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Foliar and soil nutrients

General Research

Foliar nutrient concentrations related to soil sources across a range of sites in the northeastern USA

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Abstract

Understanding the supply of nutrients from various soil sources and the sensitivity of tree species to soil nutrient availability is critical for predicting the effects on forest health and productivity of declines in base cations due to acid rain and forest harvesting. We collected soil samples from 19 sites in the northeastern US, chemically analyzed them using a sequential extraction procedure, and compared them to the chemical composition of foliage of the dominant tree species. Concentrations of calcium and magnesium in foliage were correlated with exchangeable Ca and Mg concentrations in the upper mineral soil; for most tree species they were also correlated to acid-extractable Ca and Mg in the parent material (C horizon). Foliar phosphorus was better correlated with soil P in the upper mineral soil than the C horizon, while foliar aluminum was insensitive to soil Al concentrations. In five sites in New Hampshire, the Ca/Sr of foliage was consistent with that of the Oie horizon, after taking the reported discrimination of Ca over Sr into account. In sites in New York, without an Oie horizon, the Ca/Sr of foliage was too high to be explained by any of the soil pools. A comparison of Ca/Sr ratios of foliage among species at common sites showed oak to have higher Ca/Sr ratios than sugar maple, birch, red maple and beech. The interpretation of soil Ca sources from Ca/Sr ratios is complicated at sites where a single horizon does not dominate the source.

Introduction

Soil base cations have declined in soils in the northeastern US in the 20th century (Likens et al., 1998) due to forest harvesting (Federer et al., 1989, Johnson et al., 1992) and acidic deposition (Likens et al., 1996). Reductions in exchangeable soil calcium and magnesium have been associated with declines of sugar maple (Bailey et al., 2004; Juice et al., 2006), an economically and ecologically important species. Sugar maple is thought to have high Ca requirements (Fujinuma et al., 2005; Page et al., 2008) while other species, such as beech, are less sensitive to soil base cation status (Duchesne et al., 2005; Park and Yanai, 2009). Acid deposition has also increased the concentration of dissolved inorganic aluminum in soil, which is toxic to plants (Foy et al., 1978; Delhaize and Ryan, 1995). Differences in the responses of tree species to regional variation in soil conditions may provide clues as to which species will be most sensitive to continued soil acidification and base cation depletion.

Sources of nutrients to forest soils include atmospheric deposition and mineral weathering (e.g., Graustein and Armstrong, 1983). Apatite, a ubiquitous but trace mineral in parent material, has been shown to be disproportionately important as a source of Ca and phosphorus in young soils, because of its high weathering rate (Blum et al., 2002; Nezat et al., 2004). In a site in the White Mountains of New Hampshire, 52-69% of the foliar Ca was estimated to be derived from apatite in some tree species (Dasch et al., 2006) based on Ca/Sr and $^{87}Sr/^{86}Sr$ ratios of foliage and soil (Blum et al., 2002; Dasch et al., 2006). The annual input of Ca to foliage from weathering of apatite and silicates combined is only ~1% of the Ca in the vegetation and forest floor (Nezat et a., 2004; Blum et al., 2008), since weathering inputs are small compared to biological recycling rates. Determining the role of weathering of apatite and other minerals in replenishing soil Ca will aid in determining whether weathering will help ameliorate the negative effects of acid rain on forest soils (Hamburg et al., 2003; Yanai et al., 2005).

Because strontium is chemically similar to Ca and is taken up and incorporated into plant tissue along with Ca (Runia, 1987), the Ca/Sr ratios of plant tissue have been compared to Ca/Sr ratios of parent materials and atmospheric sources to determine the relative importance of different sources of Ca for vegetation (Blum et al., 2008; Miller et al., 1993; Bailey et al., 1996). Differences in the uptake and use of Ca and Sr by trees are represented as a discrimination factor (DF), where the DF = $(\text{Ca/Sr})_{\text{plant tissue}}$ / $(\text{Ca/Sr})_{\text{nutrient source}}$. The discrimination factors for sugar maple, yellow birch and beech have been determined from the Ca/Sr ratio of the vegetation after wollastonite ($CaSiO_3$) with a known Ca/Sr ratio was applied to a watershed in the White Mountains of NH (Dasch et al. 2006). Tissues had different discrimination factors, with leaves discriminating for Ca over Sr (DF>1, Blum et al., 2008; Blum et al., in review), while roots had greater Sr than Ca relative to the source (DF<1, Dasch et al. 2006).

These discrimination factors have been used at other sites in the White Mountain region, in which the Oie horizon had a Ca/Sr ratio consistent with being the nutrient source for the foliage of sugar maple, yellow birch, beech, and red maple (Blum et al., 2008; Blum et al., in review). It is not known whether Ca/Sr ratios can be used to identify Ca sources in sites lacking the thick organic layer characteristic of Spodosols in the White Mountains. Also, the discrimination factors for many common tree species are unknown, limiting the use of Ca/Sr ratios to identify Ca sources to only those species for which DFs have been determined.

In this paper, we compare Ca, Sr, Mg, P, and aluminum in tree leaves and soils from a range of soil and parent material types in 19 sites in NH and NY. Our first objective was to compare the sensitivity of foliar nutrients to variation in soil concentrations obtained by neutral-salt and acid extractions, for a variety of tree species (10 species or species groups). We hypothesized that foliar concentrations would increase with soil Ca, Mg and P, but remain constant across a range of soil Al. We also expected sugar maple to show a greater response of foliar Ca to soil Ca, because of its known sensitivity to Ca depletion.

Second, we compared Ca/Sr ratios in leaves and soils to determine whether there was a soil pool, likely the upper (0-10 cm) exchangeable pool, that had a Ca/Sr ratio consistent with the known discrimination factors for particular species. Since previous studies showing that the Oie was supplying most of the Ca to foliage were conducted in Spodosols (Blum et al., 2008; Blum et al., in review), we wanted to see if this approach was valid across a wider range of soil types. Finally, we compared Ca/Sr ratios of foliage among co-occurring species, in an attempt to identify species groups of distinguishable discrimination factors.

Materials and methods

Study sites

Twenty-nine stands in nineteen sites in NY and NH were used for this study (Figure 1, Table 1). Soil chemical properties were previously studied at these sites (Yanai et al., 2000; Nezat et al., 2008) and they range in amount of total soil Ca in the parent material from 5 mmol Ca kg^{-1} in the Adirondacks to 1890 mmol kg^{-1} in carbonate sites in NY (Nezat et al., 2008). The sites with low soil Ca had sedimentary clastic (n=6) or crystalline silicate (n=9) parent material, while the high soil Ca sites had sedimentary carbonate (n=4) parent material.

Leaf and soil collection

We collected leaf litter from each of the dominant tree species at each stand. We combined the tree species into ten groups because many of the twenty-four species were represented at only a few sites (Tables 2 and 3). At the stands in NH (n=12), we collected leaves using multiple litter baskets or tarps in each stand, while at the stands in NY (n=15) we collected samples from the soil surface near the soil pit. Our previous comparisons of freshly fallen litter collected on tarps to litter collected in baskets showed no bias in Ca or Sr concentrations (Blum et al., 2008). For more mobile elements, such as K, the method of litter collection is important to the results (data not shown) and therefore we do not present results for K.

Three soil pits were excavated to the C horizon at each of the stands in NH (Yanai et al., 2006; Park et al., 2007; Blum et al., 2008; Schaller et al., 2010). Pits were separated by about 50 m. In the stands in NY, only one soil pit was excavated, and samples were collected from the wall of the pit. Soil samples were collected from the Oie and Oa horizons, when present. At all sites, samples were collected from the following depth increments in the mineral soil: 0-10 cm, 10-30 cm, and 30 cm to the top of the C horizon. Samples were also collected from the C horizon. At some sites, finer depth increments were sampled (10-20, 20-30, 30-50 and 50-C) and we used the average concentrations to estimate the 10-30-cm or 30-C increments. At some sites, samples were taken to multiple depths in the C horizon, and we used the uppermost C horizon sample in all cases.

Sample processing and chemical analyses

Leaves and Oie samples were oven dried at 50ºC and finely ground to increase sample homogeneity and facilitate digestion. Approximately 0.5 g of each leaf sample was digested in ultra-pure distilled HNO_3 and HCl using high-pressure microwave digestion in reinforced XP-1500 Teflon vessels (MARS 5, CEM Corporation, Matthews, NC). Samples were evaporated to dryness and then re-dissolved in ultra-pure 5% HNO_3 for analysis.

Oa and mineral soil samples were dried (105°C), sieved (2-mm), and subjected to a sequential extraction (Nezat et al., 2007). The exchangeable fraction was extracted by shaking 0.5 g of soil with 5 ml of 1 mol L^{-1} NH_4Cl at 20°C for ~18 h. The supernatant was collected and filtered through a 0.45-µm membrane. The residual material was extracted with 5 ml of 1 mol L^{-1} HNO_3 for 18 h at 10°C to dissolve the readily weathered mineral forms (apatite and carbonates). The more aggressive extractions used by Nezat et al. (2008) were not used in this analysis because these soil fractions are not readily available to plants. In the NH sites, a hydrogen peroxide extraction followed the neutral-salt extraction. This fraction was small in comparison to the neutral-salt extraction and was added numerically to the acid-extractable fraction for consistency with the other sites.

The leaf digests and soil extracts were analyzed for Ca, Mg, P, Al and Sr using inductively coupled plasma optical emission spectrometry (ICP-OES, PE-3300DV, Perkin Elmer, Norwalk, CT) with a five- to eight-point calibration curve. Analysis of a certified reference material (CRM Soil Solution A, High Purity Standards Inc.) indicated an accuracy of about ±5% for all elements.

Data Analysis

Prior to statistical analysis, we combined the tree species into ten groups (Table 2) and averaged the soil concentrations at the NH sites where three soil pits were collected. To determine the relationship between foliar and soil nutrients by tree species group, we used analysis of covariance for each nutrient (SAS Institute, Inc. 2004). Each element (Ca, Mg, P Al) and soil depth (0-10cm, C horizon) was run separately with tree species as a fixed factor and soil nutrient concentration as a covariate. If the slopes were significantly different ($\alpha = 0.05$) among species, we used Tukey's multiple comparison procedure (Zar, 1996). We also used this statistical approach using only the sites that had exchangeable Ca below 60 mmol/kg.

Results

Relation between foliar and soil chemistry

We compared the relationship between foliar and soil nutrients in the exchangeable pool in the upper mineral soil (0-10cm) and the readily weathered pool of apatite and/or calcite in the parent material (C horizon). Foliar Ca was generally higher at sites with higher exchangeable Ca at the 0-10 cm soil depth ($p<0.0003$, Figure 2a-b). For acid-extractable Ca in the C horizon, aspen, birch, red maple and sugar maple had significantly higher foliar Ca with greater soil Ca, but beech and “other conifers” had foliage that was not correlated with soil Ca (Figure 2c). When sites with high Ca (>100mmol Ca kg^{-1}) were excluded from the analysis, red maple was no longer correlated with soil Ca and the slope of red maple was significantly less than the slopes of birch, “other hardwoods” and oak (Figure 2d). The size of the exchangeable pool in the C horizon was negligible (< 56 mmol kg^{-1}; data not shown).

Foliar Mg was higher at sites with higher exchangeable Mg (p=0.01, Figure 3a-b) as expected. Species differed in their response to acid-extractable Mg in the C horizon (Figure 3c). The foliage of birch was the most highly correlated with soil Mg; the slope of birch was higher than aspen, beech, other hardwoods, and sugar maple. Differences in species were primarily driven by the high foliar Mg at sites with high Ca. When the sites with high soil Ca were excluded from the analyses, foliar Mg was significantly correlated with soil Mg (p<0.001) but species were not significantly different (p=0.5, Figure 3d).

Unlike Ca and Mg, the relationship between foliar and soil P was similar across species. Foliar P was higher at sites with higher soil P in the upper mineral soil (p<0.0001, Figure 4a). Surprisingly, there was no significant relationship of foliar P to C-horizon acid-extractable P (p=0.9, Figure 4b).

Aluminum concentrations in foliage were not sensitive to soil exchangeable Al (p=0.8, Figure 5a). There were no significant relationships of foliar Al to C-horizon acid-extractable Al (p=0.1). In fact, the highest foliar Al concentrations were observed at sites with relatively low Al in the parent material (Figure 5b).

Ca/Sr as an indicator of soil sources

We compared the Ca/Sr ratio of foliage to the Ca/Sr ratios of soil exchangeable and acid-extractable soil fractions at different soil depths (Figure 6). A consistent soil source of Ca to trees across sites would be indicated by a foliar Ca/Sr ratio that differed consistently from the Ca/Sr ratio of the soil pool, namely by the discrimination factor: 1.16 ± 0.13 (SD) for sugar maple, 1.90 ± 0.15 for red maple, 1.78 ± 0.17 for beech and 1.31 ± 0.10 for yellow birch (Blum et al., in review). These values are shown as slopes (with upper and lower confidence limits) in Figure 6.

For sugar maple and birch, at sites in NH with the highest Ca/Sr ratios (C6, C9 and M6), the Ca/Sr of foliage was higher than predicted by the Ca/Sr of the Oie, but at the other sites, the Oie was generally consistent with the Ca/Sr predicted for the source (Figure 6). For beech at the same sites, there was less consistency in the relationship between foliar and soil Ca/Sr ratios; no pool consistently fell within the range predicted by the discrimination factor. In red maple, the Ca/Sr ratio of the Oie horizon fell close to the value predicted by the discrimination factor of red maple (Blum et al., in review).

In the sites in NY, an organic horizon was not present (except at Ferris Lake and Happy Valley), so we cannot compare the foliar Ca/Sr to an organically cycling pool. In the sites in NY, none of the horizons consistently fell within the confidence interval defined by the discrimination factor for any of the species groups we studied (Figure 6). In fact, in many sites, all the soil pools had lower Ca/Sr ratios than a possible source to the foliage, so the Ca/Sr of the foliage cannot be explained by a simple mixing between the soil pools that were sampled. Only for beech do a majority of sites have possible sources with both higher and lower Ca/Sr than the foliage. However, in most cases the only source pool with a higher Ca/Sr than beech leaves is the unweathered apatite pool, indicated by the acid-extractable Ca.

We compared the Ca/Sr of sugar maple foliage to the Ca/Sr soil pools, referenced to the 0-10 cm exchangeable pool (Figure 7). If the 0-10 cm exchangeable pool were the source of Ca and Sr to the vegetation, the Ca/Sr of the foliage divided by the soil pool would be the same as the discrimination factor, shown as the line in Figure 7. Instead, Ca/Sr of the foliage is much higher than predicted by any of the measured soil pools, except in one of the stands (C1 at Bartlett). Exchangeable pools at greater depths are generally lower in Ca/Sr than the 0-10 cm exchangeable pool; the foliar Ca/Sr would appear even higher relative to possible sources if compared to these pools.

Comparing Ca/Sr across species

We compared the Ca/Sr of foliage of different tree species sharing the same site (Figure 8). The comparisons support the reported differences in discrimination factors, which were developed at common sites (Dasch et al., 2006; Blum et al., in review). Specifically, beech and red maple have higher foliar Ca/Sr relative to the soil source by a factor of 1.8-1.9, while sugar maple and yellow birch differ by a factor of 1.2-1.3 (Figure 8a). The "other hardwoods" (Table 2) are similar to sugar maple and yellow birch. Oak has higher foliar Ca/Sr than the four species for which discrimination factors have been defined (Figure 8b), suggesting that it has a higher discrimination factor than 1.9 or has a different source of Ca.

Species differences in Ca/Sr ratios are evident regardless of the species chosen for the x-axis on Figure 8, but the choice of a reference species does affect which species are statistically different. For example, red maple and beech have higher Ca/Sr ratios than birch and sugar maple when beech is used as the reference (Figure 8a) but they are indistinguishable when compared to birch (Figure 8b). Not all species are present at all sites and thus the data set available for comparison depends on the choice of the reference species.

Discussion

Foliar response to soil nutrients

Foliage showed a strong relationship to soil Ca, Mg and P but not Al in the exchangeable fraction of the upper mineral soil (Figures 2-4). Correlations between foliar and soil exchangeable Ca have been observed in sugar maple in the northeastern US (Schaberg et al., 2006). In 33 plantations across New Zealand, foliar Ca was correlated with exchangeable Ca in *Pinus radiata* but not by *Cupressus lusitanica* (Davis et al., 2007). Contrary to our study, foliar Mg was not correlated with soil exchangeable Mg in sugar maple (Schaberg et al., 2006) but was correlated in *P. radiata* and *C. lusitanica*. (Davis et al., 2007). Differences in the relationship between foliar and soil nutrients indicates that the relationship might be site or species-specific for exchangeable Ca and Mg.

The strong control that parent materials exert over Ca availability is reflected in the correlations we found between the foliar Ca and the C horizon for aspen, birch, red maple and sugar maple. As expected, sugar maple was higher in foliar Ca with increasing soil Ca (Fujinuma et al., 2005; Page et al., 2008), while beech foliage was not (Park and Yanai, 2009). Aspen, birch and red maple were also responsive to soil Ca, indicating that they may be more sensitive to base cation depletion than the "other conifers" (eastern hemlock and northern white cedar, Table 2). Birch was the most responsive to soil Mg in the C horizon, though Mg is not thought to be limiting in northeastern forests. However, the foliage of some species, such as American beech and "other conifers," reflects the Ca availability of the exchangeable nutrients more than the parent material.

Foliar P was correlated with P in the upper mineral soil but not the C horizon, indicating the possible importance of biologically driven uptake from the mineral soil into actively cycling pools (Dijkstra and Smits, 2002; Hamburg et al., 2003) or the importance of the atmospheric deposition of P (Prospero et al., 1996). Our results with P are consistent with others who suggest that P concentrations in the upper 0-10cm of the mineral soil are a good indicator of potential nutrient limitation for trees (Schoenhotz et al., 2000; Davis et al., 2007).

The relationship of foliar nutrients to soil nutrients differed by nutrient. The strongest relationship was for P, in which five out of seven species groups had high slopes, averaging 2.6. This might be expected, if P is more limiting to growth at the low-P sites, while Ca and Mg are not. Recent analysis indicates that P limitation is more widespread in terrestrial ecosystems than previously thought (Elseri et al., 2007). For Al, which is not a nutrient for trees, foliar concentrations were remarkably constant over a wide range of soil concentrations (Figure 5). Trees generally exclude Al from their foliage (Jackson 1967) and other studies have found no relationship between foliar and soil Al (e.g. Rosenberg 2010).

Soil sources indicated by Ca/Sr

One goal of this analysis was to determine whether the soil source of Ca within a species was constant across a wide range of soil types. In New Hampshire, the majority of the sites had foliar Ca/Sr consistent with uptake from the Oie horizon (Figure 6). However, we found greater Ca/Sr ratios in foliage than expected at sites with high Oie Ca/Sr. This difference could reflect a difference in soil sources, or it could be that discrimination of Ca over Sr is greater at the high Ca/Sr sites. These sites have higher foliar Ca/Sr ratios (>500) than the average foliar Ca/Sr at Hubbard Brook (foliar Ca/Sr = 413; Dasch et al., 2006), where the discrimination factor was determined. Beauregard and Côté (2008) also reported nonlinear Ca/Sr discrimination at high soil Ca/Sr by sugar maple seedlings relative to rhizosphere soil, but they found lower, not higher, Ca/Sr ratios in foliage than expected. Beech and oak were reported to show constant discrimination factors with exchangeable soil Ca over a range of 6 – 840 mmol/kg (Drouet and Herbauts 2008), compared to our range of 0.02 – 1890 mmol/kg.

In Spodosols, the forest floor is the soil pool that supplies the majority of Ca, as well as other nutrients (Yanai 1992), to plant uptake, so it's not surprising that the Oie could supply most of the Ca to foliage in our New Hampshire sites. Where detrital organic matter is incorporated more rapidly into the mineral soil, as in the NY sites, there was no such pool that we could recognize as consistent with foliar Ca/Sr ratios (Figure 6). As others have noted (Likens et al., 1998), the soil exchangeable pool of Ca is not a good indicator of the amount of Ca available to trees. Our results confirm that Ca uptake is not just from the exchangeable Ca pool. In fact, none of the measured soil pools is high enough to explain the foliar Ca/Sr we observed (Figure 7).

The high Ca/Sr of sugar maple foliage compared to all the mineral soil pools (Figure 7) suggests that a significant fraction of calcium uptake is occurring directly from decomposing organic matter, perhaps through the action of mycorrhizal fungi (Dighton, 1991; Chalot and Brun, 1998). The redistribution of detritus by soil organisms means that more of the mineralization of nutrients occurs over a greater depth in the soil profile than in the Spodosols of NH (Bohlen et al., 2004). The high Ca/Sr of foliage relative to all the soil pools suggests that direct uptake of nutrients occurs even without the formation of an organic horizon. When we sample soils by horizon or by depth increment using traditional methods, we apparently fail to isolate this actively cycling pool, except in the case of Spodosols, where this recycling occurs above the mineral soil.

We also compared the Ca/Sr of foliage between species at the same sites. We found that beech and red maple have higher Ca/Sr ratios than sugar maple and yellow birch and that oak has higher Ca/Sr ratios than beech and red maple. These results indicate that the discrimination factor differs between species (oak>beech + red maple>sugar maple + birch), as reported (except for oak) by other studies (Blum et al., 2008; Blum et al., in review) or that their soil sources differ in a very consistent way. At sites where the soil source is known, this technique holds promise for deducing discrimination factors for species for which the factor is not known, though a large sample size may be needed to statistically separate the different discrimination factors.

There are many complex and poorly understood issues involved in interpreting Ca/Sr ratios in forested ecosystems. Tissues within the trees have different discrimination factors, with leaves discriminating for Ca over Sr (DF>1, Blum et. al 2007; Blum et al. in review), while roots discriminate for Sr over Ca (Dasch et al. 2006). Therefore, to assess the effect of repeated annual uptake on the Ca/Sr of soil pools would require a mass-balance budget and knowledge of the DFs for all the species and tissue types in the ecosystem. Other factors affect the Ca/Sr of soil pools, such as transport of Ca and Sr in soil solution and recycling of nutrients through decomposition. More research on these processes will improve the interpretation of Sr as a tracer for Ca in a variety of soil types.

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Table 1. Coordinates and characteristics of each site used in this study.

Location	State	Region	Latitude	Longitude	# of stands	Parent material
NH						
Jackson (M5)	NH	White Mtns	44° 12'	71° 14'	1	Crystalline silicate
Iron Mountain (T30)	NH	White Mtns	44° 9'	71° 14'	1	Crystalline silicate
Bartlett Experimental Forest (C1, C2, C4, C6, C8, C9, H1, H4, H6)	NH	White Mtns	44° 3'	71° 17'	9	Crystalline silicate
Sabbaday Falls (M6)	NH	White Mtns	44° 0’	71° 25'	1	Crystalline silicate
NY						
Brasher Falls NW	NY	St. Lawrence Valley	44° 52'	74° 50'	1	Sedimentary (clastic)
Brasher Falls SE	NY	St. Lawrence Valley	44° 51'	74° 39'	1	Sedimentary (carbonate)
Grantville	NY	St. Lawrence Valley	44° 51'	74° 55'	1	Sedimentary (carbonate)
Fort Jackson	NY	St. Lawrence Valley	44° 43'	74° 45'	1	Sedimentary (clastic)
Southville	NY	St. Lawrence Valley	44° 41'	74° 51'	1	Sedimentary (clastic)
Black Pond	NY	Alleghany Plateau	43° 47'	76° 12'	1	Sedimentary (carbonate)
Black River	NY	Adirondack Mts	43° 34'	74° 51'	1	Crystalline silicate
Ferris Lake	NY	Adirondack Mts	43° 24'	74° 42'	1	Crystalline silicate
Happy Valley	NY	Alleghany Plateau	43° 27'	76° 2'	1	Sedimentary (clastic)
Klondike	NY	Alleghany Plateau	43° 22'	75° 59'	1	Sedimentary (clastic)
Rush	NY	Alleghany Plateau	42° 58'	77° 40'	3	Sedimentary (carbonate)
Swift Hill	NY	Alleghany Plateau	42° 27'	78° 14'	1	Sedimentary (clastic)
Lafayetteville	NY	Taconic Mts	41° 58'	73° 43'	1	Crystalline silicate
Stissing Mt.	NY	Taconic Mts	41° 56'	73° 41'	1	Crystalline silicate
Wassaic	NY	Taconic Mts	41° 47'	73° 34'	1	Crystalline silicate

Table 2. Species groups used in this study. Since some species were represented at very few sites, we grouped the species into ten groups.

Species group	Species present
Beech	American beech (*Fagus grandifolia* Ehrh.)
Birch	Yellow birch (*Betula alleghaniensis* Britt.), paper birch (*B.papyrifera* Marsh.) and grey birch (*B. populifolia* Marsh.)
Red maple	*Acer rubrum* L.
Sugar maple	*A. saccharum* Marsh.
Other hardwoods	Striped maple (*A. pennsylvaticum* L.), black cherry (*Prunus serotina* Ehrh.), pin cherry (*Prunus pensylvanica* L.f.), white ash (*Fraxinus americana* L.), black walnut (*Juglans nigra* L.) and basswood (*Tilia americana* L.)
Aspen	Quaking aspen (*Populus tremuloides* Michx.) and big-tooth aspen *(Populus grandidentata* Michaux)
Other conifers	Eastern hemlock (*Tsuga canadensis* (L.) Carriere and northern white cedar (*Thuja occidentalis* L.)
Pine	Pitch pine (*Pinus rigida* Mill.), white pine (*Pinus strobus* L.), Scots pine (*Pinus sylvestris* L.) and red pine (*Pinus resinosa* Sol. Ex Aiton)
Oak	White oak (*Quercus alba* L.) and red oak (*Quercus rubra* L.)
Spruce-fir	White spruce (*Picea glauca* (Moench) Voss and balsam fir (*Abies balsamea* (L.) Mill.

Table 3. Species sampled within each study site. “Other hardwoods” include striped maple, black cherry, pin cherry, white ash, black walnut and basswood. “Other conifers” includes eastern hemlock and northern white cedar.

Location	**Beech**	**Birch**	**Red Maple**	**Sugar Maple**	**Other hardwoods**	**Aspen**	**Other Conifers**	**Pine**	**Oak**	**Spruce-fir**
New Hampshire										
Jackson (M5)	X	X	X	X	X					
Iron Mountain (T30)	X	X	X	X	X					
Bartlett (C1)	X		X	X						
Bartlett (C2)	X	X								
Bartlett (C4)	X	X		X						
Bartlett (C6)	X			X						
Bartlett (C8)	X	X		X						
Bartlett (C9)	X	X		X						
Bartlett (H1)	X	X	X	X						
Bartlett (H4)	X	X	X	X		X				
Bartlett (H6)	X	X	X	X	X					
Sabbaday Falls (M6)	X	X	X	X	X					
New York										
Brasher Falls NW			X				X			
Brasher Falls SE	X		X		X					
Grantville	X	X			X	X				
Fort Jackson	X		X					X	X	
Southville	X						X	X	X	
Black Pond		X	X		X		X			
Black River			X		X	X				X
Ferris Lake	X	X		X						
Happy Valley			X		X			X		
Klondike	X		X				X		X	
Rush			X	X	X	X				X
Swift Hill	X			X						
Lafayetteville	X		X						X	

Stissing Mt.		X		X	X	X
Wassaic	X	X	X	X		X

Figure Captions

Figure 1. Location of study sites in the northeastern United States.

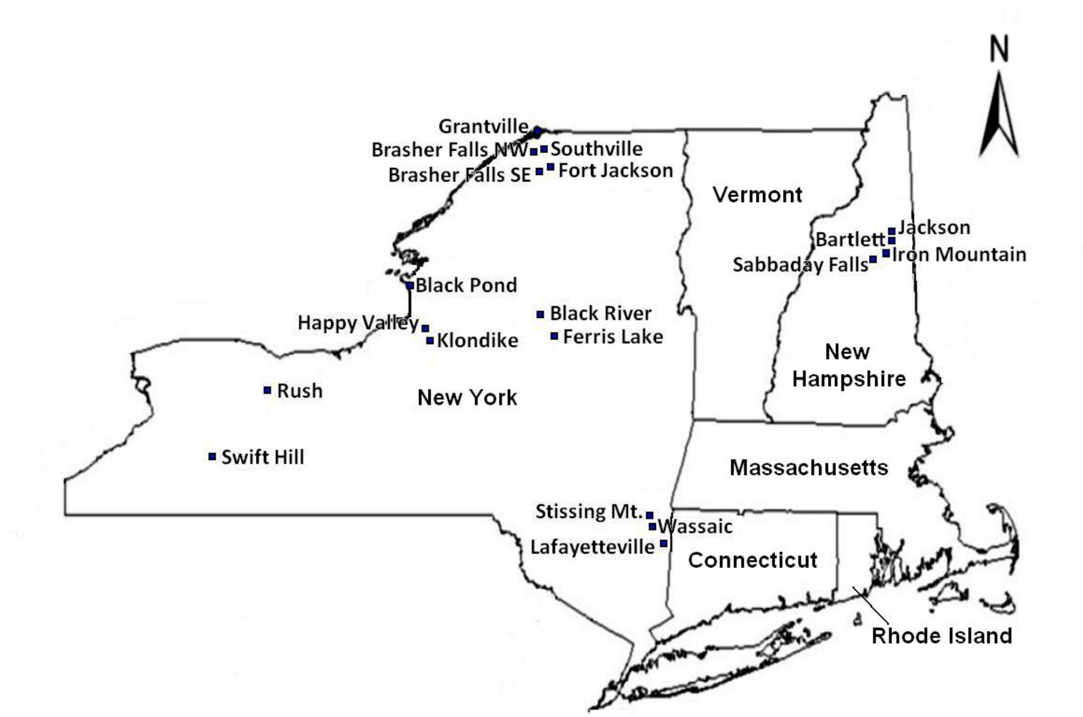

Figure 2. Foliar Ca compared to soil Ca for various tree species groups and two soil Ca fractions. (a, b) Exchangeable Ca concentrations at 0-10cm, (c, d) 1-N HNO3 extractable Ca in the C horizon. (a, c) all sites; (b, d) sites with low exchangeable Ca. Slopes with different letters differ significantly at α ≤ 0.05.

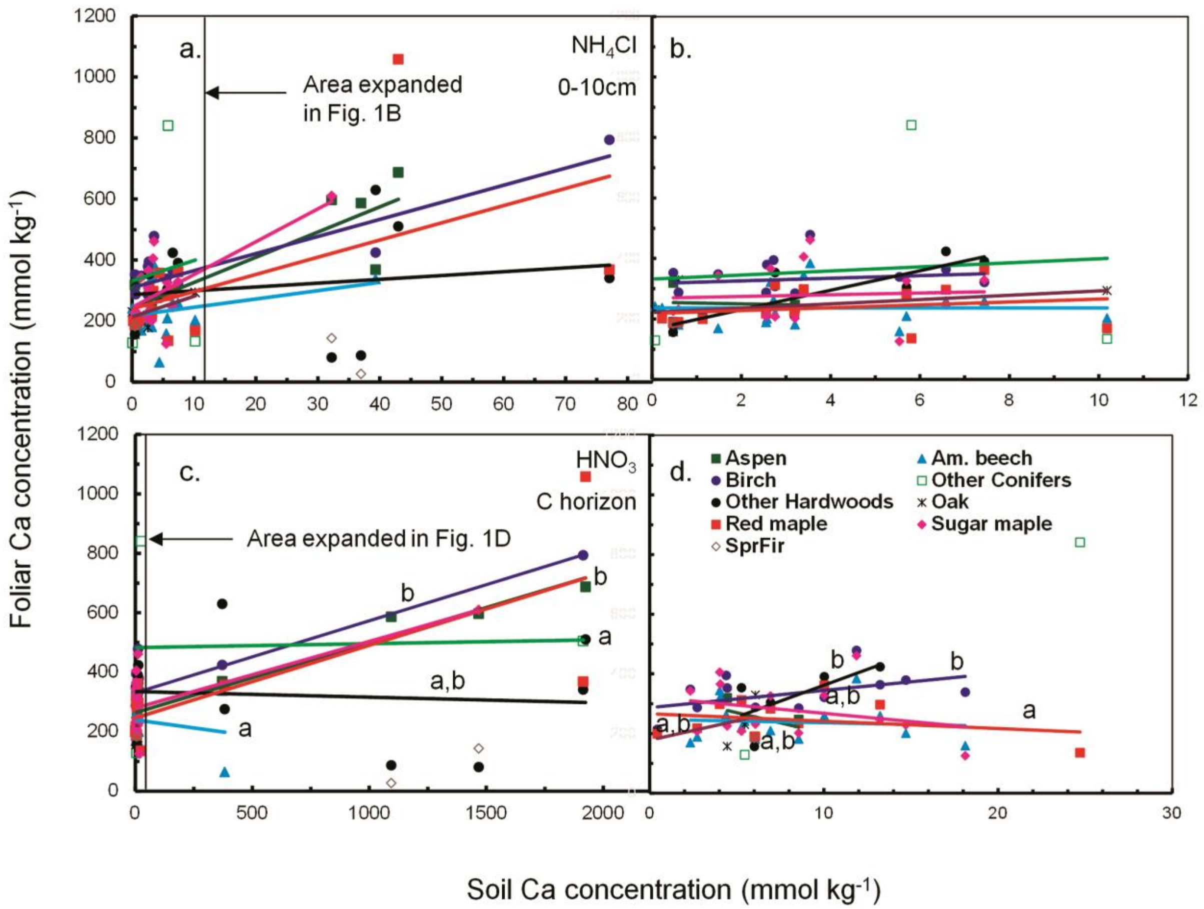

Figure 3. Foliar Mg compared to soil Mg for various tree species groups and two soil Mg fractions. (a, b) Exchangeable Mg concentrations at 0-10cm, (c, d) 1-N HNO3 extractable Mg in the C horizon. (a, c) all sites; (b, d) sites with low exchangeable Ca. Slopes with different letters differ significantly at α ≤ 0.05.

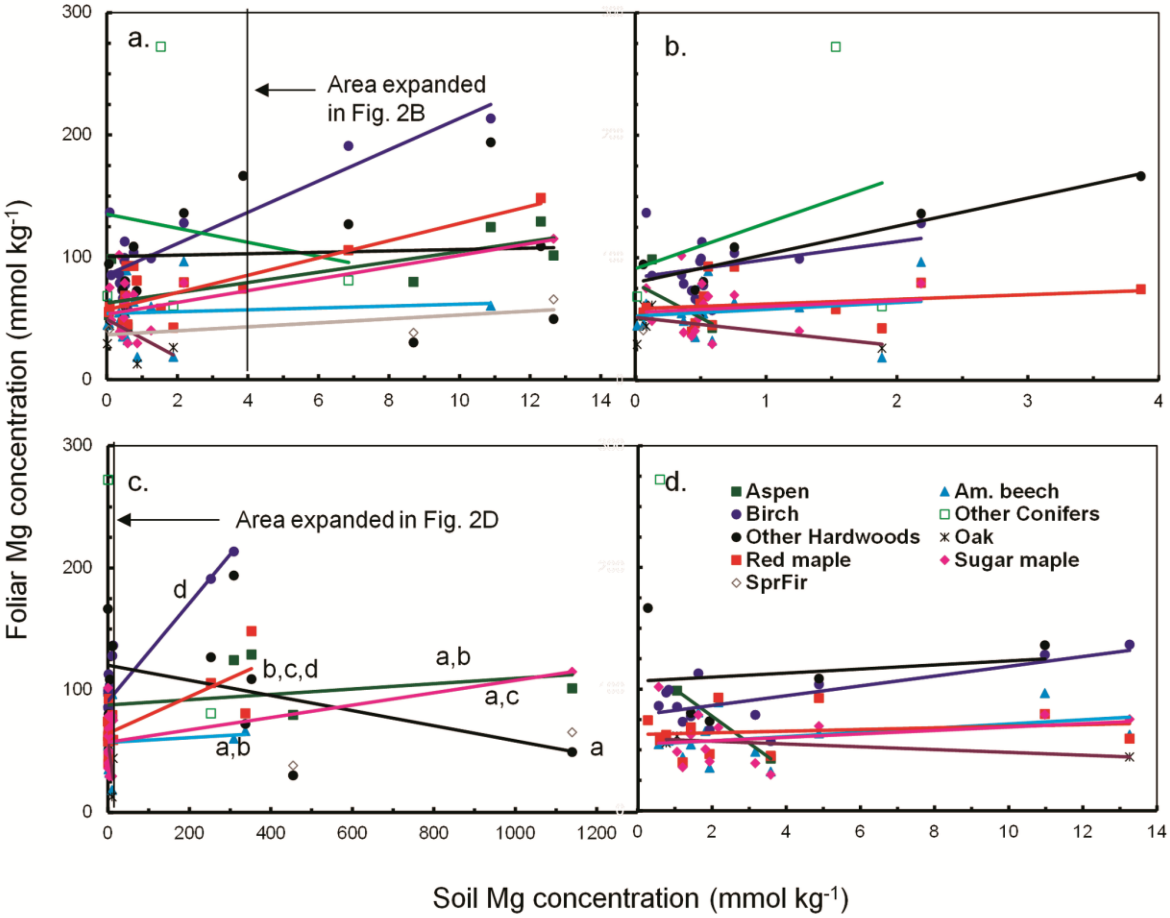

Figure 4. Foliar P compared to soil P for various tree species groups and 1-N NHO3-extractable P at two depths: (a) 0-10cm, (b) C horizon. Regression lines are shown only for 0-10cm, since there was no significant relationship between foliar and soil P in the C horizon.

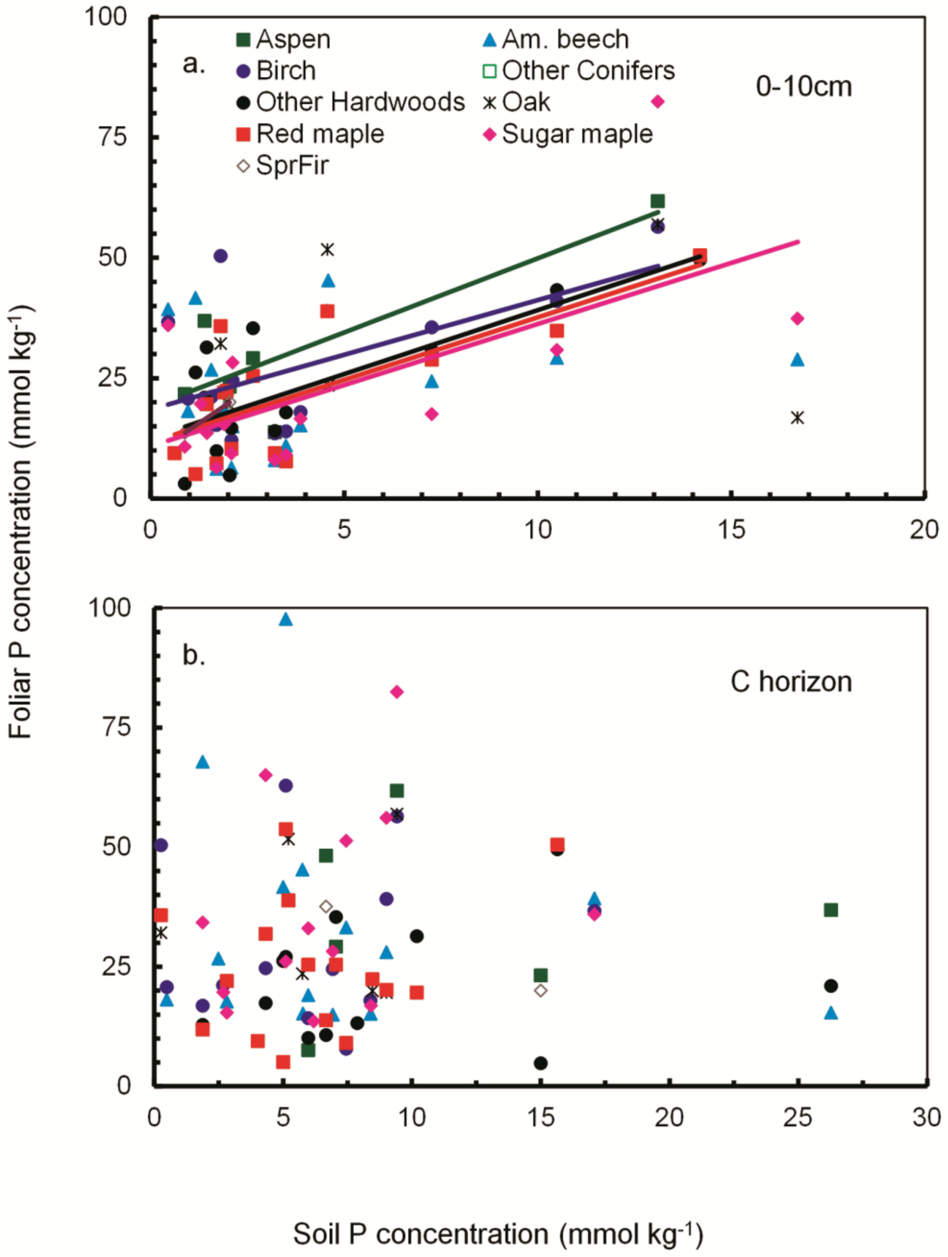

Figure 5. Foliar Al compared to soil Al for various tree species groups and two soil Al fractions. (a) Exchangeable Al concentrations at 0-10cm, (b) 1-N HNO3 extractable Al in the C horizon. Regression lines are not shown since there was no significant relationship between foliar and soil Al.

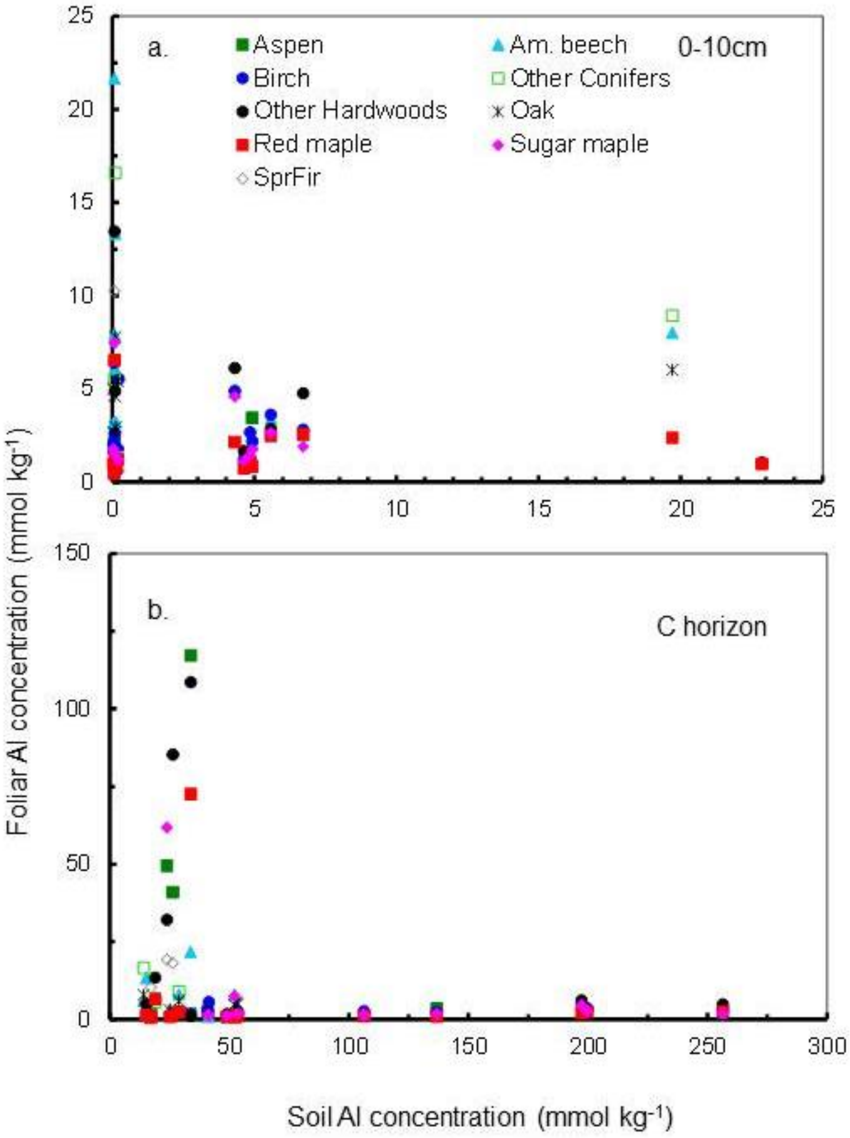

Figure 6. Foliar vs. soil molar Ca/Sr ratio at 0-10 cm, 10-30 cm, 30- C, and C horizon for exchangeable and acid-extractable fractions of beech, birch, sugar maple and red maple in NH and NY. The discrimination factor is displayed as a line with its associated standard deviation (Blum et al. in review).

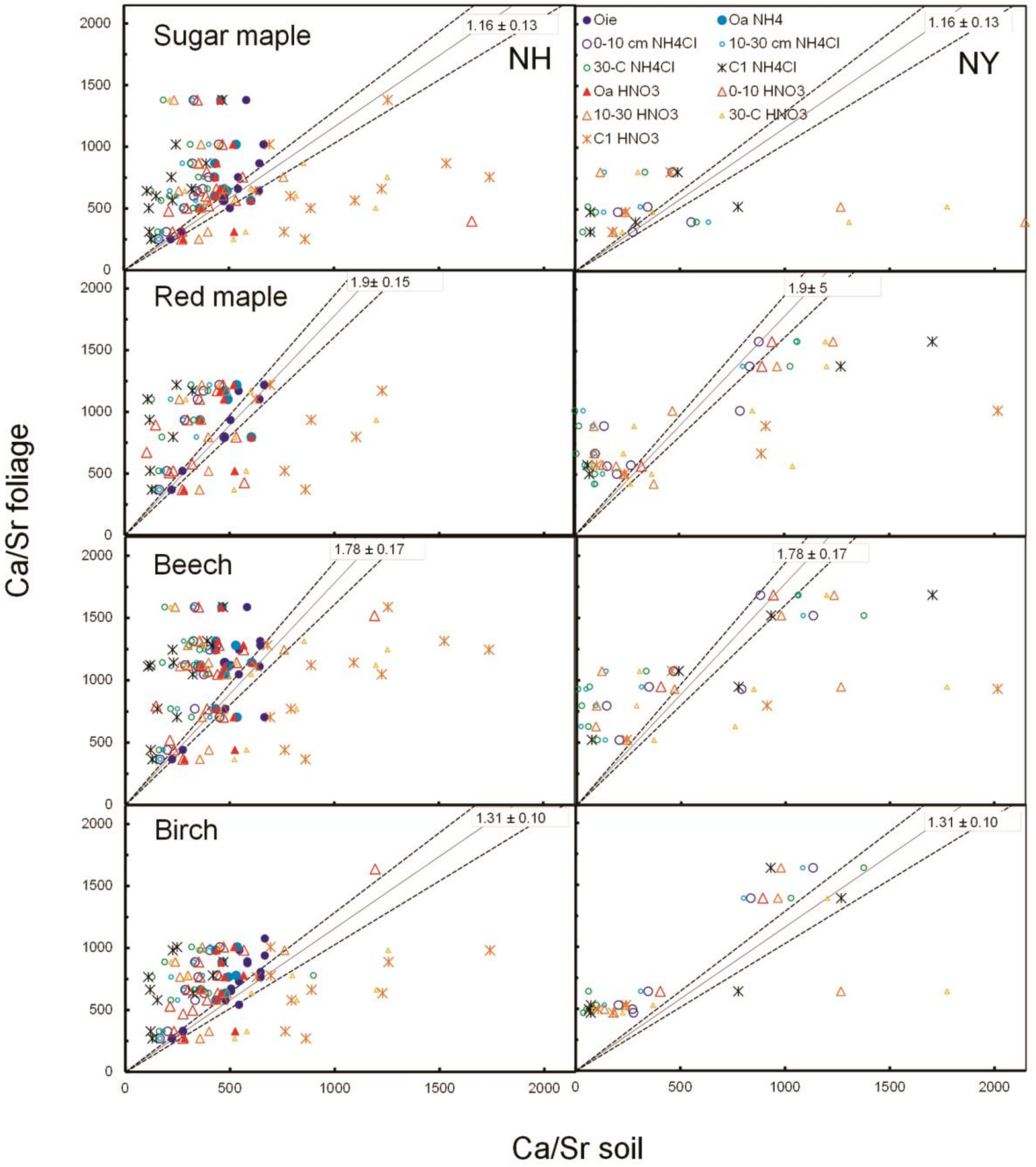

Figure 7. The Ca/Sr ratio of sugar maple leaves and the soil exchangeable pool divided by the Ca/Sr ratio of the exchangeable 0-10cm horizon plotted against the molar Ca/Sr ratio of the acid-extractable fraction of the C horizon. The discrimination factor of sugar maple is displayed as a horizontal line at 1.16 (Blum et al; in review).

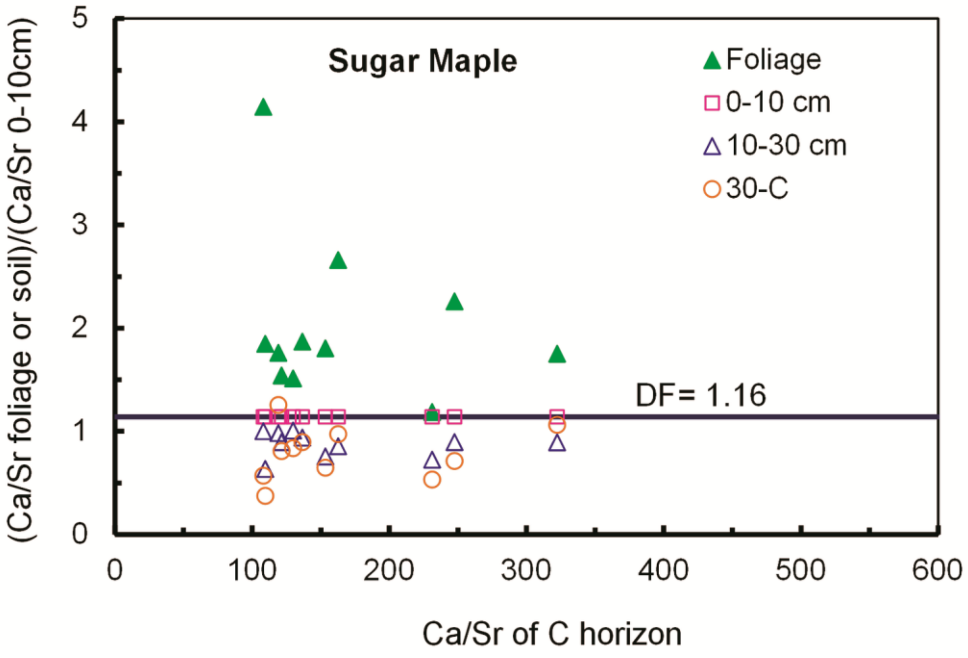

Figure 8. The Ca/Sr ratio of leaves of various species compared, at the sites where they co-occur, to that of species with known discrimination factors from Blum et al. (in review). Slopes with different letters differ significantly at $\alpha \leq 0.05$.