Sugar maple growth in relation to nutrition and stress in the northeastern United States

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Abstract. Sugar maple, *Acer saccharum*, decline disease is incited by multiple disturbance factors when imbalanced calcium (Ca), magnesium (Mg), and manganese (Mn) act as predisposing stressors. Our objective in this study was to determine whether factors affecting sugar maple health also affect growth as estimated by basal area increment (BAI). We used 76 northern hardwood stands in northern Pennsylvania, New York, Vermont, and New Hampshire, USA, and found that sugar maple growth was positively related to foliar concentrations of Ca and Mg and stand level estimates of sugar maple crown health during a high stress period from 1987 to 1996. Foliar nutrient threshold values for Ca, Mg, and Mn were used to analyze long-term BAI trends from 1937 to 1996. Significant ($P \leq 0.05$) nutrient threshold-by-time interactions indicate changing growth in relation to nutrition during this period. Healthy sugar maples sampled in the 1990s had decreased growth in the 1970s, 10–20 years in advance of the 1980s and 1990s decline episode in Pennsylvania. Even apparently healthy stands that had no defoliation, but had below-threshold amounts of Ca or Mg and above-threshold Mn (from foliage samples taken in the mid 1990s), had decreasing growth by the 1970s. Co-occurring black cherry, *Prunus serotina*, in a subset of the Pennsylvania and New York stands, showed opposite growth responses with greater growth in stands with below-threshold Ca and Mg compared with above-threshold stands. Sugar maple growing on sites with the highest concentrations of foliar Ca and Mg show a general increase in growth from 1937 to 1996 while other stands with lower Ca and Mg concentrations show a stable or decreasing growth trend. We conclude that acid deposition induced changes in soil nutrient status that crossed a threshold necessary to sustain sugar maple growth during the 1970s on some sites. While nutrition of these elements has not been considered in forest management decisions, our research shows species specific responses to Ca and Mg that may reduce health and growth of sugar maple or change species composition, if not addressed.

Key words: Acer saccharum; *basal area increment; base cations (Ca, Mg, Mn); black cherry; foliar nutrient threshold; sugar maple.*

Introduction

Sugar maple (*Acer saccharum*) health and growth in the northeastern and Lake States of the United States and eastern Canada are threatened by multiple factors including disturbance from insect defoliators that have incited periodic declines with accelerated mortality (Gross 1991, Kolb and McCormick 1993, Payette et al. 1996, Horsley et al. 2002). Predisposing stresses include nutrient imbalances that are frequently implicated in sugar maple declines (Mader and Thompson 1969, Bernier and Brazeau 1988, Bernier et al. 1989), while decreased basal area increment (BAI) has been associated with increased soil acidity (Duchesne et al. 2002). Evidence of these threats is demonstrated by numerous decline episodes in the past 50 years throughout the region (Houston 1999, Horsley et al. 2002). Nutrient base cation addition studies have shown that sugar maple health, growth, foliar nutrient status, flower and seed production, and seedling survival are limited by low soil levels of Ca and/or Mg (Long et al. 1997, 1999, Moore et al. 2000, Juice et al. 2006). Long-term acidic deposition inputs have resulted in decreased exchangeable soil base cation concentrations and decreased health and growth of sugar maple (Duchesne et al. 2002, Bailey et al. 2004, 2005).

Stress events are key factors that incite sugar maple decline (sensu Manion 1991). Fig. 1 is a conceptual model (modified from Hallett et al. 2006) showing relationships among base cations (Ca and Mg), acidification (Mn and aluminum [Al]), and the effects of stressors on net photosynthesis, stress response systems (e.g., wound repair, cold tolerance) and carbohydrate supply, factors that affect sugar maple health and
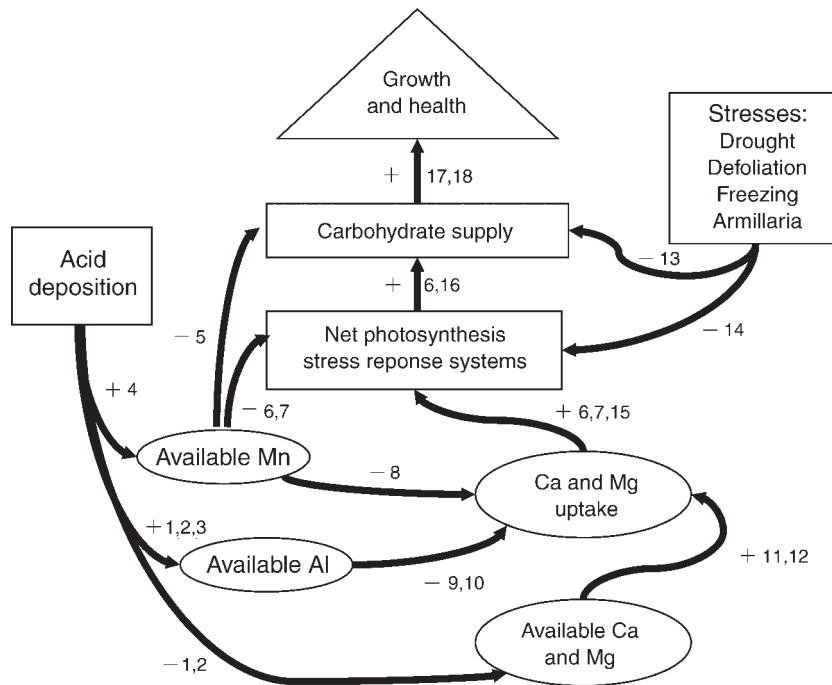
Fɪɢ. 1. Conceptual model outlining our current understanding of sugar maple health and growth. Positive and negative signs indicate the nature of the correlative relationship between variables. Numbers refer to citations: 1, Duchesne et al. (2002), 2, Bailey et al. (2005); 3, Lawrence et al. (2007); 4, Reisenaur (1988); 5, McQuattie et al. (1999); 6, St. Clair et al. (2005); 7, St. Clair et al. (2008); 8, McQuattie and Schier (2000); 9, Foy et al. (1978); 10, Cronan and Grigal (1995); 11, Long et al. (1997); 12, Bailey et al. (2004); 13, Wargo et al. (2002); 14, Pallardy and Rhoades (1993); 15, Ellsworth and Liu (1994); 16, DeHayes et al. (1999); 17, Pallardy (2008); 18, Renaud and Mauffette (1991).

growth. Insect defoliation, drought, late spring frosts, and midwinter freeze–thaw cycles frequently have been associated with sugar maple decline (Houston 1999, Horsley et al. 2002). Secondary organisms such as *Armillaria* fungi serve as mortality agents. Studies conducted in 76 stands in northern Pennsylvania, New York, Vermont, and New Hampshire identified foliar nutrient (Ca > 5500 mg/kg, Mg > 700 mg/kg, and Mn < 1900 mg/kg) and soil thresholds (Ca > 0.2 cmol$_c$/kg, Mg > 0.05 cmol$_c$/kg, Ca:Al molar ratio > 0.03) that enable trees to withstand stresses associated with defoliation and drought, but maintain healthy crown vigor (Horsley et al. 2000, Bailey et al. 2004, Hallett et al. 2006). A large number of studies have documented the interacting factors affecting sugar maple health as cited in Fig. 1, but only a few studies have addressed whether these factors also affect growth.

Several studies have contrasted BAI of healthy and declining sugar maple in relation to soil and nutrient factors. These studies show that BAI of trees that eventually declined began to decrease at least 20 years before visible symptoms of decline were observable (Kolb and McCormick 1993, Duchesne et al. 2002, 2003). Ca and Mg and the Ca:Al molar ratio were positively correlated with BAI, while Mn and N were negatively associated with BAI (Stanturf et al. 1989, Heisey 1995). Moreover, all species did not respond similarly to these elements. During a manipulative study

in northern Pennsylvania from 1985 to 1993, sugar maple basal area increased in response to dolomitic lime applications compared with control plots (Long et al. 1997). Both black cherry and American beech (*Fagus grandifolia*) showed no significant response to liming.

In this study, we used a regional network of sites to examine the influence of a range of site and environmental factors that may affect sugar maple BAI from northern Pennsylvania to New Hampshire (Fig. 2). We evaluated the influence of nutrition, crown health, topography, climate, stand structure, and stand disturbance from defoliation on sugar maple growth at the same 76 stands examined by Hallett et al. (2006). Specific objectives of this research were to (1) determine whether site nutrition, stand health, topographic, climatic, and stand structure variables affected recent short-term (10-year) trends in BAI; (2) determine the relationship between foliar nutrient thresholds (Horsley et al. 2000), soil nutrient thresholds (Bailey et al. 2004), and long-term (60-year) BAI trends; (3) determine whether the BAI of a co-occurring species, black cherry, responds to the same foliar and soil nutrient thresholds as sugar maple.

These objectives will test the relationships described in the conceptual model (Fig. 1) related to sugar maple growth and will allow us to propose guidelines for land managers.
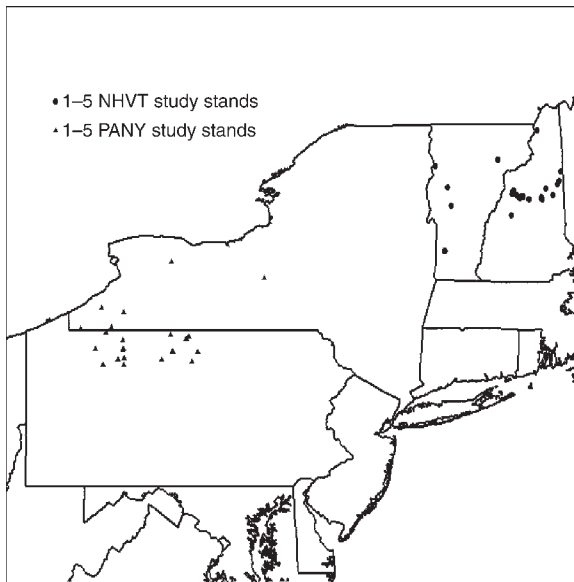
FIG. 2. Study sites located in New Hampshire and Vermont (NHVT, $n = 30$) and in Pennsylvania and New York (PANY, $n = 46$); 1–5 means that each symbol represents 1–5 stands that were sampled at that location.

METHODS

Study sites

A total of 76 sites (Fig. 2) was selected to span the range of major soil orders on which sugar maple is found in the northeastern United States (Alfisols, Inceptisols, Ultisols, and Spodosols), including 46 stands in Pennsylvania (PA) and southwestern New York (NY) and 30 stands in New Hampshire (NH) and Vermont (VT). The objective of our stand selection criteria was to span the range of site nutrition on which sugar maple grows in the northeastern United States and was not intended to provide a statistical representation of any particular area. The lithologic composition of bedrock and soil parent materials included granite, syenite, schist, phyllite, quartzite, amphibolite, marble, dolostone, sandstone, and shale. Soil parent materials included unglaciated residuum and colluvium as well as Wisconsinan glacial drift. Elevation ranged from 71 to 885 m above sea level. When not referring to sites across the entire region ($n = 76$), we combined all the Pennsylvania and New York sites ($n = 46$) and referred to these as PANY; the New Hampshire and Vermont sites ($n = 30$) are referred to as NHVT.

Stand health evaluation

Stand health was evaluated in mid to late July 1996 and 1997 for PANY stands or 1998 and 1999 for NHVT stands using modified protocols from the North American Maple Project (NAMP; Cooke et al. 1996, Horsley et al. 2000). Plots were established to represent the range of stand conditions, to characterize the vegetation composition and stand health, and to include healthy overstory sugar maples used for foliage sampling. In each stand, three circular 400-m^2 plots were established and all standing live and dead trees ≥ 10 cm in diameter at 1.4 m (diameter at breast height [dbh]) were measured and evaluated by species, dbh, and crown class (dominant, codominant, intermediate, suppressed). Crown health was assessed by estimating sugar maple crown vigor index (SMVIG) using NAMP definitions: 1 = healthy, <10% branch dieback or twig mortality; 2 = light decline with 10–25% of the crown damaged; 3 = moderate decline with 26–50% of the crown damaged or with abnormal conditions; 4 = severe decline with more than 50% of the crown damaged; and 5 = standing dead (Cooke et al. 1996). SMVIG was averaged by stand to provide an overall estimate of sugar maple health. Percent dead sugar maple basal area (PDEADSM) was used as a measure of stand health and was calculated as the proportion of the total stand basal area of sugar maple that was composed of standing dead trees (SMVIG = 5).

Defoliation and disturbance histories

To assess the impact of defoliation and disturbance on stand growth, we queried land managers and forest health specialists who maintain GIS databases of annual aerial defoliation sketch maps in the respective state forestry agencies and U.S. Forest Service, Northeastern Area State and Private Forestry. Estimates of the number and severity of defoliation events during the 10 years before health evaluation were collected. Defoliation severity was rated as 1 = light (<30% defoliation), 2 = moderate (31–60% defoliation), and 3 = severe (>60% defoliation). A defoliation severity index (DSI) was developed by summing the severity values over the preceding 10 years. For example, in the 10-year period before health evaluation a stand may have had a moderate defoliation in year 4, heavy defoliation in year 5, and no defoliation in the remaining eight years. This stand would have a DSI value of 5. No stands affected by the 1998 ice storm in New York and New England were included in this study.

Foliage sampling and analysis

We used foliage nutrient concentrations of presumably healthy overstory trees as a bioassay of site nutritional quality because foliage integrates site nutrition in both vertical and horizontal dimensions (Armson 1973, Leaf 1973, Morrison 1985). Previous research at the Pennsylvania and New York sites showed that 76% of the variation in foliar Ca and 69% of the variation in foliar Mg could be accounted for by upper B horizon soil extractions (Bailey et al. 2004). In each stand, foliage was sampled from three to six presumably healthy (vigor class = 1) dominant or codominant sugar maples at least 25 cm dbh. A mid-crown sample of sun-exposed leaves was obtained from each tree during the last two weeks of August. Foliage samples were collected by shooting small branches from the periphery of the

crown with a shotgun and were processed as described by Hallett et al. (2006). For PANY, foliage samples were obtained in 1995–1996 and for NHVT, samples were taken in 1996–1997. Previous research showed that apparently healthy trees sampled in two successive years at the same time of the growing season showed acceptable levels of repeatability ($R^2 > 0.60$) for some nutrients (R. P. Long and S. B. Horsley, *unpublished data*). Ca ($R^2 = 0.625$, $P = 0.001$), Mg ($R^2 = 0.857$, $P < 0.001$), and Mn ($R^2 = 0.715$, $P < 0.001$) all had acceptable repeatability. Foliage chemistry values from individual trees were averaged to create stand means.

The three to six sample trees in each stand were used to calculate mean stand ages and mean dbh of sampled trees for each stand. Mean age for sampled trees in PANY stands was 89.2 years (range = 55–136 years) for the 46 stands, and mean dbh of sampled trees was 39.9 cm (range = 26–56 cm). For NHVT stands mean age was 99.9 years (range = 54–152 years) while mean dbh of sampled trees was 37.5 cm (range = 31–51 cm) for the 30 sampled stands.

Increment core sampling and processing

Growth analysis was conducted on increment cores obtained from the same three to six sugar maples used for foliar sampling at a site. In total, 371 trees were sampled across the 76 sites in the region. Two cores were taken from each tree approximately 180° apart at 1.3 m above the ground, parallel with the slope contour. Cores were air-dried, glued to wooden holders, sanded to enhance ring boundaries, and visually cross-dated and measured to 0.001 mm by personnel at the Tree Ring Laboratory, Lamont-Doherty Earth Observatory (Palisades, New York, USA). Cross-dating and measurement quality control were validated using the program COFECHA (Holmes 1983). Locally absent rings were inferred from a regional chronology and were frequently associated with defoliation events (Lorimer et al. 1999). If a core could not be reliably dated, it was omitted. Data from a total of 363 trees were validated and used in subsequent growth analyses. Because sugar maple is shade tolerant and juvenile growth can be highly suppressed, we omitted any suppressed juvenile ring width data.

To compare sugar maple growth with a co-occurring species that has not had a history of regional decline episodes, we sampled 115 dominant or codominant, vigor = 1, healthy, black cherry trees growing in 23 of the 46 sugar maple stands in PANY. Sampled black cherry trees were in the same stands as the sampled sugar maples. Increment cores were sampled, cross-dated, measured, and validated as described above.

To compare growth patterns, ring-width measurements were converted to basal area increments (BAI) using the following formula:

$$BAI_t = \pi(RA_t^2 - RA_{t-1}^2)$$

where RA is the tree radius at time t that corresponds to the year of ring formation. To preserve both low and high frequency variance, and particularly to preserve any long-term trend, BAI estimates were not standardized (Duchesne et al. 2002, 2003).

Soil sampling and analyses

A representative sampling pit was located in each stand by using county soil survey maps and on-site reconnaissance. Pedons were described using protocols of the Soil Conservation Service (1993) to a depth of at least 130 cm unless bedrock was encountered at a shallower depth. For each horizon, rock fragment content, expressed as the volume percentage of coarse fragments (>2 mm to 25 cm diameter), was estimated by comparing the pit face to the percentage area charts and by examining horizon samples removed for analysis. Depth to a root-restricting layer was measured as the distance from the soil surface to a fragipan, densipan, bedrock, or to the base of the pit (130 cm) in the absence of any of the preceding. The depth from the surface to the shallowest redoximorphic features was also recorded. Seeps were recorded as present or absent.

Soils were sampled by genetic horizon for subsequent chemical analysis. Samples were air-dried and screened to remove particles >2 mm. Soil chemistry was determined as described in Bailey et al. (2004).

Although all horizons were sampled and analyzed, we confined our statistical analyses in this work to soil variables measured in the upper B horizon samples. Earlier work showed that upper B horizon soil chemistry variables had the highest correlations with foliar chemistry compared with lower B and Oa/A horizons (Bailey et al. 2004).

Because of its widely reported importance, we examined the influence of the Ca:Al molar ratio (Cronan and Grigal 1995) based on values from the upper B horizon soils. Using data from Bailey et al. (2004), we found that stands with poor crown health and high levels of sugar maple mortality had Ca:Al molar ratios <0.03 and we used this as the Ca:Al threshold value.

Topographic, climatic, and stand structure variables

Local physiography was classified for each stand using a system similar to that of the NAMP (Cooke et al. 1996). Physiographic positions were grouped together in the following classifications: summit and shoulder (physiography = 1); upper backslopes (physiography = 2); middle backslopes (physiography = 3); lower backslopes (physiography = 4); foot or toeslopes, benches, or any topographic position with concave topography (physiography = 5). At each stand we measured slope with a clinometer and used a compass to estimate aspect to the nearest degree.

Elevation was determined from topographic maps at the plot center, where GPS coordinates were recorded. USGS 7.5-minute topographic maps were used to measure the elevation and horizontal distance (m) to the highest point and lowest point directly upslope and downslope from each stand. Land index, the relative

TABLE 1. Ranges of foliage, soil, topographic, climatic, stand structure, and stand health variables for sugar maple stands in two subregions, northeastern USA, and Pearson correlations of these variables with regional basal area increment (BAI) and the associated probability levels.

Variables	NHVT (N = 30 stands)	PANY (N = 46 stands)	Correlation (N = 76 stands)	P
Foliage chemistry				
Nitrogen (mg/kg)	11 800–22 600	15 100–21 600	0.142	0.219
Phosphorus (mg/kg)	925–2447	953–2318	0.192	0.097
Potassium (mg/kg)	5187–1142	5421–11 154	−0.222	0.053
Calcium (mg/kg) L10	3161–24 106	3146–18026	**0.606**	**<0.001**
Magnesium (mg/kg) L10	457–2275	499–2867	**0.617**	**<0.001**
Manganese (mg/kg) SQR	179–3112	191–3738	**−0.408**	**<0.001**
Soil chemistry				
Exchangeable potassium, upper B horizon (cmol$_c$/kg)	0.026–0.390	0.033–0.384	−0.158	0.172
Exchangeable calcium, upper B horizon (cmol$_c$/kg) L10	0.200–21.580	0.044–9.020	**0.564**	**<0.001**
Exchangeable magnesium, upper B horizon (cmol$_c$/kg) L10	0.018–1.260	0.014–3.970	**0.452**	**<0.001**
Exchangeable aluminum, upper B horizon (cmol$_c$/kg) SQR	0.002–17.634	0.002–17.387	**−0.283**	**0.013**
pH, upper B horizon	3.14–7.04	3.22–5.71	**0.265**	**0.021**
Organic matter, upper B horizon (%)	3.52–22.10	2.41–13.02	−0.133	0.251
Site/environment/stand				
Elevation (m)	71–885	204–767	−0.222	0.054
Physiographic position	1–5	1–5	**0.267**	**0.020**
Slope (%) SQR	5–68	1–46	0.040	0.733
Aspect (degrees from true north) SQR	26–338	0–358	−0.103	0.377
Depth to mottles (cm) SQR	28–130	10–130	−0.071	0.543
Depth to pan or bedrock (cm) L10	50–130	25–130	−0.035	0.761
Seep (absent or present)	0–1	0–1	0.173	0.136
Coarse fragments (%)	1–75	1–68	−0.108	0.355
Elevation of the high point (m)	112–1034	236–771	−0.109	0.349
Elevation of the low point (m)	53–686	195–646	−0.120	0.300
Distance to the high point (m) L10	90–1661	48–1127	0.159	0.170
Distance to the low point (m) SQR	36–1598	0–1129	**−0.354**	**0.002**
Relief (m) L10	85–738	55–247	0.022	0.853
Land index (m) SQR	0.122–0.954	0.055–1.000	**0.318**	**0.005**
Mean annual temperature (°C)	3.2–7.3	5.9–8.5	0.037	0.749
Mean July temperature (°C)	16.8–21.1	18.4–21.5	0.108	0.352
Annual precipitation (mm)	843.16–1598.09	1026.75–1383.35	−0.146	0.206
Total basal area (m^2/ha)	23.763–47.270	15.150–45.111	**0.258**	**0.024**
Stand health				
Percentage of dead sugar maple basal area (%) L10	0–15	0–56	**−0.527**	**<0.001**
Sugar maple crown vigor index (SMVIG) L10	1.10–2.61	1.03–3.66	**−0.583**	**<0.001**
Number of defoliation events in the last 10 years	0–1	0–4	−0.206	0.074
Defoliation severity index, 1987–1996	0–2	0–8	**−0.268**	**0.019**

Notes: Abbreviations are: NHVT, New Hampshire and Vermont; PANY, Pennsylvania and New York. Some variables were transformed, as indicated (SQR = square root; L10 = log base 10). Significant ($P \leq 0.05$) variables are shown in boldface.

position of the study stands along the hillside, was calculated by dividing distance to the high point along a slope by the sum of the distance to the high point and the distance to the low point; a stand at a summit would have a land index value of zero while a stand at the lowest point on a hillside would have a value of one. Local relief was determined as the difference in elevation between the highest and lowest point within a 1 km radius of each stand.

Total basal area was calculated using data from the 400-m^2 plots for trees ≥10 cm dbh, and is considered an estimate of the degree of competition among trees. Climatic parameters included the 30-year normal mean annual temperature and mean annual precipitation obtained from the National Cartography and Geospatial Center (data *available online*).[6] Parameter values

for the study stands were extracted after interpolating between climate monitoring stations using the parameter-elevation regression on independent slopes model (PRISM; Daly et al. 1994). In addition, the mean July temperature was calculated for each site because other research has shown responses to growing season temperature (Lane et al. 1993).

Statistical analyses

The large number of variables considered in this study (Table 1) required a strategy to identify the most important variables affecting growth. Normal probability plots of all variables were assessed to determine whether transformations were necessary (transformations are listed in Table 1). The initial focus of these analyses was on growth of sugar maple during the most recent 10-year period from 1987 to 1996. This period was selected because it represents the recent status of sugar maple

[6] ⟨http://www.ncgc.nrcs.usda.gov⟩

growth for these stands and encompasses a period when detailed records of defoliation were available that allowed explicit statistical evaluation of the effect of stress on growth. During this period, sugar maple decline became widespread across northern Pennsylvania and was coincident with stress events such as defoliation and drought.

Pearson correlation analyses were used to reduce the number of variables under consideration, limiting the variables of interest to those having correlations with the mean 1987–1996 BAI that were significant at $P \leq 0.05$. These variables were then examined using backward selection (with $P = 0.15$ for a variable to stay in the model) to determine which variables had the most influence on growth. Backward selection assumes all variables are equal candidates at the start and eliminates those that are least significant at our chosen critical level, $\alpha = 0.15$, at each stage of the analysis. We used variance inflation factors (VIF) to evaluate the degree of mulitcollinearity among the variables. VIFs revealed collinearity between Ca and Mg variables (values from 5 to 10 or greater); thus we used separate Ca and Mg backward elimination regression models (Freund and Littell 2000).

Foliar Ca and exchangeable Ca in the upper B horizon were used with the remaining significant variables in the backward elimination regression analysis; a similar procedure was used for foliar and exchangeable Mg. Due to the disparity in mortality between NHVT and PANY subregions, and because percent dead sugar maple basal area (PDEADSM) focuses on the endpoint of decline (tree mortality), we used mean sugar maple crown vigor index (SMVIG) as the measure of health because it represents a greater range in stand health conditions across the region.

We hypothesized that changes in soil chemistry may have affected sugar maple growth over time. To test for this effect, we used mean annual basal area increments calculated by tree and stand to examine growth trends over a 60-year period (1937–1996) using 12 five-year mean basal area increments. To evaluate the potential effect of foliar nutrient thresholds and the Ca:Al molar ratio in upper B horizon soils on BAI growth, we conducted a repeated measures analysis using SAS Proc Mixed (SAS Institute, Cary, North Carolina, USA) with the restricted maximum likelihood technique along with the Kenward-Roger correction method for the denominator degrees of freedom (Littell et al. 2006). An autoregressive (AR1) covariance structure using the twelve five-year mean BAIs was selected based on comparisons of the corrected Akaike information criterion (AICC) with competing covariance structures. To determine whether the growth trends in relation to the thresholds were consistent across the entire region, we first conducted an analysis with region as a variable in the model. There were no significant ($P \geq 0.05$) differences in BAI growth between regions so this was not included in further analyses. Linear combinations of least square means were used to evaluate specific pair-wise comparisons related to factors identified as significant in the analyses (Littell et al. 2006).

RESULTS

Selection of significant independent variables for objective 1

Comparison of Pearson correlations between the two subregions showed that most correlations for the 1987 to 1996 period were similar (data not shown, see Hallett et al. 2006); thus the data were pooled for the entire region ($n = 76$; Table 1). Of the six foliage variables, Ca and Mg were positively correlated and Mn was negatively correlated with BAI growth in the 1987 to 1996 period. Exchangeable Ca, Mg, and pH in the upper B horizon were positively correlated and exchangeable Al was negatively correlated with BAI from 1987 to 1996. Among the topographic, climatic, and stand structure variables, four variables were significantly correlated with growth: physiographic position, distance to the low point on the slope, land index, and total basal area (Table 1). Three of the four stand health variables were negatively correlated with BAI: sugar maple crown vigor index, percentage of dead sugar maple basal area, and defoliation severity index.

Some of the correlations differed between the two subregions for the 1987–1996 period. As expected, the correlations for the number of defoliations and defoliation severity index were not significant for the 30 NHVT stands (number of defoliations, $r = -0.018$, $P = 0.925$), because these stands had little or no history of defoliation during 1987–1996. Climatic variables had stronger correlations with BAI during 1987–1996 in NHVT (total precipitation, $r = -0.371$, $P = 0.043$) than in PANY (total precipitation, $r = -0.037$, $P = 0.806$) stands, perhaps because of the disturbances from defoliation in many of the PANY stands. Total basal area also showed contrasting correlations by subregion. For NHVT, total basal area was correlated with BAI ($r = 0.442$, $P = 0.014$) but PANY showed no such significant relationship ($r = 0.169$, $P = 0.259$).

Factors affecting growth 1987 to 1996 (objective 1)

The backward elimination procedure identified foliar Ca and sugar maple crown vigor index as the best parameters for predicting basal area growth ($R^2 = 0.46$, Table 2). A similar analysis with foliar and exchangeable Mg produced a two variable model with foliar Mg and sugar maple crown vigor index ($R^2 = 0.44$, Table 2). Both Ca and Mg were positively related to BAI while sugar maple crown vigor index was negatively related to BAI (healthier trees with a lower crown vigor index grew better).

Long-term growth trends and nutrient thresholds (objective 2)

Long-term trends in mean basal area increment by subregion, without regard to the nutrient thresholds, are shown in Fig. 3A. Although the general trends were

TABLE 2. Best regression models predicting basal area growth in the 10-year period from 1987 to 1996.

Group/variable	Variable coefficient	Coefficient P level	R^2	Regression P level
Ca variables, backward elimination				
Foliar Ca	0.376	<0.001	0.461	<0.001
Sugar maple crown vigor index	−0.243	<0.001		
Mg variables, backward elimination				
Foliar Mg	0.460	<0.001	0.445	<0.001
Sugar maple crown vigor index	−0.218	0.005		

Note: Significant variables (shown in boldface in Table 1) were considered and eliminated or kept using a backward elimination regression analysis.

similar between subregions, the PANY subregion growth trends showed greater interannual fluctuations, both higher and lower growth, than the NHVT subregion. Examination of the subregion growth trends (Fig. 3B, C) with respect to the foliar Ca threshold (5500 mg/kg) showed that trees in below-threshold stands grew less in both subregions starting about 1970. Similar results were evident (Fig. 3D, E) for the Mg threshold (700 mg/kg); however, the PANY stands that were below the Mg threshold separate by the mid to late 1960s. Before the mid-1960s or early 1970s, BAI for both above- and below-nutrient-threshold stands was similar in both subregions.

Repeated measures analysis of mean five-year BAIs for the entire region ($n = 76$ stands) had a significant threshold-by-time interaction for separate analyses of Ca, Mg, and Mn (Table 3). A significant threshold-by-time interaction means that the differences between the groups (based on the specific threshold) are not consistent over the 60-year period. For Ca, the threshold-by-time interaction indicated that stands with below-threshold foliar Ca had significantly lower BAI starting in the 1972–1976 period compared with above-threshold stands, and this difference was sustained through the subsequent periods (Fig. 4A). The Ca threshold-by-time interaction was nonsignificant for both PANY and NHVT subregions when examined separately (Table 3).

The regional growth response to the Mg threshold also had a significant threshold-by-time interaction (Table 3) with significant pairwise differences in BAI starting in the 1972–1976 period (Fig. 4B). For the subregions, only PANY had a significant threshold-by-time interaction; growth of below Mg threshold stands was significantly less starting in the 1972–1976 period compared with above-threshold stands (data not shown).

For the Mn threshold (Mn > 1900 mg/kg), there was a significant threshold-by-time interaction, and linear combinations describing regional pairwise BAI differences were statistically significant starting in the 1977–1981 period (Table 3). Similar results were seen for the PANY subregion; stands with above-threshold Mn grew significantly less starting in the 1977 to 1981 period than stands below the Mn threshold. There was no significant Mn

threshold-by-time interaction for the NHVT stands. Repeated measures analysis did not reveal any statistically significant effect of the Ca:Al molar ratio threshold in the upper B horizon soils on basal area growth (Table 3).

Comparison of BAI growth trends of black cherry with sugar maple (Objective 3)

BAIs from 115 black cherry trees growing in 23 of the 46 PANY stands were classified based on the sugar maple foliar thresholds and upper B horizon Ca:Al molar ratio to determine whether black cherry responded to the same thresholds as sugar maple. Repeated-measures analysis showed a significant, but opposite, BAI response to the Ca threshold (Table 3; Fig. 4C), and a marginally significant ($P = 0.054$) five-year BAI response for black cherry to the Mg threshold (Table 3; Fig. 4D). Similarly, time was a significant factor, while the interaction of threshold and time for Mg was nonsignificant (Table 3; Fig. 4D). Black cherry BAI responses to the Mn threshold were also significant (Table 3). Ca, Mg, and Mn threshold BAI responses for black cherry are opposite to those of sugar maple; and the separation of the two groups, while consistent throughout the 60-year period, became wider during the mid-1960s. Black cherry growth was greater in stands where sugar maple foliar Ca was <5500 mg/kg and where foliar Mg levels were at or below the 700 mg/kg threshold value. Likewise, black cherry BAI was greater in stands with above-threshold Mn levels and greater in stands with below-threshold Ca:Al molar ratios in the upper B horizon (Table 3).

Sugar maple foliar nutrient thresholds for Ca, Mg, and Mn were derived empirically from data collected across 76 stands based on sugar maple crown health and mortality. To further explore the potential differential growth responses of sugar maple to nutrition we divided the 76 stands into six groups of 12–13 stands per group based on foliar nutrient concentrations of Ca and Mg. Fig. 5A, B show the five-year mean BAI patterns for the six groups for both Ca and Mg. Sugar maples growing on sites with the highest foliar concentrations of Ca and Mg have generally increasing BAI over this 60-year period. The middle four groups show considerable variability, but essentially there is a flattening of the BAI trend across a
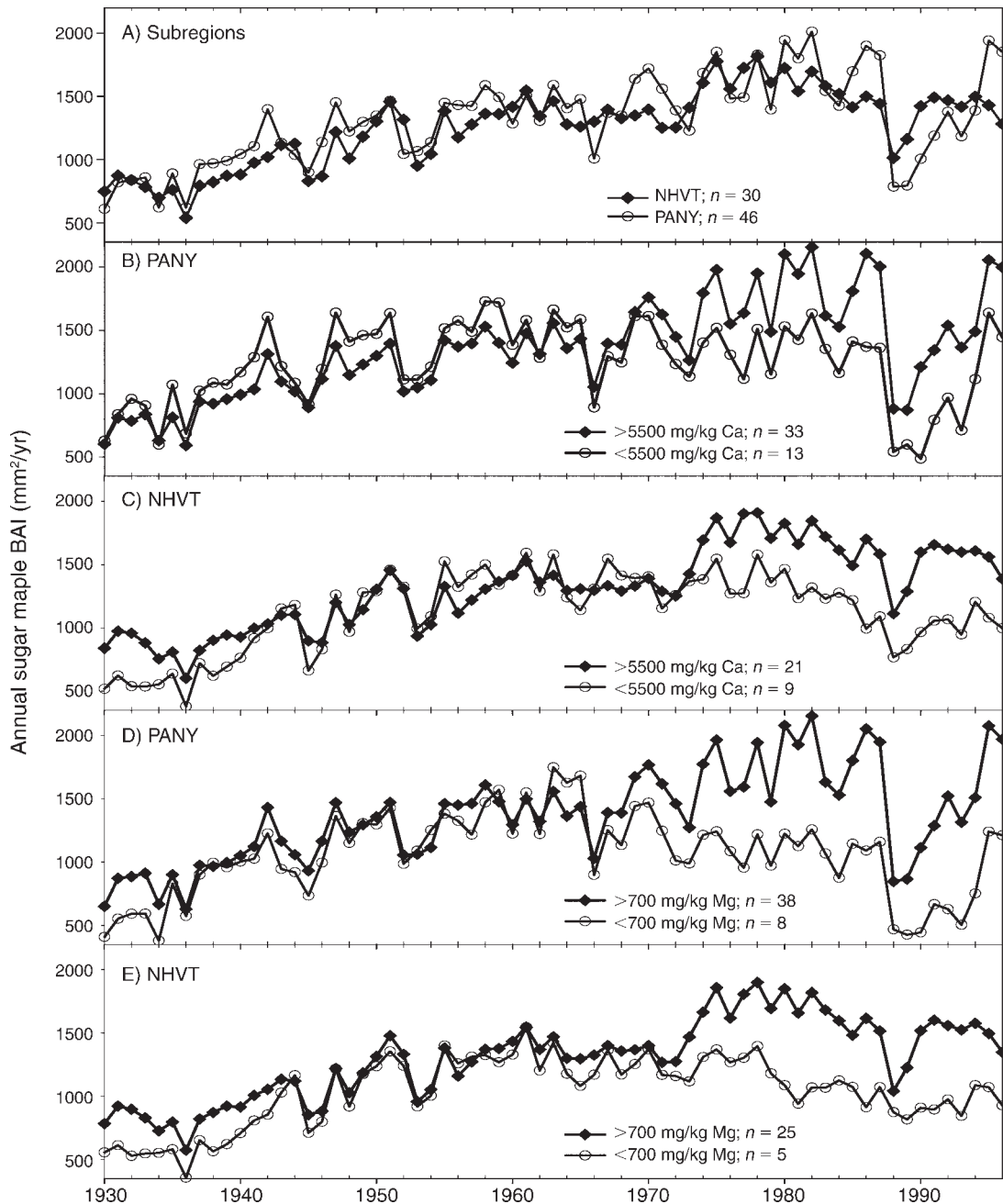
FIG. 3. Annual trends in basal area increment (BAI) for sugar maple in (A) two subregions, (B) PANY stands with groups based on the foliar Ca threshold, (C) NHVT stands with groups based on foliar Ca threshold, (D) PANY stands with groups based on the foliar Mg threshold, and (E) NHVT stands with groups based on the foliar Mg threshold. The abrupt decrease in growth in 1988 is related to a regional drought that affected these sites.

broad range of foliar nutrient concentrations. Sugar maple on sites with the lowest Ca and Mg, the below-threshold stands, had decreasing BAI after the late 1960s.

DISCUSSION

Sugar maple growth responses

The present study illustrates that even in the absence of defoliation, sugar maple BAI is affected by imbal-anced Ca, Mg, and Mn nutrition across the entire region. An inciting stress such as defoliation was required to cause decline, leading to enhanced mortality; however, imbalanced nutrition in the absence of de-foliation did cause a decrease in stand crown condition in the NHVT stands that were not defoliated in the past 30 years (Hallett et al. 2006). Foliar Ca or Mg and sugar maple crown vigor (SMVIG) had the greatest influence

TABLE 3. Repeated-measures analysis results (P values) for the effects of foliar Ca, Mg, Mn, and soil Ca:Al thresholds, time, and their interaction for sugar maple in all stands in the region ($n = 76$ stands), and for the PANY ($n = 46$) and NHVT ($n = 30$) stands.

Effect	Ca threshold	Mg threshold	Mn threshold	CA:Al threshold
Sugar maple				
Region				
Threshold	0.149	**0.019**	0.231	0.193
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Threshold × time	**0.010**	**0.003**	**0.043**	0.200
PANY				
Threshold	0.250	**0.034**	0.101	0.173
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Threshold × time	0.110	**0.008**	**0.022**	0.504
NHVT				
Threshold	0.418	0.275	0.841	0.684
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Threshold × time	0.135	0.429	0.148	0.232
Black cherry				
PANY				
Threshold	**<0.001**	0.054	**<0.001**	**<0.001**
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Threshold × time	0.260	0.267	0.091	0.129

Notes: Black cherry results are for 23 PANY stands. Values with $P \leq 0.05$ are shown in boldface.

on sugar maple growth during the high stress period from 1987 to 1996. SMVIG is a measure of visible crown health, but also provides an indication of physiological function. Correlation of mean stand total basal area with the 1987 to 1996 BAI was significant and positive for NHVT, but not for PANY. Closer examination of the data showed that the NHVT stands with the highest foliar levels of Ca and Mg also had the highest basal areas. Adequate base cation nutrition enhanced growth enough that higher levels of competition did not adversely affect sugar maple BAI in these stands.

Foliar nutrient thresholds of Ca, Mg, and Mn had a significant effect on growth in two subregions of the northeast with contrasting defoliation and stand health histories (Fig. 3). This expands on the previous research relating crown vigor and mortality measures to nutrient thresholds (Hallett et al. 2006). Stands with below-threshold amounts of foliar Ca or Mg and above-threshold Mn have decreasing BAI trends, while stands with above-threshold Ca and Mg and below-threshold Mn show a leveling off of the BAI trends (Fig. 4A, B). Basal area growth trends suggest that the separation between stands at sites with above-threshold foliar Ca and Mg and stands at below-threshold nutrition occurred sometime in the 1970s (Figs. 3, 4A, B).

Research conducted in the 1980s did not detect decreases in sugar maple growth (Hornbeck et al. 1988) because sites were not stratified by site quality. Similarly, in our study BAI flattened or leveled off at the subregional level when stands of all nutritional classes were considered together (Fig. 3A). Trees on better sites probably obscure any signal of decreasing growth detectable from trees on the sites with low base cation pools. In southern Quebec in the 1990s, research

conducted at fourteen sites showed six sites with declining BAI trends that started sometime between 1950 and 1965 (Duchesne et al. 2002). The remaining eight stands had either flat or increasing BAIs. Correlation analyses showed negative correlations of BAI trend with atmospheric N and S wet deposition, forest floor exchangeable acidity, and exchangeable K concentration in mineral B horizon. Correlations of BAI with exchangeable Mg and Ca in the mineral soil were not significant; however, the BAI trend was positively correlated with base saturation and exchangeable Ca in the forest floor (Duchesne et al. 2002). The contrast between these findings and those in our study could be related to significant differences in soil morphology, deposition inputs, and the more stressful climatic regime in Quebec.

Differences in long-term growth trends for stands above and below Ca, Mg, and Mn thresholds that became observable in the 1960s and 1970s suggest that changes in soil nutritional levels became critical for sugar maple during this period at some sites. Long-term decreases in soil pH, exchangeable Ca, and exchangeable Mg concentrations, and increases in exchangeable Al concentrations at all depths (to at least 120 cm) were documented over 30 years (1967–1997) at four forested sites on the unglaciated Allegheny Plateau in northwestern Pennsylvania (Bailey et al. 2005). Even accounting for forest growth and net biomass accumulation, the magnitude of decrease in soil pools of exchangeable Ca and Mg suggests substantial net losses. In 1967, soil exchangeable Ca and Mg were well above their respective soil nutrient thresholds, but by 1997 these values were below-threshold levels. The analysis of sugar maple growth over time suggests that growth reductions
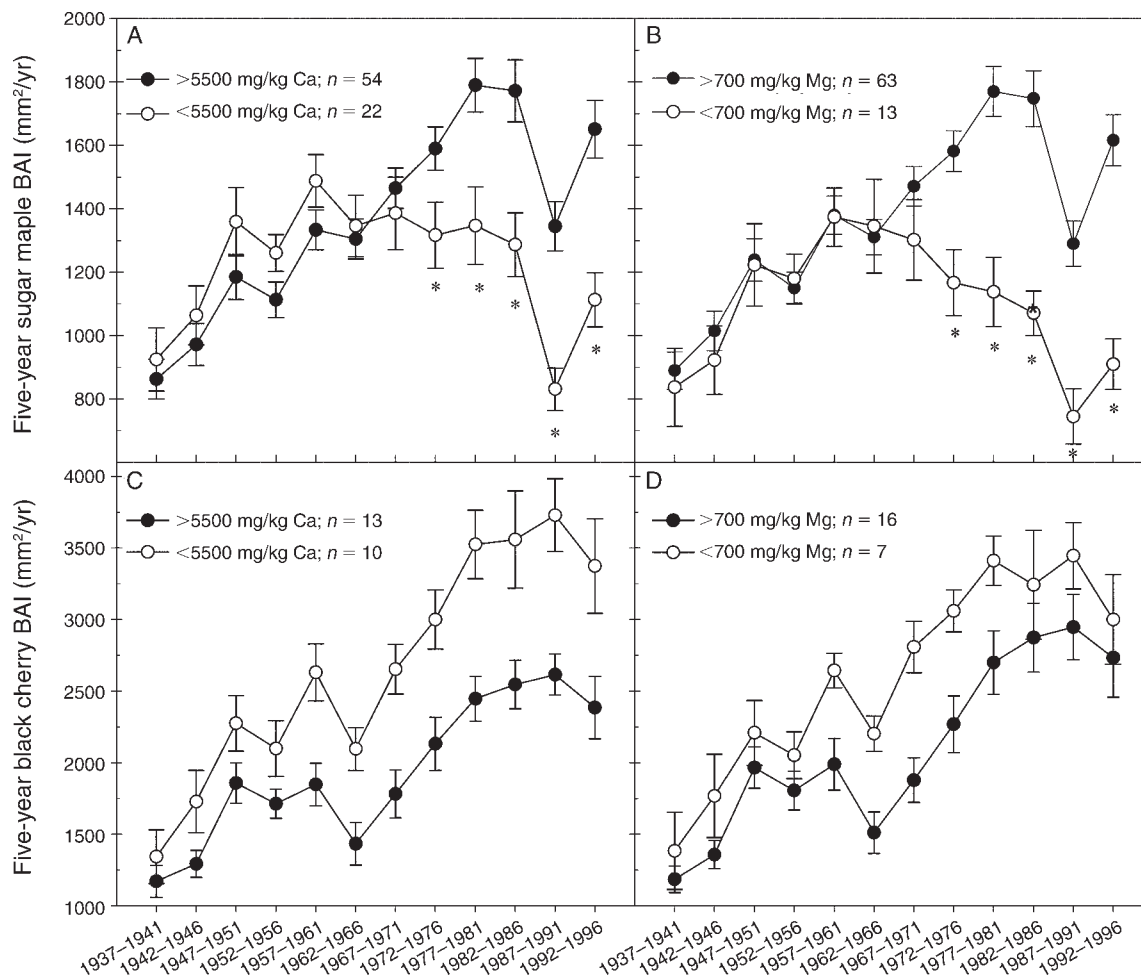
FIG. 4. (A) Mean five-year basal area increment for sugar maple in all stands based on foliar Ca thresholds and (B) in all stands based on foliar Mg thresholds, (C) mean five-year basal area increment for black cherry in 23 PANY stands that are grouped based on the Ca foliar threshold, and (D) black cherry stands grouped based on the Mg foliar threshold. Asterisks indicate significant ($P \leq 0.05$) pairwise differences. Error bars show ±SE.

in below-threshold stands began in the 1970s (Fig. 4A, B). This timing fits with data from other studies that show increasing and chronic leaching losses from forested ecosystems (Likens et al. 1998, Johnson et al. 2000) correlated with increased acidic deposition. We conclude that acidic deposition induced significant losses of exchangeable base cation pools by hydrologic leaching (Bailey et al. 2005). Landscape position, site quality, soil parent materials, and initial base cation status influence the rates of base cation losses making it difficult to determine exactly when base cations decreased below critical thresholds to sufficiently affect sugar maple stand health and growth at a particular site. While sulfate has been substantially reduced in precipitation, sulfate deposition remains well above preindustrial levels; high levels of nitrogen (NO_3^- and NH_4^+) have continued in the northeast, and base cation deposition has decreased (National Atmospheric Deposition Program [NADP] 1994–2006). Based on the

NADP data (NADP 1994–2006), we estimate that continued inputs of sulfates and nitrates will contribute to additional leaching of base cations and more sites with small base cation pools will fall below threshold quantities of Ca and Mg necessary for sustaining sugar maple growth and health. Similarly, we estimate that soil acidity will increase and greater quantities of Mn and Al will become available in the soil solution creating additional nutrient imbalances, if the deposition trends established to date by the NADP continue.

Linkage between the timing of sugar maple growth decline in the northeastern United States and increased acid deposition is supported by the incidence of red spruce, *Picea rubens*, decline in portions of the same region (Shortle and Bondietti 1992). For sensitive red spruce sites receiving acidic deposition inputs, exchangeable Ca and Mg in the forest floor decreased substantially from the 1930s to 1970s. Base cation mobilization from the forest floor was detected in red spruce xylem in
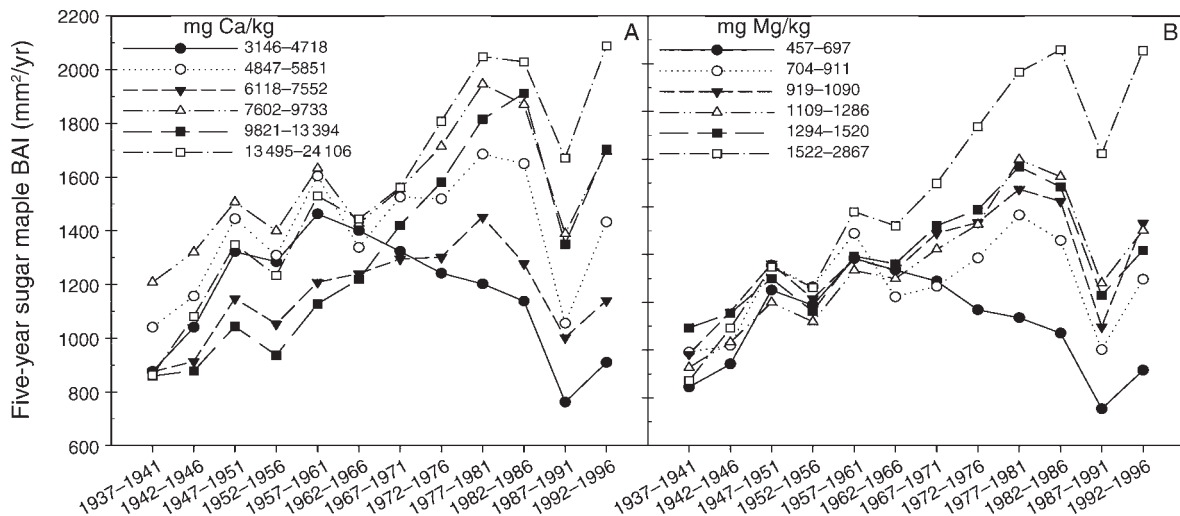
FIG. 5.   (A) Mean five-year basal area increment for sugar maple based on groupings of 12–13 stands in each of six classes spanning the range of foliar Ca levels and (B) similar groupings based on foliar Mg levels. The key shows the range in foliar Ca and Mg concentrations in mg/kg for each class.

the 1960s and this pre-dates the decline and mortality episode of the 1980s by at least 20 years (Shortle and Bondietti 1992). This is similar to the timing of the divergence of sugar maple BAI in stands with below-threshold quantities of Ca and Mg, although the timing, sites, soils, and mechanisms may be different from red spruce. Other research showed acid mist or fog induced Ca losses from current year foliage of red spruce and significantly decreased freezing tolerance (Schaberg and DeHayes 2000). Freezing injury may have weakened red spruce crown health and incited the decline and mortality of red spruce. This scenario fits the decline-disease model of Manion (1991) and is similar to the scenario associated with sugar maple decline in Fig. 1.

Species-specific responses

Black cherry, an economically valuable co-occurring species, exhibited a different growth response to an identical set of nutrient status and stress conditions on the study sites. Black cherry growth maintained linear increases in BAI on low base status sites, and BAI of black cherry, while not decreasing, was lower on sites with higher base cation levels and higher soil pH (Fig. 4C, D). Based on foliar nutrient data, sugar maple grew less on sites having below-threshold amounts of Ca or Mg and above-threshold Mn. This occurred even on sites where considerable sugar maple mortality would be expected to reduce competition for crown and root resources and allow surviving trees to increase their growth. We hypothesize that the greater black cherry BAI on low Ca and Mg sites indicates a preference for more acid soil conditions (Fig. 4C, D). This hypothesis is supported by a manipulative liming study in north central Pennsylvania initiated in 1985. In this study, species specific responses to 22.4 Mg/ha of dolomitic limestone were observed for sugar maple and black

cherry. Sugar maple growth and crown condition responded positively while black cherry and American beech crown condition and growth were unaffected by lime application (Long et al. 1997). More recent data also show that black cherry growth and survival has been negatively affected by the lime application (R. P. Long and S. B. Horsley, *unpublished data*).

Forest management implications

Maintenance of forest productivity is an important issue for forest managers. These results suggest that while individual species may be impacted by temporal changes in site quality, overall stand productivity may be maintained as other species better suited to the new conditions increase in dominance. We encourage foresters and land managers to consider species composition and base cation status when making management decisions for northern hardwood forests. Across the northern hardwood region, forests are underlain by soils having a wide range of lithologic parent materials, which interact with landscape position to produce a mosaic of base cation status. On unglaciated Allegheny Plateau sites, upper landscape positions (summit, shoulder, and upper back slope) were associated with low foliar Ca and Mg and high Mn. Middle and lower slope sites generally had base cation quantities above the established thresholds due to inputs of nutrients from colluvial processes and hydrologic inputs of weathering products derived from below the rooting zone (Bailey et al. 2004). In NHVT, lithologic sources of glacial till soil parent material are diverse and have varying amounts of base cation supplies. To guide land managers in selecting sites to culture sugar maple, vegetation indicators have been developed to identify sites with adequate base cation nutrition for sugar maple in the absence of direct data on soil quality (Horsley et al. 2008).

While it is possible to maintain site productivity with soil amendments, operational procedures have not been developed and cost effectiveness is undetermined. Silvicultural practices can be adapted to promote species composition suitable for local site conditions. Nutrient thresholds can be used to differentiate stable vs. decreasing BAI trends for sugar maple. While we interpreted the thresholds as single point values, there is a broader range where sugar maple could be "at risk" with regard to crown health or reduced growth rate (Fig. 5). We described six classes for Ca and Mg that show a range of BAI responses (Fig. 5). Stands with the lowest amounts of foliar Ca and Mg, represent below health threshold stands and show decreasing BAI trends. These stands are the most vulnerable to decline from acute stressors, such as drought or defoliation. For the PANY region, an alternative species such as black cherry will maintain productivity on these sites. Other species in the northern hardwood forest region may be suitable, but nutrient requirements are not well known. Silvicultural recommendations have emphasized soil water availability and other physical characteristics (Godman et al. 1990). Where nutrition has been considered, N, P, and K have been considered the most limiting nutrients (Lea et al. 1979, Stanturf et al. 1989). Our studies have emphasized that base cations act as limiting nutrients for the health and growth of sugar maple (Long et al. 1997, Horsley et al. 2000, Bailey et al. 2004, Hallett et al. 2006). The sites with the highest foliar concentrations of Ca ($>13\,000$ mg/kg) and Mg (>1500 mg/kg) showed increasing BAI (Fig. 5), near the putative optimal amounts for sugar maple growth in the northeastern United States. Increased effort to understand optimal nutrition for the growth and health of sugar maple and associated tree species is warranted.

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