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Abiotic and Biotic Factors Influencing Sugar Maple Health: Soils, Topography, Climate, and Defoliation

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Sugar maple (*Acer saccharum* Marsh.), a keystone species of northern hardwood forests, is susceptible to decline, especially on sites low in the soil base cations calcium (Ca) and magnesium (Mg). A common stressor of sugar maple is forest tent caterpillar (FTC; *Malacosoma disstria* Hübner), an indigenous defoliator. The recent outbreak of FTC (2002–2007) affected 600,000 ha of forest in the northeastern United States and Canada. We assessed the condition of sugar maple trees in 47 North American Maple Project stands in Massachusetts (2006–2007) and Vermont and New York (2007–2008) just after the peak of the FTC outbreak. Mortality was highest in stands with the most crown dieback the previous year (R^2 = 0.62, P < 0.001). In addition to drought, cold winter temperatures, and concave microrelief, mortality reflected an interaction of defoliation with soil base cation availability (P = 0.02), with stands defoliated in 2005 that also had low Mg saturation in the A horizon being most likely to suffer high mortality. Sites with above-average annual sugar maple mortality (>3 or 4%) occurred on soils with low concentrations of Ca (0.31–0.46 $cmol_c\ kg^{-1}$ in the upper B horizon), Mg (0.06–0.10 $cmol_c\ kg^{-1}$), and K (0.03–0.05 $cmol_c\ kg^{-1}$). This work extends the thresholds for these base cations determined by previous research on the Allegheny Plateau to a larger geographic area.

Abbreviations: AIC_C, corrected Akaike's information criterion; CEC, cation exchange capacity; FTC, forest tent caterpillar; NAMP, North American Maple Project.

Sugar maple is a keystone species of the northern hardwood forest type (Houston, 1999; Horsley et al., 2002). The species is ecologically, economically, and culturally important in the northeastern United States and southeastern Canada (Godman et al., 1990; Houston, 1999). Sugar maple is valuable to the timber products industry, and its sap is used to produce maple syrup (Houston, 1999; Nyland, 1999). Tourism in the region benefits from sugar maple each fall as people seek the vibrant colors of its foliage (Houston, 1999).

Sugar maple decline was first documented in the early 1900s but was not systemically researched until the middle of the century, when researchers in Wisconsin determined that deterioration of sugar maple, or "maple blight," was caused by a complex of factors (Giese et al., 1964). Since then, decline episodes have been reported across portions of its native range (Manion, 1991; Houston, 1999), particularly on sites marginal for sugar maple growth (Nyland, 1999). Decline is characterized by a decrease in crown vigor, showing increased foliar transparency, fine-twig dieback, and loss of major branches, ultimately leading to tree mortality (Manion, 1991; Bauce and Allen, 1991; Horsley et al., 2002).

Sugar maple decline is driven by a number of abiotic and biotic factors that predispose, incite, and contribute to tree death (Allen, 1987; Manion, 1991). Sugar

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maple is predisposed to decline on soils low in base cations, especially Ca and Mg (Wilmot et al., 1995; Long et al., 1997; Horsley et al., 2002), and high in the toxic metals aluminum (Al) (Horsley et al., 2000) and manganese (Mn) (Hallett et al., 2006). Potassium deficiency has also been linked to decline symptoms in sugar maple. Low K concentrations in foliage were associated with decreased growth and poor crown conditions of sugar maple in Quebec (Bernier and Brazeau, 1988; Bernier et al., 1989; Jones and Hendershot, 1989), and foliar K was significantly lower in declining stands than non-declining stands in Pennsylvania (Drohan et al., 2002). The role of K concentrations in soil as a predisposing factor in sugar maple decline has rarely been reported.

Physiographic factors can also predispose sugar maple to decline. Sugar maple stands with high crown dieback and mortality were found at upper slope positions on unglaciated soils in the Allegheny Plateau (Horsley et al., 2000; Bailey et al., 2004). Sugar maples in Quebec in concave microsites had more crown dieback than at planar sites due to shallow soils and excessive moisture (Roy et al., 2002). Sugar maple stands predisposed to decline by poor site conditions and cation deficiencies suffer more crown dieback and mortality when stressed by inciting factors such as defoliating insects, late spring frosts, or drought (Manion, 1991; Horsley et al., 2002; Bailey et al., 2004). Defoliating insects are the most common inciting factor in sugar maple decline (Millers et al., 1989; Manion, 1991), and severe insect defoliations can predispose otherwise healthy sugar maples to decline (Allen, 1987).

The native forest tent caterpillar (FTC, *Malacosoma disstria* Hübner) is the most important early-season defoliator of northern hardwood forests (Mattson et al., 1991), and sugar maple is its preferred host in the northeastern United States (Fitzgerald, 1995; Parry and Goyer, 2004; Wink and Allen, 2007). Some forested stands are defoliated continually by localized populations of FTC (Fitzgerald, 1995), but periodically, populations expand to region-wide outbreak levels (Hodson, 1941; Fitzgerald, 1995) that persist for two to four years (Fitzgerald, 1995; Wink and Allen, 2007). Defoliation early in the growing season can be followed by refoliation, but this depletes carbohydrate reserves in roots, which can reduce winter hardiness (Parker and Houston, 1971; Wargo et al., 1972; Manion, 1991).

The most recent FTC outbreak in the northeastern United States occurred from 2002 to 2007 and affected >600,000 ha of northern hardwood forest. Many sugar maple stands were defoliated for multiple years during this outbreak (Wood et al., 2009). Repeated defoliation can lead to crown dieback, growth reduction, and eventual death of trees (Gross, 1991; Bauce and Allen, 1991; Horsley et al., 2000). Sugar maples with crown dieback below 40% can usually recover within 2 yr following defoliation (Gross, 1991), but trees with severe crown dieback (≥50%) have a high probability of dying within 10 yr (Gross, 1991; Allen et al., 1995).

Previous research in Vermont and New York at the end of this FTC outbreak provided important insight into which sugar maple stands were vulnerable to decline following defoliation. Stands defoliated during the outbreak had higher crown dieback and mortality than undefoliated stands (Wood et al., 2009). Higher crown dieback and mortality also occurred in stands with concave microrelief and in stands with drier growing season conditions during the outbreak (Wood et al., 2009). Soil chemistry, however, was not studied by Wood et al. (2009), although soils deficient in base cations are known to predispose sugar maple to decline.

Our study built on that begun by Wood et al. (2009) to meet the following objectives. First, we determined whether sugar maple crown condition improved after the collapse of the FTC outbreak and whether sugar maple mortality could be predicted based on crown dieback observations from the previous year. We determined thresholds for high sugar maple mortality following the collapse of the FTC outbreak in terms of the soil base cations Ca, Mg, and K. We also evaluated which soil chemistry variables, in addition to the suite of variables assessed by Wood et al. (2009), best predicted sugar maple mortality in our stands when combined with defoliation history and other site and climate variables.

MATERIALS AND METHODS

Study Sites

This study used data collected from 47 northern hardwood forest stands in Massachusetts, Vermont, and New York (Fig. 1) following protocols of the North American Maple Project (NAMP; Millers et al., 1991). We used data collected by the Massachusetts Department of Conservation and Recreation from two NAMP stands in Massachusetts in 2006 and 2007; 2008 tree health data were not collected due to reallocation of resources. We used data from 27 NAMP stands in Vermont that were measured in 2007 to 2008 by the Vermont Department of Forests, Parks, and Recreation. In New York, we collected data in 2008 from 18 stands that were previously assessed in 2007

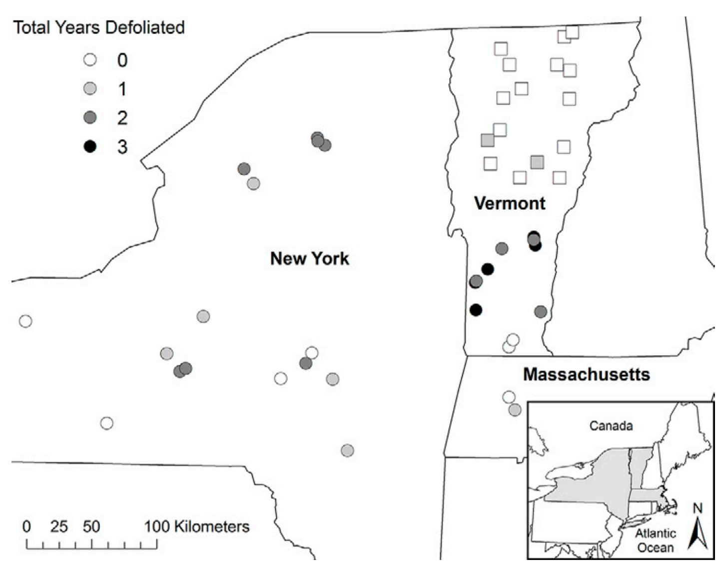

Fig. 1. Locations of the 47 sugar maple stands studied in Massachusetts in 2006 and 2007 and in Vermont and New York in 2007 and 2008. Circles indicate stands where soils were collected. Squares indicate stands where soils were not sampled. Shading of symbols indicates the number of years each stand was defoliated (>25%) during the forest tent caterpillar outbreak (2002–2007).

(Wood et al., 2009); 10 of these stands were previously monitored under the NAMP and 8 were established in 2007 by Wood et al. (2009) in areas heavily defoliated by FTC.

Each NAMP stand contained five 400-m^2 plots with a 20-m buffer between each plot. Plots within each stand were similar in site characteristics and species composition. Sugar maple comprised at least 50% of stand basal area (Millers et al., 1991). Common overstory associates were American beech (*Fagus grandifolia* Ehrh.), black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and eastern hemlock [*Tsuga canadensis* (L.) Carr.]. There had been no logging activity in any stands since at least 1983. The only management activities, besides tapping, were single-tree removals in some Vermont sugar bushes. Except for one stand in western New York that was on an Alfisol, all stands were located on Inceptisols and Spodosols based on field observations and GPS locations (Soil Survey Staff, 2009, 2010).

Tree and Site Characterization

Crown dieback estimates were used to assess crown conditions of all sugar maple trees >10-cm diameter at breast height (1.4 m) in all plots. Following NAMP methods (Millers et al., 1991), crown dieback was estimated (to the nearest 5%) as the proportion of fine twig mortality on branches with diameters <10 cm. Dieback of each tree crown was estimated by two people from perpendicular sides. To ensure consistency and accuracy, field crew members participated in the Vermont Department of Forests, Parks, and Recreation annual training in each field season. Annual sugar maple mortality was calculated from the number of sugar maple trees that died between the two years of the inventory; we did not include mortality from wind throw.

We analyzed stand and site data from 47 stands, 45 that were investigated by Wood et al. (2009) and 2 additional NAMP stands in Massachusetts. These data included crown closure (open, moderate, or full), canopy structure (single story, two story, or multistory), and terrain shape or microrelief (convex, planar, or concave) (Table 1). Annual minimum and maximum temperatures for 2008 (2007 in Massachusetts), average temperature and precipitation data for the duration of the FTC outbreak (2002–2007), and short-term drought conditions (Palmer's *Z*-index; Palmer, 1965) for the duration of the outbreak were obtained from the National Climatic Data Center (http://www.ncdc.noaa.gov/cdo-web/).

Soil Characterization

Soil samples were collected from 31 of the 47 NAMP stands in summer 2009: 11 in southern Vermont, 2 in Massachusetts, and 18 in New York (Fig. 1). Soils were not collected from stands in northern Vermont because little FTC defoliation occurred there. One soil pit was dug in each of the five 400-m^2 plots in each stand, except for five stands in which not all the plots could be relocated, including some that were salvage logged after our mortality measurements and before soil collection. Samples were collected from the A horizon and the first 10 cm of the upper B horizon along the same side of the pit. Two of the stands in northern New York did not have an A horizon in any of the pits; the A horizon averaged 9 cm in thickness in the other 29 stands. An E horizon was present in 20 stands, averaging 1.8 cm, and 25 stands had an O layer, averaging 2.3 cm.

Air-dried soils were ground with a mortar and pestle and sieved to 2 mm. Samples from the five plots in each stand were composited by horizon (A horizon and upper B). The moisture content of the air-dried soil samples was measured, and concentrations were expressed on an oven-dried basis. The pH of 1:2 soil/deionized, distilled water solution for each soil composite was measured using a pH meter. Exchangeable cations were extracted from 5 g of soil with 100 mL of 1 mol L^{-1} NH_4Cl (Blume et al., 1990). Soil extracts were analyzed to determine Ca, Mg, K, Na, and Al concentrations using inductively coupled plasma–optical emission spectrometry (PerkinElmer OPTIMA 33000DV). Exchangeable acidity was extracted using 1 mol L^{-1} KCl and determined by potentiometric titration (Thomas, 1982). Effective cation exchange capacity (CEC) is the sum of exchangeable Ca, Mg, K, Na, and acidity. Base saturation is the sum of exchangeable bases divided by the CEC.

Defoliation Data

Defoliation shapefiles for each year of the FTC outbreak (2002–2007) were provided by the New York State Department of Environmental Conservation; Vermont Department of Forests, Parks, and Recreation; and Massachusetts Department of Conservation and Recreation. These agencies aerially sketch-mapped noticeable (>25%) defoliation in hardwood stands during the outbreak (Wood, 2008). Defoliation intensity was rated as moderate (25–50%) or severe (>50%). State foresters confirmed that defoliation at these sites was by FTC.

Data Analysis

We limited our analysis to dominant and codominant sugar maple in each stand because forest decline is best indicated by trees of these crown positions (Manion, 1991). The predictor variables included all of those assessed by Wood et al. (2009; Table 1) plus the soil variables, which were the soil drainage class and, for both A and B horizons, the concentration and saturation of each of the base cations (Ca, Mg, and K), the CEC, and the pH. Physiography was ranked by slope position (upper, middle, or lower), and landform types were ranked by water and nutrient retention (Bailey et al., 2004; Table 1).

A *t*-test was used to compare crown dieback the previous year between trees that survived ($n = 1650$) and those that died ($n = 33$), with trees as the experimental units.

Mortality was calculated as the percentage of sugar maple trees in each stand that died from 2006 to 2007 in Massachusetts or from 2007 to 2008 in New York and Vermont. Pearson correlations were used to determine relationships between independent variables and sugar maple mortality. Fisher's *r*-to-*z* transformation (Preacher, 2002) was used to determine the significance of differences between correlation coefficients for soil cations.

Table 1. Variables used to explain sugar maple mortality from 2006 to 2007 in Massachusetts and 2007 to 2008 in New York and Vermont. Variables in bold indicate a correlation with sugar maple mortality at α = 0.10.

Variable	Explanation	*r*
Defoliation (*n* = 45)		
Defoliated	(0) not defoliated, (1) defoliated	0.19
Defoliation in 2002	(0) not defoliated, (1) defoliated	−0.09
Defoliation in 2004	(0) not defoliated, (1) defoliated	−0.08
Defoliation in 2005	(0) not defoliated, (1) defoliated	**−0.25**
Defoliation in 2006	(0) not defoliated, (1) defoliated	0.24
Defoliation in 2007	(0) not defoliated, (1) defoliated	0.04
Defoliation events (yr)	total number of years defoliated by forest tent caterpillar	0.17
Defoliation severity index	sum of moderate (1) and severe (2) defoliations	0.11
Stand (*n* = 45)		
Crown closure	(1) open, (2) moderate, (3) full	−0.18
Canopy structure	(1) single story, (2) two story, (3) multistory	**−0.26**
Diameter at breast height (cm)	average among all sugar maples within a stand	−0.15
Basal area ha^{-1}, all species (m^2)		**−0.30**
Basal area ha^{-1}, sugar maple (m^2)		**−0.13**
Sugar maple dominance (%)		0.06
Management	(1) sugar bush, (2) forest	0.04
Site (*n* = 45)		
Elevation (m)		0.02
Slope (%)		0.02
Terrain	(1) flat, (2) hilly, (3) mountainous	**0.29**
Landform type	(1) ridgetop, (2) spur ridge, (3) head slope, (4) nose slope, (5) sideslope, (6) draw, (7) cove, (8) flat	**0.25**
Slope position	(1) summit/shoulder, (2) backslope, (3) footslope, (4) terrace, (5) flat, (6) floodplain	0.18
Topographic position	(1) upper, (2) middle, (3) lower	0.10
Microrelief	(1) convex, (2) planar, (3) concave	**−0.38**
Site aspect	(1) north, (2)east/west, (3) south	−0.16
Rockiness	(1) >10 large rocks or bedrock exposed, (2) 2–10 large rocks in site, (3) no large rocks	0.18
Outbreak mean precipitation (cm)	May–September average during outbreak years (2002–2007)	−0.10
Outbreak mean temperature (°C)	May-September average during outbreak years	−0.18
Annual mean temperature (°C)	2007 in Massachusetts, 2008 in New York and Vermont	**−0.30**
Annual min. temperature (°C)	2007 in Massachusetts, 2008 in New York and Vermont	**−0.32**
Annual max. temperature (°C)	2007 in Massachusetts, 2008 in New York and Vermont	−0.19
Outbreak mean *Z*-index	May–September average during outbreak years	**−0.46**
A horizon soils (*n* = 29)		
Ca/Al (mol/mol)		−0.16
Ca ($cmol_c$ kg^{-1})		−0.17
Mg ($cmol_c$ kg^{-1})		−0.20
K ($cmol_c$ kg^{-1})		−0.22
Al ($cmol_c$ kg^{-1})		−0.07
pH	pH in water	−0.01
Ca saturation (%)		−0.23
Mg saturation (%)		−0.24
K saturation (%)		−0.09
Base saturation (%)		−0.20
Effective cation exchange capacity ($cmol_c$ kg^{-1})		−0.27
B horizon soils (*n* = 31)		
Ca/Al (mol/mol)		−0.14
Ca ($cmol_c$ kg^{-1})		**−0.31**
Mg ($cmol_c$ kg^{-1})		**−0.37**
K ($cmol_c$ kg^{-1})		**−0.39**
Al ($cmol_c$ kg^{-1})		−0.08
pH	pH in water	−0.13
Ca saturation (%)		−0.25
Mg saturation (%)		**−0.30**
K saturation (%)		−0.02
Base saturation (%)		−0.26
Effective cation exchange capacity ($cmol_c$ kg^{-1})		**−0.38**
Soil drainage	(1) well drained, (2) moderately well drained, (3) poorly drained	−0.05
Soil texture	(1) coarse gravel, (2) medium gravel, (3) fine gravel, (4) coarse sand, (5) medium sand, (6) fine sand, (7) silt/clay	0.01

Soil thresholds were determined as those that best predicted annual mortality >3% in defoliated stands, which is higher than the normal annual mortality rate (2%) for dominant and codominant sugar maple (Allen et al., 1995). We used the same method as Bailey et al. (2004): the threshold was placed between two stands, maximizing the number of correctly classified stands (defoliated stands below the threshold with high mortality and above the threshold with low mortality). We conducted a sensitivity analysis by recalculating thresholds with each stand removed from the data set, and we report the maximum and minimum threshold thus determined. We also calculated thresholds for mortality >4% to assess the importance of this cutoff to the determination of the threshold.

Multiple linear regression was used to determine which combination of variables best predicted sugar maple mortality in sites where soils were characterized ($n = 31$). Predictor variables were chosen from the variables determined to be important by Wood et al. (2009) and those correlated ($\alpha = 0.10$) with sugar maple mortality (shown in bold in Table 1). Class variables were coded as described in Table 1. Stepwise regression with $\alpha = 0.15$ was used to narrow the list of candidate predictors, producing a model that included microrelief, drought, terrain, summer precipitation, crown structure, crown closure, pH and K in the A horizon, and soil drainage class.

Based on the stepwise regression model, 76 candidate models were proposed, each with variables describing defoliation history, site physiography and climate, and soils. Variance inflation factors (VIFs) were calculated for variables within these categories (Table 1). To avoid multicollinearity, variables with a VIF ≥ 5 were not included when proposing candidate regression models (Freund and Littell, 2000; Long et al., 2009).

Model performance was evaluated using R^2 and corrected Akaike's information criterion (AIC_C), which is a bias adjustment of Akaike's information criterion (Burnham and Anderson, 2002). The best models were identified by low AIC_C and high R^2. Akaike's information criterion measures the model goodness of fit (Akaike, 1974), and AIC_C was used because our ratios between sample size ($n = 31$) and model parameters ($k = 4$–7) were <40 (Burnham and Anderson, 2002). In addition to reporting the best six models, we compared these models with alternate models with different base cations while keeping all of the other predictor variables the same. Models are considered different if AIC_C differs by >2 (Akaike, 1974).

Model residuals were analyzed using the chi-square test for heteroscedasticity. A nonsignificant P value resulting from the chi-square test indicates homogeneity of error variance (Freund and Littell, 2000). All candidate models had residuals with acceptable variance. Statistical analyses were performed using SAS (SAS Institute) and SigmaPlot 11.0 (Systat Software).

Table 2. Sugar maple condition by crown position across all stands ($n = 47$). Mortality was calculated as the percentage of sugar maple trees in each stand that died from 2006 to 2007 in Massachusetts or 2007 to 2008 in New York and Vermont.

Tree crown position	Measurement	Range	Mean
		%	%
Dominant or codominant ($n = 1683$)	mortality	0–14	2 ± 3†
	dieback during outbreak	5–31	10 ± 6
	dieback after outbreak	2–31	8 ± 6
Intermediate or suppressed ($n = 731$)	mortality	0–38	4 ± 8
	dieback during outbreak	5–33	10 ± 5
	dieback after outbreak	0–37	8 ± 6

† Mean ± standard deviation.

RESULTS

Sugar Maple Condition

Average crown dieback of dominant and codominant sugar maple was 10 ± 6% (mean ± SD) across all 47 stands one year after the peak of the FTC outbreak (2007 in New York and Vermont and 2006 in Massachusetts). Average crown dieback decreased to an average of 8% the following year, after the collapse of the FTC outbreak (Table 2), a statistically significant improvement ($P = 0.001$). One stand, which was defoliated for three years during the outbreak, improved from 18% average crown dieback to 7% average crown dieback (Fig. 2). The two stands with the worst crown condition had >20% crown dieback in both years, which is indicative of decline, according

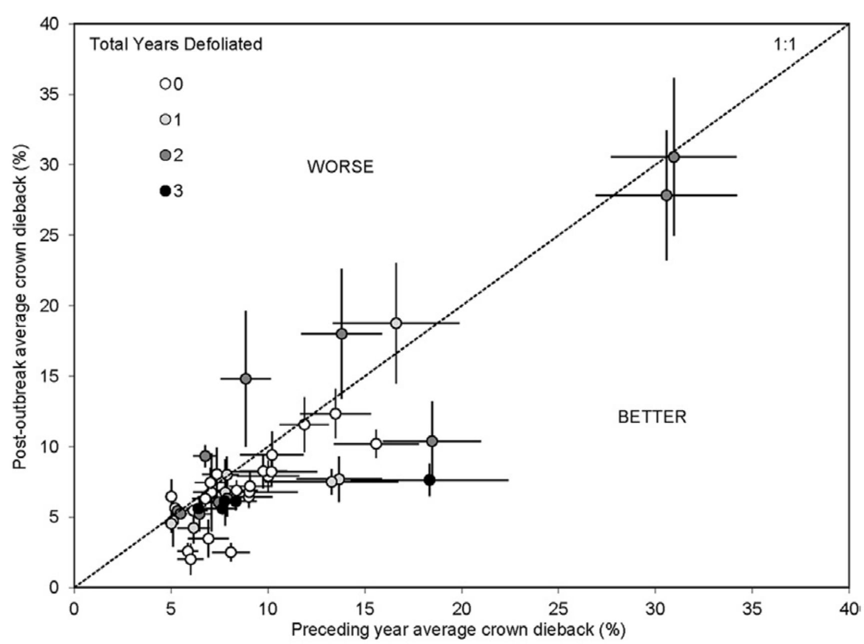

Fig. 2. Crown dieback in consecutive years (2006 and 2007 for Massachusetts; 2007 and 2008 for Vermont and New York) for dominant and codominant sugar maple trees in 47 northern hardwood forest stands. Each circle represents the average dieback percentage for one stand. Error bars represent standard errors. Shading of circles indicates the number of years each stand was defoliated during the forest tent caterpillar outbreak (2002–2007). The dotted line represents no change.

to Allen (1987). Sugar maple mortality (the percentage of all sugar maples in the stand that died within the year) was predicted by the average crown dieback from the previous year (R^2 = 0.62, $P < 0.001$; Fig. 3). Stands with the most crown dieback in 2007 (2006 for Massachusetts) had the highest sugar maple mortality in 2008 (2007 for Massachusetts; Fig. 3).

Most stands (28 of 47) had no mortality within the year we studied, which is not surprising given the small number of trees monitored in each stand. However, 19 stands had some sugar maple mortality, and 16 stands had mortality >2%, the normal rate for dominant and codominant sugar maple (Allen et al., 1999). Sugar maple mortality was >10% in two stands (5 of 37 trees or 13%; 6 of 53 trees or 11%) that suffered two years of heavy defoliation (2005 and 2006) during the FTC outbreak (Fig. 3). At the stand level, the average crown dieback the preceding year was a very significant predictor of mortality ($P < 0.001$; Fig. 3). Mortality for dominant and codominant sugar maples averaged 2 ± 3% across all stands (Table 2).

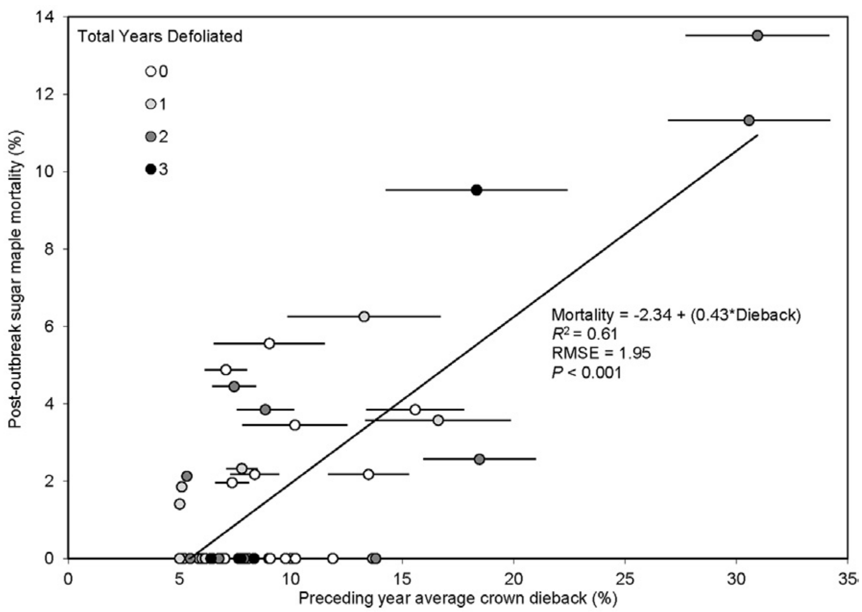

Fig. 3. Sugar maple mortality as a function of the previous year's crown dieback in 47 northern hardwood forest stands. Each circle represents a stand average. Shading of circles indicates the number of years each stand was defoliated during the forest tent caterpillar outbreak (2002–2007). Error bars represent standard errors. There is no standard error for mortality because it is a stand-level variable. The solid line shows the regression relationship.

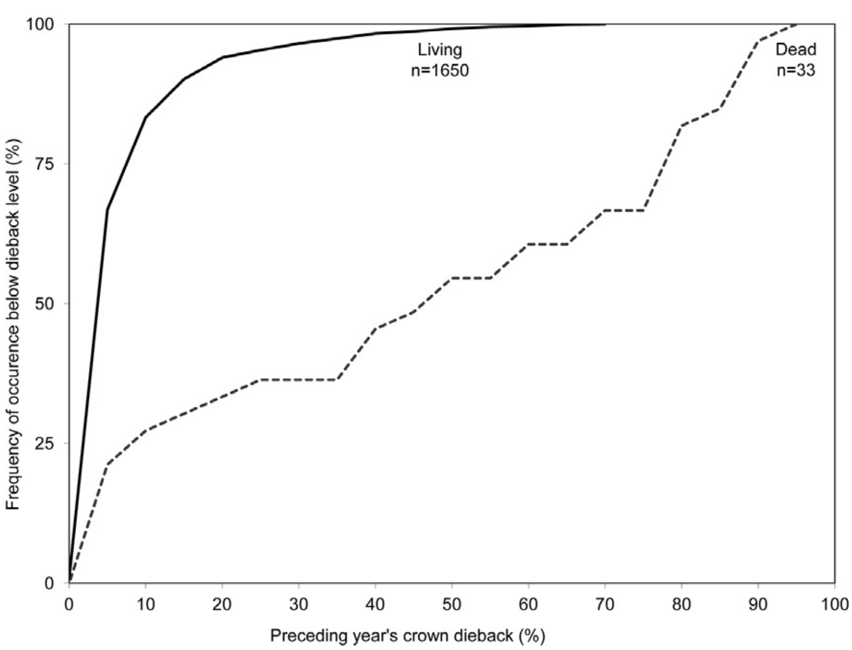

Fig. 4. Cumulative frequency diagram of the preceding year's crown dieback (2006 for Massachusetts, 2007 for Vermont and New York) of individual dominant and codominant sugar maple trees living (*n* = 1650) and dead (*n* = 33) the following year in 47 northern hardwood stands.

Dieback and mortality can also be related at the tree level. We observed mortality of 33 of 1683 (2%) dominant and codominant sugar maples (Fig. 4). The previous year's crown dieback for trees that survived (n = 1651) was 9 ± 9% compared with 48 ± 5% for trees that died ($P < 0.001$). Half of the sugar maple trees that died had crown dieback >50% the previous year (Fig. 4). Three-quarters of the trees that survived (n = 1238) had <10% dieback the previous year, and half (n = 825) had dieback ≤5%. Crown dieback in the previous year did not exceed 70% for any surviving trees (Fig. 4).

Soil Chemistry Relationship to Mortality

Concentrations of Ca, Mg, and K in the upper B horizon all had inverse correlations with mortality, with K having the strongest relationship with mortality ($r = -0.39$, $P = 0.03$; Table 1), although the correlation with K was not statistically distinguishable from correlations with Ca ($P = 0.73$) or Mg ($P = 0.93$). Sugar maple mortality was not strongly correlated with any soil chemistry variables from the A horizon (Table 1).

Stands that had been defoliated that occurred on soils with low exchangeable Ca, Mg, and K had above-normal sugar maple mortality (Fig. 5). We determined the thresholds below which stands were likely to suffer >3 or 4% annual mortality (to establish the sensitivity of the thresholds to the mortality rate we defined as above normal) and we recalculated the thresholds with each stand removed from the data set. For A horizon exchangeable cations, the thresholds for high mortality were the same whether based on 3 or 4% annual mortality (0.74–0.76cmol$_c$kg^{-1}forCa,0.12–0.16mol$_c$kg^{-1} for Mg, and 0.04–0.07 cmol$_c$ kg^{-1} for K) (Fig. 5). In the upper B horizon, thresholds for 3% mortality (0.31–0.41 cmol$_c$ kg^{-1} for Ca, 0.08–0.10 cmol$_c$ kg^{-1} for Mg, and

0.03–0.05 $cmol_c\ kg^{-1}$ for K) were slightly different than for 4% mortality (0.31–0.46 $cmol_c\ kg^{-1}$ for Ca, 0.06–0.10 $cmol_c\ kg^{-1}$ for Mg, and 0.03–0.04 $cmol_c\ kg^{-1}$ for K) (Fig. 5). We also calculated thresholds for above-normal annual mortality based on base saturation in the A horizon (0.74–0.76% for Ca, 0.12–0.16% for Mg, and 0.04–0.10% for K) and the upper B horizon (0.31–0.46% for Ca, 0.06–0.10% for Mg, and 0.03–0.05% for K saturation), combining ranges based on 3 and 4% mortality. Sites with high sugar maple mortality also had low CEC (<5.8 $cmol_c\ kg^{-1}$ in the A horizon and <1.6–1.8 $cmol_c\ kg^{-1}$ in the B horizon) and low base saturation (<24–29%) and Ca/Al ratios (0.17–0.25) in the upper B horizon.

Variables Suitable for Predicting Mortality

We determined which variables describing site physiography, climate, defoliation, and soils best predicted sugar maple mortality following the FTC outbreak. We compared candidate models with various combinations of variables in these classes, excluding combinations of variables with high multicollinearity and including the interaction of soil chemistry and defoliation variables (Table 3). The physiographic predictor variable in all the best models was site microrelief, with concave sites tending to have higher mortality. Two climate variables were significant in all the best models, namely drought during the outbreak (as indicated by the average Palmer's *Z*-index for 2002–2007) and low winter temperatures. Defoliation in 2005 was a better predictor than defoliation in any other year or the total number of years defoliated.

These variables were combined with various candidates for soil variables, and the candidate models were compared. The best model included the interaction of defoliation in 2005 with Mg saturation in the A horizon ($P = 0.02$) (Table 3). Sugar maple mortality was more sensitive to Mg availability in stands defoliated in 2005 than in stands not defoliated in 2005 (Fig. 6). Because the soil variables were highly correlated, there were many candidate models with different soil variables (Table 3). The second best model, which had the interaction of defoliation in 2005 with base saturation in the A horizon, was not much worse than the best (AIC_C of 60.1 compared with 58.4). The best model had an R^2 of 0.60 and a model weight of 0.47, meaning that it is 47% likely to be the best model for predicting mortality compared with the rest of the top models.

Base saturation and the base cations are all positively correlated. To know whether Mg was a significantly better predictor than Ca or K, we compared alternate models substituting the different base cation saturations into the top model. In the A horizon, Mg ($AIC_C = 58.4$) was significantly better than K ($AIC_C = 61.8$) or Ca ($AIC_C = 61.4$). Cation concentrations were not as good predictors as cation saturation in these models, but A horizon Mg was the best ($AIC_C = 61.9$) compared with K ($AIC_C = 66.1$) and Ca ($AIC_C = 66.5$). For the B horizon, models were not as good as for the A horizon, with AIC_C values of 62.2 or 63.8 (Mg), 66.9 or 64.7 (K), and 68.1 or 66.6 (Ca) for cation saturation or concentration, respectively.

DISCUSSION

Interacting Stresses and the Effects of Soil Chemistry on Mortality

Many of the variables included in our best models for predicting sugar maple mortality (Table 3) have been shown to be important to sugar maple health in other studies. Site microrelief, dry growing seasons during the years of the FTC outbreak, low temperatures, and defoliation by FTC were all determined to be important factors for predicting sugar maple condition in our stands by prior analyses (Wood et al., 2009). However, our results showed that when combined with these variables, soil base cation deficiencies play an important role in sugar maple health. Sugar maple mortality reflected an interaction between low base cations and defoliation events (Table 3; Fig. 6).

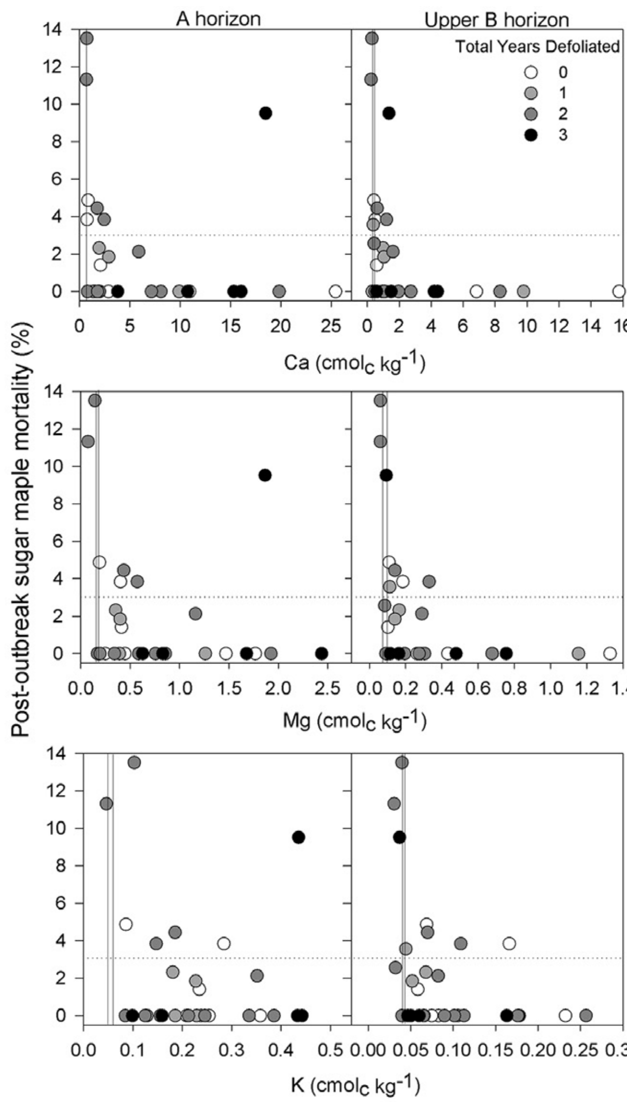

Fig. 5. Sugar maple mortality in Massachusetts, Vermont, and New York as a function of exchangeable soil cation concentrations in the A horizon (*n* = 29) and upper B horizon (*n* = 31). Shading of circles indicates the number of years each stand was defoliated during the forest tent caterpillar outbreak (2002–2007). The dotted line shows 3% mortality. The vertical lines are the upper and lower bounds of thresholds defined for all possible subsamples of *n* – 1 defoliated stands by removing each stand from the data set.

Table 3. The best six regression models for predicting sugar maple mortality (n = 31), listed in order of corrected Akaike's information criterion (AIC_C) from lowest (best) to highest. Model coefficients for variables included in the model are shown.

Variable	Model†					
	1 a	2 ab	3 b	4 bc	5 c	6 c
Intercept	3.3	5.0	5.5	5.1	7.4	2.5*
Site microrelief	2.9*	2.8*	2.9*	3.0*	2.8*	2.8*
Outbreak mean *Z*-index‡	−5.0*	−6.2*	−6.4*	−6.3*	−6.3*	−4.0*
Annual min. temperature	−1.1*	−1.1*	−1.1*	−1.0*	−1.1*	−1.0
2005 defoliation			−2.2	−2.0	−2.0	
2005 defoliation × A horizon Mg saturation	−0.26*					
2005 defoliation × A horizon effective base saturation		−0.03				
A horizon Ca saturation			−0.01			
A horizon Mg saturation				−0.1		
A horizon effective base saturation					−0.03	
Total defoliation × A horizon Mg saturation						−0.1
AIC_C	58.4	60.1	61.3	61.8	62.2	62.2
R^2	0.60	0.58	0.59	0.59	0.60	0.56
Difference in AIC_C (D_i)§	0	1.8	2.9	3.4	3.8	3.8
K (no. of model parameters)	4	4	5	4	5	5
Model weight (w_i)¶	0.47	0.19	0.11	0.09	0.07	0.07
Chi-square (P value)#	0.24	0.39	0.35	0.21	0.55	0.14

* Coefficients are significant at a = 0.05.

† Letters show which candidate models differ based on AIC_C.

‡ Palmer's Z-index for May–September for duration of forest tent caterpillar outbreak (2002–2007).

§ Models that differ by >2 in AIC_C (D_i) are statistically distinguishable.

¶ The weight of evidence in favor of the model.

\# H_0: Model residuals have constant variance (P > 0.05).

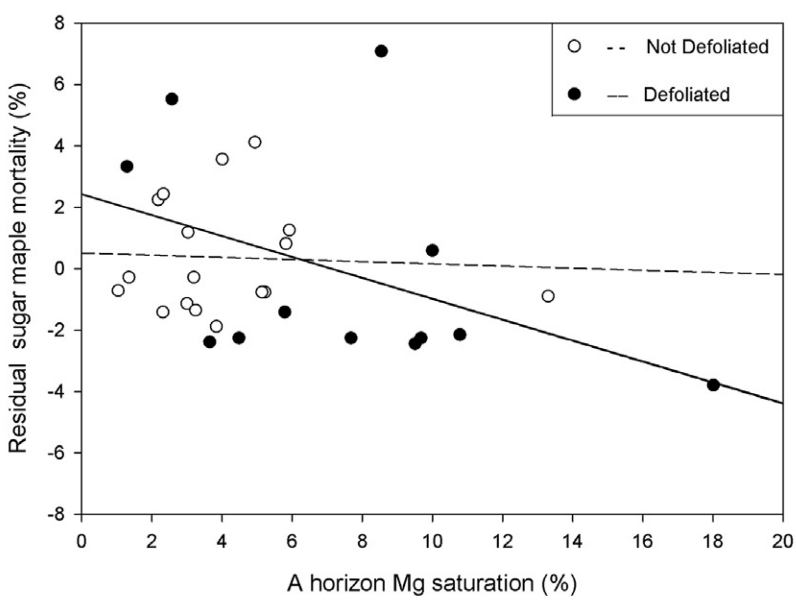

Fig. 6. Sugar maple mortality was more sensitive to Mg availability in stands defoliated in 2005 (solid regression line) than in stands not defoliated in 2005 (dashed regression line). The residual variation in mortality is that not accounted for by topography, drought, or temperature in the best regression model (Table 3).

Calcium, Mg, and K in the upper B horizon all correlated significantly with sugar maple mortality (Table 1). We sampled soil from the upper B horizon because, on the Allegheny Plateau, nutrient concentrations in sugar maple foliage correlated best with exchangeable base cation concentrations from the upper B horizon (Bailey et al., 2004). In that study, cation concentrations in the A horizon were poorly correlated with sugar maple foliar chemistry, and the upper B horizon was a more reliable indicator of sugar maple health than the lower B horizon (Bailey et al., 2004). However, our best models for predicting sugar maple mortality all included soil variables from the A horizon. Therefore, the A horizon should not be discounted during sampling and may be useful when investigating the relationship between sugar maple condition and soil base cation concentrations.

Our findings that high sugar maple mortality occurred on sites with low soil Ca and Mg (Fig. 5) are consistent with findings on the Allegheny Plateau (Horsley et al., 2000; Horsley et al., 2002; Hallett et al., 2006). Those studies observed mortality over a longer period of time and defined above-normal rates as >10%; we used annual mortality >3 or 4% as above normal. We report thresholds above which sugar maple can tolerate drought and defoliation stress that are somewhat higher than theirs for exchangeable Ca (0.3–0.5 vs. 0.2 $cmol_c$ kg^{-1}) and Mg (0.6–1.0 vs. 0.05 $cmol_c$ kg^{-1}) in the upper B horizon (Bailey et al., 2004). Unlike Bailey et al. (2004), we propose thresholds for soil base cation concentrations in the A horizon and for K concentrations (Fig. 5). The study in the Allegheny Plateau included many stands with lower base cation concentrations than our stands on glaciated soils in New York, southern Vermont, and western Massachusetts. Given the differences between that study and this, it is perhaps remarkable that the thresholds are in such good agreement.

We suggest that more attention be paid to exchangeable K in soils when investigating sugar maple condition. Low concentrations of K in foliage have been linked to sugar maple decline in Quebec and Vermont (Bernier et al., 1989; Wilmot et al., 1996), and the application of fertilizer with K was shown to decrease crown dieback and increase growth in sugar maple in these regions (Wilmot et al., 1996; Moore et al., 2000; Tripler et al., 2006). Most of the previous research relating K to sugar maple health has investigated K in foliage rather than soils. However, of the soil variables we measured, we found that K in the upper B horizons had the strongest correlation with sugar maple mortality, equivalent to correlations with Mg and Ca (Table 1). We suggest that exchangeable K in soils may contribute to sugar maple health. Magnesium was the most significant cation in our predictive models, but Ca was no better than K. To our knowledge, no threshold for adequate K in soils has been established. We propose a threshold for soil exchangeable K of 0.03 to 0.07 $cmol_c\ kg^{-1}$ (Fig. 5), below which sugar maple may be more susceptible to stress.

Sugar Maple Condition over Time

The average crown dieback of 8% across all stands in 2008 (2007 in Massachusetts; Table 2) is not a biologically significant improvement from the 10% reported by Wood et al. (2009) for sugar maple of all crown positions in 51 stands (45 of which we studied) in 2007. This amount of crown dieback is similar to levels reported for sugar maple in New York following an outbreak of pear thrips (*Taeniothrips inconsequens* Uzel) in 1988 (Allen et al., 1995). Following an earlier FTC outbreak, Wink and Allen (2007) reported a greater rate of improvement in crown condition in 14 unmanaged stands within our study area: crown dieback in trees of upper crown positions decreased by 6% in two years (1991–1993). In Ontario, Gross (1991) found that defoliated sugar maples of upper crown positions had similar crown dieback in 1978 and 1979 following the FTC outbreak that peaked in 1976 or 1977.

It is not possible to determine an exact threshold for crown dieback that would lead to tree mortality because so many factors influence tree resilience to this stress. Our results (Fig. 4) are consistent with those from earlier FTC outbreaks, in which most trees with crown dieback above 40% died within two years (Gross, 1991) and had a high probability of dying within 10 years when dieback was severe (>50%) following defoliation (Gross, 1991; Allen et al., 1995). The 0% survival probability within one year for trees with dieback >70% (Fig. 4) is a lower survival probability than the reported 33% for sugar maple with crown dieback ≥75% over a 4-yr span (1990–1993) in Quebec (Roy et al., 2006). Our study was limited to two years; longer term data could improve predictions of sugar maple mortality (Tominaga et al., 2008).

It was surprising that the best defoliation variable in our predictive models was defoliation in 2005, as defoliation in 2006 was more extensive (Wood et al., 2009). We measured mortality between 2007 and 2008 in New York and Vermont (between 2006 and 2007 in Massachusetts, where defoliation peaked earlier). It can take time for inciting factors to cause mortality, even when combined with predisposing conditions. Thus it is possible that defoliation in 2006 would be the best predictor of subsequent mortality.

Implications for Forest Management

We studied a variety of sugar maple stands across several different soil types and geographic locations that suffered different durations and intensities of defoliation during the recent (2002–2007) FTC outbreak. This allowed us to investigate soil chemistry variables that may be affecting sugar maple condition at a broader scale than most previous studies on this topic. This makes our findings applicable to a variety of stakeholders in the region.

Most stands with high sugar maple mortality occurred on soils low in Ca and Mg in both the A and upper B horizons. Base cation concentrations in soils can be a good indicator of how sugar maple is likely to respond to heavy defoliation. Fertilization could be a treatment for stands susceptible to decline (St. Clair et al., 2008). The addition of $CaCO_3$ or dolomitic limestone $[CaMg(CO_3)_2]$ has improved crown condition and increased radial growth in sugar maple (Wilmot et al., 1996; Long et al., 1997; Moore et al., 2000; Moore and Ouimet, 2006). Fertilization with K has been shown to improve crown condition, increase growth (Wilmot et al., 1996; Moore et al., 2000), and increase foliar K in sugar maple (Lea et al., 1980).

Managers can also utilize our dieback results to better prepare for salvage cuts. We suggest that trees with crown dieback >70% are very likely to die, with death most likely occurring within 1 yr. However, trees with less dieback are not immune to mortality, as half of the trees that died during this study had <50% dieback the previous year. When dieback exceeds 50%, trees have a high probability of dying within a decade (Gross, 1991; Allen et al., 1992). Managers could prioritize salvaging trees with >70% crown dieback, while paying close attention to trees with >50% dieback.

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