Measuring changes in stress and vitality indicators in limed sugar maple on the Allegheny Plateau in north-central Pennsylvania

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Abstract: A study established in 1985 in north-central Pennsylvania to determine effects of lime fertilization on declining sugar maple (*Acer saccharum* Marsh.) was evaluated in 1993 and showed that liming positively affected growth and crown vitality in sugar maple. This effect of lime on sugar maple offered an opportunity to assess other indicators of tree vitality and their response to lime additions. Foliar polyamines, starch and soluble sugars in root tissues, and cambial electrical resistance (CER) at breast height were evaluated. Foliar putrescine, soluble sugars, and CER decreased, while starch increased in lime-treated trees. Changes in these indicators were correlated with tree growth and crown vitality, which improved in limed plots. However, they were more highly correlated with lime-induced changes in foliar and soil elements and soil pH. Putrescine, soluble sugars, and CER decreased and starch increased, as Ca and Mg and molar ratios of Ca/Al and Mg/Mn increased and as Al and Mn decreased in both soil and foliage, and as soil pH increased. Results showed the beneficial effect of lime on tree vitality that was not reflected in visual assessments of crown vitality and demonstrated the potential utility of these physiological and biochemical measures as indicators of vitality in sugar maple.

Résumé : Une étude établie en 1985 dans le centre-nord de la Pennsylvanie pour déterminer les effets du chaulage sur le dépérissement de l'érable à sucre (*Acer saccharum* Marsh.) a été évaluée en 1993 et a montré que le chaulage avait un effet positif sur la croissance et la vitalité de la cime chez l'érable à sucre. L'effet du chaulage sur l'érable à sucre offrait une opportunité pour évaluer d'autres indicateurs de la vitalité des arbres et de leur réaction à l'addition de chaux. Les polyamines foliaires, l'amidon et les sucres solubles des tissus racinaires ainsi que la résistance électrique cambiale (REC) à hauteur de poitrine ont été évalués. La putrescine foliaire, les sucres solubles et la REC ont diminué tandis que l'amidon a augmenté chez les arbres traités à la chaux. Les changements dans ces indicateurs sont corrélés à la croissance des arbres et à la vitalité de la cime qui se sont améliorées dans les parcelles chaulées. Cependant, ils sont davantage corrélés aux changements dus à l'effet du chaulage sur les éléments minéraux dans les feuilles et le sol et sur le pH du sol. La putrescine, les sucres solubles et la REC ont diminué et l'amidon a augmenté avec l'augmentation du Ca, du Mg et du ratio molaire de Ca/Al et de Mg/Mn, la diminution de Al et de Mn dans le sol et le feuillage et l'augmentation du pH dans le sol. Les résultats montrent que l'effet bénéfique du chaulage sur la vitalité de la cime ne se reflétait pas dans l'évaluation visuelle de la vitalité de la cime. Ils démontrent également l'utilité potentielle de ces mesures physiologiques et biochimiques comme indicateurs de vitalité chez l'érable à sucre.

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Introduction

Premature decline and death of overstory sugar maple (*Acer saccharum* Marsh.) has occurred across the Allegheny Plateau in northern Pennsylvania since the mid-1980s, reducing stocking in affected stands (Kolb and McCormick 1993; McWilliams et al. 1996). This decline (Manion 1991; Houston 1992), like other episodes of sugar maple decline (Giese et al. 1964; McLaughlin et al. 1987; Bauce and Allen 1991; Coté and Ouimet 1996), has been associated with a variety of stressors, including insect defoliation and drought (Kolb and McCormick 1993; Long et al. 1997).

In studies to improve health and increase regeneration in stands dominated by declining sugar maple, dolomitic lime

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was applied in 1985 to four stands in north-central Pennsylvania as an experimental treatment. Its effects on growth, crown condition, and flower and seed production were compared with unlimed stands at the same sites (Long et al. 1997). These stands are characterized by soils that are unglaciated fine loams formed from sandstone, siltstone, and shale with low Ca and Mg concentrations relative to nearby glaciated sites (Long et al. 1997). Measurements on these plots indicated that liming significantly increased vitality and survivorship as measured by improved crown condition, increased diameter growth of overstory sugar maple, and the percentage of living trees remaining in the plots (Long et al. 1997). Vitality is the status of tree health at any one time, and it is the dynamic response of a tree to its surroundings and is especially affected by stress; by contrast, vigor is the genetic capacity of a tree to survive stress (Shigo 1986). Improved vitality in sugar maple was associated with increased levels of exchangeable base cations, especially Ca and Mg, and reductions in soil acidity in the upper 15 cm of soil (Long et al. 1997).

The availability of these treatment plots and improved conditions of sugar maple in limed plots presented a unique opportunity to evaluate other potential indicators of stress or vitality in forest trees. Foliar polyamines, root starch and soluble sugars, and cambial electrical resistance have been used as indicators of stress and (or) vitality in a variety of tree species including sugar maple and were used in this study.

Polyamines (putrescine, spermidine, and spermine) are organic polycations of low molecular weight found in all living organisms and play an important role in a wide range of biological processes, including growth, development, and stress responses. At the cellular level, polyamines are involved in DNA synthesis, stabilization of membranes, scavenging of free radicals, and modulation of enzyme activities (Minocha et al. 1996, 1997; Walden et al. 1997; Kumar and Minocha 1998). Abiotic stress induced by conditions such as low pH, SO_2, high salinity, drought, nutrient extremes, low temperature (Flores 1991; Bouchereau et al. 1999), high Al concentrations (Minocha et al. 1996), and pathogen infections (Musetti et al. 1999) increase concentrations of cellular putrescine. In mature red spruce trees (*Picea rubens* Sarg.) an increase in soluble putrescine in foliage was associated with a decrease in foliar and soil Ca and Mg concentrations and an increase in Al and Al/Ca ratios in the Oa soil horizon and soil solution (Minocha et al. 1997). These cations have been related to putrescine concentration in other studies (Minocha et al. 1996, 2000). The molar ratio of Ca/Al in soils has been proposed as an indicator and perhaps a cause of stress in forested ecosystems (Cronan and Grigal 1995).

Starch is the major form of reserve carbohydrate in most trees and reflects their photosynthetic capacity (genetic capacity and environment), an indicator of the vigor and vitality of a tree (Wargo 1999). Its status in unstressed trees reflects the general vigor of the tree, i.e., high starch content is equated to good vigor (Wargo 1981). In stressed trees, starch content reflects the combination of vigor and vitality (ability of an organism to grow and survive in its surroundings; see Shigo 1986). Starch content is a dynamic indicator of stress and shows the effects of defoliation (Wargo et al. 1972; Wargo 1972, 1981), drought (Parker and Patton 1975), air pollution (Miller et al. 1968), and soil acidification (Wargo et al. 1993). In urban sugar maples, trees with healthy crowns had high starch content, while those with declining crowns had low or depleted starch (Carroll et al. 1983). Preliminary analyses of root starch in sugar maple on the lime-treated plots in this study indicated a positive effect of lime on starch content (Wargo 1999).

Soluble sugars also are potential indicators of stress; abnormally high concentrations indicate stress. Increased concentrations of reducing sugars were observed in root wood of defoliated sugar maple saplings (Wargo 1972) and mature sugar maple with severe crown dieback (Renaud and Mauffette 1991). High levels of reducing sugars also were measured in sugar maple seedlings growing in "high stress" areas with poor soil nutrients and adverse temperatures (McLaughlin et al. 1996).

Cambial electrical resistance (CER) and electrical capacitance have been used as indicators of altered tree vitality after fertilization, crown release, defoliation, and other stresses; higher CER indicated reductions in vitality (Wargo 1981; Piene et al. 1984; MacDougall et al. 1988; Gagnon et al. 1988; Lindberg and Johansson 1989; Huttl et al. 1990). CER was used as a stand hazard index for rating vulnerability of balsam fir (*Abies balsamea* L.) to damage from spruce budworm (Davis et al. 1980) and also was useful in separating red spruce stands into classes of low, intermediate, and high vigor and vitality (Smith and Ostrofsky 1993). In studies with sugar maple, CER did not distinguish crown condition classes in urban trees but was correlated with visual crown symptoms in a nonurban setting (Newbanks and Tattar 1977).

In our study, these stress or vitality indicators were measured in sugar maples on plots treated with lime and compared with trees in adjacent untreated plots to determine whether the indicators were related to visual measures of tree vitality and to lime-induced changes in soil and foliar nutrients and to identify the best indicator of tree vitality and, thus, the most advantageous one to measure.

Materials and methods

Field sites and treatment applications

Information about the field sites, including treatments, soil type, land-use history, and species composition, is detailed by Long et al. (1997). In brief, these sites are located on the Susquehannock State Forest, Potter County, Pennsylvania, within the unglaciated High Plateau Section of the Appalachian Plateau Province. Four blocks, two in each of two areas and each with eight 60 × 60 m plots, were established in the summer of 1985. Half of the plots in each block were enclosed with fence. One plot in each half-block (fenced and unfenced) received a single application of (*i*) commercial pulverized dolomitic limestone (Ca = 21%, Mg = 12%, CaO equivalent = 58.8) at 22.4 $Mg \cdot ha^{-1}$, (*ii*) herbicide (glyphosate) applied to the understory at 2.2 kg a.i.$\cdot ha^{-1}$ in 308.5 $L \cdot ha^{-1}$ water, (*iii*) lime and herbicide, or (*iv*) no lime nor herbicide (control). Herbicide was applied to the entire plot including a buffer zone and lime was applied only to the 45 × 45 m interior plot area. All data in this study are from trees within the interior plot. There were 32 plots for the experiment (4 blocks × 8 plots/block).

Soluble foliar polyamines and inorganic elements

Foliage samples were removed with a shotgun from branches in the outer midcanopy of five to seven dominant and codominant sugar maples in each plot during mid-July in 1997 and 1998. Two or three healthy leaves were collected from each tree and were wiped with clean Kimwipes to remove surface contaminants. Discs of leaf tissue (60–75) with no major veins and about 6 mm in diameter (yielded 200–300 mg fresh mass) were punched from folded leaves and placed in individual preweighed microfuge tubes containing 1 mL of 5% perchloric acid. In 1998, all leaves were affected by fall cankerworm (*Alsophila pometaria* (Harr.); T.J. Hall, Pennsylvania Bureau of Forestry, personal observation) and disease, probably caused by the anthracnose fungus (*Discula campestris* (Pass.) von Arx) (Hall 1995). It was impossible to sample disease-free leaves, so leaf tissue was punched from areas free of "chewed" or diseased tissue. Samples were kept on ice in the field and during transportation to the laboratory where they were stored at –20°C until processing. Samples were processed according to the procedures described by Minocha et al. (1990, 1997). Soluble foliar elements and polyamines were extracted using the freeze–thawing method (Minocha and Shortle 1993; Minocha et al. 1994), which extracts total soluble polyamines and a concise fraction of the total elements (Minocha et al. 2000). Foliar elements and polyamines were determined as micromoles per gram fresh mass and nanomoles per gram fresh mass, respectively.

Total foliar and exchangeable soil elements

In August 1995, total foliar elements were measured in a subset of 54 overstory sugar maples; 27 trees in unlimed and 27 trees in limed plots in 22 of the 32 total plots (11 each per lime treatment) were sampled. Samples were collected from the outer midcrown by shooting small branches from each tree, then treated by methods described in Long et al. (1997), and analyzed by inductively coupled plasma (ICP) spectroscopy. Total element concentrations were measured as milligrams per kilogram dry mass. In 1996, soil samples were taken near six permanently marked sampling sites on a 22.5 × 11.3 m grid centered in each plot (Long et al. 1997). Loose litter was brushed from the surface and samples were collected at increments of 2.5 cm to a depth of 15 cm. For each plot, the six samples were composited for each increment, air dried, and sieved through a 2-mm mesh. Elements were extracted with 1 M NH_4OAc for all exchangeable elements except Al, which was extracted with 1 M KCl, and analyzed using ICP as described in Long et al. (1997). For this present study, element concentration, milligrams per kilogram dry mass, was averaged over the total 15 cm soil depth. Data for soil analyses will be published elsewhere.

Carbohydrate analyses

Root sampling

Root tissue for carbohydrate analyses was collected after leaf drop in early November 1997 from each of three randomly chosen sugar maple trees in each plot. Two randomly chosen buttress roots (first order) were excavated, and on each, a smaller, healthy, higher order branch root (second or third) was located and a section, about 10–15 cm long, was cut, placed in plastic bags on dry ice in the field, and stored in freezers at –20°C on return to the laboratory.

Visual starch

A short section (~2 cm) of frozen root was clipped from one root section for visual assessment of starch using procedures described by Wargo (1975). Previous studies indicated that a single healthy root reflected the overall starch status of mature trees (Wargo 1976). Sections stained with I_2–KI were rated for starch content as (1) none, (2) low, (3) moderate, (4) high, and (5) very high, based on the density of the stain reaction with starch (Wargo 1975). Root bark has minimal starch and was not rated. An average visual rating for each plot was calculated from the ratings of the three trees.

Chemical starch and soluble sugars

A section of root (3–4 cm) was clipped from each frozen root sample, washed, and blotted dry. Strips of bark down to the wood were removed and cut into small pieces that were placed in a centrifuge tube and immediately refrozen. The remaining wood cylinder was split longitudinally and radially into four to eight sections (depending on diameter) that were cut into small pieces, placed in a centrifuge tube and immediately refrozen. Discolored wood in the sections was discarded.

Samples were extracted and analyzed for soluble sugars according to the procedures described by Wong et al. (2001). Sugars were identified and quantified with known standards and converted to milligrams per gram residue tissue dry mass. Residue tissue dry mass was determined after starch extraction.

Starch in the residual pellet was quantified by the method described by Hendrix (1993) with some modification. Both branched and linear forms of starch were determined. The branched form of gelatinized starch was hydrolyzed to glucose with amyloglucosidase (No. 10115; Fluka Chemical Co., Milwaukee, Wis.) for 30 min at 55°C. The linear form of gelatinized starch was hydrolyzed first with α-amylase (A-6380; Sigma Chemical Co., St. Louis, Mo.) for 20 min at room temperature, followed by maltase (M-3145; Sigma) for an additional 20 min at room temperature. Enzymatic digestion was terminated after each incubation by placing the digests in a boiling water bath for 4 min. Concentration of starch was calculated from glucose standard curves and expressed as milligrams per gram residue dry mass. Quantities for branched and linear starch were combined for each tissue. This was designated as "chemical" starch in contrast to starch levels determined visually.

Cambial electrical resistance

CER was measured with a Shigometer, model OZ-67 (Osmose Wood Preserving Co., 980 Ellicott Street, Buffalo, N.Y.), in mid-July 1998, on all living overstory sugar maples in each interior plot. Four readings were taken on each tree, one on each of the north, east, south, and west faces at about breast height (1.4 m), where DBH also was measured. Electrodes (two stainless steel pins, 2.7 cm long) were inserted vertically through the bark into the outer wood. Readings were recorded as whole kiloohms after an equilibration period (3–5 s). The 32 plots were completed in mid-July on 2 consecutive days with similar air temperatures, thus avoiding confounding effects with temperature (Piene et al. 1984) or

seasonality (Smith et al. 1984; Shigo and Shortle 1986). Individual readings for each face of the tree were recorded and a mean (MEANR) for each tree was calculated. Later, mean minimum (MINR), and mean maximum (MAXR) CER readings were generated from the data for each plot and analyzed to determine if minimum or maximum readings for these trees were related differently from mean CER to treatment or to other measures of tree vitality and chemistry.

Crown vitality

Vitality of the trees ("vigor classes", sensu Long et al. 1997) was estimated by rating crown condition annually during August of 1997 and 1998 using the system described by Mader and Thompson (1969). Each tree was placed in one of six crown vitality classes by two observers. To allow the numerical crown vitality class to increase as tree health increased, the Mader–Thompson system was reversed: their class 1 became our class 6. Class 6 trees were healthy with full-size foliage and no dieback; class 5 trees had abnormally small and slightly chlorotic foliage but no dieback; class 4 trees were similar to class 5 trees but had dieback in the upper crown; class 3 trees had several large dead branches and twig dieback on less than half the crown; class 2 trees had more than half of the crown with dieback; Class 1 trees were dead (Long et al. 1997). Only the five living crown vitality classes (i.e., 2–6) were used.

Statistical analyses

Lime effects

The original study was a split-plot design with fencing as the whole-plot treatment and with lime, herbicide, lime and herbicide, and control as the subplot treatments. Analyses of diameter and basal area, crown vitality ("vigor", sensu Long et al. 1997), and foliar chemistry in a previous study on sugar maple in these lime plots indicated that only lime had a significant treatment effect on foliar chemistry, crown vitality, and growth (Long et al. 1997). Therefore, if there were no effects of fence and herbicide, data for lime effects were pooled over fence and herbicide and analyzed. Only polyamines showed a herbicide effect, and data for polyamines were not pooled over herbicide for lime analyses (data presented elsewhere). Standard ANOVA procedures using SAS version 6.12 (SAS Institute Inc. 1990) or SYSTAT version 7.01 (SYSTAT Inc., Evanston, Ill.) statistical packages were used to analyze the data. An F test at 0.05 probability level was used for determining significant differences between unlimed and lime-treated trees. There were too few trees in each crown vitality class to analyze each class separately for lime effects; therefore, vitality classes were pooled across several ratings. For both 1997 and 1998 crown vitality ratings, trees with ratings of 5 and 6 and those with 2, 3, and 4 were pooled to form two general vitality groups of good and poor trees, respectively. ANOVA was performed on each vitality group within each crown-rating year and the combined group (all five vitality classes) for both years, and unlimed and limed tress were compared. Differences were considered significant at $p \leq 0.05$. For analyses of CER, DBH was used as a covariate in the ANOVA, because CER was significantly correlated with DBH and there were significant differences in DBH among the treatments.

Intercorrelation of variables

Spearman correlation tests were performed on all data to determine significant relationships among CER, polyamines, and carbohydrates and their relationships to crown vitality measurements. Spearman correlations were used, because the crown variables were discrete and few were distributed normally. Correlations of the stress variables with 1997 and 1998 soluble and 1995 total foliar elements, and 1996 soil chemistry averaged over the total 15 cm soil depth also were determined. Pearson correlation tests were used to determine relationships between years for polyamines and soluble foliar elements in 1997 and 1998, and among 1997–1998 soluble and 1995 total foliar and 1996 soil elements, all of which were continuous variables. Unless otherwise specified, significant relationships at $p = 0.05$ or lower are reported. Correlations among individual tree variables were determined on a tree basis where there were data for the same trees. Where data were not from the same tree or where plot data only were available, e.g., soil and total foliar chemistry, correlations were based on plot-level variables.

Results

Lime effects

Foliar polyamines

Putrescine was the predominant polyamine in sugar maple leaf tissue and its concentration in 1997 and 1998 in trees on limed plots was less than in trees on unlimed plots (Table 1). Putrescine concentrations in 1998 in both unlimed and limed plots were higher (46–77%, depending on vitality class) than in 1997 (Table1). Spermidine levels also were less in trees in limed plots except for poor trees in 1997; levels were about 45% lower in 1998 than in 1997. Spermine also was present but in barely detectable levels and showed no consistent trends (Table 1). Concentration of putrescine in 1998 was not highly correlated ($r = 0.30$, $p = 0.05$, $n = 188$) with its concentration in 1997. When trees were separated by vitality classes, putrescine, although numerically lower in limed than in unlimed trees in both good and poor vitality groups in 1997 and 1998, was significantly lower only for good trees in 1997. The same relationship occurred for spermidine. Spermine showed the reverse relationship; it was lower in unlimed than in limed trees in the good crown vitality group in 1997 but not in 1998 (Table 1).

Soluble foliar elements

Concentrations of Ca and Mg and molar ratio of Mg/Mn were greater in foliage from trees in limed plots than in unlimed plots in 1997 and 1998; the molar ratio of Ca/Al was significantly higher only in 1998 (Table 2). Concentrations of K and Mn were significantly lower in lime-treated trees in both years, while Al and P were significantly lower only in 1998 (Table 2). Concentrations of Ca, K, Mg, Mn, and P in the foliage in 1997 were correlated with their counterpart ions in 1998 ($r = 0.87$, 0.36, 0.94, 0.94, and 0.37, $p \leq 0.04$, respectively). Concentrations of Al between years were not significantly correlated ($r = 0.32$, $p = 0.08$). Concentrations of soluble foliar elements measured in 1997 and 1998 also were highly correlated with their total counterpart element concentrations of Ca, Mg, and Mn measured in the foliage in 1995 and in the soil in 1996; correlations for soluble

Table 1. Polyamine concentrations in 1997 and 1998 foliage of sugar maple separated into crown vitality groups of good and poor based on crown vitality ratings in 1997 and 1998 or combined into one group in unlimed and limed plots, Susquehannock State Forest, north-central Pennsylvania.

	Putrescine concentration (nmol·g fresh mass^{-1})			Spermidine concentration (nmol·g fresh mass^{-1})			Spermine concentration (nmol·g fresh mass^{-1})		
Crown rating year and plot[a]	Good[b]	Poor[b]	Combined[b]	Good	Poor	Combined	Good	Poor	Combined
1997									
Unlimed[c]	82.2±7.4	108.5±21.4	94.5±7.4	42.2±3.7	40.4±2.9	41.8±2.7	7.3±1.8	7.2±1.7	7.1±1.4
Limed[c]	54.4±5.1	77.5±0.0[d]	54.9±6.5	33.0±2.4	54.1±10.7	33.2±2.2	11.5±1.2	9.6±6.6	11.5±1.1
p	<0.01	1.00	<0.01	0.04	0.24	0.02	0.05	0.74	0.02
1998									
Unlimed[e]	127.4±31.2	182.9±41.6	167.1±25.2	22.4±3.5	23.6±2.7	23.3±2.0	2.1±0.9	3.7±0.9	3.3±0.6
Limed[e]	83.3±15.1	112.9±88.9	87.1±22.8	17.7±1.7	17.7±5.8	17.7±1.8	3.4±0.5	2.5±2.1	3.3±0.6
p	0.21	0.48	0.02	0.23	0.36	0.04	0.25	0.61	1.00

Note: Values are means ± SEs.
[a]Crowns were rated in 1997 and 1998 as described in the Materials and methods.
[b]Crown vitality classes were pooled to form two general vitality groups of good or poor crowned trees. Crown vitality classes 5 and 6 were pooled to form the good-vitality group and classes 2, 3, and 4 were pooled to form the poor-vitality group. Combined is the pooled data for all five crown vitality classes.
[c]*n* = 25 good and 16 poor, and 53 good and 1 poor crowned trees for unlimed and limed plots, respectively, for 1997.
[d]Only one observation for putrescine in limed, poor crowned trees in 1997.
[e]*n* = 11 good and 32 poor, and 47 good and 7 poor crowned trees for unlimed and limed plots, respectively, for 1998.

Table 2. Soluble foliar elements and molar ratios in sugar maple from unlimed and limed plots, Susquehannock Forest, north-central Pennsylvania.

	Element (μmol·g fresh mass^{-1})						Molar ratio	
Year and treatment	Al	Ca	K	Mg	Mn	P	Ca/Al	Mg/Mn
1997								
Unlimed	0.21±0.08*a*	17.5±0.96*a*	57.3±1.81*b*	9.3±0.60*a*	8.9±0.41*b*	4.4±0.49*a*	289±71*a*	2.5±0.22*a*
Limed	0.08±0.02*a*	31.3±1.52*b*	52.1±2.32*a*	22.6±1.02*b*	2.3±0.25*a*	5.6±0.41*a*	463+118*a*	25.1+2.48*b*
1998								
Unlimed	0.34±0.02*b*	23.5±1.20*a*	62.4±1.67*b*	7.8±0.42*a*	13.0±0.62*b*	4.0±0.27*a*	51+4.9*a*	1.4±0.11*a*
Limed	0.25±0.01*a*	46.2±1.91*b*	49.4±1.10*a*	27.3±1.15*b*	3.0±0.26*a*	5.6±0.41*b*	127±8.4*b*	22.2±1.89*b*

Note: Values are means ± SEs. Values in columns within year followed by different letter indicates significant differences between elements at $p \leq 0.05$ ($n = 16$).

Table 3. Pearson's correlation coefficients among soluble foliar elements measured in 1997 and 1998 and their counterparts in total foliar elements measured in 1995, and exchangeable soil elements measured in 1996 in limed and unlimed sugar maple plots, Susquehannock Forest, north-central Pennsylvania.

	Soluble foliar elements				
Element source	Al	Ca	K	Mg	Mn
1997					
1995 total foliar (n = 22)	–0.17	0.82*	0.33	0.93*	0.88*
1996 exchangeable soil (n = 32)	0.27	0.81*	0.52*	0.89*	0.71*
1998					
1995 total foliar (n = 22)	0.14	0.85*	0.64*	0.97*	0.87*
1996 exchangeable soil (n = 32)	0.53*	0.83*	0.44*	0.90*	0.77*

*Significant at $p \leq 0.05$.

foliar elements K and Al were not significant for either year (Table 3).

Root carbohydrates

The visual rating of starch content in root wood as well as concentrations of "chemical" starch in both root bark and wood were consistently and sometimes significantly higher in lime-treated than in unlimed trees in the combined and good and poor vitality groups (Table 4). In contrast to starch, some soluble sugars in both root bark and wood were less in lime-treated trees (Table 4). Stachyose, raffinose, and xylose in both bark and wood were not significantly affected

Table 4. Means (±SE) for 1998 cambial electrical resistance (CER, kΩ) and 1997 root carbohydrates (mg·g dry mass^{-1}) in sugar maple separated into good and poor crown vitality groups based on crown vitality ratings in 1997 and 1998 or combined into one group on unlimed and limed plots, Susquehannock State Forest, north-central Pennsylvania.

	Crown vitality rating 1997[a]			Crown vitality rating 1998[a]		
Vitality group	Unlimed	Limed	*p*	Unlimed	Limed	*p*
CER						
Good[b]	9.9±0.9	7.3±0.3	<0.01	10.1±0.1	7.2±0.3	<0.01
Poor[b]	11.3±0.7	7.4±1.3	0.02	11.2±0.6	8.0±1.1	0.03
Combined[c]	10.8±0.5	7.3±0.3	<0.01			
Visual starch						
Good	3.9±0.2	4.2±0.1	0.13	4.1±0.2	4.3±0.1	0.27
Poor	3.6±0.2	5.0±0.0	<0.01	3.5±0.2	4.7±0.3	0.01
Combined	3.7±0.10	4.3±0.1	<0.01			
Chemical bark starch						
Good	0.70±0.14	2.40±0.44	0.01	0.69±0.12	2.36±0.44	0.01
Poor	0.81±0.14	1.46±0.46	0.08	0.83±0.15	1.59±0.44	0.05
Combined	0.77±0.10	2.27±0.39	<0.01			
Chemical wood starch						
Good	19.9±2.8	30.2±2.9	0.03	24.2±4.8	30.6±2.9	0.23
Poor	19.9±3.6	25.7±2.9	0.48	16.8±2.2	23.2±2.3	0.20
Combined	19.9±2.4	29.7±2.6	<0.01			
Bark sucrose						
Good	23.8±2.8	19.6±2.1	0.26	20.2±2.8	19.1±2.1	0.75
Poor	30.1±4.0	11.8±2.8	0.04	32.9±3.8	15.4±3.9	0.04
Combined	27.6±2.7	18.7±1.9	<0.01			
Bark glucose						
Good	4.03±0.42	3.63±0.34	0.49	4.07±0.63	3.53±0.34	0.41
Poor	5.87±0.77	1.98±0.55	0.03	5.91±0.72	2.67±0.65	0.05
Combined	5.14±0.51	3.42±0.31	<0.01			
Bark fructose						
Good	5.74±0.54	4.88±0.43	0.25	5.65±0.79	4.74±0.44	0.28
Poor	8.30±1.06	2.91±0.69	0.03	8.46±0.99	3.83±0.88	0.04
Combined	7.29±0.69	4.63±0.40	<0.01			
Wood sucrose						
Good	17.4±1.8	12.1±0.9	<0.01	14.7±1.4	12.1±0.9	0.12
Poor	18.8±2.2	10.9±2.0	0.12	20.8±2.3	10.9±2.0	0.05
Combined	18.3±1.05	11.9±0.8	<0.01			
Wood glucose						
Good	2.47±0.60	1.00±0.14	<0.01	1.56±0.24	0.98±0.15	0.03
Poor	2.76±0.48	0.51±0.12	0.04	3.42±0.57	0.65±0.15	0.03
Combined	2.64±0.37	0.94±0.13	<0.01			
Wood fructose						
Good	2.84±0.67	1.04±0.18	<0.01	1.88±0.30	1.02±0.18	0.01
Poor	3.49±0.61	0.54±0.14	0.03	4.20±0.69	0.70±0.14	0.02
Combined	3.23±0.45	0.98±0.16	<0.01			

[a]Crown vitality ratings are as described in the Materials and methods. For 1997 and 1998, crown vitality classes 5 and 6 were pooled for the good-tree group, and classes 2, 3, and 4 were pooled for the poor-tree group. Combined is pooled data for all five crown vitality classes.

[b]*n* = 19 good- and 29 poor- and 41 good- and 6 poor-crowned trees for unlimed and limed plots, respectively, for 1997 and *n* = 20 good- and 28 poor- and 42 good- and 6 poor-crowned trees for unlimed and limed plots, respectively, for 1998.

[c]Combined health class is the same for both crown vitality groups.

by lime treatment, although all concentrations were slightly lower in limed trees (data not presented). Concentrations of sucrose, glucose, and fructose were less in both bark and wood of roots from trees in limed plots (Table 4). Differences were significant for all these sugars when all vitality classes were combined. When vitality groups were analyzed separately (good and poor) the increase or decrease in carbohydrates in response to lime treatment was greater in poor vitality trees, and differences between trees in limed and unlimed plots within the poor vitality group were more often

Table 5. Spearman correlation coefficients of plot means of cambial electrical resistance (CER) in 1998, visual and chemical starch and soluble sugars (sucrose, glucose, and fructose) in 1997 in root bark and wood, with crown vitality in 1997 and 1998 of sugar maple in unlimed and unlimed plots, Susquehannock State Forest, north-central Pennsylvania.

			Chemical starch		Sucrose		Glucose		Fructose		Total	
Tree variable	CER	Visual starch	Bark	Wood	Bark	Wood	Bark	Wood	Bark	Wood	Bark	Wood
CER		–0.32	–0.30	–0.46*	0.34*	0.19	0.53*	0.63*	0.55*	0.61*	0.39*	0.22
Visual starch			0.36*	0.40*	–0.27	–0.32	–0.33	–0.61*	–0.34*	–0.53*	–0.24	–0.35*
Chemical starch												
Bark				0.43*	–0.46*	–0.39*	–0.40*	–0.35*	–0.41*	–0.37*	–0.44*	–0.37*
Wood					–0.13	0.17	–0.31	–0.33	–0.33	–0.42*	–0.24	0.21
Vitality 1997	–0.48*	0.25	0.54*	0.32	–0.36*	–0.33	–0.18	–0.46*	–0.25	–0.53*	–0.32	–0.32
Vitality 1998	–0.46*	0.29	0.48*	0.34*	–0.36*	–0.32	–0.12	–0.48*	–0.20	–0.53*	–0.29	–0.32

Note: Cambial electrical resistance was measured in July 1998. Crown vitality (crown vigor sensu Mader and Thompson 1969) determined in August 1997 and 1998 using the Mader–Thompson system modified, where class 6 is healthy with no dieback and class 2 is >50% crown dieback.

*Significant at $p \leq 0.05$ ($n = 32$).

significant in comparison with the good vitality group (Table 4).

In the bark, starch concentration was about 3 times greater in trees on limed than unlimed plots; starch content in root wood of limed trees was about 1.5 times greater than in unlimed trees (Table 4). Mean starch concentration in root wood was more than 10 times higher than that in root bark (Table 4). In the bark, sugar concentrations in limed trees were 33–37% less than in unlimed trees; in the wood, sugar levels were 35–70% less in limed than unlimed trees (Table 4). In general, sugar concentrations in bark were higher than those in wood (Table 4).

Visual starch rating was positively but not highly correlated with concentrations of chemical starch in both root bark and wood and negatively correlated with concentrations of glucose, fructose, and total sugars, especially those in root wood (Table 5). Chemical starch in the bark was positively correlated with chemical starch in the wood and negatively with all soluble sugars in bark and wood; chemical starch in the wood was correlated (negatively) only with fructose in the wood (Table 5).

Cambial electrical resistance

CER was measured on 249 sugar maples in the 32 plots and ranged from 3 to 33 kΩ. The maximum individual-tree difference between the MINR and MAXR was 19 kΩ, while the mean difference between MINR and MAXR was 3.6 ± 3.3 kΩ. The overall tree MEANR, mean MINR, and mean MAXR were 9.2 ± 4.1 (mean ± SE), 7.6 ± 3.5, and 11.2 ± 5.4 kΩ, respectively.

CER was significantly less in lime treated trees than in unlimed trees (Table 4). When trees were separated into the two vitality groups, changes in CER within vitality groups in response to lime treatment were similar to that for polyamines and carbohydrates. CER in trees in the poor-vitality group in limed plots was similar to trees in the good-vitality group in limed plots and was significantly lower than CER in unlimed trees. The difference between lime treatments within a vitality group was greater in the poor-vitality group (Table 4). CER and DBH were significantly correlated ($r = –0.61$, $p = 0.0002$), and there were significant differences in DBH between limed and unlimed trees. However, differences in all three measures of CER were significant even after CER was adjusted by covariate analysis for the effect of DBH (Table 4, only MEANR data presented).

Correlations with tree vitality

Intracorrelations of tree vitality

The tree-vitality ratings in 1997 were highly correlated with vitality ratings in 1998 ($r = 0.94$, $p = 0.0001$).

Polyamines

Foliar putrescine in 1997 was significantly ($p \leq 0.01$) but not highly correlated with crown vitality; Spearman correlations coefficients for putrescine with crown vitality in 1997 and 1998 were –0.47 and –0.49, respectively. Putrescine in 1998 was not correlated significantly with either measure of crown vitality.

Carbohydrates

The visual starch rating was not significantly correlated with crown vitality rating in 1997 or 1998; however, chemical starch in root bark was significantly correlated with crown vitality in 1997 and 1998, and chemical starch in root wood was correlated significantly with crown vitality in 1998 (Table 5). About 62% of trees with high starch were in the two high crown vitality classes (5 and 6); 54% were in the highest crown vitality class (6). More than 80% of trees in vitality class 6 were in limed plots.

All sugars affected by lime were negatively correlated with crown vitality in 1997 and 1998 but not all correlations were significant (Table 5). Sucrose in root bark and glucose and fructose in root wood were significantly correlated with crown vitality in 1997 and 1998 (Table 5).

Cambial electrical resistance

CER was negatively correlated ($p \leq 0.01$) with crown vitality in 1997 and 1998 (Table 5).

Correlations among the three stress indicators

Carbohydrates and CER with putrescine

Visual starch rating and chemical starch in root wood were not significantly correlated with putrescine measured in 1997 or 1998; starch in root bark was correlated ($p \leq 0.05$) with putrescine ($r = –0.39$). Glucose and fructose in

Table 6. Spearman correlation coefficients for plot means for foliar putrescine measured in 1997 and 1998 with soluble foliar elements measured in 1997 and 1998, total foliar elements in 1995, and exchangeable soil elements and pH in 1996 in the upper 15 cm of soil pooled across limed and unlimed sugar maple plots, Susquehannock State Forest, north-central Pennsylvania.

	Element					Molar ratio		
Putrescine	Al	Ca	K	Mg	Mn	Ca/Al	Mg/Mn	pH
1995 total foliar elements (n = 22)								
1997	0.45*	–0.41*	0.59*	–0.53*	0.48*	–0.47*	–0.55*	
1998	0.12	–0.27	0.05	–0.33	0.06	–0.24	–0.28	
1997 and 1998 soluble foliar elements (n = 32)								
1997	0.03	–0.45*	0.25	–0.50*	0.43*	–0.02	–0.40*	
1998	0.17	–0.15	0.22	–0.28	0.27	–0.20	–0.29	
1996 exchangeable soil elements (n = 32)								
1997	0.52*	–0.72*	0.02	–0.73*	0.37*	–0.65*	–0.46*	–0.54*
1998	0.36*	–0.42*	–0.11	–0.45*	0.21	–0.46*	–0.29	–0.35*

Note: The pH was measured only in soil.
*Significant at $p \leq 0.05$.

root bark were not significantly correlated with putrescine in 1997 but were correlated positively with putrescine in 1998 (r = 0.36 and 0.42, respectively, $p \leq 0.05$). Glucose and fructose in root wood were correlated ($p \leq 0.05$) positively with putrescine (r = 0.54 and 0.60, respectively) in 1997 but not in 1998. CER was correlated ($p \leq 0.05$) with putrescine in 1997 (r = 0.41) and in 1998 (r = 0.46).

CER, starch, and soluble sugars

CER was significantly correlated with chemical starch content in the wood but not with visual starch or bark chemical starch, although these relationships also were negative (Table 5). CER decreased as the concentration of starch increased. By contrast, CER was correlated with all soluble sugars in root bark and all but sucrose in root wood. CER increased as concentrations of these sugars in the root tissue increased (Table 5).

Correlations with foliar and soil cations

Polyamines

Only putrescine was significantly correlated with foliar and soil elements. Putrescine measured in 1997 was negatively correlated with 1995 total foliar Ca and Mg, and Ca/Al and Mg/Mn molar ratios and positively with Al, K, and Mn (Table 6). However, putrescine measured in 1998 was not significantly correlated with any 1995 total foliar element (Table 6). Putrescine measured in 1997 was significantly correlated with 1997 soluble foliar elements, negatively with Ca and Mg and the Mg/Mn molar ratio and positively with 1997 foliar Mn; in 1998, putrescine was not significantly correlated with any 1998 soluble foliar element (Table 6). Putrescine measured in 1997 and 1998 was significantly correlated with 1996 exchangeable soil elements, negatively with Ca and Mg, Ca/Al and Mg/Mn molar ratios, and pH and positively with Al and also Mn but only for 1997 (Table 6). Correlation coefficients of 1997 putrescine with 1996 soil elements were higher than those for 1998 putrescine and also were the highest of all correlations with any of the elements measured (Table 6).

Carbohydrates

Starch

Visual starch and chemical starch in the bark were significantly correlated with all 1995 foliar elements, positively with Ca and Mg and Ca/Al and Mg/Mn molar ratios and negatively with Al, K, and Mn; chemical starch in the wood was not significantly correlated with any 1995 foliar element (Table 7). Similar relationships of visual and chemical starch occurred with soluble foliar elements for 1997 and 1998, but correlations were not as frequent or as high as with 1995 foliar elements (data not shown). Visual starch rating was correlated significantly with 1996 soil Ca and Mg and Ca/Al and Mg/Mn molar ratios (Table 7). Chemical starch in bark was significantly correlated with all soil elements, positively with Ca and Mg and Ca/Al and Mg/Mn molar ratios as well as with soil pH and negatively with Al, K, and Mn (Table 7). Chemical starch in wood was significantly correlated with Al, Ca, Mg, Ca/Al molar ratio, and pH (Table 7).

Sugars

In contrast to starch, sugars, particularly in the wood, were negatively correlated with 1995 foliar Ca and Mg and Ca/Al and Mg/Mn molar ratios and positively correlated with Al, K, and Mn (Table 7). Sucrose was significantly correlated with all elements in root wood and with Al and Ca/Al and Mg/Mn molar ratios in root bark. Correlations of glucose, fructose, and total soluble sugars in root wood with all 1995 foliar elements were significant, while only total soluble sugar in root bark was significantly correlated with Al and Ca/Al molar ratio (Table 7).

Sugars were significantly correlated with some but not all 1997 and 1998 soluble foliar elements, but coefficients were not as high as with 1995 total foliar elements. Sugars in the wood in general were correlated with more elements, and coefficients were higher than for bark sugars; correlations were more numerous for 1998 elements (data not shown). Sugars in root wood also were significantly correlated with more 1996 soil elements than sugars in the bark (Table 7). Correlation coefficients for sugars with 1996 soil elements were slightly lower than those for 1995 total foliar elements (Table 7).

Table 7. Spearman correlation coefficients for plot means of visual and chemical starch and soluble sugars (sucrose, glucose, and fructose) in bark and wood of sugar maple roots in 1997 with 1995 total foliar and 1996 soil elements and pH pooled across limed and unlimed sugar maple plots, Susquehannock State Forest, north-central Pennsylvania.

	Element					Molar ratio		
Carbohydrate variable 1997	Al	Ca	K	Mg	Mn	Ca/Al	Mg/Mn	pH
1995 total foliar elements (*n* = 22)								
Visual starch								
Wood	–0.57*	0.61*	–0.58*	0.66*	–0.51*	0.71*	0.62*	
Chemical starch								
Bark	–0.53*	0.61*	–0.63*	0.56*	–0.54*	0.61*	0.55*	
Wood	–0.28	0.37	–0.36	0.32	–0.19	0.39	0.25	
Sucrose								
Bark	0.63*	–0.37	0.40	–0.32	0.40	–0.50*	–0.42*	
Wood	0.56*	–0.60*	0.41*	–0.54*	0.55*	–0.61*	–0.53*	
Glucose								
Bark	0.31	–0.27	0.16	–0.28	0.19	–0.32	–0.25	
Wood	0.62*	–0.68*	0.55*	–0.73*	0.62*	–0.72*	–0.68*	
Fructose								
Bark	0.38	–0.30	0.19	–0.32	0.26	–0.35	–0.31	
Wood	0.61*	–0.64*	0.56*	–0.73*	0.59*	–0.69*	–0.66*	
Total soluble sugars								
Bark	0.58*	–0.30	0.34	–0.27	0.37	–0.45	–0.37	
Wood	0.61*	–0.63*	0.48*	–0.60*	0.60*	–0.64*	–0.59*	
1996 exchangeable soil elements (*n* = 32)								
Visual starch								
Wood	–0.29	0.61*	–0.07	0.52*	–0.33	0.41*	0.38*	0.32
Chemical starch								
Bark	–0.65*	0.50*	–0.35*	0.42*	–0.48*	0.66*	0.43*	0.59*
Wood	–0.39*	0.48*	–0.02	0.39*	–0.29	0.50*	0.31	0.42*
Sucrose								
Bark	0.44*	–0.34*	0.27	–0.32	0.41*	–0.46*	–0.39*	–0.48*
Wood	0.53*	–0.35*	0.39*	–0.30	0.51*	–0.51*	–0.46*	–0.51*
Glucose								
Bark	0.21	–0.30	–0.14	–0.35*	0.18	–0.32	–0.19	–0.32
Wood	0.30	–0.72*	0.09	–0.69*	0.48*	–0.55*	–0.49*	–0.60*
Fructose								
Bark	0.30	–0.36*	–0.06	–0.43*	0.28	–0.41*	–0.30	–0.41*
Wood	0.41*	–0.73*	0.10	–0.72*	0.52*	–0.65*	–0.55*	–0.63*
Total soluble sugars								
Bark	0.33	–0.29	0.14	–0.29	0.28	–0.36*	–0.28	–0.37*
Wood	0.49*	–0.38*	0.36*	–0.33	0.50*	–0.42*	–0.46*	–0.47*

Note: The pH was measured only in soil.
*Significant at $p \leq 0.05$.

Cambial electrical resistance

CER was significantly correlated with 1995 total foliar elements, negatively with Ca and Mg and Ca/Al and Mg/Mn molar ratios and positively with Al and Mn (Table 8). CER was lower in plots where foliar Ca and Mg were higher, whereas it was higher where Al and Mn were higher. CER was significantly correlated with 1997 soluble foliar Ca, Mg, and Mn and the Mg/Mn molar ratio and all elements and ratios but Al in 1998; correlations with Al were not significant in either year (Table 8). CER also was significantly correlated with pH, Ca, Mg, and Mn and Ca/Al and Mg/Mn molar ratios in the 1996 soil elements; coefficients were highest for Ca and Mg (Table 8).

Discussion

Factors that may contribute to sugar maple decline on these sites as well as the effects of liming treatments on soil and foliar chemistry and tree recovery measured by changes in growth and crown condition are discussed in detail in Long et al. (1997). More recently, the vulnerability of sugar maple to decline after stress from defoliation has been strongly linked to foliar and soil chemistry (Horsley et al. 2000). This current study shows that recovery of sugar maple in these stands in response to liming was related to measurable changes in soil and foliar chemistry that were reflected in favorable changes in concentrations of foliar

Table 8. Spearman correlation coefficients for plot means of cambial electrical resistance (CER) for 1998 and soil and foliar elements measured in sugar maple from unlimed and limed plots, Susquehannock State Forest, north-central Pennsylvania.

	Element					Molar ratio		
Mean CER	Al	Ca	K	Mg	Mn	Ca/Al	Mg/Mn	pH
Total foliar elements, 1995 (n = 22)	0.62*	–0.61*	–0.30	–0.52*	0.57*	–0.62*	–0.59*	
Soluble foliar elements (n = 32)								
1997	0.18	–0.54*	–0.12	–0.59*	0.55*	–0.23	–0.59*	
1998	0.26	–0.54*	0.40*	–0.55*	0.45*	–0.53*	–0.51*	
Exchangeable soil elements, 1996 (n = 32)	0.26	–0.65*	–0.03	–0.65*	0.40*	–0.48*	–0.41*	–0.56*

Note: The pH was measured only in soil.
*Significant at $p \leq 0.05$.

putrescine, soluble foliar elements, starch and soluble sugars in the roots, and CER.

Polyamines

An increase in cellular putrescine in plants has been related to stress from a variety of factors, such as nutrient deficiencies, ozone exposure, pathogen infections, salt exposure, drought (Flores 1991, and references therein), and increases in Al (Minocha et al. 1996). Arginine, a precursor of putrescine, also increased in spruce and pine needles in response to higher N deposition, a form of stress (van Dijk and Roelofs 1988; Dohmen et al. 1990; Santerre et al. 1990; Ericsson et al. 1993; Nohrstedt et al. 1996; Näsholm et al. 1997). Increases in putrescine when accompanied by changes in soil chemistry can be used as an early indicator of stress in apparently healthy trees (Minocha et al. 1997, 2000).

Conversely, if stress is reduced or eliminated, putrescine should decrease. Our data support this relationship; trees on nutrient-enriched plots amended with lime had lower putrescine concentrations than trees on nutrient-deficient plots not amended with lime. These data also support previous work that showed that putrescine content was inversely proportional to elements such as Ca and Mg and positively related to Mn and K in response to Al treatment (Minocha et al. 1997). This is the first report of a decrease in foliar putrescine in forest trees in response to a treatment applied to alleviate stress and improve growth. These sugar maple trees in limed plots in Pennsylvania showed an increase in tree vitality, as indicated by improved growth rate and crown condition, both associated with an increase in foliar Ca and Mg (Long et al. 1997).

Putrescine concentrations in 1998 in both unlimed (control) and limed plots were higher than their concentrations in 1997 and probably reflected infection by the maple anthracnose fungus (Hall 1995) and damage by larvae of the fall cankerworm caterpillar. In addition, a severe drought that began in the spring of 1998 (Quimby 1998) in this area of Pennsylvania affected trees well into 1999 (Towers 2000). Although care was taken to avoid sampling necrotic leaf tissue, increases of putrescine in adjacent tissues that appeared healthy might have resulted from stress due to fungal infection, insect herbivory, or water deficit (Flores 1991) or from direct production of putrescine by fungi (Shapira et al. 1989; Walters 1995). The highly elevated concentrations of putrescine in some treatments from additional stressors in 1998 did not mask the overall effects of lime in lowering putrescine levels. However, the affects of additional stressors may have caused the lack of and (or) weak correlation between putrescine measured in 1998 and foliar and soil elements.

Soluble foliar elements

Changes observed in soluble foliar elements in response to lime treatments were similar to those for total foliar elements observed by Long et al. (1997), and concentrations of elements in both studies were correlated significantly and similarly with soil chemistry. Both studies showed that liming had a positive effect on foliar Ca, Mg, and P and a negative effect on Mn, K, and Al. The soluble foliar elements measured in this study mimicked the total foliar elements measured on these trees in 1994 (Long et al. 1997) and were highly correlated with concentrations re-measured by R.P. Long, S.B. Horsley, P.R. Liija, and T.J. Hall (unpublished data) in 1995 (foliar) and 1996 (soil). Thus, the freeze–thawing method is an easy, safe, and quick way to measure the nutritional status of trees.

Carbohydrates

Starch content

Starch content corroborated the beneficial effects of liming on sugar maple vitality (crown condition), growth, and survival reported by Long et al. (1997). Trees in limed plots had higher starch contents than those on unlimed plots in all crown vitality groups, and this difference in starch content was not related to recent stress factors. Although there was defoliation in 1992 and 1993, there were no differences in severity among the plots, and trees had recovered probably by 1998 from the effects of earlier defoliations. Starch content of trees on limed plots prior to fertilization is not known; however, the lower starch content of trees in all unlimed plots and high starch content in most of the poor-crowned trees in the limed plots suggest that starch content increased in trees in limed plots.

Starch content was positively correlated with concentrations of Ca and Mg in the soil and foliage and negatively with concentrations of Al and Mn confirming the beneficial effects of lime on foliar nutrients in these sugar maples. Long et al. (1997) related improvement in "vigor" and growth of sugar maple to increases of available Ca and Mg in the soil, increased concentrations in the foliage, and a decrease in Al and Mn in both soil and foliage. The combined data suggest that trees on nutrient-poor soils produce less

carbohydrate than trees on nutrient-enriched sites, and it is reflected in their starch contents.

Soluble sugars

Reduced concentrations of sucrose, glucose, and fructose (and corresponding higher starch content) in trees in limed plots in response to increased available Ca and Mg also reflected the beneficial effects of liming on sugar maple vitality. Increased concentrations of soluble sugars in root wood of mature sugar maples have been related to crown dieback in stressed trees (Renaud and Mauffette 1991). Concentrations of sucrose, glucose, and fructose in root wood were higher in stressed trees during autumn and were directly proportional to the amount of dieback in the crowns. Glucose and fructose were two times higher in trees in the highest dieback class (≥50%) than in trees in the lowest dieback class ("healthy" trees) with ≤10% dieback. A similar but more obvious relationship of sugars and crown dieback was detected when trees were separated by a crown deterioration index (CDI) based on rate of decline in 3 years. Trees with a higher CDI had 1.9 times higher reducing sugar levels in their roots than trees with stable crowns (Renaud and Mauffette 1991).

Concentrations of soluble sugars in both bark and wood tissues of our trees were correlated with tree vitality, i.e., higher concentrations in trees with poorer crowns (Renaud and Mauffette 1991), but correlation coefficients were low. This low correlation with crown condition probably reflects the larger decrease, in comparison with good crowned trees, of these sugar concentrations in lime-treated trees with poor crowns. Sugar concentrations were more highly correlated with foliar and soil cations suggesting that sugars are being affected more by current site nutrient condition rather than by crown condition, an effect of previous stress. Accumulation of reducing sugars in sugar maple seedlings has been related to site conditions of temperature, growing season, and soil chemistry (McLaughlin et al. 1996). Seedlings growing on a more northerly and stressful site had higher concentrations of reducing sugars than those growing on a more southerly site.

Acute stress from defoliation can cause similar increases in reducing sugar, but it lowers sucrose and total carbohydrate reserves (Wargo 1972). Concentrations of reducing sugars in defoliated trees increase as a result of mobilization of starch to translocatable sugars for sustaining tissues during the "leafless" period during the growing season. Mean concentrations of sugar in the wood from the roots of trees in the lime study were within the range of seasonal measurements at a comparable time for these sugars in mature healthy sugar maple (Wargo 1971). Thus, it is unlikely that concentrations of these sugars were elevated because of acute stress; concentrations of glucose and fructose in defoliation-stressed trees were four to five times higher (Wargo 1972) than those reported here, suggesting that the elevated concentrations of sugars reported here are a function of site and concentrations of soil and leaf cations.

Cambial electrical resistance

Although there were significant differences among MEANR, MINR, and MAXR, these measurements showed consistent results with regard to lime treatments, DBH, crown condition, carbohydrate content, or soil and foliar chemistry variables.

CER reflected the beneficial effects of fertilization with lime on the vitality of sugar maple. CER was significantly lower in trees in limed plots indicating that these trees had a wider cambial zone and, hence, faster growth rate than trees in the unlimed plots. CER measurements in balsam fir showed that trees with a CER of 9 kΩ or less grew three times faster than trees with a CER of 13 kΩ (Davis et al. 1980). Subsequent work with balsam fir indicated that CER was related to the width or number of vascular cambial cells in the current growth ring (Smith et al. 1984) and the concentration of mobile ions, principally K in the cambial zone (Blanchard et al. 1983)

CER also reflected the beneficial effects of liming on foliar- and soil-element content. Lower CER occurred in trees with higher foliar concentrations of Ca and Mg and lower levels of Al and Mn growing in the limed plots. This indicates that radial growth was better in trees in plots with increased available soil cations and improved foliar nutrients in relationship to the range of nutrient concentrations for putative healthy sugar maple trees compiled by Kolb and McCormick (1993).

Physiologically favorable changes in concentrations of foliar polyamines, principally putrescine, starch and soluble sugars in the roots, and CER of sugar maple trees in lime-fertilized plots showed the beneficial effects of liming on tree vitality and reflected to some extent the improvements in crown condition, growth, and survival observed on these trees by Long et al. (1997). These results support the hypothesis that nutrients, especially Ca and Mg, are important in the health dynamics of sugar maple in response to stress in northern hardwood forests in northern Pennsylvania (Horsley et al. 1999, 2000). The relationship of these indicators with sugar maple vigor and vitality suggest that they are potentially useful in assessing sugar maple stands for their vulnerability to decline from stress and (or) for their vitality after a stress event.

The four indicators measured in this study were not highly intercorrelated nor was any indicator highly correlated with tree crown condition; correlations of all indicators with foliage and soil elements were consistently higher than with tree condition. Indeed, poor-crowned trees responded more favorably than good-crowned trees for most of the variables measured. The lack of a strong relationship with tree crown vitality and a stronger relationship with site nutrient conditions should be considered favorable. This suggests that indicators were reflecting physiological processes that were influenced or induced by longer term and more stable conditions of site nutrients rather than by ephemeral onset of or recovery from stresses such as defoliation and drought. Interestingly, putrescine increases in 1998 over the 1997 level reflected not only the difference in the long-term nutrient status of the plots but also the short-term effects of herbivory by insects, foliar fungal infection, and drought stress.

Clearly the easiest measurement on sugar maple trees was CER, which required no collection and analyses of tissue. CER indicated differences in trees that were related to the beneficial effects of liming and was highly correlated with concentrations of foliar (both soluble and total) and soil elements. Only glucose and fructose in root wood had higher

correlations with these elements than CER. The other three indicators required significant effort to collect tissues and analyze them. Even the visual starch technique was labor intensive. However, the current observations were on sites that were treated experimentally and that are limited geographically and geologically within the large range of site conditions applicable to sugar maple. It is not clear whether these results can be applied to sugar maple universally. Information is needed on these stress or vitality indicators over a wider spectrum of soil- and foliar-nutrient conditions before we can determine which indicator or suite of indicators (of health and risk to decline disease) would be most useful in managing sugar maple.

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