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Model Estimates of Nutrient Uptake by Red Spruce Respond to Soil Temperature

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ABSTRACT

A better understanding of the mechanisms that control nutrient acquisition in the context of plant and ecosystem responses to climate change is needed. Mechanistic nutrient uptake models provide a means to investigate some of the impacts of temperature change on soil nutrient supply and root uptake kinetics through the simulation of key soil and plant processes. The NST 3.0 *model, in combination with literature values on plant and soil parameters from a red spruce* (*Picea rubens L.*) *site in the southern Appalachians, was used to conduct a series of model simulations focused on the combined effects of changes to the maximal rate of nutrient influx at high concentrations* (I_{max}), *root growth rate* (*k*), *concentration of nutrient occurring in the soil solution* (C_{li}), *and the ability of the soil solid phase to buffer changes to the soil solution nutrient concentration* (*b*). *Previous research has indicated that these four parameters are responsive to changes in root zone temperature. Simulated uptake of* NH_4 *increased by a factor of up to* 2.6 *in response to increases in soil temperature of* 1˚*C to* 5˚*C. The model also projected an increase in P uptake coupled with up to an* 80% *reduction in solution P concentration in response to a* 1˚*C -* 5˚*C increase over a* 147*-d simulation period. These hypothetical changes, if validated, have interesting implications for plant growth and competition and point to a need for additional studies to better define the impacts of soil temperature on soil nutrient supply and root uptake.*

Keywords: *Mechanistic Modeling*, I_{max}, *Root Growth Rate*, *Soil Buffer Power*

1. Introduction

Over the next 100 years, mean global temperature is projected to increase by 1.5˚C to 4.5˚C [1]. An increase in atmospheric temperature will eventually lead to an increase in soil temperature [2], and this increase in soil temperature could lead to changes in soil supply and plant nutrient uptake rates. Most studies of soil warming in the forest environment have focused on changes in plant productivity and soil nutrient availability [3-6] with only Gessler *et al.* [7] and Adam *et al.* [8] assessing the potential changes in nutrient uptake as a function of changes in root zone temperature.

In a laboratory study on the influence of temperature on solution phase nutrient concentrations in soil from a southeastern US spruce-fir stand, Kelly [9] found higher concentrations of NH_4 and P as soil temperature increased from 4˚C to 24˚C. Conversely, NO_3 concentration in solution was greatest at 4˚C and declined as temperature increased. Since nutrient uptake is thought to occur largely through root interaction with the solution phase [10], changes in soil temperature, and associated changes in soil solution chemistry have the potential to alter both nutrient availability and plant uptake. And since nutrient uptake is a physiologically mediated process, it also follows that changes in soil temperature could have an impact on the rate at which plants take up nutrients. For example, Adam *et al.* [8] in a greenhouse study found that the uptake of NO_3 by red maple plants increased by approximately 2% per degree of temperature increase as solution temperature increased to an optimum and then began to decline. Adam *et al.* [8] also report that root surface area was influenced by differences in root zone temperature, with both root length and root radius values showing a response pattern similar to that of nitrate. Similarly, Weih and Karlsson [5] found that mountain birch root-N uptake rate and plant-N concentration were positively correlated with increases in soil temperature. In a field and laboratory study of Norway spruce, Gessler *et al.* [7] found that very little NO_3 was taken up by roots when solution NH_4 concentrations were elevated and that NH_4 uptake increased by approximately 10% to 13% per ˚C increase in root zone temperature.

Agronomic studies suggest that when soil P supplies are low, P availability increases with increasing soil temperature [11-13]. It stands to reason that this relationship would also hold in unfertilized forest soils, since in both agricultural and forest soils, decomposition of organic matter is the primary source of P. These and other studies have created a body of knowledge that, when combined through a mechanistic nutrient uptake model, provide a means to explore hypothetically the impacts of soil temperature change on soil nutrient supply and nutrient uptake by an important tree species.

The NST 3.0 mechanistic nutrient uptake model provides a means to simulate the short-term impact of soil temperature change on the concentration of nutrients occurring in the soil solution as well as the impact of changes in root growth rate on nutrient acquisition. Similarly, the impacts of temperature mediated changes on physiological processes can be explored indirectly through alterations of the magnitude of the uptake kinetics parameters. NST 3.0 is available for download from the website of the Department of Crop Sciences at Göttingen University (http://wwwuser.gwdg.de/~uaac/). The NST 3.0 model, and its predecessor the Barber-Cushman model [14], have been used with a high degree of success to explore nutrient uptake under a variety of circumstances [15-19].

As noted by Claassen and Steingrobe [18], a validated mechanistic model provides a means to extrapolate plant response beyond currently available data and also provides a way to evaluate potential hypotheses. Thus, the objective of this study is to use a well-established mechanistic nutrient uptake model, NST 3.0, to explore the potential impacts of 1˚C, 2˚C, 3˚C, and 5˚C increases in simulated soil temperature on estimates of nutrient uptake by red spruce seedlings over a growing season. We will do this by altering the magnitude of the values for the initial solution concentration (C_{li}), the ability of the soil solid phase to resupply the solution phase (b), the root growth rate (k), and the maximal rate of nutrient influx at the root surface (I_{max}). The results of these comparisons should provide initial theoretical insights into the potential changes in N and P supply and uptake that might occur in response to changes in soil temperature as a consequence of global climate change.

2. Materials and Methods

Published data taken from studies conducted in the spruce-fir forest at Whitetop Mountain in southeastern Virginia and reported by Kelly and Mays [20], Thornton *et al.* [21], Kelly *et al.* [22], and Kelly [9] will form the basic data set used in this analysis (**Table 1**). These data sets will be supported by additional information from the same site reported by Joslin and Wolfe [23,26]. In some cases the values listed in **Table 1** are taken directly from

Table 1. Transport, sorption, and root parameters used in the NST 3.0 model to describe N and P uptake by red spruce seedlings under base conditions (Letters in parentheses following each value indicate the data source corresponding to the citations listed in the footnote).

	Parameter	Units	N	P
D_L	Diffusion coefficient in H_2O	$cm^2 \cdot s^{-1}$	1.9E−5 (a)†	8.9E−6 (b)
Θ	Volumetric H_2O content	cm^3 H_2O/cm^3 soil	0.22 (c)	0.22 (c)
f	Impedance factor	unitless	0.178 (c)	0.178 (c)
V_o	H_2O uptake at root	$cm \cdot s^{-1}$	6.3E−8 (d)	6.3E−8 (d)
C_{li}	Initial solution concentration	$mol \cdot cm^{-3}$	1.17E−6 (e)	3.42E−9 (e)
b	Buffer power	unitless	133 (c)	37 (d)
I_{max}	Maximum influx at high concentration	$mol \cdot cm^{-2} \cdot s^{-1}$	2.1E−11 (f)	2.68E−13 (g)
K_m	Solution concentration when influx is 0.5 I_{max}	$mol \cdot cm^{-3}$	2.06E−4 (f)	1.6E−8 (g)
C_{min}	Solution concentration when influx is zero	$mol \cdot cm^{-3}$	1.11E−9 (f)	6.0E−11 (g)
r_o	Root radius	cm	0.042 (h)	0.042 (h)
r_1	Half distance	cm	0.31 (h)	0.31 (h)
L_o	Initial root length	cm	37860 (h)	37860 (h)
k	Root growth rate	$cm \cdot d^{-1}$	315 (h)	315 (h)

†(a) [24]; (b) [25]; (c) [20]; (d) [9]; (e) calculated by model; (f) [19]; (g) [22]; (h) [21].

the published work cited in **Table 1** or re-calculated from these values when not available as a direct result of these studies. For parameters that could not be calculated or extrapolated from on-site data directly available to the authors, missing parameter values were obtained from the literature sources noted or calculated with the model using a process similar to that described in Kelly *et al.* [17]. Values for the NH_4 uptake kinetics parameters I_{max}, K_m, and C_{min} were taken from a study of white spruce conducted by Hangs *et al.* [19]. Phosphorus values for the same parameters came from a study of loblolly pine conducted by Kelly *et al.* [22]. While it would be preferable to have actual values for red spruce, values from these two conifer species are thought to provide a reasonable first approximation.

In this study we used the NST 3.0 model to focus on the impacts of temperature change on the level of nutrient occurring in the soil solution (C_l), the ability of the soil solid phase nutrients to sustain the solution phase concentration (b), the root growth rate (k), and the maximal rate of nutrient uptake under unlimited nutrient availability (I_{max}). These four parameters were chosen for evaluation because of their demonstrated sensitivity to change as a function of temperature [8,9]. Values used for these and the other parameters required for the base case simulations of N and P using NST 3.0 are listed in **Table 1** and their source identified.

Percentage modifications (+/−) to the base level values used for k and I_{max} to simulate changes in temperature (**Table 2**) are based on the relations observed by Adam *et al.* [8] for red maple. In a study of root zone temperature influence on root growth and nitrate uptake by red maple, Adam *et al.* [8] found that root growth rate increased by an average of 4.3% per degree of temperature change as the root zone temperature was increased from 14˚C to 24˚C and that the nitrate I_{max} value increased by 1.9% per degree increase over the same temperature range. Given the absence of actual measurements for red spruce, these two percentage values were assumed to represent the relative change rate in k and I_{max} for both nutrients (**Table 2**). It should be noted however, that the temperature range used by Adam *et al.* [8] exceeds the range of soil temperature increase likely to occur in soils currently supporting the growth of red spruce.

Similarly, in a controlled environment investigation of changes in soil solution NH_4 and P in the surface horizon of a soil from a spruce-fir stand on Whitetop Mountain, Kelly [9] found that NH_4 concentration increased by 10% per degree as temperature increased from 4˚C to 24˚C while soil solution P concentration increased by 13.1% per degree *C*. Using the relationship between C_{li} and b reported by Kelly *et al.* [27], the corresponding b values for NH_4 and P were estimated to decrease by 10% for NH_4 and 6.5% for P per degree of temperature increase (**Table 2**). For the purposes of this analysis all nitrogen uptake is assumed to be in the form of NH_4 because of the established preference of conifers for this form of N [7,28]. Using the change values listed in **Table 2** for the four model parameters, a suite of uptake values was calculated for each nutrient to represent simulated temperature increases of 1˚C, 2˚C, 3˚C, and 5˚C. All four values for each nutrient-temperature scenario were entered concurrently while the values for the remaining nine parameters in the model were held constant at the level specified for each nutrient in **Table 1**.

Table 2. Percentage change factors for Tests I and II (+/− %) per degree centigrade increase in simulated soil temperature for C_{li}, b, k, and I_{max} for simulations by NST 3.0 of N and P uptake by red spruce seedlings.

Parameter	N		P	
	Test I	Test II	Test I	Test II
	Change %			
C_{li}	+10	†	+13.1	
b	−10	†	−6.5	
k	+4.3	+10	+4.3	+10
I_{max}	+1.9	+10	+1.9	+10

†C_{li} and b values were unchanged in Test II, only the k and I_{max} values were modified according to the Q_{10} relationship.

In addition to the change factors for k and I_{max} identified for Test I in **Table 2**, an additional set of values was calculated for these two physiologically mediated parameters based on a simple Q_{10} relationship. Thus for the data sets based on the Q_{10} relationship (Test II, **Table 2**), k and I_{max} were each increased by 10% per ˚C of temperature increase. This level of change for Test II was chosen in part based on the study of Norway spruce by Gessler *et al.* [7] who found an increase in NH_4 uptake of approximately 10% - 13% per ˚C increase in root zone temperature. The values for C_{li} and b in the Q_{10} simulations (Test II) continued to change at the rates indicated for Test I in **Table 2**, while the remaining values for the other nine parameters listed in **Table 1** were again held constant at the levels indicated. Nine scenarios were run for each nutrient-temperature combination for a total of 18 simulations covering both nutrients.

3. Results and Discussion

3.1. Validity of Assumptions

Before proceeding further it is appropriate to consider the assumptions that have been made concerning the magnitudes and directions of change associated with the C_{li}, b, k, and I_{max} values used for each nutrient. Unfortunately, studies of soil temperature influences focused directly on these parameters are very limited for woody species. Therefore we have depended heavily on the study of Adam *et al.* [8] even though their study was conducted with a deciduous species and used a temperature range likely to exceed temperatures in red spruce forest soils. We combined the insights from Adam *et al.* [8] with actual seasonal totals of N and P uptake by red spruce seedlings from the work of Thornton *et al*. [21]. The Test I values are taken to be at the lower end of the potential response spectrum. The observations of Gessler *et al*. [7] were used to inform the other end (Test II) of what we feel is a conservative spectrum of input parameters that are consistent with observed growing season uptake based on the data of Thornton *et al.* [21]. Therefore, the focus of this study is to develop an assessment of "relative change" rather than providing "absolute values". While these uptake estimates are hypothetical, they have the potential to raise important research questions. These questions in turn could lead to the formulation of future studies specifically designed to address possible changes in nutrient uptake in response to changing soil temperature.

3.2. Nitrogen

Using the parameter values listed in **Table 1**, the model estimate of NH_4 uptake over a 147-d period was on the order of 24.0 mmols. For the purpose of this study this value is considered to be the base level of N uptake and is equivalent to the level of uptake actually observed for the red spruce seedlings described by Thornton *et al.* [21] during their second year of growth. This level of correspondence between the model calculation and observed uptake was achieved by adjusting the C_{li} value to a level that, in conjunction with the other values entered into the model (**Table 1**), would combine to produce a level of model predicted uptake equivalent to the observed uptake. The same procedure was used to establish the base level of uptake for P as well.

In the case of NH_4, this led to a higher value for C_{li} (1.17E−6 mol·cm^{-3}) being used in the model than was reported by Kelly [9] for a spruce-fir soil at the Whitetop Mountain site (5.27E−8 mol·cm^{-3}). However, it is not unreasonable to assume that even though the soil used in the pot study conducted by Thornton *et al.* [21] came from a similar site on Whitetop Mountain, the handling of the soil and the warmer environment in the chambers used by Thornton *et al.* [21] led to a higher level of N availability to the study seedlings. This supposition is consistent with the observation of Kelly [9] that soil solution NH_4 levels increased as soil incubation temperature increased, as well as the findings of Rustad and Fernandez [4] who reported that a 4˚C - 5˚C increase in soil temperature in a red spruce forest stand stimulated decomposition and the subsequent release of N from organic sources.

Estimates of N uptake derived by the model in response to each of the temperature increase scenarios indicate steady increases in uptake with the highest estimate using the Test I parameters being 1.75 times that occurring under base conditions (**Table 3**). When Q_{10} values are used to represent further increases in I_{max} and k (Test II), the level of N uptake estimated at 5˚C increases by a factor of 2.6 over base conditions. This level of increase, if realized, could stimulate the growth of established red spruce, assuming that current growth rate is N limited. The predicted level of increased uptake could also have other impacts such as the creation of imbalances with other nutrients that could slow growth, or increased susceptibility to freeze damage due to early bud out or delayed senescence [29]. Alternatively, an increase in nitrogen availability could stimulate the growth or establishment of other species that might be better suited to a more favorable nitrogen supply and warmer soil than red spruce and ultimately lead to the displacement of red spruce by another species over time [30].

To explore these model results further, a series of single factor sensitivity analyses were conducted using the approach described by Silberbush and Barber [31] to see if a particular one of the four parameters evaluated was driving the response. Using the 1˚C increase scenario as an example, the results of the sensitivity analyses indicted that for NH_4 the I_{max} and C_{li} values were the most sensitive to change and both produced essentially the same level of response (**Figure 1**). Root growth rate (k) responded to a lesser degree with NH_4 uptake exhibiting a 19% decline when the k value was reduced by 50% and a 40% increase when the k value was doubled (**Figure 1**).

Table 3. Estimates of N and P uptake by red spruce seedlings over a 147-d period as a function of simulated soil temperature changes of 1˚C, 2˚C, 3˚C, or 5˚C based on NST 3.0 calculations.

Scenario	Uptake (mmols)			
	N		P	
	Test I	Test II	Test I	Test II
Base	24.0		1.48	
+1˚C	27.3	29.7	1.61	1.66
+2˚C	30.8	37.0	1.77	1.87
+3˚C	34.4	44.8	1.86	2.01
+5˚C	42.2	63.2	2.06	2.26

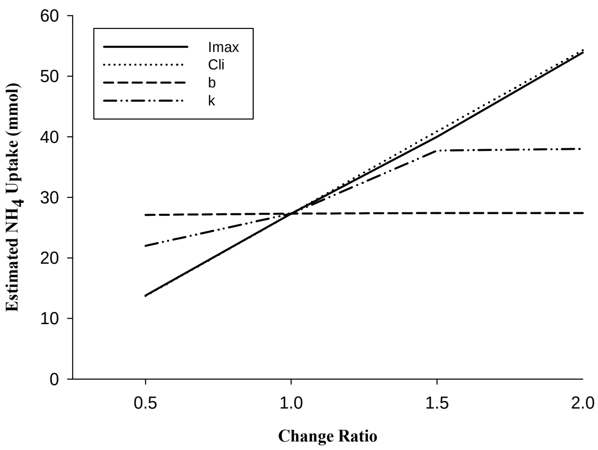

Figure 1. Sensitivity analysis of predicted NH_4 uptake in response to a simulated 1˚C increase in temperature using the NST 3.0 model showing the effect on predicted NH_4 uptake of varying individually each of the four parameters illustrated while holding all remaining model parameters constant. Each parameter has been varied from a 50% reduction (0.5 change ratio) to a doubling (2.0 change ratio).

The buffer power (*b*), although very much related to C_{li}, was not responsive and NH_4 uptake remained essentially unchanged in its response (**Figure 1**). This suggests that NH_4 supply exceeds plant demand as defined by the I_{max} value used.

To explore this further, the change in the solution NH_4 concentration profile along the radius of a cylinder of soil around a typical root, as represented by the ratio of the ending solution concentration to the initial solution concentration (C_l/C_{li}) was plotted (**Figure 2)**. This depiction generated by the model is from the 2˚C increase using the Test I values for I_{max}, C_{li}, *b*, and *k*. This example illustrates that there was no change in solution NH_4 concentration at the end of 147-d of simulated plant uptake for the 2˚C scenario or any of the other soil temperature change simulations of NH_4. **Figure 2** clearly illustrates that under the conditions investigated, that N uptake had very minimal impact on the concentration of N in the soil solution and further suggests that plant growth would be unlikely to be N limited on an annual basis under these conditions. This conjecture is also consistent with the N-saturation hypothesis of Joslin and Wolfe [26] for southern red spruce stands.

3.3. Phosphorus

Uptake of P ranged from 1.48 mmol under base conditions to a maximum of 2.26 mmol for the 5˚C scenario (**Table 3**). In contrast to NH_4, the solution concentration profile for P was substantially depleted at the end of the 147-d simulation period (**Figure 3**). The response depicted in this figure is similar to that observed for all of

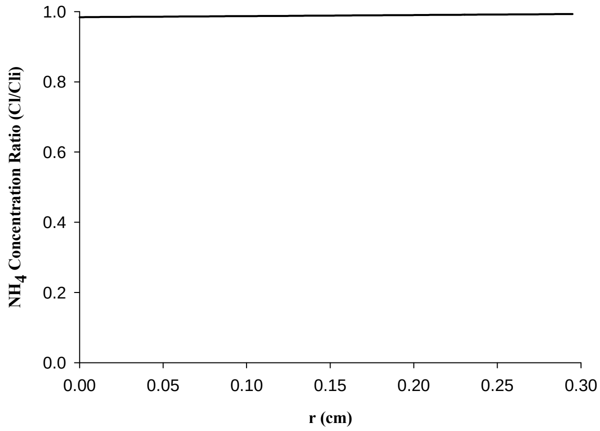

Figure 2. Effect of distance from the root surface on the ratio of the ending solution concentration to the initial solution concentration (C_l/C_{li}) of NH_4. The gradient in solution perpendicular to the root illustrates the combined impact of a change in I_{max}, *b*, *k*, and C_{li} for a 2˚C simulated change in soil temperature using Test I data.

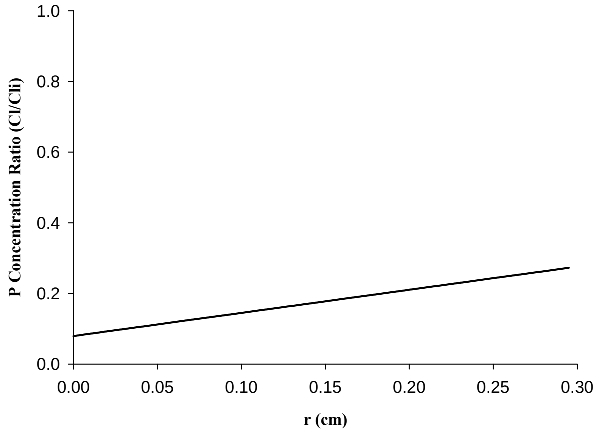

Figure 3. **Effect of distance from the root surface on the ratio of the ending solution concentration to the initial solution concentration (C_l/C_{li}) of P. The gradient in solution perpendicular to the root illustrates the combined impact of a change in I_{max}, *b*, *k*, and C_{li} for a 3˚C simulated change in soil temperature using Test I data.**

the P scenarios with the concentration profile being reduced further in the 5˚C scenario. The sensitivity analysis depicted in **Figure 4** illustrates that the model is more sensitive to changes in the C_{li} value than the b value. This seems reasonable given the availability of P for root uptake is controlled by the diffusion rate of P through the soil [10]. Since P supply is relatively low in most unfertilized soils, it is common to see steep solution concentration profiles in the soil surrounding a root [18].

The growth of new roots and mycorrhizae can also play an important role in P uptake given the relatively slow rate of P diffusion and the negligible contribution of

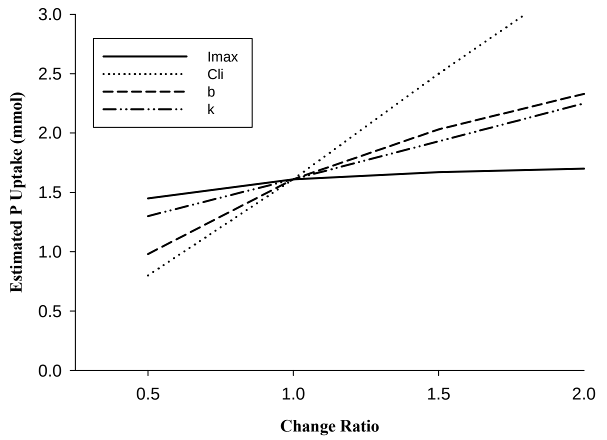

Figure 4. Sensitivity analysis of predicted P uptake in response to a 1˚C increase in temperature using the NST 3.0 model showing the effect on predicted P uptake of varying individually each of the four parameters illustrated while holding all remaining model parameters constant. Each parameter has been varied from a 50% reduction (0.5 change ratio) to a doubling (2.0 change ratio).

mass flow to P delivery. Under base case conditions, P uptake over the study period attributed to existing roots, as calculated by the model, was on the order of 912 μmols with new roots responsible for an additional 563 μmols. At the 5˚C level using Test II data, existing roots accounted for 1.17 mmols of uptake and new roots 1.09 mmols of P uptake. In the latter case, new roots account for approximately half of the uptake, while in the base case simulation new roots provide approximately 38% of the P uptake. Increasing the degree to which roots ramify the soil has a definite impact on the uptake of P as a result of shorter diffusion distance to a root.

Hyphae of mycorrhizae can serve much the same function as roots and are known to be important to P acquisition in P limited situations. We did not have information on mycorrhizal growth rates or mycorrhizal uptake kinetics values for P or NH_4. Consequently, we choose not to consider their potential contribution. Provisions have been made in NST 3.0 to estimate the contribution of root hairs to uptake. To do so, additional values for k and I_{max} are entered into the model. This same provision could be used to get an estimate of mycorrhizal contributions as well, assuming appropriate k and I_{max} values were available. However, under the conditions considered here it is likely that the addition of mycorrhizae would have increased further the rate of P uptake and contributed to the further decline of plant available P.

3.4. Implications of Results

In this study, we simulate NH_4 and P uptake using data from a southeastern US red spruce forest stand where there is evidence that growth is not consistently N-limited. The absence of red spruce responses to N fertilization on Whitetop Mt. [23] and the observation of net N-mineralization rates that exceed tree uptake requirements in various other high-elevation red spruce-fir forest sites [32,33] would indicate the absence of an N limitation for red spruce in some southeastern US locations. In light of this evidence, it appears prudent to question related assumptions given our limited knowledge of the impact that a lack of N-limitation might have.

While we were able to calibrate the model to existing data on the total uptake of N by red spruce seedlings over a 147-d period, direct information on uptake responses to changes in C_l under current conditions in the southern Appalachians was not available and the assumptions was made that NH_4 concentration in the soil solution would increase in response to increasing soil temperature in a manner similar to that observed by Kelly [9]. Both Karlsson and Nordell [3] and Weih and Karlsson [5] found an increase in N uptake and tissue concentration in mountain birch as soil temperature increased. In a study of oats, Nielsen *et al.* [34] found an increase in N uptake as soil temperature increased. Similarly, both Whitfield and Smika [35] and Gavito *et al.* [1] found an increase in N uptake in several wheat varieties as soil temperature increased. All of these responses are consistent with the findings of Adam *et al.* [8]. However, none of these studies, except for the work of Adam *et al.* [8], was conducted in a manner that allows the role of increased soil supply and increased root uptake to be assessed separately. Consequently, we assumed that I_{max} for modeled NH_4 would increase with temperature either at rates observed by Adam *et al.* [8] (Test I) or according to a Q_{10} relationship (Test II).

However, under conditions where N is not limiting growth, source-sink relationships could result in reduced NH_4 uptake capacity and lower I_{max} values than those used in our modeling effort. Studies have documented reductions in uptake capacity for NH_4 with increases in N availability for a variety of tree species, including two species closely related to red spruce—Norway spruce [36] and Engelmann spruce [28]. If these observations hold for red spruce under conditions of high N availability, the values for the increase in N uptake with increases in temperature would be lower than those predicted here. Possible secondary effects of a reduction in N uptake by red spruce include: 1) increases in the availability of NH_4 for other plant species, 2) increased production of NO_3,3) attendant elevation in cation concentrations in soil solution, and 4) leaching losses of cations.

In the case of P, we again assumed an increase in soil supply with increasing temperature based on the findings of Kelly [9]. This assumption is supported by the work of Sheppard and Rocz [11] who found that the availability of P increased as soil temperature increased from 10˚C to 25˚C. They attributed this increase to desorption of bound P. Studies of P uptake by oats [13,34] and wheat [35] found a general increase in P uptake with increases in soil temperature. Del Valle and Harmon [37] found a 300% increase in P uptake in the shoots and a 200% increase in the roots of turnip as soil temperature increased from 7˚C to 23˚C. Conversely, Nielsen and Cunningham [38] did not find an increase in P uptake by ryegrass in response to increased soil temperature while De Lucia *et al.* [39] found that foliar P in big bluestem increased but root P declined in response to soil temperature increase. Given that the P response is mixed we chose to use an increasing scenario given that in most forest soils supply of P is generally low and thus an increase in availability is most likely to lead to an increase in uptake.

4. Conclusions

Model predictions from the study indicate that even modest changes in soil temperature in response to global warming could lead to increased levels of N and P uptake in the near term. While the actual magnitude of the potential response is uncertain, if the underlying assumptions prove to be correct, there is reason to feel that trends depicted by the model are credible given that the NST 3.0 model is based on mechanistic principles and its outputs have proven reliable in a variety of situations [18,22].

Possibly the most useful outcome of this analysis is that model results point to a number of areas that deserve further exploration through experimentation. For example, the sensitivity analyses indicate that a better understanding of the impact of increasing temperature on plant nutrient uptake kinetics could be informative. This appears particularly true in the case of NH_4, since red spruce may respond differently to increases in soil supply if it is not N-limited. Similarly, changes in soil supply as reflected by changes in soil solution nutrient concentrations might be the most informative parameter and the least complicated to explore experimentally. As noted by Bassirirad [40], there is an urgent need to generate more data in this area and future studies of plant response to global warming should integrate measurements of soil nutrient supply and absorption into study plans.

Although it was not the intent of this study to explore the ecological or whole plant implications of the simulated changes, the potential ecological response to reduced P supply, in conjunction with an increase in P uptake, seems the most provocative. The potential impact of increased nitrogen availability on competition with other species for site dominance, possible changes in red spruce cold tolerance, and/or increases in nitrate production and nitrate leaching of cations also have important ecological implications and warrant further evaluation.

5. Acknowledgements

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