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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.

Reswne : Les racines jouent un r(')le important dans les flux et les reserves de nutriments des ecosystemes, mais elles sont difficiles a echantillonner pour !'analyse de tissus, surcout en profondeur. Nous avons analyse !es patrons de concentration des nutriments dans des racines vivantes d'un diametre allant jusqu'a 20mm, prelevees dans des fosses d'observation quantitative etablies dans six stations de feuillus nordiques a la for t experimentale de Bartlett, dans l'Etat du New Hampshire, aux Etats-Unis. Les concentrations racinaires d'azote (N), de phosphore (P), de calcium (Ca) et de magnesium (Mg) etaient plus elevees dans la couverture morteque dans le sol mineral, de 23a61 % dans les racines fines (0-1 et 1-2 mm de diametre). Le fait d'utiliser seulement !es echantillons preleves dans !'horizon O pour caracteriser !es racines parcout dans le profll a engendre une erreur moyenne pour !'ensemble des elements de 16% dans les estimations de la teneur en nutriments des racines. Dans le sol mineral, il y avait peu de difference dans la concentration racinaire des nutriments selon la profondeur. 11 y avait cependant des patrons significatifs selon le diametre des racines: !es concentrations de N et Mg etaient plus eleveesdans les plus petites racines, tandis que la concentration de Ca etait la plus elevee dans la dasse de diametre de 2-5 mm. Une station (C8) se demarquait des autres par des concentrations racinaires plus faibles de N mais plus elevees de P, Ca, Mg et de potassium (K). En resume, pour obtenir une evaluation juste des nutriments il est plus important d'analyser les racines par station et dasse de diametre qu'en fonction de la profondeur dans le sol mineral, mais les racines dans la couverture morte et le sol mineral diflerent grandement dans le cas de certains elements. (Traduit par la Redaction]

Mots-des: carbone, azote, phosphore, calcium, magnesium, 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 Oackson 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 (Wanget al. 2016), and in conifer forests in British Columbia (Kinun in s 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 (Hert el et al. 2009; Davidson et al. 2011). A study in the Ecuadorian Andes found no difference in root concentrations of N, phosphoms (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

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Table 1. Basal area by species of trees near the soil pits from which roots were collected (sites Cl, C2, C4, C6, CS, and C9), based on trees> 2 cm diameterat breast heightwithin3mandtrees>10cm diameterat breast heightwithin6mofthecenterof the pit;speciesare listedin decreasing order of importance.

	Basal area (m^{-2} ha^{-1})					
	Cl (14 years)"	C2 (16years)	C4 (26 years)	C6 (29 years)	cs (121years)	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 (Pnmus pennsylvanica)	4.3	1.8	3.6	7.3		
White birch (Benlla *papyrifera)*	3	1.7	6	3.7	15	2.3
Yellow birch (Benda alleghaniensis)	1.2	2	5.8	1.1		4.6
Red map le (Acer rubrum)	0.2	1.5	3.7	8.9	2.2	
Aspe n (Populus spp.)			5.2			
Eastern hemlock *(Tsuga canadensis)*		0.3		2.1	0.3	
Striped maple *(Acer* penns){vanicum)	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 laboriouscollection methods. Two studies in tropical forestsfound fine roots to be higher in concentrationsofN, P, and Mg than coarse roots, but Ca was higher in coarser size classes, and K patternsdiffered bystudy(Edwards and Grubb1982; Soethe et al. 2007). In a study of49 species across seven sitesfrom Siberia to tropical China, N and P concentrat ions 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 caincreased withincreasing root diameter, and K and Mg were highest in 0.6-1 mm roots (Faheyet 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 (Fal1eyet 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 Han1pshire. The excavation of soil pits in these sites provided access to roots ofgreater diameter and from greater soil depths than is normally possible to collect with traditional coring methods. We tested the inlportance of root diameter and soil depth in explainingvariation in root concentrations of N, P, Ca, Mg, and K. We expected to find differences in concentrationsas 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 rootsto 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 ofa larger study on nut1ient cycling during stand development (Yanai et al. 2006 ; Park et al. 2007). The climate is hmnid continental with average annual precipitation of1270 mm. The soils are Spodosols developed in granitic glacial drift. The O horizon (forest floor) averages 5.1 cm in depth in the sitesthatwestudied (Vadeboncoeur et al 2012). In the United States Soil Taxonomy, the horizons of the forest floor are designated Oi, Oe, and Oa (Soil Survey Staff1975), corresponding to **L,** F, and **Hin** the Canadian System of Soil Classificat ion (Soil Classification Working Group1998).

Forest composition around the soil pits differed by site, **in** part reflecting successional dynamics following forest harvest (Table **1).** The young stands (Cl (14years) and C2 (16 years)) were dominated by pin cherry *(Pronus pennsylvanica* L.f.) and American beech (Fagus *grandifolia* Ehrh.), followed by white birch (Berula *papynfera* 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 (Acerrubrum **L.)**was important in one of the stands. The older stands (C8 (121years) 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 san1ples 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 bycolor and turgor, were sorted intosizeclasses: 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 nun were found entirely on the screens. For the 0-1 and 1-2 mm roots, 34% and 85 %, respectively, of the massof roots reported from the pitswerecollected on the screens. Large samples were subsampled before being smted into vitality and size classes, and multiple subsan1ples were washed, dried, and weighed. In these cases, the roots were composited for analysis in proportion to the biomass represented by each san1ple.

Because it would have been prohibitively expensive to analyze eve1y root sample, we selected classes of roots to analyze across the combinations of soil depth, root dian1eter, 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 0-1111111 diameter class, which comprises the majority of root biomass <10 nun 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,wealso analyzed composite samples of additional combinations of root diameter and soil depth classes. For Cl, C6, and C8, we analyzed samples separately for each of the three pits in each site. In total,174samples were analyzed.

Rootswere ground in a Wileymill(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 analyzedfor Ca, Mg, K, and P using inductively coupled plasma optical emission spectrometry (ICP-OES) (PE-3300DV, PerkinElmer Inc., Shelton, Connecticut). For N an alysis, samples were pulverized (Zenith /DMGVariable Speed DentalAmalgan1ator, Englewood, NewJersey)and analyzed by dry combustion (Vario EL, Elementar Americas Inc., Mount Laurel, New Jersey).

We used the C content of roots to evaluate contamin ation of root samples byadheringsoil.Rootsfrom the O horizon havelittle 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 mineralsoil.We did not correct for soilcontamination 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 withinsite.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 classeswithin depths, and soildepthsforeach root dian1eter class. For the main effect of root diameter on N, P, K, Ca, and Mg concentrations, coarse (5-10 and 10-20 111111) 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 interactionswith sites nestedwithinage in a repeated-measuresANOVA. The Oie was omitted from this analysisbecause 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 wemeasured from a subset of those san1ples. Forthe 174 san1ples 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 inSAS (SAS Institute Inc.). In addition , therewere twoclasses of roots that were too rare to be included in the ANOVA but needed to be estimated for nutrient contents. First, to estin1ate concentrations in roots > 1 mm in dian1eter in the Oie, we assigned concentrations from the same diameter of roots in the Oa horizon. Second, roots > 10 mm in dian1eter 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 dian1eter . 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 withdepth (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 dian1eter, for completeness, although roots> 20mmin diameter were spatially highlyvariable 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(describedabove)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, by80% for N, 49%for Mg, and 13%for K, comparing <2 nun diameter roots with5-20 mmdiameter roots(Fig.1).ForCa, in contrast, fine roots had concentrations10% lower than the coarse roots, and the peak Ca concentrations occurred in the 2-5 mm dian1eter 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 withall 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 thancoarse 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, therewasa 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 had16% h igher concentration (p = 0.002).

Concentrations vary with soil depth

There were important differences in the nutrient concentrations of roots as a fimction 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 :-, 0.006) but not for K(p 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	Fvalue	Pvalue	Fvalue	Pvalue	Fvalue	Pvalue	Fvalue	Pvalue	Fvalue	Pvalue	Fvalue	Pvalue
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 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 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 x 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 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 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 x 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= 0.00,2) 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 withstand age and site

Theroots that we studied were collected in replicate stands of three ages. There were no significant differences in root nutrient concentrationswith stand age(p 0.17).

There was one site,CS, that differed significantly from the others for all of the nutrients studied. For N (*p* < 0.01), thissite was significantlylower than the others. ForP(p= 0.01,) Ca (p = 0.008), Mg(p<0.001), and K(*p*= 0.02), rootsinCShad significantlyhigher concentrations than roots in other sites. When C8 was removed fromthe analysis, site was not significant for any element(p>0.06).

Some of tl1e other effects that we observed depended on this site. Thesignificance of dian1eter effects on K and P differed witl1 and without CS (Table 2). Including all sites, diameter was significantforK(p=0.01) but not P(p=0.10). ExcludingsiteC8, diameter wassignificant for **P**(p=0.001) but not K(p=0.11). The significant interactions of deptl1and dian1eter on Ca and K concentr ation s, described above,were notverysignificant without C8(p= 0.09and 0.08, respectively).

Root nutrient content

Across the six sites, the elemental contents of roots< 20mm in dian1eter in the whole soil profile averaged 7.4 g-m-^{2} for Ca, 4.3 g-m-^{2} for K, 1.1 g-111-^{2} for Mg, 13.9 g-111-^{2} for N, 0.76 g-111-^{2} for P, and 851 g- m -^{2} for C (Ta ble 3). The coefficient of variation of elementalcontents a□-osssites 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 tl1eir mass or C contents, because they had higher nutrient concentrations than coarser roots (Table 3; Fig. 2). For exam ple , 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 Mgand P, the fraction found in the <l mm roots was 50%. However, for Ca, which occurs at higher concentrationsin coarser roots, the portion of root nutlientcontentsin the <l mm sizeclass averaged only 37/4.

We tested the importance of sampling roots at depth bycalculating the nutrient contents of roots up to 20 mm in dian1eter in our six sites based on roots from various depth combinations (Fig. 2). The biggest discrepancy between root nutrient content prediction metl1ods occurred between using concentrations of roots only in the Oa and the best estin1ates using all our data. For N, tl1e average error across the three soil pits ranged from 11%to 28,% depending on the site. Thisrange was1%to 58%for P an d - 3% to 68 % for Ca. For Mg and K, using roots from tl1e Oa to represent the whole profile agreed within -12% to 29 % (Mg) or -16 % to 29% (K), whid1 is consistent with a lack of significant variation in concentrations with depth (Table 2).Wealso compared tl1e root nutrient contents of the mineral soil based on sampling onlyfrom the 0-10 cm depth. The errors introduced by this sampling scheme were smaller: - T/4 to 2% for N, -4 5% 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 deptl1than in the stuiace horizons, the difference in the nutlient content of roots calculated usingdata only from superficial roots (Fig. 2) was smaller than tl1e difference in concentration (Fig.1).

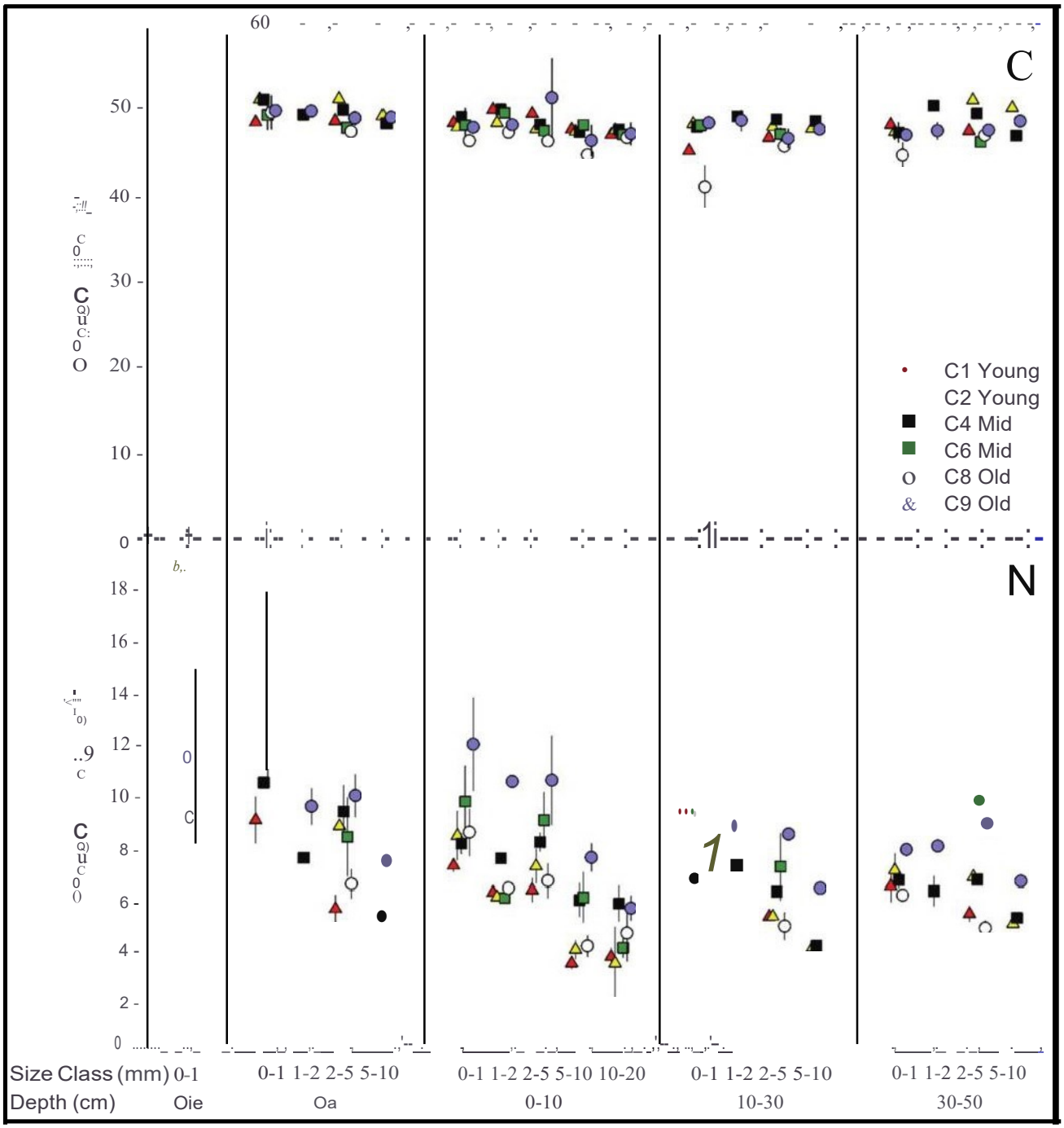
Discussion

Patt ern s withroot 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, witl1 most elements usually higher in concentration in the finest roots. At Huntington Forest in the Adirondack,s sugar maple and beech had higher concentrationsofN, P,and Mgin finer(0-1 nu n) rootsthan in coarser (2-5mm) roots (Park and Yanai 2009), as was the case in this study. Sin1ilarly, studies of N as a fun ction of root order have found the highest concentrations in the most distal roots, withdiameters rangingfrom <0.2to >3 mmin diameter for ash and sugar maple in Michigan (Pregitzer et al.1997)and for ash and larch in northeastern China (Ji.a et al. 2013). At Hubbard Brook in tl1eWhite Moun tain s, however , fine roots(<0.6 nun , 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 concentrationswere higher in the finer roots (Faheyet al.1988).

Calcium peaked at intermediate diameters in our data set (Fig.1), which was also tl1e case in a study of black spmce, Jack pine, and sugar maple in Quebec in which Ca concentrations peaked in roots 0.2-0.5 nun 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 birc,h American beech, and red spruce at Hubbard Broo k, 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, wherechanges withdiameter are nonlinear, observations

Fig. 1. Concentrations of C, N, P, Ca, Mg, and Kin roots by diameter class and soildepth in six sites at Bartlen Experintental 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.]



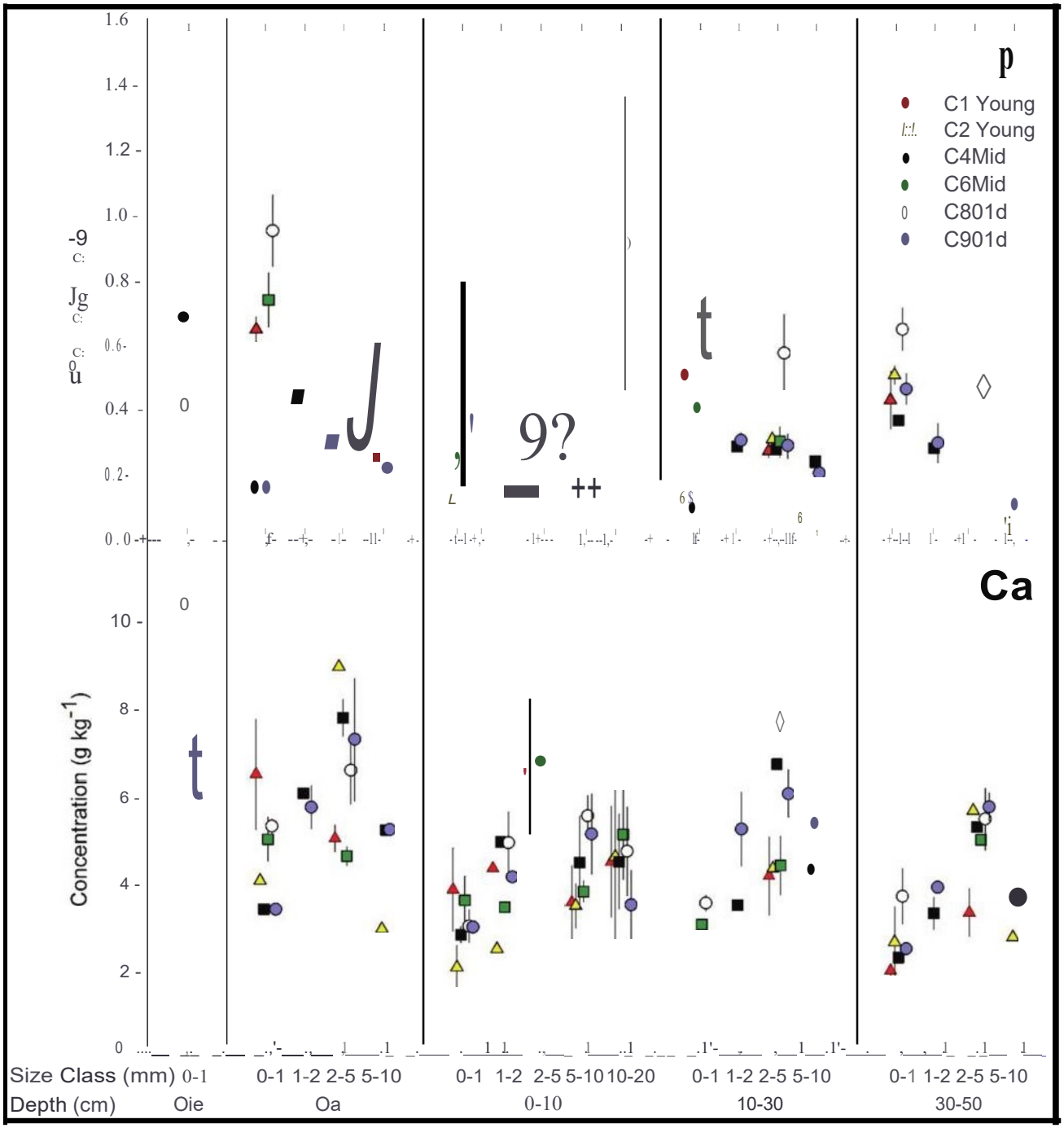
of trends with root diameter will depend on which part of the diameter range is observed.

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 Riverand 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 thatwoody roots are lower in nutrients thanfiner rootsis far from universal.

Patterns with depth

Declines **in** root concentrations of N with soil depth have been well documented (Kin-imins 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 % higherthan inthe mineral soil. These elements are likelyto be most lin-iiting to forest growth and most tightly conserved, with mineralization of organic fom-is 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.

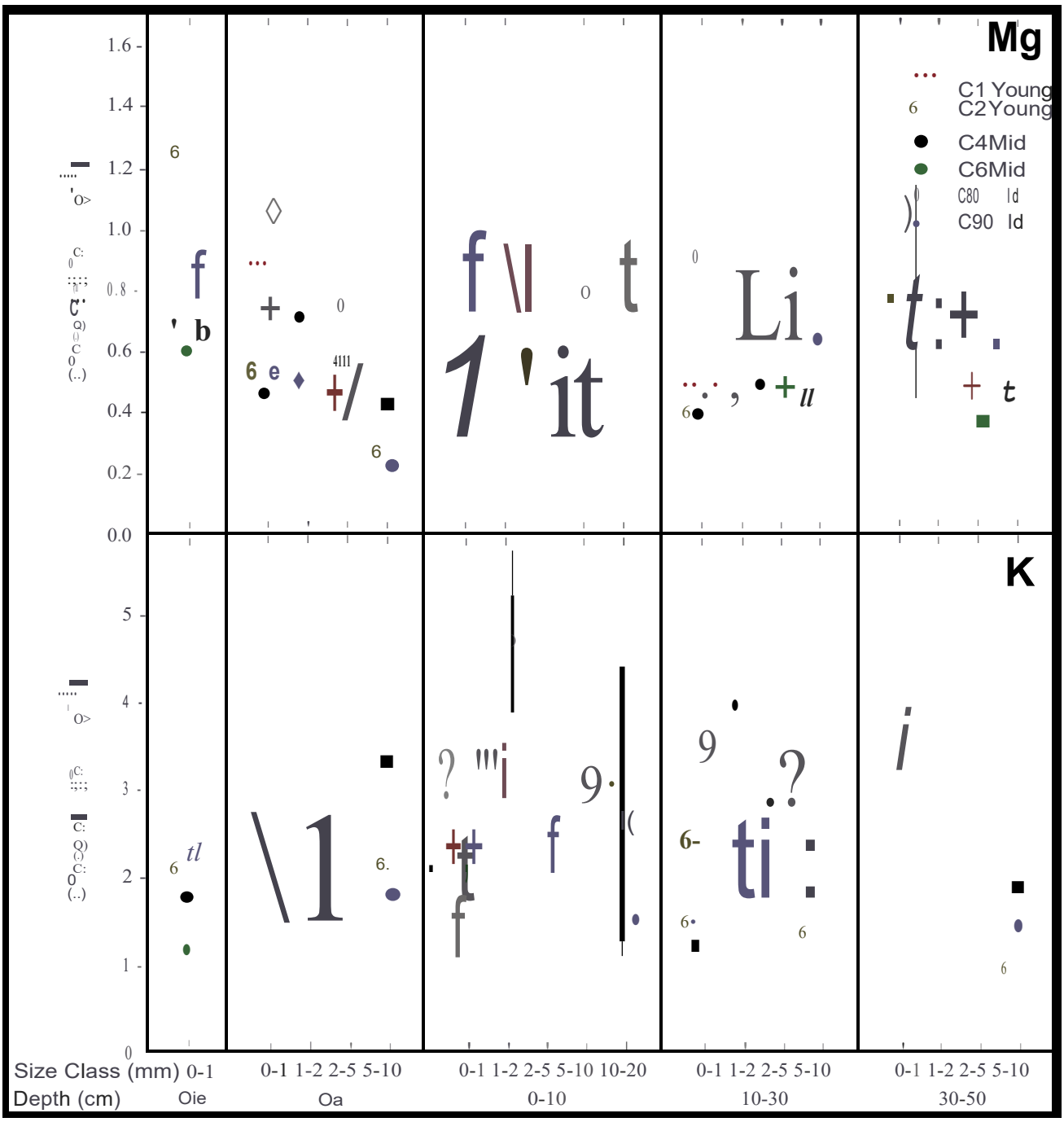
The base cations Ca, Mg, and K had differing behaviors in our study, although these elements are cycled through cation exchange, and weathering sources originate in the mineral soil. Specifically, Cadeclined most strongly, Mgwas intermediate, and K was not sensitive to soil depth. Scots pine in England had declining concentrationsof Ca and Mg from depths of O to 60 cm in the mineral soil(Vanguelovaet al. 2005). Norway spruce in Gennany had 27"/ohigherconcentrationsof Ca in rootsin organic than mineral soil, while N, P, and K showed less significant effects of soil depth across the four sites san1pled (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 concentrationswith depth within the mineral soilweregenerally small, but because of the large differences between the forest floor and mineral soil, it would be wise to san1ple roots from at least the upper mineral soil in ecosystems such as these.

Patterns withsite

One of the sites that westudied (CS) differed significantly from the othersin theconcentrationsofnutrients in roots. Differences

Fig. 1 (conduded).



in root chemistry across sites forested with northern hardwoods have been reported by other studies. For example, in Quebec, Ca, Mg, and Kconcentrations in rootswere higher in siteswith higher soil base saturation (Ouimet et al. 2008). Similarly, roots had high Ca, Mg, and Kin 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 chemist: 1.y 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 CB. The high P concentrations in roots in C8 are consisten t with high P concentrations in soil and foliage at that site (Seeet 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 (Table1), 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 withsite differences (Park and Yanai 2009).SiteCSdoes not differ dramatically in speciescomposition from the othersites in the study (Table1).

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

(a) Root nutrient contents by root diameter.

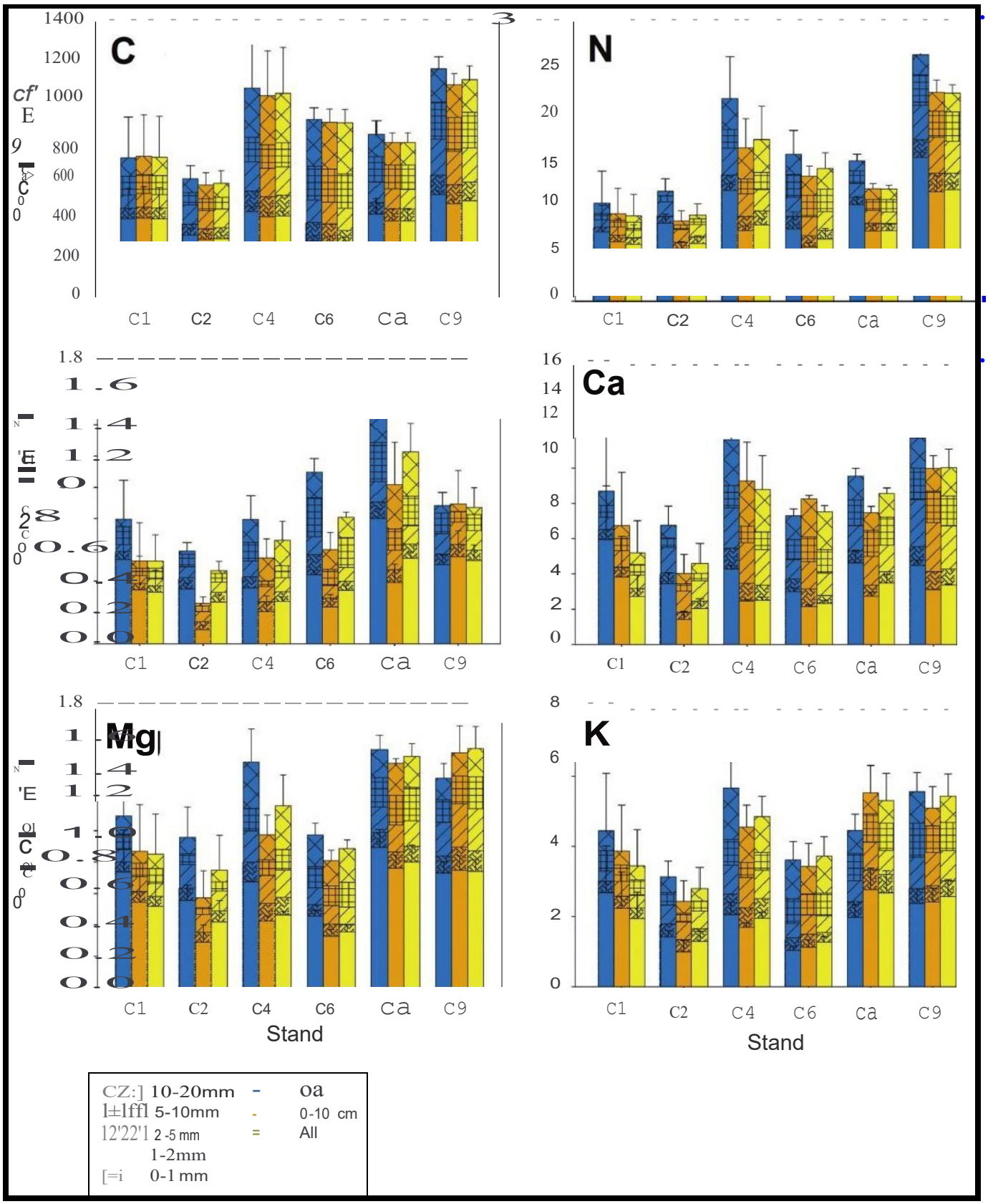
	C						N					
Root diameter	Cl	C2	C4	C6	*CB*	C9	Cl	C2	C4	C6	*CB*	C9
0-1	427±155	327±29	457±31	363±35	408±64	511±16	6. 3±2.0	6. 3±0.8	8.6±0.8	7.9±1.2	7.6±0.7	12.1±0.7
1-2	55±24	55±12	114±35	73±6	58±5	95±7	0.7±0.3	0.7±0.2	1.7±0.6	1.0±0.1	0.7±0.1	1.8±0.1
2-5	67±11	105±8	148±20	130±24	101±20	171±7	0.8±0.1	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	Cl	C2	C4	C6	*CB*	C9	Cl	C2	C4	C6	*CB*	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-+o.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	Cl	C2	C4	C6	*CB*	C9	Cl	C2	C4	C6	*CB*	C9
0-1	0.54 ±0.20	0.44-+o.13	0.50±0.0 2	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-+o.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	Cl	C2	C4	C6	*CB*	C9	Cl	C2	C4	C6	*CB*	C9
	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
	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	Cl	C2	C4	C6	*CB*	C9	Cl	C2	C4	C6	*CB*	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.OL+o.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	Cl	C2	C4	C6	*CB*	C9	Cl	C2	C4	C6	*CB*	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.OL+o.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-+o.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:Refertothe textforsiteaetaiis.TheOiecorresponas to the LanaFinthecanaaian soiltaxonomy, ana the Oacorresponas to the H.TheChorizon 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 Bartleu 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. [Colouronline.)



Tree health might also explain some variation associatedwith site; Pand Ca in fine rootswere 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.

Reco mm en dati ons

The resultsfrom thisstudy confirm the in1portance 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 wasimportant, with roots in the forest floor having significantly different concentrations tl1an roots at depth, which suggests that roots should be san1pled in botl1 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 easierto collect. In otl1erecosystem types, both the distribution ofroot biomass with depth and the possibility of concentration differences with depth need to be considered in evaluating root sampling regimes.

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