the balance between the axial and radial fluxes, (3.1) and (3.3) respectively, i.e.

$$2\pi a k_r (p - p_r) = -k_z \frac{\partial^2 p_r}{\partial z^2}. \tag{3.4}$$

We suppose that the structural properties of the root tip preclude an axial flux there, thus

$$\frac{\partial p_r}{\partial z} - \rho g = 0 \quad \text{at } z = L. \tag{3.5}$$

At the base of the root we prescribe the driving pressure:

$$p_r = P \quad \text{at } z = 0. \tag{3.6}$$

Note that P, like all the pressures, is negative (relative to atmospheric pressure). During the day time when plants breathe $P \neq 0$ and during the night time when the stromata are closed and thus no breathing takes place $P \approx 0$. Thus, in general, the driving pressure P is a function of time. Eqs. (3.4)–(3.6) were first used by Landsberg and Fowkes (1978) to calculate the root internal pressure p_r for a given soil water pressure p profile. However, in their case the water uptake did not influence the moisture conditions in the soil.

By solving the above Eqs. (3.4)–(3.6) we find that during the day when $P \neq 0$ the pressure inside thick roots, like maize zero order roots for example, is constant and approximately equal to the pressure at the base of the root, i.e. $p_r(z) \approx P$ (see Appendix A for mathematical derivation). This is because in thick long roots the limiting factor for water uptake is the radial pathway, since the water movement along the root is easy because of the large size and number of open mature xylem vessels, i.e. $k_z \gg 2\pi a k_r L^2$, where L is the length of the root. Thus, the amount of water taken up by those large roots is fully determined by the water pressure variations in the soil. However, the pressure inside small thin roots, such as first order lateral branches of maize plant, is for most part equal to the pressure in the soil apart from the small region near the base of the roots where the driving pressure P has an influence. Thus, the pressure profile inside such root is given by $p_r(z) = p(z) - [P - p(0)]\mathrm{e}^{-\kappa z}$, where $\kappa^2 = 2\pi a k_r L^2 / k_z \gg 1$ is the ratio of axial and radial conductivity of the root and L is the length of the root (see Appendix A). Thus, in small thin roots, the limiting mechanism for water movement inside the root is the low axial conductivity due to the small diameter of mature open xylem vessels, i.e. $k_z \ll 2\pi a k_r L^2$ (see Appendix A for mathematics).

At night when the plant is not breathing, $P \approx 0$, there will not be any water uptake. However, depending on the water pressure in the soil the plant can start bleeding out water. In the case of large thick roots, the root internal pressure is $p_r(z) \approx \rho g z / L$ and the bleeding can happen anywhere along the root, but the most likely site will be near the tip, since the pressure head inside the root is highest there (see Appendix A). In the case of small thin roots, like maize first order roots, bleeding out water can only happen in the very narrow region near the base of the roots (see Appendix A) since the low axial conductivity in comparison to the high radial conductivity causes the pressure inside the roots to equilibrate rapidly with the pressure outside in the soil. Thus, there is no pressure head build up in the small thin roots (see Appendix A). The bleeding can occur in the region near the base where the boundary condition $p = 0$ at $z = 0$ is still felt. However, this region is very small.

In conclusion to this section we would like to draw attention to the fact that most of the "action", i.e. water uptake or bleeding out, in the first order lateral branches of the maize roots occurs in the very small region near the base of those roots, i.e. near the branch point. The width of this "active" region is approximately of order ≈ 0.7 cm. This fact will enable us in Section 4 to handle the water uptake by the root branching system with greater ease. However before we proceed to do that, we need to discuss the water uptake influence on the water saturation profile in the soil surrounding cylindrical roots.

3.2. *Water saturation profile around a single root*

In the previous section we developed a model for the root internal water pressure p_r in terms of the soil water pressure p. Now we will discuss the second half of the problem, the flow of water in the soil. As described previously, water movement in the soil is described by the Richards equation (2.5) for unsaturated soil. We suppose that when looking at a small section of a root, the root can be considered as a straight cylinder.

Since there are many roots present in the soil we calculate the average distance between the roots based on average root radius and average root length density per unit volume of soil. On the macroscale it would seem reasonable to expect that uptake and saturation could be treated using a root density. However, it could be that on the microscale, i.e. the inter-root distance scale, there is a strong spatial variation in the water saturation. This would influence the water uptake calculation on a root system scale. Thus, the aim of this section is to find out if such microscale variations in water saturation can occur, and if they can what would be the impact on the way we model the macroscale behaviour of the plant–soil system. Thus, we approximate the presence of other roots in the soil by using the measure of average distance between the roots a_{int} and use this as a position for reflection boundary (zero flux boundary) around a single cylindrical root.

We will also ignore the effect of gravity because of the small length scale which is appropriate, i.e. we are looking at a very small section along the cylindrical root so that the gravity induced changes in the root internal pressure and in the water saturation in the soil are negligible.

The model for water uptake in cylindrical radial coordinates is then given by

$$\phi \frac{\partial S}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(D_0 D(S) r \frac{\partial S}{\partial r}\right) \tag{3.7}$$

with boundary conditions

$$D_0 D(S)\frac{\partial S}{\partial r} = k_r[p(S) - p_r] \quad \text{at } r = a,$$
$$\frac{\partial S}{\partial r} = 0 \quad \text{at } r = a_{int}, \tag{3.8}$$

where

$$p(S) = -p_c(S^{-1/m} - 1)^{1-m} \tag{3.9}$$

is the van Genuchten suction-characteristic function (2.4), a is the radius of the root, a_{int} is a measure of inter-branch distance, k_r is the root radial conductivity, and p_r is the root internal pressure, $P \leqslant p_r \leqslant p(S)$.

Non-dimensionalizing this model with $r \sim a$, $t \sim \phi a^2/D_0$ and $p_r \sim |P|$ we obtain the following dimensionless equation:

$$\frac{\partial S}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left[r D(S)\frac{\partial S}{\partial r}\right] \tag{3.10}$$

with dimensionless boundary conditions

$$D(S)\frac{\partial S}{\partial r} = \lambda[-\varepsilon_w f(S) - p_r] \quad \text{at } r = 1,$$
$$\frac{\partial S}{\partial r} = 0 \quad \text{at } r = a_{int}/a, \tag{3.11}$$

where

$$\lambda = k_r a|P|/D_0 \tag{3.12}$$

is the dimensionless water uptake parameter calculated using the scale for water pressure $|P|$ inside the plant root, i.e. it shows the relative importance of water uptake in comparison to the water mobility in the soil. The other parameter

$$\varepsilon_w = p_c/|P| \tag{3.13}$$

is a dimensionless van Genuchten parameter showing the importance of capillary suction pressure in comparison to the root internal pressure. The dimensionless suction characteristic $f(S)$ is given by Eq. (2.4).

The typical soil parameters are shown in Table 1 and typical values for the root radial conductivity, etc. are shown in Table 2. For Silt Loam G.E.3 we find that the dimensionless water uptake parameters are $\lambda \approx 2.5 \times 10^{-4}$ and $\varepsilon_w \approx 2.32 \times 10^{-2}$. Since $\lambda \ll 1$ the root surface flux $\partial S/\partial r|_{r=1} \ll 1$ for all values of root surface water saturation.

For values $\phi \sim 0.4$, $a \sim 5 \times 10^{-4}$ m, $D_0 \sim 10^{-6}$ m^2 s^{-1}, the diffusive time scale $\phi a^2/D_0$ is very small, about 0.1 s, compared with a seasonal plant growth period of four months, or 10^7 s. The water diffusive time-scale calculated based on the inter-root distance is 10 s ($a_{int}/a \sim 10$) and the diffusive time-scale based on the maximum root length is about a minute when the soil is fully saturated. Thus, the soil water movement time-scales are mostly much shorter than the plant growth time-scale, and time-scales related to environmental changes that occur over days, weeks and months. Even a rapid rainfall event is still going to be on a longer time-scale than the diffusive time-scale of water around a single root. Thus, on this longer time-scale of interest, a diffusive quasi-equilibrium between sub-branches is reached in which, since λ is very small, the saturation profile surrounding the roots is essentially flat. In computing the macroscopic water uptake by the plant root system, we can therefore simply use the expression for the flux at the root in Eq. (3.8) multiplied by the root surface area per unit volume, where S can be taken as the local average saturation in the soil.

We thus have the dimensional expression for the soil water uptake in Eq. (2.1),

$$F_w = 2\pi a l_d k_r[-p_c f(S) - p_r], \tag{3.14}$$

where l_d is the root length density [cm of roots per cm^3 of soil], and we have

$$l_d \sim [\pi(a_{int} - a)^2]^{-1} \approx [\pi a_{int}^2]^{-1}. \tag{3.15}$$

This applies for roots of a fixed radius a, but since we suppose $2\pi a k_r$ is constant for different roots, the expression can be used generally for different root sizes.

4. Water uptake by growing root branching structure

The water uptake by the root system is not simply given by Eq. (3.14), because of the interconnectedness of the root system architecture. In order to model the effect of this, we consider a simple model for the root architecture consisting of zeroth and first order lateral roots, as indicated in Fig. 3. In principle, the approach presented below can be extended to root systems of arbitrary order. The idea is to use the isolated cylinder model for the smallest roots (here first order), and then use the calculated basal flux in these roots as an input to the uptake by the roots of next lowest order. We thus begin with the description of root system growth suitable for the maize plant.

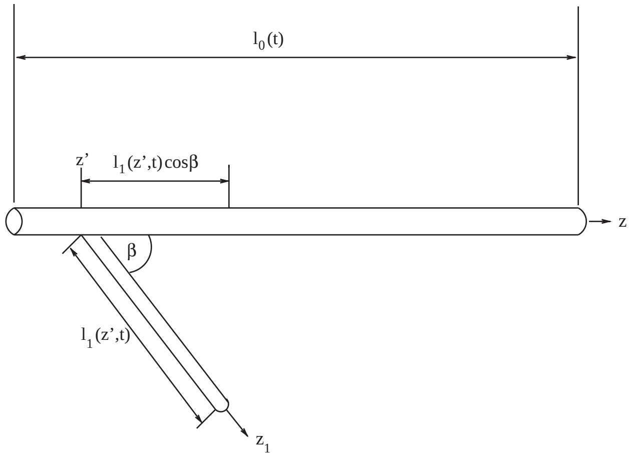

Fig. 3. Root branching structure, where β is the branching angle, l_0 and l_1 are the length of zero and first order roots, respectively, and z' is the branch-point.

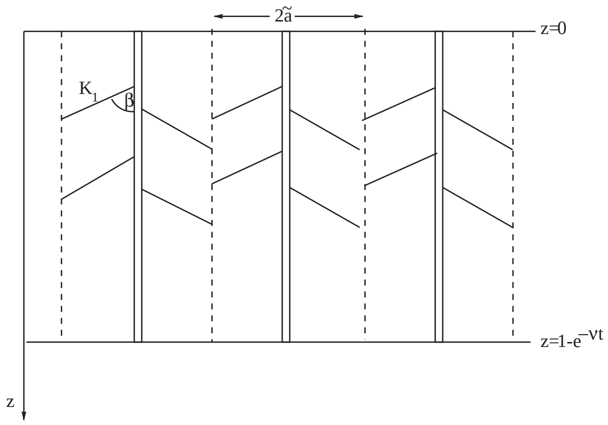

Fig. 4. Vertical root distribution.

4.1. Growth of the root system

Roots of annual plants grow by generating new root tissue at the tip of the root. Additionally, they can develop lateral branches which in turn can grow by generating new tissue at their tip. This pattern of developing lateral branches from the side of the already existing root is then repeated. It is however thought that due to the root internal hormone regulation, there is a non-branching zone near every root tip and near the base/branch point. In those non-branching zones roots cannot develop lateral branches. Thus, if the length of the apical non-branching zone is l_a and that of the basal non-branching zone is l_b, then the root can develop lateral branches only if its overall length l is larger than the sum of non-branching zones, i.e. $l > l_a + l_b$. In the case of maize plant there can be 3 orders of roots present: zero order roots are the ones growing out from the seed, first order roots branch off from the zero order roots and second order roots branch off from first order roots. In this paper we will consider maize roots with zero and first order roots only. This is because in Section 3 we found that first order branches of maize roots take up water only in a small thin region near the base. Second order roots will take up even less water and thus we can neglect them. This is also in agreement with observation of Varney et al. (1991) who found that the field grown maize plants had primarily zero and first order branches present and not very many second order branches. Even though we are making this simplifying assumption in the calculations presented in the current paper, the model developed here can easily be extended to include more root orders should this be necessary.

Clearly, since first order lateral branches grow from the zero order root, there will be a difference in directionality between the growth of the zero order root and its sub-branches. We consider that the first order lateral branches of the maize plant grow out from the side of the zero order root at an angle β. Assuming that the zero order root is growing vertically downwards into the soil, then the coordinate z_1 along a first order root is given by $z_1 = z/\cos\beta$ (see Figs. 3 and 4).

Another question that we need to address is the speed of root growth. Clearly, the rate of root growth depends on may factors: the nutrient and water status in the soil, their uptake by the plant, the temperature of the soil and air, and so on. In order to simplify the problem presented in this paper, we consider the growth of roots to be pre-determined. Thus, the model for root system growth presented here is based on the observation of root growth rather than on a mechanism of it. We also have to note that the mechanism of root growth and its dependence on the environment have only recently started to be investigated in detail due to advances in molecular biology. Thus, we do not believe that there is enough quantitative data available in the literature to tackle the mechanistic aspects of root system development with enough rigour. Therefore, we use a similar approach to that of Pages et al. (1989), Doussan et al. (1998a, b) to model the maize root system development. They considered the rate of root elongation to be given by an experimentally measured parameter r_i, where i denotes the root order. They also indicate that it is reasonable to assume that there is a maximum possible length K_i for roots of different orders. Thus, the simplest possible way to express this type of root elongation mathematically is

$$\frac{\partial l_i}{\partial t} = r_1\left(1 - \frac{l_i}{K_i}\right). \tag{4.1}$$

By solving this equation subject to the initial condition $l_i = l_{i,0}$ ($l_{i,0}$ is the initial length of ith order root) at $t = 0$ we get that the length l_i of ith order root as a function of time is given by

$$l_i(t) = K_i + [l_{i,0} - K_i]\exp\left(-\frac{r_i t}{K_i}\right). \tag{4.2}$$

4.2. Water uptake by first order lateral branches

As discussed in Section 3 (see also Appendix A), the water pressure inside the single first order branch of a maize plant is given by

$$p_r(z_1) \approx p(z_1) + [p_r(z') - p(z')]\mathrm{e}^{-\kappa z_1}, \quad \kappa^2 = \frac{2\pi a k_r L_1^2}{k_{z,1}}, \tag{4.3}$$

where k_r and $k_{z,1}$ are, respectively, the radial and axial hydraulic conductivities of first order branches, a and L_1 are, respectively, the radius and length of first order branches, z' is the location of the branch point on the zero order root, and z_1 is measured along the first order root.

As discussed in Section 3, in this situation, only a very thin region near the base, i.e. near z', of the root provides resistance to water flow, since in the rest of the region the water pressure inside the root is equal to the water pressure in the soil. In this case the limiting mechanism for water movement inside the root is the low axial conductivity due to the small diameter of the xylem vessels. The approximate expression for the dimensional *upwards* water flux delivered at the base is therefore given by

$$-q_z \approx (2\pi k_r k_{z,1})^{1/2}[p(z') - p_r(z')]. \tag{4.4}$$

We suppose that $\tilde{a}$ is the mean (radial) distance between plants, and is given by

$$\tilde{a} = a_0 + L_1 \cos\beta \tag{4.5}$$

(see Fig. 4), where a_0 is the zeroth order root radius. Let $\psi_1(z)$ be the density of first order roots on the zeroth order roots, i.e. in a length $\mathrm{d}z$ of zeroth order root there are $\psi_1(z)\,\mathrm{d}z$ first order roots; then the water uptake $F_1(z)$ by first order roots per unit volume of soil which is delivered to the zeroth order roots is given by, using Eq. (4.4),

$$F_1(z) = \frac{\{2\pi a k_r k_{z,1}\}^{1/2}\psi_1(z)}{\pi(a_0 + L_1\cos\beta)^2}[p - p_r], \tag{4.6}$$

where $p(z,t)$ is the water pressure in the soil, $p_r(z,t)$ is the water pressure inside the zero order root, and we are now supposing horizontal uniformity in the pressures, i.e. the pressure at the base of the first order sub-branch branching out from point z' is equal to the pressure inside the zero order root at position z'. The units of F_1 are m^3 (water) s^{-1} m^{-3} (soil) (ψ has units of m^{-1}).

4.3. Water uptake by zero order roots

In addition to its own radial uptake of water from the soil, a zero order root also takes up water from its sub-branches (a quantity $\pi\tilde{a}^2 F_1$, volume of water per unit time per unit zeroth order root length). Thus the total flux per unit height to the zeroth order root is

$$[2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2}\psi_1(z)](p - p_r) \tag{4.7}$$

and it follows that the corresponding equation for the zero order root internal water pressure variation is, using mass balance,

$$[2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2}\psi_1(z)](p - p_r) = -k_{z,0}\frac{\partial^2 p_r}{\partial z^2}. \tag{4.8}$$

Suitable boundary conditions for this equation are

$$p_r = P \text{ at } z = 0, \quad \frac{\partial p_r}{\partial z} - \rho g = 0 \text{ at } z = l_0, \tag{4.9}$$

where l_0 is the zeroth order root length and will depend on time as the root grows. By its definition ψ is the inverse of the average distance between the subbranches in the branching region. We now suppose branching is uniform, so that $\psi = 1/l_n$ in the branching region and $\psi = 0$ in the non-branching (apical) region. This will be appropriate in field scale studies, where an ensemble average will yield this form for ψ, and is also reasonable if $l_n \ll L$ (which we take to be the case, since appropriate values for maize are $l_n = 0.7$ cm, $L = 50$ cm). Clearly, the model presented could easily be extended to use a spatially varying function for ψ in the equations above.

For a maize plant, we use values in Table 3, together with $2\pi a k_r = 7.85 \times 10^{-10}$ m^2 MPa^{-1} s^{-1}, $L = 0.5$ m, $l_n = 0.7 \times 10^{-2}$ m. Together with the definition of ψ, we find that the parameter κ^2, which measures the relative importance of radial water flow in comparison to axial water flow (see Appendix B for details and also Section 3), is given by

$$\kappa^2 = \begin{cases} \frac{2\pi a k_r L^2}{k_{z,0}} = 0.033 & \text{for } l_0 - l_a \leqslant z \leqslant l_0, \\ & \text{branching zone,} \\ \frac{2\pi a k_r L^2}{k_{z,0}} + \frac{\{2\pi a k_r k_{z,1}\}^{1/2} L^2}{l_n k_{z,0}} & \text{for } 0 \leqslant z < l_0 - l_a, \\ \quad = 1.01 & \text{non-branching zone.} \end{cases} \tag{4.10}$$

As we can see, unlike the case of a single unbranched zero order root, presented in Section 3, the inclusion of water flow from the first order sub-branches into the zero order root results in the variations of soil water pressure p becoming important in determining the zero order root internal pressure.[2] Thus we need to couple Eqs. (4.8) and (4.9) to the equations describing the water flow in the soil and solve the resulting coupled equations numerically. Before we do this we recap the expressions for the water uptake by zero and first order roots.

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[2] This is because $\kappa^2 \sim O(1)$ and thus the approximation techniques presented in Appendix A cannot be used.

The direct water uptake F_0 by the zero order root per unit volume is given from Eq. (3.14) by

$$F_0 = \frac{2\pi a k_r}{\pi(a_0 + L_1\cos\beta)^2}[p - p_r]. \tag{4.11}$$

Thus the overall water uptake by the root system is

$$\begin{aligned} F_w &= F_0 + F_1 \\ &= \frac{2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2}\psi_1(z)}{\pi(a_0 + L_1\cos\beta)^2}[p(S) - p_r] \end{aligned} \tag{4.12}$$

and this expression is used as a volume sink in solving the Darcy–Richards equation (2.5) for S.

4.3.1. Summary: macroscopic model equations for water uptake by growing root system

The model can then be written in the form (assuming z dependence only)

$$\frac{\partial}{\partial z}\left[D_0 D(S)\frac{\partial S}{\partial z} - K_s K(S)\right] = \frac{\partial S}{\partial t} + F_w, \tag{4.13}$$

where

$$F_w = \frac{2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2}\psi_1(z)}{\pi(a_0 + L_1\cos\beta)^2}[p(S) - p_r] \tag{4.14}$$

(or $F_w = 0$ for $z > l_0$).

The boundary conditions for the model are

$$D_0 D(S)\frac{\partial S}{\partial z} - K_s K(S) = \begin{cases} -q_s & \text{at } z = 0, \\ 0 & \text{at } z = l_w. \end{cases} \tag{4.15}$$

The root internal pressure p_r is calculated from

$$\begin{aligned} &[2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2}\psi_1(z)](-p_c f(S) - p_r) \\ &\quad = -k_{z,0}\frac{\partial^2 p_r}{\partial z^2} \end{aligned} \tag{4.16}$$

with

$$p_r = -P \text{ at } z = 0, \quad \frac{\partial p_r}{\partial z} - \rho g = 0 \text{ at } z = l_0. \tag{4.17}$$

The functional forms of $D(S)$, $K(S)$, and $f(S)$ are given by

$$D(S) = S^{1/2-1/m}[(1 - S^{1/m})^{-m} + (1 - S^{1/m})^m - 2], \tag{4.18}$$

$$K(S) = S^{1/2}[1 - (1 - S^{1/m})^m]^2, \tag{4.19}$$

$$f(S) = (S^{-1/m} - 1)^{1-m}. \tag{4.20}$$

In addition, we need an initial condition for S, and we take this to be spatially uniform, i.e. at time $t = 0$ the relative water saturation is given by $S = S_\infty$. In our simulations, we choose a zero root tip growth law given by Eq. (4.2), i.e.

$$l_0 = K_0 + [l_{0,0} - K_0]\exp\left(-\frac{r_0 t}{K_0}\right). \tag{4.21}$$

As one can see this is a predetermined function for the growth of the zero order root. We would like to stress that this is in no way a limitation of this model as this growth law can easily be substituted with a different function if function (4.21) is not applicable. The dimensionless equations of this model are presented in Appendix C.

5. Numerical results

The above model consists of a nonlinear diffusion–convection equation for water movement in the soil and a second order ordinary differential equation for the root internal pressure. We solved the diffusion–convection equation using an implicit finite difference scheme for approximating the diffusive term and an upwind scheme to approximate the convective term (Morton and Mayers, 1994). The resulting system of algebraic equations was solved using the Thomas algorithm (Morton and Mayers, 1994). The equation for the zero order root internal pressure is solved using a finite difference scheme and the Thomas algorithm at each time step of the diffusion–convection equation solution.

The results of numerical experiments with this model are presented in Fig. 5. We have assumed there that the driving pressure P at the base of the root system is constant, and that the radial hydraulic conductivity k_r of water is constant along each root, however we have incorporated the effects of immature xylem vessels in the manner described earlier. There are essentially two reasons for presenting the results for this simplified case. Firstly, we aimed to observe the changes in the soil moisture conditions that occur over the time-scale of months, i.e. plant growth time-scale. Thus, the constant value of P should be considered an average daily driving pressure, i.e. driving pressure averaged over the ensemble of daily values for P. Secondly, the radial conductivity has been found to depend on the age of the root and aquaporin channel activity (Henzler et al., 1999; Javot and Maurel, 2002); however, the exact spatiotemporal parameterization of this dependence is not available. Thus we have neglected it.

As we can see in Fig. 5 the water saturation profile settles over a time-scale of order one month into a quasi-steady state in the rooting region of the soil. This quasi-steady state is characterized by a wet zone near the surface of the soil (near $z = 0$) if $W > 0$, and a dry zone just below it. If there is no surface rainfall ($W = 0$), then the dry zone develops without a surface wet zone.

Because the overall water uptake in comparison to the water mobility in the soil is small (the parameter $\lambda_w \ll 1$ in (C.2) in Appendix C), one might suppose that the relative water saturation S in the soil would relax rapidly to a quasi-equilibrium state. However, this conclusion fails if S is too small, since then D and K tend to zero. We define a critical value of S, S_c, when

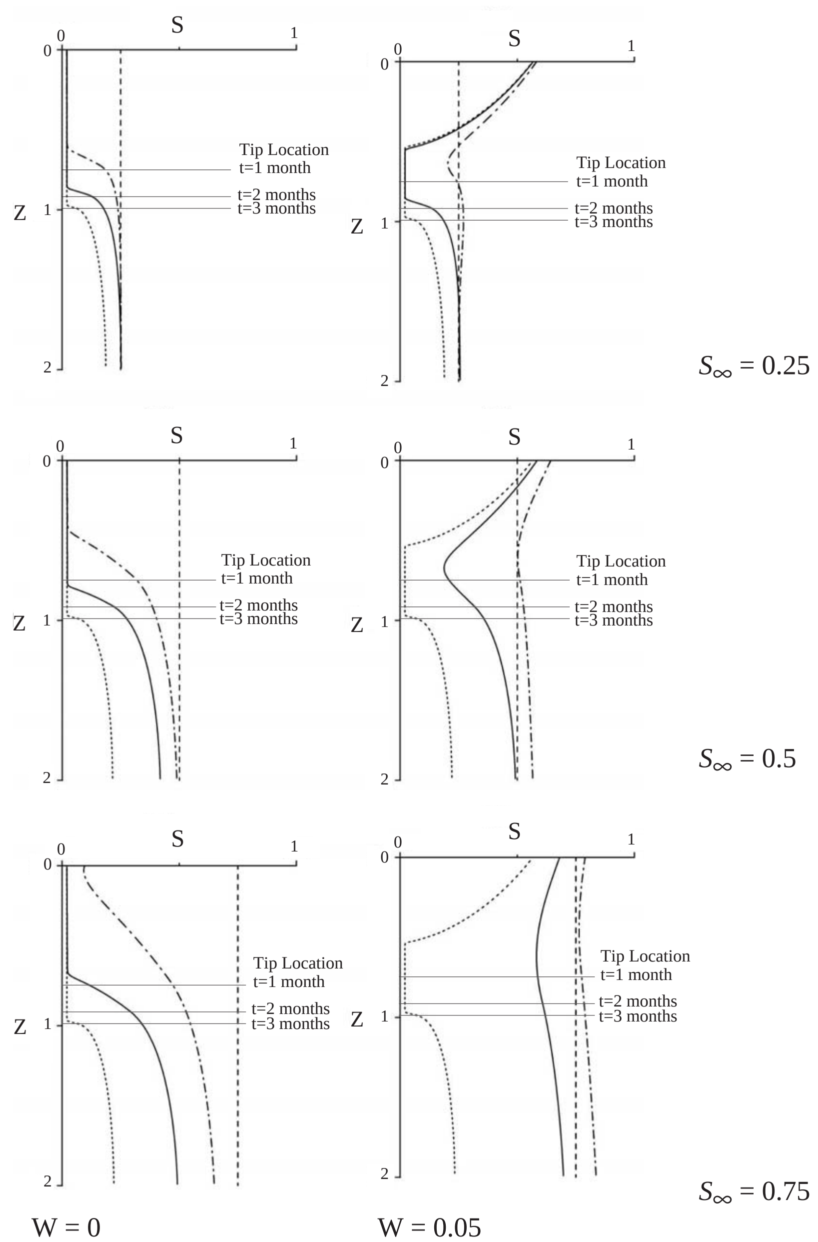

Fig. 5. Water profile due to water uptake by a developing root system for different rainfall patterns. The graphs on the left are for $W = 0$ (no rainfall), while those on the right are for $W = 0.05$, corresponding to a high average seasonal rainfall (about 3 m yr^{-1}). The dashed line shows the initial condition, the dotted–dashed line corresponds to $t = 1$ months, the solid line to $t = 2$ months, and the dotted line to $t = 3$ months. Parameters are $\varepsilon = 0.1$, $\lambda_w = 0.1$, $\varepsilon_w = 0.02$, and tip growth is given by $l_0 = 1 + (l_{0,0} - 1)e^{-\nu t}$ with $\nu = 0.9$ and $l_{0,0} = 0.1$.

this happens by the relation (see also Appendix C)

$$D_0 D(S_c) = \frac{2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2}}{\pi(a_0 + L_1 \cos\beta)^2}. \tag{5.1}$$

For a typical maize plant in a silt loam soil, $S_c \approx 0.59$. When $S < S_c$, as throughout most of the simulations, we can no longer neglect the temporal changes in relative water saturation in the soil, i.e. right-hand side of Eq. (4.13).

As t increases, we expect S to approach an equilibrium solution as the current model not only considers the water uptake from the soil, but also allows the bleeding out of water from the plant to the soil. We define the equilibrium value S^* to be the value when the uptake of water pressure at the base is equal to the soil suction pressure. Thus, we define S^* by

$$-p_c f(S^*) + p_r = 0, \tag{5.2}$$

i.e. in this case $F_w = 0$. In the case of maize, $S^* \approx 0.02$ for $p_r \approx -1$. The region where the value of S reaches S^* in a time-scale of plant growth comes about because all the water being supplied at the surface of the root has been taken up in the top region of the soil, i.e. in the region from 0 to z^*. Thus, the value z^* can be defined as a solution to

$$q_s = \int_0^{z^*} F_w \, \mathrm{d}z. \tag{5.3}$$

A more rigorous expression can also derived for z^* (see Appendix C). For a typical maize plant calculation as shown in Fig. 5, the value of z^* should be around 0.5, and we see that this is in a good agreement with numerical simulations.[3]

The region below this, $z > z^*$, corresponds to the development of a dry zone. This dry zone extends to the surface if there is no rainfall, as there is then nothing to keep $S > S^*$. The dry zone is of finite depth, since there is a further wet zone connecting to the far field water table. This lies in $z \geqslant l_0$, since we must have $F_w = 0$ in order that $R^* = W - \int_0^{z^*} F_w \, \mathrm{d}z$ can take the very small constant value which enables S to approach S_∞ in the far field. We can also derive a condition (see Appendix C) when such dry zone in the middle of the rooting region appears, i.e. if

$$q_s < \frac{2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2} \psi_1(z)}{\pi (a_0 + L_1 \cos\beta)^2} \left[1 - \frac{C}{2}\right],$$
$$C = \frac{\kappa^2 l_a}{1 + \kappa^2 l_0 l_a}, \tag{5.4}$$

then the dry zone can develop in the middle of the rooting zone.

6. Conclusions

In this article we have set out to calculate the water uptake by a typical agricultural plant such as maize. We have done this by combining a model for the soil water saturation with a model for the variation of the water pressure in the root system itself. In order to make the model tractable, we have used a number of approximations. In particular, we have found that the variation of water saturation in the vicinity of a single root is small, and this allows us to derive the individual root uptake in terms of the local saturation. We have also allowed in the model for the fact that the root system has a branched architecture, so that the n-th order roots supply water to the $(n-1)$-th order roots. In the version presented here, only zeroth order and first order roots are included.

Our principal result is that as a result of water uptake by a plant, a dry zone will develop in the soil, in the lower part of the rooting zone, providing the surface rainfall is sufficiently low. The explicit criterion is given by Eq. (5.4), and the fraction of the root system which is wet is z^*, given by Eq. (5.3). Using values in Table 2, we have $C \approx 0.23$, which is relatively small, so that Eq. (5.3) can be written approximately as

$$z^* \approx \frac{V_s}{V_r} = \frac{\pi \tilde{a}^2 q_s}{2\pi a k_r |P| L} \tag{6.1}$$

and this quantity is the perfusion ratio, i.e. V_s is the surface volume supply rate per plant, and V_r is the uptake by the root system. The approximate criterion for the occurrence of a dry zone is simply that $V_s < V_r$, and is due to the fact that the capillary suction parameter p_c is much smaller than the root internal driving pressure $|P|$. If $V_s > V_r$, then the plant becomes waterlogged, and this is easily seen in the model, because in this case

$$q_s > \int_0^{l_0} F_w \, \mathrm{d}z, \tag{6.2}$$

so that there is no steady state. For a maize root system with a maximum length of the roots 50 cm, the critical level of rainfall for this to occur is about 5 cm day^{-1}.

The modelling presented in this article also helps to address the question of where the main sites of water uptake by plant root systems are. This question has been of great interest to experimental and theoretical biologists (Varney and Canny, 1993; Doussan et al., 1998a, b). Experimental studies have found that most of the water uptake by a zero order root occurs near the tip of the root (Varney and Canny, 1993). This has been explained assuming a variation in root radial conductivity, since younger tissues of root epidermis are thought to have higher radial conductivity (Doussan et al., 1998a, b).

We indeed confirm the fact that there is, in addition to the local maximum in water uptake near the base, also a local maximum for water uptake at the root tip. Fig. 6 shows the (dimensionless) root system water uptake as a function of depth in a developing root system. With the development of a dry zone is associated a drop in the water uptake in the midst of the root system. However, this is not because of variation in the internal root conductivity, but because of the long-range water movement limitations in the soil (we have kept the root radial conductivity constant along the root). The tip of the root is continuously growing into soil which is less depleted of water and thus the tip region is able to take up more water. Because of the highly nonlinear dependence of diffusion and convection of water on the water saturation of the soil, the fast reduction in soil water content in the middle part of the rooting region causes the diffusion to become much slower there than near the tip region, therefore decreasing the flow of water into this region of low saturation. Thus we find that at low levels of rainfall the middle part of the root system takes up a negligible amount of water.

In the case of high rainfall (but not in drought) there will be another local maximum for water uptake near the top of the soil $z = 0$. Indeed, when the rainfall

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[3] Dimensionless $z^* = W/\lambda_w = 0.05/0.1 = 0.5$ (see Appendix C).

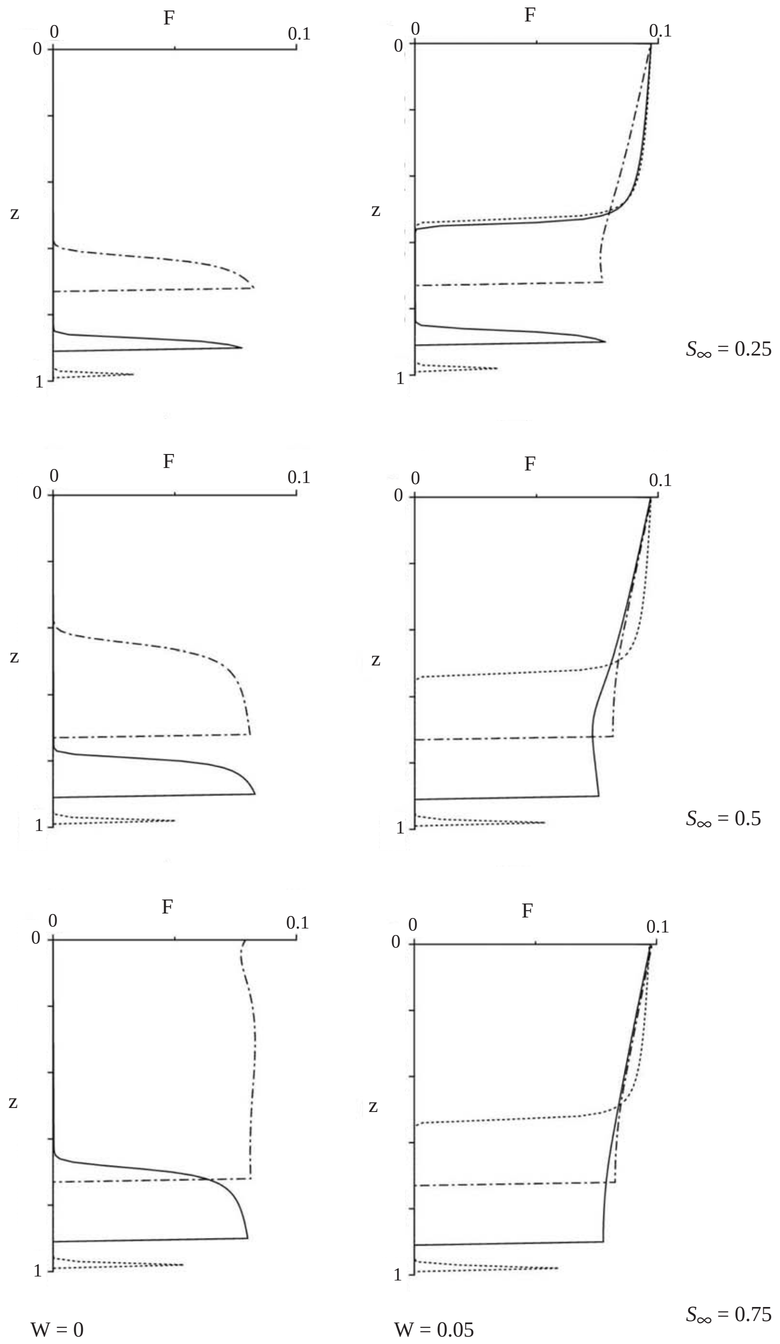

Fig. 6. Dimensionless relative rate of water uptake $F = -p_r - \varepsilon_w f(S)$ at times $t = 1$, 2, and 3 months (dotted–dashed, solid and dotted lines, respectively) for the same two rates of rainfall (dry and wet) as assumed in Fig. 5, which shows the corresponding soil water relative saturation profiles. Parameters are $\varepsilon = 0.1$, $\lambda_w = 0.1$, $\varepsilon_0 = 0.02$, and tip growth is given by $l_0 = 1 + (l_{0,0} - 1)e^{-\nu t}$ with $\nu = 0.9$ and $l_{0,0} = 0.1$.

supply rate satisfies $V_s \sim V_r$, then the saturation remains relatively high throughout the rooting zone. In that situation the dominant site for water uptake is near the base of the stem from where it is easiest to transport it to stem and leaves.

When a plant is young, the root system is not deep, and so it is supplied with water everywhere. However, as roots grow into deeper layers in the soil the total amount of water taken up increases, and once this water uptake becomes larger than the rainfall supply rate, a dry zone develops in the middle of the root system where the soil is still relatively highly saturated with water.

Fig. 7 shows graphs of the total plant water uptake as a function of time. It can be seen that when there is no water flux from the surface of the soil, then the water uptake by the plant stops after about 10–30 days

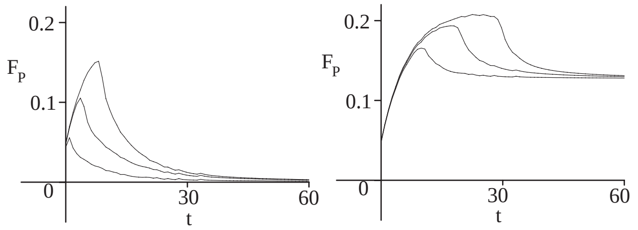

Fig. 7. Overall rate of water uptake $F_P = \pi\tilde{a}^2 L \int_0^{l_0} F_w \, dz$, where F_w is given by (4.12), by the full plant in litres per day for initial water saturations $S_\infty = 0.25$, 0.5 and 0.75; the curves increase as S_∞ increases. The left-hand graphs are for dry conditions ($W = 0$), and the right-hand graphs are for wet conditions ($W = 0.05$). The time t is measured in days.

depending on the initial saturation. However, when the water flux at the surface of the soil is non-zero then the rate of water uptake by the plant reaches a constant level. This constant level is determined directly by the equilibrium saturation profile that develops near the soil surface. The rate at which it develops is dependent on the initial water saturation in the soil.

The prediction about the development of dry zones predicted in this paper is partially supported by experimental evidence presented by Gardner (1964), Rowse et al. (1978) and Molz and Remson (1970). These authors show the development of a dry zone near the top of the soil when there is either no, or only a very small amount of water applied to the surface of the soil. This dry zone appears to be quite similar to the dry zone that is shown in Fig. 5 graphs for zero water application at the surface of the soil (left-hand column of Fig. 5). However, clearly, more controlled experiments measuring the changes in soil moisture conditions and root architecture in response to the well-defined water application and evaporation at the surface of the soil are needed.

The development of wet and dry regions as suggested here has important implications for root physiology and thus also for overall plant ecophysiology; in addition, it affects plant susceptibility to pest attack and fungal diseases, since the soil organisms responsible for these require water for survival. Plant beneficial mycorrhizal fungi have been found to increase the plant nutrient uptake by a factor of three (Marschner, 1995; Smith and Read, 1997). However, it has also been found that mycorrhizal fungi cannot grow in very dry soil (Bowling, 1976; Marschner, 1995), such as might occur in the dry zone predicted here.

The development of wet and dry regions may also act as a protection against groundwater pollution due to surface fertilization. As the water and therefore also solute mobility is very low in the dry region, the dry region acts as a barrier for water and solute movement, and decreases the risk of groundwater pollution. However, since most of the fertilizer will then be trapped in the wet surface region, the pollution of aquifers due to surface runoff may be increased. We have already developed a preliminary model for nutrient uptake by growing root system in absence of water movement (Roose et al., 2001). A detailed model for simultaneous water and nutrient uptake by a branching root system will be presented in another paper.

In this paper we found that as a result of water uptake the significant heterogeneity in vertical water saturation in the soil can develop. This modelling was applicable for a field crop where the horizontal variations in the root density are small. We expand the modelling presented in this paper to determine if similar patterns can emerge in the plant ecosystems where there are significant horizontal variations in root density. The extensions of the model to two or three dimensions requires new numerical simulations rather than a new model. However, such multidimensional numerical simulations are beyond the scope of this paper.

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Appendix A. Non-dimensionalization and analysis of the single cylindrical root model

We non-dimensionalize Eqs. (3.4)–(3.6) by choosing the following scales for the variables:

$$z \sim L, \quad p_r \sim |P|, \quad p \sim |P|, \tag{A.1}$$

where L is the length of the root, and $|P|$ is the magnitude of the root internal pressure at the base. We obtain the following dimensionless model:

$$\kappa^2(p - p_r) = -\frac{\partial^2 p_r}{\partial z^2} \tag{A.2}$$

with boundary conditions

$$p_r = p_0 \text{ at } z = 0, \quad \frac{\partial p_r}{\partial z} = \varepsilon \text{ at } z = 1, \tag{A.3}$$

where p_0 is the dimensionless water pressure at the base ($p_0 = -1$ during plant breathing and $p_0 = 0$ during non-breathing) and $\varepsilon = \rho g L/|P| \ll 1$ on the basis that $L \ll |P|/\rho g$, i.e. with $|P| = 1$ MPa, $\rho = 2.6 \times 10^3$ kg m^{-3},

$g = 9.8\ \mathrm{m\,s^{-2}}$, this is valid if $L \ll 39$ m. The most important dimensionless parameter in above model is

$$\kappa^2 = 2\pi a k_r L^2 / k_z \tag{A.4}$$

that largely determines the behaviour of the system.

The solution of above equation is given by

$$p_r(z) = p_0 - \kappa^2 \int G(x,\xi)[p(\xi) - p_0]\,\mathrm{d}\xi - \varepsilon G(x, \xi = 1), \tag{A.5}$$

where the Green's functions is given by

$$G(x,\xi) = \begin{cases} -\frac{1}{\kappa}\sinh(\kappa z)[\cosh(\kappa\xi) \\ \quad - \tanh(\kappa)\sinh(\kappa\xi)] \quad 0 \leqslant z \leqslant \xi \leqslant 1, \\ -\frac{1}{\kappa}\sinh(\kappa\xi)[\cosh(\kappa z) \\ \quad - \tanh(\kappa)\sinh(\kappa z)] \quad 0 \leqslant \xi \leqslant z \leqslant 1. \end{cases} \tag{A.6}$$

Large thick roots $\kappa \ll 1$: For long thick roots such as zero order roots of maize (see Table 3), $\kappa^2 \ll 1$ and therefore the leading $O(\kappa^0)$ solution after expanding $\mathrm{e}^{\pm\kappa z} \sim 1 \pm \kappa z + O(\kappa^2)$ becomes given by

$$p_r(z) \sim p_0 + \varepsilon z. \tag{A.7}$$

Thus, when plant is breathing and $p_0 = -1$ then the uptake of water from at any point in the soil is $q_r(z) \propto p(z) + 1 - \varepsilon z$. If however plant is not breathing and $p_0 = 0$ then $q_r \propto p(z) - \varepsilon z$ and depending on the value of ε plant can bleed out water.

Small thin roots $\kappa \gg 1$: For small thin roots like first order lateral branches of maize, $\kappa^2 \gg 1$, and leading order expansion in κ gives

$$p_r(z) \approx p(z) + [p_0 - p(0)]\mathrm{e}^{-\kappa z} - \frac{\varepsilon}{\kappa}\mathrm{e}^{-\kappa(1-z)}. \tag{A.8}$$

Thus the water uptake is in this case $q_r(z) \propto \mathrm{e}^{-\kappa z}$, i.e. the uptake of water is occurring only in a very thin region near the base of the root since $\mathrm{e}^{-\kappa z} \sim 0$ for $z \gg 1/\kappa$.

Appendix B. Dimensionless model for water movement inside the branched zero order root

Non-dimensionalizing equations (4.8)–(4.9) with

$$z \sim L, \quad p_r \sim |P|, \quad p \sim \rho g L, \tag{B.1}$$

we get the following dimensionless equations:

$$\kappa^2(z)(p - p_r) = -\frac{\partial^2 p_r}{\partial z^2}, \tag{B.2}$$

where

$$\kappa^2 = \kappa_0^2 + \kappa_{01}^2 \psi(z), \tag{B.3}$$

wherein we have defined

$$\psi = l_n \psi_1, \tag{B.4}$$

l_n is the distance between first order sub-branches. The parameters are given by

$$\kappa_0^2 = \frac{2\pi a k_r L^2}{k_{z,0}}, \tag{B.5}$$

which is the dimensionless water uptake parameter for zero order roots, and

$$\kappa_{01}^2 = \frac{\{2\pi a k_r k_{z,1}\}^{1/2} L^2}{l_n k_{z,0}}, \tag{B.6}$$

which is a parameter representing water flow from first order sub-branches into the zero order root. Suitable boundary conditions for this equation, neglecting gravity, are

$$p_r = -1 \text{ at } z = 0, \quad \frac{\partial p_r}{\partial z} = 0 \text{ at } z = l_0, \tag{B.7}$$

where l_0 is the dimensionless zeroth order root length and will depend on time, as the root grows towards its dimensionless maximum of one. By its definition, the average value of ψ is one in the branching region, and to be specific, we now suppose branching is uniform, so that $\psi = 1$ in the branching region and $\psi = 0$ in the non-branching (apical) region. For a maize plant, we use values in Table 3, together with $2\pi a k_r = 7.85 \times 10^{-10}\ \mathrm{m^2\,MPa^{-1}\,s^{-1}}$, $L = 0.5$ m, $l_n = 0.7 \times 10^{-2}$ m, to compute values of κ_0 and κ_{01} for both branching and non-branching zones (the difference being that in the branching zone, the presence of late metaxylem elements leads to an enhanced axial conductivity in zeroth order roots). Together with the definition of ψ, we then find that

$$\kappa^2 = \begin{cases} 0.033 & \text{for } l_0 - l_a^* \leqslant z \leqslant l_0, \\ 1.01 & \text{for } 0 \leqslant z < l_0 - l_a^*, \end{cases} \tag{B.8}$$

where $l_a^* = l_a/L$ is the dimensionless length of the zero order root apical non-branching zone. As we can see, including the uptake by the first order branches means the total non-dimensional water uptake is of $O(1)$, which implies that the variations in the soil pressure p can influence very strongly the zero order root internal pressure. Thus we need to solve this equation numerically.

Appendix C. Dimensionless model for water uptake by developing root branching structure

We non-dimensionalize the Darcy–Richards equation (4.13) using scales $z \sim L$,

$$t \sim t_D = \frac{\phi \pi \tilde{a}^2}{2\pi a k_r |P|}, \tag{C.1}$$

$p \sim |P|$ and $p_r \sim |P|$. The model can then be written in the form (assuming z dependence only)

$$\frac{\partial}{\partial z}\left[D(S)\frac{\partial S}{\partial z} - \varepsilon K(S)\right] = \lambda_w\left(\frac{\partial S}{\partial t} + F\right), \tag{C.2}$$

where

$$F = (1 + \delta\psi)(-\varepsilon_w f(S) - p_r) \tag{C.3}$$

(or $F = 0$ for $z > l_0$) and the parameters are

$$\lambda_w = \frac{2\pi a k_r |P| L^2}{\pi \tilde{a}^2 D_0}, \quad \delta = \left(\frac{k_{z,1}}{2\pi a k_r l_n^2}\right)^{1/2}, \quad \varepsilon = \frac{K_s L}{D_0},$$
$$\varepsilon_w = \frac{p_c}{|P|}. \tag{C.4}$$

The boundary conditions for the model are

$$D(S)\frac{\partial S}{\partial z} - \varepsilon K(S) = \begin{cases} -W & \text{at } z = 0, \\ 0 & \text{at } z = l_w, \end{cases} \tag{C.5}$$

where

$$W = \frac{q_s L}{D_0} \tag{C.6}$$

and the root internal pressure p_r is calculated from

$$\kappa^2(-\varepsilon_w f(S) - p_r) = -\frac{\partial^2 p_r}{\partial z^2} \tag{C.7}$$

with

$$p_r = -1 \text{ at } z = 0, \quad \frac{\partial p_r}{\partial z} = 0 \text{ at } z = l_0. \tag{C.8}$$

In addition, we need an initial condition for S, and we take this to be spatially uniform, thus $S = S_\infty$ at $t = 0$. In our simulations, we choose a root tip growth law given by

$$l_0 = 1 - (1 - l_{0,0})e^{-\nu t}. \tag{C.9}$$

This is a dimensionless version of Eq. (4.2) for zero order roots.

Estimated values for the parameters, using Tables 1–3, are $\lambda_w = 0.075$, $\delta = 1.11$, whence $1 + \delta\psi = 1$ for $z > l_0 - l_a^*$ (apical region), $= 2.11$ for $z < l_0 - l_a^*$ (branching region); $\varepsilon_w \approx 0.023$, $\varepsilon \approx 0.23$, $W \approx 0.013$, $l_a^* = 0.3$; κ is given by (B.8). The value of the time scale t_D is 29.6 days, so a growth time scale of 25 days (eventual length, 50 cm, divided by initial growth rate, 2 cm day^{-1} (Pagès et al., 1989)) would give $\nu = 0.84$.

In order to understand and quantify the observed wet and dry zone development, we note firstly that with the choice of $t_D \sim 29$ days as a time-scale, dimensionless times $\geqslant O(1)$ (as in Fig. 5) correspond to a plant root development time-scale of the order of weeks.

Secondly, because the parameter $\lambda_w \ll 1$ in (C.2), one might suppose that S would relax rapidly to a quasi-equilibrium state. However, this conclusion fails if S is too small, since then D and K tend to zero. We define a critical value of S, S_c, by the relation

$$D(S_c) = \lambda_w. \tag{C.10}$$

For $\lambda_w = 0.1$ and $m = 0.5$, $S_c \approx 0.59$. When $S < S_c$, as throughout most of the simulations, we can no longer neglect the right-hand side of Eq. (C.2).

As t increases, we expect S to approach an equilibrium solution of Eq. (C.2) satisfying

$$\frac{\partial S}{\partial z} = \frac{\varepsilon K(S) - R}{D(S)}, \tag{C.11}$$

where

$$R = W - \lambda_w \int_0^z F\,dz. \tag{C.12}$$

Taking ε_w to be small in Eq. (C.3), we have, approximately,

$$F \approx (1 + \delta\psi)(-p_r) \tag{C.13}$$

and F is a positive function of z (and t, through the dependence of p_r on l_0); also $F = 0$ for $z > l_0$.

Both W and λ_w are small, so that also R is small, but because $D(S)$ goes rapidly to zero as $S \to 0$, then $\partial S/\partial z \to \pm\infty$ in the same limit. Fig. 8 shows $\partial S/\partial z$ as a function of S for three different (very small) values of R. If F is positive (as is the case for S not close to zero), R decreases as z increases. Evidently, S decreases until $R \approx 0$ at a depth z^*, where $S = S^*$, say. If $z^* < l_0$, then for $z > z^*$, R becomes negative, and S will subsequently increase indefinitely. Hence $z^* \geqslant l_0$, and thus in fact $z^* = l_0$, since $F = 0$ for $z > l_0$ (and so R is constant). But with F given explicitly by Eq. (C.13), l_0 given by Eq. (C.9), R will generally not be zero at $z = l_0$. The only possibility is that S becomes so small that the neglected $\varepsilon_w f(S)$ term becomes significant, and we thus identify S^* as a zero of F; it is given by

$$S^* = f^{-1}(-p_r/\varepsilon_w). \tag{C.14}$$

In the case of maize, $S^* \approx 0.02$ for $p_r \approx -1$.

The region below the surface wet zone where $S > S^*$, i.e. for $z > z^*$, corresponds to the development of a dry

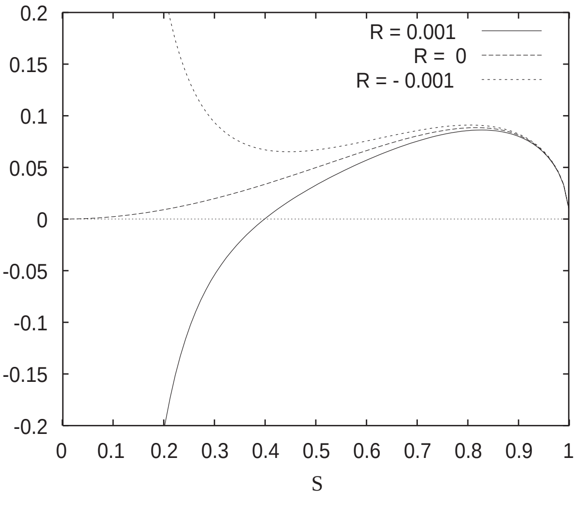

Fig. 8. $\partial S/\partial z$ as a function of S for three different values of R in Eq. (5.1), using $m = 0.5$.

zone. This dry zone extends to the surface if there is no rainfall, as there is then nothing to keep $S > S^*$. The dry zone is of finite depth, since there is a further wet zone connecting to the far field water table. This lies in $z \geqslant l_0$, since we must have $F = 0$ in order that R can take the very small constant value which enables S to approach S_∞ in the far field. The depth z^* to the dry zone is given approximately by

$$z^* \approx \frac{W}{\lambda_w} = \int_0^{z^*} -p_r \, \mathrm{d}z \tag{C.15}$$

and this dry zone exists providing $z^* < l_0$. Bearing in mind from Eq. (B.8) that κ^2 is small except near l_0, the solution for $-p_r$ is approximately

$$-p_r = 1 - Cz, \tag{C.16}$$

where

$$C = \frac{\kappa^2 l_a^*}{1 + \kappa^2 l_0 l_a^*} \tag{C.17}$$

and κ^2 takes its value at l_0. Thus we find the approximation

$$z^* = \frac{1 - \{1 - 2CW/\lambda_w\}^{1/2}}{C}, \tag{C.18}$$

since $l_0 \to 1$ as $t \to \infty$, a necessary and sufficient for a dry zone to appear is (approximately)

$$W < \lambda_w \left(1 - \frac{C}{2}\right). \tag{C.19}$$

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