Effects of chronic nitrogen additions on nitrogen cycling in a high-elevation spruce–fir stand

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A 3-year low-level (15–31 kg $N \cdot ha^{-1} \cdot year^{-1}$) fertilization treatment was conducted in a high-elevation spruce–fir stand, on Mount Ascutney, Vermont. Shortly after fertilization, large concentrations (≤900 ppm) of both NH_4-N and NO_3-N were recovered in ion-exchange resin bags buried at the base of the forest floor. Despite an initial loss of added N, we found significant correlations between the amount of fertilizer applied and measured ecosystem parameters. Bulk deposition for the plots equalled 5.1 kg $N \cdot ha^{-1} \cdot year^{-1}$, of which 50% fell as NO_3-N in snow. No correlations were found between the amount of N applied to a site and throughfall N concentration of the site. Increased Basal Area (BA) growth was recorded using two separate techniques, with the greatest increases in living BA occurring on the 25.6 kg $N \cdot ha^{-1} \cdot year^{-1}$ treatment. As N fertilization increased, foliar %N, net forest floor net N mineralization, dead BA, total (living + dead) BA, first year net N mineralization, and coniferous and deciduous litter %N also increased. On plots receiving high rates of fertilization, net N mineralization rates remained constant or decreased during the third year while low N addition plots experienced increased net N mineralization rates, suggesting a possible C limitation. These results indicate that these slow growing, nutrient conserving ecosystems are responsive to even small increases in N inputs.

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Une expérience de fertilisation à faible dose (15–31 kg $N \cdot ha^{-1} \cdot an^{-1}$) a été conduite sur une période de 3 ans dans un peuplement d'épinette–sapin de haute altitude, au Mont Ascutney dans l'etat du Vermont. Peu de temps après fertilisation, de fortes concentrations (≤900 ppm) de N-NH_4 et N-NO_3 ont été retrouvées dans les sacs de résines échangeuses d'ions enfouis à la base de la couverture morte. En dépit d'une perte initiale de N ajouté, nous avous trouvé des corrélations significatives entre la quantité de N ajouté et certains paramètres de l'écosystème. Les dépositions incidentes ont été de 5,1 kg $N \cdot ha^{-1} \cdot an^{-1}$, dont 50% était sous forme de N-NO_3 dans la neige. Aucune corrélation n'a été trouvée entre la quantité de N ajouté et la concentration de N dans le pluviolessivage. Une augmentation de l'accroissement en surface terrière (ST) a été observée avec deux méthodes différentes de mesure, et les plus grands accroissements en ST vivante ont été observées pour le traitement de 25,6 kg $N \cdot ha^{-1} \cdot an^{-1}$. La concentration foliaire en N, la minéralisation nette de N dans la couverture morte, la ST morte, la ST totale (vivante + morte), la minéralisation nette de N la première année ainsi que les concentrations en N des litières des conifères et des décidues se sont accrues avec l'augmentation du taux de fertilisation. Sur les parcelles recevant les hauts taux de fertilisation, les taux nets de minéralisation de N sont restés constants ou ont diminué durant la troisième année tandis que les parcelles recevant de faibles taux de N ont montré un accroissement du taux de minéralisation nette, suggérant une limitation possible de C. Ces résultats indiquent que ces écosystèmes à croissance faible et conservant bien les éléments répondent à de faibles apports de N.

[Traduit par la rédaction]

Introduction

Cool, highly organic, acidic soils that are nitrogen poor and lignin rich, decompose slowly (Powers 1990; Nadelhoffer et al. 1991; Meentemeyer 1978; Melillo et al. 1982; Flanagan and Van Cleve 1983; Lodhi 1982; Berg 1986). Historically, these factors characterize the forest floor of high-elevation spruce–fir forests in northern New England, which have developed under conditions of low nutrient availability. However, anthropogenic inputs of NH_4-N and NO_3-N are increasing the amount of N deposited annually into these systems.

Across New England (New York – Maine), N deposition is greatest on the western end of the region (Munger and Eisenreich 1983) and at high elevation (Lovett and Kinsman 1990). Friedland et al. (1991) reported 16.4 kg $N \cdot ha^{-1} \cdot year^{-1}$ on Whiteface Mountain, New York at elevations between 970 and 1100 m, compared with low elevation sites on the eastern end of New England which receive 2.5 kg $N \cdot ha^{-1} \cdot year^{-1}$ (National Atmospheric Deposition Program 1988, wet only deposition).

Initially, elevated inputs of N stimulate forest-floor decomposition (Adams and Attiwill 1984) and increase foliar N concentrations (Turner 1977; Weetman and Fournier 1984), which results in increased leaf productivity and forest growth. However, if N deposition continues, total N availability from net N mineralization and N deposition begins to exceed both plant and microbial demand and the ecosystem can then be defined as N saturated (Ågren and Bosatta 1988). Significant changes in soil–plant relationships, and nutrient input–output budgets may occur (Aber et al. 1989; Zoettl 1990). Additional N inputs into the ecosystem could cause a progressive series of responses beginning with a decrease in foliar lignin concentrations (Aber et al. 1989; McNulty et al. 1991), followed by an increase in foliar biomass (Turner 1977; Binkley and Reid 1984), and perhaps the initiation of nitrification (Aber et al. 1989). The final stages of N saturation could include a decrease in foliar biomass (Aber et al. 1989), imbalances in foliar nutrient concentrations (Zoettl 1990; Van Dijk and Roelofs 1988; Schulze et al. 1989), an increase in the fraction

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of N mineralization nitrified (McNulty et al. 1990), and an increase in stand mortality (Aber et al. 1989; Zoettl and Huettl 1986).

The objectives of this study were to induce N saturation in a spruce–fir ecosystem using low levels of N fertilization and to observe how the forest floor, foliar, and litter quality and quantity change in relation to induced N saturation. A series of N fertilization plots were established in the spruce–fir zone of Mount Ascutney, Vermont.

Study sites

During June 1988, ten 15 × 15 m research plots were established at an elevation of 762 m, on Mount Ascutney, Vermont (43°26′N, 72°27′W), where red spruce (*Picea rubens* Sarg.) is found in large patches (>1 ha) at elevations above 725 m. In this area red spruce comprises >80% of the total basal area, with the remainder divided between balsam fir (*Abies balsamea* (L.) Mill), red maple (*Acer rubrum* L.), mountain maple (*Acer spicatum* Lam.), and birch (*Betula* spp.). The study plots were randomly located within these patches. Prior to fertilization, no statistically significant relationships existed between amount of N added and the presence of minor tree species within each plot. Climatologically, these sites receive approximately 100 cm precipitation·year^{-1}, most of which is in frozen form (i.e., snow or sleet). Although temperature values were not recorded directly on the sites, the area is characterized as having warm summers (average July temperature 22°C) and cold winters (average January temperature −6°C) (USDC 1968).

The plots are on a soil type from the spodosol group, classified as a well-drained Houghtonville (USDA Soil Conservation Service 1989), which is found on broad areas between rock outcrops with a slope classification between 3 and 15%.

Materials and methods

Fertilization

Four sets of paired plots were amended with NH_4Cl-N and (or) $NaNO_3$-N over the course of the growing seasons of 1988–1990 (Table 1). The rates of N application were comparable to the high rates of annual N deposition recorded in other spruce–fir ecosystems located in industrialized regions (Schulze et al. 1989). Although the plots were not exhibiting any of the initial symptoms of N saturation, the sites were slightly east of an area which showed symptoms of N saturation (McNulty et al. 1990). By supplementing the long-term inputs of anthropogenic N deposition with additional N fertilizer at a rate which equalled high rates of N deposition found elsewhere, we hypothesized that N saturation could quickly be induced on these sites. Two types of N (NH_4Cl-N and (or) $NaNO_3$-N) were used to assess the ecosystems ability to absorb both ionic N forms. As an anion, we hypothesized that NO_3-N would not be adsorbed by the forest floor. Instead, added NO_3-N would simply leach out of the system and therefore have minimal ecosystem affect.

Treatments were divided randomly among plots. The fertilizer was dissolved in 15 L distilled H_2O, and applied with a Solo Backpack Sprayer. The total annual amount of fertilizer was divided into three equal amounts and applied in June, July, and August of each year (1988–1990).

Bulk precipitation collectors

In April 1989, four bulk precipitation collectors were installed on each plot and 10 collectors were randomly located in open areas surrounding the plots. The 25 cm tall collectors were made from 15 cm diameter funnels placed on top of 1-L Nalgene bottles that were then staked to the forest floor. These collectors were replaced weekly and remained on the site from April until October when they were replaced with frozen precipitation collectors.

Two frozen precipitation collectors were placed on each plot and five collectors were placed in open areas surrounding the plots. The collectors were sheet-metal tubes 122 cm long and 20 cm in diameter. Three 183-cm aluminum rods were attached to the collector such that 15 cm of rod protruded from the bottom end of the tube and 46 cm of rod from the top. To the top rod, a 36 cm diameter baffle was attached around the top of the tube. The purpose of the baffle was to reduce horizontal precipitation movement both into and out of the tube. Using the rods on the bottom of the tube and wires attached externally to the tube, each collector was secured to the ground. A plastic bag was fitted into the inside of the collector and replaced every two weeks from October through April.

TABLE 1. Design of N addition experiment on Mount Ascutney, Vermont

Plot No.	Monthly amendment (kg N·ha^{-1}·application^{-1})		Total annual amendment (kg N·ha^{-1}·year^{-1})
	NH_4Cl-N	$NaNO_3$-N	
1, 6	0	0	0
4, 10	5.2	0	15.7
2, 8	0	6.6	19.8
5, 9	5.2	3.3	25.6
3, 7	10.5	0	31.4

NOTE: All N was added in three equal doses during June, July, and August 1988–1991.

Samples were run on a TRAACS 800 Auto-Analyzer for determination of NH_4-N (Technicon Industrial Systems 1978) and NO_3-N (Technicon Industrial Systems 1977) concentration. Frozen and liquid throughfall and precipitation amounts (cm H_2O·ha^{-1}·year^{-1}), and total N (kg N·ha^{-1}·year^{-1}) were recorded.

Forest floor

Plot characteristics

Pretreatment potential net N mineralization was determined using 20 forest floor samples randomly collected from each plot in May 1988. The forest floor samples were randomly combined into five composite samples and sieved through a No. 18 mesh screen to remove all twigs, roots, and mineral particles. Combination of samples was necessary to insure sufficient sample size for analysis. NO_3-N and NH_4-N concentrations were determined before and after a 28-day incubation (described below) by placing 10 g of composited forest floor sample in 150 mL of 1M KCl for 48 h. Extracts were run on a TRAACS 800 Auto-Analyzer for NH_4-N (Technicon Industrial Systems 1978) and NO_3-N (Technicon Industrial Systems 1977) concentration. Net N mineralization potential was calculated as NH_4-N plus NO_3-N of incubated samples, minus the sum of NH_4-N and NO_3-N of initial samples. Net nitrification potential was calculated as incubated NO_3-N minus initial NO_3-N. Forest floor pH was measured on two samples from each plot, using 1:2 (w/v) forest floor to $CaCl_2$ solution (0.01 M).

In June 1988, forest floor mass was measured by extracting nine 400-cm^2 forest floor samples randomly located on each plot. If a random collection fell on an area of exposed rock, an alternative location was sampled. The material was sieved through a No. 18 mesh screen, oven dried at 70°C for 48 h, weighed, and converted to "potential" forest floor mass (kg·ha^{-1}). The percentage of forest floor covered by exposed rock was measured on each plot using 256 points on a 15 × 15 m grid. At each grid point, forest floor depth was recorded. All depths less than 2 cm were considered "rock". Potential forest floor mass was multiplied by the nonrock fraction, to produce the "actual" forest floor mass (kg·ha^{-1}).

From the nine forest floor samples collected at each plot, three samples were randomly chosen for CHN analysis. C, H, and N were measured using a Perkin-Elmer model 240B CHN analyzer at the University of New Hampshire, Durham.

Buried bags

In each month from May to October of all study years, on each plot, two sets of forest floor samples (20 cores each) were extracted

TABLE 2. Mean forest floor parameters (with standard errors in parentheses) for all plots prior to treatment

Treatment (kg N·ha^{-1}·year^{-1})	Potential mass (kg·ha^{-1})	Nonrock fraction (%)	Actual mass (kg·ha^{-1})	Depth (cm)	N (%)	C (%)	N (kg·ha^{-1})	C (kg·ha^{-1})	C/N
0	88 100 (2290)	77 (3)	68 000 (4300)	7.8 (0.1)	1.22 (0.16)	35.7 (4.3)	813 (53)	23 900 (1400)	29.4 (0.1)
15.7	112 200 (13 800)	80 (2)	89 700 (13 000)	8.7 (1.0)	1.47 (0.01)	42.9 (0.3)	1317 (184)	38 550 (5820)	29.2 (0.4)
19.8	91 500 (8200)	84 (2)	76 700 (8500)	7.1 (0.4)	1.44 (0.06)	42.3 (3.1)	1115 (171)	32 950 (5960)	29.4 (0.8)
25.6	137 900 (7000)	74 (3)	102 500 (9100)	8.9 (0.3)	1.35 (0.14)	37.9 (4.5)	1262 (249)	41 450 (8250)	29.5 (0.4)
31.4	123 500 (19 100)	79 (1)	96 000 (8900)	8.2 (0.2)	1.30 (0.04)	38.9 (0.1)	1240 (74)	37 300 (3290)	30.0 (0.9)

and placed in 1 mil polyethylene bags and sealed prior to plot fertilization. One set of bagged forest floor samples was returned to the laboratory to determine initial NH_4-N and NO_3-N concentration (described previously). The second set of buried bags was allowed to incubate in the forest floor for 28 days, except for overwintering (October–May) bags. After 28 days the buried bags were removed and returned to the laboratory to determine incubated NO_3-N and NH_4-N concentration, net N mineralization, and net nitrification. These bags were sieved, combined, and extracted as previously described.

Resin bags

Because of the shallow forest floor (≤10 cm) over a thin mineral layer, the use of lysimeters was not practical. To obtain an estimate of relative N mobility in each plot, ion exchange resin bags were used. Ten g of Dowex AG 50W-X8 cation exchange resin (H^+) or Dowex AG 1-X8 anion exchange resin (Cl^-) were placed in separate nylon bags. Ten anion and cation resin bags were randomly placed at the base of the O horizon (approximately 8 cm depth) on each plot. The first bags were installed in May 1989 and replaced in September 1989. The bags were replaced each May and September with the last bags removed in May 1991.

Resins were extracted using 100 mL of 1 M KCl dripped through a column containing the resin bag. The resin bags were placed in a 15-mL syringe which had a stopper on the bottom. Into this syringe, 5 mL of 1 M KCl was added such that the resin bag was immersed in KCl. A 60-mL syringe with an attached 22-gauge needle fitted through a rubber stopper was fitted securely into the top of the 15-mL syringe. The 60-mL syringe was then filled with 1 M KCl and the stopper was removed from the bottom of the 15-mL syringe, allowing the KCl to drip through the resin bag and into a flask placed below it. The 60-mL reservoir was refilled as the KCl was drawn into the 15-mL syringe. Approximately 45 minutes was required to pass all 100 mL of KCl through the column. Nitrate and ammonium concentration were determined using a TRAACS 800 Auto-Analyzer.

Plot biomass

Canopy

Three sunlit and three understory red spruce trees, from which foliage samples were collected, were randomly selected and tagged on each plot. In June, July, and August during 1988–1990, three randomly oriented sunlit or understory branch samples were removed from each tagged tree using a pruning pole. These branch samples contained all age-classes of needles and no effort was made to separate the age-classes. All age-classes were grouped so that foliar chemistry would be an average for the branch.

The clipped branches from each tree were placed in a single large bag and dried for 48 h at 70°C. After drying, all branch needles had fallen into the bag and were ground through a No. 10 mesh using a Wiley Mill. The samples were placed in 2-oz. (60-mL) Qorpak glass jars, dried for 24 h at 70°C, and stored in darkness at 22°C.

Percent foliar N and lignin were measured using near-infrared reflectance spectroscopy (Wessman et al. 1988). Applications of this technique have produced results with precision equal to, or better than wet chemistry procedures, for foliar analysis (Wessman et al. 1988; McLellan et al. 1991).

Basal area

In June 1988, all trees >2 cm DBH were measured at 1.5 m above forest floor with a diameter tape, and species, basal area (BA), and condition (living vs. dead) were recorded. In November 1990, the trees were again measured and compared to initial measurements. Changes in BA were divided into living, dead, and total, calculated as initial BA subtracted from final BA (measured in square meters per hectare per 3 years).

In December 1990, an increment tree corer was used to remove a complete core from all six tagged trees on each plot. In addition, four randomly selected trees in each plot were also cored. As foliage had been removed three times each year, for 3 years, we had considered the possibility that removal of foliage reduced growth rates. A comparison of ring growth between the tagged trees (foliage removed) with nontagged trees (no foliage removed) was used to quantify the potential growth loss. Cores were stored in cardboard straws and allowed to air dry. The cores were measured at the Northeastern Forest Service Laboratory in Durham, N.H. to determine tree age (years) and growth increment (measured in square centimeters per year), assuming that from a green to air-dry state, red spruce radial wood shrinks approximately 3% (USDA Forest Products Laboratory 1974). Samples not meeting Forest Service criteria for completeness or readability were excluded from analysis.

Litter

Ten litter baskets were randomly placed on each plot on October 28, 1988 (following autumn litter fall). The baskets remained on the plots until October 27, 1990, and were emptied once every 3 weeks, except during snow periods. Each 402-cm^2 basket was 20 cm deep, lined with 50% cotton – 50% polyester broadcloth. The litter was placed in bags and oven dried at 70°C for 48 h to prevent decomposition before being sorted into coniferous and deciduous litter. The sorted material was dried at 70°C for 24 h before weighing.

Litter N and lignin concentrations were measured using near-infrared spectroscopy (McLellan et al. 1991).

Results and discussion

Plot characteristics

Forest floor

High foliar or forest floor N concentrations and high nitrification:mineralization ratios may indicate the beginning of an N-saturated ecosystem (Aber et al. 1989). The initial forest floor N concentration of these plots averaged 1.35% N (Table 2). This value is on the lower end of the range (1.0–2.5% forest floor N) reported by others (Lang et al. 1981; Federer 1983; Olson and Reiners 1983; Friedland et al. 1991) and close to the nitrogen concentration (1.5% N) that may trigger the onset of nitrification in New England spruce–fir forest floor (McNulty et al. 1991). No nitrate was formed in incubated pretreatment forest floor samples collected in May 1988.

Pretreatment sample collection illustrated that average forest floor mass varied considerably across the plots (Table 2), while foliar lignin and N concentrations (Table 3)

TABLE 3. Red spruce foliar chemistry for treatments (with standard errors in parentheses)

Treatment (kg N·ha^{-1}·year^{-1})	Seasonal average (%)			Pretreatment average	Monthly average (%) for 1990		
	1988	1989	1990	May 1988 (%)	June	July	August
				Foliar N			
0	0.88 (0.03)	0.92 (0.04)	0.84 (0.03)	0.86 (0.01)	0.76 (0.03)	0.76 (0.02)	0.93 (0.02)
15.7	0.90 (0.01)	1.06 (0.01)	1.07 (0.00)	0.86 (0.01)	0.99 (0.02)	1.07 (0.01)	1.14 (0.01)
19.8	0.89 (0.00)	1.08 (0.00)	1.06 (0.02)	0.88 (0.03)	0.95 (0.02)	1.06 (0.02)	1.17 (0.04)
25.6	0.95 (0.02)	1.16 (0.01)	1.18 (0.00)	0.91 (0.01)	1.11 (0.01)	1.20 (0.02)	1.23 (0.01)
31.4	0.91 (0.03)	1.09 (0.01)	1.09 (0.02)	0.87 (0.02)	1.05 (0.01)	1.02 (0.03)	1.16 (0.01)
				Foliar lignin			
0	21.1 (0.4)	23.3 (0.3)	21.6 (0.5)	17.1 (0.0)	18.4 (0.6)	22.2 (0.4)	24.0 (0.4)
15.7	20.2 (0.4)	21.6 (0.2)	21.2 (0.1)	17.3 (0.6)	18.3 (0.1)	22.3 (0.1)	23.0 (0.0)
19.8	20.8 (0.3)	22.6 (0.2)	21.7 (0.4)	17.7 (0.5)	18.8 (0.8)	23.1 (0.2)	23.2 (0.1)
25.6	19.9 (0.2)	21.4 (0.4)	20.5 (0.3)	16.0 (0.1)	17.9 (0.3)	21.8 (0.3)	21.8 (0.3)
31.4	20.3 (0.4)	22.4 (0.4)	21.7 (0.6)	16.2 (0.2)	19.9 (0.7)	22.5 (0.8)	22.6 (0.7)
				Foliar lignin/N			
0	23.1 (1.1)	25.6 (1.3)	26.2 (1.5)	19.9 (0.1)	24.7 (1.8)	27.5 (1.7)	26.5 (1.1)
15.7	22.5 (0.1)	20.4 (0.2)	19.8 (0.2)	20.1 (0.5)	17.6 (1.1)	20.9 (0.1)	20.3 (0.3)
19.8	23.3 (0.5)	20.9 (0.3)	20.6 (0.9)	20.6 (0.5)	18.9 (0.7)	22.0 (0.9)	19.9 (0.7)
25.6	21.0 (0.9)	18.6 (0.1)	17.4 (0.3)	17.5 (0.1)	19.3 (2.0)	18.2 (0.5)	17.7 (0.1)
31.4	22.5 (1.2)	20.6 (0.6)	19.6 (0.5)	18.6 (0.5)	18.9 (0.8)	20.2 (0.4)	19.6 (0.4)

NOTE: Seasonal averages equal the values of each of the three monthly averages (June, July, and August) divided by three. Monthly averages equal the foliar values from each of the six tagged trees on each plot divided by six.

as well as forest floor C/N (Table 2) were within a narrow range. Owing to the variation in forest floor mass between plots, net N mineralization rates are expressed in both mg N·kg forest floor^{-1}·year^{-1} and kg N·ha^{-1}·year^{-1}. The forest floor had a pretreatment average pH of 2.7 (SE 0.1) and was not statistically different at the end of the experiment.

Forest floor mass (kg·ha^{-1}) was weakly correlated with forest floor C/N ($R^2 = 0.38$, $P < 0.05$). This trend has also been documented across New England where a greater range of forest floor C/N ratios exist (McNulty et al. 1991). A very strong correlation was found between forest floor C concentration and forest floor N concentration ($R^2 = 0.95$, $P < 0.0001$) for all of the Mount Ascutney sites. However, the relationship between forest floor %C and %N appears to break down under chronically elevated levels of N deposition (McNulty et al. 1991), where ecosystem N inputs may no longer be balanced by N uptake.

Baath et al. (1978), Johnson and Edwards (1979), and Foster et al. (1980), correlated forest floor C/N ratios with increased net N mineralization and N cycling. Leaf-litter decomposition is largely controlled by relative percentages of lignin and N (Melillo et al. 1982). In areas where annual N inputs exceed biological demand, decomposers may no longer be limited by N. Instead decomposition may be limited by available C (Berg and Staaf 1981; Flanagan and Van Cleve 1983; Harmer and Alexander 1986), so the relationship between decomposition and available N deteriorates.

Bulk precipitation

Open areas around the sample plots received 99 and 104 cm of precipitation during the 1989–1990 and 1990–1991 seasons, respectively. Total open-area precipitation was slightly more than total canopy throughfall during 1989–1990 and slightly less than total canopy throughfall in 1990–1991 (not statistically significant). During both years, approximately 70% of the precipitation was frozen, which can occur from October to April because of latitude and elevation.

Unlike precipitation volume, open areas received much less N compared with throughfall N inputs (Fig. 1). Open areas received 5.4 kg N·ha^{-1}·year^{-1}, mainly from frozen precipitation containing nitrate (50%), followed by frozen precipitation containing ammonium (25%), liquid precipitation containing nitrate (15%), and liquid precipitation containing ammonium (10%). The 5.4 kg N·ha^{-1}·year^{-1} of open-area bulk precipitation is slightly less than the 7 kg N·ha^{-1}·year^{-1} measured on Whiteface Mountain, New York (Friedland et al. 1991), an area west of these study sites.

Nitrogen analysis of frozen precipitation samples from one of the control plots during both years and one of the 15 kg N·ha^{-1}·year^{-1} plots during 1990–1991 contained numerous samples with N concentrations that were 10–20 times greater than other samples collected from other plots at the same time. Porcupine activity on these plots was monitored by visual sightings and bark removal. It is likely that the extremely high N concentrations from areas of porcupine activity are an artifact of a few instances of animal contamination.

Excluding contaminated samples, control plots received 14.1 and 14.3 kg throughfall N·ha^{-1}·year^{-1} during 1989–1990 and 1990–1991, respectively, while the plots fertilized with 15.7 kg N·ha^{-1}·year^{-1} received 13.2 kg throughfall N·ha^{-1}·year^{-1} in 1990–1991. These differences are not statistically different ($P > 0.05$) using a paired *t*-test (Ott 1984).

Excluding sites with contaminated N concentrations, annual throughfall N inputs to all sites equalled 150–300% of open-area N inputs. Bulk N deposition inputs indicate that there is a statistical difference ($P < 0.05$) between the open areas and any of the other treatments, the exception being the 15.7 kg N·ha^{-1}·year^{-1} treatment during the first year of the experiment. Tree morphology may increase deposition rates above open-area collections as stems and branches provide

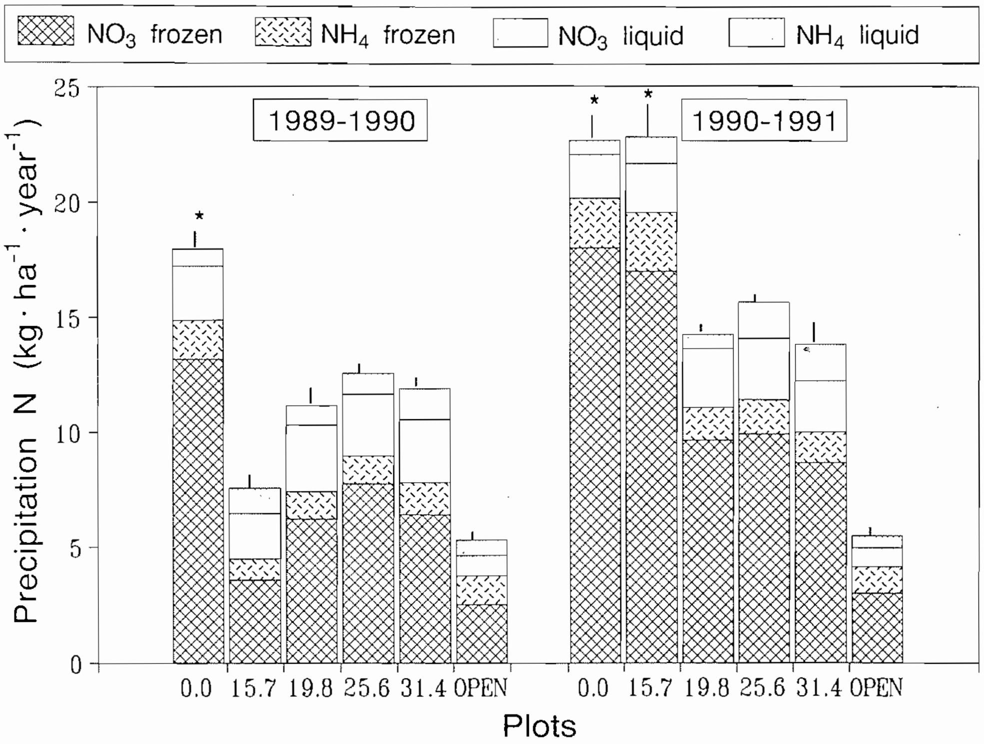

FIG. 1. Annual N inputs (kg·ha^{-1}·year^{-1}) for 2 years of the study on Mount Ascutney, Vermont, for N additions (N treatment levels are given in kg·ha^{-1}·year^{-1} below each bar). The type of N (NO_3-N or NH_4-N) and the form of input (frozen or liquid) are shown with standard error bars included. *Treatments with possible animal contamination. Open, open area bulk precipitation collectors.

greater surface area for cloud and dry deposition. Foliar leaching of N is another possible source of some N input (Lovett et al. 1985) but no pattern of increased leaching relative to increased N fertilization was found.

Buried Bags

(i) Net N mineralization

Control plots had an average net N mineralization rate of 15 kg N·ha^{-1}·year^{-1} and no statistically significant change in net N mineralization occurred during the 3 years of the study. Since no statistical difference was found in net N mineralization rates on the control plots over the 3 years of the experiment, we assume that the climatic controls (forest floor temperature and moisture) of N mineralization were annually similar throughout the experiment. While forest floor temperature was not measured, precipitation inputs (measured on open areas) were measured and were not statistically different between years.

The treatment plots had a greater annual net N mineralization variability than did the control plots. Net N mineralization initially correlated well with N added but this relationship deteriorated over time (Table 4). For the first year net N mineralization on fertilized sites was approximately equal to control site net N mineralizations plus the amount of N added as fertilizer (Table 5). However, without the use of labeled N, it is not possible to determine what fraction of the N applied was immobilized and then remineralized.

Plots receiving only NO_3-N also had elevated net N mineralization rates (Table 5). As an anion, NO_3-N is subject to leaching loss, but these results suggest that added NO_3-N may have been immobilized as it was added to the forest floor and then remineralized.

The greatest rate of net N mineralization was measured during the second year of fertilization when average net N mineralization for the eight fertilized plots equalled 56.6 kg N·ha^{-1}·year^{-1}. The third year average net N mineralization decreased to 46.4 kg N·ha^{-1}·year^{-1} for the eight fertilized plots. After the second year, net N mineralization on plots receiving <25.6 kg N·ha^{-1}·year^{-1} of fertilizer continued to increase while net N mineralization on plots receiving greater amounts of added N decreased or remained constant. Given similar climatic conditions between years, this suggests that the additional N was no longer stimulating net N mineralization. A lack of a labile C source could explain this net N mineralization pattern. Berg and Staaf (1981) found that litter N concentrations were linearly correlated with lignin-bound N when heterocyclic ring compounds (which are highly resistant to microbial decomposition) are formed as NH_4-N is fixed to litter lignin. Flanagan and Van Cleve (1983) have postulated that decomposition may be energy limited in taiga ecosystems, as a labile C source is more limiting than available N, and this study found no explanation to refute that theory.

(ii) Nitrification

Average nitrification for all N addition plots during the final year of the experiment (1990–1991) was 0.8 kg NO_3-N·ha^{-1}·year^{-1} or approximately 2% of the total net N mineralization, which is consistent with other New England spruce–fir stands receiving comparable amounts of annual N deposition (McNulty et al. 1990).

Several factors control nitrification rates including forest floor pH and plant and microbial N demand relative to N availability (Robertson 1982; Robertson and Vitousek 1981). Increases in net nitrification could occur once the ecosystem

TABLE 4. Correlations coefficients and probabilities for changes in foliar, litter-fall, and forest floor chemistry and processes

	1988		1989		1990		1991	
	R^2	P	R^2	P	R^2	P	R^2	P
Added N versus								
Deciduous litter mass (kg·ha^{-1}·year^{-1})			0.05	0.67	0.19	0.21		
Coniferous litter mass (kg·ha^{-1}·year^{-1})			0.02	0.84	0.45	0.02		
Total litter-fall mass (kg·ha^{-1}·year^{-1})			0.04	0.68	0.61	0.004		
Deciduous litter %N			0.68	0.001	0.90	0.0000		
Coniferous litter %N			0.29	0.09	0.84	0.0001		
Total litter %N			0.46	0.02	0.73	0.0006		
Deciduous litter lignin/N			0.67	0.002	0.75	0.0004		
Coniferous litter lignin/N			0.59	0.005	0.53	0.009		
Total litter lignin/N			0.66	0.002	0.50	0.01		
Net N mineralization (kg N·ha^{-1}·year^{-1})			0.57	0.006	0.59	0.005	0.11	0.42
Net N mineralization (mg N·ha^{-1}·year^{-1})			0.62	0.003	0.48	0.015	0.09	0.48
Foliar spruce %N	0.11	0.39	0.68	0.001	0.78	0.0003		
Foliar spruce %lignin	0.00	1.00	0.26	0.12	0.01	0.89		
Foliar spruce lignin/N	0.06	0.60	0.62	0.003	0.49	0.01		
Forest floor %N	0.03	0.77						
Forest floor %C	0.05	0.70						
Forest floor total N (kg·ha^{-1})	0.27	0.11						
Forest floor total C (kg·ha^{-1})	0.26	0.12						
Forest floor C/N	0.20	0.82						
Foliar red spruce %N versus								
Foliar red spruce % lignin	0.46	0.02	0.40	0.04	0.67	0.002		

TABLE 5. Average in situ net N mineralization and nitrification for all treatments (with standard errors in parentheses)

Treatment (kg N·ha^{-1}·year^{-1})	Net mineralization			Net nitrification		
	1988–1989	1989–1990	1990–1991	1988–1989	1989–1990	1990–1991
	mg N·g forest floor^{-1}·year^{-1}			**mg NO_3-N·g forest floor^{-1}·year^{-1}**		
0	0.20 (0.01)	0.23 (0.01)	0.24 (0.05)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
15.7	0.37 (0.08)	0.50 (0.04)	0.56 (0.03)	0.03 (0.02)	0.00 (0.00)	0.00 (0.00)
19.8	0.44 (0.05)	0.70 (0.06)	0.68 (0.15)	0.01 (0.01)	0.01 (0.00)	0.03 (0.02)
25.6	0.53 (0.03)	0.63 (0.18)	0.35 (0.05)	0.02 (0.01)	0.03 (0.00)	0.01 (0.01)
31.4	0.49 (0.08)	0.64 (0.08)	0.44 (0.06)	0.01 (0.01)	0.01 (0.01)	0.00 (0.00)
	kg N·ha^{-1}·year^{-1}			**kg NO_3-N·ha^{-1}·year^{-1}**		
0	13.7 (1.5)	15.7 (1.5)	16.0 (2.3)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)
15.7	35.4 (12.5)	48.2 (3.2)	51.0 (9.7)	2.5 (1.8)	0.0 (0.0)	0.0 (0.0)
19.8	34.2 (7.2)	54.3 (10.6)	54.3 (17.3)	0.8 (0.5)	0.4 (0.3)	2.1 (1.5)
25.6	53.3 (2.0)	61.4 (12.5)	36.7 (8.4)	1.4 (0.6)	2.5 (0.1)	0.9 (0.6)
31.4	45.4 (3.0)	62.3 (12.8)	43.6 (9.6)	0.7 (0.5)	0.7 (0.5)	0.0 (0.0)

becomes N saturated (Aber et al. 1989). However, even with decreases in biological demand or an increase in pH, soils can show long-term delays in the initiation of nitrification (Vitousek et al. 1982), perhaps owing to the absence of a community of nitrifying bacteria (Vitousek and Matson 1985).

While autotrophic nitrification is thought to dominate (Stams et al. 1990), a lack of available C could also regulate heterotrophic nitrification under conditions of elevated N availability. As added N stimulated production of relatively large quantities of available N (200–300% of the control level amounts) through net N mineralization, a spike in net NO_3-N was observed. With few exceptions, only the initial increase in net N mineralization triggered nitrification, despite sustained (or increased) plot net N mineralization. Therefore, the initial correlation between increased net N mineralization and increased nitrification degenerated over time. These ecosystems are naturally low in readily decomposable C sources. Before the experiment, litter lignin concentrations were very high (22%) and insufficient time had passed to significantly reduce litter lignin concentrations and increase the amount of a readily decomposable C source. In contrast, areas receiving elevated N deposition for longer periods of time have foliage with lower foliar lignin concentrations (McNulty et al. 1991), greater amounts of readily decomposable C, and thus greater capability for sustaining elevated net N mineralization and nitrification rates.

Resin bags

In control plots, only a small amount of N reached the resin bags (largely composed of NO_3-N), and mainly during the

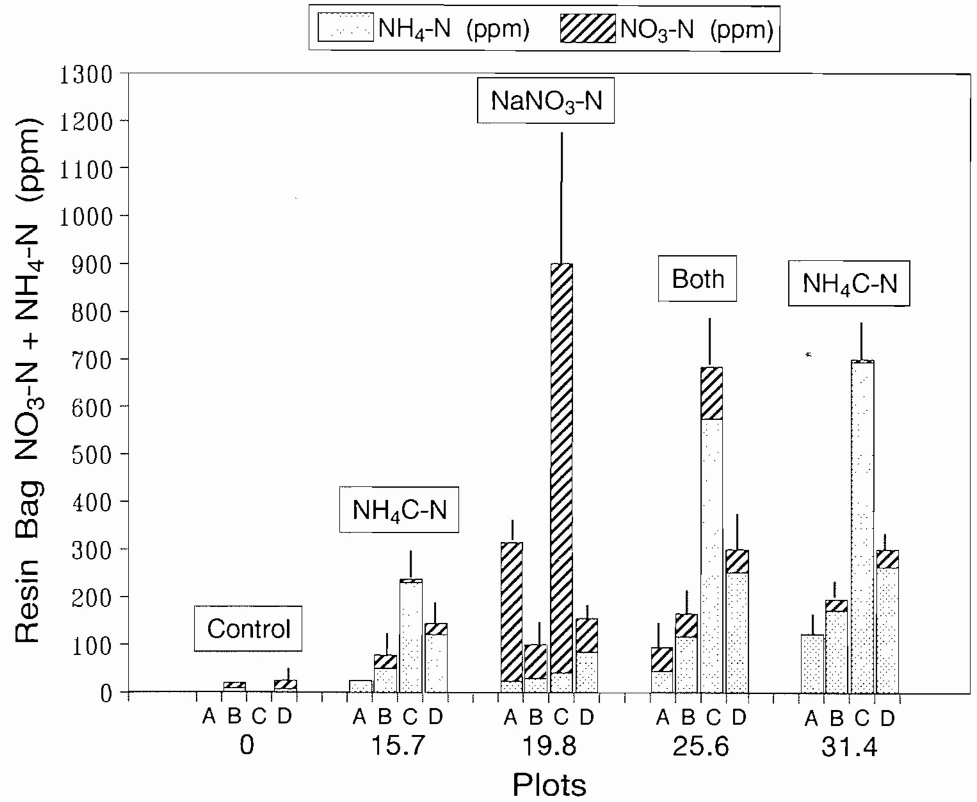

FIG. 2. Seasonal concentrations of NO_3-N or NH_4-N (ppm) for 2 years on Mount Ascutney, Vermont, where ion exchange resin bags placed at the base of the forest floor of each treatment (N treatment levels are given in $kg \cdot ha^{-1} \cdot year^{-1}$ below each set of bars). Standard error bars are included for each value. (A) Bags installed May 1989 – August 1989. (B) Bags installed August 1989 – May 1990. (C) Bags installed May 1990 – August 1990. (D) Bags installed August 1990 – May 1991.

nongrowing season months between mid-August and mid-May (Fig. 2). During this period, biological N demand is low while late spring and autumn temperatures often produce periods of warm temperatures which can stimulate net N mineralization and nitrification. Autumn rains and spring snowmelt also provide additional transport and a source of N ions to the resin bags. Nitrate as an anion is not bound to soil colloids and is, therefore, easily transported to the base of the organic horizon and to the resin bead exchange sites. For this reason, a greater proportion of the NO_3-N produced in the forest floor may have been retrieved, compared with NH_4-N, when using this technique.

On fertilized plots, large concentrations of added NH_4-N and NO_3-N (100–900 ppm $N \cdot season^{-1}$) were transported to the resin bead exchange sites following N fertilization, but the precise amount of N lost is not determinable using this methodology (Binkley 1984). Total N (NO_3-N + NH_4-N) accumulated on the resin exchange sites during the period of time when fertilizer was not added (September–May) was correlated with annual net N mineralization during 1989–1990 ($R^2 = 0.68$, $P = 0.0014$). However, as the experiment progressed the amount of N absorbed to the resin-bead exchange sites continued to increase while net N mineralization began to decrease. During 1990-1991, the relationship between resin-bag N and net N mineralization was no longer significant ($R^2 = 0.12$, $P = 0.39$). During the course of the experiment, there were no significant differences in the timing or amount of annual precipitation which would account for the changes in N transport to the resin bags. These results (increased N on resin-bag exchange sites) lend credence to the theory that the soils were becoming N saturated as less of the applied N was being immobilized (i.e., greater N leaching) as the experiment continued.

Plot biomass

Basal area

Pretreatment red spruce BA represented 82% (SE 4%), balsam fir 9% (SE 3%), and red maple and birch combined to equal 9% (SE 5%) of the total BA.

Living BA was roughly equal across all plots at the beginning of the experiment when average BA equaled 37.7 $m^2 \cdot ha^{-1}$ (SE 0.86 $m^2 \cdot ha^{-1}$). However, after 3 years, average stand BA had increased to 39.0 $m^2 \cdot ha^{-1}$ (SE 0.95 $m^2 \cdot ha^{-1}$). On control plots, living BA increased by 0.8 $m^2 \cdot ha^{-1} \cdot 3\ years^{-1}$ (2.0% greater than pretreatment area; Fig. 3). Maximum living BA occurred on the high NO_3-N plots with a 3.4 $m^2 \cdot ha^{-1} \cdot 3\ years^{-1}$ (8.7%) increase. At fertilization rates of 25.6 kg $N \cdot ha^{-1} \cdot year^{-1}$, living BA was reduced to below pretreatment areas by 0.05 $m^2 \cdot ha^{-1} \cdot 3\ years^{-1}$ (0.1%).

Average dead standing BA across all stands represented a small amount of the total area (1.99 ± 0.30 $m^2 \cdot ha^{-1}$; mean ± 1 SE) at the beginning of the treatments. On control plots, dead BA increased by 0.6 $m^2 \cdot ha^{-1} \cdot 3\ years^{-1}$ (38%) over the course of the experiment. As additional N was added, the amount of dead BA also increased with the highest N addition plots (31.4 kg $N \cdot ha^{-1} \cdot year^{-1}$) having a 4.2 $m^2 \cdot ha^{-1} \cdot 3\ years^{-1}$ (327%) increase in dead standing BA after three

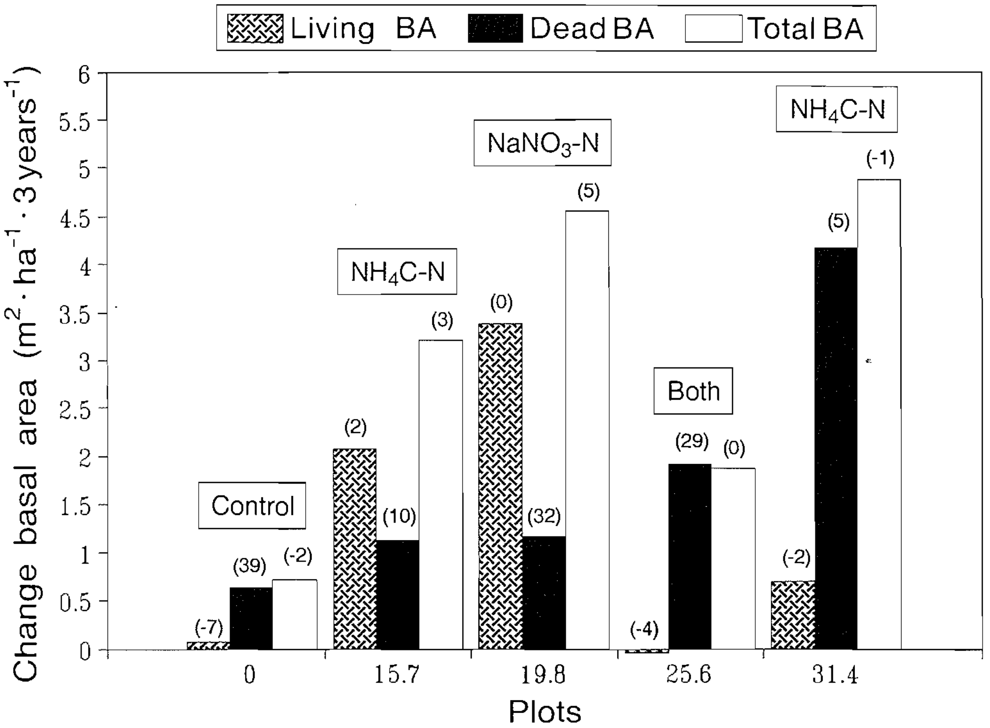

FIG. 3. Living, dead, and total basal area (BA) change ($m^2 \cdot ha^{-1} \cdot 3$ $years^{-1}$) for each treatment (N treatment levels are given in $kg \cdot ha^{-1} \cdot year^{-1}$ below each set of bars) over the 3 years of the experiment. The percent change in the number of trees per treatment are given in parentheses and the forms of N applied are given above the bars.

years. The size of the trees that died during the experiment varied inversely with N addition. The number of dead trees in the control plots increased by 39%, while on the plots with the greatest increases in dead BA (plots receiving 31.4 kg $N \cdot ha^{-1} \cdot year^{-1}$) only a 5% increase in the number of dead trees was observed (Fig. 3). On the highest N fertilization plots, smaller diameter dead standing trees fell over, hence, were removed from the count, while much larger diameter trees died, remained standing, and were included in the count. On high N fertilization plots, the number of dead standing trees increased only slightly from the beginning of the experiment, but the increase in dead standing BA was greater than on control plots.

Total BA (living + dead) increased by 0.7 $m^2 \cdot ha^{-1} \cdot$ 3 $years^{-1}$ (1.9%) on control plots compared to the starting conditions. In the 31.4 kg $N \cdot ha^{-1} \cdot year^{-1}$ plots, the greatest increase in total BA was observed (4.9 $m^2 \cdot ha^{-1} \cdot 3$ $years^{-1}$ (13%)).

Tree rings

The BA increase as measured by tree-ring analysis is significantly different than that measured by DBH. Cores were extracted from codominant trees selected from each plot while DBH measurements sampled all trees. In selecting codominant trees, suppressed trees that would decrease average tree basal growth were excluded. Both long-term growth chronology and treatment affects were assessed using tree-ring data for 49 of the 100 samples that were suitable for complete core analysis. Of the 49 trees sampled, only three trees had reached a height of 1.5 m by the early 1930s. From 1900 to 1930, BA increased slowly (≤ 1 $cm^2 \cdot tree^{-1} \cdot year^{-1}$), but from the 1940s to the 1980s, the rate of BA growth increased, peaking at a BA of 5.3 $cm^2 \cdot tree^{-1} \cdot year^{-1}$ during the 1980s.

Between 1940–1945, 21 of the 49 trees reached 1.5 m (sampling height) and most of the other sampled trees were 1.5 m within 5 years of this period. Charred wood located throughout this area and significant increases in volume growth of the three trees present by 1930 suggest that a fire caused a major change in ecosystem structure in the mid 1930s. Release of nutrients following the fire and increased light penetration into the forest likely caused a stimulation of new growth. A 1938 hurricane may also have either directly (by creating gap openings) or indirectly (by scattering debris that was subject to fire) contributed to increased forest growth. The fraction of growth that could be attributed to industrialization after the Second World War and resulting increased atmospheric N inputs cannot be determined.

Living BA per tree per year increased by 2.3% on control plots as measured using tree-ring cores. This compares with 3.3, 3.0, 2.0, and 1.6% increases in living BA per tree per year on the 15.7, 19.8, 25.6, and 31.4 kg $N \cdot ha^{-1} \cdot year^{-1}$ treatment plots, respectively, between 1988 and 1990. From 1981 to 1987, BA growth across all plots averaged 3.2–8.4 $cm^2 \cdot tree^{-1} \cdot year^{-1}$ (Fig. 4). Control plot BA increment rose from an average of 5.2 $cm^2 \cdot tree^{-1} \cdot year$ during 1981–1987 to 6.0 $cm^2 \cdot tree^{-1} \cdot year^{-1}$ (15%) during 1990. The 25.6 kg $N \cdot ha^{-1} \cdot year^{-1}$ addition plots had the greatest incremental BA increase, changing from 4.2 $cm^2 \cdot tree^{-1} \cdot year^{-1}$ between 1981 and 1987 to 7.0 $cm^2 \cdot tree^{-1} \cdot year^{-1}$ in 1990 (67% increase) (Fig. 4). Using paired *t*-test (Ott 1984), differences among treatments within a given year and among years within a treatment are expressed ($P < 0.05$). Owing to large standard errors, many of the differences among treatments and years

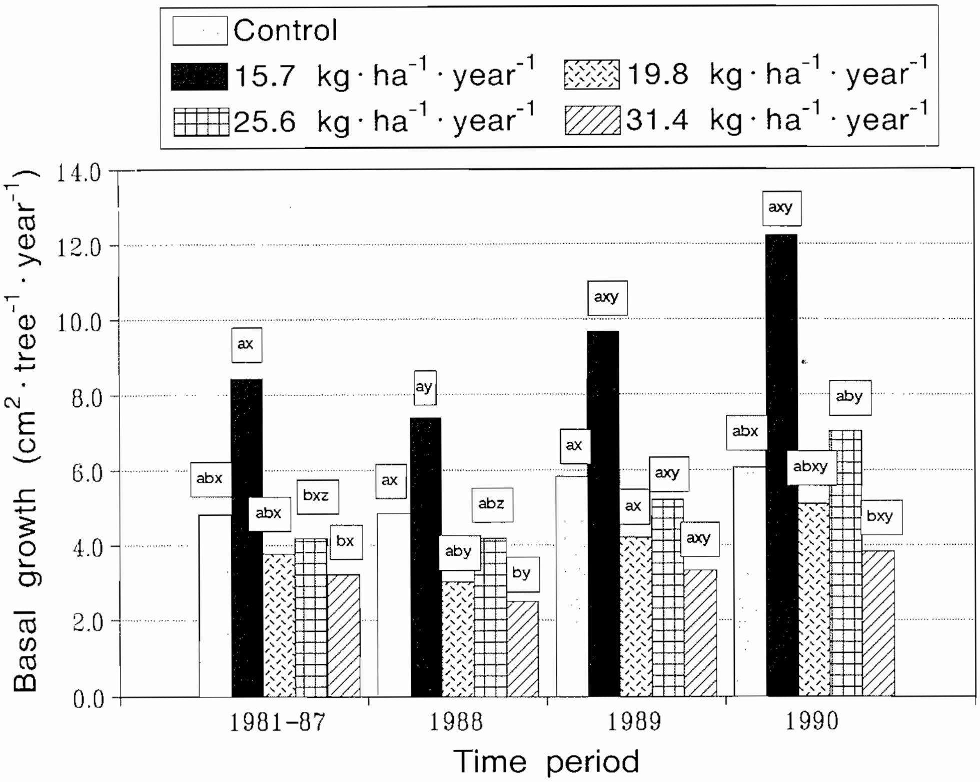

FIG. 4. Basal growth (cm^2·tree^{-1}·year^{-1}) measure using tree cores for each treatment (bars represent different N treatment levels in kg·ha^{-1}·year^{-1}) on Mount Ascutney, Vermont, from 1988 to 1990. Bars with the same letter are not significantly different by *t*-test for treatments within a year (*a* and *b*) or years within a treatment (*x*, *y*, and *z*).

were not significant. The differences in basal growth among treatments which was present before the experiment (1981–1987) continued during the experiment. All plots (including control) showed increased basal growth during the experiment (relative to pretreatment averages). The 15.7 kg N·ha^{-1}·year^{-1} plot maintained significantly greater basal growth compared with the high N treatment (31.4 kg N·ha^{-1}·year^{-1}) throughout the experiment (Fig. 4). On an annual basis, a trend in basal growth was found in all treatments; 1988 was a year of below-average growth (compared with the same plot from 1981 to 1987), 1989 was a year of above-average growth, and 1990 growth was greater than 1989 growth (Fig. 4).

Canopy chemistry

Red spruce and balsam fir retain their needles for 7–10 years (USDA 1990); thus, most of the foliage sampled in this experiment was already formed before the N additions began, because all age-classes of needles were combined for analysis. Mobile nutrients such as N can be retranslocated into new foliage, where lignin concentrations do not change after full needle development. Therefore, changes involving foliar lignin content would probably be enhanced if only current year needles were examined.

No significant differences were found in foliar chemistry between sunlit and understory spruce, so the six trees from each plot were not separated by canopy location for further statistical analyses.

Over the 3 years of foliar sampling, three patterns of foliar chemistry were found. First, foliar lignin and N concentration continued to increase over the course of the growing season as cool temperatures and late initial bud break required the entire summer to achieve full needle structure (Table 3). Second, annual variations in canopy chemistry were observed on all plots. Maximum foliar N concentration occurred in 1989 on the control plots while foliar N concentrations increased each year in the N addition plots (Table 3). The correlation between N added and foliar N concentration increased each year (Table 4).

An average foliar N concentration of 0.86%, measured during initial foliar collections (Table 3), is within the range of published values (0.8–1.1% N) for red spruce foliage during the growing season (Czapowskyj et al. 1980; Friedland et al. 1988; Fernandez et al. 1990). Fertilizer application initially increases foliar N concentration, leaf size, and leaf thickness (Mitchell and Chandler 1939; Turner 1977; Czapowskyj et al. 1980; Miller 1986; Weetman and Fournier 1984). As fertilization continues, foliar N concentrations, leaf size, and leaf thickness decrease (Weetman and Fournier 1984) while canopy mass increases (Turner 1977; Binkley and Reid 1984; Brix 1983). This progression of foliar mass and chemistry should also be observed in litter-fall changes.

On Mount Ascutney, foliar lignin concentrations were the greatest during the second year (1989) on all plots and subsequently decreased (Table 3).

The literature suggests that leaf lignin content will vary inversely with leaf N content (Flanagan and Van Cleve 1983; Waring et al. 1985) as increased foliar %N causes an increase in the fraction of available C transformed into leaf proteins, leaving little for construction of secondary carbon-based herbivore defense compounds such as lignin (Coley et al. 1985). During the third year, photosynthate used for amino-acid production may have hindered the trees' ability to construct lignin, as foliar lignin concentration was inversely correlated with foliar N concentration (Table 4).

The foliar lignin/N ratios in the control stand increased for each of the three years while the foliar lignin/N ratios of fertilized plots decreased (Table 3). On a seasonal basis, lignin/N ratios were maximized in July (Table 3). Foliar lignin/N ratios were inversely correlated with both N added and net N mineralization (Table 4).

Net N mineralization, foliar lignin/N, foliar N concentration, litter lignin/N and litter N concentration are correlated with N fertilization rates (Table 4). Melillo et al. (1982) reported that the litter concentrations of lignin and N control the rate of hardwood leaf litter decomposition. The decomposition of the forest floor and accompanying net N mineralization is the primary source of available N in forest ecosystems. Increasing the amount of available N produces foliage and litter with a lower lignin/N compared to stands with reduced available N (Tables 3 and 6). As the ecosystem approaches N saturation, increases in leaf-litter quality (lower C:N), net N mineralization and available N should also occur (Aber et al. 1989). Therefore, changes in net N mineralization or foliar lignin/N may be important indicators of ecosystem change.

Litter

Over the two years that litter was collected, no significant changes were measured in coniferous or deciduous litter mass. Each plot contained deciduous trees (mainly *Betula papyrifera* Marsh., but also *Acer spicatum*), the litter of which should respond rapidly to changes in N inputs due to annual litter fall. The correlation between N concentration of deciduous litter and N added was positive and increased with each successive year (Table 4), but no correlation was found with litter lignin concentrations and N added.

The coniferous litter lignin concentrations are largely influenced by the conditions when the needles are originally formed (pretreatment) and no trend was observed relative to the amount of N fertilization (Table 4). Therefore, decreases in the lignin/N ratio of litter from the N supplemented plots are the result of increased litter N concentration and not decreased litter lignin concentration (Table 6).

Conclusion

No differences were found between the type of fertilizer applied and ecosystem response. However, despite the small amounts of fertilizer applied, significant changes in ecosystem function occurred. Litter-fall mass, litter-fall %N, foliar %N, foliar lignin, resin-bag ionic absorption of both NO_3-N and NH_4-N, net N mineralization, dead BA, and total BA all changed with increasing N fertilization. In general, the growth and death of trees and cycling of N increased with increasing N fertilization.

The results thus far suggest that this ecosystem is changing from a closed system of slow growth and high nitrogen retention to a more open system with faster growth, higher mortality, and less effective N retention. It is perhaps significant that only very small N additions were required to effect this change. Longer term N additions will be required to determine the full impact of increased N fertilization on this system.

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TABLE 6. Average litter-fall data for treatments (with standard errors in parentheses)

Treatment ($kg\ N \cdot ha^{-1} \cdot year^{-1}$)	Mass ($kg \cdot ha^{-1} \cdot year^{-1}$) Coniferous	Mass Deciduous	Mass Total	N ($kg \cdot ha^{-1} \cdot year^{-1}$) Coniferous	N Deciduous	N Total	Lignin ($kg \cdot ha^{-1} \cdot year^{-1}$) Coniferous	Lignin Deciduous	Lignin Total	Lignin/N	%N
1988–1989											
0	1690 (10)	120 (20)	1810 (40)	15.3 (0.1)	1.5 (0.3)	16.8 (0.4)	340 (10)	19 (3)	359 (13)	21.3 (0.2)	0.93 (0.01)
15.7	2070 (290)	230 (100)	2300 (380)	19.8 (1.7)	3.8 (1.7)	23.6 (3.4)	379 (49)	34 (14)	413 (63)	17.4 (0.1)	1.03 (0.06)
19.8	1540 (130)	500 (150)	2040 (10)	16.3 (1.3)	7.2 (2.2)	23.5 (0.8)	307 (28)	77 (21)	384 (7)	16.4 (0.9)	1.16 (0.03)
25.6	2200 (330)	200 (100)	2400 (430)	21.9 (1.4)	3.7 (1.9)	25.6 (3.2)	408 (51)	36 (18)	444 (69)	17.2 (0.6)	1.09 (0.06)
31.4	1770 (280)	240 (80)	2010 (350)	18.2 (3.0)	3.9 (1.3)	22.1 (4.3)	336 (55)	36 (12)	372 (66)	17.0 (0.3)	1.09 (0.02)
1989–1990											
0	1360 (10)	140 (0)	1500 (10)	12.4 (0.1)	2.0 (0.0)	14.4 (0.1)	281 (20)	25 (1)	306 (20)	21.3 (1.5)	0.96 (0.07)
15.7	1990 (230)	250 (30)	2240 (260)	21.7 (3.1)	4.0 (0.5)	25.7 (3.6)	426 (44)	44 (5)	470 (49)	18.6 (0.7)	1.15 (0.03)
19.8	1450 (100)	440 (130)	1890 (30)	17.0 (1.1)	7.2 (2.1)	24.2 (0.9)	321 (21)	74 (21)	395 (1)	16.3 (0.6)	1.29 (0.03)
25.6	2100 (20)	330 (160)	2430 (140)	23.6 (0.1)	5.8 (5.5)	29.1 (3.0)	478 (4)	60 (28)	538 (24)	18.5 (1.07)	1.21 (0.05)
31.4	2070 (10)	330 (50)	2400 (30)	25.4 (0.7)	5.7 (0.8)	31.1 (0.1)	436 (6)	58 (9)	494 (4)	15.9 (0.07)	1.30 (0.02)

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