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Modelling Amazonian forest eddy covariance data: a comparison of big leaf versus sun/shade models for the C-14 tower at Manaus I. Canopy photosynthesis

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ABSTRACT

In this study, we concentrate on modelling gross primary productivity using two simple approaches to simulate canopy photosynthesis: "big leaf" and "sun/shade" models. Two approaches for calibration are used: scaling up of canopy photosynthetic parameters from the leaf to the canopy level and fitting canopy biochemistry to eddy covariance fluxes. Validation of the models is achieved by using eddy covariance data from the LBA site C14. Comparing the performance of both models we conclude that numerically (in terms of goodness of fit) and qualitatively, (in terms of residual response to different environmental variables) sun/shade does a better job. Compared to the sun/shade model, the big leaf model shows a lower goodness of fit and fails to respond to variations in the diffuse fraction, also having skewed responses to temperature and VPD. The separate treatment of sun and shade leaves in combination with the separation of the incoming light into direct beam and diffuse make sun/shade a strong modelling tool that catches more of the observed variability in canopy fluxes as measured by eddy covariance. In conclusion, the sun/shade approach is a relatively simple and effective tool for modelling photosynthetic carbon uptake that could be easily included in many terrestrial carbon models.

KEY WORDS

modelling canopy photosynthesis; rainforest; Amazon; eddy-covariance.

Modelagem de dados de covariância de fluxo turbulento na floresta amazônica: uma comparação entre os modelos "folha-grande" e "sol/sombra" para a torre C-14 em Manaus. I. Fotossíntese do dossel

RESUMO

Neste trabalho foi modelada a produtividade primária bruta através de duas técnicas simples para simular a fotossíntese no dossel: os modelos "folha-grande" e "sol/sombra". Para calibrar os modelos foram utilizados os parâmetros de fotossíntese da folha, estendidos à escala do dossel e um ajuste da bioquímica do dossel em relação à covariância de vórtices turbulentos. Os modelos foram validados com as medidas feitas através da técnica de covariância de vórtices turbulentos da estação C14 do projeto LBA. Ao comparar o desempenho de ambos os modelos, conclui-se que o modelo "sol/sombra" apresenta melhores resultados numericamente (do ponto de vista da qualidade do ajuste aos dados da estação C14) e qualitativamente (segundo a resposta residual às diferentes variáveis ambientais). Comparado ao modelo "sol/sombra", o modelo "folha-grande" tem menos precisão e não responde bem às variações na fração difusa da luz. O modelo "folha-grande" também apresenta resultados assimétricos em relação à temperatura do ar e ao déficit da pressão de vapor. O tratamento separado de folhas expostas ao sol e de folhas sombreadas, combinado à separação da incidência de luz direta e difusa, faz do modelo "sol/sombra" uma ferramenta de modelagem útil, capaz de reproduzir melhor a variabilidade de fluxos no dossel medidos pela técnica de covariância de vórtices turbulentos. Neste trabalho, mostramos também a importância de boas estimativas de radiação difusa e a necessidade de aprimoramento de tais medidas na região amazônica. Discutimos igualmente as dificuldades de mudança de escala desde a folha para o dossel e a importância de dados representativos para serem parametrizados nestes tipos de modelo. Em conclusão, o modelo "sol/sombra" mostrou-se relativamente simples e eficaz para modelar a fixação de carbono pela fotossíntese e poderia facilmente ser incluído em diferentes modelos de ciclo do carbono terrestre.

PALAVRAS-CHAVE

modelagem da fotossíntese no dossel, floresta tropical, Amazônia, técnica de covariância de fluxo turbulento.

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INTRODUCTION

Tropical rain forests play an important role in the global carbon budget covering 12% of the planet's land surface and containing around 40% of the carbon in the terrestrial biosphere (Taylor & Lloyd, 1992). It has been estimated that they may account for as much as 50 % to the global net primary productivity (Grace et al., 2001).

Recently, some studies have suggested the possibility that mature rainforests are currently acting as net carbon sinks. This implication comes from forest inventories (Phillips et al., 1998) eddy covariance measurements (Grace et al., 1995; Malhi et al., 1998) and global atmospheric inversions (Rödenbeck et al., 2003). Some terrestrial modelling studies (Tian et al., 1998) have also suggested that undisturbed Amazon forest can be a strong net sink of CO_2 particularly during wet years or can be a carbon source when precipitation in much of the Amazon Basin is severely reduced (i.e during strong El Niño events). The measured magnitude of the sink is still controversial due to the range of reported values and it is clear that the magnitude of the sink in Amazonia can have important implications for the global carbon cycle.

There is a need to parameterise and validate ecosystem gas exchange and vegetation models for the Amazon region in order to adequately simulate present and future carbon balances. Calibrated models for the Amazon region are also of vital importance to improved accuracy of climate models' simulations of future carbon dioxide concentration and climate.

In the absence of major disturbances such as fire, gross primary productivity together with ecosystem respiration constitute the major components of an ecosystem's carbon balance. In this study, we concentrate on modelling gross primary productivity using two simple approaches to simulate canopy photosynthesis: big leaf and sun/shade models.

Among the terrestrial ecosystem biophysical modelling community, the merit of separating the contributions from sunlit and shaded foliage to canopy photosynthesis in model simulation has been recognized for some time (Goudriaan, 1977; de Pury & Farquhar 1997). This is because the photosynthesis of shaded leaves should retain an essentially linear response to above canopy irradiance even though photosynthesis of sunlit leaves may be light saturated. The sun/shade approach is expected to give more accurate predictions because of its separation of the leaves into dynamically changing sunlit and shaded groups exposed to very different radiation environments.

A closely related issue is the importance of separating diffuse skylight and direct sunlight when considering the penetration and absorption of radiation through the canopy. This is because of their different attenuation in canopies and the temporal and spatial variation in illumination intensity (Goudriaan, 1977; de Pury & Farquhar 1997). Under clear sky conditions most of the solar irradiance is direct beam radiation, whereas under overcast conditions the radiation is almost all diffuse. The partitioning of the incoming radiation into diffuse and direct portions thus creates spatial bimodality in the illumination of the canopy: sun foliage receives diffuse and direct irradiance and shade foliage receives only diffuse irradiance.

Canopy light use efficiency (ratio of amount of CO_2 fixed to amount of absorbed photosynthetically active radiation, PAR) has been reported to be higher under diffuse irradiance than under direct radiation for individual trees and forest canopies (Lloyd et al., 1995; Gu et al., 2002; Law et al., 2002). This can be explained by the following reasoning: since photosynthesis of individual leaves saturates at high irradiances, it is at low irradiances when individual leaves present their highest efficiencies. If light is mostly diffuse, the volume of shade in the canopy is minimal and the whole canopy should be more efficient under low irradiances. If light is mainly direct, there are well defined shadows that occupy larger amounts of leaves in the canopy and light use efficiencies will be lower (Roderick et al., 2001).

Avoiding the separation of leaves into sunlit and shaded is one of the main drawbacks of big leaf models because it has a potential to lead to overestimation of canopy photosynthesis (de Pury & Farquhar 1997). Theoretically then, an accurate separation of diffuse and direct irradiance together with an accurate division of sun and shade foliage should be a crucial issue in modelling canopy photosynthesis.

Our main objective here is to calibrate and test these two approaches for modelling canopy photosynthesis, namely the big leaf and sun/shade parameterisations. The big leaf model (Lloyd et al., 1995) is calibrated against eddy covariance data and sun/shade (de Pury & Farquhar 1997) is parameterised using derived leaf level photosynthetic parameters from vertical profiles of leaf photosynthetic capacities together with data of vertical distribution of leaf area density. More specifically, we wanted to compare and evaluate the behavior of both models for an Amazonian ecosystem.

MATERIALS AND METHODS

Site

The study site is an undisturbed mature lowland rain forest in the central Brazilian Amazon, close to Manaus, (2° 35' S, 60° 06' W). It is part of the Cueiras biological reserve owned by the Instituto National de Pesquisas da Amazonia (INPA) and is located on an extensive plateau with an elevation of about 100 m. The forest has a closed canopy of about 35- 40 m height with a few emergent trees reaching up to 45m (Malhi et al., 1998). Permanent forest inventory plots established around the study area (2° 30' S, 60° 06'W) by the Biomass and Nutrient Experiment (BIONTE) and the Biological Dynamics of Forest Fragments Project (BDFFP) measured an average of stand biomass of 324.14 Mg ha^{-1} (reported in Chambers et al. (2001a)). A leaf area index of 5.7 has been measured at this site (Meir et al., 2000) with values in the range [4.1-5.7] having been measured in nearby forests by S.Patiño (pers.comm.). The landscape consists of plateaus and valleys with soil type decreasing gradually from oxisols in the uplands (where the

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measurement tower was located) and upper parts of the valleys to utisols and spodosols in the valley slopes. There is a gradual decrease in clay content from oxisols (80%-90%) to spodosols (2%-5%). This decrease in clay content is accompanied by an increase in quartz from the upper to the lower level of the toposequence (Bravard & Righi 1989).

Central Amazonia is characterized by a seasonal rainfall regime with a dry season (usually with monthly precipitation lower than 100 mm) from July to October. The annual mean temperature is 26 °C. Leopoldo *et al.* (1987) reported an average annual precipitation of 2101 mm for the Manaus region during the 1931-1960 period. Of the total precipitation, around 73% falls in short, heavy rains (Leopoldo *et al.,* 1987).

DATA

Fluxes and meteorology

Models were tested against measurements of carbon dioxide, water vapor and sensible heat fluxes made by an eddy covariance system of the type described by Moncrieff *et al.* (1997) located 5 m above the top of a 41.5 m tower, "C14", previously known as "ZF2". Meteorological data (global solar radiation, wind speed, air temperature, and wet bulb temperature) used as input data to the models come from an automatic weather station located 2.5 m below the top of the same tower. A detailed description and analysis of the carbon dioxide flux data used here has been provided by Malhi *et al*. (1998).

The data set used here to test the models was obtained towards the end of the dry season and the early wet season of the 1995 (mid October to mid December). We have used only this period to calibrate and test the models because this was the only period within the original Malhi *et al*. (1998) dataset when CO_2 canopy storage estimates were obtained.

A lack of closure of the energy balance is a well-recognized problem of the eddy covariance method (Massman *et al.*, 2002; Aubinet *et al.*, 2002). But recently this problem has been associated with a failure to take into account low frequency contributions to the overall ecosystem flux due to a short mean removal period (Finnigan *et al.*, 2003). For the Manaus C14 site described by Malhi *et al*. (1998), it was found that once turbulent transport at low frequencies (on time scales of 1 to 4 hours) was taken into account, the energy balance of the forest was much improved (Malhi *et al.*, 2002; Finnigan *et al.*, 2003). Including the low energy correction sensible heat fluxes increased by 43.3%, latent heat fluxes by 32.1% and day time CO_2 fluxes increased by 30.7%. Fluxes from this "recalculated data set" (Malhi *et al.*, 2002) have thus been used here for calibration (big leaf) and validation (big leaf and sun /shade) of the models.

Because the carbon dioxide fluxes determined by eddy covariance are net ecosystem exchange rates, in order to determine canopy CO_2 assimilation rate, A, it is necessary to take into account the ecosystem respiration rate, R_E.

$$A = N_E - R_E + \int_0^h \frac{\partial C_a}{\partial t}\, dz \qquad (1)$$

where A is net assimilation or gross primary productivity and N_E is net ecosystem exchange measured by eddy covariance, both in [μmol m^{-2} s^{-1}]. The integrand in [μmol m^{-2} s^{-1}], represents the rate of change in the CO_2 concentration (C_a) within the canopy between the forest floor and the eddy covariance measurement height, h.

Ecosystem respiration

The eddy covariance technique has become a very important and widely used tool to measure the net ecosystem exchange of CO_2 at regional levels, and theoretically, it should be possible to use the night time eddy correlation fluxes to determine the respiration of an ecosystem. But like other measuring techniques, this method has limitations and most of the limitations occur at night time when air is typically stratified which is associated to low turbulence (Aubinet *et al.*, 2002; Massman *et al.*, 2002). Massman *et al.* (2002) report eddy covariance limitations being mainly of instrumental and meteorological types. Since eddy covariance is a technique that performs best when turbulent conditions predominate, the usual stable atmospheric conditions occurring during night time might make sensor limitations a significant restriction for accurate measurements. Large footprints, gravity waves, advection and low turbulence are among the most significant meteorological restrictions (Massman *et al.*, 2002). An analysis of the database used for this study reports underestimation of the night time fluxes especially at high wind speeds (Malhi *et al.*, 1998). Specifically because of the undulated topography formed by valleys and plateaus in the Manaus region and because the C14 tower is located on a plateau, it might be possible that on calm nights, part of the CO_2 that is being respired is draining to the valleys without being registered by the tower sensors (Araújo *et al.*, 2002). Because of all these uncertainties with night time eddy correlation fluxes, ecosystem respiration rates in this study were taken from direct chamber measurements of the different contributions to the ecosystem CO_2 efflux performed in sites nearby and scaled up appropriately.

We define ecosystem respiration as the summation of different contributions from live leaves (R_C), stems and branches (R_W), soil (which includes root and fine litter decomposition in the soil surface) (R_S) and coarse litter (R_{CS}) contributions. All terms are in [μmol m^{-2} s^{-1}].

$$R_E = R_S + R_W + R_C + R_{CS} \qquad (2)$$

Leaf respiration was modelled for this site and measurements of soil and stem respiration (Chambers *et al.*, 2004) and that of coarse litter (Chambers *et al.*, 2001b) in an area nearby (permanent plots established by the BDFFP and the BIONTE projects) were used to parameterise the models.

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Coarse litter respiration was taken as a constant 0.5 μmol m^{-2} s^{-1} and stem respiration was taken as 1.1 μmol m^{-2} s^{-1} with the same temperature dependence as for canopy respiration in equation (9) below. The soil respiration measurements (Chambers *et al.*, 2004) were performed during the period (2000-2001, *La Niña* years). We used soil respiration data from October, November and December 2000. Precipitation during these months was higher in year 2000 than in 1995. In the same study, Chambers *et al.* (2004) found that there is a decrease in soil respiration with increasing volumetric water content of the soil. Because precipitation regimes were different during 1995 and 2000, soil volumetric water content might have been higher for 2000 than during 1995. Therefore, soil respiration during the period October-December 95 might have been slightly higher than the ones during the same months in year 2000. This implies that our estimations of gross photosynthesis used here to fit and test the models, using net ecosystem exchange measured by the eddy covariance system plus ecosystem respiration could have been slightly higher as well.

THEORY AND MODELS

Leaf biochemistry

The biochemistry of C3 photosynthesis is given by Farquhar & von Caemmerer (1982) as presented by Lloyd *et al.* (1995). Leaf level photosynthetic capacity is described as the sum of all the chloroplast capacities in a given unit area and the chloroplast properties are assumed to scale with the internal light gradient of the leaf (Farquhar & von Caemmerer, 1982).

The CO$_2$ assimilation rate (A) in [μmol m^{-2} s^{-1}] is controlled by the rate of carboxylation when rubisco activity is limiting (A$_v$) at low intercellular partial pressure of CO$_2$ and/or high irradiances and by the rate of carboxylation when RUBP regeneration is limiting (A$_J$) at high intercellular partial pressure of CO$_2$ and/or low irradiances (Farquhar & von Caemmerer, 1982). The rate of CO$_2$ assimilation is modelled as the minimum between A$_v$ and A$_J$.

The rubisco-limited rate, A$_v$, and electron transport-limited rate, A$_J$, both in [μmol m^{-2} s^{-1}] are defined as:

$$A_V = V_{C\max}\left(\frac{C_C - \Gamma^*}{K_C\left(1 + pO_2/K_0\right) + C_C}\right) - R_C \qquad (3)$$

$$A_J = \frac{J}{4}\left(\frac{C_C - \Gamma^*}{C_C + 2\Gamma^*}\right) - R_C \qquad (4)$$

where V$_{cmax}$ in [μmol m^{-2} s^{-1}] is the maximum rate of rubisco activity, K$_o$ and K$_c$ in [Pa] are the Michaelis-Menten constants for carboxilation and oxygenation by rubisco, C$_C$ in [Pa] is the partial pressure of CO$_2$ in the chloroplast, Γ* in [Pa] is the CO$_2$ compensation point in the absence of mitochondrial respiration and R$_C$ in [μmol m^{-2} s^{-1}] is leaf dark respiration in the light. The rubisco Michaelis constants for CO$_2$ and O$_2$ are described to follow an Arrhenius type temperature dependency as in Lloyd *et al.* (1995).

The electron transport rate, J in [μmol m^{-2} s^{-1}], is modelled by a non-rectangular hyperbolic function of the absorbed quantum flux with I$_2$ in [μmol quanta m^{-2} s^{-1}] as the absorbed irradiance that reaches photosystem II, J$_{max}$ in [μmol m^{-2} s^{-1}], as saturating value and θ as curvature factor:

$$\theta J^2 - (I_2 + J_{max})J + I_2 J_{max} = 0 \qquad (5)$$

$$I_2 = I_0 (1-f)(1-r-t)/2 \qquad (6)$$

with r and t being canopy reflectance and transmittance for PAR, f being a spectral correction factor of light and I$_0$ being the PAR reaching the leaf or canopy surface in [μmol quanta m^{-2} s^{-1}].

The temperature sensitivities for rubisco activity and electron transport are given by Farquhar & von Caemmerer (1982) as presented by Lloyd *et al.* (1995):

$$V_{c\max} = V_{C\max,25}\exp\left(\frac{E_v}{298.2R}\left(1 - \frac{292.2}{T_C}\right)\right) \qquad (7)$$

$$J_{max} = J_{max,25}\frac{\exp\left[\frac{(T_C/298.2 - 1)E_J}{RT_C}\right]\left[1 + \exp\left(\frac{298.2S_J - H_J}{298.2R}\right)\right]}{1 + \exp\left(\frac{S_J T_C - H_J}{RT_C}\right)} \qquad (8)$$

where T$_C$ is absolute temperature [K] of the leaf or canopy, R is the universal gas constant (8.314 J mol^{-1} K^{-1}), V$_{cmax,25}$ and J$_{max,25}$ are rubisco activity and electron transport capacity at 25 °C in [μmol quanta m^{-2} s^{-1}]. E$_v$ and E$_J$ in [J mol^{-1}] are activation energies. H$_J$ in [J mol^{-1}] and S$_J$ in [J mol^{-1}K^{-1}] control maximum and minimum optimum temperature dependencies of the electron transport rate.

Leaf respiration is modelled to decrease with increasing light with a temperature dependency as presented by Lloyd *et al.* (1995):

$$R_C = R_{C,25}\exp\left(308.45\left(\frac{1}{71.02} - \frac{1}{T_C - 227.13}\right)\right) \qquad (9)$$

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R_C is the rate of canopy respiration at T_C and $R_{C,25}$ is the rate of canopy respiration at 25 °C, both are given in [μmol m^{-2} s^{-1}].

Because stomatal conductance is also modelled, we prefer to use equations (3) and (4) as a function of stomatal conductance for CO_2 and ambient partial pressure of CO_2. The mathematical development of these equations is presented in appendix III of Lloyd *et al.* (1995).

The equations used here neglect the effect of the mesophyll conductance as in de Pury & Farquhar (1997). Based on measurements those authors argued that avoiding mesophyll conductance would have effects of less than 1% in canopy photosynthesis.

Big leaf model

A similar argument as has been applied to the scaling of chloroplast biochemical properties to the leaf level (Farquhar & von Caemmerer, 1982) has sometimes been applied to plant canopies. That is, if the distribution of photosynthetic capacity amongst leaves in a canopy is in proportion to the profile of absorbed irradiance, then the canopy can be treated as a big leaf and the equations used for individual leaves should be applicable to the canopy as a whole (de Pury & Farquhar 1997). The main assumption of this approach is an optimal distribution of leaf nitrogen through the canopy which means that the vertical profile of photosynthetic capacity is distributed in proportion to the time-averaged irradiance (de Pury & Farquhar 1997). The canopy is treated as an homogeneous entity and the equations usually applied to single leaves are then used for the entire canopy. Because big leaf assumes 100 % diffuse radiation, it ignores any sun fleck penetration and also the effects of leaf angles within canopy irradiance profiles. The big leaf model used in this study is described by Lloyd *et al.* (1995).

Sun/shade model

The main feature of this approach is the partitioning of the canopy into sunlit and shaded components. Each component is modelled as a single layer model using the biochemistry of single leaves as given in de Pury & Farquhar (1997) . The division of sun and shade foliage changes during the day with solar elevation, which means that the photosynthetic capacity and the irradiance absorption of the sunlit and shaded portions of the canopy are also dynamic. All leaves are model to absorb diffuse, scatter diffuse and scattered beam irradiance. Sunlit leaves also receive direct-beam irradiance. The distribution of leaf nitrogen, rubisco capacity (V_{cmax}) and electron transport (J_{max}) in the canopy is taken to decrease exponentially with cumulative leaf area index from the top of the canopy (See Figure 1c, parameterisation using leaf level data), though no implicit assumption of photosynthetic capacity varying directly with average absorbed irradiance is required (as is the case in the big-leaf model). The sun/shade model for canopy photosynthesis used here is described in detailed in de Pury & Farquhar (1997).

Stomatal conductance: "lambda model"

The "lambda model" used here is based on the assumption of optimal stomatal regulation of the rates of CO_2 assimilation and transpiration per unit leaf area in a plant at a finite interval of time with changing environmental conditions except for small changes in the amount of soil water available to the plant (Cowan & Farquhar 1977). The lambda parameter (λ) is a Lagrangean multiplier and it represents the marginal benefit of plant carbon gain relative to the cost of water loss. Lloyd *et al.* (1995) showed that if λ was a constant over a day and did not vary with light or leaf temperature then the following relationship should apply:

$$G_S = A \sqrt{\frac{1.6\lambda P}{(C_a - \Gamma^*)Dc}} \qquad (10)$$

Here A is assimilation in [mol m^{-2}s^{-1}], λ in [mol mol^{-1}], Dc vapor pressure deficit, P atmospheric pressure, C_a ambient partial pressure of CO_2 and Γ^* is the CO_2 compensation partial pressure in the absence of dark respiration, all expressed in [mol mol^{-1}].

Parameterisation of the big leaf model

From the mid October- mid December 1995 data, a selected data set was used to fit the model. Criteria of selection followed the same conditions as in Lloyd *et al.* (1995) and in Grace *et al.* (1995). Data before 9 a.m. was rejected in order to avoid the CO_2 flush or so-called morning peak. Storage terms larger than 8 μmol m^{-2} s^{-1} and smaller than -8 μmol m^{-2} s^{-1} were also neglected as were data points collected during and after rainy hours. Measurements where radiation fluctuated as a result of a moving cloud (i.e abrupt changes in solar radiation from hour to hour) were also filtered together with aerodynamic conductances lower than 0.1 μmol m^{-2} s^{-1}.

Canopy rubisco activity (V_{max}), light saturated electron transport capacity (J_{max}), rate of canopy respiration in the dark (R_C), temperature sensitivity parameters for electron transport, S_J and H_J, the curvature factor and slope of the light response curve, θ and Φ respectively, and the lambda parameter (λ), were then estimated by minimizing the error sum of squares of the model fitted to the selected data set using a simplex procedure (Nelder & Mead 1965).

Parameterisation of the Sun/shade model

Maximum canopy carboxylation capacity (V_{max}), maximum electron transport velocity (J_{max}) and canopy dark respiration (R_C) were calculated by numerical integration of the profiles of the leaf level V_{cmax}, J_{max}, R_C, and cumulative leaf area index along the canopy height as described in de Pury & Farquhar (1997). Profiles of leaf level V_{cmax}, J_{max} and R_C were derived from gas exchange measurements made at the same site where the C14 tower is located. Measurements were made at five

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different heights within the canopy (Carswell *et al.*, 2000) (See Figure 1a for the vertical profile of V_{cmax}). Since the gas exchange measurements of Carswell *et al.* (2000) were undertaken only to a height of 24m, we fitted an exponential curve to the points in Figure 1a and calculated the correspondent V_{cmax}, J_{max} and R_C values for 30 and 35 m height. The vertical distribution of leaf area index was determined using a photographic method to measure leaf area density (m² leaf m⁻³ leaf) at different heights on the same C14 tower (Meir *et al.*, 2000)(Figure 1b). Using the vertical profile of leaf area density leaf area index was calculated for each height and then the cumulative leaf area variation with height was also determined. By plotting the vertical profile of V_{cmax}, J_{max}, and R_C with cumulative leaf area index we found that there was indeed an exponential decrease of each of these canopy properties with height or with cumulative leaf area index. We then fitted an exponential function that was numerically integrated along the whole leaf area index to provide canopy V_{max}, J_{max} and R_C. Figure 1c shows the relationship between V_{cmax} at leaf level and cumulative leaf area index. The area under the curve is the canopy carboxylation capacity.

The rest of the required parameters, curvature factor of the light response curve, θ, slope of the light response curve, Φ, and temperature sensitivity parameters of the electron transport rate, S_J and H_J, were taken from the modelling study of Carswell *et al.* (2000). Same as for big leaf, the lambda (λ) parameter for stomatal conductance was fitted minimizing the error sum of squares of the model fitted to the selected data set using a simplex procedure (Nelder & Mead 1965).

RESULTS

Canopy biochemical properties

Sun/shade: Taking the parameters of Carswell *et al*. (2000) gave an integrated canopy photosynthetic rubisco capacity (V_{max}) of 205 μmol m⁻² s⁻¹ at 25 °C with V_{max} at the top of the canopy being 58 μmol m⁻² s⁻¹ at the same temperature and with a ratio of electron transport rate to rubisco activity (J_{max}/V_{max}) of 2.6. The rate of canopy respiration in the dark (R_C) was modelled to be 3.9 μmol m⁻² s⁻¹ at 25 °C with canopy respiration at the top of the canopy being 1.3 μmol m⁻² s⁻¹ at the same temperature.

To run the model, the temperature sensitivity parameters of J_{max} (S_J and H_J) and the curvature factor of the non-rectangular hyperbolic function were initially taken as given by Carswell *et al.* (2000) from A/Cᵢ and light response curve gas exchange measurements on individual leaves throughout the canopy (710 J K⁻¹mol⁻¹, 220000 J mol⁻¹ and 0.67, respectively).

When the sun/shade model was run with the above parameterisation, canopy daytime CO_2 assimilation rates were overestimated by on average 20 % (shown in Figure 2a-b), but when V_{max} and R_C at the top of the canopy were empirically reduced by 10% and the ratio of electron transport rate to rubisco activity was reduced to 1.9, a much better fit was
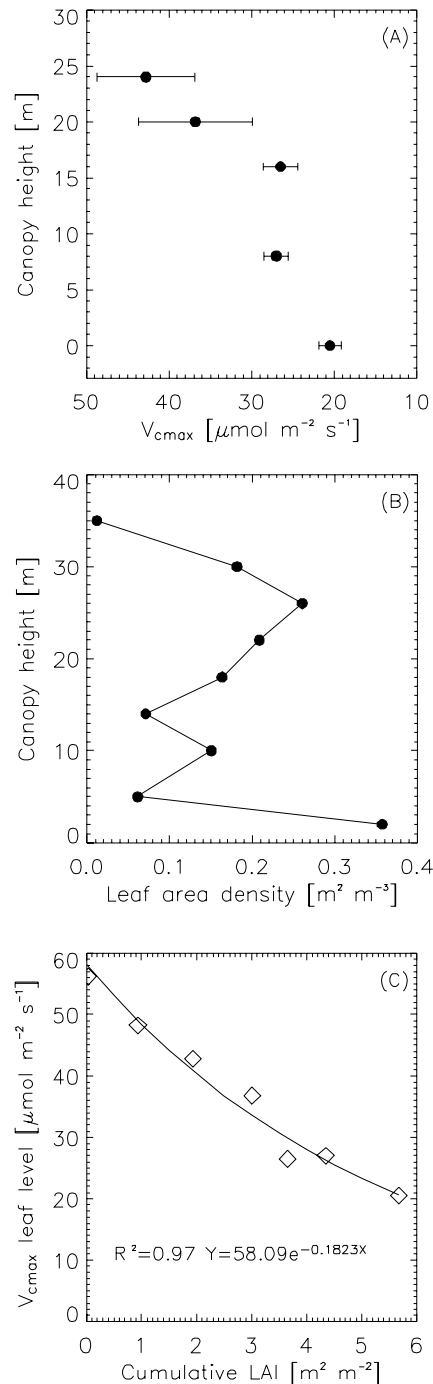

Figure 1 - Data used for parameterisation of sun/shade model. (A) Vertical profile of leaf rubisco activity V_{cmax} (Carswell *et al.*, 2000), (B) Vertical profile of leaf area density (Meir *et al.*, 2000),(C) Distribution of V_{cmax} with cumulative LAI.

obtained (Figure 2c-d). The higher initially estimated ratio had resulted in sunlit leaves never being limited by their electron transport rate which, with shaded leaves representing about

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70-85% of the canopy LAI, was the main source of the initial overestimation. The initial high ratio is also a result of the high up-scaled canopy J_{max}, related to the high nitrogen levels of the leaf level data used for up-scaling. This issue is discussed later. An even better fit was obtained when the apparent quantum yield was reduced from 0.5 (as in Carswell *et al,.* 2000) to 0.4. (Figure 2e-f) with a further improvement also being obtained when one of the Carswell *et al.* (2000) electron transport temperature response parameters was modified slightly, increasing the temperature optimum from 32 to 39 °C (Figure 2g-h). The best fitted value of S_J was 693.1 J $K^{-1}mol^{-1}$ (cf. 710.0 in Carswell *et al.*, 2000).

Big leaf: For the big leaf model the fitted values of canopy rubisco capacity and electron transport rate were 152 and 273 $\mu mol\ m^{-2}\ s^{-1}$, respectively at 25 °C. The fitted curvature factor for the light response curve was 0.17, and the best fitted quantum yield for absorbed light was 0.37. Fitted values of S_J and H_J were 687.4 $K^{-1}mol^{-1}$ and 215.6 KJ mol^{-1}, respectively. Modelled canopy dark respiration rate was 2.92 $\mu mol\ m^{-2}\ s^{-1}$ at 25 °C.

The sun/shade model predicted higher gross photosynthetic rates than the big leaf model as a result of the higher canopy V_{max} and J_{max}, but the modelled net assimilation (photosynthesis - leaf respiration) was quantitatively similar for both models (See Figures 2g-h and 3a-b). This was because of the much higher canopy respiration rates modelled by sun/shade, a consequence of the assumption in the initial leaf-level parameterisations of Carswell *et al.* (2000) that leaf respiration is not inhibited in the light. By contrast, using the parameterisation of Lloyd *et al.* (1995) the big-leaf model here assumes decreased respiration rates in the light (See Figure 4). Assuming no inhibition with light daytime foliar respiration rates have been scaled to ecosystem level for the same site in Manaus giving values between 1.8 and 7 $\mu mol\ m^{-2}\ s^{-1}$ (ground area basis), averaging 4.7 $\mu mol\ m^{-2}\ s^{-1}$ (Chambers *et al.*, 2004). Similarly, the sun/shade model predicts canopy respiration rates between 2.9 and 6.7 $\mu mol\ m^{-2}\ s^{-1}$ during the day. Leaf respiration during daylight is still a parameter with a high uncertainty because it is not easy to measure due to the difficulty in separating photosynthetic and respiratory processes (Atkin *et al.*, 2002).

The ratio J_{max}/V_{max} for big leaf and sun and shade were very similar, 1.8 and 1.9 respectively. But, in contrast to the sun/shade model the big leaf modelled photosynthesis was limited by electron transport rate at all irradiances, despite the low θ. This can be attributed to the fact that, according to the sun/shade calculations, 70-85% of the canopy LAI is shaded, which means that the majority of the photosynthesis is indeed limited by J_{max}. In the sun/shade model, the shaded leaf fraction is limited by electron transport at all the irradiances. The rate of photosynthetic uptake in the sun leaf is light-limited at low irradiances (0-500 μmol quanta $m^{-2}\ s^{-1}$ PAR), and from 500 to 1000 μmol quanta $m^{-2}\ s^{-1}$ PAR, it is typically close to being co-limited by rubisco and electron transport rates. At irradiances
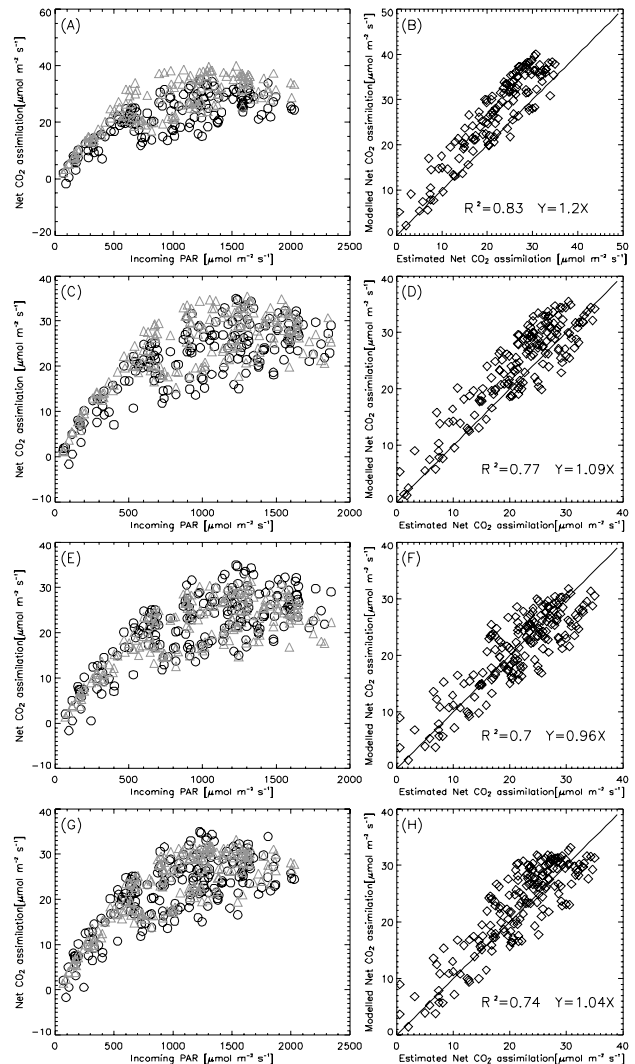

Figure 2 - Light response (left) and goodness of fit (right) by sun/shade model. (o) estimated and (∇) modelled net CO_2 assimilation. (A) and (B) using canopy parameters derived from up scaling leaf level V_{cmax}, J_{max} and R_C. (C) and (D), top canopy V_{max} and R_C are empirically reduced by 10% and the ratio of J_{max}/V_{max} is reduced from 2.6 to 1.9. (E) and (F), quantum yield of light absorption reduced from 0.5 to 0.4 and changes included in (C) and (D). (G) and (H), all the previous changes plus the use of a fitted S_J that increased the optimum temperature of J_{max} from 32 to 39 °C.

higher than 1000 μmol quanta $m^{-2}\ s^{-1}$ PAR, leaves in the sunlit fraction are light-saturated and their photosynthetic activity is then modelled to be limited by rubisco activity.

The efficiency of photosynthesis or quantum yield of absorbed light in both models was fitted and equal to 0.37 and 0.4 for big leaf and sun and shade, respectively. Even though the leaf level measurements are fitted with a value of 0.5 (Carswell *et al.*, 2000), both models overestimate the data that
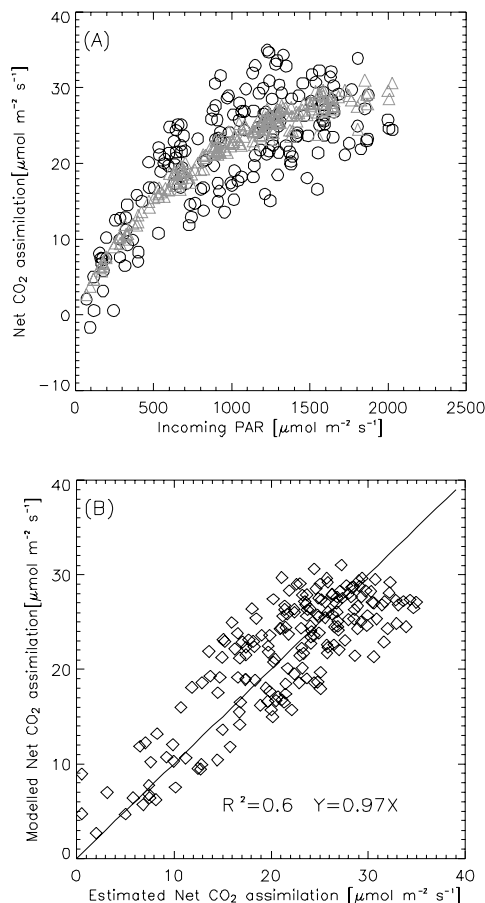
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Figure 3 - Light response curve (A) and goodness of fit as modelled by big leaf (B): (o) estimated and (∇) modelled net CO_2 assimilation.

Figure 4 - Canopy respiration rate modelled by big leaf (A) and by sun/shade (B): (o) leaf respiration by the shaded leaf, (∇) leaf respiration by the sun leaf, ($\Diamond$) canopy respiration including sun and shade contributions.

belong to the region of slope of the light response curve when using that value. In this case, the reduction of the quantum yield of absorbed light implies a reduction in the efficiency of photosynthesis without reduction of photosynthetic capacity. This light dependent reduction is associated with a long term down regulation of the quantum yield of photosystem II photochemistry through a mechanism of thermal energy dissipation (Öquist *et al.*, 1992).

The goodness of the models fit is presented in terms of R^2 (Figures 2g-h and 3) and the agreement index 'd'. The index of agreement has been used in other studies (Medlyn *et al.* 2003); it is useful to indicate the degree which a model's predictions are error-free. The index 'd' ranges from 0 to 1 with increasing agreement between model and data. The sun/shade model had a slightly better fit ($R^2 = 0.74$ vs 0.6, d = 0.93 vs 0.9) but also a higher slope (1.04 vs 0.97) than the big leaf model. In the light response for both models, it can be seen that the sun/shade model catches some of the variability measured by the eddy covariance system, whilst the big leaf simply provides an average of the data.
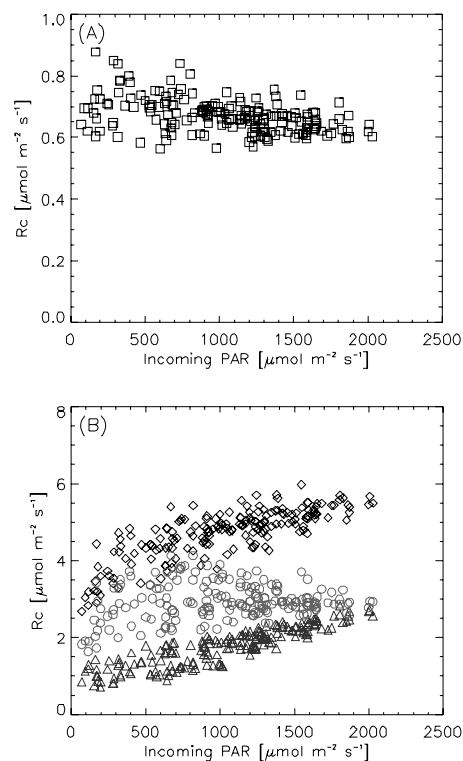
Sun/shade models can clearly predict part of the variability due to the radiation treatment as the attenuation of diffuse and scattered radiation are taken into account. This is shown in Figure 5 where model residuals are plotted as a function of both incoming PAR and the fraction of diffuse irradiance (f_d). Here it can be seen that at low values of f_d, the big leaf model residual plot skews markedly showing that the model tends to overestimate under these conditions (Figure 5a). By contrast the sun/shade has residuals relatively well distributed around the zero line (Figure 5b). The big leaf model is unresponsive to diffuse irradiance and the predictions are especially inaccurate at low values of diffuse fraction. At high values of PAR (also typically with low fractions of diffuse irradiance), big leaf tends to overestimation while sun shade presents a more uniform distribution of residuals along the zero line (Figures 5 c-d).

In Figure 6 the standardised residuals against vapour pressure difference (VPD) and temperature for both models are also presented. Again, this shows the generally superior performance of the sun-shade model (Figures 6 b,d,f,g) for which there is not bias in the model residuals when examined as a function of VPD or air and canopy temperatures. By contrast, the big leaf model (Figures 6 a,c,e) consistently overestimates fluxes at high VPD and temperatures. These are mainly values
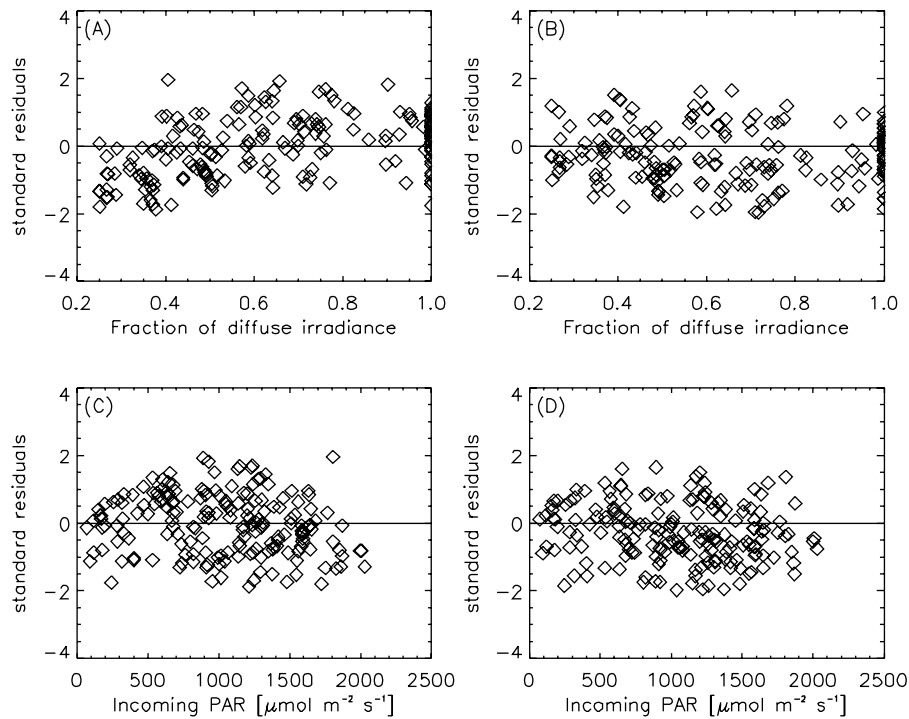
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Figure 5 - Response of standard residuals (of modelled and estimated net assimilation rates) to incoming irradiance and fraction of diffuse irradiance. (A) and (C) are residuals by big leaf, (B) and (D) correspond to sun/shade. Positive residuals mean underestimation and negative residuals mean overestimation.

that also correspond to high irradiances and low fractions of diffuse irradiance.

In the case of sun/shade model, canopy photosynthesis is mainly driven by irradiance absorbed by the shaded leaves (i.e. diffuse irradiance) because 40-60% of the total photosynthesis is undertaken by the shaded part of the canopy which constitutes 70-85% of the leaf area. A plot of the light response of diffuse irradiance is presented in Figure 7. It can be seen that it has the same shape as the light response of photosynthesis as modelled by sun/shade (Figure 2).

If light is mostly diffuse, there are minimal shadows, and photosynthesis will be enhanced. In contrast, when there is clear sky and high PAR the shadows are well defined because most of the radiation comes from a single direction and overall photosynthesis will be lower (Roderick *et al.*, 2001). Thus, an estimation of diffuse irradiance is a highly important variable for sun/shade models, and the accuracy of its calculation becomes very relevant. Here we lacked actual measurements, relying on simulations. This lack of measured diffuse irradiance makes it difficult to quantify the extent to which the modelled diffuse irradiance agrees with reality. Thus, four different models for calculation of global diffuse irradiance were tested (Figure 8): Spitters *et al.* (1986), Weiss & Norman (1985), Reindl *et al.* (1990) and Erbs *et al.* (1982) with the fraction for PAR being calculated in all cases using the relationships from Alados & Alados-Arboledas (1999). Using the models from Weiss &

Norman (1985), Reindl *et al.* (1990) and from Erbs *et al.* (1981), the sun/shade model predicted a strong trend of overestimation at high diffuse irradiances and underestimation at low diffuse fractions. The best performance of sun/shade model here was obtained using formulations from Spitters *et al.* (1986). However, at high irradiances the modelled photosynthesis still tended to slightly overestimate. This result suggests a considerable importance for actual diffuse irradiance measurements in the Amazon region to be made in order to test and parameterise diffuse irradiance models needed for canopy photosynthesis modelling.

After accounting for variation in diffuse irradiance, canopy V_{max} for the sun and shaded leaf fractions and stomatal conductance, especially for the shaded leaf fraction, were the variables with strongest influence in modelling photosynthesis using the sun/shade model. Parameterisation of canopy V_{max} was most sensitive to the V_{max} at the top of the canopy and as already mentioned the sun/shade model could only fit the data when reducing the V_{max} and R_C at the top of the canopy by 10% and the ratio J_{max}/V_{max} fom 2.6 to 1.9.

The sensitivity parameters for the temperature dependence of the light saturated potential rate of electron transport, S_J and H_J (equation 8) were also important factors in model performance, especially S_J that controls the optimum temperature of J_{max}. Figure 9 shows the temperature dependence function ($J_{max}/J_{max,25}$ from equation 8) evaluated

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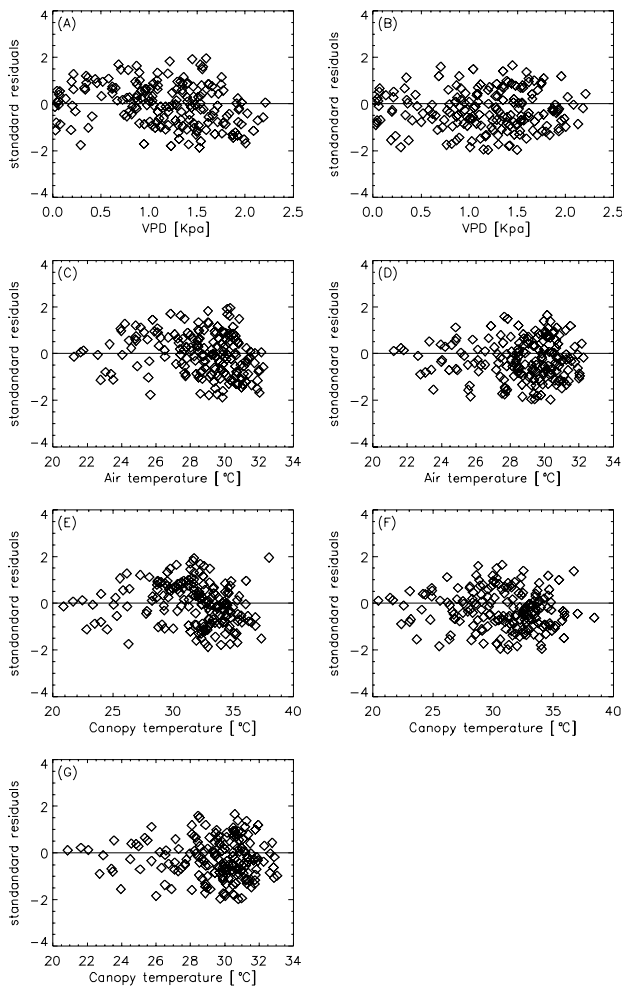THE C-14 TOWER AT MANAUS I. CANOPY PHOTOSYNTHESIS

Figure 6 - Response of standard residuals (of modelled and estimated net assimilation rates) to VPD, air temperature and canopy temperatures. (A),(C), (E) are residuals by big leaf, (B) (D), (F) and (G) correspond to sun/shade. (F) and (G) are simulated canopy temperatures by the sunlit and shaded leaves respectively. Positive residuals mean underestimation and negative residuals mean overestimation.

using S_j from Carswell *et al.* (2000), S_j fitted for big leaf, S_j fitted for sun/shade and S_j used by Lloyd *et al.* (1995). Apart from S_j used by Carswell *et al.* (2000) they all had similar values with optimum temperatures between 39 and 43 °C. Using S_j from Carswell *et al.* (2000), which has an optimum temperature of 32 °C, resulted in electron transport limited photosynthesis at canopy temperatures higher than 32 °C which implied that photosynthesis by the sunlit leaf fraction was being limited by electron transport at high irradiances. Nevertheless, we also point out that the dataset of Carswell *et al.* (2000) was not parameterised at the highest canopy temperatures observed as part of this study.
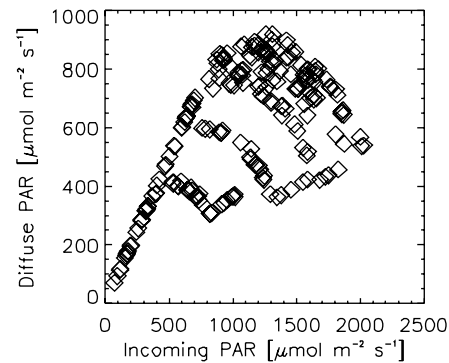

Figure 7 - Light response of diffuse irradiance using Spitters *et al.* (1986) model.

GENERAL DISCUSSION

The required reparameterisation of the sun/shade model shows the difficulties of scaling from leaf to canopy level and it is important to again note that a mixture of field data (V_{cmax}, J_{max}, R_C, Leaf area density distribution) and fitted parameters (lambda, quantum yield, S_J) were used for its initial parameterisation. Thus, this scaling and modelling exercise has been subject to the limitations of the goodness and representativeness of the data used to parameterise at the leaf level and the data used to test the model (eddy covariance flux data and respiration data). There are thus several explanations for the overestimation (20%) obtained when running the model with the directly scaled up canopy V_{max}, J_{max} and R_C. The leaf level gas exchange data used here comes from a study where only 9 species were measured. But de Oliveira & Daly (1999) determined a total of 845 species by sampling 3 hectares in the BDFFP plots. Carswell *et al.* (2000) reported an average nitrogen concentration in the leaves of 2.7 %. Results from a leaf and soil sampling study (where 20 canopies were sampled for each of plateau, valley and slope topographies) 11 km away at the K34 LBA tower, obtained an average nitrogen concentration in the top leaves of 1.8% and a whole-canopy average of 1.9% (Costa *et al.*, this issue). When using a linear relationship between the nitrogen concentration in the leaves and V_{cmax} reported in Carswell *et al.* (2000), one can easily estimate the correspondent V_{cmax} and J_{max} for the top leaves with the reported leaf nitrogen at the K34 site. The V_{cmax} and J_{max} values obtained for the top leaves are 24.4 and 57.5 μmol m^{-2} s^{-1} respectively, with a ratio of 2.3 which are 58 and 68% lower respectively than the values estimated here (58.09 and 181.7 μmol m^{-2} s^{-1} and a ratio of 3.1) using Carswell *et al.* (2000) data. The correspondent V_{cmax} and J_{max} values at the top of the canopy using the parameterisation of sun/shade used here are 52.2 and 111.5 μmol m^{-2} s^{-1} with a fitted J_{max}/V_{max} ratio of 1.9.

This suggests that the average V_{max}, J_{max} and R_C for the C14 site could indeed be lower than implied by the more limited dataset of Carswell *et al.* (2000). The obtained ratio of J_{max}/V_{cmax} reported by Carswell *et al.* (2000) at leaf level for
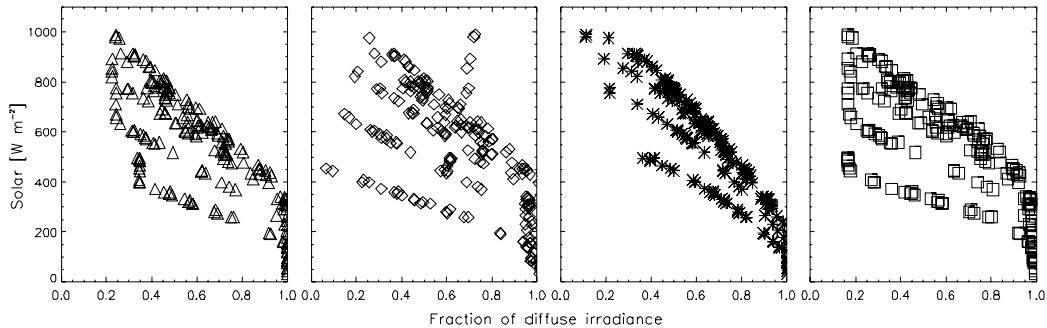
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Figure 8 - Different models for calculating the fraction of diffuse irradiance, (∇) Spitters *et al.* (1986), ($\Diamond$) Reindl *et al.* (1982), *Weiss & Norman (1985) and ($\square$) Erbs *et al.* (1981) model.
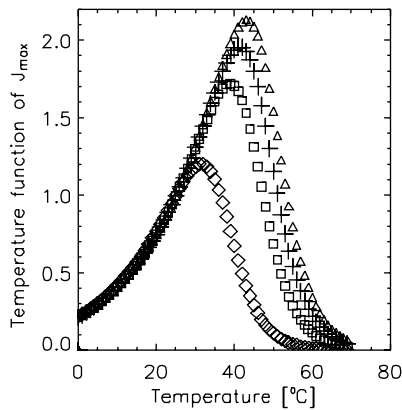

Figure 9 - Temperature function of J_{max} ($J_{max}/J_{max,25}$ in equation 8) evaluated under different S_J.

- ($\Diamond$) S_J from Carswell *et al.* (2000), S_J=710. J mol^{-1}K^{-1}, optimum temperature= 32 ^{o}C
- ($\square$) S_J fitted for sun / shade, S_J = 693.124 J mol^{-1}K^{-1}, optimum temperature= 39 °C
- (+) S_J fitted for big leaf, S_J=687.392 J mol^{-1}K^{-1}, optimum temperature= 41 °C
- (∇) S_J from Lloyd *et al.* (1995), S_J = 683.6 J mol^{-1}K^{-1}, optimum temperature= 43 ^{o}C

different heights ranges from 1.74 to 2.82. Our estimated value for the canopy was 1.9. Other measurements of leaf photosynthesis in the tropics have reported ratios ranging from (1.08 to 2.24) (Meir, 1996) for a secondary rain forest in Cameroon, Africa and a range of 1.8-2.25 for an eastern Amazonian forest (Vale R., pers.comm.). Leaf respiration is one of the three parameters that is fitted to the leaf gas exchange measurements and presents the highest standard deviations (6.34 - 57.57% of the mean value, See Figure 10). J_{max} and V_{cmax} also had a range standard deviations (of 5.5 to 13.78% and 3.15 to 23.29 % of the mean value respectively) in the Carswell *et al.* (2000) data set. The inclusion of these deviations adds also uncertainties to the estimations of canopy V_{max}, J_{max} and R_C.

However, it is also possible that there are physiological differences between the forest at sites C14 and K34 that can explain the high difference of nitrogen concentration in the leaves. Araújo *et al.* (2000) did a comparison of eddy covariance measurements of CO_2 fluxes using data from the tower here used C14 and the 11 km away second tower K34. From that study, "clear differences between the towers appear in the intensities of the peak daytime sink-strength and total daily Net Ecosystem Exchange, which are higher for the C14 forest". They recognize the possibility of physiological differences in the forest sites to explain the observed difference in CO_2 uptake.

Even though the sun/shade model needed some reparametrisation to fit the eddy covariance "recalculated data set" (mainly 10% decrease in top V_{max} and R_C and J_{max}/V_{max} ratio decrease from 2.6 to 1.92), the result obtained here with this scaling-modelling exercise supports this method of calculation of eddy covariance measurements which has yet to be widely adopted. Moreover, when comparing sun and shade to the normal data set (uncorrected for low frequency motions), a severe 50% overestimation was obtained when the leaf level parameters of Carswell *et al.* (2000) were employed without modification. In order to fit these "uncorrected" observations V_{max} at the top of the canopy needed to be decreased by 33% (results not shown).

A second important limitation in this study is the uncertainty involved in the data we are using to validate the models and to calibrate in the case of the big leaf model. Fitting a model to any data restricts the model results to the goodness of the data, in this case the eddy covariance and the respiration data. Eddy covariance technique works best under non-intermittent atmospheric conditions and over homogeneous vegetation located in flat terrain (Wesely & Hart, 1985). Eddy correlation measurements over rain forests are more complicated than over flat vegetation due to the presence of uneven tall canopies. This heterogeneity results in high roughness lengths (202-220 cm for Amazon rain forest) (Shuttleworth *et al.*, 1989) that creates large turbulent eddies that facilitate the transfer of heat and momentum between the vegetation and the atmosphere. For heights of 5- 10 m, Wesely
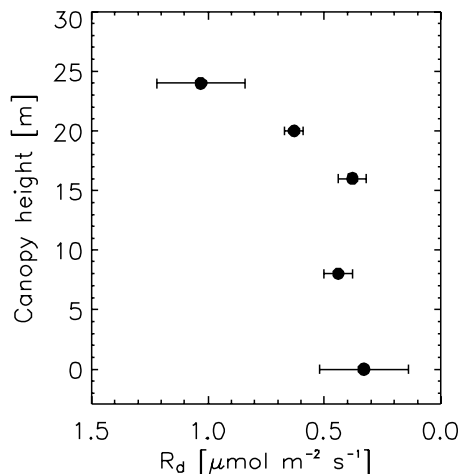
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Figure 10 - Vertical profile of leaf dark respiration (Carswell *et al*., 2000).

& Hart (1985) reported a natural turbulence variability of 10-20%. Contributing errors in day time measurements include 2-3% for calibration of infrared gas analysers, 2% associated with time lags between velocity and scalar sensors and around 7% associated with the covariance measurement (Baldocchi, 2003).

As mentioned in the methods section, in order to avoid the night time uncertainties with CO_2 flux measurements by eddy covariance, we used data that comes from measurements of the different contributions to ecosystem respiration. The soil respiration data used here was collected during October – November 2000, a year that had higher precipitation than in 1995. We recognize the possibility of higher respiration fluxes during the period covered here.

CONCLUSION

We have shown the difficulties of scaling from the leaf up to the canopy level and the importance of having representative data to parameterise canopy gas exchange models. In order to be close to the data used to validate the sun/shade model, it was necessary to empirically reduce the estimated canopy V_{max} and R_C at the top by 10% and the ratio J_{max}/V_{max} from 2.6 to 1.9. Numerical fitting techniques also showed that parameters like S_J and apparent quantum yield could be modified within reasonable ranges in order to get a better model performance.

When comparing the performance of both model types it is possible to conclude that numerically (in terms of goodness of fit) and qualitatively (in terms of residual response to different environmental variables), the sun/shade model was superior. Although the big leaf model provided a nice average curve of the canopy light response, compared to the sun/shade model, the overall fit was inferior and it failed to respond to variations in diffuse fraction, also showing skewed residual responses for both temperature and VPD. The separate treatment of sun and shade leaves in combination with the separation of the incoming light into direct beam and diffuse make sun/shade a strong modelling tool that catches part of the variability measured by eddy covariance. We have, however, also shown here the importance of good estimates of diffuse irradiance and the need of its measurement for the Amazon region for such models to provide any sort of high fidelity output. Despite some difficulties of up scaling and adequate parameterisation of the model, the sun/shade approach may provide a simple and effective tool for modelling photosynthetic carbon uptake that can be easily included in global vegetation models.

ACKNOWLEDGMENTS

LITERATURE CITED

Alados, I.; Alados-Arboledas, L. 1999. Direct and diffuse photosynthetically active radiation: measurements and modelling. *Agricultural and Forest Meteorology*, 93: 27-38.

Araújo, A.C.; Nobre, A.D.; Kruijt, B.; Elbers, J.A.; Dallarosa, R.; Stefani, P.; von Randow, C.; Manzi, A.O.; Culf, A.D.; Gash, J.H.C.; Valentini, R.; Kabat, P. 2002. Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: The Manaus LBA site. *Journal of Geophysical Research-Atmospheres*, 107(D20), 8090, doi:10.1029/2001JD000676.

Atkin, O.K.; Zhang, Q.S.; Wiskich, J.T. 2002. Effect of temperature on rates of alternative and cytochrome pathway respiration and their relationship with the redox poise of the quinone pool. *Plant Physiology*, 128: 212-222.

Aubinet, M.; Heinesch, B.; Longdoz, B. 2002. Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability. *Global Change Biology*, 8(11): 1053-1071.

Baldocchi, D.D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology*, 9: 479-492.

Bravard, S.; Righi, D. 1989. Geochemical Differences in an Oxisol Spodosol Toposequence of Amazonia, Brazil. *Geoderma*, 44: 29-42.

Carswell, F.E.; Meir, P.; Wandelli, E.V.; Bonates, L.C.M.; Kruijt, B.; Barbosa, E.M.; Nobre, A.D.; Grace, J.; Jarvis, P.G. 2000. Photosynthetic capacity in a central Amazonian rain forest. *Tree Physiology*, 20: 179-186.

Chambers, J.Q.; dos Santos, J.; Ribeiro, R.J.; Higuchi, N. 2001a. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecology and Management*, 152(1-3): 73-84.

Chambers, J.Q.; Schimel, J.P.; Nobre, A.D. 2001b. Respiration from coarse wood litter in central Amazon forests. *Biogeochemistry*, 52: 115-131.

ACTA AMAZONICA

MODELLING AMAZONIAN FOREST EDDY COVARIANCE DATA: A COMPARISON OF BIG LEAF VERSUS SUN/SHADE MODELS FOR THE C-14 TOWER AT MANAUS I. CANOPY PHOTOSYNTHESIS

Chambers, J.; Tribuzy, E.S.; Toledo, L.C.; Crispim, B.F.; Higuchi, N.; dos Santos, J.; Araújo, A.C.; Kruijt, B.; Nobre, A.; Trumbore, S. 2004. Respiration from a Tropical Forest Ecosystem: Partitioning of sources and low carbon use efficiency. *Ecological Applications*, 14(4):S72-S88

Costa, R.; Luizao, F.; Silva, L.; Quintino, R.; Monteiro, T. this issue. Variation of carbon and nitrogen cycling processes along a topographic gradient in a central amazonian forest. *Acta Amazonica.(in review)*

Cowan, I.R.; Farquhar, G.D. 1977. Stomatal function in relation to leaf metabolism and environment. *Symposium of the Society for Experimental Biology*,(31): 471-505.

de Oliveira, A.A.; Daly, D.C. 1999. Geographic distribution of tree species occurring in the region of Manaus, Brazil: implications for regional diversity and conservation. *Biodiversity and Conservation*, 8: 1245-1259.

de Pury, D.G.G.; Farquhar, G.D. 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell and Environment*, 20: 537-557.

Erbs, D.G.; Klein, S.A.; Duffie, J.A. 1982. Estimation of the Diffuse-Radiation Fraction for Hourly, Daily and Monthly-Average Global Radiation. *Solar Energy*, 28: 293-302.

Farquhar, G.D.; von Caemmerer, S. 1982. Modelling of photosynthetic response to environmental conditions. *In:* Lange, O.L.; Nobel, P.S.; Osmond, C.B.; Ziegler, H. (Eds). *Enciclopedia of Plant physiology. Vol.*12B. Springer-Verlag, Berlin. p.549-587.

Finnigan, J.J.; Clement, R.; Malhi, Y.; Leuning, R.; Cleugh, H.A. 2003. A re-evaluation of long-term flux measurement techniques - Part I: Averaging and coordinate rotation. *Boundary-Layer Meteorology*, 107: 1-48.

Goudriaan, J. 1977. *Crop micrometeorology: A simulation study.* Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, 249p.

Grace, J.; Lloyd, J.; McIntyre, J.; Miranda, A.; Meir, P.; Miranda, H.; Moncrieff, J.; Massheder, J.; Wright, I.; Gash, J. 1995. Fluxes of Carbon-Dioxide and Water-Vapor over an Undisturbed Tropical Forest in South-West Amazonia. *Global Change Biology*, 1: 1-12.

Grace, J.; Mahli, Y.; Higuchi, N.; Meir, P. 2001. Productivity and carbon fluxes of tropical rain forest. *In:* J.Roy, H.A.M. (Ed). *Global Terrestrial Productivity.* Academic Press, San Diego.

Gu, L.H.; Baldocchi, D.; Verma, S.B.; Black, T.A.; Vesala, T.; Falge, E.M.; Dowty, P.R. 2002. Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of Geophysical Research-Atmospheres*, 107(D5-D6), 4050,doi:10.1029/2001JD001242.

Law, B.E.; Falge, E.; Gu, L.; Baldocchi, D.D.; Bakwin, P.; Berbigier, P.; Davis, K.; Dolman, A.J.; Falk, M.; Fuentes, J.D.; Goldstein, A.; Granier, A.; Grelle, A.; Hollinger, D.; Janssens, I.A.; Jarvis, P.; Jensen, N.O.; Katul, G.; Mahli, Y.; Matteucci, G.; Meyers, T.; Monson, R.; Munger, W.; Oechel, W.; Olson, R.; Pilegaard, K.; Paw, K.T.; Thorgeirsson, H.; Valentini, R.; Verma, S.;

Vesala, T.; Wilson, K.; Wofsy, S. 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology*, 113(1-4): 97-120.

Leopoldo, P.R.; Franken, W.; Salati, E.; Ribeiro, M.N. 1987. Towards a Water-Balance in the Central Amazonian Region. *Experientia*, 43: 222-233.

Lloyd, J.; Grace, J.; Miranda, A.C.; Meir, P.; Wong, S.C.; Miranda, B.S.; Wright, I.R.; Gash, J.H.C.; McIntyre, J. 1995. A Simple Calibrated Model of Amazon Rain-Forest Productivity Based on Leaf Biochemical-Properties. *Plant Cell and Environment*, 18(10): 1129-1145.

Malhi, Y.; Nobre, A.D.; Grace, J.; Kruijt, B.; Pereira, M.G.P.; Culf, A.; Scott, S. 1998. Carbon dioxide transfer over a Central Amazonian rain forest. *Journal of Geophysical Research-Atmospheres*, 103(D24): 31593-31612.

Malhi, Y.; Pegoraro, E.; Nobre, A.D.; Pereira, M.G.P.; Grace, J.; Culf, A.D.; Clement, R. 2002. Energy and water dynamics of a central Amazonian rain forest. *Journal of Geophysical Research-Atmospheres*, 107(D20),8061,doi:10.1029/2001JD000623.

Massman, W.J.; Lee, X. 2002. Eddy covariance flux corrections and uncertainties in long-term studies of carbon and energy exchanges. *Agricultural and Forest Meteorology*, 113(1-4): 121-144.

Medlyn, B., D. Barrett, J. Landsberg, P. Sands, and R. Clement. 2003. Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches for regional scales. *Functional Plant Biology* 30 (2):153-169.

Meir, P. 1996. *The exchange of carbon dioxide in tropical rainforest.* Doctor of Philosophy, Institute of Ecology and Resource Management/ The University of Edinburgh, Edinburgh. 208p.

Meir, P.; Grace, J.; Miranda, A.C. 2000. Photographic method to measure the vertical distribution of leaf area density in forests. *Agricultural and Forest Meteorology*, 102(2-3): 105-111.

Moncrieff, J.B.; Massheder, J.M.; deBruin, H.; Elbers, J.; Friborg, T.; Heusinkveld, B.; Kabat, P.; Scott, S.; Soegaard, H.; Verhoef, A. 1997. A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology*, 189(1-4): 589-611.

Nelder, J.A.; Mead, R. 1965. A Simplex-Method for Function Minimization. *Computer Journal*, 7: 308-313.

Öquist, G.; Anderson, J.M.; McCaffery, S.; Chow, W.S. 1992. Mechanistic Differences in Photoinhibition of Sun and Shade Plants. *Planta*, 188: 422-431.

Phillips, O.L.; Malhi, Y.; Higuchi, N.; Laurance, W.F.; Nunez, P.V.; Vasquez, R.M.; Laurance, S.G.; Ferreira, L.V.; Stern, M.; Brown, S.; Grace, J. 1998. Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science*, 282(5388): 439-442.

Reindl, D.T.; Beckman, W.A.; Duffie, J.A. 1990. Diffuse Fraction Correlations. *Solar Energy*, 45: 1-7.

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Rödenbeck, C.; Houweling, S.; Gloor, M.; Heimann, M. 2003. CO_2 flux history 1982-2001 inferred from atmospheric data using a global inversion of atmospheric transport. *Atmospheric Chemistry and Physics,* 3:1919-1964

Roderick, M.L.; Farquhar, G.D.; Berry, S.L.; Noble, I.R. 2001. On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia*, 129: 21-30.

Shuttleworth, W.J.; Dickinson, R.E. 1989. Modeling Tropical Deforestation - a Study of Gcm Land-Surface Parametrizations - Comment. *Quarterly Journal of the Royal Meteorological Society*, 115(489): 1177-1179.

Spitters, C.J.T.; Toussaint, H.; Goudriaan, J. 1986. Separating the Diffuse and Direct Component of Global Radiation and Its Implications for Modeling Canopy Photosynthesis .1. Components of Incoming Radiation. *Agricultural and Forest Meteorology*, 38(1-3): 217-229.

Taylor, J.A.; Lloyd, J. 1992. Sources and sinks of atmospheric CO_2. *Australian Journal of Botany*, 40(4-5): 407-418.

Tian, H.Q.; Melillo, J.M.; Kicklighter, D.W.; McGuire, A.D.; Helfrich, J.V.K., III; Moore, B., III; Vörösmarty, C.J. 1998. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature*, 396(6712): 664-667.

Weiss, A.; Norman, J.M. 1985. Partitioning solar radiation into direct and diffuse, visible and near-infrared components. *Agricultural and Forest Meteorology*, 34(2-3): 205-213.

Wesely, M.L.; Hart, R.L. 1985. Variability of short term eddy-correlation estimates of mass exchange. *In:* Hutchison, B.A.; Hicks, B.B. (Eds). *The Forest-Atmosphere Interaction.* D.Reidel Publishing Company, Dordrecht/Boston/Lancaster. p.591-612.