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TELLUS

Improving the representation of radiation interception and photosynthesis for climate model applications

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ABSTRACT

The Joint UK Land Environment Simulator (JULES) (which is based on Met Office Surface Exchange Scheme MOSES), the land surface scheme of the Hadley Centre General Circulation Models (GCM) has been improved to contain an explicit description of light interception for different canopy levels, which consequently leads to a multilayer approach to scaling from leaf to canopy level photosynthesis. We test the improved JULES model at a site in the Amazonian rainforest by comparing against measurements of vertical profiles of radiation through the canopy, eddy covariance measurements of carbon and energy fluxes, and also measurements of carbon isotopic fractionation from top canopy leaves.

Overall, the new light interception formulation improves modelled photosynthetic carbon uptake compared to the standard big leaf approach used in the original JULES formulation. Additional model improvement was not significant when incorporating more realistic vertical variation of photosynthetic capacity. Even with the improved representation of radiation interception, JULES simulations of net carbon uptake underestimate eddy covariance measurements by 14%. This discrepancy can be removed by either increasing the photosynthetic capacity throughout the canopy or by explicitly including light inhibition of leaf respiration. Along with published evidence of such inhibition of leaf respiration, our study suggests this effect should be considered for inclusion in other GCMs.

1. Introduction

Realistic representation of plant physiological processes within General Circulation Models (GCMs) is of major importance for accurate prediction of changes to the global carbon and water cycles. In particular, good estimates of CO_2 and H_2O exchange at the land surface are required. These fluxes are highly dependent on the environmental and physiological controls that affect stomatal opening throughout the canopy. Such controls include the canopy structure and the related physical environment. An important step to achieving a good representation of these land-atmosphere exchanges is an accurate representation of radiation interception through plant canopies (de Pury and Farquhar, 1997).

It has long been recognized by the agricultural research community (de Wit, 1965; Duncan et al., 1967; Sinclair et al., 1976; Goudriaan, 1977; Norman, 1980; Smolander, 1984), that the different attenuation rates of diffuse and direct beam radiation in canopies makes it necessary to model their absorption separately. Similarly, because of the different absorption and scattering properties of leaves for visible and near-infrared radiation, these distinct spectral bands also require separate treatment. In GCMs (for summary see Arora (2002) and specifically for the Hadley Centre GCM, see Cox et al. (1998)) and in terrestrial carbon-exchangeregional models (Wang, 2003), radiation attenuation through canopies is generally described using the simple 'Beer's law'. Within these models, photosynthesis is simulated under the assumption that the leaf photosynthetic capacity within the plant canopy is proportional to the vertical distribution of time-averaged irradiance, the so called 'big leaf approach' (Sellers et al., 1992). Recent studies have found that the distribution of photosynthetic capacity within canopies does not exhibit a 1:1 proportionality with radiation (Carswell et al., 2000; Meir et al., 2002), thereby casting doubt on the big leaf assumption.

Many of the newer generation models that simulate carbon cycling in the plant-soil-atmosphere system, include representation of radiation interception and canopy photosynthesis by explicitly defining the diffuse and direct components of the photosynhtetically active radiation (PAR), dividing the canopy into sunlit and shaded parts [e.g. for single stands (Medlyn et al., 2003)] and regional level (e.g. Williams et al., 1996; Wang and Leuning, 1998). These models have been tested successfully against

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eddy covariance measurements (Baldocchi and Harley, 1995; Williams et al., 1998; Falge et al., 2005). It is only very recently that these land surface schemes have started to be used in GCMs [e.g. the SiB3 land surface scheme linked to the NCAR GCM (Baker et al., 2006) and the land surface scheme of the Goddard Institute for Space Studies (GISS) GCM (Friend and Kiang, 2005)]. Recent GCM simulations by Friend and Kiang (2005) have shown major influences of the land surface on other parts of the Earth System, including simulated cloud cover, large scale precipitation and surface temperatures.

These results provide motivation for better representation of land surface processes within GCMs. This paper aims to improve the representation of both canopy radiation interception and photosynthetic carbon uptake within the Hadley Centre GCM. A new canopy radiation routine has been implemented in the Joint UK Land Environment Simulator (JULES), which is based on MOSES, the original land surface scheme of Version 3 of the Hadley Centre GCM (Cox et al., 1998). The new routine uses the 'two-stream' approach (Sellers, 1985) to infer absorption of direct and diffuse radiation at different levels in the canopy and therefore provides a multilayer approach to scaling from leaf to canopy level photosynthesis. This approach has recently been tested (Jogireedy et al., 2006) for a coniferous forest; here we implement the same radiation scheme but further analyze different representations of vertical distribution of photosynthetic capacity, at a site in the Amazonian rainforest. Land-atmosphere fluxes in the Amazon region are of particular interest after the prediction of forest 'die-back' in a changing climate (Cox et al., 2004) and subsequent amplification of the effect of anthropogenic CO_2 emissions (Cox et al., 2000) by the Hadley Centre model.

This paper reports on extensive model evaluation undertaken by comparing the radiation interception model against measurements of vertical profiles of radiation through the canopy, using data from the ABRACOS project, see Cabral et al. (1996). In addition, the integrated performance of the model through the canopy is tested by comparison against eddy covariance measurement of carbon uptake and energy partitioning. Measurements of carbon isotopic fractionation from canopy leaves are also used to assess the model.

2. Methods

2.1. Sites

The data were collected at several different sites in an area of undisturbed, lowland rainforest located north of Manaus in central Amazonia. The forest has a closed canopy of about 35–40 m height with a few emergent trees reaching up to 45 m (Ranquin de Merona et al., 1992). The reported range of leaf area index for this area is 4.5–5.7 (McWilliam et al., 1993; Meir et al., 2000). Estimates of forest above-ground biomass in this area range between 265 and 300 (McWilliam et al., 1993) and 350 tonne ha^{-1} (Baker et al., 2004). The topography is undulating, with soil type decreasing gradually from oxisols on the plateaus (where the measurement tower was located) and upper parts of the valleys to utisols and spodosols on the valley slopes (Bravard and Righi, 1989). Mean annual temperature is 26.7 °C and mean annual precipitation is 2200 mm, with a relatively dry season defined as months when precipitation is less than 100 mm per month, a period usually lasting from June/July until September (Figueroa and Nobre, 1990).

2.2. Data

2.2.1. Eddy covariance. The eddy covariance measurements, made by Araújo et al. (2002) above the K34 forest site, 60 km north of Manaus (2° 36′ S, 60° 12′ W), include half-hourly average data of latent and sensible heat fluxes and Net Ecosystem Exchange (*NEE*). *NEE* is calculated as the measured flux of CO_2 by eddy covariance plus a storage term that represents the change in the CO_2 concentration (C_a) within the canopy between the forest floor and the eddy flux measurement height. The meteorological variables required to force JULES were collected using an automatic weather station located at the top of the tower. The variables measured were: global solar radiation, windspeed and air temperature, net radiation and relative humidity. Further information about flux calculation and specifications of the instruments used for measurements and methods for flux calculations are given by Araújo et al. (2002). The data used were collected from January to May covering the wet season of year 2000 (see Fig. 1)

2.3. Light profiles

Profiles of PAR through the forest canopy were measured in Reserva Ducke in 1991 as part of the study reported by Cabral et al. (1996). This site is 25 km from Manaus, with broadly similar forest to our K34 study site. Quantum radiation sensors (type SKP 215, Skye Instruments, Powys, UK) were mounted

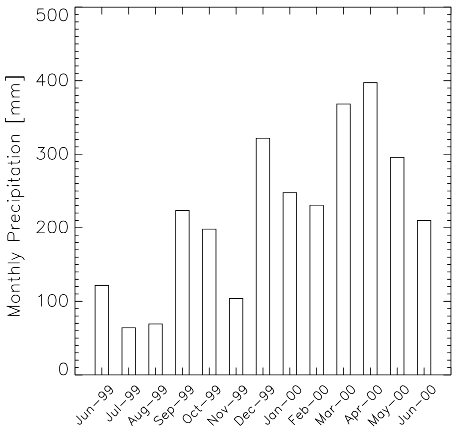

Fig. 1. Observed monthly precipitation at Manaus in mm during the period June 1999–June 2000.

on both the east- and west-facing sides of the tower above the canopy and at five heights within it. The data recorded in this analysis were collected from 12 July to 12 August (day numbers 193 to 224) and recorded as ten minute averages. To avoid the possibility of the tower shading the sensor, data from the east-facing sensors were used before midday and from the west-facing sensor after midday. Data were then grouped into five 'bins' of equal sun angle: the 2 hr immediately before and after midday, and hours plus or minus 1, 2, 3 and 4 hr from midday.

The vertical profile of cumulative leaf area was derived from the study of McWilliam et al. (1993), in which a 400 m^2 plot of forest was destructively sampled. Their site was situated roughly midway between the K34 and the Reserva Duke sites.

2.4. Model and model parameterization

2.4.1. Light interception, photosynthesis and stomatal conductance under the original JULES land surface model. The original JULES model (Cox et al., 1998) simulates photosynthesis based on the leaf photosynthesis models for C_3 and C_4 leaves from Collatz et al. (1991) and Collatz et al. (1992), respectively. These simulate potential (non-water stressed) leaf photosynthesis as the minimum of three limiting rates: (1) Rubisco limited rate, (2) light limited rate and (3) rate of transport of photosynthetic products (in the case of C_3 plants) and PEP-Carboxylase limitation (in the case of C_4 plants). The first two rates depend on the leaf internal CO_2 concentration, c_i (Pa). The overall rate of net photosynthesis (also dependent on c_i) is calculated using the c_i/c_a closure defined by Jacobs (1994), itself a function of the CO_2 compensation point (Pa), the humidity deficit at the leaf surface and two vegetation specific parameters D_c and F_0, that determine the dependence on leaf level humidity and an overall ability to photosynthesize. The rate of leaf dark respiration (R_d) is simulated as a fraction of the maximum rate of carboxylation of Rubisco (V_max), both in (μmol m^{-2} s^{-1}). The moisture stressed net leaf photosynthesis A (μmol m^{-2} s^{-1}), is related to the potential (non-stressed) leaf photosynthesis (A_n) as simply $A = A_\mathrm{n}\beta(\theta)$, where $\beta(\theta)$ is a unitless soil moisture availability factor based on soil moisture movement, and availability calculated in a four-layer soil model component of JULES.

Under the 'standard' JULES model, leaf level photosynthesis is scaled up to canopy level using the big leaf approach from Sellers et al. (1992). Leaf nitrogen (and therefore leaf photosynthetic capacity) and incident PAR are all assumed to be directly proportional to each other and decrease exponentially through the plant canopy as $I = I_0\ \mathrm{e}^{-0.5L}$ and $N = N_0\ \mathrm{e}^{-0.5L}$, where I and N are irradiance and leaf nitrogen at any level in the canopy, I_o and N_o are the irradiance and leaf nitrogen concentration at the top of the canopy, 0.5 is the PAR extinction coefficient and L is the cumulative leaf area index from the top of the canopy, down to any level in the canopy.

These approximations mean that the Collatz et al. (1991) and Collatz et al. (1992) models of leaf level photosynthetic behaviour can be scaled very simply to canopy level, including canopy conductance (g_c), net photosynthesis (A_c) and leaf respiration (R_d) as $S_\mathrm{C} = S_\mathrm{l} f_\mathrm{PAR}$ where Sc is g_c, A_c or R_dc and S_l are the corresponding leaf level values. Quantity f_PAR is given by $[(1-\mathrm{e}^{-0.5\ LAI})/0.5]$, where LAI is the total canopy leaf area index ($L = LAI$ at the bottom of the canopy). This simple leaf-to-canopy integration allows easy calculation of photosynthesis, dark respiration and the surface energy balance. However, there is increasing evidence that such scaling oversimplifies in-canopy behaviour, and this is now considered.

2.4.2. Light interception, photosynthesis and stomatal conductance under an improved version of JULES. In the improved version of JULES (Jogireedy et al., 2006), the photosynthesis and stomatal conductance models remain as previously described, but now a leaf-to-canopy scaling is introduced making explicit calculations at different levels in the canopy, and with the emphasis on a more sophisticated representation of light interception. Light interception is simulated using the two stream approximation approach from Sellers (1985), which describes absorption and scattering losses of incident radiation for both direct and diffuse radiation separately in the visible and near-infrared wavebands. The two stream approach provides a set of equations for variation of direct and diffuse, upward and downward beams through the canopy, calculating PAR as a function of L. The calculated values of PAR(L) also depend on solar zenith angle, direct and diffuse radiation incident at the top of the canopy, leaf angle distribution and leaf radiation properties for each waveband. Using the calculated absorbed light at each layer of the canopy, leaf photosynthesis, leaf respiration and stomatal conductance are calculated at each layer and summed to provide a canopy level value. Based on this additive calculation through the canopy, a canopy level stomatal conductance is defined for use in JULES calculations of the surface energy partitioning.

Moving from the 'big leaf' assumption, there is a requirement to define the foliar nitrogen value, N, (and thus, the V_max parameter) at each level. In the version of Jogireedy et al. (2006), a constant value of N is assumed (i.e a uniform vertical distribution of photosynthetic capacity). This differs from the original 'big leaf' model; where an exponential decay function is implicitly assumed (Cox et al., 1998). For the Amazonian site considered here, the improved JULES model was parameterized using the vertical distribution of measured V_max (Carswell et al., 2000) at a site 10 km from the K34 site. The Carswell et al. (2000) measurements were used to infer the decrease of V_max with height (K_n defines the vertical decrease of leaf N and therefore V_max through the canopy) by fitting an exponential function of height and V_max to the data. A value of the nitrogen allocation coefficient K_n of 0.78 was thus obtained. The V_max parameter at the top of the canopy was estimated in JULES from a linear relationship between V_max and the ratio of leaf nitrogen to leaf carbon (on a weight basis). This value was combined with the inferred profile through the canopy to enable calculation of $V_\mathrm{max}(L)$. Leaf nitrogen and leaf carbon values at the top of the canopy were

Table 1. Parameters used for simulations of this site and default parameters of JULES corresponding to the broad leaf plant functional type

Parameter	Parameterized for this site	Default parameter for broad leaf trees
N content a the top of the canopy	23.10 ± 0.59^{a} mg g^{-1}	
	0.046^{b} kg N kg C^{-1}	0.05 kg N kg C^{-1}
Rubisco capacity at the top of the canopy ($V_{\max}$)	42^{b} μmol m^{-2} s^{-1}	42 μmol m^{-2} s^{-1}
N allocation coefficient, K_n	0.17^{c}	0 (uniform distribution)
Parameters from stomatal conductance model		
F_{o}	0.875	0.875
D_{c}	0.09	0.09

[a] Mean value from 19 leaf samples at the K34 site from Luizão et al. (2004) data set.

[b] Calculated value of $V_{\max}$ using the measured values of leaf nitrogen/leaf carbon from Luizão et al. (2004) and the $V_{\max}$ vs leaf N/ leaf C (weight basis) relationship used within JULES.

[c] Inferred from Carswell et al. (2000) data set.

taken from the data set of Luizão et al. (2004) from the K34 site. JULES simulations for this site were carried out using the parameters given in Table 1.

2.5. Model evaluation

The aim of this paper is to test JULES, with both an explicit canopy-depth dependent light interception model, and different assumptions regarding the vertical distribution of $V_{\max}$. As discussed above, this is achieved by utilising measurements of the vertical distribution of PAR from the rainforest in the Reserva Ducke site and comparing simulated net carbon uptake (A_{n}) and energy fluxes against measurements from eddy covariance. However, another way to test carbon assimilation is through the carbon isotopic signature from leaves. The carbon isotope ratio ($\delta^{13}C$) of leaves provides a quantitative assessment of stomatal limitations to photosynthetic activity. This ratio varies between species and environment depending on the rate of CO_2 assimilation and stomatal conductance. This additionally provides an integrated measure of the photosynthetic water use efficiency (Farquhar et al., 1982). For this reason, $\delta^{13}C$ of leaves can be useful to constrain and check the parameterization of the stomatal conductance model. We have used measurements of $\delta^{13}C$ from top canopy leaves to evaluate simulated canopy $\delta^{13}C$. Simulated isotopic composition of the leaves $\delta^{13}C$ (‰) was calculated for the top canopy leaves following Farquhar et al. (1982) as:

$$\delta^{13}C = \delta_{\mathrm{atm}} - a - (b - a)C_i/C_a, \qquad (1)$$

where a corresponds to maximum fractionation due to diffusion of CO_2 in air (4.4‰) and b is the maximum fractionation in the carboxylation reaction (30‰) (Farquhar et al., 1982). The value δ_{atm} is $\delta^{13}C$ of the air, taken as −8.0 (‰), the late twentieth century mean atmospheric background value (Ehleringer et al., 1987). The ratio C_{i}/C_a corresponds to simulated daytime half-hourly values from the top canopy layer during the wet season of 2000. The simulated average integral of photosynthetic discrimination during the period tested $\overline{(\delta^{13}C)}$ was calculated with eq. (1) using the photosynthetic flux weighted average C_i/C_a from the top leaves:

$$\overline{\delta^{13}C} = -12.4 - 25.6\frac{\sum_{i=1}^{n} A_{ni}(C_i/C_a)}{\sum_{i=1}^{n} A_{ni}} \qquad (2)$$

where A_n are simulated daytime half-hourly values from the top canopy layer during the studied season.

When using eddy covariance to estimate net carbon uptake rates, i.e gross uptake minus canopy leaf respiration (A_n), it is necessary to know all the 'non-leaf' ecosystem respiration terms during the day (R_{E}). This is because the eddy covariance method measures Net Ecosystem Exchange of carbon (*NEE)* (i.e. $NEE = A_n - R_{\mathrm{E}}$). The ecosystem respiration term is often inferred from the night time *NEE* measured by eddy covariance by extrapolation of functional relationships between the night time *NEE* and temperature. Unfortunately, eddy covariance systems can be unreliable in the stable conditions generally encountered in nocturnal boundary layers (Aubinet et al., 2002; Massman and Lee, 2002). Further, due to the undulating topography of the site here studied, it might be possible that on calm nights, part of the CO_2 being respired is draining to the valleys without being registered by the tower sensors (Araújo et al., 2002). We therefore decided to prescribe the ecosystem respiration term (R_{E}) (μmol m^{-2} s^{-1}) based on independent measurements at adjacent sites.

The 'non-leaf' components of ecosystem respiration (R_{E}) are single compartments of the ecosystem, such as stems and branches, soil, and coarse litter (leaf respiration is already included in the net carbon uptake term). Respiration from stems and branches was taken as 1.1 μmol m^{-2} s^{-1} as measured by Chambers et al. (2004) in the forest around the K34 site, with a temperature dependency as given by Lloyd and Taylor (1994). Stem temperature was assumed to be two degrees below the measured air temperature above the canopy and for coarse litter respiration, a value of 0.5 μmol m^{-2} s^{-1} has been used as measured by Chambers et al. (2004) at the same site. Diurnal variation in coarse litter respiration with temperature was included using the Lloyd and Taylor (1994) formulation assuming that coarse litter temperature was two degrees lower than the fluctuating air temperature above the canopy.

Prescription of soil CO_2 efflux in this forest is difficult because of its spatial and seasonal variability and the strong dependency on soil temperature and soil water content (Chambers et al., 2004; Sotta et al., 2004). The only measurements reported for the studied site were made during a strong *La Niña* period (June 2000–June 2001) during which the Central Amazon received some of its highest precipitation of the 20th century. This period corresponds to a different time to the eddy covariance flux measurements (Chambers et al., 2004). Due to these different precipitation regimes and differences in measurement methodologies, the reported measurements from Chambers et al. (2004) fall into the lower rage of values reported for the Manaus area (Sotta et al., 2004). Lacking soil CO_2 efflux data collected during the studied period in the studied site, it was decided to use data from a neighbouring area of plateau forest—only 10 km away, and from where, various measurements have been reported. Carmo et al. (2006) reported an average value of 5.4 ± 1.4 SE and 5.5 ± 1.1 SE μmol m^{-2} s^{-1} during the wet and dry seasons of 2004, respectively, Sotta et al. (2004) reported average soil soil CO_2 efflux of 5.8 ± 0.05 SE μmol m^{-2} s^{-1} measured during the end of the wet season in 1997, and Silva de Suoza (2004) measured 5.64 and 5.30 μmol m^{-2} s^{-1} during the rainy and dry periods of 2003. Based on the reported values (from wet and dry seasons), the soil CO_2 flux was taken as constant at 5.5 μmol m^{-2} s^{-1}. But, being aware of the uncertainty in these estimates, we assess the sensitivity of our results to the particular choice of soil CO_2 flux.

Eddy covariance measurements above forest ecosystems often fail energy balance closure tests (Massman and Lee, 2002; Wilson et al., 2002; Baldocchi, 2003; Finnigan et al., 2003). For this reason, it is often more useful to test model performance against the observed variation in evaporative fraction (defined as the ratio between the latent heat flux and the sum of the latent and sensible heat fluxes). There is considerable variability in the half hour calculated evaporative fraction (black dots in Fig. 3, all plots on the right), therefore model performance was evaluated using the mean diurnal cycles of measured and simulated evaporative fraction.

A set of simulations was performed with the original JULES formulation (run called Big leaf) and with the improvements discussed above, including multilayer representation of light interception (i.e. using the two stream approximation model) and different [uniform (constant leaf N) and non-uniform (variable leaf N)] $V_{\max}$ profiles down through the canopy (simulations called Light-uniform-$V_{\max}$ and Light-vertical-$V_{\max}$, respectively). The multilayer simulations include nine layers corresponding to identical increments to cumulative leaf area index down through the canopy. Shuttleworth (1989) notes that only 1% of solar radiation above the canopy reaches the soil, so all simulations were undertaken under the assumption thatthere was no evaporation from the soil in this forest. As the simulations are performed for the wet season and also because the months preceding the wet season had considerable amounts of rain (Fig. 1), it was assumed that there was no soil water stress during the simulations and thus $\beta = 1$. Finally, in fitting to eddy covariance measurements, we also considered the possibility that JULES should include light inhibition of leaf respiration (run called Light-vertical-V$_{max}$-Leaf respiration).

3. Results

3.1. Model evaluation of radiation interception

Observed vertical profiles of PAR are shown in Fig. 2a. The data are plotted as a function of cumulative leaf area index descending through the canopy and are normalized by the incident PAR at the top of the canopy. The line with short dashes represents mean values of measurements at different sun angles (i.e. times of day from 0700–1700) and the thick line is the average over all the data. These measurements show that there is negligible effect of sun angle on the vertical profile of absorbed light. The remaining plots in Fig. 2 show the simulated vertical profiles of light interception by the version of JULES that uses the two-stream approximation (Sellers, 1985), under a spherical (2b) and horizontal (2c) arrangement of leaves. The non-continuous lines in Fig 2b represent different sun angles, with highest and lowest elevation angles under and over predicting the observations (thick continuous line). In contrast, under a horizontal arrangement of leaves (dashed lines, Fig 2c), there is no change on the simulated vertical profile of absorbed radiation with solar elevation angle. The line with short and long dashes in Fig. 2c represents radiation absorption under a Beer's law assumption, which below a cumulative leaf area index of 2, overestimates the measurements by more than 100%. It can be seen that for the JULES simulations, a horizontal arrangement of leaves gives the best match to the measurements for this site (single dashed line in Fig 2c). A more detailed model might include a vertical leaf angle distribution with inclined (more vertical) leaves at the canopy top, to avoid midday canopy heat load and more horizontal leaves towards the bottom to maximize light absorption, in accordance to observations (Kelly et al., 2004). Wirth et al. (2001) report a vertical distribution of leaf angles ranging from 48 to 18 degrees from the horizontal (from top to bottom of the canopy) for a tropical rainforest in Barro Colorado, Panama.

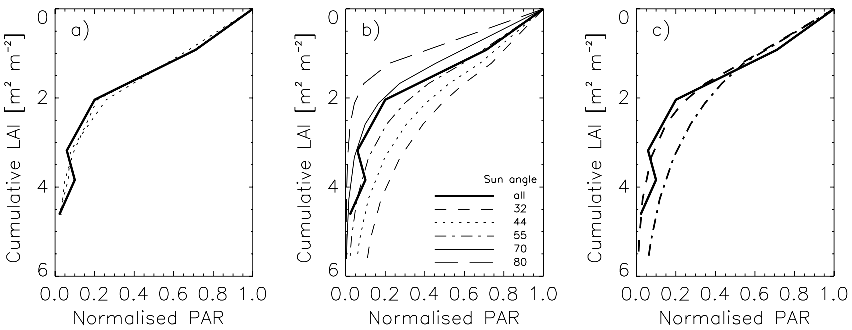

Fig. 2. Vertical profiles of normalized PAR against cumulative LAI, such that cumulative LAI is zero and normalized PAR is one at the top of the canopy. Plots correspond to (a) as measured within the canopy at different solar elevation angles (dotted lines) and mean of all solar elevation angles (solid line) and then (b) simulated vertical profile of light interception with a spherical arrangement of leaves at different solar elevation angles (non-continuous lines) and (c) is as for (b), but with a horizontal arrangement of leaves (dashed lines). The mean of all solar elevation angles plot (continuous line) in (a) is also reproduced in (b) and (c). In addition, radiation absorption under a Beer's law assumption is shown in (c) by the line with short and long dashes.

3.2. Further model testing

JULES calculations of simulated net CO_2 assimilation (A_n) and evaporative fraction are presented in Fig 3. Half-hourly measurements (presented as 'dots') of A_n are plotted against above canopy measurements of PAR and (local) time of day; the evaporative fraction is also given as a function of time of day. The triangles represent the mean values ('binned' by 200 μmol m^{-2} s^{-1} for PAR values and half-hourly for time of day). The squares are similar mean values, but for the eddy covariance data. Initially, concentrating on the top three rows of Fig. 3, these correspond to (1) the standard big leaf approach used by JULES (plots a–c), 2) the Light-uniform-$V_{\max}$ run (plots d–f) and 3) and the Light-vertical-$V_{\max}$ run (plots g–i). For these three simulations, it is noticeable that for both metrics of model predictions of A_n, inclusion of the vertical profile of light interception makes a major improvement (see Table 2 for statistics of model-data comparison). Simulated photosynthesis does not saturate rapidly with increasing solar radiation, and thus avoids the situation (plot b), where the simulated diurnal cycle of $A_{n,}$ using the big leaf approach tends to have a 'flat' response in the middle of the day. Note that at midday, there is very little difference between the three simulations. Additionally, the evaporative fraction is also more accurately predicted than with the big leaf approach, particularly for time periods late in each day.

Comparing simulations from the second and third rows of Fig. 3, i.e. using uniform and vertically varying $V_{\max}$, the difference is very small. This is because for this particular site, the dominant factor limiting photosynthesis throughout the canopy is light, and therefore photosynthesis of the lower canopy levels become independent of the $V_{\max}$ value.

Despite the inclusion of the two stream approximation (Sellers 1985) into JULES and vertical variations of $V_{\max}$ as shown in the second and third rows of Fig. 3, there is a general tendency for the model to underpredict the estimated A_n from eddy covariance by about 14% for the period tested (see Table 2). From the mean diurnal cycle of simulated and estimated A_n, particular underestimation occurs around 1000–1400 hours. This midday problem is not seen in estimates of evaporative fraction; in the three cases, simulated values were quantitatively similar to each other with some overestimation before 1000 and after 1400 hours. However, the big leaf model had slightly higher simulated evaporative fraction after 1400 hours compared with both simulations using the two stream approximation. Under the big leaf approach, the mean simulated evaporative fraction overestimated the measurements by 10–15% between 0800 and 0900 and after 1400 by 10–25%, whereas under both simulations using the two stream model (i.e. Light-uniform-$V_{\max}$ and Light-vertical-$V_{\max}$), corresponding values were between 7–13% for the 0800 and 0900 period and 5–6% after 1400 hours and about ±5% during the rest of the day.

The model tendency to underestimate the eddy covariance estimates of A_n implies that either the prescribed respiration term (R_E) used to estimate A_n from eddy covariance *NEE* is too large, or that simulated A_n is too low. We undertook a sensitivity study using three extra runs in an attempt to understand this discrepancy. In the first run, it is assumed that the prescribed ecosystem respiration is overestimated; in the second and third runs it is assumed that the simulated net photosynthesis is underestimated by two different means.

The first extra simulation assumes that ecosystem respiration was too large as a result of overestimation of the prescribed soil CO_2 efflux (5.5 μmol m^{-2} s^{-1}) from published values at the neighbouring Manaus C14 site (Silva de Souza, 2004; Sotta et al., 2004; Carmo et al., 2006). For this simulation, we use the mean value of soil CO_2 efflux reported during the wet season of 2001 by Chambers et al. (2004; Fig. 3).These are the only measurements reported for the studied site. These measurements fall into the lower range of values published for the area of Manaus (values ranging from 3 to 4 μmol m^{-2} s^{-1}). This simulation

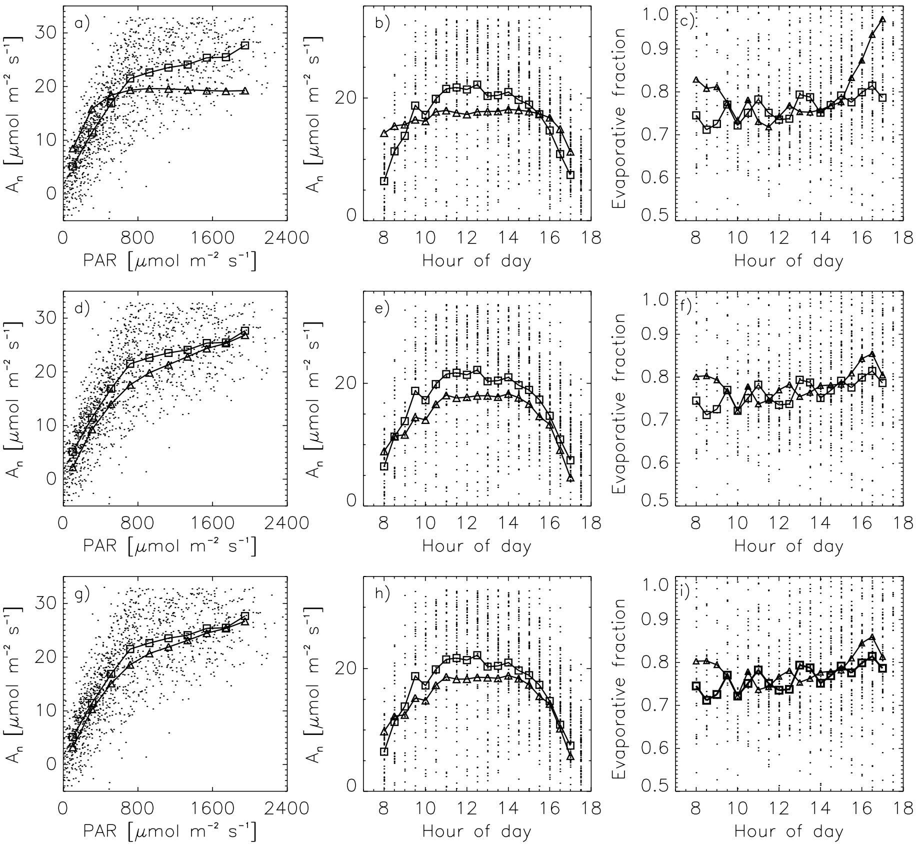

Fig. 3. Model evaluation of carbon uptake and energy partition. Plots in the left column represent the light response of net CO_2 assimilation (A_n) (lines represent data (□) and simulations (Δ) averaged over 200 μmol quanta m^{-2} s^{-1} bins). Plots in the centre and on the right correspond to the diurnal cycle of A_n and of evaporative fraction, respectively. In both cases, data (□) and simulations (Δ) are averaged over half hour time periods. In all cases, black dots represent half hourly estimates from eddy covariance. Rows represent the following JULES configurations: (1) JULES simulations under the big leaf approach, plots on the first row, (2) simulation assuming a constant $V_{\max}$ throughout the canopy, run called Light-uniform -$V_{\max}$, plots on the second row, (3) simulations using a prescribed (inferred from measurements) vertical distribution of $V_{\max}$, run called Light-vertical -$V_{\max,}$ plots on the third row.

Table 2. Statistics of model-data comparison for CO_2 assimilation (A_n) under the following JULES configurations: Big leaf, simulations under the big leaf approach, Light-uniform-$V_{\max}$, simulation assuming a constant $V_{\max}$ throughout the canopy, Light-vertical-$V_{\max}$, simulations using a prescribed (inferred from measurements) vertical distribution of $V_{\max}$, Light-vertical-$V_{\max\_18}$, same as previous and assuming an 18% increase in the canopy top $V_{\max}$, and Light-vertical-$V_{\max}$-Leaf respiration, simulation including light inhibition of leaf respiration. The regression model is modelled flux = a × measured flux

Model configuration	a	r^2
Big leaf	0.85	0.89
Light-uniform $V_{\max}$	0.83	0.92
Light-vertical $V_{\max}$	0.86	0.93
Light-vertical-$V_{\max\_18}$	0.96	0.92
Light-vertical-$V_{\max}$-Leaf respiration	0.96	0.93

retains identical parameterization of the remaining components of ecosystem respiration, i.e. decomposition by coarse litter, and stem and branch respiration simulated using a temperature dependent function (Lloyd and Taylor 1994) with parameters derived from measurements in the Manaus area (Chambers et al., 2001, 2004) assuming that these terms were reasonably well simulated. When using the ecosystem respiration term described above, the resulting comparison still showed an average underestimation in A_n of 8% by the model compared to eddy covariance estimates, with a specific tendency to underestimate A_n during 1000–1400 hours. Therefore, we conclude that the discrepancies between the model and the measurements cannot be attributed to possible errors in the prescribed soil CO_2 efflux alone. Results are not shown for this simulation.

The second extra simulation assumed that simulated A_n was too low. The main parameters of the photosynthesis model are the quantum yield of photosynthetic update, ∝, $V_{\max}$ and its sensitivity to temperature and the colimitation ('curvature') factor

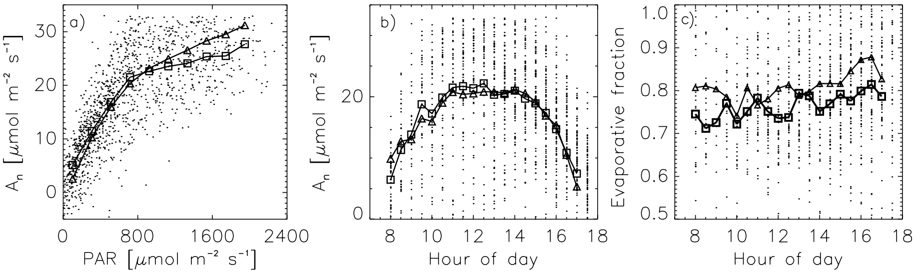

Fig. 4. Model evaluation of carbon uptake and energy partition assuming an 18% increase in the canopy top $V_{\max,}$ run called Light-vertical-$V_{\max\_18}$. The plot on the left represents the light response of net CO$_2$ assimilation (A_n) (lines represent data (□) and simulations (Δ) averaged over 200 μmol quanta m^{-2} s^{-1} bins). Plots in the centre and on the right correspond to the diurnal cycle of A_n and of evaporative fraction, respectively. In both cases data (□) and simulations (Δ) are averaged over half hour time periods. In all cases, black dots represent half hourly estimates from eddy covariance.

linking the photosynthesis limiting rates (Collatz et al., 1991). Parameter values for ∝ and the curvature factor are well known and taken from the literature and should be applicable for all C3 plants (Ehleringer and Pearcy, 1983; Collatz et al., 1990). The temperature dependencies of the remaining parameters of the leaf photosynthesis model are also taken from the literature (Collatz et al., 1991) with an optimum temperature for $V_{\max}$ set at 36 °C. However, the reported range of variation of $V_{\max}$ for the canopy leaves in the Amazon rainforest is 30–75 μmol m^{-2} s^{-1} (Carswell et al., 2000; Domingues et al., 2005). Therefore, $V_{\max}$ was varied to improve the model fit to the eddy covariance estimates of A_n, increasing $V_{\max}$ from top canopy leaves from 42.2 to 50 μmol m^{-2} s^{-1} (keeping the same nitrogen allocation coefficient), which led to a 18% increase in total canopy $V_{\max}$ (simulation called Light-vertical-$V_{\max\_18}$). Results are presented in Fig. 4 (plots a and b) and indicate that the mean diurnal cycle and light response of A_n match the observations better than the previous runs with lower $V_{\max}$ as shown in Fig. 3 (plots g and h) and in Table 2. However, simulated A_n remains slightly underestimated at the highest irradiances. Further, the higher canopy $V_{\max}$, and associated simulated stomatal conductance altered the partition between latent and sensible heat fluxes leading to an overestimation of the simulated evaporative fraction compared to the measurements by eddy covariance as shown in Fig. 4 (plot c).

In the third extra run, it was assumed that simulated net carbon uptake was too low because the leaf respiration term was too high. An attempt was made to account for this by inclusion of inhibition of leaf respiration in daylight, a phenomenon not included in JULES, or to our knowledge, in any other GCM land-surface scheme. This was based on results from various studies. Brooks and Farquhar (1985), Hoefnagel et al. (1998), Atkin et al. (1998, 2000) and Hoefnagel et al. (1998) report that the rate of leaf respiration in daylight is less than that in darkness. To implement canopy respiration with a light dependence (now called R_c) in JULES, an empirical formula is used based on observed leaf respiration in varying light and incoming irradiance levels for spinach leaves (Brooks and Farquhar, 1985, as implemented by Lloyd et al., 1995). Thus,

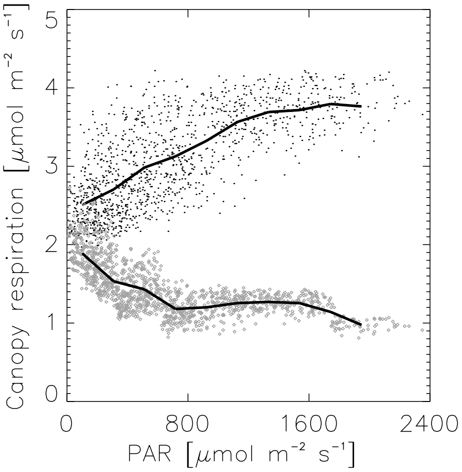

Fig. 5. Light response of (half hourly) simulated canopy respiration with (dots) and without (diamonds) light inhibition. Lines represent simulations averaged over 200 μmol quanta m^{-2} s^{-1} bins.

$$\begin{array}{ll} R_c = R_d & 0 < \mathrm{Io} < 10\ \mu\mathrm{mol\ quanta\ m^{-2}s^{-1}} \\ R_c = [0.5 - 0.05\ln(I_o)]\,R_d & \mathrm{Io} > 10\ \mu\mathrm{mol\ quanta\ m^{-2}s^{-1}} \end{array} \tag{3}$$

where R_d is the original JULES value for leaf respiration in the dark and I_o is incoming PAR in μmol quanta m^{-2} s^{-1}.

Implementation of eq. (3) combined with parameters for this site (Table 1) (simulation called Light-vertical-$V_{\max}$-Leaf respiration) reduced the simulated canopy leaf respiration by [0–50]% (compared to the Light-vertical-$V_{\max}$ simulation) at irradiances of PAR between 0 and 500 μmol quanta m^{-2} s^{-1} and by [60–75]% at irradiances of PAR between 500–2500 μmol quanta m^{-2} s^{-1}. These differences can be seen in Fig. 5, where simulated canopy respiration with and without light inhibition is presented. This simulation resulted in higher net carbon uptake, and gave a very good fit to the data (Fig. 6 and Table 2). As for the previous test, there is a lot of improvement in predicting

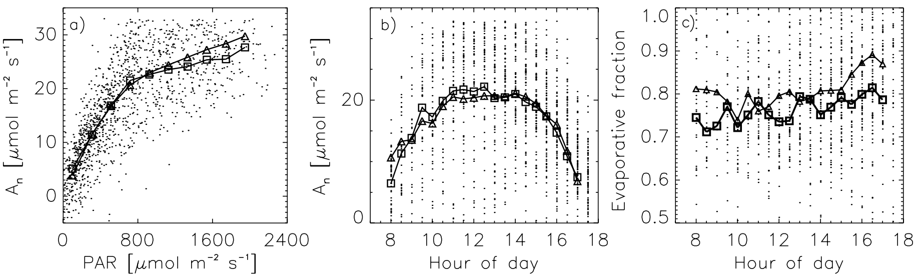

Fig. 6. Model evaluation of carbon uptake and energy partition including light inhibition of leaf respiration, run called Light-vertical-$V_{\max}$-Leaf respiration. The plot on the left represents the light response of net CO_2 assimilation (A_n) (lines represent data (□) and simulations (Δ) averaged over 200 μmol quanta m^{-2} s^{-1} bins). Plots in the centre and on the right correspond to the diurnal cycle of A_n and of evaporative fraction respectively. In both cases data (□) and simulations (Δ) are averaged over half hour time periods. In all cases black dots represent half hourly estimates from eddy covariance.

A_n, but a slightly decreased capability to model the evaporative fraction.

To address the overestimation of evaporative fraction by the model, the tunable parameters of the stomatal conductance model (F_o or D_c) were varied. By increasing F_o or D_c, in both cases, the simulated latent heat fluxes decreased, improving the comparison to evaporative fraction. However, in terms of carbon uptake, this resulted in a simultaneous move away from the good fits achieved previously (as shown in Figs 4 and 6). In addition, knowledge of the simulated C_i/C_a ratio allows calculation of simulated leaf $\delta^{13}C$. Measurements of $\delta^{13}C$ from top canopy leaves from this site (Ometto et al., 2006) were compared to the corresponding simulated values (eq. 2) for the five main simulations described above, which in all cases fell inside the range published by Ometto et al. (2006) for this site. Furthermore, changes made to F_o or D_c in the attempt to fit better evaporative fraction changed the simulated g_s and the C_i/C_a ratio and therefore, the simulated $\delta^{13}C$ changed as well. Under these cases (i.e. increased F_o or D_c), simulated $\delta^{13}C$ decreased but remained within the range reported by Ometto et al. (2006) (not shown). It is noted that for the first simulation using the Big Leaf approach (top row of Fig. 3), simulated $\delta^{13}C$ was near the lowest limit (most negative) published by Ometto et al. (2006). Furthermore, uncertainties related to the simulated $\delta^{13}C$ include the estimates of the maximum fractionation in the carboxylation reaction, the b parameter in eq. (1). Reported values for this parameter are between 24 and 31 (‰) (Farquhar et al., 1989). Measurements and simulations of $\delta^{13}C$ from top canopy leaves are presented in Table 3.

Table 3. Measured (δ^{13}C) and simulated $\overline{(\delta^{13}C)}$from top canopy leaves under different model runs

	$\delta^{13}C$ (‰)
Measurements reported by Ometto et al. (2006)	−31.65 ± 2.6
Big leaf	−34.39
Light-uniform $V_{\max}$	−34.16
Light-vertical $V_{\max}$	−34.13
Light-vertical-$V_{\max\_18}$	−34.11
Light-vertical- $V_{\max}$ Leaf respiration	−34.09

4. Discussion

The radiation data used in this study were effectively collected using only one sensor at each level in the canopy. However, the daily integrated values are comparable to the mean profile derived from the more comprehensive sampling by Carswell et al. (2000) at a site 10 km away in the same forest. Simulations presented in this study do not include the effect of leaf clumping on light transmission. This has been found to be an important factor in boreal forest (Chen et al., 1997; Kucharik et al., 1998), where it has been shown that failing to include the effect of leaf clumping when simulating light transmission within boreal forest canopies can lead to underpredictions of latent heat and *NEE* fluxes (Baldocchi and Harley, 1995). Given the good agreement between our model and the radiation observations, it appears that leaf clumping has a small effect in the type of dense rainforest canopies under consideration here. A similar conclusion was reached by Meir et al. (2000) working in the same forest. They found that leaf area density distribution derived using a photographic method, with an assumed random leaf spatial distribution, compared well with those obtained from a destructive sample. Although including leaf clumping and a more detailed leaf angle distribution might give a more realistic description of the radiation profile within the canopy, we do not believe the extra complexity can be justified in the present case. Further measurements of the separation of direct and diffuse radiation in the canopy are needed to validate this model and assess the need for a more complex description.

We have systematically compared five configurations of the JULES model against eddy covariance measurements at an Amazonian rainforest site. The model evaluation presented here is limited by the accuracy of the data used to compare simulations.

The two main limitations for this comparison were the accuracies of the estimated ecosystem respiration term (specifically the soil CO_2 flux), and the non-closure of the energy balance from eddy covariance measurements.

A correct estimate of soil CO_2 efflux in this forest is difficult due to the high spatial variability, with plateaus having higher efflux than slopes and valleys (Chambers et al., 2004), and seasonal variability mostly dependent on soil water content (Chambers et al., 2004; Sotta et al., 2004). It seems the optimum conditions for soil respiration are found at intermediate water contents with decreases in respiration at water contents both above and below the optimum (Davidson et al., 2002).

We initially used soil CO_2 efflux measurements from the neighbouring plateau forest (Araújo et al., 2002). Even though there are likely to be differences in the soil CO_2 efflux measurements among sites, we found that despite including both the low and high values of soil CO_2 efflux reported for forest in the Manaus area, the model still could not agree with the observations. Therefore we concluded that the discrepancies between the model and the estimates of A_n from eddy correlation could not be explained by errors in the soil CO_2 efflux term. Furthermore, there are considerable uncertainties in eddy correlation systems in the Amazon rainforest. For instance, there is a large sensitivity (10–25% annually) to the treatment of low frequencies and non-horizontal flow, being lower (<3% annually) for the treatment of high-frequency loss, delay corrections and data spikes (Kruijt et al., 2004). The total uncertainly in daytime measurements estimated for the studied site is ±12% (Kruijt et al., 2004). In addition to the uncertainties in the *NEE* measurements at this site, the estimates of total ecosystem respiration imposed another uncertainty on the comparison presented. Further, non-closure of the energy balance in the eddy covariance data (Aubinet et al., 2002; Massman and Lee, 2002) forced evaluation of energy partition by comparison of evaporative fraction, but due to the high variability in the measurements, we decided to test the model against mean diurnal cycles only.

The introduction of explicit calculation of light interception at different canopy levels, and a move away from the 'big leaf' concept has clearly improved JULES simulations of carbon uptake, enabling a realistic diurnal cycle of A_n to be produced. Introduction of $V_{\max}$ depth-dependence within JULES allows model aspects to be calibrated for different positions within a canopy. Different vertical configurations of in $V_{\max}$ (both uniform and non-uniform distributions) were tested, but we found simulated net canopy photosynthesis to be less sensitive to this. We believe that this is due to canopy structure, where a large percentage of the canopy is permanently shaded and photosynthesis is thus being limited by light rather than $V_{\max.}$

The introduction of the multilayer approach to light interception improved the diurnal profile of A_n when compared to the eddy covariance measurements, however, there remained a systematic underestimation in the model compared to the measurements. To overcome this underestimation, we have tested two possibilities: first by increasing $V_{\max}$ throughout the canopy and second, by including light inhibition of leaf respiration. With the implementation of either solution, JULES became capable of more accurate simulation of A_n, although calculated evaporative fraction increased in both cases and therefore moved slightly away from measurements.

The first option implies a nitrogen content of top leaves of 31.2 mg g^{-1} (according to JULES calculations), which is just outside of the reported upper limit for this site (Table 4). Further, when calculating the nitrogen content of the leaves (equivalent to the $V_{\max} = 50$ μmol m^{-2} s^{-1} from top canopy leaves) using three linear regressions of $V_{\max}$ versus leaf N inferred from measurements of leaf N and photosynthesis in tropical forest in Amazonia (presented in Table 4), the calculated values of leaf N (for two of three cases) were close to the upper limit published for this area. In the third case, using the regression from Carswell et al. (2000), estimated leaf N values were outside of the published range for this area. This was because the original leaf N data from Carswell data set are higher than reported for the C14 and for the K34 sites (Luizao et al., 2004; Ometto et al., 2006). A summary of this comparison is shown in Table 4.

The second possibility to remove the noted bias, is to introduce within JULES a description of the light inhibition of leaf respiration. This would be supported by abundant evidence showing that leaf respiration rates are lower when photosynthesis is happening at the same time (Brooks and Farquhar, 1985; Atkin et al., 1998; Hoefnagel et al., 1998; Atkin et al., 2000). Unfortunately, because biochemical models of gas exchange describing this phenomenon are not available yet, we have used the empirical description used by Lloyd et al. (1995). There are, however, uncertainties on the extent of the reduction of leaf respiration with light. Published values of leaf respiration in the light (see fig. 1 from Wohlfahrt et al. (2005)) indicate reductions in daytime leaf level respiration (relative to darkness) varying between 24 and 84%. The relationship obtained from Brooks and Farquhar (1985) implemented by Lloyd et al. (1995) and used here falls near the upper end observed range reported in the literature. In addition, previous studies assessing daytime ecosystem respiration found that failure to include light inhibition of canopy respiration resulted in overestimation of daily ecosystem respiration and hence, overestimation of gross primary productivity from eddy covariance measurements (Janssens et al., 2001; Wohlfahrt et al., 2005). Their results suggest a reduction of 11–17% of estimated gross primary productivity (GPP) from eddy covariance measurements when considering daytime inhibition of leaf respiration. Unfortunately, from the simulations presented here, it is not possible to unequivocally differentiate whether the potential agreement with the observations is due to altered rubisco capacity, or inhibition of light respiration, or some combination of both. We do note the increasing reported evidence of light inhibition of leaf respiration, and suggest that there is a good case to examine these effects in observations and models.

Table 4. Leaf nitrogen values published in the literature and inferred from $V_{\max}$ *vs* Leaf N relationships derived from measurements in tropical forest in the Brazilian Amazon

	Site	Height	Leaf N [mg g^{-1}]
Ometto et al. (2006)	K34	All heights	20.4 ± 6.0
Ometto et al. (2006)	C14	All heights	20.7 ± 0.7
Luisao et al. (2004)	K34	Top leaves	23.1 ± 5.9
Carswell et al. (2000)	C14	At 24 m	30.05 ± 0.06
Carswell et al. (2000)	C14	All heights	27.36
Equivalent to $V_{\max} = 50\ \mu$mol m^{-2} s^{-1} using JULES calculations	K34	Top leaves	31.2
Equivalent to $V_{\max} = 50\ \mu$mol m^{-2} s^{-1} using the $V_{\max}$ vs. leaf N regression derived from the Carswell et al. (2000) data set from Manaus.	K34	Top leaves	43.1
Equivalent to $V_{\max} = 50\ \mu$mol m^{-2} s^{-1} using the $V_{\max}$ vs leaf N regression derived from the Domingues et al. (2005) data set from Tapajos.	K34	Top leaves	25.8
Equivalent to $V_{\max} = 50\ \mu$mol m^{-2} s^{-1} using the $V_{\max}$ versus leaf N regression derived from the Vale et al. (2003) data set from Caxiuana.	K34	Top leaves	30.0

A novel aspect of this paper has been the use of measurements of top leaf-level $\delta^{13}C$ to check model performance. In all tested simulations, simulated $\delta^{13}C$ was inside of the published range for this site. The number of isotopic sampling studies is increasing, and isotopes are a promising tool that will aid further land surface model evaluation at different sites.

5. Conclusion

We have shown major improvement on the simulated net carbon uptake within JULES as a result of the introduction of a two stream canopy radiation model (Sellers, 1985) and a multilayer scheme to scale leaf to canopy photosynthesis. The simulated light responses and diurnal cycle of net photosynthesis compare more closely with the observations with the new approach than with the standard 'Big Leaf' algorithm. In particular, saturation of light dependence at low PAR values has been removed, yielding diurnal profiles of A_n that no longer flatten-off in high-light levels around the middle of the day. Introduction of $V_{\max}$ depth-dependence within the JULES model had less impact on the simulated A_n than initially expected. This might be a function of this particular site where light limitation dominates photosynthetic activity throughout much of the canopy, because of the high leaf area index of the forest.

Despite these improvements, JULES had a persistent bias, underestimating the eddy covariance measurements of A_n. This bias could be eliminated either by increasing $V_{\max}$ throughout the canopy (i.e. raising photosynthesis) or by suppressing leaf respiration in the light. There is increasing evidence of light inhibition of leaf respiration (Brooks and Farquhar, 1985; Atkin et al., 1998; Hoefnagel et al., 1998; Atkin et al., 2000), and we suggest that further studies are required to investigate this effect in field experiments and model sensitivity studies.

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