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Leaf nutrition and photosynthetic performance of sugar maple (*Acer saccharum*) in stands with contrasting health conditions

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Summary Leaf nutrition and photosynthetic performance of sugar maple (*Acer saccharum* Marsh.) were compared between two sugar maple stands in northwestern Vermont with contrasting health conditions as indicated by annual basal area growth, degree of crown dieback, and foliar appearance. Observations made during the diurnal cycle of both stands showed no apparent leaf water stress. In both stands, leaves had similar concentrations of major non-structural carbohydrates (starch and sucrose). Over two consecutive growing seasons (1991 and 1992), we consistently observed lower leaf Ca and Mg concentrations in the declining stand than in the healthy stand. Compared with the healthy stand, lower leaf chlorophyll concentrations and apparent leaf chlorosis were observed in the declining stand, and some trees had very low foliar Ca and Mg concentrations (0.31 ± 0.03% and 0.09 ± 0.01%, respectively). Trees in the declining stand had lower light-saturated net photosynthetic rates on a dry mass basis at both ambient CO_2 ($P_{n,amb}$) and saturating CO_2 ($P_{n,sat}$) than trees in the healthy stand. There were significant linear correlations between $P_{n,amb}$ and leaf mass per unit area (LMA) and between $P_{n,sat}$ per unit leaf area and LMA. There were also linear correlations between both $P_{n,amb}$ and $P_{n,sat}$ and leaf N when expressed on an area basis in both stands, indicating that variation in LMA may have been largely responsible for the observed photosynthesis–nitrogen relationship. The values of $P_{n,amb}$ and $P_{n,sat}$ were not significantly correlated with leaf N on a mass basis but were weakly correlated with leaf Ca and Mg on a mass basis. We conclude that low leaf Ca or Mg concentrations may limit leaf CO_2 assimilation and tree carbohydrate status in the declining stand.

Keywords: chlorophyll, forest decline, mineral nutrition, photosynthesis.

Introduction

Forest decline is evident in symptoms such as a reduction in stem wood growth, loss of foliage, change in leaf size and shape, foliage discoloration and high mortality of aboveground or belowground tissue (Mueller-Dombois 1986, McLaughlin et al. 1987, Bernier and Brazeau 1988*a*, 1988*b* and 1988*c*, Allen et al. 1992). Many alterations in physiological processes can be involved in forest decline (Mueller-Dombois 1986, Schulze 1989, McLaughlin and Kohut 1992). Therefore, an understanding of how and why forests exhibit decline will depend on a detailed understanding of the physiological basis of decline (Schulze 1989, Allen et al. 1992, McLaughlin and Kohut 1992).

Field surveys in northeastern North America have revealed localized decline symptoms in sugar maple (*Acer saccharum* Marsh.) trees, including crown dieback, reductions in basal area growth, and chlorosis of foliage (Bernier and Brazeau 1988*a*, 1988*b*, Allen et al. 1992, Kolb and McCormick 1993, Wilmot et al. 1995). These decline symptoms are accompanied by visible foliar symptoms caused by low foliar magnesium, phosphorus or potassium (Leaf 1968, Bernier and Brazeau 1988*a*, Bernier and Brazeau 1988*b*). Such deficiencies are characteristic of growth on acidic soil with low base cation availability. Although there is some evidence that dieback of declining sugar maple is related to nutrient deficiencies or low soil pH and low soil base cation availability (Bernier and Brazeau 1988*c*, Wilmot et al. 1995), there is little information on how mineral nutrient deficiency is involved in sugar maple decline (Bernier and Brazeau 1988*a*, 1988*b* and 1988*c*, Ellsworth and Liu 1994). The primary environmental stresses in declining sugar maple stands have been identified as summer drought (Gregory et al. 1986, Allen et al. 1992), and low soil pH and base cation pools (Ellsworth and Liu 1994, Wilmot et al. 1995). However, few studies of sugar maple decline have focused on the physiological processes that might underlie the relationship between nutrient deficiency and stand decline. Wilmot et al. (1995) hypothesized that the reduction in basal area growth in sugar maple decline results from carbohydrate deficiencies caused by reduction in leaf photosynthesis.

To test this hypothesis, we investigated foliar photosynthetic performance in relation to leaf characteristics, mineral nutrition and non-structural carbohydrate reserves in a healthy and a declining sugar maple stand in northwestern Vermont. Because recent experimental evidence indicates that low leaf Ca status in stands on acid soils may intensify the limitation of leaf

nitrogen on photosynthesis (Ellsworth and Liu 1994), we also examined photosynthesis–nitrogen relations to determine if there is a correlation between maximum leaf photosynthetic rate and leaf nitrogen concentration in sugar maple trees (cf. Reich et al. 1991, Ellsworth and Reich 1992, 1993). The specific objectives of the study were to determine if: (1) declining stands have low foliar nutrient content; (2) leaves with low leaf mineral nutrient concentrations have low leaf photosynthetic rates; and (3) reduced carbon assimilation capacity of foliage is involved in sugar maple decline (cf. Ellsworth and Liu 1994).

Materials and methods

Study sites

Two stands representing "healthy" and "declining" conditions typical of those observed in a reconnaissance of 15 sugarbushes in northern Vermont (Wilmot et al. 1995) were selected based on the proportion of crown branch dieback (low versus high), appearance of foliage (e.g., chlorotic versus healthy), and basal area growth rate (low versus high). During the two years of study, 1991 and 1992, the average percentage of crown branch dieback was 10 ± 2% for the declining stand and 3 ± 0.6% for the healthy stand, and the annual basal area increment was 6.5 ± 1.3 cm^2 and 12.0 ± 3.3 cm^2 for the declining and healthy stands, respectively (T.R. Wilmot, Univ. Vermont, personal communication). The soil in the declining stand is an acidic Marlow coarse loam with a pH of 3.9 ± 0.1 and low extractable calcium and magnesium status (1138 ± 88 mg kg^{-1} and 96.5 ± 5.3 mg kg^{-1} for Ca and Mg, respectively). In contrast, the soil in the healthy stand is a Stowe silt loam with a pH of 4.9 ± 0.1 and extractable Ca and Mg is 1547 ± 277 mg kg^{-1} and 162.2 ± 44.9 mg kg^{-1}, respectively (T.R. Wilmot, personal communication). During the two growing seasons studied, trees in the declining stand exhibited incidences of foliar damage and in some cases, irregular leaf size and damaged lobes, whereas leaves of trees in the healthy stand appeared normal. The healthy stand was located at Fairfield (44°48′ N, 72°59′ W, elevation 165 m), and the declining stand was located approximately 40 km away at Proctor Maple Research Center, Underhill Center (PMRC, 44°31′ N, 72°53′ W, elevation 440 m). Both stands were managed as sugarbushes, and approximately 90% of the trees in the stand were sugar maple. Tree basal area was 23.8 cm^2 m^{-2} in the healthy stand and 31.4 cm^2 m^{-2} in the declining stand. The dominant sugar maples were 200 and 125–145 years old in the healthy and declining stands, respectively (Wilmot et al. 1995). Other trees present were American beech (*Fagus grandifolia* J.F. Ehrh.), yellow birch (*Betula allegnaniensis* Britt.) and white ash (*Fraxinus americana* L.). Detailed stand information has been presented by Wilmot et al. (1995; see data for Stands 1 and 4).

Sample trees

In each stand, 12 dominant mature sugar maple (*Acer saccharum* Marsh.) trees were arbitrarily selected from within a 1000 m^2 plot previously established for long-term study (Wilmot et al. 1995). The selected trees had diameters at breast height of 35–81 cm and 37–78 cm and heights of approximately 25 m and 20 m in the healthy and declining stands, respectively. In the declining stand, six of the 12 trees selected exhibited chlorotic foliage and approximately 10% crown dieback, and preliminary data indicated that these trees had low leaf Ca and Mg concentrations (T.R. Wilmot, personal communication). In 1992, these six trees in the declining stand were selected for the study of leaf photosynthetic performance under low leaf nutrient conditions. Because many leaves in sugar maple canopies are shaded (Ellsworth and Reich 1993), eight to nine understory sugar maple seedlings in each plot were also measured. The seedlings had stem diameters of 3–5 mm and heights of 1–1.5 m, and were located in microsites receiving sunflecks during the day.

Leaf gas exchange

To avoid the difficulty of reaching intact branches in the upper crowns, detached branches from the selected trees were used to measure gas exchange. Branches on the southeast side of the upper crowns were shot down with a shot gun and the branch ends were immediately immersed in a bucket of water. The ends of the branches were recut under water, and the cut ends were smoothed with a sharp razor blade to ensure rehydration. The detached branches were typically 1–1.2 m long and 7–12 mm in diameter. While under water, the branches were attached to a clean rubber tube supplying deionized water at 0.01 MPa hydraulic pressure. Branches were allowed to acclimatize for 1 to 2 h before gas exchange was measured. Leaf water potentials of the detached branches were usually greater than −0.5 MPa. Four to six fully expanded leaves on each branch were tagged for study. Net photosynthesis (P_n) and stomatal conductance (g_s) of foliage of detached sugar maple branches measured within 48 h of cutting were comparable to values for foliage of intact branches (Liu 1995).

Leaf gas exchange was measured under natural conditions in a clearing with an LI-6200 photosynthesis system with a 1-liter chamber (Li-Cor, Inc., Lincoln, NE). Based on other studies (Ellsworth and Reich 1993, Liu and Tyree unpubl. data), photosynthetic light saturation of sugar maple occurs at photosynthetic photon flux densities (PPFD) above 400 μmol m^{-2} s^{-1}. Initially, light-saturated leaf P_n and g_s were measured in natural sunlight at ambient CO_2 concentration (320–340 ppm) ($P_{n,amb}$ and $g_{s,amb}$). Light-saturated leaf P_n and g_s were then measured at the intercellular CO_2 partial pressure (C_i) near the saturation point ($P_{n,sat}$ and $g_{s,sat}$). Near saturating C_i was determined by a P_n–C_i curve as described by Davis et al. (1987). The elevated C_i values were achieved by breathing into the leaf chamber to increase chamber CO_2 concentration, and then using the soda-lime scrubber of the LI-6200 to lower chamber CO_2 to the selected concentration (approximately 1100 ppm).

Similar measurements of $P_{n,amb}$ and $g_{s,amb}$ at ambient CO_2 and of $P_{n,sat}$ and $g_{s,sat}$ at saturating CO_2 concentration were made on 3–4 leaves exposed to sunflecks for at least 5 min on each of 8–9 intact seedlings in each plot to obtain the mean value for each seedling. The PPFDs of the sunflecks were

above 400 μmol m^{-2} s^{-1} for all leaves. The response of P_n to stepwise increases in external CO_2 concentration and leaf internal CO_2 concentration (C_i) was measured outdoors under light-saturating conditions on a detached and rehydrated branch from an apparently healthy mature sugar maple tree near the PMRC site. A P_n–C_i curve was obtained from this measurement to determine the saturating C_i for sugar maple. Intercellular CO_2 concentration was calculated based on the equations of von Caemmerer and Farquhar (1981). Data were fitted to the equation (Hanson et al. 1988):

$$P_n = P_{n,max}(1 - (1 - R_d/P_{n,max})^{(1 - C_i/CP_{CO_2})}),$$

where $P_{n,max}$ represents CO_2-saturated net photosynthesis; R_d is dark respiration; and CP_{CO_2} is the CO_2 compensation point.

All photosynthesis measurements were conducted in the field between early June and early August in 1991 and 1992. The related environmental conditions recorded during gas exchange measurements are given in the captions of the respective Figures and Tables.

Leaf element concentrations

The area of each leaf used for gas exchange measurements was determined with an LI-3100 leaf area meter (Li-Cor, Inc.). The leaves were then oven dried at 70 °C for 24 h and weighed. Dried leaves were combined for each branch and ground to pass a 40-mesh screen. Samples were analyzed for leaf element concentrations at the University of Vermont Plant and Soil Analysis Laboratory. Total leaf nitrogen (N) was assayed by the Kjeldahl procedure in 1991 or by the Dumas method in 1992–1993. Other macromineral and micromineral nutrients in leaves were assayed, after digestion in $HClO_4$ and HNO_3, with an inductively coupled plasma emission spectrometer (Plasmaspec 2.5, Leeman Labs, Lowell, MA).

Leaf chlorophyll concentrations

After leaf gas exchange measurements, branches were taken to the laboratory and a total of 70–100 leaf disks (diameter = 0.64 cm) from 7–10 fully expanded leaves were taken from each branch. Disks were placed in a test tube with 80% acetone solution, homogenized with a polytron and extracted in the dark for 15 min at room temperature. The extract was filtered through Whatman No. 1 filter paper, and its absorbance at 645 and 663 nm was measured with a Beckman spectrophotometer according to procedures and calculations described by Arnon (1949).

Leaf water potential

Leaf water potentials were measured by the pressure chamber technique to ensure that the detached branches were sufficiently rehydrated. In addition, a diurnal pattern of leaf water potential of the study trees was measured in the field. On a typical sunny day in July, small twigs in the upper section of the southeast side of the crowns of both stands were sampled by shotgun every 2 h from early morning to evening for leaf water potential measurement.

Leaf non-structural carbohydrate concentrations

Diurnal patterns of major non-structural carbohydrate (starch and sucrose) reserves were determined to provide a measure of the change in strength of leaf photosynthate sink and source, which may be related to that of carbon sinks and sources in other parts of the trees (Zampini et al. 1980, Hendrix and Huber 1986). Leaf glucose concentrations were assayed by the INT enzymatic color reaction method (Hendrix 1993). Leaf starch, sucrose and fructose concentrations were determined after conversion to glucose by amyloglucosidase, invertase and phosphoglucoisomerase, respectively. In June, after leaves had fully expanded in both stands, a branch in the upper portion on the southeast side of the crown was collected. Six expanded leaves from each branch were used, and 15 6.4-mm diameter leaf discs without the main vein were taken immediately and stored in 80% alcohol solution in a cooler with dry ice (−20 to −24 °C) for transfer to the laboratory. Assays were done immediately after sampling. Because the leaf glucose and fructose concentrations were very low, leaf starch and sucrose concentrations were used to represent leaf non-structural carbohydrate concentrations. Leaf starch and sucrose concentrations were calculated on both a leaf area and dry mass basis.

Statistical analyses

Differences in measured leaf characteristics between the two stands were evaluated by *t*-tests. Significance of the diurnal changes of the measured leaf water potential and carbohydrate concentrations, and the interaction between stand and time during the day were evaluated using SAS general linear models repeated measures procedure. Correlations between leaf characteristics were analyzed by linear regression procedures. All of the statistical analyses were done using the SAS software package (SAS Institute, Cary, NC). The slopes of two straight lines were compared by orthogonal contrasts (Kleinbaum et al. 1988). Significant differences are at $P < 0.05$, except where otherwise indicated.

Results

Diurnal patterns in leaf water potential and carbohydrates

Measurements were taken on a typical sunny day in June 1991. In both stands, leaf water potential changed significantly from early morning to evening ($P = 0.003$) (Figure 1A). Although leaf water potentials did not differ significantly between the stands from 0700 h to late afternoon (1700 h) ($P = 0.089$), leaf water potentials in the declining stand were significantly higher than in the healthy stand at 1930 h ($P < 0.05$) (Figure 1A). The lowest leaf water potential observed during the day was about −1.4 MPa in both stands. During the same period, there were no differences between the stands in leaf water potentials of seedlings growing under gap conditions (data not shown).

There were no significant diurnal changes in leaf starch and sucrose concentrations ($P \geq 0.06$), except in sucrose concentration calculated on a dry mass basis ($P = 0.038$). No signifi-

cant differences were found in the diurnal change of any leaf carbohydrate concentration (Figures 1B and 1C) between the two stands ($P \geq 0.10$). Leaves in the declining stand had similar starch and sucrose concentrations (% or g m^{-2}) to those in the healthy stand (Figures 1B and 1C) ($P \geq 0.10$) except in late afternoon (1700 h) when leaf starch concentrations (g m^{-2}) in the declining stand were marginally higher than in the healthy stand ($P = 0.065$). In both stands, leaf starch concentrations were three to four times higher than leaf sucrose concentrations (Figures 1B and 1C).

Leaf mineral nutrition and photosynthesis

In general, year to year changes in leaf macronutrient status were small and comparable for trees in both stands (Table 1) ($P > 0.21$). Leaf N concentration in the declining stand was lower than in the healthy stand. The difference was marginally significant in 1991 ($P = 0.055$), but not in 1992 ($P = 0.199$)

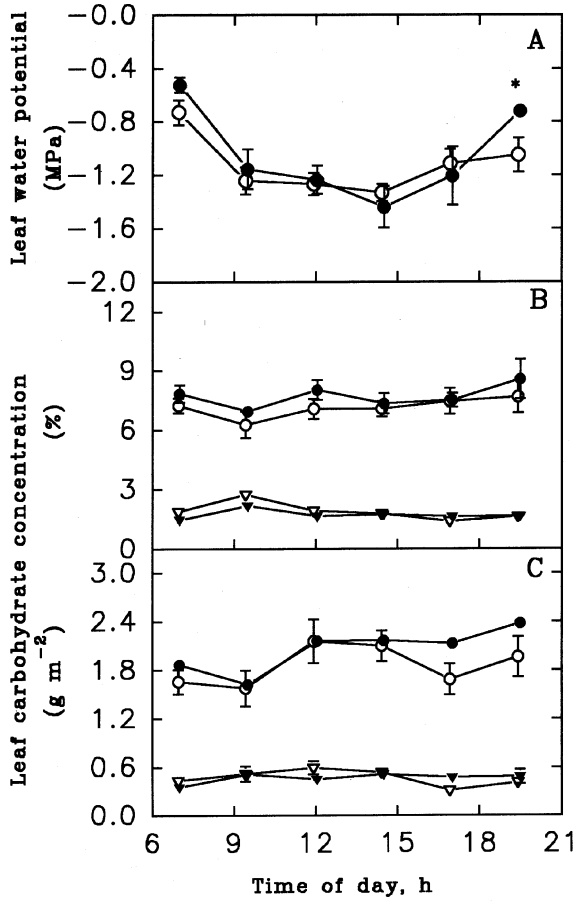

Figure 1. Diurnal changes in leaf water potential and leaf starch (circles) and sucrose (triangles) concentrations of sugar maple leaves in the healthy (open symbols, Fairfield) and declining (filled symbols, PMRC) stands. Values are means ± 1 SE. $n = 6$ trees for each plot. An asterisk indicates that there is a significant difference between the two plots at $P < 0.05$. (A) Water potential versus time of day (on a sunny day in June), (B) percent starch and sucrose versus time of day, and (C) g starch or sucrose per unit leaf area versus time of day (on the same day as A).

(Table 1). Leaf K concentrations did not differ significantly between the two stands in 1991 ($P = 0.138$), but were significantly higher in the healthy stand than in the declining stand in 1992 ($P = 0.047$). Leaf P was significantly higher in the declining stand than in the healthy stand in both 1991 and 1992 ($P = 0.001$ and $P = 0.005$, respectively) (Table 1). Leaf Ca and Mg and leaf chlorophyll concentrations in the declining stand were consistently and significantly lower than in the healthy stand in both 1991 and 1992 ($P < 0.05$) (Tables 1 and 2). In 1991, leaf mass per unit area (LMA) was higher in the declining stand than in the healthy stand (62.2 versus 52.1 g m^{-2}) ($P = 0.058$). In 1992, there was no significant difference in LMA ($P = 0.131$) between the declining and healthy stands (84.8 versus 75.3 g m^{-2}), although LMA was significantly higher in both stands in 1992 than in 1991. Stomatal conductances did not differ significantly between stands in either year ($P = 0.324$ and $P = 0.131$ for the declining and healthy stands, respectively) (Table 2).

At ambient CO_2, light-saturated net photosynthetic rates expressed on an area basis (μmol m^{-2} s^{-1}) ($P_{n,amb}$/area) were marginally higher in the declining stand than in the healthy stand ($P = 0.075$) in 1991, but not in 1992. However, when expressed on a mass basis (nmol g^{-1} s^{-1}), light-saturated net photosynthesis at ambient CO_2 ($P_{n,amb}$/mass) was similar in both stands in both years (Table 2).

The P_n–C_i curve in Figure 2 shows that light-saturated net photosynthesis was near saturation (90% of $P_{n,max}$) at $C_i \approx 700$ ppm. Light-saturated net photosynthesis at C_i near or above this point ($P_{n,sat}$) was measured to estimate the physiological potential for photosynthetic CO_2 assimilation without diffusional limitations. At ambient CO_2, area-based, light-saturated net photosynthesis ($P_{n,amb}$/area) was significantly and positively correlated with leaf mass per unit area (LMA) and leaf N concentration per unit area (N/area) according to linear regression models using the pooled data from the two stands ($P = 0.0001$) (Figures 3A and 3B). At near saturating CO_2, area-based net photosynthesis ($P_{n,sat}$/area) was more closely correlated with LMA and N/area than was $P_{n,amb}$/area (Table 3), and the slopes of these relationships were significantly higher for $P_{n,sat}$/area than for $P_{n,amb}$/area (Table 3 and Figures 3A, 3B, 3D and 3E). Mass-based $P_{n,amb}$ and $P_{n,sat}$ were not significantly related to leaf N concentration (N/mass) ($P > 0.10$ in both cases, Figures 3C and 3F).

Both $P_{n,amb}$/mass and $P_{n,sat}$/mass were significantly and positively correlated with Ca/mass and Mg/mass (Table 4 and Figures 4A, 4D, 4B and 4E). The linear correlations were weak for $P_{n,amb}$/mass ($r^2 = 0.19$ and 0.12) and stronger for $P_{n,sat}$/mass ($r^2 = 0.43$ and 0.33). The slopes of these linear regressions were significantly higher for $P_{n,sat}$/mass than for $P_{n,amb}$/mass (Table 3). Leaf Ca and Mg concentrations were both significantly positively correlated with leaf chlorophyll concentration ($r^2 = 0.21$ and $P = 0.009$, $r^2 = 0.226$ and $P = 0.006$, respectively, data not shown). The pooled data from the healthy and declining stands showed that Ca/mass was strongly positively correlated with Mg/mass across sites ($r^2 = 0.77$, $P < 0.001$) in a linear model (Figure 4C, Table 4). There was also a significant linear relation between N/mass and Ca/mass ($P = 0.0068$), but the correlation was weak

Table 1. Leaf macromineral nutrient concentrations (mg g^{-1} dry weight, expressed as means ± 1 SE) from mature sugar maple trees in a healthy stand (Fairfield) compared with values from trees in a declining stand (PMRC) (n = 6 trees for each stand). For each year, significant differences between means within a column are indicated by a different letter ($P \leq 0.05$). Data are for fully expanded leaves collected in July of each year from the upper third of the crown.

	Macromineral concentration (mg g^{-1})				
Stand	N	P	K	Ca	Mg
1991					
Fairfield	19.9 ± 1.2 a*	1.1 ± 0.1 a	5.6 ± 0.4 a	10.2 ± 0.6 a	1.8 ± 0.1 a
PMRC	17.2 ± 0.5 b	1.3 ± 0.1 a	6.5 ± 0.3 a	8.1 ± 0.4 b	1.0 ± 0.1 a
1992					
Fairfield	17.9 ± 1.0 a	1.0 ± 0.06 a	5.1 ± 0.3 a	11.0 ± 0.5 a	1.8 ± 0.2 a
PMRC	16.2 ± 0.1 a	1.4 ± 0.05 a	6.8 ± 0.2 b	7.7 ± 0.6 b	1.1 ± 0.1 b

* Marginally significant (P = 0.056).

Table 2. Comparison of light saturated net photosynthetic rate based on area and mass ($P_{n,amb}$/area and $P_{n,amb}$/mass), stomatal conductance to water vapor at ambient CO_2 ($g_{s,amb}$), leaf mass per unit area (LMA), and leaf chlorophyll concentration (Chl) of mature sugar maple trees in the healthy (Fairfield) and the declining stand (PMRC). Trees (n = 6) were the same as those sampled for data in Table 1. Values are means ± 1 SE. Within each year and column, different letters indicate a significant difference between stand means ($P < 0.05$). Measurements were made under a range of environmental conditions.[1]

Stand	$P_{n,amb}$/area (μmol m^{-2} s^{-1})	$P_{n,amb}$/mass (nmol g^{-1} s^{-1})	$g_{s,amb}$ (mmol m^{-2} s^{-1})	LMA (g m^{-2})	Chl (mg g^{-1})
1991					
Fairfield	4.9 ± 0.8 a[2]	104 ± 18 a	80 ± 24 a	52.1 ± 7.2 a[2]	7.7 ± 0.9 a
PMRC	6.8 ± 0.6 b	100 ± 9 a	112 ± 17 a	62.2 ± 3.4 b	5.1 ± 0.3 b
1992					
Fairfield	6.3 ± 1.0 a	77 ± 12 a	96 ± 16 a	75.3 ± 4.6 a	5.2 ± 0.4 a
PMRC	6.9 ± 0.3 a	80 ± 7 a	129 ± 10 a	84.8 ± 3.5 a	3.4 ± 0.2 b

[1] Gas exchange was measured under a range of environmental conditions for Fairfield and PMRC foliage. The conditions for the data for Fairfield and PMRC, respectively, were: Tl = 29.5–30.1 °C and 28.4–29.9 °C; VPD = 2.29–2.70 kPa and 2.18–2.60 kPa; C_{CO_2} = 326–335 ppm and 323–332 ppm; Ψ_L = −0.19 to −0.48 MPa and −0.18 to −0.63 MPa in 1991; and in 1992: Tl = 29.5–32.0 °C and 26.7–28.0 °C; VPD = −2.30–2.80 kPa and 2.00–2.20 kPa; C_{CO_2} = 326–335 ppm and 307–329 ppm; Ψ_L = −0.49 to −0.83 MPa and −0.44 to −0.68 MPa. (Tl = leaf temperature, VPD = leaf-to-air vapor pressure deficit, C_{CO_2} = chamber CO_2 concentration, Ψ_L = leaf water potential).

[2] Marginally significant (P = 0.075 for $P_{n,amb}$/area, P = 0.058 for LMA).

(r^2 = 0.14, Figure 4F, Table 4). Linear regression analysis showed that $g_{s,amb}$ and $g_{s,sat}$ (leaf stomatal conductance at near saturating CO_2) were not significantly related to leaf Mg or Ca on an area basis (P = 0.185 and P = 0.207 for Mg, P = 0.251 and P = 0.116 for Ca, for the declining and healthy stands, respectively).

The significance of each relationship shown in Figures 3 and 4 was the same whether data for the two stands were analyzed separately or together. The only significant difference in slopes between stands was for the relationship between leaf Mg and Ca concentrations (P = 0.05, Table 5). For the relationships between $P_{n,sat}$/area and LMA, $P_{n,amb}$/mass and Mg/mass, and $P_{n,sat}$/mass and Mg/mass, the differences in slopes between the two stands were marginally significant (P = 0.08, 0.06 and 0.08, respectively).

In the declining stand, tree crown conditions varied from tree to tree (T.R. Wilmot, personal communication), and some trees had low leaf base cation status and chlorotic foliage (Liu, unpubl. data). Foliar Ca and Mg concentrations (3.1 and 0.89 mg g^{-1}, respectively) were low compared to reported foliar concentrations in healthy trees (Kolb and McCormick 1993, Wilmot et al. 1995), and significantly lower than those of trees in our healthy stand (P = 0.0001 for both, Table 6). Correspondingly, $P_{n,amb}$/mass for nutrient-poor trees in the declining stand was lower (P = 0.057) and $P_{n,sat}$/mass was significantly lower than for trees in the healthy stand, but there were no statistically significant differences in $P_{n,amb}$/area and $P_{n,sat}$/area, g_s and $g_{s,sat}$ between the healthy and declining stands. The LMA was significantly different between the two stands (Table 6).

Discussion

We found no evidence of water stress in the declining stand. Moreover, leaf water potentials were not statistically different between stands (Figure 1). In addition, soil water content in the declining stand was significantly higher (P = 0.0005) than in the healthy stand throughout the growing season of 1992 (Liu

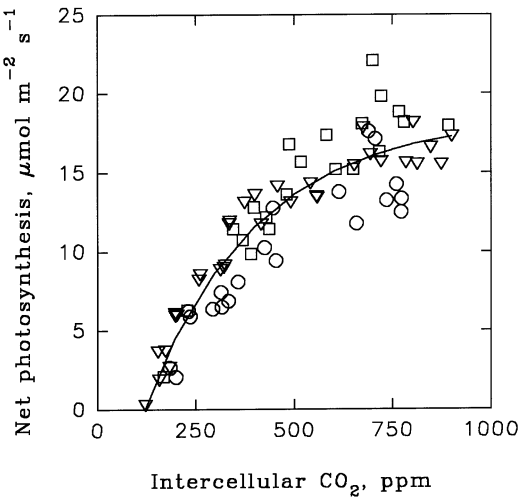

Figure 2. Relationship between light-saturated net photosynthesis and intercellular CO_2 concentration (P_n–C_i curve) of sugar maple. Different symbols represent different leaves. The curve shown was fit to the data by nonlinear regression techniques. The measurement conditions were leaf temperature: 28.2–33.1 °C, and leaf-to-air vapor pressure deficit: 2.4–3.50 kPa.

and Tyree, unpublished data). Soils rarely became dry at the decline site, where in one study (Tyree and Wilmot, unpublished observations), predawn soil water potential was never below −0.15 MPa. Therefore, water stress may be excluded as a possible cause of the lower photosynthetic rates and lower leaf Mg and Ca concentrations, and the presence of chlorotic foliage in the declining stand compared with the healthy stand.

Starch and sucrose were the primary forms of non-structural carbohydrate reserve in sugar maple leaves. Other sugars (e.g., glucose and fructose) were present only in trace concentrations. The foliar concentration of starch was three to four times higher than that of sucrose (Figure 1). Generally, the foliage in both the declining and healthy stands stored the same amount of photosynthate during the day, perhaps indicating that the strength of leaf carbon sinks was not affected by the contrasting stand conditions. The marginal difference in starch concentration on an area basis between the two stands in the late afternoon was attributed to differences in LMA (Figures 1B and 1C). Similarities in leaf sucrose concentrations between the two stands suggest that production versus utilization in leaves and translocation to other plant parts were comparable in the two stands during the day (Huber et al. 1985, Hendrix and Huber 1986).

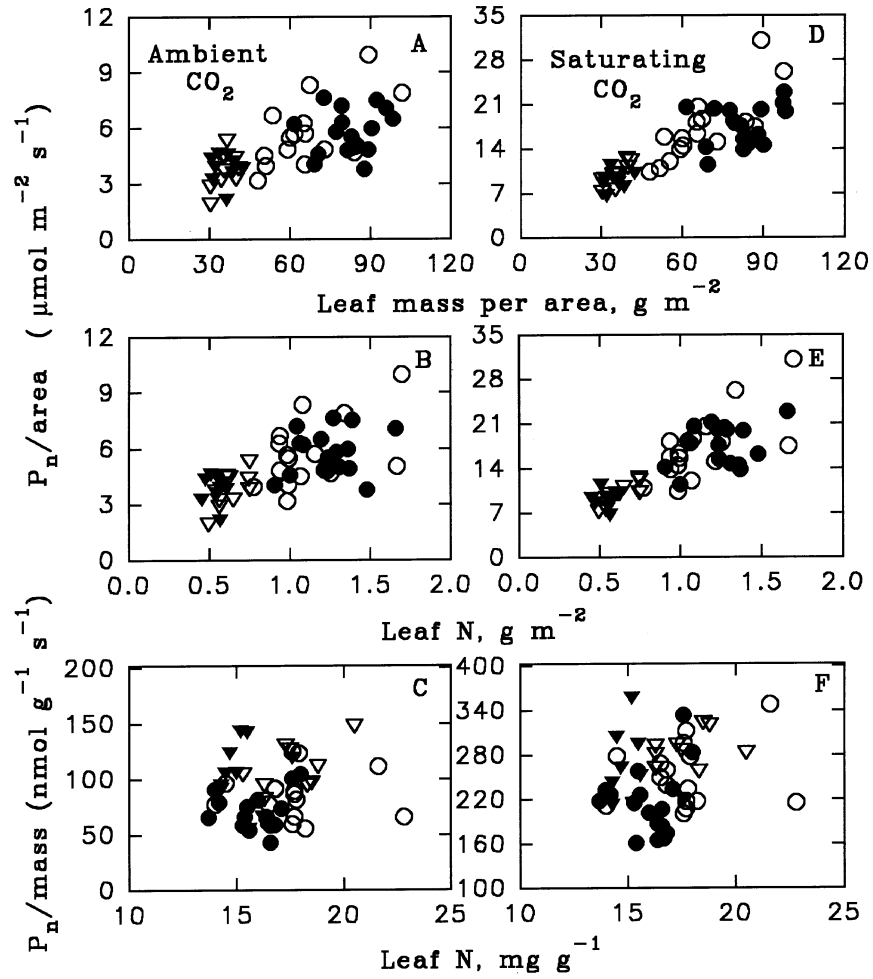

Figure 3. Sugar maple light-saturated net photosynthesis based on area at ambient CO_2 ($P_{n,amb}$/area) and at saturating CO_2 ($P_{n,sat}$/area) in relation to leaf mass per unit area (LMA) (A, D), leaf N per unit area (N/area), respectively (B, E), and light-saturated net photosynthesis based on mass at ambient CO_2 ($P_{n,amb}$/mass) and at saturating CO_2 ($P_{n,sat}$/mass) in relation to leaf N based on mass (N/mass), respectively (C, F). Data were collected between mid-June and early August in 1992 and 1993. Symbols: open = healthy stand in Fairfield, closed = declining stand at PMRC, triangles = leaves from seedlings, and circles = leaves from mature trees. The linear regression results were $P_{n,amb}$/area = 2.295 + 0.047 LMA (r^2 = 0.38, P < 0.001), $P_{n,sat}$/area = 3.133 + 0.527 LMA (r^2 = 0.63, P < 0.0001), $P_{n,amb}$/area = 2.217 + 2.933 N/area (r^2 = 0.42, P < 0.0001), $P_{n,sat}$/area = 2.855 + 12.20 N/area (r^2 = 0.68, P < 0.0001). Data in left-hand set of panels are for ambient CO_2, and data in the right-hand panels are for saturating CO_2. The measurement conditions for $P_{n,amb}$ and $P_{n,sat}$ were leaf temperature: 24.0–32.0 °C and 24.3–31.6 °C, leaf-to-air vapor pressure deficit: 2.14 ± 0.05 kPa and 2.24 ± 0.06 (± SE) kPa, respectively, and leaf water potential: less than –0.7 MPa.

Table 3. Evaluation of difference in slopes of the linear regressions for the relationships in Figure 3 and Figure 4 between the ambient CO_2 and near saturating CO_2. Dependent and independent variables are referred to in Figures 3 and 4: *b* is intercept, *m* is slope, and r^2 is correlation coefficient.

Dependent variable	Independent variable	Ambient CO_2 concentration			Saturating CO_2 concentration			*P*-value
		b	*m*	r^2	*b*	*m*	r^2	
P_n/area	LMA	2.30	0.05	0.38	3.13	0.20	0.63	0.0001
P_n/area	N/area	2.22	2.93	0.42	2.86	12.20	0.68	0.0001
P_n/mass	Ca/mass	60.9	3.58	0.19	171	9.94	0.43	0.001
P_n/mass	Mg/mass	65.9	16.5	0.12	180	49.42	0.33	0.008

Table 4. Regression equations for the relationships between light saturated net photosynthesis based on mass ($P_{n,amb}$/mass taken at ambient CO_2, and $P_{n,sat}$/mass taken at near saturating CO_2) and leaf Ca or leaf Mg based on mass (Ca/mass and Mg/mass); leaf Mg and leaf Ca based on mass; and leaf Ca or N based on mass (Ca/mass, N/mass) in Figure 4. Data are for both stands combined.

Regressions (linear model)	r^2	*P*-value
$P_{n,amb}$/mass = 60.91 + 3.583 Ca/mass	0.19	0.0014
$P_{n,sat}$/mass = 171.00 + 9.935 Ca/mass	0.43	0.0001
$P_{n,amb}$/mass = 65.87 + 16.47 Mg/mass	0.12	0.0113
$P_{n,sat}$/mass = 179.53 + 49.42 Mg/mass	0.33	0.0001
Mg/mass = 0.199 + 0.154 Ca/mass	0.77	0.0001
Ca/mass = –0.288 + 0.644 N/mass	0.14	0.0068

The ranges of foliar macronutrient concentrations in the healthy stand (Table 1) were similar to those reported elsewhere (Leaf 1968, Bernier and Brazeau, 1988*a*, 1988*b*, 1988*c*, Wilmot 1995). Foliar N, P and K concentrations in the declining stand (Table 1) were also within the range of values commonly reported (Kolb and McCormick 1993). Foliar Ca and Mg concentrations in the declining stand (≤ 8.1 mg g^{-1} and ≤ 1.1 mg g^{-1}, respectively; Figure 4C) were similar to or below critical values reported for sugar maple seedlings (Erdmann et al. 1979), and low compared to values reported for mature trees (see also Ellsworth and Liu 1994). Low foliar Ca and Mg concentrations can cause foliar chlorosis, low chlorophyll concentrations and marginal necrosis (Leaf 1968, Erdmann et al. 1979, Bernier and Brazeau 1988*c*, Oren et al. 1993). Other factors such as insect feeding, which may cause similar foliar symptoms (Houston et al. 1990), were rarely observed.

Area-based photosynthetic rate may be significantly related to LMA, depending on leaf light environment history and leaf developmental stage (Oren et al. 1986, Reich et al. 1991). Because only fully expanded leaves were measured in both stands, the correlations between P_n and LMA in Figures 3A and 3D were, in part, related to leaf position in the canopy or canopy leaf area above the sampled branches, or both (see Ellsworth and Reich 1993). These relationships were further strengthened by the inclusion of understory seedling data in the analysis. The marginally higher $P_{n,amb}$/area in the declining stand than in the healthy stand may be related to a higher average LMA (Table 2), which can be attributed to reduced canopy density, as a result of crown dieback, in the declining stand. A higher slope of $P_{n,sat}$/area than of $P_{n,amb}$/area in relation to LMA (Table 3) was primarily related to the direct stimulatory effects of CO_2 on photosynthesis. For a given leaf, $P_{n,sat}$ was, on average, 2.7 times greater than $P_{n,amb}$ using pooled data from the two stands, and accounted for most of the difference between the slopes of $P_{n,sat}$ and $P_{n,amb}$ versus LMA. The same explanation accounts for the significantly higher slope of $P_{n,sat}$ than of $P_{n,amb}$ in relation to the other leaf traits presented in Table 3.

Because leaf N/area was strongly correlated with LMA ($r^2 = 0.90$, $P < 0.0001$, data not shown), the observed correlation between leaf N/area and $P_{n,amb}$/area is likely associated with the covariation of LMA and N/area. A similar conclusion was reached by Reich et al. (1991) and Ellsworth and Reich (1992, 1993) for sugar maple: i.e., the area-based photosynthesis–nitrogen relationships can be attributed to scaling of leaf N/area with LMA when LMA varies with leaf age or light environment. In contrast, mass-based photosynthesis–nitrogen relationships are more closely related to the metabolic basis of the association between these two parameters, and thus are more likely to reflect the effects of site and microsite variation in N availability on photosynthesis (Field and Mooney 1986, Evans 1989, Ellsworth and Reich 1993, Ellsworth and Liu 1994). The absence of a mass-based photosynthesis–nitrogen relationship in our study (Figures 3C and 3F) supports the contention that variation in LMA is responsible for the observed area-based photosynthesis–nitrogen relationships (Figures 3B and 3E).

Ellsworth and Reich (1992, 1993) showed that regressions of P_n versus leaf N/area for data obtained from leaves of seedlings and mature trees had similar slopes (slope 5.9 versus 5.0 for seedlings and mature trees, respectively). Similar results were obtained for regressions of P_n versus LMA (Ellsworth and Reich 1993). The regression of P_n versus N/area of pooled seedling and mature tree data from the study of Ellsworth and Reich (1993) had a slope and intercept of 5.98 and –0.63, respectively (cf. Figure 3). A lower slope for the $P_{n,amb}$/area versus N/area relationship in our study (Table 3) could have resulted from high leaf temperature or leaf–air vapor pressure difference, or both during some of the measurements, or because of limitations of other mineral nutrients (cf. Ellsworth and Liu 1994).

The correlations between leaf Ca or Mg concentration and photosynthesis indicate that leaf Mg or Ca or both impose

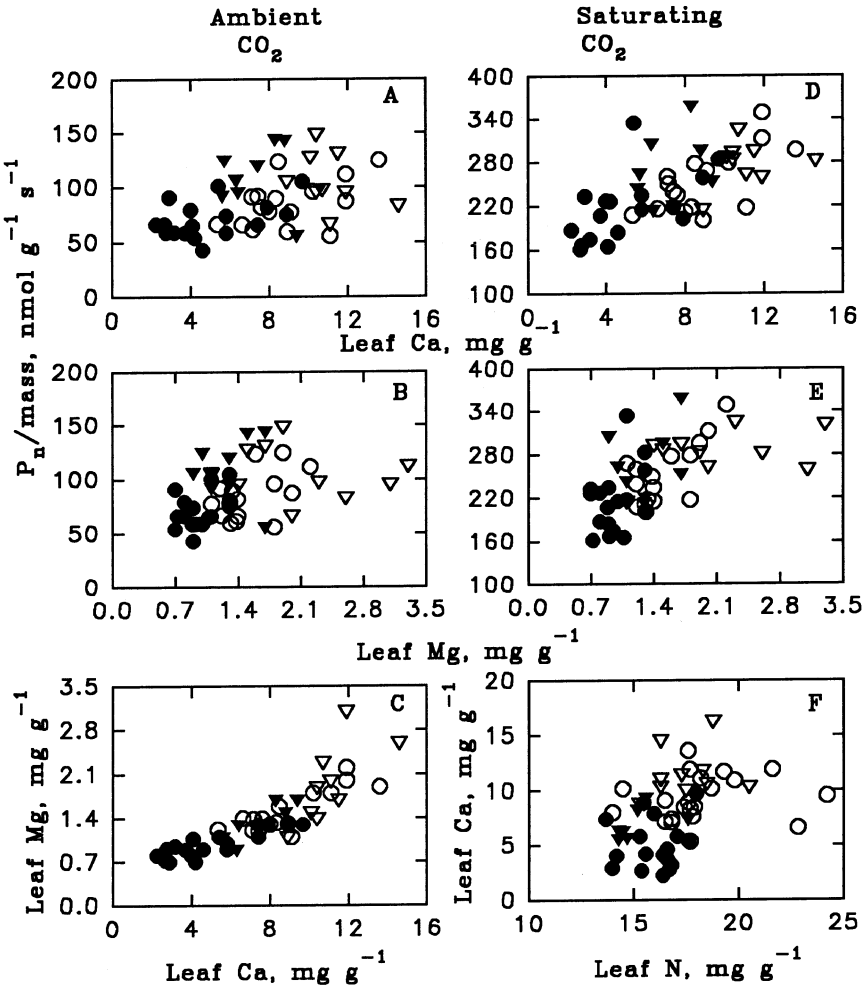

Figure 4. Sugar maple light-saturated net photosynthesis based on mass (P_n/mass at ambient and saturating CO_2) in relation to leaf Ca (Ca/mass) (A, D), leaf Mg (Mg/mass) (B, E); leaf Ca in relation to leaf Mg (C); leaf N based on mass (N/mass) in relation to leaf Ca (F). Data were collected between mid-June and early August in 1992 and 1993. Data in the left-hand set of panels are for ambient CO_2 and data in the right-hand set are for saturating CO_2. Symbols: open = healthy stand in Fairfield, closed = declining stand at PMRC, triangles = leaves from seedlings, and circles = leaves from mature trees. The linear regressions are presented in Table 4. The measurement conditions for $P_{n,amb}$ and $P_{n,sat}$ were the same as those in Figure 3.

Table 5. Evaluation of differences in slopes of linear regressions for the relationships in Figure 3 and Figure 4 between the healthy (Fairfield) and declining (PMRC) stands: m is slope and r^2 is correlation coefficient. Dependent and independent variables are referred to in Figures 3 and 4.

Dependent variable	Independent variable	Healthy stand		Declining stand		P-value
		m	r^2	m	r^2	
$P_{n,amb}$/area	LMA	0.065	0.40	0.040	0.43	0.20
$P_{n,sat}$/area	LMA	0.259	0.66	0.181	0.70	0.08
$P_{n,amb}$/area	N/area	3.71	0.46	2.37	0.41	0.20
$P_{n,sat}$/area	N/area	14.36	0.71	10.67	0.67	0.15
$P_{n,amb}$/mass	Ca/mass	3.72	0.15	6.06	0.23	0.26
$P_{n,sat}$/mass	Ca/mass	10.75	0.46	13.80	0.37	0.27
$P_{n,amb}$/mass	Mg/mass	10.69	0.06	49.42	0.34	0.06
$P_{n,sat}$/mass	Mg/mass	40.90	0.34	94.50	0.27	0.08
Mg/mass	Ca/mass	0.187	0.68	0.11	0.72	0.05

some limitation on light-saturated net photosynthesis, especially at near saturating CO_2 concentrations (Tables 2 and 5). This evidence combined with the data showing that foliar Mg and Ca concentrations were low in some trees in the declining stand (Table 6), provide support for the hypothesis that low leaf Mg or Ca nutrition status, or both, plays a role in reducing photosynthesis and hence affecting carbon availability for tree carbon balance. Because of the strong correlation between leaf Mg/mass and Ca/mass, it remains unclear whether the limitation to photosynthesis arises from foliar Mg deficieny or foliar Ca deficiency or both. Both Ca and Mg can function as essential regulators to control many biochemical reactions related to plant development and growth (Hepler and Wayne 1985, Marschner 1986). The stability and integrity of cell membranes are partly dependent on Ca, and Mg is a major component of chlorophyll and a primary ion involved in the charge

Table 6. Comparison of light saturated leaf photosynthetic rate based on area and mass, stomatal conductance to water vapor at ambient CO_2 ($P_{n,amb}$/area, $P_{n,amb}$/mass, $g_{s,amb}$) and at saturating CO_2 ($P_{n,sat}$/area, $P_{n,sat}$/mass, $g_{s,sat}$); leaf mass per unit area (LMA), leaf Ca and Mg based on mass of mature sugar maple trees in the healthy (Fairfield) stand with that in the declining (PMRC) stand. In PMRC, trees were selected to reflect extremes in leaf mineral nutrition based on earlier foliar nutrient assays (T.R. Wilmot, personal communication). Observations were made in June 1992, on a sample of 6 trees from each stand. Values are means ± 1 SE. Different letters within rows indicate significant differences ($P < 0.05$).[1]

Leaf characters	Healthy stand	Declining stand
$P_{n,amb}$/mass (nmol g^{-1} s^{-1})	83.7 ± 9.2 a	61.0 ± 2.4 b[2]
$P_{n,amb}$/area (μmol m^{-2} s^{-1})	5.1 ± 0.7 a	4.9 ± 0.3 a
$g_{s,amb}$ (mmol m^{-2} s^{-1})	92 ± 11 a	87 ± 9.0 a
$P_{n,sat}$/mass (nmol g^{-1} s^{-1})	233.8 ± 10.7 a	177.3 ± 7.0 b
$P_{n,sat}$/area (μmol m^{-2} s^{-1})	14.4 ± 1.2 a	14.1 ± 0.6 a
$g_{s,sat}$ (mmol m^{-2} s^{-1})	65.1 ± 9.9 a	66.2 ± 10.4 a
LMA (g m^{-2})	57.5 ± 3.5 a	73.2 ± 5.3 b
Ca (mg g^{-1})	7.2 ± 0.5 a	3.1 ± 0.3 b
Mg (mg g^{-1})	1.38 ± 0.05 a	0.89 ± 0.05 b

[1] Gas exchange was measured over the following range of environmental variables at Fairfield and PMRC, respectively: Tl = 26.8–29.3 °C and 25.3–29.0 °C; VPD = 1.98–2.56 kPa and 1.85–2.46, C_{CO_2} = 309–322 and 316–328; 1067–1161 and 1108 and 1167 ppm, Ψ_L = −0.21 to −0.66 MPa and −0.21 to −0.50 MPa. Names of the variables are referred to in Table 2.

[2] Marginally significant ($P = 0.057$).

balance in photosynthesis (Bangerth 1979, Marschner 1986). A possible colimitation of Ca with N on sugar maple photosynthesis has been found in stands growing on acidic soils with low base cation availability (Ellsworth and Liu 1994).

Leaf area index (LAI) was presumably lower in the declining stand than in the healthy stand because of more extensive crown dieback. Reduced P_n and decreased LAI could cause reduced whole-plant photosynthesis and thus reduce carbohydrate supply, causing reduced stem growth but not necessarily reduced leaf carbohydrates (Renaud and Mauffette 1991). In a companion paper (Liu and Tyree 1997), we show that declining sugar maple trees allocate more biomass to fine roots than healthy trees, resulting in a further drain on carbohydrate supply from the crown and leaving less for basal area growth. In addition, low Ca and Mg supply might have other direct effects on basal area growth in the declining stand, although there is no clear evidence of this.

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