

CANOPY TREE–SOIL INTERACTIONS WITHIN TEMPERATE FORESTS: SPECIES EFFECTS ON pH AND CATIONS

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Abstract. We quantified soil acidity and exchangeable cations in the forest floor and upper 7.5 cm of mineral soil beneath the canopies of individual trees of six different species in a mixed-species forest in northwestern Connecticut. Soil pH decreased in a sequence starting with sugar maple (*Acer saccharum*) > white ash (*Fraxinus americana*) > red maple (*Acer rubrum*) > beech (*Fagus grandifolia*) > red oak (*Quercus rubra*) > eastern hemlock (*Tsuga canadensis*). The differences among species were largest in the forest floor and the top 7.5 cm of mineral soil. Exchangeable Ca and Mg in the 0–7.5 cm mineral soil layer were significantly higher beneath sugar maple than all other species, with the exception of white ash. There were negligible differences among species in the quantity of exchangeable Ca and Mg in the forest floor. In the 0–7.5 cm mineral soil layer, exchangeable Ca was positively correlated with the content of unweathered Ca in the parent material, but the relationship differed among species. There was a large increase in exchangeable Ca in the soils beneath sugar maple but a negligible increase in the soils beneath hemlock and red maple. Exchangeable Al and Fe were highest beneath hemlock and lowest beneath sugar maple. The differences in pH and exchangeable cations between sugar maple and hemlock are likely due to interspecific differences in the introduction of acidity (e.g., organic acids) and Ca uptake and allocation. Observing an association between tree species and specific soil chemical properties within mixed-species stands implies that changes in the distribution and abundance of tree species alters the spatial and temporal pattern of soil acidity and cation cycling in this forest.

Key words: community; ecosystem; exchangeable cations; pH; soil acidity; soil–plant interactions; temperate forest.

INTRODUCTION

Likens et al. (1996) provided strong circumstantial evidence that base cation depletion (notably calcium) associated with acid rain was responsible for a significant decline in net primary production at the Hubbard Brook Experimental forest over the last decade. Although the concentration of acidifying agents in precipitation is currently decreasing, so are the concentrations of base cation inputs from the atmosphere (Hedin et al. 1987, 1994), suggesting that it will take many years for ecosystems to return to predisturbance states (Likens et al. 1996). In support of Likens et al. (1996), Wilmot et al. (1994, 1996) found that base cation fertilization in a base-poor, acidic site in Vermont increased rates of photosynthesis and radial growth and improved crown vigor in sugar maple (*Acer saccharum*).

Changes in soil acidity and the availability of cations are also influenced by biotic processes unrelated to human activity. The mechanisms by which tree species

influence soil acidity and exchangeable cations are severalfold and include interspecific differences in the uptake of exchangeable cations and anions (Alban 1982), nitrogen fixation, and ensuing nitrification (van Miegroet and Cole 1984), the production of litter high in organic acid content (Ovington 1953), and the stimulation of mineral weathering (Tice et al. 1996). While there is a mechanistic basis for the effects of tree species on soil acidity and the quantity of exchangeable cations, there are few studies that have examined the effect of individual trees on soil chemistry. Zinke (1962) found significant variation in soil pH around tree bases of *Pinus contorta*. Crozier and Boerner (1986) found that stemflow influenced soil pH and exchangeable calcium around tree bases in Ohio. Whether these are general patterns and whether tree-induced variation in soil pH and exchangeable cations influence forest dynamics and ecosystem processes is poorly understood.

In related research, Van Breemen et al. (1997) found that white ash (*Fraxinus americana*) trees occurred on soil parent material high in total Ca and Mg, while the parent material beneath beech (*Fraxinus americana*) and red oak (*Quercus rubra*) trees was low in total Ca

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and Mg. Individual hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), and red maple (*Acer rubrum*) trees occurred over a wide range of total Ca and Mg in the parent material. These results raised the question of whether the pH and the quantity of exchangeable cations in the soils beneath these different tree species resulted from the weathering of parent material that differed in its mineralogical composition, or from the effects of the tree species found on those sites. The objectives of this study were to (1) characterize the pH and the quantity of exchangeable cations in the forest floor and the surface mineral soil beneath different canopy tree species, and (2) assess whether the process of species replacement could influence ecosystem nutrient (e.g., Ca) cycling.

MATERIALS AND METHODS

Study sites

This research was conducted on the Canaan Mountain Plateau at elevations of 300–500 m in northwestern Connecticut (42° N, 73°15' W). One site was located on land belonging to the Bridgeport Hydraulic Company (BHC) near the Wangum Reservoir. The second site was located on land belonging to the Great Mountain Forest (GMF) east of Wampee pond. Soils at Wampee and Wangum are well-drained Typic Dystrachrepts (Hill et al. 1980). Both sites are ~2.5 ha in size. At Wampee the soils have an uneven surface topography with boulders emerging through the soil surface. The site has not been cleared for agriculture and trees range in age from 80 to 150 yr with maximum diameters near 60 cm dbh (diameter at breast height). The Wangum site has a more uniform surface topography but also shows no signs of agriculture. Apart from several large trees (>80 cm diameter), the trees at Wangum are in the same age and size classes as those found at Wampee. At both sites, the regolith consists of 0–1 m well-drained Wisconsinian sandy-loam glacial till over a mica schist bedrock.

We sampled soils beneath the canopies of the six dominant tree species at these two sites. The study species were: beech (*Fagus grandifolia* Ehrh.), hemlock (*Tsuga canadensis* Carr.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and northern red oak (*Quercus rubra* L.). At each site, we randomly selected six replicate trees of each species ($N = 72$).

Soil sampling

Two replicate soil sampling locations 0.5–5 m apart were established beneath each canopy tree. The replicate soil sampling locations were >2 m from each tree base but within the vertically projected crown of each target tree. At each of the two sampling locations, we removed two 5 × 15 cm cores. The first core sampled the forest floor (<15 cm thick) and the mineral soil. The second core, extracted immediately adjacent

to the first core, sampled the top 15 cm of mineral soil only. We cored soils using a soil bulk density sampler lined with a vertically precut polycarbonate liner.

All cores were cut with a sharp knife along the vertical division of the polycarbonate liner and separated into three layers: the forest floor, the 0–7.5 cm layer, and the 10–15 cm layer. Typically, the forest floor material was <15 cm thick and in most cases the top 7.5 cm of mineral soil was present in the first core. In the case where the top 7.5 cm of mineral soil was not recovered in the first core, we divided the second core into the top 7.5 cm of mineral soil and the lower 10–15 cm of mineral soil. The three soil layers were separated from one another using a sharp knife. The boundary between the forest floor and the mineral soil was invariably abrupt (<0.5 cm).

Sample analysis

Forest floor samples were sieved through an 8-mm mesh to remove roots, dried for 4 d at 105°C, and then weighed (± 0.01 g). The mineral soil samples were weighed, large stones removed, and the soils placed directly into the drying oven at the same temperature and for the same duration. Following drying, mineral soil samples were sieved through an 8-mm mesh to remove root material and stones (>1.0 cm diameter). Dry soil and large stones were weighed. Stone bulk density was estimated from a subsample of stones (calculated to be 2.61 g/cm³) and soil bulk density measurements were adjusted. We oven-dried our samples to allow determination of bulk density on the same material as that used for chemical analysis. Oven-drying influences the chemical composition differently from the usual air-drying: extractable nitrogen and phosphorus are commonly increased by oven-drying, but soil pH and exchangeable cations usually show little or no change, except in strongly reduced soils (Molloy and Lockman 1979, Houba et al. 1994).

Forest floor samples used in all chemical analyses were ground in a tissue pulverizer prior to analysis. For the forest floor and upper 0–7.5 cm of mineral soil, we measured soil pH and exchangeable cations. For the lower mineral soil horizon we only measured soil pH.

Soil pH in the forest floor was measured in a 10:1 slurry of deionized water and 2.0 g of sample. Soil pH in the mineral soil was measured in a 2:1 slurry of deionized water and 10.0 g of sample (Hendershot et al. 1993a). All samples were stirred once initially and after 15 min, and then allowed to settle for 0.5 h before pH was measured on an Orion pH meter 610A (Fisher, Springfield, New Jersey, USA).

All cations were extracted using 0.1 mol/L BaCl₂ (Ngewoh et al. 1989, Hendershot et al. 1993b). Prior to analysis, 1.5 g of forest floor material from each replicate sample at each tree was combined. The same was done for mineral soil samples. A 0.5-g subsample of the homogenized forest floor mix, and the 3.0-g

TABLE 1. Soil pH and the quantity (mol_e/m^2) of exchangeable Ca, Mg, Al, and Fe in the forest floor and the 0–7.5 cm of mineral soil. Row values with different superscript letters are significantly different from one another. Values are the mean followed by the standard error of the mean. NS = not significant at the $P < 0.05$ level.

Soil property	Wampee	Wangum	df	<i>F</i>	<i>P</i>
pH	4.30 \pm 0.04 ^a	4.47 \pm 0.04 ^b	1,198	11.66	<0.001
Calcium	1.590 \pm 0.24 ^a	1.962 \pm 0.20 ^a	1,47	1.06	NS
Magnesium	0.511 \pm 0.05 ^a	0.471 \pm 0.44 ^a	1,47	1.07	NS
Aluminum	2.676 \pm 0.24 ^a	2.906 \pm 0.24 ^a	1,49	0.42	NS
Iron	0.261 \pm 0.03 ^a	0.196 \pm 0.02 ^b	1,48	4.41	<0.05

sample of the homogenized mineral soil mix was used for analysis. Samples were placed into 50-mL plastic centrifuge tubes, and 30.0 mL of the 0.1 mol/L BaCl_2 solution was added to each tube. The tubes were capped and placed on a shaker table at 45 rpm for 2 h. The suspensions were centrifuged at 3500 rpm, and the supernatant filtered through Whatman Number 41 filter paper. Concentrations of exchangeable calcium, magnesium, iron, and aluminum were measured using a Perkin-Elmer Plasma 400 Emission Spectrometer P400 (Perkin Elmer, Norwalk, Connecticut, USA). Standards were prepared from 1000 and 10 000 mg/L liquid stock solutions and diluted using 0.1 mol/L BaCl_2 .

The total quantity of Ca and Mg in unweathered parent material was determined by melting soils to $\text{Li}_2\text{B}_4\text{O}_7$ beads at 1100°C followed by x-ray fluorescence microscopy as described by Van Breemen et al. (1997).

Statistical analyses

The data were analyzed as a complete factorial design using PROC GLM in SAS (1987). There were two independent variables: sites (two levels), and species (six levels). Because of the large differences in the pH and the concentration of cations with increasing depth in the soil, we analyzed differences among species and sites separately for each soil horizon. Assumptions of normality and homogeneity of variance were met. We used Tukey's test for post hoc mean comparisons for each of the main effects (site, species). This test protects the experimentwise alpha at 0.05.

To examine the effect of mineral-bound Ca and Mg on the exchangeable base cations pools, we performed an analysis of covariance (ANCOVA) using the GLM procedure of SAS (1987) where exchangeable Ca and Mg were modeled as a function of total soil Ca and Mg (covariate) and the species identity of the overstory canopy tree (treatment effect). When there was a significant species \times covariate interaction term, we performed a series of species-specific linear regressions and tested for homogeneity of slope and intercept among species (SAS 1987). Significant differences among species in slopes and intercepts were tested using paired *t* tests. For the six species, there were 15 possible pairwise comparisons. Rather than using a Bonferroni adjustment ($\alpha = 0.05/15 = 0.003$), significant slope and intercept differences among species

were accepted at the $P < 0.0002$ level protecting the overall significance level well below 0.05.

RESULTS

Soil pH was slightly but significantly higher at Wangum than at Wampee (Table 1). The total quantity (=sum of the forest floor and upper 7.5 cm of mineral soil) of exchangeable Ca, Mg, and Al was not significantly different between Wampee and Wangum (Table 1). There was a small but significant difference in the total quantity of exchangeable Fe between sites (Table 1).

The average pH of the three soil horizons decreased in the order sugar maple > white ash > red maple > beech > red oak > hemlock. The differences among species were largest in the forest floor, more subtle in the 0–7.5 cm mineral soil layer, and least pronounced in the 7.5–15 cm mineral soil layer, suggesting that a species-related pattern was attenuated with depth (Fig. 1).

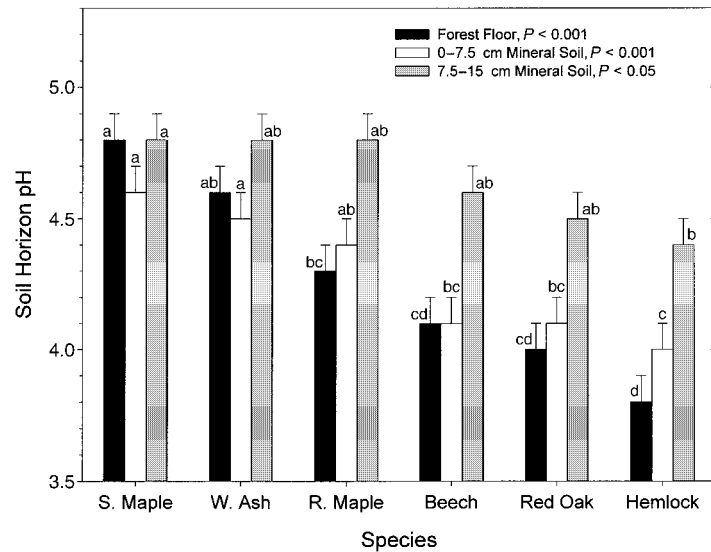
The total quantities of exchangeable Ca and Mg were highest beneath sugar maple, intermediate beneath white ash, and lowest beneath the canopies of red maple, beech, red oak, and hemlock (Fig. 2a, b). The largest differences among species in the quantity of exchangeable Ca and Mg were observed in the upper 7.5 cm of mineral soil (Fig. 2a, b).

The total quantities of exchangeable Al and Fe were highest beneath hemlock, intermediate beneath red oak, beech, and red maple, and lowest beneath white ash and sugar maple (Fig. 2c, d). The size of the total exchangeable Al and Fe pool accounted for by the forest floor pool increased significantly from sugar maple (Al = 0.041, Fe = 0.006) to hemlock (Al = 0.83, Fe = 0.107).

The ranking of species from lowest to highest exchangeable Al and Fe was nearly opposite that of pH (Fig. 1) and Ca and Mg (Fig. 2a, b). There were highly significant positive correlations between soil pH and exchangeable Ca and Mg (Table 2). Conversely, there were significant negative correlations between pH and exchangeable Al and Fe (Table 2). Exchangeable Ca was negatively correlated with exchangeable Al and Fe, while exchangeable Mg was negatively correlated with Al (Table 2).

For exchangeable Ca, the species, covariate (total

FIG. 1. The mean (± 1 SE) pH of soils at three different depths. Bars of the same color but with different superscript letters are significantly ($P < 0.05$) different from one another. S. Maple = sugar maple, W. Ash = white ash, R. Maple = red maple.



soil Ca), and species \times covariate interaction terms in the ANCOVA were all significant, violating model assumptions (SAS 1987). Therefore, the Ca data were analyzed using a series of species-specific linear regressions between total and exchangeable Ca (Fig. 3). Sugar maple had a significantly larger slope than hemlock and red maple, the two species with the smallest slopes (Fig. 3). Only the slope for sugar maple was larger than that of exchangeable Ca as a function of total Ca across all species (exchangeable Ca = $-0.45 + 0.093$ (mineral Ca); $P < 0.001$, $r^2 = 0.31$). The variation in total soil Ca beneath beech, white ash, and red oak was small, and therefore the effects of these species on exchangeable Ca should not be extrapolated to high total Ca contents.

In the Mg ANCOVA, only the covariate (total Mg content) and treatment (species) effects were significant. It was therefore possible to adjust the mean exchangeable Mg content in the mineral soil beneath the different species by the contribution of the covariate (SAS 1987). However, the difference in the quantity of exchangeable Mg in the 0-7.5 cm mineral soil layer after adjusting for the effect of the covariate differed little from those presented in Table 2. Consequently, we did not report the adjusted values.

DISCUSSION

There were large interspecific differences in the pH and the quantity of exchangeable cations in the forest floor and in the top 7.5 cm of mineral soil. The processes involved in creating the observed variation in pH and exchangeable cations among species are likely to be threefold: (1) interspecific differences in the production of organic acids from decomposing litter that change the relative quantities of exchangeable base (Ca, Mg) and acid (Al, Fe) cations in soils, (2) differences in cation uptake and allocation to biomass pools

with differing turnover times, and (3) variation in the mineral content of the parent material. Higher organic acid production and lower soil pH have been noted in sites dominated by species whose litter is relatively recalcitrant to the decomposition process (Konova 1966). Hemlock litter and bark have high concentrations of tannins (Millen 1995) that slow the rate of litter decomposition (White 1986, 1991) and are likely to have contributed to the formation of a thick and highly acidic forest floor beneath hemlock (Fig. 1; A. C. Finzi et al., *unpublished manuscript*). Low soil pH increases the solubility of aluminum and iron, which outcompete base cations for binding sites on the exchange complex (e.g., Johnson et al. 1994). Thus, beneath hemlock base cations are likely to be displaced from exchange sites to the soil solution where they are bound by organic or mineral acids and transported to lower soil horizons or lost from the ecosystem.

Calcium uptake and/or allocation to biomass pools with differing turnover times may explain the high soil pH and the large quantity of exchangeable Ca beneath sugar maple. Alban (1982), in a plantation study of deciduous and evergreen species, found that the total quantity of Ca in each of the four vegetation types did not differ significantly but that the location of the Ca pools did. He found larger quantities of exchangeable Ca in the forest floor and smaller quantities of exchangeable Ca in the mineral soil beneath white spruce and aspen than beneath red and jack pine. He attributed these differences to Ca uptake from the mineral soil and return to the forest floor via litter fall. Sugar maple trees are characterized by deep crowns (Canham et al. 1994) and relatively high leaf litter Ca concentrations ($\sim 1.35\%$, Wilmot et al. 1994). High leaf litter Ca concentrations coupled with a large quantity of leaf litterfall could increase the quantity of exchangeable Ca in the surface soils beneath sugar maple.

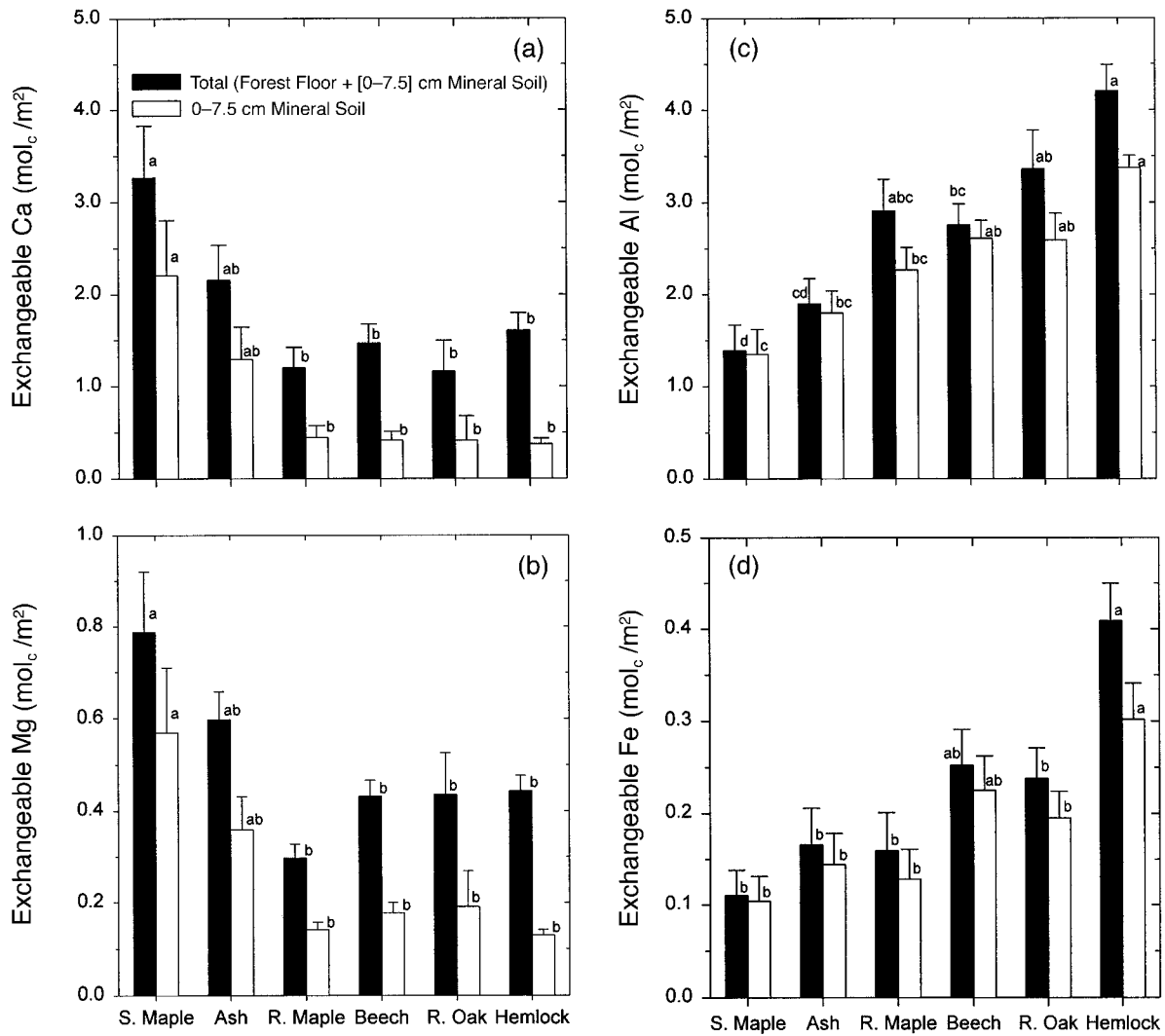


FIG. 2. Mean quantities [mol_c/m² ± 1 SE] of exchangeable Ca in the forest floor and top 7.5 cm of mineral soil beneath the different tree species. Bars with the same shading but with different letters are significantly ($P < 0.05$) different from one another. (a) Calcium, (b) magnesium, (c) aluminum, and (d) iron.

TABLE 2. Correlation analysis of soil pH and exchangeable calcium, magnesium, aluminum, and iron.

Soil property	Soil pH	Calcium	Magnesium	Aluminum	Iron
pH	1				
Calcium	0.71*** (58)	1			
Magnesium	0.54*** (61)	0.87*** (60)	1		
Aluminum	-0.73*** (61)	-0.66*** (59)	-0.60*** (62)	1	
Iron	-0.81*** (60)	-0.40** (59)	-0.20 (62)	0.62*** (61)	1

Note: Sample sizes are in parentheses. This analysis is based on the average soil pH in the forest floor and upper 7.5 cm of mineral soil and the total quantity of exchangeable cations (mol_c/m²) in the forest floor and upper 7.5 cm of mineral soil. Significant correlations are indicated as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

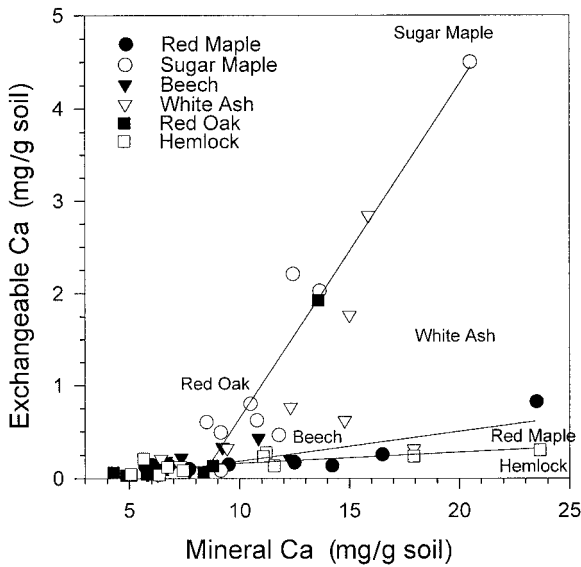


FIG. 3. Species-specific linear regressions of exchangeable calcium as a function of the mass of total soil Ca. The regression lines were significant for sugar maple ($P < 0.001$, $r^2 = 0.88$), red maple ($P < 0.01$, $r^2 = 0.68$), and hemlock ($P < 0.05$, $r^2 = 0.48$). White ash, beech, and red oak occurred over a restricted range of total soil Ca, and no regression analysis was performed for these species.

The variation in soil pH and exchangeable bases beneath beech, red oak, and white ash appear to reflect the composition of the parent material under these trees. The soil pH and the quantity of exchangeable bases beneath beech and red oak trees were low and these tree species only occur on soils low in total Ca and Mg at GMF (Van Breemen et al. 1997). The relatively thick forest floor and the slower rates of organic matter decomposition beneath these species may reinforce this pattern by increasing the quantity of organic acids produced (Konova 1966). In contrast, the soils beneath white ash had a high pH and large quantities of exchangeable bases and white ash occurs on soils with the highest total Ca and Mg contents measured at GMF (Van Breemen et al. 1997).

The soil pH was intermediate beneath red maple, but the quantity of exchangeable Ca in red maple soils was the lowest of all six species studied. The content of total (i.e., unweathered) Ca beneath red maple was not significantly different than sugar maple and hemlock (Fig. 3, Van Breemen et al. 1997), and similar to hemlock, there was a negligible increase in exchangeable Ca with an increase in total Ca beneath red maple. Red maple leaf litter decomposes rapidly (Melillo et al. 1982), and relative to the species we studied, the forest floor beneath this species is neither excessively thick (Finzi et al. 1998), nor acidic (Fig. 1). The production of organic acids is unlikely to explain the small quantity of exchangeable Ca beneath red maple. Calcium redistribution from lower soil horizons to the soil surface via litterfall is possible, but following mineralization

from organic matter Ca would have to be rapidly consumed or lost from the exchangeable pool to maintain the small exchangeable Ca pool beneath red maple. Calcium storage in wood may be an additional explanation.

The variation in soil pH and the quantity of exchangeable cations at GMF are likely to be controlled by all three mechanisms discussed—the generation of acidity and changes in the ratio of acid vs. base cation availability, interspecific differences in cation uptake and allocation to biomass pools with different turnover times, and subtle variation in the mineral composition of the parent material beneath the different species. Clearly, we need to test these hypotheses with mechanistic studies of cation cycling in this forest.

Our results are correlational and we cannot discount the possibility that prior differences in soil chemistry are responsible for the patterns we observed beneath the different species; the distribution of canopy trees in the replicate stands may not be independent of the soil properties we measured in this study (e.g., an association between the quantity of exchangeable Ca in soils and the presence of sugar maple). However, the degree of confounding in this study is likely to be much less than that in other studies. First, our analyses of exchangeable cations accounted for variation in the mineral composition of the soil parent material beneath the different tree species. Sugar maple, red maple, and hemlock trees occurred along an overlapping range of mineral soil Ca content, but differed significantly in the quantity of exchangeable Ca in the upper 7.5 cm of mineral soil. The most parsimonious explanation for this result is that the biotic processes of Ca uptake, allocation, and retention influence the availability of exchangeable Ca in the surface soil. Second, soil texture did not differ significantly between the two study sites (Van Breemen et al. 1997). Differences in soil texture are often associated with different vegetation types, both of which can contribute to variation in soil pH and exchangeable cations (e.g., Pastor et al. 1984, Binkley 1995). Third, soil pH and cation contents change beneath tree species in less time than the average age of the individuals in this study (e.g., <40 yr, Binkley 1995 and references therein).

Conclusions

If the differences in surface soil chemistry among tree species are at least partly caused by the trees themselves, then decadal changes in surface soil acidity and cation cycling will be driven by tree population and community dynamics. For example, the large differences in soil chemistry beneath sugar maple and hemlock trees could lead to different ecosystem-level stable states because these species appear to change the chemistry of an initially similar soil substrate (Figs. 2, 3). However, alternate stable states imply that the changes in soil chemistry beneath these tree species influence the outcome of interspecific seedling competition in a

manner that favors self-replacement. While there is evidence that sugar maple and hemlock self-replace in the upper Midwest (Frelich et al. 1993), differences in soil acidity and base cation availability have not been identified as the causative factors governing self-replacement. Self-replacement by sugar maple and hemlock does not appear to be widespread in New England forests. Nevertheless, there exists a potential feedback between tree species and soil chemistry at the level of individual trees that deserves further study.

Sugar maple and hemlock are two species that often dominate late-stages of succession (Forcier 1975, Frelich et al. 1993, Kobe et al. 1995, Pacala et al. 1995, 1996). Significant declines in the abundance of hemlock due to defoliation by the woolly adelgid have been reported in southern New England (Houston 1994, Steward and Horner 1994). The results of this study suggest that if sugar maple replaces hemlock following defoliation by the woolly adelgid, significant changes in soil chemistry (e.g., increases in soil pH and exchangeable bases) should follow. Identifying the mechanisms by which different tree species change soil chemistry is necessary to predict the effects of natural and anthropogenic disturbances on nutrient cycling in southern New England forests.

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