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A Steady-State Model of Nutrient Uptake Accounting for Newly Grown Roots

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ABSTRACT

A model of solute uptake that accepts root growth, water uptake, and soil solution concentration as time-varying input is required to interactively link plant and soil processes. The advantage of the steady-state approach to solute uptake over more exact numerical solutions lies in the independence of the mathematical solution to previous conditions. Uptake thus calculated can accommodate unpredictable changes in root growth and mortality, root density, water uptake rates, and sources and sinks of nutrients such as decomposition and leaching, as required in simulating plant growth for multiple seasons in a dynamic soil environment. Previous steady-state models were improved by including nonlinear uptake kinetics and the contribution of new root growth to uptake. The correction for new root growth is most important for relatively fast-growing plants and immobile nutrients. The importance of each model parameter, as indicated by sensitivity analysis, depends on the values of other parameters. For example, root surface area and uptake kinetics are important when solution concentrations at the root surface are high, while root length, water uptake rate, and diffusion become important when delivery of solute to the root surface is limiting. Because the limiting factors can vary with environmental and plant conditions, it is important to represent these aspects of nutrient uptake in modeling plant-soil interactions. A consistent derivation of the improvements and the original model is appended.

MODELING PLANT UPTAKE of dissolved soil constituents is essential to predicting plant growth under nutrient limitation. Solute uptake by plants can also be important in explaining changes in the chemistry of soil and drainage waters. Many existing models of forest growth, such as FORTNITE (Aber et al., 1978, 1982), FORCYTE (Kimmins and Scoullar, 1984), and FOREST-BGC (Running and Coughlan, 1988), and of soil chemistry at the ecosystem scale, such as the ILWAS model (Gherini et al., 1985; Davis et al., 1987), the "magic" model (Cosby et al., 1986), and STEADYQL (Furrer et al., 1989, 1990), do not include mechanistic representations of nutrient uptake. This omission occurs partly because solute uptake by plants is not entirely within the domain of either soil chemistry or plant growth models, but also because a suitable model has not been available. To be useful in long-term simulations of vegetated ecosystems, a nutrient uptake model should be capable of beginning the simulation with a fully established root system and it should allow root growth and mortality. To serve as a link between soil and plant simulators, it should accept time-varying inputs of soil solution chemistry, transpiration rates, and root dynamics during the simulation. None of the existing nutrient uptake models has all of these properties.

Bouldin (1961) formulated the mathematics of diffusion of solutes through an infinite and stationary soil solution to a cylindrical sink, assuming that the rate of uptake is proportional to the solution concentration at the root surface. Olsen et al. (1962) devised a similar model, exploring different assumptions about the boundary condition at the root surface, namely (i) constant rate of uptake and (ii) constant concentration at the root surface. These diffusion-only models were applied to explain phosphate movement and uptake. For more mobile ions, mass flow of the solution can also be an important mechanism of solute movement. Nye and Spiers (1964) presented the equations for simultaneous mass flow and diffusion, and solved them for the steady-state condition. To describe the solute uptake and concentration profile of the root with time required solving these same equations in the non-steady-state condition; Nye and Marriot (1969) and Claassen and Barber (1976) solved them numerically, allowing Michaelis–Menton uptake kinetics. Claassen and Barber (1976) further allowed for a distribution of root ages, assuming an exponentially growing root system. None of these models included interroot competition. Cushman (1979) and Barber and Cushman (1981) included interroot competition as an outer boundary condition of no nutrient movement, although the distance to this boundary was not affected by changing root density. The Barber–Cushman model has been reprogrammed for microcomputers and is easy to use (Oates and Barber, 1987). It is not, however, suitable for linking to a plant or soil simulator because, like its predecessor numerical models, it cannot accept time-varying input. The pattern of root growth (linear or exponential) must be specified in advance, and the rate of water influx and the average distance between root axes are parameters that cannot vary during the course of a simulation. Further, there can be no other sources or sinks for solute besides plant uptake, an untenable situation for long time scales.

The steady-state approach originated by Nye and Spiers (1964) offers a solution to the problem of time-varying input. This approach assumes that the concentration profile around the root can be considered to be in a steady state; change with time is accommodated by recalculating the solution at each iteration of the model. The advantage of the steady-state approach lies in the independence of the mathematical solution to previous conditions. This makes it ideal for linking plant and soil simulation models, where feedback between plant and soil makes it impossible to specify changes in root growth and soil status in advance of running the models. By calculating solute uptake at each time step, changes in root density can dictate a changing radius for the zone of influence of a root, water uptake rates can be varied with time, and the amount of solute in the system can be changed at each iteration. The concentration profile around the root develops stepwise in a manner similar to that predicted by the more exact models (Baldwin et al., 1973).

One weakness of the steady-state models to date has been the omission of the nutritional benefit incurred by new roots entering unexploited soil. Nye et al. (1975)

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provided for root length and root density to change with time, but because new roots enter the model having already attained a steady-state concentration profile, the solute taken up in attaining that profile is ignored. I extended the iterative steady-state approach of Nye and Spiers (1964) and Baldwin et al. (1973) to include the contribution made by new roots in the creation of the steady-state depletion zone. I also added the capability to substitute Michaelis–Menton uptake kinetics for the linear uptake used in the derivation of these models.

MODEL DESCRIPTION

Theoretical Approach

Three processes interact to determine the movement of solute to the root surface: (i) solute uptake by the root, (ii) flow of water toward the root, drawn by transpiration, and (iii) diffusion along the concentration gradient created by active uptake and solution flow. A zone of solute depletion or accumulation develops around the root, depending on whether the rate of uptake exceeds the rate of solution flow. Under stable conditions, in which the rate of water uptake, the relation of solute uptake to concentration at the root surface, and the solute concentration in bulk solution remain constant, a steady state will be attained, with an unchanging concentration profile around the root (Nye and Spiers, 1964). This steady-state concentration profile can be described mathematically, allowing concentration at the root surface and thus solute uptake to be calculated from the average solution concentration.

In a natural environment, of course, plant and soil conditions are far from stable; a steady state may rarely be attained. Water uptake varies daily; soil solution concentrations vary seasonally; even the relation between uptake and solute concentrations may change with plant status. For this reason, the steady state is not assumed to hold for longer than the model time step, but is solved anew at each iteration. The model should be applied at a time step shorter than the variations of interest, be they yearly, seasonal, or daily; fluctuations briefer than the model time step are ignored. An additional error is introduced by prohibiting non-steady-state concentration profiles, which must exist at least temporarily with every change in conditions. The difference between the exact solution and the approximation by iterative steady states is small (Baldwin et al., 1973).

I applied the iterative steady-state approach to simulating uptake by established roots, that is, roots that have been in place long enough to establish depletion zones. Uptake by these roots can be calculated from the solute concentration at the root surface and the appropriate uptake kinetics. The solute concentration at the root surface is, in turn, calculated from the average concentration in the bulk solution. The average concentration is a more useful state variable than concentration at the root surface because it can readily be adjusted for losses from and additions to the soil solution between time steps.

The steady-state concentration at the root surface will give the correct uptake rate for new roots only where nutrient concentrations are too high to limit uptake, such that both established and new roots are taking up the solute at their maximum possible rate (I_{max}). In concentration-limited conditions, new roots will have higher uptake rates than predicted by the steady-state calculation because of the higher than steady-state concentrations prevailing at the root surface during the time that the new roots create their depletion zones and approach the steady state. To simulate the contribution to solute uptake of new roots attaining the steady state, the amount of solute that is absent from the root zone in the steady state can be calculated and transferred to the plant. This transfer can be made gradually during the period that it takes to create the steady-state depletion zone, or, if short-term variation in root growth rates is unimportant, nutrient transfers can be credited to the plant in a single time step following root growth.

Model Assumptions

The following assumptions are inherent in the model. Solute uptake is assumed to be independent of water uptake; only active uptake is considered. Spatial variation in the soil is not treated, except for the variation radial to the root created by root activity. Roots are assumed to be uniformly distributed, such that a single average radial distance to the next root describes all roots. Roots have a uniform radius. Root hairs and mycorrhizae are not explicitly considered, although r_o could be defined as the effective radius of the root hairs. There is no change in root function (nutrient or water uptake rate) with age. These assumptions are common to preceding models; additional discussion can be found in Nye and Marriot (1969) and Claassen and Barber (1976). Mycorrhizal roots can be treated either by adjusting the uptake parameters to represent mycorrhizal roots (Yanai and Eissenstat, 1994, unpublished data) or by assuming that uptake occurs mainly through hyphae and selecting parameter values characteristic of hyphae (Yanai et al., 1994a).

The following characteristics distinguish my model from previous models. Water uptake rate, average radial distance to the next root, and root growth rate need not be constant but can be changed at each time step. Diffusion need not be independent of soil water content; the effective diffusion coefficient can be recalculated at each time step. Similarly, solute uptake at the root surface and soil buffer capacity need not be linear with solution concentration. Michaelis–Menton kinetics can be used to calculate uptake at the root surface, and any reversible form of exchange isotherm can be used to describe solute absorption.

Finally, the model is applied to each solute independently; solutes are assumed not to interact at the root surface. However, solutes may interact inside the plant or in the soil. For example, cation exchange can be calculated between iterations of the uptake calculation by calls to a solute equilibration routine (e.g., Bouldin, 1989; Yanai et al., 1994b).

Model Equations

Uptake is calculated as the product of the root surface area ($2\pi r_o L$), the concentration of solute at the root surface (C_o), a rate constant (α), and the time elapsed (Δt):

$$\text{Uptake} = 2\pi r_o L \alpha C_o \Delta t \quad [1]$$

The value of C_o is calculated from the average concentration in the bulk solution, C_{av}, because C_o is generally not measured and C_{av} is a useful state variable (variables are defined in Table 1):

$$C_o = P_c C_{av} \quad [2]$$

where

$$P_c = v_o \left[\alpha + (v_o - \alpha) \left(\frac{2}{2-\gamma} \right) \frac{(r_x/r_o)^{2-\gamma} - 1}{(r_x/r_o)^2 - 1} \right]^{-1} \quad [3]$$

and

$$\gamma = \frac{r_o v_o}{Db}$$

This relationship is derived in the Appendix. It depends on the assumption that a balance has been attained between solute

Table 1. Symbols and definitions used in the model.

A =	solute removed in the creation of the depletion zone per centimeter of root length (mol).
α =	root absorbing power (cm s^{-1}): uptake (mol cm^{-2} s^{-1}) = α C_o [optionally, $\alpha = I_{max}/(k_m + C_o)$].
b =	soil buffer power (dimensionless): $b = \theta + \rho K_d$, where θ = volumetric soil water content, ρ = soil bulk density (g cm^{-3}), and K_d is the slope of the adsorption isotherm (cm^3 g^{-1}).
C_{av} =	average concentration of substance in the soil solution (mol cm^{-3}).
C_o =	concentration of substance at the root surface (mol cm^{-3}).
C_r =	concentration of substance in the soil solution at radius r (mol cm^{-3}).
D =	effective diffusion coefficient of the solute through the soil (cm^2 s^{-1}): $D = D_l\theta f/b$, where D_l = diffusion coefficient in water (cm^2 s^{-1}), θ = volumetric soil water content, and f = impedance factor (dimensionless).
F =	outward radial flux of substance (mol cm^{-2} s^{-1}).
γ =	$r_o v_o/Db$ (dimensionless).
I_{max} =	maximal nutrient influx rate (mol cm^{-2} s^{-1}).
k_m =	half-saturation constant for uptake (mol cm^{-3}).
L =	root length (cm).
L_v =	root density, length per unit volume (cm root cm^{-3} soil).
P_c =	the proportion C_o/C_{av}.
r =	radial distance from the center of the root (cm).
r_{av} =	the r at which $C_r = C_{av}$.
r_o =	radius of the root (cm).
r_x =	average radial distance from the center of the root to the next root's zone of influence (cm).
Δt =	the model time step.
U_{new} =	uptake of solute by new roots in the process of establishing depletion zones (mol).
U_{est} =	uptake of solute by established roots in steady-state depletion zones (mol).
v_o =	inward radial velocity of water at the root surface (cm s^{-1}).
v_r =	inward radial velocity of water at radius r (cm s^{-1}).

uptake and the delivery of solute to the root surface by diffusion and solution flow (i.e., the amount of solute in the rhizosphere is at a steady state). These equations were presented by Baldwin et al. (1973) and Nye and Tinker (1977). The product Db should be calculated as $D_l\theta f$, where D_l = diffusion coefficient in water (cm^2 s^{-1}), θ = volumetric soil water content, and f, a function of θ, is the impedance (dimensionless). The soil buffer power, b, drops out of the calculation because $D = D_l\theta f/b$ (Nye and Tinker, 1977; Van Rees et al., 1990).

At high concentrations, where a solute uptake system is saturated, the linear root absorption coefficient, α, should be calculated from Michaelis–Menton parameters. Because $\alpha C_o = I_{max}C_o/(k_m + C_o)$,

$$\alpha = I_{max}/(k_m + C_o) \quad [4]$$

This calculation of α with changing C_o must be implemented iteratively, because C_o is a function of α. The value of α from the previous time step of the model is a good approximation of the value at the next step; a solution can generally be achieved in only a few iterations of Eq. [2], [3], and [4].

The above analysis applies to roots after they have attained steady-state concentrations in the depletion zone. During the period before the depletion zone is fully established, however, concentrations at the root surface are higher than at steady state (unless the solute is one for which $\alpha < v_o$ and the rhizosphere has higher concentrations than bulk soil). Uptake will therefore be underestimated if all roots are assumed to be at steady state from the time they are grown, as was assumed by Nye et al. (1975).

At the other extreme from assuming that all roots are in steady-state depletion zones, some models (Barber and Cushman, 1981; Barber, 1984) have adopted the assumption that, at the start of the simulation, soil concentrations are uniform, such that the concentration at the root surface, C_o, is the same as the average, C_{av}. Smethurst and Comerford (1993) have made modifications to the steady-state model to simulate the same condition by applying Eq. [1], [2], and [3] to a soil volume that increases with time at the rate of expansion of the depletion zone [approximated by $2\sqrt{(Dt)}$], as suggested by Nye and Tinker (1977).

Although these models have proven applicable to annual crops with small initial root systems, they seem less appropriate to perennial plants, which may have large root systems at the time a simulation is initiated. It would be most correct to assume that roots are exposed to the average or bulk soil concentration only when they are first grown. Only the established roots need be assumed to exist in the steady state. This approach has the advantage that calculated uptake at a given point in time is not sensitive to the time at which the model was first applied. Models that assume that C_o equals C_{av} at the start of a simulation would give a much higher estimate of uptake if the model were applied anew each day than if it were applied once for the entire growing season.

Uptake by roots during the formation of the depletion zone can be calculated by calculating uptake rates using Eq. [1] with C_o varying as the depletion zone develops, as implemented by Barber and Cushman (1981) and Smethurst and Comerford (1993). It is simpler, but less temporally exact, to evaluate the amount of solute absent from the depletion zone in the steady state (A), and use this total to represent the additional uptake provided by the existence of roots in undepleted soil. Uptake by new roots is calculated from the amount of new root length:

$$U_{new} = A\,\Delta L \quad [5]$$

where

$$A = \pi b\,C_{av}\left\{\left(1 - \frac{P_c\,\alpha}{v_o}\right)(r_{av}^2 - r_o^2) - \frac{2P_c}{v_o}\left(\frac{v_o - \alpha}{2 - \gamma}\right)r_o^2\left[\left(\frac{r_{av}}{r_o}\right)^{2-\gamma} - 1\right]\right\} \quad [6]$$

and where

$$r_{av} = r_o\left[\left(\frac{2}{2 - \gamma}\right)\frac{(r_x/r_o)^{2-\gamma} - 1}{(r_x/r_o)^2 - 1}\right]^{-\frac{1}{\gamma}} \quad [7]$$

These equations are derived in the Appendix.

The value of U_{new} can be less than zero when the rhizosphere has higher concentrations of the solute than the average solution. This happens whenever $\alpha < v_o$, as is not uncommon when uptake is limited by I_{max}. In this case, a negative correction is needed because uptake is higher at steady state than from unexploited soil, and so less solute has entered the root than would be predicted by U_{est} alone.

New roots become established roots, for the purpose of calculation, as soon as this U_{new} has been assessed. The simplest implementation transfers all of U_{new} to the plant in the same time step as root growth; alternatively, the transfer can be made gradually across multiple time steps. The amount of time required for the depletion zone to extend to the interroot distance, r_x, at the rate $2\sqrt{(Dt)}$, is approximately $(r_x - r_o)^2/4D$ (Baldwin and Nye, 1974). In simulations in which the contribution to uptake of new root growth is a small fraction of total uptake, the error introduced by the timing of U_{new} will be small. Even if U_{new} is large, timing errors will be small if the rate of root growth is relatively constant.

At each time step of an uptake calculation, C_{av} can be updated to account for removal of solute by uptake (as well as for other removals and additions such as those due to

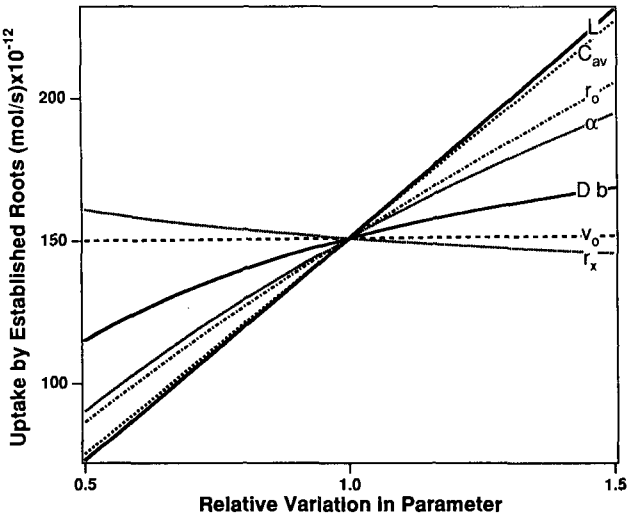

Fig. 1. Sensitivity of calculated uptake (U_{est}) as each of the parameters is varied from 0.5 to 1.5 of the value for P uptake by a loblolly pine seedling while the other parameters are held constant. Parameter values for this one-dimensional analysis are given in Table 2.

mineralization, reactions with soil surfaces, and leaching). The relation between the total amount of solute in the soil and C_{av} can be described by the buffer power, b, such that

$$\Delta C_{av} = b\ \Delta C_{total}$$

where C_{total} is the sum of the dissolved solute concentration (θC_{av}) and the adsorbed solute (C_S), combined on the basis of soil volume. The appropriate formulation of b therefore includes the contribution of dissolved solute to the total: $b = \theta + \rho K_d$, where θ = volumetric soil water content, ρ = soil bulk density (g cm^{-3}), and K_d is the slope of the adsorption isotherm (cm^3 g^{-1}) (Van Rees et al., 1990). The adsorption isotherm need not be linear, but if it is not, the value of b will depend on C_{av}, because $K_d = dC_S/dC_{av}$ (e.g., Kovar and Barber, 1990). Other models may be substituted to simulate changes in C_{av} due to uptake (e.g., Bouldin, 1989; Yanai et al., 1994b).

SENSITIVITY ANALYSIS

There are about 10 parameters required in the calculation of uptake (more or less depending on the method of calculating α, b, and D), half of which must be estimated separately for each nutrient element. Sensitivity analysis provides a basis for judging which parameters are most important to measure accurately. The importance of each parameter depends, however, on the values of all the parameters. For a particular application of the model, it is sufficient to vary each parameter value independently to assess its relative importance in that application. For example, Fig. 1 shows the variation in calculated uptake (U_{est}) as each of the parameters is varied from 0.5 to 1.5 of the value for P uptake by a loblolly pine (*Pinus taeda* L.) seedling (Kelly et al., 1992), while the other parameters are held constant. For uptake by already established roots, the root length (L) and the average solution concentration (C_{av}) are the most influential parameters, with nearly proportional effects on uptake; increasing root radius (r_o) and root absorbing

Table 2. Parameter values used in sensitivity analyses. One-dimensional sensitivity analyses used the baseline values, measured for uptake of P by loblolly pine seedlings in Lilly soil (Kelly et al., 1992). Two-dimensional sensitivity analyses used the ranges shown for the parameters that varied and the baseline values for those held constant.

Parameter	Baseline	Range
L, cm	285	
r_x, cm	2.0	0.1-2.0
r_o, cm	0.035	0.0003-0.035
v_o, cm	5.66×10^{-7}	$0.0\text{-}2.0 \times 10^{-6}$
I_{max}, mol cm^{-2} s^{-1}	2.68×10^{-13}	$2 \times 10^{-13}\text{-}5.6 \times 10^{-12}$
k_m, mol cm^{-3}	1.6×10^{-8}	
α, cm s^{-1}	1.86×10^{-5}	
C_{av}, mol cm^{-3}	0.19×10^{-6}	$0.0\text{-}2.0 \times 10^{-3}$
D, cm^2 s^{-1}	8.17×10^{-7}	$1 \times 10^{-9}\text{-}2.7 \times 10^{-16}$
b	5.84	

power (α) also have large effects. Uptake increases slightly with increasing D or b and decreases slightly with increasing interroot distance (r_x). In this parameter set, U_{est} is insensitive to the value of v_o. Similar analyses have been applied to previous models of nutrient uptake (Nye and Tinker, 1977; Barber, 1984; Kelly et al., 1992). The relative importance of parameters defined in these one-dimensional sensitivity analyses can depend quite strongly on the values of the other parameters, which are not readily considered in a one-dimensional sensitivity analysis. For example, the capacity for uptake at the root surface (defined by α or by k_m and I_{max}) is important only when C_o, the concentration at the root surface, is high. Although the existence of such interactions is well known (Barber, 1984), multidimensional sensitivity analyses of uptake models have not previously been presented in systematic or quantitative form.

A complete multidimensional sensitivity analysis can be described by partial differential equations; the derivation of these equations is straightforward but the results are complex equations that are difficult to visualize in the six or more dimensions of interest. I have chosen a few two-dimensional relationships to illustrate the effect of input parameter values on calculated uptake in more depth than can be afforded by a one-dimensional analysis. This analysis is neither systematic nor exhaustive, and there may be important interactions of two or more variables that are not revealed here. In the following discussion I consider the interactions of I_{max} and C_{av}, v_o and C_{av}, v_o and Db, and r_x and C_{av} in determining the rate of solution uptake.

The kinetics of uptake at the root surface (represented in the model by I_{max} and k_m) limit uptake only when soil solution concentrations (C_{av}) are high (Fig. 2a). Uptake increases linearly with increasing C_{av} until uptake approaches I_{max}, which it cannot exceed. This limit is reached at higher values of C_{av} with increasing I_{max}. The shape of the transition between C_{av} limitation and I_{max} limitation depends on the value of k_m (not illustrated here).

Although root surface area ($2\pi r_o L$) appears as a multiplier in the equation for uptake (uptake = $2\pi r_o L \alpha C_o \Delta t$, Eq. [1]), uptake is not always proportional to surface area, because of the dependence of C_o on r_o (Eq. [3]). In the one-dimensional sensitivity analysis of P uptake

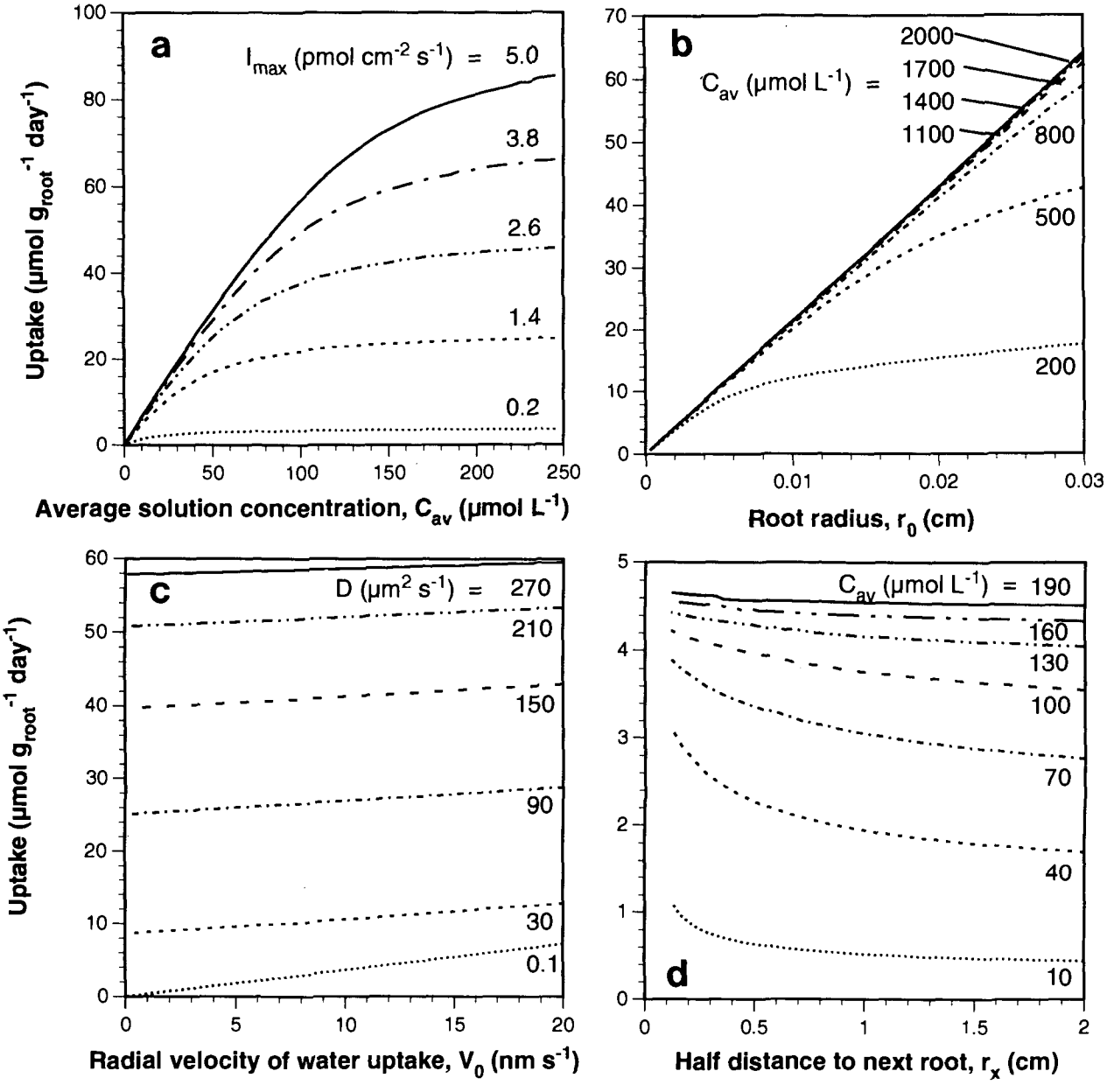

Fig. 2. Two-dimensional sensitivity analyses of calculated uptake (U_{est}): (a) as a function of the average concentration in soil solution (C_{av}) for varying values of the Michaelis-Menton uptake parameter I_{max}; (b) as a function of root radius (r_o) for various values of C_{av} with I_{max} = 4 × 10^{-12} mol cm^{-2} s^{-1} and D = 5 × 10^{-12} cm^2 s^{-1}; (c) as a function of radial velocity of water uptake (v_o) for various values of the effective diffusion coefficient (D) with I_{max} = 4 × 10^{-12} mol cm^{-2} s^{-1} and b = 1; and (d) as a function of the half-distance to the next root (r_x) for various values of the average concentration in soil solution (C_{av}) with D = 5 × 10^{-12} cm^2 s^{-1}. Variables not varied were held at the values given in Table 2 except where noted otherwise.

by loblolly seedlings, uptake was nearly proportional to L [not exactly proportional because L appears in the calculation of C_o, if r_x is calculated from it (Eq. [12])], but the effect of changes in r_o on uptake was somewhat less (Fig. 1). When uptake is limited by kinetics at the root surface (I_{max}), increases in root surface area provide a proportional increase in uptake, as illustrated by the upper curves in Fig. 2b. When uptake is limited, not by I_{max}, but by the concentration of solute at the root surface, then increases in root radius have a much smaller effect on uptake (illustrated by the lower curves in Fig. 2b). As a result, uptake is proportional to root surface area when C_o is high relative to I_{max}, but length is more predictive when delivery of solute to the root surface is limiting.

The parameters that control the rate of delivery of solute to the root surface by solution flow (v_o) and diffusion (Db) become important when C_o is low and I_{max} is not limiting. The effect of v_o is most important when Db is low (Fig. 2c), that is, when diffusion contributes little to solute movement toward the root. The parameters D and b are not independent in the model equations, as only their product appears; in fact, because b appears in the denominator in constructing D, the steady-state

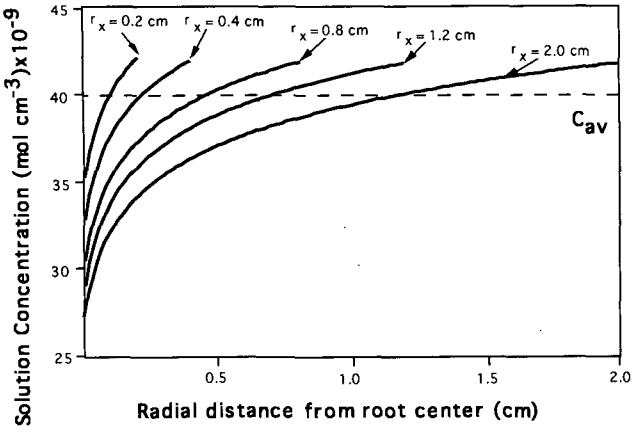

Fig. 3. Solute concentration profile around the root for various values of the half-distance to the next root (r_x). Values of the other parameters are those for P in Table 2.

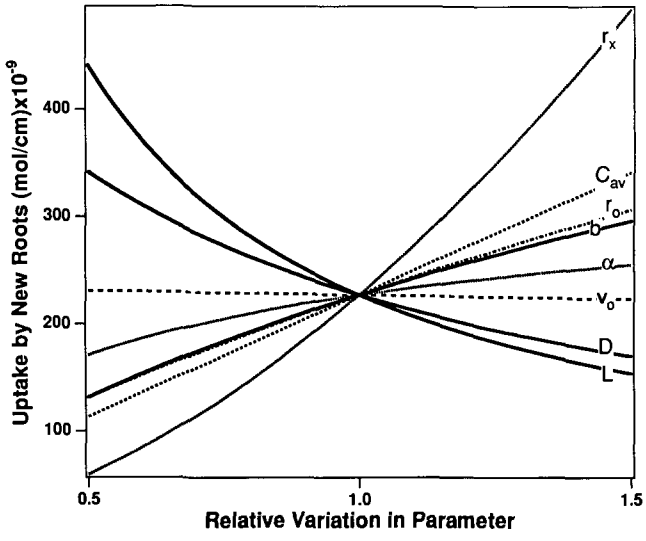

Fig. 4. Sensitivity of calculated uptake due to new root growth (U_{new}) as each of the parameters is varied from 0.5 to 1.5 of the value for P uptake by a loblolly pine seedling while the other parameters are held constant. Parameter values for this one-dimensional analysis are given in Table 2.

solution is not sensitive at all to b if its contribution to D is included. Uptake during multiple time steps would be sensitive to b, because b determines the rate of change in C_{av} with time.

There are other relationships between these variables in controlling nutrient uptake that cannot be demonstrated by calculation of a single steady-state solution to the uptake equations, but are only manifested in a simulation that allows nutrient depletion of the soil with time. For example, we expect there to be a threshold root length density, L_v, and hence a threshold interroot distance, r_x, at which competition between roots for nutrients becomes important and incremental additions of root length bring diminishing returns to the plant. This expected relationship does not hold, however, for the steady-state solution to uptake as a function of r_x (Fig. 2d). In fact, the reverse is true: uptake per unit length of root is greater at high root density (low r_x) than at low density, given the same C_{av}. This relationship obtains because r_{av} (the r at which $C_r = C_{av}$) is closer to the root when r_x is small and the gradient dC_r/dr is not very variable, and so C_o is highest at low r_x (Fig. 3). In a calculation of uptake implemented over multiple time steps, high root density would reduce C_{av} more quickly than low root density, and the expected reduction in uptake would result.

The sensitivity of uptake by new roots (U_{new}) to model parameters is illustrated with the same values for loblolly pine seedlings used in the analysis of U_{est}. Results of the one-dimensional sensitivity analysis are given per unit length of root growth (Fig. 4); the effect of root growth rate is, of course, linear on U_{new}. The most important parameter in this data set is root density (r_x) or, because $r_x = (\pi L_v)^{-1/2}$, root length (L). The value of U_{new} is also highly dependent on the average solution concentration (C_{av}) and the soil buffer capacity (b). These parameters together (bC_{av}) describe the total concentration of solute in the soil system. The root radius (r_o) has a positive effect on U_{new} by increasing the sink strength of the root and hence the steepness of the depletion zone around the root. Likewise, U_{nenew} is higher at low values of the effective diffusion coefficient (D) because the depletion zone is deepened. The parameters α and v_o are less important to the calculation of U_{new} for this combination of parameter values.

The importance of U_{new} relative to U_{est} depends partly on the growth rate of roots. For the case of loblolly pine seedlings, with a growth rate of 5% per day, U_{new} contributed 20% of total P uptake (Fig. 5). The value of U_{new} as a fraction of U_{est} is linear with root growth rate, dropping in this illustration to 10% of U_{est} if the root growth rate is only 2% per day. Diffusion rate is also an important factor in the contribution of U_{new} to total uptake: the more immobile the nutrient, the more important is the exploration of undepleted soil by new root growth. The interroot distance, r_x, increased the importance of U_{new}: as root density increases, the benefit to new roots of exploring new soil diminishes. The other parameters were not important to the ratio of U_{new} to U_{est} in this data set, v_o because it had little effect on either U_{new} or U_{est}, and the others because they had positive effects on both. The importance of these parameters, however, depends on the values of other parameters, as discussed above, and may not always be negligible.

DISCUSSION

The iterative steady-state approach provides a simple method for calculating nutrient uptake by plants that have long-lived roots and multiple periods of root growth. By considering the concentration profile around the roots to be in steady state (solute diffusion and solution flow balance uptake) at each time step, the effects of active solute uptake, diffusion, water flow, and root growth on solute uptake can be solved analytically, providing a mathematical description of uptake in terms of known plant and soil properties. Uptake can be simulated continuously as roots grow; the rate of root growth need not be predetermined, as is required by the model of Barber and Cushman (1981). Changes in root density, water

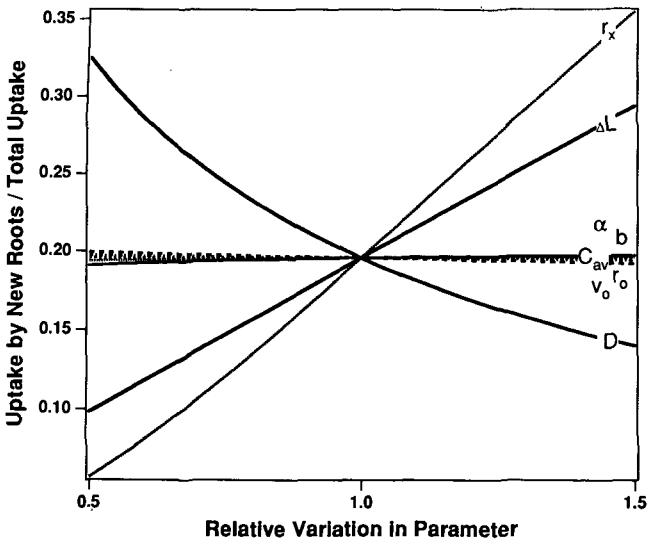

Fig. 5. Sensitivity of the ratio of uptake due to new root growth (U_{new}) to uptake by established roots (U_{est}) as each of the parameters is varied from 0.5 to 1.5 of the value for P uptake by a loblolly pine seedling while the other parameters are held constant. Parameter values for this one-dimensional analysis are given in Table 2.

uptake rate, and soil solution concentrations can also be specified arbitrarily at each time step. The model is an improvement over previous steady-state uptake models (Baldwin et al., 1973; Nye and Tinker, 1977) because the nutrient extracted from soil in the process of attaining a depletion zone is included in the uptake calculation. In addition, the inclusion of Michaelis–Menton kinetics is an improvement over linear uptake kinetics, especially at high concentrations.

Sensitivity analysis is one method of describing the behavior of a system of equations such as this model. For a specific application of the model, a simple one-dimensional sensitivity analysis, in which each of the model parameters is varied independently by some fraction while holding the other values constant, can provide insight into which parameters are most important to know precisely and which contribute the most error to the calculation. For the example studied here, root length and soil solution concentration were most influential in the calculation of uptake by established roots; root density, soil concentration, and the effective diffusion coefficient were most influential in the amount of uptake provided by the establishment of a depletion zone by growing roots. These results depend, however, on the situation studied, because the sensitivity of the model to one parameter depends on the values of other parameters. For example, the kinetics of uptake are limiting only when solution concentrations are high at the root surface. In such a situation, accurate estimation of I_{max} (or α) is critical to predicting uptake. Kelly et al. (1992) found that Mg uptake by loblolly pine seedlings was greater than model predictions; the combination of parameter values they used resulted in accumulation of Mg at the root surface, a clear indication of limitation by I_{max}. In this circumstance, uptake will be proportional to root surface area. On the other hand, when uptake is limited by the rate of delivery of solute to the root surface by mass flow and diffusion, concentrations at the root surface can be near zero. In this situation, increasing I_{max} or α has little effect on solute uptake; the rates of diffusion and water uptake are more important. The root can be viewed as a linear sink of zero concentration; in this circumstance, root length is more predictive of solute uptake than is root surface area.

Because the factors limiting uptake vary with environmental conditions and plant status, a model of solute uptake that considers only one or two limiting factors (such as root surface area and soil solution chemistry) will not be applicable under a wide range of conditions (such as changing root density). Including variables that describe uptake kinetics, diffusion and mass flow, root dynamics, and solution chemistry makes it unnecessary to assume which of these factors are limiting to uptake in a given simulation. For example, calculating the contribution of U_{new} to total uptake will not be important to all applications of the model. For NO_3 uptake by mature trees, the correction U_{new} may be small because root growth rates are low and diffusion is rapid. Calculating U_{new} is most likely to be important for fast-growing plants, such as annual plants or seedlings, and immobile nutrients, such as phosphate. The case of P uptake by loblolly pine seedlings, in which exploration of soil by new roots contributed 20% of the total uptake, may be considered an upper limit to the importance of U_{new} for tree and forest models.

Because these uptake equations allow time-varying input, they can be used to link plant and soil models such that feedbacks between the plant and soil are expressed. For example, these uptake equations are included in the tree physiological model TREGRO (Weinstein et al., 1992). TREGRO simulates increased C allocation to roots under nutrient stress; this increased root mass causes an increase in nutrient uptake, partially relieving the nutrient stress (Weinstein et al., 1991; note that in this early version of TREGRO, soil nutrient availability was fixed for the duration of a model run). Linking the soil chemistry model YASE (Yanai et al., 1994b) to TREGRO permits changes in the soil environment as well as changes in tree status to influence nutrient uptake. For example, the effect of elevated atmospheric CO_2 on plant growth should consider not only the effect of increased growth or altered C allocation on nutrient demand, but also the effect of changes in litter quality or soil warming on nutrient mineralization and availability. The steady-state approach makes the equations describing uptake very simple to evaluate. Including a detailed representation of nutrient uptake can improve the performance of plant and soil models.

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APPENDIX: DERIVATION OF EQUATIONS

The equations describing the concentration profile around the root and the average concentration were published by Baldwin et al. (1973) and Nye and Tinker (1977). The equations that are presented for the first time here describe the amount of solute contained in the depletion zone and the radius at which the average concentration occurs. I give a new derivation of the already published equations along with the derivation of the new equations for two reasons. First, Baldwin et al. (1973) and Nye and Tinker (1977) do not derive solute concentration as a function of distance from the root but cite Nye and Spiers (1964) for an equation that is not readily derived. The notation changed during the course of these studies, adding another difficulty to following the trail of the derivation. Second, Nye and Spiers (1964) made use of the variable C_i, the "initial" solution concentration, and of the boundary condition that at $t = 0$, $C_o = C_i$, which is inappropriate when simulating an already established root system. The definition of C_i and the use of this boundary condition are not necessary to the derivation. This appendix provides readers with a single derivation of the old equations, using consistent notation and making no reference to initial conditions. It also presents the new equations, which correct for the solute gained during the formation of the steady-state depletion zone. Symbols and definitions are presented in Table 1.

At any distance from the root, solute moves towards the root by mass flow (v_rC_r) and by diffusion [$Db(dC_r/dr)$]; the net effect is

$$F = -v_rC_r - Db\frac{dC_r}{d_r} \qquad [8]$$

the negative sign showing that the flux is inward. If the soil water content is not changing with time, the water flux through any radius r is equal to that at the root surface:

$$2\pi r v_r = 2\pi r_o v_o$$

Substituting for v_r in Eq. [8],

$$F = -\frac{r_o v_o}{r}C_r - Db\frac{dC_r}{dr} \qquad [9]$$

Under constant conditions, solute flux will reach a steady state in which soil and solution concentrations are stable, and the solute flux through any cylinder surrounding the root is the same as that entering the root. In this condition, the radial flux, $2\pi rF$, is independent of distance from the root. Thus rF is constant with respect to r. From Eq. [9],

$$rF = -r_o v_o C_r - Db\, r\frac{dC_r}{dr} \qquad [10]$$

To find the value of rF in the steady state, consider the flux at the root surface. Active root uptake is essential to the formation of a depletion zone and the maintenance of the concentration gradient that drives diffusion. In this treatment, I describe the rate of solute uptake as a function of nutrient concentration at the root surface. I assume that nutrient uptake is independent of plant nutrient status and water uptake rate. The relationship between concentration at the root surface (C_o) and uptake can have a variety of forms. The simplest is a linear relation, as used by Nye and Spiers (1964), Baldwin et al. (1973), and Cushman (1979), in which α is a constant:

$$F = -\alpha C_o$$

Alternatively, α can be described as a function of C_o (Eq. [4]), as in Nye and Marriott (1969), Claassen and Barber (1976), and Barber and Cushman (1981), who use Michaelis–Menton kinetics. Because α is independent of r, the following derivation will apply to any formulation of α as long as nutrient uptake is assumed to be independent of water uptake into the root. Water movement influences nutrient uptake indirectly, of course, through its effect on concentrations at the root surface. The constant rF can now be expressed in terms of conditions at the root surface:

$$rF = -r_o\alpha C_o$$

Substituting for rF from Eq. [10],

$$r_o v_o C_r + Db\, r\frac{dC_r}{dr} = r_o\alpha C_o$$

which can be solved to find C_r as a function of C_o. Rearranging and letting $\beta = r_o\alpha C_o/Db$ and $\gamma = r_o v_o/Db$,

$$\frac{dC}{\beta - \gamma C_r} = \frac{dr}{r}$$

Integrating from $C(r_o) = C_o$ to $C(r) = C_r$,

$$-\frac{1}{\gamma}\ln(\beta - \gamma C_r)\Big|_{C_o}^{C_r} = \ln(r)\Big|_{r_o}^{r}$$

gives

$$\frac{\beta - \gamma C_r}{\beta - \gamma C_o} = \left(\frac{r}{r_o}\right)^{-\gamma}$$

Selectively expanding β and γ and solving for C_r gives the concentration profile with respect to r:

$$C_r = \frac{C_o}{v_o}\left[\alpha + (v_o - \alpha)\left(\frac{r}{r_o}\right)^{-\gamma}\right] \qquad [11]$$

This equation corresponds to Eq. [8] and [10] in Nye and Spiers (1964), Eq. [vii] in Baldwin et al. (1973), and Eq. [7.14] in Nye and Tinker (1977).

In practice, the value of C_o, the solute concentration at the root surface, is rarely known. Because the average solution concentration, C_{av}, can be more readily measured or calculated, it would be preferable to describe C_o in terms of C_{av}. The average solution concentration for the whole soil can be found from the average solution concentration around an average root.

The zone of influence of the average root can be calculated from the root density by considering a regular array of parallel roots. The cross-sectional area of soil assigned to each root, πr_x^2, is $1/L_v$, where L_v is root length per unit volume, and therefore

$$r_x = \frac{1}{\sqrt{(\pi L_v)}} \qquad [12]$$

The average solution concentration, C_{av}, is the sum of solute in solution in the root zone cross section (obtained as the integral of C_r from the root surface, r_o, to the average radius

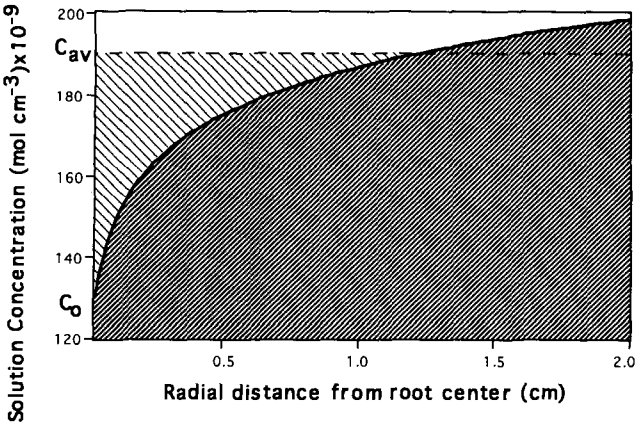

Fig. 6. The concentration profile with respect to r (C_r) from the root surface ($r = r_o$) to the average radius of the root zone (r_x) (Eq. [11]). The dark shading shows the area integrated to find the average concentration in solution (C_{av}) (Eq. [13]) and the light shading shows the area integrated to find the amount of solute absent from the root zone (A) relative to the average concentration (Eq. [15]).

of the root zone, r_x) divided by the cross-sectional area of the root zone (Fig. 6):

$$C_{av} = \frac{\int_{r_o}^{r_x} C_r 2\pi r dr}{\pi (r_x^2 - r_o^2)} \qquad [13]$$

Substituting C_r from Eq. [11],

$$C_{av} = 2\frac{\int_{r_o}^{r_x} \frac{C_o}{\nu_o}\left[\alpha + (\nu_o - \alpha)\left(\frac{r}{r_o}\right)^{-\gamma}\right] r\, dr}{(r_x^2 - r_o^2)}$$

we obtain the relationship between C_{av} and C_o:

$$C_{av} = \frac{C_o}{\nu_o}\left[\alpha + (\nu_o - \alpha)\left(\frac{2}{2-\gamma}\right)\frac{(r_x/r_o)^{2-\gamma} - 1}{(r_x/r_o)^2 - 1}\right] \qquad [14]$$

This is Eq. [viii] of Baldwin et al. (1973) and Eq. [7.16] of Nye and Tinker (1977).

The radius, r_{av}, at which $C_r = C_{av}$, can be found by equating Eq. [11] for C_r with Eq. [14] for C_{av} and solving for r:

$$r_{av} = r_o\left[\left(\frac{2}{2-\gamma}\right)\frac{(r_x/r_o)^{2-\gamma} - 1}{(r_x/r_o)^2 - 1}\right]^{-\frac{1}{\gamma}} \qquad [7]$$

For convenience we will define P_c as the proportionality between C_{av} and C_o:

$$P_c = \frac{C_o}{C_{av}} = \nu_o\left[\alpha + (\nu_o - \alpha)\left(\frac{2}{2-\gamma}\right)\frac{(r_x/r_o)^{2-\gamma} - 1}{(r_x/r_o)^2 - 1}\right]^{-1} \qquad [3]$$

Now C_o and C_r can be calculated from C_{av}. In particular, the amount of solute uptake (U_{est}) during a timestep Δt by roots of length L that have attained the steady state is

$$U_{est} = 2\pi r_o L \alpha P_c C_{av} \Delta t \qquad [1']$$

Equation [1'] gives the uptake by roots after the steady-state concentration profile has been achieved. The amount of solute that is removed by new roots, U_{new}, in the process of attaining the steady state can be calculated by comparing the amount of nutrient in the soil before root growth with the steady-state concentration profile C_r. Assume that new roots enter the soil at random and thus sample the average solution concentration C_{av}. The amount of solute (A) removed from the depletion zone per unit length of root is obtained by integrating the concentration change, $C_{av} - C_r$, across the radial distance from $r = r_o$, the root surface, to r_{av}, and including the factor b for the amount of exchangeable solute released from the soil (Fig. 6).

$$A = b\int_{r_o}^{r_{av}} (C_{av} - C_r)\, 2\pi r\, dr \qquad [15]$$

Separating the terms and substituting C_r from Eq. [11],

$$A = 2\pi b\int_{r_o}^{r_{av}} C_{av}\, r\, dr - 2\pi b\int_{r_o}^{r_{av}} \frac{C_o}{\nu_o}\left[\alpha + (\nu_o - \alpha)\left(\frac{r}{r_o}\right)^{-\gamma}\right] r\, dr$$

The first term is simply the amount of solute in the root zone at the average concentration before this root was grown. Integrating gives

$$A = \pi b\, C_{av}\left\{\left(1 - \frac{P_c\,\alpha}{\nu_o}\right)(r_{av}^2 - r_o^2) - \frac{2P_c}{\nu_o}\left(\frac{\nu_o - \alpha}{2-\gamma}\right) r_o^2\left[\left(\frac{r_{av}}{r_o}\right)^{2-\gamma} - 1\right]\right\} \qquad [6]$$

the amount of solute removed from the depletion zone per unit length of root, where r_{av} is given by Eq. [7]. Thus the amount of solute provided by an amount of root growth ΔL is

$$U_{new} = A\, \Delta L \qquad [5]$$

Total uptake for each model time step is the sum of U_{est} and U_{new}.

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