

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

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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 (Nihigård 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 μmol 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

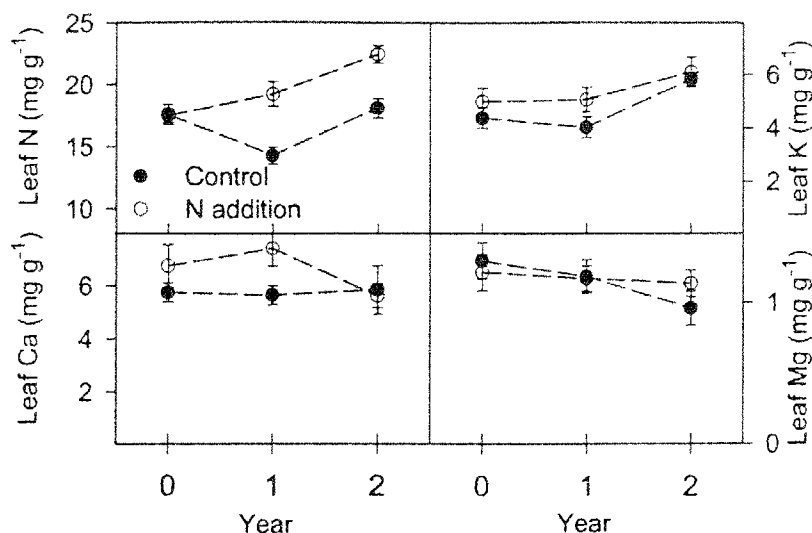


Figure 1.—Leaf nutrient levels in sugar maple foliage in the study stand during pretreatment and the subsequent two years of N addition for treatment (open circles) and control trees (closed circles). Data shown are for N, K, Ca and Mg. Error bars indicate ± 1 s.e. ANOVA results on this data are summarized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

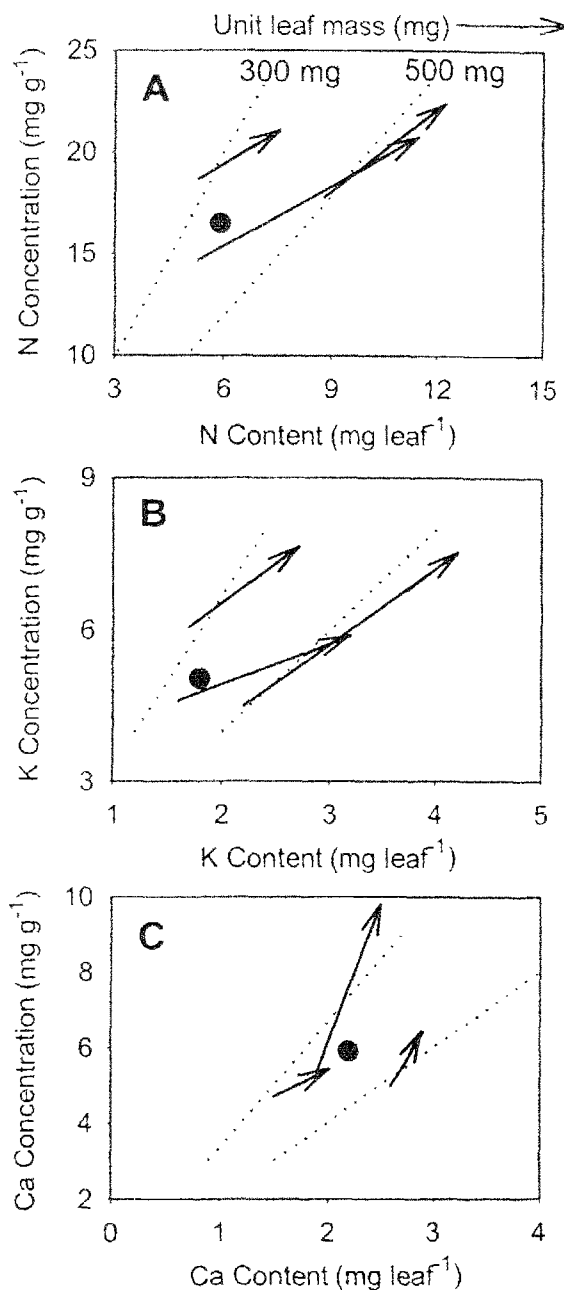


Figure 2.—A. Trajectory of changes in leaf N concentration and N content with two years of fertilization at 30 kg N ha⁻¹ shown using a vector diagram (after Timmer and Stone 1978). Arrowed lines each indicate a single tree followed from pre-treatment to two years of N fertilization (year 0 → year 2). 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.

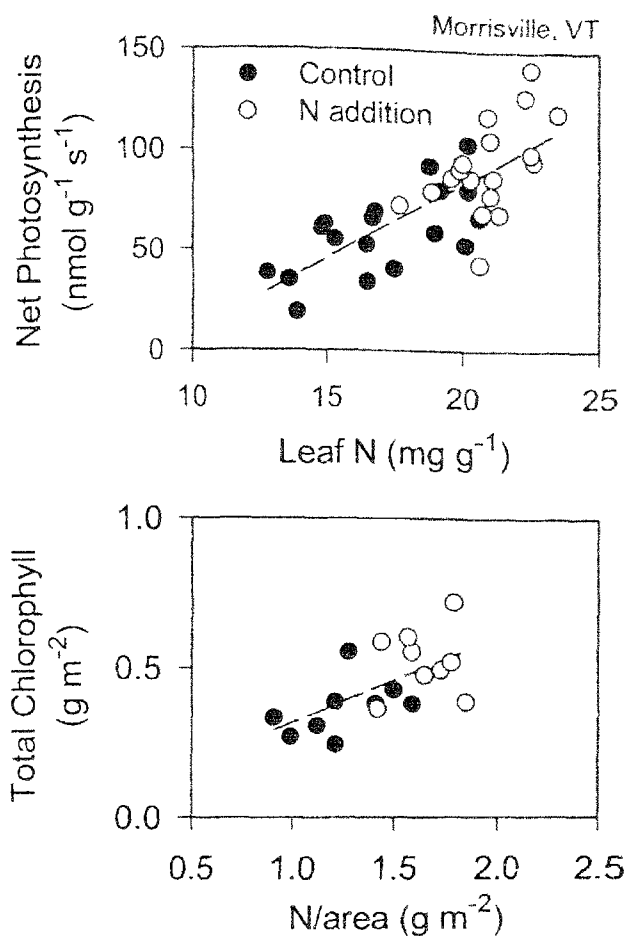


Figure 3— A. Relationship between photosynthesis and leaf N (mass-based) in upper crown *Acer saccharum* leaves for control trees (closed circles) and trees with N added (open circles). Data are pooled between two years as there was no significant effect of year on the relationship ($P > 0.10$). The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

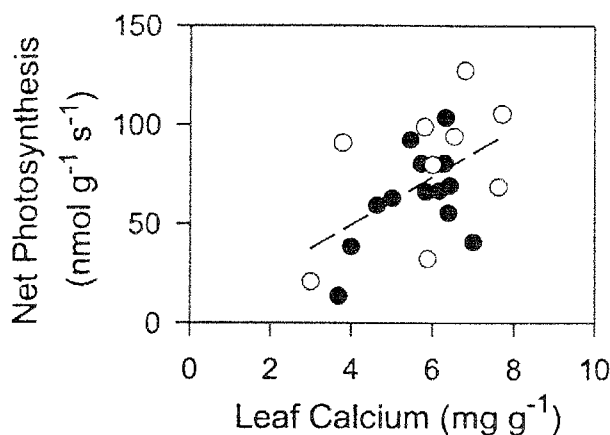


Figure 4.—Photosynthesis in relation to leaf Ca concentration for *Acer saccharum* leaves. Open circles indicated trees with N addition, and closed circles indicate control trees. The regression model shown is $Y = 1.1 + 12.09X$, $r^2 = 0.27$. There was no difference in the relationship with respect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