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Effects of nitrogen saturation on tree growth and death in a mixed-oak forest

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Abstract

Ecologists have long treated temperate forests as systems limited by nitrogen (N) availability. Widespread concern about the effects of anthropogenic N on forested ecosystems has inspired experimental simulation of the effects of chronic N addition. This study investigates the effects of 8 years (1996–2003) of simulated chronic N deposition on tree growth and mortality in an upland mixed-oak forest at the Institute of Ecosystem Studies (IES), Millbrook, NY, USA. Nitrogen was added at a rate of 50–100 kg N ha^{-1} y^{-1}, with atmospheric deposition (wet + dry, inorganic N) at the site averaging 10 kg N ha^{-1} y^{-1}. The experiment used a paired design, with six fertilized plots and six non-fertilized control plots. We measured the diameter of all of the trees in the plots, recorded mortality, and extracted increment cores and measured their annual growth rings. We found that fertilization caused both increased mortality (N-saturation effect) and increased relative growth rate of surviving trees (fertilization effect). The combined effect was a net loss of living basal area in most of the fertilized stands. Growth and mortality effects varied among sites and species. Within sites, N fertilization caused increased growth in some trees and mortality of neighboring trees in the same site, indicating that N saturation is manifest as a mosaic phenomenon mediated by sensitivity of individual trees and soil microsites. No interactions were observed between site, treatment, and species for basal area growth, but oak species suffered greater mortality. Decreased Ca:Al ratio in organic soil is a possible explanation for increased mortality, though the specific mechanism is unknown. The growth and mortality responses at this deciduous forest may be more similar to those previously observed in coniferous forests, calling into question the hypothesis that deciduous forests are less sensitive to the effects of N-saturation.

Keywords: Nitrogen deposition; Nitrogen saturation; Tree growth; Tree mortality; *Quercus rubra*; *Quercus prinus*

1. Introduction

Ecologists have long considered temperate forests systems to be limited by nitrogen (N) availability (Mitchell and Chandler, 1939). In the last century anthropogenic activities have doubled the global rate of fixation of N_2 into reactive forms of N (Driscoll et al., 2003). Atmospheric deposition of nitrogen oxides, resulting primarily from the combustion of fossil fuels, has increased the amount of N available to many natural systems. Though legislative efforts have reduced N emissions slightly, deposition persists at levels sufficient to significantly alter the chemistry of forests and surface waters in the northeastern US (Aber et al., 2003). Furthermore, global deposition rates are rising as many countries undergo rapid modernization (Galloway, 1995). Widespread concern about the effects of acid deposition has inspired numerous attempts to quantify the effects of added N on forested ecosystems. Research has shown that the forests of the eastern US are able to absorb substantial amounts of added N (Mitchell and Chandler, 1939; Magill et al., 1997; Peterjohn et al., 1996). However, as added N accumulates in excess of the demand of an ecosystem, it can have detrimental ecological effects.

In the northeastern US, studies on the effects of nitrogen on forests have included comparisons of sites along gradients of N deposition (McNulty et al., 1991; Lovett and Rueth, 1999) and experimental manipulations in which N fertilizer is added to simulate the effects of chronic N accumulation (Magill et al., 1996, 1997; McNulty et al., 1996; Lovett and Hart, 2005).

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Gradient studies provide insight into the regional-scale effects of N deposition, but are usually involve less control over other variables that could differ among sites. Nitrogen amendment experiments allow precise specification of N addition levels and good matching of control and N-amended plots, but are necessarily more limited in scale, and simulated deposition levels are often artificially high. Taken together, these studies indicate that forests vary greatly in the amount of N they can retain, and excessive N addition causes some forests to undergo what is termed a N-saturation response (Aber et al., 1998). A saturation response occurs when N availability approaches or exceeds the nutritional N-demand of plants and soil microbes (McNulty et al., 1996). Aber et al. (1998) describe a model of ecosystem responses to N-saturation that identifies three stages of progressive severity, and lists characteristic biogeochemical symptoms of each stage. They suggested that N-saturation responses vary among forests and appear to be highly influenced by local characteristics, especially the history of land use at a given site, the level of N-limitation, and the forest type, with deciduous forests possibly more resistant to N saturation than coniferous forests (Aber et al., 1998). Research in the Catskill Mountains of southeastern New York State has shown that the stage of N saturation can differ markedly among forests receiving similar amounts of N deposition (Lovett et al., 2000), and the variation is explained in part by differences in forest type and soil C/N ratio (Lovett et al., 2002).

One of the diagnostic characteristics of N saturation is excess NO_3^- leaching below the rooting zone. Nitrate leaching is usually one of the first symptoms to appear in N fertilization studies (Emmett, in press). Charge balance dictates that the leaching of NO_3^- be accompanied by equivalent leaching of cations, which can include the base cations magnesium (Mg^{2+}), potassium (K^+), sodium (Na^+), and calcium (Ca^{2+}). Loss of these base cations from the soil results in more of the soil exchange sites being occupied by H^+ or Al^{3+}, which increases the soil acidity and the concentration of Al^{3+} in soil solution. Mobilized Al^{3+} can cause tree mortality either directly from aluminum poisoning, or indirectly from nutrient imbalances that increase susceptibility to physical and pathogenic stressors (Cronan and Grigal, 1995). The inherently greater passive uptake of Al^{3+} relative to base cations by the fine root systems of trees can lead to calcium deficiency (Shortle and Smith, 1988). Calcium is an essential nutrient in sapwood production and membrane function (Aber and Melillo, 1991). Reduced Mg:N ratio from N-saturation is potentially harmful to chlorophyll production (Aber and Melillo, 1991). In addition, increased N level in plant tissues has also been tied to greater susceptibility to insect and fungal pathogens (e.g., Latty et al., 2003).

In 1996 we initiated a N addition experiment in an upland mixed-oak forest in southeastern New York State. The N addition has resulted in high levels of nitrate leaching from the fertilized stands (Lovett and Hart, 2005). The purpose of this study was to examine the effect of this N addition on tree growth and mortality as well as on calcium and aluminum in the soil.

2. Methods

2.1. Study site

All samples were collected between July 2004 and January 2005 on the grounds of the Institute of Ecosystem Studies (IES) in Millbrook, NY, USA, (41°50′N, 73°45′W). Between 1988 and 2004 the average annual temperate at IES was 9.6 °C, with monthly averages of −3.2 °C for January and 21.7 °C for July, and an average of 142 frost-free days between mid-May and late September (unpublished IES data, http://www.ecostudies.org/emp_purp.html). Average annual precipitation for this period was 1093 mm, distributed relatively evenly throughout the year. The experimental plots are located in the Cannoo Hills area of IES, in a second-growth mixed oak-hickory wood. The area once served as a woodlot (Glitzenstein et al., 1990), and was probably selectively harvested through the 1930s. Most of the trees sampled for this project were between 60 and 100 years old, with none older than approximately 180 years.

The canopy is dominated by chestnut oak (*Quercus prinus* L.), northern red oak (*Quercus rubra* L.), and hickories (*Carya* species), with eastern white pine (*Pinus strobus* L.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.) and shadblow serviceberry (*Amelanchier canadensis* (L.) Medik.) present to a lesser extent. The majority of the hickories on the plots are most likely *Carya glabra* (Mill.), but some show traits intermediate between *C. glabra* and *C. tomentosa* (Poir.) Nutt., and so are grouped at the genus-level for this study.

The substrate of the plots is late Cambrian-early Ordovician shale and slate, beneath a mantle of glacial till (Glitzenstein et al., 1990). The soils generally have a thin organic horizon over a B horizon which varies in depth up to 50 cm, and are classified as lithic dystrochrepts of the Nassau series: ‘‘slaty silty loam on glacial till, consisting of shallow, well-drained soils on uplands, derived from acidic shales and slates’’ (Secor et al., 1955; Lovett and Hart, 2005).

2.2. Nitrogen addition experiment

In 1996 a nitrogen addition experiment was established at this site. The design consisted of six pairs of plots (designated with letters A–F), with one of each pair fertilized and the other left untreated as a control. The plots are circular and 20 m in diameter. Fertilizer is applied to the entire area of the fertilized plot, but nutrient-cycling measurements are made in the central 10 m diameter inner-plot, with the outer 5 m radius ring serving as a buffer zone to reduce edge effects. The plots were chosen to be representative of the ridge top forest community of the area. Each plot pair is of similar elevation and exposure, and the two plots of each pair are separated by 4–40 m.

Nitrogen was added to the fertilized plots as pelletized ammonium nitrate (NH_4NO_3) four times per year (May–August). The N application rate was equivalent to 100 kg N ha^{-1} y^{-1} from 1996 to 1999, after which it was reduced to 50 kg N ha^{-1} y^{-1} from 2000 to the present. These fertilization rates are 5–10 times the total (wet + dry) deposition of inorganic N at the site, which averages ~10 kg N ha^{-1} y^{-1} (Kelly et al., 2002).

2.3. Soil sampling and analysis

Four soil cores, each 6.5 cm diameter and 10 cm deep, were taken from randomly chosen locations in each plot in July 2004 and were used to measure extractable Ca and Al. The samples were divided into two depths, 0–3 cm (representing primarily the organic horizons), and 3–10 cm (primarily mineral soil). Soils were taken to the lab and sieved through a 2 mm mesh. Fine root fragments were removed from the sieved soil using forceps. Subsamples of approximately 10 g were dried at 60 °C for 48 h and the dry weight was measured. The samples were extracted in 100 ml 0.1 M $BaCl_2$ in plastic specimen cups. The soil extraction mixture was vigorously shaken every 15 min for 2 h and then allowed to settle overnight. The samples were then filtered through Whatman 41 paper into 60 ml polyethylene bottles. The filtrate was analysed for Ca and Al using an inductively coupled plasma emission spectrometer (ICP).

2.4. Tree growth measurements

Increment cores were extracted at breast height from all of the standing trees in the inner plots (10 m diameter) using an increment borer and following established dendrochronological procedures (Stokes and Smiley, 1968; Schweingruber, 1988). The diameter at breast height (DBH) of each tree was measured to the nearest millimeter with a standard diameter tape at the point from which the core was extracted.

The cores were glued to wooden mounts and wrapped with twine to prevent warping while drying (Stokes and Smiley, 1968). Once dry, the cores were trimmed with razor blades, and finished with increasingly fine grit sandpapers to make the rings visible and provide an even surface to prevent distortion in viewing the rings. Each core was then digitally photographed using a system of digital photography and computer software devised by Dr. Charles Canham (Canham, 2004). First, the cores were placed in a vise underneath a digital camera fitted with a high-resolution macro-lens and mounted on a tripod perpendicular to a stage. A series of photographs were taken of each core, with a 15-cm metric ruler in the images. These photographs were transferred to a computer and measured using *Trimage* software (Canham, 2004). The software was calibrated to the ruler in the photographs and the annual rings measured to the thousandth of a millimeter. Measurement began from the bark and proceeded inwards at least 30 years, and in some cases as far as the pith.

We were able to cross-date most of the samples by lining up a particularly small growth ring caused by the severe gypsy moth defoliation of 1981 (Goodwin et al., 2005). We accomplished this by plotting ring measurements on a line graph and visually comparing the relative sizes of the rings. Cores that did not initially line up with the date were reexamined for missing or double rings, and then matched with the master chronology. Ring anomalies, such as double or missing rings, are exceedingly rare in ring-porous species, including the oaks and hickories (Schweingruber, 1988). However, many of the samples were difficult to read because of extremely small rings (hickories) and very dry sapwood (oaks). Cores that could not be satisfactorily cross-dated, or that had gaps during the fertilization period, were not used.

2.5. Calculations and statistical analysis

We converted linear ring measurements into basal area increment (BAI) assuming a circular bole. In the discussion that follows, when BAI is followed by a span of years (i.e. BAI 1996–2003) it refers to the total incremental growth in cm^2 during that time period. In order to normalize for the variation in size, species, and growth rate between individual trees, we divided the BAI of each individual by its total basal area growth up to the previous year to get a relative basal area increment (RBAI)

$$\mathrm{RBAI} = \frac{\mathrm{BAI}}{(\mathrm{BA} - \mathrm{BAI})} \qquad (1)$$

where RBAI is the relative basal area increment from time t to the time of measurement, BA the basal area of the tree at the time of measurement and BAI is the basal area increment between time t and the time of measurement. We also estimated woody biomass of trees in 1996 and 2004 using species-specific allometric equations that calculate woody biomass as a function of DBH (Jenkins et al., 2004). Woody biomass increment (WBI) was calculated as the mean annual increase in woody biomass between 1996 and 2004, and relative woody biomass increment (RWBI) was calculated as the WBI divided by the woody biomass prior to the start of the experiment in 1996.

The nonparametric Wilcoxon paired-sample test was used to make plot-wise comparisons of total BAI, RBAI, WBI and RWBI. Analysis of variance (SAS software system, Version 8) was used to evaluate individual-tree BAI, RBAI, WBI and RWBI for the main effects of site, treatment, and species, and all potential interactions. For the ANOVA, BAI, RBAI, WBI and RWBI data were log-transformed to improve the normality of the distribution.

All live trees were tagged when the plots were established in 1996. Mortality was assessed by noting the condition of the trees during our 2004 measurement. We derived the plot-level mortality statistics by taking the ratio of the total live basal area on each plot at the start of fertilization in 1996 to the live basal area of those same individuals at the time of sampling in 2004, calculated from measurements of DBH. For three trees no DBH was recorded in 1996, so we used the next available diameter measurement from 2001 to calculate the basal area. We omitted one individual from the change in live basal area calculation because its DBH was first recorded in 2004.

3. Results

3.1. Soil analysis

In the soil, extractable Ca^{2+} concentration was lower and the Al^{3+} concentration was higher in the fertilized than control plots in both the 0–3 and 3–10 cm depth horizons, but the effect was only significant in the 0–3 cm horizon (Fig. 1). The ratio of Ca:Al and the pH were significantly lower in the fertilized plots

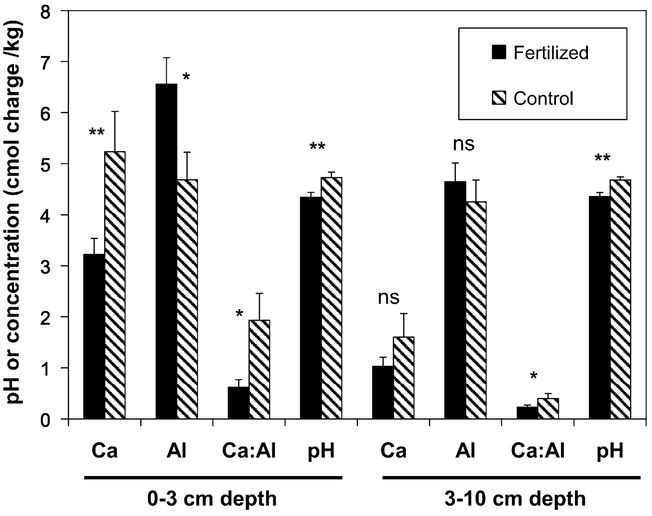

Fig. 1. Extractable Ca and Al concentration cmol charge/kg dry soil, Ca:Al ratio (equivalent basis) and pH of extraction solution for fertilized and control plots. Mean and standard error shown for two depth horizons of soils, 0–3 cm (primarily organic horizons) and 3–10 cm (primarily mineral horizon). Significance of paired t-test ($n = 6$ pairs of plots) indicated as $^{**}p < 0.01$, $^{*}p < 0.05$, ns: $p > 0.05$.

Table 1
Species distribution of trees from which cores were taken on fertilized and control plots

	Fertilized	Control	Total
Red maple (*Acer rubrum*)	1	2	3
Sugar maple (*Acer saccharum*)	1	2	3
Shadblow serviceberry (*Amelanchier canadensis*)	1	2	3
Hickories (*Carya* species)	10	11	21
Eastern white pine (*Pinus strobus*)	0	4	4
Chestnut oak (*Quercus prinus*)	5	13	18
Red oak (*Quercus rubra*)	7	8	15
Total			67

in both horizons (Fig. 1). No pre-treatment soil chemistry data are available, so any pre-existing differences between the pairs of plots are included in the unexplained variance of this analysis.

3.2. Number and species distribution of samples

Of the 74 trees in the plots at the start of the experiment, two trees had fallen over before we cored the trees in 2004 and five yielded cores that were rotten or unable to be cross-dated due to missing rings, resulting in 67 cores suitable for measurement. Table 1 shows the number and species distribution of samples. The following statistics describe the 8-year time period from the start of fertilization in 1996 through 2003, the last complete annual ring at the time of sampling.

3.3. Plot-level growth analysis

For the plot-level results in this section, statistical significance was assessed at the $p = 0.05$ level using the Wilcoxon paired-sample test with $n = 6$ pairs of plots. Although there was substantial variation among plots, there were no significant difference between fertilized and control treatments in the number or basal area of live trees in 1996, prior to the start of the N addition (Table 2). During the fertilization period, there was no significant difference in the mean plot BAI between the fertilized and control plots (Fig. 2). However, there was a strong positive relationship between the pre-fertilization basal area of the surviving trees and the BAI of those trees during the fertilization period (Fig. 3). To take this into account, we normalized the data in two ways: (1) we calculated the ratio of the mean annual BAI during the fertilization period (1996–2003) to the pre-fertilization basal area to calculate relative BAI (RBAI, Eq. (1)), analogous to the relative growth rate often used in the plant physiological literature, and (2) we calculated the ratio of the 1996–2003 BAI to the pre-fertilization BAI for the 8 years prior to fertilization (1988–1995). Both of these indices were significantly greater in the fertilized plots than in the control plots (Wilcoxon test, $p < 0.05$) (RBAI shown in Fig. 4). The BAI during the 8 years prior to fertilization (1988–1995) did not differ significantly between the fertilized and control plots, showing that there was no pre-treatment difference in the relative vigor of the fertilized and control plots (Fig. 2). Also, there was no significant change in the BAI between the first 4 years of fertilization (1996–1999) and the

Table 2
Basal area (BA, $m^2\ ha^{-1}$) and number of live trees by species in each of the plots at the start of the experiment (1996)

Plot pair	Treatment	*Q. rubra*		*Q. prinus*		Carya sp.		Other		Total	
		BA	#	BA	#	BA	#	BA	#	BA	#
A	F	49.3	3	0	0	0	0	2.0	1	54.3	4
A	C	19.4	2	0	0	1.2	1	7.6	2	31.2	5
B	F	3.0	1	14.9	3	0.0	0	0	0	21.9	4
B	C	13.7	3	33.8	3	0	0	2.8	3	56.3	9
C	F	5.8	1	3.0	1	0	0	0	0	10.8	2
C	C	7.5	1	17.5	3	0	0	3.7	2	32.7	6
D	F	9.5	2	28.6	3	1.9	3	0	0	48.0	8
D	C	2.9	2	20.7	2	8.4	2	0	0	38.0	6
E	F	7.8	1	0	0	7.2	4	0	0	19.9	5
E	C	0	0	33.7	4	9.9	4	1.4	2	53.0	10
F	F	2.0	1	20.7	2	1.6	3	2.1	2	32.5	8
F	C	0	0	10.4	1	13.5	4	1.2	2	30.1	7

Carya sp. includes all hickories, and "Other" includes all other species. Treatments are F, fertilized; C, control.

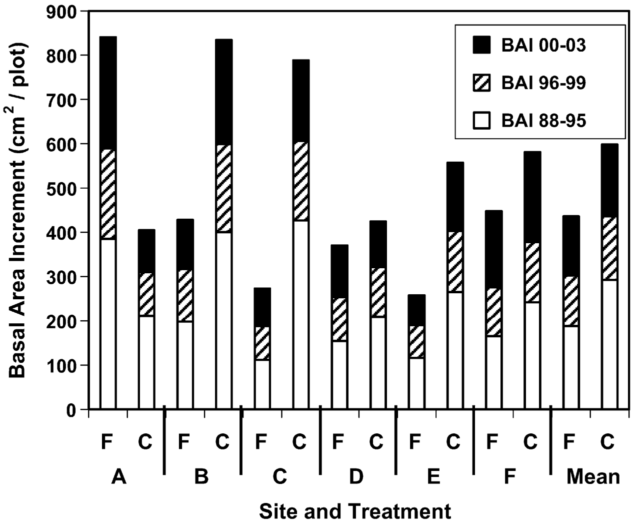

Fig. 2. Basal area increment (cm^2) of trees alive in 2004 at six pairs of plots (A–F) either fertilized with nitrogen or left non-fertilized as control. White bars show basal area of each plot during the 8 years prior to fertilization (1988–1995), striped bars show the basal area during the first 4 years of fertilization at 100 kg N ha^{-1} y^{-1} (1996–1999), and black bars show basal area during the next 4 years of fertilization at 50 kg N ha^{-1} y^{-1} (2000–2003).

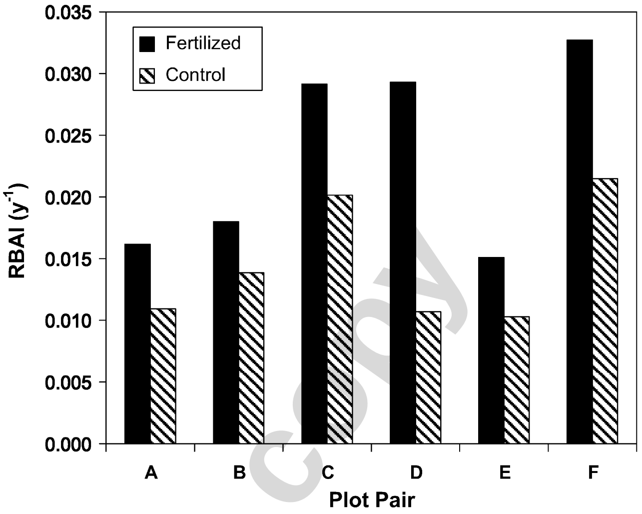

Fig. 4. Relative basal area increment (RBAI, y^{-1}) of trees alive in 2004 in six pairs of plots. The plot RBAI is the sum of mean annual BAI (1996–2003) (cm^2/y) for all surviving trees in the plot divided by the sum of 1995 basal area (cm^2) for those same trees. Across all plots, RBAI is significantly higher in fertilized plots compared to control plots ($p < 0.05$).

next 4 years of fertilization (2000–2003) on either the fertilized plots or the control plots (Fig. 2).

The mean woody biomass increment (WBI) was lower in fertilized (267 g m^{-2} y^{-1} ± 56 S.E.) than control plots (378 ± 49), but the difference was not significant with the Wilcoxon test. The mean relative woody biomass increment (RWBI) was higher in the fertilized plots (0.021 ± 0.006 y^{-1}) than in the control plots (0.017 ± 0.003), but again the difference was not significant.

3.4. Tree-level growth analysis

We examined the influence of individual tree characteristics on the fertilizer response by evaluating the response of individual-tree growth to site, treatment, species, and all potential interactions using multivariate ANOVA on log-transformed data. To gain more power in the analysis, species represented by 4 or less individuals were grouped as ‘‘other’’, while the two oak species were treated individually and the hickories were grouped on the genus level because of potential hybridizing. There were no significant differences in individual-tree BAI between different sites or N-addition treatments, but there was a significant effect of species ($p < 0.0001$) (Table 3). A post hoc Student–Newman–Keuls test showed that the two oak species (red oak and chestnut oak) grew significantly more slowly than the hickories and all other species. The individual-tree RBAI (BAI during fertilization divided by the basal area of the tree prior to fertilization), showed highly significant effects of site, treatment, and species, and no significant interactions (Table 3). Post hoc tests for RBAI showed that a tree had significantly greater RBAI if it was (1) fertilized, (2) at site F, or (3) not a chestnut oak.

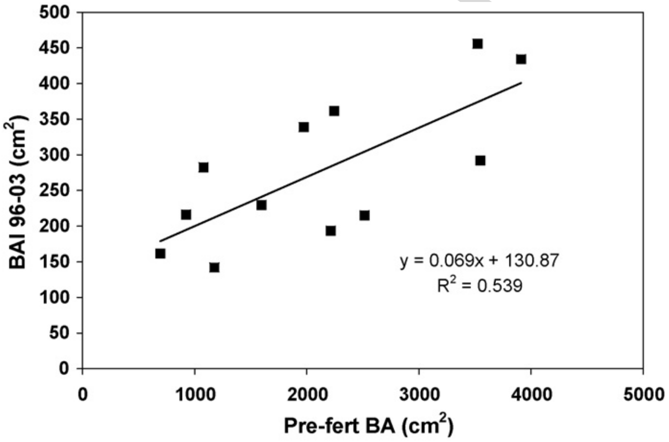

Fig. 3. Relationship between pre-fertilization basal area of the surviving trees on each plot and their basal area increment during the fertilization period. Each point represents a plot, using the summed values of BA and BAI for all surviving trees on the plot.

Responses in woody biomass increment (WBI) were similar to those of BAI, with significant species effects, but no significant effects of N treatment or site (Table 3). Relative WBI was significantly affected by site, N treatment and species, and all of the two-way interactions were also significant (Table 3).

3.5. Plot-level mortality and basal area change

A total of 11 of the 31 trees (35%) in the fertilized plots died during the fertilization period (1996–2004), compared to only 1 of 41 (2.4%) in the control plots. This difference in percent mortality is statistically significant (Wilcoxon paired-sample test, $p < 0.05$). Oaks accounted for the majority of the mortality in the fertilized plots (5 chestnut oaks and 4 red oaks), with 1 dead individual each of hickory and sugar maple. Between 1996 and 2004 all of the fertilized plots lost live basal area,

Table 3
Summary of results from analysis of variance and Wilcoxon tests comparing basal area increment (BAI), relative basal area increment (RBAI), woody biomass increment (WBI) and relative woody biomass increment (RWBI) from 1996–2003 on the individual-tree level and plot level

	Tree-level (ANOVA)				Plot-level (Wilcoxon)
	Site	N treatment	Species	Interactions	Treatment
BAI	ns	ns	$p < 0.0001$	ns	ns
RBAI	$p = 0.0006$	$p = 0.018$	$p = 0.0005$	ns	$p = 0.05$
WBI	ns	ns	$p < 0.0001$	ns	ns
RWBI	$p = 0.0001$	$p = 0.0028$	$p = 0.0006$	All two-way interactions were significant	ns

For the individual tree analysis, $n = 67$ trees. For the plot-level analysis, $n = 12$ plots in six pairs, with one of each pair fertilized with nitrogen and the other left non-fertilized as control.

except for plot B, while all of the control plots gained live basal area, except for plot A (Fig. 5). In 2004 the total live basal area in the fertilized plots had declined to 72% of its 1996 level, while the live basal area in the control plots increased to 106% of its 1996 level. We noted a non-linear relationship between soil Ca:Al ratio and the percent mortality (Fig. 6a) and the change in live basal area (Fig. 6b) of these plots between 1996 and 2004. For all of the plot pairs, the Ca:Al ratio was lower in the fertilized than in the control plot. The greatest mortality and loss of live basal area occurred for plots with a Ca:Al ratio < 1, but not all plots with Ca:Al < 1 lost live basal area (Fig. 6b).

Despite the overall loss of live basal area in the plots due to mortality, N-addition increased the growth of the trees that survived through the 9 years. The basal area of the surviving trees in the fertilized plots increased by 18% over its 1996 level, compared to 11% increase in the control plots. This difference is only marginally significant statistically (Wilcoxon test, $p < 0.1$), but the 64% greater growth in the fertilized plots may well be ecologically important.

4. Discussion

This study has documented a response to N addition in hardwood stands that differs markedly from the response of other hardwood stands in the eastern US. We discuss our results below and then compare them to other studies reported in the literature.

4.1. Growth and mortality

Nitrogen addition did not significantly affect the absolute basal area increment or woody biomass increment of the trees in the fertilized plots, but it did increase their relative basal area increment, relative woody biomass increment, and their mortality rate. The lack of a significant effect on the absolute BAI is mainly a result of the large variation among plots in the pre-fertilization basal area; the strong dependence of the BAI

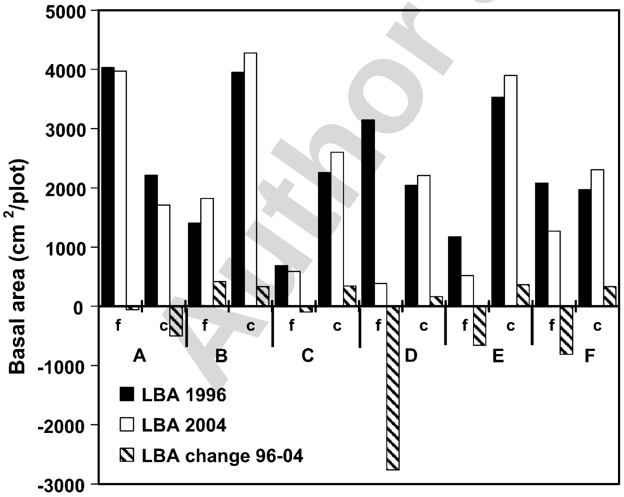

Fig. 5. Change in live basal area (LBA) between 1996 and 2004 in six pairs of plots (A–F) at fertilized (f) or control (c) sites. This calculation includes the increase in LBA resulting from tree growth as well as the loss of LBA due to mortality.

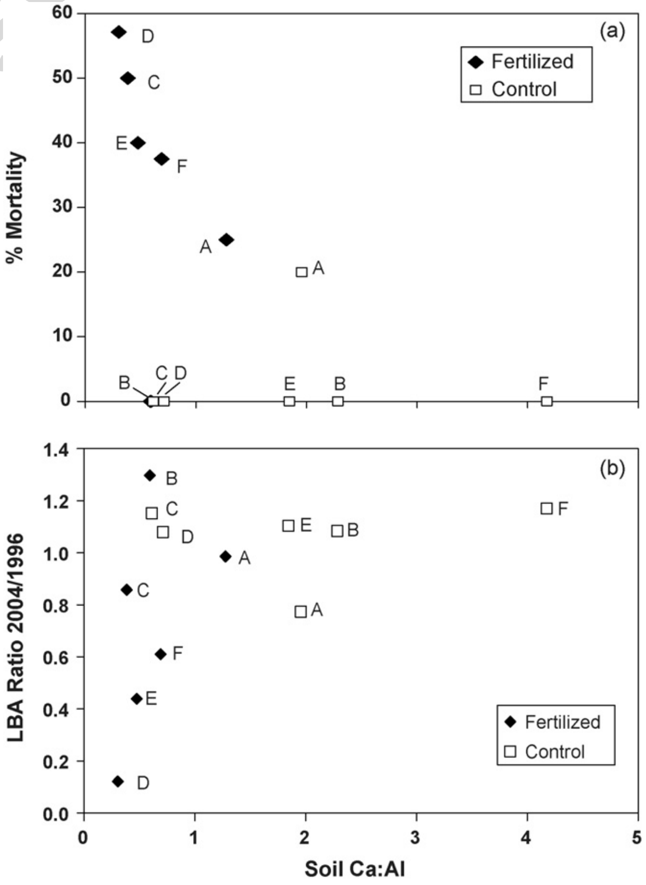

Fig. 6. Relationship between the calcium:aluminum equivalent ratio in the 0–3 cm deep soil horizon and (a) the percent mortality and (b) the ratio of live basal area (LBA) in 2004 relative to 1996 for six pairs of N-amended plots. Labels A–F denote the plot pairs.

on pre-fertilization basal area engendered a substantial amount of noise that obscured the growth signal due to fertilization. In the tree-level analysis, when the BAI or WBI was normalized by its pre-fertilization value (i.e. RBAI or RWBI was calculated), the live trees in the fertilized plots had consistently and significantly greater growth that their control plot counterparts. The increase in RBAI and RWBI confirms the presence of a fertilization effect on growth, while the increase in mortality suggests that N-saturation is damaging some trees.

Both the normalized plot- and tree-level growth statistics (RBAI) show that the application of additional N has significantly increased the relative growth of the trees in the fertilized plots, confirming the presence of a N-fertilization effect. The rate of increased growth did not change with the halving of the fertilization rate in 2000, suggesting that the reduced rate of 50 kg N ha^{-1} y^{-1} is sufficient to saturate the continuing demand, or that the effects of the 100 kg N ha^{-1} y^{-1} application rate carried over for several years following the rate reduction. Both RBAI and mortality effects varied among sites and species. The significance of the species effect in the non-normalized tree-level data shows that, regardless of their size, chestnut oaks are growing more slowly than individuals of other species. The site effects may be associated with soil acidification, as a non-linear relationship was observed between net basal area change and soil Ca:Al ratio.

Concurrent with the increased relative growth rate, there was a significant increase in tree mortality in the fertilized plots, resulting in a net loss of live basal area. The seeming paradox of increased growth and increased mortality in the fertilized plots leads us to believe that they are in the intermediate stage of a N-saturation response. It appears that the plots are currently bridging the saturation threshold, with those trees that are more sensitive to N-saturation (and associated soil acidification) suffering mortality while the less-sensitive trees benefit from the fertilization effect. It is also possible the growth of survivors in the fertilized plots may have increased because of greater light availability resulting from mortality of neighboring trees. However, the fact that the fertilized plot at site B, the only fertilized plot with no mortality, showed an increase in growth suggests that increased N rather than increased light is the major factor influencing the growth rate on the fertilized plots. There also appears to be a positive relationship between mortality and growth enhancement, with plot B showing the lowest growth increase and mortality and plot D the highest growth increase and mortality (Figs. 4 and 6). Nitrogen uptake and light availability interact, as greater access to light increases the energy available to incorporate added N into biomass, and added N generally increases the photosynthetic rate of fertilized plants. Though the relationship between increased growth and light gap dynamics from increased mortality is unclear, it is likely that there is a light-gap effect in the fertilized plots, and its relationship to the fertilization effect bears future investigation.

4.2. Species effects on growth and mortality

In the individual tree growth data, a species by treatment interaction was observed in the analysis of RWBI, though not of RBAI. Previous research has shown that single-species stands differ in their N cycling characteristics (Lovett et al., 2004), and that coniferous and deciduous stands have different growth responses to fertilization (McNulty et al., 1996). It is possible that differences in the RBAI response among species would be more evident with lower doses of fertilizer. The lack of variability in growth response to fertilization on the species-group level suggests that individual tree and micro-site characteristics are the dominant factors influencing individual growth.

While the effect of fertilization on RBAI is not species-specific, variability in mortality may correlate with species and size. Oaks show the greatest mortality from N-addition, and also have the greatest average pre-treatment individual basal area and slowest growth. In the fertilized plots, oaks (red oak + chestnut oak) had a 56% mortality between 1996 and 2004, while mortality for all other species combined was 15%. Oaks, as a genus, appear to be more susceptible to the stresses associated with N-saturation at this site.

Of the 12 trees that have died since 1996, 8 have died since 2001. Although we do not have mortality surveys prior to 2001, we observed that most of this mortality occurred after two dry summers in a row, 2001 and 2002. Precipitation in July and August was 44% below normal in 2001 and 39% below normal in 2002. Many trees in the fertilized plots were noted as having brown leaves in 2002, followed by mortality in 2003 or 2004, suggesting that drought and fertilization were interacting factors contributing to mortality.

There appears to be a non-linear relationship between Ca:Al ratio in the soil and the percent mortality and loss of live basal area in the plots (Fig. 6). It is difficult to evaluate the significance of the correlation because soil Ca:Al is less commonly used in the literature than foliar and root Ca:Al, and is thus not associated with known thresholds of toxicity (Cronan and Grigal, 1995). However, the relationship between organic horizon Ca:Al and loss of live basal area shows severe mortality and loss of basal area in the fertilized plots below a Ca:Al ratio of 1. These results are consistent with widespread reports in the literature of effects of Al on plant mortality (Cronan and Grigal, 1995), and are also consistent with Aber et al.'s conceptuals model (Aber et al., 1998). Note, however, that only the fertilized plots with a Ca:Al < 1 showed a decline in live basal area (with the exception of plot B), while the non-fertilized plots at sites C and D gained basal area despite having Ca:Al < 1. This suggests either: (1) that mortality and Ca:Al may be covarying with a third unknown effect of N-addition in the fertilized plots, or (2) that the trees are more sensitive to a decrease in the Ca:Al ratio than to a low, but stable, value.

4.3. Comparisons with other N-addition experiments

The significant influence of site characteristics and land-use history in response to N-addition makes direct comparisons between experiments challenging (Aber et al., 1998). However, comparisons across studies can help identify general patterns of response, so we summarize below the results of several N-addition studies in the Northeastern US.

At Harvard Forest, MA, USA, two hardwood plots have received experimental N addition since 1988: the high-N plot has received 150 kg N ha^{-1} y^{-1} and the low-N plot 50 kg N ha^{-1} y^{-1}. These stands are composed primarily of black oak (*Quercus velutina* Lam.), red maple (*Acer rubrum* L.), and black birch (*Betula lenta* L.). The high-N plot showed remarkable N-retention and increased growth, increasing NPP, little N-leaching, and few signs of decline over the first 7 years of treatment (Magill et al., 1997, 2004). After a drought in 1995, the high N plot suffered 49% mortality of individuals, however primarily red maples in the understory were lost (suffering 72% mortality) and the total loss of tree biomass was only 17% (Magill et al., 2004). Since 1995, the high-N plot has shown increased N leaching, but the low-N plot continues to retain almost all of the N added to it (Magill et al., 2004). After 15 years of treatment, both the high-N and low-N plots have higher net primary production than the control plot. The relatively vigorous response of these plots has been attributed to an initial state of extreme N-limitation due to land-use history (Magill et al., 2004). The marked contrast between the growth response and mortality at the Harvard forest hardwood and IES plots, all of which are oak-dominated, probably results from the soil acidification (as indicated by the reduction in Ca:Al ratio) associated with the rapid onset of N leaching at IES. In the IES plots, nitrate leaching began to increase within a year after the initiation of the N amendments, and reached 50 kg N ha^{-1} y^{-1} after 3 years (Lovett and Hart, 2005). The more stressful ridge-top location and thinner soils at IES may also have played a role.

In a plot-level N addition at the Bear Brook Watershed, Maine, USA, hardwood forest plots received between 50 and 60 kg N ha^{-1} y^{-1} over 4 years, resulting in a fractional increase in woody NPP of 10%, and a trend of heightened mortality (Magill et al., 1996). More than half of the mortality was of beech trees (*Fagus grandifolia* Ehrh.) with beech bark disease, the severity of which has been shown to increase with increasing N concentration in plant tissue (Latty et al., 2003). The Bear Brook plots received less N than the IES and Harvard Forest plots over a shorter period of time, and showed changes in mortality, leaching, and growth more similar to Harvard Forest than IES.

The trend at IES of declining live basal area from increased mortality is comparable to the response of several N-addition experiments in coniferous forests. An experiment at Mt. Ascutney, VT, USA, in which 20–26 kg N ha^{-1} y^{-1} was added to spruce-fir plots over a 7-year period, showed a net loss of living basal area and an increase in mortality (McNulty et al., 1996). The mortality at Mt. Ascutney was correlated positively with the N-addition rate and inversely with foliar Ca:Al ratio. In a red pine (*Pinus resinosa* Ait.) plot at Harvard Forest receiving high N fertilization (150 kg N ha^{-1} y^{-1}), the woody NPP decreased to 0.68 of its pre-fertilization level by 1997, and though no mortality occurred during the initial 6 years of treatment, 56% of the red pines suffered mortality by 2002, and total mortality is now expected (Magill et al., 1997, 2004). The rate of decline on the Harvard Forest pine plot is more rapid than that at IES, but still more similar to IES than any other example in the literature.

5. Conclusions

The increased mortality and decline in live basal area suggests that some of the N-fertilized plots at IES are at an advanced stage of response to N-saturation. However, the concurrence of death of some trees and increased growth in surviving trees also suggests that the conceptual model of N-saturation as a "threshold" phenomenon, initiated after the total saturation of the nutritional demand of a system, is too simplistic. The picture of decline in progress at IES shows the action of N-saturation as a mosaic process, progressing in relationship to micro-site conditions and variations in vigor of species and individuals.

We found that the positive growth response (RBAI) to fertilization does not vary among species, and is therefore likely determined by micro-site characteristics and individual life history. Mortality is associated with N fertilization, and at this point has primarily affected oaks. Calcium deficiency caused by a reduced soil Ca:Al ratio is a possible cause of mortality, but possible compounding factors include drought and individual traits such as greater size, older age and reduced individual vigor.

The growth and mortality responses observed in this hardwood forest at IES are similar to those documented in pine and spruce-fir forests at other sites, bringing into question the hypothesis that hardwood forests move more slowly towards N saturation than coniferous forests (Aber et al., 1998). Continued loss of living basal area will eventually lead to nearly total mortality of the trees included in the study in 1996. In boreal forests of New England, McNulty et al. (1996) reported regeneration of birch and maple in spruce-fir stands declining from N saturation, but little is known about successional dynamics of mixed-oak woods following N-saturation. With the dominant oaks showing the greatest mortality at IES, it is possible that maples will eventually dominate the fertilized plots; on the other hand, red maples appear to be more susceptible than oaks to N additions at the Harvard Forest site in Massachusetts. In any event, changes in species composition are likely to cause changes in many ecosystem processes such as nutrient cycling, carbon storage, and food web dynamics (Lovett et al., 2004; Lovett and Mitchell, 2004).

It is unclear how well the high doses of N in experimental studies mimic the chronic accumulation of N in forests receiving ambient deposition. A recent study of pine forests in Sweden indicated that the rate of N addition was more important than the total amount of N applied in determining soil acidification and tree growth responses (Hogberg et al., 2006). However, comparison of our study with the high-N hardwood plot at the Harvard Forest, where higher N addition rates resulted in lower N leaching and less mortality than at our site, suggests that the main factor determining tree growth and mortality in response to N addition is the inherent susceptibility of the site to nitrate leaching and consequent soil acidification. This susceptibility is mainly regulated by the N uptake capacity (both biotic and abiotic) of the soils and vegetation and thus depends on multiple interacting factors including stand age, site history, soil C:N ratio and the ability of the soils to support nitrification. Sorting out these factors may require a multi-site fertilization experiment with low rates of N application at multiple sites varying in soil and vegetation characteristics. Nonetheless, the high rates of tree mortality in this and other experimental studies suggest that forest health in the eastern US may suffer if N saturation becomes severe.

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