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A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I:
Model description and comparison with a multi-layered model

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Abstract

An one-layered, two-leaf canopy model which calculates the fluxes of sensible heat, latent heat and CO_2 separately for sunlit and shaded leaves is presented. The two-leaf model includes: (1) a simple but robust radiation model, (2) an improved leaf model accounting for the interaction of conductance and photosynthesis and the response of stomata to water vapour pressure deficit and available soil water and (3) a new parameterisation of radiative conductance which simplifies solution of the leaf energy balance equation. Comparisons with a multi-layered model show that predicted fluxes of CO_2, latent and sensible heat fluxes usually agree within 5% over a range leaf area index typical of a wheat crop grown in a temperate climate. The two-leaf model is computationally 10 times more efficient than the multi-layered model and is suitable for the incorporation into regional and global climate models. For a hypothetical canopy with a leaf area index of 5 under very dry (vapour pressure deficit of air of 2 kPa) and sunny conditions, the net canopy photosynthesis and latent heat fluxes calculated by the two-leaf model agree with those by the multi-layered model within 10% for the whole range of soil water conditions (from very dry to wet) and the sensible heat fluxes of the canopy calculated by the two-leaf model agree with those by the multi-layered model within 25 W m^{-2} (or usually within 15%). For a canopy with leaf area index less than 2, the differences in the modelled fluxes of canopy CO_2, latent or sensible heat are less than 5% between the multi-layered model and two-leaf model. Our results show that the two-leaf model can predict net photosynthesis, latent and sensible heat fluxes of a canopy quite accurately under a wide range of soil water availability and meteorological conditions, as compared with the multi-layered model. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Canopy photosynthesis and energy partition model; Canopy conductance; 'Big-leaf' model

1. Introduction

The terrestrial biosphere and regional and global climate are closely linked through the reflection and absorption of radiation at the earth's surface, the partitioning of available energy into sensible and latent heat and through variation in surface roughness (Garratt, 1992). Many models have been developed to describe the interaction between the biosphere and atmosphere and several of these surface schemes have been incorporated into regional or global climate

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models (Dickinson et al., 1986, Sellers et al., 1986, 1992, 1996, Kowalczyk et al., 1991, 1994 and Garratt et al., 1993).

The latest version of the Simple Biosphere Model (SiB2) of Sellers et al. (1992, 1996) treats the canopy as one big leaf, solves the coupled equations for leaf energy balance, stomatal conductance and photosynthesis for a leaf at the top of the canopy and then scales up to the whole canopy. A similar approach was also taken by Amthor et al. (1994) and Lloyd et al. (1995). Such simple scaling from leaf to canopy is made possible by arguing, as first proposed by Field (1983), that limited resources such as nitrogen are distributed optimally through the canopy. However, sunlit and shaded leaves are not treated separately in SiB2 (Sellers et al., 1992). This is theoretically incorrect (Norman, 1993) because the quantum response of leaf photosynthesis is non-linear and use of mean absorbed radiation in the big leaf model will significantly overestimate the canopy photosynthesis (Spitters, 1986). Furthermore, the partitioning of available energy and photosynthesis are also non-linearly related to the leaf to air temperature difference. Sunlit leaves can be several degrees warmer than shaded leaves under sunny and dry conditions, so ignoring the temperature difference between sunlit and shaded leaves will bias the estimates of photosynthesis and sensible and latent heat fluxes for the canopy.

It is conceptually convenient to formulate a big-leaf model of a canopy using the same set of equations that apply to the individual leaves. Unfortunately the equations are non-linear and it is not possible to calculate correctly canopy fluxes by using simple arithmetic averages of the leaf-level parameters which occur in these equations (Raupach and Finnigan, 1988, Baldocchi et al., 1991, Raupach, 1991, 1995 and McNaughton, 1994). It may even be mathematically impossible to define a physically consistent averaging scheme for both latent and sensible heat fluxes (Raupach, 1995), but fortunately the errors are usually small when suitable simple flux-matching averaging schemes are used (Raupach, 1995). Similarly, Leuning et al. (1995) used a multi-layered model to show that transpiration from a canopy is closely approximated when canopy conductance is calculated as the separate sums of conductances of sunlit and shaded leaves, weighted by their respective leaf area fraction within the canopy. This procedure satisfies the requirement that canopy conductance is calculated as the sum of the stomatal conductance of the individual leaves weighted by the net radiation absorbed by each leaf (McNaughton, 1994). The simple two-leaf approach was successful because net radiation and hence the weighting factor, is quite similar within sunlit or shaded leaf classes but differs strongly between them. Early work by Monsi and Saeki (1953) and Saeki (1961) also recognised this important distinction between sunlit and shaded leaves for estimating canopy photosynthesis and has been confirmed by numerous other studies (eg. Spitters, 1986 and Norman, 1993).

These findings have motivated the development of a canopy model with two big leaves, one sunlit and the other shaded, that is simple enough for incorporation in climate models but which overcomes some of the deficiencies summarised above. This paper describes a new two-leaf model and compares its performance to an earlier multi-layer model of Leuning et al. (1995). Predictions for fluxes of available energy, sensible heat, latent heat and CO_2 assimilation are shown to be very similar for the two modelling approaches. A companion paper (Leuning et al., 1998) compares model predictions against measurements taken over two wheat fields. The two-leaf canopy model developed here will be incorporated into a complete Soil-Canopy-Atmosphere Model (SCAM, Raupach et al., 1997) to become the new surface scheme in the general circulation model in CSIRO.

2. Model description

The two-leaf model is derived from the multi-layered model of Leuning et al. (1995) which predicts canopy conductance, photosynthesis and partitioning of the absorbed radiation into latent and sensible heat fluxes. In the multi-layer model the approximations developed by Goudriaan (1977) were used to calculate the amounts of radiation absorbed by sunlit and shaded leaves in the photosynthetically active, near infra-red and thermal wavebands at five levels within the canopy. The known absorbed radiation was then coupled with a leaf-level model to calculate stomatal conductances and fluxes of CO_2, H_2O and sensible heat using numerical techniques. Gaussian integration (Goudriaan, 1986) was used to calculate canopy fluxes

from leaf-level fluxes using inputs of air temperature, air humidity, solar radiation and wind speed and measured leaf area index (LAI). Several improvements are made to the original multi-layered model in this paper: (1) allowance for leaf angle distributions which are non-spherical; (2) an improved theory for the exchange of solar and thermal radiation between the air, canopy and soil; and (3) modification of the stomatal model of Leuning (1995) to account for effects of soil water deficit on stomatal conductance and photosynthesis. These extensions are also incorporated into the two-leaf model described below and allow the models to apply to a wider range of vegetation types and climate conditions than the original. Meteorological and soil moisture data required for the model may be provided by another model at large-scale or from field measurements.

One of the major differences between various surface schemes is the method of representing canopy conductance. Leuning (1995) critically reviewed several existing stomatal models and concluded that the model proposed by Ball et al. (1987); BWB hereafter) and then modified by Leuning (1990, 1995) is satisfactory when soil water stress is not significant. Because it requires fewer parameters than some other models (eg. Jarvis, 1976), the original BWB stomatal model has been implemented in the latest version of SiB2 (Sellers et al., 1996). The BWB model uses relative humidity at the leaf surface as an independent humidity variable but Leuning (1995) showed that the use of water vapour pressure deficit (VPD) is theoretically preferable and provides superior results. This approach was adopted here and the stomatal model was further modified to account for soil water deficits.

The two-leaf canopy model consists of two parts: (1) a radiation submodel which calculates the PAR, near infrared radiation (NIR) and thermal radiation absorbed by sunlit and shaded leaves and (2) a coupled model of stomatal conductance, photosynthesis and partitioning of absorbed net radiation into sensible and latent heat (Leuning et al., 1995). The coupled model for two big leaves is formulated using the same set of equations as for a single leaf (Leuning et al., 1995), but the parameters in the coupled model are first integrated separately over all the sunlit and the shaded leaves within the canopy. Integration of the equations for the two-leaf model is achieved by assuming that the intercellular CO_2 concentrations and leaf temperatures are the same within each leaf class but differ between them (cf. Fig. 2 in Leuning et al., 1995). This may not be true within a dense canopy, as the surface temperature of sunlit leaves near the bottom of the canopy can be up to $10°C$ higher than that of sunlit leaves near the canopy top, however the overall contribution of those leaves to total canopy fluxes are relatively small and this error will be neglected. As shown later in our comparison between the two-leaf and multi-layered models, our assumption is quite reasonable in most circumstances. Additional assumptions are: (1) the canopy is horizontally homogeneous and thus all structural, physical and physiological parameters only vary vertically; (2) leaf day respiration, r_d, is proportional to maximum carboxylation rate (Collatz et al., 1991) and (3) maximal carboxylation rate, v_{cmax}, maximal potential electron transport rate, j_{max} and the stomatal conductance at the light compensation point, g_0, decrease in proportional to leaf nitrogen concentration within the canopy.

In describing the model, we use lower case letters to represent leaf-level quantities and the corresponding upper case letters for the same quantities for the big leaves or the whole canopy. Subscript $i=1$ is used for sunlit leaves and $i=2$ for shaded leaves; while subscript j represent radiation wavebands, with $j=1$, 2 and 3 for PAR, NIR and thermal radiation, respectively. All symbols, their definitions and units are listed in Appendix A

As the coupled model is the core of both the multi-layered and two-leaf model, we shall describe it first.

2.1. The coupled model of stomata-photosynthesis-transpiration

Following Leuning et al. (1995), the coupled model of stomatal conductance, photosynthesis and transpiration for the big sunlit leaf ($i=1$) or big shaded leaf ($i=2$) is:

Energy balance

$$Q_{n,i} = \lambda E_{c,i} + H_{c,i} \qquad (1)$$

Evaporation

$$E_{c,i} = G_{s,i} D_{s,i} = G_{w,i}(D_a + s\Delta T_i) \qquad (2)$$

Sensible heat

$$H_{c,i} = G_{h,i} c_p \Delta T_i \qquad (3)$$

Photosynthesis-gas diffusion

$$A_{c,i} = b_{sc} G_{s,i}(C_{s,i} - C_i) = G_{c,i}(C_a - C_i) \qquad (4)$$

Stomatal conductance

$$G_{s,i} = G_{0,i} + \frac{a_1 f_w A_{c,i}}{(C_{s,i} - \Gamma)(1 + D_{s,i}/D_0)} \qquad (5)$$

Photosynthesis-biochemistry

$$A_{c,i} = V_{n,i} - R_{d,i} \qquad (6)$$

where $Q_{n,i}$ is the net available energy, which is partitioned into latent, $\lambda E_{c,i}$ and sensible $H_{c,i}$, heat fluxes and where λ is latent heat of vaporisation for H_2O ($J\ mol^{-1}$). D_a and $D_{s,i}$ are water vapour mol fraction deficits (VPD) in the ambient air and at the leaf surface, respectively. $G_{s,i}, G_{0,i}$ are the bulk stomatal and residual ($G_{s,i}$ when $A_{c,i} = 0$) conductance for water vapour, $G_{w,i}$ and $G_{c,i}$ are the total conductance from the intercellular space of the leaves to the reference height above the canopy for H_2O and CO_2, respectively; $G_{h,i}$ is the total conductance for the heat transfer from the leaf surface to the reference height above the canopy (see Appendix D), c_p is the specific heat of the air ($J\ mol^{-1}\ K^{-1}$), ΔT_i is the temperature difference between the surface of the big leaf and that of the air at the reference height, s is the slope of the function relating saturated water vapour mol fraction to temperature and b_{sc} is the ratio of diffusivity of CO_2 and H_2O through the stomata. $A_{c,i}$ is the net photosynthesis rate, $V_{n,i}$ is the net carboxylation rate, $R_{d,i}$ is the day respiration rate and C_a, $C_{s,i}$ and C_i are CO_2 mol fractions in the air, at the leaf surface and intercellular spaces, respectively, while Γ is the CO_2 compensation point. In the stomatal model D_0 is a parameter for stomatal sensitivity to VPD, while a_1 is related to the intercellular CO_2 concentration by $C_i/C_{s,i} = 1 - 1/a_1$ at maximal stomatal opening (when both $D_{s,i}$ and $G_{0,i}$ are zero and f_w=1). A major improvement over the original stomatal model is the incorporation of the function f_w to describe the sensitivity of stomata to soil water content, θ_s.

Similar to Gollan et al. (1986), the effect of soil water supply on stomatal conductance is modelled using the empirical function

$$f_w = \min\left(1.0, \frac{10(\theta_s - \theta_{min})}{3(\theta_{max} - \theta_{min})}\right) \qquad (7)$$

where θ_{min} and θ_{max} are the soil water content at the field capacity and at wilting point of the top 25 cm soil and θ_s is the measured soil water content of top 25 cm soil. Parameter f_w represents the relative availability of soil water for plants.

Parameters for the big leaves in the two-leaf model are scaled up from the corresponding parameters for the individual leaves in the canopy. Appendix C describes the scaling rules and Table 1 lists the formulae for some conductances for the two big leaves. More details about the photosynthesis model (Eq. (6)) are given in Appendix D

The coupled model consists of the above six equations. There are six unknowns (ΔT_i, $D_{s,i}$, $C_{s,i}$, C_i, $A_{c,i}$, $G_{s,i}$) for given meteorological conditions above the canopy and soil water content from which we obtain the desired fluxes $\lambda_{c,i}$ (Eq. (2)), $H_{c,i}$ (Eq. (3)) and $A_{c,i}$ (Eq. (4)) from the absorbed radiation, calculated as described in the following section.

2.2. Radiation absorption

The net energy available to the big leaf i in waveband j, is $Q_{n,i}$ calculated as:

$$Q_{n,i} = \sum_{j=1}^{3} Q_{i,j} \qquad (8)$$

Leaf temperature needs to be known for calculating the absorbed long-wave radiation ($Q_{i,3}$), because leaf temperature is a part of the solution to the coupled model. This problem is avoided by using the isothermal net radiation ($Q_{n,i}^*$) defined as

$$Q_{n,i}^* = Q_{n,i} + c_p G_{r,i} \Delta T_i \qquad (9)$$

The second term on the right-hand side of Eq. (9) accounts for the additional thermal exchange under non-isothermal conditions. Loss of thermal radiation of the big leaf to the air under non-isothermal conditions is described using $G_{r,i}[= 4\varepsilon_f \sigma T_a^3/c_p]$, the radiative conductance of the big leaf (Jones, 1983), where

Table 1
Formulation of the parameters for the two big-leaf model[a]

$G_{\text{bf},i} = g_{\text{bf}}(0)L_i$

$G_{\text{bu},1} = g_{\text{bu}}(0)\Psi\{0.5k_u + k_b\}$

$G_{\text{bu},2} = g_{\text{bu}}(0)[\Psi\{0.5k_u\} - \Psi\{0.5k_u + k_b\}]$

$G_{\text{r},1} = \left[\dfrac{4\sigma T_a^3 k_d \varepsilon_f}{c_p}\right]\left[\Psi\{k_b + k_d\} + \dfrac{\exp(-k_dL) - \exp(-k_bL)}{k_b - k_d}\right]$

$G_{\text{r},2} = \left[\dfrac{4\sigma T_a^3 k_d \varepsilon_f}{c_p}\right]\left[2\Psi\{k_d\} - \Psi\{k_b + k_d\} - \dfrac{\exp(-k_dL) - \exp(-k_bL)}{k_b - k_d}\right]$

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[a] The total conductances for CO_2, H_2O and heat, $G_{\text{c},i}$ and $G_{\text{h},i}$ are calculated as

$$G_{\text{c},i}^{-1} = G_{\text{a},i}^{-1} + (b_{\text{bc}}G_{\text{b},i})^{-1} + (b_{\text{sc}}G_{\text{s},i})^{-1}$$

$$G_{\text{w},i}^{-1} = G_{\text{a},i}^{-1} + G_{\text{b},i}^{-1} + G_{\text{s},i}^{-1}$$

$$G_{\text{h},i}^{-1} = G_{\text{a},i}^{-1} + (n b_{\text{bh}}G_{\text{b},i})^{-1}$$

$$\text{and} \quad G_{b,i} = G_{bu,i} + G_{bf,i}$$

where b_{bc}, b_{sc} and b_{bh} are constants required to convert conductances for water vapour to those for CO_2 and heat and where $n = 1$ for amphistomatous leaves and $n = 2$ for hypostomatous ones. For other parameters of the big leaves, see Appendix C.

ε_f is the leaf emissivity, σ is the Steffan Boltzman constant and T_a is air temperature (K). The radiative loss is approximately proportional to the temperature differences between the leaf and the ambient air at the reference height, ΔT_i, when ΔT_i is relatively small ($<5°C$).

Absorption of PAR and NIR is calculated using the theory developed by Goudriaan (1977) and Goudriaan and van Laar (1994) in which absorption of scattered radiation is accounted for. (See Appendix B for details concerning the calculation of $Q_{i,j}$). Compared with the radiation scheme used in SiB2 (Sellers, 1985), Goudriaan's theory is much simpler, but gives very similar amounts of total radiation absorbed by the two big leaves for both PAR and NIR (Wang and Leuning, unpublished results).

3. Implementation of the model

An analytical solution was not found for the coupled equations for stomatal conductance, photosynthesis and partitioning of available energy (Eqs. (1)–(9)), so a reliable and efficient numerical approach was adopted which minimises the number of equations to be calculated within the iteration loop (see Table 2 and Appendix E for details). The model

Table 2
Structure of the coupled, two-leaf model

Set all physical, physiological constants
Read in location and plant species-dependent parameters
Read in meteorological data (do loop)
    Initialise some variables
    Calculate radiation absorbed under isothermal conditions
    Calculate parameters of the two big leaves
    Solve the coupled model (iteration loop for two big leaves)
    End of iteration loop
    Calculate $A_{\text{c},i}$, $G_{\text{s},i}$, $\lambda E_{\text{c},i}$, $H_{\text{c},i}$
    Output results
End do loop

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is written as an independent module, so that it can be easily incorporated into land surface models, such as SCAM (Raupach, 1995) or used in regional and global climate models (McGregor et al., 1993).

4. Results

4.1. Comparison of the two-leaf model of canopy photosynthesis with that of de Pury and Farquhar (1997)

A sunlit and shaded, two-leaf model for canopy photosynthesis has recently been presented by de Pury

and Farquhar (1997). In contrast to their model which focuses on photosynthesis, the model presented here includes coupled equations for stomatal conductance, photosynthesis and the leaf energy balance. This allows calculation of intercellular CO_2 concentration, C_i and leaf temperature, $T_{f,i}$. Our parameterisation of the big shaded leaf also differs from that of de Pury and Farquhar (1997).

Canopy photosynthesis calculated using mean absorbed PAR can be significantly overestimated when the PAR absorbed by the leaves vary because of the non-linear response of photosynthesis to light, that overestimation depends on the variance of the absorbed PAR by the leaves within the canopy (Smolander and Lappi, 1985). The nonlinear response of photosynthesis to the absorbed PAR forms the justification for the sunlit and shaded, two-leaf model of de Pury and Farquhar (1997). These authors calculate photosynthesis for each of the two big leaves using the bulk formulae that provide reasonably accurate estimates of the photosynthetic rate of the two big leaves if the variance in the absorbed PAR is relatively small by the sunlit or shaded leaves within the canopy. This may not always be correct. Our calculations using the multilayer model show that while the variation in the irradiance of *sunlit* leaves only contributes errors of a few percent of the total photosynthesis of sunlit leaves when mean absorbed radiation is used, this assumption causes up to 34% overestimation of the photosynthesis of *shaded* leaves and hence 11% for the whole canopy with a nitrogen distribution coefficient, $k_n = 0.5$ and LAI=4 (Fig. 1). Because the relative variance of the PAR absorbed by shaded leaves within the canopy is larger than that for sunlit leaves, the relative errors in the big-leaf model of de Pury and Farquhar (1997) are also larger for shaded than for sunlit leaves.

The solution to the problem of non-uniform irradiance of shaded leaves adopted in this paper was to estimate J_2, the potential rate of electron transport of shaded leaves in a hypothetical canopy, with the following properties:

1. the integral of $j_{max,2}$ of all the shaded leaves within the hypothetical canopy is equal to $J_{max,2}$
2. the total amount of absorbed PAR is equal to that absorbed by all the shaded leaves $Q_{1,2}$;
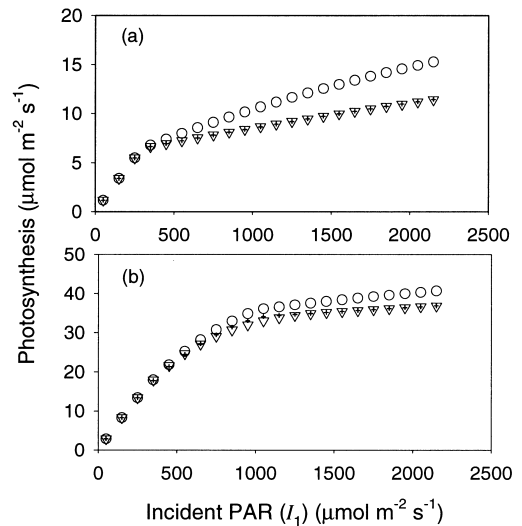

Fig. 1. Comparison of the photosynthetic rates of the big shaded leaf (a) and total canopy photosynthesis (b) calculated using our approach (cross) with that using the approach by de Pury and Farquhar (1997) (circle) or that using the multi-layered model of canopy photosynthesis (Leuning et al., 1995) (triangle). Leaf area index of the canopy is 4 and the leaf angle distribution is spherical. The zenith angle of the sun is 0. The beam fraction of incident PAR (f_b) is calculated as $f_b = \min(0, 1 - 300/I_1)$, where I_1 is the flux density of incident PAR above the canopy (μmol m^{-2} s^{-1}). In this comparison, the non-rectangular PAR response of the potential electron transport rate was used. Parameter values used are: $C_i = 245\ \mu$mol mol^{-1}; $\Gamma^* = 30\ \mu$mol mol^{-1}; $K_c(1 + O_i/K_o) = 585\ \mu$mol mol^{-1}; $\theta = 0.7$; $\alpha = 0.385$, $k_n = 0.5$; ν_{cmax} and j_{max} for the leaves at the top of the canopy were 100 and 210 μmol m^{-2} s^{-1}, respectively.

3. both j_{max} and absorbed PAR of shaded leaves within the hypothetical canopy vary in proportion to $\exp(-k_{d,1}^* \xi)$.

Where $k_{d,1}^*$ is the effective extinction coefficient for diffuse radiation and ξ is the cumulative leaf area index measured from the top of the canopy. The final expression for J_2 is presented in Eq. (D7).

Our approach provides a reasonably accurate estimate of photosynthesis of shaded leaves for a realistic range of nitrogen distributions within the canopy. For example, photosynthesis rates of shaded leaves and of the whole canopy calculated by our big-leaf model agreed with results from the multi-layered model, to within 1% and 4% respectively, for a canopy with leaf

area index of 4 and of 0.5. For $k_n > 1$ the differences in the photosynthesis of shaded leaves calculated by both two-leaf models become quite small, because in this case photosynthetic capacity is concentrated in the upper canopy where irradiance distribution of shaded leaves is more uniform. Overall our two-leaf model gives better estimates of canopy photosynthesis than the model developed by de Pury and Farquhar (1997), relative to the multilayer model.

4.2. Comparison of the two-leaf model with a multi-layered model

The multi-layered model is suitable for studying the spatial variation of leaf photosynthesis or water use within the canopy, whereas a major advantage of the two-leaf model is that it is at least ten times more efficient computationally. This makes the two-leaf model suitable for incorporating into some regional and global climate models provided there is no significant loss of accuracy. Our goal is to show that the two-leaf approximation provides results very similar to the reference multilayer model, while a companion paper (Leuning et al., 1998) compares model predictions for fluxes of available energy, sensible heat, latent heat and CO_2 measurements for a wheat crop.

Data required to run the model (meteorological variables, leaf area index and soil moisture content) were obtained during an experiment on wheat at Wagga Wagga (35°S, 147.3°E), NSW, Australia from May to November 1993. Details of the experimental site and the fertiliser treatments used on two adjacent five ha. fields can be found in Leuning et al. (1998) and in Poss et al. (1995). Meteorological measurements included incident solar radiation, windspeed and dry and wet bulb temperatures measured at ≈0.3 m above the canopy. Soil moisture was measured using Time Domain Reflectometry (Zegelin and White, 1989). Plant biomass and canopy leaf area index were also measured by harvest sampling. These data are used as input to both the two-leaf and multi-layered models and predictions from the two models are presented here. Values of the model parameters are listed in Table 3.

We included all available half-hourly data collected during vegetative growth of the crop for the model comparisons. The measurements were carried from day of year (DOY) 231 to 295 (18 August– 21 October). During that period, canopy leaf area index increased from 1.0 to 2.4 in the control (unfertilised) block and from 1.8 to 4.5 in the fertilised block. In total 228 valid half hourly measurements of net CO_2,

Table 3
Values of key parameters used in the simulation model

Class of parameter	Parameter	Value	Units
Photosynthesis	ν_{cmax}	1.5×10^{-4}	mol CO_2 m^{-2} s^{-1}
	α	0.385	mol e mol^{-1} quanta
(at $T_f = 20°C$)	K_c	3.02×10^{-4}	mol mol^{-1}
(at $T_f = 20°C$)	K_0	0.256	mol mol^{-1}
Stomatal conductance	D_0	0.01	Pa Pa^{-1}
	a_1	11.0	(−)
	g_0	0.01	mol H_2O m^{-2} s^{-1}
Leaf width	w_1	0.01	m
Leaf scattering coefficients:	$\omega_{f,1}$	0.20	(−)
	$\omega_{f,2}$	0.85	(−)
Leaf emissivity	ε_f	0.96	(−)
Leaf angle distribution	χ	0.0	(−)
[a]Soil reflectances:	$\rho_{s,1}$	0.10	(−)
Soil emissivity	ε_s	0.94	(−)
Windspeed extinction coefficient	k_u	0.5	(−)

Photosynthesis parameters are from (Leuning, 1990, Leuning, 1995).
[a] Soil reflectance of near infra-red radiation is calculated as a function of soil water content, of the top 5 cm (Garratt, 1992), i.e. $\rho_{s,2} = 0.18$ if $\theta_s > 0.5$, $\rho_{s,2} = 0.52 - 0.68\theta_s$ otherwise
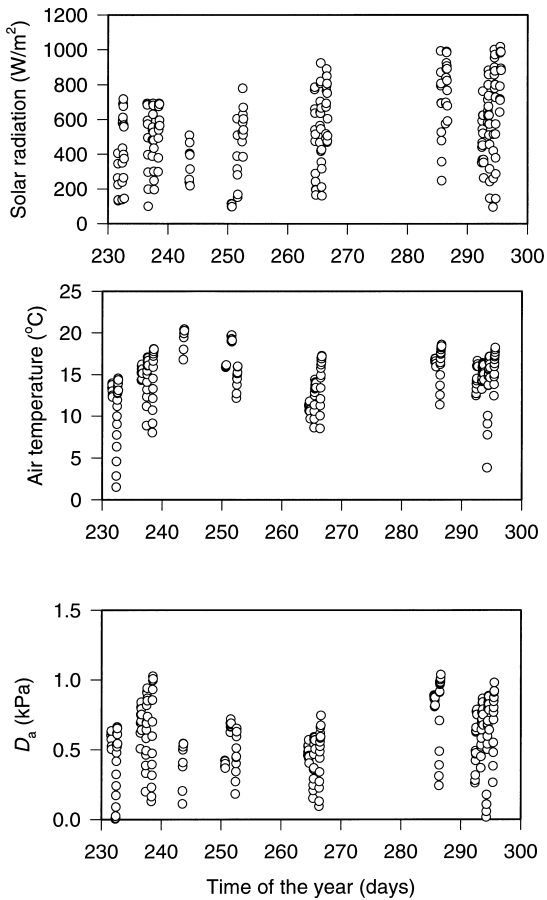
Fig. 2. Incident solar radiation, air temperature and the saturated water vapour partial pressure deficit of the ambient air (D_a) above the canopy measured in a wheat field at Wagga Wagga in 1993.

latent and sensible heat fluxes were made using micrometeorological methods during the experiments.

Incident solar radiation, ambient air temperature and VPD above the crop canopy are shown in Fig. 2. They represent typical climatic conditions experienced by spring wheat crops in much of the southeast Australian wheat growing area. Peak solar radiation increased gradually from 700 to 1000 W m^{-2} during the observation period, while there were no clear trends in maximum T_a and D_a. Most of the variation in these variables occurred diurnally.

Excellent agreement was obtained between predictions by the two-leaf and multi-layer models for

canopy fluxes of net photosynthesis, latent and sensible heat and for canopy conductance for the fertilised field (Fig. 3). Slopes of the linear regressions (are very close to 1, intercepts are close to zero, r^2 values are >0.94 and values for the agreement index (d) of Willmott (1981) are close to 1 as required for perfect agreement (Table 4). Systematic and random errors are also small, with the worst results for sensible heat fluxes where the systematic root-mean-square error, RMSE$_s$, is about 6 Wm^{-2}. Similar results were obtained for the unfertilised field and subsequently only results for the fertilised block will be presented.

Fig. 4–6 compare the predictions by the two-leaf and multi-layered models for diurnal variation of net CO_2, latent and sensible heat fluxes for six days representing the early, middle or late stages of the growing seasons, when the canopy leaf area index was 2, 4 and 3, respectively. There is little difference between the two models for net CO_2 assimilation by the shaded leaves but the two-leaf model slightly overestimated the net CO_2 fluxes for sunlit leaves for Day 265 and 294. Overall the net photosynthesis rates by the canopy predicted by the two models agree within 4%, showing that both the average and dynamic response of $A_{c,i}$ are similar in the two models.

Differences in the latent heat fluxes ($\lambda E_{c,i}$) predicted by the two models are very small for both sunlit and shaded leaves (Fig. 5). The two-leaf model tends to overestimate $\lambda E_{c,1}$ (see Fig. 5, Day 266 and 294). The mean difference in the predicted latent heat flux by the two models is less than 8 W m^{-2} for both sunlit and shaded leaves and the average relative difference in the predicted total latent heat flux by two models is about 5%.

Compared to the multi-layer model, the two-leaf model underestimates sensible heat fluxes on average by 3 W m^{-2} for sunlit or shaded leaves (Fig. 6). This can be explained by the surface temperature predicted by the two models (Fig. 7(a)). On average, the two-leaf model underestimates the mean surface temperature of the sunlit leaves by 0.07°C, but underestimates the surface temperature of the shaded leaves by 0.09°C, these differences are still too small to have any significant influences on the predicted $A_{c,i}$ and $\lambda E_{c,i}$ fluxes. As a consequence, the two-leaf model underestimates on average the Bowen ratio ($H_{c,i}/\lambda E_{c,i}$) by 6% for sunlit leaves and 24% for the shaded leaves (Fig. 7(b)).
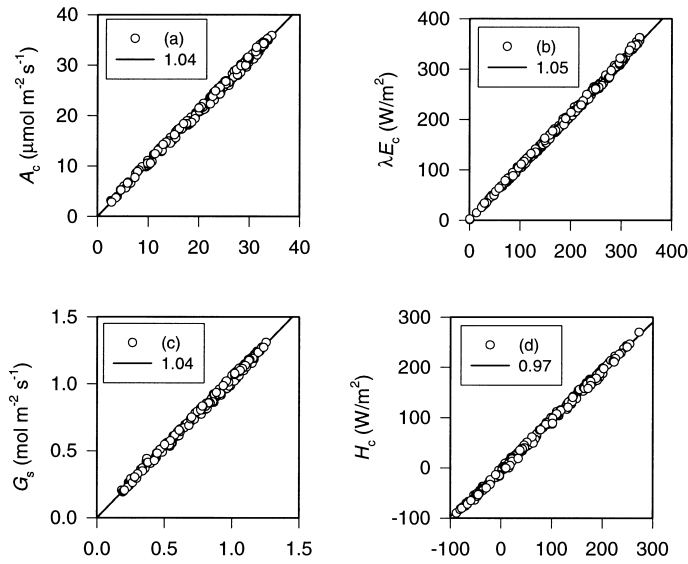
Fig. 3. Comparison of the predicted net canopy CO_2 flux (A_c), canopy conductance (G_s), canopy latent (λE_c) (and sensible) heat flux by the multi-layered model (x-axis) against those by the two-leaf model (y-axis). The lines are the best-fit linear regressions ($y=ax$) and values of a are also shown in the figure.

Because the net available energy is similar for all sunlit leaves, the two-leaf model predicts Bowen ratios and leaf to air temperature differences of the sunlit leaves better than those of the shaded leaves, when compared with the multi-layered model. Net radiation absorbed by the shaded leaves decreases more slowly from the top of the canopy than does absorbed PAR. Thus the weighting factor W_2 based on

Table 4
Results of linear regression analysis, $y=ax+b$, comparing predictions of the two-leaf model versus a multilayer model

Site	Variable	Unit	a	b	r^2	d	$RMSE_s$	$RMSE_u$
Fertilised	$A_{c,1}$	μmol m^{-2} s^{-1}	1.04	0.17	1.00	0.99	0.89	0.43
	$A_{c,2}$	μmol m^{-2} s^{-1}	1.00	0.01	1.00	1.00	0.01	0.01
	$G_{s,1}$	mol m^{-2} s^{-1}	1.04	0.01	1.00	0.99	0.03	0.02
	$G_{s,2}$	mol m^{-2} s^{-1}	0.99	0.00	1.00	1.00	0.00	0.00
	$\lambda E_{c,1}$	W m^{-2}	1.05	1	1.00	1.00	8	4
	$\lambda_{c,2}$	W m^{-2}	1.05	-1	1.00	1.00	2	1
	$H_{c,1}$	W m^{-2}	0.91	3	0.98	0.99	5	6
	$H_{c,2}$	W m^{-2}	1.19	-5	0.94	0.97	5	6
Control	$A_{c,1}$	μmol m^{-2} s^{-1}	0.99	0.48	1.00	1.00	0.33	0.34
	$A_{c,2}$	μmol m^{-2} s^{-1}	1.00	0.01	1.00	1.00	0.01	0.02
	$G_{s,1}$	mol m^{-2} s^{-1}	0.99	0.02	1.00	1.00	0.01	0.01
	$G_{s,2}$	mol m^{-2} s^{-1}	0.99	0.00	1.00	1.00	0.00	0.00
	$\lambda E_{c,1}$	W m^{-2}	1.00	3	1.00	1.00	3	3
	$\lambda E_{c,2}$	W m^{-2}	1.05	-1	1.00	1.00	1	1
	$H_{c,1}$	W m^{-2}	0.93	2	0.99	0.99	3	4
	$H_{c,2}$	W m^{-2}	1.22	-1	0.88	0.95	3	5

Also shown are the agreement index (d) and the systematic ($RMSEs$) or unsystematic ($RMSEu$) root mean square errors. For more details about agreement index, see Leuning et al. (1998).
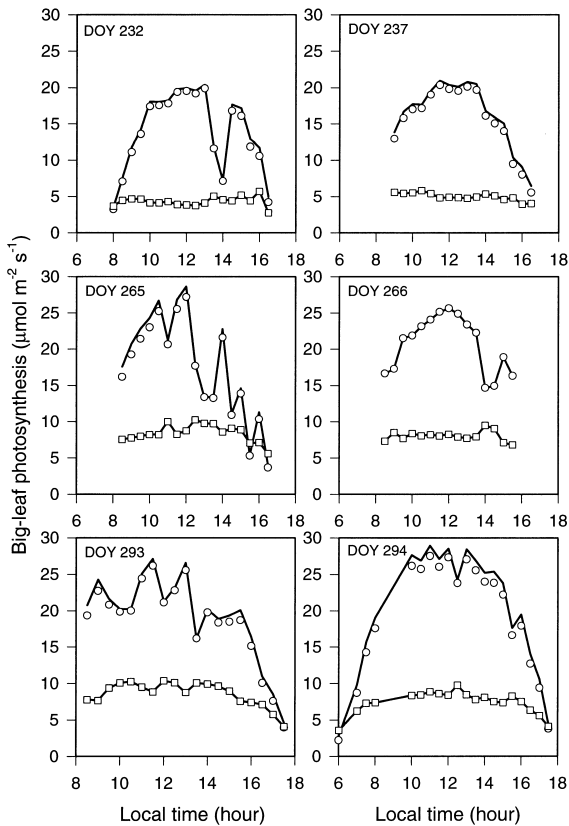
Fig. 4. The predicted net CO_2 fluxes by all the sunlit leaves or shaded leaves of the canopy by the multi-layered model ($A_{c,\,1}$, circle; $A_{c,\,2}$ square) or by the two-leaf model (solid curves) for different days during the early, middle and late times of the vegetative growth of the crop.

the vertical distribution of canopy leaf nitrogen (Eq. (C7)) is biased towards shaded leaves near the top of the canopy, causing the radiative conductance (see Table 1) to be overestimated and leaf to air temperature differences to be underestimated. The absolute difference in the total CO_2 and H_2O fluxes of all the shaded leaves predicted by the two models are relatively small and because the sunlit leaves contribute to more than 75% of the total canopy fluxes (A_c, λE_c and H_c), the predicted total canopy fluxes are not significantly different from those of the multi-layered model. But if sunlit leaves are not considered separately from the shaded leaves, as in the models by Sellers et al. (1992) and Lloyd et al. (1995), the

differences in total canopy fluxes will be significant. The one big-leaf model overestimates the latent heat flux and canopy photosynthesis by up to 40% and underestimates the sensible heat flux by as much as 100 W/m^2 under sunny conditions, as compared with our two-leaf model.

The soil during the growing season in 1993 was quite moist and crop photosynthesis and transpiration were only moderately limited by soil water late in the season (Leuning et al., 1998). To compare the predicted fluxes by the two-leaf model with those by the multi-layered model under some extreme conditions, we simulated the response of photosynthesis, latent and sensible heat fluxes of a hypothetically sparse (LAI=2) or dense (LAI=5) crop canopy under sunny and dry conditions (I_0=800 W m^{-2} and D_a=2 kPa). The results are shown in Fig. 8–11. As the availability of the soil water increases, both models predict that crop photosynthesis, total available energy and latent heat fluxes increase nonlinearly while sensible heat flux decreases. Canopy fluxes for CO_2, latent and sensible heat predicted by the multi-layer and two-leaf models differed by <5% when LAI<2 and the results are not shown here.

For a canopy with leaf area index of 5, photosynthesis of the sunlit leaves is underestimated by the two-leaf model when the fraction of available water, $f_w < 0.7$ and overestimated when $f_w > 0.7$, the difference is largest when f_w is about 0.56 (Fig. 8). The difference in the photosynthesis of the shaded leaves is very small (<0.06 µmol m^{-2} s^{-1}). The two-leaf model predicts a more rapid response of canopy photosynthesis to soil water availability than the multi-layered model, however the difference is quite small (<2 µmol m^{-2} s^{-1}).

The two-leaf model predicts a smaller sensitivity of net available energy to soil water availability than the multi-layered model, particularly when the availability of the soil water is low ($f_w < 0.5$), even though the difference is only 4% (Fig. 9). The two-leaf model overestimates $H_{c,i}$ when the availability of soil water is low to moderate ($f_w<0.7$) but underestimates $H_{c,i}$ when the availability of soil water is high ($f_w>0.7$) (Figs. 10 and 11). Overall there are only small differences between the models for predictions of $\lambda E_{c,i} + H_{c,i}$ for sunlit and shaded leaves and only 4% even when the availability of soil water is extremely low ($f_w<0.2$).
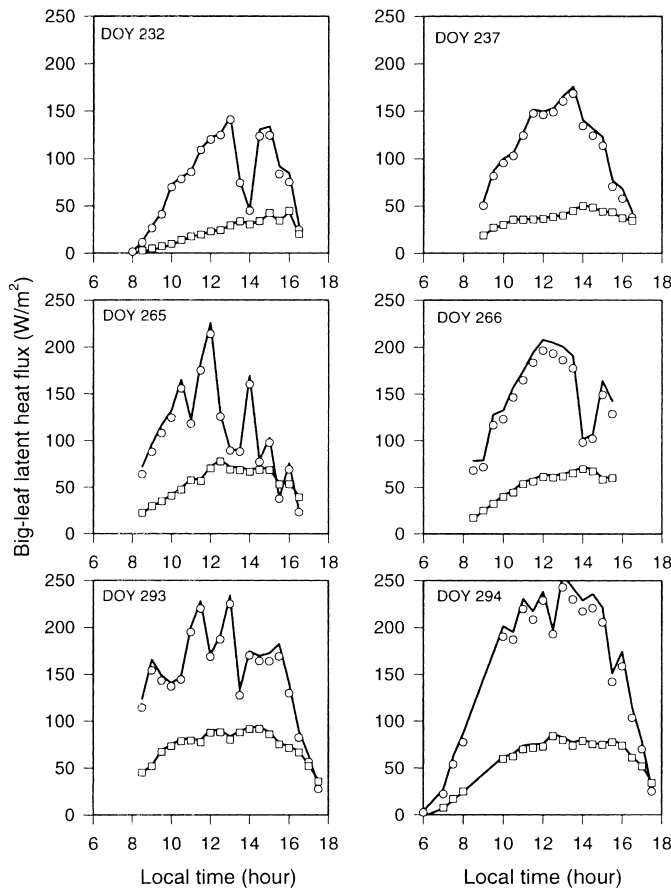
Fig. 5. As Fig. 4 but for $\lambda E_{c,1}$ and $\lambda E_{c,2}$.

When the availability of soil water is extremely low, differences in the predicted sensible heat flux by two models may result from the effect of radiative coupling. The degree of radiative coupling depends on the leaf to air temperature difference. In the two-leaf model, it is assumed that the leaf to air temperature difference is constant within the canopy for all the sunlit or shaded leaves, but is different between them. Simulations using the multi-layered model by Leuning et al. (1995) showed that leaf to air temperature difference of the sunlit leaves can vary up to $3°C$ and will be considerably greater when the availability of soil water is extremely low. This is ignored in the two-leaf model. Because both the leaf boundary conductance for free convection and loss of long-wave radia-

tion by the leaves are non-linearly related to leaf temperature, the two-leaf model gives biased predictions of the sensible heat fluxes when compared with the multi-layered model. An example is shown in Fig. 12 for sunlit leaves that have a larger leaf to air temperature difference than the shaded leaves and therefore a stronger radiative coupling. The sensible heat flux will be overestimated because the extra loss of long-wave radiation by the sunlit leaves is not considered in the energy balance equation if radiative coupling is ignored ($G_{r,1} = 0$). However radiative coupling alone has very small effect on the response of latent heat flux to the availability of soil water. Therefore the difference shown in Figs. 9–11 results from other effects, such as the exponential rise in
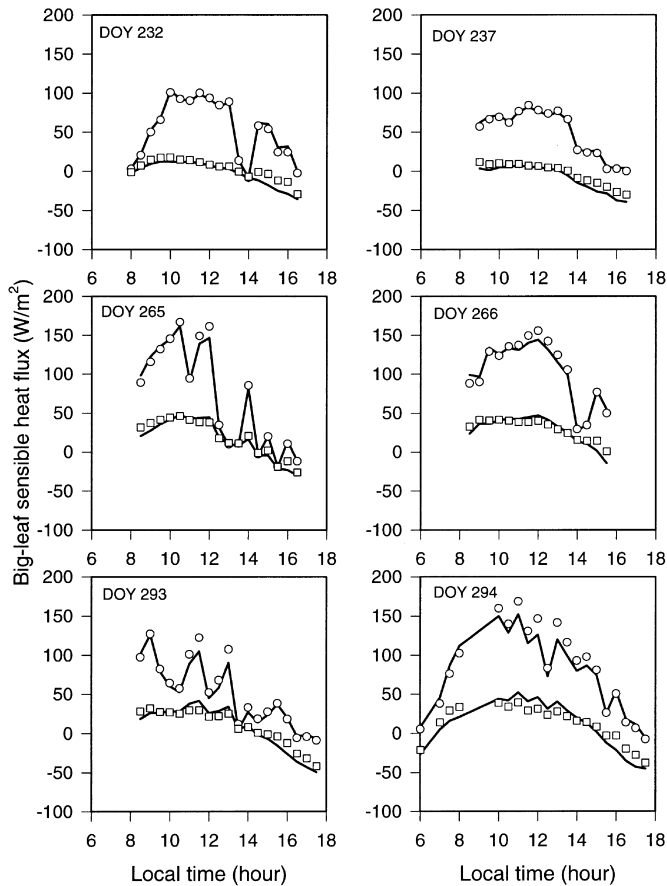
Fig. 6. As Fig. 4 for $H_{c,1}$ and $H_{c,2}$.

water vapour pressure deficit at the leaf surface with temperature. Radiation coupling has the largest effect on sensible heat flux and smallest effect on net CO_2 flux of all the sunlit or shaded leaves (data not shown). Similar results were also obtained by Baldocchi et al. (1991) and Baldocchi and Harley (1995).

5. Conclusions

A two-leaf canopy model has been developed which calculates separately the conductances and fluxes of energy and CO_2 for sunlit and shaded leaves. Separating sunlit and shaded leaves is neces-

sary because photosynthesis and partitioning of the available energy are non-linearly related to absorbed PAR and short-wave radiation. A single big-leaf model that does not account for the difference in the radiation absorbed by the two leaf classes will inevitably bias fluxes towards those for leaves near the top of the canopy and thus overestimate canopy fluxes. Our two-leaf model includes: (1) a simple but robust radiation model, (2) an improved leaf model accounting for the interaction of conductance and photosynthesis and the response of stomata to water vapour pressure deficit and available soil water and (3) a new parameterisation of radiative conductance which simplifies solution of the leaf energy balance equation. This increases the computational efficiency
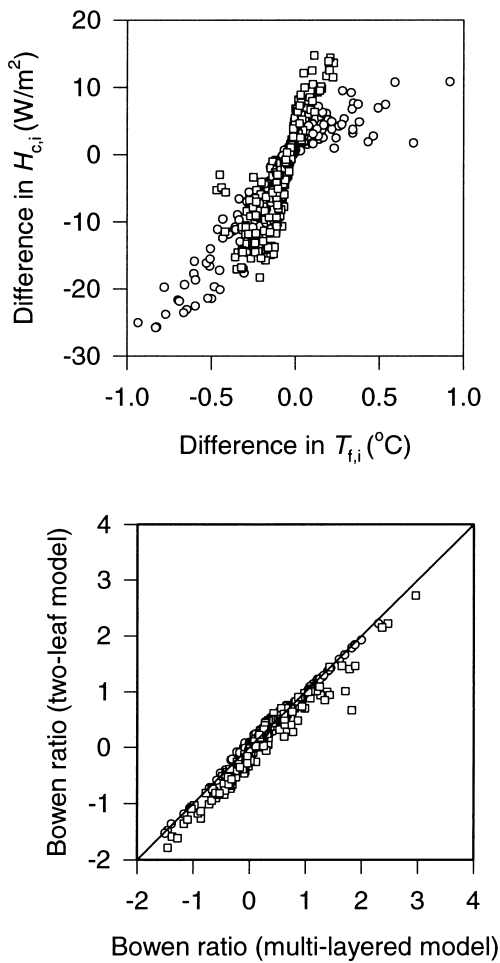
Fig. 7. (a) Difference in the sensible heat fluxes (two-leaf minus multi-layer) against the difference in the surface temperature predicted by the two-leaf and multi-layered model for sunlit leaves (circle) or shaded leaves (square) for the fertilised crop canopy at Wagga Wagga; (b) the Bowen ratio predicted by the multi-layered model (x-axis) against the Bowen ratio predicted by the two-leaf model (y-axis) for sunlit leaves (circle) or shaded leaves (square). The line represents 1 : 1 relation.

Fig. 8. The predicted responses of net CO_2 flux of the whole crop canopy (A_c), sunlit leaves ($A_{c, 1}$) and shaded leaves ($A_{c, 2}$) to the availability of soil water by the two-leaf model (curve) or the multi-layered model (circle). The canopy leaf area index was assumed to be 5 and incident solar radiation above the canopy was 800 W m^{-2}, ambient air temperature of 25°C and saturated water vapour pressure deficit of 2 kPa.

of our canopy scheme relative to a multilayer approach but without compromising model accuracy significantly.

Comparisons with a multi-layered model show that predicted fluxes of CO_2, latent and sensible heat fluxes usually agree within 5% over a range leaf area index typical of a wheat crop grown in a temperate climate. The two-leaf model is 10 times more efficient com-
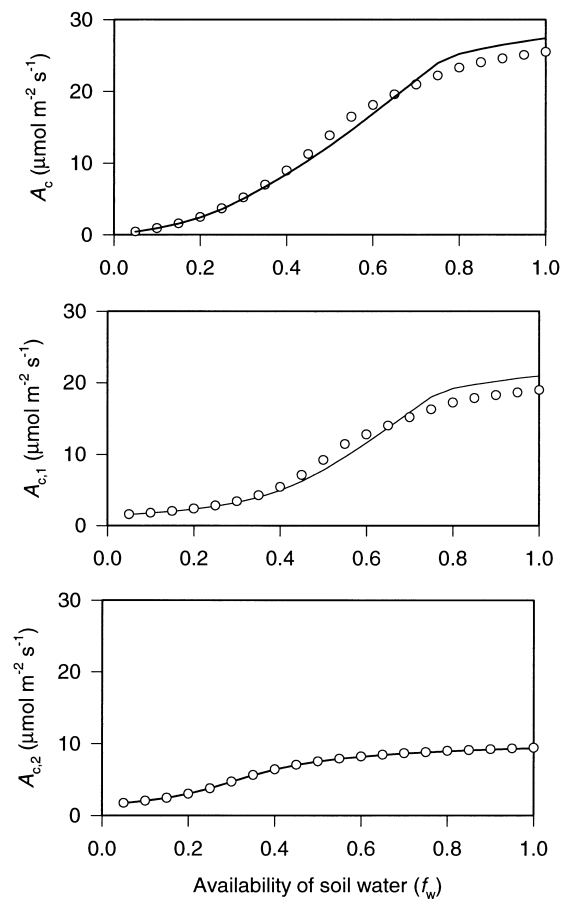
putationally and is therefore more suitable than the multi-layered model for incorporation into some regional and global-scale climate models.

For a dense canopy (LAI=5) under dry and sunny conditions (fractional available soil water <0.7) the two-leaf model overestimates the sensible heat flux by ≈20 W m^{-2} (or 10%) relative to the multi-layered model. The two-leaf model also underestimates the net canopy CO_2 fluxes by up to 2 μmol m^{-2} s^{-1} when the availability of soil water is moderately limiting (0.45<f_w<0.65) but overestimates the net canopy CO_2
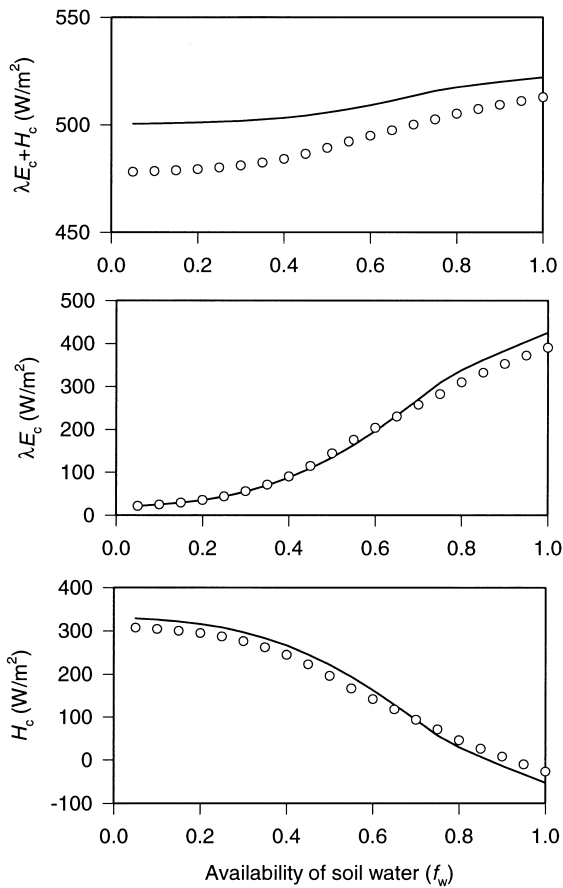
Fig. 9. The predicted responses of net available energy ($\lambda E_c + H_c$), latent (λE_c) and sensible (H_c) heat flux of the whole canopy to the availability of soil water by the two-leaf model (curve) or the multi-layered model (circle).

Fig. 10. As for Fig. 9 but for all the sunlit leaves of the canopy only.

fluxes by up to $2\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ when $f_w > 0.65$. The direct effects of radiative coupling on fluxes of water vapour and CO_2 for sunlit leaves are less important than the indirect effects via water vapour pressure deficit on stomatal conductance and therefore photosynthesis and transpiration.

Acknowledgements

Appendix A

Symbols, their definitions and units

$A_{c,i}$ net photosynthesis ($\mu\text{mol m}^{-2}\ \text{s}^{-1}$);

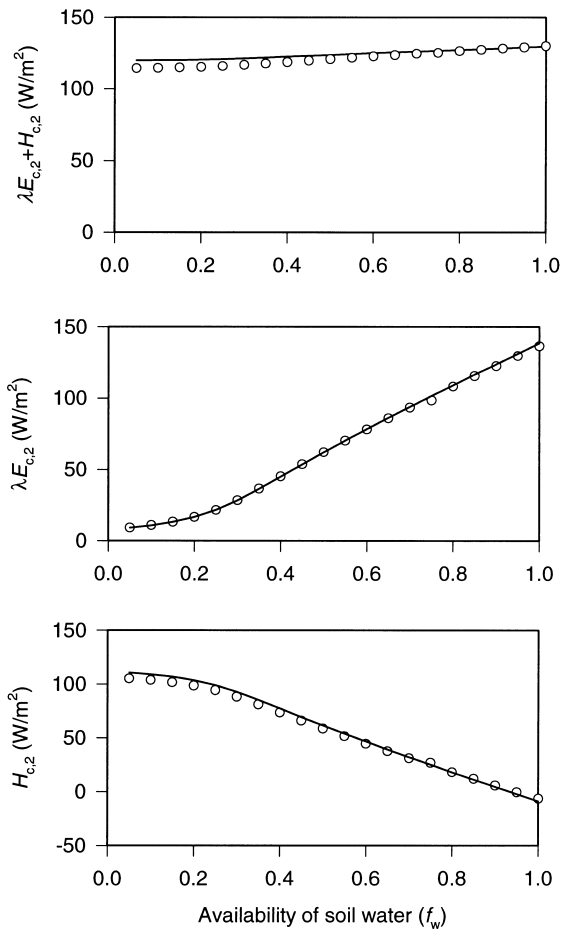a_1 an empirical parameter;

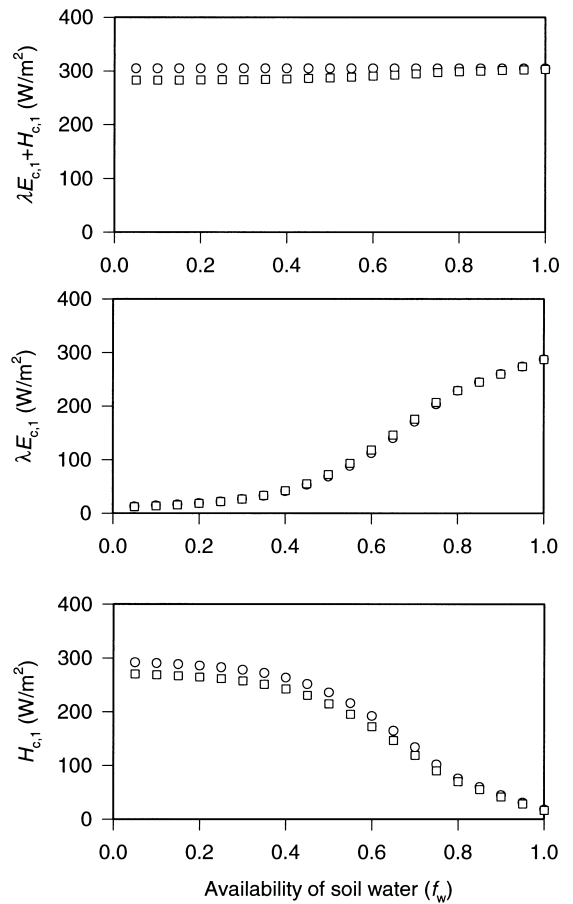Fig. 11. As for Fig. 9 but for all the shaded leaves of the canopy only.

Fig. 12. The predicted responses of net available energy ($\lambda E_{c,1} + H_{c,1}$), latent ($\lambda E_{c,1}$) and sensible ($H_{c,1}$) heat fluxes of all the sunlit leaves by the two-leaf model with (square) or without (circle) radiative coupling. When radiative coupling is absent, the radiative conductance is set to zero.

b_{bc}	ratio of the diffusivity of CO_2 to H_2O across the leaf boundary layer ($=0.73$);
b_{bh}	ratio of the diffusivity of heat to H_2O across the leaf boundary layer ($=0.93$);
b_{sc}	ratio of the diffusivity of CO_2 to H_2O across the leaf stomatal pores ($=0.64$);
c_p	specific heat of the air (J mol^{-1} K^{-1});
C_a	the ambient CO_2 concentration at the reference height above the canopy ($\mu mol\ mol^{-1}$);
$C_{s,i}$	CO_2 concentration at the leaf surface ($\mu mol\ mol^{-1}$);
C_i	intercellular CO_2 concentration of the leaf ($\mu mol\ mol^{-1}$);
d	agreement index;
D_a	the saturated deficit of water vapour pressure of the air at the reference height (Pa);
$D_{s,i}$	the saturated deficit of water vapour pressure at the leaf surface (Pa);
D_0	an empirical parameter (Pa);
E_c	canopy transpiration rate (mol H_2O m^{-2} s^{-1});
$E_{c,i}$	transpiration rate of the big leaf (mol H_2O m^{-2} s^{-1});
f_w	an empirical parameter describing the relative availability of soil water for plants;

$g_0, G_{0,i}$ — stomatal conductance of a leaf or big leaf for H_2O when net leaf photosynthesis is zero (mol m^{-2} s^{-1});

$g_s, G_{s,i}$ — stomatal conductance of a leaf or big leaf for H_2O (mol m^{-2} s^{-1});

$g_b; G_{b,i}$ — boundary conductance of a leaf or the big leaf for H_2O (mol m^{-2} s^{-1});

$g_{bu}; G_{bu,i}$ — boundary conductance due to forced convection of a leaf or a big leaf for H_2O (mol m^{-2} s^{-1});

$g_{bf}, G_{bf,i}$ — boundary conductance of the big leaf due to free convection for H_2O (mol m^{-2} s^{-1});

$G_{c,i}$ — total conductance for CO_2 from the intercellular space of the leaves to the reference height above the canopy (mol m^{-2} s^{-1});

$G_{h,i}$ — total conductance for heat transfer from the leaf surface to the reference height above the canopy (mol m^{-2} s^{-1});

$g_r, G_{r,i}$ — radiative conductance of a leaf or big leaf (mol m^{-2} s^{-1});

G_{ross} — G function as defined by Ross (1981);

$G_{w,i}$ — total conductance for H_2O from the intercellular space of the leaves to the reference height above the canopy (mol m^{-2} s^{-1});

H_c — sensible heat flux of the canopy (W m^{-2});

$H_{c,i}$ — sensible heat flux of the big leaf (W m^{-2});

I_0 — flux density of the incident short-wave radiation above the canopy (W m^{-2});

I_j — flux density of incident PAR, NIR or thermal radiation (Wm^{-2} or μmol m^{-2} s^{-1});

$I_3\downarrow$ — downward long wave radiation in the canopy (W m^{-2});

$I_3\uparrow$ — upward long wave radiation in the canopy (W m^{-2})

$I_{b,j}$ — the flux density of incident direct beam radiation above the canopy (W m^{-2});

$I_{d,j}$ — the flux density of the incident diffuse radiation above the canopy (W m^{-2});

j, J — potential electron transport rate of a leaf, or the big leaf (μe m^{-2} s^{-1});

$j_{max}, J_{max,i}$ — maximum potential electron transport rate of a leaf or the big leaf (μe m^{-2} s^{-1});

K_c — Michaelis–Menten constant for CO_2 for Rubisco carboxylation (mol mol^{-1});

K_o — Michaelis–Menten constant for O_2 for Rubisco oxygenation (mol mol^{-1});

k_b — extinction coefficient of a canopy of black leaves for direct beam radiation;

$k_{b,j}^*$ — extinction coefficient of a canopy for direct beam radiation;

$k_{d,j}^*$ — extinction coefficient of a canopy for diffuse radiation;

k_d — extinction coefficient of a canopy of black leaves for diffuse radiation;

k_n — an empirical parameter used to describe the vertical distribution of leaf nitrogen in the canopy;

k_u — an empirical parameter used to describe the vertical variation of wind speed within the canopy;

L — canopy leaf area index;

L_i — leaf area index of the big leaf;

O_i — intercellular O_2 concentration (mol mol^{-1});

$q_{i,j}, Q_{i,j}$ — radiation absorbed by a leaf or the big leaf (W m^{-2});

$Q_{i,3}^*$ — absorbed long-wave radiation under isothermal condition (W m^{-2});

$Q_{n,i}^*$ — net available energy of the big leaf under isothermal condition (W m^{-2});

$Q_{n,i}$ — net available energy of the big leaf under non-isothermal condition (W m^{-2});

$q_{i,j}$ — flux density of radiation absorbed by the sunlit or shaded leaves in the canopy (μmol m^{-2} s^{-1});

$r_{d,i}R_{d,i}$ — day respiration of a leaf or the big leaf (μmol m^{-2} s^{-1});

s — the slope of the curve relating saturation water vapour pressure to temperature (Pa K^{-1});

T_a — ambient air temperature (°C or K);

$T_{f,i}$ — leaf surface temperature (°C or K);

$v_{cmax}, V_{cmax,i}$ — maximum carboxylation rate when photosynthesis is limited by Rubisco activity of a leaf or the big leaf (μmol m^{-2} s^{-1});

$V_{n,i}$ net carboxylation rate of the big leaf (μmol m^{-2} s^{-1});

$V_{c,i}$ Rubisco-limited carboxylation rate of the big leaf (μmol m^{-2} s^{-1});

$V_{J,i}$ RuBP regeneration-limited carboxylation rate of the big leaf (μmol m^{-2} s^{-1});

w_i fraction of sunlit leaf area within the canopy;

W_i weighting factor;

ΔT_i leaf to air temperature difference (°C);

Y_i a parameter or flux of individual leaf or the big leaf;

Y parameter or flux of the whole canopy;

α quantum efficiency of RuBP regeneration (mol mol^{-1});

γ psychrometer constant (Pa K^{-1});

γ^* the modified psychrometer constant (Pa K^{-1});

$\rho_{cb,j}$ the canopy reflectance for direct beam radiation;

$\rho_{cd,j}$ the canopy reflectance for diffuse radiation;

$\rho_{tb,j}$ the effective canopy-soil reflectance for direct beam radiation;

$\rho_{td,j}$ the effective canopy-soil reflectance for diffuse radiation;

$\rho_{s,j}$ soil reflectance;

ξ cumulative leaf area index from the canopy top;

λ latent heat of vaporisation (J mol^{-1});

ε_a emissivity of the air;

ε_f emissivity of the leaf;

ε_s emissivity of the soil;

$\omega_{f,j}$ scattering coefficient of the leaf;

σ Stefen–Boltzman constant (5.67×10^{-8} W m^{-2} K^{-4});

χ an empirical parameter describing the leaf angle distribution;

θ zenith angle of the sun (radian);

θ_s volumetric fraction of soil water;

θ_{max} volumetric fraction of soil water at field capacity;

θ_{min} volumetric fraction of soil water at wilting point.

Γ CO$_2$ compensation point of leaf photosynthesis (μmol mol^{-1});

Γ^* CO$_2$ compensation point of leaf photosynthesis when leaf day respiration is zero (μmol mol^{-1});

$i=1$ for the big sunlit leaf; or $=2$ for the big shaded leaf;

$j=1$ for photosynthetically active radiation; $=2$ for near infra red radiation and $=3$ for long-wave radiation.

Appendix B

The radiation submodel

The radiation submodel uses the approximations developed by Goudriaan (1977) and Goudriaan and van Laar (1994) to calculate the radiative transfer within the canopy, including the scattered radiation.

The amount of radiation within waveband j absorbed by the big leaf ($Q_{i,j}$) is

$$Q_{i,j} = \int_0^L q_{i,j} w_i(\xi) d\xi \tag{B1}$$

where $j=1$ for PAR and $j=2$ for NIR radiation, $q_{i,j}$ is the radiation absorbed by the sunlit leaves ($i=1$) or shaded leaves ($i=2$) within the canopy, ξ is the cumulative leaf area index from the canopy top and $w_1(\xi)$ is the fraction of sunlit leaves at LAI depth ξ and $w_2(\xi)$ ($=1-w_1$) is the fraction of shaded leaves at ξ (see Eqs. (C3) and (C4)).

Radiation absorbed by sunlit and shaded leaves at ξ is given by

$$q_{1,j} = q_{2,j} + I_{b,j} k_b (1 - \omega_{f,j}) \tag{B2}$$

$$q_{2,j} = I_{d,j} k_{d,j}^* (1 - \rho_{td,j}) \exp(-k_{d,j}^* \xi)$$
$$+ I_{b,j} [k_{b,j}^* (1 - \rho_{tb,j}) \exp(-k_{b,j}^* \xi) \tag{B3}$$
$$- k_b (1 - \omega_{f,j}) \exp(-k_b \xi)]$$

where $I_{b,j}$ and $I_{d,j}$ are the incident direct beam and diffuse radiation above the canopy respectively and where $k_{d,j}^*$, $k_{b,j}^*$ and k_b are the extinction coefficients for diffuse radiation, beam radiation in real canopies and for a theoretical canopy with black leaves, $\omega_{f,j}$ is the leaf scattering coefficient, $\rho_{td,j}$ and $\rho_{td,j}$ are the

effective reflection coefficients for canopy plus soil for diffuse and direct beam radiation.

By substituting Eq. (B2) or Eq. (B3) into Eq. (B1) and then integrating, we have

$$Q_{1,j} = I_{d,j}(1 - \rho_{td,j})k_{d,j}^*\Psi\{k_{d,j}^* + k_b\}$$
$$+ I_{b,j}(1 - \rho_{tb,j})k_{b,j}^*\Psi\{k_{b,j}^* + k_b\}$$
$$+ I_{b,j}(1 - \omega_{f,j})k_b[\Psi\{k_b\} - \Psi\{2k_b\}] \quad \text{(B3b)}$$

$$Q_{2,j}1 = I_{d,j}(1 - \rho_{td,j})k_{d,j}^*[\Psi\{k_{d,j}^*\} - \Psi\{k_{d,j}^* + k_b\}]$$
$$+ I_{b,j}(1 - \rho_{tb,j})k_{b,j}^*[\Psi\{k_{b,j}^*\} - \Psi\{k_{b,j}^* + k_b\}]$$
$$- I_{b,j}(1 - \omega_{f,j})k_b[\Psi\{k_b\} - \Psi\{2k_b\}] \quad \text{(B4)}$$

in which the function Ψ is defined as

$$\Psi\{z\} = \int_0^L \exp(-z\xi)d\xi = (1 - \exp(-zL))/z \quad \text{(B5)}$$

Eqs. (B3) and (B4) have also been derived by de Pury and Farquhar (1997). Extinction coefficients ($k_{b,j}^*$ and $k_{d,j}^*$) and reflection coefficients ($\rho_{tb,j}$ and $\rho_{td,j}$) are calculated according to Goudriaan and van Laar (1994). The extinction coefficient for beam radiation and black leaves, k_b, is a function of the sun's zenith angle, θ and is calculated as

$$k_b = G_{ross}/\cos\theta \quad \text{(B6)}$$

where the function G_{ross} was defined by Ross (1981) and is the projection of the unit leaf area in the direction of the sun's beam. Following Sellers (1985) it was calculated as:

$$G_{ross} = 0.5 - (0.633 - 1.11\cos\theta)\chi$$
$$- (0.33 - 0.579\cos\theta)\chi^2$$
$$- 0.4 < \chi < 0.6 \quad \text{(B7)}$$

where χ is an empirical parameter related to the leaf angle distribution and is equal to 0 for a spherical leaf angle distribution.

The downwards ($I_3\downarrow$) and upwards ($I_3\uparrow$) long-wave radiation flux density within the canopy under isothermal condition are calculated as

$$\frac{I_3 \downarrow (\xi)}{\sigma T_{a^4}} = \varepsilon_f - (\varepsilon_f - \varepsilon_a)\exp(-k_d\xi)$$
$$+ (1 - \varepsilon_f)[1 - \exp(-k_d\xi)]$$
$$\times [\varepsilon_f - (\varepsilon_f - \varepsilon_s)\exp(-k_d(L - \xi))] \quad \text{(B8)}$$

$$\frac{I_3 \uparrow (\xi)}{\sigma T_{a^4}} = \varepsilon_f - (\varepsilon_f - \varepsilon_s)\exp[-k_d(L - \xi)]$$
$$+ [\varepsilon_f - (\varepsilon_f - \varepsilon_a)\exp(-k_d\xi)]$$
$$\times \{(1 - \varepsilon_f)[1 - \exp(-k_d(L - \xi))]$$
$$+ (1 - \varepsilon_s)\exp[-2k_d(L - \xi)]\}$$
$$+ \varepsilon_f(1 - \varepsilon_s)\exp[-k_d(L - \xi)]$$
$$\times \{1 - \exp[-k_d(L - \xi)]\} \quad \text{(B9)}$$

The long-wave radiation absorbed by sunlit and shaded leaves under isothermal condition is given by

$$Q_{1,3}^* = \int_0^L \exp(-k_b\xi)d(I_3 \uparrow - I_3 \downarrow) \quad \text{(B10)}$$

$$Q_{2,3}^* = \int_0^L (1 - \exp(-k_b\xi))d(I_3 \uparrow - I_3 \downarrow) \quad \text{(B11)}$$

By substituting Eqs. (B8) and (B9) into Eqs. (B10) and (B11), we obtain

$$Q_{1,3}^* = -k_d\sigma T_a^4[\varepsilon_f(1 - \varepsilon_a)\Psi\{k_b + k_d\} + (1 - \varepsilon_s)$$
$$\times (\varepsilon_f - \varepsilon_a)\Psi\{2k_d\}\Psi\{k_b - k_d\}] \quad \text{(B18)}$$

$$Q_{2,3}^* = -k_d\sigma T_a^4[\varepsilon_f(1 - \varepsilon_a)\Psi\{k_d\} - (1 - \varepsilon_s)$$
$$\times (\varepsilon_f - \varepsilon_a)\exp(-k_dL)\Psi\{k_d\}] - Q_{1,3}^* \quad \text{(B19)}$$

where ε_f, ε_a and ε_s are the emissivity of the leaf, sky and soil, respectively. Emissivity for clear skies was calculated using the formula of Brutsaert (1975).

Appendix C

Scaling up the parameters in the coupled model for single leaf to the big leaves

Provided sunlit and shaded leaves are treated separately, values of parameters in the coupled model for the two big leaves can be closely approximated by integrating values for individual leaves, ie.

$$Y_i = \int_0^L y_i(\xi)w_i(\xi)d\xi \quad \text{(C1)}$$

and

$$Y = Y_1 + Y_2 \quad \text{(C2)}$$

where y_i is the parameter value or flux (CO_2, net available energy, H_2O or sensible heat flux) of individual sunlit or shaded leaf within the canopy and Y_i is the value of the corresponding parameter or flux for the big leaves, ξ is the cumulative leaf area index from the canopy top and L is the total canopy leaf area index. Y represents the parameter value or the total flux of the whole canopy, $w_i(\xi)$ is the fraction of sunlit ($i=1$) or shaded ($i=2$) leaf area within the canopy and is given by

$$w_1 = \exp(-k_b\xi) \qquad (C3)$$

and

$$w_2 = 1 - \exp(-k_b\xi) \qquad (C4)$$

If $y_i(\xi)$ is proportional to leaf nitrogen and leaf nitrogen decreases exponentially from the top of the canopy, Eq. (C1) can be integrated analytically. That is

$$Y_i = \int_0^L y(0)\exp(-k_n\xi)w_i(\xi)d\xi = y(0)W_i \qquad (C5)$$

and

$$W_1 = \Psi\{k_b + k_n\} \qquad (C6)$$

$$W_2 = \Psi\{k_n\} - \Psi\{k_b + k_n\} \qquad (C7)$$

where the exponential function Ψ is defined in Eq. (B5).

The total leaf area index of the big sunlit leaf (L_1) and shaded leaf (L_2) is

$$L_1 = \Psi\{k_b\} \qquad (C8)$$

and

$$L_2 = L - \Psi\{k_b\} \qquad (C9)$$

Note that the units for y_i and Y_i are different. For example, if y_1 represents day respiration rate of sunlit leaves, its unit is mol CO_2 m^{-2} leaf area s^{-1} and the unit for Y_1 is mol of CO_2 total area of sunlit leaves per ground area per second and then the unit for Y is mol m^{-2} ground area s^{-1}.

In this study, parameters $R_{d,i}$, $G_{0,i}$, $V_{cmax,i}$, $J_{max,i}$ for the big leaves are scaled up from the values of the respective parameters for individual leaves in the canopy using Eq. (C5).

Appendix D

Parameterisation of biochemical model of photosynthesis for the big leaves

The net carboxylation rate of the big leaf is calculated as

$$V_{n,i} = \min\{V_{c,i}, V_{J,i}\} \qquad (D1)$$

where $V_{c,i}$ is the Rubisco-limited gross photosynthesis rate and $V_{j,i}$ is RuBP-limited gross photosynthesis rate of all sunlit leaves within the canopy. The Rubisco limited rate is calculated as

$$V_{c,i} = \frac{V_{cmax,i}(C_i - \Gamma_i^*)}{C_i + K_c(1 + O_i/K_o)} \qquad (D2)$$

where K_c and K_o are Michaelis-Menten coefficients for CO_2 and O_2, respectively. The RuBP-limited carboxylation rate is a function of potential electron transport rate (J_i) (von Caemmerer and Farquhar, 1981). That is:

$$V_{J,i} = \frac{(C_i - \Gamma_i^*)J_i}{4(C_i + 2\Gamma_i^*)} \qquad (D3)$$

where J_i is the potential rate of electron transport and is calculated as

$$J_i = \int_0^L j(q_{i,1})w_i(\xi)d\xi \qquad (D4)$$

and where j is calculated as

$$j = \frac{\alpha q_{i,1} j_{max}}{\alpha q_{i,1} + 2.1 j_{max}} \qquad (D5)$$

in which α is the quantum use efficiency and $j_{max,i}$ is the maximum electron transport rate. The following approximations (Eqs. (D6) and (D7)) are also applicable to the non-rectangular response function of potential electron transport rate to the absorbed quantum flux as used by de Pury and Farquhar (1997) and others.

For the big sunlit leaf, Eq. (D4) can be approximated using the big leaf parameterisation with reasonable accuracy for J_1 (the relative error usually less than 10%) as compared with the multi-layered canopy

model (Wang and Polglase, 1995 and de Pury and Farquhar, 1997). That approximation is equivalent to applying the two-point Gaussian integration to Eq. (D4) (Wang and Polglase, 1995). That is

$$J_1 = \frac{\alpha Q_{11} J_{max,1}}{\alpha Q_{11} + 2.1 J_{max,1}} \quad (D6)$$

However the big-leaf approximation as used by de Pury and Farquhar (1997) usually overestimates J_2 by 10 to 40% as compared with the multi-layered model, even though the overall relative errors in the total canopy photosynthesis is significantly much lesser. Leuning et al. (1995) numerically demonstrated that total photosynthesis of shaded leaves is relatively insensitive to the nitrogen distribution within the canopy for a given amount of total canopy nitrogen. As photosynthesis of shaded leaves within the canopy usually is limited by absorbed PAR. We assumed that J_2 is equal to the the potential electron transport rate of all shaded leaves within a hypothetical canopy having

the following properties:

1. the total j_{max} of all shaded leaves within the hypothetical canopy is equal to $J_{max,2}$;
2. the total amount of absorbed PAR is equal to $Q_{1,2}$;
3. both the j_{max} and absorbed PAR of shaded leaves within the hypothetical canopy vary in proportional to $\exp(-k_{d,1}\xi)$.

Then J_2 can be calculated as

$$J_2 = (\Psi(k_{d,1}^*) - \Psi(k_{d,1}^* + k_b)) \frac{\alpha q_{2,1}^*(0) j_{max^*}(0)}{\alpha q_{2,1}^*(0) + 2.1 j_{max}^*(0)}$$
$$(D7)$$

where $q_{2,1}^*(0)$ and $j_{max}^*(0)$ are the PAR absorbed by the shaded leaves and the maximum potential electron transport of shaded leaves at the top of the hypothetical canopy, respectively; $q_{2,1}^*$ and j_{max}^* are determined from the following equations derived from the assumed properties of the hypothe-

tical canopy:

$$\int_0^L j_{max}^*(\xi)(1 - \exp(-k_b\xi))d\xi$$
$$= \int_0^L j_{max}(\xi)(1 - \exp(-k_b\xi))d\xi \quad (D8)$$

$$\int_0^L q_{2,1}^*(\xi)(1 - \exp(-k_b\xi))d\xi$$
$$= \int_0^L q_{2,1}(\xi)(1 - \exp(-k_b\xi))d\xi \quad (D9)$$

$$q_{2,1}^*(\xi) = (1 + c_2)I_{d,1}k_{d,1}^*(1 - \rho_{td,1})\exp(-k_{d,1}^*\xi)$$
$$(D10)$$

Solving the above equations, we have

$$j_{max}^*(0) = J_{max,2}/(\Psi(k_{d,1}^*) - \Psi(k_b + k_{d,1}^*)) \quad (D11)$$

$$c_2 = \frac{I_{b,1}[(1 - \rho_{tb,1})k_{b,1}^*[\Psi\{k_{b,1}^*\} - \Psi\{k_{b,1}^* + k_b\}] - (1 - \omega_{f,1})k_b[\Psi\{k_b\} - \Psi\{2_b\}]]}{I_{d,1}(1 - \rho_{td,1})k_{d,1}^*[\Psi\{k_{d,1}^*\} - \Psi\{k_{d,1}^* + k_b\}]} \quad (D12)$$

Appendix E

Solving the coupled model of stomata-photosynthesis and energy partitioning

The equations for the coupled model for the big leaves can be written as:

$$G_{s,i} = G_{0,i} + \frac{a_1 f_w A_{c,i}}{C_{s,i}(1 + D_{s,i}/D_0)} \quad (E1)$$

$$A_{c,i} = V_{n,i} - R_{d,i} \quad (E2)$$

$$A_{c,i} = (C_{s,i} - C_i)b_{sc}G_{s,i} \quad (E3)$$

$$(C_{s,i} - C_i)b_{sc}G_{s,i} = (C_a - C_i)G_{c,i} \quad (E4)$$

$$Q_{n,i}^* - c_p G_{r,i}\Delta T_i = (D_a + s\Delta T_i)G_{w,i} + c_p G_{h,i}\Delta T_i$$
$$(E5)$$

$$D_{s,i}G_{s,i} = (D_a + s\Delta T_i)G_{w,i} \quad (E6)$$

There are six unknowns, $\Delta T_i, D_{s,i}, C_{s,i}, C_i, G_{s,i}, A_{c,i}$. Therefore at least one set of solutions exist. It is not

possible to solve the above six equations analytically. Several numerical methods can be used to solve the equations, all of them involve iteration until the solutions converge. The method for solving the equations must be efficient and reliable, the number of equations to be iterated must be minimised and evaluation of first-order or higher-order differentials should be avoided.

Eqs. (E1),(E2) and (E3) can be solved analytically for a given value of $\Delta T_i, C_{s,i}$ and $D_{s,i}$.

The analytic solution for C_i is (Leuning, 1990):

$$C_i = \frac{-b_1 + \sqrt{b_1^2 - 4b_0 b_2}}{2b_2} \qquad (E7)$$

$$A_{c,i} = d_2 \frac{C_i - \Gamma^*}{C_i + d_3} - R_{d,i} \qquad (E8)$$

where

$$b_0 = -(1 - d_1 C_{s,i})(d_2 \Gamma^* + d_3 R_{d,i}) - G_{0,i} d_3 C_{s,i}$$

$$b_1 = (1 - d_1 C_{s,i})(d_2 - R_{d,i}) + G_{0,i}(d_3 - C_{s,i})$$
$$- d_1(d_2 \Gamma^* + d_3 R_{d,i})$$

$$b_2 = G_{o,i} + d_1(d_2 - R_{d,i})$$

$$d_1 = \frac{a_1 f_w}{(C_{s,i} - \Gamma)(1 + D_{s,i}/D_0)}$$

and for Rubisco-limited photosynthesis

$$d_2 = V_{cmax}$$

$$d_3 = K_c(1 + O_i/K_o)$$

for RuBP-limited photosynthesis

$$d_2 = 0.25J$$

$$d_3 = 2\Gamma^*$$

Solution (Eq. (E7)) should be calculated for both Rubisco-limited and RuBP-limited photosynthesis and the smaller value of $A_{c,i}$ from Eq. (E8) should be used to calculate $G_{s,i}$ with Eq. (E1).

Eqs. (E5) and (E6) can be solved for ΔT_i for given values of $G_{w,i}$ and $G_{h,i}$ (Monteith and Unsworth, 1990):

$$\Delta T_i = \frac{\gamma^*}{s + \gamma^*} \frac{Q_{n,i}^*}{c_p(G_{h,i} + G_{r,i})} - \frac{D_a}{s + \gamma^*} \qquad (E9)$$

where γ^* is the modified psychrometer constant and is related to the psychrometer constant (γ) as

$$\gamma^* = \gamma \frac{G_{h,i} + G_{r,i}}{G_{w,i}}$$

Eqs. (E4) and (E6) can be re-arranged to give the values of $C_{s,i}$ and $D_{s,i}$ for a given values of ΔT_i, C_i and all conductances. They are

$$C_{s,i} = C_i + (C_a - C_i)G_{c,i}/(b_{sc} G_{s,i}) \qquad (E10)$$

$$D_{s,i} = (D_a + s\Delta T_i)G_{w,i}/G_{sw,i} \qquad (E11)$$

To solve the coupled equation numerically, initially ΔT_i is set to zero and $C_{s,i}$ and $D_{s,i}$ are assigned their respective values at the reference height above the canopy (C_a, D_a). The initial values of $C_i, A_{c,i}$ and $G_{s,i}$ are obtained from Eqs. (E7),(E8) and (E1) and these are used to update the values of $T_i, C_{s,i}$ and $D_{s,i}$ using Eqs. (E9),(E10) and (E11). The new values of ΔT_i, $C_{s,i}$ and $D_{s,i}$ are then used to update the values of C_i, $A_{c,i}$ and $G_{s,i}$ in the each iteration until the values of ΔT_i between two successive iterations is <0.01°C.

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