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Measuring nitrogen and phosphorus uptake by intact roots of mature *Acer saccharum* Marsh., *Pinus resinosa* Ait., and *Picea abies* (L.) Karst

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Abstract

A common method for measuring uptake by intact roots *in situ* is the depletion method, wherein intact fine roots are separated from soil and placed in nutrient solution. The difference between initial and final amounts of nutrient in solution is attributed to root uptake. Variations on this method include applying pretreatment solutions, training roots to grow into bags or trays, and varying concentrations of nutrient solution. We tested whether variations in methods affected measured net uptake rates of NH_4^+, NO_3^-, and PO_4^{3-}. Intact roots of 60 year-old sugar maple (*Acer saccharum* Marsh.), red pine (*Pinus resinosa* Ait.), and Norway spruce (*Picea abies* (L.) Karst.) were given one of four treatments prior to measuring net uptake. ''Trained'' roots were grown in a sand-soil mixture. ''Recovered'' roots were excavated and allowed to recover in nutrient solution for two or four days (''two-day recovery'' and ''four-day recovery'', respectively). ''No recovery'' roots were excavated and used immediately in experiments. We exposed roots to three concentrations of nutrient solutions to observe the effects of initial nutrient solution concentration. Initial nutrient solution concentration was an important source of variation in measured uptake rates, and N uptake was stimulated by low antecedent concentrations. We found no significant differences in net uptake rates between pretreatments for any of the species studied, indicating that our pretreatments were not effective in improving measurement of uptake. Such pretreatments may not be necessary for measuring net uptake and may not hinder the comparison of rates measured using variations of the depletion method.

Introduction

Measuring nutrient uptake by roots of mature trees in the field is very difficult, so our current understanding of nutrient uptake is based primarily on annual plants. Tree species have been studied as seedlings grown in the greenhouse, where root systems may be studied more easily and researchers can control growing conditions and nutrient supplies (Kelly and Barber, 1991; Kronzucker et al., 1997; Topa and Sisak, 1997). However, results from seedling studies should be applied with caution to mature trees, because nutrient demand and uptake capacity may change as trees mature (Gessler et al., 1998; Greenham, 1979).

The technique of using excised roots to study nutrient uptake was developed for agronomic species and has been adapted for use with tree roots that have been excavated (Comas et al., 2002; Lajtha, 1994) or collected in root cores (Pennell et al., 1990). Removing the roots from the plant eliminates complications associated with shoot–root interactions but may alter nutrient fluxes (Hoagland and Broyer, 1936).

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The few studies measuring uptake by intact roots of mature trees have used the depletion method. Intact root branches are excavated but left attached to the tree, washed, and placed in an artificial soil solution based on the soil solution chemistry of the site where the study is conducted. Solutions are sampled after exposure to the roots for a specified time. The change from initial nutrient content is determined and is attributed to fluxes into or out of the root (Claassen and Barber, 1974).

The depletion method has been used in studies measuring uptake of N by Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.) (Gessler et al., 1998, 2002; Marschner et al., 1991), N by red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marsh.) (BassiriRad et al., 1999), P and K by slash pine (*Pinus elliottii* Engelm var. *elliottii*) (Escamilla and Comerford, 1998a, b; 2000), and N, K, and Ca by loblolly pine (*Pinus taeda* L.) (Lucash et al., 2005). These studies have used the depletion method to study the influence of numerous factors on uptake including: temporal variation (Gessler et al., 1998, 2002; Lucash et al., 2005), N availability (Gessler et al., 1998), and oxygen availability (Escamilla and Comerford, 1998b).

Researchers have used variations of the depletion method based on individual study objectives and concerns about various aspects of the method. Prior to measuring uptake, roots must be isolated from the soil in which they grow. This generally involves gently excavating and washing roots (BassiriRad et al., 1999; Gessler et al., 1998, 2002; Rennenberg et al., 1996). The excavation processes is of particular concern as roots are highly sensitive to disturbance (Aslam et al., 1996; Bloom and Sukrapanna, 1990; Rincon and Hanson, 1986) and excavation visibly disturbs roots and severs mycorrhizal hyphae, likely altering uptake rates.

To minimize the disturbance caused during excavation, some researchers have trained roots to grow in a more controlled medium (Escamilla and Comerford, 1998a). Roots are excavated, left attached to the tree, and pruned. Roots are then placed in a bag or tray with sieved soil or a soil–sand mixture and buried. After the roots have grown for several months, they are re-excavated, washed gently, and used for experiments.

Roots may be given an experimental pretreatment solution prior to uptake measurements. For example, excavated roots may be placed in solution similar to the experimental solution to allow them to recover from physical manipulation and to adjust to the liquid medium (Marschner et al., 1991). Uptake of NO_3^- by roots that have not been previously exposed to NO_3^- may require exposure to the ion for a period of several hours to several days for full induction of NO_3^- uptake capacity (Kronzucker et al., 1995).

Alternatively, pretreatment solution that lacks nutrients of interest may be used to "starve" roots (Escamilla and Comerford 1998a, b, 2000). Starving roots of a nutrient results in higher net uptake and influx rates when the root is then exposed to the previously deficient nutrient (Hoagland and Broyer, 1936; Lee 1982). Starving roots is justified when researchers are interested in the maximum possible rate of uptake; uptake rates may be repressed when the plant is not experiencing a shortage of the nutrient (Lee 1993).

Generally, nutrient solutions used for uptake experiments are simulated soil solutions, with ion ratios based on ambient soil solution chemistry (Rennenberg et al., 1996). In contrast, solutions may contain only ions of interest (BassiriRad et al., 1999). This minimizes ion interactions, but results from these studies may not be illustrative of uptake under natural conditions where roots are simultaneously exposed to multiple ions. To ensure detectable uptake occurs, researchers have used more concentrated solutions than the ambient soil solution or have used varying time intervals from as short as 5 min (White et al., 1992) to over 100 h (Marschner et al., 1991).

In this study, we tested the effects of variations in the depletion method on net uptake of NH_4^+, NO_3^-, and PO_4^{3-} by intact roots of 60 year-old sugar maple, red pine (*Pinus resinosa* Ait.), and Norway spruce. We trained roots of each species to grow into bags, applied a pretreatment recovery solution to roots for either two or four days, or excavated roots and used them immediately for uptake experiments. We also exposed roots in all treatments to three different nutrient solutions, all with ion ratios representative of the ambient soil solution. Our objective was to test whether variations in the method affected measured rates of nutrient uptake.

Materials and methods

Site description

Uptake experiments were conducted at Turkey Hill Plantation in Dryden, New York (42°27 0 N, 76°25 0 W, elevation 427 m). The plantation consists of 0.4 ha plots that were planted in a single species or mixture of species between 1939 and 1941 (Pallant and Riha, 1990). Sugar maple, red pine, and Norway spruce in monospecific plots were chosen for uptake experiments. Use of single-species plots ensured that excavated roots were of a known species.

Training pretreatment

We installed root bags at Turkey Hill during the summer and fall of 2001. Intact coarse roots approximately 0.5 cm in diameter were excavated for training from trees of ten species: black cherry (*Prunus serotina* Ehrh.), Norway spruce, red pine, sugar maple, tulip poplar (*Liriodendron tulipifera*), white pine (*Pinus strobes* L.), red oak (*Quercus rubra*), black locust (*Robinia pseudoacacia* L.), and American beech (*Fagus grandifolia*). Excavated coarse roots were pruned and placed in 20 cm × 14 cm bags constructed of landscaping cloth. The bags were filled with a 50–50 mixture of soil and sand, stapled closed, and buried. The soil–sand mixture contained soil that was removed during root excavation, hand-picked clean of rocks and coarse organic matter, and mixed with quartz sand.

Sugar maple, red pine, and Norway spruce were chosen for this study because they showed sufficient fine root growth in at least 7 of 13 installed bags by May 2002. Black cherry also showed excellent growth, but these roots were used in preliminary studies and those results are not reported here. The morphology of the roots that were trained into the sandy medium was distinct from those we excavated immediately before the experiments. They tended to have more extension growth and fewer of the finest roots.

Recovery pretreatment

Four days prior to uptake experiments, ten "four-day recovery" intact root branches were carefully excavated and washed with distilled water to remove soil particles. Roots were placed in tubes with 27 mL of simulated soil solution (described below). We selected the simulated soil solution as a recovery medium because it best approximated ambient nutrient conditions. Solutions were aerated to prevent hypoxia using a fishing bait bubbler. Tubes were covered with Parafilm and covered by opaque plastic tarps. Two days later, the process was repeated for ten "two-day recovery" roots. At the same time, the first set of roots was given fresh solution.

Nutrient solutions

Target concentrations for the simulated soil solution (Table 1) were determined using a saturated paste slurry (Bickelhaupt et al., 1983) of bulked

Table 1. Target simulated soil solution concentrations for this study and other studies using the depletion method (μM)

Ion	Target solution	Escamilla and Comerford, (1998a, b)	Gessler et al. (1998) (spruce)	Gessler et al. (1998) (beech)	Marschner et al., 1991
NH_4^+	122	90	53	56	100
NO_3^-	17	20	618	311	1000
PO_4^{3-}	8	6	5	3	50
Ca^{2+}	42	65	95	120	500
Mg^{2+}	20	10	68	55	150
K^+	32	26	77	71	600
Na^+	37	n/a	43	19	n/a
Al^{3+}	7	n/a	128	38	n/a
pH	5	5	4	5	4

Some solutions for other studies also included micronutrients (not listed). Actual nutrient solution concentrations of NH_4, NO_3, and PO_4 for this study are shown in Figure 1.

soil samples collected in May 2002 from the research site. Nutrient solutions contained all nutrients shown in Table 1 and had an approximate pH of 5. To study the effect of solution concentration on uptake rates, nutrient solutions of 5 times (concentrated) and 10 times (highly concentrated) the simulated soil solution concentrations were also used in experiments. Solutions were made the day before the experiment and were refrigerated overnight. Each nutrient solution was sampled at the beginning of the experiment. These samples provided our "initial" values for nutrient concentration and content. Actual concentrations of NH_4^+, NO_3^-, and PO_4^{3-} in nutrient solutions for uptake experiments are shown in Figure 1.

Uptake experiments

Uptake experiments for sugar maple, red pine, and Norway spruce were conducted on June 13, June 26, and July 18, 2002, respectively. Weather conditions during experiments are shown in Table 2. On the day of each experiment, an additional set of ten "zero recovery" roots was excavated and trained roots were removed from their bags. Ten trained Norway spruce roots were used, but only seven trained roots were available for sugar maple and red pine. Trained and zero recovery roots were washed with distilled water to remove soil and sand particles and used immediately in experiments. Each root branch was placed in a plastic tube with 27 mL of fresh nutrient solution, aerated, and covered with Parafilm to minimize evaporation and contamination. Each of six tubes with no roots was also filled with 27 mL of solution, aerated, and covered. These tubes served as controls. All roots and controls were exposed for two hours to each of three concentrations of nutrient solution (1, 5, and 10 times the simulated soil solution concentration).

The purpose of using multiple solution concentrations was to study the effects of nutrient solution concentration on the uptake capacity of the roots. Using each root for multiple nutrient concentrations allows us to reduce the variation in uptake associated with variation among roots. However, this design introduces the risk that the timing of the measurement or the order of the solution treatments could affect the results. Therefore, half of the roots of each pretreatment and half of the controls were given the nutrient solutions in increasing concentration (1, then 5, then 10 times the simulated soil solution concentration) and half in decreasing concentration (10, then 5, then 1 times the simulated soil solution concentration). Splitting the roots into ascending and descending concentrations (a crossover design) allowed us to distinguish whether uptake was changing over the course of the experiment and whether the preceding treatment had an effect on uptake. At the end of each interval, roots were carefully lifted out of the experimental solution and placed in new solution.

Final solution volume was recorded to correct nutrient content calculations for evaporation or water uptake. After experiments were completed, the portion of the root exposed to solution was removed from the larger root system and fresh weight determined. Mean wet weight ($\pm$ standard error) was 1.4 g $\pm$ 0.2 for sugar maple roots, 2.4 g $\pm$ 0.3 for red pine roots, and 1.4 g $\pm$ 0.1 for Norway spruce roots.

Sample analysis

All solution samples were filtered immediately after collection using 0.4 μm polycarbonate filters, kept on ice in the field, and frozen until analysis. Samples were analyzed for NH_4^+ with a continuous flow autoanalyzer (Bran and Luebbe AA3) and for NO_3^- and PO_4^{3-} by ion chromatography (Dionix DX-500). Calcium, magnesium, potassium, and sodium were analyzed by ICP spectroscopy (Perkin Elmer OPTIMA 3300DV ICP-OES). Net uptake of Mg^{2+} and Na^+ was not significantly different from zero and net uptake of Ca^{2+} and K^+ was uniformly negative; these results are presented elsewhere (Lucash et al., in preparation).

Data analysis

Statistical analysis was conducted using the GLM procedure in SAS (SAS Institute, Inc. Cary, NC 27513). Statistical tests were conducted separately by species because experiments for each species occurred on different dates. The nutrient solution treatment is reported using the concentrations applied to the roots. These concentrations changed over the course of the

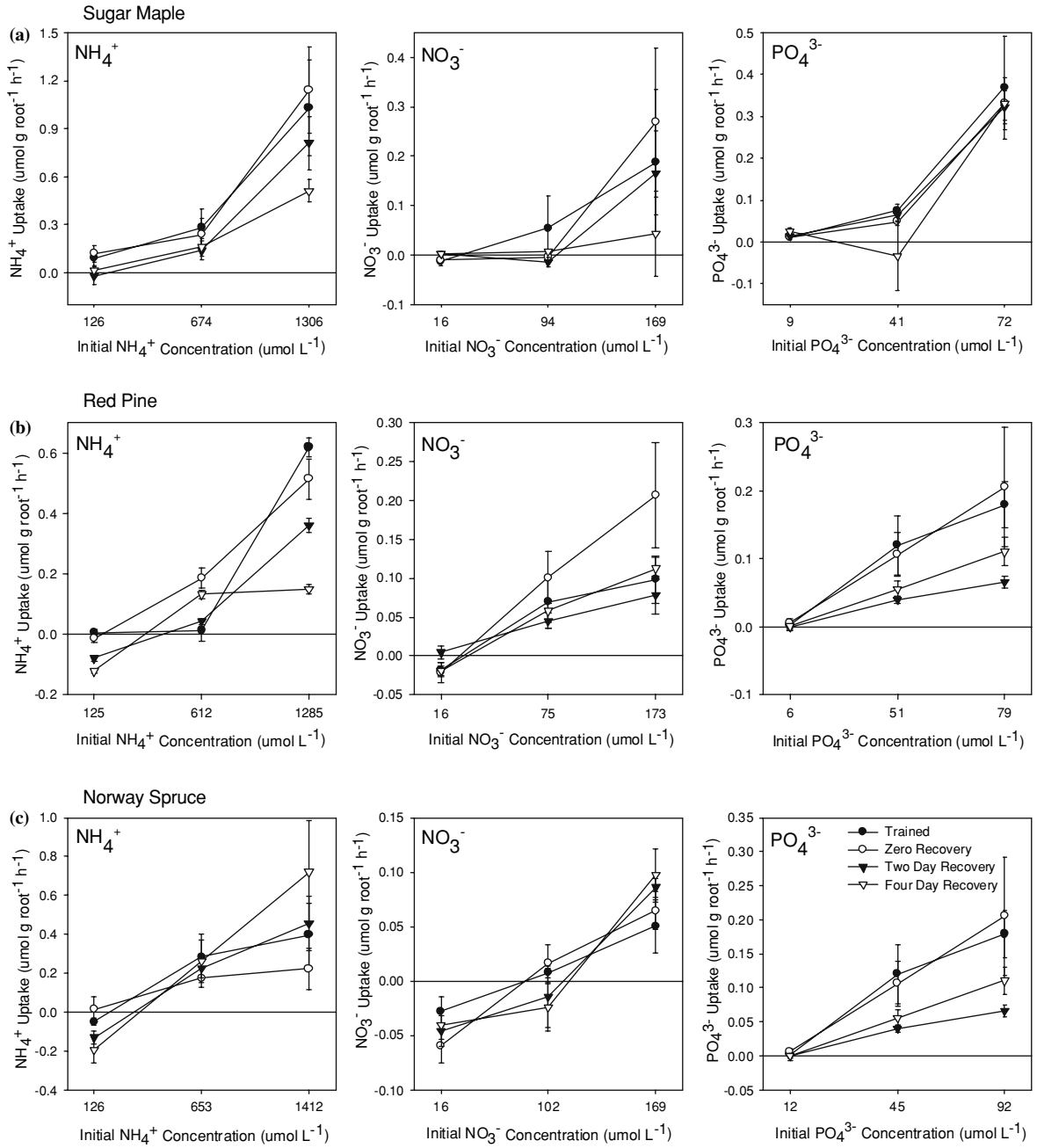

Figure 1. Mean uptake rates by pretreatment of NH_4^+, NO_3^-, and PO_4^{3-} by (a) Sugar maple, (b) Red pine, and (c), and Norway spruce. Bars represent standard errors. Actual initial nutrient solution concentrations for the simulated soil solution, concentrated solution (5×), and highly concentrated solution (10×) are on the *x*-axes. Data include roots exposed to solutions in both increasing and decreasing order. For treatment means, $n = 10$, except trained sugar maple and red pine roots for which $n = 7$.

experiments, and the rate of change in nutrient content averaged over the 2 h period provided the basis for the dependent variable, net uptake rate.

We expected the change in nutrient concentration for the controls to be negligible. No precipitates had been visible in solution and gloves were worn during experiments to minimize

Table 2. Summary of weather conditions during uptake experiments. Data collected at the Game Farm Road Weather Station, Ithaca, NY and provided by Northeast Regional Climate Center

Species	Date	Air temperature (°C)	Relative humidity (%)	Solar radiation (kJ m^{-2} d^{-1})
Sugar maple	6/13/2002	19	27	75
Red pine	6/26/2002	28	63	33
Norway spruce	7/18/2002	28	64	36

contamination. However, concentrations of NH_4^+ and PO_4^{3-} in the controls changed significantly ($P < 0.01$). Depletion by controls was significantly smaller in magnitude than the change in concentration for the roots ($P < 0.05$). For all nutrients, the variability in depletion in the controls was low. Across all experiments, controls showed a decrease from the initial concentration of NH_4 ($3.5 \pm 0.7\%$, mean ± standard error) and an increase of NO_3 ($0.3 \pm 2\%$). Surprisingly, controls showed a $26 \pm 3\%$ decrease in PO_4 concentration.

We attributed change in concentration of nutrients by controls to adhesion of ions to tubes, precipitation, evaporation, or contamination occurring during the setting up of experiments. Therefore, we subtracted change in concentration of controls from the change in concentration by roots, so as not to be attributed to uptake. Uptake in μmol g $root^{-1}$ $hour^{-1}$ was calculated as the difference between initial nutrient content of the solution (concentration times volume) and final nutrient content divided by fresh root weight and time (about 2 h).

A subsample of roots from this and similar experiments were scanned and uptake rates as a function of root surface area, total root length, dry weight, and fresh weight were determined. None of the parameters were found to be better than fresh weight as predictors of uptake (data not shown).

Effects on net uptake of pretreatment, nutrient solution concentration, and the sequence in which solutions were applied were tested by analysis of variance using a split-plot model to account for repeated measures (Kuehl, 2000). In addition to the main effects of pretreatment, sequence, and nutrient solution concentration, the statistical model included interactions between pretreatment and sequence and between pretreatment and nutrient solution concentration. Differences in net uptake rates due to pretreatment, order of solution application, and nutrient solution concentrations were tested using least squares means and linear contrasts.

Results

Roots significantly changed the nutrient concentrations of the solutions to which they were exposed ($P < 0.01$). Positive net uptake rates indicate that roots took up nutrients, while negative uptake rates indicate net efflux (Figure 1). Because uptake by different species was not measured on the same date, rates should not be compared between species. Net uptake of NH_4^+ was positive for sugar maple at all initial nutrient concentrations. Red pine and Norway spruce roots given 5× and 10× nutrient solutions also took up NH_4^+, but a small net efflux was commonly observed at the lowest concentration. Net uptake of NO_3^- by red pine was positive at the 5× and 10× nutrient solution concentration, but rates for sugar maple and Norway spruce were consistently positive only at the highest concentration. For all three species, net uptake of NH_4^+ was several times higher than that of NO_3^-. Net uptake of PO_4^{3-} was generally positive at all concentrations for all species. Efflux of Ca^{2+} and K^+ was commonly observed for all species (data not shown). For all three species, net uptake of NH_4^+ was several times higher than that of NO_3^-.

Because uptake rates vary as a function of nutrient solution concentration, rates are likely to change over time during a depletion study such as this. The amount of nutrient depletion by roots during our 2–h exposures averaged 12% for NH_4^+ (excluding the 23% of cases in which net uptake was negative). For NO_3^-, positive net uptake was observed in 61% of cases,

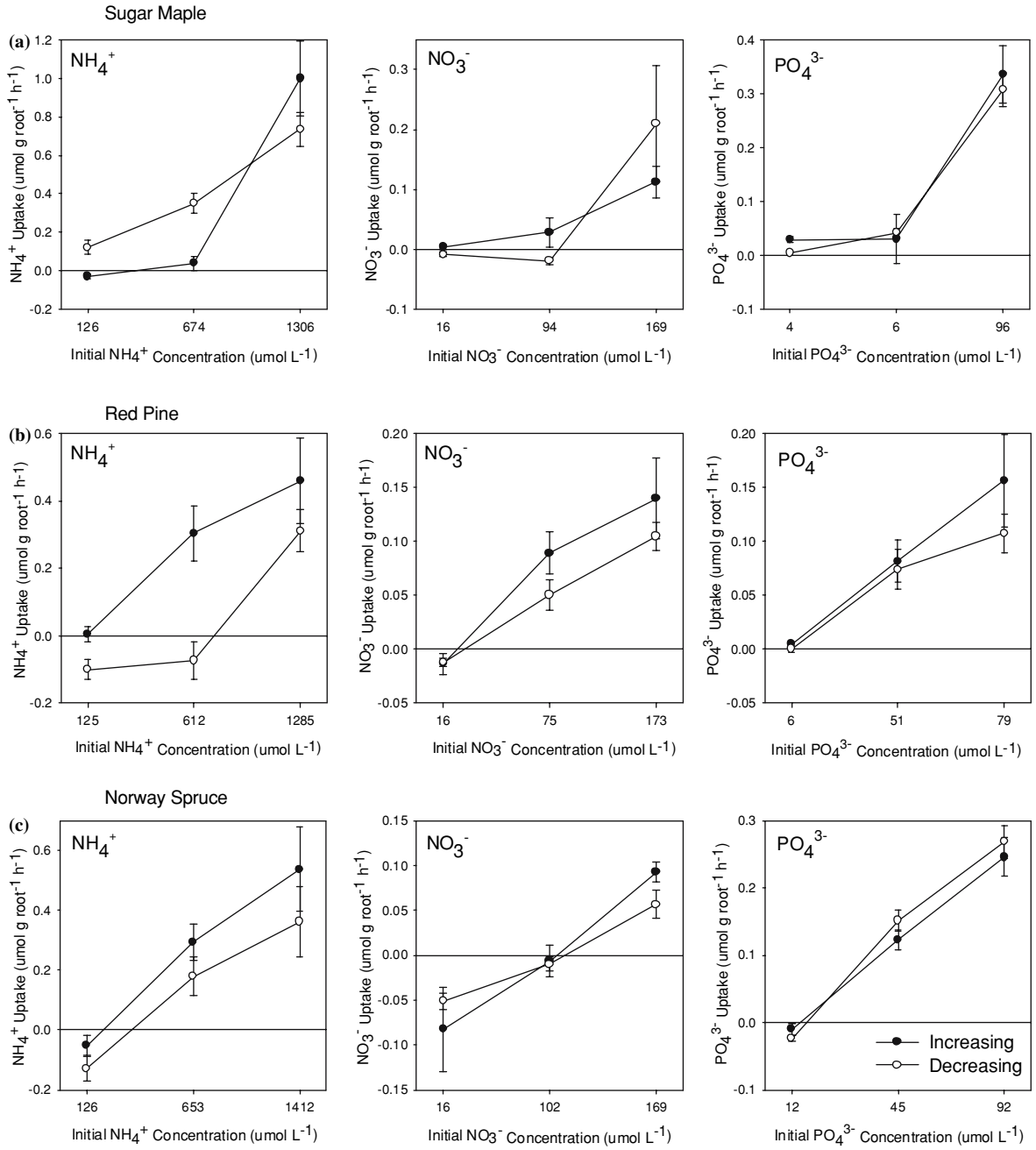

Figure 2. Mean uptake rates of NH_4^+, NO_3^-, and PO_4^{3-} by (a) Sugar maple, (b) Red pine, and (c), and Norway spruce by sequence of nutrient solution application. "Increasing" refers to roots nutrient solutions in order of increasing concentration. "Decreasing" refers to roots given nutrient solutions in order of decreasing concentration. Bars represent standard errors and *x*-axes are the same as Figure 1. Data include roots given all pretreatments. For treatment means, $n = 18$–20 depending on sequence and species.

and the amount of depletion averaged 15%. The reported uptake rates can thus be associated with the initial solution concentration with only a small overestimate of concentration over the 2-h period. In contrast, roots depleted 63% of available PO_4^{3-} (95% of cases showed net influx).

Therefore, the reported average rates of uptake of PO_4^{3-} for each time interval are probably underestimated relative to the initial solution concentration because the concentration was considerably lower for most of the experiment. We observed a large and unexplained loss of PO_4^{3-} from controls (26%), although less was lost from controls than was taken up by roots.

For the most part, the different pretreatments resulted in statistically indistinguishable net uptake rates. However, pretreatment did have a significant effect on net uptake for a few combinations of nutrient and species. Net uptake of NH_4^+ by sugar maple was higher for zero recovery roots than for 2- or 4-day recovery roots ($P = 0.04$). Red pine trained and zero recovery roots had higher net PO_4^{3-} uptake than 2- and 4-day recovery roots ($P < 0.01$). Trained roots were not different from recently excavated roots for any species or nutrient combination despite the difference in morphology induced by pruning and growth in the sandy medium.

In addition to pretreatment effects, we were interested in the effects of nutrient solution concentration and the sequence in which solutions were applied. Net uptake rates for NH_4^+, NO_3^-, and PO_4^{3-} increased significantly with increasing concentration for all three species (Figure 1, $\alpha = 0.05$). The sequence in which nutrient solutions were applied did not significantly affect PO_4^{3-} uptake (Figure 2). However, red pine and Norway spruce took up more NH_4^+ when roots were given nutrient solutions in increasing order of concentration (simulated soil solution first) than in decreasing order (highly concentrated solution first). Norway spruce showed the same effect for NO_3^-. This evidence provides support for the method of "starving" roots of a nutrient to increase measured uptake rates.

Discussion

This study and studies by others (Escamilla and Comerford, 1998a, b; Gessler et al., 1998, 2002; Lucash et al., 2005; Marschner et al., 1991; Rennenberg et al., 1996) have demonstrated positive uptake of N and P using variations of the depletion method. As a basis of comparison to other published rates, our net uptake rates ranged from 0 (or net efflux) up to 1.4 μmol g root^{-1} hr^{-1} for NH_4^+, up to 0.18 μmol g root^{-1} hr^{-1} for NO_3^-, and up to 0.36 μmol g root^{-1} hr^{-1} for PO_4^{3-}. These rates are within the range reported by other studies. For example, net uptake rates of NH_4^+ measured in situ using the depletion method ranged from 0.06–0.9 μmol g root^{-1} hr^{-1} (fresh weights) for European beech, 0.1–0.9 μmol g root^{-1} hr^{-1} for Norway spruce (Gessler et al., 1998, 2002), from 0–0.17 μmol g root^{-1} hr^{-1} of NO_3^- by Norway spruce (Rennenberg et al., 1996). Net uptake rates by Loblolly pine, also measured *in situ* with the depletion technique, were 0 (or net efflux) up to 3 μmol g root^{-1} hr^{-1} (dry weights) for NH_4^+ and up to 0.6 μmol g root^{-1} hr^{-1} for NO_3^-. To our knowledge, phosphate uptake has not been measured *in situ* using the depletion method. However, net uptake rates of PO_4^{3-} by loblolly pine seedlings measured using isotopes were 0.06–0.2 μmol g root^{-1} hr^{-1} and those for pond pine (*Pinus serotina* Michx.) seedlings were 0.2–0.5 μmol g root^{-1} hr^{-1}.

Net uptake rates measured with the depletion method depend on the length of time roots are exposed to nutrient solutions. Because the solutions are typically depleted over time (Escamilla and Comerford, 1998b), uptake rates decline, resulting in lower average rates calculated for longer time intervals (Lucash et al., 2005). Researchers using the depletion method have used time periods ranging from 15 min to several days. We selected the two-hour interval because in earlier experiments we found that two hours was sufficient to cause a measurable change in solution concentrations and that periods of one to several days incur the risk of depleting the solution to such a degree that net uptake rates approach zero. In cases where solutions are highly depleted, the average rate of uptake over the time interval is not very meaningful and the average solution concentration is unknown.

We observed much higher net uptake rates for NH_4^+ than for NO_3^- by all three species we studied. This is not surprising for a number of reasons. First, the initial nutrient solutions contained about seven times as much NH_4^+ as NO_3^-. Second, numerous studies have reported higher uptake capacity (BassiriRad et al., 1999; Marschner et al., 1991; Rennenberg et al., 1996) or lower Cmin (BassiriRad et al., 1999; Marschner et al., 1991; Rennenberg et al., 1996) for NH_4^+ than for NO_3^- by trees. In addition, high

concentrations of NH_4^+ in nutrient solutions have been shown to inhibit net uptake of NO_3^- (Gessler et al., 1998).

There are numerous reasons to question the accuracy of the depletion method. Roots are extremely sensitive to disturbance, and the excavation damages roots, likely altering uptake rates. Similarly, a realistic estimate of uptake should include extramatrical hyphae of mycorrhizae, which are excluded when measuring uptake using this method. We also recognize that although net efflux is sometimes observed by the depletion method, roots must exhibit positive net uptake over the long term. Observation of net efflux by roots in this and similar studies (Kulpa et al., *in review;* Lucash et al., 2005) suggests that the conditions during the measurement period are not representative of field conditions. This problem probably applies equally to excised root and depletion techniques. Although the rates of uptake we observed may not characterize these tree roots over the long term, we have interpreted the effect of our treatments by assuming that any artifacts of our experimental methods applied equally across treatments.

We had expected that training roots or allowing a recovery period would result in higher uptake rates and fewer cases of net efflux compared to recently excavated roots. This was not the case. The use of training and recovery period pretreatments increased the amount of time and labor required to measure uptake, but we observed no benefit compared with roots given no pretreatment. It remains possible that a recovery period longer than four days might have produced significantly different results.

Other factors, such as nutrient solution concentrations, may reduce the comparability of studies. The sensitivity of uptake rates to nutrient solution concentration has been well documented in studies of uptake kinetics and was demonstrated in this study. Field experiments of nutrient uptake generally use nutrient solutions concentrations designed to simulate ambient soil solution conditions of the site at which they are conducted. As a result, nutrient solution concentrations are variable across studies (Table 1). The importance of nutrient solution concentration should be considered when interpreting results of uptake studies.

We also tested the effects of sequence on measured uptake rates. Phosphate uptake was unaffected by the sequence of solution concentrations, but NH_4^+ and NO_3^- uptake were higher when roots were first given low concentrations than when they were given high concentrations. This observation is similar to the effect of starving roots to stimulate uptake (Hoagland and Broyer, 1936; Lee, 1982). However, starvation treatments are generally applied for a day or longer (Hoagland and Broyer, 1936; Lee, 1982), not a mere few hours. Conversely, early exposure to high concentrations may have resulted in saturation of root exchange sites (Deane-Drummond, 1982; Siddiqi et al., 1990) repressing subsequent uptake.

In conclusion, the use or absence of pretreatments such as training roots or providing a recovery or acclimation period in solution may not affect uptake rates measured by the depletion method. In contrast, solution concentrations, including initial nutrient solution concentration and antecedent conditions, are very important to measured uptake rates and should be considered when interpreting results or comparing results from different experiments.

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