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Nutrient concentrations in roots, leaves and wood of seedling and mature sugar maple and American beech at two contrasting sites

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ABSTRACT

Differences in sensitivity to soil conditions across tree species and developmental stage are important to predicting forest response to environmental change. This study was conducted to compare elemental concentrations in leaves, stems, and roots of (1) sugar maple (*Acer saccharum* Marsh.) seedlings vs. mature trees and (2) mature sugar maple vs. mature American beech (*Fagus grandifolia* Ehrh.) in two sites that differ in soil base saturation and pH. Both sites are located in Huntington Forest, NY, USA; one site (hereafter 'H') has higher soil pH and Ca, Mg, and Mn concentrations than the other site (hereafter 'L'). Sugar maple growth at H (14.8 cm² year⁻¹ per tree) was much greater than at L (8.6 cm² year⁻¹ per tree), but the growth of beech was not different between the two sites. Leaves, roots, and stem wood of mature beech trees and sugar maple seedlings and mature trees were sampled for nutrient analysis. Foliar Ca, K, and Al concentrations were positively correlated with soil elements, but Mn concentrations were negatively correlated. Sugar maple differed more than beech between sites in foliar K and Mn concentrations. Root Mg and P concentrations reflected soil chemistry differences, in contrast to foliar concentrations of Mg and P, which were indistinguishable between the sites. In sugar maple, seedlings differed more than in mature trees in nutrient concentrations in roots, especially for Mg and Mn. Although beech was not as responsive to nutrient availability as sugar maple in foliar and root nutrient concentrations, Ca and Mg concentrations in beech wood were higher in H (52% higher for Ca and 68% higher for Mg), while sugar maple did not differ between sites. Sugar maple regeneration failure on acidic soils in the same region is consistent with our finding that sugar maple seedlings were very sensitive to nutrient availability. This sensitivity could ultimately contribute to the replacement of sugar maple by American beech in regions of low pH and base cations if base cation leaching by anthropogenic deposition and tree harvesting continues.

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1. Introduction

Several factors have contributed to base cation depletion in forest soils of northeastern North America. First, acidic deposition is neutralized by cation exchange, which results in cation loss (Lawrence et al., 1995; Likens et al., 1996). Second, atmospheric deposition of base cations has declined over the past 30 years following emission controls (Likens et al., 1996). Finally, forest harvesting removes nutrients, including base cations, which must be resupplied by the soil to support regrowth (Federer et al., 1989). These changes in soil environments have raised concern over the

continued health and long-term productivity of forests in North America and Europe (Driscoll et al., 2001; Likens et al., 1996).

Studies of soil acidification commonly focus on the acid cations, aluminum and hydrogen, and the dominant base cations, calcium, magnesium, and potassium. Manganese and iron are potentially toxic elements that are more available in acid soils, and Mn, especially, has been shown to inhibit Ca and Mg uptake (Maas et al., 1969).

Foliage is the tissue most commonly used to monitor the effects of nutrient availability and long-term environmental change on tree nutrition (Duquesnay et al., 2000; Ouimet and Camiré, 1995; Wilmot et al., 1996); responses in stem wood have also been reported (DeWalle et al., 1991; Shortle and Bondietti, 1992; Watmough, 2002). Although nutrient concentrations in roots can be sensitive indicators of nutrient availability (Adams and Hutchinson, 1992; Matzner et al., 1986), less attention has been given to belowground responses, which are more difficult to measure.

Research on sugar maple (*Acer saccharum* Marsh.) response to nutrient availability has focused primarily on mature trees in the field (Ellsworth and Liu, 1994; Wilmot et al., 1995). Seedlings, in

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contrast, have been studied in controlled conditions to verify the influence of soil nutrition on plant nutrient status (Kobe et al., 2002; Langheinrich et al., 1992; McQuattie and Schier, 2000). There have been few studies comparing sugar maple seedlings with mature trees in field conditions. Understanding whether seedlings and mature trees differ in sensitivity to soil conditions is important not only for extrapolating the results of experiments with seedlings, but also for predicting forest response to environmental change. Declining recruitment of sugar maple in the Adirondacks (Jenkins, 1997), New Hampshire (Hane, 2003; Juice et al., 2006), and Quebec (Duchesne et al., 2005; Moore et al., 2008) has been attributed among other factors to the sensitivity of seedlings to cation depletion.

In addition, the responses of foliar nutrient concentrations to nutrient availability vary among species (Long et al., 1997; Clair and Lynch, 2005), which may result in some species being better indicators of environmental conditions than others. Sugar maple has been shown to respond to liming to a greater extent than American beech (*Fagus grandifolia* Ehrh.) or black cherry (*Prunus serotina* Ehrh.), as indicated by an increase in foliar nutrient, growth and crown vigor (Long et al., 1997). Differential response of species to cation depletion could result in changes in species composition over long time periods (Palmer, 1990; van Breemen et al., 1997). Simulation modeling of northern hardwoods suggests that cation depletion could lead to increases in yellow birch (*Betula alleghaniensis* Britton) and beech, at the expense of sugar maple (Kobe et al., 2002).

One approach to studying effects of cation depletion is to compare sites that differ in soil acidity and base cation concentrations. We studied sugar maple and American beech in two adjacent catchments in the Adirondack region of New York State, USA, which differ in parent material and soil chemistry, but are similar in other environmental factors affecting tree growth (Christopher et al., 2006). This experimental design allows us to compare tissue chemistry by species between our two sites, but not to test whether differences between the sites are due to any particular factor, because the site factors are not replicated (Eberhardt and Thomas, 1991; Pennock, 2004).

The purpose of this study was to compare nutrient concentrations of leaves, stems, and roots of (1) sugar maple seedlings vs. mature trees and (2) mature sugar maple vs. mature American beech in sites with contrasting soil base saturation and pH. Because tissue concentrations in roots vary with root diameter, we made our comparison of roots within diameter classes. We hypothesized that seedlings would differ more than mature trees and that sugar maple would differ more than beech between the two sites. We also compared the growth rates of sugar maple and beech between sites, which we expected to reflect the difference in soil fertility.

2. Materials and methods

2.1. Site description

This study was conducted in two contrasting catchments in Archer Creek Watershed at the Huntington Forest, New York

(43°59'N, 74°14'W). Catchment 14 (hereafter 'H') has significantly higher NO_3^- and Ca^{2+} concentrations and higher pH in streams than catchment 15 (hereafter 'L').

The two catchments are similar in average elevation (619 and 614 m for H and L, respectively), aspect (S20°W and S12°E for H and L, respectively), slope (16° and 10° for H and L, respectively), and land use history over the past two centuries (Christopher et al., 2006). The mean annual temperature is 4.4 °C, with a January mean of -10.2 °C and a July mean of 17.4 °C; precipitation averages 1010 mm per year (Shepard et al., 1989).

Although the total basal area of the two catchments are indistinguishable (37.6 and 37.8 m² ha⁻¹ for H and L, respectively), species composition differs significantly between the H and L sites (Christopher et al., 2006). Basal areas of sugar maple, American basswood (*Tilia americana* L.), and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) are significantly higher at H, and American beech and eastern white pine (*Pinus strobus* L.) are significantly higher at L. Beech bark disease is present in these stands, with 40% of beech trees showing signs of infection in 2000 and the mortality of trees >30 cm DBH having a mortality rate of 5% year⁻¹ (Forrester et al., 2003).

The soils at both sites are coarse-loamy, mixed frigid, Typic Haplorthods in the Becket–Mundal association. The soil overlying gneiss bedrock is shallow (<1 m in depth) and contains a hardpan derived from glacial till. The sites overlie the Anorthosite Massif, a large igneous intrusion composed of up to 90% Ca-rich feldspar. The mineral horizons have considerable coarse fragments (5%–32% by volume) and high organic concentrations (2–21 mol C kg⁻¹) (Mitchell et al., 1992).

Soil pH and total Ca, Mg, and Mn concentrations are significantly higher at H than L, while concentrations of P and Al are significantly lower at H than L (Christopher et al., 2006; Table 1). Total K, Na, and Fe concentrations at 15 cm depth are not significantly different between the sites. These differences are presumed to stem from differences in the composition of the glacial till in which the soils formed (Christopher et al., 2006).

2.2. Plant sampling and analysis

Leaves and roots were sampled on August 14, 26, and 27 in 2003. For mature trees, five dominant or codominant sugar maple and American beech trees were selected in each site, ranging from the bottom to the top of each catchment. Two branches (diameter less than 10 mm) from each tree were cut from the base of the crown. Twenty to 30 pathogen-free leaves were pooled from the cut branches to produce a single sample per tree. Roots from the same trees were excavated from the upper mineral soil. Several root branches less than 5 mm in diameter were collected and combined for each tree.

We sampled seedlings of sugar maple that were 70–120 cm tall and 1–2 cm in diameter at the root collar. To obtain enough material for analysis, the sampling unit for seedlings was a cluster of 10–15 seedlings; 5 clusters were randomly sampled at each site. Two fully opened leaves were collected from each seedling and

Table 1
Total elemental concentrations of Bs horizon soils from sites H and L at Huntington Forest, New York, from Christopher et al. (2006). Standard errors are in parentheses ($n = 2$ plots with three pits in each plot). The soil pH shown for 15 cm depth was measured in the forest floor (Oe and Oa horizon); that at 50 cm is from the mineral soil (Bs horizon). Means sharing the same letter are not significantly different between sites within strata at $\alpha = 0.05$.

Soil depth (cm)	Site	pH	Total concentrations (g kg ⁻¹)							
			Ca	Mg	P	K	Mn	Na	Fe	Al
15	H	5.4 ^a (0.1)	52.33 ^a (0.2)	24.43 ^a (0.4)	0.54 ^b (0.01)	17.18 ^b (0.5)	0.81 ^a (0.19)	12.80 ^a (0.3)	47.97 ^a (2.7)	54.72 ^b (0.5)
	L	4.1 ^b (0.1)	16.9 ^b (0.8)	3.9 ^b (0.1)	0.75 ^a (0.06)	19.3 ^a (0.3)	0.43 ^b (0.01)	13.9 ^a (0.8)	57.6 ^a (18.4)	66.8 ^a (5.2)
50	H	4.6 ^a (0.1)	54.6 ^a (3.4)	23.5 ^a (2.4)	0.64 ^b (0.02)	18.2 ^a (0.2)	0.72 ^a (0.07)	14.8 ^a (0.7)	43.8 ^a (4.0)	60.0 ^b (2.1)
	L	3.7 ^b (0.1)	23.1 ^b (1.8)	5.4 ^b (0.6)	0.80 ^a (0.04)	21.9 ^a (0.5)	0.50 ^b (0.02)	17.2 ^a (0.1)	44.1 ^a (3.4)	73.5 ^a (2.0)

composited within cluster for nutrient analysis. Roots were sampled from the same seedlings by excavating the root system (hence, roots from organic and mineral soil horizons were pooled). Leaves and roots of young beech were not sampled because these individuals likely originated as root sprouts. Sampled roots were refrigerated (4 °C) until further processing.

Tree boles were cored on May 14, 2004, before the growing season. Two sets of cores were sampled, one for measuring the annual growth rate and the other for chemical analysis. Thirty dominant or codominant sugar maple and American beech trees were selected along an uphill transect at each site. One core from each tree was taken to determine the recent annual growth rate. All of the tree cores were collected from the south side of the tree at a height of 1.1 m. For chemical analysis of stems, the outer sapwood (<10 mm) was collected using an increment hammer or a small chisel from the same trees that were used for measuring annual growth rate. Samples were combined for chemical analysis into 5 composited samples, based on spatial proximity; each sample represented 5–8 trees. Sampled cores were refrigerated (4 °C) until further processing.

Leaves were oven-dried at 65 °C for 1 week, then ground in a Wiley mill to pass a 1 mm screen. Concentrations of total N, P, K, Ca, Mg, Al, Mn, and Fe were determined for leaves. For total N, a pulverized subsample was analyzed using a carbon–nitrogen elemental analyzer (model NC2100, CE Elantech, Inc., Lakewood, NJ, USA). After dry ashing the samples at 470 °C, the ash was dissolved in 10 mL of 6 M HCl (Wilde et al., 1979). Concentrations of P, K, Ca, Mg, Al, Mn, and Fe in the acid solution were determined by inductively coupled plasma emission spectrometer (PerkinElmer Life and Analytical Sciences, Shelton, CT, USA).

Roots were sorted into three diameter classes: 0–1, 1–2, and 2–5 mm. Sorted roots were forcefully stirred in a plastic container with deionized water for 10 s to remove soil and organic particles from the root surfaces. Nutrient losses during brief washing are not a significant source of error (Böhm, 1979). Soil contamination was presumably insignificant, as the mean ash was less than 34 g kg⁻¹. Root samples were analyzed following the same methods as leaves, described above.

Sapwood samples were analyzed for nutrient concentrations following the same methods as leaves and roots, described above. For growth rates, tree cores were air-dried and sliced with a razor blade to expose a clean surface. The most recent five or six rings were measured to obtain the average annual growth rate for the past few years. Tree rings were measured to the nearest 0.01 mm under a microscope. The measurements were taken two times per tree core to reduce experimental error. To compare growth rates from sites where average tree diameter differs, mean basal area growth for the different sites was adjusted to a common diameter (Auchmoody, 1985). This method makes the assumption that diameter increment is constant for the period represented by the diameter difference.

2.3. Statistical analysis

Elemental concentrations of leaves, roots, and sapwood were analyzed using analysis of variance (ANOVA). The experimental unit was the tree, or, in the case of seedlings, a cluster of five seedlings. For sugar maple leaves, we analyzed effects of site ('H' and 'L') and age (seedlings vs. mature). We also analyzed the effects of site and species (sugar maple vs. American beech) for mature leaves. We did not have leaves from beech seedlings, as explained above. For roots, we used a three-factor ANOVA, using site, species, and root diameter (0–1, 1–2, and 2–5 mm). For sugar maple roots, we also compared site, age, and root diameter. There were no observations of roots of beech seedlings.

We checked the two-factor interactions of site and age and site and species. If the interactions were important ($P < 0.2$) (Stehman and Meredith, 1995), all simple effects were compared using Tukey's pairwise comparison (Kuehl, 2000). Where interactions were not important, only main effect comparisons were reported.

3. Results

3.1. Stem growth of mature sugar maple vs. American beech

Total basal area was similar between the two sites, but growth rates of trees were not (Fig. 1). Growth rates of sugar maple differed more between the two sites than did those of beech (Fig. 1). While growth of American beech was not sensitive to site ($P = 0.33$), sugar maple had 72% higher annual growth at H than L ($P < 0.01$), with average annual basal area growth of 14.8 ± 1.6 cm² per tree at H and 8.6 ± 1.4 cm² per tree at L. The rate of growth of sugar maple at H adjusted to the size of trees at L (Auchmoody, 1985) was still 26% higher than at L, and H had 40% higher annual growth rate of the trees at L adjusted to the size at H. No such calculation was needed for beech, because the sampled trees had the same diameter at the two sites.

Tree growth can be influenced by multiple factors, such as soil nutrient availability, stem density and growth stage, microclimate, topography, acid deposition, and site history. Soil N was not measured in this study, but there were no differences in leaf or root N concentrations (Figs. 2 and 3), indicating that N availability was not a major factor responsible for differences in stem growth here.

3.2. Foliar chemistry

3.2.1. Site differences

Consistent with the higher Ca status of the soil (Table 1), Ca concentrations in leaves were higher at site H (Fig. 2). For mature beech, foliar Ca concentrations were 33% higher at H than L ($P < 0.01$). For mature sugar maple, foliar Ca concentrations were 25% higher ($P = 0.10$), and seedling sugar maple foliar Ca concentrations were 56% higher ($P < 0.01$).

Soil K was lower at site H (Table 1), and foliar K reflected this difference, significantly so for mature sugar maple ($P = 0.02$), but

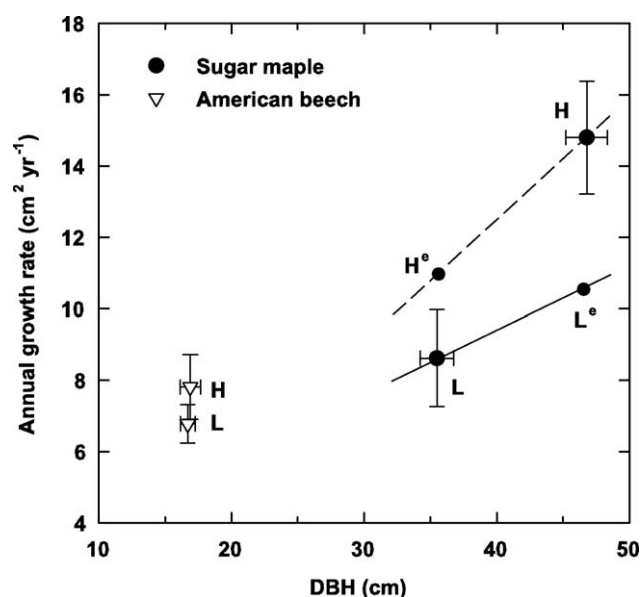


Fig. 1. Basal area growth of sugar maple and American beech at site H and site L for 1999–2004. H° is the estimated annual growth rate on the average DBH of sugar maple at L and L° is the estimated annual growth rate on the average DBH at H.

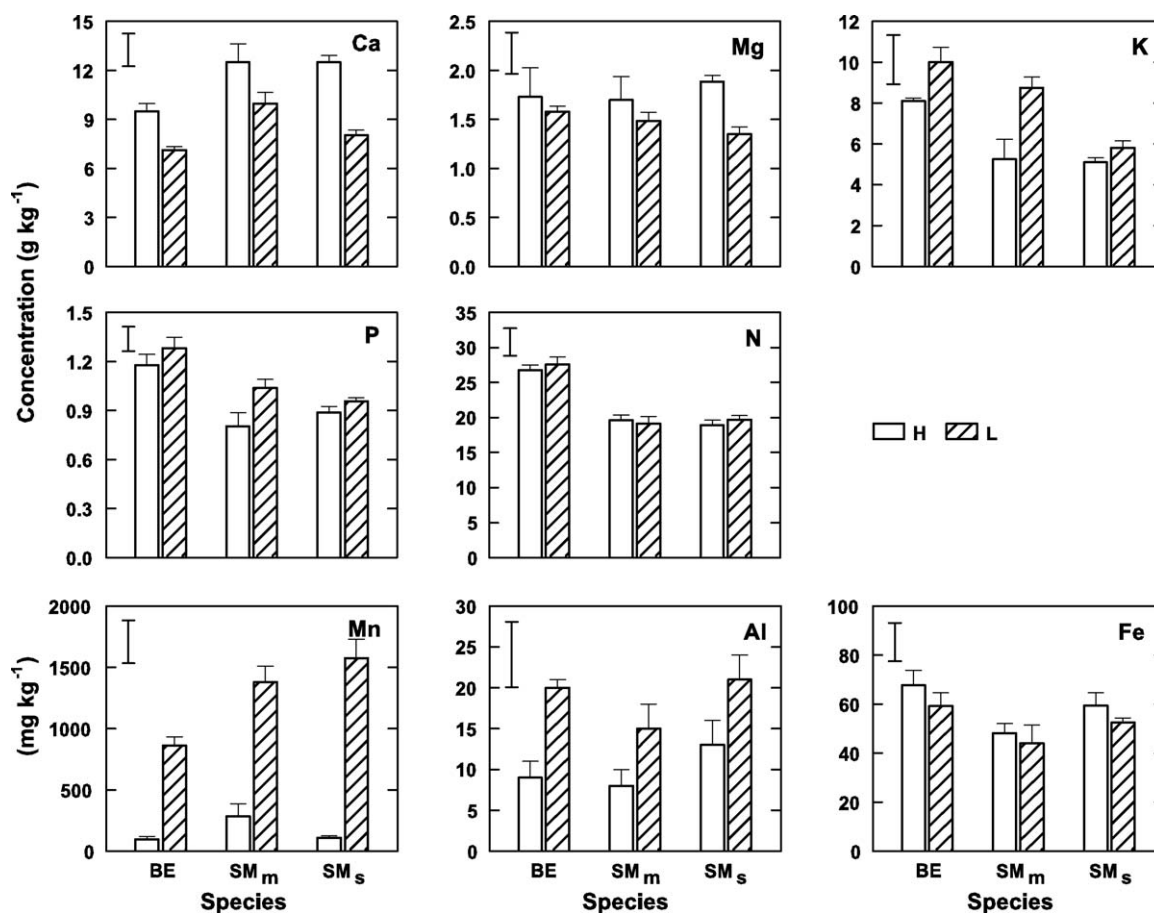


Fig. 2. Elemental concentrations in leaves of sugar maple seedlings, mature sugar maple and American beech at Huntington Forest, New York. Vertical bars represent standard errors ($n = 5$). Vertical bars in the top left corner represent the least significant differences at $\alpha = 0.05$. Abbreviations: BE, mature American beech; SM_m , mature sugar maple; SM_s , seedling sugar maple.

not for mature beech ($P = 0.37$) or sugar maple seedlings ($P = 0.12$) (Fig. 2).

There were no significant effects of site on Mg, P, N, or Fe concentrations of leaves (Fig. 2).

Soil micronutrient concentrations would predict that leaves at site H would have lower Al concentrations, but higher Mn concentrations (Table 1). Aluminum concentrations were indeed lower at H than at L for both seedling and mature sugar maple and beech ($P < 0.01$). In contrast, Mn concentrations in both species were more than five times higher at L than at H ($P < 0.01$), although soil Mn concentrations were twice as high at H than L.

3.2.2. Species differences

Mature sugar maple had higher foliar Ca concentrations than did beech ($P < 0.01$), but similar Mg ($P = 0.15$) and K concentrations ($P = 0.23$), and lower P ($P < 0.01$) and N ($P < 0.01$) concentrations (Fig. 2).

Potassium in beech leaves was not as responsive to site as K in sugar maple leaves, hence the interaction of site and species was significant ($P < 0.01$) (Fig. 2).

Beech leaves were similar to sugar maple in Fe and Al concentrations (Fig. 2). Beech leaves were not as high in Mn as sugar maple in site L. There were significant interactions of site and species in foliar Mn ($P < 0.01$) because the two species had similarly low concentrations in site H but differential responses in site L (Fig. 2). As in the case of K, sugar maple showed a greater sensitivity to site than did beech in foliar Mn concentrations.

3.2.3. Seedlings vs. mature trees

The comparison of seedling to mature sugar maple revealed greater differences within site L than H, with both Ca and K concentrations being higher in mature trees than seedlings in site L (Fig. 2). There was no difference between seedlings and mature trees in foliar Ca or K in site H, so the interaction of site and age was significant ($P = 0.02$ for Ca and $P < 0.01$ for K).

Foliar Mg, P, N, Mn, and Fe concentrations were similar in mature and seedling sugar maple (Fig. 2).

3.3. Root chemistry

3.3.1. Site differences

Calcium concentrations in roots were higher at H than L in seedling and mature sugar maple and in mature beech across all root size classes ($P < 0.01$) (Fig. 3). The magnitude of this difference in roots was more than twice the difference observed for leaves.

Magnesium concentrations in sugar maple roots also reflected site differences (Fig. 3), although foliar Mg concentrations did not, as described above (Fig. 2). Magnesium concentrations were significantly higher at H than L in the seedling sugar maple ($P = 0.01$), but not mature sugar maple ($P = 0.19$). Beech showed little sensitivity to site in root Mg concentrations; the interaction between species and site was significant for 1–2 mm ($P < 0.01$) and 2–5 mm roots ($P < 0.01$).

For P also, roots (Fig. 3) were more sensitive to site than leaves (Fig. 2), with lower concentrations at H than L, reflecting the pattern for soil (Table 1). Phosphorus concentrations were higher

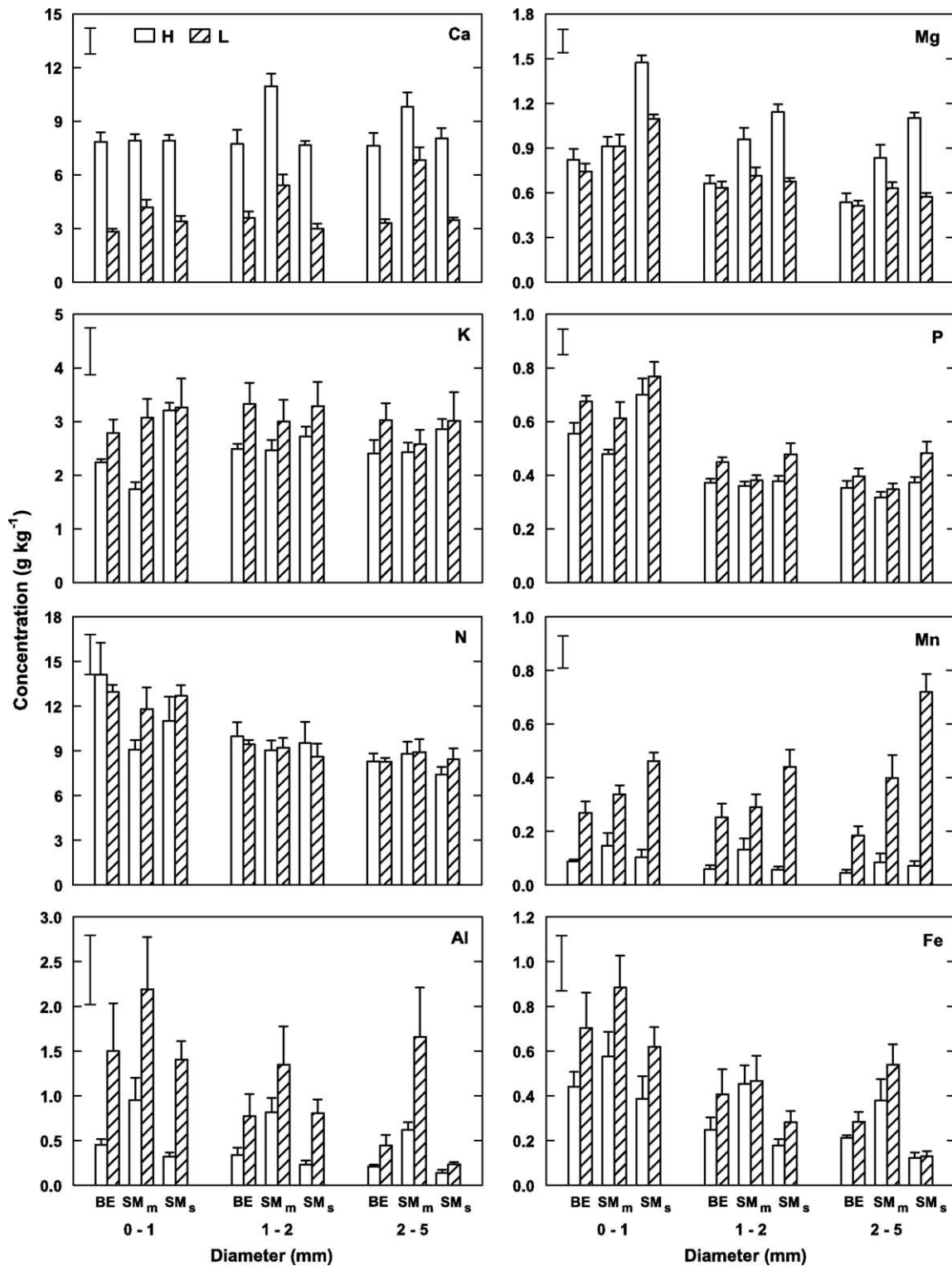


Fig. 3. Elemental concentrations in roots of sugar maple seedlings, mature sugar maple and American beech among diameter classes at Huntington Forest, New York. Vertical bars represent standard errors ($n = 5$). Vertical bars in the top left corner represent the least significant differences at $\alpha = 0.05$. Abbreviations: BE, mature American beech; SM_m, mature sugar maple; SM_s, seedling sugar maple.

in all classes of roots in L than H, significantly so in the 1–2 mm diameter class ($P = 0.03$).

Potassium concentrations were higher in all classes of roots in L than H, significantly so in the 1–2 mm diameter class ($P = 0.02$), consistent with the pattern for soil and leaves.

Although the soil concentrations of the cations Ca, Mg, and Mn were all higher at site H than L (Table 1), Mn concentrations in

sugar maple roots were lower in site H for both ages of tree and all size classes of roots ($P < 0.01$) (Fig. 3), consistent with the pattern observed for leaves (Fig. 2). There were no significant effects of site on root N concentrations.

Aluminum concentrations in roots of both seedling and mature sugar maple were lower at H than L for 0–1 mm ($P < 0.01$) and 1–2 mm roots ($P = 0.03$), as predicted from differences in soil

between the sites (Table 1). Iron concentrations of roots of both species were also lower at H than L, with the degree of significance varying by size class (Fig. 3).

3.3.2. Species differences

Roots of beech were similar to those of sugar maple in Ca concentration in all size classes ($P = 0.49, 0.17,$ and 0.15 for 0–1, 1–2, and 2–5 mm, respectively) (Fig. 3), although they were lower in leaves (Fig. 2). Similarly, there were no differences in K concentrations between sugar maple and beech roots ($P = 0.65, 0.56,$ and 0.42 for 0–1, 1–2, and 2–5 mm, respectively).

Magnesium concentrations were higher in roots of sugar maple than beech ($P = 0.07, <0.01,$ and <0.01 for 0–1, 1–2, and 2–5 mm, respectively), but for P, sugar maple had lower concentrations than beech ($P = 0.08, 0.04,$ and 0.11 for 0–1, 1–2, and 2–5 mm, respectively).

Sugar maple had higher Mn concentrations than beech in 0–1 and 2–5 mm roots ($P = 0.01$) by about 25%. Beech roots 2–5 mm in diameter were less sensitive to site than were those of sugar maple, indicating an interaction between species and site ($P = 0.03$).

Sugar maple and beech had similar concentrations of Al and Fe.

3.3.3. Seedlings vs. mature trees

The finest roots (<1 mm) were similar in Ca concentrations between seedlings and mature sugar maple (Fig. 3), but larger roots of mature trees had higher Ca concentrations than the same size roots of seedlings, significantly so in the 1–2 mm size class ($P = 0.05$).

Like site effects, age effects were significant for Mg in roots, although they were not for leaves. The finest roots of seedlings in H had 38% higher Mg concentrations than did those of mature trees ($P < 0.01$) (Fig. 3). The interaction between site and age was significant ($P < 0.01$): roots of seedlings reflected the higher Mg in soil at site H more than the mature trees did. For K, too, the finest roots of mature trees in H had higher K concentrations than did those of seedlings ($P = 0.02$); this difference was not significant for larger roots.

Phosphorus concentrations in roots at both sites were lower in mature sugar maple than seedlings for 0–1 mm ($P = 0.02$) and 2–5 mm diameter roots ($P = 0.02$).

At site L, seedlings had higher Mn concentrations in roots than did mature trees in all size classes. The interaction between site

and age was significant ($P < 0.01$): there was no difference between seedlings and mature trees in site H.

Root Al concentrations were significantly higher in mature sugar maple than seedlings in all classes ($P = 0.05, 0.03,$ and <0.01 for 0–1, 1–2, and 2–5 mm, respectively).

There were no differences with tree age in N concentrations in roots. Iron concentrations in 2–5 mm roots were lower in seedlings than in mature trees in both sites ($P = 0.01$).

3.4. Sapwood chemistry

The concentrations of nutrients in sapwood were much lower than that of leaves or roots, and some of the patterns with site and species were different. As was the case for leaves and roots, stem Ca concentrations were higher at H than L ($P = 0.05$), and higher in beech than in sugar maple at H ($P = 0.03$) (Fig. 4), but not at L. Magnesium in sugar maple stems was not as responsive to site as Mg in beech stems; hence there was a significant interaction between site and species ($P < 0.02$) (Fig. 4). In contrast to leaves and roots (Figs. 2 and 3), N concentrations in stems were significantly higher at H than L (Fig. 4). Phosphorus concentrations were significantly higher at H than L in beech ($P < 0.01$), but not in sugar maple. Potassium concentrations were not responsive to site or species.

Manganese ($P < 0.01$) concentrations in sapwood were lower at H than L in both species, but there were no differences between species (Fig. 4). Stem Al and Fe concentrations could not be obtained because concentrations were less than method detection limits (0.24 and 0.14 mg kg⁻¹ for Al and Fe, respectively).

4. Discussion

4.1. The use of different tissue types to indicate nutrient status

Our results showed that root tissues may be useful for diagnosing soil nutrient conditions. For example, root Mg and P concentrations differed strongly between sites in roots (Fig. 3) but not in leaves (Fig. 2), reflecting differences in soil chemistry (Table 1). It is difficult, however, to clean roots free of soil particles without losing mobile nutrients. The optimal regime for washing roots may depend on the elements of interest.

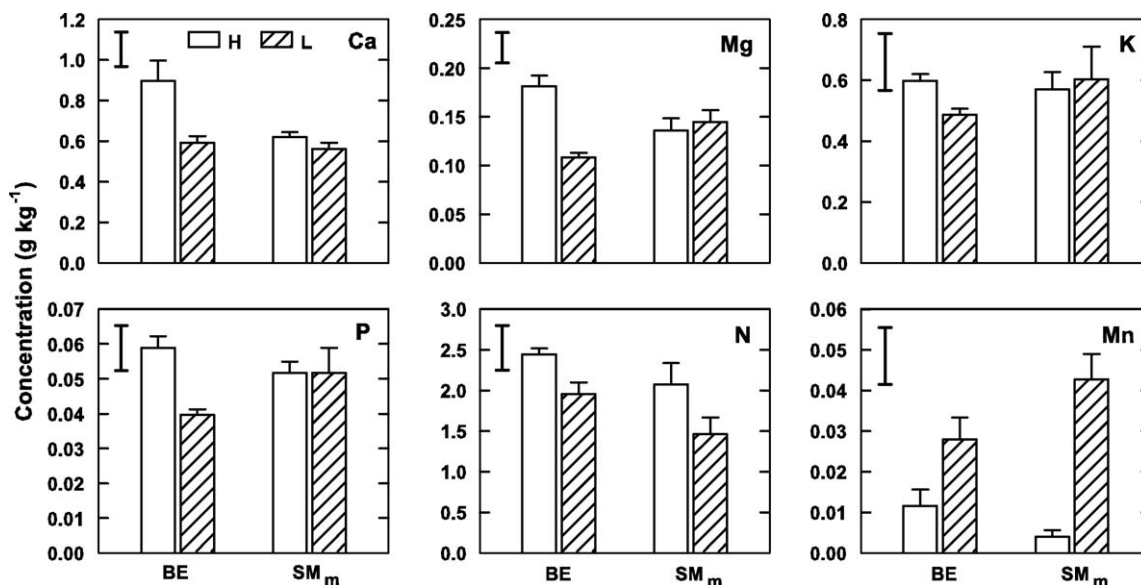


Fig. 4. Elemental concentrations in the sapwood of mature sugar maple vs. American beech at Huntington Forest, New York. Vertical bars represent standard errors ($n = 5$). Vertical bars in the top left corner represent the least significant differences at $\alpha = 0.05$. Abbreviations: BE, mature American beech; SM_m, mature sugar maple.

Nutrient concentrations in sapwood have been used to investigate the effect of long-term environmental change (DeWalle et al., 1991). Although we found significant differences in wood chemistry in some nutrients by species, the patterns were different from those of leaf and root chemistry (Figs. 2–4). Beech was not as sensitive to site as sugar maple in leaf and root nutrient concentrations, but in wood, Ca and Mg concentrations in beech were dramatically higher in the rich site (52% higher for Ca and 68% higher for Mg). Different responses in wood chemistry by species could be due to differential translocation to perennial tissues (Arp and Manasc, 1988) or redistribution of Ca and Mg after wood formation (McClenahan et al., 1989).

It is important to note that these concentrations are not in the deficient range. Even foliar Ca in seedlings at site L (8 g kg^{-1}), which was the lowest in our study, is high compared to values reported for infertile and declining sugar maple stands, where the low values are $4\text{--}6 \text{ g kg}^{-1}$ (Ellsworth and Liu, 1994; Wilmot et al., 1995, 1996; Moore and Ouimet, 2006). Similarly, we observed high root concentrations of Ca and Mg relative to those reported for sugar maple in Quebec (Ouimet et al., 2008) and sugar maple and beech in New Hampshire (Fahey et al., 1988). Manganese concentrations in our seedlings were not at toxic levels (McQuattie and Schier, 2000).

4.2. Site effects and element interactions

Some foliar nutrient concentrations, such as Ca, K, and Al, reflected soil element availability (Fig. 2). In contrast, Mn concentrations in leaves in H were one sixth that at L, in spite of Mn concentrations being 1.7 times higher in the soil at H than L (Table 1). Similarly, roots at L had Mn concentrations four times higher than at H. Low soil pH, as observed at the poor site, can enhance Mn availability. Since high soil Ca or Mg can have antagonistic effects on Mn uptake (Maas et al., 1969), the lower Ca and Mg at L may also contribute to higher Mn uptake there. Conversely, increased Mn concentrations can reduce foliar Ca and Mg concentrations in sugar maple seedlings and other trees (El-Jaoual and Cox, 1998; Marschner, 1995; McQuattie and Schier, 2000).

4.3. Ecological implications

In this study comparing two sites with contrasting nutrient availability, mature sugar maple and American beech differed in their ability to accumulate nutrients in leaves, roots, and stem wood, with sugar maple generally more sensitive to nutrient availability than American beech. Sugar maple seedlings were more sensitive to site differences than mature trees for Ca and Mg in leaves and Mg in roots. Although Mn concentrations were higher in the poor site for both seedlings and mature trees, the magnitude of this difference in seedlings was significantly greater than mature trees.

Other studies have also found sugar maple to be sensitive to nutrient availability (Watmough, 2002; Wilmot et al., 1995). In northern Pennsylvania, liming increased diameter growth by 11% over 7 years and improved crown vigor of sugar maple, but did not affect the growth or vigor of black cherry or American beech (Long et al., 1997). In experiments involving transplanted seedlings, only sugar maple showed significant increases in relative diameter growth of seedlings in CaCl_2 amended plots vs. controls; there were no significant responses in diameter growth of American beech, yellow birch, balsam fir (*Abies balsamea* (L.) Mill.), or red spruce (*Picea rubens* Sarg.) to Ca treatments (Kobe et al., 2002). In our study, high Ca or Mg availability associated with soil of moderate pH (>5.0) may be responsible for the relatively high stem growth in sugar maple compared with trees growing in more

acidic soil ($\text{pH} < 4.1$) (Fig. 1). However, beech appears not to be sensitive to soil Ca and Mg availability in these sites.

Sugar maple regeneration failure has been widely reported in northeastern North America (Jenkins, 1997; Hane, 2003; Juice et al., 2006; Duchesne et al., 2005). The increase in beech saplings associated with beech bark disease may limit the survival of sugar maple seedlings (Hane, 2003). Additionally, environmental stress may contribute to the recent decline in sugar maple seed production and seedling survival in the Adirondack Mountains (Jenkins, 1997). Similarly, in Quebec, liming enhanced sugar maple regeneration as well as mature tree condition (Moore et al., 2008). Our findings support this interpretation; sugar maple regeneration failure in acidic sites is consistent with our finding that sugar maple seedlings were very sensitive to nutrient availability. Sugar maple could ultimately be susceptible to replacement by American beech in regions of low pH and base cations if base cation depletion by anthropogenic deposition and tree harvesting continues.

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