

DIVISION S-7—FOREST & RANGE SOILS

Simulating Nutrient Uptake by Single or Competing and Contrasting Root Systems

P. J. Smethurst and N. B. Comerford*

ABSTRACT

Simulation of nutrient uptake by competing root systems is necessary to assist in the quantitative understanding of these processes, to predict the consequences of competition for nutrients, and to prioritize future research on the mechanisms of nutrient competition. Our objective was to apply previously published concepts to a computer model based on solute transport theory that would have the ability to simulate nutrient uptake by root systems of one or two competing plant species. Analytical solutions were used for calculating the volume of soil allocated to each root system and the concentrations of solute at the root surfaces. We included in the model (i) a depletion zone that increased with time until it reached the no-transfer boundary, (ii) an adjustment of the average concentration in the depletion zone to account for newly encountered solute as the zone increased in radius, (iii) a variable root-absorbing power (α), and (iv) a routine to correctly account for all soil in simulations with two contrasting root systems. Predicted uptake for single-species scenarios in soils of contrasting nutrient supply characteristics was verified against that predicted by the commonly used Barber-Cushman model, NUTRIENT UPTAKE (maximum discrepancy was 23%), which utilizes a numerical solution. The ratio of uptakes predicted by both models was a function of α , root radius, effective-diffusion coefficient, and buffer power in a more complex way than previously suggested in the literature. Sensitivity analysis indicated that, of all parameters, K uptake by slash pine (*Pinus elliottii* Engelm. var. *elliottii*) relative to competing grass would be most sensitive to variations in root-length density of the grass, or in soil water content, if only soil parameters were examined.

NUTRIENT UPTAKE by plant roots has been simulated since 1961 using computer models with increasing degrees of sophistication. Amijee et al. (1991) summarized the key attributes of 21 models published between 1961 and 1989. All of these models relied on solute-transport theory to determine the supply of nutrients to the root surface. Uptake by the root was then described in most cases by Michaelis-Menten relationships.

A major dichotomy in the evolution of these models is that some depend on an accurate numerical method for determining the concentration at the root surface, while others depend on a less accurate, but faster, analytical solution. Numerical methods, as the terminology is used here, are those that iteratively solve a system of simultaneous equations developed from approximations of the differential equation for solute transport (Nye and Marriott, 1969). Numerical meth-

ods, in general, are accurate if the appropriate number of time and space nodes are used and if the code converges to a solution. One disadvantage of employing a numerical solution has been the necessity to keep interroot distances constant during a simulation, because the concentration profile away from a root is developed with time across fixed nodes in space.

Analytical methods are those that require the solution of only one equation, namely, a solution to the differential equation for solute transport with some simplifying assumptions (Baldwin et al., 1973). Hence, analytical methods require fewer computations than numerical methods, and are thereby faster. Analytical solutions also have permitted interroot distances to change, and the concentration profile calculated at each time step is independent of the profile at the previous time step. Within a time step, the concentration profile and the concentration at the root surface are approximated in the analytical approach by a steady-state solution in which all derivatives with respect to time are equal to zero. The physical interpretation of this condition is that solute enters with the transpiration stream and by diffusion at the outer edge of the soil cylinder at a rate that exactly equals the rate of uptake by the root at the center of the cylinder and that maintains the steady-state concentration profile. Successive time steps, each with a new steady-state approximation, develop a concentration profile that has been shown to change in a similar manner to that given by a numerical solution if the ratio of sink strength to diffusive supply ($\alpha a/Db$ where α is the root absorbing power, a is the root radius, D is the effective-diffusion coefficient, and b is the soil buffer power; abbreviations are defined also in Table 1) is <5 (Baldwin et al., 1973; Nye and Tinker, 1977). This ratio has been suggested as an important criterion for predicting whether uptake calculated by an analytical solution is close to that calculated by a more accurate numerical solution (fractional uptake = prediction by analytical solution/prediction by numerical solution). However, the relationship between $\alpha a/Db$ and fractional uptake has been examined only for a range of values of a with fixed values of the plant and soil parameters α , D , and b .

Apparently, a mathematical technique that combines the accuracy of a numerical solution with the flexibility of an analytical solution does not yet exist. The use of an acceptably accurate analytical method over a tedious but exact numerical method is justified because "there is little point in getting exact solutions of the flow equation for boundary and other conditions which are only approximate" (Passioura and Cowan, 1968, p. 130). Fortunately, the accuracy of the ana-

P.J. Smethurst, CSIRO Division of Forestry, Tasmanian Laboratory, Locked Bag no. 2, Post Office, Sandy Bay, Tasmania 7005, Australia; N.B. Comerford, Soil Science Dep., McCarty Hall 2169, Univ. of Florida, Gainesville FL 32611. A contribution of the Agric. Exp. Stn. Journal Series no. R-02521. Received 8 July 1992. *Corresponding author.

Table 1. List of abbreviations used in the models

Symbol	Description (units)
\bar{C}_l	Average concentration of liquid-phase solute in bulk soil solution ($\times 10^{-3}$ mol L $^{-1}$)
C_l	Concentration of liquid-phase solute ($\times 10^{-3}$ mol L $^{-1}$ solution)
C_{la}	Concentration of liquid-phase solute at the root surface ($\times 10^{-3}$ mol L $^{-1}$ solution)
C_{ave}	Average concentration of liquid-phase solute in the depletion zone ($\times 10^{-3}$ mol L $^{-1}$ solution)
C_{li}	Initial concentration of liquid-phase solute ($\times 10^{-3}$ mol L $^{-1}$ solution)
C_{min}	Concentration of solute at the root surface at which efflux equals influx ($\times 10^{-3}$ mol L $^{-1}$ solution)
C_T	Total concentration of solute in soil (mol m $^{-3}$ soil)
D	Effective-diffusion coefficient of solute in soil ($\times 10^{-4}$ m 2 s $^{-1}$)
D_l	Diffusion coefficient of solute in liquid ($\times 10^{-4}$ m 2 s $^{-1}$)
DZ	Depletion zone; also used as a subscript
I_{max}	Michaelis-Menten parameter for maximum rate of influx of solute ($\times 10^{-2}$ mol m $^{-2}$ s $^{-1}$)
IRD	Interroot distance ($\times 10^{-2}$ m); also used as a subscript
K_d	Solid-liquid partition coefficient for solute
K_m	Michaelis-Menten parameter for solute concentration at one-half I_{max} ($\times 10^{-3}$ mol L $^{-1}$ solution)
L_v	Root-length density ($\times 10^4$ m m $^{-3}$ soil)
NTB	No-transfer boundary; also used as a subscript
P	Of Root P; also used as a subscript
Q	Of Root Q; also used as a subscript
a	At the root surface (if subscript), otherwise radius of the root ($\times 10^2$ m)
b	Buffer power of soil (dC_T/dC_l)
f	Impedance factor for solute diffusion
i	Initial value; used as a subscript
l	Liquid phase; used as a subscript
r	Radial distance from the center of the root ($\times 10^{-2}$ m)
t	Time (s)
v_a	Water flux at the root surface ($\times 10$ L water m $^{-2}$ s $^{-1}$)
y	Radial distance from the center of the root to the NTB ($\times 10^2$ m)
α	Root absorbing power, i.e., $I_{max}/(K_m + C_{la} - C_{min})$ ($\times 10^{-2}$ m s $^{-1}$)
θ	Soil water content by volume ($\times 10^3$ L water m $^{-3}$ soil)
ρ	Soil bulk density (g cm $^{-3}$ soil)

lytical solution is adequate to justify its use in nutrient uptake modeling (Baldwin et al., 1973).

In applying an analytical solution, Baldwin and Nye (1974) defined the zone of nutrient depletion around a root to be that radial distance coincident with a 5% lowering of the initial concentration (Fig. 1). They found that the position of this boundary (r_{DZ}) at any time was roughly equal to $2\sqrt{(Dt)}$, where t is time, and that a model with an analytical solution for the concentration at the root surface (C_{la}), that incorporated this modification, provided a good approximation of the concentration profile away from the root, compared with that provided by a numerical solution. They stated that this modification was particularly important during the early stages of uptake, but further details were not provided. Nye and Tinker (1977) also described this modification as an option, but they did not describe how the average concentration in the de-

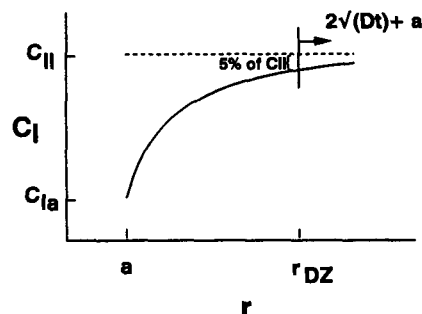


Fig. 1. Schematic representation of a depletion zone around a root increasing with time. The x axis (r) is the radial distance from the center of the root, with r_a and r_{DZ} being the distances at the surface of the root and at the end of the depletion zone, respectively. The y axis (C_{la}) represents the nutrient concentration in the soil solution, with C_{la} and C_{li} representing the solution concentrations at the root surface and the initial bulk solution concentration, respectively. The rate of spread of the depletion zone is given by the equation, where D is the effective diffusion coefficient and t is time.

pletion zone (C_{ave}) should be adjusted to account for the increasing width of the depletion zone.

Nye and Tinker (1977) also suggested that α may need to vary as a function of C_{la} if it was to correctly operate as the coefficient that, when multiplied by the concentration at the root surface, gave the rate of flow of solute into the root. They defined α as a constant, because at concentrations approaching C_{min} (the concentration below which no net influx occurs, which they expected to occur at most root surfaces whenever nutrient depletion occurs) the Michaelis-Menten relationship defining inflow $I = I_{max}(C_{la} - C_{min})/(K_m + C_{la} - C_{min})$ approaches a constant value (where I_{max} is the maximum rate of inflow and K_m is the concentration at $I_{max}/2$). However, C_{la} initially for most roots can be much greater than C_{min} . Reexamination of this option is therefore justified.

The model presented by Barber and Cushman (1981) and by Oates and Barber (1987, referred to below as the BC model) employs a numerical solution that has been verified in a variety of situations (Silberbush and Barber, 1984; Van Rees et al., 1990a). However, this model can simulate uptake by roots of only one species in one homogeneous volume of soil. Nye and Tinker (1977) presented a mathematical and conceptual basis for simulating uptake by competing roots of contrasting species. These concepts utilized an analytical solution to determine the position of the no-transfer boundary between two competing roots. However, Nye and Tinker (1977) did not describe how to apply this approach while accounting for the total soil volume containing competing root systems of contrasting length and absorbing power. In such situations, the sum of the calculated soil volumes allocated to each root is not equal to the total volume of soil available. Note that two adjacent cylinders of equal radii have a different volume than two adjacent cylinders of different radii but of the same center spacing.

To advance the application of these concepts of competition for nutrients we also need an understanding of the sensitivity of uptake by the two plant species

to variations in the various soil and plant parameters. Such an analysis could be used to prioritize continuing research in competition experiments.

The objectives of this study were, using a computer model based on the concepts and analytical solutions provided by Nye and Tinker (1977), to (i) determine the importance of allowing the radius of the depletion zone to increase with time from the root surface to the no-transfer boundary, (ii) determine the importance of how C_{ave} is calculated during annular growth of this zone, (iii) determine the importance of using a variable value for α , (iv) determine the extent to which variations in $\alpha a/Db$ caused by variations in the parameters α , a , D , or b can be used as a guide to conditions in which the analytical solution is applicable, (v) determine the importance of correctly accounting for the total soil volume when simulating uptake by competing and contrasting root systems, (vi) determine the sensitivity of simulated uptake by competing root systems to variations in soil and plant parameters, and (vii) thereby present and critique a model based on these concepts.

METHODS

A computer model (COMP8, i.e., competition model version 8) was written in QuickBASIC based on the concepts and assumptions of Nye and Tinker (1977). Two key equations provided by those authors included one for calculating the position of the no-transfer boundary (y) between two competing roots P and Q within a time step (their Eq. [8.14]):

$$\frac{C_{1aP}}{C_{1aQ}} = \frac{(\alpha\alpha)_Q y^2}{(\alpha\alpha)_P (IRD - y)^2} \quad [1]$$

where y is the distance from root P to the no-transfer boundary (r_{NTB}) between roots P and Q. Other symbols are as defined in Table 1. This equation is implicit for y and is therefore solved in COMP8 using a binary search routine. The other key equation is used to calculate the concentration of solute at a root surface, i.e., C_{1aP} and C_{1aQ} (their Eq. [7.16]):

$$C_{1a} = \bar{C}_1 \left/ \left\{ \frac{\alpha}{v_a} + \frac{2(1 - \alpha/v_a)[(r_{DZ}/a)^2 - (a v_a/Db) - 1]}{[(r_{DZ}/a)^2 - 1](2 - a v_a/Db)} \right\} \right. \quad [2]$$

where v_a is the rate of water influx at the root surface, and \bar{C}_1 is the average concentration in the depletion zone only (not the average for the bulk soil).

The model enables simulations of uptake by one or two species in one to six separate soil volumes, and includes a depletion zone that increases in radius until it reaches and remains at the no-transfer boundary. During the growth of this zone, C_{ave} at the beginning of each time step is calculated as the weighted average of the concentration of the solute in the previous depletion zone (after uptake) and the concentration of newly encountered solute (C_{ii}). The model also includes variations in α as a function of C_{1a} , a variable b ($b = \theta + \rho K_d$; Van Rees et al., 1990b) and a variable D ($D = D_0 \theta f/b$). A copy of the model is available from either author.

Increasing Depletion Zone

The importance of an increasing depletion zone was determined by comparing uptake estimated by the model [which included $r_{DZ} = 2\sqrt{(Dt)} + a$ (Fig. 1) until it reached and was

fixed at $r_{DZ} = r_{NTB}$] with that estimated by a version (COMP8G) that set $r_{DZ} = r_{NTB}$ throughout the simulation. Root-length densities ranged from 0.1×10^4 to 8×10^4 m m⁻³ for three one-species scenarios, for which values were selected from Barber (1984) and Van Rees et al. (1990a) to provide a range of soil and plant conditions including NO₃ with high C_{ii} and low b , phosphate with low C_{ii} and high b , and K with intermediate C_{ii} and b (Table 2). Uptake simulated by COMP8 and COMP8G is presented relative to the highest value of uptake for each nutrient as simulated by COMP8, i.e. relative uptake (Fig. 2).

Adjustment of Average Concentration in the Depletion Zone

The COMP8 model includes newly encountered solute in the calculation of C_{ave} as the depletion zone increases by calculating $C_{ave} = (1/r^2)[C_{ave,prev} r_{prev}^2 + C_{ii}(r^2 - r_{prev}^2)]$. Here C_{ave} and $C_{ave,prev}$ are the average concentrations in the depletion zone of the current and previous time steps, respectively, and r and r_{prev} are the radii of the current and previous depletion zones, respectively. The importance of including this calculation was determined by comparing outputs of COMP8 with outputs from a version without this adjustment (COMP8D).

Variable Root-Absorbing Power

The importance of using a variable α , equal to $I_{max}/(K_m + C_{1a} - C_{min})$, was determined by comparing outputs of COMP8

Table 2. Inputs and derived values used in the simulations.

Parameter	Values for examining versions of COMP8 and the Barber-Cushman model			Base values for examining fractional uptake and sensitivity
	N†	P‡	K§	K¶
Volume, $\times 10^{-3}$ L	1000	1000	1000	1000
Atomic weight	14.01	30.97	39.1	39.1
Diffusion coefficient, $\times 10^{-9}$ m ² s ⁻¹	8.8	1.3	4.5	2.0
Effective diffusion coefficient, $\times 10^{-10}$ m ² s ⁻¹	2.5	2.3	4.0	1.35
Volumetric water content, m ³ m ⁻³	0.2	0.2	0.2	0.187
Bulk density, g cm ⁻³	1.4	1.4	1.4	1.51
Solid liquid partition coefficient	0.5714	116.3	2.143	2.141
Soil buffer power	1.0	163.0	3.2	3.42
Initial solution concentration, $\times 10^{-3}$ mol L ⁻¹	5.0	0.0136	0.05	0.05
Plant	corn	soybean	pine	grass
Water influx rate to root, $\times 10^{-6}$ L m ⁻² s ⁻¹	1.0	5.0	3.8	19.0
Root-length density, $\times 10^4$ m m ⁻³	—	0.1, 0.5, 1, 2, 4, 8	—	3.0
Root radius, $\times 10^{-2}$ m	0.02	0.015	0.04	0.0112
Maximum influx of solute, $\times 10^{-8}$ mol m ⁻² s ⁻¹	10.0	0.643	3.61	3.61
Michaelis-Menten parameter, $\times 10^{-6}$ mol L ⁻¹	25.0	5.45	29.0	29.0
Minimum concentration at root for net uptake, $\times 10^{-6}$ mol L ⁻¹	2.0	0.2	1.0	1.0
Time, d	10	10	10	10

† For NO₃-N uptake by corn from a silt loam (Barber, 1984).

‡ For P uptake by soybeans from a silt loam (Silberbush and Barber, 1983).

§ For K uptake by pine from a sand (Van Rees et al., 1990a).

¶ For K uptake by grass from a sand (Smethurst and Comerford, 1992, personal communication).

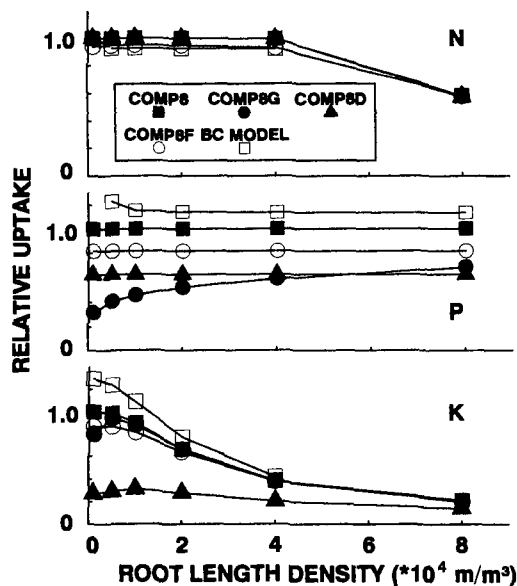


Fig. 2. Comparison of uptake estimated by the Barber-Cushman (BC) model with uptake estimated by COMP8 and by versions that either fix the depletion zone at the no-transfer boundary (COMP8G), do not adjust the average concentration in the depletion zone as it increases (COMP8D), or use a fixed value for the root absorbing power (COMP8F). Values of estimated uptake are compared for a range of root-length density (L_v) values, and presented relative to the uptake estimated by COMP8 for an L_v value of $0.1 \times 10^4 \text{ m m}^{-3}$ ($107.9 \text{ } \mu\text{mol N}$, $1.5 \text{ } \mu\text{mol P}$, and $9.0 \text{ } \mu\text{mol K}$).

with outputs from a version where α was fixed at $I_{\max}/(K_m - C_{\min})$ (version COMP8F) for the range of inputs provided in Table 2.

Verification of Single-Plant-Species Simulations

For single-plant-species scenarios, uptake simulated by the BC model for the parameter values given in Table 2 was used to verify uptake simulated by COMP8. All BC model simulations were run with 200 time and space nodes, because predicted uptake under contrasting conditions in preliminary studies varied by <0.1% for simulations using 200 to 500 time and space nodes.

Ratio of Sink Strength to Diffusive Flow as a Guide for the Appropriate Use of the Analytical Solution

The relationship between $\alpha a/Db$ and fractional uptake was explored for the base values of the sensitivity analysis given in Table 2. The value of L_v was fixed at $3 \times 10^4 \text{ m m}^{-3}$ and I_{\max} , K_m , a , D , and b were changed separately by factors of 0.1, 0.5, 2, or 10 to result in $\alpha a/Db$ values that ranged from 0.302 to 30.2. During each simulation, C_{la} decreased rapidly and resulted in values of $\alpha a/Db$ that approached a constant value of $[I_{\max}/(K_m - C_{\min})](a/Db)$. Hence, final values of $\alpha a/Db$ were used to explore this relationship.

Accounting for All Soil in Two-Plant-Species Simulations

In COMP8, the interroot distance (IRD) is adjusted (but not L_v) to ensure that the sum of the soil volumes allocated to each root system equals the total soil volume. This is achieved by iteratively solving for the NTB using Eq. [1], calculating the total soil volume simulated ($L_v \times \text{total soil volume} \times \pi \times \text{radius of the depletion zone squared}$, summed for both species), and adjusting the IRD until the volume tolerance (<1%) is met. Only if the two types of roots are exactly the same will

the NTB be equidistant from each root and the simulated volume exactly correct. The importance of this correction was determined for two-plant-species scenarios with the same soil properties as given for N, P, and K in Table 2. Plant Species 1, slash pine, had thick roots (radius 0.04 cm) and low L_v (modified from Van Rees et al., 1990a). In contrast, Plant Species 2, grass, had thin roots (radius 0.0112 cm) and L_v values that were either constantly low, intermediate, or high. For these simulations, a version of COMP8 (COMP8C) was used that omitted the internal check on soil volume.

Sensitivity Analyses for Two Plant Species

Several authors have provided sensitivity analyses for single-plant-species scenarios using the BC model, including Silberbush and Barber (1983) and Van Rees et al. (1990a). Similar analyses are not repeated here. Instead, the sensitivity of uptake by each of two plant species is examined in relation to variations in soil parameters and characteristics of Plant Species 2 only (characteristics of Plant Species 1 were kept constant). The effects of varying bulk density (ρ) are not shown, because these variations had exactly the same result as varying K_d . Both these parameters function in the same manner to determine soil buffer power: $b = \theta + \rho K_d$ (Van Rees et al. 1990b). Basic inputs (Table 2) were chosen from Van Rees et al. (1990a) and Escamilla et al. (1991) to simulate K uptake by competing roots of slash pine and *Panicum* grass. Rooting densities were held constant within each simulation, and simulations were for 10 d. Data are presented as relative uptake values, i.e., simulated uptake relative to that simulated for the same plant species in the base scenario, or in terms of relative proportional uptake of Plant Species 1, i.e., uptake by Plant Species 1 as a proportion of the total uptake (Species 1 plus Species 2) relative to this proportion for the base scenario.

RESULTS AND DISCUSSION

Allowing the Radius of the Depletion Zone to Develop

Fixing the radius of the depletion zone had little (<5% discrepancy) or no effect on N or K uptake at any root-length density, except for a 20% discrepancy in K uptake at a low L_v value of $0.1 \times 10^4 \text{ m m}^{-3}$. However, this modification led to large changes in simulated P uptake, ranging from a 69% discrepancy at $0.1 \times 10^4 \text{ m m}^{-3}$ to a 31% discrepancy at $8 \times 10^4 \text{ m m}^{-3}$ (Fig. 2). Therefore, allowing a depletion zone to develop led to substantially different estimates of uptake if the nutrient had a large buffer power, or if it had a small buffer power and root-length density was low. These were situations that resulted in no overlapping of depletion zones, and hence in no interroot competition.

Adjustment of Average Concentration as Depletion Zone Radius Develops

Omitting the adjustment of C_{ave} had no effect on N uptake, but resulted in a 38% lower estimate of P uptake (Fig. 2). Estimates of K uptake ranged from 73% lower at low root-length densities to 15% lower at high root-length densities if the adjustment was omitted. Underestimates of uptake were the result of underestimates of C_{ave} (and thereby C_{la}), and were lowest in cases where depletion zones were slowest to overlap, i.e., due to a high value of b or IRD.

Effect of Variable Root Absorbing Power

If α was fixed, estimated N uptake ranged from 5 to 6% lower at $L_v \leq 4 \times 10^4 \text{ m m}^{-3}$ to <1% lower at 8

$\times 10^4 \text{ m m}^{-3}$ (Fig. 2). This adjustment resulted in 19% less estimated uptake of P irrespective of the value of L_v , and underestimates of K uptake decreased from 13% at $0.1 \times 10^4 \text{ m m}^{-3}$ to <1% at $8 \times 10^4 \text{ m m}^{-3}$. Hence, use of a variable α resulted in substantially higher estimates of uptake for all nutrients, except in cases of high L_v and low soil buffer power.

Verification of Single-Plant-Species Simulations

Estimates by COMP8 of N uptake (per meter of root) were 8% higher than those by the BC model at L_v values of 0.5×10^4 to $4 \times 10^4 \text{ m m}^{-3}$ (Fig. 2). A comparison of simulated N uptake was not possible at an L_v of $8 \times 10^4 \text{ m m}^{-3}$, because the BC model's numerical method failed to converge during its iterative process. At this L_v , COMP8 predicted reduced relative uptake, and hence interroot competition.

Estimates by COMP8 of P uptake were 12% lower than those by the BC model at L_v values of 1×10^4 to $8 \times 10^4 \text{ m m}^{-3}$ (Fig. 2). Estimates by the BC model of P uptake per meter of root were 7% higher at an L_v of $0.5 \times 10^4 \text{ m m}^{-3}$ than at an L_v of $1.0 \times 10^4 \text{ m m}^{-3}$. This result was apparently not due to interroot competition, because further increases in L_v had no effect on uptake, and interroot competition was not evident in the COMP8 simulations.

Estimates by COMP8 of K uptake were 23% lower than those by the BC model at $0.1 \times 10^4 \text{ m m}^{-3}$, and only 8% lower at $4 \times 10^4 \text{ m m}^{-3}$ (Fig. 2). The BC model failed to converge for K uptake at higher values of L_v . Lower predicted uptake by COMP8 than by the BC model can be attributed directly to a lower estimate of concentration at the root surface, because both models used the same root surface area and Michaelis-Menten parameters. For example, at an L_v of $0.1 \times 10^4 \text{ m m}^{-3}$, COMP8 predicted C_{la} to be $0.004 \times 10^{-3} \text{ mol K L}^{-3}$, whereas the BC model predicted $0.005 \times 10^{-3} \text{ mol K L}^{-3}$. Predictions by all models of K uptake converged at high L_v values, because under these conditions almost all available solute was taken up irrespective of difference between models.

The COMP8 model was considerably faster than the BC model. For example, a 10-d, one-plant-species, one-horizon simulation required 27 s on a 386/33 MHz IBM-compatible computer with a math coprocessor. This was 13.6 times faster than the BC model.

Despite the wide range of soil and plant conditions tested and the different procedures for calculating uptake, the maximum discrepancy between the two models was a 23% lower estimate by COMP8 for K uptake at an L_v of $0.1 \times 10^4 \text{ m m}^{-3}$. Hence, these comparisons indicated good agreement between the two models for simulated solute uptake across a wide range of parameter values.

Ratio of Sink Strength to Diffusive Flow as a Guide for the Appropriate Use of the Analytical Solution

The effect of varying $\alpha a/Db$ on fractional uptake (predictions by analytical solution/predictions by numerical solution) was dependent on which parameter caused the variation (Fig. 3). Fractional uptake for the base values of parameters was 0.82, indicating that COMP8 gave an 18% lower estimate than the BC model. Lower $\alpha a/Db$

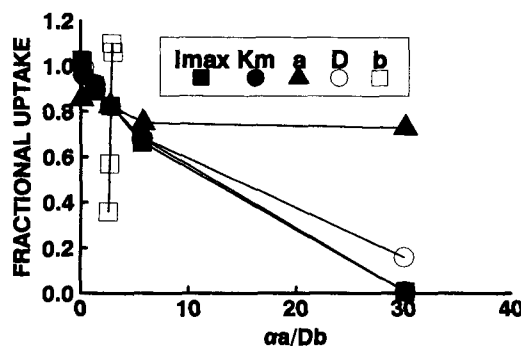


Fig. 3. Uptake estimated by COMP8 relative to that estimated by the Barber-Cushman model (fractional uptake) for a range of values of $\alpha a/Db$ caused by changes in maximum rate of solute influx (I_{\max}), solute concentration at $I_{\max}/2$ (K_m), root radius (a), effective-diffusion coefficient (D), or soil buffer power (b). Note that the root absorbing power $\alpha = I_{\max}/(K_m + C_{la} - C_{min})$.

values caused by variations in I_{\max} , K_m , a , or D resulted in higher fractional uptake. At a value of 30.2, fractional uptake was <0.2 for variations caused by changes in I_{\max} , K_m , or D . However, at this same value of $\alpha a/Db$ caused by a change in root radius (a), fractional uptake remained high at 0.73.

Variations in b did not result in an appreciable change in $\alpha a/Db$ from a value of 3, because a change in b is canceled by an equivalent but inverse change in D , which equals $D_0 \theta f/b$ (Nye and Tinker, 1977). Fractional uptake was >0.8 if b was <3.4, and <0.6 if b was 6.8 or larger (Fig. 4). However, this should not be construed to imply that fractional uptake will be low in all scenarios with a high buffer power. For example, fractional uptake of P in Fig. 2 was consistently >0.80 despite a buffer power of 163. The value of $\alpha a/Db$ in this case was 4.7.

Baldwin et al. (1973) evaluated fractional uptake as predicted by their model by varying α between 2×10^{-6} and $2 \times 10^{-9} \text{ m s}^{-1}$ while keeping a and Db constant. As a result, $\alpha a/Db$ ranged from 0.055 to 11.1, and fractional uptake was close to 1 if $\alpha a/Db$ was <5. Our results show that the relationship between $\alpha a/Db$ and fractional uptake is not simple. Similar to the observation of Baldwin et al. (1973), values of >5 consistently indicated low (<0.80) fractional uptake. However, values of $\alpha a/Db$ <5 were not consistently associated with high fractional uptake (>0.80). We therefore recommend that, for any particular set of conditions, and irrespective of

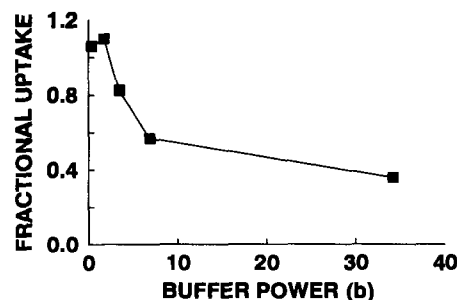


Fig. 4. Uptake estimated by the analytical solution in COMP8 relative to that estimated by the Barber-Cushman model (fractional uptake) for a range in values of soil buffer power (b).

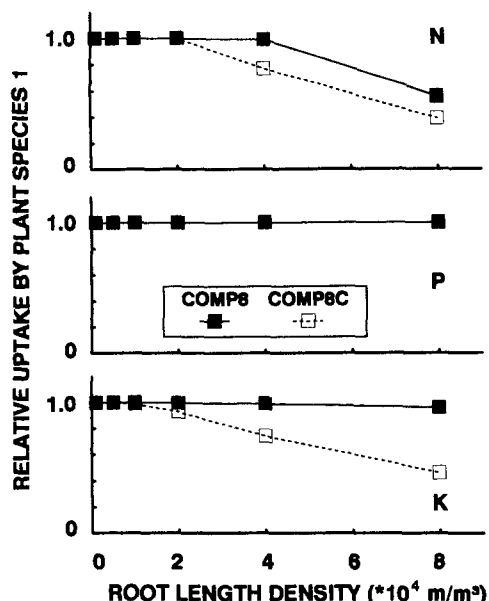


Fig. 5. Comparison of estimated uptake by Plant Species 1 (at a root length density $[L_v] = 0.1 \times 10^4 \text{ m m}^{-3}$) with (COMP8) and without (COMP8C) correctly accounting for the total volume of soil, for a range in L_v values of Plant Species 2. Uptake is expressed relative to that estimated by COMP8 (215.8 $\mu\text{mol N}$, 3.0 $\mu\text{mol P}$, and 9.0 $\mu\text{mol K}$) at an L_v value for Plant Species 2 of $0.1 \times 10^4 \text{ m m}^{-3}$.

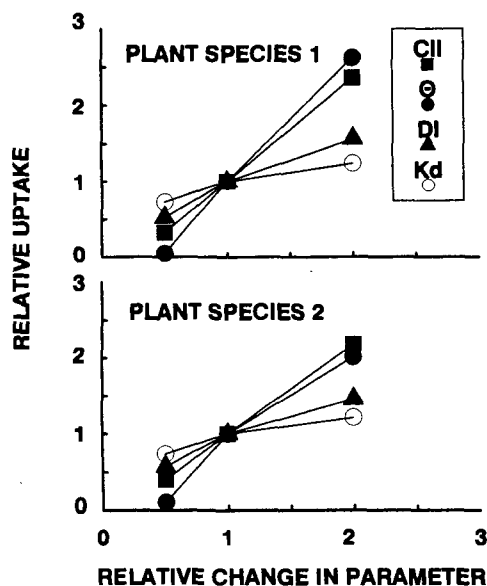


Fig. 6. Sensitivity of estimated uptake by both plant species to variations in soil parameters; C_{li} is the initial concentration of liquid-phase solute, D_l is the diffusion coefficient in liquid, and K_d is the solid-liquid partition coefficient.

the value of $\alpha a/Db$, one should compare outputs of representative scenarios run with both the COMP8 and BC models (or equivalent).

Importance of Correctly Accounting for All Soil in Two-Plant-Species Simulations

At an L_v value of $8 \times 10^4 \text{ m m}^{-3}$ for Plant Species 2, incorrect simulation of the soil volume caused esti-

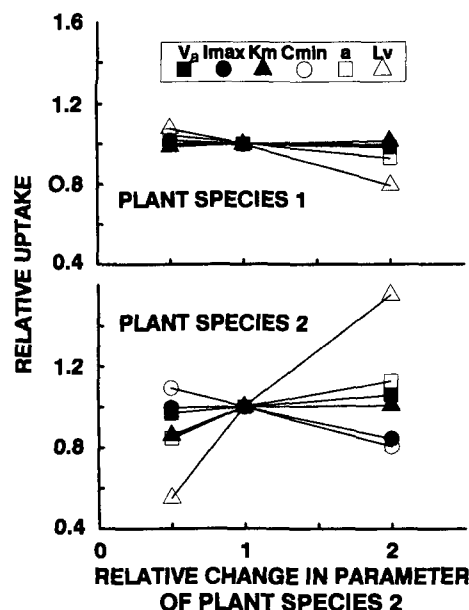


Fig. 7. Sensitivity of estimated K uptake by both plant species to variations in parameters of Plant Species 2; v_r is the water flux at the root surface, I_{\max} is the maximum rate of solute influx, K_m is the solute concentration at $I_{\max}/2$, C_{\min} is the solute concentration at the root surface at which efflux equals influx, a is the root radius, and L_v is the root-length density.

mated uptake by Plant Species 1 to be lower by 30% for N, 0% for P, and 52% for K (Fig. 5). At L_v values lower than $2 \times 10^4 \text{ m m}^{-3}$ for Plant Species 2, the correction had no effect on estimated uptake of either N, P, or K due to the absence of interroot competition.

Sensitivity Analyses for Two Plant Species

Soil parameters affected both plant species similarly, i.e., uptake was quite sensitive to variations in θ and C_{li} , but rather insensitive to variations in D_l and K_d (Fig. 6). Doubling the L_v of Plant Species 2 (but with parameter values for Species 1 unchanged) increased uptake by that species by 50% and decreased uptake by Plant Species 1 by 22% (Fig. 7). Variations in other plant parameters had little effect on relative uptake by either plant species.

Uptake by Plant Species 1 as a proportion of total uptake by the two plant species was calculated for each scenario and expressed relative to the same proportion resulting from the base parameter values. Variations in L_v of Plant Species 2 and in θ had the two largest effects on relative proportional uptake by Plant Species 1 (Fig. 8). If relative proportional uptake is an index of competitiveness, this analysis suggests that θ is positively correlated with the competitiveness of Plant Species 1 and that, as expected, the L_v value of Plant Species 2 is negatively correlated with the competitiveness of Plant Species 1. The importance of variations in soil and plant parameters under any particular set of conditions will depend not only on the sensitivities exhibited here, but also on the actual ranges of values likely to be experienced. For example, in a glasshouse experiment, θ may be controlled within a narrow range while I_{\max} and C_{\min} may vary by an order of magnitude. In a mature slash pine plantation, L_v may remain relatively constant, while

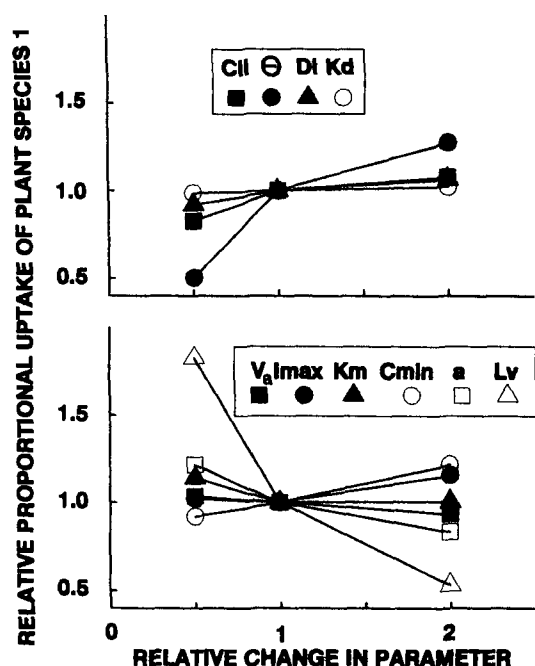


Fig. 8. Sensitivity of K uptake by Plant Species 1, as a proportion of that taken up by both species, to variations in soil parameters (top) and parameters of Plant Species 2 (bottom). Proportional uptake is presented relative to that for the base scenario; C_{li} is the initial concentration of liquid-phase solute, θ is the volumetric soil water content, D_i is the diffusion coefficient in liquid, K_d is the solid-liquid partition coefficient, v_a is the water flux at the root surface, I_{max} is the maximum rate of solute influx, K_m is the solute concentration at $I_{max}/2$, C_{min} is the solute concentration at the root surface at which efflux equals influx, α is the root radius, and L_v is the root-length density.

C_{li} may vary by two orders of magnitude due to fertilization and seasonal variability. Hence, the results presented here are an illustration of a sensitivity analysis for competing species, and are representative only of scenarios with similar base values.

CONCLUSIONS

All considered inclusions to the model (increasing depletion zone, adjustment of C_{ave} , variable root absorbing power, and accounting for all soil volume) were important for particular cases of nutrient uptake. This information advances the concepts outlined by Nye and Tinker (1977), and indicates the strengths and weaknesses of using an analytical solution for calculating C_{la} . By making use of the ratio $\alpha a/Db$ and comparing simulated uptake by the COMP8 and BC models for representative scenarios, COMP8 appears to be useful for simulating nutrient uptake across a wide range of situations, including competition.

The COMP8 model has several characteristics that are attractive: (i) for a wide range of soil and plant conditions, estimated uptake is similar to that given by a numerical model with the same theoretical basis; (ii) the parameters D and b are not inputs that are held constant throughout a simulation, but instead are derived from D_i , θ , ρ and the solid-liquid phase equilibrium, and hence thereby vary within a simulation as C_{la} changes; (iii) the parameter IRD is not set constant, but may change with time; (iv) uptake by either one or two plant species may be simulated; (v) inputs of a solute can be accounted for as well, if their effects on soil-solution concentration are known; and (vi) the analytical solution enables rapid simulation of nutrient uptake.

ACKNOWLEDGMENTS

This research was funded by the U.S. Forest Service and the National Science Foundation (Grant no. BSR-9019788). Special thanks goes to Dr. Ruth Yanai for her suggestions on using a variable α .

REFERENCES

- Amijee, F., P.B. Barraclough, and P.B. Tinker. 1991. Modeling phosphorus uptake and utilization by plants. p. 63-75. In C. Johansen et al. (ed.) Phosphorus nutrition of grain legumes in the semi-arid tropics. ICRISAT, Patancheru, India.
- Baldwin, J.P., and P.H. Nye. 1974. A model to calculate the uptake by a developing root system or root hair system of solutes with concentration variable diffusion coefficients. *Plant Soil* 40:703-706.
- Baldwin, J.P., P.H. Nye, and P.B. Tinker. 1973. Uptake of solutes by multiple root systems from soil. III: A model for calculating the solute uptake by a randomly dispersed root system developing in a finite volume of soil. *Plant Soil* 38:621-635.
- Barber, S.A. 1984. Soil nutrient bioavailability. John Wiley & Sons, New York.
- Barber, S.A., and J.H. Cushman. 1981. Nitrogen uptake model for agronomic crops. p. 382-409. In I.K. Iskandar (ed.) Modeling waste-water renovation. John Wiley & Sons, New York.
- Escamilla, J.A., N.B. Comerford, and D.G. Neary. 1991. Spatial pattern of slash pine roots and its effect on nutrient uptake. *Soil Sci. Soc. Am. J.* 55:1716-1722.
- Nye, P.H., and F.H.C. Marriott. 1969. A theoretical study of the distribution of substances around roots resulting from simultaneous diffusion and mass-flow. *Plant Soil* 30:459-472.
- Nye, P.H., and P.B. Tinker. 1977. Solute movement in the soil-root system. Blackwell Scientific, Oxford, England.
- Oates, K., and S.A. Barber. 1987. NUTRIENT UPTAKE: A microcomputer program to predict nutrient absorption from soil by roots. *J. Agron. Educ.* 16:65-68.
- Passioura, J.B., and I.R. Cowan. 1968. On solving the non-linear diffusion equation for the radial flow of water to roots. *Agric. Meteorol.* 5:129-134.
- Silberbush, M., and S.A. Barber. 1983. Sensitivity analysis of parameters used in simulating K uptake with a mechanistic mathematical model. *Agron. J.* 75:851-854.
- Silberbush, M., and S.A. Barber. 1984. Phosphorus and potassium uptake of field-grown soybean cultivars predicted by a simulation model. *Soil Sci. Soc. Am. J.* 48:592-596.
- Van Rees, K.C.J., N.B. Comerford, and W.W. McFee. 1990a. Modeling potassium uptake by slash pine seedlings from low-potassium-supplying soils. *Soil Sci. Soc. Am. J.* 54:1413-1421.
- Van Rees, K.C.J., N.B. Comerford, and P.S.C. Rao. 1990b. Defining soil buffer power: Implications for ion diffusion and nutrient uptake modeling. *Soil Sci. Soc. Am. J.* 54:1505-1507.