

# Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis

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## ABSTRACT

Tropical rain forests account for a significant fraction of global net primary productivity, and are important latent energy (LE) sources, affecting extra-tropical atmospheric circulation. The influence of environmental factors on these fluxes has until recently been poorly understood, largely due to a paucity of data, but in recent years the amount of available data has been increased greatly by use of eddy covariance techniques. In this paper we examine the factors that control daily and seasonal carbon (C) and LE fluxes, by comparing a detailed model of the soil–plant–atmosphere continuum against a unique long-term data-set collected using eddy covariance at an undisturbed rain forest site north of Manaus, Brazil. Our initial application of the model was parametrized with simple measurements of canopy structure, and driven with local meteorological data. It made effective predictions of C and LE exchange during the wet season, but dry season predictions were overestimates in both cases. Sensitivity analyses indicated that the best explanation for this behaviour was a seasonal change in soil and root hydraulic resistances ( $R_b$ ). An optimization routine was then used to estimate the increase in  $R_b$  during the dry season that would be required to explain the reduced dry season fluxes. The local soil, a clay latosol, is typical of much of Amazônia, having very low available water and low hydraulic conductivity. We conclude that an increase in soil–root hydraulic resistance in the dry season introduces a significant seasonal cycle to carbon and water fluxes from this tropical forest. Furthermore, our model structure appears to be an effective tool for regional and temporal scaling of C and LE fluxes, with primary data requirements being regional and temporal information on meteorology, leaf area index (LAI), foliar N, critical leaf water potentials, and plant and soil hydraulic characteristics.

**Keywords:** Amazon basin; biosphere – atmosphere interactions; eddy covariance; hydraulic resistance; photosynthesis; soil–plant–atmosphere model.

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## INTRODUCTION

Among the most important components of global biogeochemical cycling are the processes that mediate the fluxes of C, water and energy between biosphere and atmosphere. A major difficulty in improving our understanding of the functioning of the biosphere–atmosphere system lies in the problem of effectively scaling measurements of the key processes, such as photosynthesis and evapotranspiration, to generate regional estimates of these fluxes (Ehleringer & Field 1993). Generally, the ability to make measurements of the various components of these coupled systems is strictly limited in some dimension of space and time, according to particular financial and technical constraints. Often it is only possible to collect data at a limited number of sites and/or for restricted periods. Yet, to understand the regional and global issues of present concern, there is a requirement for detailed understanding of processes as they occur over vast areas and long time scales (including the future).

Tropical rain forests are among the most important biomes in terms of annual C turnover and evapotranspiration. Although tropical rain forests extend over only about 8% of the global land surface ( $\approx 12 \times 10^6 \text{ km}^2$ ; Whittaker & Likens 1973), they contain about 40% of the biomass (240 Gt C; Skole & Tucker 1993) and account for about 50% of the annual net primary production of the biosphere ( $\approx 30 \text{ Gt C a}^{-1}$ ; Grace *et al.*, in press). Recent indications are that these ecosystems may also be a significant net sink for C (Grace *et al.* 1995b). Tropical forests are also important latent energy sources, with significant impacts on local climate. Studies investigating the effects of tropical deforestation have shown that resulting alterations in land surface characteristics are likely to increase soil and air temperatures, reduce evapotranspiration and increase runoff (Dickinson & Henderson-Sellers 1988; Nobre, Sellers & Shukla 1991). Latent energy fluxes from tropical forests have also been shown to have significant impacts on extra-tropical atmospheric circulation patterns (Paegle 1987).

The largest continuous area of tropical rain forest in the world is located in the Amazon basin, covering an area of over 4 million  $\text{km}^2$ , almost one half of the earth's undisturbed tropical evergreen forest. There has been a long history of vegetation–atmosphere research in this region. From 1983 to 1985, the Amazon Region Micrometeorological Experiment (ARME) was undertaken in the

primary rain forest in Reserva Ducke near Manaus (Shuttleworth *et al.* 1984; Shuttleworth 1988). Following this, the Anglo-Brazilian Amazonian Climate Observation Study (ABRACOS) undertook a series of campaigns looking at ecosystem–atmosphere interactions at three sites within the Amazon basin, between 1990 and 1994; much of this research is detailed in Gash *et al.* (1996). Other unconnected studies have provided information on both ecosystem level fluxes (Fan *et al.* 1990; Fitzjarrald *et al.* 1990), and leaf-level ecophysiology in Amazônia (Reich *et al.* 1994; Meinzer *et al.* 1995).

The ARME and ABRACOS studies have described the major environmental controls on tropical canopy gas and energy exchange. These controls are physical (e.g. temperature, irradiance, soil moisture), chemical (e.g. photosynthetic capacity, enzyme reaction rates) and biological (e.g. leaf area, stomatal opening). But quantifying the interactions between these controls, and the links between C and energy exchange, is more complicated, and necessitates the use of mathematical models based on a mechanistic understanding of the coupled mechanisms of photosynthesis and transpiration. Once these models have been parametrized from leaf-level data, they can be tested against independent whole canopy process measurements. Once validated, the models can be used to generate regional and long-term predictions of gas exchange. A vital component of model testing is the identification of where knowledge is most limited; i.e. under what conditions do model predictions break down. In these instances the model can then be used to explore new hypotheses and set questions that can influence the next generation of experimental studies. In summary, a model should serve two functions; firstly, it aids interpretation of complex data-sets, identifies weaknesses in understanding and allows rapid hypothesis testing. Secondly, it provides a tool for scaling up the knowledge derived in experimental studies, and can serve as a link from these to remotely sensed data sets.

As part of the ABRACOS study, 55 d of ecosystem gas exchange data were gathered by eddy covariance at a site in Rondônia, south-west Amazônia (Grace *et al.* 1995b). The data suggested similar rates of C uptake during dry and wet seasons, a result that agreed with other, leaf-level ABRACOS studies, that did not identify distinct seasonality in gas exchange (McWilliam *et al.* 1996; Roberts *et al.* 1996; Sá, Costa & Roberts 1996). Lloyd *et al.* (1995) developed a simple, big-leaf calibrated model of C exchange using the Rondônia gas exchange data. This model used an empirical stomatal model connected to a biochemical photosynthesis model (Farquhar & von Caemmerer 1982) to predict an annual gross primary productivity (GPP) of 2450 gC m<sup>-2</sup> a<sup>-1</sup>, with very little seasonality.

In an extension of the ABRACOS study, a long-term experiment in central Amazônia has recently provided the first long-term data-set for gas exchange in a tropical rain forest, using eddy covariance methods (Malhi *et al.*, in press). The importance of these data is that they describe the diurnal variations and seasonality of photosynthesis and transpiration over a period of 12 months. In contrast

with earlier studies, these data demonstrate a profound seasonality in water and C exchange.

We have used a new model of vegetation–atmosphere interactions (Williams *et al.* 1996) to investigate this ABRACOS data-set quantitatively. There are important differences (De Pury & Farquhar 1997) between the soil–plant–atmosphere (SPA) model we apply and models such as that used by Lloyd *et al.* (1995) in Rondônia. (1) The SPA model represents the canopy with multiple layers, separated into sunlit and shaded components, rather than as a ‘big leaf’ – the latter technique is problematic in that it does not generate truly scaled models, and tends to require empirical tuning. (2) The SPA model has a unique stomatal submodel whereby stomatal conductance operates to maximize C assimilation, while balancing atmospheric demand for water with plant–soil hydraulic supply. (3) The parameters for the SPA model are not derived from the eddy covariance data, so the latter can provide an independent test of model predictions. (4) The SPA model requires more detailed parameters, specifically those describing canopy structure, and plant–soil hydraulic properties.

## OBJECTIVES

Our intention in this paper is to test the hypotheses embodied in a detailed model of canopy processes (Williams *et al.* 1996) against the long-term data set collected at an undisturbed rain forest site during the Anglo-Brazilian Amazonian Climate Observation Study (ABRACOS). Our goals are to use this comparison to: (1) isolate the key variables that control C and water fluxes in this stand; (2) identify the nature and relative importance of the interactions between the controlling physical, chemical and biological factors; (3) investigate how these controls vary with seasonal cycles, and predict the magnitude of variation required to explain observed seasonality; (4) determine the weaknesses in our current understanding of tropical canopy gas exchange, and (5) set out a strategy for best employing our model to develop regional predictions of C and water exchange.

## METHODS

### The study site

The tower is located in a stand of virgin *terra firme* rain forest, in the Reserva Biológica do Cuieiras (a forest reserve belonging to Instituto Nacional de Pesquisas da Amazônia, used by the ABRACOS-Jacarex project). The stand is 60 km north of Manaus, in the state of Amazonas, Brazil (2°35′22″ S, 60°06′55″ W). The data reported here were collected over a 12 month period from 1 September 1995 (Project day 1, or PD 1) to 31 August 1996.

The soils at the site are deeply weathered yellow-clay latosols (oxisols), 3–8 m thick. The soils are acid, pH 4.3–5.0, nutrient poor, with a porosity range of 50–80% (Chauvel, Grimaldi & Tessier 1991). The sand and clay content is ≈ 10% and 80%, respectively (Sanchez

1989). Although the soils have a very high clay content, they exhibit a high hydraulic conductivity at and close to saturation because of the influence of macro- and large meso-pores in the top meter of the profile (Tomasella & Hodnett 1996). The parameter values derived at this site for the van Genuchten model (Van Genuchten 1980) are different from those found in the literature for clay soils in temperate zones (Tomasella & Hodnett 1996). The available water in these soils is very low, with a capacity of only about  $70 \text{ mm m}^{-1}$  in the upper metre of the profile (Correa 1984). Hodnett *et al.* (1996b) estimate that in local soils the water availability below 2 m depth is only  $30 \text{ mm m}^{-1}$ . Their calculations indicate that maximum water uptake below 2 m can reach over 250 mm in a year. This low soil water availability means that the vegetation has to extract water from the top 9 m of soil to satisfy its water requirements in the driest years. Water release curves at the forest site show very small changes in available moisture between  $-33$  and  $-1500 \text{ kPa}$  (Ranzani 1980; Tomasella & Hodnett 1996); soil only begins to free significant amounts of water below  $-4 \text{ MPa}$  (Tomasella & Hodnett 1996), well beyond the capability of plant extraction. Thus, most of the plant available water is released from the soil only at relatively high soil water potentials (above  $-70 \text{ kPa}$ ).

The climate of the site is typical equatorial, warm with frequent precipitation, with a short dry season running from July to October. Over the 12 month study period the estimated precipitation was 2088 mm. 1616 mm of rain, 77% of the annual total, fell during the 6 month period from 1 January 1996 to 30 June. There were 211 rain-days, and the longest rain-free interval was 30 d, running from 13 July 1996 to 11 August. Annual mean temperature was  $25.7 \text{ }^\circ\text{C}$ , with a maximum monthly mean value of  $27.3 \text{ }^\circ\text{C}$  in September 1995, and a minimum of  $24.9 \text{ }^\circ\text{C}$  in January. Daily maximum vapour pressure deficit (VPD) peaked in September ( $\approx 2.0 \text{ kPa}$ ), while values were lowest ( $\approx 1.0 \text{ kPa}$ ) from January through March. Monthly patterns of irradiance were related to cloud-cover and thus precipitation; the driest months (August and September) had the highest mean irradiance.

The forest canopy is  $\approx 30 \text{ m}$  tall, with occasional emergents to  $45 \text{ m}$ . The stand is comprised of a mix of species – in a nearby site there were 179 species per hectare with a diameter at breast height  $> 15 \text{ cm}$  (Prance, Rodrigues & Da Silva 1976) – mostly broad-leaved hardwoods with some palms in the understorey. Leaf area index (LAI;  $\text{m}^2$  one-sided leaf area  $\text{m}^{-2}$  ground area) values for nearby sites range from 5.7 to 6.6 (Klinge 1973; Klinge *et al.* 1975; Da Conceição 1977; Medina & Klinge 1982; McWilliam *et al.* 1993; Roberts *et al.* 1996). McWilliam *et al.* (1993) determined the vertical stratification of leaf area, showing a peak leaf area density at around 15–20 m above ground-level, with lowest values at around 10 m and lower. Above-ground biomass density in nearby stands is 300–400 t DW  $\text{ha}^{-1}$  (Klinge *et al.* 1975). Past human disturbance in this area is very unlikely, as the area was only made accessible by road in the 1970s, and infertile plateau soils were not usually farmed by indigenous peoples.

Foliage samples were obtained at the site to determine nitrogen (N) concentration, a key determinant of leaf metabolic capacity (Harley *et al.* 1992). The data showed that foliar N concentrations varied from 1.5 to  $4.0 \text{ g m}^{-2}$  leaf area (Meir *et al.*, University of Edinburgh, manuscript in preparation). These values are around 50% higher than those measured in Rondônia (Meir 1996) and in Venezuela (Reich & Walters 1994; Reich *et al.* 1994). Using a vertical leaf area profile from a nearby site (McWilliam *et al.* 1993), we estimated that total canopy N was  $\approx 16 \text{ g N m}^{-2}$  ground area.

### Eddy covariance measurements

The technique of eddy covariance determines the vertical flux of  $\text{CO}_2/\text{H}_2\text{O}$  by calculating the covariance between fluctuations in vertical wind velocity and  $\text{CO}_2/\text{H}_2\text{O}$  concentration over all frequencies (Moncrieff *et al.* 1997). The 'EdiSol' eddy covariance system, described by Moncrieff *et al.* (1997), was installed at the site in mid-October 1995. The system was mounted on a 5 m pole attached to a 41.5 m tower (of 6 m cross-section). A sonic anemometer (Solent, Gill Instruments, Lymington, UK) recorded wind velocity, and a Li-Cor 6262 IRGA (Li-Cor, Lincoln, NE, USA) determined the concentrations of  $\text{CO}_2$  and water vapour. Data were stored on a personal computer located on the tower and were analysed using EdiSol software (Moncrieff *et al.* 1997). The storage of  $\text{CO}_2$  within the canopy was monitored using a six-level profile sampling system (sampling at heights from 46.5 to 1.0 m). A weather station mounted on the tower recorded complete meteorological data with no temporal discontinuity. The flux instruments were prone to occasional failure; data were available for 54% of the time during the full annual cycle discussed in this paper. A more detailed description of the data collection, results and analysis can be found in a related paper (Malhi *et al.*, in press).

### Field results

A detailed description of the eddy covariance measurements is presented in a companion paper (Malhi *et al.*, in press). For C fluxes, net ecosystem productivity (NEP) is the net exchange of C between the biota (autotrophic and heterotrophic) and the atmosphere, with a positive flux representing ecosystem net C uptake. At the study site daily NEP averaged  $\approx 1 \text{ g C m}^{-2} \text{ d}^{-1}$ , but it ranged from  $-4$  to  $+4 \text{ g C m}^{-2} \text{ d}^{-1}$ . Soil respiration did not vary greatly over the diurnal cycle, and thus photosynthetic rates determined the bulk of the diurnal variation. Average night-time NEP was  $-6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and day-time NEP typically reached peak values of  $15\text{--}20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Note, for comparison, that  $1 \mu\text{mol m}^{-2} \text{ s}^{-1}$  scales to  $\approx 1 \text{ g C m}^{-2} \text{ d}^{-1}$ . The observed magnitudes and diurnal patterns were similar to those reported in other Amazonian studies (Fan *et al.* 1990; Grace *et al.* 1995a). Latent energy fluxes were approximately zero at night and reached values of up to  $400 \text{ W m}^{-2}$  during the day. Total daily fluxes ranged from

near zero up to  $11 \text{ MJ m}^{-2} \text{ d}^{-1}$  ( $\approx 4.5 \text{ mm d}^{-1}$ ). There was significant seasonal variation in flux rates, with increased evapotranspiration and photosynthetic uptake in the wet season. Peak daytime NEP varied from  $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the dry season, to  $25 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the wet season. Peak daytime latent energy fluxes ranged from  $250 \text{ W m}^{-2}$  in the dry season, to  $400 \text{ W m}^{-2}$  in the wet.

## THE SOIL-PLANT-ATMOSPHERE MODEL

The fine-scale, soil-plant-atmosphere canopy model (SPA; see Williams *et al.* 1996 for a full description) is a multilayer simulation of  $C_3$ -canopy processes. The model employs some well tested theoretical representations of eco-physiological processes, such as the Farquhar model of leaf-level photosynthesis (Farquhar & von Caemmerer 1982), and the Penman-Monteith equation to determine leaf-level transpiration (Jones 1992). These two processes are linked by a unique model of stomatal conductance ( $g_s$ ) that optimizes daily C gain per unit leaf N, within the limitations of canopy water storage and soil-to-canopy water transport. The model assumes that maximum carboxylation capacity ( $V_{\text{cmax}}$ ) and maximum electron transport rate ( $J_{\text{max}}$ ) are proportional to foliar N concentration (Harley *et al.* 1992). The model does not treat each species in the ecosystem individually, but instead treats the system as a single functional type, described by vertical variations in light absorbing area (LAI), photosynthetic capacity (foliar N), and plant hydraulic properties (see below).

The unique feature of this model lies in its treatment of stomatal opening, explicitly coupling water flows from soil to atmosphere with C fixation. The rate at which water can be supplied to the canopy is restricted by plant hydraulics and soil water availability. This rate ultimately limits transpiration because stomata will close at a threshold or critical minimum leaf water potential to prevent xylem cavitation (Jones 1992). However, forest canopies also use water accumulated and stored in the trees themselves during periods of low transpiration (e.g. at night) (Holbrook 1995). We argue that this stored water is used conservatively in the morning to delay the onset of stomatal closure in the early afternoon when atmospheric saturation deficits are high. By delaying stomatal closure, the canopy can maximize daily C assimilation. We assume that the photosynthetic apparatus itself is resistant to drought and variation in leaf water potential (Cornic *et al.* 1989; Epron & Dreyer 1993).

To ensure the efficient use of stored water in our model, stomatal conductance ( $g_s$ ) in each canopy layer is adjusted until the incremental increase in net C assimilation ( $A$ ) per incremental increase in  $g_s$  falls to a critical value of diminishing return. This adjustment of  $g_s$  is used until stored water in a layer is exhausted, at which point leaves must be irrigated by water transported from the soil (Meinzer & Grantz 1990). To avoid xylem cavitation,  $g_s$  is decreased until the transpiration rate ( $E$ ) from a canopy layer, as determined from the Penman-Monteith equation, equals the rate of water supply to that layer from the soil, so that leaf water potential ( $\Psi_1$ ) remains above a critical threshold

value (Sperry & Tyree 1988; Jones & Sutherland 1991). The change in  $\Psi_1$  is determined from a simple electrical analogue model that incorporates soil water potential ( $\Psi_s$ ), plant hydraulic resistance ( $R_p$ ), below-ground hydraulic resistances ( $R_b$ ) and plant capacitance ( $C$ ).

$$\Delta\Psi_1 = \Delta_t \frac{\Psi_s - \rho_w gh - E(R_b + R_p) - \Psi_1}{C(R_b + R_p)} \quad (1)$$

$\rho_w$  is the density of water,  $g$  is acceleration due to gravity and  $h$  is height above the reference plane; these terms defines the gravitational component of leaf water potential. Stomatal closure, and the consequent decrease in  $A$ , is most pronounced in the upper canopy where atmospheric saturation deficits and plant hydraulic resistances (which increase with layer height) tend to be highest. As the canopy grows taller, hydraulic limitations on GPP are expected to increase.

There are four key components in the description of the canopy hydraulic system:

**1** Plant hydraulic resistance ( $R_p$ ) is determined from xylem path length and the leaf specific conductivity ( $G_p$ ). In tropical trees  $G_p$  varies between  $40$  and  $550 \text{ mmol m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ , somewhat higher than temperate species (Tyree & Ewers 1996). The higher values are more typical of rapidly growing gap specialists. To reflect the dominance of canopy trees at our site, we used a value of  $100 \text{ mmol m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ , so that  $R_p$  for the canopy varied from  $0.01$  (canopy bottom,  $1 \text{ m}$ ) to  $0.3$  (canopy top,  $30 \text{ m}$ )  $\text{MPa s m}^2 \text{ mmol}^{-1}$ . We investigate the sensitivity of this parameter below.

**2** Below-ground hydraulic resistance ( $R_b$ ) can be subdivided into two parts. (a) the soil hydraulic resistance ( $R_s$ ), which determines the resistance of water flux from the soil to the root surface. This term is dependent on total root surface area, rooting density, and soil hydraulic conductivity (Newman 1969). Fine-root ( $< 1 \text{ mm}$ ) density in Amazonian soils has been determined at  $\approx 1000 \text{ m m}^{-3}$  (Nepstad *et al.* 1994) and hydraulic conductivity by Tomasella & Hodnett (1996). With water content close to field capacity,  $R_s$  is close to zero, and thus negligible. But  $R_s$  increases rapidly once reductions in soil water content reduce both the area of roots in contact with moisture and the soil hydraulic conductivity. (b) Fine root resistance ( $R_r$ ), which describes the flow from the surface of the fine roots to the xylem.  $R_r$  is likely to be at least as large as  $R_p$  (Tyree & Ewers 1996); in a potted apple tree Landsberg *et al.* (1976) measured  $R_s + R_r$  at  $4.7 \text{ MPa s m}^2 \text{ mmol}^{-1}$ .  $R_r$  was initially set to  $1.5 \text{ MPa s m}^2 \text{ mmol}^{-1}$  for each of the hydraulically independent canopy layers.

**3** The difference between the critical leaf water potential and soil water potential (MPa) describes the maximum tension that can be applied to the hydraulic system. Soil water potential can be determined from water release curves (Tomasella & Hodnett 1996). Threshold leaf water potentials were estimated from data describing daily minimum leaf water potentials for Brazilian canopy species; these typically vary between  $-2.4$  and  $-3.8 \text{ MPa}$  (Roberts *et al.* 1996).

4 Canopy capacitance describes the available water stored in the canopy foliage, which is set to 8000 mmol MPa<sup>-1</sup>m<sup>-2</sup> leaf area (Schulze *et al.* 1985).

The model has been modified to introduce a revised radiation subroutine that calculates sun-lit and shaded fractions of the foliage in each canopy layer (Norman 1981). Sun-lit fractions are lit by both incident direct and diffuse radiation, while the shaded fractions receive only diffuse radiation. For each layer the model calculates gas exchange separately for the sun-lit and shaded fractions, then sums the two values to give a prediction for the whole layer.

This fine-scale model provides an explicit link between canopy structure, soil properties (including soil moisture), atmospheric conditions and stomatal conductance. The submodels from which our fine-scale model is constructed (the Farquhar and Penman-Monteith models, Darcy's Law, a multilayer model of radiation absorption) are mechanistically based and should therefore be valid in tropical ecosystems. However, because of the uncertainty associated with some parameter values, especially those describing the hydraulic system, a sensitivity analysis was undertaken. This analysis also provides a useful basis for hypothesising how the ecosystem might respond to variation in climate, atmospheric composition, soil hydrology and vegetation structure.

## MODEL SENSITIVITY ANALYSIS

### Methods

Sensitivity analyses were performed to determine the relative importance of variation in the key factors controlling C and LE exchange in a typical tropical rain forest canopy. In a previous analysis with the SPA model (Williams *et al.* 1997) nine key factors were identified as critical in explaining global variations in daily total canopy photosynthesis (GPP). The most sensitive controls were identified as LAI and total daily irradiance. Next most important were average foliar N concentration, ambient CO<sub>2</sub> concentration and soil moisture stress. Still important, but least influential, were solar elevation and daylength, canopy height, average temperature and daily temperature range (which defined

maximum vapour pressure deficit). From this basis, we undertook a new analysis, examining in turn the importance of these factors specifically in tropical forest ecosystems. The analysis was expanded to include all those parameters describing the hydraulic system (leaf specific conductivity, canopy capacitance, and total below-ground hydraulic resistance), because the relevant site-specific data were unavailable. The descriptions of canopy structure and climate outlined above (see 'The study site') were used to generate a typical tropical rain forest environment, to provide both a baseline for comparison and the range over which the key factors involved in canopy processes were expected to vary in a tropical forest habitat (see Table 1). For the analyses, each factor was changed individually across its range, and model predictions were generated, while the other factors were held at their baseline values (indicated by arrows in Fig. 1). The resultant changes in predicted daily GPP and LE fluxes are plotted on the specific graphs associated with each factor (Fig. 1).

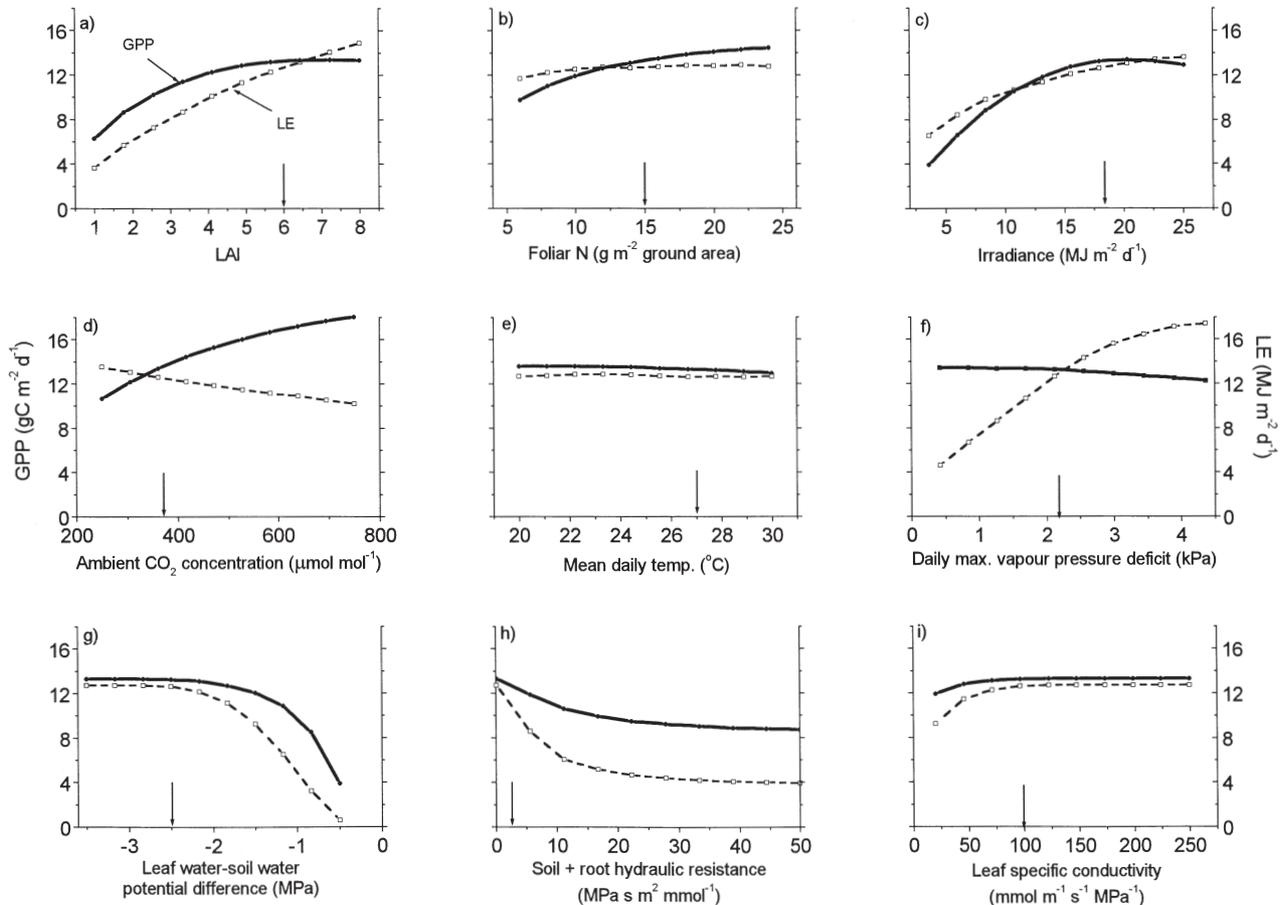
Where changing a variable would cause correlated variation in another driver, corrective steps were taken. For example, when varying LAI, instead of leaving average foliar N constant, which would result in total canopy N varying in proportion to LAI, total canopy N was held constant at 15 g m<sup>-2</sup> ground area, allowing average N concentration to vary. When mean temperature was increased, the daily temperature range was reduced, so that maximum daily VPD remained constant at 2.1 kPa throughout (assuming dew-point at daily minimum temperature). The assumptions involved in generating hourly meteorological values from daily means or totals are described in another paper (Williams *et al.* 1997).

## RESULTS AND DISCUSSION

Gross primary productivity (GPP) is most sensitive to those factors controlling the three component processes of photosynthesis – light reactions, dark reactions and CO<sub>2</sub> supply. The rate of the light reactions is determined by light absorption (LAI, Fig. 1a, and irradiance, Fig. 1c). The dark reactions are controlled by Rubisco concentration, related to foliar N (Fig. 1b). CO<sub>2</sub> supply is affected by ambient

Factor	Standard	Low	High
Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	6.0	1.0	8.0
Mean daily temperature (°C)	27.0	20.0	30.0
Daily temperature range (°C)	5.0	1.0	10
Mean foliar N concentration (gN m <sup>-2</sup> leaf area)	2.5	1.0	4.0
Cloudiness (fraction)	0.5	0.1	0.7
Ambient CO <sub>2</sub> concentration (μmol mol <sup>-1</sup> )	355	250	750
Leaf water–soil water potential difference (MPa)	-2.5	-0.5	-3.5
Canopy capacitance (mol MPa <sup>-1</sup> m <sup>-2</sup> leaf area)	8.0	1.0	15.0
Soil + root hydraulic resistance (MPa s m <sup>2</sup> mmol <sup>-1</sup> )	1.5	0.5	50.0
Leaf specific conductivity (mmol m <sup>-1</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	100.0	20.0	250.0

**Table 1.** The determinants of canopy processes: standard values for tropical rain forests, and their high and low values, as applied in a sensitivity analysis. Latitude was held constant at 2 °S and canopy height at 30 m. Temperature range = 0.5 × (daily maximum temperature – minimum temperature). Dew point is assumed at the daily minimum temperature; thus daily temperature range and mean temperature define the daily vapour pressure deficit. Total daily extra-terrestrial radiation is calculated from day of year and latitude (Gates 1980); the cloudiness factor determines what proportion of this potential radiation reaches the top of the canopy



**Figure 1.** One-dimensional sensitivity analyses for nine variables on daily gross primary productivity (GPP) and daily latent energy flux (LE). Arrows indicate the baseline values derived from Table 1. The units of irradiance ( $\text{MJ m}^{-2} \text{d}^{-1}$ ) can be converted to an estimate of photosynthetic photon flux density ( $\text{mol m}^{-2} \text{d}^{-1}$ ) by multiplying by the approximate conversion factor of  $2.3 \mu\text{mol}$  photosynthetically active radiation  $\text{MJ}^{-1}$ .

$\text{CO}_2$  concentration (Fig. 1d), and by factors affecting stomatal conductance. Stomata operate to balance atmospheric demand (VPD, Fig. 1f, and irradiance, Fig. 1c) with water supply (the hydraulic constraints, Fig. 1g, h, & i). The saturating response observed in several of the analyses occurs as the major constraint on C uptake shifts from one of the three component processes to another.

LE fluxes are highly responsive to the total canopy surface area (LAI, Fig. 1a), and to the variable components of the Penman-Monteith equation – radiation (Fig. 1c), VPD (Fig. 1f) and stomatal conductance. Because the canopy is relatively tall and thus aerodynamically rough, leaf boundary layer conductance is relatively large, and so also is the de-coupling coefficient (McNaughton & Jarvis 1983). The vegetation is well coupled to the environment and thus LE fluxes are more sensitive to variation in VPD (imposed evaporation) than to irradiance (equilibrium evaporation). (Note that we have not incorporated in our analysis the impact of changing LAI on the turbulence regime, which may damp the response of canopy LE fluxes to higher LAIs.) The stomata operate to match atmospheric demand for water, as determined by the Penman-Monteith equation, with hydraulic supply. Thus, when demand exceeds

supply, stomata are forced to close to reduce demand. However, the absolute quantity of water transpired rises with VPD (Fig. 1f) because the hydraulic system operates at maximum capacity for longer periods of the day and deeper into the canopy. Levels of water supply are reduced by both lower soil water potentials – or higher critical leaf water potentials – (Fig. 1g), and by increased resistance in the hydraulic pathway (Fig. 1h & i). In either case, as supply rates fall, stomata close to maintain leaf water potential above the critical value, and LE fluxes fall. As soil water potential falls towards the critical leaf water potential, LE fluxes decline at an increasing rate. LE fluxes also decline as hydraulic resistance rises, but at a decreasing rate after the initial fall. Even with high resistance there is plentiful soil water, and fluxes can be maintained down the water potential gradient. Sensitivity to canopy capacitance (not shown) and leaf specific conductivity (Fig. 1i) only occurs at the lower end of their expected ranges.

Several authors report that radiation-use efficiency is higher under cloudy skies than under clear skies (Hollinger *et al.* 1994; Baldocchi 1997). In a simple analysis with the base-line data set, with total incident radiation held constant, the diffuse fraction of total incident radiation was

varied from 0% to 100%. Across this range, daily GPP increased by 64%, and LE flux by 17%. With increased diffuse fraction, the canopy was more evenly illuminated, and because of the nonlinear response of photosynthesis to light, this led to more efficient C fixation. However, GPP remained very sensitive to the total incident radiation (Fig. 1c), so that if an increase in diffuse fraction was accompanied by a reduction in total irradiance, then the beneficial effects of increased diffuse radiation would be out-weighted by the overall reduction in irradiance. Foliar respiration was insensitive to changes in diffuse fraction, because alterations in leaf temperature were minor. At present an empirical relationship is used to estimate diffuse radiation fraction from the ratio of total above canopy radiation to calculated extra-terrestrial radiation for that day and latitude (Erbs, Klein & Duffie 1982). It would be advantageous to use locally derived data to describe the diffuse component.

We looked at two final issues in the sensitivity analysis. First, what were the differences in modelled behaviour between a uniform canopy leaf area density distribution, and the measured, more stratified distribution, with enhanced leaf area near the top and bottom of the profile? Only minor differences in daily model predictions were found. Second, what impact did leaf size have on modelled gas exchange, through effects on boundary layer resistance? Leaf size ranged from  $\approx 5$  to  $\approx 12$  cm at the field site (personal observation); we used a value of 8 cm in the model, with a constant windspeed of  $2 \text{ ms}^{-1}$ . Sensitivity analyses across the observed range indicated insignificant impacts on C uptake, but did predict daily LE flux alterations of  $\pm 4\%$ , higher fluxes occurring with smaller leaves.

## MODEL APPLICATION

### Model validation

The model generates predictions of gross canopy photosynthesis (i.e. gross canopy C uptake = GPP) and total canopy transpiration ( $T_{\text{can}}$ ). Although completely independent, the available validation data (net ecosystem C and latent energy exchange) do not directly match the model outputs. Predictions of total canopy transpiration ( $T_{\text{can}}$ ) are related to measured ecosystem water exchange ( $E_{\text{total}}$ ) by

$$T_{\text{can}} = E_{\text{total}} - E_{\text{soil}}, \quad (2)$$

where  $E_{\text{soil}}$  is soil evaporation, which is determined from a simple soil evaporation model (Choudhury & Monteith 1988). Predicted soil evaporation is generally an order of magnitude less than predicted transpiration rates in dense forest, so errors in the soil evaporation model are not of great concern. However, GPP (a positive flux) is equal to net ecosystem production (positive or negative) minus total ecosystem respiration (a negative flux). Thus, a reliable comparison requires respiration data for leaves, stems and soils. Chamber measurements undertaken in an undisturbed rain-forest in Rondônia, Brazil, estimated total ecosystem respiration at  $7.1 \mu\text{mol m}^{-2} \text{ ground area s}^{-1}$

(Meir 1996), close to the night-time measurements of NEP at Cuieiras. Chamber data derived in Rondônia (Meir 1996) was used to develop a relationship between foliar N concentration, leaf temperature and respiration (Ryan 1991; Williams *et al.* 1996). This submodel estimated that night-time whole-canopy leaf respiration was  $\approx 2.7 \mu\text{mol m}^{-2} \text{ ground area s}^{-1}$ . By difference the combined soil and stem respiration was  $4.4 \mu\text{mol m}^{-2} \text{ ground area s}^{-1}$ . There was little diurnal variation in soil temperatures, and thus in rates of soil respiration (which is the main component of nonfoliar respiration), so soil/stem respiration is held constant through the diurnal cycle and unchanged each season. The leaf respiration submodel was responsive to temperature, with a  $Q_{10}$  of 2.0. Although there is evidence that foliar dark respiration in the light may be significantly less than in the dark (Villar, Held & Merino 1994), this is not taken into account in this study. Were dark respiration to be less in the light, predictions of ecosystem C uptake would be slightly, but systematically, increased. The uncertainty in the effects of light suppression on respiration is of the same magnitude as net ecosystem production, and is thus of some importance; however, it is unlikely to affect the form of our predictions, or their relative seasonal variation.

In the results that follow the choice of validation data is dependent on the time-scale of interest. On the hourly time-scale, examining diurnal behaviour, the comparison is between modelled and predicted NEP (so modelled GPP is converted into a NEP estimate, see above). However, for daily predictions the comparison is between GPP (gross photosynthesis over 24 h), and so measured NEP is converted to GPP.

### Simulations

Hourly gas exchange at the Cuieiras study site was simulated over the course of 12 months. The initial comparison is with the independent data-sets derived from eddy covariance measurements over an intensively studied 45 d period from mid-October through early December 1995 (PD55–100). The results from this period are investigated in detail for two reasons; (a) during this period the profile sampling system was generating estimates of within-canopy C storage. While it is legitimate to estimate 24 h NEP purely using eddy covariance data (assuming that the summation runs from one well mixed period to another, e.g. 5 pm to 5 pm), the profile system is required to generate hourly  $\text{CO}_2$  exchange data, because of the significant within-canopy C storage term noted in Amazonian forests (Grace *et al.* 1995a); (b) this period covered the transition from the dry to wet season, and so allowed investigation of the issues related to the seasonality of canopy processes. We estimate that the dry season runs until PD60, and the wet season is underway by PD90; the days between 60 and 90 are a transition period.

Next, daily predictions of LE and GPP are compared with measured values across the whole year. Using these analyses, hypotheses are developed to explain discrepancies between

modelled and measured behaviours, and further model simulations are used to test and develop these ideas.

### Initial gas-exchange predictions

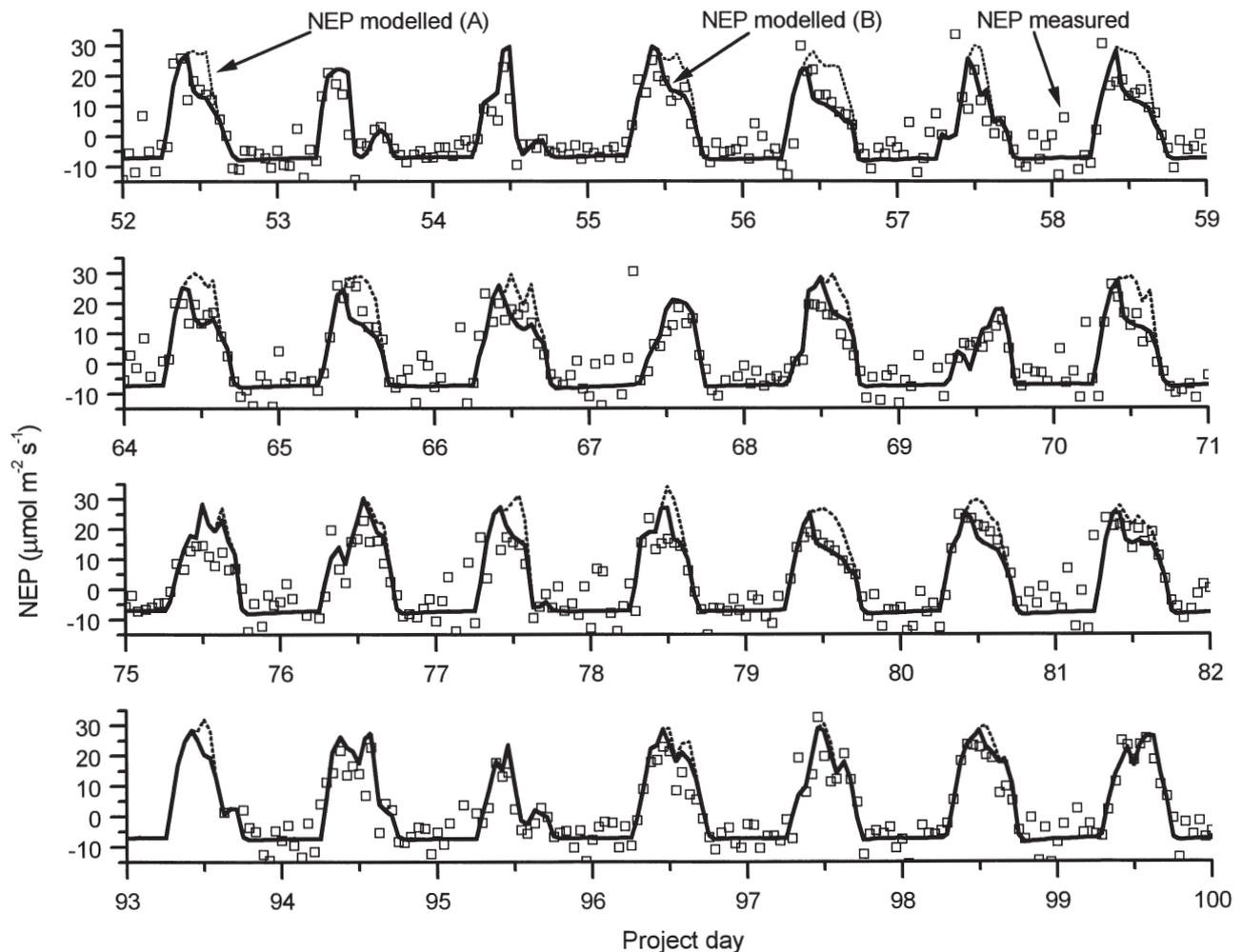
The initial simulations investigate the extent to which variation in canopy gas-exchange over a 12 month period can be explained purely by light, temperature and VPD. Thus, soil moisture is kept at field capacity throughout, and there is no variation in phenology (LAI = 5.7 throughout) or hydraulics (critical leaf water potential = -2.5 MPa).

#### Hourly predictions during the intensive period

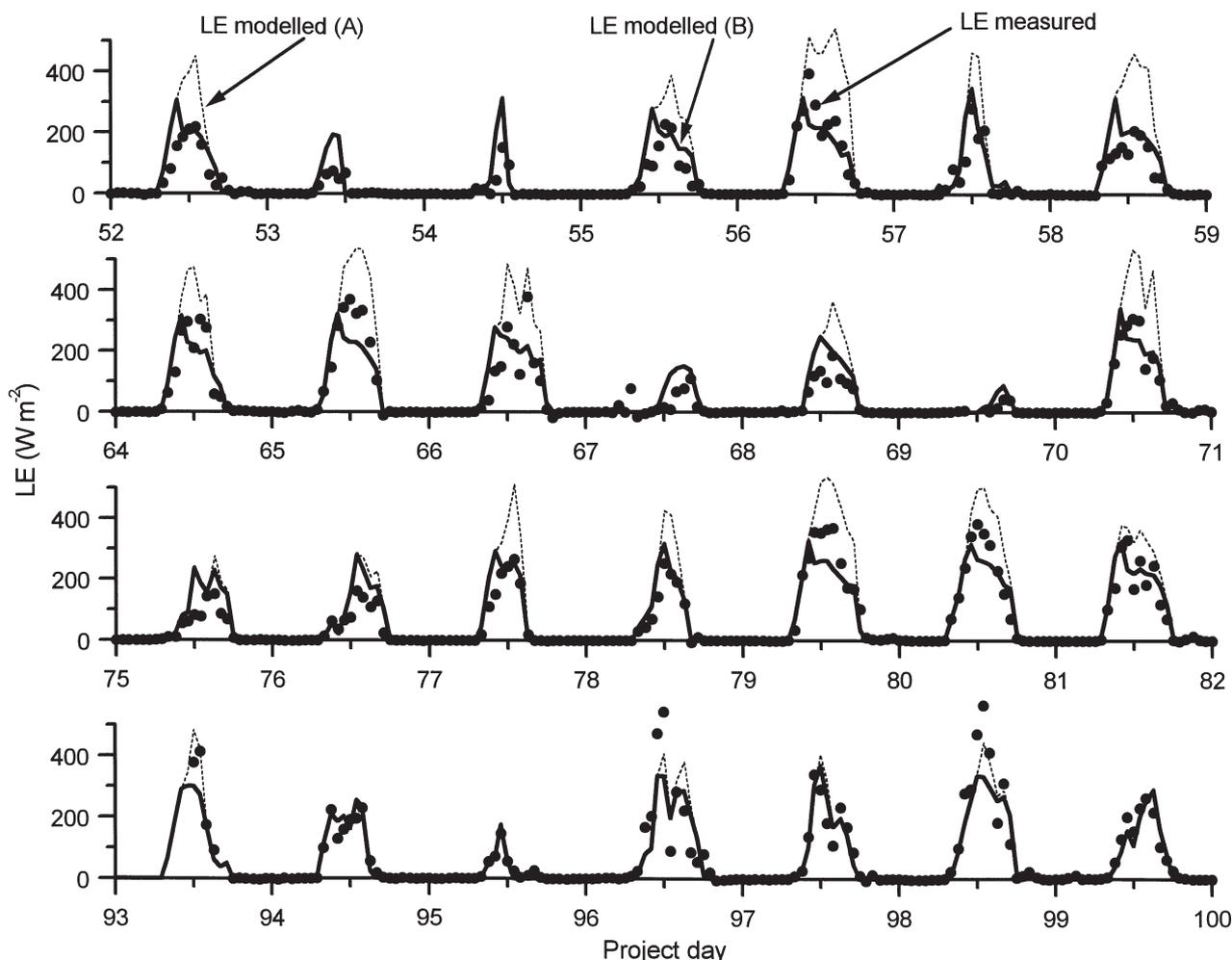
Predictions of hourly CO<sub>2</sub> fluxes show a systematic over-estimation of ecosystem sink strength through much of the period (Fig. 2, model A). The exceptions are those days with relatively low productivity (associated with cloudy days; e.g. PD 67), and days towards the end of the period,

after the transition from dry to wet seasons. Night-time simulated NEP matched the data more accurately throughout. Though the measurements did show a relatively high degree of scatter, the assumptions applied in generating predictions of respiration seem valid. However, estimates of photosynthesis are too high for much of the period – only in the final week do the predictions match the measured diurnal behaviour. While VPDs are higher during the dry season (reaching values of 2.5 kPa), the sensitivity analysis indicates that in well watered conditions these deficits are not large enough to have an important impact on C uptake. Thus, in the early part of the period we suggest that the full photosynthetic limitation cannot be explained purely by the impacts of meteorology.

Similarly, predicted latent energy fluxes are significantly larger than measured values in the early part of the intensive period, i.e. late in the dry season (Fig. 3, model A). The trend in the data was for maximum flux rates to increase over the period, from  $\approx 250 \text{ W m}^{-2}$  to



**Figure 2.** Modelled (lines) and measured (symbols) hourly net ecosystem production (NEP) during 28 d between project day (PD) 55, 28 October 1995, and PD 100, 9 December 1995. The predictions of two models are shown; models A (variable climate only) and B (variable below-ground hydraulic resistance).



**Figure 3.** Modelled (lines) and measured (symbols) hourly ecosystem latent energy flux (LE) during 28 d between project day (PD) 55, 28 October 1995, and PD 100, 9 December 1995. The predictions of two models are shown; models A (variable climate only) and B (variable below-ground hydraulic resistance).

$\approx 400 \text{ W m}^{-2}$ . In contrast, the model predicted a decrease in LE fluxes over time, because VPD, maximum temperature and irradiance all declined over the intensive period. As expected, the most significant impacts on daily LE fluxes were irradiance and VPD (Fig. 1c & f); on cloudy days when both these factors were at their minima, measured and modelled LE fluxes were reduced near to zero. Bowen ratios derived from the data declined over time; values in the early part of the period varied between 1.0 and 3.0, but fell to between 0.2 and 1.4 by the end. Model predictions were less variable; they remained between 0.5 and 1.4 throughout the period, and showed reasonable agreement with the data only during the last 15 d.

#### Daily predictions through the year

On the basis purely of meteorological variation, the model could explain 53% of the annual variability in daily gross C fixation. However, during the wet season (here set to PDs 100–200) our predictions were more accurate ( $r^2 = 0.76$ ).

Much of the day-to-day variability throughout the year was explained as a result of cloudiness, with overcast conditions reducing GPP by 50% or more. The highest gross photosynthetic uptake was measured between PDs 130 and 180, and lower mean values were recorded before PD 100 and after PD 250. Although the model predicted similar maximum rates ( $13\text{--}15 \text{ g C m}^{-2} \text{ d}^{-1}$ ), it did not predict any seasonality in fixation.

During the early wet season (PDs 100–200) the model could explain 89% of the variance in daily LE fluxes, though estimates were around 10% larger than measurements. Over the full year, however, predictions were less effective, and the overestimates were relatively larger ( $r^2 = 0.71$ ). Outside the wet season the model predicted relatively large LE fluxes, because these periods had high VPD and irradiance (Fig. 1c & f).

Assuming full soil moisture availability and unchanging phenology, the model could explain much of the variability in C and LE fluxes in the early wet season, in the period from PD 100–200. However, over the whole year the predictions

were less accurate. During the dry season, or transitions between seasons, there was a tendency to overpredict both hourly C uptake and total transpiration, and the model failed to predict the pronounced seasonality in C uptake identified in the data. The model predicted that changes in VPD would result in a significant increase in dry season latent energy flux (Fig. 1f), while the data did not support this.

There are several hypotheses to explain the observed seasonal responses.

**1** Variations in soil moisture availability. From the sensitivity analyses (Fig. 1g & h), a reduction in available soil moisture, or an increase in a component of total hydraulic resistance would reduce both LE fluxes and C sink strength, with a relatively stronger impact on the water fluxes.

**2** Variation in leaf area/foliar N. The sensitivity analyses indicate that this would have the required effects on gas exchange (Fig. 1a); however, while actual leaf fall data are lacking, the variation at the site is very unlikely to be such that LAI ever fell below 4.0 (Roberts *et al.* 1996), and this limits the potential explicatory power of a leaf area change.

**3** Impairment of photosynthetic machinery by drought stress. While this could explain reduced C uptake, it would not satisfactorily explain the impact on latent energy fluxes.

Thus, the sensitivity analyses suggest that hypothesis (1) is the most promising explanation [although effects from (2) and (3) cannot be ruled out completely], and the model was employed to test it further.

### The effects of seasonal variation in soil moisture availability

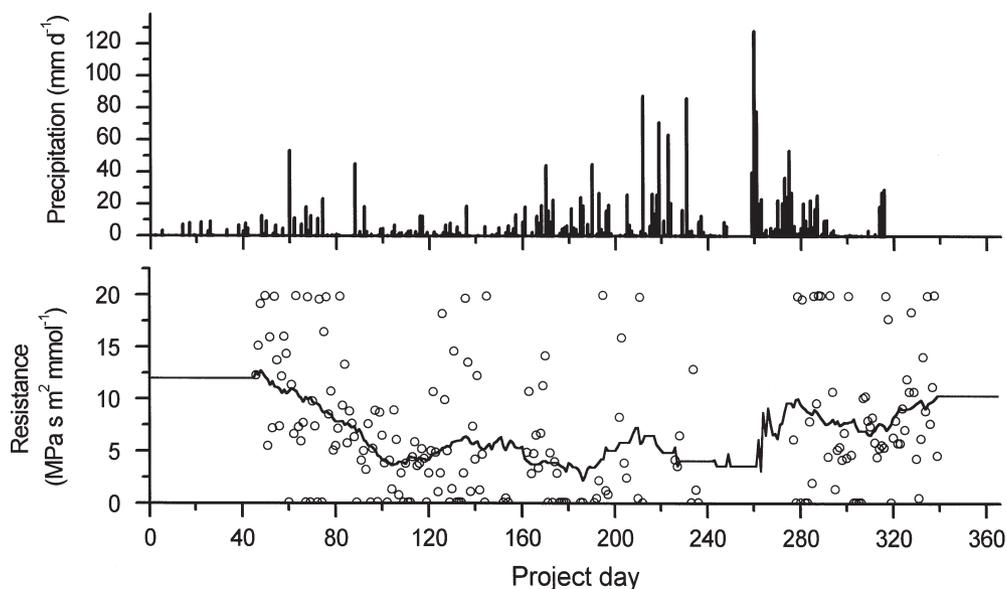
There are three ways in which the rate of plant water uptake is reduced as absolute soil moisture declines. First, the decline in moisture reduces the soil water potential, because the water remaining in the soil is held at more negative hydrostatic pressures. A decline in the potential gradient between soil and leaf will reduce total flux rate. Second, as soil moisture declines the total surface area of roots in contact with soil water is reduced, thus precipitating a loss in hydraulic continuity and an increase in the soil–root hydraulic resistance. And third, the decline in soil moisture reduces the hydraulic continuity of soil water itself, and this leads to a sharp increase in total soil–root hydraulic resistance.

Studies undertaken at the site at the end of the 1992 dry season indicated that predawn leaf water potential in dominant canopy trees was never much below  $-0.5$  MPa, even during the dry season (McWilliam *et al.* 1996), indicating that some portion of the fine roots remained in contact with freely available soil moisture throughout the year. This evidence argues against the likelihood of a soil water potential limitation on stomatal opening. Instead we argue that as water extraction exceeds recharge by precipitation, the successive drying of the soil profile effectively reduces the surface area of roots in contact with soil solution (Passioura 1988), interrupts soil hydraulic continuity and causes a precipitous decline in soil hydraulic conductivity

(Tomasella & Hodnett 1996). Thus, soil hydraulic resistance to water uptake increases as soil moisture declines, and this increase in resistance is the primary cause of seasonality in canopy gas exchange.

For present purposes it is difficult to distinguish between the two components of below-ground resistance, the soil and root hydraulic resistances, though we expect that soil resistance is most responsive to soil water depletion. The model was employed to determine the total below-ground hydraulic resistance ( $R_b = R_s + R_r$ ; MPa s m<sup>2</sup> mmol<sup>-1</sup>) that must be invoked to explain the observed pattern of latent energy fluxes through the intensive study period. A golden section search (Press *et al.* 1986) was used to vary the daily value of  $R_b$  within SPA, one day at a time, between values of 0 and 20 MPa s m<sup>2</sup> mmol<sup>-1</sup>. These bounds were chosen with reference to the sensitivity analysis (Fig. 1h); LE fluxes are not very responsive above an  $R_b$  of 20 MPa s m<sup>2</sup> mmol<sup>-1</sup>. The search routine sought to minimize the total sum-of-squares error between predicted and measured hourly daytime LE fluxes. The above-ground plant resistance calculation was left unchanged.

Our hypothesis was that over the course of the intensive period, as soil moisture was recharged, there would be a decline in  $R_b$ . The results of the fitting routine (Fig. 4) confirm this hypothesis in broad terms. While the day-to-day variability in predicted  $R_b$  is large in many cases, a 30-day adjacent smoothing indicates that  $R_b$  is  $\approx 12$  MPa s m<sup>2</sup> mmol<sup>-1</sup> at the end of the dry season (PD 45), and falls steadily to around 4 MPa s m<sup>2</sup> mmol<sup>-1</sup> by PD 100 (20 and 10 d smoothing indicate a similar low frequency trend, with greater degrees of high frequency variability). The resistance fluctuates around this value until PD 280, and then increases to 10 MPa s m<sup>2</sup> mmol<sup>-1</sup> by the end of the study year. Variation in  $R_b$  is responsive to the occurrence of precipitation events; for example, the initial decline in  $R_b$  is linked to the onset of the wet season (from PD 60–100), and the increase around PD 280 is correlated with a period of both less frequent and less intense rain (Fig. 4). On some days the fitting routine indicates that resistance was close to zero; these are generally days where atmospheric demand was low (low irradiance and VPD), so that hydraulic supply of water greatly exceeded demand. On other days estimated  $R_b$  approached the maximum bound of the fitting routine, and this was often at odds with the general pattern of change in  $R_b$ . The unusual feature of these days is that their Bowen ratios ranged between 1.5 and 6.0, whereas on most days values ranged between 0 and 2.0. However, while optimal fits required very high  $R_b$  for these days, we expected that the highly non-linear response of gas fluxes to declining  $R_b$  (Fig. 1h) would mean that a much smaller resistance term would still lead to a decline in LE flux, and effectively explain observed values. So, while fitting  $R_b$  was very effective in improving our predictions of daily LE fluxes ( $r^2 = 0.93$ , slope =  $0.93 \pm 0.02$ ), we deemed it a stronger test of our hypothesis to rerun the model using the 30 d smoothed average  $R_b$  (Fig. 4) to ascertain whether this improved our estimates of both hourly and daily gas exchange.



**Figure 4.** The lower panel shows the individual predictions of total below-ground hydraulic resistance as fitted by golden search over the project year (PD 1 = 1 September 1995). The line is the 30 d moving average. The upper panel shows daily precipitation over the same time period.

#### Hourly predictions, intensive period

Predictions of hourly latent energy fluxes were improved by the optimization (Fig. 3, model B), as expected. Once hydraulic resistance was allowed to vary, the over-predictions noted in the earlier runs diminished, and the diurnal character of transpiration was more effectively represented (PDs 56,58). In the early (dry season) part of the intensive study period, the increase in hydraulic resistance reduced predicted midday LE fluxes by up to 33% (Fig. 3, Model B).

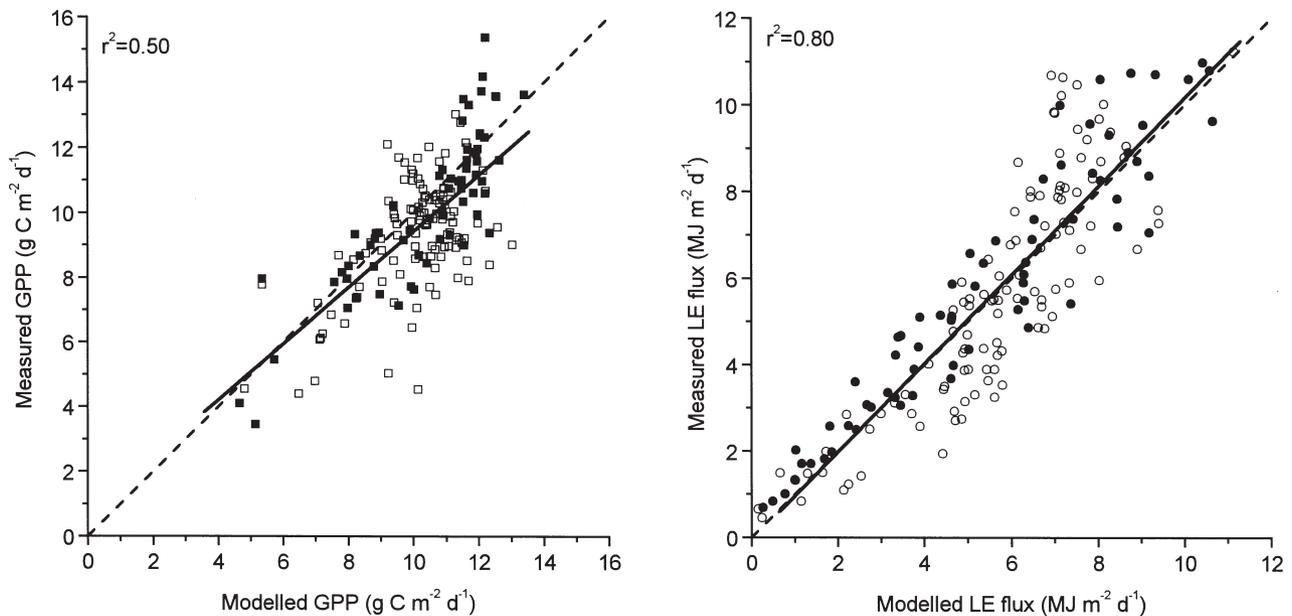
Model B, with variable below-ground hydraulic resistance, also explained a greater part of the variance in daytime hourly NEP, and improved the accuracy of predictions (Fig. 2, model B). The afternoon decline in ecosystem C uptake recorded early in the period (PDs 52–82) can now be explained as the result of a stomatal limitation on photosynthesis resulting from increased below-ground hydraulic resistance. This was a satisfying test of the variable  $R_b$  hypothesis, because the optimization was undertaken with LE flux data only, not with NEP data.

The stomatal behaviour across the period is determined by the interaction of VPD with  $R_b$ . At the start of the period, both these are relatively high. The high hydraulic resistance sets the maximum flux of water; since VPD is high, stomatal conductance must be small to bring the Penman-Monteith equation into balance with the hydraulic flux. Thus, stomatal constraints on afternoon C uptake are large. With the onset of the wet season, the rise in soil moisture reduces  $R_b$ , and the maximum sustainable hydraulic flux increases. Because VPD is lower,  $g_s$  can be higher; stomatal constraints are eased, and productivity rises.

#### Daily predictions over 12 months

The introduction of a variable below-ground resistance improved predictions of both GPP and LE flux through the whole year: in each case the root mean square error of prediction versus measurement was reduced (Fig. 5). Predictions of GPP actually explained slightly less of the variance in measurements, but the slope of the regression line was closer to 1.0, meaning our predictions were more accurate. However, predictions through the year are still not as accurate as those during the early wet season (filled symbols in Fig. 5), and the tendency is for predicted GPP to be greater than measured values. There are several hypotheses to account for the discrepancy. First, a reduced LAI (and associated reduction in total canopy N) during the dry season would slightly decrease the prediction of GPP. Second, intrinsic photosynthetic parameters may vary seasonally. Third, to estimate GPP the measured daily NEP has been combined with a constant soil and stem respiration estimate throughout the year. Daily and seasonal variability in the actual respiration may account for the discrepancy. Fourth, other below-ground hydraulic constraints, including reduced soil water potentials, may be important cofactors.

At the annual time-scale, estimated GPP of the forest over the experimental period was  $37.0 \text{ t C ha}^{-1} \text{ a}^{-1}$ . This value is higher than the value determined from the empirically interpolated data,  $30.6 \text{ t C ha}^{-1} \text{ a}^{-1}$  (Malhi *et al.* 1998), and results because the modelled daily values are often higher than the measurements (Fig. 5). Our estimate is also much greater than that for a rain forest in Rondônia made by Lloyd *et al.* (1995),  $24.5 \text{ t C ha}^{-1} \text{ a}^{-1}$ . However, the LAI and total foliar N in Rondônia were only  $\approx 70\%$  of the values at the Cuieiras site. As a further comparison,



**Figure 5.** Measured versus modelled daily gross primary productivity (GPP,  $n = 161$ ) and ecosystem latent energy flux (LE,  $n = 174$ ). Both 1:1 lines (---) and regression lines (—) are plotted. Filled symbols are for days between PD 100 and 200 (early wet season).

measured GPP in a temperate forest in north-eastern USA varied between 10.7 and 12.7 t C ha<sup>-1</sup> a<sup>-1</sup> over a 5-year period (Goulden *et al.* 1996). The prediction of total LE fluxes at Cuieiras was 1991 MJ m<sup>-2</sup> a<sup>-1</sup>, 35% of the total measured short-wave irradiance. Estimated annual evapotranspiration was 818 mm, 39% of the measured precipitation. Because our modelled LE fluxes were in close agreement with the LE data (Fig. 5), it is likely that the annual prediction is accurate. On the other hand, using the Priestly Taylor equation, and data on hourly net radiation and air temperature, the annual estimate of LE flux was 3944 MJ m<sup>-2</sup> a<sup>-1</sup>. Shuttleworth *et al.* (1984) also noted that the Priestly Taylor equation considerably over-estimated evapotranspiration in Amazonian rain forests.

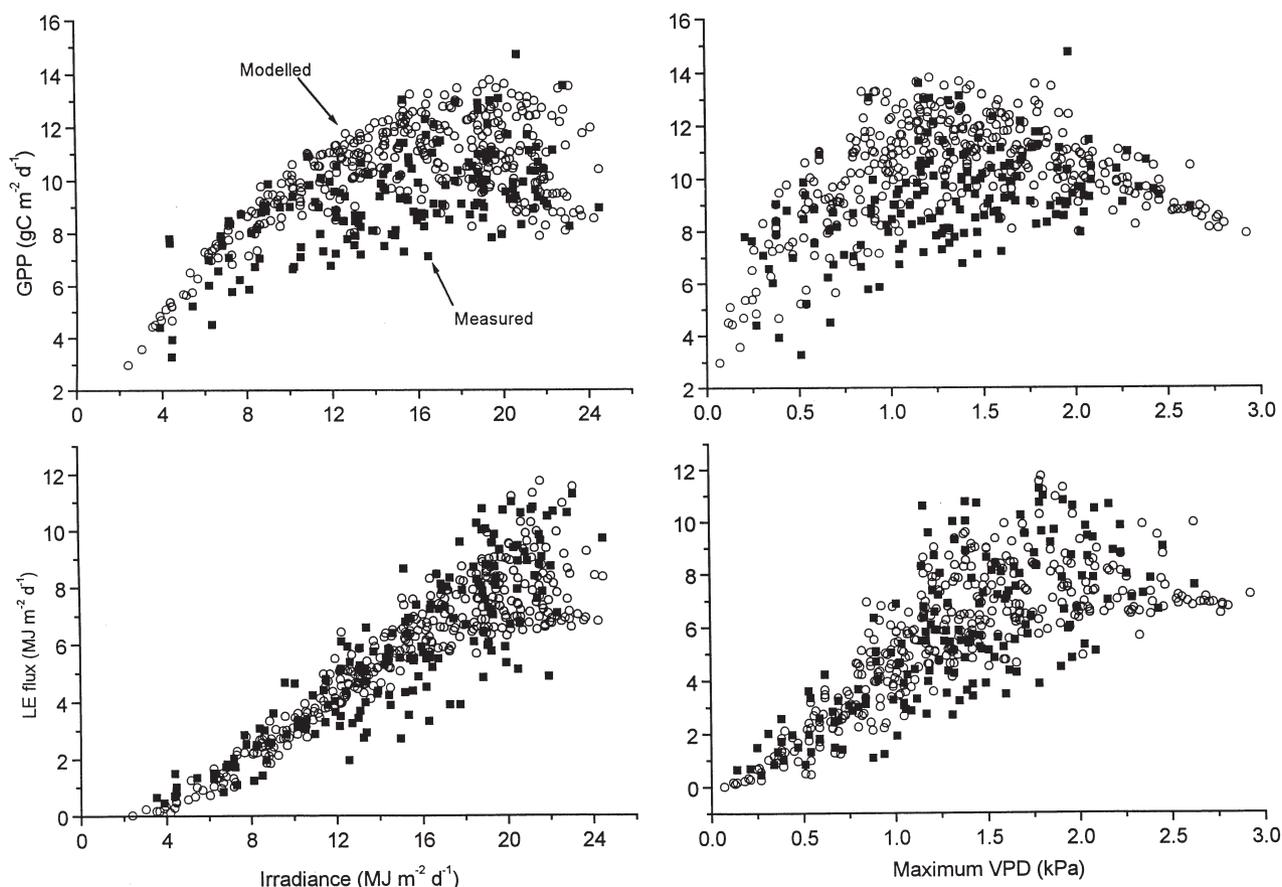
## DISCUSSION

The sensitivity analyses showed that of the potentially influential controls on canopy processes, the most important were likely to be either climatic (irradiance and VPD) or related to seasonal changes in plant-soil hydraulics, given that LAI variation is small. In its application to this data set the model has been able to describe quantitatively the interaction between the atmospheric and edaphic controls on water fluxes, the stomatal behaviour required to balance these, and the resulting constraints on C uptake. Across the 12-month period the modelled responses of daily LE flux and GPP to the climatic controls show similar patterns to those described by the data (Fig. 6). For example, the measured response of daily gross C fixation to irradiance is in both cases asymptotic. The initial slope is determined by radiation absorption, which controls the rate of the light reactions. The maximum rate is limited either by the rate of the dark reactions, controlled by canopy N con-

tent, or by CO<sub>2</sub> supply. As hydraulic constraints increase in the dry season the latter effect becomes dominant, with stomatal closure reducing maximum photosynthetic rates. This is also clearly demonstrated in the response of GPP to VPD. Peak C assimilation declines above a VPD of 1.5 kPa and the degree of reduction depends on the magnitude of the below-ground hydraulic resistance.

The response of daily total LE flux to irradiance was more linear, which was unexpected, given the inflected response noted in the sensitivity analysis (Fig. 1c). However, in the natural environment, other climatic conditions were correlated with irradiance (temperature, VPD); the concurrent increase in these variables may account for the observed linearity. The response of LE to VPD is also linear, with day to day variability in soil hydraulic resistance explaining the range in flux magnitude for a given VPD. The highest fluxes occur at VPDs of ≈2.0 kPa; these are days when atmospheric demand for water is high, but soil hydraulic resistance is not limiting. Days with VPDs > 2.0 kPa are dry season days, and so are associated with increased soil hydraulic resistance. Larger  $R_s$  means that water supply can no longer meet atmospheric demand, and stomata close so that maximum flux rates decline to match the supply constraint.

The model analyses have revealed biosphere-atmosphere interactions on two timescales. First, there is a daily interaction related to the covariance that exists between daily maximum VPD and total irradiance. Because LE fluxes respond similarly to increases in either irradiance or VPD, the covariance between the two meteorological conditions is complementary. The response of GPP is more complicated; higher irradiance boosts potential productivity, but also tends to be correlated with increased VPD, which increases stomatal limitation to C fixation. Second,



**Figure 6.** The responses of both measured (closed symbols) and modelled (open symbols) daily gross primary productivity (GPP) and ecosystem latent energy flux (LE) to variation in total daily short-wave irradiance and maximum daily vapour pressure deficit (VPD) are shown.

there is a strong seasonal interaction related to moisture. The movements of the intertropical convergence zone control local precipitation. In periods of low rainfall, continuing canopy evapotranspiration leads to a decline in soil moisture and an increase in  $R_s$ , which limits maximal daily LE flux. The sensible heat flux is increased, leading to higher air temperatures, increased VPD, and thus further reductions in stomatal opening and C fixation. When soil moisture is readily available, latent energy flux is high, and biosphere-atmosphere feedbacks act to restrict the maximum VPDs. The increased transpiration reduces both the sensible heat flux and incident radiation, the latter effect arising through increased cloudiness.

The pronounced seasonality in both C and LE exchange, indicated in our unique, long-term data-set, and our model analysis that has linked this seasonality to alterations in soil moisture, are important and novel findings for an Amazonian rain forest. Previous studies have failed to locate evidence for an affect of soil moisture on transpiration or leaf level gas exchange (Gash *et al.* 1996). However, earlier components of the ABRACOS project did record an extensive use of deep soil moisture by forests, and noted that transpiration can exceed rainfall in about one year in three in any of the months between June and November (Hodnett *et al.* 1996b). Other

studies have indicated that soil water availability in central Amazonia is low and decreases with depth (Tomasella & Hodnett 1996), and that without deep rooting, evapotranspiration could not be maintained during the dry season (Hodnett *et al.* 1996a). These data provide additional support for our conclusions, providing evidence that soil moisture availability may limit water supply in the dry season.

While the model can explain general behaviours with great success in both diurnal and seasonal cycles, we conclude that our greatest ignorance lies in the arenas of canopy-soil and canopy-atmosphere feedbacks.

**1** Is the soil hydraulic resistance hypothesis valid throughout the Amazon Basin and other tropical areas? We expect that in regions underlain by less clayey soils, and with higher soil hydraulic conductivity, the dry season decline in soil water potential, rather than an increase in hydraulic resistance, may be the primary limitation on C and LE fluxes. The sensitivity analyses show that a soil water potential limitation may have different characteristics than a soil resistance limitation (compare Fig. 1g & h). Measurements of dry season predawn leaf water potential across an Amazonian transect should identify the presence and extent of such an effect.

**2** Biosphere–atmosphere interactions are of critical importance, being centrally involved in determining the seasonal cycles. The canopy energy balance is intimately connected with air temperature, VPD and the growth of the boundary layer. Thus, there is a need to interface canopy models with boundary-layer meteorological models to explore these interactions.

**3** Relative ignorance of the respiration terms in the ecosystem C balance needs to be rectified. Are there seasonal differences to be incorporated? Soil temperatures are relatively constant throughout the year, but a change in soil water and seasonal pulses of litter inputs could impact microbial activity, and fine root growth and activity may also vary by season.

**4** GPP is over-predicted during some parts of the year. For instance, our predictions are better during the early wet season (PDs 100–200) than during the later wet season (PDs 200–300; but note there is less validation data from this period). This might be due in part to leaf phenology, such as subtle changes in LAI, or age-related alterations in the parameters for the Farquhar photosynthesis model. Some further leaf level studies to determine these parameters experimentally would be valuable.

Any strategy for regional extrapolation of the model must incorporate a compromise between accuracy and feasibility. The characteristics of the vegetation (LAI, foliar N, critical leaf water potential), soils (moisture content and water retention characteristics) and climate (irradiance, temperature, VPD) are all critical for accurate predictions of C and water fluxes over the full annual cycle. For a spatially detailed extrapolation, fields for each of the parameters are a requisite; daily climate variables, and monthly phenology and soil moisture data. The difficulty in extrapolation will arise from correctly incorporating interactions of canopy, soils and atmosphere. For example, with soils of a lower clay content, the alterations in water holding capacity and soil hydraulic conductivity are likely to alter the magnitude and timing of the seasonal cycle. More information on rooting depths and plant and soil hydraulic conductivity, and soil water retention curves will improve estimates of seasonal cycles across Amazônia. Detailed spatial and temporal data on soil moisture variability are required; it seems likely that, to fully understand such variability, soil hydrological models will need to be linked to canopy models such as the one presented here.

## CONCLUSIONS

A simplified but mechanistic model of canopy processes, previously applied in a temperate system, was successfully applied in a tropical rain forest. In the initial application the only changes made to the model were to use locally derived data on LAI, foliar N concentration, and meteorology, and also hydraulic parameters derived from the literature. With these simple changes the model could effectively simulate the diurnal course of C and LE

exchange during the wet season. Thus, the high species diversity of the tropical rain forest did not present any problems to understanding and predicting gas and energy exchange at the canopy scale.

While the eddy covariance studies had uncovered a strong seasonality in gas exchange at the site, the direct causes of this were not clear. The data indicate that the seasonal variation in maximum canopy C uptake was around  $5 \text{ gC m}^{-2} \text{ d}^{-1}$ , and in LE fluxes was close to  $3 \text{ MJ m}^{-2} \text{ d}^{-1}$ . These values represent a large fraction of daily totals, so it is critical that any scaling exercise incorporate the best understanding of the mechanisms of seasonality. Our analyses suggest that, while there is evidence for a seasonal change in LAI, it is not enough to account for the large variation in C and LE exchange. Although leaf area variability will have some influence, it is not the major control. Instead, these analyses suggest that below-ground constraints on water uptake were responsible for increased stomatal restrictions on gas exchange during the dry season. Using an optimization procedure, we predicted the daily variation in soil and root hydraulic resistance that would account for the observed LE fluxes. The pattern revealed varied in synchrony with seasonal precipitation. We applied a smoothed version of this daily pattern of resistance to the model to generate C and LE flux predictions through the annual cycle, and our predictive ability was improved. For example, we were able to account for the strongly asymmetrical daily photosynthetic data, and the relatively low LE fluxes observed in the dry season.

A regional scaling exercise will require further combined research on canopy hydraulics, gas exchange, sap flow measurements, and investigations of soil hydraulic properties. It is essential that these are undertaken along precipitation gradients and that they provide coverage of the other major Amazônian soil types. Our analysis suggests that a relatively simple scaling protocol can then be applied given the availability of this spatially and temporally referenced data.

We have demonstrated how the concept of a soil–plant–atmosphere continuum is helpful to understanding the pattern of vegetation–atmosphere interactions observed in central Amazônia. We show that the higher VPDs of the dry season are not sufficient to explain reduced C uptake, and in fact would not reduce LE flux if soil water were readily available. Instead, the supply of water to the plants must be limiting. We show that seasonal variations in this limitation can explain the changing nature of the vegetation–atmosphere interaction over diurnal periods. This study shows the strength of the interaction between the components of the continuum, with plant process both affecting and responding to soil hydrology and boundary layer meteorology. Our hypotheses require further testing; specifically we require more detailed studies of processes at the root–soil interface. Nevertheless, they provide a sound quantitative and theoretical footing for further exploration of this component of the biosphere–atmosphere system.

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