

Analysis of gas exchange in seedlings of *Acer saccharum*: integration of field and laboratory studies

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Abstract. In the field, photosynthesis of *Acer saccharum* seedlings was rarely light saturated, even though light saturation occurs at about 100 μmol quanta $\text{m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD). PPFD during more than 75% of the daylight period was 50 μmol $\text{m}^{-2} \text{s}^{-1}$ or less. At these low PPFD's there is a marked interaction of PPFD with the initial slope (CE) of the CO_2 response. At PPFD-saturation CE was 0.018 μmol $\text{m}^{-2} \text{s}^{-1}/(\mu\text{l/l})$. The apparent quantum efficiency (incident PPFD) at saturating CO_2 was 0.05–0.08 mol/mol. CO_2 - and PPFD-saturated CO_2 exchange was 6–8 μmol $\text{m}^{-2} \text{s}^{-1}$. The ratio of internal CO_2 concentration to external (C_i/C_a) was 0.7 to 0.8 except during sunflecks when it decreased to 0.5. The decrease in C_i/C_a during sunflecks was the result of the slow response of stomata to increased PPFD compared to the response of net photosynthesis. An empirical model, which included the above parameters was used to simulate the measured CO_2

exchange rate for portions of two days. Parameter values for the model were determined in experiments separate from the daily time courses being simulated. Analysis of the field data, partly through the use of simulations, indicate that the elimination of sunflecks would reduce net carbon gain by 5–10%.

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List of symbols

A : measured photosynthetic rate under any set of conditions (μmol $\text{m}^{-2} \text{s}^{-1}$); A_m (atm): measured photosynthetic rate at saturating PPFD, 350 $\mu\text{l/l}$ CO_2 and 21% (v/v) O_2 (μmol $\text{m}^{-2} \text{s}^{-1}$); C : constant in equation of Smith (1937, 1938); C_a : CO_2 concentration in the air ($\mu\text{l/l}$); C_i : CO_2 concentration in the intercellular air space ($\mu\text{l/l}$); C_i^* : C_i corrected for CO_2 compensation point, i.e., $C_i - I^*$, ($\mu\text{l/l}$); CE: initial slope of the CO_2 response of photosynthesis (μmol $\text{m}^{-2} \text{s}^{-1}/(\mu\text{l/l})$); CEM: CE at PPFD saturation; E : transpiration rate (mmol $\text{m}^{-2} \text{s}^{-1}$); F : predicted photosynthetic rate (μmol $\text{m}^{-2} \text{s}^{-1}$); G : leaf conductance to H_2O (mol $\text{m}^{-2} \text{s}^{-1}$); I : photosynthetic photon flux density (μmol $\text{m}^{-2} \text{s}^{-1}$); N : number of data points; P_m : predicted photosynthetic rate at saturating CO_2 and given PPFD (μmol $\text{m}^{-2} \text{s}^{-1}$); P_{m1} : predicted photosynthetic rate at saturating CO_2 and PPFD (μmol $\text{m}^{-2} \text{s}^{-1}$); R_d : residual respiratory rate (μmol $\text{m}^{-2} \text{s}^{-1}$); T_a : air temperature ($^\circ\text{C}$); T_l : leaf temperature ($^\circ\text{C}$); V : reaction velocity in equation of Smith (1937, 1938); V_{max} : saturated reaction velocity in equation of Smith (1937, 1938); VPA: vapor pressure of water in the air (mbar/bar); VPD: vapor pressure difference between leaf and air (mbar/bar); X : substrate concentration in equation of Smith (1937, 1938); α : initial slope of the PPFD response of photosynthesis at saturating CO_2 (mol CO_2 /mol quanta); α (atm): initial slope of the PPFD response of photosynthesis at 340 $\mu\text{l/l}$ CO_2 and 21% (v/v) O_2 (mol CO_2 /mol quanta); I^* : CO_2 compensation point after correction for residual respiration ($\mu\text{l/l}$); A : PPFD compensation point (μmol $\text{m}^{-2} \text{s}^{-1}$)

On the forest floor, light intensity, measured as photosynthetic photon flux density (PPFD), often remains below saturating values for net photosynthesis (Malkina et al. 1970; Percy 1983), in spite of adaptation of understory plants to low PPFD. Shade adapted leaves exhibit very efficient light utilization, low maximum photosynthetic and respiratory rates per unit area, and low light compensation points (Björkman 1968; Björkman, Ludlow and Morrow 1972; Boardman 1977; Larcher 1980; Percy and Calkin 1983). In an extremely dense rainforest of Queensland, Australia, Björkman et al. (1972) observed positive CO_2 exchange rates in *Alocasia macrorrhiza* at PPFD below 10 μmol $\text{m}^{-2} \text{s}^{-1}$. Percy and Calkin (1983) found a similar response in *Claoxylon sandwicense* growing in an Hawaiian rainforest. The low photosynthetic capacities of shade-adapted species as measured at PPFD-saturation appear to be genetically fixed and do not change markedly with variation in PPFD during growth (Logan and Krotkov 1968; Leverenz and Jarvis 1980; McMillan and McClendon 1983). While studies such as those of Björkman et al. (1972) and Percy and Calkin (1983) have demonstrated daily variation in CO_2 exchange of understory species, these studies concentrated on the extreme shade habitats found in rainforests. Little is known about the daily time course response of understory woody plants in cold temperate deciduous forests. Existing data on photosynthesis of leaves of seedlings and saplings of shade-adapted, late successional species are mostly limited to studies in the laboratory, greenhouse, and nursery (Leverenz and Jarvis 1980; Logan and Krotkov 1968; Ledig and Korbobo 1983; McMillan and McClendon 1983) or to understory herbs (Young and Smith 1983).

In nature, seedlings of *Acer saccharum* grow in a low light environment characterized by relatively mild, constant conditions and moist, fertile soils with undisturbed litter. Leaves of these plants experience low PPFD except for brief periods when sunflecks fall on them (Spurr and Barnes 1980; Curtis 1959). The success of sugar maple in achieving

dominance in later stages of forest development depends in part on its ability to survive under low light conditions until an opening in the canopy occurs. Demographic studies have shown that the seedlings may survive for a decade or more exhibiting only very slow growth (Hett and Loucks 1971). That *A. saccharum* is a shade species is demonstrated by the very limited ability of this species to acclimate to high light intensity (Logan and Krotkov 1968; McMillan and McClendon 1983).

In the present study we have analyzed the photosynthetic response of *A. saccharum* seedlings to variation in environmental conditions using both laboratory and field data. We assume that long term survival in nature is associated with a slightly positive carbon balance and that slow accumulation of carbon adequately provides for respiratory maintenance during the winter, reestablishment of the foliage during spring, and a small increment of growth of stems and roots. We have determined the total daily carbon gain per unit leaf area on typical days and extrapolated this daily gain to the growing season, fully recognizing the difficulties in such a projection. We have also investigated the importance of sunflecks to total carbon gain. Finally, we have examined the utility of simulating daily time course of net photosynthesis with a simple model of net photosynthetic response. The model allows us to study more fully the effect of a particular photosynthetic capacity, PPFD utilization efficiency, and stomatal behavior on primary production of maple seedlings growing in their natural habitat.

Materials and methods

Field experiments

In situ measurements of gas exchange were made on mature leaves of *A. saccharum* seedlings growing in a natural mixed hardwood forest at the University of Michigan Biological Station (Pellston, Michigan, USA) within 100 m of Douglas Lake. The soil is sandy (Rubicon sand, U.S. Soil Survey) with a moderately rich layer of humus in the A horizon. The seedlings were about 10 years old as estimated from budscale scars, but no more than 40 cm tall. Data obtained on 12 and 13 September, 1981 are representative of results obtained during the summer of 1981 and are analyzed in detail in the results section. For these experiments the leaf was inserted into the gas exchange cuvette on the evening before the measurements. Between 1 and 11 September, 3.45 cm of rain fell including 1.6 cm on 7 September. Temperatures were measured in a standard meteorological enclosure about 0.25 km distant from the study site. Average maximum temperature for the preceding month was 25°C with a high extreme of 28°C; average minimum, 14°C, with a low extreme of 10°C. Maximum air temperatures on the forest floor tended to be a few degrees less than those measured in the meteorological enclosure.

Measurements of gas exchange were made using an open flow gas exchange system (Walz, Effeltrich, FRG), (Lange et al. 1967; Koch et al. 1971; Jurik et al. 1984). The leaf chamber was made of plexiglass the interior surfaces of which were covered with Teflon film (du Pont S-115) to reduce water vapor absorption. Volume of the chamber was 6 l. Flow rate through the chamber was 1–2 l/min. During the measurement of the diurnal time courses the air temperature inside the leaf chamber was controlled to be equal to air temperature at a position similar to that of

the leaf being measured. Air for the system was collected 7 m above-ground and 15 m upwind of the experimental site and was pumped through a 0.1 m³ buffer box before entering the system. Carbon dioxide and water vapor concentrations of the incoming air were not controlled.

Laboratory experiments

Five to ten-year old seedlings were collected in May 1982 from a site north of Douglas Lake. They were brought to the University of Michigan Matthaei Botanical Gardens where they were potted in 15 cm diameter pots with 2,500 cm³ of soil (peat:leaf mold:perlite:vermiculite:sand, 4:2:1:1:2) and fertilized with a 12:12:12 (% N:P:K) fertilizer. After potting, the seedlings were placed outside under three layers of greenhouse shade cloth to simulate light conditions on the forest floor. PPFD, measured with a quantum sensor (LI-190S, LICOR, Lincoln, Nebraska, USA), was approximately 10% of that in the open at mid-day, about 2 times that measured in the natural habitat during periods without sunflecks. Plants were watered regularly to avoid water stress. A wide range of gas mixtures (experimental gas) was produced using 4 Wösthoff (Bochum, FRG) gas mixing pumps in series and pure CO₂, O₂, and N₂. A portion of the mixed gas was used as a reference for the differential infrared gas analyzer (Sensors, Ann Arbor, Michigan, USA). Gas entering the gas analyzer (IRGA) was dried with Mg(ClO₄)₂. The IRGA was calibrated for each CO₂ concentration during each experiment by measuring a zero differential, i.e., experimental gas on both sides of the IRGA, and a gas of known differential (span gas) from the experimental gas. The span gas was produced by diluting a portion of the experimental gas by 1–10% with nitrogen using a gas mixing pump (Wösthoff). The slope of the line connecting the zero and span readings was used to calculate the differential in CO₂ concentration across the leaf chamber. To the extent possible, the CO₂ in the span gas was adjusted to be near the concentration of CO₂ in the gas exiting the leaf chamber. The remaining gas was humidified by passing it through a sparging bottle. The dew point of the gas entering the leaf chamber was set in a temperature conditioning column. Flow rates to the leaf chamber, reference side of the gas analyzer, and the upscale reference pump were controlled with flow controllers (Condyne, Pasadena, California, USA). Excess gas was vented through a pressure control valve which maintained pressure upstream of the flow controllers at 50 kPa. Flow rate into the leaf chamber, after humidification, was measured with a mass flow meter (Teledyne Hastings-Raydist, Hampton, Virginia, USA). The lucite leaf chamber was 14 cm in diameter and 5 cm deep with an anodized aluminum plate on the bottom to aid in heat exchange. Except for the aluminum, the walls of the chamber were covered with a Teflon film (du Pont S-115) to reduce adsorption of water (Bloom et al. 1981). Leaf temperature was controlled to ±0.1°C with a water jacket above and below the leaf chamber. Temperature of the water jacket was controlled using an electronic temperature controller which directed water through solenoids to constant temperature hot and cold baths. Concentration of CO₂ in the leaf chamber was corrected for dilution by transpired water vapor. Carbon dioxide concentration inside the leaf was calculated according to the equation of Wong et al. (1980). Rates are expressed on a projected leaf area basis.

Net photosynthesis model

The response of photosynthesis (A) to increasing CO_2 or PPF level has three phases: 1) an initial nearly linear increase with CO_2 concentration or PPF, 2) a transition zone, and 3) CO_2 or PPF saturated region. Smith (1937, 1938) noted that the transition occurs more rapidly than would be expected for simple Michaelis-Menten kinetics. He proposed an empirical equation for light and CO_2 responses which has the property of being nearly linear through the limited phase then rapidly reaching a plateau:

$$V = \frac{C \cdot V_{\max} \cdot X}{(V_{\max}^2 + C^2 \cdot X^2)^{1/2}}, \quad (1)$$

where: V_{\max} is saturated rate of reaction for substrate X ; V is the exhibited rate of reaction; X is substrate concentration; and C is a constant.

Tenhunen et al. (1976) used a rearrangement of Eq. (1) to describe the CO_2 -saturated light response of photosynthesis:

$$P_m = \frac{\alpha \cdot I \cdot P_{ml}}{(P_{ml}^2 + \alpha^2 \cdot I^2)^{1/2}}, \quad (2)$$

where: P_{ml} is the light and CO_2 -saturated rate of photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$); α is the initial slope of the light response (mol CO_2 /mol quanta); I is PPF ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$); P_m is the CO_2 -saturated rate at a particular PPF and given temperature ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

A similar equation can be used to describe the CO_2 response:

$$F = \frac{CE \cdot C_i^* \cdot P_m}{(P_m^2 + CE^2 \cdot C_i^{*2})^{1/2}} - R_d, \quad (3)$$

where: P_m is the CO_2 -saturated rate at a given PPF ($\mu\text{mol m}^{-2} \text{s}^{-1}$); CE is initial slope of the CO_2 response ($\mu\text{mol m}^{-2} \text{s}^{-1}$); C_i^* is the difference between CO_2 concentration in the intercellular air space (C_i) and Γ^* ($\mu\text{l/l}$); Γ^* is the CO_2 compensation point at a given temperature as determined from the CO_2 response which has been corrected for R_d ($\mu\text{l/l}$); R_d is the axis correction needed to compensate for dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$); and F is the photosynthetic rate at a given temperature, CO_2 concentration, and PPF ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

In the present model we assume that R_d is not affected by PPF and represents the continued contribution of non-photosynthetic (dark) respiration in the leaf. Subtraction of R_d from measured assimilation rate, A , and of Γ^* from C_i are the only respiratory corrections in the model. By substituting Eq. (2) into Eq. (3) and rearranging, we obtain:

$$F = \frac{CE \cdot C_i^* \cdot \alpha \cdot P_{ml}}{((\alpha \cdot I \cdot P_{ml})^2 + (CE \cdot C_i^* \cdot P_{ml})^2 + (CE \cdot C_i^* \cdot \alpha \cdot I)^2)^{1/2}} - R_d, \quad (4)$$

Temperature effects on the parameters, P_{ml} , α , Γ^* , CE , and R_d can be included using either the Arrhenius equation or an equation by Johnson et al. (1954) (see discussion by Tenhunen et al. 1976). For our purposes the Arrhenius equation proved adequate.

Parameter determination

Model parameters were determined from response curves of net CO_2 exchange by two methods. When data for a complete response curve were available, the parameters were estimated from a non-linear least squares fit using

a program from the Biomedical Computer Programs package (BMDX85; Dixon 1969) to the appropriate equation after correction for dark respiration (R_d). The CO_2 response was also adjusted so that the response curve passed through the origin by subtracting Γ^* from C_i . Each fit gave estimates of the initial slopes (CE or α) and the PPF- and CO_2 -saturated rate (P_{ml}). The second method was employed for determination of the CO_2 and PPF compensation points (Γ^* and A) for data sets that had only data near saturation and near the compensation point. In this case a linear regression based on the lowest three points for the independent variable (C_i or PPF) was used to estimate the initial slope and compensation point. Maximum rates were estimated at PPF of $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$ or greater and at an external CO_2 (C_a) of approximately $2,000 \mu\text{l/l}$ for P_{ML} . Both methods gave similar results.

The diurnal course of CO_2 exchange was simulated using Eq. (4) and the Arrhenius equation for the effect of temperature on P_{ml} and R_d (see below). A linear equation was used for Γ^* . Parameters were estimated, as described above, from independent sets of field and laboratory data. Input variables for simulation of field responses were PPF, chamber CO_2 , leaf temperature, and leaf conductance to water vapor.

Results

Response curves

In order to estimate the seasonal variability of photosynthesis in *A. saccharum*, several response curves of net photosynthesis to PPF for plants in the natural habitat were measured throughout the growing season at concentrations of CO_2 between 300 and 350 $\mu\text{l/l}$ and 21% O_2 . Under these conditions the apparent incident quantum efficiency, α (atm), and the PPF-saturated photosynthetic rate, A_m (atm), were determined as the initial slope and maximum of each response curve, respectively. It should be noted that α (atm) is less than α (Table 1) because the latter is measured under non-photorespiratory conditions whereas the former is not. For responses obtained between 20 and 25° C, neither α (atm) nor A_m (atm) changed significantly between the end of May, when the leaves had just completed expansion, and the end of the growing season in September (Table 1A). The decrease in the light compensation point (A) was likely related to a decrease in respiration of the leaves. It seems that the production system in *A. saccharum* leaves is relatively stable for long periods allowing the application over most of the growing season of a photosynthetic model developed for such leaves. A similar situation was found for mature apricot leaves (Tenhunen et al. 1980).

The parameter values obtained from analysis of net photosynthetic response curves obtained in the field and in the laboratory are summarized in Table 1. The maximum quantum efficiency (α) was determined as the initial slope of the response of A to incident PPF under non-photorespiring conditions, i.e., at high CO_2 concentration (Fig. 1, bottom). At 25° C the value obtained for α was 0.05–0.08 mol CO_2 /mol quanta. From the response of A to C_i (Fig. 1, top) a value of CE (initial slope of the response) at 25° C of $0.019 \mu\text{mol m}^{-2} \text{s}^{-1}/(\mu\text{l/l})$ was found. The saturated rates of both response curves, which were 6.89 and $7.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, provide estimates of P_{ml} for 25° C.

Table 1. PPFD and CO₂ response characteristics as determined in the field and in the laboratory. A. The initial slope (α (atm)), PPFD compensation point (A), and PPFD-saturated rate at approximately 350 $\mu\text{l/l}$ CO₂ and 21% O₂ (A_m (atm)). B. Initial slopes for CO₂ (CE) response at saturating PPFD and for PPFD response (α) at saturating CO₂ and the CO₂- and PPFD-saturated rate as measured at 25 C and 21% O₂. C. Activation energies for P_{m1} and R_d

A. Field response, atmospheric gas concentrations, 20–25° C

Dates	α (atm) mol/mol	A_m (atm) $\mu\text{mol m}^{-2} \text{s}^{-1}$	A $\mu\text{mol m}^{-2} \text{s}^{-1}$	N
26–31 May	0.038 ± 0.002	3.4 ± 0.3	6.8 ± 1.7	5
1–24 June	0.039 ± 0.004	3.5 ± 0.7	5.3 ± 1.0	6
6 Aug.–17 Sep.	0.040 ± 0.003	3.8 ± 0.5	3.2 ± 3.3	5

B. Response characteristics at 25° C and saturating CO₂ and PPFD

	CE $\mu\text{mol m}^{-2} \text{s}^{-1}/\mu\text{l/l}$	α mol/mol	P_{m1} $\mu\text{mol m}^{-2} \text{s}^{-1}$
Field	0.018	0.05–0.08	6.3–7.5
Laboratory	0.018	0.06 ± 0.01	7.0–9.0

C. Temperature responses

Parameter	kJoule/mol	Constant
Arrhenius equation		
P_{m1}	28	13.02
R_d	42	14.76
CO ₂ Compensation point		
$\Gamma^* = (4.0 * T_1 + 34.4) * \text{Atm. Press}/(T_1 + 273.16)$		

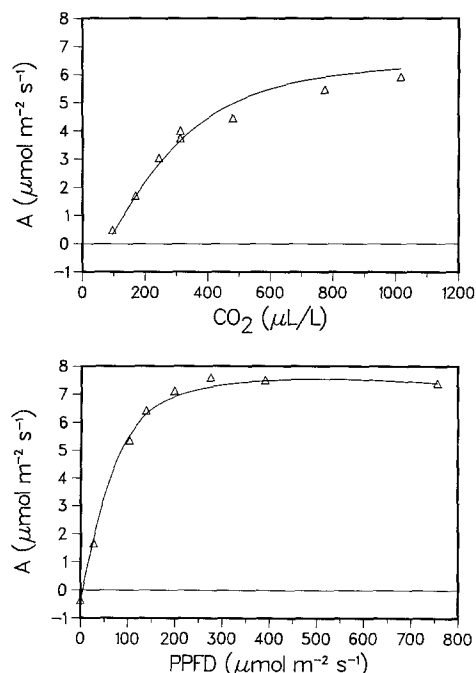


Fig. 1. Top. Photosynthetic response to CO₂ at saturating PPFD ($1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$). $P_{m1} = 6.89 \mu\text{mol m}^{-2} \text{s}^{-1}$. CE = $0.019 \mu\text{mol m}^{-2} \text{s}^{-1}/(\mu\text{l/l})$. $\Gamma^* = 66 \mu\text{l/l}$. Bottom. Photosynthetic response to PPFD at saturating CO₂ ($C_a = 2,000 \mu\text{l/l}$) and 25° C. $P_{m1} = 7.5 \mu\text{mol m}^{-2} \text{s}^{-1}$. $\alpha = 0.08 \text{ mol/mol}$. $R_d = 0.35 \mu\text{mol m}^{-2} \text{s}^{-1}$. Measurements made in the field

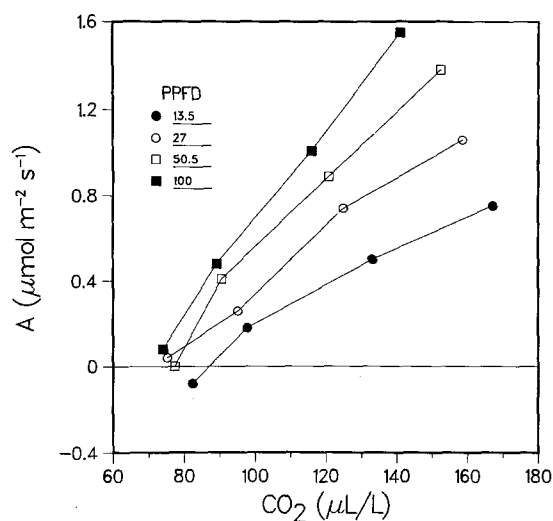


Fig. 2. The effect of variation of PPFD on the initial slope of the CO₂ response. T_1 : 25° C. Laboratory data

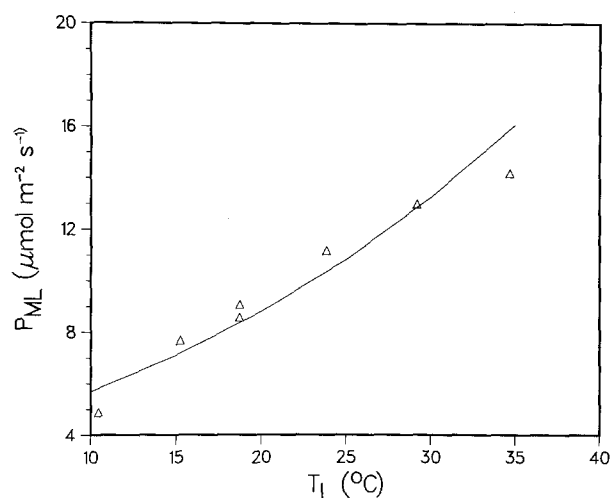


Fig. 3. The effect of leaf temperature (T_1) on the CO₂- and PPFD-saturated photosynthetic rate (P_{m1}). $C_a = 1,900 \mu\text{l/l}$. PPFD = $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$. Activation energy = 28 kJoule/mol. Constant = 13.02. Laboratory data

In order to clarify temperature dependencies of the parameters, detailed laboratory investigations were undertaken. In these experiments, the five parameters – α , Γ^* , CE, R_d , and P_{m1} – were determined for each replicate leaf. An average value for α of $0.058 \pm 0.0011 \text{ mol CO}_2/\text{mol quanta}$ was obtained. The light compensation point (A) was estimated as $3.4 \pm 1.6 \mu\text{mol m}^{-2} \text{s}^{-1}$. There was no detectable effect of temperature on either α or A over the temperature range of interest.

Analysis of the response of net photosynthesis to CO₂ concentration showed that CE was not significantly affected by temperature between 18 and 28° C, the temperature range of interest in the natural habitat. We did find, however, that CE was affected by PPFD (Fig. 2) when determined between 80 and 160 $\mu\text{l/l}$ C_i . The decrease of the slope (CE) with decreasing PPFD is quite important because leaves of *A. saccharum* seedlings experience PPFD in the range which was found to influence CE during most of the day. The CO₂ compensation point (Γ^*) increased with temperature being 38 $\mu\text{l/l}$ at 20° C and 44 at 25° C.

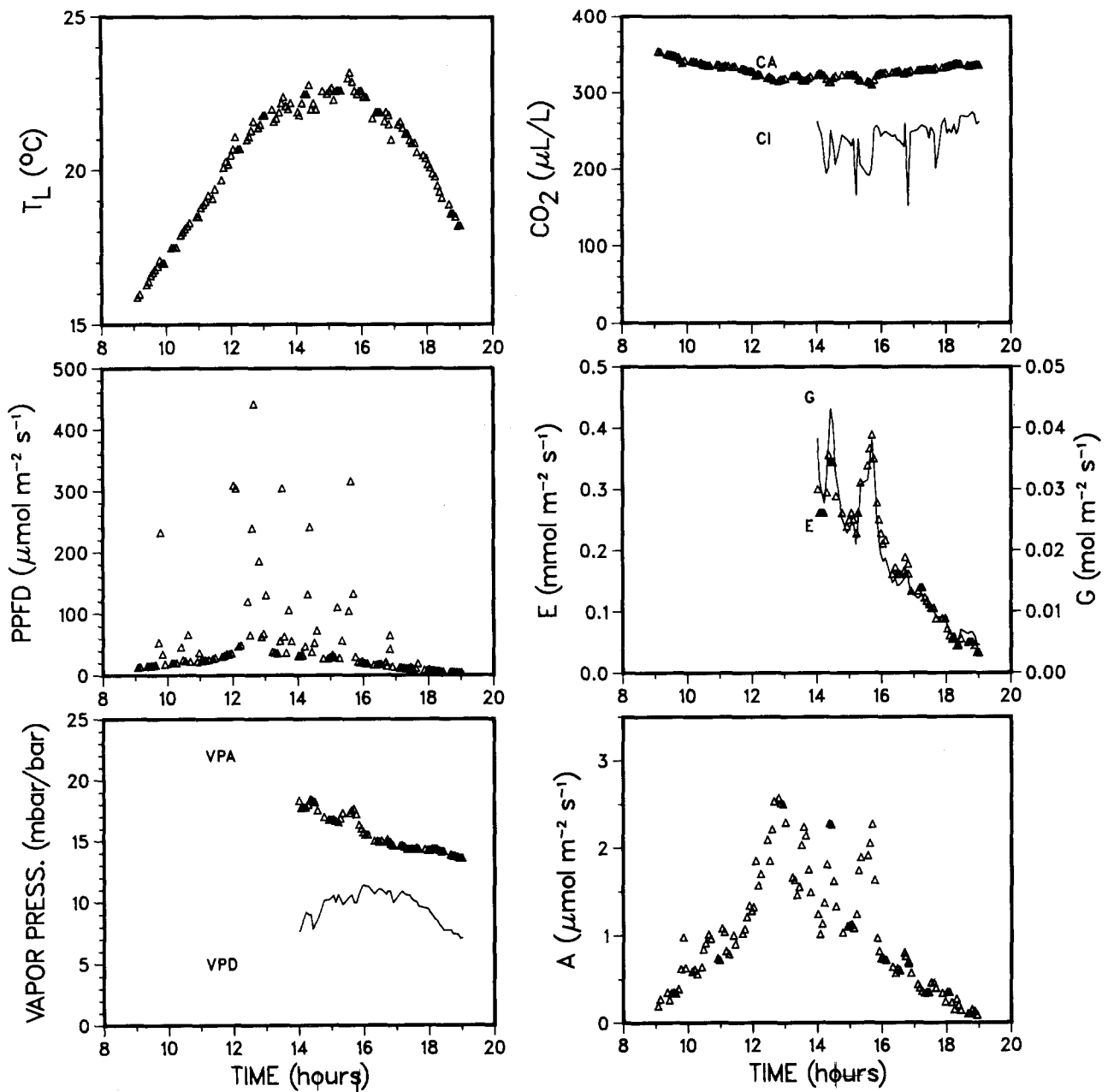


Fig. 4. Diurnal course of photosynthesis A , transpiration E , leaf conductance to water vapor G , and environmental factors for 12 Sept 1981. Condensation in the leaf chamber interfered with transpiration measurements until about 14:00

The rate of photosynthesis at saturating PPFD and CO_2 concentration, P_{m1} , was strongly affected by leaf temperature (Fig. 3). Since leaf temperatures measured in the natural habitat were below 25°C and, therefore below the temperature optimum for P_{m1} , the data were fit to the Arrhenius equation. The activation energy for P_{m1} was approximately 28 kJ/mol . Dark respiration, R_d , measured in the field measurements and in the laboratory was quite low. At 25°C R_d was approximately $0.2\ \mu\text{mol m}^{-2}\text{ s}^{-1}$. The activation energy was estimated at 42 kJ/mol .

Time course of gas exchange in the field

Time courses for PPFD, leaf temperature (T_l), water vapor pressure in the air (VPA) and the vapor pressure difference

between the leaf and air (VPD), CO_2 pressure in the chamber (C_a) and in the leaf (C_i), transpiration rate (E), net photosynthetic rate (A), and leaf conductance to water vapor (G) are shown in Figs. 4 and 5 for leaves of *A. saccharum* measured on 12 and 13 September 1981. It is apparent from the figures that of the environmental factors shown, PPFD shows the greatest variation, changing 5 to 10 fold within minutes. The peaks in PPFD occur as the solar beam reaches the forest floor through breaks in the canopy. Net photosynthetic rate is positively correlated with T_l , PPFD, VPA, and G , but negatively correlated with C_a (Table 2). The negative correlation of A with C_a is the result of a decrease in CO_2 concentration in the incoming air during the middle of the day when A was the highest. Ignoring temperature and conductance effects on A and

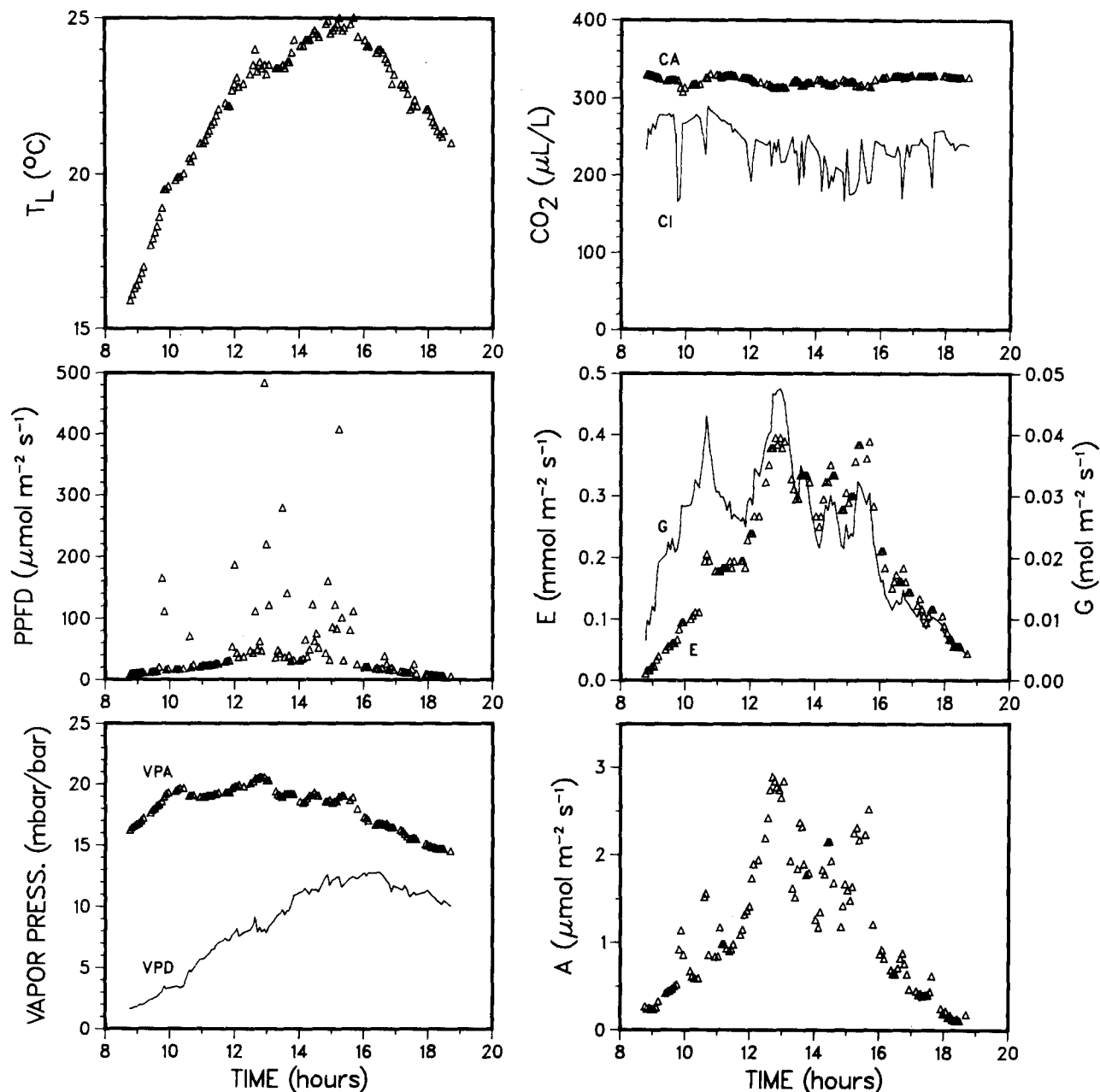


Fig. 5. Diurnal course of photosynthesis A , transpiration E , leaf conductance to water vapor G , and environmental factors for 13 Sept 1981

fitting the data to Eq. (2) with non-linear regression techniques, variation in PPFD alone can account for 70% of the variation in A (Fig. 6).

On both days, 15 distinct peaks in PPFD occur. Associated with these peaks in PPFD are maxima in A although the maxima in A are delayed by 5 to 10 min. The lag in the response is caused by the low flow rate through the system. In addition the maxima in A are much broader (extended over a much longer period) for two reasons. First, the low flow rate and large volume of the chamber increases mixing time of the gas in the chamber. Second, the sensing area of the quantum sensor and the area of the leaf did not coincide and were of different sizes (0.78 cm^2 and $30\text{--}50 \text{ cm}^2$, respectively) so that there may have been a difference between actual incident on the leaf and measured PPFD.

The apparent quantum efficiency for incident PPFD at

normal CO_2 and O_2 concentrations (α (atm)), A divided by incident PPFD estimated for each measurement point obtained at low PPFD (diffuse light below $50 \mu\text{mol m}^{-2} \text{ s}^{-1}$), was about $0.04 \text{ mol CO}_2/\text{mol quanta}$. Comparing this apparent quantum efficiency with that obtained from light response curves (Table 1A), it is evident that the leaves were operating at near maximum quantum efficiency for the CO_2 and O_2 concentrations experienced in the field. More than 75% of the time PPFD remains at less than $50 \mu\text{mol m}^{-2} \text{ s}^{-1}$, and during these periods 60% of the total CO_2 fixation takes place (Table 3). At PPFD greater than $50 \mu\text{mol m}^{-2} \text{ s}^{-1}$ the apparent quantum efficiency, calculated as A divided by I , decreased as expected.

Stomatal conductance (G) was positively correlated with PPFD, T_L , and VPA; and negatively with VPD and C_a (Table 2). Statistical selection methods indicated that 90%

Table 2. Correlation table for photosynthesis and conductance with environmental factors using data from the daily time course measurements

Environmental factors	A		G	
	12 Sept.	13 Sept.	12 Sept.	13 Sept.
T_l	0.77**	0.59**	0.78**	0.25**
VPA	0.92**	0.78**	0.98**	0.94**
VPD	0.17	0.24*	0.11	-0.20*
I	0.71**	0.54**	0.59**	0.42**
C_a	-0.96**	-0.75**	-0.93**	-0.68**
G_a	0.94**	0.84**	-	-
N	51	89	51	89

* Significant at $P=0.05$

** Significant at $P=0.01$

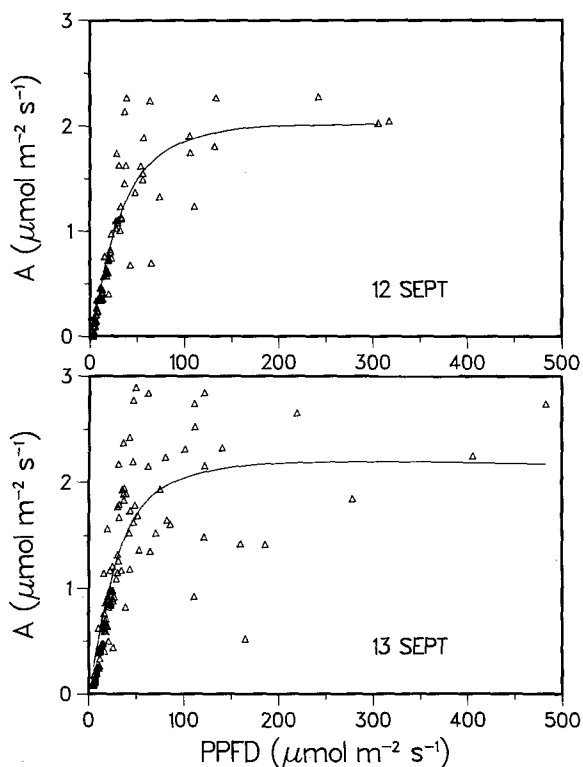


Fig. 6. Photosynthesis rates of daily time course data plotted as a function of PPFD. Solid line in each Fig is the regression line for Eq. (2). A. A_M (atm) = $2.04 \mu\text{mol m}^{-2} \text{s}^{-1}$. α (atm) = 0.0442 mol/mol . B. A^M (atm) = $2.22 \mu\text{mol m}^{-2} \text{s}^{-1}$. α (atm) = 0.0519 mol/mol

of the variation in stomatal conductance could be accounted for by a multiple linear regression on T_l , C_a , and VPD. Ball and Berry (1982) have proposed that stomatal conductance is regulated such that the ratio C_i/C_s , where C_s is the CO_2 concentration at the leaf surface, is maintained constant. Since all measurements were made at constant wind velocity, and therefore constant boundary layer conductance, the ratio C_i/C_a should also be constant. There is a general tendency for this ratio to be between 0.7 and 0.8 (Fig. 7). This value is approached slowly during the morning and is disturbed during sunflecks.

At low PPFD the transpiration ratio (E/A) is approximately $200 \text{ mol H}_2\text{O/mol CO}_2$ (Fig. 8). At higher PPFD

Table 3. Analysis of the photosynthetic response during daily time course on 13 September 1981 according to PPFD categories. Numbers in parentheses are percentages of total

	PPFD category ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				
	0-25	26-50	51-75	76-100	>100
Photon flux mol/m ²	0.262	0.379	0.118	0.120	0.761
%	(16.0)	(23.1)	(7.2)	(7.3)	(46.4)
Measured A mmol/m ²	9.67	16.82	3.30	2.90	8.02
%	(23.8)	(41.2)	(8.1)	(7.1)	(19.7)
Simulated A mmol/m ²	11.41	15.23	4.12	3.16	9.51
%	(27.3)	(35.1)	(9.5)	(7.3)	(21.9)
Time sec	17,856	10,548	1,872	1,476	3,996
%	(48.9)	(29.5)	(5.2)	(4.1)	(11.2)
Measured α (atm)	0.037	0.044	0.028	0.024	0.011
Simulated α (atm)	0.044	0.040	0.035	0.026	0.012

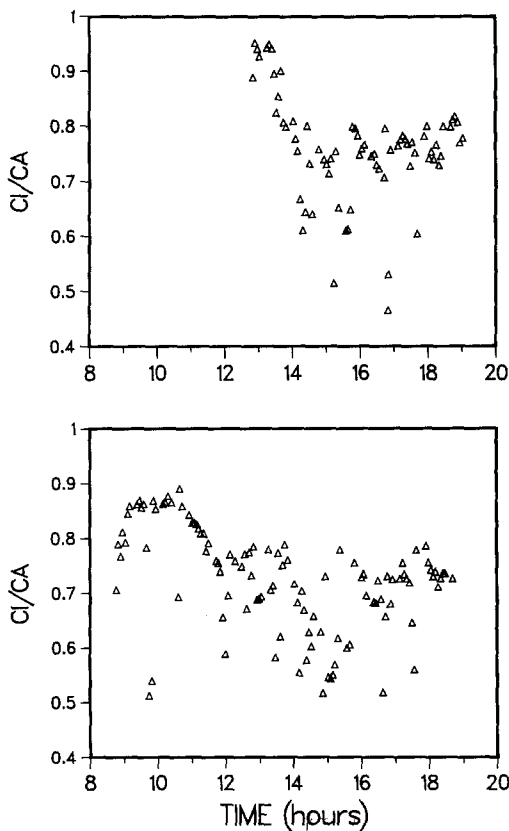


Fig. 7. Variation of C_i/C_a throughout the day. Top: 12 September. Bottom: 13 September

the leaves use water more effectively and E/A declines to approximately 140. In part this effective water use may result from sluggish reaction of stomata to increased PPFD during sunflecks, whereas A increases quickly and draws C_i down (Fig. 7). There is a strong correlation between A and G (Fig. 8), except for data obtained during the early

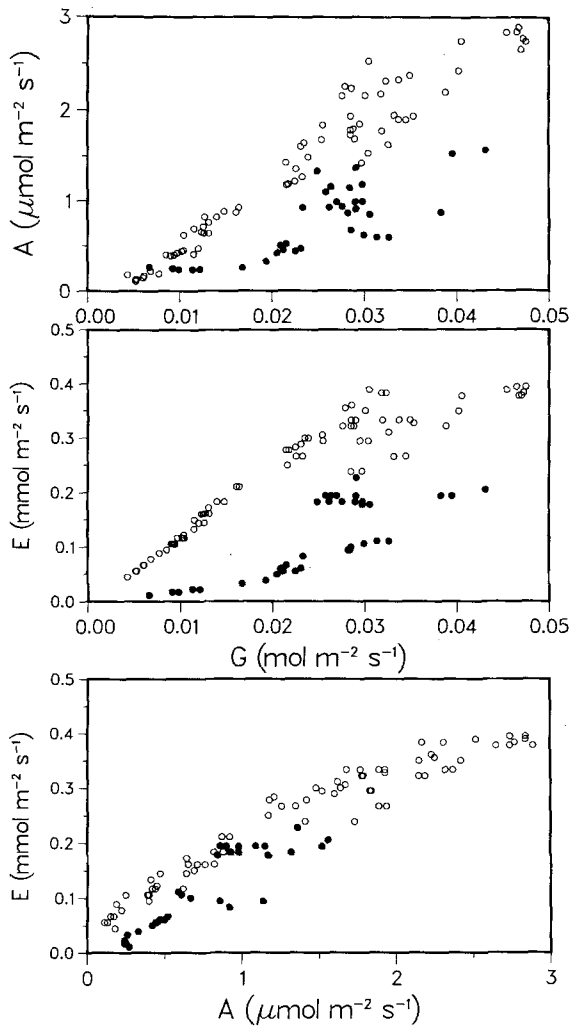


Fig. 8. Relationship of leaf conductance G to transpiration E , top, and photosynthesis A , middle. Relationship between transpiration E and photosynthesis A , bottom. Daily time course data for 13 September 1981. Solid symbols represent data taken in the morning

morning period. During the early morning when VPA is high, stomata open rapidly and photosynthesis increases relatively slowly due to low T_l and low PPFD. In the afternoon, when VPA is lower and VPD is substantial, water use is more effectively regulated. In this situation, G and A decrease simultaneously.

Integrating over 24 h periods, we obtain a net carbon gain of 32.1 mol m^{-2} on 12 September and 38.9 mol m^{-2} on 13 September, an average of 35.5 mol m^{-2} . If this average carbon gain occurs over a 120 day growing season, the estimated total carbon gain for the season would be $4.3 \text{ mol CO}_2 \text{ m}^{-2}$ or $0.72 \text{ mol glucose m}^{-2}$. Maintenance respiration costs of leaves are included in this estimate. An estimate of the amount of glucose needed to produce new leaves in the following growing season may be obtained by multiplying specific leaf weight ($25\text{--}30 \text{ g m}^{-2}$) by the conversion factor for synthesis of leaf material from glucose determined by Penning de Vries (1974; $1.5 \text{ g glucose/g tissue}$). It is assumed that NO_3^- and SO_4^{2-} are the sources of nitrogen and sulfur. We calculate that $0.2\text{--}0.23 \text{ mol}$ glucose are required to produce 1 m^2 leaf, which is approximately 30% of the carbon gained.

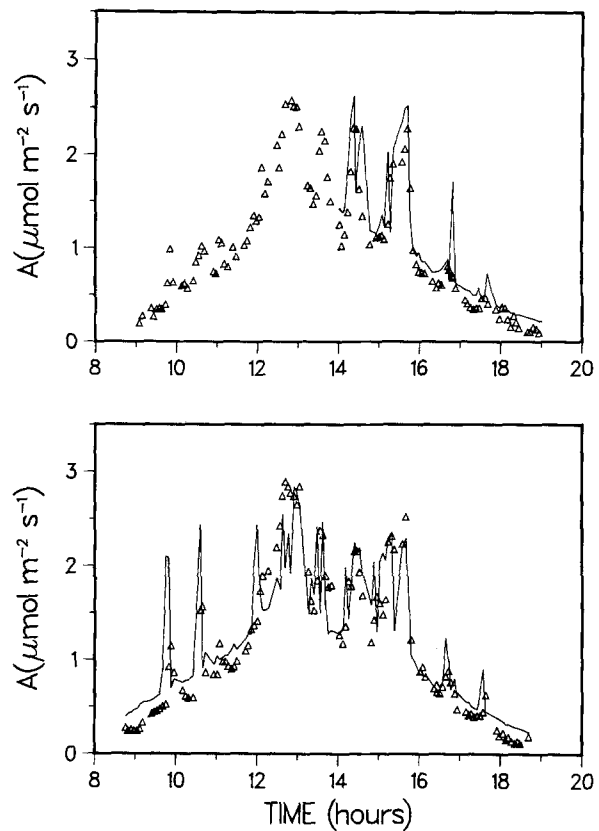


Fig. 9. Comparison of measured (symbols) and simulated (solid line) daily time course of photosynthesis for 12 Sept (top) and 13 Sept (bottom). Parameter values in Table 1 B and C

Simulation of the time course of A

Equation (4) and parameter values given in Table 1 were used to simulate the measured A (Fig. 9). We do not test extensively the model or describe detailed applications. The purpose here is to demonstrate how laboratory determination of parameters may be related meaningfully to the leaf response under fluctuating environmental conditions, to examine whether such a model reproduces the general behavior of the leaves, and to identify problems specific to modeling of gas exchange in the shade environment of the forest floor. More detailed studies with the model, including examination of water use efficiency, will be described later.

Equation (4) was used to calculate a simulated value for net CO_2 exchange (F) at each point where valid measurements had been obtained for PPFD, T_l , C_a , and G . The parameters P_m and R_d were considered to vary with T_l according to the Arrhenius equation; I^* varied with T_l over the temperature of interest (Table 1). The parameter CE was treated as as function of PPFD

$$\text{CE} = \min \begin{cases} I \cdot 0.0003 \\ \text{CEM} \end{cases} \quad (5)$$

where: CEM is the PPFD-saturated carboxylation efficiency, and $\min \{$ means the minimum value is chosen.

The increase in CE with I at low PPFD ($0.0003 \mu\text{mol CO}_2/(\mu\text{l/l})/\mu\text{mol quanta}$) was estimated from several data sets similar to that shown in Fig. 2. Equation (5) was used because preliminary data indicate that CE as measured here rises rapidly with increasing PPFD then rapidly saturates. The value for α was held constant at $0.06 \text{ mol CO}_2/\text{mol}$

quanta. Internal CO₂ concentration, C_i , was obtained iteratively.

The general pattern of F is similar to A but the simulation is characterized by a series of extremely sharp peaks where measurements indicate broad ones (Fig. 9). Rapid light fluctuations cause overestimation and underestimation of the measured chamber rate by the calculated rate because mixing in the chamber tends to dampen the oscillations in A produced by rapid changes in PPFD. Integrated F is 107% of integrated A for 13 September, and 122% of the portion of the day simulated for 12 September.

Discussion

The results obtained in this study are in many ways similar to those obtained by Björkman et al. (1972) with *Alocasia macrorrhiza* and *Cordyline rubra* growing on the floor of a rainforest in Queensland, Australia and by Pearcy and Calkin (1983) with *Claoxylon sandwicense* in Hawaii. In contrast, however, direct and diffuse radiation fluxes were approximately one order of magnitude greater on the floor of this mixed hardwood forest. In addition greater change in C_a and VPA occurred. Compared to the rainforest species, *Acer saccharum* had a specific leaf weight approximately the same, A_m (atm) was about the same, average A during the day was about 3 times greater, and apparent maximum quantum efficiency α (atm) was lower (0.04 mol/mol compared to 0.05 for *C. sandwicense* and 0.07 for *A. macrorrhiza*). As in the studies of Björkman et al. (1972) and Pearcy and Calkin (1983) the pattern observed in the daily time course of A was primarily determined by available PPFD. Stomata were seen to respond to large changes in PPFD during sunflecks but much less than did photosynthesis.

Approximately 45–55% of the total photon flux occurred during periods of high PPFD ($> 100 \mu\text{mol m}^{-2} \text{s}^{-1}$), while 35–40% occurred during the low PPFD ($> 50 \mu\text{mol m}^{-2} \text{s}^{-1}$) periods (Table 3). Net carbon gain during high PPFD was 20–30% of the total, whereas 55–65% of the carbon was fixed during low PPFD. While it seems clear that sunflecks provide an important contribution to productivity of maple seedlings on the forest floor as has been concluded in other studies (Björkman et al. 1972; Young and Smith 1983), it is necessary to compare the photosynthate accumulated with and without the additional input from sunflecks. To this end we calculated the net CO₂ exchange assuming that PPFD's for the high PPFD period were in the range indicated in category 2 or 3 (Table 3). With only diffuse light (PPFD $< 50 \mu\text{mol m}^{-2} \text{s}^{-1}$) the reduction in net CO₂ fixation is about 5%. Estimates using the model are a reduction of 12% at most. A similar estimate for the data on A of *A. macrorrhiza* obtained by Björkman et al. (1972) suggests that total carbon gain would be reduced by 10% if there were no sunflecks. This result is apparently caused coincidentally by differences in length of time spent at various PPFD's and by the low PPFD required to saturate photosynthesis in *A. saccharum*. With similar lengths of time during sunflecks *A. macrorrhiza* would be expected to utilize the period more efficiently than *A. saccharum* because *A. macrorrhiza* has 1) a greater quantum efficiency, and 2) a greater stomatal conductance.

In spite of significant problems confronted in assessing average PPFD (see also Pearcy 1983) it was possible to simulate mathematically A as a function of PPFD, T_1 , G , and C_a . Parameter estimates were obtained from single fac-

tor response curves in the laboratory and in the field. Favorable comparison of F with A suggests that the approach taken here should be further pursued in order to develop methods which will aid in linking laboratory studies to response under natural conditions. The importance of the interaction between CO₂ and PPFD is indicated by the decrease in CE, assessed between 80 and 160 $\mu\text{l/l } C_i$, with decreasing PPFD (Fig. 2). While previous studies have shown the interaction (Ludlow and Wilson 1971; Ku et al. 1977), relatively little work has been directed toward accurately describing this interaction. A dependency of CE on PPFD is an absolutely essential component of any mathematical model intended to simulate gas exchange of *A. saccharum* shade leaves. Further experimentation suggests that the same conclusion may be drawn for any leaves growing under shade conditions, and it appears to us that correct description of the PPFD dependency of CE will be extremely important in description of canopy function. While CE is a function of C_i at which its value is estimated, at least in *A. saccharum* we feel that CE is influenced as well by actual metabolic components. As PPFD decreases, RuBP production decreases, leading to decreased steady-state levels (Collatz 1972; Sharkey 1983; Jensen et al. 1983). The activation state of RuBP carboxylase also changes, with less activation occurring at low PPFD (Perchorowicz et al. 1981; Jensen et al. 1983). Either change could be involved in the dependence of CE on PPFD.

During the growing season, the potential rates of carbon fixation of *A. saccharum* leaves remain quite constant. It appears relatively safe to make an initial estimate of the total seasonal carbon gain by the methods indicated in the results section. We conclude that after supplying maintenance respiration and reserving adequate carbon to reconstruct new leaves during the following growing season, *A. saccharum* leaves provide substantial amounts of carbon for maintenance respiration of stems and roots and for storage (70% of seasonal fixation). Further studies are planned to examine the ways in which this carbon pool is utilized over the annual cycle.

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