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ARTICLE

Differential impacts of calcium and aluminum treatments on sugar maple and American beech growth dynamics

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Abstract: Acid deposition induced losses of calcium (Ca) from northeastern forests have had negative effects on forest health for decades, including the mobilization of potentially phytotoxic aluminum (Al) from soils. To evaluate the impact of changes in Ca and Al availability on sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) growth and forest composition following a major ice storm in 1998, we measured xylem annual increment, foliar cation concentrations, American beech root sprouting, and tree mortality at the Hubbard Brook Experimental Forest (Thornton, New Hampshire) in control plots and in plots amended with Ca or Al (treated plots) beginning in 1995. Dominant sugar maple trees were unaffected by the treatment, but nondominant sugar maple tree growth responded positively to Ca treatment. Although plots were mainly composed of sugar maple, American beech experienced the greatest growth on Al-treated plots. Increases in tree mortality on Al-treated plots may have released surviving American beech and increased their growth. The Al tolerance of American beech and the Ca:Al sensitivity of sugar maple contributed to divergent growth patterns that influenced stand productivity and composition. Given that acidic inputs are expected to continue, the growth dynamics associated with Al treatment may have direct relevance to future conditions in native forests.

Key words: acid deposition, dendrochronology, ice storm, tree growth, Hubbard Brook.

Résumé : Les pertes de calcium (Ca) provoquées par les dépôts acides dans les forêts du nord-est ont eu des effets néfastes sur la santé des forêts pendant plusieurs décennies, incluant la mobilisation de l'aluminium (Al) dans le sol, un élément potentiellement phytotoxique. Pour évaluer l'impact des changements dans la disponibilité de Ca et Al sur la croissance de l'érable à sucre (*Acer saccharum* Marshall) et du hêtre d'Amérique (*Fagus grandifolia* Ehrh.) ainsi que sur la composition de la forêt à la suite d'un verglas important survenu en 1998, nous avons mesuré l'accroissement annuel du xylème, la concentration des cations dans les feuilles, la production de drageons par le hêtre d'Amérique et la mortalité des arbres à la forêt expérimentale de Hubbard Brook (Thornton, New Hampshire) dans des placettes témoins et traitées depuis 1995 par l'apport de Ca ou Al. Le traitement n'a pas eu d'effet sur les érables à sucre dominants mais la croissance des érables à sucre non dominants a réagi positivement à l'apport de Ca. Bien que les placettes aient été principalement composées d'érable à sucre, le hêtre d'Amérique a connu une meilleure croissance dans les placettes traitées avec Al. Une plus forte mortalité des arbres dans les placettes traitées avec Al pourrait avoir dégagé les hêtres d'Amérique qui avaient survécu et favoriser leur croissance. La tolérance du hêtre d'Amérique à Al et la sensibilité de l'érable à sucre à Ca:Al ont engendré des patrons de croissance divergents qui influencent la productivité et la composition du peuplement. Comme on s'attend à ce que les dépôts acides persistent, la dynamique de croissance associée au traitement avec Al représente probablement les conditions futures dans les forêts naturelles. [Traduit par la Rédaction]

Mots-clés : dépôts acides, dendrochronologie, verglas, croissance des arbres, Hubbard Brook.

Introduction

Acidification of forests in northeastern North America has been a widespread problem for tree health for decades. Causal factors include high acid loading from anthropogenic sources (Likens and Bormann 1974), the low buffering capacity of forest soils (Lawrence et al. 1997), and the subsequent leaching of base cations (Likens et al. 1996; DeHayes et al. 1999). Evidence now suggests that climate change may also contribute to acidification by increasing the frequency and (or) severity of soil-freezing events that damage roots, reduce nitrate uptake, and leach base cations from soils (Comerford et al. 2013). Depletion of base cations, most notably calcium (Ca), can disrupt fundamental components of tree function, including photosynthesis, carbohydrate metabolism, and cold tolerance (McLaughlin and Wimmer 1999; Halman

et al. 2008). Such physiological disruptions have contributed to declines in tree species (e.g., red spruce (*Picea rubens* Sarg.) and paper birch (*Betula papyrifera* Marsh.)) in the northeastern United States (US). Beyond changes in Ca-mediated physiology, continued acid deposition has the ability to mobilize soil aluminum (Al), which renders tree roots, and indirectly other tissues, vulnerable to damage by this phytotoxic element (Rengel and Zhang 2003; Šimonovičová et al. 2004). One measure that integrates physiological disruption due to a variety of stressors (e.g., drought, flooding, and nutrient perturbations) is the radial increment of xylem (Schweingruber 1996).

The positive relationship between Ca nutrition and growth is well understood for seedlings, saplings, and mature trees (Kobe et al. 2002; Schaberg et al. 2006; Huggett et al. 2007; Halman et al.

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2011). One reason for this is that Ca is a component of the xylem and is required for maintaining the structural integrity of plant cell walls by way of pectin binding in the middle lamella (Demarty et al. 1984). Ca also helps to regulate certain aspects of carbohydrate metabolism that influence tree growth (e.g., photosynthesis and respiration) (McLaughlin and Wimmer 1999; Snedden and Fromm 2001; Marschner 2012).

The availability of Ca and Al in northern forests has a strong influence on the health of sugar maple (*Acer saccharum* Marsh.). Sugar maple has exhibited reduced crown vigor, seedling survival, and radial growth coincident with reductions in Ca in the northeastern US and in southern Quebec, Canada (Duchesne et al. 2002; Juice et al. 2006; Schaberg et al. 2006; Huggett et al. 2007; Gravel et al. 2011). In the same region, elevated soil Al has been shown to increase the mortality of sugar maple seedlings (Kobe et al. 2002; Bigelow and Canham 2010). In southern New England, sugar maple seedling survival was greatest on sites with higher available Ca and was lowest on sites with higher available Al (Bigelow and Canham 2010). Although sugar maple appears to be sensitive to both low Ca and high Al concentrations, not all sympatric species in the region exhibit these same characteristics.

In recent years, shifts in species abundance have been noted in the northern forest, whereby American beech (*Fagus grandifolia* Ehrh.) has begun to outpace sugar maple regeneration (Duchesne et al. 2005; Duchesne and Ouimet 2009). This is particularly interesting considering the presence of beech bark disease (a disease complex caused by an insect pest (*Cryptococcus fagisuga* Lind.) and a fungal pathogen (*Nectria* spp.); Ehrlich 1934), which has been responsible for high levels of American beech mortality in this region for decades (Houston 1975). Studies conducted in southern Quebec suggest that there may be a link between soil nutrition and the aforementioned shift (Duchesne and Ouimet 2009), consistent with the fact that sugar maple appears to be Al sensitive, whereas other sympatric species, including American beech, may be more Al tolerant (Cronan et al. 1989). In the state of New York, sugar maple seedlings have been shown to be far more sensitive to nutrient availability (particularly Ca and Al) than American beech, resulting in growth reductions of sugar maple (Park and Yanai 2009). However, the impact of differing concentrations of Ca and Al on the growth of mature trees has seldom been evaluated.

Recent evidence has shown that at least for some tree species (e.g., paper birch and heart-leafed paper birch (*Betula papyrifera* var. *cordifolia* (Regel) Fern.)), adequate soil Ca and low available Al concentrations contribute to the ability of trees to recover from disturbance events (e.g., a major ice storm in 1998) and rebuild their crowns (Halman et al. 2011). Because such disturbances are often widespread regional phenomena, it stands to reason that other co-occurring Ca-sensitive species such as sugar maple may require similar stores of available Ca to recover from these environmental stresses.

To evaluate the dynamics of mature sugar maple and American beech to soil Ca and Al perturbation, a study was initiated at the Hubbard Brook Experimental Forest (HBEF; Thornton, New Hampshire) to observe long-term (here 13 years) trends in growth, including responses to a significant ice storm. Based on the findings of Huggett et al. (2007), we hypothesized that the 1998 ice storm likely reduced the growth of dominant trees that experienced substantial crown damage and improved the growth of minimally damaged codominant and intermediate trees (hereafter referred to as "nondominant" trees) that experienced a release as the overshadowing crowns were thinned. We also hypothesized that the impact of the 1998 ice storm would vary between species and among soil treatments, with sugar maple exhibiting greater sensitivity to soil Ca and Al perturbation. Because changes in xylem increment may result from impacts on the tree itself (e.g., changing nutrition) or nearby competition (treatment-induced changes in stocking, sprouting, and mortality of other trees in a stand), these factors were assessed to better understand the causes of any differences in radial growth.

Materials and methods

Study site

The HBEF has long been documented as a site exposed to acidic inputs and subsequent Ca depletion (Bormann and Likens 1979; Likens et al. 1998). To better evaluate the interaction of Ca depletion and Al mobilization on a northern hardwood forest, the Nutrient Perturbation (NuPert) study was initiated in 1995, west of the biogeochemical reference watershed (W6) at the HBEF (43.95411°N, 71.74779°W). The study area is on a south-facing slope, with an elevational range of 700–760 m, and most soils are classified as either Aquic Haplorthods or Aquic Haplumbredts (Berger et al. 2001). Twelve sugar maple dominated plots (45 m × 45 m) were randomly assigned to one of three treatments (Ca addition, Al addition, or control (no addition)), yielding four replicates of each treatment in the study. In addition to sugar maple, American beech and yellow birch (*Betula alleghaniensis* Britt.) are co-occurring tree species in these plots, whereas hobblebush (*Viburnum lantanoides* Michx.) and striped maple (*Acer pensylvanicum* L.) dominate the understory. Although present in the forest, beech bark disease was not severe in these plots and did not differ among treatments. Treatments began in 1995 with annual $CaCl_2$ (2.5 g·m^{-2}) and $AlCl_3$ (0.9 g·m^{-2}) applications occurring each fall or spring during leafless periods. The use of $CaCl_2$ was halted in 1999 in favor of a one-time application (38 g·m^{-2}) of wollastonite ($CaSiO_3$, a slow-release form of Ca). Thereafter, $AlCl_3$ additions occurred in alternate years in fall or spring.

Foliar nutrition

To confirm the influence of treatments, foliage was collected from sunlit branches in the upper third of the crowns from the three following groups of trees on each NuPert plot: dominant sugar maple, nondominant sugar maple, and codominant American beech. Five trees per plot of each group were selected for sampling in August 2008. Mean tree size did not differ among treatments for individual tree groups. Fresh samples were collected with shotguns, sealed in plastic bags for transport, and dried for two weeks at 65 °C upon return to the laboratory. Samples were ground to pass through a 2 mm sieve, digested by heating with nitric acid and hydrogen peroxide using a block digester (adapted from Jones and Case 1990), and analyzed for total foliar cations (Ca, Al, K, Mg, and Mn) by inductively coupled plasma atomic emission spectroscopy (ICP-AES; Optima DV 3000, Perkin-Elmer Corp., Norwalk, Connecticut). Peach leaves from the National Bureau of Standards and Technology (SRM 1547), sample duplicates, and blanks were analyzed for procedural verification. Tissue standards were within 5% of certified values.

Increment core collection and growth analysis

In early November 2008, increment cores were collected from the sample trees (see above), and the diameter at breast height (DBH; 1.3 m) was recorded. Two increment cores per tree were removed at 180° from one another at breast height and perpendicular to the slope. Cores were mounted, dried, and sanded, and annual growth rings were measured to the nearest 0.01 mm. Cores were then visually crossdated and aged using standard dendrochronological methods (Stokes and Smiley 1968). The computer program COFECHA was used to crossdate and identify areas of cores that may contain false or locally absent rings. Locally absent rings were also identified by subsequent visual inspection of the cores. Basal area increment (BAI) was calculated to evaluate growth on an area basis and subsequently divided by the 5-year pretreatment growth mean for each tree to generate a BAI ratio of posttreatment to pretreatment growth and allow for comparisons among tree groups.

Table 1. Mean foliar calcium (Ca) and aluminum (Al) concentrations and molar ratios of Ca to Al (Ca:Al) for dominant sugar maples, nondominant sugar maples, and codominant American beech (±SE) from NuPert plots at Hubbard Brook Experimental Forest (n = 60 trees per tree group).

Tree group	Treatment	Foliar cation concentration		
		Ca (mg·kg⁻¹)	Al (mg·kg⁻¹)	Ca:Al (mol·L⁻¹)
American beech	Al addition	4821±378	29±3	119±17
	Control	5973±340	22±1	172±14
	Ca addition	5897±342	24±2	176±18
Sugar maple (dominant)	Al addition	5155±382b	15±1	243±22b
	Control	5593±404ab	15±1	264±21b
	Ca addition	7778±419a	12±1	438±32a
Sugar maple (nondominant)	Al addition	3877±350b	47±3	61±8b
	Control	4246±303ab	46±3	66±6b
	Ca addition	6357±323a	42±2	108±9a

Note: Means within tree groups and columns with different letters are significantly different based on Tukey–Kramer HSD ($P < 0.05$).

Assessment of vegetative reproduction and survival

To assess other contributions to growth, we also assessed the number and size of root sprouts, the basal area density of living trees (stocking), and recent mortality (e.g., new gap formation) in all plots. We quantified the number and basal area of root sprouts likely associated with individual mature American beech that were sampled (e.g., within a 3 m radius of each sampled tree, based on findings of Jones and Raynal 1986). We also conducted a full inventory of root sprouts with a DBH of less than 5 cm in the fall of 2010 to calculate the total basal area of sprouts per plot. Variable radius plots were established from the plot center to quantify stocking using a factor 10 prism. All trees included in prism plots were identified by species, and DBH was measured. Recent mortality was evaluated by taking inventory of all dead standing or down trees that qualified as deceased within the last 15 years based on the standard decay class scale (1 = fine branches present, 2 = fine branches absent and medium branches present, 3 = fine and medium branches absent; bark was present for each decay class) for northern hardwood forests (Fast et al. 2008). Species were identified by bark characteristics, and the basal area of deceased trees was calculated by species for each plot. Tree position (i.e., standing or down) was also noted.

Statistical analysis

For parameters that did not involve multiyear measurements (i.e., foliar nutrition, the number and basal area of American beech sprouts, species-specific and overall basal area, and species-specific and total basal area of dead stems), treatment differences among means were tested using a nested analyses of variance (ANOVA). To test for overall differences in nutrition between tree groups, a crossed ANOVA model was used with treatment, tree group, and the treatment × tree group interaction as the sources of variation. Significant differences among treatment means were tested using Tukey–Kramer HSD multiple comparison tests. Differences in growth trends among the three species and canopy-class groups (i.e., dominant sugar maple, nondominant sugar maple, and codominant American beech) and soil cation manipulations over time were tested using a repeated measures analysis. The MIXED procedure in the SAS system for Windows (version 9.4) was used to perform these analyses, assuming an autoregressive covariance structure for the repeated measures. Whenever interactions with year were significant, tests of simple effects within the interaction were performed to assess differences among groups or treatments for each year. Growth data did not satisfy the assumption of equal variances; therefore, the data were square-root transformed prior to statistical analyses. Means were considered statistically different if $P < 0.05$, unless otherwise noted.

Results and discussion

Foliar nutrition differences among treatments and tree groups

Both dominant and nondominant sugar maple foliage from Ca-treated plots contained significantly higher concentrations of Ca than sugar maple foliage from Al-treated plots, whereas trees grown in the control plots were intermediate (Table 1). Additions of Ca to plots resulted in a nearly 40% increase in dominant sugar maple foliar Ca compared with control plots and a nearly 50% increase for nondominant sugar maples over control plots. Additions of Al to plots resulted in lower foliar Ca concentrations than in Ca-treated plots, but these were not significantly different (and only 8% lower) than control plots.

No significant differences were found for Al (Table 1) or other cations (data not shown) in dominant and nondominant sugar maple foliage. Ca addition did result in the lowest mean Al concentrations for dominant and nondominant sugar maples (Table 1). For both canopy classes of sugar maples, molar ratios of Ca to Al (hereafter Ca:Al) were significantly higher in the foliage of trees from Ca-treated plots than in either Al-treated or control trees (Table 1). Mean ratios for all tree groups and treatments were well above previously established foliar toxicity thresholds (e.g., 9.9 for sugar maple and 26.1 for American beech; Cronan and Grigal 1995), suggesting that these trees are not at imminent risk of impairment due to an imbalance of these cations.

American beech foliage showed no significant difference in cation concentrations among treatments. Although a trend was apparent for lower Ca and higher Al in trees from Al-treated plots, means were not significantly different. Ca:Al in American beech leaves were not significantly different among treatments.

Differences in Ca among tree groups were not significant; however, significant interaction effects were found between treatment and tree group for both foliar Ca concentrations and Ca:Al ($P = 0.019$ and $P < 0.001$, respectively). Perhaps most interesting were the large significant differences in foliar Al concentrations found among tree groups, a consistent pattern seen across both treatment and control plots (Table 1). Dominant sugar maples contained the lowest concentrations of foliar Al (14 ± 0.5; mean ± SE) among the tree groups sampled, whereas nondominant sugar maples contained the highest concentrations of foliar Al (45 ± 2) and American beech had intermediate levels of Al (27 ± 2) ($P < 0.001$). Few comparisons between foliar-Al levels in mature sugar maple and American beech have been reported. In untreated plots at the Bear Brook Watershed in Maine, no differences in foliar Al were found between sugar maple and American beech in multiple sampling years (Elvir et al. 2006, 2010). Park and Yanai (2009) evaluated

foliar nutrition (including Al) of mature sugar maple and American beech in New York and found no significant species differences. They also assessed differences in foliar nutrition between sugar maple seedlings and mature trees and similarly found no differences. At HBEF, Juice et al. (2006) assessed the foliar nutrition of new sugar maple germinants and 1-year-old seedlings from a Ca-treated watershed and control sites. Although a trend was apparent, with higher Al concentrations in new germinants than in 1-year-old seedlings on control sites, statistical testing of the differences was not conducted (Juice et al. 2006). To our knowledge, these data are the first to suggest that differences in sugar maple foliar Al may be influenced by tree size or canopy position and that inherent differences in sugar maple and American beech foliage from the same canopy class may exist. More specific analysis is needed to determine the possible reasons for low foliar Al in dominant sugar maples (e.g., perhaps through greater Al scavenging by xylem cation exchange sites distal to the leaves in these large trees) or for lower foliar Al in American beech versus nondominant sugar maples (e.g., possibly due to better root exclusion or sequestration of Al in American beech).
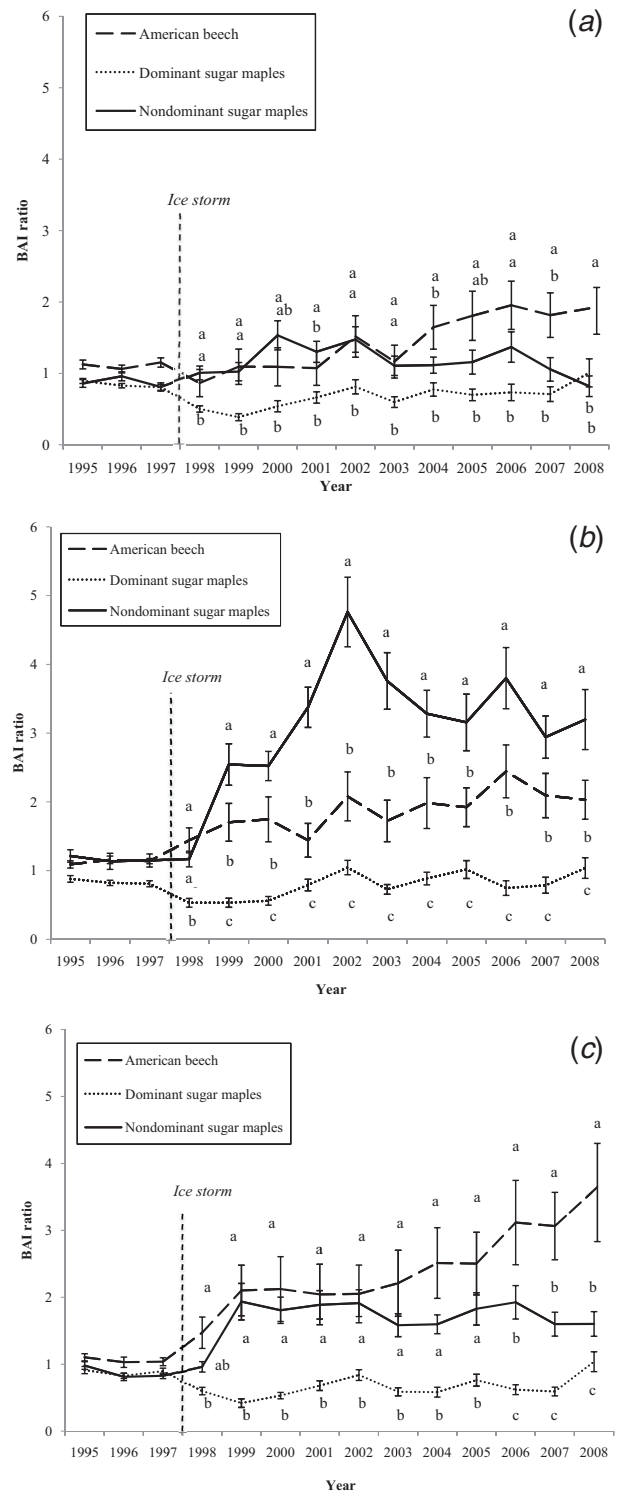
Trends in radial growth of tree groups

For all growth comparisons among tree groups, a significant interaction effect was found between year and tree group (Fig. 1). Control plots exhibited a moderate and significant reduction in growth for dominant sugar maples relative to nondominant sugar maples and American beech following the 1998 ice storm (Fig. 1a). This growth reduction in dominant sugar maples compared with nondominant sugar maples and American beech was maintained throughout most of the 11 growing seasons following the ice storm, with 7 of the 11 years showing a significant difference in growth (Fig. 1a). However, in 3 of the last 5 years of recorded growth, American beech outpaced both sugar maple tree groups (Fig. 1a). The improved performance of American beech over sugar maple elsewhere has been attributed to the greater Al tolerance of American beech (Duchesne and Ouimet 2009). The timing of this on control plots may suggest a recent change in Al status and (or) tree response under ambient conditions.

The 1998 ice storm damaged large portions of forests from New York through Maine when high ice loading weighed down and snapped off branches from trees (Miller-Weeks and Eagar 1999). At NuPert, a poststorm damage survey of 340 trees showed that there was substantial injury to trees, but that this damage was significantly greater ($P < 0.001$) for larger trees (>22 cm DBH) than smaller trees (10–21.9 cm DBH) (Huggett et al. 2007). Importantly, this assessment verified that there were no differences in ice-storm damage associated with NuPert soil treatments (Huggett et al. 2007). Following the ice storm, growth differences were greater on treated plots than the control plots (Figs. 1b and 1c). Ca-treated plots exhibited large differences in growth between tree groups for 11 growing seasons after 1998 (Fig. 1b). Similar to control plots, dominant sugar maple growth was reduced following the ice storm, and they sustained lower growth than both nondominant sugar maples and American beech (which were indistinguishable from one another) for that time period (Fig. 1b). After 1998, nondominant sugar maples and American beech on Ca-treated plots increased their growth rates relative to years prior to the ice storm, whereas dominant sugar maples maintained growth rates similar to those in previous years (Fig. 1b). Consistent with the species' known sensitivity to Ca, the response of nondominant sugar maples to the combined release following the ice storm and Ca addition was greater than the response of American beech.

In Al-treated plots, dominant sugar maples did not exceed growth rates preceding the 1998 ice storm for 11 years following the ice storm (Fig. 1c). Dominant sugar maple growth was significantly lower than both nondominant sugar maples and American beech for 10 seasons following 1998 (Fig. 1c). The difference in

Fig. 1. Radial growth trends for dominant and nondominant sugar maples and codominant American beech in (*a*) control plots, (*b*) Ca-treated plots, and (*c*) Al-treated plots. Annual growth data were converted to basal area increment (BAI) and divided by the 5-year pretreatment BAI mean for each tree (BAI ratio). Data were square root transformed for statistical testing to satisfy assumptions of the ANOVA. Means (±SE) are displayed, and those with different lowercase letters in a given year are significantly different based on tests of simple effects following repeated measures ANOVA ($P < 0.05$). The absence of lowercase letters for a given year indicates no significant differences among means.

growth trends between these tree groups became even more apparent over time, with the greatest differences occurring during the last 3 years of measured growth, where American beech growth on Al-treated plots was nearly threefold greater than both dominant and nondominant sugar maples (Fig. 1c). This surprising growth increase with Al addition lends further credence to the concept of American beech as an Al-tolerant hardwood species (Cronan et al. 1989).

Treatment impacts on growth of tree groups

The effects of the year × treatment interaction and of treatment itself were not found to be significant for dominant sugar maple growth based on repeated measures analysis. However, year did significantly impact growth among dominant sugar maples ($P < 0.001$). Comparisons of growth among treatments for each tree group suggest that the dominant sugar maple trees in the NuPert plots were negatively impacted by the 1998 ice storm and responded with growth reductions for at least 2 years following the event (Fig. 2a). After this growth reduction, all dominant sugar maples, regardless of treatment, recovered to growth rates preceding the ice storm and began to increase their annual radial growth (Fig. 2a).

Nondominant sugar maples in the Ca-treated plots exhibited a rapid increase in growth following the 1998 ice storm compared with trees on control and Al-treated plots, and this trend continued until the end of recorded growth (Fig. 2b). Past work at NuPert indicated that the growth release following the ice storm was particularly strong for nondominant sugar maples on Ca-treated plots, although at the time, growth increases were measured only until 2004 (Huggett et al. 2007). Here we detected a protracted (e.g., 10-year) benefit of Ca addition to nondominant sugar maple (Fig. 2b). Although growth on control and Al-treated plots was generally similar, in 3 of the 11 years, growth rates of nondominant sugar maples after the ice storm were greater on Al-treated plots than on control plots. We suspect that the cause of this unexpected finding is similar to that for the increased growth of American beech with Al addition (see below).

American beech trees in all treatments increased in growth following the 1998 ice storm (Fig. 2c). However, American beech growth on Al-treated plots increased more rapidly than American beech growing on Ca-treated plots, whereas control plots were intermediate based on differences in linear slope of growth trends from 1998 to 2008 ($P = 0.040$). American beech growth was first affected by treatment from 1999 to 2001 following the ice storm and again in 2003, presumably due to the impaired response of competing species on Al-treated plots. Following this period, the last 2 years of the growth record indicated that American beech growing on Al-treated plots grew significantly more than American beech in other treatments (Fig. 2c). The general trend of American beech growth outpacing that of sugar maple under ambient conditions (Fig. 1a) and especially in Al-treated plots (Fig. 1c), suggested that elevated Al levels may impact interspecific competition in these plots.

Possible contributors to enhanced American beech growth

The increase in American beech growth compared with both dominant and nondominant sugar maple on control plots that have received years of acid inputs (Fig. 1a) and Al-treated plots (Fig. 1c), as well as increases in growth of American beech from Al-treated plots over trees from Ca-treated or control plots (Fig. 2c), suggests that there may be indirect effects of Al addition on the growth of these trees. One possible explanation for greater American beech growth with Al addition could be the preferential release of dormant buds on American beech roots caused by the oxidative stress (oxidative processes are a key trigger for the release of dormant buds; Arora et al. 2003) introduced by Al treatment (Naik et al. 2009). An Al-induced increase in root sprouting could create an understory of vegetative American beech sprouts

Fig. 2. Treatment impacts on radial growth trends of (*a*) dominant sugar maple, (*b*) nondominant sugar maple, and (*c*) codominant American beech. Annual growth data were converted to basal area increment (BAI) and divided by the 5-year pretreatment BAI mean for each tree (BAI ratio). Data were square root transformed for statistical testing to satisfy assumptions of the ANOVA. Means (±SE) are displayed, and those with different lowercase letters in a given year are significantly different based on tests of simple effects following repeated measures ANOVA ($P < 0.05$). The absence of lowercase letters for a given year indicates no significant differences among means.
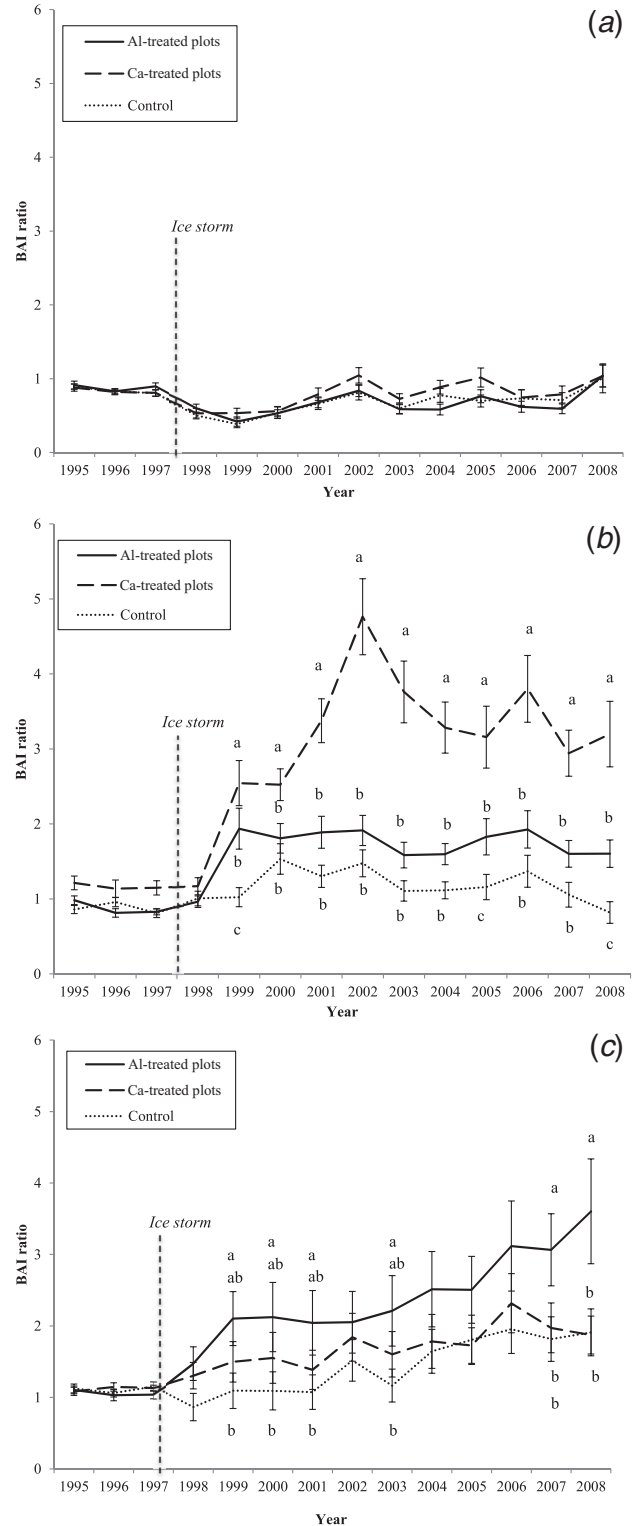
Table 2. American beech sprout survey for all plots (each 45 m × 45 m) in the NuPert study.

	Full survey of beech sprouts		Localized survey of beech sprouts	
Treatment	No. of sprouts	Sprout basal area (m²·ha⁻¹)	No. of sprouts	Sprout basal area (m²·ha⁻¹)
Al addition	975	1.2	365	0.3
Control	1232	1.2	310	0.3
Ca addition	1030	1.1	240	0.2

Note: Full survey data contains all American beech sprouts less than 10 cm in diameter, whereas localized data include only sprouts within a 3 m radius from sampled mature trees. No significant differences were found among treatments.

Table 3. Mean (±SE) basal area of dead stems present in all treatment plots.

	Mean plot basal area (m²·ha⁻¹)			
Treatment	ACSA	FAGR	BEAL	Total
Al addition	2.4±1.1	1.4±0.6	3.5±0.8b	8.1±0.8b
Control	1.6±0.6	1.3±0.8	3.0±0.5ab	6.6±0.4ab
Ca addition	1.2±0.4	0.7±0.2	1.5±0.4a	4.5±1.1a

Note: Only stems estimated to have died during the treatment period (15 years) were included in the analysis. Means with different letters are significantly different based on Tukey–Kramer HSD ($P < 0.05$). Species abbreviations: ACSA, *Acer saccharum*; FAGR, *Fagus grandifolia*; BEAL, *Betula alleghaniensis*.

that are attached to mature trees and could contribute carbohydrate stores to larger American beech, thus fueling greater growth for these trees. American beech sprouting is often the result of root stress, whether by mechanical means, pathogenic stress, or other disruptions to root health (Beaudet and Messier 2008). Therefore, this would be more likely to happen on Al-treated plots, where elevated Al concentrations behave as both a toxin and an oxidative stressor (Yamamoto et al. 2003; Marschner 2012) on roots.

Although an interesting possibility, our assessment of root sprouting prevalence on the NuPert plots found little evidence of an Al-induced increase in sprouting. Plot surveys of root sprouts revealed no significant differences in either the number or the basal area of sprouts (Table 2). This was also true for our localized survey, where only sprouts present in a 3 m radius from cored trees were included. Mean root-sprout counts for this latter survey were lowest in Ca-treated plots and highest in Al-treated plots, although these means were not statistically different. The pervasiveness of beech bark disease, which is known to incite root sprouting (Jones and Raynal 1986), may have resulted in similar cohorts of root sprouts, regardless of soil treatment. Beech bark disease was present in northern hardwood forests long before the NuPert plots were established, thus the legacy of the disease may be more important in determining sprout cohort size and extent than the influences of our comparatively short-term study. Furthermore, beech bark disease did not differ among treatments, based on a 2006 survey of all plots (J.M. Halman, unpublished data).

To assess whether the density of living trees had any effect on American beech growth (e.g., fewer trees on Al-treated plots resulting in greater ability for light capture and carbon gains for American beech there), we measured the live basal area of trees at the plot center using a factor 10 prism. We found no significant differences in total plot basal area among trees on Ca-treated (22.4 ± 3.6 m²·ha⁻¹), control (23.0 ± 2.5 m²·ha⁻¹), or Al-treated (29.8 ± 3.4 m²·ha⁻¹) plots. Similarly, no differences in plot basal area of individual tree species among treatments were detected (data not shown). Quantifying light availability, although an attractive option, would not have provided any insight into light

regimes for years other than the current sampling year (i.e., would not have assisted evaluations of growth differences in past years).

In contrast to assessments of root sprouting and stand density, our survey of total tree mortality since treatments began revealed that significantly higher mortality levels were present on Al-treated plots than Ca-treated plots, with control plots having intermediate mortality levels (Table 3). This pattern of response could be caused by either Al-induced increases in tree mortality, Ca-related reductions in mortality, or some combination of the two. The lack of a difference between Ca- or Al-treated plots and control plots makes it difficult to distinguish which of these possibilities is more likely.

For individual species, there was a trend for greater mortality of sugar maple and American beech on Al- versus Ca-treated plots, but these differences were not statistically significant ($P = 0.54$ and 0.62, respectively; Table 3). In contrast to these species but similar to total mortality measurements, there was significantly higher mortality levels of yellow birch on Al-treated plots than on Ca-treated plots, with levels of yellow birch mortality on control plots being intermediate (Table 3). Treatment differences in total mortality appear to integrate trends among sugar maple and American beech, with more definitive patterns for yellow birch. In particular, the greater mortality of yellow birch on Al-treated plots may help to explain the recent surge in American beech growth on these plots — elevated mortality of an apparently Al-sensitive species may have increased light and other resources for an Al-tolerant species. Although Al-sensitive sugar maples were presumably exposed to the same influx of light, they were likely at a disadvantage and were less able to capitalize on the increase in light levels associated with mortality. A notable exception to this was the sporadic and small, but significant, increase in growth for nondominant sugar maples on Al-treated plots (Fig. 2*b*). Although this growth increase was minor relative to the growth increase following the ice storm and Ca addition (Fig. 1*b*), it suggests that these nondominant trees responded to release even in the presence of enhanced Al availability. Differences in growth between American beech on Al-treated and control plots could not be accounted for by treatment-induced differences in mortality because no significant differences were detected (Table 3). It is possible that growth measurements are more precise and dateable (assuring that they occurred during the treatment period) than more crude measures of mortality (e.g., the dates of which had to be estimated based on bark characteristics; Fast et al. 2008).

The significantly greater mortality of yellow birch on Al-treated plots may have broader implications as well. A recent survey of the entire Hubbard Brook valley between 1995 and 2006 found that of all species inventoried, yellow birch was undergoing the greatest loss of biomass compared with other tree species due to its high rate of mortality in the forest (van Doorn et al. 2011). The authors suggest that this trend may be due to the age of yellow birch throughout the valley, with approximately 57% of yellow birch sampled being 80 years old or older. However, yellow birch have been shown to live well over 200 years (Burns and Honkala 1990). In contrast to the proposition that yellow birch mortality at Hubbard Brook was solely age dependent, our data provide evidence that elevated Al availability may exacerbate the decline of yellow birch (Table 3).

Acidic inputs and acidification due to soil freezing are expected to continue in the region (Howarth et al. 2002; Comerford et al. 2013) and, as such, have the potential to increase the mobilization of Al in already poorly buffered forest soils. The increase in yellow birch mortality and growth patterns that favor American beech health over sugar maple coincident with Al treatment at NuPert suggests that continued acidification may induce shifts in species composition. Indeed, some shifts are already being seen in Quebec, where American beech is expanding its dominance in forests once composed primarily of sugar maple (Duchesne et al. 2005). Reasons for this shift include the decline of sugar maple in the

region, as well as sugar maple sensitivity to cation depletion and changes in the acid–base soil status (Duchesne and Ouimet 2009). Yellow birch decline has been observed in Canada, and some studies suggest that reduced snowpack, soil freezing, and associated freeze-induced root mortality have contributed to this phenomenon (Zhu et al. 2002). In fact, recent studies with sugar maple have shown that freeze-induced root injury can reduce root nitrate uptake, leading to soil acidification and Ca:Al imbalances (Fitzhugh et al. 2003) that reduce growth (Comerford et al. 2013). Though not yet tested, the decline of yellow birch induced by soil freezing could also include both direct root injury and subsequent alterations to soil cation availability that influence tree health and productivity. Declines in other species (notably red spruce and paper birch) in the region have already been associated with soil acidification and disruptions in Ca and Al nutrition (DeHayes et al. 1999; Halman et al. 2008, 2011). The alterations in American beech and yellow birch health that we describe here likely contribute to the existing changes in growth and mortality already noted for other species and indicate that regional forests are balanced near the limits of hospitable soil cation conditions.

Conclusions

Our data show that dominant sugar maple from all plots were damaged by the 1998 ice storm, which likely resulted in changes to radial growth of the less dominant sugar maple and American beech. Calcium treatment resulted in a greater growth response of nondominant sugar maples following overstory crown damage, whereas American beech growth response following the 1998 ice storm was not affected by Ca treatment. This finding provides further evidence that Ca availability directly influences the stress response of sugar maple, whereas American beech appears to be less Ca sensitive. The growth of American beech was ultimately affected by Al treatment beginning in 2007, when Al addition was associated with increased radial growth following elevated tree mortality that decreased competition for Al-tolerant American beech. On Al-treated plots, tree mortality was highest for yellow birch, and although sugar maple and American beech showed similar trends, they were not statistically significant. As anthropogenic acidification continues either through continued pollutant inputs (Greaver et al. 2012) or as a secondary effect of climate change (Groffman et al. 2012; Comerford et al. 2013), it will be important to monitor untreated forest areas for signs of decline, as detected at NuPert (Huggett et al. 2007; Halman et al. 2013; and this study), that are associated with reduced Ca availability and (or) increased Al availability.

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