NRC Research Press

ARTICLE

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

Ruth D. Yanai, Griffin E. Walsh, Yang Yang, Corrie A. Blodgett, Kikang Bae, and Byung Bae Park

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 (N), phosphorus (P), calcium (Ca), and magnesium (Mg) 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 potassium (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.

Key words: carbon, nitrogen, phosphorus, calcium, magnesium, potassium.

Résumé : Les racines jouent un rôle important dans les flux et les réserves de nutriments des écosystèmes, mais elles sont difficiles à échantillonner pour l'analyse de tissus, surtout en profondeur. Nous avons analysé les patrons de concentration des nutriments dans des racines vivantes d'un diamètre allant jusqu'à 20 mm, prélevées dans des fosses d'observation quantitative établies dans six stations de feuillus nordiques à la forêt expérimentale de Bartlett, dans l'État du New Hampshire, aux États-Unis. Les concentrations racinaires d'azote (N), de phosphore (P), de calcium (Ca) et de magnésium (Mg) étaient plus élevées dans la couverture morte que dans le sol minéral, de 23 à 61 % dans les racines fines (0–1 et 1–2 mm de diamètre). Le fait d'utiliser seulement les échantillons prélevés dans l'horizon O pour caractériser les racines partout dans le profil a engendré une erreur moyenne pour l'ensemble des éléments de 16 % dans les estimations de la teneur en nutriments des racines. Dans le sol minéral, il y avait peu de différence dans la concentration racinaire des nutriments selon la profondeur. Il y avait cependant des patrons significatifs selon le diamètre des racines : les concentrations de N et Mg étaient plus élevées dans les plus petites racines, tandis que la concentration de Ca était la plus élevée dans la classe de diamètre de 2–5 mm. Une station (C8) se démarquait des autres par des concentrations racinaires plus faibles de N mais plus élevées de P, Ca, Mg et de potassium (K). En résumé, pour obtenir une évaluation juste des nutriments il est plus important d'analyser les racines par station et classe de diamètre qu'en fonction de la profondeur dans le sol minéral, mais les racines dans la couverture morte et le sol minéral diffèrent grandement dans le cas de certains éléments. [Traduit par la Rédaction]

Mots-clés : carbone, azote, phosphore, calcium, magnésium, potassium.

Introduction

Roots are very difficult to sample for tissue analysis compared with aboveground vegetation (Fahey et al. 2017), but they make up an important portion of ecosystem nutrient contents and nutrient turnover (Jackson et al. 1997). It is especially difficult to sample roots at depth; roots obtained by coring methods are restricted to the top 30 cm, or even less, in stony forest soils (Park et al. 2007). For this reason, it is important to know whether there are systematic changes in root tissue concentrations with depth in the soil. Such differences with soil depth have been described for nitrogen (N) concentrations in fine roots of sugar maple (*Acer saccharum* Marsh.) in Michigan (Pregitzer et al. 1998), in hardwoods in Japan (Makita et al. 2011) and northeastern China (Wang et al. 2016), and in conifer forests in British Columbia (Kimmins and Hawkes 1978) and Japan (Ugawa et al. 2010). In deeply weathered tropical soils, roots have been excavated from depths of several metres and characterized for biomass but not nutrient concentrations (Hertel et al. 2009; Davidson et al. 2011). A study in the Ecuadorian Andes found no difference in root concentrations of N, phosphorus (P), sulfur (S), calcium (Ca), magnesium (Mg), or potassium (K) between organic and mineral soils, but it did not test for differences with depth in the mineral soil (Soethe et al. 2007). If there were a

Received 6 June 2017. Accepted 5 September 2017.

R.D. Yanai, G.E. Walsh,* Y. Yang, C.A. Blodgett, and K. Bae.† SUNY College of Environmental Science and Forestry, 210 Marshall Hall, 1 Forestry Drive, Syracuse, NY 13210, U.S.A.
B.B. Park. Department of Environment and Forest Resources, Chungnam National University, College of Agriculture and Life Sciences, 99 Daehak-ro, Yuseong-gu, Daejeon 305-764, Republic of Korea.
Corresponding author: Ruth D. Yanai (email: rdyanai@syr.edu).
*Present address: Yale University, New Haven, CT 06520, U.S.A.
†Present address: International Cooperation Division, Korea Forest Service, Government Complex-Daejeon, Bldg 1, 189 Cheongsa-ro, Seo-gu Daejeon 302-701, Republic of Korea.

Table 1. Basal area by species of trees near the soil pits from which roots were collected (sites C1, C2, C4, C6, C8, and C9), based on trees > 2 cm diameter at breast height within 3 m and trees > 10 cm diameter at breast height within 6 m of the center of the pit; species are listed in decreasing order of importance.

	Basal area ($m^2 \cdot ha^{-1}$)					
	C1 (14 years)*	C2 (16 years)	C4 (26 years)	C6 (29 years)	C8 (121 years)	C9 (114 years)
American beech (*Fagus grandifolia*)	2	6.5	3.5	8	7.3	12.7
Sugar maple (*Acer saccharum*)		0.3			16.3	19.1
Pin cherry (*Prunus pennsylvanica*)	4.3	1.8	3.6	7.3		
White birch (*Betula papyrifera*)	3	1.7	6	3.7	1.5	2.3
Yellow birch (*Betula alleghaniensis*)	1.2	2	5.8	1.1		4.6
Red maple (*Acer rubrum*)	0.2	1.5	3.7	8.9	2.2	
Aspen (*Populus* spp.)			5.2			
Eastern hemlock (*Tsuga canadensis*)		0.3		2.1	0.3	
Striped maple (*Acer pennsylvanicum*)	0.2	0.04	0.2	0.4		
Ash (*Fraxinus* spp.)	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.

significant pattern of concentration with depth, then using roots collected near the soil surface to describe all of the roots in the ecosystem would result in a bias in estimates of their nutrient contents.

Root diameter is known to be important to nutrient concentrations, with finer roots generally having higher concentrations (Gordon and Jackson 2000). Again, soil cores are appropriate for the collection of fine roots (<2 mm), but collecting larger roots requires more laborious collection methods. Two studies in tropical forests found fine roots to be higher in concentrations of N, P, and Mg than coarse roots, 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 that we studied (Vadeboncoeur et al. 2012). In the United States Soil Taxonomy, the horizons of the forest floor are designated Oi, Oe, and Oa (Soil Survey Staff 1975), corresponding to L, F, and H in the Canadian System of Soil Classification (Soil Classification Working Group 1998).

Forest composition around the soil pits differed by site, in part reflecting successional dynamics following forest harvest (Table 1). The young stands (C1 (14 years) and C2 (16 years)) 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 (*Betula allegheniensis* Britton). The young–transitional stands (C4 (26 years) and C6 (29 years)) had a smaller proportion of pin cherry; red maple (*Acer rubrum* L.) was important in one of the stands. The older stands (C8 (121 years) and C9 (114 years)) were dominated by sugar maple and American beech.

Root collection

In each site, roots were collected in summer 2004 from three 0.5 m^2 quantitative soil 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 cannot be sieved for roots, three 100 cm^2 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 and roots picked from the sieved soil are included in our estimates of biomass. More detail on root collection and processing was reported by Park et al. (2007).

Root analysis

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

Because it would have been prohibitively expensive to analyze every root sample, we selected classes of roots to analyze across the combinations of soil depth, root diameter, and site. For a comprehensive comparison of the five diameter classes, we chose

the 0–10 cm soil depth, which has the greatest representation of size classes. This soil depth also tended to have the greatest root mass, though in the older stands, there was more biomass in the 10–30 cm depth (Park et al. 2007). To compare concentrations of roots from multiple soil depths, we focused on the 0–1 mm diameter class, which comprises the majority of root biomass < 10 mm in diameter (Park et al. 2007). We also analyzed 2–5 mm diameter roots from all depths except the Oie, where such coarse roots are rare. In some depth increments and size classes, to reduce the 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 Wiley mill (2 mm screen) and oven-dried at 60 °C, and then 0.25–1.0 g samples were weighed out for analysis. The samples were ashed at 470 °C and dissolved in 10 mL of 6 mol·L^{-1} 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, PerkinElmer Inc., Shelton, Connecticut). For N analysis, samples were pulverized (Zenith/DMG Variable Speed Dental Amalgamator, Englewood, New Jersey) and analyzed by dry combustion (Vario EL, Elementar Americas Inc., Mount Laurel, New Jersey).

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 with 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 (ANOVA) with repeated measures of the soil pits using PROC MIXED in SAS (SAS Institute Inc., Cary, North Carolina). We assessed the effect of site (six levels), root diameter (five levels), and soil depth (five levels), with the three pits nested within site. We included all of the two-way interaction terms in the model. We repeated the analysis after excluding one site (C8) from the above analyses to assess the degree to which it controlled the results by site.

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

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

Calculation of root nutrient content

To calculate root nutrient contents, we used the mass of roots previously reported (Park et al. 2007) and the nutrient concentrations that we measured from a subset of those samples. For the 174 samples that were analyzed, we used the observed concentrations. Because we did not analyze concentrations for every combination of root size and depth classes, we estimated the other nutrient concentrations using the coefficients from the repeated-measures ANOVA described above, using PROC PLM for postfitting in SAS (SAS Institute Inc.). In addition, there were two classes of roots that were too rare to be included in the ANOVA but needed to be estimated for nutrient contents. First, to estimate concentrations in roots > 1 mm in diameter in the Oie, we assigned concentrations from the same diameter of roots in the Oa horizon. Second, roots > 10 mm in diameter were analyzed for concentration only at 0–10 cm depth, but occasionally this size class occurred at other depths. For C, N, and P, we used root concentrations for this size class from the 0–10 cm depth roots, because these elements showed a strong relationship with diameter. For Ca, Mg, and K, we used concentrations from the 5–10 mm diameter class from the same depth, because these elements showed a stronger trend with depth (Fig. 2). Root nutrient content was calculated as the product of root biomass and root chemical concentration. We included roots up to 100 mm in diameter, for completeness, although roots > 20 mm in diameter were spatially highly variable in this data set as they are not adequately sampled by quantitative soil pits (Yanai et al. 2006).

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

Results

Concentrations vary with root diameter

Concentrations varied significantly with root diameter for N ($p < 0.001$), Ca ($p < 0.001$), Mg ($p < 0.001$), and K ($p = 0.01$) (Table 2). For N, Mg, and K, fine roots were higher in concentration, by 80% for N, 49% for Mg, and 13% for K, comparing <2 mm diameter roots with 5–20 mm diameter roots (Fig. 1). For Ca, in contrast, fine roots had concentrations 10% lower than the coarse roots, and the peak Ca concentrations occurred in the 2–5 mm diameter class. For P, the effect of root diameter was much stronger if site C8 was excluded from the analysis. Compared with coarse roots, fine roots were 62% higher in concentration with all sites included ($p = 0.10$) but 91% higher excluding C8 ($p = 0.001$), which was high in concentrations of P and other elements, as described below.

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

Concentrations vary with soil depth

There were important differences in the nutrient concentrations of roots as a function of soil depth (Fig. 1; Table 2), with significant declines in concentration with depth for N ($p < 0.001$), P ($p < 0.001$), Ca ($p < 0.001$), and Mg ($p \leq 0.006$) but not for K ($p \geq 0.67$). For fine roots (0–1 mm and 1–2 mm), concentrations in the O horizons were 40% higher for N ($p = 0.01$), 61% higher for P ($p < 0.001$), 56%

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

		N		P		K		Ca		Mg		C	
	df	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Based on all six sites													
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 × 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 × diameter	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 × diameter	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 five sites, excluding site C8													
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 × 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 × diameter	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 × diameter	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												

Note: Bold font indicates $P < 0.05$.

higher for Ca ($p = 0.002$), 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 that 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 of the nutrients studied. 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 that 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 nutrient concentrations than coarser roots (Table 3; Fig. 2). For example, 55% of N was in the <1 mm roots, on average, although this size class accounted for 44% of the total mass of <20 mm roots. For both Mg and P, the fraction found in the <1 mm roots was 50%. However, for Ca, which occurs at higher concentrations in coarser roots, the portion of root nutrient contents in the <1 mm size class averaged only 37%.

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

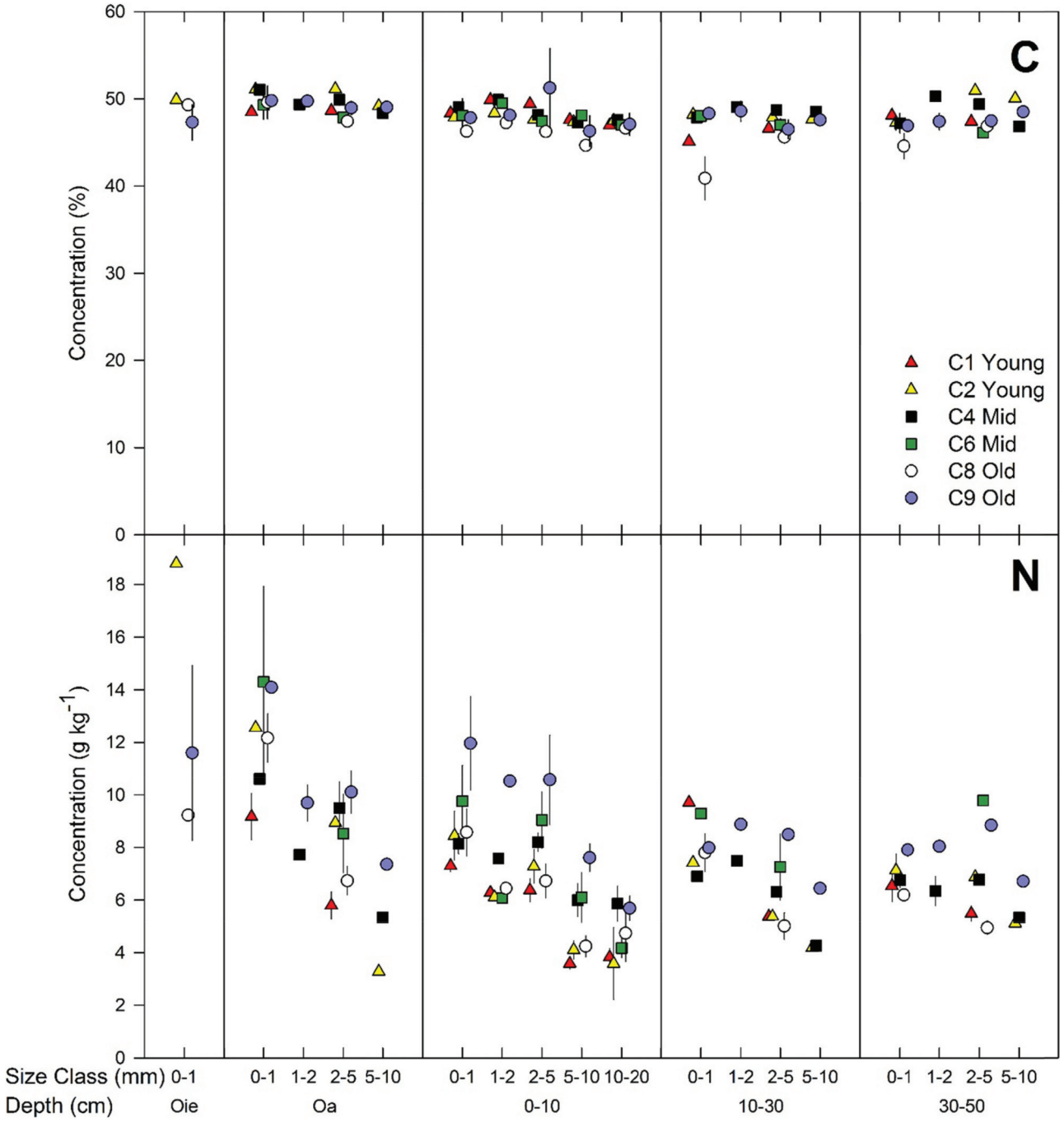
Discussion

Patterns with root diameter

In aboveground tissues, nutrient concentrations are generally lowest in boles and 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) roots than in 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 in diameter and then decreased with diameter to >10 mm (Ouimet et al. 2008). In contrast, in roots of sugar maple, yellow birch, American beech, and red spruce at Hubbard Brook, Ca concentrations increased up to roots > 10 mm in diameter (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 nonlinear, observations

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



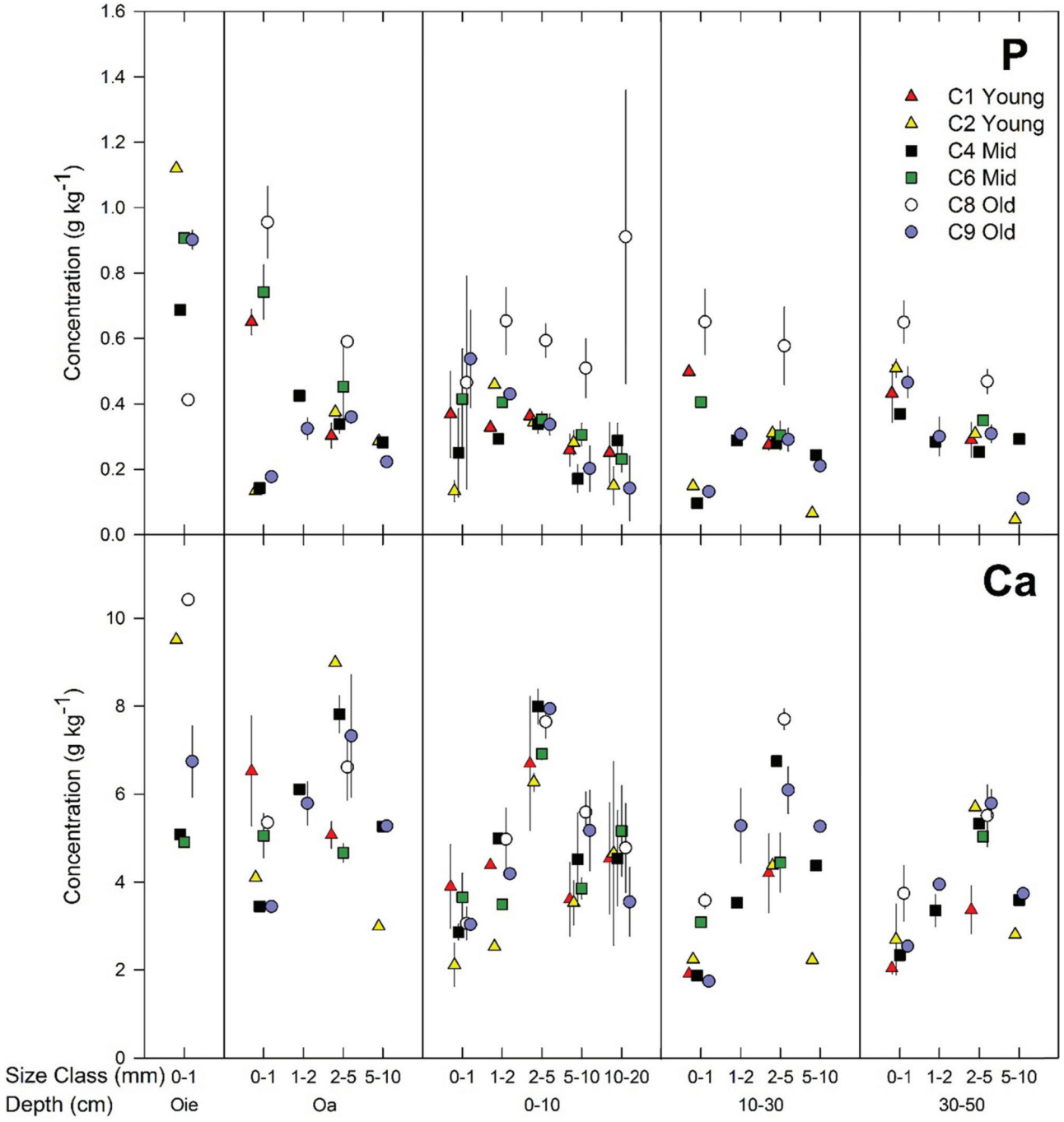
of trends with root diameter will depend on which part of the diameter range is observed.

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

Patterns with depth

Declines in root concentrations of N with soil depth have been well documented (Kimmins and Hawkes 1978; Pregitzer et al. 1998; Ugawa et al. 2010). In our sites, we found impressive declines in N and P in roots with depth, with fine roots in the forest floor having concentrations 40% to 60% higher than in the mineral soil. These elements are likely to be most limiting to forest growth and most tightly conserved, with mineralization of organic forms in the forest floor playing an important role in nutrient conserva-

Fig. 1 (*continued*).



tion. Roots also differ in function with depth, and a greater concentration of proteins, which are high in N, is presumably of more value near the soil surface, where more nutrient uptake occurs, than at depth, where roots may be serving more for water than nutrient uptake.

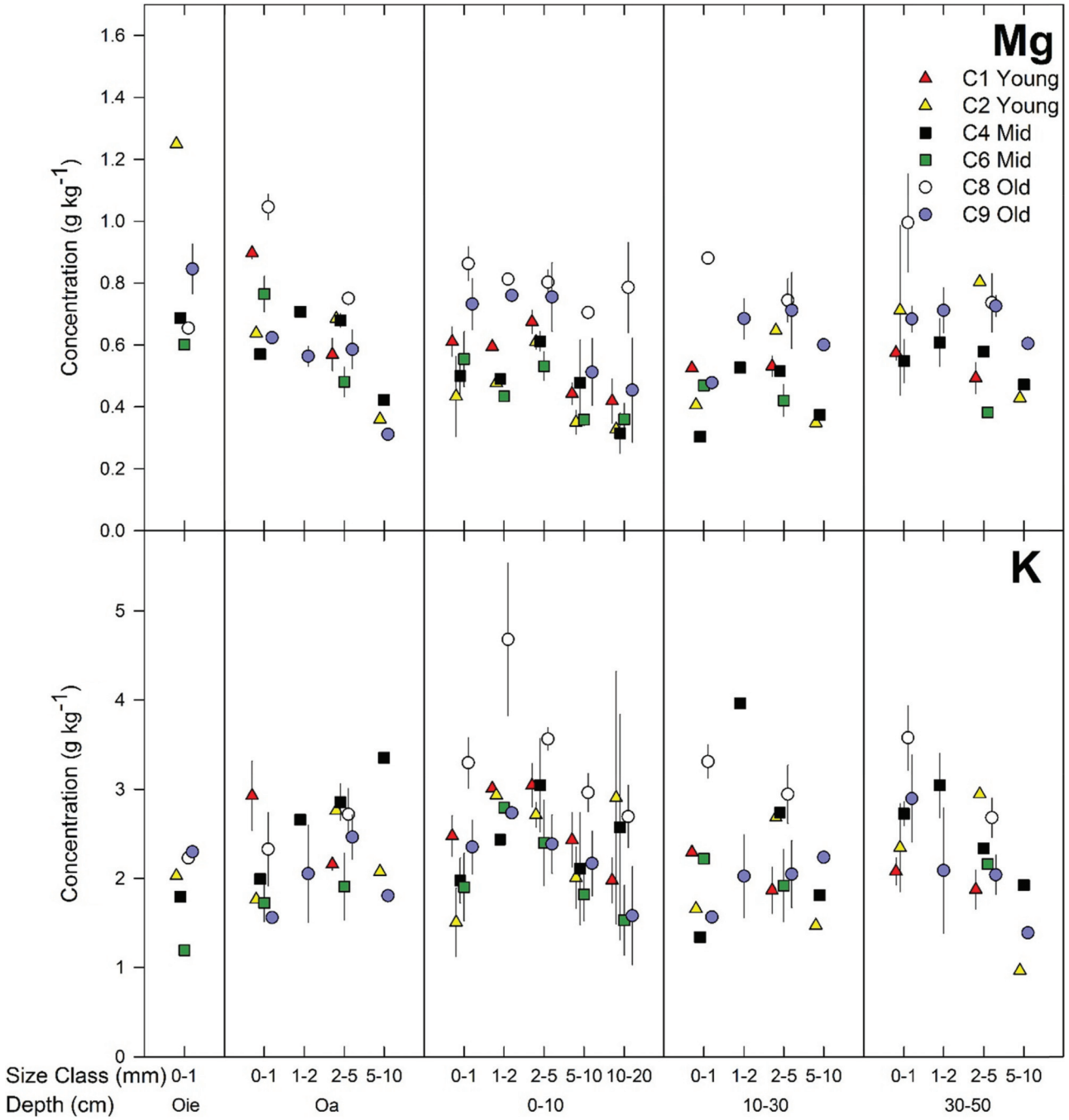
The base cations Ca, Mg, and K had differing behaviors in our study, although these elements are cycled through cation exchange, and weathering sources originate in the mineral soil. Specifically, Ca declined most strongly, Mg was intermediate, and K was not sensitive to soil depth. Scots pine in England had declining concentrations of Ca and Mg from depths of 0 to 60 cm in the mineral soil (Vanguelova et al. 2005). Norway spruce in Germany had 27% higher concentrations of Ca in roots in organic than mineral soil, while N, P, and K showed less significant effects of soil depth across the four sites sampled (Borken et al. 2007).

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

Patterns with site

One of the sites that we studied (C8) differed significantly from the others in the concentrations of nutrients in roots. Differences

Fig. 1 (*concluded*).



in root chemistry across sites forested with northern hardwoods have been reported by other studies. For example, in Quebec, Ca, Mg, and K concentrations in roots were higher in sites with higher soil base saturation (Ouimet et al. 2008). Similarly, roots had high Ca, Mg, and K in at Sleepers River, Vermont, a site with high base saturation, compared with Hubbard Brook and Cone Pond, while P concentrations were highest at Hubbard Brook (Park 2006). At Huntington Forest, New York, catchments with contrasting soils differed in root chemistry by a factor of five for Ca and two for Mg, whereas K concentrations showed no trends with soil nutrient availability (Park and Yanai 2009). We have data on exchangeable bases in our soil pits (Schaller et al. 2010), but they do not explain the high concentrations of Ca, Mg, and K in site C8. The high P concentrations in roots in C8 are consistent with high P concentrations in soil and foliage at that site (See et al. 2015), though site C9 had even higher soil P (Vadeboncoeur et al. 2014). Low N in roots at this site is consistent with high P availability, as this site is likely N-limited, while the rest are more P-limited (Gonzales 2017).

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

Table 3. Root nutrient contents (g·m^{-2}; mean ± standard error (SE)) by (*a*) root diameter (mm) and (*b*) soil depth (cm) for sites C1, C2, C4, C6, C8, and C9.

(*a*) Root nutrient contents by root diameter.

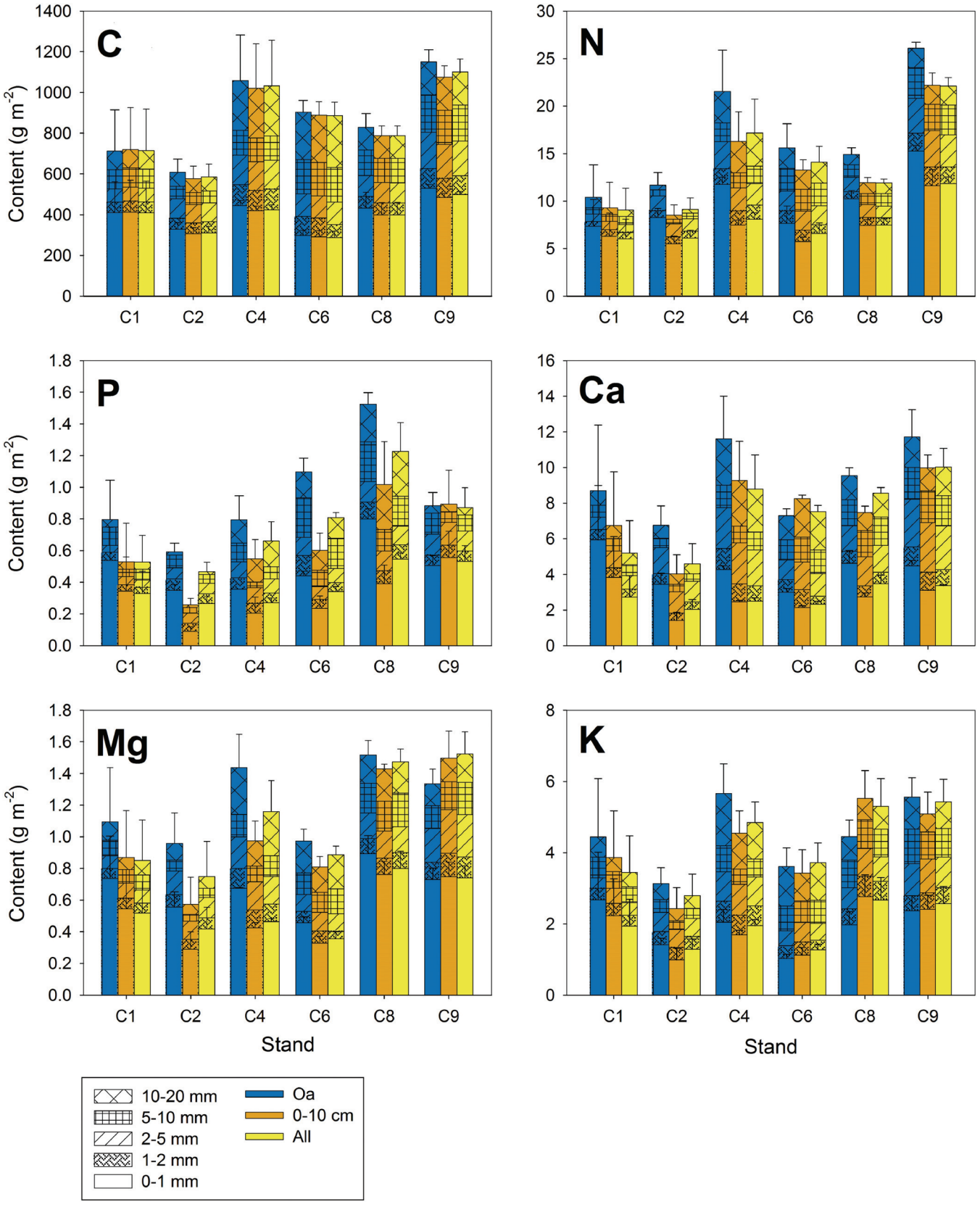
	C						N					
Root diameter	C1	C2	C4	C6	C8	C9	C1	C2	C4	C6	C8	C9
0–1	427±155	327±29	457±31	363±35	408±64	511±16	6.3±2.0	6.3±0.8	8.6±0.8	7.9±1.2	7.6±0.7	12.1±0.7
1–2	55±24	55±12	114±35	73±6	58±5	95±7	0.7±0.3	0.7±0.2	1.7±0.6	1.0±0.1	0.7±0.1	1.8±0.1
2–5	67±11	105±8	148±20	130±24	101±20	171±7	0.8±0.1	1.5±0.1	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					
Root diameter	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					
Root diameter	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

(*b*) Root nutrient contents by soil depth.

	C						N					
Soil depth	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					
Soil depth	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					
Soil depth	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

Note: Refer to the text for site details. The Oie corresponds to the L and F in the Canadian soil taxonomy, and the Oa corresponds to the H. The C horizon is the parent material.

Fig. 2. Nutrient content of C, N, P, Ca, Mg, and K of roots up to 20 mm in diameter for six sites at Bartlett Experimental Forest based on concentration data from all of the roots that were analyzed ("All") or on a subset of the data, either the roots in the Oa horizon only ("Oa") or the roots from the top 10 cm of the mineral soil ("0–10 cm"). Error bars represent the standard error of three soil pits. [Colour online.]



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

Recommendations

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

Acknowledgements

The excavation of 6.44 metric tons of soil and roots was accomplished by Robin Averbeck, Corrie Blodgett, Molly Deringer, Colin Fuss, Meredith Germain, Shefije Miftari, Nicole Shapiro, Dan Tucker, and Brian Weeks under the direction of Matt Vadeboncoeur and Steve Hamburg. Sorting roots, an equally arduous task, was accomplished by Asuka Matsuzaki, Mutsumi Nishii, Gwen Kernan, Byung Kwon Park, and Amber Knowlden. The roots were exhumed from the archives, selected, and processed by Andrew Mishler, Bill O'Neill, Christina Allison, and Griffin Walsh. The digested samples were analyzed by Sanae Kuwagaki, Dusty Wood, Sarah Worsham, and Griffin Walsh. Nitrogen was run in the lab of Christy Goodale with help from Alexis Heinz and Guin Fredriksen. Eddie Bevilacqua provided guidance on statistical analyses. This work was funded by grants from the National Science Foundation (DEB 0235650 and 0949550).

References

Borken, W., Kossmann, G., and Matzner, E. 2007. Biomass, morphology and nutrient contents of fine roots in four Norway spruce stands. Plant Soil, **292**: 79–93. doi:10.1007/s11104-007-9204-x.

Davidson, E., Lefebvre, P.A., Brando, P.M., Ray, D.M., Trumbore, S.E., Solorzano, L.A., Ferreira, J.N., Bustamante, M.M. da C., and Nepstad, D.C. 2011. Carbon inputs and water uptake in deep soils of an eastern Amazon forest. For. Sci. **57**(1): 51–58.

Edwards, P.J., and Grubb, P.J. 1982. Studies of mineral cycling in a montane rainforest in New Guinea: IV. Soil characteristics and the division of mineral elements between the vegetation and soil. J. Ecol. **70**(2): 649–666. doi:10.2307/2259929.

Fahey, T.J., Hughes, J.W., Pu, M., and Arthur, M.A. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. For. Sci. **34**: 744–768.

Fahey, T.J., Yanai, R.D., Gonzales, K.E., and Lombardi, J.A. 2017. Sampling and processing roots from rocky forest soils. Ecosphere, **8**(6): e01863. doi:10.1002/ecs2.1863.

Gonzales, K.E. 2017. Effects of calcium, nitrogen, and phosphorus fertilization on foliar nutrient dynamics of three northern hardwood tree species. M.Sc. thesis, SUNY College of Environmental Science and Forestry, Syracuse, N.Y.

Gordon, W.S., and Jackson, R.B. 2000. Nutrient concentrations in fine roots. Ecology, **81**: 275–280. doi:10.1890/0012-9658(2000)081[0275:NCIFR]2.0.CO;2.

Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., and Leuschner, C. 2009. Below- and above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi, Indonesia) as compared to neotropical forests. For. Ecol. Manage. **258**: 1904–1912. doi:10.1016/j.foreco.2009.07.019.

Jackson, R.B., Mooney, H.A., and Schulze, E.-D. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl. Acad. Sci. U.S.A. **94**: 7362–7366. doi:10.1073/pnas.94.14.7362. PMID:11038557.

Jia, S., McLaughlin, N.B., Gu, J., Li, X., and Wang, Z. 2013. Relationships between root respiration rate and root morphology, chemistry and anatomy in *Larix gmelinii* and *Fraxinus mandshurica*. Tree Physiol. **33**: 579–589. doi:10.1093/treephys/tpt040. PMID:23824239.

Kimmins, J.P., and Hawkes, B.C. 1978. Distribution and chemistry of fine roots in a white spruce – subalpine fir stand in British Columbia: implications for management. Can. J. For. Res. **8**(3): 265–279. doi:10.1139/x78-042.

Li, A., Guo, D., Wang, Z., and Liu, H. 2010. Nitrogen and phosphorus allocation in leaves, twigs, and fine roots across 49 temperate, subtropical and tropical tree species: a hierarchical pattern. Funct. Ecol. **24**: 224–232. doi:10.1111/j.1365-2435.2009.01603.x.

Makita, N., Hirano, Y., Mizoguchi, T., Kominami, Y., Dannoura, M., Ishii, H., Finér, L., and Kanazawa, Y. 2011. Very fine roots respond to soil depth: biomass allocation, morphology, and physiology in a broad-leaved temperate forest. Ecol. Res. **26**(1): 95–104. doi:10.1007/s11284-010-0764-5.

Ouimet, R., Camiré, C., and Furlan, V. 1995. Endomycorrhizal status of sugar maple in relation to tree decline and foliar, fine-roots, and soil chemistry in the Beauce region, Quebec. Can. J. Bot. **73**: 1168–1175. doi:10.1139/b95-126.

Ouimet, R., Camiré, C., Brazeau, M., and Moore, J.-D. 2008. Estimation of coarse root biomass and nutrient content for sugar maple, Jack pine, and black spruce using stem diameter at breast height. Can. J. For. Res. **38**: 92–100. doi:10.1139/X07-134.

Park, B.B. 2006. Fine root dynamics and tissue chemistry across a calcium gradient in temperate hardwood and softwood forest ecosystems. Ph.D. thesis, SUNY College of Environmental Science and Forestry, Syracuse, N.Y.

Park, B.B., and Yanai, R.D. 2009. Nutrient concentrations in roots, leaves and wood of seedling and mature sugar maple and American beech at two contrasting sites. For. Ecol. Manage. **258**(7): 1153–1160. doi:10.1016/j.foreco.2009.06.003.

Park, B.B., Yanai, R.D., Vadeboncoeur, M.A., and Hamburg, S.P. 2007. Estimating root biomass in rocky soils using pits, cores, and allometric equations. Soil. Sci. Soc. Am. J. **71**: 206–213. doi:10.2136/sssaj2005.0329.

Pregitzer, K.S., Kubiske, M.E., Yu, C.K., and Hendrick, R.L. 1997. Relationships among root branch order, carbon, and nitrogen in four temperate species. Oecologia, **111**: 302–308. doi:10.1007/s004420050239. PMID:28308123.

Pregitzer, K.S., Laskowski, M.J., Burton, A.J., Lessard, V.C., and Zak, D.R. 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol. **18**: 665–670. doi:10.1093/treephys/18.10.665. PMID:12651416.

Schaller, M., Blum, J.D., Hamburg, S.P., and Vadeboncoeur, M.A. 2010. Spatial variability of long-term chemical weathering rates in the White Mountains, New Hampshire, USA. Geoderma, **154**: 294–301. doi:10.1016/j.geoderma.2009.10.017.

See, C.R., Yanai, R.D., Fisk, M.C., Vadeboncoeur, M.A., Quintero, B.A., and Fahey, T.J. 2015. Soil nitrogen affects phosphorus recycling: foliar resorption and plant–soil feedbacks in a northern hardwood forest. Ecology, **96**: 2488–2498. doi:10.1890/15-0188.1. PMID:26594705.

Soethe, N., Lehmann, J., and Engels, C. 2007. Carbon and nutrient stocks in roots of forests at different altitudes in the Ecuadorian Andes. J. Trop. Ecol. **23**: 319–328. doi:10.1017/S0266467407004002.

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd ed. Agric. and Agri-Food Can. Publ. 1646. NRC Research Press, Ottawa, Canada.

Soil Survey Staff. 1975. Soil taxonomy, a basic system of soil classification for making and interpreting soil surveys. USDA-SCS Agric. U.S. Government Printing Office, Washington, D.C.

Ugawa, S., Miura, S., Iwamoto, K., Kaneko, S., and Fukuda, K. 2010. Vertical patterns of fine root biomass, morphology and nitrogen concentration in a subalpine fir-wave forest. Plant Soil, **335**: 469–478. doi:10.1007/s11104-010-0434-y.

Vadeboncoeur, M.A., Hamburg, S.P., Blum, J.D., Pennino, M.J., Yanai, R.D., and Johnson, C.E. 2012. The quantitative soil pit method for measuring belowground carbon and nitrogen stocks. Soil Sci. Soc. Am. J. **76**: 2241–2255. doi:10.2136/sssaj2012.0111.

Vadeboncoeur, M.A., Hamburg, S.P., Yanai, R.D., and Blum, J.D. 2014. Rates of sustainable forest harvest depend on rotation length and weathering of soil minerals. For. Ecol. Manage. **318**: 194–205. doi:10.1016/j.foreco.2014.01.012.

Vanguelova, E.I., Nortcliff, S., Moffat, A.J., and Kennedy, F. 2005. Morphology, biomass and nutrient status of fine roots of Scots pine (*Pinus sylvestris*) as influenced by seasonal fluctuations in soil moisture and soil solution chemistry. Plant Soil, **270**: 233–247. doi:10.1007/s11104-004-1523-6.

Vanguelova, E.I., Hirano, Y., Eldhuset, T.D., Sas-Paszt, L., Bakker, M.R., Püttsepp, Ü., Brunner, I., Lõhmus, K., and Godbold, D. 2007. Tree fine root Ca/Al molar ratio — indicator of Al and acidity stress. Plant Biosyst. **141**(3): 460–480. doi:10.1080/11263500701626192.

Wang, Y., Dong, X., Wang, H., Wang, Z., and Gu, J. 2016. Root tip morphology, anatomy, chemistry and potential hydraulic conductivity vary with soil depth in three temperate hardwood species. Tree Physiol. **36**: 99–108. doi:10.1093/treephys/tpv094. PMID:26423336.

Wargo, P.M., Vogt, K., Vogt, D., Holifield, Q., Tilley, J., Lawrence, G., and David, M. 2003. Vitality and chemistry of roots of red spruce in forest floors of stands with a gradient of soil Al/Ca ratios in the northeastern United States. Can. J. For. Res. **33**(4): 635–652. doi:10.1139/x02-195.

Yanai, R.D., Park, B.B., and Hamburg, S.P. 2006. The vertical and horizontal distribution of roots in northern hardwood stands of varying age. Can. J. For. Res. **36**: 450–459. doi:10.1139/x05-254.