Similarity of nutrient uptake and root dimensions of Engelmann spruce and subalpine fir at two contrasting sites in Colorado

Ruth D. Yanai,*, Karis J. McFarlane, Melissa S. Lucasha, Sarah E. Kulpa, Dustin M. Wood

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 NH₄⁺ and NO₃⁻ uptake capacities than those grown under ambient N (Rothstein et al., 2000). Uptake capacity of NH₄⁺ 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 (Bouna 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 year⁻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 effects by the orographic effect of the mountains (Fenn et al., 2003), resulting in total N deposition of only 1–2 kg N ha⁻¹ year⁻¹ (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 NH₄⁺, NO₃⁻, Ca²⁺, Mg²⁺, 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 12 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 (P. engelmannii) and subalpine fir (A. lasiocarpa). Engelmann spruce is longer lived than subalpine fir, and the spruce trees are generally older (400+ years, compared to 200+ years for fir) and bigger (Table 1) than the fir trees (Arthur, 1992). 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, 1982; Stottlemyer 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 NH₄⁺ with the remaining two-thirds as NO₃⁻ (Fenn et al., 2003).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Loch Vale</th>
<th>Fraser</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>40°17' N</td>
<td>39°54' N</td>
</tr>
<tr>
<td>Longitude</td>
<td>105°39' W</td>
<td>105°52' W</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>3100</td>
<td>3250</td>
</tr>
<tr>
<td>MAP (cm)</td>
<td>100⁰</td>
<td>82⁰</td>
</tr>
<tr>
<td>MAT (°C)</td>
<td>1.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Winter low T (°C)</td>
<td>-7.6⁰</td>
<td>-10.3⁰</td>
</tr>
<tr>
<td>Summer high T (°C)</td>
<td>12.3⁰</td>
<td>11.8⁰</td>
</tr>
<tr>
<td>Soil subgroup</td>
<td>Lithic Cryoboralf</td>
<td>Dystric Cryochrept</td>
</tr>
<tr>
<td>N deposition (kg N ha⁻¹ year⁻¹)</td>
<td>4.1⁰</td>
<td>1.7⁰</td>
</tr>
<tr>
<td>Quadratic mean diameter (cm)³</td>
<td>30.5 (0.9)</td>
<td>21.8 (0.5)</td>
</tr>
<tr>
<td>Engelmann spruce</td>
<td>15.5 (0.9)</td>
<td>13.3 (1.6)</td>
</tr>
<tr>
<td>Subalpine fir</td>
<td>38.6 (0.5)</td>
<td>17.1 (11.9)</td>
</tr>
<tr>
<td>Subalpine fir</td>
<td>26.9 (9.7)</td>
<td>34.4 (9.9)</td>
</tr>
<tr>
<td>Stem density (stems ha⁻¹)</td>
<td>531 (37)</td>
<td>679 (61)</td>
</tr>
<tr>
<td>Engelmann spruce</td>
<td>1371 (333)</td>
<td>3334 (371)</td>
</tr>
</tbody>
</table>

*Arthur and Fahey (1992).*  
¹Altstatt and Miles (1983).  
²Measured at Fraser Experimental Forest Headquarters (Stottlemyer and Troendle, 1992).  
³Alexander et al. (1985).  
⁵Calculated from data provided by Stottlemyer et al., 1997 for Lexen Creek Watershed for the 1990 water year.  
⁶Diameter of the tree of mean basal area.

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 kg N ha⁻¹ year⁻¹ in 1990 (calculated from Stottlemyer et al., 1997); two other watersheds at Fraser Experimental Forest also averaged 1.7 kg N ha⁻¹ year⁻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 (1×) or to a solution of five (5×) or ten (10×) times the simulated soil solution concentrations. The range of actual concentrations used in the field in our 1× solutions at the two sites was 3–22 μM NH₄⁺, 4–9 μM NO₃⁻, 50–81 μM Ca²⁺, 8–11 μM Mg²⁺, and 10–25 μM K⁺ as measured in control tubes, described below. Concentrations in 5× and 10× solutions were proportionately higher (averages are shown in Fig. 1). We included PO₄³⁻, Na⁺, and Al³⁺ in the simulated solutions, but these were not analyzed for uptake. 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 to 25 and at Fraser from June 27 to 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 O₂ 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 h and 11 roots were measured for 2, 24, and 44 h. At Fraser, 7 roots were measured for 2, 66, and 4 h, and 5 roots were measured for 1, 20, and 22 h. The initial solution concentrations (1×, 5×, and 10×) 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 NO₃⁻ and NH₄⁺ by continuous flow analyzer (model AA3; Bran and Luebbe, Norderstedt, Germany). Not all the samples were analyzed for NO₃⁻; results for the 10× nutrient solution concentrations for Fraser are therefore not reported. Concentrations of Ca²⁺, Mg²⁺, K⁺, and Al³⁺ 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

Fig. 1. Solution concentrations of ammonium, calcium, magnesium, and 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 1× to 10×.
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 10 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, 6 red spruce); Similkameen Experimental Forest, British Columbia (5 Picea engelmannii [Engelmann spruce], 6 Picea rubens Sarg., 8 American beech and 7 yellow birch); Huntingdon 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 (5 lobolly 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 control “uptake” for each site and solution concentration. Uptake rates are reported in units of micrograms of nutrient per gram fresh root per hour. We used fresh weight (not dry) 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 (two levels), species (two levels), initial nutrient solution concentration (three levels), duration of the experiment (nine 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 α 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 solution concentrations were very low, and solutions exposed to roots proved indistinguishable in concentration from controls.

We also computed average uptake rates for 2-h 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 (Fig. 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 (Fig. 1). 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 5× and 10× treatments were drawn down to about the 1× level, the concentration of NH$_4^+$ in soil solution reported by Arthur and Fabey (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 (Fig. 1). Concentrations depleted very gradually over time, relative to initial conditions (controls without roots). Unlike NH$_4^+$, differences among the 1×, 5×, and 10× 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.

Nitrile concentrations, like those of Ca$^{2+}$ and Mg$^{2+}$, were not rapidly depleted (Fig. 1). Concentrations in the 5× and 10× 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 (Fig. 2).

Potassium (Fig. 1) 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 (Fig. 2).
Uptake rates of all nutrients were indistinguishable between spruce and fir ($P = 0.11$ for $\text{NO}_3^-$ 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 $\text{NH}_4^+$ ($P = 0.01$) and less so for $\text{NO}_3^-$ ($P = 0.15$) and $\text{K}^+$ ($P = 0.18$). Uptake of $\text{Ca}^{2+}$ was significantly greater at Fraser than at Loch Vale only at the $10 \times$ nutrient solution concentration ($P < 0.01$), resulting in an interaction of site and initial solution concentration ($P < 0.01$). For $\text{Mg}^{2+}$, uptake rates were higher at Fraser only at ambient solution concentrations ($P = 0.14$) and were higher at Loch Vale under the $5 \times$ 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 (Fig. 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 $\text{Ca}^{2+}$ and $\text{Mg}^{2+}$ uptake ($P < 0.01$) and $\text{NH}_4^+$ uptake ($P = 0.06$) but not for $\text{K}^+$ efflux or $\text{NO}_3^-$ 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 (Fig. 2). For $\text{NH}_4^+$, this decline could conceivably be attributed to the progressive depletion of nutrients from the solutions (Fig. 1), but for base cations, the concentrations in $5 \times$ and $10 \times$ treatments were still high at the end of long experiments (Fig. 1). The consistent near-zero uptake rates of base cations in long experiments show 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-h 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 (Fig. 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 (Fig. 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 12 species we studied (Fig. 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 (Fig. 4).

Frequency distributions of fine root diameters (Fig. 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

Table 2

<table>
<thead>
<tr>
<th>Site</th>
<th>Concentration</th>
<th>n</th>
<th>NH₄⁺</th>
<th>NO₃⁻</th>
<th>Ca²⁺</th>
<th>Mg²⁺</th>
<th>K⁺</th>
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<tbody>
<tr>
<td>Loch Vale</td>
<td>1×</td>
<td>4</td>
<td>0.07 (0.01)</td>
<td>0.023 (0.008)</td>
<td>18 (0.11)</td>
<td>0.02 (0.004)</td>
<td>−0.47 (0.13)</td>
</tr>
<tr>
<td>Fraser</td>
<td>1×</td>
<td>2</td>
<td>0.17 (0.02)</td>
<td>0.027 (0.013)</td>
<td>47 (0.15)</td>
<td>0.07 (0.03)</td>
<td>−0.57 (0.05)</td>
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<tr>
<td>Loch Vale</td>
<td>5×</td>
<td>4</td>
<td>0.18 (0.04)</td>
<td>0.024 (0.013)</td>
<td>63 (0.33)</td>
<td>0.12 (0.04)</td>
<td>−0.26 (0.2)</td>
</tr>
<tr>
<td>Fraser</td>
<td>5×</td>
<td>3</td>
<td>0.24 (0.06)</td>
<td>0.37 (0.16)</td>
<td>55 (0.15)</td>
<td>0.04 (0.03)</td>
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<tr>
<td>Loch Vale</td>
<td>10×</td>
<td>2</td>
<td>0.36 (0.12)</td>
<td>0.34 (0.01)</td>
<td>0.0 (0.54)</td>
<td>0.26 (0.05)</td>
<td>−0.38 (0.14)</td>
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<tr>
<td>Fraser</td>
<td>10×</td>
<td>2</td>
<td>0.41 (0.09)</td>
<td>n.a.</td>
<td>86 (0.31)</td>
<td>0.16 (0.03)</td>
<td>−0.39 (0.09)</td>
</tr>
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</table>

Uptake rates (μmol g⁻¹ h⁻¹) for short-term (2-h) experiments. Means by site and solution concentration include both spruce and fir; species did not differ significantly in uptake rates. Standard errors are given in parentheses. For nitrate, fewer observations were available (in the case of 10× at Fraser, we have none) and we report experiments up to 4 h in duration.
study (0.1−0.4 μmol g\textsubscript{rdw} h\textsuperscript{-1} for 2-h experiments, Table 2) was lower than uptake by Norway spruce (0.6 μmol g\textsubscript{rdw} h\textsuperscript{-1}, Gessler et al., 1998), sugar maple (0.1−1.1 μmol g\textsubscript{sdw} h\textsuperscript{-1}, McFarlane and Yanai, 2006) and American beech (0.5 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Gessler et al., 1998) trees in the field and loblolly pine (1 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Lucash et al., 2008) and Norway spruce seedlings (0.3 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Eltrop and Marschner, 1996) in sand culture. However, McFarlane and Yanai (2006) reported similar NH\textsubscript{4}\textsuperscript{+} uptake rates by Norway spruce (0.01−0.2 μmol g\textsubscript{sdw} h\textsuperscript{-1} and red pine (0−0.5 μmol g\textsubscript{sdw} h\textsuperscript{-1}) to those shown in Table 2. The same study reported higher NO\textsubscript{3}\textsuperscript{−} uptake rates (up to 0.2 μmol g\textsubscript{sdw} h\textsuperscript{-1} for red pine) than were observed in this study (0.02−0.04 μmol g\textsubscript{sdw} h\textsuperscript{-1}).

Converted to a dry-weight basis, our NH\textsubscript{4}\textsuperscript{+} uptake rates (1−2 μmol g\textsubscript{rdw} h\textsuperscript{-1}) were lower than loblolly pine trees in the field (10 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Lucash et al., 2005). Similarly, in solution culture, higher rates of NH\textsubscript{4}\textsuperscript{+} uptake than those we have been reported for seedlings of loblolly pine (10 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Constable et al., 2001), sugar maple (16 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Rothstein et al., 1996; 8 μmol g\textsubscript{sdw} h\textsuperscript{-1} BassiriRad et al., 1996), American beech (9 μmol g\textsubscript{sdw} h\textsuperscript{-1}, BassiriRad et al., 1996), and quaking aspen (8−12 μmol g\textsubscript{sdw} h\textsuperscript{-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\textsubscript{4}\textsuperscript{+} uptake rates of 15, 17, and 13 μmol g\textsubscript{sdw} h\textsuperscript{-1}, respectively, at solution concentrations similar to ours (Lajtha, 1994).

Uptake rates of Ca\textsuperscript{2+}, Mg\textsuperscript{2+} and K\textsuperscript{+} were generally similar to other studies. Our Ca\textsuperscript{2+} uptake rates (1−7 μmol g\textsubscript{sdw} h\textsuperscript{-1}) were slightly lower than loblolly pine trees in the field (8 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Lucash et al., 2007) and sycamore maple (Acer pseudoplatanus L.) seedlings in hydroponics (8 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Gloser and Gloser, 2000). Magnesium uptake rates (0.1−1.2 μmol g\textsubscript{sdw} h\textsuperscript{-1}) were similar to sycamore maple seedlings in hydroponics (0.2 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Gloser and Gloser, 2000) but lower than loblolly pine trees in the field (3 μmol g\textsubscript{sdw} h\textsuperscript{-1}, Lucash et al., 2007). Uptake rates of K\textsuperscript{+} were negative (−0.6 to −3.2 μmol g\textsubscript{sdw} h\textsuperscript{-1}) and fell within the large range we found for loblolly pine trees in the field (−120 to 40 μmol g\textsubscript{sdw} h\textsuperscript{-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\textsuperscript{-2} for roots < 2 mm; Arthur and Fahey, 1992), our observed uptake rates from 1× 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\textsuperscript{2+} (60 times) and Mg\textsuperscript{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 (Kelli 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\textsuperscript{+}, is clearly not descriptive of long-term root behavior in nature. We have observed efflux of K\textsuperscript{+}, NH\textsubscript{4}\textsuperscript{+}, Mg\textsuperscript{2+}, and PO\textsubscript{4}\textsuperscript{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\textsuperscript{+} 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 averted our solutions and simulated ambient solute concentrations and pH in our soil solutions. Whatever the mechanism, we believe that it acts sufficiently consistent 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.

Engelmann spruce and subalpine fir have similar root morphology. The similarity in specific root length between the two species (Fig. 4) is consistent with their similar nutrient uptake rates. They also had the most similar frequency distribution of root diameters among the 12 tree species we studied (Fig. 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, does not 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.

Fig. 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.
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 h 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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