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## Interseasonal comparison of CO<sub>2</sub> concentrations, isotopic composition, and carbon dynamics in an Amazonian rainforest (French Guiana)

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**Abstract** Canopy CO<sub>2</sub> concentrations in a tropical rainforest in French Guiana were measured continuously for 5 days during the 1994 dry season and the 1995 wet season. Carbon dioxide concentrations ([CO<sub>2</sub>]) throughout the canopy (0.02–38 m) showed a distinct daily pattern, were well-stratified and decreased with increasing height into the canopy. During both seasons, daytime [CO<sub>2</sub>] in the upper and middle canopy decreased on average 7–10 μmol mol<sup>-1</sup> below tropospheric baseline values measured at Barbados. Within the main part of the canopy (≥ 0.7 m), [CO<sub>2</sub>] did not differ between the wet and dry seasons. In contrast, [CO<sub>2</sub>] below 0.7 m were generally higher during the dry season, resulting in larger [CO<sub>2</sub>] gradients. Supporting this observation, soil CO<sub>2</sub> efflux was on average higher during the dry season than during the wet season, either due to diffusive limitations and/or to oxygen deficiency of root and microbial respiration. Soil respiration rates decreased by 40% after strong rain events, resulting in a rapid decrease in canopy [CO<sub>2</sub>] immediately above the forest floor of about 50 μmol mol<sup>-1</sup>. Temporal and spatial variations in [CO<sub>2</sub>]<sub>canopy</sub> were reflected in changes of δ<sup>13</sup>C<sub>canopy</sub> and δ<sup>18</sup>O<sub>canopy</sub> values. Tight relationships were observed between δ<sup>13</sup>C and δ<sup>18</sup>O of canopy CO<sub>2</sub> during both seasons ( $r^2 > 0.86$ ). The most depleted δ<sup>13</sup>C<sub>canopy</sub> and δ<sup>18</sup>O<sub>canopy</sub>

values were measured immediately above the forest floor (δ<sup>13</sup>C = -16.4‰; δ<sup>18</sup>O = 39.1‰ SMOW). Gradients in the isotope ratios of CO<sub>2</sub> between the top of the canopy and the forest floor ranged between 2.0‰ and 6.3‰ for δ<sup>13</sup>C, and between 1.0‰ and 3.5‰ for δ<sup>18</sup>O. The δ<sup>13</sup>C<sub>leaf</sub> and calculated *c<sub>i</sub>/c<sub>a</sub>* of foliage at three different positions were similar for the dry and wet seasons indicating that the canopy maintained a constant ratio of photosynthesis to stomatal conductance. About 20% of the differences in δ<sup>13</sup>C<sub>leaf</sub> within the canopy was accounted for by source air effects, the remaining 80% must be due to changes in *c<sub>i</sub>/c<sub>a</sub>*. Plotting 1/[CO<sub>2</sub>] vs. the corresponding δ<sup>13</sup>C ratios resulted in very tight, linear relationships ( $r^2 = 0.99$ ), with no significant differences between the two seasons, suggesting negligible seasonal variability in turbulent mixing relative to ecosystem gas exchange. The intercepts of these relationships that should be indicative of the δ<sup>13</sup>C of respired sources were close to the measured δ<sup>13</sup>C of soil respired CO<sub>2</sub> and to the δ<sup>13</sup>C of litter and soil organic matter. Estimates of carbon isotope discrimination of the entire ecosystem, Δ<sub>e</sub>, were calculated as 20.3‰ during the dry season and as 20.5‰ during the wet season.

**Key words** Carbon discrimination · δ<sup>13</sup>C · δ<sup>18</sup>O · Canopy CO<sub>2</sub> profiles · Soil respiration.

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### Introduction

Tropical forests, covering about 17% of the earth's continents (Olson et al. 1983), store large amounts of the world's carbon pools. Approximately 53% of the carbon in terrestrial above- and below-ground biomass, and 28% of the global soil carbon pool are found in tropical forests and woodlands (Solomon et al. 1993). Although these overall carbon budgets indicate the global importance of tropical forests, information about carbon fluxes within tropical ecosystems and their controlling factors is needed to elucidate the role of tropical forests for global carbon dioxide exchange.

Canopy  $\text{CO}_2$  concentrations ( $[\text{CO}_2]$ ) can be used as an indicator of differences in gas exchange activities among forest components and of interactions between the soil and the atmosphere. In response to turbulent mixing as well as to photosynthesis and respiration,  $[\text{CO}_2]$  varies daily, from very high nocturnal  $[\text{CO}_2]$  to low concentrations during the day (Richards 1952; Lemon et al. 1970; Odum and Pigeon 1970; Aoki et al. 1975; Schnell et al. 1981; Wofsy et al. 1988). Daytime  $[\text{CO}_2]$  can decrease below tropospheric baseline levels due to active photosynthesis, often by as much as  $20 \mu\text{mol mol}^{-1}$  (Raupach et al. 1992; Buchmann et al. 1996, 1997a). Furthermore, canopy  $[\text{CO}_2]$  generally increases near the ground surface. High concentrations immediately above the forest floor can reach values more than  $100\text{--}150 \mu\text{mol mol}^{-1}$  above tropospheric background  $[\text{CO}_2]$ , indicating the dominant influence of soil respiration on canopy  $\text{CO}_2$  profiles. Using static  $\text{CO}_2$  concentration profiles allows for separation into different canopy strata, thus providing insight into how stand structure (e.g. stand density, understory vegetation) influences stand carbon dynamics (Buchmann et al. 1996).

Internal carbon fluxes within forest canopies and their interactions with soil and atmospheric exchange processes can be addressed using carbon isotopes. As concluded from canopy  $\text{CO}_2$  profile measurements, canopy air is influenced by two main  $\text{CO}_2$  sources, tropospheric  $\text{CO}_2$  and respired  $\text{CO}_2$  (Keeling 1958). Both sources have very distinct carbon isotope ratios ( $\delta^{13}\text{C}$ ; Keeling 1958): about  $-8\text{‰}$  for the tropospheric pool, and  $-28\text{‰}$  for respired  $\text{CO}_2$ , similar to leaf litter. Turbulent mixing between these two sources within the canopy and discrimination against  $^{13}\text{CO}_2$  during photosynthesis results in  $\delta^{13}\text{C}$  ratios of canopy air that are more depleted near the soil surface than at the top of the canopy (Francey et al. 1985; van der Merwe and Medina 1989; Sternberg et al. 1989a; Quay et al. 1989; Broadmeadow et al. 1992; Lloyd et al. 1996). Frequent observations that  $\delta^{13}\text{C}$  ratios of foliage typically decrease with decreasing height above the forest floor (Vogel 1978; Medina and Minchin 1980), have fuelled speculations about the importance of source air effects in relation to changes associated with photosynthesis. Empirical models that relate gas exchange characteristics and the  $\delta^{13}\text{C}$  ratio of source air to leaf carbon isotope composition (Farquhar et al. 1982; Schleser and Jayasekera 1985) provide a valuable tool for quantifying the importance of these two factors.

However, within the last ten years, only a limited number of field studies addressed aspects of internal  $\text{CO}_2$  fluxes within tropical forests (Sternberg 1989; Sternberg et al. 1989a; Quay et al. 1989; Broadmeadow et al. 1992; Grace et al. 1996; Kruijt et al. 1996; Lloyd et al. 1996) or provided quantitative estimates of  $\text{CO}_2$  dynamics and of carbon isotope discrimination at the leaf ( $\Delta_{\text{leaf}}$ ; Francey et al. 1985; van der Merwe and Medina 1989; Kruijt et al. 1996) and the ecosystem level ( $\Delta_{\text{e}}$ ; Buchmann et al. 1997b). Ecosystem carbon isotope

discrimination integrates over  $\Delta_{\text{leaf}}$  within a canopy, but also includes information about  $\text{CO}_2$  released by respiration of plants and soils. Field measures of the  $\delta^{13}\text{C}$  of respired sources are essential to calculate  $\Delta_{\text{e}}$ , however, actual isotopic analyses of soil respired  $\text{CO}_2$  are rare and, instead, data are mostly extrapolated from leaf and litter values. Moreover, only limited information is available about temporal variations of  $\Delta_{\text{e}}$  in the wet and dry seasons. As pointed out by Lloyd and Farquhar (1994), temporal variability of canopy as well as ecosystem carbon isotope discrimination is critical for our understanding of the global carbon budget and our ability to model carbon fluxes. Oxygen isotope ratios of atmospheric  $\text{CO}_2$  can provide further information about a system's carbon and water fluxes, because  $\delta^{18}\text{O}$  of atmospheric  $\text{CO}_2$  is not only influenced by exchange processes with oceans and clouds, but also by exchange with the terrestrial biosphere and pedosphere (Friedli et al. 1987; Farquhar and Lloyd 1993). However, no information is available about the  $\delta^{18}\text{O}$  of canopy air in tropical forests, although this aspect is attracting increasingly attention for global models (Ciais et al. 1996).

In this study, we address the questions of how concentrations and carbon and oxygen isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) of canopy  $\text{CO}_2$  profiles change daily and seasonally in a tropical rainforest, and how well the  $\delta^{13}\text{C}$  of litter or soil organic matter matches the  $\delta^{13}\text{C}$  of soil respired  $\text{CO}_2$ . Furthermore, we estimate ecosystem carbon isotope discrimination and its seasonal variability.

## Materials and methods

### Site

The study site Paracou (managed by "CIRAD-forêts") is located in the equatorial lowland rainforest of French Guiana ( $53^{\circ}\text{W}$   $5^{\circ}\text{N}$ , 40 m asl), approximately 50 km west of Kourou. The dense primary forest (Leaf area index, LAI 8; A. Granier, personal communication) had a basal area of about  $35 \text{ m}^2 \text{ ha}^{-1}$ . The canopy is stratified in three layers: an upper canopy formed by trees 25–35 m tall, a middle canopy at about 15–20 m, and an understory regeneration with saplings < 2 m tall. Three angiosperm families (out of 73 total) make up 60% of the rainforest in French Guiana, i.e., the Lecythidaceae (genera *Eschweilera* and *Lecythis*), the Caesalpiniaceae (genera *Eperua* and *Dycorinia*) and the Chrysobalanaceae (genera *Licania* and *Parinari*; Favrichon 1994; Loubry 1994). The soil is a well-drained Oxisol on Precambrian bedrock. Clay contents increase continuously with depth, from sandy upper horizons to a sandy clay below 1.50 m depth (Huc et al. 1994). The regional climate is characterized by a distinct seasonal pattern: a wet season (December–August), which is normally interrupted in February or March by a short dry period (petite saison sèche), and a long dry season (grande saison sèche; September–November; Loubry 1994) with monthly precipitation of less than 150 mm. Average annual precipitation is 2200 mm (Huc et al. 1994).

### Continuous $[\text{CO}_2]$ and micrometeorological measurements

Canopy  $[\text{CO}_2]$  was measured continuously for 5 days during the 1994 dry season (26–30 September), and for 5 days during the 1995 wet season (9–13 July). Canopy air was sampled from different heights within the canopy (0.02, 0.75, 2.00, 13.3, 28.3 and 36.8 m in

1994; 0.10, 0.70, 2.00, 18.2, 31.6 m and 37.1 m in 1995). Dry air (dried with magnesium perchlorate and Gelman filters) was drawn at a flow rate of 10 ml/s through tubing (Dekoron 1300; 0.625 cm outer diameter; Aurora, Ohio, USA), and pumped into an infra-red CO<sub>2</sub> gas analyzer (LI-6262; LiCor, Lincoln, Neb., USA). The set-up provided sampling of air from six heights and two standards (one CO<sub>2</sub>-free air source and a calibrated CO<sub>2</sub> source; Buchmann et al. 1996). A run of the entire profile with six heights was completed within 10 minutes; each height was measured for 90 s. The last 15 of the 90 CO<sub>2</sub> readings at each height were averaged and stored. Every 3 h, calibration gases were measured. Continuous CO<sub>2</sub> data are presented as the hourly averages of 10-min records.

Air temperatures were measured at 1.00 and 36.8 m (37.1 m in 1995) height, and soil temperatures at 0.05 m soil depth by using copper-constantan thermocouples. Thermocouples for air temperature were shielded against direct sunlight, but installation allowed free air movement. During both seasons, bulk precipitation and photosynthetically active radiation (PAR) above the canopy were measured approximately 2 m above the canopy of a nearby plantation. PAR at 1.00 m height was measured at our site in 1995 with a photodiode (GaAsP 1118, Hamamatsu, Bridgewater, N. J., USA) after calibration against a quantum sensor (LI-190; LiCor, Lincoln, Neb., USA). Bulk precipitation summed up to 0.4 mm during the 5 days in the 1994 dry season, and to 42 mm during the 5 days in the 1995 wet season.

#### Collection of canopy air for isotope analyses

Canopy air was collected for isotopic analyses from the same heights as used for the continuous CO<sub>2</sub> measurements from a second set of tubings. Using a battery-operated 12-V pump (TD-3LS, Brailsford and Company Inc., Rye, N. Y., USA), dry air (by dried magnesium perchlorate) was drawn through the tubing and a pre-evacuated 1.7-l glass flask (with two high-vacuum stopcocks) at a flow rate of 10 ml/s. After pumping for 20 min, [CO<sub>2</sub>] coming out of the flask was measured with a portable photosynthesis system (LI-6200; LiCor, Lincoln, Neb., USA), and then both stopcocks of the flask were closed. Up to four flasks were collected at the same time. Over the 5 days during the 1994 dry season, 62 flask samples were collected between 0700 and 2200 hours; over the 5 days during the 1995 wet season, 36 flask samples were collected between 0600 and 1730 hours.

#### Measurement of soil CO<sub>2</sub> efflux and soil moisture

Soil respiration rates were measured using a soil respiration chamber (LI-6000-09S; LiCor, Lincoln, Neb., USA) connected to a portable photosynthesis system (LI-6200). Two PVC tubes (0.25 m long, 0.10 m inside diameter) to which the chamber could be attached without leaks to the atmosphere, were inserted into the soil, 24 h prior to measurement. The protocol recommended by LiCor (LI-6000-09S manual) was changed to five observations of 5 μmol mol<sup>-1</sup> change per measurement (J. Norman personal communication). CO<sub>2</sub> concentrations were scrubbed with soda lime in an open configuration until the CO<sub>2</sub> level was 50 μmol mol<sup>-1</sup> below ambient. After closing the system, [CO<sub>2</sub>] was allowed to increase by 20 μmol mol<sup>-1</sup> before measurements were taken: 16 measurements were taken during the 1994 dry season, and a total of 12 measurements during the 1995 wet season. Gravimetric soil water content was determined with three replicates per measurement. The wet soil samples were weighed, then dried until weight constancy, and weighed again. Soil moisture is expressed as per cent dry weight (% dw).

#### Collection of soil respired CO<sub>2</sub> for isotope analyses

The set-up described for soil respiration measurements was modified to collect soil respired CO<sub>2</sub> for isotopic analyses. A closed

system was designed where soil CO<sub>2</sub> efflux was drawn from the soil respiration chamber through the LI-6200 and an ethanol-dry ice water trap into a glass flask and pushed back into the chamber. The 1.7-l glass flask was filled with CO<sub>2</sub>-free N<sub>2</sub> gas and connected to the top inlet of the soil respiration chamber. The air within the entire system was scrubbed by soda lime for 10–20 min. As soon as [CO<sub>2</sub>] decreased below 50 μmol mol<sup>-1</sup>, the soda lime was taken out of line. The system's [CO<sub>2</sub>] was allowed to increase to approximately 350 μmol mol<sup>-1</sup> before the stopcocks of the flask were closed. Four flasks were collected in each season.

#### Sampling and isotope analyses

Foliage samples for carbon isotope analyses (δ<sup>13</sup>C<sub>leaf</sub>) were collected using the "shotgun-removal" method from three positions in the canopy: upper canopy (> 30 m, 5 dominant trees of different species), middle canopy (15 m, 5 co-dominant trees of different species) and understory (2 m, 5 saplings of different species). Litter and soil samples (3 replicates each) were taken at the site that was used for soil respiration measurements. Plant samples were dried for 48 h at 70°C and then ground with mortar and pestle to a fine powder. Soil materials were acid-washed and then sieved (mesh size 1 mm). A 2-mg subsample was combusted and analyzed for <sup>13</sup>C/<sup>12</sup>C using an isotope ratio mass spectrometer (delta S, Finnigan MAT, Bremen, Germany).

CO<sub>2</sub> of the flask samples was extracted cryogenically using a three-trap vacuum line and transferred into a sampling tube within 12 h after flask collection. Due to possible interferences at mass 44, CO<sub>2</sub> was separated from N<sub>2</sub>O by using a gas chromatograph (GC-14A; Poraplot Q column, Shimadzu Corporation, Kyoto, Japan) prior to isotope analysis. The CO<sub>2</sub> gas was introduced manually into the mass spectrometer, and carbon and oxygen isotope ratios of canopy air (δ<sup>13</sup>C<sub>canopy</sub>, δ<sup>18</sup>O<sub>canopy</sub>) were analyzed from the same sample.

The isotope ratio (δX) was calculated as

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \text{ ‰} \quad (1)$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the <sup>13</sup>C/<sup>12</sup>C or <sup>18</sup>O/<sup>16</sup>O ratios of the sample and the standard (PDB for carbon; SMOW for oxygen), respectively (Farquhar et al. 1989). The overall precision of the carbon isotope measurements was ± 0.11‰ for organic carbon, and 0.03‰ for carbon and 0.15‰ for oxygen isotopes in gas samples.

Carbon isotope discrimination (δ<sub>leaf</sub>) of a leaf was calculated as

$$\Delta_{\text{leaf}} = (\delta^{13}\text{C}_{\text{canopy}} - \delta^{13}\text{C}_{\text{leaf}})/(1 + \delta^{13}\text{C}_{\text{leaf}}) \quad (2)$$

where δ<sup>13</sup>C is expressed in absolute units (e.g., 0.026 instead of 26), not in the per mil notation used in Eq. 1. The δ<sup>13</sup>C<sub>canopy</sub> was calculated for each canopy height by first weighting the [CO<sub>2</sub>]<sub>canopy</sub> measured during each season by the above-canopy PAR, and then applying the corresponding linear regression equation (δ<sup>13</sup>C<sub>canopy</sub> as a function of 1/[CO<sub>2</sub>]<sub>canopy</sub>) obtained from all flask samples collected during this season.

The ratio of internal CO<sub>2</sub> concentration in the mesophyll air-spaces to the ambient atmospheric concentration of carbon dioxide (c<sub>i</sub>/c<sub>a</sub>) was calculated from (Farquhar et al. 1982).

$$\Delta_{\text{leaf}} = a + (b - a) \times c_i/c_a \quad (3)$$

which includes discrimination factors associated with diffusion in air ( $a$ ; 4.4‰), and with photosynthetic carboxylation ( $b$ ; 29‰; O'Leary 1993).

#### Modeling of δ<sup>13</sup>C<sub>canopy</sub> and estimates of Δ<sub>e</sub>

Carbon isotope ratios of canopy air (δ<sup>13</sup>C<sub>canopy</sub>) are the result of turbulent mixing of two major CO<sub>2</sub> sources with different δ<sup>13</sup>C (troposphere and respired CO<sub>2</sub>), and of a photosynthetic effect due to discrimination during carbon assimilation (Keeling 1958;

Sternberg 1989). In addition,  $\delta^{13}\text{C}_{\text{canopy}}$  are linearly related to the inverse of the corresponding  $[\text{CO}_2]_{\text{canopy}}$ .

The intercept of this linear regression is an indicator of the isotopic composition of respired  $\text{CO}_2$  and was used to estimate ecosystem discrimination against the heavier  $^{13}\text{C}$  during photosynthesis of the entire stand ( $\Delta_e$ ; Buchmann et al. 1997b). Provided no fractionation occurs during respiration,  $\Delta_e$  can be calculated as

$$\Delta_e = (\delta^{13}\text{C}_{\text{trop}} - \delta^{13}\text{C}_{\text{resp}}) / (1 + \delta^{13}\text{C}_{\text{resp}}) \quad (4)$$

where  $\delta^{13}\text{C}_{\text{trop}}$  describes the tropospheric  $\text{CO}_2$  and  $\delta^{13}\text{C}_{\text{resp}}$  the respired  $\text{CO}_2$ . Tropospheric data were collected on a weekly basis during daytime hours at Barbados ( $59^\circ 26' \text{W}$   $13^\circ 10' \text{N}$ , 3 m asl) within the NOAA Cooperative Flask Sampling Network (Conway et al. 1994; Ciais et al. 1995). Monthly mean  $[\text{CO}_2]_{\text{trop}}$  was provided by Thomas Conway (NOAA/CMDL; September 1994:  $353.7 \mu\text{mol mol}^{-1}$ , July 1995:  $360.4 \mu\text{mol mol}^{-1}$ ); monthly mean  $\delta^{13}\text{C}_{\text{trop}}$  was provided by M. Trolier (University of Colorado, INSTAAR; September 1994:  $-7.73\text{‰}$ , July 1995:  $-7.96\text{‰}$ ). The precision of the NOAA data is  $< 0.5 \mu\text{mol mol}^{-1}$  for  $[\text{CO}_2]$ , and  $\pm 0.03\text{‰}$  for  $\delta^{13}\text{C}$ . Natural temporal variability for data, collected at the same station over a one month period is  $< 0.2\text{‰}$  (M. Trolier, personal communication). Variability between stations at a similar latitude is between  $0.5$  and  $1 \mu\text{mol mol}^{-1}$  and around  $0.25\text{‰}$  (see Conway et al. 1994; Ciais et al. 1995, respectively).

#### Statistics

The statistical package JMP (Version 3, SAS Institute Inc., Cary, N.C., USA) was used for most of the data analyses. Analyses of variance (ANOVA) were done with a nested design, e.g., season within height or with multiple main factors such as season, daytime, height. If the interaction terms were not significant ( $P > 0.05$ ), data were pooled and reanalyzed. The Student's *t*-test or Tukey-Kramer HSD (honestly significant difference) test (at the 0.05 level) were used to distinguish among the means of two or more groups, respectively. All linear regressions are stated with  $r^2_{\text{adjusted}}$ . When both *x* and *y* variables were associated with an error (such as for  $1/[\text{CO}_2]$  vs.  $\delta^{13}\text{C}$ ), slopes and intercepts were calculated by geometric mean regressions (Sokal and Rohlf 1981). Slopes and intercepts of two regressions were tested against each other by introducing indicator variables ("dummy" variables) into a multiple regression model (Neter et al. 1985).

## Results

### Temporal and spatial variations of canopy $[\text{CO}_2]$ profiles

$\text{CO}_2$  concentrations throughout the canopy were well-stratified (Table 1), and decreased steadily with increasing height in the canopy. Highest concentrations were measured immediately above the forest floor, where they peaked at values as high as  $707 \mu\text{mol mol}^{-1}$  during the dry season and at  $560 \mu\text{mol mol}^{-1}$  during the wet season. This stratification of canopy  $[\text{CO}_2]$  was similar for both dry and wet seasons, although the absolute values of  $[\text{CO}_2]$  for comparable heights tended to be different. During the wet season, nighttime  $[\text{CO}_2]$  (Table 1; 0730 hours) above, and within the upper and middle canopy were slightly lower than in the dry season, whereas daytime concentrations (1300 hours) were higher. For example, daytime  $[\text{CO}_2]$  at the top of the canopy was about  $10 \mu\text{mol mol}^{-1}$  higher in the wet season than in the dry season ( $t = 7.27$ ,  $P < 0.0001$ ), mainly reflecting the  $7 \mu\text{mol mol}^{-1}$  increase in the Barbados

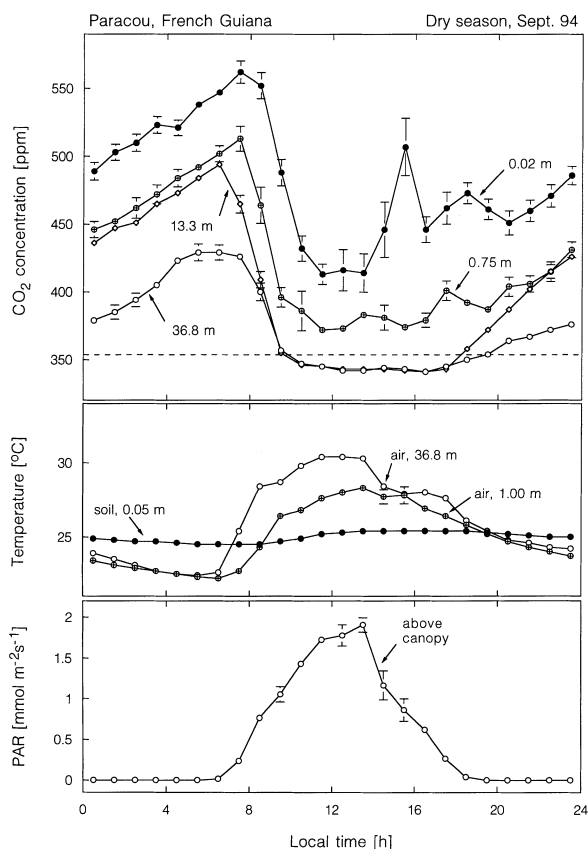
**Table 1**  $\text{CO}_2$  concentrations within the canopy profile of a primary rainforest in Paracou, French Guiana during the 1994 dry season and the 1995 wet season, for two times during the day (0730 hours  $\pm$  30 min in the morning; 1300 hours  $\pm$  30 min mid-day). Means and standard errors are presented ( $n = 24$  for 1994, 0730 hours;  $n = 15$  for 1994, 1300 hours;  $n = 18$  for 1995, 0730 hours;  $n = 15$  for 1995, 1300 hours). Different letters following the means represent significantly different  $\text{CO}_2$  concentrations within a daytime comparing across seasons ( $18 < F < 605$ ,  $P < 0.0001$ , height as main factor; Turkey-Kramer test, 0.05 level)

Season	Height (m)	$[\text{CO}_2]$ ( $\mu\text{mol mol}^{-1}$ )	
		0730	1300
Dry	36.8	$425.9 \pm 4.2^a$	$342.1 \pm 0.4^a$
	28.3	$433.7 \pm 3.4^a$	$342.6 \pm 0.3^a$
	13.3	$464.5 \pm 6.5^b$	$342.2 \pm 0.2^a$
	2.00	$498.7 \pm 5.9^d$	$349.8 \pm 1.1^{ab}$
	0.75	$503.8 \pm 6.0^d$	$366.3 \pm 1.3^{ab}$
	0.02	$562.4 \pm 8.2^e$	$443.5 \pm 24.1^c$
Wet	37.1	$412.1 \pm 3.1^a$	$351.8 \pm 1.2^{ab}$
	31.6	$420.4 \pm 3.1^a$	$350.7 \pm 1.3^{ab}$
	18.2	$467.9 \pm 10.3^{bc}$	$352.4 \pm 2.2^{ab}$
	2.00	$492.8 \pm 4.6^{cd}$	$367.7 \pm 4.7^{ab}$
	0.70	$496.5 \pm 4.8^d$	$377.8 \pm 2.4^b$
	0.10	$510.1 \pm 7.8^d$	$412.6 \pm 4.6^c$

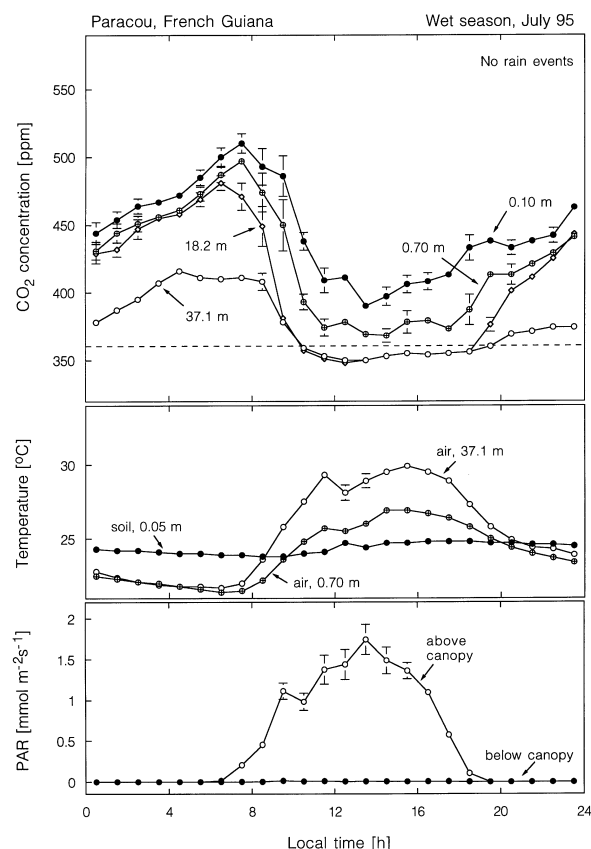
tropospheric baseline concentration. However,  $[\text{CO}_2]$  above the forest floor were always lower during the wet season than compared to the dry season.

Moreover, canopy  $[\text{CO}_2]$  showed a distinct daily pattern that was similar for both seasons (Figs. 1 and 2). Over night, as respiratory fluxes were high but turbulent mixing low,  $\text{CO}_2$  accumulated within the canopy, reaching peak  $[\text{CO}_2]$  around 0730 hours in the morning. This nocturnal buildup of  $[\text{CO}_2]$  was followed by a rapid draw-down in the morning (between 0800 and 1000 hours), when turbulent mixing and wind speed increased due to increasing solar radiation and air temperatures. Therefore, the strong stratification that was present at night throughout the canopy in both seasons, weakened during the day, especially in the wet season (Table 1). Later in the day (between 1030 hours and 1630 hours),  $[\text{CO}_2]$  within the upper and middle canopy stayed almost constant, on average  $10 \mu\text{mol mol}^{-1}$  below the Barbados baseline during the dry season (Fig. 1), and by approximately  $7 \mu\text{mol mol}^{-1}$  during the wet season (Figs. 1 and 2). In contrast to the canopy  $[\text{CO}_2] \geq 2.00$  m, daytime concentrations at 0.7 m always remained above baseline levels during both seasons. As soon as above-canopy light levels decreased below  $0.2 \text{ mmol m}^{-2} \text{ s}^{-1}$ ,  $[\text{CO}_2]$  in the upper and middle canopy followed those in the lower strata and started to increase again (1800 hours).

Canopy  $\text{CO}_2$  gradients within the canopy ( $\geq 2$  m) were always larger during the night than during the day (Table 2), whereas gradients below the canopy ( $\leq 0.7$  m) increased during the day for both seasons. Furthermore, total canopy  $\text{CO}_2$  gradients tended to be smaller during the wet season than during the dry season, although  $\text{CO}_2$  gradients of single canopy strata were very similar for



**Fig. 1** Mean daily course of canopy  $\text{CO}_2$  concentrations ( $[\text{CO}_2]$ ), air and soil temperatures, and photosynthetically active radiation (PAR) during the 1994 dry season. Hourly averages of 10-min records ( $\text{CO}_2$  and temperatures) or 30-min records (PAR) ( $\pm$  SE) from a 5-day period are presented. The dashed line represents the average daytime tropospheric  $[\text{CO}_2]$  at Barbados (provided by T. Conway, NOAA/CMDL)



**Fig. 2** Mean daily course of canopy  $\text{CO}_2$  concentrations, air and soil temperatures, and PAR of a dry period during the 1995 wet season. Hourly averages of 10-min records ( $\text{CO}_2$ , temperatures, PAR below canopy) or 15-min records (PAR above canopy) ( $\pm$  SE) from a 3-day period are presented. The dashed line represents the average daytime baseline  $[\text{CO}_2]$  at Barbados (provided by T. Conway, NOAA/CMDL)

**Table 2** Canopy  $[\text{CO}_2]$  gradients within a primary rainforest in Paracou, French Guiana during the 1994 dry season and the 1995 wet season at 0730 hours ( $\pm$  30 min in the morning) and at 1300 hours ( $\pm$  30 min midday). Gradients are calculated as the differences between the top and the bottom of each stratum. Means and standard errors are presented ( $n = 24$  for 1994, 0730 hours;  $n = 15$  for 1994, 1300 hours;  $n = 18$  for 1995, 0730 hours;  $n = 15$  for 1995, 1300 hours). Asterisks denote significantly different gradients between seasons (Student's  $t$ -test, 0.05 level)

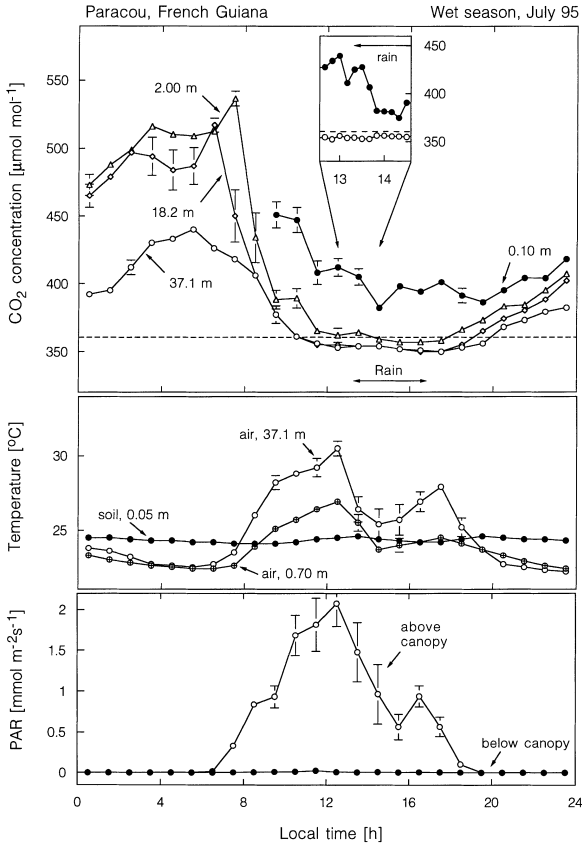
Time	Canopy strata (m)	$[\text{CO}_2]$ gradients ( $\mu\text{mol mol}^{-1}$ )	
		Dry season	Wet season
0730	Upper ( $\geq 30$ m)	$7.7 \pm 1.4$	$8.3 \pm 3.1^{\text{NS}}$
	Middle (15–30 m)	$30.8 \pm 7.2$	$47.4 \pm 9.8^{\text{NS}}$
	Lower (2–15 m)	$34.2 \pm 3.0$	$23.2 \pm 1.8^{\text{NS}}$
	Below ( $\leq 0.7$ m)	$58.6 \pm 5.5$	$13.5 \pm 6.4^{***}$
	Total	$136.5 \pm 10.7$	$97.9 \pm 9.6^*$
1300	Upper ( $\geq 30$ m)	$0.5 \pm 0.4$	$-1.1 \pm 0.4^*$
	Middle (15–30 m)	$-0.4 \pm 0.3$	$1.7 \pm 1.4^{\text{NS}}$
	Lower (2–15 m)	$7.6 \pm 1.9$	$15.3 \pm 4.7^{\text{NS}}$
	Below ( $\leq 0.7$ m)	$77.2 \pm 24.4$	$34.8 \pm 4.7^{\text{NS}}$
	Total	$101.4 \pm 24.4$	$60.8 \pm 4.1^{\text{NS}}$

<sup>NS</sup> non significant, \* $P < 0.05$ , \*\*\* $P < 0.0001$

both seasons (Table 2). The upper canopy ( $\geq 30$  m) contributed least to the overall canopy gradient, independent of time or season, whereas the stratum below the actual canopy ( $\leq 0.7$  m) contributed the most, indicating high soil respiration rates. While during the night, the middle canopy (15–30 m) might have impeded air-flow out of the canopy, thus contributing to a large nocturnal build-up of  $\text{CO}_2$ , it clearly showed a photosynthetic effect during the day, with low or negative gradients at 1300 hours.

#### Effect of precipitation on canopy $\text{CO}_2$ profiles and soil respiration

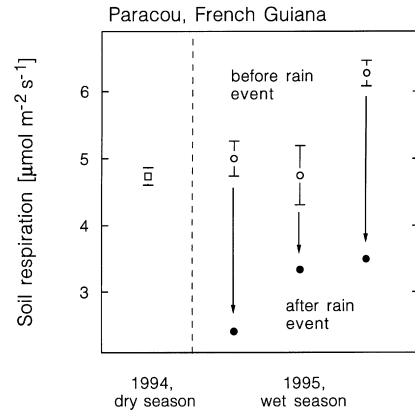
Among other abiotic factors such as temperature and light, precipitation also influenced canopy  $\text{CO}_2$  profiles, as seen during two rainy days of the 1995 wet season (Fig. 3). Within the 2 h after the 17.8 mm rain event had started, air temperature above the canopy decreased by  $9.7^\circ\text{C}$ , air temperature in 1 m height decreased by  $5.2^\circ\text{C}$ . Soil temperatures responded with a decrease of  $0.9^\circ\text{C}$



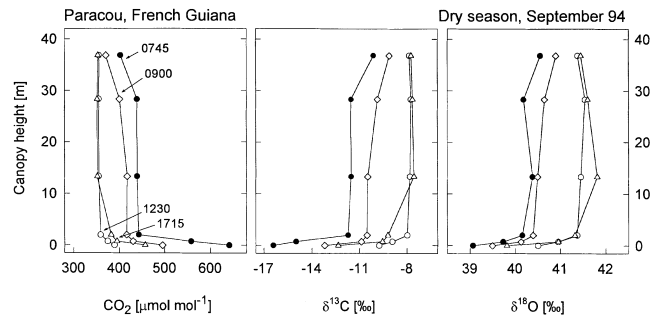
**Fig. 3** Mean daily course of canopy CO<sub>2</sub> concentrations, air and soil temperatures, and PAR during days with afternoon rains in the 1995 wet season. Hourly averages of 10-min records (CO<sub>2</sub>, temperatures, PAR below canopy) or 15-min records (PAR above canopy) ( $\pm$  SE) from two days are presented. The *dashed line* represents the tropospheric baseline [CO<sub>2</sub>] at Barbados (provided by T. Conway, NOAA/CMDL). The *insert* emphasizes one rain event; CO<sub>2</sub> concentrations at 0.10 m and 37.10 m are shown

after a lag-time of 3 h. In spite of this profound influence on canopy air temperatures, CO<sub>2</sub> concentrations of the upper and middle canopy were not affected. However, [CO<sub>2</sub>] above the forest floor (0.10 m) decreased by about 50  $\mu\text{mol mol}^{-1}$  within 1 h after the rain (Fig. 3, insert), indicating a rapid decrease in soil CO<sub>2</sub> efflux.

Soil respiration rates during the 1994 dry season ( $4.7 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were similar to rates measured during the 1995 wet season, before rain events occurred ( $5.3 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Fig. 4). However, rates decreased substantially after two strong precipitation events, reaching average values of  $3.1 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Although soil temperatures immediately after the rain were approximately 0.2°C lower than before the rain had started, this small change in soil temperature does not seem to be enough to explain a 40% decrease in CO<sub>2</sub> efflux. Soil respiration rates measured during days without rain in the wet season were not significantly different from those measured in the dry season, in spite of soil temperatures that were 0.9°C higher in the dry season.



**Fig. 4** Influence of precipitation on the soil respiration rates of a tropical rainforest. During the wet season, soil CO<sub>2</sub> efflux was measured at two different sites; one site was measured on two consecutive days just before and after rain events of 23 and 17.8 mm, the other site was measured only on one day before and after the 17.8 mm rain event. Means ( $\pm$  SE) are presented ( $n = 16$  for 1994,  $n = 2-3$  in 1995)

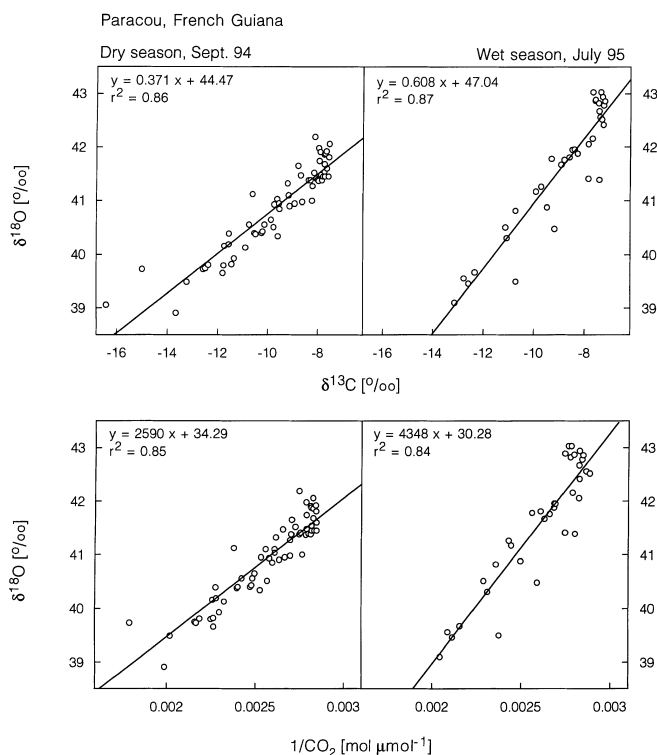


**Fig. 5** Canopy profiles of CO<sub>2</sub> concentrations,  $\delta^{13}\text{C}_{\text{canopy}}$ , and  $\delta^{18}\text{O}_{\text{canopy}}$  at four different times of the day during the 1994 dry season. Original flask data (collected over a 5-day period) are presented

### $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of canopy CO<sub>2</sub>

Fluctuations in canopy [CO<sub>2</sub>], spatial as well as temporal, were accompanied by changes in  $\delta^{13}\text{C}_{\text{canopy}}$  and  $\delta^{18}\text{O}_{\text{canopy}}$  ratios (Fig. 5). The strong vertical stratification seen for [CO<sub>2</sub>] was also evident for the isotope ratios of CO<sub>2</sub>, with most depleted  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  immediately above the forest floor and highest ratios at the top of the canopy. Both isotope ratios of canopy CO<sub>2</sub> followed the daily course of [CO<sub>2</sub>]. Early in the morning (0745 hours), when [CO<sub>2</sub>] was highest due to low turbulent mixing,  $\delta^{13}\text{C}_{\text{canopy}}$  and  $\delta^{18}\text{O}_{\text{canopy}}$  were most depleted.

Most negative  $\delta^{13}\text{C}_{\text{canopy}}$  ratios were measured immediately above the forest floor with  $-16.4\text{‰}$  at a corresponding [CO<sub>2</sub>] of  $641.8 \mu\text{mol mol}^{-1}$ . During the course of the day, carbon isotope ratios of canopy CO<sub>2</sub> increased with decreasing [CO<sub>2</sub>]. The  $\delta^{13}\text{C}_{\text{canopy}}$  in the upper and middle canopy was about  $-7.8\text{‰}$ , almost reaching the Barbados baseline of  $-7.7\text{‰}$ .  $\delta^{13}\text{C}_{\text{canopy}}$



**Fig. 6** Relationships between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in canopy air (*top panel*), and  $1/[\text{CO}_2]$  and  $\delta^{18}\text{O}$  in canopy air (*bottom panel*) during both dry and wet seasons. Original flask data are presented ( $n = 62$  for 1994,  $n = 36$  for 1995)

gradients within the canopy were large in the morning (0745 hours), with a 6.3‰ difference between the top of the canopy and the forest floor. During midday (1230 hours), small  $\delta^{13}\text{C}_{\text{canopy}}$  gradients of about 2.0‰ were measured before they increased again in the evening (4.3‰; 1900 hours). Variations of  $\delta^{13}\text{C}_{\text{canopy}}$  at any position in the canopy ranged between 1.1‰ (36.8 m) and 3.5‰ (0.02 m), with fluctuations of about 2.5‰ in the upper and middle canopy.

Similarly to the vertical stratification and daily pattern of carbon isotopes,  $\delta^{18}\text{O}_{\text{canopy}}$  ratios were most depleted early in the morning (39.1‰; 0745 hours) and most enriched during midday (42.2‰; 1430 hours). Differences in  $\delta^{18}\text{O}_{\text{canopy}}$  between the top of the canopy and the forest floor were lowest during midday (1.0‰), but highest in the late afternoon (2.0‰; 1730 hours). This close relationship of  $\delta^{13}\text{C}_{\text{canopy}}$  and  $\delta^{18}\text{O}_{\text{canopy}}$  was seen during both seasons (Fig. 6;  $r^2_{\text{adjusted}} > 0.8$ ), although  $\delta^{18}\text{O}_{\text{canopy}}$  values increased faster with increasing  $\delta^{13}\text{C}_{\text{canopy}}$  or decreasing  $[\text{CO}_2]$  (increasing  $1/[\text{CO}_2]$ ) in the wet season compared to those in the dry season (multiple regression analysis with indicator variables; intercept:  $P < 0.0001$ , slope:  $P < 0.0001$ ).

#### Leaf carbon isotope ratios

We sampled foliage from ten different tree species, including trees of the three angiosperm families that

comprise about two thirds of the French Guiana forest (i.e., Lecythidaceae, Caesalpiniaceae and Chrysobalanaceae). Foliage growing at different positions within the canopy showed the typical pattern of decreasing  $\delta^{13}\text{C}_{\text{leaf}}$  with decreasing height above the forest floor (Table 3). Foliage in the upper canopy ( $\delta^{13}\text{C}_{\text{leaf}}$  about  $-29‰$ ) was significantly less negative than foliage in the middle canopy or in the understory in both years ( $\delta^{13}\text{C}_{\text{leaf}}$  about  $-33‰$ ; position as main factor:  $P < 0.0001$ ; interaction term:  $P = 0.4957$ ;  $F = 19.00$  of the whole-model test). No differences were found between years (season as main factor:  $P = 0.0927$ ). Leaf isotope ratios of the middle canopy and the understory vegetation did not differ from each other, in spite of differences in light levels and source air effects.

Furthermore, we calculated how much of the variability in  $\delta^{13}\text{C}_{\text{leaf}}$  within the canopy profile can be explained by differences in the  $\delta^{13}\text{C}$  of canopy air (between 2 m and 30 m). While the height difference between  $\delta^{13}\text{C}_{\text{leaf}}$  values within the canopy was between 4 and 5‰ for both seasons, the gradient of weighted  $\delta^{13}\text{C}_{\text{canopy}}$  was only about 1‰. Consequently, source air effects accounted for about 20% of the difference in carbon isotope ratios of foliage within this tropical canopy, and the remaining 80% of the difference must have resulted from changes in  $c_i/c_a$  values.

#### Carbon isotope discrimination at the ecosystem level and at the leaf level

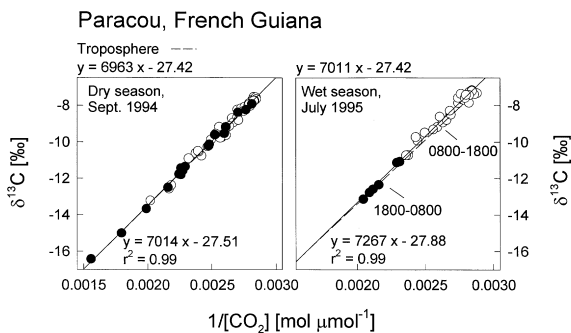
Plotting the inverse of canopy  $[\text{CO}_2]$  versus the corresponding  $\delta^{13}\text{C}_{\text{canopy}}$  ratios resulted in very tight, linear relationships for both seasons ( $r^2 = 0.99$ ;  $P < 0.0001$ ; Fig. 7). Testing slopes ( $7014 \pm 75.5$  and  $7267 \pm 145.7$  for dry and wet seasons, respectively) and intercepts ( $-27.51 \pm 0.2‰$  and  $-27.88 \pm 0.4‰$  for dry and wet seasons, respectively) of both regressions revealed no significant differences between the two seasons ( $P = 0.46$  for slope,  $P = 0.14$  for intercept). Furthermore, both intercepts were close to the  $\delta^{13}\text{C}$  of soil respired  $\text{CO}_2$  and to the  $\delta^{13}\text{C}$  of litter and soil organic matter (Table 4). Using the  $\delta^{13}\text{C}$  value of tropospheric  $\text{CO}_2$  and the intercept of the regressions as  $\delta^{13}\text{C}$  value of soil respired  $\text{CO}_2$ , we calculated  $\Delta_e$  as 20.3‰ during the dry season and as 20.5‰ during the wet season.

Leaf carbon isotope discrimination was calculated for foliage of the understory (2 m) and the middle and upper canopy (15 m and 30 m; Table 5). During both seasons, leaves in the understory showed similar  $\Delta_{\text{leaf}}$  against  $^{13}\text{C}$  compared to leaves in the middle canopy (about 26.4‰), while  $\Delta_{\text{leaf}}$  was lower in the upper canopy (22‰ during the dry season and 23‰ during the wet season). During both dry and wet seasons, internal  $\text{CO}_2$  concentrations ( $c_i$ ) steadily decreased with increasing height above the ground, while  $c_i/c_a$  was higher in the understory and middle canopy than in the upper canopy.

**Table 3** Leaf carbon isotope composition of tropical tree species in a primary rainforest, French Guiana. Foliage was collected during the 1994 dry season (September) and the 1995 wet season (July).

Different letters following the means represent significantly different  $\delta^{13}\text{C}$  ratios across all combinations (Tukey-Kramer test at the 0.05 level)

Canopy	Species	Family	Common name	$\delta^{13}\text{C}$ (‰) Dry season	$\delta^{13}\text{C}$ (‰) Wet season
Upper, > 30 m	<i>Eschweilera odora</i> Miers	Lecythidaceae	Mahot noir	-30.3	-31.7
	<i>Eperua grandiflora</i> Benth	Caesalpiniaceae	Wapa	-28.4	-31.9
	<i>Minuartia guianensis</i> Aublet.	Oleaceae	Maaka	-27.7	-27.6
	<i>Recordoxylon speciosum</i> Norm.	Caesalpiniaceae	Wacapou guitin	-26.6	-27.6
	<i>Vouacapoua americana</i> Aublet.	Caesalpiniaceae	Wacapou	-29.7	-30.3
	Mean			-28.6 <sup>a</sup>	-29.9 <sup>a</sup>
	Standard error ( $n = 5$ )		0.7	0.9	
Middle, 15 m	<i>Eschweilera amara</i> Ndz.	Lecythidaceae	Mahot rouge	-33.4	-34.0
	<i>Eschweilera odora</i> Miers	Lecythidaceae	Mahot noir	-32.8	-32.8
	<i>Licania alba</i> Cuatr.	Chrysobalanaceae	Gaulette	-33.5	-33.5
	<i>Ocotea glomerata</i> Benth. Hook	Lauraceae	Cèdre noir	-34.4	-33.3
	<i>Oxandra asbeckii</i> Pulle	Annonaceae	Mouamba	-31.9	-32.6
	Mean			-33.2 <sup>b</sup>	-33.3 <sup>b</sup>
	Standard error ( $n = 5$ )		0.4	0.3	
Understory, 2 m	<i>Eschweilera amara</i> Ndz.	Lecythidaceae	Mahot rouge	-33.1	-34.0
	<i>Eschweilera odora</i> Miers	Lecythidaceae	Mahot noir	-34.0	-34.4
	<i>Licania alba</i> Cuatr.	Chrysobalanaceae	Gaulette	-34.4	-34.2
	<i>Nectandra grandis</i> Kostern.	Lauraceae	Cèdre jaune	-33.6	-35.1
	<i>Oxandra asbeckii</i> Pulle	Annonaceae	Mouamba	-33.2	-33.2
	Mean			-33.6 <sup>b</sup>	-34.2 <sup>b</sup>
	Standard error ( $n = 5$ )		0.2	0.3	



**Fig. 7** Relationship of the inverse of canopy  $\text{CO}_2$  concentrations and their corresponding  $\delta^{13}\text{C}$  for the 1994 dry season and the 1995 wet season. Regression equations (solid lines) are given for day (open symbols) and night (closed symbols) flask data together ( $P < 0.0001$ ,  $n = 62$  for 1994,  $n = 36$  for 1995). See text for details on the gas mixing model of tropospheric and respired  $\text{CO}_2$  (dashed line). Baseline  $\delta^{13}\text{C}$  of the troposphere was provided by M. Trolier (University of Colorado, INSTAAR)

**Table 4** Comparison of the carbon isotope composition of soil respired  $\text{CO}_2$ , litter, soil organic matter (SOM) and the intercept of the relationship  $1/[\text{CO}_2]_{\text{canopy}}$  vs.  $\delta^{13}\text{C}_{\text{canopy}}$ . Means and standard errors are presented ( $n = 4$  for soil respired  $\text{CO}_2$ ,  $n = 3$  for litter,  $n = 6$  for SOM)

	Dry season	Wet season
Soil respired $\text{CO}_2$	$-26.5 \pm 0.1$	$-26.8 \pm 0.3$
Litter	$-30.5 \pm 0.5$	$-28.9 \pm 0.2$
SOM	$-28.3 \pm 0.3$	$-28.0 \pm 0.1$
Intercept	$-27.5 \pm 0.2$	$-27.9 \pm 0.4$

## Discussion

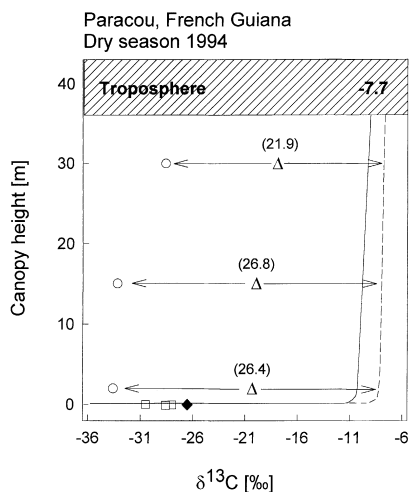
Fluctuations in canopy  $[\text{CO}_2]$  and isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) of canopy  $\text{CO}_2$  were larger on a daily than on a seasonal basis, although rain events during the wet season had profound effects on soil respiration and  $[\text{CO}_2]$  immediately above the forest floor. Close relationships were observed between  $1/[\text{CO}_2]$  and the corresponding  $\delta^{13}\text{C}$  as well as between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  of canopy  $\text{CO}_2$ . Estimates of  $\Delta_\epsilon$  averaged  $20.4\text{‰}$  for both seasons.

Concentrations as well as carbon and oxygen isotope ratios of  $\text{CO}_2$  in the tropical canopy were well stratified and followed the typical daily course known for a variety of different forest ecosystems (Fig. 8). However, in contrast to canopy  $[\text{CO}_2]$  in temperate deciduous forests, which frequently decreased  $20 \mu\text{mol mol}^{-1}$  below tropospheric values (Buchmann et al. 1996), midday depletions of  $[\text{CO}_2]$  within tropical canopies were smaller (between 7 and  $11 \mu\text{mol mol}^{-1}$ ) and rarely observed (Quay et al. 1989,  $11 \mu\text{mol mol}^{-1}$ ; Fan et al. 1990,  $7\text{--}8 \mu\text{mol mol}^{-1}$ ). Grace et al. (1996) reported canopy  $[\text{CO}_2]$  during the afternoon close to the free troposphere that remained at this baseline until around 1800 hours. Changes in wind speed and turbulent mixing were responsible for either  $[\text{CO}_2]$  buildups or a well-ventilated canopy airspace. Furthermore, daytime  $[\text{CO}_2]$  gradients in the French Guiana rainforest frequently reached values  $> 200 \mu\text{mol mol}^{-1}$ , and thus were considerably higher than daytime gradients in temperate forests



**Table 5** Estimates of leaf carbon discrimination ( $\text{‰}$ ),  $c_i$  ( $\mu\text{mol mol}^{-1}$ ) and  $c_i/c_a$  ( $\mu\text{mol mol}^{-1}$ ) for a tropical rainforest during the dry and wet seasons.  $[\text{CO}_2]_{\text{canopy}}$  ( $\mu\text{mol mol}^{-1}$ ) and  $\delta^{13}\text{C}_{\text{canopy}}$  ( $\text{‰}$ ) are weighted by above-canopy photosynthetically active radiation PAR.  $\delta^{13}\text{C}_{\text{leaf}}$  is averaged for each canopy position

	Dry season			Wet season		
	2.00 m	13.3 m	28.3 m	2.00 m	18.2 m	31.6 m
$[\text{CO}_2]_{\text{canopy}}$	366.4	351.4	350.3	375.7	362.6	359.6
$\delta^{13}\text{C}_{\text{canopy}}$	-8.37	-7.55	-7.49	-8.54	-7.84	-7.67
$\delta^{13}\text{C}_{\text{leaf}}$	-33.6	-33.2	-28.6	-34.2	-33.3	-29.9
$\Delta_{\text{leaf}}$	26.14	26.53	121.68	26.57	26.34	22.92
$c_i$	324	316	249	339	323	271
$c_i/c_a$	0.88	0.90	0.70	0.90	0.89	0.75



**Fig. 8** Conceptual model of the isotopic composition of different carbon pools in a tropical rainforest during the dry season.  $\delta^{13}\text{C}_{\text{canopy}}$  is presented for the original flask data (solid line nighttime, dashed line daytime);  $n = 5$  for foliage samples per canopy position (open circle),  $n = 3-5$  for litter and soils (open square),  $n = 4$  for soil-respired  $\text{CO}_2$  (closed diamond).  $\Delta_{\text{leaf}}$  was calculated according to Eq. 3. Baseline  $\delta^{13}\text{C}$  is given for the Barbados station of the NOAA network (provided by M. Troler, University of Colorado, INSTAAR)

(always  $< 100 \mu\text{mol mol}^{-1}$ ; Buchmann et al. 1996), whereas nighttime  $[\text{CO}_2]$  gradients were similar to canopy gradients observed in other forest types. An equivalent pattern of larger daytime gradients in tropical than temperate forests was also observed for gradients of  $\delta^{13}\text{C}_{\text{canopy}}$  between the forest floor and the top of the canopy. Dependent on the time of the day,  $\delta^{13}\text{C}_{\text{canopy}}$  gradients in the French Guiana forest ranged between  $2\text{‰}$  and  $6.3\text{‰}$ , similar to gradients observed in tropical seasonal forests in Trinidad (Broadmeadow et al. 1992,  $2\text{‰}$ ), and evergreen Amazonian forests (van der Merwe and Medina 1989,  $5-6\text{‰}$ ; Quay et al. 1989,  $5\text{‰}$ ; Lloyd et al. 1996,  $2-6\text{‰}$ ; Kruijt et al. 1996,  $2-7\text{‰}$ ). Daily fluctuations in  $\delta^{18}\text{O}_{\text{canopy}}$  were relatively small in this tropical canopy (about  $1\text{‰}$  for a given canopy height) compared to those in a temperate forest (*Pinus resinosa*; approximately  $2-4\text{‰}$ ; Flanagan and Varney 1995), and consistent with small variations in the water vapor deficit in this tropical canopy. Soil respiration, a dominant factor shaping canopy  $[\text{CO}_2]$  profiles (Buchmann et al. 1996), was measured at rates of  $3-5 \mu\text{mol m}^{-2} \text{s}^{-1}$ , well

within the range reported for other tropical soils (Schlesinger 1977), and comparable to rates measured in temperate forest soils (Buchmann et al. 1996).

Although  $[\text{CO}_2]$  profiles in temperate forests exhibited strong seasonal variations (Bazzaz and Williams 1991; Buchmann et al. 1996),  $[\text{CO}_2]$  values in the main part of the tropical canopy were similar for both dry and wet seasons. Furthermore, the draw-down in the upper and middle canopy was very similar for both seasons, about  $10 \mu\text{mol mol}^{-1}$  during the dry season and  $7 \mu\text{mol mol}^{-1}$  during the wet season. This lack of seasonality in main canopy carbon fluxes, indicated by  $[\text{CO}_2]$  profile measurements, is supported by both gas exchange measurements and carbon isotope analyses of foliage and canopy  $\text{CO}_2$ . Photosynthetic rates of late stage tropical tree species measured at a nearby plantation (Huc et al. 1994) either slightly decreased or remained stable during the transition from wet to dry season. Moreover, we found no differences in  $\delta^{13}\text{C}_{\text{leaf}}$  in any canopy stratum between the two seasons. For both wet and dry seasons, about 20% of the vertical  $\delta^{13}\text{C}_{\text{leaf}}$  gradient was due to source air effects ( $\delta^{13}\text{C}_{\text{canopy}}$ ), while the remaining 80% must have been due to changes in  $c_i/c_a$ . Thus, changes in Barbados tropospheric baseline  $\delta^{13}\text{C}$  values by approximately  $0.3\text{‰}$ , which were reflected by the  $\delta^{13}\text{C}_{\text{canopy}}$  at the top of the canopy, did not have a major effect. Using  $\delta^{13}\text{C}_{\text{leaf}}$  and our  $\delta^{13}\text{C}_{\text{canopy}}$  values (weighted by PAR) to calculate long-term  $c_i/c_a$  for these leaves revealed almost constant ratios for both seasons in spite of changing precipitation and therefore vapor pressure deficit between seasons, indicating that plants maintained a constant balance between stomatal conductance ( $g$ ) and photosynthesis through both wet and dry seasons. Integrating over the entire canopy by using the relationship of  $1/[\text{CO}_2]$  and  $\delta^{13}\text{C}_{\text{canopy}}$  strengthened these observations even more; neither slopes nor intercepts of the two regressions differed from each other, indicating high similarity in turbulent mixing with the troposphere relative to photosynthetic effects on canopy  $[\text{CO}_2]$  in both seasons. Another indicator that the balance between  $g$  and photosynthesis was maintained over both seasons is the tightness of the relationship between  $\delta^{13}\text{C}_{\text{canopy}}$  and  $\delta^{18}\text{O}_{\text{canopy}}$  (for both seasons:  $r^2 > 0.8$ ). Both isotope ratios are strongly influenced by this physiological balance, diffusion of  $\text{CO}_2$  into and out of a leaf may be influenced by humidity (which will also influence isotopic composition) or by other factors such as water potentials

(Schulze 1986) and leaf temperature (Ball et al. 1988). Sternberg et al. (1989b) for example found a strong relationship for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in leaf cellulose only for plants growing on irrigated plots, but not for control plants which did not receive additional water.

Seasonal variability was evident in soil respiration. These rates were on average lower in the wet than in the dry season, as heavy rains decreased soil  $\text{CO}_2$  efflux by about 40% when compared to non-rain periods and thus decreased  $[\text{CO}_2]$  immediately above the forest floor. As a result, total canopy  $[\text{CO}_2]$  gradients during the wet season were about  $40 \mu\text{mol mol}^{-1}$  lower than those during the dry season. Since high decay factors have been reported for tropical forests (turnover rates = 1.2–3.2  $\text{year}^{-1}$ ; Whitmore 1990; Wieder and Wright 1995), and maximum litterfall in French Guiana forests generally occurs during July and August (Loubry 1994), lower soil respiration rates during the wet season were unexpected and counterintuitive. However, Wofsy et al. (1988) attributed lower soil  $\text{CO}_2$  efflux from an Amazonian forest soil during the wet season to a lower solar flux, which could reduce carbon allocation of plants to roots. Although we found a small seasonal difference of  $0.9^\circ\text{C}$  in French Guiana soil temperatures, these cannot be solely responsible for the large decrease in soil respiration. Instead, in spite of the sandy substrate, we observed standing water during and just after the two heavy rain events that accounted for 17.8 and 23 mm within 3- and 1-h periods, respectively, suggesting that the upper soil profile might have been water-saturated and therefore diffusion of  $\text{CO}_2$  out of the soil and/or microbial respiration oxygen-limited.

Within the canopy,  $\delta^{13}\text{C}_{\text{leaf}}$  were influenced more by physiological regulation on a leaf-level than by source air (Fig. 8). Although  $\delta^{13}\text{C}_{\text{leaf}}$  decreased with decreasing height throughout the canopy, as described earlier (Medina and Minchin 1980; Ehleringer et al. 1986, 1987; Medina et al. 1991; Huc et al. 1994), about 80% of this decrease was due to physiological responses to either decreasing PAR or increasing  $[\text{CO}_2]$  with decreasing height in the canopy. Similar patterns were found in another tropical forest (Kruijt et al. 1996), and also for boreal (Brooks et al. 1996) and temperate forests (Buchmann et al. 1997a).  $\Delta$  and long-term  $c_i$  increased from the upper to the middle canopy (Fig. 8; from 30 m to 15 m). This indicated that the decrease of photosynthetic rates with decreasing light was faster than any decrease in  $g$  with increasing  $[\text{CO}_2]$  and decreasing light. A similar pattern was observed by Ehleringer et al. (1986) in a subtropical monsoon forest where  $c_i/c_a$  increased with decreasing light. Relative humidity appeared to remain nearly constant, as indicated by very stable  $\delta^{18}\text{O}_{\text{canopy}}$  above 2 m. Similar to variations in  $\delta^{18}\text{O}$  of leaf water that is strongly influenced by changes in relative humidity (Flanagan 1993), one could expect a similar effect on  $\delta^{18}\text{O}_{\text{canopy}}$ . Lower in the canopy (< 15 m), both  $\Delta$  and long-term  $c_i$  remained stable, suggesting a proportional change in stomatal conductance and photosynthetic rates.

As seen from  $[\text{CO}_2]$  profile measurements as well as isotope analyses of canopy air and foliage, internal carbon fluxes seem to be quite stable for both seasons in this tropical canopy. This stability was also reflected in the  $\delta^{13}\text{C}$  of soil respired  $\text{CO}_2$ , either estimated by the intercept of the regression  $1/[\text{CO}_2]$  against  $\delta^{13}\text{C}_{\text{canopy}}$  or actually measured, indicating that the same carbon sources were respired during the wet and dry seasons. However, these results from natural conditions stand in contrast to results from irrigation experiments in Panama (Sternberg et al. 1989).  $\delta^{13}\text{C}_{\text{resp}}$  (estimated from intercept) of irrigated plots was more positive than that of control plots, suggesting less diffusion of lighter soil  $\text{CO}_2$ , thus enriching the carbon isotope signal of soil  $\text{CO}_2$  efflux from the wet soil. Although we measured  $\delta^{13}\text{C}_{\text{resp}}$  at the end of the wet season (July), and found profound effects of heavy rains on soil respiration rates, the integrated mean value still indicates an overall lack of seasonality of  $\delta^{13}\text{C}_{\text{resp}}$ . Furthermore, the estimates of  $\delta^{13}\text{C}_{\text{resp}}$  (from the intercepts:  $-27.5$  to  $-27.9\text{‰}$ ) were very close to the actual measurements of  $\delta^{13}\text{C}$  of soil  $\text{CO}_2$  efflux ( $-26.5$  to  $-26.8\text{‰}$ ), indicating that the two-ended mixing model (Keeling 1958) describes the two mixing pools during day and night quite well. Similar  $\delta^{13}\text{C}$  of soil  $\text{CO}_2$  efflux were measured in an Amazonian forest ( $-24.8$  to  $-27.4\text{‰}$ ; Quay et al. 1989). Although we did not find seasonal variations of the respired carbon sources, the  $\delta^{18}\text{O}_{\text{canopy}}$  suggested seasonal changes in water sources. The regressions of  $1/[\text{CO}_2]$  versus  $\delta^{18}\text{O}_{\text{canopy}}$  showed very different slopes and intercepts for both dry and wet seasons. Analogously to  $1/[\text{CO}_2]$  against  $\delta^{13}\text{C}_{\text{canopy}}$ , the intercept describes one of the two mixing pools. In contrast to  $\delta^{13}\text{C}_{\text{resp}}$ , the  $\delta^{18}\text{O}$  intercept for the dry season was more positive ( $34\text{‰}$ ) than that of the wet season ( $30\text{‰}$ ), indicating either a shift in the isotopic signal of the water source (precipitation) and/or a temperature dependent enrichment due to the higher temperatures in the dry season (Friedli et al. 1987).

Lloyd and Farquhar (1994) modeled canopy carbon isotope discrimination  $\Delta_A$  globally, based on datasets for climate, vegetation distribution, and gas exchange of the dominant plant species. However, only very limited datasets are available yet to evaluate the modeled values, despite the need of an integrative measure for ecosystems that can be used in modeling carbon dioxide exchange between oceans, biosphere and atmosphere (Ciais et al. 1995). Ideally, one would use photosynthetically weighted  $\delta^{13}\text{C}$  of canopy air for all canopy layers, weighted over the day and the life span of the foliage as well as weighted  $\delta^{13}\text{C}_{\text{leaf}}$  values to validate  $\Delta_A$  with field data. Because this is not feasible, we used another approach to integrate over the stand. By using the isotope ratios of tropospheric and respired  $\text{CO}_2$  to estimate  $\Delta_e$ , we integrate not only over  $\Delta_{\text{leaf}}$  of all leaves photosynthesizing, but we include information about the  $\delta^{13}\text{C}$  of soil organic matter as well (Buchmann et al. 1997b). The consideration of the large soil carbon stocks and their turnover dynamics (Bird et al. 1996; Trumbore et al. 1996) are appropriate for an integrative measure of

carbon isotope discrimination of ecosystems, especially in regard of the potential role soils might play for future climate (Houghton et al. 1996).

While  $\Delta_A$  for tropical rainforests was initially modeled as 18.4‰ (Lloyd and Farquhar 1994), our  $\Delta_e$  estimates averaged  $20.4 \pm 0.1$ ‰ for both seasons, again indicating strong regulation of ecosystem carbon and water fluxes, thus keeping  $\Delta_e$  and therefore ecosystem water use efficiency constant. Recalculating  $\Delta_e$  for other tropical datasets resulted generally in similar  $\Delta_e$  estimates (20.3‰, Quay et al. 1989; 21.1‰, Sternberg et al. 1989; 19.5‰, Lloyd et al. 1996). This 2‰ difference between  $\Delta_A$  and  $\Delta_e$  estimates for tropical forests might have several reasons, including analytical and statistical uncertainties as well as ecophysiological differences between the modeled vegetation and the actual study sites. Whereas the modeled  $\Delta_A$  values can vary by 2–3‰ (J. Lloyd, personal communication), the  $\Delta_e$  estimates are influenced by natural variability of tropospheric  $\text{CO}_2$  as well as by errors introduced by the estimates of  $\delta^{13}\text{C}_{\text{resp}}$ . Latitudinal as well as vertical variations of the tropospheric baseline are generally  $< 5 \mu\text{mol mol}^{-1}$  during the photosynthetically active period or  $< 0.25$ ‰ (Ciais et al. 1995; Tans et al. 1996); the error around the  $\delta^{13}\text{C}_{\text{resp}}$  estimate in this study was 0.2 and 0.4‰, but can average about 1‰ (Buchmann et al. 1997b). Thus, any uncertainty introduced by the use of tropospheric baseline values to estimate  $\Delta_e$  is overcome by the precision of estimation of  $\delta^{13}\text{C}$  of respired  $\text{CO}_2$ . Other factors influencing both estimates might be differences in stand ecophysiology or associated with the soil compartment. Short-term changes in air temperature and water vapor deficit will influence gas exchange parameters such as  $g$  or  $c_i$  and therefore alter carbon isotope discrimination of the ecosystem. Isotopic shifts in the  $\delta^{13}\text{C}$  values of litter and soil organic carbon that temporally and spatially integrate previous years' foliage and decomposition processes affect  $\Delta_e$  estimates and might increase natural variability. Further studies are needed to separate these effects.

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