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Nitrogen saturation in a high elevation New England spruce–fir stand ¹

Steven G. McNulty ^{a,*}, John D. Aber ^b, Steven D. Newman ^b

^a *Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Rd., Otto, NC 28734, USA*

^b *Complex Systems Research Center, Morse Hall, University of New Hampshire, Durham, NH 03824, USA*

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Nitrogen saturation in a high elevation New England spruce–fir stand¹

Steven G. McNulty^{a,*}, John D. Aber^b, Steven D. Newman^b

^a *Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Rd., Otto, NC 28734, USA*

^b *Complex Systems Research Center, Morse Hall, University of New Hampshire, Durham, NH 03824, USA*

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Abstract

High-rates of nitrogen (N) deposition were first postulated as a cause of N saturation (i.e. the availability of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in excess of total combined plant and microbial nutritional demand) and spruce mortality during the 1980s. To test this hypothesis, N addition plots were established in 1988, in a high elevation spruce–fir forest in southeastern Vermont, an area of relatively low N deposition ($5.4 \text{ kg N bulk deposition ha}^{-1} \text{ year}^{-1}$). To test how the form of applied N may influence forest growth and N-cycling, four replicated treatment plots received either $\text{NH}_4\text{Cl-N}$, $\text{NaNO}_3\text{-N}$, or a combination of both N forms at rates ranging from 15.7 to $31.4 \text{ kg N ha}^{-1} \text{ year}^{-1}$. The N additions were applied in three equal doses each year between June and August from 1988 to 1994. In addition to N treatments, two control plots were also established. Between 1988 and 1990, annual in situ net N mineralization and net nitrification in the forest floor, litterfall and forest floor mass and elemental concentration, foliar elemental concentration, and basal area growth by species were measured on each plot. In July 1994, basal area growth by species, net N mineralization potential and net nitrification potential in the forest floor, and foliar and forest floor elemental concentration were again measured on all plots. Inter-treatment and intra-treatment basal area growth changed substantially between 1988 and 1994. Spruce, fir, and birch trees on the N addition plots receiving $< 20 \text{ kg N ha}^{-1} \text{ year}^{-1}$ had the highest rate of growth between 1988 and 1990 and then had the highest rate of decline between 1991 and 1994. Spruce, fir, and birch trees on the N addition plots receiving $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$ showed moderate rates of decline from 1988 to 1994. Numerous birch and maple sprouts were noted on the sites with the highest rates of decline, but no spruce or fir seedlings were observed. In July 1994, net N mineralization potential was highest on the control plots and net nitrification potential of the forest floor was highest on the plots receiving $15.7 \text{ kg N ha}^{-1} \text{ year}^{-1}$. A strong positive correlation existed between forest floor %N and net nitrification potential. Foliar %N was positively correlated with added N and negatively correlated with the change in net basal area growth. Foliar Ca:Al concentrations may also be negatively related to changes in net basal area growth. Our results suggest that N saturation has caused foliar nutrient imbalances on the N addition plots, and that the stands may be changing in species composition and structure. No long-term effects of N-form additions on N saturation and forest health were observed. Continued N additions

* Corresponding author.

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may change the stands from a slow growing and slow N-cycling coniferous forest, to a fast N-cycling and fast growing deciduous forest.

Keywords: N saturation; Mt. Ascutney; Red spruce; *Picea rubens*; Nutrient imbalance; Mortality; Fertilization

1. Introduction

During the last 2 decades, high rates of spruce decline have occurred across the northern and southern Appalachians (Peart et al., 1992) and Europe (Nihlgard, 1985; Schulze et al., 1989). Possible causes of this decline are nitrogen (N) availability in excess of plant demand (Nihlgard, 1985; Aber et al., 1989; Schulze et al., 1989), drought (Johnson and Siccama, 1983), Al toxicity in roots (Shortle and Smith, 1988), foliar nutrient imbalance (Zoettl and Huettl, 1986; Cronan and Grigal, 1995), reduced cold tolerance (Sheppard, 1994), and freezing injury (DeHayes, 1992). In areas where spruce decline is the highest, many pollutants have high deposition rates (e.g. SO_x , NO_x , heavy metals). Increases in pollutant loading are often accompanied by reductions in forest floor pH (Shortle and Smith, 1988; Cronan and Schofield, 1990), increased forest floor heavy metal concentrations (Andresen et al., 1980; Friedland et al., 1984a, Friedland et al., 1984b; Herrick and Friedland, 1990), and leaching of soil Al and Ca (Cronan and Schofield, 1979; Berg, 1986; Johnson et al., 1994).

The interactions among pollutants and changes in forest processes make it difficult to identify the cause(s) for the decline. Although the 1990 United States (US) Clean Air Act has targeted a 50% reduction in S deposition, only about a 10% reduction in N deposition is required (and expected). Therefore, N deposition is more likely to have potential impacts on forest structure and function in the future. To examine the influence of N inputs alone on spruce–fir forest N-cycling and forest health (i.e. tree mortality and growth), we established a series of N addition plots on Mt. Ascutney, Vermont, in 1988 (McNulty and Aber, 1993). Our objective was to observe changes in N-cycling associated with varying rates and forms of N inputs, to determine if and when N saturation (i.e. the availability of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in excess of total combined plant and microbial nutritional demand) occurred within each treatment,

and to observe changes in forest health associated with N saturation. We used two types of N-fertilizer to assess the ecosystem's ability to absorb anionic and cationic forms of N. As an anion, we hypothesized that $\text{NO}_3\text{-N}$ would not be absorbed by the forest floor, but would leach through the ecosystem, and deplete cations, such as Ca, from soil colloids. Therefore, $\text{NO}_3\text{-N}$ additions could have a minimal impact on N availability, but a potentially large impact on cation availability, soil acidification, and Al mobility (Aber et al., 1989; Raloff, 1995). Conversely, the cation $\text{NH}_4\text{-N}$ would more likely be retained by the ecosystem, thus conserving cations and potentially increasing N availability. During this period, annual in situ net N mineralization and net nitrification in the forest floor, litterfall and forest floor amount and elemental concentration, foliar elemental concentration, and basal area (BA) growth by species were measured on each plot. Results from 1988 to 1991 suggest that N addition plots receiving $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$ may have been in the early stages of N saturation, while plots receiving $< 20 \text{ kg N ha}^{-1} \text{ year}^{-1}$ still had increased BA growth compared with control and high N input plots (McNulty and Aber, 1993). No substantial long-term (after 3 years of treatment) changes were detected between the form of N applied and forest health or N saturation. As N additions continued from 1991 to 1994, forest processes and stand composition changed. This paper discusses the effects of continued N additions on N-cycling and tree growth and mortality and presents a possible scenario for future forest structural and functional changes given continued additions of N.

2. Materials and methods

2.1. Study plots

During June 1988, ten $15 \times 15 \text{ m}$ plots were established at an elevation of 762 m a.s.l., on Mount

Ascutney, Vermont (42°26'N, 72°27'W), where red spruce (*Picea rubens* Sarg.) grows in large patches (> 1 ha) at elevations above 725 m. Red spruce comprises > 80% of the total basal area; the remainder is divided between balsam fir (*Abies balsamea*), red maple (*Acer rubrum*), mountain maple (*Acer spicatum*), and birch (*Betula* spp.) (McNulty and Aber, 1993). Study plots were randomly located within these patches. Before N additions, no statistically significant (paired t -test $P > 0.05$) differences in stand structure, stand species composition, net N mineralization and net nitrification of the forest floor or foliar chemistry existed among plots (McNulty, 1991; McNulty and Aber, 1993).

These plots receive approximately 1000 mm of precipitation year⁻¹, 70% in frozen form as sleet or snow (McNulty and Aber, 1993). The area is characterized by warm summers (average July air temperature 22°C) and cold winters (average January air temperature -6°C) (USDC, 1968). Located on broad areas between rock outcrops, the plots are on Houghtonville soils classified as frigid Typic Haplorthods. The soils are well-drained and have 3 to 15% slopes (USDA Soil Conservation Service, 1989).

2.2. Nitrogen additions

One pair of plots (controls) received no N-fertilizer. Four pairs of plots were randomly selected to be amended with NH₄Cl-N and (or) NaNO₃-N during June, July, and August from 1988 to 1994 (Table 1). The rates of N application were comparable to annual N deposition rates recorded in spruce-fir ecosystems located in industrialized regions in the US (e.g. 16 kg N ha⁻¹ year⁻¹, Friedland et al.,

1991) and western Europe (e.g. 30 to 40 kg N ha⁻¹ year⁻¹, Grennfelt and Hultberg, 1986). Across New England, N deposition increases from east to west (McNulty et al., 1990). The Mt. Ascutney plots are located slightly east of the area where signs of N saturation have been observed (McNulty et al., 1991), and the plots did not exhibit any of the initial symptoms of N saturation presented by Aber et al. (1989). Bulk precipitation collectors measured 5.4 kg N ha⁻¹ year⁻¹ in open areas adjacent to the research plots (McNulty and Aber, 1993). By supplementing the long-term inputs of anthropogenic N deposition with additional N-fertilizer at a rate equal to high rates of N deposition found elsewhere, we hypothesized that N saturation could be induced on these plots.

2.3. Basal area change

In June 1988, prior to the start of N additions, basal area (BA), species, and tree condition (i.e. living vs. dead) were recorded for all trees > 2 cm at 1.5 m above the forest floor. In November 1990, and July 1994, the trees within each plot were again measured and compared to initial measurements. Changes in BA were divided into two growth periods: 1988 to 1990 (Period 1) and 1991 to 1994 (Period 2). Net BA growth was calculated by subtracting total BA death from total BA growth.

2.4. Forest floor net N mineralization and net nitrification

From July 1988 to June 1991, 40 forest floor samples with an average area of 150 cm² were

Table 1
Design of N addition experiment on Mount Ascutney, Vermont. Nitrogen was added in three equal doses during June, July, and August 1988 to 1994

Plot number	Monthly amendment (kg N ha ⁻¹ per application)		Total annual amendment (kg N ha ⁻¹ year ⁻¹)
	NH ₄ Cl-N	NaNO ₃ -N	
1,6	0.0	0.0	0.0
4,10	5.2	0.0	15.7
2,8	0.0	6.6	19.8
5,9	5.2	3.3	25.6
3,7	10.5	0.0	31.4

collected monthly (except over-winter samples which were incubated in situ from September to April), from each plot. Twenty samples from each plot were randomly combined into five samples per plot and sieved through a No. 18 mesh screen to remove twigs, coarse roots, and stones. Combining samples ensured sufficient sample mass for analysis. Approximately 10 g of each of the five composite samples from each plot were placed into 150 ml of 1 M KCl for 48 h. After 48 h, approximately 20 ml of solution extract was removed and frozen at 0°C until analyzed for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations.

The remaining 20 samples from each plot were placed into 1-ml (2.54×10^{-4} mm) thick polyethylene bags, replaced into the forest floor and incubated in situ for 28 days. The 20 incubated samples were then composite, sieved, and extracted as previously described. Initial and incubated extracts were run on a TRAACS 800 Auto-analyzer for $\text{NH}_4\text{-N}$ (Technicon Industrial Systems, 1978) and $\text{NO}_3\text{-N}$ (Technicon Industrial Systems, 1977) concentrations. Net annual N mineralization was calculated as the sum of monthly incubated sample ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) minus initial monthly sample ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$). Net annual nitrification was calculated as the sum of monthly incubated sample $\text{NO}_3\text{-N}$ minus initial monthly sample minus $\text{NO}_3\text{-N}$.

In July 1994, 40 forest floor samples were collected and sieved as previously described. Half of the samples were composite, placed in KCl for 48 h, extracted, and run on the auto-analyzer to measure initial $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ concentration, while the other half were lab. incubated at 22°C for 28 days. After 28 days the samples were composited as previously described, placed in KCl for 48 h, extracted, and run on a auto-analyzer to measure incubated $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ concentration. Net N mineralization and net nitrification potentials were calculated as previously described.

2.5. Forest floor chemistry

In June, 1988 (before the first N additions), and in July 1994, 20 forest floor samples, each with an average area of 150 cm² were collected from each plot and randomly composited into five samples per plot. The samples were sieved through a 5 × 5-mm mesh screen to remove all twigs, coarse roots, and

stones. Carbon (C), hydrogen (H), and N were measured in these samples using a Perkin-Elmer model 240B CHN analyzer. Two (of the five) forest floor samples were randomly selected for pH measurements, using a 1:2 (w/v) forest floor to CaCl_2 (0.01 M) solution.

2.6. Foliar chemistry

Three randomly selected dominant red spruce trees were tagged on each plot at the beginning of the experiment. In July 1988, 1990, and 1994, three randomly oriented, sunlit, or understory branch samples, each containing needles from all age classes were removed from each tagged tree using a pruning pole. The clipped branches from each tree were placed in a large paper bag and dried for 48 h at 70°C. After drying, all branch needles had fallen into the bag. The contents of the bag were shaken to homogenize the age classes, and a randomly selected sub-sample was sieved through a 2 × 2-mm mesh screen to remove twigs and detritus, and ground through a No. 10 mesh using a Wiley Mill. The samples were placed in 60-ml acid-washed 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). After determination of N and lignin concentration, cation concentration of the foliar samples were measured using 0.5 g of leaf tissue ashed at 450°C for 4 h and added to 10 ml of plant buffer. One liter of buffer consisted of 300 ml HCl, 100 ml HNO_3 , 20 ml of 1000 ppm Mo Standard, and both to volume (Jones, 1988). The extracts were analyzed using inductively coupled argon plasma emission spectroscopy (Jarrell-Ash 965 Atomcomp).

3. Results and discussion

3.1. Basal area change

A substantial shift in net BA growth occurred on the fertilized plots between Period 1 (1988 to 1990) and Period 2 (1991 to 1994) (Fig. 1). During Period 1, total plot net BA growth was highest for plots receiving $< 20 \text{ kg N ha}^{-1} \text{ year}^{-1}$, suggesting a

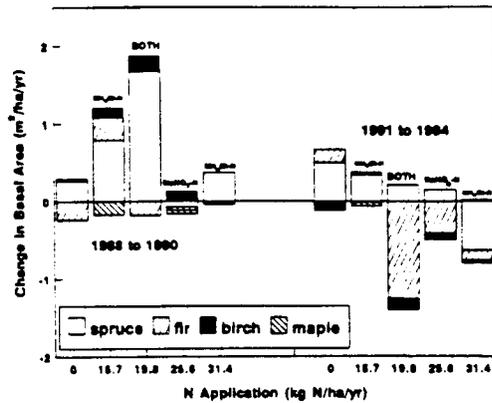


Fig. 1. Average basal area growth by species on ten spruce-fir plots (four paired N addition treatments, and one paired control) on Mt. Ascutney, Vermont, during Period 1 (1988 to 1990) and Period 2 (1991 to 1994).

fertilization response at these rates of N addition. Plots receiving $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$ showed little or no growth increase, suggesting that N was no longer limiting growth. The $25.6 \text{ kg NaNO}_3\text{-N ha}^{-1} \text{ year}^{-1}$ plots were the only treatments to have a negative total growth rate (i.e. net mortality), but rates of mortality were not significantly different (paired τ -test $P > 0.05$, $n = 2$) from the high $31.4 \text{ kg NH}_4\text{Cl-N ha}^{-1} \text{ year}^{-1}$ plots or the control plots. The plots receiving a combination of N-fertilizer at a rate of $19.8 \text{ kg N ha}^{-1} \text{ year}^{-1}$ had the highest average annual spruce BA growth.

During Period 2, net BA growth was the highest on the control plots ($+0.55 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$) and lowest in the $19.8 \text{ kg N ha}^{-1} \text{ year}^{-1}$ addition plots ($-1.19 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$). Most of the negative net BA growth on the $19.8 \text{ kg N ha}^{-1} \text{ year}^{-1}$ plots can be attributed to a large reduction in living balsam fir. The $15.7 \text{ kg N ha}^{-1} \text{ year}^{-1}$ plots were the only N additions plots to show a positive net BA growth rate ($+0.31 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$), but net BA growth decreased on all the plots receiving N-fertilizer, compared with Period 1 (Fig. 1). Red spruce net BA growth was positive for all plots except those receiving $31.4 \text{ kg NH}_4\text{Cl-N ha}^{-1} \text{ year}^{-1}$, and red spruce net BA growth was inversely correlated to the amount of N added (Fig. 1).

3.2. Mortality

Stand mortality is defined as the fraction of trees in each stand, separated by species, that die each

period. Because mortality expresses change as a percentage, variation in initial stand stocking is removed from the assessment of tree mortality at the plot level. During both periods (1 and 2), the trees in the two control plots had a mortality rate of approximately $3\% \text{ year}^{-1}$ (standard error (σ) = 4% (Period 1), and 3% (Period 2)) (Fig. 2). In Period 1, all N-fertilized plots had very low rates of average stand mortality ($< 1\% \text{ year}^{-1}$) and inter-plot variation in mortality ($\sigma = 1\%$). In the plots receiving $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$ during Period 1, the number of ingrowth stems was greater than or equal to the number of dying trees, thus net stand mortality was $\leq 0\%$.

During Period 2 (1991 to 1994), stand mortality in the N addition plots increased to 5 to $9\% \text{ year}^{-1}$ ($\sigma = 2$ to 3%) because no species had sufficient ingrowth of stems to replace dying individuals, mortality rates were positive for all plots and species (Fig. 2). N addition plots receiving $< 20 \text{ kg N ha}^{-1} \text{ year}^{-1}$ had the highest rates of mortality ($> 8\% \text{ year}^{-1}$), but because there were only two plots per treatment, the differences in mortality rates between treatments were not statistically significant using a paired τ -test ($P > 0.05$, $n = 2$).

Although not quantified, we observed increased stump sprouting and seedling establishment of maple (*Acer* spp.) and birch (*Betula* spp.) species on the plots with the highest mortality. The reason for this

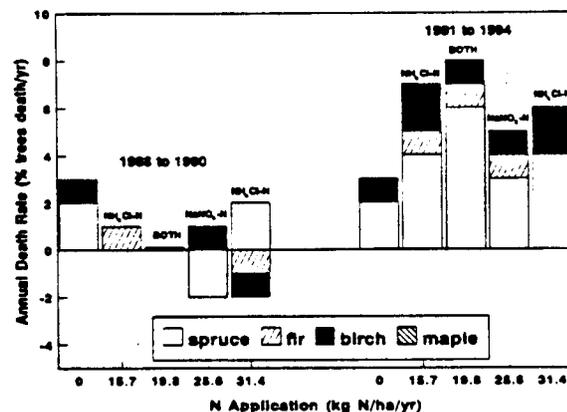


Fig. 2. Average annual mortality by species on ten spruce-fir plots (four paired N addition treatments, and one paired control) on Mt. Ascutney, Vermont, during Period 1 (1988 to 1990) and Period 2 (1991 to 1994).

increase in deciduous species regeneration is not clear (i.e. increased light availability onto the forest floor, increased forest floor temperature, or increased N availability), but a shift in species composition may be occurring on the N addition plots.

3.3. Net N mineralization and net nitrification potential

The possible reason trees in the N-fertilized plots were growing more slowly or had a higher mortality rate than those in the control plots was then examined. Net N mineralization and net nitrification patterns have changed since N additions began in 1988. The plot receiving $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$ had the highest rates of annual in situ net N mineralization during Period 1 (1988–1990), but annual in situ net N mineralization declined over time with the $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$ plots having the lowest rates of net N mineralization at the end of Period 1 (McNulty and Aber, 1993). The same pattern of declining net N mineralization was observed in July 1994, when net N mineralization potential was measured in the laboratory (Table 2). In July 1994, the highest rates of net N mineralization potential were on the control and $15.7 \text{ kg NH}_4\text{Cl-N ha}^{-1} \text{ year}^{-1}$ plots (Table 2). Using the July 1994 forest floor samples, no pattern was observed regarding the form of N applied and net N mineralization potential or net nitrification potential.

Over the years, as N additions continued on plots, the total amount of net N mineralization and net

nitrification potential decreased, but the percentage of mineralized N that was nitrified increased. Before the N additions, no net nitrification was detected on any of the plots (McNulty and Aber, 1993) suggesting that forest floor N concentrations may have been too low to support nitrifiers. These results are supported by McNulty et al. (1990), who found no net nitrification potential in undisturbed spruce–fir sites located in areas of low N deposition. Following the first year of N application, the fraction of net mineralized N which was nitrified rose to approximately 5% on plots receiving $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$ and no net nitrification occurred on the plots receiving $< 20 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (McNulty and Aber, 1993). In the July 1994 sampling, the fraction of mineralized N that was nitrified was approximately 12% of total net N mineralization potential on the plots receiving $< 20 \text{ kg N ha}^{-1} \text{ year}^{-1}$, and a strong correlation was observed between forest floor %N and net nitrification potential (Fig. 3). When forest floor N was below 1.35%, no net nitrification potential was observed, but when forest floor N was $> 1.35\%$, net nitrification was linearly correlated with forest floor %N ($r^2 = 0.92$, $P < 0.05$, $n = 4$) (Fig. 3). Both the intercept and slope of this relationship are very similar to earlier work (McNulty et al., 1991), that related forest floor %N and net nitrification potential on 161 plots located in 11 areas across New England (Fig. 3). The Mt. Ascutney data support the hypothesis that nitrifiers living in these very acidic, organic soil horizons need forest floor N concentrations $> 1.4\%$ to nitrify. If forest decline

Table 2

Change in forest floor %N, C:N ratio, net N mineralization potential (N miner.), net nitrification potential (nitrif.), and the percent of mineralized N that was nitrified (% nitrif.) on Mt. Ascutney, Vermont, spruce–fir plots between 1988 (pre-N additions) and 1994. The standard error for the mean of each value is in parentheses. Five forest floor samples were collected from each of two plots per treatment for a total of ten samples per treatment

Treatment (kg N ha^{-1} year^{-1})	Forest floor N (%)		Forest floor C:N (kg:kg)		July, 1994, collected forest floor (mg N kg^{-1} soil per 28 days)		
	1988	1994	1988	1994	N miner.	Nitrif.	% Nitrif.
0	1.22 (0.16)	1.36 (0.05)	29.4 (0.1)	32.1 (0.8)	50.0 (12.8)	0.0 (0.0)	0
15.7	1.47 (0.01)	1.47 (0.05)	29.2 (0.4)	32.01 (1.0)	56.6 (21.5)	6.8 (3.3)	12
19.8	1.44 (0.06)	1.39 (0.07)	29.4 (0.8)	31.7 (0.9)	38.6 (15.1)	1.8 (1.1)	5
25.6	1.35 (0.14)	1.28 (0.11)	29.5 (0.4)	28.3 (0.4)	9.6 (5.7)	0.0 (0.4)	0
31.4	1.30 (0.04)	1.40 (0.06)	30.0 (0.9)	29.7 (0.4)	38.7 (27.9)	0.7 (0.6)	2

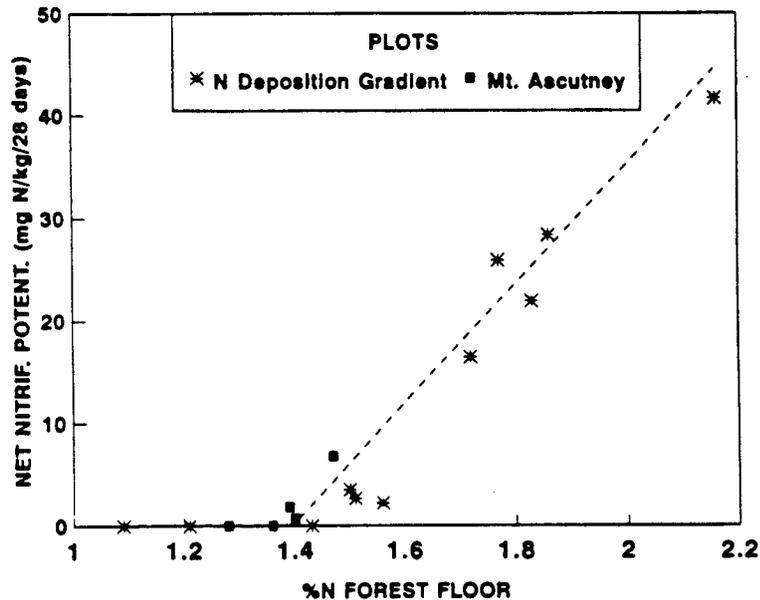


Fig. 3. Relationship between average forest floor %N and 28-day net nitrification potential on ten spruce–fir plots (four paired N addition treatments, and one paired control) on Mt. Ascutey, Vermont, sampled in July 1994, and average forest floor %N and 28-day net nitrification potential for 11 sites across a New England N deposition gradient sampled from June to August in 1987 and 1988.

(i.e. reduced N demand) occurs in conjunction with increased net nitrification, significant losses of nitrate are possible (Durka et al., 1994).

No relationships were found between the form of N addition and the rate of net N mineralization or net nitrification between 1988 and 1991, or between net N mineralization or net nitrification potential in July 1994.

3.4. Forest floor chemistry

From 1988 to 1994, up to 220 kg $\text{NH}_4\text{Cl-N ha}^{-1}$ (31.4 kg $\text{NH}_4\text{Cl-N ha}^{-1}$ year $^{-1}$ plots), or 180 kg $\text{NaNO}_3\text{-N ha}^{-1}$ (25.6 kg $\text{NaNO}_3\text{-N ha}^{-1}$ year $^{-1}$) representing up to a 20% addition to the existing 1150 kg N ha $^{-1}$ average forest floor N content (McNulty and Aber, 1993) have been added to the plots. Despite these additions, forest floor %N has not significantly changed on any of the plots (Table 2), suggesting that N is immobilized in decomposing wood, taken up by the vegetation, is leaching from the ecosystem or that variation in forest floor chemistry is too large relative to the change in N to detect any noticeable differences. Loss of N as $\text{N}_2\text{O-N}$ was

also not significant because < 0.1 kg $\text{N}_2\text{O-N ha}^{-1}$ per growing season is released from either the high N addition or control plots (Castro et al., 1993). The change in woody debris N concentration and mass have not been measured over time, but the significant increase in foliar N concentrations (Fig. 4) partially account for the lack of change in forest

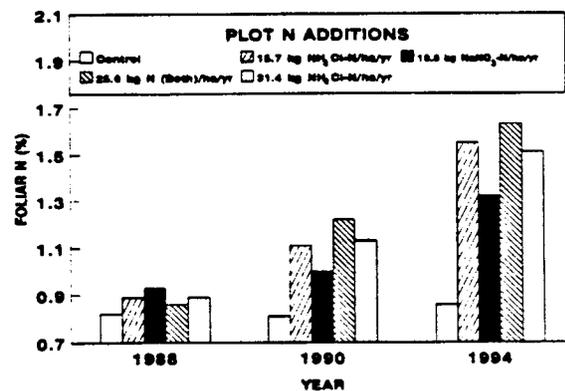


Fig. 4. Average red spruce foliar %N collected in July 1988, 1990, and 1994 on ten spruce–fir plots (four paired N addition treatments, and one paired control) on Mt. Ascutey, Vermont.

floor %N. During the first 2 years of treatment (1988 and 1990), control and N addition plot litterfall mass and quality were measured (McNulty and Aber, 1993). Red spruce litterfall from the control plots averaged $1500 \text{ kg ha}^{-1} \text{ year}^{-1}$, and using a foliar retention time of 8 years, total spruce foliar biomass on control plots was equal to $12.0 \text{ t foliage ha}^{-1}$. Using 0.90% N for spruce foliage, the control plots contained approximately $110 \text{ kg organic N ha}^{-1}$ in foliage. Assuming that the high N addition plots also contained $12 \text{ t foliage ha}^{-1}$, these plots would retain $180 \text{ kg organic N ha}^{-1}$ (given a 1.5% N of green leaf tissue). The difference between control and high N addition plots foliar N storage is only 80 kg N . Because forest growth is now less on the treatment plots than on controls, and the treatment plots were losing more litter each year than control plots (McNulty and Aber, 1993), the differences in N storage between control and N addition plots is likely $< 80 \text{ kg organic N}$.

The greatest loss of N (especially N applied as $\text{NO}_3\text{-N}$) may occur through leaching of N from the forest floor. Potential loss of N through leaching was supported by McNulty and Aber (1993), who found higher levels of N in resin bags located at the base of the forest floor in N-fertilized plots ($> 800 \text{ ppm NO}_3\text{-N } 10\text{g}^{-1}$ resin and $> 600 \text{ ppm NH}_4\text{-N } 10\text{g}^{-1}$ resin) than in control plots ($< 20 \text{ ppm NO}_3\text{-N } 10\text{g}^{-1}$ resin and $< 15 \text{ ppm NH}_4\text{-N } 10\text{g}^{-1}$ resin). Between 1989 and 1991, ion exchange resin bags placed at the base of the forest floor detected substantial differences in $\text{HN}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations relating to the form of N applied to each plot (McNulty and Aber, 1993). No clear trend was observed between the amount of N added and changes in the forest floor C:N ratio, which also suggests that N is not

retained in the forest floor. Across all plots, forest floor pH was very low (2.7 to 3.0) at the beginning of N-fertilization in 1988 and had not changed significantly (paired τ -test $P > 0.05$, $n = 4$) when measured during the 1994 sampling (i.e. pH ranged from 2.6 to 3.0).

3.5. Spruce foliar chemistry

From the July 1994 sampling, the control plots had the lowest average foliar %N, while the 25.6 and $31.4 \text{ kg N ha}^{-1} \text{ year}^{-1}$ plots had the highest average foliar %N (Table 3). Foliar N concentration increased significantly between the July 1990 sampling and the July 1994 sampling (paired τ -test, $\tau = 8.18$, $P < 0.0001$, $n = 12$) on the N-fertilized plots, but the foliar N concentrations on the control plots were not statistically different between measurement periods (paired τ -test $P > 0.05$, $n = 12$) (Fig. 4). Control plot foliar N was significantly lower (paired τ -test, $\tau = 8.6$, $P < 0.0001$, $n = 12$) than the foliar concentrations of plots receiving $> 20 \text{ kg N ha}^{-1} \text{ year}^{-1}$, and the foliar N concentration of spruce from the $25.6 \text{ kg N ha}^{-1} \text{ year}^{-1}$ was significantly higher (paired τ -test, $\tau = 16.9$, $P < 0.0001$, $n = 12$) than all other treatment or control plots. These foliar N concentrations are higher than any values reported for red spruce across an N deposition gradient in New England (Fernandez and Struchtemeyer, 1984; Friedland et al., 1988; Huntington et al., 1990; McNulty et al., 1991) and may represent the upper limit of that red spruce foliar N concentrations under N addition field conditions.

The July 1994 foliar N concentration was inversely correlated to BA growth up to the 25.6 kg N

Table 3

Variation in red spruce foliar chemistry on Mt. Ascutney, Vermont, spruce-fir plots collected in July 1994. The standard error for the mean of each value is in parentheses. Six foliage samples were collected from each of two plots per treatment for a total of 12 samples per treatment

Treatment ($\text{kg N ha}^{-1} \text{ year}^{-1}$)	N (%)	Lignin (%)	Ca (g kg^{-1})	Al (mg kg^{-1})	N:Ca (molar ratio)	Ca:Al (molar ratio)
0	0.85 (0.03)	24.1 (0.6)	3.5 (0.3)	34 (4)	7.1 (0.11)	69 (8)
15.7	1.30 (0.05)	24.6 (0.9)	3.5 (0.5)	32 (4)	11.0 (0.09)	73 (7)
19.8	1.23 (0.06)	23.8 (0.7)	3.1 (0.4)	32 (3)	11.3 (0.12)	65 (7)
25.6	1.51 (0.07)	23.4 (1.1)	3.4 (0.4)	36 (4)	13.1 (0.18)	63 (6)
31.6	1.47 (0.07)	24.2 (0.7)	3.1 (0.3)	38 (3)	14.0 (0.18)	55 (5)

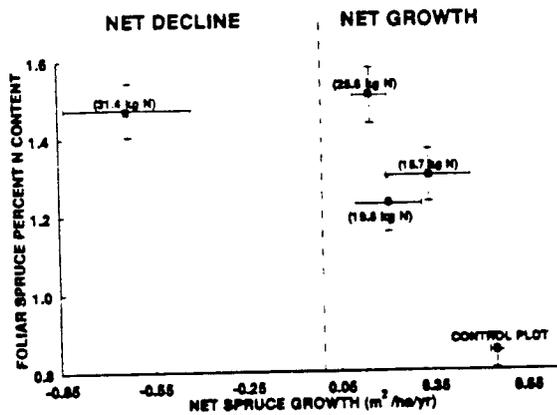


Fig. 5. Relationship between foliar N% collected in July 1994 and red spruce annual BA growth from 1991 to 1994 on ten spruce–fir plots (four paired N addition treatments, and one paired control) on Mt. Ascutney, Vermont.

ha⁻¹ year⁻¹ addition level (Fig. 5). Although the 31.4 kg N ha⁻¹ year⁻¹ addition plots, had the highest rate of decline, the foliar N concentration were not higher than in the 25.6 kg N ha⁻¹ year⁻¹ addition plots. These results indicate that even relatively low additions of chronically applied N can potentially cause reduction in forest growth and ultimately stand decline. No differences in BA growth or mortality rates relating to the form or N applied were observed.

In July 1994, red spruce foliar Ca concentrations in control and fertilized plots did not differ significantly (paired τ -test $P > 0.05$, $n = 12$) (Table 3). Our measured foliar Ca concentrations are in the mid-to-upper range of values reported by others including MacLean and Robertson (1981) (1.8 to 3.1 g Ca kg⁻¹); Fernandez and Struchtemeyer (1984) (1.9 to 11.6 g Ca kg⁻¹, mean 4.5 g Ca kg⁻¹); Friedland et al. (1988) (1.8 to 4.1 g Ca kg⁻¹); Joslin et al. (1992) (2.7 g Ca kg⁻¹ (low elevation), 2.4 g Ca kg⁻¹ (high elevation)); and Thornton et al. (1994) (0.9 g Ca kg⁻¹ to 1.1 g Ca kg⁻¹). Foliar Ca concentrations are well above the minimum level of 0.5 g Ca kg⁻¹ to 0.8 g Ca kg⁻¹ which serve as an indicator of Ca deficiency (Swan, 1971). However, these minimum deficiency levels were developed under greenhouse conditions (Swan, 1971), and levels of nutrient deficiency may be different for mature trees (Joslin et al., 1992). Thornton et al. (1994)

suggested that a minimum deficiency level of 0.17% may be a more accurate level for mature red spruce. However, the Mt. Ascutney red spruce foliar samples were also well above this Ca concentration (Table 3).

Foliar Al concentrations from the July 1994 collection were restricted to a narrow range across the plots (Table 3), and are within the spruce foliar Al concentration averages reported by Joslin et al. (1992) for several low elevation (31 mg kg⁻¹ Al) and high elevation (39 mg kg⁻¹ Al) spruce stands. Any analysis of variance correlation between N added and foliar Al concentration was not significant (paired τ -test $P > 0.05$, $n = 12$) in this study.

The proportion of nutrients (e.g. Al, N, Ca) may be a better measure of forest health than the absolute concentration of each individual nutrient because disproportionate levels of nutrients could lead to an imbalance even if neither nutrient level in itself is deficient (van Dijk and Roelofs, 1988; Cronan and Grigal, 1995). Foliar Ca:Al molar ratios from the July 1994 collection had a wider range of mean plot values (i.e. 55 to 69) because foliar Ca concentration tended to decrease and foliar Al concentration tended to increase with increased N additions to plots (Table 3). Because there were only two plots per treatment, the intra-treatment standard deviation is large enough that the difference in foliar Ca:Al concentrations are not statistically significant (paired τ -test $P > 0.05$, $n = 2$). However, the average treatment foliar Ca:Al

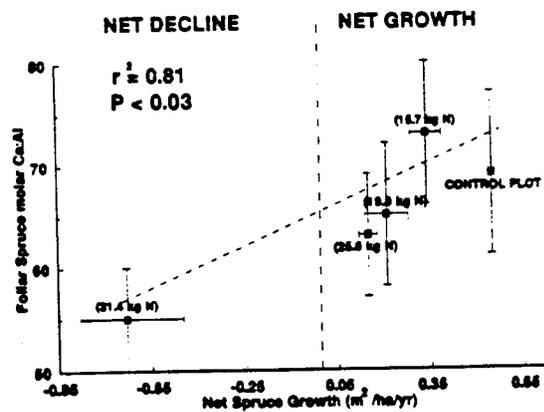


Fig. 6. Relationship between foliar Ca:Al molar ratios collected in July 1994 and red spruce annual basal area growth from 1991 to 1994 on ten spruce–fir plots (four paired N addition treatments, and one paired control) on Mt. Ascutney, Vermont.

was inversely related to N-fertilization ($r^2 = 0.93$, $P = 0.04$, $n = 5$) and net spruce BA growth (Fig. 6). A literature review by Cronan and Grigal (1995) found that foliar Ca:Al molar ratios between 11.4 and 14 can adversely affect forest growth. Cronan and Grigal (1995) note that the reported levels of impact (i.e. threshold levels) were often observed at the lowest level of foliar Al concentration and the actual threshold level may be higher. Also, of the 36 studies of plant Ca:Al ratios affecting growth, only three studies used forest soils (but not necessarily in situ soils), indicating the need for increased research under field conditions. The lowest foliar spruce Ca:Al molar ratio on Mt. Ascutney was 55 and occurred on the highest N addition plot (Table 3). This ratio is approximately four times higher than values reported by Cronan and Grigal (1995) as causing adversely affecting forest growth.

On Mt. Ascutney plots, excessive N may be adversely affecting forest health before large increases in foliar Al, or decreases in foliar Ca or Ca:Al ratio occur. McLaughlin et al. (1991) concluded that low foliar Ca:Al ratios may be related to decreased leaf carbon balances among conifers growing on sites altered by pollutant additions, including N. Although mechanisms by which N inputs might alter plant Ca nutrition have been suggested (McLaughlin and Kohut, 1992), how N availability, Ca, and Al interrelate and affect plant carbohydrate production and use remains unknown. Measurements of photosynthetic capacity have been used to evaluate the carbon economies of red spruce to relate differences in leaf N and Ca concentrations to tree vigor. Field assessments of red spruce in the southern extent of its range in the US have shown that trees at high elevations and declining trees at any elevation have higher rates of dark respiration, lower foliar Ca concentrations, and higher foliar Al concentrations than trees at lower elevations and healthy trees at any elevation (McLaughlin et al., 1990, McLaughlin et al., 1991). Nutrient deficiencies, imbalances, or both may lead to carbon depletions which predispose trees to the detrimental impacts of other stresses such as drought or freezing injury (DeHayes, 1992; McLaughlin and Kohut, 1992). Winter physiological studies on Mt. Ascutney plots during January of 1994 and 1995 indicate an inverse correlation between N addition and cold tolerance of red spruce

foliage (T.D. Perkins and S.G. McNulty, unpublished data, 1995).

3.6. Potential future changes in plot structure and function

In areas of low N deposition, N availability is primarily dependent on net N mineralization. However, as N deposition increases, a larger portion of the N needed for plant growth and development can be supplied directly from atmospheric sources. As N-fertilization continues, the linkage between net N mineralization, N uptake, foliar N concentration, and litter quality degenerates. From 1988 to 1990, fertilized plots had increased net N mineralization, foliar %N, forest growth, and litter quality. However, as fertilization continued, net N mineralization potential and forest growth decreased while foliar %N remained high. These results suggest that N is no longer limiting, and that excess N may be leaching from the ecosystem (McNulty and Aber, 1993) causing foliar nutrient imbalances and forest decline. If anion leaching continues (McNulty and Aber, 1993), Ca and Mg may be leached and nutrient imbalances increase (Table 3). Much of the available Ca is obtained through the weathering of parent material (Woodwell and Whittaker, 1967; Likens et al., 1970). If nutrient leaching could be reduced, cation weathering could increase Ca availability and reduce nutrient imbalances despite continued N-fertilization. On the plots receiving $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$ as fertilizer, a total of approximately $50 \text{ kg N ha}^{-1} \text{ year}^{-1}$ ($30 \text{ kg N ha}^{-1} \text{ year}^{-1}$ from fertilization and $5 \text{ kg N ha}^{-1} \text{ year}^{-1}$ from bulk N deposition, and $15 \text{ kg N ha}^{-1} \text{ year}^{-1}$ from net N mineralization) is available for plant, mycorrhizae and microbial uptake. This level of N availability is at the low end of measured values for deciduous broad-leaved forests (Pastor et al., 1984), which typically have higher foliar N contents, better litter quality (lower lignin:N), and higher N demand than needle-leaved evergreens. Greater N demand by deciduous broad-leaved species (e.g. *Betula* spp. and *Acer* spp.) could decrease $\text{NO}_3\text{-N}$ leaching by reducing available $\text{NO}_3\text{-N}$ through increased leaf-based nitrate reductase activity (Smirnov et al., 1984; Smirnov and Stewart, 1985). Downs et al. (1993) found higher rates of foliar nitrate reductase activity in *Acer rubrum* (red

maple) seedlings exposed to levels of $\text{NO}_3\text{-N}$ equal to $\text{NO}_3\text{-N}$ deposition rates experienced across New England than in seedlings not exposed to elevated levels of $\text{NO}_3\text{-N}$.

In this study, growth declined in both coniferous and deciduous trees when fertilization continued after 1990 (Period 2). However, in the plots with the greatest percentage of tree mortality, numerous deciduous stump sprouts, and some deciduous seedlings emerged, while spruce or fir did not regenerate. Heavy birch and maple regeneration was also observed in areas of high N deposition and spruce–fir decline across New England in 1987 and 1988 (S.G. McNulty and J.D. Aber, unpublished data, 1988). We propose that additional N will continue to reduce spruce–fir dominance in the fertilized plots, and that spruce–fir will be replaced by the cold tolerant, N demanding species already present on the plots in low numbers (i.e. *Betula* spp. and *Acer* spp.) With improved litter quality (lower C:N ratio), net N mineralization and nitrification may also increase. Eventually, the N-cycle and forest growth could be re-established at a new, higher equilibrium (Fig. 7).

4. Conclusion

The results of 7 years (1988 to 1994) of N-fertilization to spruce–fir stands on Mt. Ascutney, Vermont suggest that the early stages of N saturation are occurring on all fertilized plots. Despite the low level

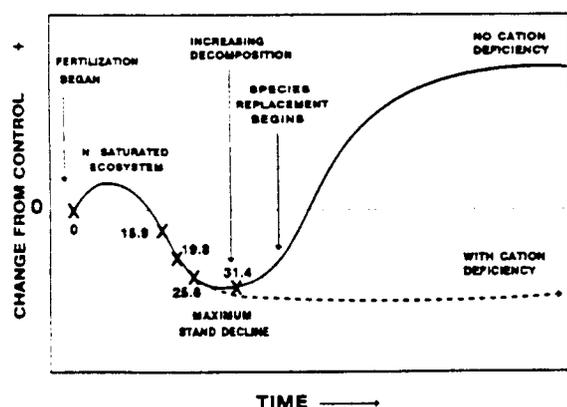


Fig. 7. Conceptual curve of changes in N availability (net N mineralization plus N deposition) and forest growth with continued N additions to high elevation spruce–fir forests.

of added N; spruce foliage %N, BA growth, net N mineralization and net nitrification were significantly different between treatment and control plots after 7 years of N additions. These differences appear to be related to the amount of N applied and not the form of N. We predict that these changes are only the beginning of a series of ecosystem alterations that could eventually lead to a shift in species composition (assuming no serious cation deficiencies develop in replacement species), forest growth, and N-cycling. If N additions continue, both on Mt. Ascutney through N-fertilization, and across New England from anthropogenic sources, high elevation spruce–fir forests could eventually be converted into stands of birch, maple, or both.

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