

# Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies

R. LEUNING,<sup>1</sup> F. M. KELLIHER,<sup>2</sup> D. G. G. DE PURY<sup>3</sup> & E.-D. SCHULZE<sup>4</sup>

<sup>1</sup>CSIRO, Centre for Environmental Mechanics, PO Box 821, Canberra, ACT 2601, Australia, <sup>2</sup>Manaaki Whenua – Landcare Research, PO Box 69, Lincoln, New Zealand, <sup>3</sup>Research School of Biological Sciences, Australian National University, GPO Box 475, Canberra, ACT 2601, Australia, and <sup>4</sup>Lehrstuhl Pflanzenökologie, Universität Bayreuth, Germany

## ABSTRACT

A model is presented which solves simultaneously for leaf-scale stomatal conductance, CO<sub>2</sub> assimilation and the energy balance as a function of leaf position within canopies of well-watered vegetation. Fluxes and conductances were calculated separately for sunlit and shaded leaves. A linear dependence of photosynthetic capacity on leaf nitrogen content was assumed, while leaf nitrogen content and light intensity were assumed to decrease exponentially within canopies. Separate extinction coefficients were used for diffuse and direct beam radiation. An efficient Gaussian integration technique was used to compute fluxes and mean conductances for the canopy. The multi-layer model synthesizes current knowledge of radiation penetration, leaf physiology and the physics of evaporation and provides insights into the response of whole canopies to multiple, interacting factors. The model was also used to explore sources of variation in the slopes of two simple parametric models (nitrogen- and light-use efficiency), and to set bounds on the magnitudes of the parameters.

For canopies low in total N, daily assimilation rates are ~10% lower when leaf N is distributed uniformly than when the same total N is distributed according to the exponentially decreasing profile of absorbed radiation. However, gains are negligible for plants with high N concentrations. Canopy conductance,  $G_c$ , should be calculated as  $G_c = \Lambda \sum (f_{sl}g_{sl} + f_{sh}g_{sh})$ , where  $\Lambda$  is leaf area index,  $f_{sl}$  and  $f_{sh}$  are the fractions of sunlit and shaded leaves at each level, and  $g_{sl}$  and  $g_{sh}$  are the corresponding stomatal conductances. Simple addition of conductances without this weighting causes errors in transpiration calculated using the ‘big-leaf’ version of the Penman–Monteith equation. Partitioning of available energy between sensible and latent heat is very responsive to the parameter describing the sensitivity of stomata to the atmospheric humidity deficit. This parameter also affects canopy conductance, but has a relatively small impact on canopy assimilation.

Simple parametric models are useful for extrapolating understanding from small to large scales, but the complexity of real ecosystems is thus subsumed in unexplained

variations in parameter values. Simulations with the multilayer model show that both nitrogen- and radiation-use efficiencies depend on plant nutritional status and the diffuse component of incident radiation, causing a 2- to 3-fold variation in these efficiencies.

**Key-words:** energy balance; leaf nitrogen; photosynthesis; plant simulation modelling; stomatal conductance.

## INTRODUCTION

Important advances have been made in the last two decades in our understanding of the biochemistry of photosynthesis (Farquhar *et al.* 1980; Harley *et al.* 1992), the physiology of stomatal behaviour (Jarvis 1976; Cowan 1977, 1982; Ball *et al.* 1987) and the physics of transpiration (Monteith 1965). It is now possible to construct coupled models for photosynthesis and transpiration which summarize this knowledge and successfully predict the observed behaviour of individual leaves (Collatz *et al.* 1991; Leuning 1995). A major challenge is to extend this understanding from the scale of leaves to canopies.

‘Scaling up’ involves integration of processes in both space and time. To predict long-term responses of canopies to environmental perturbations such as increased global CO<sub>2</sub> concentrations requires a full description of not only photosynthesis and transpiration of leaves, but the functioning of roots and the resource allocation involved in respiration, growth and reproduction. This task is beyond the scope of the present paper, and scaling up is restricted to the more limited goal of describing the spatial distribution of fluxes of radiation, CO<sub>2</sub>, heat and water vapour within canopies, and integrating fluxes over all leaves. Temporal integration will be restricted to the daily time scale, in which canopy properties such as leaf area index are constant.

Canopies may be characterized using multilayer or ‘big leaf’ models (Raupach & Finnigan 1988). A multilayer model integrates the fluxes for each layer to give the total flux (e.g. Wang & Jarvis 1990; Collatz *et al.* 1991); while the big leaf approach maps properties of the whole canopy on to a single leaf before calculating the fluxes (e.g. Sellers *et al.* 1992; Amthor 1994; de Pury 1995). A major distinction between the methods lies in how the non-linear relationships describing assimilation and transpiration are

parametrized. A multilayer model uses functions with parameters that are measurable at the leaf level, but requires knowledge of the spatial distribution of the parameters as well as other factors such as irradiance, temperature, humidity deficit and boundary layer conductance. These factors may be obtained by measurements or through other models. Parameters required for a big-leaf model cannot be measured directly, nor can they be defined as the arithmetic mean of leaf level parameters because of the non-linearity of the functions. Instead, *a priori* assumptions must be made concerning canopy behaviour, for example the single-leaf model of photosynthesis applies to the whole canopy provided that photosynthetic capacity and absorbed photosynthetically active radiation have an identical distribution through the canopy (Farquhar 1989). In a further example, McNaughton (1994) illustrated the problem of non-linearities involved in combining stomatal conductances to define a canopy conductance that ensure canopy transpiration is the same when computed using multiple layers or the canopy conductance. The multilayer approach was adopted in this paper to avoid the problems encountered in defining big-leaf parameters, and because all non-linearities are maintained at the leaf level and the resultant fluxes are simply additive.

A sound model of stomatal behaviour is central to describing the rates of photosynthesis and transpiration of leaves. Many modellers have followed Jarvis (1976) in assuming that stomatal response to environmental factors may be modelled as the product of several independent functions. This approach treats stomatal conductance as an entity that is independent of both photosynthesis and transpiration. Following a detailed examination of the models of Jarvis (1976) and Ball *et al.* (1987), Leuning (1995) concluded that assimilation and stomatal conductance were well described using a set of coupled equations for the biochemical demand for CO<sub>2</sub>, the molecular diffusion of CO<sub>2</sub> through the stomata, plus the equation  $g_{sc} = g_{c0} + a_1 A / [(c_s - \Gamma)(1 + D_s/D_{s0})]$ , where  $g_{sc}$  is stomatal conductance for CO<sub>2</sub>,  $g_{c0}$  is a residual conductance at the light compensation point,  $\Gamma$  is the CO<sub>2</sub> compensation point,  $a_1$  and  $D_{s0}$  are coefficients, and  $D_s$  is the humidity deficit at the leaf surface. Conductance and assimilation are intimately linked in this approach: photosynthetic capacity determines maximum stomatal conductance (Wong *et al.* 1979). Because photosynthetic capacity is linearly correlated to leaf nitrogen concentration (Field 1983), the distribution of key physiological parameters within the canopy is fully specified by the distribution of leaf nitrogen. These relationships greatly simplify construction of a multilayer model.

To complete the canopy model, the relationships for stomatal conductance and photosynthesis were combined with equations for the distribution of diffuse and direct beam radiation within plant canopies, and the Penman–Monteith equation for transpiration. Many of these algorithms are now regarded as standard and are included without critical comment in models by other workers (e.g. Wang & Jarvis 1990; Collatz *et al.* 1991;

Sellers *et al.* 1992).

With the objective of identifying limitations in the assumptions and functions used, model output was compared with selected field measurements. The impact of varying the distribution and amounts of leaf area, leaf nitrogen and photosynthetically active radiation on canopy assimilation and transpiration was investigated using the model. The model was then used to explore sources of variation in the slopes of two simple parametric models (nitrogen- and light-use efficiency), and to set bounds on the magnitudes of the parameters.

## MODEL DESCRIPTION

The model provides a fully coupled solution for assimilation, stomatal conductance, net radiation, transpiration, sensible heat transfer and leaf temperature at several levels within plant canopies using numerical methods. Key features of the model are: (1) the separation of radiation absorption by sunlit and shaded leaves having an assumed spherical leaf angle distribution; (2) use of coupled equations for assimilation and stomatal conductance; (3) solution of the leaf energy balance equations; (4) inclusion of the influence of leaf temperature on assimilation and conductance; (5) use of an exponential profile for the distribution of canopy nitrogen concentration and hence photosynthetic capacity; and (6) use of an efficient five-point Gaussian integration technique to calculate canopy fluxes.

## Radiation absorption

Because the light response of photosynthesis is non-linear, radiation absorbed by shaded and sunlit leaves must be calculated separately to avoid the overestimation of canopy assimilation obtained when mean irradiance is used (Spitters 1986). The bimodal distribution of irradiance of leaves occurs because shaded leaves receive diffuse light only, while sunlit leaves receive both diffuse and direct radiation. Scattering of beam radiation creates further diffuse radiation, thus complicating description of the radiation field. Incoming radiation must also be partitioned into diffuse and direct components because radiation attenuation is dependent on the angle of incidence relative to the distribution of foliage angles: beam radiation is incident at a fixed solar elevation at a given time, while diffuse radiation is distributed over all angles. The most detailed approach uses numerical models to calculate radiation absorption by leaves with differing classes of leaf angle (Goudriaan 1977; Ross 1981), and may consider the problem of leaf clumping. Such models required detailed knowledge of canopy architecture, which is generally unavailable. A simpler approach is to assume a spherical leaf angle distribution and to approximate distributions of direct and diffuse radiation using exponential profiles (Spitters 1986). Comparison with more detailed models shows that the simpler method, adopted in this paper, provides an excellent description of the radiation field within simple canopies (Goudriaan & van Laar 1994).

Following Spitters (1986), photosynthetically active radiation absorbed by shaded leaves,  $Q_{sh}$ , may be written as

$$Q_{sh}(\xi) = Q_{ld}'(\xi) + Q_{lbs}(\xi), \quad (1)$$

in which  $\xi$  is the cumulative leaf area index measured downwards from the top of the canopy, and  $Q_{ld}'$  and  $Q_{lbs}$  are the absorbed components of incoming diffuse and scattered beam radiation, respectively (see Appendix G for a list of symbols). These quantities are estimated using the approximate exponential expressions

$$Q_{ld}'(\xi) = Q_{d0}k_d'(1 - \rho_{cd}) \exp(-k_d'\xi) \quad (2)$$

and

$$Q_{lbs}(\xi) = Q_{b0}[k_b'(1 - \rho_{cb}) \exp(-k_b'\xi) - k_b(1 - \sigma_l) \exp(-k_b\xi)], \quad (3)$$

where  $Q_{d0}$  and  $Q_{b0}$  are incoming diffuse and beam radiation,  $k_d'$ ,  $k_b'$  and  $k_b$  are extinction coefficients for diffuse radiation, for scattered beam radiation and for theoretical canopies with black leaves (no reflection or transmission),  $\sigma_l$  is the scattering coefficient (reflection plus transmission), and  $\rho_{cd}$  and  $\rho_{cb}$  are canopy reflection coefficients for diffuse and beam radiation, respectively. Scattered beam radiation (Eqn 3) is calculated as the difference between total absorbed beam radiation (including scattering: first term) and the absorbed direct beam alone (second term). Incident radiation ( $Q_{d0}$ ,  $Q_{b0}$ ) is expressed per unit area of *ground*, whereas the absorbed radiation at level  $\xi$  within the canopy is expressed per unit of *leaf* area.

Radiation absorbed by sunlit leaves is expressed as

$$Q_{sl}(\xi) = k_b Q_{b0}(1 - \sigma_l) + Q_{sh}(\xi), \quad (4)$$

where the first term is absorbed beam radiation and the second term is the diffuse radiation absorbed by all leaves at depth  $\xi$ . Note that the intensity of direct beam per unit leaf area does not change with depth in the canopy. Appendices A and B provide methods to estimate incoming beam and diffuse radiation, and the extinction and reflection coefficients required in Eqns 1–4.

## Leaf photosynthesis and stomatal conductance

A complete description of  $\text{CO}_2$  uptake of leaves requires a model of the demand for  $\text{CO}_2$  of the biochemical reactions of photosynthesis, an equation for the supply of  $\text{CO}_2$  by diffusion from the external air to the intercellular spaces plus a model of the stomatal response to physiological and environmental factors. Simultaneous solution of these coupled equations yields the three required quantities: stomatal conductance for  $\text{CO}_2$ ,  $g_{sc}$ , intercellular  $\text{CO}_2$  concentration,  $c_i$ , and the net assimilation rate,  $A$  (Leuning 1990, 1995; Tenhunen *et al.* 1990).

Biochemical demand for  $\text{CO}_2$  is written as

$$A = \min\{A_v, A_j\} - R_d, \quad (5)$$

where  $A_v$  and  $A_j$  are the gross rates of photosynthesis limited by Ribulose bisphosphate carboxylase-oxygenase

(Rubisco) activity and the rate of Ribulose bisphosphate ( $\text{RuP}_2$ ) regeneration through electron transport, respectively. The term  $\min\{A_v, A_j\}$  represents the minimum of  $A_v$  and  $A_j$ . Both  $A_v$  and  $A_j$  are functions of  $c_i$  and temperature, while  $A_j$  also depends on absorbed radiation. Respiration that continues during the light,  $R_d$ , is also strongly dependent on leaf temperature. The model for  $\text{C}_3$  photosynthesis used in this paper closely follows that developed by Farquhar *et al.* (1980) and von Caemmerer & Farquhar (1981), and the required equations used are summarized in Appendix C.

Supply of  $\text{CO}_2$  by diffusion through the stomata and the leaf boundary layers is given by

$$A = g_{sc}(c_s - c_i) = g_{bc}(c_a - c_s), \quad (6)$$

in which  $g_{sc}$  and  $g_{bc}$  are the stomatal and boundary layer conductances for  $\text{CO}_2$ , and  $c_a$  and  $c_s$  are the  $\text{CO}_2$  concentrations in the free air and at the leaf surface, respectively. The first of these equations ignores interactions between molecules of water leaving and entering the stomata (Leuning 1983).

A semi-empirical model for stomatal conductance first proposed by Ball *et al.* (1987) and modified by Leuning (1990, 1995) completes the set of required equations. The model relates stomatal conductance to assimilation rate and to humidity deficit and  $\text{CO}_2$  concentration at the leaf surface according to

$$g_{sc} = g_{c0} + \frac{a_1 A}{(c_s - \Gamma)(1 + D_s/D_{s0})}, \quad (7)$$

where  $g_{c0}$  is a residual stomatal conductance at the light compensation point,  $\Gamma$  is the  $\text{CO}_2$  compensation point,  $D_s$  is the humidity deficit at the leaf surface, and  $D_{s0}$  is an empirical coefficient reflecting the sensitivity of the stomata to  $D_s$ . The parameter  $a_1$  is related to intercellular  $\text{CO}_2$  concentration at saturating irradiance by  $1/a_1 = 1 - c_i/c_s$ . Leuning (1995) critically examined the coupled model for stomatal conductance and assimilation (Eqns 5–7) and found that it reproduced the observed behaviour of individual leaves over a wide range of environmental conditions.

## Spatial distribution of physiological parameters

Specification of the spatial distribution of physiological parameters is a key problem in constructing multilayer models. A significant advantage of the coupled model for photosynthesis and stomatal conductance described above is that the vertical profile of photosynthetic capacity also characterizes the distribution of stomatal conductance.

A large fraction of nitrogen within leaves is incorporated into the enzymes involved in photosynthesis (Stocking & Ongun 1962). Field (1983), Leuning *et al.* (1991) and Harley *et al.* (1992), amongst others, obtained linear relationships between photosynthetic capacity and leaf nitrogen concentration. While Field (1983) obtained better correlations between photosynthetic capacity and nitrogen concentration expressed per unit leaf mass than per unit area,  $c_N$ , the latter basis is used here, since exchanges of

mass and energy occur across leaf surfaces. A linear relationship

$$V_{\text{cmax}} = a_N(c_N - c_{Nt}) \quad (8)$$

is assumed in this paper, where  $V_{\text{cmax}}$  is the maximum catalytic activity of Rubisco in the presence of saturating levels of RuP<sub>2</sub> and CO<sub>2</sub> (see Appendix C for the relationships between  $A_v$  and  $V_{\text{cmax}}$ ),  $c_{Nt}$  is a threshold value of  $c_N$  below which there is no photosynthesis, and  $a_N$  is an empirical coefficient.

An exponential decrease in  $c_N$  has been observed by many workers (e.g. Hirose & Werger 1987; Schieving *et al.* 1992), and Evans (1993) observed that nitrogen concentrations in leaves of lucerne were dependent on position within the canopy, but independent of time. The N distribution was thus assumed to follow  $c_N = (c_{N0} - c_{Nt}) \exp(-k_N \xi) + c_{Nt}$ , where  $c_{N0}$  is the N concentration of leaves at the top of the canopy and  $k_N$  is the nitrogen distribution coefficient. [Note that Hirose & Werger (1987) use relative cumulative leaf area index  $\xi/\Lambda$  when defining their N-distribution coefficient.] Combination of the above expression with Eqn 8 shows that photosynthetic capacity is also expected to decline exponentially with  $\xi$ , i.e.

$$V_{\text{cmax}}(\xi) = V_{\text{cmax}}(0) \exp(-k_N \xi), \quad (9)$$

where  $V_{\text{cmax}}(0) = a_N(c_{N0} - c_{Nt})$  is the value of  $V_{\text{cmax}}$  for leaves at the top of the canopy.

### Leaf energy balance

The above models for radiation absorption, photosynthesis and stomatal conductance need to be coupled to a model for the leaf energy balance, because this determines the heat load and temperature of the leaf, and temperature determines the rates of most biochemical reactions. A further reason for including the energy balance is that the stomatal model (Eqn 7) is specified in terms of CO<sub>2</sub> concentration and humidity deficit at the leaf surface. These differ from corresponding values in the free air surrounding leaves because of resistances to diffusion presented by the laminar boundary layer that exists on all surfaces. The magnitude of the differences depends on the fluxes themselves, as well as the boundary layer conductance, and thus the evaporation rate must be calculated to determine  $D_s$ .

The 'isothermal' form of the Penman-Monteith combination equation (Monteith 1965; Jones 1976) was used to partition net radiation absorbed by the leaves into sensible and latent heat, i.e.

$$\lambda E = \frac{s Y R_n^* + \rho_a c_p D_a g_{bh}}{s Y + \gamma g_{bw}(1/g_{bw} + 1/g_{sw})}, \quad (10)$$

where  $E$  is the transpiration rate,  $\lambda$  is the latent heat of vaporization of water vapour,  $D_a$  is the humidity deficit of the air,  $s$  is the slope of the curve relating saturation water vapour pressure to temperature,  $\gamma$  is the psychrometric constant,  $\rho_a$  is air density,  $c_p$  is the specific heat of air at constant pressure,  $g_{bw}$  and  $g_{bh}$  are the boundary layer conductances for water vapour and heat, and  $R_n^*$  is the net

'isothermal' radiation absorbed by the leaf. Stomatal conductance for water vapour is  $g_{sw} = 1.56 g_{sc}/C$ , where the factor 1.56 is the ratio of molecular diffusivities for water vapour and CO<sub>2</sub> in air, and  $C$  is molar density of air, which is required to convert  $g_{sc}$  (Eqn 7) from molar to velocity units. Expressions necessary to calculate  $R_n^*$ ,  $Y$  and the boundary layer conductances  $g_{bw}$  and  $g_{bh}$  are presented in Appendices D and E. The outward flux of thermal radiation from a leaf, and hence net radiation, are a function of leaf temperature. The isothermal form of the combination equation uses air temperature to calculate  $R_n^*$ , thereby eliminating one iteration in the numerical solution of the complete model.

From the energy balance equation, the sensible heat exchange between a leaf and its surroundings is given by

$$H = Y(R_n^* - \lambda E), \quad (11)$$

from which we may calculate the departure of leaf temperature from that of air:

$$T_l - T_a = H/(\rho_a c_p g_{bh}). \quad (12)$$

Equations 10–12 apply to symmetrical, amphistomatous leaves, and the boundary layer and stomatal conductances for both sides of the leaf are added together. Many broad-leaved trees have hypostomatous leaves, in which case sensible heat exchange occurs from both leaf surfaces whereas transpiration occurs on only one side. In this case, single-sided values for  $g_{bw}$  and  $g_{sw}$  must be used, while doubling  $g_{bh}$  (Jarvis & McNaughton 1986).

In formulating the above equations, reference conditions for temperature, humidity deficit and CO<sub>2</sub> concentrations have implicitly been assumed to be those outside the leaf boundary layer. If the reference point is moved to above the canopy, then the boundary layer conductances must be modified to account for the resistance to turbulent transport of heat and mass through the canopy air space. This is a complex topic (Raupach 1989) and beyond the scope of this paper, so for simplicity constant vertical profiles of  $T_a$ ,  $D_a$  and  $c_a$  were assumed for the simulations at any instant.

### Integration over space and time

Goudriaan (1986) and Spitters (1986) showed that Gaussian integration provides an accurate and fast method to calculate instantaneous and daily canopy photosynthesis. The five-point method was adopted for this paper, using the normalized Gaussian distances  $G_x(n) = 0.04691$ ,  $0.23075$ ,  $0.5000$ ,  $0.76925$  and  $0.95309$ , with corresponding weights  $G_w(n) = 0.11846$ ,  $0.23931$ ,  $0.28444$ ,  $0.23931$  and  $0.11846$  (Goudriaan & van Laar 1994). Gaussian distances were used to select times during the day [ $t = t_{dl} G_x(n) + t_{sunrise}$ ] at which to evaluate the canopy fluxes ( $t_{dl}$  is daylength; see Appendix A). To obtain the total canopy assimilation at these times, radiation absorption was evaluated at canopy depths  $\xi = \Lambda G_w(n)$ , ( $n = 1–5$ ), where  $\Lambda$  is the total leaf area index  $\Lambda = \int d\xi$ . The resultant solutions for fluxes, conductances and concentrations were obtained separately for sunlit and shaded leaves at these

values of  $\xi$ .

The fraction of sunlit leaves at canopy depth  $\xi$  is equal to the fraction of direct beam reaching that layer (Spitters 1986), i.e.

$$f_{\text{sl}} = \exp(-k_b \xi), \quad (13)$$

and the fraction of shaded leaves is  $f_{\text{sh}} = 1 - f_{\text{sl}}$ . Fluxes at each  $\xi$  were calculated using the weighted contributions from sunlit and shaded leaves. As an example, canopy assimilation at time  $t$  was evaluated as

$$A_c(t) = \Lambda \sum_{n=1}^5 [A_{\text{sl}} f_{\text{sl}} + A_{\text{sh}} f_{\text{sh}}] G_w(n), \quad (14)$$

where  $G_w(n)$  are the Gaussian weights given above. Similarly, the Gaussian weights were applied to the spatially integrated values  $A_c(t)$  to obtain daily integrals or means for the whole canopy,  $A_d$ . Parameter values used in the model are given in Tables 1, 2 and 3.

### Comparison with other models

Despite differences in detail, there is now significant convergence in the structure of multilayer models and the algorithms used by various authors. There is consensus concerning the models for C<sub>3</sub> photosynthesis and the leaf energy balance, but differences occur in the treatment of radiation distribution in plant canopies and in the stomatal model used. Wang & Jarvis (1990) described a model similar in structure to that above, but used a more detailed model for radiation distribution within canopies and calculated stomatal conductances using the empirical relationships of Jarvis (1976). Collatz *et al.* (1991) solved simultaneously equations for assimilation, conductance and leaf energy balance, but adopted the stomatal model of Ball *et al.* (1987) which uses relative humidity to describe stomatal response instead of humidity deficit, which is physiologically more appropriate (Leuning 1995). Collatz *et al.* (1991) simplified radiation absorption by treating the canopy as a horizontal, single-sided surface. Sellers *et al.*

**Table 2.** Parameter values used to define low-N and high-N plants

Parameter	Low-N	High-N	Units
$V_{\text{cmax}0}$	50	150	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
$a_1$	4	9	—
$D_{\text{so}}$	1.5	3.5	kPa

(1992) used a coupled conductance-assimilation model for C<sub>3</sub> leaves, and exponential profiles to describe the extinction of radiation and the distribution of leaf nitrogen within the canopy. However, they did not separate radiation absorbed by sunlit and shaded leaves, and also used the stomatal model of Ball *et al.* (1987). They also assumed equality between leaf and air temperatures and thus did not include the leaf energy balance equations.

The model in this paper presents a coupled set of relationships between stomatal conductance, assimilation and the leaf energy balance using a simplified description of radiation absorption by sunlit and shaded leaves in canopies. This is a compromise between the complexity of the radiation model of Wang & Jarvis (1990), and the simple approximation of no separation of radiation absorption by sunlit and shaded leaves.

## RESULTS AND DISCUSSION

### Leaf response to nitrogen concentration and environment

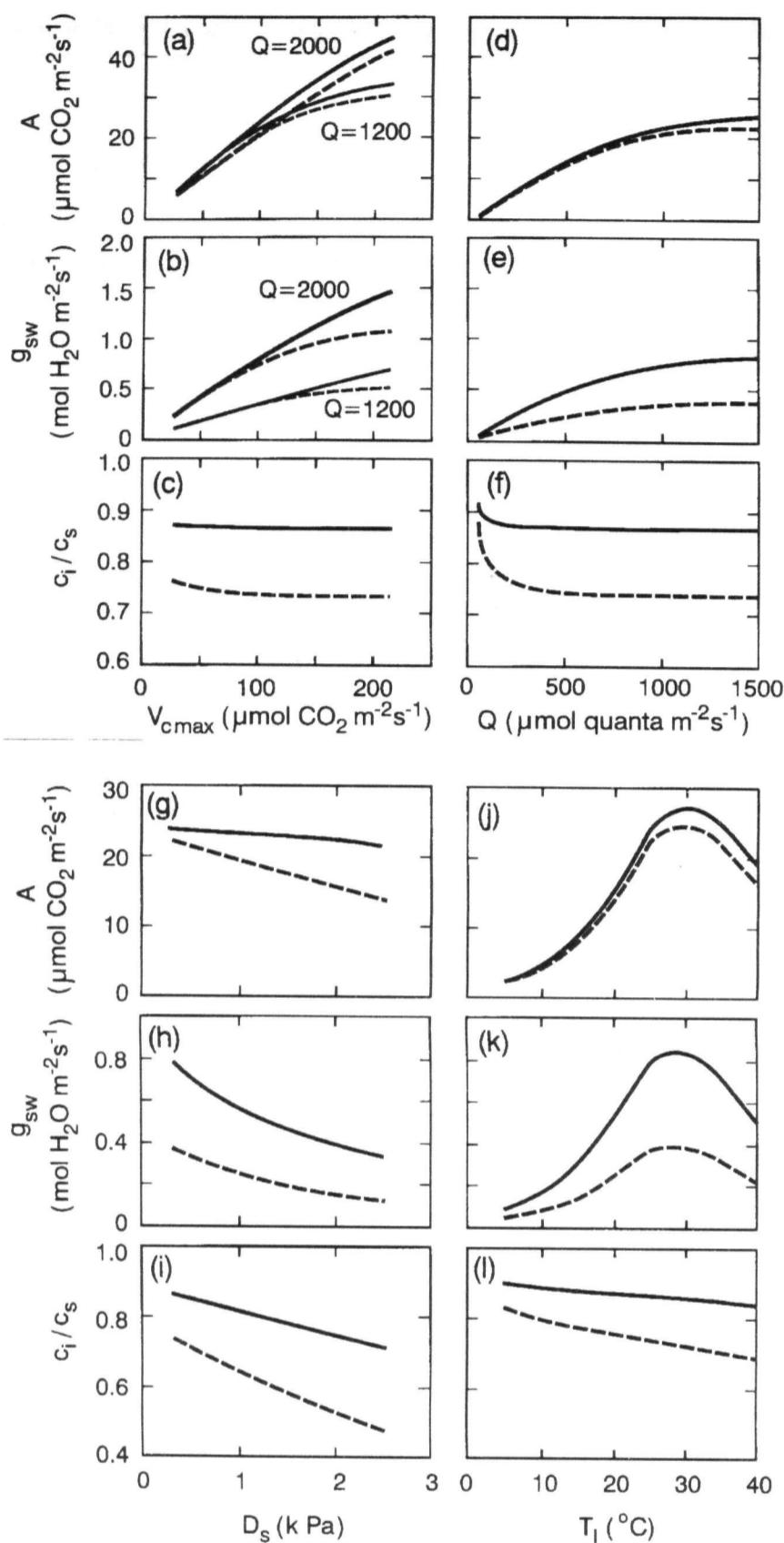
The coupled model for assimilation and stomatal conductance (the section 'Leaf photosynthesis and stomatal conductance' above) is central to the multilayer canopy model adopted in this paper. It is thus instructive to examine the

**Table 3.** List of parameters and their values used in the model for C<sub>3</sub> photosynthesis. Values for  $V_{\text{cmax}0}$  are given in Table 2. Parameter values marked with an asterisk are from Harley *et al.* (1992), the others from Leuning (1990). Symbol definitions are given in Appendix G

Parameter	Value	Units
$\theta$	0.9	—
$\alpha$	0.20	$\text{mol e mol}^{-1} \text{ quanta}$
$T_0$	293.2	K
$K_{\text{c}0}$	302	$\mu\text{mol mol}^{-1}$
$K_{\text{o}0}$	256	$\text{mmol mol}^{-1}$
$R_{\text{d}0}$	0.32	$\mu\text{mol mol}^{-1}$
$H_{\text{Kc}}$	59430*	$\text{J mol}^{-1}$
$H_{\text{Ko}}$	36000*	$\text{J mol}^{-1}$
$H_{\text{Rd}}$	53000*	$\text{J mol}^{-1}$
$H_{\text{vVcmax}}$	116300*	$\text{J mol}^{-1}$
$H_{\text{dVcmax}}$	202900*	$\text{J mol}^{-1}$
$H_{\text{vJmax}}$	79500*	$\text{J mol}^{-1}$
$H_{\text{dJmax}}$	201000*	$\text{J mol}^{-1}$
$S_v$	650*	$\text{J mol}^{-1}$
$\gamma_0$	34.6	$\mu\text{mol mol}^{-1}$
$\gamma_1$	0.0451	—
$\gamma_2$	0.000347	—

**Table 1.** List of parameters used in multilayer model (see Appendix G for definition of symbols)

Parameter	Value	Units
$t_d$	276	day of year
$w_l$	0.01	m
$\lambda_l$	-35	degrees
$T_{\text{an}}, T_{\text{ax}}$	15, 24	°C
$T_{\text{wn}}, T_{\text{wx}}$	15, 19	°C
$U_n, U_x$	1.4, 2.4	$\text{m s}^{-1}$
$t_{\text{mT}}, t_{\text{mu}}$	6, 3	h
$k_d$ (black leaves)	0.8	—
$\rho_{\text{cd}}, \sigma_l$ (visible)	0.057, 0.2	—
$\rho_{\text{cd}}, \sigma_l$ (NIR)	0.389, 0.8	—
$\tau_a$	0.8, 0.3	—
$k_N$	0.0, 0.6, 1.2	—
$k_u$	0.5	—
$\Lambda$	0.5–6.0	—



**Figure 1.** Predictions of the response of  $A$ ,  $g_{sw}$  and  $c_i/c_s$ , as a function of  $V_{cmax}$  (a, b, c);  $Q$  (d, e, f);  $D_s$  (g, h, i), and  $T_l$  (j, k, l). Except for the independent variable, reference conditions for each simulation were  $T_l = 20^\circ\text{C}$ , relative humidity = 0.9,  $c_s = 350 \mu\text{mol CO}_2 \text{ mol}^{-1}$ ,  $Q = 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and  $V_{cmax0} = 100 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ . In (a, b, c) the  $A-V_{cmax}$  response is shown for  $Q = 1200$  and  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Results for two values of the stomatal parameter,  $a_1$ , are shown (see Eqn 7): solid lines,  $a_1 = 8$ ; dashed lines,  $a_1 = 4$ .

predicted responses of  $A$ ,  $g_{sw}$  and  $c_i/c_s$  of individual leaves to internal ( $c_N$ ) and external ( $Q$ ,  $D_s$  and  $T_l$ ) factors, before integrating these responses over all leaves. The simulations shown in Fig. 1 highlight the non-linearity and complexity of the response surfaces for photosynthesis and stomatal conductance. The leaf-scale responses will later be compared with simplified relationships at the canopy scale.

Both  $A$  and  $g_{sw}$  become saturated at high values of  $V_{cmax}$  (Figs 1a & b), when insufficient radiation is absorbed to

utilize the photosynthetic capacity, but the response is approximately linear when radiation is increased to  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  under full sunlight. (Although  $V_{cmax}$  is used as the independent variable, this is equivalent to  $c_i$  through Eqn 8.)  $A$  and  $g_{sw}$  also become saturated at high values of  $Q$  when there is insufficient photosynthetic capacity (Figs 1d & e). The model predicts that  $c_i/c_s$  does not vary substantially with  $V_{cmax}$  when the stomatal parameter  $a_1$  is fixed (Fig. 1c). As  $Q$  approaches the light compensation point,  $c_i/c_s \rightarrow 1$ , but this ratio remains essentially constant for  $Q > 200 \mu\text{mol m}^{-2} \text{s}^{-1}$ , at constant  $D_s$  (Fig. 1f).

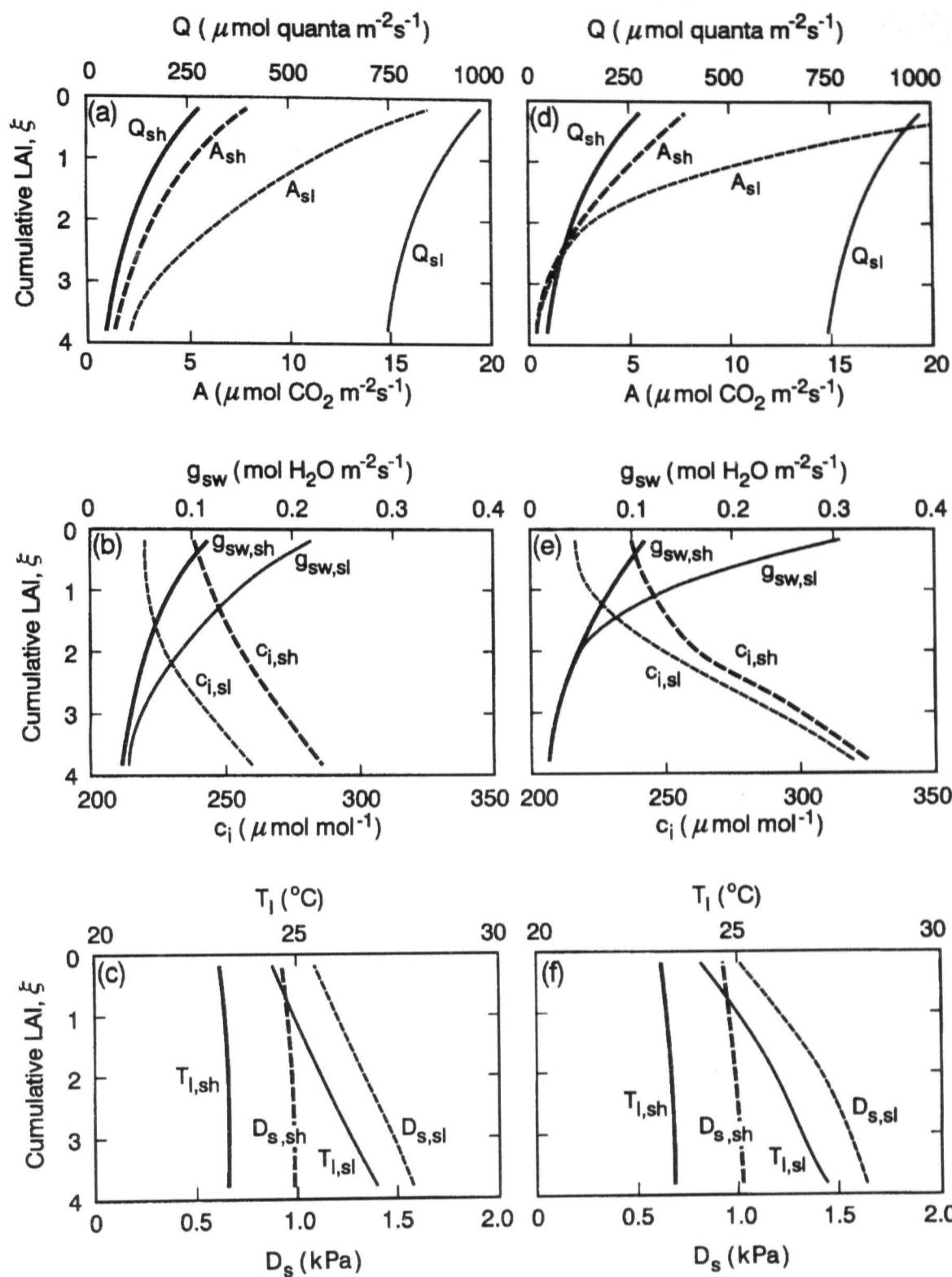
Higher values of  $a_1$  in the stomatal model (Eqn 7) correspond to leaves with higher stomatal conductances for a given value of  $A$ , and hence higher  $c_i/c_s$  (Figs 1c & f). Whereas  $A$  depends only marginally on the value of  $a_1$ , both  $g_{sw}$  and  $c_i/c_s$  depend strongly on  $a_1$  when either  $V_{cmax}$  or  $Q$  varies (Figs 1b–f). Humidity deficit is predicted to cause  $A$  and  $c_i/c_s$  to decrease approximately linearly (Figs 1g & i), and  $g_{sw}$  to decrease hyperbolically (Fig. 1h). A low value of  $a_1$  causes  $A$  and  $c_i/c_s$  to decrease more rapidly with  $D_s$  than a high value of  $a_1$ .

An approximately linear decline was expected for  $c_i/c_s$  in response to increasing temperature when relative humidity was held constant at  $r_h = 0.9$  (Fig. 1l). In contrast, both  $A$  and  $g_{sw}$  peaked at about  $30^\circ\text{C}$  (Figs 1j & k). The fact that  $r_h$  was maintained at a fixed value in the simulations meant that the humidity deficit increased more slowly with increasing temperature than occurs naturally, when daytime absolute humidity is often approximately constant.

### Leaves within a canopy—spatial integration

While the model structure and many of the functions used in this paper may not be controversial, choice of parameter values for those functions critically affects model predictions. This has led some (e.g. Passioura 1973) to question the usefulness of complex models because of the difficulty of validating them against field data, without resorting to ‘fine tuning’. Despite these reservations, the interaction of subsystems within the model can be explored by varying parameter values, leading to testable hypotheses.

Field (1983), Field & Mooney (1986), Hirose & Werger (1987) and others have suggested that plants distribute their available nitrogen to maximize canopy assimilation. Optimization theory indicates that maximum photosynthesis occurs when leaf nitrogen concentration and absorbed radiation have the same distribution within the canopy (Field 1983; Sands 1995). However, radiation penetration varies with time of day and season (de Pury 1995), and it is not clear what constitutes an optimal distribution for  $c_N$ . Leaf nitrogen concentrations have been found to decrease exponentially with depth in many canopies, but reported values of the distribution coefficient,  $k_N$ , differ considerably. Hirose & Werger (1987) obtained values for  $k_N/\Lambda$  of between 0.67 and 0.86 for dense canopies of *Solidago altissima*, and between 0.35 and 0.89 for dense stands, while Schieving *et al.* (1992) observed  $k_N/\Lambda = 0.45$  and 2.8 for open and dense stands of *Carex acutiformis*, respec-



**Figure 2.** Vertical profiles as a function of  $\xi$ , for  $Q$ ,  $A$  (a, d);  $g_{sw}$ ,  $c_i$  (b, e), and  $T_l$ ,  $D_s$  (c, f) when  $\Lambda=4$ . Separate profiles are shown for sunlit and shaded leaves for  $k_N=0.6$  (a, b, c) and  $k_N=1.2$  (d, e, f).

tively. The model was thus first used to assess the influence of varying  $k_N$  on the profiles of  $A$ ,  $g_{sw}$ ,  $c_i$ ,  $T_l$  and  $D_s$  for representative sunlit and shaded leaves within the canopy. We then examined the effects of varying  $k_N$  and changing the balance between the diffuse and direct components of incident radiation on net daytime assimilation for leaves with two levels of N.

Values of  $Q$ ,  $A$  and  $g_{sw}$  for sunlit and shaded leaves are predicted to diminish with  $\xi$ , while  $c_i$ ,  $D_s$  and  $T_s$  are all expected to increase (Fig. 2), although  $D_s$  and  $T_s$  are expected to increase only slightly for shaded leaves. Shaded leaves absorb less radiation than sunlit ones, causing  $A$ ,  $g_{sw}$ ,  $T_l$  and  $D_s$  to have lower values, and  $c_i$  to be higher, at all depths within the canopy. Note that the relative fractions of sunlit and shaded leaves change with canopy depth (Eqn 13) and thus mean values of  $A$  and  $Q$  at

each  $\xi$  change from being close to those of sunlit leaves at the top of the canopy to those of shaded leaves at the bottom. Even though direct rays passing through gaps are not intercepted, radiation absorbed by sunlit leaves decreases with  $\xi$  because of a decrease in the diffuse component. However, lower sunlit leaves are predicted to be warmer than those higher in the canopy, despite smaller radiation loads, because of two factors: (1) the sharp reduction in stomatal conductance with depth reduces latent heat flux in favour of sensible heat, and (2) the assumed wind speed profile reduces boundary layer conductances lower in the canopy, leading to larger leaf-to-air temperature differences for a given heat flux. The shapes of all profiles, except  $Q$ , depend strongly on the assumed value of  $k_N$  (Fig. 2). Total canopy N was kept constant for this comparison, so integration of the exponential profiles (Eqn 9) shows that the

**Table 3.** Variation in daytime total assimilation rate ( $A_d$  mol CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>), as a function of the leaf area index,  $\Lambda$ , the atmospheric transmission coefficient,  $\tau_a$ , and the nitrogen distribution coefficient,  $k_N$ , for plants with low and high leaf N contents.  $Q_d$  is total absorbed photosynthetically active radiation (mol quanta m<sup>-2</sup> d<sup>-1</sup>)

$\Lambda$	$\tau_a$	$Q_d$	Low-N			High-N		
			$k_N=0.0$	$k_N=0.6$	$k_N=1.2$	$k_N=0.0$	$k_N=0.6$	$k_N=1.2$
2	0.3	14.4	0.366	0.409	0.406	0.428	0.417	0.407
	0.8	37.7	0.464	0.608	0.679	1.020	1.100	1.090
4	0.3	17.8	0.455	0.508	0.471	0.480	0.513	0.515
	0.8	47.0	0.629	0.732	0.741	1.250	1.310	1.230

ratio of  $V_{cmax}$  at the top of the canopy for the two cases is given by

$$\frac{V_{cmax}(1.2)}{V_{cmax}(0.6)} = 2 \frac{1-e^{-2.4}}{1-e^{-4.8}} = 1.834 \quad (15)$$

at  $\Lambda=4$ . Both  $A$  and  $g_{sw}$  have higher values at the top of the canopy at  $k_N=1.2$  for sunlit leaves, but there was little impact of  $k_N$  on shaded leaves. This suggests that Rubisco activity limits photosynthesis of the sunlit leaves at the lower value of  $k_N$  (Fig. 1a), but not that of the shaded leaves, where RuP<sub>2</sub> regeneration limits  $A$ . As a result of feedback between stomatal conductance, the leaf energy balance, leaf temperature and photosynthesis, surface temperatures and humidity deficits are predicted to be lower at the top of the canopy and higher at the bottom when  $k_N=1.2$  than when  $k_N=0.6$ . While experimental verification of these predictions is currently lacking, they may be tested in future using the micrometeorological techniques described by Raupach (1989) in combination with suitable physiological measurements.

Atmospheric transmission,  $\tau_a$ , affects both the amount of incident radiation and the fraction of the diffuse component (Appendix A), and hence will affect canopy assimilation rates. The effect of varying  $\tau_a$  and  $k_N$  on the total daytime absorbed radiation and canopy assimilation is shown in Table 4 for plants with low and high leaf N contents,  $c_N$ . For leaves with relatively low  $c_N$ , daily assimilation rates,  $A_d$ , increase by 10–16% as  $k_N$  is raised from 0.0 to 0.6, at both values of  $\Lambda$  and for overcast ( $\tau_a=0.3$ ) and clear ( $\tau_a=0.8$ ) skies. In contrast, there is little difference in  $A_d$  for  $k_N=0.6$  and 1.2 for these leaves. A uniform N distribution resulted in the lowest  $A_d$  for all combinations of  $\Lambda$  and  $\tau_a$  for leaves with low  $c_N$ , but variation in  $k_N$  resulted in little change in  $A_d$  at any given value of  $Q$  for leaves with high  $c_N$ . A change of  $\tau_a$  for 0.3 to 0.8 increased the radiation absorbed by a factor of 2.6 for both  $\Lambda$ , but this did not cause a commensurate increase in  $A_d$  at low  $c_N$ , because the uppermost leaves were light-saturated for part of the day under these conditions. Leaves with higher  $c_N$  were able to utilize the extra radiation under clear skies, since  $A_d$  increased by 2.6 except for uniform N at  $\Lambda=2$ . The higher assimilation rates at  $\Lambda=4$  than at  $\Lambda=2$  resulted from a doubling of total canopy N, since no

adjustment was made to  $V_{cmax}$  for the topmost leaves, in contrast to the adjustment made when varying  $k_N$  (Eqn 15). The results of Table 4 emphasize that the optimum N distribution is not simply a function of light distribution, but also depends on the level of leaf nutrition.

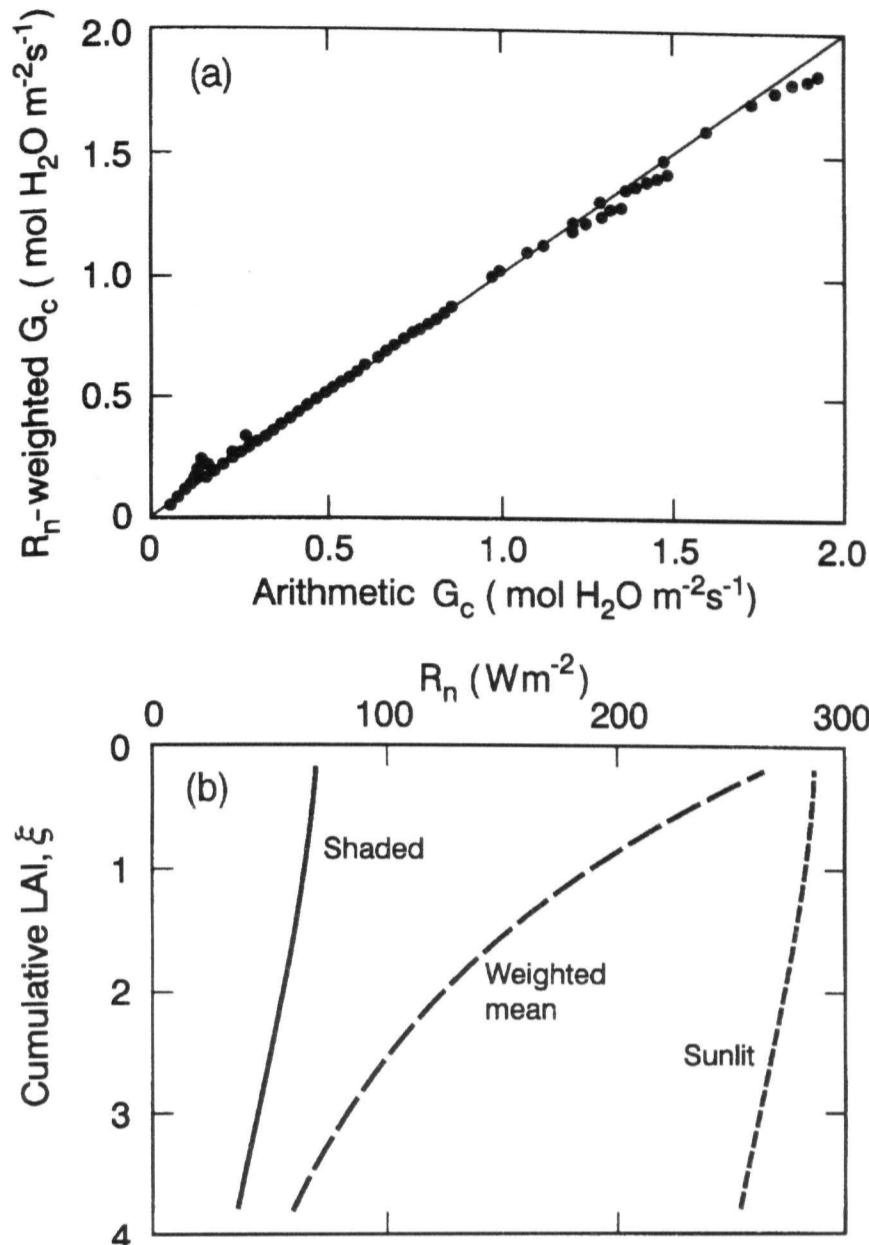
The simplest definition of mean canopy conductance is the sum of stomatal conductances for each layer, using the Gaussian weights shown in Eqn 14. Finnigan & Raupach (1987), Raupach (1991) and McNaughton (1994) showed that this simple definition is not correct because it may not give the correct canopy evaporation when used in a ‘big leaf’ version of the Penman–Monteith equation (Eqn 10). McNaughton (1994) demonstrated that vertically averaged canopy conductance should be calculated as

$$\langle G_s \rangle = \frac{\sum b_n \omega_n \sum b_n R_{n,n}}{\sum b_n R_{n,n} \omega_n r_{sw,n}}, \quad (16)$$

where

$$\omega_n = \frac{1}{r_{sw,n} + r_{bw,n} + \epsilon r_{bh,n}} \quad (17)$$

and where the weighting factors  $b_n$  for each layer are given by  $\Lambda^*G(n)$ , when Gaussian integration is used. Note that leaf-level resistances are used instead of conductances in Eqns 16 and 17, and that sunlit and shaded leaves need to be considered separately. These equations apply to symmetrical amphistomatous leaves;  $r_{bh}$  should be halved for hypostomatous leaves. There is little difference between canopy conductances calculated by the arithmetic and radiation-weighted approaches (Fig. 3), when variation in conductance results from diurnal variations in temperature, humidity deficit, leaf area index or leaf nutrition (Table 2). The two approaches give similar results because there is relatively little variation in net radiation absorbed by sunlit and shaded leaves when considered separately (Fig. 3b). Examination of Eqn 16 shows that the weighting is not required if  $R_n$  is constant with depth. The weighting is needed when stomatal conductances measured on randomly selected leaves are used to estimate canopy conductance, because mean net radiation varies with height as the relative fractions of sunlit and shaded leaves vary (Fig. 3b).



**Figure 3.** (a) Comparison of canopy conductances calculated using net radiation-weighted  $g_{sw}$  (Eqn 16) with those computed using  $g_{sw}$  for sunlit and shaded leaves, weighted by their relative proportions at depth  $\xi$ . The 1:1 line is also shown. (b) Vertical profiles of  $R_n$  for sunlit and shaded leaves and their weighted mean.

### Diurnal variation of fluxes

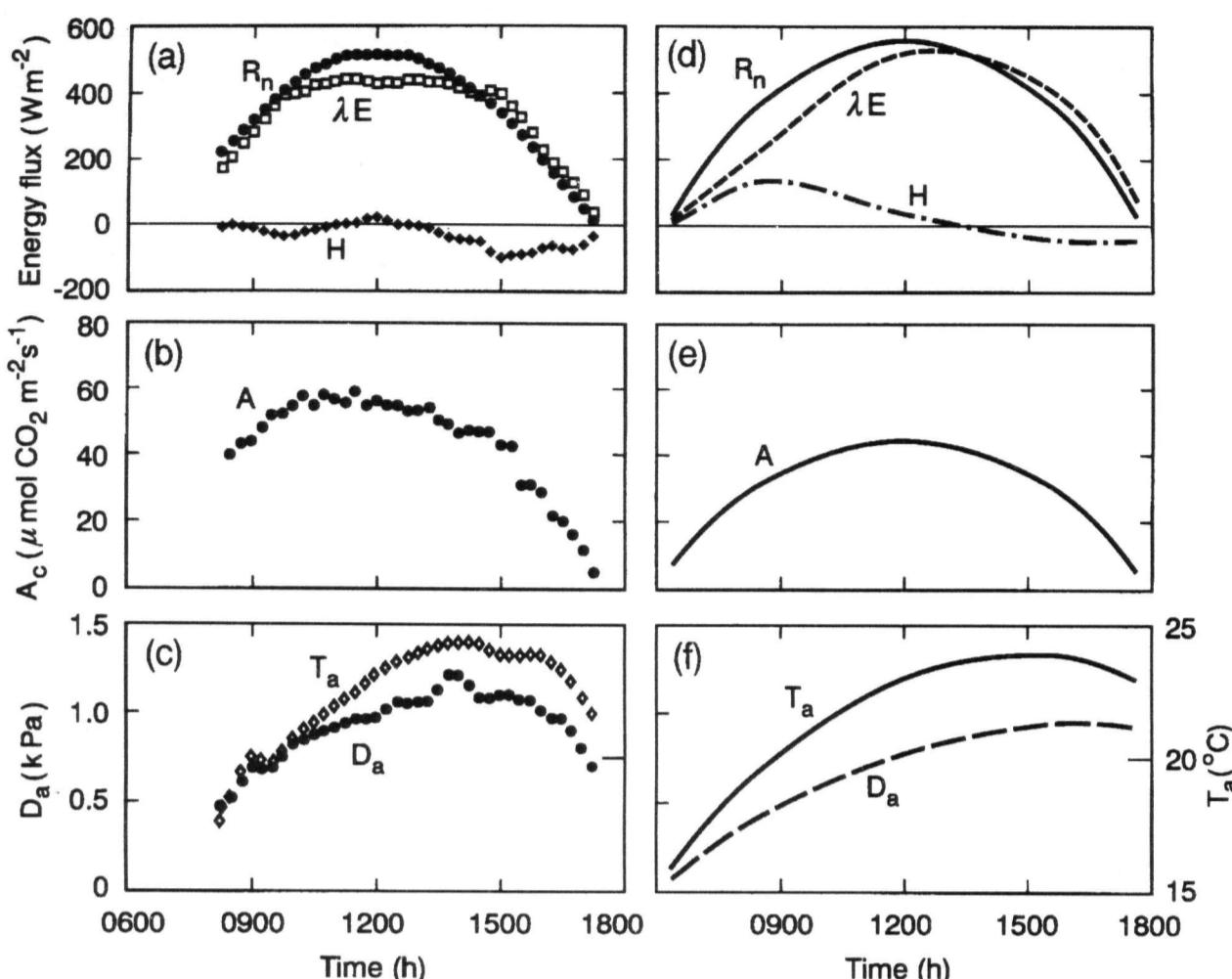
Fluxes of net radiation, sensible and latent heat and CO<sub>2</sub>, measured on 3 October 1991 over a 5 ha field of wheat at Wagga Wagga, NSW, using micrometeorological techniques (Dunin *et al.* 1989), are compared in Fig. 4 to predictions of the current model using parameter values for high-nutrient vegetation (Table 2). Many features of the data are reproduced by the model, including the variation in net radiation, air temperature and humidity deficit. The model predicts a negative sensible heat flux from mid-afternoon onwards, with the consequence that latent heat flux exceeds net radiation at these times. As shown by Leuning *et al.* (1994), soil evaporation was 0.4 mm d<sup>-1</sup> (25 W m<sup>-2</sup>) and thus contributed little to total evapotranspiration. The data showed that sensible heat fluxes were close to zero in the morning, whereas the model predicted fluxes of up to 100 W m<sup>-2</sup>. This discrepancy is explained by the presence of dew on the real canopy typically until about 1000 h, effectively reducing stomatal control of evaporation. Only dry canopies are considered in the model.

Significant disagreement between model and data arises in the CO<sub>2</sub> fluxes (Fig. 4), and this could not be improved by selecting higher values of  $V_{cmax0}$ , the maximum catalytic activity of Rubisco at the reference temperature. An increase of  $V_{cmax0}$  above 150  $\mu\text{mol m}^{-2} \text{s}^{-1}$  causes little increase in  $A_c$  because of limitation in regeneration of RuP<sub>2</sub> ( $J_{max0}/V_{cmax0}=2.1$  is assumed in the model; Wullschleger 1993). A change in the temperature optimum for photosynthesis (Eqn C6) also has little effect on the predictions because simulation temperatures were less than 24 °C.

Predicted diurnal patterns of canopy conductance, and the fluxes of CO<sub>2</sub> and water vapour, are sensitive to the choice of the parameters  $a_1$  and  $D_{s0}$  in the stomatal conductance model (Eqn 7). Leaves with a low value of  $D_{s0}$  are more sensitive to humidity deficit than ones with a high value. To examine the effect of stomatal sensitivity to humidity deficit on  $E$ ,  $A$  and  $G_c$ , the simulation in Fig. 4 was repeated, but with a value of  $D_{s0}=0.5 \text{ kPa}$ , rather than  $D_{s0}=3.5 \text{ kPa}$ . For low  $D_{s0}$ , canopy conductance is predicted to peak early in the morning and then decrease steadily during the day, whereas for high  $D_{s0}$ ,  $G_c$  peaks around midday (Fig. 5c). The lower value of  $D_{s0}$  has little impact on  $A$  (Fig. 5b), but approximately halves  $E$  and shifts the time of peak transpiration from mid-afternoon to around noon (Fig. 5a). These predictions are in accord with observations for well-watered crops, but for forests and water-stressed crops the observed decline in  $G_c$  is somewhat more rapid than shown in Fig. 5c for low  $D_{s0}$  (e.g. Köstner *et al.* 1992; Kelliher *et al.* 1992). The rapid decline in  $G_c$  during the day will be enhanced by plant water stress, and there is evidence that photosynthetic capacity varies during the day (e.g. Küppers *et al.* 1986), neither of which features have been included in the stomatal model.

### Simple parametric models

Sellers *et al.* (1992) suggested that mechanistic canopy models may be used to calculate fluxes consistent with regional and global studies of biogeochemical cycles. This approach is unlikely to succeed because process models require a large number of parameters which are not 'universal constants', but vary in time and space and are unknown for most ecosystems. Instead, extrapolation from small to large scales requires simple models which are readily parametrized, but then system complexity is subsumed into a small number of parameters whose variation depends on the underlying processes. Detailed models may bridge the gap between simplicity and complexity by placing bounds on parameter values in simple models, and identifying major factors contributing to their variability. Two examples are considered below: the first provides an interpretation of linear correlations relating leaf nitrogen concentrations to maximum canopy assimilation (Schulze *et al.* 1994), and the second examines causes of variation in light-use efficiency employed by Ruimy & Saugier (1994) to estimate net primary production.



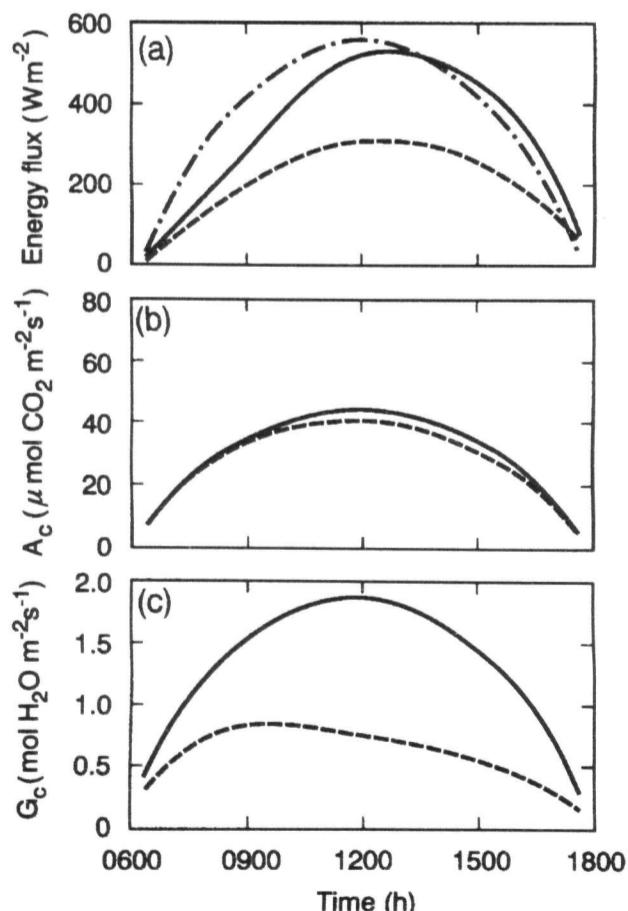
**Figure 4.** Diurnal variation in  $R_n$ ,  $H$ ,  $\lambda E$  (a, d);  $A_c$  (b, e), and  $T_a$ ,  $D_a$  (c, f). Results shown in (a, b, c) were obtained using micrometeorological techniques over a field of wheat at Wagga Wagga, NSW, while those in (d, e, f) are simulations.

#### Nitrogen-use efficiency

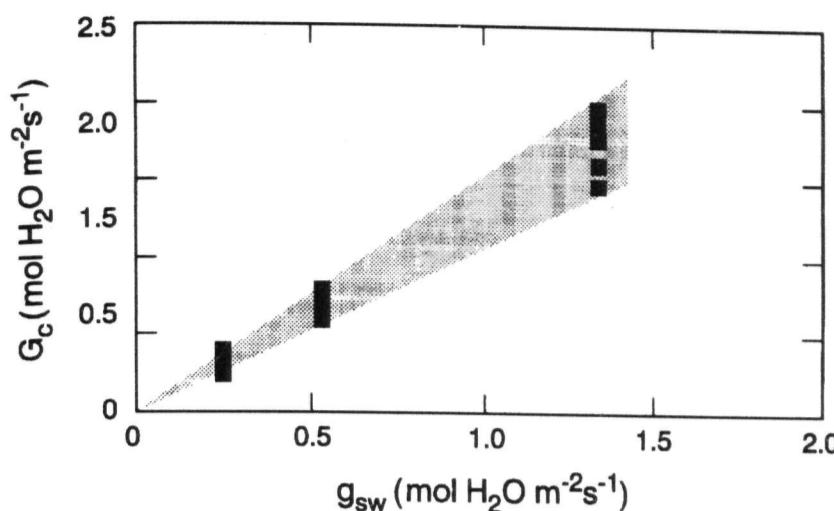
Schulze *et al.* (1994) collated data for a large variety of vegetation types and found strong linear correlations between: (1) leaf-scale nitrogen status and maximum

stomatal conductance, (2) maximum stomatal and canopy conductances, and (3) canopy conductance and maximum canopy assimilation. Distribution of leaf-scale nitrogen status was then used to infer maximum assimilation rates for various world ecosystems. The first correlation is supported by Fig. 1b, which shows that the relationship between  $g_{sw}$  and  $V_{cmax}$  (and hence  $c_N$ ) is almost linear over the full range of  $V_{cmax}$ , provided that absorbed radiation is very high ( $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ , full sunlight). However, the relationships are non-linear for leaves with high  $c_N$  that absorb lower levels of radiation.

Support for the second correlation is shown in Fig. 6, where maximum canopy conductances calculated using the multilayer model are plotted as a function of stomatal conductances of sunlit leaves at the top of the canopy. The results, which were restricted to  $\Lambda \geq 2$ , show a strong relationship between  $G_c$  and  $g_{sw}$ , with variation in  $G_c$  at each stomatal conductance resulting from changes in  $\Lambda$ . The slopes bounding the points range from 1.1 at  $\Lambda = 2$  to 1.5 at  $\Lambda = 6$ . The maximum slope of the line is considerably less than the value of 3 obtained by Kelliher *et al.* (1995) and Schulze *et al.* (1994) when they plotted surface conductance,  $G_s$ , as a function of maximum stomatal conductance. A clear distinction must be made between canopy and surface conductances; the former describes the control of transpiration by vegetation, while surface conductance applies to evapotranspiration from the soil plus vegetation. Canopy conductance will thus always be less than surface conductance. As  $\Lambda \rightarrow 0$ , and all evaporation is



**Figure 5.** Simulated diurnal variation in  $R_n$  (dot-dashed line),  $\lambda E$  (solid and dashed lines) (a);  $A_c$  (b), and  $G_c$  (c) as a function of  $D_{so} = 3.5 \text{ kPa}$  (solid lines) and  $D_{so} = 0.5 \text{ kPa}$  (dashed lines).



**Figure 6.** Predicted correlation between maximum canopy conductance,  $G_c$ , at 1200 h and  $g_{sw}$  of sunlit leaves at the top of the canopy. Results have been restricted to  $2 \leq \Lambda \leq 6$ .

from the soil, then  $G_s$  is dependent on turbulent transport and on soil properties. Surface and canopy conductances will converge at high  $\Lambda$  because shading will reduce soil evaporation. Surface conductances reported by Kelliher *et al.* (1995) were obtained by inverting the Penman-Monteith equation (Eqn 10, with  $G_s$  replacing  $g_{sw}$ ), using micrometeorological measurements of evaporation. Because of lack of concurrent measurements, maximum stomatal conductances reported by Schulze *et al.* (1994) were usually estimated from separate measurements on similar vegetation types. The necessity of combining data from disparate sources, plus the distinction between canopy and surface conductances, may account for the discrepancy between the slope obtained by Kelliher *et al.* (1995) and that obtained in the present analysis. Choice of stomatal conductance of sunlit leaves at the top of the canopy, rather than conductance of a mean leaf, also reduces the slope in Fig. 6. There is a clear need for concurrent physiological and micrometeorological measurements for a variety of ecosystems.

Daily canopy assimilation is shown in Fig. 7 as a function of mean daily canopy conductance  $G_c$  for 'low-N' and 'high-N' plants, having parameter values shown in Table 2. (Note that low-N plants also have a lower value of the stomatal parameters  $a_1$  and  $D_{so}$ .) The simulations were repeated for clear and overcast skies ( $\tau_a = 0.8$  and 0.3, respectively). An approximately linear relationship was found between  $A_c$  and  $G_c$  for the high-N plants under both clear and overcast skies, but separate curves were obtained for the low-N vegetation. A linear correlation between  $A_c$  and  $G_c$  implies a constant  $\bar{c}_i/c_s$ , since, treating the canopy as a big leaf, we may write  $A_c \approx G_c(c_s - \bar{c}_i)$ , where  $\bar{c}_i$  is mean intercellular  $\text{CO}_2$  concentration of leaves within the canopy. For a given canopy conductance, assimilation rates are ~2.3 times higher for plants with low N than for those with high N (Fig. 6). This apparently paradoxical result is explained by Fig. 1c, which shows that  $c_i$  is lower for plants with lower values of  $a_1$  at all values of  $V_{cmax0}$ , thus resulting in a higher value of  $A_c$  for any given  $G_c$ . Data presented by Schulze *et al.* (1994) yield  $\bar{c}_i/c_s = 0.9$ , which corre-

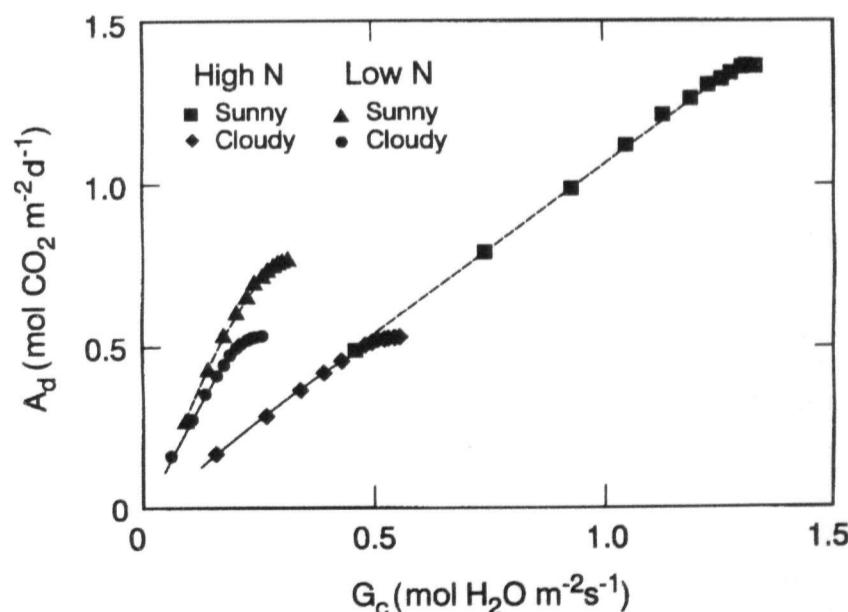
sponds to leaves with relatively high stomatal conductances and is consistent with results obtained for well-watered vegetation.

Results from the detailed model show the limitations of combining three sets of linear correlations produced by Schulze *et al.* (1994) to form the parametric equation  $A_c = \alpha_N c_N$ , where  $\alpha_N$  is a nitrogen-use efficiency. Our analysis suggests that estimates of maximum daily assimilation for various ecosystems may be correct to within a factor of ~3. Further sensitivity analysis using detailed models and comparison with field data are needed to confirm this conclusion.

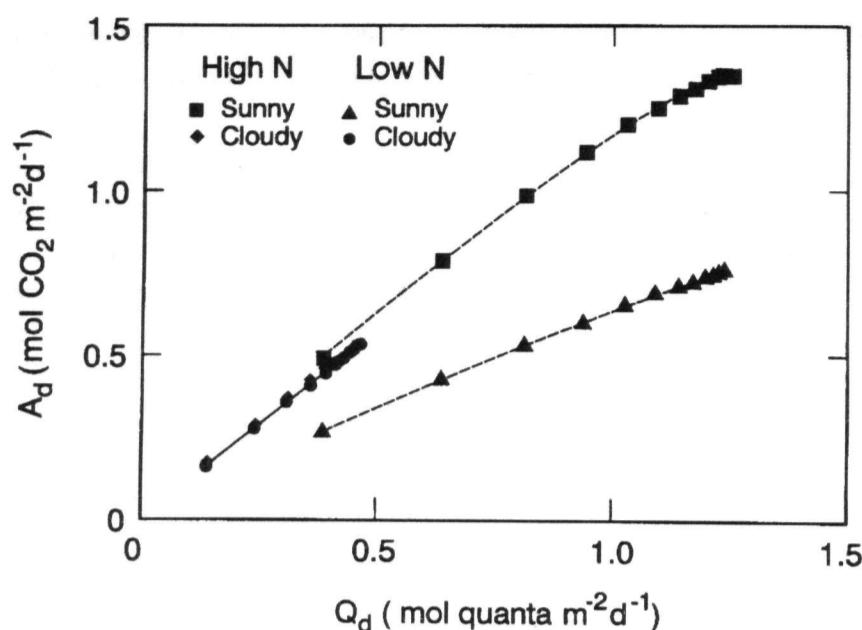
#### Radiation-use efficiency

Monteith (1977) and Ruimy & Saugier (1994) estimated the net primary productivity (NPP) of terrestrial ecosystems using the parametric model  $P(t) = e(t)f(t)S_0(t)$ , where  $P(t)$  is net primary production,  $f(t)$  is the fraction of incoming solar radiation  $S_0(t)$  that is absorbed, and  $e(t)$  is the efficiency of converting absorbed solar radiation to organic dry matter. All quantities are a function of time  $t$ . This equation is attractive because remote sensing techniques can be used to estimate  $f(t)$ , and  $S_0(t)$  can be estimated using climate models. Unfortunately,  $e(t)$  is not constant, but depends on factors such as leaf nitrogen status, plant type (woody, herbaceous), temperature, water availability and photosynthetic pathway ( $C_3, C_4$ ). Daily carbon assimilation is a major component of  $P(t)$ , so the multilayer model was used to see whether daily integration over all leaves produced simpler relations than found at the single leaf scale.

Non-linearities observed in the  $A-Q$  relationship for individual leaves (Fig. 1d) are largely eliminated when daily totals are calculated for the canopy (Fig. 8). However, the slopes between  $A_c$  and  $Q_c$  vary with both



**Figure 7.** Daily canopy assimilation,  $A_d$ , as a function of mean daily canopy conductance,  $G_c$ , for high-N and low-N plants (Table 2) under clear and cloudy skies.  $\Lambda$  ranged from 0.5 to 6.



**Figure 8.** Daily canopy assimilation,  $A_d$ , as a function of total daily absorbed radiation for high-N and low-N plants (Table 2) under clear and cloudy skies.  $\Lambda$  ranged from 0.5 to 6.

leaf nutrient status ( $V_{c\max}$ ) and the stomatal parameter  $a_1$ . As pointed out by Hollinger *et al.* (1994), varying the proportions of direct and diffuse radiation will also alter the relationship between absorbed radiation and canopy assimilation because diffuse radiation is absorbed by canopies more efficiently than beam radiation. This was confirmed for low-N plants (Fig. 8), but not for high-N vegetation, where assimilation rates under diffuse radiation fell on the same curve as for clear skies. Under cloudy skies, there is little differentiation between  $A_c$  values for high- and low-N plants. As for N-use efficiency, there is no unique relationship between daily absorbed radiation and daily assimilation.

## CONCLUSIONS

Two major uses have been identified for the multilayer canopy model presented in this paper. Firstly, it synthesizes much of what is currently known about radiation penetration, leaf physiology and the physics of evaporation. The model was reasonably successful in predicting diurnal variation in canopy conductances and fluxes of  $\text{CO}_2$ , net radiation, sensible heat and water vapour for a typical crop. Consequences of altering the distribution of leaf nitrogen on profiles of assimilation and stomatal conductance were also explored. This type of sensitivity analysis allows examination of the relative importance of various parameters of the model, and hence provides insight into the behaviour of real plant canopies. Secondly, the detailed model was used to explore sources of variation in the slope of two simple parametric models, and for setting bounds on the magnitude of the parameters.

In comparison to plants with uniform N distributions with depth, model results showed that significant gains in daily canopy assimilation are obtained for plants with low N concentrations when leaf N is distributed according to the profile of absorbed radiation. The gains are

small for plants with high N concentrations. Canopy conductance,  $G_c$ , should be calculated as  $G_c = \Lambda \Sigma (f_{sl}g_{sl} + f_{sh}g_{sh})$ , where  $f_{sl}$  and  $f_{sh}$  are the fractions of sunlit and shaded leaves at each level, and  $g_{sl}$  and  $g_{sh}$  are the corresponding stomatal conductances. Simple addition of conductances without this weighting causes errors in transpiration calculated in the 'big leaf' version of the Penman-Monteith equation. Calculated energy partitioning between sensible and latent heat is very responsive to the parameter describing the sensitivity of stomata to atmospheric humidity deficit. This parameter also affects canopy conductance, but has a relatively small impact on canopy assimilation.

Simple parametric models are useful for extrapolating understanding from small to large scales, but the complexity of real ecosystems causes variation in parameter values. Both nitrogen- and radiation-use efficiencies depend on plant nutritional status and the diffuse component of incident radiation.

## ACKNOWLEDGMENTS

R.L. thanks Ms Christine Hofmann, Department of Plant Ecology, University of Bayreuth for invaluable bibliographic assistance and for critical reading of the manuscript. Messrs F. X. Dunin and W. Reyenga, CSIRO Division of Plant Industry are gratefully thanked for the micrometeorological data presented in Fig. 4. F.M.K. thanks the New Zealand Foundation for Research, Science and Technology for their continued support of international atmospheric research.

## REFERENCES

- Amthor J.S. (1994) Scaling  $\text{CO}_2$ -photosynthesis relationships from the leaf to the canopy. *Photosynthesis Research* **39**, 321–350.
- Ball J.T., Woodrow I.E. & Berry J.A. (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In *Progress in Photosynthesis Research* (ed. J. Biggens), pp. 221–224. Martinus Nijhoff Publishers, The Netherlands.
- Brooks A. & Farquhar G.D. (1985) Effect of temperature on the  $\text{CO}_2/\text{O}_2$  specificity of Ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. Estimates from gas-exchange measurements on spinach. *Planta* **165**, 397–406.
- Brutsaert, W. (1975) On a derivable formula for long-wave radiation from clear skies. *Water Resources Research* **11**, 742–744.
- Caemmerer, S. von & Farquhar G.D. (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* **153**, 376–387.
- Collatz G.J., Ball J.T., Grivet C. & Berry J.A. (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer. *Agricultural and Forest Meteorology* **54**, 107–136.
- Cowan I.R. (1977) Stomatal behaviour and environment. *Advances in Botanical Research* **4**, 117–228.
- Cowan I.R. (1982) Regulations and water use in relation to carbon gain in higher plants. In *Encyclopedia of Plant*

- Physiology, New Series*, Vol. 12B (eds L. Lange, P.S. Nobel & C.B. Osmond), pp. 589–613. Springer-Verlag, Berlin.
- de Pury D.D.G. (1995) *Scaling Photosynthesis and Water use from Leaves to Paddocks*. PhD thesis, Australian National University, Canberra.
- Deacon E.L. (1970) The derivation of Swinbank's long-wave radiation formula. *Quarterly Journal of the Royal Meteorological Society* **96**, 313–319.
- Dunin F.X., Meyers W.S., Wong S.C. & Reyenga W. (1989) Seasonal change in water use and carbon assimilation of irrigated wheat. *Agricultural and Forest Meteorology* **45**, 231–250.
- Evans J.R. (1993) Photosynthetic acclimation and nitrogen partitioning within a lucerne canopy. II Stability through time and comparison with a theoretical optimum. *Australian Journal of Plant Physiology* **20**, 69–82.
- Farquhar G.D. (1989) Models of integrated photosynthesis of cells and leaves. *Philosophical Transactions of the Royal Society of London B* **323**, 357–367.
- Farquhar G.D. & Wong S.C. (1984) An empirical model of stomatal conductance. *Australian Journal of Plant Physiology* **11**, 191–210.
- Farquhar G.D., Caemmerer S. von & Berry J.A. (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* **149**, 78–90.
- Field C. (1983) Allocating leaf nitrogen for the maximisation of carbon gain: Leaf age as a control on the allocation program. *Oecologia* **56**, 341–347.
- Field C. & Mooney H.A. (1986) The photosynthesis-nitrogen relationship in wild plants. In *On the Economy of Plant Form and Function* (ed. T.J. Givnish), pp. 25–55. Cambridge University Press, Cambridge.
- Finnigan J.J. & Raupach M.R. (1987) Transfer processes in plant canopies in relation to stomatal characteristics. In *Stomatal Function* (eds E. Zeiger, G.D. Farquhar & I.R. Cowan), pp. 385–429. Stanford University Press, Stanford, CA.
- Gates D.M. (1965) Heat, radiant and sensible. Chapter 1: Radiant energy, its receipt and disposal. *Meteorological Monographs* **6**, 1–26.
- Goudriaan J. (1977) *Crop Micrometeorology: A Simulation Study*. Centre for Agricultural Publishing and Documentation, Wageningen.
- Goudriaan J. (1986) A simple and fast numerical method for the computation of daily totals of crop photosynthesis. *Agricultural and Forest Meteorology* **38**, 249–254.
- Goudriaan J. (1988) The bare bones of leaf angle distribution in radiation models for canopy photosynthesis and energy exchange. *Agricultural and Forest Meteorology* **43**, 155–169.
- Goudriaan J. & van Laar H.H. (1994) *Modelling Crop Growth Processes*. Kluwer, Amsterdam.
- Harley P.C., Thomas R.B., Reynolds J.F. & Strain B.R. (1992) Modelling photosynthesis of cotton grown in elevated CO<sub>2</sub>. *Plant, Cell and Environment* **15**, 271–282.
- Hatfield J.L., Reginato R.J. & Idso S.B. (1983) Comparison of long-wave radiation calculation methods over the United States. *Water Resources Research* **19**, 285–288.
- Hirose T. & Werger M.J.A. (1987) Maximising daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* **72**, 520–526.
- Hollinger D.Y., Kelliher F.M., Byers J.N., Hunt J.E., McSeveny T.M. & Weir P.L. (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* **75**, 134–150.
- Jarvis P.G. (1976) The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London Series B* **273**, 593–610.
- Jarvis P.G. & McNaughton K.C. (1986) Predicting effects of vegetation changes on transpiration and evaporation. *Advances in Ecological Research* **15**, 1–49.
- Jones H.G. (1976) Crop characteristics and the ratio between assimilation and transpiration. *Journal of Applied Ecology* **13**, 605–622.
- Kelliher F.M., Köstner B.M.M., Hollinger D.Y., Byers J.N., Hunt J.E., McSeveny T.M., Meserth R., Weir P.L. & Schulze E.-D. (1992) Evaporation, xylem sap flow, and tree transpiration in a New Zealand broad-leaved forest. *Agricultural and Forest Meteorology* **62**, 53–73.
- Kelliher F.M., Leuning R., Raupach M.R. & Schulze E.-D. (1995) Maximum conductances for evaporation from global vegetation types. *Agriculture and Forest Meteorology* **73**, 1–16.
- Köstner B.M.M., Schulze E.-D., Kelliher F.M., Hollinger D.Y., Byers J.N., Hunt J.E., McSeveny T.M., Meserth R. & Weir P.L. (1992) Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia* **91**, 350–359.
- Küppers M., Wheeler A.M., Küppers B.I.L., Kirschbaum M.U.F. & Farquhar G.D. (1986) Carbon fixation in eucalypts in the field. *Oecologia* **70**, 237–282.
- Leuning R. (1983) Transport of gases into leaves. *Plant, Cell and Environment* **6**, 181–194.
- Leuning R. (1990) Modelling stomatal behaviour and photosynthesis of *Eucalyptus grandis*. *Australian Journal of Plant Physiology* **17**, 159–175.
- Leuning R. (1995) A critical appraisal of a combined stomatal-photosynthesis model for C<sub>3</sub> plants. *Plant, Cell and Environment* **18**, 339–357.
- Leuning R., Cromer R.N. & Rance S. (1991) Spatial distributions of foliar nitrogen and phosphorus in crowns of *Eucalyptus grandis*. *Oecologia* **88**, 504–510.
- Leuning R., Condon A.G., Dunin F.X., Zegelin S. & Denmead O.T. (1994) Rainfall interception and evaporation from soil below a wheat canopy. *Agricultural and Forest Meteorology* **67**, 221–238.
- McNaughton K.G. (1994) Effective stomatal and boundary-layer resistances of heterogeneous surfaces. *Plant, Cell and Environment* **17**, 1061–1068.
- Monteith J.L. (1965) Evaporation and Environment. The State and Movement of Water in Living Organisms. *Symposium of the Society of Experimental Biology* **19**, 205–234. Cambridge University Press.
- Monteith J.L. (1973) *Principles of Environmental Physics*. Edward Arnold, London.
- Monteith J.L. (1977) Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London Series B* **281**, 277–294.
- Passioura J.B. (1973) Sense and nonsense in crop simulation. *Journal of the Australian Institute of Agricultural Science* **39**, 181–183.
- Raupach M.R. (1989) A practical Lagrangian method for relating concentrations to source distributions in vegetation canopies. *Quarterly Journal of the Royal Meteorological Society* **115**, 609–632.
- Raupach M.R. (1991) Vegetation-atmosphere interaction in homogeneous and heterogeneous terrain—Some implications of mixed-layer dynamics. *Vegetatio* **91**, 105–120.
- Raupach M.R. & Finnigan J.J. (1988) Single-layer models of evaporation from plant canopies are incorrect but useful, whereas, multilayer models are correct but useless: Discuss. *Australian Journal of Plant Physiology* **15**, 705–716.
- Ross J. (1981) *The Radiation Regime and Architecture of Plant*

- Stands*. W. Junk, London.
- Ruimy A. & Saugier B. (1994) Methodology for estimation of terrestrial net primary production from remotely sensed data. *Journal of Geophysical Research—Atmospheres* **99**, D3, 5263–5283.
- Sands P.J. (1995) Modelling canopy production: I. Optimal distribution of photosynthetic resources. *Australian Journal of Plant Physiology*, in press.
- Scheibling F., Pons T.L., Werger M.J.A. & Hirose T. (1992) The vertical distribution of nitrogen and photosynthetic activity at different plant densities in *Carex acutiformis*. *Plant and Soil* **14**, 9–17.
- Schulze E.-D., Kelliher F.M., Körner C., Lloyd J. & Leuning R. (1994) Relationships between maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate and plant nitrogen nutrition: A global ecology scaling exercise. *Annual Reviews of Ecology and Systematics* **25**, 629–660.
- Sellers P.J., Berry J.A., Collatz G.J., Field C.B. & Hall F.G. (1992) Canopy reflectance, photosynthesis and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing Environment* **42**, 187–216.
- Spitters C.J.T. (1986) Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis. Part II. Calculation of canopy photosynthesis. *Agricultural and Forest Meteorology* **38**, 231–242.
- Spitters C.J.T., Toussaint H.A.J.M. & Goudriaan J. (1986) Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis. Part I. Components of incoming radiation. *Agricultural and Forest Meteorology* **38**, 225–237.
- Stocking C.R. & Ongun A. (1962) The intercellular distribution of some metallic elements in leaves. *American Journal of Botany* **49**, 284–289.
- Tenhunen J.D., Sala Serra A., Harley P.C., Dougherty R.L. & Reynolds J.F. (1990) Factors influencing carbon fixation and water use by mediterranean sclerophyll shrubs during summer drought. *Oecologia* **82**, 381–393.
- Wang Y.P. & Jarvis P.G. (1990) Description and validation of an array model—MAESTRO. *Agricultural and Forest Meteorology* **51**, 257–280.
- Wong S.C., Cowan I.R. & Farquhar G.D. (1979) Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**, 424–426.
- Wullschleger S.D. (1993) Biochemical limitations to carbon assimilation in C<sub>3</sub> plants—A retrospective analysis of the A/c<sub>i</sub> curves from 109 species. *Journal of Experimental Botany* **44**, 907–920.

## APPENDIX A: TOTAL SOLAR RADIATION AT THE EARTH'S SURFACE AND ITS PARTITIONING INTO DIRECT AND DIFFUSE COMPONENTS

While many of the equations in the following appendices are well known, they appear in diverse sources, so they are collected here to allow interested readers to reconstruct the full model should they wish.

According to Goudriaan & van Laar (1994), the direct radiation incident on a horizontal plane at the Earth's surface may be written as

$$S_0 = \tau_a S_c \sin\beta, \quad (\text{A1})$$

where  $\tau_a$  is the atmospheric transmissivity and  $S_c$  is the flux density of solar radiation normal to the sun's beam outside the Earth's atmosphere:

$$S_c = 1367 \{ 1 + 0.033 \cos[2\pi(t_d - 10)/365] \}, \quad (\text{A2})$$

where  $t_d$  is the day of the year (1 = 1 Jan). The term in brackets corrects the solar constant (1367 W m<sup>-2</sup>) for eccentricity of the sun's orbit. The solar elevation  $\sin\beta$  is

$$\sin\beta = a + b \cos[2\pi(t_h - 12)/24], \quad (\text{A3})$$

where  $t_h$  is the solar time in hours, and

$$a = \sin\lambda_1 \sin\delta_s, \quad b = \cos\lambda_1 \cos\delta_s \quad (\text{A4})$$

with

$$\sin\delta_s = -\sin(23.5\pi/180) \cos[2\pi(t_d + 10)/365], \quad (\text{A5})$$

in which  $\lambda_1$  is the degree of latitude and  $\delta_s$  is the declination of the sun with respect to the equator. The number 23.5 is the latitude of the tropics in degrees.

The quantities  $a$  and  $b$  may be used to evaluate the daylength in hours:

$$t_{dl} = 12[1 + (2/\pi) \operatorname{asin}(a/b)]. \quad (\text{A6})$$

This expression is required for the Gaussian integration technique (see main text) and for scaling temperatures and wind speeds (Appendix F).

Incident solar radiation consists of a direct beam component,  $S_{b0}$ , and a diffuse component,  $S_{d0}$ . Following Goudriaan & van Laar (1994), the fraction of diffuse radiation,  $f_d$ , is estimated as a simple function of the atmospheric transmissivity,  $\tau_a$ , such that

$$\begin{aligned} f_d &= 1, & \tau_a < 0.3, \\ f_d &= 1 - 2(\tau_a - 0.3), & 0.3 \leq \tau_a \leq 0.7, \\ f_d &= 0.2, & \tau_a > 0.7. \end{aligned} \quad (\text{A7})$$

The diffuse component of incoming radiation is  $S_{d0} = f_d S_0$  and the direct beam component is  $S_{b0} = (1 - f_d) S_0$ . More detailed methods for estimating the direct and diffuse components of incoming radiation using only the measured daily global irradiance were presented by Spitters *et al.* (1986). For present purposes, values of  $\tau_a$  will be specified *a priori* (see Table 1).

The model for photosynthesis requires quantum flux density for photosynthetically active radiation,  $Q$ , rather than solar energy,  $S$ , and a simple conversion factor of 1 W m<sup>-2</sup> (total solar) = 2 μmol m<sup>-2</sup> s<sup>-1</sup> was used in the calculations.

## APPENDIX B: CANOPY EXTINCTION AND REFLECTION COEFFICIENTS

Extinction coefficients for diffuse and beam radiation required for Eqns 1 and 2 are given by

$$k_d' = k_d (1 - \sigma_l)^{1/2}, \quad (\text{B1})$$

$$k_b' = k_b (1 - \sigma_l)^{1/2}, \quad (\text{B2})$$

where  $\sigma_l$  is the scattering coefficient for leaves, and  $k_d$  is the extinction coefficient for diffuse radiation and a canopy of black leaves. Although  $k_d$  is a function of the distribution of radiance from the sky, leaf angle distribution and leaf area index (Goudriaan 1988), it may be approximated to first order by the constant  $k_d=0.8$  for leaves with a spherical leaf angle distribution (Goudriaan & van Laar 1994). The coefficient  $k_b$  is a function of the mean projected leaf area in the direction of the sun's beam,  $G(\beta)$ , and the solar elevation  $\sin(\beta)$  [see Appendix A for equations to determine  $\sin(\beta)$ ]. A spherical leaf angle distribution is assumed here, in which case  $G(\beta)=0.5$  and  $k_b=0.5/\sin(\beta)$ . Goudriaan (1977) showed that the canopy reflection coefficient for beam radiation,  $\rho_{cb}$  in Eqn 3, is related to the canopy reflection coefficient for horizontal leaves,  $\rho_h$ , by

$$\rho_{cb} = 1 - \exp[(-2\rho_h k_b)/(1 + k_b)], \quad (B3)$$

where

$$\rho_h = \frac{1 - (1 - \sigma_l)^{1/2}}{1 + (1 - \sigma_l)^{1/2}}. \quad (B4)$$

Scattering coefficients are typically  $\sigma_l=0.2$  for visible radiation and  $\sigma_l=0.8$  in the NIR. The reflection coefficient for diffuse radiation (Eqn 2) is  $\rho_{cd}=0.057$  (visible) and  $\rho_{cd}=0.389$  (NIR) for canopies with a spherical leaf angle distribution when incoming diffuse radiation is distributed uniformly across the sky (Goudriaan & van Laar 1994).

## APPENDIX C: BRIEF DESCRIPTION OF C<sub>3</sub> PHOTOSYNTHESIS MODEL

According to Farquhar *et al.* (1980) and von Caemmerer & Farquhar (1981), the assimilation rate,  $A_v$ , limited by Rubisco activity in Eqn 5 is given by

$$A_v = V_{cmax} \frac{c_i - \Gamma_*}{c_i + K_c(1 + o_i/K_o)}, \quad (C1)$$

in which  $V_{cmax}$  is the maximum catalytic activity of Rubisco in the presence of saturating levels of RuP<sub>2</sub> and CO<sub>2</sub>,  $\Gamma_*$  is the CO<sub>2</sub> compensation point in the absence of day respiration,  $o_i$  is the intercellular oxygen concentration, and  $K_c$  and  $K_o$  are Michaelis coefficients for CO<sub>2</sub> and O<sub>2</sub>, respectively.

When photosynthetic electron transport limits RuP<sub>2</sub> regeneration, assimilation rate is given by

$$A_j = \frac{J}{4} \frac{c_i - \Gamma_*}{(c_i + 2\Gamma_*)}, \quad (C2)$$

where  $J$  is the electron transport rate for a given absorbed photon irradiance,  $Q$ . Farquhar & Wong (1984) used a non-rectangular hyperbolic function to describe  $J$  in terms of  $Q$ :

$$\theta J^2 - (\alpha Q + J_{max}) J + \alpha Q J_{max} = 0, \quad (C3)$$

where  $\theta$  determines the shape of the non-rectangular

hyperbola,  $J_{max}$  is the potential rate of whole-chain electron transport and  $\alpha$  is the quantum yield of whole-chain electron transport. Parameter values used in the photosynthesis model are given in Table 3.

## Dependence on leaf temperature

The kinetic parameters  $K_c$  and  $K_o$ , day respiration  $R_d$ , and the CO<sub>2</sub> compensation point,  $\Gamma_*$ , are dependent on leaf temperature. A second-order polynomial (Brooks & Farquhar 1985) was used to describe the temperature dependence of  $\Gamma_*$ , namely

$$\Gamma_* = \gamma_0 [1 + \gamma_1 (T_l - T_0) + \gamma_2 (T_l - T_0)^2], \quad (C4)$$

where  $\gamma_0$ ,  $\gamma_1$  and  $\gamma_2$  are empirical constants,  $T_l$  is leaf temperature and  $T_0$  is a reference temperature (293.2 K). A normalized Arrhenius equation was used to represent the temperature dependence of  $K_c$  and  $K_o$ ,

$$K_x = K_{x0} \exp[(H_x/RT_0)(1 - T_0/T_l)], \quad (C5)$$

in which temperatures are in degrees K,  $R$  is the universal gas constant,  $H_x$  is the activation energy for  $K_x$ , where the subscript x stands for either c or o, and  $K_{x0}$  is the value of  $K_x$  at a reference temperature  $T_0$ .

The temperature dependence of  $V_{cmax}$  was modelled according to Farquhar *et al.* (1980) and Harley *et al.* (1992):

$$V_{cmax} = \frac{V_{cmax0} \exp[(H_v/RT_0)(1 - T_0/T_l)]}{1 + \exp[(S_v T_l - H_d)/(RT_1)]}, \quad (C6)$$

where  $V_{cmax0}$  is the value of  $V_{cmax}$  at  $T_0$ ,  $H_v$  is the energy of activation,  $H_d$  is the energy of deactivation and  $S_v$  is an entropy term. Wullschleger (1993) reviewed data for the ratio  $J_{max}/V_{cmax}$  and found that a fixed value of 2.1 applied to a wide variety of leaves examined. This ratio was used in the present model.

Leaf respiration that continues in the light,  $R_d$ , was assumed to be a fixed proportion of Rubisco capacity, and we assume that  $R_d=0.0089 V_{cmax}$ . This amounts to assuming a fixed CO<sub>2</sub> compensation point,  $\Gamma$  (de Pury 1995). A complete list of parameters used in the photosynthesis model is given in Table 3.

## APPENDIX D: ISOTHERMAL NET RADIATION AND RADIATION CONDUCTANCE

The isothermal net radiation required in the combination equation (Eqn 10) has two components, absorbed solar radiation and net thermal radiation, and is given by

$$R_n^* = S_n - B_{n,0} k_d \exp(-k_d \xi), \quad (D1)$$

where  $k_d$  is the extinction coefficient for diffuse radiation and black leaves with a spherical leaf angle distribution. Absorbed solar radiation,  $S_n$ , can be calculated using the equations presented in the section 'Radiation absorption' and Appendix A, while noting that approxi-

mately half of the incident solar radiation is in the visible and the other half is in the NIR waveband (Gates 1965). Reflection and transmission coefficients of leaves typically have values of 0.1 in the visible waveband and 0.4 in the NIR. This ensures maximum capture of energy in the photosynthetically active region, while reducing the energy load on leaves from absorption of NIR radiation. Appropriate values for the scattering, reflecting and extinction coefficients must thus be used for each waveband (Table 1), and separate values for  $R_n^*$  need to be computed for sunlit and shaded leaves.

Isothermal net longwave radiation exchange at the top of the canopy,  $B_{n,0}$  is expressed as

$$B_{n,0} = \varepsilon_c \sigma T_a^4 - R_{L\downarrow}, \quad (D2)$$

where  $\varepsilon_c$  is the emissivity of the canopy and  $R_{L\downarrow}$  is the downward thermal radiation from the sky. This quantity should preferably be measured, but for clear skies  $R_{L\downarrow}$  may be estimated using

$$R_{L\downarrow} = \varepsilon_{atm} \sigma T_a^4, \quad (D3)$$

where  $\varepsilon_{atm}$  is an apparent emissivity for a hemisphere radiating at air temperature ( $T_a$ , in degrees K). Hatfield *et al.* (1983) compared several formulae for estimating  $\varepsilon_{atm}$  and found that the following equation proposed by Brutsaert (1975) gave the best results:

$$\varepsilon_{atm} = 0.642(e_a/T_a)^{1/7}, \quad (D4)$$

where  $e_a$  is atmospheric water vapour pressure (Pa). This formula is successful because downward thermal radiation is dominated by emission from air and water vapour molecules within the lowest tens of metres of the atmosphere (Deacon 1970).

When Eqns D2 and D3 are combined with the assumption that  $\varepsilon_c = 1$ , we obtain

$$B_{n,0} = (1 - \varepsilon_{atm}) \sigma T_a^4. \quad (D5)$$

The coefficient  $Y$  in Eqn 10 is given by

$$Y = \frac{1}{1 + g_{RN}/g_{BH}}, \quad (D6)$$

in which the 'radiation conductance' is defined as

$$g_{RN} = 4\varepsilon_l \sigma T_a^3 k_d \exp(-k_d \xi) / \rho_a c_p, \quad (D7)$$

where  $T_a$  is the air temperature (K),  $\varepsilon_l$  is the emissivity of the leaf, and  $\sigma$  is the Steffan–Boltzman constant. Calculation of the boundary layer conductance for heat,  $g_{BH}$ , is presented in Appendix E.

## APPENDIX E: BOUNDARY LAYER CONDUCTANCE FOR HEAT

Both forced and free convection contribute to exchange of heat and mass through leaf boundary layers at the wind speeds typically encountered within plant canopies ( $<0.5 \text{ m s}^{-1}$ ). It is particularly important to include the contribution of buoyancy forces to the boundary conductance for sunlit leaves deep within the canopy where

wind speeds are low, for without this mechanism computed leaf temperatures become excessively high.

From Monteith (1973), the boundary layer conductance for one side of a leaf resulting from forced convection may be calculated using

$$g_{BHw} = 0.003(U/w_l)^{1/2}, \quad (E1)$$

in which  $U$  is the wind speed ( $\text{m s}^{-1}$ ) and  $w_l$  is the leaf width (m). The wind speed within the canopy was assumed to decrease exponentially with depth in the canopy according to

$$U(\xi) = U_0 \exp(-k_u \xi), \quad (E2)$$

where  $U_0$  is the wind speed just above the canopy.

Monteith (1973) showed that for free convection the leaf boundary layer conductance is

$$g_{BHf} = 0.5 D_H Gr^{1/4} / w_l, \quad (E3)$$

in which  $D_H$  is the molecular diffusivity for heat and the Grashof number is

$$Gr = 1.6 \times 10^8 |T_l - T_a| w_l^3, \quad (E4)$$

where  $T_l$  and  $T_a$  are leaf and air temperatures, respectively.

Total boundary layer conductance to heat for one side of a leaf is

$$g_{BH} = g_{BHw} + g_{BHf}. \quad (E5)$$

The boundary layer conductance for water vapour is  $g_{bw} = 1.075 g_{BH}$ . All conductances must be doubled when used to describe transpiration of amphistomatous leaves (Eqn 10), but for hypostomatous leaves only  $g_{BH}$  should be doubled and the single-sided value used for  $g_{bw}$ .

## APPENDIX F: AIR TEMPERATURE, HUMIDITY DEFICIT AND WIND SPEED

Diurnal variations in air temperature, humidity deficit and wind speed were estimated using the following functions.

The air temperature between sunrise and sunset was calculated as

$$T_a = T_{an} + (T_{ax} - T_{an}) \sin[\pi(t_h + t_{dl}/2 - 12)/(t_{dl} + t_{mT})]. \quad (F1)$$

A similar function was used for the wet bulb temperature, and the psychrometric equation was used to calculate the water vapour pressure and the humidity deficit of the air at any desired time. In Eqn F1,  $T_{an}$  and  $T_{ax}$  are the minimum and maximum temperatures for the day,  $t_h$  is the time of day (h),  $t_{dl}$  is the daylength and  $t_{mT}$  is twice the number of hours between noon and the time of maximum temperature.

The wind speed at the reference height was estimated using

$$U_0 = U_n + (U_x - U_n) \sin[\pi(t_h + t_{dl}/2 - 12)/(t_{dl} + t_{mu})], \quad (F2)$$

where  $U_n$  and  $U_x$  are minimum and maximum wind speeds and  $t_{mu}$  is twice the number of hours between noon and the time of maximum wind speed.

## APPENDIX G: LIST OF SYMBOLS (with units)

$a$	Eqn A3 (-)	$g_{RN}$	radiation conductance ( $\text{m s}^{-1}$ )
$a_1$	empirical coefficient in Eqn 13 (-)	$g_{SC}$	stomatal conductance for $\text{CO}_2$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )
$a_N$	empirical coefficient in Eqn 8 [ $\text{mol CO}_2 \text{m}^{-2} \text{d}^{-1}$ ( $\text{mol N m}^{-2}$ ) $^{-1}$ ]	$g_{SW}$	stomatal conductance for $\text{H}_2\text{O}$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )
$A$	$\text{CO}_2$ assimilation rate of leaves ( $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )	$G_c$	canopy conductance for water vapour ( $\text{mol m}^{-2} \text{s}^{-1}$ )
$A_c$	canopy assimilation rate ( $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )	$\langle G_s \rangle$	radiation-weighted sum of stomatal conductances ( $\text{mol m}^{-2} \text{s}^{-1}$ )
$A_d$	total daytime canopy assimilation ( $\text{mol CO}_2 \text{m}^{-2} \text{d}^{-1}$ )	$Gr$	Grashof number (-)
$A_j$	gross rate of photosynthesis limited by RuP <sub>2</sub> regeneration ( $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )	$G_w(n)$	normalized Gaussian weights (-)
$A_{sl}$	$\text{CO}_2$ assimilation rate of sunlit leaves ( $\text{mol CO}_2 \text{m}^{-2} \text{d}^{-1}$ )	$G_x(n)$	normalized Gaussian distances (-)
$A_{sh}$	$\text{CO}_2$ assimilation rate of shaded leaves ( $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )	$H$	sensible heat flux density ( $\text{W m}^{-2}$ )
$A_v$	gross rate of photosynthesis limited by Rubisco activity ( $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )	$H_d$	deactivation energy ( $\text{J mol}^{-1}$ )
$b$	Eqn A3 (-)	$H_v$	activation energy ( $\text{J mol}^{-1}$ )
$b_n$	weighting factor (Eqn 16)	$J$	electron transport rate ( $\text{mol e m}^{-2} \text{s}^{-1}$ )
$B_{n,0}$	isothermal net longwave radiation at canopy top ( $\text{W m}^{-2}$ )	$J_{max}$	potential rate of whole-chain electron transport ( $\text{mol e m}^{-2} \text{s}^{-1}$ )
$c_a$	$\text{CO}_2$ concentration in the free air ( $\text{mol CO}_2 \text{mol}^{-1}$ )	$J_{max0}$	potential rate of whole-chain electron transport at $T_0$ ( $\text{mol e m}^{-2} \text{s}^{-1}$ )
$c_i$	intercellular $\text{CO}_2$ concentration ( $\text{mol CO}_2 \text{mol}^{-1}$ )	$k_b$	extinction coefficient for theoretical canopies with black leaves ( $\text{m}^2 \text{ground m}^{-2} \text{leaf}$ )
$c_N$	leaf nitrogen concentration ( $\text{mol N m}^{-2} \text{leaf}$ )	$k_b'$	extinction coefficient for scattered beam ( $\text{m}^2 \text{ground m}^{-2} \text{leaf}$ )
$c_{N0}$	leaf nitrogen concentration at canopy top ( $\text{mol N m}^{-2} \text{leaf}$ )	$k_d$	extinction coefficient for diffuse radiation and black leaves ( $\text{m}^2 \text{ground m}^{-2} \text{leaf}$ )
$c_{Nt}$	threshold value of $c_N$ ( $\text{mol N m}^{-2} \text{leaf}$ )	$k_d'$	extinction coefficient for diffuse beam ( $\text{m}^2 \text{ground m}^{-2} \text{leaf}$ )
$c_p$	specific heat of air ( $\text{J kg}^{-1} \text{C}^{-1}$ )	$k_N$	distribution coefficient for leaf N ( $\text{m}^2 \text{ground m}^{-2} \text{leaf}$ )
$c_s$	$\text{CO}_2$ concentration at the leaf surface ( $\text{mol CO}_2 \text{mol}^{-1}$ )	$k_u$	extinction coefficient for wind speed ( $\text{m}^2 \text{ground m}^{-2} \text{leaf}$ )
$C$	molar density of air ( $\text{mol m}^{-3}$ )	$K_c$	Michaelis coefficient for $\text{CO}_2$ ( $\text{mol CO}_2 \text{mol}^{-1}$ )
$D_a$	water vapour pressure saturation deficit of the air (Pa)	$K_o$	Michaelis coefficient for $\text{O}_2$ ( $\text{mol O}_2 \text{mol}^{-1}$ )
$D_H$	molecular diffusivity for heat ( $\text{m}^2 \text{s}^{-1}$ )	$o_i$	intercellular $\text{O}_2$ concentration ( $\text{mol O}_2 \text{mol}^{-1}$ )
$D_s$	humidity deficit at the leaf surface (Pa)	$Q$	quantum flux density for photosynthetically active radiation ( $\text{mol quanta m}^{-2} \text{s}^{-1}$ )
$D_{s0}$	empirical coefficient reflecting sensitivity of the stomata to $D_s$ (Pa)	$Q_{bo}$	direct beam component of $Q$ ( $\text{mol quanta m}^{-2} \text{s}^{-1}$ )
$e_a$	atmospheric water vapour pressure (Pa)	$Q_{do}$	diffuse component of $Q$ ( $\text{mol quanta m}^{-2} \text{s}^{-1}$ )
$E$	evaporation rate ( $\text{kg H}_2\text{O m}^{-2} \text{s}^{-1}$ )	$Q_{lbs}$	absorbed scattered beam radiation ( $\text{mol quanta m}^{-2} \text{s}^{-1}$ )
$f_d$	fraction of diffuse radiation in $S_0$ (-)	$Q_{ld}'$	absorbed diffuse radiation ( $\text{mol quanta m}^{-2} \text{s}^{-1}$ )
$f_{sh}$	fraction of shaded leaves at canopy depth $\xi$ (-)	$Q_{sh}$	radiation absorbed by shaded leaves ( $\text{mol quanta m}^{-2} \text{s}^{-1}$ )
$f_{sl}$	fraction of sunlit leaves at canopy depth $\xi$ (-)	$Q_{sl}$	radiation absorbed by sunlit leaves ( $\text{mol quanta m}^{-2} \text{s}^{-1}$ )
$g_{bc}$	boundary layer conductance for $\text{CO}_2$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$r_{bw}$	boundary layer resistance for water vapour ( $\text{s m}^{-1}$ )
$g_{bh}$	leaf boundary layer conductance for heat ( $\text{m s}^{-1}$ )	$r_h$	relative humidity
$g_{bHf}$	leaf boundary layer conductance for heat-free convection ( $\text{m s}^{-1}$ )	$r_{sw}$	stomatal resistance for water vapour ( $\text{s m}^{-1}$ )
$g_{bHw}$	leaf boundary layer conductance for heat-forced convection ( $\text{m s}^{-1}$ )	$R$	universal gas constant ( $\text{J mol}^{-1} \text{K}^{-1}$ )
$g_{bw}$	leaf boundary layer conductance for water vapour ( $\text{m s}^{-1}$ )	$R_d$	day respiration ( $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )
$g_{co}$	residual stomatal conductance for $\text{CO}_2$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$R_{L\downarrow}$	downward thermal radiation from the sky ( $\text{W m}^{-2}$ )
		$R_n^*$	net isothermal radiation absorbed by the leaf ( $\text{W m}^{-2}$ )
		$S_0$	solar radiation incident on a horizontal surface ( $\text{W m}^{-2}$ )

$S_{b0}$	direct beam component of $S_0$ ( $\text{W m}^{-2}$ )	$\alpha_N$	N-use efficiency
$S_c$	solar constant ( $\text{W m}^{-2}$ )	$\gamma_0, \gamma_1, \gamma_2$	empirical constants (Eqn C4)
$S_{d0}$	diffuse component of $S_0$ ( $\text{W m}^{-2}$ )	$\Gamma$	$\text{CO}_2$ compensation point ( $\text{mol CO}_2 \text{ mol}^{-1}$ )
$\beta$	solar elevation (degrees)	$\Gamma^*$	$\text{CO}_2$ compensation point in the absence of day respiration ( $\text{mol CO}_2 \text{ mol}^{-1}$ )
$S_n$	absorbed solar radiation ( $\text{W m}^{-2}$ )	$\delta_s$	declination of the sun (rad)
$S_v$	entropy ( $\text{J mol}^{-1}$ )	$\varepsilon_{\text{atm}}$	apparent emissivity for a hemisphere radiating at air temperature (-)
$t$	time of day (h)	$\varepsilon_c$	canopy emissivity (-)
$t_d$	day of the year (d)	$\varepsilon_l$	leaf emissivity (-)
$t_{dl}$	daylength (h)	$\theta$	shape coefficient of the non-rectangular hyperbola (-)
$t_h$	solar time (h)	$\lambda$	latent heat of vaporization for water ( $\text{J kg}^{-1}$ )
$t_{mT}$	2 × number of hours between noon and time of maximum temperature (h)	$\lambda_l$	latitude (degrees)
$t_{mu}$	2 × number of hours between noon and time of maximum wind speed (h)	$\Lambda$	total leaf area index ( $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$ )
$T_0$	reference temperature (293.2 K)	$\xi$	cumulative leaf area index ( $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$ )
$T_a$	air temperature at a reference point ( $^\circ\text{C}$ )	$\rho_a$	air density ( $\text{kg m}^{-3}$ )
$T_n, T_x$	minimum and maximum air temperatures ( $^\circ\text{C}$ )	$\rho_{cb}$	canopy reflection coefficient for beam radiation (-)
$T_l$	leaf temperature ( $^\circ\text{C}$ )	$\rho_{cd}$	canopy reflection coefficient for diffuse radiation (-)
$U$	wind speed at $\xi$ ( $\text{m s}^{-1}$ )	$\rho_h$	canopy reflection coefficient for horizontal leaves (-)
$U_n, U_x$	minimum and maximum wind speeds ( $\text{m s}^{-1}$ )	$\sigma_l$	scattering coefficient (-)
$U_0$	wind speed above the canopy ( $\text{m s}^{-1}$ )	$\sigma$	Stefan–Boltzman constant ( $\text{J mol}^{-1} \text{ K}^{-4}$ )
$V_{\text{cmax}}$	maximum catalytic activity of Rubisco ( $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$\tau_a$	atmospheric transmissivity (-)
$V_{\text{cmax}0}$	value of $V_{\text{cmax}}$ at $T_0$ ( $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$\omega_n$	reciprocal resistance (Eqn 17)
$V_{\text{cmax}}(0)$	value of $V_{\text{cmax}}$ at $\xi=0$		
$w_l$	leaf width (m)		
$Y$	Eqn D6		
$\alpha$	quantum yield of whole-chain electron transport ( $\text{mol e mol}^{-1}$ quanta)		

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.