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SOIL NITROGEN TRANSFORMATIONS IN BEECH AND MAPLE STANDS ALONG A NITROGEN DEPOSITION GRADIENT

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Abstract. A gradient of atmospheric nitrogen deposition exists across the northeastern United States due to the concentration of urban and industrial sources of nitrogen oxides in the southern and western parts of the region. We examined possible effects of N deposition on N cycling in forests by measuring potential net mineralization and nitrification of soils under single-species plots of sugar maple and American beech along this gradient. The total atmospheric deposition of nitrogen was estimated to range from 11.1 kg $N \cdot ha^{-1} \cdot yr^{-1}$ at a site in southern New York to 4.2 kg $N \cdot ha^{-1} \cdot yr^{-1}$ at a site in western Maine. Although potential net mineralization and nitrification rates were extremely variable, highly significant positive correlations were observed between N deposition and mineralization and nitrification rates in organic horizons in maple plots, but not in beech plots. The correlation between deposition and N cycling variables was weaker in mineral horizons than in organic horizons for maple plots, and no significant correlations between these variables were found for beech mineral horizons. Many beech soils showed no net nitrification even under the higher deposition conditions. Percentage nitrogen (%N) of the organic horizons increased with increasing deposition in sugar maple, but not in beech plots. In organic horizons of both species, mineralization and nitrification increased with increasing %N, although the slopes of the increases were steeper for maple than for beech. Nitrogen deposition, mean annual temperature, and mean annual precipitation were intercorrelated across the sites of this study, but the data indicate that the observed patterns of N mineralization in maple plots resulted from the N deposition gradient rather than the climate gradient. These results suggest that the two species respond differently to N accumulation from atmospheric deposition. Species differences in the responses of forests to N deposition should be considered in both the prediction of forest response and the management of forest composition which could affect that response.

Key words: Acer saccharum; *American beech;* Fagus grandifolia; *gradient studies; nitrification; nitrogen deposition; nitrogen mineralization; sugar maple; United States, northeastern.*

INTRODUCTION

In the eastern United States, release of nitrogen oxides from the burning of fossil fuels has increased atmospheric deposition of nitrogen by roughly a factor of 10 compared to preindustrial times (Hicks et al. 1990). The largest sources of nitrogen oxides are the east-coast urban centers and the industrialized region of the Great Lakes and the Ohio River Valley. In general, the deposition of nitrogen is thought to decrease along a southwest-to-northeast gradient from Pennsylvania to Maine in the northeastern United States because the nitrogen oxides are depleted from air masses as they move downwind from these major source areas (Ollinger et al. 1993). The enhanced deposition of nitrogen engendered by this air pollution has been of concern because of possible effects on the functioning of ecosystems, particularly forests (Aber 1992), streams (Murdoch and Stoddard 1992), and coastal waters and estuaries (Valiela et al. 1997). Hypothesized effects in forests include increases in foliar N concentrations, N mineralization and nitrification rates, and leaching of N into stream water or groundwater, perhaps leading to a general decline of forest productivity (Aber et al. 1989).

Investigations of the effects of N deposition using nitrogen fertilization experiments have shown mixed results. In some fertilized plots net nitrogen mineralization rates have increased initially and then decreased after several years (Aber et al. 1995, Magill et al. 1996), while in others no effect is seen (Aber et al. 1993, Emmett et al. 1995). The response to N fertilization of net nitrification rates and subsequent nitrate losses is similarly variable, with some studies showing continual increases during fertilization (Magill et al. 1996), some showing initial increases which fade over time (McNulty and Aber 1993), and some showing no effects (Aber et al. 1993, Christ et al. 1995, Emmett et al. 1995). Variation between studies is probably a function of the timing, quantity, and chemical form of the applied N as well as the history of the experimental plot (Magill et al. 1996).

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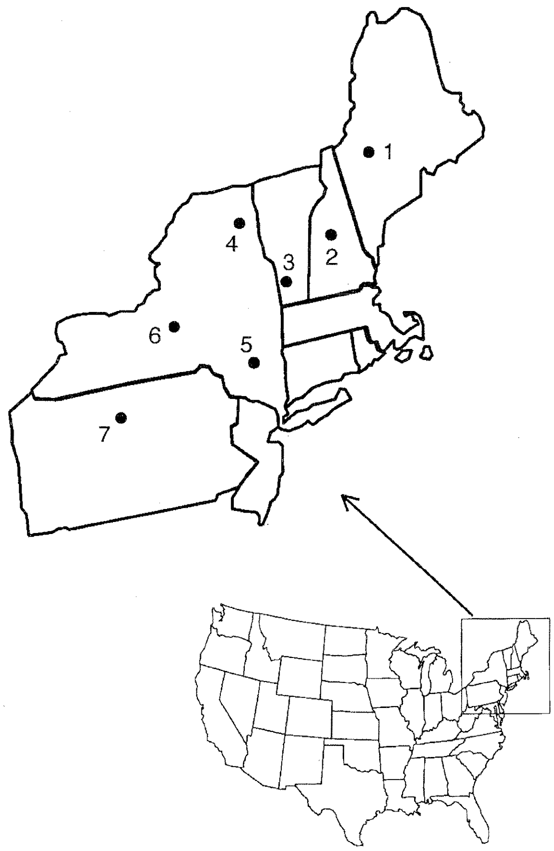

FIG. 1. Map showing location of study sites and site identification codes. (1) Sugarloaf area, Maine (MES); (2) Hubbard Brook, New Hampshire (NHH); (3) Lye Brook, Vermont (VTL); (4) Whiteface Mt., New York (NYW); (5) Catskill Mountains, New York (NYC); (6) Ithaca, New York (NYI); (7) Potter County, Pennsylvania (PAP).

An alternative method that avoids unrealistic doses of nitrogen is to compare ecosystems along an existing gradient of N deposition. This approach has been used by McNulty et al. (1991), who studied spruce–fir forests along an N deposition gradient in the northeastern United States and found correlations between estimated N deposition and forest floor C:N, forest floor percent N, net mineralization, and net nitrification, among other N cycling variables. In a similar study along a deposition gradient from Ohio to Minnesota, N deposition was not correlated with nitrate leaching from the soil or N concentration in foliage or litter, but it was correlated with N flux in litterfall because of higher litter mass at the high-deposition end of the gradient (MacDonald et al. 1992, Pregitzer et al. 1992).

Forest species composition is thought to be a major factor controlling nitrogen cycling, primarily because species differ in the decomposability of their litter (Melillo et al. 1982), which can lead to differences in nitrogen mineralization rates and thus in nitrogen availability to plants and microbes (Pastor and Post 1986, Stump and Binkley 1993). Lignin and nitrogen concentrations are thought to be key litter quality variables (Melillo et al. 1982, Stump and Binkley 1993, Scott and Binkley 1997). Thus, in order to observe any possible effects of N deposition along a gradient, it is important to control for variation in forest species composition.

In this paper we report the results of a study of potential net N mineralization and nitrification along an 800-km gradient of N deposition in the northeastern United States. We focused on N mineralization and nitrification because those processes are usually the rate-limiting steps in the nitrogen cycle, and thus control the rate of N cycling and loss in temperate forest stands. Our objectives were (1) to determine if potential net N mineralization and nitrification rates change across the N deposition gradient in the northeastern United States and (2) to determine if different tree species influence the response. Our measurements at each location along the gradient took place in single-species plots of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) in order to separate N deposition effects from species-related effects. Beech and maple, along with yellow birch (*Betula alleghaniensis*), are the dominant tree species in the northern hardwood forest, the most widespread forest type in the uplands of the northeastern United States. These two species provide a good contrast because beech litter has higher lignin concentration and lower decomposition rates than sugar maple litter (Melillo et al. 1982).

METHODS

Field methods

Seven study sites were identified along the N deposition gradient in the northeastern United States (Fig. 1). These sites were chosen to be on glaciated terrain, to be near atmospheric deposition monitoring stations of the Clean Air Status and Trends Network (Clarke et al. 1997), and to be dominated by northern hardwood forests, in which we could find single-species plots of sugar maple and beech. At each site, we searched until we found two or three plots of each species meeting these criteria: (1) the plot should be roughly 10 m in diameter, encompassing several canopy trees of the target species; (2) the target species should comprise at least 90% of the leaf area in the canopy by visual observation, and the litter of that species should dominate the forest floor; (3) the canopy trees should be at least 20 cm in diameter; and (4) there should be no evidence of recent disturbance (e.g., logging or agriculture). The latter two criteria were used to ensure as much as possible that the target species had dominated the site for several decades and that the forest floor was relatively undisturbed during that time.

In each plot we took five soil samples in early July of 1995, yielding 10–15 samples for each species at each site. To sample the soils, we brushed away the

TABLE 1. Atmospheric deposition and climate data for the study sites.

Site code	Total N dep. ($kgN \cdot ha^{-1} \cdot yr^{-1}$)	Nearest NADP/NTN site	Distance (km)	Nearest CASTNet site	Distance (km)	CASTNet data record	MAT (°C)	MAP (cm)
NYC	11.1	Biscuit Brook, New York	8	Catskills, New York	10	5/1994–1/1996	4.6	153
NYI	10.5	Aurora Research Farm, New York	51	Connecticut Hill, New York	13	1/1989–9/1995	7.1	96
PAP	9.1	Kane Experimental Forest, Pennsylvania	73	Kane Experimental Forest	73	1/1989–9/1995	6.6	107
VTL	8.9	Bennington, Vermont	23	Lye Brook, Vermont	5	3/1994–9/1995	6.6	115
NYW	7.1	Whiteface Mt., New York	<5	Whiteface Mt., New York	<5	1/1989–3/1993	5.6	101
NHH	6.8	Hubbard Brook, New Hampshire	<5	Woodstock, New Hampshire	<5	1/1989–1/1996	5.6	131
MES	4.2	Greenville, Maine	65	Howland, Maine	125	1/1993–9/1995	3.4	96

Notes: Estimated total N deposition, nearest NADP/NTN (wet deposition) and (CASTNet (dry deposition) sites, and approximate distances from NADP/NTN and CASTNet sites to study sites are given. Also listed are mean annual temperature (MAT) and mean annual precipitation (MAP) for the sites. Site codes are as shown in Fig. 1

fresh litter (Oi horizon) and obtained a 20 × 20 cm block of the lower organic horizons (Oe and/or Oa) by cutting around a template with a knife and saw. The mineral soil below was sampled by taking two 6.5 cm diameter cores, each 10 cm deep or to the depth of impenetrable rock, whichever was less. The two mineral soil cores were composited into a single sample. Organic and mineral horizon samples were placed in separate plastic bags and kept on ice in a cooler while they were returned to the laboratory for processing.

Laboratory methods

In the laboratory, the samples were passed through an 8-mm sieve, homogenized, weighed, and wetted to 60% of field capacity (determined gravimetrically on a subsample). One 15-g subsample was extracted with 100 mL of 2 mol/L KCl and a second 15-g subsample was placed in a plastic specimen cup covered with plastic wrap and incubated in a constant-temperature room at 20°C in the dark for 29 d. At the end of the incubation period, the incubated samples were extracted with KCl as were the initial samples. If 15 g of the sample were not available, a 7.5-g subsample was extracted in 50 mL of KCl. In each extraction, the sample and solution were agitated four times in the first hour and then allowed to stand overnight. The extract solution was filtered through Whatman 41 filter paper, preserved with ~100 μL of chloroform per 60 mL, and stored at 4°C until chemical analysis could be performed. The samples were analyzed for NH_4^+ and NO_3^- by automated colorimetry on an Alpkem autoanalyzer (Alpkem Corporation, Wilsonville, Oregon, USA).

Separate subsamples of each soil sample were passed through a 2-mm sieve, dried, ground, and analyzed for percent C and N on a Carlo-Erba NA1500 CN analyzer (Carlo-Erba Instruments, Milan, Italy), and another sample was ashed in a muffle furnace to determine organic matter content by mass loss on ignition. Other subsamples were used to determine pH (in deionized water, 4:1 for organic horizons and 1:1 for mineral horizons) and texture (percent sand, silt, and clay by the Bouyoucos [1962] method).

Potential net N mineralization (sensu Zak et al. 1994) was calculated as the difference in extractable N (NH_4^+ plus NO_3^-) between the incubated and initial samples. Potential net nitrification was calculated as the difference in NO_3^- between incubated and initial samples. Potential net mineralization and nitrification rates were calculated as μg N released per day and expressed in three ways: per gram dry mass (DM) of soil, per gram of organic matter (OM) in the soil, and per gram N in the soil. The mineralization rates on these three bases are referred to as MinDM, MinOM, and MinN, respectively, and the corresponding nitrification rates are referred to as NitDM, NitOM, and NitN. Expressing the rates per gram DM gives the potential rate in the bulk soil. Rates expressed per gram OM reflect mineralization and nitrification potential of the organic material in the soil, and minimize the effects of differences in OM content among the samples. Rates expressed per gram N show the relative lability of the N in the soil.

Atmospheric deposition

Atmospheric wet deposition data for 1989–1995 were obtained from the reports of the National Atmospheric Deposition Program (e.g., NADP 1991), using the nearest site to each sampling location (Table 1). These data represent NH_4^+ and NO_3^- in wet-only precipitation collected weekly. Dry deposition data for 1989–1995 were obtained from the Clean Air Status and Trends Network (CASTNet) of the Environmental Protection Agency Office of Research and Development (Research Triangle Park, North Carolina). These data included weekly filter-pack measurements of atmospheric concentrations of HNO_3 vapor, and NO_3^- and NH_4^+ particulate material, as well as estimates of dry deposition velocity (deposition velocity = dry deposition flux/atmospheric concentration) calculated from a model parameterized with site-specific canopy data and meteorological data measured hourly on site (Clarke et al. 1997). The EPA-calculated deposition velocities varied by more than a factor of two among sites with no consistent pattern across the gradient, illustrating the strong influence of local micrometeorological and canopy conditions at the dry deposition measurement station. Because our soil sampling sites were often some distance from the dry deposition station (Table 1), the calculated deposition velocities are probably a poor estimate of deposition conditions at our sites. Our sites were chosen to be in upland areas and to have a particular species composition, and were probably more similar to each other than the deposition calculations would suggest. Consequently, we calculated the average deposition velocity for HNO_3 vapor and fine particles from all of the measurement sites and applied the average deposition velocity to the mean measured atmospheric concentrations at each site. The average deposition velocities used were 2.14 cm/s for HNO_3 vapor and 0.12 cm/s for fine-particle NH_4^+ and NO_3^-. If the entire period 1989–1995 was not available for a site, the longest available period was used (Table 1).

Climate

Mean annual temperature and precipitation data were obtained for the PAP, NYI, NYC, VTL, and MES sites from the Northeastern Regional Climate Center at Cornell University, using data from the National Weather Service station closest to each of the sites. For the Whiteface Mt., New York (NYW) site, climate data were obtained from the State University of New York Atmospheric Sciences Research Center, and for the Hubbard Brook, New Hampshire site (NHH) data were obtained from the U.S. Department of Agriculture/Forest Service's Hubbard Brook Experimental Forest. Both of these stations use collection procedures equivalent to those of the National Weather Service, and their measurement sites were much closer to our research sites than were the nearest National Weather Service stations. For all sites, we used the 1961–1990 mean annual temperature and precipitation, or if the record was incomplete for that period, we used the longest record available.

Data screening and analysis

Our samples included a large range of organic matter (OM) contents within each soil horizon category. Samples labeled "mineral" based on color and texture, actually ranged from 4 to 72% OM. "Organic" samples ranged from 21 to 90% OM. This variation in OM causes a large variation among samples in nitrogen transformations, which can obscure other sources of variation. Expressing the rates of mineralization and nitrification per gram OM in the soil did not completely solve the problem because both MinOM and NitOM were significantly correlated with %OM in the organic soils. Because our objective was to compare similar samples of organic and mineral soils across sites, we omitted from the analysis any samples that we called organic in the field but had <60% OM. Likewise, we omitted any samples called mineral in the field but which had >25% OM. This screening eliminated 79 of the 298 samples (27%), and resulted in a data set in which %OM was not significantly correlated with the mineralization and nitrification variables. Some effects of this data screening are discussed below.

The large range in %OM in the original samples also led us to doubt that our measurements of organic horizon depth were comparable across sites. Consequently, we focused our analysis of the data primarily on chemical characteristics of the soil and rates of N cycling processes expressed per gram DM, per gram OM, and per gram N, rather than on pool sizes or rates expressed per unit area.

Many of the variables we measured showed significant departures from a normal distribution (using the Shapiro-Wilk W statistic at $P = 0.05$). Neither logarithmic, square-root, nor arcsine transformations eliminated this problem, which was particularly acute for the nitrification variables. Consequently, we used nonparametric correlation analysis (Spearman's rank correlation, Zar [1996]) as our principal means of testing the relationships between N cycling response variable and potential driving variables. We analyzed the screened data set ($n = 219$ individual samples) for the species and soil horizons separately for correlation between response variables and total N deposition, soil %N, soil C:N, and mean annual temperature and precipitation. Response variables included potential net N mineralization and nitrification rates per gram dry mass of soil (MinDM and NitDM), per gram OM in the soil (MinOM and NitOM), and per gram N in the soil (MinN and NitN). We also used as response variables the nitrification fraction (Nitfrac = nitrification/mineralization), the C:N ratio (mass basis), percent N, and the extractable NH_4^+ and NO_3^- in the soil (Ext. NH_4^+ and Ext. NO_3^-). In graphing data, we used simple linear regression to calculate the parameters of the best-fit regression lines (slope, intercept, coefficients of determination), which do not require assumptions about normality and homoscedasticity in the data.

We performed several multivariate analyses to evaluate the differences between species and the interactions of climate and N deposition across the sites. These multivariate procedures were performed only on the response variables that did not depart significantly from a normal distribution (C:N ratio in the mineral horizons, and MinDM, MinOM, MinN, and %N in the organic horizons). To test for differences between the species, we used a general linear model to evaluate the response to deposition (a continuous variable), species (a categorical value), and the interaction of deposition

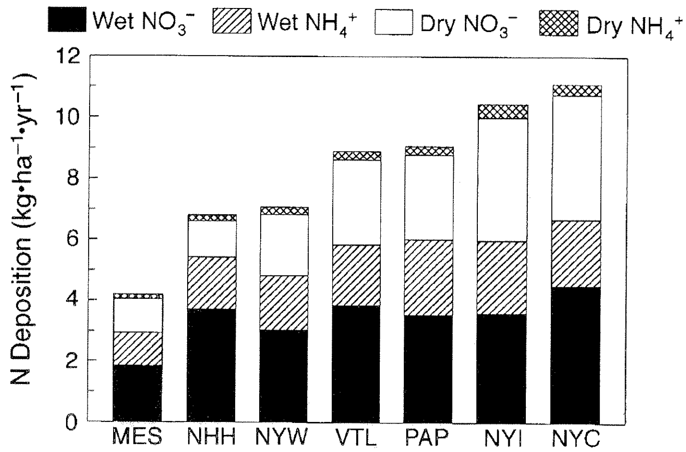

FIG 2. Estimated wet and dry deposition at the study sites.

and species. Another general linear model analysis was performed using %N, species, and the interaction of %N and species as the independent variables. Stepwise multiple linear regression was used to analyze the relative influence of N deposition, precipitation, and temperature on the normally distributed response variables.

Data were analyzed using the SAS statistical package (GLM, CORR, and REG procedures, SAS 1989). Statistical significance was chosen to be at the $P = 0.05$ level.

RESULTS

Atmospheric deposition

Calculated total N deposition (wet plus dry) ranged from 4.2 kg $N \cdot ha^{-1} \cdot yr^{-1}$ at the Maine sites (MES) to 11.1 kg $N \cdot ha^{-1} \cdot yr^{-1}$ at the Catskill Mt., New York site (NYC) (Fig. 2). The order of sites deviates somewhat from the SW to NE gradient, which we expected based on the results of Ollinger et al. (1993). The highest deposition site, the Catskill site in New York (NYC), is not the furthest to the SW but is the closest to the urban centers of the Atlantic coast (Fig. 1).

Soil texture and pH

Soil texture was quite variable among the sites, with sand content ranging from 27 to 65% (Fig. 3) and clay content ranging from 2 to 32%. There was no consistent pattern of soil texture corresponding to the N deposition gradient, but there was a tendency for the more northerly sites to be sandier. However, there was no significant correlation ($P > 0.05$) between percent sand or percent clay and mean mineralization or nitrification rates (expressed per gram DM, OM, or N) in the plots, nor were there significant differences in soil texture between stands dominated by the two species ($P > 0.05$), so we do not believe that soil texture confounded our analysis of the N deposition gradient or species effects. Mean soil pH at the sites ranged from 3.75 to 4.82 in the mineral horizons and 4.29 to 5.14 in the organic horizons (Fig. 3). There was an inconsistent tendency toward higher soil pH at the more northerly (low-deposition) end of the gradient (Fig. 3), and there was a significant negative relationship between the pH and mineralization and nitrification rates ($P = 0.01$ for MinOM and $P = 0.006$ for NitOM in the mineral horizons and $P = 0.006$ and $P = 0.007$ for the same variables in the organic horizons). The relationship is such that the more acid soils had higher net mineralization and nitrification rates, which does not indicate an inhibition of microbial activity by low pH, but rather suggests some acidification of the soil at the high-deposition sites, either from direct leaching of deposited NO_3^- or from enhanced nitrification at those sites.

Nitrogen cycling

In the organic horizons, mineralization and nitrification rates expressed on all three bases (per gram DM, OM, and N) were significantly and positively correlated with total N deposition in the maple but not in the beech plots (Table 2, Figs. 4 and 5). The response of N mineralization to N deposition was significantly different in maple soils compared to beech soils, as illustrated by the highly significant deposition × species interaction terms in the general linear model analysis (Table 3). (The general linear model analysis was not done for other response variables because of the non-normal distribution of the data.) Nitrogen deposition was also positively correlated with percent N and extractable NH_4^+ and NO_3^- in the maple but not the beech soils (Table 2, Fig. 6). In the mineral horizons, NitDM, MinOM, NitOM, NitN, nitrification fraction, and extractable NH_4^+ and NO_3^- all increased, and C:N decreased, with increasing deposition in maple plots, but beech plots showed no significant responses (Table 2).

Soil percent N was highly significantly correlated with the mineralization and nitrification variables in the organic horizons of both beech and maple plots (Table 2). We caution that the relationship between rates expressed per gram DM and %N are probably a result of the differences in OM content among the sam-

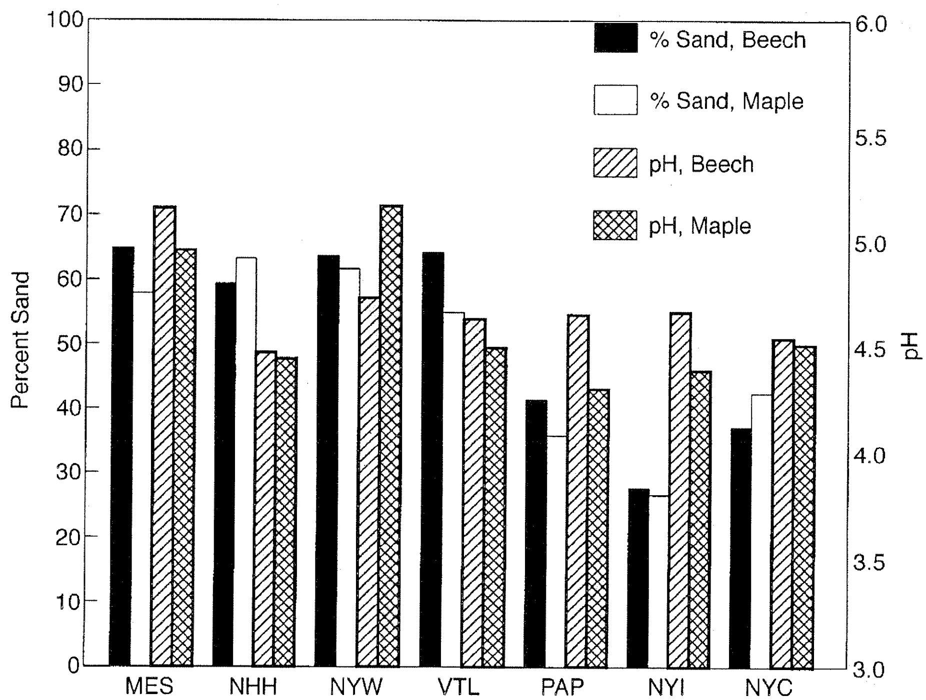

FIG. 3. Mean percentage sand and mean organic horizon pH in beech and maple plots at sites used in the study. See Fig. 1 for site codes.

ples due to sampling variability, rather than differences in the concentration or lability of N in the organic matter. To minimize the effect of the OM variation among samples, it is more instructive to examine the relationship between %N and mineralization or nitrification expressed per gram OM or per gram N. Organic soils under both species showed significant correlations between %N and the response variables expressed per gram OM and per gram N, but the maple responses had both higher correlation coefficients (Table 2) and higher slopes (Figs. 7 and 8), especially for net N mineralization. This suggests that increased concentration of N in the organic horizons increases N mineralization under both species, but the increases are stronger in maple soils than in beech soils. This interpretation is further supported by the general linear model analysis, which showed significant responses of N mineralization to %N, species, and the interaction of %N × species (Table 3). Net nitrification rates showed more of a threshold effect, with near zero rates of net nitrification for low values of %N or high values of C:N (Figs. 8 and 9). For %N values greater than about 1.7% (or C:N ratios <23), measurable net nitrification occurs in all of the maple but only some of the beech plots. A substantial fraction of the beech samples show no net nitrification even at low C:N ratios (Fig. 9).

Mean annual temperature and precipitation were also strongly correlated with some of the nitrogen cycling response variables in both beech and maple plots, as illustrated for some of the important response variables in Table 4. Stepwise multiple regression was employed to separate the relative effects of N deposition, mean annual temperature (MAT), and mean annual precipitation (MAP) on the response variables that were normally distributed. For N mineralization rates (MinDM, MinOM, and MinN) in the organic horizons, MAT was the only variable of the three that was significant in the beech plots, but N deposition was the only variable that was significant in the maple plots (Table 5). The coefficients of determination (R^2) for the N mineralization regression models were low in the beech plots, ranging from 0.14 to 0.21, and somewhat higher in the maple plots, ranging from 0.35 to 0.45 (Table 5). Precipitation was the only significant predictor of %N in the beech plots, and precipitation and temperature are the only significant predictors of %N in the maple plots (Table 5). In the stepwise regression for %N in the maple plots, N deposition was the first variable entered (highest partial R^2), but after MAT and MAP were entered, the significance of the N deposition term decreased and the sign of its regression coefficient switched from positive to negative. This erratic behavior suggests that collinearity among N deposition, MAT, and MAP may have been problematic in this case, and the results of the regression analysis for %N should be interpreted with caution.

The data screening procedure we employed greatly reduced the correlation between OM and the mineralization and nitrification variables, thereby reducing the variance among samples resulting from the uncer-

TABLE 2. Results of Spearman rank correlations of response variables (see *Methods: Laboratory* for abbreviations) with total N deposition (Dep.), soil %N, and soil C:N ratio.

Response variables	Mineral horizon		Organic horizon	
	Beech (n = 54)	Maple (n = 75)	Beech (n = 55)	Maple (n = 36)
Dep. vs.				
MinDM	NS	NS	NS	+0.51 (0.0017)
NitDM	NS	+0.29 (0.0104)	NS	+0.55 (0.0005)
MinOM	NS	+0.24 (0.0351)	NS	+0.54 (0.0008)
NitOM	NS	+0.33 (0.0043)	NS	+0.51 (0.0016)
MinN	NS	NS	NS	+0.56 (0.0003)
NitN	NS	+0.34 (0.0024)	NS	+0.54 (0.0006)
Nitfrac	NS	+0.37 (0.0010)	NS	+0.43 (0.0081)
C:N	NS	−0.27 (0.0187)	NS	NS
%N	NS	NS	NS	+0.46 (0.0047)
Extractable NH_4^+	NS	+0.28 (0.0163)	NS	+0.42 (0.0098)
Extractable NO_3^-	NS	+0.36 (0.0013)	NS	+0.59 (0.0002)
%N vs.				
MinDM	+0.38 (0.0047)†	+0.29 (0.0104)†	+0.52 (0.0001)†	+0.75 (0.0001)†
NitDM	NS	+0.29 (0.0110)†	+0.42 (0.0014)†	+0.50 (0.0019)†
MinOM	NS	NS	+0.37 (0.0048)	+0.60 (0.0001)
NitOM	NS	NS	+0.39 (0.0032)	+0.43 (0.0096)
MinN	NS	NS	+0.33 (0.0125)	+0.57 (0.0003)
NitN	NS	NS	+0.38 (0.0043)	+0.40 (0.0164)
Nitfrac	NS	−0.29 (0.0126)	+0.45 (0.0006)	NS
Extractable NH_4^+	NS	+0.28 (0.0163)	NS	0.76 (0.0001)
Extractable NO_3^-	+0.39 (0.0038)	+0.36 (0.0013)	+0.32 (0.0181)	0.39 (0.0178)
C:N vs.				
MinDM	+0.32 (0.0200)	NS	NS	−0.44 (0.0075)
NitDM	NS	NS	−0.29 (0.0330)	−0.50 (0.0021)
MinOM	NS	−0.28 (0.0138)	NS	−0.52 (0.0011)
NitOM	−0.28 (0.0425)	−0.40 (0.0004)	−0.30 (0.0280)	−0.54 (0.0007)
MinN	NS	NS	NS	−0.35 (0.0366)
NitN	NS	−0.23 (0.0429)	−0.27 (0.0479)	−0.45 (0.0059)
Nitfrac	−0.29 (0.0372)	−0.40 (0.0004)	−0.43 (0.0011)	−0.49 (0.0025)
Extractable NH_4^+	0.36 (0.0075)	NS	NS	NS
Extractable NO_3^-	NS	NS	−0.32 (0.0166)	−0.45 (0.0053)

Note: A table entry of "NS" indicates $P > 0.05$; if $P < 0.05$, then information given is: correlation coefficient (P value).
† The relationship between %N and variables expressed per gram DM may be partially due to varying OM content among samples. See *Results: Nitrogen cycling.*

tainty in horizon definition during field sampling. Analysis of correlations in the full (unscreened) data set yielded similar patterns to those in the screened data set, although usually the unscreened data set had weaker correlations between N deposition and the N cycling response variables. Specifically, in the unscreened data set, all of the response variables in Table 2 except MinDM showed significant positive correlations with N deposition in the maple organic soils, but none were significant in the beech organic soils. All of the response variables were significantly correlated with %N in both beech and maple organic soils, as in the screened data set, with the exception of nitrification fraction in the maple plots. In the mineral soils, the unscreened data set had no significant correlations between deposition and any of the response variables in the beech plots, but significant correlations with NitDM, MinOM, NitOM, MinN, NitN, Nitfrac, and C:N in the maple plots, a set of results that is similar but not identical to the results from the screened data set (Table 2).

DISCUSSION

A consistent pattern emerged from the data set despite a large amount of variability among individual samples. While we cannot interpret causality directly from a gradient study, the results indicate a significant increase in potential net N mineralization and nitrification associated with higher N deposition levels in maple but not in beech plots. This result is echoed by the general linear model analysis on the N mineralization rates (Table 3), which showed highly significant interaction between N deposition and species, indicating that the soils under the two species respond differently to N deposition. Organic horizons under both species showed highly significant increases in net N mineralization and nitrification rates associated with higher %N in the soil. Although many factors interact to influence N cycling rates and a large amount of small-scale spatial variation is present, N deposition and accumulation of N in the soil appear to have an influence on mean rates observed across the N deposition gradient.

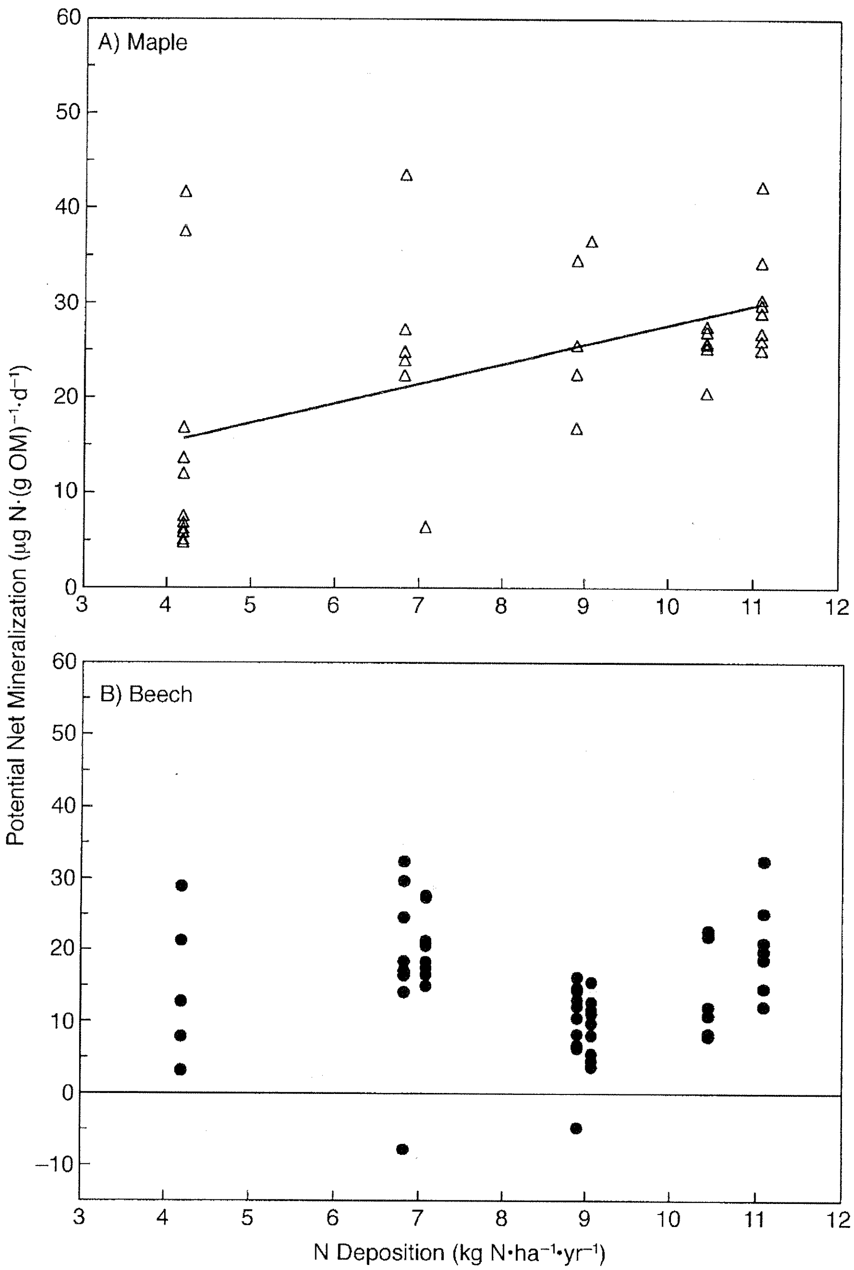

FIG. 4. Potential net mineralization per gram organic matter (OM) in organic soils vs. total N deposition in (A) maple and (B) beech plots. The line in A is the best-fit linear regression for maple ($y = 7.045 + 2.064x$, $r^2 = 0.28$). The relationship for beech is not statistically significant.

Gradient studies are often difficult to interpret because of the possibility of more than one variable changing simultaneously across the gradient. For this study, using an 800-km gradient from Pennsylvania to Maine, we tried to eliminate some confounding variables through the experimental design. By choosing single-species plots, we eliminated the effects of changes in forest composition across the gradient. We also stratified the sampling by soil horizon to minimize the influence of different horizon development in the different plots, and measured soil texture to evaluate its effect. Another possible source of variation is the history of the sampling site, e.g., cutting, burning, or agriculture. We do not know the history of all of our sites, but it is likely that they all were logged, at least selectively, during the past century. Because we chose

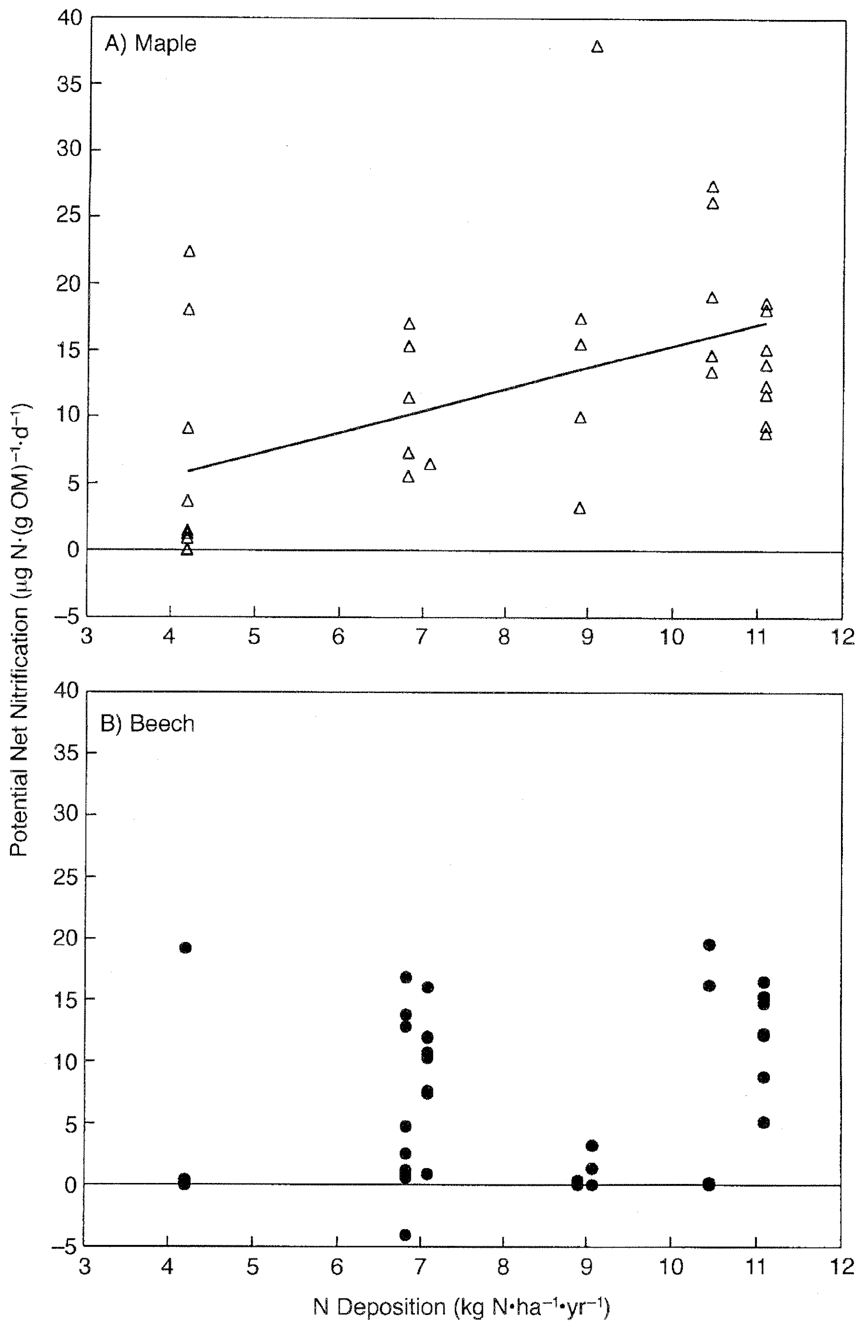

FIG. 5. Potential net nitrification per gram organic matter (OM) in organic soils vs. total N deposition in (A) maple and (B) beech plots. The line in A is the best-fit linear regression for maple ($y = -1.026 + 1.641x$, $r^2 = 0.28$). The relationship for beech is not statistically significant.

small single-species patches within mixed forests, and the beech and maple plots were usually close together, it is unlikely that the species differences we see are confounded by different site histories.

A change in climate across the gradient is another possible confounding factor. By incubating the soils in the laboratory under constant temperature and moisture conditions, we eliminated the direct effects of climate on mineralization and nitrification, although indirect effects of climate are possible. The most likely mechanism of indirect response is a cold- or drought-induced accumulation of organic matter in the samples, leading to greater rates of potential N mineralization and nitrification (Burke 1989, Zak et al. 1994). However, the

TABLE 3. (A) Results of general linear model analysis to test for effects of deposition, species, and their interaction on response variables that did not depart significantly from the normal distribution. (B) Results of generated linear model analysis for %N, species, and their interaction.

A)			Independent variable		
Horizon	Response variable	df	Deposition	Species	Deposition × Species
Mineral	C:N	128	5.22 (0.0240)	0.38 (NS)	1.64 (NS)
Organic	MinDM	90	5.20 (0.0250)	3.38 (NS)	8.70 (0.0041)
	MinOM	90	4.58 (0.0352)	2.42 (NS)	8.74 (0.0040)
	MinN	90	3.26 (NS)	4.14 (0.0448)	10.96 (0.0014)
	%N	92	9.71 (0.0025)	0.73 (NS)	0.50 (NS)
B)			**Independent variable**		
Horizon	**Response variable**	**df**	**%N**	**Species**	**%N × Species**
Mineral	C:N	128	9.22 (0.0029)	1.11 (NS)	2.53 (NS)
Organic	MinDM	90	63.1 (0.0001)	7.07 (0.0093)	11.3 (0.0012)
	MinOM	90	43.7 (0.0001)	7.60 (0.0071)	12.8 (0.0006)
	MinN	90	31.1 (0.0001)	5.11 (0.0262)	8.69 (0.0041)

Notes: See *Methods:Laboratory* for response variable abbreviations. Values given are F values (P in parentheses); NS indicates $P > 0.05$.

pattern of change across the gradient in maple plots, and the lack of response in beech plots, was observed even when the N mineralization and nitrification rates were expressed per gram OM (Tables 2 and 4), suggesting that some factor other than the *quantity* of OM influenced the pattern. In a similar study, Vinton and Burke (1997) showed that the ratio of C respired to N mineralized varied in grassland soils collected across a climate gradient in the central United States, suggesting that climate can also influence the *quality* of the labile organic matter. In our data set, the multiple regression analysis showed that MAT had a weak but statistically significant effect on MinOM in the beech plots (Table 5). In the maple plots, however, N mineralization was much more strongly related to N deposition than to climate. Thus, we conclude that potential N mineralization rates may be influenced by both N deposition and climate, and beech and maple soils appear to differ in their sensitivity to these two factors.

As a check on the increases in forest floor %N we observe across the gradient, we can calculate how long it would take to produce such a difference under current deposition conditions. For maple organic soils, the regression line in Fig. 6A indicates an increase in mean %N from 1.84% at a deposition rate of 4.2 kg $N \cdot ha^{-1} \cdot yr^{-1}$ to 2.20% at 11.1 kg $N \cdot ha^{-1} \cdot yr^{-1}$. The mean mass of organic soils at these sites was 49 629 kg/ha, so that the increase in %N corresponds to a difference in N content of 179 kg N/ha. At the current deposition rates, this difference in N content could be generated in 26 yr. Trends in nitrogen oxide emissions in the eastern United States indicate that nitrogen deposition rates have been impacted by pollution for much longer than that, and have been relatively stable at current levels for at least that long (National Acid Precipitation Assessment Program, 1992).

The species could have different responses to N deposition (1) if their soils accumulated N at different rates, or (2) if they accumulated N similarly but responded to it differently. Our results are inconclusive on the former but strongly support the latter. We found a significant correlation between deposition and organic horizon %N in maple but not in beech plots (Table 2), suggesting that the soils under these single-species plots accumulate N at different rates. In contrast, the general linear model analysis indicated a significant effect of N deposition on %N, but no effect of species or the interaction of species and deposition (Table 3). Thus our analyses of species differences in %N across the gradient are inconsistent. It is clear, however, that both N mineralization and nitrification respond more strongly to increased %N in maple than in beech soils (Figs. 7 and 8). The onset of nitrification occurs once the C:N ratio of the soils decreases below a threshold level of about 23, at which point nitrification occurs in all maple plots, but only some of the beech plots (Fig. 9). McNulty et al. (1996) found a similar threshold effect for net nitrification potential in spruce–fir forest floors from New York and New England.

The two species have soils for which the net mineralization and nitrification potentials are similar under low-N conditions, but diverge as N is accumulated (Figs. 7 and 8). Thus the differences in nitrogen cycling associated with these two species may not be evident under low deposition conditions, but the differences may increase as deposition increases. The lack of response of the beech soils to increased N deposition may be the result of the poor beech litter quality (e.g., high lignin : N ratio, Melillo et al. 1982) reducing gross mineralization rates, high carbon availability enhancing microbial immobilization of N, allelochemical inhibition of nitrification, or some combination of these factors.

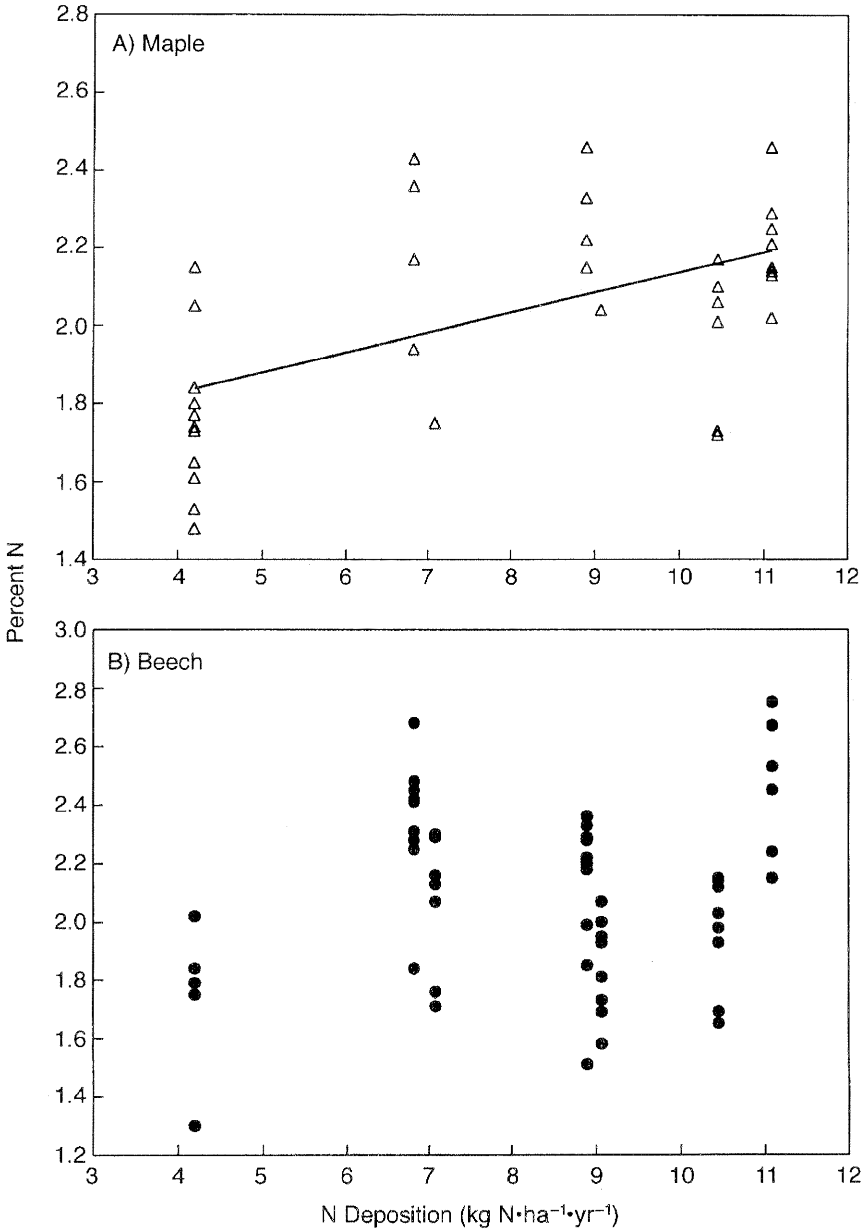

FIG. 6. Percentage N in organic soils vs. N deposition in (A) maple and (B) beech plots. The line in A is the best-fit linear regression for maple ($y = 1.621 + 0.052x$, $r^2 = 0.29$). The relationship for beech is not statistically significant.

It is important to note that the spatial patterns observed across this gradient may not be analogous to the temporal trends in N cycling experienced by a forest as it begins to receive enhanced N inputs. Because emissions of nitrogen oxides have been relatively constant in the United States for at least two decades (National Acid Precipitation Assessment Program 1992), N cycling in these forests may be approaching a steady state with respect to N inputs. Increasing the N deposition to a previously unimpacted forest may result in transient responses in N cycling, which could be quite different from the responses we observe in this study. For example, in fertilizer studies of N deposition, forest soils often show an initial increase in N mineralization, followed by a decrease relative to control (unfertilized) plots (Magill et al. 1996, McNulty et al. 1996). One might interpret this to mean that a forest receiving higher N deposition would eventually have a lower N mineralization rate than a forest receiving lower N deposition. The results of our gradient study indicate a monotonic increase in N mineralization potential associated with increas-

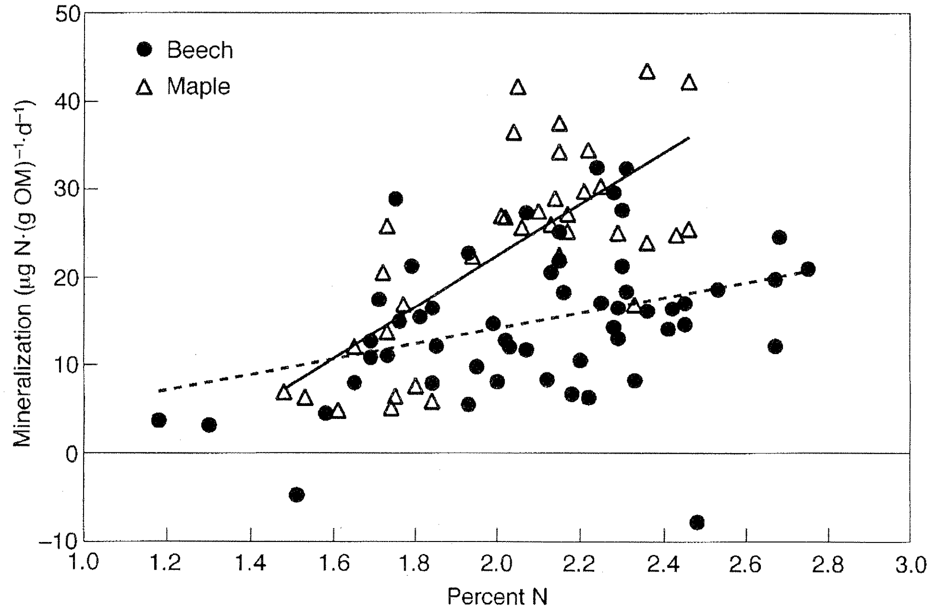

FIG. 7. Potential net mineralization per gram organic matter (OM) vs. percentage N in organic soils. Lines are best-fit linear regressions for each species: solid line for maple ($y = -36.24 + 29.36x$, $r^2 = 0.52$) and dashed line for beech ($y = -3.381 + 8.770x$, $r^2 = 0.13$).

es in N deposition in maple soils, and no response in beech soils. This suggests to us that the response to fertilizers may be an artifact of the rate or timing of application, for instance if the fertilizations "primed" the soil (sensu Paul and Clark 1989) resulting in increased availability of carbon which could then fuel nitrogen immobilization by microbes. Gradient studies such as this one and those of McNulty et al. (1991)

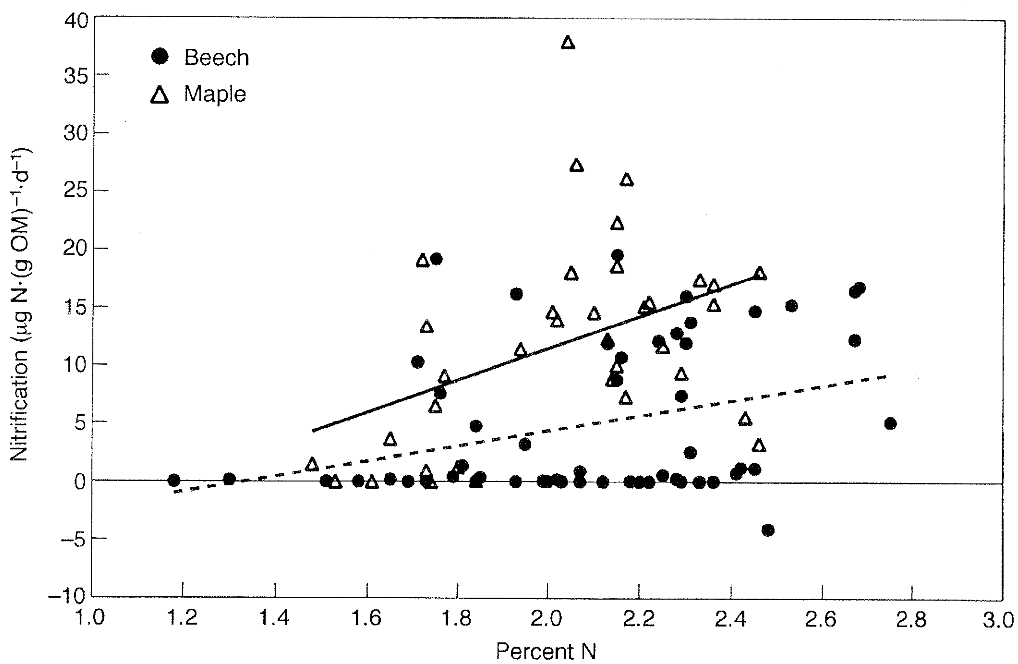

FIG. 8. Potential net nitrification per gram organic matter (OM) vs. percentage N in organic soils. Lines are best-fit linear regressions for each species: solid line for maple ($y = -16.27 + 13.89x$, $r^2 = 0.19$) and dashed line for beech ($y = -8.674 + 6.523x$, $r^2 = 0.11$).

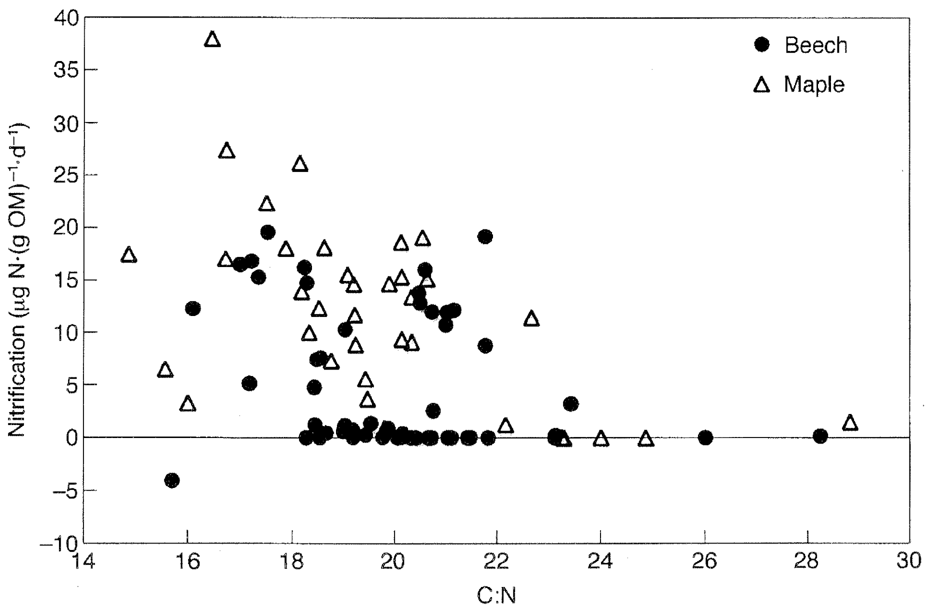

FIG. 9. Potential net nitrification per gram organic matter (OM) vs. C:N ratio in organic soils.

and Pregitzer at al. (1992) are a crucial complement to fertilizer studies in that they permit observation of long-term ecosystem responses to realistic, low doses of nitrogen.

Implications for science and policy

The results of this study highlight some complexities in the hypotheses previously put forward on the response of forests to nitrogen deposition (Agren and Bosatta 1988, Aber et al. 1989, 1995). These hypotheses predict increases in N mineralization, followed by increases in nitrification, as a result of enhanced N deposition. Our study suggests that these changes can occur, but are strongly mediated by tree species, such that soils under some species may not show enhanced mineralization or nitrification at all.

This result has three important implications. First, the net mineralization and nitrification of an entire forested watershed, and the response of nitrification to elevated N deposition, may depend on the species composition of that watershed. For beech and sugar maple, species differences in these processes are most likely to be manifested in areas of higher deposition. Since nitrification produces nitrate, which can be lost in drainage waters, stream nitrate concentration, the key indicator of nitrogen saturation (Stoddard 1994), may depend on species composition as well as nitrogen accumulation in the watershed.

TABLE 4. Results of Spearman rank correlations of response variables (see *Methods:Laboratory* for abbreviations) with mean annual temperature (MAT) and mean annual precipitation (MAP).

	Mineral soils		Organic soils	
Variables	Beech (n = 54)	Maple (n = 75)	Beech (n = 55)	Maple (n = 36)
MAT vs.				
MinOM	−0.37 (0.0071)	NS	−0.42 (0.0012)	NS
NitOM	−0.28 (0.0391)	NS	−0.46 (0.0025)	0.54 (0.0006)
C:N	NS	−0.41 (0.0002)	NS	−0.44 (0.0071)
%N	−0.31 (0.0216)	−0.29 (0.0132)	−0.31 (0.0177)	0.36 (0.0321)
%OM	NS	−0.25 (0.0316)	NS	NS
MAP vs.				
MinOM	0.31 (0.0263)	0.69 (0.0001)	NS	0.53 (0.0008)
NitOM	NS	0.71 (0.0001)	NS	NS
C:N	NS	NS	−0.35 (0.0072)	NS
%N	NS	0.28 (0.0133)	0.65 (0.0001)	0.69 (0.0001)
%OM	NS	NS	0.50 (0.0001)	0.43 (0.0092)

Note: A table entry of "NS" indicates $P > 0.05$; if $P < 0.05$, then information given is: correlation coefficient (P values).

TABLE 5. Results of stepwise linear regressions using N deposition, mean annual temperature (MAT), and mean annual precipitation (MAP) as independent variables.

Horizon, species	Response variable	MAT	MAP	N dep.	R^2 (P)
Organic, beech	MinDM	2.73 (0.0017)	NS	NS	0.21 (0.0068)
	MinOM	−2.36 (0.0141)	NS	NS	0.13 (0.0141)
	MinN	−84.3 (0.0124)	NS	NS	0.14 (0.0124)
	%N	NS	0.01 (0.0001)	NS	0.38 (0.0001)
Organic, maple	MinDM	NS	NS	1.21 (0.0002)	0.45 (0.0002)
	MinOM	NS	NS	2.23 (0.0004)	0.35 (0.0004)
	MinN	NS	NS	73.1 (0.0003)	0.37 (0.0003)
	%N	0.19 (0.0090)	0.01 (0.0022)	NS	0.60 (0.0001)
Mineral, beech	C:N	NS	NS	NS	NS
Mineral, maple	C:N	−0.83 (0.0007)	NS	NS	0.18 (0.0007)

Notes: Response variables are those that did not depart significantly from a normal distribution. Data are regression coefficients (P values); NS indicates $P > 0.05$. For each regression, the R^2 value (P value in parentheses) of the final regression model is shown.

Second, increased N deposition may increase the patchiness of N cycling associated in a mixed-species forests. For instance, under high-deposition conditions we would expect the soils under sugar maple trees to have higher rates of N mineralization and nitrification than the soils under beech trees, whereas under low-deposition conditions the soils under the two species would be similar. Thus, ecosystem processes that respond to small-scale changes in N availability (such as seedling or understory plant growth) may become more spatially heterogeneous in mixed-species forests under high deposition conditions.

Third, changes that affect the species composition of forests may also affect their responses to nitrogen deposition. If the ratio of beech to maple in the northern hardwood forest were altered, for instance, we would expect subsequent changes in N cycling and perhaps in NO_3^- losses in stream water. Many processes could act to change species composition, for instance, selective harvesting or climate change, but of particular concern for beech is the spread of the beech bark disease, which is currently causing elevated beech mortality throughout the northeastern United States (Houston 1994). Our results suggest that the decline of beech, if it were accompanied by an increase in the abundance of sugar maple, would make the forests more likely to show higher rates of N cycling and loss in response to increased N deposition.

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