DIVISION S-3—SOIL BIOLOGY & BIOCHEMISTRY

Landscape Patterns of Net Nitrification in a Northern Hardwood-Conifer Forest

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ABSTRACT

The production of NO_3^- in forest soils is an important process influencing the form of N available for plant uptake and the potential for off-site N losses. We sampled mineral and organic soil horizons in 100 plots distributed across a 3160-ha hardwood-conifer forest in central New Hampshire to examine patterns of net nitrification rate (NR) and NO_3^- concentration associated with physiographic features and vegetation abundances. Net NR and NO_3^- concentrations each varied by a factor of 150 across the forest. Greater rates of net NO_3^- production were associated with higher plot elevation, extent of southerly aspect, greater abundance of sugar maple (*Acer saccharum* Marsh.) and striped maple (*Acer pensylvanicum* L.), and lower abundances of coniferous trees. Regression models incorporating these factors accounted for 52% of the variance in NR across the entire valley. Higher soil water contents, N mineralization rates, and total N concentrations in higher elevation plots and higher N mineralization and respiration rates in more south-facing plots contributed to the landscape patterns. Incorporation of measured soil C/N ratios together with landscape factors accounted for an additional 10% of the variation. Regression models incorporating vegetation, physiographic, and soils data explained 62 to 73% of the variance in soil C/N ratios across the valley. Our results demonstrate how multiple biotic and abiotic factors combine to generate wide variation in NO_3^- production, and provide a quantitative basis for estimating how vegetation shifts and climate change may influence N cycling in heterogeneous landscapes characteristic of many temperate forest ecosystems.

T HE PRODUCTION OF NO_3^- via nitrification in forest soils is an important process influencing both the form of N available for plant uptake and the potential for N losses via NO_3^- leaching or gas emission. In temperate forests, perhaps the most important impact of nitrification is its influence on NO_3^- inputs to headwater streams, which in turn may affect downstream water quality (Goodale and Aber, 2001; Likens and Bormann, 1995). Patterns of soil NO_3^- production across a broad forested landscape are likely to influence the variation in stream NO_3^- levels among different watersheds and the spatial distribution of soil NO_3^- inputs within each watershed. These patterns may influence the potential for in-stream retention or transformation of NO_3^- in lower order streams before discharge to larger stream systems where NO_3^- processing rates may be lower (Peterson et al., 2001). Nitrification also generates soil acid-ity and may promote the leaching of base cations from the plant-soil system (Likens and Bormann, 1995).

Nitrification is influenced by a variety of soil factors including water content, pH, temperature, texture, oxygen and NH_4^+ availability, and the numbers and types of active nitrifying microbes (Schmidt, 1982). Across any single forest landscape, NRs may vary widely due, in part, to variation in vegetation type which affects the competition for N between plants, fungi and bacteria (Romell, 1935), the quality of organic substrates undergoing decomposition (Melillo et al., 1982; Scott and Binkley, 1997), the presence of secondary plant compounds (Fierer et al., 2001), and the soil chemical environment in general (Finzi et al., 1998a; Jenny, 1941). Some studies have indicated that the soil C/N ratio, which is greatly influenced by vegetation inputs, may provide a strong index of soil nitrification and NO_3^- leaching potential (Lovett et al., 2002; Christ et al., 2002; Ollinger et al., 2002; Goodale and Aber, 2001; Lovett and Rueth, 1999). In addition to vegetation, variations in localized climatic influences due to physiography (e.g., elevation, aspect, slope) affect soil temperature and water content over the short term, and soil development over the long term. Thus, it is not surprising that several studies have found that NRs within temperate forest ecosystems can vary spatially by factors of 10 to 1000 (Ollinger et al., 2002; Lovett and Rueth, 1999; Zak et al., 1989; Federer, 1983).

Several studies have examined the influence of vegetation on soil N dynamics by comparing data from distinct stands dominated by individual species or vegetation types (e.g., hardwoods vs. conifers) (Ollinger et al., 2002; Giardina et al., 2001; Verchot et al., 2001; Lovett and Rueth, 1999; Finzi et al., 1998b; Zak and Pregitzer, 1990). A major limitation of this categorical approach is that many temperate forests in North America are composed largely of heterogenous mixtures of species including different deciduous and coniferous trees in close proximity (Ollinger et al., 2002; Schwarz et al., 2001; Finzi and Canham, 1998). There is very little information relating soil N cycling process rates or soil C/N ratios directly to vegetation abundances in multiple-species stands. In a study in the Catskills Mountains of New York state, Lovett et al. (2002) found that soil C/N ratio in mixed stands was positively related to abundance of red oak (*Quercus rubra* L.) and negatively related to abundance of sugar maple. With respect to physiography, a few studies have examined interactions between topography and vegetation in controlling nitrification (Christ et al., 2002; Bohlen et al., 2001; Knoepp

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Abbreviations: BA, basal area; CV, coefficient of variation; HBEF, Hubbard Brook Experimental Forest; NR, nitrification rates; S, southness.

and Swank, 1998; Zak et al., 1991). But few, if any, studies have utilized comprehensive sets of vegetation, physiographic, and soils data for robust analysis of potential controls over net NR across a broad and heterogenous landscape. Such an analysis may be useful not only as a means of characterizing extant patterns, but also for understanding how NO_3^- leaching and N oxide gas emission rates may respond to climate change directly or to vegetation shifts due to disease or climate change.

The main objective of this study was to examine landscape patterns of net nitrification in a mixed hardwood-conifer forest during the middle of the growing season. We measured potential net NR in soils collected from 100 plots distributed across the Hubbard Brook Valley in central New Hampshire. Our analysis was primarily aimed at determining how much of the overall valley-wide variation in net nitrification could be explained by plot-scale landscape factors alone, and how much additional variation could be explained by supplementing landscape data with soils information. The soils data also were used to evaluate the underlying proximal controls mediating any observed landscape patterns.

METHODS AND MATERIALS

Site Description

The study was conducted in the Hubbard Brook Experimental Forest (HBEF), which encompasses a 3160-ha valley within the White Mountain National Forest of central New Hampshire, USA (43° 56′ N lat., 71° 45′ W long.) (Fig. 1; http://www.hubbardbrook.org/). The HBEF has been the site of numerous biogeochemical investigations centered largely on a series of small (10–40 ha) watersheds in the northeast corner of the valley (e.g., Likens and Bormann, 1995). The study described here was part of a multi-investigator effort to characterize variation in ecosystem properties across the entire valley. The HBEF is composed of 30% (basal area, [BA]) yellow birch (*Betula alleghaniensis* Britton), 17% sugar maple, 12 to 13% each of red spruce (*Picea rubens* Sarg.), and American beech (*Fagus grandifolia* Ehrh.), approximately 7% each of paper birch (*Betula papyrifera* Marsh.) and balsam fir (*Abies balsamea*), and <6% each of red maple (*Acer rubrum*), Eastern hemlock (*Tsuga canadensis*), white ash (*Fraxinus americana*), and striped maple (Schwarz, 2001). The mean air temperatures are 19°C in July and −9°C in January. Annual precipitation of approximately 1400 mm is spread evenly throughout the year, of which approximately 30% occurs as snow (Likens and Bormann, 1995). Soils are mainly acidic (pH 3.5–5.5) and consist of well-drained, Typic Haplorthods of sandy loam texture derived from glacial till (USDA, 1996).

Between 1995 and 1998, a system of 395 permanent 0.05-ha plots (25.2 m diam.) distributed along 16 north-south transects across the HBEF were established as the basis for a comprehensive study of forest vegetation structure and composition (Schwarz et al., 2001; Schwarz, 2001). Transects were spaced at 500-m intervals, and plots were spaced at 100- and 200-m intervals within each transect. No plots were established within the long-term experimental watersheds. Each plot was characterized for live tree species abundance (BAs), elevation, aspect and slope angle by field measurement. A digital elevation model with 10-m resolution and geographic information system software (Arc/Info, ESRI, Inc., Redlands, CA) were also used to perform a digital terrain analysis (Schwarz, 2001),
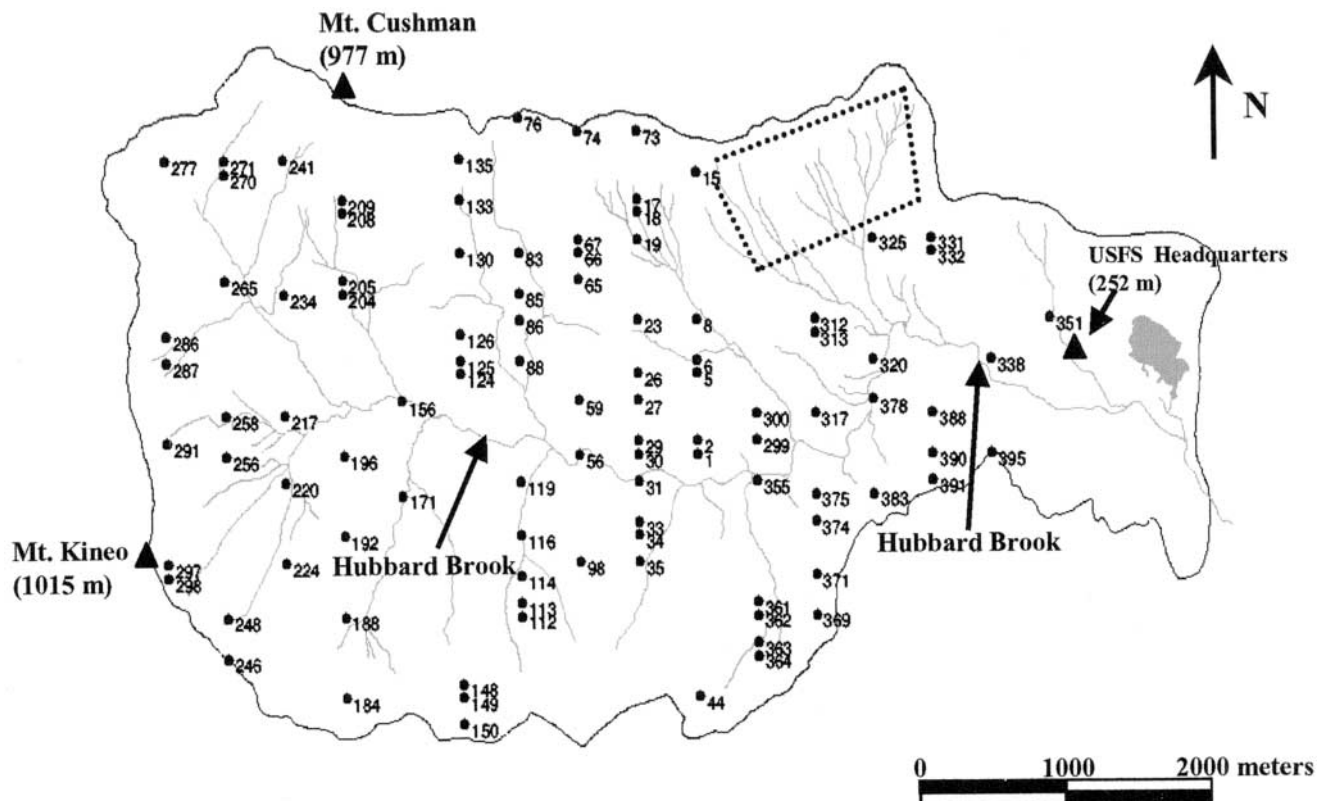

Fig. 1. Representation of Hubbard Brook Experimental Forest, showing 100 plot locations utilized in present study. Numbers are plot designations previously established by Schwarz et al. (2001). Dashed lines are approximate boundaries of areas used in previous watershed-scale studies (Likens and Bormann, 1995).

which allowed for estimation of a topographic wetness index for each plot, defined as natural logarithm (A/tan β), where A is the upslope area drained per unit contour (m^2 m^{-1}) and β is the slope angle (°) (Moore et al., 1993). This index has been previously used to characterize forest and agricultural soils with respect to zones of surface saturation and soil water content (Johnson et al., 2000; Moore et al., 1993). Before June 2000, 100 plots were randomly selected for the present study. The plots were uniformly distributed across the valley, with 58 plots on the north side and 42 plots on the south side of the Hubbard Brook (Fig. 1). Plots ranged in elevation from 330 to 900 m above sea level.

Soil Sampling

Soils were collected on four occasions in June and early July of 2000 (12–14 June, 19–21 June, 26–28 June, and 3–5 July). At each plot, five soil cores were taken at evenly spaced locations along a 12-m diam. circle concentric within the 25.2-m diam. plot boundary. Any loose litter (O$_i$ horizon) was removed before insertion of a 5-cm diam. by 17-cm polyvinyl chloride (PVC) coring tool to a depth of at least 7 cm and at most 15 cm. The entire thickness of the O horizon and the thickness of the mineral horizon to the bottom of each core sample were determined. Soil cores were separated in the field into organic (O$_e$ + O$_a$) and mineral horizons, and then aggregated to form a single organic and single mineral soil composite per plot. After collection, soils were stored in polyethylene bags at 4°C for 1 to 3 d. Six of the 100 plots (plots 31, 56, 196, 299, 312, and 325) were sampled during each sampling event to examine the extent of temporal variability in net NR occurring during the 4-wk sampling period.

Soil Analysis

Within 1 to 3 d of sample collection, soils were passed through an 8-mm sieve, manually homogenized, and weighed before analysis. Two subsamples (approximately 5 g each) of each mineral and organic soil composite were extracted overnight in 25 mL of 1.2 M KCl. Extracts were filtered (Whatman no. 42 paper, Whatman Ltd., Maidstone, Kent, UK) into 60-mL polyethylene bottles and stored at 4°C before analysis of inorganic N (NH$_4^+$–N and total NO$_2^-$–N + NO$_3^-$–N) levels using an automated colorometric analyzer (3000 series, Perstorp Analytical, silver Springs, MD). Concurrently with the initial extraction, two additional 50-g subsamples of each composite were placed into separate 1-L glass jars. The jars were sealed with polyethylene plastic wrap, and a small piece (approximately 4 cm^2) of filter paper moistened with deionized water was suspended above the incubating soil to minimize drying. Jars were incubated at room temperature (20–25°C) for 28 d, at which time the entire jar contents were extracted overnight with 250 mL of 1.2 M KCl. Extracts were filtered and stored as above before determination of final inorganic N concentrations. Potential net nitrification rates on a dry mass basis (mg N kg^{-1} d^{-1}) were calculated from the net increase in total NO$_2^-$–N + NO$_3^-$–N concentration occurring during the incubation period. Potential net mineralization rates were calculated from the net increase in total inorganic N. Mean values of the two laboratory replicates were reported for each composite sample.

Three times during the above incubations (at 8, 19, and 27 d), seals on the incubation jars were removed for approximately 30 min to allow equilibration of the jar headspace with ambient (room) air. Jars were then sealed with metal screw-on lids equipped with butyl rubber septa. After 20 to 28 h, 9-mL headspace samples were removed by plastic syringe and transferred to evacuated 9-mL glass vials, which were stored at room temperature before determination of CO$_2$ concentrations using gas chromatography with thermal conductivity detection. Rates of CO$_2$ production (mg C kg^{-1} soil d^{-1}) were calculated from the concentration at the end of the 20- to 28-h incubation and concentrations in room air samples collected during the 30-min equilibration period. Rates were corrected to account for the dry mass of soil present and the headspace volume occupied by soil. No consistent temporal trends during the incubation period were evident, so the mean of the three measurements was used in subsequent analysis.

Concurrently with the above analyses, 15- to 25-g subsamples of each composite were dried overnight at 60°C for determination of gravimetric soil water content. Dried soil was retained and subsequently analyzed for pH, relative water content, and total C and N concentrations. Soil pH was determined in approximately 5-g subsamples by manually mixing soil with 1 M KCl at a mass ratio of 2:1 (soil/solution) for mineral soil and 5:1 for organic soil, and measuring pH in supernatant solution after settling for 1 h. Because of a shortage of sample mass, pH was not determined in 22 of the 100 organic soils. Soil water-holding capacity was determined in 5- to 10-g subsamples by measuring the mass of water retained in initially saturated samples following 24 h of gravity drainage while placed in a funnel-filter apparatus. An index of relative water content was then calculated from the ratio of the gravimetric water content to the water-holding capacity, each expressed on a dry mass basis (g H$_2$O dry g^{-1} soil). Separate subsamples were ground with a Kleco Tissue Pulverizer and analyzed for total N and C (Carlo Erba NS 1500, Carlo Erba, Milan, Italy). Sample masses for total C and N analysis (8–16 mg) were determined using a microbalance accurate to ±0.001 mg (Mettler-Toledo, Columbus, OH).

Data Analysis and Statistics

Slope aspect data were converted from compass readings (γ°) to continuous indices of southness (S) (S = cos [γ°+ 180°]) and eastness (E = sin[γ°]) with values ranging from −1 to +1 for each index, that is, maximum eastness values occurred on sites with a measured aspect of 90°, and maximum southness values occurred on sites with a measured aspect of 180° (Schwarz, 2001). Net NR, NO$_3^-$ concentrations, and C/N ratios on a per mass soil basis were converted to areal units (e.g., kg N ha^{-1}) using the total dry mass of soil sampled and total area sampled within each plot. Overall plot areal values were determined from the sum of the areal values for the entire organic horizon and the mineral horizon to the sampled depth (>90% of plots had an average core depth of 13–15 cm). The calculated areal values are meant to provide a measure of process rates and concentrations integrated over the organic and mineral horizons and to provide some estimate of field areal values. The calculated values are subject to some error, since we did not quantitatively account for areal and vertical distributions of soil mass versus nonsoil material (e.g., rocks and roots) within each plot. To examine soil-property controls, multiple regression analyses were performed with net NR and NO$_3^-$ concentrations expressed on a per mass soil basis as dependent variables against soil properties separately for mineral and organic soils. To examine landscape-scale trends, regression analyses were done using net NR, NO$_3^-$ concentrations, and C/N ratios expressed on an areal basis as dependent variables. Separate analyses were performed using the following combinations of independent (explanatory) variables: (i) vegetation factors, (ii) physiographic and vegetation factors (hereafter collectively referred to as landscape factors), (iii) landscape factors combined with chemical and physical soil

Table 1. Means, ranges, and variability of laboratory-measured rates of potential net nitrification and ambient concentrations of NO$_3^-$ in 100 plots distributed across the Hubbard Brook Experimental Forest.

	Units	Mean†	Range‡	CV§
		Net Nitrification rate		
areal	kg N ha^{-1} d^{-1}	0.58	−0.010–1.5 (0.010)	69%
organic soil	mg N kg^{-1} d^{-1}	3.2 (35%)	−0.27–14 (0.011)	97%
mineral soil	mg N kg^{-1} d^{-1}	1.2 (65%)	−0.036–3.4 (0.011)	70%
		NO$_3^-$ Concentration		
areal	kg N ha^{-1}	1.3	0.030–4.5	81%
organic soil	mg N kg^{-1}	5.0 (29%)	0.10–21	94%
mineral soil	mg N kg^{-1}	2.8 (71%)	0.090–12	75%

† Values in parentheses are mean contributions or organic and mineral horizons as percentage of total areal rate of concentration
‡ Values in parentheses are the minimum positive values of net nitrification rate.
§ Coefficient of variation.

properties, and (iv) landscape factors combined with chemical, physical, and microbial soil properties (process rates). Microbial process rates (i.e., respiration rate and N mineralization rate) were not considered in explanatory models of soil C/N ratio. Models describing soil C/N ratio were developed using untransformed C/N ratio values. Distributions of net nitrification rates and NO$_3^-$ concentrations expressed both on an areal and per mass soil basis were somewhat skewed to the right. Kolmogorov-Smirnov goodness-of-fit tests showed that distributions resulting from square-root transformations improved the normality of the distributions. The deviations from normality were not extreme, and variable transformation had negligible effects on single-factor correlation analyses, so Pearson product-moment correlation coefficients using untransformed variables are reported for single-factor analysis. Multiple regression models using transformed and nontransformed variables generally yielded similar coefficients of multiple determinations (R^2). Square-root transformation generated multiple-factor models with residuals that were more homoscedastic and normally distributed, so their results are reported and presented graphically (Zar, 1996). Stepwise regression analysis with a criterion of $p < 0.05$ was used to derive multiple factor regression models. The regression models developed here can be expressed in the general form

$$D = \left[\left(\sum_{i=1}^{k} a_i A_i \right) + b \right]^{\phi} - c \qquad [1]$$

where D is the predicted dependent variable, i is the independent variable index, k is the total number of independent variables in the model, a_i is the regression coefficient for independent variable A_i, b is the regression constant, and c is a constant to correct for negative values of D ($c \neq 0$ for net nitrification rate only). The exponent ϕ is equal to 2 for models using square root transformed variables (i.e., for net NR and NO$_3^-$ concentration), and $\phi = 1$ for models using untransformed variables (i.e., for C/N ratio). In addition to R^2 values obtained with transformed variables, R^2 values were calculated after back-transforming the dependent variables, as an additional and more conservative measure of model efficiency (hereafter referred to as R_b^2 values). Because of the high ratio between the number of data points ($n = 100$ plots) and the number of independent variables in each model (≤ 5), adjustments based on the number of independent variables did not change R^2 values substantially and are therefore not reported. Statistical analysis was performed using the Statgraphics software package (Manugistics, Rockville, MD).

RESULTS

Valley-Wide Variation

Laboratory-measured rates of potential net NR and concentrations of NO$_3^-$ showed wide variation across the HBEF (Table 1), ranging over two orders of magnitude, with coefficients of variation (CV) of 69 to 97%. Initial soil NO$_3^-$ concentrations were positively correlated with NR in mineral ($r^2 = 0.58$) and organic soil ($r^2 = 0.69$) on a mass basis, and on an areal basis ($r^2 = 0.73$, Fig. 2). On a per mass soil basis, NR and NO$_3^-$ levels were significantly higher in the organic than the mineral soil horizon ($p < 0.001$). However, the importance of mineral soil processes was demonstrated in that the organic horizon contributed on average ≤35% of the total areal values because of the greater soil bulk density in the upper mineral horizon ($\bar{x} = 0.47$ g cm^{-3}) compared with the organic horizon ($\bar{x} = 0.09$ g cm^{-3}). The average total C contents were 9.9% (±0.4%) in mineral and 43% (±0.6%) in organic soil. In the six plots that were sampled at each of the four 1-wk sampling periods, there was no consistent temporal pattern in NR. The mean NR in these plots did not differ significantly by week ($p > 0.89$). There was also very little variation and no evident temporal pattern in soil water
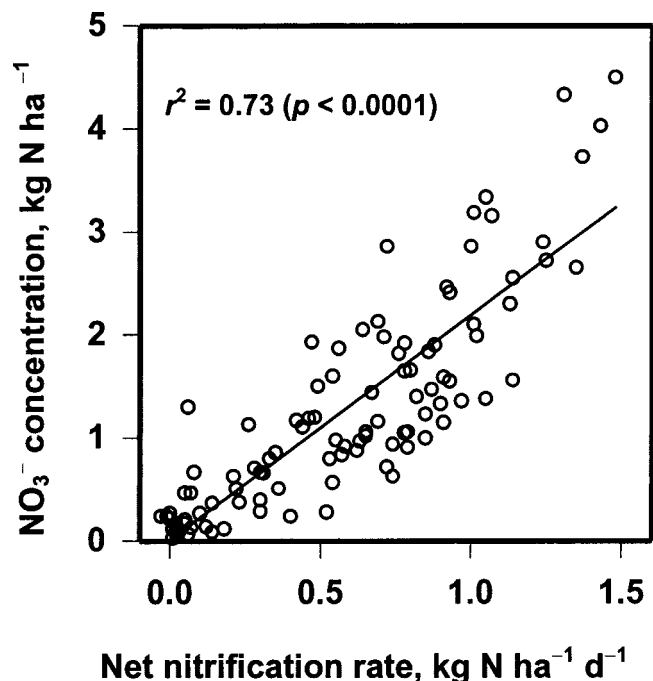

Fig. 2. Net nitrification rates versus NO$_3^-$–N concentrations determined in soils stored at 4°C for 1 to 3 d following field collection for 100 plots distributed across the Hubbard Brook Experimental Forest.

Table 2. Single-factor correlation results for soil factors.

	r†			
	Net nitrification rate‡		Nitrate-N concentration‡	
Factor, units	Mineral	Organic	Mineral	Organic
Physical properties				
water content, kg H_2O kg^{-1}	0.53***	0.03	0.38***	−0.01
relative water content§, −	0.55***	0.06	0.40***	0.02
Chemical properties				
pH, −	0.32**	0.41***	0.27**	0.31*
total N, %	0.58***	0.20*	0.40***	0.21*
total C, %	0.38***	−0.41***	0.23*	−.35***
C/N, kg C kg^{-1} N	−0.46***	−0.55***	−0.42***	−.50***
NH_4^+, mg N kg^{-1} soil	0.01	−0.15	−0.05	−0.06
Microbial process rates				
Mineralization rate, mg N kg^{-1} d^{-1}	0.73***	0.61***	0.45***	0.38***
Respiration rate, mg C kg^{-1} d^{-1}	0.33***	−0.05	0.03	−0.23*

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Pearson product-moment correlation coefficient.
‡ Nitrification rates and nitrate concentrations expressed on per mass dry soil basis (mg N kg^{-1} soil d^{-1} and mg N kg^{-1} soil, respectively).
§ Water content as a fraction of water-holding capacity.

content during the 4-wk period, with CV values for each plot ranging from 4 to 17%.

Soil Controls

Soil C/N ratios, pH, total N concentrations, and net N mineralization rates were all significantly correlated with NR and NO_3^- concentrations (Table 2). The rate of N mineralization was the most highly correlated single variable (positively), accounting for 53 and 37% of the variance in NR in mineral and organic soil, respectively. Soil C/N ratio was also strongly correlated (negatively) with NR in both mineral and organic soil. Multiple regression models incorporating relative water content, soil pH, N mineralization rate, C/N ratio and total N and C concentrations as explanatory variables described 68 and 51% of the variability (based on R_b^2 values) in NR in mineral and organic soil, respectively (Fig. 3).

Vegetation Factors

Net NRs were positively correlated with plot BAs of sugar maple and striped maple, and negatively with BAs of red maple, red spruce, eastern hemlock, and total coniferous trees (Table 3). Relationships between NO_3^- concentrations and BA of these tree species were similar. In general, tree species that were negatively corre-
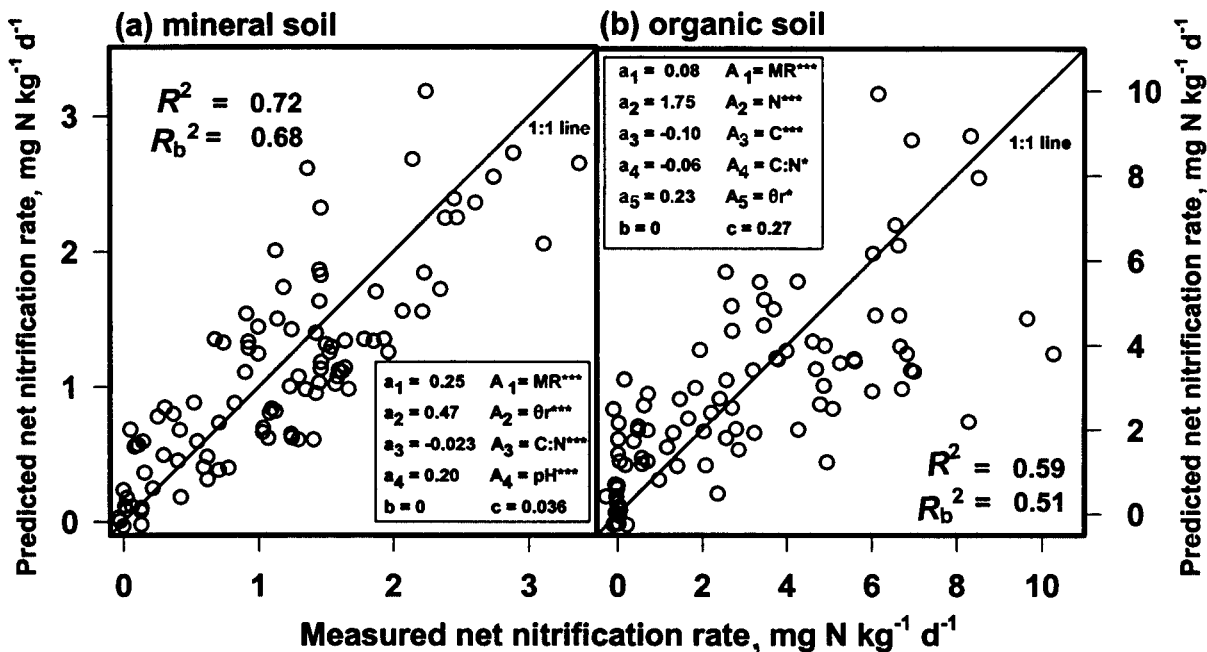

Fig. 3. Net nitrification rates (NR) per mass soil in (a) mineral and (b) organic horizon soils versus NR predicted from multiple regression models in the form of Eq. [1] with φ = 2. Regression coefficients (a_i) shown for each independent variable (A_i) in order of decreasing importance to overall model. $θ_r$ = relative water content; C/N = kg C per kg N; M_r = net N mineralization rate (mg N kg^{-1} d^{-1}); N = g N per 100 g soil; C = g C per 100 g soil. * signifies $p < 0.05$; ** signifies $p < 0.01$; *** signifies $p < 0.001$.

Table 3. Single-factor correlation results for vegetation abundances and physiographic factors.†

			Correlation coefficient (r)‡													
		C/N ratio		pH		N mineralization rate		Total N		Respiration rate		Water content		Relative water content	
	NR§	NO$_3$§	mineral	organic	mineral	organic	mineral	organic	NR§	NO$_3$§	mineral	organic	mineral	organic	mineral	organic
¶SM basal area	0.29**	0.18	−0.34***	−0.33***	0.33***	0.29*	0.01	0.27**	−0.01	−0.07	0.06	0.15	0.09	−0.07	0.09	−0.04
RS basal area	−0.33***	−0.28**	0.61***	0.58***	−0.23*	−0.31**	−0.06	−0.26**	0.09	−0.23*	0.12	0.01	0.12	0.13	−0.06	0.04
BF basal area	−0.10	−0.13	0.09	0.08	−0.28*	−0.11	0.12	−0.12	0.05	0.01	0.10	0.13	0.04	0.18	0.15	0.27*
RM basal area	−0.38***	−0.27**	0.45***	0.33***	−0.23*	−0.41***	0.24*	−0.24*	−0.14	0.01	0.14	−0.11	−0.15	−0.15	0.24*	0.18
WA basal area	0.03	0.15	−0.25*	−0.32*	0.26*	0.17	−0.20	0.03	−0.22*	0.06	−0.12	−0.11	−0.22*	−0.33***	−0.19	−0.23*
EH basal area	−0.34***	−0.23*	0.36***	0.37***	−0.18	−0.36**	−0.28**	−0.29**	−0.25*	−0.16	−0.13	−0.20	−0.31**	−0.11	−0.32**	−0.14
StM basal area	0.22*	0.26*	−0.08	−0.14	0.04	0.14	−0.03	0.07	−0.01	0.12	−0.23*	−0.30**	−0.04	−0.14	−0.01	0.06
Conifer basal area	−0.43***	−0.36***	0.61***	0.59***	−0.41***	−0.44***	−0.08	0.37***	−0.02	−0.22*	0.08	0.01	−0.04	0.15	−0.08	0.13
Total basal area	−0.14	0.06	0.23*	0.13	−0.14	−0.32**	−0.11	−0.22*	−0.17	−0.22*	−0.05	−0.08	−0.15	−0.07	−0.09	−0.08
Elevation	0.48***	0.31**	−0.15	−0.19	−0.04	0.10	0.48***	0.31**	0.33***	0.11	0.14	0.18	0.41***	0.17	0.47***	0.26*
Southness	0.22*	0.10	−0.16	−0.10	−0.06	0.09	0.38***	0.32**	0.07	0.07	0.25*	0.49***	−0.03	−0.01	0.04	−0.10
Wetness index	0.18	0.12	−0.26*	−0.26	0.09	0.25*	−0.04	0.14	−0.05	0.04	−0.04	0.06	0.07	−0.23*	0.10	−0.02

† Results for yellow birch, American beech, paper birch, and physiographic factors not shown were not significant ($p > 0.05$).
‡ Pearson product-moment correlation coefficient.
§ Net nitrification rates (NR) and NO$_3^-$–N concentrations expressed on areal basis.
¶ SM = sugar maple; RS = red spruce; BF = balsam fir; RM = red maple; WA = white ash; EH = eastern hemlock; StM = striped maple. Conifer = RS + EH + BF.
* Significant at the 0.05 probability level.
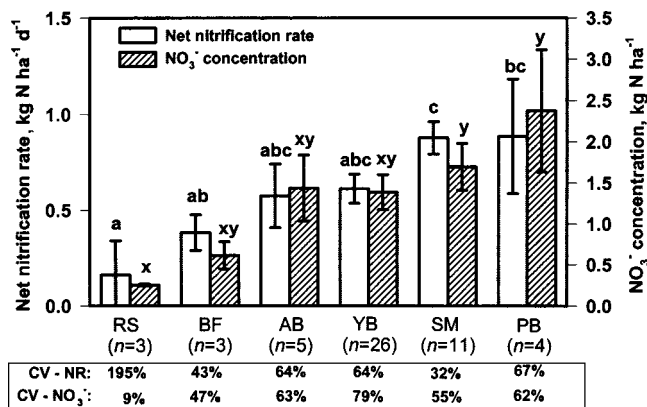** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.

lated with NR showed a consistent pattern of positive correlation with C/N ratio and negative correlation with both soil pH and N mineralization rate. This pattern was consistent for red spruce, eastern hemlock, and red maple. Conversely, sugar maple abundance, which was positively correlated with NR, was correlated negatively with C/N ratio, and positively with soil pH and N mineralization rate. Total conifer BA explained 18 and 13% of the variance in NR and NO$_3^-$ concentrations, respectively. Regression models incorporating multiple species BA terms could not explain much more of the variance in NR than using conifer BA alone in a single-factor model. Models using total conifer, sugar maple, striped maple, and paper birch BA as explanatory variables yielded an R_b^2 value of 0.28 ($R^2 = 0.33$). Models incorporating vegetation abundance factors together with physiographic factors did considerably better than models using vegetation factors alone (below).

Consistent with the heterogeneous nature of the HBEF, the vast majority of the 0.05-ha plots sampled in this study were comprised of a diverse mixture of overstory tree species. Over 75% of the plots contained some mixture of deciduous and conifer trees. Less than 20% of plots were comprised of ≥70% BA of a single species, and only six plots contained ≥80% of a single species. A total of 56 plots did contain ≥50% BA of a single species. Analysis of variance performed on data from 52 of these plots (using only species for which $n \geq 3$ plots) revealed some significant differences which were generally consistent with the correlation analysis results, that is, net NR and NO$_3^-$ concentrations were higher in plots containing mostly sugar maple, and lower in plots comprised mostly of red spruce or balsam fir (Fig. 4). Plots containing mostly paper birch also had higher rates and NO$_3^-$ concentrations, although no significant correlations with paper birch BA were evident overall (Table 3). The CV values for NR and NO$_3^-$ concentrations in plots containing ≥50% of a single species were generally >40% (Fig. 4).

	RS (n=3)	BF (n=3)	AB (n=5)	YB (n=26)	SM (n=11)	PB (n=4)
CV - NR:	195%	43%	64%	64%	32%	67%
CV - NO$_3^-$:	9%	47%	63%	79%	55%	62%

Fig. 4. Net nitrification rates (NR) and NO$_3^-$–N concentrations determined in soils stored at 4°C for 1 to 3 d following field collection in plots comprised of 50% or more basal area of a single species. RS = red spruce; BF = balsam fir; AB = American beech; YB = yellow birch; SM = sugar maple; PB = paper birch. Species with the same letter designations for each parameter are not significantly different ($p > 0.05$), using least significant differences multiple range test. Coefficients of variation (CV) values are tabulated.

Physiographic Factors

Plots at higher elevation in the HBEF had higher rates of potential net nitrification (Table 3). Elevation accounted for the greatest amount (23%) of the overall variance in NR of any single landscape factor. Plots at higher elevation also tended to have higher soil water contents and also had higher total N concentrations in mineral soil (Table 3). Variation in species abundances with elevation included increases in balsam fir ($r^2 = 0.26$) and paper birch ($r^2 = 0.25$), and decreases in eastern hemlock ($r^2 = 0.23$) and white ash ($r^2 = 0.11$) ($p < 0.001$). There was also a decrease in plot total BA with elevation, although the correlation was relatively weak ($r^2 = 0.04$, $p < 0.05$). Plots with greater S of aspect also tended to have higher rates of net nitrification (Table 3). Southness was also positively correlated with net N mineralization rates in mineral and organic soil and respiration rates in organic soil only. The only trend in species distribution with plot aspect was a relatively weak negative correlation between S and striped maple BA ($r^2 = 0.06$, $p < 0.05$). Topographic wetness index was negatively correlated with C/N ratio and positively with soil pH, but a showed a nonsignificant ($p < 0.10$) correlation with NR (Table 3). No other physiographic factors displayed a significant correlation with NR or NO_3^- concentration.

While no single vegetation or physiographic factor alone could account for more than 23% for the variability in NR across the HBEF, the percentage increased to 52% when vegetation and physiographic variables were combined into multiple regression models (Fig. 5a). Plot elevation was a highly significant explanatory variable ($p < 0.001$), and S was also significant ($p < 0.01$), when included in regression models with BA of total conifers, striped maple, and sugar maple. A similar model explained 40% of the variability in areal NO_3^- concentrations using total BAs of all trees in replace of sugar maple BA (Fig. 6a). The amount of the total variance in NR and NO_3^- concentrations explained by multiple regression models increased with the incorporation of soil chemical factors into the models (C/N ratio was significant, Fig. 5b and 6b), and increased further with the incorporation of soil microbial process rates (net N mineralization rate was significant, Fig. 5c and 6c). Models describing NR tended toward underprediction when the measured NR was approximately 1 kg N ha^{-1} d^{-1} or greater (Fig. 5). Regression models were less able to account for variation in NO_3^- concentrations than variation in potential rates of net nitrification. Models describing NO_3^- concentration also tended toward underprediction at measured concentrations >2 kg N ha^{-1} (Fig. 6). The trends toward underprediction at high levels of NR and NO_3^- may in part have derived from nonlinear relationships between soil C/N ratio and NR that were found in this data set (not shown) and that have generally been observed (Ollinger et al., 2002; Goodale and Aber, 2001; Lovett and Rueth, 1999). Attempts to account for this by incorporating nonlinear terms in regression models were not effective in improving the overall models or removing these trends in residuals.

Soil Carbon/Nitrogen Ratio

Soil C/N ratio was significantly correlated with plot BA of five of the 10 tree species identified as important at HBEF (Table 3). Two of three major conifer trees (eastern hemlock and red spruce) and one of seven hardwood trees (red maple) were associated with higher C/N ratios, and also with lower pH, net N mineralization rates, net nitrification rates, and NO_3^- concentrations (Table 3). Multiple regression models using plot BA of red spruce, eastern hemlock, and white ash could account for 62% of the overall variance in soil C/N ratio calculated on an areal basis (Fig. 7a). Models incorporating plot BA of these same trees together with striped maple BA and S of aspect explained 66% of the variance (Fig. 7b), and the incorporation of mineral soil pH improved the explanatory power to 73% (Fig. 7c). A similar model using organic soil pH in place of mineral soil pH explained 72% of the variance (not shown). Southness, striped maple and white ash all contributed similar (minor) explanatory power to the models, each improving the overall R^2 values by approximately 0.02 when incorporated with the other variables. Soil pH and C/N ratio were negatively correlated ($p < 0.001$) in organic ($r^2 = 0.41$) and mineral soil ($r^2 = 0.26$).

DISCUSSION

Physiographic Patterns

Elevation had the strongest effect of any single landscape variable on potential net NR. The pattern with elevation appeared to be driven in part by soil water content, which we found to increase with elevation, presumably because of increases in precipitation (Martin et al., 2000) and decreases in evapotranspiration due to decreased total BA (Bormann et al., 1970) higher in the Hubbard Brook Valley. Soil water content is known to enhance NR as long as water contents are not high enough to limit O_2 availability within soil pores (Schmidt, 1982). Soil moisture levels in the high elevation soils here were observed to be well below the point of saturation.

Other factors may have contributed to the elevation trend. We found higher total N content in mineral soil with elevation. A small watershed study at HBEF which also found higher net NR in higher elevation plots (Bohlen et al., 2001) found that the N content of beech and maple leaf litter increased, and litter C/N ratios decreased, with elevation, and that microbial biomass N in mineral soil increased with elevation. There is some evidence that rates of wet N deposition may increase with elevation at HBEF because of greater precipitation (Martin et al., 2000). Both dry deposition and cloud water deposition are also likely to increase with elevation in forests like the HBEF because of a variety of climatic and vegetation factors (Lovett and Kinsman, 1990). Notwithstanding elevation differences in N deposition, reduced plant competition for N at higher elevation would be expected to increase the amount of N available for soil microbes and thereby enhance nitrification potential (Robertson, 1982).
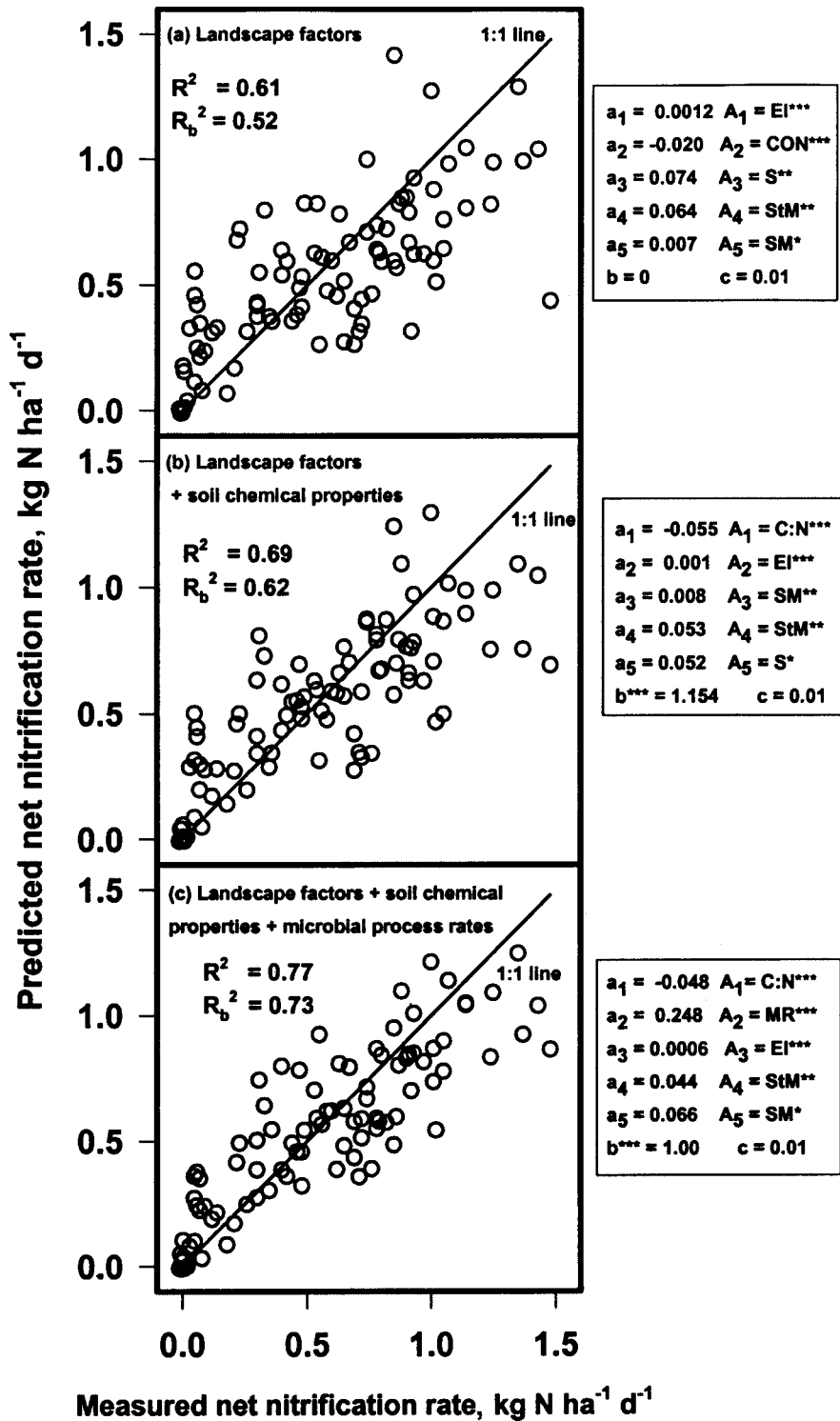
Fig. 5. Net nitrification rates (NR) on an areal basis versus NR predicted from multiple regression models in the form of Eq. [1] with $\phi = 2$, using (a) landscape factors, (b) landscape factors and soil chemical properties, and (c) landscape factors, soil chemical properties, and microbial process rates. Regression coefficients (a_i) shown for each independent variable (A_i) in order of decreasing importance to overall model. El = elevation (m); S = Southness; SM = sugar maple basal area; StM = striped maple basal area; CON = conifer basal area (m^2 ha^{-1}); C/N = kg C kg^{-1} N on areal basis; M_r = net N mineralization rate (kg N ha^{-1} d^{-1}); * signifies $p < 0.05$; **signifies $p < 0.01$; * signifies $p < 0.001$.**

A recent study by Ollinger et al. (2002) found strong relationships between foliar N concentrations and soil NR across a fairly wide spectrum of forest types in New Hampshire. Considering the results of Ollinger, at al. (2002) together with the elevation trends in leaf litter

N contents (Bohlen et al., 2001), it is logical to hypothesize that the elevation trends in nitrification that we observed may be well described as a function of variations in foliar chemistry across the HBEF. However, our data also suggest that soil moisture availability will
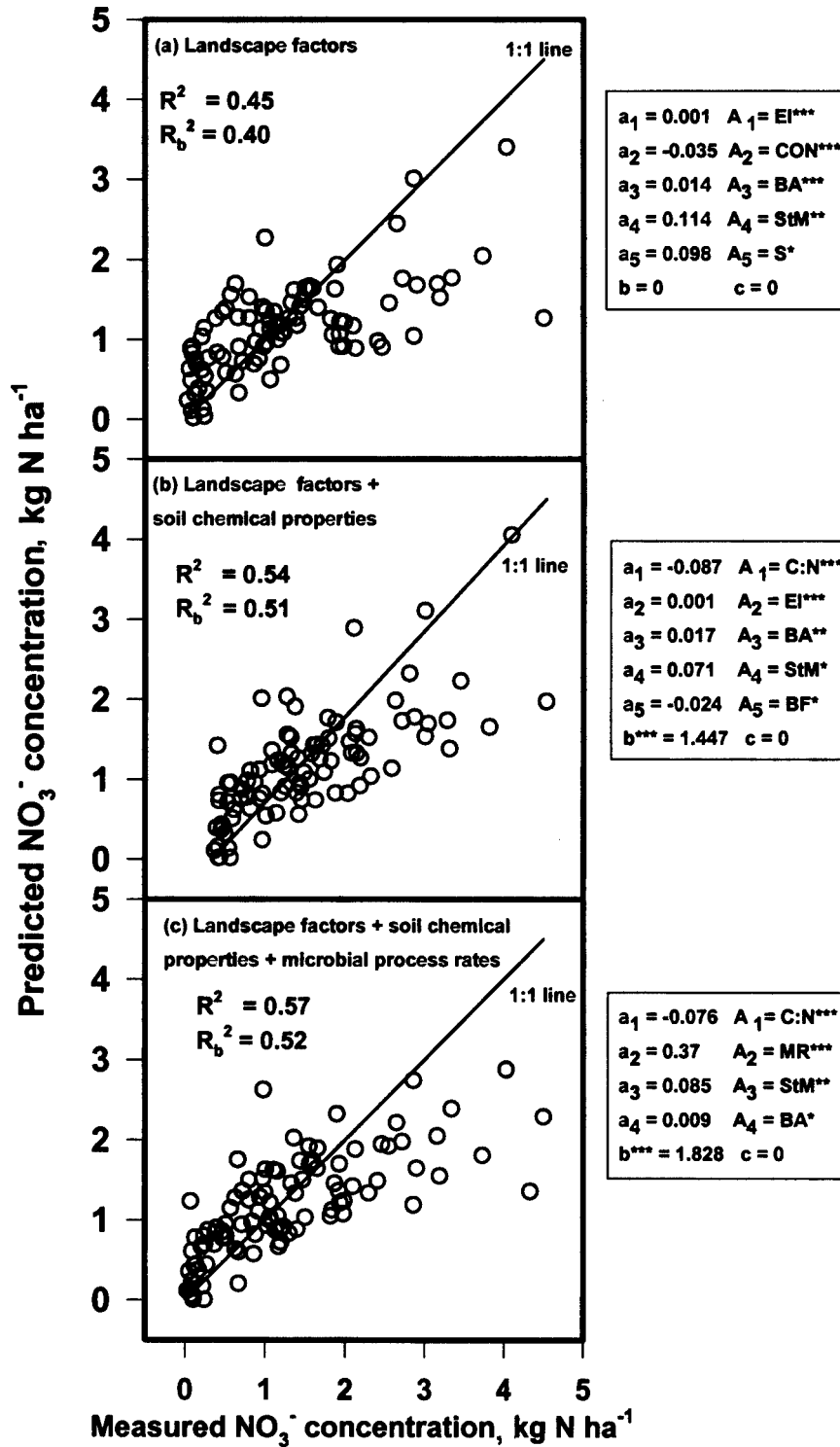
Fig. 6. Measured NO₃⁻ concentrations on an areal basis versus NO₃⁻ predicted from multiple regression models in the form of Eq. [1] with φ = 2, using (a) landscape factors, (b) landscape factors and soil chemical properties, and (c) landscape factors, soil chemical properties, and microbial process rates. Regression coefficients (a_i) shown for each independent variable (A_i) in order of decreasing importance to overall model. El = elevation (m); S = Southness; BF = balsam fir basal area; StM = striped maple basal area; BA = total basal area (m² ha⁻¹); C/N = kg C kg⁻¹ N on areal basis; M_r = net N mineralization rate (kg N ha⁻¹ d⁻¹); * signifies $p < 0.05$; ** signifies $p < 0.01$; * signifies $p < 0.001$.**

play an important role in this trend. Another recent study in West Virginia found higher rates of potential net nitrification and NO₃⁻ export to streams in a higher elevation, less dense, watershed compared with an adjacent watershed with a similar management history (Christ et al., 2002). Significant differences in predominant vegetation between watersheds (greater sugar maple at the high nitrifying site) likely contributed to the
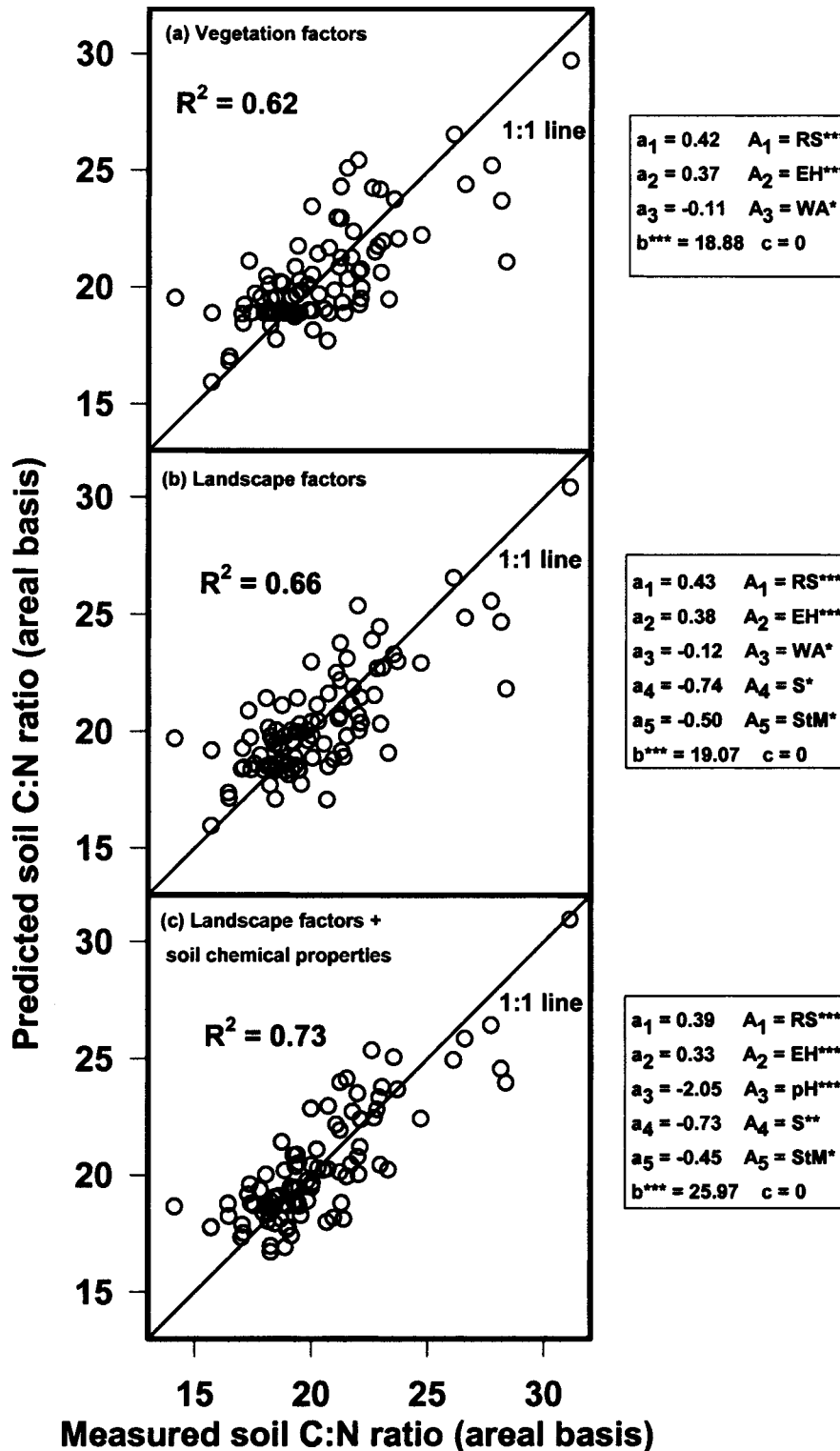
Fig. 7. Measured soil C/N ratios on an areal basis versus C/N ratios predicted from multiple regression models in the form of Eq. [1] with ϕ = 1, using (a) vegetation factors, (b) landscape factors, and (c) landscape factors and soil chemical properties as independent variables. Regression coefficients (a_i) shown for each independent variable (A_i) in order of decreasing importance to overall model. S = Southness; RS = red spruce basal area; EH = eastern hemlock basal area; StM = striped maple basal area; WA = white ash basal area (m^2 ha^{-1}); pH = mineral soil pH; * signifies $p < 0.05$; ** signifies $p < 0.01$; * signifies $p < 0.001$.**

differences found by Christ et al. (2002). In a study in the Catskill Mountains, Lovett et al. (2002) found no significant effect of elevation on soil C/N ratio in multiple regression models that included species composition.

At HBEF, elevation trends in species distributions included increases in balsam fir and paper birch, and decreases in eastern hemlock and white ash, with elevation. The common co-occurrence of paper birch, our

highest nitrifying species in the species-dominated plots (Fig. 4), with fir at high elevation complicates the interpretation of elevation patterns. This is the case at Hubbard Brook and throughout the northern hardwood forests (Evans et al., 1998). Our data suggest that these vegetation trends may have at least partly counteracted each other with respect to the elevation trend in net nitrification at HBEF (Table 3, Fig. 4). Thus, factors other than tree-species affects—that is, soil water content, N deposition, and N content of litter within species—may have been more important.

The pattern with respect to aspect that we observed was weaker than the elevation pattern. Southness of aspect accounted for only about 5% of the valley-wide variation in net nitrification as a single factor (Table 3), and contributed about 3% of the explanatory power in multiple regression models (Fig. 5 and 6). Relationships between S and rates of soil respiration and N mineralization were stronger than for S and net nitrification (Table 3). Some part of this trend was likely driven by soil temperature. Although all soils were incubated at the same temperature, earlier snow melt in the spring and warmer temperatures throughout the growing season provide more favorable conditions for microbial growth, and thus possibly resulted in higher populations of decomposing and nitrifying organisms in these soils at the time of collection. Multiple regression also indicates that C/N ratios are slightly lower on more south-facing slopes when vegetation factors are held constant (Fig. 7), although the reasons for this are not readily apparent. In contrast with our findings, Gilliam et al. (2001) found lower NO_3^- concentrations on south- and southwest-facing slopes in forested watersheds in West Virginia and hypothesized that greater rates of weathering-induced nutrient loss and acidification may have contributed to the trend.

The Role of Vegetation

Many studies have shown that forest canopy tree species composition and litter quality are key factors controlling variation in N cycling in temperate forest soils (Lovett et al., 2002; Lawrence et al., 2000; Lovett and Rueth, 1999; Finzi et al., 1998b; Hart et al., 1997; Zak et al., 1989; Pastor et al., 1984). The low rates of net nitrification in the conifer species and relatively high rates in sugar maple that we observed are particularly consistent with previous studies (cited above). Our results, as summarized by the relationships in Fig. 5 through 7 and Table 3, further indicate that some degree of landscape-scale pattern in potential net NO_3^- production and soil C/N ratio can be identified across a broad forested area which is heterogeneous with respect to both biotic and abiotic influences. Our results also point out the value of utilizing comprehensive vegetation abundance data in analyses, which allow for detection of multiple species influences. Restricting our consideration to species-dominated stands at HBEF would have greatly limited the robustness of the analysis, since there were few plots (six out of 100) comprised of more than 80% of a single species. The high variability in net nitrifi-

cation potential and NO_3^- levels within plots comprised of more than 50% of a single species (Fig. 4) further supports the value of our approach in elucidating landscape patterns.

While regression models utilizing comprehensive vegetation abundance data together with basic physiographic information accounted for 40 to 52% of the variation in NO_3^- concentrations and potential net nitrification rates (Fig. 5a and 6a), supplementation of the landscape information with soil C/N ratio data generated models which explained considerably more of the variation (51–62%, Fig. 5b and 6b). This may indicate that vegetation influences were not fully accounted for by species BA. For example, litter inputs from each species may not have been proportional to their respective BA within each 0.05-ha plot. Also, litter inputs from outside plot boundaries may have had considerable influence on soil N cycling rates within the plot. This is further suggested by multiple regression results for C/N ratio, that is, supplementing plot-scale information with mineral or organic soil pH data also increased the model effectiveness (Fig. 7). Conifer litter inputs from outside the plots, not accounted for in the plot basal area data, may have influenced soil chemistry with respect to both pH (lower) and C/N ratio (higher) resulting in slower rates of net N mineralization and nitrification. This certainly raises questions about ideal sampling protocols for landscape characterizations of soil processes. While a larger plot size would appear to decrease this affect, it would likely also result in higher intra-plot variability in landscapes as heterogeneous as the HBEF, possibly masking the influence of controls that operate on the scale of a few meters or less (e.g., Boerner and Koslowsky, 1989). Little information is available on the relative effectiveness of varying plot size in capturing vegetation influences on N cycling. The results presented here suggest that studies of this nature would be valuable.

Implications and Limitations

The regression models developed here are primarily useful in identifying important controlling factors, and in better understanding how multiple factors can contribute to net process rates. Depending on the categories of information available for any particular site or study (i.e., vegetation, physiographic, and different types of soils data), one of the several relationships obtained here should allow for useful cross-site comparisons. The primary aim of the current study was to identify patterns and potential controls over net nitrification, since it is exactly this net rate (i.e., the sum of gross nitrification and gross NO_3^- immobilization rates), which would be expected to ultimately control NO_3^- accumulation and leaching potential in forest ecosystems. Our measurements do not provide any direct evidence regarding controls over these separate processes. Thus, factors that have been identified as proximal controls mediating the observed patterns of net nitrification (i.e., soil C/N ratio, N mineralization rates, water content, pH) may have influenced gross NR, gross microbial NO_3^- immobilization rates, or both.

While our findings are consistent with other studies (Christ et al., 2002; Ollinger et al., 2002; Goodale and Aber, 2001; Lovett and Rueth, 1999) in demonstrating a negative correlation between soil C/N ratio and net nitrification, our data do not clarify precisely how C/N ratio may directly or indirectly mediate net nitrification on an individual process level. There are several possible mechanisms involved, all of which would tend to favor enhanced net nitrification at lower C/N ratios, including: (i) lower soil C/N ratio generally promotes higher rates of net N mineralization during decomposition (Jansson and Persson, 1982), generating a supply of NH_4^+ above the demands of heterotrophic microbial assimilation, which in the short term provides primary substrate for gross nitrification and in the long term may support the development of robust nitrifying populations, (ii) increased NH_4^+ availability deriving from increased N mineralization may act to inhibit heterotrophic assimilation of NO_3^- because of microbial preference for NH_4^+ (Stark and Hart, 1997; Jansson and Persson, 1982), and (iii) it is possible that high soil C/N ratio may be empirically associated with chemical factors which may inhibit nitrification, such as low pH (as in the current study) or tannins (e.g., Rice and Pancholy, 1973; Fierer et al., 2001), although these relationships have not been well explored. It should also be noted that bulk soil C/N ratios do not necessarily represent the chemical composition of the most labile organic matter that is undergoing decomposition and most strongly influencing N dynamics. Therefore, the soil C/N ratio may be primarily useful in this context as a general index of nitrification and NO_3^- leaching potential, that is, without necessarily suggesting the exact mechanism(s) of control. Recent studies in Europe and North America have in fact shown that soil C/N ratio is a strong indicator of NO_3^- leaching potential in forested watersheds (Gundersen et al., 1998; Lovett et al., 2002). Thus, our findings with respect to landscape and soil influences over soil C/N ratio (Fig. 7) have important implications for understanding and possibly predicting NO_3^- leaching.

The relationship between laboratory-measured rates of net nitrification and NO_3^- levels found here (Fig. 2) may be interpreted as support for the laboratory assays in representing field N cycling processes, similar to previous results (Ollinger et al., 2002). However, our NO_3^- data should be interpreted with some caution, since soil samples were extracted for initial NO_3^- determinations 1 to 3 d after collection. It is possible that some nitrification could have occurred during storage, to an extent that may in fact have been proportional to the subsequently measured net nitrification rates. We attempted to minimize this artifact by storing soils at 4°C, and by sieving the soils immediately before the initial extraction, although we did not test the effectiveness of these procedures in minimizing changes in NO_3^- levels during storage.

Extension of our models for purposes of predicting NO_3^- inputs to streams would require consideration of additional factors, including hydrology, which can be complex in many forest systems (e.g., Hagedorn et al., 1999), and other processes regulating the fate of NO_3^- once produced via net nitrification (e.g., plant uptake and deni-

trification). This is also suggested by the reduced effectiveness of models obtained here in describing NO_3^- concentration compared with net NR (Fig. 5 and 6). The impact of seasonal changes in plant nutrient uptake, climate and other factors on the relationships identified here needs to be investigated. More generally, the fact that a substantial portion of the variance remains unexplained by our models indicates that our knowledge of the controls on the nitrification process in forest soils is incomplete, and that predictive models derived from them would be subject to significant uncertainty. However, the relationships observed here might be useful in estimating broad differences in NO_3^- leaching potential between distinct watersheds within or across landscapes, or between different areas within a single watershed.

Our findings also may be useful in estimating the general response of watersheds or landscapes to alterations in species composition because of climate change, which are predicted to be significant (Iverson and Prasad, 1998), as well as to species shifts because of selective harvest or disease. Indeed, tree species which proved to be strongly related to NO_3^- production in this study (sugar maple and eastern hemlock), as well as one of the most predominant species at HBEF (American beech), are all presently being threatened by invasive diseases (USDA, 1999; Jenkins et al., 1999; DiGregorio et al., 1999). Thus, for example, our results suggest that decreases in the latitudinal range of coniferous trees under global warming scenarios could promote NO_3^- leaching potential in some regions, while decreases in sugar maple abundance because of Asian longhorned beetle (*Anoplophora glabripennis*) infestation could have the reverse effect. In summary, while further data are certainly required in evaluating the generality of our findings to different forest systems, the relationships obtained here provide a quantitative basis for estimating spatial patterns given vegetation, physiographic, and soils data, and an opportunity for testing against data from future studies.

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