Photosynthesis and canopy nutrition of four sugar maple forests on acid soils in northern Vermont

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Canopy nutrition, leaf chlorophyll concentration, and leaf CO_2 assimilation capacity (A_{max}) were examined in sugar maple (*Acer saccharum* Marsh.) trees exhibiting symptoms of crown dieback in four stands on acid soils (pH ≈ 4.0) in northern Vermont. Leaf CO_2 assimilation capacity was measured on foliage from detached and rehydrated branches harvested from the upper portion of the canopy. Leaf calcium (Ca) and magnesium (Mg) concentrations were among the lowest reported for sugar maple in its natural range. Total leaf chlorophyll concentrations of canopy leaves were lowest on the sites exhibiting the lowest leaf nitrogen (N) and Ca, and CO_2 assimilation capacity was correlated with chlorophyll concentration among canopy leaves from all sites. Strong linear relationships were observed between leaf CO_2 assimilation capacity per unit leaf mass and leaf N ($r^2 = 0.60$) as well as leaf Ca ($r^2 = 0.51$) among the four sites. On the basis of the observed strong correlation between leaf Ca and leaf N ($r^2 = 0.64$) and the lack of clear enhancement of leaf CO_2 assimilation capacity in trees fertilized with base cations (K, Ca, and Mg), it appears that leaf CO_2 assimilation capacity and leaf Ca may not necessarily be functionally related. However, since low leaf CO_2 assimilation capacity and photosynthetic N-use efficiency were common in unfertilized trees with low Ca (Ca < 0.6%), CO_2 assimilation processes in sugar maple on acid soils may be limited by N and Ca × Mg interactions. The strongly acidic nature of the soils in these stands and the magnitude of acidic deposition in the region may precondition sugar maple trees on some sites to levels of cation deficiency that may be associated with low CO_2 assimilation in the forest canopy.

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La nutrition du couvert, la concentration de chlorophylle dans les feuilles et la capacité d'assimilation de CO_2 (A_{max}) des feuilles furent étudiées chez des érables à sucre (*Acer saccharum* Marsh.) montrant des symptômes de dépérissement de la cime et situés dans quatre peuplements sur des sols acides (pH ≈ 4,0) dans le nord du Vermont. La capacité d'assimilation foliaire de CO_2 a été mesurée sur les feuilles de branches détachées et réhydratées récoltées dans la partie supérieure du couvert. Les concentrations foliaires de calcium (Ca) et de magnésium (Mg) étaient parmi les plus faibles rapportées pour l'érable à sucre dans son aire naturelle de distribution. Les concentrations totales de chlorophylle foliaire des feuilles du couvert étaient les plus faibles sur les sites où les concentrations d'azote (N) foliaire et de Ca foliaire étaient les plus faibles. La capacité d'assimilation de CO_2 était corrélée avec la concentration de chlorophylle dans les feuilles du couvert dans tous les sites. De fortes corrélations linéaires ont été observées entre la capacité d'assimilation de CO_2 par unité de masse foliaire et N ($r^2 = 0,60$) et Ca ($r^2 = 0,51$) foliaire dans les quatre sites. Étant donné la forte corrélation entre Ca et N dans les feuilles ($r^2 = 0,64$) et l'absence d'une nette augmentation de la capacité d'assimilation de CO_2 dans les feuilles des arbres fertilisés avec des cations basiques (K, Ca et Mg), il semble que la capacité d'assimilation de CO_2 dans les feuilles et le Ca foliaire ne seraient pas fonctionnellement reliés. Cependant, étant donné que la capacité d'assimilation de CO_2 dans les feuilles et l'efficacité d'utilisation de l'azote dans la photosynthèse étaient faibles chez les arbres non fertilisés et avec une faible concentration de Ca (Ca < 0,6%), N et les interactions Ca × Mg pourraient entraver les processus d'assimilation du CO_2 chez l'érable à sucre sur des sols acides. La nature très acide des sols dans ces peuplements et l'importance des dépôts acides dans cette région pourraient sur certains sites prédisposer les érables à sucre à des niveaux de carence en cations qui pourraient être associés à une assimilation réduite du CO_2 dans le couvert.

[Traduit par la Rédaction]

Introduction

The importance of adequate mineral nutrition to normal physiological and growth processes in forest trees is well known; however, increasing recognition of the possibility of nutritional imbalances in trees as a result of anthropogenic alterations in atmospheric chemistry (Richter et al. 1992) and subsequent effects on forest soil chemistry (Driscoll et al. 1985; Ulrich and Matzner 1986) has raised concern over the continued health and long-term productivity of forests in industrialized regions (Pitelka and Raynal 1989; Barnard et al. 1990). Recent work has implicated nutrient deficiencies and imbalances in preconditioning trees to foliar chlorosis, progressive shoot dieback, and overall stand decline in forests on acid soils in central Europe (Zöttl and Hüttl 1986; Oren and Schulze 1989), high-elevation ecosystems in eastern North America (McLaughlin and Kohut 1992), and more recently in other forests in eastern North America (Bernier et al. 1989; Raynal et al. 1992). Documentation of the relationships between nutritional deficiencies and leaf carbon balance in coniferous forest species exhibiting decline symptoms (Zimmermann et al. 1988; McLaughlin et al. 1991) has led to the development of mechanistic hypotheses to explain physiological responses to

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dieback and stand decline (Schulze 1989; McLaughlin and Kohut 1992); however, there is little of this information currently available for mature deciduous forest trees growing on acid soils (pH ≤ 4.0).

A progressive dieback of the crown of sugar maple (*Acer saccharum* Marsh.) trees in localized areas within the species range has recently been observed by a number of investigators (Bernier and Brazeau 1988; Gagnon et al. 1990; Allen et al. 1992*a*). Despite numerous hypotheses to explain this dieback phenomenon (Bernier et al. 1989; Allen et al. 1992b; Raynal et al. 1992), a comprehensive understanding of the role of nutrient deficiencies in the metabolism and overall carbon balance of sugar maple is lacking. Inadequate nitrogen (Mader and Thompson 1969), phosphorus (Paré and Bernier 1989), potassium and magnesium (Bernier and Brazeau 1988; Bernier et al. 1989; Oimet and Fortin 1992), and calcium (Mader and Thompson 1969; Wilmot et al. 1995) levels have been associated with the sugar maple crown dieback phenomenon, although the physiological basis of the putative nutritional dysfunction (cf. Oren and Schulze 1989) and the potential impacts on tree carbon balance have largely remained uninvestigated. Current theory concerning plant resource limitations suggests that plant responses to nutrient deficiencies and (or) imbalances may be important in mediating physiological responses to other environmental stresses (Bloom et al. 1985; Chapin 1991). Hence it has been hypothesized that soil infertility may precondition trees to carbon depletion in combination with other stresses such as drought or defoliation (Gregory et al. 1986; Bernier et al. 1989; McLaughlin and Kohut 1992). In sugar maple, stored root carbohydrates may be reduced in trees exhibiting severe symptoms of dieback (Renaud and Mauffette 1991), indicating that incidence of severe dieback may be associated with insufficient carbon balance in the tree crown and hence depletion of internal stored carbohydrates. It remains unclear whether a reduction in leaf carbon balance related to site nutrient stress is involved, or whether reductions in whole-tree carbon balance are instead directly related to stress-induced alteration of carbon balance and subsequent reductions in leaf area, which may further decrease the whole-plant assimilation rate.

The objectives of the present study were to characterize leaf-level photosynthetic carbon assimilation patterns in sugar maple trees currently showing dieback symptoms among different sites and examine inter-relationships between leaf net photosynthesis, leaf chlorophyll, and canopy nutrition in sugar maple trees on acid soils in northern Vermont. Photosynthetic measurements were designed to reflect overall physiological capacity of foliage for CO_2 fixation in trees currently showing dieback symptoms. Chlorophyll was examined because of the reports of foliar chlorosis associated with dieback and growth declines (Bernier and Brazeau 1988; Lange et al. 1987). Nutrient manipulations were achieved by use of a fertilizer mixture of K, Ca, and Mg designed to experimentally expand the potential range of cation nutrition observed in sugar maple trees on acid soils in northern Vermont.

Materials and methods

Study sites

Four sugar maple forests located within 100 km of one another in northwestern and north central Vermont were selected for this study (Table 1). Two study sites each were located on the west and east sides of the Green Mountain cordillera. The regional climate is cool, moist, and submontane–continental with warm summers and cool winters. Average annual precipitation at the Proctor Maple Research Center in Underhill Center, Vermont (Table 1), a site in the Green Mountain foothills, is 1120 mm (1982–1992 data; NADP 1993) with approximately 40% of annual precipitation falling as snow. Average precipitation pH at the Proctor Maple Research Center is 4.35, and average annual NO_3^- and SO_4^{2-} deposition is 15.9 and 23.1 kg·ha^{-1}, respectively, for 1982–1992 (NADP 1993). All study sites were located on glacial till or glaciolacustrine substrates derived from schists and gneisses of Cambrian origin, which tend to weather to base-cation-poor, acid soils (pH_{water} of upper 5 cm of soil ranges from 3.9 to 4.3; Table 1). Sites were located on well-developed soils in the Haplorthod great group (Humo-Ferric or Ferro-Humic Podzols, Canada Soil Survey Committee 1978). Cation exchange capacity of the soils ranged from 18 to 26 cmol·kg^{-1} (T. Wilmot, unpublished data). A description of the nutrient content of these soils is presented elsewhere (Wilmot et al. 1995).

A portion of the sugar maple stand on each site (approximately 0.5 ha) exhibiting apparent symptoms of crown dieback was selected for study. Average crown dieback of 20–25 representative overstory trees in the study plot in each stand exceeded approximately 10% (based on visual estimates of the projected crown area) in 1990–1991 (Wilmot et al. 1995; T. Wilmot, unpublished data). The incidence of dieback was not directly attributable to primary pathogens, as there was no evidence of pathogens or apparent trunk defects on the dominant overstory trees sampled (T. Wilmot and D. Ellsworth, unpublished data). Stands were uneven aged and composed largely of sugar maple (at least 80% of the trees in the stand were >10 cm DBH), with minor overstory components of yellow birch (*Betula alleghaniensis* Britt.), red maple (*Acer rubrum* L.), and various other tree species (Wilmot et al. 1995). Three of the stands were managed as sugarbushes, which included the occasional removal of standing dead trees, while the fourth stand (MORR) was unmanaged at the time of the study. On each of the sites, 4–6 individual overstory trees showing symptoms of dieback (dieback evident for more than 5% of the projected crown area), determined by visual surveys, were selected for the measurements. Although subjective, dieback estimates were made to ensure that trees showing similar dieback symptoms, and of similar overall apparent condition, were used in this study.

Three of the stands (PMRC, JOHN, and FLET) were fertilized with base cations (K, Ca, and Mg) in the spring before leaf emergence for 2 years during 1990–1992. In each of the fertilized stands, a 0.35-ha plot located within 100–300 m of the control trees was manually fertilized with the base-cation mixture to investigate the possible physiological effect of increasing base-cation availability to sugar maple trees growing on acid soils (pH ≈ 4.0). Commercially available agricultural fertilizers were applied in the form of K_2SO_4, $CaCO_3$, and $Ca,Mg(CO_3)_2$ at a rate equivalent to 107 kg·ha^{-1} K, 53 kg·ha^{-1} Ca, and 11 kg·ha^{-1} Mg.

Sample collection

During the latter part of the growing season when foliage was fully expanded, branches were collected from the forest canopy using a shotgun and steel shot for leaf photosynthesis measurements and analyses of foliar nutrient content. Branches were obtained from the periphery of the upper third of the crown of dominant or codominant mature sugar maple trees in each plot. Foliage from these locations corresponded to leaves that would be sunlit on sunny days and are expected to contribute the majority of daily canopy carbon assimilation (Ellsworth and Reich 1993). In the field, branch sections 0.7–1.5 m in length and typically 1–1.5 cm in diameter at the base were collected, and the distal end was immediately placed in a wide bucket of tap water. Branches were rehydrated by cutting the stem underwater, after which a fresh razor blade or clean knife was used to carefully

TABLE 1. Description of the four sugar maple forest sites in northern Vermont

Site	Location	Elevation (m)	Soil type	Soil pH
Underhill Center (PMRC)	44°31′N 72°51′W	410	Marlow coarse loam	4.1
Johnson (JOHN)	44°41′N 72°42′W	400	Lyman–Tunbridge loam	3.9
Fletcher (FLET)	44°42′N 72°55′W	220	Stowe fine sandy loam	4.3
Morrisville (MORR)	44°32′N 72°34′W	240	Salmon coarse silty loam	3.9

NOTE: Sites are referred to in the text according to the abbreviations listed under the site column. Soil type was determined from a detailed analysis of soil pits dug at each site (T.R. Wilmot, unpublished data). Soil pH_{water} was measured in the laboratory using an analytical pH electrode (Beckman Instruments, Fullerton, Calif.) on five homogenized, replicate samples of the upper 5 cm of soil (O + A horizons) collected from each site.

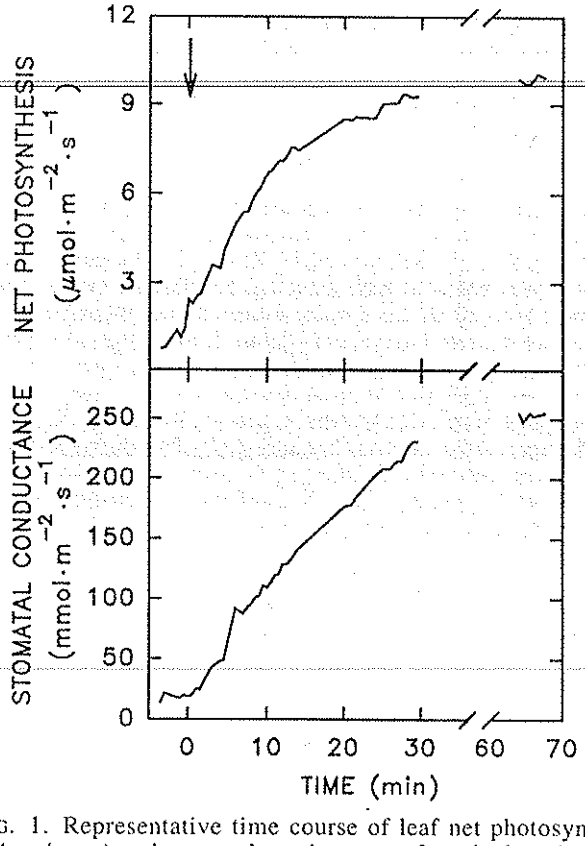

FIG. 1. Representative time course of leaf net photosynthesis (A_{mass}/mass) and stomatal conductance of a rehydrated sugar maple leaf upon continuous illumination by an artificial light source. The arrow in the upper left corner (at time = 0) indicates a stepwise increase in PFD from 90 μmol·m^{-2}·s^{-1} (in shade) to 800 μmol·m^{-2}·s^{-1} upon illumination. Chamber air temperature ranged from 27.4 to 28.3°C during the measurements, VPD in the leaf chamber was maintained at 1.7 Pa·kPa^{-1}, and ambient CO_2 concentration of incoming air was 300–315 μmol·mol^{-1} during the course of the measurements. The broken axis at time = 30 min indicates a period when the leaf remained illuminated in the chamber with a constant airflow, but measurements were not recorded. Measurements were made at PMRC (elevation 410 m).

shave the cut end of the branch. Branches were transferred to clean water while keeping the cut end underwater and stored in the shade until photosynthesis measurements could be made. Leaf water potential measurements indicated no evidence of water stress for any of the measurement trees prior to rehydration, as water potentials were always greater than −1.5 MPa. The measurements reported here were made on fully-expanded leaves collected between late July and the first week of September. There was no evidence of the onset of leaf senescence in any of the experimental trees at the time measurements were made, and foliar nutrients remain relatively stable during this period of the growing season (Lea et al. 1979).

Photosynthesis measurements

Photosynthesis measurements were conducted either at each respective field site (Table 1) or at the PMRC site. Photosynthesis and transpiration were monitored simultaneously using a field-portable infrared gas analyzer (IRGA) and leaf chamber (LCA-3, Analytical Development Corp., Hoddesdon, Herts., U.K.) in an open-system configuration. A rigid sampling protocol was used to ensure that photosynthetic measurements would as closely as possible reflect the physiological capacity of each leaf for light-saturated photosynthetic CO_2 assimilation capacity (A_{max}) at ambient CO_2 and temperature conditions and that measurements were excluded when photosynthetic limitations were likely to occur as a result of partially closed and (or) unresponsive stomata.

All measurements were made in the field under moderate ambient air temperatures (air temperature always between 20°C and 30°C) and at ambient CO_2 concentrations CO_2 = 322 ± 11 μmol·mol^{-1} (mean ± SD) for n = 47 leaves). A 50-W metal halogen projector lamp (EXT, Ushio, Inc., Tokyo, Japan) powered by a car battery provided saturating photon flux densities (PFD; ≥800 μmol·m^{-2}·s^{-1}). Leaf to air vapor pressure difference (VPD) was always ≤1.8 Pa·kPa^{-1} during measurements to reduce the possibility of VPD-induced stomatal closure. Air temperature, PFD, and VPD conditions were within the range considered to be optimal for photosynthesis in sugar maple (Ellsworth and Reich 1993; D. Ellsworth, unpublished data). Instantaneous measurements of net photosynthetic CO_2 assimilation and stomatal conductance (g_s) were monitored for 20–60 min from the initial time of illumination, until leaf A reached a stable maximum (Fig. 1). Leaves not exhibiting (*i*) a stomatal opening response to light as indicated by a lack of noticeable increase in g_s upon illumination or (*ii*) a stable photosynthetic rate for at least 5 min were eliminated from the analysis. In some cases, branches were stored in a humid container overnight, recut in fresh tap water, and remeasured. On these occasions, photosynthetic rates were similar to those measured on the previous day.

Two to five leaves were measured on branches collected from each of four to six control (unfertilized) trees at each study site. A similar number of leaves were measured from a limited set of fertilized trees on three sites. Usually at least two leaves from each tree satisfied the constraints of the sampling protocol for analysis of A_{max}. Leaves for which A_{max} was achieved were collected after measurements were taken, and leaf area was determined on fresh leaves or leaf silhouettes to the nearest 0.1 cm^2

TABLE 2. Leaf net photosynthesis (A_{max}, $\mu mol \cdot m^{-2} \cdot s^{-1}$), total chlorophyll concentration ($mg \cdot g$ dry $mass^{-1}$) and leaf nutrient concentrations (% dry mass) of canopy leaves from unfertilized sugar maple trees on four sites in northern Vermont

Site	A_{max}	Total chlorophyll	N	P	K	Ca	Mg
PMRC	4.57*ab*	11.3*b*	1.67*ab*	0.11*a*	0.75*a*	0.44*b*	0.06*a*
	(0.63)	(1.0)	(0.08)	(0.01)	(0.04)	(0.04)	(0.01)
JOHN	7.54*a*	15.9*a*	2.02*a*	0.18*a*	0.59*ab*	0.68*a*	0.10*a*
	(0.97)	(0.5)	(0.06)	(0.05)	(0.03)	(0.05)	(0.02)
FLET	6.13*ab*	15.3*a*	1.75*ab*	0.18*a*	0.74*a*	0.58*ab*	0.09*a*
	(0.85)	(1.2)	(0.13)	(0.02)	(0.06)	(0.05)	(0.02)
MORR	3.62*b*	6.3*c*	1.55*b*	0.21*a*	0.48*b*	0.51*ab*	0.13*a*
	(0.91)	(0.8)	(0.16)	(0.04)	(0.06)	(0.06)	(0.02)

NOTE: $n = 4$ trees, except at PMRC, where $n = 6$. Data are means with standard errors in parentheses. Within a column, means that are significantly different ($P < 0.05$, Tukey's studentized range test) are followed by a different letter.

with an optical scanning device (CID Model 201 Area Meter, Moscow, Idaho).

To determine whether photosynthetic rates of leaves from detached and rehydrated branches were representative of in situ leaf photosynthetic capacity, instantaneous measurements of net photosynthetic CO_2 assimilation were taken for sugar maple leaves in the field from intact branches in a clearing and at the top of the forest canopy (at 16.5 m height, accessed via a tower) at the Proctor Maple Research Center, using the protocol described above. Subsequent measurements of A_{max} made on the same leaves after branch detachment and rehydration indicated that A_{max} was always within ±5% of the rate measured on intact branches (data not shown).

Photosynthetic responses to CO_2 in the intercellular spaces (c_i, $\mu mol \cdot mol^{-1}$) were measured in the field to extend interpretations to the physiological mechanism of photosynthesis. After leaf A had reached a stable maximum (light saturation; Fig. 1), CO_2 supply to the leaf was varied by rerouting a portion of the airstream entering the leaf chamber through a CO_2-absorbing column and using a ball inflated by breath to supply elevated CO_2 to the system. Although the system was not maintained at isothermal conditions, leaf and chamber air temperatures varied by less than 1.5°C throughout a measurement cycle. Other environmental conditions during the measurements were the same as specified above for A_{max} at ambient CO_2. The IRGA was calibrated against at least two primary CO_2 standards (Scott Specialty Gases, Plumsteadville, Pa.) before and after conducting the experiments. Calculations of c_i were made according to the equations in von Caemmerer and Farquhar (1981) with corrections for the diluting effect of water vapor in air. All A_{max}–c_i response curves were conducted at PMRC (elevation 410 m) and are not compensated for pressure. A rectangular hyperbola model described in Gunderson et al. (1993) was fitted to the data for A_{max} and c_i using nonlinear least squares modelling techniques (SAS Institute Inc. 1990).

Leaf chemical analyses

Chlorophyll analysis was performed on leaf disks taken from leaves adjacent to those used for photosynthesis measurements. Chlorophyll was extracted using dimethyl sulfoxide as the solvent, and absorbance was measured on a spectrophotometer (Spectronic Model 1001, Milton-Roy, Rochester, N.Y.) at 648 and 665 nm. Chlorophyll content (chlorophyll *a* and *b*) was calculated using solution-specific absorption coefficients in Barnes et al. (1992). In some cases, chlorophyll samples were stored frozen at 4°C for 1–5 days prior to analysis, but chlorophyll may remain stable for up to 1 week when frozen in dimethyl sulfoxide (Barnes et al. 1992; D. Ellsworth, unpublished data).

Total leaf nitrogen (N) was measured on individual leaves for which A_{max} had been measured. Leaves were oven-dried, ground and homogenized, and analyzed using the Dumas combustion method (AOAC 1990) on a CHN analyzer (Elemental Analyzer, Leeman Labs, Lowell, Mass.) at the University of Vermont Plant and Soil Analysis Laboratory. A pooled sample of adjacent leaves from the same branch was submitted to the University of Vermont Plant and Soil Analysis Laboratory for determinations of leaf macronutrient and trace metal content using inductively coupled plasma-emission spectrometry (Plasma Emission Spectrometer, Leeman Labs, Lowell, Mass.). Leaves showing obvious morphological evidence of pear thrips (*Taeniothrips inconsequens* Uzel) damage or mite infestations (Houston et al. 1990) were not included in samples submitted for leaf nutrient analyses. Blind standards from the National Bureau of Standards submitted along with the sugar maple leaf samples indicated concentrations for N, P, and K to be within at least 7% of the reference concentrations at all times.

Data were analyzed using the general linear models procedures and regression techniques in SAS (SAS Institute Inc. 1990). The main effects of the model were site and fertilization treatment, using site × treatment as the error term. Site means were statistically compared using Tukey's studentized range test when main effects were significant at the appropriate level ($P < 0.05$). Data were transformed when necessary to satisfy statistical assumptions, and residual plots were examined for all regressions to confirm that error variances were stable (Sokal and Rohlf 1981).

Results

Leaf A_{max} was generally achieved within 30 min of illumination for foliage on detached and rehydrated branches (Fig. 1). A_{max} varied considerably among sites (CV = 31.5%; Table 2) and also among trees within a site (CV = 33.5%). A_{max} of control trees was significantly higher ($P < 0.05$) at JOHN than at MORR, as was leaf N concentration and leaf chlorophyll concentration (Table 2). Leaf Ca concentration was significantly higher ($P < 0.05$) at JOHN than at PMRC, and leaf K was lowest at MORR (Table 2). Sugar maple foliar Ca was low (less than ≈0.50%) at both PMRC and MORR (Table 2), and foliar Al was <50 $\mu g \cdot g^{-1}$ at all sites (data not shown). Field notes indicated that leaf-tip and marginal necroses were occasionally observed for foliage collected from both PMRC and MORR sites but not from JOHN and FLET. Leaves also appeared chlorotic on some trees at PMRC and MORR, and leaf chlorophyll concentrations were lowest at these sites ($P < 0.05$; Table 2).

Photosynthesis and leaf nutrients

Although leaf mass per unit area was high for all foliage sampled (76.0 $g \cdot m^{-2}$, range 62–97 $g \cdot m^{-2}$), as would be

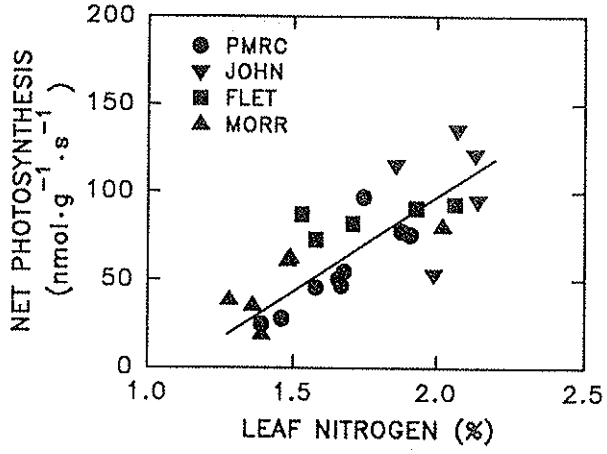

FIG. 2. Relationship between leaf net photosynthesis (A_{max}/mass) and leaf N concentration for canopy leaves of sugar maple from four sites in northern Vermont. The relationship shown is A_{max}/mass = −88.7 + 91.9(leaf N) ($P < 0.0001$, $r^2 = 0.60$, $n = 25$).

expected for "sun" foliage near the top of sugar maple forest canopies (Ellsworth and Reich 1993), A_{max} was expressed per unit leaf dry mass (A_{max}/mass) in order to examine intrinsic variation in A_{max} unrelated to variation in leaf mass per unit area and to permit comparisons between A_{max} and leaf mineral nutrient concentrations. Transformations of leaf mineral nutrient data from a mass to area basis tend to increase the variability as a result of offsetting variation in leaf mass per unit area and mass-based leaf nutrient concentrations (Field and Mooney 1986; Reich et al. 1994*a*). There was no significant correlation between A_{max} and leaf mass per unit area ($P > 0.05$; hence, data not shown).

Among canopy leaves from all four sites, A_{max}/mass was strongly related to leaf N concentration ($P < 0.0001$, $r^2 = 0.60$; Fig. 2). This relationship was also significant or marginally significant for data among trees at PMRC and MORR ($P < 0.003$, $r^2 = 0.74$ for PMRC data; and $P < 0.084$, $r^2 = 0.68$ for MORR data) but not at JOHN or FLET. There was also a significant, although weaker, relation between area-based A_{max} and leaf N among all four sites (A_{max} = −1.05 + 4.73[leaf N, in g N·m^{-2}], $P = 0.004$, $r^2 = 0.31$). Light harvesting is intrinsically an area-based phenomenon, but for the purpose of examination of trends in leaf chlorophyll with respect to nutrient concentrations among the different sites, total leaf chlorophyll (chlorophyll *a* + *b*) was expressed on a leaf dry mass basis (mg·g^{-1}). Among all four sites, leaf A_{max}/mass was significantly correlated with mass-based leaf chlorophyll ($P = 0.0065$, $r^2 = 0.54$; Fig. 3A). The corresponding area-based relationship (leaf chlorophyll in g·m^{-2} versus leaf N per unit area in g N·m^{-2}) was also significant but somewhat weaker ($P = 0.028$, $r^2 = 0.40$; hence, data not shown). Mass-based leaf chlorophyll concentration was significantly correlated with leaf N concentration ($P = 0.0041$, $r^2 = 0.58$; Fig. 3B) but not with any other leaf macronutrient.

Among the three sites that were fertilized with base cations, leaf Ca was apparently greater for fertilized than for unfertilized trees at the FLET site only (leaf Ca > 1.0%; outlier points in Fig. 4). There were no other obvious differences in leaf macronutrients between fertilized and unfertilized trees within or among any of the sites. Fertilization effects on A_{max} were examined with correlation analyses using individual tree nutrient data because (*i*) the overall ANOVA on

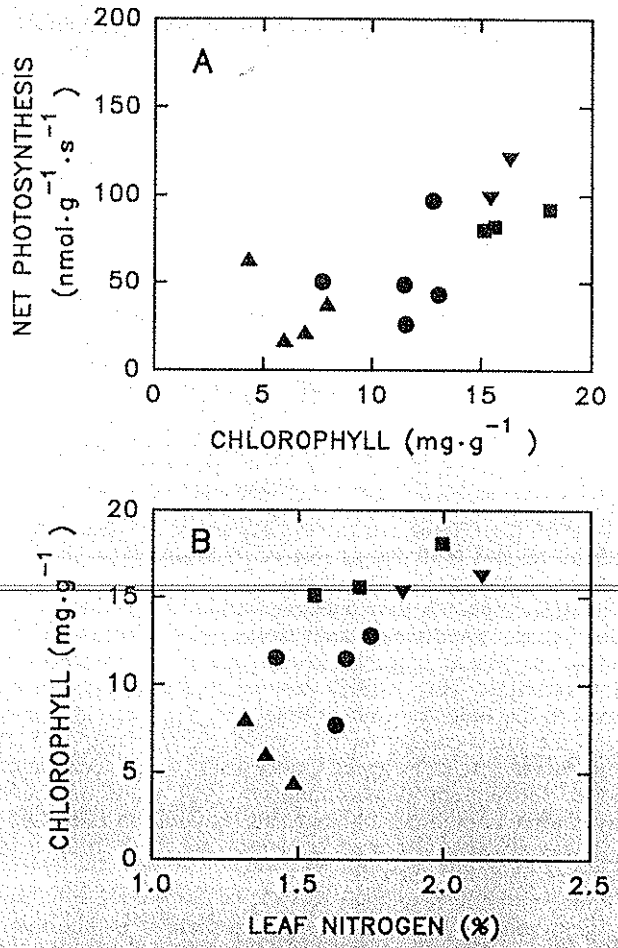

FIG. 3. (A) Relationship between leaf net photosynthesis (A_{max}/mass) and mass-based leaf chlorophyll concentration among canopy leaves of sugar maple from the four sites ($P = 0.0065$, $r^2 = 0.54$). Symbols as in Fig. 2. (B) Relationship between mass-based leaf chlorophyll concentration and leaf N concentration ($P = 0.0041$, $r^2 = 0.58$).

mass and area-based A_{max} (unbalanced design) were not significant (area-based A_{max}: $F = 2.31$, df = 17, MSE = 2.96, $P = 0.096$; A_{max}/mass: $F = 2.69$, df = 17, MSE = 682.9, $P = 0.063$), (*ii*) plot and site effects cannot be separated in the experimental design, (*iii*) pretreatment A_{max} data were not available, and (*iv*) logistic considerations limited the number of trees that could be sampled on any site–plot combination ($n = 2$–4 trees sampled for each of the three sites).

Correlation analyses of A_{max}/mass among trees on all four sites with leaf mineral nutrient concentrations other than N were conducted in order to examine the possible importance of leaf nutrients with respect to leaf carbon assimilation capacity. For unfertilized trees among the four study sites, A_{max}/mass was significantly correlated ($P < 0.0001$, $r^2 = 0.51$) with leaf Ca concentration (Fig. 4A). This relationship was also significant ($P < 0.001$) for the pooled data set using both fertilized and unfertilized trees among all sites. However, the within-site relation between A_{max}/mass and Ca was significant for PMRC data only ($P < 0.018$, $r^2 = 0.34$). The addition of leaf N concentration to the model improved r^2 to 0.62 ($P < 0.0001$) and 0.66 ($P < 0.0001$) for the unfertilized trees alone and for the combined data sets, respectively. For unfertilized trees there was a tendency (17 of 19 leaves measured) for A_{max}/mass to be low (<80 nmol·g^{-1}·s^{-1}) at

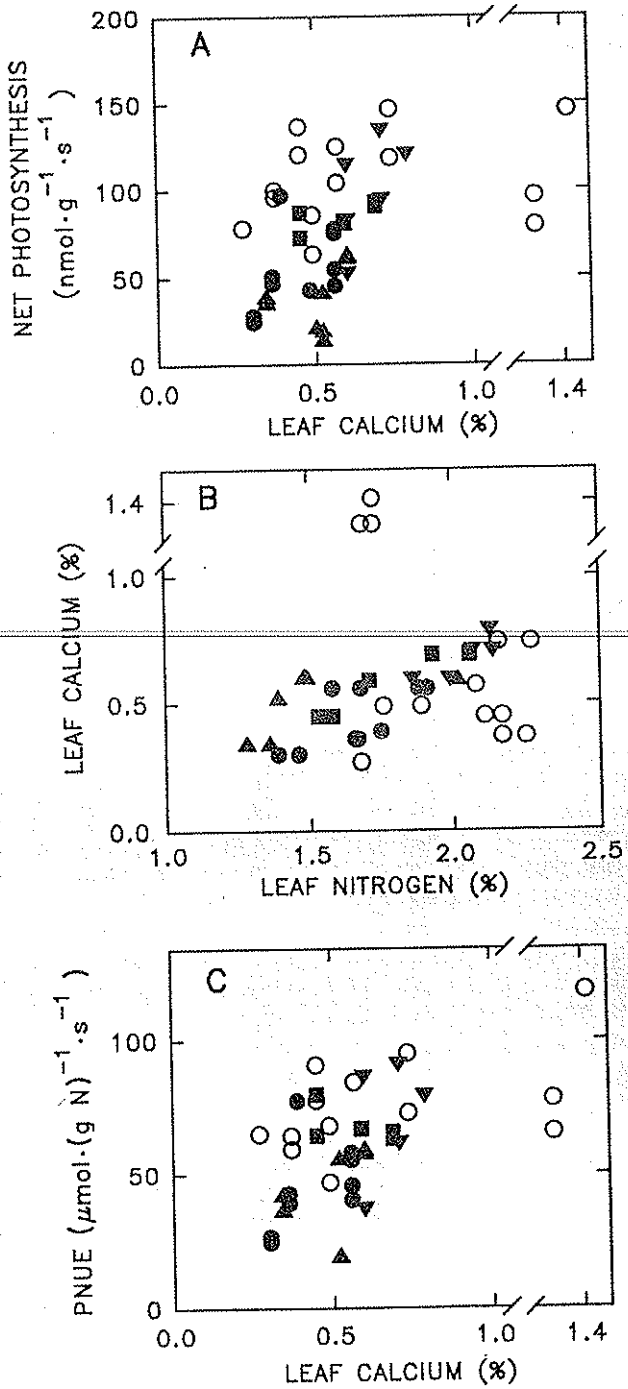

FIG. 4. (A) Correlation between leaf net photosynthesis (A_{max}/mass) and leaf Ca concentration for canopy leaves of sugar maple on four sites. Data for unfertilized trees from each site are indicated by a different filled symbol (see Fig. 2). Open circles indicate data for fertilized trees pooled for the three sites where this treatment was applied. The relationship is significant using data for unfertilized trees ($P < 0.0001$, $r^2 = 0.51$) and using data for fertilized and unfertilized trees on all sites combined ($P = 0.001$, $r^2 = 0.23$). (B) Correlation between leaf Ca and leaf N concentration for canopy leaves of sugar maple. Symbols are as in Fig. 4A. The relationship is significant using data for unfertilized trees only ($P < 0.0001$, $r^2 = 0.64$). (C) Scatterplot of instantaneous photosynthetic nitrogen-use efficiency (PNUE) as a function of leaf Ca concentration. Symbols are as in Fig. 4A. The correlation is significant using data for unfertilized trees ($P = 0.0036$, $r^2 = 0.32$) and for unfertilized and fertilized trees pooled ($P = 0.0008$, $r^2 = 0.28$).

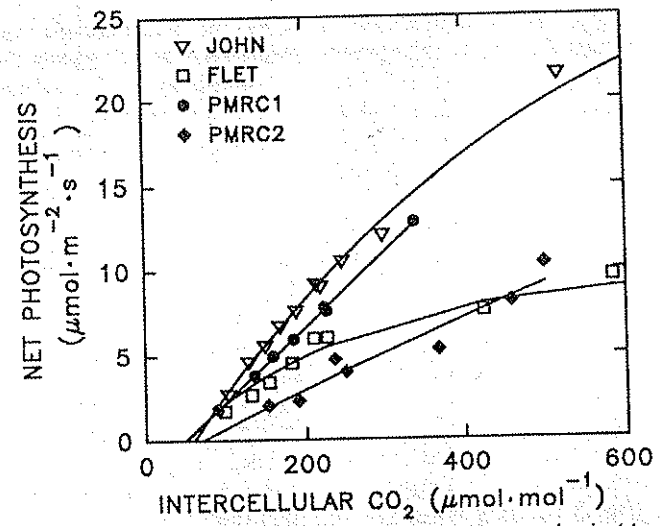

FIG. 5. Representative curves of leaf net photosynthesis (A_{max}/mass) as a function of intercellular CO_2 (c_i) for four representative canopy leaves with contrasting N and Ca status. Open symbols, leaves with "adequate" Ca (leaf Ca = 0.60% dry mass); closed symbols, leaves with low Ca concentration (leaf Ca < 0.40%). Upper curves (JOHN and PMRC1) are for high-N leaves (leaf N = 1.86% and 1.99%, respectively); lower curves (FLET and PMRC2) are for lower N leaves (leaf N = 1.71% and 1.67%, respectively). Curves represent a rectangular hyperbola function fitted to the data. Initial slopes of A_{max} vs. c_i are shown in Table 3. Data have not been corrected for temperature.

leaf Ca less than approximately 0.6% (Fig. 4A). There was a marginal, weak relationship ($P = 0.068$, $r^2 = 0.14$) between A_{max}/mass and leaf Mg concentration among sites for unfertilized trees alone (data not shown). Correlations between A_{max}/mass and other leaf macronutrients (P, K, S) were examined individually for both the unfertilized trees alone and for the pooled data sets, but none of these relationships were significant ($P > 0.05$; data not shown). Among leaf macronutrients, Ca concentration was strongly correlated with leaf N concentration when unfertilized trees were analyzed alone ($P < 0.0001$, $r^2 = 0.64$), but there was no significant relationship between these variables for the pooled data sets (Fig. 4B). There was also a significant relationship between leaf Ca concentration and leaf Mg concentration for unfertilized trees ($P = 0.0014$, $r^2 = 0.38$) and for the unfertilized and fertilized trees combined ($P = 0.0001$, $r^2 = 0.35$; data not shown). Examination of instantaneous leaf photosynthetic nutrient-use efficiency (PNUE), expressed as the ratio of A_{max}/leaf N concentration, can be used to calculate A_{max} on a leaf N basis and indicate whether the correlation between A_{max}/mass and leaf Ca concentration arises as a result of the correlation between leaf Ca and N in Fig. 4B. PNUE was correlated with leaf N concentration, as expected ($P = 0.0009$, $r^2 = 0.27$; data not shown); however, there was also a significant correlation between PNUE and leaf Ca concentration for unfertilized trees ($P = 0.0036$, $r^2 = 0.32$) as well as for the pooled data sets (fertilized and unfertilized trees; $P = 0.0008$, $r^2 = 0.28$; Fig. 4C).

For the purpose of determining whether the low leaf Ca concentrations (Ca < 0.50%) observed in this study in sugar maple were related to possible biochemical dysfunction of photosynthetic processes, curves of A_{max} as a function of leaf intercellular CO_2 concentration (c_i) were examined (Fig. 5). Representative curves of A_{max}–c_i for leaves of

TABLE 3. Characteristics of the A_{max}–c_i curves shown in Fig. 5

Site and leaf	Slope ($mol \cdot m^{-2} \cdot s^{-1}$)	Temp. (°C)	Predicted A_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Leaf N/area (g N·(m^2 leaf)$^{-1}$)
JOHN	0.051	28.2–28.5	9.82	1.67
PMRC1	0.044	23.8–24.9	7.96	1.38
FLET	0.026	21.5–22.5	5.41	1.14
PMRC2	0.022	27.9–28.4	3.63	1.08

NOTE: Data are organized in descending order by slope. Slopes were determined by linear regressions of A_{max} on c_i at c_i = 20–400 $\mu mol \cdot mol^{-1}$. The range in air temperatures for which each curve was measured is indicated along with the predicted A_{max} at the "operational" c_i (Farquhar and Sharkey 1982) using the nonlinear regression models. The operational c_i was determined as the average c_i for all measurements of A_{max} at ambient CO_2 (n = 38).

contrasting N and Ca status were chosen from among 10 such curves that were developed using canopy leaves from the study sites (D. Ellsworth, unpublished data). For leaves in Fig. 5 of similar leaf N status (high N ≈ 1.9%, JOHN and PMRC1; low N ≈ 1.7%, FLET and PMRC2), low Ca leaves (arbitrarily defined as leaf Ca < 0.40%) did not show noticeable reductions in the initial slope of the A_{max}–c_i curve relative to leaves with higher Ca (Ca = 0.60% for both JOHN and FLET). The initial slopes of the A_{max}–c_i curves in Fig. 5 (slope from c_i = 20 to 400 $\mu mol \cdot mol^{-1}$) ranged from 0.022 to 0.051, and the ranks of the slopes (JOHN > PMRC1 > FLET > PMRC2) corresponded to the ranks of the area-based measure of leaf N (Table 3).

Discussion

Leaf Ca concentrations in the canopy at PMRC and MORR (Table 2) are among the lowest values reported for sugar maple. According to other studies of mature sugar maple, leaf Ca concentrations generally exceed 0.60% in other areas of northeastern North America (Chandler 1939; Lea et al. 1979; Bernier and Brazeau 1988; Oimet and Fortin 1992; but see Kolb and McCormick 1993). In a bioassay of seedlings grown in sand culture with a complete nutrient solution except Ca^{2+}, Erdmann et al. (1979) observed visual deficiency symptoms such as leaf chlorosis and leaf-tip and marginal necroses at leaf Ca concentrations of 0.86%, higher than in the present study for mature sugar maple. Similar foliar symptoms were occasionally observed in the field for mature canopy trees with evidence of past dieback at PMRC and MORR, where total leaf chlorophyll concentrations were also low (Table 2), although nutrient deficiency cannot be ascribed as the only likely cause of such visual symptoms. Some visual symptoms such as chlorotic mottling and marginal necrosis are nonspecific and may also indicate feeding damage by pear thrips (Houston et al. 1990), yet the incidence of damage by pear thrips was locally low in the year of this study (H.B. Teillon and S.H. Wilmot, Vermont Department of Forests and Parks, unpublished data).

Leaf Mg concentrations among the study sites were also low (≤0.10% for all sites except MORR; Table 2) relative to values reported for sugar maple forests exhibiting dieback in Quebec (Mg concentrations generally >0.12%; Bernier and Brazeau 1988; Kolb and McCormick 1993). Although leaf Mg concentrations may be associated with the concentration of green pigments in leaves because of plant Mg requirements for synthesizing chlorophylls (Lange et al. 1987; Oren et al. 1993), there was no correlation between leaf Mg and leaf chlorophyll concentration in this study. In fact, leaf chlorophyll concentration was lowest at MORR, where leaf Mg concentration was highest (Table 2). Leaf K was comparable to concentrations reported in Oimet and Fortin (1992) for unfertilized sugar maple stands in Quebec.

Crown position effects could have accounted, in part, for low Ca and Mg concentrations in sugar maple foliage in this study compared with others; some investigators (Mader and Thompson 1969; Bernier and Brazeau 1988; Oimet and Fortin 1992) have sampled more shaded foliage near the midcrown, where there is a tendency for somewhat higher but also less variable leaf nutrient concentrations, than in upper crown positions (Morrison 1985). In this study, upper canopy foliage was specifically chosen for sampling because crown dieback is generally observed on branches in upper canopy positions (Allen et al. 1992*b*; T. Wilmot and D. Ellsworth, personal observation) and because a large part of the canopy carbon gain in sugar maple comes from upper canopy foliage (Ellsworth and Reich 1993).

Leaf chlorophyll concentrations can provide an indication of the extent of foliar chlorosis in forests exhibiting decline symptoms (Oren et al. 1993). Variation in leaf chlorophyll concentration among trees and sites appeared to be most closely related to leaf N concentration in this study (Fig. 3B). The correlation between A_{max} and leaf chlorophyll concentration for leaves grown in high-light positions near the top of the canopy (Fig. 3A) may not arise based on strictly functional considerations because of the strong correlation between leaf chlorophyll and leaf N concentration, and because the light-harvesting and energy-transducing components of the photosynthetic apparatus are frequently not limiting CO_2 fixation under sunny conditions (Evans 1989). If taken as an index of leaf chlorosis, however, a correlation between A_{max} and leaf chlorophyll concentration may indicate a possible relationship between the overall degree of foliar chlorosis and reduced net photosynthesis for upper canopy leaves.

Photosynthesis and leaf nutrients

For many species, there are strong linear relationships between A_{max} and leaf N that are associated with the limitations of soil N availability in terrestrial communities and with the central role of N-based compounds in regulating leaf CO_2 fixation capacity (Field and Mooney 1986; Evans 1989). The form of the A_{max}–N relationship may vary depending on whether variation in leaf N arises as a result of (*i*) soil nutrient availability, (*ii*) variation in the microenvironment (Ellsworth and Reich 1993), or (*iii*) an endogenous control such as leaf aging (Reich et al. 1991; 1994*a*). For sugar maple, Ellsworth and Reich (1993) observed strong A_{max}–N relationships using the area-based expressions (A_{max} and leaf N per unit area) for leaves among microsites of

contrasting light availability, whereas there were no mass-based A_{max}–N relationships. Strong area-based A_{max}–N relationships appear to be most common when leaf N per unit area varies more than leaf N concentration. This occurs as a result of variation in leaf mass per unit area, which has been observed among leaves arrayed along a forest canopy light gradient (Ellsworth and Reich 1993). In contrast, A_{max}/mass was most closely related to leaf N concentration in the present study (Fig. 2), as was also found by Reich et al. (1991). Since variation in leaf microenvironment and aging were minimized by collecting foliage near the upper portion of the crown and sampling fully expanded non-senescent leaves, leaf N most likely varied among trees and sites as a result of differences in nutrient availability within and among sites and (or) because of tree to tree variation in nutrient supply capacity to foliage in the upper crown. Although the area-based A_{max}–N relationship was weak ($r^2 = 0.31$, data not shown), the lower slope for this relationship compared with previously published values (see Reich et al. 1991; Ellsworth and Reich 1993) may indicate co-limitation of photosynthesis by other nutrients (Reich and Schoettle 1988; Reich et al. 1994*a*).

The observed correlation between A_{max}/mass and leaf Ca concentration (Fig. 4A) may indicate that Ca limitations or interactions with other mineral elements are also important in controlling leaf-level carbon balance in sugar maple trees on these sites. Although reports of limitations to leaf photosynthesis by mineral nutrients other than N are not common (Reich and Schoettle 1988), there is evidence that low leaf Ca, low leaf Mg, or high foliar Al:Ca may be related to decreased leaf carbon balance in coniferous trees growing on nutrient-poor soils or soils altered by pollutant deposition (Lange et al. 1987; Zimmerman et al. 1988; McLaughlin et al. 1991; Reich et al. 1994b). Although Ca may not play a direct role in leaf photosynthetic carbon fixation, low foliar Ca (0.3–0.4% Ca) was associated with elevated leaf respiration and reduced leaf carbon balance in red spruce (*Picea rubens* Sarg.) saplings on acid soils in the southern Appalachians (McLaughlin et al. 1991; McLaughlin and Kohut 1992). Low A_{max}/mass in sugar maple was common at leaf Ca < 0.5–0.6% among the four stands on acid soils in Vermont (Fig. 4A). Cytosolic Ca^{2+} is important in maintaining cell integrity and membrane stability (Kirkby and Pilbeam 1984), and reduced Ca may be associated with reductions in the leaf carbon balance or photosynthetic efficiency through perturbations of membrane-related processes (Marschner 1986; McLaughlin and Kohut 1992).

Previous interpretations of the functional significance of A_{max}–nutrient relationships have been predicated on the basis of the prominent role of an element in key functional biochemical constituents associated with photosynthetic processes (Reich and Schoettle 1988; Evans 1989). Since these relationships are only correlative, caution must be taken in their interpretation (Field and Mooney 1986). On the basis of the strong arguments made previously in favor of the generality of A_{max}–N relationships among species (Field and Mooney 1986) as well as for sugar maple alone (Reich et al. 1991; Ellsworth and Reich 1993), and the strong correlation between leaf N and Ca among trees sampled in this study (Fig. 4B), it cannot be concluded that the correlation between A_{max}/mass and leaf Ca observed for sugar maple in this study (Fig. 4A) is necessarily attributable to a direct functional relationship between these parameters. Co-variation in A_{max}/mass and leaf Ca is largely driven by differences in Ca among sites (Table 2, Fig. 4) and may also be related to differences in fine-root function among stands and to the associated capacity for water and nutrient uptake (see Adams and Hutchinson 1992). Moreover, the relationship between A_{max}/mass and leaf N was stronger ($r^2 = 0.60$, Fig. 2) than the correlation between A_{max}/mass and leaf Ca ($r^2 = 0.51$ for unfertilized trees only, Fig. 4A) and was only improved slightly (to $r^2 = 0.62$) by the inclusion of Ca in the regression model. Examination of A–c_i curves (Fig. 5) supports this interpretation, since the initial slopes of the curves is proportional to leaf carboxylation capacity (Farquhar and Sharkey 1982). The initial slopes corresponded closely to leaf N status (Table 3), but these data do not demonstrate a clear interaction of reduced Ca at moderate (leaf N = 1.9%) or low N (leaf N = 1.7%).

Interactions between N and Ca nutrition may affect A_{max} in canopy leaves, since there was a tendency for higher A_{max}/mass in fertilized trees (Fig. 4A) and lower PNUE at low Ca (Ca < 0.5%; Fig. 4C). Other investigators (cf. Reich and Schoettle 1988; Reich et al. 1994*a*) have attributed reductions in PNUE to interactions between N nutrition and other mineral elements. It is possible that base-cation fertilization may enhance fine-root growth and function (Adams and Hutchinson 1992), which could result in increased N supply to leaves, or that physiologically active Ca pools in leaf mesophyll cells may increase (Marschner 1986). Since the availability of several base-cations may co-vary in acid, podzolic soils with low base cation status (Wilmot et al. 1995), more carefully controlled experiments are needed to determine whether low foliar Ca has a more direct role in reduced A_{max} and adverse leaf carbon balance for sugar maple on acid soils.

While there is concern over the potential for cation deficiencies in northern hardwood forests (Bernier et al. 1989; Federer et al. 1989; Leichty et al. 1993), in the absence of biogeochemical and root physiology data it remains unclear whether low foliar Ca and Mg in sugar maple on these sites resulted from low soil availability of these cations, from the inhibition of base-cation uptake in acid soils, or from losses of Ca^{2+} and Mg^{2+} ions from upper soil horizons as a result of acid deposition (Raynal et al. 1992). Regardless of the proximal cause of the adverse nutritional status of sugar maple on these sites, this study represents one of the first efforts to address canopy physiological responses to nutrition that may be associated with dieback in mature sugar maple trees in northern Vermont. Low leaf Ca (<0.60%) and Mg (<0.10%) were observed in stands exhibiting dieback in this region, and low leaf chlorophyll concentrations may also be common in these cases. While N has a primary role in CO_2 assimilation processes (Evans 1989), there is also limited evidence of Ca-related disturbances to leaf carbon balance in sugar maple (Figs. 4A and 4C), suggesting possible co-limitation of photosynthetic processes by N and Ca or interactions between Ca and other mineral nutrients such as Mg. Because sugar maple trees exhibiting marginal nutritional status appear to show lower A_{max} (Table 2), further reductions in net photosynthesis beyond site preconditioning such as may occur as a result of defoliation and damage by pear thrips (Ellsworth et al. 1994), drought, or other environmental stresses could potentially reduce the tree carbon economy enough to trigger crown dieback. Despite recent improvements in sugar maple crown condition in Vermont

(Teillon and Wilmot 1993) and in other parts of northeastern North America (Allen et al. 1992*a*), it is also likely that recovery will be retarded on strongly acidic and low-nutrient sites where maple canopy carbon balance may be reduced by N limitations and N and Ca × Mg interactions.

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