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Soil CO_2 efflux in a tropical forest in the central Amazon

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Abstract

This study investigated the spatial and temporal variation in soil carbon dioxide (CO_2) efflux and its relationship with soil temperature, soil moisture and rainfall in a forest near Manaus, Amazonas, Brazil. The mean rate of efflux was 6.45 ± 0.25 SE µmol $CO_2\,m^{-2}s^{-1}$ at 25.6 ± 0.22 SE °C (5 cm depth) ranging from 4.35 to 9.76 µmol $CO_2\,m^{-2}s^{-1}$; diel changes in efflux were correlated with soil temperature ($r^2 = 0.60$). However, the efflux response to the diel cycle in temperature was not always a clear exponential function. During period of low soil water content, temperature in deeper layers had a better relationship with CO_2 efflux than with the temperature nearer the soil surface. Soil water content may limit CO_2 production during the drying-down period that appeared to be an important factor controlling the efflux rate ($r^2 = 0.39$). On the other hand, during the rewetting period microbial activity may be the main controlling factor, which may quickly induce very high rates of efflux. The CO_2 flux chamber was adapted to mimic the effects of rainfall on soil CO_2 efflux and the results showed that efflux rates reduced 30% immediately after a rainfall event. Measurements of the CO_2 concentration gradient in the soil profile showed a buildup in the concentration of CO_2 after rain on the top soil. This higher CO_2 concentration developed shortly after rainfall when the soil pores in the upper layers were filled with water, which created a barrier for gas exchange between the soil and the atmosphere.

Keywords: carbon dioxide, rainfall effect, soil carbon, soil respiration, soil temperature, soil water content

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Introduction

The efflux of carbon dioxide (CO_2) from soil results almost entirely from the combined rates of autotrophic (root) and heterotrophic (microbial and fungal) respiration; it is often called 'soil respiration'. Globally, soil respiration comprises a release of carbon to the atmosphere of approximately $80\,Pg\,C\,yr^{-1}$ to which the largest contributions come from tropical and subtropical broadleaved forests (Raich *et al.*, 2002). While together these and other terrestrial ecosystems show significant interannual variability in gross primary productivity (e.g., Schimel *et al.*, 2001), the relative variation of global soil respiration is lower, responding (globally) less strongly to water than to temperature (Schlesinger, 1977; Raich *et al.*, 2002).

Over smaller spatial and temporal scales much more variation in soil respiration can be discerned. Distinct vegetation types exhibit large differences in the relative contribution from autotrophic respiration, ranging from croplands to tundra by 12–93%, with an approximate value of 50% estimated for forests (Hanson *et al.*, 2000; Raich & Tufekcioglu, 2000). Temperature is a dominant factor determining soil respiration rates at a forest stand level or at smaller scales (Jenkinson *et al.*, 1991; Katterer *et al.*, 1998) but respiratory processes in soil are also strongly influenced by soil moisture, with drier soils tending to yield lower effluxes of CO_2 (Parker *et al.*, 1984; Davidson *et al.*, 2000).

The relatively recent use of micrometeorological measurement methods has significantly advanced our understanding of whole ecosystem carbon processing by yielding estimates of stand-scale CO_2 fluxes, the combined balance of photosynthetic and respiratory processes (e.g., Moncrieff *et al.*, 1997; Baldocchi &

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Wilson, 2001). However, despite this advance, the measurement of total (including night-time) respiration remains uncertain (Araujo *et al.*, 2002) and in this context component-scale measurements can help to constrain the value for total respiration and hence estimates of net ecosystem productivity (Meir & Grace, 2002). Mean soil respiration rates for forests in Amazonia range from 3.2 to 6.2 μmol m^{-2} s^{-1} for reported soil temperatures between 22 °C and 25 °C (Trumbore *et al.*, 1995; Meir *et al.*, 1996, Davidson *et al.*, 2000; Chambers *et al.*, 2004). These studies suggest that 50–84% of total respiration comes from the soil (Meir, 1996; Malhi *et al.*, 1999; Chambers *et al.*, 2004) and consequently it is the largest component of ecosystem respiration in Amazonian forests.

Soil respiration can vary strongly over space, with CO_2 efflux rates for individual microsites (e.g. 0.25 m^2) changing by over an order of magnitude over just a few meters (Schlesinger, 1977). Variation also occurs in response to changes in soil temperature and moisture, reflecting the biochemical basis of the component respiratory processes that occur simultaneously at different depths within the soil profile (Davidson *et al.*, 2000). Finally, physical constraints also act upon the measured efflux rate of CO_2 from soil. These include the repression of effluxes from soils that have been temporarily or chronically saturated by water, and the potentially positive influence of ambient pressure changes on efflux rates that are not accounted for using closed chamber measurement systems (Hutchinson & Mosier, 1981; Norman *et al.*, 1997; Conen & Smith, 1998). Closed chamber systems may also slightly (~ 10%) underestimate true efflux rates because of the difficulty of measuring the volume of the soil air space, a requirement of the method (Rayment, 2000). The soil respiration rate for our study site (see below) inferred from above-canopy eddy covariance measurements (Malhi *et al.*, 1998), was 5.4 μmol m^{-2} s^{-1} in 1995/1996, while measurements made approximately at 10 km distance from this site using a closed chamber system gave lower efflux rates (3.2 μmol m^{-2} s^{-1}; Chambers *et al.*, 2004). The measurements in this study were made with an open-dynamic chamber system designed to obviate possible measurement artifacts associated with ambient pressure changes at the soil surface (Kanemasu *et al.*, 1974; Rayment & Jarvis, 1997).

The principal objective of our work was to quantify soil respiration in a primary tropical rainforest at the Cuieiras Reserve in central Amazonia. The area in which measurements were made coincided with the flux footprint (*sensu* Schuepp *et al.*, 1990) of the measurements made by Malhi *et al.* (1998). We examined spatial variability in soil respiration, including its variation with respect to aboveground biomass, and measured the temporal variability in respiration rates in relation to temperature, soil moisture status and rainfall events.

Material and methods

Site description

The measurements were made in the Reserva Biológica do Cuieiras (2°35′22″S, 60°06′55″W), a forest reserve belonging to the Instituto Nacional de Pesquisas da Amazônia (INPA), some 60 km north of Manaus, Amazonas, Brazil. This is an undisturbed dense lowland terra firme forest with a mean annual rainfall of 2200 mm; canopy height, 30 m; aboveground dry biomass, 300–350 t ha^{-1} and leaf area index, 5–6 (Malhi *et al.*, 1998). The soil is a yellow clay latosol (Brazilian classification) or oxisol (US Department of Agriculture soil taxonomy), with a high (80%) clay content, low nutrient content, low pH (4.3), very high porosity (50–80%, Chauvel *et al.*, 1991), and a low available water capacity (Correa, 1984; Hodnett *et al.*, 1995). This highly weathered, nutrient-poor soil type is typical of much of lowland central and eastern Amazonia (Sanchez, 1989).

Sampling and sample processing

Gas exchange measurements. Spatial variation in soil CO_2 efflux was assessed in a 60 m × 180 m plot (500 m from the eddy measurements tower). A dynamic open measurement system of the type described by Rayment & Jarvis (1997) was used in conjunction with an infrared gas analyzer (IRGA) (LCA3, ADC Ltd, Herts, UK) to measure soil CO_2 efflux. To make a measurement, the chamber was sealed onto steel collars (13 cm diameter) that had 24 h previously been gently pushed 1 cm into the soil, taking care to minimize disturbance to any roots. Soil CO_2 efflux (R, μmol m^{-2} s^{-1}) was calculated as a function of the difference in CO_2 concentration between air entering and leaving the chamber ($\Delta[S]_{ch}$, μmol m^{-3}), the molar flow rate through the chamber (F_{ch}, m^3 s^{-1}), and the area of soil under the chamber (A_{ch}, m^{-2}), using the following equation:

$$R\,(\mu\mathrm{mol\,m^{-2}\,s^{-1}}) = \Delta[S]_{ch}\,F_{ch}/A_{ch}. \tag{1}$$

In order to mimic the effects of rainfall during measurements, rainfall was collected above the chamber (using a funnel of the same diameter) and evenly distributed over the soil in the chamber by channeling it through a stainless-steel perforated membrane (perforation diameter = 1.59 mm) placed very close to the soil in order to avoid any air

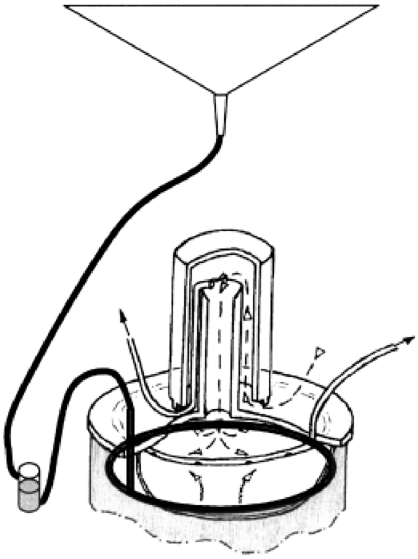

Fig. 1 Diagram of the open chamber (Rayment & Jarvis, 1997) with the adaptation for rainfall. For the sealing of the tubing from the funnel to inside the chamber an inverted 'J' seal was used. The fluxes after the adaptation were compared with a LiCor 6400 soil efflux chamber.

movement. A water seal was used to prevent leakage of CO_2 through the perforated membrane (Fig. 1).

The site was presampled in order to establish the number of samples needed to represent the area adequately. Data from six measurement points were used to obtain the coefficient of variation (CV) in CO_2 efflux. The following equation was used to calculate the minimum number of measurements necessary to represent the sample area with 95% confidence (i.e., $LE = 0.05$), which was 18 (Pellico Neto & Brena, 1997):

$$n = \frac{t^2 \mathrm{CV}^2}{\mathrm{LE}^2}, \qquad (2)$$

where n is number of samples units, t is Student's t-value at $\alpha = 0.05$ and degrees of freedom = 5, CV is the coefficient of variation and LE is the selected relative limit of error (confidence limit).

The plot was divided into 27 subplots (20 m × 20 m) from which 20 were selected using a random number table. Within each subplot the positions of two points (microsites) were further determined using a random number table. At each microsite soil CO_2 efflux measurements were made for approximately 2.5 h; all 40 measurements were completed between 20 May 1997 and 12 June 1997. The measurements were made between 08:00 and 19:00 hours and, in order of the difficulty of moving the equipment in the forest, they followed a zigzag order from NW to SE inside the plot.

Temporal variation was evaluated during two periods, 16 June–9 July 1997, during the transition from wet to dry season, and 7 October–12 December 1997 (not continuously) during the period in which the transition from dry to wet season normally occurs.

For the first period of evaluation of short-term temporal variation in CO_2 effluxes, three subplots out of the sample of 20 used in the spatial variability assessment were chosen for further study (the subplot with an efflux rate closest to the mean value, and two further subplots with the highest and lowest measured values). We sampled one subplot at a time because of the limitation of the equipment. For each subplot two chambers (series 'a' and 'b') were placed on the same microsites used to assess spatial variation measurements, but only after an interval of more then 25 days, in order to avoid any influence from the previous measurements. Soil CO_2 efflux data were recorded from 16 to 20 June 1997 in subplot 4, from 25 to 29 June 1997 in subplot 10 and from 2–4 and 7–10 June 1997 in subplot 27.

For the second period of temporal variation only subplot 4 was reassessed. Soil efflux data was recorded on the following dates 7–8 October, 14 October, 5 November, 11 November, 17 November and 12 December. Except for the 7–8 October full 24 h measurement, all other measurements were recorded only between 10:00 and 16:00 hours.

Soil temperature was monitored using copper–constantan thermocouples placed at 0, 1, 5, 10 and 25 cm into the soil profile immediately adjacent to the chamber. The thermocouples were referenced to a calibrated thermistor placed at 50 cm. The data were stored using a 21X datalogger (Campbell Scientific Ltd, Leicester, UK).

Ancillary measurements

Biomass data. The basal area of the plot was obtained by measuring the total diameter at breast height (dbh, 1.30 m) of all trees >10 cm dbh. Biomass in this forest is approximated as a linear function of this value (Araujo *et al.*, 1996).

Micrometeorological data and soil water content. During the period of data collection, meteorological (rainfall, air and soil temperature) and soil moisture measurements were taken at the same site by INPA. Soil moisture was measured with a neutron probe in three profiles on 6 February, 10 April, 22 May, 05 June, 19 June, 31 July 1997, 14 August, 28 August, 09 October, 21 October and 17 December at depths of 10 and 20 cm and then at 20 cm intervals to the maximum depths (either 380 or 400 cm) (A. Marques, unpublished data). A water balance approach, using locally measured rainfall, was used to estimate soil moisture in the intervals between neutron probe measurements.

The estimated soil water storage (SWS) was fitted to the data using the following equation:

$$\mathrm{SWS} = \mathrm{SWS}_{i-1} + \mathrm{RF} - D - \mathrm{ET}, \qquad (3)$$

where SWS_{i-1} is the measured SWS, RF is the rainfall, D is drainage and ET is evapotranspiration.

Soil profile measurements. The gradient in soil CO_2 concentration was measured at two randomly chosen points inside the subplot 4, 3 m away from each other (this experiment was only carried out in December, in the beginning of the wet season). At each point a hole of 40 cm depth was made, and after inserting the stainless-steel tubes at 2, 5, 10, 20 and 40 cm depth, the hole was back-filled with the soil. Samples of gas in the soil air space were obtained using a syringe attached to the gas sampling tubes. The gas samples were collected from these two points on 3 days with differing soil water tensions in the first 10 cm of soil:

(a) 9 December 1997, high water tension in top soil (6 days without rain).
(b) 10 December 1997, low water tension in top soil (just after a rain event with 22.4 mm precipitation).
(c) 13 December 1997, higher water tension again (48 h without rain).

Further gas samples were collected 30 min, 1 and 3 h after the initial sampling. Soil CO_2 concentrations were measured using an IRGA (Licor LI 6262, Licor Inc., Lincoln, Nebraska, USA); a 20 mL gas sample was injected into a CO_2-free air stream and then through the IRGA sample cell. The IRGA response with time was recorded at 1 Hz and the CO_2 concentration was calculated using a calibration curve derived from injections of three standard concentrations (Davidson & Trumbore, 1995).

Tensiometers were built using a 1 cm OD × 10 cm porous ceramic cup, 1 bar air entry value (Soilmoisture Equipment Corp., Santa Barbara, CA, USA) and installed at 2, 5 and 10 cm depth into the soil column 1.5 m from the CO_2 concentration profiles. Water tension measurements in the soil were made at the same time as gas samples were taken using a pressure transducer (Current Transducer 5301, Soilmoisture Equipment Corp.).

Data analysis

The data examining spatial variation were checked for a pattern in relation to the time of sampling, due to the difference in soil moisture between the first and last measurements of CO_2 efflux. The effluxes were normalized using an exponential function for temperature in order to minimize the effect of temperature variations (Fig. 5).

Any possible relationship between soil CO_2 efflux (R) and tree basal area (g) was investigated using regression analysis on the matching data of the measured CO_2 efflux and the corresponding integrated points of basal area, excluding those at the edges of the plot. For the integration of the basal area data, kriging interpolation was used.

Pearson correlation analysis was used to check the relationship between temperature and moisture profile within the whole dataset and between temperature profile and CO_2 efflux.

Linear regression analysis was used to examine relationships between each depth of soil temperature and soil CO_2 efflux as well as the relationship between temperature and soil moisture separated by series. Regression analysis was also used to examine the relationship between soil CO_2 efflux and soil moisture. The temperature sensitivity in the rate of CO_2 efflux was analyzed using measurements made at 5 cm depth, excluding data collected during rain events. The data were fitted to an exponential model:

$$R = R_0 e^{kT}, \qquad (4)$$

where R is the CO_2 efflux ($\mu\mathrm{mol\,m^{-2}\,s^{-1}}$), R_0 is the CO_2 efflux at average soil temperature ($\mu\mathrm{mol\,m^{-2}\,s^{-1}}$), k is the CO_2 efflux exponential response coefficient for temperature, and T is the soil temperature at 5 cm depth (°C).

Results

Meteorological characterization of the data collection period

The first period of data collection (20 May–9 July 1997) was characterized by the transition from the wet to the dry season. The start of the second period of data collection (7 October–13 December 1997) followed a long period with little rainfall. After 2 November, rainfall was more frequent and this period can be characterized as the early part of the transition to the wet season (the upper layers of the soil profile were kept wetted by rainfall, although the deeper layers – below 1 m – were still very dry indeed). Figure 2 shows the air and soil temperature, soil moisture and rainfall for the period of data collection. The data for temperature and rainfall from 19 February to 3 May 1997 and from 19 July to 10 September 1997 are not shown because during these two periods of the year, the instruments were not functioning.

During the experiment for spatial variation (20 May–12 June 1997) the average soil temperature at 5 cm depth was 25.6 ± 0.22 °C (mean ± SE). Soil temperature slightly decreased with depth, the highest soil temperature was at 0 cm (25.9 ± 0.20 °C) and the lowest at 50 cm depth (25.1 ± 0.25 °C). The average temperature

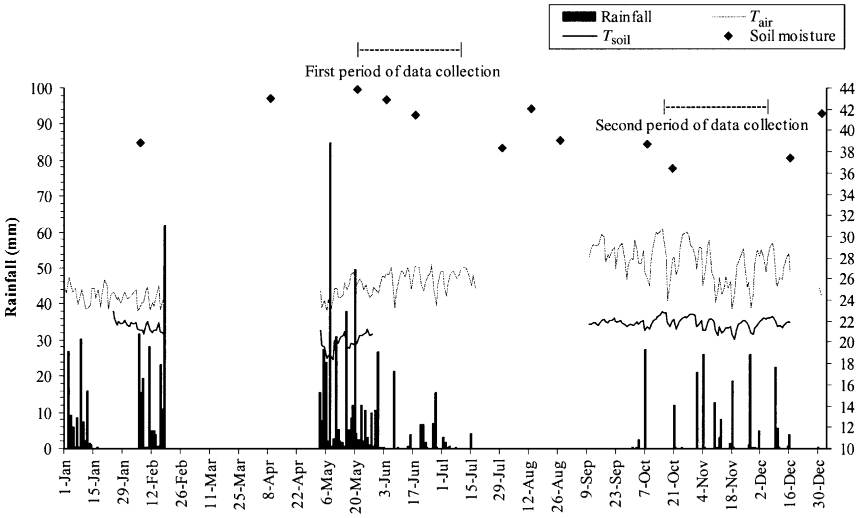

Fig. 2 Micrometeorological data for the data collection periods. Soil temperature measured at 10 cm depth and soil moisture representing the average of three neutron tubes from 0 to 100 cm depth.

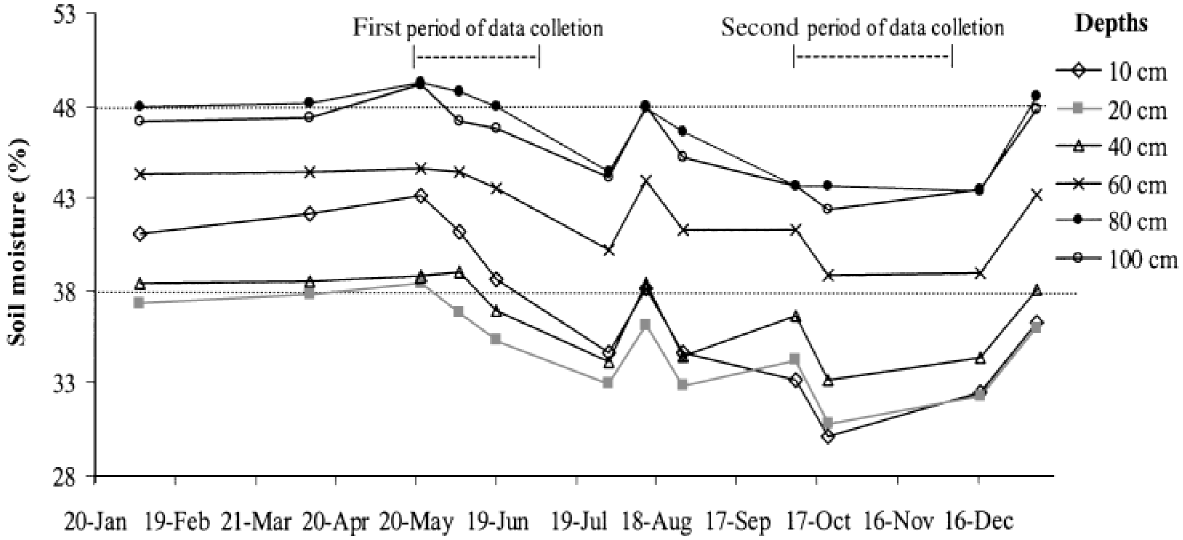

Fig. 3 Soil moisture profile separated by depth layers. Average values of three neutron probe profiles during the year of data collection (1997).

at 5 cm depth during the temporal variation measurements (16 June–9 July 1997) was 25.4 ± 0.36 °C.

Profile of soil water content and estimate of SWS

The volumetric water content of the top 100 cm of the soil varied by $0.07\,m^3\,m^{-3}$, drying from $0.439\,m^3\,m^{-3}$ (field capacity) to $0.365\,m^3\,m^{-3}$ (low available water capacity). The 10 cm layer varied from 0.41 to $0.20\,m^3\,m^{-3}$, while the layers 80 and 100 cm varied only from 0.49 to $0.42\,m^3\,m^{-3}$ (Fig. 3). During the period of data collection for spatial variation the mean volumetric water content in the 0–100 cm layer decreased from 43.7% ($0.437\,m^{-3}m^{-3}$, the highest value of the year) to 41.5% ($0.415\,m^{-3}\,m^{-3}$). At the beginning of the second period of data collection, on 7 October 1997, the mean soil moisture in the 0–100 cm layer was 36.1% ($0.361\,m^{-3}\,m^{-3}$), and it kept falling until the end of October.

As reflected in the soil water content, the SWS for the entire period of data collection decreased with a slight increase in the end of the second period (November–December) (Fig. 4). The first period of data collection started with normal storage for the wet season (436.5 mm) and decreased gradually as the dry season started (382.7 mm). Before it rained on 8 October the profile was very dry and probably with almost no more

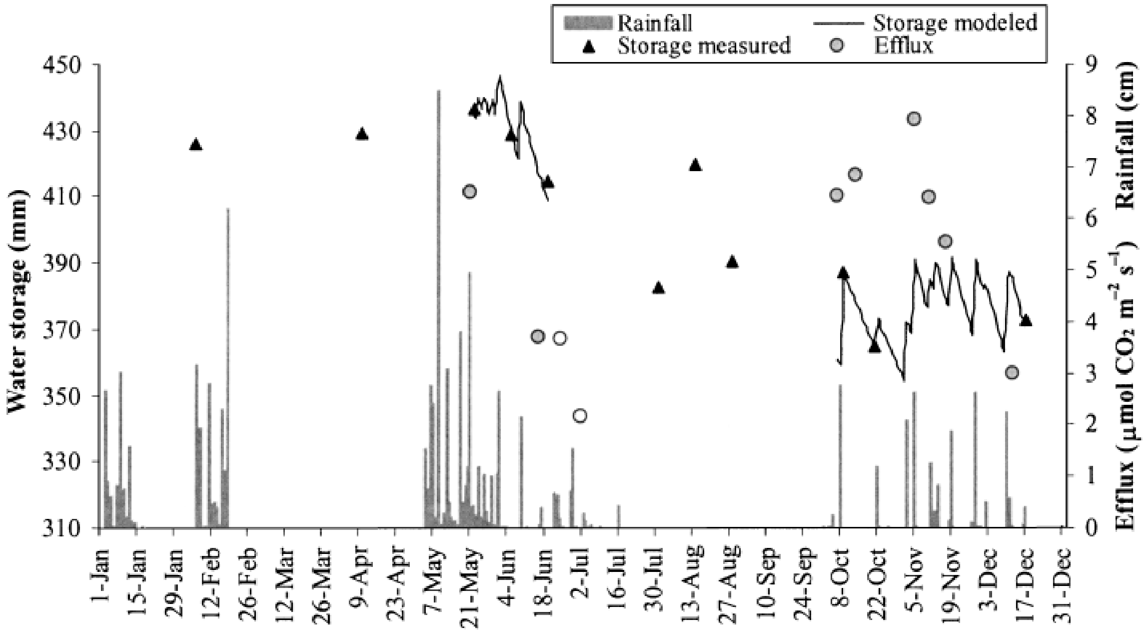

Fig. 4 Rainfall, soil water storage, estimate of soil water storage and soil CO_2 efflux for the year of data collection. Soil water storage was estimated for the periods of data collection using the rainfall data. The white points (subplots 10 and 27) shown for efflux are not measured in the same site as the dark points (subplot 4).

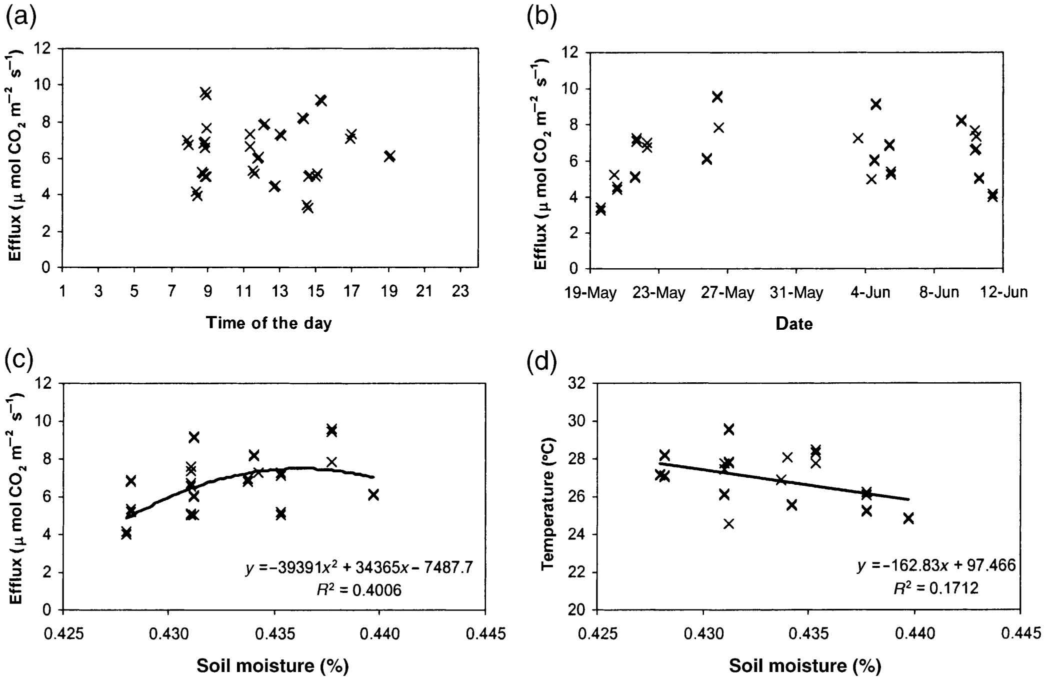

Fig. 5 Spatial variation data plotted against some parallel variation factors during the 23 days of sampling: (a) relationship between time of the day and efflux, (b) relationship between day of measurement and efflux, (c) relationship between soil moisture and efflux, (d) relationship between soil moisture and temperature.

available water (359.1 mm). In the first phase of the second period of data collection the top soil was extremely dry (except in the few days after rainfall events), and in the second phase (after 2 November) the conditions were a little wetter, except possibly around 26–27 November (after a dry spell) and again around

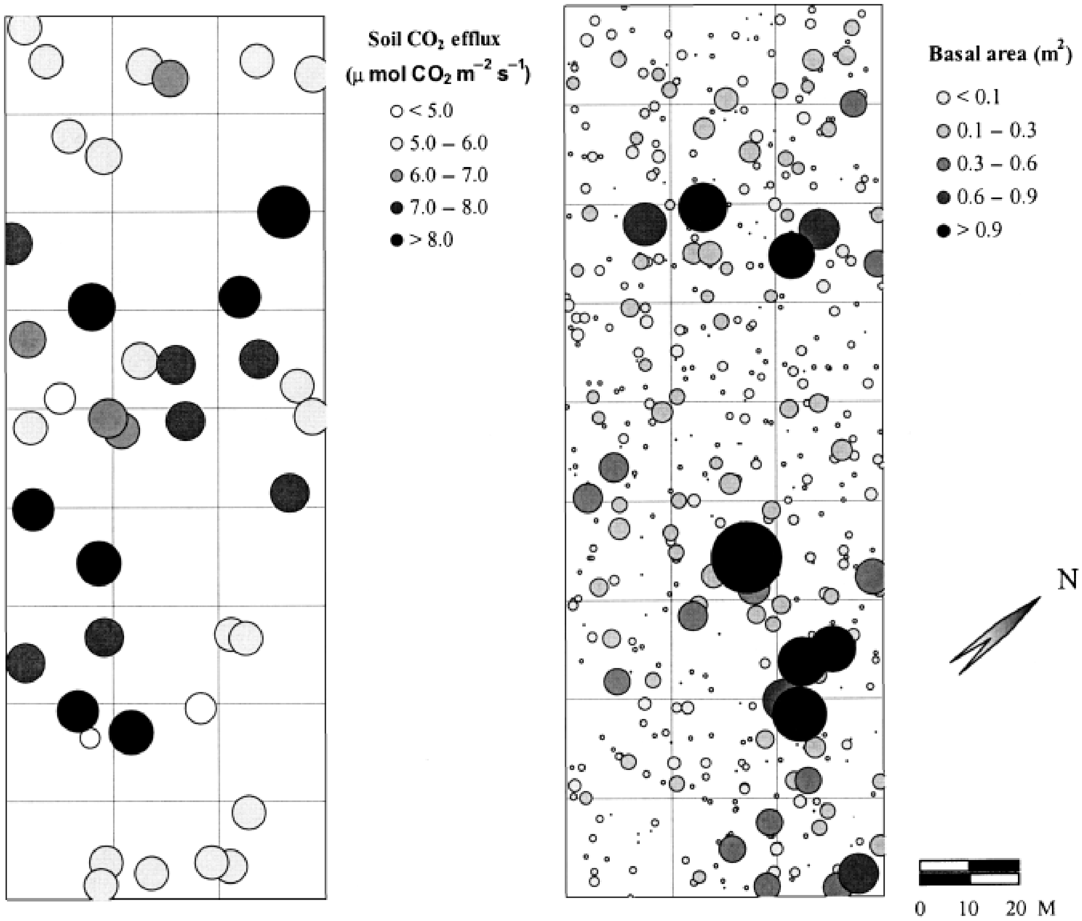

Fig. 6 Soil CO$_2$ efflux (a) and trees basal area (b) ordered in classes of size: (a) soil CO$_2$ efflux distribution (each point corresponds to a sample point) and (b) trees basal area distribution (each point corresponds to one measured tree).

7–10 December. The periods from 17–21 October to 26 October–1 November were very dry indeed and the topsoil reached its lowest water content since April 1995.

Spatial variation of the soil CO$_2$ efflux. We plotted the spatial soil CO$_2$ efflux data against date of measurement to look for any evidence of a temporal trend due to the change in soil moisture between the beginning and the end of the experiment and the difference in the time of the day.

Soil moisture seems to have had influenced the spatial sampling ($r^2 = 0.40$), although it was probably not a limiting factor during the sampling period and hence only a minor influence. Soil moisture was also weakly inversely related to temperature ($r^2 = 0.17$). Variation on efflux rate may have been influenced by time of measurement during this 23-day period (Fig. 5).

The mean soil CO$_2$ efflux was 6.45 ± 0.25 SE μmol CO$_2$ m^{-2} s^{-1} at 25.6 °C (5 cm depth), and 6.46 μmol CO$_2$ m^{-2} s^{-1} when corrected to the average temperature of the sampling period using Eqn (4) (where k value was calculated from temporal efflux data). The CV for soil CO$_2$ efflux at the 40 microsites was 24% with almost 85% of efflux rates between 5.0 and 9.0 μmol CO$_2$ m^{-2} s^{-1} and almost 50% between 6.0 and 7.0 μmol CO$_2$ m^{-2} s^{-1}.

The tree basal area ranged from 0.05 to 0.16 m^2 and the higher basal area points were frequently far from the border (Fig. 6). We investigated the spatial correlation between the soil CO$_2$ efflux and tree basal area and found no correlation ($r^2 = 0.0008$, $P = 0.87$, $n = 32$).

Temporal variation of the soil CO$_2$ efflux

Diurnal variation. Mean daytime efflux was 3.2 ± 0.02 SE μmol CO$_2$ m^{-2} s^{-1} ($n = 1728$) and night-time efflux was 2.7 ± 0.02 SE μmol CO$_2$ m^{-2} s^{-1} ($n = 2934$) for the first period of data collection. Twenty-four hours efflux ranged from 1.2 to 4.7 μmol CO$_2$ m^{-2}s^{-1}. The amplitude of the diurnal cycle was 1.3 μmol CO$_2$ m^{-2} s^{-1} in the end of the wet season (soil moisture = 0.42 m^3 m^{-3}), 16 June

Table 1 The regression data obtained from fitting the temporal series data to Eqn (4)

Series	R_0	k	r^2	P-value
1a	−1.1557	0.1150	0.95	0.001
1b	−1.1207	0.1136	0.94	0.001
2a	−2.4509	0.1573	0.25	0.001
2b	−2.4903	0.1588	0.27	0.001
3a	−7.7716	0.3778	0.89	0.001
3b	−7.7285	0.3762	0.89	0.001
4a	−0.7555	0.0736	0.70	0.001
4b	−0.8941	0.0788	0.70	0.001
5a	−0.6449	0.0686	0.53	0.001
5b	−0.6700	0.0695	0.56	0.001
6a	−1.9560	0.0933	0.89	0.001
6b	−1.9373	0.0928	0.90	0.001
7a	9.3036	−0.3944	0.68	0.001
7b	9.7611	−0.4136	0.65	0.001
8a	0.4549	0.0196	0.07	0.001
8b	0.0449	0.0303	0.12	0.001
9a	0.8965	0.0031	0.005*	0.415
9b	0.2162	0.0249	0.18	0.001

Each series corresponds to a 24 h period from 16 June to 9 July 1997, excluded the data during rainfall events. Q_{10} (1.8) was calculated from the mean k value (0.0581) given from all series. *Except series 9a that had nonsignificant relationship.

1997; while at the beginning of the dry season (soil moisture = 0.37 $m^3 m^{-3}$) it was only 0.6 μmol CO_2 $m^{-2} s^{-1}$ (11 July 1997).

For the second period of data collection day and night efflux did not differ, day efflux was 5.8 ± 0.11 SE μmol CO_2 $m^{-2} s^{-1}$ ($n = 110$) and night efflux was 5.8 ± 0.05 SE μmol CO_2 $m^{-2} s^{-1}$ ($n = 144$). The 24 h efflux ranged from 4.5 to 9.1 μmol CO_2 $m^{-2} s^{-1}$ and the amplitude of the diurnal cycle was 4.6 μmol CO_2 $m^{-2} s^{-1}$.

Diel (24 h) efflux variation. The temporal relationships between diel cycle in CO_2 efflux and the measured temperature at various depths were investigated. For all depths of 0, 1, 5, 10, 25 and 50 cm the corresponding r^2 coefficients were 0.56, 0.50, 0.68, 0.65, 0.42 and 0.40, respectively, with $P < 0.05$. Hence the diurnal variation in soil respiration seems most directly driven by metabolic activity at about 5 cm depth. The temperature time series were always inversely correlated with the soil moisture time series with the degree of correlation increasing with depth ($r^2 = 0.30$, 0.31, 0.33, 0.36, 0.41 and 0.41 for depths of 0, 1, 5, 10, 25 and 50 cm, respectively).

The temporal variation data, for the first period of data collection, were divided into 24 h series (Fig. 9). For some series, efflux was explained to a large extent by temperature at 5 cm depth (Table 1), excluding the efflux during rainfall events. However in other series, temperature did not explain much of the diurnal soil CO_2 efflux variability, yielding an overall mean r^2 value of 0.60 ± 0.08 SE ($n = 17$). The lowest relationships occurred on days at the end of the first period of data collection (series 8a, 8b and 9b) and there were negative relationships for series 7a and 7b (series 9a had a nonsignificant relationship, $P > 0.05$). Furthermore, temperature in deeper layers had a better relationship with CO_2 efflux than the temperature nearer the soil surface during periods of lower soil moisture. The relationship between soil CO_2 efflux and soil temperature profile is shown in Fig. 7 as an average for series 1–5 (soil moisture 41%) and 6–9 (soil moisture 39%).

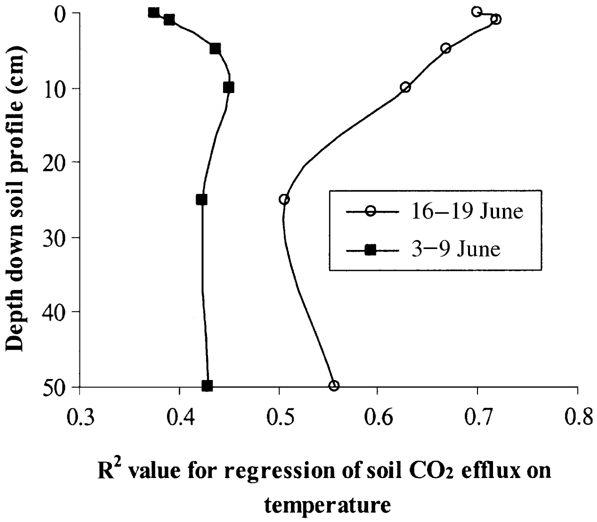

Fig. 7 r^2 values for soil CO_2 efflux and temperature regressions for temperature down the soil profile from 0 to 50 cm. Profile with white circles represents an average from 16 to 19 June (higher soil moisture) and profile with black squares represents an average from 3 to 9 July (lower soil moisture).

During the second period of data collection there was only one 24 h series (8 October 1997). However it was not possible to calculate a relationship because the temperature at 5 cm depth was not registered.

The k values ranged from –0.4136 to 0.3778 with an average of 0.0613 ± 0.0494 SE. The Q_{10} calculated with the average k was 1.8.

Period of drought and successive rewetting. During the second period of data collection, the efflux was initially high and decreased with time. The highest efflux measured was on 5 November (7.92 μmol CO_2 $m^{-2} s^{-1}$), which followed a >20 mm rainfall event, after a dry spell. Over subsequent rewetting events the efflux gradually decreased (Fig. 4) The average efflux for the second period was 6.02 ± 0.28 SE μmol CO$_2$ m^{-2} s^{-1} ($n = 6$).

The effect of rain on the soil CO$_2$ efflux

On average, soil CO$_2$ efflux dropped by 0.94 ± 0.50 SE μmol CO$_2$ m^{-2} s^{-1} ($n = 4$) at the start of a rainfall event. This corresponded with a drop in soil temperature (5 cm depth) by 3.0 ± 1.2 SE °C ($n = 3$) due to water infiltration in the soil (Table 2). Using eqn (4) and the average k value from temporal variation we calculated the drop in efflux due to the temperature reduction. The difference in soil temperature could explain 75% of the reduction on the efflux (0.7 μmol CO$_2$ m^{-2} s^{-1}).

A descriptive analysis was made using measurements of CO$_2$ concentration in the soil profile in order to understand this decrease in efflux when rain falls. There were three measurements of soil CO$_2$ concentration during rain days (soil water tension ranging from 0 to 0.73 kPa) and nonrain days (soil water tension ranging from 0 to 2.93 kPa) in an attempt to capture the influence of the water infiltrating the soil on the soil CO$_2$ efflux:

(a) 9 December 1997, when the top soil had high water tension (1.30 ± 0.24 kPa).
(b) 10 December 1997, when the top soil had low water tension (0.35 ± 0.15 kPa). Measurement made just after a rainfall of 22.4 mm.
(c) 13 December 1997, when the top soil had higher water tension again (0.64 ± 0.26 kPa).

The average CO$_2$ concentration in the top 10 cm of the soil from the third measurement was 2230 ± 447 ppm of CO$_2$, similar to the levels of the first measurement (2208 ± 296 ppm of CO$_2$), while for the second measurement (the wettest day) it was 2877 ± 570 ppm of CO$_2$. Water potential data indicated a higher ratio of air-filled pores to water-filled pores on drier days compared with wetter days (Fig. 10).

Discussion

Spatial variation of the efflux

The daytime temperature did not appear to be an important influence on spatial variation sampling (Fig. 5a), nevertheless it is possible that the low values found in the beginning and in the end of the data collection (Fig. 5b) reflected the soil water content exceeding field capacity and the lack of soil water content at the time of the measurement (Fig. 5c), respectively. Although soil CO$_2$ effluxes are affected by soil water availability, moisture only tends to strongly influence efflux rates below or above critical extreme values of soil moisture.

Table 2 Date and time for the beginning and end of the rainfall during the temporal soil efflux measurements

Day and time		Rainfall		Efflux (μmol CO$_2$ m^{-2} s^{-1})		Temperature at 1 cm (°C)		Temperature at 5 cm (°C)	
Beginning	End	Duration (min)	(mm)	Before	After	Before	After	Before	After
15 Jun 18:00	15 Jun 21:15	3:15	1.4	7.36	5.02	28.2	23.5	27.9	24.1
16 Jun 12:38	16 Jun 15:13	2:34	3.0	4.20	3.74	25.5	24.2	24.6	23.9
27 Jun 15:07	27 Jun 16:04	0:57	6.2	3.57	2.68	–	–	–	–
02 Jul 16:10	02 Jul 16:28	0:17	0.8	1.62	1.57	29.1	23.5	28.6	23.9

For each rainfall the duration and volume of the rainfall is given, the rate of CO$_2$ efflux and temperature at 1 and 5 cm depth before and after the rain.

Table 3 Studies with soil CO_2 efflux measurements for the Amazon region

Author	Season	Location	Vegetation	Temperature	Efflux (μmol CO_2 $m^{-2}s^{-1}$)	Methodology
Coutinho & Lamberti(1971)	Dry season (Aug–Sep)	Barcelos, AM, Brazil	*Floresta Ombrófila Densa*	25–28 °C soil temperature	2.8*	Aqueous solution 0.5 N KOH
Martins & Matthes (1978)	Dry season (Jul)	Manaus, AM, Brazil	*Campinarana, Campina*	Not stated	1.4 ± 0.5*	Chemical system – aqueous solution 0.5 N KOH
Medina *et al.* (1980)	2 years long	San Carlos do Rio Negro, Venezuela	Laterite Forest	22–27 °C forest floor	3.1 ± 0.5*	Chemical system – aqueous solution 0.5 N KOH
Wofsy *et al.* (1988)		Reserva Ducke, Manaus, AM, Brazil	*Floresta Ombrófila Densa*	Not stated	4.5	
Fan *et al.* (1990)	Wet season (Apr–May)	Reserva Ducke, Manaus, AM, Brazil	*Floresta Ombrófila Densa*	Not stated	5.9*	IRGA – closed dynamic system
Meir *et al.* (1996)		Reserva do Jarú, RO, Brazil	*Floresta Ombrófila Aberta*	22.9 °C soil temperature	5.5 ± 1.6*	IRGA – closed dynamic system
Davidson *et al.* (2000)	Year long	Fazenda Vitória, Paragominas, PA, Brazil	*Floresta Ombrófila Densa*	22–24 °C soil temperature at 10 cm depth	5.3*	IRGA – closed dynamic system
Chambers *et al.* (2004)	Year long	Manaus, AM, Brazil	*Floresta Ombrófila Densa* (plateau)	Not stated	3.8	IRGA – closed dynamic system
Present study	End of wet season	Manaus, AM, Brazil	*Floresta Ombrófila Densa* (plateau)	25.6 °C soil temperature at 5 cm depth	6.4 ± 0.25	IRGA – open dynamic system

*Transformed values by a factor of 0.023148 (mg m^{-2} h^{-1}).
The results were all transformed to the same unit.

Thus the influence of soil water on our measured efflux rates was probably small, but in any case will be included in our mean value, which itself is consistent with those from other studies in the Amazon region (see Table 3).

Lower soil CO_2 efflux was measured by Chambers *et al.* (2004) in a forest approximately 10 km distant from the site studied. The difference may be due mainly to the restricted time of the year (May/June) of our data collection and perhaps to the difference in measurement techniques. Chambers *et al.* (2004) also measured higher effluxes in May/June and plateaus compared with other time in the year and slopes and valleys. The efflux measured in this study is also higher than that estimated by Malhi *et al.* (1998) using above-canopy net CO_2 efflux data collected in the same area and considering that soil respiration may be as much as 84% (using the higher limit) of the total forest efflux (4.9–5.6 μmol CO_2 m^{-2} s^{-1}, Meir *et al.*, 1996). The higher efflux may be due to the limited range of topographic situations (i.e. plateau only) considered in our study compared with the variety of conditions covered by the footprint of the eddy covariance measurements, or due to an underestimation of night-time effluxes by the eddy covariance system (Malhi & Grace, 2000). A lower efflux was noted for slope and valleys soils, than for plateau soils in the forest in this area (Chambers *et al.*, 2004).

Temperature and soil water content have been frequently identified as dominant factors in controlling soil CO_2 efflux; however, they can mostly only explain temporal variation, especially in relatively uniform ecosystems. Our attempt to find a relationship with aboveground biomass was based on the idea that root distribution and litter microbes in the humus layer and mineral soil are more likely to be the factors defining spatial variation of soil CO_2 efflux (Schlesinger, 1977; Medina *et al.*, 1980; Kira, 1987; Raich & Nadelhoffer, 1989; Barbosa & Fearnside, 1996). However, basal area, indicative of aboveground biomass, did not show any significant relationship with efflux.

We suggest two hypotheses to explain why soil CO_2 efflux and tree basal area were not significantly correlated, although both together may explain partially the lack of relationship: (i) there is no relationship between basal area and litter or fine root production. The root distribution and litterfall in the soil is very heterogeneous. Root growth is influenced by the characteristics of the soil and litterfall by the position and form of the crown rather than the position of the trunk; (ii) there was a small contribution of litter decomposition on the efflux during the end of the wet season. The thinner litter layer on the soil surface, usual in tropical forests during the end of the wet season (Luizão & Schubart, 1987; Luizão *et al.*, 1992), may not contribute significantly (through organic matter breakdown) to the efflux. This would reduce the influence of litter on the spatial variation in efflux rate. The experiment was carried out when there was very little litter on the forest floor (at the end of the wet season and beginning of dry season).

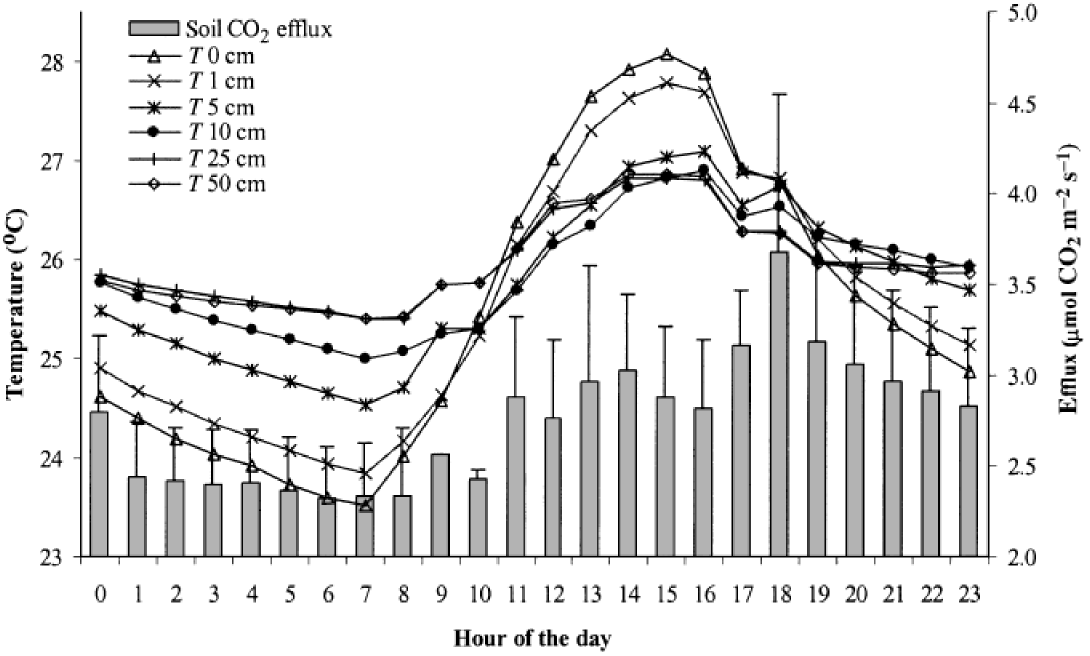

Fig. 8 Relationship between diel cycle variation in soil CO_2 efflux and temperature profile at depths from 0 to 50 cm. Average data for the temporal variation period.

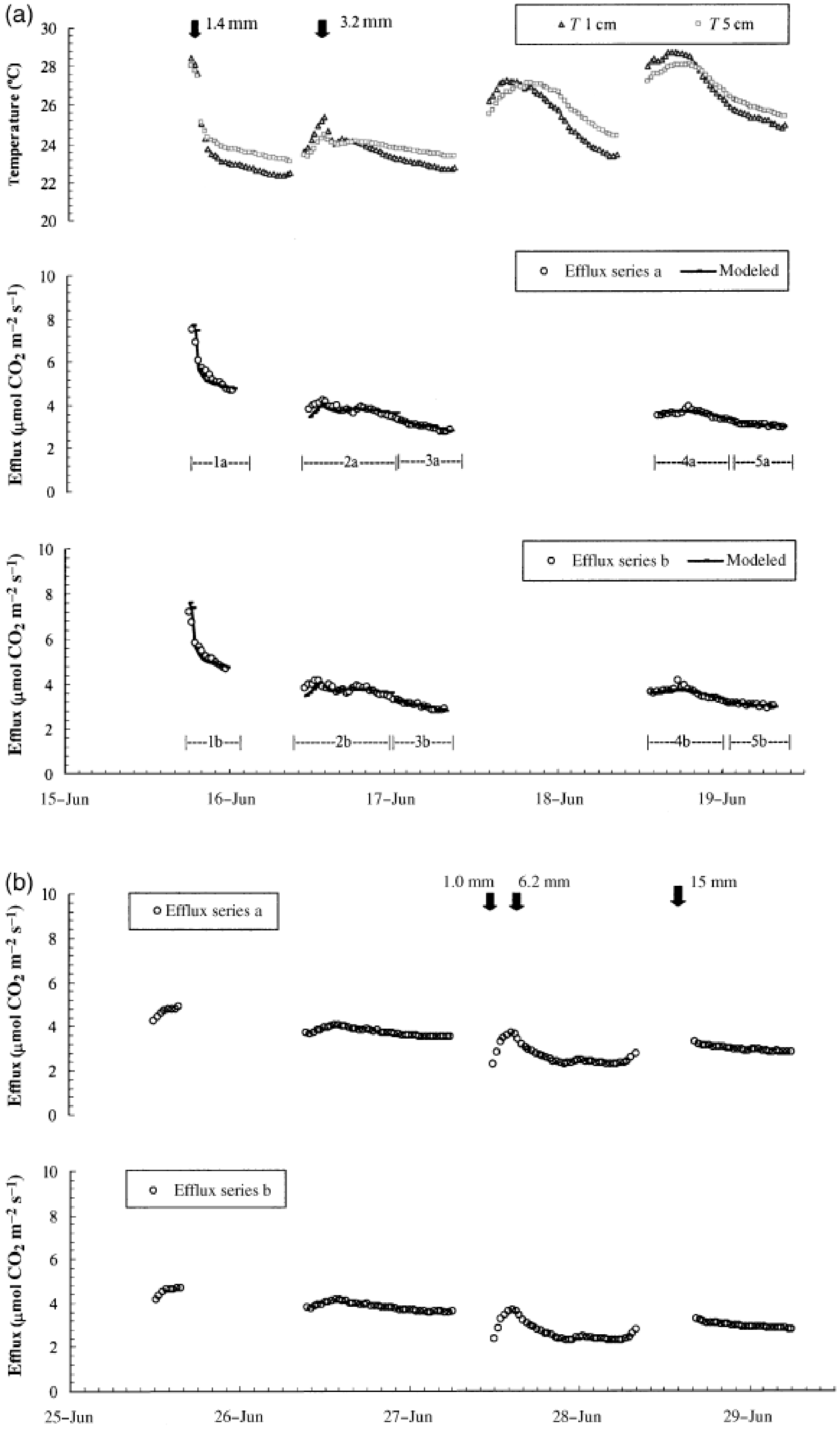

Fig. 9 (*continued*).

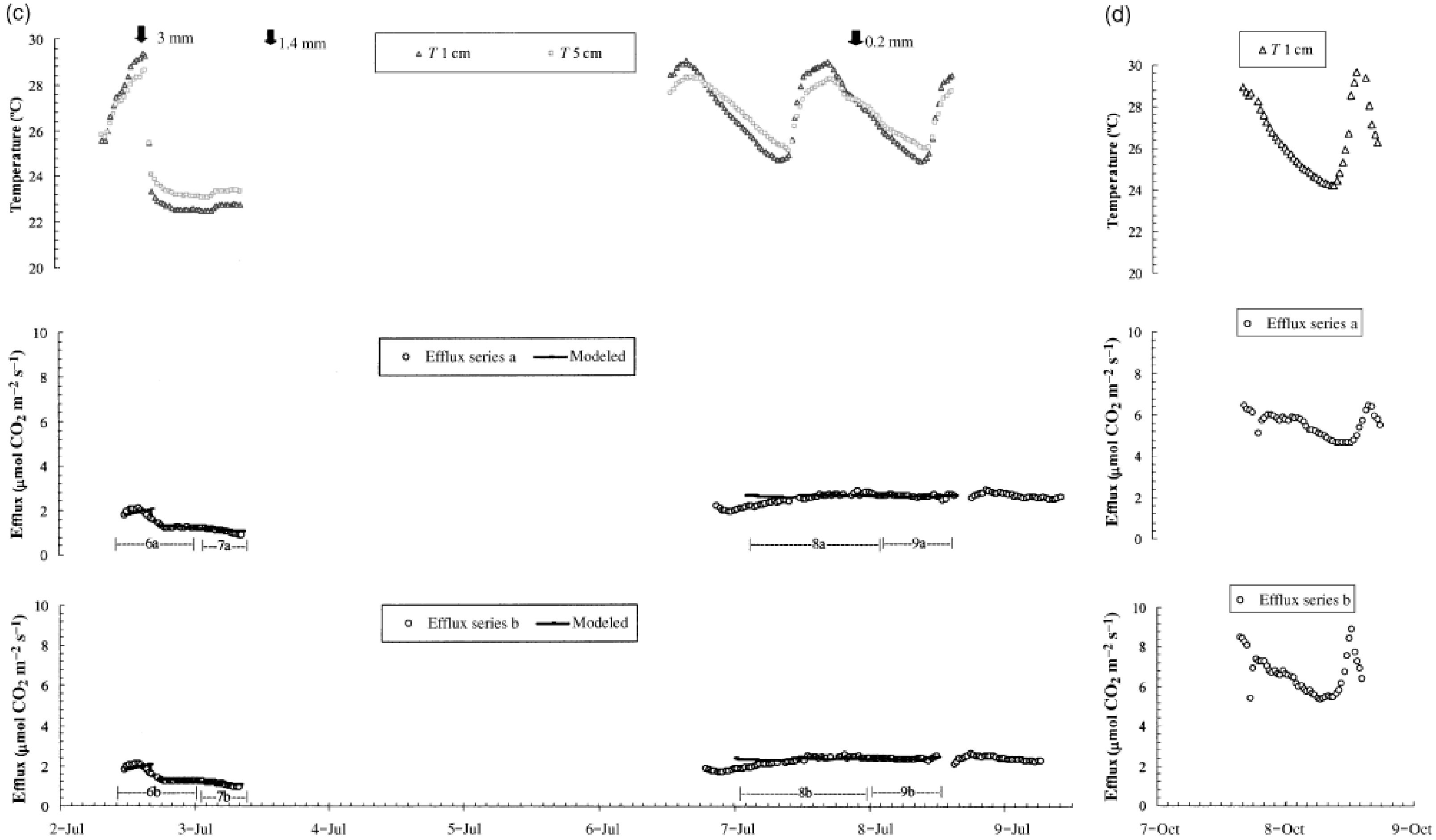

Fig. 9 Soil temperature at 1 and 5 cm depth, soil CO$_2$ efflux for series 'a' and 'b' and modeled efflux using the temperature exponential equation of individual series for the temporal variation measurements: (a) from 16 to 19 June 1997, (b) from 25 to 29 June 1997, this plot did not have temperature measurements for failure of the datalogger, (c) from 2 to 9 July 1997, (d) from 7 to 8 October 1997, the second period of data collection had only temperature at 1 cm depth registered.

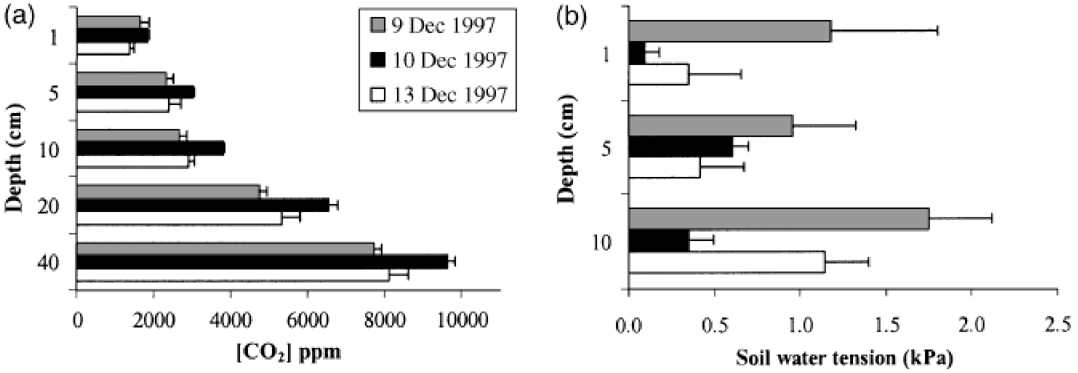

Fig. 10 Soil CO_2 concentration for soil layers at 0–40 cm depth and soil water tension at 0–10 cm depth for 3 sampling days. Each value of efflux is composed of two sampling points and four successive samplings (30 min, 1 and 3 h after the first sampling), while soil water tension values are composed of one sample point and four successive samplings.

Temporal variation

The soil CO_2 efflux diel cycle is characterized by lower and more constant values during the night and higher and more variable values during the day (Fig. 8). For measuring the night-time variation of the efflux two measurements appear to be sufficient, one in the beginning of the night (around 20:00 hours) and another in the early morning (around 07:00 hours). The efflux during the night can be estimated considering a linear decline. However, for capturing the variation during the day it would be necessary to measure the soil CO_2 efflux every hour or two. The diel cycle was dependent on temperature (60%) but also was influenced by soil moisture (39%, Fig. 9) and disturbed by the rain events (drop around 30% on the efflux).

Response of soil CO_2 efflux to temperature. Meir *et al.* (1996) found, for a tropical forest in Rondonia, southwestern Amazonia, that the temperature at 5 cm depth is responsible for 76–88% of the temporal variation. Similar observations have been made for different ecosystems (Hanson *et al.*, 1993; Lloyd & Taylor, 1994; Fang, 1997). Our study found a lower dependence of the temporal variation due to temperature at 5 cm depth ($r^2 = 0.60$), and as observed by Davidson *et al.* (2000), our study also found that the efflux response on diel cycle temperature was not always a clear exponential function (Table 1).

The poor relationship between soil efflux and temperature frequently occurred when soil water content was low, which indicates that by the days 7–9 July 1997 water content was almost certainly acting as a limiting factor for soil CO_2 efflux (Davidson *et al.*, 1998, 2000; Schwendenmann *et al.*, 2003). During this period negative k values were also recorded that may have been a result of an inverse correlation between temperature and surface soil moisture. The large variation in k, probably a result of a combination of physical and biological processes, should alert modelers to reconsider the constant value often used in the modeling equations (Davidson *et al.*, 1998).

Day to day variation and soil water content. The poor relationship between soil CO_2 efflux and temperature for the days 7–9 July 1997 must be a response of both plant and soil microbial metabolism to water stress (Kutsch & Kappen, 1997; Malhi *et al.*, 1998). The impact of water stress on photosynthesis may result from higher vapor pressure deficit and lower soil water content (Malhi *et al.*, 1998). The increased hydraulic resistance requires restrictions in transpiration, and thus causes stomatal closure and a reduction in photosynthesis. With the lower metabolism the production of fine roots is lower (Priess *et al.*, 1999) and the population of microbes and fine roots diminishes. Because plateau soils in Central Amazonian have high root density in the top meter (Chauvel *et al.*, 1987) they are likely to respond fairly strongly to such conditions. Thus, under moisture-limited conditions, soil CO_2 efflux may follow temperature cycle from deep soil layers that still have access to water (Nepstad *et al.*, 1994; Hodnett *et al.*, 1997). As a result, during the dry season the soil CO_2 efflux is essentially dependent on deep roots, which can reach more than 8 m deep in Amazonian forests (Nepstad *et al.*, 1994).

Drying and rewetting effect on the soil CO_2 efflux. The drying effect alone reduces the soil efflux (as observed in the first period of measurements). However, when combined with periods of rewetting, the rate of soil CO_2 efflux can rise considerably.

During the second period of measurements, it was possible to observe the effect of drying and successive rewetting in the soil CO_2 efflux, as already described by Birch (1958). When the very dry soil was rewetted by the rain (during October and November), the efflux was higher due to the high initial rate of decomposition resulting from the rapid early stages of bacterial population growth (Birch, 1958). The initial higher rate of CO_2 production, which results from high microbial metabolic activity, reduces subsequently. This reduction was observed during the second phase of the second period of data collection and may be a result of the successive dry periods alternating with periods with rainfall.

The effect of rainfall on soil CO_2 efflux. Independent of the effect of the water supply on the source of the CO_2, an immediate response in soil CO_2 efflux caused by rain events is an observed reduction in the efflux rate. The drop in temperature may be responsible for almost all the change in the efflux. However, rainfall events are also related to the immediate replacement of the air-filled pores by water that may form a cap and prevent gas diffusion of CO_2 through the soil to the atmosphere. We observed a steep fall of soil CO_2 efflux just after rainfall (about 30% when compared with nonrain periods), but a higher CO_2 concentration in the top soil layer. The higher CO_2 concentration found in the upper soil during the second measurement of the CO_2 concentration profile is not likely to be a result from a higher rate of CO_2 production but a result of a reduction in the rate of diffusion of air within the top soil pore space. This effect seems to happen only in the very top layer of soil (10 cm) and the retained CO_2 may be released to the atmosphere shortly after the drainage of the upper soil layer. This rain effect was also observed by Buchmann *et al.* (1997) in an equatorial lowland rainforest in French Guiana. They found that heavy rains decreased soil CO_2 efflux by about 40% when compared with nonrain periods.

Conclusion

The average soil CO_2 efflux in this study was higher than the value calculated from eddy covariance measurements for the same site, and was not correlated with tree basal area.

The short-term temporal variation in soil respiration was dependent on soil temperature, but the diel cycle did not always have an exponential response with temperature. Soil water supply appeared to be an important controlling factor during the drying period, while the rewetting effect was more marked during the drought. Rainfall reduced soil CO_2 efflux and soil temperature, and increased CO_2 concentration in the top soil, and for a short period after the event.

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