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Forest liming increases forest floor carbon and nitrogen stocks in a mixed hardwood forest

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Abstract. In acid-impacted forests, decreased soil pH and calcium (Ca) availability have the potential to influence biotic and abiotic controls on carbon (C) and nitrogen (N) cycling. We investigated the effects of liming on above- and belowground C and N pools and fluxes 19 years after lime addition to the Woods Lake Watershed, Adirondack Park, New York, USA. Soil pH and exchangeable Ca remained elevated in the forest floor and upper mineral soil of limed areas. Forest floor C and N stocks were significantly larger in limed plots (68 vs. 31 Mg C/ha, and 3.0 vs. 1.5 Mg N/ha), resulting from a larger mass of Oa material. Liming reduced soil basal respiration rates by 17% and 43% in the Oe and Oa horizons, respectively. Net N mineralization was significantly lower in the limed soils for both forest floor horizons. Additional measurements of forest floor depth outside of our study plots, but within the treatment and control subcatchments also showed a deeper forest floor in limed areas; however, the mean depth of limed forest floor was 5 cm shallower than that observed in our study plots. Using a differential equation model of forest floor C dynamics, we found that liming effects on C fluxes measured within our study plots could explain the small observed increase in the Oe C stock but were not large enough to explain the increase in the Oa. Our catchment-wide assessment of forest floor depth, however, indicates that our plot analysis may be an overestimate of ecosystem-scale C and N stocks. Our results suggest that the mechanisms identified in our study, primarily liming-induced reduction in decomposition rates, may account for much of the observed increase in forest floor C. These findings emphasize the importance of understanding of the effects of liming in hardwood forests, and the long-term impacts of acid deposition on forest C and N uptake and retention.

Key words: acidification; Adirondack Park, New York, USA; calcium; carbon; forest; lime; nitrogen; soil; Woods Lake.

Introduction

Nutrient availability in northeastern U.S. forests has been dramatically altered by anthropogenic activities. Acid deposition has increased nitrogen (N) availability and forest growth, but has also been linked to soil acidification, base cation losses, and declines in some temperate tree species (Siccama et al. 1982, van Breemen et al. 1983, Likens et al. 1996, Driscoll et al. 2001, Thomas et al. 2010). Amendments to the Clean Air Act have reduced the deposition of sulfate, a strong acid anion; however, N deposition remains high (National Atmospheric Deposition Program [NADP], *available online* 2008),[4] and declines in soil pH and exchangeable base cations, especially calcium (Ca), are continuing throughout the region (Bailey et al. 2005, Johnson et al. 2008, Warby et al. 2009). Calcium is typically the most abundant base cation on the soil exchange complex and is important in neutralizing acids in soil (Likens et al. 1998, Driscoll et al. 2001). As a result of this important function, studies of Ca cycling have focused largely on the links between Ca and acidification, including how Ca availability affects soil pH, mobilization of aluminum (Al), and the acid-neutralizing capacity of freshwaters (Cronan and Schofield 1990, Driscoll et al. 2001). Far fewer studies have investigated how altered soil Ca concentrations and changes in pH influence forest carbon (C) sequestration and storage, and response to increased N deposition.

Calcium has many roles in forest ecosystems that can directly affect C and N stocks and fluxes. Trees utilize Ca for numerous biological functions that dictate C and N uptake and storage in tissues. This includes growth, stomatal regulation, carbohydrate metabolism, cell wall synthesis and structure, and response to environmental stress (McLaughlin and Wimmer 1999, Lautner and Fromm 2010). Changes in pH and soil Ca concentration can also influence microbial and faunal communities, with higher Ca availability and soil pH leading to increased microbial activity (Illmer and Schinner 1991, Andersson and Nilsson 2001, Nilsson et al. 2001), higher earthworm abundance, and higher rates of litter

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decomposition (Reich et al. 2005, Hobbie et al. 2006). In contrast, Ca can reduce the mobility and solubility of dissolved organic matter (OM) in some mineral soils by forming cation bridges that stabilize OM and reduce decomposition, leading to greater OM retention (Muneer and Oades 1989, Romkens et al. 1996, Chan and Heenan 1999, Oste et al. 2002, Mikutta et al. 2007). Recent work has also demonstrated that increased Ca availability can lead to greater N uptake by plants and reduced microbial N cycling, thereby reducing potential ecosystem N losses via leaching (Groffman and Fisk 2011*a*).

Forest liming (with calcium carbonate, $CaCO_3$) can reduce the effects of acidification by increasing soil pH and exchangeable Ca concentrations in the forest floor and upper mineral soils. Liming studies, therefore, provide an opportunity to explore how soil Ca availability influences C and N cycling, and to identify how this management practice affects ecosystem nutrient availability. Liming studies have been widely conducted across Europe in conifer plantations (Huettl and Zoettl 1993, Lundstrom et al. 2003). In North America, Ca additions have been conducted in conifer stands (Kulmatiski et al. 2007) and mixed hardwood forests (Peng and Thomas 2010, Kluber et al. 2012), but have been most common in stands of sugar maple (*Acer saccharum*), a species that typically responds positively to increased soil Ca availability (Long et al. 1997, Huggett et al. 2007, Moore et al. 2012).

Here, we investigated changes in C and N pools and fluxes ~20 years after an experimental lime addition to the Woods Lake Watershed, a mixed northern hardwood forest located in the Adirondack Park, New York, USA. In 1989, lime was added to half of the catchment area to assess whether forest liming could be an effective strategy to reduce acidification of surface waters (Driscoll et al. 1996). We hypothesized that the lime addition would improve forest health and that this improvement would be evident in increased aboveground live tree biomass, leaf litter, and fine-root production. Within the forest floor, we anticipated that the increased pH associated with liming would stimulate microbial activity resulting in increased decomposition, soil basal respiration, and net N mineralization. We also expected enhanced decomposition to lead to reduced C and N stocks in limed forest floor horizons relative to controls. Conversely, we hypothesized that increased Ca availability would enhance Ca–OM complexation in the upper mineral soils, leading to larger C and N stocks within limed mineral soils.

Methods

Site description

Research was conducted in the Woods Lake Watershed, the site of an Experimental Watershed Liming Study, located in Herkimer County, New York, within the Adirondack Park (43°52′ N, 74°57′ W). In 1989, $CaCO_3$ was applied by helicopter to two ~50-ha subcatchments (L1 and L2 in this study; II and IV, respectively, in orginal study) in a single application of 6.89 tons/ha (2.76 Mg/Ca ha) (Driscoll et al. 1996). The lime pellet was 82% $CaCO_3$, 8% $MgCO_3$, and 4% organic binder (Driscoll et al. 1996). Two additional subcatchments were maintained as controls (C1 and C2 in this study; III and V in the original study). Mean annual precipitation at this site is 1230 mm, and mean annual temperature is 5.2°C (Yavitt et al. 1995).

This watershed has 98% forest cover (Staubitz and Zarriello 1989) and is dominated by American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*), with lesser amounts of red spruce (*Picea rubens*), sugar maple (*Acer saccharum*), and striped maple (*Acer pensylvanicum*) (Smallidge and Leopold 1994). The site is underlain by hornblende granitic gneiss bedrock covered by a sandy glacial till comprised of quartz and feldspar, with some interspersed hornblende, ilmenite, and magnetite (April and Newton 1985). The soils are classified as Orthod Spodosols (Smallidge and Leopold 1994), and mean mineral soil depth is 30–35 cm (Brocksen et al. 1988). Calcium is the dominant base cation in these soils (Blette and Newton 1996). Within 1–2 years after liming, the pH in the forest floor rose from 3.7 to 4.9 in the Oe horizon and from 3.7 to 4.0 in the Oa (Simmons et al. 1996). Exchangeable Ca concentrations also increased during this period, from 8.5 to 35 $cmol_c$/kg soil in the Oe and from 6 to 10 $cmol_c$/kg soil in the Oa (Blette and Newton 1996). Following these early studies, little research has been conducted within the forest at this site.

Plot selection

Vegetation and soil sampling was conducted in five 0.04-ha plots located in each subcatchment. These 20 plots were a subset of 99 plots established during the original vegetation sampling in 1989 (Smallidge and Leopold 1994) and were chosen to span the spatial heterogeneity of the landscape and to minimize differences in tree species composition, slope, and aspect between control and limed subcatchments.

Aboveground vegetation measurements

When the plots were established in 1989, all trees ≥10 cm diameter at breast height (dbh) were tagged, and dbh was recorded (P. Smallidge, *personal communication*). In August 2009, dbh was measured on all trees ≥10 cm within each study plot, including both tagged and untagged trees meeting this size criteria. Aboveground live tree biomass for both 2009 and 1989 was calculated using allometric equations from Jenkins et al. (2003). To convert to units of C, we assumed that woody biomass is 50% C (Fahey et al. 2005*a*). Plot mortality and changes in aboveground live biomass were calculated using newly collected data from 2009 and measurements taken in 1989. Litterfall was collected from May 2009 to May 2010 using five 0.23-m^2 (40.6 × 55.9 cm) litter baskets distributed across each plot. Baskets were secured in

place with stakes and lined with fiberglass window screen to prevent litter material from resting on the bottom of the basket.

Litter was air dried, then sorted into components including: foliage (sorted by species), seeds, branches and wood, and miscellaneous components. Sorted samples were then dried at 50°C for at least 3 d and weighed. Foliar litter from all baskets within a plot was combined by tree species into one composite sample per plot for analysis of C, N, Ca, and lignin. The composite foliar samples were ground to a fine powder using a Cyclone Sample Mill (Udy, Fort Collins, Colorado, USA). Total C and N concentrations were measured via high temperature combustion using a Vario EL III elemental analyzer (Elementar, Hanau, Germany) at Cornell University, Ithaca, New York, USA. Total Ca concentration was analyzed by nitric acid microwave digestion followed by analysis using a Varian Vista AX inductively coupled plasma atomic emission spectrometer at the U.S. Forest Service Laboratory, Durham, New Hampshire, USA. Foliar-litter lignin concentration was determined at the Dairy One Forage Laboratory, Ithaca, New York. Samples were digested in an ANKOM A200 fiber analyzer using the ANKOM A200 filter bag technique (ANKOM Technology, Macedon, New York, USA). First, samples were placed in filter bags and submerged in acid detergent fiber solution for 75 min in an ANKOM A200 digestion unit. Samples were then rinsed in boiling water, then in acetone, before being dried at 100°C for 2 h. The remaining residue was combined with 72% sulfuric acid for 3 h in an ANKOM A200 DaisyII Incubator. Lignin concentration was then determined using a FOSS NIRSystems Model 6500 VIS-NIR spectrometer (FOSS, Laurel, Maryland, USA).

Soil collection

In the summer of 2007, forest floor and mineral soils were collected from five locations within each of the 20 intensively studied plots. The forest floor was collected by placing a 15 × 15 cm wood frame on the surface of the Oe horizon and cutting out a block of OM using a knife. Roots within the block were clipped with pruners at the edges of the frame and all forest floor material was removed, either as an intact block, or by hand and with a spoon. After removal of the block, forest floor depth was recorded. The interface between the forest floor and mineral soil was usually easy to identify due to the presence of an E horizon immediately below the Oa horizon. A spoon was used to collect as much organic matter as possible from this E–Oa boundary, with care taken to minimize mixing of mineral and organic horizons. Mineral soils were sampled incrementally for depths 0–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm using a diamond-tipped rotary coring device with 9.5-cm internal diameter, which provides a quantitative sample of soil bulk density and OM stocks (Rau et al. 2011). Collected mineral soil samples were used to quantify soil pH, exchangeable Ca availability, and C and N stocks.

The 2007 sampling revealed differences in forest floor mass between limed and control plots. In 2008, we improved the resolution of our forest floor sampling by collecting Oe and Oa horizons separately from six locations within each plot. Similar to the 2007 sampling, we used a knife to cut out 15 × 15 cm blocks. First, we removed the Oe layer, which consisted of partially fragmented litter, had a light brown color, and typically was removed as a solid block held together by hyphae and roots. Next, we removed the Oa horizon, which was dark brown to black in color, very moist, and contained no recognizable litter material.

An in situ net N mineralization study was conducted in 2008 and included the collected Oe and Oa samples and a new measurement of the top 10 cm of mineral soil. At each of the six sampling locations, two samples of Oe, Oa, and 0–10 cm mineral soil were taken side by side. Mineral soil was collected using a tulip bulb corer (7 cm diameter). One set of samples (initial) were kept on ice packs and returned to the laboratory shortly after collection. The initial Oe and Oa samples were used to quantify forest floor pH, exchangeable Ca availability, C and N stocks, and pools of ammonium (NH_4^+) and nitrate (NO_3^-), and the mineral soils were used only to estimate NH_4^+ and NO_3^-. The second set of soil samples (incubated) were sealed in polyethylene bags in the field and placed back in the soil from which they were removed. After a 30-d in situ incubation, samples were retrieved, placed on ice packs, and returned to the laboratory for analysis.

In September 2010, five additional Oe and Oa samples were collected within each plot from a 15 × 15 cm area using a square-edged shovel. Samples were kept on ice packs during transport and later used to assess soil basal respiration. Finally, to assess whether our 20 study plots represented forest floor dynamics across the 200-ha watershed, we took an additional 100 forest floor depth measurements at random locations in each of the study subcatchments in 2010 ($n = 400$).

Soil laboratory analyses

The forest floor and mineral soil samples collected in 2007 were dried at 50°C for approximately one week. These samples were then weighed, but no chemical analyses were performed. Mineral soils collected in 2007 were passed through a 2-mm sieve and rock and roots were removed and weighed. The Oe and Oa samples collected in 2008 were passed field moist through 5.6-mm and 4-mm sieves, respectively. All roots were removed from these samples while sieving. Large root pieces that slipped through the sieve were retrieved for quantification. Samples were then dried at 50°C for at least 3 d. Forest floor fine-root biomass was estimated later on Oe and Oa samples by sorting the dried samples into >2-mm and <2-mm size classes, then re-drying and weighing the <2-mm roots. Two 10-g subsamples of

moist Oe and Oa material were collected to determine moisture content and to measure net N mineralization and were kept refrigerated until analysis. The remaining sample was dried at 50°C for at least 5 d, then three additional ~10-g subsamples were removed for analysis of total C, N, exchangeable Ca, and pH.

A subsample of forest floor (2008 collection) and mineral soil (2007 collection) samples were ground to a fine powder using a Retsch mixer mill, type MM200 (Retsch, Haan, Germany), and analyzed for total C and N on a Vario EL III elemental analyzer. Exchangeable cation concentrations were measured using a 1 mol/L ammonium chloride (NH_4Cl) extraction. Five grams of forest floor material were combined with 50 mL of NH_4Cl, and 10 g of mineral soil were mixed with 100 mL of NH_4Cl. Each sample was placed on a shaker table for 1 h. After shaking, solutions were vacuum filtered through Pall brand type A/E glass fiber filters (Port Washington, New York, USA). Extracts were frozen until analysis, using inductively coupled plasma emission spectroscopy at the State University of New York College of Environmental Science and Forestry, Syracuse, New York. Soil pH analysis was performed using an Accumet basic AB15 pH meter (Accumet, Hampton, New Hampshire, USA) with a flushable junction soil probe. For the mineral soils, a 10-g subsample of soil was mixed thoroughly with 20 mL of deionized water. For forest floor material, 5 g of sample were mixed with 50 mL of water. After a 30-min equilibration, samples were gently swirled, and a reading was taken after pH stabilized.

To assess net N mineralization and nitrification of both initial and incubated Oe, Oa and 0–10 cm mineral soil samples, 10 g of field moist soil was mixed with 100 mL of 1 mol/L potassium chloride and placed on a shaker table for 1 h. After shaking, samples were passed through a Whatman Type GF/F glass fiber filter via vacuum filtration. All extractions were performed on the same day the sample was sieved, and within one week of collection. Extracts were then frozen until analysis using the automated flow injection phenate method on a Lachat QuikChem 8000 automated ion analyzer at the Cary Institute of Ecosystem Studies, Millbrook, New York. Net N mineralization was calculated as the difference between the incubated and initial sample concentrations of NH_4^+ and NO_3^- in the paired samples for each depth increment studied. Net nitrification was calculated as the accumulation of NO_3^- between the incubated and initial samples.

To measure heterotrophic soil basal respiration, the five samples collected within each plot in 2010 were sieved, then composited by depth increment shortly after collection, creating one composite Oe and Oa sample for each plot. Samples were then kept at 4°C for 5 months, until analysis. We assume that this delay in initiating measurements allowed the most labile C substrates to be respired prior to our sampling period. Approximately one week before measuring soil basal respiration, four subsamples weighing 20 g each (field moist), of each composite sample were placed in 355-mL Ball glass jelly jars and left in the dark at 22°C. A 10-g subsample of each composite was dried for at least 24 h at 110°C to calculate soil moisture content. Soil basal respiration was measured on two occasions approximately three weeks apart. Sample moisture was maintained by weighing samples weekly and adding deionized water as needed to return soils to field moisture. The last water addition occurred one week prior to the second respiration measurement. Soil basal respiration was measured by capping samples with an air-tight lid and allowing CO_2 to accumulate in the headspace. After 24 h, 2 mL of headspace was removed using a syringe and immediately injected into an infrared gas analyzer (LI-6200, LI-COR, Lincoln, Nebraska, USA). One replicate of each composite sample was incubated a third time and the collected headspace was analyzed for ^{13}C, to determine whether any undissolved lime pellets in the limed forest floor samples had contributed to the measured CO_2 accumulation during the incubation. Following the incubation, ~5 g of each sample were ground and analyzed for total C and N concentration using the same forest floor analytical methods used to determine forest floor C and N stocks.

Statistics

Statistical analysis was performed using JMP 9.0 (SAS Institute 2011). A mixed model was constructed containing treatment (control vs. limed) and subcatchment (C1, C2, L1, L2) nested within treatment as fixed effects. Plot and samples obtained within plots were included as random effects. Main liming effects were confirmed using this model, then subcatchment mean comparisons were made using Tukey's test ($P < 0.05$). When data were not normally distributed, natural log-transformations were performed. These transformations did not change the statistical outcomes, and values reported here are for the observed values.

Modeling forest floor C dynamics

We used an ordinary differential equation (ODE) model to quantify the impacts of liming on the dynamics of the forest floor Oe and Oa C stocks over the 19-year period post-liming. Specifically, we sought to quantify if the observed liming effects on litterfall, root biomass, and heterotrophic respiration in our study plots were sufficient to explain observed differences in Oe and Oa C stocks. The ODE model is

$$dC_e/dt = \mathrm{Lit} + \mathrm{CWD} + \mathrm{Root_e} + \mathrm{Rhizo_e} - (r_e + \tau_{ea})C_e \quad (1)$$

$$dC_a/dt = \tau_{ea}C_e + \mathrm{Root_a} + \mathrm{Rhizo_a} - (r_a + \tau_{am})C_a \quad (2)$$

where the subscripts e, a, and m denote the Oe, Oa, and mineral soil layers, respectively; C_e and C_a are Oe and Oa C stocks (Mg/ha); Lit and CWD are leaf litter and

TABLE 1. Live tree aboveground biomass estimates (Mg C/ha; mean ± SE) for all tree species found within the control (C1 and C2) and limed (L1 and L2) subcatchments in the Woods Lake Watershed, Adirondack Park, New York, USA.

	Subcatchment and year measured							
	C1		C2		L1		L2	
Tree species	1989	2009	1989	2009	1989	2009	1989	2009
Beech	25.8 ± 12.8	18.3 ± 5.7	75.7 ± 15.6	41.2 ± 13.4	36.2 ± 5.9	15.7 ± 3.1	62.8 ± 16.4	12.5 ± 3.0
Red maple	27.9 ± 16.3	26.9 ± 10.1	27.0 ± 6.4	19.7 ± 13.5	25.7 ± 12.3	18.3 ± 5.1	14.5 ± 4.5	19.9 ± 7.5
Red spruce	6.9 ± 4.3	5.4 ± 3.0	5.9 ± 5.2	0.9 ± 0.5	10.7 ± 6.6	6.2 ± 2.5	14.6 ± 6.6	4.8 ± 3.3
Striped maple	2.0 ± 1.7	3.1 ± 2.0	0.0	3.9 ± 3.2	2.4 ± 1.5	1.9 ± 1.4	0.2 ± 0.2	1.9 ± 0.7
Sugar maple	17.0 ± 9.3	22.8 ± 14.3	0.8 ± 0.8	1.6 ± 1.6	0.9 ± 0.6	0.7 ± 0.7	2.2 ± 1.0	7.2 ± 3.1
Yellow birch	46.0 ± 32.2	14.9 ± 7.3	7.2 ± 3.1	2.0 ± 1.3	60.6 ± 26.8	64.8 ± 34.2	14.6 ± 7.9	14.5 ± 6.7
Other	5.6 ± 6.0	0.0	0.1 ± 0.1	0.0	0.0	0.0	0.0	0.0
Total	131.5 ± 34.2	91.3 ± 10.6	116.8 ± 12.6	69.3 ± 7.7	136.6 ± 22.5	107.6 ± 29.7	108.8 ± 14.3	60.8 ± 6.0

Note: See *Methods: Site description* for scientific names of tree species.

coarse woody debris fluxes ($Mg \cdot ha^{-1} \cdot yr^{-1}$) entering the Oe C pool; Root and Rhizo are C inputs ($Mg \cdot ha^{-1} \cdot yr^{-1}$) to the Oe and Oa pools resulting from root mortality and rhizosphere transfers (root exudation and allocation to micorrhyzae); r is heterotrophic respiration (yr^{-1}); and τ is the transfer rate (yr^{-1}) between C pools in different soil layers (τ_{ea} from Oe to Oa; τ_{am} from Oa to the mineral layer).

We did not measure all fluxes in Eqs. 1–2; therefore, we combined our data with values reported by Fahey et al. (2005*b*) to parameterize the ODE model. We briefly outline the approach here and provide a detailed account in the Appendix. Fahey et al. (2005*b*) report a complete C budget for forest floor and mineral soil layers for mixed Northern hardwood forests at the Hubbard Brook Experimental Forest, New Hampshire. Their reported stocks and fluxes imply that their system is close to equilibrium. We used the ratio of Oe:Oa C pool sizes at our study site to partition the Fahey et al. (2005*b*) forest floor values into Oe and Oa layers. We then solved their system for equilibrium and perturbed it with a liming treatment by multiplying the Lit, Root, r and τ terms in Eqs. 1–2 by the relevant limed : control ratios observed in our study. We simulated the transient dynamics of the perturbed system for 19 years and compared the ratios of final (year 19) to initial (year 0; i.e., the pre-liming equilibrium) C pool sizes from Eqs. 1–2 to the limed : control ratios of C stocks observed at our study site. Sensitivity analysis showed that the comparison between the ODE model (Eqs. 1–2) and our observed pool-size effects depended strongly on the limed : control ratios for Lit, Root, r and τ, but not on the literature-derived parameter values. Therefore, we propagated uncertainty in the limed : control ratios using 10 000 Monte Carlo simulations of the ODE model.

RESULTS

Tree response to liming

In 1989, live tree biomass averaged 123.4 Mg C/ha in study plots (Table 1). During the 20-year interval since lime application, there was a net decline in live tree biomass in all subcatchments, averaging 2.1 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ and resulting in a mean standing biomass of 82.2 Mg C/ha in 2009. There were no significant differences in biomass loss between limed and control subcatchments ($P = 0.76$). Aboveground biomass declines differed among species, however, with American beech exhibiting the largest biomass loss across the watershed.

Total annual aboveground litter inputs were 3.9 Mg $OM \cdot ha^{-1} \cdot yr^{-1}$ across the watershed and did not differ significantly between limed and control subcatchments ($P = 0.65$). Similarly, no differences were observed between any of the measured litter components (data not shown). There was a trend toward larger foliar-litter inputs in the limed subcatchments (2.96 vs. 2.76 Mg $OM \cdot ha^{-1} \cdot yr^{-1}$), but this relationship was not statistically significant ($P = 0.36$). All tree species exhibited significantly larger Ca concentrations in foliar litter in limed plots relative to controls, resulting in significantly higher total foliar Ca inputs in limed plots (Table 2).

TABLE 2. Foliar-litter C, N, and Ca inputs, and Ca and lignin concentrations.

	Subcatchment				
Foliar chemistry	C1	C2	L1	L2	Lime effect (P value)
Ca (%)	0.81^{a} ± 0.02	1.1^{b} ± 0.04	1.7^{c} ± 0.1	1.5^{c} ± 0.04	<0.001
Ca ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	0.02^{a} ± 0.002	0.02^{a} ± 0.002	0.04^{b} ± 0.008	0.04^{ab} ± 0.001	0.001
C ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	1.35 ± 0.08	1.36 ± 0.08	1.39 ± 0.19	1.44 ± 0.04	0.60
N ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	0.03 ± 0.002	0.03 ± 0.002	0.03 ± 0.004	0.03 ± 0.002	0.12
Lignin (%)	30.9 ± 4.0	32.4 ± 3.8	28.1 ± 3.0	27.8 ± 3.2	0.01

Notes: Row values with different superscript letters indicate significant differences among control (C1 and C2) and limed (L1 and L2) subcatchments ($P < 0.05$). Lime-effect P values indicate significant responses to liming. Values are reported as mean ± SE.

TABLE 3. Fine-root biomass <2 mm diameter (Mg C/ha) for forest floor Oe and Oa horizons, reported as mean ± SE.

Forest floor horizon	Subcatchment				Lime effect (P value)
	C1	C2	L1	L2	
Oe	$0.26^{a} \pm 0.04$	$0.31^{a} \pm 0.06$	$0.59^{b} \pm 0.05$	$0.27^{a} \pm 0.04$	0.01
Oa	0.22 ± 0.05	0.44 ± 0.05	0.40 ± 0.08	0.45 ± 0.05	0.11

Notes: Different superscript letters within a row indicate significant differences ($P < 0.05$) among the control (C1 and C2) and limed (L1 and L2) subcatchments.

Total foliar inputs of C and N did not differ between limed and control plots (Table 2); however, significantly larger C concentrations were observed in the control plot foliar litter of all species, except yellow birch (data not shown). Foliar litter in control plots exhibited significantly higher lignin concentrations (Table 2).

Fine-root (<2 mm) biomass in the Oe horizon was significantly greater in the limed sites relative to controls (Table 3). This pattern was driven by significantly greater root biomass in the L1 subcatchment relative to all other subcatchments. There was no effect of liming on fine-root biomass in the Oa horizon ($P = 0.11$); however, there was a trend toward greater biomass in limed soils.

Soil response to liming

Nineteen years after the lime addition, 48% of the added Ca was present in an exchangeable form within the forest floor and top 40 cm of mineral soil. Total soil exchangeable Ca stocks were significantly higher in limed soils for all measured depths, with the largest stock differences being present in the Oa horizon (Table 4). Similarly, the largest pools of exchangeable Ca were present in the forest floor, where both limed subcatchments showed significantly higher exchangeable Ca concentrations than controls ($P < 0.001$ for both Oe and Oa; Fig. 1A). Liming also resulted in significantly higher exchangeable Ca availability in the top 40 cm of mineral soil ($P \leq 0.01$ for all depth increments). The forest floor pH was significantly higher in the forest floor of limed plots, increasing from 4.1 to 5.3 in the Oe ($P < 0.001$) and from 3.9 to 4.7 in the Oa ($P < 0.001$; Fig. 1B). In the mineral soil, significantly higher pH was observed only in the 0–10 cm increment ($P = 0.05$). No differences were observed in exchange magnesium for any measured depth increment (data not shown).

The forest floor mass was significantly larger in limed soils relative to controls (175 vs. 94 Mg OM/ha), resulting in larger forest floor C and N stocks in limed plots (Fig. 2 A, B). This difference in C and N content was driven primarily by greater accumulation of Oa material in the limed subcatchments, which contained 57.6 Mg C/ha relative to 22.8 Mg C/ha ($P < 0.001$) in controls and 2.5 vs. 1.1 Mg N/ha ($P < 0.001$). The Oe also contained significantly larger C and N stocks in the limed subcatchments, but treatment differences were not as large as those observed in the Oa (10.4 vs. 7.9 Mg C/ha; $P = 0.01$; and 0.5 vs. 0.4 Mg N/ha, $P = 0.01$). A significantly higher C concentration in the limed Oa horizon was also observed (36.0% ± 4.4% vs. 29.0% ± 4.1%, in limed and control, respectively; $P = 0.009$). No differences in C concentration were present in the Oe horizon (limed 44.3% ± 2.7% and control 45.2% ± 2.3%; $P = 0.44$) or in N concentration for either forest floor horizon (Oe limed 2.2% ± 0.2%, control 2.2% ± 0.1%; $P = 0.47$; and Oa limed 1.6% ± 0.2%, control 1.4 ± 0.2%; $P = 0.09$). Additional forest floor depth measurements taken across the watershed support our plot observations and showed a deeper forest floor in limed subcatchments relative to controls. However, the mean depth of the forest floor in limed plots across the subcatchments was only 13 cm, compared to a mean of 18 cm found in our study plots. Control areas exhibited a mean forest floor depth of 10 cm across the subcatchments and 11 cm within plots.

No significant differences in soil C stocks were observed for any of the measured mineral soil depth

TABLE 4. Mean (±SE) soil exchangeable Ca pools (kmol Ca/ha) in the soils of the Woods Lake Watershed in 2007–2008.

Soil depth	Subcatchment				Lime effect (P value)
	C1	C2	L1	L2	
Oe	$1.4^{a} \pm 0.3$	$0.9^{a} \pm 0.3$	$6.1^{b} \pm 1.6$	$4.7^{b} \pm 1.0$	<0.001
Oa	$1.1^{a} \pm 0.5$	$1.5^{a} \pm 1.0$	$19.3^{b} \pm 5.2$	$20.0^{b} \pm 5.0$	<0.001
0–10 cm	$1.4^{a} \pm 0.4$	$1.9^{a} \pm 0.9$	$6.7^{b} \pm 2.3$	$7.5^{b} \pm 3.2$	<0.001
10–20 cm	$0.8^{a} \pm 0.2$	$1.3^{ab} \pm 0.6$	$2.6^{bc} \pm 0.6$	$3.2^{c} \pm 0.8$	<0.001
20–30 cm	$0.6^{a} \pm 0.2$	$0.9^{a} \pm 0.3$	$1.7^{ab} \pm 0.4$	$2.5^{b} \pm 0.6$	<0.001
30–40 cm	$0.6^{a} \pm 0.1$	$0.8^{ab} \pm 0.3$	$1.5^{bc} \pm 0.4$	$2.0^{c} \pm 0.4$	<0.001

Notes: Row values with different superscript letters indicate significant differences among control (C1 and C2) and limed (L1 and L2) subcatchments ($P < 0.05$). Lime effect indicates significant responses to liming.

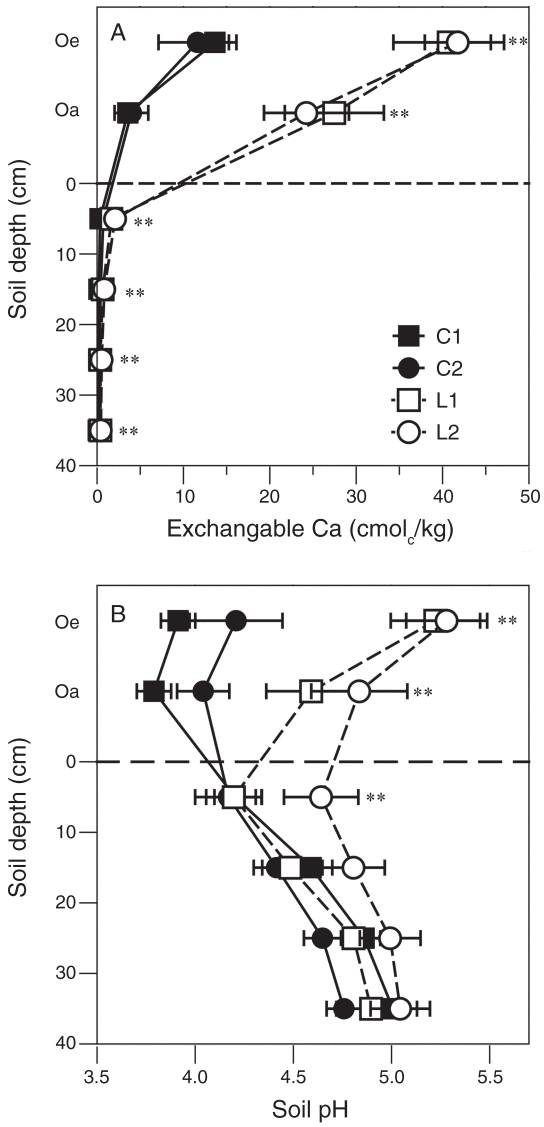

FIG. 1. (A) Exchangeable Ca concentration and (B) soil pH (mean ± SE) for all measured forest floor and mineral soil depth increments in control (C1 and C2) and limed (L1 and L2) subcatchments.
** $P < 0.01$.

increments (Table 5). Significantly higher N stocks were observed in the 0–10 cm and 10–20 cm depth increments in control soils; however, this appeared to be driven primarily by larger stocks in the C2 control subcatchment. The soil C:N ratio increased with soil depth from a mean value of 21 in the Oe horizon to 27 in the 30–40 cm mineral soil depth increment (Table 5). Liming resulted in significantly larger C:N ratios in the Oa forest floor horizon and in the mineral soil depth increments 0–10 cm, 10–20 cm, and 20–30 cm. These differences were driven primarily by a larger C:N ratio within the L1 limed subcatchment.

Heterotrophic soil basal respiration was significantly lower in the forest floor of limed soils relative to controls, particularly for the Oa horizon (Fig. 3A, B). Soil basal respiration was 17% lower in the Oe horizon of limed soils and reduced by 43% in the Oa layer. The ^{13}C values of C respired as CO_2 did not differ significantly between limed and control forest floor material for either horizon ($P = 0.10$ for Oe and $P = 0.30$ for Oa; data not shown), suggesting that abiotic CO_2 production caused by dissolution of any remaining lime pellets did not influence observed values.

Net N mineralization expressed on a mg N/kg soil basis indicated significantly lower rates in the limed soils for both forest floor horizons ($P = <0.001$ and 0.003 for Oe and Oa, respectively; Fig. 4A, C). No effect of liming on N mineralization in the top 10 cm of mineral soil was observed ($P = 0.74$; Fig. 4E). Net nitrification was significantly higher in the limed soils in the Oe horizon ($P < 0.001$; Fig. 4B), while no differences were evident in the Oa ($P = 0.95$; Fig. 4D) or upper mineral soils ($P = 0.60$; Fig. 4F). Scaling these N cycling measurements to the plot scale (kg N/ha) revealed little difference in net N mineralization rates for any measured depth ($P = 0.06$, 0.05, and 0.80 for Oe, Oa, and 0–10 cm, respectively). Net nitrification rates at this scale were significantly higher in both Oe and Oa forest floor horizons ($P = <0.001$ and 0.03, respectively).

Modeled dynamics of Oe and Oa C stocks

Perturbing Eqs. 1–2 from their equilibrium by applying the observed limed:control ratios for fluxes (decomposition, litterfall, and fine-root production; see the Appendix for details) caused the Oe C stock to increase and then equilibrate after about five years (Fig. 5A), whereas the Oa C stock continued to increase over the 19 years of simulated dynamics (Fig. 5B). The predicted Oe stock 19 years after liming (Fig. 5A; black line and gray-shaded area) was very similar to the stock expected from applying our observed limed : control Oe stock ratio to the initial equilibrium state of the model (Fig. 5A; filled circle and error bars). In contrast, the predicted Oa C stock tended to be smaller ($P = 0.038$) than that expected from the observed limed : control Oa stock ratio within our study plots (Fig. 5B).

DISCUSSION

Liming effects on forest floor C and N cycling and stocks

Liming in the Woods Lake Watershed showed large and unexpected effects on C and N cycling 19 years after the lime addition. Perhaps most dramatically, the forest floor in the limed subcatchments was much larger than in the controls, resulting in over twice the C and N storage in the organic horizons. We had hypothesized that the increase in pH associated with liming would stimulate decomposition. Increased pH can lead to greater solubility of organic carbon compounds, making them more readily available for microbial processing (Kalbitz et al. 2000), and in later stages of decomposition substrates high in Ca tend to decompose more fully than those with low Ca concentrations, possibly due to

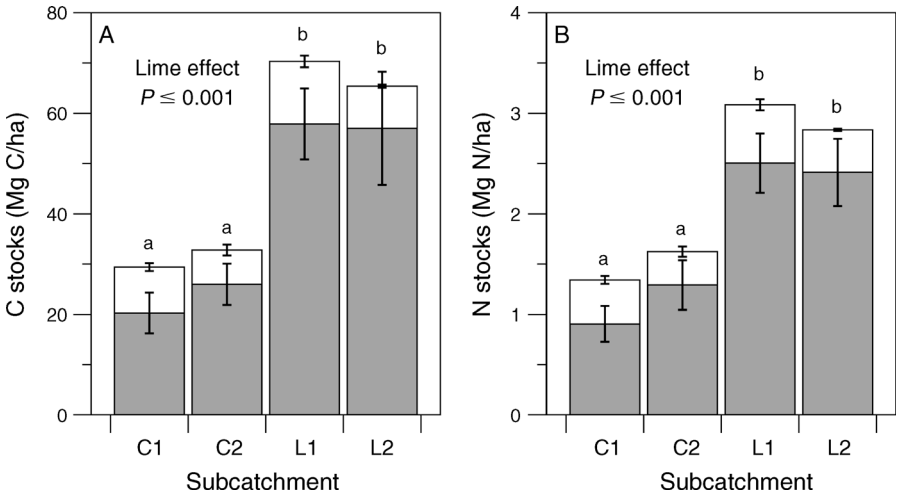

FIG. 2. Cumulative forest floor (A) carbon and (B) nitrogen stocks (mean ± SE) in control (C1 and C2) and limed (L1 and L2) subcatchments. The forest floor Oe horizon is displayed in white, and Oa in gray. Different letters indicate significant differences ($P < 0.05$) among subcatchments, and lime effect indicates the overall response to liming.

increased growth of white-rot fungi (Berg 2000). Observations of increased decomposition with liming have also been widely reported in the literature (Brumme and Beese 1992, Valeur and Nilsson 1993, Andersson and Valeur 1994, Baath and Arnebrant 1994, Priha and Smolander 1994, Andersson and Nilsson 2001), and have shown reduced OM accumulation in the forest floor of limed soils (Kreutzer 1995, Persson et al. 1995). In contrast, however, others have observed a decline in respiration after an initial enhancement period of weeks to a few years post-liming (Persson et al. 1989, Illmer and Schinner 1991, Groffman et al. 2006). In situ measurements of soil respiration conducted at Woods Lake within the first year after liming showed a trend toward lower CO_2 efflux in limed soils relative to controls, with significantly lower values in the peak of summer (Yavitt et al. 1995). Enhanced forest floor accumulation with liming has also been observed previously across 40 sites in Sweden and was attributed to increased OM inputs from ground vegetation, although inputs were not quantified in the study (Derome 1990). Reasons for these differential responses in C stocks remain unclear. At Woods Lake, it appears that a decrease in decomposition rate is the primary driver of forest floor accumulation, rather than an increase in litter or root inputs.

TABLE 5. Mean (±SE) soil C and N stocks and C:N ratios for control (C1 and C2) and limed (L1 and L2) subcatchments.

Soil depth	Subcatchment				Lime effect (P value)
	C1	C2	L1	L2	
C (Mg/ha)					
0–10 cm	$36.3^{a} \pm 3.8$	$49.7^{b} \pm 4.8$	$40.0^{ab} \pm 4.8$	$43.1^{ab} \pm 5.2$	0.54
10–20 cm	$39.3^{a} \pm 5.5$	$54.6^{b} \pm 5.8$	$43.0^{ab} \pm 6.8$	$43.7^{ab} \pm 4.7$	0.31
20–30 cm	$37.5^{a} \pm 5.1$	$56.2^{b} \pm 7.5$	$44.3^{ab} \pm 7.9$	$41.2^{ab} \pm 5.1$	0.36
30–40 cm	32.7 ± 5.4	49.0 ± 6.8	41.0 ± 7.6	34.5 ± 5.4	0.41
N (Mg/ha)					
0–10 cm	$1.7^{a} \pm 0.2$	$2.3^{b} \pm 0.2$	$1.6^{a} \pm 0.2$	$1.8^{ab} \pm 0.2$	0.04
10–20 cm	$1.6^{a} \pm 0.2$	$2.3^{b} \pm 0.2$	$1.5^{a} \pm 0.2$	$1.8^{a} \pm 0.2$	0.01
20–30 cm	$1.5^{a} \pm 0.2$	$2.2^{b} \pm 0.3$	$1.5^{a} \pm 0.3$	$1.6^{a} \pm 0.2$	0.07
30–40 cm	1.3 ± 0.2	1.9 ± 0.3	1.4 ± 0.3	1.3 ± 0.2	0.12
C:N ratio					
Oe	$20.9^{ab} \pm 0.7$	$20.2^{ab} \pm 0.7$	$21.5^{a} \pm 1.0$	$20.0^{b} \pm 0.8$	0.57
Oa	20.6 ± 1.6	20.8 ± 1.2	23.3 ± 1.4	22.6 ± 1.9	0.03
0–10 cm	$21.9^{a} \pm 1.2$	$21.9^{a} \pm 1.0$	$25.3^{b} \pm 1.2$	$24.1^{ab} \pm 1.6$	0.002
10–20 cm	$24.6^{a} \pm 1.2$	$23.6^{a} \pm 1.3$	$28.1^{b} \pm 1.2$	$24.9^{a} \pm 1.1$	0.005
20–30 cm	25.3 ± 1.3	25.1 ± 1.6	29.2 ± 1.3	26.1 ± 1.0	0.04
30–40 cm	24.6 ± 1.2	26.8 ± 1.9	28.4 ± 1.3	26.9 ± 1.8	0.13

Notes: Different superscript letters within a row indicate significant differences among subcatchments. Lime-effect P values indicate significant treatment differences.

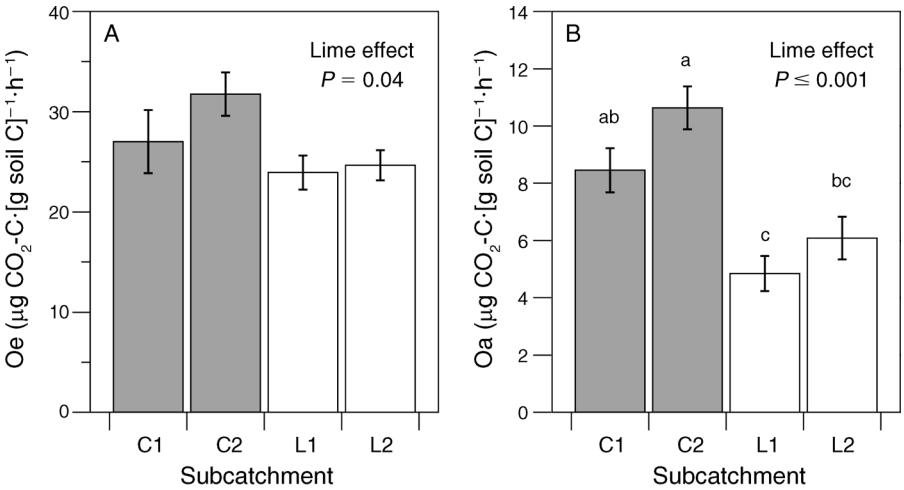

FIG. 3. Soil basal respiration for (A) Oe and (B) Oa forest floor horizons. Values represent plot means ± SE within each control (C1 and C2) and limed (L1 and L2) subcatchment for the two sampling dates. Different letters indicate significant differences among subcatchments ($P < 0.05$), and lime effect indicates the overall effect of liming.

The large reduction in heterotrophic soil basal respiration that we observed suggests that liming has altered the relationship between the microbial community and the OM it mineralizes. There are many ways in which liming could influence soil–microbe interactions, including changes in the microbial community, altered recalcitrance of the OM produced, or physical stabilization of OM. Others have shown increases in the activity of the bacterial community after liming (Baath and Arnebrant 1994, Andersson and Nilsson 2001), as well as reductions in fungal activity (Ivarson 1977), suggesting that a shift in the microbial community may have occurred. A new community may be unable to utilize the C substrate as effectively due to a change in microbial population size, enzyme activity, or efficiency. It is also possible that increased pH has influenced the available of other potentially limiting nutrients such as phosphorus (P), thereby altering microbial activity and community composition (DeForest and Scott 2010). Addition of Ca has been shown to increase resin-sorbed P and plant P uptake (Fiorentino et al. 2003), but others have found Ca to have little effect on metrics of P availability (Groffman and Fisk 2011*b*). At our site, the increased pH may have affected P availability and contributed to our observed changes in C and N cycling, but additional measurements would be needed to explore this potential interaction.

Alternatively, decomposition rates could decrease if plants respond to liming by producing more recalcitrant litter. Plant physiological research has shown that higher Ca availability can increase the lignin concentration in cell walls of tree seedling shoots (Eklund and Eliasson 1990). We hypothesized that increased Ca availability could enhance lignin production, leading to more recalcitrant litter inputs in limed plots. Our findings indicated the opposite, however, that leaf litter lignin concentration was larger in controls than in limed plots, and that the lignin : N ratio in litter did not differ by liming treatment, suggesting that a shift in litter lignin concentrations is not a primary driver of reduced decomposition rate. It is possible that liming may have increased quantities of other recalcitrant compounds that we did not measure in this study.

Another potential explanation for the observed increase in Oa mass is that the OM has become physically stabilized via Ca–OM bridging. This mechanism is well studied in laboratory experiments using pure minerals and agricultural soils (Oades 1988, Muneer and Oades 1989, Mikutta et al. 2007) and has been suggested as a factor influencing soil C and N accumulation in forest soils with neutral pH (5–8; Paul et al. 2003, Morris et al. 2007) and in tundra ecosystems (Hobbie et al. 2002). In acidic forest soils, Al is typically the dominant binding element (Oades 1988), and therefore, little research has been done to explore Ca–OM bridging. In managed forests that are limed, however, this may be a plausible mechanism to enhance soil C and N stocks. Calcium concentration can have a greater influence over Ca–OM binding at pH as low as 4 (Temminghoff et al. 1998), and some studies indicate that Ca–OM complexation can occur in the forest floor (Kalbitz et al. 2000). While greater research would be needed to confirm this mechanism, we suggest that the increased pH and exchangeable Ca concentration in the forest floor of limed plots provides an environment in which transient Ca–OM complexation could occur, thereby reducing microbial access to OM and reducing decomposition.

Forest floor net N mineralization rates (per kg) were smaller in limed forest floor, while net nitrification was significantly higher in the Oe horizon of limed plots. Reduced net N mineralization was observed at Woods Lake in the two years immediately following the lime addition (Simmons et al. 1996), and at other study sites (De Boer et al. 1993, Groffman et al. 2006). In our

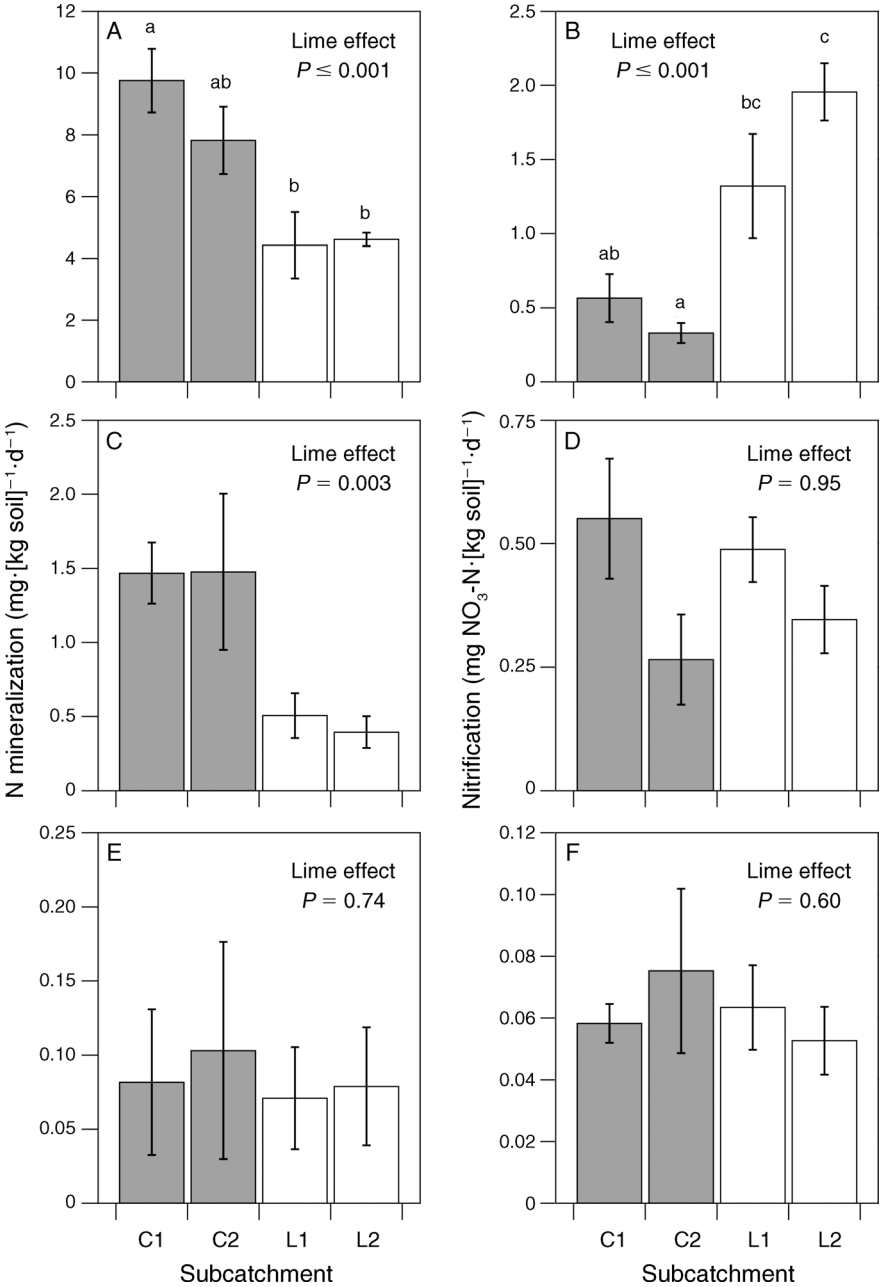

FIG. 4. (A, C, E) Net N mineralization for (A) Oe, (C) Oa, and (E) 0–10 cm mineral soil, and (B, D, F) nitrification for the same depths displayed as mean ± SE for each control (C1 and C2) and limed (L1 and L2) subcatchment. Different letters indicated significant differences among studied subcatchments ($P < 0.05$), and lime effect indicates the overall effect of liming.

study, it seems likely that a reduction in gross N mineralization is occurring, concurrent to the reduction in soil basal respiration. The greater net nitrification observed in limed soils has commonly been observed and attributed to a stimulation of nitrifiers caused by increased soil pH (Dancer et al. 1973, De Boer et al. 1993, Andersson and Valeur 1994, De Boer and Kowalchuk 2001, Groffman et al. 2006). This finding demonstrates that the microbial community in limed soils is producing greater quantities of NO_3^-, while utilizing a smaller pool of available NH_4^+.

Forest floor C stocks

The forest floor C stock in limed plots was 54% (37 Mg/ha) larger than in controls. Our empirically parameterized model of forest floor C dynamics matched measured Oe stocks, but predicted smaller Oa stocks than we observed in our study plots. Thus, the observed

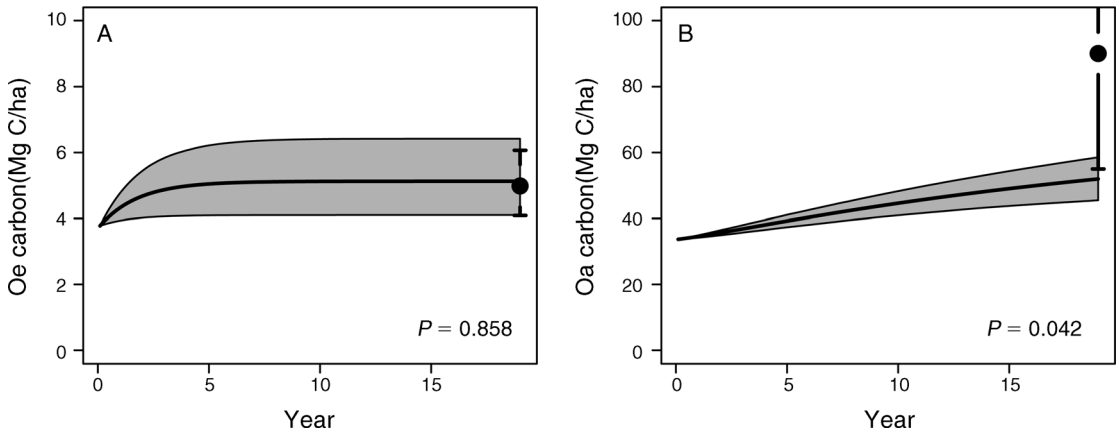

FIG. 5. Predicted dynamics of (A) Oe and (B) Oa forest floor C stocks over 19 years following liming at year 0. Predictions are from Eqs. 1–2 (black line is the mean, and the gray shaded area indicates the 95% confidence region). The dynamics begin from a non-limed equilibrium state estimated from values reported in this study and in Fahey et al. (2005*b*). The predictions at year 19 are compared to observed stocks 19 years post-liming (black circles and error bars), which were estimated by combining information in Fahey et al. (2005*b*) with the ratios of limed : control C stocks observed in this study. *P* values are for the null hypothesis that the predicted and observed stocks at year 19 are equal. See the Appendix for details.

differences between limed and control plots in forest floor fluxes (primarily in soil basal respiration) suggest our model can only partially explain the observed differences in C stocks. These results, however, may not be representative of the entire watershed. Our watershed-wide assessment of forest floor depth showed greater forest floor mass in limed soils relative to controls, but the mean limed forest floor depth was 5 cm lower than that observed within our study plots, indicating our plot values may be an overestimate of the watershed scale soil C stocks. It is also possible that C fluxes were very different during the 19-year period that we do not have measurements for. Our dynamic model assumed constant liming effects on C fluxes throughout the 19-year post-liming period, which may be an inaccurate representation of C dynamics during this time period. If there was an initial stimulation of aboveground and/or root C inputs and/or a more pronounced reduction of soil basal respiration immediately following liming, our model would generate an underestimate of C stocks. Pre-existing site heterogeneity and plot selection could have also influenced observed patterns in forest floor. Unfortunately, we were unable to obtain pretreatment data on forest floor mass or nutrient stocks, so we cannot confirm whether this was the case. However, no prior published studies from Woods Lake report large intra-site soil heterogeneity.

Forest floor N stocks

The additional 1.5 Mg N/ha observed in limed forest floor is also difficult to reconcile. This increase in N must stem from either enhanced inputs to or reduced losses from limed soils. Total foliar N inputs did not differ between treatment and controls. Slightly higher fine-root biomass observed in limed soils also seems unlikely to account for the observed difference. It is possible that the trees may have acquired N from deeper mineral soils, and then deposited it as litter in the forest floor. If this were occurring, however, we would expect this to be evident in increased N concentrations in foliar litter, which we did not observe. It may also be possible that liming increased N fixation in the forest floor, but this process is not typically observed in temperate forests (Davidson 2008) and seems an unlikely cause of the large N stocks at our study site.

Greater losses of N from control subcatchments could contribute to the pattern we observed. Net N mineralization was significantly higher in the control soils relative to limed, which suggests the microbial community may have utilized a larger fraction of the available N, thereby reducing N stocks. However, removal of this N from the ecosystem would occur most readily through NO_3^- leaching, and we observed smaller NO_3^- pools in control plots. If more N was leaching deeper into the soils in controls, we might have expected to see higher N concentrations in the mineral soils. This pattern was evident in the C2 control, but not in the C1 subcatchment (Table 5). Alternatively, it is possible that the trees in limed soils took up less N from the forest floor. We did not see a relative difference in tree growth or in the N concentrations in foliar litter, however, which might be expected with a change in N acquisition. Additional analysis of fresh foliage and wood N concentration could help to determine whether the trees are acting as an enhanced N sink.

Although our plot C and N stock data for limed soils may overestimate watershed values, the pattern of enhanced C and N accumulation with liming is well supported by our data. Both limed subcatchments show similar relative increases in C and N accumulation relative to both control subcatchments. Watershed-scale forest floor depth sampling also showed a pattern of deeper forest floor in limed subcatchments relative to controls. Finally, our soil basal respiration measurements

show a strong suppression of CO_2 efflux, indicating that mineralization of available C has been reduced in limed soils, and our C balance estimates suggest that this can account for much of the observed enhanced C accumulation in limed forest floor.

Liming effects on mineral soil C and N cycling

We had hypothesized that increased exchangeable Ca availability would increase soil C and N stocks in mineral soils as a result of enhanced OM stabilization via cation bridging. While we saw significantly larger exchangeable Ca availability within mineral soils, the difference between limed and control Ca pools was small, suggesting that if increased Ca–OM bridging is occurring, it is not great enough to influence stock measurements.

Tree response to lime addition

We had expected to see a positive tree growth response and increased litter inputs following liming. Instead, we observed a net decline in biomass across the watershed that was unrelated to treatment and no significant differences in litter production. American beech was a dominant species in our study plots and showed the largest biomass loss, which was likely caused by beech bark disease in the Adirondack region, where 55% of beech trees in second-growth forests are infected, and nearly 10% of standing beech stems are dead (Latty et al. 2003). Previous research has also shown that beech does not respond to Ca addition (Long et al. 1997). The lack of response in litter production may be driven by forest age. This is a closed-canopy, mature forest, and therefore, leaf area has likely reached a maximum capacity, such that an increase in production in response to liming would not benefit the tree (Ryan et al. 1997). There was a trend towards greater annual foliar-litter production in limed plots, but this difference was not significant. Since we lack data from the years immediately following the lime addition, it is possible that litter inputs were elevated after the lime addition and our measurements captured the late stages of this enhancement. Unfortunately, our lack of information during the 19 years post-liming limit our assessment of cumulative changes in litter inputs.

We also expected that the enhanced Ca and forest floor pH might stimulate fine-root growth or shift root allocation toward surface horizons. Although a larger stock of fine-root biomass was observed in the limed Oe, this pattern was driven by much higher values in the L1 subcatchment relative to all other subcatchments. Some studies have shown increased root production in Norway spruce (Hahn and Marschner 1998, Nowotny et al. 1998), but this does not appear to be occurring in our mixed northern hardwood forest.

Conclusions

Our results highlight the importance of the coupled interactions among C, N, and Ca cycles and suggest that liming can have large effects on ecosystem C and N balance. While these findings conform with some Ca addition studies, we also observed some dramatic differences. Most strikingly, the large difference in forest floor C and N stocks and the suppression of soil basal respiration differ from most published Ca addition research. Since most other studies have been conducted in conifer plantations, our observations generate many new questions about the controls on decomposition following lime addition in mixed northern hardwood forests. Additional research is needed to identify the primary drivers of altered decomposition rates in response to liming and should include study of microbial community dynamics, OM recalcitrance, and physical stabilization. The northeastern United States has experienced high acid deposition rates, declines in soil pH and exchangeable Ca availability, which may have long-term, detrimental effects on C sequestration and storage and ecosystem N retention. Refining our understanding of the mechanisms driving changes in soil OM dynamics and the specific role of Ca is essential to understanding C and N fluxes in acid-impacted forest ecosystems.

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Supplemental Material

Appendix

Modeling the dynamics of the Oe and Oa soil carbon stocks (*Ecological Archives* A023-096-A1).