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**Nutrient concentrations of roots vary with diameter, depth,
and site in New Hampshire northern hardwoods**

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Abstract

Roots are important to ecosystem nutrient pools and fluxes, but they are difficult to sample for tissue analysis, especially at depth. We analyzed patterns of nutrient concentrations in live roots up to 20 mm in diameter collected from quantitative soil pits in six northern hardwood sites at the Bartlett Experimental Forest, New Hampshire, USA. Root concentrations of nitrogen, phosphorus, calcium, and magnesium were higher in the forest floor than in the mineral soil, by 23-61% in fine roots (0-1 mm and 1-2 mm in diameter). Using only samples collected from the O-horizon to characterize roots throughout the profile resulted in an average error across all elements of 16% in estimates of root nutrient contents. Within the mineral soil, there was little difference in root nutrient concentrations with depth. There were significant patterns with root diameter: N and Mg concentrations were highest in the finest roots, while Ca concentrations peaked in the 2-5 mm diameter class. One site (C8) differed from the others in having lower N but higher P, Ca, Mg, and K concentrations in roots. In summary, analyzing roots by site and diameter class is more important to accurate nutrient accounting than is analyzing roots from depth in the mineral soil, but roots in the forest floor and the mineral soil differ dramatically for some elements.

Keywords:

Carbon, nitrogen, phosphorus, calcium, magnesium, potassium

38 **Introduction**

39 Roots are very difficult to sample for tissue analysis compared to aboveground
40 vegetation (Fahey et al. 2017), but they make up an important portion of ecosystem
41 nutrient contents and nutrient turnover (Jackson et al 1997). It is especially difficult to
42 sample roots at depth; roots obtained by coring methods are restricted to the top 30 cm
43 or even less, in stony forest soils (Park et al. 2007). For this reason, it is important to
44 know whether there are systematic changes in root tissue concentrations with depth in
45 the soil. Such differences with soil depth have been described for nitrogen
46 concentrations in fine roots of sugar maple in Michigan (Pregitzer et al. 1998), in
47 hardwoods in Japan (Makita et al. 2011) and northeastern China (Wang et al. 2015), and
48 in conifer forests in British Columbia (Kimmins and Hawkes 1978) and Japan (Ugawa
49 et al. 2010). In deeply weathered tropical soils, roots have been excavated from depths
50 of several meters and characterized for biomass but not nutrient concentrations (Hertel
51 et al. 2009, Davidson et al. 2011). A study in the Ecuadorian Andes found no difference
52 in root concentrations of nitrogen, phosphorus, sulfur, calcium, magnesium or
53 potassium between organic and mineral soils, but did not test for differences with depth
54 in the mineral soil (Soethe et al. 2007). If there were a significant pattern of
55 concentration with depth, then using roots collected near the soil surface to describe all
56 the roots in the ecosystem would result in a bias in estimates of their nutrient contents.

57 Root diameter is known to be important to nutrient concentrations, with finer
58 roots generally having higher concentrations (Gordon and Jackson 2000). Again, soil
59 cores are appropriate for the collection of fine roots (< 2 mm), but collecting larger
60 roots requires more laborious collection methods. Two studies in tropical forests found
61 fine roots to be higher than coarse roots in concentrations of N, P and Mg, but Ca was

higher in coarser size classes, and K patterns differed by study (Edwards and Grubb 1982, Soethe et al. 2007). In a study of 49 species across seven sites from Siberia to tropical China, N and P concentrations decreased with increasing root order, which corresponds to increasing root diameter (Li et al. 2010). In roots collected from soil pits at the Hubbard Brook Experimental Forest in New Hampshire, N and P concentrations decreased as root diameter increased (from <0.6 mm to >10 mm), but Ca increased with increasing root diameter and K and Mg were highest in 0.6 – 1 mm roots (Fahey et al. 1988). For Ca, the bark of these roots had much higher concentration than the wood, so root concentrations by species depended on the proportion of bark to wood (Fahey et al. 1988).

The objective of this study was to describe elemental concentrations in live roots in six northern hardwood stands in the Bartlett Experimental Forest in New Hampshire. The excavation of soil pits in these sites provided access to roots of greater diameter and from greater soil depths than is normally possible to collect with traditional coring methods. We tested the importance of root diameter and soil depth in explaining variation in root concentrations of N, P, Ca, Mg, and K. We expected to find differences in concentrations as a function of root diameter, but because of the difficulty of sampling deep roots, we hoped to find only minor differences in root chemistry with soil depth. We calculated the nutrient contents of roots to evaluate the importance of information about concentration as a function of soil depth.

Methods

Site Description

We studied roots in six sites of three stand ages in the Bartlett Experimental Forest (44° 02-04' N, 71° 16-19' W), as part of a larger study on nutrient cycling during

stand development (Yanai et al. 2006, Park et al. 2007). The climate is humid continental with average annual precipitation of 1270 mm. The soils are Spodosols developed in granitic glacial drift. The O horizon (forest floor) averages 5.1 cm in depth in the sites we studied (Vadeboncoeur et al. 2012). In the U.S. Soil Taxonomy, the horizons of the forest floor are designated Oi, Oe, Oa (Soil Survey Staff 1975), corresponding to L, F, and H in the Canadian System of Soil Classification (Soil Classification Group 1998).

Forest composition around the soil pits differed by site, in part reflecting successional dynamics following forest harvest (Table 1). The young stands (age 14 and 16) were dominated by pin cherry (*Prunus pennsylvanica* L.f.) and American beech (*Fagus grandifolia* Ehrh.), followed by white birch (*Betula papyrifera* Marsh.) and yellow birch (*B. allegheniensis* Britton). The young-transitional stands (age 26 and 29) had a smaller proportion of pin cherry; red maple (*Acer rubrum* L.) was important in one of the stands. The older stands (age 114 and 121) were dominated by sugar maple (*Acer saccharum* Marsh.) and American beech.

Root Collection

In each site, roots were collected in summer 2004 from three 0.5 m² quantitative soils pits, each located in one of three replicate 0.25-ha plots in each site, resulting in pit separations of 40 to 130 m within sites. For the Oie, which can't be sieved for roots, three 100-cm² samples were cut with a template and returned to the lab for root picking. The Oa was removed and sieved through a 6-mm screen. The mineral soil was excavated by depth increment (0-10, 10-30, and 30-50 cm) and sieved through a 12-mm screen. The roots that remained on the screen were returned to the lab and refrigerated until they could be processed. Material that passed through the screen was subsampled

110 and roots picked from the sieved soil are included in our estimates of biomass. More
111 detail on root collection and processing was reported by Park et al. (2007).

112 *Root Analysis*

113 Roots were sorted, washed, dried, and weighed in 2004 as part of the earlier
114 study (Park et al. 2007). Live roots, identified by color and turgor, were sorted into size
115 classes: 0-1, 1-2, 2-5, 5-10, 10-20, and >20 mm in diameter. For the analysis of root
116 chemistry, we used the roots collected on the screens in the field or picked from the Oie
117 blocks. For the larger roots (>2 mm), these were all the roots found in the pits; for the 0-
118 1 and 1-2 mm roots, these were 34 and 85%, respectively, of the mass of roots reported
119 from the pits. Large samples were subsampled before being sorted into vitality and size
120 classes, and multiple subsamples were washed, dried, and weighed. In these cases, the
121 roots were composited for analysis in proportion to the biomass represented by each
122 sample.

123 Because it would have been prohibitively expensive to analyze every root
124 sample, we selected classes of roots to analyze across the combinations of soil depth,
125 root diameter, and site. For a comprehensive comparison of the five diameter classes,
126 we chose the 0-10 cm soil depth, which has the greatest representation of size classes.
127 This soil depth also tended to have the greatest root mass, though in the older stands,
128 there was more biomass in the 10-30 cm depth (Park et al. 2007). To compare
129 concentrations of roots from multiple soil depths, we focused on the 0-1 mm diameter
130 class, which comprises the majority of root biomass < 10 mm in diameter (Park et al.
131 2007). We also analyzed 2-5 mm diameter roots from all depths except the Oie, where
132 such coarse roots are rare. In some depth increments and size classes, to reduce the
133 analytical load, we composited roots across pits within sites for one of the sites in each

age class (C2, C4, and C9). In these three sites, we also analyzed composite samples of additional combinations of root diameter and soil depth classes. For C1, C6, and C8, we analyzed samples separately for each of the three pits in each site. In total, 174 samples were analyzed.

Roots were ground in a Willey mill (2 mm screen) and oven-dried at 60 °C before weighing out 0.25 – 1.0 g for analysis. The samples were ashed at 470 °C and dissolved in 10 mL of 6N nitric acid. The solutions were filtered, diluted to 50 mL with distilled, deionized water, and analyzed for Ca, Mg, K, and P using inductively coupled plasma optical emission spectrometry (ICP-OES) (PE-3300DV, Perkin Elmer, Shelton, CT). For N analysis, samples were pulverized (Zenith/DMG Variable Speed Dental Amalgamator, Englewood, NJ) and analyzed by dry combustion (Vario EL, Elementar Americas, Mount Laurel, NJ).

We used the C content of roots to evaluate contamination of root samples by adhering soil. Roots from the O horizon have little mineral material associated with them, compared to roots from greater depths. There was a slight but significant difference in C concentration with depth ($p = 0.02$ for the main effect of depth in ANOVA): the average C concentration of roots was 49% in the Oa and 47% in the mineral soil. There were no differences with depth within the mineral soil. We did not correct for soil contamination of roots, as the difference amounted to only 2% of the mass of the roots.

Statistical Analysis

Root concentrations were compared separately for each element using analysis of variance with repeated measures of the soil pits using proc mixed in SAS. We assessed the effect of site (6 levels), root diameter (5 levels) and soil depth (5 levels),

158 with the 3 pits nested within site. We included all the two-way interaction terms in the
159 model. We repeated the analysis after excluding one site (C8) from the above analyses
160 to assess the degree to which it controlled the results by site.

161 Least-square means were used to compare sites, root diameter classes within
162 depths, and soil depths for each root diameter class. For the main effect of root diameter
163 on N, P, K, Ca and Mg concentrations, coarse (5-10 and 10-20 mm) and fine roots (0-1
164 mm and 1-2 mm) were compared with a contrast statement. To describe the effect of
165 soil depth on coarse and fine root concentrations, we compared weighted concentrations
166 from the O horizon with those from the mineral soil. We report the difference as a
167 percentage of the mineral soil concentration.

168 To test the effect of stand age (3 levels), we included root diameter (5 levels),
169 soil depth (4 level) and their interactions, with sites nested within age, in a repeated-
170 measures ANOVA. The Oie was omitted from this analysis because of a lack of
171 replication in the youngest age class. We repeated the analysis of stand age after
172 excluding one site (C8) from the analysis to assess the degree to which it controlled the
173 results by stand age.

174 ***Calculation of Root Nutrient Content***

175 To calculate root nutrient contents, we used the mass of roots previously
176 reported (Park et al. 2007) and the nutrient concentrations we measured from a subset of
177 those samples. For the 174 samples that were analyzed, we used the observed
178 concentrations. Because we did not analyze concentrations for every combination of
179 root size and depth classes, we estimated the other nutrient concentrations using the
180 coefficients from the repeated-measures ANOVA described above, using proc plm for
181 postfitting in SAS. In addition, there were two classes of roots that were too rare to be

182 included in the ANOVA, but which needed to be estimated for nutrient contents. First,
183 to estimate concentrations in roots >1 mm in diameter in the Oie, we assigned
184 concentrations from the same diameter of roots in the Oa horizon. Second, roots > 10
185 mm in diameter were analyzed for concentration only at 0-10 cm depth, but
186 occasionally this size class occurred at other depths. For C, N, and P, we used root
187 concentrations for this size class from the 0-10 cm depth roots, because these elements
188 showed a strong relationship with diameter. For Ca, Mg, and K, we used concentrations
189 from the 5-10 mm diameter class from the same depth, because these elements showed
190 a stronger trend with depth (Fig. 2). Root nutrient content was calculated as the product
191 of root biomass and root chemical concentration. We included roots up to 100 mm in
192 diameter, for completeness, although roots > 20 mm in diameter were spatially highly
193 variable in this data set as they are not adequately sampled by quantitative soil pits
194 (Yanai et al. 2006).

195 To quantify the error introduced by using root concentrations from surficial
196 horizons to calculate root nutrient contents, we compared estimates of the nutrient
197 content of roots up to 20 mm in diameter based on all our data (described above) with
198 estimates that used concentration data from only the Oa horizon or only the surface 10
199 cm of the mineral soil. We compared the estimates based on the reduced data sets to the
200 estimates based on all our data for each of the six sites, using the three soil pits within
201 each site as replicates.

202 **Results**

203 ***Concentrations vary with root diameter***

204 Concentrations varied significantly with root diameter for N ($p < 0.001$), Ca ($p <$
205 0.001), Mg ($p < 0.001$), and K ($p = 0.01$) (Table 2). For N, Mg, and K, fine roots were

206 higher in concentration, by 80% for N, 49% for Mg, and 13% for K, comparing < 2 mm
207 roots to roots 5-20 mm in diameter (Fig. 1). For Ca, in contrast, fine roots had
208 concentrations 10% lower than the coarse roots, and the peak Ca concentrations
209 occurred in the 2-5 mm diameter class. For P, the effect of root diameter was much
210 stronger if site C8 was excluded from the analysis. Compared to coarse roots, fine roots
211 were 62% higher in concentration with all sites included P ($p = 0.10$), but 91% higher
212 excluding C8 ($p = 0.001$), which was high in concentrations of P and other elements, as
213 described below.

214 The effect of diameter on concentration depended on depth for three elements.
215 For N ($p < 0.001$), fine roots were higher N concentrations than coarse roots at all
216 depths, but the differences between fine and coarse roots were greater in the Oa horizon
217 (120%) than in the 30-50 cm mineral soil depth (21%) ($p < 0.01$). For K, there was a
218 reversal of the difference with depth ($p = 0.03$): fine roots were 93% higher in K
219 concentration than coarse roots at 30-50 cm ($p < 0.01$), but in the Oa horizon, the fine
220 roots had 8% lower concentration ($p = 0.23$). For Ca, fine roots were 15-23% lower in
221 Ca concentration than coarse roots at 0-10, 10-30 and 30-50 cm ($p < 0.01$), but in the Oa
222 horizon, the fine roots had 16% higher concentration ($p = 0.002$).

223 *Concentrations vary with soil depth*

224 There were important differences in the nutrient concentrations of roots as a
225 function of soil depth (Fig. 1, Table 2), with significant declines in concentration with
226 depth for N ($p < 0.001$), P ($p < 0.001$), Ca ($p < 0.001$), and Mg ($p \leq 0.006$) but not K (p
227 ≥ 0.67). For fine roots (0-1 mm and 1-2 mm), concentrations in the O horizons were
228 40% higher for N ($p = 0.01$), 61% higher for P ($p < 0.001$), 56% higher for Ca ($p =$
229 0.002) and 23% higher for Mg ($p = 0.02$) than those in the mineral soil (Fig. 1). For

coarse roots (5-10 and 10-20 mm), the differences with soil depth were not significant for any element.

Concentration patterns with stand age and site

The roots we studied were collected in replicate stands of three ages. There were no significant differences in root nutrient concentrations with stand age ($p \geq 0.17$).

There was one site, C8, that differed significantly from the others for all the nutrients. For N ($p < 0.01$), this site was significantly lower than the others. For P ($p = 0.01$), Ca ($p = 0.008$), Mg ($p < 0.001$), and K ($p = 0.02$), roots in C8 had significantly higher concentrations than roots in other sites. When C8 was removed from the analysis, site was not significant for any element ($p > 0.06$).

Some of the other effects we observed depended on this site. The significance of diameter effects on K and P differed with and without C8 (Table 2). Including all sites, diameter was significant for K ($p = 0.01$) but not P ($p = 0.10$). Excluding site C8, diameter was significant for P ($p = 0.001$) but not K ($p = 0.11$). The significant interactions of depth and diameter on Ca and K concentrations, described above, were not very significant without C8 ($p = 0.09$ and 0.08 , respectively).

Root nutrient content

Across the six sites, the elemental contents of roots < 20 mm in diameter in the whole soil profile averaged 7.4 g m^{-2} for Ca, 4.3 g m^{-2} for K, 1.1 g m^{-2} for Mg, 13.9 g m^{-2} for N, 0.76 g m^{-2} for P, and 851 g m^{-2} for C (Table 3). The coefficient of variation of elemental contents across sites was the largest for P and N (both 36%) and smallest for C (23%). With the exception of Ca, roots < 1 mm accounted for a greater fraction of total root nutrient contents than their mass or C contents, because they had higher

253 nutrient concentrations than coarser roots (Table 3, Fig. 2). For example, 55% of N was
254 in the < 1 mm roots, on average, although this size class accounted for 44% of the total
255 root mass < 20 mm in diameter. For both Mg and P, the fraction found in the < 1 mm
256 roots was 50%. However, for Ca, which occurs at higher concentration in coarser roots,
257 the portion of root nutrient contents in the < 1 mm size class averaged only 37%.

258 We tested the importance of sampling roots at depth by calculating the nutrient
259 contents of roots up to 20 mm in diameter in our six sites based on roots from various
260 depth combinations (Fig. 2). The biggest discrepancy between root nutrient content
261 prediction methods occurred between using concentrations of roots only in the Oa and
262 the best estimates using all our data. For N, the average error across the three soil pits
263 ranged from 11-28%, depending on the site. For P, this range was 1-58% and for Ca, -3-
264 68%. For Mg and K, using roots from the Oa to represent the whole profile agreed
265 within -12-29% (Mg) or -16-29% (K), which is consistent with a lack of significant
266 variation in concentrations with depth (Table 2). We also compared the root nutrient
267 contents of the mineral soil based on sampling only from the 0-10 cm depth. The errors
268 introduced by this sampling scheme were smaller: -7-2% for N, -45-2% for P, -13-30%
269 for Ca, -23-2% for Mg, and -13-12% for K. Because fewer roots occur at depth than in
270 the surface horizons, the difference in the nutrient content of roots calculated using data
271 only from superficial roots (Fig. 2) was smaller than the difference in concentration
272 (Fig. 1).

273 Discussion

274 *Patterns with root diameter*

275 In aboveground tissues, nutrient concentrations are generally lowest in boles and
276 higher in branches and twigs, because wood is low in nutrients. Nutrient concentrations

of roots of different diameters have been compared at other northern hardwood sites, with most elements usually higher in concentration in the finest roots. At Huntington Forest, in the Adirondacks, sugar maple and beech had higher concentrations of N, P, and Mg in finer (0-1 mm) than coarser (2-5 mm) roots (Park and Yanai 2009), as was the case in this study. Similarly, studies of N as a function of root order have found the highest concentrations in the most distal roots, with diameters ranging from <0.2 to >3 mm in diameter for ash and sugar maple in Michigan (Pregitzer et al. 1997) and for ash and larch in northeastern China (Jia et al. 2013). At Hubbard Brook in the White Mountains, however, fine roots (<0.6 mm, all species combined) had lower Mg concentrations than small woody roots (0.6-10 mm) in sugar maple, beech, yellow birch, and red spruce, although other nutrient concentrations were higher in the finer roots (Fahey et al. 1988).

Calcium peaked at intermediate diameters in our data set (Fig. 1), which was also the case in a study of black spruce, Jack pine, and sugar maple in Quebec, in which Ca concentrations peaked in roots 0.2-0.5 mm and 0.5-1 mm, then decreased with diameter to >10 mm (Ouimet et al. 2008). In contrast, roots of sugar maple, yellow birch, American beech, and red spruce at Hubbard Brook, Ca concentrations increased up to roots > 10 mm, Fahey et al. 1988). Some studies that have found Ca to increase with root diameter have not sampled roots >5 mm (Wargo et al. 2003, Park 2006, Park and Yanai 2009). Clearly, where changes with diameter are non-linear, observations of trends with root diameter will depend on which part of the diameter range is observed.

For K, we did not find a consistent difference between fine and coarse roots, but rather an interaction between depth and diameter (Table 2, Fig. 1). The Hubbard Brook data set shows coarser roots (>10 mm) to be lower in K concentration than finer roots

301 (Fahey et al. 1988), which we observed at 30-50 cm depth. In a cross-site comparison
302 that included Sleepers River and Cone Pond as well as Hubbard Brook (Park 2006),
303 roots from softwood and hardwood stands at all three sites had higher K concentrations
304 in the 1-2 mm diameter class than in two finer size classes, but coarser roots were not
305 studied (Park 2006). The generalization that woody roots are lower in nutrients than
306 finer roots is far from universal.

307 *Patterns with depth*

308 Declines in root concentrations of N with soil depth have been well documented
309 (Kimmins and Hawkes 1978, Pregitzer et al. 1998, Ugawa et al 2010). In our sites, we
310 found impressive declines in N and P in roots with depth, with fine roots in the forest
311 floor having concentrations 40 to 60% higher than in the mineral soil. These elements
312 are likely to be most limiting to forest growth and most tightly conserved, with
313 mineralization of organic forms in the forest floor playing an important role in nutrient
314 conservation. Roots also differ in function with depth, and a greater concentration of
315 proteins, which are high in N, is presumably of more value near the soil surface, where
316 more nutrient uptake occurs, than at depth, where roots may be serving more for water
317 than nutrient uptake.

318 The base cations Ca, Mg, and K had differing behaviors in our study, although
319 these elements are cycled through cation exchange, and weathering sources originate in
320 the mineral soil. Specifically, Ca declined most strongly, Mg was intermediate, and K
321 was not sensitive to soil depth. Scots pine in England had declining concentrations of
322 Ca and Mg from 0 to 60 cm depth in the mineral soil (Vanguelova et al. 2005). Norway
323 spruce in Germany had 27% higher concentrations of Ca in roots in organic than

324 mineral soil, while N, P, and K showed less significant effects of soil depth across the
325 four sites sampled (Borken et al. 2007).

326 The high cost of sampling roots deep in the soil profile means that it may not be
327 practical to include this source of variation when constructing nutrient budgets. The
328 differences in nutrient concentrations with depth within the mineral soil were generally
329 small, but because of the large differences between the forest floor and mineral soil, it
330 would be wise to sample roots from at least the upper mineral soil in ecosystems such as
331 these.

332 *Patterns with site*

333 One of the sites we studied (C8) differed significantly from the others in the
334 concentrations of nutrients in roots. Differences in root chemistry across sites forested
335 with northern hardwoods have been reported by other studies. For example, in Quebec,
336 Ca, Mg, and K concentrations in roots were higher in sites with higher soil base
337 saturation (Ouimet et al. 2008). Similarly, roots had high Ca, Mg, and K in at Sleepers
338 River, VT, a site with high base saturation, compared to Hubbard Brook and Cone Pond,
339 while P concentrations were highest at Hubbard Brook (Park 2006). At Huntington
340 Forest, NY, catchments with contrasting soils differed in root chemistry by a factor of 5
341 for Ca and 2 for Mg, whereas K concentrations showed no trends with soil nutrient
342 availability (Park and Yanai 2009). We have data on exchangeable bases in our soil pits
343 (Schaller et al. 2010), but they do not explain the high concentrations of Ca, Mg and K
344 in site C8. The high P concentrations in roots in C8 are consistent with high P
345 concentrations in soil and foliage at that site (See et al. 2015), though site C9 had even
346 higher soil P (Vadeboncoeur et al. 2014). Low N in roots at this site is consistent with

347 high P availability, as this site is likely N limited, while the rest are more P limited
348 (Gonzales 2017).

349 Species differences in root chemistry were not addressed in this study but could
350 contribute to variation across sites. Sugar maple, which was important only in the two
351 mature sites (Table 1), was reported to be high in P at Hubbard Brook (Fahey et al.
352 1988). However, at Huntington Forest, where beech and sugar maple were studied in
353 contrasting sites, species differences were small compared to site differences (Park and
354 Yanai 2009). Site C8 does not differ dramatically in species composition from the other
355 sites in the study (Table 1).

356 Tree health might also explain some variation associated with site; P and Ca in
357 fine roots were lower in declining sugar maples in Quebec than in healthy trees (Ouimet
358 et al. 1995). Sugar maples in our sites were healthy, but beech, which comprised from
359 12 to 45% of basal area in our stands (Table 1) suffered from beech bark disease.

360 ***Recommendations***

361 The results from this study confirm the importance of sampling roots by site,
362 since concentrations of nutrients in roots varied by a factor of two, even in similar
363 forests at nearby sites. Variation in root chemistry with depth was important, with roots
364 in the forest floor having significantly different concentrations than roots at depth,
365 which suggests that roots should be sampled in both organic and mineral horizons, in
366 forests where the forest floor is important. In the sites we studied, differences with depth
367 within the mineral soil were not as important, suggesting that sampling in the mineral
368 soil could be focused on roots near the surface, which are easier to collect. In other
369 ecosystem types, both the distribution of root biomass with depth and the possibility of

370 concentration differences with depth need to be considered in evaluating root sampling
371 regimes.

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Table 1. Basal area by species of trees near the soil pits from which roots were collected, based on trees >2 cm dbh within 3 m and trees > 10 cm dbh within 6 m of the center of the pit; species are listed in decreasing order of importance.

Site Stand Age (years) *	Basal Area (m ² ha ⁻¹)					
	C1 14	C2 16	C4 26	C6 29	C8 121	C9 114
American beech (<i>Fagus grandifolia</i>)	2	6.5	3.5	8	7.3	12.7
Sugar maple (<i>Acer saccharum</i>)		0.3			16.3	19.1
Pin cherry (<i>Prunus pennsylvanica</i>)	4.3	1.8	3.6	7.3		
White birch (<i>Betula papyrifera</i>)	3	1.7	6	3.7	1.5	2.3
Yellow birch (<i>B. alleghaniensis</i>)	1.2	2	5.8	1.1		4.6
Red maple (<i>A. rubrum</i>)	0.2	1.5	3.7	8.9	2.2	
Aspen (<i>Populus spp.</i>)			5.2			
Eastern hemlock (<i>Tsuga canadensis</i>)		0.3		2.1	0.3	
Striped maple (<i>A. pennsylvanicum</i>)	0.2	0.04	0.2	0.4		
Ash (<i>Fraxinus spp.</i>)	0.1	0.3				
Other			0.7			
Total	11.0	14.5	28.8	31.4	27.6	38.8

* Stand ages pertain to 2004, when the roots were collected.

Table 2. Analysis of variance of root nutrient concentration as a function of site, soil depth, and root diameter

Based on all 6 sites

Elements	df	N		P		K		Ca		Mg		C	
		F value	P value	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
site	5	3.79	0.02	2.82	0.05	1.25	0.34	2.42	0.08	3.83	0.02	2.08	0.12
soil depth	4	35.61	<0.001	11.98	<0.001	0.59	0.67	19.85	<0.001	3.85	0.006	6.02	<0.001
root diameter	4	38.52	<0.001	2.03	0.10	3.43	0.01	33.84	<0.001	7.72	<0.001	1.35	0.26
site x depth	19	3.49	<0.001	2.02	0.01	1.34	0.18	1.84	0.03	2.99	<0.001	2.04	0.01
site x dia	20	1.03	0.43	1.83	0.03	1.59	0.07	1.96	0.02	1.52	0.09	1.10	0.36
depth x dia	9	4.72	<0.001	1.34	0.23	2.25	0.03	2.56	0.01	1.68	0.10	1.73	0.09
Error	112												

Based on 5 sites, excluding site C8.

Elements	df	N		P		K		Ca		Mg		C	
		F value	P value	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
site	4	1.54	0.25	1.45	0.27	0.87	0.51	0.79	0.55	2.66	0.08	1.62	0.23
soil depth	4	36.37	<0.001	25.77	<0.001	0.36	0.84	14.14	<0.001	8.34	<0.001	4.30	0.004
root diameter	4	30.47	<0.001	4.93	0.001	1.99	0.11	25.15	<0.001	8.47	<0.001	2.10	0.09
site x depth	15	2.56	0.004	1.93	0.03	1.07	0.40	1.54	0.11	2.85	0.001	2.29	0.01
site x dia	16	0.81	0.68	1.82	0.04	1.53	0.11	2.22	0.01	1.05	0.42	1.21	0.28
depth x dia	9	3.29	0.002	1.56	0.14	1.78	0.08	1.77	0.09	1.64	0.12	1.21	0.30
Error	89												

499 Table 3a. Root nutrient contents (g m⁻³) by root diameter (Mean±SE).

C							N					
Elements												
Site	C1	C2	C4	C6	C8	C9	C1	C2	C4	C6	C8	C9
0-1	427±155	327±29	457±31	363±35	408±64	511±16	6.3±2.0	6.3±0.8	8.6±0.8	7.9±1.2	7.6±0.7	12.1±0.7
1-2	55±24	55±12	114±35	73±6	58±5	95±7	0.7±0.3	0.7±0.2	1.7±0.6	1.0±0.1	0.7±0.1	1.8±0.1
2-5	67±11	105±8	148±20	130±24	101±20	171±7	0.8±0.1	1.5±0.1	2.3±0.4	2.3±0.5	1.3±0.2	3.4±0.1
5-10	96±14	61±9	131±49	178±33	120±19	177±26	0.9±0.1	0.6±0.1	2.0±0.8	2.5±0.7	1.3±0.2	3.1±0.4
10-20	91±43	69±31	249±125	262±46	111±41	163±35	0.7±0.3	0.4±0.2	3.5±2.1	2.3±0.2	1.2±0.4	2.0±0.6
20-100	687±341	198±142	423±356	121±63	7±7	491±262	5.7±3.1	1.5±1.1	5.3±4.4	1.0±0.5	0.1±0.1	5.8±2.9

P							Ca					
Elements												
Site	C1	C2	C4	C6	C8	C9	C1	C2	C4	C6	C8	C9
0-1	0.35±0.14	0.28±0.04	0.30±0.02	0.42±0.04	0.56±0.04	0.55±0.10	2.8±1.2	2.1±0.6	2.7±0.2	2.8±0.2	3.6±0.5	3.4±0.1
1-2	0.04±0.01	0.06±0.01	0.07±0.02	0.06±0.01	0.09±0.01	0.07±0.01	0.4±0.1	0.4±0.1	0.9±0.3	0.5±0.01	0.6±0.04	0.9±0.1
2-5	0.05±0.01	0.07±0.01	0.09±0.01	0.10±0.02	0.12±0.02	0.13±0.01	0.8±0.2	1.3±0.1	2.1±0.2	1.4±0.3	1.5±0.3	2.5±0.3
5-10	0.07±0.01	0.06±0.01	0.08±0.02	0.20±0.05	0.19±0.04	0.10±0.01	0.6±0.2	0.4±0.03	1.1±0.3	1.4±0.4	1.6±0.2	1.7±0.2
10-20	0.04±0.03	0.02±0.01	0.17±0.10	0.13±0.04	0.28±0.14	0.05±0.03	0.6±0.3	0.6±0.3	2.4±1.4	2.2±0.1	1.3±0.4	1.6±0.4
20-100	0.35±0.20	0.14±0.13	0.18±0.13	0.06±0.03	0.02±0.02	0.05±0.02	4.1±1.7	1.4±0.9	3.4±2.7	0.8±0.4	0.1±0.1	4.6±2.4

Mg							K					
Elements												
Site	C1	C2	C4	C6	C8	C9	C1	C2	C4	C6	C8	C9
0-1	0.54±0.20	0.44±0.13	0.50±0.02	0.43±0.05	0.82±0.12	0.76±0.08	2.0±0.8	1.4±0.3	2.1±0.2	1.7±0.2	2.7±0.7	2.7±0.5
1-2	0.06±0.02	0.07±0.03	0.12±0.03	0.05±0.01	0.10±0.01	0.14±0.01	0.3±0.1	0.4±0.1	0.6±0.1	0.3±0.04	0.5±0.1	0.5±0.1
2-5	0.09±0.02	0.15±0.02	0.18±0.02	0.13±0.02	0.16±0.04	0.27±0.02	0.4±0.1	0.6±0.05	0.8±0.1	0.6±0.1	0.7±0.2	0.9±0.1
5-10	0.10±0.04	0.06±0.01	0.14±0.04	0.16±0.04	0.21±0.03	0.20±0.02	0.4±0.04	0.3±0.04	0.5±0.1	0.7±0.1	0.8±0.2	0.8±0.1
10-20	0.09±0.05	0.07±0.04	0.28±0.15	0.22±0.04	0.20±0.08	0.18±0.04	0.4±0.2	0.4±0.2	1.0±0.4	1.1±0.3	0.6±0.2	0.7±0.04
20-100	0.69±0.33	0.20±0.12	0.37±0.30	0.10±0.05	0.01±0.01	0.64±0.43	3.9±1.9	1.0±0.6	1.6±1.2	0.5±0.3	0.04±0.04	2.3±1.5

500

501 Table 3b. Root nutrient contents (g m⁻³) by soil depth (Mean±SE).

C							N					
Elements												
Site	C1	C2	C4	C6	C8	C9	C1	C2	C4	C6	C8	C9
Oie	560±323	2±1	83±69	73±21	14±1	233±208	4.7±2.8	0.4±0.1	1.7±1.2	1.8±0.1	0.3±0.03	3.7±2.9
Oa	98±44	225±93	292±77	308±139	151±54	339±175	1.1±0.3	2.9±1.0	4.7±0.6	4.3±2.1	2.7±0.9	6.7±3.1
0-10	355±68	306±64	537±209	340±30	255±41	349±84	4.1±0.7	3.6±0.1	7.8±2.5	4.6±0.2	3.8±0.5	5.9±1.1
10-30	160±54	131±20	341±74	202±21	259±13	455±57	2.2±0.7	1.8±0.1	5.3±1.1	2.9±0.6	3.7±0.3	7.9±0.9
30-50	187±150	82±22	109±18	67±11	90±19	146±36	2.1±1.7	1.2±0.4	1.5±0.2	1.1±0.2	1.1±0.2	2.5±0.6
50-C	41±15	22±17	95±47	14±14	26±17	69±25	0.5±0.2	0.3±0.3	1.4±0.7	0.3±0.3	0.3±0.2	1.2±0.4
C	21±7	32±17	66±27	123±29	10±4	15±6	0.3±0.1	0.4±0.2	1.0±0.4	2.0±0.5	0.1±0.1	0.3±0.1

P							Ca					
Elements												
Site	C1	C2	C4	C6	C8	C9	C1	C2	C4	C6	C8	C9
Oie	0.31±0.23	0.36±0.19	0.09±0.06	0.12±0.03	0.02±0.002	0.14±0.09	3.3±1.8	0.4±0.2	0.9±0.7	0.8±0.3	0.3±0.0	2.7±2.4
Oa	0.06±0.01	0.22±0.12	0.17±0.01	0.28±0.11	0.29±0.11	0.17±0.05	0.8±0.2	2.1±0.7	3.2±0.8	2.2±0.9	1.8±0.7	3.4±1.9
0-10	0.23±0.06	0.12±0.005	0.25±0.12	0.23±0.05	0.30±0.05	0.18±0.02	3.1±0.9	2.1±0.3	3.9±1.1	3.3±0.3	2.5±0.4	2.9±0.8
10-30	0.12±0.04	0.11±0.01	0.19±0.04	0.16±0.02	0.46±0.10	0.24±0.06	1.1±0.5	0.7±0.1	2.7±0.7	1.4±0.3	3.1±0.1	4.0±0.2
30-50	0.13±0.10	0.08±0.02	0.08±0.01	0.07±0.01	0.14±0.03	0.12±0.04	0.9±0.7	0.6±0.3	0.8±0.1	0.5±0.05	0.8±0.1	1.1±0.3
50-C	0.03±0.01	0.02±0.02	0.06±0.03	0.01±0.01	0.03±0.02	0.06±0.02	0.2±0.1	0.2±0.1	0.7±0.3	0.1±0.1	0.2±0.1	0.6±0.2
C	0.02±0.01	0.03±0.01	0.05±0.02	0.11±0.01	0.01±0.01	0.02±0.01	0.1±0.03	0.2±0.1	0.4±0.2	0.8±0.2	0.1±0.05	0.1±0.04

Mg							K					
Elements												
Site	C1	C2	C4	C6	C8	C9	C1	C2	C4	C6	C8	C9
Oie	0.57±0.32	0.36±0.19	0.13±0.11	0.10±0.03	0.02±0.002	0.49±0.43	3.3±1.8	0.4±0.2	0.3±0.2	0.2±0.1	0.1±0.01	1.6±1.5
Oa	0.12±0.04	0.30±0.12	0.40±0.12	0.30±0.13	0.29±0.11	0.33±0.13	0.6±0.2	1.3±0.5	1.7±0.4	1.3±0.6	0.8±0.2	1.5±0.6
0-10	0.39±0.07	0.28±0.0	0.40±0.11	0.30±0.05	0.45±0.06	0.37±0.02	1.8±0.4	1.2±0.2	1.8±0.2	1.3±0.4	1.8±0.4	1.3±0.1
10-30	0.20±0.07	0.15±0.03	0.36±0.10	0.20±0.01	0.50±0.01	0.63±0.08	0.8±0.3	0.6±0.1	1.6±9.2	0.9±0.03	1.8±0.1	2.2±0.5
30-50	0.21±0.17	0.14±0.08	0.13±0.03	0.06±0.01	0.18±0.03	0.22±0.07	0.7±0.6	0.4±0.2	0.6±0.04	0.4±0.1	0.7±0.2	0.8±0.3
50-C	0.05±0.02	0.02±0.01	0.11±0.05	0.01±0.01	0.05±0.03	0.11±0.05	0.2±0.1	0.1±0.1	0.4±0.2	0.1±0.1	0.2±0.2	0.4±0.2
C	0.02±0.01	0.04±0.03	0.07±0.03	0.11±0.02	0.02±0.01	0.02±0.01	0.1±0.04	0.2±0.1	0.3±0.1	0.6±0.1	0.1±0.04	0.1±0.1

502 **Figure captions**

503 Figure 1. Concentrations of C, N, P, Ca, Mg, and K in roots by diameter class and soil
504 depth in six sites at Bartlett Experimental Forest. Error bars represent the standard error
505 of three soil pits. Samples without bars represent means of three pits composited before
506 chemical analysis.

507

508 Figure 2. Nutrient content of C, N, P, Ca, Mg, and K of roots up to 20 mm in diameter
509 for six sites at Bartlett Experimental Forest based on concentration data from all the
510 roots that were analyzed (“All”) or on a subset of the data, either the roots in the Oa
511 horizon only (“Oa”) or the roots from the top 10 cm of the mineral soil (“0-10 cm”).
512 Error bars represent the standard error of three soil pits.

Figure 1.

Figure 1, cont.

Figure 1, cont.

Fig. 2.