



Soil nitrification in a large forested watershed, Ranch Brook (Vermont), mirrors patterns in smaller northeastern USA catchments

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ABSTRACT

Soil nitrification rates in northeastern USA forested ecosystems appear to be regulated by a number of factors and are likely influenced by continuing N deposition. Among other factors, rates across small watersheds have been found to relate to the soil C/N ratio and tree species composition. We measured potential net nitrification rates in the Ranch Brook watershed, a relatively large (9.6 km²) forested basin in north central Vermont, to determine if relationships found in smaller catchments were evident at a larger scale. The stream network was divided into eight reaches to determine the variability within the watershed. Sampling points (6–15 along each reach, total of 74) were established along transects that paralleled the major watershed tributaries. At each point, we measured net rates of nitrification and ammonification in the uppermost humified soil horizon (Oa or A), using a one-day lab incubation. The basal area and density of all tree species were measured in a 10-m radius plot, along with a number of topographic metrics such as slope, aspect and elevation. In a stepwise regression, 39% of the variability in net nitrification rates was explained by the density of *Picea rubens*, elevation and the thickness of the forest floor. When net nitrification rates were normalized to soil C concentration, 60% of the variability was explained by soil N concentration, C/N ratio, elevation and the density of *P. rubens*. The significant negative influence of *P. rubens* density, and not basal area, was consistent with a previous cross-site study of 10 smaller northeastern USA watersheds. No influence of sugar maple basal area or density was found. Other relationships, similar to those found in smaller watersheds, were net nitrification rates predicted by the fraction of inorganic N as NO₃⁻, net nitrification predicted by the C/N ratio and the C/N ratio predicted by tree species. The consistent influence of tree species on potential net nitrification rates demonstrates a role for future forest management in influencing ecosystem processes.

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1. Introduction

In both Europe and North America, increases in N deposition on forested ecosystems have been linked to increased net nitrification, leading to greater N leaching and stream export (Driscoll et al., 2003; Gundersen et al., 2006). However, a connection between higher N deposition and increased nitrification rates has not always been clear (Aber et al., 2003). Different catchments have responded differently to increases in N deposition and there continues to be a need for greater clarity on the factors that control net nitrification (Campbell et al., 2004). Many variables have been related to nitrification rates, either within small (≤ 1 km²) watersheds (e.g., Ohri et al., 1999; Bohlen et al., 2001); across a number of small watersheds (e.g., Gilliam et al., 2001; Ross et al., 2009);

within larger (10¹–10² km²) watersheds (e.g., Venterea et al., 2003), or across geographic regions (10³–10⁴ km²) (e.g., Goodale and Aber, 2001; Lovett et al., 2002; Ollinger et al., 2002). High spatial variability of nitrification in forest soils has been well documented and may be one reason for variation in the documented controls on nitrification rates.

Another factor contributing to variation among studies is that a number of different methods have been used to measure nitrification (Jefts et al., 2004). Most measure only net nitrification and all measure only potential rates because the act of measurement necessarily involves some type of disturbance that, at least in some sites, can greatly accelerate net nitrification rates (Hart et al., 1994; Ross and Hales, 2003). Minor methodological differences among studies can obscure cross-site comparisons. Both the high spatial variability and the method variability make generalizations difficult.

Controls on nitrification can be roughly divided into soil factors, vegetation influences, topographic metrics (slope, aspect, elevation, land-form), environmental factors (moisture, temperature)

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and land-use history. A large number of studies have shown that the soil C/N ratio influences net nitrification, with little or no NO_3^- persisting above a ratio of between 23–25 (e.g., Christ et al., 2002; Lovett et al., 2002; Vervaet et al., 2003; Ross et al., 2004). Quite a few other studies have shown the influence of vegetation, especially the dominant tree species (e.g., Finzi et al., 1998; Lovett et al., 2004; Templer et al., 2005; Christopher et al., 2006; Christenson et al., 2009; Ross et al., 2009). As stated by Knoepp and Vose (2007), soil properties as influenced by vegetation communities may be the best approach for understanding controls. Land-use enters as a factor through its influence on the plant community, that is, stand age and fire history (Goodale and Aber, 2001); and through legacy effects of past agricultural practices (Compton and Boone, 2000). Other contributing regulatory factors, such as soil moisture and temperature, may be confounded by both topographical influences such as aspect and elevation and by differences in vegetation. For example, Gilliam et al. (2001) found that, in one watershed in the Fernow Experimental Forest, sites with a southwestern aspect had lower net nitrification. While this aspect would be expected to be warmer and drier, the main influence appeared to be the presence of ericaceous shrubs known to inhibit net nitrification. Teasing out primary controls and interactive effects on soil nitrification rates is still a work in progress.

Cross-site studies have been used to find factors common to more than one watershed. Sampling across 10 northeast USA watersheds, Ross et al. (2009) confirmed the importance of the soil C/N ratio and found that conifer basal area and density were the best plant community predictors of net rates. Contrary to other studies (e.g. Lovett et al., 2004; Ross et al., 2004), the presence or absence of sugar maple alone was not a robust predictor; although in combination with yellow birch it was well related to the soil C/N ratio. No influence was found of topographic metrics, or other soil characteristics such as soil pH or soil Ca status.

Compared to small watersheds, studies conducted within larger basins (10^1 – 10^2 km²) provide a wider range in the landscape variables examined. Venterea et al. (2004) sampled throughout the Hubbard Brook Experimental Forest boundaries (31.6 km²) and found that net nitrification was significantly higher with five landscape factors: higher elevation, southerly aspect, greater abundance of sugar maple and striped maple, and lower abundance of conifer species. Soil C/N ratio was also a significant explanatory variable. The influence of elevation has been found in other studies. Bonito et al. (2003) concluded that higher N transformation rates with elevation at the Coweeta Hydrological Laboratory were a function of the higher N pools, both in the soil and the vegetation. Higher precipitation in areas receiving elevated N deposition may have created this gradient. If so, this represents an external factor that may, in time, create additional changes in both soil and plant community characteristics.

In this study, we explored whether soil nitrification rates documented across the northeastern U.S. in a cross-site study of small watersheds (Ross et al., 2009) would be consistent with those measured along small reaches nested within a larger northeastern watershed. Of particular interest was whether we could see consistent controlling variables for nitrification across the region, regardless of the spatial scale of the study site and lower intensity of sampling within a larger study site. Ross et al. (2009) sampled 10 forested watersheds in New York, Vermont and New Hampshire with sampling, at most sites, along transects oriented parallel to the stream channels. This design was used to examine the relationship between soil net nitrification rates and stream nitrate export (in review). These 10 watersheds had a range in size from 7–217 ha (median 33 ha) and a watershed-mean elevation range of 557–945 m. This range in elevation among watersheds prevented a valid statistical examination of the independent effect of elevation on nitrification rates. Other topographic metrics, such as aspect, also

varied more among these small watersheds than within them. By locating this study within a larger watershed than those represented by the cross-site study (Ross et al., 2009), we also aimed to sample across a range of topographic conditions within a single site and determine the relative importance of landscape controls vs. soil and vegetation controls on soil nitrification rates. Our study was located in the Ranch Brook watershed in Vermont's Green Mountains, a 9.6 km² forested watershed within the Mt. Mansfield State Forest (Wemple et al., 2007). This area continues to receive elevated N in deposition, although regional rates have declined somewhat over the past decade (Aleksic et al., 2009). This anthropogenic deposition is a regional driver of stream nitrate export (Howarth et al., 2006). Both environmental management, through control of NO_x emissions, and forest management, through control of harvesting practices, will influence watershed N cycling.

2. Methods

2.1. Site description

The Ranch Brook watershed is located in the town of Stowe, Vermont on the eastern slopes of Mt. Mansfield (Fig. 1). The watershed is undeveloped, except for a network of recreation trails (Wemple et al., 2007). Elevation ranges from 335 to 1173 m. Upper elevations are generally steep with shallow, cryic soils and coniferous vegetation (balsam fir, *Abies balsamea* (L.) Mill., and red spruce, *Picea rubens* Sarg). Below about 750 m, the dominant vegetation is mixed northern hardwoods (sugar maple, *Acer saccharum* Marsh., yellow birch *Betula alleghaniensis* Britt. and American beech, *Fagus grandifolia* Ehrh.) with some other minor species including Eastern hemlock, *Tsuga canadensis* (L.) Carr. Soils below ~900 m are mostly Spodosols with the major mapping units being the Marlow very stony fine sandy loam, Colton-Duxbury loamy sands and sandy loams, and Tunbridge-Lyman fine sandy loams (Soil Survey Staff, 2009). The Marlow series (coarse-loamy, isotic, frigid Oxyaquic Haplorthods) can be relatively deep but with densic material (Cd horizon) near 70 cm. This Cd horizon restricts downward water movement. The Tunbridge (coarse-loamy, isotic, frigid Typic Haplorthods) and Lyman (loamy, isotic, frigid Lithic Haplorthods) series differ in their depth to bedrock (50–100 and 25–50 cm, respectively) but neither have a Cd horizon. Both series are generally found at somewhat higher elevations than the Marlow. The Colton (sandy-skeletal, isotic, frigid Typic Haplorthods) and Duxbury (sandy, isotic, frigid Typic Haplorthods) series are both relatively deep (bedrock > 150 cm), sandy and have no densic materials restricting downward water movement. These series are mapped along the main branch of Ranch Brook (Soil Survey Staff, 2009). All these soil series are typically acidic podzols.

2.2. Field procedures

Our sampling design was motivated by an interest in how spatial patterns of soil nitrification might drive stream NO_3^- export. Recent studies have demonstrated the importance of stream-proximal zones in connecting hillslopes and channels (Sidle et al., 2000; Jencso et al., 2009) and we intentionally biased our sampling points towards the stream channels. Transects were laid out parallel to the major tributaries within eight subwatersheds of the Ranch Brook watershed (Fig. 1), consistent with transect design at most of the sites sampled in Ross et al. (2009). The relationship between nitrification and stream nitrate export is still being explored, but the similar sampling design in this study and Ross et al. (2009) allows for a comparison of factors affecting net nitrification rates. Although the scale in Fig. 1 suggests that the sampling points were often quite close to the stream, they were

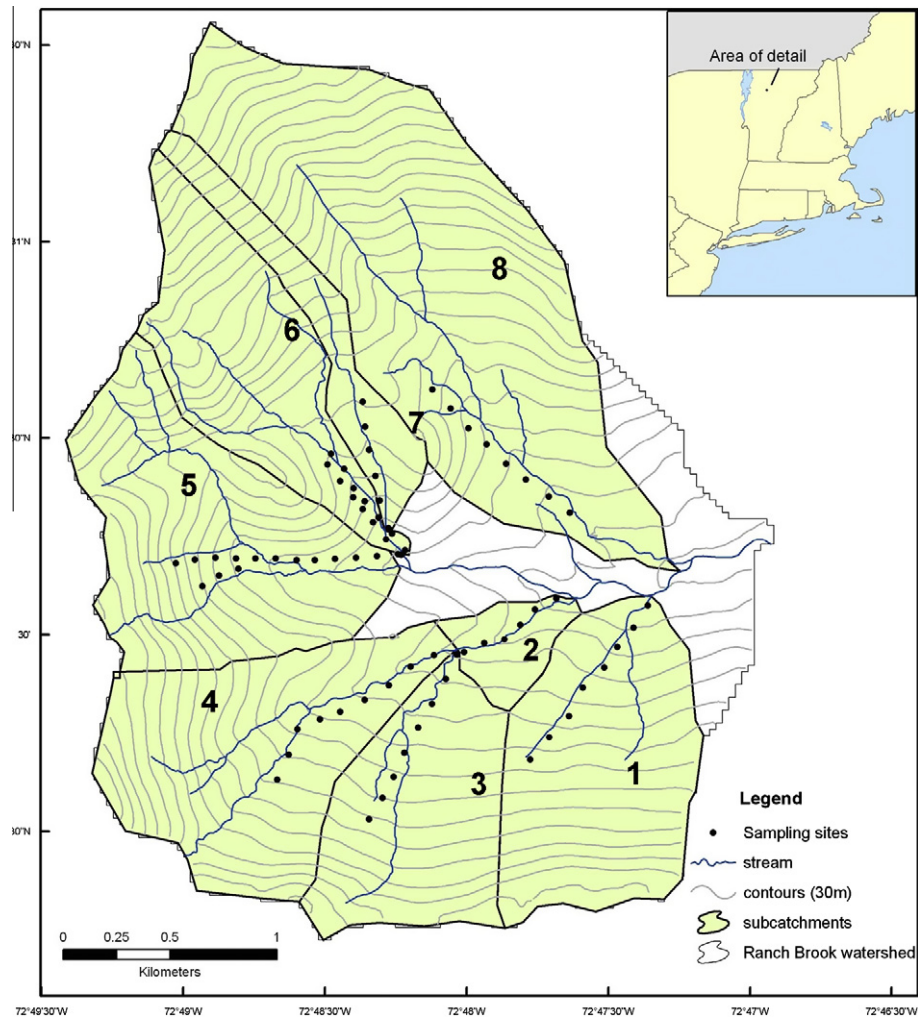


Fig. 1. Map of the Ranch Brook watershed showing the eight reaches and their contributing area, sampling transects, stream network and 30-m contours.

purposefully kept out of the riparian zone, which we defined as the saturated area adjacent to the stream, typically less than 1–2 channel widths. Sampling points were spaced approximately 125 m apart and three separate soil samples were taken, one from the center point and one each 1.0 m north and south (magnetic or 15° from true). Transects 2–6 were sampled during the 2004 field season and the rest were sampled in 2005. The topmost humified horizon (Oa or A) that was at least 2 cm thick was sampled after removing a small square ($\sim 300 \text{ cm}^2$) of Oi/Oe material. These soils usually had either an Oa ($>20\% \text{ C}$) or an A ($<20\% \text{ C}$) horizon just below the Oe, and not both. We sampled only the near-surface Oa or A horizon instead of, or in addition to, a depth increment of the mineral soil. The higher organic matter near-surface horizons are relatively easy to sample and have been used to show clear differences in net nitrification rates among plots and watersheds (Ross et al., 2004, 2009). About 250 mL of this horizon was sampled with a trowel and mixed by hand, with larger roots, rocks and other debris discarded. Potential net nitrification and ammonification were measured with the 1-day method of Ross et al. (2006). This method simply uses a short-term incubation of a disturbed, composite sample and has been shown to correlate well with both longer incubations of disturbed samples and intact cores (Ross et al., 2004; Ross et al., 2006). Briefly, the method is as follows: as soon as feasible after sampling, duplicate 10 mL of soil were packed into a volumetric spoon, transferred to 50-mL centrifuge tubes, shaken with 25 mL of $2 \text{ mol L}^{-1} \text{ KCl}$ for 15 min and put under ice in a por-

table cooler. The remaining soil was sealed in a polyethylene bag, stored in the field under ice packs, returned to the lab later the same day and incubated overnight at 10°C in the dark. The field-extracted samples were centrifuged in the lab the next day. Duplicate sub-samples from the stored bags were extracted approximately 24 h later in the lab. All soil subsamples with added KCl, field or lab, were stored under similar conditions and for approximately the same amount of time (20 h) before centrifugation.

In addition to the sampling described above, we measured the thickness of the combined Oi/Oe horizon and of the Oa or A horizon sampled. The local topography at each sampling point was estimated using a 60-cm level and tape measure to determine the short-range slope, i.e. microtopography. Other topographical metrics for each transect point were measured from the central sampling point. A clinometer was used to determine the 10-m slope downhill from each center point. A compass was used to determine aspect and 'southness' was calculated 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. Elevation was taken from the available digital elevation model (DEM) using ArcGIS and GPS data from a Trimble GeoExplorer 3. The GPS data were differentially corrected post-collection using a nearby base station to improve horizontal accuracy to about 2 m.

Tree species density and basal area were measured in a 10 m radius plot around the central point. Any tree with a diameter-breast-height $> 10 \text{ cm}$ was measured and identified by species.

All stems greater than 1 m in height were counted by species. This size plot was used to encompass the possible influence of nearby species on the soil properties through leaf litter and root inputs.

2.3. Lab procedures

Nitrate and NH_4^+ were determined by flow injection on an automated colorimeter (Lachat QuickChem AE, Hach Inc., Loveland, CO) using the Cd-reduction method for NO_3^- and the salicylate–nitroprusside method for NH_4^+ . The KCl extracts were kept refrigerated or frozen if the analysis did not take place within a few days. We have found that the extracts slowly increase in NH_4^+ , but not NO_3^- , concentration with storage time, presumably from hydrolysis of organically bound N (Ross et al., 2006). Samples from transect 3 were not run in a timely manner nor frozen and the NH_4^+ concentrations were obviously elevated relative to other samples. For this reason, NH_4^+ results from this transect have been omitted from the data. To determine soil moisture and dry weights for rate calculation, duplicate 10-mL samples were weighed and dried at 80 °C. Net N potential transformation rates were calculated by final NO_3^- or NH_4^+ concentrations minus initial field concentrations. The results were expressed per kg of dry soil, using a solution:soil ratio that incorporated the field soil moisture. The NO_3^- fraction of the total inorganic N after 1 day of incubation was also calculated.

The wetness ratio developed by Ross (2007) was calculated to compare actual moisture vs. that predicted at field capacity by soil C. Gravimetric soil moisture at field capacity ($\text{kg}^{-1} \text{kg}^{-1}$) was predicted by $0.080 + 0.057 \times C$ (g kg^{-1}), an equation developed using a large dataset of Oa and A horizons from across the northeastern USA. The wetness ratio is the actual gravimetric water content at sampling ($\text{kg}^{-1} \text{kg}^{-1}$) divided by the predicted. Ross (2007) showed that wetness ratios above 1.25 were associated with poorly drained soils and a ratio as low as 0.49 could be found after extended drought.

Total soil C and N were determined by a CN elemental analyzer (Flash EA-1112, CE Elantech, Lakewood, NJ) on the same subsamples used to determine dry weights, after grinding to pass through a 0.125 mm screen. Standards and quality control samples were soil standards obtained from the North American Proficiency Testing program. Because Ross et al. (2009) found no cross-site effect of soil pH or Ca and Al (extracted with pH 4.8 NH_4 -acetate), we did not include these analyses in our study. A small subset of 21 samples (7 points from transect 5) did have pH measured (2:1 V:V in $10^{-3} \text{ mol L}^{-1} \text{ CaCl}_2$) and the mean pH of these samples was 3.69 (the mean of watershed averages from Ross et al. (2009) was 3.62).

2.4. Statistical methods

All statistical analysis was performed using SAS 9.1 (SAS Institute, Cary, NC). For most comparisons, results from the three soils sampled at each transect point were averaged before analysis. Initial examination of overall relationships was done by Spearman's rank correlation because not all data were normally distributed. Regression analysis was performed to determine controlling variables of nitrification. Soil N rate measurements (field- NO_3^- and NH_4^+ concentrations, net nitrification and ammonification rates and their sum, and the fraction of inorganic N as NO_3^- found after 1 day) were treated as dependent variables in a forward step-wise multiple regression using 24 predictor variables (soil C, N, C/N, wetness, two horizon thicknesses, two slopes, southness, elevation, plot basal area, relative dominance of nine tree species, and stem density of the three major hardwood species and red spruce). The same regressions were performed with the net nitrification normalized to both C and N concentrations ($\mu\text{mol kg}^{-1} \text{ C h}^{-1}$ and $\mu\text{mol kg}^{-1} \text{ N h}^{-1}$, respectively). Inclusion and exclusion criteria were set at 0.05. Studentized residuals were plotted against pre-

Table 1
Reach characteristics.

Reach	Contributing area (ha)	Number of points	Average point elevation (m)	Average point slope (°)	Average point southness ^a
1	87	8	516	11.8	−0.95
2	58	6	469	8.8	0.23
3	63	8	597	7.9	−0.73
4	125	9	593	11.9	−0.59
5	142	15	592	17.3	0.70
6	91	14	569	9.4	0.75
7	33	6	603	15.8	0.41
8	246	8	530	12.9	0.52
Overall	844	74	564	12.2	0.12

^a A value of 1.0 is due magnetic south and −1.0 due magnetic north.

dicted values to assess distribution of variance and a normalized probability plot of residuals was examined for linearity. These assumptions were not met for all variables except net nitrification and the fraction of inorganic N as NO_3^- . Log transformation of the remaining dependent variables resulted in satisfactory residual variance distribution and normality.

For within basin comparisons, the sampling was divided into eight reaches with 6–15 transect points within each subwatershed (Fig. 1, Table 1). Three samples, 1 m apart, were taken at each transect point and, for statistical comparison of reaches, these would normally be averaged. To examine the relative contribution of variance from data compared among reaches, transect points and sampling units, we used the VARCOMP procedure (SAS, 2003). For nitrification, the variance ascribed to sampling units (59.8) was higher than that found among transect points (47.1) and both were much higher than among reaches (3.2). Because of this, it can be argued that the distribution of sampling units was as random as the distribution of transect points and an ANOVA of the reach nitrification data can be performed using data from all sampling units. This increases the sample *n* by a factor of 3. Results from two approaches are presented, i.e. one with transect point as the experimental unit, as would be typical, and one with each sample as the experimental unit. The ANOVA was performed using the general linear model procedure and the Student–Newman–Keuls multiple range test was used to contrast reach means (SAS, 2003). We also tested the minimum number of transect points needed, based on the variability within our data, to detect a significant difference in nitrification rates among reaches using the least significant number test in JMP software (SAS, 2008).

Statistical comparison of the relationship between the fraction of inorganic N as NO_3^- and net nitrification rates in this study with that found by Ross et al. (2009) was performed in SAS by the homogeneity of slopes test (SAS, 2003). The confidence intervals for net nitrification rates predicted by equations derived from Ross et al. (2009) were also generated in SAS using the simple regression function in analyst mode (SAS, 2003).

3. Results

3.1. Nitrification and ammonification rates

The overall mean nitrification rate of $12.5 \mu\text{mol kg}^{-1} \text{ h}^{-1}$ (Table 2) was close to the mean ($12.4 \mu\text{mol kg}^{-1} \text{ h}^{-1}$) found in 10 much smaller northeastern watersheds by Ross et al. (2009). The range of rates among reaches in this study, 8.2–17.0 $\mu\text{mol kg}^{-1} \text{ h}^{-1}$, was somewhat narrower than the range found in the smaller watershed study, 1.3–22.1 $\mu\text{mol kg}^{-1} \text{ h}^{-1}$ (Ross et al., 2009). The fraction of inorganic N found as nitrate after 1 day was a good

Table 2
Nitrification and ammonification rates from points within each reach. Different letters within a column denote significant differences among reach means with all replicates treated as random samples (i.e. not averaged by point). No significant differences were found in ammonification rates; few significant differences in any column were found if replicates were averaged before analysis.

Reach	NO ₃ ⁻ at time 0 (mmol kg ⁻¹)	1-day nitrification (μmol kg ⁻¹ h ⁻¹)	NH ₄ ⁺ at time 0 (mmol kg ⁻¹)	1-day ammonification (μmol kg ⁻¹ h ⁻¹)	Sum of 1-day rates (μmol kg ⁻¹ h ⁻¹)	Fraction of inorganic N as NO ₃ ⁻
1	0.15 ^b	16.5 ^{ab}	0.44 ^b	9.1	25.6 ^{ab}	0.42 ^a
2	0.05 ^b	8.2 ^b	0.45 ^{ab}	9.9	18.1 ^b	0.26 ^{bc}
3	0.31 ^a	12.6 ^{ab}	nd	nd	nd	nd
4	0.13 ^b	14.0 ^{ab}	0.49 ^{ab}	16.9	31.0 ^a	0.33 ^{abc}
5	0.04 ^b	13.0 ^{ab}	0.49 ^{ab}	8.3	21.3 ^{ab}	0.37 ^{ab}
6	0.05 ^b	9.0 ^{ab}	0.55 ^{ab}	20.5	29.4 ^{ab}	0.20 ^c
7	0.07 ^b	10.1 ^{ab}	0.60 ^a	8.0	18.1 ^b	0.26 ^{bc}
8	0.32 ^a	17.0 ^a	0.40 ^b	15.0	32.1 ^a	0.48 ^a
Overall mean	0.13	12.5	0.49	13.1	25.6	0.33
Overall std. err.	0.02	1.0	0.02	1.4	1.4	0.02

predictor ($R^2 = 0.87$, $P = 0.001$) of net nitrification rates (Fig. 2) and quite similar to the finding in Ross et al. (2009). The slopes of the least-squared linear fits of the two data sets in Fig. 2 are not significantly different ($P = 0.37$). The confidence intervals overlap the measured data for nitrification rates predicted from the fraction of inorganic N as NO₃⁻ in this study by using the relationship from Ross et al. (2009).

Examining all data across the watershed, forward stepwise multiple regression analysis found that only about 40% of the variation in nitrification rates could be explained by the 24 variables (soil C, N, C/N, wetness, horizon depths, four topographic metrics, total basal area and 13 species metrics of relative dominance and density). The first variable entered was red spruce density (partial $R^2 = 0.19$), which had a negative influence on nitrification. Although red spruce was a relatively minor component of ≥ 10 cm-basal area, stem density (which included small stems) was relatively high compared with others species. Red spruce density also was a significant explanatory variable in the larger data set from 10 watersheds in Ross et al. (2009). In the present study, two additional variables met the inclusion criteria ($\alpha = 0.05$). Elevation had a positive influence (partial $R^2 = 0.14$) and surface soil thickness (Oa or A + Oi + Oe) was a minimally significant negative factor (partial $R^2 = 0.05$). The resulting equation was:

$$\begin{aligned} \text{Nitrification } (\mu\text{mol kg}^{-1}\text{h}^{-1}) \\ = -8.12 - 42.55 \times \text{RSD} + 0.050 \times \text{Elev} - 0.33 \times \text{TSH}, \\ R^2 = 0.39, \quad n = 71 \end{aligned}$$

RSD = red spruce density (m² ha⁻¹), Elev = elevation (m), TSH = thickness of surface horizons (cm).

If the regression was performed with nitrification rates normalized to the soil's C concentration, and C removed as an independent variable, the overall relationship was stronger, with red spruce density and elevation still explanatory variables:

$$\begin{aligned} \text{Nitrification } (\mu\text{mol kg}^{-1}\text{C h}^{-1}) = 105.4 - 4.28 \times \text{N} - 4.89 \times \text{C/N} \\ + 0.21 \times \text{Elev} - 134.7 \times \text{RSD}, \\ R^2 = 0.60, \quad n = 71 \end{aligned}$$

N = total soil nitrogen in g kg⁻¹, C/N = is the ratio of soil carbon to nitrogen and other terms are as defined above.

Similar results ($R^2 = 0.56$) were found using the nitrification rates normalized to N, with the selected variables being C concentration along the same three selected above for the unadjusted nitrification rates. The fraction of inorganic N as NO₃⁻ was also predicted by the same set of independent variables:

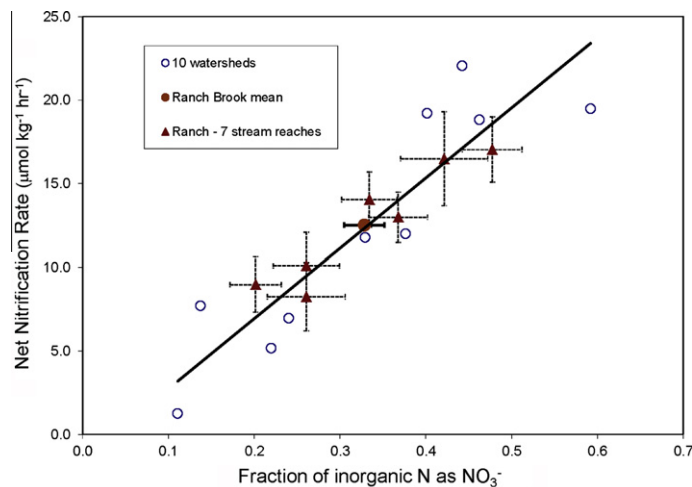


Fig. 2. The fraction of inorganic N as NO₃⁻ after 1 day of incubation vs. the potential net nitrification rate. The regression line and 10 watershed points are from Ross et al. (2009). Error bars represent the standard error of all data (replicate soil samples within each transect point treated as random). Data from reach 3 for NH₄⁺ was not valid and not included.

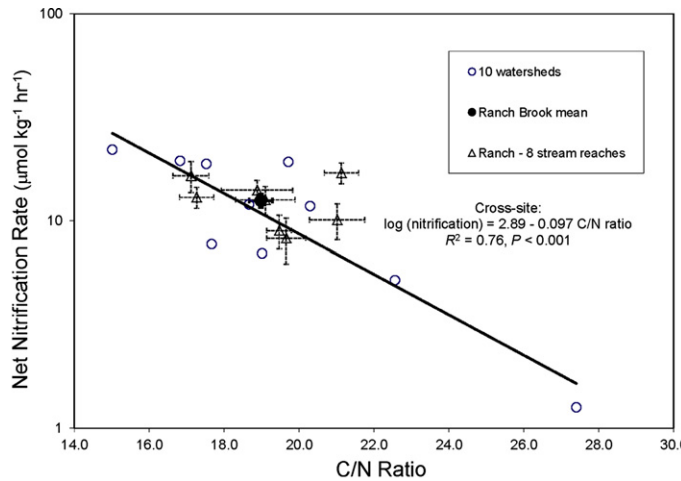


Fig. 3. Potential net nitrification rate as predicted by the C/N ratio. The exponential regression line and 10 watershed points are from Ross et al. (2009). Error bars represent the standard error of all data, (replicate soil samples within each transect point treated as random).

$$\text{Fraction as NO}_3^- = 0.20 - 1.04 \times \text{RSD} + 0.001 \times \text{Elev} - 0.007 \times \text{TSH} - 0.016 \times \text{C/N},$$

$$R^2 = 0.48, \quad n = 63, \quad \text{terms defined above.}$$

Stepwise multiple regression for ammonification and mineralization (sum of rates), both log transformed to meet the assumptions for the test, gave only two significant variables and low R^2 of 0.18 and 0.17, respectively.

The C/N ratio has been found in many studies to provide a threshold, between 23 and 25, above which little or no net nitrification is found. Net nitrification rates below this threshold are often scattered, but, in some studies, a linear or curvilinear relationship between the C/N ratio and net nitrification rates has been shown (e.g., Goodale and Aber, 2001; Lovett et al., 2004; Ross et al., 2004). In this study the overall mean in net nitrification was closely predicted by the exponential relationship with C/N developed in Ross et al. (2009): predicted rate = $11.8 \mu\text{mol kg}^{-1} \text{h}^{-1}$, actual = $12.5 \mu\text{mol kg}^{-1} \text{h}^{-1}$. The C/N vs. nitrification relationship in the individual reaches generally followed the trendline from this relationship (linearized in Fig. 3). However, the prediction confidence intervals for these rates, using the Ross et al. (2009) equation, did not include the measured rates for two of the reaches (those furthest from the line in Fig. 3). Ross et al. (2009) also provided linear equations to predict the C/N ratio from the basal area of either red spruce or the sum of sugar maple and yellow birch. Applying them to our data (overall C/N mean = 19.0), red spruce

predicted a mean C/N ratio of 17.7 and the maple and birch sum predicted 19.0, both within the prediction confidence intervals. Thus, the relationships found across the 10 small northeastern watersheds, using similar methods, appear to transfer well to a much larger basin.

3.2. Plot and reach characteristics

The eight sampled reaches were located in subwatersheds that had a combined contributing area of 8.4 km^2 and represented 88% of the total 9.6 km^2 basin. However, the transects themselves did not extend into the upper elevations of many of the watersheds and did not extend away from the stream channels. Therefore, we are not presenting the reach data as representative of the entire subwatershed. The overall range in transect point elevation was 431–714 m whereas the maximum watershed elevation was 1173 m, found in subwatershed 8 (Fig. 1). The factors limiting higher sampling along some of the reaches were extreme slope and bedrock outcrops. For example, of the highest two points in transect 5 (~700 m), one had no measurable trees because of bedrock and the other had a slope of 40° . The southness of individual transect points ranged fully between -1.0 and $+1.0$, or an aspect of due magnetic south to due magnetic north. The average aspect of the transect points within each reach also had a wide range (Table 1) reflecting the bowl-like topography of the basin.

Tree species composition in the plots was typical of the region's northern hardwood forest with sugar maple, yellow birch and American beech representing an average of 82% of the basal area (stems with dbh ≥ 10 cm, Table 3). Of these three, yellow birch was highest overall (39%) and highest in six of the eight reaches. The remaining hardwood species were red maple, *Acer rubrum* L. (4.7%), paper birch, *Betula papyrifera* Marsh. (3.4%), striped maple, *Acer pensylvanicum* L. (2.3%) and mountain maple, *Acer spicatum* Lam. (1.5%). Conifer basal area was relatively low in the plots, averaging between $<0.2\%$ and 13% of the measured basal area of each reach. Eastern hemlock basal area was higher than red spruce overall and in six of the eight reaches. Red spruce stem (≥ 1 m) density in each reach ranged between 0.01 and $0.16 \text{ stems m}^{-2}$ and its variability was not well correlated with its basal area (Table 3), i.e. a high number of small stems (<10 cm) were often found in plots with little measureable basal area. Plot conifer basal area was weakly negatively correlated with elevation (Spearman's $r = -0.31$, $P = 0.008$); plot elevation was always <750 m, above which the forest transitioned to mostly conifer species.

The mean C concentration in the horizons sampled was 305 g kg^{-1} with a range of $221\text{--}368 \text{ g kg}^{-1}$ in averages for the eight reaches (Table 4). Of all samples, 76% had $>20\%$ C and would be classified as Oa horizons, with the remaining being A horizons (Soil Survey Staff, 2006). The average reach N concentrations ranged be-

Table 3

Mean plot basal area of major tree species and red spruce density for each reach. Basal area was measured on all stems with dbh ≥ 10 cm. Stem density was measured on all stems ≥ 1 m.

Reach	Average plot basal area ($\text{m}^2 \text{ ha}^{-1}$)	Sugar maple <i>A. saccharum</i> dominance	Yellow birch <i>B. alleghaniensis</i> dominance	American beech <i>F. grandifolia</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	Red Spruce density (stems m^{-1})
1	22.2	0.53	0.04	0.27	0.00	0.00	0.04	0.06	0.011
2	28.2	0.27	0.37	0.21	0.05	0.01	0.01	0.06	0.028
3	23.7	0.30	0.29	0.21	0.00	0.05	0.03	0.02	0.027
4	30.3	0.24	0.47	0.26	0.00	0.01	0.00	0.00	0.048
5	19.1	0.20	0.55	0.14	0.04	0.06	0.00	0.00	0.017
6	29.2	0.04	0.45	0.16	0.19	0.06	0.04	0.05	0.164
7	27.4	0.20	0.47	0.07	0.00	0.05	0.04	0.05	0.127
8	26.3	0.26	0.29	0.27	0.00	0.00	0.02	0.11	0.011
Overall mean	25.5	0.23	0.39	0.19	0.05	0.03	0.02	0.05	0.058

tween 12.5 and 18.8 g kg⁻¹ (overall mean 15.8 g kg⁻¹) and C/N ratios were between 17.1 and 21.1 (overall mean 19.0). These C and N values were close to the means found in the 10 small (median size 0.023 km²) northeastern watersheds studied by Ross et al. (2009) using similar methods: 307 g kg⁻¹ C, 15.6 g kg⁻¹ N, C/N 19.5. The average thickness of the horizon sampled for nitrification rate measurements in this study (9.3 cm) was somewhat higher than the mean of 6.6 cm in the small watershed study of Ross et al. (2009).

Moisture content generally correlated with C concentration but, using the wetness ratio of Ross (2007), there was a range between somewhat dry conditions in transects 1 and 4 (ratios of actual water content to field capacity predictions of 0.76 and 0.72, respectively) and relatively wet in transect 6 with a ratio of 1.43 (Table 4). The low wetness ratios were the result of dry summer conditions in June and July of 2005, whereas the high wetness resulted from some points being located in or near seeps. Although moisture has been found to affect N transformation rates (e.g., Knoepp and Swank, 2002), in this study we found no correlation between the wetness ratio and nitrification ($P = 0.51$). The effect may have been masked by variability due to other factors or the range in moisture may have been insufficient to affect rates.

3.3. Variability within and among reaches

We found that the variability in net nitrification rates among three soil samples taken 1 m apart at a transect point was similar to the variability among points about 125 m apart within a reach (see Section 2.4). The number of transect points within each reach was not sufficient to provide significant differences, even though the range in net nitrification was fairly broad (8.2–17.0 $\mu\text{mol kg}^{-1} \text{h}^{-1}$, Table 2). Power analysis revealed that 109 points, or 13–14 points in each reach, would be needed to show any differences, assuming similar variability. The difference between the high and low values for nitrification was only significant if all individual replicates (i.e. three separate soil samples per point) were treated as independent values rather than averaged before analysis (Table 2). This was a function of both small transect point numbers and high variability in each reach. No differences were found in the 1-day ammonification rates across transect points whereas mineralization (the sum of nitrification and ammonification) showed differences similar to the nitrification rates alone (Table 2). The fraction of inorganic N as NO₃⁻ after 1 day of incubation was less variable within reaches and thus showed more significant differences (Table 2). If the analysis of variance was performed on transect point averages rather than individual replicates (see Section 2 for details), only the highest and lowest reach means

were significantly different. This was the only such difference found in any dependent variable when the statistical analysis was done in this manner.

4. Discussion

4.1. Tree species control on net nitrification rates

Many studies have shown that specific tree species are associated with higher net nitrification rates, e.g. sugar maple, or lower rates, e.g. oak and conifer species (Finzi et al., 1998; Christ et al., 2002; Lovett et al., 2004; Ross et al., 2004). Using our statistical approach, red spruce density was the only tree species metric that explained any of the variability across all plots even though sugar maple dominance varied from 0% to 92% across all plots. Sugar maple has been widely reported to foster high rates but we found identical net nitrification in plots having >50% sugar maple dominance (14.2 $\mu\text{mol kg}^{-1} \text{h}^{-1}$, $n = 9$) to those having >50% yellow birch dominance (14.2 $\mu\text{mol kg}^{-1} \text{h}^{-1}$, $n = 19$), while plots with >50% American beech were numerically higher but not statistically different (15.8 $\mu\text{mol kg}^{-1} \text{h}^{-1}$, $n = 7$). The number of plots being compared here is low but results are similar to plots in the cross site study of Ross et al. (2009). Two recent studies on species effects, which included the above three northern hardwood species along with red oak and eastern hemlock, have been performed on the same single-species plots in the Catskills of New York (Lovett et al., 2004; Christenson et al., 2009). Lovett et al. (2004), using a 28-d incubation, found higher net nitrification rates in the combined Oe/Oa horizons under sugar maple and American beech compared to the other three species. In the mineral soil (A and/or B horizon), net nitrification rates were not significantly different in the maple, beech or birch plots but these three were higher than the oak and hemlock plots. Christenson et al. (2009), using shorter incubations, found that among-species differences in net and gross nitrification rates in the organic horizons were similar to those found by Lovett et al. (2004). However, sugar maple rates were numerically highest in both studies and, in the mineral soils studied by Christenson et al. (2009), both gross and net nitrification rates were significantly higher than all other species. Thus, although it is clear that high nitrification rates are likely to be found associated with sugar maple, these rates are not necessarily higher than the two other common northern hardwoods—yellow birch and American beech. No red oak was found in our plots as its current range is at lower elevations and/or latitudes. Low rates of net nitrification have often been found associated with conifer species, e.g. eastern hemlock in the above studies and red spruce

Table 4
Mean soil characteristics within each reach.

Reach	Carbon (g kg ⁻¹)	Nitrogen (g kg ⁻¹)	C/N ratio ^a	Oa or A horizon thickness (cm)	Depth of Oi, Oe and Oa or A ^b (cm)	Soil moisture content (kg kg ⁻¹)	Wetness ratio ^c
1	220.8	12.53	17.1	9.1	13.1	1.95	0.76
2	368.3	18.76	19.7	11.3	15.2	2.57	0.92
3	354.8	18.62	19.1	10.4	14.5	2.20	1.10
4	285.0	14.94	18.9	9.8	14.4	2.60	0.72
5	243.9	13.65	17.3	8.0	11.3	1.61	1.25
6	353.3	18.21	19.5	9.2	13.7	3.00	1.43
7	360.3	17.45	21.0	12.2	18.3	2.01	1.10
8	318.3	14.98	21.1	7.2	11.0	1.68	1.20
Overall mean	306.6	15.95	19.0	9.4	13.5	2.19	1.10
Overall standard error	11.7	0.53	0.3	0.6	0.6	0.12	0.05

^a Mass basis.

^b The horizon sampled was either an Oa or A directly below the Oe.

^c Sample water content relative to field capacity predicted by C, calculated from the equation given in Ross (2007).

in this study and in Ross et al. (2009). A number of reports have shown that volatile compounds (monoterpenes) from coniferous species can inhibit N mineralization, especially nitrification (White, 1986; Paavolainen et al., 1998; Smolander et al., 2006; Uusitalo et al., 2008). Whether or not this was the case in our study is unknown, but it is intriguing that the stem density of red spruce was a significant, albeit weak, negative correlate of net nitrification. Historically, larger red spruce stems were selectively logged from these forests and many remaining red spruce suffered die-back (Whitney, 1988; Cogbill et al., 2002). Perhaps the influence of spruce saplings on nitrification is from inhibition or perhaps the effect is from other landscape factors related to the regeneration of red spruce.

As stated, the basal area of red spruce in our plots was relatively low and, in most reaches, Eastern hemlock basal area was greater (although the average stem density of hemlock was much lower: 0.002 stems m^{-2} vs. 0.058 stems m^{-2} for red spruce). Eastern hemlock basal area was weakly negatively correlated with net nitrification (Spearman's $r = -0.40$, $P < 0.001$) and with elevation (Spearman's $r = -0.40$, $P < 0.001$). The interaction with elevation is discussed further below.

4.2. Elevation as a control on net nitrification

A number of studies have found higher net nitrification rates with higher elevation (Knoepp and Swank, 1998; Bohlen et al., 2001; Groffman et al., 2009) and, in a large watershed study similar to ours, Venterea et al. (2003) found elevation to be a significant, positive predictor of net nitrification rates in the Hubbard Brook valley. All these studies ascribed the effect of elevation to higher soil moisture. Venterea et al. (2003) sampled 100 plots in the HBEF (3.6 km^2) that had an elevation gradient of 570 m (range between 330 and 900 m). They developed a regression model that explained 52% of the variability in net nitrification rates, with independent variables being elevation, southness of aspect, and the abundance of sugar maple, striped maple and conifer species (all but the latter being positive factors). Both organic and mineral soil horizons were sampled but soil moisture was only a significant correlate with net nitrification in the mineral soil. Elevation was also significant in our regression model but we had a weak *negative* correlation of elevation with soil moisture (Spearman's $r = -0.25$, $P = 0.04$) and only a weak positive correlation with the wetness ratio (Spearman's $r = +0.28$, $P = 0.02$). The reason for these opposite effects is that C concentrations tended to get lower with higher elevation (Spearman's $r = -0.23$, $P = 0.05$) but the relative amount of soil moisture predicted by soil C (the wetness ratio) actually tended higher. It should be reiterated that these relationships were very weak as evidenced by the low correlation coefficients. We also had a lower range in elevation, 283 m between our lowest and highest transect points, than the other studies. The most likely explanation of the positive influence of elevation on net nitrification rates was the lower basal area of eastern hemlock found at higher elevation, as mentioned above, and not soil moisture as found in other studies.

4.3. Soil controls on net nitrification

The third and final significant component in our regression analysis of net nitrification rates was the thickness of the combined Oi, Oe and Oa or A horizons as a negative factor. As stated, the horizon sampled was either an Oa or A as defined by its C concentration (an A horizon with 19% C is difficult to differentiate from an Oa horizon with 21% C). This combined 'forest floor' thickness was highly correlated with the thickness of the Oa or A horizon sampled (Spearman's $r = 0.95$, $P < 0.001$) but was a superior predictor in the regression analysis. The relationship be-

tween net nitrification rates and the C/N ratio in these soils is somewhat confounded by relationships between C/N, C concentration and horizon thickness. In the Ranch Brook watershed and in the smaller watersheds from Ross et al. (2009), these three variables were linearly and positively related (Ross et al., *in press*). Thus, sampling points with thicker A or Oa horizons had both higher C concentrations in those horizons and a higher C/N ratio. There was also a significant linear increase in C concentration with increased combined basal area of American beech and red spruce (Ross et al., *in press*). In this study, there was a weak correlation (Spearman's $r = 0.33$, $P = 0.003$) between red spruce and 'forest floor' thickness, probably responsible for the inclusion of thickness in the multiple regression shown above. Many of these controlling factors for net nitrification rates are obviously interrelated.

We did not examine the effect of other soil chemical characteristics, such as pH and available Ca and Al, on N transformation rates. While there is evidence to support their influence (e.g. Gilliam et al., 2005; Christopher et al., 2006), no influence of these factors was found by Ross et al. (2009) and therefore we did not measure them for the present study. Our focus was on examining the application of significant results from the cross-site study (Ross et al., 2009) to the larger Ranch Brook watershed.

4.4. Methodological considerations

A large number of methods have been used to estimate forest soil net nitrification rates and it has long been recognized that the procedure used can affect the rate measured (Hart et al., 1994), thus necessitating the label 'potential' rates. Sampling disturbance can stimulate net rates (Ross and Hales, 2003), apparently through altering patterns of NH_4^+ consumption (Kaur et al., 2010); i.e. a greater proportion of the gross production of NH_4^+ is nitrified. Gross rates of NO_3^- and NH_4^+ production can, with some difficulty, be measured and, as long as disturbance artifacts are not introduced, should provide insight into soil N transformation processes. Most studies only measure potential net rates with the intention of linking these rates to watershed processes such as response to anthropogenic N inputs or stream NO_3^- export. The one-day rate method (Ross et al., 2006) that we used has the advantage of providing *in situ* concentrations of both NO_3^- and NH_4^+ . Taking advantage of the rapid soil response to disturbance, a wide range of rates can be obtained after only 1 day of incubation. However, processing samples in the field is not always practical. Potential net nitrification rates measured by other procedures should provide a similar separation of rates, with similar analytical variability, assuming that the timing of the initial, baseline extractions for NO_3^- and NH_4^+ is consistent.

Limiting variability due to analysis is critical because high spatial variation in forest soil N processes is well documented (e.g. Laverman et al., 2002; Lorz et al., 2010; Gilliam et al. 2011). Comparing variance among studies is difficult because of the differences in methodology and how results are expressed. Laverman et al. (2002) studied spatial variability in a 400 m^2 coniferous forest soil plot, measuring NO_3^- production after a 3-wk incubation of 210 intact cores. They found a CV of 75.3% in their data; comparable to the CV of 83.5% for 1-day net nitrification in our combined data of 221 total samples (representing 74 transect points with one missing value). Unless a different statistical approach is used, comparing even relatively small plots will require a large sample size. How well transect points represent a watershed or subwatershed is another difficult issue. Our sampling scheme was not intended to represent the entire subwatershed that contained the transect but, instead, to provide a series of potential net nitrification rates spatially referenced to the stream channels.

5. Conclusions

The Ranch Brook watershed mean for potential net nitrification rates in the near-surface horizon ($12.5 \mu\text{mol kg}^{-1} \text{h}^{-1}$) was near the median of the rates found in the 10 much smaller watersheds by Ross et al. (2009), using similar methods. The fraction of inorganic N as NO_3^- was also close to the 10-watershed median and matched well with the small watershed relationship to net nitrification rates (Fig. 2). Other relationships developed in Ross et al. (2009) also held true for the Ranch Brook watershed means, such as the equation that predicted net nitrification rate from the C/N ratio (Fig. 3) and the close prediction of C/N ratio from the sum of sugar maple and yellow birch basal area. Sugar maple was associated with relatively high rates of net nitrification but no higher than those associated with other major hardwood species. We also found a similar influence of vegetation on net nitrification rates, with red spruce density being significant and sugar maple basal area or density not contributing in regression analysis. Thus, widely spaced sampling in a 9.6 km^2 basin gave results that fit well with more intensive sampling in much smaller watersheds (median 0.23 km^2). Elevation was a significant explanatory variable in this study, similar to the basin-wide study of Venterea et al. (2003); however, unlike that study, the effect of elevation did not appear to be related to soil moisture differences. The division of the watershed into eight reaches provided a relatively wide range in nitrification rates but, because of high variability, the number of points within each reach was insufficient to show significant differences among reaches. The data from the individual reaches did, however, provide a useful comparison of the N transformation rates measured in this study with those measured across the northeastern USA.

Tree species composition is affected by management, both in harvesting and in regeneration. As stated above, red spruce was historically selectively removed from the lower elevations in much of the New England forest (Whitney, 1988; Cogbill et al., 2002). If the relationships developed in this and a previous study (Ross et al., 2009) hold true, increasing red spruce density could reduce soil net nitrification rates and, in turn, reduce stream nitrate export. Whether or not greater retention of N by these watersheds is a positive outcome is under debate. Some would argue that the additional N is required for any additional C sequestration while others would argue that excesses of N will have deleterious effects on the forest ecosystem.

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References

Aber, J.D., Goodale, C.L., Olinger, S.V., Smith, M.L., Magill, A.H., Martin, R.A., Hallett, R.A., Stoddard, J.L., 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? *Bioscience* 53, 375–389.

Aleksic, N., Roy, K., Sistla, G., Dukett, J., Houck, N., Casson, P., 2009. Analysis of cloud and precipitation chemistry at Whiteface Mountain, NY. *Atmospheric Environment* 43, 2709–2716.

Bohlen, P.J., Groffman, P., Driscoll, C.T., Fahey, T.J., Siccama, T.G., 2001. Plant-soil-microbial interactions in a northern hardwood forest. *Ecology* 82, 965–978.

Bonito, G.M., Coleman, D.C., Haines, B.L., Cabrera, M.L., 2003. Can nitrogen budgets explain differences in soil nitrogen mineralization rates of forest stands along an elevation gradient? *Forest Ecology and Management* 176, 563–574.

Campbell, J.L., Hornbeck, J.W., Mitchell, M.J., Adams, M.B., Castro, M., Driscoll, C.T., Kahl, J.S., Kochenderfer, J.N., Likens, G.E., Lynch, J.A., Murdoch, P.S., Nelson, S.J., Shanley, J.B., 2004. Input-output budgets of inorganic nitrogen for 24 forest watersheds in the northeastern United States: a review. *Water Air and Soil Pollution* 151, 373–396.

Christ, M.J., Peterjohn, W.T., Cumming, J.R., Adams, M.B., 2002. Nitrification potentials and landscape, soil and vegetation characteristics in two Central Appalachian watersheds differing in NO_3^- export. *Forest Ecology and Management* 159, 145–158.

Christenson, L.M., Arthur, M.A., Weathers, K.C., Lovett, G.M., 2009. The influence of tree species, nitrogen fertilization, and soil C to N ratio on gross soil nitrogen transformations. *Soil Science Society of America Journal* 73, 638–646.

Christopher, S.F., Page, B.D., Campbell, J.L., Mitchell, M.J., 2006. Contrasting stream water NO_3^- and Ca^{2+} in two nearly adjacent catchments: the role of soil Ca and forest vegetation. *Global Change Biology* 12, 364–381.

Cogbill, C.V., Burk, J., Motzkin, G., 2002. The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys. *Journal of Biogeography* 29, 1279.

Compton, J.E., Boone, R.D., 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology* 81, 2314–2330.

Driscoll, C.T., Whittall, D., Aber, J.D., Boyer, E.W., Castro, M., Cronan, C., Goodale, C.L., Groffman, P., Hopkinson, C., Lambert, K., Lawrence, G.B., Ollinger, S.V., 2003. Nitrogen pollution in the northeastern U.S.: sources, effects and management options. *Bioscience* 53, 357–374.

Finzi, A.C., Van Breemen, N., Canham, C.D., 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications* 8, 440–446.

Gilliam, F.S., Lytle, N.L., Thomas, A., Adams, M.B., 2005. Soil variability along a nitrogen mineralization and nitrification gradient in a nitrogen-saturated hardwood forest. *Soil Science Society of America Journal* 69, 247–256.

Gilliam, F.S., McCulley, R.L., Nelson, J.A., 2011. Spatial variability in soil microbial communities in a nitrogen-saturated hardwood forest watershed. *Soil Science Society of America Journal* 75, 280–286.

Gilliam, F.S., Yurish, B.M., Adams, M.B., 2001. Temporal and spatial variation of nitrogen transformations in nitrogen-saturated soils of a central Appalachian hardwood forest. *Canadian Journal of Forest Research* 31, 1768–1785.

Goodale, C.L., Aber, J.D., 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecological Applications* 11, 253–267.

Groffman, P.M., Hardy, J.P., Fisk, M.C., Fahey, T.J., Driscoll, C.T., 2009. Climate variation and soil carbon and nitrogen cycling processes in a northern hardwood forest. *Ecosystems* 12, 927–943.

Gundersen, P., Schmidt, I.K., Raulund-Rasmussen, K., 2006. Leaching of nitrate from temperate forests – effects of air pollution and forest management. *Environmental Reviews* 14, 1–57.

Hart, S.C., Stark, J.M., Davidson, E.A., Firestone, M.K., Weaver, R.L., 1994. Nitrogen mineralization, immobilization, and nitrification. *Methods of Soil Analysis, Part 2*. Soil Sci. Soc. Am, Madison.

Howarth, R.W., Swaney, D.P., Boyer, E.W., Marino, R., Jaworski, N., Goodale, C., 2006. The influence of climate on average nitrogen export from large watersheds in the Northeastern United States. *Biogeochemistry* 79, 163–186.

Jefts, S.S., Fernandez, I.J., Rustad, L.E., Dail, D.B., 2004. Comparing methods for assessing forest soil net nitrogen mineralization and net nitrification. *Communications in Soil Science and Plant Analysis* 35, 2875–2890.

Jencso, K.G., McGlynn, B.L., Gooseff, M.N., Wondzell, S.M., Bencala, K.E., Marshall, L.A., 2009. Hydrologic connectivity between landscapes and streams: transferring reach- and plot-scale understanding to the catchment scale. *Water Resources Research* 45, W04428.

Kaur, A., Ross, D., Fredriksen, G., 2010. Effect of soil mixing on nitrification rates in soils of two deciduous forests of Vermont, USA. *Plant and Soil* 331, 289–298.

Knoepp, J.D., Swank, W.T., 1998. Rates of nitrogen mineralization across an elevation and vegetation gradient in the southern Appalachians. *Plant and Soil* 204, 235–241.

Knoepp, J., Swank, W., 2002. Using soil temperature and moisture to predict forest soil nitrogen mineralization. *Biology and Fertility of Soils* 36, 177–182.

Knoepp, J.D., Vose, J.M., 2007. Regulation of nitrogen mineralization and nitrification in Southern Appalachian ecosystems: separating the relative importance of biotic vs. abiotic controls. *Pedobiologia* 51, 89–97.

Laverman, A.M., Borgers, P., Verhoef, H.A., 2002. Spatial variation in net nitrate production in a N-saturated coniferous forest soil. *Forest Ecology and Management* 161, 123–132.

Lorz, C., Schneider, B., Lethmate, J., Eissner, C., 2010. Spatial and temporal small-scale variability of nitrogen mobilization in a forest ecosystem with high N deposition in NW-Germany. *Environmental Pollution* 158, 424–439.

Lovett, G.M., Weathers, K.C., Arthur, M.A., 2002. Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. *Ecosystems* 5, 712–718.

Lovett, G.M., Weathers, K.C., Arthur, M.A., Schultz, J.C., 2004. Nitrogen cycling in a northern hardwood forest: do species matter? *Biogeochemistry* 67, 289–308.

Ohrui, K., Mitchell, M.J., Bischoff, J.M., 1999. Effect of landscape position on N mineralization and nitrification in a forested watershed in the Adirondack Mountains of New York. *Canadian Journal of Forest Research* 29, 497–508.

- Ollinger, S.V., Smith, M.L., Martin, M.E., Hallett, R.A., Goodale, C.L., Aber, J.D., 2002. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. *Ecology* 83, 339–355.
- Paavolainen, L., Kitunen, V., Smolander, A., 1998. Inhibition of nitrification in forest soil by monoterpenes. *Plant and Soil* 205, 147–154.
- Ross, D.S., 2007. A carbon-based method for estimating the wetness of forest surface soil horizons. *Canadian Journal of Forest Research* 37, 846–852.
- Ross, D.S., Bailey, S.W., Lawrence, G.B., Shanley, J.B., Fredriksen, G., Jamison, A.E., in press. Near-surface soil carbon, C/N ratio and tree species are tightly linked across northeastern USA watersheds. *Forest Science*.
- Ross, D.S., Fredriksen, G., Jamison, A.E., Wemple, B.C., Bailey, S.W., Shanley, J.B., Lawrence, G.B., 2006. One-day rate measurements for estimating net nitrification potential in humid forest soils. *Forest Ecology and Management* 230, 91–95.
- Ross, D.S., Hales, H.C., 2003. Sampling-induced increases in net nitrification in the Brush Brook (Vermont) watershed. *Soil Science Society of America Journal* 67, 318–326.
- Ross, D.S., Lawrence, G.B., Fredriksen, G., 2004. Mineralization and nitrification patterns at eight northeastern US forested research sites. *Forest Ecology and Management* 188, 317–335.
- Ross, D.S., Wemple, B.C., Jamison, A.E., Fredriksen, G., Shanley, J.B., Lawrence, G.B., Bailey, S.W., Campbell, J.L., 2009. A cross-site comparison of factors influencing soil nitrification rates in northeastern USA forested watersheds. *Ecosystems* 12, 158–178.
- SAS Institute, 2003. The SAS system for windows. Release 9.1. SAS Inst., Cary, North Carolina, USA.
- SAS Institute, 2008. JMP Statistical Discovery Software, version 8. SAS Institute Inc., Cary, North Carolina, USA.
- Sidele, R.C., Tsuboyama, Y., Noguchi, S., Hosoda, I., Fujieda, M., Shimizu, T., 2000. Stormflow generation in steep forested headwaters: a linked hydrogeomorphic paradigm. *Hydrological Processes* 14, 369–385.
- Smolander, A., Ketola, R.A., Kotiaho, T., Kanerva, S., Suominen, K., Kitunen, V., 2006. Volatile monoterpenes in soil atmosphere under birch and conifers: effects on soil N transformations. *Soil Biology and Biochemistry* 38, 3436–3442.
- Soil Survey Staff, 2006. Keys to soil taxonomy, 10th edition. United States Department of Agriculture Natural Resource Conservation Service, Washington, D.C.
- Soil Survey Staff, 2009. United States Department of Agriculture Natural Resource Conservation Service Web Soil Survey. Available from: <http://websoilsurvey.nrcs.usda.gov/app/HomePage.htm> (accessed 11.1.09.).
- Templer, P.H., Lovett, G.M., Weathers, K.C., Findlay, S.E., Dawson, T.E., 2005. Influence of tree species on forest nitrogen retention in the Catskill Mountains, New York, USA. *Ecosystems* 8, 1–16.
- Uusitalo, M., Kitunen, V., Smolander, A., 2008. Response of C and N transformations in birch soil to coniferous resin volatiles. *Soil Biology and Biochemistry* 40, 2643–2649.
- Venterea, R.T., Groffman, P.M., Verchot, L.V., Magill, A.H., Aber, J.D., 2004. Gross nitrogen process rates in temperate forest soils exhibiting symptoms of nitrogen saturation. *Forest Ecology and Management* 196, 129–142.
- Venterea, R., Lovett, G., Groffman, P., 2003. Landscape patterns of nitrification and nitrous oxide production in a northern hardwood forest. *Soil Science Society of America Journal* 67, 527–539.
- Vervaeke, 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. *Biology and Fertility of Soils* 36, 93–101.
- Wemple, B., Shanley, J., Denner, J., Ross, D., Mills, K., 2007. Hydrology and water quality in two mountain basins of the northeastern US: assessing baseline conditions and effects of ski area development. *Hydrological Processes* 21, 1639–1650.
- White, C.S., 1986. Volatile and water-soluble inhibitors of nitrogen mineralisation and nitrification in a ponderosa pine ecosystem. *Biology and Fertility of Soils* 2, 97–104.
- Whitney, H.E., 1988. Disturbance and Vegetation Change on Camel's Hump, Vermont, Ph.D. thesis, Botany Department, University of Vermont, Burlington, p. 126.