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The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment

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16. Modeling Nutrient Uptake as a Component of Loblolly Pine Response to Environmental Stress

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The ability of plants to acquire nutrients and fix carbon depends on the below ground processes associated with soil-nutrient supply, uptake kinetics, and root-surface area, combined with the physiological processes that capture, fix, and redistribute carbon from the aboveground portions of the plant to the belowground parts. Plants are exposed to multiple environmental stresses that act both individually and collectively to limit plant growth, by reducing rates of photosynthesis, growth, and carbon storage. Although the relative importance of various stresses depends on the site, for southern forests, available water and nutrient supplies in addition to tropospheric ozone are generally the factors of greatest concern (McLaughlin, 1985). Any stress that directly or indirectly impairs the ability of the plant to fix and store carbon can exacerbate nutrient and water stress, because root growth, the development of mycorrhizal associations, and active uptake of nutrients all depend on carbon supply.

Unfortunately for predictive purposes, in real world situations the various combinations of multiple stresses can be either competitive or offsetting. Although single-factor studies can clearly define the impact of an individual stress, the much-needed experiments with multiple stress factors are frequently more costly and time-consuming to conduct, difficult to design, and more problematic to interpret. Consequently, it is difficult to determine experimentally those processes that probably will control overall plant behavior under various circumstances. Mechanistic models provide a means to circumvent some of the limitations and investigate the effects of combinations of stresses. To be effective as

well as accurate, nutrient-uptake models must be combined with detailed whole plant carbon allocation models so that interactions between the two models can occur and the results can describe verifiable changes in key parameters.

Model Descriptions

We employed two nutrient-uptake models, the Barber-Cushman model (Barber, 1984) as modified for the personal computer by Oates and Barber (1987) and a steady-state model (Yanai, 1994). The two models are similar in approach and share many assumptions with their predecessors (Nye and Spiers, 1964; Nye and Marriot, 1969; Claassen and Barber, 1976; Cushman, 1979; Barber and Cushman, 1981). They simulate uptake by the average absorbing root in the average soil; there is no consideration of the geometry of the root system or of differences in root properties with age or morphology. The root is essentially a uniform, linear sink and the amount of soil surrounding the root is defined by the average distance to the next root. In both models, nutrients move toward the root by both mass flow (the movement of solution to the root to support the transpiration stream) and by diffusion along the concentration gradient created by active uptake at the root surface. Uptake at the root surface is described by Michaelis-Menten kinetics. Neither model considers mycorrhizal association, except as it affects the values of parameters in the model, nor root modification of the rhizosphere, except for nutrient depletion.

Both modeling approaches have been extensively tested in a number of applications through comparison of model predictions to observed responses. Although this is not a fail-safe process, experience has shown that opportunities for error propagation through these modeling approaches lie more with the development of the data used to provide initial values than with the concepts or codes within the models. Consequently, a portion of the discussion in this chapter is devoted to an analysis of how best to develop key initial values.

The major difference between the models is that the Barber-Cushman model simulates uptake of a growing root system over a period of time, but without time-varying input. The rate of root growth is one of the values input to the model; that is, it must be specified in advance. Similarly, there are no inputs of nutrients to the soil system during the duration of a model run except as defined by the ability of the solid phase (C_s) to maintain solution-phase concentration (C_l) through buffering. We applied this model with considerable success in a simulation of loblolly pine seedlings for one growing season (Kelly et al., 1992). However, the Barber-Cushman model as presently configured could not be effectively linked to a plant simulator because it does not accept time-varying input to root growth and soil conditions. We also wanted to allow such feedback as the effect of nutrient uptake on root growth and the effect of litter quality on nutrient supply. Therefore, in addition to using the Barber-Cushman model, we developed a new model to allow a more dynamic simulation of nutrient uptake (Yanai, 1994). This model calculates the steady-state solution for uptake at any point in time and can be invoked

repeatedly to simulate uptake over time under changing plant and soil conditions. Dissimilar to prior steady-state models (Baldwin et al., 1973; Nye and Tinker, 1977), which ignored the effect of root growth into unexplored soil, this new model includes the nutrient extracted from soil in the process of forming a depletion zone. At the other extreme, the Barber-Cushman model assumes that all roots start the simulation in unexplored soil, which is not realistic for the uptake of immobile nutrients by mature plants.

Results and Discussion

Factors Controlling Nutrient Uptake

Many factors interact in determining nutrient uptake by plants. In the uptake models we used, these factors are represented as parameters, which can be divided into those related to the plant and those describing the supply of nutrient from soil. Factors related to the plant can be further divided into those describing uptake kinetics (defined per unit surface of root) and those describing the development of the root system, which determine the absorbing length and surface area.

Uptake Kinetics

The three processes that combine to determine the movement of nutrients to the root surface are (1) nutrient uptake at the root, which tends to create a concentration gradient in the vicinity of the root, (2) flow of water to the root to support the transpiration stream, and (3) diffusion in response to the concentration gradient created by active uptake and solution flow. As soon as nutrients are delivered to the root surface, uptake in the natural environment will reflect the combined influences of varying degrees of active and passive uptake. Both the Barber-Cushman (Barber, 1984) and Yanai (1994) models use Michaelis-Menton parameters to describe nutrient uptake as a function of nutrient concentration at the root surface.

To use the Michaelis-Menton approach, it is necessary to conduct solution studies to find values of parameters representing (1) the maximum rate of nutrient influx (I_{max}) at high solution concentrations, (2) the nutrient concentration in solution (k_m) at which influx is one-half of I_{max} , and (3) the concentration in solution below which influx ceases (C_{min}) (Barber, 1984). Typical values for these three parameters by nutrient for loblolly pine are presented in Table 16.1; these values are consistent with values reported by others (Van Rees et al., 1990a; Williams and Yanai, 1996). Experimental work and modeling efforts revealed some important factors that need to be considered when attempting to model nutrient uptake.

First, as illustrated by the sensitivity analysis depicted in Figure 16.1, I_{max} is the most influential of the uptake kinetics parameters for the situation modeled and therefore must be chosen very carefully. In this case, high solution concentrations (C_1) relative to I_{max} account for the dominance of I_{max} (Figure 16.2a). A very low

Table 16.1. Root Uptake Kinetics Variables Used in the Barber-Cushman Model to Predict Mg, K, and P Uptake

Variable	Units	Mg	K	P
I_{\max}	$\mu\text{mol cm}^{-2} \text{s}^{-1}$	$1.29\text{E}-7$	$1.40\text{E}-6$	$2.68\text{E}-7$
k_m	$\mu\text{mol cm}^{-3}$	$9.83\text{E}-3$	$3.0\text{E}-2$	$1.60\text{E}-2$
C_{\min}	$\mu\text{mol cm}^{-3}$	0.001	0.001	0.0006

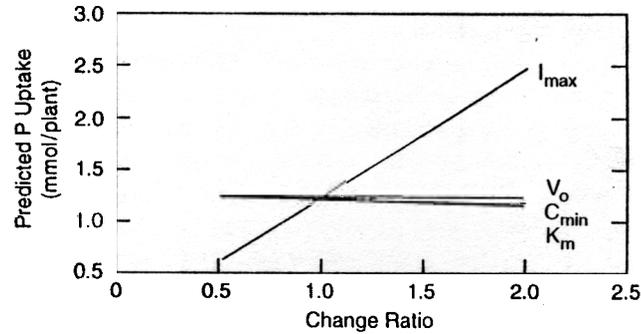


Figure 16.1. Sensitivity analysis of predicted phosphorus uptake in response to changing the maximum influx rate (I_{\max}), solution-nutrient concentration at $0.5 I_{\max}$ (k_m), solution concentration at which influx is zero (C_{\min}), and water-uptake rate (v_o). Each parameter was varied individually by the indicated ratio while all other parameters were held constant. Figure redrawn from Kelly et al. (1992).

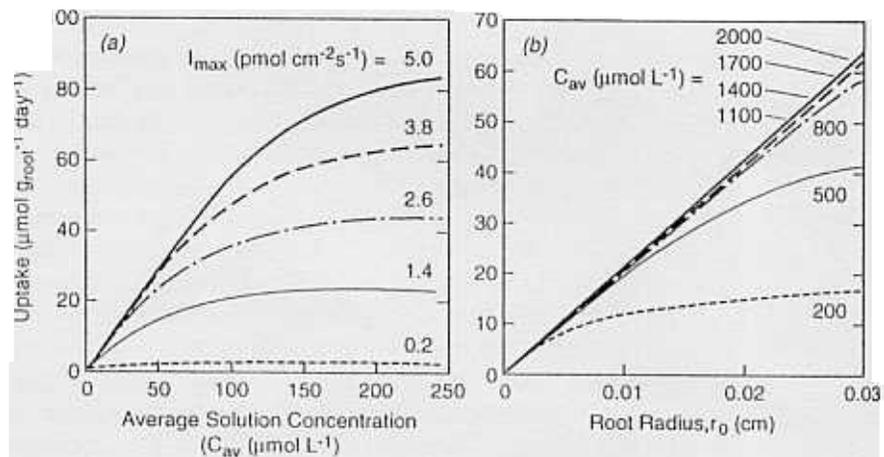


Figure 16.2. Two dimensional sensitivity analyses of calculated uptake (U_{cal}) as (a) a function of the average concentration in soil solution (C_{av}) for varying values of the Michaelis-Menton uptake parameter I_{\max} ; and (b) a function of root radius (r_0) for various values of C_{av} , with $I_{\max} = 4 \text{E}-12 \text{ mol cm}^{-2} \text{ s}^{-1}$ and $D = 5 \text{E}-12 \text{ cm}^{-2} \text{ s}^{-1}$. Other variables were held constant. Figure redrawn from Yanai (1994).

concentrations, uptake at the maximum rate may not occur or is relatively short-lived and therefore has only limited effect on uptake. Uptake will increase linearly with increasing C_i until the uptake approaches I_{max} , which it cannot exceed. The rate of approach of the I_{max} limitation with increasing C_i depends on the value of k_m (Yanai, 1994). When influx rates are close to I_{max} , k_m is not important in defining uptake (Kelly et al., 1992; Yanai, 1994). The C_{min} value, similar to k_m , often is not important to estimate nutrient uptake, because it is much lower than simulated uptake rates. Very low values of C_{min} , such as those of loblolly seedlings for NH_4-N (Kelly et al., 1995a), mean that nutrient uptake can continue even when nutrient depletion is severe.

The I_{max} value is both the most important and the most problematic of the uptake kinetics parameters to define for perennial plants. Kelly and Barber (1991) noted differences in the magnesium I_{max} value of at least an order of magnitude when they compared values for 365-d and 180-d seedlings. Similarly, Kelly et al. (1995a) found that I_{max} values can vary between loblolly pine families, as well as possibly differing across the growing season. The latter possibility is supported in part by an earlier observation (Kelly and Barber, 1991) in which seedlings that were not experiencing a shoot-growth flush exhibited a lower I_{max} than would have been observed if the experiments were performed during a growth flush. Although there are circumstances when this value will be less critical (for example, conditions of very low nutrient availability), finding appropriate methods for measuring I_{max} and mechanisms to describe its dynamic nature are key to future progress in nutrient uptake modeling.

Root Length and Surface Area

In addition to the parameters that define uptake kinetics, the parameters that define root length and surface area are extremely important in determining rates of nutrient uptake. In the steady-state models, these parameters are root radius and root length; root-growth rate is a factor in calculating nutrients acquired in the formation of depletion zones. In the Barber-Cushman model, the parameters are root radius, initial root length, and the rate of increase of root length. Both models calculate uptake as the product of root-surface area and the simulated uptake rate per unit area. For this reason, uptake might be expected to be proportional to root-surface area, and a number of one-dimensional sensitivity analyses (Nye and Tinker, 1977; Barber, 1984; Kelly et al., 1992) support this relationship (Figure 16.3). This relationship holds as long as uptake is proportional to the absorbing surface area, even if variation in surface area is the result of root radius (Figure 16.2b). On the other hand, when uptake is controlled by soil supply, increases in root radius offer little improvement in nutrient uptake. Uptake kinetics are not a limiting factor in this situation as the roots take up all the solute that arrives at the root surface; the limiting factor is the rate of delivery of solute to the root surface. (The parameters controlling the supply of nutrients by the soil will be discussed in the next section.) When the rate of delivery of solute to the roots is a limiting factor, the root behaves approximately as a linear sink. Uptake under th

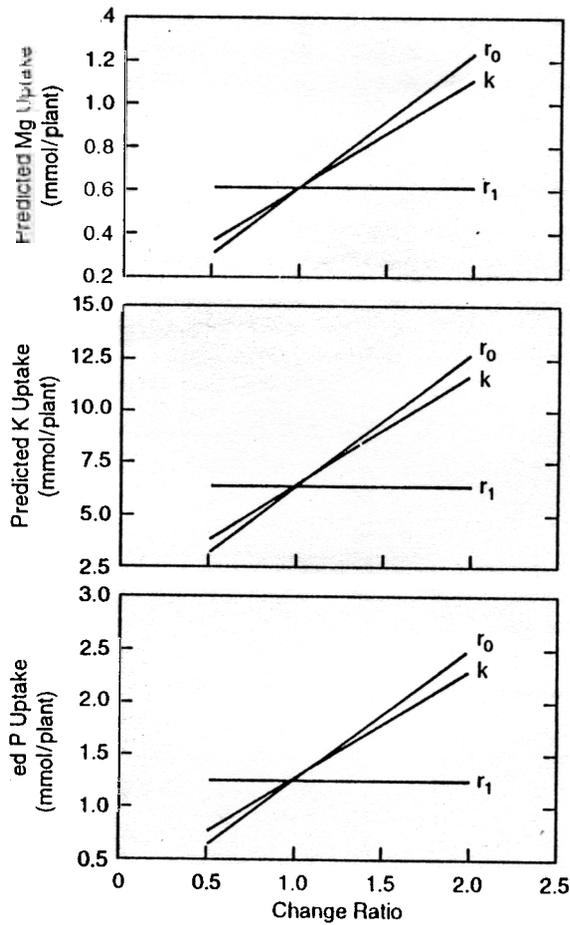


Figure 16.3. Sensitivity analysis of predicted Mg, K, and P uptake in response to changing the initial root length (L_0), root-growth rate (k), mean root radius (r_0), and half-distance between root axes (r_1). Each parameter was varied individually by the indicated ratio while all other parameters were held constant. Figure redrawn from Kelly et al. (1992).

tions will be more dependent on root length than on root-surface area (Yanai, 1994; Williams and Yanai, 1996).

Increased root length will result in increased nutrient uptake, but as root density increases, incremental additions of root length bring diminished returns to the plant. In the models, root-length density is represented by the interroot distance, r_1 , which describes the average radius of the zone of influence of the root. In the Barber-Cushman model, this distance is constant; the plant is assumed to occupy a proportionately larger soil volume as the root length increases. In the steady-state models, the interroot distance is calculated at each timestep.

The separate treatment of new root growth in the steady-state model made it

possible to assess the importance of the solute obtained in the formation of depletion zones. This contribution to uptake is most important for immobile nutrients and rapidly growing root systems (Yanai, 1994).

Soil Supply

Defining soil-supply parameters for modeling purposes is less problematic than defining plant parameters. The solution concentration (C_1) is often the most influential of the soil-supply parameters (Figure 16.4). As illustrated by the ammonium data plotted in Figure 16.5, the C_1 value not only varied among the four fertility treatments depicted, but also changed substantially from the initial sampling in early May through the final sampling in October. Although one of the weaknesses

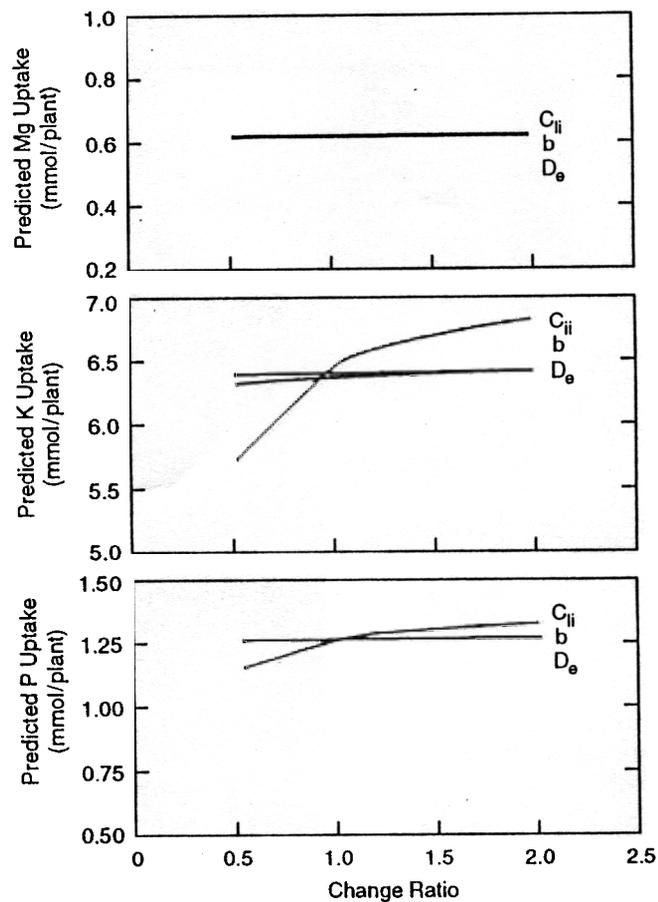


Figure 16.4. Sensitivity analysis of predicted Mg, K, and P uptake in response to changing the initial soil solution concentration (C_{1i}), the diffusion coefficient (D_e), and buffer power (b). Each parameter was varied individually by the indicated ratio while all other parameters were held constant. Figure redrawn from Kelly et al. (1992).

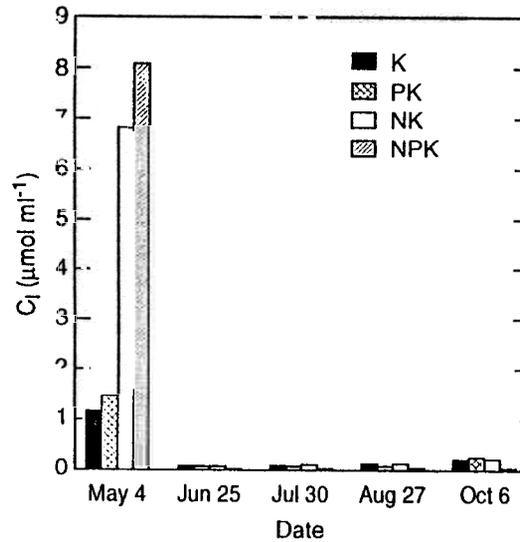


Figure 16.5. Mean equilibrium solution-phase concentrations (C_1) of ammonium by harvest date and fertility regime in soil collected from pots in which a single loblolly pine seedling was growing. Figure redrawn from Kelly et al. (1995a).

of the Barber-Cushman approach (Barber, 1984) is the lack of a mechanism in the model to allow resupply of nutrient except through transfer from the solid to the liquid phase, the actual soil-solution concentration data plotted in Figure 16.5 indicate that little or no resupply occurred during the growing season. However, had these data been collected under field conditions, it is more probable that resupply would have been observed.

Measured solid-phase values (C_s) also exhibit variation across the growing season as illustrated by the potassium values plotted in Figure 16.6. As might be anticipated, the values generally decline as the growing season progresses, reflecting a transfer to the solution phase in response to plant uptake or leaching loss (Kelly et al., 1995a). This relationship between the solution and solid phases is represented in the model through the buffer power (b), which is roughly C_s/C_1 (Van Rees et al., 1990b). Although Kelly et al. (1992) found uptake to be relatively insensitive to changes in the b value using a single-factor sensitivity analysis, Yanai (1994), who worked with essentially the same data set, found the b value to be somewhat more influential in her multifactor approach to sensitivity.

Modeling Nutrient Uptake and Supply

The Barber-Cushman approach, although successful at simulating growth over a growing season, could not be linked to a plant simulator because it, as with similar

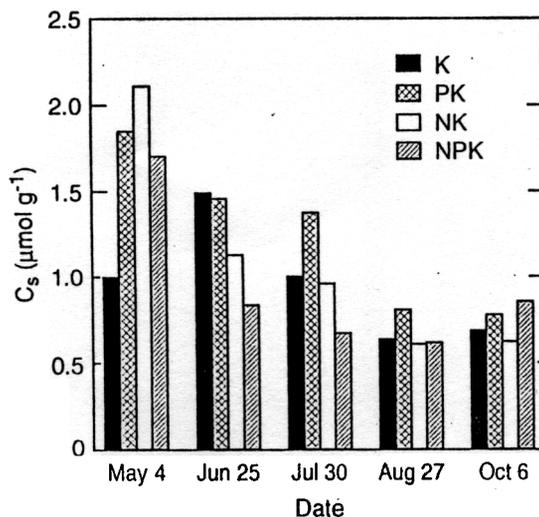


Figure 16.6. Mean concentrations of potassium in the solid phase (C_s) by harvest date and fertility regime in soils collected from pots in which a single loblolly pine seedling was growing. Figure redrawn from Kelly et al. (1995a).

numerical models, cannot accept time-varying input. As an alternative, the iterative steady-state approach (Nye and Tinker, 1977) provides a simple method for calculating nutrient uptake that is more appropriate to plants that have long-lived roots and multiple periods of root growth. Our version (Yanai, 1994) is an improvement over prior steady-state uptake models (Baldwin et al., 1973; Nye and Tinker, 1977) because the nutrient extracted from soil in the process of forming a depletion zone is included in the uptake calculation. Additionally, the inclusion of Michaelis-Menton kinetics is an improvement if non-linear uptake kinetics are required.

In the case of loblolly pine seedlings, the calculation of uptake by established roots was most sensitive to root length and soil-solution concentration (Yanai, 1994). The amount of uptake provided by the formation of a depletion zone by growing roots was most sensitive to root density, solution concentration, and the effective diffusion coefficient. These results, however, are dependent on the situation studied because model sensitivity to one parameter is dependent on the values of other parameters (Williams and Yanai, 1996).

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 mass and soil-solution concentration, will not be applicable under a wide range of conditions. Such multifactor models, as those discussed here are therefore better suited to assess plant response to environmental stress. For example, the Barber-Cushman model can simulate nutrient uptake for a single growing season (Van Rees et al., 1990a; Kelly et al., 1992). The steady-state model of nutrient uptake (Yanai 1994) has been incorporated in the plant model

TREGRO (Weinstein et al., 1992), allowing feedbacks between the plant and soil that influence estimates of nutrient uptake and plant growth.

Nutrient Availability and Plant Response to Stress

The effects of multiple environmental stresses can be difficult to predict because the combined effects of individual stresses are often not additive (Van Heerde and Yanai, 1995). For example, Temple et al. (1993), as well as Runeckles and Chevone (1992), found that drought stressed plants responded less to ozone than did well-watered plants. Conversely, trees weakened by ozone can be more susceptible to damage from other stresses (Hain, 1987; Davidson et al., 1988; Edwards et al., 1990). Understanding the impact of nutrient limitation in combination with other stresses on the plant is essential to predicting the response of vegetation to air pollutants and other environmental changes.

Experimental work with loblolly pine (Kelly et al., 1993) and northern red oak (Kelly et al., 1995b) showed that ozone reduced root growth, presumably as a result of carbon allocation to foliar repair. Under nutrient limitation, decreased allocation of carbon to the root system could exacerbate a nutrient stress. Conversely, if nutrient limitation results in a reduced carbon supply, a plant could become more susceptible to damage from ozone exposure as a result of an insufficient supply of carbon to compensate for damage (Pell et al., 1994). Simulation models provide a means of assessing the possible interactions of nutrient limitation with other environmental factors.

Summary

Mechanistic models of nutrient uptake are useful tools in refining our understanding of the chemical, physical, and biological processes that control plant nutrition. Prior work with woody species has raised important questions on how best to derive model input values given that many of these values change substantially over a growing season. For example, models using fixed-root morphology should use weighted seasonal average values rather than values describing initial conditions. Alternatively, variable growth rates across the growing season based on actual observation can be used in an iterative steady-state model. Decisions on these two options will be influenced by the intent of the modeling exercise and the data available. Changes in soil-supply parameters should also be taken into consideration; again, seasonal variation must be examined even if time-varying input is not used. Equally important to reasonable model representations is the recognition that the age and growth stage of the plant can influence the kinetics of nutrient uptake and carbon allocation to roots.

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 from prior conditions. Uptake thus calculated can accommodate unpredict-

able changes in root growth and mortality, root density, water-uptake rates, and such sources and sinks of nutrients as decomposition and leaching. This level of flexibility is required in simulating plant growth for multiple seasons in a dynamic soil environment. Prior steady-state models were modified to include nonlinear uptake kinetics and the contributions of new root growth to uptake.

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