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## **A mathematical model of plant nutrient uptake**

Received: 1 September 1999 / Revised version: 2 November 2000 /  
Published online: 16 March 2001 – © Springer-Verlag 2001

**Abstract.** The classical model of plant root nutrient uptake due to Nye, Tinker and Barber is developed and extended. We provide an explicit closed formula for the uptake by a single cylindrical root for all cases of practical interest by solving the absorption-diffusion equation for the soil nutrient concentration asymptotically in the limit of large time. We then use this single root model as a building block to construct a model which allows for root size distribution in a more realistic plant root system, and we include the effects of root branching and growth. The results are compared with previous theoretical and experimental studies.

### **1. Introduction**

Conventional agriculture requires the use of fertilisers to maximise crop yields and this is an issue of concern for several reasons. Many fertilisers are applied in excess because the amounts required for optimum economic yield cannot be estimated with precision (Swoboda, 1990). The surplus pollutes groundwater with nitrate and surface water with both nitrates and phosphate, decreasing drinking water quality and amenity value. Neither the economics nor the environmental impact of such practices are sustainable (Magdoff et al., 1997). A further concern is that of understanding how climatic change will affect crop yield and nutrient uptake, through variation in CO<sub>2</sub> concentration, sunlight, temperature and rainfall (Wullschleger et al., 1994). A better understanding of the rates at which plants assimilate nutrients would therefore be welcome.

Plants require thirteen nutrients from the soil for their growth and deficiencies in their uptake can have profound dietary consequences for human health (Welch and Graham, 1999). The principal nutrients are nitrogen, phosphorus, sulphur, potassium, magnesium and calcium, and are taken up mainly as ionic species (e.g. nitrate, phosphate) from soil water. Nutrient uptake is thought to occur through binding to certain specific ion-binding proteins in the root wall (Bowling, 1976), so that the uptake mechanism is kinetically similar to the Michaelis-Menten reaction of enzyme kinetics (Murray, 1993). In this paper we will consider the root as a uniform

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*Key words or phrases:* Plant nutrient uptake – Root system – Mathematical model

cylindrical structure with uptake localised on the surface. We shall not consider the extra complications associated with root hairs or an internal uptake pathway, nor indeed shall we consider the extra nutrient uptake due to mycorrhizae, which essentially act as fungal nutrient conduits to the root system (Marschner, 1995).

The classical model for nutrient uptake is due to Nye and Tinker (1977) and Barber (1984). It supposes a single cylindrical root to be surrounded by an infinite extent of soil, with prescribed far field soil water concentration. The nutrient diffuses through the soil water (via the pore water), and its uptake at the root is given by a Michaelis-Menten dependence on concentration. This absorption-diffusion model thus consists of a linear diffusion equation with the nonlinear root surface absorption condition. Because of the nonlinearity, Nye and Tinker (1977) and Barber (1984) were forced to solve the problem numerically. Although this is straightforward, it requires a separate calculation for each parameter set, which is time consuming and in addition means that the extension of the single root model to more realistic root systems is hazardous. In this paper we deal with this problem by providing a fully explicit approximation to the basic Nye-Tinker-Barber model; we are then able to build a more realistic model which incorporates root size distribution.

On a larger scale, root systems are similar to tree branch systems. As roots grow, they form sub-branches of smaller radius, which themselves grow and form their own sub-branches. Root structure depends on the plant (genetics), and also on the soil characteristics (phenotypic plasticity). For example, Marschner (1995) showed that there is a prevalence of proteoid roots in *Lupinus albus* L. (the white lupin) when grown in a phosphorus-deficient environment. We do *not* try to account for the ability of a root system to evolve according to the environment it finds itself in.

As described above, the Nye-Tinker-Barber model combines diffusion of nutrient through the soil with its absorption at the root surface. It also includes convection by soil water; Jungk and Claassen (1997) observed that for most nutrients, the convective transport was negligible, and we confirm this here.

The plan for the rest of this paper is as follows. In section 2 we present and analyse the Nye-Tinker-Barber model, deriving an explicit formula for the nutrient uptake by a single cylindrical root. In section 3 a root system model is presented and analysed, using the results of section 2 as an ingredient. Concluding remarks follow in section 4.

## 2. The Nye-Tinker-Barber model

We will derive the diffusion model in some detail, since the nutrient in the soil can exist in solution but also as adsorbed particulate in the soil phase. Let  $c$  be the concentration of nutrient in pore water (mass per unit volume of pore water) and  $c_s$  the ion concentration in solid form, mass per unit volume of soil. The relevant solid concentration is that adsorbed at solid surfaces, and more properly  $c_s$  might be measured as mass per unit surface area of solid phase. This simply involves subsequent multiplication by the soil specific surface area (surface area per unit volume of soil) to convert to a volume concentration. Although this needs to be borne in mind, it does not effect the derivation of the model and is therefore ignored.

Conservation of  $c$  and  $c_s$  follows from an approximate two-phase model, which can be written

$$\frac{\partial c_s}{\partial t} = d_s,$$

$$\frac{\partial}{\partial t}(\phi c) + \nabla \cdot (c\mathbf{u}) = \nabla \cdot [\phi D \nabla c] - d_s, \tag{2.1}$$

where  $\phi$  is the liquid saturation (equal to the porosity if the soil is saturated),  $\mathbf{u}$  is the Darcy flux of pore water,  $D$  is the diffusion coefficient of nutrient in pore water,  $d_s$  is the interfacial ion transport, which is non-zero if the liquid is below saturation.

In order to derive an equation for  $c$  alone, we need to prescribe how ion adsorption occurs. A simple assumption is that adsorption and desorption of ions at the soil particle surface are proportional to the respective concentrations, whence we can write

$$d_s = k_a c - k_d c_s, \tag{2.2}$$

and if  $k_d$  is large (relative to the diffusion time) then (2.1) implies

$$c_s = b c, \tag{2.3}$$

where  $b = k_a/k_d$  is called the soil buffer power (Barber, 1984; Nye and Tinker, 1977).

We now obtain an equation for  $c$  by adding the equations for  $c_s$  and  $c$  in (2.1), using (2.3), so that ( $\phi$  and  $D$  being constant)

$$(\phi + b) \frac{\partial c}{\partial t} + \nabla \cdot (c\mathbf{u}) = \phi D \nabla^2 c. \tag{2.4}$$

In general  $\mathbf{u}$  is determined through solution of local groundwater flow to the root surface. We presume this is prescribed.

### 2.1. Boundary conditions

At the root surface, we presume an uptake flux of Michaelis-Menten type. If  $\mathbf{n}$  is a unit vector at the root surface pointing into the soil, then the flux is taken to be

$$\phi D \frac{\partial c}{\partial n} - c u_n = \frac{F_m c}{K_m + c}, \tag{2.5}$$

where  $F_m$  and  $K_m$  are properties of the root surface. It is common to add an extra term  $-E$  to the right hand side of (2.5), to represent the fact that there is a minimum nutrient level in the soil below which no uptake occurs. Practical values of  $E$  are so low, however, that this term appears generally to be negligible, and hence we omit its consideration henceforth.

The initial soil concentration is prescribed, and equal to the farfield concentration away from the root:

$$c \rightarrow c_0 \quad \text{as} \quad |\mathbf{x}| \rightarrow \infty. \tag{2.6}$$

For the specific case of a cylindrical root the problem can be written in terms of polar radius  $r$ , and moreover the Darcy flux (satisfying  $\nabla \cdot \mathbf{u} = 0$ ) is given as

$u = -aV/r$ , where  $V$  is the water flux to the root and  $a$  is the root radius. The absorption-diffusion model is then

$$\begin{aligned}(\phi + b)\frac{\partial c}{\partial t} - \frac{aV}{r}\frac{\partial c}{\partial r} &= \frac{\phi D}{r}\frac{\partial}{\partial r}\left(r\frac{\partial c}{\partial r}\right), \\ \phi D\frac{\partial c}{\partial r} + Vc &= \frac{F_m c}{K_m + c} \quad \text{on } r = a, \\ c &\rightarrow c_0 \quad \text{as } r \rightarrow \infty,\end{aligned}\tag{2.7}$$

and  $c = c_0$  at  $t = 0$ .

## 2.2. Non-dimensionalisation

We scale the variables by writing

$$c = K_m c^*, \quad r = ar^*, \quad t = \frac{(\phi + b)a^2}{\phi D} t^*,\tag{2.8}$$

so that the dimensionless model is, on dropping asterisks,

$$\begin{aligned}\frac{\partial c}{\partial t} - Pe\frac{1}{r}\frac{\partial c}{\partial r} &= \frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial c}{\partial r}\right), \\ \frac{\partial c}{\partial r} + Pec &= \frac{\lambda c}{1 + c} \quad \text{at } r = 1, \\ c &\rightarrow c_\infty \quad \text{as } r \rightarrow \infty, \quad t \rightarrow 0,\end{aligned}\tag{2.9}$$

where the parameters are the Péclet number

$$Pe = \frac{aV}{\phi D},\tag{2.10}$$

the uptake coefficient

$$\lambda = \frac{F_m a}{\phi D K_m},\tag{2.11}$$

and the farfield scaled concentration

$$c_\infty = \frac{c_0}{K_m}.\tag{2.12}$$

The dimensionless (scaled with  $\phi D K_m/a = F_m/\lambda$ ) nutrient flux to the root is

$$F = \left. \frac{\lambda c}{1 + c} \right|_{r=1},\tag{2.13}$$

and our object is to calculate this as a function of  $t$ ; evidently it depends on the parameters  $Pe$ ,  $\lambda$  and  $c_\infty$ , which implies  $F$  may vary widely with different plant and soil characteristics.

2.3. Parameter estimation

Typical estimates of soil water movement and diffusion coefficients are  $V \sim 10^{-7}$  cm s<sup>-1</sup>,  $D \lesssim 10^{-5}$  cm<sup>2</sup>s<sup>-1</sup>, while root radii of interest are  $a \sim 5 \times 10^{-4} - 6 \times 10^{-2}$  cm. Even for  $a = 10^{-1}$  cm, and if  $\phi$  is as low as 0.1,  $Pe \sim 10^{-2}$ , and mostly will be lower. This implies that the Péclet number is generally negligible, and we begin by ignoring it. Obviously, this assumption needs to be scrutinised in (2.9) if, for example,  $\lambda \sim Pe$ , and this warning needs to be borne in mind: we return to this case later.

We give typical plant macro-nutrient characteristics for maize in a normal soil, according to Barber (1984), in Table 1. Computed values of  $\lambda$  and  $c_\infty$  are then as shown in Table 2. Typically we see that  $\lambda \gtrsim 1$ , while  $c_\infty$  may be large or small. If instead we focus on the nutrient, phosphorus, then the values of the parameters for soybean, lettuce and tomato are shown in Table 3; for this mineral,  $\lambda$  and  $c_\infty$  are  $O(1)$  for different plants.

In Table 1 we see that the diffusional time scale  $a^2(\phi + b)/D\phi$  is typically of order 10<sup>5</sup> seconds or less, i. e. of the order of one day. We are specifically concerned in this paper with the growth of agricultural plants over a growing season of about four months  $\approx 10^7$  seconds, and thus we see that in the dimensionless model, we are interested in the evolution of the solution over long time scales of  $O(10^2)$ .

**Table 1.** Dimensional parameter estimation for maize after Barber (1984). In the right hand column, values of  $a$ ,  $\phi$  and  $D$  are taken as 0.02 cm, 0.3 and  $0.3 \times 10^{-5}$  cm<sup>2</sup> s<sup>-1</sup>, respectively.

Parameter	$c_0$ ( $\mu\text{mol cm}^{-3}$ )	$b$ –	$F_m$ ( $\mu\text{mol cm}^{-2}\text{s}^{-1}$ )	$K_m$ ( $\mu\text{mol cm}^{-3}$ )	$\frac{a^2(\phi + b)}{D\phi}$ (s)
NO <sub>3</sub> <sup>-</sup>	5	1.0	10 <sup>-5</sup>	0.025	$0.58 \times 10^3$
K	0.046	39	$3 \times 10^{-5}$	$14 \times 10^{-3}$	$1.75 \times 10^4$
S	0.1	2	$3 \times 10^{-7}$	10 <sup>-2</sup>	$1.02 \times 10^3$
P	$2.9 \times 10^{-3}$	239	$3.26 \times 10^{-6}$	$5.8 \times 10^{-3}$	$1.06 \times 10^5$
Mg	10 <sup>-3</sup>	1.2	$4 \times 10^{-6}$	0.15	$0.67 \times 10^3$
Ca	$0.8 \times 10^{-3}$	156	10 <sup>-6</sup>	4	$0.69 \times 10^5$

**Table 2.** Non-dimensional parameter estimation for maize with  $D = D_f f$ , where  $D_f = 10^{-5}$  cm<sup>2</sup> s<sup>-1</sup>,  $f = \phi = 0.3$ .

Parameter	$\lambda$	$c_\infty$
NO <sub>3</sub> <sup>-</sup>	8.8	200
K	47	3.28
S	0.66	10
P	12.3	0.5
Mg	0.55	$6.7 \times 10^{-3}$
Ca	$5.5 \times 10^{-3}$	$2 \times 10^{-4}$

**Table 3.** Parameter estimation for phosphorus for different plants.

Plant	$F_m$	$K_m$	$\lambda$	$c_\infty$
Soybean	$6.4 \times 10^{-7}$	$2.7 \times 10^{-3}$	5.2	1.07
Lettuce	$10.6 \times 10^{-7}$	$2 \times 10^{-3}$	11.7	1.45
Tomato	$49.9 \times 10^{-7}$	$6.1 \times 10^{-3}$	18.2	0.475

2.4. Solution strategy

In view of the wide variety of parameter values for  $\lambda$  and  $c_\infty$ , which we see in table 2, it is possible to attempt to solve the model in various asymptotic limits ( $\lambda \gg 1$ ,  $c_\infty \gg 1$ , etc.), and this approach was adopted by Roose (2000). However, a more direct observation is that from Table 1, we see that the longest diffusive timescale is for phosphorus in maize, and is approximately one day. Since the time scale for plant growth is much larger than this, we only require the solution of (2.9) for large times. By restricting ourselves in this way, we can derive an approximate solution which is valid for all values of  $\lambda$  and  $c_\infty$  (so long as  $Pe$  is negligible). With  $Pe = 0$ , we have to solve

$$\begin{aligned} \frac{\partial c}{\partial t} &= \frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial c}{\partial r} \right), \\ \frac{\partial c}{\partial r} &= \frac{\lambda c}{1 + c} \quad \text{on } r = 1, \\ c &\rightarrow c_\infty \quad \text{as } r \rightarrow \infty, \end{aligned} \tag{2.14}$$

and we wish to compute the dimensionless flux  $F = \frac{\partial c}{\partial r} |_{r=1}$ . At large times, the concentration profile has spread out over a large distance. To specify this, we write

$$t = \frac{\tau}{\sigma^2}, \quad r = \frac{R}{\sigma}, \tag{2.15}$$

where  $\sigma \ll 1$ . The concentration field in  $R \sim 1$  sees a boundary at  $R = \sigma \ll 1$ , and it seems reasonable to anticipate that a farfield similarity solution will be appropriate. In terms of a similarity variable  $R^2/\tau$ , a solution of the far field diffusion equation is

$$c = c_\infty - B E_1 \left( \frac{R^2}{4\tau} \right), \tag{2.16}$$

where

$$E_1(x) = \int_x^\infty \frac{e^{-y}}{y} dy, \tag{2.17}$$

is the exponential integral.

There is an inner region near the root, where we revert to the variable  $r$ , so that

$$\sigma^2 \frac{\partial c}{\partial \tau} = \frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial c}{\partial r} \right), \tag{2.18}$$

with solution

$$c = c_1 + F \ln r + O(\sigma^2), \tag{2.19}$$

where  $F$  is the dimensionless flux at the root. Note that  $c_1$  and  $F$  may be functions of  $\tau$  in (2.19). We determine  $F$  by matching (2.19) and (2.16). As  $x \rightarrow 0$ , the exponential integral is given by

$$E_1(x) \sim -\gamma - \ln x + O(x), \tag{2.20}$$

where  $\gamma$  is Euler’s constant, so that (2.16) as  $R \rightarrow 0$  is given by

$$c \sim c_\infty + \gamma B - B \ln 4\tau + 2B \ln \sigma + 2B \ln r + O(\sigma^2). \tag{2.21}$$

This indicates that (2.16) is correct to order  $O(\sigma^2)$ , and also determines  $B$  and  $c_1$  through the matching conditions

$$B = \frac{F}{2}, \quad c_1 = c_\infty + \frac{F}{2}(\gamma - \ln 4\tau + 2 \ln \sigma), \tag{2.22}$$

and the flux is finally determined through application of the root surface boundary condition:

$$F = \frac{\lambda[c_\infty + \frac{F}{2}\{\gamma - \ln 4t\}]}{1 + c_\infty + \frac{F}{2}\{\gamma - \ln 4t\}}. \tag{2.23}$$

As  $t \rightarrow 0$ , the two roots of this quadratic equation approach  $\lambda$  and 0, and the correct root is determined as that which approaches  $\lambda$ . Evidently the expression for  $F$  is not valid for times of  $O(1)$ . It is algebraically convenient to ‘fix’ this by introducing a time origin shift which forces  $F \rightarrow \lambda c_\infty / (1 + c_\infty)$  at  $t = 0$ . From (2.23), we can evidently do this by replacing  $\ln 4t$  by  $\ln(4t + e^\gamma)$ ; after some algebra, the correct solution for  $F$  can be written as

$$F(t) = \frac{2\lambda c_\infty}{1 + c_\infty + \frac{\lambda}{2} \ln(4e^{-\gamma}t + 1) + [4c_\infty + \{1 - c_\infty + \frac{\lambda}{2} \ln(4e^{-\gamma}t + 1)\}^2]^{1/2}}. \tag{2.24}$$

### 2.5. Pore water convection

The Equation (2.24) gives an explicit expression for the root uptake flux, valid for all  $t \gg 1$  and for all  $\lambda$  and  $c_\infty$ , providing the Péclet number is sufficiently small, the precise condition being, from (2.9) and (2.22),

$$Pe \ll \frac{\lambda}{1 + c_\infty - \frac{F}{2} \ln(4e^{-\gamma}t + 1)}, \tag{2.25}$$

and this is valid for all  $t$  if  $Pe \ll \lambda / (1 + c_\infty)$ . Consulting Table 2, we see that the dangerous ions are nitrate, where  $\lambda / (1 + c_\infty) \approx 0.044$ , and sulphur, where  $\lambda / (1 + c_\infty) \approx 0.06$ . (calcium is less significant, since it has  $\lambda \ll 1$ .) These can be comparable to  $Pe$  if root radii are larger than 0.5 cm. However, note that as long as  $Pe$  is small, it can still be neglected in solving the diffusion equation, so that the only modification to (2.24) if  $Pe \sim \lambda / (1 + c_\infty)$  is that  $F = \partial c / \partial r|_{r=1}$  in (2.22), which is no longer the total flux. In fact, the total flux is then

$$F_{\text{tot}} = Pe c_1 + F = \frac{\lambda c_1}{1 + c_1}; \tag{2.26}$$

solving this as before, and making the time origin shift (which is the same), we find, for  $Pe \ll 1$ ,

$$F_{\text{tot}} = \frac{2\lambda c_\infty}{1 + c_\infty + \frac{L}{2}(\lambda - Pe) + \left\{ [1 - c_\infty + \frac{L}{2}(\lambda - Pe)]^2 + 4c_\infty(1 - \frac{L}{2}Pe) \right\}^{1/2}}, \tag{2.27}$$

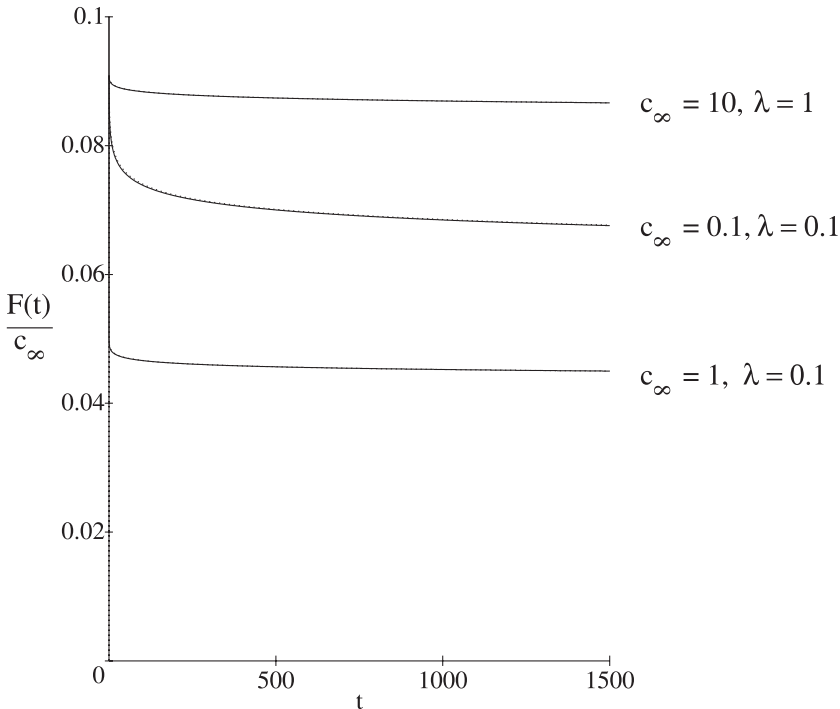
where

$$L = \ln(4e^{-\gamma}t + 1). \tag{2.28}$$

Figure 1 shows comparisons of the formula (2.24) to numerical solutions of the model (with  $Pe = 0$ ) for several different parameter values of  $c_\infty$  and  $\lambda$ . It can be seen that the agreement is good.

Finally we point out that it is straightforward to extend the results above if  $Pe \sim 1$ . The only difference is that the far field solution which replaces (2.16) is

$$c = c_\infty - B \int_{R^2/4\tau}^\infty \frac{e^{-\eta}d\eta}{\eta^{1+Pe/2}}, \tag{2.29}$$



**Fig. 1.** Comparison of the formula (2.24) for the scaled flux  $F/c_\infty$  with that obtained by numerical solution of the full model, for three different values of  $\lambda$  and  $c_\infty$ . The approximating formula is virtually exact.



while the inner solution for  $r \sim 1$  is ( $F = \frac{\partial c}{\partial r} \Big|_{r=1}$ )

$$c = c_1 + \frac{F}{Pe}(1 - r^{-Pe}), \tag{2.30}$$

and the solution procedure then follows as before. We leave the details to the reader, in view of the common irrelevance of such large values of  $Pe$ .

### 3. Root system model

We wish to calculate the nutrient uptake by the root system of an agricultural plant like maize. We will use the nutrient uptake by a single isolated root as a constituent in calculating this expression. Specifically, we will suppose that in a developing root system, the roots are of a typical radius  $a$ , and are separated by distances much larger than  $a$ . If this is the case, then the single root uptake can be used for each root, and we have what might be called ‘dilute network theory’. Maize has root radii in the range 0.001–0.05 cm and inter-root distances of the order of 1 cm (Pagès *et al.*, 1989), and thus this assumption of root sparseness is well satisfied. More generally, we will always suppose that roots are separated by a distance that is much larger than their radius (Varney *et al.*, 1991), and hence we can use the expression for the flux that was derived in the preceding section.

The dimensional flux  $F_D$  into a root of radius  $a$  is given from (2.24), if  $Pe$  is negligible, by using (2.13) to obtain

$$F_D = \frac{2F_m c_\infty}{1 + c_\infty + \frac{1}{2}L + [4c_\infty + (1 - c_\infty + \frac{1}{2}L)^2]^{1/2}}, \tag{3.1}$$

where, in terms of dimensional time  $t_D$  in (2.8),

$$L = \ln[1 + 4e^{-\gamma} \frac{\phi D}{(\phi + b)a^2} t_D], \tag{3.2}$$

where  $\gamma \approx 0.5772$ , so  $e^{-\gamma} \approx 0.56$ . We now wish to use (3.1) to construct a model for the nutrient uptake of a plant root system. We conceptualise the root mass as consisting of a distribution of roots of radius  $a$  and length  $l(a)$ . In the soil, we visualise a network of well separated roots, so that the flux to each root can be represented by (3.1), which, it can be seen, is a highly non-linear function of  $a$ . We suppose that the roots are distributed homogeneously in the soil, and are distinguished by their order (Nye and Tinker, 1977): the roots which emerge from the seed are zero order roots, and so on. Roots of cereal plants, such as maize, typically have three or four orders. Root branching is described as follows. Mature roots consist of a basal non-branching zone of length  $l_a$ , an apical non-branching zone of length  $l_b$ , and (if  $l > l_a + l_b$ ) a branching zone between these, wherein new branches develop at intervals of  $l_n$ , the inter-nodal distance. Hence, a root of length  $l$  has  $[(l - l_a - l_b)/l_n]_+$  branches, where  $[x]_+ = \text{int}(x)$ , assumed non-negative.

We suppose roots of different orders  $i$  have different radii  $a_i$ , and that they grow at a rate which decreases with age. Specifically, we take the elongation of roots of order  $i$  to be

$$L_i = r_i(1 - \frac{l}{K_i}). \tag{3.3}$$

The above description of root order development is similar to that of Pagès *et al.*, (1989) in studying the evolution of root architecture. The details are not essential to the structure of the model, now to be described, but some such constitutive detail must be provided.

Let the root size density function of order  $i$  roots be  $\phi_i(l, t)$ , so that  $\phi_i dl$  is the number density of roots of order  $i$  and lengths between  $l$  and  $l + dl$ , measured as a number of roots per unit volume of soil. We are assuming that root spacing is sufficiently small that a ‘representative elementary volume’ of soil can be chosen, large enough so that  $\phi_i$  is well defined in the sense of the continuum hypothesis.

The structure of the model is essentially that of an age-dependent population growth model, where root length masquerades as age, and the rate of ‘aging’ is non-uniform. Conservation of root density leads to the hyperbolic equation

$$\frac{\partial \phi_i}{\partial t} + \frac{\partial}{\partial l}(L_i \phi_i) = -\mu_i \phi_i, \tag{3.4}$$

where  $\mu_i$  is the mortality rate of order  $i$  roots.

At  $t = 0$  we take

$$\begin{aligned} \phi_0(l, 0) &= \phi_{00}(l), \\ \phi_i(l, 0) &= 0, \quad t > 0, \end{aligned} \tag{3.5}$$

where  $\phi_{00}(l)$  is prescribed: the plant has germinated but no root development has taken place. At  $l = 0$ , the renewal equation describes the generation of new roots, and we have

$$\begin{aligned} \phi_0(0, t) &= 0, \\ r_i \phi_i(0, t) &= \int_0^\infty L_{i-1}(l) G_{i-1}(l) \phi_{i-1}(l, t) dl, \end{aligned} \tag{3.6}$$

where  $G_{i-1}(l)$  is the length specific root generation rate, i.e., the number of roots of order  $i$  created per root of order  $i - 1$  per unit length. For the particular branching rule described above

$$G_{i-1}(l) = \sum_{k=0}^\infty \delta[l - l_{0,i-1} - kl_{n,i-1}], \tag{3.7}$$

where  $l_0 = l_a + l_b$  is the sum of apical and basal non-branching zones, and  $l_n$  is the inter-nodal distance.

The solution of (3.4) can be determined using characteristics. There is a dividing characteristic from  $l = 0, t = 0$ , which is

$$l = l^*(t) = K_i(1 - e^{-r_i t/K_i}), \tag{3.8}$$

and then for  $l > l^*$ ,

$$\phi_i = \phi_i[K_i - (K_i - l)e^{r_i t/K_i}, 0] \exp\left[\left(\frac{r_i}{K_i} - \mu_i\right)t\right], \tag{3.9}$$

while for  $l < l^*$ ,

$$\phi_i = \frac{\phi_i[0, t - \frac{K_i}{r_i} \ln\{\frac{1}{1-l/K_i}\}]}{[1 - \frac{l}{K_i}]^{1-\mu_i K_i/r_i}}, \tag{3.10}$$

where the initial values  $\phi_i(\xi, 0)$ ,  $\xi > 0$ ,  $\phi_i(0, \tau)$ ,  $\tau > 0$ , are given by (3.5) and (3.6), the latter of which determines  $\phi_i$  in terms of  $\phi_{i-1}$ .

The total length of order  $i$  roots per unit volume of soil is

$$l_i = \int_0^{K_i} l\phi_i(l, t) dl, \tag{3.11}$$

and the nutrient uptake by order  $i$  roots per unit volume is therefore

$$F_i = 2\pi a_i l_i F_D(t; a_i), \tag{3.12}$$

where  $F_D$  is given by (3.1) with  $a = a_i$  in (3.2) and  $\lambda = F_m a_i / DK_m$ ; the total uptake per volume by the root system is then

$$F_{\text{sys}} = \sum_i F_i. \tag{3.13}$$

Figure 2 shows the nutrient uptake rate and the cumulative uptake calculated from this model using the root branching parameters shown in Table 4, following Pagès et al., (1989);  $\mu_i$  is taken to be zero in these calculations. In order to compare this solution with the Barber–Nye–Tinker derived flux, we need to consider the average root radius of the root system. In their calculations, Nye and Tinker (1977) and Barber (1984) use an average root radius derived from experiments. For example, Barber (1984) and Schenck and Barber (1979) use a root volume averaged radius evaluated at the end of the experiment. The total root length development in the case of the ‘Barber experiment’ is calculated using the total length of the root system at the beginning and end of the experiment assuming that the elongation rate  $\kappa$  is given by  $\kappa = (\ln(l_B(\tau)) - \ln(l_B(0))) / \tau$ , where  $l_B(t)$  is the total length of the root system at time  $t$ , i.e.,  $l_B = \sum_i l_i$ ;  $\tau$  is the duration of the experiment (typically  $\tau = 21$  days). Hence the total length as a function of time in the case of the Barber experiment is then given by

$$l_B(t) = l_B(0)e^{\kappa t}. \tag{3.14}$$

In terms of the root size distribution  $\phi_i(l, t)$ , the total root volume per unit volume of soil at time  $t$  is

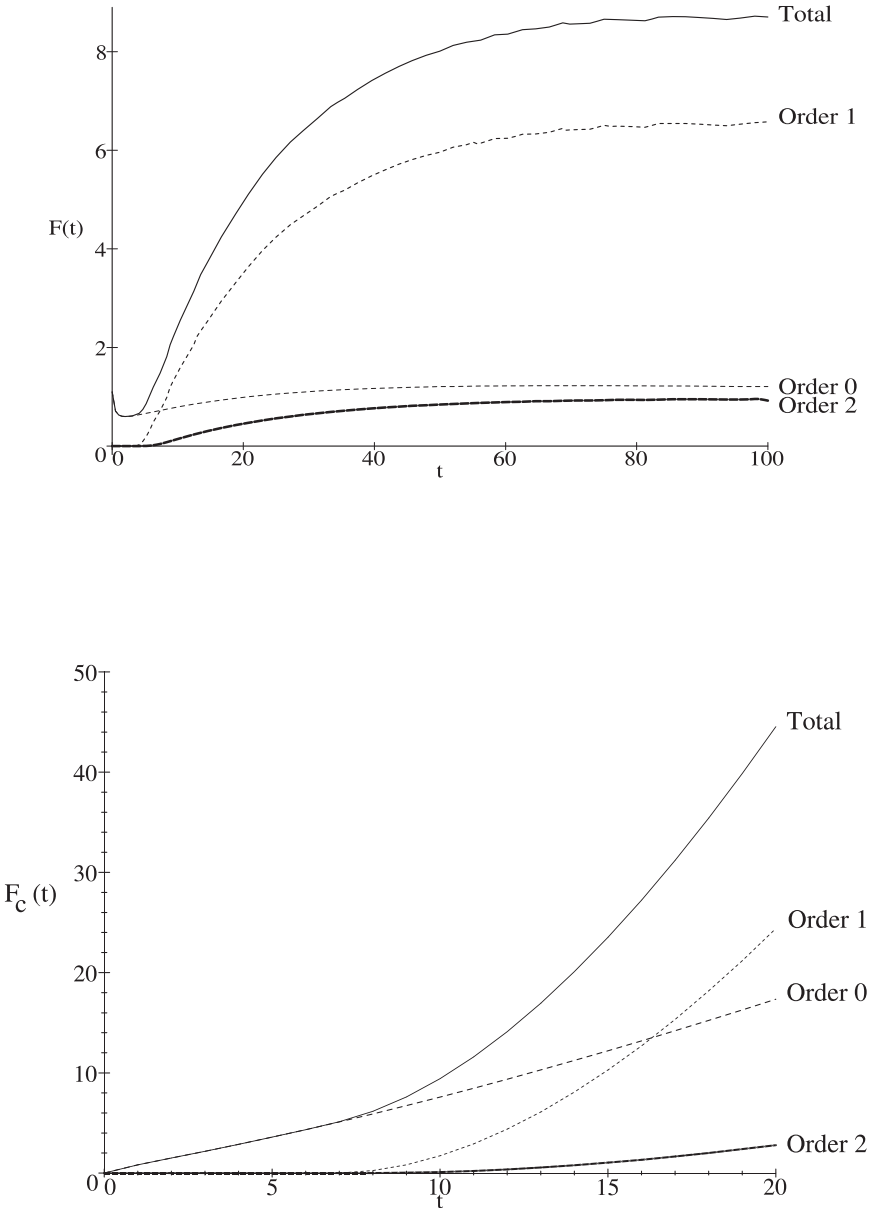
$$V = \sum_i \pi a_i^2 \int_0^{K_i} l\phi_i(l, t) dl, \tag{3.15}$$

where the total root length is given by (3.11). Hence the mean volume averaged root radius at time  $t$  is

$$\bar{a}_v = \left( \frac{\sum_i a_i^2 \int_0^{K_i} l\phi_i dl}{\sum_i \int_0^{K_i} l\phi_i dl} \right)^{1/2}, \tag{3.16}$$

and we define the Barber flux to be  $2\pi\bar{a}_v(\tau)l_B(t)F_D(t; \bar{a}_v)$ , based on this representative radius; i.e.,

$$F_B = 2\pi \left( \frac{\sum_i a_i^2 \int_0^{K_i} l\phi_i dl}{\sum_i \int_0^{K_i} l\phi_i dl} \right)_{t=\tau}^{1/2} l_B(t)F_D(t; \bar{a}_v), \tag{3.17}$$



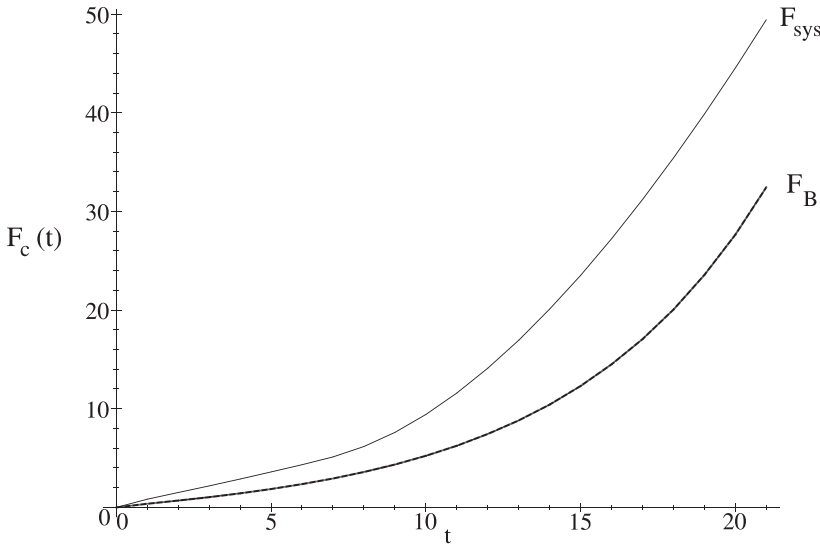
**Fig. 2.** Nutrient uptake curves for the root branching model. The upper figure gives the rate of uptake for each order of roots, together with the total uptake, while the lower figure gives the integral of these curves in time, i.e. the cumulative uptake.

as compared to the ‘correct’ value from (3.13),

$$F_{\text{sys}} = 2\pi \sum_i a_i \int_0^{K_i} l \phi_i dl F_D(t; a_i). \tag{3.18}$$

**Table 4.** Root branching parameters.

Order $i$	0	1	2
$K_i$ [cm]	51	8	0.1875
$r_i$ [cm day <sup>-1</sup> ]	2	6.4	1.5
$l_{0,i}$ [cm]	15.7	2.7	—
$l_{n,i}$ [cm]	0.7	0.7	—



**Fig. 3.** A comparison of the root branching model calculated cumulative uptake  $F_{sys}$  with the Barber uptake  $F_B$  given by (3.17).

Figure 3 compares the calculated Barber flux  $F_B$  with the root system value  $F_{sys}$  for the system developing according to the branching rules developed earlier. It can be seen that there is a significant difference in the results.

**4. Conclusions**

The classical model of nutrient uptake by a plant root system assumes an appropriately equivalent cylindrical root, with the Barber flux (3.17) being determined in terms of the advection-diffusion-absorption flux  $F_D$ , which depends on the effective root radius and time. In previous studies, this flux has been calculated numerically, and so must be recalculated for each plant and each effective root radius. We have shown in this paper that for most macronutrients, with the exception of sulphur and also nitrate in nitrogen rich soils, that pore water advection is negligible, and also that the plant growth time scale is always much longer than the nutrient diffusional time scale. In this circumstance, it is possible to find an explicit closed form solution

to the diffusion-adsorption problem, and in fact this can be extended to include the effects of pore water advection of sulphur and nitrate.

The existence of the resulting explicit formula for the nutrient uptake renders the numerical solution of the advection-diffusion-adsorption model obsolete, and in addition provides a basis for a rational calculation of the nutrient uptake in a distributed root mass. We show how a root system distribution model can be formulated similarly to an age-structured population model, and indeed the equation for the evolving size distribution can be solved explicitly. This leads to a correctly formulated calculation of the system nutrient uptake, which differs significantly from the equivalent Barber flux calculated using the Nye–Tinker–Barber formulation.

This result provides the basis for future experimental work, and will also provide a platform for the development of whole plant nutrient uptake models, with a view to establishing the interaction of plant growth and yield with rainfall levels and fertilisation programmes.

*Acknowledgements.* Tiina Roose acknowledges the award of a studentship through a grant from Oxford University to its Environmental Change Institute.

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