Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forests

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Abstract: The declining health of high-elevation red spruce (*Picea rubens* Sarg.) and Fraser fir (*Abies fraseri* (Pursh) Poir.) in the southern Appalachian region has long been linked to nitrogen (N) deposition. Recently, N deposition has also been proposed as a source of negative health impacts in lower elevation deciduous forests. In 1998 we established 46 plots on six sites in North Carolina and Virginia dominated by American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britt). We evaluated several response variables across an N deposition gradient, including annual basal area growth; foliage percent N, Al, P, K, Mg, and Ca; and forest floor percent N, Mg, and C, pH, and potential net nitrification and N mineralization rates. We found a significant linear relationship between N deposition and basal area growth in sugar maple, but not in American beech or yellow birch. In addition, we found a significant relationship between N deposition and foliar chemistry (foliar %N in all species, foliar Mg/N and %K in sugar maple, and %P in sugar maple and yellow birch). Foliar %N of the three studied species was high relative to values reported in other studies in the United States and Canada. Several forest floor response variables (%N, C/N, pH, Mg/N, and potential net nitrification and N mineralization rates and nitrification/mineralization fractions) were also correlated with N deposition. The correlations between the above response variables and N deposition are consistent with the influence of chronic N deposition on forested ecosystems measured in other regions and suggest that chronic N deposition may be influencing forest structure and chemistry within the southern region.

Résumé : Le dépérissement de l'épinette rouge (*Picea rubens* Sarg.) et du sapin de Fraser (*Abies fraseri* (Pursh) Poir.) croissant en altitude dans le sud des Appalaches a depuis longtemps été associé aux dépôts d'azote (N). Récemment, des impacts négatifs sur la santé des forêts décidues croissant à plus faible altitude ont aussi été attribués aux dépôts de N. En 1998, nous avons établi 46 placettes, en Caroline du Nord et en Virginie, dans six stations dominées par le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.), l'érable à sucre (*Acer saccharum* Marsh.) et le bouleau jaune (*Betula alleghaniensis* Britt.). Nous avons évalué le comportement de plusieurs variables le long d'un gradient de dépôts de N, incluant : la croissance annuelle en surface terrière, le pourcentage de N, Al, P, K, Mg et Ca dans le feuillage, le pourcentage de N, Mg et C dans la couverture morte, le pH et les taux potentiels de nitrification nette et de minéralisation. Nous avons observé une relation linéaire significative entre les dépôts de N et la croissance en surface terrière chez l'érable à sucre mais non chez le hêtre à grandes feuilles ni chez le bouleau jaune. De plus, nous avons observé une relation significative entre les dépôts de N et les caractéristiques chimiques du feuillage (pourcentage de N foliaire chez toutes les espèces, Mg/N et pourcentage de K foliaire chez l'érable à sucre et pourcentage de P foliaire chez l'érable à sucre et le bouleau jaune. Le pourcentage de N dans les feuilles des trois espèces étudiées était élevé comparativement à ce qui a été rapporté dans d'autres études aux É.-U. et au Canada. Plusieurs variables de la couverture morte (%N, C/N, pH, Mg/N et taux de minéralisation et de nitrification nette potentiels et rapport nitrification/minéralisation) étaient également corrélées avec les dépôts de N. Les corrélations entre les variables ci-dessus et les dépôts de N sont consistantes avec les effets des dépôts chroniques de N sur les écosystèmes forestiers mesurés dans d'autres régions et indiquent que les dépôts chroniques de N pourraient influencer la structure et les caractéristiques chimiques de la forêt dans cette région du sud.

[Traduit par la Rédaction]

Introduction

In the northeastern United States, the highest nitrogen (N) deposition values generally occur along the southwestern edge of the region, and in the southeastern United States, the highest N deposition values are found in the northern part of the region (National Atmospheric Deposition Program 1998). The 1970 Clean Air Act and its 1990 amendments set reduced thresholds for annual N and sulfur (S) deposition in response to increases in N deposition that have occurred

Received 13 September 2004. Accepted 8 June 2005. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 8 September 2005.

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 doi: 10.1139/X05-128 © 2005 NRC Canada

since the beginning of the industrial era (Hicks et al. 1990). Implementation of the Clean Air Acts helped reduce S emissions, but trend analyses of N deposition have not been significantly reduced from levels in the 1980s (NADP 1998).

Historically, the greatest concerns about the impacts of N deposition on forests focused on the northeastern United States, particularly on high-elevation spruce–fir (*Picea–Abies*) forests that receive some of the highest levels of N deposition as a result of cloud deposition (Heilman et al. 2000). Cloud deposition coupled with wet and dry deposition can result in a total N deposition 6 to 20 times higher than N deposition levels in lower elevation forests (Baumgardner et al. 2003).

Previous studies have shown that forest ecosystems in the northeastern United States have been altered by N deposition. McNulty et al. (1991) examined forest floor and foliar chemistry across northeast spruce–fir forests along a gradient of N deposition. Their results showed that there was a correlation between N deposition and forest floor inorganic N and foliar lignin/N ratio. They suggested that these relationships across the region indicated that these forests may be progressing toward more advanced N-saturated conditions (defined as N in excess of plant and microbial biological demand (Aber et al. 1989)). In another study, McNulty et al. (1996) used N amendments to simulate the potential impacts of increased N deposition on spruce–fir forest structure and function. Their results showed a decrease in tree growth rates associated with a foliar nutrient imbalance (i.e., N, calcium (Ca), magnesium (Mg)), increases in forest floor %N, and increases in forest floor potential net nitrification/mineralization ratios. Foliar nutrient imbalances are generally thought to be caused by either soil depletion or the addition of nutrients. However, Schaberg et al. (2001) found that Ca, in particular, can be leached from the needles of red spruce (*Picea rubens* Sarg.) during exposure to acidic deposition, thus predisposing the tree species to Ca deficiency. Schaberg et al. (1997) and Perkins et al. (2000) found that increases in forest floor %N increase freezing injury to spruce foliage, thus making the tree species more susceptible to mortality.

McLaughlin et al. (1998) reported that N deposition in southern Appalachian spruce–fir forests can cause leaching of Ca and Mg from soils where base cation stores are very low and the ability of the ecosystems to retain N is minimal. In another study on southern Appalachian spruce–fir forests, Flum and Nodvin (1995) found the highest occurrence of nitrate (NO_3-N) leaching (an indicator of N saturation) in watersheds dominated by a spruce–fir overstory. Fenn et al. (1998) found that N saturation conditions are more likely to develop in mature forests that receive high N deposition inputs and have low soil C/N ratios.

Since the 1980s, there have been indications that N deposition may be negatively affecting forest ecosystems, particularly in the southern Appalachian region. Bruck (1984) and Bruck et al. (1989) indicated a relationship between N and S deposition and reduced growth and early senescence of needles. This relationship suggests a direct impact of N deposition on species dynamics that may predispose species to growth decline. Additional studies in the region (Southern Appalachian Man and Biosphere 1996; Fernandez and Adams 2000) suggest that N saturation is not confined to high-elevation conifer forests, but may also develop in deciduous forests. The cited studies suggest how N deposition may change forest structure and function and increase the rate of forest mortality relative to low N deposition areas.

The southern Appalachian physiographic region consists of about 15.1×10^6 ha; 70% of the region is forested, with deciduous trees accounting for 47% of the forested area (Boone and Aplet 1994). Southern Appalachian deciduous forests contain the largest plant species diversity of any forest ecosystem in North America (Great Smoky Mountain National Park, http://www.nps.gov/grsm/pphtml/facts.html). The area is also a center for recreation in the eastern United States, with over 9 million people visiting the Great Smoky Mountains National Park every year (Great Smoky Mountain National Park). The loss of deciduous forest tree species could have significant ecological and economic implications for the region. The objectives of this study are to correlate the response of tree species basal area growth rates, foliar chemistry, and N cycling with a gradient of N deposition in the southern Appalachians and to determine if any of these relationships could be characteristic of declining forest health.

Material and methods

Plot location

During the summer of 1998, we established 46 plots on six deciduous forest sites in the southern Appalachian Mountains (Table 1). Figure 1 shows the locations of the six sites with the estimated N deposition across the area. The 46 plots, each with a radius of 10 m, were located at elevations between 1126 to 1661 m and were divided evenly along each of the cardinal aspects on each site. At each site a semi-randomized block design was applied to select plots that contained greater than 70% combined basal area of yellow birch, American beech, and sugar maple. Since site selection was based on the level of N deposition inputs (Fig. 1) and on occurrence and composition of these three deciduous tree species, the distance between plots and the slope of the plots varied among sites.

Climate and estimated wet N deposition inputs

Both temperature and precipitation data were extracted from the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) (Kittel et al. 2000) monthly climate data set. We identified VEMAP grid cell numbers for each sample plot by a GIS overlay. Precipitation and temperature data for years 1978 through 1993 were pulled from the historical climate table, and the data for years 1994 through 1998, from the Hadley Centre's climate change scenario table (http://www.metoffice.com/research/hadleycentre). Annual averages were then calculated in centimetres for precipitation and in degrees Celsius for temperature for each plot.

The wet N deposition rates were determined for each plot by kriging mean annual N deposition data from 1978 through 1990 from 62 sites in the southern 13 states from the National Atmospheric Deposition Program (NADP 1998). Several krig algorithms were evaluated. The spatial distribution of NADP sites was log skewed, and with consideration of the work of Finkelstein (1983), a spherical model with a 100-km separation distance was selected to minimize error in the krig estimates.

We then acquired the site names and coordinates (latitude, longitude) for all points from NADP; a point site coverage

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Table 1. Site description.

Site	N deposition (kg N·ha^{-1}·year^{-1})	No. of plots	Latitude (°N)	Longitude (°W)	Elevation (m)	Precipitation (cm)	Temperature (°C)	MDBP (m)	Soil, family-level class
Corner Rock, N.C.	9	8	35.8	82.4	1151–1661	126.08	12.44	84	Typic Dystrochrepts, coarse-loamy, mixed, mesic
Dill Falls, N.C.	12	6	36.3	82	1150–1500	191.49	12.21	116	Umbric Dystrochrepts, coarse-loamy, mixed, mesic
HighKnob, Va.	13	12	36.9	82.6	1126–1265	117.53	11.37	90	Typic Dystrochrepts, loamy-skeletal, mixed, mesic
Mount Rogers, Va.	14	7	36.6	81.5	1295–1434	123.14	12.73	218	Typic Hapludults, loamy-skeletal, siliceous, mesic
Balsam Mountain, Va.	14	3	36.7	81.6	1382–1482	117.53	11.37	146	Typic Hapludults, loamy-skeletal, siliceous, mesic
Whitetop, Va.	15	10	36.6	81.6	1169–1569	117.53	11.37	44	Typic Hapludults, loamy-skeletal, siliceous, mesic

Note: MDBP, minimal distance between plots.

was built using Arc/Info (ESRI 2005). Quality assurance and quality control of the data were based on an NADP document that described their measurements and provided suggestions for working with the data (NADP 1998). The point site coverage was then joined to the N deposition data. We then used the Arc/Info to krig point coverages into a surface with a 0.5° grid spatial resolution previously developed by VEMAP (Kittel et al. 1995). We chose the 0.5° resolution to allow us to work the estimates into other projects. The mean regional wet N deposition for the southeastern United States between 1978 and 1990 was 11.3 kg N·ha^{-1}·year^{-1}, with minimum and maximum values of 2.9 and 23.1 kg N·ha^{-1}·year^{-1}, respectively. The highest regional N values (>16 kg N·ha^{-1}·year^{-1}) were generally found in the northern sections of the southern Appalachian region (Fig. 1). The sources for N deposition in this region are emissions from all 31 states east of the Mississippi River (Nash et al. 1992), with the emission sources being mainly automobiles and coal-burning electricity-generating facilities.

Estimated wet-only N deposition rates for our plots ranged from 9 to 15 kg N·ha^{-1}·year^{-1} (Table 1). Mean annual dry deposition ($HNO_3 + NO_3^- + NH_4^+$) from the period 1997–2000 for our study area was approximately 2 kg/ha (Baumgardner et al. 2002). Dry deposition values were not included in our correlation analyses.

Basal area growth analysis

We used a Haglof increment borer to collect two tree cores at 1.5 m above the forest floor from three dominant or codominant trees from each of the three tree species in each of the 46 plots. The first core was collected at a random azimuth, and the second core was extracted 90° from the first core. Each sample was cored to the pith, air dried, mounted, and sanded prior to measuring ring widths. The cores were cross-dated, and ring widths were measured using a dendrochronometer with an accuracy of 0.01 mm. Each core was measured twice to provide an average measurement of yearly ring growth. If the difference in measurements between readings was greater than 10%, the core was measured a third time, and a mean of the values was recorded from the two cores taken from each tree. Annual basal growth (square centimetres) was calculated as πr^2 of the current-year ring width minus πr^2 of the previous-year ring width (USDA Forest Products Laboratory 1974). The data were summarized as the mean annual basal area growth for the period 1980–1998, for each of the three species within the study area.

Foliage analysis

Between mid-July and mid-August 1998, we randomly collected sun and shade foliar samples from three dominant or codominant trees from each of the three tree species in each of the 46 plots. We placed at least 5 g of each sample in separate paper bags. The foliar samples were oven-dried for 48 h at 70 °C, ground through a 1-mm sieve, placed in 60-mL acid-washed glass jars, and stored in darkness at 22 °C until analysis. The foliar cation percentages were measured using the dry-ash procedure where 2.5 g of leaf tissue was ashed at 500 °C overnight. The sample was then dehydrated with 6 mol/L HCl and then brought to volume (50 mL) with distilled water in a volumetric flask. The analyses for Ca, Mg, and aluminum (Al) were conducted using an ion

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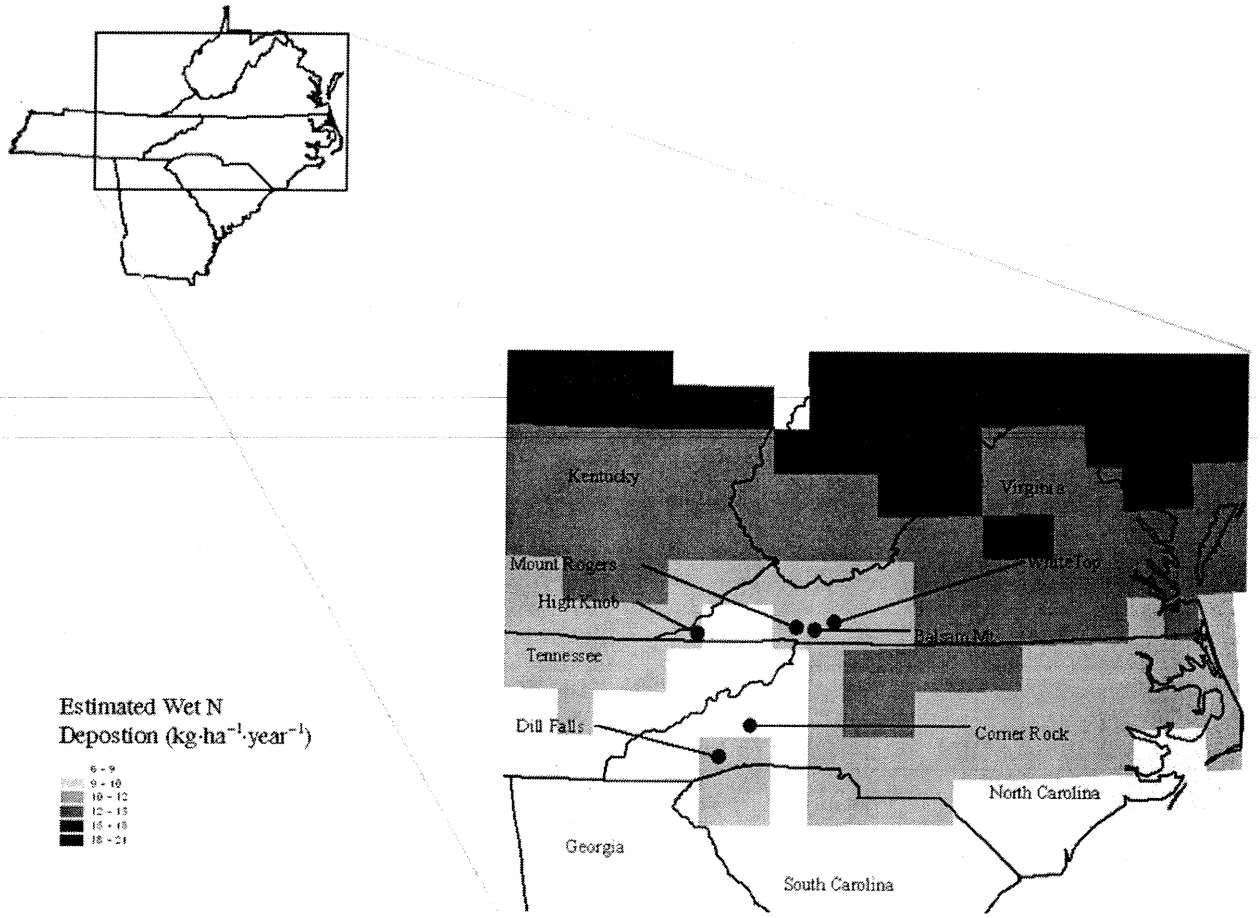
Fig. 1. Site locations and estimated N deposition across the southern Appalachian deciduous forests.



coupled plasma analyzer. Standards that spanned the range of foliar cation concentrations were used for quality assurance and quality control. Foliar percent N and percent carbon (C) were measured using a Perkin-Elmer model 240B CHN analyzer. Two standards from the National Institute of Standards and Technology were used in the analysis: National Bureau of Standards 1572 (citrus leaves) and 1567 (wheat flour).

Forest floor analysis

We randomly collected 20 forest floor samples to a depth of 15 cm from each of the 10-m-radius plots. Mineral soil was removed if it was attached to the base of the forest floor sample. At each plot 20 samples were randomly distributed into five composite samples, stored in 25-μm thick polyethylene bags, and kept at 5 °C until time of analysis. The five composite samples were sieved using a 2-mm screen. Potential net nitrification and N mineralization were calculated based on a ratio of wet mass to dry mass that was determined by weighing 10.0 g of the sieved sample, then oven-drying the sample at 105 °C for 48 h prior to reweighing. Another 10.0-g replicate was placed in 150 mL of 1 mol/L KCl, shaken for 30 min, and centrifuged to collect the extract. The extract of these initial samples was frozen at 0 °C until analysis for ammonium (NH_4-N) and nitrate (NO_3-N) concentrations. The remaining forest floor sample material from each bag was incubated for 28 days at 22 °C and then extracted as previously described. We used a TRAACS 800 auto-analyzer to analyze the initial and incubated extract for NH_4 (Technicon Industrial Systems 1978) and NO_3 (Technicon Industrial Systems 1977). Monthly potential net nitrification was calculated as the incubated sample NO_3-N minus the initial sample NO_3-N. Monthly potential net N mineralization was calculated as the incubated sample (NH_4 + NO_3) minus the initial sample (NH_4 + NO_3).

Percent forest floor C and N were determined by burning each forest floor sample in a pure-oxygen environment using a Perkins-Elmer CHN 2400 analyzer to collect and measure the resulting combustion gases.

We analyzed each forest floor sample for percent Ca, Mg, and Al by placing 2.5 g of sieved sample into a 500 °C muffle furnace for 12 h. Distilled water (2 mL), 4 mL of 6 mol/L HCl, and the ashed sample were added to a 50-mL volumetric flask. The flask was filled to volume, mixed, filtered, and analyzed using inductively coupled plasma. Two forest floor samples from each plot were randomly selected for pH measurements, using a 1:2 (*m*/*v*) forest floor to calcium chloride ($CaCl_2$) (0.01 mol/L) solution.

Statistical analysis

All data analysis were completed using SYSTAT version 9, and all correlations (Pearson correlation, $p < 0.05$) and re-

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Table 2. Mean forest floor potential net N mineralization and nitrification, pH, %N, %C, and Ca/Al, Mg/N, and C/N ratios across a gradient of N deposition.

Site	Potential net N mineralization ($mg \cdot kg^{-1} \cdot 28\ days^{-1}$)	Potential net nitrification ($mg \cdot kg^{-1} \cdot 28\ days^{-1}$)	Nitrification/ mineralization ratio	pH	%N	%C	Ca/Al	Mg/N	C/N
Corner Rock, N.C.	81.4 (19.12)	58.1 (8.90)	0.71 (0.37)	4.20 (0.49)	0.71 (0.44)	11.16 (5.94)	0.03 (0.02)	1.28 (0.83)	16.62 (2.74)
Dill Falls, N.C.	41.8 (14.01)	24.3 (7.72)	0.60 (0.40)	3.64 (0.49)	0.81 (0.34)	15.04 (8.89)	0.04 (0.07)	0.83 (0.44)	18.09 (2.85)
High Knob, Va.	112.5 (27.75)	91.1 (24.84)	0.81 (0.24)	3.79 (0.25)	0.64 (0.17)	9.58 (2.78)	0.04 (0.03)	0.52 (0.21)	14.90 (1.26)
Mount Rogers, Va.	145.1 (32.19)	83.2 (20.41)	0.57 (0.15)	3.44 (0.24)	0.97 (0.32)	15.47 (5.76)	0.04 (0.05)	0.21 (0.09)	15.49 (1.88)
Balsam Mountain, Va.	163.8 (40.23)	162.6 (35.31)	0.99 (0.09)	3.56 (0.18)	1.40 (0.22)	18.31 (3.70)	0.03 (0.01)	0.95 (0.58)	13.00 (0.82)
Whitetop, Va.	174.8 (41.80)	142.4 (39.56)	0.81 (0.15)	3.70 (0.46)	1.17 (0.45)	16.78 (7.79)	0.08 (0.09)	0.39 (0.22)	14.05 (1.71)

Note: Numbers in parentheses represent standard deviations.

Table 3. Correlations between forest floor %C and C/N, and potential net N mineralization and nitrification (with and without HighKnob data).

	R^2	P	n
Forest floor %C vs.			
Potential net nitrification			
With HighKnob	0.24	0.001	46
Without HighKnob	0.27	0.001	34
Potential net N mineralization			
With HighKnob	0.43	<0.001	46
Without HighKnob	0.47	<0.001	34
Forest floor C/N vs.			
Potential net nitrification			
With HighKnob	0.37*	<0.001	46
Without HighKnob	0.50*	<0.001	34
Potential net N mineralization			
With HighKnob	0.23*	0.001	46
Without HighKnob	0.31*	0.001	34

*Negative correlation.

gression analyses were derived from plot-level (as opposed to site-level) data. There was only one N deposition value for each site because of the coarse resolution of the N deposition data, but each plot on a site may have unique combination of past plot disturbance, management, or microclimate. Thus, we could begin to evaluate the relative contribution of the other non-N-deposition controls on plot-level foliar and soil chemistry by comparing these plot-level parameters with regional N deposition. A tight grouping (i.e., low intrasite variability) of foliar or forest floor chemistry within a site is one indication that N deposition is the major controlling factor for foliar and forest floor chemistry within the species type. A wide grouping (i.e., high intrasite variability) of foliar or forest floor chemistry within a site could indicate that other non-N-deposition factors are significantly controlling intrasite chemistry. This information would be lost if only site-level average foliar and forest floor values were used.

Basal area growth data for all species were significantly skewed. Skewness was considered to be significant if the absolute value was greater or equal to two times the standard errors for skewness (SES) (Tabachnick and Fidell 1996). The SES was calculated as SES = $(6/n)^{1/2}$, where n is the number of samples (Tabachnick and Fidell 1996). Logarithmic transformations of the basal area growth data were done to correct the skewed data before we performed correlation and regression analyses.

Nitrogen deposition gradient studies have been conducted to understand the effects of naturally varying N inputs on nutrient cycling and overall forest health (McNulty et al. 1991; Lovett and Rueth 1999). However, inherent soil, climate, and vegetation variability among plots can make data from gradient studies difficult to interpret. To minimize among-plot variability in this study, we tried to select sites with similar forest floor and species physical characteristics. Table 1 shows the variability of soil types that exist across the sampled plots, as recorded in the STATSGO database (http://www.essc.psu.edu/soil_info/index.cgi?soil_data&statsgo). Most of the soils across the N deposition gradient originated from coarse-loamy, mixed, mesic Typic Dystrochrepts and

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Table 4. Foliar chemistry means, tree age, and mean annual basal area growth.

Site	*n*	%N	%Al	%Mg	%Ca	Ca/Al	Mg/N	Age (years)	Mean basal area growth ($cm^2 \cdot year^{-1}$)
American beech									
Corner Rock, N.C.	12	2.4 (0.24)	0.008 (0.002)	0.19 (0.07)	0.70 (0.07)	101 (34.86)	0.08 (0.04)	65 (6.5)	2.40 (1.4)
Dill Falls, N.C.	9	2.2 (0.80)	0.003 (0.001)	0.21 (0.02)	0.49 (0.06)	170 (28.27)	0.10 (0.01)	—	—
HighKnob, Va.	6	2.4 (0.08)	0.006 (0.000)	0.18 (0.02)	0.74 (0.07)	127 (10.89)	0.08 (0.01)	61 (0.0)	4.32 (0)*
Mount Rogers, Va.	20	2.7 (0.08)	0.005 (0.002)	0.16 (0.04)	0.56 (0.14)	114 (51.55)	0.06 (0.02)	80 (11.9)	3.77 (2.3)
Balsam Mountain, Va.	9	2.8 (0.05)	0.008 (0.002)	0.20 (0.04)	0.86 (0.09)	109 (34.23)	0.07 (0.02)	—	—
Whitetop, Va,	14	2.8 (0.14)	0.010 (0.005)	0.17 (0.04)	0.67 (0.16)	82 (49.48)	0.06 (0.02)	77 (10.2)	2.51 (1.0)
Sugar maple									
Corner Rock, N.C.	12	2.1 (0.29)	0.005 (0.002)	0.22 (0.11)	0.82 (0.15)	207 (90.15)	0.11 (0.07)	72 (30)	2.77 (3.4)
Dill Falls, N.C.	3	2.1 (0.38)	0.004 (0.001)	0.22 (0.02)	0.58 (0.19)	163 (0.26)	0.11 (0.01)	—	—
HighKnob, Va.	33	2.3 (0.24)	0.006 (0.010)	0.16 (0.04)	0.86 (0.16)	163 (62.03)	0.07 (0.02)	49 (14.5)	5.41 (4.6)
Mount Rogers, Va.	9	2.3 (0.16)	0.004 (0.001)	0.16 (0.05)	0.74 (0.29)	187 (94.39)	0.07 (0.02)	77 (34.6)	2.11 (0.03)
Balsam Mountain, Va.	6	2.4 (0.14)	0.006 (0.002)	0.13 (0.02)	0.66 (0.09)	117 (33.36)	0.06 (0.01)	—	—
Whitetop, Va,	18	2.5 (0.17)	0.005 (0.002)	0.16 (0.05)	1.02 (0.40)	264 (179.26)	0.06 (0.02)	48 (14.1)	5.59 (3.1)
Yellow birch									
Corner Rock, N.C.	9	2.4 (0.02)	0.011 (0.01)	0.19 (0.01)	0.92 (0.16)	88 (26.09)	0.08 (0.00)	58 (8.5)	3.04 (2.0)
Dill Falls, N.C.	16	2.4 (0.28)	0.005 (0.001)	0.30 (0.04)	0.77 (0.11)	162 (56.37)	0.13 (0.02)	—	—
HighKnob, Va.	26	2.6 (0.22)	0.010 (0.002)	0.26 (0.03)	1.03 (0.13)	107 (30.57)	0.10 (0.01)	41 (13.1)	6.56 (4.1)
Mount Rogers, Va.	17	2.7 (0.22)	0.008 (0.002)	0.23 (0.08)	0.89 (0.31)	114 (34.78)	0.09 (0.03)	59 (13.2)	7.84 (5.8)
Balsam Mountain, Va.	22	2.7 (0.18)	0.008 (0.001)	0.23 (0.02)	0.91 (0.15)	116 (32.09)	0.09 (0.01)	—	—
Whitetop, Va,	7	3.2 (0.34)	0.015 (0.01)	0.22 (0.05)	0.90 (0.30)	71 (46.86)	0.07 (0.02)	42 (9.8)	4.82 (3.8)

Note: Numbers in parentheses represent standard deviations. —, no data.
*Standard deviation of zero due to one tree available for analysis.

loamy-skeletal, siliceous, mesic Typic Hapludults. These soils, in general, have a moderately rapid permeability and are moderately deep, well drained, and found on ridges and hillslopes. The soils were acidic with a pH range of 3.7 to 4.2 (Table 2). Climate data varied slightly across the gradient with the highest precipitation and temperature occurring on Dill Falls and Mount Rogers, respectively (Table 1).

Variations in plot aspect, elevation, and N deposition were inherently incorporated into the sampling design. We then tested whether or not forest floor and foliar chemistry were significantly different across aspect and elevation with a two-sample *t* test. We found no significant differences in plot-level forest floor and foliar chemistry among different aspects and elevations across all sites. This could be due to the small range in elevation across the N deposition gradient. For this reason, statistical analyses of ecosystem chemical components were not separated based on aspect or elevation.

The forest floor %C from the HighKnob site was significantly lower than that of all other sites, suggesting that the forest floor samples from this site contained higher concentrations of mineral soil. However, when HighKnob data were removed from the statistical analysis, the relationship between %C and potential net nitrification and that between %C and N mineralization were not changed significantly (Table 3). Forest floor C/N correlations with N-cycling components were also unchanged with and without the HighKnob data (Table 3). All statistical analyses examining the relationships between N deposition and forest floor N cycling and foliar chemistry were completed using data from all six sites, which included HighKnob.

Approximately 60% of the 144 extracted tree cores were suitable for determining tree age and basal area tree growth. The remaining 40% of the cores had broken pieces and (or) undistinguishable tree rings and were not included in the analysis. Correlations analysis between basal area tree growth and the following independent variables will be presented: N deposition; air temperature; tree age; and forest floor N cycling, %N, and C/N ratio. Data from four sites (Corner Rock, HighKnob, Mount Rogers, and Whitetop) were use to perform the correlation analyses between basal area growth and the independent variables. Dill Falls and Balsam Mountain were excluded from this part of the analysis because of the limited number of readable cores from two of the sites.

Results

Basal area growth

Species basal area growth and tree age varied across the N deposition gradient (Table 4). The American beech trees were 61 to 80 years old, and annual basal area growth for this species ranged from 2.40 to 4.32 $cm^2 \cdot year^{-1}$. Across all sites, the sampled sugar maple trees were 48 to 77 years old, and annual basal area growth ranged from 2.11 to 5.59 $cm^2 \cdot year^{-1}$. Yellow birch trees were 41 to 59 years old, and annual basal area growth ranged from 3.04 to 7.84 $cm^2 \cdot year^{-1}$.

Foliage chemistry

Foliar %N for all three species on Whitetop Mountain was within the range of concentrations cited in other studies in the United States and Canada (Table 5). Foliar Mg/N and

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Table 5. Comparison of foliar %N and foliar Mg/N and Ca/Al ratios from various studies.

Source	%N	Mg/N	Ca/Al	Location
American beech				
This study, low N deposition	2.40	0.08	101	Southern Appalachians
This study, high N deposition	2.80	0.06	82	Southern Appalachians
Coté et al. 2002	1.98			Quebec
Coté et al. 2002	2.24			Quebec
Ollinger et al. 2002	2.10			New Hampshire
White et al. 1999	2.28	0.07	327	Bear Brook
Bolster et al. 1996	2.00			Harvard Forest
Fahey et al. 1997	2.13			New Hampshire
Aber et al. 1995	1.98	0.08	307	Bear Brook
Aber et al. 1995	2.25	0.07	199	Bear Brook
Boerner 1984	2.27			Ohio
Boerner 1984	2.32			Ohio
Mitchell and Chandler 1939	1.78			New York
Mitchell and Chandler 1939	2.44			New York
Mitchell and Chandler 1939	2.03			New York
ACCP 2005	1.97			Howland, Maine
ACCP 2005	2.36			Harvard Forest
Sugar maple				
This study, low N deposition	2.10	0.11	207	Southern Appalachians
This study, high N deposition	2.50	0.06	264	Southern Appalachians
Hutchinson et al. 1999	1.34	0.07	349	Canada
White et al. 1999	1.56	0.07	500	Bear Brook
Bolster et al. 1996	1.69			Harvard Forest
Ellsworth et al. 1994	1.67	0.04		Vermont
Ellsworth et al. 1994	2.02	0.05		Vermont
Ellsworth et al. 1994	1.75	0.05		Vermont
Ellsworth et al. 1994	1.55	0.08		Vermont
Zak et al. 1986	0.74			Michigan
Zak et al. 1986	1.02			Michigan
Heisey 1995	2.18	0.07	450	Pennsylvania – New York
Pastor et al. 1984	1.88	0.10		Wisconsin
Yellow birch				
This study, low N deposition	2.40	0.08	88	Southern Appalachians
This study, high N deposition	3.20	0.07	71	Southern Appalachians
Coté et al. 2002	2.44			Quebec
Nadelhoffer et al. 1999	3.02			Spruce forest in N.H.
Nadelhoffer et al. 1999	2.57			Spruce–hardwood forest in N.H.
Nadelhoffer et al. 1999	2.49			Hardwood forest in N.H.
Fahey et al. 1997	2.30	0.14		White Mountain National Forest
Bolster et al. 1996	2.30			Harvard Forest
Fownes 1985	2.21			Wisconsin
Day and Monk 1977	2.14			Coweeta
NERC 2005	2.36			New England
ACCP 2005	2.98			Harvard Forest

Note: ACCP, Accelerated Canopy Chemistry Program (http://www.daac.ornl.gov/ACCP/accp.html); NERC, Northeastern Ecosystem Research Cooperative.

Ca/Al were low or within the range of values found in other studies (Table 5).

Foliar chemistry concentrations varied across sites and by tree species (Table 4). Foliar %N and %P for American beech and sugar maple correlated significantly with N deposition. American beech foliar %K did not correlate with N deposition. Foliar Mg/N in sugar maple also correlated ($R^2 = -0.22$, $p = 0.004$) with N deposition but foliar Ca/Al did not correlate with N deposition. Sugar maple was the only species for which foliar Mg/N and %K correlated with N deposition. There was no relationship between N deposition and foliar Ca/Al and Mg/N and %K and %P in yellow birch.

Forest floor chemistry

Forest floor potential net nitrification ranged from 24.3 to 162.6 $mg \cdot kg^{-1} \cdot 28\ days^{-1}$, and potential net N mineralization

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Table 6. Correlations between N deposition and foliar %N, %P, %K; foliar Mg/N and Ca/Al ratios; and forest floor N cycling and nutrients.

N deposition vs.	R^2	P	n
Foliar %N			
American beech	0.40	<0.001	26
Sugar maple	0.22	0.004	36
Yellow birch	0.38	<0.001	35
Foliar %P			
American beech	0.20	0.020	26
Sugar maple	0.15	0.018	36
Yellow birch	0.09	ns	35
Foliar %K			
American beech	0.01	ns	26
Sugar maple	0.35	0.004	36
Yellow birch	0.04	ns	35
Foliar Mg/N			
American beech	0.13*	ns	26
Sugar maple	0.22*	0.004	36
Yellow birch	0.08*	ns	35
Foliar Ca/Al			
American beech	0.03*	ns	26
Sugar maple	0.01	ns	36
Yellow birch	0.05*	ns	35
Forest floor			
Potential net nitrification	0.22	0.001	46
Potential net mineralization	0.23	0.001	46
Nitrification/mineralization	0.15	0.009	46
pH	0.14*	0.013	44
%N	0.16	0.005	46
C/N	0.19*	0.002	46
Mg/N	0.37*	<0.001	46

Note: ns, not significant at $p < 0.05$.
*Negative correlation.

ranged from 41.8 to 174.8 $mg \cdot kg^{-1} \cdot 28\ days^{-1}$ (Table 2). Mean forest floor %N ranged from 0.64% to 1.40% (Table 2) across all sites and was correlated with N deposition (Table 6). Lovett and Rueth (1999) found that in pure maple forests, potential net nitrification occurred when forest floor N was >1.7%. In this study of beech–maple–birch forests, we first observed potential net nitrification when forest floor N was >0.30% (Fig. 2).

Potential net nitrification and N mineralization rates and nitrification/mineralization fraction correlated significantly with N deposition (Table 6). Across sites, the onset of potential net nitrification occurred when forest floor C/N ratios decreased below a threshold of 20:1 (Fig. 3). Forest floor C/N correlated significantly and negatively with N deposition (Table 6).

Forest floor Ca/Al did not correlate significantly with N deposition. However, both forest floor Mg/N and pH were negatively and significantly correlated with N deposition (Table 6).

Discussion

Examining general changes in ecosystem processes such as species growth rates, foliar chemistry, and potential net nitrification and N mineralization can help delineate the response of ecosystem dynamics to chronic N deposition loading. In this study, we observed several trends in ecosystem response variables that were consistent with the influences of N deposition and the Aber et al. (1989) model of N saturation.

Basal area growth

A general linear regression model between basal area growth and species indicated a significant correlation ($R^2 = 0.10$, $p = 0.02$, $n = 85$), suggesting to some extent that species type influences tree growth. A stepwise linear regression model suggested that across the gradient, species type, N deposition, C/N, and tree age were more strongly correlated with basal area growth than were potential net nitrification and N mineralization, forest floor %N, and mean annual air temperature. Species, N deposition, and tree age improved the overall R^2 from 0.10 to 0.25.

A linear correlation analysis of individual tree species indicated that sugar maple was the only species in which basal area growth correlated significantly with N deposition, potential net nitrification, forest floor C/N, mean annual air temperature, and tree age (Table 7). Yellow birch basal area growth did, however, correlate significantly with potential net N mineralization rates. None of the measured American beech components correlated with the independent variables (i.e., N deposition, forest floor %N, C/N, potential net nitrification and N mineralization, mean annual air temperature, or tree age). The growth patterns for sugar maple were consistent with early-stage N saturation. When increases in N deposition correlate with basal area growth, N deposition is acting as a fertilizer. Yellow birch and American beech basal area growth are consistent with later stages of N saturation, in that the trees growth patterns have reached the crest of the N saturation curve and have started a downward trend (Fig. 4). These growth patterns indicated that a linear correlation was not the best fit to explain the relationship between N deposition and yellow birch and American beech basal area growth. We then performed quadratic correlation analyses between yellow birch and American beech basal area growth rates and N deposition. The quadratic correlation was significantly correlated for yellow birch ($R^2 = 0.19$, $p = 0.03$, $n = 37$), but not for American beech ($R^2 = 0.13$, $p = 0.25$, $n = 23$). Figure 4 also shows that the growth rates of the three species were similar at the lowest N deposition value and then diverge as N deposition increases, with yellow birch and American beech basal area growth decreasing at the high N deposition values. Duchesne et al. (2002) found that forest growth decline in Quebec was, in part, due to soil acidification and acid deposition.

Lovett and Rueth (1999) found that in pure maple and beech stands, maple and beech respond differently to N deposition inputs, with maple having the strongest correlation to N accumulation. This suggests that sugar maple is more likely to have a positive growth-related response (Fig. 4) to N deposition as long as N deposition did not induce N saturation. LeBlanc et al. (1987) also found a relationship between basal area growth in trees and changes in acid deposition (i.e., N deposition). Further, LeBlanc (1990) found a negative trend between acid deposition and basal area is a strong indicator of growth decline.

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Fig. 2. Relationship between forest floor N and potential net nitrification across a gradient of N deposition in the southern Appalachian deciduous forests.

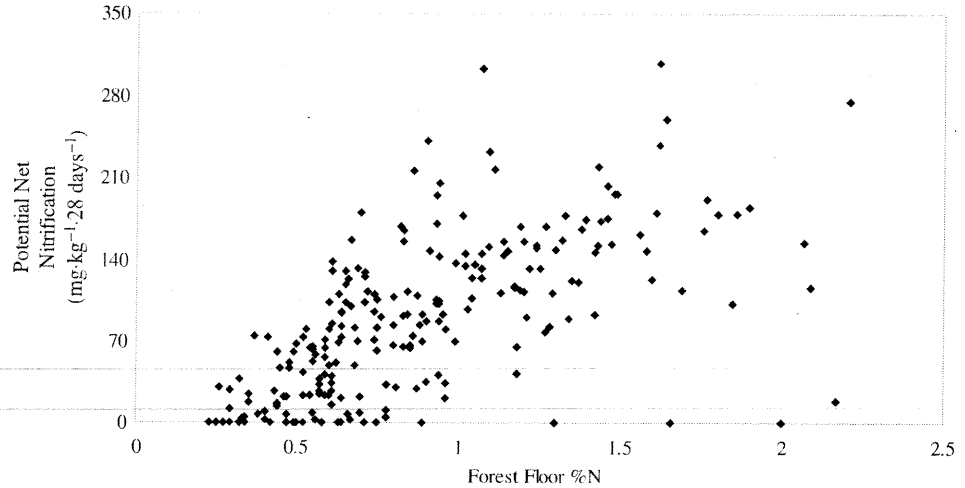
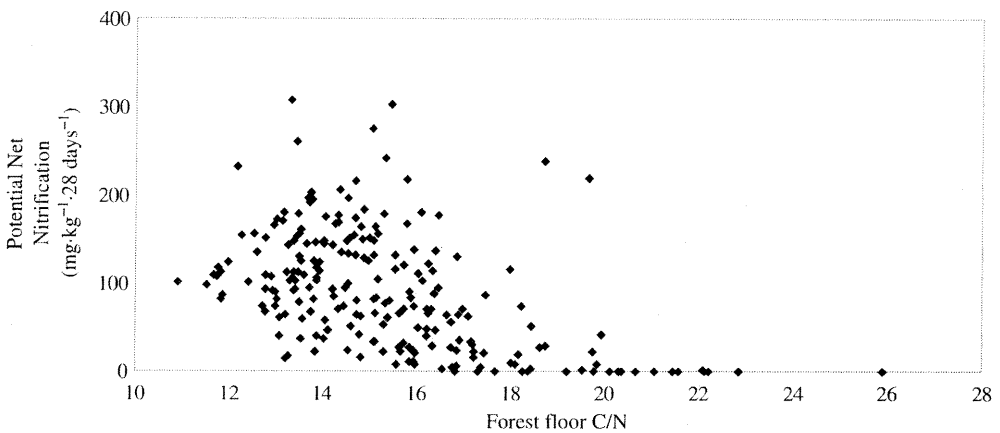


Fig. 3. Relationship between C/N and potential net nitrification across a gradient of N deposition in the southern Appalachian deciduous forests.



Foliage

The pattern of foliar %N in this study relative to that in other studies was consistent with influence of N deposition on foliar chemistry. However, our foliar data does not provide evidence that N deposition is damaging the overall health of these deciduous forests. Foliar %N has been shown to be a useful index of ecosystem processes, N cycling, and productivity (Reich et al. 1999; Ollinger et al. 2002).

Table 5 shows foliar %N, Ca/Al, and Mg/N values in American beech, sugar maple, and yellow birch in sites throughout the United States and Canada. Our foliar %N concentrations are at the high end of the cited values (Table 5). In particular, the foliar %N pattern for American beech appears to consistently reach a concentration of 2.8% when N deposition is greater than 13 kg $N{\cdot}ha^{-1}{\cdot}year^{-1}$ and was 20% higher than data collected from a beech–maple–spruce forest at the N fertilization site in Bear Brook, Maine (Nadelhoffer et al. 1995). Ollinger et al. (2002) and Bolster et al. (1996) have reported American beech foliar %N values that were 33% and 40%, respectively, lower than American beech foliar %N on our high N deposition plots. This appearance of a foliar %N plateau and high foliar %N at our site relative to other studies suggest that foliar %N for American beech is progressing toward a permanently elevated state, particularly on Mount Rogers, Balsam Mountain, and Whitetop Mountain where wet N deposition was greater than 13 kg $N{\cdot}ha^{-1}{\cdot}year^{-1}$.

The negative correlation between foliar Mg/N and N deposition in sugar maple is consistent with early-stage N saturation. In addition, the positive correlations between foliar %N, %P, and %K and N deposition in sugar maple are consistent with a fertilization effect of N deposition (Table 6). Damaged or declining sugar maple trees have been found to be K deficient (Ouimet and Fortin 1992). Ouimet and Fortin (1992) further noted that fertilization of these trees leads to enhanced tree vigor, as reflected by increased stem growth and increased foliar %N, %K, and %Ca.

Whitetop Mountain receives 15 kg $N{\cdot}ha^{-1}{\cdot}year^{-1}$ and had a yellow birch foliar N concentration of 3.2% (Table 4). Nadelhoffer et al. (1999) found a 2.41% foliar N concentration for yellow birch from a beech–maple–spruce forest fertilized with 56 kg $N{\cdot}ha^{-1}{\cdot}year^{-1}$; prior to fertilization, the ambient deposition (wet) at the study site was 4 kg $N{\cdot}ha^{-1}{\cdot}year^{-1}$. The difference in foliar %N between this study and our study could be due in part to Whitetop receiving 15 kg $N{\cdot}ha^{-1}{\cdot}year^{-1}$ for a longer time (chronic)

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Table 7. Correlation between basal area growth of American beech, sugar maple, and yellow birch and N deposition, N cycling, forest floor %N and C/N, air temperature, and tree age.

Response variable	Species	N deposition	Nitrification	Mineralization	%N	C/N	Temperature	Tree age	*n*
Basal area growth	American beech	ns	ns	ns	ns	ns	ns	ns	23
	Sugar maple	0.17 (0.04)	0.18 (0.03)	ns	ns	0.31 (0.004)*	0.17 (0.04)*	0.18 (0.04)	25
	Yellow birch	ns	ns	ns	ns	ns	ns	ns	37

Note: R^2 values are shown with p values in parenthesis. ns, not significant at $p < 0.05$. Nitrification is potential net nitrification, mineralization is potential net N mineralization, and temperature is mean annual air temperature.
*Negative correlation.

Fig. 4. Basal area growth (logarithmic transformation) patterns across a N deposition gradient for (*a*) American beech, (*b*) sugar maple, and (*c*) yellow birch.

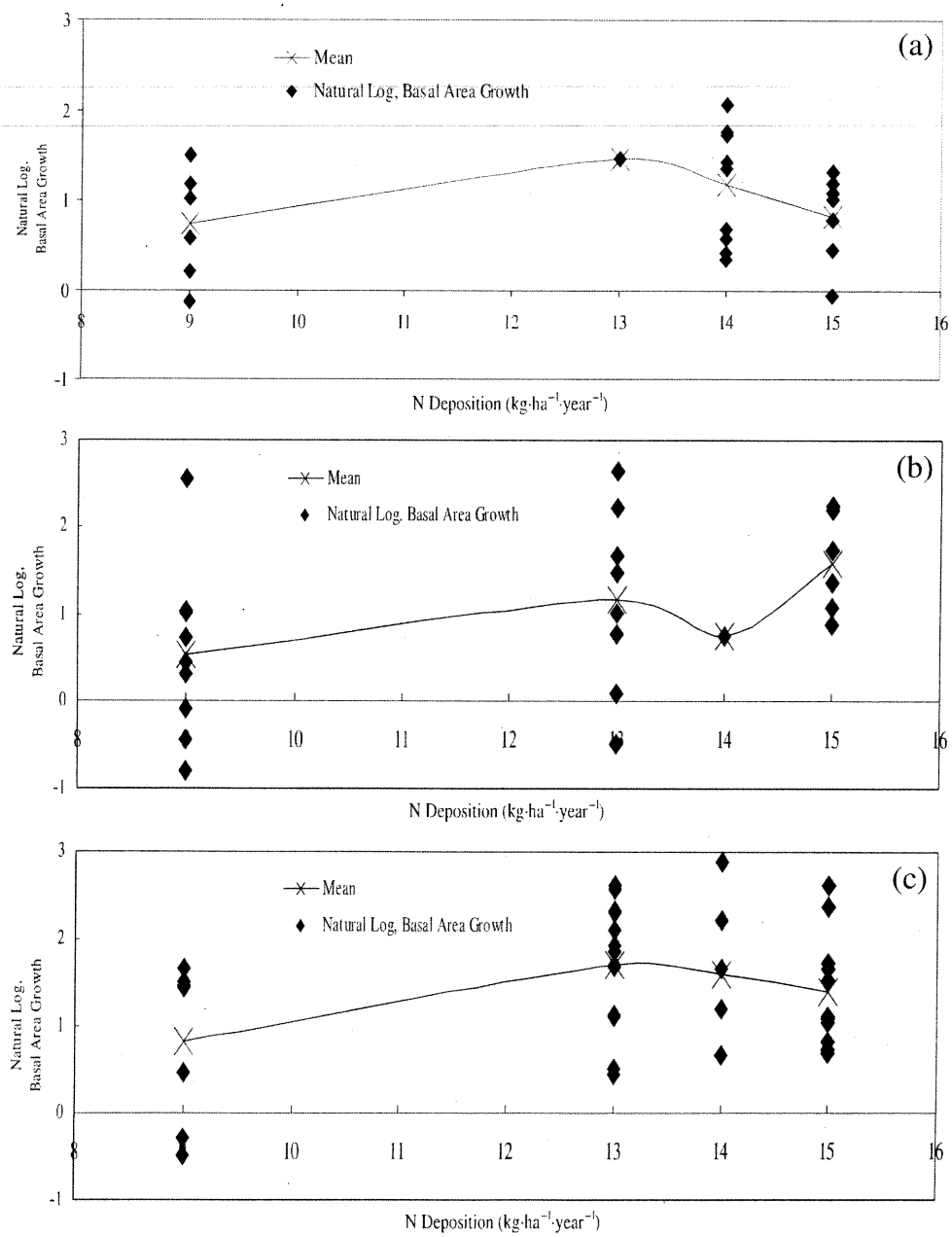

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Table 8. Stepwise linear regression analysis between potential net N mineralization and nitrification and the following independent variables: N deposition, forest floor C/N, and air temperature.

Response variable	N deposition	C/N	Temperature	R^2	n
Potential net N mineralization	12.0 (0.02)	11.0 (<0.02)*	ns	0.32 (<0.001)	46
Potential net nitrification	ns	17.0 (<0.001)*	ns	0.38 (<0.001)	46

Note: Coefficients are shown with p values in parenthesis ns, not significant at $p < 0.05$. Temperature is mean annual air temperature.
*Negative correlation.

than the fertilized forests (acute) of the Nadelhoffer study. Yellow birch foliar %N values reported by Fahey et al. (1997) and Bolster et al. (1996) from untreated sites were 30% less than what we found on our highest N deposition site, Whitetop (Table 4).

Forest floor

Overall, the relationships between N deposition and N cycling and nutrient pools are consistent with the influence of N deposition on N cycling. In addition, a stepwise linear regression model indicated that N deposition and forest floor C/N had a greater influence on potential net nitrification and N mineralization rates than air temperature (Table 8). Rustad et al. (2001), however, found that temperature significantly increased (46%) N net mineralization. Their temperatures from the meta-analysis of experimental ecosystem warming projects ranged from 0.3 to 6.0 °C.

Forest floor %N was significantly correlated with N deposition. The relative values of forest floor nutrients (i.e., Mg/N) have been shown to be better indicator of tree health (McNulty et al. 1996) than the absolute concentrations (i.e., %Mg). In this study, our results indicated that as the N deposition increased, forest floor Mg/N decreased (Table 6). Ouimet and Camiré (1995) found that in sensitive forests, acid deposition may increase the displacement of base cations, resulting in nutrient imbalances. Our forest floor pH values were acidic and were significantly and negatively correlated with N deposition (Table 6). Forest floor acidification on our sites, which is due in part to chronic N deposition, may have caused leaching of the base cation Mg.

Potential net nitrification and N mineralization rates and nitrification/mineralization ratios were significantly and positively correlated with N deposition (Table 6). The nitrification/mineralization fractions ranged from 57% to 99% with the highest percentages occurring on Balsam Mountain. A nitrification/mineralization fraction of about 100% was also found at Fernow Experimental Forests (Gilliam et al. 2001). Our high nitrification/mineralization fractions and their correlations with N deposition suggest that chronic high levels of N deposition are continuing to stimulate potential net nitrification and N mineralization rates. Aber et al. (1995), Magill et al. (1996), and McNulty et al. (1996) have shown that potential net N mineralization rates increase initially with N fertilization and then decrease after several years, thus suggesting that southern Appalachian forests may be in an early phase of N saturation. The onset of potential net nitrification occurred when the C/N ratio of the forest floor decreased below a threshold of approximately 20 across all sites (Fig. 3). Lovett and Rueth (1999) reported a C/N ratio of 23 in a pure sugar maple stand in the northeastern United States.

Forest floor C/N ratios indicated a significant negative correlation when compared with forest floor potential net nitrification and N mineralization rates (Table 3). Forest floor %N was significantly correlated with potential net N mineralization ($R^2 = 0.65$, $p < 0.001$, $n = 46$) and nitrification ($R^2 = 0.35$, $p < 0.001$, $n = 46$). These results suggest that an adequate supply of NH_4-N (ammonium N) was available for microbial activity (McNulty et al. 1996).

Forest ecosystems under chronically elevated levels of N deposition have shown a breakdown in the relationship between forest floor %C and %N (McNulty et al. 1991; Michel and Matzner 2002). In areas where N deposition exceeds plant and microbial biological demand, decomposers may no longer be limited by N. Instead, decomposition may be limited by C availability (Bowden et al. 2004), reducing the relationship between C and N. The data from this study indicated a very strong correlation ($R^2 = 0.88$, $p < 0.001$, $n = 46$) between forest floor %C and %N, suggesting an adequate amount of available C substrate is still available.

Conclusion

Studies have shown differences in the relationships between N deposition and response variables in deciduous forests. Payette et al. (1996) used tree ring data to show that sugar maple decline was related more to drought and insect infestations than to anthropogenic pollution in Canada. Duchesne et al. (2002) found that the appearance of forest growth decline in a sugar maple forests was due in part to soil acidification and acid deposition. Deciduous forests in the southern United States are generally not considered sensitive to N deposition, and these ecosystems generally have adequate stores of base cation nutrients and the forest floor maintains considerable capacity to retain added N. However, in our study on a limited number of high-elevation sites across the southern Appalachian, we observed several response variables that were correlated with the N deposition gradient (Table 6). The growth trend (Fig. 4) of yellow birch was mostly consistent with a negative influence of high N deposition inputs, as explained by the quadratic regression model. The growth trend for American beech was not explained by the linear or quadratic regression model. Sugar maple basal area growth pattern and foliar %N, %P, and %K were consistent with N fertilization effects. The relationships between N deposition and potential net nitrification and N mineralization suggest N deposition is changing the overall N cycle. Our results also provide a regional baseline against which the effects of long-term N deposition can be assessed. These findings further indicate the need for a more intensive sampling of deciduous forests across the southern Appalachian mountains and for the es-

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tablishment of permanent monitoring plots to quantify change in forest growth, N cycling, and foliar chemistry over time.

Acknowledgments

This research was funded by the Southern Global Change Program (SGCP) of the Southern Research Station, USDA Forest Service. The SGCP would like to thank Harvard Ayers for his collaboration and Aaron Hohl, Taryn Bayer, Mya Williams, Gretta Guzzman, and Sara Strickland for their diligent work in the field and laboratory. Further, we would like to thank Robert Mickler and the USDA Southern Research Station Communication staff for editing this manuscript.

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