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Implications of CO₂ pooling on $\delta^{13}\text{C}$ of ecosystem respiration and leaves in Amazonian forest

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Abstract

The carbon isotope of a leaf ($\delta^{13}\text{C}_{\text{leaf}}$) is generally more negative in riparian zones than in areas with low soil moisture content or rainfall input. In Central Amazonia, the small-scale topography is composed of plateaus and valleys, with plateaus generally being drier than the valley edges in the dry season. The nocturnal accumulation of CO_2 is higher in the valleys than on the plateaus in the dry season. The CO_2 stored in the valleys takes longer to be released than that on the plateaus, and sometimes the atmospheric CO_2 concentration (c_a) does not drop to the same level as on the plateaus at any time during the day. Samples of sunlit leaves and atmospheric air were collected along a topographical gradient to test whether the $\delta^{13}\text{C}_{\text{leaf}}$ of sunlit leaves and the carbon isotope ratio of ecosystem respired CO_2 ($\delta^{13}\text{C}_R$) may be more negative in the valley than those on the plateau.

The $\delta^{13}\text{C}_{\text{leaf}}$ was significantly more negative in the valley than on the plateau. Factors considered to be driving the observed variability in $\delta^{13}\text{C}_{\text{leaf}}$ were: leaf nitrogen concentration, leaf mass per unit area (LMA), soil moisture availability, more negative carbon isotope ratio of atmospheric CO_2 ($\delta^{13}\text{C}_a$) in the valleys during daytime hours, and leaf discrimination (Δ_{leaf}). The observed pattern of $\delta^{13}\text{C}_{\text{leaf}}$ suggests that water-use efficiency (WUE) may be higher on the plateaus than in the valleys. The $\delta^{13}\text{C}_R$ was more negative in the valleys than on the plateaus on some nights, whereas in others it was not. It is likely that lateral drainage of CO_2 enriched in ^{13}C from upslope areas might have happened when the nights were less stable. Biotic factors such as soil CO_2 efflux (R_{soil}) and the responses of plants to environmental variables such as vapor pressure deficit (D) may also play a role.

1 Introduction

The use of isotopic tracers in organic matter, water, and atmospheric gases has emerged as a powerful tool that integrates biotic and physical processes over space

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and time, improving our understanding of plant physiology, biogeochemistry, and ecosystem function (Pataki et al., 2003b; Pataki et al., 2007). The mean carbon isotope ratio of atmospheric CO₂ ($\delta^{13}\text{C}_a$) is currently -8‰ (Keeling et al., 2005a; Keeling et al., 2005b). Plants utilizing the C₃ photosynthetic pathway (the majority of terrestrial plants) typically have values of $\delta^{13}\text{C}$ that range from -21 to -35‰ (Pataki et al., 2007). An expression for discrimination in leaves (Δ_{leaf}) of C₃ plants can be stated as follows

$$\Delta_{\text{leaf}} = a + (b - a) \frac{c_i}{c_a} \quad (1)$$

where a is the fractionation associated with diffusion (4.4‰), b is the net kinetic/enzymatic fractionation associated with carboxylation (27‰), and c_i and c_a are the intercellular and atmospheric concentrations of CO₂, respectively. Thus, Δ_{leaf} is a function of c_i/c_a ratio, which is sensitive to a variety of factors that influence the balance of stomatal conductance and assimilation rate, for example light and water availability (Pataki et al., 2003b).

The carbon isotope ratio of a leaf ($\delta^{13}\text{C}_{\text{leaf}}$) is a measure that integrates the photosynthetic activity over the period of weeks to months during which the leaf tissue was synthesized (Ometto et al., 2002; Dawson et al., 2002; Ometto et al., 2006). In tropical forests, $\delta^{13}\text{C}_{\text{leaf}}$ is strongly correlated with the height of the leaf within the canopy. Low $\delta^{13}\text{C}_{\text{leaf}}$ (more negative) is observed in the understory vegetation, and high $\delta^{13}\text{C}_{\text{leaf}}$ (less negative) is observed in the upper canopy (Medina and Minchin, 1980; Medina, 1986; Medina et al., 1991; Vandermerwe and Medina, 1989; Sternberg, 1989; Zimmerman and Ehleringer, 1990; Broadmeadow, 1992; Buchmann et al., 1997; Guehl, 1998; Martinelli, 1998; Bonal, 2000; Ometto et al., 2002; Ometto et al., 2006). This trend in $\delta^{13}\text{C}_{\text{leaf}}$ through the canopy is related to the reassimilation of respired CO₂ and differences in conditions such as light and vapor pressure deficit through the canopy, resulting in changes in c_i/c_a ratios (Sternberg et al., 1989; Lloyd et al., 1996; Sternberg et al., 1997; Buchmann et al., 1997; Ometto et al., 2002; Ometto et al., 2006).

The temporal and spatial variability of $\delta^{13}\text{C}_{\text{leaf}}$ in forested landscapes and along environmental gradients has shown that $\delta^{13}\text{C}_{\text{leaf}}$ is more negative in riparian zones

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or in areas with high soil moisture content or rainfall input than in areas with low soil moisture content or rainfall input (Medina and Minchin, 1980; Ehleringer et al., 1986; Ehleringer et al., 1987; Korner et al., 1988; Korner et al., 1991; Garten and Taylor, 1992; Marshall and Zhang, 1993; Stewart et al., 1995; Sparks and Ehleringer, 1997; Hanba et al., 2000; Bowling et al., 2002). Yet, plants growing in dry environments have shown lower Δ_{leaf} and higher water-use efficiency (WUE) than those grown at low altitudes or in wet environments.

In Central Amazonia, the small-scale topography is composed of plateaus and valleys. These give rise to a high variability of soil moisture contents (θ) in the unsaturated zone, with plateaus generally being drier than the valley edges in the dry season (J. S. de Souza, data not published). de Araújo et al. (in press) made nocturnal measurements of c_a along a topographical gradient at a site in Central Amazonia. They showed that in the dry season, depending on the atmospheric stability, larger amounts of CO_2 were stored on the slopes and in the valleys than on the plateaus of this undulating landscape. Lateral drainage of respired CO_2 downslope and high soil CO_2 efflux (R_{soil}) in the valleys were considered as possible causes for the observed variability in c_a , respectively. In addition, these authors observed that the CO_2 stored in the air in the valley took longer to be released than that on the plateau, and that c_a in the valley did not decrease to the same level as on the plateau at any time during the day. This leads to two hypotheses for dry season conditions. The first is that the $\delta^{13}\text{C}_{\text{leaf}}$ in the valleys may be more negative than that on the plateaus due to both higher soil water availability and longer time of exposure to high c_a with low $\delta^{13}\text{C}_a$. The second is that the carbon isotope ratio of ecosystem respired CO_2 ($\delta^{13}\text{C}_R$) may be less negative on the plateaus than in the valleys.

This study aims to investigate how $\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{13}\text{C}_a$ vary in time and space along a topographical gradient at a site in Central Amazonia and analyses the biotic and physical factors controlling the stable carbon isotope discrimination.

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2 Site description

Measurements were made at the Manaus LBA site (2°36'32" S, 60°12'33" W, 45–110 m a.s.l. – above sea level), located in the Asu catchment in the Reserva Biológica do Cuieiras. The forest belongs to the Instituto Nacional de Pesquisas da Amazônia (INPA). The exchange of CO₂, sensible and latent heat, momentum transfer, and meteorological variables have been measured almost continuously on two micrometeorological towers, installed in July 1999 and in May 2006, respectively. The first tower, known as K34 (Araujo et al., 2002), is on a medium sized plateau, whereas the second one, known as B34 (de Araújo et al., 2007¹), is at the bottom of a U-shaped valley.

The mean air temperature was 26°C between July 1999 and June 2000 (Araújo et al., 2002). Average annual rainfall is about 2400 mm, with a distinct dry season during July, August and September when there is less than 100 mm rainfall per month (Araújo et al., 2002).

There is very little large-scale variation in topography in the region, but at a smaller scale, the dense drainage network has formed a pattern of plateaus and valleys. The mean elevation is about 100 m a.s.l. with about 40–60 m difference between plateaus and valley bottoms. The soils along a typical toposequence consist of well-drained Oxisols and Ultisols on plateaus and slopes, respectively, and of poorly drained Spodosols in the valleys (Chauvel et al., 1987). From the plateau down to the valley, the soil (top 5 cm) clay fraction decreases (from about 75% to 5%) and the sand fraction increases (from about 10% to 85%) (Ferraz et al., 1998; Chambers et al., 2004; Souza, 2004; Luizao et al., 2004).

The vegetation is old-growth closed-canopy *terra firme* (non-flooded) forest. Variation in soil type, topography and drainage status has created distinct patterns in forest vegetation composition. On the plateaus, well drained clay soils favor high biomass forests 35–40 m in height with emergent trees over 45 m tall: typical *terra firme* forest.

¹de Araújo, A. C., Dolman, A.J., Waterloo, M.J., Kruijt, B., et al.: Comparative measurements of CO₂ fluxes from a plateau and valley in Amazonian forest, in preparation, 2007.

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Along the slopes, where a layer of sandy soil is deepening towards the valley bottom, forest biomass is lower and height is around 20–35 m with few emerging trees. In the valleys, the sandy soils are poorly drained and usually they remain waterlogged during the rainy season, supporting low biomass and low tree height (20–35 m), with very few emerging trees. A distinct forest type, classified as *Campinarana* (as it resembles the *Campina* forest that develops on white sand areas), also occurs between the lower slope and valley bottom areas. This vegetation has lower biomass, tree diversity and tree height (15–25 m) (Guillaumet, 1987; Luizão et al., 2004). The forest canopy is stratified in four layers. The first layer is that formed by emergent trees, reaching heights of 35–45 m above ground level (a.g.l.). Below this layer, there are trees with their canopies between 20 and 35 m. The third layer is formed by understory regeneration, whereas shrubs and seedlings form a fourth layer close to the ground. More elaborate descriptions of the site can be found in Araújo et al. (2002), Andreae et al. (2002), Chambers et al. (2004), Luizão et al. (2004), and Waterloo et al. (2006).

3 Material and methods

3.1 Air sampling collection and data conditioning

All sampling was carried out in representative plots along a transect that was divided into 3 topographical sections: plateau, slope and valley (Fig. 1). See also Fig. 1 in de Araújo et al. (in press). In each plot, air samples were collected at different levels above and within the canopy for $\delta^{13}\text{C}_a$ and c_a analysis. Each profile sampling system consisted of HDPE-lined tubes (Dekoron 1300, 6.25 mm OD, non-buffering ethylene copolymer coating, USA) with intakes at different heights (Table 1). Nylon funnels with stainless steel filters were installed on the air intakes to avoid sample contamination by particles. A battery-operated air pump (Capex V2X, UK) was used to draw air through the tubing, a desiccant tube containing magnesium perchlorate and a glass sample flask. The flow rate was 10 L min^{-1} . The longest air sampling tube had an internal

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5 volume of about 0.65 L that corresponds to a maximum residence time of 4 s. All air samples were collected in pre-evacuated 100 mL glass flasks that were closed with two high-vacuum Teflon stopcocks (34-5671, Kontes Glass Co., USA) after air had been pumped through the flask for about 3 minutes. The c_a was measured at the same time with an infrared gas analyzer (IRGA) (LI-800, LI-COR, Inc., USA). For this a “T” piece was connected at the air pump output, which allowed a low subsampling flow of about 800 mL min⁻¹ to be passed through the IRGA.

10 Plateau air samples were collected at the K34 tower (118 m a.s.l.) with a tube system attached to the tower. The slope profile system was suspended from the highest branch of a tall tree located about midway down the slope (89.2 m a.s.l.) at 550 m from the K34 tower, whereas the valley profile system, which was suspended in the same way as that on the slope, was installed in the valley (77.3 m a.s.l.) at about 850 m from the K34 tower (de Araújo et al., in press). This latter system had its highest intake at 11 m a.g.l. in 2002 (de Araújo et al., in press) and was extended to reach up to 30 m a.g.l. in August 2004. In October 2006, the valley profile system was relocated 500 m to the west and attached to the newly erected B34 tower (Fig. 1).

15 Nighttime sampling began about one hour after sunset (about 19:30 local time) and ended about one hour before sunrise (about 05:30 local time) to avoid any effects of photosynthesis on the estimates of $\delta^{13}C_R$. In order to increase statistical confidence in $\delta^{13}C_R$ values, we aimed to collect samples with a minimum c_a difference of about 75 ppm between samples, which was set a priori as the minimum difference that shall be observed among the flasks sampled at each nighttime sampling (Pataki et al., 2003a; Lai et al., 2004; Lai et al., 2005). Daytime values of $\delta^{13}C_a$ and c_a within and above the canopy were obtained between 07:00 and 18:00 hours (Table 1). Due to both strong rainfall on 10 October and technical problems, the last sampling of atmospheric air during daytime hours occurred on 16 October at both plateau and valley.

25 The flasks were shipped to the Centro de Energia Nuclear na Agricultura (CENA) in São Paulo, Brazil, for stable isotope ratio and c_a analyses. Details about the analytical procedures at CENA are given by Ometto et al. (2002).

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3.2 Sampling of foliage and litter

In August 2004, leaf samples were collected from trees at each topographical section, sampling a vertical profile through the forest canopy. There was no botanical classification for the trees sampled in August 2004. In October 2006, sun leaves at the top of the canopy were collected by a tree climber at plateau and valley sections. Trees with botanical classification to species level were now systematically selected according to either their importance value index (IVI) or occurrence at both plateau and valley areas (Oliveira and Amaral, 2004; Oliveira and Amaral, 2005; I. L. do Amaral, personal communication). Each sample from a single tree consisted of at least five healthy leaves that were combined according to their status (either mature or young). In August 2004, litter samples were randomly collected at each topographical section. These were bulked by topographic section to form single samples. The samples were pre-dried at ambient air temperature for 3 days in a home-made greenhouse located in an open-sky area and shipped to CENA for stable isotope ratio and elementary analyses.

3.3 Soil-respired CO₂ sampling

In August 2004, CO₂ released from the soil was sampled at each topographical section using the protocol described by Flanagan et al. (1999) and Ometto et al. (2002). The sampling was repeated at plateau and valley sites in October 2006 and now included the *Campinarana* site. Samples were collected using a stainless steel chamber with an internal volume of about 40 L and a small electric fan to enhance mixing within the chamber. Samples were collected at two sites in each topographical section. At each site, five sample flasks were filled using five minutes time intervals between sampling for determining the carbon isotope ratio of soil respired CO₂ ($\delta^{13}\text{C}_{\text{soil}}$) (explained further). All samples were shipped to CENA for stable isotope ratio and c_a analyses.

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3.4 Laboratory analyses

The $\delta^{13}\text{C}_a$ in sample flasks were measured using a continuous-flow isotope-ratio mass spectrometer (IRMS) (Delta Plus, Finnigan MAT, Germany) as described by Ehleringer and Cook (1998) and Ometto et al. (2002). Measurement precision of this method was 0.13‰ for ^{13}C (Ometto et al., 2002). The air remaining in the flask after stable isotope ratio analysis was used to measure c_a using a system similar to that described by Bowling et al. (2001a). Measurement precision and accuracy of this method were 0.2 and 0.3 ppm, respectively (Ometto et al., 2002).

Leaf and litter samples were dried at 65°C to constant weight, then ground with mortar and pestle to a fine powder. A 1–2 mg subsample of ground organic material was sealed in a tin capsule and placed into an elemental analyzer (Carlo Erba Instruments, Model EA 1110 CHNS-O, Milan, Italy) for combustion and subsequent elemental C and N analysis. The CO_2 generated by combustion was purified in a gas chromatograph column and passed directly to the inlet of the IRMS (Delta Plus, Finnigan MAT, USA) operating in continuous-flow mode.

This provided stable isotope ratios of carbon, oxygen and nitrogen ($^{13}\text{C}/^{12}\text{C}$; $^{18}\text{O}/^{16}\text{O}$; $^{15}\text{N}/^{14}\text{N}$) with a measurement precision of 0.2‰ (Ometto et al., 2006). The carbon isotope ratio was expressed in the delta notation

$$\delta^{13}\text{C} = \left(\frac{R_s}{R_{\text{std}}} - 1 \right) \times 1000 \quad (2)$$

where R_s and R_{std} correspond to the measured $^{13}\text{C}/^{12}\text{C}$ molar ratio of the sample and the international Pee Dee Belemnite (PDB) limestone standard, respectively (Ehleringer and Rundel, 1989). The $\delta^{13}\text{C}$ values are presented in parts per thousand (‰).

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3.5 Carbon isotope discrimination by sunlit leaves

It may be that Δ_{leaf} is higher in the valley than on the plateau, thus the carbon isotope discrimination by sunlit leaves at both plateau and valley, as well their c_i/c_a ratios and c_i were investigated. According to Farquhar et al. (1989a, b), Δ_{leaf} can be calculated from

$$\Delta_{\text{leaf}} = \left(\frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}_{\text{leaf}}}{1 + \delta^{13}\text{C}_{\text{leaf}}} \right) \quad (3)$$

We have used the averaged $\delta^{13}\text{C}_{\text{leaf}}$ (Table 2) and daytime values of $\delta^{13}\text{C}_a$ from the canopy layer level on October 2006 to obtain temporal series of Δ_{leaf} for every topographical section. The results of Eq. (3) were used in Eq. (1), together with daytime values of c_a on October 2006 to obtain temporal series of c_i/c_a ratio and c_i .

3.6 Correlation between $\delta^{13}\text{C}_R$ and water vapor saturation deficit

The possibility of a correlation with fine time lag between environmental variables and $\delta^{13}\text{C}_R$ may confound our analysis, so we investigated the relation between ambient vapor pressure deficit and $\delta^{13}\text{C}_R$ (Ekblad and Hogberg, 2001; Bowling et al., 2002; McDowell et al., 2004; Knohl et al., 2005; Werner et al., 2006). We selected the water vapor saturation deficit in the air (D) as a suitable variable because it may influence $\delta^{13}\text{C}_R$ at a short time scale, possibly through changes in photosynthetic discrimination (Bowling et al., 2002). Daytime mean values were used unless specified otherwise. Because there may be a significant delay between the time that a given carbon atom is assimilated by photosynthesis and the time that it is respired by various ecosystem components (Ekblad and Hogberg, 2001), correlations between D and $\delta^{13}\text{C}_R$ were examined over a range of time lags (e.g. relationships between D on day X and $\delta^{13}\text{C}_R$ on day $X+n$). We calculated averages of daytime D (from 10:00 to 17:00) from 1–5 days, and then shifted these averages back in time by 0–15 days. A 1-day average

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and a 0-day time lag correspond to the average daytime D on the day prior to the night of sampling. For a more detailed description of lag analysis see Bowling et al. (2002), Ekblad and Hogberg (2001) and McDowell et al. (2004).

3.7 Statistical analyses

5 3.7.1 Keeling plots for $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_{\text{soil}}$

A two-source mixing model proposed by Keeling (1958) was used to obtain $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_{\text{soil}}$ (Flanagan et al., 1999; Ometto et al., 2002; Pataki et al., 2003a). The Model II regression or geometric mean regression (GMR) has been recommended to determine the Y-intercept (Pataki et al., 2003a). However, Zobitz et al. (2006) argued that the use of Model II regression to obtain $\delta^{13}\text{C}_R$ is inappropriate because it is a biased estimator of $\delta^{13}\text{C}_R$ and the relative error in the $\delta^{13}\text{C}_a$ measurements is significantly greater than the relative error in c_a measurements. They suggested therefore the use of Model I regression or ordinary least squares (OLS) to determine the Y-intercept (a) and slope ($b_{y,x}$). We have decided to follow their recommendation, though we also present the slope ($v_{y,x}$) and Y-intercept (a_v) of Model II regression for $\delta^{13}\text{C}_R$ in Table 3. Uncertainty for the Y-intercept is reported as standard error estimate from a Model I regression or standard linear regression intercept (SE_a) (Sokal and Rohlf, 1995; Pataki et al., 2003a; Zobitz et al., 2006). Because we followed the suggested guidelines made by Pataki et al. (2003a) to reduce errors when using the two-source mixing approach for estimating $\delta^{13}\text{C}_R$, the majority of the standard errors of the Y-intercept reported here are smaller than 1‰ (Table 3).

3.7.2 Organic samples ($\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{13}\text{C}_{\text{litter}}$)

Statistical comparisons were made using Model I ANOVA, and comparisons between means were evaluated with Bonferroni t tests (Glover and Mitchell, 2002; Sokal and Rohlf, 1995). Unless otherwise indicated, a significance level of 99% was used in all

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hypothesis testing.

3.7.3 Correlation between $\delta^{13}\text{C}_R$ and D

First-order linear regression was used except in cases where scatter plots suggested nonlinear or second-order equations were appropriate. The Pearson product-moment correlation coefficient, usually known by correlation coefficient (r), was used as the index of association of two variables (Glover and Mitchell, 2002).

3.8 Altitude measurements

We applied the same altitude measurements as described by de Araújo et al. (in press). The altitude presented here refers to the vertical distance above mean sea level.

4 Results

4.1 Meteorological and turbulent variables

4.1.1 Dry season campaign on 2–5 August 2004

Figure 2 shows the diurnal variation of selected meteorological and turbulent variables measured at the top of K34 tower (53 m a.g.l.) during the sampling period. Rainfall (12 mm) occurred in the late afternoon of 4 August (data not shown), with a corresponding increase in the friction velocity (u_*) from about 0.2 m s^{-1} to 0.8 m s^{-1} and D decreased from about 2 kPa to 0.5 kPa (Fig. 2a, b). Nighttime values of u_* were higher at 0.2 m s^{-1} from 3–4 August than during the other nighttime periods (Fig. 2a), implying enhanced vertical mixing on 3–4 August. The nighttime periods from 3–4 and 4–5 August were ranked as the least and most stable, respectively. Pre-dawn values of c_a were greater on 5 August (about $372.8 \pm 5.7 \text{ ppm}$) than on 3 August (about $366.1 \pm 1.4 \text{ ppm}$) and 4 August (about $365.6 \pm 2.1 \text{ ppm}$) (Fig. 2a). Nighttime values of

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above-canopy turbulent exchanges of CO_2 (F_c) were higher from 3–4 August (about $2.7 \pm 0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$) than from 2–3 August (about $0.02 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) and 4–5 August (about $0.2 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 2c).

4.1.2 Dry season campaign on 7–10 October 2006

5 Due to a lightning strike on the B34 valley tower neither meteorological nor turbulent data were measured at this site during the sampling period (between 27 September and 12 October). Figure 2d–f therefore shows the diurnal variability of meteorological and turbulent variables measured at the top of K34 tower on the plateau. Rainfall occurred in the morning of 8 October (0.2 mm) and 10 October (27 mm), respectively
10 (data not shown). Nighttime values of u_* were higher for 9–10 October than at the other nighttime periods (Fig. 2d). The nighttime periods of 9–10 and 7–8 October were ranked as the least and most stable, respectively. The nighttime values of c_a and F_c were higher on 9–10 October than on the other nighttime periods (Fig. 2d, f). On 8 and 9 October, between 06:00 to 08:00 local time (LT), the values of F_c were very high showing considerable amounts of CO_2 from ecosystem respiration (R_{eco}) released in a short time interval (Fig. 2f). Daytime values of F_c were lower on 10 October than on 8 October due to high morning rainfall on 10 October (Fig. 2f).

4.2 Spatial variability of $\delta^{13}\text{C}_{\text{leaf}}$, $\delta^{13}\text{C}_{\text{litter}}$ and canopy and litter $C:N$ ratio

In August 2004, the vertical profile of $\delta^{13}\text{C}_{\text{leaf}}$ through the canopy showed a similar
20 pattern for every topographical section, decreasing with depth into the canopy (data not shown). However, $\delta^{13}\text{C}_{\text{leaf}}$ of canopy layer was significantly more negative in the valley than on the plateau, with values of -32.34‰ and -28.86‰ , respectively (Table 2). On other hand, $\delta^{13}\text{C}_{\text{litter}}$ showed no significant difference among the topographical sections (Table 2).

25 The $C:N$ ratios of leaves from the canopy layer and litter showed no significant difference between the means (Table 2). In October 2006, $\delta^{13}\text{C}_{\text{leaf}}$ at the top of the canopy

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was significantly more negative in the valley than on the plateau, about -30.55‰ and -29.71‰ , respectively (Table 2). Yet, the $C:N$ ratios of leaves from the top of the canopy were higher in the valley and *Campinarana* than on the plateau, though there was no significant difference between the means at the 99% level (Table 2). No significant difference was observed between the $\delta^{13}\text{C}_{\text{leaf}}$ of old and new leaves sampled in October 2006 (data not shown).

4.3 Temporal and spatial variability of $\delta^{13}\text{C}_a$, c_a , $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_{\text{soil}}$

4.3.1 Campaigns on 8–9 October and 17–18 November 2002

These trial campaigns, on 8–9 October and 17–18 November 2002, provided the first insights into the variation of $\delta^{13}\text{C}_a$ and c_a with time and topography. They suggested that the atmospheric air below the canopy was more ^{13}C depleted in the valley than on the plateau (data not shown). Yet, $\delta^{13}\text{C}_a$ was uniform with height a.g.l. in the valley, whereas on slope and plateau it was quite variable. In addition, c_a was higher in the valley and slope than on the plateau, and it was uniform with height a.g.l. in the valley (data not shown).

4.3.2 Dry season campaign on 2–5 August 2004

The dry season campaign on 2–5 August 2004 revealed that nighttime values of $\delta^{13}\text{C}_a$ were significantly different among the topographical sections. The $\delta^{13}\text{C}_a$ was more negative in the valley and slope plots than on the plateau (Fig. 3a–c). The $\delta^{13}\text{C}_a$ difference between the canopy layer (35–20 m a.g.l.) and shrub layer (from 5 m a.g.l. downwards) was larger on the plateau than at the slope and valley, respectively. Post-sunset or pre-dawn values of the $\delta^{13}\text{C}_a$ in the canopy layer were always more negative at both slope and valley plots than on the plateau by at least 1.5‰ or 2.5‰ , respectively (Fig. 3a–c). Before dawn, on 4 August, the $\delta^{13}\text{C}_a$ measured at 30 m a.g.l. increased sharply at both slope and valley, this was not observed on 3 and 5 August (Fig. 3b, c).

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Opposing the isotopic signatures along the topographical sections, the nighttime values of c_a were higher at both slope and valley than on the plateau (Fig. 3d–f). In addition, the c_a difference between the canopy layer and shrub layer was higher on the plateau than on the slope and in the valley, respectively. Before dawn, on 4 August, the c_a measured at 30 m a.g.l. decreased sharply at both slope and valley, this was different on 3 and 5 August (Fig. 3e, f).

The relationship between c_a and $\delta^{13}C_a$ for each topographical section during the three consecutive nighttime periods is shown in Fig. 4. Although the second-order regressions for the plateau were quite similar, they showed that the values of $\delta^{13}C_a$ for 4–5 August were slightly less negative than for 2–3 August and 3–4 August, respectively (Fig. 4a). At both slope and valley, regressions were quite variable and data seemed to be clustered in two distinct ranges of c_a and $\delta^{13}C_a$. The first range (from 420 to 480 ppm and from -10 to -13%) is for data measured from early in the evening until late at night (23:00 LT), whereas the second range (from 540 to 560 ppm and from -14 to -15%) consists of data measured before dawn (Fig. 4b, c). Particularly in the valley, the regressions showed that for the first range values of $\delta^{13}C_a$ on 2–3 August were higher than on 3–4 August and 4–5 August (Fig. 4c). For the second range, the values of $\delta^{13}C_a$ from 3–4 August were higher than from 4–5 August and 2–3 August (Fig. 4c).

The nighttime variability of c_a and $\delta^{13}C_a$ was also observed in the values of $\delta^{13}C_R$ (Table 3). From 2–3 August, $\delta^{13}C_R$ was less negative on the plateau than at both slope and valley (Fig. 5a). On the following day, 3–4 August, $\delta^{13}C_R$ became progressively less negative moving from the valley to the slope and onto the plateau. Finally, from 4–5 August, $\delta^{13}C_R$ was less negative on the slope than on both plateau and valley (Fig. 5a). On the plateau, the values of $\delta^{13}C_R$ agreed very well with the predictions based on the regressions in Fig. 4a. In the valley, the values of $\delta^{13}C_R$ also agreed very well with the predictions based on the regressions in Fig. 4c, but only for the pre-dawn data cluster (from 540 to 560 ppm and from -14 to -15%). This could suggest that in the valley, $\delta^{13}C_R$ is biased by data measured between midnight and dawn. This possibility

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was investigated by comparing the $\delta^{13}\text{C}_R$ determined from data collected either before midnight or after midnight (data not shown). The c_a range was below 75 ppm for both cases, except after midnight on 3–4 August, and the uncertainty therefore was higher than 1‰ (ranging from 1.3 to 7.2‰). The $\delta^{13}\text{C}_R$ increased for the periods of 2–3 and 4–5 August using both datasets, so that the valley became more enriched in ^{13}C relative to the plateau. Moreover, $\delta^{13}\text{C}_R$ decreased for the period of 3–4 August also using both datasets, but the valley remained more enriched in ^{13}C relative to the plateau. The differences in $\delta^{13}\text{C}_R$ that were observed between plateau, slope and valley cancelled out when the values of $\delta^{13}\text{C}_R$ were averaged for each topographical section (data not shown). The $\delta^{13}\text{C}_{\text{soil}}$ was also variable among the topographical sections. It was less negative on the plateau than in the valley, but the minimum was found on the slope (Fig. 5b).

4.3.3 Dry season campaign on 7–10 October 2006

Nighttime values of $\delta^{13}\text{C}_a$ were more negative in the valley than on the plateau. High $\delta^{13}\text{C}_a$ was observed early in the night, whereas low $\delta^{13}\text{C}_a$ occurred before dawn. The $\delta^{13}\text{C}_a$ was highest on 7 October on the plateau and on 8 October in the valley. The $\delta^{13}\text{C}_a$ was lowest on 8 October at both plateau and valley (Fig. 6a, b). Before dawn on 8 October, the $\delta^{13}\text{C}_a$ measured at 42 m a.g.l. on the plateau and at 30 m a.g.l. in the valley were about 4‰ and 1‰ more enriched in ^{13}C , respectively, than the levels below them (Fig. 6a, b). From 8–9 October, the values of $\delta^{13}\text{C}_a$ from the canopy layer downwards on the plateau and from middle layer downwards in the valley were almost uniform with height a.g.l. (Fig. 6a, b).

Nighttime values of c_a were higher in the valley than on the plateau. Low c_a was observed early at night and high c_a before dawn (Fig. 6c, d). From the canopy layer to the middle layer (20–5 m a.g.l.), on the plateau, c_a was lowest on 7 October and highest on 8 October (Fig. 6c). From about 20 m a.g.l. downwards, in the valley, c_a was highest and lowest on 8 October (Fig. 6d). On 8–9 October, the values of c_a from

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the canopy layer downwards on the plateau and from middle layer downwards in the valley were almost uniform with height a.g.l. (Fig. 6c, d). Before dawn on 8 October, the c_a measured at 42 m a.g.l. on the plateau and at 30 m a.g.l. in the valley were about 120 ppm and 30 ppm lower, respectively, than at lower levels (Fig. 6c, d).

The relation between c_a and $\delta^{13}C_a$ for each topographical section during the three consecutive nighttime periods was also investigated. The second-order regressions for the plateau had the same shape as those shown in Fig. 4a. In addition, the regressions showed that the values of $\delta^{13}C_a$ from 9–10 October were less negative than those of 7–8 October and 8–9 October, respectively (data not shown). The regressions for the valley also had a similar shape as those shown in Fig. 4c, except now the regression for 8–9 October. The values of $\delta^{13}C_a$ on 7–8 October were less negative than those observed on 8–9 October and 9–10 October (data not shown).

Nighttime variability of c_a and $\delta^{13}C_a$ was also observed in the values of $\delta^{13}C_R$ (Table 3). The values of $\delta^{13}C_R$ were more negative in the valley than on the plateau on 7–8 October and 9–10 October and more positive on 8–9 October (Fig. 5c). On the plateau, the values of $\delta^{13}C_R$ agreed very well with the predictions based on the regressions, whereas this was not the case for the valley. In addition, the values of $\delta^{13}C_R$ were higher than those measured on August 2004. The $\delta^{13}C_{soil}$ was greater on the plateau than at the *Campinarana* and in the valley, respectively (Fig. 5d).

Daytime values of $\delta^{13}C_a$ were typically less negative on the plateau than in the valley by about 1‰ (Table 4).

4.4 Correlation between $\delta^{13}C_R$ and D

There were strong correlations between $\delta^{13}C_R$ and D at all topographical sections. In August 2004, the highest correlations were observed with 1 and 3-day average and 2 and 4-day lag times for plateau, slope and valley (Table 5). The regression coefficients (a and $b_{y.x}$) for the plateau (about -34% and 3% kPa^{-1}) were higher and lower, respectively, than those for slope (about -75% and 27% kPa^{-1}) and valley (about

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–160‰ and 75‰ kPa⁻¹) (Table 5). Figure 7a shows that on the plateau, according to Table 5, the $\delta^{13}\text{C}_R$ on 2–3, 3–4 and 4–5 August had a maximum correlation with the averaged D of 31 July, 1 and 2 August, respectively. In October 2006, the highest correlations were observed with 1 and 2-day average and 7 and 6-day lag times for plateau and valley, respectively (Table 5). The regression coefficients (a and $b_{y,x}$) for plateau (about –40‰ and 7‰ kPa⁻¹) and valley (about –35‰ and 4‰ kPa⁻¹) were of similar magnitude (Table 5). Figure 7b shows that in the valley, according to Table 5, the $\delta^{13}\text{C}_R$ on 7–8, 8–9 and 9–10 October had a maximum correlation with the averaged D for the period from 30 September to October, from 1 to 2 October, and from 2 to 3 October, respectively. Figure 7c shows the relationship between $\delta^{13}\text{C}_R$ and D for each topographical section, according to the results of Table 5. In August 2004, the $\delta^{13}\text{C}_R$ was more responsive to changes on the slope and in the valley than on the plateau (Fig. 7c). However, on the slope and in the valley, $\delta^{13}\text{C}_R$ ranged from about –26 to –33‰ with almost no variation in D . In October 2006, on both plateau and valley, $\delta^{13}\text{C}_R$ was positively correlated with D (Fig. 7c). The $\delta^{13}\text{C}_R$ was here more responsive to changes in D on the plateau than in the valley.

4.5 Temporal and spatial variability of Δ_{leaf} , c_i/c_a ratio and c_i

There was a strong correlation between the c_i/c_a ratio and Δ_{leaf} for both plateau and valley sites. The values of the c_i/c_a ratio and Δ_{leaf} were evenly distributed in the ranges of 0.7–0.8 and 20.5–22.5‰, respectively (Fig. 8a). However, there was no clear relationship between plateau and valley when the variables Δ_{leaf} , c_i/c_a ratio, and c_i were used. Daytime values of Δ_{leaf} , c_i/c_a ratio, and c_i were quite variable both between plateau and valley and among days on October 2006. For example, on 8 October, Δ_{leaf} was higher in the valley than on the plateau, except at noon (Fig. 8b). However, on 9 and 16 October, Δ_{leaf} was higher on the plateau than in the valley, except about midday and late in the afternoon on 16 October (Fig. 8c, d). An increase in Δ_{leaf} with time was observed on 9 October, notably on the plateau (Fig. 8c). The averaged Δ_{leaf}

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was similar for plateau (about $21.45 \pm 0.1\text{‰}$) and valley (about $21.39 \pm 0.1\text{‰}$).

5 Discussion

5.1 Spatial variability of $\delta^{13}\text{C}_{\text{leaf}}$ and link to WUE

The $\delta^{13}\text{C}_{\text{leaf}}$ decreased from the plateau towards the valley (Table 2). This result is consistent with the work of Medina and Minchin (1980) in Amazonian rainforests in the southern part of Venezuela. These authors reported averaged $\delta^{13}\text{C}_{\text{leaf}}$ of -28.7 and -30.5‰ for the upper canopy levels of forests on lateritic outcrops and sandy spodosols soils, respectively. Increased leaf-level photosynthetic capacity of plants has been linked to higher leaf nitrogen content and leaf mass per unit area (LMA), and increased leaf thickness (Sparks and Ehleringer, 1997; Hanba et al., 2000; Vitousek et al., 1990; Korner and Woodward, 1987; Friend et al., 1989). Increased leaf-level photosynthetic capacity would decrease c_i at the carboxylation site, thus reducing Δ_{leaf} and consequently increasing $\delta^{13}\text{C}_{\text{leaf}}$ (Sparks and Ehleringer, 1997). At our study site, Luizão et al. (2004) observed that leaf nitrogen concentration was significantly higher on the plateau than in the valley. Furthermore, Nardoto (2005) showed that LMA was higher on the plateau than in the valley. These results support our findings.

The $\delta^{13}\text{C}_{\text{leaf}}$ may also be affected by c_a , $\delta^{13}\text{C}_a$ and soil moisture. Even though daytime values of c_a were about 20 ppm lower on the plateau than in the valley (Fig. 6c, d) it is unlikely that this difference would have contributed much to the observed pattern in $\delta^{13}\text{C}_{\text{leaf}}$. Daytime values of $\delta^{13}\text{C}_a$ were about 1‰ lower in the valley than on the plateau (Table 4, Fig. 6a, b). Lower $\delta^{13}\text{C}_a$ may have a significant contribution to lowering the values of $\delta^{13}\text{C}_{\text{leaf}}$ in the valley. Because leaf conductance may be more sensitive to soil moisture than photosynthesis (Schulze, 1986), decreased soil moisture content on the plateau would lead to a decrease in leaf conductance and a subsequent decrease of the c_i/c_a ratio and therefore increase in $\delta^{13}\text{C}_{\text{leaf}}$. Thus, at this site, it seems that it is not only Δ_{leaf} that explains the pattern in $\delta^{13}\text{C}_{\text{leaf}}$, but rather the

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combination of factors such as the $\delta^{13}\text{C}_a$ in air surrounding the leaves, soil moisture availability, leaf nitrogen concentration, and LMA.

5.2 Temporal and spatial variability of $\delta^{13}\text{C}_a$ and c_a

In general, $\delta^{13}\text{C}_a$ was more negative in the valley than on the plateau at night, whereas c_a showed an opposite pattern, i.e. it was higher in the valley than on the plateau. This is consistent with the findings of de Araújo et al. (in press), who observed that in the dry season, depending on the atmospheric stability, there was a preferential pooling of c_a in the lower topographical areas of this landscape.

Larger differences in $\delta^{13}\text{C}_a$ and c_a between canopy layer and shrub layer on the plateau than in the valley may result from horizontal stratification of the nocturnal CO_2 buildup. According to de Araújo et al. (2007), c_a was stratified horizontally in layers of increasing concentration (from top to bottom) along the topographical gradient. They argued that horizontal stratification was caused by inversion layers that develop above and underneath the canopy. Figure 9 shows the evolution of vertical profiles of $\delta^{13}\text{C}_a$ along the topographical gradient during 3–4 and 4–5 August, which is consistent with the pattern described by de Araújo et al. (in press). The horizontal stratification of $\delta^{13}\text{C}_a$ was clearer on the plateau than on the slope or in the valley, particularly before dawn, when the $\delta^{13}\text{C}_a$ profiles on the slope and in the valley were fairly uniform with altitude (Fig. 9). The uniformity of $\delta^{13}\text{C}_a$ and c_a with height in the valley suggests that the air is well mixed (vertical mixing), most likely as a consequence of the nocturnal thermal belts that might have occurred (Goulden et al., 2006; de Araújo et al., in press). Vertical mixing might also have happened on the plateau during the nighttime period from 8–9 October, when the values of $\delta^{13}\text{C}_a$ and c_a from the canopy layer downwards were almost uniform with height a.g.l. (Fig. 6). This period was however rather turbulent. The high values of c_a and F_c suggest that part of the nocturnal CO_2 buildup might have been released (Fig. 2d, f).

The $\delta^{13}\text{C}_a$ measured at about 160 m a.s.l. (42 m a.g.l. on the plateau) was consis-

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tently higher than that measured at the levels below (Fig. 9), as a result of the inversion layer that separated the canopy air from the free atmospheric air. Before dawn on 4 August, there was a sharp increase and decrease of $\delta^{13}\text{C}_a$ and c_a measured at 30 m a.g.l. at both slope and valley, respectively (Fig. 3b, c, e and f). In addition, in the same period on 8 October, the $\delta^{13}\text{C}_a$ and c_a measured above the canopy layer on both plateau and valley (42 and 30 m a.g.l., respectively) were also much higher and lower than those measured at the levels below, respectively (Fig. 6). This suggests that the erosion of the nighttime buildup in the valley had already started. However, in contrast to 4 August, on 8 October neither u_* nor F_c showed any significant change during the pre-dawn hours (Fig. 2a, c, d and f). As mentioned before, the nighttime period from 7–8 October was ranked as the most stable in October 2006.

During the transition from day to night the atmosphere underneath the canopy shifts from stable to either neutral or unstable, and this is most likely when the CO_2 stored in the layers just above the forest floor is released (Kruijtt et al., 2000; Goulden et al., 2006; de Araújo et al., in press). This could explain the strong decrease and increase of $\delta^{13}\text{C}_a$ at 0.2 m a.g.l. on the plateau observed early in the night of 7 and 9 October (Fig. 6a).

The $\delta^{13}\text{C}_a$ was more negative in the valley than on the plateau during daytime periods, whereas c_a was higher. In addition, the decrease of c_a with time of the day was faster on the plateau than in the valley (Fig. 6). This is consistent with the findings of de Araújo et al. (in press), who observed that in the dry season the CO_2 stored in the valley took longer to be released than that on the plateau, and that c_a in the valley did not decrease to the same level as on the plateau at any time during the day. Weak vertical mixing and high R_{soil} (discussed below) in the valleys were considered driving the observed variability in c_a .

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5.3 Temporal and spatial variability of $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_{\text{soil}}$

The $\delta^{13}\text{C}_R$ is more closely associated with that of sun foliage than with the shade foliage across a variety of ecosystems. In addition, $\delta^{13}\text{C}_R$ of an entire ecosystem can be either more enriched or more depleted in ^{13}C than sun foliage (Pataki et al., 2003a). This association also holds at our site, even considering the high variability in $\delta^{13}\text{C}_R$ in both space and time (Table 2, Fig. 5). Yet, the averaged $\delta^{13}\text{C}_{\text{leaf}}$ of the most exposed sun foliage of the dominant tree species of some tropical forests was similar to the $\delta^{13}\text{C}_R$ value. This suggests that the major portion of recently respired CO_2 in these forests was metabolized carbohydrate fixed by the sun leaves at the top of the forest canopy (Buchmann et al., 1997; Ometto et al., 2002). The $\delta^{13}\text{C}_R$ is a dynamic indicator of plant physiological response to short-term changes in environmental conditions. Tu and Dawson (2005) showed that $\delta^{13}\text{C}_{\text{soil}}$ (root plus microbial) is often enriched in ^{13}C relative to $\delta^{13}\text{C}_R$ whereas aboveground respiration (leaf plus stem) is often depleted across a variety of ecosystems. In our site, although there were some exceptions, $\delta^{13}\text{C}_{\text{soil}}$ was higher than $\delta^{13}\text{C}_R$ (Fig. 5). This is in agreement with Buchmann et al. (1997) and Flanagan et al. (1999), who also observed higher $\delta^{13}\text{C}_{\text{soil}}$ than $\delta^{13}\text{C}_R$ in both tropical and boreal forests. In contrast, Ometto et al. (2002) observed that $\delta^{13}\text{C}_{\text{soil}}$ and $\delta^{13}\text{C}_R$ were of similar magnitude in a forest about 700 km east of our site.

During the present study, the associations among $\delta^{13}\text{C}_{\text{leaf}}$, $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_{\text{soil}}$ held reasonably well for the plateau, whereas for the valley they did not. For example, there were periods such as on 3–4 August and on 8–9 October (Fig. 5a, c) in which $\delta^{13}\text{C}_R$ was higher in the valley than on the plateau. This was somewhat unexpected because in the valley the $\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{13}\text{C}_{\text{soil}}$ were well depleted in ^{13}C relative to the plateau. Galvão (2005) also observed that $\delta^{13}\text{C}_{\text{soil}}$ was lower in the valley than on the plateau in the dry season of 2003. Leaf respiration and R_{soil} correspond to about 80% of R_{eco} at our site (Chambers et al., 2004). Yet, R_{soil} measurements made during the dry

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season of 2003 showed that R_{soil} was lower on the plateau than in the valley (Souza, 2004). Particularly during these two nighttime periods, there was some vertical mixing as shown by the measurements of u_* and F_c (Fig. 2). It is unlikely that R_{soil} from the valley might have contributed to $\delta^{13}\text{C}_R$ being enriched in ^{13}C rather than being depleted in ^{13}C . Higher $\delta^{13}\text{C}_R$ in the valley than on the plateau therefore points to a combination of physical (mixing and transport) and biotic (respiration) processes as in de Araújo et al. (in press). These authors argued that respired CO_2 drains downslope and high R_{soil} in the valleys was driving the observed variability in c_a along this topographical gradient. Because there were no advection measurements during the periods sampled at this study, we cannot corroborate the lateral drainage with empirical data.

5.4 Correlation between $\delta^{13}\text{C}_R$ and D

According to the highest correlations between $\delta^{13}\text{C}_R$ and D , the time elapsed for a given carbon atom to be assimilated by photosynthesis and to be respired by various ecosystem components varied between 1 and 7 days at this site (Table 5). Similar investigations in boreal, temperate and Mediterranean forest ecosystems have shown time lags ranging between 0 and 10 days (Bowling et al., 2002; Knohl et al., 2005; Werner et al., 2006; Ekblad and Hogberg, 2001; McDowell et al., 2004; Mortazavi et al., 2005). It is important to note that at these forest ecosystems the diversity of species per unit area is very low, whereas the forests of Central Amazonia have more than 200 species ha^{-1} (Oliveira and Mori, 1999; Oliveira and Amaral, 2004; Oliveira and Amaral, 2005).

Prior to nocturnal sampling periods, there were several rainfall events in August 2004 rather than in October 2006 (data not shown). This is reflected in the values of D between August 2004 and October 2006 (Fig. 7a, b). We do not have a clear explanation for the time lag of plateau being shorter than for the slope and valley in August 2004. However, it is likely that the high variability of $\delta^{13}\text{C}_R$ on the slope and in the valley may have contributed to this. Yet, the regression coefficients for both slope and valley

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were very different from those for the plateau (Table 5, Fig. 7c). It is likely that lateral drainage of air enriched in ^{13}C from upslope areas occurs at our site. The 6 and 7-day time lag observed for plateau and valley in October 2006 shows that the time elapsed for a carbon atom to move from foliage to the site of respiration is not constant, but rather, it probably shifts with changes in carbon allocation, tissue metabolism, dark discrimination, assimilation rates, environmental conditions, etc. (McDowell et al., 2004; Bowling et al., 2002; Knohl et al., 2005; Werner et al., 2006).

In October 2006, $\delta^{13}\text{C}_R$ was more responsive to changes in D on the plateau than in the valley. As mentioned before, prior to nocturnal sampling periods, there was almost no rainfall in October 2006. Thus, it is likely that high D in combination with low soil water availability on the plateau have driven the observed pattern. Unfortunately, there were no measurements of θ available for the valley to corroborate our hypothesis with empirical data. However, for the plateau, there were. There was a strong negative correlation between $\delta^{13}\text{C}_R$ and θ , and the maximum correlation was observed with 1-day average and 1-day time lag ($r^2=0.91$). This is consistent with Lai et al. (2005), McDowell et al. (2004), Werner et al. (2006), Ponton et al. (2006) and Mortazavi et al. (2005). The shorter time lag for θ in comparison with that for D suggests that soil conditions have a faster and likely more direct effect on $\delta^{13}\text{C}_R$. For example, it may indicate that the proportion of $\delta^{13}\text{C}_R$ released from heterotrophic R_{soil} responds faster to changes in edaphic conditions (Werner et al., 2006). This effect was shown by Goulden et al. (2004) at a site in Central Amazonia.

5.5 Temporal and spatial variability of Δ_{leaf} and c_i/c_a ratio

There is a strong positive correlation between the c_i/c_a ratio and Δ_{leaf} (Farquhar et al., 1989a; Farquhar et al., 1989b; Lauteri et al., 1993; Ehleringer et al., 2002). The variation of the c_i/c_a ratio was within the expected range of values (0.5–0.8) for C_3 plants (Ehleringer et al., 2002). In addition, the values of the c_i/c_a ratio and Δ_{leaf} were close to 0.70 and 21.68‰, respectively, reported for an Amazonian rainforest canopy layer

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in French Guiana in the dry season (Buchmann et al., 1997). The calculated values of Δ_{leaf} showed no clear pattern and they were similar for plateau and valley (Fig. 8). Daytime values of carbon isotope discrimination by the canopy (Δ_{canopy}) were modelled for a tropical rainforest in southern Amazonia (Lloyd et al., 1996). The modelled Δ_{canopy} was highest in the morning and afternoon hours (about 20‰), with a minimum value around midday of about 18‰. Furthermore, Harwood et al., (1998) measured on-line Δ_{leaf} from sunlit leaves of *Piper anducum* (a tropical pioneering tree) and observed that Δ_{leaf} declined gradually over the day, from about 30‰ in the morning to about 10‰ in the late afternoon. The estimates of Δ_{leaf} by Bowling et al. (2001b) showed the same pattern as in Harwood et al. (1998). Nonetheless, Harwood et al. (1998) observed that the modelled Δ_{leaf} remained constant during daytime (between 20 and 25‰). The daytime values of Δ_{leaf} for the present study were consistent with the range of modelled Δ_{leaf} by Harwood et al. (1998). Diurnal curves of Δ_{leaf} from the upper canopy of two species of Mediterranean trees showed no clear pattern (Hymus et al., 2005). These authors acknowledged the dependence of Δ_{leaf} on the relative changes in assimilation rate and stomatal conductance, but also stressed that the resulting changes in $\delta^{13}\text{C}$ of respiratory substrates due to fractionation during dark respiration could also play an important role. As suggested in Sect. 5.1, at this site, the pattern of $\delta^{13}\text{C}_{\text{leaf}}$ was not only determined by Δ_{leaf} , but rather by a combination of factors such as, leaf nitrogen concentration, LMA, soil moisture availability and $\delta^{13}\text{C}_a$ in air surrounding the leaves.

6 Conclusions

We formulated two hypotheses to be tested in this study. The first one proposed that $\delta^{13}\text{C}_{\text{leaf}}$ is more negative in the valley than on the plateau as a consequence of both higher soil water availability in the valley and longer time of exposure to high c_a with low $\delta^{13}\text{C}_a$ in the valley than on the plateau during daytime hours. The second one proposed that the $\delta^{13}\text{C}_R$ is more negative in the valley than on the plateau.

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There is substantial evidence that $\delta^{13}\text{C}_{\text{leaf}}$ is more negative in the valley than on the plateau (Sect. 5.1). The processes and factors that may be playing a role at our site are leaf nitrogen concentration, LMA, soil moisture availability, Δ_{leaf} and lower $\delta^{13}\text{C}_a$ in the valley during daytime hours.

According to the literature, there is a strong positive relationship between $\delta^{13}\text{C}_{\text{leaf}}$ and WUE. Thus, at this site, according to the pattern of $\delta^{13}\text{C}_{\text{leaf}}$ it is likely that WUE is higher on the plateau than in the valley.

The use of Δ_{leaf} allows us to test the hypothesis that $\delta^{13}\text{C}_{\text{leaf}}$ is more negative in the valley, as it is likely that Δ_{leaf} is higher there. However, we were not able to provide full supporting evidence for this from our dataset mainly because at this site, the pattern of $\delta^{13}\text{C}_{\text{leaf}}$ was not only determined by Δ_{leaf} , but rather by a combination of factors such as, leaf nitrogen concentration, LMA, soil moisture availability and $\delta^{13}\text{C}_a$ in air surrounding the leaves.

The $\delta^{13}\text{C}_{\text{leaf}}$, $\delta^{13}\text{C}_a$ and $\delta^{13}\text{C}_{\text{soil}}$ were more negative in the valley than on the plateau. Thus, $\delta^{13}\text{C}_R$ is expected to be also more negative in the valley than on the plateau. This was observed on some nights, whereas on others it was not. The most likely explanation for this was sought in lateral drainage of CO_2 enriched in ^{13}C from upslope areas, when the nights are less stable. This argument is purely based on physical factors only, such as stability parameters, lateral drainage, nocturnal thermal stratification, thermal belts, etc.

However, biotic factors, such as R_{soil} and the responses of plants to environmental variables such as D may also play a role. For example, R_{soil} varies spatial and seasonally along this topography and the response of heterotrophic R_{soil} to hydration is faster than that of autotrophic R_{soil} . The soluble sugars produced at the top of the trees are used at the sites of respiration (e.g. stem, leaves, and roots) and their signature should reflect the environmental conditions that prevailed when they were biosynthesized. The relationship between $\delta^{13}\text{C}_R$ and D sheds light on this issue.

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Table 1. Periods during which nocturnal samples of atmospheric air were collected along a topographical gradient in central Amazonia for stable carbon isotopes ratio and CO₂ concentration analyses. Time is presented as Local Time.

Place	Period	Height (m, a.g.l.)										
		0.2	2	3	7	11	13	20	22	30	42	52
Plateau	08–09 Oct 2002		✓		✓				✓ ¹		✓ ¹	✓ ¹
	17–18 Nov 2002	✓ ²			✓			✓ ²		✓ ²		
	02–05 Aug 2004	✓			✓			✓		✓ ³		
	07–16 Oct 2006	✓			✓ ⁴			✓ ⁴		✓ ⁴		
Slope	17–18 Nov 2002	✓			✓		✓ ¹	✓		✓		
	02–05 Aug 2004	✓			✓			✓		✓		
Valley	08–09 Oct 2002			✓ ¹		✓ ¹						
	17–18 Nov 2002	✓		✓		✓						
	02–05 Aug 2004	✓			✓			✓		✓		
	07–16 Oct 2006	✓			✓ ⁴			✓ ⁴		✓ ⁴		

¹ Extra samples collected between 07:00 and 14:00

² Extra samples collected between 12:00 and 14:00

³ Extra samples collected between 14:00 and 16:00

⁴ Extra samples collected between 09:00 and 18:00

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Table 2. Stable carbon isotope and C:N ratios of leaves and litter along a topographical gradient in central Amazonia. Leaves were sampled in the canopy layer in August 2004 and at the top of the canopy in October 2006. The $\delta^{13}\text{C}_{\text{leaf}}$, $\delta^{13}\text{C}_{\text{litter}}$, C:N_{leaf} and C:N_{litter} are presented as average (\pm standard error). Averages in the same column followed by different letters are significantly different at $\alpha=0.01$ (Bonferroni *t* tests).

Date	Place	$\delta^{13}\text{C}_{\text{leaf}}$ (‰)	C:N _{leaf}	$\delta^{13}\text{C}_{\text{litter}}$ (‰)	C:N _{litter}	<i>n</i> ₁	<i>n</i> ₂
August 2004	Plateau	-28.86 ^a ±0.84	28.01 ^a ±5.5	-30.75 ^a	27.84 ^a	5	1
	Slope	-31.54 ^{ab} ±1.00	35.15 ^a ±5.1	-30.22 ^a	26.67 ^a	4	1
	Valley	-32.34 ^b ±0.79	35.34 ^a ±5.5	-30.12 ^a	30.84 ^a	5	1
October 2006	Plateau	-29.71 ^a ±0.32	30.92 ^a ±2.3			13	
	Campinarana	-30.31 ^b ±0.36	35.24 ^a ±2.8			11	
	Valley	-30.55 ^b ±0.25	37.88 ^a ±2.7			11	

The number of samples collected at each topographical section is presented as *n*₁ and *n*₂, and refer to leaf and litter samples, respectively.

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Table 3. Statistics of Keeling plots used to obtain the $\delta^{13}\text{C}_R$ along a topographical gradient in central Amazonia. The values of a and a_v are expressed in ‰ (per mil), c_a in ppm, and $b_{y,x}$ and $v_{y,x}$ in ‰ ppm.

Place	Period	$b_{y,x}$	a	$v_{y,x}$	a_v	r	r^2	SE_a	c_a min	c_a max	c_a range	n
Plateau	2–3 Aug 2004	8066.06	−29.76	8221.10	−30.14	0.98	0.96	0.91	379.5	483.7	104.2	20
	3–4 Aug 2004	8487.91	−30.79	8562.05	−30.97	0.99	0.98	0.71	388.1	476.3	88.2	16
	4–5 Aug 2004	8069.02	−29.62	8107.45	−29.71	0.99	0.99	0.43	374.3	551.9	177.6	20
	7–8 Oct 2006	7377.16	−28.02	7403.43	−28.09	0.99	0.99	0.37	374.2	513.2	139	17
	8–9 Oct 2006	7698.18	−28.70	7780.70	−28.89	0.99	0.98	0.68	408.7	456.5	47.8	17
	9–10 Oct 2006	5609.03	−23.64	5797.74	−24.04	0.96	0.94	0.81	419.4	553.4	134	17
Slope	2–3 Aug 2004	9441.98	−32.46	9605.08	−32.81	0.98	0.97	0.89	394.2	545.3	151.1	18
	3–4 Aug 2004	8278.19	−29.39	8447.39	−29.74	0.98	0.96	0.82	428.5	545.7	117.2	20
	4–5 Aug 2004	7496.50	−28.30	7517.47	−28.35	0.99	0.99	0.28	410.8	578.7	167.9	18
Valley	2–3 Aug 2004	9658.42	−32.44	9779.97	−32.69	0.99	0.98	0.73	447.7	560.6	112.9	20
	3–4 Aug 2004	6489.37	−26.08	6679.55	−26.46	0.97	0.94	0.77	455.7	558.6	102.9	19
	4–5 Aug 2004	8299.85	−29.69	8340.31	−29.78	0.99	0.99	0.40	422.2	559.6	137.4	20
	7–8 Oct 2006	7523.61	−28.13	7615.30	−28.30	0.99	0.98	0.59	476.2	595.0	118.8	16
	8–9 Oct 2006	6671.87	−26.64	7052.79	−27.48	0.93	0.89	1.29	405.1	488.4	83.3	17
	9–10 Oct 2006	5809.47	−25.10	5989.76	−25.48	0.94	0.94	0.79	418.7	523.8	105.1	14

The slope of Model I regression ($b_{y,x}$), the Y-intercept of Model I regression (a), the slope of Model II regression ($v_{y,x}$), the Y-intercept of Model II regression (a_v), the correlation coefficient (r), the coefficient of determination (r^2), the standard error of the Y-intercept of Model I regression (SE_a), and the c_a minimum, maximum and range are presented. The SE_a higher than 1‰ is in bold.

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Table 4. Statistics of daytime values of $\delta^{13}\text{C}_a$ measured along a topographical gradient in central Amazonia. The averaged $\delta^{13}\text{C}_a$ (\pm standard error), $\delta^{13}\text{C}_a$ min and $\delta^{13}\text{C}_a$ max are expressed in ‰ (per mil).

Place	z (m, a.g.l.)	08 Oct 2006				Date 09 Oct 2006				16 Oct 2006			
		$\delta^{13}\text{C}_a$	$\delta^{13}\text{C}_a$ min	$\delta^{13}\text{C}_a$ max	n	$\delta^{13}\text{C}_a$	$\delta^{13}\text{C}_a$ min	$\delta^{13}\text{C}_a$ max	n	$\delta^{13}\text{C}_a$	$\delta^{13}\text{C}_a$ min	$\delta^{13}\text{C}_a$ max	n
Plateau	42*	-9.01	-9.02	-8.99	2	-8.20			1	-9.72			1
	22	-8.76 \pm 0.2	-9.12	-7.99	6	-8.61 \pm 0.1	-9.19	-8.34	6	-9.08 \pm 0.2	-9.56	-8.68	6
	7	-8.90 \pm 0.2	-9.33	-8.07	6	-8.91 \pm 0.2	-9.31	-8.37	5	-9.61 \pm 0.3	-10.87	-8.48	6
Valley	30*	-9.35			1	-9.72			1	-10.14			1
	20	-9.36 \pm 0.2	-9.89	-8.91	6	-10.01 \pm 0.2	-10.23	-9.84	6	-10.11 \pm 0.3	-10.56	-9.74	6
	7	-10.09 \pm 0.4	-11.12	-8.76	6	-10.12 \pm 0.2	-10.76	-9.70	6	-10.97 \pm 0.8	-12.02	-9.76	6

(*) Air samples collected late in the afternoon (between 15:00 and 17:00) at these heights.

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Table 5. Summary of correlation analyses between $\delta^{13}\text{C}_R$ and water vapor saturation deficit in the air (D) at a forest site in central Amazonia in the dry season. The values of a are expressed in ‰ (per mil) and $b_{y,x}$ in ‰ kPa⁻¹. Unless otherwise indicated, $n=3$ for every topographical section.

Date	Place	n -day average	n -day time lag	r	r^2	P	a	$b_{y,x}$
August 2004	Plateau	1	2	0.99	0.99	0.046	-33.98	2.41
	Slope	3	4	0.99	0.99	0.003	-75.36	27.31
	Valley	1	4	0.99	0.98	0.094	-158.65	74.90
October 2006	Plateau	1	7	0.97	0.94	0.160	-39.71	7.18
	Valley	2	6	0.99	0.99	0.008	-34.88	4.26

The number of days averaged (n -day average), the number of days lagged (n -day time lag), the correlation coefficient (r), the coefficient of determination (r^2), the P -value of the regression, the Y -intercept of Model I regression (a), and the slope of Model I regression ($b_{y,x}$) are presented.

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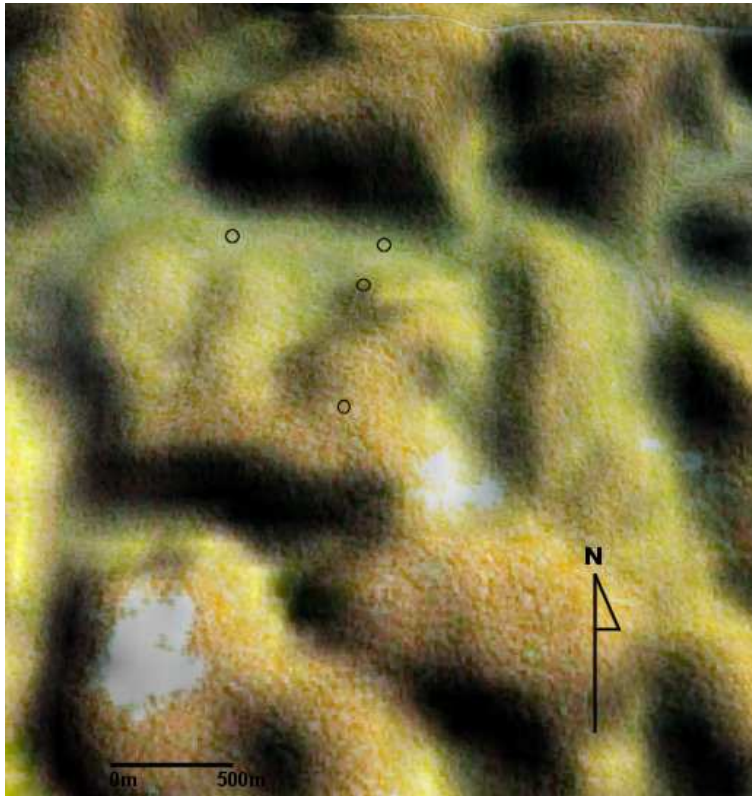


Fig. 1. Composite of satellite images from a topographical gradient in Central Amazonia along which $\delta^{13}\text{C}_a$, c_a , $\delta^{13}\text{C}_{\text{leaf}}$, $\delta^{13}\text{C}_{\text{litter}}$ and $\delta^{13}\text{C}_{\text{soil}}$ were measured. An IKONOS image was overlaid on a SRTM image to generate the composite. The black open circles denote the places where the measurements were made.

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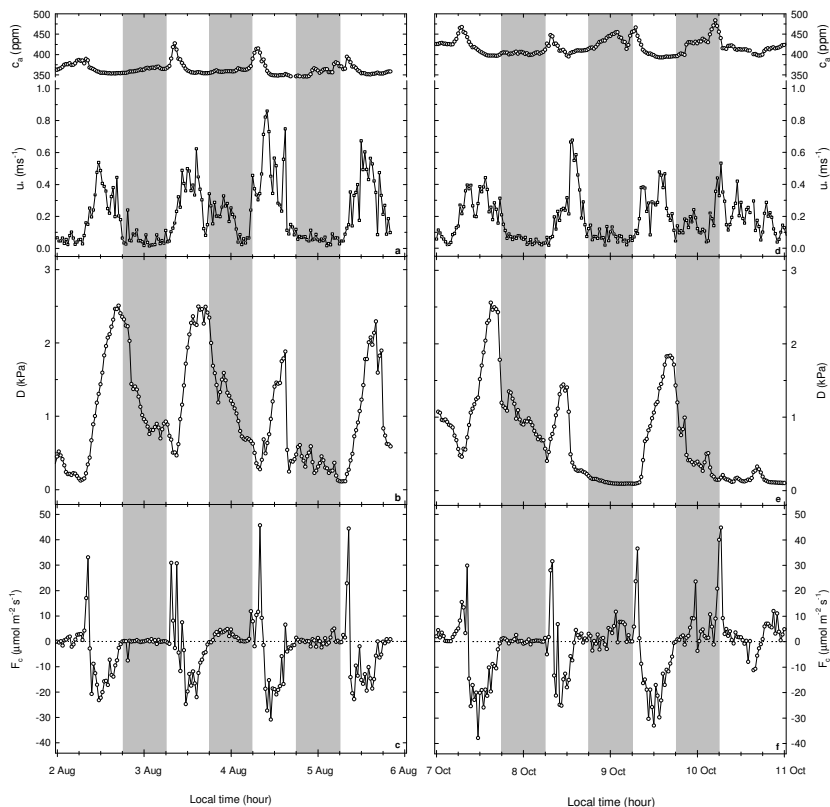


Fig. 2. Diurnal variation of some meteorological and turbulent variables measured at the top of K34 tower (53 m a.g.l. on the plateau): from 2–5 August 2004 (**a–c**) and from 7–10 October 2006 (**d–f**). Points correspond to half-an-hour averages. The shaded boxes indicate the nighttime periods. Points above the horizontal dotted line (**c** and **f**) denote CO_2 release, and below the line CO_2 uptake.

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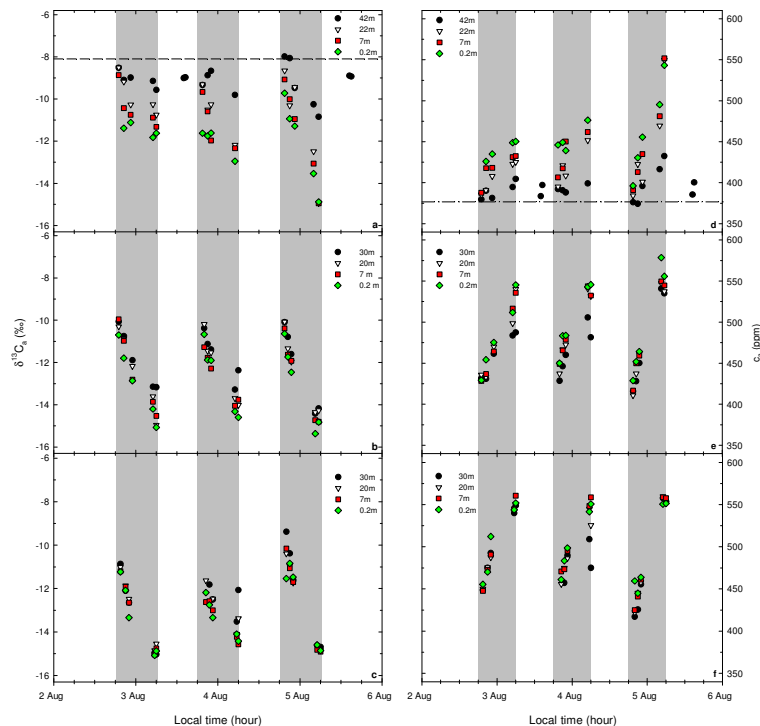


Fig. 3. Evolution of $\delta^{13}\text{C}_a$ and c_a along a topographical gradient in Central Amazonia from sunset until dawn on 2–5 August 2004: on the plateau (**a, d**), slope (**b, e**) and valley (**c, f**); and measurements of $\delta^{13}\text{C}_a$ and c_a at 42 m a.g.l. on the plateau late in the afternoon on 5 August 2004 (**a, d**). Points correspond to the single measurement made at each sampling level. The dashed line in (**a**) and the dash-dotted line in (**d**) represent the carbon isotope ratio of tropospheric background CO_2 ($\delta^{13}\text{C}_b$) and the tropospheric background $[\text{CO}_2]$ (c_b) measured in the marine boundary layer at Ascension Island, UK (7.92°S 14.42°W; 54 m a.s.l.), respectively, on August 2004 (about -8.094‰ and 376.71 ppm) (White and Vaughn, 2007; Conway et al., 2007). The shaded boxes indicate the nighttime periods.

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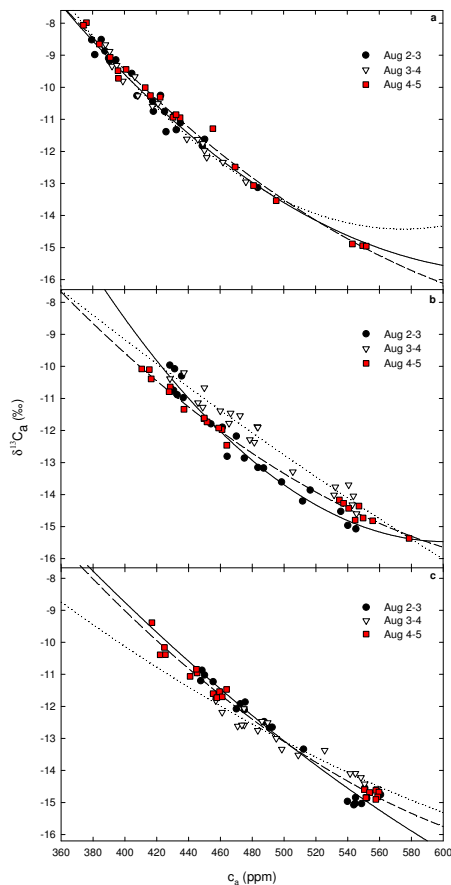


Fig. 4. Relationship between c_a and $\delta^{13}\text{C}_a$ along a topographical gradient in Central Amazonia from sunset until dawn on 2–5 August 2004: **(a)** on the plateau, **(b)** slope and **(c)** valley. Points correspond to the single measurement made at each sampling level. The solid, dotted and dashed lines denote the second-order regressions for the periods of 2–3 August, 3–4 August and 4–5 August, respectively.

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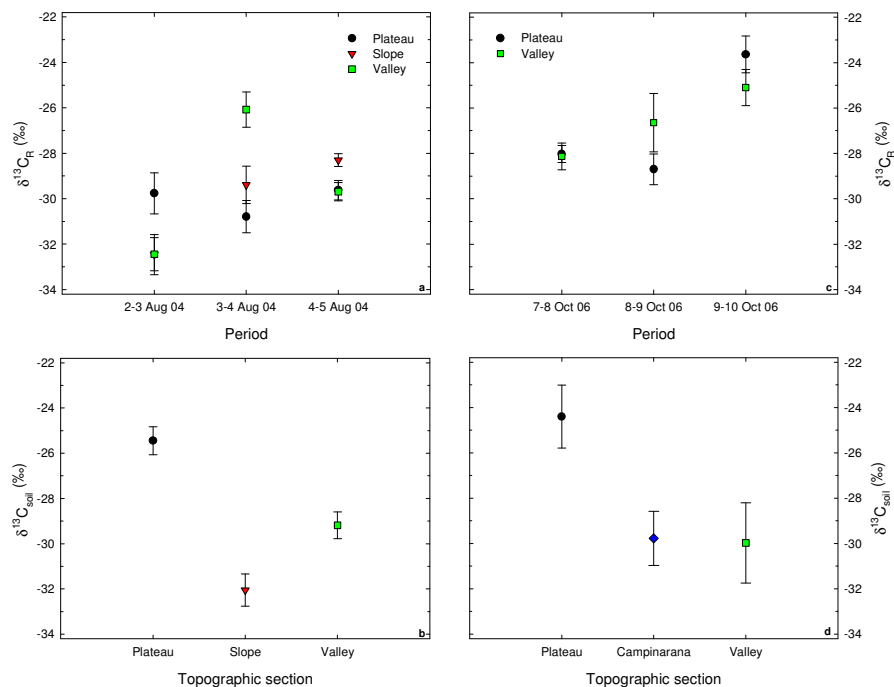


Fig. 5. $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_{\text{soil}}$ measured along a topographical gradient in Central Amazonia in August 2004 (a, b) and October 2006 (c, d). Points in (a) and (c) correspond to the Y-intercept of the Keeling plot (\pm standard error) for every nighttime period at each topographical position. Each point in (b) and (d) corresponds to the Y-intercept of the Keeling plot (\pm standard error) at each topographical position on 6 August 2004 and 9 October 2006, respectively.

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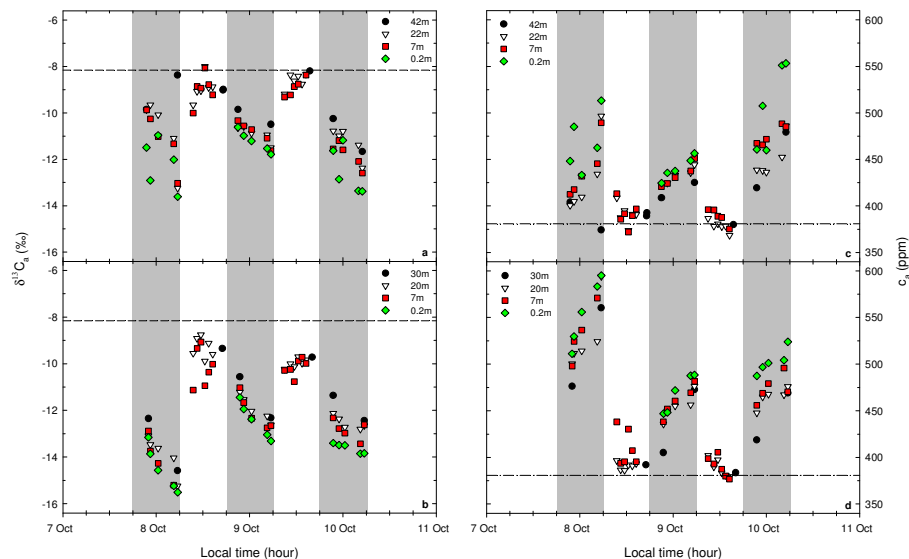


Fig. 6. Diurnal curves of $\delta^{13}\text{C}_a$ and c_a along a topographical gradient in Central Amazonia on 7–10 October 2006: on the plateau (**a**, **c**) and in the valley (**b**, **d**). Points correspond to the single measurements made at each sampling level. The dashed line (a, b) and the dash-dotted line (c, d) represent the carbon isotope ratio of tropospheric background CO_2 ($\delta^{13}\text{C}_b$) and the tropospheric background $[\text{CO}_2]$ (c_b) measured in the marine boundary layer at Ascension Island, UK (7.92°S 14.42°W; 54 m a.s.l.), respectively, on October 2006 (about -8.156‰ and 380.77 ppm). The $\delta^{13}\text{C}_b$ was determined by linear interpolation using the data from October 2004 and 2005, as these were the last data available (about -8.105 and -8.152‰ , respectively). The c_b was determined by adding the annual $[\text{CO}_2]$ growth rate for the year 2006 (about 1.73 ppm yr^{-1}) to the $[\text{CO}_2]$ on October 2005 (about 379.04 ppm) (White and Vaughn, 2007; Conway et al., 2007). The shaded boxes indicate the nighttime periods.

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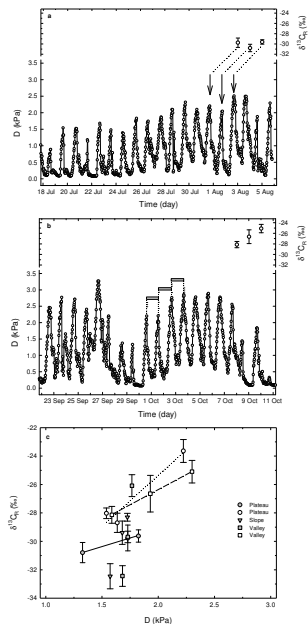


Fig. 7. Diurnal curves of half-an-hour averages of water vapor saturation deficit in the air (D) measured at the top of K34 tower (53 m a.g.l. on the plateau): from 18 July to 5 August 2004 **(a)** and from 22 September to 10 October 2006 **(b)**. Carbon isotope ratio of ecosystem respired CO_2 ($\delta^{13}\text{C}_R$) (\pm standard error) on the plateau from 2–5 August 2004 (a) and in the valley from 7–10 October 2006 (b). The n -day average and n -day time lag that presented the maximum correlation between $\delta^{13}\text{C}_R$ and D on the plateau and in the valley (Table 5) are indicated by arrows (a) and horizontal bars (b), respectively. The length of the horizontal bar denotes the 2-day averaged (Table 5), and each horizontal bar has a corresponding $\delta^{13}\text{C}_R$, from left to right. **(c)** Relationship between $\delta^{13}\text{C}_R$ and (averaged and time-lagged) D along a topographical gradient in Central Amazonia in August 2004 (shaded symbols) and October 2006 (open symbols) according to the results of Table 5. The linear regressions for slope and valley in August 2004 were omitted for clarity. The error bars denote the standard error.

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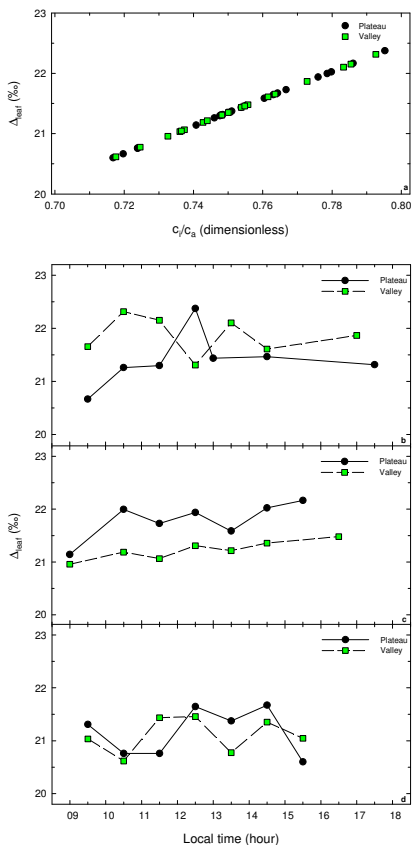


Fig. 8. (a) Relationship between carbon isotope discrimination by a leaf (Δ_{leaf}) and the ratio of intercellular (c_i) to atmospheric CO_2 (c_a) concentrations along a topographical gradient in Central Amazonia on October 2006. Evolution of Δ_{leaf} on the plateau and in the valley on 9 (b), 10 (c) and 16 (d) October 2006.

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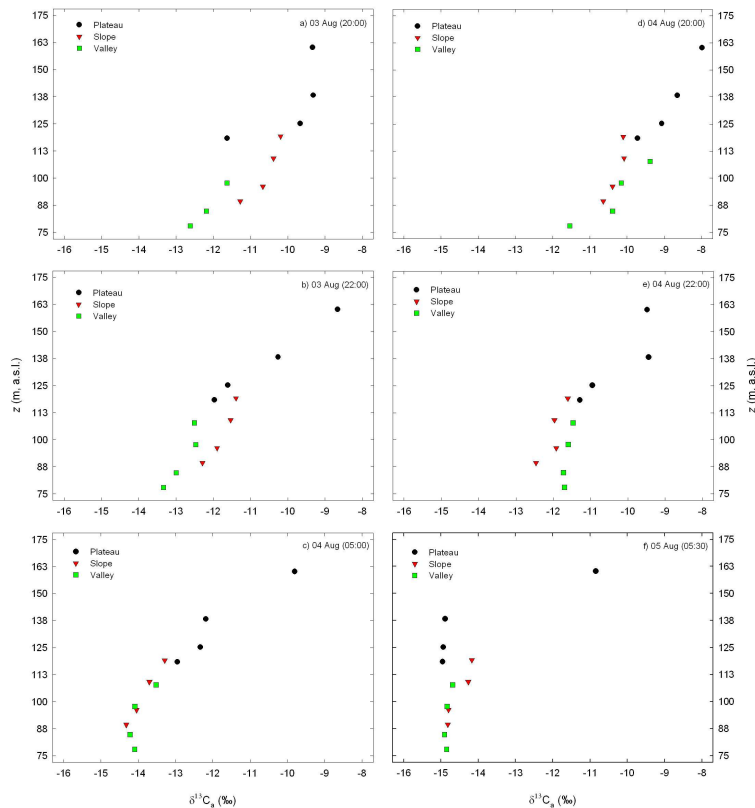


Fig. 9. Composite of vertical profiles of $\delta^{13}\text{C}_a$ from three different positions along a topographical gradient in Central Amazonia during the nighttime periods from 3–4 August (a–c) and 4–5 August (d–f) 2004. The reference altitude corresponds to the soil surface level at 850 m in the valley (about 77.3 m a.s.l.). Points correspond to the single measurement made at each sampling level. Time is presented as Local Time.

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