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Nitrogen cycling in a northern hardwood forest: Do species matter?

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Abstract. To investigate the influence of individual tree species on nitrogen (N) cycling in forests, we measured key characteristics of the N cycle in small single-species plots of five dominant tree species in the Catskill Mountains of New York State. The species studied were sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), eastern hemlock (*Tsuga canadensis*), and red oak (*Quercus rubra*). The five species varied markedly in N cycling characteristics. For example, hemlock plots consistently showed characteristics associated with ″slow″ N cycling, including low foliar and litter N, high soil C:N, low extractable N pools, low rates of potential net N mineralization and nitrification and low NO_3^- amounts trapped in ion-exchange resin bags buried in the mineral soil. Sugar maple plots had the lowest soil C:N, and the highest levels of soil characteristics associated with NO_3^- production and loss (nitrification, extractable NO_3^-, and resin bag NO_3^-). In contrast, red oak plots had near-average net mineralization rates and soil C:N ratios, but very low values of the variables associated with NO_3^- production and loss. Correlations between soil N transformations and litter concentrations of N, lignin, lignin:N ratio, or phenolic constituents were generally weak. The inverse correlation between net nitrification rate and soil C:N that has been reported in the literature was present in this data set only if red oak plots were excluded from the analysis. This study indicates that tree species can exert a strong control on N cycling in forest ecosystems that appears to be mediated through the quality of soil organic matter, but that standard measures of litter quality cannot explain the mechanism of control.

Introduction

Despite several decades of research, our understanding of the controls on nitrogen (N) cycling and retention in forested watersheds remains incomplete. In rapidly growing forests, sequestration of N in vegetative biomass produces a very strong N sink that can minimize N losses from the ecosystem (Vitousek and Reiners 1975). However, in mature forests the major sink for N is usually in the soil organic matter (Nadelhoffer et al. 1999a, 1999b; Templer 2001). Mature forests can retain a surprisingly large amount of added N despite little or no biomass increment, largely

through incorporation of N into soil organic matter (Magill et al. 2000). However, the mechanisms of N incorporation into soil organic matter are not well understood (Aber et al. 1998; Johnson et al. 2000), and the retention capacity is apparently quite variable among forest stands (McNulty et al. 1996; Magill et al. 2000; Lovett et al. 2000).

In recent studies, we reported that small, forested watersheds in the Catskill Mountains of New York State vary markedly in their ability to retain atmospheric N (Lovett et al. 2000, 2002). We identified differences in species composition among the watersheds as one possible source of that variation. However, the influence of species composition is difficult to predict because the literature does not give a clear picture of how dominant tree species affect the N cycle.

Several recent papers have shown substantial variation in N cycling across forested landscapes (Knoepp and Swank 1998; Ferrari 1999; Peterjohn et al. 1999; Christ et al. 2002; Ollinger et al. 2002). In these studies, the variation appeared to be related to forest type, yet the influence of particular species was difficult to distinguish from other factors that vary across the landscape. One recent study reported significant differences in soil C:N ratios and N transformations under single individuals of six northeastern tree species (Finzi et al. 1998).

Many potential mechanisms by which species can control N cycling have been identified, including fixing atmospheric N, sequestering varying amounts of N in plant biomass, or by altering the distribution of N to aboveground and belowground plant parts (Vitousek et al. 1987; Fahey et al. 1998; Hobbie 1992). One of the most important controls is in the chemical quality of the litter produced. Litters with high ratios of lignin:N tend to decompose slowly (Melillo et al. 1982) and soils produced by those litters have been reported to have low N mineralization rates (Scott and Binkley 1997). Phenolic compounds in litter have also been shown to have effects on nutrient cycling processes in the soil through multiple mechanisms (see review by Hattenschwiler and Vitousek (2000)) including enhancing N immobilization in litter (Gallardo and Merino 1992), altering the proportion of dissolved organic to inorganic N in soil solution (Northup et al. 1995), acting as general microbial inhibitors or as sources of labile C (Schimel et al. 1998; Fierer et al. 2001), or specifically inhibiting nitrification (Baldwin et al. 1983).

This study was designed to elucidate the role of five important tree species in modifying the N cycle in forested watersheds of the Catskill Mountains. We used a comparative approach, in which we contrasted N cycling properties of small, single-species plots within mixed-species forest stands.

Methods

The study was performed in the Catskill Mountains, an area of flat-topped mountains and deeply incised valleys encompassing about 5000 km^2 in southeastern New York State. There are 35 peaks over 1067 m (3,500 ft), the highest being Slide Mountain at 1274 m (4,180 ft). 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 the region are primarily thin Inceptisols of moderate to high acidity (Stoddard and Murdoch 1991). 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.

We studied the five most dominant trees in the Catskill region (McIntosh 1972): sugar maple (*Acer saccharum* Marsh), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), eastern hemlock (*Tsuga canadensis* L.), and red oak (*Quercus rubra* L.). For each species we chose six 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. Each plot was 3 m in radius and included 2 or 3 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. The plots were chosen with the following criteria estimated by observation in the field: 1) > 90% dominance of the canopy by the mature trees of the target species, 2) pure or nearly pure litter composition from target species, and 3) no evidence of recent disturbance such as logging or fire.

In each of the 30 plots we measured several key characteristics of the N cycle in a forest: foliar and litter N concentrations, litter lignin and polyphenol concentrations, soil C:N ratio and potential N mineralization and nitrification, and an index of NO_3^- leaching.

Foliar N concentration was measured in early August 1998 by shooting foliage from the mature canopy trees in the plot with a shotgun using steel shot. Three samples of sunlit leaves near the tops of the trees were collected per plot. For each sample we measured leaf area with a Li-Cor LI-3000A Leaf Area Meter, fresh weight and dry weight, and the samples were dried in a 60 °C oven, ground in a ball mill, and N concentration was measured by dry combustion with a Leco CN2000 analyzer.

Litterfall was collected using 3 plastic baskets (each 0.23 m^2 area) per plot. Each basket contained a fiberglass screen that trapped the litter and kept it off the bottom of the basket. Litter collections were made biweekly during September–November 1998 except during the heaviest litterfall period of early October, when weekly collections were made. Collections for each basket were composited across all time periods before being sorted by species, dried in an oven at 60 °C, ground, and analyzed for N concentration in the CN analyzer.

Litter lignin concentration was determined as follows. Samples were ground through a 1 mm screen with a Cyclotec (Foss Tecator, Hoeganaes, Sweden) sample mill. Duplicate 0.5 g samples were placed into filter bags (Ankom #F57, Ankom Technology, Fairport, NY) and refluxed for 60 min with acid detergent solution (Robertson and Van Soest 1981) using an Ankom200 Fiber Analyzer. Samples were washed three times with hot (95 °C) distilled water and then once with acetone.

Air-dried bags were dried in a forced-air oven (100 °C) for a minimum of 4 h before weighing to determine amount of fiber residue present. Bags were then submerged in 72% H_2SO_4 for 3 h, washed with boiling, distilled water until the pH of rinse water was neutral, rinsed once with acetone, and dried in a forced-air oven (100 °C) for a minimum of 4 h before weighing to determine the amount of lignin residue. Bags were then ashed in a muffle furnace at 550 °C and residual ash weights were obtained. Lignin concentrations were calculated as the difference between the lignin residue weight and the ash residue weight (including blank bag correction), divided by the weight of the original sample dry matter.

Litter phenolic concentrations were measured on a composite sample of litter collected from each plot in the autumn of 2000, using the following procedures. *Polyphenol extraction and purification*. Five g of lyophilized leaf powder were washed in 100 ml of ether for 30 minutes to remove pigments and waxes, and then extracted 3 × in 125 ml 70% acetone at 40 °C for 1 h under sonication. Ascorbate (10 mM) was added to the acetone to prevent oxidation. Acetone was removed by evaporation under reduced pressure, and distilled water was added to the aqueous extracts to a constant volume of 125 ml.

Semipurified polyphenol standards were prepared as described by Hagerman and Klucher (1986). A slurry of 50 g of Sephadex LH_2O (Pharmacia, Piscataway, NJ) and approximately 1 liter of 95% reagent grade ethanol was equilibrated overnight, and then mixed thoroughly with 125 ml of crude extract from the procedure described above. Using a large Buchner funnel and vacuum filtration, monomeric polyphenols were eluted from the slurry by washing it with 95% ethanol. Mostly-polymeric polyphenols (= tannins) were subsequently eluted with 70% acetone, which was removed from the filtrate by evaporation under reduced pressure. The extract was freeze-dried and stored under nitrogen at −10 °C. Yields of the off-white powder averaged 5% of the dry weight of the leaf. Use of standards comprising the actual polyphenols present in samples provides an accurate dry weight-based quantification (Appel et al. 2001).

Polyphenol assays. Purified tannins of each species were assayed for (1) *″total phenolics″* using the Folin-Denis assay (Swain and Hillis 1959; Swain and Goldstein 1964) which measures the ability of phenolics to reduce a mixture of phosphomolybdic and phosphotungstic acids, (2) *condensed tannins* using the butanol-HCl assay (Bate-Smith 1977) which quantifies hydrolyzed proanthocyanidin residues, and (3) *hydrolyzable tannins* using the potassium iodate method modified for quantitative use (Schultz and Baldwin 1982; Hartzfeld et al. 2002) which quantifies galloyl esters. Polyphenol contents are reported as means of triplicate absorbance measurements of single extracts from each sample.

The colorimetric Folin-Denis ″total phenolics″ measure assesses the redox potential of a phenolic-containing extract. When used with a standard having the same composition as the samples (prepared as described above), this measure approximates the total concentration of all phenolic molecules, plus any other reducing agents that may be present. This fraction comprises a complex mixture of protein-binding, antioxidant, toxic, and signaling phenolic molecules. The tannin fractions contain protein- and cation-binding phenolic polymers. Condensed tannins are com-

posed of anthocyanin monomers, are only slightly soluble in acidified water, and can be hydrolyzed only with strong acid. Condensed tannins have been shown to influence N mineralization by several studies (Fierer et al. 2001; Schimel et al. 1998; Hattenschwiler and Vitousek 2000). Hydrolyzable tannins are polymers of glucose and esterified phenolic acids; they are quite water-soluble and hydrolyze readily in slightly acidic water, producing phenolic acid residues that may be antifeedant or toxic to decomposer organisms (Zimmer 1999). While their impact on nutrient cycling has not been reported, hydrolyzable tannins may comprise the major portion of the polyphenols in litter from the tree species studied here.

Soil properties were measured on four soil samples per plot collected in July 1998. Fresh litter was brushed away, and a soil core was taken to a depth of 12 cm unless a rock or large root obstructed. The core was separated into two samples representing organic (Oe + Oa) and mineral (A and/or B) horizons. The 12-cm core generally included the entire organic horizon and a variable depth of mineral soil. In cases where mineral soil was not encountered at a depth of 12 cm, the core was deepened until a mineral horizon was reached and a sample was taken from approximately the top 5 cm of the mineral soil. Extractable NH_4^+ and NO_3^-, total C and N, and potential net N mineralization and nitrification were measured on each sample. The samples were returned to the laboratory, passed through an 8 mm sieve, and thoroughly homogenized. A subsample was dried in an oven at 60 °C to determine moisture content; a second subsample was used to determine field capacity gravimetrically after saturating the sample and allowing it to drain overnight. Each sample was then wetted with deionized water to a moisture content of 60% of the field capacity. A subsample of approximately 10 g was extracted by adding 100 mL of 2 M KCl to the sample, shaking the sample twice within the first hour, allowing it to stand overnight, and then filtering the extract into clean polyethylene bottles through Whatman 41 filter paper. Another 10 g subsample was incubated for 28 d at 20 ± 4 °C in a plastic specimen cup covered with polyethylene film. After the 28 d incubation, the sample was extracted as above. Potential net N mineralization was calculated from the change in extractable N (NH_4^+ + NO_3^-) from initial to final extractions, and the potential net nitrification was calculated from the change in NO_3^-. Another subsample was dried, ground, and analyzed for percent C and N by dry combustion on the CN analyzer. On a composite mineral soil sample from each plot we also measured pH (in a 1:1 mixture with water), and soil texture using the Lowy pipette method, with pretreatment to destroy organic matter (Gee and Bauder 1986).

Resin bags were used as relative indicators of NO_3^- leaching from the plots. Approximately 10 g (dry weight basis) of Sybron IONAC ASB-1P resin were enclosed in small bags made of pre-cleaned nylon stockings. The resins were charged by soaking overnight in 0.5 M NaOH. Four bags per plot were buried in the mineral soil at a depth of 10–20 cm by pounding in a flat pry bar to make a slit in the soil, inserting the bag in the slit, and closing the slit with gentle pressure. The bags were left in the soil from October 1998 through May 1999. The winter and spring are the periods of highest NO_3^- leaching loss in these forests (Murdoch and Stoddard 1992), and these resin bags were intended to provide an index of potential differ-

ences in leaching among plots. After the resin bags were retrieved from the plots, they were extracted twice in 2 M KCl, and the two extracts were combined to determine total N exchanged from the resin. The extracts were analyzed for NO_3^- on an Alpkem Flow Solutions III auto-analyzer using the cadmium reduction method. Concentrations were expressed per g dry mass of the resin.

Statistical analysis was performed using the SAS system (SAS Institute 1989). Species differences were tested by analysis of variance using the GLM procedure. When multiple samples were taken within a plot, the ANOVA was performed on plot means with n = 30 (5 species × 6 plots per species). Differences among individual means were tested with the Student-Neuman-Keuls procedure. Correlation was tested with the Pearson correlation coefficient using the CORR procedure in SAS.

Results

Foliar and litter N concentrations

The species differed significantly in N concentration in full-sun foliage (Figure 1, $p < 0.0001$). Hemlock had the lowest foliar N concentration and the other species were statistically indistinguishable. Litterfall N concentrations were also significantly different among species ($p = 0.0013$), and within a species, were always lower than foliar N concentrations (Figure 1). Yellow birch had the highest litter N concentrations, while the other species were not significantly different from one another. The ratio of N concentration in foliage to that in litterfall is an index of resorption efficiency, and this index indicates the most efficient resorption occurred in sugar maple and the least efficient in hemlock (Figure 1).

Litter lignin and phenolic concentrations

Litter lignin and phenolic concentrations also varied significantly among species (Figure 2). Lignin concentrations were highest in yellow birch and beech, and lowest in hemlock and sugar maple. Although mean lignin:N ratios varied from 19 in hemlock to 28 in beech, these means were not significantly different among species (Figure 2). Sugar maple had the highest concentrations of Folin-reactive phenolics and condensed tannins, but hydrolyzable tannins were high in both hemlock and sugar maple. Red oak and beech had the lowest concentrations of Folin-reactive phenolics; hemlock, oak and birch had the lowest condensed tannins; and beech had the lowest hydrolyzable tannins (Figure 2).

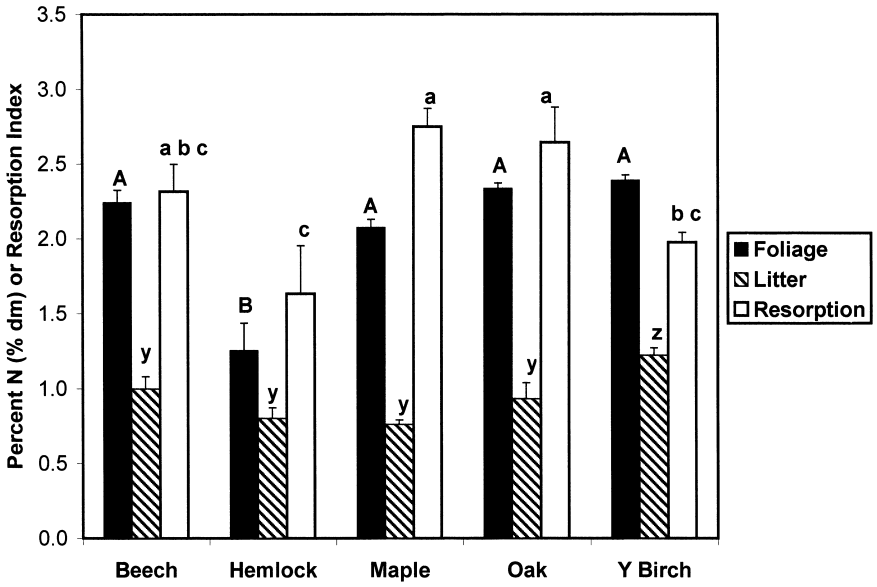

Figure 1. Mean N concentration (percent dry mass) for fresh foliage (black bars) and litter (striped bars) in the five species. The white bar is the resorption index, or the ratio of fresh foliage:litter N concentration. Error bars are standard errors. A,B denote significant differences in fresh foliage; y,z denote differences in litter N, and a,b,c denote differences in resorption index. Within each group of letters, species sharing common letters are not significantly different.

Soil texture and pH

Although individual stands varied in soil texture, there were no significant differences among species in percent sand, silt or clay (Table 1). The average texture across all plots was 56% sand, 30% silt, and 14% clay.

There were significant differences in mineral soil pH among the species ($p = 0.005$). A comparison of means indicated that maple plots were not significantly different from oak plots but that those two species had higher soil pH than a group including yellow birch, beech and hemlock (Table 1).

Soil N

There were significant differences among species in C:N ratios in both organic and mineral horizons ($p < 0.0001$ and $p = 0.03$, respectively) with hemlock having the highest C:N and maple the lowest (Table 1) in both the mineral and organic horizon. There were significant differences among species in organic-horizon extractable NO_3^- ($p = 0.0004$) but not in extractable NH_4^+ ($p = 0.38$) prior to the 30-d incubation (Table 1). Extractable NO_3^- concentrations were highest in maple plots and lowest in oak and hemlock plots (Table 1). The same patterns were observed after the incubation. Similar among-species patterns of extractable NH_4^+ and NO_3^-

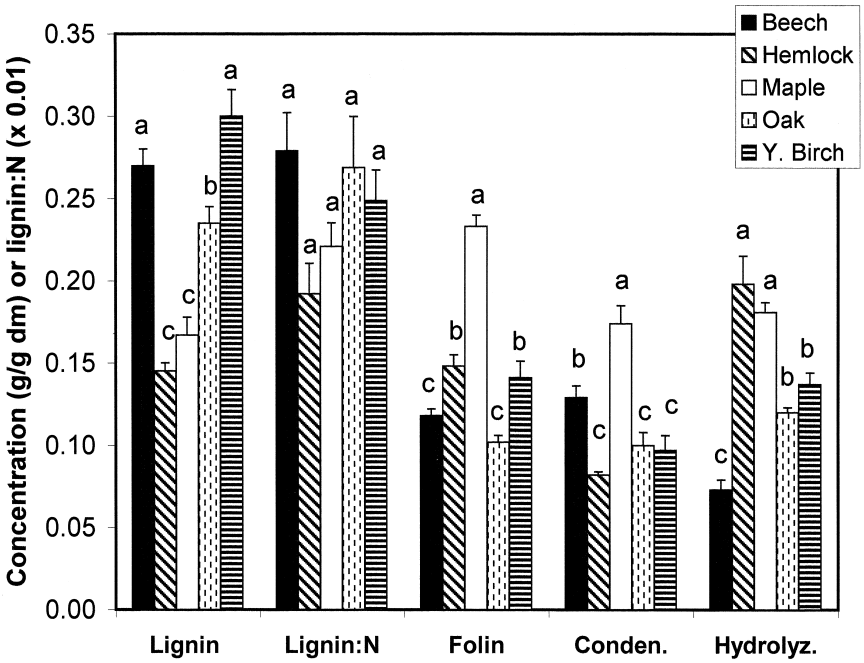

Figure 2. Mean concentrations of lignin and phenolic constituents and the lignin:N ratio in the foliar litter of the five tree species. Data are means and standard errors of n = 6 plots per species. Folin = Folin-reactive phenolics; Conden. = condensed tannins, Hydrolyz. = hydrolyzable tannins. Letters indicate significant differences among species for each constituent. Within a single bar cluster, species with common letters are not significantly different in concentration of that constituent.

concentrations were found in the mineral horizons, although absolute concentrations were lower (Table 1).

Potential net N mineralization and nitrification rates also varied significantly among species ($p = 0.0027$ for mineralization and $p = 0.0017$ for nitrification in organic horizons). Maple and beech had high mineralization rates and high nitrification rates, and hemlock had low rates of both processes (Figure 3a). Oak and birch had moderate rates of mineralization but low rates of nitrification. The nitrification fraction, which is the percentage of mineralized N that was nitrified, varied from 59% in maple plots to 8% in oak plots. Nitrogen mineralization and nitrification rates per g dry weight of soil were generally lower in the mineral horizons than in the organic horizons, but the differences among species were similar in the two horizons (Figure 3a).

We also calculated the net N mineralization rates and nitrification rates per g of N in the soil, as a measure of the lability of the N in the soil. Interestingly, the rates of net N mineralization and nitrification per g N were substantially higher in the mineral soil than in the organic soils (Figure 3b). This is the reverse of the pattern seen for the rates expressed per g DW of soil (Figure 3a).

Table 1. Mean soil properties in the research plots. Under extractable N, ″ext″ indicates the initial extraction of the soil and ″inc″ indicates the extraction after the 30-day incubation. Within a row, means sharing a letter are not significantly different. If there are no letters in a row, none of the means are significantly different from one another.

Parameter	Horizon		Beech	Hemlock	Maple	Oak	Y Birch
Texture	Mineral	%sand	57.7	51.6	56.3	48.4	65.0
		%silt	29.7	35.4	26.3	35.6	24.2
		%clay	12.8	13.0	17.4	16.0	10.9
pH	Mineral		3.27 b	3.21 b	3.92 a	3.88 a	3.32 b
C:N	Organic		21.5 b	24.9 a	19.2 c	21.1 b	22.1 b
	Mineral		20.1 a,b	24.9 a	17.3 b	19.5 a,b	21.4 a,b
Extractable N	Organic	NH_4 ext	19.3	14.3	17.0	14.7	14.9
		NH_4 inc	132.3	72.8	93.2	125.5	109.7
		NO_3 ext	7.9 a,b	1.5 c	12.2 a	0.8 c	3.6 b,c
		NO_3 inc	80.9 a,b	11.9 c	111.0 a	21.9 c	46.3 b,c
	Mineral	NH_4 ext	11.1	13.4	11.6	11.6	12.3
		NH_4 inc	47.8 a,b	49.3 a,b	32.2 b	56.6 a,b	64.4 a
		NO_3 ext	10.1 a,b	1.6 c	13.2 a	1.3 c	6.7 b
		NO_3 inc	63.8 a	14.0 b	83.9 a	17.1 b	52.1 a

Relationships between litter and soil properties

We looked for correlations between N mineralization and nitrification and possible controlling variables such as soil C:N and litter lignin and phenolic concentrations. Correlations with litter N and lignin concentrations were weak and nonsignificant (Table 2). There were some marginally significant correlations among soil N transformations and litter phenolics. Condensed tannin concentrations were positively, but weakly, correlated with N mineralization, nitrification, and nitrification fraction. This positive correlation was contrary to what might be expected from the reported inhibitory role of tannins in decomposition processes (Hattenschwiler and Vitousek 2000), although some tannins are known to enhance microbial activity (Schimel et al. 1998; Fierer et al. 2001). There was a slight negative correlation between hydrolyzable tannins and N mineralization in the organic soils, and a positive correlation between Folin-reactive phenolics and nitrification fraction in both the organic and mineral soils (Table 2). There were moderately strong negative correlations between the soil N transformations and soil C:N ratio, and to a lesser extent, soil percent C. Closer examination of the relationship between soil C:N and nitrification in the organic horizon reveals an increase in nitrification with decreasing soil C:N for maple, beech, and birch plots (Figure 4). This relationship did not hold for the oak plots, which in general had very low nitrification rates across the entire range of C:N, with the exception of one oak plot that had a relatively high nitrification rate for reasons that remain a mystery to us. None of our hemlock plots had C:N ratios below 23, so from these data it is impossible to determine if nitrification rates in hemlock stands would increase at lower C:N ratios.

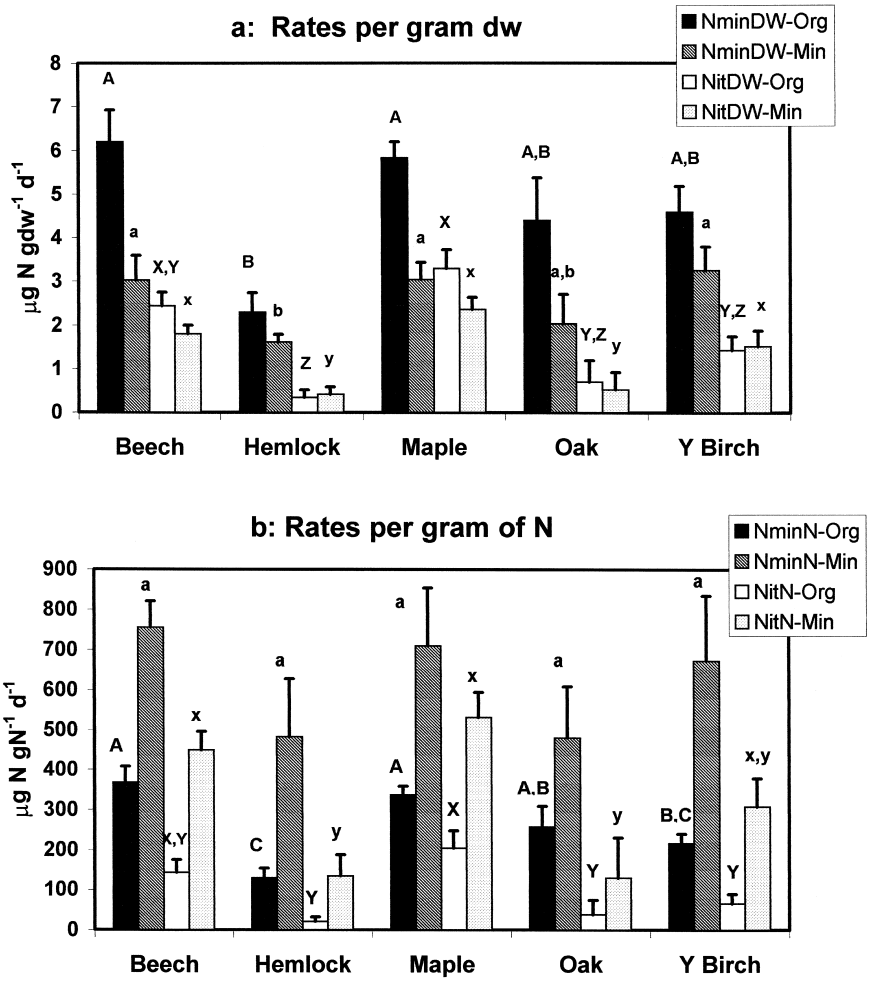

Figure 3. a) Mean rates of potential net N mineralization and nitrification per g DW per day under the five species. b) Mean rates of potential net N mineralization and nitrification per g N per day in soil under the five species. Error bars are standard errors. A,B denote differences in mineralization in organic horizons; a,b denote differences in mineralization in mineral horizons; X,Y,Z denote differences in mineralization in mineral horizons, and x,y denote differences in nitrification in mineral horizons. Within each group of letters, species sharing common letters are not significantly different.

Because our soil sampling protocol resulted in variation among plots in the depth of the mineral soil samples, changes in organic matter or N content with depth in the mineral soil could obscure relationships between litter and soil variables. However, all of the correlations in Table 2 were also calculated for N mineralization and nitrification expressed per gram of N (to normalize for the amount of N in the soil), and these correlations did not differ substantially from those shown in Table 2,

Table 2. Pearson product moment coefficients for correlations between soil N transformations and possible controlling variables.

	Organic Horizons			Mineral Horizons		
	NminDW	NitDW	Nit. Fraction	NminDW	NitDW	Nit. Fraction
Soil %N	0.08	–0.04	–0.09	0.34	0.30	0.14
Soil %C	–0.27	–0.43*	–0.43*	0.16	0.02	–0.13
Soil C:N	–0.51**	–0.61***	–0.60***	–0.23	–0.47**	–.51**
Litter % Lignin	0.26	–0.07	–0.16	0.30	0.01	–0.11
Litter % N	0.09	–0.04	–0.03	0.23	0.09	0.02
Litter Lignin:N	0.20	–0.08	–0.21	0.07	–0.12	–0.18
Litter Folin Reactive Phenols	0.06	0.32	0.43*	0.13	0.38	0.49**
Litter Condensed Tannins	0.37*	0.42*	0.41*	0.25	0.46*	0.55**
Litter Hydrolyzable Tannins	–0.38*	–0.16	–0.01	–0.26	–0.12	–0.03

*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

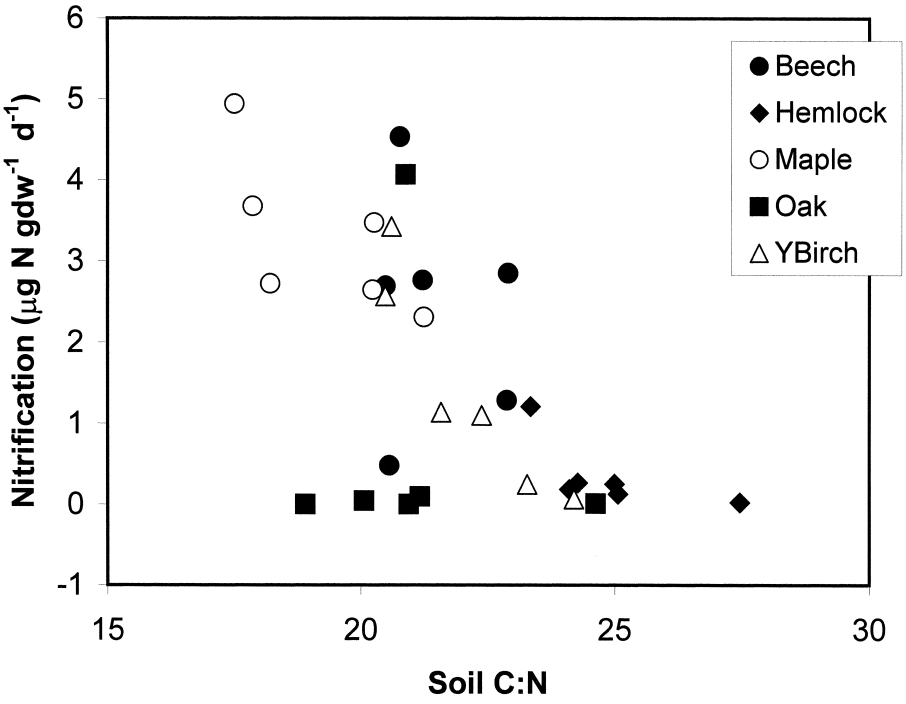

Figure 4. Potential net nitrification rate in organic horizons as a function of C:N ratio.

suggesting that the depth of mineral soil sampling was not an important confounding factor.

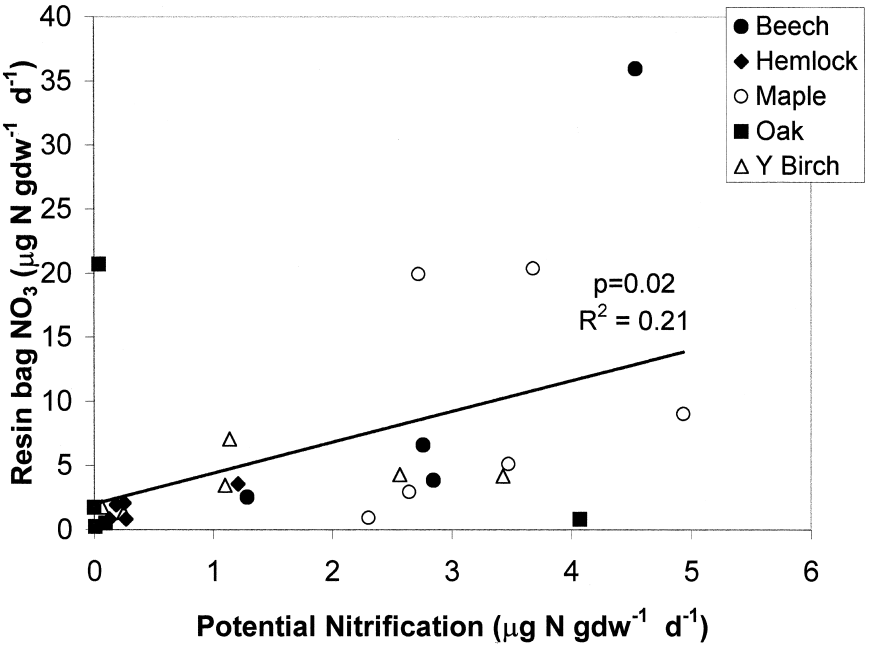

Figure 5. Mean extractable NO_3^- from resin bags buried in mineral soil beneath the research plots vs. potential net nitrification in organic soils in the plots. Each point represents the mean of measurements within a single plot. Regression line is for all plots combined.

Ion exchange resins

The amount of NO_3^- trapped in the ion exchange resin bags varied among species in a similar manner to soil extractable NO_3^- and nitrification rates–maple and beech were highest, and hemlock, oak, and birch lowest. However, among-species differences in the resin bag NO_3^- values were not statistically significant, despite the 6.5-fold range in mean values, because of the extremely high variability within and among plots (Figure 5). The relationship between potential net nitrification and resin bag NO_3^- was significant but weak ($p = 0.02$, $r^2 = 0.21$, Figure 5)

Discussion

Marked variation among species was observed in most of the N cycling characteristics measured in this study. The suite of measurements taken together comprises a profile of each species' N cycling characteristics. To summarize and display these profiles, we calculated for each variable the percentage difference between the mean for an individual species and the mean across all species. This expresses the values of a variable for each species as a relative deviation from the mean of all species.

The species show individualistic N cycling profiles (Figure 6). Beech has near average levels of foliar and litterfall N, but above average levels of soil N availability as indicated by extractable NH_4^+ and NO_3^-, N mineralization and nitrification. The resin bag NO_3^- concentration, which we interpret to be a relative index of NO_3^- leaching, was also relatively high. Hemlock consistently showed characteristics typically associated with ″slow″ N cycling. It had low foliar and litter N, high soil C:N, low extractable N pools, low mineralization and nitrification rates, and low resin bag NO_3^-. Sugar maple had near-average foliar N, but low litter N, giving the highest resorption efficiency of the species in this study. It had the lowest C:N measured, and its other soil N cycling characteristics were consistently above the average, especially those associated with NO_3^- production and loss (nitrification, extractable NO_3^-, and resin bag NO_3^-). Red oak showed a very different profile–it had relatively high foliar N, near average mineralization rates and extractable NH_4^+, but very low values of the variables associated with NO_3^- production and loss. Yellow birch had the highest foliar and litter N values, near-average soil C:N, mineralization rate, and extractable NH_4^+, and moderately low values of the NO_3^--associated variables.

In contrast to previous studies (Stump and Binkley 1993; Scott and Binkley 1997) we did not find strong correlations between litter lignin and N characteristics (% N, % lignin, lignin:N) and soil N mineralization or nitrification rates. These previous studies compiled data sets that differed in several ways from ours: 1) Their studies compiled literature data from a range of species growing in different soil and climatic conditions, 2) they included litter with higher lignin:N ratios than we observed in our 5 species, and 3) they used rates of *in situ* net N mineralization, as opposed to the laboratory potential rates measured in our study. It is possible that the larger range of lignin:N may have permitted a correlation between lignin:N and N mineralization to emerge in their data sets but not in ours. Within the range of lignin:N values we observed in this study, the correlation in the Scott and Binkley (1997) data set does not appear to be much stronger than what we observe (see Figure 3 in Scott and Binkley (1997)). Furthermore, if litter characteristics do in fact control N mineralization, one might expect to see a higher correlation in our data set because 1) we measured laboratory potential rates under controlled conditions of temperature and moisture, using identical procedures for all species, and 2) the sites we sampled had very similar soil types, elevations, and climatic conditions. These factors should minimize the noise in the relationship between litter lignin:N and N mineralization, yet the correlation we observed was poor (Table 1).

We conclude that the set of species we investigated vary in some important characteristics that overshadow the influence of the litter lignin:N ratio. One possibility is the level of polyphenols in the litter and soil organic matter, because polyphenols have been shown in several previous studies to affect soil N cycling processes (Gallardo and Merino 1992; Northup et al. 1995; Schimel et al. 1996). However, our data showed only weak correlations between the N transformations and the litter polyphenol measures that we used (Folin-reactive phenolics, condensed tannins, and hydrolyzable tannins). In fact, for Folin-reactive phenolics and condensed tannins, the correlations are positive, the opposite of what would be ex-

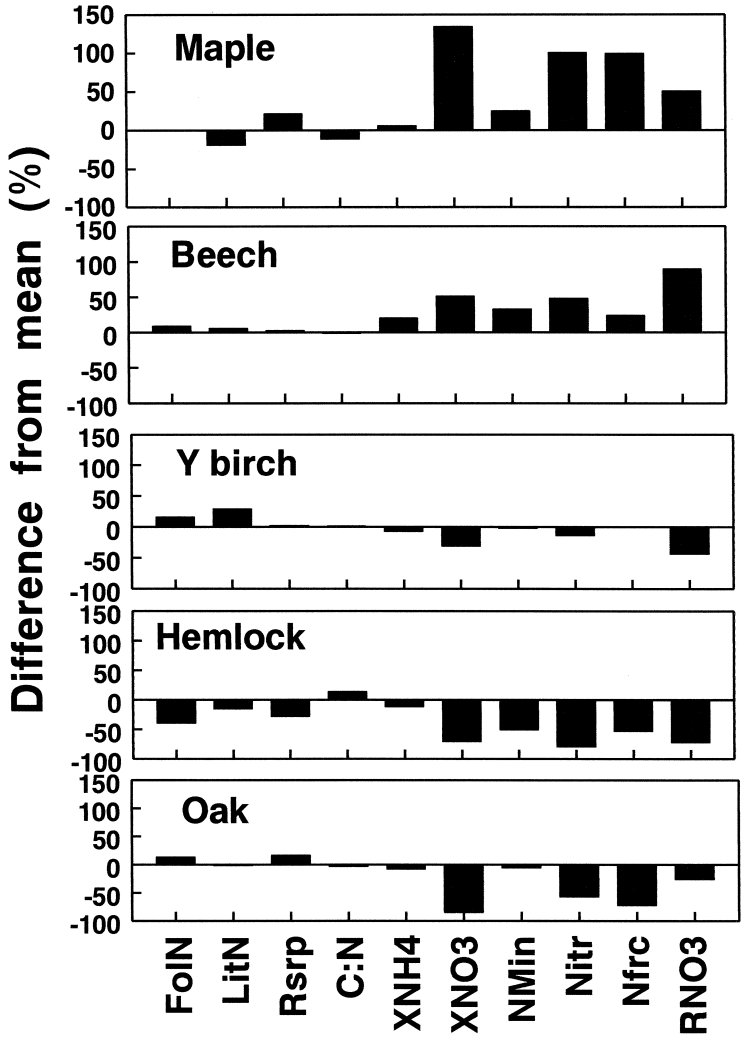

Figure 6. ″Species profiles″ of relative values of N cycling variables. The Y axes represent the species mean for each variable relative to the mean across all 5 species. Abbreviations on the X axis are as follows: FolN, foliar %N; LitN, litter %N; Rsrp, resorption index (see Figure 1); C:N, soil C:N; XNH_4^+, soil extractable NH_4^+; XNO_3^-, soil extractable NO_3^-, Nmin, potential net N mineralization; Nitr, potential net nitrification; Nfrc, nitrification fraction (nitrification/mineralization); RNO_3, resin bag NO_3^-. All soil data are for organic horizons.

pected. The species with the highest tannin concentrations, sugar maple, also had the highest nitrification rates and nearly the highest N mineralization rates. There are several possible explanations for these results. The most important of these is probably variation in polyphenol quality (composition), as opposed to quantity (concentrations). Our assays focused on polymeric polyphenols (″tannins″), which previous studies have also emphasized (Gallardo and Merino 1992; Northup et al.

1995; Fierer et al. 2001). The foliage phenolic composition of these tree species is much more complex than the polyphenol fraction is likely to reveal, and species- or site-specific monomeric or oligomeric phenolics could be responsible for the patterns we observed. Indeed, we found that the standard curves (relating absorbance to polyphenol concentrations) were species-specific, suggesting that composition of the polyphenol mixtures from these tree species differed qualitatively. This difference in composition would produce differential activity independent of concentration. Previous studies, which did not use standards made from the litter they studied, may have confused effects of concentration with those of composition.

Tannin-protein interactions (a likely mechanism of their impact on nutrient cycling phenomena) are also pH dependent, and some polyphenolic mixtures may have been more active than others in the acidic systems encountered in this study. Finally, local microbial communities are likely to adapt to the quality of incoming litter, and the stand age, history, and microbial community composition should be accounted for in comparing polyphenol impacts on different systems.

While it is possible that tannins may not affect these N transformation processes, we consider it more likely that the general phenolic assays we used in this study, which are commonly used for leaf tissue, are not optimal for identifying the phenolics important to soil microbes. Even within the category ″condensed tannins,″ variations in the degree of polymerization can produce widely varying effects on microbial processes (Fierer et al. 2001). It is clear that the impacts of litter polyphenols warrant closer scrutiny and would benefit from development of an assay specifically targeted at polyphenolic effects on soil N cycling processes.

Examination of the species profiles (Figure 6) suggests that the factors controlling N mineralization are different from those controlling nitrification. For instance, hemlock has low rates of both N mineralization and nitrification, maple has moderate rates of mineralization and very high rates of nitrification, and red oak has moderate rates of mineralization and very low rates of nitrification. Thus, referring to species as having ″faster″ or ″slower″ N cycles involves unwarranted generalization, as the rates of different parts of the N cycle may vary independently.

We found that N mineralization and nitrification are higher in the organic horizon than in the mineral soil when expressed per gram of dry weight (DW), but are higher in the mineral soil when expressed per gram of N in the soil (Figures 3a and 3b). The lower rates per g DW in the mineral soil probably reflect the fact that the mineral soil has less organic matter and thus less mineralization than the organic soils. The observation that the rates in the mineral soil are higher per g of N suggests that either 1) the N in the mineral soil is more labile than the N in the organic soil, or 2) there are lower levels of microbial N immobilization in the mineral soil because of lower labile C availability.

Our data lend some support to the idea that soil C:N ratio is related to the rates of soil N transformations, especially nitrification. Several studies have suggested that net nitrification rates increase with decreasing C:N below a threshold value of C:N of about 22–25 (McNulty et al. 1991; Gundersen et al. 1998; Lovett and Rueth 1999; Goodale and Aber 2001). Our data indicate that this relationship is a reasonable approximation of the behavior of beech, maple, birch and hemlock stands

taken together, although no single species spans the range above and below the threshold point of about C:N = 24 (Figure 8). Oaks do not follow this generalization, however, as most of the oak stands in our study had very little potential net nitrification even at quite low values of C:N. Overall, soil C:N explained only about 25–36% of the variation of net N mineralization and nitrification (squares of correlation coefficients in Table 2). In a multiple-watershed study in the Catskill Mountains, Lovett et al. (2002) reported that 57% of the variance in stream water NO_3^- concentrations could be explained by variation in the C:N ratio of watershed soils. They also found that in mixed-species stands, increasing oak dominance was associated with a higher C:N ratio, and increasing sugar maple dominance with a lower C:N ratio. In a study of the fate of ^{15}N applied as a tracer to a subset of these plots, Templer (2001) found oak plots to be more retentive of added $^{15}NH_4^+$ than maple plots, but in all plots the ^{15}N was retained predominantly in the forest floor.

The reason for the low nitrification rates in oak stands is not apparent from these data. If there were some inhibition of the NH_4^+ oxidation step in nitrification, one might expect NH_4^+ to accumulate in soils during our laboratory incubations, but that did not occur to any unusual extent in oaks (Table 1). Another possibility is the abiotic retention of NO_2^- in soil organic matter, a process known as nitrosation (Stevenson and Swaby 1964; Dail et al. 2001). However, a recent experiment on these soils shows that although nitrosation may be important in these soils, it proceeds at a similar rate in maple, beech and oak soils (Fitzhugh et al. in press). Thus, this process does not account for an unusually low net nitrification in oak stands. A third possible process is biotic or abiotic consumption of NO_3^- (Berntson and Aber 2000; Dail et al. 2001). We are currently investigating the roles of the many N-consuming processes in these stands.

Previous studies that have examined the nutrient cycling associated with these tree species have generally compared mixed-species stands, sometimes with varying soil texture, making it more difficult to isolate species effects. However, some similar trends have been reported–for instance, sugar maple has been associated with high nitrification rates in studies in New Hampshire (Ollinger et al. 2002), Wisconsin (Mladenoff 1987), Connecticut (Finzi et al. 1998) and West Virginia (Christ et al. 2002). The study most comparable to ours was the work by Finzi et al. (1998) in Connecticut, which involved sampling of soil N properties under single-tree canopies of four of the five species we studied. Finzi et al. reported that, compared to sugar maple, soils under hemlock, beech and red oak trees had significantly higher soil C:N ratios and tended to have lower (but not significantly lower) mineralization and nitrification rates. Our study found also found higher C:N ratios in soils under hemlock, and in addition we found that hemlock stands had significantly lower N mineralization rates, and both hemlock and oak stands had significantly lower nitrification rates (in organic horizons), than maple and beech stands.

Our approach of sampling small single-species plots was necessary for the measurements we made, but this approach has several limitations. First, it is possible that the single-species plots were present because of some inherent edaphic difference (e.g., soil texture) in the plots that could influence our results. In other words,

are the species causing differences in N cycling or is their presence a response to characteristics of the site? While a comparative study like this one cannot conclusively answer that question, we believe that the N-cycling differences we observed were caused primarily by the species present on the site for four reasons: 1) Our analysis is focused on the organic soil horizons, the properties of which are strongly influenced by organic matter generated by the trees; 2) We focus on N, an element whose cycling is, under most circumstances, under biological more than geochemical control; 3) We chose small single-species plots growing within mixed-species forest, increasing the probability that the tree clusters are present because of the vagaries of dispersal rather than as a result of edaphic characteristics. We also chose plots of mature trees, so that N cycling properties of the soil would have been influenced by the same species for decades prior to our sampling; 4) We found no significant soil textural differences among species. Soil texture is a likely mechanism for edaphic control of both species composition and N cycling (e.g., Pastor et al. (1984)). We did find differences in soil pH among species, but it remains uncertain whether those differences are a cause of the species dominance on the plot, or a result of them. Further, our data do not suggest that soil pH has a strong effect on N cycling processes. Acid soils are known to inhibit nitrification, but in our study the two species having the highest mean soil pH had the highest and lowest nitrification rates (maple and oak, respectively).

A second limitation of the single-species plot approach is that we cannot easily use the results of this study to determine the characteristics of the N cycle in mixed-species stands. Synergistic or antagonistic effects between different species, particularly in the soil, may produce non-linear effects in species mixtures that would not be obvious in single-species stands (Finzi and Canham 1998). However, our results are consistent with our vegetation and soil surveys in mixed species plots in the Catskills. These surveys indicate that increasing dominance by sugar maple is associated with lower soil C:N ratios and higher NO_3^- leaching, while increasing red oak dominance is associated with higher C:N ratios and lower NO_3^- leaching (Lovett et al. 2002). Although on average oak stands in the Catskills have a relatively high C:N ratio, the results of the current study indicate that oaks influence nitrification rates by a mechanism that is not yet clear but goes beyond the C:N effect. Similar influences of maples and oaks in mixed-species stands have been noted elsewhere (Christ et al. 2002; Ollinger et al. 2002; Lewis and Likens 2000, 2000).

In summary, our study indicates that tree species can exert a strong control on N cycling in forest ecosystems that appears to be mediated through the quality of the soil organic matter they produce. However, the mechanisms of that control appear to be more complex than the simple litter and soil characteristics that have been previously reported in the literature, such as litter lignin:N ratio and polyphenolic concentration or soil C:N ratio. Nonetheless, the differences among species suggest that N cycling in forests is likely to be patchy and dependent on the dominant trees in the patch. In addition, it suggests that changes in forest composition resulting from such factors as selective harvest, tree diseases, or climatic change, could substantially alter the N cycling in a forest. In particular, introduced pests and diseases

are currently having a strong effect on tree species composition in the Catskills. The beech bark disease complex (Houston 1994) is decreasing the abundance of beech, thereby increasing the dominance of its principal competition, sugar maple (McIntosh 1962). In the past few years, the hemlock woolly adelgid has begun to infest the Catskills and has the potential to decimate the hemlock population as it has elsewhere (Orwig and Foster 1998). It is clear that models that attempt to predict how forest N cycling will respond to such perturbations as enhanced atmospheric N deposition and climate change should account for possible changes in species composition that could profoundly alter the N cycling characteristics of the ecosystem.

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