# Factors associated with the decline disease of sugar maple on the Allegheny Plateau

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**Abstract**: Mortality of sugar maple (*Acer saccharum* Marsh.) has reached unusually high levels across northern Pennsylvania since the early to mid-1980s. We evaluated the influence of glaciation, topographic position, foliage chemistry, defoliation history, and stand characteristics (species composition, structure, density) on the health of sugar maple in 43 stands at 19 sites on the northern Allegheny Plateau. Using percent dead sugar maple basal area as the measure of health, we found that all moderately to severely declining stands were on unglaciated summits, shoulders, or upper backslopes. Stands on glaciated sites and unglaciated lower topographic positions were not declining. The most important factors associated with sugar maple health were foliar levels of Mg and Mn and defoliation history. The lowest foliar Mg, highest foliar Mn, and highest number and severity of insect defoliations were associated with unglaciated summits, shoulders, and upper backslopes. Declining stands had less than ~700 mg·kg$^{-1}$ Mg and two or more moderate to severe defoliations in the past 10 years; both conditions were associated with moderately to severely declining stands. The decline disease of sugar maple seems to result from an interaction between Mg (and perhaps Mn) nutrition and stress caused by defoliation.

**Résumé** : La mortalité de l'érable à sucre (*Acer saccharum* Marsh.) a atteint des proportions anormalement élevées partout dans le nord de la Pennsylvanie depuis le début ou le milieu des années 1980. Nous avons étudié l'influence de la glaciation, de la topographie, de la chimie foliaire, des défoliations passées, et des caractéristiques du peuplement (composition, structure et densité) sur la santé de l'érable à sucre dans 43 peuplements établis sur 19 sites dans la partie nord du plateau alléghanien. En utilisant le pourcentage de surface terrière que représentent les érables à sucre morts comme mesure de l'état de santé, nous avons trouvé que tous les peuplements où le dépérissement était modéré à sévère étaient situés sur les sommets, les contreforts, ou le haut des revers qui n'avaient pas subi la glaciation. Les peuplements situés sur des sites exposés à la glaciation ou des sites plus bas qui n'avaient pas subi la glaciation ne dépérissaient pas. Les facteurs les plus importants associés à la santé de l'érable à sucre étaient les concentrations foliaires de Mg et Mn et les défoliations passées. La plus faible concentration foliaire de Mg, la plus forte concentration foliaire de Mn, la sévérité la plus élevée et le plus grand nombre de défoliations d'insectes étaient associés aux sommets, aux contreforts, ou au haut des revers qui n'avaient pas subi la glaciation. Les peuplements dépérissants avaient moins d'environ 700 mg·kg$^{-1}$ de Mg et avaient subi au moins deux défoliations modérées à sévères au cours des 10 dernières années. Ces deux facteurs étaient associés à des peuplements où le dépérissement était modéré à sévère. Le dépérissement de l'érable à sucre semble être le résultat d'une interaction entre la nutrition en Mg (et peut-être en Mn) et le stress causé par la défoliation.

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## Introduction

Overstory sugar maple (*Acer saccharum* Marsh.) trees have been declining (sensu Manion 1991) across the unglaciated Allegheny Plateau in northwestern and north-central Pennsylvania since the early to middle 1980s (Kolb

and McCormick 1993; McWilliams et al. 1996; Long et al. 1997). Declining trees are typified by a slow loss of crown vigor, dieback of fine twigs, and reduced radial increment over a period of years, frequently ending in death (Kolb and McCormick 1993; Long et al. 1997). Surveys conducted since 1989 in the northeastern United States and eastern Canada by the joint United States – Canadian North American Maple Project (NAMP) health monitoring network generally have shown that sugar maple is healthy throughout this range, though declines in Quebec were noted in the middle and late 1980s (Allen et al. 1992*a*, 1995, 1999). However, the current levels of crown dieback and mortality in northwestern and north central Pennsylvania, which are not included in the NAMP, are substantially higher than other areas in the northeastern United States and eastern Canada surveyed by the NAMP. For example, mortality of dominant and codominant, non-sugarbush trees monitored by the NAMP was 0.5% per year from 1989 to 1994 (Allen et al.

1995). Mortality of dominant and codominant sugar maple on a series of "NAMP-like" plots installed on the Allegheny National Forest (ANF) in 1990 using NAMP protocols was 3.5% per year in uncut forest stands and 2.3% per year in thinned stands from 1990 to 1995 (R.P. Long, unpublished data). These unusually high levels of mortality are corroborated by aerial surveys and ground inventories conducted by land-management agencies (Laudermilch 1995; McWilliams et al. 1996). Moreover, observations by land managers suggested that sugar maple declines typically began or were most severe on upper slopes or sites above an elevation of about 600 m (Towers 1984; Bills 1997; S. Wingate and S. Kobielski, ANF, personal communication).

Insect defoliation, drought, late spring frost, and midwinter freeze–thaw cycles have been associated with the decline and mortality of sugar maple (Giese et al. 1964; Kelley 1988; Bernier et al. 1989; Bauce and Allen 1991; Allen et al. 1992*a*, 1992*b*; Kolb and McCormick 1993; Payette et al. 1996; Robitaille et al. 1995; Auclair et al. 1997). Sugar maple decline in Pennsylvania has occurred against a background of unusual defoliations and untimely climatic stresses. Between 1991 and 1996, native defoliators including fall cankerworm (*Alsophila pometaria* Harris), elm spanworm (*Ennomus subsignarius* Hubner), forest tent caterpillar (*Malacosoma disstria* Hubner), and linden looper (*Erannis tiliaria* Harris) defoliated 247 268 ha; the exotic insect, pear thrips (*Taeniothrips inconsequens* Uzel), also caused significant defoliations during the 1980s. Summer droughts of mild or greater severity (June–August mean Palmer drought severity index (PDSI) –1 or lower) occurred in the region in 1952, 1954, 1962, 1963, 1966, 1971, 1988, 1991, and 1995. Snowfall during the decade of the 1980s frequently was lower than normal in northwestern and north-central Pennsylvania (NOAA 1995), although soils in the region typically do not freeze (Carter and Ciolkosz 1980; L.R. Auchmoody, unpublished data).

Nutrient deficiency, particularly of base cations, seems to be a common thread in sugar maple decline. While not usually identified as primary causal factors, nutrients (N, P, K, Ca, and Mg) have been recognized as important stressors contributing to sugar maple declines in western Massachusetts (Mader and Thompson 1969), Quebec (Bernier and Brazeau 1988*a*, 1988*b*, 1988*c*; Bernier et al. 1989; Côté et al. 1995; Ouimet and Camiré 1995), northern New York (Bauce and Allen 1992), Vermont (Wilmot et al. 1995, 1996), and Pennsylvania (Kolb and McCormick 1993). Long et al. (1997) showed that the addition of 22.4 Mg·ha$^{-1}$ of dolomitic limestone to the soil surface at four high-elevation unglaciated sites on the Susquehannock State Forest in north-central Pennsylvania significantly increased sugar maple survival, crown vigor, diameter, and basal area increment, and flower and seed crop production. Black cherry (*Prunus serotina* Ehrh.) and American beech (*Fagus grandifolia* Ehrh.) at these sites were unaffected by lime application. On unlimed plots, sugar maple with high crown vigor and few symptoms of twig dieback had higher foliar concentrations of Ca and Mg than low vigor trees. Mean sugar maple basal area increment for limed and unlimed trees was positively correlated with foliar concentrations of Ca and Mg and negatively correlated with Al and Mn.

Stress associated with high levels of stand density (competition) was suggested as a predisposing factor in the decline–disease of sugar maple in central New York (Bauce and Allen 1991) and Wisconsin (Giese et al. 1964). During development of the second-growth forest on the Allegheny Plateau in northern Pennsylvania and southwestern New York, shade-tolerant species like sugar maple and beech were typically outgrown by black cherry and red maple (*Acer rubrum* L.) where the proportion of these less shade-tolerant species was high. Under these conditions, sugar maple was relegated to lower crown classes and smaller relative diameters, where it may be more vulnerable to decline (Marquis 1992).

Northwestern and north central Pennsylvania and adjacent portions of southwestern New York are at the southern edge of the Wisconsin glacial advances. There have been few observations of sugar maple decline reported in the glaciated areas of the western Allegheny Plateau (Drohan et al. 1999), although declines have been significant in glaciated areas of northeastern Pennsylvania (Hall et al. 1999). Soils on the unglaciated portion of the Plateau are dominated by Ultisols, whereas glaciated portions are dominated by Inceptisols. Because of their longer period of formation, Ultisols have fewer weatherable minerals within the rooting zone, possibly limiting nutrient supply. Detailed knowledge of variation in soil nutrient content with glaciation, topographic position, geology, and elevation is lacking.

In previous studies of sugar maple decline, the contribution of nutrition, stress, and stand factors usually have been addressed as single factors. Some investigators have qualitatively dealt with more than one factor, but none have evaluated multiple factors in a spatially explicit way. The work presented here began with our liming study (Long et al. 1997) which showed a species-specific response of sugar maple to dolomitic limestone addition and the observation of practicing foresters that decline symptoms appeared to be concentrated on the upper slopes of unglaciated sites. Although the boundary of the Wisconsin glacial advances bisects this area, there has been little comparison of forest health or growth across this boundary, nor has work been done to elucidate geologic and pedologic processes responsible for differences in nutrient distribution in the landscape.

Manion (1991) and Houston (1992) have proposed that decline diseases such as sugar maple decline result from the interaction of predisposing, inciting, and contributing factors. The objective of our work is to develop a working hypothesis for a mechanistic study of the cause(s) of sugar maple decline by studying correlations among factors in stands containing sugar maple on the Allegheny Plateau. Our specific objectives are (*i*) to determine whether sugar maple health, foliar nutrition, stress history, and stand characteristics differ with glaciation and topographic position and (*ii*) to determine whether foliar nutrition, stress history, and stand characteristics or their interaction are related to sugar maple health. To investigate these relationships, we established a series of plots in 43 stands along topographic gradients at 19 sites across the glaciated and unglaciated portions of the Allegheny Plateau in Pennsylvania and New York. In each stand we evaluated the health of overstory trees and assessed the role of potential interacting factors by collecting

**Fig. 1.** Location of study sites in northwestern Pennsylvania and southwestern New York. The broken line represents the southern extent of the Wisconsin glacial advances in the area. Study sites: AK, Akeley; BH, Baldwin Hollow; BO, Boutwell Hill; BT, Brooks Trail; CL, Clymer; CO, Costello; CP, Colton Point; DH, Dodge Hollow; HH, Hemlock Hollow; HR, Hardwood Ridge Trail; ID, Indian Doctor; KA, Kane Experimental Forest; LV, Little Valley; MC, Mill Creek; ON, Onoville; RB, Red Bridge; RC, Russell City; SR, Sugar Run; TB, Tanbark Trail.
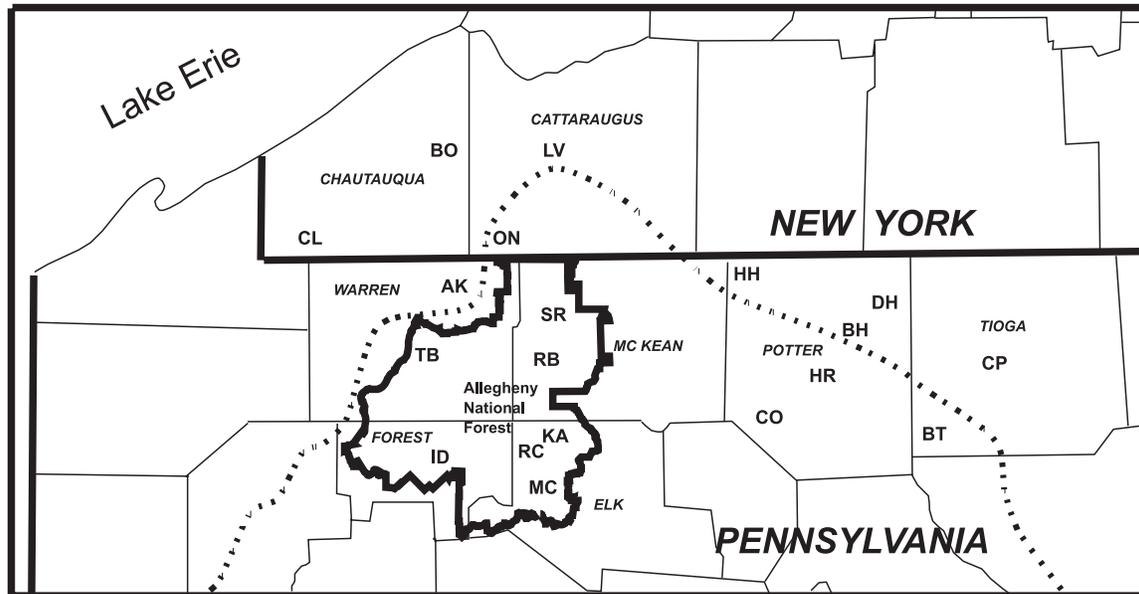


samples of or information on foliage chemistry, defoliation history, site characteristics (glaciation and physiography), and stand characteristics (species composition, structure, density).

## Methods

### Study sites

Sites were established with the assistance of federal, state, and private land managers at locations where sugar maple was present along topographic gradients and were selected to represent the range of sugar maple health conditions across a >18 000 km$^2$ portion of the Allegheny Plateau in northwestern and north-central Pennsylvania and southwestern New York. Sites were stratified by glaciation and topographic position. In 1995, five sites were selected, three on unglaciated soils (HR, KA, RB) and two on glaciated soils (CL, DH) (Fig. 1). At each site, stands were located in upper (U), mid (M), and lower (L) topographic positions. In 1996, an additional 14 sites were selected; eight were on unglaciated soils (BT, CO, ID, MC, ON, RC, SR, TB), and six were on glaciated soils (AK, BH, BO, CP, HH, LV) (Fig. 1). At the sites established in 1996, only stands in upper and lower topographic positions were chosen. Within each stand, we selected five presumably healthy dominant and codominant sugar maples with no symptoms of crown dieback for foliage sampling. We selected these trees so that we could distinguish between effects due to site nutritional quality and those due to poor tree health (Kolb and McCormick 1993; Long et al. 1997). 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). These trees also formed the locus for establishing plots to evaluate other site and stand characteristics. In all, 43 stands were sampled (1995: 5 sites × 3 stands/site = 15 stands; 1996: 14 sites × 2 stands/site = 28

stands); 18 were on glaciated soils, and 25 were on unglaciated soils.

### Stand health evaluation

Stand health was evaluated in middle to late July 1996 (15 stands established in 1995) or 1997 (28 stands established in 1996). Protocols used for plot establishment and tree health evaluation were similar to those used by the NAMP (Cooke et al. 1996). In each stand, three 400-m$^2$ circular plots were established in the vicinity of trees selected for foliage samples. All standing living and dead trees ≥10 cm in diameter at a height of 1.4 m height (diameter at breast height (DBH)) were evaluated by species, DBH, and crown class (dominant, codominant, intermediate, suppressed). Over all 43 stands, we evaluated the health of 1499 sugar maple trees. The following parameters of tree health were estimated for each tree: crown vigor index, percent branch dieback, and percent crown transparency. Crown vigor index was estimated as follows: (1) healthy (no major branch mortality); (2) light decline; (3) moderate decline; (4) severe decline; and (5) dead (for more complete definitions, see Cooke et al. 1996). Percent branch dieback, including dead branches less than 2.5 cm diameter, where mortality begins at the terminal portion of the limb and progresses inward, was estimated for each tree using a 12-class system (Cooke et al. 1996). Percent crown transparency was estimated with the same system as percent branch dieback (Cooke et al. 1996).

To characterize sugar maple health, percent dead sugar maple basal area (PDEADSM), was calculated from crown vigor index (SMVIG) data as the proportion of the sugar maple basal area in category 5 (dead) compared with the total stand basal area of sugar maple. Mean sugar maple crown vigor (SMVIG) was calculated for all sugar maple trees in the stand (all three plots) as the mean of all five vigor classes. Similarly, mean percent sugar maple dieback (PSMDIE), based on estimates of branch dieback and mean percent sugar maple transparency (PSMTRANS), were determined for each stand. All crown health measurements were

estimated by two observers, both of whom attended the annual NAMP crown-rating certification training.

## Site characteristics

At each site, percent slope was recorded with a clinometer. Aspect was estimated with a compass and assigned to north, south, east, and west categories; each category was ±45° from the cardinal direction. Stand elevations were determined from 7.5′ topographic maps after the sites were geolocated (±2 m) in December 1996 with a Trimble Pro-XL global positioning system unit.

Local physiography was determined for each stand using a classification system similar to that used by the NAMP that considered moisture and nutrient retention along with local physiography in classifying a stand (Cooke et al. 1996). Summit and shoulder physiographic positions were grouped together (physiography = 1) and represented sites with the least moisture and nutrient retention. Stands on upper backslopes (physiography = 2) were the next most susceptible to deficiencies in moisture or nutrient retention, followed by middle backslope stands (physiography = 3), and lower backslope stands (physiography = 4). A fifth category represented sites with the most moisture and nutrient retention (physiography = 5) and included stands on foot- or toe-slopes, benches, or any topographic position with concave microtopography. Also, because seeps may be a source of additional water and nutrition that could affect or moderate the effects of other stressors on tree health, their presence or absence in each stand was noted.

## Foliage sampling and analysis

In each stand, foliage was sampled from the five presumably healthy (NAMP vigor class 1, ≤10% crown dieback, and foliage transparency) dominant or codominant sugar maples marked at the time of site selection. A midcrown sample of 25 healthy sun leaves was obtained from each tree during the last 2 weeks of August 1995 (15 stands) or 1996 (28 stands) by shooting small branches from the periphery of the crown with a shotgun. Surface area for each 25-leaf sample was determined using a LI-COR LI-3000/3050A area meter (LI-COR Inc., Lincoln, Neb.). Samples were dried to constant mass at 65°C. Mean leaf area and leaf mass was determined for each 25-leaf sample. Foliage samples were dry ashed at 485°C; taken up in 10% HCl; and analyzed for P, K, Ca, Mg, Al, and Mn (mg·kg$^{-1}$) by inductively coupled plasma spectroscopy at the University of Minnesota Research Analytical Laboratory (Munter 1982). National Institute of Standards and Technology (NIST) pine needles were used as a reference standard. Percent recovery for certifiable elements (P, K, Ca, Mn, and Al) 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 generally less than 3%. Total Kjeldahl N was determined with a Lachat autoanalyzer (QuikChem method 13-107-06-2-D; Lachat Instruments, Milwaukee, WI 53218, U.S.A.) in our laboratory. NIST pine needles were used as a reference standard. Percent recovery of N, a noncertified element, was ±10% of the noncertified value. Similarly, the percent relative difference for duplicate samples was 6%. For data analysis, foliar chemistry was expressed on a concentration (mg·kg$^{-1}$), content (mg/leaf), and unit leaf area (mg·cm$^{-2}$) basis. There was no difference in the results based on these different expressions; only results based on concentration are reported in this paper.

Previous research showed that apparently healthy trees sampled in two successive years at the same time of the growing season showed varying levels of repeatability in nutrient concentrations (R.P. Long and S.B. Horsley, unpublished). Phosphorus ($R^2$ = 0.643, $p < 0.001$), K ($R^2$ = 0.439, $p$ = 0.005), Ca ($R^2$ = 0.625, $p$ = 0.001), Mg ($R^2$ = 0.857, $p < 0.001$), and Mn ($R^2$ = 0.715, $p < 0.001$) showed good repeatability. Nitrogen ($R^2$ = 0.310, $p$ = 0.047)

and Al ($R^2$ = 0.268, $p$ = 0.040) were less repeatable. Statistical analyses of nutrient data showed no significant relationship between sugar maple health and foliar concentrations of N, P, and K, so results for these elements are not presented here.

## Stand disturbance and defoliation histories

Disturbances caused by stand management activities and those associated with defoliation were determined for each stand. Two primary sources of information were used. First, a geographic information system data base consisting of annual layers of digitized defoliation sketch maps was queried to determine the timing, agent, and severity of defoliation (light, <30%; moderate, 30–60%; or heavy, >60%) during the past 20 years for the Pennsylvania stands (P. Drohan, personal communication). These data were provided by the Pennsylvania Bureau of Forestry, Middletown, and the USDA Forest Service, Northeastern Area State and Private Forestry, Morgantown, W.V. Second, land managers responsible for the specific stands were contacted regarding management activities such as thinning or other removals and additional information on defoliation incidence and severity. All disturbance information for stands in New York was provided by local land managers at the New York Department of Environmental Conservation and International Paper Co. This information was tabulated for use in a correlation matrix to evaluate the influence of defoliation and management on tree health. Several variables were created from the disturbance database: the number of defoliation events (NDE) at each site that affected sugar maple in the last 10 and 20 years was determined. A defoliation severity index (DSI), combining number and severity of defoliations (1, light; 2, moderate; and 3, heavy) over the 10- or 20-year period prior to evaluation of overstory health, was calculated by summing severity values for the appropriate period. Preliminary analysis showed that thinning was unrelated to PDEADSM or SMVIG over the 10- or 20-year period prior to health evaluation, so results are not presented.

## Stand characteristics

Measures of species composition, stand structure, and stand density were calculated from data collected on the three 400-m$^2$ plots in each stand during the evaluation of overstory health. Species composition was evaluated as the percent of the total basal area that was sugar maple (PSMBA) or the percentage of the total basal area that was black cherry (PBCBA). Relative diameter of sugar maple (RDIASM) was the measure of stand structure. It expresses the relative position of sugar maple in the diameter distribution of the entire stand and was used as an estimate of competitive position of sugar maple in the stand. The parameter was calculated as the ratio of the mean medial diameter of sugar maple to the mean stand medial diameter (diameter of the tree at the midpoint of the basal area distribution of all species) (Hillebrand et al. 1992). Relative density (RD) was used as the measure of stand density, because unlike absolute measures such as basal area, it is independent of site quality and stand age (Stout 1983). RD compares absolute density with the average maximum density characteristic of undisturbed stands of a forest type. Equations in SILVAH were used to calculate relative density on unglaciated sites (Marquis et al. 1992; Marquis and Ernst 1992). These equations were developed for stands of the Allegheny hardwood type, which have ≥25% of their basal area in black cherry. Equations developed by S.L. Stout (unpublished data) were used to calculate RD of stands on glaciated sites, which have <25% of their basal area in black cherry, because they more accurately represent density of these stands.

## Statistical methods

To determine which of the health measures was the best for discriminating natural health groupings among stands (dependent health variable), we used the *K*-means clustering algorithm in

SYSTAT version 7.0 (Wilkinson 1997). This algorithm split the original 43 health-rating observations into two well-separated groups by maximizing among-cluster relative to within-cluster variation. The procedure generates an $F$ statistic (not Fisher's $F$), the largest value of which represents the measure with the greatest ability to discriminate differences in the dependent variable. Standardization of health variables before $K$-means cluster analysis made no difference in the outcome, so unstandardized data were used. Based on the $F$ statistic, PDEADSM was the best discriminator ($F = 211$) of groups, followed by SMVIG ($F = 147$), PSMDIE ($F = 77$), and PSMTRANS ($F = 20$). Both PDEADSM (a continuous variable) and SMVIG (a categorical variable) identified the same group of six declining stands, HR-U, KA-U, KA-M, MC-U, RB-U, and RB-M. In this manuscript, the term non-declining includes stands with 0–11 PDEADSM and is empirically derived from the cluster analysis; SMVIG for these stands ranged from 1.0 to 2.2. Similarly, moderately to severely declining stands includes those with PDEADSM from 21 to 56 and with SMVIG from 2.4 to 3.7. Both PDEADSM and SMVIG gave the same interpretations in all analyses; only results using PDEADSM as the dependent variable are presented.

Variables describing stand health (PDEADSM), foliage chemistry, defoliation incidence, and severity, and stand characteristics were analyzed by a mixed model analysis of variance (SAS version 6.12). For these analyses, the glaciation by topographic position variable classes were combined into a single classification variable that included the four combinations of glaciation and topographic position (GU, glaciated upper slopes; GL, glaciated lower slopes: UU, unglaciated upper slopes; and UL, unglaciated lower slopes:); this factor was considered a fixed effect in the analysis. The second factor was sites nested within glaciation–topographic position (random effect) (Littell, et al. 1996). The five mid-topographic position stands were omitted from these analyses because of the small sample size. Three orthogonal a priori contrasts were used to test for differences between glaciated versus unglaciated sites, glaciated upper slopes versus glaciated lower slopes, and unglaciated upper slopes versus unglaciated lower slopes. Homogeneity of variance and normality of data were checked by analysis of residuals and the use of normal probability plots (SYSTAT, version 7.0). To further identify variables that may be correlated with stand decline status, Pearson correlation analysis ($r$) with Bonferroni adjusted probabilities and linear regression ($R^2$) were used. In these analyses, data from all 43 stands were used to assess the relationship between PDEADSM and foliage chemistry, defoliation history, and stand characteristics (SYSTAT, version 7.0). All analyses were conducted with the dependent variable untransformed and log transformed; differences in the results of these analyses were negligible and there were no differences in the interpretation of results. Thus, we have presented all results using the untransformed data. An $\alpha$ value of 0.05 was the nominal indicator of statistical significance, although $p$ values >0.05 and ≤ 0.15 were considered worthy of additional investigation.

## Results

### Site characteristics

Thirty-three of the 43 stands were on north (19) and east (14) aspects; the remaining 10 stands were on south (5) and west (5) aspects. Elevation ranged from 474 to 707 m on glaciated sites and from 386 to 767 m on unglaciated sites. Sugar maple was healthier in stands on glaciated sites than on unglaciated sites ($p = 0.036$) (Table 1). There were no trends in health of sugar maple between the upper and lower slopes of glaciated sites ($p = 0.698$), but stands on the upper slopes of unglaciated sites were less healthy than those on the lower slopes of unglaciated sites ($p = 0.005$).

Assignment of a physiographic classification to each stand gave a more precise location of stands in the landscape. The unglaciated upper topographic position included the summit, shoulder, and upper backslope physiographic positions. All stands with moderate to severe decline (PDEADSM = 21–56) were on summits, shoulders, or upper backslopes of unglaciated sites, although all stands in these positions were not declining, e.g., ID-U, CO-U, ON-U, BT-U, TB-U, SR-U, RC-U (PDEADSM = 4) (Fig. 2). Unglaciated middle and lower backslopes, foot- and toe-slopes, or enriched locations such as benches, sites with concave microtopography or seeps contained only non-declining sugar maple stands (PDEADSM = 0–11). There were no trends in sugar maple health with physiographic position on glaciated sites (Fig. 2).

### Foliage chemistry

*Trends in leaf area and leaf dry weight*

Mean leaf area and mean leaf dry weight of the presumably healthy sugar maple trees generally were unrelated to glaciation or topographic position. Over all topographic positions, both attributes were similar for trees on glaciated and unglaciated sites ($p \geq 0.170$). Both parameters were similar for trees on the upper and lower topographic positions of glaciated ($p \geq 0.180$) and unglaciated ($p \geq 0.226$) sites.

*Relation to glaciation, topographic position, and physiographic position*

Data on concentrations of Ca, Mg, Al, Mn and molar ratios of Ca/Al, Ca/Mn, and Mg/Mn in the foliage of presumably healthy sugar maple trees are found in Table 1. The foliage of trees on glaciated and unglaciated sites had similar concentrations of Al ($p = 0.679$). Glaciated sites had higher concentrations of Ca ($p = 0.001$) and Mg ($p = 0.007$) and molar ratios of Ca/Al ($p = 0.026$), Ca/Mn ($p = 0.017$), and Mg/Mn ($p = 0.014$), while unglaciated sites had higher levels of Mn ($p < 0.001$).

Comparison of foliage from trees on glaciated upper and lower slopes showed that concentrations of Ca ($p = 0.149$), Mg ($p = 0.774$), and Al ($p = 0.300$) and molar ratios of Ca/Al ($p = 0.650$), Ca/Mn ($p = 0.990$), and Mg/Mn ($p = 0.216$) were similar. Foliar Mn concentration was higher on glaciated upper than lower slopes ($p = 0.038$). There were differences in the foliar chemistry of sugar maple trees on unglaciated upper and lower slope sites. Foliage of trees on upper slopes contained lower concentrations of Ca ($p = 0.006$) and Mg ($p = 0.005$); lower molar ratios of Ca/Al ($p = 0.003$), Ca/Mn ($p < 0.001$), and Mg/Mn ($p < 0.001$); and more Al ($p = 0.003$) and Mn ($p < 0.001$) than those on lower slope sites.

Differences in foliar concentrations between unglaciated upper and lower slope sites also were reflected in trends recorded by physiographic position (Table 2). Foliar Ca, Mg, and Mn concentrations and molar ratios of Ca/Mn and Mg/Mn were significantly correlated, and the molar ratio of Ca/Al was marginally correlated with physiographic position (Ca: $r = 0.637$, $p = 0.034$; Mg: $r = 0.703$, $p = 0.005$; Mn: $r = -0.770$, $p < 0.001$; Ca/Mn: $r = 0.701$, $p = 0.005$ and Mg/Mn: $r = 0.848$, $p < 0.001$; Ca/Al: $r = 0.745$, $p = 0.109$). Ca and Mg levels and molar ratios of Ca/Al, Ca/Mn, and Mg/Mn were lowest on summits and shoulders, intermediate on

**Table 1.** Means (with SE given in parentheses), ranges, and analysis of results for tests among the four glaciation – topographic position categories for stand health, foliar nutrition, defoliation history, and stand characteristics variables.

| Variable | Overall mean (n = 38) | Range (n = 38) | Glaciated (G) vs. unglaciated (U) | | | Glaciated upper (GU) vs. lower (GL) slopes | | | Unglaciated upper (UU) vs. lower (UL) slopes | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | G (n = 16) | U (n = 22) | p | GU (n = 8) | GL (n = 8) | p | UU (n = 11) | UL (n = 11) | p |
| **Stand health** | | | | | | | | | | | |
| PDEADSM | 7.6 (2.1) | 0–56.4 | 3.0 (2.8) | 11.0 (2.4) | 0.036 | 2.0 (3.8) | 4.0 (3.8) | 0.698 | 18.0 (3.2) | 4.0 (3.2) | 0.005 |
| **Foliar nutrition (mg·kg$^{-1}$ or molar ratio)** | | | | | | | | | | | |
| Calcium | 8100 (500) | 3600 – 17 400 | 9700 (500) | 7000 (400) | 0.001 | 10 400 (700) | 8900 (700) | 0.149 | 5700 (600) | 8300 (600) | 0.006 |
| Magnesium | 1100 (50) | 450–1780 | 1250 (60) | 990 (50) | 0.007 | 1230 (90) | 1270 (90) | 0.774 | 810 (80) | 1170 (80) | 0.005 |
| Aluminum | 29 (2) | 15–62 | 30 (1) | 29 (1) | 0.679 | 31 (2) | 28 (2) | 0.300 | 33 (2) | 25 (2) | 0.003 |
| Manganese | 1700 (120) | 720–3740 | 1380 (100) | 1930 (80) | <0.001 | 1600 (140) | 1160 (140) | 0.038 | 2520 (120) | 1340 (120) | <0.001 |
| Ca/Al | 214 (18) | 54–463 | 249 (19) | 189 (16) | 0.026 | 258 (26) | 240 (26) | 0.650 | 132 (23) | 245 (23) | 0.003 |
| Ca/Mn | 8.6 (1.0) | 1.8–26.9 | 10.8 (1.1) | 7.0 (0.9) | 0.017 | 10.8 (1.5) | 10.8 (1.5) | 0.990 | 3.6 (1.3) | 10.4 (1.3) | 0.002 |
| Mg/Mn | 1.9 (0.2) | 0.4–4.2 | 2.3 (0.2) | 1.6 (0.2) | 0.014 | 2.1 (0.3) | 2.6 (0.3) | 0.216 | 0.9 (0.2) | 2.4 (0.2) | <0.001 |
| **Defoliation history** | | | | | | | | | | | |
| NDE(10) | 1.2 (0.20) | 0–4 | 1.4 (0.38) | 1.1 (0.32) | 0.208 | 1.6 (0.42) | 1.3 (0.42) | 0.339 | 1.5 (0.36) | 0.7 (0.36) | 0.039 |
| NDE(20) | 1.7 (0.26) | 0–6 | 1.9 (0.47) | 1.5 (0.40) | 0.247 | 2.1 (0.54) | 1.8 (0.54) | 0.485 | 2.0 (0.46) | 1.0 (0.46) | 0.039 |
| DSI(10) | 2.3 (0.39) | 0–8 | 2.3 (0.74) | 2.4 (0.63) | 0.750 | 2.6 (0.82) | 1.9 (0.82) | 0.304 | 3.2 (0.70) | 1.6 (0.70) | 0.020 |
| DSI(20) | 3.2 (0.53) | 0–13 | 3.5 (0.95) | 3.0 (0.81) | 0.512 | 3.9 (1.09) | 3.1 (1.09) | 0.494 | 4.1 (0.93) | 1.9 (0.93) | 0.029 |
| **Stand characteristics** | | | | | | | | | | | |
| PSMBA | 59.4 (3.5) | 23–95 | 64.9 (5.6) | 55.4 (4.8) | 0.102 | 70.8 (6.8) | 59.0 (6.8) | 0.155 | 47.5 (5.8) | 63.3 (5.8) | 0.032 |
| PBCBA | 13.9 (2.5) | 0–71 | 9.2 (4.0) | 17.3 (3.5) | 0.075 | 4.5 (5.1) | 13.9 (5.1) | 0.145 | 16.9 (4.3) | 17.6 (4.3) | 0.891 |
| RDIASM | 0.93 (0.02) | 0.63–1.10 | 0.96 (0.03) | 0.91 (0.02) | 0.140 | 0.98 (0.04) | 0.94 (0.04) | 0.386 | 0.84 (0.03) | 0.98 (0.03) | 0.002 |
| RD | 102 (3) | 77–139 | 99 (4) | 105 (3) | 0.199 | 96 (5) | 102 (5) | 0.383 | 99 (4) | 111 (4) | 0.057 |

**Note:** Data are for 38 stands that were in upper and lower topographic positions. The five midslope stands are omitted. PDEADSM, percent dead sugar maple basal area; NDE(10), number of defoliation events in the last 10 years; NDE(20), number of defoliation events in the last 20 years; DSI(10), defoliation severity index for the last 10 years; DSI(20), defoliation severity index for the last 20 years; PSMBA, percent sugar maple basal area; PBCBA, percent black cherry basal area; RDIASM, relative diameter of sugar maple; RD, relative stand density (%).

**Fig. 2.** Relationship between sugar maple health as measured by PDEADSM and stand physiographic position. S–Sh, summit and shoulder; UB, upper backslope; MB, mid-backslope; LB, lower backslope; Enr, enriched sites including benches, seeps, and concave microtopography. △, stands on unglaciated upper slope sites; +, stands on unglaciated lower slope sites; ×, stands on glaciated upper slope sites; ○, stands on glaciated lower slope sites; ▲, unglaciated upper slope stands with moderate to severe decline. All other stands are non-declining.
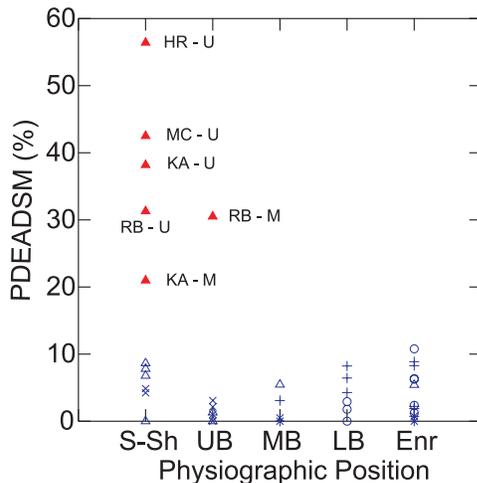


upper and middle backslopes, and highest on lower backslopes and enriched sites (Table 2); values of Mn were highest on summits and shoulders, intermediate on upper and middle backslopes, and least on lower backslopes and enriched sites. Aluminum was not significantly correlated with physiographic position on unglaciated sites ($r = -0.061$, $p = 1.000$); the highest values of Al were associated only with the summits and shoulders. On glaciated sites, there were no significant trends in nutrient elements or element molar ratios with physiographic position (Table 2).

*Relation to sugar maple health*

Correlation analysis showed that Mg ($r = -0.620$, $p = 0.001$) and Mn ($r = 0.573$, $p = 0.004$) and the Mg/Mn molar ratio ($r = 0.781$, $p = 0.033$) were the only foliar nutrients or molar ratios consistently correlated with PDEADSM. Foliar Ca was poorly related to PDEADSM ($r = -0.455$, $p = 0.144$) and the Ca/Al molar ratio was related marginally to PDEADSM ($r = -0.476$, $p = 0.083$).

The linear regression of PDEADSM on foliar Mg concentration using all 43 stands accounted for 38.4% of the variability ($p < 0.001$) (Fig. 3a). The six stands identified by the cluster analysis as moderately to severely declining had mean Mg concentrations less than ~700 mg·kg$^{-1}$. Two stands, ID-U and RC-U, were outliers in that they had low foliar Mg but had values of PDEADSM that fell within the non-declining group of stands. Foliar Mg and Ca were closely related (Fig. 3b) ($R^2 = 0.617$, $p < 0.001$), but foliar Ca concentration ($R^2 = 0.207$, $p = 0.002$) did not distinguish decline status of stands as well as foliar Mg concentration (Fig. 3c). Foliar Mn also was related to PDEADSM ($R^2 = 0.328$, $p < 0.001$), but foliar Mn alone could not be used to distinguish stand decline status (Fig. 3d). All stands with declining sugar maple had relatively high foliar Mn concentra-

tions, but in some stands, trees with foliar Mn as high or higher than stands with declining trees were evaluated as non-declining stands, including AK-U, BH-U, BT-U, CO-U, CO-L, CP-U, ID-U, ID-L, and RC-U. Scatterplots of foliar Mn concentration on foliar Mg concentration showed that all stands that were classified as declining had both low foliar Mg and high foliar Mn ($R^2 = 0.518$, $p \leq 0.001$) (except ID-U and RC-U) (Fig. 3e). This figure also shows that non-declining sugar maple that had high foliar Mn concentrations also had greater than ~700 mg·kg$^{-1}$ of foliar Mg. The molar ratio of Mg/Mn (Fig. 3f) did not distinguish decline status of stands ($R^2 = 0.259$, $p < 0.001$) as well as foliar Mg concentration alone (Fig. 3a) or foliar Mg on foliar Mn (Fig. 3e). As with foliar Mn, foliar Al did not distinguish stand decline status ($R^2 = 0.128$, $p = 0.018$) (Fig. 3g). Although all stands with unhealthy sugar maple had high foliar Al concentrations, trees in stands with foliar Al as high or higher than those with declining sugar maple showed no symptoms of decline. Furthermore, stands with high foliar Al were not always the same as those with high foliar Mn. Again, trees with high foliar Al in stands that were evaluated as non-declining had greater than ~700 mg·kg$^{-1}$ of foliar Mg (Fig. 3h).

**Defoliation history**

The NDE and DSI for the 10 and 20 years prior to overstory health evaluation varied substantially among the 38 sites in upper or lower slopes on glaciated or unglaciated areas (Table 1). The NDE ranged from 0 to 4 over the previous 10 years and from 0 to 6 over the previous 20 years; DSI ranged from 0 to 8 over the previous 10 years and from 0 to 13 over the previous 20 years. There were no differences in defoliation history parameters between glaciated upper and lower slopes ($p \geq 0.304$); however, on unglaciated sites, stands on upper slopes were defoliated more often and more severely than stands on lower slopes for both the 10- and 20-year periods prior to health evaluation ($p \leq 0.039$).

There was a relationship between defoliation history as measured by the number of defoliation events and the defoliation severity index and sugar maple health (Fig. 4); the strongest relationship was between PDEADSM and DSI for the 10 years preceding health evaluation ($R^2 = 0.158$, $p = 0.008$). Moderately to severely declining stands had two or more defoliations in the past 10 years with a DSI ≥ 4, equivalent to two moderate defoliations (Fig. 4). However, some stands with these defoliation history criteria were classified as non-declining. These stands were located on glaciated areas (BH-L, CL-U, CL-M, CL-L, CP-U, DH-U, DH-M, DH-L), unglaciated lower backslopes (MC-L), unglaciated areas with seeps (RC-L, SR-U), or unglaciated areas with concave microtopography (KA-L). Only RC-U did not fit these descriptions (Fig. 4a).

**Stand characteristics**

Means, ranges, and statistical tests of the effects of glaciation and topographic position on stand variables measuring species composition (PSMBA, PBCBA), stand structure (RDIASM), and stand density (RD) are found in Table 1. There were no differences among stand variables for glaciated versus unglaciated sites or for glaciated upper versus lower slopes. On unglaciated sites, PSMBA ($p = 0.032$),

**Fig. 3.** Relationship between sugar maple health as measured by PDEADSM and foliar nutrition (mg·kg$^{-1}$) of (*a*) Mg, (*c*) Ca, (*d*) Mn, (*f*) Mg/Mn molar ratio, and (*g*) Al; and between foliar elements (mg·kg $^{-1}$) (*b*) Ca versus Mg, (*e*) Mn versus Mg, and (*h*) Al versus Mg. Solid symbols show stands with moderate to severe decline. Open symbols show non-declining stands.

**Table 2.** Sugar maple foliar concentrations (mg·kg $^{-1}$) of calcium, magnesium, aluminum, and manganese and molar ratios of Ca/Al, Ca/Mn, and Mg/Mn by physiographic position for 43 stands on glaciated and unglaciated sites.

| Element or ratio | Physiographic position | | | | |
| --- | --- | --- | --- | --- | --- |
| | Summit or shoulder | Upper back | Mid-back | Lower back | Enriched |
| **Glaciated sites** | | | | | |
| *n* | 2 | 4 | 2 | 3 | 7 |
| Calcium | 11 800 (2000) | 9300 (2900) | 11 100 (2000) | 7800 (300) | 9600 (1100) |
| Magnesium | 1160 (90) | 1160 (170) | 1290 (200) | 1110 (70) | 1380 (100) |
| Aluminum | 26 (4) | 38 (8) | 26 (4) | 30 (5) | 30 (5) |
| Manganese | 1780 (10) | 1690 (350) | 1270 (220) | 1220 (170) | 1140 (60) |
| Ca/Al | 313 (2) | 198 (75) | 292 (12) | 187 (26) | 257 (45) |
| Ca/Mn | 9.1 (1.5) | 10.1 (5.6) | 12.7 (4.3) | 9.0 (0.9) | 12.0 (1.8) |
| Mg/Mn | 1.5 (0.1) | 1.9 (0.7) | 2.5 (0.8) | 2.1 (0.2) | 2.9 (0.3) |
| **Unglaciated sites** | | | | | |
| *n* | 9 | 3 | 3 | 3 | 7 |
| Calcium | 4500 (300) | 7300 (2500) | 7100 (1200) | 9400 (2100) | 8800 (900) |
| Magnesium | 630 (60) | 1150 (250) | 1060 (180) | 1170 (60) | 1260 (100) |
| Aluminum | 37 (2) | 28 (5) | 23 (2) | 24 (1) | 29 (4) |
| Manganese | 2770 (170) | 1740 (310) | 1720 (340) | 1220 (120) | 1280 (200) |
| Ca/Al | 88 (9) | 196 (71) | 224 (56) | 270 (64) | 232 (43) |
| Ca/Mn | 2.2 (0.1) | 6.5 (2.5) | 6.7 (2.6) | 11.2 (3.7) | 11.4 (2.2) |
| Mg/Mn | 0.5 (0.1) | 1.7 (0.5) | 1.6 (0.6) | 2.2 (0.4) | 2.8 (0.4) |

**Note:** Values are means with SE given in parentheses. *n*, number of stands used to calculate each mean.

RDIASM ($p = 0.002$), and RD ($p = 0.057$) were greater on lower than on upper slope sites. However, stand health as measured by PDEADSM was unrelated to PSMBA ($R^2 \leq 0.006$, $p \geq 0.641$) and RD ($R^2 \leq 0.012$, $p \geq 0.490$) and marginally related to PBCBA ($R^2 = 0.073$, $p = 0.079$) and RDIASM ($R^2 = 0.078$, $p = 0.070$).

**Interaction of foliar nutrition and defoliation**

There was evidence of an interaction between foliar Mg and defoliation history. All stands in which sugar maple was moderately or severely declining had in common foliar Mg less than ~700 mg·kg$^{-1}$ and at least two moderate or severe defoliations (DSI $\geq 4$) during the 10 years prior to health evaluation (Figs. 5*a* and 5*b*). Non-declining sugar maple were associated with foliar Mg at or above 700 mg·kg$^{-1}$ and with greater numbers and severity of defoliation without developing symptoms of decline. Some stands with as many as four defoliation events in the 10 years prior to health evaluation were classified as non-declining (CL-U, CL-M, CL-L, DH-U, DH-M) (Fig. 5*a*). Sugar maple in these stands had foliar Mg $\geq 700$ mg·kg$^{-1}$. Similarly, stands with a DSI as high as 6 for the 10 years prior to health evaluation had values of PDEADSM which were classified as non-declining (CL-U, CL-M, CL-L, DH-U, DH-M, RC-U, RC-L); sugar maple in these stands also had foliar Mg $\geq 700$ mg·kg$^{-1}$ (Fig. 5*b*). By contrast, in the ID-U stand, sugar maple with 529 mg Mg·kg$^{-1}$ and only one moderate defoliation in the 10 years prior to health evaluation (DSI = 2) was classified as non-declining.

Using data from all 43 stands, a multiple linear regression containing a constant, foliar Mg and Mn concentration, and the defoliation severity index for the 10 years prior to health evaluation accounted for 46.4% of the variation in PDEADSM ($p < 0.001$); including the stand variables, PBCBA and RSMD, did not significantly increase the proportion of the variability accounted for by the regression (2.4%). A similar multiple linear regression for the 25 unglaciated stands accounted for 54.6% of the variability in PDEADSM ($p < 0.001$); including the stand variables increased the $R^2$ by only 2.8%.

## Discussion

### Association of nutrition with glaciation, topographic position, and sugar maple health

Nutrition, particularly of Mg and Mn and defoliation stress during the preceding 10 years, were the most important factors associated with sugar maple health; competitive stresses due to stand conditions had relatively little effect on stand health. Our results not only suggest the importance of base cations, particularly Mg, for health of sugar maple (Mader and Thompson 1969; Bernier and Brazeau 1988*c*; Bernier et al. 1989; Bauce and Allen 1992; Kolb and McCormick 1993; Côté et al. 1995; Ouimet and Camiré 1995; Wilmot et al. 1995, 1996; Long et al. 1997) but also point to a potential role for Mn toxicity. Manganese toxicity only recently has been associated with sugar maple decline (Timmer and Teng 1999), though Mn-induced Ca and Mg
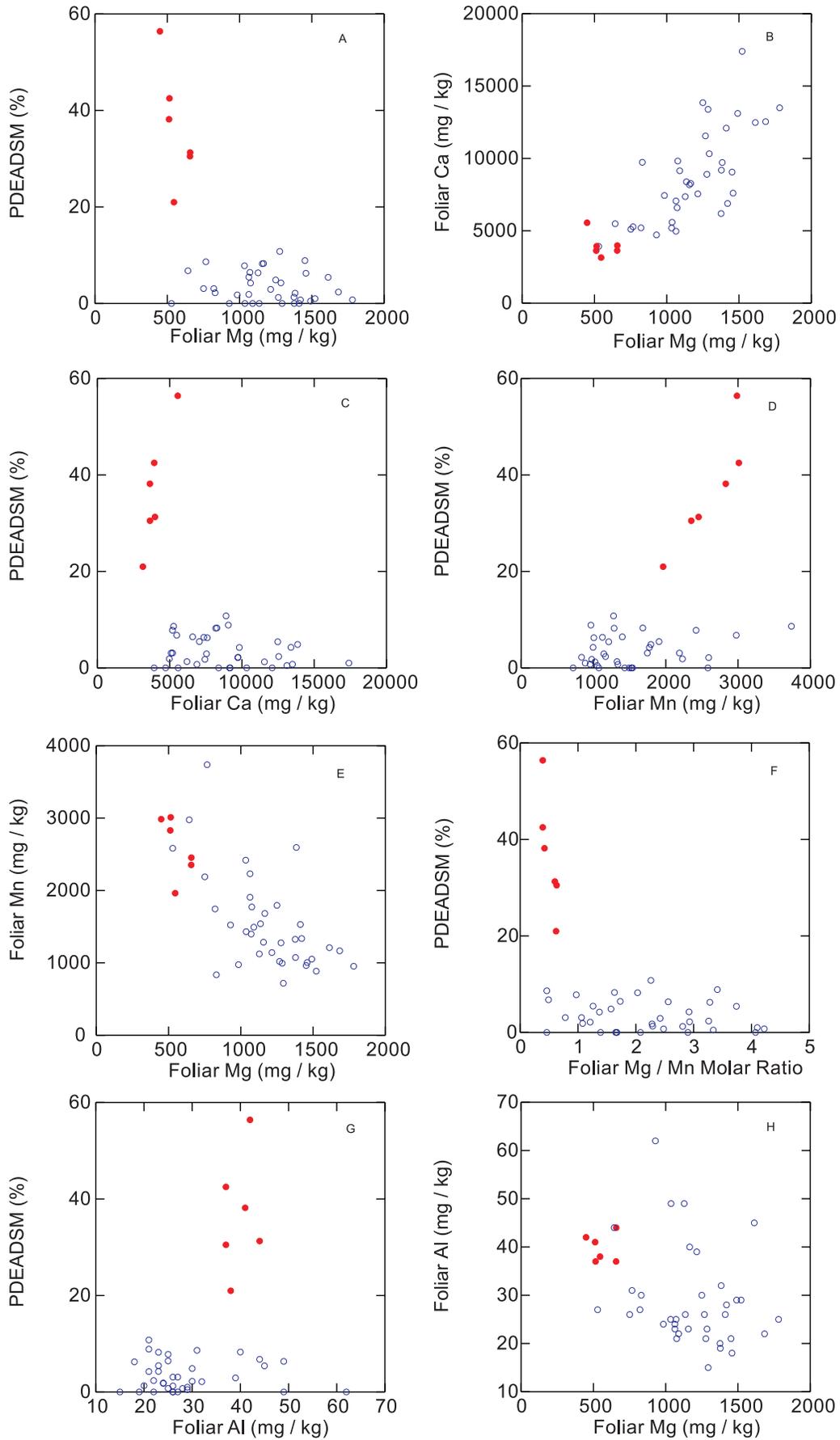
**Fig. 4.** Relationship between sugar maple health as measured by PDEADSM and (*a*) the number of defoliation events in the past 10 years ($R^2 = 0.072$, $p = 0.083$) or (*b*) in the past 20 years ($R^2 = 0.062$, $p = 0.107$) and between sugar maple health and the defoliation severity index (*c*) in the past 10 years ($R^2 = 0.158$, $p = 0.008$) or (*d*) in the past 20 years ($R^2 = 0.138$, $p = 0.014$). Solid symbols show stands with moderate to severe decline. Open symbols show non-declining stands.
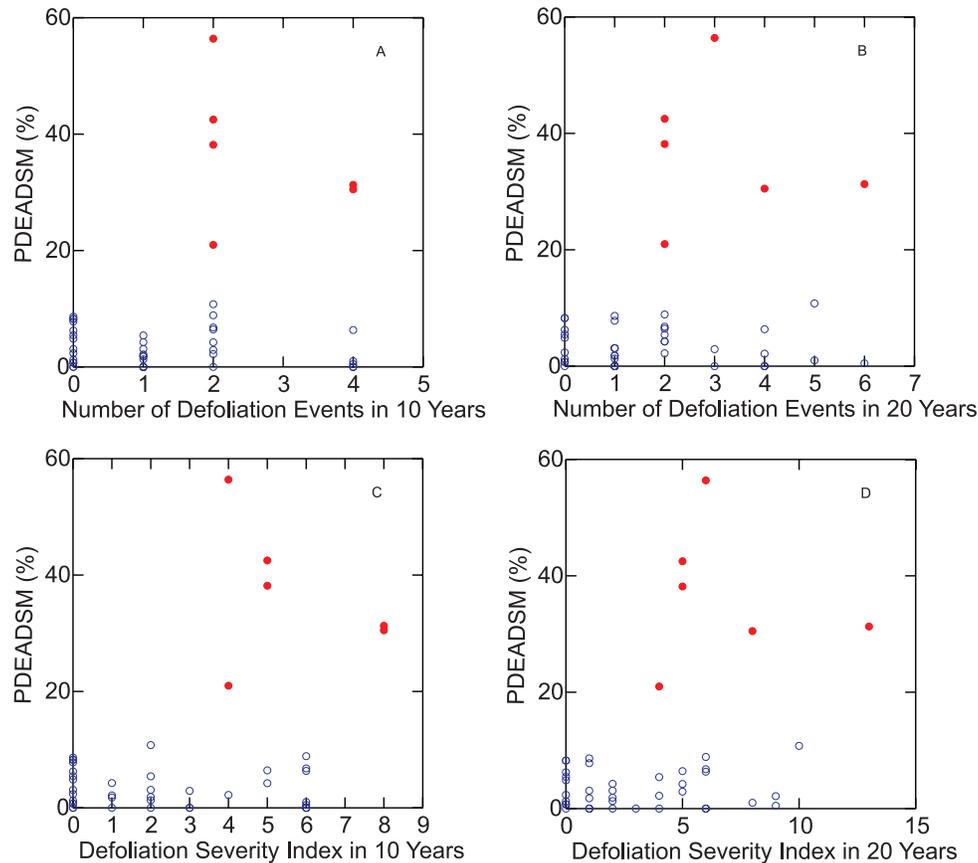


deficiencies have been reported for agricultural crops (Horst 1988; Marschner 1995).

Glaciation, topographic and physiographic position, and elevation were surrogates for foliar nutrition of Mg (and Ca) and appear to delineate landscape positions with inadequate base cation supply where sugar maple may be vulnerable to other stresses. All six stands with unhealthy sugar maple were associated with unglaciated upper slopes on summits, shoulders, and upper backslopes. Sugar maple sample trees on these vulnerable sites had the lowest foliar levels of Mg and Ca, lowest molar ratios of Mg/Mn and Ca/Al, and the highest foliar levels of Mn and Al (Table 2). Soils on the unglaciated portions of the Allegheny Plateau are dominated by Ultisols with low base cation status inherited from the parent material (Ciolkosz et al. 1989). On the basis of geologic and pedologic studies on these sites, Bailey et al. (1999) have proposed a model to explain the observed differences in base cation nutrition with glaciation and landscape position: on unglaciated sites, weatherable minerals are located well below the rooting zone or in bedrock and, thus, are unavailable to trees growing on the summit or upper slopes. On middle or lower slopes weathering products such as Mg and Ca probably become available as a result of water flowpaths that bring weathering products from deeper

soil layers or bedrock to the rooting zone; hence, the importance of seeps. By contrast, soils on glaciated portions of the Allegheny Plateau were derived from material more recently exposed by glacial erosion; these soils are Inceptisols containing weatherable materials within the rooting zone. It should be noted that the contrast between glaciated and unglaciated soils is not universal. For example, glacial till derived primarily from an orthoquartzite would be expected to contain few weatherable minerals. In New England, nutrient-budget studies have identified glaciated sites with low base cation status that are susceptible to accelerated acidification (Bailey et al. 1996; Likens et al. 1998).

Acid deposition may contribute to the low base cation status on upper slope Ultisols, although its influence relative to geologic factors is unclear. Northwestern Pennsylvania receives relatively high levels of $NO_3^-$ and $SO_4^{2-}$ via acidic deposition (Lynch et al. 1997). Such inputs accelerate loss of base cations (Knoepp and Swank 1994; Bailey et al. 1996; Likens et al. 1998; Markewitz et al. 1998). Limited resampling of soils at forested sites in northwestern Pennsylvania using the analytical methods of the original sampling suggested a trend of increasing soil acidity since the 1960s (Drohan and Sharpe 1997), although these results have not been confirmed by reanalysis of archived soils or nutrient

**Fig. 5.** Relationship between foliar Mg (mg·kg$^{-1}$) and defoliation stress as measured by (*a*) the number of defoliation events in the past 10 years and (*b*) the defoliation severity index for the past 10 years. Solid symbols show stands with moderate to severe decline. Open symbols show non-declining stands.
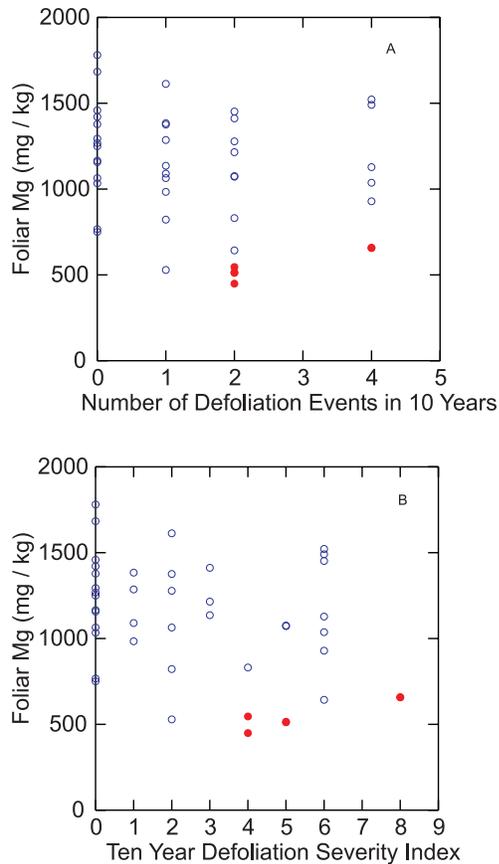


budgets. In northern Pennsylvania, the relative contributions of geologic factors and acidic deposition to low base cation status and sugar maple decline remain unquantified.

## Association of stress with sugar maple decline

Disturbance caused by insect defoliation was an important form of stress in our study. Both NDE and DSI were significantly related to PDEADSM (Table 1); the DSI for the past decade produced the strongest relationships. Studies of defoliation effects on sugar maple have shown that effects on nonstructural carbohydrates, particularly root starch reserves, play a critical role in tree vigor (Parker and Houston 1971; Wargo et al. 1972; Wargo 1981*a*, 1988*b*, 1988*c*, 1999; Gregory and Wargo 1986; Gregory et al. 1986; Renaud and Mauffette 1991). These studies show that the number, severity, and timing (both within a growing season and number of consecutive years) of defoliations and the physiological condition of the tree when defoliation occurs contribute to the outcome (Parker 1981). Both the number and the severity of defoliations have a strong negative relationship with root starch reserves at the beginning of the dormant season; defoliations that cause refoliation have the greatest effect (Wargo 1981*a*, 1988*b*, 1988*c*; Gregory and Wargo 1986). Sugar maple in some of our stands were more resilient than those in

others; some stands with NDE ≥ 2 and DSI ≥ 4 did not have symptoms of decline, while trees with the same number and severity of defoliations in other stands were declining. These resilient stands were on sites where foliar Mg was greater than ~700 mg·kg$^{-1}$, suggesting that Mg nutrition conveys better physiological condition. Furthermore, stands with low Mg status were found among the non-declining stands if DSI < 4 (ID-U, CO-U) or if other factors that promote tree vigor, like thinning (Nowak 1996), had occurred relatively recently (RC-U).

We did not study the effects of drought per se. Kolb and McCormick (1993) suggested the involvement of drought stress alone or in association with defoliation in the decline of sugar maple in Pennsylvania on sites similar to our upper slope unglaciated sites. Upper slopes are the driest positions in the landscape. Like defoliation, drought has negative effects on accumulation of root starch, although the effects of drought seem to be less than those of defoliation (Parker and Patton 1975).

Defoliation and drought have been associated with biochemical changes that encourage attack of sugar maple by secondary organisms, such as *Armillaria* (Wargo and Harrington 1991; Bauce and Allen 1992). In addition to reduced root starch supplies, defoliation and drought increase reducing sugars and alter the composition of amino acids and phenolic defensive compounds, which increase root susceptibility to *Armillaria* infection (Wargo and Houston 1974; Garraway et al. 1991; Wargo and Harrington 1991).

## Interaction of nutrition and stress

Our data suggest that the sugar maple decline on the unglaciated Allegheny Plateau is the result of an interaction between nutrition and stress. Past research on sugar maple decline generally has focused on stress or nutrition without providing spatially explicit quantitative data (Mader and Thompson 1969; Giese et al. 1964; Bernier and Brazeau 1988*c*; Kelley 1988; Hendershot and Jones 1989; Bauce and Allen 1991; Allen et al. 1992*a*, 1992*b*; Côté et al. 1993; Kolb and McCormick 1993; Côté et al. 1995; Robitaille et al. 1995; Wilmot et al. 1995; Payette et al. 1996). Stress alone can result in mortality even if nutrition is sufficient but only if the stress is severe or prolonged (Houston 1992).

The roles of Mg and Mn in sugar maple decline may be linked to their physiological and biochemical functions and to interactions between them (Maas et al. 1969). Much of what is known comes from work on agricultural crops. Magnesium deficiency due to Mg uptake inhibition by other cations, including K, NH$_4$ (Kurvits and Kirkby 1980), Ca, Mn (Heenan and Campbell 1981), and H (Marschner 1995), is well known in agriculture. The roles of Mg and Mn nutrition and defoliation (and drought) stress in plant carbohydrate economy suggest that root storage carbohydrates may be an integrating factor in sugar maple decline. In studies with other plants, both Mg deficiency and Mn excess have been associated with reduced leaf chlorophyll, net photosynthesis, and transport of leaf carbohydrates (Hecht-Buchholz et al. 1987; Marschner 1995). Observations of sugar maple trees and seedlings in field studies corroborate these results. Trees with low foliar Mg and (or) Ca had reduced foliar levels (mass basis) of chlorophyll (Liu et al. 1997; T. Noland, personal communication) and lower net photosynthesis

(Ellsworth and Liu 1994; Liu et al. 1997) than trees with higher Ca and Mg. Ultrastructural evaluation of leaves from seedlings with high foliar Mn showed evidence of an accumulation of foliar starch compared with those with low foliar Mn (McQuattie et al. 1999). Reduced production and transport of carbohydrates from leaves typically leads to a decrease in carbohydrates at sinks such as roots (Marschner 1995). There is abundant evidence that severe defoliation events or multiple defoliation events that result in reduction in crown area by >50% result in lower root storage carbohydrate levels (Wargo et al. 1972; Wargo 1981*a*, 1981*b*, 1981*c*, 1999; Gregory et al. 1986; Renaud and Mauffette 1991; Kolb et al. 1992). Single light to moderate defoliations do not seem to reduce root starch reserves at the beginning of the dormant season. However, the effects of chronic reductions in photosynthetic rate on root starch reserves that result from deficiencies in base cations are not known. It also is not clear whether carbohydrate starvation alone is the cause of sugar maple mortality or whether mortality results from the action of secondary organisms such as *Armillaria* (Parker and Houston 1971; Wargo and Houston 1974; Garraway et al. 1991; Wargo and Harrington 1991).

The decline of sugar maple in Pennsylvania fits the definition of a decline disease suggested by Manion (1991) and Houston (1992): a syndrome of canopy-dominant trees characterized by a gradual deterioration in health and vigor that frequently ends in death. Decline diseases seem to result from complex interactions of abiotic and biotic factors that predispose or weaken trees, followed by inciting or triggering events that result in dieback and mortality. Our study suggests that sugar maple is predisposed to decline by imbalanced Mg (and Ca) and Mn nutrition and incited to decline by excessive stress, particularly from defoliation (and perhaps drought).

## Acknowledgments

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