Potential role of soil calcium in recovery of paper birch following ice storm injury in Vermont, USA

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ABSTRACT

In recent years, an increased number of mature paper birch (*Betula papyrifera* Marsh.) and heart-leafed paper birch (*B. papyrifera var. cordifolia* (Regel) Fern.) in northeastern United States forests have exhibited decline symptoms including foliar loss, reduced fine branching, and tree mortality. We assessed crown health, radial growth, and available soil cations in 2006 as a preliminary assessment of factors that may be influencing paper birch decline. Tree rings began to decrease in width in 1998—the year of a severe region-wide ice storm. All trees (regardless of their current decline status) experienced reduced growth starting in 1998 and tree growth continued to decrease for two years following the ice storm. After this generalized growth decrease, trees that now have vigorous crowns showed a marked increase in growth, whereas trees that now have low crown vigor did not rebound in growth, but instead exhibited a significantly higher incidence of locally absent annual rings. Extractable soil-aluminum (Al), a phytotoxic element mobilized by acid deposition, was significantly higher in soils associated with declining trees compared to those adjacent to vigorous trees. Higher soil calcium (Ca) availability was associated with both vigorous crowns and increased radial growth following the 1998 ice storm. Furthermore, increased soil Ca availability was negatively correlated to the percentage of declining trees, and positively related to increased radial growth, whereas elevation was not significantly associated with either parameter. Although previously overlooked as a factor influencing paper birch recovery from injury, we found that available soil Ca was linked to crown vigor and rebounds in growth following an inciting event.

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1. Introduction

Populations of paper birch (*Betula papyrifera* Marsh.) and yellow birch (*Betula allagheniensis* Britt.) trees in the eastern United States (US) and Canada have experienced periodic incidences of dieback (i.e., the death of fine branches beginning at terminal portions of branches and proceeding towards the trunk; USDA Forest Service, 2004) during the last century (Ward and Stephens, 1997; Bourque et al., 2005). Much research has been devoted to elucidating the causative factors associated with fine branch death in yellow birch, paper birch, and heart-leafed paper birch (*B. papyrifera var. cordifolia* (Regel) Fern.), and multiple causes have been suggested, including the severity of freeze–thaw events, fungal or insect infestations, high temperature and drought, dry summers and cold winters, and xylem embolism (Sperry, 1993; Cox and Malcolm, 1997; Zhu et al., 2000, 2002; Bourque et al., 2005). While these studies have examined some potential initiators of birch dieback and subsequent decline (i.e., reductions in growth and increases in

tree mortality), little research has evaluated potential connections between dieback and other climate-associated disturbances that may influence decline. Notably, a large increase in dieback and mortality of paper birch trees was noted in New York and New England (Decker et al., 2005; Maine Forest Service, 2007; McDonnell, 2007; NH-DRED, 2007), which occurred following a severe ice storm in 1998.

From 5 to 10 January 1998, a severe region-wide ice storm affected Ontario and Quebec, Canada, and New York, Vermont, New Hampshire and Maine, US. Ice loading on tree branches was as much as 10 cm in some areas, and persisted until 10 January 1998 when a thaw began to melt the accumulated ice (Miller-Weeks and Eager, 1999). The ice storm of 1998 damaged large portions of the forest from New York to Maine by bending saplings and breaking branches from mature trees. Damage was generally greater in hardwoods than softwoods (Miller-Weeks and Eager, 1999). However, the causes of inadequate wound response and other possible connections between ice storm damage and birch decline remain unresolved.

Tree species decline in the region is not a new phenomenon as evidenced by sugar maple (*Acer saccharum* Marsh.) and red spruce (*Picea rubens* Sarg.) declines in the last half-century, both

Table 1
Location and composition of sites used to evaluate birch decline in Vermont. Latitude and longitude are based on NAD83 datum and measured at plot center. Vigor ratings of 1 or 2 qualified a tree for "vigorous" status, and a rating of 3 or 4 resulted in "declining" status.

Plot location	Latitude (° north)	Longitude (° west)	Mean elevation (m)	Trees (n)	Vigor rating (# of trees)				Vigorous (%)	Declining (%)
					1	2	3	4		
Granville	44.00225	−72.88116	537	19	7	8	2	2	78.9	21.1
MHW – Low	44.39705	−72.65977	666	10	1	9	0	0	100.0	0.0
MHM – Low	44.38836	−72.64488	689	10	1	7	2	0	80.0	20.0
CH – Low	44.30930	−72.86731	703	10	7	3	0	0	100.0	0.0
Appalachian Gap	44.21164	−72.93179	715	18	1	6	8	3	38.9	61.1
CH – Mid	44.31083	−72.87067	745	20	6	5	5	4	55.0	45.0
MHW – Mid	44.39603	−72.65552	785	20	0	6	7	7	30.0	70.0
Roxbury	44.07214	−72.80988	797	20	4	8	3	5	60.0	40.0
MHM – Mid	44.39152	−72.64003	800	19	0	11	5	3	57.9	42.1
CH – High	44.31450	−72.87745	856	10	0	5	5	0	50.0	50.0
MHW – High	44.39618	−72.65204	888	9	0	1	5	3	11.1	88.9
MHM – High	44.39326	−72.64180	899	7	0	1	5	1	14.3	85.7

Abbreviations: CH = Camel's Hump, MHM = Mount Hunger (Middlesex), and MHW = Mount Hunger (Waterbury). Mount Hunger sites were located on opposing sides of the same mountain.

of which have been linked to acid deposition and subsequent calcium (Ca) depletion (Shortle and Smith, 1988; DeHayes et al., 1999; Schaberg et al., 2006). Because Ca is a biologically essential element, anthropogenic alterations in the availability of this cation may have serious implications to forest health and productivity. In particular, Ca is an important structural component of woody cell walls (Marschner, 2002), and its availability modulates aspects of carbohydrate metabolism including photosynthesis and respiration (McLaughlin and Wimmer, 1999; Dilley, 2004) and the formation and breakdown of various carbohydrates (Snedden and Fromm, 2001). Considering these functions, one likely consequence of tree Ca deficiencies is a reduction in structural carbon gains (woody growth/biomass)—a defining characteristic of species declines (DeHayes et al., 1999; Huggett et al., 2007). Ca depletion may also predispose trees to decline by impairing physiological response systems that help trees sense and adapt to environmental stresses (e.g., low temperatures, drought, oxidative stress and wounding; Huggett et al., 2007; Halman et al., 2008). In light of the connections between reduced Ca availability and a predisposition to decline, and because birch decline is occurring in the same vicinity (regionally and elevationally) where Ca depletion predisposes red spruce and sugar maple trees to decline, it is possible that Ca depletion also contributes to birch decline. Nevertheless, in these regions not all trees are declining, and in fact some appear to have rebuilt their crowns following ice storm damage. Determining the nutritional status of areas where ice loading occurred and decline exists may provide some insight into the possible involvement of Ca availability in paper birch recovery (e.g., increased growth and crown vigor following a period of decline) following ice storm damage. We posit that the 1998 ice storm initiated the decline of paper birch in Vermont, but that birch trees growing in areas with greater soil Ca availability were more likely to rebound in crown vigor and radial growth following ice damage.

To assess if recent extreme weather events contributed to current birch decline, and if differences in soil cation availability were associated with differences in paper birch recovery in the northeastern United States, we analyzed xylem increment cores and soil samples from forested plots throughout the Green Mountains in Vermont where varying degrees of paper birch decline exist. We employed visual assessments of crown vigor and dendrochronological techniques cross-referenced with existing climate and weather data to identify potential factors that contributed to the current decline of paper birch in the region, and assessed soil cation nutrition to investigate the relationship between Ca availability and potential recovery.

2. Materials and methods

2.1. Study site

Twelve sites containing 7–20 dominant or co-dominant mature paper birch each were selected in the north-central region of the Green Mountains in Vermont. All sites overlapped with previous aerial mapping of birch decline in Vermont, and we avoided areas known to have been affected by insect outbreaks in 2004 and 2005 (Dupigny-Giroux et al., 2003; Decker et al., 2005). Descriptive data were collected, including elevation and latitude/longitude of each site (Table 1). Nine of the sites were located at three different elevations on each of three different mountain-slopes in order to assess tree health and soil nutrition across an elevational gradient that could influence factors predisposing trees to decline (e.g., soil nutrition) and environmental factors that could trigger decline (e.g., temperature extremes, ice storm loading, etc.). In particular, soil Ca often decreases as elevation increases due to the presence of thinner soils and greater inputs of acid deposition, which leaches Ca from soils (Schaberg et al., 2010). To help evaluate spatial variability with elevation, three plots per site were established using GPS points within areas known to have experienced moderate ice storm damage in 1998 (VT-DFPR, 1999). Choosing plots with similar levels of ice impact in 1998 helped reduce variability associated with differential damage. The three-to-four birch closest to each GPS plot center were sampled for tree and soil assessments. All sites contained dominant and co-dominant paper birch with sugar maple and/or red spruce as companion species. At higher elevations, sample trees included the heart-leafed variety of paper birch. Understory vegetation was highly variable depending on both aspect and elevation, though hobblebush (*Viburnum alnifolium* Marsh.) and striped maple (*Acer pensylvanicum* L.) were present on most plots. Soils were usually Spodosols with generally well defined O_a, E, and B horizons, except at some upper elevations where soils were either Histosols or Entisols (i.e., no B horizon present).

2.2. Crown vigor assessments

For all paper birch trees sampled, crown vigor was visually assessed using previously established methods that employ a 1–5 scale to rate the health of individual tree crowns as having either (1) highly vigorous crowns without major branch dieback and less than 10% branch or twig mortality, (2) light decline with branch and twig mortality present and between 10 and 25%, (3) moderate decline with branch and twig mortality between 25 and 50%, (4) severe decline with extensive branch mortality and greater than

50% branch and twig dieback, or (5) dead (Cooke et al., 1996). Vigor ratings were made using binoculars by groups of two researchers per tree to avoid observer bias. Trees were initially assessed in late fall of 2006, and ratings were repeated on the same trees in summer 2007 after leaf-out. Those trees given a vigor rating of 1 or 2 were deemed "vigorous" within our analysis, and those with a rating of 3 or 4 were considered "declining." Trees with minimal transparency in their crowns often contained branch mortality low in the crown—presumably due to self-shading and natural crown thinning. These trees received a rating of two. However, because these trees showed no other visible injury, we feel confident in categorizing them as being vigorous.

2.3. Dendrochronology

For the 172 trees assessed, two increment cores per tree were taken at 180° from one another at 1.3 m above ground level, perpendicular to the slope. Cores were mounted, dried, and sanded. All cores were measured to the nearest 0.01 mm, visually crossdated and aged per 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 (Holmes, 1983). Locally absent rings were identified by subsequent visual inspection of the cores. Basal area increment (BAI) was calculated to evaluate growth on an area basis and was expressed as percent of total basal area per tree.

Regional weather and climate information was obtained from the Vermont State Climatologist website (Dupigny-Giroux, 2009), and included data from the National Climate Data Center (NCDC) and the National Oceanic and Atmospheric Administration (NOAA). Being regional data, these highlighted major climatic trends in our study area (i.e., Green Mountains, VT) rather than site-specific information. All data were screened for anomalies or events that aligned with recent years of xylem growth suppression in the paper birch we assessed. Because injured paper birch crowns were first reported in 1998, we evaluated weather events and/or conditions between 10 years prior to 1998 and the time of sampling.

2.4. Soil nutrition

In order to determine the relationship between available soil Ca and paper birch crown vigor and growth, we sampled the O_a and B soil horizons around individual sample trees from a subset of nine sites (three sites on each of three mountain-slopes: Camel's Hump, Mount Hunger (Middlesex), and Mount Hunger (Waterbury)). Approximately 10 trees were randomly selected per site (Table 1). On opposite sides of each tree ($n = 86$), we excavated small (30 cm × 30 cm) soil pits from which we collected approximately 500 g of soil each from the O_a and upper 10 cm of B horizons. Samples were kept moist and extracted using standard procedures with a 5:1 (v:v) ratio of pH 4.8 ammonium acetate to soil (Ross et al., 1994). Samples were then filtered and analyzed on an ICP-AES (Optima DV 3000, PerkinElmer Corp., Norwalk CT) to quantify concentrations of extractable cations (mg nutrient kg^{-1} soil). Duplicates were processed to ensure accuracy. Although this method of extraction is standard and provides an accurate assessment of available Ca, estimates of aluminum (Al) availability derived using this technique slightly overestimate exchangeable Al (Soon, 1993).

2.5. Statistical approach

Differences in measurement parameters between crown vigor groupings (i.e., vigorous versus declining trees) were tested for significant differences using one-way analyses of variance (ANOVA). We employed regression analysis to test and quantify linear relationships between both the proportion of declining trees and mean

BAI per plot with soil cation concentrations or elevation, with mountain-slope as a covariate. Sites from which we collected soil and that contained a mix of crown vigor types (i.e., at least five trees each from vigorous and declining crown condition per site) were used for plot mean-based regression analysis. By focusing on sites with a mix of healthy and declining trees we hoped to better identify factors associated with a transition in crown health. We excluded from these analyses sites where trees were uniformly in decline in order to reduce potential confounding sources of variation (e.g., increased decomposition and reduced Ca uptake with advanced decline) that could mask relationships between Ca availability and recovery. Regression analyses were also used to evaluate BAI data from 2000 to 2006 and test for differences in growth trends between vigorous and declining trees. Assumptions of normality and equal variance were met for all datasets, and no data transformations were necessary. Two plots originally intended for use in regression analyses were excluded due to laboratory complications. For all analyses, means were considered statistically significant if $P \leq 0.05$.

3. Results and discussion

3.1. Factors influencing paper birch recovery

A mixture of crown vigor classes were found, ranging from fully vigorous crowns, to crowns with substantial foliar loss (Table 1). Some dead trees were found as well, though they were not included in our analysis. Ultimately, 97 vigorous and 75 declining trees were assessed and used for subsequent analyses. Reassessment of crown vigor in summer 2007 confirmed that we were 87% accurate in our ratings in 2006. Errors in our 2006 ratings were likely due to minor leaf drop prior to crown assessments that occurred in the fall. Vigor ratings from 2007 were used for all comparisons. Composition of sites ranged from primarily vigorous, to a mix of vigorous and declining, to primarily declining trees (Table 1). No significant differences in age were found between vigor classes, with mean age of declining trees being 93.0 years versus 92.8 years for vigorous trees. Considering these striking similarities, age-related differences in physiology (e.g., older trees having a greater respiratory demand relative to photosynthetic potential (Yoder et al., 1994)) or stress exposure (older trees having greater exposure to stochastic stress events like droughts, wounds, etc.) are unlikely to account for differences in tree vigor. However, the relatively advanced age of sample trees may explain the gradual reduction in growth for all trees prior to recent precipitous growth reductions (Fig. 1a).

Prior to 1998, both vigorous and declining trees experienced sometimes sudden and dramatic reductions in growth. However, during this period, growth rates also recovered for trees in both crown vigor categories (Fig. 1). This rebound in growth was also documented by Bourque et al. (2005) for yellow birch trees in eastern North America following freeze–thaw events that occurred during winter or early spring in 1936 and 1944. Indeed, sudden reductions and then rebounds in growth were evident for paper birch trees in our study in both of these years (Fig. 1a)—suggesting that paper birch in Vermont may also have been subject to regional freeze–thaw events.

Following a severe region-wide ice storm in 1998 that affected low-lying (<305 m) and mid-elevation (548–975 m) areas (Dupigny-Giroux et al., 2003), both vigorous and declining paper birch experienced marked reductions in growth, which continued for at least two years (Fig. 1a). Aerial overflight data of ice-storm damage in Vermont confirm that the paper birch stands we assessed for vigor and growth were moderately damaged by the 1998 ice-storm (Dupigny-Giroux et al., 2003), although estimates of relative damage for individual trees or plots were not avail-
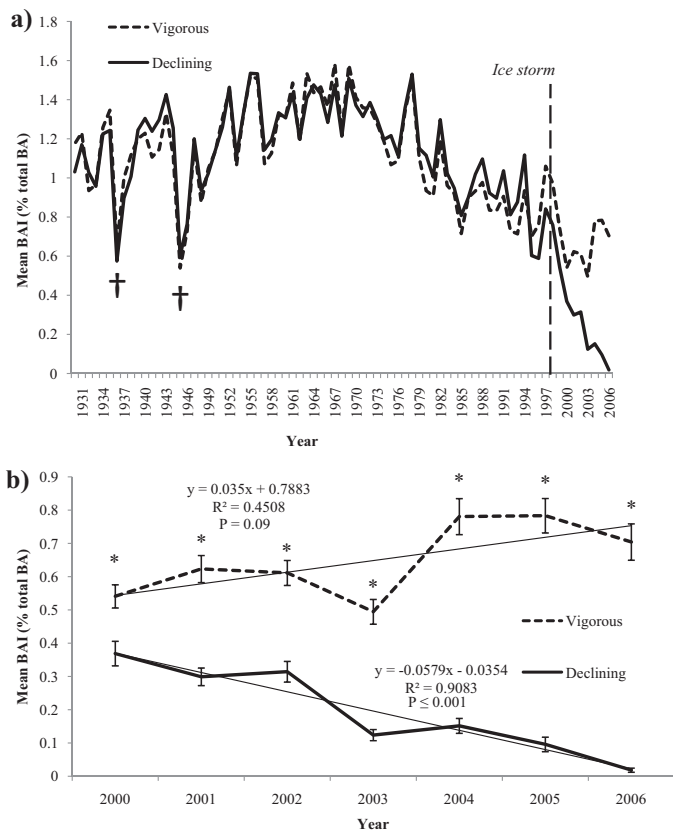
Fig. 1. Increment core analysis of the basal area increment (BAI) associated with paper birch decline. (a) Growth chronology of vigorous and declining trees with (b) mean BAI (±SE) for years post-2000 highlighted to show the rebound in growth of vigorous trees and a continued reduction in growth for declining trees (n = 172). Crosses (†) denote years of significant yellow birch dieback in the region as reported by Bourque et al. (2005). (*) Indicates P ≤ 0.05 for differences in BAI between vigorous and declining trees in a given year based on ANOVA.

able. Direct reductions in radial growth were associated with crown damage from the ice storm in other species as well (sugar maple, yellow birch, white ash (*Fraxinus americana* L.), and red maple (*Acer rubrum* L.); Smith and Shortle, 2003). By 2000, BAI of vigorous and declining trees was 49% and 56% lower, respectively, than BAI from the year prior to the ice storm. Patterns in growth reductions (i.e., slope of percent change in BAI) from 1998 through 2000 in our study did not differ between trees in vigorous and declining crown classes (P = 0.92), suggesting that there were no differences in initial injury for trees in these groups.

Climate data also indicated that a moderate to severe drought occurred in Vermont towards the end of 1998, and continued through the growing season of 1999 with Palmer Drought Severity Index (PDSI) readings ranging from −2.4 to −4.7 (Brewer, 2008; Dupigny-Giroux, 2009). However, based on the analysis of spectral satellite data used to evaluate the timing and nature of changes in vegetation (e.g., leaf phenology and amount, species composition, etc.), Dupigny-Giroux et al. (2003) concluded that the 1998 ice storm had a far more profound and lasting influence on vegetation health than the later drought. In fact, they classified the 1998 ice storm as a relatively inelastic disturbance—one with a greater capacity to alter physiological and ecosystem processes than the 1998/1999 drought, which they categorized as an elastic (i.e., transient) disturbance (Dupigny-Giroux et al., 2003). This characterization of the elasticity of stress response based on broader landscape-based data corresponds closely to patterns of BAI response to past stress events (e.g., the regional freeze–thaw events of 1936 and 1944; Bourque et al., 2005) versus the 1998

ice storm (Fig. 1). Variations in the elasticity of stress response and rebounds in growth likely reflect basic differences in the extent of damage associated with stress agents. For example, the loss of foliage and branches, as well as increases in wounding associated with ice storm damage would be expected to have a greater influence on long-term vigor than more transient reductions in stomatal conductance or foliar loss associated with drought.

Potential sources of continued low growth through the 2000 growing season include the influences of other weather events. However, no other climatic factors or weather events captured by state climatological records were consistent with declines or releases in paper birch growth from 1998 onward. The more likely explanation for lingering growth disruptions is the severity of stress exposure and damage in 1998. Especially if weather events result in a significant loss of crown biomass, reductions in tree growth may persist for at least two years beyond the year of initial injury (Schaberg et al., 2011).

Following the 2000 growing season, trees with currently vigorous crowns were able to rebound in BAI and continued to increase in growth, whereas trees with currently declining crowns maintained annual decreases in BAI (Fig. 1b). Overall, the regression of mean BAI for vigorous trees from 2000 to 2006 showed a positive, though only marginally significant growth rate (P = 0.09; Fig. 1b), whereas the regression for declining trees for the same period was significant and negative (P = 0.001; Fig. 1b). ANOVA analysis showed significant differences in tree growth for each year from 2000 to 2006 between declining and vigorous trees (P ≤ 0.001, Fig. 1b). Mean BAI for declining trees was 32% lower than vigorous trees in 2000 and by 2006 was 97% lower than BAI of vigorous trees. The rapid growth decrease of declining trees by 2006 is similar to patterns of predicted dieback for the region. Auclair (2005) generated two models roughly predicting regional dieback through 2017, each of which hinged on the cyclic nature of dieback in the northeastern US, and both of which predicted a spike in dieback in 2006. This spike in multi-species dieback for 2006 is consistent with growth patterns of birch currently declining but not for the vigorous trees surveyed—a discrepancy that highlights the difficulty in predicting dieback in a region with high climatic and nutritional variability. In contrast to previous elastic growth responses following stress, trees that now appear to be declining did not rebound in growth after 1998. This absence of a normal growth rebound suggests either (1) the influence of more severe or multi-stress impositions that caused more extensive physiological damage, and/or (2) the influence of other factors that impaired the stress response systems of trees and predisposed trees to decline.

During the last ten years of growth that we evaluated (1997–2006), the prevalence of locally absent annual growth rings increased in both health classes of trees, though the incidence of these rings in declining trees surpassed the level in vigorous trees by more than 6-fold (Fig. 2). An abundance of locally absent rings is often indicative of severe stress or injury (Lorimer et al., 1999). For the trees that we assessed, the number of locally absent rings was highly correlated with BAI growth (r = −0.532, P ≤ 0.001). Especially for trees now in decline, the prominence of low growth and locally absent annual rings highlight the negative trajectories of tree C relations.

Species differences in the amount of crown damage experienced or re-growth following crown injury would undoubtedly influence growth responses to ice damage. For instance, although American beech (*Fagus grandifolia* Ehrh.) and yellow birch may sustain more ice-related injury than sugar maple and paper birch trees, paper birch can exhibit greater long-term impacts perhaps because of the relative weakness of the wood of this species (Dupigny-Giroux et al., 2003), or because of the less effective wound closure and compartmentalization of disease in paper birch (Shortle et al., 2003). However, the inter-specific differences noted by others may do
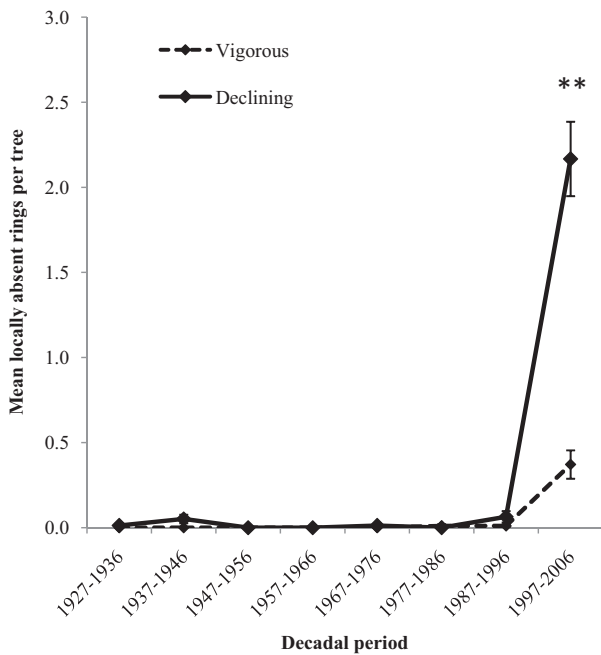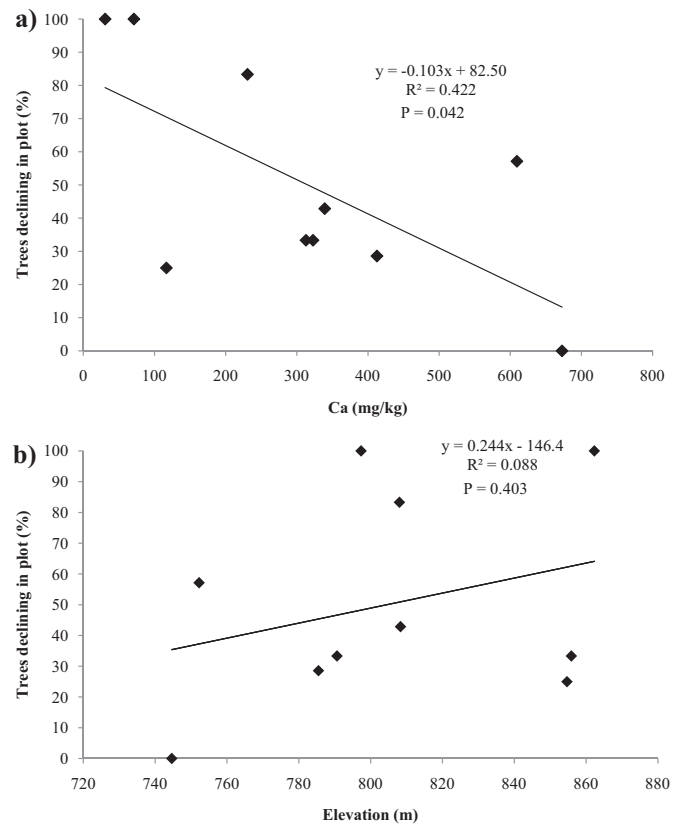
Fig. 2. Mean (±SE) locally absent xylem rings per tree per decadal period of vigorous and declining crown condition groups. For all but the most recent decade, error bars are smaller than symbols for means. Decadal periods began in 1927 where greater than 75% of trees were present. (**) Indicates $P \le 0.001$ based on ANOVA ($n = 172$).

Fig. 3. Linear relationships between the percent of declining trees and (a) Ca concentrations in the O_a horizon of soils or (b) elevation. Data are means from plots ($n = 10$) that contained both vigorous and declining trees, generally from moderate elevations.

little to inform the intra-specific differences in growth we found for vigorous versus declining birch. Shortle et al. (2003) report a poor response of paper birch to ice storm damage—although they note that trees with suppressed growth prior to the 1998 ice storm exhibited higher mortality three years after the storm. In contrast, we found that currently vigorous and declining trees showed near identical growth prior to the 1998 ice storm and yet showed dramatically different growth responses afterward (Fig. 1)—suggesting that some factor other than pre-disturbance growth contributed to damage recovery. One factor that may have influenced the differential ability of paper birch to respond to ice storm damage was the Ca availability in soils surrounding these trees.

3.2. Ca and elevation impacts

Vigorous trees grew in soils with an average of over three times greater Ca in O_a horizons than trees with declining crowns ($P \le 0.001$, Table 2). Additionally, Al, a competitor for Ca-uptake and a potentially phytotoxic element, was significantly higher in O_a horizons adjacent to declining trees compared to vigorous trees ($P \le 0.001$, Table 2). Significantly greater Ca was also found in B horizons surrounding vigorous trees, though no differences in Al concentrations were found in this horizon (Table 2). No significant differences associated with crown health were found for other soil cations assayed (i.e., potassium, magnesium and manganese). Acid

deposition-induced soil Ca depletion has resulted in tree Ca deficiencies that have been implicated in the reduced productivity and decline of red spruce and sugar maple trees in the northeastern US (Shortle and Smith, 1988; DeHayes et al., 1999; Schaberg et al., 2006). The soil-Ca concentrations reported here are supported by these findings for other species, but are the first measures that link reduced paper birch health to Ca-depletion. The significantly greater soil-Ca and lower soil-Al measured for O_a horizons, and the higher Ca concentrations in B horizons adjacent to vigorous trees relative to soils around declining trees is consistent with the possibility that Ca availability influenced the ability of trees to rebound in growth and recover from the 1998 ice storm. Adequate Ca nutrition is required to support at least three processes that are fundamental to overcoming a severe stress such as the crown loss and wounding associated with ice storm damage: (1) structural compartmentalization (Lachaud et al., 1999), (2) the optimization and regulation of carbon (C) relations (including respiration, growth, and C storage/transport; Marschner, 2002; Lautner et al., 2007), and (3) the metabolic control of stress response systems (including systems

Table 2
Mean (±SE) concentrations of Ca and Al extracted from soil Oa (n = 86) and B (n = 81) horizons adjacent to sampled trees based on crown vigor grouping. Sample size was lower for B horizons due to its absence in some locations.

Crown condition	Soil horizon			
	O_a		B	
	Ca (mg/kg)	Al (mg/kg)	Ca (mg/kg)	Al (mg/kg)
Vigorous	375.2 ± 44.2[**]	99.8 ± 14.9[**]	19.1 ± 1.6[*]	402.3 ± 24.5
Declining	107.9 ± 16.9[**]	223.1 ± 25.2[**]	13.8 ± 1.7[*]	368.1 ± 26.2

[*] Concentrations are significant at $P \le 0.05$ within each column.
[**] Concentrations are significant at $P \le 0.001$ within each column.

a)

b)
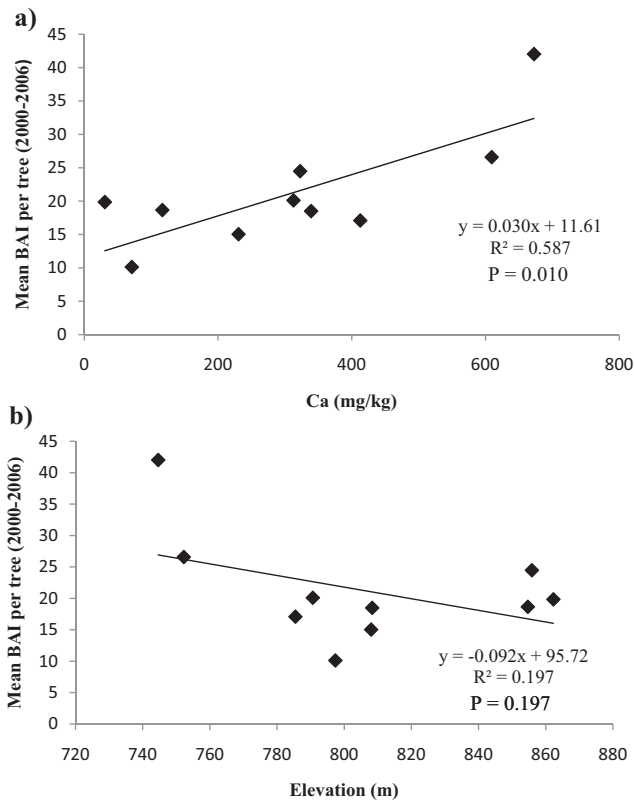
Fig. 4. Linear relationships between the basal area increment (BAI) from 2000 until 2006 with (a) Ca concentrations in the O_a horizons of soil or (b) elevation. Data are means from plots ($n = 10$) that contained both vigorous and declining trees, generally from moderate elevations.

that support wound closure and defense against fungal pathogens; Medvedev, 2005; Huggett et al., 2007). Considering this, deficiencies in biological Ca pools may predispose trees to reduced response in growth, wound closure and pathogen defense, thereby resulting in continued decreases in annual growth for declining (low Ca) trees, whereas vigorous (higher Ca) trees can adjust their physiology and rebound in crown condition and growth following damage.

To better separate the potentially confounding influences of elevation and Ca availability, we conducted regression analyses between the percentage of declining trees and (1) the average Ca concentration of soil O_a horizons and (2) average elevation using plot means from the three mountain-slopes ($n = 10$). We found that soil-Ca concentration explained approximately 42% of the variation and was significantly and negatively related to the percentage of declining trees within plots ($P = 0.042$). In contrast, elevation was not linearly associated with the percentage of declining trees ($P = 0.403$, Fig. 3). Although a greater frequency of declining trees existed at higher elevations (Table 1), it appears that the association of decline and elevation was an artifact of the coupling of reduced soil-Ca availability with increased elevation. Soils at higher elevations are typically thinner and cation-poor (Schaberg et al., 2010), and generally receive greater inputs of acid precipitation that further reduce levels of soil-Ca availability (DeHayes et al., 1999). To further assess the influence of Ca availability and elevation on tree health, we also conducted regression analyses between mean BAI during the period of potential growth rebound (summed from 2000 to 2006) and (1) Ca concentrations of soil O_a horizons and (2) elevations of plots. We found that O_a horizon Ca availability was significantly associated with the amount of growth trees experienced ($P = 0.010$) and explained over 58% of the variation, whereas elevation was not linearly associated with growth after 2000 ($P = 0.197$; Fig. 4). It is well documented that Ca plays a role

in the growth of sugar maple, particularly following site disturbance (Wargo et al., 2002; Huggett et al., 2007). However, to our knowledge, this is the first evidence that Ca availability influences the growth of mature paper birch following a physical disturbance (i.e., the 1998 ice storm).

In addition to the possible confounding of elevation and soil Ca status, elevation can be confounded with gradients in other environmental factors (e.g., differential ice loading during the 1998 ice storm, or more generalized exposures to low temperatures or water availability) that result in differential stress exposure. However, the lack of a relationship between decline and elevation seems to discount the likely influence of differential stress exposure with elevation for our sample trees. Indeed, at least one possible stressor, drought exposure during 1998/1999, should have decreased with elevation because precipitation levels generally increase with elevation (Basist et al., 1994).

One shortcoming of our current study was an inability to directly measure the Ca nutrition of trees via foliar analysis (the standard metric) because declining trees often have little foliage and residual crowns may not be sun-exposed (needed for the transpirationally induced uptake of Ca; Marschner, 2002). Future work should include the manipulation of tree Ca nutrition and evaluate the influence of this manipulation on Ca-dependent carbohydrate and stress response measures.

4. Conclusions and implications

Our data show that following the 1998 ice storm, paper birch growing in soils with greater Ca concentrations were able to recover more fully from injury (e.g., rebound in growth) than birch growing on Ca-depleted soils. Paper birch is not the first species in the region to undergo decline in the last half-century due to Ca-limitations. Red spruce has experienced large-scale decline due to acid deposition-induced Ca leaching and associated alterations in physiology, foliar loss and growth (Vogelmann et al., 1985; Beckage et al., 2008). Additionally, sugar maple has experienced decline throughout the region and has been adversely impacted by acid deposition-associated factors such as reduced Ca availability that contribute to crown thinning, reduced growth and tree mortality (Schaberg et al., 2006; Huggett et al., 2007). Paper birch is the third species in the region to undergo crown decline and high mortality in recent years (Shortle et al., 2003). The work presented here suggests that there is a link between soil-Ca deficiency and the decline of paper birch (Figs. 3 and 4). We propose that a unique scenario may be unfolding in the region in which three tree species, generally occupying similar habitat (sugar maple decline has predominated at the species' upper elevational limits, and red spruce and paper birch commonly occupy an overlapping habitat), are experiencing a roughly synchronous reduction in health and increase in mortality. To date, the loss of red spruce has been far more prominent, whereas maple decline has been more site-specific (Horsley et al., 2000), and paper birch decline only recently prevalent (Decker et al., 2005). Indeed, Beckage et al. (2008) have shown that red spruce mortality has allowed other species (e.g., sugar maple) to become established in what was once largely red spruce-balsam fir (*Abies balsamea* (L.) Mill.) habitat, and that at certain elevations, paper birch has increased in abundance where red spruce has declined. However, if declines in sugar maple and paper birch health persist, replacement species for lost red spruce may themselves be jeopardized. In montane ecosystems with relatively limited diversity among woody species, the simultaneous decline of three prominent tree species would likely create gaps that could disrupt multiple trophic levels and the production of numerous essential ecosystem services. Furthermore, the risk posed to montane ecosystems may increase over time if acidic inputs continue to leach Ca from sensitive soils.

Acknowledgments

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