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Spatial changes in forest floor and foliar chemistry of spruce-fir forests across New England

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Abstract. In the U.S., high elevation spruce-fir forests receive greater amounts of nitrogen deposition relative to low elevation areas. At high elevations the cycling of nitrogen is naturally low due to slower decomposition and low biological N demand. The combination of these factors make spruce-fir ecosystems potentially responsive to changes in N inputs.

Excess nitrogen deposition across the northeastern United States and Europe has provided an opportunity to observe ecosystem response to changing N inputs. Effects on foliar and forest floor chemistry were examined in a field study of 161 spruce-fir sites across a longitudinal (west-to-east) N deposition gradient. Both foliar elemental concentrations and forest floor elemental concentrations and rates of potential N mineralization were correlated with position along this gradient.

Nitrogen deposition was positively correlated with potential forest floor nitrification and mineralization, negatively correlated with forest floor C:N and Mg concentrations and with spruce foliar lignin, lignin:N and Mg:N ratios. Foliar lignin:N and forest floor C:N were positively correlated and both were negatively correlated with nitrification and mineralization. Correlations found between forest floor and foliar N and Mg concentrations support the theory of nutrient imbalance as a potential cause of forest decline.

Introduction

Across northern New England, N deposition increases from east to west (Munger & Eisenreich 1982), and with elevation. In the U.S., high elevation spruce-fir forests may receive over 20 kg N $ha^{-1}.yr^{-1}$ compared with 3—6 kg N $ha^{-1}.yr^{-1}$ at low elevations in the same area (Anonymous 1988; Lovett & Kinsman 1990). There is a limit to the amount of added N that can be accumulated and utilized in these ecosystems (Aber et al. 1989; Agren & Bosatta 1988). As N inputs increase, the cycling of N within the system could be altered. High rates of N deposition increased foliar N concentrations and decreased foliar Mg and Ca concentrations (Friedland et al. 1988; Czapowskyj et al. 1980), possibly resulting in foliar imbalances (Friedland et al. 1984; Nihlgard 1985; Schulze et al. 1989), or a loss of forest hardiness (Friedland et al. 1984; Hadley et al. 1990). Foliar lignin concentrations may also decrease (Waring et al. 1986). Secondary effects of these alterations may include higher rates of litter decomposition (Meentemeyer 1978; Melillo et al. 1982), lower forest floor C:N ratios, increasing rates of nitrification (McNulty et al. 1990), and nitrate leaching to streams.

The purpose of this paper is to present data on regional trends in N deposition, forest floor chemistry and foliar chemistry in spruce-fir forests across northern New England. Regional patterns in N deposition in spruce-fir forests provide a context in which to interpret the possible effects of regional differences in N dynamics.

Materials and methods

Field methods

Study sites

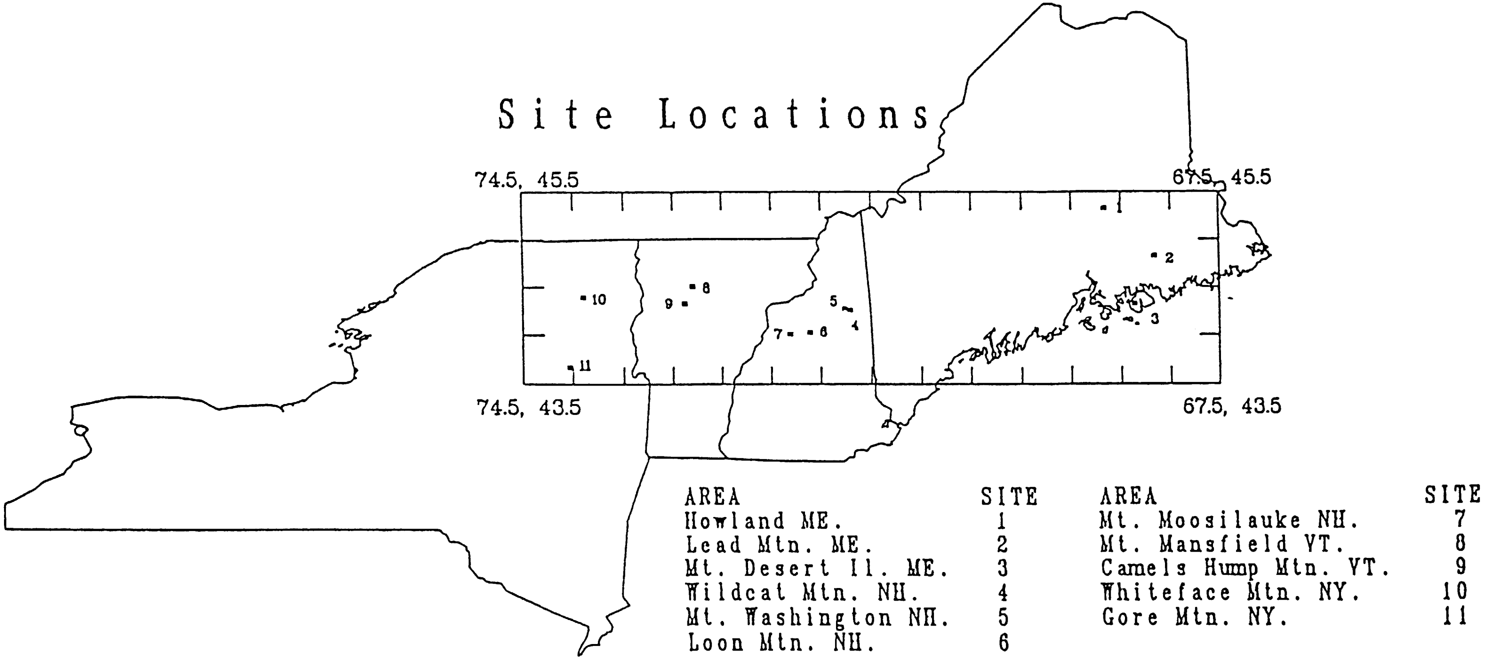
Between mid-June and mid-August in 1987 and 1988, 161 15 × 15 m spruce-fir sites were sampled from eleven areas within the northeastern United States (Fig. 1). A variable number of sites were examined in each study area (Table 1), depending on the size of the area and the occurrence of spruce-fir forest.

The eleven areas are positioned along a regional N deposition gradient.

Table 1. List of eleven areas used in this study.

Location	Area No.	Longitude	Latitude	N. dep.[1] (kg $ha^{-1}yr^{-1}$)	Elev. range (m)	No. of sites
Howland ME	1	68°40′	45°20′	2.9	80—100	5
Lead Mtn. ME	2	68°10′	44°50′	3.4	90—240	7
Acadia ME	3	68°22′	44°20′	3.9	10—60	8
Wildcat Mtn. NH	4	71°13′	44°16′	4.0	930—1210	20
Mt. Washington NH	5	71°16′	44°17′	4.1	630—1460	40
Loon Mtn. NH	6	71°37′	44°02′	4.5	690—910	20
Mt. Moosilauke VT	7	71°49′	44°01′	5.1	810—1400	11
Mt. Mansfield VT	8	72°48′	44°31′	5.7	900—1210	4
Camels Hump VT	9	72°53′	44°20′	5.6	590—1040	9
Whiteface Mtn. NY	10	73°54′	44°24′	5.2	840—1190	20
Gore Mtn. NY	11	74°02′	43°41′	5.1	880—1010	17

[1] Interpolated, low elevation NADP wet N deposition.



AREA	SITE	AREA	SITE
Howland ME.	1	Mt. Moosilauke NH.	7
Lead Mtn. ME.	2	Mt. Mansfield VT.	8
Mt. Desert Il. ME.	3	Camels Hump Mtn. VT.	9
Wildcat Mtn. NH.	4	Whiteface Mtn. NY.	10
Mt. Washington NH.	5	Gore Mtn. NY.	11
Loon Mtn. NH.	6		

Fig. 1. The location of the 11 areas sampled between June and August, 1987—1988.

Estimated low-elevation N deposition was determined for each area by a kriging technique applied to mean annual N deposition data reported by National Atmospheric Deposition Program (NADP) stations located in the northeastern region (McNulty et al. 1990).

Although the exact pattern of change in N deposition with slope, aspect and elevation has not been determined, it is known that high elevation sites receive several times the deposition of adjacent, low elevation sites (Lovett & Kinsman 1990). Therefore, the N deposition rates reported in this paper represent relative differences in N inputs across New England and not absolute annual inputs. The eight western-most areas of this study were all at high elevation, with individual sites covering a broadly overlapping range of elevations. The three Maine areas were all at lower elevations where N deposition would not be increased by topographic effects. Less severe climatic conditions at the Maine areas should also lead to a more favorable C balance and a higher potential for N uptake and cycling. Thus we feel that the eleven areas represent the maximum range in the relative availability of C and N for spruce within the forest type and region.

Individual site selection within an area was not random, but was determined in part by the availability and accessibility of spruce-fir stands. The spruce-fir were often found in pockets, especially on the western half of the sampled gradient. Spruce comprised a minimum of 50% of each sampled stand, and spruce-plus-fir comprised a minimum of 90% of each stands' basal area. Spruce was more commonly found as a component (5—15%) of deciduous (*Betula sp., Acer sp.*) stands across this region but these stands were not sampled.

Forest floor

Collections of forest floor and foliar samples occurred simultaneously at each site between mid-June and mid-August in each year. The eleven areas were sampled in a random order. Twenty replicate 50g samples of the entire O_e plus O_a horizons were taken from the forest floor at each site. Soils were kept in 25 μm thick polyethylene bags and placed on ice for transportation to the laboratory. After all twigs, roots and mineral particles >1 mm were removed, the 20 samples from each site were randomly grouped into five composites.

Foliage collection

A pruning pole was used to collect foliar samples from random crown positions on each site at the same time as forest floor samples. Spruce needles from three trees judged to receive direct sunlight for at least 50% of the daylight hours were collected and composited into a single sample.

All needle age classes were composited to measure overall foliar nutrient status and to provide an average value for correlations with future remote sensing measurements. Since these samples represent all age classes caution should be taken when comparing foliar concentrations from this study, and those studies where foliar concentrations were separated by age class.

Potential net N mineralization, potential net nitrification and forest floor pH were determined for each site, as described in McNulty et al. (1990). Total C and N concentrations for the organic horizons of all 161 sites were determined on a Perkin-Elmer model 240B CHN analyzer at the University of New Hampshire.

Composited forest floor samples from 102 of the 161 sites from across the region were selected for ash-free elemental analysis (Jones 1988) using inductively Coupled Argon Plasma Emission Spectroscopy (Jarrell-Ash 965 Atomcomp) at the University of Georgia's Institute of Ecology. For areas with 20 or fewer sites, all samples were individually analyzed; a subsample of approximately 50% of the sites was used for areas with 21 or more sites. Selected samples represented a proportional subsample of the range of potential nitrification rates for each area.

Foliage representing all needle age classes were placed in paper bags and oven dried at 70 °C for 48 hours. Dried needles were sieved through a #18 mesh to remove detritus, ground through a #10 mesh Wiley Mill and stored in the dark in glass jars. Foliar concentrations of lignin, cellulose and N were measured using Pacific Scientific's model 6250 near-infrared spectrophotometer (Wessman et al. 1988; McLellan et al. in press).

Overstory needles from 139 of the 161 sites across the gradient were selected for elemental analysis of macro/micro nutrients and heavy metals using the dry ash method (Jones 1988) described above.

Results

Depending on the element or process, foliar and forest floor values varied to different extents across New England (Tables 2—4). Estimated low elevation N deposition was correlated with foliar elemental concentrations and forest floor elemental concentrations and processes (Table 5 and 6). N deposition and longitude were highly correlated (Table 5), so longitude could be substituted for N deposition in correlations with foliar and forest floor values. If accurate measures of N deposition were available for each site, we expect that annual N deposition would increase roughly sevenfold for high elevation areas (Lovett & Kinsman 1990). This would further

Table 2. Forest floor and red spruce foliar C, N and lignin concentrations for eleven areas.

	Forest floor concentration (%)				Red spruce foliage concentration (%)			
Area	*n*	C	N	C:N	*n*	Lignin	N	Lignin:N
1	5	51.9 (0.4)	1.21 (0.0)	43.1 (1.3)	5	25.3 (0.3)	0.88 (0.02)	28.7 (0.4)
2	5	49.6 (1.4)	1.43 (0.1)	35.1 (1.8)	7	22.6 (0.7)	1.02 (0.02)	22.4 (1.2)
3	4	52.8 (1.7)	1.09 (0.1)	48.7 (1.5)	8	21.8 (0.6)	0.84 (0.02)	26.2 (0.9)
4	5	43.6 (6.5)	1.51 (0.2)	28.4 (2.8)	20	17.1 (0.2)	0.85 (0.02)	20.2 (0.5)
5	6	40.2 (4.6)	1.50 (0.1)	27.7 (4.1)	34	21.5 (0.2)	1.04 (0.01)	20.7 (0.4)
6	5	44.9 (1.2)	1.56 (0.2)	30.2 (3.5)	20	16.7 (0.2)	0.88 (0.02)	19.1 (0.5)
7	5	36.3 (2.7)	1.72 (0.1)	21.1 (0.4)	7	17.7 (0.7)	0.89 (0.06)	20.2 (0.9)
8	4	48.0 (0.3)	2.16 (0.1)	22.3 (1.0)	3	17.6 (0.6)	0.98 (0.07)	18.0 (1.1)
9	4	35.3 (4.0)	1.86 (0.2)	18.9 (0.6)	9	18.3 (0.6)	1.01 (0.04)	18.3 (0.8)
10	4	44.6 (7.0)	1.77 (0.3)	25.2 (2.0)	19	20.6 (0.5)	1.03 (0.03)	20.0 (0.6)
11	4	43.8 (4.9)	1.83 (0.1)	24.3 (3.3)	16	22.5 (0.3)	1.07 (0.02)	21.2 (0.6)
ave.	51	44.5 (1.3)	1.59 (0.1)	29.7 (1.4)	148	20.0 (0.2)	0.97 (0.01)	20.8 (0.3)

Values are means (± SE).

separate N deposition input to the three Maine areas from the eight remaining high elevation areas because orographic affects. The major results presented here would not be altered.

Several of the relationships between N deposition and foliar and forest floor chemistry suggest positive feedbacks between N deposition and the quality of litter and forest floor material. Increased N deposition across the gradient was correlated with regional decreases in lignin:N ratios in foliage and forest floor C:N ratios (Fig. 2) and with increased forest floor %N (Fig. 3). This suggests that the shift in lignin:N ratio within spruce foliage across the gradient, is translated into changes in forest floor %N and C:N ratio through litter fall and decomposition (Fig. 4). Forest floor N concentrations were significantly correlated with nitrification potential (Table 5). The relationship between forest floor N concentration and potential nitrification (Fig. 5) suggests a critical threshold (1.4% N) above which nitrification increases linearly.

Concentrations of Cu, Cd and Pb are similar to those measured by Herrick and Friedland (1990) and Friedland et al. (1986). However, few correlations were found between Cu, Cd, Pb and other elements. An interaction between N deposition and forest floor Ca, Cu, and Mg, and between forest floor and foliar concentrations of Ca and Mg are suggested (Table 6). Foliar concentrations of Pb, Ca and Mg were related to foliar lignin concentrations (Table 6). No relationships between N deposition, soil pH and foliar Al, Al:Ca ratios or P were found.

Table 3. Forest floor and foliar concentrations of Pb, Cu, Al and Cd, for the eleven areas in this study.

		Forest floor concentration (mg kg^{-1})					Red spruce foliage concentration (mg kg^{-1})			
Area	*n*	Pb	Cu	Al	Cd	*n*	Pb	Cu	Al	Cd
1	6	90 (12)	0.75 (0.7)	1310 (40)	0.26 (0.04)	8	0.24 (0.2)	1.99 (0.31)	48 (3)	0.12 (0.02)
2	7	154 (13)	4.52 (0.9)	1360 (70)	0.43 (0.06)	11	1.76 (0.6)	2.46 (0.26)	57 (7)	0.09 (0.02)
3	9	73 (3)	0.58 (0.6)	1100 (30)	0.35 (0.03)	13	0.54 (0.3)	1.45 (0.11)	51 (4)	0.09 (0.02)
4	11	134 (13)	6.19 (1.8)	1180 (80)	0.45 (0.05)	20	1.50 (0.3)	2.64 (0.45)	33 (2)	0.11 (0.02)
5	12	93 (12)	5.04 (3.0)	1140 (90)	0.33 (0.05)	17	3.84 (0.8)	2.22 (0.22)	36 (3)	0.09 (0.01)
6	10	149 (13)	1.18 (1.0)	1010 (60)	0.40 (0.05)	6	2.43 (0.9)	1.64 (0.09)	36 (2)	0.17 (0.03)
7	11	151 (20)	6.49 (1.5)	880 (110)	0.35 (0.07)	7	0.77 (0.2)	2.31 (0.30)	101 (21)	0.06 (0.03)
8	4	230 (18)	11.10 (1.6)	1120 (80)	0.66 (0.19)	4	2.30 (1.1)	2.58 (0.37)	107 (24)	0.06 (0.04)
9	9	207 (26)	8.10 (2.6)	1180 (90)	0.45 (0.09)	12	2.72 (0.5)	2.91 (0.36)	56 (7)	0.07 (0.03)
10	11	74 (14)	1.51 (0.8)	1490 (120)	0.36 (0.11)	22	1.14 (0.3)	2.74 (0.15)	121 (27)	0.02 (0.01)
11	12	105 (13)	1.10 (0.6)	1470 (120)	0.30 (0.06)	19	0.26 (0.1)	2.60 (0.20)	116 (31)	0.15 (0.03)
Average		127 (6)	3.92 (0.6)	1200 (100)	0.38 (0.02)		1.55 (0.2)	2.40 (0.10)	80 (22)	0.09 (0.01)

Values are means (± SE).

Table 4. Forest floor and foliar concentrations of Mg, Ca, K and P for the eleven areas used in this study.

		Forests floor total amounts (mg kg^{-1})					Red spruce foliage total amounts (mg kg^{-1})			
Area	*n*	Mg	Ca	K	P	*n*	Mg	Ca	K	P
1	6	449 (55)	2060 (320)	535 (53)	538 (25)	8	1107 (160)	3750 (500)	4600 (260)	850 (29)
2	7	458 (34)	2010 (250)	307 (31)	581 (33)	11	1122 (180)	3310 (950)	4570 (260)	760 (53)
3	9	719 (32)	2160 (290)	530 (41)	508 (36)	13	1197 (130)	4020 (710)	4260 (210)	790 (59)
4	11	370 (24)	2360 (280)	544 (63)	744 (39)	20	1057 (120)	3380 (560)	3270 (120)	850 (53)
5	12	338 (51)	2210 (420)	434 (40)	642 (88)	17	1092 (140)	3590 (670)	4630 (150)	990 (53)
6	10	205 (17)	1550 (664)	592 (30)	580 (28)	6	596 (110)	3070 (710)	4590 (230)	770 (56)
7	11	237 (24)	1300 (190)	424 (56)	673 (54)	7	801 (190)	2690 (410)	3520 (150)	910 (38)
8	4	272 (30)	1360 (280)	328 (35)	648 (58)	4	943 (170)	2490 (500)	3660 (620)	870 (67)
9	9	253 (35)	1930 (350)	520 (67)	675 (53)	12	970 (180)	3250 (320)	3970 (210)	1010 (62)
10	11	182 (46)	1920 (480)	212 (17)	491 (44)	22	1061 (250)	3730 (870)	4510 (220)	930 (57)
11	12	302 (47)	2300 (370)	353 (20)	647 (44)	19	859 (150)	3070 (710)	4280 (200)	870 (46)
Average		328 (18)	1940 (100)	435 (17)	614 (17)		1012 (220)	3411 (760)	4180 (70)	880 (18)

Values are means (± SE).

Table 5. Significant correlations between estimated low elevation N deposition, foliar and forest floor C and N contents, and rates of mineralization and nitrification.

	R	*P*
annual N deposition v. longitude	0.87	< 0.001
deposition/foliage correlations		
annual N deposition v. spruce foliar lignin:N	−0.79	< 0.01
annual N deposition v. spruce foliar lignin	−0.61	< 0.05
foliage/forest floor state correlations		
spruce foliar lignin:N v. forest floor C:N	0.88	0.000
spruce foliar lignin plus foliar %N v. f.f. C:N	0.90	< 0.001
spruce foliar lignin plus foliar %N v. f.f. %N	0.86	< 0.001
foliage/forest floor process correlation		
spruce foliar lignin:N v. nitrification	−0.61	< 0.05
spruce foliar lignin:N v. mineralization	−0.62	< 0.05
forest floor condition/process correlations		
f.f. C:N v. nitrification:mineralization	−0.67	< 0.05
f.f. %N v. nitrification:mineralization	0.77	< 0.01
f.f. %N v. nitrification	0.92	0.000
deposition/forest floor correlations		
annual N deposition v. forest floor C:N	−0.81	< 0.001
annual N deposition v. forest floor %N	0.88	0.000
annual N deposition v. mineralization	0.66	< 0.05
annual N deposition v. nitrification	0.89	0.000

"Plus" means a multiple linear regression of the two variable, and f.f.= forest floor.

Discussion

Few studies have examined forests floor or foliar chemistry across the range of northeast spruce-fir forests encompassed by this study. Though many researchers have examined foliage and/or forest floor chemistry from a single mountain within the northeastern region (Huntington et al. 1990; Fernandez & Struchtemeyer 1984; Lang et al. 1981), or have focused on metal concentrations in the forest floor alone (Andresen et al. 1980; Friedland et al. 1984, 1986), this study combines large spatial scale, with analysis of both foliage and the forest floor.

The large regional changes in N concentration of forest floor material reported here are relevant to the current discussion of critical N input/output balances and N saturation of forest ecosystems (Agren & Bosatta 1988; Aber et al. 1989; Zottl 1990). A compilation of available literature

Table 6. Significant (0.05 C.I.) correlations between N deposition and forest floor, and foliar Mg, Ca and Al.

Forest floor state correlations	*R*	*P*
forest floor %Mg v. annual N deposition	−0.64	<0.05
f.f. umol Mg:mmol N v. N deposition	−0.57	0.05
forest floor %Mg v. forest floor %N	−0.87	<0.0005
forest floor %Mg v. forest floor C:N	0.77	<0.0005
f.f. %Al v. mineralization potential	−0.60	<0.05
foliage correlations		
foliar umol Mg:mmol N v. annual N deposition	−0.59	<0.05
foliar %Mg v. foliar %lignin	0.63	<0.05
foliar %Mg v. forest floor %Mg	0.67	<0.05
foliar %Ca v. annual N deposition	−0.66	<0.05
foliar %Ca v. foliar %lignin	0.66	<0.05
foliar %Ca v. forest floor %Ca	0.73	0.005
foliar %Cu v. annual N deposition	0.62	<0.05

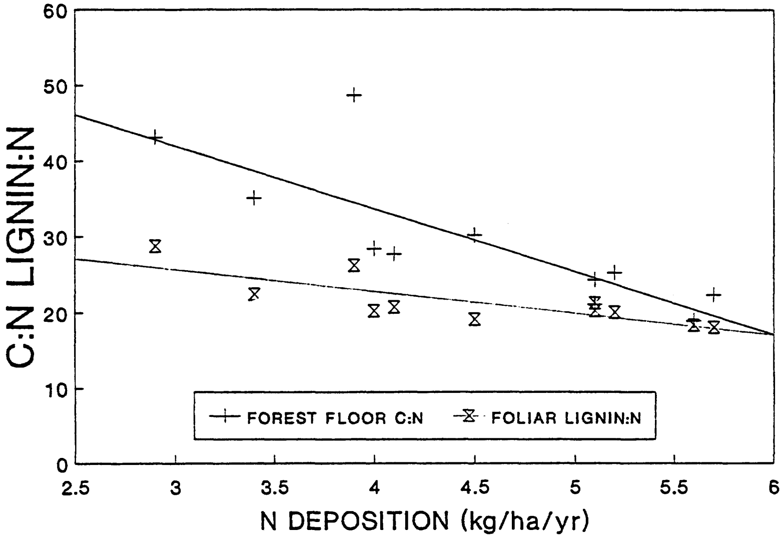


Fig. 2. Red spruce foliar lignin:N in relation to regional trends in low elevation wet N deposition.

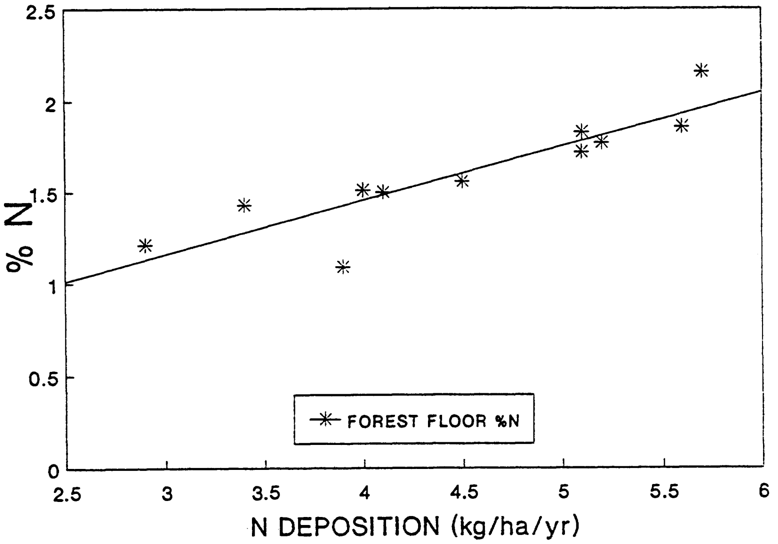


Fig. 3. Forest floor nitrogen concentration in spruce-fir forests in relation to regional trends in low elevation wet N deposition.

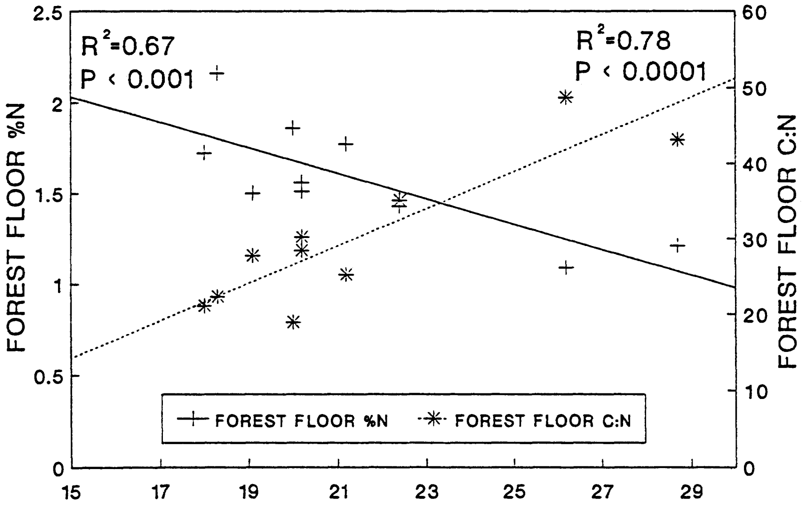


Fig. 4. Forest floor N concentration and C:N ratio in spruce-fir forests in relation to lignin:N ratio of spruce foliage.

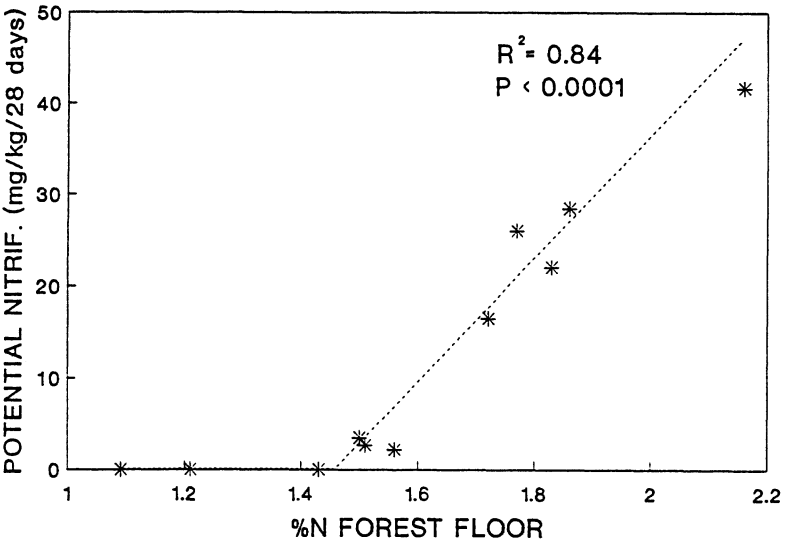
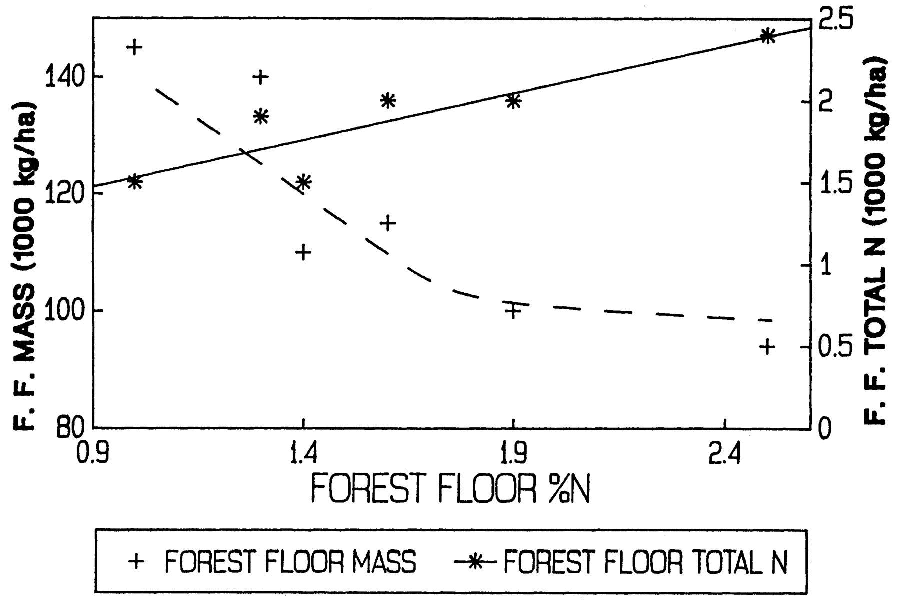


Fig. 5. Potential net nitrification rate (28 day laboratory incubation) for forest floor samples from spruce-fir forests in relation to C:N ratio of these samples.

data suggest that as floor N concentrations increase, forest floor mass decreases (Fig. 6). This may be due in part to increased litter quality (lower lignin, higher N content) resulting in faster and more complete decay at the high end of the N deposition gradient (Meentemeyer 1978; Vitousek & Melillo 1979; Aber & Melillo 1982; Mladenoff 1987). Decreased forest floor mass and increasing forest floor N concentration do not completely offset each other, so there is a net increase in total forest floor N (kg ha^{-1}) with increasing N deposition. Maximum forest floor N storage was found at Mt. Moosilauke (2200 kg N ha^{-1}) which also had the highest N mineralization, nitrification and lowest foliar lignin:N ratio of any examined area. All of these parameters suggest increased N cycling and storage with increased N deposition.

Both foliar and forest floor concentrations of heavy metals were examined across the gradient (Table 3), with few correlations (Table 6). The correlation between forest floor Pb and foliar lignin concentrations (Table 6) may be due to the decreased decomposition rate of foliage with high lignin concentrations, as organic matter which is resistant to decomposition may be providing increased bonding sites for Pb in the forest floor. No spatial pattern in concentrations of Pb, Cu, Al or Cd were found across the gradient and no correlations were found with patterns of mineralization, nitrification or foliar concentrations of nutrients (Tables 2–4). Literature citing increased forest floor heavy metal concentrations



Site	Source
Weymouth Point ME	Federer 1983
Mt. Ascutney VT	McNulty (unpublished)
Mt. Moosilauke NH	Olson & Reiners 1983
Mt. Moosilauke NH	Lang et al. 1981[1]
Camels Hump VT	Freidland et al. 1986[2]
Howland ME	Fernandez (unpublished)

[1] ash-free measurements

[2] N concentration from this paper

Fig 6. Data from the literature relating forest floor mass in spruce-fir forests to forest floor N concentrations.

as a cause for decreased litter decomposition (Strojan 1978), soil enzyme activity (Freedman & Hutchinson 1980), or reduced plant growth (Whitby & Hutchinson 1974), were all close to point sources. In lower concentrations, the affect of heavy metals on ecosystems is less conclusive. Shortle & Smith (1988) and Raynal et al. (1990) have suggested that decreased pH could elevate Al in forest floor solution which could impede red spruce root uptake of Mg and Ca. This study did not measure root nutrient uptake or solubilized Al but no correlation was found between forest floor pH and foliar Mg, N or Ca concentrations (Table 4).

Foliar nutrient concentrations have been used as an indicator of nutrient deficiencies in plants. The time of year that foliage is collected can greatly affect nutrient concentrations. In red spruce, N, P and K concentrations are lowest in midsummer, early spring and in the fall, these periods correspond with the highest concentrations of Ca (Maclean & Robertson 1981). We chose to examine foliar nutrient status during the mid-growing season (Mid-June to Mid-August), when nutrient imbalances would be the most critical to plant growth. Additionally, stand age (Maclean & Robertson 1981), year to year variation (Friedland et al. 1988) and needle age (Cape et al. 1990) may also affect elemental foliar concentrations. It was not possible to sample all sites simultaneously. Although seasonal variability in foliar chemistry may have contributed to the variance in this analysis, it should not have added any significant bias, as all samples were collected in the same season.

Foliar N plus lignin was correlated with mineralization and nitrification (Table 5). Waring et al. (1986) has observed similar relationships between changing ratios of C:N in other forest tree species. In this study a foliar lignin:N ratio of < 22:1 or a forest floor C:N ratio < 31:1 correlated with the onset of forest floor nitrification. As N deposition increases foliar lignin:N and forest floor C:N converge at approximately 18:1 (Fig. 2). The convergence between foliar lignin:N and forest floor C:N ratio, suggests either a decrease in foliar N retranslocation before needle sensence, decreased foliar N leaching, and/or more complete forest floor decomposition, with increasing N deposition. Mineralization potential was correlated with N deposition (Table 5) due to either direct inputs of N onto the forest floor or increased litter quality (decreased lignin:N litter).

Although variable, both forest floor and foliar Mg concentrations decreased with increasing N concentration in the forest floor. Schulze et al. (1989) have suggested that foliar Mg deficiencies are contributing to forest decline in Europe. Swan (1971), cited moderate foliar Mg deficiency beginning at 0.04–0.06% Mg in pot cultured 26 week old spruce seedlings. Foliar Mg concentrations for all age class foliage in this study ranged from 0.06–0.12% but a better indicator of deficiency may be the ratio of elements. Below a molar ratio of 28 (umol Mg:N mmol) in *Picea abies* foliage, nutrient imbalance may occur (Schulze et al. 1989). The red spruce foliage of this study had molar ratios between 39–82. While the differences in species precludes direct comparisons, there is a definite trend toward lower Mg:N ratios with increasing N deposition (Table 6).

Conclusion

Changes in forest floor and foliar chemistry along an N deposition gradient in spruce-fir forests were examined and a number of significant relationships were found. First, there appear to be critical values for the onset of nitrification at 1.4% N (Fig. 5) or a C:N ratio < 31:1 in the forest floor, and a lignin:N ratio of < 22:1 in red spruce foliage. If the occurrence of nitrification is an indicator of N saturation (Aber et al. 1989), then these values may represent important thresholds beyond which significant changes in ecosystem function occur in New England spruce-fir forests.

Second, a relationship exists between N deposition and forest floor N concentration but we cannot determine whether this is an equilibrium condition.

Finally, a correlation was found between the lignin:N ratio of spruce foliage and the forest floor C:N ratio., which in turn can be used to predict other site processes such as N mineralization and nitrification. This suggests that the development of remote sensing systems designed to measure lignin and N concentrations of whole forest canopies (eg. Wessman et al. 1988; Goetz et al. 1985) would be useful in monitoring regional changes in N cycling and storage in spruce-fir forests.

Of the other elements, foliar and forest floor Mg negatively correlated with N content in both the forest floor and foliage. This suggests the possible development of a N:Mg imbalance in red spruce.

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