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Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parametrization

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ABSTRACT

In order to parametrize a leaf submodel of a canopy level gas-exchange model, a series of photosynthesis and stomatal conductance measurements were made on leaves of white oak (*Quercus alba* L.) and red maple (*Acer rubrum* L.) in a mature deciduous forest near Oak Ridge, TN. Gas-exchange characteristics of sun leaves growing at the top of a 30 m canopy and of shade leaves growing at a depth of 3–4 m from the top of the canopy were determined. Measured rates of net photosynthesis at a leaf temperature of 30 °C and saturating photosynthetic photon flux density, expressed on a leaf area basis, were significantly lower ($P = 0{\cdot}01$; $n = 8$) in shade leaves (7·9 μmol m^{-2} s^{-1}) than in sun leaves (11·5 μmol m^{-2} s^{-1}). Specific leaf area increased significantly with depth in the canopy, and when photosynthesis rates were expressed on a dry mass basis, they were not significantly different for shade and sun leaves. The percentage leaf nitrogen did not vary significantly with height in the canopy; thus, rates expressed on a per unit nitrogen basis were also not significantly different in shade and sun leaves. A widely used model integrating photosynthesis and stomatal conductance was parametrized independently for sun and shade leaves, enabling us to model successfully diurnal variations in photosynthesis and evapotranspiration of both classes of leaves. Key photosynthesis model parameters were found to scale with leaf nitrogen levels. The leaf model parametrizations were then incorporated into a canopy-scale gas-exchange model that is discussed and tested in a companion paper (Baldocchi & Harley 1995, *Plant, Cell and Environment* 18, 1157–1173).

Key-words: Quercus alba L.; Fagaceae; modelling; photosynthesis; scaling; stomatal conductance; white oak.

INTRODUCTION

Simulation models are important tools for integrating physiological information across scales of organization. Particularly in the context of global change, in which plant communities will be subject to hitherto unfamiliar combinations of environmental inputs, the empirical data base is necessarily small and predictions of responses at whole-plant and ecosystem scales will increasingly rely on simulation models of the system in question. Although in the later stages of model development, when system behaviour is better understood, it may be desirable to simplify certain aspects of the overall model, we believe that in the initial stages it is beneficial to incorporate a considerable amount of mechanistic detail, particularly when a large empirical data base does not exist and where models are used to make predictions outside the range of empirical measurements.

At the level of the individual C_3 leaf, the model first proposed by Farquhar, von Caemmerer & Berry (1980) and subsequently modified (Farquhar & von Caemmerer 1982; Sharkey 1985; Collatz *et al.* 1991) enjoys general acceptance. It has been widely used to interpret leaf-scale photosynthesis data, and has been used successfully in canopy scaling schemes (Leuning 1990; Caldwell *et al.* 1986). Although there has been considerable research on gas exchange of deciduous temperate forest species, we found no information sufficiently detailed to allow rigorous parametrization of both the Farquhar photosynthesis model and an accompanying model of stomatal conductance (Ball, Woodrow & Berry 1987).

During the summer of 1992, therefore, we conducted a comprehensive physiological/micrometeorological study of the carbon and water vapour exchange of a temperate, broadleaf deciduous forest. In this paper, we describe leaf-scale measurements and parametrization of the leaf gas-exchange model for leaves of white oak (*Quercus alba* L.) and red maple (*Acer rubrum* L.). Of particular interest were the effect of canopy position and light environment on leaf physiological properties, and ways to incorporate such information into leaf- and canopy-scale models.

In a companion paper (Baldocchi & Harley 1995, this issue) we incorporate these leaf-scale data and model parameters into a canopy gas-exchange model and test our ability to scale CO_2 and water vapour fluxes from leaves to canopy by comparing model predictions with canopy-scale measurements made using micrometeorological techniques.

METHODS

Site

Physiological and micrometeorological measurements

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were made in a mixed deciduous forest dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.) and maples (*Acer* spp.). The field site was located on the United States Department of Energy reservation near Oak Ridge, TN (latitude 35°57'30"N; longitude 84°17'15"W; elevation 365 m above sea level). The canopy height was *c.* 30 m, and a 44 m walk-up tower provided access to leaves of white oak and red maple at both the canopy top and depth of *c.* 3–4 m from the top of the canopy where leaves were significantly shaded.

EXPERIMENTAL METHODS

Rates of leaf photosynthesis and transpiration were measured using a commercially available open-path gas-exchange system (MPH-1000, Campbell Scientific, Logan, UT), consisting of a temperature-controlled, fan-stirred cuvette attached to a measurement and control system. Air of specified water vapour and CO_2 concentrations was generated using mass flow controllers (Model 825, Edwards High Vacuum International, Wilmington, MA) and passed to the cuvette. The flow rate of gas entering the cuvette was measured using a mass flow meter (Model 831, Edwards), water vapour concentrations before and after the cuvette were measured using two chilled-mirror hygrometers (General Eastern, Watertown, MA), and the CO_2 exchanged by the leaf was measured using an infrared gas analyser (LI-6251, Li-Cor Inc., Lincoln, NE) in differential mode.

Except when natural light was used, light was provided using a portable system consisting of a quartz halogen bulb (ELH 120V-300W, General Electric, Cleveland, OH) mounted in a slide projector lamp holder and directed at a Tempax cold mirror (Optical Coating Labs Inc., Santa Rosa, CA) mounted at a 45° angle to reflect visible light onto the cuvette. Neutral density filters of blackened window screen were inserted in the light path to vary the intensity. Photosynthetic photon flux density (PPFD) was measured using a gallium arsenide photodiode which had been calibrated against a quantum sensor (LI-190SA, Li-Cor Inc.) and placed at leaf height inside the cuvette. The area of leaf within the cuvette was traced onto cardboard and subsequently measured using a leaf area meter (CID, Moscow, ID). All measured leaves were collected, oven-dried at 60°C for 48 h, and weighed. Leaves were accessible from the tower at only two heights, at the canopy top and 3–4 m down. Only fully expanded leaves were measured.

Calculations of net photosynthetic rate, transpiration, stomatal conductance and internal CO_2 partial pressure were made using the equations of von Caemmerer & Farquhar (1981). For the purpose of parametrizing the leaf gas-exchange model (see Harley & Tenhunen 1991), extensive measurements of net photosynthesis and conductance were made on leaves of white oak at the canopy top and within the canopy. Measurements were made to determine the effect of varying PPFD over a range of leaf temperatures, the effect of varying temperature at saturating PPFD, and the effect of varying intercellular CO_2 concentration at 30°C and saturating PPFD. In addition, the relationship between leaf gas exchange and intercellular CO_2 concentration at 30°C and saturating PPFD was determined for two leaves of red maple at different levels within the canopy, and a single leaf at the canopy top.

Leaf gas-exchange model

We employ the integrated leaf biochemistry/stomatal conductance model discussed above, in the form presented in Harley *et al.* (1992) with the following slight changes in the functions used to describe the temperature dependences of parameters. The shape of the functions remains identical, but certain parameters which were difficult to interpret (e.g. dimensionless scaling factors and entropy terms) are replaced. The photosynthesis model employs seven major parameters (Table 1), six of which are dependent on temperature. K_c and K_o, Michaelis-Menten constants for carboxylation and oxygenation, respectively, τ, the specificity factor for Rubisco, and R_d, the rate of CO_2 evolution in the light by processes other than photorespiration, are described by an exponential temperature function,

$$f(T_k) = f(298) \exp\left[\frac{(T_k - 298)\, H_a}{\mathbf{R}\, T_k\, 298}\right], \quad (1)$$

where $f(T_k)$ is the value of a given parameter at leaf temperature T_k (K), f(298) is the value of that parameter at 25°C, **R** is the gas constant (0·00831 kJ mol^{-1}) and H_a is the activation energy for that parameter (kJ mol^{-1}).

Two parameters, V_{cmax} and J_{max}, the maximum rates of carboxylation and electron transport, respectively, are described by

$$f(T_k) = f(\text{opt}) \frac{H_d \exp\{(H_a/\mathbf{R})\,[(1/T_{opt}) - (1/T_k)]\}}{H_d - H_a\,[1 - \exp\{(H_a/\mathbf{R})\,[(1/T_{opt}) - (1/T_k)]\}]}, \quad (2)$$

where f(opt) is the value of the parameter at its temperature optimum (T_{opt}; K) and H_d is the energy of deactivation for that parameter (kJ mol^{-1}).

Stomatal conductance to water vapour (g_s) is modelled after Ball *et al.* (1987), with slight modifications; namely, relative humidity (h) and CO_2 partial pressure outside rather than inside the leaf boundary layer (C_a) are used to drive the model, as noted in Harley *et al.* (1992). Thus

$$g_s = g_0 + g_1 A \frac{h}{C_a}, \quad (3)$$

where g_0 is the minimum stomatal conductance to H_2O vapour when A=0 at the PPFD compensation point, and g_1 is an empirical coefficient which represents the composite sensitivity of conductance to assimilation, pCO_2, humidity and temperature.

The partial pressure of CO_2 in the intercellular air space (C_i), which is used to drive the biochemical model, results from the interaction of A and g_s, according to the familiar Fick's Law relationship

$$C_i = C_a - \frac{1{\cdot}6\, A}{g_s}, \quad (4)$$

where the factor 1.6 corrects for the difference in diffusiv-

Parameter	Units	Temperature Parameters	Sun leaves	Shade leaves	Units
K_c	Pa CO_2	$K_c(25°)$	(27·5)		Pa
		$H_a(K_c)$	(80·5)		kJ mol^{-1}
K_o	kPa O_2	$K_o(25°)$	(42·0)		kPa
		$H_a(K_o)$	(14·5)		kJ mol^{-1}
τ	—	$\tau(25°)$	(2321·0)		—
		$H_a(\tau)$	(–29.0)		kJ mol^{-1}
R_d	$\frac{\mu mol\ CO_2}{m^2\ s}$	$R_d(25°)$	0.34	0.42	$\mu mol\ m^{-2}\ s^{-1}$
		$H_a(R_d)$	38.7	38.7	kJ mol^{-1}
V_{cmax}	$\frac{\mu mol\ CO_2}{m^2\ s}$	$T_{opt}(V_{cmax})$	(311)	(311)	K
		$V_{cmax}(T_{opt})$	73.0	52.0	$\mu mol\ m^{-2}\ s^{-1}$
		$H_a(V_{cmax})$	55.0	55.0	kJ mol^{-1}
		$H_d(V_{cmax})$	(200)	(200)	kJ mol^{-1}
J_{max}	$\frac{\mu mol\ electrons}{m^2\ s}$	$T_{opt}(J_{max})$	(311)	(311)	K
		$J_{max}(T_{opt})$	170.0	115.0	$\mu mol\ m^{-2}\ s^{-1}$
		$H_a(J_{max})$	48.0	48.0	kJ mol^{-1}
		$H_d(J_{max})$	(200)	(200)	kJ mol^{-1}
α	$\frac{mol\ electrons}{mol\ photons}$	—	0.20	0.24	—
g_0	mmol $H_2O\ m^{-2}\ s^{-1}$	—	17.5	17.5	—
g_1	$\frac{mmol\ H_2O\ Pa\ CO_2}{\mu mol\ CO_2}$	—	9·50	9·50	—

Table 1. List of model parameters and the parameters used to describe their temperature dependence. Values in parentheses are held constant in this version of the model; all other values have been determined from measured data as described in the text

ity between CO_2 and H_2O. Because A and g_s are not independent, the value of C_i must be determined in an iterative fashion.

RESULTS

Experimental data

Despite the fact that leaf morphology and physiology are likely to change in a continuous manner with reductions in growth PPFD with depth in a tree canopy (Sellers *et al.* 1992), the discrete terms 'sun' and 'shade' leaves will be employed here to distinguish between leaves growing at the top of the canopy and those found at a depth of 3–4 m from the top of the canopy. Although no systematic study of the light environment within the canopy was conducted, a comparison of PPFD measurements made above and 3–4 m within the canopy between 1000 and 1500 h on two successive clear days indicated that the average PPFD within the canopy was between 10 and 15% of that above the canopy. That the two groups of leaves were morphologically distinct was shown by large differences in specific leaf area (SLA; area/mass). SLA of shade leaves within the canopy averaged $0·0134 \pm 0·0004$ $m^2\ g^{-1}$ ($n=8$; range: 0·0110–0·0147), while that of sun leaves at the canopy top averaged $0·0090 \pm 0·0002$ $m^2\ g^{-1}$ ($n=8$; range: 0·0085–0·0099). These means are significantly different at $P=0·01$. Thus, although percentage leaf nitrogen values were not significantly different between sun leaves ($1·89 \pm 0·05\%$) and shade leaves ($1·83 \pm 0·15\%$), nitrogen per unit leaf area was significantly greater ($P=0·01$) in sun ($2·11 \pm 0·12$ g N m^{-2}) than in shade leaves ($1·40 \pm 0·12$ g N m^{-2}).

When expressed on a leaf area basis, photosynthetic rates of sun leaves measured at 30°C and PPFD>1200 $\mu mol\ m^{-2}\ s^{-1}$ averaged $11·5 \pm 0·7$ $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ ($n=8$) whereas the mean for shade leaves was $7·9 \pm 0·5$ ($n=8$). These mean values are significantly different at $P=0·01$. Mean stomatal conductance was also lower in shade leaves (159 versus 190 mmol $m^{-2}\ s^{-1}$ for sun leaves), with the result that there was no significant difference in mean measured values of C_i (25·4 Pa for shade leaves versus 24·9 Pa for sun leaves). When rates of photosynthesis were expressed on a dry mass basis, the systematic variation in SLA caused measured CO_2 assimilation rates of sun and shade leaves to converge. The mean for sun leaves was 373 ± 25 and that for shade leaves was 383 ± 21 $\mu mol\ g^{-1}\ h^{-1}$ (not significantly different at $P=0·1$). Similarly, mean rates of net photosynthesis per unit leaf N were not significantly different for shade ($5·76 \pm 0·34$ $\mu mol\ g^{-1}$ N s^{-1}) and sun ($5·49 \pm 0·38$ $\mu mol\ g^{-1}$ N s^{-1}) leaves.

The response of net photosynthesis to varying C_i at 30 °C and saturating PPFD was measured on two shade (Figs 1a&b) and two sun (Figs 1c&d) leaves of white oak

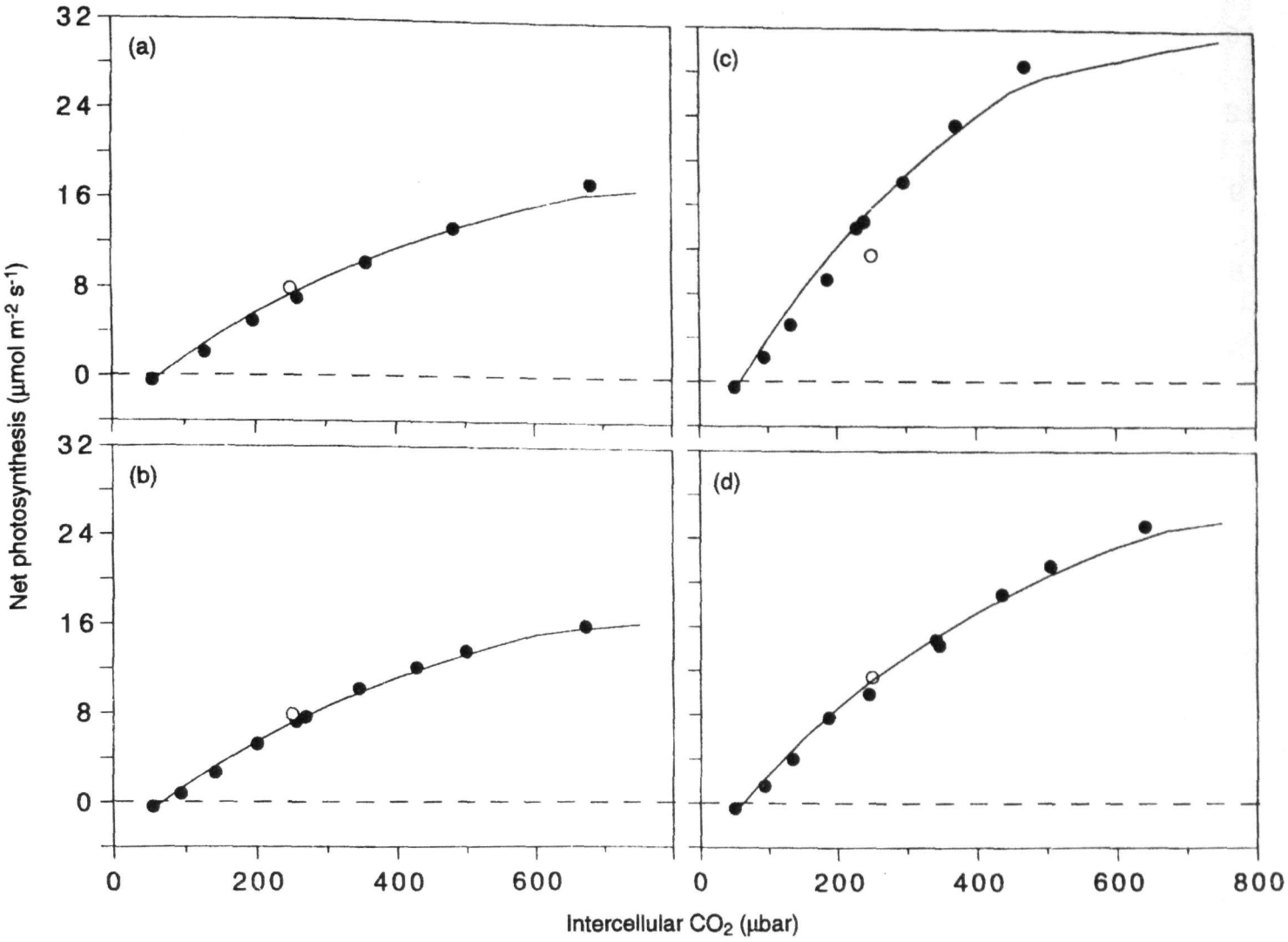

Figure 1. Relationship between net photosynthesis and intercellular pCO_2 for two shade leaves (a,b) and two sun leaves (c,d) of *Quercus alba*. Leaf temperature is 30°C and PPFD>1400 μmol m^{-2} s^{-1}. Solid lines are model fits to measured data, and closed circles are measured values. Open circles represent mean values of photosynthesis measured at ambient CO_2 for shade and sun leaves ($n=7$ for each).

and on three maple leaves (data not shown). The open circles in Fig. 1 indicate the mean values of net photosynthetic rates for shade and sun leaves of white oak measured at C_a=35·0 Pa and 30 °C. Figure 2 illustrates the measured responses of net photosynthesis to leaf temperature at ambient C_a and saturating PPFD (>1200 μmol m^{-2} s^{-1}) for six shade leaves (Fig. 2a) and four sun leaves (Fig. 2b) of oak, with mean values measured at 30 °C denoted by open circles. Finally, the measured responses of net photosynthesis to PPFD at both 25 and 30°C are shown for shade (Figs 3a&b) and sun (Figs 3c&d) leaves of oak. For comparison, a single PPFD response curve measured on a shade leaf of red maple at 30 °C is included.

The stomatal model (Ball *et al.* 1987) states that stomatal conductance is a linear function of CO_2 assimilation rate, modified by the ratio of ambient relative humidity to ambient CO_2 (Eqn 3). This assumption was tested for our data by plotting stomatal conductance data from all the measured PPFD and temperature response curves against Ah/C_a (Fig. 4a). In the accompanying paper (Baldocchi & Harley 1995), we make inferences about the canopy response to elevated atmospheric CO_2. Stomatal conductance values obtained from four oak and three maple leaves as C_a was varied, while PPFD (1500 μmol m^{-2} s^{-1}) and leaf temperature (30 °C) were held constant, are plotted against Ah/C_a in Fig. 4b.

In order to test the ability of the fully parametrized model to simulate measured data, we measured the diurnal courses of photosynthesis and evapotranspiration for a single shade leaf and a single sun leaf, measured on different days under natural conditions of PPFD and temperature. These data are depicted in Fig. 5.

Model parametrization

Harley & Tenhunen (1991) describe techniques for model parametrization given an ideal data set. The present data set is less than ideal, and the resulting model parametrization is necessarily less robust. In particular, A–C_i curves were obtained only at 30 °C, and were too few to characterize an entire population of leaves. For that reason, parameter estimates obtained from the A–C_i curves shown in Fig. 1 were modified to reflect more accurately the overall population mean photosynthetic rates determined at 30 °C and saturating PPFD for a larger sample of both sun and shade leaves. In addition, the temperature dependences of model parameters (Eqns 1 and 2) could not be obtained explicitly, and parameters were adjusted to mimic the temperature responses of photosynthesis measured at ambient CO_2 and saturating PPFD on a larger sample of leaves. These procedures are described below.

From the four A–C_i curves measured on oaks (Fig. 1) and the three measured on maples (data not shown), we obtained estimates of R_d by running a linear regression

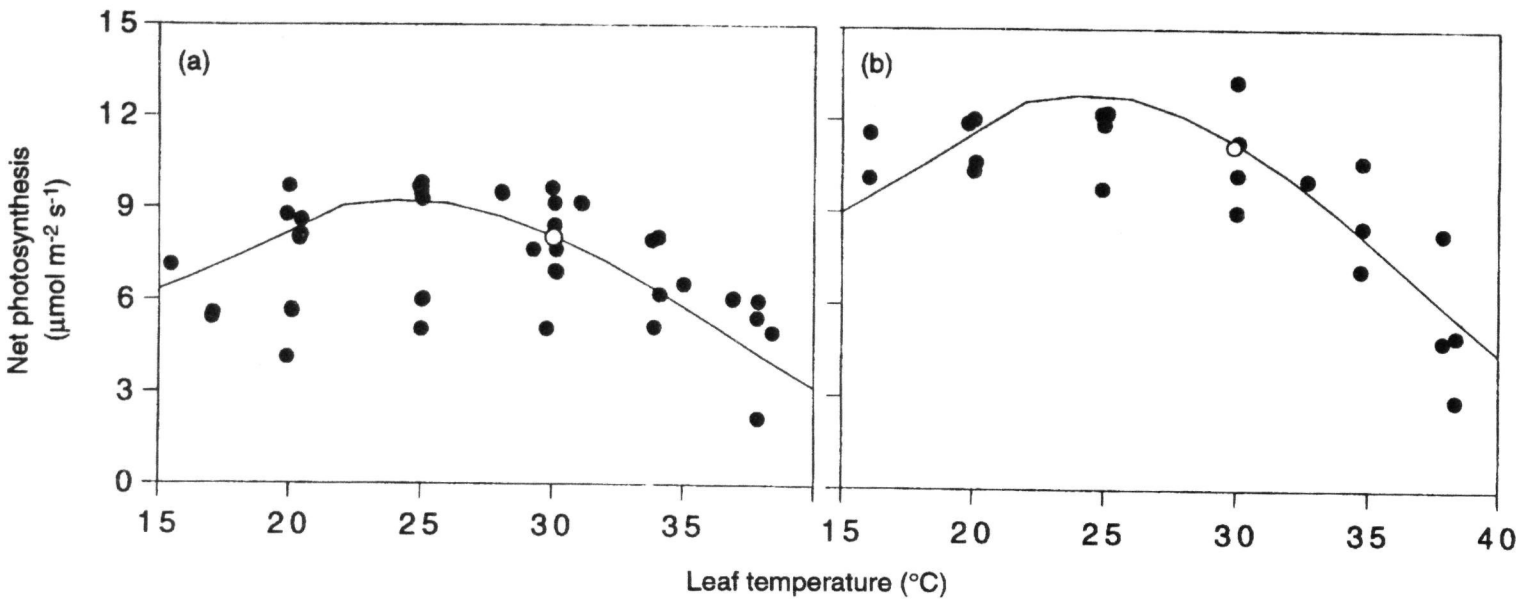

Figure 2. Relationship between net photosynthesis and leaf temperature for shade leaves (a; $n=6$) and sun leaves (b; $n=4$) of *Quercus alba*. External pCO_2=35·0 Pa and PPFD>1400 μmol m^{-2} s^{-1}. Solid lines are model simulations. ——, predicted values; ●, measured values; ○, mean values of photosynthesis measured at 30°C.

through the lowest four points of each curve, and solving for A at $C_i=\Gamma_*=5{\cdot}49$ Pa, where Γ_* (=500 O_2/τ) is the CO_2 compensation point at 30 °C in the absence of day respiration (Brooks & Farquhar 1985). With the value of R_d thus fixed, estimates of V_{cmax} were obtained using non-linear least-squares analysis (Systat, Evanston, IL) to fit the lowest six points on each curve. Finally, using all data points from each curve, and with R_d and V_{cmax} fixed, estimates of J_{max} were determined using non-linear least-squares analysis. The best-fitting estimates of parameter values determined for each curve are shown in Table 2, expressed in units based on leaf area, and the solid lines in Fig. 1 are the resulting model fits. Table 2 also provides the SLA and leaf nitrogen content (g N m^{-2}) for each of the leaves for

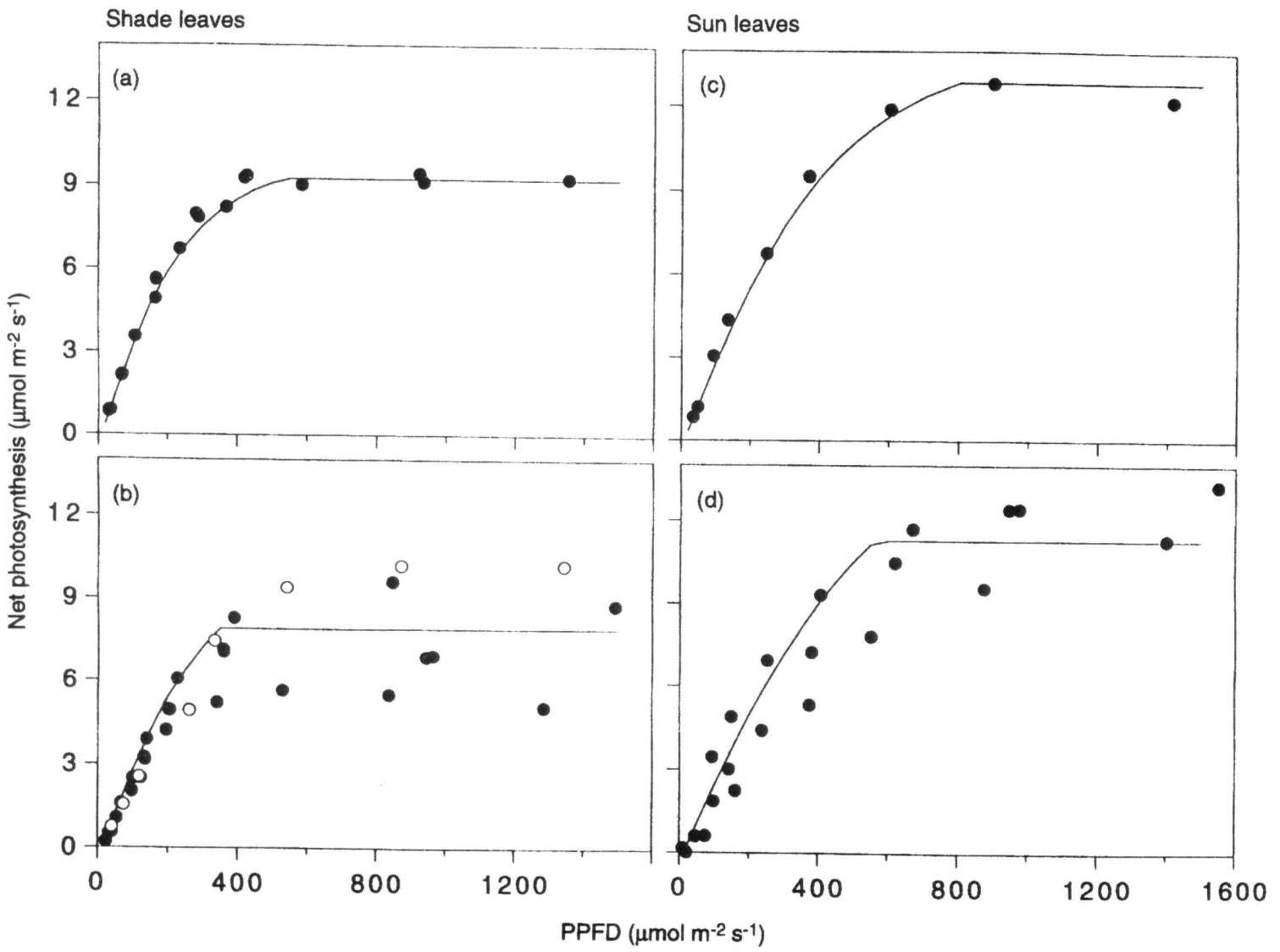

Figure 3. Relationship between net photosynthesis and incident PPFD for shade leaves (a,b) and sun leaves (c,d) of *Quercus alba* measured at ambient CO_2 and either 25 °C (a,c) or 30°C (b,d). Also shown (open symbols in b) is the PPFD response for a single shade leaf of *Acer rubrum*. Solid lines are model simulations and closed symbols are measured values. For shade leaves, $\alpha = 0{\cdot}24$; for sun leaves, $\alpha = 0{\cdot}20$.

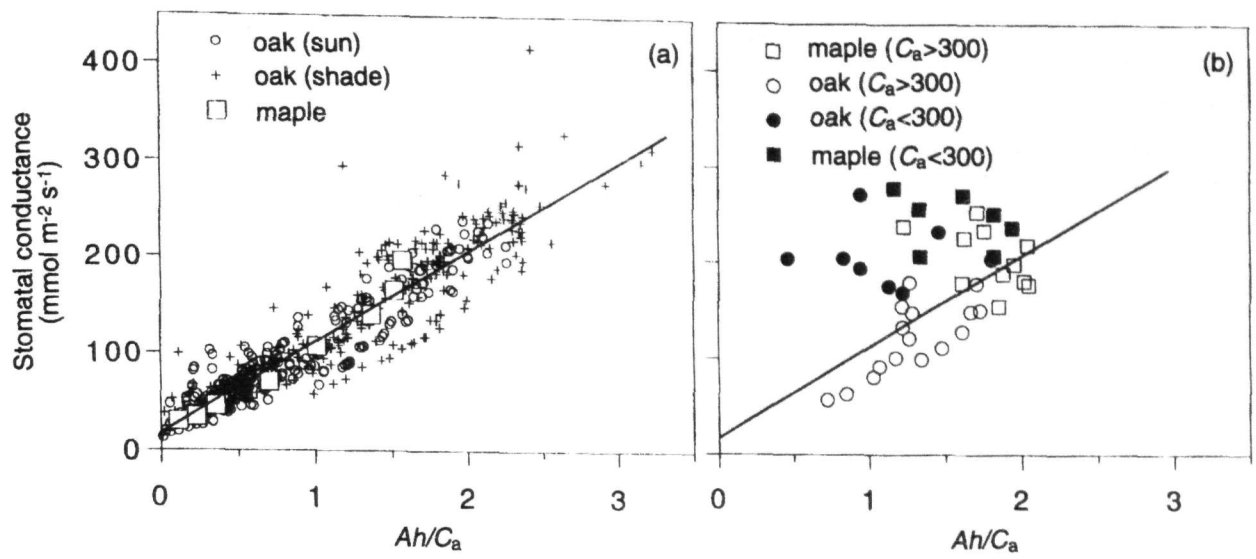

Figure 4. Relationship between stomatal conductance to water vapour and the factor Ah/C_a for leaves of *Quercus alba* and *Acer rubrum*. (a) Data collected with C_a=350 Pa and PPFD and temperature variable. (b) Data collected at constant leaf temperature (30 °C) and high PPFD as C_a is varied. Data collected at C_a above 300 Pa (open symbols) and below 300 Pa (closed symbols) are shown. Solid lines are a linear fit to measured data using the following equation: $g_s = 17{\cdot}5 + 95{\cdot}0Ah/C_a$.

which photosynthetic parameters were obtained, allowing one to convert parameters from a leaf area basis to a leaf mass or leaf nitrogen basis. Although large differences in both V_{cmax} and J_{max} between sun and shade leaves are apparent when parameters are expressed per unit leaf area, the differences are almost eliminated when parameters are expressed either per unit nitrogen or per unit dry weight.

A comparison between the curve fits in Fig. 1 and the mean values for the entire population of measured sun and shade leaves (open circles) indicated that the value of V_{cmax} determined from these individual curves needed to be adjusted, up slightly in the case of shade leaves and down slightly for sun leaves, to represent the entire population more accurately. The value of V_{cmax} was subsequently modified until the parameterizations used for both sun and shade leaves resulted in model predictions closely approximating the mean measured values at 30°C and PPFD=1500 μmol m^{-2} s^{-1}. Given those values of V_{cmax}, we adjusted the value of J_{max} independently for sun and shade leaves until an acceptable fit to the light response data at 30 °C in Fig. 3 was obtained. Given those values of V_{cmax} and J_{max}, which provided reasonable fits to data obtained at 30 °C, we needed to establish reasonable temperature dependences for both parameters. Based on temperature dependences of V_{cmax} and J_{max} for cotton (Harley *et al.* 1992), we held the values of H_d and T_{opt} in Eqn 2 constant at 200 kJ mol^{-1} and 311 K, respectively, and varied the values of H_a and f(opt) to achieve both the appropriate values of V_{cmax} and J_{max} at 30°C, and a reasonable fit to the data in Figs 2 and 3, which is indicated by the solid lines. The values of H_a and the values of V_{cmax} and J_{max} at the temperature optimum arrived at for both sun and shade leaves are given in Table 1.

Estimates of α, the efficiency of light energy conversion on an incident-light basis (mol electrons mol^{-1} photons), were chosen which provided the best overall fit to the initial slope of measured PPFD response curves for sun and shade leaves (Fig. 3). Resulting fits at 25 and 30°C are shown in Fig. 3, using values of α of 0·20 and 0·24 mol electrons mol^{-1} photons for sun and shade leaves, respectively. The value of 0·24 for shade leaves of oaks also provides a good fit to the quantum yield portion of the PPFD response curve for the shade leaf of red maple, although PPFD-saturated rates of photosynthesis for the maple exceeded those of the oaks.

Based on Fig. 4a, the assumption of linearity between stomatal conductance and Ah/C_a appears valid (r^2=0·87) when C_a is held constant at 35·0 Pa, and a linear fit to the data provides values for the slope and intercept of that function. Furthermore, a single set of values is adequate to fit conductance data from both sun and shade leaves of oak and from the single PPFD response curve of red maple. When C_a is varied as PPFD and temperature are held constant, however, the relationship is no longer linear. The model captures reasonably well the increase in conductance as C_a falls from very high values of >80·0 Pa) to 30·0 Pa (Fig. 4b, open symbols). When C_a falls below 30·0 Pa, however, the model no longer behaves realistically (Fig. 4b, closed symbols).

Having parametrized the model as described above for both sun and shade leaves of white oak (Table 1), we simulated the diurnal courses of photosynthesis and evapotranspiration for a single shade leaf and a single sun leaf (Fig. 5), using as driving variables the measured values of leaf temperature and PPFD (Figs 5a&b) as well as measured C_a and h. The resulting simulations were compared with the measured rates of transpiration (Figs 5c&d) and net photosynthesis (Figs 5e&f). The photosynthetic rates of both the sun and shade leaves, determined at 30°C and PPFD=1000 μmol m^{-2} s^{-1}, were below average for their respective leaf classes, and thus model simulations using the parameters in Table 1 overestimated measured values of net photosynthesis and transpiration, especially for the shade leaf when PPFD exceeded 200 μmol m^{-2} s^{-1}. Comparing the daily integrated totals of carbon fixed and water lost, the model overestimated CO_2 fixation by 6·7

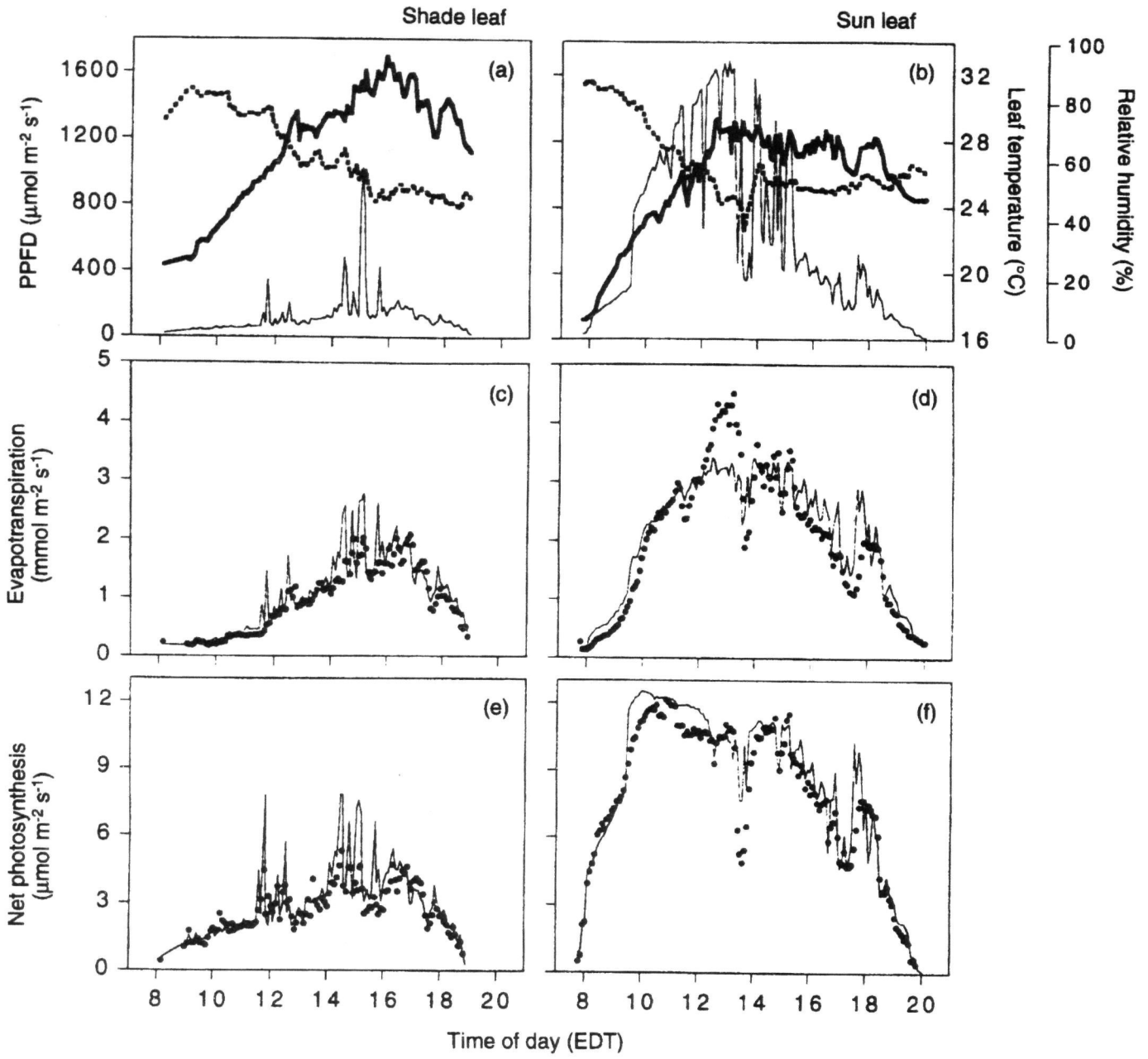

Figure 5. The diurnal pattern of evapotranspiration (c,d) and net photosynthesis (e,f) measured for a shade leaf (on 29 July 1992; left panels) and a sun leaf (on 2 August 1992; right panels) of *Quercus alba*. Solid lines are model simulations based on average sun and shade leaf model parameters given in Table 1, and closed circles are measured values. Measured values of leaf temperature (——), PPFD (——) and relative humidity (– – – –) used to drive shade and sun simulations are shown in panels (a) and (b), respectively.

and 13·1% for the sun and shade leaves, respectively, and overestimated daily water loss by 4·8 and 12·0%. Despite these overestimations, the model captured the diurnal patterns resulting from variations in PPFD and temperature, and effectively represents the response of the average sun and shade leaf.

DISCUSSION

Model parametrization

We feel that the parametrizations developed here effectively capture the important PPFD, temperature and CO_2 dependences of CO_2 assimilation and water loss from individual leaves of white oak at different levels of a forest canopy. We have also attempted to deal with the problem of leaf-to-leaf variation in leaf gas-exchange properties, although we readily admit that sample size ($n=8$ for both sun and shade leaves) remains a potential difficulty in that regard.

The ideal way to estimate values of V_{cmax}, J_{max} and R_d and their temperature dependences is to analyse A versus C_i response curves measured carefully over a range of leaf temperatures (Harley & Tenhunen 1991). Unfortunately, the curves measured in this study (Fig. 1) were somewhat problematic. At low C_i (typically <30·0 Pa) and high PPFD (>1000 μmol m^{-2} s^{-1}), RuBP is present in excess and photosynthesis is limited by the kinetic properties of Rubisco, determined in the model by the value of V_{cmax} (K_c, K_o and τ being considered constants at a given temperature) (see Farquhar & von Caemmerer 1982; Sharkey 1985; Harley & Tenhunen 1991 for discussion). As C_i increases and/or PPFD decreases, the rate of regeneration of RuBP in the Calvin cycle, determined by the value of J_{max} in the model, becomes limiting. For our curves (Fig. 1), PPFD was sufficiently high (>1400 μmol m^{-2} s^{-1}) and C_i values sufficiently low that RuBP, if limiting at all, was only so at the highest calculated C_i value. For this reason, our estimates of J_{max} should be regarded as minimum estimates.

Despite this difficulty, it remains relatively easy to parametrize our gas-exchange model for a single leaf temperature; a few A versus C_i response curves, perhaps supplemented by a few A versus PPFD responses, are sufficient (Harley & Tenhunen 1991). In order for the model to be of use in predicting leaf response under the whole range of

Species	Figure	Depth in canopy (m)	R_d	V_{cmax} (μmol m^{-2} s^{-1})	J_{max}	SLA m^2 g^{-1}	[N] g m^{-2}
white oak	Fig. 1a	3	0.5	37.6	89.2	0.0144	1.22
white oak	Fig. 1b	3.5	0.6	37.0	85.0	0.0147	1.21
white oak	Fig. 1c	0	0.4	76.8	185.3	0.0094	2.00
white oak	Fig. 1d	0	0.5	56.0	136.5	0.0086	2.15
red maple	not shown	4.5	0.8	48.8	118.5	0.0111	1.23
red maple	not shown	3	0.4	57.7	149.9	0.0132	1.53
red maple	not shown	0	0.6	65.3	164.9	0.0084	1.67

Table 2. Values of 'day' respiration (R_d, μmol m^{-2} s^{-1}), the maximum rate of carboxylation (V_{cmax}, μmol m^{-2} s^{-1}) and the maximum rate of electron transport (J_{max}, μmol electrons m^{-2} s^{-1}) determined by least-squares regression analysis from A versus C_i response curves measured at 30 °C and PPFD>1400 μmol m^{-2} s^{-1} for leaves of white oak and red maple at different canopy depths. Also shown are the specific leaf area (SLA, m^2 g^{-1}) and leaf nitrogen content (g N m^{-2}) for each leaf

environmental input values, each model parameter must also be given a temperature dependence, described for this model by Eqns 1 and 2. Ideally, one could repeat the procedure outlined above for a range of leaf temperatures, but this involves considerable effort, particularly if one hopes to establish leaf-to-leaf variability within a canopy.

Here we have opted to determine in a rigorous fashion parameter values at a single leaf temperature (30 °C) and subsequently establish temperature dependences based on measured A versus leaf temperature responses on a larger number of leaves, as described above. Although the measured data (Fig. 2) are scattered, the overall fit describes the average response. That the resulting temperature dependences adequately predict effects of leaf temperature on both photosynthesis and leaf conductance is indicated by the generally good fit to the diurnal response data (Fig. 5) in which leaf temperature varied over a 15 °C range.

The model of stomatal conductance is empirical and has been verified for only a few experimental situations (Ball *et al.* 1987; Leuning 1990; Harley & Tenhunen 1991; Harley *et al.* 1992). Furthermore, the use of ambient relative humidity rather than explicit dependences on temperature and vapour pressure deficit at the leaf surface has been criticized (Aphalo & Jarvis 1993). As leaf temperature was varied between 15 and 42 °C in this study, vapour pressure in the cuvette was not held constant; as a result, relative humidity varied between 30 and 80% while VPD varied between 0·5 and 7·0 kPa. Based on our measurements, however, the model effectively describes the complex interactive effects of PPFD and temperature, mediated through relative humidity (or vapour pressure deficit), on conductance at ambient C_a (Fig. 4a).

When C_a varies, however, the model breaks down (Fig. 4b). Stomata typically open with decreasing CO_2, and the model captures reasonably well the increase in conductance as C_a falls from very high values of >80·0 Pa to 30·0 Pa (Fig. 4b, open symbols). When C_a falls below 30·0 Pa, which is unlikely under natural conditions, the model no longer fits the data (Fig. 4b, closed symbols). As C_a falls below 30·0 Pa, predicted net photosynthesis (A) declines faster than does C_a, resulting in a decrease in Ah/C_a and a decrease in predicted conductance. Contrary to model predictions, however, measured conductance continues to increase with decreasing C_a. None the less, in ambient CO_2 the model behaves well (Fig. 4a), and for scenarios of elevated atmospheric CO_2 (i.e., C_a>35·0 Pa) the relationship remains relatively robust (Fig. 4b, open symbols).

In the companion paper (Baldocchi & Harley 1995), we use this relationship to make some inferences about canopy-scale gas-exchange under elevated CO_2. The point should be made that the results in Fig. 4 (and those of the canopy modelling exercise) apply only to short-term exposure to high CO_2, and not necessarily to stomatal responses of plants grown for extended periods under elevated CO_2 conditions. In the case of cotton plants grown under both 35·0 and 65·0 Pa CO_2, however, Harley *et al.* (1992) found that a single set of stomatal model parameters could be applied to leaves from both ambient and elevated CO_2 growth treatments.

It has long been recognized that there exists a strong correlation between leaf net photosynthesis and leaf nitrogen content (Field & Mooney 1986; Evans 1989), and a similar relationship has been found between leaf nitrogen and key photosynthetic model parameters such as V_{cmax} and J_{max} (Leuning *et al.* 1991; Harley *et al.* 1992). Although the data from the current study are limited, they extend the notion that both V_{cmax} and J_{max} increase more or less linearly with leaf nitrogen for leaves of both oak and maple (Fig. 6).

Sun versus shade leaves of white oak

Our data clearly indicate that photosynthetic parameters of both red maple and white oak (expressed on a leaf area basis) vary with canopy depth (Table 2) and contribute to decreasing photosynthetic rates. This is somewhat at variance with data of Aubuchon, Thompson & Hinckley (1978), who also studied variation in photosynthesis with canopy position in white oak. Although photosynthetic rates measured under prevailing conditions were 50% higher for leaves at the top of the canopy than for those near the bottom, the authors attributed this variation primarily to reduced PPFD at the lower levels, rather than to variation in photosynthetic capacity *per se*, which was not measured. When they took into account differences in PPFD between the different levels, re-calculated rates of photosynthesis declined only slightly with canopy depth. However, it appears that a single PPFD function was used to adjust the photosynthetic rate of leaves from all canopy positions, i.e. it was assumed *a priori* that there was no difference in the response of sun and shade leaves to PPFD, whereas numer-

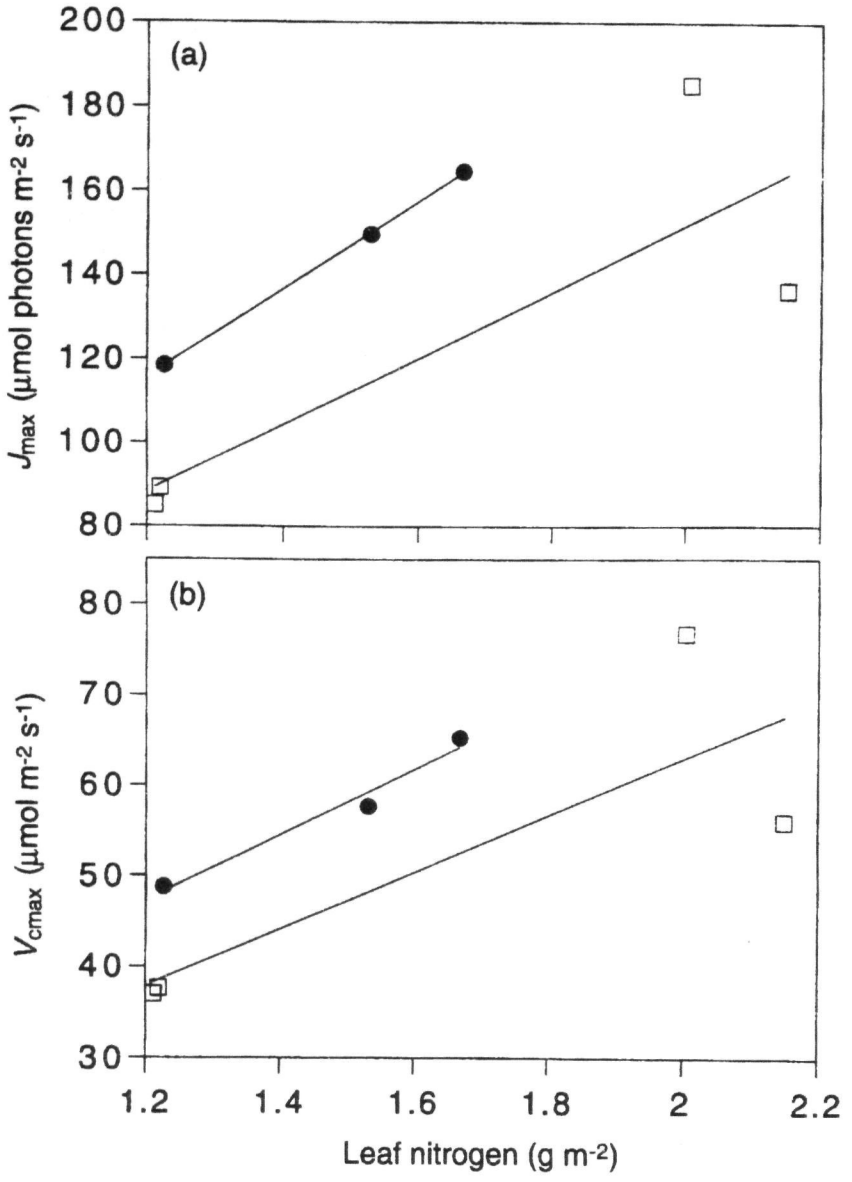

Figure 6. Calculated values of J_{max} (a) and V_{cmax} (b) for sun and shade leaves of both white oak (□) and red maple (●), expressed on a leaf area basis, as a function of leaf nitrogen content, also expressed on a leaf area basis.

ous studies have shown that shade leaves saturate at lower values of PPFD than sun leaves (Jarvis, James & Landsberg 1976; Boardman 1977). Had the PPFD-saturated photosynthetic rate been measured at each canopy layer, their results might have been more consistent with the present findings.

The differences in parameter values between sun and shade leaves presented in Table 2 are consistent with the general trends reported by Boardman (1977) for sun versus shade ecotypes, including lower rates of PPFD-saturated photosynthesis (leaf area basis) and higher quantum use efficiencies for shade-acclimated leaves. Reductions in photosynthetic capacity (on a leaf area basis) as a result of shading are reflected in reduced values of both V_{cmax} and J_{max}. Although dark respiration is generally lower in shade leaves, reflecting reduced physiological activity (Boardman 1977), no significant differences in R_d appear in this study. Estimated values of R_d also failed to show the expected positive correlation with leaf nitrogen. Estimates of R_d are very sensitive to errors in the data at low C_i values, and we lack confidence in our ability to discern differences in such a small parameter that is so difficult to estimate unless greater care is taken with the measurements (Brooks & Farquhar 1985).

The value of α for shade leaves given in Table 1 (0·24 mol electrons mol^{-1} photons) is identical to values determined previously for leaves of *Arbutus unedo* (Harley, Tenhunen & Lange 1986) and cotton (Harley *et al.* 1992). A value of 0·24 mol electrons mol^{-1} photons is equivalent to 0·06 mol CO_2 mol^{-1} photons, assuming four electrons pass through the electron transport chain per molecule of CO_2 fixed (see Farquhar & von Caemmerer 1982 for a discussion of alternative assumptions). These values are based on incident PPFD; assuming a reasonable value of 82% absorption, they are comparable to the average value for α of 0·073 mol CO_2 mol^{-1} photons (absorbed PPFD) for C_3 leaves (Ehleringer & Björkman 1977).

The only comparable previous estimates of Farquhar model parameters for *Quercus alba* of which we are aware are those of Wullschleger (1993) using data of Ni & Pallardy (1992) collected on greenhouse-grown seedlings (midday PPFD≈1000 μmol m^{-2} s^{-1}). Using procedures similar to ours, Wullschleger (1993) calculated V_{cmax}= 55±3 μmol m^{-2} s^{-1}, but, for reasons similar to those cited above, he was unable to estimate J_{max}. Our estimates of V_{cmax} (Table 2) for sun leaves exceed those of Wullschleger, while those for shade leaves are approximately 30% lower. Although he published no estimates of J_{max} for white oak, Wullschleger (1993) provides a figure and a linear function describing the general relationship between V_{cmax} and J_{max} for 109 C_3 species. Given the values of V_{cmax} in Table 2 and using this linear relationship, the predicted value of J_{max} for oak would fall within 5% of the estimated value for our two shade leaves, and within 15–20% for the sun leaves.

Figure 5 demonstrates that the integrated photosynthesis/stomatal conductance model effectively describes the variation in fluxes resulting from variable PPFD and leaf temperature, even when average parameter values (Table 1) are used to describe individual leaves having slightly below-average photosynthetic characteristics.

Extrapolating leaf-scale results to a canopy

The leaf-scale model relies on instantaneously measured values of PPFD, incident on and normal to the leaf, and leaf temperature to drive the physiological processes. The primary purpose of upscaling to the canopy scale is to describe the effects of canopy structure on leaf temperature and light penetration with depth in the canopy. As described in the companion paper (Baldocchi & Harley 1995), this can involve models of varying levels of detail, depending on whether such factors as leaf angle distribution, leaf clumping and leaf energy budget are considered important for modelling a given canopy.

The results of this study make it clear that any but the very simplest canopy models should incorporate variation in leaf physiological and/or morphological properties with leaf position in the canopy. Although we have measured physiological characteristics at only two canopy levels, these changes are likely to be continuous with depth in a canopy (Jarvis *et al.* 1976; Jarvis & Sanford 1986). Unless

a large number of measurements are made at several canopy levels, it is important to develop some more easily measured surrogate for physiological changes with level which can be inserted into a canopy-scale model. One such surrogate might be leaf nitrogen content (g N m^{-2}), which decreases with canopy depth (Leuning *et al.* 1991; Chen *et al.* 1993) and has a major influence on V_{cmax} and J_{max} (Fig. 6) (Leuning *et al.* 1991; Harley *et al.* 1992). Photosynthetic parameters might also be scaled based on the average amount of PPFD incident on a given leaf layer (Sellers *et al.* 1992). However, SLA, which is much easier to characterize, co-varies with leaf nitrogen and with integrated light interception (Sellers *et al.* 1992) and is utilized in the companion paper (Baldocchi & Harley 1995).

Boardman (1977) maintained that, although the higher capacity for CO_2 fixation of sun leaves results from larger amounts of carboxylating enzymes (and nitrogen) on a leaf area basis, photosynthetic capacity per unit volume of leaf is little affected by growth PPFD. Similarly, McMillen & McClendon (1983) studied 10 deciduous tree species, including *Quercus rubra*, and found that, although PPFD-saturated rates of net photosynthesis expressed per unit leaf area or unit chlorophyll were approximately 1.5 times higher in sun than shade leaves, when expressed per unit fresh mass or unit protein, rates of photosynthesis of sun and shade leaves were essentially equal.

If SLA can be shown to 'explain' (in a statistical sense) a significant amount of the variation in leaf-scale photosynthetic properties, those properties can be characterized for a small subset of leaves in a canopy, and the results scaled appropriately using SLA data obtained at different canopy positions. Gutschick & Wiegel (1988) predicted that SLA should increase with canopy depth in order to optimize canopy carbon assimilation, and discuss theoretical considerations leading to optimal distribution of SLA within a canopy. Unlike parameters which determine photosynthetic capacity (i.e. V_{cmax}, J_{max}), quantum use efficiency (α) is independent of whether rates are expressed on an area or weight basis. If variation in α is deemed important to overall canopy model performance, α should be determined experimentally at different canopy levels and inserted explicitly into the model rather than scaled with SLA.

This paper has provided a reasonable set of leaf-scale parameters for a biochemically based photosynthesis model for white oak. These parameter estimates are based on a reasonably large sample of leaves from two levels of a white oak canopy experiencing quite different average light environments. In addition, parameters were determined for an empirical model of leaf conductance to water vapour for leaves at both levels. In the companion article (Baldocchi & Harley 1995), the parametrizations thus arrived at are incorporated into a canopy-scale model which is used to predict canopy-scale fluxes that are compared with canopy CO_2 and water vapour flux measurements obtained using micrometeorological techniques.

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