Research Article

Modeling Phosphorus Capture by Plants Growing in a Multispecies Riparian Buffer

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The NST 3.0 mechanistic nutrient uptake model was used to explore P uptake to a depth of 120 cm over a 126 d growing season in simulated buffer communities composed of mixtures of cottonwood (*Populus deltoids* Bartr.), switchgrass (*Panicum virgatum* L.), and smooth brome (*Bromus inermis* Leyss). Model estimates of P uptake from pure stands of smooth brome and cottonwood were 18.9 and 24.5 kg ha^{-1}, respectively. Uptake estimates for mixed stands of trees and grasses were intermediate to pure stands. A single factor sensitivity analysis of parameters used to calculate P uptake for each cover type indicated that I_{max}, k, r_o, and L_o were consistently the most responsive to changes ranging from −50% to +100%. Model exploration of P uptake as a function of soil depth interval indicated that uptake was highest in the 0–30 cm intervals, with values ranging from 85% of total for cottonwood to 56% for switchgrass.

1. Introduction

The loss of P from agricultural lands has been a subject of growing interest in the environmental community for the past two decades. The shift in regulatory focus in the latter half of the 1990s from point sources to diffuse sources and the associated requirement that total maximum daily load (TMDL) estimates be developed has led to the extensive use of a variety of P transport models to describe both particulate and solution phase movement of P [1, 2].

Paralleling the evolution of P transport models has been the development and implementation of various types of riparian buffers intended to retard the movement of P to surface waters [3, 4]. Buffers can significantly reduce particulate P entering surface waters [5]. Control of dissolved P inputs is more challenging [6]. Given that plant roots remove P from soil solution, it follows that plant uptake (mining) can reduce losses of dissolved P to some extent as noted by van der Salm et al. [7].

In an earlier study, Kelly et al. [8] investigated the ability of various plant cover types to capture P from a loess soil in Western Iowa over a four-year period. By the end of the study period the four vegetation cover types exhibited differences in the amount of P incorporated into standing biomass. Given that there are likely differences in plant uptake of P as a result of cover type and soil conditions, it could prove useful to the TMDL process to have a means of mechanistically projecting vegetative uptake of P under a variety of conditions.

As noted by Claassen and Steingrobe [9], a validated mechanistic nutrient uptake model provides a means to extrapolate plant response beyond currently available data, as well as to evaluate potential hypotheses. In a recent review Hinsinger et al. [10] concur with the above statement and further discuss both the utility and efficacy of mechanistic models to describe P uptake. The NST 3.0 model [11] and its predecessor the Barber Cushman model [12, 13] have been used with a high degree of success to explore nutrient uptake under a variety of circumstances [9, 14]. NST 3.0 provides a means to simulate the impacts of changes in both plant and soil processes on the uptake of P for a variety of plant species. In a recent study Lin and Kelly [15] found that NST

3.0 provided the best estimates of P uptake in a three-model comparison utilizing a common set of input values.

The first objective of this study was to use the NST 3.0 model to explore the uptake of P to a depth of 120 cm over a single growing season in simulated buffer communities composed of varying percentages of cottonwood, switchgrass, and smooth brome; three plant species commonly used in riparian buffers in the Midwestern U.S. The second objective was to use the model to explore the impacts of changes in key soil supply and plant parameters, as determined by sensitivity analysis, on estimates of P uptake by the three test species. And finally, the third objective was to use the model to explore potential P capture from each of three soil depth increments (0–30, 30–60, and 60–120 cm) over a 126-d growing season. The buffer species tend to be deep-rooted, so we hypothesized that P uptake from subsoil could be significant.

2. Materials and Methods

The NST 3.0 model was used to make all the calculations in this study. It is a transient model that requires numerical solution. The model along with necessary documentation is available for download from the website of the Department of Crop Sciences at Göttingen University (http://wwwuser.gwdg.de/~uaac/download.htm). In order to operate, the model requires the user to provide information describing: (i) the availability of water and the ability of the soil to supply the nutrient of interest, (ii) the beginning length and growth rate of the root system, and (iii) a suite of values describing the uptake of the nutrient at the root surface, utilizing Michaelis-Menten kinetics. The required parameters along with numerical values for each parameter for each of the three plant cover types investigated are listed by depth interval in Tables 1, 2, and 3. These values were obtained from samples collected and measurements made in support of the study described by Kelly et al. [8] and from related studies conducted by Kovar and Claassen [16] and Kelly and Ericsson [17]. As described by Kelly et al. [8] the study site was divided into five 22 × 20 m blocks. The number of samples collected varied by parameter but in all cases sample size was sufficient to provide representative mean values. Data for this analysis were taken from the 2003 growing season.

2.1. Determination of Parameters Describing P Uptake Kinetics.
A solution depletion technique using intact plants and transient conditions, as described by Claassen and Barber [19] and Edwards and Barber [20] was used to determine the Michaelis-Menten P uptake kinetics values I_{max} (maximum influx at high concentrations), K_m (nutrient concentration in solution when influx is one-half of I_{max}), and C_{min} (concentration in solution below which influx ceases) needed to run the NST 3.0 model.

For smooth brome, the depletion study was conducted at 49 d after germination and for switchgrass the plants were 54 d after germination [16]. Initial solution P concentration for both studies was approximately $50 \, \mu mol \, L^{-1}$. In both

cases, samples were collected at 30 min intervals and C_{min} was achieved at approximately 14 hr.

The cottonwood depletion study followed procedures described in Kelly and Ericsson [17] using green-stem single node cuttings. The cuttings were allowed to grow for 48 d prior to initiating the depletion study. Initial solution P concentration was approximately $7 \, \mu mol \, L^{-1}$. Samples were collected at 15 min intervals until the solution concentration reached the minimum root uptake at approximately 12 hr.

2.2. Determination of Parameters Describing Root Growth.
A field study was used to obtain estimates of the mean half-distance between roots (r_1), mean root radius (r_o), initial root length (L_o), and root growth rate (k). A tractor-mounted hydraulic probe (Giddings Machine Co., Inc.; Windsor, CO) was used to collect 5.0 cm diameter root sample cores to a depth of 120 cm. Details of the field sampling procedures used to collect the cottonwood, switchgrass, and smooth brome buffer segments can be found in Kelly et al. [8]. Sample cores were dispersed in tap water and the roots collected using methods described by Kelly and Ericsson [17]. Total root length of each sample was then determined using the line intercept method of Tennant [21]. Mean root radius was calculated based on the fresh weight using the method described by Mackay and Barber [22].

2.3. Determination of Parameters Describing Soil Supply of P.
Soil samples collected at the start of the 2003 growing season were used to determine the solution and solid phase P concentrations in the soil. Soil solution was collected using the displacement column procedure described by Kovar and Barber [23] followed by ICP analysis of P concentration as described by Clesceri et al. [24]. For the solid phase determination, soil samples were air-dried and extractable P ($0.025 \, M \, HCl$ in $0.03 \, M \, NH_4F$) was determined by ICP analysis [25]. Solution and solid phase P concentrations were then used to calculate the effective diffusion coefficient (D_e), buffer power (b), and initial equilibrium solution concentration (C_{li}) according to the procedures described by Kelly et al. [26].

2.4. Model Simulation Procedures.
Preliminary model runs were made using the 0–120 cm values listed in Tables 1, 2, and 3 for each species, with the exception that the I_{max} values for each species were adjusted from the experimentally derived values to a level that would provide a model calculated uptake equivalent to the observed uptake based on field measurements. This generally required that the I_{max} value is adjusted downward by an order of magnitude using the approach described in Kelly et al. [27]. The simulation ran for a period of 126 days, the time between the initial harvest in early May and the final harvest in late September.

To explore model results further, a series of single factor sensitivity analyses were conducted with the 0–120 cm and 0–30 cm data using the approach described by Silberbush and Barber [28]. Working from the base case scenario, each parameter value in the model was adjusted in turn to three different levels; 0.5, 1.5, or 2.0 times the base case value, while

TABLE 1: Transport, sorption, and root parameters used in the NST 3.0 model to describe P uptake by cottonwood for the 0–120, 0–30, 30–60, and 60–120 cm soil depths.

Parameter		Units	0–120 cm	0–30 cm	30–60 cm	60–120 cm
D_e	Diffusion coefficient in water[†]	$cm^2\,s^{-1}$	$8.9E-6$	$8.9E-6$	$8.9E-6$	$8.9E-6$
Θ	Volumetric soil water content	$cm^3\,H_2O/cm^3$ soil	0.32	0.32	0.33	0.31
f	Impedance factor	Unitless	0.33	0.33	0.35	0.32
V_o	Water uptake at root	$cm\,s^{-1}$	$7.45E-7$	$7.45E-7$	$7.45E-7$	$7.45E-7$
C_{li}	Initial solution concentration	$\mu mol\,cm^{-3}$	$9.39E-3$	$2.69E-2$	$6.45E-4$	$6.45E-4$
b	Buffer power	Unitless	314	45	477	421
I_{max}	Maximum influx at high concentration	$\mu mol\,cm^{-2}\,s^{-1}$	$1.64E-8$	$1.647E-8$	$1.647E-8$	$1.647E-8$
K_m	Solution concentration when influx is $0.5\,I_{max}$	$\mu mol\,cm^{-3}$	$8.7E-4$	$8.7E-4$	$8.7E-4$	$8.7E-4$
C_{min}	Solution concentration when influx is zero	$\mu mol\,cm^{-3}$	$1.0E-6$	$1.0E-6$	$1.00E-6$	$1.00E-6$
r_o	Root radius	cm	0.023	0.0241	0.0217	0.0217
r_1	Half distance	cm	1.05	0.213	0.378	2.578
L_o	Initial root length	$cm\,m^{-3}$	3,041,322	2,094,524	663,672	283,126
k	Root growth rate	$cm\,d^{-1}$	4,812	6,631	6,816	991

[†] From Edwards and Huffman [18].

TABLE 2: Transport, sorption, and root parameters used in the NST 3.0 model to describe P uptake by switchgrass for the 0–120, 0–30, 30–60, and 60–120 cm soil depths.

Parameter		Units	0–120 cm	0–30 cm	30–60 cm	60–120 cm
D_e	Diffusion coefficient in water[†]	$cm^2\,s^{-1}$	$8.9E-6$	$8.9E-6$	$8.9E-6$	$8.9E-6$
Θ	Volumetric soil water content	$cm^3\,H_2O/cm^3$ soil	0.37	0.39	0.36	0.36
f	Impedance factor	Unitless	0.42	0.45	0.40	0.40
V_o	Water uptake at root	$cm\,s^{-1}$	$8.43E-7$	$8.43E-7$	$8.43E-7$	$8.43E-7$
C_{li}	Initial solution concentration	$\mu mol\,cm^{-3}$	$1.28E-2$	$2.95E-2$	$4.52E-3$	$4.52E-3$
b	Buffer power	Unitless	63	47	74	69
I_{max}	Maximum influx at high concentration	$\mu mol\,cm^{-2}\,s^{-1}$	$2.30E-8$	$2.30E-8$	$2.30E-8$	$2.30E-8$
K_m	Solution concentration when influx is $0.5\,I_{max}$	$\mu mol\,cm^{-3}$	$3.22E-5$	$3.22E-5$	$3.22E-5$	$3.22E-5$
C_{min}	Solution concentration when influx is zero	$\mu mol\,cm^{-3}$	$102E-6$	$1.02E-6$	$1.02E-6$	$1.02E-6$
r_o	Root radius	cm	0.009	0.0121	0.0075	0.0085
r_1	Half distance	cm	0.304	0.198	0.227	0.489
L_o	Initial root length	$cm\,m^{-3}$	4,162,621	1,935,508	1,371,549	855,564
k	Root growth rate	$cm\,d^{-1}$	8,484	10,506	10,306	4,641

[†] From Edwards and Huffman [18].

TABLE 3: Transport, sorption, and root parameters used in the NST 3.0 model to describe P uptake by smooth brome for the 0–120, 0–30, 30–60, and 60–120 cm soil depths.

Parameter		Units	0–120 cm	0–30 cm	30–60 cm	60–120 cm
D_e	Diffusion coefficient in water[†]	$cm^2\,s^{-1}$	$8.9E-6$	$8.9E-6$	$8.9E-6$	$8.9E-6$
Θ	Volumetric soil water content	$cm^3\,H_2O/cm^3$ soil	0.256	0.25	0.26	0.26
f	Impedance factor	Unitless	0.243	0.23	0.25	0.25
V_o	Water uptake at root	$cm\,s^{-1}$	$8.16E-7$	$8.16E-7$	$8.16E-7$	$8.16E-7$
C_{li}	Initial solution concentration	$\mu mol\,cm^{-3}$	$1.141E-2$	$3.74E-2$	$2.58E-3$	$2.58E-3$
b	Buffer power	Unitless	73	28	98	92
I_{max}	Maximum influx at high concentration	$\mu mol\,cm^{-2}\,s^{-1}$	$3.27E-8$	$3.27E-8$	$3.27E-8$	$3.27E-8$
K_m	Solution concentration when influx is $0.5\,I_{max}$	$\mu mol\,cm^{-3}$	$2.71E-5$	$2.71E-5$	$2.71E-5$	$2.71E-5$
C_{min}	Solution concentration when influx is zero	$\mu mol\,cm^{-3}$	$1.22E-6$	$1.22E-6$	$1.22E-6$	$1.22E-6$
r_o	Root radius	cm	0.0114	0.0135	0.009	0.0117
r_1	Half distance	cm	0.505	0.255	0.347	0.914
L_o	Initial root length	$cm\,m^{-3}$	2,486,379	1,464,477	793,155	228,747
k	Root growth rate	$cm\,d^{-1}$	3,572	8,631	1,622	464

[†] From Edwards and Huffman [18].

holding all other parameters used in the model at the base level. Calculated estimates of uptake were compared with the base case value as a way of assessing whether a particular model parameter was more or less influential in determining the level of P uptake predicted by the model. One hundred and four model simulations were conducted for each of the three vegetation types in support of the sensitivity analyses.

To explore the uptake of P in the 0–30, 30–60, and 60–120 cm soil depths, soil supply and root growth values were developed for each depth interval (Tables 1, 2, and 3). The water uptake rate and Michaelis-Menten kinetics values used in the 0–120 cm simulation for each cover type were assumed to represent uptake in each cover type for the three depth intervals.

3. Results and Discussion

Total estimated P uptake for the 126 d simulation period was 79.1 mmols m^{-3} for cottonwood, 69.5 mmols m^{-3} for switchgrass, and 61.0 mmols m^{-3} for smooth brome, all to a depth of 120 cm. Using these rates of uptake as a base, estimates of uptake on a per hectare basis were calculated for buffers composed of various percentages of the three cover types (Table 4). Model estimates of P uptake over a single growing season ranged from 18.9 kg ha^{-1} for the smooth brome only to 24.5 kg ha^{-1} for cottonwood only (Table 4). Simulated buffers with mixtures of trees and grasses were intermediate to the pure stands noted above. Simulated uptake in a buffer composed of 50% smooth brome and 50% switchgrass exceeded the uptake in a simulated smooth brome only buffer by 1.33 kg ha^{-1}, but was 1.29 kg ha^{-1} less than a switchgrass only buffer.

Based on these simulations, the greatest amount of P is captured in a pure stand of cottonwood when compared to other buffer configurations. Assuming that this relationship holds for the longer term, the potential to capture and retain P on site is greater with the cottonwood given its longer lifespan and substantially larger level of standing biomass with the passage of time. The standing crop of the perennial grasses will come to relative equilibrium after a few years and the annual level of P intercepted will stabilize. If the grasses are removed annually, or even more frequently, the potential for P uptake will increase due to the fact that the level of P recycled annually by the standing vegetation will be reduced. The same would be true for the removal of the aboveground portion of the cottonwood, although it would be more practical to harvest the trees on a 7-to-10-year cycle as a fiber or fuel byproduct. For example, Kelly et al. [8] found that a total of 101 kg ha^{-1} of P would be removed over a 4 yr period from a mixed stand buffer compared to a 62 kg of P ha^{-1} for a smooth brome control. Although a pure stand of cottonwood would be more effective in the capture of solution P, it should be kept in mind that the grass communities will be more effective in retarding or preventing the loss of P due to soil erosion [29].

Each of the parameters used in the model was subjected to a single factor sensitivity analysis using the 0–120 cm and 0–30 cm values for each of the three cover type species.

Results indicated that four factors, I_{max}, k, r_o and L_o, were consistently responsive at both depths across species to changes ranging from −50% to +100%. The response of each of these four parameters for each species is illustrated for the 0–120 cm analysis in Figure 1. All other parameters were either minimally responsive or nonresponsive to change at both intervals. As illustrated in Figure 1, the response to change in root growth rate (k) was lower than those of the other three parameters. A doubling of the root growth rate increased P uptake by cottonwood by approximately 9% while the same change induced a 26% increase in switchgrass P uptake. Changes in root radius (r_o) and initial root length (L_o) had larger impacts on uptake estimates than did changes to the root growth rate (Figure 1). Comparison of the 0–30 cm response to the 0–120 cm response produced essentially the same response pattern for both depth intervals. However, the r_o response in the 0–120 cm sensitivity analysis was slightly more responsive to change than in the 0–30 cm simulations (data not shown). These results point to the importance of designing a sampling scheme that is capable of providing as accurate an estimate of the initial root length and mean root radius as possible since the model will be responsive to over or under estimates in either or both of these values.

As noted in Figure 1, the I_{max} value is the single most influential parameter in the model for all three of the test species. In all three cases, a 50% decrease or a 100% increase in I_{max} leads to an identical decrease or increase in estimated P uptake. As suggested earlier, this points to the fact that P supply in this soil exceeds the ability of all three of these species to take up P, even when the maximum rate of uptake is doubled. If the goal is to capture as much solution phase P as possible, it will be useful to create additional demand through periodic harvests and removal of the P contained in the biomass. Additionally, it could be useful to screen other species to determine if they might have higher rates of P uptake and storage in accumulated biomass.

Values used to evaluate P uptake in each of the three depth intervals for each plant cover type are presented in Tables 1, 2, and 3. As noted above, it was assumed that the Michaelis-Menten uptake kinetics values (I_{max}, K_{min}, C_{min}) and the water uptake rate at the root (V_o) within a cover type would not vary as a function of soil depth interval. We cannot verify the validity of this assumption, and thus it should be considered as a reasonable first approximation. In future studies the collection of depth dependent values for these parameters would test the validity of this assumption and help refine future model applications. Soil supply and root geometry values were unique to the particular depth interval.

Model exploration of the level of P uptake as a function of soil depth indicated that in all three cover types the level of uptake was highest in the 0–30 cm intervals (Table 5) although the values ranged from 85% of total uptake for cottonwood to 56% of total uptake for switchgrass. A partial explanation for these differences in uptake can be found by comparing the root length values (Tables 1 and 2) for the 0–30 cm depth interval where 68% of the cottonwood root length occurs compared to 46% of the switchgrass

TABLE 4: NST 3.0 model estimates of phosphorus uptake in kilograms per hectare to a depth of 120 cm over a 126 d growing season for buffers composed of varying percentages on an area basis of cottonwood, switchgrass, and smooth brome.

| Plant community | Percentage contribution cottonwood/switchgrass/smooth brome | | | | | |
| | 66/17/17 | 33/33/33 | 0/50/50 | 100/0/0 | 0/100/0 | 0/0/100 |
	kg P ha^{-1}					
Cottonwood	16.3	8.1	0	24.5	0	0
Switchgrass	3.6	7.1	10.8	0	21.5	0
Smooth brome	3.2	6.2	9.4	0	0	18.9
Σ	23.1	21.4	20.2	24.5	21.5	18.9

TABLE 5: NST 3.0 model estimates of phosphorus uptake in kilograms per hectare for four depth increments at the end of a 126 d simulated growing season for buffers composed of cottonwood, switchgrass, and smooth brome.

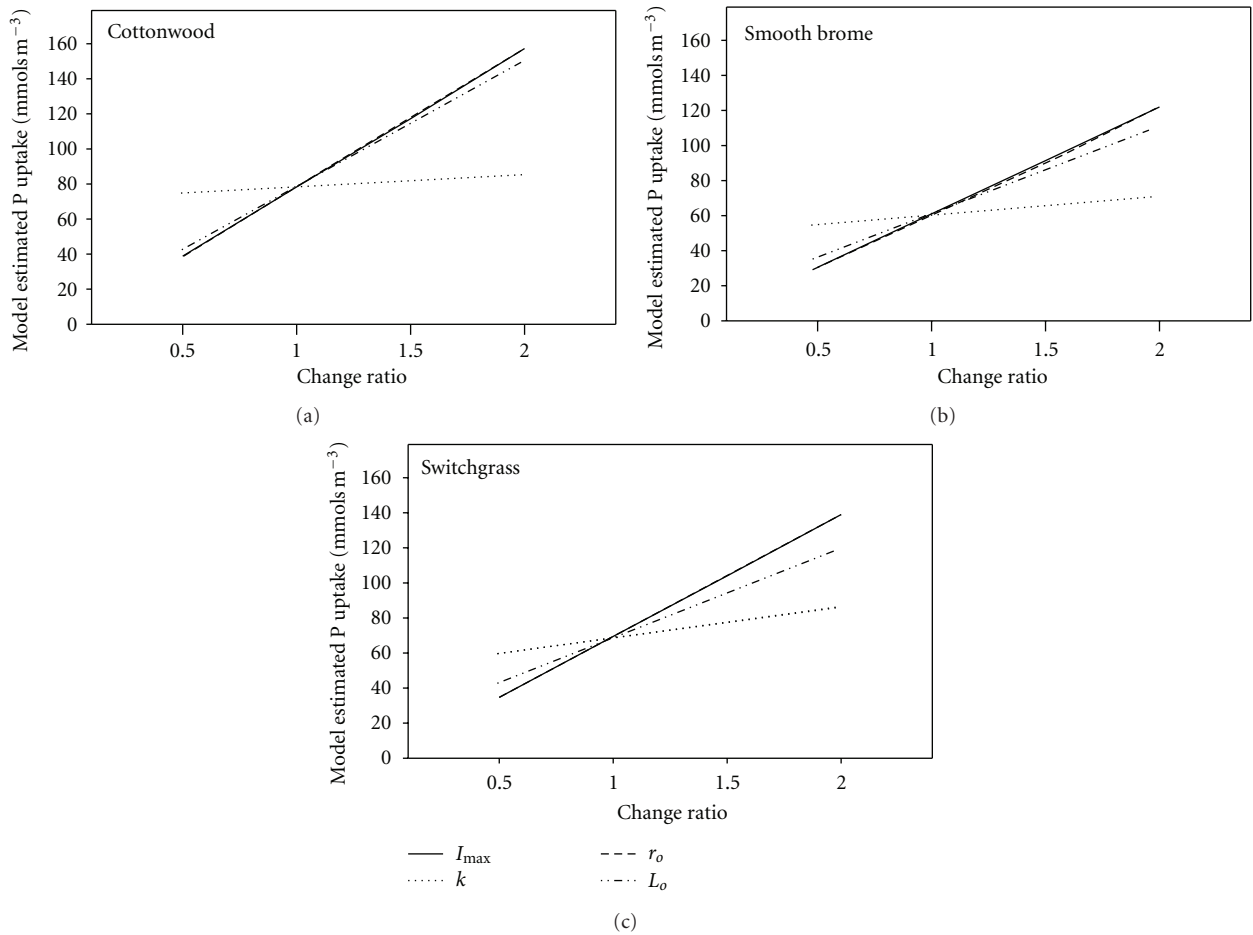| Plant community | Depth of soil increment (cm) | | | |
| | 0–120 | 0–30 | 30–60 | 60–120 |
	kg P ha^{-1}			
Cottonwood	24.5	20.4	2.7	0.8
Switchgrass	21.5	15.3	7.3	4.7
Smooth brome	21.4	18.8	5.4	2.0

FIGURE 1: Sensitivity analysis of predicted P uptake by cottonwood, smooth brome, and switchgrass using the NST 3.0 model showing the effect on predicted P uptake of varying individually the maximum nutrient influx rate at high concentration (I_{max}), root growth rate (k), root radius (r_o), and initial root length (L_o) values while holding all remaining model parameters constant. Each parameter has been varied from a 50% reduction (0.5 change ratio) to a doubling (2.0 change ratio).
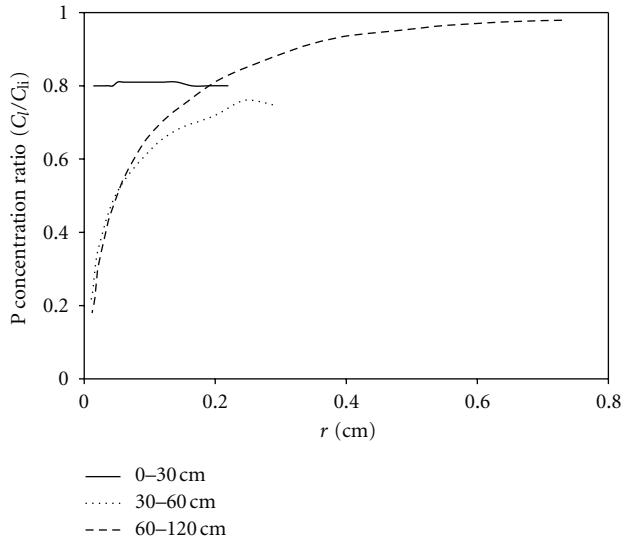
FIGURE 2: Effect of the distance from the root surface, as defined by the r_1 value, on the ratio of the final solution concentration to the initial solution concentration (C_l/C_{li}) of P for the 0–30, 30–60, and 60–120 cm soil depths in the smooth brome cover type.

60–120 simulations, the P concentration at the end of the simulation is approximately 80% lower than it was at the start of the simulation. Similar C_l/C_{li} ratio patterns were observed for the three depth intervals in the cottonwood and switchgrass simulations. These observations are consistent with the findings from several studies, as summarized by Hinsinger et al. [10], which attribute the formation of similar gradients to the relatively slow diffusion rate of P through the soil to the root surface with little or no contribution attributable to mass flow. However, Roose et al. [31] suggest that the numerical solution used in the NST 3.0 model has limitations when describing more complex roots systems. To address this concern, Roose and Kirk [32] explored the use of a simplified analytical solution that would more fully allow for both convection and diffusion. Their findings warrant further consideration as we continue the evolution and application of mechanistic nutrient uptake models.

root length. This is also consistent with the results of the sensitivity analysis with respect to the influence of increasing root length on P uptake (Figure 1). However, it is also important to note that P uptake is not totally a function of root length since switchgrass had the highest total root length (Table 2), but was second in total uptake and just barely exceeded the level of uptake by smooth brome which had only 59% of the total root length of switchgrass (Table 3).

If the amount of P uptake for each of the three depth intervals within a cover type is summed, the estimate of total uptake obtained for switchgrass and smooth brome as compared to the value obtained for the same two cover types in the 0–120 cm simulation (Table 5), increases by approximately 20% in both cases. A similar comparison of the cottonwood data reveals that the total by summation of the three layers is approximately 2% lower than the 0–120 cm simulation (Table 5). We speculate that the differences associated with the summed values may be attributable to small differences in the observed uptake-based approach used for the calculation of the Michaelis-Menten values, since previous studies have shown uptake to be particularly sensitive to changes in I_{max} values [30].

Figure 2 depicts solution P concentration in relation to the initial concentration as determined by the model for each of the three depth intervals in the smooth brome cover type at the end of 126 days of simulated uptake. The decline in solution P concentration in the surface layer is fairly uniform throughout the soil surrounding the root. A different pattern is seen in the concentration profiles for the 30–60 and 60–120 cm depths. Due to the slow rate of P diffusion through the soil and the relatively lower initial P concentration, a fairly steep gradient develops with much greater depletion of P near the root surface and a lower level of P depletion as distance from the root increases. In both the 30–60 and
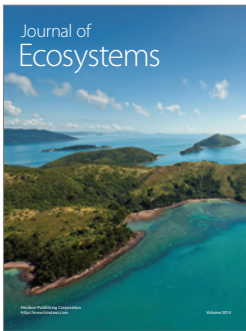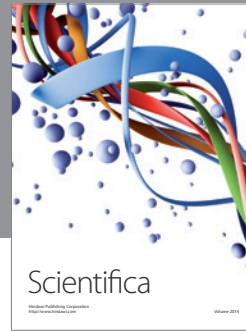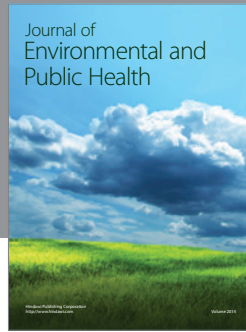
4. Conclusions

Results of this study indicate that a simulation model such as NST 3.0 can provide both useful insights into the ability of various plant cover types to capture solution P and a means to explore which soil and plant factors are the most influential in predicting plant P uptake. A single factor sensitivity analysis for each cover type identified I_{max}, k, r_o and L_o as the parameters having the most impact on model estimates of P uptake. This result indicates in this case that soil supply of P did not limit uptake. Model evaluation of P uptake as a function of soil layer indicated that in all three cover types uptake was highest from the 0–30 cm layer. Consequently, our hypothesis that subsoil uptake might play a proportionally greater role in total uptake by these deep rooted species was not supported by model predictions. Although results indicate a pure stand of cottonwood would be more effective in capturing solution P, it should be kept in mind that the grass communities will be more effective in mitigating or preventing the loss of particulate P due to soil erosion. While the results of this study are most encouraging, recent evaluations of the current approaches to mechanistic modeling [10, 15, 32] point to the need for a further evolution of the structure of minimalistic mechanistic nutrient uptake models. In the final analysis, it is important to remind ourselves that the validity of predictions produced by this or any model, is highly dependent on the quality of the data used to represent each of the parameters.

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