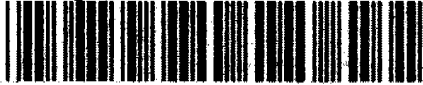


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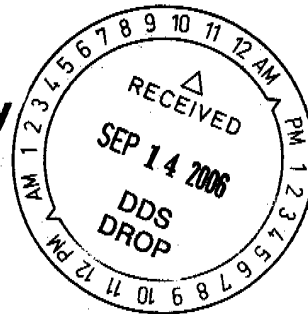
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# Tree Species Effects on Calcium Cycling: The Role of Calcium Uptake in Deep Soils

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## ABSTRACT

Soil acidity and calcium (Ca) availability in the surface soil differ substantially beneath sugar maple (*Acer saccharum*) and eastern hemlock (*Tsuga canadensis*) trees in a mixed forest in northwestern Connecticut. We determined the effect of pumping of Ca from deep soil (rooting zone below 20-cm mineral soil) to explain the higher available Ca content in the surface soil beneath sugar maple. We measured the atmospheric input of Ca with bulk deposition collectors and estimated Ca weathering and Ca mineralization in the surface soil (rooting zone above 20-cm mineral soil) from strontium isotope measurements and observed changes in exchangeable Ca in soils during field incubation. Calcium leaching at 20 cm was calculated by combining modeled hydrology with measured Ca soil solution concentrations at 20-cm depth. We measured root length distribution with depth beneath both tree species. Calcium leaching from the surface soil was much higher beneath sugar maple than hemlock and was positively related with the amount of Ca

available in the surface soil. Calcium leaching from the surface soil beneath sugar maple was higher than the combined Ca input from atmospheric deposition and soil weathering. Without Ca uptake in the deep soil, surface soils are being depleted in Ca, especially beneath sugar maple. More organically bound Ca was mineralized beneath sugar maple than beneath hemlock. A relatively small part of this Ca release was leached below the surface soil, suggesting that, beneath both tree species, most of the Ca cycling is occurring in the surface soil. Sugar maple had more fine roots in the deep soil than hemlock and a greater potential to absorb Ca in the deep soil. With a simple model, we showed that a relatively small amount of Ca uptake in the deep soil beneath sugar maple is able to sustain high amounts of available Ca in the surface soil.

**Key words:** calcium uptake; calcium cycling; calcium depletion; tree species; deep soil; roots; model.

## INTRODUCTION

It is well known that individual trees alter soil acidity and available Ca content in surface soils (for example, see Zinke 1962; Boettcher and Kalisz 1990; Nordén 1994; Bockheim 1997; Finzi and others 1998; Amiotti and others 2000). In a mixed forest, therefore, temporal and spatial alterations of

soil acidity and available Ca content may develop and subsequently affect the distribution of the forest vegetation. In addition, trees growing in soils of different base cation availability may react differently to human-induced stresses such as acid rain. Different mechanisms may help trees to alter soil acidity and available Ca content in the surface soil, but their relative importance remains unclear.

Biotic control over Ca availability in the surface soil can be established through different pathways (Figure 1). Several studies have shown that Ca uptake and allocation to biomass pools are the main

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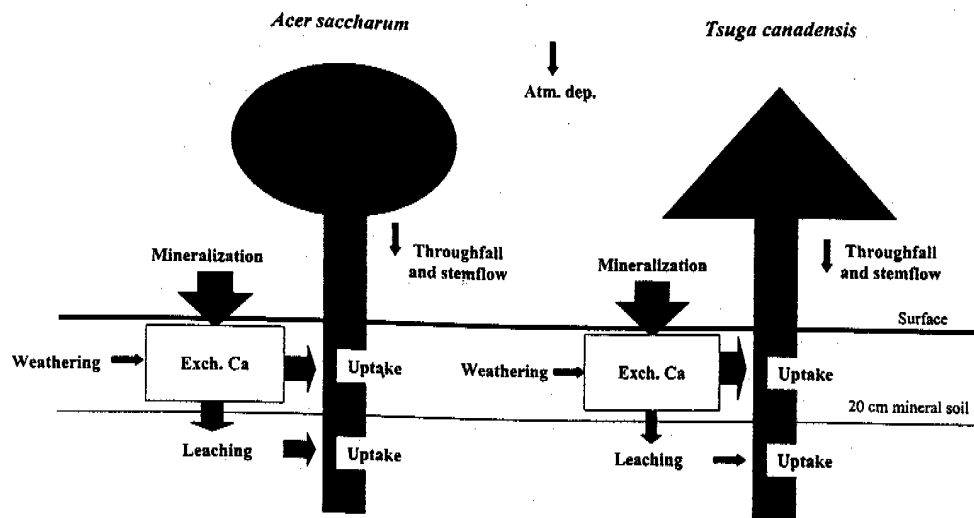


Figure 1. The Ca pools and fluxes influenced by *Acer saccharum* and *Tsuga canadensis*. The width of the arrows corresponds to the hypothesized size of the Ca flux.

cause for changes in Ca content in the surface soil (Alban 1982; Johnson and Todd 1987, 1990; Eriksson and Rosen 1994). Bockheim (1997) found lower contents of Ca in the surface soil beneath hardwood stands dominated by sugar maple compared to hemlock stands and attributed this to higher Ca biomass fixation in sugar maple trees. However, at sites similar to ours, Finzi and others (1998) found higher Ca content in the surface soil beneath sugar maple than beneath hemlock stands of similar age. Their results therefore cannot be explained by higher Ca biomass fixation in sugar maple.

A potential mechanism by which trees may affect the exchangeable Ca content in surface soils is through their influence on chemical weathering in the soil. Several authors have reported apparent differences in soil weathering caused by different tree species (Spyridakis and others 1967; Bouabid and others 1995; Quideau and others 1996; Tice and others 1996; Augusto and others 2000). Organic acid production and increased soil acidity are two of the mechanisms that have been suggested to influence soil weathering (for example, see Tan 1980; Kodama and others 1983; Lundström and Öhman 1990). Hemlock stands in our study area showed higher concentrations of dissolved organic acids in the forest floor than sugar maple (Dijkstra and others 2001). However, in soils developed from granitic material, such as at our sites, the role of organic acids in mineral weathering processes appears to be limited (Drever and Vance 1994; Raulund-Rasmussen and others 1998).

The production of organic acids from decomposing litter and root or mycorrhizal exudation lowers soil pH and increases the solubility of alu-

minum and iron, which compete with base cations for binding sites on the exchange complex (for example, see Johnson and others 1994; Lawrence and others 1995). The exchanged base cations are then likely to leach with drainage water to deeper soil layers. High organic acid production in forest floors beneath hemlock did not increase actual leaching of Ca with organic anions, which was greatest beneath sugar maple where the forest floor contained more exchangeable base cations (Dijkstra and others 2001).

How then, in spite of greater Ca leaching rates, do sugar maple trees enhance the pool of available surface soil Ca? As shown in Figure 1, the flux that can maintain a high available Ca content in the surface soil is the recapture of appreciable amounts of Ca leached from the surface soil via deep roots. We postulated that sugar maple takes up appreciably larger quantities of Ca from the deeper soil than hemlock. Even when enough Ca is released by mineral weathering to potentially increase the available pool of Ca in the surface soil under hemlock, this pool will remain low because hemlock lacks a root system capable of retaining Ca lost from the surface soil.

To test our hypothesis, we compared Ca inputs from atmospheric deposition, soil weathering, and release through organic matter decomposition with Ca leaching below 20 cm in the mineral soil beneath sugar maple and hemlock stands. After measuring the presence of roots at depth in the soil, we developed a simple model to calculate and compare plant uptake from surface and deep soil and to illustrate the effect of plant uptake from deep soil on Ca availability in the surface soil.

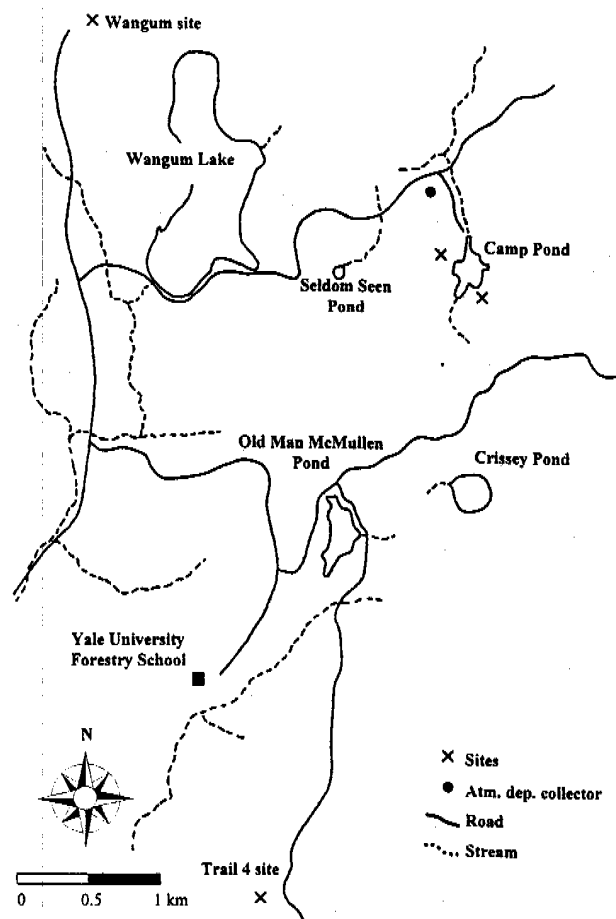


Figure 2. Site locations at Great Mountain Forest (GMF).

## METHODS

### Study Site

This research was done on the Canaan Mountain Plateau at elevations of 300–500 m in northwestern Connecticut. The sites were located near Camp Pond, Wangum Reservoir, and Trail 4 (Figure 2). Soils at these fairly flat sites are acidic, well-drained sandy loams (Typic Dystrachrepts) derived from glacial till over mica-schist bedrock. X-ray diffraction showed that significant amounts of plagioclase, alkali-feldspars, and mica (biotite) are present in the soil (F. A. Dijkstra unpublished). The dense glacial till at all sites starts at a depth of approximately 60 cm. The sites have not been cleared for agriculture, but some selective logging has occurred. Forest structure is relatively simple, with no major shrub or subcanopy tree species present.

We selected sites (diameter, approximately 20 m) that were dominated by either mature sugar maple (*Acer saccharum* Marsh.) or hemlock (*Tsuga canadensis* Carr.) trees (around 80–130 years old). There were six sugar maple and six hemlock sites at Camp

Pond, two sugar maple and two hemlock sites at Wangum, and one sugar maple and one hemlock site at Trail 4. At Camp Pond, soil texture at three different soil depths, analyzed on a Coulter LS230 laser grain-sizer (Buurman and others 1997), was similar among sites (Table 1). At Camp Pond, all trees with a diameter at breast height (dbh) of at least 5 cm were identified and their dbh measured within a circle of 10-m radius at each site (average, 22 trees at each site). Total basal area density and the proportion of the dominant tree (sugar maple or hemlock) were calculated for each site. The total aboveground biomass was calculated according to biomass equations found for each tree species in the literature (Ter-Mikaelian and Korzukhin 1997). The average total basal area density was significantly higher for hemlock sites than for sugar maple sites (Table 2). Also, the average total biomass was higher, but not significantly so.

### Total and Exchangeable Calcium in the Soil

At all 12 sites at Camp Pond, the first 20 cm of the mineral soil was sampled in the spring of 1997 for determination of total mineral Ca concentration. At each site, three cores (diameter, 4.5 cm) were randomly pushed into the soil and bulked for each layer. At these same sites, forest floor and mineral soil from a depth of 0 to 5 and 10 to 20 cm were sampled in the same way in the summer of 1998 for exchangeable Ca determination. Forest floor and mineral soil samples were dried for 48 h at 105°C and sieved (through 8- and 2-mm mesh, respectively) to remove roots and stones. Soil bulk density was determined by dividing dry weight of the sieved sample over the volume of the soil core. Soil samples from 0- to 20-cm depth were analyzed for total Ca with x-ray fluorescence. Ground samples (0.6 g) were melted with 2.4 g of  $\text{Li}_2\text{Br}_4\text{O}_7$  at 1100°C for 4 h. The resulting glass beads were analyzed using a Philips PW 1404 XRF spectrometer, using standard reference samples similarly prepared (Buurman and others 1996). Exchangeable Ca was extracted with 0.1 M  $\text{BaCl}_2$  (Hendershot and others 1993). A 0.5-g subsample of the homogenized forest floor and a 3-g subsample of the mineral soil with 30 ml of 0.1 M  $\text{BaCl}_2$  were placed on a shaker table at 45 rpm for 2 h. The suspensions were centrifuged at 2000 rpm for 15 min, extracts were filtered through Whatman 41 filter paper, and concentrations of Ca were measured by AAS (Perkin Elmer AA 300) at Wageningen University, The Netherlands. For each layer, we calculated the exchangeable Ca content ( $\text{mol m}^{-2}$ ) using the bulk density that was measured for each layer. To calculate the total exchangeable Ca content in the forest

**Table 1.** Average Sand, Silt, and Clay Fraction of the Mineral Soil at 0- to 10-cm, 20- to 30-cm, and 50- to 70-cm Depth beneath Sugar Maple (*Acer saccharum*) and Hemlock (*Tsuga canadensis*) Sites at Camp Pond

Depth (cm)	<i>Acer saccharum</i>			<i>Tsuga canadensis</i>		
	Sand (%)	Silt (%)	Clay (%)	Sand (%)	Silt (%)	Clay (%)
0-10	41.4 (4.9)	49.3 (3.7)	9.3 (1.2)	43.2 (2.8)	48.0 (3.5)	8.8 (0.9)
20-30	45.1 (4.5)	46.9 (4.9)	7.9 (0.4)	43.1 (3.7)	49.2 (3.5)	7.6 (0.5)
50-70	46.2 (4.6)	47.4 (3.6)	6.3 (1.1)	47.4 (3.7)	46.6 (3.6)	6.0 (0.5)

Standard error in parentheses;  $n = 3$

**Table 2.** Average Aboveground Biomass Measurements at Sugar Maple and Hemlock Sites at Camp Pond

Site	Total Basal Area Density ( $\text{cm}^2 \text{m}^{-2}$ )	Basal Area Dominant Tree (%)	Total Aboveground Biomass <sup>a</sup> ( $\text{kg m}^{-2}$ )
<i>Acer saccharum</i>	30.1 (4.3)	72.9 (8.7)	22.7 (3.1)
<i>Tsuga canadensis</i>	49.3 (4.1)	70.8 (5.3)	28.5 (1.8)
Significance <sup>b</sup>	c	n.s.	n.s.

n.s., not significant

<sup>a</sup>Biomass equations for *Acer rubrum*, *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, and *Tsuga canadensis* are from Young and others (1980); those for *Fraxinus americana* and *Quercus rubra* are from Peralta and Alban (1994); and those for *Prunus serotina* are from Wiant and others (1979). All cited in Ter-Mikaelian and Korzukhin (1997).

<sup>b</sup>Independent samples *t* test.

<sup>c</sup>Significance at  $P < 0.05$

Standard error in parentheses;  $n = 6$

floor and the first 20 cm of the mineral soil, the content of each layer was totaled. We assumed that the exchangeable Ca concentration in the 5- to 10-cm layer was equal to the concentration in the 10- to 20-cm layer. Judging from field observations, we estimated that 30% of the volume in the first 20 cm of the mineral soil consisted of large rocks, stones, and roots; and the Ca content in this layer was adjusted accordingly. We will refer to the forest floor and first 20 cm of the mineral soil as "surface soil", while the rooting zone below 20-cm mineral soil will be called the "deep soil".

### Calcium from Bulk Atmospheric Deposition

Bulk atmospheric deposition was collected in two collectors (for quality control), 1 m above the ground, at a clearing close to Camp Pond (Figure 2). Collectors were made of a polyethylene funnel (diameter, 20 cm) connected to a polyethylene bottle. Bulk atmospheric deposition was collected weekly from May until October in 1997, 1998, and 1999 and directly measured for pH and electric conductivity. A subsample was stored in the dark at 4°C prior to analysis for Ca. Samples from the two collectors that differed in pH and/or electric conductivity were discarded, but this rarely occurred. All materials for solution sampling were cleaned in

50% hydrochloric acid and rinsed with nanopure water before use. Solutions were analyzed for Ca with an Inductively Coupled Plasma Emission Spectrometer (ICP; Perkin-Elmer) at the Institute of Ecosystem Studies in Millbrook, New York. Average annual bulk atmospheric deposition of Ca was calculated from volume-adjusted Ca concentrations and from precipitation data that were collected at a weather station within 10 km from our site in Norfolk, Connecticut.

### Calcium Leaching

At Camp Pond, tension lysimeters (Rhizon SMS; Eijkelkamp) were installed at six sites (three replicates per tree species) in the summer of 1997 and at the other six sites in the summer of 1998. The lysimeters, 10 cm long with a diameter of 0.5 cm, consisted of a hydrophilic porous polymer sheath fitted around a stainless steel wire and connected to PVC tubing. At each site, a small pit was dug and six lysimeters were pushed into the sidewall at 20-cm depth in the mineral soil (the minimum distance between any two lysimeters was 10 cm); thereafter, the pit was backfilled. Soil solutions were obtained by connecting vacuumed bottles (40 kPa) to the PVC tubes. The six lysimeters at one site were connected to two bottles (three to each bottle) to en-

sure enough solution for analysis and so that solutions could be sampled in duplicate. Soil solutions were obtained from the bottles after 24 h. Soil solutions were collected on 4 September and 2 October 1997, 23 April, 6 May, 21 May, and 20 October 1998, and 27 April 1999 and stored before analyses at 4°C in the dark. Soil solutions were analyzed for Ca by AAS at Wageningen University, The Netherlands.

We estimated average annual Ca leaching below 20-cm mineral soil by multiplying Ca concentrations with weekly water fluxes at 20-cm mineral soil that were calculated with a hydrologic model (BROOK90), (Federer 1995; Lawrence and others 1995). We used daily values for minimum and maximum temperature and precipitation, as measured at the weather station in Norfolk, Connecticut, and our root distribution data (see below) as input parameters for the model. We used soil and vegetation parameters (a deciduous tree species parameter file for sugar maple sites and a coniferous tree species parameter file for hemlock sites) that were calibrated for sites at the Hubbard Brook Experimental Forest, New Hampshire (Federer 1995). To calculate annual Ca leaching, we interpolated Ca concentrations for time periods for which we did not have data.

### Calcium Weathering

Because of the similar geochemical behavior of Ca and Strontium (Sr) (Graustein 1989), we used strontium isotopes to estimate Ca weathering rates in the first 20 cm of the mineral soil (for example, see Miller and others 1993; Bailey and others 1996). At three sugar maple and three hemlock sites at Camp Pond, we sampled soil at 0- to 20-cm and 50- to 70-cm depth with a soil corer (diameter, 4.5 cm) during the summer of 1997. At the same time, at each of these sites we sampled stem wood of one tree (three cores [diameter, 0.5 cm] to the center of the stem at breast height). Together with four bulk atmospheric deposition samples (taken between 15 May 1998 and 17 October 1998) and soil solutions taken at 20-cm depth from the same sites (on 21 May 1998), these samples were analyzed for total Ca and Sr concentrations (ICP; Perkin-Elmer) and  $^{87}\text{Sr}/^{86}\text{Sr}$  by mass spectrometry (Finigan Mat 261 and 262 RPQ-Plus) at the Vrije Universiteit, Amsterdam, The Netherlands. Using a linear mixing equation (Graustein 1989), with the average  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio measured in atmospheric deposition and the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio measured in the organic-poor but mineral-rich 50–70-cm deep soil at each site as the atmospheric and weathering end member, respectively, the proportion of Sr fixed in

stem wood that was originally derived from soil weathering was calculated. With  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios measured in soil solution and Ca/Sr ratios measured in the first 20 cm of the mineral soil, we then calculated the Ca weathering rate in this soil layer for each site (Dijkstra 2001).

### Ca Release through Organic Matter Decomposition

At the three sugar maple and hemlock sites where Ca weathering was estimated, net Ca release through organic matter decomposition in the forest floor and first 15 cm of mineral soil was estimated (Dijkstra 2001). We used the buried polyethylene bag technique that previously has been used for N mineralization (Eno 1960; Pastor and others 1984; Vitousek and Matson 1985). Because the mineralization:available pool ratio in the forest floor and mineral soil was expected to be much smaller for Ca than for nitrogen (N) the incubation period required to observe significant changes in exchangeable Ca was longer than is commonly used for N mineralization studies. Samples were incubated for 1 year divided into two periods. The first period was from 18 June 1999 until 3 November and the second period began on 3 November, at which time freshly fallen leaf litter was included in the forest floor samples, and lasted until 18 June 2000.

Forest floor was sampled by cutting around the edges of an acrylic square (20 × 20 cm) that was randomly placed on top of the forest floor within each site. Forest floor was then gently removed from the mineral soil beneath it with a sharp knife. Where the forest floor was removed, we recorded the depth of the forest floor, and two soil cores (diameter, 4.5 cm) were taken to a depth of 15 cm and bulked. Samples were weighed and thoroughly homogenized. One subsample (initial sample) was dried (105°C for 48 h) for soil moisture content; another subsample was dried, sieved (8-mm mesh), and used for exchangeable Ca extraction. The remainder of the forest floor and mineral soil samples was divided into four equal portions. Each portion was weighed and put in a polyethylene bag that was closed with a knot, returned to the spot from which the samples came, and covered with forest litter and a piece of poultry wire to protect the bags from shifting. After the field incubation, the bags were brought back to the laboratory, where intact bags (more than 90% of all bags and at least one from each site and depth) were weighed, subsampled for moisture content, and then bulked for forest floor and mineral soil at each site. Bulked samples (final samples) were dried and sieved (8-mm mesh). Initial and final samples were ex-

tracted with 0.1 M BaCl<sub>2</sub>. Exchangeable Ca and weight loss during incubation were based on oven-dried (105°C) samples. Net Ca release through organic matter decomposition was calculated as the difference between initial and final exchangeable Ca that was measured by ICP at the Institute of Ecosystem Studies, Millbrook, New York, and corrected for weight loss during incubation, Ca weathering in the mineral soil, and volume taken by rocks and roots in the mineral soil (estimated at 30%).

### Root Density Characterization

One mature tree was selected at four sugar maple and four hemlock sites to measure the root density at different soil depths during the summer of 2000. Around each tree within a circle of 1-m radius, eight cores (diameter, 5 cm) were taken to a depth of 60 cm. Each core was subdivided into the forest floor, 0- to 5-cm, 5- to 15-cm, 15- to 30-cm, 30- to 45-cm, and 45- to 60-cm samples, and each individual sample was analyzed separately. Power analysis showed that eight cores were enough to characterize the root density for each layer accurately (SE less than 10%) (M. Smits unpublished). Tree roots were collected by sieving and gently rinsing samples with water and were then divided into fine (diameter, less than 2 mm) and coarse roots. Fine and coarse root length was measured by counting intersections of roots laid on a grid (Newman 1966). The root density (cm cm<sup>-3</sup>) of each layer was calculated by dividing the root length with the volume of each layer for each core. For each site, the mean root density per layer was then calculated by taking the average of the eight cores.

### Statistical Analysis

We used a repeated measures analysis of variance (ANOVA) on measured Ca concentrations in soil solution over time, where duplicate samples at each site were averaged. The variance of the solution concentrations from the two solution samples at one site did not differ significantly from that between tree species (nested ANOVA with tree species as a fixed factor and solution sample as a random factor). Analyses of covariance (ANCOVA) were done on exchangeable Ca content (mmol m<sup>-2</sup>), Ca leaching (mmol m<sup>-2</sup> y<sup>-1</sup>), Ca weathering (mmol m<sup>-2</sup> y<sup>-1</sup>), and Ca release through organic matter decomposition (mmol m<sup>-2</sup> y<sup>-1</sup>), with total mineral Ca concentration in the surface soil (mg g<sup>-1</sup>) as covariate and species identity as fixed factor. Significant differences were accepted at  $P < 0.05$ . The mean root density of each layer was compared between sugar maple and hemlock trees with  $t$ -tests.

We used a Bonferroni adjustment and considered significant differences between tree species at  $P < 0.05/6 = 0.0083$ . All statistical analyses were done in SPSS (version 7.5).

### Model

A simple model was developed to illustrate the effect of Ca uptake from surface and deep soil on the exchangeable Ca content in the surface soil. The exchangeable Ca content (mmol m<sup>-2</sup>) in the surface soil at time step  $t$  ( $E_{s,t}$ ) can be calculated as:

$$E_{s,t} = E_{s,t-1} + A + W_s + R_s - U_s - L_{s,t} \quad (1)$$

where  $E_{s,t-1}$  is the exchangeable Ca content in the surface soil at time step  $t-1$  (mmol m<sup>-2</sup>),  $A$  is Ca atmospheric deposition,  $W_s$  is Ca weathering in the surface soil,  $R_s$  is Ca release through organic matter decomposition in the surface soil,  $U_s$  is Ca uptake in the surface soil, and  $L_{s,t}$  is the Ca leaching below the surface soil at time step  $t$  (mmol m<sup>-2</sup> y<sup>-1</sup>) where  $t$  is in years. Calcium leaching below the surface soil at time step  $t$  is modeled as a fixed proportion of the exchangeable Ca content  $\alpha$  in the surface soil at time step  $t-1$ :

$$L_{s,t} = \alpha E_{s,t-1} \quad (2)$$

For the sake of simplicity, we ignored the flux of Ca throughfall and stemflow and considered this flux as part of Ca release through organic matter decomposition (see Results and Discussion below). When the exchangeable Ca content in the surface soil is in steady state, Ca uptake in the surface soil can be calculated as:

$$U_s = A + W_s + R_s - L_{s,t=\text{steady state}} \quad (3)$$

Using the values of  $A$ ,  $W_s$ ,  $R_s$ , and  $L_{s,t}$  that we measured at sugar maple and hemlock sites at Camp Pond as steady-state values, we then calculated Ca uptake in the surface soil at these sites. To illustrate the effect of Ca uptake from deep soil on exchangeable Ca in the surface soil, we further set Ca release through organic matter decomposition equal to total Ca uptake by the tree. We then could calculate Ca uptake in the deep soil ( $U_d$ ) by sugar maple and hemlock with:

$$U_d = R_s - U_s \quad (4)$$

and Eq. (1) becomes:

$$E_{s,t} = E_{s,t-1} + A + W_s + U_d - \alpha E_{s,t-1} \quad (5)$$

With this equation, we could model the exchangeable Ca content in the surface soil over time be-

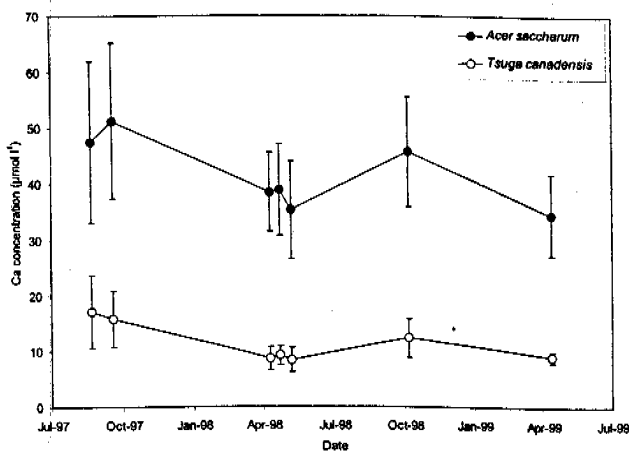


Figure 3. The Ca concentration ( $\mu\text{mol l}^{-1}$ ) in soil solution at 20-cm mineral soil depth beneath *Acer saccharum* and *Tsuga canadensis* sites at Camp Pond during September 1997 through April 1999.

neath different sugar maple and hemlock sites, assuming that Ca uptake from the deep soil is unlimited and constant over time but tree species is dependent. The model is now independent of Ca release through decomposition because of the linkage of Ca release with Ca uptake in the surface soil. Even though our sites are probably not in steady state as defined here, the model is useful to illustrate divergent effects of differences in Ca uptake from surface versus deep soil on available Ca content in the surface soil beneath sugar maple and hemlock.

## RESULTS AND DISCUSSION

### Ca Pools and Fluxes

Ca concentrations that were measured in soil solution at 20-cm depth were much higher beneath sugar maple than beneath hemlock ( $P = 0.007$ ) (Figure 3). Ca concentrations showed some seasonal fluctuations (they were higher during the fall), but we did not observe any year-to-year changes. The installation of the lysimeters in the soil seemed to have had minimal effects on Ca concentrations during the time of measurement.

Exchangeable Ca contents and rates of Ca leaching in the surface soil were significantly higher beneath sugar maple than beneath hemlock ( $P = 0.003$  for exchangeable Ca and  $P = 0.010$  for Ca leaching) (Figure 4A and B). The covariate (total mineral Ca concentration in the top 20 cm of the mineral soil) and species  $\times$  covariate interaction terms were nonsignificant in the ANCOVA. A study by Finzi and others (1998) in the same study area

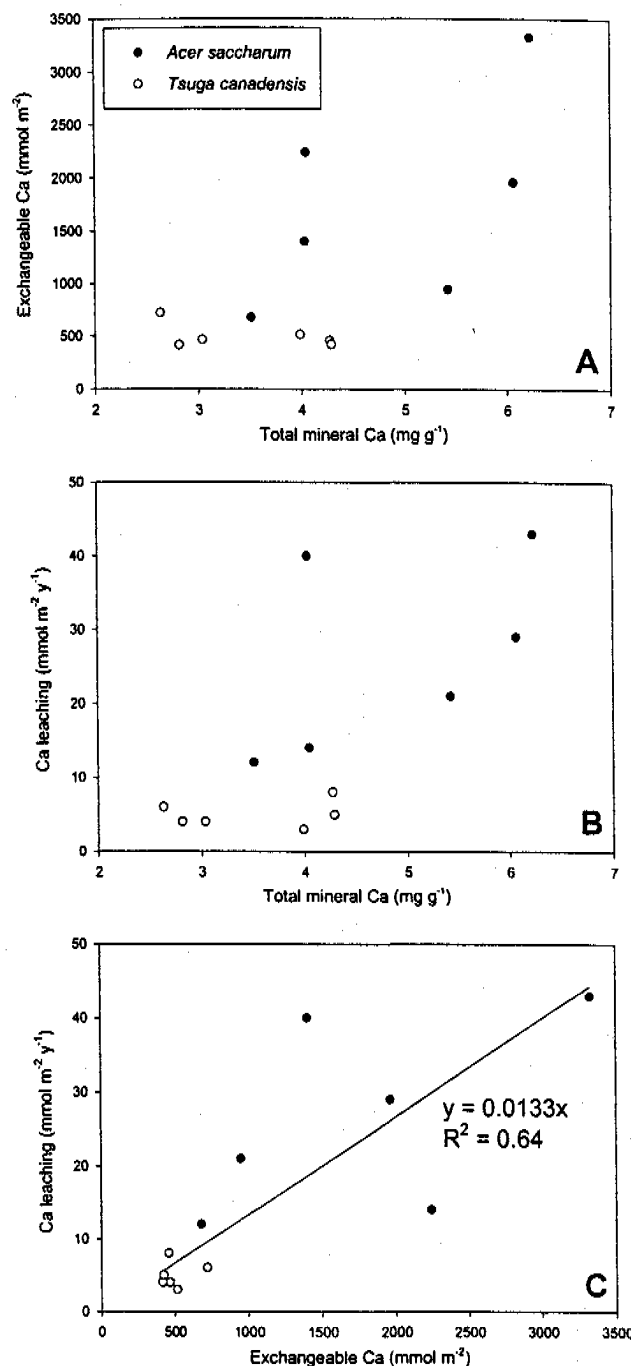


Figure 4. Exchangeable Ca ( $\text{mmol m}^{-2}$ ) and Ca leaching ( $\text{mmol m}^{-2} \text{y}^{-1}$ ) below the surface soil beneath *Acer saccharum* and *Tsuga canadensis* sites at Camp Pond. (A) Exchangeable Ca as a function of total mineral Ca concentration in the soil ( $\text{mg g}^{-1}$ ). (B) Ca leaching as a function of total mineral Ca concentration in the soil. (C) Ca leaching as a function of exchangeable Ca content.

found a significantly higher slope for sugar maple than for hemlock when the exchangeable Ca concentration was plotted against the mineral Ca concentration in the top 7.5 cm of the soil. Our sites



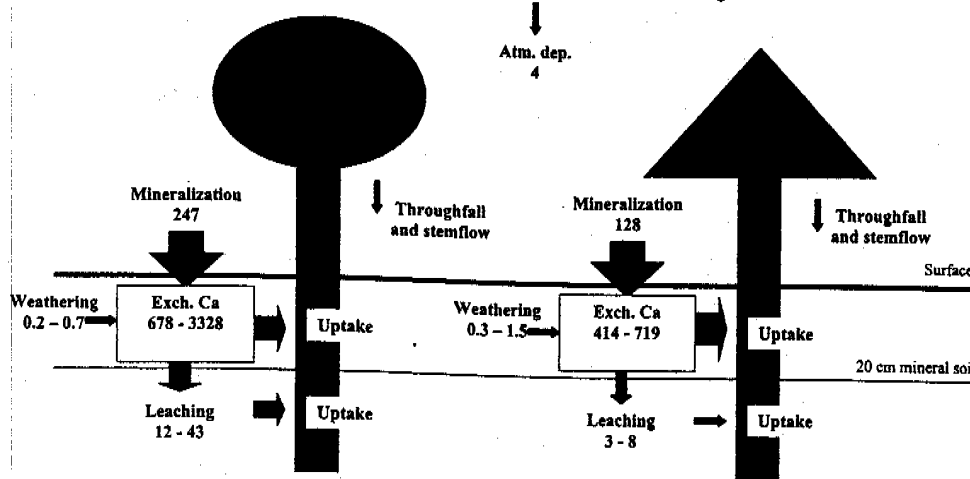
*Acer saccharum**Tsuga canadensis*

Figure 5. Ca content in the surface soil ( $\text{mmol m}^{-2}$ ) and Ca fluxes ( $\text{mmol m}^{-2} \text{y}^{-1}$ ) at *Acer saccharum* and *Tsuga canadensis* sites at Camp Pond.

had a smaller range in total mineral Ca concentration than reported by Finzi and others (1998), but we observed similar trends. Exchangeable Ca content and Ca leaching at our sites generally increased with total mineral Ca concentration beneath sugar maple, whereas for the hemlock sites exchangeable Ca content and Ca leaching remained low over their range of total mineral Ca concentration (Figure 4A and B). Our results and those reported by Finzi and others (1998) indicate that both soil parent material (total mineral Ca concentration) and tree species affect the Ca availability in the surface soil and the amount of Ca that is leached from the surface soil. Other soil properties in the surface soil, such as exchangeable magnesium (Mg) and acidity, were to a lesser degree also affected by tree species (Finzi and others 1998; Dijkstra and others 2001).

There was a positive trend between exchangeable Ca content in the surface soil and Ca leaching for the sugar maple sites, but the range of exchangeable Ca content was too small beneath hemlock sites for a significant relationship (Figure 4C). The significant regression through all data points in Figure 4C ( $R^2 = 0.64$ ,  $P = 0.002$ ) shows that Ca leaching can be roughly estimated from the exchangeable Ca content. These results suggest that Ca leaching below the surface soil is tightly controlled by the amount of Ca that is available in the surface soil for leaching.

Our exchangeable Ca content estimates are based on the assumption that 30% of the volume in the first 20 cm of the mineral soil is occupied by large rocks, stones, and roots (coarse fraction). Although we have not measured the coarse fraction in the soil quantitatively and our estimate may diverge by  $\pm 10\%$ , we have no reason to believe that there are systematic difference in the coarse fraction between

the two tree species. Therefore, the trends that we found with total mineral Ca concentration and Ca leaching remain the same (as our tree species effects on Ca release through organic matter decomposition). Spatial variability in exchangeable Ca content within a site may also confound the results. We did find the same pattern of exchangeable Ca content, and its relationship to total mineral Ca concentration, for sugar maple and hemlock sites as reported by Finzi and others (1998). Thus, we believe that we did adequately capture the spatial variability within each site with our soil-sampling scheme.

Inaccuracies in our Ca leaching estimates may derive from (a) errors of the hydrologic model to calculate water fluxes, (b) errors from interpolation of Ca concentration data points, and (c) spatial variation unaccounted for within a site. The hydrologic model was calibrated for a site with similar soil properties and vegetation (Hubbard Brook Experimental Forest, New Hampshire), where annual evapotranspiration and soil water flux are similarly related to temperature and precipitation as at our sites. We found little variation in Ca concentration in solution over time, and between the two spatial samples within a site, compared to differences between tree species. Thus, we are confident that we have constrained the error in estimating Ca leaching rates from the surface soil sufficiently.

We estimated an average annual bulk atmospheric deposition of Ca at our sites of  $4 \text{ mmol m}^{-2} \text{y}^{-1}$  (Figure 5). This is higher than estimated at the Hubbard Brook Experimental Forest in New Hampshire (average of  $2.9 \text{ mmol m}^{-2} \text{y}^{-1}$  during 1987–92) (Likens and others 1998). We did not measure Ca atmospheric input from November to April and assumed the same input rates as measured from May to October, averaged over the 3 years of mea-

surement. Likens and others (1998) showed that Ca atmospheric deposition at Hubbard Brook Experimental Forest was evenly distributed over the year from 1963–92. Although canopy trees affect acid deposition (Bergkvist and Folkeson 1995), there is no clear evidence that they have a significant influence on the deposition of Ca in northeastern forests of the United States. According to Lindberg and others (1986), most of the dry deposition in temperate forests of the northeastern United States is in particles greater than 2  $\mu\text{m}$  in diameter and occurs under the influence of gravity. We assume that our annual Ca atmospheric deposition flux has been estimated with fairly high accuracy.

Results from the Sr isotope study showed that Ca weathering in the surface soil was generally very low at Camp Pond sites, and no significant differences could be detected among tree species (Figure 5). A sensitivity analysis, using soil mineralogical data obtained from different soil depths, demonstrated that calculated Ca weathering rates in the surface soil could have an error of up to 100%, but they still remained relatively low (never higher than 1.5  $\text{mmol m}^{-2} \text{y}^{-1}$ ) (Dijkstra 2001). The parent material of the soil (total mineral Ca concentration, mainly from plagioclase) had a greater effect than tree species on Ca weathering.

Net Ca release through organic matter decomposition in the surface soil was significantly lower for hemlock than for sugar maple ( $P = 0.008$ ) (Figure 5). The net Ca release in the surface soil was not correlated to the initial exchangeable Ca content or the total mineral Ca concentration in the surface soil. The net Ca release in the forest floor was significantly correlated with mass loss (Dijkstra 2001), as was also demonstrated by Attiwill (1968) and Gosz and others (1973), suggesting that Ca is an important structural litter component (Kramer and Kozlowski 1979). We used relatively long incubations where moisture content remained constant in the bags. Also, samples were disturbed and were not accessible to soil invertebrates such as earthworms. Therefore, net Ca release rates in the bags may have been different from actual Ca release through organic decomposition in the field.

Throughfall and stemflow are other Ca sources to the surface soil. Likens and others (1998) estimated an annual Ca flux in throughfall and stemflow of 11  $\text{mmol m}^{-2} \text{y}^{-1}$  at the Hubbard Brook Experimental Forest in New Hampshire. Compared to our sites, the Ca flux in throughfall and stemflow would be 4% and 9% of net Ca release through organic matter decomposition for sugar maple and hemlock, respectively. Other studies did not find significant differences in the Ca flux in throughfall among tree

species (Lovett and others 1985; Johnson and Todd 1987, 1990). The annual internal cycling of Ca via Ca release through organic matter decomposition (plus inputs from throughfall and stemflow) greatly exceeds the fluxes into and out of the system for sugar maple and hemlock sites (Figure 5), implying a tight Ca cycling for both tree species.

Although the aboveground biomass is slightly, but not significantly, higher for the hemlock sites (Table 2), a higher aboveground biomass for hemlock sites cannot explain the large difference in exchangeable Ca content in the surface soil between sugar maple and hemlock. Calcium concentrations in stem wood of the six most common tree species at Great Mountain Forest (GMF) were similar and around 1  $\text{g kg}^{-1}$  dry weight (Dijkstra 2001). On average, an extra 5.8  $\text{g m}^{-2}$  or 145  $\text{mmol m}^{-2}$  of Ca would then be stored in aboveground biomass at the hemlock sites compared to the sugar maple sites. The calculated aboveground biomass should be viewed with some caution, since biomass equations were used from different regions. For instance, Ter-Mikaelian and Korzukhin (1997) reported nine different biomass equations to estimate aboveground biomass for sugar maple from different regions in the United States. For a tree with a dbh of 40 cm, the calculated biomass with the different equations ranged between  $\pm 20\%$  of the average. Because we used biomass equations from regions that were geographically closest to our study area, we assume that the error in our aboveground biomass estimates is smaller than 20%.

By setting the boundary of the tree-soil system at 20-cm mineral soil, we compared the fluxes into and out of the system for sugar maple and hemlock sites. Ca inputs from atmospheric deposition and weathering were almost the same as Ca leaching below 20-cm mineral soil at hemlock sites. At all sugar maple sites, however, Ca leaching exceeded inputs from atmospheric deposition and soil weathering (Figure 5). To maintain appreciable amounts of exchangeable Ca in the surface soil, sugar maple needs to take up Ca below 20-cm mineral soil (deep soil). This Ca is then transferred in litterfall to the surface soil, where it is mineralized and augments the Ca content in the surface soil beneath sugar maple. Annual net storage of Ca in the biomass and forest floor in the tree-soil system would require further Ca uptake in the deep soil to maintain Ca levels in the surface soil, both for sugar maple and hemlock. At present, we do not have data on annual net Ca storage at our sites. Likens and others (1998) estimated a relatively low average net Ca uptake in above- and belowground biomass of 5.4

$\text{mmol m}^{-2} \text{y}^{-1}$ , based on the difference in biomass storage between 1982 and 1992 at the Hubbard Brook Experimental Forest (Watershed 6).

Without Ca uptake in the deep soil, surface soils beneath sugar maple sites lose Ca at rates between 8 and  $37 \text{ mmol m}^{-2} \text{y}^{-1}$ . Without Ca uptake in the deep soil, surface soils beneath hemlock would undergo little or no Ca depletion. Calcium depletion would be higher if there is a net increment in biomass and forest floor at sugar maple and hemlock sites. There is substantial evidence that Ca is depleted in northeastern forests of the United States under the influence of acid atmospheric deposition (Lawrence and others 1995; Likens and others 1996, 1998). Likens and others (1998) estimated that the total amount of Ca lost from the complete soil profile between 1965 and 1992 at the Hubbard Brook Experimental Forest was  $9.9\text{--}11.5 \text{ kmol ha}^{-1}$  or on average between  $37$  and  $43 \text{ mmol m}^{-2} \text{y}^{-1}$ . However, Yanai and others (1999) concluded that during the last 20 years there was no Ca depletion in the forest floor at the Hubbard Brook Experimental Forest.

Considering the large influence of trees on Ca cycling at our sites, a possible explanation for the discrepancy is that most of the Ca depletion occurs at greater soil depths.

### Root Density

For a mobile cation such as Ca, mass flow of soil solution is thought to be an important mechanism in the supply of Ca to the root surface (Rengel 1993; Yanai 1994). Higher fine-root densities would therefore increase the potential for Ca uptake by the tree. To test the difference in potential Ca uptake in the deep soil under sugar maple and hemlock, we measured fine-root density at different depths beneath these two species. Fine-root density beneath sugar maple was higher than beneath hemlock in each layer (Figure 6A), but this difference was insignificant after applying the Bonferroni adjustment. Because the forest floor beneath hemlock was much thicker than the floor beneath sugar maple (average,  $6.9 \text{ cm}$  for hemlock and  $1.3 \text{ cm}$  for sugar maple), the fine-root length per area forest floor was significantly higher beneath hemlock ( $43.6 \text{ cm cm}^{-2}$  for hemlock and  $16.2 \text{ cm cm}^{-2}$  for sugar maple). We compared the fine-root length measured below a depth of  $30 \text{ cm}$  as a fraction of root length in the total profile between sugar maple and hemlock. Although no differences in total fine-root length were found, the fraction of fine-root length below  $30 \text{ cm}$  was significantly higher under sugar maple (Figure 6B). Root densities were not corrected for volume occupied by the coarse frac-

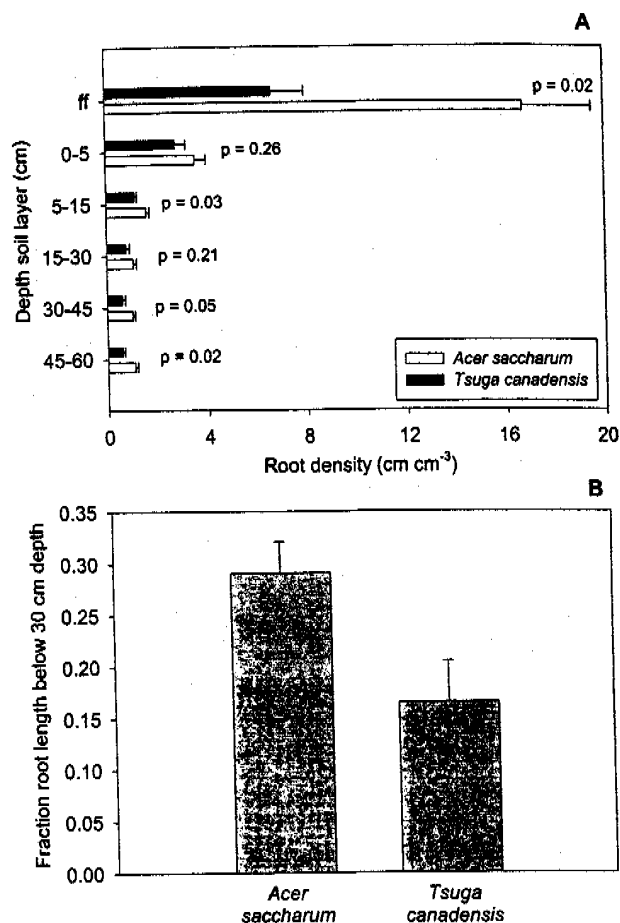


Figure 6. Average fine-root density in different soil layers (A) and average fine-root length below 30-cm depth as a fraction of total root length (B) for *Acer saccharum* and *Tsuga canadensis*.

tion in the soil at different depths. Because the volume occupied by rocks and stones may increase with soil depth at our sites, we may have overestimated the fraction of fine-root length below  $30 \text{ cm}$  for both tree species. Systematic differences in the coarse fraction between the two tree species are not expected; therefore, they do not affect relative differences in root density and fraction of root length below  $30 \text{ cm}$  between the two tree species. Many fine roots of hemlock were infected with ectomycorrhiza, especially in the upper soil layers (M. M. Smits unpublished). These results indicate that sugar maple has a higher potential for Ca uptake in the deep soil than hemlock. Higher fine-root densities, extended with mycorrhizal mycelium, in the surface soil beneath hemlock suggest that this tree has a higher potential to explore and absorb Ca in the surface soil.

High Ca uptake rates in the surface soil that are close to release rates of Ca through organic matter

**Table 3.** Calcium (Ca) Uptake ( $\text{mmol m}^{-2} \text{y}^{-1}$ ) for Sugar Maple and Hemlock Sites at Camp Pond in Steady State

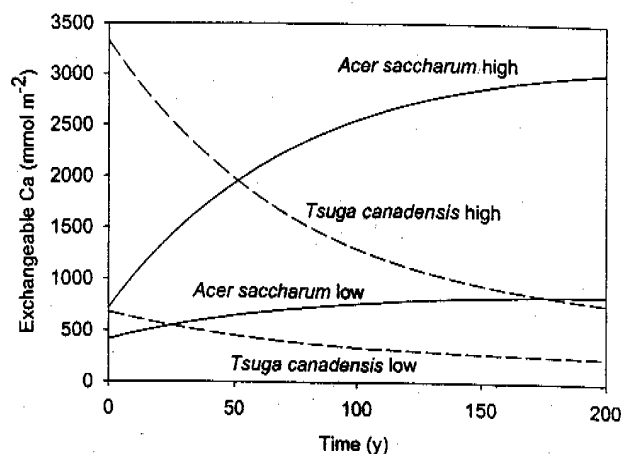
Ca uptake ( $\text{mmol m}^{-2} \text{y}^{-2}$ )	<i>Acer saccharum</i> Total mineral Ca concentration		<i>Tsuga canadensis</i> Total mineral Ca concentration	
	Low	High	Low	High
Surface soil	239 (97)	209 (85)	128 (100)	125 (98)
Deep soil	8 (3)	38 (15)	0 (0)	3 (2)

Percentage of total given in parentheses

decomposition could keep the available Ca pool low in the surface soil beneath hemlock. As soon as Ca is released through organic matter decomposition, the tree may take it up before any buildup of Ca can occur in the surface soil. Beneath sugar maple, Ca uptake rates in the surface soil may not be as high as Ca release rates through organic matter decomposition; therefore, the available Ca pool in the surface soil could increase, which would stimulate Ca leaching to deeper soil layers. Because it has more fine roots in the deep soil than hemlock, sugar maple could then take up part of the leached Ca in the deep soil.

## MODEL

We used our model to test the possibility that differences in deep uptake of Ca could explain the differences in contents of exchangeable Ca in the surface soil that were measured beneath sugar maple and hemlock. First, we used Eqs. (3) and (4) to calculate Ca uptake in the surface and deep soil respectively, assuming steady-state Ca levels under sugar maple and hemlock sites, for the lowest and highest total mineral Ca concentration in the soil observed beneath each species (Table 3). Our calculations suggest that Ca uptake from the surface soil is much higher than from the deep soil for both tree species due to the high input of Ca release through organic matter decomposition at the surface. Fluxes of Ca release through uptake, litterfall, and mineralization should indeed be high because Ca is not retranslocated within the tree before leaf abscission (Kramer and Kozlowski 1979). Under steady-state conditions, Ca uptake from the deep soil is slightly higher beneath sugar maple than beneath hemlock, and Ca uptake from the deep soil becomes only substantial at the high total mineral Ca site beneath sugar maple. These results indicate



**Figure 7.** Exchangeable Ca in the surface soil modeled with time for *Acer saccharum* and *Tsuga canadensis* sites with low and high total mineral Ca concentrations in the soil.

that Ca uptake in the deep soil depends not only on tree species but also on the parent material of the soil.

We modeled the exchangeable Ca content in the surface soil over time for sites with low and high total mineral Ca concentration in the soil for sugar maple and hemlock ("low" and "high" sites), using Eq. (5). We evaluated the effect of each of the two tree species on the Ca availability in a surface soil that at the start had the exchangeable Ca content typical of the other species. Thus, we started our model at  $t = 0$  with an exchangeable Ca content of 414 and 719  $\text{mmol m}^{-2}$  in the surface soil for low and high sugar maple sites and of 678 and 3328  $\text{mmol m}^{-2}$  for low and high hemlock sites. These values correspond with exchangeable Ca contents measured at hemlock and sugar maple sites respectively (Figure 5). We further used parameters that were measured ( $A$ ,  $W_s$ ) (Figure 5) and calculated ( $\alpha$ ,  $U_d$ ) (Table 3) at these sites. Note that in this model we do not need to parameterize Ca uptake in the surface soil. We assumed  $\alpha$  to be the same for all sites by taking the slope of the regression through all points in Figure 4C ( $\alpha = 0.0133$ ). Our model suggests that small differences in Ca uptake from the deep soil had a large effect on the exchangeable Ca content in the surface soil over a few centuries, that is, the life time of old-growth canopy dominants (Figure 7). The exchangeable Ca content in the surface soil beneath the "high" sugar maple site increased much faster over time than the "low" sugar maple site. This is caused by the higher Ca uptake from the deep soil at the sugar maple site with a high total mineral Ca concentration (Table 3). While the exchangeable

Ca content in the surface soil increases with time beneath sugar maple, so does Ca leaching below the surface soil until Ca leaching equals Ca uptake from the deep soil plus the Ca inputs from atmospheric deposition and weathering and steady state is reached. Because of a lack of sufficient Ca uptake from the deep soil beneath hemlock, the exchangeable Ca content in the surface soil drops until Ca leaching has decreased sufficiently.

These results suggest that Ca uptake in the deep soil, with varying total mineral Ca concentration, has the effect of bringing the exchangeable Ca content in surface soils beneath sugar maple into a fairly wide range. The lack of Ca uptake in the deep soil beneath hemlock results in a convergence of exchangeable Ca, no matter what the parent material Ca concentration is. The divergent relationships between exchangeable and total mineral Ca under these two tree species are in agreement with observations at the Canaan Mountain plateau by Finzi and others (1998), van Breemen and others (1997), and ourselves. Our model shows that a change in tree composition can alter the exchangeable Ca content in the surface soil significantly within the life span of the tree.

Our modeling results depend on the accuracy of the Ca pools and fluxes that we estimated and on the likelihood of our assumptions. The Ca flux that we measured with the largest possible error is from Ca release through organic matter decomposition in the surface soil ( $R_d$ ). We also created errors by ignoring Ca input from throughfall and stemflow. However, these errors are only relevant to the internal Ca cycling (for example, Ca uptake in the surface soil) within our set boundary of the tree-soil system—the mineral soil at 20-cm depth,—but they do not affect Ca uptake in the deep soil that we estimated under the condition that the exchangeable Ca content in the surface soil is maintained. As discussed earlier, annual net Ca storage in the biomass should increase our estimate of net Ca uptake in the deep soil, if exchangeable Ca content in the surface soil is maintained. Our deep uptake estimates rely further on the error of our estimates on Ca input from atmospheric deposition and weathering, compared to Ca leaching below the surface soil at each site, which we fairly constrained. Whether or not our sites are being depleted in exchangeable Ca in the surface soil, our model clearly illustrated the importance of Ca uptake in deep soils as a means of altering Ca availability in the surface soil.

## CONCLUSIONS

The release of Ca through organic matter decomposition was significantly higher beneath sugar maple than beneath hemlock. The high flux of Ca release through organic matter decomposition compared to the low Ca leaching below the surface soil indicates that for both tree species most of the Ca released through decomposition is taken up again in the surface soil (more than 85%). Calcium leaching to soil depths below 20 cm was much higher beneath sugar maple than beneath hemlock. Beneath sugar maple, Ca leaching was positively correlated with the total mineral Ca concentration in the soil and was always higher than the sum of Ca input from atmospheric deposition and weathering in the surface soil. There are two possible explanations for these results: (a) Ca depletion from the surface soil (forest floor + upper 20 cm of the mineral soil) occurs much faster beneath sugar maple than beneath hemlock, and (b) appreciable Ca uptake in the deep soil helps to maintain high exchangeable Ca contents in the surface soil beneath sugar maple. A higher Ca uptake in the deep soil beneath sugar maple was supported by higher fine-root densities in the deep soil beneath sugar maple than beneath hemlock. In contrast, more fine roots were present in the forest floor beneath hemlock, where possibly, with the aid of ectomycorrhizal mycelium, Ca uptake efficiency by hemlock was greater while the organic matter decomposition rate was slower. This would keep the exchangeable Ca content in the surface soil beneath hemlock small resulting in minimal Ca leaching losses to deeper soil layers. Using a simple model, we showed that even a slightly higher Ca uptake from the deep soil can substantially increase Ca availability in the surface soil within the life span of these trees.

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