Influence of nutrition and stress on sugar maple at a regional scale

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Abstract: Sugar maple (*Acer saccharum* Marsh.) decline disease on the Allegheny Plateau (region 1) resulted in high levels of mortality during the 1990s. Sugar maple was predisposed to decline because of an imbalance in Mg, Ca, and Mn nutrition and incited to decline by repeated defoliation. We sampled 33 stands in New York, Vermont, and New Hampshire (region 2) to determine if this model of sugar maple decline applies to a broader region. Low Ca and Mg and higher Mn levels were correlated with poorer tree health in both regions, but region 2 stands had little defoliation and few dead trees, suggesting that both unbalanced nutrition and stress are required for mortality to occur. We predict that stands with low foliar Ca and Mg and high Mn levels would incur increased mortality if stressed. In region 2, relationships between Ca, Mg, and Mn levels and dieback suggested that impacts on sugar maple may be caused by nutritional imbalance alone. Partial correlation analysis suggests that antagonism between Mg and Mn is the most important nutritional factor in region 1, while Mn supply is most important in region 2. We suggest that more research is needed on the interacting roles played by Ca, Mg, Al, and Mn in sugar maple performance.

Résumé : Le dépérissement de l'érable à sucre (*Acer saccharum* Marsh.) sur le plateau des Appalaches (région 1) a causé beaucoup de mortalité durant les années 1990. L'érable à sucre était prédisposé au dépérissement à cause d'un déséquilibre nutritionnel impliquant Mg, Ca et Mn et le dépérissement a été déclenché par des défoliations répétées. Dans cette étude, nous avons échantillonné 33 peuplements dans les États de New York, du Vermont et du New Hampshire (région 2) pour déterminer si ce modèle de dépérissement de l'érable à sucre pouvait être appliqué à une région plus vaste. Une concentration faible de Ca et de Mg et élevée de Mn était corrélée avec le mauvais état de santé des arbres dans les deux régions mais il y avait peu de défoliation et d'arbres morts dans les peuplements de la région 2, ce qui indique que le déséquilibre nutritionnel et le stress sont tous les deux nécessaires pour qu'il y ait de la mortalité. Nous prédisons que la mortalité augmentera dans les peuplements dont la concentration foliaire de Ca et Mg est faible et celle de Mn est élevée s'ils subissent un stress. Dans la région 2, les relations entre Ca, Mg et Mn et le dépérissement indiquaient que les impacts sur l'érable à sucre pourraient être causés par le déséquilibre nutritionnel seul. L'analyse de corrélation partielle indique que l'antagonisme entre Mg et Mn est le facteur nutritionnel le plus important dans la région 1 tandis que l'apport de Mn est plus important dans la région 2. Nous croyons qu'il faudrait plus de recherches sur les interactions entre Ca, Mg, Al et Mn et sur leur rôle dans la performance de l'érable à sucre.

[Traduit par la Rédaction]

Introduction

Decline diseases of trees are thought to be the result of interactions among abiotic and biotic factors, in contrast to tree dieback or mortality events that are attributable to single abiotic or biotic factors (Manion and Lachance 1992). Declines are ephemeral events that typically result in a gradual loss in tree vigor, which often ends in tree mortality. Manion (1991) defined decline as "an interaction of interchangeable, specifically ordered abiotic and biotic factors to produce a gradual general deterioration, often ending in death of trees". Manion categorized these factors as predisposing, inciting (or triggering), and contributing, to describe the way each factor might participate in the tree-decline process.

Houston (1992) developed a similar concept of tree decline from studies on Wisconsin sugar maple (*Acer saccharum* Marsh.) blight during the late 1950s and subsequent physiological and biochemical studies (Houston 1999). Houston (1992) proposed that "disease manifestation (progressive crown dieback sometimes leading to continued tree decline and death) results when one or more predisposing (*sensu stricto*) stress factors reduces resistance to invasion by opportunistic, secondary-action organisms that result in death of tissues — sometimes of trees". The scientific team investigating the Wisconsin sugar maple blight episode documented the decline scenario as 10 months of drought (Skilling 1964) followed closely by a complex of three insect species (the leaf rollers *Sparganothus acerivorana* and *Acleris chalybeana* and the maple webworm, *Tetralopha asperatella*) defoliating the trees at different times of the

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growing season (Giese et al. 1964), and finally attack by the opportunistic fungus *Armillaria mellea* (Houston and Kuntz 1964). Defoliation and mortality occurred for 2 years, then began to subside with the collapse of the defoliator population. Houston's (1992) model suggests that drought and defoliation stress predisposed trees to decline by altering the resistance of sugar maple tissue to invasion by *Armillaria* spp., which subsequently triggered decline. Houston and others subsequently clarified that stress from an abiotic factor such as drought and a biotic factor such as defoliation lowered tree resistance by altering carbohydrate, nitrogen, and phenolic defense chemistry, making root tissue susceptible to invasion by *Armillaria* spp. (Houston 1992).

More recently, well-documented episodes of sugar maple decline occurred in Massachusetts in the 1960s (Mader and Thompson 1969), in Ontario in the 1970s (Hendershot and Jones 1989; Gross 1991), in Quebec, New York, and Vermont in the 1980s (Bernier and Brazeau 1988; Kelley 1988; Allen et al. 1992*b*; Ouimet and Camiré 1995), and in Pennsylvania in the 1980s and 1990s (Kolb and McCormick 1993; Long et al. 1997; Horsley et al. 2000). Decline events were usually characterized by a loss of crown vigor, including increased foliage transparency, fine-twig dieback, and loss of major branches, and by increased whole-tree mortality.

Stress events including defoliations, droughts, and extreme weather events (late spring frosts, midwinter thaw/freeze cycles) were common themes in all of these declines. However, foliage and soil sampling in the more recent sugar maple declines suggests that deficiency of the base cations Ca, Mg, and K and (or) excesses of the potentially toxic cations Al and Mn may have been a predisposing factor in sugar maple decline (Bernier and Brazeau 1988; Côté et al. 1995; Wilmot et al. 1995).

The goal in our initial work was to develop a broadly applicable working hypothesis to account for sugar maple decline by studying correlations among factors in stands containing sugar maple on the Allegheny Plateau of western Pennsylvania and New York in a spatially explicit way (Horsley et al. 2000; Wargo et al. 2002; Bailey et al. 2004). We found that sugar maple decline, measured as percent dead sugar maple basal area (PDEADSM), was associated with low foliar and soil concentrations of the base cations Mg and Ca, a high foliar concentration of the antagonistic cation Mn, and high levels of insect defoliation stress. More specifically, sugar maple decline was associated with foliar Mg, Ca, and Mn concentrations of <700, <5500, and >1900 mg·kg^{-1}, respectively, and two or more moderate to severe insect defoliations during the 10 years prior to evaluation of tree health (defoliation severity index (DSI 10) = 4; Horsley et al. 2000). Mg was a better predictor of decline than Ca or Mn; when Mg was used as the predictor of tree health, only one misclassification occurred among the 43 stands evaluated — a thinned stand where trees in poor health had probably been removed. The rate of misclassification was higher when Ca or Mn, or a molar ratio of Mg or Ca to Mn or Al, was used as the predictor. When the foliar Mg concentration was <700 mg·kg^{-1} and DSI 10 was ≥4, sugar maple stands contained >21 PDEADSM and were termed unhealthy. In contrast, when the Mg concentration was ≥700 mg·kg^{-1}, stands remained healthy (≤11 PDEADSM), regardless of defoliation history (DSI 10 = 0–8). There was a strong positive relationship between foliar chemistry and exchangeable Ca and Mg in B-horizon soil and a negative relationship with exchangeable Al (Bailey et al. 2004). In addition, Marcais and Wargo (2000) found that although liming increased the aggressiveness of *Armillaria calvescens*, the major *Armillaria* species on sugar maple, there were no increases in infection, presumably because of the increase in overall vigor of the limed trees. We concluded that sugar maple decline in western Pennsylvania and New York fit the decline-disease hypothesis of Manion (1991) and Houston (1992): sugar maple is predisposed to decline by an imbalance in Mg, Ca, Al, and Mn concentrations and incited to decline by excessive defoliation stress.

Despite this evidence, some have concluded that insect defoliation or other stress events are not required for sugar maple decline to occur, but that an imbalance in base cation nutrition is sufficient to cause decline. "In order to conclude that insect defoliations are important in the observed decline of sugar maple, the no-insect defoliation and low Ca-to-Al ratio case also needs to be evaluated" (Sharpe 2002).

In this study, we contrast data from western Pennsylvania and New York (region 1) with stands in adjacent areas of central New York, Vermont, and New Hampshire (region 2) where trees have not been defoliated for 20 or more years and have a range of base cation nutrition similar to that of trees in western Pennsylvania and New York. Our goal was to (*i*) determine whether nutritional imbalances similar to those identified on the Allegheny Plateau occur in region 2, and (*ii*) answer the question Is low foliar base cation status sufficient to cause sugar maple decline?

Materials and methods

Study sites

In addition to the 43 stands in region 1 studied in 1995 and 1996 (Horsley et al. 2000), 33 additional stands in region 2 were studied; 11 stands were installed in 1996 and 23 in 1997. Stands were chosen to include a broad range of soil types and elevations containing mature stands of sugar maple (Fig. 1). The study sites represented the major soil orders on which sugar maple is found in the northeastern United States (Spodosols, Inceptisols, Alfisols, and Ultisols). The lithologic composition of bedrock and soil parent materials included granite, syenite, schist, phyllite, quartzite, amphibolite, marble, dolostone, sandstone, and shale. Elevation ranged from 71 to 885 m a.s.l. (Table 1). Note that our goal was not to select stands to be proportional to the importance of sugar maple in certain states, but to span the nutritional range experienced by sugar maple in the northeastern United States. Taking regions 1 and 2 together, the range of soils on which sugar maple health was evaluated is broader than in any previous study. In the present study, foliage chemistry was used as a bioassay of site nutritional quality because of its ability to integrate horizontal and vertical differences in soil nutrition within stands (Armson 1973; Leaf 1973; Morrison 1985). Bailey et al. (2004) show that 76% of the variation in foliar Ca and 69% of the variation in foliar Mg can

Fig. 1. Locations of study sites in the northeastern United States, showing stands in region 1 (▲; reported in Horsley et al. 2000) and region 2 (●).

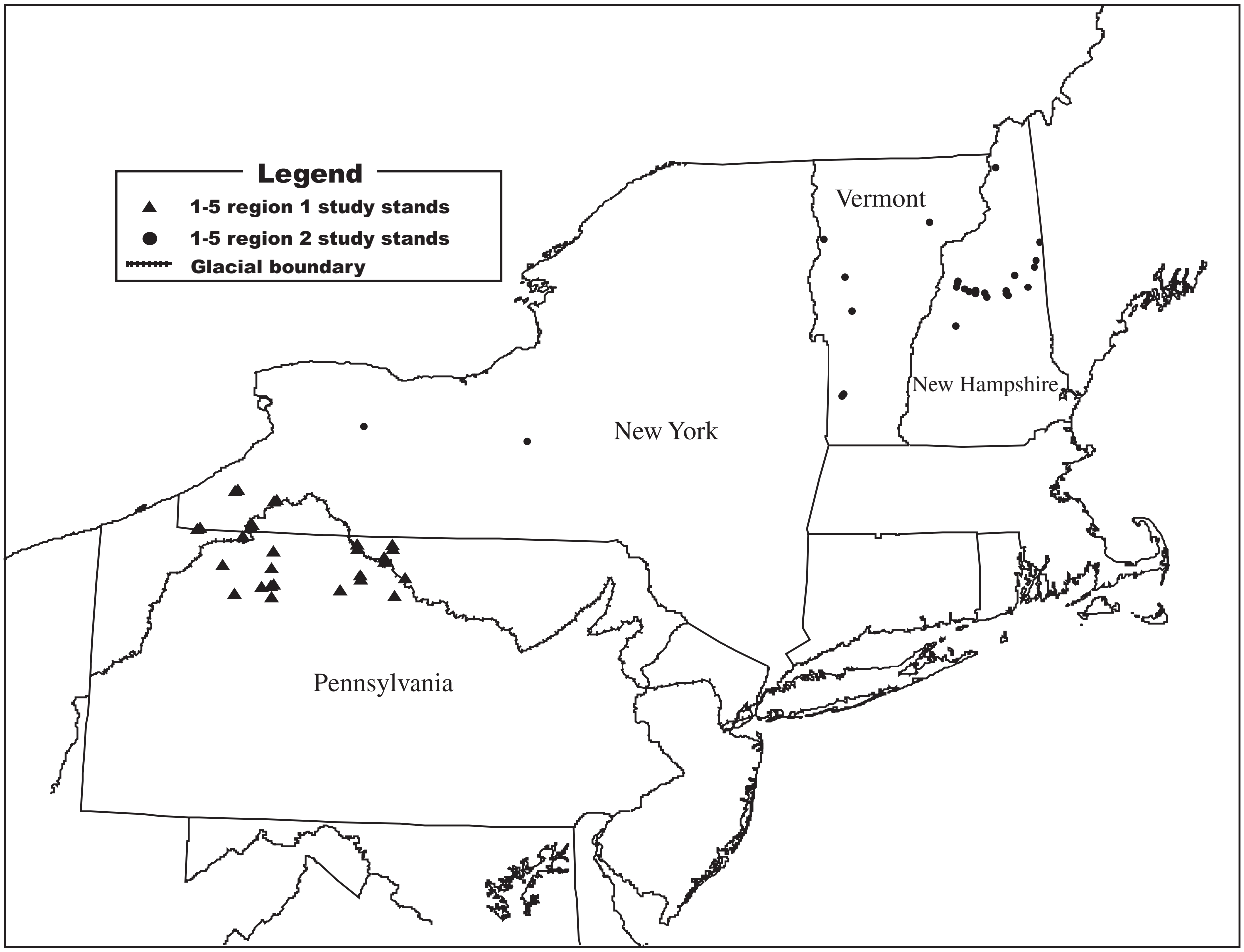


Table 1. Stand characteristics and sugar maple foliar nutrition (mg·kg dry mass^{-1}) in regions 1 and 2.

	Region 1 (n = 43)			Region 2 (n = 33)	
Variable	Mean	Range	p	Mean	Range
Stand characteristic					
Basal area (m^{2}·ha^{-1})	30 (0.97)	15–45	**0.01**	34 (1.00)	24–47
Percent sugar maple basal area	59 (0.03)	23–95	0.10	67 (0.04)	25–99
Elevation (m a.s.l.)	570 (12)	386–767	0.07	511 (30.00)	71–885
DSI 10	2.7 (0.4)	0–8	**<0.001**	0.06 (0.06)	0–2
Foliar nutrition					
Calcium concn. (mg·kg^{-1})	8062 (519)	3146–17399	0.16	9539 (894)	3161–24106
Magnesium concn. (mg·kg^{-1})	1100 (52)	499–1781	0.37	1200 (100)	457–2867
Manganese concn. (mg·kg^{-1})	1686 (112)	718–3738	**<0.001**	1011 (115)	179–3113
Phosphorus concn. (mg·kg^{-1})	1314 (41)	953–2073	0.54	1357 (59)	926–2448
Potassium concn. (mg·kg^{-1})	7993 (185)	5693–11154	0.87	8046 (280)	5187–11420
Ca:Mn molar ratio	9 (1)	2–27	**0.004**	25-(5)	2–103
Mg:Mn molar ratio	2 (0.2)	0.4-4	**0.005**	5 (1)	0.5–26

Note: Values are regional means (with standard error of the mean in parentheses) and ranges. The p values are for between-region comparisons (t tests); values in boldface type denote significant differences between regions at $p < 0.05$. "DSI 10" is the defoliation severity index, which defines the number and severity of defoliations during the previous decade.

be explained by soil properties emphasizing the chemistry of the B horizon (Leaf 1973; Morrison 1985; Bailey et al. 2004).

Evaluation of stand health

Stand health was evaluated in mid to late July in 1996 and 1997 (region 1) or 1998 and 1999 (region 2) using North American Maple Project protocols (Cooke et al. 1996), following the modifications made by Horsley et al. (2000). Note that no stands that were impacted by the January 1998 ice storm were included in this study. Within each stand, three 400 m^2 circular plots were established to evaluate stand and site characteristics. Within each of the three 400 m^2 circular plots, all standing live and dead trees ≥10 cm in diameter at a height of 1.4 m (diameter at breast height (DBH)) were evaluated by species, DBH, and crown class (dominant, codominant, intermediate, suppressed).

We used three variables that integrate sugar maple health over varying lengths of time: percent dead sugar maple basal area (PDEADSM), crown-vigor index (SMVIG), and percent fine-twig dieback (PSMDIE). PDEADSM integrates tree health over a relatively long period of time. Dead trees were included as long as they were standing and had a measurable DBH (1.4 m). The measure may not be useful for distinguishing stands in which sugar maple is healthy or declining during the early stages of decline where minimal tree mortality has occurred. However, where enough time has elapsed for dead trees to accumulate, PDEADSM is a discriminating measure; in our work it had the highest *F* value in a cluster analysis to determine healthy and unhealthy stands in region 1 (Horsley et al. 2000). SMVIG integrates crown health over a relatively long period of time. The measure includes dead trees and, depending upon the stage of decline, may include trees with crowns that are continuing to deteriorate, as well as those that are recovering or have recovered. PSMDIE integrates health over a somewhat shorter period of time. The measure includes only living trees and integrates health conditions as long as fine twigs (<2.5 cm diameter) remain attached and visible (2–5 years). Consequently, PSMDIE is a useful indicator of incipient decline, but is of lesser value where dead trees are abundant and recovering live trees have few visible dead fine twigs. Measures of health were estimated for each tree.

PDEADSM was calculated as the proportion of the total stand basal area of sugar maple that is dead (SMVIG = 5).

SMVIG increases as crown health decreases. Values were estimated according to Cooke et al. (1996): 1, healthy (no major branch mortality); 2, light decline (10%–25% of the crown damaged); 3, moderate decline (26%–50% of the crown damaged); 4, severe decline (>50% of the crown damaged); 5, dead.

SMVIG ratings are a proven repeatable measurement in the North American Maple Project. When different rating teams are used, QA/QC data have shown that SMVIG estimates are repeatable for >75% of trees (C. Barnett, USDA Forest Servce, unpublished data).

For PSMDIE, dead branches are <2.5 cm diameter with mortality beginning at the terminal portion of the limb and progressing inward, and the value was estimated for each tree using a 12-class system (Cooke et al. 1996). Dieback estimates were repeatable within ±1 class for >95% of the trees (Burkman et al. 1991; Allen et al. 1995).

To characterize overall sugar maple health for each stand, these tree health parameters were aggregated for each stand (all three plots, sugar maple only) as the mean of all classes.

Stand-disturbance and -defoliation histories

In both regions, disturbances caused by stand-management activities and defoliation were determined for each stand. Two primary sources of information were used: (1) GIS databases consisting of annual layers of digitized defoliation sketch maps were acquired from the Pennsylvania Bureau of Forestry, Middletown, and the USDA Forest Service, State and Private Forestry, in Morgantown, West Virginia, and Durham, New Hampshire, and (2) land managers were contacted for information on management activities and defoliation stress for each stand. From this information, DSI 10, which combines the number and severity of defoliations over the 10- year period prior to evaluation of overstory health, was calculated by summing severity values (1 = light (<30% defoliation); 2, moderate (30%–60% defoliation); 3, heavy (>60% defoliation)). For example, in the 10-year period prior to health evaluation, a stand with moderate defoliation in year 4, heavy defoliation in year 5, and no defoliation in the remaining 8 years would be assigned a DSI 10 value of 5.

Foliage sampling and analysis

In each stand, foliage was sampled from three to six presumably healthy (North American Maple Project vigor class 1, ≤10% crown dieback) dominant or codominant sugar maples at least 25 cm DBH between 1995 and 1997 and values were averaged to create a stand mean. For all stands in the study, mean coefficients of variation for Ca, Mg, and Mn concentrations ranged from 21% to 27%. A mid-crown sample of healthy sun-exposed leaves was obtained from each tree during the last 2 weeks of August in the year the plot was established. The sample was collected by shooting small branches from the periphery of the crown with a shotgun. Foliage samples were ground and oven-dried at 70 °C. Dried and ground foliage was digested using a microwave-assisted acid digestion procedure (EPA Method 3052, 1996) and analyzed for Al, P, K, Ca, Mg, and Mn by inductively coupled plasma spectroscopy. National Institute of Standards and Technology pine needles were used as a reference standard. Percent recovery for certifiable elements (Vogt et al. 1987) ranged from 90% for Al to 108% for Ca. Repeatability of determinations for both standards and duplicate samples, expressed as the percent relative difference (maximum value minus minimum value expressed as a percentage of the mean) was typically <3%. Similarly, the percent relative difference for duplicate samples was 6%. Total Kjeldahl N was determined with a Lachat autoanalyzer as detailed by Horsley et al. (2000). For data analysis, foliar chemistry was expressed as concentration ($mg \cdot kg$ dry $mass^{-1}$). Foliar N and Al were not included in the statistical analyses because of high interannual variability (Horsley et al. 2000).

Statistical methods

Differences in foliar chemistry between regions were assessed using an independent *t* test. Pearson's correlation coefficients (r) with Bonferroni-adjusted probabilities were used to measure the strength of association between foliar element concentrations and the health measures used in this study. Partial correlation analysis was conducted on only those elements that had statistically significant Pearson's correlation coefficients ($\alpha \leq 0.05$) with health measures in both regions. Partial correlation analysis was conducted because the foliar elements with the strongest relationship to health (Ca, Mg, Mn) were highly correlated with each other (Ca, Mg: $r = 0.86$; Ca, Mn: $r = -0.51$; Mg, Mn: $r = -0.55$). This allowed us to examine correlations between health variables and foliar element concentrations without the confounding effects of the strong correlations between the foliar elements themselves. Analysis of variance was used to test for differences among the four categories of foliar concentration × defoliation stress (DSI 10) in region 1 — (1) high concentration, low stress; (2) high concentration, high stress; (3) low concentration low stress; and (4) low concentration, high stress — and the two foliar concentrations at low defoliation stress in region 2 (the same as categories 1 and 3 in region 1). Single degree of freedom polynomial contrasts were used to separate the means of categories 4 vs. 1, 2, and 3; the mean of categories 1 vs. 2, and the mean of categories 1 vs. 3 in region 1. Thresholds of high versus low foliar concentration and high versus low defoliation stress were those empirically determined for region 1 by Horsley et al. (2000): Mg: 700 $\text{mg}\cdot\text{kg}^{-1}$; Ca, 5500 $\text{mg}\cdot\text{kg}^{-1}$; Mn, 1900 $\text{mg}\cdot\text{kg}^{-1}$; DSI 10 = 4. An α value of 0.05 was the nominal indicator of statistical significance for all tests. Statistical tests were conducted using SYSTAT® version 10.2 (Wilkinson 2002).

Results

Stand characteristics

Study stands were relatively mature northern hardwoods. Mean basal area was 32 $\text{m}^2\cdot\text{ha}^{-1}$ for all study stands regionwide and region 2 had a slightly higher mean basal area than region 1 (Table 1). PDEADSM ranged from 23% to 99% of total stand basal area and values were similar within each region (Tables 1 and 2,). In addition to sugar maple, species that commonly occurred in the study stands included black cherry (*Prunus serotina* Ehrh.) and white ash (*Fraxinus americana* L.) in region 1 and American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Britt.) in region 2 (Table 2). The range of elevations at which sugar maple stands were located was marginally greater (both higher and lower) in region 2 than in region 1 (Table 1). The incidence of defoliation was significantly greater in region 1 than in region 2. Over the past decade the stands in region 1were defoliated an average of 2.7 times versus an average of 0.06 defoliations for the stands in region 2 (Table 1). Of the region 2 stands sampled, 1 stand was defoliated once in the past decade, 1 stand was defoliated once in the past two decades, and 11 stands were defoliated once or twice in the past 30 years. None of the stands in region 2 approached the number and severity of defoliations associated with declining stands in region 1.

Table 2. Number of stands containing each species and average percent basal area of each species by region.

	Region 1		Region 2	
	No. of stands	Percent basal area	No. of stands	Percent basal area
Sugar maple	43	59	33	67
American beech	34	4	27	14
Black cherry	35	19	2	3
Basswood	17	9	0	0
Eastern hemlock	13	8	6	1
Paper birch	0	0	3	2
Red maple	24	7	9	16
White ash	22	15	14	12
Yellow birch	20	3	23	10

Foliar nutrients

The mean and range for all nutrients were similar in regions 1 and 2 (Table 1). There were no significant differences between the regions except that foliar Mn concentration and the molar ratios of Ca and Mg with Mn were higher in region 1.

Sugar maple health

PDEADSM ranged from 0 to 56 in region 1 and fell between 0 and 15 in region 2. SMVIG values ranged from 1 to 3.7 for all study plots. PSMDIE values were between 3.8 and 17.7 regionwide.

Correlations between foliar nutrients and health

Region 1

Correlations between health measures and concentrations of foliar nutrients in region 1 stands are listed in Table 3. Ca and Mg showed a strong relationship with tree health as indicated by the relatively high negative correlations with PDEADSM, SMVIG, and PSMDIE. Manganese had a relatively high positive correlation with PDEADSM and SMVIG; the relationship with PSMDIE was marginal. P and K were not related to any of the health measures.

Region 2

PDEADSM was not significantly related to concentrations of any of the foliar elements measured (Table 3). However, Ca and Mg were negatively correlated with SMVIG and PSMDIE. Mn showed a strong positive correlation with PSMDIE. Again, P and K were unrelated to health measures.

Foliar nutrient ratios in regions 1 and 2

Correlations of Ca:Mn and Mg:Mn molar ratios with health variables were generally weaker than those for Ca, Mg, and Mn alone. In region 1, the Ca:Mn molar ratio was marginally correlated with PDEADSM and SMVIG; the Mg:Mn molar ratio was correlated with all health variables. In region 2 the Ca:Mn molar ratio was correlated with SMVIG and marginally correlated with PSMDIE; the Mg:Mn molar ratio was marginally correlated with SMVIG.

Foliar nutrient thresholds

In region 1, all declining (>21 PDEADSM) stands exhibited one or more of the following conditions: foliar Mg concentration below 700 mg·kg^{-1}, Ca concentration below 5500 mg·kg^{-1}, and foliar Mn concentration above 1900 mg·kg^{-1}. In addition, Ca, Mg, and Mn concentrations were all significantly correlated with PDEADSM in region 1. In region 2, 7 stands fell below this empirical threshold for Mg, 4 stands had Mn concentrations greater than the threshold, and 11 stands had Ca concentrations below the empirical threshold (Fig. 2).

The graphs of Mg and Ca concentrations (Fig. 3) versus SMVIG show that all region 2 stands with sugar maple SMVIG >2 fell near or below thresholds determined by Horsley et al. (2000). In region 1, all stands with high PDEADSM had >1900 mg·kg^{-1} foliar Mn. However, despite the imbalance in foliar Ca, Mg, and Mn status in many region 2 stands, mortality levels were not elevated (Fig. 4).

Partial correlations

Because of covariance of foliar Ca, Mg, and Mn concentrations, a partial correlation analysis was conducted to evaluate the relative importance of foliar elements to each health variable (Table 4). In region 1, partial correlation analysis suggests that Mg and Mn have similar importance to PDEADSM and SMVIG, but in opposite directions, suggesting an antagonistic relationship. For PSMDIE, Mg alone has high relative importance. With covariance among foliar elements removed, Ca has low relative importance to all health measures for region 1. In the region 2 stands, Ca and Mg had the strongest relationships with SMVIG; Mn had the highest partial correlation with PSMDIE.

Nutrition and stress interactions

Stands were categorized by their relative Ca, Mg, and Mn nutritional level and defoliation stress levels to examine the interaction between foliar nutrient status and stress within each region (Figs. 4–6). Figure 4 shows the interaction of Ca concentration with stress. In region 1, increases in PDEADSM (p < 0.001), SMVIG (poorer crown condition; p < 0.001), and PSMDIE (p < 0.001) occurred only when foliar Ca was low and stress was high. In region 2 stands, where stress levels were low, the level of Ca nutrition was not correlated with PDEADSM or SMVIG. However, there was a small (3%) but significant (p = 0.018) difference in PSMDIE when foliar Ca was low.

Figure 5 shows the interaction of Mg concentration with defoliation stress. In region 1, results for Mg were similar to those for Ca (PDEADSM: p < 0.001; SMVIG: p < 0.001; PSMDIE: p < 0.001). Again, in region 2 foliar Mg status was unrelated to PDEADSM when stress was low. However, crown health was poorer, as evaluated by SMVIG (0.6, p = 0.001) and PSMDIE (4%, p = 0.001), when foliar Mg was low.

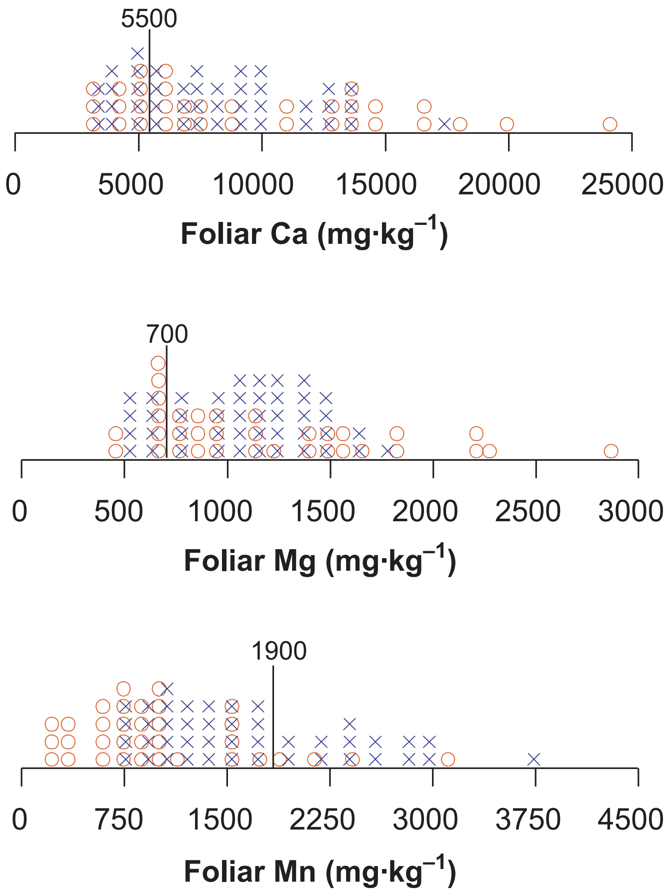
Figure 6 shows the interaction of Mn concentration with defoliation stress. In region 1, high PDEADSM (p < 0.001), SMVIG (p < 0.001), and PSMDIE (p < 0.001) occurred only when both foliar Mn concentration and stress were high. In region 2, high foliar Mn concentration was correlated with a small (6%) but significant (p < 0.001) increase in PSMDIE.

Table 3. Pearson's correlation coefficients (Bonferroni p values) between foliar element concentrations and health variables for sugar maple stands in regions 1 and 2.

Health variable	Ca concn.	Mg concn.	Mn concn.	P concn.	K concn.	Ca:Mn molar ratio	Mg:Mn molar ratio
Region 1							
Dead sugar maple basal area (%)	**−0.46 (0.044**	**−0.62 (<0.001)**	**0.57 (0.001)**	−0.33 (0.667)	0.04 (1.000)	−0.45 (0.057)	**−0.52 (0.008)**
Crown-vigor index	**−0.48 (0.023)**	**−0.61 (<0.001)**	**0.55 (0.003)**	−0.36 (0.392)	0.07 (1.000)	−0.45 (0.056)	**−0.51 (0.011)**
Fine-twig dieback (%)	**−0.45 (0.047)**	**−0.54 (0.004)**	0.43 (0.080	−0.36 (0.406)	0.19 (1.000)	−0.40 (0.185)	**−0.46 (0.044)**
Region 2							
Dead sugar maple basal area (%)	−0.14 (1.000)	−0.20 (1.000)	0.19 (1.000)	0.09 (1.000)	0.16 (1.000)	−0.26 (1.000)	−0.25 (1.000)
Crown-vigor index	**−0.58 (0.009)**	**−0.58 (0.008)**	0.32 (1.000)	−0.11 (1.000)	0.34 (1.000)	**−0.52 (0.036)**	−0.49 (0.077)
Fine-twig dieback (%)	**−0.56 (0.014)**	**−0.60 (0.004)**	**0.65 (0.001)**	0.11 (1.000)	0.11 (1.000)	−0.49 (0.085)	−0.48 (0.102)

Note: Values in boldface type denote significant correlations at p < 0.05.

Fig. 2. Histograms showing the number of stands in region 1 (×) and region 2 (○) that fall below the empirical foliar Ca and Mg thresholds and above the empirical foliar Mn threshold for health, using percent dead sugar maple basal area (PDEADSM) as the measure of health.



Discussion

The present work expands the geographic range considered by Horsley et al. (2000) to gain insight into sugar maple health over a broader regional scale and to understand the role of nutrition in sugar maple health in the absence of defoliation stress. Because stands were selected to represent a broad range of soil and site types where sugar maple occurs, the information presented here is broadly applicable to sugar maple in the northeastern United States.

The goals of this study were to (*i*) determine whether nutritional imbalances similar to those identified on the Allegheny Plateau (region 1) occur in region 2 as well, and (*ii*) answer the question: Is imbalance in base cation nutrition alone sufficient to cause sugar maple decline? Our findings show that region 2 stands had foliar nutritional imbalances similar to those observed in region 1 as demonstrated by low Ca and Mg and high Mn concentrations (Fig. 2). The major difference between regions 1 and 2 was the high stress levels at some sites in region 1 caused by repeated insect defoliation.

In region 1, foliar nutritional imbalances coupled with excessive defoliation led to increased sugar maple mortality

Fig. 3. Foliar element concentrations versus sugar maple crown vigor index as the measure of health (1 = healthy (no major branch mortality); 2 = light decline (10%– 25% of the crown damaged); 3 = moderate decline (26%–50% of the crown damaged); 4 = severe decline (>50% of the crown damaged)), showing stands in region 1 that are considered to be declining (percent dead sugar maple basal area >21%) as defined by Horsley et al. (2000) (▲), healthy stands in region 1 (△), and stands in region 2 (○). The vertical lines represent empirical foliar element thresholds representing the best fit of data (Horsley et al. 2000). For Ca and Mg, all declining stands (▲) had foliar chemistry values that were less than the empirical thresholds. For Mn, all declining stands (▲) had foliar chemistry values that were greater than the empirical threshold.

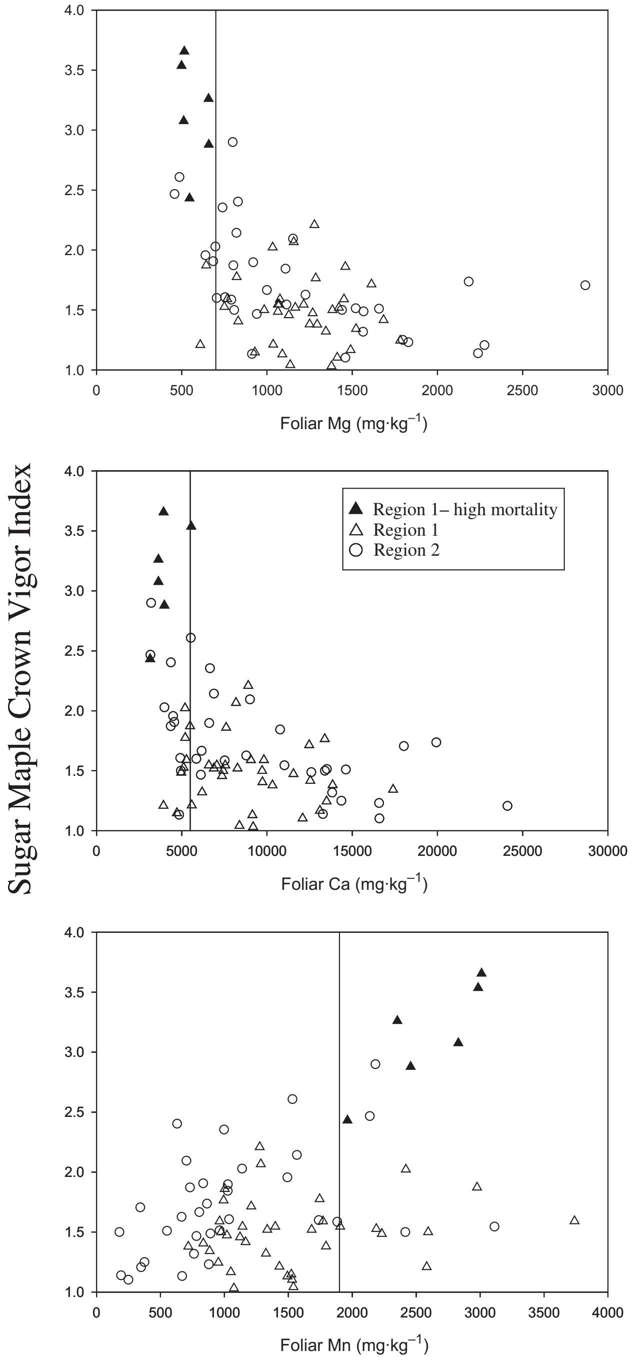


Table 4. Partial correlation coefficients for each health variable versus foliar Ca, Mg, and Mn concentrations for sugar maple stands.

Health variable	Ca concn.	Mg concn.	Mn concn.
Region 1			
Dead sugar maple basal area (%)	0.10	–0.35	0.25
Crown-vigor index	0.02	–0.31	0.20
Fine-twig dieback (%)	–0.05	–0.26	0.07
Region 2			
Crown-vigor index	–0.15	–0.15	0.02
Fine-twig dieback (%)	–0.13	–0.08	0.49

(PDEADSM). In region 2, where defoliation stress was absent, slightly poorer crown health (SMVIG, PSMDIE) was found in stands with imbalanced Ca, Mg, and Mn nutrition but did not result in increased sugar maple mortality. Stands with low Ca or Mg and high Mn concentrations and low defoliation-stress levels in region 1 did not have poorer crown health as in region 2. In region 1, all stands with imbalance in nutrition and low stress levels were defoliated once in the preceding 10 years. Some fine-twig dieback may have occurred for a few years following defoliation. However, there is an abundance of evidence that once stress, e.g., insect defoliation, abates, crown vigor and growth of surviving trees improve, often returning to predecline levels (Giese et al. 1964; Houston and Kuntz 1964; Hendershot and Jones 1989; Gross 1991; Allen et al. 1992*a*; Houston 1992; Payette et al. 1996; Long et al. 1999). By the time of our crown-health evaluations, many of the dead twigs had fallen from the trees and were no longer observable. Thus, as pointed out earlier, PSMDIE may not reflect stand health as well as PDEADSM or SMVIG does in situations where decline has been occurring for a long period of time and both recovering and dying trees may be present. Overall, we conclude that imbalance in Ca, Mg, and Mn nutrition alone is not sufficient to increase sugar maple mortality; an inciting stress factor also is required.

However, imbalance in Ca, Mg, and Mn nutrition in the absence of defoliation stress is sufficient to cause a decrease in stand health. This suggests that many stands on sites with low Ca and Mg supplies and high Mn levels, particularly in region 2, where significant defoliation stress has not occurred in many parts of the region for 20 or more years, would be at risk of increased mortality if severe defoliation or other stresses occurred. Further, we cannot rule out the possibility that other unmeasured stress factors may have contributed to the decrease in crown health observed in some stands in region 2. For instance, many of the stands that showed poorer crown health were either at higher elevations or in upper landscape positions near the limit of deeper soils. This is consistent with the possibility that these stands could have experienced greater climatic stress due to low water availability during dry years or more injury in winter. Insufficient detailed climatic data are available to address historical spatial variability in these factors at a regional scale.

The conclusions from this study, coupled with what is already known about sugar maple decline, provide the basis for a conceptual model outlining the complex nature of sugar maple decline as we currently understand it (Fig. 7). The stands where sugar maple decline has occurred or has the potential to occur in the future are situated on acid, low base cation soils. For the past half century, soils in both regions have been impacted by relatively high inputs of wet and dry sulfate and nitrate deposition (Lynch et al. 1999; National Atmospheric Deposition Program 2002). Recently, using archived soil samples from upper-slope sites on the Allegheny Plateau, Bailey et al. (2005) found that during the 30-year interval between 1967 and 1997 there were significant decreases in exchangeable Ca, Mg, and pH and an increase in exchangeable Al in all soil horizons to a depth of >120 cm. Soil acidification resulted in pH decreases of 0.9 in the Oa/A horizon and 0.2–0.3 in the B horizons. While soil Mn was not measured in this study, one can assume that soil acidification also increased the availability of soil Mn, since Mn availability begins to increase rapidly as the pH decreases below 5.5 (Reisenauer 1988). Hutchinson et al. (1998) found that after applications of ammonium sulfate to sugar maple stands, soil pH decreased, water-extractable soil Mn increased, and foliar Mn concentration increased. Bailey et al. (2004) also showed that there is a strong positive relationship between exchangeable Ca and Mg in upper and lower B horizon soils and foliar chemistry of sugar maple. They also developed empirical soil Ca and Mg thresholds for sugar maple health. Sugar maple that declined were found on sites with <0.5% Mg or <2% Ca saturation in the upper B horizon and <0.6% Mg or <4% Ca saturation in the lower B horizon. When these thresholds are viewed against the amount of change in region 1 soil chemistry between 1967 and 1997, they show that in 1967, soils contained adequate Ca and Mg for sugar maple to remain healthy, even with multiple stresses. By 1997, Ca and Mg had diminished to less than the threshold levels required for health of sugar maple under stress. Soil Al also increased during the same time period (Bailey et al. 2005). Defoliation stress and sugar maple decline began to increase in the early to mid-1980s in region 1 (Bonstedt 1985; Kolb and McCormick 1993) at about the time the thresholds for healthy levels of Ca and Mg in the soil were being passed.

In acid soils, Al interference with availability and uptake of Ca and Mg is well known in agricultural crops and trees, though its transport to the foliage is limited in many species (Foy et al. 1978; Cronan and Grigal 1995). Mn is an essential micronutrient, but in acid soils Mn also interferes with Ca and Mg uptake and under these conditions Mn is easily transported to the foliage in quantities >50 times the plant requirement (Reisenauer 1988). The partial correlation results suggest that the potential importance of Mn as an antagonistic cation is consistent with these studies.

Fig. 4. Foliar Ca concentration and stress interaction categories (mean ± SD) for different measures of sugar maple health (PDEADSM, SMVIG, PSMDIE) by region. Nutrition categories are defined as follows: "high Ca" denotes a foliar Ca concentration of 5500 mg·kg^{-1} and "low Ca" a foliar Ca concentration of <5500 mg·kg^{-1}. Stress categories are defined as follows: "high defoliation stress" denotes a DSI 10 value of 4 and "low defoliation stress" a DSI 10 value <4. Regions 1 and 2 were analyzed separately; the same lower case letter above the bar indicates that values were not statistically different within a region (p = 0.05).

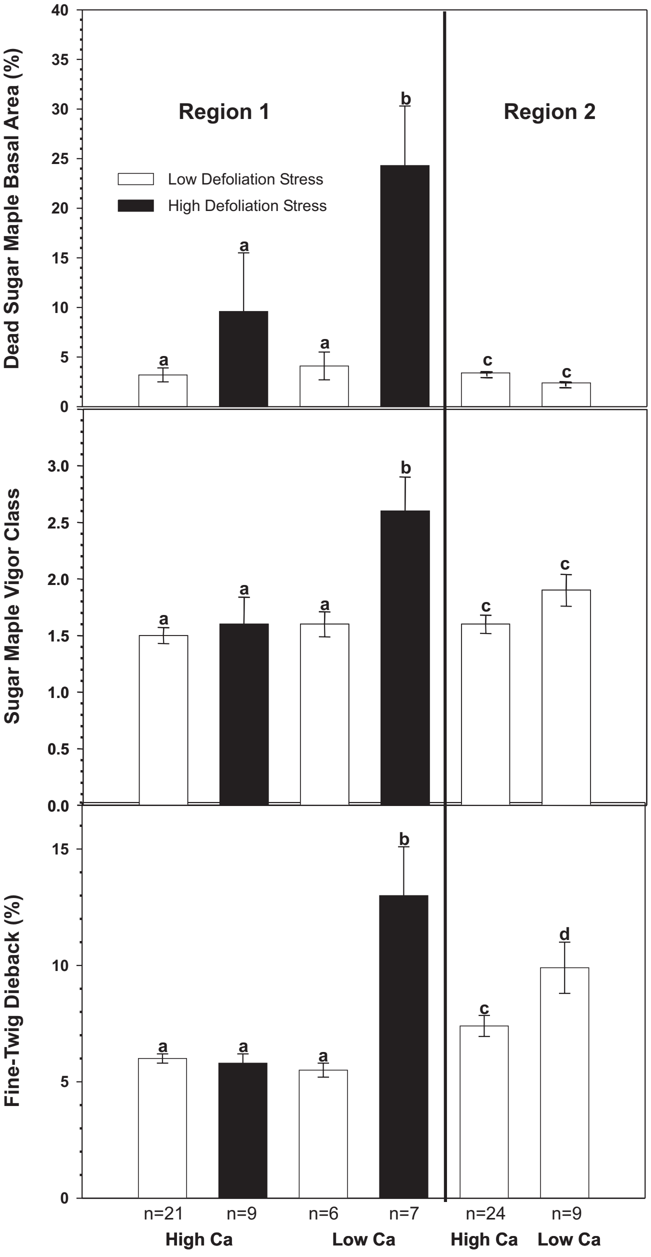
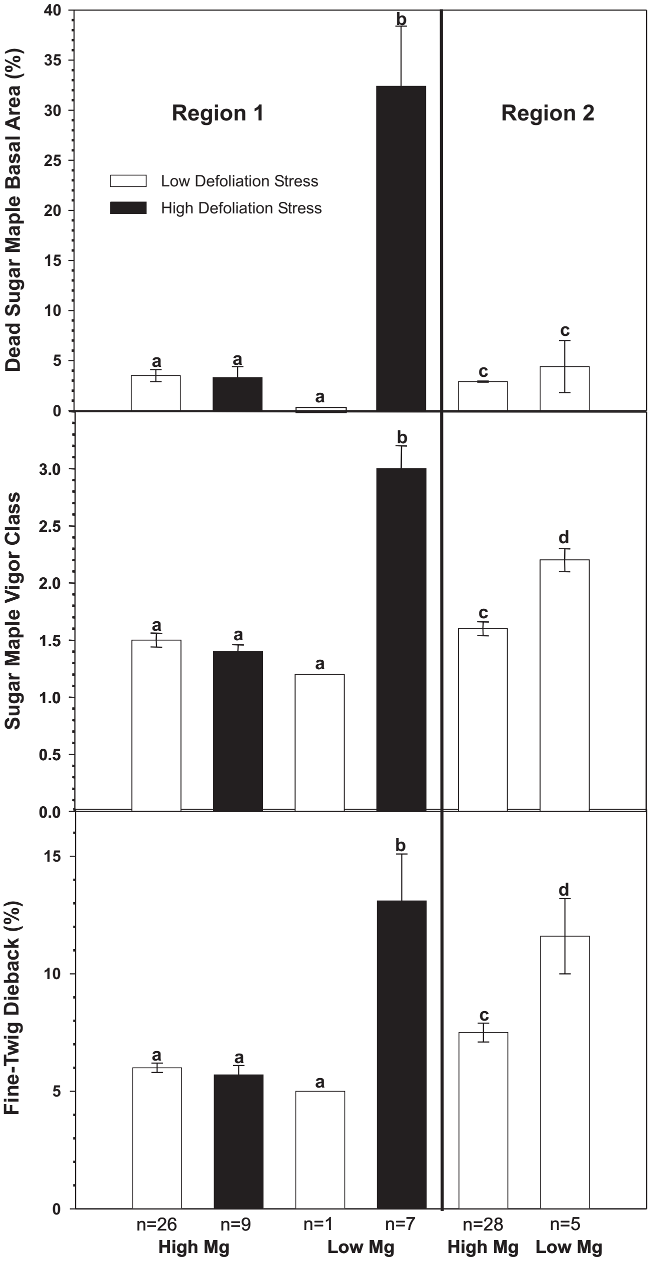


Fig. 5. Foliar Mg concentration and stress interaction categories (mean ± SD) for different measures of sugar maple health (PDEADSM, SMVIG, PSMDIE) by region. Nutrition categories are defined as follows: "high Mg" denotes a foliar Mg concentration of 700 mg·kg^{-1} and "low Ca" a foliar Mg concentration of <700 mg·kg^{-1}; stress categories are defined as follows: "high defoliation stress" denotes a DSI 10 value of 4 and "low defoliation stress" a DSI 10 value <4. Regions 1 and 2 were analyzed separately; the same lower case letter above the bar indicates that values were not statistically different within a region.



Mn functions in plant metabolism in several important ways: in photosynthesis, particularly electron transport in photosystem II, photodestruction of chlorophyll and chloroplast structure; in N metabolism, particularly the sequential reduction of nitrate; in aromatic ring compounds as precursors for aromatic amino acids, hormones (auxins), phenols, and lignins (Campbell and Nable 1988). In excess, Mn has been associated with reduced leaf chlorophyll, net photosynthesis, and leaf carbohydrates (Hecht-Buchholz et al. 1987; Nable et al. 1988; Marschner 1995; St. Clair et al. 2005; Kitao et al. 1997). The negative effect of high Mn concentration on sugar maple health is supported by McQuattie and

Fig. 6. Foliar Mn concentration and stress interaction categories for different measures of sugar maple health (PDEADSM, SMVIG, PSMDIE) by region. Nutrition categories are defined as follows: “high Mn” denotes a foliar Mn concentration of 1900 mg·kg^{-1} and “low Mn” a foliar Mn concentration of >1900 mg·kg^{-1}; stress categories are defined as follows: “high defoliation stress” denotes a DSI 10 value of 4 and “low defoliation stress” a DSI 10 value <4. Regions 1 and 2 were analyzed separately; the same lower case letter above the bar indicates that values were not statistically different within a region.

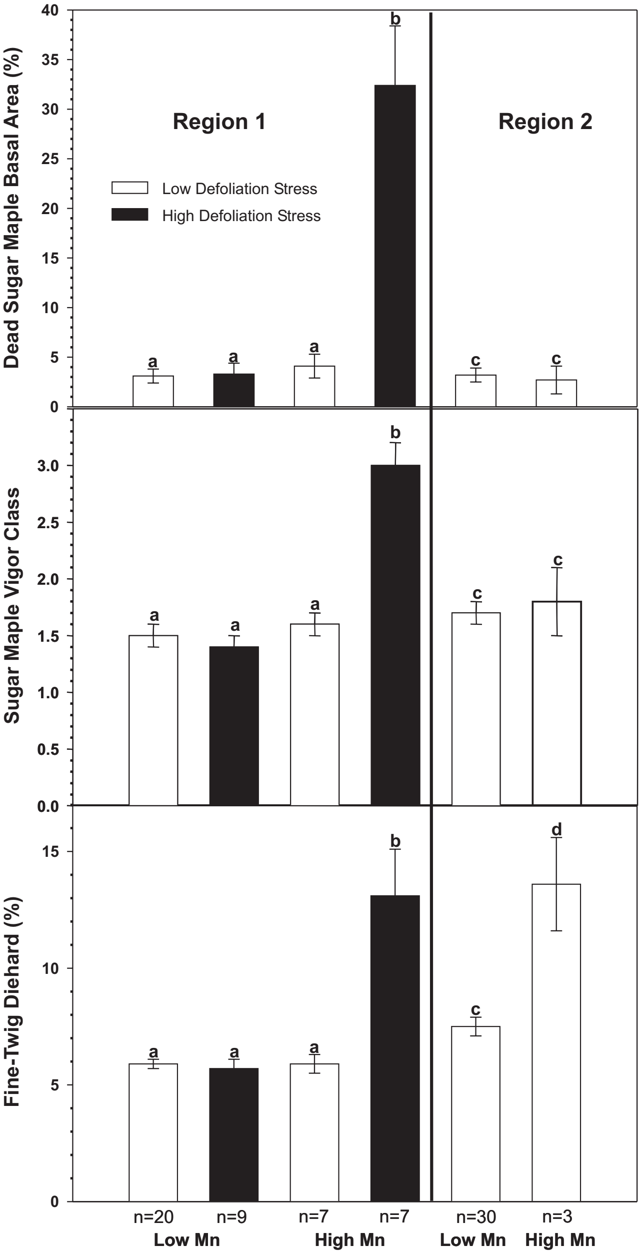
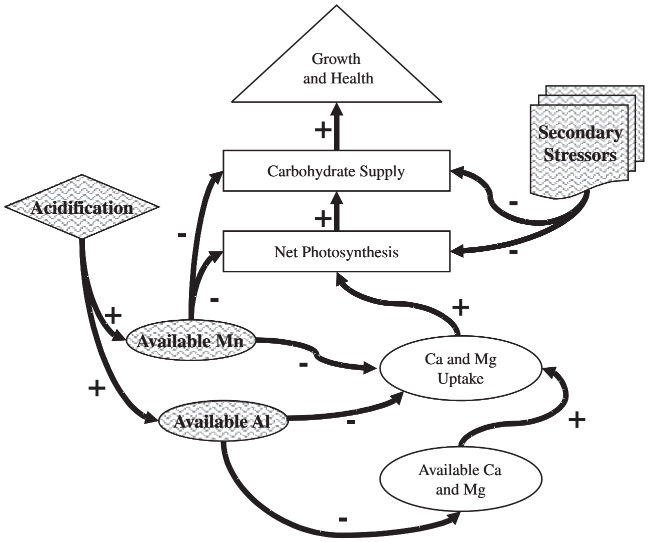


Fig. 7. Conceptual diagram outlining our current understanding of sugar maple decline. Positive and negative signs indicate the nature of the correlative relationship between variables.



Schier (2000), who conducted a dose–response study on sugar maple seedlings and found that increased Mn levels reduced concentrations of all foliar nutrients except P. Moreover, on three of our region 1 sites with low sugar maple foliar Ca and Mg and high foliar Mn concentrations, St. Clair et al. (2005) found a strong relationship between impaired photosynthesis and high late-season antioxidant enzyme activity in the foliage of dominant and codominant trees. The impact of low Ca and Mg supply and Mn toxicity on photosynthesis leads to a direct effect on levels of carbohydrate and energy that are available to build new tissues and repair damaged tissues. Using electron microscopy and energy-dispersive X-ray microanalysis, McQuattie et al. (1999) have demonstrated dense Mn-containing material in sugar maple leaf chloroplasts and delayed transport of starch out of chloroplasts to roots and other carbohydrate-storage locations. Applications of dolomitic limestone to stands containing sugar maple (Long et al. 1997) that increased soil pH and foliar and soil Ca and Mg concentrations and decreased foliar and soil Al and Mn concentrations resulted in an increase in crown vigor and root starch content (Wargo et al. 2002).

Defoliation stress creates a massive demand for carbohydrates to repair the damaged crown (Wargo 1972; Wargo 1981*a*, 1981*b*; Gregory and Wargo 1986; Renaud and Mauffette 1991; Wargo and Harrington 1991; Kolb and McCormick 1993; Wargo 1999). Starch reserves at the end of the growing season may be unaffected by defoliations that occur very early in the growing season, but defoliations that are followed by refoliation during the same growing season or multiple defoliations in the same or subsequent years can reduce carbohydrate reserves to the point where they are inadequate to support over-winter respiratory demands, resulting in mortality of fine twigs and branches or invasion of poorly defended roots by secondary stressors such as *Armillaria* spp. (Parker and Houston 1971; Wargo and Houston 1974; Houston 1999; Wong et al. 2001).

The present study expands the range of inference drawn from our work in western Pennsylvania and New York to the northeastern United States. Within this region, the decline of sugar maple fits the decline-disease hypothesis of Manion (1991) and Houston (1992). Decline diseases result from complex abiotic and biotic factors that predispose or weaken trees, followed by inciting or triggering events that result in dieback and mortality. Furthermore, the results of this study suggest that foliar nutrient (Ca, Mg, and Mn) thresholds could provide land managers with a diagnostic tool to help determine which sugar maple stands are “at risk” of experiencing an increase in mortality in the face of excessive stress, such as deep soil freezing, drought, and (or) insect defoliations.

The results of our study suggest that sugar maple is predisposed to decline by imbalance in Ca, Mg, Mn (and Al) and incited to decline by excessive stress, particularly from defoliation. Increased effort to study the interacting roles of Ca, Mg, Mn, and Al in the physiology, health, and growth of sugar maple is warranted.

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