Changes in conifer and deciduous forest foliar and forest floor chemistry and basal area tree growth across a nitrogen (N) deposition gradient in the northeastern US

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Data from the 1999 remeasurement of the red spruce forests suggest that N deposition, to some extent, is continuing to influence red spruce across the northeastern US as illustrated by a significant correlation between N deposition and red spruce foliar %N. Our data also suggest that the decrease in forest floor %N and net nitrification potential across sites from 1987 to 1999 may be due to factors other than N deposition, such as climatic factors and N immobilization in fine woody material (<5 cm diameter).

Abstract

We evaluated foliar and forest floor chemistry across a gradient of N deposition in the Northeast at 11 red spruce (*Picea rubens* Sarg.) sites in 1987/1988 and foliar and forest floor chemistry and basal area growth at six paired spruce and deciduous sites in 1999. The six red spruce plots were a subset of the original 1987/1988 spruce sites. In 1999, we observed a significant correlation between mean growing season temperature and red spruce basal area growth. Red spruce and deciduous foliar %N correlated significantly with N deposition. Although N deposition has not changed significantly from 1987/1988 to 1999, net nitrification potential decreased significantly at Whiteface. This decrease in net potential nitrification is not consistent with the N saturation hypothesis and suggests that non-N deposition controls, such as climatic factors and immobilization of down dead wood, might have limited N cycling.
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1. Introduction

Since the beginning of the industrial era, atmospheric nitrogen (N) emissions (i.e., acid deposition) have increased dramatically (Hicks et al., 1990; Galloway et al., 2003). Acid deposition is formed from nitric oxides (NO_x) and sulfur dioxide (SO_x) emission from automobiles and power plants. In the northeastern US, N deposition ranges from 4 to 13 kg N ha^{-1} yr^{-1}, with the highest N deposition values generally occurring along the southwestern edge of the region (National Atmospheric Deposition Program, 1998; Ollinger et al., 1993). These N deposition inputs were reported to be associated with red spruce (*Picea rubens* Sarg.) mortality and growth decline (Johnson et al., 1988; Siccama et al., 1982; Foster and Reiners, 1983), N saturation conditions (i.e., N in excess of plant and microbial biological demand; Aber et al., 1989), Al toxicity in roots (Shortle and Smith, 1988), reduced cold tolerance (Sheppard, 1994), and freezing injury (DeHayes, 1992) across the northeastern US.

N deposition gradient and controlled N fertilization experimental studies in high elevation red spruce and lower elevation deciduous forests have also linked N deposition to foliar

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and forest floor chemistry. McNulty et al. (1991) examined forest floor and foliar chemistry across a range of northeastern spruce-fir forests along a gradient of N deposition. They found significant relationships between measures of ecosystem N status (N cycling, forest floor and foliar chemistry, and foliar lignin:N ratio) and N deposition. Lovett and Rueth (1999) found that pure maple and beech stands respond differently across a gradient of N deposition, with maple having stronger correlation to N accumulation. They also noted that species differences should be considered in the prediction of forest response and the management of forest composition.

Controlled experimental studies by Magill et al. (2004) and McNulty et al. (2005) revealed that tree growth, nutrient imbalances, forest floor and foliar %N and net nitrification potential and N mineralization have been adversely affected by increased N inputs over time. Elvir et al. (2006) also found that in a treated watershed (25.2 kg N ha^{-1} yr^{-1}), foliar N concentration in deciduous and conifer trees increased significantly and foliar Ca, Mg, and Zn concentrations decreased significantly when compared to the trees in the reference watershed. Schaberg et al. (1997) found that calcium (Ca) can be leached from the needles of red spruce during exposure to acid deposition, thus predisposing the tree species to Ca deficiency.

Historically, the greatest concerns about N deposition impacts on forests in the US have focused on the northeast, particularly on high elevation spruce-fir (*Picea abies*) forests. Although these forests receive some of the highest levels of N deposition in the US due in part to cloud deposition (Heilman et al., 2000), studies in the southern Appalachian region suggest that the influence of N deposition may not be confined to high elevation conifer forests, but may also affect deciduous forests (Southern Appalachian Man and the Biosphere, 1996; Fernandez and Adams, 2000; Boggs et al., 2005). In 1999, we resampled six of the eleven spruce sites along a gradient of N deposition in the northeastern US that had previously been sampled in 1987/1988 by McNulty et al. (1991). Additionally, we sampled deciduous trees from six sites located adjacent to the six spruce sites. The remeasurement of the spruce sites and the establishment of new deciduous sites across a gradient of N deposition allowed us to evaluate the long-term influence of N deposition on the structure, composition, and function of high elevation conifer forests. This study also allowed us to compare the influence of how equal amounts of N deposition on cycling in conifer and deciduous stands. The objective of this study was to examine whether forest floor and foliar chemistry in red spruce forests across the northeast have changed from 1987/1988 to 1999 and to examine if patterns of foliar and forest floor chemistry across the N gradient in both conifer and deciduous forests are consistent with progression toward N saturation.

2. Materials and methods

2.1. Plot location

In 1987/1988, McNulty et al. (1991) established 161 10-m radius red spruce plots across 11 sites in the northeastern US at elevations ranging from 100 to 1460 m. During the summer of 1999, we resampled a sub-sample of 42 red spruce (*P. rubens* Sarg.) plots across six sites (Fig. 1, Table 1). At the same time, we established 49 deciduous plots near the original red spruce plots at six of the sites. Across sites, the dominant species in the deciduous plots were yellow birch (*Betula alleghaniensis* Britt.) and paper birch (*Betula papyrifera* Marsh.), with the exception of two sites, Howland and Mount Washington. Red maple (*Acer rubrum* Sarg.) and paper birch were the dominant species on the Howland site, while paper birch and sugar maple (*Acer saccharum*) were the dominant species on Mount Washington. Because site and plot selections were based primarily on N deposition input, species composition, elevation, slope, and aspect varied across sites and plots. Estimates of N
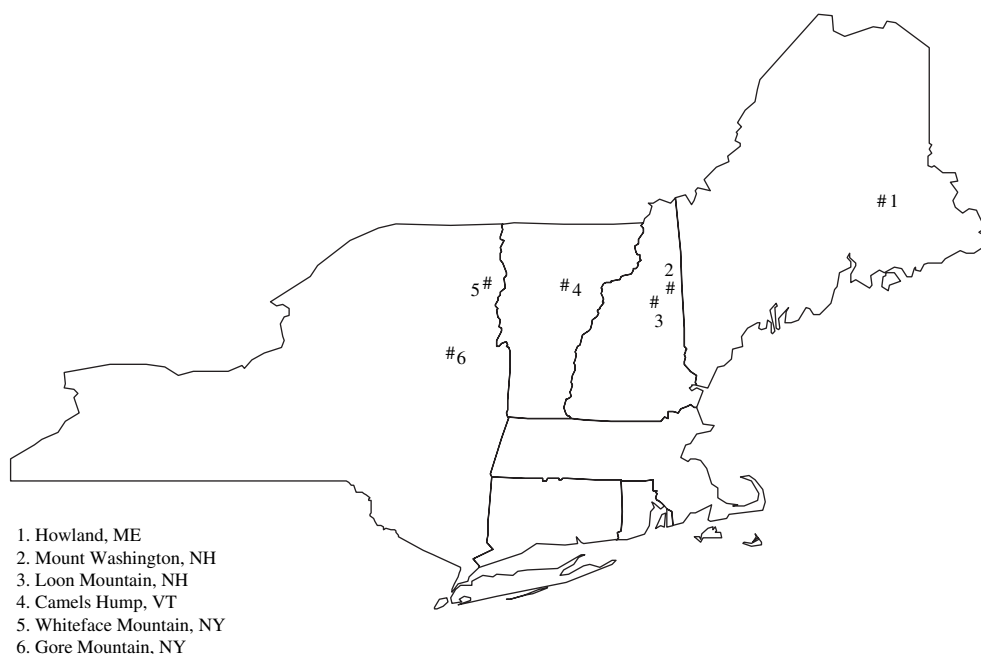

1. Howland, ME
2. Mount Washington, NH
3. Loon Mountain, NH
4. Camels Hump, VT
5. Whiteface Mountain, NY
6. Gore Mountain, NY

Fig. 1. Site locations.

Table 1
Site description

Sites	Longitude (°W)	Latitude (°N)	N deposition (kg^{-1} N ha^{-1} yr)	No. of plots			Elevation (m)	%Basal area of site					
				Conifer 1987/1988	Conifer 1999	Deciduous 1999		YB/PB	S/F	Other	S/F	YB/PB	Other
								Deciduous			Conifer		
Howland, ME	68″40′	45″20′	5.0	5	10	11	80–100	13	34	53	50	0	50
Mount Washington, NH	71″16′	44″17′	8.4	40	14	11	630–910	38	12	50	91	0	9
Loon Mountain, NH	71″37′	44″02′	8.9	20	8	7	690–910	73	23	4	70	12	18
Camels Hump, VT	72″53′	44″20′	9.3	9	8	8	590–1040	72	21	7	81	11	8
Whiteface Mountain, NY	73″54′	44″24′	10.7	20	10	10	840–1190	46	40	14	90	6	4
Gore Mountain, NY	74″02′	43″41′	11.0	5	7	7	880–1010	84	15	1	78	15	7

MGST (°C)		MGSP (cm)	
1987/1988	1999	1987/1988	1999
17.68	19.70	6.33	12.38
15.70	17.59	11.50	16.81
17.47	19.14	11.06	15.41
17.15	18.91	11.06	15.33
17.53	18.75	10.63	14.59
16.70	17.96	12.13	13.66

YB, yellow birch (*Betula alleghaniensis* Britt.); PB, paper birch (*Betula papyrifera* Marsh.); S/F, spruce/fir (*Picea rubens* Sarg.)/(*Abies balsamea* (L.) Mill. Other — American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), mountain ash (*Sorbus americana* Marsh.), red maple (*Acer rubrum* L.), and striped maple (*Acer pensylvanicum* L.). MGST, mean growing season temperature; MGSP, mean growing season precipitation.

deposition were determined from ClimCalc, a model that estimates wet and dry depositions based on latitude, longitude, and elevation (Ollinger et al., 1993). This model was modified slightly with updated dry deposition coefficients from Lovett and Rueth (1999). The temperature and precipitation data were extracted from 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 way of a GIS overlay. Precipitation and temperature data for years 1960 through 1993 were pulled from the historical climate table, and years 1994 through 2000 from the Had2CMSul table. Mean growing season (June–August) averages were then calculated in centimeters for precipitation and in degree Celsius for temperature for each site.

2.2. Foliage analysis

Foliar samples were collected during the summer of 1999 from the six sites as indicated in Table 1 (Fig. 1). Green foliage was collected using a pole pruner (for shorter trees) or by shooting small branches from the canopy with a shotgun. Samples were collected from up to three randomly selected dominant or co-dominant species in each plot. All age class needles were included in conifer foliage samples. Leaves were stored and air dried in paper bags; they were then oven dried at 65 °C for 24 h. Foliar cation percentages were measured from all age classes of needles 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 N HCl and then brought to volume (50 ml) with distilled water in a volumetric flask. The analyses for Ca and Mg were conducted using an Ion Coupled Plasma Analyzer. Standards that spanned the range of foliar cation concentrations were used for quality assurance and quality control. Foliar %N and carbon (C) were measured using a Perkin–Elmer model 240B CHN analyzer. The National Institute of Standards and Technology (NIST) 1572 (citrus leaves) and NBS 1567 (wheat flour) Standards were used in the analysis.

2.3. Forest floor analysis

We collected and analyzed 20 randomly located forest floor (Oe + Oa) samples to a depth of 15 cm from each of the 10 m radius plots sampled in 1987/1988 and 1999 (McNulty et al., 1991). 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 the time of analysis. The five composite samples were sieved using a 6-mm screen. Net nitrification potential and N mineralization were calculated based on a ratio of wet weight to dry weight that was determined by weighing 10.0 g of the sieved sample, then oven drying the sample at 65 °C for 48 h prior to re-weighing. Another 10.0 g replicate was placed in 150 ml of 1 M KCl, mechanically 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 autoanalyzer to analyze the initial and incubated extracts for NH_4 (Technicon Industrial Systems, 1978) and NO_3 (Technicon Industrial Systems, 1977). Twenty-eight day potential net nitrification was calculated as the incubated sample nitrate minus the initial sample nitrate. Twenty-eight day net N mineralization potential was calculated as the incubated sample (NH_4 + NO_3) minus the initial sample (NH_4 + NO_3). Forest floor samples used for N cycling calculations were collected during the summer, June–August.

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

Two forest floor samples from each plot were randomly selected for pH measurements, using a 1:2 ratio (mass forest floor/volume calcium chloride, $CaCl_2$) using a solution (0.01 M).

2.4. Basal area growth analysis

In 1999, we used a Haglof Increment Borer to collect two tree cores at breast height (1.5 m above the forest floor) from three red spruce trees in each conifer plot and from three dominant or co-dominant trees in each deciduous plot. 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 (cm^2) 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). Approximately 75% of the 171 extracted red spruce tree cores were suitable for determining basal area tree growth. The remaining 25% of the cores had broken pieces and/or undistinguishable tree rings. Less than 10% of the deciduous tree cores were suitable for determining basal area tree growth, as the growth rings of birches (*Betula* spp.) and maples (*Acer* spp.) were difficult to differentiate. Therefore, the deciduous growth data are not presented in this manuscript. No tree cores were collected in the 1987/1988 survey.

2.5. Basal area (BA) and stem density measurements

In 1999, we measured the basal area, species types, and tree condition (i.e., living vs. dead based on the presence or absence of leaves) on all trees >2 cm in diameter 1.5 m above the forest floor. In 1987, tree condition was estimated based on visual observations of the proportion of live vs. dead stand basal area.

2.6. Statistical analysis

All data analyses were conducted using SYSTAT Version 9 and all possible significant differences between means were tested with a one-way ANOVA, Tukey adjustment at $\alpha = 0.05$. The Tukey's test was used to determine if the mean of the measured ecosystem parameters varied from year to year within site and from site to site within year. Correlation analyses between foliar and forest floor chemistry and N deposition were determined using Pearson's correlation ($\alpha = 0.05$) from mean plot data instead of site averages to evaluate measurable differences in intra-site variability.

3. Results

3.1. Resampled red spruce plots

3.1.1. Forest floor

Forest floor %N on the Howland site showed a significant decrease from 1987 to 1999 (Table 2). Differences in forest floor %C and C:N ratio over time at most sites were also small, with only the Howland site having a significantly lower %C and the Camels Hump site having a significantly higher C:N from 1987 to 1999. Net N mineralization potential increased over time significantly on Mount Washington and Gore (Table 2). Net nitrification potential and nitrification/mineralization decreased significantly over time at Whiteface. Forest floor pH did not change significantly over time (Table 2).

Forest floor %N was not significantly different among sites in 1987 with %N ranging from 1.22 to 1.85 (Table 2). However, measurements from 1999 indicated that forest floor %N at Howland, the site receiving the lowest N inputs, was significantly lower than the other sites (Table 2). Forest floor %C was not significantly different among sites in either sampling period, but the C:N ratio at the Howland site was significantly higher than the C:N ratio at all other sites in both sampling periods (Table 2). The overall average rate of net nitrification potential was significantly ($r = 0.59$, $p = 0.040$, $n = 12$) lower in 1999 than in 1987, 1.36 vs. 12.77 mg kg^{-1} 28 days^{-1}, respectively.

Table 2
Forest floor chemistry in spruce forests from two sampling periods

Sites	Year	n	N (%)	C (%)	C:N	pH	Nitri (mg kg^{-1} 28 days^{-1})	Min (mg kg^{-1} 28 days^{-1})	Nitri/min
Howland, ME	1987	5	1.22 (0.05)Aa	51.90 (0.36)Aa	42.79 (1.72)Aa	2.70 (0.03)Aa	0.00 (0.00)ABCa	50.60 (9.51)Aa	0.00 (0.00)ABa
Howland, ME	1999	5	0.90 (0.09)Ab	37.27 (3.60)Ab	42.09 (1.88)Aa	2.87 (0.19)Aa	0.00 (0.17)Aa	39.01 (7.66)Aa	0.00 (0.00)Aa
Mount Washington, NH	1987	6	1.52 (0.05)Aa	40.23 (1.79)Aa	27.32 (1.57)Ba	2.66 (0.05)Aa	3.16 (1.24)Ca	152.41 (17.91)ABa	0.04 (0.02)Aa
Mount Washington, NH	1999	8	1.41 (0.11)Ba	38.83 (2.69)Aa	27.70 (1.22)Ba	2.84 (0.08)Aa	1.21 (1.06)Aa	254.57 (40.90)Ab	0.00 (0.00)Aa
Loon Mountain, NH	1987	5	1.56 (0.08)Aa	44.92 (0.61)Aa	30.33 (1.95)Ba	2.78 (0.03)Aa	5.68 (4.20)BCa	212.34 (32.41)Ba	0.02 (0.02)Aa
Loon Mountain, NH	1999	6	1.48 (0.12)Ba	41.31 (1.93)Aa	28.31 (1.22)Ba	2.75 (0.11)Aa	−0.52 (0.22)Aa	218.43 (59.00)Aa	0.00 (0.00)Aa
Camels Hump, VT	1987	4	1.85 (0.11)Aa	35.35 (2.68)Aa	19.00 (0.51)Ba	2.79 (0.07)Aa	27.93 (14.41)ABa	203.79 (22.07)Ba	0.11 (0.05)ABa
Camels Hump, VT	1999	7	1.66 (0.15)Ba	41.48 (3.70)Aa	25.09 (1.32)Bb	2.72 (0.05)Aa	0.22 (0.67)Aa	150.09 (159.22)Aa	0.00 (0.00)Aa
Whiteface Mountain, NY	1987	4	1.75 (0.11)Aa	44.58 (3.10)Aa	25.39 (1.01)Ba	3.01 (0.05)Aa	25.78 (6.01)Aa	117.27 (13.12)Aa	0.21 (0.04)Ba
Whiteface Mountain, NY	1999	9	1.33 (0.12)ABa	34.79 (2.83)Aa	26.46 (1.00)Ba	2.99 (0.06)Aa	0.70 (0.41)Ab	95.34 (43.62)Aa	0.00 (0.00)Ab
Gore Mountain, NY	1987	4	1.85 (0.06)Aa	43.83 (2.35)Aa	24.02 (1.65)Ba	2.79 (0.04)Aa	14.09 (5.52)ABCa	93.91 (8.80)Aa	0.14 (0.04)ABa
Gore Mountain, NY	1999	7	1.74 (0.11)Ba	40.75 (1.70)Ba	25.27 (2.73)Ba	2.89 (0.07)Aa	6.53 (4.50)Aa	232.89 (17.13)Ab	0.02 (0.01)Aa

Means with the same letters are not significantly different (Tukey, $\alpha = 0.05$), year vs. year within site (lowercase) and site vs. site within year (uppercase). The standard error for the mean of each value is in parenthesis. n = Number of plots. Nitri, net potential nitrification; Min, net potential N mineralization; Nitri/min, nitrification/mineralization.

3.1.2. Basal area growth

Mean basal area growth across sites ranged from 4.39 to 6.41 cm^2 yr^{-1} and average tree age ranged from 67 to 95 years (Fig. 2). We also observed the well-documented regional decrease in ring width or basal area growth after 1960 across all sites (Johnson and McLaughlin, 1986; Hornbeck et al., 1986; Shortle et al., 2000). However, in the mid- to late-1980s basal area growth in red spruce increased through about 1993 then started to decrease slightly across all sites. Camels Hump showed the smallest and Gore the greatest variability in basal area growth.

3.1.3. Foliage

Foliar %N on Loon, Whiteface, and Gore increased significantly between 1987 and 1999 while foliar %C increased significantly at all sites. Loon Mountain was the only site with significantly lower foliar %Ca in 1999 when compared to 1987. With the exception of Mount Washington, foliar %Mg and Mg:N were significantly lower in 1999 when compared to 1987.

Among sites in 1987, foliar %N ranged from 0.88 to 1.07% with foliar %N at Howland and Loon being significantly lower than at the other sites but not significantly different from each other. By 1999, foliar %N ranged from 0.84 to 1.18% with foliar %N being significantly lower only on the Howland site. In 1999, there were no longer any significant differences in

foliar %C across sites (Table 3). Foliar %Ca did not change across sites from 1987 to 1999, showing no significant differences between sampling periods. Foliar %Mg and Mg:N were slightly more variable with Loon Mountain being significantly lower than the other sites.

3.2. Deciduous plots

3.2.1. Forest floor

There were no significant differences in forest floor %N and %C between sites (Table 4). However, the low N deposition site (Howland) had a significantly lower C:N ratio compared to the C:N ratio on the other sites (Table 4). There were no significant differences in net nitrification potential and N mineralization across sites due to the high intra-site variability. The nitrification/mineralization ratio was significantly higher on Mount Washington than on the Howland site.

3.2.2. Foliage

Yellow and paper birch species were the only species that were present across all sites, thus our data analyses focus primarily on these two deciduous species. Yellow and paper birch foliar %N across the gradient were similar to the pattern seen between the 1999 red spruce foliar %N and N deposition; foliar %N on Howland was significantly lower when compared to the other sites (Table 5). Paper birch foliar %Ca and Mg and
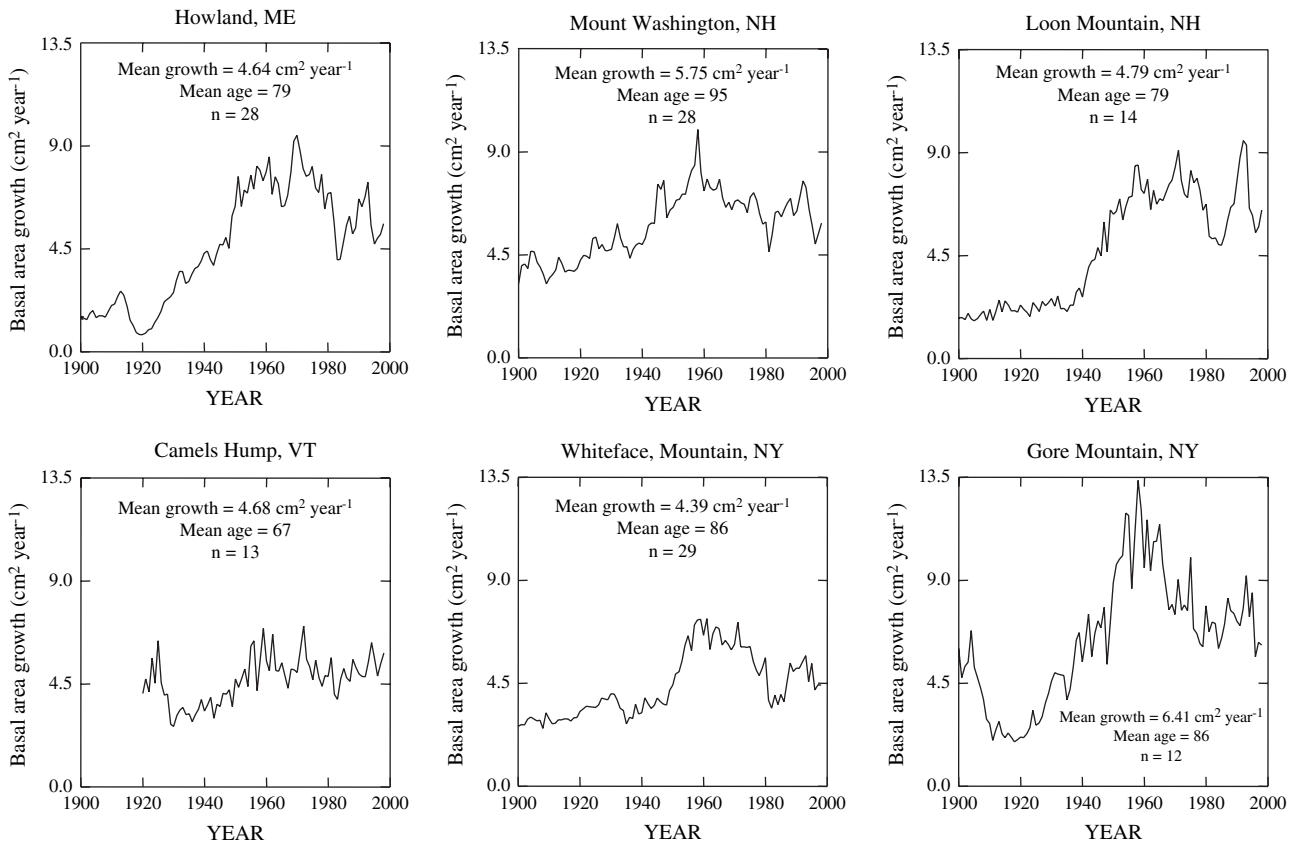

Fig. 2. Red spruce basal area growth across six sites in the Northeastern US in 1999. Basal area growth at all sites showed a decrease during the period from early 1960s to early 1980s, and increase during the period early from 1980s to early 1990s, and a decrease from the early/mid-1990s to 1998.

Table 3
Foliar chemistry in spruce forests from two sampling periods

Sites	Year	n	N (%)	C (%)	Ca (%)	Mg (%)	C:N	Mg:N
Howland, ME	1987	5	0.88 (0.02)Aa	36.0 (0.53)Aa	–	–	40.94 (0.79)Aab	–
Howland, ME	1999	5	0.84 (0.02)Aa	49.0 (0.12)Ab	–	–	58.41 (1.13)Ab	–
Mount Washington, NH	1987	10	1.06 (0.03)Ba	38.8 (0.24)BCa	0.36 (0.03)Aa	0.10 (0.01)Aa	36.84 (0.84)Aa	0.10 (0.03)Aa
Mount Washington, NH	1999	10	1.14 (0.05)Ba	49.1 (0.14)Ab	0.40 (0.02)Aa	0.09 (0.01)Aa	43.47 (1.41)Bb	0.08 (0.02)Aa
Loon Mountain, NH	1987	8	0.88 (0.03)Aa	39.4 (0.37)Ba	0.32 (0.03)Aa	0.10 (0.01)Aa	45.41 (1.78)Ba	0.11 (0.03)Aa
Loon Mountain, NH	1999	8	1.07 (0.09)Bb	48.8 (0.14)Ab	0.45 (0.04)Ab	0.05 (0.00)Bb	47.39 (3.04)Ba	0.05 (0.01)Bb
Camels Hump, VT	1987	7	1.03 (0.04)Ba	38.3 (0.59)BCa	0.37 (0.05)Aa	0.12 (0.01)Aa	37.45 (1.54)Aa	0.12 (0.03)Aa
Camels Hump, VT	1999	7	1.13 (0.04)Ba	49.0 (0.08)Ab	0.39 (0.01)Aa	0.08 (0.01)Ab	43.67 (1.38)Bb	0.08 (0.02)Ab
Whiteface Mountain, NY	1987	7	1.06 (0.03)Ba	37.3 (0.66)ACa	0.37 (0.04)Aa	0.11 (0.01)Aa	35.37 (1.00)Aa	0.10 (0.03)Aa
Whiteface Mountain, NY	1999	7	1.21 (0.03)Bb	49.2 (0.13)Ab	0.39 (0.04)Aa	0.08 (0.00)Ab	40.90 (1.08)Bb	0.07 (0.01)Ab
Gore Mountain, NY	1987	5	1.07 (0.04)Ba	35.1 (0.90)Aa	–	–	32.95 (0.73)Ca	–
Gore Mountain, NY	1999	5	1.18 (0.01)Bb	49.0 (0.16)Ab	–	–	41.84 (0.53)Bb	–

No data. Means with the same letters are not significantly different (Tukey, $\alpha = 0.05$), year vs. year within site (lowercase) and site vs. site within year (uppercase). The standard error for the mean of each value is in parenthesis. n = Number of species.

Mg:N on Howland were significantly lower than all other sites. Yellow birch foliar %Ca was not significantly different across the gradient while foliar %Mg and Mg:N varied across the gradient.

3.3. Deciduous vs. conifer

Across forest types, patterns between forest floor and foliar chemistry were similar in many respects, with foliar %N in both conifer and deciduous species increasing significantly with N deposition (Fig. 3a). A general linear regression model analysis also revealed that forest type (i.e., red spruce dominated forests compared to yellow and paper birch dominated forests) has an effect on forest floor chemistry and N cycling (Table 6).

Individual tree species in our mixed deciduous forests responded slightly differently to N deposition, with yellow birch foliar %N indicating a stronger correlation to N deposition and forest floor C:N than paper birch (Fig. 3a and c). Foliar %N in conifer and paper birch was significantly related to forest floor %N, with similar r values (Fig. 3d).

The relationship between forest floor C:N and net nitrification potential showed similar patterns in deciduous and conifer forests, with the onset of nitrification occurring in both forest types when forest floor C:N reached approximately 20–25 (Fig. 4).

4. Discussion

4.1. Resampled red spruce plots

4.1.1. Forest floor

McNulty et al. (1991) found that in 1987/1988 foliar and forest floor chemistry and N cycling were correlated with N deposition across the northeastern US. Results from the 1999 remeasurement indicated that some of the relationships have not changed significantly across sites since then (e.g., N deposition vs. pH, forest floor C:N and %C and foliar Ca). Even though regional N deposition inputs have not changed significantly from 1987/1988 to 1999, forest floor %N and net nitrification potential have decreased (Table 2) and the relationship between forest floor %N and net nitrification potential has become weaker over time (Fig. 5).

These changes from 1987/1988 to 1999 do not align with the progression of a forest toward nitrogen saturation conditions. We do not know the underlying processes governing these regional changes even though gradient and controlled experimental studies have shown relationships between N deposition inputs and forest response variables (McNulty et al., 1991; Lovett and Rueth, 1999; Magill et al., 2004). We are proposing two plausible explanations that might have limited N cycling across the regional gradient. First, the percent of dead red spruce trees has increased over time across sites

Table 4
Forest floor chemistry in deciduous forests from 1999 sampling period

Sites	n	N (%)	C (%)	C:N	Net potential N mineralization (mg kg^{-1} 28 days^{-1})	Net potential nitrification (mg kg^{-1} 28 days^{-1})	Nitrification/ mineralization
Howland, ME	9	1.15 (0.12)a	38.44 (1.69)a	35.24 (2.22)a	101.10 (28.18)a	−0.27 (0.19)a	−0.01 (0.01)a
Mount Washington, NH	10	1.49 (0.09)a	32.75 (2.28)a	22.35 (1.14)b	277.93 (31.80)a	21.05 (11.70)a	0.10 (0.04)b
Loon Mountain, NH	7	1.31 (0.09)a	36.09 (2.62)a	27.48 (0.66)b	210.41 (30.92)a	2.53 (1.80)a	0.005 (0.01)ab
Camels Hump, VT	7	1.37 (0.12)a	30.28 (3.08)a	22.25 (0.70)b	251.78 (150.98)a	1.56 (0.86)a	0.00 (0.00)ab
Whiteface Mountain, NY	9	1.26 (0.10)a	29.99 (3.18)a	23.62 (0.87)b	−60.94 (90.27)b	3.24 (1.05)a	0.02 (0.01)ab
Gore Mountain, NY	7	1.46 (0.13)a	30.89 (4.14)a	20.74 (1.23)b	182.45 (113.02)a	7.27 (3.06)a	0.05 (0.02)ab

Means with the same letters are not significantly different (Tukey, $\alpha = 0.05$). The standard error for the mean of each value is in parenthesis. n = Number of plots.

Table 5
Paper and yellow birch foliar chemistry across the N deposition gradient in 1999

Sites	n	N (%)	C (%)	Ca (%)	Mg (%)	Mg:N
Paper birch						
Howland, ME	5	1.68 (0.24)a	46.32 (0.56)a	0.78 (0.23)a	0.24 (0.09)a	0.14 (0.03)a
Mount Washington, NH	24	2.71 (0.10)b	46.53 (0.36)a	0.31 (0.02)b	0.13 (0.01)b	0.05 (0.002)b
Loon Mountain, NH	23	2.50 (0.09)b	47.20 (0.19)ab	0.38 (0.02)b	0.10 (0.004)b	0.04 (0.001)b
Camels Hump, VT	23	2.44 (0.07)b	47.08 (0.18)ab	0.40 (0.02)b	0.14 (0.01)b	0.06 (0.003)b
Whiteface Mountain, NY	28	2.57 (0.07)b	47.72 (0.13)b	0.39 (0.03)b	0.12 (0.01)b	0.05 (0.003)b
Gore Mountain, NY	18	2.43 (0.06)b	46.90 (0.18)ab	0.39 (0.02)b	0.12 (0.01)b	0.05 (0.003)b
Yellow birch						
Howland, ME	1	1.46 (0.00)a	44.37 (0.00)a	0.85 (0.00)a	0.25 (0.00)ab	0.17 (0.00)ac
Mount Washington, NH	4	2.86 (0.10)b	45.99 (0.46)b	0.88 (0.16)a	0.29 (0.02)a	0.10 (0.010)cd
Loon Mountain, NH	20	2.63 (0.14)b	46.38 (0.21)b	0.58 (0.04)a	0.14 (0.01)b	0.05 (0.004)b
Camels Hump, VT	2	2.39 (0.02)b	46.13 (0.68)b	0.85 (0.21)a	0.28 (0.08)ab	0.12 (0.034)bcd
Whiteface Mountain, NY	2	3.07 (0.00)b	46.28 (0.00)b	0.69 (0.00)a	0.19 (0.00)a	0.06 (0.00)b
Gore Mountain, NY	8	2.91 (0.09)b	46.90 (0.35)b	0.69 (0.12)a	0.25 (0.05)a	0.09 (0.015)bd

Means with the same letters are not significantly different (Tukey, $\alpha = 0.05$). The standard error for the mean of each value is in parenthesis.

(Fig. 6); the lack of significant change in forest floor %C and forest floor C:N ratio (Table 2) may suggest that woody material was not incorporated into the forest floor during this time period. One possible explanation is that the addition of the N-poor detritus from dying tree roots and stems is immobilizing the N deposition input across sites, consequently reducing the impacts on forest floor N cycling. McNulty et al. (2005) postulated a similar hypothesis for the small increase in forest floor C concentration and decrease in forest floor C:N observed in a long-term N fertilization experiment. However, Currie et al. (2002) found that the increase in N immobilization in fine woody material in N addition hardwood and softwood plots (5 g N m^{-2} yr^{-1}) over a 10-year period to be minimal.
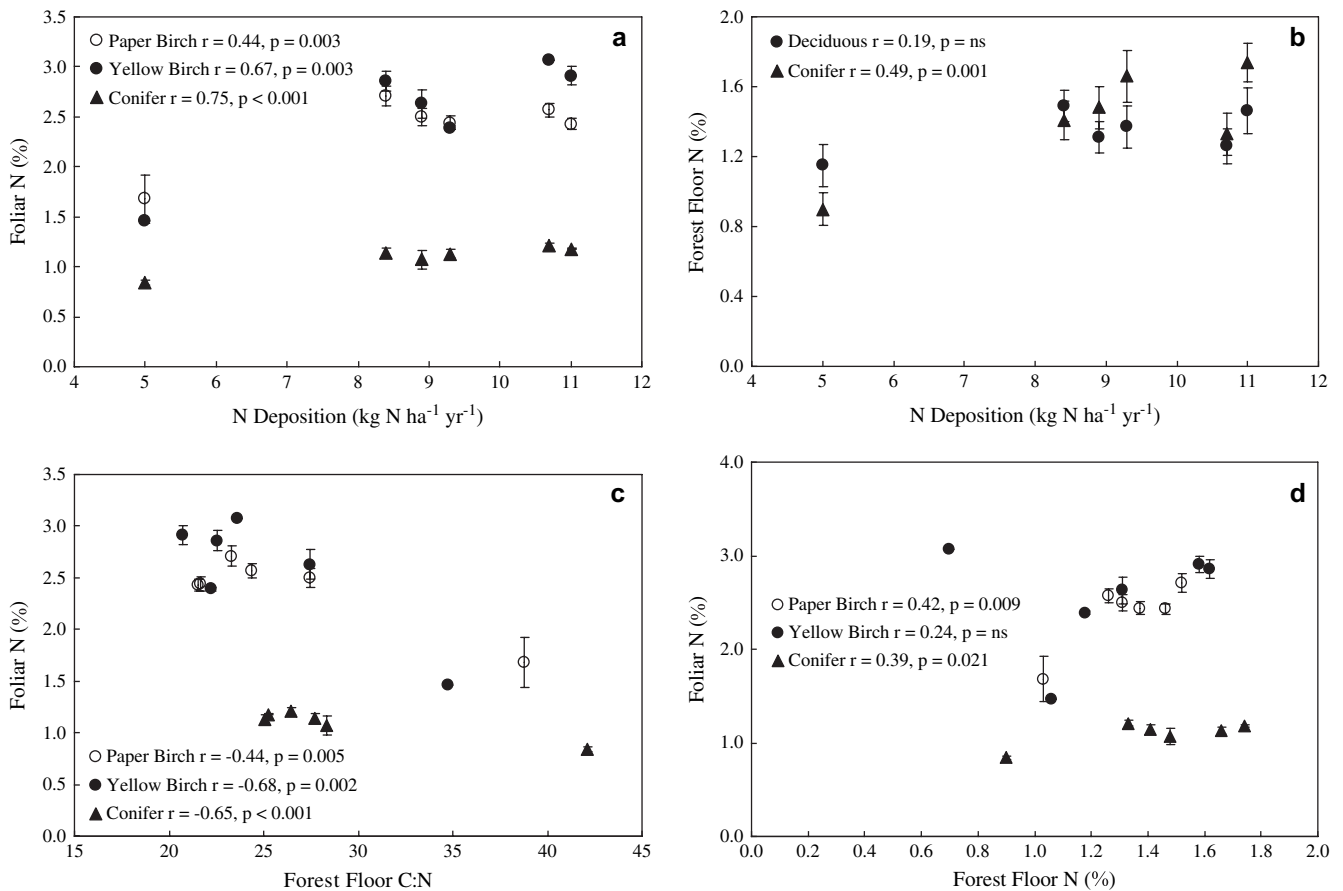

Fig. 3. Relationship between (a) N deposition and foliar %N, (b) N deposition and forest floor %N, (c) forest floor C:N and foliar %N, and (d) forest floor %N and foliar %N.

Table 6
General linear regression model analysis comparing several response variables from 1999 to the following independent variables: MGST, MGSP, N deposition, forest type and their interaction

Response variables	N deposition	Forest type	N deposition × forest type
Forest floor %N	78.76 (0.000)	9.03 (0.003)	27.44 (0.000)
Forest floor C:N	452.29 (0.000)	18.95 (0.000)	13.16 (0.000)
Net N mineralization potential	6.32 (0.012)	0.06 (NS)	2.52 (NS)
Net nitrification potential	6.86 (0.009)	11.67 (0.001)	1.71 (NS)
Nitrification/ mineralization	11.47 (0.001)	18.21 (0.000)	5.33 (0.022)
	MGST	MGSP	MGST × MGSP
Net nitrification potential	2.13 (NS)	0.21 (NS)	22.77 (0.04)

F values are shown with *p* values in parenthesis. NS, not significant at $p < 0.05$. Forest type is defined as conifer or deciduous. A plot was labeled as conifer or deciduous forest based on which species occupied 70% of the plot area. MGST, mean growing season air temperature; MGSP, mean growing season precipitation.

A second plausible explanation for the decrease in regional net nitrification potential in 1999 is climatic. Net nitrification potential from our 1999 measurement was significantly related to the interaction terms of mean growing season air temperature and precipitation (Table 6). Although in-lab incubation (i.e., net nitrification potential) does remove the direct effects on climate on N cycling (Lovett and Rueth, 1999), increases in N input and climate have been shown to affect availability of labile C and consequently nitrification (Wallenstein et al., 2006; Burke, 1989). It is possible that the quality of labile C of forest floor samples we collected in 1999 has been reduced when compared to the 1987/1999 survey, thus limiting net nitrification potential. Nitrification is the primary process that mobilizes N from forest ecosystems that are in late stage N saturation. This mobilized N is then leached from forest into lakes and streams (i.e., nitrate loss). Goodale et al. (2003) suggested that the temporal trend of nitrate loss across New Hampshire streams could be explained in part by interannual climate variation. They also noted that there is uncertainty as to which climate factor is driving the nitrate loss. More
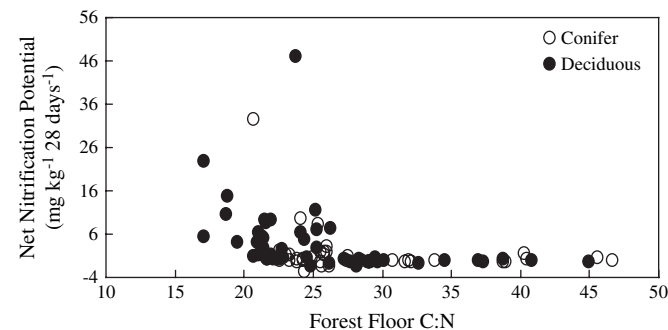

Fig. 4. Forest floor C:N and net nitrification potential in conifer and deciduous forests in 1999.
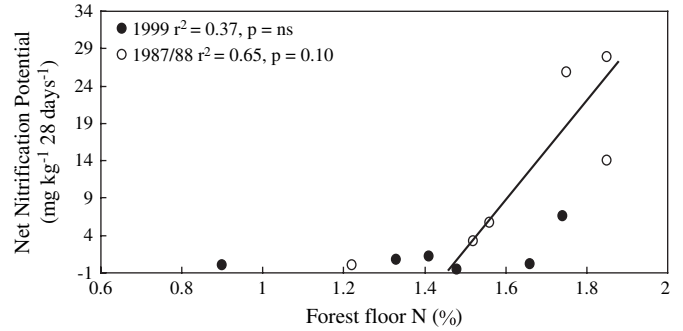

Fig. 5. Relationship between forest floor %N and net nitrification potential in red spruce forests. As explained in McNulty et al. (1991), the regression line for the 1987/1988 data suggests a critical threshold (∼ forest floor N 1.5%) above which net nitrification potential increases linearly. By the 1999 sampling, the threshold was less pronounced.

research is needed to accurately assess to what extent regional climate and N deposition are affecting N cycling and nitrate loss across the northeast.

4.1.2. Red spruce basal area growth

Regional climate and N deposition data have been linked to ring width or basal area tree growth. The significant red spruce growth decline after 1960 in the mountains of New York and western New England as reported by Johnson et al. (1988) was associated with temperature variables. Johnson and McLaughlin (1986) also reported that stand conditions and environmental factors stressed red spruce and a subsequent growth decline followed during this same period. Our data support the finding that there was a significant decrease in red spruce basal area growth after 1960, regardless of mean tree age (Fig. 2). But by the mid- to late-1980s, red spruce basal area growth
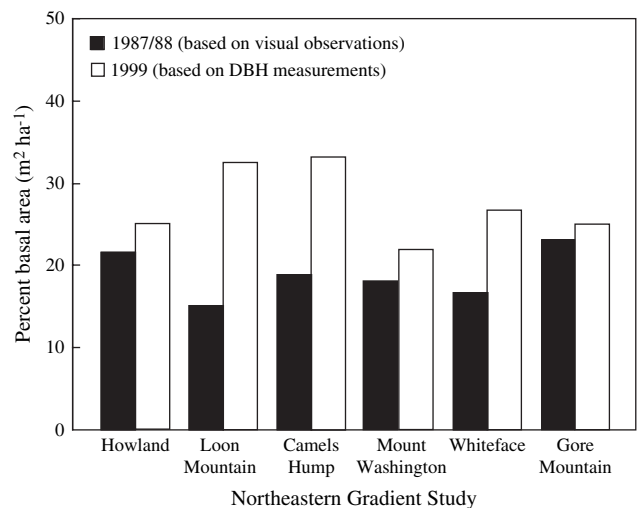

Fig. 6. Percent basal area (m² ha⁻¹) occupied by dead red spruce trees across the northeastern US. In 1999, we measured the basal area, species types, and tree condition (i.e., living vs. dead based on the presence or absence of leaves) on all trees > 2 cm in diameter 1.5 m above the forest floor. In 1987, tree condition was determined based on visual observations of the proportion of live vs. dead stand basal area.

rates across the region started increasing and continued to increase through the early 1990s. Then, interestingly, we observed a regional decrease in red spruce basal area tree growth from about 1993 to 1998. Mean growing season temperature and red spruce basal area growth data from 1960 to 1998 were inversely correlated (Fig. 7), as mean annual air temperature decreased across all sites basal area growth increased. Between 1960 and 1999, the warmest mean growing season temperature (June–August) on record across our sites was in 1999, averaging 18.7 °C across sites. The next warmest year at each site, except Howland, was 1996, averaging 18.3 °C. Increased temperature, with the potential for increased red spruce evapotranspiration rates can trigger tree stress (Mitchell et al., 1990; Rosenberg et al., 1990) and could be one reason that we observed regional decreases in basal area tree growth during the 1960s to early 1980s and early 1990s to late-1990s.

4.1.3. Foliage

Although we observed a decrease in forest floor %N and net nitrification potential, foliar %N increased over time. As noted earlier, in the late-1990s climatic conditions did not favor red spruce growth, suggesting that the tree species might have been stressed during our 1999 sampling. Our companion paper (Pardo et al., 2007) in this special issue presents possible explanations for the contrasting patterns in foliar %N and net nitrification potential.

The decrease in foliar %Mg and Mg:N we observed on Loon, Camels Hump, and Whiteface is consistent with the influence of chronic N deposition on forested ecosystems and suggests that chronic N deposition may be continuing to influence red spruce foliar chemistry within the northeastern region. Elvir et al. (2005) found that a decrease in the availability of base cations in the soil made Ca and Mg less available for plant uptake; consequently, the American beech and red spruce foliar Ca and Mg concentrations from the treated watershed (25.2 kg N ha^{-1} yr^{-1}) in their study were lower than the reference watershed in 2002 and 2003. A controlled experimental study found that red spruce foliar Ca and Mg decreased as a result of both N fertilizer (15 and 31 kg N ha^{-1} yr^{-1}) and anthropogenic N deposition (5 kg N ha^{-1} yr^{-1}) (McNulty et al., 2005). Decreases in red spruce foliar Ca can lead to reduced

cold tolerance and increased freezing injury (DeHayes et al., 1999; Schaberg et al., 2002).

4.1.4. N deposition gradient vs. N fertilization experiment

Inherent soil, climate, and vegetation variability among plots can make data from gradient studies difficult to interpret. A series of small-scale N fertilization plots were established on Mount Ascutney, Vermont in 1988 (McNulty et al., 2005) which minimize the effect of this inter-site variability. Forest floor %N increased from 1988 to 2000 on Mount Ascutney (Fig. 8b). In contrast, across our gradient study forest floor %N decreased from 1987 to 1999 (Fig. 8a). The relationship between N deposition and foliar %N from our gradient study was consistent with the same relationship on the Mount Ascutney N fertilization experiment (Fig. 8c and d). In each study, slope steepness between N deposition and foliar %N increased through time, suggesting that over time foliar %N is better reflecting N deposition. Results from Mount Ascutney during the past 18 years are consistent with the patterns of N saturation conditions as described by Aber et al. (1989). Given that the patterns of some of our response variables align with the patterns of response variables from the long-term N fertilization study on Mount Ascutney, we infer that over time, regional pattern of various stages of N saturation could develop across northeastern US red spruce forests. Pardo et al. (2007) also noted other relationships between our gradient study and Mount Ascutney that suggest an influence of N deposition on these red spruce forests across the region.

4.2. Deciduous vs. conifer

Conifer and deciduous forest floor and foliar chemical/physical compositions are inherently different, which may cause each forest type to respond differently to equal doses of N deposition over time. Southern Forest Resource Assessment (2002) reported that high elevation red spruce forests were the only forests considered sensitive to N deposition in that region. More recently, regional scale studies have shown links between N deposition and forest response variables in deciduous forests in the eastern US (Lovett and Rueth, 1999; Boggs et al., 2005). We also found links between N deposition and forest floor and foliar %N in conifer and deciduous forests (Fig. 3a and b). This suggests that both conifer and deciduous forests are behaving similarly to N deposition. However, because of the high buffering capacity of deciduous forests to N deposition, we believe that the point where N deposition becomes problematic differs among forest type.

A general linear model analysis that examined N deposition, forest type and their interaction on forest response variables indicated that N deposition and forest type do have an impact on forest response variables (Table 6). Several studies have also shown that tree species and forest type influence N cycling (Finzi et al., 1998; Ollinger et al., 2002; Lovett et al., 2004). Lovett et al. (2004) also reported that pure stands of sugar maple had the lowest soil C:N ratios and the highest nitrification rates when compared to pure stands of American beech (*Fagus grandifolia* Ehrh.), yellow birch, eastern hemlock
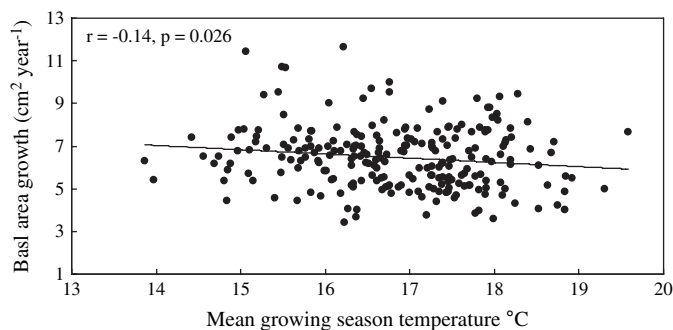
Fig. 7. Relationship between basal area growth and mean annual air temperature (MAT) from 1960 to 1998 across all sites.
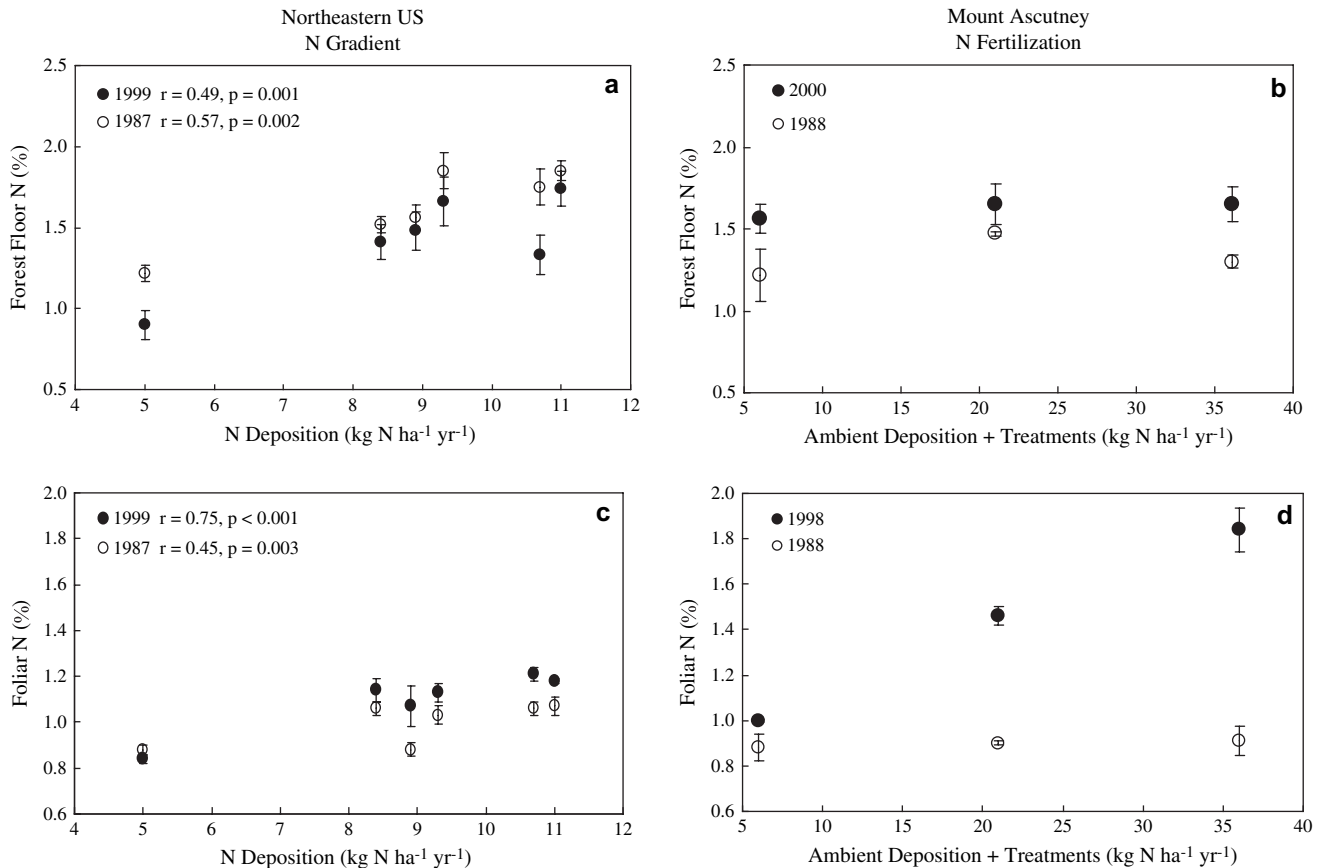
Fig. 8. Comparison between our northeastern US N deposition gradient study and Mount Ascutney N fertilization (McNulty et al., 2005) in high elevation red spruce forests.

(*Tsuga canadensis* L.), and red oak (*Quercus rubra* L.). Mount Washington was the only site in our study where sugar maple was a co-dominant species. This might account for the high net N mineralization potential and nitrification rates we observed on that site (Table 4).

The difference in yellow and paper birch foliar %N pattern across the N deposition gradient (Fig. 3a) and forest floor C:N (Fig. 3c) could be due in part to the physiological differences between these two species. Paper birch is considered shade intolerant whereas yellow birch is classed as intermediate in shade tolerance and competitive ability (Gilbert, 1965). Walters et al. (1993) found that N uptake rates per gram of root mass were highest for yellow birch when compared to paper birch under high light exposure; tree uptake of available N varied by species.

5. Conclusions

Data from the 1999 remeasurement of the red spruce forests suggest that N deposition, to some extent, is continuing to influence red spruce across the northeastern US as illustrated by a significant correlation between N deposition and red spruce foliar %N. Our data also suggest that the decrease in forest floor %N and net nitrification potential across sites from 1987 to 1999 may be due to factors other than N deposition,

such as climatic factors and N immobilization in fine woody material (<5 cm diameter). Additional research between climatic factors and N cycling are needed to determine what underlying mechanisms are controlling the contrasting patterns in foliar %N and forest floor %N and net nitrification potential.

Negative impacts of N deposition have typically been associated with high elevation red spruce forests because of their inherent low buffering capacity and low pH in the forest floor and their low biological N demand, leading to nutrient imbalance and increased risk of forest mortality. In this study, we examined whether these negative impacts were limited to high elevation red spruce forests. Results indicated that forest floor and foliar chemical characteristics in conifer and deciduous forests responded similarly. However, the point at which harmful ecological effect will occur as a result of chronic N deposition inputs differs between forest types.

Acknowledgments

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