

THE LONG-TERM EFFECTS OF LAND-USE HISTORY ON NITROGEN CYCLING IN NORTHERN HARDWOOD FORESTS

CHRISTINE L. GOODALE¹ AND JOHN D. ABER

Complex Systems Research Center, University of New Hampshire, Durham, New Hampshire 03824 USA

Abstract. Nearly all northeastern U.S. forests have been disturbed by wind, logging, fire, or agriculture over the past several centuries. These disturbances may have long-term impacts on forest carbon and nitrogen cycling, affecting forests' vulnerability to N saturation and their future capacity to store C. We evaluated the long-term (80–110 yr) effects of logging and fire on aboveground biomass, foliar N (%), soil C and N pools, net N mineralization and nitrification, and NO_3^- leaching in northern hardwood forests in the White Mountain National Forest, New Hampshire. Historical land-use maps were used to identify five areas each containing previously logged, burned, and relatively undisturbed (old-growth) forests. Aboveground biomass averaged 192 Mg/ha on the historically disturbed sites and 261 Mg/ha on the old-growth sites, and species dominance shifted from early-successional and mid-successional species (*Betula papyrifera* and *Acer rubrum*) to late-successional species (*Fagus grandifolia* and particularly *A. saccharum*). Forest floors in the old-growth stands had less organic matter and lower C:N ratios than those in historically burned or logged sites. Estimated net N mineralization did not vary by land-use history ($113 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$); mean ($\pm 1 \text{ SE}$) nitrification rates at old-growth sites ($63 \pm 4.3 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) doubled those at burned ($34 \pm 4.4 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and logged ($29 \pm 4.7 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) sites. Across all plots, nitrification increased as forest floor C:N ratio decreased, and NO_3^- concentrations in streamwater increased with nitrification. These results indicate that forest N cycling is affected by century-old disturbances. The increased nitrification at the old-growth sites may have resulted from excess N accumulation relative to C accumulation in forest soils, due in part to low productivity of old-aged forests and chronic N deposition.

Key words: C:N ratio; disturbance; fire; land-use history; logging; New Hampshire; nitrification; nitrogen saturation; nitrogen mineralization; old growth; succession; White Mountains (New Hampshire, USA).

INTRODUCTION

Over the past several centuries, most northeastern U.S. forests have experienced human-induced disturbances such as forest harvests, fire, or agriculture (e.g., Cronon 1983, Foster 1992). Successional forests in the eastern United States currently act as a net carbon sink (Birdsey et al. 1993, Turner et al. 1995, Houghton et al. 1999), a sink possibly augmented by fertilization from atmospheric carbon dioxide or deposited nitrogen (Schimel 1995, Townsend et al. 1996). These aggrading forests also provide a substantial sink for atmospheric N deposition, and differences in successional status or disturbance history may partially explain the observed variety of forest responses to similar rates of N deposition (Aber and Driscoll 1997). Understanding the long-term impacts of historical disturbances on N cycling is important for predicting the potential amount of additional C and N that may be stored in forest biomass and soils.

Chronic N deposition may lead to N saturation, which is N availability in excess of plant and microbial demand, accompanied by elevated nitrification and NO_3^- losses (Aber et al. 1989, Stoddard 1994). Field measurements have demonstrated that N losses do not necessarily increase directly with N inputs (Van Mieghroet et al. 1992, Dise et al. 1998b, Gundersen et al. 1998b), and northern hardwood forests with similar N inputs can have vastly different N outputs (Pardo et al. 1995, Hornbeck et al. 1997, Lovett et al. 2000). These authors and others have inferred that land-use history may influence nitrate output.

While the short-term impacts of disturbances on forest nutrient cycling have been well studied (e.g., Likens et al. 1970, Raison 1979, Vitousek et al. 1979), long-term impacts are often overlooked. Modeling efforts suggest that disturbance can influence C and N cycling for hundreds of years (Aber and Driscoll 1997, Schimel et al. 1997), but few field studies have measured responses on this time scale, due in part to the difficulty of establishing disturbance histories over such long periods. In this study, an unusually complete record of forest disturbance provided the opportunity to examine the effects of century-old fires and logging on current N cycling in northern hardwood forests in the White Mountains, New Hampshire.

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¹ Present address: Carnegie Institution of Washington, Department of Plant Biology, 260 Panama St., Stanford, California 94305 USA. E-mail: christy@jasper.stanford.edu

The White Mountain National Forest (WMNF) was established in 1911, largely in response to public outcries over widespread clearcutting and subsequent slash fires across the region during preceding decades. These relatively synchronous and human-induced disturbances differed greatly from the natural disturbance regime, and arguably represent the most extensive disturbance to affect northern hardwood forests in the White Mountains during the last 3000 yr (Spear et al. 1994). Wind is the primary natural disturbance agent, and episodic ice damage may also be important; natural fires are extremely rare in the northern hardwood zone (Lorimer 1977, Bormann and Likens 1979, Fahey and Reiners 1981, Seischab et al. 1993, Spear et al. 1994). Reforestation after agricultural abandonment is the dominant form of land-use history throughout most of New England (e.g., Cronon 1983, Foster et al. 1998), but within the WMNF, agriculture was of minor importance and was generally restricted to lowland valleys and floodplains.

The pulse of harvesting in the late 19th and early 20th centuries removed large quantities of C and N from White Mountain forests. Modern sawlog harvests of eastern hardwoods remove $\approx 100\text{--}200$ kg N/ha; whole-tree harvests remove $\approx 200\text{--}300$ kg N/ha (Hornbeck and Kropelin 1982, Johnson et al. 1982, Tritton et al. 1987). Harvests can induce up to 40–60 kg/ha of N loss through nitrate leaching (Martin et al. 1986). Historical harvest practices in the White Mountains varied widely, from selective cutting of large-diameter spruce to intensive clearcutting on steep slopes. Slash was left on-site, and fires frequently struck cutover lands and spread to uncut forest. Period accounts often reported combustion of both woody material and soil organic matter (Chittenden 1904, and unpublished surveys, WMNF Headquarters, Laconia, New Hampshire), and because N volatilization in fire corresponds directly with combustion of organic matter (Raison 1979, Raison et al. 1985), we expected that the White Mountain fires led to large losses of N. Fire-induced losses of N from the forest floor can be substantial but variable: In humid forests, site preparation burns typically remove 100–300 kg N/ha, but can range from small gains to losses of 600 kg N/ha (Little and Ohmann 1988, Vose and Swank 1993, Johnson et al. 1998). Soil organic matter losses from slash and wildfires may be even greater than site preparation or prescribed burns, as they generally have greater fuel loads which burn hotter and longer (Raison 1979).

We examined whether logging and fire had long-term impacts on N cycling in northern hardwood forests. We tested whether 80–110 yr old disturbances affected foliar chemistry, net N mineralization and nitrification rates, soil C and N pools, and NO_3^- leaching losses relative to undisturbed stands, and whether logging effects differed from fire effects. We predicted that N pools, availability, and loss would differ as a function of past N removals, with the lowest levels in the burned

stands, intermediate levels in the logged stands, and the highest levels in the old-growth stands. Across all plots, we expected that effects of land-use history on N cycling would relate to measurable differences in soil or vegetation properties.

METHODS

Site description

The WMNF covers 3000 km² in north-central New Hampshire (43.8–44.6° N, 71.0–72.0° W; Fig. 1). The mountains consist largely of highly metamorphosed Devonian aluminum schists or Mesozoic granites (Hatch and Moench 1984). Soils in the northern hardwood zone are primarily Haplorthods developed on stony glacial till. The Hubbard Brook Experimental Forest, at 250 m elevation in the southwestern WMNF, receives an average of 1300 mm precipitation annually, and mean monthly temperatures range from -8.7°C in January to 18.8°C in July (Federer et al. 1990). Bulk inorganic N ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) deposition averages $6.5\text{--}8.0$ kg N $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ at Hubbard Brook and nearby Cone Pond (Hornbeck et al. 1997). Temperatures decrease, and precipitation and N deposition increase with elevation (Lovett and Kinsman 1990, Ollinger et al. 1995).

Within the northern hardwood zone, tree species' distributions and abundances differ due to shade tolerance and successional status. Shade intolerant species such as paper birch (*Betula papyrifera*) and aspen (*Populus* spp.), and midsuccessional species such as yellow birch (*B. alleghaniensis*), and red maple (*Acer rubrum*) are common after heavy logging, while American beech (*Fagus grandifolia*), sugar maple (*A. saccharum*), eastern hemlock (*Tsuga canadensis*), and red spruce (*Picea rubens*) increase in abundance later in succession (Leak 1991). The full transition in species dominance generally requires at least 170 to 250 yr (Leak 1991).

Site selection

Old-growth, historically logged, and historically burned northern hardwood stands were located within each of five different regions (Fig. 1, Table 1). This design allowed replication of land-use categories while controlling for local differences in geology and climate. Disturbance histories were identified from published (Chittenden 1904, Belcher 1980) and unpublished WMNF records. As the federal government purchased forest land to form the WMNF (primarily 1911–1939), foresters were sent out to survey and map forest condition. These unpublished survey documents (WMNF Headquarters, Laconia, New Hampshire) identify forest type (northern hardwood, spruce–fir, or subalpine) and condition (burned, lightly logged, heavily logged, second growth, or virgin) at the time of federal purchase. We chose stands that were mapped as burned or heavily logged northern hardwoods; additional information on

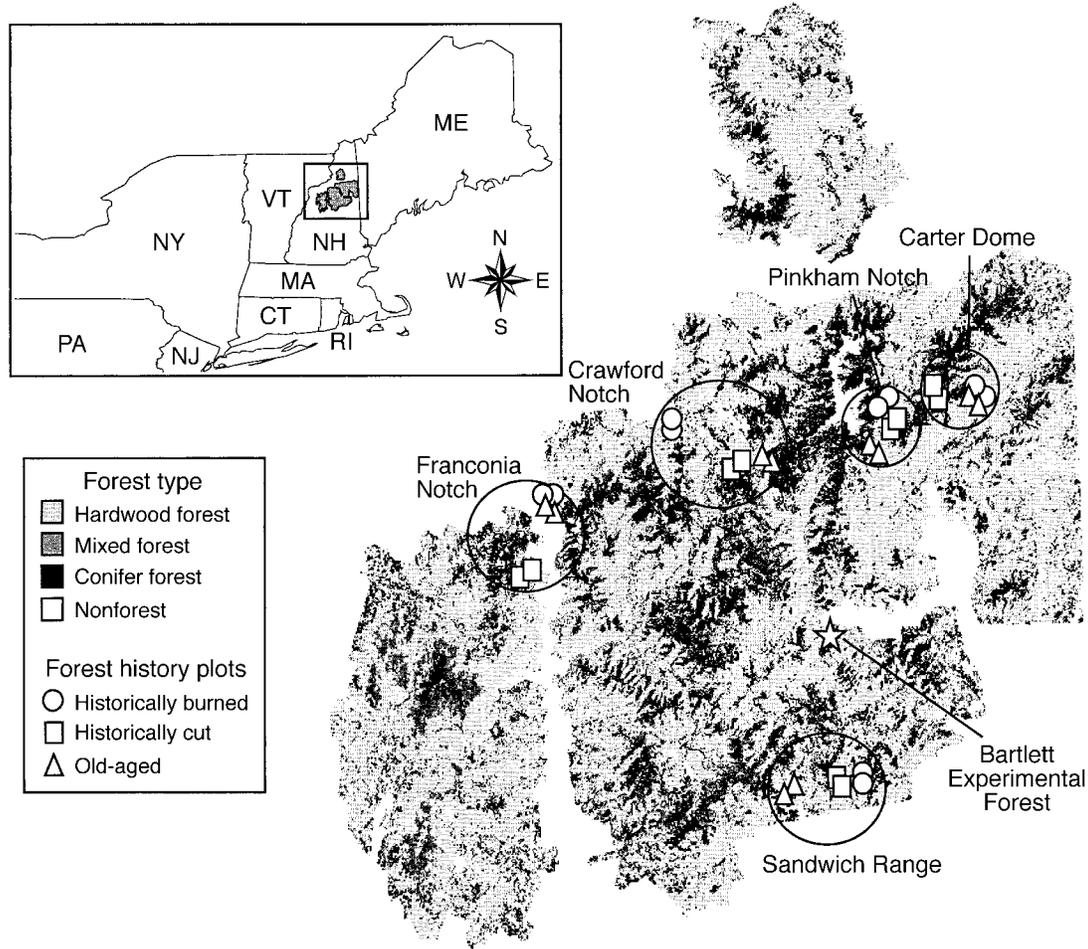


FIG. 1. Soil sampling locations by land-use history (symbols) and region (large circle outlines) in the White Mountain National Forest, New Hampshire.

the exact species composition was not available. The burned sites all occurred in areas of heavy logging and were probably, but not necessarily, first logged and then burned by accidental slash fires. For convenience, we refer to these sites as “burned” rather than “logged and burned” throughout the paper. All of the burned sites contained soil charcoal fragments, usually located at the contact between the forest floor and the mineral soil. Charcoal was not found at any of the other sites. Chittenden (1904), Belcher (1980), or the WMNF surveys confirmed the burn dates for all fires but that at

the George’s Gorge, Pinkham Notch site, which was approximated from tree increment cores. Information from the WMNF surveys was used to constrain the dates of cutting in the logged stands.

There are few known old-growth northern hardwood stands in the WMNF. As official or candidate Research Natural Areas, the Bowl (Leak 1974, Martin 1977, 1979) and Gibbs Brook (Foster and Reiners 1983) are well-documented old-growth sites (Table 1). The New Hampshire Natural Heritage Inventory identified potential old-growth stands in the Lafayette Brook Scenic

TABLE 1. Location and sampling date (1996) of soil collection sites.

Region	Date	Old-growth site	Burned site (year)	Logged site (possible years)
Sandwich Range	10–11 June	The Bowl	Mt. Chocorua (1915)	Mt. Paugus (~1915)
Pinkham Notch	17–18 June	Glen Boulder†	George’s Gorge (~1903)†	Lost Pond (1896–1915)†
Crawford Notch	24–25 June	Gibbs Brook†	Zealand Valley (1886)†	Mt. Tom (1880–1915)
Franconia Notch	1–2 July	Lafayette Brook†	Mt. Bickford (1903)†	Cascade Brook (~1895)
Carter Dome	8–9 July	Spruce Brook	Wild River (1903)	Carter Dome Tr. (1896–1915)

Note: Dates of fires and possible dates of cutting are indicated in parentheses.

† Sites with streamwater collections.

Area (Sperduto and Engstrom 1993) and in the Spruce Brook watershed of the Wild River valley (Engstrom and Sperduto 1994). The Glen Boulder site is a probable old-growth stand that was described as "virgin hardwoods and spruce" in its purchase survey in 1912; compartment records (U.S. Forest Service, Conway, New Hampshire) indicate no harvesting since then. Consistent with other old-growth stands in the region, the Glen Boulder site contains large individuals of late-successional species (including red spruce) and large dead boles with no evidence of harvesting; however, the site has not been fully surveyed. Very light selective cutting could have occurred in the late 1800s or early 1900s in any of these stands, but they represent some of the best available examples of old-growth northern hardwoods in the WMNF.

At each burned, logged, and old-growth site, two 20 × 20 m plots were established on drained, midslope positions dominated by northern hardwoods. An altimeter was used to match plot elevations among the three land-use histories within each of the five regions. Once the appropriate elevations were reached, plot locations were chosen by walking a predetermined random number of paces along the contour, although recent canopy gaps or poorly drained sites were rejected. Exact plot locations were later determined with a Trimble Pro XR Global Positioning System (Sunnyvale, California), which indicated that on average the logged plots were 40 m lower than the old-growth plots, a statistically significant but minor difference (see *Results*). Given the constrained locations of accessible sites with known land-use histories, we were unable to match aspects as well as elevations, although no biases were apparent.

Soil measurements

Net N mineralization and nitrification, soil C, N, and organic matter content, and soil pH were measured at all 30 plots (5 regions × 3 land-use histories × 2 plots/site). Net N mineralization and nitrification were estimated with 28-d laboratory incubations of intact cores intended to mimic the buried bag method (Eno 1960, Pastor et al. 1984). Cores were incubated at room temperature (21°C) rather than fluctuating field temperatures. This laboratory method differed from laboratory potential mineralizations in that soils were not sieved, nor were soil moisture levels adjusted prior to incubation.

Soils were collected in early summer (Table 1) from three randomly chosen 5 × 5 m subplots within each 20 × 20 m plot. After removing recent litter (Oi), three pairs of 5.5 cm diameter soil cores were collected at each subplot. Each core was divided into forest floor (Oe + Oa) and mineral soil (0–10 cm) horizons, which were placed into separate polyethylene bags. Cores were refrigerated until return to the laboratory. One core from each pair was extracted within 24 h of return, while the other was incubated in the dark for 28 d. Forest floor and mineral soil horizons were each com-

posited by subplot, sieved through a 5.6-mm mesh sieve, and then weighed. Soil moisture was determined for subsamples of the composited soils by drying at 105°C for 48 h. Ten grams of sieved, composited, field-moist soil were extracted in 100 mL of 1 mol/L KCl over 48 h. Extracts were filtered (Gelman Sciences A/E) and frozen until later analysis. Extract NO_3^- -N and NH_4^+ -N concentrations were determined colorimetrically with a Technicon TRAACS 800 Autoanalyzer using Technicon methods 782–86T (hydrazine reduction) and 780–86T (indophenol blue), respectively. Net N mineralization was calculated as: $([\text{NO}_3^-\text{-N}] + [\text{NH}_4^+\text{-N}])_{\text{incubated}} - ([\text{NO}_3^-\text{-N}] + [\text{NH}_4^+\text{-N}])_{\text{initial}}$, and net nitrification was calculated as $[\text{NO}_3^-\text{-N}]_{\text{incubated}} - [\text{NO}_3^-\text{-N}]_{\text{initial}}$.

The laboratory incubation method was compared with annual in situ incubations at 24 plots in the WMNF (Ollinger et al., *in press*). The traditional buried-bag technique was used to measure annual N mineralization at 14 plots at the Bartlett Experimental Forest in 1996–1997 (Fig. 1), and at 10 other WMNF plots in 1998–1999. Soil cores were collected from these plots in mid-summer 1996 and 1998, respectively, for 28-d laboratory incubations. Laboratory estimates of net N mineralization (Eq. 1) and nitrification (Eq. 2) reliably predicted annual field measurements across the 24 plots (Ollinger et al., *in press*). For net N mineralization (kg/ha),

$$\text{annual} = 2.44 \times \text{lab} + 5.94 \quad (1)$$

($R^2 = 0.88$, $P < 0.0001$); for net nitrification (kg/ha),

$$\text{annual} = 2.52 \times \text{lab} + 0.60 \quad (2)$$

($R^2 = 0.96$, $P < 0.0001$). These relationships were used to extrapolate measurements from the 28-d laboratory incubations to estimates of net annual N mineralization and nitrification at the plots in this study.

Composited soils from the initial cores were air dried, and analyzed for pH and total C, N, and organic matter. Soil pH was measured with an Orion glass pH electrode in a 1:10 g/g (forest floor), or 1:4 g/g (mineral soil) 0.01 mol/L CaCl_2 slurry. Soil organic matter content was determined by loss-on-ignition at 500°C for 5 h. Total C and N were determined on dried, ground (Brinkman mechanized ceramic mortar and pestle) samples by thermal combustion (Fisons NA 1500 Series 2 CHN analyzer).

Vegetation measurements

On all 30 plots, diameter at breast height (dbh) and species were recorded for all trees ≥ 9.5 cm dbh. Allometric equations were used to estimate foliar and total aboveground biomass from dbh. Equations from Whittaker et al. (1974) with modifications by Siccama et al. (1994) were used for yellow birch, sugar maple, American beech, and red spruce; equations from Hocker and Early (1983) were used for paper birch, red

maple, aspen, and eastern hemlock. In August, 1997, foliage was collected from the mid- to upper canopy of one to three individuals of each canopy species on each plot using 12-gauge shotguns and Number 4 steel shot. Foliage samples were air dried and ground with a Wiley mill to pass through a 1-mm mesh sieve. Nitrogen and lignin concentrations were determined with near-infrared reflectance spectroscopy (McLellan et al. 1991, Bolster et al. 1996). On each plot, foliar chemistry was averaged by tree species, and then weighted by species' estimated foliar biomass to obtain plot-averaged foliar chemistry.

Stream nitrate

Stream NO_3^- -N concentrations were determined for streams draining 7 of the 15 soil-collection sites (Table 1) as part of a larger survey of stream chemistry (Goodale et al., *in press*). Two to four small streams were sampled at each site. Each stream's watershed fell wholly within the identified land-use history. Monthly streamwater samples were collected from October 1996 until September 1997 for all but the Mt. Bickford site, which was sampled from May to September 1997. Its mean annual flux was approximated from its growing season flux, and the ratio of growing season to annual nitrate flux in the other historically burned streams. Monthly streamflow was modeled with PnET-II (Aber et al. 1995), and annual NO_3^- -N flux was estimated as the sum of monthly water flux \times NO_3^- -N concentration. Goodale et al. (*in press*) describe the stream sampling, analytical, and modeling methods in detail.

Statistical analyses

Plot-level properties were compared across the three land-use history categories (burned, logged, and old growth) with analysis of variance. The ANOVAs were blocked by region (five levels, Table 1) as a fixed factor, and a land-use history \times region interaction term was included. Scheffé's tests were used for post hoc comparisons among land-use histories. Relationships among plot-level soil and vegetation properties were examined with correlation analyses and Bonferroni corrections for multiple comparisons. Stepwise multiple linear regression was used to determine which properties best explained variability in net N mineralization and nitrification rates.

RESULTS

Effects of land-use history

The forest floors of old-growth sites had significantly less organic matter, C, and slightly less N than historically logged or burned sites (Fig. 2, Table 2). Land-use history was only one of several factors affecting forest floor C and N contents, as differences among the five regions were larger than the differences among land-use histories (Table 2). Strong, but nonsignificant, land-use history \times region interaction terms ($P = 0.06$ –

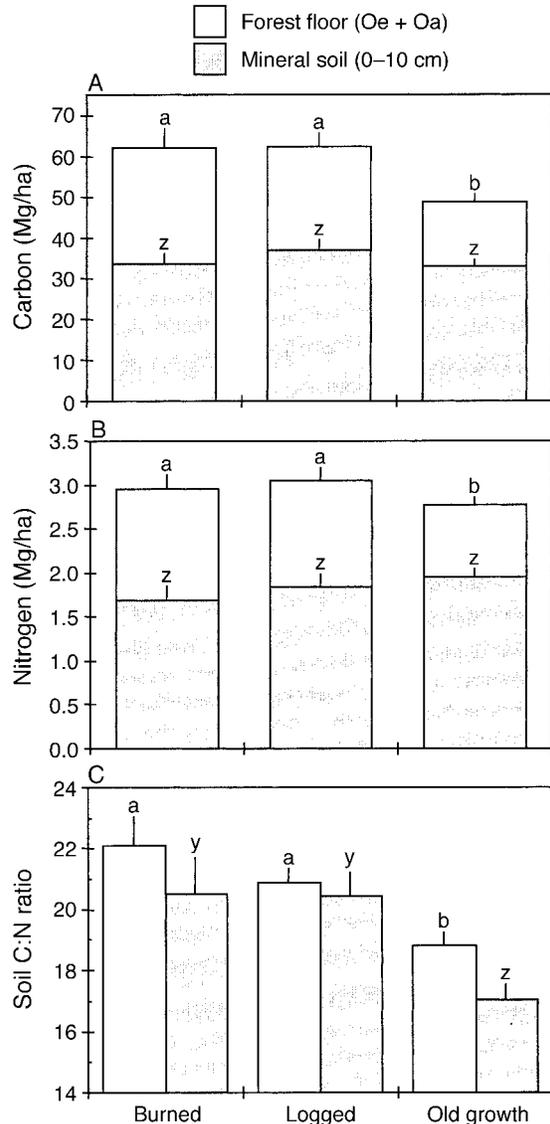


FIG. 2. (A) Carbon, and (B) nitrogen content, and (C) C:N ratio by land-use history. Bars are mean (± 1 SE) values, and different letters (a,b or y,z) indicate significant differences among land-use histories; $n = 10$ plots/land use. Table 2 contains additional statistics.

0.10; Table 2) suggested that the mean land-use differences were influenced by large differences in some regions. In the mineral soil (0–10 cm), land-use history did not significantly affect organic matter, C or N content. Soil C:N ratios (grams per gram) varied consistently by land-use history in both the mineral soil and the forest floor (Table 2). C:N ratios were lowest in the old-growth stands, and did not differ between the logged and burned sites (Fig. 2). Neither soil moisture, nor soil pH differed by land-use history (Table 2). Soil moisture averaged 186% of dry mass in the forest floor, and 61% in the mineral soil. Soils were acidic: pH

TABLE 2. Analysis of variance of soil properties by land-use history (burned, logged, and old-growth), region (see Table 1), and interactions.

Soil property	Soil type†	Land-use (L) (df = 2)			Region (R) (df = 4)		
		MS	F	P	MS	F	P
Carbon (Mg/ha)	Forest floor	462	6.8	0.008	290	4.3	0.017
	Mineral soil	42	1.5	0.25	205	7.3	0.002
	Total	611	6.1	0.011	569	5.7	0.005
Nitrogen (Mg/ha)	Forest floor	0.58	5.8	0.014	0.58	5.8	0.005
	Mineral soil	0.17	1.4	0.28	0.74	6.0	0.004
	Total	0.21	1.5	0.26	1.41	10.1	<0.001
C:N ratio	Forest floor	27.7	10.3	0.002	12.7	4.7	0.01
	Mineral soil	39.4	11.1	0.001	23.7	6.7	0.003
Net N mineralization (kg·ha ⁻¹ ·yr ⁻¹)	Forest floor	73	1.0	0.37	514	7.6	0.002
	Mineral soil	37	0.1	0.90	731	2.2	0.11
	Total	180	0.5	0.63	1188	3.1	0.05
Net N mineralization (mg·g OM ⁻¹ ·yr ⁻¹)	Forest floor	2.64	7.0	0.007	1.33	3.5	0.03
	Mineral soil	0.01	0.1	0.89	0.22	2.5	0.09
Net N turnover (%/yr)	Forest floor	25.4	9.0	0.003	12.0	4.2	0.02
	Mineral soil	2.0	0.8	0.47	10.0	3.9	0.02
Net nitrification (kg·ha ⁻¹ ·yr ⁻¹)	Forest floor	587	10.6	0.001	89	1.6	0.22
	Mineral soil	1175	3.7	0.05	404	1.3	0.33
	Total	3421	6.6	0.009	505	1.0	0.45
pH	Forest floor	0.07	0.9	0.42	0.12	1.6	0.23
	Mineral soil	0.17	1.8	0.20	0.08	0.8	0.53
Soil moisture (% dry mass)	Forest floor	0.17	1.0	0.40	0.17	1.0	0.45
	Mineral soil	0.01	0.3	0.78	0.13	5.4	0.007

Note: Significant effects of land-use history are indicated in boldface.

† Forest floor consisted of Oe + Oa, mineral soil consisted of 0–10 cm, and total indicates forest floor + mineral soil.

averaged 3.4 in the forest floor, and 3.5 in the mineral soil.

Estimated net annual N mineralization rates averaged 113 kg·ha⁻¹·yr⁻¹, and did not differ significantly by land-use history in either the forest floor or the mineral soil (Fig. 3, Table 2). As the old-growth stands had lower forest floor organic matter and N contents, net N mineralization rates per unit organic matter or unit N (net N turnover) were greater in old-growth forest floors (2.3 mg·g⁻¹·yr⁻¹ and 8.0%/yr, respectively) than in the historically disturbed stands (1.4 g·mg⁻¹·yr⁻¹ and 5.2%/yr, respectively; Table 2). Mineral soil net N turnover averaged 3.6%/yr, and did not differ by land-use history. Net nitrification rates varied strongly by land-use history. Nitrification rates at the old-growth sites approximately doubled those at historically burned or logged sites, which did not differ from each other (Fig. 3). This pattern was consistent across all five regions (Fig. 4).

Mean aboveground biomass was greater on the old-growth plots than on the historically disturbed stands ($P = 0.04$, Fig. 5), although biomass estimates were quite variable due to small plot size (400 m²), and chance inclusion of large individuals. The estimates of aboveground biomass were comparable within this study, but may be slightly higher than forest-wide values because our site selection excluded plots with recent canopy gaps. Estimates from allometric equations

suggested that burned sites had greater foliar biomass than old-growth sites, even though the old-growth sites had greater total aboveground biomass (Table 3). Stand basal area averaged 30 m²/ha, and did not vary by land-use history. Mean stem density was lower ($P < 0.001$, Fig. 5), and hence mean tree size was greater on the old-growth plots than on the logged and burned plots. Species composition differed by land-use history: Early-successional paper birch and red maple occurred only on the historically disturbed sites, while late-successional sugar maple and American beech occurred on all three site types, but were most important in the old-growth stands (Fig. 5). American beech increased in both number of stems and biomass on the old-growth stands relative to the disturbed stands, while sugar maple decreased slightly in numbers but increased greatly in biomass. Conifers (generally red spruce) averaged 7% of the stems on old-growth and logged plots, and ranged up to 27%. Land-use history did not affect plot-level foliar percentages of N (%N), lignin, or the lignin:N ratio (Table 3), nor were there any differences in foliar chemistry by land use within individual species.

Nitrification and nitrate losses

Estimated annual stream NO₃⁻-N flux correlated strongly with soil nitrification, even though plots covered very small portions of the watersheds (Fig. 6).

TABLE 2. Extended.

L × R (df = 8)			Residual (df = 15)
MS	F	P	MS
157	2.3	0.08	68
55	1.9	0.13	28
287	2.9	0.04	100
0.24	2.4	0.06	0.10
0.13	1.0	0.45	0.12
0.38	2.7	0.04	0.14
3.4	1.3	0.34	2.7
8.0	2.3	0.08	3.5
265	3.9	0.01	68
602	1.8	0.15	327
808	2.1	0.10	381
0.38	1.0	0.47	0.38
0.23	2.6	0.06	0.09
4.5	1.6	0.21	2.8
5.1	2.0	0.12	2.6
22	0.4	0.91	55
276	0.9	0.57	321
285	0.5	0.80	520
0.02	0.2	0.98	0.07
0.06	0.6	0.76	0.09
0.19	1.1	0.43	0.18
0.05	2.0	0.11	0.02

The old-growth sites had high nitrification rates and high stream NO₃⁻-N concentrations and fluxes, while the historically disturbed sites had much lower nitrification rates and stream NO₃⁻-N fluxes. Nitrification rates varied greatly within both the Gibbs Brook old-

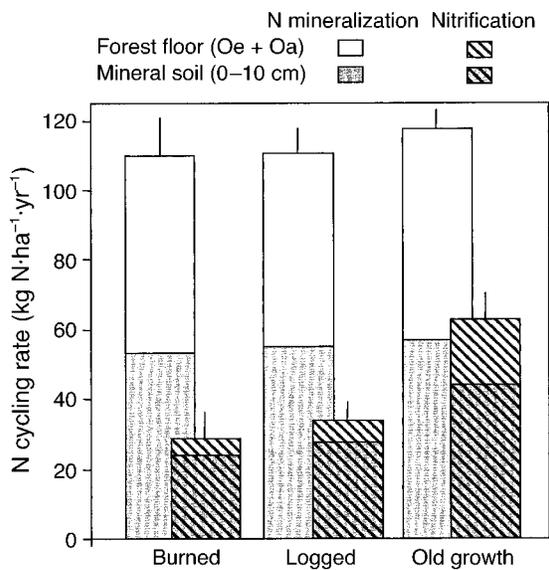


FIG. 3. Annual net N mineralization and nitrification by land-use history. Bars are total mean (+1 SE) values, and are divided into forest floor and mineral soil; n = 10 plots/land use. Table 2 contains additional statistics.

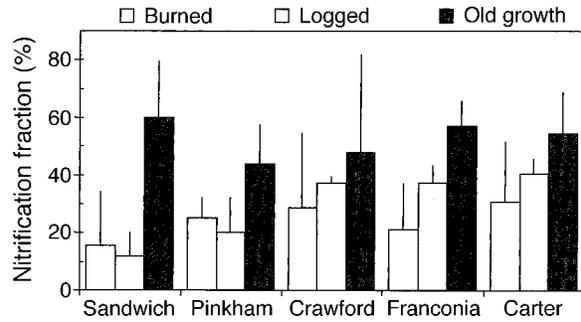


FIG. 4. Percentage nitrification (net nitrification/net mineralization) by region and land use history. Bars are mean values (+1 SD) of 2 plots/site.

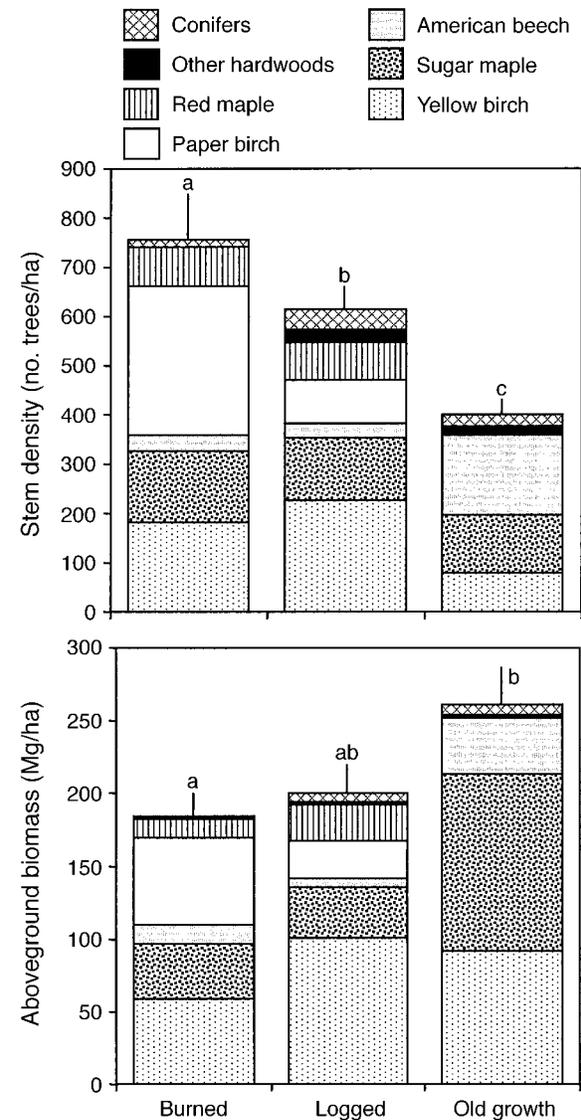


FIG. 5. Mean stem density (number of trees/ha) and aboveground biomass (Mg/ha) by tree species and land-use histories for all trees ≥9.5 cm dbh.

TABLE 3. Analysis of variance of foliar properties by land-use history, region, and interactions.

Variable	Burned	Logged	Old growth	Land-use (L) (df = 2)		
				MS	F	P
Elevation (m)	660 ± 35 ^{ab}	634 ± 24 ^a	673 ± 30 ^b	3997	4.0	0.04
Foliar mass (Mg/ha)	5.0 ± 0.43 ^a	4.1 ± 0.47 ^{ab}	3.6 ± 0.18 ^b	4.86	6.4	0.010
Foliar N (%)	2.37 ± 0.05	2.30 ± 0.04	2.34 ± 0.08	0.02	0.5	0.63
Foliar lignin (%)	20.0 ± 0.47	21.0 ± 0.39	20.8 ± 0.49	1.27	1.5	0.25
Foliar lignin:N	8.62 ± 0.18	9.19 ± 0.16	8.90 ± 0.34	0.35	0.9	0.41

Note: Significant effects of land-use history are indicated in boldface.

growth site and the Zealand Valley burned site, suggesting patchy nitrification in both areas. Within the Gibbs Brook site, the plot with the low nitrification rates typified the mixed hardwood-conifer forest of the three large watersheds yielding very low NO_3^- -N fluxes, while the plot with high nitrification rates typified the sugar maple/yellow birch composition of the small watershed yielding relatively high NO_3^- -N fluxes (indicated by open triangles in Fig. 6).

Nitrogen cycling covariates

Net nitrification rates correlated significantly with forest floor C:N ratio, forest floor organic matter content, net N mineralization, and mineral soil pH (Table 4). Forest floor C:N ratio was a better predictor of whole-core nitrification than mineral soil C:N ratio, even though most of the nitrification occurred in the mineral soil. Nitrification increased sharply below a forest floor C:N ratio of ≈ 23 –25 (Fig. 7). The only significant correlation between net N mineralization rate and any plot-level property was with forest floor C:N ratio (Table 4). This relationship was weak ($R^2 = 0.40$; Fig. 7), so that differences in C:N ratio among land-use histories (Fig. 2) were not sufficient to yield statistically different N mineralization rates by land-use history. Sugar maple was the only species whose abundance correlated significantly with any measured soil property: Forest floor mass and mineral soil C:N ratio decreased as sugar maple percent of total biomass increased. Yet direct correlations between sugar maple abundance and nitrification ($P = 0.32$) and N mineralization ($P = 1.00$) were not significant.

Foliar chemistry did not correlate directly with any soil property (Table 4), but did improve predictions of N cycling in multiple regression models. Multiple regression analysis using stepwise elimination of the variables in Table 4 retained forest floor C:N ratio, mineral soil pH, and foliar lignin:N ratio as the strongest predictors of net nitrification (adjusted $R^2 = 0.63$). Net N mineralization was best predicted by forest floor C:N ratio and foliar %N (adjusted $R^2 = 0.47$).

DISCUSSION

The comparison between the historically disturbed and old-growth stands suggests that after 80–110 yr, aboveground biomass has reaccumulated to $\approx 75\%$ of

that in comparable old-growth stands, while net N mineralization rates and soil C and N pools have fully recovered from any losses that may have occurred. We expected that recovery from slash fires would take longer than from clearcutting alone, yet the historically disturbed sites did not differ in aboveground biomass, N cycling rates, or soil C and N pools. Either historical fires were less intense than presumed, or both logged and burned soils have had sufficient time to reach a similar stage of recovery. Yet nitrification rates at the historically disturbed sites were much lower than those at the old-growth sites. The 80–110-yr-old forests may still be accumulating N in woody biomass, but this process is unlikely to account for more than a few (~ 2 –6) $\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in these forests, and differences in plant uptake do not immediately explain the large (~ 30 $\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) differences in nitrification observed in soil cores where roots were excluded. What other factors explain the differences in nitrification between the historically disturbed and the old-growth sites?

Net nitrification rates have previously been shown to relate to foliar chemistry, soil pH, ammonium supply, tree species, and soil C:N ratio (e.g., Robertson 1982, Vitousek et al. 1982, Pastor et al. 1984, McNulty et al. 1991, Van Miegroet et al. 1992, Finzi et al. 1998, Gundersen et al. 1998b). The strong, direct correlation between foliar chemistry (lignin:N ratio or %N) and soil properties (C:N or nitrification) observed by McNulty et al. (1991) and Gundersen et al. (1988b) in conifer forests was not observed here, although foliar chemistry did improve predictions of N cycling in multiple regression models. While McNulty et al. (1991) reported a wide range of lignin:N ratios across high-elevation spruce–fir forests (18.0 to 28.7), the northern hardwood stands studied here had a very narrow range of lignin:N values (7.4 to 10.2), with relatively high foliar %N values across all sites.

Nitrification did correlate with soil pH, N mineralization, and soil C:N ratio (Table 4), but neither soil pH, nor N mineralization varied by land-use history, and so they were not likely to explain the large differences in nitrification rates between the historically disturbed and old-growth plots. Only tree species composition and soil C:N ratio varied by land-use history and could possibly explain the systematically elevated nitrification rates at the old-growth sites.

TABLE 3. Extended.

Region (R) (df = 4)			L × R (df = 8)			Residual (df = 15)
MS	F	P	MS	F	P	MS
47 705	48.0	<0.001	1969	2.0	0.12	994
2.27	3.0	0.05	2.42	3.2	0.03	0.76
0.03	1.0	0.42	0.04	1.2	0.35	0.03
3.03	3.6	0.03	2.95	3.5	0.02	0.84
0.68	1.8	0.18	0.91	2.5	0.06	0.37

Species composition

The main differences in species composition between the historically disturbed and old-growth sites were the elimination of paper birch and red maple, and increased biomass of beech and particularly sugar maple at the old-growth sites. These shifts in species composition over succession are typical for many northern hardwood stands (Leak 1991). It is difficult to infer the composition of the presettlement forests of the WMNF from remnant old-growth patches, witness tree data, or isolated stands with historical inventory data (e.g., Hamburg and Cogbill 1988); the limited data that exist suggest that red spruce and American beech may have been more common, and sugar maple less common, than represented by the old-growth stands in which we worked. Our selection process of choosing stands marked as "northern hardwoods" on their original timber surveys may have biased our selection against areas where spruce was more common. Yet this same bias occurred when choosing the disturbed sites, and we believe that the old-growth stands we studied reasonably represented the species composition of the nearby logged and burned stands, had they not been disturbed. For example, on the eastern flank of Carter Dome, old-growth and burned sites were <150 m apart, with the

same slope, aspect, elevation, and probable predisturbance species compositions, yet sugar maple made up 80% of the 317 Mg/ha of biomass on two old-growth plots, but only 48% of the 205 Mg/ha on two plots burned in 1903. The species composition of the old-growth stands in this study strongly resembled that of old-growth northern hardwood stands in the Adirondack Mountains, New York, where large tracts of old-growth forest were preserved (McGee et al. 1999). It is always difficult to infer temporal patterns from space-for-time (or disturbance history) substitutions; we specifically designed this study with five independent replications of disturbance histories in order to reduce the likelihood of spurious conclusions about the role of disturbance.

Sugar maple is a shade-tolerant, late-successional dominant, and nitrification rates under sugar maple frequently exceed those under other northern hardwood species (Pastor et al. 1984, Finzi et al. 1998, Lovett and Rueth 1999). However, it is difficult to discern whether the reported trends in nitrification are due to a particular property of sugar maple itself (Finzi et al. 1998, Lovett and Rueth 1999), or to covariation with underlying gradients in soil pH, texture, or mineralogy (Pastor et al. 1984, van Breeman et al. 1997). This distinction is important for predicting the potential effects of increased sugar maple dominance over succession. If nitrification rates relate to an underlying soil property, then we would expect little change in nitrification due to successional changes in species dominance on the same site; if some property of sugar maple itself induces or augments nitrification, then we would expect increases in nitrification due to successional increases in sugar maple abundance, regardless of any other changes in biogeochemical cycling over the course of succession. Lovett and Rueth (1999) determined that soils with similar texture and %N had higher nitrification rates under sugar maple than under beech, suggesting a direct species effect. Sugar maple foliage does not have particularly high N concentrations (in this study, mean = 2.08% N), but its low lignin content leads to low lignin:N ratios in leaf litter, with rapid decomposition and little net N immobilization (Aber and Melillo 1982, Melillo et al. 1982). In the present study, the direct correlation between sugar maple abundance and nitrification was not significant ($R = 0.51$,

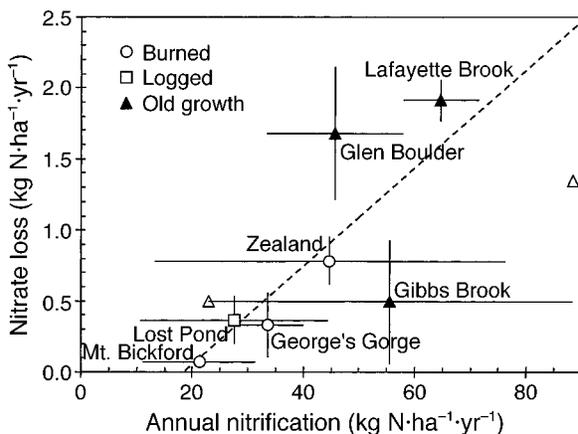


FIG. 6. Estimated N fluxes in stream nitrate export and soil nitrification. Nitrification data are the mean (\pm range) of two plots per site, and stream data are averages (\pm 1 SD) of 2–4 streams per site. Regression line (dashed): $Y = 0.035X - 0.65$, $R^2 = 0.56$, $n = 7$.

TABLE 4. Matrix of Pearson correlation coefficients (*R*) for net nitrification, mineralization, and other measured soil and vegetation properties.

Property	Nitrification	N Mineralization	Forest floor C:N	Mineral soil C:N	Forest floor pH
Nitrification (kg N·ha ⁻¹ ·yr ⁻¹)	1				
N mineralization (kg N·ha ⁻¹ ·yr ⁻¹)	0.63*	1			
Forest floor C:N ratio	-0.70***	-0.62*	1		
Mineral soil C:N ratio	-0.50	-0.27	0.65**	1	
Forest floor pH	0.47	0.19	-0.49	-0.35	1
Mineral soil pH	0.64*	0.32	-0.51	-0.32	0.86***
Forest floor OM (Mg/ha)	-0.66**	-0.46	0.69**	0.57	-0.74***
Foliar N (%)	0.26	0.33	0.01	-0.05	-0.09
Foliar lignin (%)	0.03	0.22	-0.08	0.06	-0.36
Foliar lignin:N ratio	-0.32	-0.24	0.12	-0.03	-0.04
Aboveground biomass (Mg/ha)	0.49	0.27	-0.45	-0.64*	0.22
Sugar maple biomass (%)	0.51	0.17	-0.53	-0.66**	0.56
Conifer biomass (%)	-0.07	-0.22	0.03	0.07	-0.31

Notes: Forest floor consisted of Oe = Oa; mineral soil consisted of 0–10 cm. There were *n* = 30 plots.

* *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001. All are Bonferroni-corrected values.

P = 0.32), indicating that some other property of the old-growth sites accounted for the elevated nitrification rates. Yet forest floor mass and mineral soil C:N ratio decreased as sugar maple abundance increased, suggesting a possible indirect effect on nitrification. Whether the increased nitrification at the old-growth sites was due to successional increases in sugar maple dominance or to some other aspect of old-growth biogeochemistry, species composition itself was affected by the disturbances 80–110 yr ago, and the observed differences in N cycling reflect the net effect of disturbance on both species composition and stand biogeochemistry.

Soil C:N ratio

The concept of critical soil organic matter C:N thresholds for N mineralization and nitrification was recognized long ago (reviewed in Harmsen and van Schreven 1955), but has received renewed attention in the current discussion of N saturation. Forest floor C:N ratio has emerged as a predictor of net nitrification and nitrate leaching in European and eastern U.S. forests (McNulty et al. 1991, Dise et al. 1998a, b, Emmett et al. 1998, Gundersen et al. 1998a, Currie 1999). Emmett et al. (1998) suggested a critical forest floor (minus fresh leaf litter) C:N ratio of 24 for the onset of nitrate leaching from European conifer plantations, a value consistent with the onset of net nitrification in this study (Fig. 7) and in other northern hardwood stands (Lovett and Rueth 1999; Ollinger et al., *in press*).

Forest floor C:N ratios integrate site history of both C and N accumulation, and critical C:N ratios should be reached fastest in areas where forest floor N accumulates faster than forest floor C, or where C inputs are reduced. Soil N is derived from plant litter and from N inputs in fixation or deposition, while soil C accumulation is controlled by the balance between decomposition and inputs of leaf, fine root, and woody litter. Rates and quality of soil C and N inputs may

change during forest succession due to changes in allocation patterns (Vitousek et al. 1988) or species composition (Van Cleve et al. 1991).

In the present study, nitrification correlated with forest floor C:N ratio and organic matter content (Table 4), but not with N content of the forest floor or mineral soil. Forest floor mass and C:N ratio covaried, and McNulty et al. (1991) and Gundersen et al. (1998b) also report positive correlations between forest floor mass and C:N ratio. The forest floors of the old-growth stands contained less C than those of the historically disturbed stands, although this trend could have been driven by site-specific factors in a few regions. However, forest floor and mineral soil organic matter and N contents in the old-growth stands were nearly identical to those of the Integrated Forest Study's (IFS) Turkey Lakes site, an old-growth northern hardwood stand in Ontario (Johnson and Lindberg 1992). The historically disturbed sites had soil organic matter and N contents that strongly resembled those at the Hubbard Brook Experimental Forest (Johnson 1995) and the IFS's Huntington Forest (Johnson and Lindberg 1992), both northern hardwood sites that experienced heavy logging ≈80 yr ago. The implied trend of declining forest floor mass in old-growth sites differs from the asymptotic rise in forest floor mass to a steady state at 60–80 Mg/ha predicted by Covington (1981) and Federer (1984). Yet Yanai et al. (2000) suggest that changes in forest floor mass over time can be quite variable in both direction and magnitude. If net primary production (NPP) and litter inputs decline in late stages of succession (e.g., Ryan and Waring 1992), we would expect forest floor mass to decline as well. As C becomes limiting to heterotrophic microbes, gross N immobilization should decrease, allowing net nitrification to occur (Hart et al. 1994). Furthermore, chronically reduced competition for mineralized N by old-growth vegetation may have allowed N to accumulate in soil, decreasing soil C:N ratios and heterotrophic demand for N, and allowing net nitrification to increase.

TABLE 4. Extended.

Mineral soil pH	Forest floor OM	Foliar N (%)	Foliar lignin (%)	Foliar lignin : N	Aboveground biomass	Sugar maple biomass (%)
1						
-0.77**	1					
0.05	-0.03	1				
-0.11	0.03	0.24	1			
0.01	0.14	-0.32	0.22	1		
0.30	-0.44	0.15	0.14	-0.01	1	
0.44	-0.71***	0.05	-0.37	-0.36	0.41	1
-0.35	0.23	-0.46	0.01	0.28	-0.15	-0.20

Nitrification, succession, and N saturation

This study contributes to the long-running and often contradictory discussion of the role of succession in regulating N cycling and NO_3^- loss (e.g., Odum 1969, Rice and Panchoy 1972, Vitousek and Reiners 1975, Robertson and Vitousek 1981, Vitousek et al. 1989, Hedin et al. 1995). Temporal changes in C production and regional differences in N deposition may partially explain the variety of reported trends of N cycling over succession, with C:N ratio as a common regulator.

Vitousek and Reiners (1975) proposed that retention of limiting nutrients should decrease over successional time, and they demonstrated that New Hampshire streams draining old-growth stands had higher NO_3^- losses than stands logged ≈ 30 yr previously. The theory asserts that old-growth forests, with low rates of net ecosystem production, should retain few of the nu-

trients made available by atmospheric deposition or weathering. With decreased forest demand for N, nitrification and nitrate leaching are expected to increase over successional time. This pattern of elevated net nitrification rates or nitrate losses in old-growth stands relative to successional forests has been demonstrated elsewhere in the southeastern (Sasser and Binkley 1989, Flum and Nodvin 1995) and the northeastern (Leak and Martin 1975, Martin 1979, Robertson and Vitousek 1981) United States. Across the eastern United States, N deposition rates are greatly enhanced over preindustrial levels (Galloway et al. 1995, Holland et al. 1999), and forest floor C:N ratios have been shown to correlate inversely with N deposition (McNulty et al. 1991, Van Miegroet et al. 1992, Tietema and Beier 1995, Lovett and Rueth 1999). Eastern old-growth forests with reduced carbon inputs, little net demand for N, and elevated N inputs are likely candidates to achieve the critical C:N ratios needed to induce net nitrification and nitrate losses.

In contrast, successional sequences that lead from old-field grasses to forests in regions of moderate N deposition frequently report decreasing nitrification rates and increasing soil C:N ratios over the first several decades of succession (Thorne and Hamburg 1985, Zak et al. 1990, Compton et al. 1998). In these old-field studies, the rate of soil C accumulation outpaced the rate of soil N accumulation for at least several decades, and decreasing net nitrification rates corresponded with increasing soil C:N ratios. The 80–110 yr old forests we studied may be similar to these recovered old-field stands, after several decades of relatively faster rates of C accumulation than N accumulation. If C production declines in later stages of stand development, we would expect forest floor C:N ratios to decline toward those observed in the old-growth stands, and net nitrification to increase.

Areas that receive very little N deposition may require an extremely long time to receive enough N to narrow soil C:N ratios through N accrual over time; several hundred years may not suffice. Temperate old-

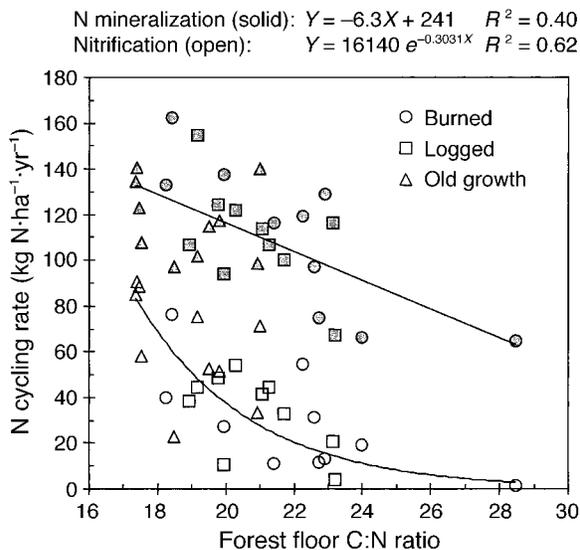


FIG. 7. Annual net N mineralization (solid symbols) and nitrification (open symbols) as a function of forest floor C:N ratio; $n = 30$.

growth forests on the west coast of North (Sollins et al. 1980) and South (Hedin et al. 1995) America often have low rates of net nitrification and nitrate loss. Old-growth angiosperm (*Nothofagus*) forests in western Chile receive very little N deposition, have relatively high soil C:N ratios (forest floor >45, 0–10 cm = 33; Pérez et al. 1998), and lose extraordinarily small amounts of nitrate in streams (Hedin et al. 1995). In contrast, the old-growth northern hardwood forests in this study and at Turkey Lakes receive elevated rates of N deposition, have low forest floor C:N ratios (18–19), and leak nitrate (Foster et al. 1989, Johnson and Lindberg 1992, Mitchell et al. 1992).

We conclude that disturbances 80–110 yr ago have had long-term effects on N cycling by allowing these aggrading forests to continue to retain deposited N in both soils and aboveground vegetation. For decades to centuries following disturbance, differences in the relative accumulation in C and N in different ecosystem pools with varying turnover times can greatly prolong the return to steady-state balances of C and N (e.g., Aber and Driscoll 1997, Schimel et al. 1997). Species-level differences in C and N cycling, and shifts in species composition over the course of succession may further modify patterns of C and N cycling with succession. Even though soil N pools in the historically disturbed stands have reaccumulated from any losses that may have occurred 80–110 yr ago, nitrate production and losses to streamwater were low relative to old-growth stands. The elevated nitrification rates in the old-growth stands corresponded with smaller forest floors and low C:N ratios, likely resulting from chronic N deposition combined with age-induced reductions in organic matter inputs or species-induced changes in litter quality. The combination of reduced organic matter production and chronic N deposition makes eastern old-growth forests particularly sensitive indicators of N saturation.

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