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Seasonality in CO_2 and H_2O flux at an eastern Amazonian rain forest

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[1] Previous studies of CO_2 fluxes in Amazonia have suggested seasonal variation in net ecosystem exchange. We find little evidence of this seasonality at a new site in eastern Amazonia, despite the expectation that this site would be particularly sensitive to seasonal fluctuation of rainfall. The average rate of peak net ecosystem exchange was -19 ± 0.9 (1 S.E.) μmol CO_2 m^{-2} s^{-1}. Canopy conductance, evaporation, and vapour pressure deficit were all increased during the dry season, consistent with an increase in bulk temperature and solar radiation. The lack of a dry season decrease in photosynthesis was thought to be due to the observed increase in leaf area following dry season flushing. This was accompanied by an increase in solar radiation, and we suggest that the effect of "dryness" was merely to preclude optimality of photosynthetic response to this increase in radiation. The gross primary productivity of this site was estimated to be 36 t C ha^{-1} yr^{-1}. This is similar to that reported for other Amazon forest stands. The year may have been a particularly productive one due to the lack of an El Niño event. *INDEX TERMS:* 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 0312 Atmospheric Composition and Structure: Air/sea constituent fluxes (3339, 4504); 0322 Atmospheric Composition and Structure: Constituent sources and sinks; 1615 Global Change: Biogeochemical processes (4805); *KEYWORDS:* Eddy covariance, photosynthesis, seasonality, NEE, Amazonia

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1. Introduction

[2] Tropical forests cover approximately 60% of the forested area of the world [*Dixon et al.*, 1994], and their net primary productivity has been estimated as 30 Pg C yr^{-1}, approximately half of the global total [*Malhi et al.*, 1998]. Recently, attention has been drawn to the possible role of these forests as a carbon sink [*Phillips et al.*, 1998; *Malhi et al.,* 1999] but only a handful of authors have tried to quantify the change in carbon stored in this unique ecosystem. The Amazon rain forest represents the largest undisturbed example of such forest, and attention is now turning to estimates of CO_2 exchange during short timescales (for a forest e.g. 1–5 years), in an attempt to reduce the uncertainty associated with current predictions of sink strength.

[3] Early eddy covariance studies in Amazonia quantified first water vapour [*Shuttleworth et al.*, 1984], then carbon dioxide exchange [*Fan et al.*, 1990]. The second study measured a net uptake of CO_2 (1 t C ha^{-1} yr^{-1}) over a very short (12 day) timescale. The studies that followed measured a greater sink strength (up to 6 t C ha^{-1} yr^{-1}) over longer periods of time [*Grace et al.*, 1995a; *Malhi et al.*, 1998]. Data from long-term forest inventory plots provide independent evidence of a net carbon sink in moist humid forests of South America, although the sink strength is less than that indicated by eddy covariance [*Phillips et al.*, 1998]. Discrepancies between the two measurements are thought to be largely attributable to a lack of replication of eddy covariance data in both space and time, coupled with a potential loss of nighttime efflux of CO_2 [*Malhi et al.*, 1999].

[4] The discovery of the ability of humid tropical forest to maintain a green canopy through five-month dry periods [*Nepstad et al.*, 1994] suggests constancy in CO_2 uptake within any given year. However, only one previous study of eddy covariance in the Brazilian Amazon has considered seasonality in CO_2 exchange [*Malhi et al.*, 1998]. That study was located near Manaus in central Amazonia and the authors suggested that carbon uptake is reduced during the dry season, despite increases in solar radiation, because of soil water restrictions [*Williams et al.*, 1998]. This pattern has also been observed in droughted temperate forests [e.g., *Baldocchi*, 1997; *Arneth et al.*, 1998a].

[5] The current study was designed to test the hypothesis that the carbon flux is seasonal, following the above demonstration of seasonality in Central Amazonia. The site

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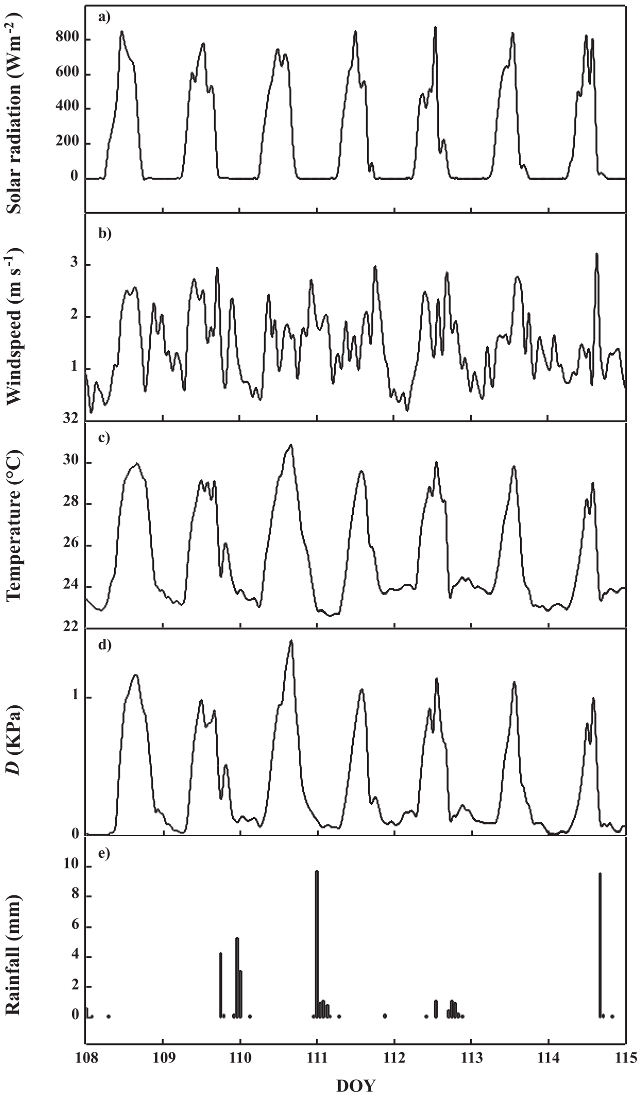


Figure 1. Hourly averaged meteorological data collected at 53 m height at Caxiuanã for a typical week (days 108 to 114, 18–24 April), including (a) solar radiation (measured at 46 m height, W m^{-2}), (b) wind speed (m s^{-1}), (c) air temperature (°C), (d) water vapour deficit (*D*, kPa), and (e) rainfall (mm).

was located at Caxiuanã forest, 350 km west of the city of Belém in north-eastern Amazonia, a region predicted to experience increasing seasonal drought over the next century [*Friend*, 1998; *Cox et al.*, 2000; *White et al.*, 2000]. Current annual rainfall is comparable to that of the majority of the Amazon basin. Satellite data gathered in years prior to the current study, but only recently published, show a large variation in seasonal greenness in this part of the Amazon, which can be largely attributed to high variation in seasonal rainfall [*Potter et al.*, 2001]. This pattern is particularly obvious during "El Niño" years where there is less rainfall overall and a greater difference in rainfall between seasons. We expected that the net carbon exchange at Caxiuanã would be reduced during the dry season. This would have a significant influence on global predictions of tropical carbon sink strength. Models would need to be constrained not only by rainfall, but also by seasonal pattern of rainfall. Here, we present data on carbon dioxide exchange and some of its environmental drivers measured over a wet — dry cycle.

2. Methods

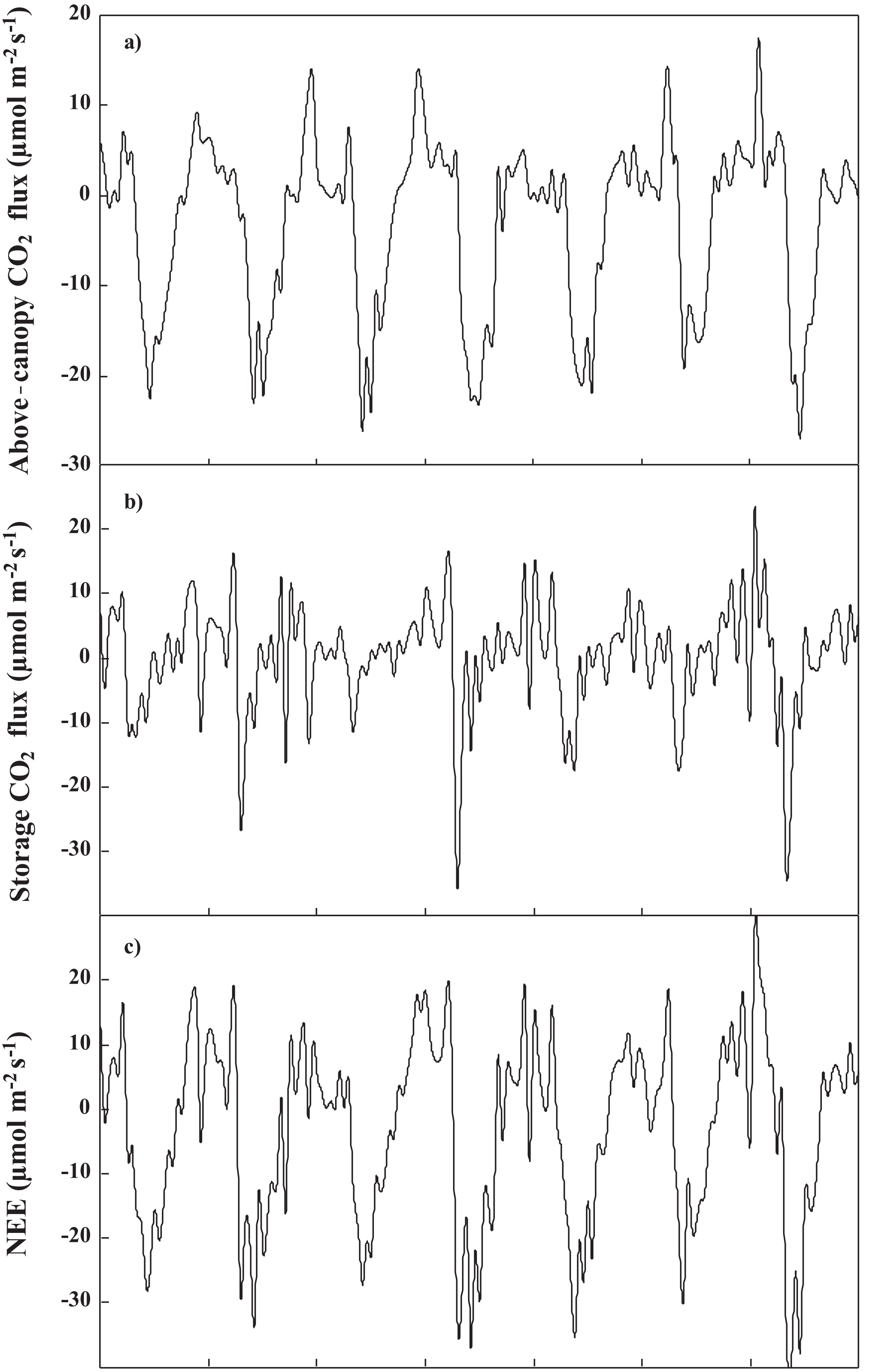
2.1. Site

[6] The Floresta Nacional de Caxiuanã (1°43′3.5″S, 51°27′36″W) is situated approximately 350 km to the west of the city of Belém, Pará, Brazil. The site is administered by the Estação Cientifica Ferreira Penna (ECFPn) which belongs to the Museu Paraense Emílio Goeldi (MPEG). The forest is extensive (33 000 hectares) and largely undisturbed, having been a reserve since the mid 1970s and is dense lowland *terra firme* forest with a mean annual rainfall of 2500 mm, a canopy height of 35 m, an aboveground dry biomass of 200 m^3 ha^{-1} [*Lisboa and Ferraz*, 1999], a basal area of 30–35 m^2 ha^{-1} (S. S. de Almeida, unpublished data, 1999) and a leaf area index of 5–6. Families with the greatest number of species present are the Sapotaceae, Chrysobalanaceae and Lauraceae families. The soil is largely a yellow latosol (oxisol in U.S. Department of Agriculture soil taxonomy), but has areas of iron sand approximately 3–5 m below the surface. The tower used for flux measurements was situated approximately 2 km to the north of the ECFPn field station. The Edisol eddy covariance system [*Moncrieff et al.*, 1997], was mounted above the 51.5 m-high aluminum tower, 2 m × 1 m wide. Due to its proximity to the Baía de Caxiuanã (lying 6 km to the south-east) the study area likely experiences a more riverine climate than two previously studied Amazonian forest sites (e.g., Manaus [*Malhi et al.*, 1998] and Jaru [*Grace et al.*, 1995a]). The tower was positioned on a plateau, the closest small river being 400 m to the south-west. Another small river was located 600 m to the east but was thought not to contribute substantially to the north-easterly fetch. The closest disturbed area was the site of the field station (approximately 1 ha), 2 km to the south, connected to the tower only by walking track. Eddy covariance sensors were mounted 4 m above the tower (i.e. at a height aboveground of 55.5 m) on the easterly side so as to minimize flow distortion for the prevailing wind direction. Please refer to the overview paper (JGR, this issue) for further site details.

2.2. Wind Direction and Fetch

[7] Despite a prevailing wind direction of north-east (NE, 45°), some day-time variation was observed both within and between seasons. The NE quarter accounted for only 44% of wet season day-time wind, but 61% of wind in the dry season. A large proportion (19%) of day-time wind came from 95° to 115° during the dry season and this is thought to represent the formation of squalls on the Baía de Caxiuanã, SE of the tower. During the dry season, long periods (3–5 h) of intense

Figure 2. (opposite) Hourly averaged CO_2 flux data at Caxiuanã for the same week as Figure 1, including (a) eddy covariance CO_2 flux at 55.5 m height, (b) flux of CO_2 into storage below 55.5 m (calculated from CO_2 profiles), and (c) NEE (net ecosystem exchange, derived as the sum of the other two fluxes).


a)
b)
c)
Above-canopy CO2 flux (µmol m-2 s-1)
Storage CO2 flux (µmol m-2 s-1)
NEE (µmol m-2 s-1)
20
10
0
-10
-20
-30
20
10
0
-10
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-30
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10
0
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108
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DOY

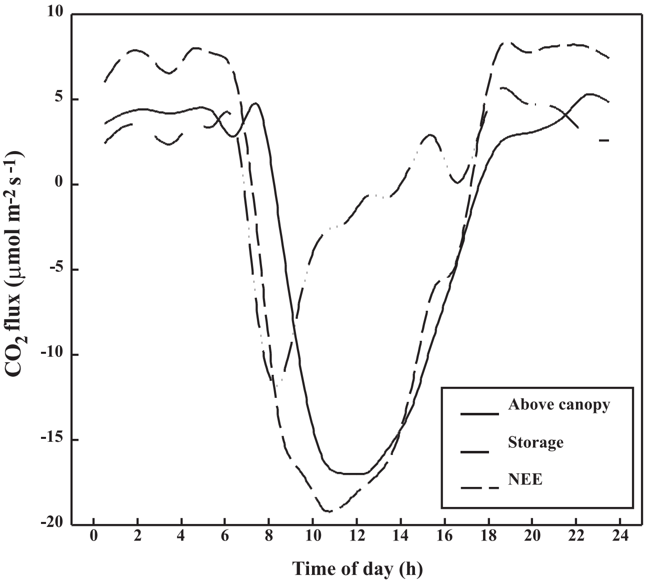


Figure 3. Mean diurnal cycle of the above-canopy CO_2 flux, the within-canopy storage flux, and the net ecosystem exchange (NEE) for the entire study period 16 April 1999 to 19 October 1999 at Caxiuanã.

sunshine cause convective build-up of cumulus clouds at the forest margins of the Baía de Caxiuanã. This is the prevalent direction from which rain arrives at the tower. Night-time wind direction was less variable but again the NE quarter only accounted for 59% of wind sampled during the wet season compared with 85% during the late dry season.

[8] An estimate of the fetch of the flux system was made using the method of *Schuepp et al.* [1990], corrected for stability according to *Lloyd* [1995]. We estimate that 80% of the measured day-time flux originated within 500 m of the tower, with the average peak occurring at 67 m. During the night, 80% of the flux originated within 1410 m, with the peak at 606 m. The fetch is marginally larger during the day in the wet season, as a result of the lower mean wind speed. Taking into account the wind directions and the fetch distribution we estimate that 80% of the fetch comes from within an area of 19 ha during the day and 167 ha at night.

2.3. Measurement of Above-Canopy Fluxes

[9] The eddy covariance technique was used to calculate fluxes of CO_2, H_2O, and energy between the forest and the atmosphere [*Baldocchi et al.*, 1988]. Instantaneous (20.8 Hz) vertical wind velocities were measured with a three-dimensional sonic anemometer (Solent, Gill Instruments, Lymington, UK) and CO_2 and H_2O concentrations were measured using a fast-response (5 Hz) Li-6262 infrared gas analyzer (LICOR, Lincoln, Nebraska, USA). Copper tubing was used to minimize temperature gradient between the point of air intake and the analyzer. Small bore (3.4 mm, 10 m in length) tubing was used until day 224 (12/8/99), at which point the tube was replaced by that of wider bore (7.5 mm, 12 m in length). The analogue output signal from the gas analyzer was sent to the sonic anemometer where it was digitized and combined with the wind data. The combined digital output was collected at 20.8 Hz on a laptop computer, and fluxes were calculated in real time, allowing for lags in CO_2 and H_2O concentrations, using University of Edinburgh Edisol software [*Moncrieff et al.*, 1997]. The analyzer was calibrated approximately weekly, using zero and fixed concentration CO_2 and water vapour samples (generated by a Licor Li-610 dew point generator in the case of the fixed water vapour supply). Power was supplied to all instruments by 12 solar panels mounted on brackets attached to the tower at 45.5 m of height.

[10] The system is designed to function correctly in all weather [*Malhi et al.*, 1998]. However, large gaps in the data occurred as a result of failure in the power supply, such that data was recorded on only 75% of the days occurring between 11 April 1999 and 19 October 1999. A further 28 days of data have been excluded from the analysis due to problems with the pumps supplying air to the gas analyzer, leaving only 59% of the total number of possible sample days.

2.4. Measurement of Storage Fluxes

[11] Within- and above-canopy measurements of CO_2 and H_2O concentrations were made at six heights (0.2, 2.0, 8.0, 16.0, 32.0, 55.5 m), with the topmost intake being the outflow from the eddy covariance system to enable comparison of readings from the two gas analyzers. The profile system sampled each height for 5 min, cycling through the entire profile every half hour. At each height, 2 min was allowed for flushing residual air from the tube before measurement using an infrared gas analyzer (PP Systems, Hitchin, UK). This instrument was also calibrated approximately weekly in the same manner as the Li-6262 analyzer. Data were stored on a logger (21X, Campbell Scientific, Leicester, UK) and downloaded approximately weekly. Vertical profiles of CO_2 and H_2O concentration were collected in batches as follows: between 16/4/99 and 11/6/99, between 24/6/99 and 8/8/99, between 6/9/99 and 9/9/99 and between 7/10/99 and 19/10/99.

2.5. Measurement of Meteorological Variables

[12] All meteorological sensors were mounted at 53 m on the top of the tower, with the exception of the net radiometer that measured incoming and reflected solar and longwave radiation (CNR1, Kipp & Zonen, Delft, Netherlands) and the downward-facing quantum sensor (Skye Instruments, Powys, UK). These were installed at 45.5 m to avoid reflection from the solar panels mounted at the same height. These two instruments were used to resolve the net radiation (CNR1) and the amount of reflected photosynthetic photon flux density (PPFD, Skye quantum sensor) respectively. Both were mounted on a 5 m pole projecting horizontally from the tower. Incoming PPFD was measured at 52 m, on a pole projecting 1.5 m from the tower, using an upward-facing Skye quantum sensor. Rainfall was measured on the top of the tower using two tipping bucket gauges with a resolution of 0.2 mm (Campbell Scientific). Air temperature was measured at heights of 16 m and 32 m using shielded thermistors. Thermocouple probes for measuring soil temperature were installed at 5 cm depth. Saturation deficit was measured on top of the tower using an aspirated Delta T psychrometer (WP1-UM2, Delta-T Devices, Cambridge, UK). Wind speed and direction were measured using an anemometer (accurate to 1%) and wind vane (accurate to ± 2°) respectively (Campbell Scientific) and all meteorological data were stored on a

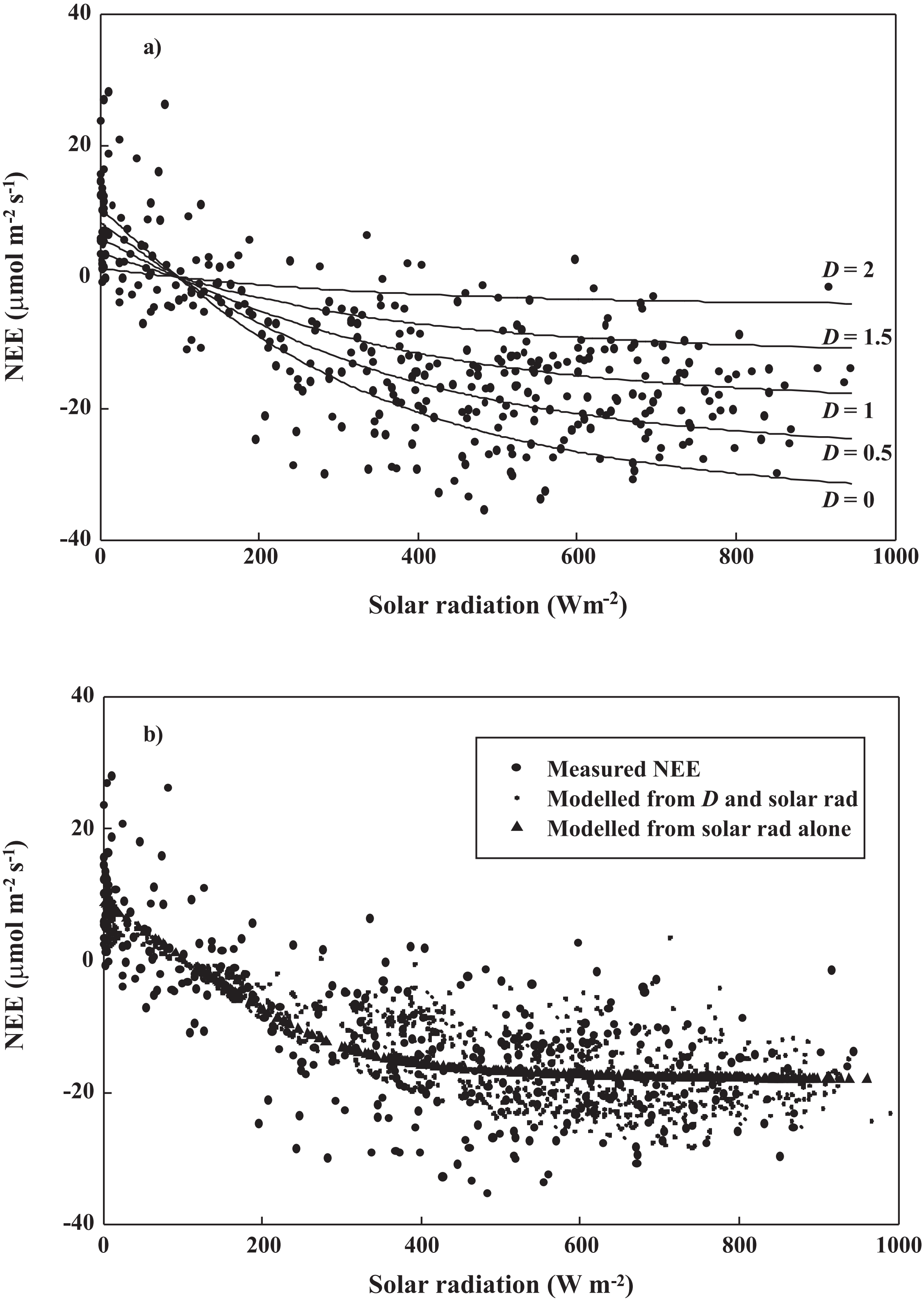


Figure 4. Hourly averaged NEE against solar radiation, using all available data from the entire study period at Caxiuanã and including (a) lines of best-fit for the modelled response of NEE to both solar radiation and *D*, and (b) data estimated from either the modelled response shown in (a) or from solar radiation alone (whenever *D* was missing).

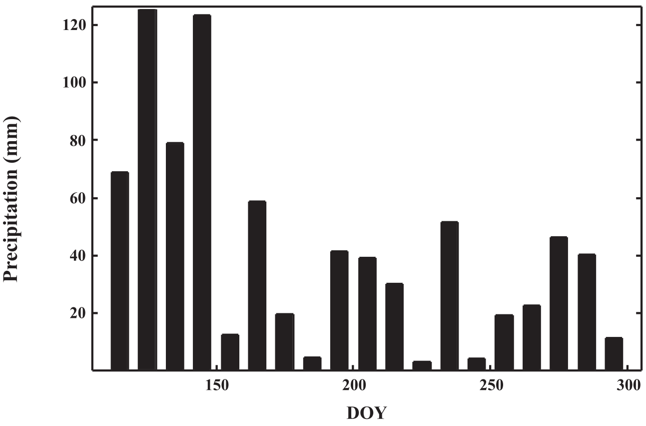


Figure 5. Total of precipitation (mm) per 10 days (represented as day of year, DOY) at Caxiuanã.

logger (21X, Campbell Scientific). All meteorological variables were measured every 10 s and averaged per half hour. The data were continuous with the exception of ten days of missing data from 1000 on Day 149 (29/5/99). In addition, there were occasional gaps in the data from a particular instrument, most commonly the psychrometer.

2.6. Derivation of Leaf Area

[13] Supplementary measurements of albedo were obtained as the ratio of reflected to incident solar radiation. An estimate of leaf area was obtained from percent cover of canopy, using a spherical densiometer [*Lemmon*, 1956] at monthly intervals at eight fixed points around the tower. These were converted to leaf area index (LAI, L) assuming a spherical leaf distribution and consequent extinction coefficient, k, of 0.5, such that:

$$I = I_o e^{-kL} \tag{1}$$

where I = transmitted irradiance and I_o = incident irradiance [*Monteith and Unsworth*, 1990].

2.7. Data Processing and Gap Filling

[14] Raw data were filtered by the Edisol program, using a digital recursive filter (time constant 800 s, effective averaging period 60 min). The wind field (u, v, w) coordinates were rotated such that mean v and w were zero over 60 min periods (refer to *Moncrieff et al.* [1997] for full details). Real-time data were collected as hourly averages, but several months of continuous raw data (20.8 Hz) were also stored for subsequent comparison with hourly averages.

[15] Corrections were applied to allow for the dampening of fluctuations at high frequencies using the approach outlined by *Moore* [1986] and *Moncrieff et al.* [1997]. Transfer functions were calculated for the loss of signal due to tube length, finite instrument response times, density fluctuation, sensor separation (0.2 m between gas analyzer inlet and sonic anemometer) and path length (0.15 m). No corrections were made for low frequency signal loss due to detrending as the semiempirical relationships between surface layer covariance spectra and wind speed and stability proposed by *Kaimal et al.* [1972] are thought to be inappropriate for low frequency fluctuations over forest canopies [*Anderson et al.*, 1986]. However, losses of high frequency signal were corrected for using the EUROFLUX methodology [*Aubinet et al.*, 2000]. A zero-plane displacement of 30 m was assumed. An additional correction was made for a change in tube attenuation of H_2O, dependent upon vapour pressure deficit of the air (R. J. Clement, unpublished data, 2000). For CO_2 fluxes, the total correction ranged from 2 to 74% in day-time conditions (mean = 4%) and from 2 to 96% in night-time conditions (mean = 8%).

[16] Within-canopy storage of CO_2 was calculated using the profile measurements interpolated by a cubic spline both through time and canopy height.

[17] Where it was necessary to fill gaps for the purpose of estimating net ecosystem exchange (NEE) over the entire duration of the study period, an empirical light response model with a vapour pressure deficit (D, kPa) function was used for day-time estimates. Light response was modeled as a nonrectangular function after *Farquhar et al.* [1980], in the form:

$$q.A^2 - (kS + A_{\max})A + kSA_{\max} = 0 \tag{2}$$

where A = NEE, $A_{\max}$ = maximum rate of NEE (μmol m^{-2} s^{-1}), k = initial slope of curve (apparent quantum yield × 2.16), S = incident solar radiation (W m^{-2}) and q = convexity of the hyperbola ($0 < q < 1$). The fit of the light response model was improved by the addition of a linear D function (r^2 increased from 0.62 to 0.66), as follows:

$$A = f(S)(1 - wD) \tag{3}$$

where w is a constant (kPa^{-1}). Where D was not available the light response function alone was used.

[18] Gaps in night-time NEE were estimated using the average NEE for a given hour in either season. Soil temperature readings were not sufficiently reliable for use in a model of soil respiration, and the relationship between NEE and above-canopy temperature was too variable to allow fitting of a function. When the mean nightly NEE was compared with the mean nightly friction velocity, u_*, a correlation was observed (r^2 = 0.48), but because the gaps in NEE were coincident with gaps in the data required to calculate u_* mean night-time NEE was the best estimate. The previous study of *Malhi et al.* [1998] in central Amazonia, showed little variation in night-time NEE throughout the year.

3. Results and Discussion

3.1. Diurnal Trends

[19] Figures 1 and 2 show a representative week of meteorological and CO_2 flux data (days 108 to 114, 18–24 April 1999). Micrometeorological sign convention is used for fluxes, with negative values indicating a net downward flux into the canopy. Above-canopy CO_2 flux is that measured by eddy covariance, to which is added the within-canopy storage flux to obtain the biotic CO_2 flux or net ecosystem exchange (NEE). Nights are less windy than days and the peak of solar radiation occurs around midday, typically just before the peak of above-canopy air temperature and vapour pressure deficit (D). Rainfall is accompanied by a drop in

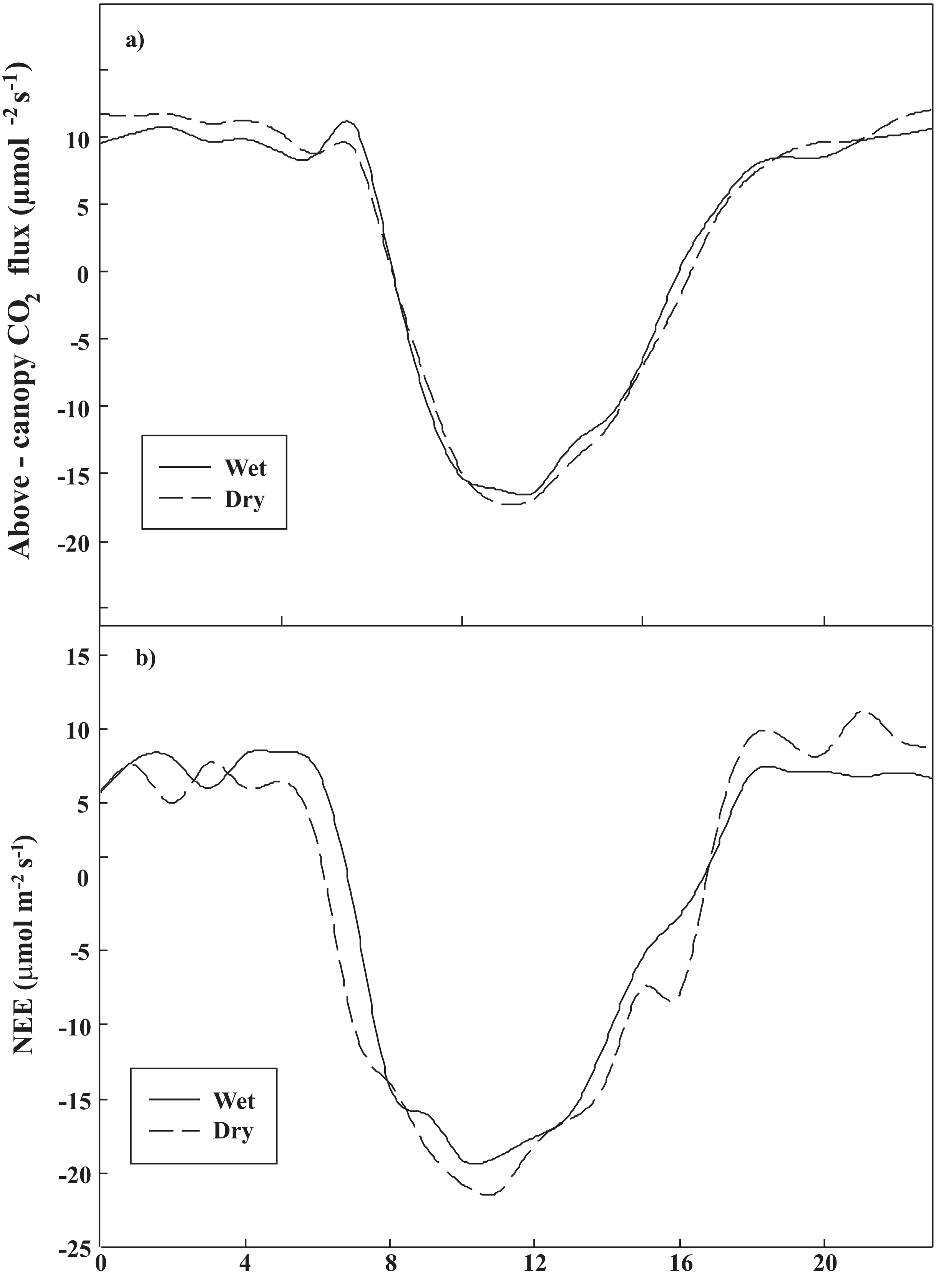


Figure 6. Mean diurnal cycle at Caxiuanã, grouped by season, of (a) the above-canopy CO_2 flux, and (b) the net ecosystem exchange (NEE), using measured data only.

day-time solar radiation and temperature, and is often preceded by an increase in mean wind speed.

[20] There is little decrease in the average CO_2 flux with rain provided that the period of rain is relatively short (<2 hours). Within-canopy storage accounts for most of the nocturnal respired CO_2 but there is a noticeable increase in above-canopy efflux after/during windy nocturnal hours. There is some evidence of a spike in above-canopy efflux around 0930 local time (LT). This is the time at which an increase in wind speed is commonly observed. The mean nocturnal NEE was 7.55 ± 0.69 μmol CO_2 m^{-2} s^{-1} (95% confidence, number of samples n = 462). Peak day time NEE was reached around 1100 and was about −19 μmol CO_2 m^{-2} s^{-1} on average (± S.E. of 0.9). The mean diurnal cycle for all collected data is shown in Figure 3. Average peak NEE is a little higher than the peak of −18 μmol CO_2 m^{-2} s^{-1} recorded in previous studies in central Amazonia [*Fan et al.*, 1990; *Malhi et al.*, 1998] and mean nocturnal respiration is substantially greater than the mean of 6.46 μmol CO_2 m^{-2} s^{-1} recorded at the Cuieiras site near Manaus [*Malhi et al.*, 1998].

[21] Day-time NEE was clearly related to incident solar radiation. All data collected with nonzero solar radiation are plotted in Figure 4a. A light response model [*Farquhar et al.*, 1980] was fitted to these data, which had a coefficient of determination, r^2, of 0.62 and a convexity of 0.95. The addition of a linear response to vapour pressure deficit, D, improved the r^2 to 0.66 and reduced the convexity to 0.7, such that for a fixed D the photosynthesis did not saturate at high light. Although low values of D are likely to be autocorrelated with higher proportions of diffuse radiation [*Hollinger et al.,* 1994], i.e. both occur on cloudy days, the relationship between net ecosystem exchange and D was the same on sunny and cloudy days (data not shown). Light compensation occurred at insolations of 98 ± 7 (1 S.E.) μmol m^{-2} s^{-1} and the maximum apparent quantum yield was 0.055 ± 0.013 mol CO_2 produced per mol of photons. These results are comparable with those obtained by previous studies. For example *Fan et al.* [1990] measured a light compensation point of 120 μmol m^{-2} s^{-1} and an apparent quantum yield of 0.051 mol of CO_2 per mol of photons at a site in central Amazonia. *Grace et al.* [1995b] give slightly different figures of 260 μmol m^{-2} s^{-1} and 0.024 mol of CO_2 per mol of photons at a site in south-western Amazonia, which may be a consequence of the lower leaf area index of that site or the different floristic composition [*Roberts et al.*, 1996].

[22] The lack of saturation in high light has been observed in other similar studies [e.g., *Malhi et al.*, 1998] and indicates the imperfection in treating the canopy as a "big leaf" as individual leaves will differ in their light interception and response [*de Pury and Farquhar*, 1997]. In fact, the majority of direct light will be captured by the uppermost layer of the canopy. The lower leaves will be receiving largely diffuse light and therefore will not be photosynthesizing at a maximum rate. In addition, the replication of measurements of the light/photosynthesis response at a canopy scale over a long period of time tends to linearize this relationship effectively reducing saturation [*Ruimy et al.*, 1995].

3.2. Seasonal Patterns in CO_2 Exchange

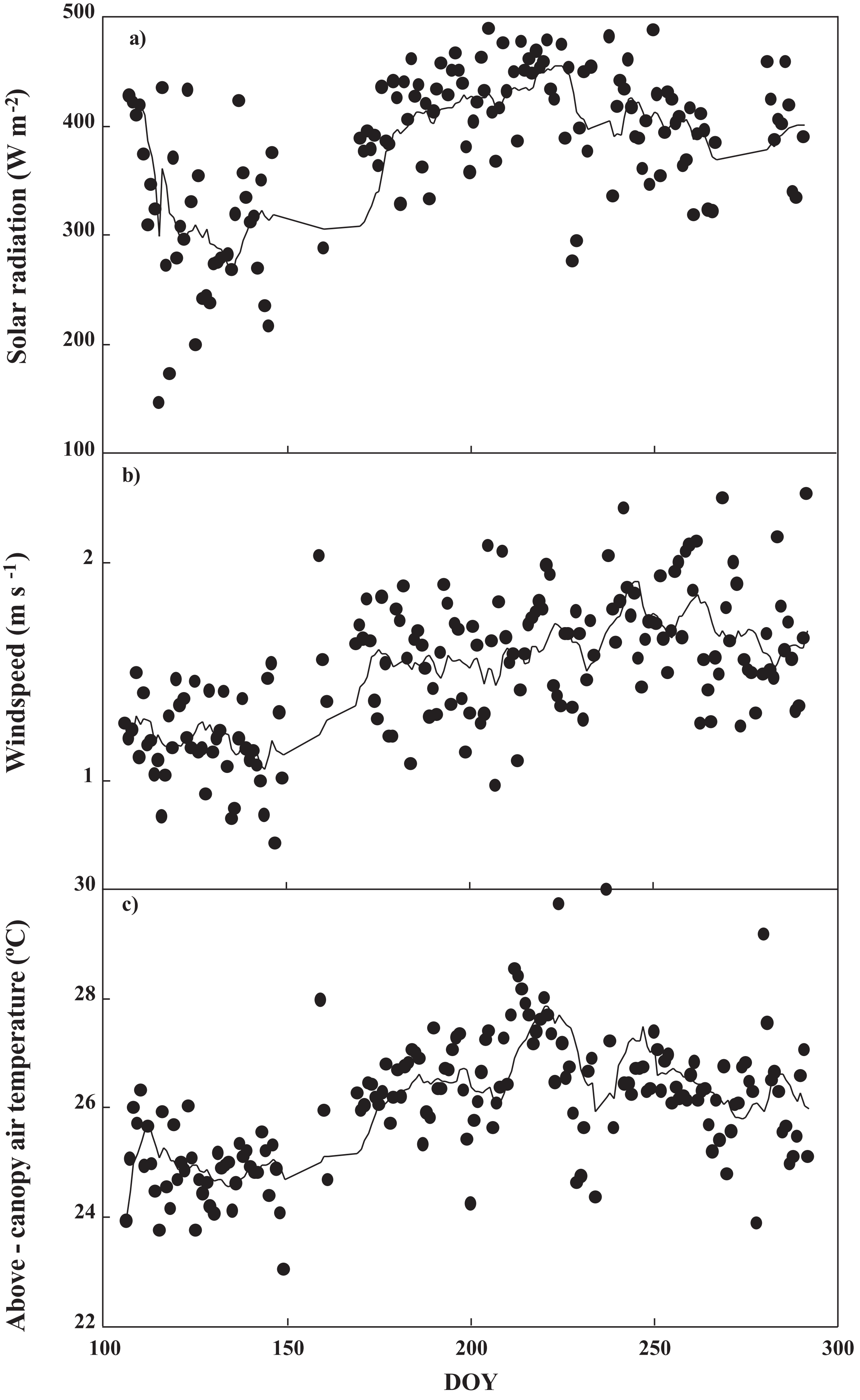
[23] Wet and dry seasons were defined simply on the basis of precipitation (Figure 5). The wet season was the period of maximum rainfall, with rain falling just about every day (up to day 150). The mean rainfall per day was 9.3 mm in the wet season and 2.8 mm in the dry season. No difference in CO_2 exchange could be detected between wet and dry seasons (Figure 6). Both seasons showed a peak above-canopy flux of around 19 μmol CO_2 m^{-2} s^{-1}.

[24] Seasonal trends in wind speed, air temperature and solar radiation are shown in Figure 7. Wind speed and air temperature were noticeably lower in the wet season (April−May) than in the dry season. Total radiation received per day was less during the wet season but the most obvious difference in solar radiation between the two seasons lies in the large variability between days of the wet season.

[25] Increases in both albedo and leaf area index were observed over the studied period (Figure 8). Leaf flush is generally believed to occur approximately a month after the start of the dry season [*Roberts et al.*, 1998], an event which would give an increase in both albedo and peak photosynthesis following the initial leaf-shed then reestablishment phase. In the current study albedo steadily increases throughout the year (presumably reflecting, in part, the "drying" of the canopy [see *Culf et al.,* 1995]. Supporting measurements of leaf area index near the tower suggest a period of relative constancy in leaf area following an initial increase, with another peak toward the end of the dry season (Figure 8b). Dry season leaf flush is thought to be a response to rehydration of stems following the shedding of transpirational load in the form of older leaves [*Borchert*, 1994]. Leaf flush also implies an increase in nitrogen content of leaves, which should confer an increase in photosynthetic capacity of the canopy [*Leuning et al.*, 1995]. We suggest that during the current "La Niña" year the influence of phenology (i.e. an increase in leaf area and associated increase in nitrogen content of leaves) balanced the opposing influence of the environmental drivers (namely solar radiation and D) of photosynthesis, at the whole-stand scale.

[26] Nocturnal respiration was marginally higher in the dry season compared with the wet season. Mean respiration rate during the wet season was 7.1 ± 0.4 μmol CO_2 m^{-2} s^{-1} compared with 8.2 ± 0.9 μmol CO_2 m^{-2} s^{-1} in the dry season. Although not significant ($p > 0.05$), an increase in soil respiration would be expected during the dry season as a result of an increased soil temperature. Nocturnal air temperature was approximately one degree higher during the dry season than in the wet (23.75 ± 0.04°C compared with 24.8 ± 0.2°C, $p > 0.05$). Another study has shown a maximum diurnal temperature range for soil of 2°C in a south-western Amazonian rain forest [*Meir et al.*, 1996]

Figure 7. (opposite) Mean daily values of meteorological data at Caxiuanã collected at 53 m height (except for solar radiation which was at 46 m) including (a) solar radiation (W m^{-2}), (b) wind speed (m s^{-1}), and (c) air temperature (°C). Also shown is the moving average for 10 day periods. Note that the mean values for radiation include only day-light hours (0700−1900).


a)
Solar radiation (W m^{-2})
500
400
300
200
100
b)
Windspeed (m s^{-1})
2
1
c)
Above - canopy air temperature (°C)
30
28
26
24
22
100
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200
250
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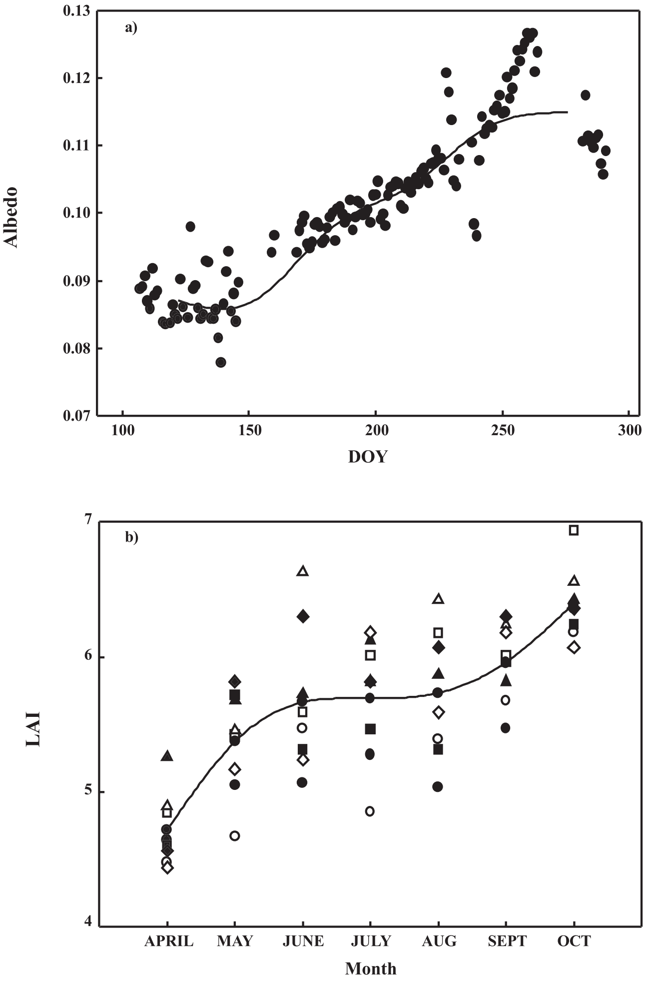

Figure 8. Changes in canopy properties during the entire observation period (16 April 1999 to 19 October 1999) at Caxiuanã including (a) albedo, shown as the daily mean for data between 1100 and 1300 hours, and (b) leaf area index (LAI) per month at eight different locations around the tower. Different symbols represent each location. The monthly mean of the eight locations is shown as a splinal curve.

compared with our mean above-canopy range of 6°C. However, soil generally mirrors the aboveground response albeit at a smaller amplitude and with a several hour time delay. The same study showed a delay of four to five hours rendering the lag insignificant for night-time estimates [*Meir*, 1996]. The relationship between nocturnal above-canopy temperature and respiration was too variable to fit a function to but is thought to be a composite of soil temperature, soil moisture and friction velocity, u_*.

[27] If the above-canopy fluxes of the dry season are split into two time periods, early and late (corresponding to before or after day 250, the end of August), there is some evidence of a difference in photosynthesis during these periods. Figure 9 shows that the late part of the dry season has the highest mean rate of above-canopy exchange for the measured period, with the early part of the dry season dropping below the rate of the wet season. Peak rates reached -22.6 ± 0.6 μmol CO_2 m^{-2} s^{-1} late in the dry season compared with -18.6 ± 0.9 earlier on. Without supporting measurements of soil water content, it is difficult to establish the significance of this late season increase in photosynthesis. A modest increase in rainfall (*ca.* 1 mm per day) was observed at this time but this increase would be unlikely to reduce soil water deficit. A high soil water deficit has been cited as the most likely cause of a reduction in photosynthesis during the dry season in previously studied Amazonian forests [*Malhi et al.*, 1998; *Williams et al.*, 1998]. However, good evidence suggests that trees rely on deep roots in dry seasons [*Nepstad et al.*, 1994] and that the movement of water stored at depths greater than 2 m may prevent drought stress in these forests [*Hodnett et al.*, 1996]. Phenologically, we again observed an increase in albedo and leaf area index during the later part of the dry season. This may represent the completion of the growth of new leaves with the small increase in rainfall [*Reich and Borchert*, 1982].

3.3. Seasonal Patterns in Light Response

[28] Above-canopy CO_2 flux was strongly related to photosynthetic photon flux density (PPFD) regardless of season (Figure 10, $r^2 > 0.66$). However, both apparent quantum yield and maximum CO_2 flux ($A_{\max}$) were decreased during the dry season compared with the wet season while the light compensation point was increased (Table 1), all indicating a suppression in photosynthetic response to light at the ecosystem level. Both estimates of apparent quantum yield fall within the range reported for forests across a wide range of biomes where the mean was reported to be 0.035 mol mol^{-1} for quantum yield assessed by micrometeorological methods [*Ruimy et al.*, 1995]. If a response to D (of the same form as that applied to NEE) is included in the light response model, the fit improves slightly and it appears as if $A_{\max}$ for the dry season is now greater than that for the wet season (22.95 ± 1.7 μmol m^{-2} s^{-1} compared with 24.46 ± 1.4 μmol m^{-2} s^{-1}). This response is difficult to assess given that a reduced data set was used to fit the relationship (due to missing D data). However, it does suggest that D may be restricting photosynthetic capacity during the dry season. A reduction in photosynthetic capacity during the dry season would have the effect of counteracting the observed increase in LAI. More data would be required to test this hypothesis.

[29] Because the difference between tropical seasons is weak [*Whitmore*, 1990], it is difficult to compare seasonal responses with those from nontropical forests, especially deciduous forests. However, temperate evergreen forests have shown little difference in the PPFD/flux relationship between early and late parts of Summer but a large difference between Summer and Winter [e.g., *Hollinger et al.*, 1994]. Some studies have shown relative insensitivity to PPFD when soil water is thought to be severely restrictive [e.g., *Baldocchi*, 1997; *Arneth et al.*, 1998b]. In a different type of tropical forest (cerradão), there was a huge increase in $A_{\max}$ with increasing wetness [*Vourlitis et al.*, 2001]. This type of forest occupies a transitional position between humid tropical rain forest and savanna so we would expect to see an increased seasonality compared with humid tropical rain forest. However, these authors find no change in quantum yield with the transition from wet to dry season.

[30] The ecosystem "dark" respiration calculated from these above-canopy flux measurements when PPFD = 0 was

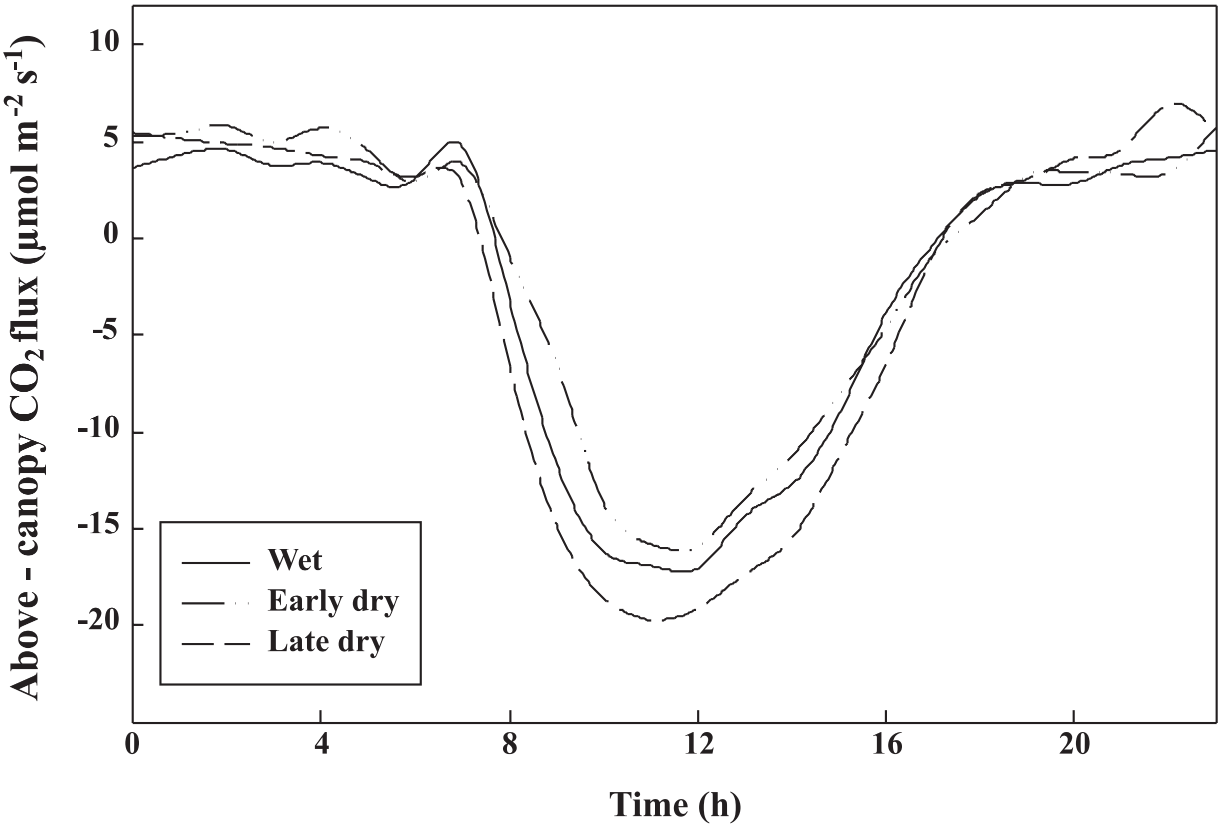

Figure 9. Mean diurnal cycle of the above-canopy CO_2 flux at Caxiuanã, when the dry season is broken into early (31 May 1999 to 7 September 1999) and late (8 September 1999 to 19 October 1999) components, using measured data only.

approximately 4 μmol CO_2 m^{-2} s^{-1} in both seasons. After adding the mean day-time within-canopy storage of 3.5 μmol m^{-2} s^{-1} the estimated value of respiration is very close to that measured at night (7.1 and 8.2 μmol m^{-2} s^{-1} for wet and dry seasons respectively).

3.4. Seasonal Patterns in Canopy Conductance

[31] Figure 11 shows the change in canopy conductance and evaporation (*E*) with vapour pressure deficit (*D*) and season. Error bars represent one standard error of the mean. *D* and *E* are both higher in the dry season, reflecting the increase in net radiation and temperature. Canopy conductance shows little seasonal difference between the hours of 1000 and 1500 but an early peak around 0900 is observed during the dry season (Figure 11c). This early morning peak of conductance has been observed in other studies of Amazon forest species both at the canopy [*Grace et al.*, 1995b] and leaf [*Roberts et al.*, 1990; *McWilliam et al.*, 1996] levels. Maximum values of canopy stomatal conductance were around 1 mol m^{-2} s^{-1}, the same as those reported in the study of *Grace et al.* [1995b]. Conductance showed little relationship with *D* beyond the daily connection with maximum rates occurring at lowest *D*.

3.5. Ecosystem Characteristics

[32] When averaged over a day the NEE did not show as good an agreement with incident solar radiation as NEE did on an hourly basis (data not shown). There was still a weak correlation (r^2 = 0.15 for a curvilinear relationship) but the night-time fluxes showed little correlation with day-time solar radiation. The strongest indicator of mean nightly above-canopy flux was friction velocity, u_* (r^2 = 0.48). This relationship between night-time above-canopy flux and u_* consequently explained a similar proportion of the variation in NEE but because the periods of missing nocturnal data coincided with missing u_* nocturnal gaps were interpolated with the use of the mean NEE for that time of the year (Figure 12). There was no relationship between storage flux and u_*. After filling gaps and upscaling the estimate of NEE to 365 days the predicted yearly NEE for the Caxiuanã ecosystem was −5.6 t C ha^{-1} yr^{-1} i.e. 5.6 t C is estimated to have accumulated in this forest stand per hectare in 1999. However, as a number of studies have indicated problems with the correct measurement of the nocturnal efflux of CO_2 from tropical forests, this value is likely to be an overestimate of the true carbon uptake [*Malhi and Grace*, 2000]. A more detailed understanding of night-time CO_2 exchange is required before a definitive value of NEE can be calculated. When calculating gross primary productivity (GPP) for Caxiuanã, respiration was allowed to vary with season to produce an estimated GPP of 36.3 t C ha^{-1} yr^{-1}. This is higher than the 30.4 estimated by Malhi et al., largely because of the higher rate of respiration at the current site. We suggest that in the current year, photosynthesis and respiration were largely unconstrained by soil water, compared with in 1995, when the study site of Malhi et al. experienced soil water restrictions.

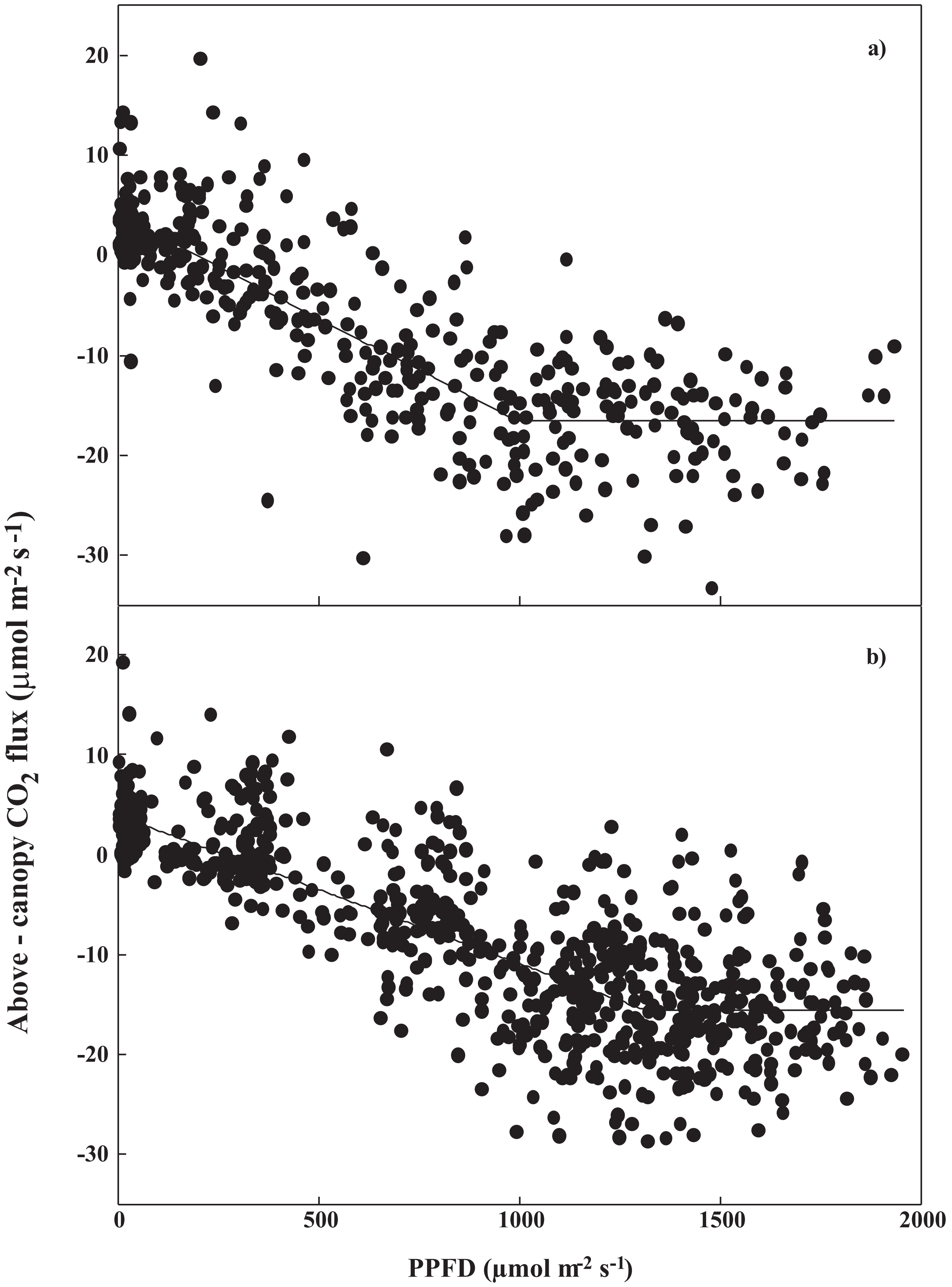

Figure 10. Hourly averaged above-canopy CO_2 flux against incident photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) for each season, (a) wet, and (b) dry, at Caxiuanã. Lines indicate the best fit of the light-response model.

Table 1. Comparison of Light Response Parameters for Two Seasons of Eddy Covariance Data at Caxiuanã Forest

Season	Apparent Maximum Quantum Yield, mol CO_2/mol photons	Light Compensation Point ± S.E. of Estimate, μmol m^{-2} s^{-1}	Maximum CO_2 Flux, μmol m^{-2} s^{-1}
Wet	0.045 ± 0.002	195 ± 5	20.5 ± 0.7
Dry	0.032 ± 0.001	275 ± 5	19.6 ± 0.5

[33] Studies using eddy covariance to estimate Amazonian NEE, including this one, have consistently measured a net uptake of C on an annual basis [*Fan et al.*, 1990; *Grace et al.*, 1995a; *Malhi et al.*, 1998]. This has now been corroborated by evidence of biomass increase, albeit of a smaller magnitude, in mostly South American permanent sample plots [*Phillips et al.*, 1998]. The difference in magnitude has been explained by a possible lack of accounting for C accumulation in soil and litter pools in the permanent sample plots, a potential undersampling of night-time efflux of CO_2 in eddy flux experiments [*Goulden et al.*, 1996], and also by the limited replication, to date, of tropical eddy covariance studies in both time and space. The LBA project attempts to address all of these possibilities. Another synthesis of net primary productivity in tropical forests has shown a net increase with an upper limit of 22 t C ha^{-1} yr^{-1} [*Clark et al.*, 2001]. Our estimate falls well within the reported range.

[34] The current study shows a different pattern of C uptake within a year, compared with the study of *Malhi et al.* [1998]. The most important distinction between the two studies is thought to be the occurrence of the El Niño Southern Oscillation (ENSO) in 1995, which was absent from the present study. The ENSO is most likely to cause a drier-than-usual dry season [*Zeng*, 1999]. Analyses of net ecosystem productivity (NEP) using satellite data to characterize the Amazon basin suggest that interannual variability due to rainfall may be sufficiently large to make forest sinks into sources in dry (El Niño) years [*Potter et al.*, 2001]. Potter and coworkers also give evidence of a decrease in seasonality of NEP in wet years. Continued measurement of fluxes at Caxiuanã will give us the opportunity to further investigate interannual variability in carbon exchange and environmental drivers of this process. In addition, permanent sample plots are being established for the purpose of comparison. Metaanalysis of flux data from LBA sites should provide further clues to the impact of the ENSO on interannual variability compared with site effects. Data from three years of eddy covariance monitoring in Costa Rica is also about to be published (Ameriflux), which, when coupled with data from Maeklong in Thailand (Asiaflux), will allow comparison of data across three distinct tropical regions. It seems likely that there is a net terrestrial carbon sink, the proportion of which can be attributed to the tropics, remains to be resolved [*Malhi et al.*, 1999].

4. Conclusions

[35] The amount of carbon exchanged by this site at Caxiuanã shows similarity with predictions from other sites of similar forest types. No significant reduction in maximum photosynthesis rate or NEE was observed during the dry season. The observed increase in canopy leaf area appears to have equaled any environmental reduction of photosynthesis with increased dryness during the dry season. By the same token, the increase in solar radiation during the dry season did not increase photosynthesis, suggesting a delicate balance between increased *D* and radiation at this time. We suggest that during a year with greater seasonal variation in rainfall (i.e. an El Niño year) a seasonal reduction in photosynthesis would be likely.

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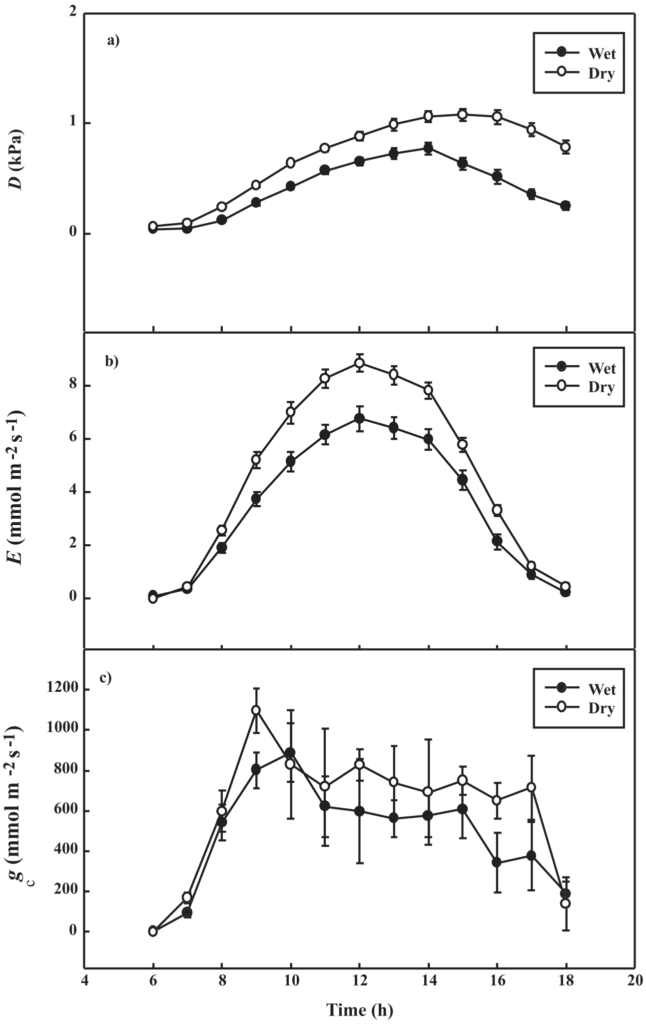

Figure 11. Mean diurnal cycle at Caxiuanã, grouped by season, of (a) vapour pressure deficit (*D*, kPa), (b) evapotranspiration (*E*, mmol m^{-2} s^{-1}) and (c) canopy conductance (g_c, mmol m^{-2} s^{-1}).

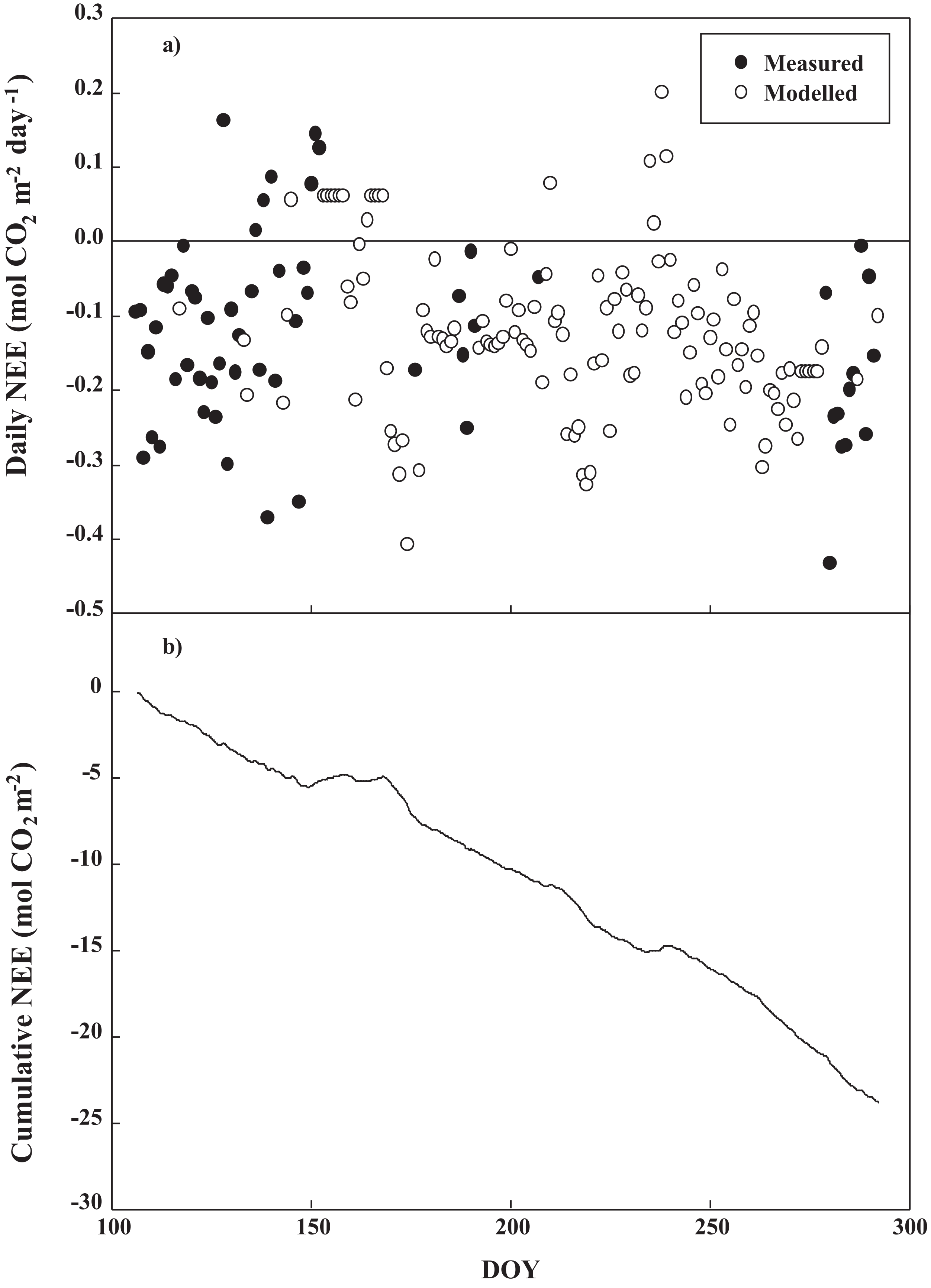

Figure 12. Data used to calculate Caxiuanã net ecosystem exchange (NEE) for the entire study period (16 April 1999 to 19 October 1999), shown as (a) totals for both measured and modelled individual days and (b) the cumulative total over 186 days.

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