Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest[1]

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Abstract: To assess potential forest compositional responses to exchangeable soil calcium (Ca_{exch}) and aluminum (Al_{exch}), we characterized light-dependent growth and mortality of tree seedlings under amendments of $CaCl_2$ and $AlCl_3$ at Hubbard Brook Experimental Forest (HBEF), New Hampshire, U.S.A. Seedlings of *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh., *Betula alleghaniensis* Britton, *Abies balsamea* (L.) Mill., and *Picea rubens* Sarg. were transplanted into field plots, which were randomly assigned to control, $CaCl_2$, or $AlCl_3$ treatments and stratified across <1 to 35% full sun. *Acer saccharum* and *P. rubens* exhibited significantly higher mortality in Al-amended than Ca-amended or control plots. *Acer saccharum* showed significant increases in relative diameter growth in Ca-amended plots versus controls; all other species showed nonsignificantly higher relative diameter growth under Ca amendments. We incorporated significant seedling responses into a model of forest dynamics (SORTIE) to assess potential changes in species composition under Al_{exch} increases and Ca_{exch} losses. SORTIE predicts that further increases in Al_{exch} would have negligible effects on canopy composition within 200 years but that the estimated Ca_{exch} depleted from HBEF between 1968 and 1995 and its influence on seedling dynamics could lead to substantial decreases in *A. saccharum* canopy dominance within a single forest generation (<125 years).

Résumé : Afin d'évaluer les changements dans la composition de la forêt en réponse au calcium échangeable (Ca_{exch}) du sol et à l'aluminium échangeable (Al_{exch}), nous avons caractérisé la croissance et la mortalité de semis en relation avec la lumière dans un sol amendé avec $CaCl_2$ ou $AlCl_3$ à la forêt expérimentale de Hubbard Brook dans le New Hampshire, aux États-Unis. Des semis d'*Acer saccharum* Marsh., de *Fagus grandifolia* Ehrh., de *Betula alleghaniensis* Britton, d'*Abies balsamea* (L.) Mill. et de *Picea rubens* Sarg. ont été transplantés dans des parcelles au champ, lesquelles étaient assignées de façon aléatoire au traitement témoin et aux traitements avec $CaCl_2$ ou $AlCl_3$ et stratifiées en fonction d'un gradient de lumière (<1 à 35% du plein soleil). *Acer saccharum* et *P. rubens* ont subi une plus forte mortalité dans le traitement avec Al que dans le traitement avec Ca ou le témoin. *Acer saccharum* a montré un accroissement significatif de la croissance relative en diamètre dans les parcelles amendées avec Ca comparativement aux parcelles témoins; toutes les autres espèces ont montré un accroissement non significatif de la croissance relative en diamètre dans les parcelles amendées avec Ca. Nous avons incorporé les réponses significatives des semis dans un modèle de dynamique forestière (SORTIE) afin d'évaluer les changements potentiels dans la composition des espèces soumises à des augmentations de Al_{exch} et des pertes de Ca_{exch}. Le modèle SORTIE prédit que des augmentations supplémentaires de Al_{exch} auraient des effets négligeables sur la composition de la canopée pour les 200 prochaines années mais que les pertes estimées de Ca_{exch} à Hubbard Brook entre 1968 et 1995 et son influence sur la dynamique des semis pourraient conduire à une diminution importante de *A. saccharum* dans la strate dominante à l'intérieur d'une seule révolution (<125 ans).

[Traduit par la Rédaction]

Introduction

Decreases in soil exchangeable calcium (Ca_{exch}) and concomitant increases in aluminum (Al_{exch}) have been reported throughout the eastern United States (e.g., Markewitz et al. 1998; Likens et al. 1998). These changes likely arise from a combination of internal ecosystem processes (Markewitz et al. 1998), continued atmospheric inputs of acid anions (Likens et al. 1996, 1998; National Atmospheric Deposition Program (NADP), http://nadp.sws.uiuc.edu/), and decreased atmospheric inputs of base cations (Hedin et al. 1994; Likens et al. 1996; NADP, http://nadp.sws.uiuc.edu/).

Several lines of evidence, including physiology, species–soil relationships, and ecosystem-level nutrient budgets, sug-

Received 29 August 2001. Accepted 8 January 2002. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 17 May 2002.

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[1]Contribution of the Hubbard Brook Ecosystem Study and to the program of the Institute of Ecosystem Studies, Millbrook, N.Y.
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 DOI: 10.1139/X02-018

gest that documented changes in Ca_{exch} and Al_{exch} likely influence forest dynamics. At the level of individual leaves, photosynthetic rates normalized by nitrogen concentration (i.e., photosynthetic nitrogen use efficiency or A_{max}/g N) are correlated with foliar Ca concentrations for *Acer saccharum* Marsh. (sugar maple) trees experiencing crown dieback in northern Vermont (Ellsworth and Liu 1994). Similarly, among Amazonian tree species with low nitrogen (N), phosphorus (P), and Ca concentrations, maximum photosynthetic rates are strongly correlated with Ca concentrations but not with N or P (Reich et al. 1995). Foliar Ca concentrations also are correlated with dark respiration rates in *Picea rubens* Sarg. (red spruce) (McLaughlin et al. 1991, 1993) and *Pinus sylvestris* L. (Scots pine) (Reich et al. 1994). In addition to gas exchange, Ca plays a role in cold tolerance of red spruce (DeHayes et al. 1999), fine-root growth of sugar maple (Adams and Hutchinson 1992), and several other physiological processes including disease resistance, signal transduction, synthesis and function of membranes and cell walls, and regulation of stomata. McLaughlin and Wimmer (1999) provide a comprehensive review of Ca physiology in trees. Dissolved Al can be directly toxic to plants or can interfere with root uptake of Ca and other nutrients (Shortle and Smith 1988). Although the actions of Ca and Al in physiology suggest their potential importance in forest dynamics, it is not clear how these physiological responses scale to whole-tree growth and survival.

At the community and ecosystem levels, Ca availability is associated with community composition, mature tree growth, crown vigor, and ecosystem productivity. Calcium availability correlates with species composition across forest stands in North Carolina Piedmont (Palmer 1990) and within stands in southern New England (van Breemen et al. 1997). Across 15 forest stands in New England and northern New York, *Quercus rubra* L. (red oak) basal area increment is related to foliar Ca but not N; *Pinus strobus* L. (white pine) basal area increment is highly correlated with both foliar Ca and N but more strongly with Ca (Hallett and Hornbeck 1997). In northern Pennsylvania, sugar maple mortality is associated with Mg, Mn, and Ca nutrition and defoliation history (Horsley et al. 2000). In a related study, Long et al. (1997) fertilized mixed stands of sugar maple, *Fagus grandifolia* Ehrh. (American beech), and *Prunus serotina* Ehrh. (black cherry) with dolomitic lime, which resulted in increased sugar maple growth, survivorship, and reproduction, presumably in response to increased Ca, Mg, or pH. At Hubbard Brook Experimental Forest (HBEF) in New Hampshire, a decrease in forest biomass accumulation has occurred concomitant with depletions of Ca_{exch} (Likens et al. 1996, 1998). Evidence from these community- and ecosystem-level studies suggests the importance of Ca and Al in forest dynamics, thus providing the motivation for experimental manipulations of Ca and Al (independent of pH) to test cause–effect relationships.

We focus here on species-specific responses to soil Ca and Al availability as mechanisms of forest community dynamics and composition. We first characterized growth and mortality responses of seedlings of dominant tree species to experimentally manipulated levels of Ca_{exch} and Al_{exch}. Results of our field experiments then were integrated into an individual tree based model of forest dynamics (SORTIE; Pacala et al. 1996) to assess whether the magnitude of changes in seedling performance had the potential to influence canopy composition.

Methods

Field

This experiment took place at HBEF (43°56′N, 71°45′W), located near West Thornton, N.H., within the White Mountain National Forest. North-central New Hampshire's climate is classified as humid continental with short, cool summers and long, cold winters (Likens and Bormann 1995), but local climate varies with altitude and topography.

We located seedling transplant plots on a south-facing slope at approximately 700–800 m above mean sea level, a transitional zone from more deciduous to more conifer-dominated forests. The transplant plots were stratified across a range of light availability caused by recent tree fall gaps; 28 light-stratified plots were assigned to each of the three treatments (Al, Ca, and control).

To avoid confounding increases in Ca availability with increases in pH, we applied Ca as $CaCl_2$ in solid form and Al as $AlCl_3$ in solution. Over the course of this experiment (September 1995 through January 1998), we applied a total of 10 g/m^2 of Ca to the Ca plots, supplying approximately the amount of Ca_{exch} that was estimated to have been depleted from the forest floor from 1968 to 1995 (Likens et al. 1996, 1998). To maintain chloride and charge equivalency between Ca and Al treatments, we applied 4.49 g Al/m^2 to Al-addition plots. $CaCl_2$ powder was hand broadcast, and $AlCl_3$ solution was applied with a backpack sprayer. Total dosages were attained over four application dates: October 1995, May and October 1996, and May 1997.

Each transplant plot was laid out as a 4 × 5 matrix with 25-cm spacing between seedlings, resulting in 1 × 1.25 m plots with 20 positions. Four individuals of each of five species were planted to randomly chosen positions. Thus the experiment was initiated with 1680 seedlings (3 treatments × 28 plots/treatment × 4 seedlings/plot of each species × 5 species).

We transplanted seedlings of sugar maple, American beech, *Betula alleghaniensis* Britton (yellow birch), *Abies balsamea* (L.) Mill. (balsam fir), and red spruce. These five species account for most of the canopy tree basal area of our field sites and sites of similar elevation and aspect in the White Mountains (Bormann et al. 1970). To provide planting stock, we collected wild seedlings (all 2–3 years old) along trails from a similar elevational range near our sites in the HBEF. Seedlings usually were transplanted into experimental plots on the same day that they were collected. The collected seedlings were kept in plastic bags with moistened native soil until transplanting to avoid desiccation. All planting took place during September and October 1995. To minimize artifacts of transplant shock, all seedlings dying through 3 July 1996 were replaced. In addition, all seedlings surviving for less than 136 days from the date of transplant (i.e., approximately the length of one growing season) were eliminated from statistical analyses.

In June 1996, we estimated seedling light availability using color hemispherical canopy photography (a modification of Canham 1988) to compute the gap light index (GLI, in

units of percent full sun). Just above the foliage of the seedlings, we positioned a Nikon N70 camera with a Sigma 180° fish-eye lens, which was leveled and oriented so that the top of the camera corresponded with true north. Color slides were taken and developed images were scanned with a Polaroid QuickScan slide scanner. To analyze the digitized images we used GLI software, which imposes on the image latitude-specific, daily solar tracks for the growing season and calculates an estimate of the direct and diffuse light reaching the location of the photograph (and thus the seedlings). We specified the growing season as 15 May – 15 September. To characterize light heterogeneity within the 4 × 5 seedling matrix of the plots, one photograph was taken near each corner of the plot and light levels were interpolated to each seedling.

On a monthly basis from May to November in 1996 and 1997, we censused the seedlings for survivorship and evidence of dieback and damage. Seedling diameter and leader extension growth were measured once annually (in 1996 and 1997) from mid-September through early November. To minimize diameter measurement error, a permanent ink marker indicated the point of diameter measurement along the stem, which generally was within 5 cm of ground level but above the influence of the root collar. In January 1998, a severe ice storm damaged some of the seedling plots and generally increased understory light levels. Thus, we report results for only the 1996 and 1997 growing seasons.

Nutrient analyses

To assess the effectiveness of nutrient manipulations, during the 1997 growing season we collected soil solution with tension lysimeters (Super Quartz soil water samplers; Prenart Corp). Lysimeters were placed below the organic horizon in twelve 25 × 25 m plots in a companion study receiving the same experimental treatments; tension was applied to the lysimeters for 24 h before each sample collection on 7 May, 3 June, 11 July, 16 September, and 28 October. We obtained soil solution samples from 13 lysimeters in four $CaCl_2$ plots, 11 lysimeters in four control plots, and 12 lysimeters in four $AlCl_3$ plots. The pH of samples was determined immediately after collection. We used inductively coupled plasma emission spectrophotometry (ICP; Varian Corp.) to analyze soil solutions samples for Ca, Mg, K, Na, and Fe. Inorganic monomeric Al, NH_4, NO_3, and Cl were analyzed using a continuous-flow autoanalyzer (Technicon); determination of inorganic monomeric Al followed McAvoy et al. (1992).

We also sampled senesced leaves in fall 1996 to further assess the effectiveness of nutrient manipulations. We collected senesced leaves in the fall instead of mature leaves during the growing season to minimize interference with seedling performance. The use of senesced leaf nutrient content as an index of nutritional status is supported by a strong correlation between mature and senesced leaf nutrient content (R.K. Kobe, C.A. Lepczyk, and M. Iyer, unpublished data). In addition, Ca concentrations in mature and senesced leaves are not expected to differ appreciably, as Ca is not retranslocated (Likens et al. 1998). Foliar nutrients were not analyzed for red spruce and balsam fir, because we were not able to collect senesced needles that had developed post-fertilization.

Leaf samples were oven-dried at 70°C for at least 48 h. Dried leaf samples were ground with a canister-ball pulverizer (Kinetic Laboratory Equipment Co., Visalia, Calif.). To digest the leaf samples for nutrient analyses, the samples from each seedling were placed in 100-mL digestor tubes with 5 mL concentrated nitric acid (HNO_3) for at least 14 h. The tubes were placed in a block digestor, ramped to 155°C for 20–25 min, and maintained at 155°C for 1 h. We added 2.5 mL of perchloric acid ($HClO_4$) to each sample, increased the block digestor temperature to 220°C, and maintained it for 2 h. We used a direct current plasma atomic emission spectrometer (DCP–AES, SMI Inc.) to analyze the digested foliar samples for Ca, Al, Mg, K, P, Fe, Mn, Zn, and Cu. Pine needles from the National Bureau of Standards were used for quality control.

Statistical analyses

We tested for significant differences among treatments in senesced leaf nutrient contents, soil solution ion concentrations, and 2-year diameter growth (combined 1996 and 1997) with the nonparametric Kruskall–Wallis one-way ANOVA and parametric one-way ANOVA using S-Plus 2000 (Mathsoft Inc). Dunn–Šidák corrected Mann–Whitney U tests and t tests, respectively, corresponding with nonparametric and parametric comparisons, were used to identify significantly different pairs among treatments.

We also characterized 2-year (1996–1997) diameter growth as a function of light availability for each species–treatment combination with log–linear and Michaelis–Menten models. The log–linear model was as follows: $\ln(1 + \Delta\text{diameter}_{1996-1997}) = \alpha + \beta \times \ln(1 + \text{light})$, where α and β are estimated from the data and correspond with the y intercept and slope. Similar to Pacala et al. (1994), the Michaelis–Menten model was specified as

$$[1] \qquad \Delta\text{diameter}_{1996-1997} = \text{diameter}_{1996} \times \frac{P_1 \times \text{light}}{P_1/P_2 + \text{light}}$$

where P_1 and P_2 are parameters estimated from the data and govern asymptotic and low-light growth, respectively. We fit the models and calculated 95% support (equivalent to 95% confidence intervals, but "support" is used in conjunction with likelihood methods) for the parameter estimates using SYSTAT version 7.0 (SPSS Inc., Chicago, Ill.).

To test for treatment effects on survivorship, we used the G test of independence to compare the number of surviving and dying seedlings among the control, Ca, and Al treatments (Sokal and Rohlf 1981). These analyses were performed for each species without consideration of variation in light availability. Furthermore, these analyses do not take into account differences among treatments in survival times.

We also examined treatment effects on species-specific survivorship by fitting models of mortality as a function of light and as a function of growth, using survival analysis and maximum likelihood methods. Cox and Oakes (1984) provide a detailed overview of survival analysis. Here we summarize how we applied these methods to our data. In contrast to the G test and other categorical analyses, survival analysis is based on distributions of survival times and enables testing factors that predict mortality. In our experiment, seedling survival times followed a continuous

distribution because (*i*) seedlings entered the experiment at various times because we replaced seedlings that died before 3 July 1996, conservatively ascribing death before this date to transplant shock; (*ii*) we frequently censused seedlings (at least monthly from May through October), thus increasing resolution in identifying a particular death date; and (*iii*) seedlings died during every census interval. Likelihood methods are used to fit models, including survival distributions, through finding the set of parameters underlying the distributions of a particular data set that results in the highest probability (i.e., maximum likelihood) of obtaining the data set (Hilborn and Mangel 1997).

Analogous to the distribution function for a binomial random variable, the likelihood function for a continuous distribution of survival times is

$$[2] \qquad L = \prod_{i=1}^{D} f(t_i; \phi) \prod_{i=1}^{N-D} S(c_i; \phi)$$

where the contribution to the likelihood of a seedling observed to die at time t is $f(t_i; \phi)$ (i.e., the density of failure at time t) and the contribution to the likelihood of an individual surviving beyond time c is $S(c_i; \phi)$ (i.e., the survivor function), ϕ is a vector of parameters, and D represents the number of individuals dying, and $N - D$ is the number of individuals surviving beyond time c, both indexed by i (Cox and Oakes 1984). Using an exponential distribution of survival times, which is supported by seedling deaths occurring in each census interval, the likelihood becomes

$$[3] \qquad L = \prod_{i=1}^{D} M(x, \phi) e^{-tM(x,\phi)} \prod_{i=1}^{N-D} e^{-cM(x,\phi)}$$

where $M(x, \phi)$ is a function composed of x as an explanatory variable and set of parameters ϕ. For each species–treatment combination, we used the Metropolis Search Algorithm to identify the set of parameters ϕ that resulted in the highest likelihood of obtaining the data set. In the present situation, we tested light availability and recent growth rates (x) as factors in predicting mortality. To characterize this relationship, we used a negative exponential function, $M(x, \phi) = A\, e^{-Bx}$, with parameters A and B estimated from the data set. To test for the significance of light availability and recent growth rates (as a surrogate for carbon balance), we used likelihood ratio tests (LRTs) to compare models with B estimated from the data versus $B = 0$. Similarly, to simplify the model, we used LRTs to compare models with A estimated from the data versus A set to a constant (i.e., $A = 0.04$ and $A = 0.05$) for all species and treatment combinations. All survival analyses were completed in programs that we wrote in Borland Delphi.

SORTIE simulations (Pacala et al. 1996) were used to assess potential community-level effects of observed seedling responses to our experimental manipulations. SORTIE is a mechanistic (i.e., resource-based), individual-tree based, spatially explicit model of forest community dynamics that operates on a 5-year time step. SORTIE is based on four species-specific submodels: (*i*) seedling recruitment (production of new seedlings as a function of parent size and seedling dispersion as a function of distance to the parent); (*ii*) calculation of the amount of light available to each tree as a function of the species, size of, and distance to neighboring trees; (*iii*) growth as a function of light availability; and (*iv*) mortality as a function of growth. In contrast to other forest dynamic models (JABOWA, FORET, and descendants), all the parameters governing the behavior of SORTIE have been determined by field experiments on individual trees, and all of the community level predictions of SORTIE arise solely from species-specific individual tree performance (i.e., no community-level properties are used to calibrate the model). SORTIE's community-level predictions are in close agreement with available data (e.g., changes in species composition through succession, old-growth composition) (Pacala et al. 1996), supporting that the model has encapsulated the processes important for predicting community dynamics and composition. Thus, SORTIE provides a tool with which to scale empirically observed individual tree behavior to the community level. Accordingly in this paper, we address the following question: would the magnitude of changes in species-specific performance of seedlings that have been observed under enhanced Ca and Al availability alter canopy composition?

We did SORTIE simulations of 1-ha plots for control, enhanced Ca, and enhanced Al conditions for the five species that we examined in the transplant experiment. These sets of simulations can be viewed as respectively representing current, past, and future conditions under atmospheric deposition of acid anions. Note that we are assuming that significant seedling responses to Ca and Al are maintained over the time of the simulations (i.e., there is no seedling acclimation to enhanced Ca or Al). Although SORTIE has not been calibrated for HBEF, our interest was not to simulate HBEF per se but to assess if the magnitude of seedling growth and mortality responses that we observed had the potential to alter species composition and successional trajectories, regardless of the particular community that was being simulated. Thus, we used model parameters as reported for Great Mountain Forest in northwestern Connecticut (Pacala et al. 1996) for the control simulations. Balsam fir and red spruce were not included in the original calibration of SORTIE but are similar to *Tsuga canadensis* (L.) Carrière (eastern hemlock) in several respects (all are evergreen, very shade tolerant, and have high foliage density). Thus, we substituted eastern hemlock parameter values for balsam fir and red spruce in the simulations.

For the enhanced Al and Ca simulations, we adjusted the parameters of the control seedling or sapling growth and mortality submodels of SORTIE to reflect the same magnitude of change observed in our field experiment for statistically significant effects only. Thus, for the enhanced Ca simulations, only sugar maple seedling growth was changed. Seedling and sapling growth in SORTIE are governed by a Michaelis–Menten function, as in eq. 1. Because a given percentage increase in the growth model's parameters results in the same percentage increase in diameter growth, we simply increased the asymptotic (P_1) and low-light (P_2) growth parameters of sugar maple by 49.4%, which is sugar maple's empirically determined increase in diameter growth under Ca fertilization.

We also scaled sugar maple and red spruce mortality submodels to result in empirically observed percentage increases in mortality under enhanced Al relative to controls

through spring 1998. SORTIE's seedling or sapling mortality submodel is

[4] Probability of mortality (2.5 years)

$$= M1 \times e^{-M2 \times \text{mean recent radial growth}}$$

where M1 (y intercept or mortality at zero growth) and M2 (decay or sensitivity of mortality to increased growth) are estimated parameters and $0 < M1 < 1$ (Kobe et al. 1995). The mean mortality across all positive growth rates is the integral of eq. 4, which is simply M1/M2. Thus, we characterized Al-induced increases in mortality by multiplying M1 or dividing M2 by the empirically observed ratio of mortality probabilities in the Al-amended plots relative to the controls. In practice, this meant increasing M1 for spruce under the Al simulations, because $M1_{spruce} << 1$. For sugar maple in the Al simulations, M2 was decreased because increasing M1 ($M1_{sugar\ maple} = 0.99$) would have resulted in an Al-adjusted $M1 > 1$, which is biologically impossible.

All other parameters in the SORTIE simulations of increased Ca and Al were the same as in the control simulations (i.e., all parameters controlling seedling recruitment, tree allometric relationships, mature tree growth and mortality, and attenuation of light availability). Each scenario was run 100 times with different random number seeds. We report the mean relative basal area for each scenario and the central 94% of the runs to estimate stochastic uncertainty in the model predictions (Pacala et al. 1996). Each simulation ran for 1000 years (first 200 years shown) with the only source of disturbance being canopy gaps originating from mature tree deaths.

Results

Effectiveness of nutrient manipulations

We tested for treatment effects on soil ion concentrations averaged over the growing season (samples in May, June, July, September, and October 1997) and for the 3 June 1997 sample date, a time when plant nutrient demand was expected to be high. $CaCl_2$ additions significantly increased mean and median soil solution Ca concentrations for both the growing season mean and June measurement (Table 1) (June mean, uncorrected $p = 0.03$). $CaCl_2$ additions also significantly increased Mg concentrations (both growing season and June) in comparison with the controls and median Ca/Al ratios marginally in comparison with the controls (June sample date, uncorrected $p = 0.07$). The $AlCl_3$ treatment significantly increased median Al concentrations for the growing season mean and resulted in nonsignificant increases in Al concentrations for the June sampling date (uncorrected $p = 0.05$). The $AlCl_3$ treatment also increased Ca levels in comparison with the controls, but median Ca/Al ratios were significantly lower in the $AlCl_3$ treatment and highest in the $CaCl_2$ treatments. We did not observe significant effects of treatments on Na, K, Fe, NH_3, and H concentrations. As expected, Cl concentrations were significantly higher in both treatments in comparison with the control. In summary, these data show that the $CaCl_2$ treatment raised Ca soil solution concentrations and Ca/Al ratios and that the $AlCl_3$ treatment raised Al soil solution concentrations and lowered Ca/Al ratios.

Table 1. Ion concentrations (ppm) of soil solution under $CaCl_2$ and $AlCl_3$ additions and controls.

Element	Control	$CaCl_2$ addition	$AlCl_3$ addition
Growing season mean			
Ca			
Median	0.75*a*	5.45*b*	2.40*b*
Mean	1.03*a*	5.49*b*	3.89*b*
Al (inorganic)			
Median	0.14*a*	0.17*ab**	0.45*b*†
Mean	0.15*a**	0.33*a*	1.36*a*†
Ca/Al			
Median	9.13*ab*	26.29*b*	6.31*a*
Mean	62.78*ab*	65.76*b*	7.15*a*
Mg			
Median	0.14*a*	0.75*b*	0.38*ab*
Mean	0.18*a*	0.81*b*	0.57*ab*
June sampling			
Ca			
Median	0.46*a*	13.69*b*†	1.35*ab**
Mean	1.04*a**	15.92*a*†	3.60*a**
Al (inorganic)			
Median	0.15*a**	0.38*a*†	0.32*a*†
Mean	0.15	1.11	0.65
Ca/Al			
Median	6.6*ab**	22.43*b*†	3.86*a*
Mean	43.51*a*†	31.63*a*†	9.25*a**
Mg			
Median	0.09*a*	2.79*b*	0.53*b*
Mean	0.13*a**	2.50*b*‡	0.76*ab*†

Note: Within rows, values with different letters are significantly different at $\alpha = 0.05$ among the three treatments. Dunn–Šidák corrected significance level of 0.017 is used for paired comparisons. Marginally significant pairwise comparisons (uncorrected $p < 0.07$) are indicated by different superscript symbols.

All three species that we examined for foliar nutrients, sugar maple, American beech, and yellow birch, had significantly higher mean and median concentrations of Ca in senesced leaves under Ca fertilization than under control and Al treatments ($p < 0.05$) (Table 2). These results demonstrate that our experimental applications of $CaCl_2$ influenced the nutrient status of the seedlings. Note that because Ca is not retranslocated, concentrations in senesced and mature leaves are normally very similar. The Al fertilizations led to increased mean and median Al concentrations in yellow birch leaves and increased mean concentrations in American beech (Table 2).

The Ca fertilization had indirect effects on foliar concentrations of other nutrients, increasing median P concentrations in the senesced leaves of all three species (sugar maple and yellow birch, $p < 0.05$; American beech, $p < 0.06$) and mean concentrations in sugar maple and American beech ($p < 0.05$). In response to the Ca fertilization, more foliar elements were influenced in sugar maple than the other two species. In addition to significantly higher Ca and P concentrations, median and mean concentrations of Mg and K and median concentrations of Fe also were significantly higher under enhanced Ca in the sugar maple senesced leaves in comparison with the control and (or) Al treatment. Indirect

Table 2. Median and mean element concentrations (ppm) of senesced leaves under $AlCl_3$ and $CaCl_2$ additions and controls.

Species	Treatment	Ca	Al	Mg	K	P	Mn	Fe	Zn	Cu
Median concentrations										
American beech	Al	6086*a*	128	1548	6050	1659*ab*	1370*a*	180	44.3	10.0*b**
	Ca	7282*b**	111	1522	5179	1977*b**	2078*b**	141	45.3	7.45*a*
	Control	6200*a*	104	1361	6576	1644*a*	1212*a*	144	38.6	8.41*ab*
	N	48, 48, 47	48, 48, 47	48, 49, 47	48, 48, 47	48, 50, 42	48, 48, 46	21, 36, 26	48, 50, 47	48, 50, 47
Sugar maple	Al	6736*a*	112	1642*ab*	6116*a*	1135*a*	1838	108*a*	52.1	8.07
	Ca	10 850*b**	95	1886*b**	7000*b**	1533*b**	2177	140*b**	52.7	6.69
	Control	7536*a*	77	1561*a*	5769*a*	1187*a*	1631	85*a*	48.4	7.53
	N	46, 47, 48	47, 47, 47	47, 44, 48	47, 48, 48	47, 47, 44	47, 44, 48	17, 32, 27	47, 48, 48	47, 48, 48
Yellow birch	Al	9802*a*	139*b**	3420	10 240	1691*a*	4344	131	361.5	9.35*b**
	Ca	12 780*b**	103*ab*	3810	10 323	1957*b**	5779	141	391.3	7.88*a*
	Control	9564*a*	88*a*	3880	8854	1619*a*	4399	135	402.7	7.95*ab*
	N	48, 44, 48	46, 44, 46	47, 44, 48	46, 45, 48	47, 47, 47	45, 39, 46	25, 35, 37	48, 47, 48	47, 46, 48
Mean concentrations										
American beech	Al	6509*a*	319*b**	1628	6927	1838*ab*	1616*a*	159	65.7	15.1
	Ca	8348*b**	200*ab*	1779	6678	2014*b**	2379*b**	183	70.9	13.1
	Control	6661*a*	131*a*	1573	6478	1675*a*	1688*a*	176	48.0	10.8
Sugar maple	Al	7918*a*	168	1781*ab*	6218*a*	1236*a*	2231	126	60.1	9.16
	Ca	12 110*b**	160	2043*b**	8323*b**	1684*b**	2702	173	77.4	10.4
	Control	7424*a*	158	1644*a*	6122*a*	1280*a*	2042	134	64.2	10.7
Yellow birch	Al	10 780*a*	513*b**	3615	10 700	1850	5153	185	449.8	17.0
	Ca	12 800*b**	297*a*	3775	11 000	2139	5841	189	565.3	14.7
	Control	9849*a*	210*a*	3928	9336	1878	4688	159	431.8	11.0

Note: Values within columns with different letters are significantly different among treatments for a species ($p < 0.05$). For sugar maple, K and Fe median concentrations in the $AlCl_3$ versus control are significant at $p = 0.06$ and P median concentrations in American beech at $p = 0.08$. *N*, sample size for Al, Ca, and control, respectively.

*Highest element concentration in each statistically significant comparison.

Table 3. Median and mean relative diameter growth (mm) over 2 years by species and treatment. *N*, sample size.

Species	Treatment	*N*	Relative diameter growth		
			Median	Mean	SD
American beech	Al	53	0.50	0.49	0.21
	Ca	70	0.50	0.57	0.37
	Control	61	0.40	0.48	0.28
Balsam fir	Al	94	0.90	0.95	0.38
	Ca	95	1.00	1.07	0.46
	Control	95	0.90	0.96	0.43
Sugar maple	Al	36	0.60*a*	0.61*a*	0.23
	Ca	68	0.70*b*	0.82*b*	0.41
	Control	68	0.50*a*	0.54*a*	0.24
Red spruce	Al	88	0.80	0.83	0.37
	Ca	98	1.00	0.98	0.54
	Control	98	0.90	0.91	0.47
Yellow birch	Al	61	0.70	0.75	0.40
	Ca	59	0.90	1.03	0.71
	Control	51	0.70	0.85	0.55

Note: Values within columns with different letters are significantly different ($p < 0.05$).

effects of the Al fertilization were limited to higher median Cu concentrations in beech and yellow birch ($p < 0.05$) (Table 2).

Growth

Averaged across light levels, all species showed higher 1996–1997 relative diameter growth (RDGR) under the Ca fertilization in comparison with the control and Al treatments, but only sugar maple showed a significant ($p < 0.05$) growth enhancement (Table 3). Our caliper measurements of diameter were coarse and more susceptible to measurement error than measuring annual area increments of stem cross sections or biomass accumulation through sequential harvests. Thus, detection of significant results is conservative.

Light availability was a significant, although generally weak, predictor of RDGR for all species–site combinations except for sugar maple and beech in the Al-amended plots. The log–linear model provided better fits than the Michaelis–Menten function in 11 of 13 species–treatment combinations where light was a significant predictor, as assessed by LRTs and R^2 values. Thus, we report results only for the log–linear model (Table 4).

All species showed the highest RDGR at a given light level under the Ca treatment and the lowest under the Al treatment (Fig. 1, Table 4). However, only the sugar maple seedlings in the Ca-amended plots showed significantly higher RDGR compared with the control. For both sugar maple and beech, the Al additions resulted in nonsignificant regressions of RDGR on light and the lowest R^2 values. For these species, Al additions appear to introduce additional noise in the potential relationship between relative diameter growth and light availability to the extent that light availability is not a significant predictor of RDGR.

Mortality

Through our last census before the January 1998 ice storm, sugar maple showed significantly higher mortality across all light levels in the Al-amended plots in comparison with the controls and Ca-amended plots ($p < 0.001$, *G* test), beech mortality was marginally higher in the Al versus Ca plots ($p = 0.06$, *G* test), and red spruce showed nonsignificantly higher mortality in the Al versus control plots ($p < 0.12$, *G* test) (Table 5). Based on our first census after the January 1998 ice storm, red spruce joined sugar maple in exhibiting significantly higher mortality in the Al treatment ($p < 0.05$, *G* test), but there were no significant treatment differences in beech mortality (Table 5).

We also examined treatment effects on mortality by developing separate treatment regressions of the probability of mortality against light availability and diameter growth. Light availability was not significant in predicting mortality for any of the 15 species–treatment combinations; that is, in $M(\text{factor}, \beta) = A_{\text{light}} \times e^{(-B_{\text{light}} \times \text{light})}$, B_{light} was not significantly different from zero ($p > 0.05$, LRT).

In contrast to light availability, diameter growth in 1996 was a significant predictor of mortality in 1997 for all species–treatment combinations. That is, $B_{(\text{diameter growth 1996})}$ was significantly greater than zero in $A_{(\text{diameter growth 1996})} \times e^{-B_{\text{diameter growth 1996}} \times \text{diameter growth 1996}}$ ($p < 0.05$, LRT). Furthermore, for all species except red spruce, LRTs indicated no significant differences for models with $A_{(\text{diameter growth 1996})} = 0.05$ versus $A_{(\text{diameter growth 1996})}$ fit to the data ($p > 0.05$). For red spruce in all treatments, there were no significant differences in models with $A_{(\text{diameter growth 1996})} = 0.015$ versus $A_{(\text{diameter growth 1996})}$ fit to the data ($p > 0.05$). Therefore, models with one estimated parameter (B) were sufficient to characterize mortality as a function of growth for all species–treatment combinations (Table 6).

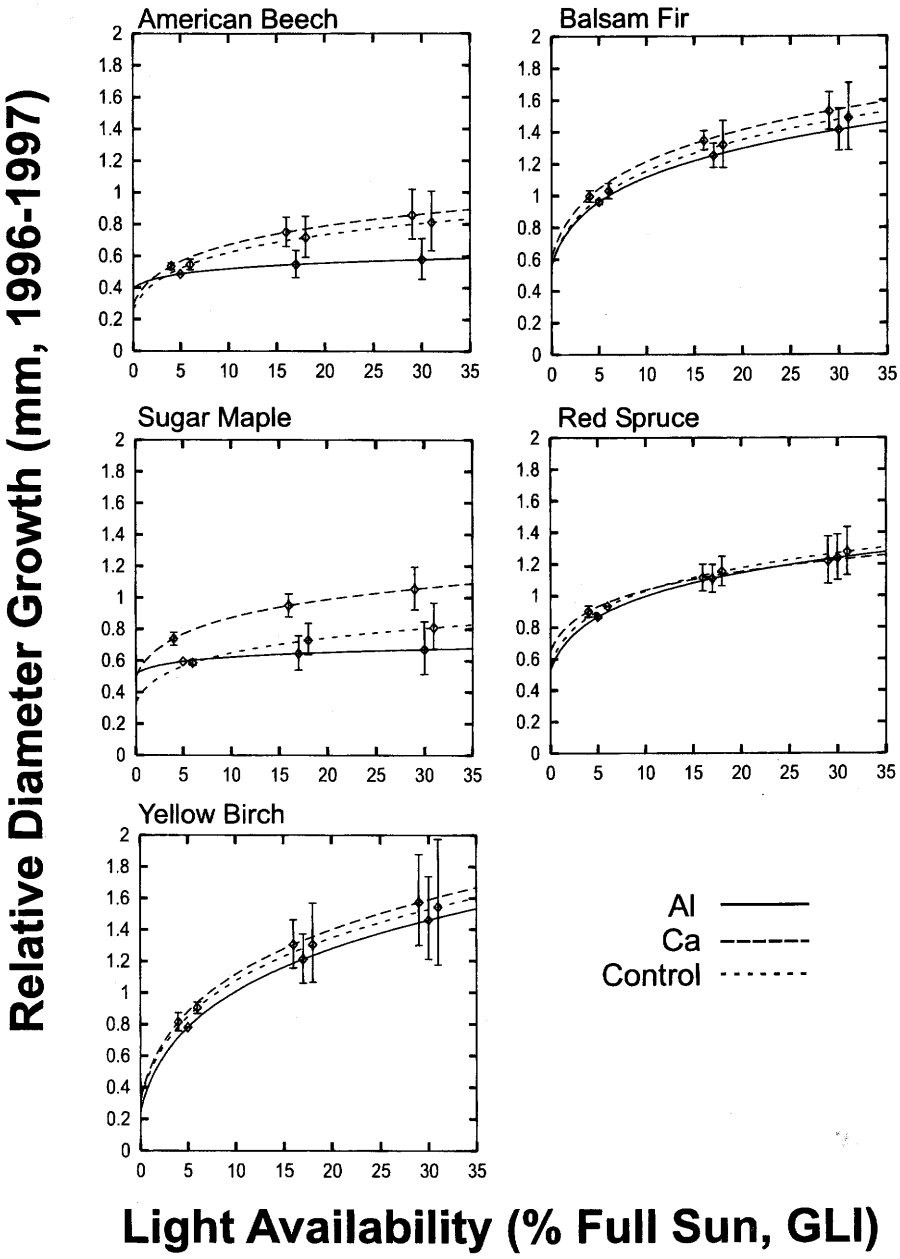
For all species–treatment combinations except yellow birch, the fitted models indicated that at any given growth rate, mortality was highest in the Al treatment (Fig. 2). However, only sugar maple's increased growth-dependent mortality was significantly higher in the Al treatment as indicated by non-overlapping 95% support limits for B among treatments (Table 6).

Predicted species composition

Species composition as reflected by relative basal area shows little variation between the control and Al treatments at 50, 125, and 200 years of forest succession (Fig. 3). The enhanced Ca simulations, however, contrast sharply with the control and enhanced Al simulations. Within a single tree generation (<125 years), sugar maple has more than twice the relative basal area under enhanced Ca in comparison with both the control and enhanced Al simulations. Sugar maple shows further increases in canopy dominance at 200 years under enhanced Ca. The effects of enhanced Ca at 50 years are less pronounced because of an expected lag in the effects of seedling dynamics on canopy composition.

These results suggest that the increases in red spruce and sugar maple seedling mortality under enhanced Al have relatively minor effects on relative species composition (Fig. 3). In contrast, the increase in sugar maple seedling growth under enhanced Ca has strong effects on sugar maple relative basal area. This substantial change in sugar maple relative basal area was effected by increased seedling growth only.

Fig. 1. Fitted models and 95% confidence intervals of 2-year relative diameter growth (1996–1997) in relation to light availability (% full sun) under Al, Ca, and control treatments. See Table 4 for model form, parameter estimates, and parameter 95% support (used to develop the confidence intervals here). Light availability was a significant predictor of diameter growth for all species–treatment combinations except sugar maple and beech under Al fertilization. GLI, gap light index.



Discussion

The amount of Ca added to these experimental plots was approximately equivalent to the amount of Ca calculated to have been depleted from the forest floor of HBEF from 1968 to 1995 (Likens et al. 1998). Thus, our experimental treatments of soil Ca amendments, controls, and Al amendments, respectively, represent past (pre-1968), current (1995–1997), and possible future states of soil Ca/Al status in northern New England.

Incorporating significant treatment differences on seedling growth and mortality (Table 7) into a model of forest community dynamics (SORTIE: Pacala et al. 1996) suggest that the loss of Ca_{exch} that has already taken place in these ecosystems could lead to a decline in the relative basal area of sugar maple in the canopy within a single tree generation (<125 years) mediated through seedling dynamics. In contrast, SORTIE results do not show a strong effect of Al on canopy tree composition within 200 years. However, after 300 years (results not shown), both sugar maple and red spruce show declines in relative canopy composition. We emphasize the qualitative results of the forest succession simulations as applied to HBEF, because SORTIE has not been calibrated for HBEF; thus, we assess the potential im-

Table 4. Maximum likelihood estimates (MLE) of growth model parameters and associated 95% support (equivalent to 95% confidence intervals).

Species	Treatment	α MLE	95% support α lower	95% support α upper	β MLE	95% support β lower	95% support β upper	R^2
American beech	Al	0.333	0.249	0.417	0.036	–0.012	0.084	0.04
	Ca	0.259	0.159	0.359	0.106	0.052	0.16	0.18
	Control	0.234	0.15	0.318	0.104	0.05	0.158	0.22
Balsam fir	Al	0.448	0.372	0.524	0.126	0.088	0.164	0.31
	Ca	0.479	0.403	0.555	0.132	0.096	0.168	0.35
	Control	0.447	0.393	0.501	0.134	0.094	0.174	0.32
Sugar maple	Al	0.415	0.305	0.525	0.029	–0.032	0.09	0.02
	Ca	0.404	0.3	0.508	0.093	0.043	0.143	0.17
	Control	0.292	0.216	0.368	0.087	0.043	0.131	0.19
Red spruce	Al	0.425	0.345	0.505	0.111	0.069	0.153	0.23
	Ca	0.502	0.406	0.598	0.087	0.039	0.135	0.12
	Control	0.449	0.363	0.535	0.108	0.064	0.152	0.20
Yellow birch	Al	0.224	0.104	0.344	0.197	0.131	0.263	0.38
	Ca	0.282	0.122	0.442	0.195	0.115	0.275	0.30
	Control	0.272	0.116	0.428	0.191	0.101	0.281	0.23

Note: The growth model is as follows: $\ln(\text{diameter growth}_{1996\text{–}1997} + 1) = \alpha + \beta \times \ln(1 + \text{GLI})$, where α and β are parameters estimated from the data and GLI is gap light index, a measure of light availability in units of percent full sun. Sample sizes are as in Table 3.

Table 5. Sample sizes and percent mortality through November 1997 and June 1998.

Species	Treatment	N	Mortality (%) Through November 1997	Mortality (%) Through June 1998
American beech	Al	101	45*b*	52
	Ca	103	32*a*	43
	Control	99	35*ab*	44
Balsam fir	Al	102	7	8
	Ca	104	9	10
	Control	104	7	7
Sugar maple	Al	103	60*b*	68*b*
	Ca	104	34*a*	43*a*
	Control	104	35*a*	42*a*
Red spruce	Al	101	12	15*b*
	Ca	106	7	8*a*
	Control	104	6	6*a*
Yellow birch	Al	102	36	44
	Ca	104	41	46
	Control	99	47	52

Note: Values with different letters are significantly different among treatments (G tests on categorical data, $p < 0.05$; $p = 0.06$ for American beech Ca vs. Al through 1997).

Table 6. Maximum likelihood estimates (MLE) and 95% support for the following mortality model: probability of $\text{mortality}_{(1997)} = 1 - \exp(-tA \times \exp(-B(\text{diameter growth}_{1996})))$ where $A = 0.015$ for red spruce and 0.05 for all other species and t is time (months).

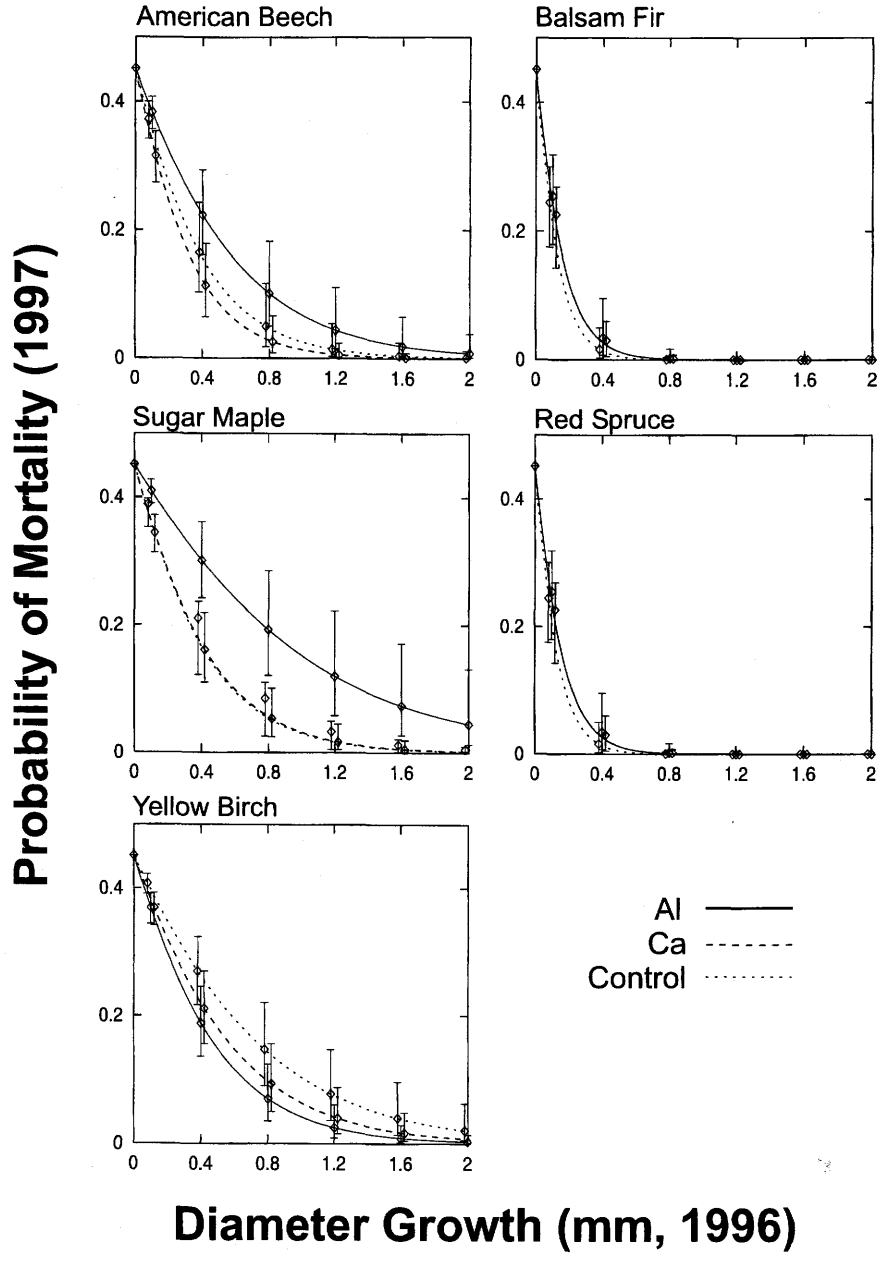
Species	Treatment	B_{MLE}	95% support Lower	95% support Upper
American beech	Al	2.159	1.363	3.066
	Ca	3.824	2.648	5.226
	Control	3.164	2.017	4.502
Balsam fir	Al	7.124	4.459	11.08
	Ca	7.096	5.406	11.32
	Control	9.501	6.469	14.20
Sugar maple	Al	1.289	0.725	1.923
	Ca	2.924	2.113	3.896
	Control	2.449	2.099	4.022
Red spruce	Al	5.424	4.433	8.064
	Ca	9.027	6.243	13.06
	Control	7.191	5.176	9.946
Yellow birch	Al	2.640	1.885	3.518
	Ca	2.207	1.537	3.000
	Control	1.699	1.125	2.364

Note: Treatments within a species are significantly different if 95% support regions for the B estimate do not overlap.

pact of the observed treatment differences rather than simulating HBEF per se. In addition, we assumed that the observed seedling responses to enhanced Ca and Al would apply to seedlings over the length of the simulations. Although we have no a priori reason to expect it, long-term seedling acclimation to enhanced Ca and Al is not known but obviously would influence predictions of the model. On the other hand, the model predictions here can be regarded as conservative, because they were based solely on changes in seedling growth and mortality even though Ca/Al ratios likely change other processes that could directly or indirectly affect relative species basal areas. For example, Ca availability might also be expected to influence the growth and reproductive output of sugar maple canopy trees (e.g., Wilmot et al. 1996; Long et al. 1997), direct effects that were not characterized by these simulations but would reinforce the predicted outcomes.

Model predictions of increased sugar maple basal area under enhanced Ca_{exch} are consistent with sugar maple's association with high pH and Ca across sites in the northeastern United States (R.A. Hallett, S.B. Horsley, R.B. Long, S.W. Bailey, and T.J. Hall, unpublished data) and northernwestern

Fig. 2. Fitted models and 95% confidence intervals of probability of mortality in 1997 (through November 1997 census) as a function of diameter growth in 1996 under Al, Ca, and control treatments. See Table 6 for model form, parameter estimates, and parameter 95% support (used to develop the confidence intervals here).



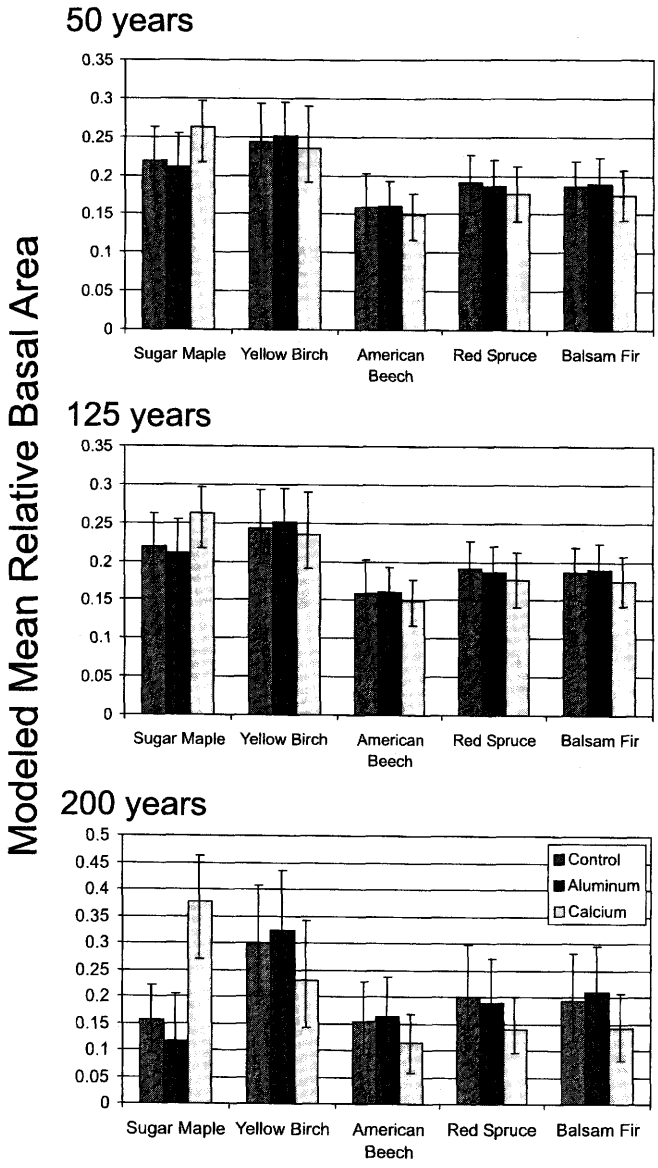
lower Michigan (Schreeg and Kobe 2001), and among- and within-stands in northwestern Connecticut (Kobe 1996; van Breemen et al. 1997). Presumably, this association reflects differences in sugar maple performance in relation to Ca availability, as demonstrated in this study and as suggested previously for sites differing in species composition and soil parent material in northwestern Connecticut (Kobe 1996). Liming ($CaCO_3$ and $MgCO_3$ additions) also increased the growth, survival, and reproductive output of sugar maple canopy trees (Long et al. 1997); however, results of liming studies are more difficult to interpret, because they are confounded with increases in soil pH.

There have been numerous reports of the decline of red spruce canopy trees (Hornbeck and Smith 1985), presumably because of the leaching of membrane-bound Ca from needles in the presence of acid precipitation (DeHayes et al. 1999). Here, we have shown a potential consequence of acid precipitation on the mortality of red spruce seedlings that is not due to foliar leaching but that results from increased availability of soil Al (also see Raynal et al. (1990) and Kelly et al. (1990)).

Whole-plant physiological responses

The ratios of Ca/Al in soil solution and foliage and their effects on plant carbon balance have been emphasized in assessing plant physiological responses to Ca and Al. Low Ca/Al ratios lead to high Al saturation of root exchange sites, possibly leading to both Al interference in biochemical

Fig. 3. Mean species relative basal area under control, Al amendments, and Ca amendments as predicted by SORTIE after 50, 125, and 200 years. The error bars are stochastic variation in model runs, indicating the outer bounds of the central 94% of simulations.



processes (i.e., toxicity) and interference with the uptake of other nutrients including Ca (Cronan and Grigal 1995), which then influences plant growth (Raynal et al. 1990; Kelly et al. 1990). Based on the extensive literature on Ca/Al ratios, we expected that seedlings would respond in terms of both growth and mortality to both the Ca and Al treatments. Furthermore, we expected decreased foliar nutrients under the Al treatment. However, our results after 2 years are not consistent with these predictions.

We found that Ca additions significantly increased growth in sugar maple but that maple survivorship was nearly identical in the Ca (66.3% through fall 1997) and control (65.4%) treatments. Furthermore, Al additions significantly decreased survivorship in both sugar maple and spruce but did not significantly change sugar maple and spruce RDGR. It should be noted, however, that Al additions appeared to introduce additional noise in the relationship between RDGR and light availability in sugar maple and beech (but not spruce), as indicated by light dropping out as a significant predictor of RDGR and lower R^2 values. Nevertheless, if Ca and Al acted as a single influence (i.e., Ca/Al ratio) on seedling performance, then the expectations are that Ca additions also would have decreased sugar maple mortality and that Al additions also would have decreased sugar maple and spruce growth. In addition, foliar concentrations of all measured elements were minimally affected under the Al fertilization but were broadly influenced by the Ca additions; these results are consistent with those of Berger et al. (2001) for sugar maple canopy trees on the same plots.

These results suggest that Ca and Al can act on different aspects of seedling performance, which may depend on soil solution Ca/Al ratio. Exchange sites in the soil complex at HBEF are dominated by Al^{n+} (Likens et al. 1998); moreover, our $AlCl_3$ additions decreased the Ca/Al ratio in O horizon soil solution, perhaps crossing an Al toxicity threshold for some sugar maple and spruce seedlings and resulting in increased mortality. However, most of the seedlings that escaped or recovered from Al toxicity were able to attain similar growth rates to the seedlings in the controls. Current Ca/Al ratios in the control plots likely are not at toxic levels (Cronan and Grigal 1995), which may explain why Ca additions did not affect seedling mortality.

While Al toxicity likely is influencing seedling mortality, Ca availability may be influencing seedling carbohydrate metabolism, as all species showed increases in relative diameter growth rate in the Ca treatment (although only increases in sugar maple were significant). Among sugar maple canopy trees experiencing crown dieback in northern Vermont, maximum rates of photosynthesis are highly correlated with both foliar N and Ca concentrations, which themselves are highly correlated. However, photosynthetic nitrogen use efficiency (PNUE; A_{max}/leaf N concentration) also increased with increases in foliar Ca, suggesting that Ca plays a role in carbon balance (Ellsworth and Liu 1994). Similarly, Reich et al. (1995) found a strong correlation between A_{max} and foliar Ca concentrations, but not with N or P, among Amazonian tree species with low N, P, and Ca concentrations. In addition to the effects of Ca on photosynthesis, increased Ca availability is associated with decreased rates of respiration (McLaughlin et al. 1991, 1993; Reich et al. 1994). Calcium availability may also positively affect carbon balance through increased nutrient uptake mediated through increased fine root production (Adams and Hutchinson 1992). The broad positive effects of Ca additions on foliar nutrient status that we found are consistent with Ca enhancement of nutrient uptake mediated through fine root growth. Another mechanism that could be operating simultaneously is that $CaCl_2$ additions may have increased base cation concentrations in soil solution through Ca displacing other cations from exchange sites in the soil complex. Significant increases in Mg concentrations under both fertilization treatments are consistent with this mechanism.

In summary, these results show that Ca and Al may act on different aspects of seedling whole-plant physiology and that seedling responses are not entirely mediated through carbon

Table 7. Summary of species-specific responses to $AlCl_3$ and $CaCl_2$ additions in terms of foliar nutrients, relative diameter growth (RDGR), mortality, and predicted community composition.

Amendment	Response
Nutrients in senesced leaves of deciduous species	
$AlCl_3$	Increased mean and median Al in yellow birch
	Increased median Cu in yellow birch and American beech
$CaCl_2$	Increased mean and median Ca in sugar maple, American beech, and yellow birch
	Increased mean and median P in sugar maple and American beech and median P in yellow birch
	Increased mean and median Mg and K and median Fe in sugar maple
Relative diameter growth (RDGR)	
$AlCl_3$	No significant effects on RDGR (but generally lower light-corrected growth)
	Disrupted RDGR–light relationship in sugar maple and American beech
$CaCl_2$	Significant increase in sugar maple RDGR
	Nonsignificant increases in RDGR of all other species
Mortality	
$AlCl_3$	Increased sugar maple and red spruce mortality
	Marginal increase in American beech mortality
$CaCl_2$	No effect
Predicted community composition	
$AlCl_3$	Little effect on composition within 200 years
	Decrease in red spruce and sugar maple basal area after 300 years
$CaCl_2$	Increased dominance of sugar maple within a tree generation (<125 years)

balance. For example, the relationships between mortality and recent growth, a surrogate for carbon balance (Kobe et al. 1995), follow significantly different lines for sugar maple in the Al versus Ca and control treatments. If carbon balance were to mediate effects of Al on mortality, then there would be a single relationship between mortality and recent growth with the treatments occupying distinct ranges of recent growth.

In this study, we have shown that under realistic field conditions, the amount of exchangeable Ca estimated to have been depleted from this northern hardwood forest significantly influenced the growth of sugar maple seedlings. Charge equivalent additions of Al significantly increased mortality of sugar maple and red spruce seedlings. The magnitude of sugar maple seedling growth responses to Ca are sufficient to cause substantial changes in canopy composition within a single tree generation (<125 years). Large changes in Ca/Al status in northeastern U.S. soils have occurred over at least the past 50 years. Given the long lifespans of trees, our results suggest further decreases in the dominance of sugar maple (and possibly red spruce) that are mediated through altered seedling dynamics, especially on soils with low base saturation.

Acknowledgements

Funding for this research was provided by an National Science Foundation Postdoctoral Fellowship to R.K.K. (DEB 9509428), support from the A.W. Mellon Foundation to G.E.L., Regional Research Support from the Michigan Agricultural Experiment Station (NRSP-3) to R.K.K., and the USDA Forest Service Northeastern Research Station. Vincent Levasseur, Ian Halm, and Amey Bailey provided crucial assistance in the field. We are grateful for the critical reviews of this manuscript by John Genet and Laura Schreeg. This research was conducted at Hubbard Brook Experimental Forest, which is owned and operated by the Northeastern Research Station, USDA Forest Service.

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