

The Effects of Land-use History on Soil Properties and Nutrient Dynamics in Northern Hardwood Forests of the Adirondack Mountains

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ABSTRACT

Soil nutrient pools and nitrogen dynamics in old-growth forests were compared with selectively logged stands and stands that were selectively logged and then burned approximately 100 years ago to test the hypothesis that land-use history exerts persistent controls on nutrient capital and nitrogen (N) transformation rates. We provide estimates of net N mineralization and nitrification rates for old-growth forests from the northeastern United States, a region in which few old-growth forests remain and for which few published accounts of mineralization rates exist. At the plot level, no effects of the dominant tree species were observed on any measured soil properties or N-cycling rates. Effects of alternate disturbance histories were detected in soil carbon (C) and N pools. Old-growth forest soils had higher total C ($67 \text{ Mg}\cdot\text{ha}^{-1}$) and N capital ($3.3 \text{ Mg}\cdot\text{ha}^{-1}$) than that of historically logged then burned soils ($\text{C} = 50 \text{ Mg}\cdot\text{ha}^{-1}$ and $\text{N} = 54$

$\text{Mg}\cdot\text{ha}^{-1}$ and $\text{N} = 2.7 \text{ Mg}\cdot\text{ha}^{-1}$) in the stands that were historically logged. Despite these differences in C and N content, corresponding differences in C–N ratio, net N mineralization rates, and net nitrification rates were not observed. The N concentration in the green foliage of American beech trees (*Fagus grandifolia*) was also highest from canopy trees growing in old-growth stands (3.0%), followed by logged stands (2.6%), and lowest in the logged/burned stands (2.2%). These data suggest that some legacies of light harvesting on ecosystem processes may be detected nearly 100 years following the disturbance event. These results are discussed in the context of how multiple forest disturbances act in concert to affect forest dynamics.

Key words: Adirondack Park; disturbance; fire; logging; nitrogen cycling; old growth; temperate forest.

INTRODUCTION

Research regarding ecological disturbance has been a major focus of forest ecologists and ecosystem scientists for decades (Watt 1947; Odum 1969; Borrmann and Likens 1979; Pickett and White 1985; Foster and others 1997; Canham and others 2001).

These studies have produced a comprehensive understanding of how disturbance shapes the landscape and have led to innovative hypotheses regarding how alternate disturbance scenarios, particularly those generated by human activities, differ in their ecological consequences. For example, several researchers have recently argued that variation in rates of inorganic nitrogen (N) loss from forested catchments is determined, in part, by land-use histories that range from variable fire intensities to clear-cutting logging practices (Pardo

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and others 1995; Aber and Driscoll 1997; Goodale and others 2000; Lovett and others 2000). Understanding the time span required for disturbed forests to become structurally, compositionally, and biogeochemically equivalent to old-growth forests is increasingly valuable as second-growth forests, particularly in the northeastern and southern United States, mature.

The nature of the disturbance event responsible for resetting the successional trajectory is likely to influence the length of the recovery period and the severity of the impairment to a given ecosystem function. Models simulating forest response to the effects of high-intensity land uses on N and carbon (C) cycling demonstrate enduring legacies of such disturbances on the storage and release of these elements (Harmon and others 1990; Aber and others 1997). One model describing changes in C storage following clear-cut logging in the Pacific Northwest (Harmon and others 1990) indicated that at least 200 years were required to restore C to pre-harvest levels. These results suggest that understanding historical land-use has broad implications for understanding the global C and N cycles. As N is thought to limit the productivity of many ecosystems (Vitousek and Howarth 1991), comparisons involving the N cycle of primary and secondary forests are of considerable ecological interest. Through such comparisons, catastrophic disturbances such as heavy forest cutting have been demonstrated to influence forest nutrient cycling (Goodale and Aber 2001; Fisk and others 2002). However, forested stands originating from less intensive disturbances also exist on the landscape, and comparisons of these stands with nearby old-growth forests add to our growing understanding of disturbance legacies on ecosystem processes.

Old-growth forests are characterized by late-successional species and are generally assumed to lack a history of direct anthropogenic disturbance (for example, logging, agriculture, or settlement). However, modern old-growth forests are not pristine examples of ancient forests, but have been subject to a variety of indirect, human-induced disturbances including exotic species introductions and elevated deposition of atmospheric N. As such, present-day old-growth forests are not necessarily representative of pre-Euro-American settlement forests in terms of their C and N capital. Despite these caveats, useful conclusions can be drawn from comparisons made between old-growth and human-altered stands regarding the relative influence of logging or fire on nutrient pools when the forests being compared are chosen from areas receiving comparable amounts of atmospheric N dep-

osition delivered over the same time period. Notwithstanding the importance of ecological studies in old-growth forests to both basic science and management (Foster and others 1996), there are few reports of soil element pools and N transformation rates in old-growth forests of the northeastern United States [see Goodale and Aber (2001)], compared to other regions (Sollins and others 1980; Mladenoff 1987; Hart and Firestone 1991; Perez and others 1998; Fisk and others 2002).

The relative paucity of nutrient pool descriptions from old-growth forests in the northeastern United States is principally due to the lack of extensive old-growth forests in the region. Most forests are currently recovering from a suite of human disturbances, including clearing for agriculture, logging, and fire (Foster 1995; Niering 1998). Landscapes in this region have shifted from a predominantly forested state in the precolonial period to an agricultural setting in the mid-19th century and are presently regenerating as forest in many areas. In some locales, forest cover has increased by as much as 50%–80% in the last 100 years (Smith and others 1993; Askins 1998). The legacies of previous farming activities generally include changes in the physical properties of the soil as well as effects on nutrient cycling and vegetation patterns in these *new* forests [Compton and others (1998) and Fuller and others (1998), but see Kalisz (1986)]. Similarly, lasting effects of past fire and selective logging on ecosystem processes are likely to exist as well. Structural differences between these latter types of stands and old growth have been demonstrated (Hardt and Swank 1997; McGee and others 1999; Ziegler 2000). For example, historic fire and partial harvesting result in low coarse woody debris volume compared to old-growth stands (McGee and others 1999; Ziegler 2000). However, variation in nutrient pools between these three forest types has not been well quantified. The Adirondack region of northern New York offers the opportunity to measure such variation as it contains both old-growth forests and forests recovering from disturbances of variable intensities.

At the landscape scale, fire was probably not uniformly important prior to European settlement in northeastern forests (Clark 1997). However, local importance of fires set by Native American peoples in some areas (Day 1953; Russell 1983; Niering 1998) has been recognized. Post-European settlement increases in fire frequency, attributed to logging, railroads, and other industrial activities, were followed by a decline in fire frequency as a result of fire-control measures (Abrams and others 1995). In the Adirondack landscape, thousands of hectares

burned in the early 20th century, notably in 1903 and 1908 following logging and drought (Hicks 1947; Pilcher 1987). Fires create significant pathways for nutrient loss through ash convection and volatilization, as well as by promoting increases in N mineralization and nitrification; the magnitude of nutrient loss depends on fire intensity (Neary and others 1999). In the northeastern United States, logging was often accompanied by fire, a situation likely to result in even greater nutrient depletion than would fire alone.

Much of New England and New York had been subjected to logging by the middle to late 1800s (Graham 1985; Niering 1998). Nutrient removal, mainly through biomass export and hydrologic losses, is associated with most logging practices (Bormann and Likens 1979; Sollins and McCorison 1981; Tritton and others 1987; Mann and others 1988), and calcium and N are particularly susceptible to logging-induced losses (Bormann and Likens 1979; Tritton and others 1987). Other effects of logging have been observed in soil organic matter content, but the direction and magnitude of the changes are debated. Comparisons of chronosequences of stands of different ages have suggested that logging also results in decreased forest-floor organic matter (Covington 1981; Federer 1984), whereas other studies have demonstrated the opposite pattern (Brais and Camire 1995). Such disparate results may be related to high spatial variability of organic C, in addition to the fact that logging practices have changed over time, thereby confounding the results of chronosequence studies (Yanai and others 2000). Although these studies commonly consider heavily disturbed stands in their analyses, light harvesting may also be expected to influence nutrient stocks as the largest trees, containing the highest concentrations of nutrients (Martinelli and others 2000; Latty and others 2003), are preferentially removed from the stand.

The objective of this study was to characterize the N dynamics and soil properties of forests with different disturbance histories. We were interested in whether modest logging that occurred nearly a century ago has long-lasting implications on N and C pools in soils. The disturbed forests had two distinctly different histories: one set had been selectively logged about 100 years ago, and the second set was burned in 1903 following selective logging. Specifically, we examined physical characteristics, element contents and concentrations, N transformation rates, and concentrations of foliar N between old-growth and second-growth forests. Overall, we expected the stands subjected to both logging and burning to have the most depleted

nutrient pools compared to old-growth stands, with stands that were only logged being intermediate. As a result of the depleted nutrient pools in the most severely disturbed stands, we also anticipated that trees growing in the logged and burned stands would exhibit the most conservative nutrient use.

METHODS

Study Area

Fieldwork was conducted in and around the Five Ponds Wilderness Area (FPWA, 44°05'N, 74°15'W) in the western portion of the Adirondack Park, New York. The region is characterized by rugged topography, numerous lakes and ponds, and northern hardwood forests. The dominant tree species were American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), red spruce (*Picea rubens* Sarg.), and eastern hemlock (*Tsuga canadensis* L.). The understory was composed mainly of American beech saplings and the shrub *Viburnum alnifolium* Marsh. All stands were underlain by well-drained, loamy spodosols derived from glacial till [Beckett-Peru association (humic and typic haplorthods) and the Potsdam-Crary association (typic and aquic fragiorthods)] (Canham 1988).

The old-growth forests were located within the FPWA, north of the Stillwater Reservoir. This region was spared cutting when access to the forest was blocked by dam construction in 1886 (Roman 1980). At 20,000 ha, the region is one of the largest old-growth landscapes in the Northeast (Leopold and others 1988). The selectively logged stands were located roughly 10 km to the southwest of the FPWA southern boundary. Clear-cutting rarely occurred in Adirondack forests, and the second-growth forests used in this study were selectively harvested for pulpwood (for example, conifers) between 1890 and 1910 (McMartin 1994). Our data from the old-growth stands indicate that hemlock and red spruce made up approximately 11% of the stand basal area. If we assume that the current species composition of the old-growth stands is a reasonable approximation of the historically logged stands prior to harvest, then only about 10% of the basal area was removed during a logging event. Logging was likely to have been conducted primarily with horses, because bulldozers and skidders were not readily available until after 1928 (Graham 1985). The logged and then burned stands were situated approximately 10 km to the southeast of the FPWA eastern boundary. These stands burned in 1903 (Schmitt 1916; McMartin 1994), and their

location adjacent to now-defunct railroad tracks provides a probable source of ignition. Moreover, the high abundance of sugar maple in these stands may be indicative of historical fire (Ziegler 2000). These stands were also likely to have been logged previous to burning, as the majority of forests in that area had been cut by that year (McMartin 1994). Further evidence corroborating this last point is that when old-growth forests burned in 1903 they received disproportionate attention at the time and their loss was reported in several sources (McMartin 1994). The lack of such reports for our stands suggests that they had been logged at the time of burning. In most cases, fires from this time were reported as stand-replacing fires (Suter 1904); however, we have no data to confirm this last point. We sought to minimize differences in climate and edaphic conditions by locating old-growth, logged, and logged, then burned, stands on upland sites with similar physiography in close proximity to one another (all stands were within 15 km of each other).

Field-Sampling Techniques

In each forest type (old growth, logged, or logged/burned), we sampled four stands at least 1 km apart. At each stand, field sampling was done in a randomly placed 0.2-ha circular plot (50-m diameter). In each plot, the species identification and diameter of every tree larger than 10 cm DBH (diameter at breast height, 1.4 m) were recorded. Within each plot, four 10-m transects were established in each of the cardinal directions. To measure soil properties and quantify N transformation rates, soil samples were taken at 5 and 10 m from the plot center, along each transect ($n = 8$). Exact sampling points depended upon a minimal soil depth of 15 cm. These measurements focused on the upper 15 cm of the soil because much nutrient uptake occurs within this zone where the fine roots are concentrated (Zimmerman and Brown 1974).

Net N transformation rates were measured using in situ modified buried-bag incubations [Eno (1960), as modified by Finzi and others (1998)]. Monthly incubations were conducted for May, June, July, August, and September of 1998. A 7-month incubation was performed from October through April. Soil cores were taken with polycarbonate tubes, 15 cm long with a 5-cm diameter. Prior to sampling, the tubes had been cut in half vertically and then taped together to form a whole. The whole tubes were inserted into metal sleeves on soil bulk-density samplers. Leaf litter was removed from the sampling area prior to inserting the tubes. After a soil core was taken, it was removed

from the metal sleeve and cut in half vertically. Half of the core was covered with a gas-permeable polyethylene bag and returned to the original hole, covered with leaf litter, incubated for 4 weeks, removed, and then treated as described below for the second half. The other half was divided into forest floor and mineral soil sections; the depth of each layer was recorded. For each plot, the eight half-cores were bulked by soil horizon and kept cool until processed for extraction (within 10 h).

The bulked samples were homogenized by sieving with an 8-mm sieve to remove coarse rocks and roots, and 10-g subsamples of field-moist soil were extracted for nitrate (NO_3^-) and ammonium (NH_4^+) with 100 mL of 2.0 M potassium chloride (KCl). Extractions were shaken and allowed to settle overnight.

Fresh foliage samples were collected in late July, the peak of the growing season (Kudish 1992), from a random sample of four beech trees (more than 20 cm DBH) in each plot. Beech trees were chosen for foliage sampling because they were a dominant canopy tree in all plots and they have demonstrated sensitivity to soil N levels (Nadelhoffer and others 1995). As nutrient levels are known to differ among sun and shade leaves (McVickar 1949), care was taken to sample full-sun leaves only. Twelve sun leaves were collected per tree by a professional arborist, using tree-climbing equipment and a pole pruner. Of the 12 leaves, six were collected from 1–2 branches from each of the north-facing and south-facing aspects of the tree canopy. During September and October, freshly fallen litter was collected from eight litter traps, 26×39 cm, per plot at weekly intervals to minimize leaching losses. All leaves were returned to the laboratory for N analyses.

Laboratory Analyses

Soil/KCl extractions used to determine N transformation rates and inorganic soil N pools were analyzed within 24 h for ammonium and nitrate on an Alpken Enviroflow Analyzer, (Alpken, Wilsonville, Oregon, USA) model 3590. Ammonium concentrations were determined by the phenate method, and nitrate concentrations were measured by using cadmium diazotization. Net N mineralization rates were calculated by subtracting concentrations of inorganic nitrogen (NH_4^+ and NO_3^-) in the initial samples from the incubated samples. Net nitrification was calculated as the net change in nitrate concentrations between the incubated and initial samples. Mineralization rates per gram of soil organic matter (SOM) were calculated based on the

average percentage of SOM determined by loss on ignition.

A subsample of the midsummer initial samples were ground in a Kleco Tissue Pulverizer, (Kleco, Visolio, California, USA) model 4200. Total C and N of these samples were determined by chromatographic analyses following combustion on a Carlo Erba NA 1500 Analyzer (CE Elantech, Milan, Italy). Separate 50-g subsamples of the midsummer initial soil samples were submitted to the Cornell Nutrient Analyses Laboratory for analysis of extractable potassium (K), magnesium (Mg), calcium (Ca), iron (Fe), aluminium (Al), zinc (Zn), copper (Cu), manganese (Mn), and sulfur (S). These elements were extracted with Morgan's solution, a sodium acetate-acetic acid solution (pH = 4.8), and their concentrations were measured using an inductively coupled plasma spectrophotometer. Phosphorus (P) was determined colorimetrically by stannous chloride reduction on an autoanalyzer-type system. Using a standard pH meter and electrodes, soil pH was measured 1 h after mixing 1 part water with 1 part soil at room temperature. To estimate the cation-exchange capacity (CEC), the acidic compounds in the soil were neutralized using a highly buffered solution of barium chloride and triethanolamine. A portion of the equilibrium solution was titrated with 0.03 N hydrochloric acid, and the exchange acidity (EA), in meq/100 g, was determined. The estimated CEC was computed as the sum of the basic and acid cation groups (Reid 1997).

Leaf areas of green and senesced leaves were recorded using a Li-Cor Leaf Area Meter (Li-Cor, Lincoln, Nebraska, USA). Leaves were dried for 48 h at 70°C, weighed, and pulverized. Total C and N concentrations were determined through combustion on a Carlo Erba NA 1500 Analyzer. A subsample of leaves from single trees demonstrated analytical error to be within 3% independent of whether the leaves had been sampled from the north face or south face of the canopy. Subsequently, leaves were pooled by tree for C and N analyses.

Statistical Analyses

Differences in community composition and structure by forest history were analyzed by one-way multivariate analysis of variance (MANOVA), using forest history as the independent variable, and species relative basal area (American beech, black cherry, eastern hemlock, red maple, red spruce, striped maple, sugar maple, and yellow birch), total basal area, and stem density as dependent variables. Nitrogen transformation rates, physical characteristics of the soil, and element pools were analyzed

using a multivariate general linear models design [PROC GLM in SAS (1989)]. The independent variable was forest history (old growth, logged, logged/burned) or dominant tree species (maple, birch, beech), and the dependent variables included the soil mass, bulk density, % SOM, pH, CEC, net N mineralization, net nitrification, percent nitrification, C-N ratio, total N ($\text{g}\cdot\text{kg}^{-1}$), total C ($\text{g}\cdot\text{kg}^{-1}$) and extractable pools ($\text{g}\cdot\text{m}^{-2}$) of the following elements: P, base cations (Ca, K, and Mg), Fe, Al, NH_4^+ , and NO_3^- . Because birch was only dominant in two of the three forest histories, a factorial design of forest history and dominant tree species was not conducted. Assumptions of normality and homogeneity of variance were met. We used Tukey's studentized range test for post-hoc comparisons. Correlation procedures were used to investigate relationships between measured soil properties within and among soil horizons.

In estimating the percentage of N resorbed prior to leaf abscission, N was expressed per unit leaf area rather than per unit weight. This corrects for the fact that weight may change considerably during senescence due to differential resorption or the deposition of materials onto the leaf surface, whereas area is expected to remain relatively constant (Ostman and Weaver 1982; Fahey and Birk 1991). The percent resorption was calculated as (Fahey and Birk 1991)

$$\% \text{ resorbed} = \frac{(\text{green nutrient content} - \text{senesced nutrient content})}{\text{green nutrient content}} \times 100^*$$

Foliage data were analyzed using one-way analyses of variance (ANOVAs) with forest history (old growth, logged, and logged/burned) as the independent variable. Dependent variables included the N contents and concentrations of green and senesced leaves, and resorption efficiencies.

RESULTS

Species Effects on Soils

The old-growth, logged, and logged/burned forest stands were similar in overstory species composition. The tree species composition of the stands was mixed with no one species accounting for over half of the relative basal area in any forest type (Table 1). No significant differences in the total basal area or stem density of all species were detected between different forest types (GLM: $df = 2, 9$, $F = 1.85$ and $P = 0.21$, and $F = 1.26$ and $P = 0.33$, respectively). There were also no significant differences when the relative basal area was compared by canopy tree

Table 1. Relative Basal Area (%) of Canopy Tree Species by Forest History

Canopy Tree Species	Old Growth	Logged	Logged/Burned
<i>Acer pensylvanicum</i>	0.00 (0.0)	1.4 (0.90)	0.870 (0.47)
<i>Acer rubrum</i>	3.21 (1.8)	12.3 (8.8)	7.10 (4.9)
<i>Acer saccharum</i>	34.3 (8.0)	8.90 (5.2)	41.7 (11)
<i>Betula alleghaniensis</i>	8.60 (3.7)	25.1 (9.7)	22.6 (14)
<i>Fagus grandifolia</i>	41.1 (12)	49.9 (10)	17.2 (5.4)
<i>Picea rubens</i>	9.50 (5.2)	1.20 (0.90)	5.50 (0.70)
<i>Prunus serotina</i>	1.60 (1.6)	0.97 (0.95)	1.50 (0.90)
<i>Tsuga canadensis</i>	1.70 (1.1)	0.10 (0.05)	3.60 (2.1)
Total basal area ^a	34.4 (5.0)	34.6 (2.9)	30.1 (2.3)
Stem density ^b	613 (110)	523 (90)	455 (22)

Means are shown with standard errors in parentheses ($n = 4$).

^aTotal basal area values ($m^2 \cdot ha^{-1}$) are for all species.

^bTotal stem density values ($no. stems \cdot ha^{-1}$) are for all species.

species (Table 1, MANOVA: Wilks's lambda = 0.07, $F(14, 6) = 1.24$ and $P = 0.42$).

At the scale of individual plots, there were no species-specific effects on measured soil properties or N transformation rates in the three types of forests. When analyzed by dominant tree species at the plot scale (either sugar maple, beech, or birch, as determined by relative basal area), no significant differences were found for soil pH, total carbon ($g \cdot m^{-2}$), total nitrogen ($g \cdot m^{-2}$), C–N ratio, net N mineralization ($kg \cdot ha^{-1} \cdot y^{-1}$) or net nitrification ($kg \cdot ha^{-1} \cdot y^{-1}$) (MANOVA: Wilks's lambda = 0.15, $F(12, 8) = 1.07$ and $P = 0.48$). Because this region is heavily impacted by beech bark disease (Latty and others 2003) and sugar maple has been suggested as a possible replacement for dying beech (Twery and Patterson 1984), we also examined net mineralization and nitrification rates as a function of the ratio of sugar maple to beech basal area in these stands. However, this relationship was nonsignificant for both N cycling rates (Figure 1; for N mineralization, $P = 0.62$; and for nitrification, $P = 0.39$).

Forest-history Effects on Soil Properties and Element Pools

Although soil properties did not differ by dominant species, they did differ significantly by stand history (Table 2). Bulk density, the percentage of SOM, and CEC differed significantly by forest history as determined by GLM (Table 2). Bulk density in the top 15 cm of the soil profile was highest in burned sites and lowest in logged sites, whereas the opposite was true for the percentage of SOM and CEC. There were no significant differences in soil pH between the different forests (GLM: $df = 2, 9, F = 2.84$ and $P > 0.11$), and on average it was low, 3.8 and 4.0 in

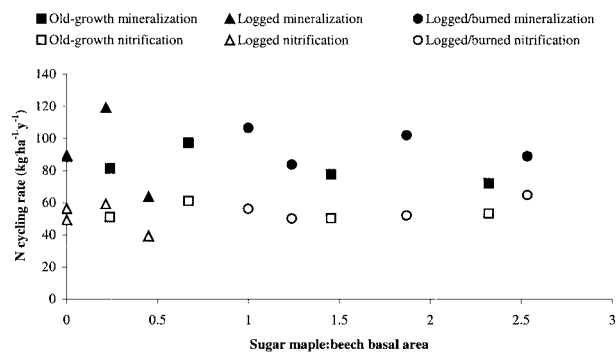


Figure 1. Annual net N mineralization rate (*solid symbols*) and nitrification (*open symbols*) as a function of the ratio of sugar maple to beech basal area for forest with different land-use histories. The mineralization relationship is described by $y = -2.8x + 92$ ($r^2 = 0.03$) and the nitrification relationship by $y = 2.0x + 52$ ($r^2 = 0.08$).

the forest floor and mineral horizon, respectively. Old-growth sites were intermediate between the logged and logged/burned sites for all significantly different soil properties.

The largest C and N pools were measured in the old-growth forests and in those that were logged only (Figure 2). These forests had larger total soil C and N concentrations at both soil depths compared to the logged/burned forests (data not shown). The magnitude of these differences is offset by the strong differences in soil bulk density, but a similar pattern in total C and N content emerged (Figures 2a and b). The forest floor C–N ratios (gram per gram) were lowest in the old-growth soils and highest in the logged/burned stands (Figure 2c, GLM: $df = 9, 11, F = 5.73$ and $P = 0.03$) with no significant differences observed in the mineral horizons. Over-

Table 2. Comparisons of Select Properties of Forest Soils with Different Histories

Soil Property	Old Growth	Logged	Logged/Burned
Bulk density ($\text{g}\cdot\text{cm}^{-3}$)***	0.502 (0.035) ^b	0.370 (0.019) ^c	0.633 (0.024) ^a
Forest floor*	0.103 (0.0050) ^{a,b}	0.0846 (0.0049) ^b	0.110 (0.0085) ^a
Mineral soil***	0.398 (0.032) ^b	0.286 (0.020) ^c	0.523 (0.023) ^a
pH			
Forest floor	3.90 (0.085)	3.78 (0.06)	3.65 (0.075)
Mineral soil	4.19 (0.090)	3.77 (0.22)	3.90 (0.075)
CEC ($\text{meq}\cdot\text{kg}^{-1}$)*	174 (18) ^{a,b}	195 (9.0) ^a	133 (9.5) ^b
Forest floor*	127 (15) ^{a,b}	140 (4.2) ^a	100 (9.5) ^b
Mineral soil*	47.6 (4.1) ^{a,b}	55.3 (7.2) ^a	32.9 (4.6) ^b
Soil organic matter (%)			
Forest floor**	58.7 (5.3) ^b	75.9 (2.2) ^a	54.8 (3.1) ^b
Mineral soil	7.71 (0.60)	9.44 (1.2)	6.32 (0.85)
¹ Base cations ($\text{Mg}\cdot\text{ha}^{-1}$)	20.2 (1.8)	20.5 (2.2)	17.7 (2.4)
Forest floor	17.7 (1.4)	16.8 (3.5)	15.3 (2.3)
Mineral soil	2.50 (0.43)	3.64 (0.85)	1.98 (0.15)
Mass NH_4 ($\text{g}\cdot\text{m}^{-2}$)	0.473 (0.012)	0.438 (0.023)	0.484 (0.011)
Forest floor	0.166 (0.010)	0.190 (0.018)	0.162 (0.010)
Mineral soil**	0.306 (0.014) ^a	0.248 (0.013) ^b	0.332 (0.009) ^a
Mass NO_3 ($\text{g}\cdot\text{m}^{-2}$)	0.217 (0.023)	0.186 (0.022)	0.215 (0.010)
Forest floor	0.068 (0.016)	0.069 (0.013)	0.055 (0.003)
Mineral soil*	0.149 (0.010) ^{a,b}	0.118 (0.010) ^b	0.160 (0.009) ^a
Mass Fe ($\text{g}\cdot\text{m}^{-2}$)*	4.81 (0.79) ^a	0.92 (0.25) ^b	4.18 (0.74) ^a
Forest floor	0.112 (0.025)	0.069 (0.015)	0.152 (0.054)
Mineral soil*	4.70 (0.75) ^a	0.85 (0.24) ^b	4.03 (0.76) ^a

Means are shown with standard errors in parentheses ($n = 4$). Forest-history effects are determined by one-way analysis of variance: * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Different lowercase letters indicate significant differences by Tukey's HSD at $P < 0.05$. CEC, cation-exchange capacity. Base cations are the sum of extractable K, Mg, and Ca.

all, the C–N ratios of the mineral horizons were consistently higher than those measured in the forest floors.

Aside from the differences in total C and N, inorganic N (NO_3^- and NH_4^+) and Fe pools were the only extractable elements to show significant differences by forest history (Table 2). The mineral horizons of old-growth and logged forests had the highest concentrations and contents of NH_4^+ and NO_3^- (concentration data not shown). None of the sampled forests demonstrated significant differences in base cation (Ca + Mg + K) concentrations (forest-floor average, $9.3 \text{ g}\cdot\text{m}^{-2}$; and mineral soil average, $8.9 \text{ g}\cdot\text{m}^{-2}$), Al (forest floor average, $0.89 \text{ g}\cdot\text{m}^{-2}$; and mineral soil average, $6.3 \text{ g}\cdot\text{m}^{-2}$), and P (forest floor average, $0.16 \text{ g}\cdot\text{m}^{-2}$; and mineral soil average, $0.059 \text{ g}\cdot\text{m}^{-2}$) contents or concentrations regardless of soil horizon.

Forest-history Effects on Nitrogen Transformation Rates

Across all plots, the estimated mean annual rates of total net N mineralization ranged from 64

$\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ to $119 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ with less variation in nitrification rates ($39\text{--}65 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$). On a mass basis, the average rate of net nitrification was positively correlated with the average rate of net N mineralization (linear regression: $n = 12$, $P = 0.001$ and $r^2 = 0.66$). Similar results were obtained when the rates were expressed per unit area (linear regression: $n = 12$, $P = 0.03$ and $r^2 = 0.39$). Within both the forest floor and mineral soil horizons, N mineralization was significantly correlated with net nitrification and the percentage of soil organic matter (Table 3). Forest-floor nitrification rates were also related to organic matter. Soil pH and C–N ratios were not significantly correlated with any N-cycling parameters. Both soil base cation content and the percentage of soil organic matter showed strong relationships between soil horizons.

Despite differences in total N pools between forests with different histories, the estimated net annual N mineralization and nitrification rates did not differ significantly by land-use history (Figure 3). When expressed per kilogram of soil, annual net mineralization rates and nitrification rates were

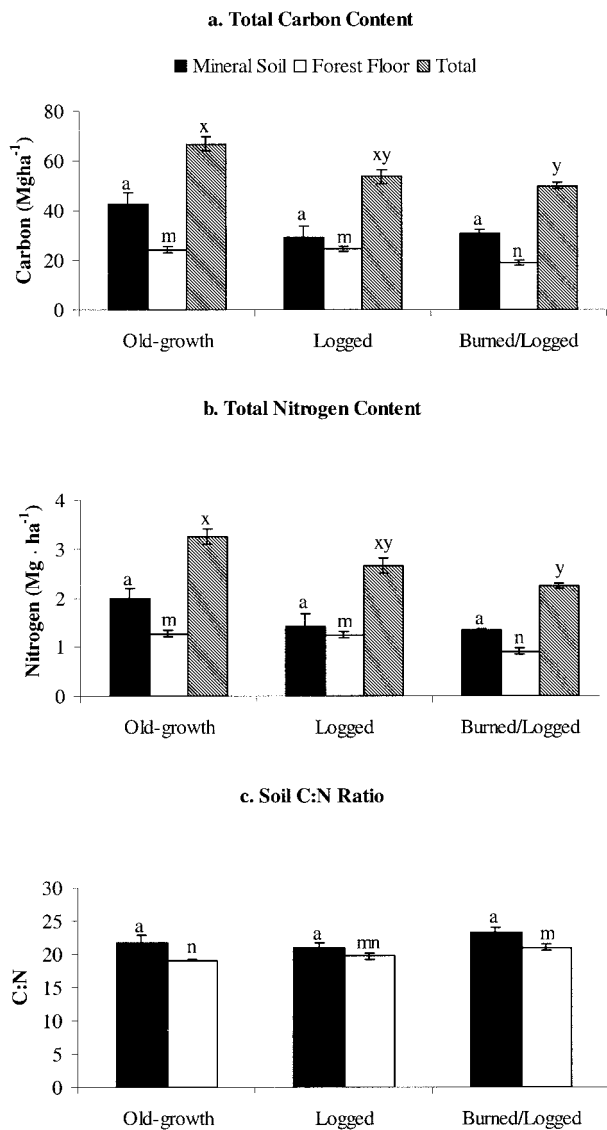


Figure 2. Average midsummer (a) total carbon (C) content ($\text{g}\cdot\text{m}^{-2}$), (b) total nitrogen (N) content ($\text{g}\cdot\text{m}^{-2}$), and (c) C:N ratio in the forest floor and upper 0–15 cm of the mineral fraction in old-growth, logged, and logged/burned soils. Bars are mean values (± 1 SE) of four stands per forest-history class. Lowercase letters indicate Tukey's honestly significantly different (HSD) test at $P < 0.05$ within either the mineral soil, forest floor, or combined data.

highest in the logged forest soils (N mineralization, $1.16 \text{ gN}\cdot\text{kg}^{-1}\cdot\text{y}^{-1}$, and nitrification, $0.390 \text{ gNO}_3\cdot\text{kg}^{-1}\cdot\text{y}^{-1}$ for the forest floor plus the mineral horizon) and generally lowest in the logged/burned soils (N mineralization, $0.847 \text{ gN}\cdot\text{kg}^{-1}\cdot\text{y}^{-1}$, and nitrification, $0.388 \text{ gNO}_3\cdot\text{kg}^{-1}\cdot\text{y}^{-1}$, for both soil horizons), but these differences were only mildly significant in the 0- to 15-cm portion of the mineral soil

(GLM: N mineralization, $df = 2, 9, F = 5.29$ and $P = 0.03$; and nitrification, $F = 6.10$ and $P = 0.02$). When adjusted for bulk-density differences, the lowest average mineralization rates were measured in the old-growth sites, but this result was nonsignificant for all soil horizons (Figure 3, GLM: forest floor, $df = 2, 9, F = 1.21$ and $P = 0.34$; and mineral soil, $F = 1.3$, and $P = 0.32$). The percentage of mineralization that was nitrified did not vary significantly among forest histories for either soil horizon (GLM: forest floor, $df = 2, 9, F = 0.75$ and $P = 0.50$; and mineral soil, $F = 0.90$ and $P = 0.44$), but the highest nitrification fractions were observed in the old-growth forest soils (Figure 3).

Forest-history Effects on Foliar Nitrogen

Mass-based mean canopy N concentrations of fresh beech foliage ranged from a low of 2.2% in the logged/burned stands to 2.6% in the logged stands, with the highest values recorded in the old-growth stands at 3.0%. These differences between forest histories were significant (GLM, $df = 2, 21, F = 89.98$ and $P < 0.0001$) and translated into significant differences in N content, as the relative mass per unit area of litter as a fraction of green foliage was statistically similar between trees from the different forest types (0.60 on average, one-way ANOVA, $df = 2, 21, F = 0.086$ and $P = 0.918$). Nitrogen content was generally highest in the green and senesced leaves of the old-growth trees and lowest in the trees from the disturbed forests (Figure 4). On average, the percentage of N resorption prior to leaf fall was highest in trees from the disturbed forests and lowest in trees growing in old-growth forests. Direct correlations between the N content of green foliage and soil N cycling variables, including soil C:N ratio ($P = 0.90$), net mineralization ($P = 0.84$), nitrification ($P = 0.67$), and the nitrification fraction ($P = 0.70$), were not significant.

DISCUSSION

Nitrogen Transformation Rates in Eastern Old-growth Forests

One goal of this study was to characterize soil processes in northeastern old-growth forests, an understudied type of ecosystem in this region. We were unable to find many published estimates of net N mineralization rates for comparable old-growth in the Northeast, although several reports exist for Midwest forests. Our estimated rates of net N mineralization in the old-growth stands, which averaged $82 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ (Figure 3), fell within the

Table 3. Correlation Matrix for Forest-floor (FF) and Mineral Soil (MS) Properties

Soil Property	Nmin		Nit		CN		pH		BC		OM FF
	FF	MS	FF	MS	FF	MS	FF	MS	FF	MS	
Nmin											
FF	1.0										
MS	-0.61*	1.0									
Nit											
FF	0.85***	-0.47	1.0								
MS	-0.37	0.91***	-0.18	1.0							
CN											
FF	-0.44	0.47	-0.12	0.31	1.0						
MS	-0.50	-0.12	-0.43	-0.40	0.45	1.0					
pH											
FF	0.12	-0.31	0.01	-0.19	-0.46	-0.33	1.0				
MS	-0.28	-0.05	-0.43	-0.11	-0.03	0.08	0.73**	1.0			
BC											
FF	-0.15	-0.04	0.03	-0.02	0.21	0.15	-0.45	-0.43	1.0		
MS	-0.33	0.51	-0.06	0.66*	0.24	-0.20	-0.28	-0.28	0.67*	1.0	
OM											
FF	0.61*	-0.37	0.72**	-0.13	-0.21	-0.46	0.33	-0.20	-0.17	-0.16	1.0
MS	0.75**	-0.57*	0.81**	-0.33	-0.37	-0.39	0.23	-0.29	-0.25	-0.36	0.88***

Data are Pearson correlation coefficients with significant relationships indicated in boldface: * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Variables include midsummer net nitrogen (N) mineralization (Nmin), net nitrification (Nit), soil carbon–N ratio (CN), soil pH, base cation content (BC), and the percentage of soil organic matter (OM).

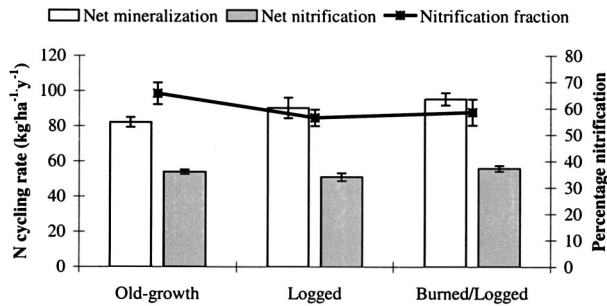


Figure 3. Comparison of annual net nitrogen (N) mineralization rates, nitrification rates, and nitrification fraction by forest history. Bars are mean values (± 1 SE) of N-cycling rates for four stands per forest-history class. Points are mean percent nitrification (± 1 SE).

range of rates published for old-growth forests from other regions. A recent study from old-growth northern hardwood forests in New Hampshire estimated mean mineralization rates at $113 \text{ kg N}\cdot\text{ha}\cdot\text{y}^{-1}$ (Goodale and Aber 2001), and lower values have been reported from old-growth hemlock–hardwood forests in the Upper Peninsula (UP) of Michigan: $68.0 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ (Ferrari 1999), and $93 \text{ kg}\cdot\text{ha}^{-1}$ from a 5-month study (Fisk and others 2002). Net nitrification rates in this study averaged $54 \text{ kg ha}^{-1}\cdot\text{y}^{-1}$ and were again similar to nitrification rates reported from other eastern forests, 63

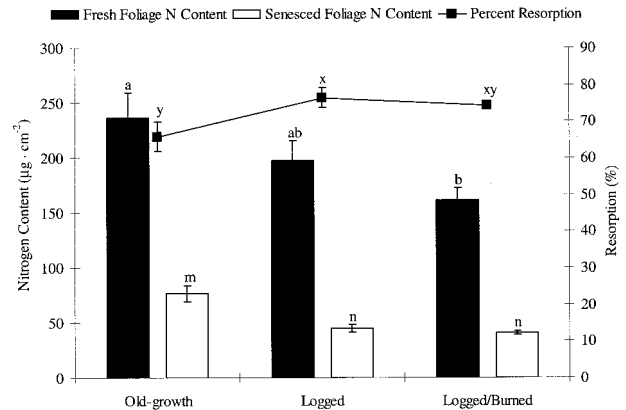


Figure 4. Nitrogen (N) content of green and senesced foliage from beech trees growing in old-growth, logged, and logged/burned stands. Bars are mean values (± 1 SE) of eight trees per forest-history class. Points are mean percent N resorption (± 1 SE) at leaf senescence. Lowercase letters indicate Tukey's honestly significantly different (HSD) test at $P < 0.05$.

$\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$ (Goodale and Aber 2001). On average, nitrification accounted for 64% of the mineralization rates (Figure 3), which was also bracketed by values obtained for old-growth forests in the Midwest, ranging from 31% (Mladenoff 1987) to 75% (Fisk and others 2002). These differences among studies are likely due to a combination of factors,

including variation in climate, atmospheric N inputs, experimental techniques, soils, topography, and tree species composition. For example, temperate old-growth forests of southern Chile receive extremely low atmospheric inputs of N, which is reflected in relatively low net N mineralization rates of 22–34 kg·ha⁻¹·y⁻¹ (Perez and others 1998). Furthermore, within those forests, higher net N mineralization rates have been associated with angiosperm-dominated forests in contrast with gymnosperm-dominated forests that inhabit gentle, north-facing slopes (Perez and others 1998).

Tree species composition has the potential to influence soil properties through many pathways, including species-specific effects on litter quality and mass (Finzi and others 1998; Ferrari 1999; Ollinger and others 2002). Although the role of canopy species in determining rates of nutrient transformation appears to be important in explaining large, regional differences, we did not detect significant effects of dominant tree species at the scale of 0.20-ha plots on any measured soil properties or nutrient transformation rates within our study. Reports of species-specific controls on soil parameters at a fine spatial scale are common in forests with distinct monospecific patches (Boettcher and Kalisz 1989; Reich and others 1997; Finzi and others 1998; Ferrari 1999). However, when averaged across larger, mixed-species plots, the species-specific effects became obfuscated and land-use history exerted stronger control over N dynamics than did canopy tree species composition.

Soil Pools and Processes and Disturbance Intensity

Within our study area, historical disturbances of low-intensity logging plus fire, but not of light logging alone, have resulted in long-term changes in the total soil C and N pools with few lasting legacies in regard to other element pools or N-cycling parameters. These findings are not surprising given the selective nature of the historical logging, which removed mainly a small amount of softwood timber. However, ensuing fire would be expected to result in further elemental deficits through additional biomass removal and nutrient volatilization. In this study, fire following logging did result in substantial losses of key elements like C and N that remain measurable nearly 100 years later (Figure 1), whereas differences were not detected in other nutrient pools.

There were no measurable effects of either logging or logging plus burning on the base cation content of the soils (Table 2). However, most of these elements volatilize at higher temperatures

than those required for C and N (Neary and others 1999), so low-intensity fires may result in reduced C and N pools while leaving other element pools unchanged. Other studies have demonstrated that substantial losses of these elements, particularly Ca, often accompany logging and ash convection by fire (Hornbeck and others 1986; Tritton and others 1987; Federer and others 1989; Neary and others 1999). On the other hand, logging-induced losses of base cations may still be small relative to those brought about by leaching of Ca and Mg resulting from acid rain (Likens and others 1996, 1998), a process that we assume to have exerted uniform effects on our stands due to their close proximity. In addition, not all clear-cut logging has been shown to result in reduced base cation pools (Johnson and others 1997). The similarities between these element pools from the three forest types provide further evidence that both the logging intensity and the severity of the fires in our study area were on the low end of the disturbance intensity spectrum.

Despite the low intensity of the logging event, differences between the logged-only sites and the other forest types were manifested in terms of the high percentages of SOM and cation-exchange capacity in the logged soils (Table 2). Clear-cut logging may result in elevated CEC, presumably by altering the charge properties of organic matter (Johnson and others 1997). However, it seems unlikely that century-old selective logging could account for the observed differences in organic matter and CEC in our stands, particularly when these soil parameters were similar between the old-growth and more heavily impacted logged/burned stands. It is more likely that these differences are explained by the high spatial variability of SOM. A number of studies have documented increases in forest-floor mass following logging (Hendrickson and others 1989; Johnson and others 1995; Goodale and Aber 2001), whereas others have reported losses (Covington 1981; Federer 1984; Yanai and others 1999). The high organic content of historically logged soils has been related to increased litter inputs resulting from the high net primary productivity of young stands relative to mature stands (Ryan and Waring 1992; Goodale and Aber 2001). However, in a study by Yanai and colleagues (2000), the oldest stands had twice as much organic mass in the forest floor as recently cut stands. These authors suggested that the amount of time elapsed since logging as well as the logging method (that is, skidders versus horses) can influence the organic mass of the forest floor, and this may in part explain confounding trends across studies. We tried to avoid confusing disturbance intensity with time, since disturbance

through our choice of study areas. We assume that both the logged and the logged/burned stands were harvested similarly, and prior to the advent of mechanized logging. As such, these stands are likely to have experienced less mixing of organic matter into the mineral soil than occurs using more modern techniques. However, the organic matter differences observed in this study are likely a result of stand level factors and not a result of forest-history effects.

The strong differences between the low total C pools of the logged/burned forest soils relative to both the old-growth stands and those that were only logged are likely a result of the intensity of the historical disturbance (Figure 2). In a similar comparison of old-growth, logged, and burned stands in the northern hardwood forests of New Hampshire, a distinctly opposite picture emerged where C pools were smallest in the old-growth stands and largest in the historically disturbed stands (Goodale and Aber 2001). However, in that study, heavily burned and/or logged stands were sampled in contrast to the relatively lightly disturbed stands of the present study. The different patterns observed from the two studies may also be related to site-specific factors like climate and species composition. Our C pool results did agree with a simulation model of northeastern mixed coniferous forests that predicted maximum C storage in the oldest stands followed by a 100-year-old logged forest and then by a 175-year-old burned stand (Aber and Driscoll 1997). These authors concluded that the degree and timing of major disturbances resulting in losses of SOM were critical in determining total C storage. Although our data do not allow us to examine the strength of the C sink in forests originating from different land uses, they do suggest that mature forests with histories of minimal human use have the potential to store greater quantities of C than do forests originating from more extensive human disturbance.

Nitrogen content and concentration were similar for the old-growth and logged second-growth stands (Figure 2), a result consistent with findings reported by Fisk and coworkers (2002), who also did not detect differences in soil N content in mid-western old- and second-growth forests and opposite that reported by Goodale and colleagues (2001). It is likely that the variable intensities of separate logging events play an important role in determining N pool reductions in these different regions. In our Adirondack sites, N content and concentration were higher in the old-growth and logged-only soils relative to the logged/burned soils. This result is not surprising, as forest fire has been

shown to exert long-lasting effects on N as well as C dynamics (Klopatek 1987; Aber and Driscoll 1997; Hornbeck and others 1997). The mechanisms responsible for such long-term effects of fire on C and N pools include changes to the physical characteristics of the soil, organic matter content, and microbial community structure. After fire, soil structure may be altered by changes in clay minerals and organic matter combustion (Neary and others 1999). Biotic changes may occur as well; for example, heterotrophic microbes are generally found to decrease, whereas autotrophic microbes tend to increase following moderate to severe fires (Neary and others 1999). Whether this shift in microbial communities occurred in the lightly to moderately burned stands in our study is not known.

Despite significant variation in total C and N content among the three disturbance histories, the C–N ratios and net N mineralization and nitrification rates were relatively similar (Figure 2 and 3). This contrasts with a study comparing a 300-year-old hardwood forest in Canada with a 100-year-old forest in the Adirondacks (Mitchell and others 1991). The older stands had a substantially narrower C–N ratio (16:1 as opposed to 34:1 for the 100-year-old stands) and higher ammonification and nitrification rates, as well as elevated levels of NO_3^- leaching. In keeping with the nutrient-retention hypotheses [sensu Vitousek and Reiners (1975)], Mitchell and colleagues (1991) attributed the differences to stand age and tree mortality, as the net N requirement in the old stands was significantly lower than that of the younger stands. However, our results are similar to those from other studies that have compared mineralization rates in old/second-growth systems (Goodale and Aber 2001; Fisk and others 2002) and, as a result, argued that the nutrient-retention hypothesis should be modified to provide a mechanism for ecosystem retention of nutrients beyond the point at which net ecosystem productivity no longer serves as the main sink for N (Fisk and others 2002). Fisk and coworkers (2002) suggest that in late-successional forests a heterotrophic N sink becomes an important N storage mechanism. This mechanism could be important in Adirondack old growth and help to explain the large quantities of total N in the soil.

Plant–Soil Interactions

Patterns in the soil N pools among forests with contrasting histories were broadly reflected in the chemistry of canopy beech foliage, with the highest N content measured in green and senesced foliage of old-growth trees (Figure 4). Considerable attention has been focused on the use of foliar chemistry

as a potential indicator of forest N saturation (Aber and others 1998; Ollinger and others 2002), where N inputs exceed biological demand resulting in elevated NO_3^- and acidity in surface waters and base cation losses from soils (Aber and others 1998). Our old-growth study sites in the western Adirondacks may be particularly at risk of N saturation for two reasons: (a) they are located in an area that receives regionally high N deposition (Ollinger and others 1993; Fenn and others 1998), and (b) due to age-induced changes in tree physiology old-growth stands have reduced biotic demand of N relative to its supply (Vitousek and Reiners 1975; Hedin and others 1995; Goodale and Aber 2001). If resorption is a mechanism by which plants conserve nutrients (Killingbeck 1996), then the low N resorption rates of old-growth beech trees relative to the historically disturbed sites suggest tighter conservation of nutrients in the disturbed stands and support the hypothesis that the old-growth stands are becoming less N limited. This alleviation of N limitation on plant processes is also likely to apply to herbivores, which are commonly N limited (Mattson 1980), and may help to explain the high severity of beech bark disease in these old-growth forests (Latty and others 2003). Beech bark disease is a tree disease initiated by an exotic scale insect, *Cryptococcus fagisuga*, which has substantial dietary N requirements (Wargo 1988; Houston 1994). The N-rich feeding substrate provided by old-growth trees with access to larger soil N pools may increase insect fitness, leading to the high proportion of diseased trees in old-growth forests relative to the historically disturbed forests (Latty and others 2003). The greater preponderance of disease in the old-growth stands is also illustrated by the relatively high number of stems in the old-growth stands when contrasted with the historically disturbed stands (Table 1), as dying beech are known to sprout prolifically (Houston 1994).

CONCLUSIONS

Knowledge of ecosystem processes in old-growth forests has become increasingly important as new research highlights the effects of land-use as one of the principal factors determining forest response to anthropogenically mediated environmental changes (Dale and others 2000). Northern hardwood forests of the eastern United States are subjected to a wide range of disturbance intensities, and the results presented here clarify the effects of low-intensity anthropogenic disturbances on these systems. Comparisons of selectively logged and logged/burned second-growth with old-growth for-

ests demonstrated that light logging plus burning resulted in more persistent effects on nutrient capital and N dynamics than did light logging acting alone, although some logging effects were still observed such as relatively high N resorption rates. Overall, total N capital was highest in the old-growth soils, but this did not translate into higher net mineralization rates, as these rates were similar to those measured in the historically disturbed soils. Larger C pools were also observed in old-growth soils versus the most severely disturbed forests, emphasizing that forest history must be taken into account when estimating the strengths of C sinks in forested ecosystems.

Ironically, it is perhaps the sensitivity of old-growth forests to elevated N deposition that will prove the greatest limitation in using these forests to determine baseline conditions from which to assess change in forest processes. However, if we consider high concentrations of N in foliage as a potential indicator of N saturation, then our data suggest that the old-growth forests in this region are approaching a situation where N is no longer limiting to either autotrophic or perhaps even heterotrophic production. In such forested areas, this could have implications for patterns of the spread of tree diseases, like beech bark disease, that are caused by N-limited herbivores. These types of interactions between introduced pests (in the case of beech bark disease) and abiotic disturbances, like elevated atmospheric N deposition and land use, have the potential to control successional trajectories, thereby altering landscape patterns and processes (Castello and others 1995). Changes in species composition as a result of these interacting disturbances could be expected to have further ramifications on forest function through soil-plant feedbacks resulting from changes in litter quality. We conclude that previous land use can influence current biogeochemical processes, which in turn have the potential to interact with novel disturbances, such as exotic species, to shape future forest dynamics and the study of these synergistic effects merits further investigation.

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