A mathematical model for water and nutrient uptake by plant root systems

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Abstract

This article deals with modelling the simultaneous uptake of water and highly buffered nutrient, such as phosphate, by root branching structures from partially saturated soil. We use the simultaneous water and nutrient uptake model to investigate the effect that water movement has on nutrient uptake. With the aid of this model we are also able to show that the previous models by Barber (Soil Nutrient Bioavailability. A Mechanistic Approach, Wiley-Interscience, New York) and Tinker and Nye (Solute Movement in the Rhizosphere, Oxford University Press, Oxford) systematically underestimated the phosphate uptake, due to the oversimplified approach in dealing with root branching structure. In this article we show how this discrepancy can be remedied and the root branching structure included in the models of plant nutrient uptake. We will also discuss the differences in the results for continuous and spot fertilization combined with variable rainfall.
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1. Introduction

Most fundamental questions in soil science in relation to plant science deal with factors controlling nutrient uptake by plant roots. In this paper we will develop a mathematical model to estimate the rate of nutrient uptake by a plant root system in variable soil moisture conditions. We use the model to estimate the increase in the rate of nutrient uptake due to fertilizer application and fertilizer movement due to water movement. In particular, we will deal with the nutrients that have high buffer power in the soil, i.e. phosphate.

Substantial amounts of phosphate fertilizer are applied in areas with highly weathered soil like the West African Savannah, Malaya, and South Australia (Nye, 1992). Even when the intensity of phosphate fertilization is high, there are virtually no governmental or international regulations on its levels in groundwater and rivers. According to Binkley et al. (1999) this might be because phosphate is not toxic. However, during recent years concerns have mounted over the effect of phosphate on aquatic ecosystems. For example, an

increase 10 parts per billion phosphate–phosphorus in the Kuparuk River in Alaska resulted in an immediate increase of algal growth by 20-fold in a region 10 km down from the phosphate placement site (Peterson et al., 1985). Indeed, in some cases phosphate fertilizer has been used to increase the productivity of fisheries. These kind of practices can however adversely alter the biodiversity of environment. Ingerpuu et al. (1998) present the results of a 30 year fertilization study of the wooded meadow Laelatu on the west coast of Estonia. This site has been found to be one of the most species rich sites[1] in temperate Eurasia. Amongst the factors Ingerpuu et al. (1998) monitored was the response of species richness to the application of nitrate–phosphate–potassium fertilizer. They found that fertilization increased the coverage and decreased the number of different vascular plants, but had the opposite effect on byrophytes. Caldwell et al. (1985) have also found that the phosphate levels in soil influenced greatly the competitiveness of different grass species in respect of

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[1] It is the most species rich site on the small scale, i.e. the number of different plant species detected on 10 m² plot is up to 68. Overall number of different plant species found in Laelatu is approximately 371.

their ability to acquire phosphate from the soil. Thus, phosphate fertilization and pollution can have huge effects on the plant ecosystems and can make some of the less adapted species almost extinct since their root systems might not be well adapted to changes in the phosphate levels in the soil (Jackson et al., 1990).

This paper will present a mathematical model that would be useful in dealing with the problems discussed above. In Section 2 of this paper we present a model for water and nutrient conservation in the soil. In Section 3 the typical parameter values for phosphate transport in silt loam soil are discussed. Using the parameter values presented, we then non-dimensionalize the model and point out the significance of the resulting dimensionless parameter values for the further modelling. The main result of non-dimensionalization is the discovery that the phosphate and water transport in the soil occur over very different time-scales. This enables us in Section 4 to derive the term for phosphate uptake by the plant root branching system and thus complete the model. The results of numerical simulations based on the model are presented in Section 5, where the mathematical analysis of the model, and biological interpretation of the results are also presented. In Section 6, the results of numerical experiments in relation to previous models, i.e. the Nye–Tinker–Barber model (Barber, 1984; Nye and Tinker, 1977; Tinker and Nye, 2000), are presented and the discrepancies between those previous approaches and ours are discussed. In this paper we are assuming that the soil is homogeneous and we will also neglect the horizontal variations in the soil moisture conditions and in the nutrient levels. We believe these assumptions to be applicable to a field crop situation where the horizontal variation in the root length density is small. However, this is by no means a limitation of the model since extension of the model to two and three dimensions would be fairly simple if the experimental situation requires it.

2. Model for water and nutrient conservation in the soil

2.1. Water conservation equation

In this article we use the model for water movement in the soil and uptake by the root branching structure first developed by Roose and Fowler (2004). This model considers the equation for conservation of water in the soil and couples it with Darcy's law for flow in porous media resulting in the Richards equation for water flow in the soil. Thus, after Roose and Fowler (2004), the relative water saturation $S = \phi_l/\phi$, where ϕ_l is the volumetric water content and ϕ is the porosity of the soil, the Richards equation will be given by

$$\phi \frac{\partial S}{\partial t} = \nabla \cdot [D_0 D(S) \nabla S - K_s k(S) \hat{\mathbf{k}}] - F_w(S, z, t), \quad (2.1)$$

where D_0 and K_s are the parameters for water diffusivity and conductivity, respectively, $D(S)$ and $k(S)$ characterize reduction in water diffusivity and conductivity in response to the relative water saturation decrease, $\hat{\mathbf{k}}$ is the vector pointing vertically downwards from the surface of the soil and F_w is the rate of water uptake by plant roots per unit volume of soil at a given position (see Roose and Fowler (2004) for discussion). The functional forms of $D(S)$ and $k(S)$ for partially saturated soil are given by (van Genuchten, 1980)

$$D(S) = S^{1/2-1/m}[(1 - S^{1/m})^{-m} + (1 - S^{1/m})^m - 2]$$
$$= m^2 S^{1/2+1/m} + m^2 S^{1/2+2/m} + \cdots \quad (2.2)$$

and

$$k(S) = S^{1/2}[1 - (1 - S^{1/m})^m]^2$$
$$= m^2 S^{1/2+2/m} - m^2 (\tfrac{2}{3} - m) S^{1/2+3/m} + \cdots. \quad (2.3)$$

The above functional forms for $D(S)$ and $k(S)$ imply that the water mobility in the partially saturated soil is nonlinearly dependent on the level of saturation in the soil, i.e. at lower levels of saturation the water is less mobile in the soil than at higher levels of saturation (see also Fig. 1).

The water uptake term $F_w(S, z, t)$ for a typical maize plant is given, after Roose and Fowler (2004), by

$$F_w(S, z, t) = \frac{2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2} \psi_1(z)}{\pi (a_0 + L_1 \cos \beta)^2} [p(S) - p_r],$$
$$(2.4)$$

where $2\pi a k_r$ is the axial conductivity of the maize roots $k_{z,1}$ is the axial conductivity of the first order lateral
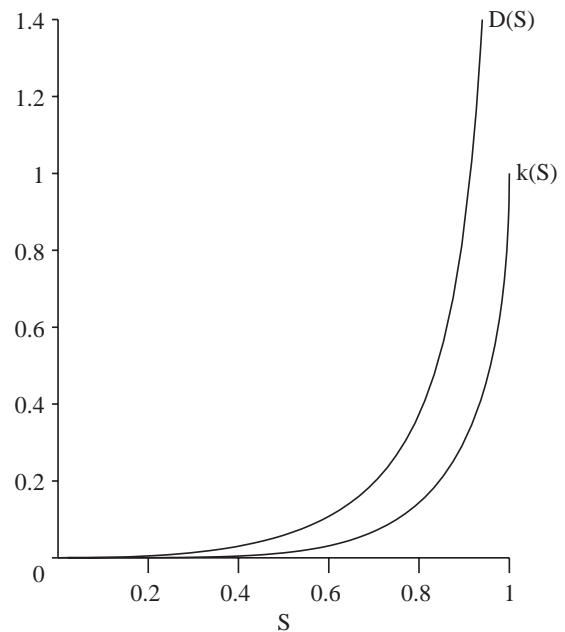

Fig. 1. Soil water "diffusivity" $D(S)$ and conductivity $k(S)$, given by Eqs. (2.2) and (2.3), as a function of soil water saturation for typical loam soil.

branches, a_0 is the radius of zero order root, L_1 is the maximum length of first order lateral branches, β is the branching angle between first and zero order roots, $\psi_1(z)$ is the distribution of first order root branch points on a zero order root, i.e. number of branch points per unit length of zero order root. The soil suction characteristic parametrizing the dependence of the soil water pressure on relative water saturation is given by

$$p(S) = -p_c (S^{-1/m} - 1)^{1/m} \qquad (2.5)$$

with p_c being experimentally determined for each soil type (van Genuchten, 1980). The pressure inside the zero order root xylem vessels, p_r, is described by the following equation that considers the balance between the axial water movement inside the zero order root and the radial water uptake by zero order roots in addition to the water flowing into zero order root xylem vessels from the first order lateral branches, i.e. after Roose and Fowler (2004)

$$[2\pi a k_r + \{2\pi a k_r k_{z,1}\}^{1/2}\psi_1(z)](p(S) - p_r) = -k_{z,0}\frac{\partial^2 p_r}{\partial z^2} \qquad (2.6)$$

with boundary conditions representing an impermeable root tip, $z = L$, and a constant root internal pressure, P, at the base of the zero order root, $z = 0$, i.e. the boundary conditions are given by

$$p_r = P \text{ at } z = 0 \quad \text{and} \quad \frac{\partial p_r}{\partial z} = 0 \text{ at } z = L. \qquad (2.7)$$

2.2. Nutrient conservation equation

The equation for nutrient conservation in the soil, assuming that there is an instantaneous equilibrium between nutrients bound to the solid surfaces in the soil and nutrients in the soil pore water, is given (after Barber, 1984; Tinker and Nye, 2000; Roose et al., 2001) by

$$\frac{\partial}{\partial t}[(b + \phi S)c] + \nabla \cdot [c\mathbf{u}]$$
$$= \nabla \cdot [D_f \phi^{d+1} S^{d+1} \nabla c] - F(c, S, t), \qquad (2.8)$$

where b is the buffer power of the soil. We have also taken the diffusivity of nutrient in the partially saturated soil to be given by $D_{nut} = D_f f = D_f \phi^d S^d$ with D_f being the nutrient diffusivity in free water and the impedance factor, f, for nutrient diffusion in the partially saturated soil is given by the following power law $f = \phi^d S^d$ in terms of soil water content. The value for the impedance factor parameter d is, according to Barber (1984) and Nye and Tinker (1977), in the range $1/2 \leqslant d \leqslant 2$. The term $F(c, S, t)$ describes the rate of nutrient uptake by the root branching structure. We will discuss the functional form of this term in a later section of this

article after having non-dimensionalized the above equations for water and nutrient conservation.

In this article we will assume that the buffer power of the soil does not change when the moisture conditions of the soil change. This is supported by experimental measurements conducted by Kuchenbuch et al. (1986). They found that the buffer power variation with soil moisture conditions is negligible in comparison to the changes in the impedance factor for nutrient diffusion. This is expected, since all soil particles will retain a water film over them even in very dry soils. This film is where the exchange between the two nutrient phases occurs (see Barber, 1984; Tinker and Nye, 2000). Thus we take the change in the nutrient ion mobility due to the changes in the soil moisture conditions to occur only due to the diffusion limitation, i.e. the impedance factor $f(S) = \phi^d S^d$.

In the above nutrient movement equation the speed of water movement $\mathbf{u}$ in the soil will be given by Darcy's law written in terms of relative water saturation using the van Genuchten suction characteristic (van Genuchten, 1980), i.e.

$$\mathbf{u} = -D_0 D(S)\nabla S + K_s k(S)\hat{\mathbf{k}}. \qquad (2.9)$$

Thus the equation for nutrient conservation, written in terms of relative water saturation S and nutrient concentration c, is

$$\frac{\partial}{\partial t}[(b + \phi S)c] = \nabla \cdot \{D_f \phi^{d+1} S^{d+1}\nabla c$$
$$+ c[D_0 D(S)\nabla S$$
$$- K_s k(S)\hat{\mathbf{k}}]\} - F(c, S, t), \qquad (2.10)$$

where $\hat{\mathbf{k}}$ is the unit vector pointing vertically downwards into the soil.

2.3. Boundary conditions

2.3.1. Soil surface boundary condition
We assume that there is a flux of water due to rainfall at the surface of the soil, i.e.

$$-D_0 D(S)\frac{\partial S}{\partial z} + K_s k(S) = W_{dim} \quad \text{at } z = 0, \qquad (2.11)$$

where W_{dim} (cm s^{-1}) is the volume flux of water per unit soil surface area in unit time. This boundary equation implies that we will be neglecting the effects of surface water ponding due to very high rainfall. However, it would not be very difficult to modify the model to include the effects of surface ponding since in the case of surface ponding the effective boundary condition at the soil surface becomes $S = 1$ at $z = 0$, i.e. fully saturated soil surface, and the flow of water into the soil will be driven by changes in water pressure via Darcy's law.

If the rate of fertilizer application at the root surface is ϱ_{dim} (μmol cm^{-2} s^{-1}), then the nutrient soil surface

Table 1
Soil and nutrient uptake parameters used in numerical simulations

Param.	Description	Value	Unit
K_s	Soil saturated hydraulic conductivity	5	cm day^{-1}
m	Non-saturated water flow parameter in Eqs. (2.2) and (2.3)	1/2	—
D_0	"Diffusivity" of water in non-saturated soil	10^3	cm^2 day^{-1}
b	Nutrient buffer power in soil (for phosphate)	239	—
ϕ	Soil porosity	0.4	—
D_f	Nutrient diffusivity in water (for phosphate)	10^{-5}	cm^2 day^{-1}
d	Parameter for nutrient diffusivity impedance in soil	2	—
K_0	Max. length of maize zero order root	50	cm
K_m	Nutrient Michaelis–Menten parameter (for phosphate)	5.8×10^{-3}	μmol cm^{-3}
F_m	Max. rate of nutrient uptake (for phosphate)	3.26×10^{-6}	μmol cm^{-2} s^{-1}

boundary condition will be given by

$$-D_f \phi^{1+d} S^{1+d} \frac{\partial c}{\partial z} + W_{dim} c = \varrho_{dim} \quad \text{at } z = 0. \tag{2.12}$$

2.3.2. Boundary condition at the "bottom" of the soil

To calculate the movement of fertilizer into the groundwater and from there to the lakes and rivers, the boundary condition at the groundwater level would need to be derived from a model for large-scale groundwater movement. However, for the purposes of simplicity we will prescribe a zero flux boundary condition at a given level in the soil. This will correspond to the situation when the soil is overlaying an aquitarol and also to pot experiments where the pot has an impermeable bottom. The zero flux boundary condition at a given level l_w for water and nutrient is thus at leading order given by

$$-D_0 D(S) \frac{\partial S}{\partial z} + K_s k(S) = 0 \quad \text{at } z = l_w, \tag{2.13}$$

$$-D_f \phi^{1+d} S^{1+d} \frac{\partial c}{\partial z} = 0 \quad \text{at } z = l_w. \tag{2.14}$$

3. Non-dimensionalization of the model and values of dimensionless parameters

We non-dimensionalize the above equations using the following scaling: $z \sim K_0$, $t \sim bK_0^2/D_0$ and $c \sim K_m$, where K_0 is the maximum length of the zero order root, K_m is the nutrient uptake Michaelis–Menten parameter (after Roose et al., 2001), b is the buffer power of the soil, and D_0 is the soil water "diffusivity" parameter (see Barber, 1984; Tinker and Nye, 2000; Roose et al., 2001). The dimensionless model is thus given by

$$\delta \frac{\partial S}{\partial t} = \frac{\partial}{\partial z} \left[D(S) \frac{\partial S}{\partial z} - \varepsilon k(S) \right] - F_w, \tag{3.1}$$

$$(1 + \delta S)\frac{\partial c}{\partial t} - \left[D(S)\frac{\partial S}{\partial z} - \varepsilon k(S) \right]\frac{\partial c}{\partial z}$$
$$= D_\varepsilon \frac{\partial}{\partial z}\left[S^{1+d}\frac{\partial c}{\partial z} \right] - F + F_w c, \tag{3.2}$$

where three dimensionless parameters are $\delta = \phi/b$, $\varepsilon = K_s K_0/D_0$ and $D_\varepsilon = D_f \phi^{1+d}/D_0$.

The dimensionless boundary conditions are given by

$$-D(S)\frac{\partial S}{\partial z} + \varepsilon k(S) = W \quad \text{at } z = 0, \tag{3.3}$$

$$Wc - D_\varepsilon S^{1+d}\frac{\partial c}{\partial z} = \varrho \quad \text{at } z = 0, \tag{3.4}$$

$$-D(S)\frac{\partial S}{\partial z} + \varepsilon k(S) = 0 \quad \text{at } z = l_w, \tag{3.5}$$

$$\frac{\partial c}{\partial z} = 0 \quad \text{at } z = l_w, \tag{3.6}$$

where the dimensionless rate of rainfall is given by $W = W_{dim}K_0/D_0$ and the dimensionless rate of fertilization is given by $\varrho = \varrho_{dim}K_0/(D_0 K_m)$.

The values for dimensional parameters are shown in Table 1. The values of the dimensionless parameters for typical loam soil (data from van Genuchten, 1980) are: $D_\varepsilon \sim 10^{-5}$, $\varepsilon \sim 0.2$. The average seasonal rainfall is in England of order 1 m yr^{-1} thus $0 \leqslant W \leqslant 10^{-2}$; and the average rate of phosphate fertilization in England is 30 kg h^{-1}, i.e. approximately 10^{-7} μmol cm^{-2} s^{-1}, thus $\varrho \sim 0.1$ (Dawson, 1998). We can see that as expected, the nutrient diffusion in the soil pore water on the chosen root system length scale is negligible in comparison to the nutrient movement due to the water movement, i.e. $D_\varepsilon \ll 1$ and $D_\varepsilon \ll \varepsilon$.

4. Two time-scales and nutrient uptake

In the above dimensionless equations (3.1) and (3.2) one of the most important parameters is $\delta = \phi/b$, which shows the importance of relative water movement

time-scale in comparison to the nutrient movement time-scale. When the buffer power b is large, as it is in the case of phosphate, potassium and calcium for example, then $\delta \ll 1$ since the porosity $\phi < 1$ anyway. Thus, the water saturation relaxes to a fast pseudo-steady state over a time-scale of highly buffered nutrient movement. Similarly, the term for nutrient concentration change due to the water saturation and resulting release of nutrient from the soil particles becomes $(1 + \delta S)\partial c/\partial t \approx \partial c/\partial t$ for $\delta \ll 1$.

Since $\delta \ll 1$ we can at the leading order take the water saturation at any given point in the soil to be constant in time. Thus, we can use the analytic formula derived by Roose et al. (2001) for the nutrient uptake by a single root. Roose et al. (2001) derived the formulae for the rate of nutrient uptake F_{dim} (μmol cm^{-1} s^{-1}) by single cylindrical root using the model originally developed by Barber (1984) and Nye and Tinker (1977)[2] and the method of matched asymptotic expansions (Hinch, 1991). The formula they derived was valid only for the case when the water saturation in the soil is in equilibrium and the water saturation profile around individual root is flat (as shown in Roose and Fowler, 2004). Thus, since in our case the water saturation is in equilibrium we can use Roose et al.'s (2001) formula locally for each sub-branch in the root system. The formula Roose et al. (2001) derived gives the rate of nutrient uptake per unit of root surface area per unit time by

$$F_{dim} = \frac{2F_m c/K_m}{1 + c/K_m + L(t) + \sqrt{4c/K_m + (1 - c/K_m + L(t))^2}},$$
(4.1)

where

$$L(t) = \frac{\lambda}{2} \ln[\alpha(t - t_0) + 1]$$
(4.2)

and the dimensionless nutrient uptake parameter λ and time parameter α (s^{-1}) are given by

$$\lambda = \frac{F_m a}{D_f \phi^{1+d} S^{1+d} K_m} \quad \text{and} \quad \alpha = 4e^{-\gamma} \frac{D_f \phi^{1+d} S^{1+d}}{a^2 b(1 + \delta S)}. \quad (4.3)$$

Dimensional parameters in above formulas are (see Roose et al., 2001): F_m (μmol cm^{-2} s^{-1}) is the maximum rate of nutrient uptake, K_m (μmol cm^{-3}) is the Michaelis–Menten nutrient uptake parameter (it corresponds to the nutrient concentration when the rate of nutrient uptake by plant root is half of maximum possible), t_0 (s) is the time when the nutrient uptake at a given physical location started, a (cm) is the radius of the root, b is the buffer power, D_f is the diffusion coefficient of nutrient

in a water, ϕ is the porosity, d is the diffusion impedance factor power, and $\gamma = 0.5772\ldots$ is the Euler constant (see Table 1 for representative values for phosphate).

4.1. Root branching structure

The root systems of agricultural plants like maize, wheat, etc. have typically 2–3 branching orders. The roots growing out from the seed are called zero order roots, roots branching out from those zero order roots are called first order roots, and roots branching out from the first order roots are called second order roots (see Fig. 2). Each of those branches has non-branching zones near the base of the root and near the tip. Thus, the higher order branches can only be developed in the so-called branching region located in a middle part of the root system (see Fig. 2).

As discussed in Roose et al. (2001) the rate of elongation dl_i/dt of a single root of order i and length l_i can be taken to be

$$\frac{dl_i}{dt} = r_i \left(1 - \frac{l_i}{K_i}\right),$$
(4.4)

where r_i is the initial, maximum rate of elongation of a newly born root, K_i is the maximum possible i-th order root length and l_i is the length of i-th order root at time t.

Solving the above equation gives that the length of a root created at time $t = T^*$ is given by

$$l_i(t) = K_i(1 - e^{-r_i(t - T^*)/K_i}).$$
(4.5)

4.1.1. Nutrient uptake by zero order roots

The zero order root, created at time $t = 0$ at a position $z = 0$ and growing vertically downwards along the positive z-axis, will reach position z in time

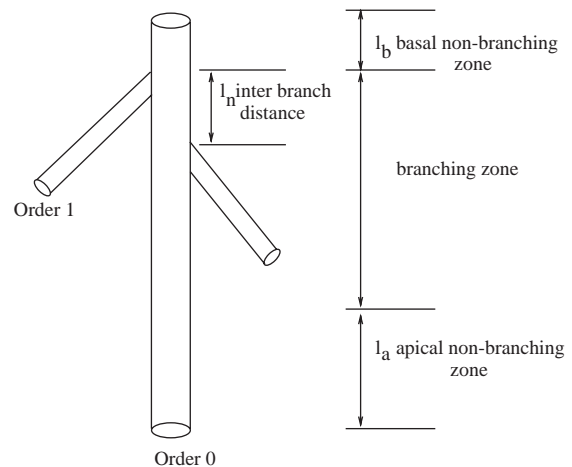$$t_0 = -\frac{K_0}{r_0} \ln\left(1 - \frac{z}{K_0}\right).$$
(4.6)

Fig. 2. Schematic structure of the maize root branching structure after Pagès et al. (1989).

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[2] Barber (1984) and Nye and Tinker (1977) solved the model only numerically. This need for numerical solution of cylindrical root model made it difficult to expand the modelling to include more realistic root structures, i.e. root branching structures.
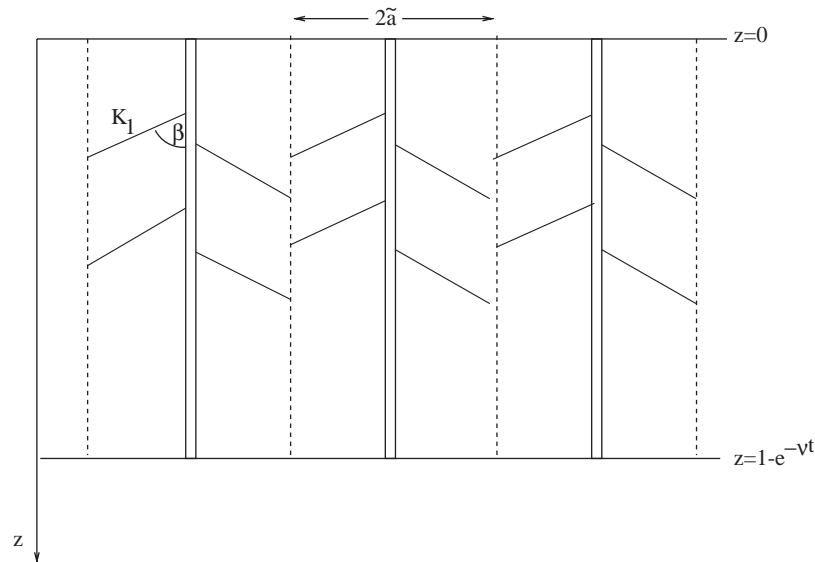
Fig. 3. Vertical root distribution.

Therefore, the rate of nutrient uptake as a function of z and t by this zero order root of radius a_0 and unit length dz is

$$F_0(z, t)\, dz$$
$$= 2\pi a_0\, dz$$
$$\times \frac{2F_m c/K_m}{1 + c/K_m + L_0(t) + \sqrt{4c/K_m + (1 - c/K_m + L_0(t))^2}},$$
$$(4.7)$$

where

$$L_0(t) = \frac{\lambda_0}{2} \ln \left[\alpha_0 t + \alpha_0 \frac{K_0}{r_0} \ln \left(1 - \frac{z}{K_0} \right) + 1 \right] \qquad (4.8)$$

with

$$\lambda_0 = \frac{F_m a_0}{D_f \phi^{1+d} S^{1+d} K_m} \quad \text{and} \quad \alpha_0 = 4e^{-\gamma} \frac{D_f \phi^{1+d} S^{1+d}}{a_0^2 b(1 + \delta S)}. \qquad (4.9)$$

4.1.2. Nutrient uptake by first order lateral branches

For the first order roots we need to take into account the time $\tau(z')$ after they are created at z' before they start taking up nutrients. Thus, the first order root created at the branch point position z' has a length

$$l_1(z', t) = K_1(1 - e^{-r_1(t - \tau(z'))/K_1}). \qquad (4.10)$$

The time-delay τ can be calculated from Eq. (4.5) since the zero order root will develop first order lateral branches at position z' only if the overall length of zero order root is larger than z' by the amount equal to the apical non-branching zone $l_{a,0}$ (see Roose et al. (2001) for discussion on root branching). Thus, the time of

creation of first order branch at z' is given by

$$\tau(z') = -\frac{K_0}{r_0} \ln \left(1 - \frac{z' + l_{a,0}}{K_0} \right) \qquad (4.11)$$

and therefore the length of first order root is given by

$$l_1(z', t) = \begin{cases} K_1 \Big[1 - e^{-r_1 t/K_1} \\ \quad \times \left(1 - \dfrac{z' + l_{a,0}}{K_0} \right)^{-\frac{r_1 K_0}{r_0 K_1}} \Big] & \text{for} \quad t \geqslant \tau(z'), \\ \\ 0 & \text{for} \quad t < \tau(z'). \end{cases} \qquad (4.12)$$

Thus, the time in which the first order root branching out from z' reaches position z is given by

$$t_1(z, z') = -\frac{K_0}{r_0} \ln \left(1 - \frac{z' + l_{a,0}}{K_0} \right)$$
$$\qquad -\frac{K_1}{r_1} \ln \left(1 - \frac{z - z'}{K_1 \cos \beta} \right), \qquad (4.13)$$

where β is the angle between the zero order root and first order branch (see Fig. 3).

The first order root with radius a_1 and length in z direction[3] dz, branching out from the branch point at z' is therefore taking up nutrients from the interval

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[3] The first order roots branch out from the zero order root making an angle β between them (see Fig. 3). Thus, if the zero order root is in direction of z axis, then the first order root length in the z direction translates into the length $dz/\cos \beta$ along each first order root.

$[z', z' + l_1(z', t) \cos \beta]$ at a rate

$$f_1(z', z, t) \, \mathrm{d}z$$

$$= 2\pi a_1 \frac{\mathrm{d}z}{\cos \beta}$$

$$\times \frac{2F_m c / K_m}{1 + c/K_m + L_1(t) + \sqrt{4c/K_m + (1 - c/K_m + L_1(t))^2}}, \tag{4.14}$$

where

$$L_1(t) = \frac{\lambda_1}{2} \ln \left[\alpha_1 t + \alpha_1 \frac{K_0}{r_0} \ln \left(1 - \frac{z}{K_0} \right) \right.$$
$$\left. + \alpha_1 \frac{K_1}{r_1} \ln \left(1 - \frac{z - z'}{K_1 \cos \beta} \right) + 1 \right] \tag{4.15}$$

with

$$\lambda_1 = \frac{F_m a_1}{D_f \phi^{1+d} S^{1+d} K_m} \quad \text{and} \quad \alpha_1 = 4 \mathrm{e}^{-\gamma} \frac{D_f \phi^{1+d} S^{1+d}}{a_1^2 b (1 + \delta S)}. \tag{4.16}$$

However, at any given point z there is more than one first order root taking up nutrients since roots from more than one branch point reach this position. In order to determine the branching interval on the zero order root from where the roots can reach position z we have to do a back calculation, i.e. the first order roots branching out from the interval $(\hat{z}, z)$ reach z, where $\hat{z}$ is defined as a solution to

$$z = \hat{z} + K_1 \cos \beta \left[1 - \mathrm{e}^{-r_1 t / K_1} \left(1 - \frac{\hat{z} + l_{a,0}}{K_0} \right)^{-r_1 K_0 / r_0 K_1} \right]$$
$$\text{for } t \geqslant \tau(\hat{z}). \tag{4.17}$$

If the branch point distribution is given by $\psi(z)$, i.e. there are $\psi(z) \, \mathrm{d}z$ branching points in the interval $(z, z + \mathrm{d}z)$, then the cumulative rate of uptake per unit depth by all first order branches reaching the position z is given by

$$F_1(z, t) = \int_{\hat{z}}^{z} \psi(z') f_1(z', z, t) \, \mathrm{d}z'. \tag{4.18}$$

4.1.3. Rate of nutrient uptake per unit volume of soil

We have described above the rate of nutrient uptake by zero and first order roots. We will limit ourselves to including these two orders, since Roose et al. (2001) found that the second order roots do not take up substantial amounts of nutrient if inter-root branch competition is neglected. This is due to the very small length and radius of second order branches. In fact, interbranch competition is going to decrease the uptake even further. Thus, for the purposes of simplicity and clarity we will neglect the nutrient uptake by second order branches. This approach is also supported by the observations of Varney et al. (1991) who studied the branching structure of soil grown maize plants and

noted that there were not very many second order branches present. Clearly, if the second order roots were to be found important for a particular plant, their effect in the model can be incorporated in a similar manner to first order branch uptake presented in this paper.

Considering the representative soil volume element to be of thickness $\mathrm{d}z$ and radius $a_0 + K_1 \cos \beta$, i.e. the first order branches of parallel zero order roots do not overlap (see Fig. 3), we write the uptake of nutrients by the root system per unit volume of soil to be given by (using the averaging of Eqs. (4.7) and (4.18) with $\mathrm{d}V = \pi(a_0 + K_1 \cos \beta)^2 \, \mathrm{d}z$)

$$F(c, z, t) = \frac{F_0 + F_1}{\pi(a_0 + K_1 \cos \beta)^2}. \tag{4.19}$$

4.1.4. Dimensionless nutrient uptake per unit volume of soil

Using the non-dimensional scaling presented above in Section 3 with the nutrient scale given by $c \sim K_m$, the Michaelis–Menten nutrient uptake parameter (Roose et al., 2001), the dimensionless nutrient uptake that appears in Eq. (3.2) is given by Eq. (4.19), i.e.

$$F = F_0^* + F_1^*, \tag{4.20}$$

where dimensionless zero order nutrient uptake is given by

$$F_0^* = \frac{2\Lambda_0 c}{1 + c + L_0(z, t) + \sqrt{4c + (1 - c + L_0(z, t))^2}} \tag{4.21}$$

with

$$L_0(z, t) = \frac{\lambda_0}{2S^{d+1}} \ln \left[(\alpha_0 t + \alpha_{00} \ln(1 - z)) \frac{S^{d+1}}{1 + \delta S} + 1 \right], \tag{4.22}$$

$$\lambda_0 = \frac{F_m a_0}{D_f \phi^{d+1} K_m}, \quad \alpha_0 = 4 \mathrm{e}^{-\gamma} \frac{D_f \phi^{d+1} [t]}{a_0^2 b},$$

$$\alpha_{00} = 4 \mathrm{e}^{-\gamma} \frac{D_f \phi^{d+1}}{a_0^2 b} \frac{K_0}{r_0}, \tag{4.23}$$

$$\Lambda_0 = \frac{2 a_0 F_m K_0^2}{(a_0 + K_1 \cos \beta)^2 K_m D_0}. \tag{4.24}$$

The dimensionless nutrient uptake by first order roots is given by

$$F_1^* = \int_{\hat{z}}^{z} \frac{2\Lambda_1 c \psi(z') \, \mathrm{d}z'}{1 + c + L_1(z, t; z') + \sqrt{4c + (1 - c + L_1(z, t; z'))^2}} \tag{4.25}$$

with

$$L_1(z, t; z') = \frac{\lambda_1}{2S^{1+d}} \ln\left\{ \left[\alpha_1 t + \alpha_{11} \ln(1 - (z' + l_{a,0})) \right.\right.$$
$$\left.\left. + \alpha_{111} \ln\left(1 - \frac{z - z'}{K_1 \cos \beta}\right)\right] \frac{S^{d+1}}{1 + \delta S} + 1 \right\},$$

(4.26)

$$\alpha_1 = 4e^{-\gamma} \frac{D_f \phi^{d+1}[t]}{a_1^2 b}, \quad \alpha_{11} = 4e^{-\gamma} \frac{D_f \phi^{d+1}}{a_1^2 b} \frac{K_0}{r_0},$$

$$\alpha_{111} = 4e^{-\gamma} \frac{D_f \phi^{d+1}}{a_1^2 b} \frac{K_1}{r_1},$$

(4.27)

$$\Lambda_1 = \frac{2a_1 F_m K_0^3}{\cos \beta (a_0 + K_1 \cos \beta)^2 D_0 K_m l_{n,0}},$$

$$\lambda_1 = \frac{F_m a_1}{D_f \phi^{d+1} K_m}.$$

(4.28)

The values of dimensionless parameters presented above are shown in Table 2.

5. Results of numerical simulations and simple analysis of the model

We solved the model described above using the implicit finite difference scheme for the diffusion terms and the upwind scheme for the convection terms (Morton and Myers, 1994). The results of numerical simulations are presented in Figs. 4 and 5. For those figures the results are calculated using a constant rate of rainfall $W = 0.05$ and constant rate of fertilization $\varrho = 0.1$. We can see from Fig. 4 (a) that the value of phosphate concentration at the soil surface is approximately 2. This can be explained by considering the boundary condition at the soil surface and neglecting

Table 2
Dimensionless nutrient uptake parameters for phosphate and potassium in Silt loam G.E.3 soil

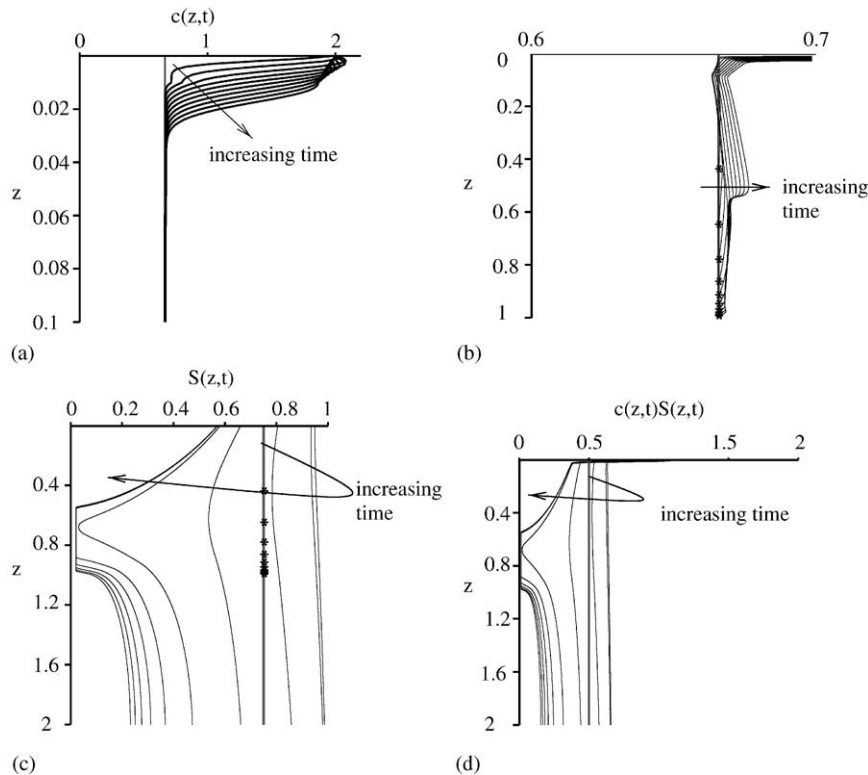|	Λ_0	Λ_1	λ_0	λ_1	α_0	α_{00}	α_1	α_{11}	α_{111}	v	$[t]$ (days)
P	0.733	4.335	43	17	111	5.196	694	34.5	1.6	21.4	505.5
K	2.532	16.55	167	67	198	32	675	199	10	3.4	82.5

Fig. 4. Numerical solution for phosphate uptake with initial water saturation profile $S_\infty = 0.75$. Corresponding initial condition for $S_\infty c_\infty = 0.5$ is $c_\infty = 0.66$ at $t = 0$. Calculations are for constant rate of rainfall $W = 0.05$ and rate of fertilizer application $\varrho = 0.1$. Flat lines on (a)–(d) show the initial conditions, others lines present the numerical solution after equal time intervals of 12 days. (a) the change in phosphate concentration due to the fertilizer movement near the soil surface; (b) change in phosphate concentration on the larger spatial scale (∗ shows the successive positions of zero order tip); (c) the water saturation profile in the soil; (d) the total amount of soluble phosphate in the soil.
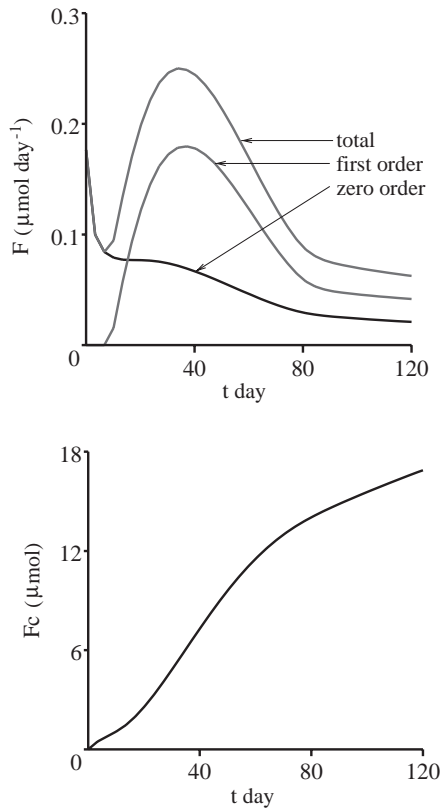
Fig. 5. Top graph shows the rate of phosphate uptake (μmol day^{-1}) by the root system as a function of time (days). Bottom graph shows the cumulative uptake (μmol) as a function of time (days).

the small D_ε term, i.e.

$$Wc - \varrho = D_\varepsilon S^{d+1} \frac{\partial c}{\partial z} \ll 1 \quad \text{thus } c \approx \frac{\varrho}{W} \text{ at } z = 0. \quad (5.1)$$

For $W = 0.05$ and $\varrho = 0.1$ we thus get that $c(0, t) \approx 2$.

We also see that the fertilizer moves relatively slowly into the main rooting region (see Fig. 4(a)). The speed of this movement can be determined from the nutrient movement equation (3.2). Neglecting the small $O(D_\varepsilon)$ diffusion term, we find that the leading order nutrient equation is the following hyperbolic partial differential equation:

$$(1 + \delta S)\frac{\partial c}{\partial t} - \left[D(S)\frac{\partial S}{\partial z} - \varepsilon k(S) \right]\frac{\partial c}{\partial z} = -F + F_w c, \quad (5.2)$$

which has characteristic nutrient movement speed[4] given by

$$\frac{dz}{dt} = -\left[D(S)\frac{\partial S}{\partial z} - \varepsilon k(S) \right]\frac{1}{1 + \delta S}. \quad (5.3)$$

We also notice that the water saturation has relaxed into pseudo-steady state giving rise to wet and dry regions in the soil, as first reported by Roose and Fowler (2004).

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[4]See Ockendon et al. (1999) for the method of characteristics for solving hyperbolic equations.

At this water pseudo-steady state $S(z, t) = S^*(z)$. Since in this case, near the soil surface, $z \approx 0$, we have $-D(S)\partial S/\partial z + \varepsilon k(S) \approx W$, expression (5.3) for the characteristic speed of nutrient movement simplifies to

$$\frac{dz}{dt} = \frac{W}{1 + \delta S^*}, \quad (5.4)$$

where S^* is the pseudo-steady state water saturation profile. For $W = 0.05$, $\delta = 1.67 \times 10^{-3}$ we find that near the soil surface $S^* \approx 0.6$, and thus the distance between the curves plotted in Fig. 4(a) should be of order $dz = 0.05 \times dt = 10^{-3}$ for dimensionless time interval $dt = 12(\text{days})/505(\text{days})$, which is what one observes also numerically.[5] Thus, in dimensional terms, the phosphate fertilizer moves into the soil at approximate speed of 4×10^{-3} cm day^{-1}, i.e. during the full 4 month long growing season fertilizer would move only to 0.5 cm depth in the soil. Thus, any effect of phosphate fertilizer on groundwater will occur on a long time-scale. However, because of its accumulation at the soil surface, we envisage the risk of phosphate pollution to be mainly due to its runoff from the soil surface.

The small-scale changes in the phosphate concentration profile due to the simultaneous water and nutrient uptake in the rooting region are presented in Fig. 4(b). As we see, the resulting concentration profiles are quite complex, however, they can be explained by the effective nutrient sink/source term in Eq. (3.2). The effective sink/source term for nutrient in that equation is given as a balance between the nutrient uptake and rise in nutrient concentration in the soil pore water due to the water uptake, i.e. by $-F + c F_w$ in Eq. (3.2). Thus, if the water uptake is large enough, then the nutrient concentration will increase, however, if it is small then the nutrient concentration will decrease due to the nutrient uptake. The characteristic step profile observed in the region $0 < z < 0.1$ develops because the initially uniform uptake of nutrients in this region is over balanced by the non-uniform water uptake.[6] We also observe the effect of the apical non-branching zone in the region $0.5 < z < 1$ where initially due to the water uptake the concentration increases but once the pseudo-steady state in the water saturation has developed and thus the water uptake in that "dry region" stops (see also Fig. 4(c) for water saturation profile), the nutrient uptake by the roots will start decreasing the nutrient concentration.

The total amount of phosphate available for plant uptake in the soil pore water is shown in Fig. 4(d). We observe that the total amount of phosphate available to the plant increases as the water saturation increases and vice versa. This is due to the fast equilibration between phosphate in solid and liquid fractions.

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[5]Estimating the distance between the curves numerically at $c = 1$ in Fig. 4(a) we find that it varies between 1.1×10^{-3} and 7.6×10^{-4}.

[6]We are modelling the simultaneous water flow inside the root system and outside in the soil as described in Roose and Fowler (2004).
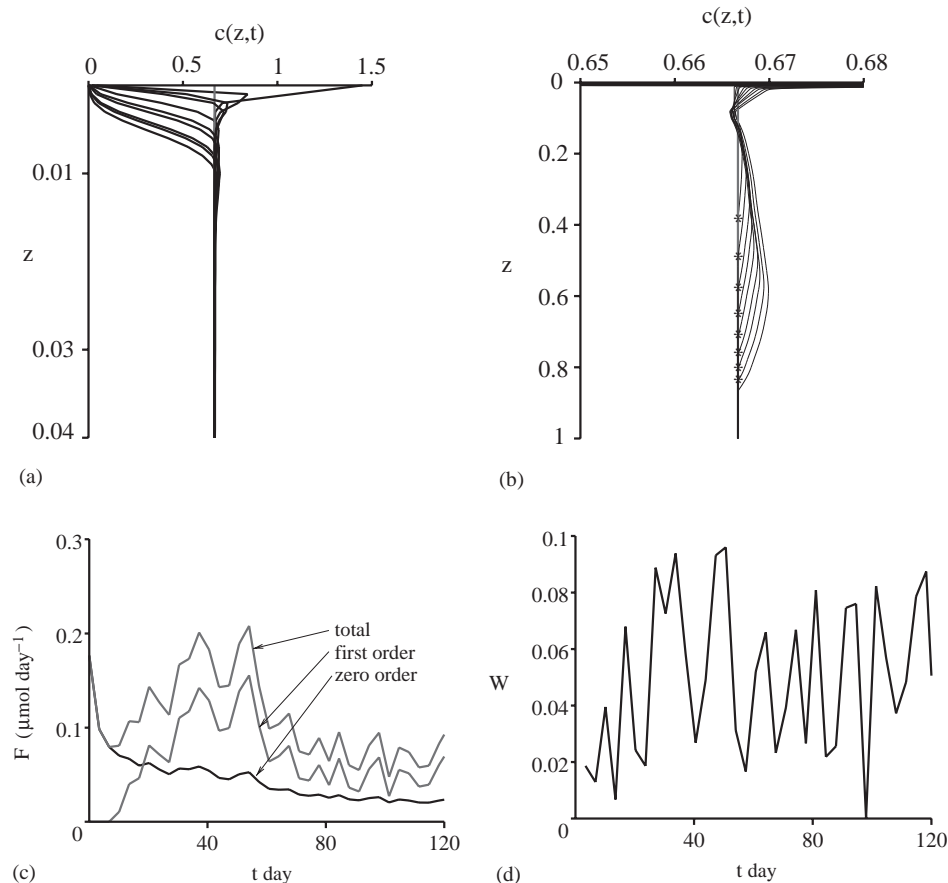
Fig. 6. Numerical solution for phosphate uptake for uniformly distributed random rainfall with average $\hat{W} = 0.05$ and single fertilization event in the beginning of growing season, i.e. $\varrho = 12$ for time $0 < t < 1$ (day) and $\varrho = 0$ for the rest of time. Thus, the overall amount of fertilizer applied is the same as in the case of constant rate of fertilization calculations presented in Figs. 4 and 5. Lines shown after equal time interval 3 days. (a) the changes in phosphate levels near the soil surface due to the single fertilization event and phosphate uptake by the plant roots; (b) changes in the phosphate concentration levels in the main rooting region (∗ shows the position of the zero order root tip); (c) the rate of phosphate uptake (μmol day^{-1}) by the plant root system as a function of time (days); (d) the rainfall pattern $W(t)$.

The rate of phosphate uptake is shown in Fig. 5. The rate of phosphate uptake by first order lateral sub-branches is at least twice as much as the rate of uptake by zero order roots. We also see that maximum rate of uptake occurs during the main growing season on about the 40th day from planting.

In Fig. 6 we can see the results of numerical experiments with spot fertilization, i.e. duration of fertilization is 1 day and the dimensionless rate of fertilization $\varrho = 12$ so that overall amount of fertilizer applied to the soil is equal to the continuous 4 month fertilization shown in Figs. 4 and 5. In Fig. 6 we have also taken the rate of rainfall to be varying in time, i.e. the average rate of rainfall is $\hat{W} = 0.05$ as in Fig. 4, but at any given time the rate of rainfall is a random number drawn from uniform distribution in the interval $0 < W < 0.1$. As we see due to the single fertilization event, the phosphate concentration at the soil surface rises initially quite high. However, at later times, when there is no fertilization, the phosphate concentration at the soil surface falls to a low level due to the removal of

it by the plant roots and due to the vertical infiltration of water. As we see, the influence of fertilizer does not reach out into the deeper layers in the soil (Figs. 6(a) and (b)). In this situation the rate of phosphate uptake by plant roots is strongly dependent on the rate of rainfall. The interesting feature to note here is that in comparison to zero order root phosphate uptake, the uptake by first order lateral branches is much more sensitive to the changes in rainfall. However, the first order lateral branches still take up most of the phosphate.

6. Comparison of this model with previous models

The most interesting result of the phosphate uptake calculation is found by comparing the cumulative uptake in the absence of water movement to that when water movement is included (see Fig. 7). We observe that the nutrient uptake in the latter case is lower than in the former case. This is because water uptake leads to the reduction in relative water saturation in the soil and
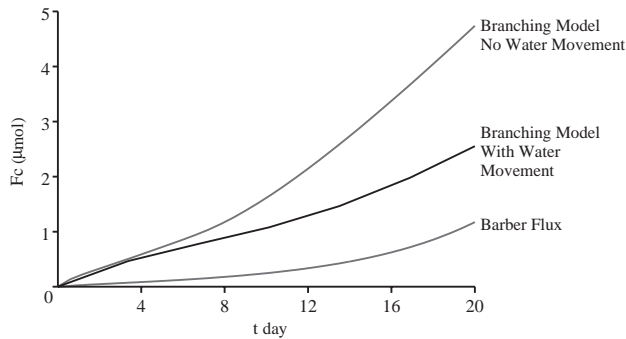
Fig. 7. A comparison between three different models used to calculate phosphate uptake by branched root systems. The curve entitled "Barber Flux" is the result of a calculation based on the model presented in Barber (1984). This model neglects water movement and inter-root competition and represents higher order roots by using a zeroth order root with an effective radius calculated using the weight of the root system, material density of roots (equal to water) and overall length of the root system. The curve entitled "Branching Model No Water Movement" is calculated using the model presented in this paper for nutrient uptake by a root branching system with the water saturation kept constant spatially and temporally. The curve entitled "Branching Model With Water Movement" is calculated using the model presented in this paper including water movement (corresponding to results shown in Fig. 4).

thus a reduction in the phosphate available for uptake. As we will now discuss, this suggests an explanation for why the Barber model only agrees with some of the experimental measurements and not others.

In the article by Roose et al. (2001) it has been shown that the classical Barber volume averaged and exponentially growing[7] (Barber, 1984; Schenk and Barber, 1979a, b) phosphate uptake model will typically underestimate the phosphate uptake when there are low levels of phosphate in the soil. However, the Barber calculation has often been found to agree with the experimental measurements in situations when there is a high level of phosphate in the soil. Barber explains this discrepancy between the measured and predicted uptake of phosphate at low soil phosphate values by the absence of root hair and mychorrizae influence in his model and because he neglects "additional chemical effects".[8] However, there are reasons to doubt each of these three explanations. Firstly, the discrepancy between measured and predicted uptake cannot be due to the neglect of root hairs, since the plant root nutrient uptake parameters were measured using roots that do have root hairs. Thus the effect of the root hairs has been "absorbed" into the experimentally measured values of Michaelis–Menten nutrient uptake coefficients F_m and K_m. Secondly, Barber often heated the soil for 6 days at

70°C in order to "stabilize" the phosphate conditions. However, because of this procedure it is unlikely that substantial quantities of fungi and their spores survived in this soil. Thus in the beginning of the experiment the probability that there was any fungi left in the soil is low, however it cannot be ruled out completely. One way of verifying the hypothesis that the mycorrhizae are important would be to quantify the amount of mycorrhizae in the soil during these experiments. Thirdly, the additional chemical effect of root exudates on nutrient uptake is quite controversial and all the phenomena observed are qualitative and not quantitative. We think that the differences between Barber's measured and predicted phosphate uptake can be explained by the failure of Barber's model to take into account the root branching structure and effects of water uptake.

The results on cumulative uptake of phosphate by a root branching structure are presented in Fig. 7. We see that the Barber calculation clearly underestimates the uptake of phosphate from the soil. Inclusion of the branching structure and root competition to the classical cylindrical root model will indeed correct the estimate of phosphate uptake "upwards". However, the inclusion of water movement in the model corrects the estimate of phosphate uptake "downwards".

We now need to discuss why Barber's model agrees so well with experimental measurements at high phosphate values, but underestimates the uptake at low phosphate values. Barber found in his experiments on root morphology and nutrient uptake Schenk and Barber (1979a, b) that the overall mass of roots in the case of high phosphate content was much higher than in the case of low phosphate content. When the root mass is higher then the water uptake is higher and therefore the water movement correction "downwards" in comparison to the branching correction "upwards" might well be such that it causes the Barber calculation to agree with the measured uptake. However, if the root mass is lower, as it is in the case of low phosphate soil, the water uptake "downward" correction is smaller and thus the Barber calculation does not agree with the experimental measurements, instead it underestimates it.

7. Conclusions

In this paper we presented a model for simultaneous water and nutrient uptake by plant root systems. We found that phosphate, due to its large buffer power, remains relatively immobile in the soil despite large-scale water movement. The risk of surface runoff due to the phosphate fertilizer application was found to be considerable since due to the continuous fertilizer application, nutrient started accumulating on the surface of the soil. However, when the continuous fertilizer application was replaced by the spot fertilization, the

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[7] Barber neglects the root branching structure and water movement in his models, however, he constantly tops up the nutrient levels in the soil.

[8] He probably means that these "additional chemical effects" are linked to the root exudates that are present on the root surface.

risk of surface runoff was reduced. We also saw that groundwater pollution with phosphate is strongly dependent on water movement and the soil's ability to resupply phosphate from the solid fraction, i.e. buffer power. Thus, if there is a substantial increase in the soil moisture, then more phosphate is released from the solid fraction and carried to the deeper layers in the soil. The future avenues of mathematical modelling work should clearly take into account the higher dimensional variation in the nutrient uptake. Although the results presented in this paper were calculated in one dimension (vertical in soil depth), the extensions of this model to two and three dimension are possible and could be carried out if the experimental conditions require it.

Using the model presented in this paper we were also able to give new insight into the discrepancies and inaccuracies present in previous models. However, in order to clarify and verify this, more accurate simultaneous measurements of nutrient and water uptake together with root branching structure development should be carried out. In order to get conclusive experimental verification of different mechanisms that control plant nutrient uptake this consistent experimental effort has to be made in order to determine if the error rises from inaccuracies in the single root model (i.e. Nye–Tinker–Barber model), as argued by Barber and coworkers, or from neglecting water movement and not treating the root branching structure adequately. With this article we have developed a consistent systematic way for calculating highly buffered nutrient uptake by the root branching structures, thus enabling the results of such consistent experiments to be analysed in an easily interpretable manner.

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