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Similarity of Nutrient Uptake and Root Dimensions of Engelmann Spruce and Subalpine Fir at Two Contrasting Sites in Colorado

*R. Yanai, K. McFarlane, M. Lucash, S. Kulpa,
and D. Wood*

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Abstract

Nutrient uptake capacity is an important parameter in modeling nutrient uptake by plants. Researchers commonly assume that uptake capacity measured for a species can be used across sites. We tested this assumption by measuring the nutrient uptake capacity of intact roots of Engelmann spruce (*Picea engelmanni* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) at Loch Vale Watershed and Fraser Experimental Forest in the Rocky Mountains of central Colorado. Roots still attached to the tree were exposed to one of three concentrations of nutrient solutions for time periods ranging from 1 to 96 hours, and solutions were analyzed for ammonium, nitrate, calcium, magnesium, and potassium. Surprisingly, the two species were indistinguishable in nutrient uptake within site for all nutrients ($P > 0.25$), but uptake rates differed by site. In general, nutrient uptake was higher at Fraser ($P = 0.01, 0.15, 0.03, 0.18$ for NH_4^+ , NO_3^- , Ca^{2+} , and K^+ , respectively), which is west of the Continental Divide and has lower atmospheric deposition of N than Loch Vale. Mean uptake rates by site for ambient solution concentrations were $0.12 \mu\text{mol NH}_4^+ \text{ g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, $0.02 \mu\text{mol NO}_3^- \text{ g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, $0.21 \mu\text{mol Ca}^{2+} \text{ g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, and $0.01 \mu\text{mol Mg}^{2+} \text{ g}_{\text{fwt}}^{-1} \text{ h}^{-1}$ at Loch Vale, and $0.21 \mu\text{mol NH}_4^+ \text{ g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, $0.04 \mu\text{mol NO}_3^- \text{ g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, $0.51 \mu\text{mol Ca}^{2+} \text{ g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, and $0.07 \mu\text{mol Mg}^{2+} \text{ g}_{\text{fwt}}^{-1} \text{ h}^{-1}$ at Fraser. The importance of site conditions in determining uptake capacity should not be overlooked when parameterizing nutrient uptake models.

We also characterized the root morphology of these two species and compared them to other tree species we have measured at various sites in the northeastern USA. Engelmann spruce and subalpine fir were indistinguishable in specific root length and diameter distribution, while most of the other ten species had statistically distinct diameter distributions across five diameter classes < 2 mm. Based on specific root length, subalpine fir and Engelmann spruce had

significantly coarser roots than red pine (*Pinus resinosa* Soland), yellow birch (*Betula allegheniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), chestnut oak (*Quercus prinus* L.), black cherry (*Prunus serotina* Ehrh.), and red spruce (*Picea rubens* Sarg.). White oak (*Quercus alba* L.), balsam fir (*Abies balsamea* (L.) Mill.), American beech (*Fagus grandifolia* Ehrh.) and loblolly pine (*Pinus taeda* L.) were intermediate in SRL (indistinguishable from Engelmann spruce and subalpine fir by ANOVA). Species that differ more in physiology and morphology than the two species we compared would likely show dissimilar uptake characteristics even at the same site.

1. Introduction

Nutrient uptake capacity, which describes uptake rates at the root surface as a function of solution concentration, is known to differ dramatically by species even when they are growing in similar conditions (Chapin et al. 1986). Uptake capacity for a given species may also vary depending on site conditions, notably nutrient availability. For example, roots exposed to high nutrient concentrations often have lower uptake capacity than roots exposed to low nutrient concentrations (Lee and Rudge 1986; Siddiqi et al. 1989). Roots of quaking aspen (*Populus tremuloides* Michx.) grown under elevated N availability had lower NH_4^+ and NO_3^- uptake capacities than those grown under ambient N (Rothstein et al., 2000). Uptake capacity of NH_4^+ by Scots pine (*Pinus sylvestris* L.) was reduced following long-term fertilization experiments in Sweden (Jones et al., 1994). Ammonium uptake capacity by Norway spruce (*Picea abies* L.) decreased with increasing N inputs along a N-deposition gradient in Europe (Högberg et al., 1998). This type of variation between species or between sites is not generally included in ecosystem models but could be important to predicting plant response to environmental change.

Species have inherent differences in root morphology as well as physiology, and these differences may contribute to differences in uptake capacity. American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.) and sugar maple (*Acer saccharum* Marsh.) differed in their root diameter distributions and SRL at a field site in NH (Fahey and Hughes 1994). Apple trees (*Malus domestica* Borkh.) have lower root length density and higher P uptake than citrus (*Citrus paradisi* Macf.) grown in the field (Bouma et al 2001). Site factors can contribute to variation in root morphology as well. For example, roots grown under low nutrient conditions can be thicker and have a lower specific root length (SRL) than those grown under high nutrient conditions (Eissenstat 1992; Fahey and Hughes 1994).

Rocky Mountain subalpine forests are subjected to a range of N deposition rates, providing an opportunity to investigate the effects of varying levels of N deposition on nutrient uptake capacity. Subalpine forests on the east of the Continental divide have total N deposition of 3–5 kg N ha⁻¹ yr⁻¹ due to their proximity to anthropogenic N emissions from urban populations and animal husbandry operations (Baron et al., 2000; Rueth and Baron, 2002). Westside subalpine forests are protected from pollution affecting areas east of the Divide by wind patterns and the orographic effect of the mountains (Fenn et al., 2003), resulting in total N deposition of only 1–2 kg N ha⁻¹ yr⁻¹ in (Rueth and Baron, 2002). Eastside subalpine forests have higher foliar N concentrations, lower foliar and mineral soil C:N and lignin:N ratios, and higher net N mineralization potential in mineral soil (Baron et al., 2000). In addition, eastside forests have greater forest floor N concentrations and storage and higher N mineralization rates in forest floors than westside forests (Rueth and Baron, 2002). Finally, eastside lakes have demonstrated symptoms of eutrophication and disturbance and increased NO₃⁻ concentrations relative to westside lakes (Baron et al., 2000; Campbell et al., 2000).

We explored the hypotheses that nutrient uptake capacity differs among sites and species due to differences in (1) nutrient availability in different locations and (2) root morphology across species. We measured nutrient uptake in the field by intact roots of Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) at two sites in the Colorado Rocky Mountains with similar forest composition and structure but contrasting N deposition. We were thus able to test the effects of species and site on rates of uptake of NH_4^+ , NO_3^- , Ca^{2+} , Mg^{2+} , and K^+ . To further explore the similarity in behavior of Engelmann spruce and subalpine fir, we compared specific root length and frequency distribution of root diameters of twelve tree species across seven sites.

2. Methods

2.1. Site Descriptions

We measured nutrient uptake and collected roots from trees at two subalpine forests in central Colorado (Table 1). The vegetation at both sites is old-growth subalpine forest dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Engelmann spruce is longer lived than subalpine fir, and the spruce trees are generally older (up to 400 years, compared to 200 years for fir) and bigger (Table 1) than the fir trees. *Vaccinium* species dominate the understory of both sites. Soils at both sites have loamy textures and were formed in gravel and glacial till parent materials derived from gneiss and schist (Retzer, 1962; Stottlemeyer et al., 1997). The sites experience similar climate, with long cold winters and short summers that are relatively cool and dry (Alexander et al., 1985; Arthur and Fahey, 1992). The main difference between sites is their proximity to anthropogenic N sources, which results in differences in atmospheric N deposition (Rueth and Baron, 2002). Across the region, about one-third of

inorganic N deposition is in the form of NH_4^{+3} with the remaining two-thirds as NO_3^- (Fenn et al., 2003).

Loch Vale Watershed, the site that receives greater rates of N deposition, is located high on the eastern slope of the Continental Divide in Rocky Mountain National Park, Colorado about 80 km northwest of Denver. Annual precipitation is 100 cm, 70% of which falls as snow. Total inorganic N deposition averaged $4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ from 1992–1997 (Campbell et al., 2000). Soils are shallow loamy-skeletal, mixed, cryic Lithic Cryoboralfs, formed in glacial till on gneiss and schist bedrock. Our study is limited to the uneven-aged forest of Engelmann spruce and subalpine fir in the lower elevations ($\sim 3100 \text{ m}$). Soil solution chemistry has been analyzed and is assumed the major source of available nutrients for vegetation at Loch Vale (Arthur and Fahey, 1993).

Fraser Experimental Forest, which receives less N deposition than Loch Vale, is located on the west slope of the Continental Divide, about 70 km west of Denver. Our measurements were made in Lexen Creek watershed near the old snow course site number 22. Wet inorganic N deposition at Lexen Creek watershed was $1.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in 1990 (calculated from Stottlemeyer et al., 1997); two other watersheds at Fraser Experimental Forest also averaged $1.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for 1984–86.

2.2 Simulated Soil Solution

The nutrient solutions we used during uptake experiments were based on soil solution chemistry for Loch Vale (Arthur and Fahey, 1993); soil solution concentrations were not available for Fraser. Using this approach makes it possible to compare the behavior of roots between the two sites at common initial concentrations. To ensure that nutrients were available in high enough concentrations for measurable uptake to occur and to determine uptake as a

function of concentration, roots were exposed to the simulated soil solution (1x) or to a solution of five (5x) or ten (10x) times the simulated soil solution concentrations. The actual average concentrations used in the field in our 1x solutions at the two sites were 3-21 μM NH_4^+ , 4-9 μM NO_3^- , 0-0.3 μM PO_4^{3-} , 10-25 μM K^+ , 50-81 μM Ca^{2+} , 8-10 μM Mg^{2+} , 100-250 μM Na^+ , and 0-2 μM Al^{3+} , as measured in control tubes, described below. Concentrations in 5x and 10x solutions were proportionately higher (shown in Figure 1). We adjusted the pH of our solutions in the field, if necessary, to mimic the reported pH of 4.9-5.0 (Arthur and Fahey, 1993).

2.3 Uptake Experiments

Uptake experiments were conducted at Loch Vale from June 22 – 25 and at Fraser from June 27 – 30, 2001. At each site, we excavated small branches of roots of each species, leaving them attached to the tree. Species were identified by tracing each root back to a tree or to a root coarse enough to have distinguishing bark characteristics. The roots were washed with distilled water to remove soil particles and placed in a tube containing 30 ml (Loch Vale) or 27 ml (Fraser) of nutrient solution. The solutions were aerated to provide roots with O_2 and to prevent depletion zones from forming around the roots. Tubes were sealed with Parafilm and covered with tarps to minimize evaporation and contamination. We did not use a pre-treatment period in these experiments. Roots were used in multiple experiments, as follows. At Loch Vale, 10 roots were measured for 4 and 96 hours and 11 roots were measured for 2, 24, and 44 hours. At Fraser, 7 roots were measured for 2, 66 and 4 hours, and 5 roots were measured for 1, 20, and 22 hours. The initial solution concentrations (1x, 5x, and 10x) were applied to roots within each experiment, and the roots received the same nutrient treatment in subsequent experiments. Tubes with aerated solution and no roots served as controls (two for each concentration and duration at Loch Vale; one for each concentration and duration at Fraser). At the end of each experiment,

solution samples were measured for volume and filtered using 0.4 μm polycarbonate filters.

Samples were frozen upon returning from the field each day.

Solution samples were analyzed for NO_3^- and NH_4^+ by continuous flow analyzer (model AA3; Bran and Luebbe, Norderstedt, Germany). Not all the samples were analyzed for NO_3^- ; results for the 10x nutrient solution concentrations for Fraser are therefore not reported.

Concentrations of Ca^{2+} , Mg^{2+} , K^+ , and Al^{3+} were measured using inductively coupled plasma emission spectroscopy (model FMA-03, Spectro Analytical Instruments, Kleve, Germany).

2.4 Root analysis

After experiments were completed, the roots were severed and returned to the lab, where they were stored in alcohol. They were weighed wet before they were analyzed for length and surface area. Each root branch was analyzed separately. We cut the roots into small pieces and oriented them in the direction of the scan to minimize shadows in the image. The roots were spread in a tray of water on a flatbed scanner, and scanned at a resolution of 600 dpi using transmitted, not reflected, light. The image was converted to a bitmap (black and white) using an automated threshold, to avoid operator bias. Stray pixels were removed with a 2-pixel noise filter. The final images were analyzed with software from Delta-T Scan. We defined diameter classes for scanning as follows: ≤ 0.1 , 0.1-0.2, 0.2-0.5, 0.5-1.0, 1.0-2.0, and >2.0 mm. Root sections with diameters > 2 mm were removed after scanning and the < 2 mm roots were dried at 65 °C and weighed. Specific root length (SRL) of the < 2 mm root fraction was calculated as total length divided by dry weight. We analyzed root weight and SRL across species and sites using ANOVA in SAS.

For comparison to the roots from Loch Vale and Fraser, we present the results of the same analysis of ten other species collected at five additional sites. Some of these other

experiments have been described elsewhere (Lucash et al., 2005; McFarlane and Yanai, 2006), but none of the root dimensions have been previously reported. The number of roots analyzed from each site and species varied, as follows: Hubbard Brook Experimental Forest, New Hampshire (5 balsam fir (*Abies balsamea* (L.) Mill.), 6 red spruce (*Picea rubens* Sarg.), 8 American beech and 7 yellow birch); Huntington Forest, New York (17 American beech and 10 sugar maple); Turkey Hill Plantation, New York (12 black cherry (*Prunus serotina* Ehrh.) and 8 red pine); Calhoun Experimental Forest, South Carolina (59 loblolly pine (*Pinus taeda* L.)); and Walker Branch, Tennessee (7 chestnut oak (*Quercus prinus* L.) and 6 white oak). The numbers of root branches analyzed from our Colorado sites were 9 Engelmann spruce and 12 subalpine fir at Loch Vale and 5 Engelmann spruce and 6 subalpine fir at Fraser.

The root distribution data were analyzed by root branch, because the individual observations of proportion within a size class were not independent within root branch. Multivariate analysis of variance was conducted using the General Linear Models procedure in SAS (SAS Institute Inc., 2004). Contrasts between species within a diameter class were evaluated using the Waller-Duncan K-ratio t-test, based on the < 2 mm portion of the root branch. We also identified species that differed in the proportion of root length in at least one diameter class.

2.5 Data analysis

Uptake was calculated from the change over time in the amount of nutrient in the tube, calculated as the product of concentration and volume. The same calculation was made for control tubes (without roots) and these differences were subtracted from the changes observed for roots. Control concentrations did not differ with duration of the experiment, so we used the means of control "uptake" for each site and solution concentration. The average loss of solution

volume averaged 7 % in roots and 3 % in control tubes (1-2 ml) and did not differ by site ($P = 0.36$). Uptake rates are reported in units of micrograms of nutrient per gram fresh root per hour. We used fresh weight because it was as good a predictor of uptake as dry weight, length or surface area (McFarlane and Yanai, 2006) and because not all of our roots were scanned.

We used analysis of variance with repeated measures to reflect the use of the same roots in multiple experiments. We assessed the effect of site (2 levels), species (2 levels), initial nutrient solution concentration (3 levels), duration of the experiments (9 levels), and their interactions on the final concentrations and calculated uptake rates of NH_4^+ , Ca^{2+} , Mg^{2+} and K^+ , using proc mixed in SAS. When interactions including site or species effects were significant at a 0.1 alpha level, we conducted slicing tests and multiple comparisons tests using a Tukey adjustment to interpret those interactions. We intended to analyze PO_4^{3-} uptake, but this was not possible because the initial solutions concentrations were very low, and solutions exposed to roots proved indistinguishable in concentration from controls.

We also computed average uptake rates for 2-hour experiments at each of the three initial solution concentrations. We report these by site but not by species, since species did not differ significantly in uptake rates.

3. Results

3.1 Roots deplete nutrients in simulated soil solutions

We observed progressive nutrient uptake over time: final nutrient concentrations in solutions exposed to roots in the field were generally lower in tubes that held roots for longer time intervals (Figure 1). For K^+ , however, the concentrations measured after applying the solutions were generally greater than 100% of the initial solution concentrations, indicating that nutrient efflux exceeded nutrient uptake.

For NH_4^+ , uptake exceeded efflux for every root and time interval measured, and concentrations declined rapidly over time (Figure 1 a). Ammonium concentrations at Fraser, the more N-limited site, declined more rapidly than at Loch Vale. Within a day or two, the solutions in the 5x and 10x treatments were drawn down to about the 1x level, the concentration of NH_4^+ in soil solution reported by Arthur and Fahey (1993). This observation suggests that the ambient solution concentrations may be controlled in part by the minimum concentration for root uptake.

Declines in concentrations of the divalent cations Ca^{2+} and Mg^{2+} were similar in their behavior (Figure 1 c, d). Concentrations depleted very gradually over time, relative to initial conditions (controls without roots). Unlike NH_4^+ , differences among the 1x, 5x, and 10x treatments persisted over the three or four days of our longest experiments. Clearly, roots did not take up these ions to the minimum concentration for root uptake. It appears that Ca^{2+} and Mg^{2+} are available in excess of tree demand, unlike NH_4^+ , consistent with limitation by N. However, concentrations were generally lower at Fraser than at Loch Vale, indicating more rapid uptake of Ca^{2+} and Mg^{2+} at the more nutrient-limited site.

Nitrate concentrations, like those of Ca^{2+} and Mg^{2+} , were not rapidly depleted (Figure 1 b). Concentrations in the 5x and 10x treatments remained relatively high, unlike NH_4^+ concentrations. The exception was the 96-h experiment, where depletion was more complete than expected based on the shorter experiments. Recall that the observations for each experimental duration represent the end point of an experiment, rather than the progress over time of a single exposure. The rate of uptake over 96 h is not as impressive as suggested by the log scale, but is similar to that at 44 and 66 h (Figure 2).

Potassium (Figure 1 e) had consistent net nutrient efflux across all treatments, at least initially. After about a day of net K^+ efflux, concentrations were reduced (net uptake occurred)

but not to levels much below the initial simulated soil solution. Like Ca^{2+} and Mg^{2+} , solution concentrations of K^{+} were generally higher at Loch Vale than at Fraser.

3.2 Uptake rates

Uptake rates were calculated using the concentration and volume of solutions at the beginning and end of each experiment, subtracting the values from the controls (tubes without roots). These rates reflect the average for the duration of each experiment; they also take into account the measured mass of each root (Figure 2).

Uptake rates of all nutrients were indistinguishable between spruce and fir ($P = 0.11$ for NO_3^{-} and $P > 0.32$ for other ions) in a repeated-measures analysis of variance including species, site, initial solution concentration, and duration of the exposure. Uptake rates were generally higher at Fraser than at Loch Vale, most significantly for NH_4^{+} ($P = 0.01$) and less so for NO_3^{-} ($P = 0.15$) and K (0.18). Uptake of Ca^{2+} was significantly greater at Fraser than at Loch Vale only at the 10x nutrient solution concentration ($P < 0.01$), resulting in an interaction of site and initial solution concentration ($p < 0.01$). For Mg, uptake rates were higher at Fraser only at ambient solution concentrations ($p = 0.14$) and were higher at Loch Vale under the 5x nutrient solution ($P = 0.03$) and not different among sites at the highest solution concentration ($P = 0.27$).

Uptake rates were higher at higher concentrations, especially in short-term exposures (Figure 2), resulting in significant interactions with the duration of the experiments. In repeated-measures ANOVA the main effect of initial solution concentration was important for Ca^{2+} and Mg^{2+} uptake ($P < 0.01$) and NH_4^{+} uptake ($P = 0.06$) but not for K^{+} efflux or NO_3^{-} uptake ($P > 0.50$). There were no significant three-way interactions.

Uptake rates differed significantly with the duration of the experiments for all nutrients ($P < 0.01$). Specifically, nutrient uptake (averaged over the time period) declined over longer

periods (Figure 2). For NH_4^+ , this decline could conceivably be attributed to the progressive depletion of nutrients from the solutions (Figure 1), but for base cations, the concentrations in 5x and 10x treatments were still high at the end of long experiments (Figure 1). The consistent near-zero uptake rates of base cations in long experiments shows that uptake was not a consistent function of nutrient concentration over four days, but declined with time.

Because of the declining uptake rates in longer experiments, we used the 2-hour experiments as the best representation of uptake by roots *in situ*. In general, uptake rates increased with solution concentration and were higher at Fraser than Loch Vale (Table 2). We averaged uptake rates by Engelmann spruce and subalpine fir because they were statistically indistinguishable and numerically similar.

3.3 Root morphology

Engelmann spruce and subalpine fir were remarkably similar in root morphology (Figure 3). The specific root length (length per unit mass) was 8.8 m g^{-1} for Engelmann spruce and 7.5 m g^{-1} for subalpine fir (Figure 4). Analysis of variance showed that neither species ($P = 0.34$) nor site ($P = 0.29$) differences were significant.

Engelmann spruce and subalpine fir were the two coarsest root systems of the twelve species we studied (Figure 4). Red pine, yellow birch, sugar maple, chestnut oak, black cherry, and red spruce had significantly finer roots (higher SRL). White oak, balsam fir, American beech and loblolly pine were intermediate in SRL (indistinguishable from Engelmann spruce and subalpine fir by ANOVA). We expected congeneric species to have similar SRL, but this was not generally true. Engelmann spruce had significantly coarser roots than red spruce, and loblolly pine had significantly coarser roots than red pine (Figure 4).

Frequency distributions of fine root diameters (Figure 5) support the similarity of Engelmann spruce and subalpine fir. Consistent with low SRL, these species have as much or more root length in the 0.5–1 mm diameter class than in the 0.2–0.5 mm class. For most of the other species, the diameter class with the greatest root length was the 0.2–0.5 class. In all species, the two smallest size classes (< 0.2 mm) accounted for less of the root length than the next two size classes (0.2–1 mm), and the amount of root length in the 1–2 mm size class was less than in the 0.5–1 mm size class.

4. Discussion

4.1 Magnitude of uptake rates

Ammonium uptake rates in this study were slightly lower than rates reported for other tree species. Ammonium uptake in our study ($0.1\text{--}0.4 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$ for 2-hr experiments, Table 2) was lower than uptake by Norway spruce ($0.6 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, Gessler et al., 1998), sugar maple ($0.1\text{--}1.1 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, McFarlane and Yanai, 2006) and American beech ($0.5 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, Gessler et al., 1998) trees in the field and loblolly pine ($1 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, Lucash et al., 2008) and Norway spruce seedlings ($0.3 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$, Eltrop and Marschner, 1996) in sand culture. However, McFarlane and Yanai, (2006) reported similar NH_4^+ uptake rates by Norway spruce ($0.01\text{--}0.2 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$) and red pine ($0\text{--}0.5 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$) to those shown in Table 2. The same study reported higher NO_3^- uptake rates (up to $0.2 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$ for red pine) than were observed in this study ($0.02\text{--}0.04 \mu\text{mol g}_{\text{fwt}}^{-1} \text{ h}^{-1}$).

Converted to a dry-weight basis, our NH_4^+ uptake rates ($1\text{--}2 \mu\text{mol g}_{\text{dwt}}^{-1} \text{ h}^{-1}$) were lower than loblolly pine trees in the field ($10 \mu\text{mol g}_{\text{dwt}}^{-1} \text{ h}^{-1}$, Lucash et al., 2005). Similarly, in solution culture, higher rates of NH_4^+ uptake than those we measured have been reported for seedlings of loblolly pine ($10 \mu\text{mol g}_{\text{dwt}}^{-1} \text{ h}^{-1}$, Constable et al., 2001), sugar maple ($16 \mu\text{mol g}_{\text{dwt}}^{-1} \text{ h}^{-1}$,

Rothstein et al., 1996; $8 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$ BassiriRad et al., 1996), American beech ($9 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$, BassiriRad et al., 1996), and quaking aspen ($8\text{--}12 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$, Rothstein et al., 2000). Seedlings of European beech (*Fagus sylvatica* L.), white ash, (*Fraxinus americana* L.) and willow oak (*Quercus phellos* L.) had NH_4^+ uptake rates of 15, 17, and $13 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$, respectively, at solution concentrations similar to ours (Lajtha, 1994).

Uptake rates of Ca^{2+} , Mg^{2+} and K^+ were generally similar to other studies. Our Ca^{2+} uptake rates ($1\text{--}7 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$) were slightly lower than loblolly pine trees in the field ($8 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$, Lucash et al., 2007) and sycamore maple (*Acer pseudoplatanus* L.) seedlings in hydroponics ($8 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$, Gloser and Gloser, 2000). Magnesium uptake rates ($0.1\text{--}1.2 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$) were similar to sycamore maple seedlings in hydroponics ($0.2 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$, Gloser and Gloser, 2000) but lower than loblolly pine trees in the field ($3 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$, Lucash et al., 2007). Uptake rates of K^+ were negative (-0.6 to $-3.2 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$) and fell within the large range we found for loblolly pine trees in the field (-120 to $40 \mu\text{mol g}_{\text{dwt}}^{-1} \text{h}^{-1}$, Lucash et al., 2007).

4.2 Comparison to ecosystem uptake

Although our rates seem reasonable, or even somewhat low, relative to other reported studies of tree roots, they are quite high compared to the reported ecosystem uptake rates reported for Loch Vale (Arthur and Fahey, 1992). We estimated ecosystem uptake using the mass of roots reported for Loch Vale (900 g m^{-2} for roots $< 2 \text{ mm}$; Arthur and Fahey, 1992), our observed uptake rates from 1x solutions at Loch Vale (Table 2), and a conservative estimate of growing season length (150 days, based on temperatures over 0°C ; <http://www.wcc.nrcs.usda.gov/climate/foguide.html#growth>). Scaling up our field measurements results in rates at least an order of magnitude higher than needed to explain Arthur

and Fahey's (1992) budgeted rates of N (12 times), Ca^{2+} (60 times) and Mg^{2+} uptake (19 times too high).

Rates in the field are likely variable over space and time, with high rates, such as those we observed, reserved for roots in particularly favorable environments and seasons. Tree phenology can contribute to temporal variation in nutrient uptake, being higher in loblolly pine seedlings experiencing needle flushing (Kelly and Barber 1991). Scaling up measurements of nutrient uptake based on seedlings or roots of mature trees in nutrient solutions may give unrealistically high estimates of ecosystem nutrient uptake.

4.3 Methodological challenges

We used intact roots in the field to measure nutrient uptake, which we believe should give more realistic estimates than methods involving excised roots or seedlings (Lucash et al. 2007). However, net nutrient efflux, which we observed for K^+ , is clearly not descriptive of long-term root behavior in nature. We have observed net efflux of K^+ , NH^+ , Mg^{2+} , and PO_4^{3-} in various forest types using these methods (Lucash et al. 2005, 2007). We also conducted experiments using various pre-treatments to reduce the disturbance to roots of excavating and manipulating them, but failed to eliminate negative rates (McFarlane and Yanai, 2006; Lucash et al., 2008). Potassium is a highly mobile element in plant tissues, and we found net efflux of K^+ in every ecosystem and every tree species we tested (Lucash et al., 2007). Possible causes besides mechanical disturbance include chemical disturbance and anoxia, though we aerated our solutions and simulated ambient solute concentrations and pH in our soil solutions. Whatever the mechanism, we believe that it acts sufficiently consistently that our comparisons of sites and species in response to applied nutrient concentrations are valid.

4.4 Importance of species and site in determining nutrient uptake capacity

The observation that nutrient uptake rates were more disparate between sites than between species is perhaps the most important result of this study. There are many instances of ecosystem calculations in which some necessary information is unavailable for the site in question. When this is the case, ecosystem scientists commonly substitute values for the relevant species measured at other sites. This problem is not unique to nutrient uptake parameters, and the solution may be different for different types of data. Leaf concentrations, for example, differ significantly by site within species, whereas the mass of leaves may be reasonably predicted by allometric equations not specific to the site (Yanai et al., in prep). For nutrient uptake capacity, our results suggest that site-specific measurements may be important. Higher uptake rates measured at Fraser presumably reflect greater nutrient limitation at Fraser than at Loch Vale.

Engelman spruce and subalpine fir have similar root morphology. The similarity in specific root length between the two species (Figure 4) is consistent with their similar nutrient uptake rates. They also had the most similar frequency distribution of root diameters among the twelve tree species we studied (Figure 5). This similarity makes it less surprising that the two species do not differ much in nutrient uptake capacity at either site. Similarity in root morphology, however, doesn't necessarily mean uptake rates will be similar. Root order is a better predictor of root anatomy than root diameter across species (Guo et al. 2008), though no studies to date have linked root order with nutrient uptake of trees. While site was more important than species in this study, we do not suggest that species can always be ignored when estimating nutrient uptake characteristics. Both species characteristics and environmental factors are important to understanding nutrient uptake capacity of trees in field conditions.

4.5 Recommendations for future research

There is a need, clearly, for more field studies to compare nutrient uptake capacity of species across a range of environmental conditions. This information will shed light on the differential capability of species to acclimate to past and future conditions, for example under changing atmospheric N deposition. Selection of species or genotypes for restoration or reforestation projects could benefit from understanding the controls on nutrient uptake capacity. Optimal nutrient management requires predicting nutrient uptake in response to soil amendments.

Before this information can be used to quantitatively predict uptake at the ecosystem scale, there is also a need for methods that better characterize uptake in field conditions. Our observations of roots exposed for 2 hours to reported soil solution concentrations vastly overestimated annual ecosystem uptake rates, as described above. Although we used intact roots in the field, our method is still unrealistic in that the entire surface area of the roots is in contact with the solution, depletion zones do not form, and mycorrhizal hyphae are disturbed. Seasonal and diurnal patterns in nutrient availability (Kelly 1993, Kelly and Mays 1999) and nutrient uptake capacity (Lucash et al. 2005) also deserve more attention.

Nutrient uptake models (Barber 1984, Yanai 1994) provide a means for scaling observations of nutrient uptake capacity of individual roots up to the scale of the forest stand. Comparing these estimates to uptake at the ecosystem scale, estimated as the sum of turnover in ephemeral tissues plus accumulation in perennial tissues, could provide a basis for evaluating the realism of techniques for measuring nutrient uptake at the root surface. These comparisons could also help improve our understanding of uptake processes, by revealing the importance of mycorrhizal associations, enhanced mineral weathering, mineralization of organic N and P, or other processes not currently represented in models of nutrient uptake.

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501

Table 1. Site characteristics.

Characteristic	Loch Vale	Fraser
Latitude	40° 17' N	39° 54' N
Longitude	105° 39' W	105° 52' W
Elevation (m)	3100	3250
MAP (cm)	100 ^a	82 ^b
MAT (° C)	1.5 ^a	0.5 ^c
Winter low T (° C)	-7.6 ^a	-10.3 ^d
Summer high T (° C)	12.3 ^a	11.8 ^d
Soil Subgroup	Lithic Cryoboralf ^a	Dystic Cryochrept ^b
N deposition (kg N ha ⁻¹ yr ⁻¹)	4.1 ^e	1.7 ^f
Quadratic Mean Diameter (cm) ^{g,h}		
Engelmann spruce	30.5 (0.9)	21.8 (0.5)
Subalpine fir	15.5 (0.9)	13.3 (1.6)
Basal area (m ² ha ⁻¹) ^h		
Engelmann spruce	38.6 (0.5)	17.1 (11.9)
Subalpine fir	26.9 (9.7)	34.4 (9.9)
Stem density (stems ha ⁻¹)		
Engelmann spruce	531 (37)	679 (61)
Subalpine fir	1371 (333)	3334 (371)

^a Arthur and Fahey 1992.

^b Alstatt and Miles 1983.

^c Measured at Fraser Experimental Forest Headquarters (Stottlemeyer and Troendle 1992).

^d Alexander et al. 1985.

^e Annual average for 1992-1997 (Campbell et al. 2000).

^f Calculated from data provided by Stottlemeyer et al. 1997 for Lexen Creek Watershed for the 1990 water year.

^g Diameter of the tree of mean basal area

^h Based on trees > 5 cm diameter surveyed in plots 8 and 16 at Loch Vale in 2002 (Mary Arthur, unpublished data) and plots LSC115 and LIP085 in 1991 and 1993 at Lexen (Wayne Shepperd, unpublished data). Standard errors are given in parentheses.

516 Table 2. Uptake rates ($\mu\text{mol g}_{\text{fw}}^{-1} \text{h}^{-1}$) for short-term (2-h) experiments. Means by site and
517 solution concentration include both spruce and fir; species did not differ significantly in uptake
518 rates. Standard errors are given in parentheses. For nitrate, fewer observations were available
519 (in the case of 10x at Fraser, we have none) and we report experiments up to 4 hours in duration.

Site	Concentration	n	NH_4^+	NO_3^-	Ca^{2+}	Mg^{2+}	K^+
Loch Vale	1x	4	0.07 (0.01)	0.023 (0.008)	0.18 (0.11)	0.02 (0.004)	-0.47 (0.13)
Fraser	1x	2	0.17 (0.02)	0.027 (0.013)	0.47 (0.15)	0.07 (0.03)	-0.57 (0.05)
Loch Vale	5x	4	0.18 (0.04)	0.024 (0.013)	0.63 (0.33)	0.12 (0.04)	-0.26 (0.2)
Fraser	5x	3	0.24 (0.06)	0.037 (0.016)	0.55 (0.15)	0.04 (0.03)	-0.43 (0.09)
Loch Vale	10x	2	0.36 (0.12)	0.034 (0.01)	1.00 (0.54)	0.26 (0.05)	-0.38 (0.14)
Fraser	10x	2	0.41 (0.09)	n.a.	1.86 (0.31)	0.16 (0.03)	-0.39 (0.09)

520

521

Figure Captions

Figure 1. Solution concentrations of (a) ammonium, (b) calcium, (c) magnesium, and (d) potassium after exposure to roots for various lengths of time. Observations are means of 1-2 roots; means from the same site, species and initial solution concentration are connected by lines. Concentrations of controls (tubes without roots) are denoted on the y axis by open squares for Fraser and filled squares for Loch Vale, increasing in size from 1x to 10x.

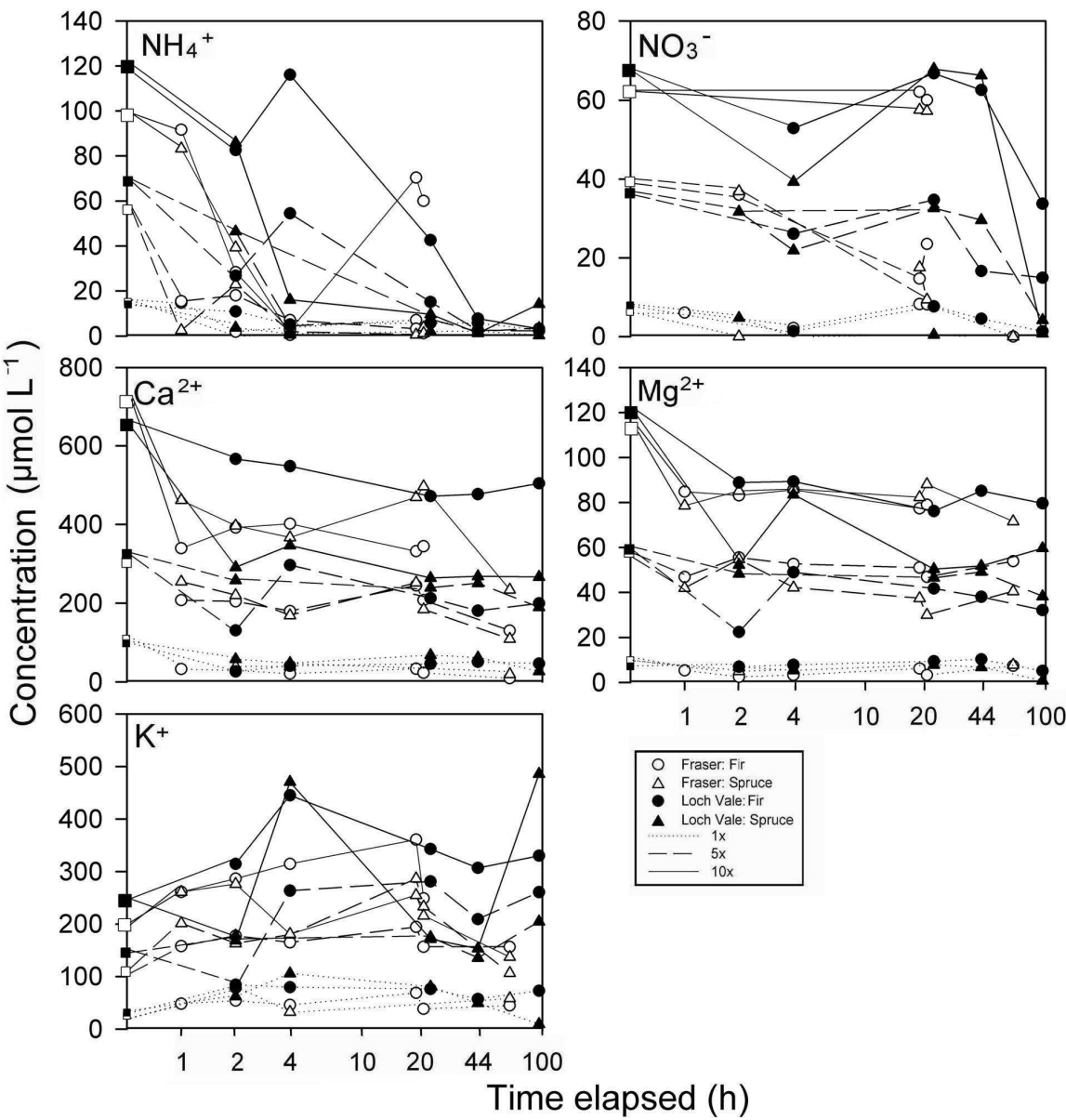
Figure 2. Uptake rates of (a) ammonium, (b) calcium, (c) magnesium, and (d) potassium during exposure to roots of various durations. Rates are reported on fresh weight basis. Rates less than zero indicate net efflux.

Figure 3. Morphology of representative root branches used in nutrient uptake experiments.

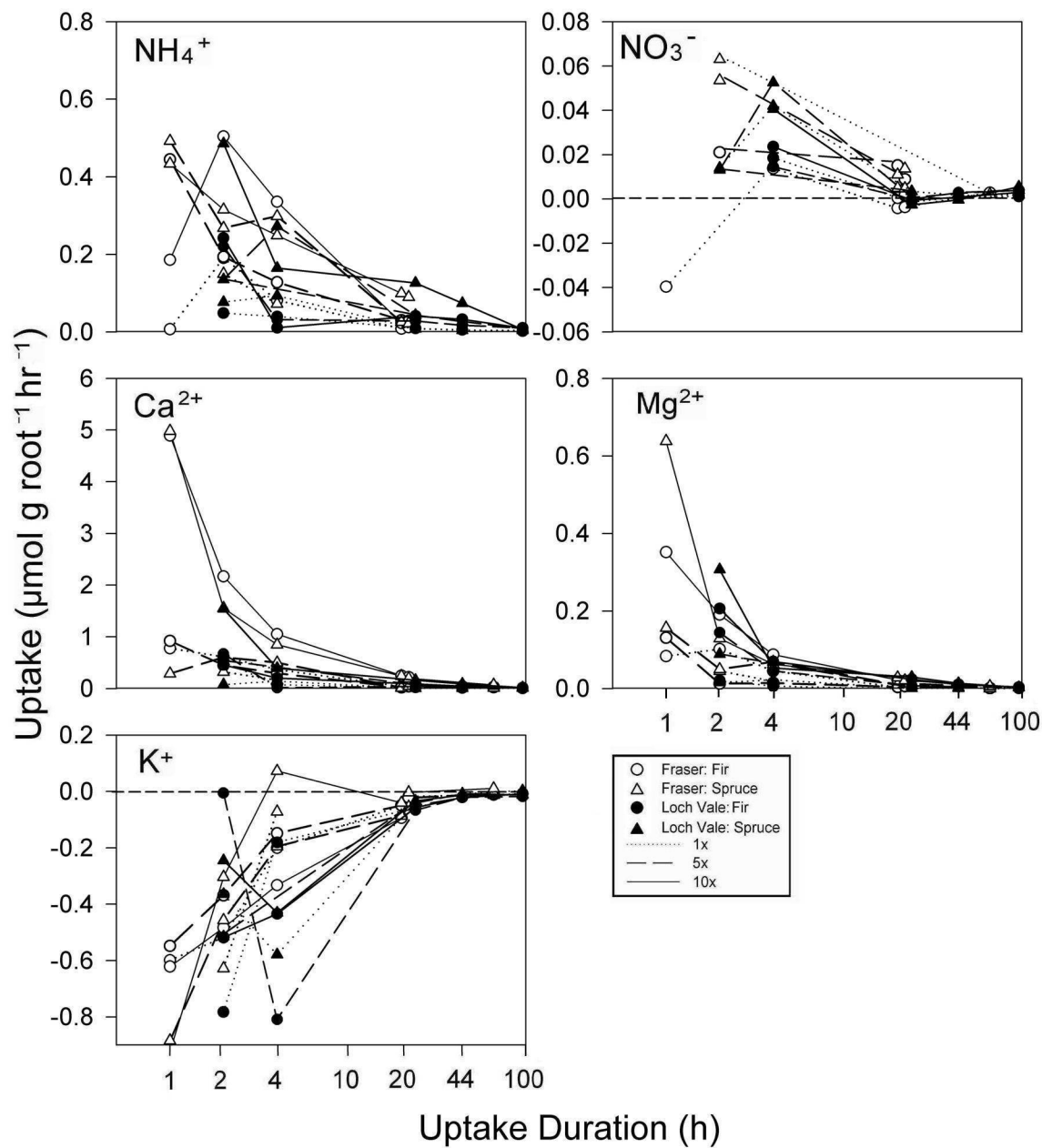
Figure 4. Specific root length of 12 tree species. Means sharing the same letter do not differ significantly at $\alpha=0.05$.

Figure 5. Frequency distributions by diameter class of 12 tree species. Means within a diameter class sharing the same lowercase letter do not differ significantly across species at $\alpha=0.05$. Species sharing the same uppercase letter do not differ significantly in any diameter class.

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552

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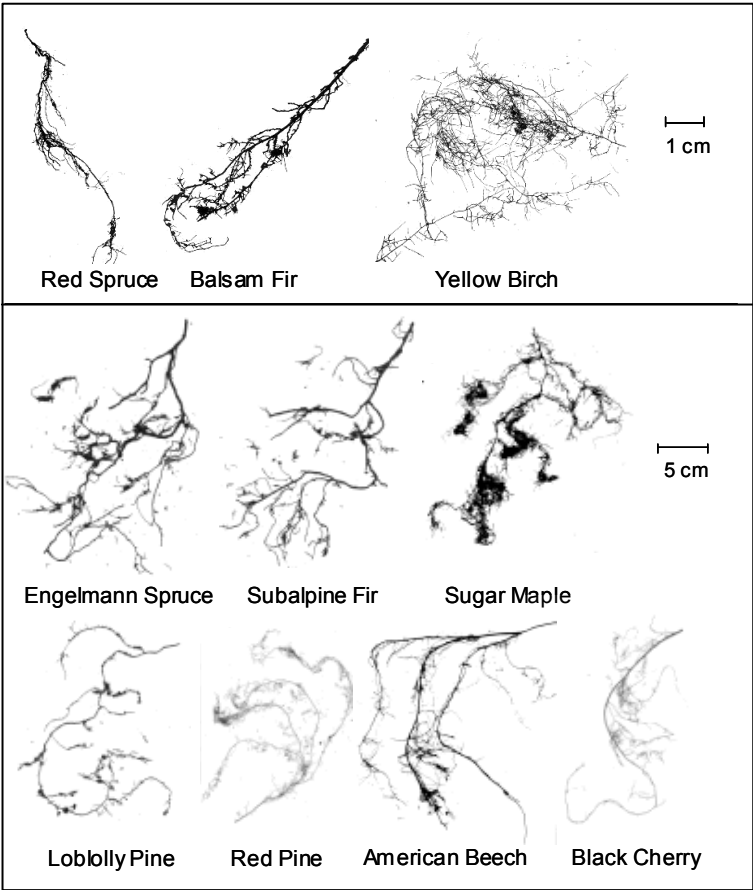


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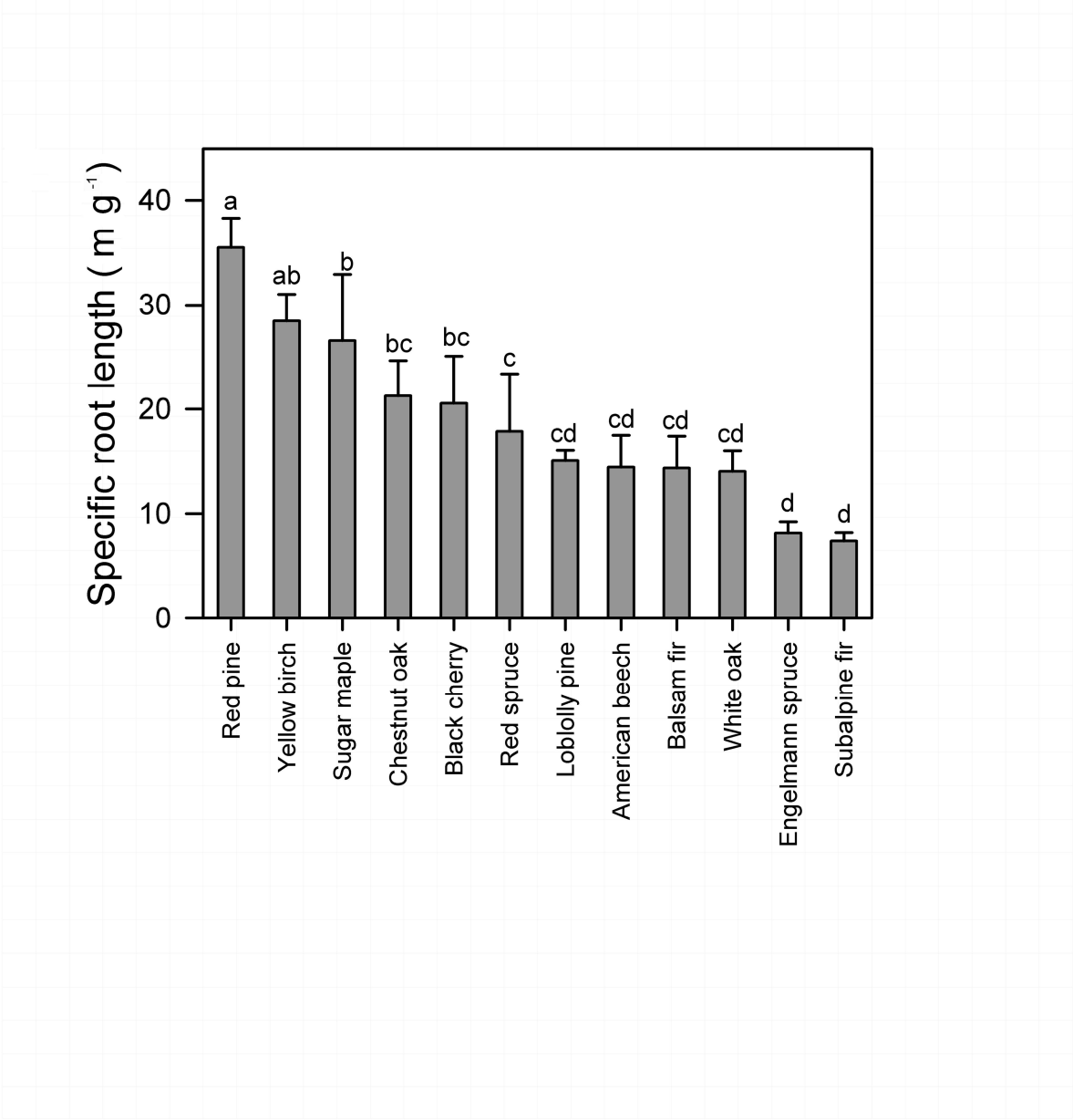


Figure 5. Frequency distributions by diameter class of 12 tree species. Means across species within a diameter class sharing the same lowercase letter do not differ significantly at $\alpha=0.05$. Species sharing the same uppercase letter do not differ significantly in any diameter class.

