

A Cross-Site Comparison of Factors Influencing Soil Nitrification Rates in Northeastern USA Forested Watersheds

Donald S. Ross,^{1*} Beverley C. Wemple,² Austin E. Jamison,³
Guinevere Fredriksen,⁴ James B. Shanley,⁵ Gregory B. Lawrence,⁶
Scott W. Bailey,⁷ and John L. Campbell⁸

¹Department of Plant and Soil Science, University of Vermont, Burlington, Vermont 05405, USA; ²Geography Department, University of Vermont, Burlington, Vermont 05405, USA; ³Blue Ridge Division, Chesapeake Wildlife Heritage, 5497 Wyant Lane, Charlottesville, Virginia 22903, USA; ⁴Ecology & Evolutionary Biology, Cornell University, E213 Corson Hall, Ithaca, New York 14853, USA; ⁵United States Geological Survey, P.O. Box 628, Montpelier, Vermont 05601, USA; ⁶United States Geological Survey, Water Resources Division, 425 Jordan Road, Troy, New York 12180, USA; ⁷United States Forest Service, Hubbard Brook Experimental Forest, 234 Mirror Lake Road, North Woodstock, New Hampshire 03262, USA; ⁸United States Forest Service, 271 Mast Road, Durham, New Hampshire 03824, USA

ABSTRACT

Elevated N deposition is continuing on many forested landscapes around the world and our understanding of ecosystem response is incomplete. Soil processes, especially nitrification, are critical. Many studies of soil N transformations have focused on identifying relationships within a single watershed but these results are often not transferable. We studied 10 small forested research watersheds in the northeastern USA to determine if there were common factors related to soil ammonification and nitrification. Vegetation varied between mixed northern hardwoods and mixed conifers. Watershed surface soils (Oa or A horizons) were sampled at grid or transect points and analyzed for a suite of chemical characteristics. At each sampling point, vegetation and topographic metrics (field and GIS-based) were also obtained. Results were examined by watershed averages ($n = 10$), seasonal/watershed averages ($n = 28$), and individual sampling points ($n = 608$). Using both linear

and tree regression techniques, the proportion of conifer species was the single best predictor of nitrification rates, with lower rates at higher conifer dominance. Similar to other studies, the soil C/N ratio was also a good predictor and was well correlated with conifer dominance. Unlike other studies, the presence of *Acer saccharum* was not by itself a strong predictor, but was when combined with the presence of *Betula alleghaniensis*. Topographic metrics (slope, aspect, relative elevation, and the topographic index) were not related to N transformation rates across the watersheds. Although found to be significant in other studies, neither soil pH, Ca nor Al was related to nitrification. Results showed a strong relationship between dominant vegetation, soil C, and soil C/N.

Key words: acidic deposition; ammonification; nitrogen transformations; conifers; *Acer saccharum*; *Picea rubens*; soil calcium.

Received 1 March 2008; accepted 2 October 2008; published online 12 November 2008

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-008-9214-4) contains supplementary material, which is available to authorized users.

*Corresponding author; e-mail: dross@uvm.edu

INTRODUCTION

Continued N deposition in many areas of the world, including the northeastern USA (for example, Driscoll and others 2003), will likely

change patterns of N cycling and N export from forested watersheds. However, changes predicted from N saturation theory (Aber and others 1998; Aber and others 2003) have not always occurred (Goodale and others 2003; Emmett 2007) and our understanding of ecosystem response is far from complete. Recent evidence suggests that anthropogenic N deposition has increased C sequestration (Magnani and others 2007). But increases in N deposition have also been associated with increased NO_3^- leaching. Gundersen and others (2006) reviewed a large number of studies from Europe and North America and found that elevated concentrations of NO_3^- in seepage and surface waters were associated with three primary factors: increased N input, reduced plant uptake, or enhanced mineralization of soil N.

Because of the complexity of the N cycle, numerous factors can affect soil nitrification rates. These factors are often interrelated and, assuming the nitrification is carried out by autotrophs, may be condensed into (i) the availability of NH_4^+ to the autotrophic ammonia oxidizers and (ii) the activity of this component of the microbial community. Understanding what controls nitrification rates in forest soils is complicated by the fact that only net rates are usually measured and that these rates also reflect consumption of the NO_3^- produced, which is often substantial (for example, Stark and Hart 1997). Further complicating our understanding is the sensitivity of many forest soils to sampling disturbance, which enhances net nitrification rates (Romell 1935; Van Miegroet 1995; Ross and Hales 2003; Ross and others 2004). Measured net rates are aptly termed 'potential net rates' because they may or may not accurately reflect in situ transformations (Hart and others 1994).

Numerous studies have examined various watershed characteristics in relation to soil nitrification rates. These include vegetation, both overstory and understory; physical attributes such as slope, elevation, and topographical index; soil chemistry; and land-use history. Many of these factors interrelate and the primary effect may not be directly due to the measured variable. Of all the factors affecting nitrification, the most focus has been on either the soil C/N ratio or the overstory tree species composition. In U.S., European, and New Zealand studies, the C/N ratio has usually been found to be a significant explanatory variable (for example, Dise and others 1998; Gundersen and others 1998; Christ and others 2002; Lovett and others 2002; Vervaet and others 2003; Parfitt and others 2005), although occasionally an insignificant one (for example, Gilliam and others 2001;

Falkengren-Grerup and Diekmann 2003; Templer and others 2003). There appears to be a threshold C/N ratio of 23–25, above which net nitrification rates are minimal. In the USA and Canada, the presence of *Acer saccharum* has often been associated with higher rates (Zak and Pregitzer 1990; Finzi and others 1998; Lovett and Rueth 1999; Lovett and Mitchell 2004; Lovett and others 2004; Ross and others 2004; Ste-Marie and Houle 2006). In Europe, Aubert and coworkers (2005) found greater nitrification under a mixed European beech–hornbeam forest compared with a pure beech stand. The combination of 'base-loving' species, higher soil Ca^{2+} availability, and sometimes higher soil pH is thought to promote net nitrification (Finzi and others 1998; Christ and others 2002; Mitchell and others 2004; Christopher and others 2006). Litter from these species has been found to decompose faster and both soil C and C/N are usually lower (Lovett and others 2004). The reverse has often been found with conifer species—higher soil C/N and lower net nitrification in the forest floor than under nearby deciduous trees (Campbell and others 2000; Jefts and others 2004a; Vesterdal and others 2008). Thus, soil C/N can be correlated with tree species and their effect on nitrification is difficult to separate.

Soil nitrification rates have been linked to land-use history in the northeastern USA (Goodale and Aber 2001; Compton and Boone 2002; Ollinger and others 2002). Differences in site history create long lasting differences in both vegetation and soil C/N ratios, and the effect of past land-use may be through these attributes. Topographic measurements have been used to predict net nitrification rates with variable results. Elevation, aspect, and slope appear to have a secondary effect on nitrification through differences in vegetation and in soil moisture and temperature (Kneopp and Swank 1998; Bohlen and others 2001; Gilliam and others 2001) but elevation also affects N deposition amounts (Ollinger and others 2002). Soil chemical properties, such as exchangeable aluminum and low pH, may have negative impacts on mineralization (De Boer and Kowalchuk 2001; Gilliam and others 2005). A further complication is the possibility of inhibition promoted by soil factors associated with ericaceous shrubs (Gilliam and others 2001) and red oak (Lovett and others 2004).

Many studies examining these factors have focused on individual watersheds or locales and relationships found do not consistently hold up across different sites. Our objective was to determine the factors common across the northeast US by conducting a cross-site study, using 10 small

research watersheds in the Catskill and Adirondack Mountains of New York, the Green Mountains of Vermont, and the White Mountains of New Hampshire. Identical analytical methods were used at all sites and a large number of commonly used soil, vegetation, and topographic metrics were obtained. The watersheds spanned a relatively narrow gradient of N deposition and 9 of the 10 had a similar land-use history of mature second growth forest with some history of logging. Our hypothesis was that soil C/N ratio would be the best cross-site predictor of net nitrification rates but that other metrics, such as tree species or topographical metrics, would be significant.

METHODS

Site Descriptions

Ten forested watersheds from seven sites in three states were chosen for this study (Figure 1, Table 1) to provide a range in geographical location and forest type. All watersheds were gauged allowing calculation of N flux via stream export. The Winnisook watershed in the Catskill Mountains of New York is both the largest and has the highest elevation of the study watersheds with the lower portions of the watershed most likely having been last cut about 55 years ago (Johnson and others 2000; Lawrence and others 2000). Buck Creek North and

South watersheds are located in the Adirondack Mountains of New York and have not been logged for at least 50–60 years (Gregory Lawrence, personal communication). The Lye watershed in southern Vermont refers to the catchment containing a first-order stream within the greater Lye Brook watershed. The watershed was last logged about 85 years ago (Campbell and others 2000). Sleepers River W9-A and W9-C in northeastern Vermont have been part of a larger U.S. government research site, the Sleepers River Research Watershed, since 1957 (Shanley and others 2002). The last logging to take place there was a clearcut in 1929 (Thorne and others 1988). Brush Brook D and G are located in Camels Hump State Forest in central Vermont, where logging operations ceased in the early 1960s (Helen Whitney, personal communication). The two sites in New Hampshire are the Cone Pond watershed (Bailey and others 1996) and watershed 7 (W7) in the Hubbard Brook Experimental Forest (HBEF). The Cone Pond watershed has no known history of human habitation or forest harvest but did experience a large fire around 1820 (Buso and others 1984) whereas W7 in the HBEF was last cut about 80 years ago (Likens and Bormann 1995). The watersheds cover a range of elevation and sizes (Table 1), but all have similar forest histories with the exception of Cone Pond. Annual precipitation (117–158 cm) and inorganic

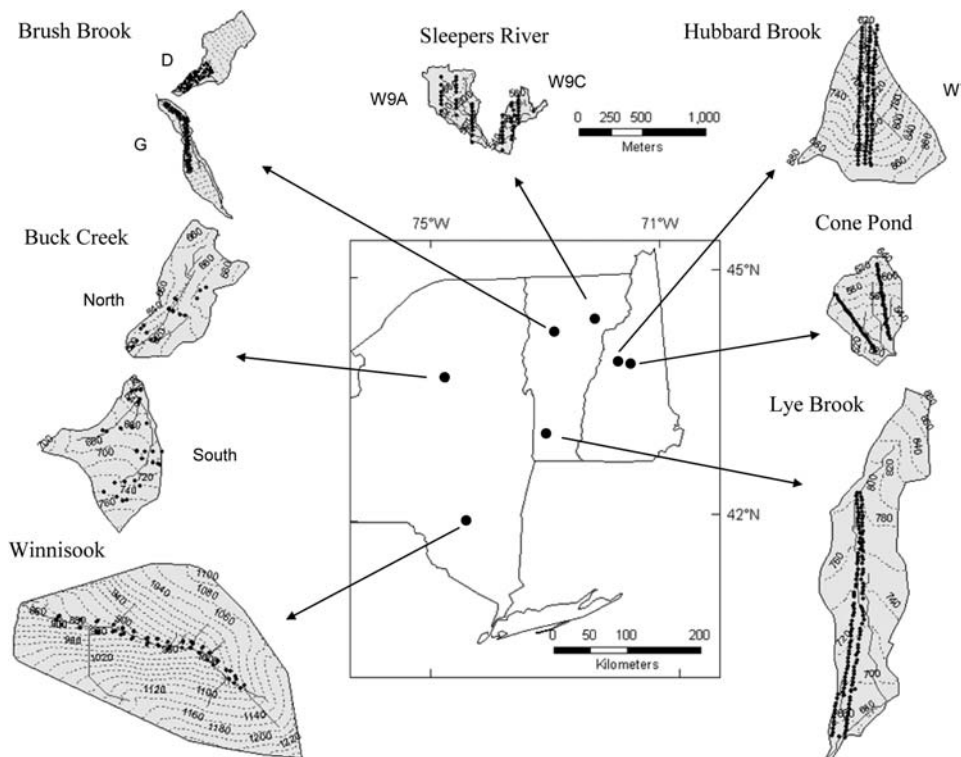


Figure 1. Map of New York, Vermont and New Hampshire showing the location of the watersheds studied. All watersheds are displayed at 1:30,000 with contours at 20 m intervals. Points are locations of transect samples.

Table 1. Watershed Locations, Physical Data from GIS Delineations, Wet N Deposition, Annual Precipitation and Sampling Information

Watershed	Location	Area (ha)	Average elevation (m)	Average slope (°)	Average Annual wet N deposition ^a (kg ha ⁻¹)	Annual precip. ^a (cm)	Number of transect points	Total numbers of samples	Dates Sampled ^b
Sleepers W9-A	Walden, VT	16	636	10	4.8	133	27	82	S02, F02, S03, S04
Brush Brook G	Huntington/Duxbury, Vermont	11.4	839	21	5.3	130	66	66	F01, S02, F02
Winnisook	Olivera, New York	217	1038	17	6.3	158	64	64	S03, S04
Brush Brook D	Huntington/Duxbury, Vermont	15.4	841	22	5.3	130	80	80	F01, S02, F02, S04
Lye	Sunderland, VT	121	759	5	5.7	120	130	130	F02, S03, F03, S04
Buck Creek South	Inlet, New York	52	692	8	4.7	117	21	58	S02, F02, S03, S04
Sleepers W9-C	Walden, Vermont	7	566	5	4.8	133	27	73	S02, F02, S03, S04
HBEF W7	Ellsworth, New Hampshire	76	772	14	4.3	125	113	114	F02, S03, F03, S04
Buck Creek North	Inlet, New York	33.7	649	8	4.7	117	21	57	S02, F02, S03, S04
Cone Pond	Thornton, New Hampshire	33	564	11	4.3	125	59	60	S03, F03

^aInorganic N (NO₃ + NH₄) deposition and precipitation data are the average of the years 2002–2004. Brush Brook data from Underhill NADP site, 27 km distant, 399 m elevation; Winnisook data from nearby Biscuit Brook NADP site, 634 m elevation; Lye data from Bennington NADP site, 21 km distant, 305 m elevation; Buck Creek data from Moss Creek NADP site, 11 km distant, 558 m elevation; HBEF W7 and Cone Pond data from the Hubbard Brook NADP site, 250 m elevation; Sleepers lies halfway between the Underhill and Hubbard Brook NADP sites and data are averages.

^bDates sampled: S01 = spring, 2001; F01 = fall 2001; S02 = spring, 2002, so on. The deposition and precipitation data are from the nearest NADP site. Watersheds are listed in descending order of nitrification rates.

N wet deposition (4.3–6.3 kg ha⁻¹) generally decreased from southwest to northeast (Table 1), with the highest values for both found at the Winnisook watershed in the Catskills of New York. Campbell and others (2004) reported a range in N wet deposition from 2.7 to 8.1 kg N ha⁻¹ y⁻¹ (mean 6.3) for a broader region of the northeastern USA (West Virginia to Maine).

Soil Sampling Procedures

We sampled the Oa or A horizon because it has been found to have the highest nitrification rates in the profile (Verchot and others 2001; Jefts and others 2004a; Parfitt and others 2005) and is well suited for rapid sampling. In our study sites, there was usually either an Oa or an A horizon, rather than an Oa over an A, with the distinction being that an A horizon had less than 200 g kg⁻¹ C (NRCS 2006).

All soil sampling took place between the fall of 2001 and the spring of 2004. At Brush Brook, HBEF W-7, Lye, and Winnisook, samples were collected along transects parallel to the stream, usually 50 m apart (10 m at Brush because of narrowness), with 30 m between sampling points (Figure 1). Although the sampling points as shown in Figure 1 often appear to be close to the streams, few samples were actually within the narrow riparian zones. At Cone, the two transects were not parallel but, instead, diverged upslope to encompass more of the watershed, with 20 m between sampling points. In all the above watersheds, repeated samplings were designed to spatially overlap (for example, alternating points along a transect sampled on two different dates). Soil sampling in Sleepers W9-A and W9-C, and Buck Creek North and South took place along previously established transects. At Sleepers, points were located on north–south transects at a spacing of 30.5 m (100 feet) with 122 m between transects. At Buck, seven transects with two to five points each had been established perpendicular to each stream. Repeated samplings at specific transect points at Sleepers and Buck took place at different specific compass directions from a central point, with at least 3 m separating sample locations. Most points were sampled on two different dates (for example, different seasons or years). Transect points were resampled if the nitrification rates were not within 10% of each other. Results are presented as the averages from all sampling dates for each transect point. The difference in the size of the individual watersheds, along with differences in sampling design, produced a range per

watershed of 57–130 total samples representing 21–130 points (Table 1).

Net rates for nitrification and ammonification were determined using the 1-day method of Ross and others (2006). At each point, an approximately 300 cm² area of forest floor (Oi/Oe) was removed to expose the underlying (Oa or A) horizon. About 250 ml of this horizon (first horizon below the Oi/Oe that was at least 2 cm thick) was collected and mixed by hand. Ten milliliters of soil was mixed with 25 ml of 2 mol l⁻¹ KCl in the field in duplicate, shaken intermittently for 15 min, and then put on ice in a cooler. The rest of the bulk sample was put into a polyethylene bag, stored in a separate cooler under ice packs, and incubated at 10°C in the dark after returning to the lab later the same day. Field extracted samples were centrifuged in the lab, usually the next day. Additional subsamples from the bulked samples were extracted one more time, approximately 24 h later in the lab. Soil subsamples with KCl added were stored under ice in a cooler for about the same duration as the initial field extractions. Other soil properties measured in the field included Oi/Oe and Oa/A horizon thickness, the presence or absence of an E horizon, and soil temperature in the sampled horizon.

Nitrate and ammonium were determined using a flow injection autoanalyzer (Lachat QuickChem AE, Hach Inc., Loveland, Colorado) using the Cd-reduction method for NO₃⁻ and the salicylate-nitroprusside method for NH₄⁺. Ten milliliters of samples were weighed and dried (80°C) in duplicate to determine dry weights to calculate the solution:soil ratio of the extractions. Carbon and nitrogen were determined by a CHN elemental analyzer (CE440, Exeter Analytical, North Chelmsford, Massachusetts) on the same subsamples ground to pass through a 0.125 mm screen. The instrument was standardized using soil standards obtained from the North American Proficiency Testing program. The soil wetness ratio, actual moisture versus that predicted by soil C, was calculated by the equation developed by Ross (2007). Soil pH was determined on field-moist 5-ml subsamples in 10 ml of both water (pH_w) and 1 mmol l⁻¹ CaCl₂ (pH_{ca}). Extractable Al, Ca, Mg, K, Na, Fe, Mn, and S were determined on air-dried 2-mm-sieved samples using the Modified Morgan's soil test procedure (Wolf and Beegle 1995). In this method, 4 ml of soil was shaken for 15 min with 20 ml of 1.25 mol l⁻¹ NH₄-acetate (pH 4.8), filtered, and the extract analyzed on a Perkin-Elmer 3000 DV ICP (Perkin-Elmer Inc., Norwalk, CT). The dry weight of the 4 ml of soil was measured before extraction and used to calculate the results on a soil

dry weight basis. This extraction procedure removes exchangeable Ca, Mg, K, and Na but, because of the low pH and acetate, it removes a portion of organically complexed Al that is greater than exchangeable that is operationally defined by a neutral salt extraction (Bartlett 1982).

Net nitrogen potential transformation rates were determined by final nitrate or ammonium concentrations minus initial (in situ) concentrations. N transformation rates were expressed in terms of μmol of N produced per hour per kg of soil. Rates were also normalized to the C and N content of the soil and expressed as per kg of C or N (rather than kg of soil). The nitrate fraction of the total inorganic N after 1 day of incubation was also calculated.

Topographic Measurements

In the field, slope aspect was measured at every soil sampling point using a handheld compass. All aspect readings were converted to an index of southness by taking the cosine of 180° added to that compass reading. This results in a southness value of 1.0 for due south (magnetic) and a value of -1.0 for north. Local slope angle was measured with a ruler and a level in a 60 cm area over the sampling location and then converted to a measure of slope in degrees. Ten-meter slope downhill from each point was also determined using a handheld clinometer. A handheld GPS unit (Trimble Geo-Explorer 3) was used to locate the position of each sampling point. All locations were differentially corrected using data from the nearest base station to improve horizontal accuracy to less than 1 m (accuracy is not available for the first Winnisook sampling in which a different GPS unit was used).

Watershed boundaries and maps of slope and the topographic index (TI, Beven and Kirkby 1979) were delineated from digital elevation models using the hydrologic functions in ArcGIS v. 9.2 (ESRI 2006) and the USGS GIS Weasel (Leavesley and others 2002). Adjustments to watershed boundaries for Brush D and G were made using field GPS points of ridgeline locations. The ArcGIS "zonal statistics" function was used to extract elevation, TI, and slope data for each sampling point. Histograms of elevation, slope, and TI values by grid cell for each watershed were compared to histograms for transect sampling points to ensure that sampling sites adequately reflected the distribution of topographic metrics within the watersheds.

Vegetation Sampling

In most watersheds, live trees over 10 cm diameter-breast-height (dbh) were measured in a 10 m

radius around each sampling point and smaller diameter stems were counted by species in a 5 m radius. At Brush Brook, both measurements were done in 5 m plots because many sampling points were only 10 m apart. For Buck Creek North and South, both measurements were made in previously established 9 m radius plots. Vegetation data were not collected for the first sampling at Winnisook because plots could not be accurately relocated. Plots consisting of more than 50% basal area of conifers (*Abies balsamea*, *Picea rubens*, *Tsuga canadensis*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), or American beech (*Fagus grandifolia*) were also identified for further analysis.

Statistical Methods

Our statistical analyses were used to examine patterns among the 10 watershed averages and, in some cases, among the 608 individual soil samples. Because of an n of 10 watersheds, we also included analyses of watershed by sampling date averages ($n = 28$). To examine patterns across watersheds, we used analysis of variance (ANOVA) to detect between watershed differences in nitrification and ammonification rates. We used correlation analysis, ANOVA, and linear regression analysis to examine relationships between these rates and the chemical and physical properties of the sampled soils and topographic and vegetation characteristics of plots surrounding our samples. Spearman's rank correlations were used because some data were not normally distributed and some were categorical. Following ANOVA, Student-Newman-Keuls (SNK) contrasts were used to compare means.

Seasonal variation was tested in each watershed on log-transformed nitrification rates from all samples (before averaging by transect point for Sleepers and Buck). Because different watersheds were sampled in different seasons, a test for a specific season (for example, fall versus spring of 2003) could not be done. Only two watersheds showed rate differences between seasons/years and the data from one of these, Buck North, has been averaged by transect point (over season) for all data presented. Brush G had higher net nitrification rates in the spring of 2002 than either the fall of 2001 or 2002 ($P < 0.01$). A simple t -test comparing log-transformed net nitrification rates in all samples from all watersheds taken in the spring ($n = 311$) versus the fall ($n = 473$) showed a significant difference ($P < 0.01$) but the means of 10.3 and 13.7 $\mu\text{mol kg}^{-1} \text{h}^{-1}$, respectively, were close numerically, relative to the overall range.

From these results of the tests for differences between seasons and years, we concluded that there was no overall bias in nitrification rates based on sampling date and all dates were combined for further analyses.

For the dataset of 608 soil samples, we used regression tree analysis to explore the importance of our measured independent variables and stepwise multiple linear regression analysis to build models to predict net nitrification rates. Regression tree (RT) analysis (Breiman and others 1984) is a data partitioning technique that repeatedly parses a continuous dependent variable into two mutually exclusive groups using successive explanatory variables that best discriminate between the groups. We constrained our tree using a criterion that no variable could enter the model unless it produced a partition in the dataset that included at least 10% ($n > 6$) of the observations. To select the size or maximum number of branches in the tree, we followed the approach described in De'ath and Fabricius (2000), whereby we iteratively partitioned the data, used a 10-fold cross validation at each iteration to compute a cross-validation error, plotted model cross-validation error against tree size, and ultimately pruned the tree to the smallest (most parsimonious) size that produced no more than a 10% increase in prediction error.

Because of missing data, a series of stepwise multiple linear regression analyses were performed to build a model with the greatest number of observations. Each successive run eliminated variables that were not selected by the previous procedure and had missing values. Initial independent variables included all parameters listed in Tables 2, 3, 4 and Supplementary Appendices B–D with the exception of elevation (spurious correlation with nitrification) and soil moisture content (highly correlated with soil C). The significance level for inclusion or exclusion was set at $P < 0.01$ and the normality and variance of residuals were examined graphically. To achieve an acceptable distribution of the residuals, the net nitrification rates were natural-log transformed. All statistical analyses were performed using SAS 9.1 (SAS Institute 2003b) and JMP 5.1 (SAS Institute 2003a).

RESULTS AND DISCUSSION

Net Potential Rates of Nitrification and Mineralization

Average watershed net nitrification potential rates, measured over a 1-day period, ranged between 1.3 and 22.1 $\mu\text{mol N kg}^{-1} \text{h}^{-1}$ (Figure 2 and

Table 2. Basal Area and Tree Species Composition Averaged for the Plots in Each Watershed

Watershed	Average plot basal area (m ² ha ⁻¹)	Conifer dominance	Sugar Maple <i>A. saccharum</i> dominance	Yellow Birch <i>B. alleghaniensis</i> dominance	American Beech <i>F. grandifolia</i> dominance	White Ash <i>F. americana</i> dominance	Red Maple <i>A. rubrum</i> dominance	Paper Birch <i>B. papyrifera</i> dominance	Red Spruce <i>P. rubens</i> dominance	Eastern Hemlock <i>T. canadensis</i> dominance
Sleepers W9-A	28.9	0.04	0.69	0.11	0.19	0.00	0.00	0.00	0.00	0.00
Brush G	28.6	0.04	0.31	0.38	0.03	0.00	0.00	0.16	0.02	0.00
Winnisook	24.3	0.02	0.00	0.62	0.29	0.00	0.03	0.00	0.00	0.00
Brush D	30.0	0.13	0.18	0.46	0.13	0.00	0.00	0.05	0.02	0.00
Lye	21.7	0.20	0.33	0.19	0.14	0.00	0.05	0.09	0.12	0.00
Buck South	25.7	0.06	0.23	0.07	0.61	0.00	0.00	0.00	0.02	0.00
Sleepers W9-C	30.2	0.10	0.60	0.19	0.00	0.08	0.00	0.02	0.04	0.00
HBEF W-7	27.4	0.18	0.14	0.49	0.03	0.00	0.00	0.16	0.11	0.00
Buck North	30.9	0.34	0.02	0.08	0.30	0.00	0.26	0.00	0.17	0.15
Cone Pond	19.9	0.64	0.03	0.05	0.09	0.00	0.10	0.08	0.41	0.23

Minor species measured but not included here were American basswood (*Tilia americana*), striped maple (*Acer pensylvanicum*) and balsam fir (*Abies balsamea*). Dominance is the fraction of the total basal area represented by each species averaged by plot (values above 0.10 given in bold).

Table 3. Net Potential N Transformation Rates in Plots in Which more Than 50% of the Basal Area was Dominated by Either Conifer Species or Individual Northern Hardwoods Species

Tree species with > 50% plot dominance	1-day nitrification all watersheds (μmol kg ⁻¹ h ⁻¹)		1-day nitrification no Sleepers W9C (μmol kg ⁻¹ h ⁻¹)		1-day ammonification all watersheds (μmol kg ⁻¹ h ⁻¹)		1-day ammonification no Sleepers W9C (μmol kg ⁻¹ h ⁻¹)		1-day overall mineralization all watersheds (μmol kg ⁻¹ h ⁻¹)		1-day overall mineralization no Sleepers W9C (μmol kg ⁻¹ h ⁻¹)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Conifer species	3.9a	0.7	3.8a	0.7	8.0a	1.9	7.5a	1.9	11.8a	2.3	11.3a	2.3
Sugar maple <i>A. saccharum</i>	86	86	85	85	86	86	85	86	86	86	85	85
Yellow birch <i>B. alleghaniensis</i>	15.6b	1.1	17.3b	1.1	13.5a	1.8	10.9a	1.5	29.1b	1.9	28.2b	1.7
American beech <i>F. grandifolia</i>	118	118	100	100	118	118	100	100	118	118	100	100
	15.2b	1.0	15.3bc	1.0	13.4a	1.7	13.5a	1.7	28.7b	1.7	28.7b	1.7
	163	163	159	159	163	163	159	159	163	163	159	159
	12.9b	1.7	12.9c	1.7	25.3b	3.1	25.3b	3.1	38.1c	3.0	38.1c	3.0
	43	43	43	43	43	43	43	43	43	43	43	43

In each column, different letters following the mean indicate significant differences using SNK contrasts ($P < 0.05$).

Table 4. Soil Chemical Data Averaged Across the Plots Within Each Watershed

Watershed	C (g kg ⁻¹)	N (g kg ⁻¹)	C/N ratio ^a	pH _{Ca} ^b	Ca (mmol kg ⁻¹)	Al (mmol kg ⁻¹)	K (mmol kg ⁻¹)	Mg (mmol kg ⁻¹)	Na (mmol kg ⁻¹)	Mn (mmol kg ⁻¹)
Sleepers W9-A	Mean	186.7	12.07	15.0	4.87	4.03	4.67	8.91	1.20	1.93
	SE	17.5	0.95	0.4	0.18	1.06	0.26	0.99	0.13	0.33
Brush G	Mean	232.3	13.34	16.8	3.72	3.45	5.08	9.97	0.98	1.36
	SE	15.3	0.73	0.3	0.07	0.37	0.27	1.17	0.05	0.33
Winnisook	Mean	344.5	17.56	19.7	3.11	7.85	8.68	6.12	1.72	1.13
	SE	12.7	0.58	0.5	0.04	1.33	0.46	0.38	0.08	0.15
Brush D	Mean	270.1	15.33	17.5	3.33	9.11	5.19	4.29	1.04	0.41
	SE	10.7	0.53	0.3	0.03	0.99	0.21	0.22	0.04	0.03
Lye	Mean	311.5	16.42	18.7	3.43	11.69	5.17	4.44	1.51	0.30
	SE	10.2	0.45	0.2	0.03	1.00	0.17	0.21	0.07	0.05
Buck South	Mean	334.5	16.37	20.3	3.35	8.14	5.91	4.51	1.47	0.79
	SE	16.2	0.76	0.3	0.04	3.40	0.30	0.48	0.07	0.18
Sleepers W9-C	Mean	273.2	15.39	17.7	4.47	3.59	7.97	11.17	1.48	1.48
	SE	21.5	1.17	0.4	0.15	0.65	0.47	0.76	0.10	0.20
HBEF W-7	Mean	317.4	16.46	19.0	3.50	13.27	6.97	5.68	1.46	0.36
	SE	10.6	0.46	0.2	0.03	1.52	0.28	0.33	0.05	0.03
Buck North	Mean	440.7	19.60	22.6	3.11	3.48	5.40	6.25	1.61	0.20
	SE	13.7	0.52	0.6	0.02	0.82	0.42	0.51	0.07	0.02
Cone Pond	Mean	354.7	13.09	27.4	3.35	8.54	11.32	6.01	2.53	1.11
	SE	14.8	0.52	0.9	0.04	1.53	0.75	0.40	0.12	0.14

^aMass basis. ^bSalt pH in 10⁻³ M CaCl₂.

Supplementary Appendix A). These 1-day rates have been found to be approximately three times the rates found in a typical 4-week incubation of mixed soil samples (Ross and others 2006). Four-week rates in mixed (bulked) soil samples from some of the same watersheds were found to be about two times those found in lab-incubated (10°C) intact cores (Ross and others 2004). Thus, for comparison with other reports of potential net nitrification rates, our samples would range between 0.2 and 2.5 mg N kg⁻¹ d⁻¹ for 4-week incubations of mixed samples (for example, buried bags) and 0.1 to 1.2 mg N kg⁻¹ d⁻¹ for 4-week incubations of intact cores. These rates are difficult to compare with rates reported on an area basis (that is, kg ha⁻¹ or g m⁻²) because of uncertainty in conversion factors but they are within the range of weight-based reports by a number of other investigators. For example, Ste-Marie and Houle (2006) found rates in three forest types in Quebec to range between 0.1 and 2.3 mg N kg⁻¹ d⁻¹ for 4-week in situ buried bag incubations; Jefts and others (2004a) reported rates between 0.06 and 2.80 mg N kg⁻¹ d⁻¹ for in situ and laboratory incubations of soils from the Bear Brook Watershed in Maine; Lovett and others (2004) reported 4-week lab rates between 0.0 and about 5.0 mg N kg⁻¹ d⁻¹ under different tree species in the Catskills of New York; Boggs and others (2005), in southern Appalachian deciduous forests, found somewhat higher net nitrification rates of 2.1–5.8 mg N kg⁻¹ d⁻¹ for 4-week laboratory incubations at 22°C. The net

nitrification rates we report in this study, therefore, appear comparable.

Although variability was relatively high within each watershed, there were significant differences between watersheds (Figure 2). The watersheds fell into four groups that we characterized as high (Sleepers W9-A, Brush-G, Brush-D, and Winnisook), medium (Lye and Buck-South), low (HBEF W-7, Buck-North, and Sleepers W9-C), and very low (Cone Pond) net nitrification potential. These results are consistent with previous studies at the same sites that used a variety of methods (Ross and Hales 2003; Ross and others 2004).

The fraction of inorganic N as NO₃⁻ (after 1 day of incubation) increased with increasing net nitrification rates (Figure 3 and Supplementary Appendix A). Our best fit model for watershed averages is expressed as:

$$\begin{aligned} \text{Fraction inorg. N as NO}_3^- \\ = 0.090 + 0.019 \times \text{nitrification rate} \\ (\mu\text{mol kg}^{-1} \text{ h}^{-1}; R^2 = 0.79, P < 0.001) \end{aligned}$$

Other researchers have proposed a link between high N deposition and a high fraction of NO₃⁻ (for example, Gilliam and others 2001; Boggs and others 2005). This fraction is highly dependent on the length of incubation, becoming higher with time (Ross and others 2004) and, thus, it is difficult to compare studies with only slightly different methods. However, it does appear that, even with the

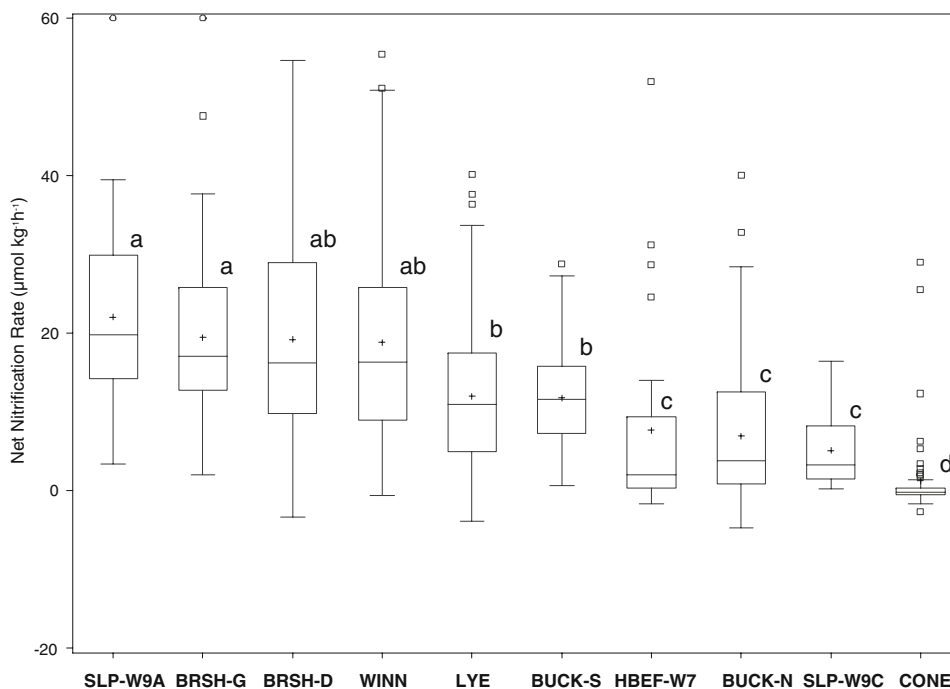


Figure 2. Boxplots of net potential nitrification rates of all sampling points in each watershed. The length of the *box* represents the interquartile range, the *plus sign* within the box is the mean and the *horizontal line* the median. The whiskers are 1.5× the upper and lower interquartile ranges. A different letter above each box indicates a significant difference ($P < 0.05$) between the watershed means using SNK contrasts and an ANOVA performed on log-transformed values (to provide a normal distribution of the data).

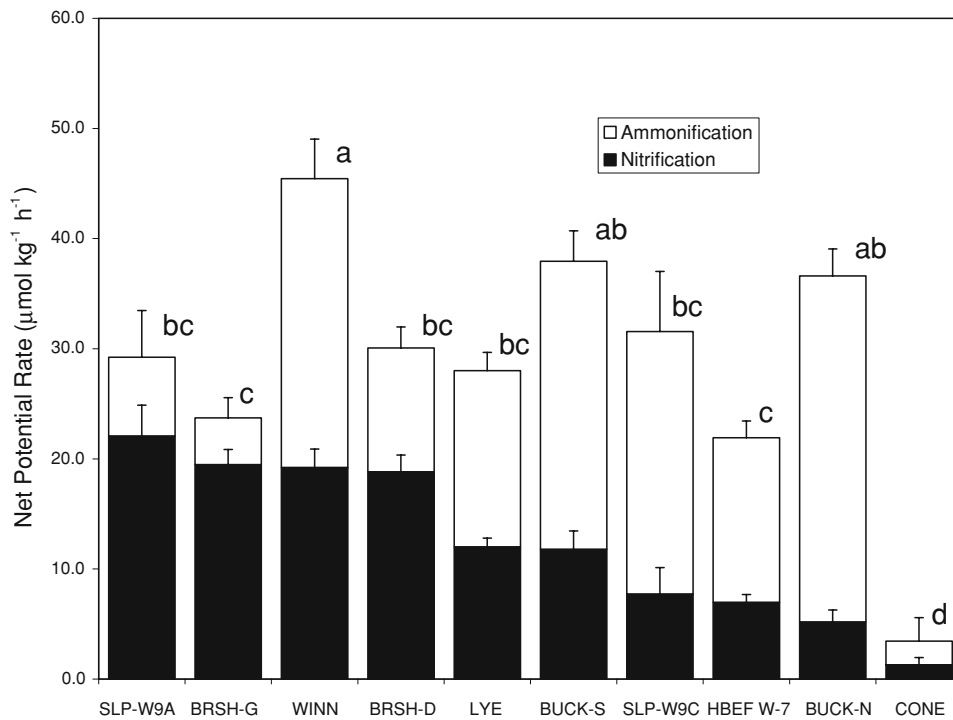


Figure 3. Mean potential net rates of mineralization (nitrification + ammonification) for each watershed measured by the 1-day method. Error bars represent the SE of the mean for each type of rate measurement. A different letter above each box indicates a significant difference ($P < 0.05$) between the watershed means for the sum of the two rates, using SNK contrasts.

1-day incubation, higher net nitrification rates will result in a higher fraction of NO_3^- regardless of the net ammonification rate.

The pattern of either net mineralization (sum of ammonification and nitrification) or 1-day net ammonification rates did not match that of nitrification (Figure 3). There were significant differences between watersheds in both the ammonification rates and the mineralization rates, but these rates did not fall into distinct groupings. It is interesting to note that the mineralization rates for the two watersheds at Buck and the two watersheds at Sleepers were not different whereas the nitrification rates were quite different. Although there was a higher net nitrification in one of the watersheds, the adjacent watershed had a higher ammonification rate, making the sums about equal.

Relationships with Topographical Metrics

No significant correlations (Spearman's rank) were found between watershed averages for N transformation rates and topographical metrics. These included the 10-m slope (GIS or field derived), point slope (60-cm slope), southness, elevation, and topographical index (TI) (Supplementary Appendix B). When correlating data from all transect points (a range of n from 575–608 because some topographical measurements were missing), nitrification was very weakly correlated with the TI

($r = 0.10$, $P = 0.013$) and better correlated with elevation ($r = 0.41$, $P < 0.001$). However, this relationship with elevation is likely spurious in that the watershed with the lowest nitrification rates (Cone Pond) was at the lowest elevation. When elevation for each point was expressed as relative to the lowest point in each watershed, no correlation was found. Within each watershed, there were some significant correlations between nitrification rates and topographic metrics (12 out of 60 pairs tested) but no patterns were evident (Table 5). For example, 10-m slope, measured either by GIS or by clinometer, was correlated in three watersheds, but not the same three and the correlations were both positive and negative. Other studies have found relationships with topographic features (Garten and others 1994; Ohrui and others 1999; Bohlen and others 2001). It may be that these features are proxies for other properties that more directly influence nitrification but are not found consistently at different watersheds. For example, aspect (or southness) in a watershed in the Appalachians of West Virginia may have a strong influence on soil moisture, affecting the distribution of ericaceous shrubs that, in turn, inhibit nitrification (Gilliam and others 2001). Working in similar watersheds, Christ and others (2002) did not find any topographical effect on net nitrification. Elevation differences across the Hubbard Brook Research Forest related to nitrification but also to changes in tree species and soil moisture (Bohlen

Table 5. Spearman's Rank Correlation Coefficients Between One-Day Net Nitrification Rates and Topographic Metrics Within Each Watershed

		Point slope	Southness	GIS slope	Clinometer slope	Topographic index	Elevation
Sleepers W9-A	<i>r</i>	-0.50	0.53	-0.51	-0.35	ns	ns
	<i>P</i>	0.008	0.004	0.007	0.077		
Brush G	<i>r</i>	ns	ns	ns	-0.25	ns	ns
	<i>P</i>				0.046		
Winnisook	<i>r</i>	ns	ns	ns	ns	ns	ns
	<i>P</i>						
Brush D	<i>r</i>	-0.41	ns	-0.33	-0.27	ns	0.40
	<i>P</i>	<0.001		0.003	0.015		<0.001
Lye	<i>r</i>	ns	ns	ns	0.16	-0.28	ns
	<i>P</i>				0.064	0.001	
Buck South	<i>r</i>	ns	-0.39	0.62	0.49	ns	ns
	<i>P</i>		0.081	0.003	0.028		
Sleepers W9-C	<i>r</i>	ns	ns	-0.35	ns	ns	ns
	<i>P</i>			0.076			
HBEF W-7	<i>r</i>	ns	ns	ns	ns	ns	0.20
	<i>P</i>						0.036
Buck North	<i>r</i>	-0.41	ns	ns	ns	ns	ns
	<i>P</i>	0.085					
Cone Pond	<i>r</i>	ns	-0.25	-0.24	ns	ns	ns
	<i>P</i>		0.061	0.065			

Only values with a significance of $P < 0.10$ are given; those with $P < 0.05$ are bold.

and others 2001). Greater N transformation rates at higher elevation in the Coweeta Hydrologic Laboratory (Kneopp and Swank 1998) may be explained by greater N pools at higher elevation from higher atmospheric inputs (Bonito and others 2003). A number of studies have found no linkage between a variety of topographical metrics and net nitrification rates at research sites in eastern USA and Canada (for example, Strader and others 1989; Zak and others 1991; Walley and others 1996; Foster and others 2005). Our data support the conclusions of these studies. If topographic features are important, their effect is secondary and this effect is not consistent across the northeastern USA.

Relationships with Tree Species Composition

Of the ten watersheds, eight would be classified as northern hardwood systems but with varying importance of the three dominant species (Table 2). Of the remaining two watersheds, Cone Pond was predominantly mixed conifer (*Picea rubens* and *Tsuga canadensis*) and Buck North a mix of these two conifer species with *Fagus grandifolia* and *Acer rubrum*. In the northern hardwood watersheds, the two at Sleepers were dominated by *Acer saccharum*; Brush D, Winnisook, and HBEF

W-7 had a high percentage basal area of *Betula alleghaniensis*; Buck South had a strong component of *Fagus grandifolia*; and Brush G and Lye were more mixed. The stem densities (including saplings) of the major species also varied among watersheds (Supplementary Appendix C) but not always in a pattern that matched the dominance values for trees with a dbh above 10 cm in Table 2.

Average watershed net nitrification rates showed a negative relationship to *Picea rubens* basal area (Figure 4). A similar strong exponential relationship was found with total conifer basal area and with conifer dominance, as the three were closely related.

$$\begin{aligned} \text{Ln of net nitrification rate } (\mu\text{mol kg}^{-1} \text{ h}^{-1}) \\ = 3.00 - 0.173 \times \text{conifer basal area } (\text{m}^2 \text{ ha}^{-1}) \\ (R^2 = 0.82, P < 0.001, n = 10) \end{aligned}$$

$$\begin{aligned} \text{Ln of net nitrification rate } (\mu\text{mol kg}^{-1} \text{ h}^{-1}) \\ = 3.03 - 4.29 \times \text{conifer dominance} \\ (R^2 = 0.82, P < 0.001, n = 10) \end{aligned}$$

No other averaged vegetation variable (species basal area, dominance, or density) was correlated with the averaged watershed rates of net nitrification, ammonification, or their sum. When exam-

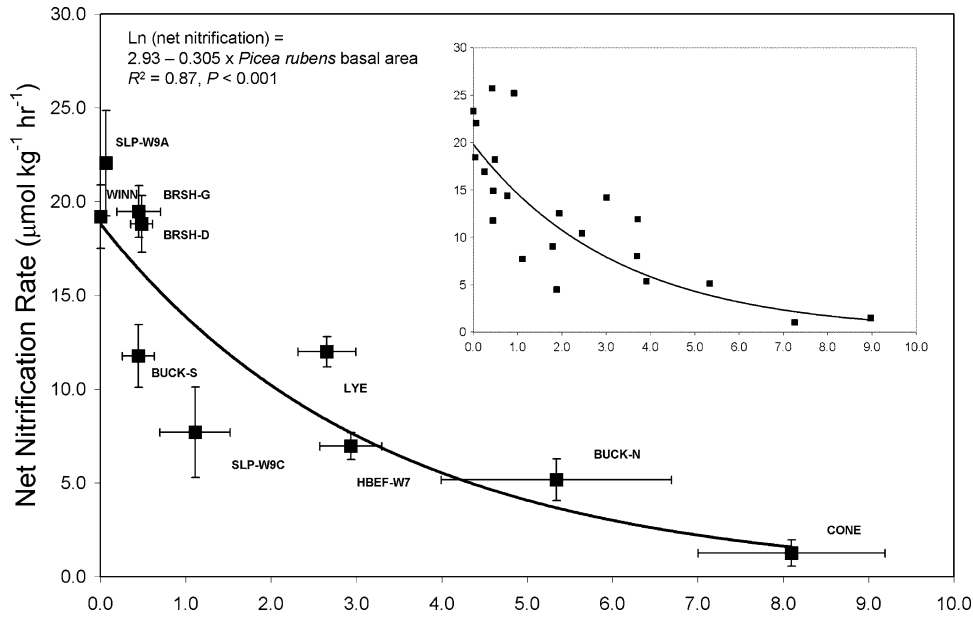


Figure 4. Average watershed potential net nitrification rates versus the watershed plot averages of *Picea rubens* basal area. Error bars represent the standard error. Points ($n = 28$) on the inset graph are means of individual sampling dates for all watersheds except Sleepers River and Buck Creek (which are represented by a single mean).

ining correlations between data from all the individual plots ($n = 572$ instead of 608 because vegetation from one sampling date at Winnisook was missing), weak positive relationships were found between net nitrification rates and either the basal area or dominance values for both *A. saccharum* and *B. alleghaniensis* ($0.19 < r < 0.22$, $P < 0.001$, $n = 572$). To further examine tree species effects, we separated the transect point data into plots having a dominance value above 0.50 for any of the three major hardwood species or conifers. Sleepers River W9-C had a high number of *A. saccharum*-dominated plots (18 of 27) but relatively low net nitrification rates. Because of possible bias from this one unusual watershed, statistical analysis was run both with and without W9-C data included. Net nitrification rates were much lower in the conifer-dominated plots than in any of the hardwood-dominated plots (Figure 5, Table 3). With all data included, there were no differences in net nitrification rates between the three hardwood species. With W9-C excluded, *A. saccharum* plots had higher rates than *F. grandifolia*-dominated plots (Figure 5, Table 3). Because of significantly higher 1-day ammonification rates in the *F. grandifolia*-dominated plots relative to the other three plots ($P < 0.001$), the mineralization rates were also highest under this species (Table 3). Some caution is needed in interpreting these results because the different watersheds were not represented equally in the different species-dominated plots. However, there appears to be ample evidence that plots dominated by *A. saccharum* did not have higher

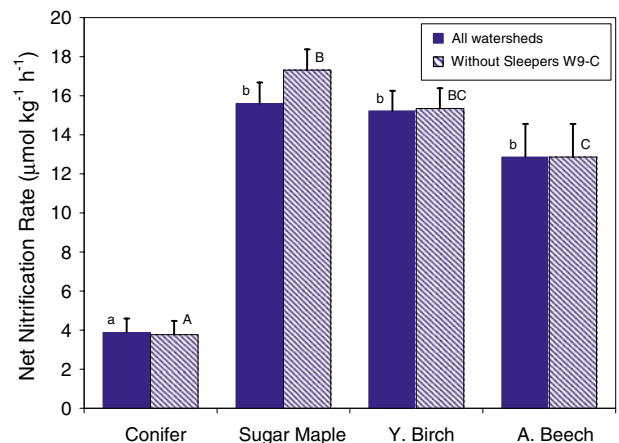


Figure 5. Mean of potential net nitrification rates for all plots dominated by more than 50% of either conifers or individual hardwood species. The hatched bars include all watersheds except Sleepers River W9-C, which appeared to have unusually low nitrification rates associated with high *Acer saccharum* dominance. Error bars represent the standard error. A different letter above each bar indicates a significant difference ($P < 0.05$) between the species means, using SNK contrasts. Separate contrasts were calculated with all watersheds (small letters) and without Sleepers River W9-C (capital letters).

net nitrification rates than those dominated by *B. alleghaniensis*. This is not consistent with previous studies in the northeastern USA (for example, Lovett and others 2004; Lovett and Mitchell 2004). If data were separated into plots containing no *A. saccharum* with dbh above 10 cm ($n = 250$) and those with at least one such stem ($n = 322$), there

was a significantly greater net nitrification rate in the plots with *A. saccharum* (13.7 vs. 10.7 $\mu\text{mol kg}^{-1} \text{h}^{-1}$, $P < 0.002$). Ross and others (2004) found a similar influence of the simple presence or absence of *A. saccharum* in a study that included many of the present watersheds. In the present study, we found better relationships between net nitrification rates and conifer species than with hardwood species but we cannot unequivocally conclude whether the effect is due to presence or absence. It is likely an interaction between the species and our data show the strongest effect of the presence of conifers on both soil C/N and net nitrification rates.

Relationships with Soil Physical Characteristics

The average forest floor (Oi, Oe, and Oa/A) depth for most watersheds was approximately 9–11 cm (range in averages of 6.5 to 20.5 cm, Supplementary Appendix D). There was no correlation between the watershed averages for horizon thickness and any of the N transformation rates. Within each of the ten watersheds, only three significant correlations were found between the thickness measurements and nitrification rates, with Spearman's r values all below absolute 0.50. Thus, the depth of the forest floor and the individual soil horizons within it does not appear to be a driving factor in determining nitrification rates.

Soil moisture content (Supplementary Appendix D) was strongly related to C (Ross 2007) and, thus, it is difficult to separate the effect of moisture from that of C. Ross (2007) developed a wetness ratio that expressed the moisture content as a fraction of that predicted by the soil's C content. A value above 1.0 indicates a condition wetter than normal field capacity. A wetness ratio of above 1.3 was usually associated with field observations of seeps or wetlands. Two watersheds, Lye and Sleepers W9-A, had relatively high average wetness ratios, indicating a large number of sampling points in wet areas. The nature of the wet areas was different in each watershed and affected the relationship to net nitrification. Lye had the lowest average slope (9.4°) and highest TI (8.08) of any watershed (Supplementary Appendix B) and its wet areas were topographical low spots or typical wetlands. Sleepers W9-A had a higher average slope and contained both typical wetlands and enriched seeps (that is, high pH and high Ca) not readily associated with surface topography ('sidehill swamps'). Soils in and near these enriched seeps had the highest net nitrification rates found throughout this study. Similar groundwater seeps have been shown to be

important sources of NO_3^- at Brush Brook (Hales and others 2007) and in the Catskills (Burns and others 1998). However, all such groundwater seeps are not necessarily sources of NO_3^- but appear to be limited to watersheds with high nitrification rates (West and others 2001). Because of these two differing sources of wetness, net nitrification correlated positively with the wetness ratio at Sleepers W9-A (Spearman's $r = 0.49$, $P < 0.49$) but not at Lye. Beyond this, there were no negative correlations within any watershed between net nitrification rates and either the wetness ratio or the soil moisture content. Excessive moisture does not appear to have limited net nitrification.

Relationships with Soil Chemical Characteristics

Watershed averages for a suite of soil chemical data on the sampled horizons (Table 4) showed a wide range in C, N, C/N ratio, pH, Ca, and extractable Al. For example, the two Sleepers River watersheds, underlain by partially calcareous bedrock, were relatively high in Ca and pH although low in C, N, and C/N. The low C and C/N are likely due to the richness of the site promoting high densities of *A. saccharum* and *T. americana* and the corresponding tendency to develop an A horizon rather than an Oa horizon. The average pH of the other watersheds ranged from 3.11 at Winnisook and Buck Creek North to 3.72 at Brush G (a watershed containing some high-pH seeps, also reflected in the somewhat higher average Ca). The two conifer-dominated watersheds (Cone Pond and Buck Creek North) had both the highest C concentrations and C/N ratios. Interestingly, extractable Al (that is, that removed with pH 4.8 ammonium acetate) was not highest in the conifer-dominated watersheds but, instead, at HBEF W-7 and Lye. This extractant removes both exchangeable (as defined by a neutral salt extraction) and some organically bound Al (Bartlett 1982) and it has been shown that Al buffers these organic soils (Skjyllberg 1999). Thus the most acid soils likely are higher in exchangeable H^+ and lower in exchangeable and complexed Al (Ross and others 1996). With the exception of some of the soils near high-pH seeps in the Brush Brook and Sleepers River watersheds, as discussed above, these soils were typical of acidic forested Spodosols and Inceptisols found in the northeastern USA (Ross and others 1996; David and Lawrence 1997).

The watershed means of net nitrification showed a curvilinear relationship to average watershed soil C/N ratio (Figure 6). A linear regression of the data

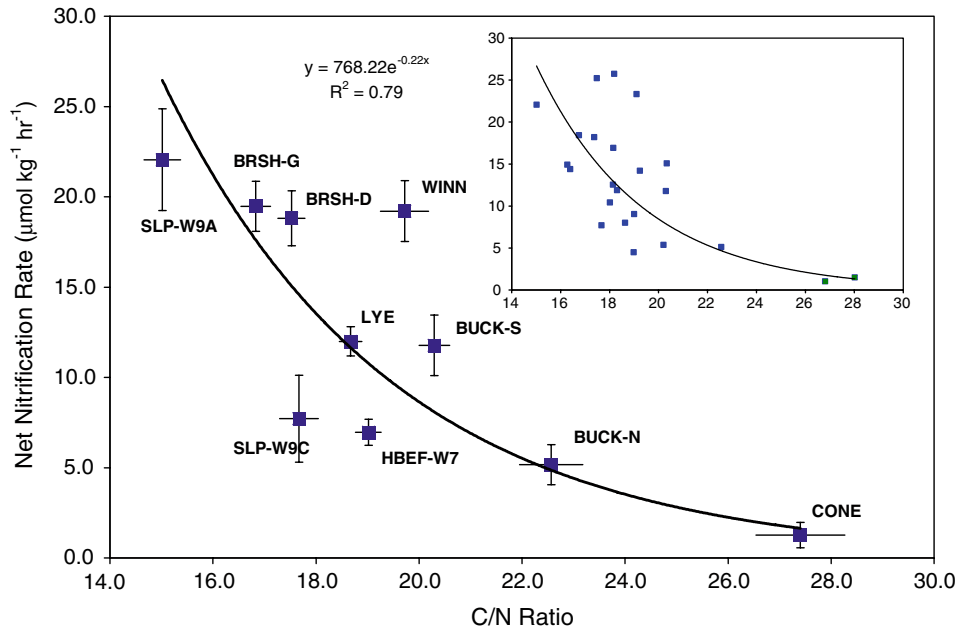


Figure 6. Average watershed potential net nitrification rates versus the watershed plot averages of the soil C/N ratio. Error bars represent the standard error. Points ($n = 28$) on the inset graph are means of individual sampling dates for all watersheds except Sleepers River and Buck Creek (which are represented by a single mean).

from all watersheds except Cone Pond showed 0 net nitrification at a C/N ratio of 25.7. The critical value, above which negligible net nitrification was found, was consistent with the range of 23 to 25 (mass basis) found in numerous other studies in North America, Europe, and New Zealand (Dise and others 1998; Gundersen and others 1998; Goodale and Aber 2001; Christ and others 2002; Lovett and others 2002; Vervaet and others 2003; Ross and others 2004; Parfitt and others 2005). Below a C/N of about 25, most other studies have found net nitrification but a linear relationship with the C/N ratio was usually lacking. When the nitrification rates were normalized to the soil C concentration in plots containing *A. saccharum*, Ross and others (2004) showed a linear relationship between these rates and the C/N ratio. In the present study, normalizing the data in this manner improved the linearity versus the C/N ratio but, in both methods of expressing the net rates, Sleepers River W9-C had a high residual. Higher net nitrification rates would have been predicted based on the relatively low C/N ratios. Again, this correlative analysis does not show cause and effect and more factors than the C/N ratio are apparently involved.

When examining the relationship between net nitrification rates and the C/N ratio in all 608 plots (Figure 7), the same general trend was observed. However, there was no relation at Winnisook where many samples had relatively high rates at C/N ratios above the range of 23 to 25. The other watersheds, more or less, all fit the curvilinear

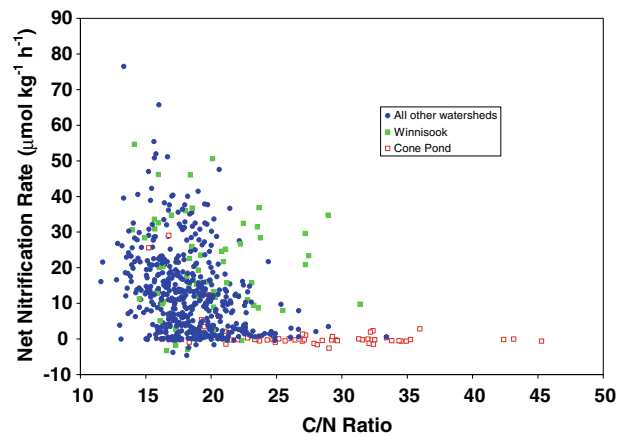


Figure 7. Potential net nitrification rates versus the soil C/N ratio for all plots ($n = 608$). The data from Cone Pond represent most of the soils with the highest C/N ratios. The nitrification rates at Winnisook did not conform to the general trend.

trend with very few points having measurable nitrification rates above a C/N ratio of 23 (although four of the watersheds had no samples above this value). Even Cone Pond samples, most of which were high C/N with negligible rates, showed this trend in a few low C/N samples (not coincidentally from a pocket of northern hardwoods) that had relatively high rates (Figure 7). No reason is evident for the anomalous behavior of the Winnisook samples, although it is likely the watershed most impacted by acidic deposition (see Table 1) and also by insect defoliation (Lovett and others 2006).

Table 6. Spearman's Rank Correlation Coefficients Between One-Day Net Nitrification or Ammonification Rates and pH, Extractable Al, and Extractable Ca Performed Within and Across All Watersheds

		Nitrification			Ammonification		
		pH	Al	Ca	pH	Al	Ca
Sleepers W9-A	<i>r</i>	ns	-0.52	0.33	ns	ns	ns
	<i>P</i>		0.005	0.088			
Brush G	<i>r</i>	ns	ns	0.28	ns	ns	ns
	<i>P</i>			0.027			
Winnisook	<i>r</i>	ns	ns	ns	ns	-0.25	0.25
	<i>P</i>					0.054	0.055
Brush D	<i>r</i>	ns	0.36	-0.29	-0.25	-0.27	0.44
	<i>P</i>		0.002	0.011	0.029	0.019	<0.001
Lye	<i>r</i>	ns	ns	ns	-0.27	-0.45	0.43
	<i>P</i>				0.002	<0.0001	<.0001
Buck South	<i>r</i>	ns	ns	ns	ns	ns	ns
	<i>P</i>						
Sleepers W9-C	<i>r</i>	0.38	ns	0.56	-0.55	ns	ns
	<i>P</i>	0.050		0.002	0.003		
HBEF W-7	<i>r</i>	ns	0.31	-0.39	ns	ns	0.18
	<i>P</i>		0.001	<0.001			0.054
Buck North	<i>r</i>	ns	ns	ns	ns	0.52	ns
	<i>P</i>					0.017	
Cone Pond	<i>r</i>	ns	ns	-0.22	ns	ns	ns
	<i>P</i>			0.092			
All watersheds	<i>r</i>	0.06	-0.07	0.02	-0.20	-0.18	0.10
	<i>P</i>	0.173	0.087	0.628	<0.001	<0.001	<0.001

Only values with a significance of $P < 0.10$ are given for the individual watersheds; those with $P < 0.05$ are bold.

Other soil factors that have been hypothesized to have a negative effect on net nitrification rates include low pH, low Ca, and high Al (Ste-Marie and Pare 1999; De Boer and Kowalchuk 2001; Gilliam and others 2005). None of these hypotheses were supported by our data. Although the highest nitrification rates were found at Sleepers River W9-A in high-pH, high-Ca soils, there were no correlations across all watersheds either between the averaged data or the individual plot data. The same was true with extractable Al concentrations, although it must be reiterated that this measure of Al is not the same as exchangeable, used in other studies—it is a measure of 'available' Al (Bartlett 1982). There were, however, weak correlations between net ammonification rates and pH, Ca, or Al when all plots were analyzed (Table 6), but not with the watershed averages. When correlations were performed within individual watersheds, there were interesting results (Table 6). Soil pH was only weakly correlated with net nitrification rates in one watershed, Sleepers W9-C. Although soil Ca concentration correlated with net nitrification in five of the ten watersheds, only three of these were positive correlations. Similarly, there were three

significant correlations with Al concentrations but two of these were positive. Net nitrification rates in soils from HBEF W-7 were the opposite of what would be predicted by the hypotheses; they were negatively correlated with Ca concentration and positively correlated with Al (Table 6). These correlations have relatively low *r* values and the inconsistency across watersheds suggests that these soil characteristics are not important factors in determining net nitrification rates. A number of studies have found a positive correlation between Ca and net nitrification rates (for example, Christopher and others 2006) but there is also usually an interaction with tree species and pH, that is, greater *A. saccharum* and higher pH with higher Ca. Because these variables covary, it is difficult to identify which exert the greatest influence on nitrification rates. Groffman and others (2006) found a decrease in net nitrification rates after watershed addition of Ca as wollastonite at HBEF, even though the pH had increased 0.5 and 1.0 units in the Oa and Oi/Oe horizons, respectively. The lack of response may be related to a microbial community that was adapted to the existing conditions. De Boer and others (1992), Martikainen

and De Boer (1993) and Rudebeck and Persson (1998) all showed either a lack of response or a decrease in net nitrification in response to liming acid forest soils. In southern Sweden, Falkengren-Grerup and others (1998) found the highest net nitrification rates in the most acid soils. The concept that low pH will limit nitrification may be an artifact from the time period when it was assumed that ammonia oxidizing autotrophs could not function in acid forest soils because the only culturable species required high pH. Similarly Al may be toxic to some species but there is no evidence that it limits autotroph function in acid forest soils where high soluble Al is natural. That being said, the combination of high Ca and high pH does create enriched sites with higher species diversity and likely higher biological activity. Continued addition of N to such systems might be expected to increase N transformation rates, and likely net nitrate production (Lovett and Mitchell 2004).

Watershed means of one-day net ammonification rates were linearly and positively related to the average soil N concentration:

$$\begin{aligned} \text{Net ammonification } (\mu\text{mol kg}^{-1} \text{ h}^{-1}) \\ = 3.95 \times \text{Soil N (g kg}^{-1}); R^2 = 0.73, P < 0.001 \end{aligned}$$

No such relationship was found with net nitrification, which was better correlated with average soil C, or mineralization. Caution is required in interpreting this relationship because low net ammonification rates can be the result of low mineralization rates, or, in the case of Sleepers W9-A, high nitrification rates and a high fraction of inorganic N as NO_3^- . The highest net ammonification rates were found at Buck Creek South, which had one of the lowest fractions of inorganic N as NO_3^- . These high rates at Buck Creek South could be related to the dominance of *F. grandifolia* that are in poor health because of the beech bark disease complex. Because NH_4^+ is retained by soil much more so than NO_3^- , higher 1-day net ammonification rates, regardless of overall inorganic rates, may relate to greater watershed soil N content.

Interrelationships

Exploratory analysis of the 608 transect data points using regression tree analysis illustrates complex interrelationships among the measured independent variables (Figure 8). Essentially, the presence or absence of larger than 10-cm dbh *P. rubens* was the single best discriminator of variation in nitrification rates (only 2 of 302 plots in the branch with *P. rubens* $< 0.11 \text{ m}^2 \text{ ha}^{-1}$ contained any measur-

able stems). The regression tree model shows the importance of the C/N ratio in discriminating low ($< 11 \mu\text{mol kg}^{-1} \text{ h}^{-1}$) nitrification rates for sites containing larger than 10-cm dbh *P. rubens* and the successive importance of extractable sulfur concentration, organic horizons (Oi + Oe) depth, conifer density, and density of *B. alleghaniensis* on discriminating high ($> 13 \mu\text{mol kg}^{-1} \text{ h}^{-1}$) rates for sites with negligible ($< 0.11 \text{ m}^2 \text{ ha}^{-1}$) *P. rubens* basal area.

Stepwise multiple regression analysis of all the data yielded similar explanatory variables for net nitrification rates. The first two variables selected were the C/N ratio and *P. rubens* density, respectively. The C/N variable was dropped in the last step of the analysis but both C and N concentration remained:

$$\begin{aligned} \text{Ln of net nitrification } (\mu\text{mol kg}^{-1} \text{ h}^{-1}) \\ = 2.70 - 0.0040 \text{ C} + 0.10 \text{ N} \\ - 0.48 \text{ conifer dominance} \\ - 1.24 \text{ } P. \text{ rubens density} \\ - 0.053 \text{ K} + 0.14 \text{ P } (R^2 = 0.41, n = 558) \end{aligned}$$

Interestingly, the extractable S concentration was chosen in the third step, similar to the regression tree analysis (Figure 8), but was dropped after the addition of K and P concentration. *A. saccharum* and *B. alleghaniensis* dominance or basal area were not chosen at any step ($P < 0.01$).

Stepwise regression analyses were also performed on the watershed averages ($n = 10$) and the seasonal/watershed averages ($n = 23$ with vegetation measurements), using the above variables. The number of explanatory variables that could be used was limited by the small n for both data sets but only conifer dominance was found to be significant, providing the same equation, for the watershed averages, given above under the section "Relationships with Tree Species Composition." For the seasonal/watershed averages:

$$\begin{aligned} \text{Ln of season/watershed avg. net nitr.} \\ (\mu\text{mol kg}^{-1} \text{ h}^{-1}) \\ = 3.07 - 4.25 \times \text{conifer density (m}^2 \text{ ha}^{-1}) \\ R^2 = 0.76, P < 0.001, n = 23 \end{aligned}$$

Because conifer dominance and *P. rubens* basal area were strongly correlated, the relationship for each with nitrification was similar, curvilinear when the nitrification rates were not log transformed, as in Figure 4, and strongly linear when transformed as in the above equations.

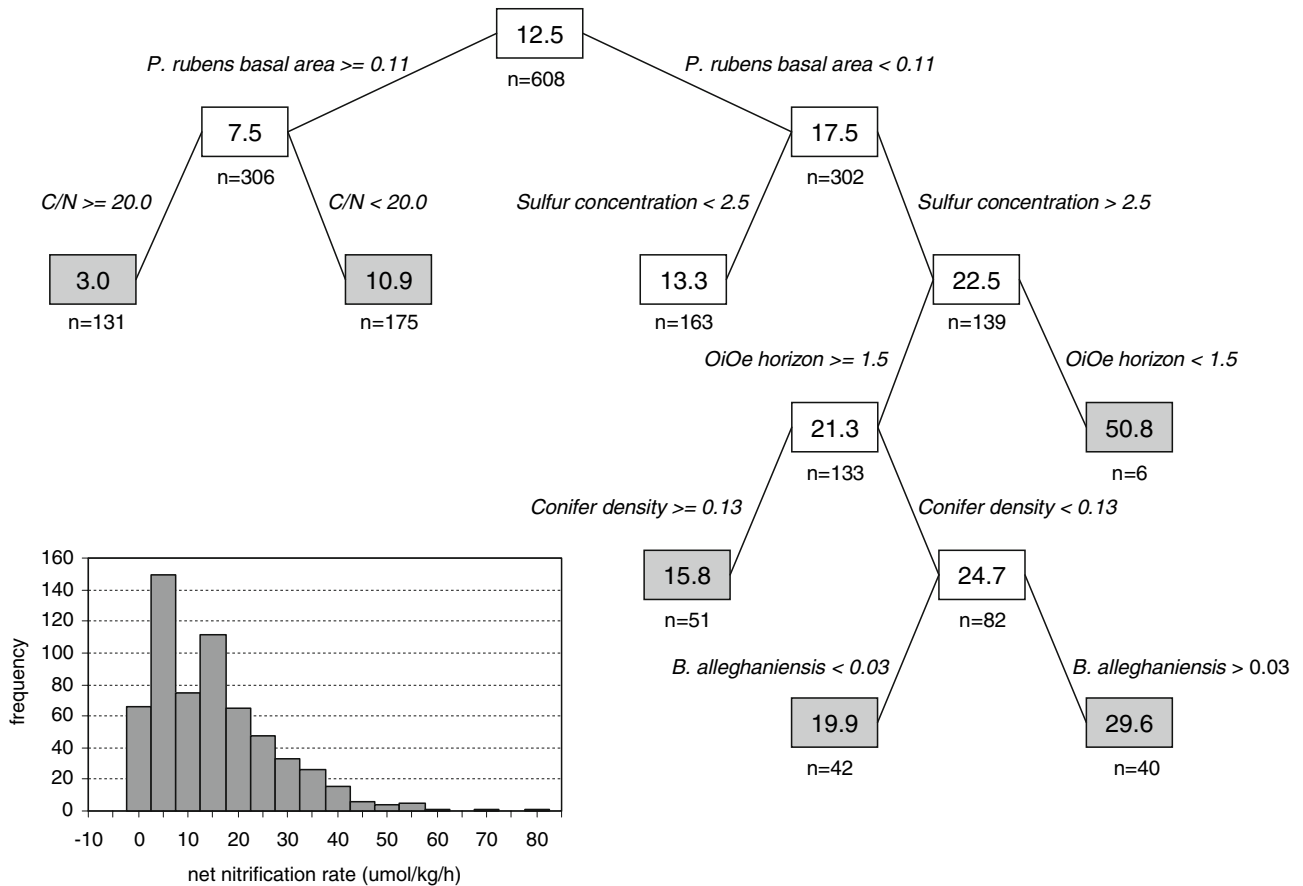


Figure 8. Regression tree model for 608 transect data points illustrating the effect of measured independent variables on partitioning nitrification rates. Values in boxes are 1-day net nitrification rates ($\mu\text{mol/kg/h}$), independent variables are in italics with threshold values that partition the groups. The number of observations in each group is given below the box. Gray boxes represent terminal branches on the tree. Inset graph shows distribution of nitrification rates for the 608 sample points.

Thus, similar to simple regression and regression tree analyses, stepwise multiple regression showed that the presence or absence of conifers was a better predictor of nitrification rates than any of the hardwood species, alone or combined. It is well established that different tree species can result in differences in forest floor C and C/N ratios (Finzi and others 1998; Lovett and others 2004).

Thus, there is an interaction between species, C/N, and net nitrification. The variation in average watershed C/N can be largely explained by either *P. rubens* basal area or the sum of the basal area of *A. saccharum* and *B. alleghaniensis* (Figure 9). Similar plots were obtained using the species dominance values (Table 2) or substituting all conifer species for *P. rubens*. Inclusion of *F. grandifolia* in the sum of the hardwood species, or using *A. saccharum* alone, decreased the significance of the relationship. This is consistent with the results for single-specie-dominated plots (Figure 5) in that

there was no difference in average C/N between *A. saccharum* and *B. alleghaniensis* (17.3 and 17.9, respectively) but a clear separation between these two species and conifers (average C/N of plots with > 50% conifer basal area = 24.4).

Watershed Uniqueness

Although there was a wide range in most of the variables measured, the uniqueness of individual watersheds sometimes confounds interpretations. The best example is Cone Pond which had by far the lowest ammonification and nitrification rates (Figure 3). This watershed has a history of widespread fire, the highest C/N ratios in the study, and the highest dominance of *P. rubens* and total conifers. These factors have been associated with low net nitrification potential rates (Goodale and Aber 2001). On the other hand, the forest floor was relatively thin and there was evidence of charcoal

in the horizons sampled. These factors have been associated with increased potential net rates of nitrification (DeLuca and others 2006). The very high C/N combined with high conifer dominance is probably the controlling factor for the very low rates (although the high C/N is partially due to the presence of charcoal). This is supported by higher rates from a few hardwood-dominated, lower C/N plots. Sleepers River W9-C was also unique in that it contained a strong component of *A. saccharum* yet had relatively low net nitrification potential rates.

For example, two plots located near each other had *A. saccharum* dominance values of 0.93 and 0.99, low C/N ratios of 13.1 and 15.1, and yet well-replicated average negative net nitrification.

CONCLUSIONS

Similar methods applied to this cross-site comparison of these ten watersheds revealed a number of factors that were clearly related to net nitrification rates and a number that were not.

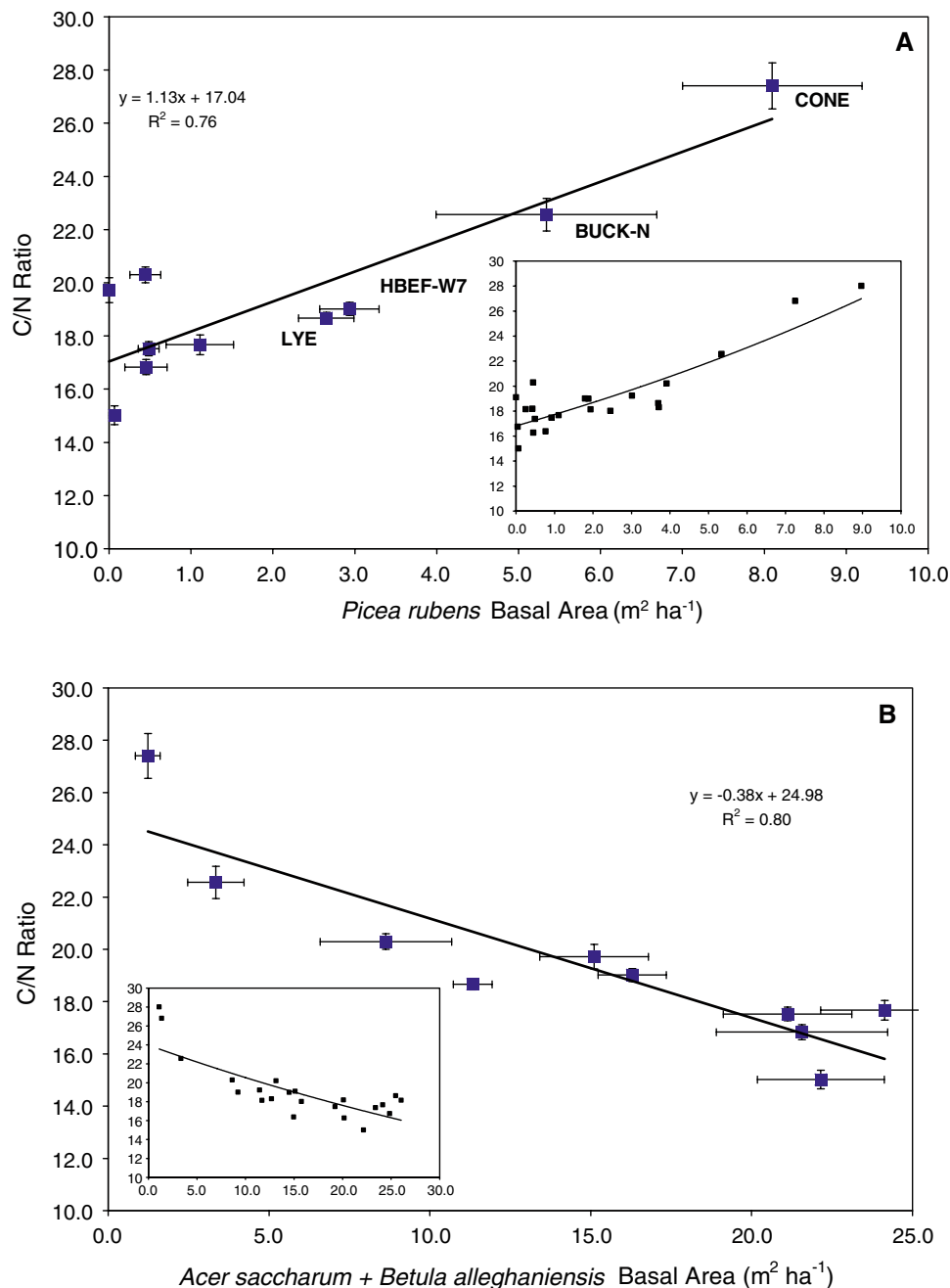


Figure 9. A Positive relationship between watershed plot averages of the soil C/N ratio and *Picea rubens* basal area. **B** Negative relationship between watershed plot averages of the soil C/N ratio and the sum of the basal areas of *Acer saccharum* and *Betula alleghaniensis*. Error bars represent the standard error. Points ($n = 28$) on the inset graphs are means of individual sampling dates for all watersheds except Sleepers River and Buck Creek (which are represented by a single mean).

- a. Topographical metrics did not explain any trends in the rates. In other studies of individual watersheds that found such relationships, it is likely that factors such as elevation or aspect were closely related to other causal factors such as tree species or moisture.
- b. We did not find any negative influence of soil acidity on nitrification rates.
- c. There was no apparent negative effect of relatively high concentrations of extractable Al.
- d. There was no overall positive effect of soil Ca on net nitrification rates. Although the highest rates were found in high-pH, high-Ca enriched sites, there was no overall correlation between Ca and nitrification. It is difficult to separate the effect of Ca from that of pH and also from that of tree species. Relationships found within individual watersheds between Ca and nitrification rates may reflect other causal factors.
- e. The dominance value, density, or basal area of *Acer saccharum* alone was not a robust predictor of nitrification rates.
- f. Either conifer dominance or *Picea rubens* basal area was the best single predictor of average watershed net nitrification.

Our study of 10 watersheds focused on the surface horizon (Oa or A) to provide a large sample *n*. Even though N cycling is generally much higher in O horizons, the greater mass of the B horizon makes the lower soil layer an important contributor (Bohlen and others 2001; Ollinger and others 2002; Jefts and others 2004b). The impact of continued N deposition will likely be seen throughout the soil profile as it appears to be a sink (Dittman and others 2007). Although there may be common factors across sites that explain the variation in net N transformation potential rates, there are as of yet unknown factors. Future studies should continue to explore these cross-site common factors and probe the interrelationships between tree species, soil properties, soil biota, and N transformations.

ACKNOWLEDGMENTS

This work was supported by the Northern States Research Cooperative (USDA award 02CA11242343 110) and USDA Hatch funds (VT-PS-00912). Numerous undergraduate students assisted with the field and laboratory efforts, including Abby Boak, Graham Burkhart, Shea Hagy, Rachel Hanish, Joe Ibrahim, Natalia Fajardo, Audrey Leduc, Isaac Paul, Lilah Ross, Chris Savastio, Stacy Thompson, Will Wheeler, Jason Wiener, and Kristin Williams. Cooperators at the research sites include Nancy Burt,

Kathy Donna, and Hal Bell of the US Forest Service at Lye; Ralph Perron of the US Forest Service at Cone Pond; Jon Denner of the USGS at Sleepers and Brush Brook; and Tom Suleski of the USGS at Buck Creek and Lye.

REFERENCES

- Aber JD, McDowell WH, Nadelhoffer KJ, Magill A, Berntson G, Kamakea M, McNulty SG, Currie W, Rustad L, Fernandez IJ. 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. *Bioscience* 48:921–34.
- Aber JD, Goodale CL, Ollinger SV, Smith ML, Magill AH, Martin RA, Hallett RA, Stoddard JL. 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? *Bioscience* 53:375–89.
- Aubert M, Bureau F, Vincelas-Akpa M. 2005. Sources of spatial and temporal variability of inorganic nitrogen in pure and mixed deciduous temperate forests. *Soil Biol Biochem* 37:67–79.
- Bailey SW, Hornbeck JW, Driscoll CT, Gaudette HE. 1996. Calcium inputs and transport in a base-poor forest ecosystem as interpreted by Sr isotopes. *Water Resour Res* 32:707–19.
- Bartlett RJ. 1982. Reactive Al in the Vermont soil test. *Commun Soil Sci Plant Anal* 13:497–506.
- Beven K, Kirkby MJ. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrol Sci Bull* 24:43–69.
- Boggs JLB, McNulty SGM, Gavazzi MJG, Myers JMM. 2005. Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forests. *Can J For Res* 35:1901–13.
- Bohlen PJ, Groffman P, Driscoll CT, Fahey TJ, Siccama TG. 2001. Plant-soil-microbial interactions in a northern hardwood forest. *Ecology* 82:965–78.
- Bonito GM, Coleman DC, Haines BL, Cabrera ML. 2003. Can nitrogen budgets explain differences in soil nitrogen mineralization rates of forest stands along an elevation gradient? *For Ecol Manage* 176:563–74.
- Breiman L, Friedman JH, Olshen RA, Stone CG. 1984. Classification and regression trees. Belmont, California: Wadsworth International Group, p 358.
- Burns DA, Murdoch PS, Lawrence GB. 1998. Effect of ground-water springs on NO₃⁻ concentrations during summer in Catskill Mountain streams. *Water Resour Res* 34:1987–96.
- Buso DC, Martin CW, Hornbeck JW. 1984. Potential for acidification of six remote ponds in the White Mountains of New Hampshire. Research Report Number 43. Durham, New Hampshire: Water Resources Research Center, p 157.
- Campbell JL, Eagar C, McDowell WH, Hornbeck JW. 2000. Analysis of nitrogen dynamics in the Lye Brook Wilderness Area, Vermont, USA. *Water Air Soil Pollut* 122:63–75.
- Campbell JI, Hornbeck JW, Mitchell MJ, Adams MB, Castro M, Driscoll CT, Kahl JS, Kochenderfer JN, Likens GE, Lynch JA, Murdoch PS, Nelson SJ, Shanley JB. 2004. Input-output budgets of inorganic nitrogen for 24 forest watersheds in the northeastern United States: a review. *Water Air Soil Pollut* 151:373–96.
- Christ MJ, Peterjohn WT, Cumming JR, Adams MB. 2002. Nitrification potentials and landscape, soil and vegetation characteristics in two Central Appalachian watersheds differing in NO₃⁻ export. *For Ecol Manage* 159:145–58.

- Christopher SF, Page BD, Campbell JL, Mitchell MJ. 2006. Contrasting stream water NO_3^- and Ca^{2+} in two nearly adjacent catchments: the role of soil Ca and forest vegetation. *Glob Chang Biol* 12:364–81.
- Compton JE, Boone RD. 2002. Soil nitrogen transformations and the role of light fraction organic matter in forest soils. *Soil Biol Biochem* 34:933–43.
- David MB, Lawrence GB. 1997. Soil and soil solution chemistry under red spruce stands across the United States. *Soil Sci* 161:314–28.
- De'ath G, Fabricius KE. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–92.
- De Boer W, Kowalchuk GA. 2001. Nitrification in acid soils: micro-organisms and mechanisms. *Soil Biol Biochem* 33:853–66.
- De Boer W, Tietema A, Klein Gunnewiek PJA, Laanbroek HJ. 1992. The chemolithotrophic ammonium-oxidizing community in a nitrogen-saturated acid forest soil in relation to pH-dependent nitrifying activity. *Soil Biol Biochem* 24:229–34.
- DeLuca TH, MacKenzie MD, Gundale MJ, Holben WE. 2006. Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. *Soil Sci Soc Am J* 70:448–53.
- Dise NB, Matzner E, Forsius M. 1998. Evaluation of organic horizon C:N ratio as an indicator of nitrate leaching in conifer forests across Europe. *Environ Pollut* 102:453–6.
- Dittman JA, Driscoll CT, Groffman PM, Fahey TJ. 2007. Dynamics of nitrogen and dissolved organic carbon at the Hubbard Brook Experimental Forest. *Ecology* 88:1153–66.
- Driscoll CT, Whittall D, Aber JD, Boyer EW, Castro M, Cronan C, Goodale CL, Groffman P, Hopkinson C, Lambert K, Lawrence GB, Ollinger SV. 2003. Nitrogen pollution in the northeastern U.S.: sources, effects and management options. *Bioscience* 53:357–74.
- Emmett BA. 2007. Nitrogen saturation of terrestrial ecosystems: some recent findings and their implications for our conceptual framework. *Water Air Soil Pollut Focus* 7:99–109.
- ESRI. 2006. ArcGIS geoprocessing tools. v.9.2. Redlands, California: Environmental System Research Institute.
- Falkengren-Grerup U, Diekmann M. 2003. Use of a gradient of N-deposition to calculate effect-related soil and vegetation measures in deciduous forests. *For Ecol Manage* 180:113–24.
- Falkengren-Grerup U, Brunet J, Diekmann M. 1998. Nitrogen mineralisation in deciduous forest soils in south Sweden in gradients of soil acidity and deposition. *Environ Pollut* 102:415–20.
- Finzi AC, Van Breemen N, Canham CD. 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecol Appl* 8:440–6.
- Foster N, Spoelstra J, Hazlett P, Schiff S, Beall F, Creed I, David C. 2005. Heterogeneity in soil nitrogen within first-order forested catchments at the Turkey Lakes Watershed. *Can J For Res* 35:797–805.
- Garten CT, Huston MA, Thoms CA. 1994. Topographic variation of soil nitrogen dynamics at Walker Branch watershed, Tennessee. *For Sci* 40:497–512.
- Gilliam FS, Yurish BM, Adams MB. 2001. Temporal and spatial variation of nitrogen transformations in nitrogen-saturated soils of a central Appalachian hardwood forest. *Can J For Res* 31:1768–85.
- Gilliam FS, Lyttle NL, Thomas A, Adams MB. 2005. Soil variability along a nitrogen mineralization and nitrification gradient in a nitrogen-saturated hardwood forest. *Soil Sci Soc Am J* 69:247–56.
- Goodale CL, Aber JD. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecol Appl* 11:253–67.
- Goodale CL, Aber JD, Vitousek PM. 2003. An unexpected nitrate decline in New Hampshire streams. *Ecosystems* 6:75–86.
- Groffman P, Fisk M, Driscoll C, Likens G, Fahey T, Eagar C, Pardo L. 2006. Calcium additions and microbial nitrogen cycle processes in a northern hardwood forest. *Ecosystems* 9:1289–305.
- Gundersen P, Callesen I, Dorich DA. 1998. Nitrate leaching in forest ecosystems is related to forest floor C/N ratios. *Environ Pollut* 102:403–7.
- Gundersen P, Schmidt IK, Raulund-Rasmussen K. 2006. Leaching of nitrate from temperate forests – effects of air pollution and forest management. *Environ Rev* 14:1–57.
- Hales HC, Ross DS, Lini A. 2007. Isotopic signature of nitrate in two contrasting watersheds of Brush Brook, VT. *Biogeochemistry* 84:51–66.
- Hart SC, Stark JM, Davidson EA, Firestone MK, Weaver RL. 1994. Nitrogen mineralization, immobilization, and nitrification. *Methods of soil analysis, part 2*. Madison: Soil Science Society of America, p 985–1018.
- Jefts SS, Fernandez IJ, Rustad LE, Dail DB. 2004. Comparing methods for assessing forest soil net nitrogen mineralization and net nitrification. *Commun Soil Sci Plant Anal* 35:2875–90.
- Jefts SS, Fernandez IJ, Rustad LE, Dail DB. 2004. Decadal responses in soil N dynamics at the Bear Brook Watershed in Maine, USA. *For Ecol Manage* 189:189–205.
- Johnson CE, Ruiz-Méndez JJ, Lawrence GB. 2000. Forest soil chemistry and terrain attributes in a Catskills watershed. *Soil Sci Soc Am J* 64:1804–14.
- Kneopp JD, Swank WT. 1998. Rates of nitrogen mineralization across an elevation and vegetation gradient in the southern Appalachians. *Plant Soil* 204:235–41.
- Lawrence GB, Lovett GM, Baevsky YH. 2000. Atmospheric deposition and watershed nitrogen export along an elevational gradient in the Catskill Mountains, New York. *Biogeochemistry* 50:21–43.
- Leavesley GH, Markstrom SL, Restrepo PJ, Viger RJ. 2002. A modular approach to addressing model design, scale and parameter estimation issues in distributed hydrological modelling. *Hydrol Processes* 16:173–87.
- Likens GE, Bormann FH. 1995. *Biogeochemistry of a forested ecosystem*. New York: Springer-Verlag, p 159.
- Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience* 56:395–405.
- Lovett GM, Mitchell MJ. 2004. Sugar maple and nitrogen cycling in the forests of eastern North America. *Front Ecol Environ* 2:81–8.
- Lovett GM, Rueth H. 1999. Soil nitrogen transformation in beech and maple stands along a nitrogen deposition gradient. *Ecol Appl* 9:1330–44.
- Lovett GM, Weathers KC, Arthur MA. 2002. Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. *Ecosystems* 5:712–8.
- Lovett GM, Weathers KC, Arthur MA, Schultz JC. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? *Biogeochemistry* 67:289–308.

- Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle A, Hari P, Jarvis PG, Kolari P, Kowalski AS, Lankreijer H, Law BE, Lindroth A, Loustau D, Manca G, Moncrieff JB, Rayment M, Tedeschi V, Valentini R, Grace J. 2007. The human footprint in the carbon cycle of temperate and boreal forests. *Nature* 447:849–51.
- Martikainen P, De Boer W. 1993. Nitrous oxide production and nitrification in acidic soil from a Dutch coniferous forest. *Soil Biol Biochem* 25:343–7.
- Mitchell MJ, Driscoll CT, Inamdar S, McGee GG, Mbila MO, Raynal DJ. 2004. Nitrogen biogeochemistry in the Adirondack Mountains of New York: hardwood ecosystems and associated surface waters. *Environ Pollut* 123:355–64.
- NRCS Soil Survey Staff. 2006. Keys to soil taxonomy. 10th edn. Washington DC: USDA Natural Resource Conservation Service. 332 p.
- Ohruj K, Mitchell MJ, Bischoff JM. 1999. Effect of landscape position on N mineralization and nitrification in a forested watershed in the Adirondack Mountains of New York. *Can J For Res* 29:497–508.
- Ollinger SV, Smith ML, Martin ME, Hallett RA, Goodale CL, Aber JD. 2002. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. *Ecology* 83:339–55.
- Parfitt RL, Ross DJ, Coomes DA, Richardson SJ, Smale MC, Dahlgren RA. 2005. N and P in New Zealand soil chronosequences and relationships with foliar N and P. *Biogeochemistry* 75:305–28.
- Romell LG. 1935. Ecological problems of the humus layer in the forest. Ithaca, New York: Cornell University, p 28.
- Ross DS. 2007. A carbon-based method for estimating the wetness of forest surface soil horizons. *Can J For Res* 37:846–52.
- Ross DS, Hales HC. 2003. Sampling-induced increases in net nitrification in the Brush Brook (Vermont) watershed. *Soil Sci Soc Am J* 67:318–26.
- Ross DS, David MB, Lawrence GB, Bartlett RJ. 1996. Exchangeable hydrogen explains the pH of Spodosol Oa horizons. *Soil Sci Soc Am J* 60:1926–32.
- Ross DS, Lawrence GB, Fredriksen G. 2004. Mineralization and nitrification patterns at eight northeastern US forested research sites. *For Ecol Manage* 188:317–35.
- Ross DS, Fredriksen G, Jamison AE, Wemple BC, Bailey SW, Shanley JB, Lawrence GB. 2006. One-day rate measurements for estimating net nitrification potential in humid forest soils. *For Ecol Manage* 230:91–5.
- Rudebeck A, Persson T. 1998. Nitrification in organic and mineral soil layers in coniferous forests in response to acidity. *Environ Pollut* 102:377–83.
- SAS Institute. 2003a. JMP statistical discovery software, version 5.1. Cary, North Carolina, USA: SAS Institute Inc.
- SAS Institute. 2003b. The SAS system for windows. Release 9.1. Cary, North Carolina, USA: SAS Institute Inc.
- Shanley JB, Kendall C, Smith TE, Wolock DM, McDonnell JJ. 2002. Controls on old and new water contributions to streamflow in some nested catchments in Vermont, USA. *Hydrological Processes* 16:589–609.
- Skyllberg U. 1999. pH and solubility of aluminium in acidic forest soils: a consequence of reactions between organic acidity and aluminium alkalinity. *Eur J Soil Sci* 50:95–106.
- Stark JM, Hart SC. 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature* 385:61–4.
- Ste-Marie C, Houle D. 2006. Forest floor gross and net nitrogen mineralization in three forest types in Quebec, Canada. *Soil Biol Biochem* 38:2135–43.
- Ste-Marie C, Pare D. 1999. Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. *Soil Biol Biochem* 31:1579–89.
- Strader R, Binkley D, Wells C. 1989. Nitrogen mineralization in high elevation forests of the Appalachians. I. Regional patterns in southern spruce-fir forests. *Biodegradation* 7:131–45.
- Templer P, Findlay S, Lovett G. 2003. Soil microbial biomass and nitrogen transformations among five tree species of the Catskill Mountains, New York, USA. *Soil Biol Biochem* 35:607–13.
- Thorne JF, Anderson JE, Horiuchi KM. 1988. Cation cycling in a base-poor and base-rich northern hardwood forest ecosystem. *J Environ Qual* 17:95–101.
- Van Miegroet H. 1995. Inorganic nitrogen determined by laboratory and field extractions of two forest soils. *Soil Sci Soc Am J* 59:549–53.
- Verchot LV, Holmes Z, Mulon L, Groffman PM, Lovett GM. 2001. Gross vs net rates of N mineralization and nitrification as indicators of functional differences between forest types. *Soil Biol Biochem* 33:1889–901.
- Vervaet H, Massart B, Boeckx P, Van Cleemput O, Hofman G. 2003. Use of principal component analysis to assess factors controlling net N mineralization in deciduous and coniferous forest soils. *Biol Fertil Soils* 36:93–101.
- Vesterdal L, Schmidt IK, Callesen I, Nilsson LO, Gundersen P. 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *For Ecol Manage* 255:35–48.
- Walley FL, van Kessel C, Pennock DJ. 1996. Landscape-scale variability of N mineralization in forest soils. *Soil Biol Biochem* 28:383–91.
- Wolf A, Beegle D. 1995. Recommended soil tests for macronutrients: phosphorus, potassium, calcium and magnesium. In: Sims JT, Wolf A, Eds. Recommended soil testing procedures for the northeastern United States. Newark, DE: University of Delaware. p 31–8.
- Zak DR, Pregitzer KS. 1990. Spatial and temporal variability of nitrogen cycling in northern Lower Michigan. *For Sci* 36:367–80.
- Zak DR, Hairston A, Grigal DF. 1991. Topographic influences on nitrogen cycling within an upland pin oak ecosystem. *For Sci* 37:45–53.