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Role of Climate in the Dieback of Northern Hardwoods

Allan N.D. Auclair

Abstract

The incidence of freezing and drought stresses, reconstructed from daily minimum/maximum temperature and precipitation records in areas of severe, recurrent dieback on sugar maple, was not happenstance but clustered at intervals of 8 to 12 years over the 1910 to 1995 period. Initial episodes of severe dieback on sugar maple (*Acer saccharum* Marsh.), as well as ash (*Fraxinus* spp.),

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white/yellow birch (*Betula papyrifera* Marsh. and *B. allegheniensis* Brit.), and red spruce (*Picea rubens* Sarg.) occurred within five years of rotation age and coincided with extreme winter thaw followed by sudden freezing. Regional thaw-freeze events correlated significantly with high El Niño-low Southern Oscillation Index, and hence with elements of change in global climate. New insights on biome-wide and century-long patterns of dieback and on climate mechanisms are being applied to innovative management approaches including early warning of risk and optimization of stand resistance to dieback.



The Effects of Defoliation and Thinning on the Dieback, Mortality, and Growth of Sugar Maple in the Tug Hill Region of New York

Robert A. Wink and Douglas C. Allen¹

Abstract

Some recent literature suggests that thinning should not be conducted immediately prior to, during, or immediately following an outbreak of defoliating insects. Although the individual effects of both defoliation and thinning are well documented in the literature, no study has assessed the combined effect of these two stressors. An outbreak of forest tent caterpillar, *Malacosoma disstria* Hbn., in the Tug Hill region of New York from 1990 to 1993 afforded the opportunity to assess the combined effects using a 2X2 factorial design. The two factors were recent defoliation and recent thinning. The two levels of defoliation were undefoliated and severely defoliated. Stands defined as severely defoliated were those in which a majority of the sugar maple (*Acer saccharum* Marsh.) had a midsummer flush of foliage for two consecutive years. The two levels of recent thinning were unthinned and thinned. Thinned stands were those that had been treated between fall 1989 and fall 1992. Five defoliated and thinned, eight defoliated and unthinned, five undefoliated and thinned, and six undefoliated and unthinned stands were selected. Five 0.02 hectare (0.05 acre) plots per stand were established to determine the extent of mortality and to assess crown condition. Crown dieback was estimated in 1995 and again in 1997 on 250 dominant and codominant (DC), 112 intermediate (INT), and 260 suppressed (SUP) sugar maple

using North American Maple Project (NAMP) protocol. Growth analyses were conducted on 220 DC sugar maple in 1995.

In both 1995 and 1997, DC sugar maple in defoliated stands had significantly greater average dieback (22 percent and 26 percent) than did DC sugar maple in undefoliated stands (9 percent and 11 percent). In both 1995 and 1997, the percent mortality of DC sugar maple was significantly higher in the defoliated stands (10 percent and 22 percent) than in the undefoliated stands (1 percent and 1 percent). Also, DC sugar maple in defoliated stands had significantly reduced growth in 1992, 1993, and 1994 when compared to trees from undefoliated stands during the same years. In

1995, INT sugar maple in defoliated stands had significantly greater average dieback (19 percent) than did INT sugar maple in undefoliated stands (7 percent). Also, in 1995, the percent mortality of INT sugar maple was significantly greater in defoliated stands (14 percent) than in undefoliated stands (1 percent). In 1995, SUP sugar maple in thinned stands had significantly greater average dieback (21 percent) than SUP sugar maple in unthinned stands (13 percent). In 1997, the percent mortality of SUP sugar maple was significantly greater in thinned stands (30.0 percent) than in unthinned stands (10 percent). No defoliation by thinning interactions were detected indicating that during the most recent outbreak of *M. disstria* in the Tug Hill region of New York State, thinning did not exacerbate the effects of defoliation.

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Relationship Between Foliar Chemistry and Insect Performance: the Forest Tent Caterpillar

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Popular Summary

Forest tent caterpillar (FTC) feeds on several species of deciduous trees (Stehr and Cook 1968). In northeastern North America, quaking aspen is the preferred host of this spring-feeding insect. FTC commonly defoliates several thousands of hectares of aspen stands each year in Québec (Bordeleau 1990), although its secondary hosts seldom are attacked. Between 1979 and 1982, large outbreaks of FTC occurred in both aspen and sugar maple stands of the southern region of Québec (Bauce et al. 1990). These outbreaks coincided with an episode of crown dieback which affected many broadleaf species. The symptoms were particularly apparent in sugar maple, but aspen was completely unaffected. Although herbivory by FTC was not a major factor explaining sugar maple crown dieback in Québec (Bauce et al. 1990), physical and physiological changes in foliage associated with decline (Houston 1981; Klein and Perkins 1988) are likely to affect foliage quality for herbivorous insects. Despite that forest decline and insect outbreaks often coincide and that foliar chemistry of declining trees is likely to change in ways relevant to insect performance, the response of herbivorous insects to these changes seldom has been investigated (but see Landsberg 1990 *a b c*). Here, we present results of a study in which the performance of FTC larvae on aspen, and healthy and declining maples was compared; we also report leaf chemistry and compare insect performance to these data.

Material and Methods

Sampling of Foliage

Foliage of quaking aspen was collected on trees ($n=5$) in a stand in Ste-Foy, Québec ($46^{\circ}47' N$, $71^{\circ}21' W$). The foliage of sugar maple was sampled from trees in a stand in the southern part of Québec ($46^{\circ}10' N$, $71^{\circ}42' W$). Condition of sugar maple trees was evaluated following the classification of Bauce and Allen (1991). Trees with less than 15 percent of the foliage missing from the crown were classified as healthy. Those with more than 50 percent missing foliage were classified having severe dieback. Three (1989) and five (1990) maple trees in each of these two classes were randomly selected for insect rearing and chemical analyses. Foliage of both species was collected early in the morning every 2 to 3 days from the top third of the crown. Leaves for chemical analyses were removed immediately from the twigs

and placed on ice in a cooler until they were stored at $-80^{\circ}C$. Foliage for insect rearing was left on the twigs and brought in a cooler to the laboratory where it was placed in distilled water.

Constituents of Foliage

Variables measured were water content (1990 only), total micro-Kjeldahl nitrogen (1990 only) (Allen 1974), free soluble sugars (Renaud and Mauffette 1991), total phenolics (Swain and Hillis 1959), and condensed tannins (Govindarajan and Mathew 1965). Free soluble sugars, total phenolics, and condensed tannins were not measured on aspen in 1989.

Insect Rearing

Egg masses of the FTC were provided by G. Bonneau (Ministry of Natural Resources) and were collected during Marsh from one location in 1989 and from two locations in 1990. At both locations, populations of the FTC were established on aspen. Egg masses were kept at $4^{\circ}C$ until rearing started. Rearing started within 3 to 4 days following budburst in the maple stand and was conducted in growth chambers ($22^{\circ}C$, 80 percent relative humidity, and 16 hr photoperiod). Newly hatched larvae from several egg masses were randomly assigned to feed on the foliage of aspen or on healthy or on declining maples until they reached pupation. Individual leaves were offered to the larvae in Petri dishes. A vial of distilled water was glued to the side of the dish and the leaf petiole was inserted in the vial to maintain turgor. Pupal weight and time to pupation were recorded. Because of the gregarious life-style of FTC, five larvae were reared per Petri dish. To avoid pseudoreplication (Hurlbert 1984), performance data used in statistical analyses were mean pupal weight and mean development time per dish. $\alpha=0.05$ was the nominal indicator of significance.

Results and Discussion

Foliar Chemistry

Water content decreased in foliage of all species as the season advanced, but the rate of decrease was faster in aspen than in either healthy or declining maples (Fig. 1); a test for the homogeneity of slopes had significant foliage by day interaction term (test performed on \log_{10} -transformed data to linearize; $F_{2, 110} = 4.00$, $p = 0.0210$). The total nitrogen content decreased at the same rate in foliage of all species as the season advanced (\log_{10} -transformed data, F -value for the foliage by day interaction term = 2.73, $d.f. = 2, 63$, $p = 0.0730$). The mean nitrogen content was lower in declining maple than in either healthy maple or aspen (Fig. 1; adjusted least-square means, $p < 0.05$). Multivariate analysis of variance (MANOVA) for repeated measures was used to compare soluble sugar (SS) content among the three foliage

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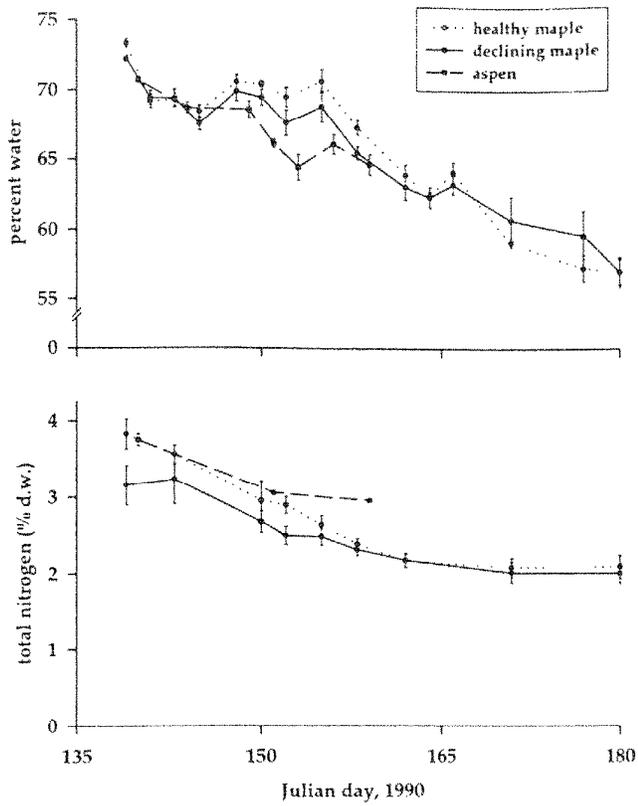


Figure 1.—Water and total nitrogen content of hosts.

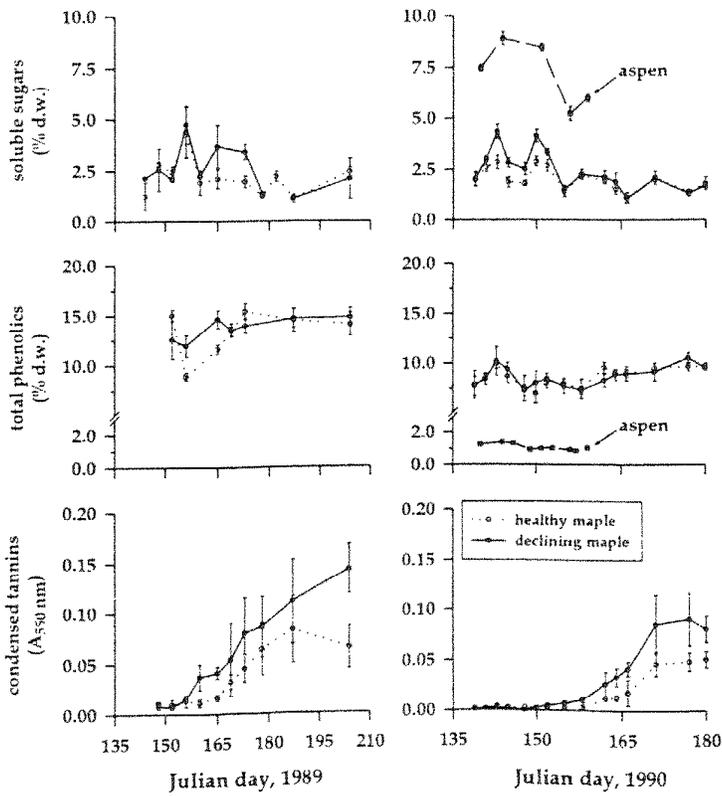


Figure 2.—Total soluble sugar, total phenolic, and condensed tannin content of hosts.

sources. Data included in the analyses were determined by inspecting plots of SS content versus Julian day (Fig. 2). For example, a visual inspection of such plots suggested that the SS content of declining maple foliage was higher than in healthy maple foliage between Julian days 160 and 178 for 1989, and between Julian days 139 and 155 of 1990. Results indicated that there was indeed more SS in the foliage of declining trees for 1990 ($F_{1,7} = 15.01$, $p = 0.0061$), whereas no significant difference was found between healthy and declining trees in 1989 ($F_{1,4} = 5.76$, $p = 0.0743$). Data for aspen were not included in the analysis because the SS content of aspen foliage was more than twice that in maples (Fig. 2). Interestingly, both species showed the same variation with respect to Julian day, despite the fact that the maple and the aspen stands were separated by 80 kilometers. The mean total phenolics (TP) content in maples was more than 50 percent higher in 1989 (13.5 percent dry weight [d.w.]) than in 1990 (8.6 percent d.w.) (Fig. 2). There was no significant linear trend in either year, as determined by a repeated measures MANOVA (1989: Wilk's Lambda = 0.0027, $p = 0.0780$; 1990: Wilk's Lambda = 0.0111, $p = 0.2127$). No significant difference was found between healthy and declining trees (1989: $F_{1,4} = 1.10$, $p = 0.3544$; 1990: $F_{1,7} = 1.10$, $p = 0.7898$). The TP content was nearly eight times less in aspen than in the maples (Fig. 2). Condensed tannins (CT) started to accumulate in the leaves of maples after Julian day 152 in 1989 and after Julian day 150 in 1990 (Fig. 2), though no significant linear trend was detected by the repeated measures MANOVA (1989: Wilk's Lambda = 0.0342, $p = 0.2742$; 1990: Wilk's Lambda = 0.7442, $p = 0.0555$). This may be due to the large variation among trees, but also to variation between sampling dates within the same tree. Baldwin et al. (1987) reported a similar pattern in their study of leaf tannin variation in sugar maple and yellow birch. In 1990, however, the mean CT content was significantly higher for declining compared to healthy trees ($F_{1,7} = 6.33$, $p = 0.0400$). In 1989, the mean CT content tended to be higher in declining trees (Figure 2), but not significantly so ($F_{1,4} = 1.93$, $p = 0.2370$). CT were practically absent in aspen ($A_{550nm} < 0.008$, all dates).

Insect Performance

In both years and in both sexes, FTC larvae developed significantly faster on aspen than on maple (Fig. 3; 1989, males: $F_{2,12} = 16.16$, $p = 0.0004$; 1989, females: $F_{2,12} = 26.83$, $p = 0.0001$; 1990, males: $F_{2,25} = 57.25$, $p < 0.0001$; 1990, females: $F_{2,25} = 93.47$, $p < 0.0001$). Development time was not significantly different between healthy and declining maples in either year or in either sex (Fig. 3; Waller-Duncan test at $p = 0.05$). In 1989, differences in pupal weight were marginally significant in males (Fig. 3; $F_{2,12} = 3.72$, $p = 0.0554$), whereas differences were highly significant in females (Fig. 3; $F_{2,12} = 23.18$, $p = 0.0001$). In 1990, differences in pupal weight were highly significant in both sexes (Fig. 3; males: $F_{2,25} = 100.12$, $p < 0.0001$; females: $F_{2,25} = 220.22$, $p < 0.0001$). Both male and female FTC

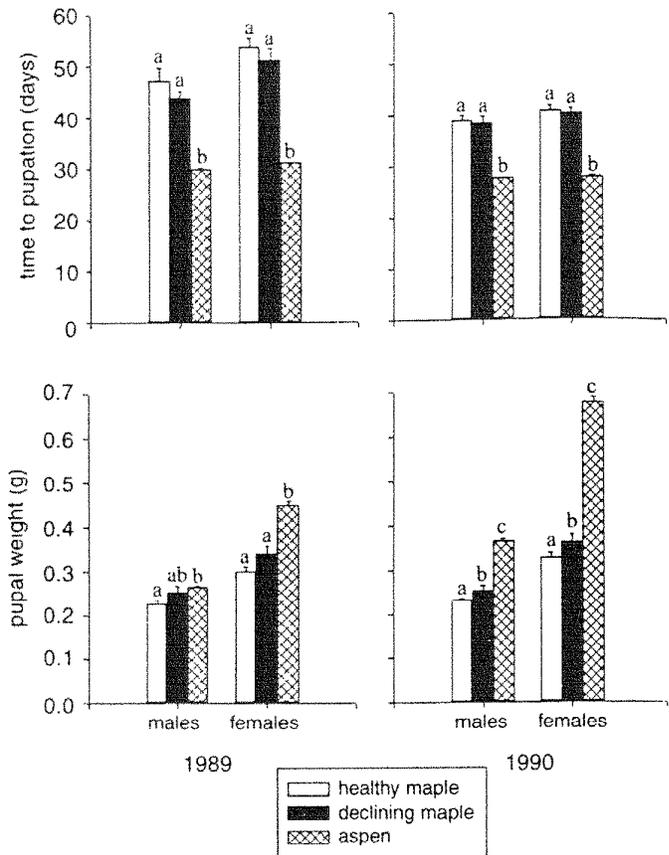


Figure 3.—Time to pupation and pupal weight of Forest Tent Caterpillar on hosts. Different letters above the bars indicate significant differences among hosts within sexes (Waller-Duncan, $p = 0.05$).

pupae were significantly heavier on declining maple than on healthy maple in 1990 (Fig. 3; Waller-Duncan test at $p = 0.05$), but not in 1989. FTC pupae were significantly heavier on aspen than on maple, but not in males in 1989 (Fig. 3; Waller-Duncan test at $p = 0.05$). In both years and in both sexes, ranking of pupal weight was, however, consistent (healthy maple < declining maple < aspen; Fig. 3).

Insect Performance vs Leaf Chemistry

High water and nitrogen contents are predicted to increase insect performance (Scriber and Slansky Jr. 1981). Here, variations in water and nitrogen contents among hosts observed in 1990, and the associated response of FTC larvae are inconsistent with this prediction. In aspen, water content was lower than in maples, yet FTC pupae were significantly heavier on aspen than on maples. Declining maple had a lower nitrogen content than healthy maple, yet FTC pupae were heavier on declining maple. Defensive compounds such as soluble phenolics and condensed tannins are generally detrimental to herbivores (Feeny 1968). Here, condensed tannins tended to be higher (1989),

or were significantly higher (1990), in declining than in healthy maple, yet FTC pupae were heavier on declining maple. The only consistent relationship between host chemistry and FTC performance that emerges from the results obtained here is between pupal weight and the soluble sugar content of the hosts. In fact, it is possible to correlate pupal weight with the soluble sugar content on a per tree basis, across hosts and across years (Fig. 4). Female pupal weight increased exponentially with increasing soluble sugar content ($y = a e^{bx}$; $a = 0.239 \pm 0.008$, $b = 0.137 \pm 0.006$, $R^2_{adj} = 0.97$, $p < 0.0001$), while the relation was linear for males ($y = ax + b$; $a = 0.025 \pm 0.002$, $b = 0.179 \pm 0.007$, $R^2_{adj} = 0.94$, $p < 0.0001$). The exponential relationship for females can be explained by the allometric relationship between pupal weight and the number of eggs at adult emergence (data not shown). When the number of eggs is used, female performance is linearly related to the soluble sugar content of the foliage (Fig. 4; $y = ax + b$; $a = 26.9 \pm 2.1$, $b = 55.8 \pm 10.4$, $R^2_{adj} = 0.93$, $p < 0.0001$). Although the very high proportion of the variation in insect performance explained by these models can be due to the gap in the data set at intermediate values of sugar content, it can be seen that the scatter around the predicted values is in general very small (Fig. 4). The results presented here do not necessarily mean that other constituents of leaves have no effect on the performance of the FTC. For example, FTC larvae took longer to develop on maples in 1989 than in 1990 (Fig. 3), and the total phenolics content of maples were higher in 1989 than in 1990, a pattern consistent with the general mode of action of these defensive compounds. The results do, however, indicate the overriding importance of soluble sugars in the diet of the FTC, especially when fecundity is concerned. Only a few other studies have reported increased insect performance with increasing sugar content in the diet (Chippendale and Reddy 1974; Harvey 1974; Valentine et al. 1983).

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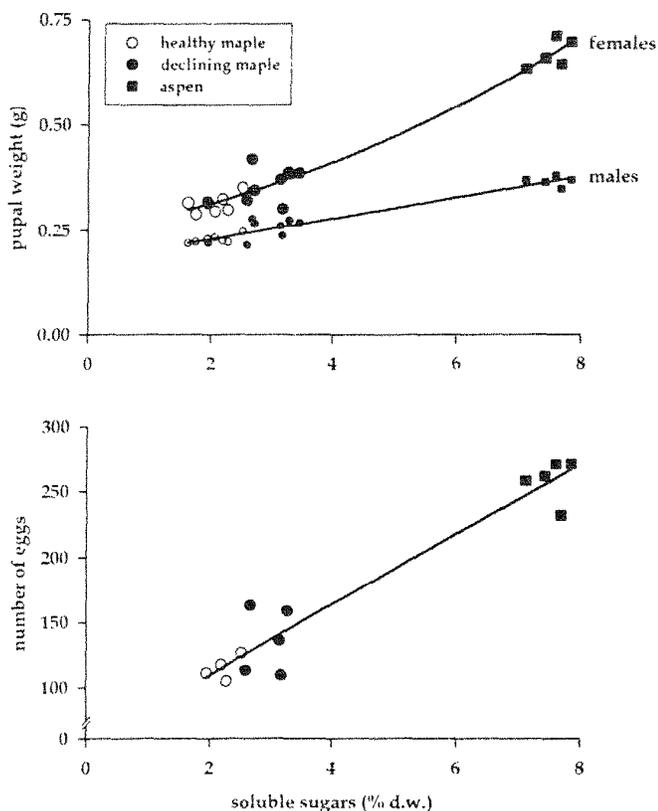


Figure 4.—Mean pupal weight and mean number of eggs per tree in relation to the soluble sugar content of foliage.

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Nitrogen addition affects leaf nutrition and photosynthesis in sugar maple in a nutrient-poor northern Vermont forest

David S. Ellsworth¹

Abstract

Sugar maple-dominated forest ecosystems in the northeastern U.S. have been receiving precipitation nitrogen (N) inputs of 15-20 kg N ha⁻¹ year⁻¹ since at least the mid 1980's. Sustained chronic N inputs of this magnitude into nutrient-poor forest ecosystems may cause eutrophication and affect ecosystem functioning as well as the nutritional balance of mineral elements in the tree crown. Canopy responses to N addition at a low rate (30 kg N ha⁻¹ year⁻¹) over two years were studied in a sugar maple stand on a highly organic, acid soil in northern Vermont to understand the potential effects of N loading on crown nutrition and photosynthesis. In each year, NO₃-N was added just prior to budbreak at a rate of 30 kg ha⁻¹ which was approximately 2× the atmospheric wet deposition rate measured at nearby sites. In late July and early August, fully-expanded canopy leaves were collected for measurements of foliar nutrition and leaf photosynthetic measurements under optimal field conditions. Foliar N increased by an average of approximately 4 mg g⁻¹ or 28% each year in response to N addition, and maximum leaf photosynthetic rate rose 35% with N fertilization. Changes in leaf N concentration and content were consistent with the interpretation that N was limiting leaf biomass production in the stand. Although stand growth and photosynthetic function appear to be strongly limited by N, there is evidence of other limitations to photosynthesis and/or nutritional imbalances in the stand. However, there was no evidence that N addition at the rate used exacerbated other nutrient limitations in the first two years following fertilization. Thus, the sugar maple forest appears to have the potential to continue to store carbon as photosynthate as a result of continuing N deposition to the region.

Introduction

In northern temperate forests, nitrogen (N) is frequently considered to be the nutrient most commonly limiting net primary productivity (Mitchell and Chandler 1939, Vitousek and Howarth 1991). However, forest ecosystems in the northeastern U.S. currently receive 5-15 kg ha⁻¹ of nitrogen annually in the form of wet and dry atmospheric deposition, primarily NO₃ and HNO₃ (Lovett and Lindberg 1993, Townsend et al. 1996, Holland et al. 1997). These anthropogenic inputs of N over many years have the potential to alter tree nutrient balance, internal physiological processes such as leaf carbon fixation, and carbon allocation patterns which ultimately may influence plant responses to other environmental factors such as ozone or elevated CO₂ (Taylor et al. 1994, Magill et al.

1997, Vitousek et al. 1997). It has been suggested that elevated atmospheric N inputs into forest ecosystems may lead to growth dilution of other nutrients, causing nutrient deficiency (Nihlgård 1985, Ågren and Bosatta 1988) although this hypothesis has rarely been tested (but see Lea et al. 1980).

To test for possible effects of increased soil N supply on mineral nutrition and physiological function in sugar maple (*Acer saccharum* Marsh.), individual trees in a nutrient-poor forest in northern Vermont were fertilized with NO₃-N at a low addition rate, equivalent to 2× the current rate of N deposition in the region. The site was typical of sugar maple forests on acidic soils in low-elevation stands in the region which are frequently low in base cations, particularly potassium and calcium (K and Ca; Wilmot et al. 1995). Base cation limitations have been implicated in recent reductions in growth and crown condition in sugar maples throughout the northeastern U.S. (Kolb and McCormick 1993, Wilmot et al. 1995, Wilmot et al. 1996, Long et al. 1997). It was hypothesized that additions of NO₃-N to an acidic soil in a nutrient-poor sugar maple stand would 1) alter tree nutrient balance and internal partitioning of N among photosynthetic processes, and 2) exacerbate leaf K and Ca deficiencies already identified within the stand (Ellsworth and Liu 1994). As a result, both effects would contribute to a relatively minor or negligible photosynthetic response of sugar maple to N addition. Therefore, I asked the following questions: Does increased N input lead to development of other mineral nutrient limitations to tree crown physiology? Does enhanced N supply have a significant effect on tree processes when other nutrients are in short supply? To help answer these questions, a nutrient-poor stand of sugar maple showing evidence of recent crown dieback was selected as a case where marginal nutrient levels would be most likely to interact with N addition in the manner hypothesized above. Leaf nutrients and maximum photosynthesis were monitored for two growing seasons following N addition to the sugar maple forest in northern Vermont.

Materials and Methods

The study was conducted in a stand in Lamoille County in rural northern Vermont (44° 32'N, 72° 34'W). The stand is located at 240 m elevation in the foothills east of the Green Mountains and is found on an acidic soil with pH of soil A horizon < 4.0. The soil is a Salmon coarse silty loam in the Haplorthod group, derived from schistic parent material and low in base cation availability (18 cmol kg⁻¹ cation exchange capacity, T. Wilmot, unpubl. data). When the study was initiated in 1991, extractable soil Ca in the O + A horizons was 529 ± 57 µg g⁻¹ and extractable Al was 44 ± 16 µg g⁻¹, following techniques described in Wilmot et al. (1995). The 80 to 100-year old stand was comprised of pole to sawlog-sized trees of sugar maple, with minor components of red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga*

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canadensis L. [Carr.], ash (*Fraxinus americana* L.) and balsam fir (*Abies balsamea* L. [Mill]). The ground flora was comprised largely of ferns, particularly *Dennstaedtia punctilobula* (Michx.) Moore and *Dryopteris* spp. The stand had been unmanaged for 15 years at the time of the study, but had been briefly managed as a sugarbush and had also undergone some timber removal in 1978 to reduce stand basal area. A partial defoliation in the stand by forest tent caterpillar (*Malacosoma disstria* Hubner) was noted in 1982-83. Mean annual rainfall <5 km from the site is 970 mm and NO₃⁻ and SO₄²⁻ deposition at a similar sugar maple site 20 km to the west (Table 1) were 15.9 kg ha⁻¹ and 23.1 kg ha⁻¹, respectively for the years 1982-1992 (National Atmospheric Deposition Program [NADP] 1993).

Sixteen individual dominant sugar maple trees in the stand were selected for the study. Trees were 25-40 cm in diameter at breast height and were separated from one another by at least 15m to minimize contamination. All trees were rated with some degree of previous crown dieback present according to the protocol given in Wilmot et al. (1995) and following the North American Maple Project (Millers et al. 1991). The average crown dieback rating of the trees at the start of the study was 20 ± 2% (mean ± s.e. for n=30 trees in the stand) and did not appreciably change during the study (data not shown). This indicates that the crown dieback that was initiated in 1988-90 (according to observations of VT Division of Forests and Parks personnel, pers. comm.) was no longer progressing in the stand. Eight randomly-selected trees were fertilized with an application of NaNO₃ at a rate of 30 kg N ha⁻¹ by hand-broadcasting the fertilizer within a 5m-radius of the designated study trees. The application rate was selected to be equivalent to approximately 2' the present rate of ambient NO₃⁻ wet deposition in the region (see NADP 1993). N addition was carried out in a single application before budbreak in both 1992 and 1993. The N addition treatment was not specifically designed to mimic elevated N deposition to forests, which typically occurs as a variety of N species deposited continuously over the season. Rather, N addition was used to test the effects of increased N supply in soil on leaf physiological processes and nutrient dynamics, and determine if the forest was approaching critical N loads as have been hypothesized for other forests (Nihlgård 1985, McNulty et al. 1996, Fenn et al. 1998). The experiment was originally designed as a N × Ca factorial experiment with a Ca application (40 kg ha⁻¹) or N and Ca to a separate set of trees. However, there was no significant effect of Ca addition on leaf Ca (P > 0.10; data not shown) and the Ca addition rate was judged too low for the acid soil to increase Ca availability to the trees by at least an order of magnitude (see Wilmot et al. 1995). Thus Ca-amended trees were not included in the present analysis.

Pretreatment leaf macronutrient concentrations were measured on 16 study trees (8 each for the N addition and control treatments). Green foliage was sampled in August in the three years of this study (two treatment years), before the onset of senescence. In each year, two minor branches

Table 1.—Description of growing-season rainfall (mm) and mean daily temperature (°C) for the study years compared to the 8-year mean as measured at the Proctor Maple Center, a similar site in the Green Mountains in northern Vermont. Data for the Proctor Maple Center, Underhill VT were provided courtesy of the Vermont Monitoring Cooperative. The site is 20 km from the main study site in an adjacent county.

Parameter (mm rainfall or °C temperature)	1991	1992	1993	Mean (1988-1995)
Rainfall (May-Sept.)	503	407	582	548
June temperature	17.1	16.0	15.8	16.7
July temperature	17.8	16.5	19.3	19.0
August temperature	18.6	17.3	18.7	17.6

were harvested from the upper portion of the tree crown using a shotgun and a subset of healthy leaves was collected for analysis of nutrient content. Leaves were oven-dried, ground and homogenized, and analyzed for total N content on a CHN analyzer (CEC-440 Analyzer, Leeman Labs, Lowell, MA) at the University of Vermont Plant and Soil Analysis Laboratory. Single leaf samples measured for photosynthesis were generally not large enough for determining concentrations of multiple nutrient elements, so a pooled sample of adjacent leaves on the same branch was submitted to the University of Vermont Plant and Soil Analysis Laboratory for determinations of leaf macronutrient content using plasma-emission spectrometry (Plasma emission spectrometer, Leeman Labs, Lowell, MA) following digestion.

Measurements of net CO₂ assimilation (A_{net}) were made on leaves from rehydrated upper crown branches from treatment and control trees in late July through mid- August according to methods described in Ellsworth and Liu (1994). The leaves were harvested from near the top of the crown usually concurrent with leaf nutrient sampling described above, and exhibited typical 'sun' leaf characteristics. Immediately upon collection the branches were placed in a bucket of water and recut under water to rehydrate leaves. The leaf CO₂ exchange measurements were made in the field with a portable photosynthesis system (LCA-3, Analytical Development Corp., Hoddesdon, Herts. U.K.) at light saturation achieved with a metal halide lamp (photon flux densities > 1000 μmol m⁻² s⁻¹). Other measurement conditions were near-ambient CO₂ concentrations (340 mmol mol⁻¹ at site elevation) and temperatures (22-27°C). The measurements were made for at least two replicate leaves per tree following the protocol used in a related study, and represented maximum values at the physiological measurement conditions (Ellsworth and Liu 1994). Measurement leaves were selected to represent those in the upper crown of the sample trees and appeared healthy with the exception of minor cases of pear thrips (*Taeniothrips inconsequens* Uzel) feeding or mite-induced gall formation. Ellsworth et al. (1994) found that pear thrips feeding has

Table 2.—Results from repeated measures ANOVA for different leaf nutrients with two years of N addition in a nutrient-poor sugar maple stand northern Vermont. Results are for the main effect (Treatment) and interaction (Treatment x Year). Replicates are seven dominant sugar maple trees for which data are available in all three years (one year pre-treatment and two years of N addition). In cases where $P > 0.10$, the effect was considered not significant (n.s.).

Parameter	Main effect			Interaction		
	F	MSE	P-value	F	MSE	P-value
N	12.83	0.734	0.0072	3.40	0.194	0.0856
K	4.33	0.0247	0.0710	1.54	0.0088	n.s.
Ca	0.58	0.007	n.s.	2.78	0.0344	n.s.
Mg	1.30	0.0004	n.s.	1.83	0.0005	n.s.

minimal effects on area-based rates of photosynthesis and instead principally affects leaf size.

While within-crown variation can be an important factor causing variability in leaf nutrient concentrations and physiology, upper crown branches facing four cardinal directions did not differ in foliar nutrition, and repeat measurements made on different crown branches collected from the same tree on different days had similar photosynthetic rates and nutrient concentrations (data not shown). Previous studies with sugar maple have shown that differences between sun and shade leaves are responsible for most within-crown variability (Ellsworth and Reich 1993). All leaves used in gas exchange measurements were collected and total lamina area and dry mass were determined prior to analysis of leaf chemical content. Leaf punches were taken from the leaf opposite to that used in photosynthesis measurements for measurement of total chlorophyll content (chlorophyll *a* + *b*) using the dimethyl sulfoxide extraction technique as described previously (Ellsworth and Liu 1994).

Data Analyses

One tree in each treatment had to be omitted from the analysis due to missing data in one of the years. Leaf nutrient content over the three years of the study was analyzed using repeated measures analyses of variance (SAS Institute Inc. 1990) for those trees measured in all three years ($n=7$ trees per treatment). Differences between fertilized and control trees were tested using variation among trees as the error term. The significance associated with the differences between yearly means of the treatments was evaluated using the replicates within each treatment with the tree by year interaction as the error term (Sokal and Rohlf 1995). Orthogonal polynomials were used to partition the trend over time and its interaction with tree and treatment into linear or nonlinear components. The leaf photosynthesis data were analyzed using ANOVA and linear regression models of area- and mass-based leaf photosynthesis on leaf nutrients across both treatment years. A graphical analysis of leaf nutrients based on the

trajectory of leaf nutrient concentration and content from pre-treatment to the end of the treatment period was also employed, as described by Timmer and Stone (1978), to help interpret foliar nutrient limitations. This analysis was only conducted on three trees due to missing data.

Results and Discussion

Pretreatment leaf N, P, K, and Mg concentrations of upper crown leaves were 17.6 ± 0.5 mg g⁻¹, 2.3 ± 0.1 mg g⁻¹, 4.7 ± 0.3 mg g⁻¹, and 1.3 ± 0.1 mg g⁻¹, respectively. Leaf calcium (Ca) concentration was 6.3 ± 0.4 mg g⁻¹, among the lowest values reported in the literature for sugar maple (see Kolb and McCormick 1993, Wilmot et al. 1995, Long et al. 1997). There was significant year-to-year variation in leaf N in control trees ($P < 0.001$; Fig. 1), which may have been caused by low leaf N related to a mast-seeding event of sugar maples in spring, or a cool summer in 1992 (year 1 of study; Table 1). It is likely that the observed year-to-year differences in leaf N cannot be ascribed to random sampling variability since I did not observe significant differences in leaf nutrients among sampling dates in the same year or with crown aspect (see Methods). Fyles et al. (1994) noted that such year-year variability necessitates multi-year studies in order to draw conclusions regarding fertilization effects on leaf nutrients and tree vigor, along with pre-treatment data. In the two years of N addition, leaf N was significantly enhanced by the treatment ($P < 0.007$; Fig. 1 and Table 2) with an enhancement of approximately 4 mg g⁻¹ in both fertilization years. Hence leaf N was increased by 28% over the two years in treatment compared to control trees. Given the year-to-year variability in leaf N in control trees, it is unclear if there was diminishing N uptake and allocation into foliage through time although year x treatment was marginally significant for N (Table 2).

In addition to N, there were significant effects of sampling year on leaf P ($P < 0.0017$) and K concentrations ($P < 0.0036$) but not other macronutrients (Fig. 1). There were no significant treatment effects on leaf macronutrients besides N ($P > 0.10$), and no apparent statistical effect of N addition

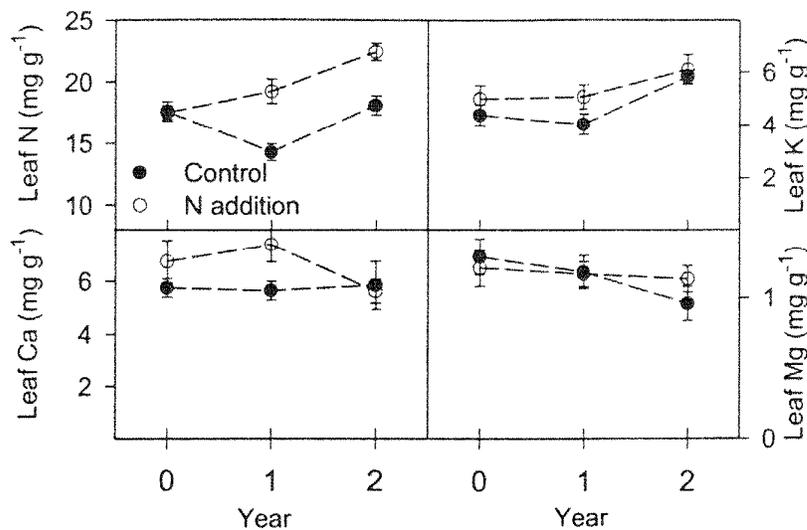


Figure 1.—Leaf nutrient levels in sugar maple foliage in the study stand during pretreatment and the subsequent two years of N addition for treatment (open circles) and control trees (closed circles). Data shown are for N, K, Ca and Mg. Error bars indicate ± 1 s.e. ANOVA results on this data are summarized in Table 2.

on leaf K, Ca or Mg concentrations (Fig. 1; Table 2). When pre-treatment and 2 year-treatment nutrient concentration and content data were plotted as vector diagrams (Timmer and Stone 1978), the trajectories of N upon fertilization showed that unit leaf mass, N concentration and N content all increased from year 0 to year 2 (Fig. 2A), although trees varied in the magnitude of this response. The increases in leaf size and leaf N content shown for all three trees are consistent with the interpretation that the stand was N limited (c.f. Timmer and Stone 1978). The vector diagram for leaf K yielded similar results suggesting that this element also may have been limiting in the stand (Fig. 2B). However, increases in leaf Ca concentration and Ca content followed the unit leaf mass isoline (Fig. 2C), suggesting that leaf Ca was accumulated in proportion to the leaf biomass response to N in Fig. 2A. It is important to note that bulk leaf Ca pools may not adequately assess the physiologically-relevant Ca in leaves since a large proportion of the Ca pool in leaves can occur as inert oxalate crystals. Moreover, it is possible that the addition of nitrate-N may have had 'hidden effects' in altering soil chemistry and Ca availability (Johnson et al. 1996).

Leaf maximum CO_2 assimilation rate was significantly related to leaf N ($r^2=0.57$, $P < 0.0001$; Fig. 3). Since leaves were sampled as 'sun' leaves near the top of the tree crown, mass and area-based photosynthesis and N can be considered roughly equivalent in this situation. The slope of this relationship was similar to those published previously for sugar maple in Vermont (Ellsworth and Liu 1994) and Wisconsin (Reich et al. 1991), and was not significantly different between control and N treatment trees ($P > 0.10$). On average, A_{net} was $91 \pm 6 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ for N treatment trees vs. $60 \pm 6 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ for control trees, with a leaf mass to area ratio of $75 \pm 1 \text{ g m}^{-2}$ for both groups pooled. Overall, mass-based photosynthesis was enhanced by an average of 34% across the two years. Leaf chlorophyll per

unit area was also significantly correlated with leaf N ($r^2=0.38$, $P < 0.0001$; Fig. 3B), and showed enhancement for N treatment trees compared to control trees. Thus both CO_2 assimilation and light energy capture were significantly increased with increases in leaf N due to N addition.

There was a significant but weak correlation between photosynthesis and leaf Ca concentration ($r^2=0.27$, $P < 0.013$; Fig. 4). As I found previously (Ellsworth and Liu 1994), there was a significant correlation ($r^2=0.18$, $P < 0.01$) between leaf Ca and N concentrations (data not shown). Thus it is difficult to ascribe a strictly functional relationship between photosynthesis and leaf Ca that is unique from that of N. Instead, since Ca is deposited in leaf tissue in the transpiration stream and both leaf photosynthesis (Fig. 3a) and stomatal conductance to water vapor (not shown) are correlated with leaf N, it is likely that more Ca is deposited in leaf tissue when leaf N is higher as a result of N effects on gas exchange that produce a greater cumulative transpiration (over the season) with higher leaf N. This argument is consistent with the observation of possible Ca 'luxury consumption' in leaves with N addition (Fig. 2C). Together the available evidence indicates that even though leaf Ca concentrations were low in the stand, Ca was likely not limiting to physiological processes responsible for tree growth via mechanisms involving carbohydrate production in leaves. In fact, root biomass and turnover may be more sensitive to soil Ca than any leaf processes (Liu and Tyree 1997).

The data presented here indicate that this sugar maple stand responds strongly to N addition despite its low cation status. Generally, N fertilization on N-limited sites can be expected to increase stand net primary production relative to the control as a result of 1) enhanced photosynthesis per unit leaf area or leaf mass, 2) more or larger leaves per tree, 3) increased leaf duration and/or 4) more relative

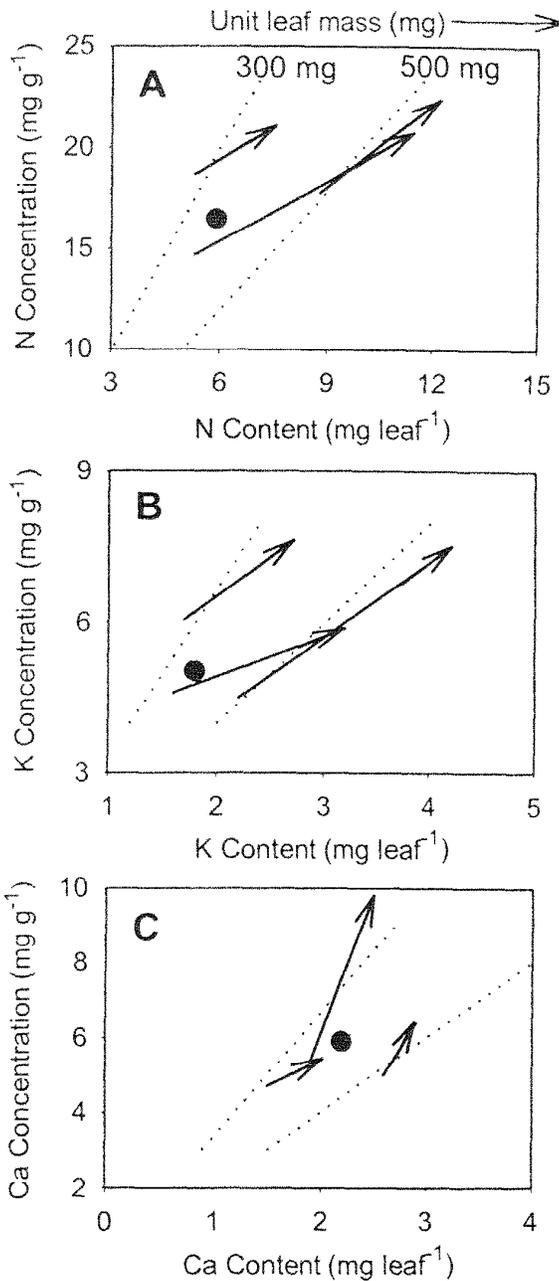


Figure 2.—A. Trajectory of changes in leaf N concentration and N content with two years of fertilization at 30 kg N ha⁻¹ shown using a vector diagram (after Timmer and Stone 1978). Arrowed lines each indicate a single tree followed from pre-treatment to two years of N fertilization (year 0 → year 2). Dashed lines indicate the unit leaf mass isolines for 300 and 500 mg per leaf. The dot denotes mean N concentration and N content of control trees in year 2 of the study. B. Vector diagram of changes in leaf K concentration and K content with N fertilization. Symbols are as in A. C. Vector diagram of changes in leaf Ca concentration and Ca content with N fertilization. Changes in Ca generally follow leaf mass isolines. Symbols are as in A.

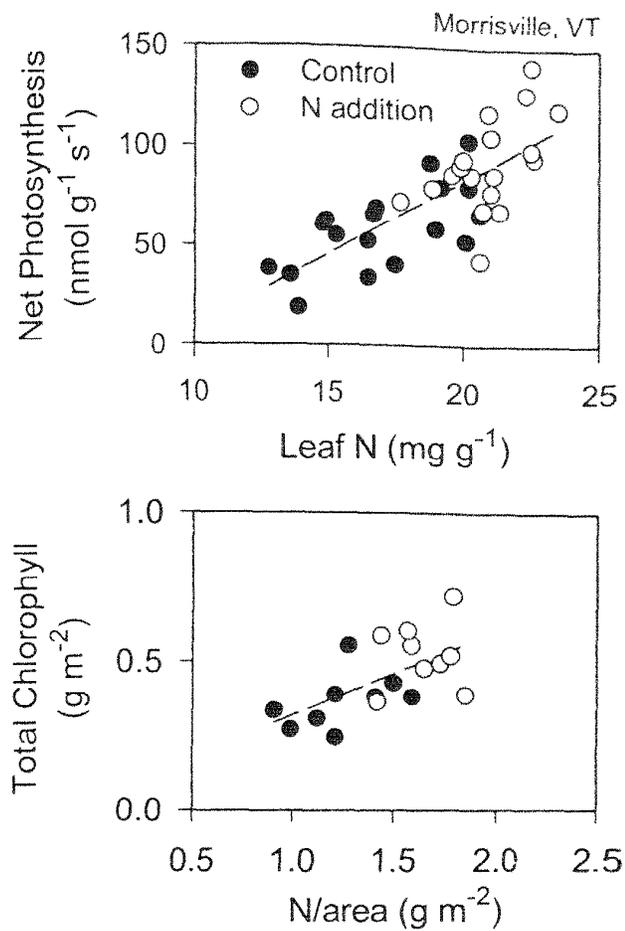


Figure 3— A. Relationship between photosynthesis and leaf N (mass-based) in upper crown *Acer saccharum* leaves for control trees (closed circles) and trees with N added (open circles). Data are pooled between two years as there was no significant effect of year on the relationship ($P > 0.10$). The regression model shown is $Y = -67.1 + 7.53 \cdot X$, $r^2 = 0.57$. B. Relationship between leaf chlorophyll and leaf N (area-based) in *Acer saccharum*. The regression model shown is $Y = 0.08 + 0.283 \cdot X$, $r^2 = 0.38$.

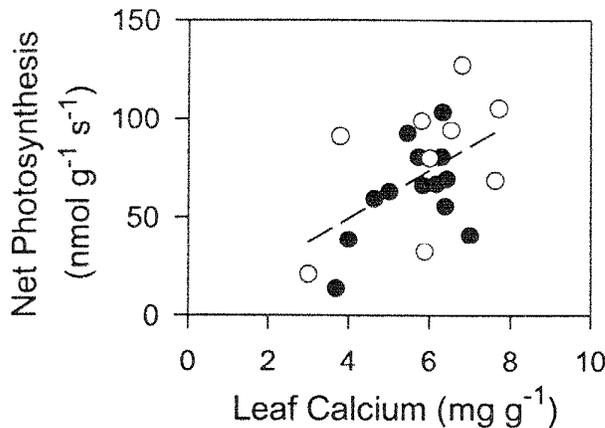


Figure 4.—Photosynthesis in relation to leaf Ca concentration for *Acer saccharum* leaves. Open circles indicated trees with N addition, and closed circles indicate control trees. The regression model shown is $Y = 1.1 + 12.09 \cdot X$, $r^2 = 0.27$. There was no difference in the relationship with respect to N treatment ($P > 0.10$).

carbon allocation to the tree crown versus roots. The current study showed that photosynthesis per unit leaf mass (A_{net}) was indeed greatly enhanced by N addition. While leaf mass in the upper crown also increased with N addition (Fig. 2A), a related plot-level N addition experiment on the same site did not significantly increase total leaf area index of trees (Ellsworth, unpubl. data). Observations at the site also indicated that there was no obvious difference in leaf duration in sugar maple with N addition vs. control trees. Thus the main contributor to increased productivity with N addition at this site was likely the enhancement in leaf photosynthesis with N addition. The increased leaf-level photosynthesis was likely due to greater photosynthetic machinery in N fertilized leaves as a result of increases in the carboxylation enzyme Rubisco (Evans 1989).

The available evidence suggests that the sugar maple forest in this study has a strong potential to respond to increasing N with increased productivity in terms of carbon assimilation in the canopy. Sugar maple responses to N addition were also demonstrated by Mitchell and Chandler (1939), Lea et al. (1980), and Stanturf et al. (1989) in New York, Fahey et al. (1998) in New Hampshire, and Carmean and Watt (1975) in Wisconsin. Magill et al. (1997) also observed increases in leaf N and stand productivity in red maple at Harvard Forest, Massachusetts. These results reinforce the conclusion that sugar maple and related hardwood forests in the northeastern U.S. may respond positively to anthropogenic N addition, at least in the near-term (see Magill et al. 1997 and Fenn et al. 1998). However, in some cases these responses diminished in subsequent years of fertilization (Carmean and Watt 1975, Lea et al. 1980, Magill et al. 1997). Moreover, the fact that similar stands also respond to liming which alters soil chemistry in a number of ways that

can also impact the N cycle (Fyles et al. 1994, Wilmot et al. 1996, Long et al. 1996) suggests that sugar maple stands on poor sites are likely co-limited by multiple nutrient elements. From the results here and in nearby sugar maple stands in Wilmot et al. (1996), N and Ca and possibly K together limit tree growth on sites in northern Vermont. Such multiple limitations may arise as a result of differential sensitivity of tree organs to different mineral nutrients, e.g. sensitivity of canopy processes to N while root processes are sensitive to Ca. As such, caution is warranted when comparing canopy response results such as those shown here with studies that evaluate nutrient responses in terms of wood or root growth.

From a management perspective, N addition to forest stands is costly and may have negative impacts on water quality (Ågren and Bosatta 1988, Fenn et al. 1998) and therefore cannot necessarily be recommended for large-scale use. However, it is also clear that in a stand expected to be K and Ca-limited on the basis of leaf nutrient concentrations and regional liming of similar stands on closely related soils (Wilmot et al. 1995, Wilmot et al. 1996), large nutritional and physiological responses of tree crowns to N addition are possible although it is unclear how long these responses may be sustained. It can be concluded from this two-year study that there is no evidence to suggest that N deposition at the present rate or even 1.5 current deposition will have significant effects on leaf nutrient concentrations or cause increases in Ca deficiencies, although N addition to the stand did have marginal effects on foliar K (Table 2). These results also suggest that longer-term experimentation (> 5 years) of this type is needed in a range of sugar maple stands in order to draw firm conclusions that are more widely applicable, and more relevant to projections for continuing N deposition in the region into the future.

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Markers of Environmental Stress in Forest Trees.

Rakesh Minocha¹

Abstract

Gradual long-term changes in soil and environmental factors due to human activity, may affect forest trees and lead to loss of forest productivity. In most cases, the symptoms of stress appear too late for their effects to be reversed through management and/or treatment. The availability of early biochemical indicators/markers that can assess the current status of stress in visually healthy trees in a forest is crucial for planning a potential treatment or management practice for either alleviating the deleterious effects of the stress or removing the cause of stress. Recently, considerable attention has been paid to the study of changes in polyamine metabolism in plants subjected to various kinds of environmental stress. Polyamines (putrescine, spermidine, and spermine) are open-chain polycations of low molecular weight found in all organisms. They play an important role in the growth and development of plants.

Abiotic stress conditions such as low pH, atmospheric SO₂, high salinity, osmotic shock, nutrient stress such as K or Ca deficiency, low temperature, ozone, and Al stress all lead to an increase in cellular putrescine levels within hours to days. Polyamine concentrations are inversely related to concentrations of cellular ions such as Ca, Mg, Mn, and K in response to Al treatment. The present studies were aimed at studying the relationship between soil nutrients and foliar putrescine in trees growing under varying soil conditions. We have evaluated the use of polyamines as "early markers/indicators" of stress in "visually asymptomatic trees". Trees growing in soils having variable soil Al:Ca ratios or trees growing in soils treated with chronic nitrogen additions, liming, herbicide, or ozone were analyzed for foliar polyamine levels. The results showed a strong correlation between soil nutrient deficiencies (e.g. Ca and/or Mg) and increased foliar putrescine. Our data support the hypothesis that in conjunction with soil chemistry, foliar putrescine can be used as a marker of general stress in visually healthy trees.

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Integrating the Role of Stressors Through Carbohydrate Dynamics

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Popular Summary

Introduction

Stress Definition

Biological stress is defined as any environmental factor (stressors) capable of inducing a potentially injurious strain in living organisms (Levitt 1972). Organisms respond to these stresses physiologically or developmentally, and depending on the duration and severity of the stress, may or may not be injured. Injury may occur directly from the stress, or indirectly when a stress reduces the capacity of organisms to resist additional or associated stresses. Injury occurs when the stress creates strain that exceeds the ability of organisms to resist the stress either by avoiding or tolerating it.

Stressor/Host/Pathogen Interactions: Decline Disease

Because trees are long-lived perennial-growing plants, they are exposed to numerous biotic and abiotic stressors (agents that cause stress) during their life time. The longevity of trees is testimony to their capacity to resist stress and their resilience to recover from injury when stressed beyond their capacity to resist. However, sometimes stress results in the premature death of a portion or all of a tree.

Decline diseases of forest trees are excellent examples of this deleterious stressor/host interaction and result in excessive and pre-mature mortality of canopy trees. Manion (1991) proposes that trees are predisposed by relatively static factors to inciting stressors that induce attack and colonization by contributing biotic factors which ultimately result in tree mortality. Houston (1992) proposed a similar but simpler model in which trees are predisposed by stressors to secondary pathogens (insects and disease organisms) that colonize and kill stress-weakened trees. The decline syndrome of dieback and progressive deterioration of the crown and eventual mortality illustrates the direct effects of stress and injury (dieback), and the indirect effects wherein the tree becomes susceptible and vulnerable to other stressors, i.e. secondary pathogens that cause additional and sometimes fatal injurious strain.

The effects of stress depend on the tree's genetic capacity (vigor) to resist the stress, the health or vitality of the tree when stressed, and the severity (e.g. % defoliation, millibars of moisture tension), duration or frequency (e.g. successive years of defoliation, length of drought), timing (when in the growing or dormant season), interacting or concert stressors (e.g. defoliation and drought, winter injury and drought), and

the presence and aggressiveness of opportunistic pathogens (Wargo 1977, 1978, 1981a; Wargo and Auclair 1999).

These relationships are illustrated in Figure 1. Depending on their health or vitality class - here depicted as crown condition - trees in good, fair, or poor condition respond differently to different levels of stress ($S1 < S2 < S3$). The time relationship shows that trees change in health status more or less rapidly depending on the severity of the stress, and also that some trees can recover, the time of recovery dependent on initial tree health, and severity of stress. Also the figure illustrates that there is a threshold range where stress reduces the capacity of the tree to defend itself against secondary pathogenic organisms, and trees succumb to their attack and die. Interactions of health, stress level, and time are also illustrated in this threshold relationship.

Carbon Allocation

The threshold level of vulnerability of trees to attack by opportunistic secondary pathogens is a function of the abundance and aggressiveness of the secondary organism and the abundance of carbon allocated, or available to be allocated to defense in the case of organism attack, whether it be inhibitory compounds in tissues attacked by fungi or rapid growth to resist physical damage from insect infestations.

Source-sink Relationships

A simple model of carbohydrate allocation is given in *Physiology of Woody Plants* (Kramer and Kozlowski 1979):

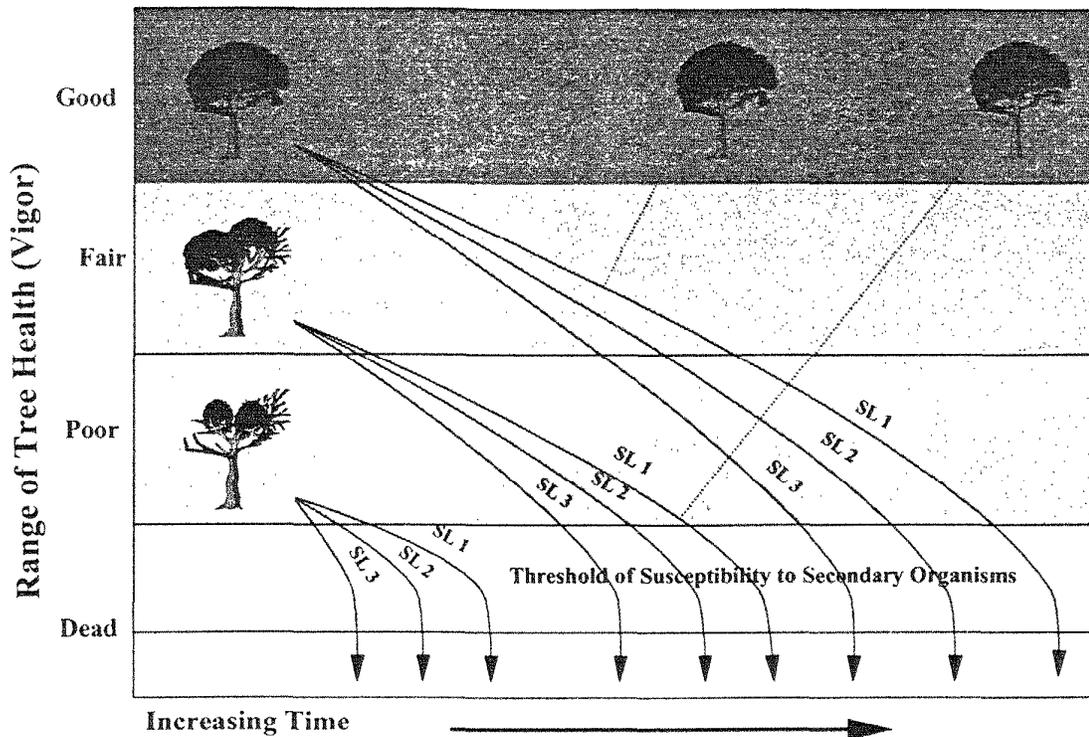
income = carbohydrates manufactured by photosynthesis (source)

expenditures = carbohydrates used in assimilation and respiration (sinks)

balance = carbohydrates accumulated (sinks)

Although a simple model, it nicely illustrates the major uses of carbohydrates in forest trees and indicates where and how stressors can influence carbon allocation. Stressors can affect the carbon budget by directly affecting the source and reducing photosynthesis and carbohydrate production. Defoliating insects, fungi, and frost and drought can cause reductions in photosynthesis. Other stressors can affect the sinks for carbon allocation by accelerating the use of carbohydrates in assimilation or in increased respiration or both. Drought for example can result in an increase in fine root production which increases the amount of carbon needed for production and growth of the root system (Sharp and Davies 1979; Turner 1986). Reduced calcium in the

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Interaction of Stress (SL1, SL2, SL3), Tree Condition, Secondary Organisms, and Time in the Decline and Death of Trees

Figure 1.—An illustration of the relationships and interactions of tree health, stress severity (levels $S_1 < S_2 < S_3$), secondary organisms, and time in the dieback, decline, recovery, or death of trees.

foliage because of aluminum-induced calcium depletion or reduced uptake can increase dark period respiration and increase the carbohydrates used in respiration (McLaughlin et al. 1991).

Both the direct effects of stressors on photosynthesis and carbohydrate production and the increased use of carbon for assimilation and respiration can have effects on the third part of the budget, carbohydrate accumulation. Stresses such as defoliation can result in reduced carbohydrate storage by reducing the total amount of photosynthate available for storage, and by triggering the conversion of stored carbohydrate to assimilable or respirable soluble carbohydrates during the stress period. The effects would depend on the severity, frequency, and timing of the stress event.

Stressors In Northeastern Forests

Lists of abiotic and biotic environmental factors, that can act as primary stressors in northeastern forests are found in Houston (1987), Manion (1991), and Millers et al (1989). Drought and defoliation are listed as the most common stressors, but sucking insects, such as the beech scale and

hemlock woolly adelgid, and defoliation from late spring frosts or fungal pathogens are also prevalent. The most recent and widespread ice storm in the Northeast in January of 1998 has emphasized that ice injury also is a common stressor in our northeastern forests.

Stressors will continue to play a large role in forest health issues in northeastern forests partly because this region has experienced more change in climate, air chemistry, land use, site alterations and other human impacts than any other region in the United States (Wargo and Auclair, in press) and partly because more non-indigenous pests have been introduced and have become established in northeastern forests (Mattson et al. 1993; Liebhold et al. 1995). These "exotic" pests have caused significant damage (mortality) and have resulted in large changes in forest composition, structure, and function throughout the Northeast.

Measuring the Effects of Stressors

Carbohydrate Dynamics and Defoliation

Carbohydrate content, especially reserves stored as starch, has been used as a monitor or indicator of the effects of

stressors on hosts, especially the effects of defoliating insects. In work on sugar maple, *Acer saccharum* Marsh. (Parker and Houston 1971; Wargo 1971, 1972; Wargo et al. 1972) starch content of the roots was an excellent indicator of tree response to defoliation. In stands of sugar maple defoliated by the saddled prominent, *Heterocampa guttivita* (Webr.) starch content of the roots not only reflected the severity of defoliation, but also the frequency (Wargo et al. 1972).

Artificial defoliation experiments on sugar maple saplings illustrated the timing and magnitude of change in carbohydrate levels in response to normal seasonal cycles and to defoliation (Wargo 1971, 1972). These studies indicated that changes caused by defoliation were far greater than those occurring because of normal seasonal change in production and use of carbohydrates. These studies also showed that the effects of defoliation depended on when in the growing season trees were defoliated. Effects depended mainly on whether the trees re-foliated in response to defoliation and the length of the remaining growing season after re-foliation. However, there was a strong interaction with carbohydrate status (starch) at the time of defoliation. Trees with low starch reserves were more likely to die than those with higher reserves, which in general increased as the season progressed. Starch reserves were also important to how these saplings responded to wounding. Wound areas were larger on defoliated trees and were highly and negatively correlated with starch content of the trees (Wargo 1977).

In field studies from 1972 to 1975 on mature oaks, (*Quercus alba* L., *Q. coccinea* Muench, *Q. prinus* L., *Q. rubra* L., and *Q. velutina* Lamarck) defoliated by the gypsy moth, *Lymantria dispar* L., starch content of the roots not only showed the effects of defoliation levels measured in 1972-75 but also revealed that trees had been defoliated prior to 1972 (Wargo 1981c). Although this defoliation was not severe enough to be recorded in earlier years, it still had a significant physiological consequence on the trees. Starch content in these trees was monitored after defoliation ceased and had not recovered to predefoliation levels even after two years of no or very low defoliation (Wargo 1981c).

Starch content in roots of oaks also indicated their vulnerability to mortality associated with defoliation (Wargo 1981c). Trees in the red or white oak groups were assigned a risk of mortality based on root starch content and then monitored for two years after a single heavy defoliation. Mortality was consistently higher in the low starch-high risk trees in both oak groups. Starch was a better indicator of risk of mortality than crown condition.

This relationship of low starch to high risk of mortality was demonstrated experimentally (Wargo 1981b). In these studies, starch content in maple and oak saplings at the time of defoliation determined their response to defoliation. Trees with lower initial starch contents died first after 1 or 2 years of defoliation, while trees with higher initial contents after 3 years of defoliation died later, and trees with still higher starch levels survived the ordeal entirely.

Starch and soluble carbohydrate status in the root system has also been related to crown dieback, rate of crown deterioration and growth loss, in declining mature sugar maple in Canada (Renaud and Muaffette 1991).

Consequences of Altered Carbohydrate Dynamics

Corresponding to decreases in starch content as a result of stress, are substantial increases in reducing sugars, especially in the root system. These increases can be four to five times higher than in unstressed trees at the same time of year and also than the normal seasonal high that occurs in spring when carbohydrates are mobilized for growth (Wargo 1971, 1972). Coupled with changes in nitrogen metabolism, these carbohydrate levels are important to opportunistic organisms, particularly species of *Armillaria* which can attack and kill stressed trees (Wargo and Houston 1974). Reducing sugars, especially glucose, not only stimulates the growth of this fungus, but also enables it to grow in the presence of inhibitory phenols such as gallic acid (Wargo 1972, 1980, 1981d).

Winter starch reserves in roots of white oak were related to susceptibility and vulnerability to attack by the twolined chestnut borer, *Agilus bilineatus* (Weber) (Dunn et al. 1987). White oaks with low starch reserves attracted more beetles than moderate or high starch trees. And only trees that had extremely low root starch were heavily attacked by the beetle and subsequently died.

Even susceptibility to aggressive primary pathogens have relationships with carbohydrate dynamics. Time of highest susceptibility of American elm, *Ulmus americana* L. to colonization by *Ophiostoma ulmi* (Ceratocystis), the Dutch elm disease fungus, is during leaf expansion when starch reserves in the growth rings were lowest (Shigo et al. 1986). In addition, infected trees stored less starch than healthy trees making them even more vulnerable to death after additional infections.

Carbohydrate Status in Declining Sugar Maple - Allegheny Plateau

Carbohydrate status of healthy and declining sugar maple on the Allegheny Plateau in northcentral Pennsylvania were assessed in a series of lime fertilization treatment plots established in 1985 (Auchmoody 1985, Long et al. 1997). Samples were collected in autumn 1997 after leaf drop. Second order woody roots were collected from each of three sugar maple trees within each treatment plot within each block. Approximately 45 cm of root 1 to 2.5 cm in diameter was collected for a series of carbohydrate and phenol analyses. Roots were frozen on dry ice in the field and placed in freezers upon return to the laboratory. A small portion (2 to 3 cm long) was cut from a section of harvested root and used for a visual determination of starch content in the roots of each tree (Wargo 1975, 1978).

Root pieces were thawed quickly in tap water, washed, and trimmed for sectioning and staining as described by Wargo (1975). Root sections were then rated for starch content as very high, high, moderate, low or none based on the density

Table 1.—Visual ratings for starch content in roots of sugar maple trees in a series of lime-treated plots on the Susquehannock State Forest on the Allegheny Plateau in northcentral Pennsylvania

Treatments ^b	Blocks ^a				Average
	BD1	BD2	CS3	CS4	
Control	3.0	3.3	2.7	3.3	3.1
Control Fence	4.7	4.3	4.0	4.3	4.3
Herbicide	2.7	4.3	3.3	3.7	3.5
Herbicide Fence	3.3	4.0	4.7	3.7	3.9
	3.4	4.0	3.7	3.7	3.7
Limed	4.0	4.3	4.7	4.7	4.4
Limed Fence	4.0	4.7	5.0	3.7	4.3
Limed Herbicide	4.3	4.0	4.7	4.7	4.4
Lime Herbicide Fence	3.7	4.0	5.0	4.0	4.2
	4.0	4.2	4.8	4.3	4.3

^aBlocks were located in 2 sections of the Susquehannock State Forest, Pennsylvania, Black Diamond Road (BD and BD2) and Cherry Springs (CS3 and CS4).

^bTreatments were arranged in a split-plot design with deer fencing (fence, no fence) as the whole-plot treatment and four sub-plots treatments (herbicide, dolomitic lime, herbicide + dolomitic lime, and no herbicide or lime) within each whole plot (Auchmoody 1985, Long et al. 1997).

^cStarch rating scale: 1=none, 2=low, 3=moderate, 4=high, 5=very high.

Table 2.—Starch ratings and vigor class of sugar maple trees in the lime treated series of plots in northcentral Pennsylvania

Starch ratings	Vigor of living trees ¹				Total
	1	2	3	4	
Very high	20	2	10	5	37
High	17	3	7	4	31
Moderate	8	0	8	4	20
Low	1	0	0	7	8
None	0	0	0	0	0
Total	46	5	25	20	96

¹Mader-Thompson System (Mader and Thompson 1969)

of purple-black staining in the ray and xylem parenchyma. A descending numerical value of 5 for very high to 1 for none was assigned each rating and an average for each treatment was determined.

Preliminary results indicated that on average all limed treated plots had high starch contents (Table 1). Lowest starch levels were in untreated control plots. Cherry trees were sampled in only the fenced portion of block CS4. Three trees were sampled per plot. All cherry trees were rated very

high or high. The average starch content for cherry was 5.0 for control plot, 4.3 for the herbicide plot, 4.3 for the limed plot and 4.7 for the limed herbicide plot.

Most trees rated as low in starch were in vigor class 4 or greater (vigor 1=healthy, 2=light decline, 3=moderate decline, 4=severe decline, 5=dead; Mader and Thompson 1969); however not all poor vigor trees had low starch contents (Table 2). Seven of the 8 low starch trees were from unlimed plots and all were in class 4 vigor.

Conclusions

Carbohydrate status, especially storage carbohydrates primarily starch, integrates the effects of stress on trees vitality and largely determine their ultimate response to stress. Energy reserves are necessary for mobilization to support respiration and assimilation prior to new leaf production at the beginning of the growing season. They are also necessary to support these processes during times of stress. Inadequate carbohydrate reserves predisposes trees to injury from the stress itself but also and especially from opportunistic organisms that are ubiquitous in the environment and depend on stress weakened trees as energy sources.

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Widespread Sugar Maple Decline and Regeneration Failure in the Adirondacks

Jerry C. Jenkins, Elizabeth Moffett, and Daphne Ross¹

Poster Abstract

Over large areas of the Adirondacks, hardwood stands whose canopies are dominated by or contain abundant mature sugar maple (*Acer saccharum* Marsh.) have almost no sugar maple saplings or seedlings in the understory. Coring shows that most (>80%) of these stands reproduced well in the first half of this century but have added few or no trees to the canopy or subcanopy since 1950. Such forests contrast sharply with maple stands elsewhere in the state and the northeast, which typically have a persistent bank of suppressed seedlings, abundant maple saplings in small gaps, and continuing recruitment of young maples to the canopy and subcanopy. Our research has been designed to assess the incidence, chronology, and ecological correlates

of this problem. We find that sugar maple regeneration failure is a) widespread in the east Adirondacks and almost ubiquitous in the western Adirondacks; b) equally common in commercial, ex-commercial, and old-growth forests; c) characterized by the early death of seedlings and hence by sparse seedling banks; d) commonly associated with an abundance of young beech but not restricted to points at which beech is locally abundant; e) found across a range of light levels and not restricted to extremely dark forests; and f) most likely to occur on soils with low (<300 ppm) amounts of exchangeable calcium and least likely to occur on soils with high (>700 ppm) amounts of exchangeable calcium. Our results are consistent with studies from Pennsylvania showing high sugar maple seedling mortality on soils with depleted calcium pools. We suggest that the remarkably uniform occurrence of regeneration failure is ecologically and economically alarming and that our results are consistent with, but do not establish, a central role for soil cation changes, possibly caused by acid rain.

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Relationships Between Stream Acid Anion-Base Cation Chemistry and Watershed Soil Types on the Allegheny High Plateau

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Poster Abstract

The leaching of calcium and magnesium from forests by atmospherically-deposited strong acid anions (sulfate and nitrate) is evidenced in some watersheds by the positive correlation in stream water between concentrations of these base cations and acid anions. However, in other watersheds, stream concentrations of base cations and acid anions are negatively correlated, even where acidic deposition is high. The goal of this study was to determine if base cation-acid anion relations in headwater streams were related to proportions of soils with shallow perched water tables (SWT) and soils without perched water tables in a watershed. I sampled stream water from 18 forested watersheds in the Allegheny National Forest, Pennsylvania, between August 1996 and June 1997. I placed each watershed into one of three groups according to the base cation-acid anion relationships of its primary stream: (1) positive correlation between base cations and acid anions ($p \leq 0.05$; $n=10$), (2) negative correlations between base cations and acid anions ($n=4$), or (3) either a combination of positive and negative correlations or no significant relationship between base cations and acid anions ($n=4$). Percentages of watershed area covered by soils with shallow perched water tables (%SWT) differed significantly (ANOVA, $p=0.01$) among the

three groups of watersheds. The percent of the watershed covered with SWT for positively correlated cation-anion relationships was significantly greater ($p < 0.05$, Scheffe test) than the percent of the watershed area with SWT for negatively correlated cation-anion relationships, and was marginally ($p=0.055$) greater than the percent of watershed area covered by soils with SWT for mixed or non-significant cation-anion relationships. In two watersheds covered mostly (80-90%) by soils with shallow perched water tables, the streams were flashy (*i.e.*, streams rose quickly in response to precipitation inputs) and calcium, magnesium, and sulfate concentrations all increased similarly with increasing discharge. In contrast, at a watershed with $< 32\%$ of its area covered by soils with shallow perched water tables, the stream was less flashy, and base cation concentrations declined sharply with increasing discharge, even though sulfate concentrations increased and nitrate concentrations remained essentially unchanged. These results suggest that flowpaths of groundwater that contribute to stream water are influenced by physical properties of soils in the watershed: where an impermeable layer (*e.g.*, a fragipan) supports a perched water table, most stream water might originate from soil horizons above the impermeable layer. However, where impermeable layers are less extensive, stream water might originate mostly from deeper (more base-rich) groundwater at low flow and shallower (more acidic, base-dilute) groundwater at high flow (*e.g.*, after storms).

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Effects of CaCl_2 and AlCl_3 Additions on Sugar Maple Fine Roots and Exchangeable Ions in Rhizosphere and Bulk Soils of a Northern Hardwood Forest

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Poster Abstract

Increased mobilization of aluminum and accelerated leaching of calcium and magnesium from the rooting zone have been linked to strong acidic inputs to northern hardwood forests. Changes in soil chemistry have been hypothesized to adversely affect Ca and Mg uptake and stress tolerance of sugar maple (*Acer saccharum* Marsh.) on base-poor soils. From 1995 to 1997, three experimental treatments were applied to four replicate northern hardwood plots: CaCl_2 (10 g/m²), AlCl_3 (4.5 g/m²) and control (no chemical additions). We sampled bulk soil, rhizosphere soil

and fine roots from four overstory sugar maples in each plot. The AlCl_3 treatment resulted in 68% lower (Ca+Mg)/Al molar ratios in bulk soils and 63% lower ratios in rhizosphere soils. Other differences in Al, Ca and Mg concentrations between treatments were too small to be significant. We found the rhizosphere to be depleted in exchangeable and organically-bound Al and enriched in Ca and Mg relative to bulk soil. Fine root concentrations of Al were significantly greater (64%) in AlCl_3 treated plots than controls. These results suggest increased mobilization of Al due to decreases in the (Ca+Mg)/Al molar ratios in bulk and rhizosphere soils may lead to preferential adsorption of Al on root exchange sites. Interference of Ca and Mg uptake may have long-term implications for sugar maple nutrition in base-poor soils.

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