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

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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 •vigorousŽ status, and a rating of 3 or 4 resulted in •decliningŽ 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	Š72.88116	537	19	7	8	2	2	78.9	21.1
MHW … Low	44.39705	Š72.65977	666	10	1	9	0	0	100.0	0.0
MHM … Low	44.38836	Š72.64488	689	10	1	7	2	0	80.0	20.0
CH … Low	44.30930	Š72.86731	703	10	7	3	0	0	100.0	0.0
Appalachian Gap	44.21164	Š72.93179	715	18	1	6	8	3	38.9	61.1
CH … Mid	44.31083	Š72.87067	745	20	6	5	5	4	55.0	45.0
MHW … Mid	44.39603	Š72.65552	785	20	0	6	7	7	30.0	70.0
Roxbury	44.07214	Š72.80988	797	20	4	8	3	5	60.0	40.0
MHM … Mid	44.39152	Š72.64003	800	19	0	11	5	3	57.9	42.1
CH … High	44.31450	Š72.87745	856	10	0	5	5	0	50.0	50.0
MHW … High	44.39618	Š72.65204	888	9	0	1	5	3	11.1	88.9
MHM … High	44.39326	Š72.64180	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).

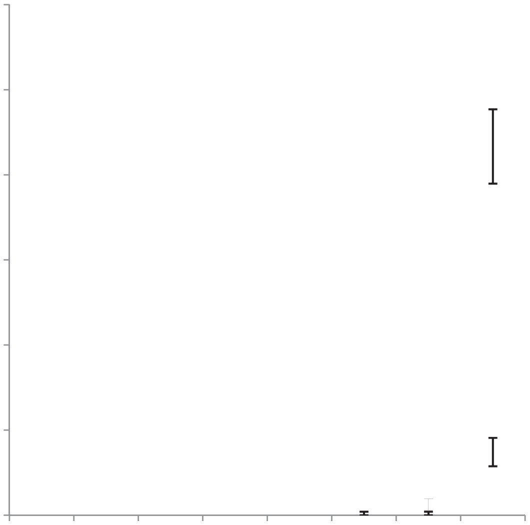
2.5. Statistical approach

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 $P \le 0.05$.

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



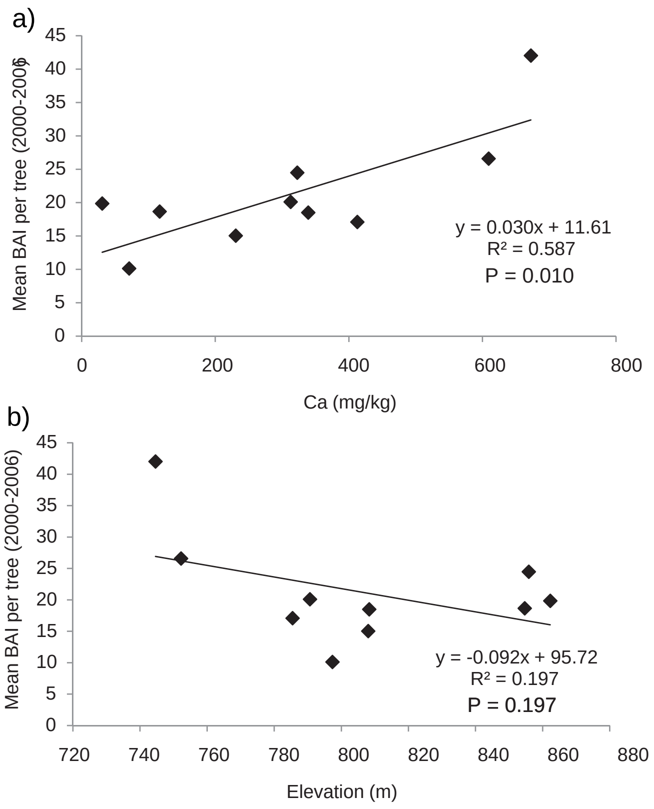


Fig. 4. Linear relationships between the basal area increment (BAI) from 2000 until 2006 with (a) Ca concentrations in the O_a horizons of soil or (b) elevation. Data are means from plots ($n = 10$) that contained both vigorous and declining trees, generally from moderate elevations.

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