# Soil supply and nutrient demand (SSAND): A general nutrient uptake model and an example of its application to forest management

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Comerford, N. B., Cropper, W. P., Jr., Li, H., Smethurst, P. J., Van Rees, K. C. J., Jokela, E. J., Adégbidi, H. and Barros, N. F. 2006. Soil supply and nutrient demand (SSAND): A general nutrient uptake model and an example of its application to forest management. Can. J. Soil Sci. 86: 665–673. Models of soil nutrient bioavailability and uptake assist in nutrient management and lead to a better understanding of nutrient dynamics in the soil-plant system. SSAND (Soil Supply and Nutrient Demand) is a steady state, mechanistic nutrient uptake simulation model based on mass flow and diffusive supply of nutrients to roots. It requires user inputs for soil and plant parameters to calculate a nutrient's concentration at the root surface and the subsequent uptake by a plant root and/or extrametrical mycorrhizal hyphae. It can be considered a sub-model linked to hydrological or plant growth models. SSAND provides a basis for simulating nutrient uptake under different soil-plant scenarios, including multiple soil compartments, net mineralization inputs, changing root growth, changing mycorrhizal hyphae growth, changing soil water content and multiple fertilizer events. It incorporates uptake from roots and mycorrhizal hyphae, including the potential competition between these entities. It should be useful for simulating the effects of climate change on soil nutrient bioavailability. It should also be a useful tool for managers in evaluating fertilizer regime options.

Key words: Nutrient bioavailability, nutrient uptake modeling, phosphorus uptake, mycorrhizae, Spodosols, climate change

Comerford, N. B., Cropper, W. P., Jr., Li, H., Smethurst, P. J., Van Rees, K. C. J., Jokela, E. J., Adégbidi, H. et Barros, N. F. 2006. Le modèle SSAND (*Soil Supply and Nutrient Demand*), modèle général de l'absorption des éléments nutritifs, et une illustration de son application en aménagement forestier. Can. J. Soil Sci. 86: 665–673. Les modèles expliquant la biodisponibilité et l'absorption des éléments nutritifs du sol facilitent la gestion de ces derniers et mènent à une meilleure compréhension de leur dynamique dans le système sol-plante. Le modèle SSAND (*Soil Supply and Nutrient Demand*) est un modèle mécaniste, à état stable, simulant l'absorption des éléments nutritifs. Il repose sur le débit massique et l'apport d'éléments nutritifs aux racines par la diffusion. Le modèle exige que l'utilisateur saisisse les paramètres du sol et des végétaux pour calculer la concentration de tel ou tel élément nutritif à la surface des racines et son absorption subséquente par celles-ci ou par les hyphes d'un mycorhize externe au système. On peut le considérer comme un modèle auxiliaire des modèles reproduisant l'hydrologie ou la croissance des plantes. Le modèle SSAND simule l'absorption des éléments nutritifs dans divers scénarios sol-plante, notamment des cellules multiples de sol, les apports nets de la minéralisation, l'évolution de la croissance des racines et des hyphes des mycorhizes, la modification de la teneur en eau du sol et la multiplicité des amendements. Le modèle tient compte de l'absorption par les racines et par les hyphes des mycorhizes, y compris la concurrence éventuelle entre ces éléments. Il pourrait avoir son utilité pour simuler les répercussions du changement climatique sur la biodisponibilité des éléments nutritifs dans le sol, mais aussi pour les gestionnaires qui évaluent les divers régimes d'amendement possibles.

**Mots clés**: Biodisponibilité des éléments nutritifs, modélisation de l'absorption des éléments nutritifs, absorption du phosphore, mycorhizes, podzols, changement climatique

The processes of plant root systems in a soil environment are among the most poorly understood in both managed and unmanaged ecosystems. However, nutrient uptake from the soil is one of the best documented of the root functions. Nutrients enter the soil solution by release from a solid phase via desorption, dissolution, or mineralization; or they enter by leaching from the surrounding soil. Once in solution, they move to the root or mycorrhizal hyphal surface by way of mass flow and diffusion, interacting with soil surfaces and organisms en route. At the root-hyphae surface, the nutrient is absorbed at a rate controlled by the external soil solution concentration and the uptake characteristics of the root-hyphae surfaces.

This conceptual model of soil nutrient bioavailability has been incorporated into an assortment of mechanistic nutrient uptake models that differ only in their initial assumptions and the management of sub-processes. The original models were based on a single root approach employing Michaelis-Menten kinetic equations to describe uptake at the root surface (Nye and Marriott 1969). Intra-root competition was added by controlling the distance of the no-transfer boundary in the soil surrounding an average root (Barley 1970; Baldwin et al. 1973; Barber and Cushman 1981; Yanai 1994). Root hairs were added to describe a unique component of the root surface (Bhat et al. 1976; Itoh and Barber 1983), while multi-ion uptake was considered (Bouldin 1989; Silberbush et al. 1993) along with the development of depletion zones around the root (Nye and Tinker 1977; Smethurst and Comerford 1993).

Instead of the soil solution concentration at the root surface driving root uptake, a moving boundary approach has been suggested (Reginato et al. 2000; Reginato and Tarzia 2002). When single, homogeneous, evenly-spaced parallel roots were not considered appropriate, both root diameter distribution and root spatial distribution within a modeled soil volume were incorporated (Barley 1970; Escamilla et al. 1991; Comerford et al. 1994; Roose et al. 2001). Interroot competition between species has been integrated (Smethurst and Comerford 1993); and finally, this conceptual approach has been used to predict fertilizer requirements (Van Noordwijk et al. 1990; Cropper and Comerford 2005).

The models mentioned above should be considered submodels of a soil-plant-water model. They generally require input from hydrological or plant growth routines. Inputs such as root length density development with time, water content, initial soil solution concentration, as well as a number of other soil and plant parameters must be provided by the user or by the output of other linked sub-models.

The mass flow-diffusion approach to modeling nutrient uptake by plants has been tested and found to be useful under a variety of soil-plant conditions. However, the simulation models have also been shown to be lacking when important components of the soil-root system are not adequately represented, such as mycorrhizal hyphae, root branching structure (Roose and Fowler 2004) or efficiency of inter-root competition (Smethurst and Comerford 1993; Reginato et al. 2000).

Here we describe, and provide a simple example of, a model named Soil Supply and Nutrient Demand (SSAND), which is a revision of the previously published COMP8 model (Smethurst and Comerford 1993; Smethurst et al. 1993a, b). SSAND model addresses some of the above mentioned problems by incorporating extramatrical mycorrhizal hyphae associated with roots of two competing species and permitting the simulation of nutrient competition between roots and mycorrhizae. It allows variable inputs for net root growth, net hyphal growth, net mineralization (which can also be used for leaching or weathering inputs), and water content change, making it suited as a sub-model for plant growth or a model to work side-by-side with a hydrological model that supplies some of the inputs to SSAND. The model is soil-based and appropriate for all soil borne nutrients. It also includes the capacity to interactively test the nutrient delivery efficiency of varying fertilizer regimes. SSAND is a useful tool for plant and soil scientists who study nutrient uptake by roots under a variety of conditions such as changing soil water content, dynamic mineralization rates, root growth patterns with time and depth, competition between two similar or dissimilar species, and the influence of mycorrhizal hyphae. It should also help in the design of optimal fertilization regimes, along with the testing of nutrient uptake as a consequence of changing soil conditions.

The objectives of this paper are to: (i) describe the model's general architecture and functionality, (ii) explain how mycorrhizae were incorporated, (iii) provide an example of the model and its fertilization routine under field conditions, (iv) illustrate the use of the mycorrhizal hyphae component, (v) illustrate the influence of changes in the soil water regime on nutrient uptake, and (vi) provide a sensitivity analysis of nutrient uptake to changes in model parameters for our specific soil condition.

## MATERIAL AND METHODS

### System Architecture and Functionality

The functional view of the system architecture is depicted in Fig. 1. This is a two-dimensional model in that multiple soil compartments can be incorporated to represent horizontal soil variability and/or the soil profile. Plant nutrient demand is calculated by defining the desired plant growth profile. This is accomplished by defining total biomass accumulation and nutrient use efficiency (NUE) over time. Ideally, NUE should be the total amount of nutrient absorbed to produce a unit weight of biomass. Biomass and NUE are combined to calculate the desired nutrient uptake profile that is necessary to support the desired growth (i.e. nutrient demand). Nutrient uptake is simulated through a root uptake module (Smethurst and Comerford 1993) based on that described by Nye and Tinker (1977). Nutrient demand from the desired growth profile and simulated nutrient uptake from the uptake routine can be compared, and if the discrepancy is deemed unacceptable (nutrient demand is much greater than supply), fertilization can be imposed and a new uptake simulation performed. The cycle of Comparison  $\rightarrow$ Fertilization  $\rightarrow$  Root Uptake Simulation  $\rightarrow$  Comparison may be repeated until the user is satisfied that the uptake simulation coincides with the desired nutrient uptake profile.

The desired profile routine determines nutrient demand (ND) for a given plant species based on the chosen nutrient, plant age, NUE and biomass databanks. It allows plotting of ND, NUE, and biomass for any given age range.

The nutrient uptake component of SSAND simulates root/hyphae uptake of a single nutrient for (i) multiple soil compartments, (ii) two species inter-root competition, (iii) soil desorption and adsorption isotherms expressed as either Freundlich or Langmuir curves, (iv) multiple fertilization events and rates, (v) dynamic mineralization rates based on a user input file, (vi) soil water content fluctuations, (vii) root length density changes with time and soil depth, and (viii) mycorrhizal association for each plant species, with dynamic mycorrhizal surface area with time. For single-



**Fig. 1.** System architecture and functionality of the SSAND model showing the relationship between the desired plant growth profile routine, nutrient uptake routine, comparison routine and fertilization routine. There are two inputs groups. The first defines the desired plant growth profile that the user will want to replicate with plant growth. The second are the inputs for the nutrient uptake routine. The uptake routine is then run and the result is compared with the nutrient demand from the plant growth profile. If the nutrient uptake meets demand, then the simulation is stopped. If demand exceeds simulated uptake, then a fertilization regime is applied and the processes starts again: nutrient uptake simulation – comparison with the plant growth profile – new fertilizer regime if required.

species simulations, both plants have the same root/hyphae parameters and results are summed for the two plants. SSAND incorporates a steady-state solution, within time steps defined by the user, of the continuity equation where the fluxes in that equation are mass flow and diffusion. That solution is found in Nye and Tinker (1977):

$$C_{la} = C_{lAVG} / \{ \{ (\alpha/v_a) + (2 [1-(\alpha/v_a)] [(r_{DZ}/a)^{\wedge} [2-(av_a/Db)] - 1 \} / [(r_{DZ}/a)^2 - 1] [2 - av_a/Db) \}$$
(1)

where  $C_{la}$  is the nutrient concentration at the root or hyphal surface (µg cm<sup>-3</sup>),  $C_{lAVG}$  is the average concentration in the depletion zone around a root or hyphae, a is the average root or hyphal radius (cm) and  $\alpha$  is the absorption coefficient of the root or hyphae defined by the Michaelis-Menten equation:

$$\alpha = I_{MAX} / (K_M + [C_{la} - C_{MIN}])$$
<sup>(2)</sup>

The other input parameters are the water influx rate to the root or hyphae ( $v_a$ , 3 cm s<sup>-1</sup>), the extent of the depletion zone ( $r_{DZ}$ , cm), the effective diffusion coefficient of the nutrient

(D, cm<sup>2</sup> s<sup>-1</sup>), the soil buffer power for the nutrient (b, mL cm<sup>-3</sup>), the maximum influx rate of the root or hyphae (I<sub>MAX</sub>,  $\mu$ g cm<sup>-2</sup> s<sup>-1</sup>), the Michaelis-Menten constant (K<sub>M</sub>,  $\mu$ g cm<sup>-3</sup>) and the solution concentration where net influx into the root or hyphae equals the net efflux out of the root or hyphae (C<sub>MIN</sub>,  $\mu$ g cm<sup>-3</sup>).

Mineralization is an internal transformation as defined by the continuity equation. At each time step the model incorporates inputs from mineralization and/or fertilization and nutrient exchange through sorption and desorption reactions with the soil mineral phase. Inorganic nutrients react with the soil mineral phase based on partition coefficients defined by the first derivative of sorption (following mineralization or fertilization) and desorption (for the maintenance of the soil solution concentration) isotherms. As uptake proceeds, a depletion zone develops around the root as described by the equation

$$2(Dt)^{1/2}$$
 (3)

where D is the effective diffusion coefficient of the nutrient in the soil solution (cm<sup>2</sup> s<sup>-1</sup>) and *t* is time (s) since initiation of the simulation. The effective diffusion coefficient is defined as:

$$\left(\mathsf{D}_{1}\,\boldsymbol{\theta}\,f\right)\,/\left(\boldsymbol{\theta}+\boldsymbol{\rho}\mathsf{K}_{\mathsf{d}}\right)\tag{4}$$

where  $D_1$  is the diffusion coefficient of the nutrient in water,  $\theta$  is volumetric water content (cm<sup>3</sup> water cm<sup>-3</sup> soil), *f* is the impedance factor (unitless),  $\rho$  is soil bulk density (g cm<sup>-3</sup>) and K<sub>d</sub> (mL cm<sup>-3</sup>) is the partition coefficient. The impedance factor, *f*, is the inverse of the tortuosity, which is the path length the nutrient travels divided by the straight line distance of travel. When depletion zones of two roots overlap, competition begins.

Uptake kinetics at the root surface is simulated using a Michaelis-Menten approach defined by:

Net influx = 
$$[I_{MAX} (C_{la} - C_{MIN})] / [K_M + (C_{la} - C_{MIN})]$$
 (5)

The inclusion of the mycorrhizal component, separation of adsorption and desorption isotherms, fertilization, and the dynamic nature of mineralization and water content make this model distinctly different from COMP8 and most other mechanistic uptake models mentioned above which are based on mass flow-diffusion dynamics

The utility functions include graphing outputs for viewing results, saving graphs, printing of outputs and graphs, running multiple sets of simulations from a user-input file, providing multiple input and output units to accommodate user needs, and storing databanks as files so the user can manipulate the data easily.

# Extramatrical Mycorrhizal Hyphae and Iterative Fertilization

When modeling uptake by an individual root, a depletion zone develops radially outward from the root surface when the root's uptake demand is greater than the nutrient supplied by mass flow. The boundaries of a depletion zone extend from the root surface to where the initial soil solution concentration is decreased by about 10% (Nye and Tinker 1977). Extramatrical mycorrhizal hyphae were incorporated into the model in a manner that is consistent with the single root approach. The initial hyphal length, average diameter, hyphal length growth dynamics and uptake kinetic parameters (I<sub>MAX</sub>, K<sub>M</sub>, C<sub>MIN</sub>) are user inputs, allowing the user to test a variety of mycorrhizal uptake scenarios. Extramatrical hyphae, as with roots, were assumed to be parallel, regularly spaced cylinders. The extramatrical hyphae extend perpendicularly from the roots into the soil. While it is understood that the spatial arrangement away from the root is not well-established, this approach was consistent with assumptions typically made for roots in soils. As previously mentioned there are methods to overcome the assumption of regular spacing if this assumption is an over simplification. However, there are no data that describe the spatial pattern of extramatrical hyphae, so this assumption was incorporated until the time that such data do exist and can be incorporated.

The development of a depletion zone around each hyphae and uptake by hyphae proceeds in the same fashion as described above for roots. A critical assumption incorporated into the model is that only the hyphal length that falls outside the root's depletion zone participates in nutrient absorption. A common observation associated with mycorrhizal uptake of nutrients is that mycorrhizae are not effective absorbers of nutrients that are highly mobile in the soil. A high mobility nutrient is one that has a high diffusion coefficient and a rapidly increasing depletion zone as defined in Eq. 3. A rapidly developing depletion zone around a root that quickly occupies the entire soil volume indicates that the root is extracting nutrients from the entire soil volume. Therefore, the advantage of hyphae extending beyond the influence of root uptake is lost under these conditions. Assuming that nutrient uptake by hyphae occurs only outside the depletion zone of roots, while not totally accurate, is a simplification that accounts for observations of hyphal uptake.

Mycorrhizal hyphal characteristics are assigned to each root species. When the user defines two different root species, each species can be assigned its own type of mycorrhizae. This allows the user to contrast two different uptake systems; however, it is possible to assign two types of hyphae to a single species of root. This is done by assigning one portion of the root system to one mycorrhizal species identifier and the other root portion to another mycorrhizal identifier. Then, a set of mycorrhizal hyphae characteristics is assigned to each of the two mycorrhizal species with the root input characteristics being identical.

The modeling of mycorrhizae is a complex problem. One limitation to the current model version is that there is no feedback between the uptake by mycorrhizal hyphae and the uptake by the roots themselves. This could be a problem if the uptake by hyphae reduces the tendency for root epidermal uptake, as suggested by Smith et al. (2004). By describing the root's Michaelis-Menten uptake parameters as a function of uptake by hyphae, this feedback could be incorporated. However, there are insufficient data to attempt a reasonable approximation of this process. Another potential problem is that posed by mycorrhizal networks. While there is evidence that they exist (Simard and Durall 2004), data on their activity are still not sufficient to make an approximation that would adequately fit into this model. Once the function and action of these systems are better known, their incorporation will be possible.

The fertilization routine is based on a water soluble form of the nutrient being applied to the soil. Fertilizer is assumed to be evenly mixed in the soil volume to which it is applied. When simulating multiple soil compartments in a soil profile, and when fertilizing with a nutrient with low soil mobility, it is useful to assign a shallow depth to the upper mineral soil horizon in order to best describe the incorporation of the fertilizer into the soil. The model allows the user to define the timing, amount and chemical form of the elemental nutrient added. The nutrient is partitioned between the liquid and solid phase based on a user-defined adsorption isotherm. The subsequent release of the nutrient from the solid to solution phases uses a separate user-defined desorption isotherm. Partition coefficients, which are the first derivative of the isotherm, are dependent on the nutrient's soil solution concentration. As mentioned above, once a fertilization regime is defined, the uptake simulation sub-routine is run with fertilizer inputs and then compared with the desired plant uptake profile until a decision to iteratively employ another fertilizer regime is made by the user (Fig. 1).

### Data Used in the Model Runs

SSAND was applied to 1-yr growth data of fast-growing loblolly pine (Pinus taeda L.) on Coastal Plain Spodosols of southeastern Georgia and Florida, USA. The input files for biomass and NUE of fast-growing loblolly pine were based on the work of Adegbidi et al. (2002), which documented total stand biomass and nutrient concentration of all tree components at age 1 year. These data established the end value for total nutrient content. Biomass accretion during the first year was estimated by partitioning the end biomass on a weekly basis using the pattern described by Neary et al. (1985) and Cooksey (1986) on a similar soil type at the same age. From these data, NUE and biomass files were developed for the desired growth profile portion of the model. This component is a user-defined input that subsequently generates a desired cumulative plant nutrient uptake curve with time and describes the nutrient demand required to reach the user's desired growth profile.

Soil parameters required as input for the nutrient uptake subroutine included initial soil solution nutrient concentration, soil bulk density, soil water content in each soil compartment over time, net mineralization rate over time, and adsorption/desorption isotherms for each soil compartment. Soil bulk density was measured in the same locations where roots were sampled (Adegbidi et al. 2004); the initial soil solution nutrient concentration was based on the data of Smethurst and Comerford (1993) and Smethurst et al. (1993a, b); phosphorus desorption and adsorption isotherms were from the work of Smethurst (1992) on a similar soil; water content change with time was based on records of the local water table fluctuation during the year (unpublished data from a local timber company) and the relationships between water table and soil water content above the water table described in Phillips et al. (1989); and mineralization was estimated as a function of soil water content as described by Grierson et al. (1999).

Plant parameters in the nutrient uptake model were root water influx rate, Michaelis-Menten equation parameters  $(I_{MAX}, K_M, C_{MIN})$ , root length density development and average root radius. Preliminary work indicated that P uptake under these conditions was not sensitive to water influx rate,  $I_{MAX}$ ,  $K_M$  or  $C_{MIN}$ ; therefore, order of magnitude estimates of these parameters were used based on the work of Escamilla (1997). One-year old root length density and average diameter were measured at the study sites (Adegbidi et al. 2004). Root development during the first year of growth was partitioned within each soil compartment based on the work of Smethurst and Comerford (1993) and Smethurst et al. (1993a, b). These data were combined with the above-ground growth pattern measured by Cooksey (1986). Both data sets were used to develop a first-year relative root growth curve for fast growing loblolly pine.

SSAND was run as described in the System Architecture and Functionality section above for P uptake in an unfertil-

Table 1. Parameter inputs for SSAND for the simulation of phosphorus uptake by three root/mycorrhizae systems. Water Flux,  $I_{MAX},\,K_M$  and  $C_{MIN}$  were the same values for both roots and hyphae

Important parameters Mycorrhizal evalua	
Duration of simulation	90 d
Soil volume (dm <sup>3</sup> )	$2 \times 10^{6}$
Initial soil solution concentration ( $\mu g m L^{-1}$ )	0.1
Volumetric soil water content ( $\theta$ , cm <sup>3</sup> cm <sup>-3</sup> )	0.15
Bulk density (g cm <sup>-3</sup> )	1.32
Impedance $(f = a \times \theta^b)$	
a	1
b	0.5
Partition coefficient (K <sub>d</sub> )	
Adsorption	60
Desorption	0 or 30
Water flux into root/hyphae ( $cm^3 cm^{-2} s^{-1}$ )	$2 \times 10^{-6}$
Average root radius (cm)	0.04
Average hyphal radius (cm)	$1.5 \times 10^{-4}$
Root length density (cm cm <sup>-3</sup> )	0.4
Hyphal length density (cm cm <sup>-3</sup> )	4 or 40
$I_{MAX}$ (µmole cm <sup>-2</sup> s <sup>-1</sup> )	$6.4 \times 10^{-7}$
$K_{\rm M}$ (µmole cm <sup>-3</sup> )	0.00545
$C_{MIN}$ (µmole cm <sup>-3</sup> )	0

ized soil. When the simulated nutrient uptake profile was less than the desired uptake profile, a fertilizer input of 33 kg P ha<sup>-1</sup> on day 100 was incorporated and the uptake routine was run again for the entire simulation time but now reflecting the fertilizer addition at day 100. This rate of fertilization was used because it was the actual rate of P added to the soil in the field study. For a demonstration of the mycorrhizal component of SSAND, the inputs are as defined in Table 1.

A sensitivity analysis was run using the inputs in Table 1 then changing one selected plant input while all other inputs remained constant. This was run for the base solution concentration of 0.1  $\mu$ g mL<sup>-1</sup>, then for solution concentrations that were 0.1 times and 10 times the base. The sensitivity of P uptake to the selected input parameters were evaluated for a root only system and a root + mycorrhizal hyphae system.

#### **RESULTS AND DISCUSSION**

The soil's ability to supply P to young loblolly pine in the first year of growth fell short of that required to maintain the desired level of productivity (Fig. 2a). The simulated uptake curve began to deviate from the desired uptake curve between day 100 and 125, indicating that phosphorus fertilization should occur prior to that time in order to maintain the desired growth trajectory. When a simulated application of 33 kg of water soluble P ha<sup>-1</sup> was applied at day 100, simulated uptake exceeded desired uptake until approximately day 325, where the two curves converged (Fig. 2b).

The input data for day 365 of the desired plant growth profile shown in the above figure was based on field data from this study. Therefore, in plant nutrient content of the desired plant growth profile represents the actual P plant content measured in the field that resulted from the application of 33 kg of P ha<sup>-1</sup>, and illustrates the utility of SSAND under these field conditions. Cropper and Comerford (2005) have investigated a Genetic Algorithm for use with mecha-



**Fig. 2.** A comparison of a desired plant growth profile of phosphorus uptake (DEMAND) for fast-growing loblolly pine during the first growing season with phosphorus uptake simulated using SSAND (UPTAKE). In (a), the simulated uptake is for an unfertilized soil. In (b), the soil was fertilized with 33 kg P ha<sup>-1</sup> on day 100 to match the fertilization history of the field study. The phosphorus uptake at day 365 for the desired plant growth profile is derived from the field sampling. The dotted lines represent  $\pm$  15% of the desired plant uptake profile.

nistic nutrient uptake models that optimizes the fertilization regime. The routine of Cropper and Comerford (2005) does not require manual iteration, although manual iteration can provide the user with a feel for the workings of the soil/plant nutrient delivery/uptake system.

Mechanistic uptake models are potentially useful in evaluating the effect of climate change on soil fertility because one result of climate change should be changes in root growth and soil water regimes. Using the same data from the loblolly pine study, the soil water regime was varied in order to evaluate the influence that soil drying would have on fertilizer uptake efficiency in these sandy, Coastal Plain soils (Table 2). The average soil volumetric water content was varied from near field capacity (0.1 cm<sup>3</sup> cm<sup>-3</sup>) to the driest values recorded under field conditions in forest stands (0.02 cm<sup>3</sup> cm<sup>-3</sup>). For an unfertilized condition, P uptake was over 4.7 times higher from soils at field capacity than from those under the driest condition due to the influence that water content has on the rate of nutrient diffusion in porous media. All simulations assumed similar root length densities. With fertilization, the uptake efficiency of fertilizer ([fertilizer absorbed / fertilizer applied]  $\times$  100) was fivefold higher under the best water regime.

Mycorrhizal hyphae perform an essential role in uptake of immobile nutrients like  $H_2PO_4$ -P, but usually are not considered important in the uptake of highly mobile nutrients like NO<sub>3</sub>-N. Mycorrhizal uptake of NO<sub>3</sub>-N should not be important because the effective diffusion coefficient of NO<sub>3</sub>-N in the soil solution is generally so high that the depletion zone quickly extends from the root surface to include the entire soil volume between roots. Under these conditions, since the root system is extracting nutrients from the entire soil volume, there should be little advantage to mycorrhizal hyphae.

Volumetrie weter content	Uptake without	Uptake with 33 kg ha <sup>-1</sup> of B at day 100 (kg ha <sup>-1</sup> )	Fertilizer use efficiency
Volumente water content	Tertilizer (kg lia )	of 1 at day 100 (kg fia )	at day 505 ( <i>n</i> )
0.10	0.19	5.14	15
0.08	0.16	4.30	12
0.06	0.10	2.67	8
0.04	0.05	1.42	4
0.02	0.04	1.00	3

Table 2. Simulated phosphorus plant uptake and fertilizer use efficiency with varying soil water content regimes. All simulations were produced using the nutrient uptake routine of SSAND

Conversely, P usually has a low diffusion coefficient that results in a narrow depletion zone and leaves much of the bulk soil untapped by the roots. Under this condition, extramatrical hyphae absorb nutrients from soil that the root system is not able to access, and do so with a relatively low carbon investment.

Figure 3a represents simulated nutrient uptake for an immobile nutrient (high  $K_d$ ). It estimates (i) uptake by roots alone, (ii) uptake by roots (root length density of 0.4 cm root cm<sup>-3</sup> soil) plus a low hyphal length density (4 cm hyphae cm<sup>-3</sup> soil) and (iii) uptake by roots plus a higher hyphal length density (40 cm hyphae cm<sup>-3</sup> soil). In contrast, Fig. 3b illustrates the simulated  $H_2PO_4$ -P uptake of the same three root/hyphae systems in a soil that allows the depletion zone around a root to expand very rapidly (low  $K_d$ ). The former shows the advantage of the symbiotic association, while the latter indicates no nutrient uptake benefit from extramatrical mycorrhizae.

To our knowledge, no other nutrient uptake model incorporates the mycorrhizal component in this fashion. The model illustrates that the benefit of mycorrhizae in absorbing an inorganic source of  $H_2PO_4$ -P is marginal in soils that have little capacity for chemical sorption of P. Spodosols of the southeastern Coastal Plain are well known for their low ability to sorb inorganic P (Fox et al. 1990; Harris et al. 1996; Zhou et al. 1997).

The sensitivity analysis for a root only system (Fig. 4) showed a consistent interpretation across all three initial soil solution concentrations. Input parameters that defined the root surface area available for uptake, root length density and root radius, greatly influenced uptake. Water influx into the root that is the nutrient supplying power for mass flow did not affect uptake, indicating that diffusive flow is the dominant supply mechanism under these soil conditions for P; and the inputs that define the kinetics of root uptake, I<sub>MAX</sub>, K<sub>M</sub> and C<sub>MIN</sub>, were also not influencing uptake significantly. These results suggest that these parameters do not have to be well documented to model P uptake under these conditions.

The sensitivity of the root plus mycorrhizal system (Fig. 5) provided a different interpretation. There was very little sensitivity of uptake to changes in the input parameters. Changes in the parameters related to the uptake kinetics of roots and the water influx rate also did not influence uptake predictions. Under the base soil solution condition and the low initial soil solution level, changes in root surface area also did not greatly influence P uptake. However, under the high soil solution level, a 50% change in the root length and root radius changed



**Fig. 3.** Simulation result of phosphorus uptake by root systems with 0.4 cm root cm<sup>-3</sup> soil that have no extramatrical mycorrhizal hyphae, that have 4 cm hyphae cm<sup>-3</sup> of soil and that have 40 cm hyphae cm<sup>-3</sup> of soil. The dark bars represent a soil that has a Kd of 30 and the white set of bars are for a soil with a Kd of 0. Simulation inputs are given in Table 1.

predicted uptake by about 20%. The model supports the premise that extramatrical mycorrhizal hyphae are very effective in using the entire soil volume under native and low soil solution concentrations and that increased root surface area is ineffective in increasing uptake under these conditions. Increased rooting would only be effective under higher soil solution concentrations.

#### SUMMARY

SSAND is a steady state, mechanistic, nutrient uptake model based on mass flow and diffusive supply of nutrients to roots. As such it requires user inputs for soil and plant parameters that allow the calculation of a nutrient's concentration at the root/hyphae surface and the subsequent uptake by a plant root and/or extramatrical mycorrhizal hyphae. It should be considered a sub-model linked to hydrological or plant growth models that would furnish inputs such as water content change, root and mycorrhizal hyphae dynamics and mineralization dynamics. In this version those inputs are currently user-defined. The model provides a basis for simulating nutrient uptake under different soil-plant scenarios, including multiple fertilizer events. It incorporates uptake from both roots and extramatrical mycorrhizal hyphae, including the potential competition between these entities. It



**Fig. 4.** Sensitivity analysis showing the effect of changing the root input parameters in a root-only system on simulated nutrient uptake by the root system. Root input parameters were the root length density (Lv), average root radius (radius), the water influx rate, which drives mass flow (v), the Michaelis-Menton constant ( $K_M$ ), the roots maximum nutrient influx rate ( $I_{MAX}$ ) and the soil solution concentration were influx equals efflux ( $C_{MIN}$ ). The analyses were run at three initial soil solution concentrations, being 0.1 µg P mL<sup>-1</sup> (A), 0.01 µg P mL<sup>-1</sup> (B), and 1.0 µg P mL<sup>-1</sup> (C). Other input parameters were those used for Fig. 3.

should be useful for assisting managers in evaluating the efficacy of fertilization regimes or in simulating the effects of changing soil and root growth conditions, such as with climate change, on soil nutrient bioavailability.



**Fig. 5.** Sensitivity analysis showing the effect of changing the root input parameters of a root plus mycorrhizae system on simulated nutrient uptake by the root plus mycorrhizal system. Root input parameters were the root length density (Lv), average root radius (radius), the water influx rate, which drives mass flow (v), the Michaelis-Menton constant ( $K_M$ ), the roots maximum nutrient influx rate ( $I_{MAX}$ ) and the soil solution concentration were influx equals efflux ( $C_{MIN}$ ). The analyses were run at three initial soil solution concentrations, being 0.1 µg P mL<sup>-1</sup> (A), 0.01 µg P mL<sup>-1</sup> (B), and 1.0 µg P mL<sup>-1</sup> (C). Other Input parameters were those used for Fig. 3.

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