

REGIONAL VARIATION IN FOLIAR CHEMISTRY AND N CYCLING AMONG FORESTS OF DIVERSE HISTORY AND COMPOSITION

S. V. OLLINGER,^{1,4} M. L. SMITH,² M. E. MARTIN,¹ R. A. HALLETT,² C. L. GOODALE,³ AND J. D. ABER¹

¹Complex Systems Research Center, Morse Hall, University of New Hampshire, Durham, New Hampshire 03824 USA

²USDA Forest Service Northeastern Forest Research Station, Durham, New Hampshire 03824 USA

³The Woods Hole Research Center, P.O. Box 296, Woods Hole, Massachusetts 02543 USA

Abstract. Although understanding of nitrogen cycling and nitrification in forest ecosystems has improved greatly over the past several decades, our ability to characterize spatial patterns is still quite limited. A number of studies have shown linkages between canopy chemistry and N cycling, but few have considered the degree to which these trends can provide an indicator of forest N status across large, heterogeneous landscapes. In this study, we examined relationships among canopy chemistry, nitrogen cycling, and soil carbon:nitrogen ratios across 30 forested stands in the White Mountains of New Hampshire. Plots included a range of species (sugar maple, red maple, American beech, yellow birch, paper birch, red spruce, balsam fir, eastern hemlock) and were broadly grouped into two disturbance categories: those that were historically affected by intensive logging and/or fire and those that experienced minimal human disturbance.

Across all plots, rates of net N mineralization and net nitrification were correlated with canopy nitrogen concentrations, but the relationships differed between disturbance treatments. In deciduous forests, historically undisturbed stands had significantly higher rates of net N mineralization and net nitrification than previously disturbed stands, but these differences were not clearly reflected in patterns of stand-level canopy chemistry. Although soil C:N ratios also differed between disturbed and undisturbed stands, a relationship between soil C:N ratios and canopy lignin:N ratios did not vary with either forest type or disturbance, suggesting that this trend is more consistent across diverse conditions.

Relationships between foliar chemistry and N cycling within individual species revealed interesting differences between species and functional groups. For four out of five deciduous species, foliar N increased with increasing net N mineralization, indicating that species were responsive to changes in N availability and suggesting a positive feedback between foliar chemistry and soil N status. These patterns led to significant differences in foliar N between disturbance treatments for some species, but at the stand level, these differences were masked by successional changes in species composition. Among coniferous species, foliar N showed no variation across wide N-cycling gradients, suggesting a fundamentally different plant-soil interaction.

We also examined the potential for extending observed field relationships to the regional level using a high-quality data set of high spectral resolution remote sensing, obtained from NASA's AVIRIS instrument (Airborne Visible and InfraRed Imaging Spectrometer). Cloud-free AVIRIS data from 56 scenes covering the White Mountain National Forest were calibrated to canopy lignin:N ratios and were applied to prediction of C:N ratios in soils. Validation at 10 independent plots showed good prediction accuracy but suggested some overprediction at the low end of the range. Preliminary regional estimates of soil C:N ratios indicate that 63% of the region's land area falls below a value of 22. This value is significant because our field data identified this as a critical threshold for the onset of nitrification. Below C:N = 22, we expect increasing but variable rates of nitrification, depending on other factors such as disturbance or species composition.

Key words: AVIRIS; canopy chemistry; C:N ratio; disturbance; foliar nitrogen; land use history; nitrification; nitrogen mineralization; plant-soil relations; regional variation; remote sensing; succession; White Mountains, New Hampshire (USA).

INTRODUCTION

The net production of nitrate in forest soils represents a key ecological process that can affect the chemistry

and nutrient capital of soils and drainage waters and can alter the dynamics of plant communities. Following disturbances that reduce plant demand for available N, production and leaching of nitrate can lead to depletion of soil N pools and elevated NO_3^- concentrations in streams (Bormann and Likens 1979, Vitousek et al. 1979, Aber et al. 1997). In intact ecosystems, nitrate production is sometimes associated with reduced plant

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⁴ E-mail: scott.ollinger@unh.edu

demand relative to N supply, for example, as biomass accumulation declines (Vitousek and Reiners 1975, Bormann and Likens 1979, Aber et al. 1997), or as excess N accumulates from high levels of atmospheric N deposition (e.g., Aber et al. 1989, Gundersen et al. 1998). In all cases, NO_3^- production is considered an important issue because of the potential for elevated NO_3^- concentrations and acidity in surface waters and removal of base cations from soils (e.g., Aber et al. 1989, Murdoch and Stoddard 1992, Bailey et al. 1996, Likens et al. 1996, Peterjohn et al. 1996).

Despite considerable attention given to studying patterns of nitrogen cycling and nitrate production during forest development, our understanding of environmental controls remains incomplete and our ability to predict and/or detect spatial patterns across forested landscapes is presently very limited. The identification of simple and observable indicators of forest nitrogen status would greatly enhance our ability to characterize spatial patterns and would help to resolve relationships with possible environmental drivers. A large and growing body of literature has documented linkages among foliar chemistry, decomposition, N cycling, and productivity in forest ecosystems (e.g., Fogel and Cromack 1977, Melillo et al. 1982, Pastor et al. 1984, McClougherty and Berg 1987, Aber et al. 1990, Stump and Binkley 1993, Scott and Binkley 1997), which raises the question of whether foliar chemistry might serve as such an indicator.

At local to continental scales, N mineralization has been related to foliar and litterfall N (Nadelhoffer et al. 1985, Yin 1992), lignin (Wessman et al. 1988), and the ratio of lignin to N (Stump and Binkley 1993, Scott and Binkley 1997). Aboveground production has been related to litterfall N (Pastor et al. 1984, Nadelhoffer et al. 1985), foliar N content or concentration (Pastor et al. 1984, Smith 2000), and N mineralization (Pastor et al. 1984, Reich et al. 1997). Experimental N additions in the United States and Europe have shown that forest response to N amendments consists of simultaneous changes in N mineralization, soil C:N ratios, nitrification potential, productivity, and foliar N concentrations (Magill et al. 1996, 1997, Gundersen et al. 1998). Concurrent with these changes are increased potential for NO_3^- losses to ground and streamwater, a response that has been related to both soil C:N ratios (Dise and Wright 1995, Gundersen et al. 1998) and foliar N concentrations (Tietema and Beier 1995).

Although foliar chemistry is not an easily observable property across broad spatial scales, the capacity for detection with high spectral resolution remote sensing has been recognized for some time (Wessman et al. 1988) and this ability has been identified as a useful approach to studying terrestrial biogeochemical cycles (Schimel 1995). Further, recent advances with hyperspectral remote-sensing capabilities (ACCP 1994, Martin and Aber 1997) and planned development of space-

borne sensors make this a reasonable avenue for further investigation.

In this study, we use spatially extensive field measurements to examine relationships among canopy chemistry, soil C:N ratios and soil N transformations across the White Mountain National Forest in New Hampshire, USA. Results are presented with respect to variation in species composition and disturbance history. We also present estimates of soil C:N ratios for the White Mountain region, derived by combining observed field relationships with image data collected by an airborne high spectral resolution remote sensing-instrument.

METHODS

Study area

The White Mountain National Forest covers 3650 km² in central New Hampshire and includes areas of low, rolling hills as well as large mountains that extend above treeline. The White Mountain region includes a wide variety of vegetation and site types, representative of those present across most of the northeastern United States. These types range from oak–pine valley bottoms on lacustrine and glacio-fluvial substrates, to northern hardwood mid-slopes on basal and ablation glacial tills, to spruce–fir on upper mountain slopes and alpine tundra mountain tops. Soils are coarse-textured spodosols and inceptisols formed on glacially deposited tills or sandy outwash with shallow histosols on upper slopes. Soils have high stone contents, and this property often exerts an influence on water-holding capacity equal or greater to that of texture.

For the current analysis, a network of 30 plots was established for sampling of foliar chemistry and soil nitrogen fluxes (Fig. 1). Plot selection was aimed at capturing a range of forest communities and disturbance histories, although these factors are often interdependent. Plot elevations ranged from ~300 to 800 m and all sites were on well-drained glacial till soils, with the exception of conifer stands on areas of shallow bedrock. Major tree species represented included paper birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), sugar maple (*Acer saccharum* L.), American beech (*Fagus grandifolia* Ehrn.), eastern hemlock (*Tsuga canadensis* L. Carr.), red spruce (*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* L. Mill.). Most plots contained mixtures of two or more species.

Prior to European settlement, the most common natural disturbances in the White Mountain region were wind and fire, which occurred at intervals of hundreds to thousands of years (Lorimer 1977, Fahey and Reiners 1981). Between approximately 1870 and 1920, large tracts of forest were intensively logged, and severe slash fires followed by heavy soil erosion were common (Chittenden 1905). Public concern led to the

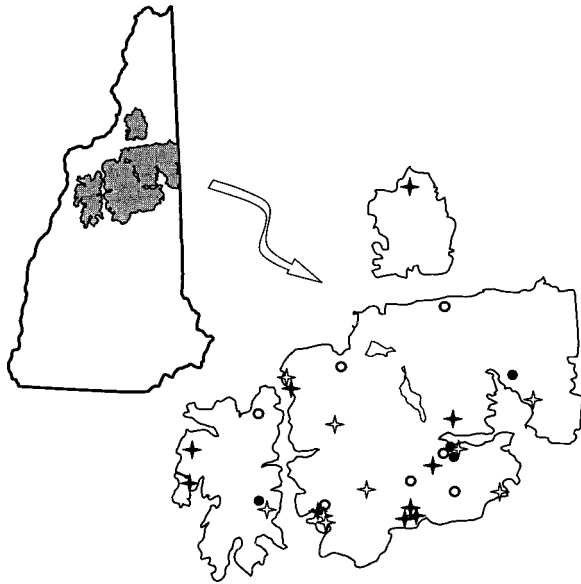


FIG. 1. Map of the White Mountain National Forest, New Hampshire, USA, showing locations of individual sample sites. Symbols are as follows: stars, hardwood stands; circles, conifer stands. Open symbols indicate stands that were historically affected by logging or fire, and closed symbols indicate stands with minimal human disturbance.

Weeks Act in 1911, which allowed federal purchase of the White Mountain National Forest (WMNF), largely as a means of reducing soil erosion and river sedimentation. At present, most of the region has returned to forest, but many areas continue to be harvested as successional forests mature.

When land was purchased for the National Forest, forest surveyors mapped forest type (hardwood, spruce–fir, or subalpine) and condition, making reference to the locations of major disturbances that had occurred. Major categories of forest condition included undisturbed forest, lightly culled, second growth and cutover (both of which indicate large areas of clearcut forest), and burned (which often indicates slash fires that occurred after major cutting activities). Following Goodale and Aber (2001), who found differences in nitrification and soil C:N ratios between old growth and disturbed sites, but not between areas that had been burned vs. those that had been logged, we grouped logged and burned sites into a single class. For stands with minimal human disturbance, we grouped sites determined to be old growth, of which there were relatively few, with plots that were mapped as lightly culled, which represent areas where low-intensity selective cutting occurred. Today, these areas share many structural characteristics with old-growth stands, suggesting that disturbance was either absent or relatively minor compared to the large-scale clearcuts and fires that occurred elsewhere. We refer to this group as “undisturbed” for simplicity, although “undisturbed and minimally disturbed” would be more accurate. In all,

14 plots were undisturbed or minimally disturbed (10 hardwood and four conifer) and 16 plots had been heavily disturbed by logging and/or fire (nine hardwood and seven conifer).

Field sample collection and analysis

Soils.—Net rates of N mineralization and nitrification were measured using the polyethylene bag method (Nadelhoffer et al. 1983, Pastor et al. 1984) and a combination of field and laboratory incubations. The widespread distribution of plots in remote locations prevented us from conducting repeat in situ incubations on all sites. As an alternative, we used 4-wk laboratory incubations on all plots, and on a subset of 10 plots we conducted annual measurements using successive field incubations.

Following the results of Zak et al. (1989) and Carlyle et al. (1998), we anticipated that within plots where both lab and annual field incubations were performed, a correlation between the two would provide confidence that the laboratory method adequately captured spatial variability and would allow estimation of annual cycling rates on all 30 plots. A similar data set collected for a related study at the Bartlett Experimental Forest in the central White Mountains allowed us to expand this comparison from 10 to 24 plots (Goodale and Aber 2001; S. V. Ollinger, unpublished data). All groups of plots (Bartlett, WMNF field, and WMNF lab) contain all major forest types included in this study.

For plots where annual N cycling measurements were made, soils were incubated in situ for 5–6 wk periods throughout the 1998 growing season, with one overwinter incubation from October 1998 to May 1999. Two plots were sampled during the 1997 growing season through May 1998. Two other plots that were sampled in both years (1997 and 1998) revealed little between-year variation, so we included the 1997 plots in the present analysis. For each incubation, net N mineralization and net nitrification were determined as the increase in $\text{NH}_4^+\text{-N}$ plus $\text{NO}_3^-\text{-N}$ (mineralization) or $\text{NO}_3^-\text{-N}$ (nitrification) relative to an initial soil core, taken from alongside the incubated core. Soil cores were 6 cm in diameter and included the organic horizon plus the top 10 cm of mineral soil, unless restricted by impenetrable soil material or bedrock. Within each 0.1-ha plot, five subplots were established and, for each sample period, three cores were incubated at each subplot, making a total of 15 soil cores per plot.

For laboratory incubations, samples were collected during mid-July using the same plot design and sampling methods as used for annual measurements, but soil cores were incubated for 4 wk in the laboratory at $\sim 22^\circ\text{C}$ before KCl extraction and chemical analysis. A limitation of the buried-bag method is that core moisture contents remain constant throughout the incubation period, whereas moisture levels in natural soils typically fluctuate. We attempted to avoid the potential bias of extreme conditions by sampling when soils were

moist but not saturated (not within two days of a hard rainfall event).

After collection (initial samples) or incubation (field- and lab-incubated samples), we separated samples into organic and mineral horizons, homogenized and composited by subplot. We then extracted ~10 g of each sample in 1 mol/L KCl for 48 h. A subsample was oven-dried at 105°C for determination of soil moisture contents. Soil extracts were filtered and analyzed for NH_4^+ and NO_3^- on a Bran and Leubbe TrAAcs 800 autoanalyzer (Bran & Leubbe, Buffalo Grove, Illinois, USA). Net N mineralization was calculated as the difference between extractable NH_4^+ -N plus NO_3^- -N in the incubated vs. initial samples. Net nitrification was determined similarly, but using extractable NO_3^- -N only. We stress that the buried-bag method measures *net* N transformations, which can vary considerably from *gross* rates because N can be released and assimilated in soils over much shorter intervals than the long duration of soil incubations (e.g., Stark and Hart 1997).

Total carbon and nitrogen contents were determined for both organic and mineral soils using a Fisons CHN Elemental Analyzer (Fisons Instruments, Beverly, Massachusetts, USA). Organic and mineral soil samples were also analyzed for pH in 0.02 mol/L CaCl_2 . Values presented for all soil variables are plot-level averages. Values presented for N mineralization and nitrification are totals for organic plus mineral soil unless otherwise noted.

Foliar chemistry.—Shotguns were used to obtain upper- and mid-canopy foliage from 3–5 trees each for all dominant and codominant species on a plot. Green foliage samples were obtained in late July to coincide with the peak of the growing season and with overflights of an airborne remote-sensing instrument. Samples were dried (70°C) and ground through a 1-mm mesh sieve and were analyzed for nitrogen and lignin using previously tested methods of near-infrared spectroscopy (McLellan et al. 1991, Bolster et al. 1996).

The relative abundance of each species by fraction of leaf area in the canopy was determined using a camera point-sampling technique developed by Aber (1979) and Smith and Martin (2001). Canopy profiles were obtained by varying the focal plane of a 35-mm camera and recording the presence of foliage by species and position within the canopy. Species abundance values determined in this way were used to weight species' foliar chemistry measurements in calculating plot-level canopy chemistry. Plot-level canopy concentrations of nitrogen and lignin were calculated as the mean of foliar concentrations among all species, weighted by the mass-based fraction of the canopy represented by each. The fraction of species by leaf area was converted to fraction by mass using measured specific leaf weights. We used this method of quantifying canopy composition instead of an approach based on tree basal areas, because the latter approach was found to yield less accurate results in stands with mixed (conifer/hard-

wood) composition. The accuracy of the camera point method was validated against canopy composition measurements obtained directly from leaf litter collections (Smith 2000).

Remote Sensing.—High spectral resolution remote-sensing image data were obtained for the White Mountain region using NASA's Airborne Visible/Infrared Imaging Spectrometer (AVIRIS). The AVIRIS instrument is flown on an ER-2 aircraft at an altitude of 20 000 m and measures upwelling radiance from the solar reflected spectrum in 224 contiguous channels from 0.4 to 2.5 μm , with a spectral resolution of 0.01 μm (Green et al. 1998). On 12 August 1997, we obtained 56 contiguous 10×10 km scenes with a spatial resolution of ~17 m covering the entire White Mountain region under cloud-free conditions. On the ground, foliar chemistry data were collected at 81 plots (using the same methods described in the preceding section) within three days of the AVIRIS overflight. Although image data from the same year as our soil analyses would be ideal, complete coverage could not be obtained in 1998 because of cloud cover. Multiyear foliar chemistry data for a number of plots indicated that between-year differences were minimal, particularly with respect to the degree of spatial variation encountered over the region (Smith 2000).

AVIRIS at-sensor radiance data were transformed to apparent surface reflectance using the ATREM model (Gao et al. 1992). After geometric registration, AVIRIS reflectance spectra for 2×2 pixel areas covering each sample plot were extracted. Reflectance spectra were converted to absorbance prior to calibration in order to linearize spectral response to chemical constituent concentration. A first-order derivative transformation was then applied to each absorbance spectrum in order to resolve overlapping spectral peaks and to remove baseline offsets, caused by varying sun-sensor-target geometry over the study area (Hruschka 1987).

Partial least squares (PLS) regression was used to relate AVIRIS spectral response to canopy chemistry data for each sample stand. PLS regression methods reduce the full spectrum data to a smaller set of independent latent variables, or factors, with the constituent concentration data used directly during the spectral decomposition process (Shenk and Westerhaus 1991). As a result, full-spectrum wavelength loadings for significant PLS factors, from which regression coefficients are derived, are directly related to constituent concentration, and thus describe the spectral variation most relevant to the modeling of variation in the chemical data.

RESULTS

Soil N transformations

At plots where net N mineralization and net nitrification were measured using both lab incubations and successive field incubations, there was a strong cor-

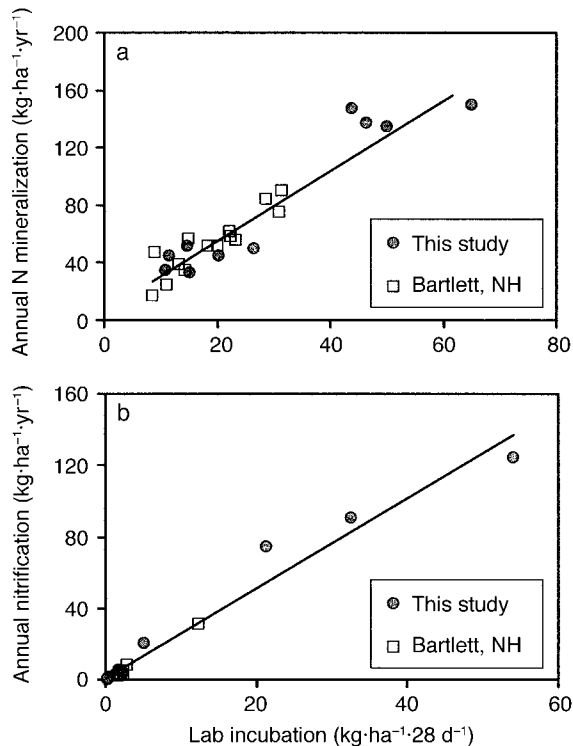


FIG. 2. Comparison of annual field-measured ($\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and lab-incubated ($\text{kg N}\cdot\text{ha}^{-1}\cdot 28 \text{ d}^{-1}$) rates of (a) net N mineralization and (b) net nitrification. The mineralization relationship is described by $N_{\text{min}}(\text{annual}) = 2.44 \times N_{\text{min}}(\text{lab}) - 5.94$ ($R^2 = 0.88$). The nitrification relationship is $N_{\text{itr}}(\text{annual}) = 2.52 \times N_{\text{itr}}(\text{lab}) + 0.60$ ($R^2 = 0.96$).

relation between the two methods (Fig. 2). Similar results were obtained from a related study at the Bartlett Experimental Forest located in the central White Mountains of New Hampshire, USA (Goodale and Aber 2001; S. V. Ollinger, *unpublished data*). Together, these relationships indicate that lab incubations were a good measure of relative N cycling across the study area and are reliable in estimating annual rates. Because annual rates are more easily compared to results published elsewhere, we used these trends to extrapolate lab incubation data to annual N transformation rates and will refer to these values throughout the remainder of this paper. Relationships reported between soils and other variables (e.g., foliage) are qualitatively similar using either lab or field N cycling data, given the linear relation between the two.

Across all plots, mean annual net N mineralization ranged from 32.0 to 162.2 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Table 1). In general, mineralization was lowest on plots dominated by red spruce or hemlock and highest in northern hardwood-dominated plots, although considerable variation was observed in both groups. Net nitrification ranged from near zero to 135.9 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, or 0–84% of N mineralized, and was strongly related to net N min-

eralization ($R^2 = 0.77$, $P < 0.001$ for log-transformed nitrification vs. N mineralization; Fig. 3).

Within soils, net N mineralization and net nitrification were related to soil C:N ratios (calculated as total soil N to total soil C across organic and mineral horizons; Fig. 4), but the relationship was stronger for nitrification than for mineralization. For both mineralization and nitrification, the observed trends were fit with exponential functions (net N mineralization, $N_{\text{min}} = 277 \times \exp[-0.0057 \times \text{soil C:N}]$, $R^2 = 0.51$, $P < 0.001$; net nitrification, $N_{\text{itr}} = 1996 \times \exp[-0.2343 \times \text{soil C:N}]$, $R^2 = 0.73$, $P < 0.001$), but both could also be described as linear below a threshold C:N ratio of ~ 22 . Above this threshold, net nitrification remained at or close to zero. It is worth noting that forest floor C:N ratios are typically somewhat higher than those of mineral soil (Table 1); if we consider forest floor material only, the threshold C:N ratio increases to ~ 24 , which is in agreement with a number of other studies (McNulty et al. 1991, Emmett et al. 1998, Lovett and Reuth 1999, Goodale and Aber 2001).

Trends between C:N ratios and N cycling variables were significant within both organic (O) and mineral (M) soil horizons (Table 2). Although the relationships had higher R^2 values within mineral horizons (e.g., C:N-M vs. $N_{\text{min}}\text{-M}$ > C:N-O vs. $N_{\text{min}}\text{-O}$), organic C:N ratios showed better overall correlations with all four N cycling terms ($N_{\text{min}}\text{-O}$, $N_{\text{min}}\text{-M}$, $N_{\text{itr}}\text{-O}$, $N_{\text{itr}}\text{-M}$). Soil C:N ratios were also related to soil pH, although the relationship was stronger in organic than mineral horizons (Table 2). Soil pH was not related to net N mineralization in either horizon, and was only weakly related to net nitrification in the organic horizon.

Within hardwood-dominated plots, there were significant differences in N cycling rates between plots with different disturbance histories (Fig. 5a; differences in mean values were tested with one-way ANOVA at $P < 0.05$). Plots that were undisturbed had significantly higher rates of net N mineralization and net nitrification and slightly, but significantly, lower soil C:N ratios than heavily disturbed sites. For undisturbed sites, net N mineralization and net nitrification averaged 121.3 and 58.6 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, respectively, whereas soil C:N ratios averaged 17.8. For disturbed sites, net N mineralization and net nitrification averaged 77.2 and 17.4 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, respectively, whereas soil C:N ratios averaged 20.0. It should be noted that we did not control for differences between sites other than disturbance history and forest type. Although all hardwood stands were located on well-drained till soils that typically support northern hardwood forest communities, variation in factors such as soil texture or mineralogy could explain some of the observed differences in N cycling. However, it is noteworthy that N mineralization rates on undisturbed plots showed relatively little variation, whereas disturbed plots had consistently lower values and exhibited much greater variability.

TABLE 1. Site characteristics, foliar chemistry, and soil properties of 30 plots in the white Mountain National Forest, New Hampshire, USA.

Study sites			Foliar chemistry [‡]		Soil C:N ratios [§]			
Plot	Species [†]	History	N (%)	Lignin (%)	Forest floor		Mineral	
					Mean	1 SE	Mean	1 SE
10	SM	select cut	2.35	19.09	16.5	1.16	13.4	0.31
14	SM	select cut	2.13	18.69	17.2	1.52	15.6	1.87
7	SM	uncut	2.27	19.28	18.1	0.70	16.0	0.78
6	SM/AB	select cut	2.13	21.13	18.7	0.90	15.6	0.70
5	SM/AB	select cut	1.87	20.42	18.6	0.18	17.7	0.11
13	AB/SM/PB	uncut	21.2	0.89	18.2	0.70
12	AB/SM	uncut	20.4	0.79	17.5	0.93
9	AB/YB	uncut	2.13	23.82	17.9	0.05	19.6	0.38
11	AB/SM/PB	uncut	19.3	0.39	19.3	0.53
8	AB	select cut	2.36	23.02	23.3	0.74	20.2	1.28
29	SM	heavy logging	2.10	17.9	15.9	0.31	13.1	0.41
26	AB/YB	logged/burned	2.21	25.37	20.0	0.77	16.5	0.30
24	SM/PB	heavy logging	2.28	18.41	20.7	0.50	18.6	0.99
21	SM/AB	logged/burned	1.77	17.82	21.2	0.37	19.1	0.98
23	PB/AB	burned	2.28	21.12	20.6	0.37	19.8	0.79
25	RM/AB	heavy logging	2.27	21.59	21.4	1.07	20.4	0.85
20	RM/AB/PB	heavy logging	1.61	20.14	23.4	0.71	20.1	0.49
22	SM/YB	heavy logging	2.01	21.93	22.7	1.28	21.4	1.16
27	AB/RM	logged/burned	1.72	22.79	25.1	1.04	23.9	1.70
3	RS	select cut	1.38	23.18	23.1	0.96	22.6	0.58
2	EH	uncut	1.22	15.97	28.8	1.09	26.6	1.36
4	RS	select cut	1.49	25.75	31.9	1.00	27.0	1.52
1	RS	select cut	1.17	23.96	34.6	1.25	35.3	1.93
30	BF	heavy logging	1.75	23.62	20.7	1.78	21.0	0.97
19	BF/RS	heavy logging	1.54	23.59	22.6	1.61	20.5	0.83
28	BF/RS	heavy logging	1.54	24.07	23.2	1.81	22.9	1.25
15	RS/EH	heavy logging	0.98	22.03	28.9	2.24	22.5	1.93
16	EH/RS	logged/burned	1.05	19.87	33.2	0.91	29.1	1.85
18	RS	burned	1.33	24.07	35.8	1.54	30.7	1.29
17	RS/EH	logged/burned	1.1	22.65	41.1	0.82	31.9	1.53

Note: Ellipses (...) indicate that data are not available.

[†] Species abbreviations are: AB, American beech; BF, balsam fir; EH, eastern hemlock; PB, paper birch; RM, red maple; SM, sugar maple; RS, red spruce; and YB, yellow birch.

[‡] Foliar nitrogen and lignin values are mass-based concentrations.

[§] Ratios are given for the forest floor, top 10 cm of mineral soil, and the total for organic plus mineral soil. Values are plot-level means and standard errors.

|| Annual N cycling rates were calculated by combining measured data from 28-d laboratory incubations with the relationship between lab and annual values shown in Fig. 2. Values are plot-level means and standard errors.

¶ Values are plot-level means and standard errors.

Within conifer-dominated stands, disturbance effects were the reverse of those observed in hardwoods; net N mineralization and net nitrification rates were higher in stands that had been disturbed than in those that had not (Fig. 5b). However, our sample size for undisturbed conifers was small ($n = 4$) and these differences were not significant. Soil C:N ratios were nearly identical between the two groups, averaging 28.6 and 28.1 in undisturbed and disturbed sites, respectively.

Foliar chemistry and soil N status

Mass-based canopy nitrogen concentrations ranged from 1.61% to 2.36% in hardwood-dominated stands and from 0.98% to 1.75% in conifer-dominated stands (Table 1). Lignin concentrations were 17.82–25.38% in hardwood stands and 15.97–25.75% in conifer stands. Conifer stands typically had higher lignin than deciduous stands, with the exception of plots dominated by eastern hemlock, a species that has much low-

er lignin concentrations than most other conifers. Canopy N concentrations showed a strong linear correlation with soil C:N ratios ($R^2 = 0.65$, $P < 0.001$) and were also related to both net N mineralization and net nitrification. For mineralization, the trend was best fit with a linear regression ($R^2 = 0.54$, $P < 0.001$). For nitrification, the trend was nonlinear and was best fit with regression of log-transformed net nitrification against foliar N concentration ($R^2 = 0.64$, $P < 0.001$).

Relationships between foliar chemistry and nitrification showed significantly different patterns between disturbed and undisturbed sites, with undisturbed sites having higher net nitrification per unit foliar N than previously disturbed sites (Fig. 6). Differences in these trends were tested using regression of log-transformed net nitrification on foliar N concentrations, with inclusion of slope (significant) and intercept (not significant) dummy variables for disturbance history (Table 3). If only hardwood stands were considered, the disturbance

TABLE 1. Extended.

Soil C:N ratio§		N cycling (kg·ha ⁻¹ ·yr ⁻¹)				Soil pH¶			
Total		Net N mineralization		Net nitrification		Forest floor		Mineral soil	
Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE
13.6	0.32	162.2	21.8	135.9	15.2	3.86	0.03	3.62	0.04
16.3	1.66	111.6	14.0	34.0	7.6	4.64	0.08	4.46	0.07
16.5	0.57	126.1	22.3	82.2	5.2	3.72	0.11	3.78	0.16
16.5	0.40	143.1	42.3	78.8	25.8	4.03	0.28	4.08	0.12
17.9	0.12	101.7	13.3	34.8	11.0	3.65	0.07	3.65	0.06
18.6	0.61	122.2	23.8	20.7	4.2	3.36	0.04	3.71	0.12
18.9	0.85	122.0	11.9	31.9	6.5	3.31	0.06	3.64	0.06
19.2	0.25	111.2	8.8	54.1	6.7	3.21	0.04	3.51	0.11
19.3	0.39	110.8	6.8	36.8	7.3	3.37	0.04	3.60	0.08
21.4	1.21	102.2	9.5	27.1	9.7	3.44	0.10	3.46	0.07
13.5	0.37	74.8	11.0	29.1	2.1	4.75	0.13	4.64	0.13
18.2	0.56	51.3	15.1	16.5	5.6	3.81	0.09	3.78	0.05
19.1	0.86	69.6	11.7	13.7	1.6	3.56	0.05	3.93	0.05
19.9	0.69	69.5	10.9	6.2	3.5	3.41	0.06	3.72	0.17
20.2	0.50	117.4	9.6	13.3	3.9	3.28	0.06	3.32	0.10
21.1	0.86	117.1	11.5	41.2	16.5	3.56	0.04	3.93	0.08
21.8	0.58	33.4	7.3	1.9	16.8	3.68	0.18	3.85	0.18
22.0	0.99	92.9	7.3	30.7	6.7	3.35	0.07	3.51	0.11
24.2	0.78	68.7	11.8	3.4	2.4	3.68	0.14	4.04	0.15
22.9	0.74	41.5	9.0	9.1	3.0	3.22	0.09	3.05	0.05
28.2	1.09	47.3	14.4	3.4	0.2
30.2	0.39	54.5	14.2	1.5	0.9	3.03	0.04	3.40	0.11
33.0	1.26	47.7	13.4	0.2	0.4
21.0	1.63	114.7	8.2	48.2	2.1	3.37	0.05	3.39	0.10
22.1	1.35	117.0	16.5	20.3	7.9	3.22	0.12	3.54	0.19
23.0	1.56	82.2	17.3	2.9	2.1	3.33	0.07	3.09	0.04
26.1	1.96	42.6	10.1	1.6	2.1	3.22	0.03	3.34	0.03
31.8	1.39	42.4	6.9	1.5	60.7	3.14	0.05	3.50	0.12
34.8	1.40	47.9	9.1	1.1	1.7	2.75	0.04	3.27	0.18
36.0	0.96	32.0	7.9	1.4	1.1	2.64	0.04	3.40	0.21

interaction increased the regression R^2 from 0.51 to 0.70 over using foliar nitrogen alone, indicating that differences in net nitrification between disturbance treatments were not clearly reflected in foliar N concentrations. Foliar nitrogen was the best predictor of net nitrification among conifers (Table 3), although our sample set for conifer stands was limited and nitrification was generally much lower than in hardwood stands.

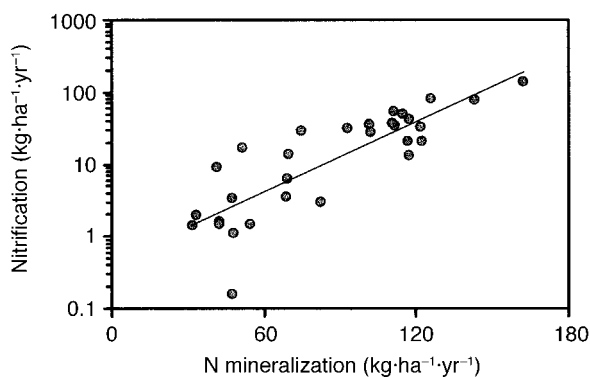


FIG. 3. Net nitrification (shown on a log scale) in relation to net N mineralization ($R^2 = 0.77$, $P < 0.001$).

Relationships between foliar chemistry and net N mineralization showed differences across disturbance treatments similar to those seen for net nitrification, and also differed between coniferous and deciduous forests, with conifers having lower foliar N concentrations at a given mineralization rate than did hardwoods (Table 3). Foliar lignin was not related to N mineralization, but was weakly correlated with soil C:N ratios ($R^2 = 0.13$, $P = 0.06$), and the lignin:N ratio improved the fit slightly over using foliar N alone (R^2 increased from 0.65 to 0.72; Fig. 7). Although soil C:N ratios differed between undisturbed and disturbed stands, there were no differences in the relationships with foliar nitrogen or lignin:N ratios, suggesting that disturbance effects on C:N ratios were reflected in foliar chemistry. Nevertheless, differences in plot-level foliar N concentrations between disturbance regimes were relatively small and not significant. Among hardwoods, foliar N averaged 2.18% in undisturbed stands and 2.04% in disturbed stands, but again, this difference was not significant. That foliar chemistry appeared to capture disturbance effects on C:N ratios, but not net N mineralization or net nitrification, may stem from the small magnitude of change in C:N ratios and the nonlinearity of trends in N cycling, especially nitrifi-

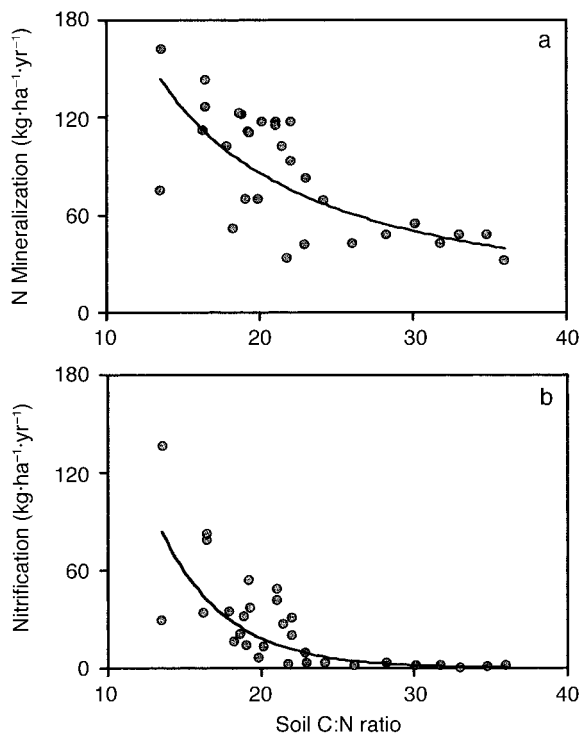


FIG. 4. Soil C:N ratios (forest floor plus top 10 cm mineral soil) in relation to (a) net N mineralization and (b) net nitrification.

cation. Similarly, conifer foliar N averaged 1.32% and 1.35%, respectively, in disturbed vs. undisturbed stands, differences that were not significant.

Species interactions with N cycling and foliar chemistry

Another factor to consider in explaining variability surrounding trends between N cycling and foliar chemistry is the concurrent effect of species composition,

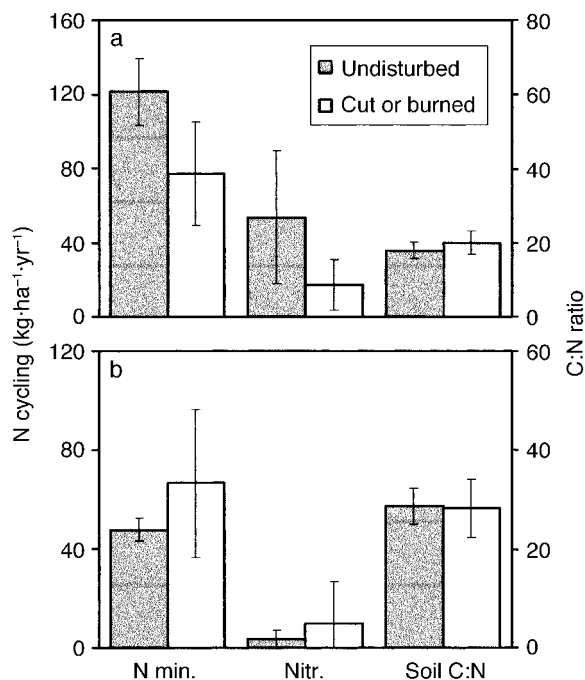


FIG. 5. Comparison of mean values (± 1 SD) for net N mineralization ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), net nitrification ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), and soil C:N ratios between undisturbed (old-growth or lightly culled) and disturbed (heavily logged and/or burned) stands for (a) deciduous and (b) coniferous forests.

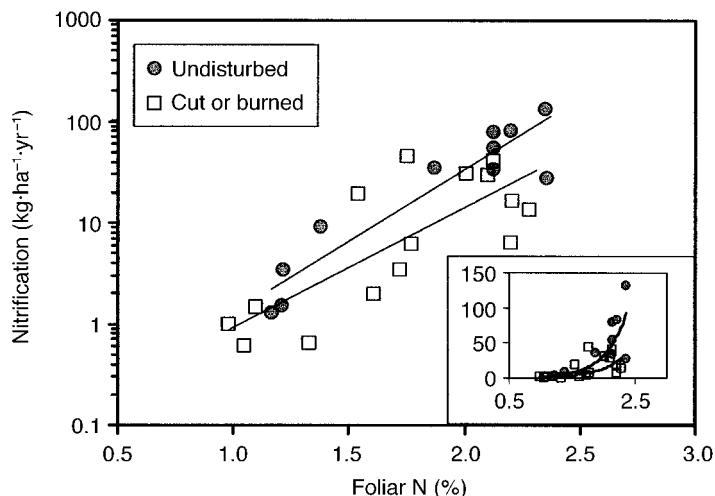
which normally changes over the course of succession and, in our study, differed between disturbed and undisturbed sites (Table 4). Among deciduous forests, disturbed stands had greater overall canopy diversity than undisturbed stands, with mixtures of sugar maple and beech, early- to mid-successional species such as paper birch and red maple, and a small presence of conifers. In undisturbed deciduous stands, overall canopy diversity was lower, conifers were less abundant, and sugar maple and/or beech had become dominant.

TABLE 2. Correlation matrix for relationships within and between organic (O) and mineral (M) soil horizons among net N mineralization (Nmin), net nitrification (Nitr.), soil C:N ratios (CN), and soil pH.

Variable	Nmin-M	Nmin-O	Nitr.-M	Nitr.-O	CN-M	CN-O	pH-M
Nmin-O	NS						
Nitr.-M	+0.89 (<0.001)	NS					
Nitr.-O	+0.59 (0.001)	+0.55 (0.003)	+0.77 (<0.001)				
CN-M	-0.67 (<0.001)	NS	-0.73 (<0.001)	-0.53 (0.004)			
CN-O	-0.85 (<0.001)	-0.33 (0.05)	-0.83 (<0.001)	-0.59 (0.001)	+0.92 (<0.001)		
pH-M	NS	NS	NS	NS	-0.57 (0.002)	-0.50 (0.015)	
pH-O	NS	NS	+0.36 (0.05)	+0.39 (0.05)	-0.79 (<0.001)	-0.71 (<0.001)	+0.85 (<0.001)

Note: Data are correlation coefficients (r values), with P values below in parentheses; NS indicates that correlations are not significant at $P < 0.05$.

FIG. 6. Net nitrification in relation to mass-based foliar N concentrations for disturbed and undisturbed stands. The relationship is shown on a log scale because of the nonlinear response of nitrification (see inset). The trends are described by $\log(\text{NO}_3) = 2.75(\text{foliar N}) - 2.96$ ($R^2 = 0.81$, $P < 0.001$) for undisturbed stands and $\log(\text{NO}_3) = 2.94(\text{foliar N}) - 4.28$ ($R^2 = 0.63$, $P < 0.001$) for disturbed stands.



These differences are important because there were significant relationships between N cycling and the abundance of some tree species in the canopy, with sugar maple in particular showing a significant positive correlation with net N mineralization and net nitrification and a negative correlation with soil C:N ratios (Table 5). Because sugar maple abundance is related to disturbance history, it is difficult to assess whether trends in soil properties reflect the singular effects of one of these factors or are the result of an interaction between the two, i.e., whereby disturbance alters the length of time over which a particular plant-soil feedback can occur. However, an analysis for deciduous

stands using stepwise linear regression of log-transformed net nitrification against foliar nitrogen, percentage of sugar maple in the canopy, and disturbance history interaction terms (slope and intercept dummy variables) indicated that disturbance history explained a greater amount of variation than did sugar maple abundance, which was not significant in the combined regression ($R^2 = 0.70$; Table 3), but was significant when the disturbance interaction variables were left out. This does not mean that variation in net nitrification is caused solely by direct disturbance effects, irrespective of associated changes in species composition, but it does suggest that there is at least some

TABLE 3. Stepwise regression results showing best-fit predictions of soil N variables against foliar chemistry along with dummy variables for disturbance history (0, undisturbed; 1, disturbed) and forest type (0, hardwood; 1, conifer) to test for differences in slope and intercept.

Plot type and measurement	Foliar chemistry		Disturbance		Forest type		R^2 †
	% N	Lignin/N	Slope	Intercept	Slope	Intercept	
All plots							
Soil C:N ratio		1.212 (<0.001)					0.71 (<0.001)
N mineralization	86.760 (<0.001)		-11.421 (0.026)		21.053 (0.044)		0.68 (<0.001)
Nitrification (log)	2.372 (<0.001)			-1.003 (0.016)			0.73 (<0.001)
Hardwoods							
Soil C:N ratio		1.320 (0.040)					0.47 (0.040)
N mineralization	64.667 (0.029)			-35.381 (0.02)			0.63 (0.002)
Nitrification (log)	2.556 (0.008)		-1.220 (0.01)				0.70 (<0.001)
Conifers							
Soil C:N ratio	-14.52 (0.040)						0.40 (0.040)
N mineralization	96.392 (0.003)						0.63 (0.003)
Nitrification (log)	3.700 (0.021)						0.52 (0.021)

Note: Data are coefficients for each variable that was significant at $P < 0.05$, with P values given in parentheses below.

† Overall regression R^2 values and associated P values in parentheses below.

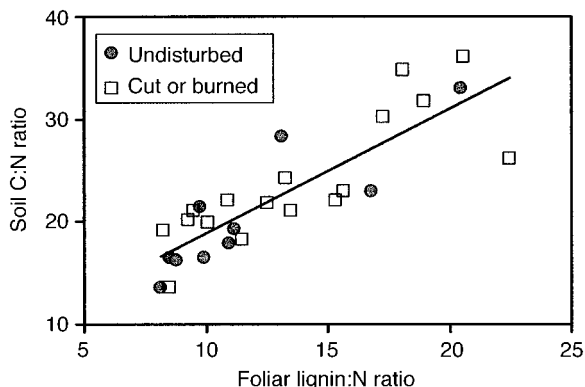


FIG. 7. Soil C:N ratios (organic plus mineral) in relation to mass-based foliar lignin:N ratios. The relationship is described by $\text{Soil C:N} = 1.2118(\text{foliar lignin:N}) + 6.7717$ ($R^2 = 0.72$, $P < 0.001$). Lignin:N ratios explained only slightly more variation than foliar N concentrations alone, which produced a regression R^2 value of 0.65.

effect of disturbance that is not also explained by the increase in sugar maple.

Other species whose abundance in the canopy was correlated with soil characteristics were red spruce and balsam fir. Red spruce was inversely related to net N mineralization and net nitrification, and positively related to soil C:N ratios (Table 5). Trends for balsam fir were opposite those of red spruce, being positively related to net N mineralization and net nitrification and negatively related to soil C:N ratio. Although net nitrification was generally low among conifer stands, ranging from near zero to ~24% of N mineralized (Table 1), the percentage of the canopy occupied by balsam fir was a strong correlate of log-transformed nitrification rates, explaining 51% of the observed variation within conifer stands ($R^2 = 0.51$, $P < 0.04$). Because balsam fir also had the highest foliar N concentration among conifers, these trends were reflected in patterns of foliar chemistry (Table 3).

Foliar N concentrations also exhibited interesting trends within and between species. For sugar maple, red maple, American beech, and yellow birch, but not paper birch, foliar N increased with increasing N min-

eralization. Further, these trends showed distinct differences between species (Fig. 8a). Yellow birch had the highest foliar N concentrations, followed by American beech, red maple, and sugar maple. These trends were pronounced enough that sugar maple and red maple growing on rich sites often had foliar N concentrations similar to those of birch and beech on poorer sites. In addition, although there were no differences in plot-level foliar chemistry across disturbance treatments, there were differences within individual species. Sugar maple and beech both had significantly lower foliar N concentrations in disturbed than undisturbed stands (one-way ANOVA at $P < 0.05$). Foliar N concentrations for red maple, yellow birch, and paper birch also tended to be lower on heavily disturbed sites, but differences were not significant.

In contrast to the patterns observed among hardwoods, there were no significant trends between foliar N and net N mineralization for individual conifer species (Fig. 8b). Hemlock foliage was collected along a relatively small N-cycling gradient, but additional data from a related study (S. V. Ollinger, unpublished data) show no change in foliar N along a greater range of N-cycling rates.

Remote detection of canopy chemistry and soil C:N ratios

Previous remote-sensing analyses have demonstrated that high spectral resolution data can be used to estimate nitrogen and lignin concentrations in forest canopies (Wessman et al. 1988, Martin and Aber 1997). Using Partial Least Squares regression (PLS), we obtained a two-factor calibration equation relating AVIRIS spectral data to measured canopy lignin:N ratios from 81 plots across the White Mountain study area. The equation had a calibration R^2 of 0.69 and a standard error of calibration (SEC) of 2.3, or 16.7% of measured lignin:N ratios from Table 1. This level of accuracy is within that required to detect important spatial patterns over the range of canopy chemistry values experienced (Schimel 1995). Although greater calibration accuracy has been achieved for single remote-sensing scenes covering relatively small areas, our calibration includ-

TABLE 4. Fractional species abundance in the canopies of sample plots by forest type and disturbance history.

Stand type and history	Conifer species			Hardwood species					
	BF	EH	RS	AB	PB	RM	SM	YB	Other
Hardwood stands									
Undisturbed	0.00	0.00	0.05	0.30	0.03	0.03	0.47	0.08	0.04
Cut/burned	0.02	0.07	0.02	0.16	0.15	0.12	0.28	0.11	0.08
Conifer stands									
Undisturbed	0.09	0.25	0.49	0.01	0.05	0.07	0.00	0.01	0.03
Cut/burned	0.26	0.12	0.42	0.01	0.08	0.04	0.02	0.04	0.01

Notes: Species abbreviations are: AB, American beech; BF, balsam fir; EH, eastern hemlock; PB, paper birch; RM, red maple; SM, sugar maple; and YB, yellow birch. Other species that occurred at low frequencies included white ash, mountain ash, and striped maple.

TABLE 5. Regression coefficients (Coeff.), *P*, and *R*² values for relationships between species abundance in the canopy and soil C:N ratio (forest floor plus mineral soil), net N mineralization, and net nitrification (measured in kg·ha⁻¹·yr⁻¹) for three species that exhibited significant trends across hardwood (sugar maple) and conifer (red spruce and balsam fir) plots sampled.

Nitrogen measurement	Sugar maple (<i>n</i> = 12)			Red spruce (<i>n</i> = 10)			Balsam fir (<i>n</i> = 8)		
	Coeff.	<i>P</i>	<i>R</i> ²	Coeff.	<i>P</i>	<i>R</i> ²	Coeff.	<i>P</i>	<i>R</i> ²
C:N ratio	-14.69	0.01	0.62	10.75	0.08	0.29	-18.03	0.02	0.46
Net N mineralization	82.323	0.04	0.35	-83.356	0.03	0.43	107.665	0.03	0.51
log(Net nitrification)	3.757	0.01	0.53	-3.604	0.09	0.34	4.376	0.05	0.51

ed 36 of the 56 scenes that cover the entire White Mountain region.

The ability to detect canopy lignin:nitrogen ratios with a reasonable level of accuracy allowed us to extend the relationship in Fig. 7 to estimate spatial patterns of soil C:N ratios across the White Mountain region (Fig. 9). Although 20 of the 30 plots used in this study were also sampled for foliar chemistry image calibration, the remaining 10 provide some means of assessing prediction accuracy against independent data. Comparison of AVIRIS-predicted vs. measured values (Fig. 10) for these plots showed generally good agree-

ment, with a standard error of prediction of 2.34, or 12.8% of observed C:N ratios, but suggested a tendency toward overprediction at the low end of the range. Although we do not consider this small validation exercise to be adequate for such a large region, it does provide some confidence that hyperspectral image data can be used to detect important spatial variability in soils through related patterns in canopy chemistry.

Fig. 11 shows the distribution of predicted values over the White Mountain region, indicating that ~63% of the area is predicted to fall below 22, the observed threshold for net nitrification. Below this, we expect increasing, but variable, rates of nitrification depending on additional factors such as disturbance history and species composition, and perhaps others that we have not addressed (e.g., soil mineralogy; Hornbeck et al. 1997). We view these results as preliminary, given the lack of comprehensive validation, and we anticipate that future improvement in image calibration can be achieved by more careful correction for atmospheric effects and within-scene sun-sensor-target geometry effects (Smith 2000).

DISCUSSION

Plant-soil interactions

Across the White Mountain study area, patterns of net nitrification in soils were strongly related to rates of net N mineralization and soil C:N ratios, and these were broadly reflected in forest canopy chemistry. These results are consistent with previous analyses of N cycling and leaf chemistry (most of which have come from the western and mid-western United States) in demonstrating the coupled nature of carbon-nitrogen interactions between forest canopies and soils (e.g., Wessman et al. 1988, Scott and Binkley 1997, Ferrari 1999), but differ in that foliar nitrogen but not lignin showed a greater degree of connection with soil N status. This could stem from differences between the chemistry of leaf litter, which has been the focus of many prior analyses, and that of whole-canopy green foliar chemistry, which we have examined here to evaluate its potential use as an indicator of ecosystem nitrogen status.

Our results also show that variation surrounding relationships between foliar chemistry and N cycling is

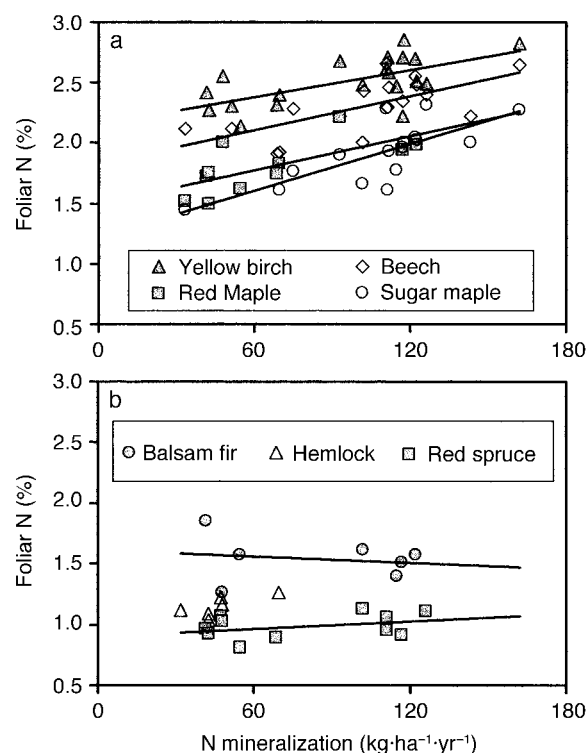


FIG. 8. Mass-based foliar N concentrations for individual species within (a) deciduous and (b) coniferous forests in relation to net N mineralization rates for plots on which they were sampled. Relationships were significant at *P* < 0.05 for all deciduous species except paper birch. Regression *R*² values were 0.42 for yellow birch, 0.49 for American beech, 0.51 for red maple, and 0.57 for sugar maple. Trends were not significant for coniferous species.

related to differences in disturbance history, with previously disturbed hardwood stands having lower N-cycling rates per unit foliar N than stands with minimal prior disturbance. Relationships between foliar chemistry and soil C:N ratios did not show a significant disturbance effect, indicating that foliar chemistry is a good predictor of C:N ratios across forest types and disturbance history gradients. This is due, in part, to the linear nature of foliar chemistry–soil C:N relationships and the relatively small difference in C:N ratios between disturbance regimes. In contrast, net nitrification varied more dramatically between disturbance treatments and increased exponentially with both foliar N concentrations and soil C:N ratios. Despite the relatively strong overall relationship between foliar N and net nitrification, this nonlinearity produces increasing variation at sites with high foliar N concentrations and low C:N ratios (see inset of Fig. 6).

Although distinguishing cause from effect is an inherent problem in studies of plant–soil interactions, trends between net N mineralization and foliar nitrogen concentrations within species suggest that some species are responsive to differences in site quality and that observed patterns of N cycling were not simply due to different combinations of species, each with characteristic and implastic leaf traits. The increase in foliar N concentrations with increasing rates of N mineralization observed for most (but not all) deciduous species is indicative of a positive feedback between plant and soil N status whereby plants respond to increased N availability in such a way that can further increase N cycling rates—by producing foliage with higher N contents, which leads to faster leaf litter turnover, narrower soil C:N ratios, and increased N mineralization (e.g., Hobbie 1992). The higher rate of N mineralization in undisturbed vs. disturbed hardwood stands is probably the result of this feedback being reiterated over longer periods of time than have occurred on heavily disturbed sites. This should emphasize the fact that plant–soil relations are interactive and can lead to changes in both over time.

These patterns should also be considered with respect to changes in species composition because individual species showed distinct patterns of foliar N along N-cycling gradients. Sugar maple was the most dominant late-successional species in deciduous forests among our sample set, and yet it had the lowest foliar N concentration of all hardwood species examined. Based on this alone, we might expect undisturbed stands with high sugar maple abundance to have lower foliar nitrogen, wider soil C:N ratios, and to exhibit lower rates of net nitrification than early-successional hardwood stands. However, sugar maple on undisturbed sites had higher foliar N than sugar maple on disturbed sites, reaching concentrations similar to those of early-successional species growing on disturbed sites with lower N-cycling rates (Fig. 8a). This, along with higher foliar N concentrations in co-occurring spe-

cies (e.g., American beech and yellow birch), led to the small, but not significant, increase in plot-level foliar N in undisturbed stands. The association between sugar maple abundance and net nitrification is consistent with a number of other studies that have linked sugar maple with nitrate production (Finzi et al. 1998, Ferrari 1999, Lovett and Reuth 1999). In our study, we could not identify a direct effect of sugar maple that was separate from that of disturbance history, making it difficult to determine the extent to which our results reflect the singular effects of either factor or an interaction between the two. However, Lovett and Reuth (1999) found higher rates of net nitrification in sugar maple stands than in American beech stands of similar age and soil texture, indicating a significant species effect that did not appear to be related to differences in disturbance history.

In marked contrast to hardwood species, conifers had consistently lower and less plastic foliar N concentrations across relatively wide N cycling gradients. These patterns suggest a different plant–soil interaction for conifers, in which continued low-quality litter inputs can cause N cycling rates to decline over time (e.g., Pastor et al. 1987, Van Cleve et al. 1993). However, the association between balsam fir abundance and elevated net nitrification might represent an exception. Although our sample size was relatively small (balsam fir occurred on eight out of 11 conifer plots sampled) and most conifer stands had low net nitrification, balsam fir abundance was the best overall correlate, explaining 51% of the variation in nitrate production among stands dominated by conifers.

There are at least two possible explanations for the trends observed for balsam fir. The first is that balsam fir has a positive effect on net N mineralization and nitrification, relative to other conifer species with which it coexists (primarily red spruce). Balsam fir does have high foliar N concentrations relative to other conifers (Fig. 8b), and soils under balsam fir tended to have proportionately lower C:N ratios (Table 5). However, balsam fir foliage also has high concentrations of lignin and has previously been associated with inhibition, not stimulation, of nitrification (Olson and Reiners 1983). The second is that balsam fir abundance and net nitrification both reflect some other site property such as the severity or timing of past disturbance. Balsam fir is adapted to growth in disturbed environments, often occurring in upper elevation areas that are characterized by frequent wind damage (Reiners and Lang 1979). Although our plots were at lower to middle elevations where wind stress is less of a factor, balsam fir was more common in plots with a history of disturbance (Table 4). If disturbance leads to conditions that favor elevated N cycling over prolonged periods in these systems, a relationship between N cycling and balsam fir abundance could be observed without implying a causal effect. Sasser and Binkley (1989) studied patterns of nitrogen cycling with stand development

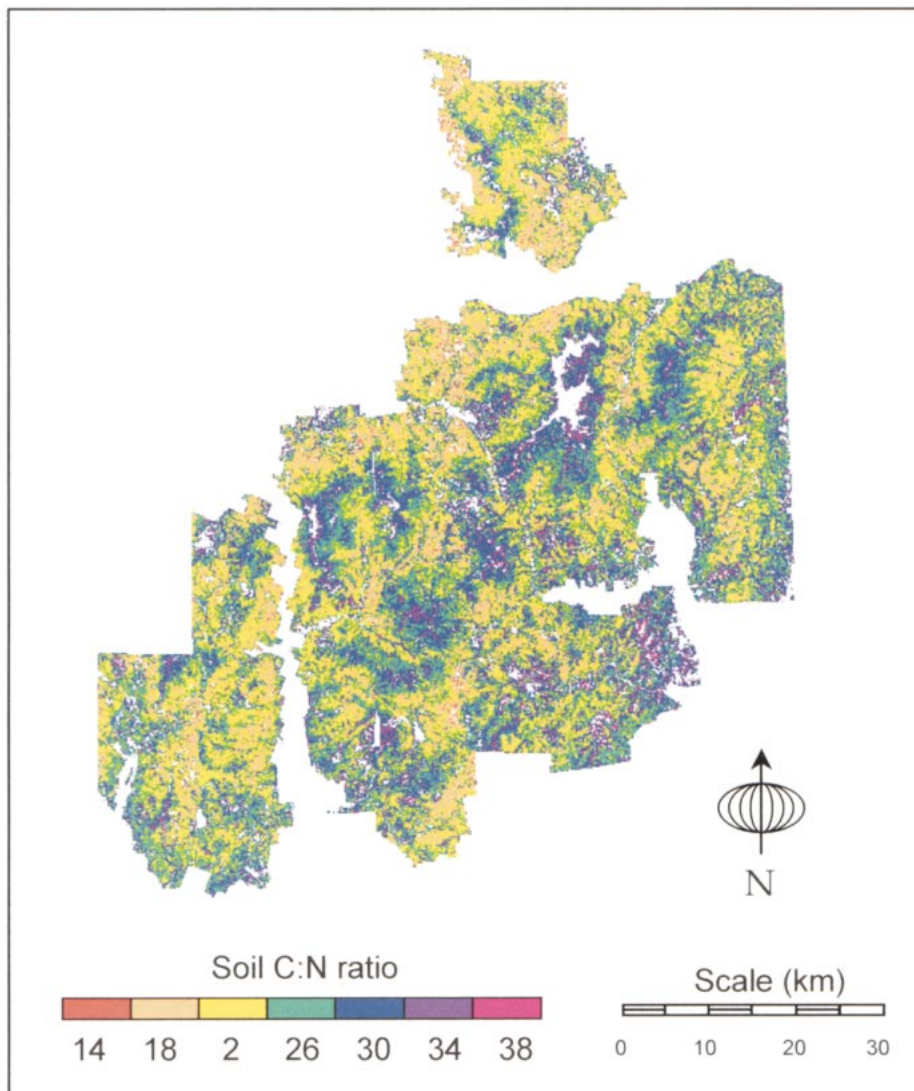


FIG. 9. Predicted soil C:N ratios (organic plus mineral) for the White Mountain National Forest of New Hampshire, USA, derived by combining the trend in Fig. 7 with AVIRIS-estimated foliar lignin:N ratios.

in wind-generated fir waves, and found that nitrification was high following mortality and declined in regenerating stands, but then became elevated again in mature stands. These observations could reflect either possibility, but in combination with our data, they suggest that differences in foliar chemistry–N cycling interactions between red spruce and balsam fir warrant further consideration, particularly when making generalizations about nutrient cycles in spruce–fir forest types.

Disturbance history

Our results support the hypothesis that past disturbance by logging and/or fire has had long-term impacts on N cycling compared to relatively undisturbed stands. Model analyses have suggested that, in the absence of disturbance, maximum rates of N cycling would ultimately be determined by energy or moisture avail-

ability, as they constrain plant growth and N turnover via organic matter inputs (Schimel et al. 1996, Aber et al. 1997). The fact that undisturbed or lightly cut hardwood forests in our study had higher and less variable rates of N cycling may be an indication that these stands have reached such a state. Heavily disturbed hardwood stands, on the other hand, exhibited lower and more variable N cycling rates, presumably reflecting variation in the severity or timing of the disturbances experienced. Although the disturbance effects we observed for conifers were not significant, our data suggest that disturbance may have had the opposite effect on N cycling in conifer stands than among hardwoods, and that this difference stems from inherently different feedbacks between litter quality and N availability. It should also be noted that hypotheses regarding disturbance effects depend on the assumption that distur-

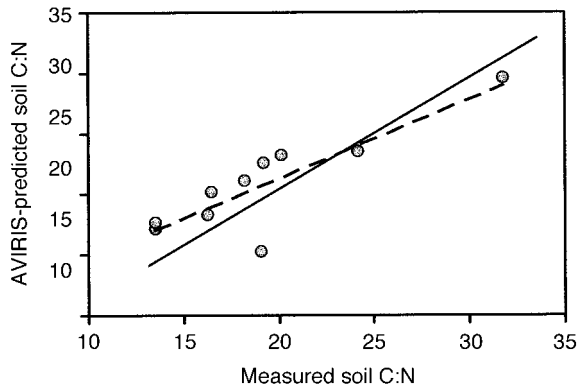


FIG. 10. Soil C:N ratios (organic plus mineral) as predicted from AVIRIS imagery (Fig. 9) in relation to measured values at 10 plots that were not used in AVIRIS foliar chemistry calibrations. The dashed line shows a predicted vs. observed linear regression, and the solid line is the 1:1 relationship.

bance history was the most significant underlying difference between the sites examined in our comparisons. Variation in some other factor such as soil texture or mineralogy could conceivably explain some or all of the observed variation in N cycling. This would be especially true if historical disturbance patterns were related to such site factors, although investigation into the specific histories of our sites suggested that logged stands were selected on the basis of logistical factors such as accessibility or proximity to railroads, rather than to specific properties of the sites themselves. Similarly, burned and unburned sites frequently occurred adjacent to one another at locations with similar slope, aspect, and elevation, but separated by natural fire breaks.

A related analysis of land use history in White Mountain northern hardwoods found results similar to those in this study, with old-growth stands having lower C:N ratios and higher rates of net nitrification than nearby stands that were logged or burned 80–110 yr ago (Goodale and Aber 2001). Mean net N mineralization rates at old-growth sites were nearly identical to those of undisturbed stands in this study ($\sim 120 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), but disturbed stands had higher rates ($110 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) than were observed for disturbed stands in this study ($77 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$). The cause of this difference is unclear, but could be due to differences in either the intensity or timing of disturbance, or to unknown variation in other site factors.

Finally, in contrast to the pattern of increased nitrification with successional status seen in both this study and in Goodale and Aber (2001), a study conducted in the White Mountains by Thorne and Hamburg (1985) found decreasing net nitrification potentials in the forest floor with increasing stand age along a 70-yr, old-field chronosequence. These different patterns of nitrification with succession are probably due to the different forms of disturbance (logging/fire vs. agricul-

ture) and to the different stages of succession examined. The decrease in net nitrification observed by Thorne and Hamburg was related to declines in forest floor pH and N concentration from initial values in young stands that were relatively high for soils of this region (including those recently disturbed by clear-cutting; Johnson et al. 1991), but not uncommon in abandoned agricultural fields (Robertson and Vitousek 1981, Richter et al. 1994). This suggests that agricultural practices caused elevated soil pH and reduced soil C:N ratios, and that the decline in nitrification potential reflected a return to conditions more characteristic of forest soils. Our study did not include agricultural disturbance and, although net nitrification was weakly correlated with forest floor pH, we did not observe a difference in pH between disturbance treatments. The different trends among these studies may also reflect differences in stand age and successional status. Although Thorne and Hamburg (1985) reported on the first ~ 70 yr of succession, our study represented stands in later stages of recovery relative to stands that experienced minimal prior disturbance. Goodale and Aber (2001) suggested that increasing soil C:N ratios in early succession could result from faster accumulation of soil carbon relative to nitrogen, whereas declining C:N ratios during late succession may stem from reduced N demand by vegetation or by age-related declines in productivity and litter production.

Collectively, these results suggest that different patterns of nitrogen cycling with ecosystem development during secondary succession can result from differences in the nature or timing of the disturbance experienced and from differences in the dominant plant-soil feedbacks that exist during forest regrowth. These differences can lead to contrasting conclusions regarding disturbance effects in forests, and so should be carefully considered before making generalizations

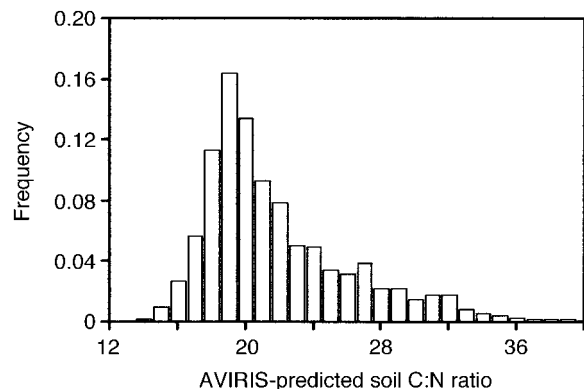


FIG. 11. Distribution of predicted soil C:N ratios across the White Mountain National Forest. Approximately 63% of the region contains predicted values below 22, the observed threshold for net nitrification. Below that value, we expect increasing, but variable, net nitrification rates, depending on disturbance history, species composition, and perhaps other factors that are not reflected in foliar chemistry.

about patterns of nutrient cycling during stand development.

Remote detection of canopy chemistry and regional ecological analysis

Early work with hyperspectral remote sensing held much promise for its role in analyses of ecosystem biogeochemistry (Wessman et al. 1988). Although there have been significant improvements in detector technology and application techniques since that time (e.g., ACCP 1994, Asner 1998), its use has been relatively limited, owing, in part, to the limited availability of hyperspectral data and the large data-processing requirements. Nevertheless, interest in the approach has persisted, or even grown, as a result of the increasing scientific importance of terrestrial carbon and nitrogen cycles (e.g., Schimel 1995), leading to development of new hyperspectral sensors for orbital platforms (e.g., NASA's Hyperion sensor aboard the New Millennium Program EO-1 satellite platform).

Although previous hyperspectral analyses have been limited to single remote-sensing scenes covering relatively small areas, here we have shown that applications across large, multi-scene landscapes are also possible. That the observed relationship between foliar chemistry and soil C:N ratios was consistent across a range of conditions suggests that patterns of soil C:N ratios across complex forested landscapes can be reliably characterized by patterns of canopy chemistry. A number of studies in both Europe and North America have identified soil C:N ratios as a key ecological variable; several, in addition to this study, have identified C:N ratios of between 22 and 24 as a critical threshold for the onset of net nitrification or nitrate leaching (McNulty et al. 1991, Emmett et al. 1998, Lovett and Reuth 1999, Goodale and Aber 2001). In addition, Aitkenhead and McDowell (2000) showed that soil C:N ratios are a strong predictor of freshwater dissolved organic carbon flux at both local and global scales. Although our analysis also indicates that information regarding disturbance history or species composition will be needed before we can make precise estimates of soil N transformations across large landscapes, the ability to detect spatial patterns of foliar chemistry and soil C:N ratios represents a useful step toward conducting regional biogeochemical analyses.

Although high spectral resolution remote sensing is not likely to replace more conventional sensors that provide data over larger areas and at greater frequencies, continued development of the approach that we have applied here stands to benefit regional analyses by making it possible to derive spatially explicit data that could not be attained through even the most ambitious field campaign nor through conventional remote sensing. If such efforts incorporate rigorous field analyses, they can even complement broader scale, coarser resolution sensors by providing a much-needed bridge

between kilometer-scale grid cells and plot-based field measurements.

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