



## Temporal variation in nutrient uptake capacity by intact roots of mature loblolly pine

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### Abstract

Nutrient uptake is generally thought to exhibit a simple seasonal pattern, but few studies have measured temporal variation of nutrient uptake capacity in mature trees. We measured net uptake capacity of K,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , Mg and Ca across a range of solution concentrations by roots of mature loblolly pine at Calhoun Experimental Forest in October 2001, July 2001, and April 2002. Uptake capacity was generally lowest in July; rates in October were similar to those in April. Across a range of concentrations, antecedent nutrient solution concentrations affected the temporal patterns in uptake in July but not in October or April. In July, uptake of  $\text{NH}_4^+$ , Mg and Ca was positively correlated with concentration when roots were exposed to successively lower concentrations, but negatively correlated with concentration when exposed to successively higher concentrations. In contrast, uptake in October was constant across the range of concentrations, while uptake increased with concentration in April. As in studies of other species, we found greater uptake of  $\text{NH}_4^+$  than  $\text{NO}_3^-$ . Temporal patterns of uptake capacity are difficult to predict, and our results indicate that experimental conditions, such as experiment duration, antecedent root conditions and nutrient solution concentration, affect measured rates of nutrient uptake.

### Introduction

The seasonality of nutrient uptake by roots affects fertilizer use efficiency, soil solution concentrations, and stream export of nutrients. For example, the timing of fertilizer application to fast-growing trees, such as loblolly pine (*Pinus taeda* L.), is critical to maximize nutrient uptake and storage capacity (Johnson and Todd, 1988; Miller, 1981). Since some studies have shown that less than 15% of nitrogen fertilizer applied may be retained by trees (Heilman and Gessel, 1963; Van Miegroet et al., 1994), understanding

what controls the timing of uptake is important to minimize nutrient leaching into groundwater and streams and to maximize fertilizer use efficiency.

Plant growth and foliar nutrients vary during the growing season (Adams et al., 1987; Nelson et al., 1970; Valentine and Allen, 1990), but these patterns may not reflect seasonal patterns of nutrient uptake because a significant fraction of nutrients are remobilized from within the plant (Millard and Proe, 1992; Proe et al., 2000). Such remobilization enables plants to grow during periods of low nutrient availability and uptake (Millard, 1994).

Temporal patterns of ion uptake in trees have been measured primarily using seedlings, and

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simple seasonal trends have been observed. Nitrogen uptake of young *Pinus radiata* (D. Don) in the field was higher in spring and summer than autumn and winter (Smethurst and Nambiar, 1989). Phosphorus uptake of three-year-old *Picea sitchensis* (Bongard) Carrière grown in the greenhouse was similar in spring and late summer (Proe and Millard, 1995).

Mature trees may differ from seedlings in their temporal pattern of uptake, since plant age affects root anatomy (Eissenstat and Achor, 1999; Wells and Eissenstat, 2003), root respiration (Wells and Eissenstat, 2003), and nitrogen and phosphorus uptake capacity (Dong et al., 2001; Wells and Eissenstat, 2003). Only one study to date has examined temporal trends in uptake using intact roots of mature trees. Net ammonium uptake was highest in the summer in subalpine *Fagus sylvatica* L. (beech) and *Picea abies* (L.) Karst (spruce) (Gessler et al., 1998).

Temporal patterns in nutrient uptake through the year are driven by variations in soil nutrient availability and the plant's capacity to take up nutrients. These factors are not independent, since plants regulate uptake capacity based on nutrient supply (BassiriRad et al., 1993; Drew et al., 1984; Lee, 1982). Plants have high  $\text{NO}_3^-$  uptake rates following a period of deficiency (Lee and Rudge, 1986; Siddiqi et al., 1989), and exhibit low uptake after exposure to high  $\text{NO}_3^-$  concentrations, due to saturation of exchange sites at the root surface (Dean-Drummond, 1982; Siddiqi et al., 1990).

We examined nutrient uptake capacity in a commercially important conifer, loblolly pine, by exposing roots to known concentrations of nutrient solutions. Using this approach, changes in uptake capacity over time can be measured independent of variation in ambient soil solution concentrations and soil moisture conditions. The objective of our study was to quantify temporal variation in potassium, ammonium, nitrate, magnesium and calcium uptake capacity by measuring net uptake across a range of nutrient concentrations in July, October and April. We hypothesized that uptake capacity would decline between late summer and fall and then increase to a maximum in spring. We also examined how uptake differed with experimental conditions, such as nutrient solution concentration, experiment length and antecedent nutrient

solution concentration. We expected net nutrient uptake rates to increase with nutrient solution concentration and experiment duration. We also predicted that uptake capacity would be higher when plants were given low antecedent nutrient solution concentrations. Finally, we compared the time course of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake, predicting that uptake of  $\text{NH}_4^+$  would be more rapid than that of  $\text{NO}_3^-$ .

## Materials and methods

### Study area

This study was conducted in the Calhoun Experimental Forest of the Sumter National Forest in Union County, South Carolina (82°N, 34.5°W). Annual precipitation averages 1228 mm (1971–2000) and mean annual temperature is 15 °C (NOAA Administration, 2002). Soils are well-developed Ultisols of the series Appling and Cataula (clayey, mixed, thermic Typic Kanhapludults) (Overstreet and Bell, 1965). Soils are acidic with low exchangeable Ca and Mg, especially in the upper 15 cm (0.05  $\text{cmol}_c \text{ kg}^{-1}$  Ca and 0.02  $\text{cmol}_c \text{ kg}^{-1}$  Mg) (Markewitz et al., 1998). Average concentrations of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  were low in soil solutions collected from the forest floor (35  $\mu\text{mol}_c \text{ L}^{-1}$   $\text{NH}_4\text{-N}$  and 10  $\mu\text{mol}_c \text{ L}^{-1}$   $\text{NO}_3\text{-N}$ ) and from 15 cm (8  $\mu\text{mol}_c \text{ L}^{-1}$   $\text{NH}_4\text{-N}$  and 3  $\mu\text{mol}_c \text{ L}^{-1}$   $\text{NO}_3\text{-N}$ ). Virtually no nitrogen in either form was detected below 60 cm depth (Markewitz et al., 1998). Cumulative precipitation was 285, 350, and 463 mm for the 2 weeks preceding our measurements in July 2001, October 2001, and April 2002, respectively (NOAA Administration, 2002). Mean daily high (low) temperatures were 28 °C (19 °C) in July; 19 °C (7 °C) in October and 19 °C (5 °C) in April.

Cotton (*Gossypium hirsutum* L.), corn (*Zea mays* L.) and wheat (*Triticum aestivum* L.) were grown at the site for many decades prior to 1954 (Urrego, 1993). Loblolly pine seedlings were planted at Calhoun in 1956. The rate of biomass accumulation was highest from 1966 to 1976, and total biomass reached a peak of 211–247  $\text{Mg ha}^{-1}$  in 1984 (Markewitz et al., 1998). Total live biomass has recently declined, reaching 174  $\text{Mg ha}^{-1}$  in 2000 (D. Richter, pers. comm.) as a result of mortality from southern pine beetle

(*Dendroctonus frontalis*) attacks and wind damage from heavy storms.

### Overview of methods

Nutrient uptake capacity of loblolly pine roots was measured using the depletion technique (BassiriRad et al., 1999; Gessler et al., 1998; Rennenberg et al., 1996). We carefully excavated terminal fine root branches of loblolly pine near the soil surface. Fine root branches of loblolly pine were identified to species by tracing them to coarse roots, which differed in color and texture from roots of understory deciduous trees and shrubs. Root branches used in our experiments were composed of roots primarily less than 2 mm in diameter, which are considered most active in nutrient uptake. These excavated root branches contained mycorrhizal short roots, but most of the extramatrical hyphae were severed during the excavation and cleaning process.

During excavation, we washed roots with deionized water to remove soil particles and adhering organic matter. Each root was placed in a 50-mL tube containing 27 mL of nutrient solution. Nutrient solutions were prepared in the laboratory, using concentrations based on data from soil solution collected by low-tension lysimeters at 15 cm (Markewitz et al., 1998). Nutrient concentrations were intended to represent a range of values from one to ten times the average soil solution concentrations (1×, 3×, 5×, 7×, 10×). The actual concentrations differed somewhat from the predicted values. In our analyses, we used the actual concentrations to which the root branches were exposed (Table 1). Tubes containing nutrient solution but no roots were used as controls to determine the amount of evaporation and contamination that occurred during the experiments. Tubes with and without roots were covered with parafilm to reduce evaporation and were aerated with ambient air using a battery-powered pump system comprised of tubing linked to pipette tips inserted in the tubes. Nutrient solutions were collected after specified intervals, and the volume of solution was measured in order to correct for uptake or evaporation of water. Solutions were filtered on site using syringe filters with 0.4  $\mu\text{m}$  membrane filters. Samples were transported in coolers to the laboratory where they were frozen until analysis. After the uptake experiments were

Table 1. Average concentration (1× to 10×) to which the roots were exposed in July 2001, October 2001 and April 2002. Concentrations were based on soil solution data at a depth of 15 cm at Calhoun Experimental Forest, SC (Target 1×; Markewitz et al., 1998). Values are expressed as the average concentration ( $\mu\text{M}$ ) and standard error ( $n = 30$ , except for Target 1× where  $n = 8$ )

Average concentration ( $\pm$ SE)( $\mu\text{M}$ )				
Concentration	K	$\text{NH}_4^+$	Mg	Ca
1×	46 $\pm$ 2	10 $\pm$ 1	19 $\pm$ 5	28 $\pm$ 5
3×	133 $\pm$ 9	31 $\pm$ 6	60 $\pm$ 13	88 $\pm$ 30
5×	223 $\pm$ 16	40 $\pm$ 1	100 $\pm$ 19	185 $\pm$ 27
7×	350 $\pm$ 10	60 $\pm$ 6	156 $\pm$ 20	156 $\pm$ 45
10×	408 $\pm$ 24	78 $\pm$ 12	360 $\pm$ 32	360 $\pm$ 71
Target 1×	39 $\pm$ 4	8 $\pm$ 4	21 $\pm$ 2	33 $\pm$ 3

completed, the portion of the root immersed in the solution was severed from the tree, weighed, and stored in 50% ethanol. Roots were weighed after oven-drying at 70 °C.

Nitrate and  $\text{NH}_4^+$  concentrations were determined by continuous flow analyzer and autoanalyzer (model AA3; Bran and Luebbe, Norderstedt, Germany). Cation ( $\text{Ca}^{+2}$ ,  $\text{Mg}^{+2}$ , and  $\text{K}^+$ ) concentrations were determined using inductively coupled plasma emission spectroscopy (model FMA-03, Spectro Analytical Instruments, Kleve, Germany). Net nutrient uptake rates were calculated from the change in nutrient content of the solution (concentration times volume) over the time period. Rates were expressed as a function of dry weight for each root. Since we did not measure influx and efflux independently, our rates are expressed as net uptake rates with positive values indicating net uptake of nutrients and negative values indicating net efflux of nutrients. These rates include any change in nutrient storage by microbes on the roots, which we could not control, but was probably small. Contamination and evaporation were also generally small; the K,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , Mg and Ca concentrations of controls were not significantly different from the initial concentration in 72% of the cases.

### Temporal trends in uptake

In July 2001, October 2001 and April 2002, 10 loblolly pine root branches were excavated, washed with deionized water and placed in a 50-mL tube with 27 mL of nutrient solution. A 15-mL tube was inserted into the 50-mL tube to displace

solution and increase the ratio of root surface area to solution volume.

To determine if uptake capacity was affected by antecedent nutrient solution concentration, we initially exposed half of the roots to average soil solution concentrations (1×) and the remaining roots to 10× solutions (Table 1). Following the initial 2-h period, each root branch was removed and placed in a new tube containing a new solution. Roots exposed to 1× were subjected over successive 2-h intervals to increasing concentrations of solutions (approximately 3×, 5×, 7× and 10×; Table 1). The remaining roots were exposed to concentrations of solution decreasing from 10× to 1×. Since 2 days were needed to excavate the roots and implement the treatments, we exposed all roots to the same nutrient solution concentration (5×) overnight for 15–19 h.

#### *Comparison of $\text{NH}_4^+$ and $\text{NO}_3^-$ uptake in spring*

In March 2001, we excavated 12 terminal fine root branches of loblolly pine. Roots were washed with deionized water and placed in a 50-mL tube with 30 mL of nutrient solution. Four roots were randomly allocated to each nutrient solution concentration: 1×, 5× and 20×. Five millilitre aliquots of solution were removed from the nutrient solution after 14, 29 and 100 h. Following each aliquot removal, 5 mL of deionized water was added to the tubes to keep volume constant and provide a descending sequence of concentrations. The nutrient solutions were filtered and frozen until analysis. Since the roots from this experiment were accidentally discarded before analysis, we present changes in nutrient concentration over time but not uptake per unit root.

#### *Statistical analysis*

To determine how sampling date (July, October or April) and prior treatment (increasing or decreasing sequence of concentration treatments) affected uptake capacity, data were analyzed using generalized linear models (SAS Institute, 1985) with nutrient solution concentration treatment (1×, 3×, 5×, 7×, 10×) as a repeated measure. Since the 3-way interaction of sampling date, prior treatment and concentration was

significant for most solutes at  $\alpha = 0.05$ , we compared temporal trends at our mid-range concentration (5×) at both 2-h and overnight time intervals. We also compared the slopes of the regression lines of uptake with concentration between sampling dates and between prior treatments.

To determine how concentration changed with time in our March 2001 comparison of  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , we used time as a class variable in our model. Since each root was only given one concentration in our preliminary experiment, data for each concentration (1×, 5× and 20×) were analyzed separately.

## **Results**

The analysis of our measurements of K,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , Mg and Ca uptake at five different nutrient concentrations (1×, 3×, 5×, 7×, 10×) and two different antecedent condition in 3 months of the growing season resulted in a three-way interaction of concentration, antecedent condition and time of year for most nutrients. We first present temporal variation in net uptake capacity at our mid-range concentration (5×) to show how uptake varied with experiment duration and sampling date. Next, we discuss the effects of antecedent conditions and nutrient solution concentration on temporal trends of uptake capacity. Finally, we compare the rates of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake.

#### *Temporal trends of net uptake at 5× in 2-h experiments*

We predicted that net uptake capacity of all nutrients would be highest in April, when plants at this location are most physiologically active, and lowest in October. Surprisingly, net uptake of K and  $\text{NH}_4^+$  at the 5× concentration was similar in April and October (Figure 1). In July, efflux of K and  $\text{NH}_4^+$  exceeded uptake. Net uptake of Mg and Ca was positive at all sampling dates, and the rates were statistically indistinguishable across dates. High variation among roots precluded detection of differences smaller than  $4 \mu\text{mol gdw}^{-1} \text{h}^{-1}$  for Mg and  $7 \mu\text{mol gdw}^{-1} \text{h}^{-1}$  for Ca.

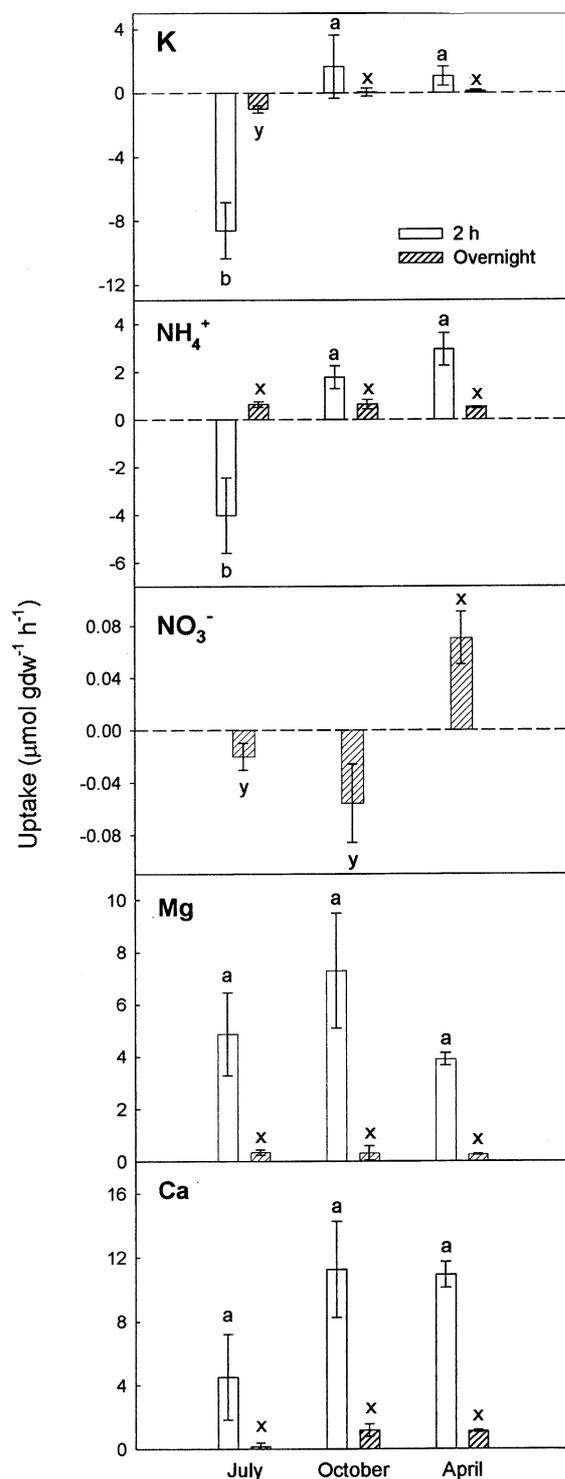


Figure 1. Uptake of K,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , Mg, and Ca by intact roots of mature loblolly trees, expressed on a per dry-weight of root per hour basis, in July 2001, October 2001 and April 2002 at concentrations five times higher than lysimeter soil solution concentrations ( $5\times$ ). Roots were left in solution for a 2-h interval and overnight (15–19 h). In the case of  $\text{NO}_3^-$ , only overnight data is presented. Error bars show standard errors of the mean ( $n = 10$ ). Means with different letters differ significantly at  $\alpha \leq 0.05$ .

#### Temporal trends of net uptake capacity at $5\times$ in overnight experiments

We also examined how net uptake of K,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , Mg and Ca differed in July, October and April when roots were left in solution for 15–19 h. The comparisons of uptake across the three seasonal times were similar between 2 h and overnight experiments, except for  $\text{NH}_4^+$  (Figure 1). Ammonium uptake did not vary by sampling date in the overnight experiments, because nearly all of the  $\text{NH}_4^+$  (92%) was taken up in the first two hours.

Nitrate was measured only in the overnight experiments since uptake rates were too low to be detectable in 2 h. As expected, net nitrate uptake was highest in April (Figure 1). In July and October, efflux of  $\text{NO}_3^-$  exceeded uptake.

Uptake of Mg and Ca was higher in the 2 h than overnight experiments, but not because there was not enough solute remaining in the tubes to sustain uptake at the 2-h rate as observed with  $\text{NH}_4^+$ . In fact, the final concentration of K, Mg, Ca in the tubes was similar in the overnight (averaging  $241 \mu\text{M}$  K,  $82 \mu\text{M}$  Mg and  $85 \mu\text{M}$  Ca) and the 2 h experiments ( $233 \mu\text{M}$  K,  $75 \mu\text{M}$  Mg and  $70 \mu\text{M}$  Ca). The average rate of net uptake ( $\mu\text{mol gdw}^{-1} \text{h}^{-1}$ ) is thus much lower for the overnight experiments although the net amount of uptake ( $\mu\text{mol gdw}^{-1}$ ) was similar. This suggests that net uptake was positive for no more than 2 h, after which efflux equaled influx.

#### Effects of antecedent conditions on temporal trends of net uptake capacity

To examine how antecedent conditions affect net uptake, we exposed our roots to either increasing ( $1\times$ – $10\times$ ) or decreasing ( $10\times$ – $1\times$ ) nutrient solution concentrations. We found that the sequence of treatments affected uptake rates of  $\text{NH}_4^+$ , Mg and Ca in July but not in October or April. In

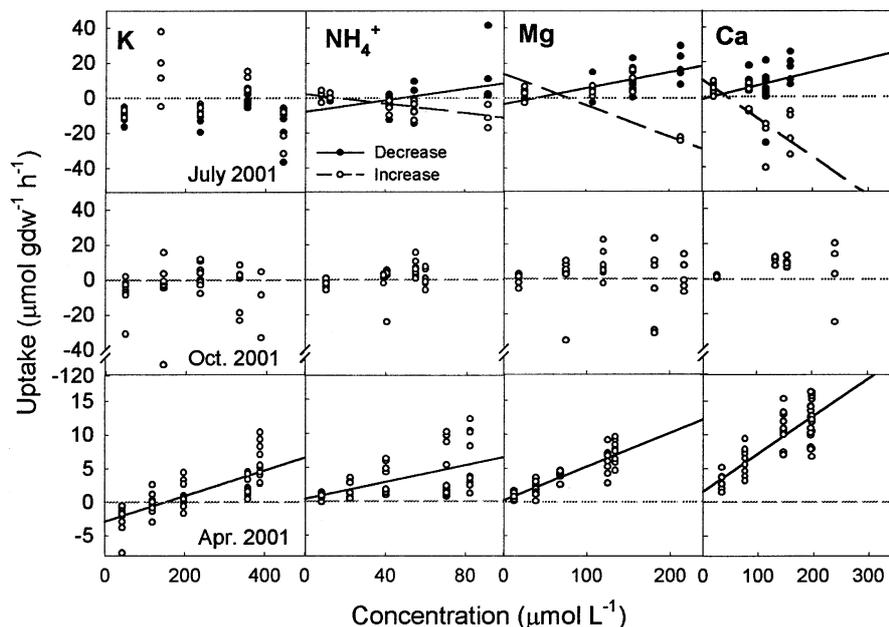


Figure 2. Uptake of K,  $\text{NH}_4^+$ , Mg and Ca on a dry-weight basis by intact roots of mature loblolly trees as a function of nutrient solution concentration in July 2001, October 2001 and April 2002. Measurements were conducted over 2-h intervals. In July, uptake was significantly different when roots were exposed to successively higher concentrations (increasing, - - - -) than successively lower (decreasing, —) concentrations. In October and April, there was no difference in uptake based on antecedent concentrations and therefore only lines for regressions that are significantly different from zero ( $P \leq 0.05$ ) are shown through all the data ( $n = 10$ ). None of the regressions for October were statistically significant.

July, antecedent conditions affected the relationship between uptake and concentration for  $\text{NH}_4^+$  ( $P = 0.03$ ), Mg ( $P < 0.0001$ ) and Ca ( $P = 0.01$ ). In contrast to our prediction, roots exposed to initially high concentrations ('decreasing') had higher uptake of  $\text{NH}_4^+$ , Mg and Ca than roots exposed to lower concentrations first ('increasing', Figure 2). In July, K uptake was relatively constant across concentration and was unaffected by antecedent nutrient concentrations.

In October and April, net uptake was not affected by antecedent root conditions, but the pattern of uptake with concentration differed between these two sampling times. Although we predicted that uptake would increase with concentration, uptake of Ca, Mg, K and  $\text{NH}_4^+$  was relatively constant across concentration in October (Figure 2). In April, when plant roots may be more physiologically active, Ca, Mg, K and  $\text{NH}_4^+$  uptake significantly increased with nutrient solution concentration ( $R^2 = 0.56, 0.75, 0.36,$  and  $0.38$ , respectively).

#### Timing of net $\text{NO}_3^-$ and $\text{NH}_4^+$ uptake

We predicted that net  $\text{NH}_4^+$  uptake of loblolly pine roots would exceed net  $\text{NO}_3^-$  uptake in our March 2001 experiment. During the first 14 h,  $\text{NH}_4^+$  was rapidly depleted at all three initial concentrations ( $P \leq 0.0001$  at  $1\times$ ,  $P \leq 0.0001$  at  $5\times$ ,  $P = 0.03$  at  $20\times$ ; Figure 3). At  $5\times$  and  $1\times$ ,  $\text{NH}_4^+$  concentrations dropped by 98 and 96% after only 14 h. Even at the highest concentration ( $20\times$ ), average  $\text{NH}_4^+$  concentration dropped by 60% after 14 h, and solutions were 97% depleted at 100 h.

In contrast, net  $\text{NO}_3^-$  uptake was delayed. In the first 14 h, there was no significant net uptake, and nitrate efflux exceeded nitrate uptake at all concentrations (Figure 3). Between 14 and 100 h, depletion of at least 89% occurred at all three concentrations ( $P = 0.02$  at  $1\times$ ,  $P = 0.04$  at  $5\times$ ,  $P = 0.004$  at  $20\times$ ), indicating that net nitrate uptake capacity was induced after an initial lag period.

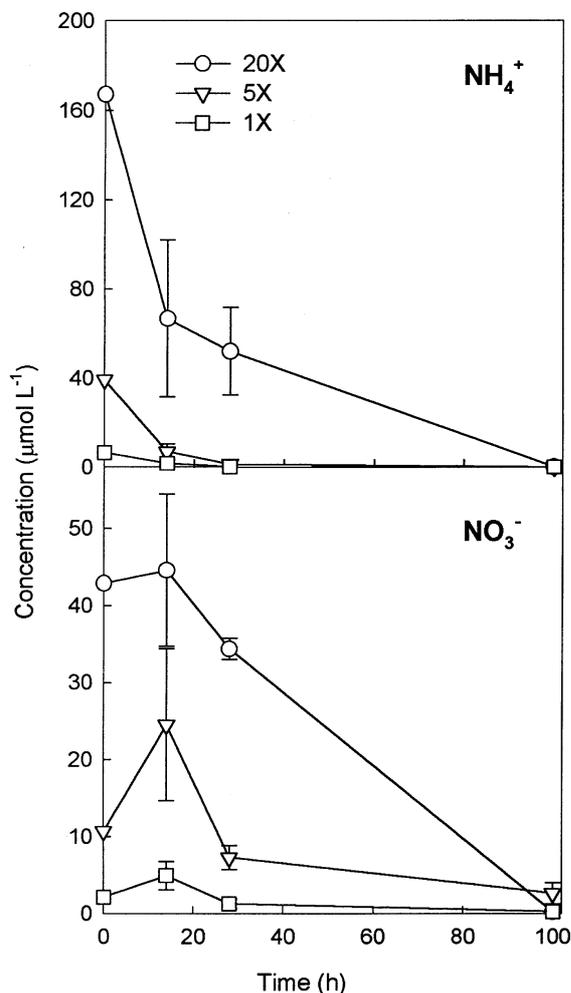


Figure 3. Time course of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentration over a 100-h period using intact roots of mature loblolly pine trees in March 2001 exposed to three initial concentrations (1X, 5X, 20X). Error bars show standard errors of the mean ( $n = 10$ ). Concentrations were diluted by additions of distilled water at each sampling time.

## Discussion

Nutrient accumulation in trees is generally thought to vary seasonally, with maximum uptake of nitrogen in summer (Gessler et al., 1998; Millard, 1994; Millard and Proe, 1992) and of cations (K, Mg and Ca) in spring (Stassen and Stadler, 1988). We measured uptake capacity, rather than uptake at ambient conditions, in our study with loblolly pine at Calhoun Experimental Forest to determine whether changes in uptake capacity might contribute to changes in nutrient accumulation over time. We found that uptake

capacity did not follow the seasonal pattern expected of plant nutrient accumulation.

In general,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake capacity in mature loblolly at Calhoun was lower in July than April. In contrast, N accumulation was lower in spring than summer in sand-grown *Picea sitchensis* (Millard and Proe, 1992) and field-grown *P. sitchensis* and *Acer pseudoplatanus* (Millard, 1994). In those studies, remobilized N apparently satisfied plant demand for N in spring, while uptake supplied N in summer. Although different species were used, these studies demonstrate that seasonal patterns of nutrient uptake capacity may differ from those of nutrient accumulation.

Temporal patterns in uptake have sometimes been attributed to variation in soil temperature. Intact roots of subalpine beech and spruce had their highest  $\text{NH}_4^+$  uptake in July and uptake was significantly correlated with soil temperature (Gessler et al., 1998). In contrast, we observed low uptake capacity in July when air temperature was highest. Uptake capacity may have been limited by soil water availability in July, though the roots were in nutrient solutions when we measured uptake. Since we measured uptake at ambient temperatures, we cannot address how temperature affects uptake capacity independent of other seasonally varying environmental factors.

Nitrate uptake of mature loblolly pine was negligible in the 2-h experiments and extremely low in the overnight experiments, indicating that short-term measurements of  $\text{NO}_3^-$  uptake may not be providing reliable estimates of uptake capacity in mature trees. In a previous study, nitrate uptake by subalpine spruce and beech was generally not detectable if measured over a 4-h time interval (Gessler et al., 1998). Since  $\text{NO}_3^-$  concentrations in soil solution ranged from only 3 to  $10.1 \mu\text{mol}_c \text{L}^{-1} \text{NO}_3\text{-N}$  in the top 15 cm at Calhoun (Markewitz et al., 1998), nitrate reductase activity may have been low in the loblolly pine roots (Li and Gresshoff, 1990). The nitrate present in the nutrient solution should increase nitrogen reductase activity, but induction and transport to the roots may take several hours. In our longest experiment, we induced  $\text{NO}_3^-$  uptake sometime between 14 and 100 h (Figure 3).

Since  $\text{NH}_4^+$  can inhibit  $\text{NO}_3^-$  influx (Lee and Drew, 1989) and induce  $\text{NO}_3^-$  efflux

(Dean-Drummond and Glass, 1983), the low rates of net  $\text{NO}_3^-$  uptake we observed may have been affected by  $\text{NH}_4^+$  in the nutrient solution. Ammonium uptake occurred at a much faster rate than  $\text{NO}_3^-$ , a result that agrees with previous studies showing a preference for  $\text{NH}_4^+$  by conifers (BassiriRad et al., 1997; Cole, 1981; Gessler et al., 1998; Gijsman, 1990; Marschner et al., 1991; Rygiewicz and Bledsoe, 1986). The higher capacity for uptake of  $\text{NH}_4^+$  than  $\text{NO}_3^-$  may be an adaptation to the greater availability of  $\text{NH}_4^+$  in the forest floor at Calhoun (Markewitz et al., 1998) or it may reflect the lower energetic costs of uptake and assimilation of  $\text{NH}_4^+$  relative to  $\text{NO}_3^-$  (Bloom et al., 1992).

Potassium uptake capacity was highest in the spring, consistent with observations of K accumulation in peach trees (Stassen and Stadler, 1988). Seasonal changes in K uptake have been studied primarily using young fruit trees (Gries et al., 1993; Picchioni et al., 1997) and agricultural crops (Clark and Smith, 1992; Hocking, 1994); more studies are needed to assess seasonal changes in uptake by mature forest trees.

Although K efflux of roots may indicate hypoxic conditions (Escamilla and Comerford, 1998), all roots were aerated in our study. We observed net K efflux by loblolly pine in July but not October or April. In a previous study, however, intact slash pine roots took up K in July (Escamilla and Comerford, 1998). Differences in starting concentrations do not explain the differences in uptake. We observed net K efflux by loblolly pine at concentrations of  $48 \mu\text{M}$  while slash pine roots took up K at  $25.6 \mu\text{M}$  (Escamilla and Comerford, 1998).

Root disturbance may be partly responsible for the K efflux in our study. Slash pine roots were excavated six months prior to measurement by Escamilla and Comerford (1998), while the plant roots in our study were excavated just prior to analysis. In previous studies, root disturbance stimulated  $\text{NO}_3^-$  efflux (Aslam et al., 1996) and decreased uptake of K,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  (Bloom and Caldwell, 1988). Exposing roots to different pretreatments designed to minimize disturbance, however, did not decrease cation efflux by mature sugar maple, red pine and Norway spruce (McFarlane and Yanai, unpublished data).

There were no statistically significant temporal variations in the capacity for uptake of Ca and

Mg by mature loblolly pine at Calhoun. No studies to date have examined seasonal trends in Ca and Mg uptake by roots, although studies of seasonal changes in foliar concentrations indicate that plant demand is higher in spring and summer than in fall (Gries et al., 1993).

Nutrient uptake capacity is sometimes observed to follow saturation kinetics (Epstein, 1976). We found that the relationship between uptake and concentration, when there was one, was generally linear, such that uptake would be best described with a slope and intercept. Our most important finding, however, was that uptake kinetics were not constant over time, such that using a relationship measured at one point in time could fail to predict rates at another point in time.

Experimental conditions, such as nutrient solution concentration and experiment length, may affect uptake rates observed in the field. In our study,  $\text{NH}_4^+$  uptake ( $-3.6 \mu\text{mol gdw}^{-1} \text{h}^{-1}$ ) was much lower than previously reported for intact roots of loblolly pine in August ( $18.8 \mu\text{mol gdw}^{-1} \text{h}^{-1}$ ) (BassiriRad et al., 1997). That study used higher concentrations ( $1700 \mu\text{mol L}^{-1}$ ) than ours ( $5\text{--}92 \mu\text{mol L}^{-1}$ ) and a longer exposure time (24 h, compared to our 2 h).

In our study, net uptake rates of  $\text{NH}_4^+$ , Mg and Ca declined with exposure times. Declining  $\text{NH}_4^+$  uptake rates over time were associated with depletion of  $\text{NH}_4^+$  in the applied solution. In contrast, Mg and Ca concentrations were similar at the end of the 2 h as compared to the overnight experiments, suggesting that net uptake was negligible after the first 2 h. Declining uptake rates of Mg and Ca could be associated with the duration of the experiments or with attaining a concentration below which net uptake was not possible. In any case, it can be misleading to report uptake rates as instantaneous rates, when the duration of experiments has such significant effects on uptake.

Species may differ in their uptake rates, even when experimental conditions are similar. In July, spruce and beech roots had higher average  $\text{NH}_4^+$  uptake rates ( $1.4, 0.9 \mu\text{mol gfw}^{-1} \text{h}^{-1}$ ) (Gessler et al., 1998) than loblolly pine in our study ( $-4.0 \mu\text{mol gfw}^{-1} \text{h}^{-1}$ ) when trees were exposed to similar  $\text{NH}_4^+$  concentrations (approximately  $55 \mu\text{M}$ ). In April, however, our loblolly pine had higher uptake rates ( $2.9 \mu\text{mol gfw}^{-1} \text{h}^{-1}$ ) than

spruce ( $0.02 \mu\text{mol gfw}^{-1} \text{h}^{-1}$ ), and beech ( $0.3 \mu\text{mol gfw}^{-1} \text{h}^{-1}$ ) Gessler et al. (1998).

This is the first study to show that the effects of antecedent conditions on uptake capacity vary temporally. Antecedent nutrient conditions influenced root uptake in July but not in October or April. In July, loblolly pine roots exposed to high initial concentrations had high  $\text{NH}_4^+$ , Mg and Ca uptake rates, indicating that the roots may have been exposed to low levels of these elements in the soil (Lee, 1993). Roots exposed to successively higher concentrations had lower uptake at high concentrations, due perhaps to saturation of exchange sites at the root surface (Dean-Drummond, 1982; Siddiqi et al., 1990).

The technique used in this study to obtain intact roots required removal of the roots from the surrounding soil, which disrupts the extramatrical hyphae of mycorrhizae. Since ectomycorrhizae play an important role in nutrient uptake of loblolly pine seedlings (Smith and Read, 1997), additional studies are needed to assess the importance of mycorrhizae on the temporal pattern of nutrient uptake capacity of mature trees.

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