The Influence of Tree Species, Nitrogen Fertilization, and Soil C to N ratio on Gross Soil Nitrogen Transformations

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To investigate controls on gross N transformations in forest soils, a ^{15}N pool dilution technique was used on soils of single-species plots of five major tree species (red oak [*Quercus rubra* L.], sugar maple[*Acer saccharum* Marsh.], hemlock [*Tsuga canadensis* (L.) Carr], beech [*Fagus grandifolia* Ehrh.] and yellow birch [*Betula alleghaniensis* Britton]) in the Catskill Mountains of New York State. Catskill forest soils had high rates of gross mineralization and NH_4^+ consumption, indicating rapid NH_4^+ cycling, a pattern not captured by net N mineralization assays. Sugar maple had the highest rates of gross mineralization and NH_4^+ consumption. Rates of gross nitrification were similar to rates of net nitrification for all species. Sugar maple had the highest gross nitrification rates, while hemlock and red oak had the lowest rates. There were no significant species differences in NO_3^- consumption. Fertilization of the plots did not significantly alter N cycling rates with the exception of yellow birch, where N fertilization decreased NO_3^- consumption. We observed a significant negative relationship between net nitrification and soil C/N ratio in both organic and mineral horizons, but our results indicate that the mechanism underlying that relationship was different in the two horizons. In the mineral horizon, limitation of net nitrification in soils of high C/N ratio probably resulted from low gross NH_4^+ production. In organic horizons, low NH_4^+ production was not a significant factor and higher NO_3^- consumption explained some of the pattern. Understanding the roles individual tree species as well as excess N input play in regulation of the N cycle will improve forest management and prediction of forest responses to elevated N deposition.

A current and important focus in forest ecology is how forest ecosystems process and retain atmospherically deposited N and how those potential retentive mechanisms are influenced by rates of N deposition. It has long been held that northern temperate forests are usually N limited (Paul and Clark, 1989; Vitousek and Howarth, 1991) and that accumulation of organic matter in these forests will provide a strong sink for N deposited from the atmosphere (Vitousek and Reiners, 1975; Van Miegroet et al., 1992). However, it has been hypothesized that chronic addition of N from air pollution will lead to a series of changes in the ecosystem over time, including enhanced losses of N via leaching from the soil in a process termed N saturation (Agren and Bosatta, 1988; Aber et al., 1989). In northeastern North America, N released by fossil fuel combustion has been deposited at current and even higher levels, for nearly 40 yr (Driscoll et al., 2003). Empirical evidence from this region indicates that in general, increased N deposition results in increased leaching of N to surface waters (Aber et al., 2003), but that ecosystems exposed to the same N deposition may vary widely in the amount of N leaching because of differences in N cycling in forests and their soils (Lovett et al., 2000). Thus, understanding the processes involved in N retention is critical to predicting the future responses of forests to changes in N deposition.

Individual tree species influence soil N cycling via many mechanisms, including direct effects of N uptake through the roots, and indirect effects mediated through differences in characteristics such as mycorrhizal associations, root exudates, and the chemical quality of the litter produced. In particular, N, lignin, and tannin contents of litter have been shown to influence microbial processes such as decomposition, net N mineralization, and net nitrification (Mellilo et al., 1982; Scott and Binkley, 1997; Olson and Reiners, 1983; Schimel et al., 1998). Differences in litter chemistry are thought to be at least partially responsible for observed differences among tree species in rates of net N mineralization and nitrification in northeastern U.S. forests (Finzi et al., 1998; Lovett and Rueth, 1999; Lawrence et al., 2000) although the relationships between litter properties and N cycling are not always apparent (Lovett et al., 2004). While there is some variation in the results from previous research, rates of net nitrification in soil organic horizons are generally observed to be high under sugar maple stands and low under stands of red oak and eastern hemlock (Finzi et al., 1998; Lovett and Mitchell, 2004; Lovett et al., 2004).

Our previous studies in the forests of the Catskill Mountains, NY, have shown that the major tree species vary in

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many key N-cycling characteristics, including net N mineralization and nitrification, microbial biomass N, and retention of added ^{15}N (Lovett et al., 2004; Templer et al., 2003, 2005). In our studies as well as others from Europe and North America, net nitrification and nitrate leaching show a strong inverse relationship with soil C/N ratio (Gundersen et al., 1998; Dise and Wright, 1995; Goodale and Aber, 2001; Lovett et al., 2002, 2004). As a consequence of this empirical relationship, soil C/N has been proposed as a criterion with which to evaluate a site's susceptibility to N saturation and nitrate leaching (MacDonald et al., 2002). The mechanism behind the relationship between soil C/N and net nitrification is not clear, but one hypothesis is that soils with high C/N ratios will have greater microbial consumption of NO_3^-, thus limiting net nitrification (Lovett et al., 2002). Another possible mechanism is that N mineralization may be inversely related to soil C/N, and that mineralization rates drive net nitrification rates. In this paper we examine whether observed rates of gross N transformations support either of those possible mechanisms.

We measured gross rates of N mineralization and nitrification in soils under five different tree species and in fertilized and unfertilized soils. Laboratory incubations were used to reduce the variance due to among-plot differences in temperature and moisture conditions in the field. We expected that gross rates of N mineralization and nitrification would differ among species and fertilizer treatments; the objectives of this study were to quantify those differences, compare them to differences in net rates, and evaluate the hypotheses that: (i) gross N mineralization is inversely correlated to soil C/N, and (ii) gross NO_3^- consumption is positively correlated to soil C/N. We focused on soil C/N as a predictive variable because it has been observed consistently to be related to net nitrification rate and because it is an easily measured soil characteristic that may be useful as an indicator of soil susceptibility to N leaching induced by elevated N deposition. We also examined the effects of total soil C and N on these gross N transformations.

MATERIALS AND METHODS
Site Description

The soils for this study were taken from the Catskill Mountains, an area of flat-topped mountains and deeply incised valleys encompassing about 5000 km^2 in southeastern New York State. The bedrock in the higher elevations (>500 m) is relatively homogeneous, consisting primarily of flat-lying sandstones, shales and conglomerates of Devonian age (Stoddard and Murdoch, 1991), and is overlain by glacial till of variable depth (Rich, 1934). Soils of this region are classified as Lithic Dystrochrepts (Loamy skeletal, mixed, mesic). They are shallow, moderately to somewhat excessively well drained and are formed on glacial till derived from sandstone, siltstone, and shale (Tornes 1979). Mean soil texture in our research plots was 56% sand, 30% silt, and 14% clay (Table 1) (Lovett et al., 2004). The climate of the area is characterized by cool summers and cold winters. The Slide Mountain weather station at 808 m in the central Catskills has a mean annual temperature of 4.3°C (January mean = –8.5°C, July mean = 16.7°C) and a mean annual precipitation of 153 cm, about 20% of which falls as snow. Annual atmospheric inorganic N de-

position to the Catskills, while variable across the landscape (Weathers et al., 2000), is on average, approximately 11 kgN ha^{-1} (Lovett and Rueth, 1999).

Forests of the Catskill Mountains are dominated by the Northern Hard wood forest type (McIntosh, 1972). We studied five of the most dominant species: sugar maple, American beech, yellow birch, eastern hemlock and red oak. For each species we chose six pairs of monospecific plots located throughout the central Catskills in a region of about 60 × 60 km roughly centered on 42°07′ N and 74°15′ W. For each species, plots were chosen in three different watersheds to encompass spatial variation across the Catskill region. Each plot was 3 m in radius and included two or three canopy dominant trees. These small plots were located within a 6-m radius buffer zone of nearly monospecific composition to minimize the edge effects from neighboring trees of other species. Single-species paired plots were located within about 20 m of each other, and one of each pair was fertilized with N (see below) and the other was left unfertilized. Thus there were 60 plots in total: 5 species × 2 N treatments × 6 replicates. The single-species plots were chosen within mixed-species stands with the following criteria estimated by observation in the field: (i) >90% dominance of the canopy by mature trees of the target species, (ii) pure or nearly pure litter composition from target species, and (iii) no evidence of recent disturbance such as logging or fire. Nitrogen fertilizer (granular NH_4NO_3) was added to the forest floor of one plot of each pair starting in November 1997. The total annual dose was equivalent to 50 kg N ha^{-1} yr^{-1} added in 12.5 kg ha^{-1} quantities four times per year (June, July, August and November) (Templer et al., 2005). At the time of sampling in July 2001 each plot had received a cumulative dose (from 1997–2001) equivalent to 187.5 kg N ha^{-1}. The sampling occurred at least 2 wk after a fertilizer addition. Granular NH_4NO_3 disappears quickly from the surface of the soil in these mesic forests, and at the time of the soil sampling no visible fertilizer was present. Both fertilized and control plots also receive the ambient N deposition of the Catskill region of approximately 11 kg N ha^{-1} yr^{-1} (Lovett and Rueth 1999).

Field and Laboratory Methods

Soils from the organic and mineral horizons were collected during the last week of July and the first week of August, 2001. Soils were sampled to a depth of 12 cm using a 2-cm diam. stainless steel corer and separated into organic (Oe + Oa) and mineral (A and/or B) horizons (following Lovett et al., 2004). Three samples were taken per plot

Table 1. Mean soil properties by species and fertilization treatment.†

Species	Treatment	pH	% Sand	% Silt	% Clay	C/N
Beech	C	3.27 (0.09)	58 (8)	30 (6)	13 (2)	19 (1.2)
Beech	F	3.23 (0.08)	54 (7)	32 (5)	13 (2)	19.5 (1)
Hemlock	C	3.20 (0.07)	45 (12)	40 (8)	15 (4)	20.6 (1.4)
Hemlock	F	3.07 (0.22)	41 (17)	43 (10)	16 (7)	22.1 (1.3)
Maple	C	3.91 (0.30)	56 (7)	26 (4)	17 (4)	14 (1.2)
Maple	F	3.95 (0.13)	52 (10)	26 (4)	22 (7)	14 (1.1)
Oak	C	3.87 (0.12)	48 (5)	36 (2)	16 (4)	16.4 (0.8)
Oak	F	3.62 (0.08)	49 (5)	35 (4)	15 (1)	18.3 (1.3)
Birch	C	3.31 (0.08)	62 (9)	26 (6)	12 (3)	18.6 (1.7)
Birch	F	3.32 (0.12)	53 (10)	32 (6)	15 (3)	18.8 (1)

†Soil texture and pH were measured on mineral soil from the plots before start of fertilization in 1997, using methods described by Lovett et al. (2004). C/N was measured in 2000. Data are means with standard error in parentheses from $n = 6$ plots per category. C = Control (unfertilized) F = fertilized with N.

and were composited by horizon within each plot. Soils were stored in a cooler (~10°C) for transport back to the laboratory where they were stored overnight at ~5°C until processing the next day. Processing included sieving (through 8-mm mesh) to remove stones, fine roots, and woody debris, determination of moisture content and calculation of water holding capacity. Addition of the labeled N and initial extractions occurred within 24 h of the time the soil was collected.

The isotope dilution method (Hart et al., 1994) was used to calculate gross rates of N mineralization and nitrification. In this method, the product pool is labeled and the rate at which this pool is diluted is measured. To estimate the gross rate of N mineralization, 90 μg of $(^{15}NH_4)_2SO_4$–N (99 atom % enriched) was added to 40 g of field moist soil. The label was added along with sufficient deionized water to bring the sample to 60% of its water holding capacity. The water and label were added by thinly spreading the soil sample in a plastic tub, then evenly distributing the labeled solution from a syringe. Once the labeled solution was added, the sample was thoroughly mixed and divided into four subsamples (approximately 10 g each). Two of the subsamples were extracted within 15 min with 2 M KCl. These subsamples served as method replicates to assure that the label was evenly distributed in the original 40 g of soil and are the measure of the initial NH_4^+ pool (Davidson et al., 1991). The remaining two subsamples were put in 120-mL plastic specimen cups, covered with plastic wrap and incubated at room temperature (20°C) for 72 h (following Venterea et al., 2004). The 72-h incubation was chosen to ensure adequate NH_4^+ and NO_3^- production in the low-activity soil samples such as hemlock and oak (Lovett et al., 2004). After incubation these samples were also extracted with KCl. The same procedure was followed for the determination of gross nitrification except that 45 μg of $^{15}KNO_3$–N (99 atom % enriched) was added. On average, the addition of the label increased the NH_4^+ pool by 33% and the NO_3^- pool by 53%.

By standardizing the temperature and moisture during the incubation, we eliminated the variability in temperature and water content across the sites and focused the study on the differences in soil organic matter quality and N availability. Because these samples were sieved, moistened, and incubated at room temperature, the rates we measured are not comparable to in situ N transformation rates (e.g., Hart et al., 1994). Rather, we conducted this study so that the rates would be comparable with the standard potential net N mineralization assay common in the soil ecology literature, and more specifically, to the

net potential N mineralization rates reported for these sites by Lovett et al. (2004).

After extraction, all samples were analyzed for NH_4^+ (salicylate method) and NO_3^- (cadmium reduction method) using a Perstorp Analytical Flow Solution 3000 autoanalyzer (Perstorp Analytical Oatley, NSW), 0.02 mg L^{-1} detection limit). The N-diffusion method (modified from Stark and Hart, 1996; Brookes et al., 1989) was used to determine ^{15}N abundance in the KCl extractions for NH_4^+ and NO_3^- separately. Briefly, MgO is added to the extract to make the sample alkaline, causing volatilization of the NH_4^+ as NH_3, which is subsequently trapped on acidified filter disks. Devardas alloy is added to the extracts, along with new acidified filter disks to reduce the NO_3^- to NH_4^+, which is then volatilized as NH_3 and trapped on the acidified disks. The disks were submitted to the stable isotope laboratory at the University of California at Davis for analysis of ^{15}N enrichment using a Europa Scientific Integra, a continuous flow Isotope Ratio Mass Spectrometer (IRMS) integrated with on-line combustion (PDZ Europa, Chesire, England). Measurement precision reported by University of California–Davis is <0.2‰ δ ^{15}N between reference and check standards. An in-lab (Cary Institute of Ecosystem Studies) standard was also run in triplicate with samples submitted to University of California–Davis. The isotopic values for these standards varied by <3%.

Isotope dilution was calculated using the equations in Hart et al. (1994). Gross nitrification was calculated from the $^{15}NO_3^-$ treatment using the same equations, substituting NO_3^- for NH_4^+ concentration. Consumption of NH_4^+ and NO_3 was calculated as the difference between the gross and net rates of mineralization and nitrification, respectively. Consumption refers to the sum of all consumptive processes, including microbial immobilization, abiotic retention and gaseous loss (Davidson et al., 1991). It should be noted that consumption of NH_4^+ may be overestimated using this method, while NO_3^- consumption is less influenced by the additional substrate (Hart et al., 1994, Booth et al., 2005).

Total soil percent C and N values used in this paper were determined by Lovett et al. (2004) on samples collected from the same plots (both fertilized and reference plots) in 2000. These samples were dried at 60°C, ground to a fine powder using a KLECO pulverizer (Visalia, CA) and analyzed by dry combustion with a Leco CN2000 analyzer (Leco Corp., St. Joseph, MI).

A mixed model ANOVA (PROC MIXED; SAS Institute, 1989) was used to determine the effects of species, fertilization and the species × fertilization interaction. Species (five categories) and fertilization (two categories) were fixed in the model, while site was a random effect, nested within species. When main effects or interactions were significant, statistical differences among subgroup means were tested by a Student–Neuman–Keuls test. Least-squares regression was used to determine the strength of linear relationships among variables and correlations were tested with the Pearson correlation coefficient (PROC CORR; SAS Institute, 1989).

RESULTS
Nitrogen Mineralization and NH_4^+ Consumption

Mineral soils from plots of the five species differed significantly in rates of gross N mineralization and NH_4^+ consumption (Table 2). None of the three variables (net mineralization, gross mineralization, or NH_4^+ consumption) showed a significant fertilization effect or a species × fertilization interaction. Gross N mineralization rates and NH_4^+ consump-

Table 2. Results of ANOVA comparing species, fertilization, and their interaction.

Horizon	Variable	Species effect (p value)	F value
Organic Soil	Gross N mineralization	Ns†	0.22
	NH_4^+ consumption	Ns	0.91
	Gross Nitrification	< 0.0001	9.59
	NO_3^- consumption	Ns	0.9
	Net N mineralization	0.04	2.99
	Net Nitrification	< 0.0001	9.45
Mineral Soil	Gross N mineralization	0.008	4.41
	NH_4^+ consumption	0.009	4.32
	Gross Nitrification	0.002	5.68
	NO_3^- consumption	Ns	2.57
	Net N mineralization	Ns	2.43
	Net Nitrification	< 0.0001	14.2

†Ns = not significant ($p > 0.05$).

tion were significantly increased in yellow birch mineral soils in the fertilized treatment plots (Fig. 1). In the mineral horizons, sugar maple control plots had the highest rates of gross N mineralization and NH_4^+ consumption compared with the other species ($p = 0.003$ and $p = 0.0001$ respectively) (Fig. 1). For net N mineralization, the species effect was not significant in the mineral horizons (Table 2). Fertilization did significantly decrease net N mineralization in maple plot mineral soils (Fig. 1). For all species and fertilization treatments, gross N mineralization was much higher than net N mineralization, indicating substantial NH_4^+ consumption. Both gross mineralization and consumption of NH_4^+ showed a negative correlation to soil C/N in the mineral horizons ($r = -0.52$ and -0.65 respectively, Table 3). There was a correlation between soil C/N and net N mineralization in the mineral horizon (Table 3).

Species composition did not significantly affect gross rates of N mineralization or NH_4^+ consumption in the organic horizon (Table 2). Net N mineralization was significantly affected by species (Table 2) but not by the fertilization treatment (Fig. 1). As in the mineral horizon, gross N mineralization rates were higher than net rates in the organic horizon, regardless of species or fertilizer treatment (Fig. 1). In organic horizons, however, no significant correlations were found between soil C/N and gross mineralization, net mineralization, or NH_4^+ consumption (Fig. 2a and b). Gross N mineralization rates were correlated to gross nitrification in organic and mineral horizons (Fig. 3a and b). Ammonium consumption was significantly correlated with gross N mineralization rates in both organic and mineral horizons (Fig. 4a and b). Ammonium consumption was also correlated with gross nitrification rates in the organic and mineral horizons ($r = 0.66$ and 0.38, respectively). The proportion of NH_4^+ production that is immobilized is greater than the proportion that is nitrified in all species in both horizons and fertilization did not change this relationship (Fig. 5a and b).

Nitrification and NO_3^- Consumption

Significant species differences in both gross and net nitrification were evident in organic and mineral horizons (Table 2). In both horizons, gross and net nitrification were highest in soils from sugar maple plots, lowest in hemlock and red oak plots, and intermediate in beech and yellow birch plots (Fig. 6a and b). Rates of nitrate consumption were generally low compared with rates of gross and net nitrification (Fig. 6a and b), and showed no significant species effects (Table 2). The effect of the fertilization treatment was not significant for any of these variables in either horizon. There was a significant fertilization × species interaction for NO_3^- consumption in the organic horizon ($p = 0.02$), which occurred primarily because of a significant ($p = 0.006$) decline in NO_3^- consumption in yellow birch following fertilization (Fig. 6a). No other species × fertilization interactions were statistically significant.

In both mineral and organic horizons there were significant correlations between soil C/N and rates of nitrification, both gross and net (Table 3). There was a significant correlation between the total soil %N and gross nitrification, consumption of NO_3^- and net nitrification in the mineral soils (Table 3). Nitrate production and consumption were significantly correlated with soil C/N in the organic horizon (Fig. 2c and d).

There were no correlations between NO_3^- consumption and gross nitrification in the organic soil horizon while there was a significant correlation in the mineral horizons (Fig. 7a and b).

DISCUSSION
Species Effects on Gross and Net Nitrogen Transformations

Highly significant differences were found among plots of these different species in gross N transformations. There was a significant species effect on gross N mineralization and NH_4^+ consumption in mineral horizons, and on gross and net nitrification in both organic and mineral horizons. For nitrification in particular, the differences among species are similar to those observed in 28-d net nitrification assays in these same plots (Lovett et al., 2004), with high rates of gross and net
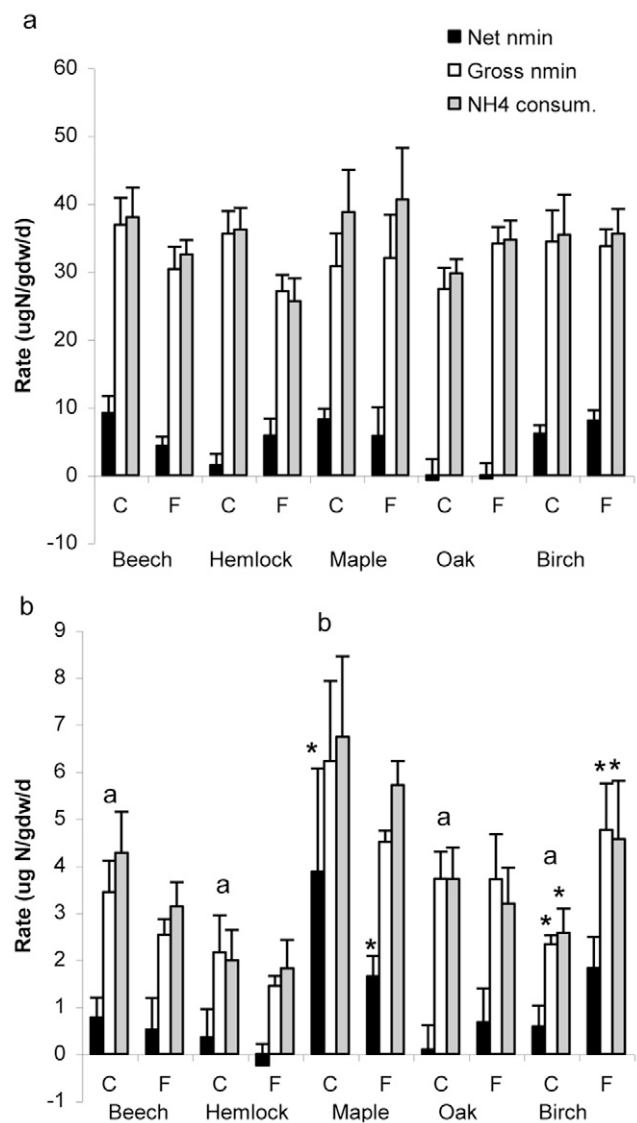

Fig. 1. Comparison of N mineralization and consumption of NH_4^+ in organic (a) and mineral (b) soils among the five tree species and fertlized vs. non-fertilized treatment. Net nmin is measured over 3 d. 'C' and 'F' refers to the control, non-fertilized treatment and the fertilized treatment. *($p \leq 0.05$) differences between C vs. F within a species using least square means. Different letters denote a statistically significant difference among species for Gross nmin and NH_4^+ consumption.

nitrification in maple stands and low rates in oak and hemlock stands. In that study it was hypothesized that high NO_3^- consumption (biotic or abiotic) may have accounted for the low net nitrification in oak and hemlock soils, but the results of our current study do not support that hypothesis: nitrate consumption rates are low and do not vary significantly among species. In the case of hemlock soils, the low nitrification rates (net and gross) appear to be related to their high C/N ratios (Fig. 2c) and low gross N mineralization rates (Fig. 3). For oak soils, the nitrification rates are low irrespective of the soil C/N ratio or gross mineralization rate (Fig. 2c, 3) suggesting that some other factor controls nitrification in oak soils. Low nitrification rates could be caused by chemical inhibition of nitrification, low available NH_4^+ concentrations and/or low nitrifier populations. These oak plots have been found to have net N mineralization rates and extractable NH_4^+ concentrations that are not significantly lower than the other hardwood species in the study (Lovett et al., 2004). Together, these results suggest to us that if nitrifier populations are low it is for some reason other than lack of substrate. We speculate that there may be chemical inhibition of nitrifiers in the oak plots, but we do not have direct evidence to evaluate this.

For all species and horizons studied, gross rates of N mineralization were much higher than net rates, and NH_4^+ consumption was substantial. High rates of gross NH_4^+ production and turnover (relative to net N mineralization) are frequently observed in temperate forest soils (e.g., Davidson et al., 1992; Verchot et al., 2001; Corre et al., 2003). The assay does not distinguish among the various processes that consume

NH_4^+, including microbial immobilization, abiotic retention of NH_4^+ and nitrification. However, previous studies in these plots showed that abiotic retention of NH_4^+ is only a minor sink for N (Fitzhugh et al., 2003), so microbial immobilization and nitrification are probably responsible for most of the NH_4^+ consumption observed here. As has been reported by other studies of gross N mineralization, these results indicate substantial short-term fluxes of NH_4^+ that would not be observed in the typical longer-term incubations used to measure net N mineralization (e.g., Davidson et al., 1992; Hart et al., 1994).

Net N mineralization rates were low, and sometimes negative, in oak and hemlock plots. However, results from this study are based on a 3-d assay which differs from the results of a 28-d assay performed on soil samples from these same plots (Lovett et al., 2004) which showed positive net N mineralization rates in all horizons and species. It is possible that soil disturbance at the start of the experiment or the addition of extra NH_4^+ with the ^{15}N label may have accelerated the consumption of NH_4^+. However, it should be noted that we did not observe increased NO_3^- production (i.e., nitrification) in the $^{15}NH_4^+$ treatment (data not shown), indicating that the label addition did not stimulate nitrification.

In contrast to the N mineralization results, gross rates of nitrification were similar to net rates, and NO_3^- consumption was low across nearly all the species, fertilization treatments and horizons in this study. As a result, gross nitrification and NO_3^- consumption were uncorrelated (Fig. 7a and b). This result differs from the conclusions from studies of conifer forest soils in the western U.S. (Davidson and Hackler, 1994;
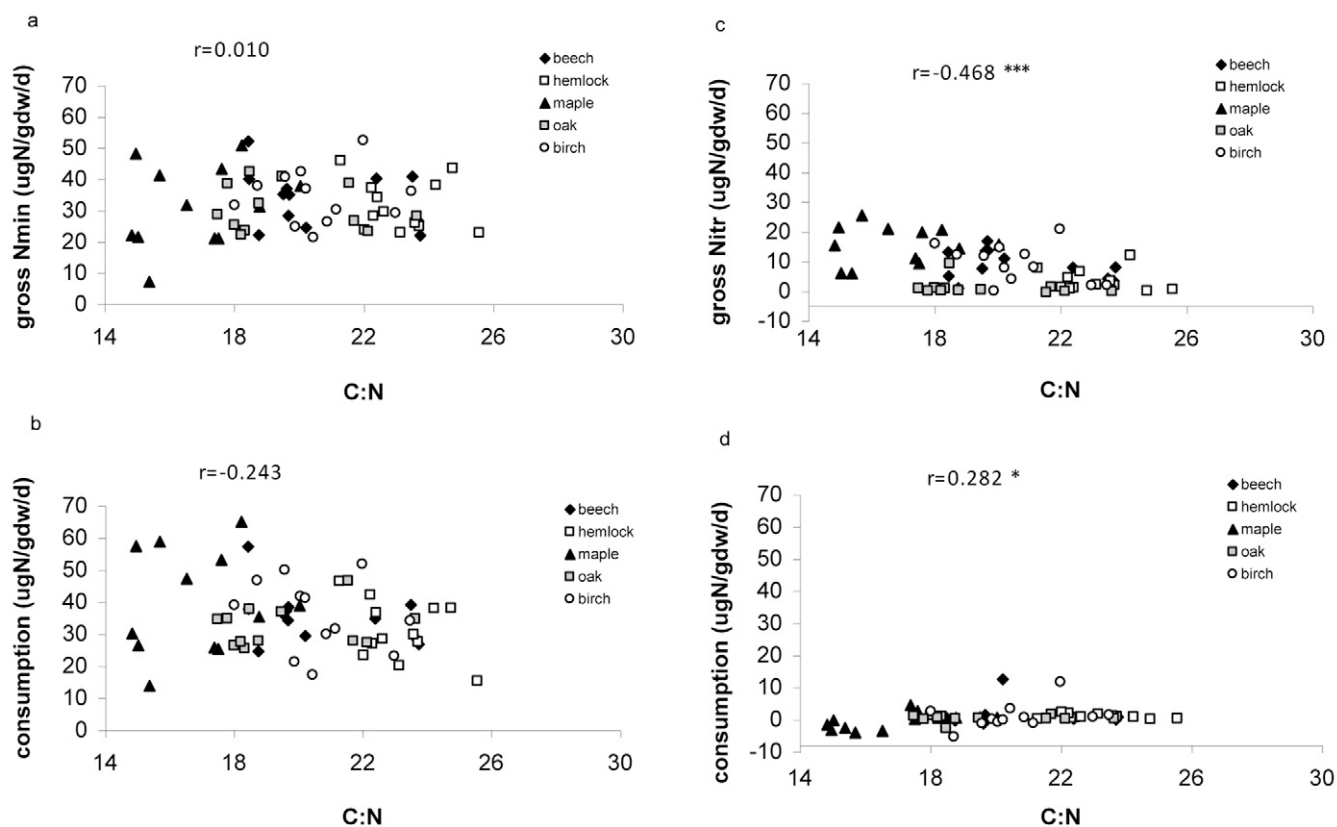

Fig. 2. Correlations of (a) gross mineralization, and (b) consumption of NH_4^+ versus C/N and (c) gross nitrification, and (d) consumption of NO_3^- vs. C/N in organic soils. Pearson correlation coefficients (*r*) shown. * signifies *p* < 0.05, *** signifies *p* < 0.001. *N* = 12 for each species illustrated combining fertilized and control treatments.

Hart et al., 1994; Stark and Hart, 1997) and of beech forests in Germany (Corre et al., 2003) where nitrate turnover (both gross production and consumption) has been reported to be high relative to rates of net nitrification. The review by Booth et al. (2005) indicate that studies using sieved cores (as used in our study) in general have lower NO_3^- consumption rates than studies using intact cores, which may partially account for the low rates that we report here. Fitzhugh et al. (2003) also report low rates of abiotic NO_3^- incorporation in the soils of the same plots examined in our study. It is unclear why NO_3^- consumption is so low in these plots, but it may be a consequence of accumulated N deposition over the past half century.

Species differences in nitrification rates may be important in determining how effectively forests can either retain atmospheric N deposition or leach N into surface waters. For instance, sugar maple stands are often associated with high rates of net nitrification and nitrate leaching and low N retention (Lovett and Mitchell 2004) while red oak stands often have low rates of net nitrification and nitrate leaching and high N retention (Lewis and Likens 2000, Lovett et al., 2004). This study indicates that the species differences in net nitrification rates are also evident in gross nitrification rates and that the differences are not due to microbial NO_3^- consumption. In sugar maple stands, the combination of low microbial NO_3^- consumption observed here, low abiotic NO_3^- consumption (Fitzhugh et al., 2003) and low NO_3^- uptake capacity by trees (Templer and Dawson, 2004, Eddy et al., 2008) could result

in the high rates of NO_3^- leaching often observed (Lovett and Mitchell 2004).

Effects of Nitrogen Fertilization

At the Harvard Forest Chronic N Amendment Study in Massachusetts, N fertilization resulted in no significant effect on gross N mineralization (Venterea et al., 2004, consistent with the results reported here. However, in contrast to our study, N fertilization did increase gross nitrification in the Harvard Forest study, although in some cases the effect was only observed at the highest rate of N fertilization (150 kg N ha^{-1}yr^{-1}). At Harvard Forest, NO_3^- consumption increased with amount of N added to the plots (Venterea et al., 2004, and in our study we also saw a trend toward increased NO_3^- consumption with fertilizer addition in our beech, hemlock, and maple soils, though the differences were not statistically significant. However, in yellow birch soils, there was a significant decline in NO_3^- consumption in response to fertilization. The pool dilution assay does not distinguish among the multiple possible fates of NO_3^- in the soil, including microbial immobilization, denitrification, dissimilatory NO_3^- reduction, and abiotic NO_3^- retention. However, in a study comparing sterilized and unsterilized soils from some of these Catskill plots, Fitzhugh et al. (2003) found that more NO_3^- was consumed by microbial immobilization than by abiotic processes.
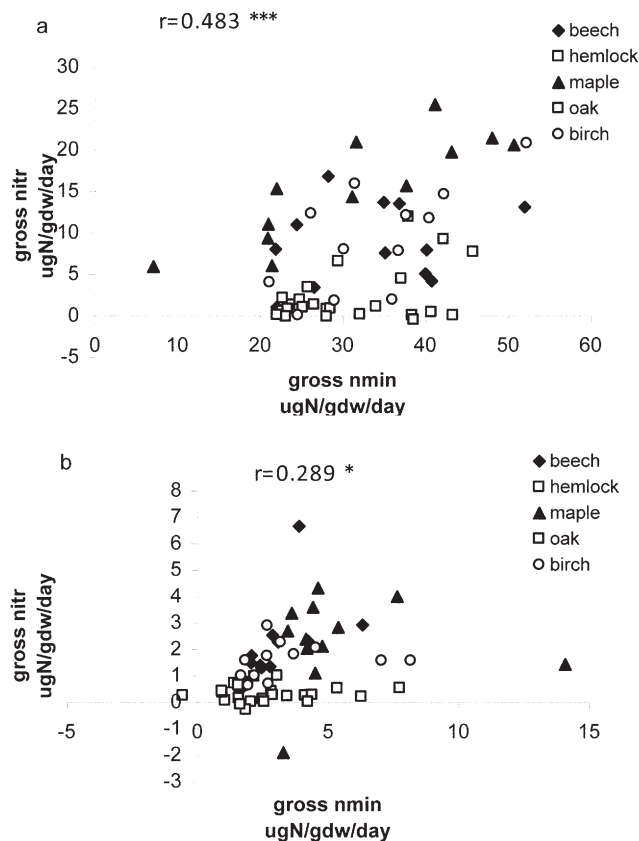

Fig. 3. Correlations of gross N mineralization vs. gross nitrification in (a) organic and (b) mineral soils. Pearson correlations coefficients (r) are shown. * signifies p < 0.05, *** signifies p < 0.001. N = 12 for each species illustrated combining fertilized and control treatments.
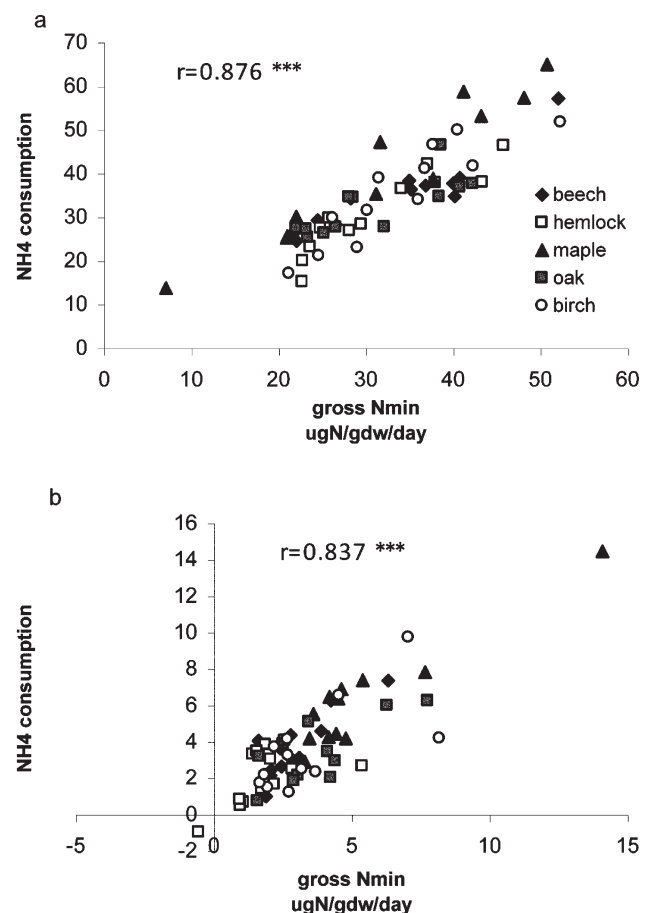
Fig. 4. Correlations of NH$_4^+$ production vs. NH$_4^+$ consumption in (a) organic and (b) mineral soils. Pearson correlation coefficients (r) shown. *** signifies p < 0.001. N = 12 for each species illustrated combining fertilized and control treatments.

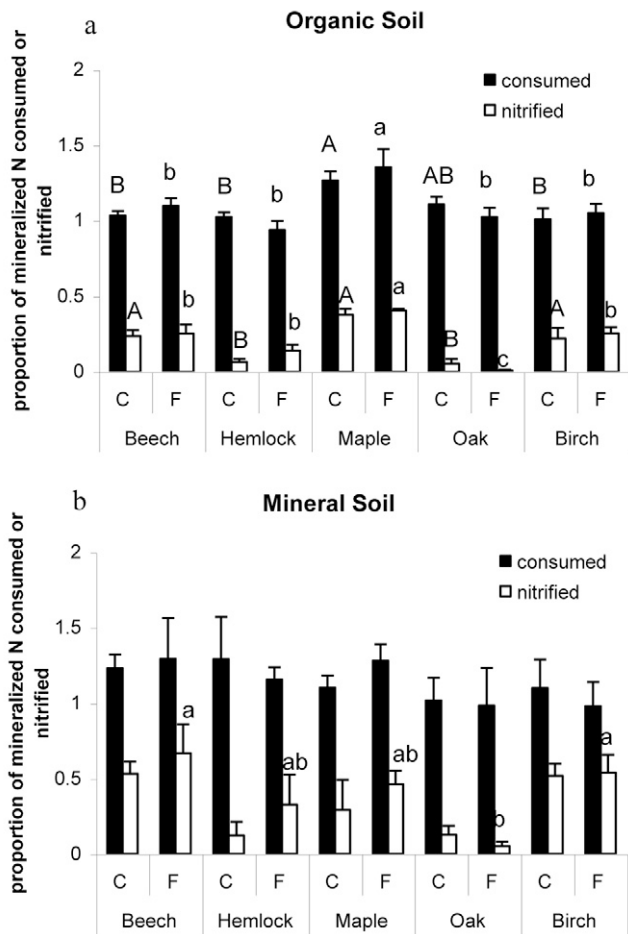Fig. 5. Proportion of mineralized N (gross NH_4^+ production) that is consumed (NH_4^+ consumption) or nitrified (gross NO_3^- production) in the (a) organic and (b) mineral soil horizons. 'C' refers to control and 'F' refers to fertilized treatment. Species with the same letter designation for each parameter within a treatment are not significantly different ($p > 0.05$).

Surprisingly, none of the N cycling processes we measured showed significant responses to N fertilization. At the time the soil sampling for this study occurred, the plots had been fertilized for 3.5 yr and had received a cumulative N addition equivalent to 187.5 kg N ha^{-1} plus the ambient atmospheric deposition of approximately 11 kg N ha^{-1}yr^{-1} (Lovett and Rueth 1999). We found no significant differences between the control and fertilized plots for %C and %N. Measurements made by Templer et al. (2005) in some of these same plots 1 yr before our samples were taken indicate that there was no significant difference in the soil N pool between fertilized and control plots. These data suggest that either the amount of N added was insufficient to elicit a response, or that there is a substantial lag between the beginning of N application and onset of changes in soil N transformations. The significant interaction between species and fertilization for NO_3^- consumption is interesting, however. Pairwise comparisons indicate that this significant interaction resulted from the decrease in NO_3^- consumption in fertilized yellow birch plots. Yellow birch was the only species that showed significant NO_3^- consumption in the control plots, and this result indicates that NO_3^- consumption, when it occurs, may be very sensitive to N additions.

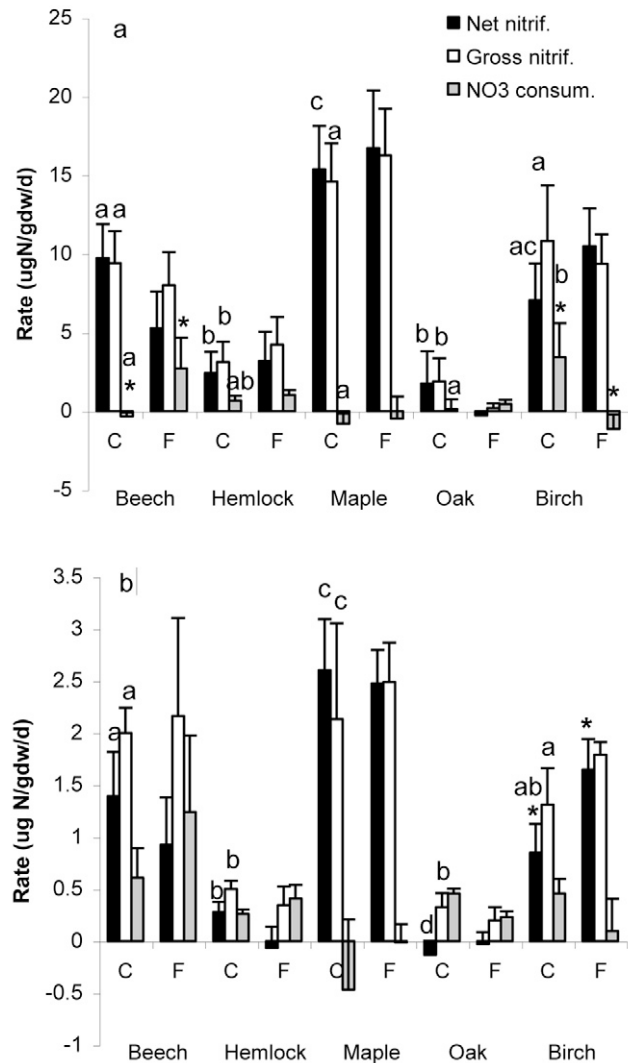Fig. 6. Comparison of nitrification and consumption of NO_3^- in (a) organic and (b) mineral soils among the five tree species and fertilized vs. non-fertilized treatment. Net nitrification is measured over 3 d. 'C' and 'F' refers to the control, non-fertilized treatment and the fertilized treatment. *($p \leq 0.05$) differences between C vs. F within a species using least square means. Different letters denote a statistically significant ($p \leq 0.05$) difference between species for net and gross nitrification and NO_3^- consumption.

Relationship between Nitrogen Transformation Rates and Soil Carbon/Nitrogen

Many previous studies have observed a negative relationship between soil C/N ratio and net nitrification or NO_3^- leaching (e.g., Gundersen et al., 1998; Dise and Wright, 1995; Goodale and Aber, 2001; Lovett et al., 2002, 2004), but the mechanism for that relationship is not clear. We hypothesized that high C/N ratios would be associated with either (i) low NH_4^+ production, or (ii) high NO_3^- consumption, either of which would help explain the negative relationship between C/N ratio and net nitrification. In both organic and mineral horizons, we observed highly significant inverse relationships between C/N ratio and net nitrification, but our results suggest that the response may have occurred for different reasons in the two horizons.

In the organic horizons, C/N ratio was not correlated with NH_4^+ production, but there was a highly significant negative

correlation with gross nitrification and a only a weak (but significant) positive correlation with NO_3^- consumption (Table 3). These results indicate that NO_3^- consumption may explain some but not all of the relationship between C/N and net nitrification in the organic horizons, and that some additional factor must also be involved. In contrast, in the mineral horizons soil C/N was negatively correlated with both gross production and consumption of NH_4^+, but not with NO_3^- consumption (Table 3), indicating that the relationship between C/N and net nitrification in the mineral horizons may, in part, reflect the underlying influence of C/N on the supply of NH_4^+. Nonetheless, all of the correlation coefficients in Table 3 are <0.7, indicating that C/N ratio explains less than half of the variance in the N transformations that we measured, and other factors are clearly involved in the regulation of these processes.

Booth et al. (2005) in an extensive review of gross N rates across a number of ecosystem types found a positive correlation between gross N mineralization and total soil N concentration while we did not see this relationship in our data (Table 3). The Booth et al. (2005) study spanned a much wider range of soil N concentrations than our study, which may have allowed this relationship to emerge. Högberg et al. (2007) found a strong negative correlation between gross mineralization and the fungi/bacteria ratio, as well as C/N ratio, indicating that these two ratios are interrelated in Swedish forests subjected to long-term N amendment. In contrast, Holub et al. (2005) found no relationship between gross N transformations and soil C/N ratio in forests in which litter input was manipulated. Taken as a whole, these contrasting studies indicate that controls on gross N transformations are likely to be more complex and variable than a simple C/N ratio would indicate, and distinguishing the multiple components of soil C will probably be necessary to improve our predictive ability.

CONCLUSIONS

This study demonstrated that Catskill forest soils have high rates of gross mineralization and NH_4^+ consumption, indicating rapid NH_4^+ cycling not measured by assays of net N mineralization. Our results compare well with N cycling rates measured in other forested systems. However, unlike some other forests, rates of gross and net nitrification were similar to one another, and nitrate consumption in the soils was generally low. Soils under five different tree species showed highly significant differences in rates of soil N transformations, especially gross and net nitrification. Three years of fertilization with nitrogen (approximately 187.4 Kg N ha^{-1}) had in general no significant effect on the N cycling rates we measured, and patterns among plots were largely influenced by tree species differences. Net nitrification rate is a key variable controlling the efficiency of N retention and release in forested watersheds, and the results reported here suggest that species differences in net nitrification are caused by differences in gross nitrification rates rather than NO_3^- consumption. Further research on the mechanisms responsible for this variation in nitrification rate will improve our capacity to model response of watersheds to elevated levels of N deposition.

Table 3. Correlations of N transformations with soil % C, %N, and C/N ratios.

Variable	Organic Horizon			Mineral Horizon		
	C%	N%	C/N	C%	N%	C/N
Gross N mineralization	+0.123	+0.172	–0.016	–0.116	+0.193	–0.517 ***
NH_4^+ consumption	–0.52	+0.133	–0.266	–0.069	+0.317 *	–0.649 ***
Net N mineralization	+0.198	+0.331	–0.092	+0.021	+0.237	–0.278 *
Gross nitrification	–0.115	+0.186	–0.469 ***	+0.098	+0.287*	–0.327 **
NO_3^- consumption	+0.182	+0.053	+0.282 *	+0.072	+0.287*	0.157
Net nitrification	–0.164	+0.166	–0.529 ***	+0.056	+0.341**	–0.484 ***

r†

* Significant at the 0.05 probability level.
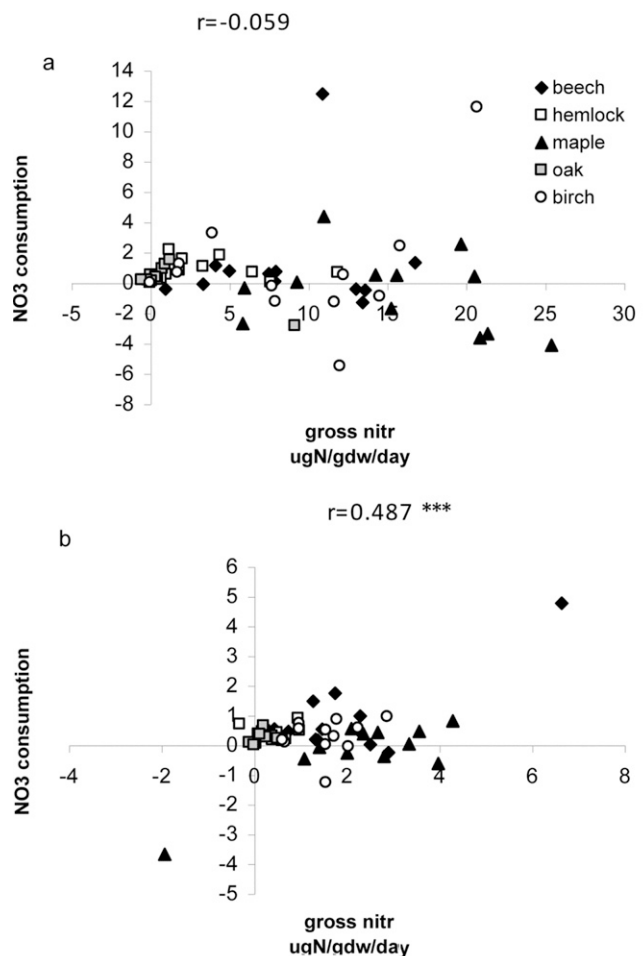** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Pearson correlation coefficient.

Fig. 7. Correlations of NO_3^- production vs. consumption in (a) organic and (b) mineral soils. Pearson correlation coefficients (*r*) are shown. *** signifies $p < 0.001$. N = 12 for each species illustrated combining fertilized and control treatments.

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