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A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. II. Comparison with measurements

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Abstract

A new two-leaf canopy model for predicting fluxes of net radiation, sensible heat, latent heat and CO₂ between plant canopies and the atmosphere was tested against 228 half-hourly micrometeorological flux measurements spanning over two months during the vegetative growth of two wheat crops. During that period green area index ranged from 1.8 to 4.5 for the fertilised crop and from 1.0 to 2.7 for the control crop. Excellent agreement was obtained between simulations and measurements for fluxes of net radiation, latent heat and CO₂, although sensible heat fluxes were less satisfactory. Uncertainties in estimates for fluxes of water vapour and CO₂ from the underlying soil contributed to discrepancies between measurements and simulations. Modelled canopy fluxes of both CO₂ and latent heat are highly sensitive to the quantum yield of photosynthesis ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ quanta). Fluxes of latent heat are more sensitive than CO₂ to parameters describing stomatal function, while CO₂ flux was more sensitive than transpiration to maximum carboxylation rates. The two-leaf model requires only a few parameters that may vary with plant species. It is computationally 10 times more efficient than an earlier described multi-layered model and is suited for incorporation into regional- or global-scale climate models. © 1998 Published by Elsevier Science B.V. All rights reserved.

1. Introduction

In an accompanying paper, Wang and Leuning (1998) describe a two-leaf model for calculating the coupled fluxes of CO₂, sensible heat and latent heat between horizontally uniform plant canopies and the atmosphere. The model separates leaves into sunlit and shaded classes, a distinction which is necessary because of the non-linear response of photosynthesis to absorbed radiation. Failure to make this distinction

and use of average radiation absorbed by leaves leads to overestimates in calculated canopy assimilation rates of 5–25% as leaf area index ranges from 1 to 5 (Spitters, 1986). In a detailed analysis, DePury and Farquhar (1997) also concluded that single “big-leaf” models introduce significant errors into CO₂ flux calculations. Because of the non-linearity of the governing equations, problems also occur in calculating sensible and latent heat fluxes if simple arithmetic means of stomatal conductances are used to calculate canopy conductance (McNaughton, 1994). Fluxes of heat, water vapour and CO₂ between a plant canopy and the atmosphere calculated using the two-leaf

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model of Wang and Leuning (1998) were within –5% of results from the more detailed multilayer model of Leuning et al. (1995). The resultant increase in computational efficiency without a significant penalty in precision makes the new two-leaf model suitable for incorporation in global circulation models (e.g. Sellers et al., 1992), regional transport models (McGregor et al., 1993) and Soil-Vegetation-Atmosphere models (Kowalczyk et al., 1992). Before this is attempted, performance of the two-leaf model must be evaluated by comparing predictions of fluxes with measurements, ideally over a variety of ecosystems and climatic regimes. As part of the validation process, this paper compares model estimates for fluxes of radiation, CO₂, sensible heat and latent heat with fluxes measured during the growing season, above two contrasting fields of wheat in a temperate climate.

2. Materials and methods

2.1. Flux measurements

The well known Bowen ratio-energy balance technique (McIlroy, 1972; Dunin et al., 1989) was used to partition energy available to the underlying surface (crop plus soil), i.e.

$$\lambda E = (Q_n - G)/(1 + \beta) \quad (1)$$

and

$$H = Q_n - G - \lambda E \quad (2)$$

where E is the water vapour flux density, λ is the latent heat of vaporisation for water vapour, Q_n is net radiation, G is soil flux, H is the sensible heat flux, and β is the Bowen ratio given by

$$\beta = H/\lambda E = (c_p/\lambda)(\Delta\bar{T}/\Delta\bar{q}) \quad (3)$$

in which c_p is the specific heat capacity of air, and where $\Delta\bar{T}$ and $\Delta\bar{q}$ are the mean differences in temperature and specific humidity measured over a suitable height interval in the air above the crop. The net exchange of CO₂ between the atmosphere and the crop plus soil was calculated using

$$A = E(M_c/M_w)(\Delta\bar{c}/\Delta\bar{q}) \quad (4)$$

where $\Delta\bar{c}$ is the difference in CO₂ mixing ratio relative to dry air (Webb et al., 1980), and M_c and M_w are the

molecular masses of CO₂ and water vapour, respectively.

2.2. Partitioning of fluxes between canopy and soil

Because the two-leaf model estimates only canopy fluxes, comparison of model predictions and measurements required the partitioning of total fluxes of net radiation, sensible heat, latent heat and CO₂ into canopy and soil components according to

$$\begin{aligned} Q_{nc} &= Q_n - Q_{ns} & H_c &= H - H_s & \lambda E_c &= \lambda E - \lambda E_s \\ A_c &= A + R_{root} + R_{soil} \end{aligned} \quad (5)$$

Absorption of net radiation by the crop, Q_{nc} , and soil, Q_{ns} , was calculated using the methods outlined by Wang and Leuning (1998). Estimates of Q_{ns} were combined with measurements of G and λE_s as described below (see Eq. (9)) to estimate the flux of sensible heat from the soil using the energy balance at the soil surface $H_s = Q_{ns} - \lambda E_s - G$.

To estimate the uptake of CO₂ by the canopy during the day, CO₂ efflux from soil microorganisms and root respiration must be added to the micrometeorological measurements. The empirical relationship

$$R_{soil} = 0.79 + 0.0676T_a \quad (6)$$

obtained by Raich and Schlesinger (1992) was used to estimate respiration by the soil, and the following formula was used to estimate respiration by the roots

$$R_{root} = 0.1A_{root} \exp(0.084T_a) \quad (7)$$

($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), where T_a is air temperature, A_{root} is root area index estimated as $0.003m_{root}$, where m_{root} is the mass of root per unit land area. Air temperature is used in Eq. (7) for lack of information on soil temperatures.

2.3. Experimental site and instrumentation

Measurements were made in a 15 ha field at Charles Sturt University, near Wagga Wagga, New South Wales (35°4'S, 147°21'E, altitude 219 m). Wheat (*Triticum aestivum* cv. Janz) was sown at a rate of 78 kg ha⁻¹ on 6 June 1993 with addition of di-ammonium phosphate at a rate of 17 kg N ha⁻¹ (Poss et al., 1995a). Two adjacent areas of 5 ha within the field were used for separate treatments. Supplementary

urea fertiliser was applied to the northern treatment block at 140 kg N ha^{-1} on 6 August, while no extra fertiliser was added to the southern control block. Anthesis occurred on 25 October and the crop was harvested on 9 December.

Green leaf and stem area index was estimated every two weeks using biomass harvests from 12 plots 0.5 m^2 in area. Subsamples from the harvests were separated into stem and leaf components and their area and mass measured to obtain specific areas. The dry mass of the total harvest was apportioned according to their ratios in the subsamples, and specific areas were used to estimate component areas from their biomass. The leaf-area index at the time of supplementary fertiliser application was 0.65 and 0.50 for the fertilised and control blocks. Total nitrogen content was determined using an autoanalyser following micro-Kjeldahl digestion of plant material which had been dried at 70°C and passed through a 0.42 mm mesh sieve. Seasonal variation in green-area index (GAI), leaf-area index (LAI), total above ground biomass and nitrogen concentrations of stems plus leaves are presented in Fig. 1 for both the fertilised and control blocks. The nitrogen concentrations of leaves shown in Fig. 1(c) were not measured directly but were estimated by assuming that concentrations within the stems were 0.33 that of the leaves, the average ratio found by van Herwaarden (1995) for wheat plants subject to fertiliser application of 0, 80 and 120 kg N ha^{-1} . With this assumption the mean N concentration in the leaves is given by

$$C_{N,L} + (m_S = m_L)\bar{C}_N / (0.33m_S + m_L) \quad (8)$$

where m_S and m_L are the dry mass of stems and leaves, respectively, and \bar{C}_N is the mean N concentration of leaves plus stems.

Soil at the site grades from a fine sandy loam at the surface (23 g kg^{-1} clay) to a mild clay (55 g kg^{-1} clay) at 0.6 m with a band of fine iron-manganese nodules (see Poss et al. (1995b) for details). Soil moisture content used to modulate stomatal conductance (Wang and Leuning, 1998) was measured using TDR (Time Domain Reflectometry; Zegelin and White, 1989), with probes inserted horizontally at the depths of 0.05, 0.10, 0.25, 0.38, 0.58, 0.88 and 1.02 m . Measurements were replicated at two sites in each of the two blocks. Moisture contents were measured every 15 min and then averaged to daily values.

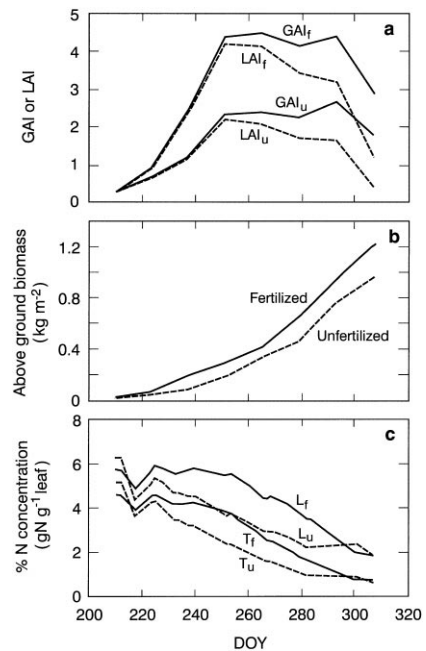


Fig. 1. Measured seasonal variation in (a) leaf-area index (LAI) and green-area index (GAI); (b) above-ground biomass; and (c) mean nitrogen concentration, C_N ($\% \text{ g N g}^{-1}$ leaf) for leaves plus stems (T), and leaves only (L). DOY stands for Day of Year (1 August = DOY 213), while subscripts f and u represent fertilised and unfertilised fields. N concentrations for leaves were estimated using Eq. (8).

Rainfall of 543 mm for 1993 was near average, although above average rainfall in July, September and October maintained high soil water contents during the growing season (Poss et al., 1995b).

Two aspirated psychrometers in radiation shields, placed 1 m apart vertically, were used to measure $\Delta\bar{T}$; and $\Delta\bar{q}$; required to estimate the Bowen ratio. The psychrometers were interchanged every 15 min using a reversing boom to reduce errors caused by sensor offsets, and measurements for each 15 min period were combined to form half-hourly estimates of the fluxes (Dunin et al., 1989). The instrument array was raised periodically throughout the season to ensure that the lower psychrometer was about 0.3 m above the canopy. Net radiation was measured using Funk-type radiometers with domes inflated with dry air, and a set of four soil heat flux plates buried at 0.02 m was used to measure soil heat flux. Soil thermometers were not installed so no correction was made for the change in energy stored between the soil surface and the heat

flux plates associated with changes in soil temperature.

Concentrations of CO₂ were measured using an infrared analyser (Binos, 4.2T, Leybold Heraeus, Germany). Air collected from sampling arms located at the same heights as the psychrometers was passed through heated airlines to avoid water condensation, and then to the CO₂ analyser in a field laboratory. The analyser was calibrated daily using cylinders of dry air containing CO₂ which had previously been calibrated against gas mixing pumps (H. Wosthoff Apparatebau, Bochum, Germany).

2.4. Soil evaporation

Miniature lysimeters described by Leuning et al. (1994) were used to measure soil evaporation, E_s . The lysimeters consisted of open PVC cylinders 285 mm long and 160 mm O.D., which is similar to the inter-row spacing of 170 mm. Four sets of 25 cylinders were pressed into the moist soil early in the growing season (LAI~0.5). The cylinders were distributed at random along four 300 m transects running N–S and spaced ~65 m apart across the 350 m wide field. Each week, a new set of four soil cylinders were extracted from the soil after removal of plant tops. The bottoms of the extracted cylinders were then sealed to prevent water exchange except at the soil surface. The cores were taken to a field laboratory where they were weighed to a precision of 0.1 g (0.005 mm resolution) before being returned to the field. The lysimeters were weighed at intervals of one to four days between 13 July and 25 November 1993. Because micrometeorological measurements and model calculations were made on a half-hourly basis, it was necessary to partition the accumulated evaporation rates measured by the lysimeters, $\sum \lambda E_s$ (the summation is over the time interval between weighings). To do so, we assumed that soil evaporation was proportional to solar radiation absorbed at the soil surface, Q_s such that

$$\lambda E_s = \frac{sQ_s/(s+\gamma)}{\sum sQ_s/(s+\gamma)} \sum \gamma E_s \quad (9)$$

where s is the slope of the curve relating saturation water vapour pressure to temperature and γ is the psychrometric constant. Normally, the factor $s/(s+\gamma)$ is used to convert net radiation at the soil surface, Q_{ns} ,

to equilibrium evaporation, but here we have assumed a constant scaling factor between net and solar radiation at the soil surface when using Eq. (9) because Q_s was not measured.

Input meteorological data required for the model are air temperature, T_a , water vapour pressure deficit, D_a , incoming solar radiation, I_0 , and windspeed, U . These quantities were measured using the psychrometers required for Bowen ratio measurements (T_a and D_a), a dual glass dome solarimeter (Kipp and Zonen, Delft, The Netherlands) for I_0 , and a cup anemometer for U with resolution of 1 km wind run. Diurnal variation of I_0 , T_a and D_a used in the current simulations are shown in Fig. 2 of the accompanying paper (Wang and Leuning, 1998). Measured leaf area indices shown in Fig. 1 were also used as input in the calculations. Soil moisture content from TDR measurements was used to evaluate the stomatal response function given in Wang and Leuning (1998).

2.5. Modelling

Model performance depends critically on model structure and the choice of parameter values (see Table 3 of Wang and Leuning, 1998 for values of key parameters used). Except for sensitivity analyses reported later, parameter values were held constant for the entire growing season and no attempt was made to adjust daily parameter values to maximise agreement between measurements and the simulations. In particular, the coupled model for stomatal conductance and CO₂ assimilation describes response functions for single leaves, and the same parameter values were used for leaves of both unfertilised and fertilised crops. Therefore the only difference between the unfertilised and fertilised crops in the model is green area index (see Fig. 1). Optical properties such as albedo of the canopy plus soil were calculated using the assigned optical properties of the soil, the component leaves and the assumed leaf angle distribution.

In the following simulations, predictions from the two-leaf model are compared to 228 half-hourly daytime micrometeorological flux measurements spanning a period of 62 days from 18 August to 21 October 1993 (DOY 230–294). During this period green area index ranged from 1.8 to 4.5 for the fertilised field and from 1.0 to 2.7 for the control (Fig. 1).

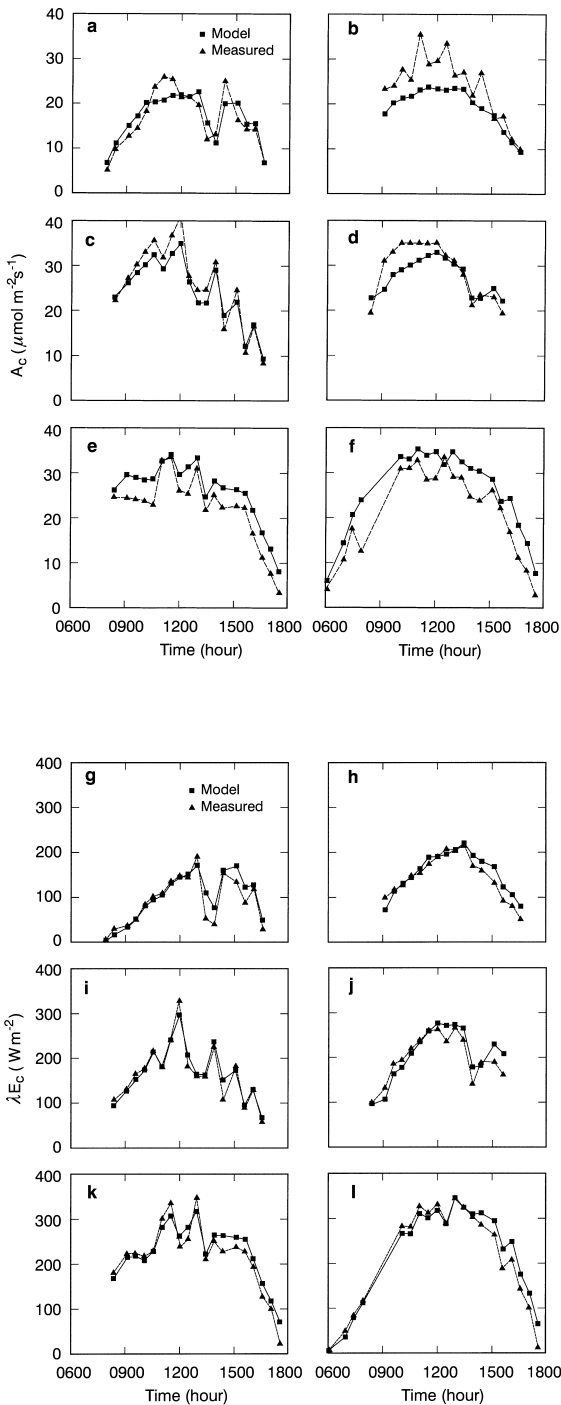


Fig. 2. Diurnal variation of measured and simulated canopy fluxes: A_c and λE_c for six selected days in 1993: (a, g) 20 August, (b, h) 25 August, (c, i) 22 September, (d, j) 23 September, (e, k) 20 October and (f, l) 21 October. Results are for fertilised field.

2.6. Criteria for evaluation of model performance

In a discussion of methods to evaluate model performance, Willmott (1981) criticised the use of r^2 values obtained from linear regression of model predictions, P_i , plotted against observations, O_i , because the magnitude of r^2 does not relate consistently to the accuracy of prediction. Accuracy is defined as “the degree to which model-predicted observations approach their observed counterparts”. Following a comparison of various measures of model accuracy Willmott (1981) recommended an index of agreement defined as

$$d = 1 - \left[\frac{\sum_{i=1}^N (P_i - O_i)^2}{\sum_{i=1}^N (|P'_i| + |O'_i|)^2} \right] \quad (10)$$

where \bar{O} is the mean of the observations, $P'_i = P_i - \bar{O}$; and $O'_i = O_i - \bar{O}$. The value of d ranges from $d=1$ to $d=0$ as agreement between predicted values and observations changes from perfect to none. As pointed out by Figuerola and Mazzeo (1997), this index becomes unstable when the denominator is small so it is useful to include other measures of model performance. Willmott (1981) separated the total mean square error, MSE, into systematic and unsystematic components

$$MSE_s = N^{-1} \sum_{i=1}^N (\hat{P}_i - O_i)^2 \quad (11)$$

and

$$MSE_u = N^{-1} \sum_{i=1}^N (P_i - \hat{P}_i)^2 \quad (12)$$

where $\hat{P}_i = aO_i + b$, in which a and b are the coefficients obtained from linear regression analysis. Note that $MSE = MSE_s + MSE_u$.

3. Results and discussion

Diurnal variation in canopy fluxes of transpiration and photosynthesis for both the fertilised and unfertilised treatments are presented for six selected days in Figs. 2 and 3. These days were selected to represent the early, middle, and late stages of vegetative growth,

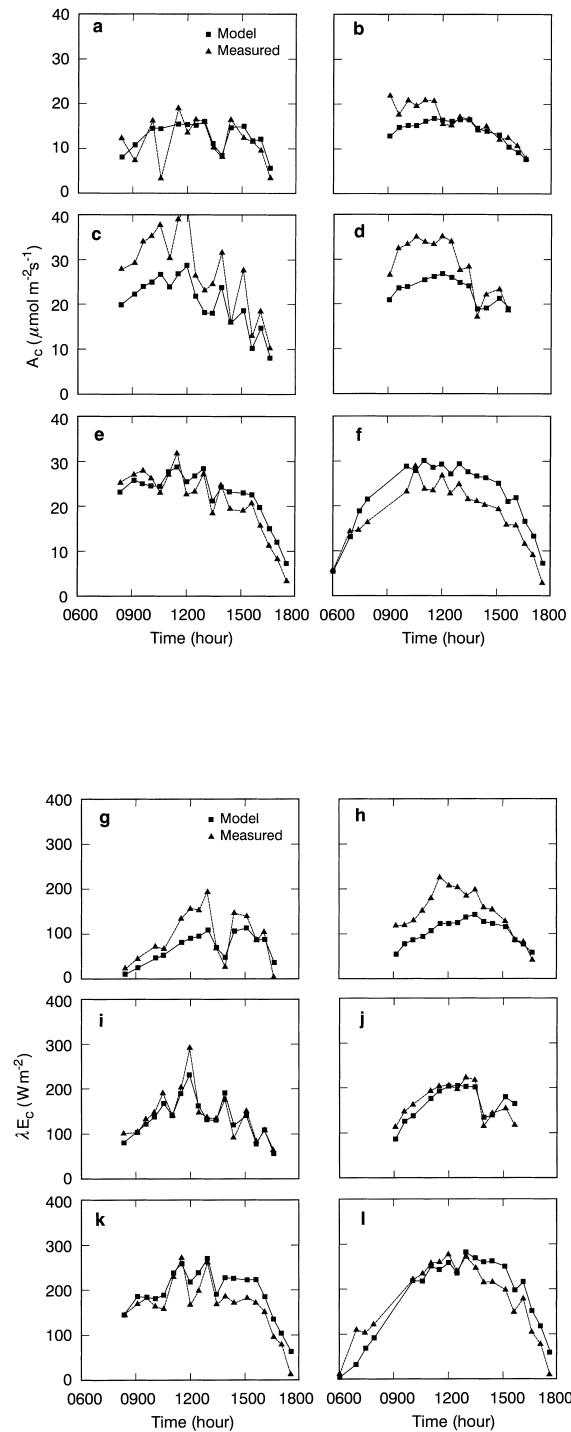


Fig. 3. Diurnal variation of measured and simulated canopy fluxes: A_c (a–f) and λE_c (g–l) for six days in 1993 (see Fig. 2). Results are for unfertilised field.

and included days which were largely sunny (Doy 232, 237, 266 and 293) or cloudy (Doy 265, 293). Each figure compares model predictions with micro-meteorological measurements adjusted for soil fluxes according to Eq. (5) for the two months before flowering. Simulations of both transpiration and photosynthesis for the fertilised treatment, with its higher green area index, match the observations more closely than do the simulations for the control. There is also a tendency for simulations of λE_c and A_c to underestimate observations early in the season while overestimating later on. These discrepancies may arise from overestimating the amount of plant area involved in transpiration and photosynthesis late in the season since an estimated 30–40% of total area consisted of stems by day 295 (Fig. 1). Alternatively, use of a constant value of V_{cmax} (J_{max}) for the whole season may cause overestimates in assimilation rates and conductances later in the season as leaf nitrogen concentrations decline. This is discussed in more detail later.

Plots comparing model simulations and observations of fluxes to the canopy alone, Q_{nc} , H_c , λE_c and A_c , for the fertilised and unfertilised plots are shown in Figs. 4 and 5, respectively. Model results cluster along the 1:1 line in each case, although there is some scatter (see also Table 1). Predictions of Q_{nc} are in excellent agreement with observations at values below 350 W m^{-2} but tend to overestimate above this value,

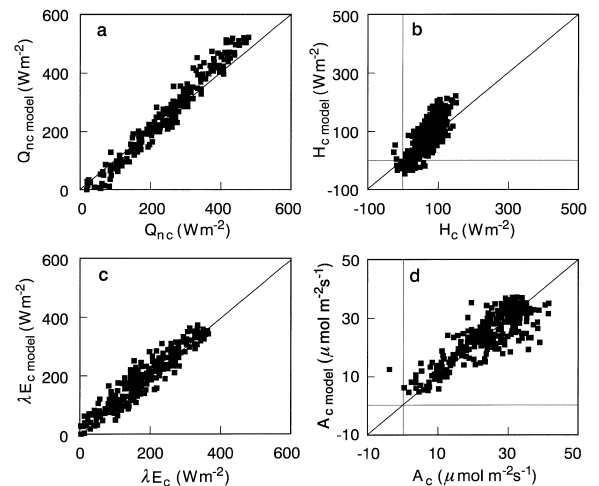


Fig. 4. Comparison of modelled vs. measured fluxes for (a) Q_{nc} , (b) H_c , (c) λE_c and (d) A_c for the fertilised field. A total of 228 half-hourly data points are shown spanning DOY 231–295.

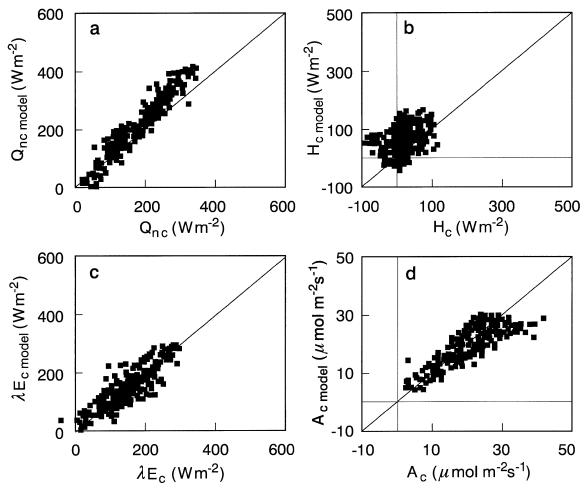


Fig. 5. Comparison of modelled vs. measured fluxes for (a) Q_{nc} , (b) H_c , (c) λE_c and (d) A_c for the unfertilised field. A total of 228 half-hourly data points are shown spanning DOY 231–295.

resulting in linear regression lines ($y = ax + b$) with slopes greater than unity (Table 1). The model typically overestimates net radiation for the canopy alone, Q_{nc} , by 10% at 500 W m^{-2} , with a similar result when total net radiation, Q_n , is compared with measurements (data not shown). The reasons for this are unclear but underestimates in calculated canopy plus soil albedo appear to be the most likely cause. Total albedo increases with GAI (e.g. $\rho=0.180, 0.215$ and 0.230 for $\text{GAI}=1, 3$ and 5 when the beam fraction=1 and solar zenith angle= 35°) Albedo also increases with the beam fraction of incoming solar radiation at

all sun zenith angles for $\text{GAI}>2$. Underestimates in the unmeasured soil albedo, GAI and calculated beam fraction will thus cause an overestimation in absorbed shortwave radiation. The formation of fair-weather cumulus clouds between 1000 and 1500 h in this region may also contribute to the observed discrepancies. Further detailed measurements of the radiation components contributing to Q_{nc} are required to resolve this issue.

Agreement between the model and observations is excellent for λE_c for both the fertilised and unfertilised plots. However, slopes of regression lines for A_c are significantly <1 (Table 1). This occurs because the centroid of the data points lies at values around $20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, thereby biasing the results away from the origin in the regression analysis. Forcing the linear regression through the origin increases the slope to 1.02 and 0.99 for the fertilised and unfertilised plots, respectively. Part of the scatter in the results also derive from errors in the measurements. In the case of transpiration, soil evaporative fluxes estimated according to Eq. (9) were subtracted from total fluxes measured using micrometeorological techniques Eq. (1). Canopy assimilation was calculated according to Eq. (5), whereby CO_2 efflux from the soil and roots (Eqs. (6) and (7)) were added to fluxes measured above the canopy Eq. (4). Fig. 6 shows that estimated soil and root respiration were fairly constant at $2 \mu\text{mol m}^{-2} \text{ s}^{-1}$, while λE_s was typically 20% of the total flux. Table 1 shows that systematic errors are substantially less than random errors for all fluxes except Q_{nc} in both treatments and

Table 1

Results of linear regression analysis, $p_i = aO_i + b$, or $p_i = a^*O_i$ where O_i are observations and p_i are predictions from the two-leaf model. Also shown are the ‘‘Agreement Index’’, d Eq. (10) and the systematic and unsystematic root mean square errors (RMSE_s and RMSE_u) obtained by taking the square root of the MSE’s given in Eq. (11) and Eq. (12). A total of 228 half-hourly data points were used in the analysis for each treatment

Site	Variable	Units	<i>a</i>	SE <i>a</i>	<i>b</i>	SE <i>b</i>	<i>r</i> ²	<i>d</i>	RMSE _s	RMSE _u	<i>a</i> [*]
Fertilised	λE_c	W m^{-2}	0.93	0.02	20	30	0.89	0.97	10.0	29.0	1.02
	H_c	W m^{-2}	1.38	0.07	-10	40	0.66	0.82	20.0	38.6	1.17
	Q_{nc}	W m^{-2}	1.20	0.02	-38	27	0.96	0.98	24.7	26.0	1.05
	A_c	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	0.71	0.03	6.7	4.6	0.67	0.90	2.7	4.5	1.02
Unfertilised	λE_c	W m^{-2}	0.88	0.03	19	36	0.75	0.93	8.3	35.3	0.99
	H_c	W m^{-2}	0.40	0.07	52	47	0.12	0.53	47.8	45.6	0.66
	Q_{nc}	W m^{-2}	1.23	0.03	-7	32	0.91	0.93	37.2	31.5	1.17
	A_c	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	0.71	0.03	4.9	3.8	0.71	0.90	2.3	3.7	0.99

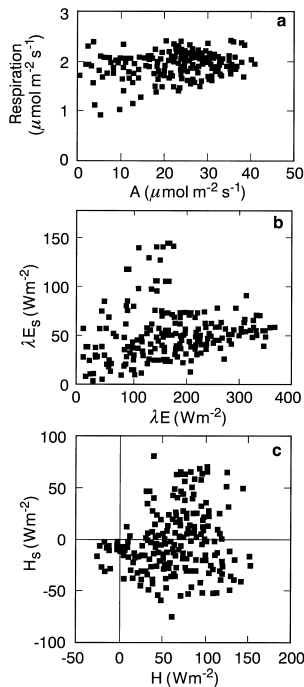


Fig. 6. Plots of (a) estimated root plus soil respiration vs. measured total CO_2 flux, (b) measured evaporation from soil vs. measured total latent heat flux, and (c) measured sensible heat flux at soil vs. measured total latent heat flux. Measurements were made using micrometeorological methods. To estimate canopy CO_2 flux, respiration is added to the measured flux, while soil λE_s and H_s are subtracted.

H_c for the unfertilised block, indicating that the model provides satisfactory unbiased results for the diurnal variation for these variables.

It is clear from both Figs. 4 and 5 that agreement between model and observed values of H_c is somewhat worse than for the other three variables. This is confirmed by the agreement index, d , and the RMSE values for systematic and unsystematic errors shown in Table 1. Several reasons for the relatively poor results for H_c are: 1) the over estimation of Q_{nc} , 2) the relatively large contribution of the estimated sensible heat flux at the soil surface to the measured sensible heat flux (Fig. 6(c)), 3) the use of too simple a formulation for the aerodynamic resistance to heat transfer (see Wang and Leuning, 1998), and 4) errors in calculating leaf temperatures. Baldocchi and Harley (1995) noted that H is expected to be more sensitive than λE to the latter two errors because H is dependent only on leaf temperature and aerodynamic resistance,

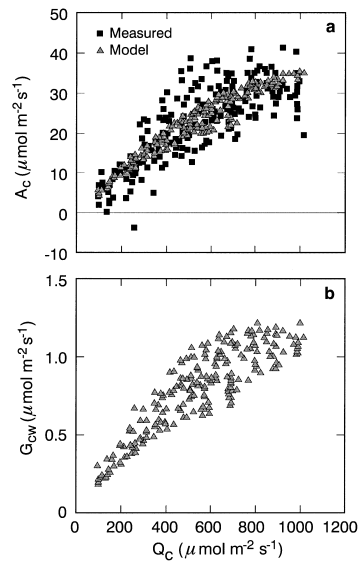


Fig. 7. (a) Measured and simulated net assimilation for the fertilised crop canopy, and (b) canopy conductance as a function of solar radiation absorbed by the canopy $Q_{c,1}$.

r_a , while λE depends on the sum of r_a and stomatal resistance, r_s . In many cases, $r_a < r_s$ so uncertainties in r_a introduce small errors into λE . For both fertiliser treatments the agreement index values for Q_{nc} , E_c and A_c are ≥ 0.90 , while that for H_c is 0.82 in the fertilised block and 0.53 for the control.

Simulated canopy CO_2 fluxes plotted as a function of solar radiation (Fig. 7(a)) shows much less scatter than do the measured values. This is to be expected for the model results since variation in radiation absorbed by the canopy is the primary determinant of canopy CO_2 fluxes, but it does suggest that a significant component of the scatter seen in Figs. 4 and 5 results from errors in both measurements and estimates of respiration from the soil and roots. While the non-linear relationship between modelled A_c and total absorbed solar radiation, Q_c , resembles the light-response curves for individual leaves, the degree of curvature for the canopy is considerably less than normally observed for leaves. This is because irradiance of leaves within canopies ranges over two orders of magnitude, and thus many leaves operate in the linear, light-limited region of the light response curve. Only leaves in full sunlight are likely to be light-saturated. A similar nexus exists between the light response of individual chloroplasts and that of the

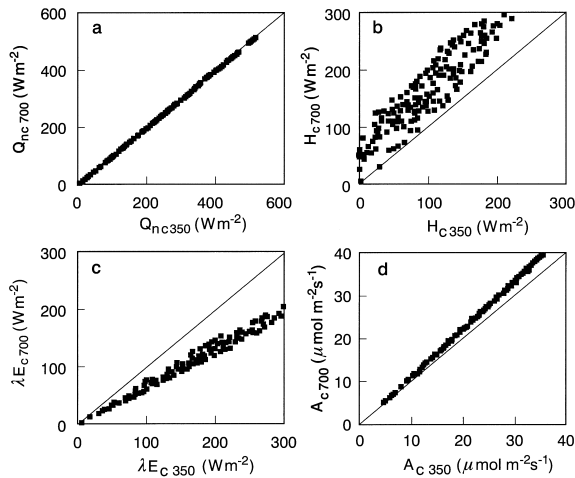


Fig. 8. Simulated fluxes for (a) Q_{nc} , (b) H_c , (c) λE_c , and (d) A_c for the fertilised field at $C_a = 700$ ppm compared to predictions for $C_a = 350$ ppm. All other parameters were held constant in the simulations.

ensemble of chloroplasts in a whole leaf (Farquhar, 1989). The relationship between predicted canopy conductance, G_{cw} , and Q_c , is shown in Fig. 7(b). Stomatal conductance responds to leaf irradiance, humidity deficit and to soil water deficits, and the increased scatter in Fig. 7(b) compared to Fig. 7(a) for predicted quantities shows that these factors influence canopy conductance more strongly than canopy CO_2 assimilation rates according to the model.

To examine the sensitivity of the model to variations in key parameters, the model was re-run using new

values of each parameter, while holding the others unchanged. In each case a linear relationship was obtained when simulation results using the new parameter value were plotted against output obtained with the reference parameters, as shown in the example of Fig. 8 when atmospheric CO_2 concentration, C_a , is doubled from 350 to 700 ppm. These simulations were run using the pattern of leaf area development and weather conditions observed during 1993, and no attempt was made to model the accelerated leaf area development during early growth stages expected under high CO_2 (Leuning et al., 1993; Wang and Connor, 1995). Doubling atmospheric CO_2 concentrations is predicted to cause latent heat fluxes to decrease by 34% and that for CO_2 to increase by 12% (Table 2). A 2% decrease in Q_{nc} is predicted because canopy temperature rises a little thereby increasing outgoing long wave radiation. It is apparent from Fig. 8 that model response of λE_c and A_c at 700 ppm CO_2 is a linear function of model output at 350 ppm CO_2 for all LAI and irradiances, implying that photosynthesis was not saturated by CO_2 at the higher concentration.

A simulation using $C_a = 550$ ppm was also run to compare with results obtained by Grant et al. (1995) in a free-air CO_2 enrichment (FACE) experiment on wheat in Arizona. According to their accumulated daily measurements, total evapotranspiration from plants grown at 550 ppm was 11% lower than for control plants grown at 370 ppm. This is about half the 23% reduction in transpiration predicted using the two-leaf model in this paper (data not shown). The

Table 2

Sensitivity of λE_c and A_c to variation in values of key parameters, expressed as slope of model output with parameter value in bold type vs. model output with standard parameter values (first line). Input data are for the fertilised treatment

Parameter					Flux	
C_a (ppm)	a_1 (-)	D_0 (Pa)	α (mol CO_2 mol ⁻¹ quanta)	V_{cmax} (μ mol CO_2 m ⁻² s ⁻¹)	λE_c (-)	A_c (-)
350	11	1000	0.385	150	1.00	1.00
700	11	1000	0.385	150	0.66	1.12
350	8	1000	0.385	150	0.79	0.97
350	16.5	1000	0.385	150	1.29	1.02
350	11	700	0.385	150	0.90	0.99
350	11	1300	0.385	150	1.06	1.01
350	11	1000	0.385	100	0.92	0.88
350	11	1000	0.385	200	1.04	1.07
350	11	1000	0.200	150	0.67	0.58

difference between FACE results and our simulation may arise from: 1) higher leaf-area index in the crop grown at elevated CO₂ than for the control, 2) higher saturation deficits in Arizona (peak 2.7 kPa) than in Wagga (<1 kPa), leading to greater evaporative demand for a given canopy conductance, and 3) compensation between evaporation from soil and plants. The latter explanation is suggested by results obtained from two wheat cultivars (Quarrion and Matong) grown at Wagga Wagga during 1991. These cultivars have similar phenological development but have differing stomatal conductances (maximum g_s for Quarrion is 60% that of Matong). One of the responses of leaves to elevated CO₂ is a reduction in stomatal conductance, and thus Quarrion provides a partial analog for expected plant response under elevated CO₂ – a decreased conductance but no high CO₂. While seasonal cumulative transpiration from Quarrion was 38% lower than for Matong (both as a result of lower leaf area and canopy conductances), this was largely offset by increased evaporation from the soil below Quarrion, with the net result that seasonal evapotranspiration for the two cultivars differed by only 6% (O.T. Denmead, F.X. Dunin and R. Leuning, unpublished data). A similar result may be expected for plants grown at elevated CO₂. It is clear that prediction of crop responses to future climates requires a complete description of leaf level responses, crop growth patterns and soil evaporation.

Table 2 presents results obtained when C_a , a_1 , D_0 , V_{cmax} and α were changed as indicated. Canopy assimilation is relatively insensitive to 30% variations in parameters a_1 and D_0 of the stomatal conductance model, while λE_c (and hence H_c) responds significantly to these parameters. Leuning et al. (1995) pointed out that, when the stomata are fully open at saturating irradiance and zero humidity deficit, a_1 is related to the intercellular CO₂ concentration, C_i , by $C_i/C_a = 1 - 1/a_1$. Varying a_1 from 8 to 16.5 (Table 2) is equivalent to varying C_i/C_a from 0.875 to 0.939 when the stomata are fully open, leading to a change of $\pm 3\%$ in maximum assimilation rate and thus explaining the insensitivity of A_c to a_1 . The parameter D_0 is the VPD at which stomatal conductance is reduced by a factor of two; thus less sensitive leaves have higher values of D_0 , and vice versa. A 30% decrease in D_0 causes a 10% reduction in λE_c , and a corresponding increase in D_0 produces a 6% increase in λE , while changes in A_c

are <1%. Canopy assimilation is slightly more sensitive to variations in the biochemical parameters α and V_{cmax} than is transpiration, with a 33% reduction in V_{cmax} leading to a 12% drop in A_c , while a 33% increase in V_{cmax} produces a 7% increase in A_c . Corresponding changes in λE_c are -8% and $+4\%$ respectively. (Note: while V_{cmax} is used in Table 2, in the model we assume $J_{max} = 2.7 V_{cmax}$ at 20°C (Leuning, 1997), so photosynthesis may be limited by either RuBP₂ regeneration or Rubisco activity, depending on C_i and absorbed PAR, $Q_{1.}$) Responses of A_c and λE_c to symmetrical changes in parameter values are not the same, emphasising the non-linear character of the response surface describing photosynthesis, stomatal conductance and the leaf energy balance.

The mean quantum yield for CO₂ assimilation, α' , was found by Ehleringer and Pearcy (1983) to be $\alpha' = 0.052 \pm 0.01$ mol CO₂ mol⁻¹ quanta for a diverse number of C₃ species when measured at a leaf temperature of 30°C. These authors found that α' decreased by 0.0013 mol CO₂ mol⁻¹°C⁻¹, thus increasing α' to 0.065 at the reference temperature of 20°C used in this paper. Following von Caemmerer and Farquhar (1981), to convert from the quantum yield for photosynthesis so that for electron transport we use $\alpha = 4\alpha' (C_i + 2\Gamma^*) / (C_i - \Gamma^*)$, which yields $\alpha = 0.39$, for $C_i = 350$ ppm and $\Gamma^* = 50$ ppm. This agrees closely with the value $\alpha = 0.385$ (mol electrons mol⁻¹ quanta) adopted in this paper and used by Farquhar et al. (1980), but contrasts to values of 0.20–0.24 obtained by Harley et al. (1992) and Harley and Baldocchi (1995) when fitting light-response curves to photosynthetic data measured on individual leaves of cotton, *Quercus* and *Acer*, and by Leuning (1990, 1995) for *Eucalyptus grandis*. With $\alpha = 0.20$, λE_c decreased to 0.67 and A_c dropped to 0.58 compared to results obtained with $\alpha = 0.385$ (Table 2), indicating that quantum yield for electron transport is a critical parameter in the model. The model provided a satisfactory fit to the measured canopy fluxes with $\alpha = 0.385$, and this value was used in all other simulations.

The current canopy model assumes an exponential decline in photosynthetic capacity, V_{cmax} (J_{max}), with depth into the canopy in response to decreasing leaf nitrogen concentrations (Hirose and Werger, 1987; Leuning et al., 1995). The nitrogen distribution

coefficient, k_n , is assumed in the model to equal the effective extinction coefficient for diffuse PAR $k_{d,1}^*$, as the vertical distribution of leaf nitrogen in the canopy was not measured (however, the two-leaf model is applicable to a canopy with any vertical distributions of leaf nitrogen). The coefficient $k_{d,1}^*$ varies with LAI but has a value ≈ 0.8 for $L < 3$ (Goudriaan and van Laar, 1994), implying that at canopy depth $L=3$, V_{cmax} is $\approx 10\%$ of V_{cmax} for leaves at the top of the canopy. Mean leaf nitrogen concentrations declined progressively during the growing season (Fig. 1(c)), and consistency with the above approach suggests that V_{cmax} should also be varied as the season progresses, rather than being held constant as in the above simulations. To test the consequence of varying V_{cmax} during the season, the model was re-run using the arbitrary function

$$V_{cmax} = 0.2C_N V_{cmax,ref} \quad (13)$$

where C_N is %N (g N g^{-1} DM leaves) and $V_{cmax,ref}$ is the value of V_{cmax} at 5% N ($150 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Comparison of Fig. 4 and Fig. 9 shows that the modified model produced results only slightly less satisfactory than when V_{cmax} is held constant. The revised

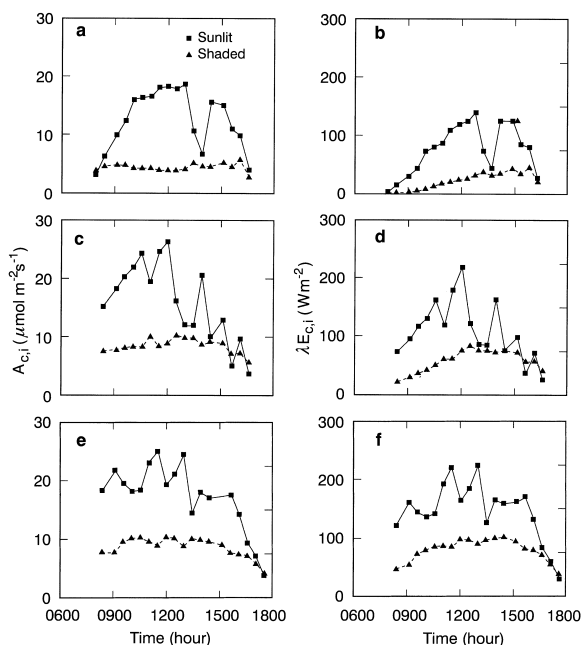


Fig. 10. Diurnal variation of simulated $A_{c,i}$ (a, c, e) and $\lambda E_{c,i}$ (b, d, f) for sunlit and shaded leaves on six days in 1993 (see Fig. 2). Sunlit leaves contribute significantly more to canopy fluxes than shaded ones, particularly during sunny conditions.

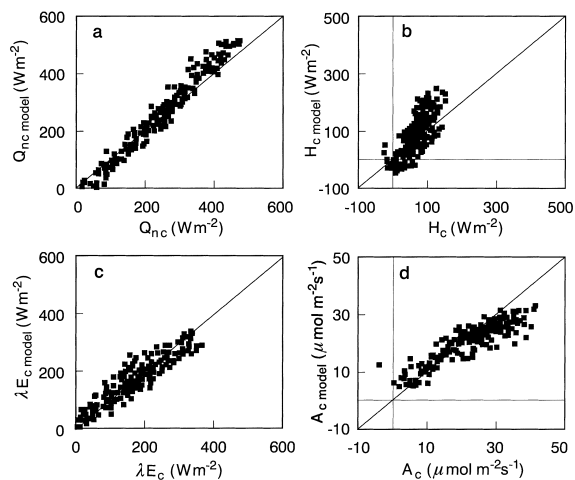


Fig. 9. Comparison of simulated vs. measured fluxes for (a) Q_{nc} , (b) H_c , (c) λE_c and (d) A_c . Results are for the fertilised field but with V_{cmax} (and hence J_{max}) allowed to vary with mean leaf N concentration during the season (see Fig. 1). Under these constraints, simulation results for λE_c and A_c agree with measurements early in the season (lower fluxes), but are lower late in the season (higher fluxes).

model tends to underestimate both A_c and λE_c at higher values (late in the season when $I_{0,1}$ and D_a are high), resulting in an overestimate in H_c because there is little change in the calculated net radiation. A possible explanation for the poorer performance of the modified model lies in the assumed distribution of C_N for leaves within the canopy as the season progressed. Mean C_N for leaves (Fig. 1) was estimated from the measured mean of stems plus leaves using Eq. (8), and this value was used in Eq. (13) to calculate V_{cmax} for leaves at the top of the canopy. However, the uppermost sunlit leaves contribute predominantly to the carbon and water fluxes of the canopy (Fig. 10), and these leaves have higher C_N than the mean, particularly at higher LAI. It is likely that C_N and hence V_{cmax} of these leaves has been underestimated by Eq. (13). To resolve this question the distribution of photosynthetic capacity and nitrogen concentrations of leaves within the canopy should be measured throughout the growing season. In the meantime, satisfactory results can be obtained using a constant value for V_{cmax} .

3.1. The limits to simulation

Validation of complex non-linear models is difficult because many sub-processes are modelled, such as radiation absorption, and stomatal conductance in response to multiple factors, while only a limited number of measurements (e.g. fluxes) are available to test the model. Nevertheless, the model used in this paper accurately captures most of the diurnal and seasonal variation in the fluxes of net radiation, sensible and latent heat and CO₂ observed for two wheat crops grown under identical meteorological conditions. Agreement between simulations and measurements is not perfect however, with systematic errors in each of the fluxes (Table 1). The model requires a large number of parameters, and this may be expected to yield a close fit between measurements and model output if the parameters had been estimated using a linear least-squares procedure, for example. This approach was not adopted here, instead leaf-level characteristics such as radiation scattering coefficients, stomatal response to saturation deficit and V_{cmax} were used, along with a priori assumptions concerning their variation within the canopy. Better agreement between measurements and simulations could probably be obtained but at the expense of greater complexity and an increased number of parameters. It is unlikely that this information will be available for any but the most intensively studied ecosystems and hence, there is little to be gained from increasing model complexity. A major challenge for research is development of simpler models with fewer parameters but which can still provide high predictive capacity for energy partitioning and carbon assimilation. One role for validated simulation models is the testing of simple parametric models over a wider range of physiological and environmental conditions than is usually possible experimentally (Leuning et al., 1995).

4. Conclusions

A two-leaf model for predicting fluxes of net radiation, sensible heat, latent heat and carbon dioxide between plant canopies and the atmosphere was tested for two wheat field using fluxes measured by micrometeorological methods. Excellent agreement was obtained between simulations and measurements for fluxes of net radiation, latent heat and CO₂, while

sensible heat fluxes were somewhat less satisfactory. Uncertainties in estimates for fluxes from the underlying soil contributed to discrepancies between measurements and model simulations. Sensitivity analysis indicated that both transpiration and canopy assimilation were most sensitive to the quantum yield for photosynthesis. The two-leaf canopy model is computationally efficient and is suitable for incorporation into comprehensive soil-vegetation-atmosphere models.

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