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Calcium mineralization in the forest floor and surface soil beneath different tree species in the northeastern US

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Abstract

Calcium (Ca) is an important element for neutralizing soil acidity in temperate forests. The immediate availability of Ca in forested acid soils is largely dependent on mineralization of organic Ca, which may differ significantly among tree species. I estimated net Ca mineralization in the forest floor and upper 15 cm of mineral soil beneath six tree species in a mixed-species forest in northwestern Connecticut, using the buried bag method. Net Ca mineralization in the forest floor was significantly correlated with mass loss of the decomposing forest floor litter. Higher mass loss fractions during the summer and in forest floors beneath sugar maple (*Acer saccharum*) and white ash (*Fraxinus americana*) coincided with higher net Ca mineralization rates. More Ca was released per unit mass loss of forest floor beneath sugar maple and white ash (362 and 390 mmol kg^{-1}, respectively) than beneath American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), red oak (*Quercus rubra*) and hemlock (*Tsuga canadensis*) (183, 133, 147, and 190 mmol kg^{-1}, respectively). Due to the high forest floor mass beneath red maple, beech, red oak, and hemlock, net Ca mineralization in the forest floor per unit area beneath these tree species did not differ significantly from sugar maple and white ash (ranging between 80 mmol m^{-2} per year for beech and 141 mmol m^{-2} per year for sugar maple). Net Ca mineralization in the mineral soil was significantly larger beneath sugar maple (142 mmol m^{-2} per year) than beneath the other tree species (ranging between -10 mmol m^{-2} per year for beech and 55 mmol m^{-2} per year for white ash). These results show that Ca mineralization rates are large and differ significantly among tree species, affecting the spatial pattern of soil acidity and Ca availability in a mixed-species forest stand.

Keywords: Buried bag method; Calcium availability; Calcium immobilization; Soil acidity; Temperate forest; Tree species effects

1. Introduction

Acid rain has depleted exchangeable Ca pools in many soils of forests throughout the northeastern United States (Federer et al., 1989; Joslin et al., 1992; Likens et al., 1996, 1998), and Ca depletion in soils have been associated with increased canopy dieback (Wilmot et al., 1995, 1996). Calcium availability influences soil acidity, and it has been suggested that soil pH and the supply of base cations affect plant productivity and community composition mainly via their effects on N supply (Giesler et al., 1998). Net Ca mineralization from decomposing litter is one of the highest Ca fluxes within temperate forest ecosystems and determines to a large extent the immediate Ca availability for plant uptake in these systems (e.g. Likens et al., 1998).

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A few studies have attempted to quantify net Ca mineralization rates of fresh litter by using litter bags and measuring concentrations and absolute amounts of Ca in decomposing litter. While some studies showed a net release of Ca closely related to weight loss (Attiwill, 1968; Gosz et al., 1973) indicating that Ca is a structural litter component, others found Ca immobilization during the first years of litter decomposition (Bockheim et al., 1991; Van Wesemael, 1993). Calcium immobilization can occur through adsorption of Ca on exchange sites that are created in litter during decomposition (Staaf and Berg, 1982; Van Wesemael, 1993). Different fractions of litter (e.g. leave, bark) have different rates of decomposition and of net Ca mineralization. Thomas (1969) showed that Ca and weight loss of decomposing leaves, fruits, and twigs of dogwood trees (*Cornus florida* L.) proceeded at considerably different rates, influencing the overall net Ca mineralization in magnitude and time. I am not aware of any studies that have estimated net Ca mineralization from the combined organic matter accumulated in the forest floor and the surface soil.

Rates of weight loss of litter vary widely among northeastern US tree species (e.g. Melillo et al., 1982; Aber et al., 1990). Species with slow rates of litter decomposition accumulate significantly thicker forest floors beneath their crowns (Finzi et al., 1998), and it is unclear whether total net Ca mineralization from the forest floor and upper mineral soil organic matter varies significantly beneath different tree species. Differences in the supply of Ca from litter decomposition among tree species, both in time and space, may have large effects on forest dynamics. The objective of this study was to identify tree species effects on net Ca mineralization for six most common tree species in a forest in northwestern Connecticut. I estimated net Ca mineralization beneath five temperate hardwood and one coniferous tree species by measuring changes in exchangeable Ca from forest floor and surface soil samples incubated in plastic bags that were buried in the field.

2. Materials and methods

2.1. Study site

This study was done at Great Mountain Forest (GMF) in northwestern Connecticut. It is a second growth forest stand (~80–130 years old) that has experienced some logging activities but no recent history of agriculture. Soils are acidic, well drained, sandy loams (Typic Dystrochrepts) derived from glacial till over mica-schist bedrock. Net Ca mineralization was investigated beneath the six most common tree species at this site: sugar maple (*Acer saccharum*), hemlock (*Tsuga canadensis* Carr.), American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana*) and red oak (*Quercus rubra* L.). A sparse and scattered under story vegetation is present consisting primarily of hay scented fern (*Dennstaedtia punctilobula*). Within GMF 36 plots were selected where four to ten mature trees of one of the six tree species dominated each plot. Within the area of each plot (diameter of 25 m) the target species occupied between 50 and 85% of total basal area, except for three white ash plots that occupied 40% of total basal area.

2.2. Sampling

Net Ca mineralization in the field was estimated by the buried polyethylene bag technique (Eno, 1960) that has been widely used for N mineralization in the past (e.g. Pastor et al., 1984; Vitousek and Matson, 1985). Effects of daily and seasonal temperature fluctuations on decomposition are accounted for, but moisture conditions do not change in the bags during the incubation. The incubation periods need to be long enough to establish significant changes in exchangeable Ca concentrations. Because the mineralization/available pool ratio in the forest floor and mineral soil was expected to be much smaller for Ca than for N, the incubation period required to observe significant changes in exchangeable Ca is longer than is commonly used for N mineralization studies. Samples therefore were incubated during one year divided in two periods. The first was from 18 June 1999 until 3 November 1999 (summer incubation). The second started at 3 November, where freshly fallen leaf litter was included in the forest floor samples, and lasted until 18 June 2000 (winter incubation).

One forest floor sample was taken by cutting around the edges of an acrylic square (20×20 cm^2) that was randomly placed on top of the forest floor within the vertically projected crown of a mature tree of the target species, but at least 2 m away from the stem,

within each plot. Forest floor was removed gently by cutting forest floor from the mineral soil beneath. Depth of the forest floor was measured. Where the forest floor was removed, two soil cores (diameter 4.5 cm) were taken to a depth of 15 cm, and the two cores were bulked. In the laboratory samples of forest floor and mineral soil samples were thoroughly homogenized separately. A sub-sample (initial sample) of the forest floor and mineral soil was taken for water content, exchangeable Ca, and pH measurement. The remainders of the forest floor and mineral soil samples were divided into four equal portions. Each portion was weighed and put in a polyethylene bag that was closed with a knot. The bags were returned to the exact spot where they were sampled. Mineral soil bags were pushed back into the holes that were cored and forest floor bags were laid on top in the $20 \times 20\ cm^2$ area where forest floor was removed. The samples were then covered with fresh forest litter and a piece of poultry wire to protect bags from shifting. After the field incubation, the bags were returned to the laboratory where intact bags with forest floor and mineral soil were each bulked for each plot (final samples). Burst bags were discarded (<10%).

2.3. Analyses

Initial and final samples were dried (70 °C for 72 h), weighed, sieved (8 mm mesh) and sub-sampled for gravimetric moisture content (105 °C for 48 h). Gravimetric moisture content in incubated forest floor and mineral soil samples did not differ among tree species. Gravimetric moisture content in the mineral soil was on average slightly higher during the winter incubation than during the summer incubation (7.8 and 5.9%, respectively). Calculated weight loss during the incubation was based on oven dried (105 °C) samples. Initial and final samples were measured for pH in 10:1 slurries of de-ionized water with forest floor and 2:1 slurries with mineral soil (glass electrode, Accumet). All samples were stirred once initially and after 15 min and then allowed to settle for 0.5 h before pH was measured. Exchangeable Ca was measured according to a slightly modified method by Hendershot et al. (1993). Five grams of forest floor and ten grams of mineral soil were extracted with 100 ml of 0.1 M $BaCl_2$. Samples were shaken for 2 h on a shaker table and then filtered through Whatman no. 41 filter paper. Calcium concentrations were determined with an Inductively Coupled Plasma Emission Spectrometer (Perkin-Elmer). Changes in exchangeable Ca concentrations between initial and final forest floor samples were corrected for weight loss. The mineral soil samples did not show a measurable change in weight during the incubation.

Differences between initial and final pH and between initial exchangeable Ca from summer and winter incubation were tested with a paired *t*-test. To test differences among tree species in initial exchangeable Ca concentrations (mmol kg^{-1}), net Ca mineralization per unit mass (mmol kg^{-1} per day) and per unit area (mmol m^{-2} per year), and forest floor mass and forest floor mass loss, I used post-hoc ANOVA analyses (Tukey's test). An ANCOVA was done on net Ca mineralization in the forest floor per unit mass with forest floor mass loss as covariate and species identity as fixed factor. When there was a significant species × covariate interaction term, I did a series of species-specific linear regressions. All statistical analyses were done in SPSS (version 7.5).

3. Results

The forest floor pH was always higher for summer and winter incubations in the final sample than in the initial sample (Table 1). In the mineral soil, pH also increased during the winter incubation, but decreased during the summer incubation. Differences in pH of forest floor and mineral soil were more pronounced and always significant for the winter incubation (beech forest floor at $P < 0.1$, all other samples at $P < 0.01$) where the incubation period was longer (7.5 months).

Initial exchangeable Ca concentrations in the forest floor and mineral soil differed significantly among tree species ($P = 0.001$ and 0.007 for forest floor and mineral soil on 18 June 1999 and $P < 0.001$ and 0.005 on 3 November 1999) and were highest beneath sugar maple and white ash and lowest beneath red maple, red oak and hemlock (Fig. 1). Initial Ca concentrations were sometimes lower and sometimes higher at the start of the winter incubation than at the start of the summer incubation, but mostly not significantly. Tree species significantly affected net Ca mineralization per unit mass in the forest floor during winter incubation ($P = 0.007$) and in the mineral soil

Table 1
Mean pH with standard error in brackets ($n = 6$), in the forest floor and first 15 cm of the mineral soil during summer and winter incubation beneath the different tree species

Species	pH			
	Summer		Winter	
	Initial	Final	Initial	Final
Forest floor				
A. saccharum	4.57 (0.15)	4.73 (0.17) ns[a]	4.47 (0.16)	5.27 (0.30)**
F. americana	4.76 (0.27)	4.76 (0.38) ns	4.30 (0.22)	5.03 (0.28)**
F. grandifolia	4.21 (0.16)	4.30 (0.10) ns	4.16 (0.27)	4.75 (0.30)*
A. rubrum	3.89 (0.08)	3.92 (0.06) ns	3.72 (0.12)	4.16 (0.16)**
Q. rubra	4.06 (0.14)	4.19 (0.13)*	3.79 (0.13)	4.40 (0.16)**
T. canadensis	3.71 (0.07)	3.79 (0.07) ns	3.51 (0.14)	3.84 (0.11)**
Mineral soil				
A. saccharum	4.48 (0.18)	4.18 (0.12)*	4.69 (0.32)	5.03 (0.29)**
F. americana	4.66 (0.14)	4.41 (0.23)*	4.16 (0.17)	4.48 (0.17)**
F. grandifolia	4.34 (0.10)	4.14 (0.05)*	4.02 (0.09)	4.49 (0.13)**
A. rubrum	3.93 (0.16)	3.91 (0.15) ns	3.88 (0.15)	4.19 (0.17)**
Q. rubra	4.23 (0.09)	4.13 (0.08)**	3.86 (0.16)	4.13 (0.18)**
T. canadensis	3.74 (0.14)	3.64 (0.12)*	3.83 (0.17)	4.14 (0.14)**

[a] Not significant.
* $P < 0.1$.
** $P < 0.01$.

during summer incubation ($P = 0.01$). Daily net Ca mineralization per unit mass (mmol kg^{-1} per day) in the forest floor and mineral soil during both incubations was highest beneath sugar maple and white ash (Fig. 2). Net Ca mineralization per unit mass was lower during the winter than during the summer and it was much lower in the mineral soil than in the forest floor.

Yearly net Ca mineralization per unit area (mmol m^{-2} per year) in the forest floor did not show significant differences among tree species (Fig. 3). Significant differences were found among tree species in net Ca mineralization per unit area in the mineral soil ($P < 0.001$) and in the total soil profile ($P = 0.005$, Fig. 3). Net Ca mineralization per unit area in the mineral soil was much higher under sugar maple and also under white ash than under the other tree species.

Forest floor mass differed significantly among tree species ($P = 0.001$) and was greatest for hemlock and smallest for sugar maple and white ash (Table 2). The forest floor mass loss during incubation was higher during the summer than during the winter incubation for all tree species. The forest floor mass loss fraction (g kg^{-1} per day) during incubation differed significantly among tree species for both summer and winter incubation ($P = 0.04$ and <0.001, respectively) and was highest for sugar maple and white ash (Table 2). Expressed on an area basis (g m^{-2} per day), however, forest floor mass loss was similar among the six tree species. The ANCOVA, where the net Ca mineralization per unit mass in the forest floor was modeled as a function of mass loss fraction (covariate) and species identity (fixed factor), resulted in a significant species × covariate interaction term ($P < 0.001$), violating the assumption of homogeneity of slope among species. Therefore tree species-specific linear regressions were done. The slope for each species, representing the average amount of Ca that becomes available per amount of decomposed litter (mmol kg^{-1}) is shown in Table 3. Litter of sugar maple and white ash had the highest and red maple the lowest amount of net Ca mineralization per amount of decomposed litter.

4. Discussion

Different processes simultaneously affect the pH during incubation. For instance, mineralization of base

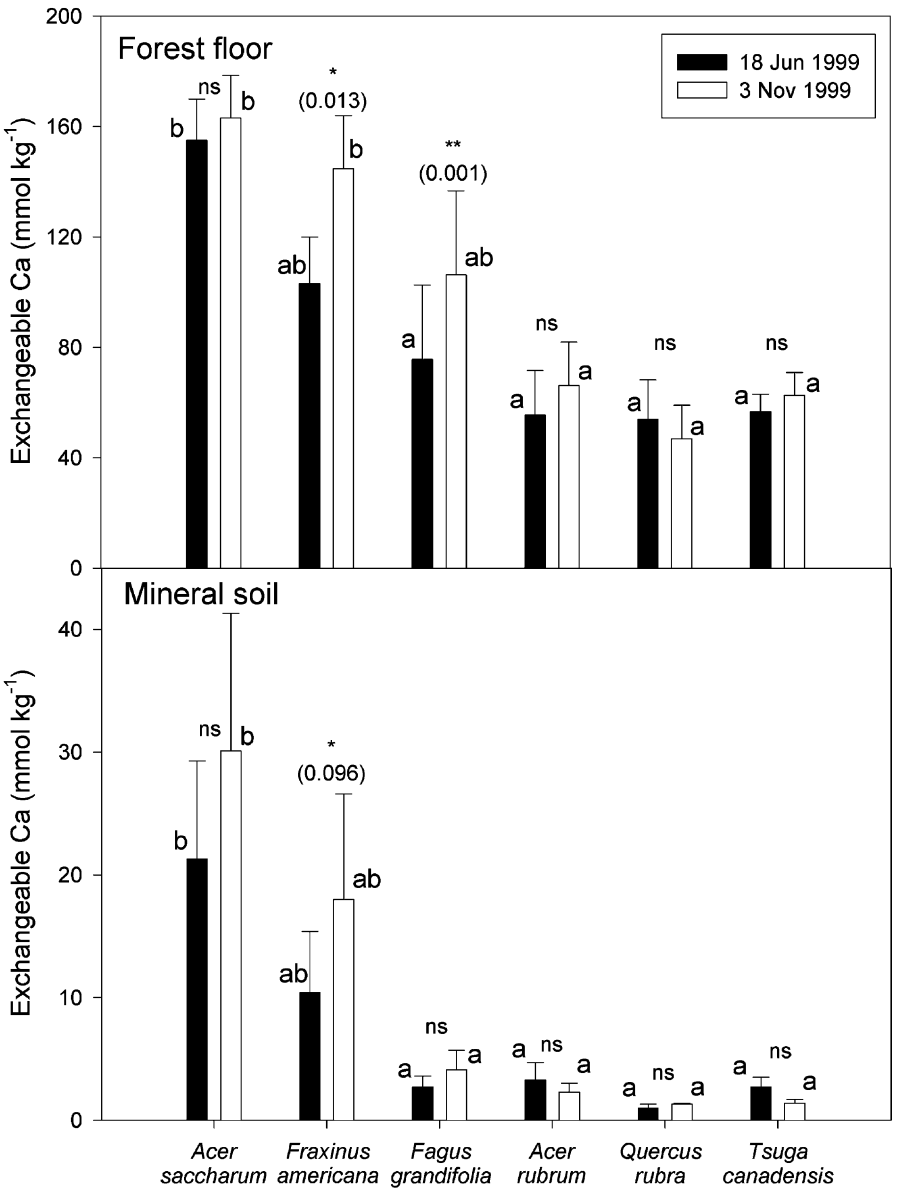

Fig. 1. Mean exchangeable Ca concentrations (±S.E.) in the forest floor and mineral soil at the start of each incubation beneath the different tree species. Significant differences between concentrations from 18 June and 3 November 1999 are indicated as: ns: not significant; *: $P < 0.1$; **: $P < 0.01$. In each panel, bars of the same color with different letters are significantly different from one another at $P < 0.05$.

cations causes an increase in pH, while nitrification leads to a decrease in pH (Van Breemen et al., 1983). The overall increase in pH during incubation of the forest floor, suggests that the effect of base cation mineralization on pH may have been stronger than that of nitrification and other acidifying processes. Nitrification may have played in important role in the pH decrease in the mineral soil during the summer incubation. The low pH values measured in the forest floor and mineral soil beneath red maple, red oak and hemlock, may have slowed down microbial activity and adversely affected Ca mineralization. The initial

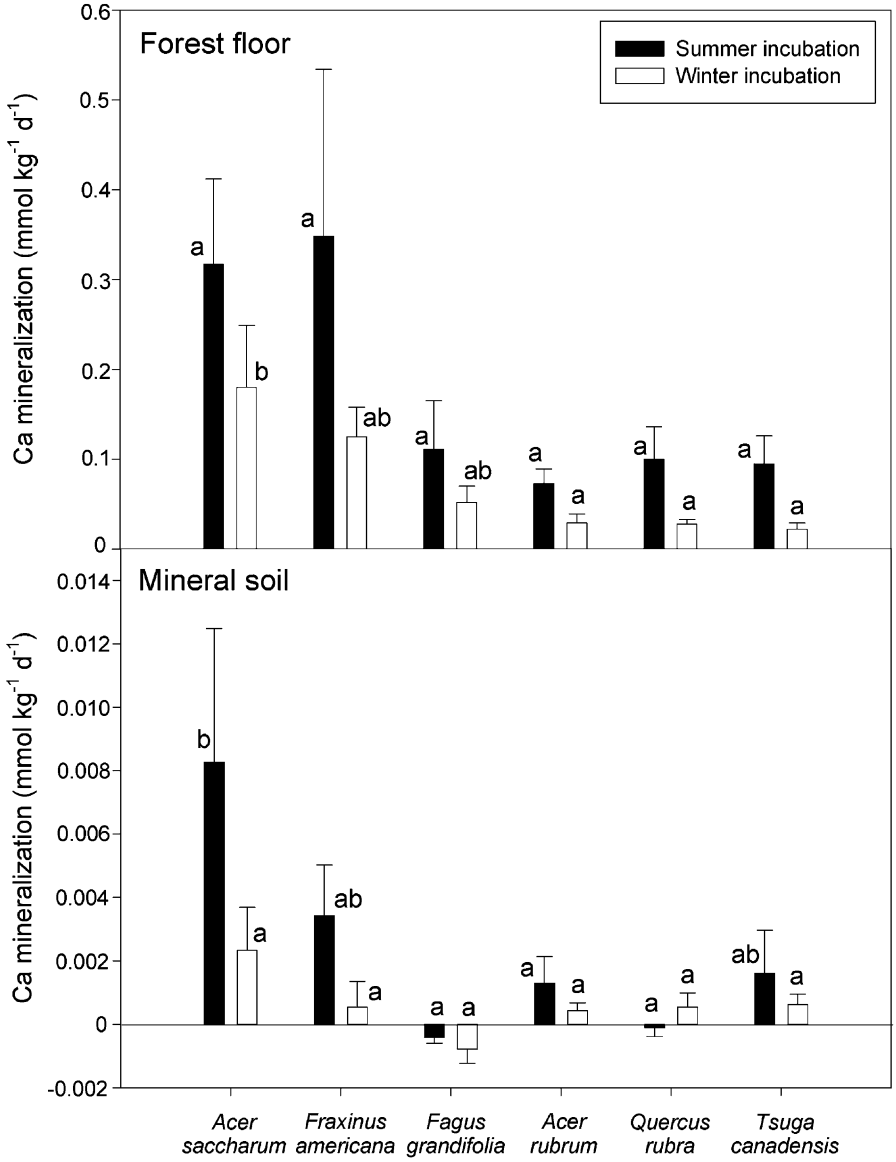

Fig. 2. Mean changes in exchangeable Ca concentrations (±S.E.) in the forest floor and mineral soil during summer and winter incubation beneath the different tree species. In each panel, bars of the same color with different letters are significantly different from one another at $P < 0.05$.

pH and Ca mineralization per unit mass, where summer and winter incubation were combined, showed a significant positive correlation in the forest floor ($R^2 = 0.677$, $P < 0.001$) and a slightly positive correlation in the mineral soil ($R^2 = 0.190$, $P = 0.121$).

Samples from the summer incubation showed a larger average net Ca mineralization per unit mass than samples from the winter incubation for all tree species (except the mineral soil under red oak). Although the winter incubation included fresh litter, the forest floor mass loss fractions were higher during the summer than during the winter incubation and were significantly related to the net Ca mineralization per unit mass. Higher temperatures during the first

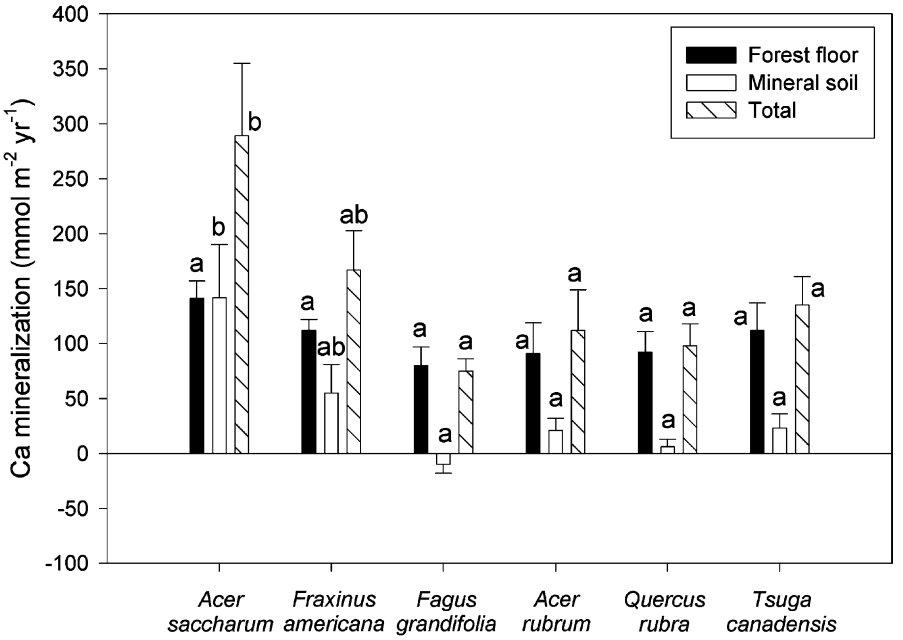

Fig. 3. Mean Ca mineralization in the forest floor, mineral soil and total soil profile beneath the different tree species. Bars of the same color with different letters are significantly different from one another at $P < 0.05$.

incubation may have resulted in increased decomposition and net Ca mineralization during the summer incubation.

Net Ca mineralization rates in the forest floor per amount of decomposed litter were significantly higher for sugar maple and white ash litter than for the other tree species. Low total Ca concentrations of the incoming litter may have caused lower net Ca mineralization rates per amount of decomposed litter beneath red maple, beech, red oak and hemlock. Leaf litter fall that was collected at the same plots during autumn of 1999 showed significantly higher Ca concentrations from sugar maple and white ash plots than from the other tree species plots (G.M. Lovett et al., in preparation). Vesterdal (1999) found increased net Ca release from decomposing foliage litter of beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) with higher initial Ca concentration. Calcium immobilization may also have been responsible for the low net Ca mineralization per amount of

Table 2
Forest floor mass (kg m^{-2}) and its loss (g kg^{-1} per day and g m^{-2} per day) during summer and winter incubation. Values are the mean followed by the standard error in brackets ($n = 6$)

Species	Forest floor mass[a]		Forest floor mass loss[a]			
	Summer (kg m^{-2})	Winter (kg m^{-2})	Summer (g kg^{-1} per day)	Winter (g kg^{-1} per day)	Summer (g m^{-2} per day)	Winter (g m^{-2} per day)
A. saccharum	2.4 (0.8) a	2.5 (0.6) a	1.00 (0.17) b	0.49 (0.08) b	1.8 (0.2) a	1.0 (0.1) a
F. americana	2.2 (0.6) a	2.6 (0.6) a	0.85 (0.14) ab	0.49 (0.10) b	1.6 (0.4) a	1.0 (0.2) a
F. grandifolia	4.0 (1.3) ab	3.8 (0.8) ab	0.62 (0.12) ab	0.36 (0.03) ab	2.2 (0.8) a	1.3 (0.3) a
A. rubrum	5.5 (0.6) ab	5.4 (0.8) ab	0.51 (0.08) a	0.22 (0.04) a	2.9 (0.6) a	1.1 (0.2) a
Q. rubra	4.8 (0.4) ab	5.4 (0.5) ab	0.64 (0.13) ab	0.25 (0.04) ab	2.9 (0.4) a	1.3 (0.1) a
T. canadensis	7.0 (0.8) b	6.5 (0.8) b	0.48 (0.06) a	0.14 (0.01) a	3.3 (0.4) a	0.9 (0.1) a

[a] Values with different letters in a row are significantly different from one another ($P < 0.05$).

Table 3
The slope with standard error (S.E.) and *P*-values calculated from linear regressions between net Ca mineralization per unit mass and forest floor mass loss during incubation for each tree species, representing the amount of Ca that becomes available per amount of decomposed litter (mmol kg^{-1}) in the forest floor

Species	Slope (mmol kg^{-1})	S.E.	*P*-value
A. saccharum	362	49	<0.001
F. americana	390	78	<0.001
F. grandifolia	183	32	0.004
A. rubrum	133	23	0.095
Q. rubra	147	22	0.021
T. canadensis	190	37	0.047

decomposed litter beneath red maple, beech, red oak, and hemlock. Litters beneath these tree species had the smallest mass loss fractions during incubation. The remaining more recalcitrant litter from these tree species can form more exchange sites during decomposition that adsorb Ca (Staaf and Berg, 1982; Van Wesemael, 1993), immobilizing mineralized Ca.

The greater forest floor mass beneath beech, red maple, red oak, and hemlock helped increase the net Ca mineralization per unit area in the forest floor to the same level as under sugar maple and white ash, where the mineralization per unit mass (mmol kg^{-1} per day) was higher but where forest floors were thinner. Differences among tree species therefore decreased and were non-significant on an area basis.

Net Ca mineralization in the first 15 cm of the mineral soil showed significant tree species effects. Especially beneath sugar maple and white ash net Ca mineralization in the mineral soil was appreciable, especially at plots where much earthworm activity was observed. It is plausible that earthworms and other soil invertebrates move organic matter from the forest floor to the upper mineral soil where the organic matter can still release substantial amounts of Ca through decomposition after downward movement of the organic matter. It must be noted, however, that increases in Ca concentration during incubation were relatively small, but involved an appreciable mass of Ca. Small increases in Ca concentration during incubation could have been caused by disturbance of the soil, accelerating Ca release through organic mineralization or mineral weathering.

To extrapolate net Ca mineralization measured in buried bags to actual net Ca mineralization in the field, a number of potential errors are introduced. First, the activity of earthworms within the bag is limited and is therefore probably much lower inside than outside the bag. As a result, decomposition and net Ca mineralization will be underestimated. This error may have been large for sugar maple and white ash forest floors where at some plots earthworms were observed in the field. Second, samples were disturbed and moisture conditions remained constant in the bags during incubation. Disturbance markedly affects N mineralization in the mineral soil (e.g. Raison et al., 1987). Ca mineralization in this study may have been overestimated because of disturbance, but it is reasonable to assume that the magnitude of overestimation is similar between N and Ca. Third, the long incubation periods that were used may have induced decomposition of fresh fine roots that were killed during sampling and were incorporated within the bags, and may have overestimated net Ca mineralization. Based on fine root mass that was measured in forest floor and mineral soil of hemlock and sugar maple plots at GMF (Dijkstra and Smits, in press) and Ca root concentrations reported by Fahey et al. (1988), maximum release of Ca due to decomposition of fresh fine roots during each incubation could not have been more than 10 mmol m^{-2}. Further, Fahey et al. (1988) showed that there was little release of Ca during the first year of fine root decomposition. Therefore, errors due to freshly cut root decomposition in net Ca mineralization estimates were probably small. However, annual fine root turnover may return substantial amounts of Ca to the soil. Likens et al. (1998) estimated for the Hubbard Brook Experimental Forest an annual Ca return from fine root turnover of 27 mmol m^{-2} per year, with 19 mmol m^{-2} per year contributed to the forest floor and 8 mmol m^{-2} per year to the mineral soil. Compared to the net Ca mineralization rates that I estimated, fine root turnover could contribute up to 30% of the net Ca mineralization in forest floor and mineral soil.

In spite of uncertainties about translating measured values to actual rates of net Ca mineralization in the field, it is evident that net Ca mineralization in the forest floor and mineral soil is an important source of Ca for immediate plant uptake for all tree species. Other inputs of Ca input at GMF are much smaller than net Ca mineralization. Atmospheric deposition is close to 4 mmol m^{-2} per year at this site, while

estimates of Ca released through mineral weathering in the surface soil, using the abundance of natural strontium isotopes as a tracer, were very low and not more than 2 mmol m^{-2} per year (Dijkstra et al., in press). No studies have been encountered in the literature where net Ca mineralization in the entire forest floor and upper mineral soil was measured. Gosz et al. (1973) estimated Ca release from fresh litter (both leaves and branches) of 17,260 g ha^{-1} per year (43 mmol m^{-2} per year) during the first 12 months in the Hubbard Brook Experimental Forest, New Hampshire, or 42% of the Ca content of the yearly litter fall. This number is lower than the lowest net Ca mineralization rate observed under beech at GMF. They stated however that their number underestimated the yearly release from the entire forest floor since release of Ca from tissues of previous litter fall was not taken into account. To estimate the amount of Ca that becomes available through organic mineralization in temperate forests, all soil litter that has been accumulated over time has to be considered.

My results show that large amounts of net Ca mineralization occur in the forest floor, and for sugar maple and white ash also in the upper mineral soil (possibly due to earthworm activity), with highest rates occurring during the summer. Large tree-specific temporal and spatial fluxes of Ca release through litter decomposition suggest that Ca mineralization has to occur in conjunction with uptake dynamics to minimize Ca depletion (Dijkstra and Smits, in press). Differences in Ca cycling among tree species affect nutrient balances in the soil and may have significant implications for growth and survival of future tree generations.

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