Nutrient limitation of juvenile trees in a northern hardwood forest: Calcium and nitrate are preeminent

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Abstract

Nitrogen (N) has historically been considered the most important mineral nutrient affecting performance of saplings in transitional northern hardwood forest of eastern North America, but recent attention has focused on the role of exchangeable soil calcium. Relative limitation by these factors may be changing because of enrichment of soil N from atmospheric deposition, and concomitant depletion of soil calcium due to leaching by acidic precipitation. We conducted a fertilization experiment to determine the relative importance of calcium, other base cations, several forms of nitrogen, and aluminum toxicity for the growth of saplings in a forest in northeastern Connecticut, USA. Five broadleaved deciduous and one needle-leaved evergreen species were examined; two of the broadleaved species are most abundant on fertile soil patches, and the other four are most abundant on the more prevalent low-fertility soils. Fertilizer was applied over 3 years to naturally established plants growing across the fertility gradient, and likelihood methods were used to determine whether light-dependent growth rate was affected. Of the two species that occur most frequently on fertile soils, one species responded most strongly to calcium application, and the other to nitrate. Of the four species of poorer soils, one responded to both calcium and ammonium, and the other three showed little response to any soil factor. The results suggest that calcium and nitrogen are of equal importance in determining juvenile growth across the suite of canopy tree species in transitional northern hardwood forest. The strong response of species occurring most commonly on fertile soils is suggestive of fundamental niche differentiation mode of community organization. Ongoing processes of atmospheric nitrogen deposition and soil calcium depletion from acidic precipitation may change competitive relationships of the canopy tree community of northern hardwood forests.
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1. Introduction

Detection of sorting of forest trees along local soil gradients is common, but the mechanisms are rarely understood well (Leak, 1976; Clark et al., 1998; Hall et al., 2004). One hypothesized mechanism is that nutrient availability may have a direct effect on light-dependent performance (Kobe et al., 1995). Simulations using field-parameterized data have shown that the ability to persist and grow in the poorly lit understory of closed-canopy forests is a strong determinant of eventual success as a canopy tree (Pacala et al., 1996). If increased nutrient availability enhances light-dependent growth, particularly at low light, then local nutrient availability could have a direct effect on successional pathways and local species composition. Tests of this proposition using measurements of ambient nutrient and light availability to individual saplings have demonstrated nutrient availability effects on high-light growth (e.g., Bigelow and Canham, 2002), but low-light effects have been elusive. Nevertheless, in situ measurement of plant nutrient availability is bedeviled by many technical issues, and direct augmentation of nutrient availability may be a better solution (e.g., Kobe et al., 2002).

Canopy tree species of the transitional northern hardwood forests of eastern North America are segregated along axes of soil nutrient availability. *Acer saccharum* Marsh. (sugar maple) and *Fraxinus americana* L. (white ash) occur on high Ca^{2+} (calcium), high N (nitrogen) soils, and other common tree species, e.g., *Tsuga canadensis* (L.) Carr., (eastern hemlock),

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Fagus grandifolia Ehrh. (American beech), and *Quercus rubra* L. (northern red oak) occur at the low end of Ca^{2+} and N gradients (Pearson, 1962; Finzi et al., 1998a,b; Schwarz et al., 2003). Nitrogen has traditionally been considered to have a preeminent role in regulating plant community composition, tree growth, and other aspects of ecosystem function in these forests (Mitchell and Chandler, 1939; Auchmoody and Filip, 1973; Aber et al., 1993; Catovsky et al., 2002), but soil Ca^{2+} and other base-forming cations are gaining increased attention (Schaberg et al., 2001; Juice et al., 2006). The relative importance of N compared to other factors is likely to have decreased over the past century (Gradowski and Thomas, 2006), because N availability has increased due to atmospheric deposition (Aber et al., 1998), and Ca^{2+}, Mg^{2+} and other cations have become depleted in the soil due to leaching by acidic precipitation (Likens et al., 1998; but see Yanai et al., 2005).

We carried out an experiment to clarify the relative importance of Ca^{2+} and other potentially limiting soil chemical factors in determining sapling growth and species replacement dynamics in a transitional northern hardwood forest in the Berkshires range of the northern Appalachian Mountains. Resource availability was manipulated by addition of fertilizer, and low versus high-light responses were determined by fitting models of growth with respect to light availability with maximum likelihood methods. Our working hypothesis was that Ca^{2+} is the main growth-limiting factor, but we tested alternative hypotheses suggested by previous research and the natural history and geology of the study site. Alternative hypotheses were (1) another base cation (potassium or magnesium) is limiting, (2) Al toxicity is limiting, (3) N is limiting as NH_4^+ (ammonium) or NO_3^- (nitrate), or (4) there is a synergistic limitation between Ca^{2+} and NO_3^-.

2. Materials and methods

2.1. Study site and experimental design

Research was conducted at Great Mountain Forest (GMF) in northwestern Connecticut (42°N, 73°15′W). The forest is located on the 300–500 m elevation Canaan Mountain plateau, a mica-schist slab overlying the Stockbridge formation, itself a several hundred meter thick slab of marble and limestone rich in Ca^{2+} and Mg^{2+}. The plateau was completely glaciated during the Pleistocene, and glacial scouring of limestone from the surrounding valleys has left small areas on the plateau that are influenced by limestone-derived glacial till (Dijkstra et al., 2003). These areas are identified by the abundance of *Carpinus caroliniana* Walt. (blue beech) and a species-rich herbaceous flora that includes limestone indicator species such as *Adiantum pedatum* L. (northern maidenhair fern). Most soils on the plateau, however, are formed from glacial till derived from mica-schist bedrock, and are acidic and low in base saturation (Finzi et al., 1998a,b). With the exception of limited areas of old-growth forest (e.g., Winer and Childs, 1956), most forests on the plateau are second growth stands with no history of agriculture but which underwent intensive logging during the 19th century (Winer, 1955). These stands are dominated by

deciduous broadleaved trees, the most common of which are *Q. rubra* L. (northern red oak), *Acer rubrum* L. (red maple), *A. saccharum*, *F. americana*, and *F. grandifolia* Ehrh. (beech). Two evergreen conifers, *T. canadensis* Carr. (eastern hemlock) and *Pinus strobus* L. (white pine), are also common.

In June and July 1998, ~180 naturally occurring saplings were found for each of six species (*A. rubrum*, *A. saccharum*, *F. americana*, *F. grandifolia*, *Q. rubra*, and *T. canadensis*) by searching stands near access roads. Saplings were randomly assigned to one of seven fertilization treatments or two controls. Most saplings occurred on soils in the Millsite, Westminster, or Bice series (Gonick et al., 1970). These soils are loamy, mixed, active, frigid Dystrudepts formed in a thin mantle of friable acidic glacial till over metamorphosed mica-schist bedrock. They differ mainly in depth to bedrock: Westminster soils have hard bedrock within 0.5 m of the surface, Millsite within 0.5–1 m, and Bice within 1–2 m. Some saplings were on Typic Eutrudepts, which are soils influenced by calcareous till, and many *A. rubrum* saplings were at the edges of wetlands on Aeric Epiaquepts or Humic Endoaquepts. Pre-treatment soil chemistry data are provided in Bigelow and Canham (2002).

The experimental design involved application of chemical fertilizer to the soil surrounding individual saplings (Table 1). Calcium limitation was tested with $CaSO_4$ (calcium sulfate). Ammonium sulfate ((NH_4)$_2SO_4$) and $NaNO_3$ (sodium nitrate) were used to test for N limitation. Research with crop plants has shown high demand for Ca^{2+} to maintain charge balance during NO_3^- uptake (Ward et al., 1986), so we used a $Ca(NO_3)_2$ (calcium nitrate) treatment to test the hypothesis that Ca^{2+} is not directly limiting but rather is required as an adjunct to NO_3^- uptake. Because exchangeable Ca^{2+} and Mg^{2+} are highly correlated in the soils at the study site (Bigelow and Canham, 2002) we tested the hypothesis that Mg^{2+} rather than Ca^{2+} is limiting, using magnesium sulfate ($MgSO_4$). We tested for K^+ limitation (with K_2SO_4; potassium sulfate) despite the K^+ present in the mica-schist parent material, because of the role of K^+ in *A. saccharum* decline in eastern North America (Fyles et al., 1994; Ouimet and Camire, 1995; Wilmot et al., 1996). Concerns about effects of acid deposition on soil aluminum levels led us to test for growth limitation due to aluminum toxicity (Cronan and Grigal, 1995). We elected not to do a P application because of the recent genesis of the soils, and we omitted a watering treatment because soil moisture is only rarely limiting at our site (Caspersen et al., 1999). One treatment was a procedural control consisting of sodium sulfate (Na_2SO_4) because Ca^{2+}, Mg^{2+}, K^+, and NH_4^+ were applied as sulfate salts.

Annual applications of fertilizer were split between early spring (before leaf-out) and early summer. All fertilizer was in granular, water-soluble form. The ground around each sapling was fertilized to a distance 1.5 times the crown radius. The Ca^{2+}, Mg^{2+}, and K^+ applied annually was half the mean amount in exchangeable form in the organic soil horizon and upper 75 mm of mineral soil beneath the crown of the canopy tree species with the largest amount of each cation (Finzi et al., 1998b; A. Finzi, unpublished).

Table 1
Fertilizer application rates ($mol_c \, m^{-2} \, year^{-1}$) and suppliers

Treatment	Rate	kg/ha	Year	Form	Supplier
Ca^{2+}	1.6	320	1999–2001	$CaSO_4$	Crop Production Services (CPS), Amenia, NY
SO_4^{2-}	1.6	768	1999–2001	Na_2SO_4	Prince Agri Products, Quincy, IL
Mg^{2+}	0.4	49	1999–2001	$MgSO_4$	Giles, Waynesboro, NC
K^+	0.4	156	1999–2001	K_2SO_4	CPS
CO_3^{2-}	1.3	390	1999–2001	Na_2CO_3	Leslie's Poolmart, Chatsworth, CA
NH_4^+	0.5	70	1999	$(NH_4)_2SO_4$	CPS
NH_4^+	1.0	140	2000	$(NH_4)_2SO_4$	CPS
NH_4^+	2.0	280	2001	$(NH_4)_2SO_4$	CPS
NO_3^-	0.5	70	1999	$NaNO_3$	Chilean Nitrate Corporation, Atlanta, GA
NO_3^-	1.0	140	2000	$NaNO_3$	Chilean Nitrate Corporation, Atlanta, GA
NO_3^-	2.0	280	2001	$NaNO_3$	Chilean Nitrate Corporation, Atlanta, GA
NO_3^-/Ca^{2+}	0.5	70[a]/100	1999	$Ca(NO_3)_2$	Hydro Agri, Tampa, FL
NO_3^-/Ca^{2+}	1.0	140[a]/200	2000	$Ca(NO_3)_2$	Hydro Agri, Tampa, FL
NO_3^-/Ca^{2+}	2.0	280[a]/400	2001	$Ca(NO_3)_2$	Hydro Agri, Tampa, FL

[a] Per-ha equivalents for NH_4^+, NO_3^- given as kg of N.

The test for growth limitation due to Al toxicity was done by raising soil pH through application of sodium carbonate (Na_2CO_3). Solubility of Al^{3+} drops sharply with increases in pH over the 3.0–6.5 pH range of the study site soils, and although pH also affects availability of base cations Al^{3+} is much more sensitive in this range (Bohn et al., 1985; Côté et al., 1993). Application rates were determined from the amount of negative charge from carbonate (CO_3^{2-}) necessary to raise the pH of the soils under the canopy tree with highest exchangeable Al^{3+} by 0.5 pH units (Sims, 1996). In the first year, Na_2CO_3 was applied at the beginning of the growing season, and in subsequent years the dose was split between early- and mid-season applications.

Ammonium and NO_3^- addition rates in the first season of the experiment provided the amount of N mineralized in 1 year at the study site (0.5 mol m^{-2} $year^{-1}$ = 70 kg ha^{-1} $year^{-1}$; Finzi et al., 1998a). This amount was doubled in the second year and quadrupled in the third year when soil exchangeable NH_4^+ and NO_3^- did not increase in response to fertilization.

3. Environmental and growth measurements

Light availability was assessed using the transmission of incident radiation through canopy openings as a percentage of growing season incident radiation. Calculations were done on fisheye photographs taken at the beginning and end of the study, using the GLA software package (Frazer et al., 2000; details in Bigelow and Canham, 2002). All saplings were harvested at the end of the 2001 growing season. Widths of the five most recent annual rings (1996–2001 growing seasons) were measured on stem sections at 10 cm above the ground. Rings were measured to the nearest 0.01 mm along the widest radius and perpendicular to this axis, using a dissecting microscope and a movable stage interfaced to a desktop computer. Growth was expressed as the average annual relative growth rate (i.e., radial growth divided by radius) for the 2 years after the first year in which fertilizer was applied (i.e., the 2000 and 2001 growing seasons). Use of relative growth rate as a response variable may inflate growth estimates of small trees and diminish those of large ones (MacFarlane and Kobe, 2006), and we tested for this

artifact by linear regression of residuals from the fitted growth–light relationship against height measured 1 year after the beginning of the study.

Soil samples were collected to assess effectiveness of fertilization treatments. A composite soil sample of five sub-samples was taken at the base of each sapling prior to fertilization (Bigelow and Canham, 2002), and additional samples were taken annually from ~20% of saplings.

4. Data analysis

Fertilization effects on soil chemistry (pH in water and extractable Ca^{2+}, Mg^{2+}, K^+, Al^{3+}, NH_4^+ and NO_3^-) were tested with analysis of covariance (General Linear Model procedure, SAS, 1999). The response variable was the difference between soil factors prior to fertilization and 3 years after fertilization. Fertilizer treatment was the main effect and the pre-fertilization value of the soil factor was a covariate. When the analysis of covariance was significant at $\alpha = 0.05$, the Dunnett–Hsu method was used to determine whether a treatment was significantly different from the unfertilized control.

We used a maximum-likelihood approach because it is a powerful and flexible means of accommodating non-linear growth responses to light. With this approach, the best-fit parameters for a mathematical model of the data are obtained via optimization. The likelihood of any data point is determined by the magnitude of its departure from the model prediction, interpreted via a probability density function. The sum of the natural logs of likelihoods of all the observations in a dataset constitutes the log-likelihood. Akaike's corrected information criterion (AIC_c) is calculated from -2 times the log-likelihood plus a term that corrects for sample size and number of estimated parameters; it is an estimate of the information contained in a model and associated data. (Because we used the normal distribution as our probability density function, it was necessary to estimate a variance parameter, σ, which is included in the parameter count.) Lower AIC_c indicates a better model. If two models having the same number of parameters are applied to a dataset, a difference of two AIC_c units would denote a

~2.7-fold difference (i.e., the natural logarithm base e) in the likelihood of the models. A difference of 2AIC$_c$ units is often used as an empirical guide for when one model, or one set of parameter values for a model, becomes more convincing than another (Burnham and Anderson, 2002).

The model used for growth analysis was the Michaelis–Menten,

$$G = \frac{aI}{a/s + I} + \varepsilon, \quad \varepsilon \sim N(0, \sigma), \tag{1}$$

a non-linear model of growth with respect to light in which the variables G and I represent relative radial growth rate and light availability or irradiance, respectively, and the parameters a and s represent maximum or *a*symptotic growth rate and the *s*lope of the relationship of G with respect to I when I is zero. The error term (ε) was assumed to have a mean of zero and to be normally distributed; a separate variance (σ) was estimated for each treatment group. Maximum likelihood estimates of a, s, and σ for each treatment group (including the two controls) were found using simulated annealing, a global optimization algorithm (Goffe et al., 1994). The optimization was done using software written in Delphi 7 (Borland Inc., Cupertino, California).

The effect of a given fertilizer on a species' growth was tested by fitting data to the Michaelis–Menten model twice: once with data for treatment and control combined, and once with treatment and control done separately. The procedure for AIC$_c$ comparisons resulted in two sets of parameters: one set of three parameters (a, s, and σ) for control and treatment combined in a single-group, and another set of six parameters (two each of a, s, and σ) for control and treatment in separate groups. We denote AIC$_c$ for the single-group set as AIC$_{c1}$ and

for the two-group set as AIC$_{c2}$, and denote the difference AIC$_{c1}$ − AIC$_{c2}$ as Δi. We evaluated both Δi and the asymptotic support intervals around parameter estimates as evidence for treatment effects. If AIC$_c$ indicated that separating the data for control and treatment gave a more likely explanation of the data than grouping it (i.e., $\Delta i > 0$), we considered that the fertilization treatment had had an effect.

5. Results

5.1. Treatment effects on soil chemistry

Application of Ca^{2+}, Mg^{2+}, and K$^+$ salts all had the desired effect on soil chemistry without undue alteration of non-targeted soil properties (Fig. 1; Table 2). Calcium sulfate application increased exchangeable Ca^{2+} by (median) 33 mmol$_c$/kg, MgSO$_4$ increased Mg^{2+} by 7.5 mmol$_c$/kg, and K$_2$SO$_4$ increased K$^+$ by 4 mmol$_c$/kg. Sodium carbonate application had the desired effect of decreasing exchangeable Al^{3+}, and although the effects on soil pH were greater than anticipated (median increase of 1.7 pH units), base cation availability was unaffected. Sodium sulfate application unexpectedly raised median pH, and since this effect was not observed in any of the other formulations involving SO$_4^-$ it rendered the Na$_2$SO$_4$ treatment moot as a procedural control.

The large quantities of N applied caused unwanted deviations in soil pH with little change in measured N availability to show for it: (NH$_4$)$_2$SO$_4$ acidified the soils but did not change exchangeable NO$_3^-$ or NH$_4^+$, and both NO$_3^-$ formulations raised soil pH but only NaNO$_3$ produced a significant increase in exchangeable NO$_3^-$. Another side effect of fertilization was that the soil around some *T. canadensis*
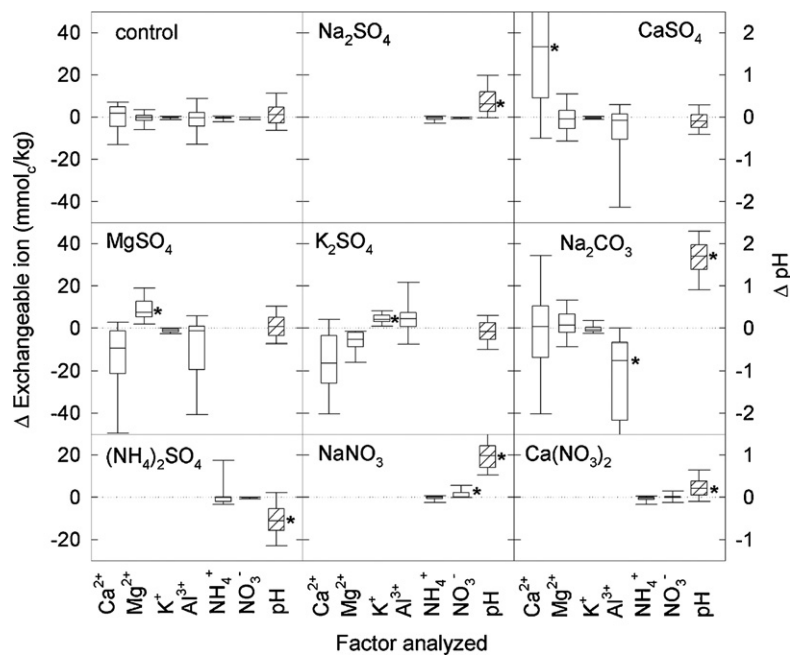

Fig. 1. Changes in soil chemistry due to fertilization of saplings in a northern hardwood forest. Fertilization treatment is identified in the upper left corner of each graph; box plots show median and 10th, 25th, 75th, and 90th percentiles. Data are difference between pre- and post-fertilization measurements (samples taken in 1998 and 2001, respectively) of soil factors identified at bottom. An asterisk to the right of a distribution signifies a difference (Dunnett–Hsu test, $\alpha = 0.10$) from the control distribution shown in upper left graph.

Table 2
Summary of analyses of variance of changes in soil chemical factors due to 3 years of fertilization

Variable	N	Expt. p	r^2	Trt. p	Cov. p	Cov. est.
ΔCa^{2+}	107	<0.0001	0.422	<0.0001	<0.0001	−0.356
ΔMg^{2+}	107	<0.0001	0.374	<0.0001	0.036	−0.127
ΔK^+	108	<0.0001	0.630	<0.0001	0.013	−0.215
ΔAl^{3+}	101	<0.0001	0.626	<0.0001	<0.0001	−0.485
ΔNH_4^+	88	0.053	0.122	0.224	0.019	−1.205
ΔNO_3^-	88	<0.0001	0.343	0.001	<0.0001	−0.880
ΔpH	949	<0.0001	0.653	<0.0001	<0.0001	−0.103

Data are probability of significant F test (Expt. p) and coefficient of determination (r^2) for overall experiment, probability of significant F test for fertilizer treatment (Trt. p) and covariate (Cov. p; initial level of soil factor), and estimate of effect size of covariate (Cov. est.).

saplings fertilized with Na_2CO_3 was disturbed by animals, presumably white-tailed deer.

5.2. Treatment effects on growth

AIC_c differences indicated that growth of five of the six species was affected by at least one fertilization treatment (Table 3); only *F. grandifolia* did not respond to any treatment. *A. saccharum* showed an unequivocal positive response to $CaSO_4$ fertilization ($\Delta i = 2.3$), with decreased low-light growth, increased high-light growth, and no support-interval overlap between treatment and control for parameters of the scientific model (Fig. 2; Table 4). *F. americana* growth was influenced by $NaNO_3$ ($\Delta i = 5.2$) and $Ca(NO_3)_2$ ($\Delta i = 0.9$), with both treatments producing decreased low-light and increased high-light growth.

The results for *A. rubrum* highlighted an issue that can arise from the need to estimate a variance parameter as well as parameters for the scientific model. The AIC_c difference suggested that the $Ca(NO_3)_2$ treatment had a strong effect on growth, but support intervals for parameter estimates for the growth model (a and s) were not clearly segregated from those of the corresponding parameters of the control treatment. In contrast, estimates of the variance parameter (σ) were widely divergent and well separated; the control had much higher σ than the fertilization treatment. (Support for the a parameter of the K_2SO_4 treatment did not overlap with the corresponding control parameter, suggesting that K_2SO_4 caused *decreased* high-light growth.) The same situation occurred for *T. canadensis*; the AIC_c difference suggested that growth was

influenced by the Na_2CO_3 treatment ($\Delta i = 6.3$), but support intervals for a, s and σ imply that the large Δi derived from differences in σ parameters rather than the parameters of the Michaelis–Menten equation.

Q. rubra growth was affected by $CaSO_4$ ($\Delta i = 4.4$), $(NH_4)_2SO_4$ ($\Delta i = 5.7$), and $Ca(NO_3)_2$ ($\Delta i = 1.6$); in all cases the treatment caused decreased low-light growth and increased high-light growth. There was separation between support intervals of treatment and control parameters for all but s of the $(NH_4)_2SO_4$ treatment.

5.3. Height effects on relative growth rate

For four of six species (*A. rubrum, F. grandifolia, Q. rubra,* and *T. canadensis*) there was no trend between residual relative growth rate and sapling height as indicated by linear regression ($p \gg 0.05$). For two species there was a weak trend (*A. saccharum*, $p = 0.047$, *F. americana*, $p = 0.047$) of slope −0.007 % per cm between residuals and height, indicating that use of relative stem radial growth as a response variable may have biased growth estimates upwards in small individuals, and downwards in large individuals, of these species.

6. Discussion

6.1. Effectiveness of soil resource manipulations

Confidence in experimental results requires examination of treatment effectiveness. Our philosophy of nutrient additions

Table 3
Coefficients of multiple determination and AIC_c for control and treatment data, with control and treatment combined in one group (R_1^2 and AIC_1) or separated in two groups (R_2^2 and AIC_2)

Species	Treatments	N	R_1^2	R_2^2	AIC_{c1}	AIC_{c2}	Δi
A. saccharum	C, Ca	39	0.186	0.357	219.2	216.9	2.3
F. americana	C, NO_3	36	0.158	0.364	197.9	192.7	5.2
F. americana	C, $CaNO_3$	39	0.124	0.284	233.3	232.4	0.9
A. rubrum	C, K	39	0.074	0.131	235.6	226.5	9.1
A. rubrum	C, $CaNO_3$	37	0.060	0.224	225.5	220.0	5.5
Q. rubra	C, Ca	35	0.090	0.165	222.8	218.4	4.4
Q. rubra	C, NH_4	32	0.156	0.450	178.6	172.9	5.7
Q. rubra	C, $CaNO_3$	30	0.165	0.379	174.5	172.9	1.6
T. canadensis	C, Na_2CO_3	34	0.170	0.269	200.1	193.8	6.3

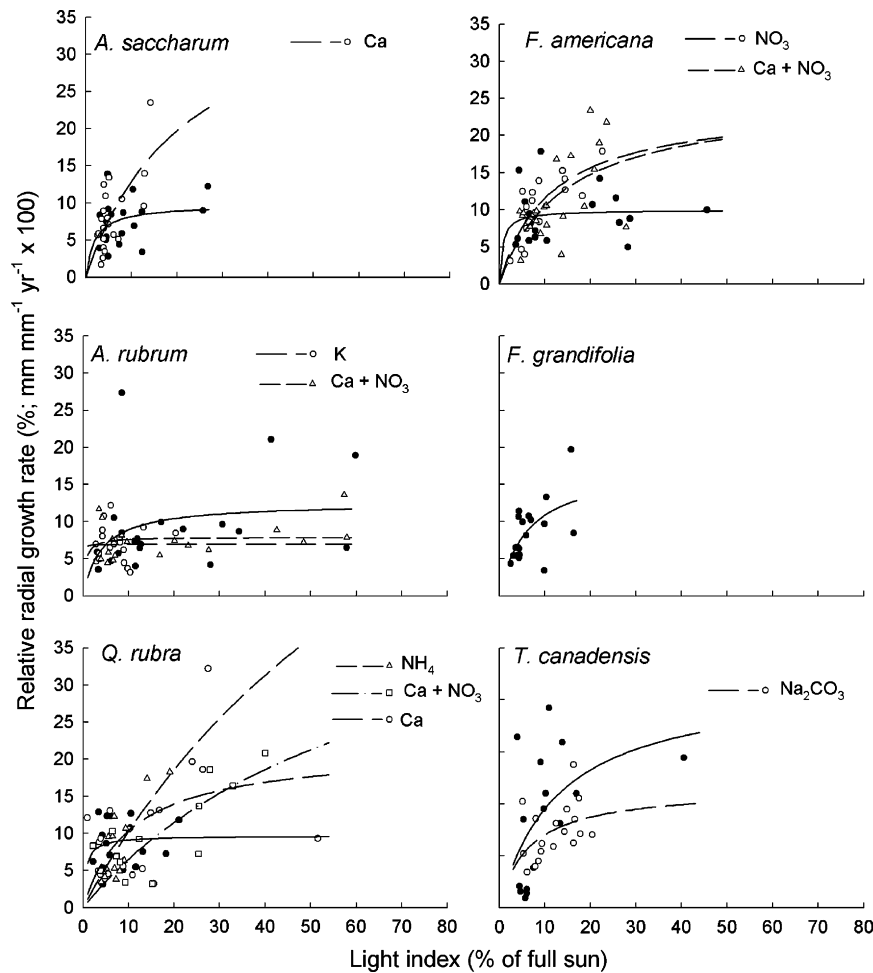Only treatments resulting in a smaller AIC_c (i.e., $AIC_{c1} - AIC_{c2} = \Delta i > 0$) are shown.

Fig. 2. Relative growth rates (RGR) of stem radii of saplings in a northern hardwood forest. Solid circles show growth rates in the control, and open circles show growth rates in fertilization treatments which produced lower AIC$_c$ than control. Solid and dashed lines indicate modeled growth rates of these same respective groups.

contrasted with those of Chapin et al. (1986), who advocate application of large quantities of nutrients to overwhelm microbial and chemical fixation processes. Instead, we calibrated application rates to sapling crown radius, existing amounts of exchangeable nutrients in the upper rooting zone, and N mineralization rates. This protocol was effective for most of the nutrient treatments except for N additions. Given the large quantities of N added there can be little question that N

Table 4
Estimates of Michaelis–Menten equation parameters (a, s), variance (σ), and associated two-likelihood-unit support intervals for controls and for fertilization treatments identified as having an effect on growth (i.e., with $\Delta i > 0$)

Species	Treatment	N	s	s S.I.	a	a S.I.	σ	σ S.I.
A. saccharum	Control	18	4.94	2.43–14.05	9.78	7.64–12.0	8.44	4.62–17.8
A. saccharum	Ca	21	1.85	1.43–2.33	42.1	23.6–89.1	12.7	7.27–25.3
F. americana	Control	18	14.3	3.71–1000[a]	9.97	8.09–11.9	12.4	6.85–26.4
F. americana	NO$_3$	18	2.21	1.81–2.69	24.2	19.7–29.5	5.48	2.97–11.4
F. americana	Ca(NO$_3$)$_2$	21	1.80	1.29–2.51	25.0	18.3–33.8	19.0	10.8–37.8
A. rubrum	Control	20	3.08	1.07–15.28	12.5	8.47–16.8	33.0	18.6–67.0
A. rubrum	K	19	198	7.00–1000[a]	6.96	5.92–8.03	5.18	2.89–10.7
A. rubrum	Ca(NO$_3$)$_2$	17	17.6	3.66–1000[a]	7.92	6.61–9.21	5.91	3.20–12.8
F. grandifolia	Control	19	2.88	2.04–4.07	17.4	12.9–23.0	9.32	5.21–19.3
Q. rubra	Control	17	15.5	4.93–1000[a]	9.61	7.91–11.4	9.08	4.89–19.4
Q. rubra	Ca	18	2.01	1.00–3.98	21.4	13.1–32.2	41.7	22.8–88.0
Q. rubra	NH$_4$	15	1.14	0.94–1.37	99.9	42.3–100[a]	7.25	3.80–16.7
Q. rubra	Ca(NO$_3$)$_2$	13	0.75	0.55–0.98	49.1	26.2–100[a]	15.0	7.54–37.2
T. canadensis	Control	16	1.69	0.97–2.79	21.8	12.4–35.9	26.1	31.9–58.5
T. canadensis	Na$_2$CO$_3$	18	1.80	1.20–2.87	11.5	9.12–14.2	5.37	2.98–11.4

[a] Upper boundary.

availability was increased, and in hindsight it would have been better to either split N applications into smaller, more frequent doses or to have used ion exchange resin bags or lysimeters to capture N as it moved through the soil (e.g., Kobe et al., 2002).

Effects of N application on soil pH (Fig. 1) are explained by plant mechanisms to maintain internal cation–anion balance and intracellular pH (Marschner, 1995). The decrease in soil pH with NH_4^+ application may have occurred because a hydrogen (H^+) molecule is returned to solution for every molecule of NH_4^+ taken up, and the increase in soil pH from NO_3^- because a hydroxyl (OH^-) ion is returned to solution for each NO_3^- molecule taken up.

Other treatment effects on soil pH are understandable from Brønsted–Lowry acid–base equilibria. Cations formed from the alkaline earth metals Ca and Mg act as weak conjugate acids by combining with OH^-, and SO_4^- acts as a weak base by combining with H^+. Thus, the soil pH increase when $Ca(NO_3)_2$ was applied was less than for $NaNO_3$ because the tendency of Ca^{2+} to acidify partly counterbalanced the tendency of NO_3^- to make the soil alkaline. Similarly, SO_4^- increased soil pH when combined with Na^+ but not with Ca^{2+} or Mg^{2+} because the acidity of the alkaline earth metal cations balanced the tendency of SO_4^- to make the soil alkaline.

6.2. Species' responses to nutrient manipulations

Reports of positive *A. saccharum* growth responses to Ca^{2+} additions are becoming commonplace (Wilmot et al., 1996; Kobe et al., 2002; Juice et al., 2006; Moore and Ouimet, 2006). In the current study, the increase in high-light growth with Ca^{2+} addition appears to be the dominant element of the growth response; the decrease in low-light growth is probably an artifact of the large numbers of saplings in the Ca^{2+} treatment group that were sampled at <5% light (Fig. 2). The positive response of *A. saccharum* to Ca^{2+} is at odds with the lack of correlation of growth and natural gradients of Ca^{2+} availability (Table 5; Bigelow and Canham, 2002). The most likely explanation is that exchangeable Ca^{2+} was not a sensitive measure of availability; calcium mineralization would have been better (Dijkstra, 2003). Regardless, the fertilization experiment is a stronger test of limitation, and it is clear that Ca^{2+} is an important growth-limiting nutrient in juvenile and adult phases of the *A. saccharum* life cycle in northern hardwood forests of eastern North America.

The vigorous high-light response of *F. americana* to NO_3^- in the present study was consistent with the characterization of the species as N-demanding (Mitchell and Chandler, 1939; but see Ellis, 1979; Stanturf et al., 1989), and with its traits of rapid growth and shade-intolerance. The similar response to $NaNO_3$ and $Ca(NO_3)_2$ fertilization suggests that there was no synergism between Ca^{2+} and NO_3^- nutrition. A previous study at our site did not detect N limitation of saplings of this species, but the formulation applied was urea, which must undergo several chemical transformations before providing available NO_3^- (Tripler et al., 2002). Neither Bigelow and Canham (2002) nor Finzi and Canham (2000) found any correlation between leader extension growth of *F. americana* and availability of NH_3^+ or NO_3^-; it is conceivable that extension growth responds differently to N availability than radial growth in this species.

The salient finding for *A. rubrum* was the large variance of the control compared to treatments. Inspection of the graph of growth plotted against light (Fig. 2) shows three rapidly growing saplings in the control treatment that are most responsible for the high variance. These saplings were located in hydric soils at the verges of ponds or streams, although other similarly located *A. rubrum* individuals were not growing rapidly. Past work has not strongly linked moisture status with radial growth for *A. rubrum* or any other species at GMF (Pacala et al., 1994; Caspersen et al., 1999; but see Kobe, 2006), but it is conceivable that the differences in variance between control and treatment were related to aspects of soil heterogeneity that went unmeasured in the current study. The other finding, of decreased high-light growth under K_2SO_4 fertilization, is undermined by the poor sampling of individuals under that treatment at >20% full sun (Fig. 2). The suggestion from previous studies that *A. rubrum* is limited by N (Catovsky et al., 2002; Finzi and Canham, 2000; Kobe, 2006) or by Al^{3+} (Bigelow and Canham, 2002) was not confirmed in our study.

F. grandifolia, the dominant species on the low-nutrient soils at GMF (Pacala et al., 1996), has usually proved unresponsive to fertilization, whether with N (Lea et al., 1979; Tripler et al., 2002), lime (Safford, 1973; Long et al., 1997), or Ca^{2+} (Kobe et al., 2002). Only Mitchell and Chandler (1939) have elicited a growth response to N. Bigelow and Canham (2002) found a weak positive correlation between Ca^{2+} and low-light growth of *F. grandifolia*; this species has low foliar Ca^{2+} (Chandler, 1939) and is not Ca^{2+}-demanding. Caspersen and co-workers (1999) have shown that mortality of *F. grandifolia* saplings at GMF is strongly influenced by drought stress. *F. grandifolia* is a

Table 5
Comparison of results from the present experimental study with results of previous observational study (Bigelow and Canham, 2002)

Species	Experimental		Observational	
	Treatment	Result[a]	Factor	Result[a]
A. saccharum	$CaSO_4$	$(\downarrow\uparrow)$	~	~
F. americana	$NaNO_3$, $Ca(NO_3)_2$	$(\downarrow\uparrow)$	Mg^{2+}, pH	$(\sim\downarrow)$
A. rubrum	K_2SO_4, $Ca(NO_3)_2$	$(\sim\downarrow)$	Al^{3+}, pH	$(\sim\uparrow)$, $(\sim\downarrow)$
F. grandifolia	~	$(\sim\sim)$	Ca^{2+}	$(\uparrow\downarrow)$
Q. rubra	$CaSO_4$, $(NH_4)_2SO_4$, $Ca(NO_3)_2$	$(\downarrow\uparrow)$	Ca^{2+}, pH	$(\uparrow\sim)$
T. canadensis	Na_2CO_3	$(\ )$	NO_3^-	$(\sim\uparrow)$

[a] Arrows in parentheses show direction of growth effect at high-light (first arrow) and high-light (second arrow) with increase in factor or treatment.

low-resource specialist, a stress-tolerator (sensu Grime, 1977) with limited ability to respond to pulsed inputs of additional soil nutrients.

Q. rubra was the only species that was strongly co-limited by two factors, Ca^{2+} and NH_4^+. Presumably the response to $Ca(NO_3)_2$ was due to Ca^{2+} rather than NO_3^-, because *Q. rubra* did not respond to $NaNO_3$. The NH_4^+ limitation in *Q. rubra* was consistent with many prior studies (Mitchell and Chandler, 1939 and other studies reviewed in Auchmoody and Filip, 1973); the urea form of N has not been as effective at eliciting a growth response (Auchmoody and Smith, 1977; Tripler et al., 2002). We are unaware of previous *Q. rubra* Ca^{2+} fertilization studies. The growth results from the direct fertilization of *Q. rubra* in the present study showed only partial correspondence with results from the earlier, non-experimental studies at GMF; the natural gradient study showed a correlation between low-light growth and soil Ca^{2+} and pH (Bigelow and Canham, 2002), but not with N availability.

The few fertilization trials of *T. canadensis* have shown it to be unresponsive to N (Catovsky and Bazzaz, 2000; Catovsky et al., 2002; Tripler et al., 2002) and other nutrients. There was a correlation between high-light growth and NO_3^- concentrations in the natural gradient study (Table 5), but the present study is consistent with the characterization of *T. canadensis* as non-responsive. High variance in the control treatment was related to the location of saplings; the six saplings with extremely low growth in the control group (Fig. 2) were located at a single site, and the reason for slow growth at this site is not known. A study comparing *T. canadensis* growth on the acid upland soils of the present study and more basic limestone-derived soils found slower growth on the latter (Kobe, 1996). Taken together, these results suggest that *T. canadensis* is second only to *F. grandifolia* in its lack of response to nutrient augmentation.

6.3. Community dynamics along nutrient gradients

The northern hardwood forest tree species at GMF tend to alter the light environment in ways that enhance the growth and survival of their own offspring (e.g., species that cast the densest shade tend to be shade-tolerant; Canham et al., 1994), and similar effects are evident with respect to the soil environment. *A. saccharum* has elevated rates of Ca^{2+} mineralization in forest floor (per-weight basis) and mineral soil compared to co-occurring species (Dijkstra, 2003), and juvenile *A. saccharum* have increased growth rates at elevated Ca^{2+}. *T. canadensis* has multiple traits associated with low rates of N cycling, including low potential net N mineralization and nitrification in its soils (Lovett et al., 2004), and as a juvenile is not responsive to N augmentation (present study and Catovsky et al., 2002). *Q. rubra* inhibits nitrification (Lovett et al., 2004), and in the present study showed a growth response to NH_4^+ (although as a seedling has equal affinity for NH_4^+ and NO_3^-; Templer and Dawson, 2004). These facts suggest that there are positive feedbacks on soil properties, or at the least, trees are influencing soil properties in ways that disadvantage potential competitors without adversely affecting themselves. This conclusion is consistent with other forms of evidence: a study

on spatial distribution of trees showed that *A. saccharum* and *T. canadensis* have positive self-association and negative reciprocal associations (Frelich et al., 1993), and a palynological study showed that stands dominated by either species can remain stable over millennia (Davis et al., 1998).

Stand simulations using the forest simulator SORTIE have shown that patterns of species replacement and succession are most strongly determined by growth and survival at low-light levels in the forest understory (Kobe et al., 1995; Pacala et al., 1996), but the growth responses observed in the present study mainly occurred under high-light conditions. Thus, local enrichment of the soil in particular nutrients (especially Ca^{2+} and N), whether as a result of feedbacks or abiotic processes, should select for improved growth of certain species, perhaps enhancing competitive ability and over time increasing the relative basal area and dominance of a species yet not necessarily affecting the species composition.

In a study on the same species (and individuals, prior to fertilization) at GMF (Table 5; Bigelow and Canham, 2002), growth responses of species along natural gradients were interpreted with respect to opposing views of niche theory and community organization (Keddy, 2001; Latham, 1992). The species that occur on the richest soils, *A. saccharum*, showed no consistent variation in growth across the soil gradient, but one of the species that occurs on more impoverished soils, *Q. rubra*, showed a strong correlation of growth with Ca^{2+}. Kobe (2006), working in Michigan with a similar suite of species, found a similar trend with respect to foliar nitrogen. This pattern is consistent with shifting competitive hierarchy theory, which emphasizes that individuals of some species may be displaced far from their optimal growth conditions by competition (see also Canham et al., 2006).

The present study lends more support for the opposing theory of fundamental niche differentiation, in that most species tended to have growth optima on the soil types on which they were most commonly found. For example, *A. saccharum* and *F. americana* each occur on rich sites with high exchangeable Ca^{2+} and rapid nitrification rates (Finzi et al., 1998a,b) and as saplings each showed a growth response to one of these nutrients (Ca^{2+} for *A. saccharum*, NO_3^- for *F. americana*). Conversely, the species that occur most frequently on impoverished soils (*T. canadensis*, *F. grandifolia*) had no growth response to nutrient augmentation, a result that is contrary to the predictions of shifting competitive hierarchy theory but is consistent with fundamental niche differentiation. The pattern of positive growth response to nutrient augmentation from species that normally occur on rich sites, and no response from species that are normally on poor sites, is also consistent with the view of community nutrient limitation espoused by Chapin et al. (1986). *Q. rubra*, though, fails to fit comfortably in any paradigm; limited by both Ca^{2+} and NH_4^+, it occurs on soils that are low in exchangeable Ca^{2+} but high in NH_4^+ availability.

7. Conclusions

One of the most obvious observations from this study is that plant species within a community can be limited by

different nutrients. Although it is often useful to treat limitation in mixed stands as though it were due to a single nutrient, differing demands and strategies of species almost guarantee that this is never the case. In the southern New England transitional hardwood forest that we examined, exchangeable Ca^{2+} and N (NO_3^- and NH_4^+) both played important roles in forest successional dynamics; in contrast, there were no growth increases from augmentation of K^+ or Mg^{2+}, alleviation of potential Al^{3+} toxicity, or synergism between Ca^{2+} and NO_3^-. The response of *A. saccharum* and *Q. rubra* saplings to Ca^{2+} augmentation indicates that anthropogenic processes that deplete surface soil Ca^{2+} (e.g., leaching by acidic precipitation) are likely to affect forest dynamics by slowing the growth of these species. Such a scenario might favor growth of low-Ca^{2+} tolerant species (*F. grandifolia*, *T. canadensis*), but there is no evidence from the present study to suggest that the course of succession would be altered. Finally, although the growth responses of the trees in this study were generally consistent with the concept of fundamental niche differentiation, when combined with other studies of effects of trees on soil properties there is a strong suggestion that positive feedback processes, which fundamental niche differentiation does not encompass, are important in the dynamics of these forests.

Acknowledgments

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