Chapter 3

Insights into the carbon dynamics of tropical primary rainforests using stable carbon isotope analyses

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Abstract – Analyzing the carbon isotopic composition of ecosystem carbon pools and fluxes provides valuable information about the origin of carbon compounds, the partitioning of composite fluxes into individual flux components, as well as their major environmental and biotic controls. We synthesize the stable isotope data available for undisturbed lowland tropical rainforests, assess reasons for their variability, and address the representativeness of the French Guiana site Paracou. At Paracou, $\delta^{13}C_{leaf}$ values decreased from about $-29‰$ at the top of the canopy to about $-34‰$ in the understory. These intra-canopy changes of $\delta^{13}C_{leaf}$ values were mainly due to changes in leaf function and, to a minor extent, to changes in $\delta^{13}C_{air}$. Leaf carbon isotope discrimination (Δ_{leaf}) was lowest for leaves growing at the top of the canopy (approximately $22‰$) and highest for shade leaves in the understory (approximately $26‰$), reflecting increasing foliar C_i/C_a ratios from about 0.7 at the top of the canopy to 0.90 in the understory. Very similar patterns were found for other tropical lowland forests. A progressive enrichment in ^{13}C was found along the leaf–litter–soil continuum at Paracou, as observed in many tropical forest soils. Surprisingly, constant $\delta^{13}C$ values for soil organic matter were found for all tropical lowland forests, ranging from $-28.3‰$ to $-28.0‰$. Canopy air CO_2 concentrations [CO_2] throughout the Paracou canopy showed a pronounced daily pattern: [CO_2] profiles were well stratified, showing decreasing [CO_2] with increasing height above the ground. Clear seasonal patterns (wet and dry seasons) were observed only for [CO_2] close to the ground, indicating lower soil respiration fluxes in the wet season. In general, soil respiration rates measured at Paracou averaged 4 μmol CO_2 m^{-2} s^{-1} and fit well within the range reported for other lowland tropical forests, most of them studied in the neotropics. Temporal and spatial variations in [CO_2] in the Paracou canopy as well as in tropical forests of other regions were reflected in changes of $\delta^{13}C_{air}$. Isotopic mixing equations provided estimates of (1) the isotopic composition of CO_2 originating from ecosystem respiration, $\delta^{13}C_{ER}$, and (2) the integrated ecosystem carbon isotope discrimination, Δ_e. No intra-annual variability was detectable for the two parameters: $\delta^{13}C_{ER}$ was $-27.5‰$ in the dry season and

−27.9‰ in the wet season; (Δ_e) was estimated as 20.3‰ and 20.5‰, respectively. Both integrating isotopic measures, $\delta^{13}C_{ER}$ and Δ_e, for the Paracou site were in the median range reported for other primary rainforests. Thus, for all ecosystem compartments and at all levels examined, carbon isotopic signatures demonstrated the representativeness of the French Guiana site Paracou for lowland pristine forests globally.

Keywords: CO_2, $\delta^{13}C$, Carbon isotope discrimination, Canopy profiles, Soil respiration, Tropical ecosystems

1. Introduction

Detailed information about carbon pools and fluxes, and their controlling factors, is needed to elucidate the role of tropical forests for the global carbon budget. Tropical forests cover 17% of the earth's continents (Olson et al., 1983). More than half of the carbon in the terrestrial biomass (above and below ground) and about one third of the world's soil carbon are found here (Solomon et al., 1993). However, ecosystem studies in the tropics, which use a combination of classical and modern techniques (from biomass estimates and nutrient analyses to measurements of net ecosystem exchange and stable isotope analyses), are still limited. This lack of information considerably increases the uncertainty for global carbon models.

Internal carbon fluxes within tropical forest canopies and their interactions with soil and atmospheric exchange processes can be addressed by various means. Canopy air CO_2 concentrations ($[CO_2]$) can be used as an indicator of differences in gas exchange activities among different forest components and of interactions between the soil and the atmosphere. In response to turbulent mixing as well as to photosynthesis and respiration by vegetation and soil, $[CO_2]$ vary daily, from very high nocturnal $[CO_2]$ to low concentrations during the day (Wofsy et al., 1988). Stable isotopes (e.g. ^{13}C, ^{18}O) can be used to separate the different flux components of the biospheric–atmospheric net CO_2 exchange, because atmospheric–biospheric CO_2 sources have typically different isotopic signatures. Turbulent mixing between these two sources within the canopy and discrimination against $^{13}CO_2$ during photosynthesis results in $\delta^{13}C$ ratios of canopy air that are more depleted near the soil surface than at the top of the canopy (Buchmann et al., 1997; Lloyd et al., 1996). This effect is even more pronounced, the denser the canopy or the more active the soils or vegetation

(Buchmann et al., 1996). At the leaf level, carbon isotope ratios, $^{13}C_{leaf}$, and leaf carbon isotope discrimination (Δ_{leaf}) provide useful information about long-term gas exchange, particularly in combination with classical, short-term measurements of plant water potentials or leaf assimilation rates (Bonal et al., 2000a). Analyzing the change of carbon isotopic composition along the leaf–litter–soil continuum and its spatial variability provides useful information about the carbon cycling within ecosystems (Buchmann et al., 1997, 1998a; Guehl et al., 1998). Thus, the knowledge of the isotopic signature of carbon pools and fluxes provides additional information that could not be obtained otherwise.

Tropical forests are very diverse, not only in terms of species composition and their ecophysiology or biogeochemistry, but also in their services to human society. Thus, current tropical ecology needs to answer the questions of how representative any given field site is for a certain forest type, e.g. for lowland primary tropical forests, by which factors ecological processes are controlled under current conditions, and how these processes might behave under changing climate and land use regimes. In this chapter, we will synthesize our results on isotopic signatures of carbon pools and fluxes at Paracou, a lowland primary forest site in French Guiana. We will compile a database on carbon isotope signatures for undisturbed lowland tropical forests, assess their spatial and temporal variability, and address potential reasons for those patterns. Finally, we will ask whether or not our results from Paracou are representative for primary lowland forests in the humid tropics.

2. Experimental site and methodology

In the following, we compare several datasets collected at Paracou to datasets from other lowland primary

tropical forests. However, we consider only data for undisturbed forests in the humid tropics; data for dry tropical forests or for forests subjected to anthropogenic land use change were omitted.

The most detailed data sets described here were collected at the Paracou site, close to the CIRAD-Forêt experimental plots (see Part I of this book for a description of the site and its environment). This lowland tropical forest with a leaf area index of about eight (Granier, pers. comm.) consists of three canopy layers, with the top canopy reaching 30–35 m height, the middle layer ranging from about 15 to 20 m and an understory layer of less than 2 m height.

$[CO_2]$ were measured continuously during 5 days in the dry season in 1994 and the wet season in 1995. Air was sampled from six different heights in the canopy (between 0.02 and 37 m) and $[CO_2]$ were analyzed using an infra-red gas analyzer (LI-6200, LiCor, Lincoln, Nebraska, USA). Flasks, filled with canopy air, were sampled during day- and nighttime for isotopic analyses ($n = 62$ in 1994 and 36 in 1995; Buchmann et al., 1997). The CO_2 was extracted cryogenically using a three-trap vacuum line in the laboratory within 12 h after collection. Soil respiration rates were measured regularly using a soil respiration chamber connected to a portable photosynthesis system (LI-6200). PVC tubes were installed at the site 24 h prior to measurements. This set-up was changed to collect soil- respired CO_2 for isotopic analyses by introducing a flask (filled with nitrogen) and a water trap into the closed circuit between the chamber and the analyzer ($n = 4$ in each year). Gravimetric soil water contents and soil temperatures were measured each time the flux rate was determined. Foliage samples were collected from all three canopy layers using a shot-gun in 1994 and 1995 ($n = 5$ per species and canopy layer). During the 1998 short dry season (February/March), sunlit, mature foliage ($n = 10$–15 per tree) was sampled for analyses of carbon isotope ratios and nitrogen concentrations from 187 individual trees representing 64 species (Bonal et al., 2000b). All samples were dried for 48 h at 70 °C and then ground to a fine powder. A 1-mg subsample was used for isotopic analyses (Delta S, Finnigan MAT, Bremen, Germany). For more details on the methods, see Buchmann et al. (1997).

The carbon isotope ratio ($\delta^{13}C$) was calculated as:

$$\delta^{13}C = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000‰ \qquad (1)$$

where R_{sample} and $R_{standard}$ are the molar $^{13}C/^{12}C$ ratios of the sample and the standard (PDB), respectively (Farquhar et al., 1989). The overall precision for the carbon isotope measurements was 0.03‰ for gas samples and 0.11‰ for foliage samples. Leaf carbon discrimination was calculated as:

$$\Delta_{leaf} = \frac{\delta^{13}C_{air} - \delta^{13}C_{leaf}}{1 + \delta^{13}C_{leaf}} \qquad (2)$$

where $\delta^{13}C_{air}$ and $\delta^{13}C_{leaf}$ represent the carbon isotope ratios of canopy CO_2 and foliage, respectively. For more details, see Buchmann et al. (1997). The ratio of internal mesophyll $[CO_2]$ to ambient concentrations (C_i/C_a) was calculated as:

$$\Delta_{leaf} = a + (b - a) \times \frac{C_i}{C_a} \qquad (3)$$

where a and b are fractionation factors associated with fractionation against ^{13}C during diffusion ($a = 4.4‰$) and photosynthetic carboxylation ($b = 29‰$; O'Leary et al., 1992).

3. Leaf and soil isotopic signatures

3.1. Inter-specific variability of $\delta^{13}C_{leaf}$

Foliar $\delta^{13}C$ ratios ($\delta^{13}C_{leaf}$) and Δ_{leaf} varied considerably among different tree species within the Paracou site (Table 1). At the top canopy, inter-specific variability was higher (approximately 4‰ at 28–32 m height) than in the mid-canopy (approximately 1.5–2.5‰ at 13–18 m height) or in the understory (approximately 1.5–2‰ at 2 m height). No significant differences in $\delta^{13}C_{leaf}$ or Δ_{leaf} were found between the dry and the wet seasons. A larger survey in the same area with 102 species (406 individuals) supported these results (Bonal et al., 2000b). Mean species $\delta^{13}C$ values for sunlit, mature leaves varied by over 6‰, reflecting differences in leaf phenology (deciduous vs. evergreen) and shade tolerance (see Chapter 2, Part II, in this volume). Leaf stomatal regulation was considered to be dominating this inter-specific variation while nitrogen concentrations, varying widely, had no effect on $\delta^{13}C_{leaf}$ (Fig. 1). Sun foliage $\delta^{13}C_{leaf}$ values averaged $-31.2 \pm 1.0‰$ for evergreen species and $-30.4 \pm 1.6‰$ for deciduous tree species ($\pm$S.D.; Bonal et al., 2000b). Generally, standard deviations of sunlit $\delta^{13}C_{leaf}$ are reported as 1–2‰ for tropical forests (Broadmeadow et al., 1992; Ducatti et al., 1991; Kapos et al., 1993;

Table 1

Inter-specific variability of leaf carbon isotopic signatures ($\delta^{13}C_{leaf}$ and Δ_{leaf} in ‰) and C_i/C_a estimates (µmol mol^{-1}) within a tropical lowland forest in French Guiana (modified after Buchmann et al., 1997)

	$\delta^{13}C_{air}$	$\delta^{13}C_{leaf}$	Δ_{leaf}	C_i/C_a
Dry season (September 1994)				
Top canopy, 28 m	−7.49			
Eschweilera odora		−30.3	23.52	0.78
Eperua grandiflora		−28.4	21.52	0.70
Minquartia guianensis		−27.7	20.79	0.67
Recordoxylon speciosum		−26.6	19.63	0.62
Vouacapoua americana		−29.7	22.89	0.75
Mid-canopy, 13 m	−7.55			
Eschweilera amara		−33.4	26.74	0.91
Eschweilera odora		−32.8	26.11	0.88
Licania alba		−33.5	26.85	0.91
Ocotea glomerata		−34.4	27.81	0.95
Oxandra asbeckii		−31.9	25.15	0.84
Understory trees, 2 m	−8.37			
Eschweilera amara		−33.1	25.58	0.86
Eschweilera odora		−34.0	26.53	0.90
Licania alba		−34.4	26.96	0.92
Nectandra grandis		−33.6	26.11	0.88
Oxandra asbeckii		−33.2	25.68	0.87
Wet season (July 1995)				
Top canopy, 32 m	−7.67			
Eschweilera odora		−31.7	24.82	0.83
Eperua grandiflora		−31.9	25.03	0.84
Minquartia guianensis		−27.6	20.50	0.65
Recordoxylon speciosum		−27.6	20.50	0.65
Vouacapoua americana		−30.3	23.34	0.77
Mid-canopy, 18 m	−7.84			
Eschweilera amara		−34.0	27.08	0.92
Eschweilera odora		−32.8	25.81	0.87
Licania alba		−33.5	26.55	0.90
Ocotea glomerata		−33.3	26.34	0.89
Oxandra asbeckii		−32.6	25.59	0.86
Understory trees, 2 m	−8.54			
Eschweilera amara		−34.0	26.36	0.89
Eschweilera odora		−34.4	26.78	0.91
Licania alba		−34.2	26.57	0.90
Nectandra grandis		−35.1	27.53	0.94
Oxandra asbeckii		−33.2	25.51	0.86

All values, including the carbon isotope ratios of canopy air ($\delta^{13}C_{air}$ in ‰), are given for the dry and the wet season.
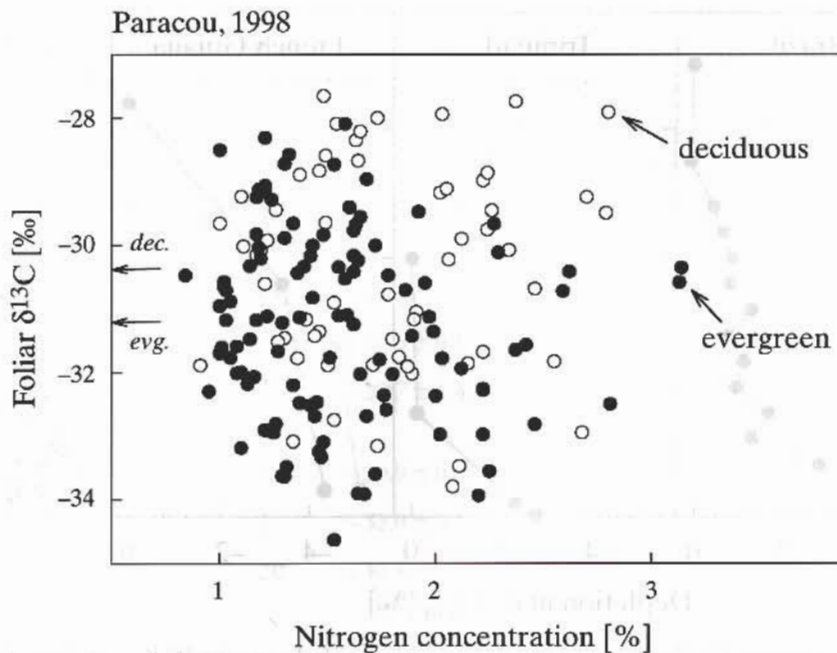
Paracou, 1998

Fig. 1. Relationship between foliar $\delta^{13}C$ values and nitrogen concentrations for deciduous and evergreen tree species ($n = 171$). Each data point represents a bulk sample of 10 to 15 sunlit, mature leaves per tree individual. Arrows indicate mean values for deciduous and evergreen foliage (data from Bonal et al., 2000b).

Martinelli et al., 1998; Medina and Minchin 1980; van der Merwe and Medina 1989). Thus, the French Guiana site falls well within this range of variability for other tropical lowland forests in Brazil, Venezuela or Trinidad. The similarity among these tropical South American forests was further supported by the fact that different geographical distributions could not explain any variation in the $\delta^{13}C_{leaf}$ values of tree species growing at Paracou (Bonal et al., 2000b).

3.2. Spatial variations in $^{13}C_{leaf}$

Foliar $\delta^{13}C$ values were always higher for leaves growing in the sunny, top canopy than for leaves growing in the shade, closer to the ground (Table 1). While $\delta^{13}C_{leaf}$ values averaged -28.6 ± 0.7‰ (dry season) and -29.9 ± 0.9‰ (wet season) in the top canopy, mean foliar $\delta^{13}C$ values ranged from -33.6‰ to -33.2‰ (dry season) and from -34.2‰ to -33.3‰ (wet season) in the two lower canopy strata. For the Paracou forest, the most pronounced change in $\delta^{13}C_{leaf}$ occurred between the top and the mid-canopy, while other forests, e.g. in Brazil or Trinidad showed a more gradual change with decreasing height above the ground (Fig. 2). At

Paracou, foliage in the mid- and understory canopy strata was about 4–5‰ depleted relative to the top, sunlit foliage, while in other lowland tropical forests, this depletion of shade foliage was smaller (about 3‰). However, whether these differences are consistent across all lowland rainforests cannot be decided, because the dataset on intra-canopy variation of foliar carbon isotope ratios from moist tropical lowland forests is still very limited (Table 2). In general, the isotopic signatures of sunlit, mature leaves at the top of the canopy stayed surprisingly constant, around –30‰. The depletion in $\delta^{13}C_{leaf}$ with decreasing height above the ground varied between 0.06‰ and 0.37‰ m^{-1} for all the sites, averaging 0.17‰ m^{-1} height. The French Guiana site, with 0.19‰ m^{-1} for the dry season and 0.14‰ m^{-1} for the wet season, was well within the typical range, similar to the south Venezuelan sites (between 0.13‰ and 0.37‰ m^{-1}) and the Brazilian sites (between 0.06‰ and 0.26 ‰ m^{-1}).

Source air effects could not explain the vertical gradients in $\delta^{13}C_{leaf}$ values at Paracou: $\delta^{13}C_{air}$ differed by only 1‰ within the canopy while $\delta^{13}C_{leaf}$ differed by 4‰–5‰ (Table 1). Thus, ecophysiological responses to changing environmental factors, e.g.
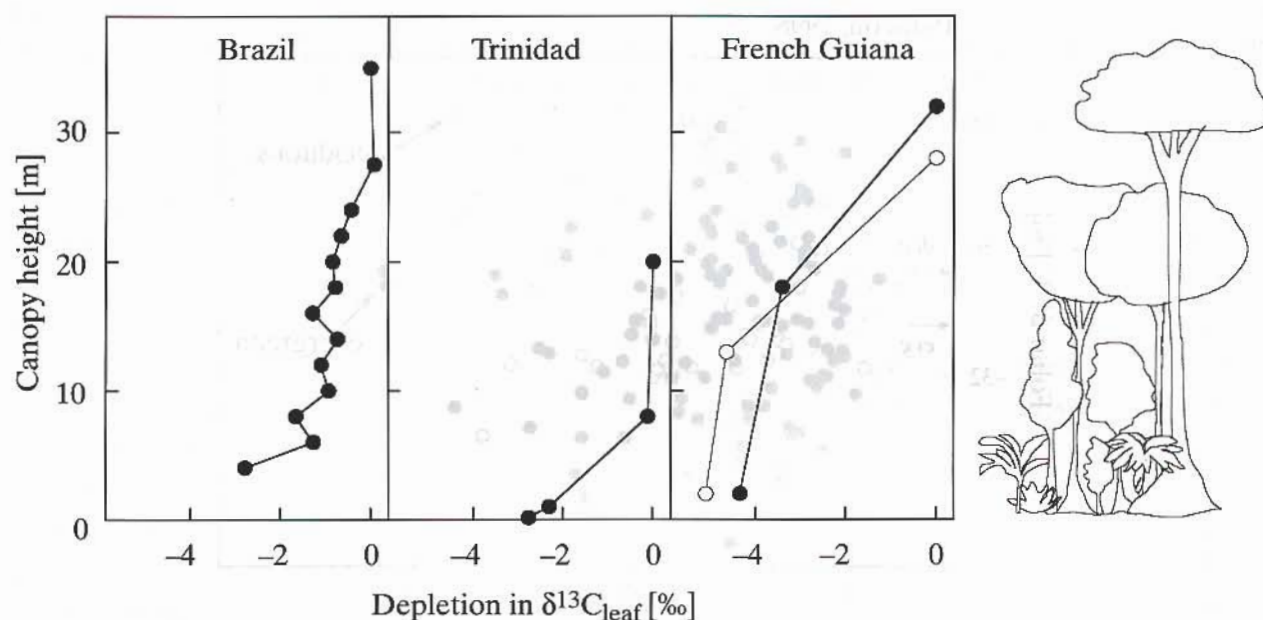
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Fig. 2. Typical spatial pattern of leaf carbon isotope ratios within tropical canopies ($\delta^{13}C_{leaf}$ in ‰). The $\delta^{13}C_{leaf}$ of foliage at the top of the canopy was used as a reference to calculate the intra-canopy depletion in $\delta^{13}C_{leaf}$ with decreasing height above the ground. Examples are taken from three lowland tropical forests in Brazil (Martinelli et al., 1998), Trinidad (Broadmeadow et al., 1992) and French Guiana (Buchmann et al., 1997). Data for French Guiana are given for the 1994 dry season (open symbols) and the 1995 wet season (closed symbols).

Table 2

Comparison of carbon isotope ratios of foliage ($\delta^{13}C_{leaf}$), litter ($\delta^{13}C_{litter}$), soil organic matter at 10 cm depth ($\delta^{13}C_{SOM}$) and soil respired CO_2 ($\delta^{13}C_{SR}$) in undisturbed tropical forests

Site	Latitude/ longitude	Time	Height (m)	$\delta^{13}C_{leaf}$ (‰)	$\delta^{13}C_{litter}$ (‰)	$\delta^{13}C_{SOM}$ (‰)	$\delta^{13}C_{SR}$ (‰)	Reference
Paracou, French Guiana	5° 2′ N 53° 0′ W	September 1994	28	−28.6 ± 0.7	−30.5 ± 0.5	−28.3 ± 0.3	−26.5 ± 0.1	Buchmann et al. (1997)
			13	−33.2 ± 0.4				
			2	−33.6 ± 0.2				
		July 1995	32	−29.9 ± 0.9	−28.9 ± 0.2	−28.0 ± 0.1	−26.8 ± 0.3	Buchmann et al. (1997)
			18	−33.3 ± 0.3				
			2	−34.2 ± 0.3				
Paracou, French Guiana	5° 2′ N 53° 0′ W	March 1993	30	−29.5 ± 0.1	−29.5 ± 0.2	−28.0 ± 0.2		Guehl et al. (1998)
Paracou, French Guiana	5° 2′ N 53° 0′ W	February 1998	30	−31.0 ± 0.1				Bonal et al. (2000b)

Table 2 *(continued)*

Comparison of carbon isotope ratios of foliage ($\delta^{13}C_{leaf}$), litter ($\delta^{13}C_{litter}$), soil organic matter at 10 cm depth ($\delta^{13}C_{SOM}$) and soil respired CO_2 ($\delta^{13}C_{SR}$) in undisturbed tropical forests

Site	Latitude/ longitude	Time	Height (m)	$\delta^{13}C_{leaf}$ (‰)	$\delta^{13}C_{litter}$ (‰)	$\delta^{13}C_{SOM}$ (‰)	$\delta^{13}C_{SR}$ (‰)	Reference
Simla, Trinidad	10° N 61° W	n.a.	20	−24.7 ± 0.1				Broadmeadow et al. (1992)
			8	−28.6± 0.7				
			1	−29.0 ± 0.5				
Aripo, Trinidad	10° N 61° W	n.a.	20	−29.7 ± 1.4				Broadmeadow et al. (1992)
			8	−29.9 ± 0.8				
			1	−32.0 ± 0.8				
South Venezuela	2° N 67° W	n.a.	20	−30.4	−30.9			van der Merwe and Medina (1989)
			8	−33.4				
			1	−32.9				
South Venezuela	2° N 67° W	n.a.	>20	−28.7 ± 0.8				Medina and Minchin (1980)
			<5	−34.3 ± 0.7				
South Venezuela	2° N 67° W	n.a.	>20	−30.5 ± 0.7	−29.4			Medina and Minchin (1980)
			2–10	−33.4 ± 0.5				
			>2	−35.2 ± 0.4				
Dimona Ranch, Brazil	2° S 60° W	September/ October 89	>20	−30.7 ± 0.3				Kapos et al. (1993)
		January/ July 90	1.3	−35.5				
Reserva Ducke, Brazil	2° 6′ S 59° 6′ W	July 1985					−24.8/−27.4	Quay et al. (1989)
Rondônia, Brazil	3° 8′ S 60° 1′ W	1974– 1976	17.5	−30.5 ± 0.4	−30.5 ± 0.4			Ducatti et al. (1991)
			9	−31.1 ± 0.6				
			3.5	−31.6 ± 1.1				

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Table 2 *(continued)*

Comparison of carbon isotope ratios of foliage ($\delta^{13}C_{leaf}$), litter ($\delta^{13}C_{litter}$), soil organic matter at 10 cm depth ($\delta^{13}C_{SOM}$) and soil respired CO_2 ($\delta^{13}C_{SR}$) in undisturbed tropical forests

Site	Latitude/ longitude	Time	Height (m)	$\delta^{13}C_{leaf}$ (‰)	$\delta^{13}C_{litter}$ (‰)	$\delta^{13}C_{SOM}$ (‰)	$\delta^{13}C_{SR}$ (‰)	Reference
Rondônia, Brazil	3° 8′ S 60° 1′ W	1974–1976	17.5	-30.2 ± 0.6	-29.9 ± 0.4			Ducatti et al. (1991)
			9	-30.1 ± 0.5				
			3.5	-31.1 ± 0.4				
Rondônia, Brazil	8° 45′ S 63° 23′ W	n.a.	35	-31.2	-28.7 ± 0.5			Martinelli et al. (1998)
			20–32.1					
			4	-34.0				
Rondônia, Brazil	10° 1′ S 62° 49′ W	n.a.				-28.3		Pessenda et al. (1998)
Bahia, Brazil	n.a.	October 1993			-29.4 ± 0.1	-28.0 ± 0.1		Cadisch et al. (1996)

n.a.: not available.

[CO_2], light or relative air humidity, contributed more to those vertical patterns in $\delta^{13}C_{leaf}$ than did $\delta^{13}C_{air}$. An important parameter for plant gas exchange, the C_i/C_a ratio, indicated changing gas exchange patterns within the canopy. Leaves at the top canopy had lower C_i/C_a (between 0.62 and 0.78) than foliage in the mid- and the understory canopy strata (between 0.84 and 0.95). Obviously, photosynthetic rates within this tropical forest decreased faster than stomatal conductance rates with increasing [CO_2] and decreasing light intensity (i.e. with decreasing height above the ground). Similar patterns were also found in other forest canopies (e.g. Brooks et al., 1997; Ehleringer et al., 1986).

3.3. $\delta^{13}C$ along the leaf–litter–soil continuum and its spatial variability

The $\delta^{13}C$ values along the leaf–litter–soil continuum tended to increase steadily at the French Guiana site (Table 2), with the effect being most obvious from litter to soil. The total enrichment in ^{13}C from leaf to soil organic carbon varied between 1‰ and 2‰ (relative to sun foliage) or 2–4‰ (relative to mid canopy foliage). In other lowland tropical forests, very similar patterns were observed. The $\delta^{13}C_{litter}$ values were either close to the corresponding $\delta^{13}C_{leaf}$ values of sun foliage (Ducatti

et al., 1991; van der Merwe and Medina, 1989) or increased by 1–2‰ (Cadisch et al., 1996; Martinelli et al., 1998; Medina and Minchin, 1980). In general, $\delta^{13}C_{litter}$ showed a smaller within-site variation than did $\delta^{13}C_{leaf}$ for all sites where data are available (S.D. of 0.3‰ vs. 0.5‰, respectively), indicating spatial and temporal integration of plant organic matter of different origins. Further ^{13}C enrichment could be observed for soil organic matter (at 10 cm depth) and soil respired CO_2 at the French Guiana site. Surprisingly constant $\delta^{13}C$ values for soil organic matter ($\delta^{13}C_{SOM}$) were found for all tropical lowland forests, ranging from −28.3‰ to −28.0‰. The same trend of progressive enrichment was observed in temperate and boreal forest ecosystems (Buchmann et al., 1997, 1998a; Flanagan et al., 1996) and is probably due mainly to a gradual shift in the relative contributions of microbial vs. plant components in the residual soil organic matter (Ehleringer et al., 2000).

Unfortunately, the isotopic data for soil respired CO_2 ($\delta^{13}C_{SR}$) at Paracou cannot be compared to any other tropical forest site since no other datasets are known to the authors. No significant differences were found between $\delta^{13}C_{SR}$ of the wet and the dry seasons (−26.8‰ vs. −26.5‰). Neill et al. (1996) determined the $\delta^{13}C$ of soil respired CO_2 using lab incubations

(sieved soil, no roots) with soil organic matter from a forest in Rondônia, Brazil and found a very similar $\delta^{13}C_{SR}$ value of –26.5‰.

Guehl et al. (1998) assessed the spatial variability of $\delta^{13}C$ in litter and soil organic matter under dominant trees in the Paracou forest, as they relate to the variability of sunlit leaf $\delta^{13}C$ values. In contrast to findings in a mixed temperate forest (Balesdent et al., 1993), Guehl and co-workers did not observe significant correlations between litter $\delta^{13}C$ values or leaf and soil $\delta^{13}C$ values (Fig. 3). Due to the non-synchronous leaf fall of the Paracou tree species (Loubry, 1994) and the high turnover rate of litter, both characteristic for tropical rainforests, litter $\delta^{13}C$ values are likely to display seasonal changes at a given site, whereas the isotopic signatures of soil organic matter are expected to be more stable over time, integrating time periods of about 5 years (Bird et al.,

1996). It is also noteworthy that the spatial variability of soil $\delta^{13}C$ was low in this highly heterogeneous pristine forest, with a maximum range of 1.5‰ among different sampling locations. Using a similar sampling design, Balesdent et al. (1993) found a range of approximately 4‰ for soil $\delta^{13}C$ values for mixed broad-leaved and coniferous temperate forests.

4. Variation in $[CO_2]$ and $^{13}C_{air}$

The source air for foliage photosynthesis is highly variable temporally and spatially in both its $[CO_2]$ and $\delta^{13}C$ ratios (Fig. 4). For the French Guiana site, daily variations were larger than seasonal variations. Changes in turbulent mixing of the atmosphere, varying soil respiration rates as well as changing contributions of canopy assimilation or respiration do affect these canopy profiles. Generally, $[CO_2]$ are the
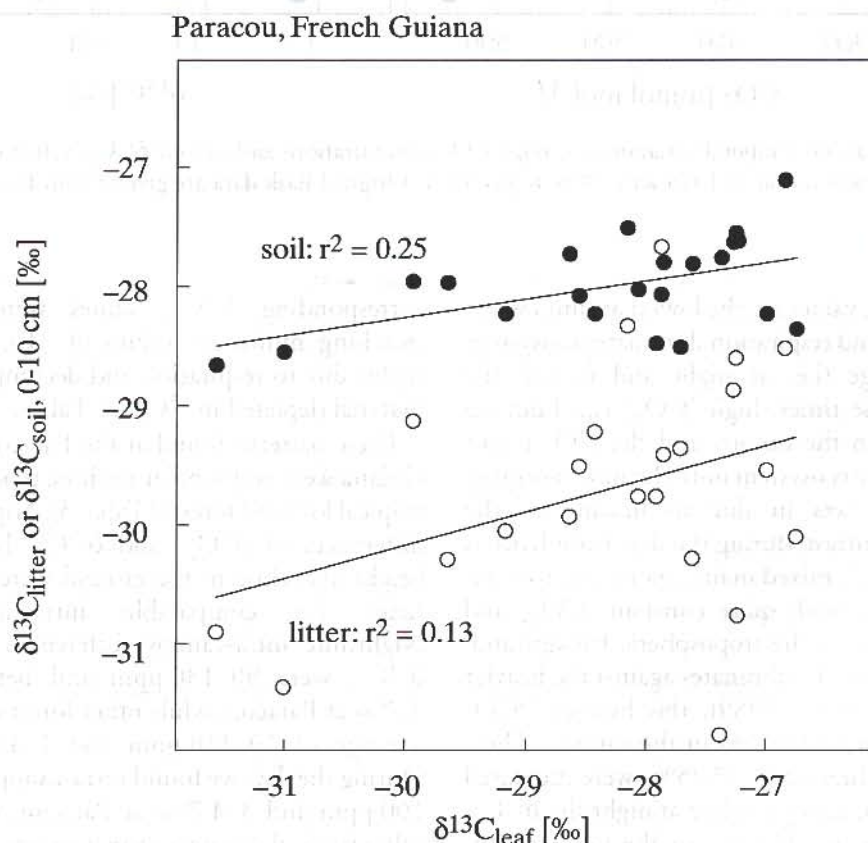

Fig. 3. Relationships between foliar $\delta^{13}C$ (sun leaves) and litter $\delta^{13}C$ (open circles) or soil $\delta^{13}C$ (0–10 cm depth; closed circles). Litter and soil samples were taken under those trees from which leaf samples were collected (data from Guehl et al., 1998). None of the regressions were significant at the 0.05 level.
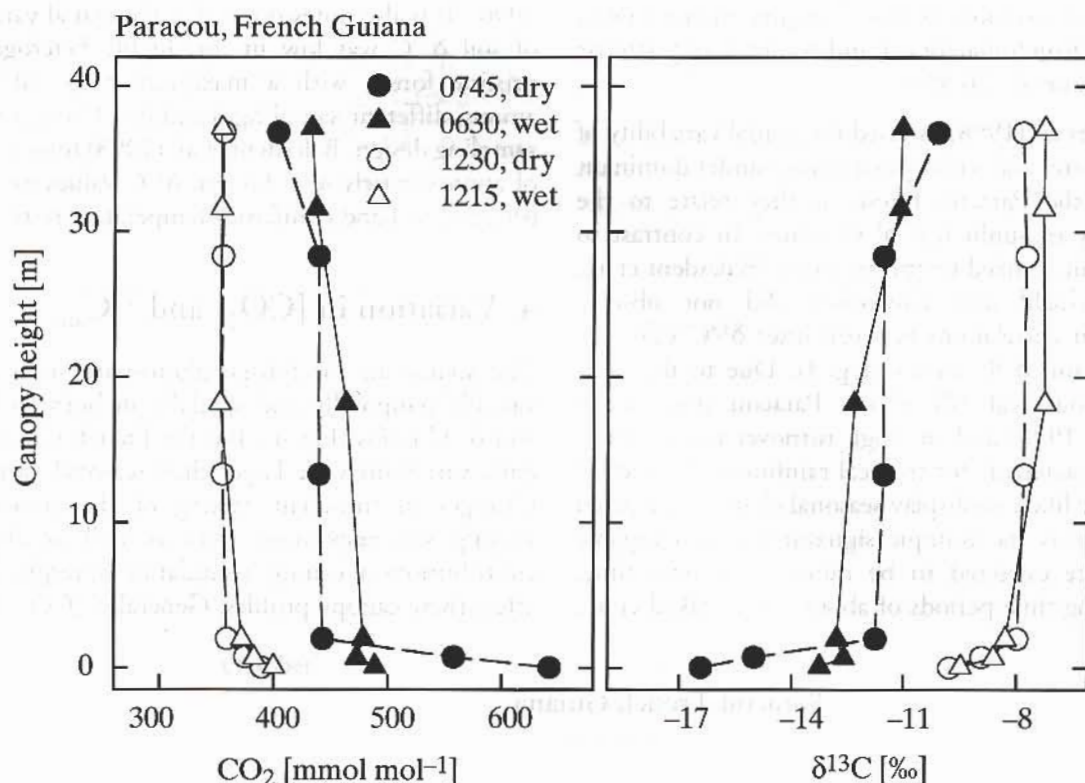
Fig. 4. Spatial and temporal variation in canopy CO_2 concentrations and canopy $\delta^{13}C_{air}$ values during the dry and the wet season in 1994 and 1995, respectively. Original flask data are given (from Buchmann et al., 1997).

highest and $\delta^{13}C_{air}$ values are the lowest at times when turbulence is low and respiration dominates ecosystem CO_2 gas exchange (i.e. at night and during the morning). At these times, high $[CO_2]$ can built up from respiration in the canopy and the CO_2 is not "flushed" out of the ecosystem until the next morning, when turbulence sets in due to heating of the atmosphere. In contrast, during the day, turbulence is high, ensuring a well-mixed main canopy (i.e. top and mid-canopy strata) with quite constant $[CO_2]$ and $\delta^{13}C_{air}$ values, close to the tropospheric background. Since photosynthesis discriminates against the heavier $^{13}CO_2$ (Farquhar et al., 1989), this heavier $^{13}CO_2$ (higher $\delta^{13}C_{air}$ values) remains in the canopy. Thus, daytime $\delta^{13}C_{air}$ values up to −7.75‰ were measured for the top Paracou canopy, while at night the $\delta^{13}C_{air}$ values were as low as −11.6‰ for the same height. Closer to the ground, the effect of soil respiration became apparent. $[CO_2]$ were always higher (up to 400 ppm during the day) compared to those in the main canopy due to the constant soil CO_2 efflux. The

corresponding $\delta^{13}C_{air}$ values were always lower (reaching minimum values of −16.4‰ during the night) due to respiration and decomposition of plant material depleted in ^{13}C (see Tables 1 and 2).

These patterns found at the Paracou site in French Guiana were very similar to those reported from other tropical lowland forests (Table 3). Night- and daytime differences of $[CO_2]$ and $\delta^{13}C_{air}$ between the top height and close to the ground were well within the range for comparable intra-canopy profiles. Nighttime intra-canopy differences for $[CO_2]$ and $\delta^{13}C_{air}$ were 90–130 ppm and between 3‰ and 3.7‰ at Paracou, while other forest canopies showed a range of 10–110 ppm and 1–4‰, respectively. During the day, we found intra-canopy profiles of 60–100 ppm and 3–4.7‰ at Paracou, while profiles in other tropical canopies were between 10 and 130 ppm and between 1‰ and 3‰. Differences in stand structure (and therefore turbulence regime), as well as species composition and water availability (and therefore ecosystem gas exchange), might be

Table 3

Intra-canopy differences for CO_2 concentrations (ΔC in ppm) and carbon isotope ratios of canopy air ($\Delta \delta_{air}$ in ‰) along height profiles (in m) in low land tropical forests for two different times (nighttime/early morning vs. noon)

Site	Latitude/ longitude	Season	Month	Profile (m)	Night/morning		Noon		Reference
					ΔC (ppm)	$\Delta \delta_{air}$ (‰)	ΔC (ppm)	$\Delta \delta_{air}$ (‰)	
Paracou, French Guiana	5° 2' N 53° 0' W	D	September 1994	0.02–28	130	3.7	100	4.7	Buchmann et al. (1997)
		W	July 1995	0.10–32	90	3.0	60	3.0	
Simla, Trinidad	10° N 61° W	W + D	n.a.	0.15–20	40	1	12	1	Broadmeadow et al. (1992)
Aripo, Trinidad	10° N 61° W	W + D	n.a.	0.15–20	40	1	30	1	Broadmeadow et al. (1992)
BCI, Panama	9° 10' N 79° 51' W	W + D	1985–1987	0.5–25	n.a.	n.a.	40	2.5	Sternberg et al. (1989)
Turrialba, Costa Rica	9° 6' N 83° 4' W	n.a.	November 1967	1–40	40	n.a.	15	n.a.	Lemon et al. (1970)
Reserva Ducke, Brazil	2° 6' S 59° 6' W	D	July 1985	0–28	70	4	70	2	Quay et al. (1989)
		D	August 1985	0–27	110	3	120	1.5	Wofsy et al. (1988)
		W	April/May 1987	0.02–37	60	n.a.	100	n.a.	Fan et al. (1990); Trumbore et al. (1990)
Para, Brazil	2° 6' S 47° 31' W	D	June 1995	0.5–18	50	2	120	4	Sternberg et al. (1997)
		D	October 1995	0.5–18	40	2	30	2	
		D	December 1995	0.5–18	40	2	40	3	
Rondônia, Brazil	3° 8' S 60° 1' W	D	May 1995	0.5–45	60	3	40	1	Sternberg et al. (1997)
		D	October 1995	0.5–45	20	1	50	1	
		D	December 1995	0.5–45	30	2	10	2	
Rondônia, Brazil	10° 5' S 61° 55' W	W	April/June '93	1–31	40	1	70	2	Grace et al. (1996)
Rondônia, Brazil	10° 5' S 61° 55' W	W	May 1993	1–26	10	n.a.	15	3	Kruijt et al. (1996)
		D	September 1992	1–26	10	n.a.	130	2.8	
West Malaysia	2° 59' N 102° 18' E	n.a.	November 1973	0.05–30	50	n.a.	115	n.a.	Aoki et al. (1975)

D = dry season, W = wet season, n.a. = not available.

responsible for the regional differences among various tropical forests for $[CO_2]$ and $\delta^{13}C_{air}$. Although the dataset is small, intra-canopy differences during the dry season seem to be often larger than those during the wet season (Table 3). Effects of cloudiness and soil water logging, reducing both canopy assimilation and soil respiration rates during the wet season, could be responsible for this observation.

Net ecosystem CO_2 exchange (NEE) measurements in the Amazon (using eddy covariance techniques) might provide further insight (Malhi et al., 1998, 1999). However, the annual NEE between an Amazon tropical forest and the atmosphere was relatively constant during the year. Although canopy photosynthetic capacity declined during the dry season, this decrease was compensated by increased hours of sunshine. Nevertheless, highest daytime CO_2 uptake rates were measured during the wet season. In addition, ecosystem respiration showed no pronounced seasonal fluctuation. Although temperatures were typically higher during the dry season, soil moisture was lower compared to the wet season. The authors concluded that NEE peaked in the early wet season and then declined progressively to minimum numbers in the late dry season (Malhi et al., 1999). Thus, the interplay between phenology (including litterfall), cloudiness and water availability determined NEE, which in turn will affect canopy $[CO_2]$ and $\delta^{13}C_{air}$ profiles.

5. Soil CO_2 efflux

Reduced soil respiration rates during the wet season were indeed found at Paracou (Table 4). Whereas soil CO_2 efflux from this well-drained site averaged 4.8 μmol CO_2 m^{-2} s^{-1} during the dry season, it fluctuated between 2.4 and 6.3 μmol CO_2 m^{-2} s^{-1} during the wet season. Just after heavy rain events (about 20 mm), soil respiration rates dropped by 30–50% relative to the rates prior to rain. Similar results were reported for a tropical forest on Barro Colorado Island (BCI), Panama (Kursar, 1989). There, soil respiration rates dropped by 29% 1.5 h after a 17 mm rain event. Five hours later, the rates were back to those prior to the rain. However, despite these short-term reductions immediately following rain events, it cannot be concluded that soil respiratory losses during the entire wet season are significantly smaller than those during the dry season. To the contrary, maximum rates have also been measured during the wet season, including at the Paracou site (Table 5; see also Kursar, 1989; Maggs and Hewett, 1990). In general, soil respiration rates measured in French Guiana (Buchmann et al., 1997; Janssens et al., 1998) fit well within the range reported for other lowland tropical forests, most of them studied in the neotropics. While the rates can vary between 1 and 16 μmol CO_2 m^{-2} s^{-1}, the average value was closer to 4 μmol CO_2 m^{-2} s^{-1}.

Similar to temperate and boreal forest soils, temporal and spatial variations in soil CO_2 efflux are typically large (S.D. between 0.3 and 1 μmol CO_2 m^{-2} s^{-1}). At the French Guiana site, soil temperature could not explain this variation since it stayed rather constant. Soil moisture (see Table 4), but also biological parameters such as root density were found to be important factors (Janssens et al., 1998). This is in contrast to the situation in most temperate and boreal

Table 4

The effect of precipitation events on soil respiration rates at the primary lowland forest site in Paracou (after Buchmann et al., 1997)

Time	Soil CO_2 efflux (μmol m^{-2} s^{-1})		
	Before rain	After rain	Reduction by
Wet season 1995	5.00 ± 0.26	2.41 ± 0.05	52%
	4.75 ± 0.44	3.34 ± 0.08	30%
	6.27 ± 0.19	3.50 ± 0.02	44%
Dry season 1994	4.77 ± 0.12		

For more details see text.

Table 5
Soil respiration rates in moist tropical forests

Site	Latitude/longitude	Season	Time	Soil respiration rate (μmol CO_2 m^{-2} s^{-1})		Reference
				Range	Average	
Paracou, French Guiana	5° 2′ N 53° 0′ W	D	September 1994		4.8 ± 0.1	Buchmann et al. (1997)
		W	July 1995	2.4–6.3		Buchmann et al. (1997)
Paracou, French Guiana	5° 2′ N 53° 0′ W	W + D	July–September 1994	2.0–2.7	2.3	Janssens et al. (1998)
Hawaii, high elevation	19° 45′ N 155° 15′ W	W + D	1991–1992	1.0–2.3		Raich (1998)
BCI, Panama	9° 10′ N 79° 51′ W	W + D	1984–1986		3.8	Kursar (1989)
South Venezuela, podsol	2° N 67° W		n.a.		3.8	Medina et al. (1980)
South Venezuela, laterite	2° N 67° W		n.a.		2.7	Medina et al. (1980)
Reserva Ducke, Brazil	2° 6′ S 59° 6′ W	W	April/May 1987		5.3	Fan et al. (1990)
		D	August 1985		4.1	Wofsy et al. (1988)
Para, Brazil	2° 6′ S 47° 31′ W	W	May 1992		6.7 ± 0.5	Davidson and Trumbore (1995)
		D	November 1992		5.6 ± 0.5	
Rondônia, Brazil	10° 5′ S 61° 57′ W	W + D	1992 and 1993		5.5 ± 1.6	Meir et al. (1996)
Orissa, India	21.5° N 83.5° E	D	September 1988		8.1 ± 0.6	Behera et al. (1990)
Sarawak, Malaysia	2° N 11° E	n.a.	June 1970	4.1–6.2		Wanner et al. (1973)
NE Queensland, Australia	17° 17′ S 145° 37′ E	W + D	July 1986–October 1987	7–14		Maggs and Hewett (1990)
Multiple sites	1–18° N or S		n.a.	1.0–16.1		Schlesinger (1977)
Multiple sites	1–18° N or S		n.a.		3.3 ± 0.2	Raich and Schlesinger (1992)

D = dry season, W = wet season, n.a. = not available.

forests, where variability of soil CO_2 efflux is mainly explained by those two factors, temperature and moisture (typically between 60% and 80%). Only limited knowledge is available about the contribution of root/rhizosphere vs. microbial respiration. Medina et al. (1980) conclude that root respiration is responsible for 67–82% of bulk soil respiration. No information about the partitioning between different sources is available for the Paracou site.

6. Integrating ecosystem $^{13}CO_2$ exchange

Integrating information from all ecosystem compartments is of major importance in order to understand ecosystem fluxes, particularly within a global context. Using canopy air and its isotopic signatures can help in both spatial and temporal integration since the major ecosystem processes, assimilation and respiration, leave their "fingerprint" on $\delta^{13}C_{air}$. Two parameters are available to characterize the $^{13}CO_2$ exchange of ecosystems: the isotopic signature of ecosystem respiration ($\delta^{13}C_{ER}$) and ecosystem discrimination (Δ_e).

6.1. Ecosystem respiration

The $\delta^{13}C_{ER}$ was estimated from a so-called "Keeling plot" (Buchmann et al., 1997; Keeling 1958). If one plots the inverse $[CO_2]$ vs. the corresponding $\delta^{13}C_{air}$ value, a linear relationship evolves that often holds for day- and nighttime data (Fig. 5). This relationship depicts a two-ended mixing model: two CO_2 sources with different $\delta^{13}C$ values mix within the canopy. Atmospheric CO_2 with its $\delta^{13}C$ of about −7.8‰ mixes with respired CO_2 that typically has a much lower $\delta^{13}C$ value (about −26‰ for C_3 stands or −13‰ for C_4 stands). The intercept from a geometric mean regression analysis represents the isotopic signature of total ecosystem respiration, the second source of CO_2 within any given canopy. Typically, the error associated with this approach is about 1‰ for $\delta^{13}C_{ER}$ estimates (Buchmann et al., 1998b).

For the primary forest at Paracou, the $\delta^{13}C_{ER}$ values were −27.5‰ during the dry season and −27.9‰ during the wet season (Table 6). Thus, intra-annual variability was negligible. The $\delta^{13}C_{ER}$ estimates for this lowland tropical forest were well within estimates for other tropical forests, ranging from −28.3‰ to 22.8‰. Most of the $\delta^{13}C_{ER}$ estimates were higher than the corresponding $\delta^{13}C_{leaf}$ values (compare Table 2),

indicating the influence of soil respiratory fluxes to ecosystem respiration. Based on chamber measurements for soil, stem and foliage respiration, Meir et al. (1996) scaled these flux rates to the ecosystem level and compared this estimate to total ecosystem respiration measured by eddy covariance techniques. Both approaches gave very similar results for ecosystem respiration: 7.2 µmol CO_2 m^{-2} s^{-1} based on scaling and 6.6 µmol CO_2 m^{-2} s^{-1} based on eddy covariance techniques. Soil respiration accounted for 76% of the total ecosystem flux, compared to 10% for stem respiration and 14% for foliage respiration. Thus, stable isotope analyses can provide important information about the dominant flux component, although only the combination of isotope and flux measurements allows the quantitative partitioning of net ecosystem exchange (e.g. Bowling et al., 1999, 2001).

6.2. Ecosystem discrimination

Both $\delta^{13}C_{ER}$ as well as ecosystem discrimination (Δ_e) integrate over all the fluxes from all compartments within a given ecosystem (Buchmann et al., 1998b; Flanagan and Ehleringer, 1998). While $\delta^{13}C_{ER}$ gives direct information about the isotopic signature of the respiratory CO_2 leaving the ecosystem, ecosystem discrimination provides information about the CO_2 assimilated by the canopy and potentially about the ratio between CO_2 assimilation and canopy conductance (Buchmann and Kaplan, 2001). The well-known relationship between Δ_{leaf} and $\delta^{13}C_{leaf}$ (Farquhar et al., 1989) is transferred to the next higher organizational level, by replacing the $\delta^{13}C_{leaf}$ with $\delta^{13}C_{ER}$ and $\delta^{13}C_{air}$ with $\delta^{13}C_{trop}$. Δ_e was calculated as:

$$\Delta_e = \frac{\delta^{13}C_{trop} - \delta^{13}C_{ER}}{1 + \delta^{13}C_{ER}} \qquad (4)$$

where $\delta^{13}C_{ER}$ represents the intercept of the corresponding Keeling plot (see Fig. 5) and $\delta^{13}C_{trop}$ represents the tropospheric background value.

Ecosystem discrimination of the Paracou site was estimated as 20.3‰ during the dry season and 20.5‰ during the wet season, reflecting the small intra-annual variability already seen in the $\delta^{13}C_{ER}$ values (Table 6). Both Δ_e estimates were well within the range reported in the literature, from 17.3‰ to 21.1‰. Thus, the similarity among different lowland tropical forests growing within a 20° latitudinal band that we found for all individual compartments of these
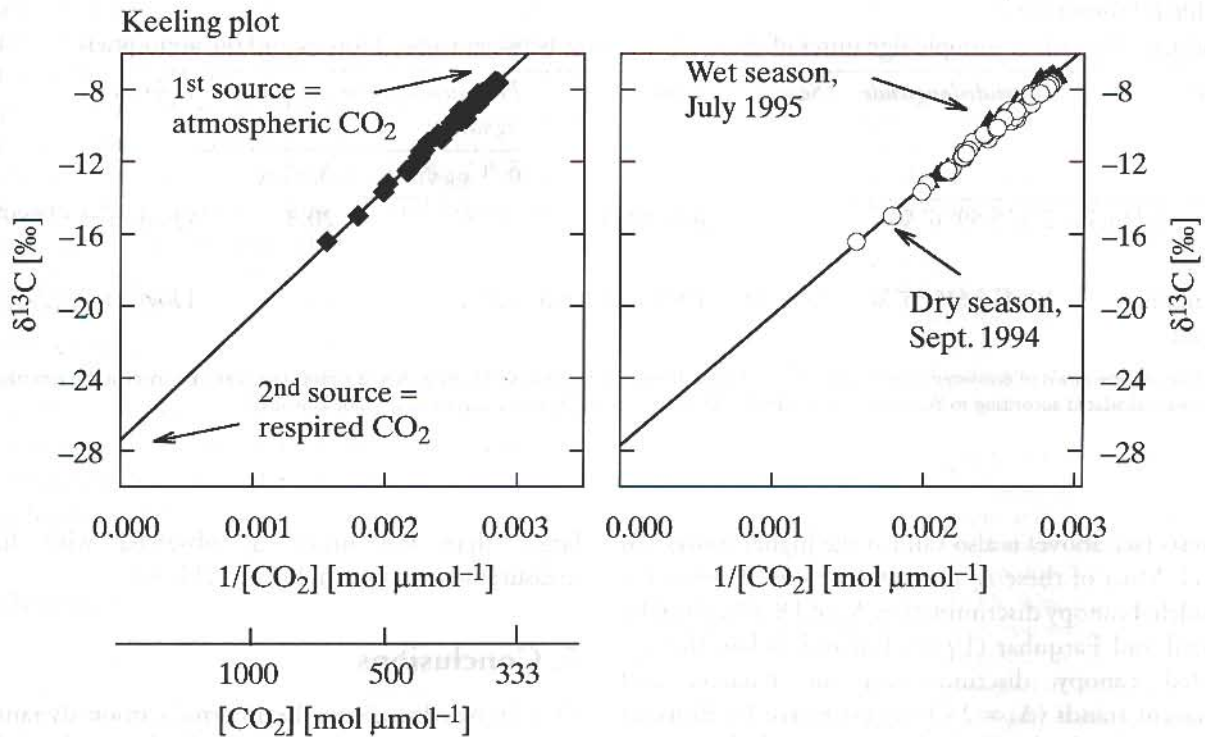
Fig. 5. Relationship between the inverse canopy CO_2 concentrations and the respective $\delta^{13}C_{air}$ values. A. Conceptual Keeling plot. B. Keeling plots for the dry and the wet season in 1994 and 1995, respectively. Original flask data are presented (from Buchmann et al., 1997).

Table 6
Estimates for carbon isotopic signatures of the CO_2 exchange between tropical forests and the atmosphere

Site	Latitude/longitude	Season	Time	Ecosystem carbon isotopic signature		Reference
				$\delta^{13}C_{ER}$ (‰)	Δ_e (‰)	
Paracou, French Guiana	5° 2' N 53° 0' W	D	September 1994	−27.5 ± 0.2	20.3 ± 0.2	Buchmann et al. (1997)
		W	July 1995	−27.9 ± 0.4	20.5 ± 0.4	Buchmann et al. (1997)
Chamela, Mexico	20° N 105° W	n.a.	October 88	−27.3	20.2	Lancaster (1990)
BCI, Panama	9° 10' N 79° 51' W	W + D	1985 and 1987	−28.3	21.1	Sternberg et al. (1989)
BCI, Panama	9° 10' N 79° 51' W	n.a.	March 88	−27.8	20.7	Lancaster (1990)
Trinidad	10° N 61° W	W + D	n.a.	−22.8	17.3	Broadmeadow et al. (1992)
Rondônia, Brazil	2° S 60° W	W	1990	−25.8	18.6	Kapos et al. (1993)

Table 6 *(continued)*

Estimates for carbon isotopic signatures of the CO_2 exchange between tropical forests and the atmosphere

Site	Latitude/longitude	Season	Time	Ecosystem carbon isotopic signature		Reference
				$\delta^{13}C_{ER}$ (‰)	Δ_e (‰)	
Reserva Ducke, Brazil	2° 6′ S 59° 6′ W	D	July 1985	−27.6	20.3	Quay et al. (1989)
Rondônia, Brazil	10° 5′ S 61° 55′ W	W + D	1992 and 1993	−27.1	19.5	Lloyd et al. (1996)

Carbon isotope ratios of ecosystem respiration ($\delta^{13}C_{ER}$) were determined as the intercepts of Keeling plots (see text). Ecosystem discrimination (Δ_e) was calculated according to Buchmann et al. (1997). D = dry season, W = wet season. n.a. = not available.

forests (see above) is also valid at the higher ecosystem level. Most of these Δ_e estimates were well above the modeled canopy discrimination Δ_A of 18.4‰ given by Lloyd and Farquhar (1994), but well below the up-scaled canopy discrimination for Paracou and adjacent stands ($\Delta_A = 23.1‰$) estimated by Bonal et al. (2000b), both of which do not include the soil compartment. The estimate by Lloyd and Farquhar (1994) is based on a limited dataset for $\delta^{13}C_{leaf}$, with variations around this value of about 2–3‰ (personal communication J. Lloyd). Bonal et al. (2000b) scaled up $\delta^{13}C_{leaf}$ to the canopy level, weighing $\delta^{13}C_{leaf}$ of all species present by their basal stem area. Thus, identifying the reasons for this 3.8‰ spread in Δ_e and for the discrepancy between Δ_e and Δ_A will be the next major task for biogeochemical ecosystem research.

Global carbon models increasingly use stable carbon and oxygen isotopes to identify the distribution and the magnitude of global carbon sinks and sources (e.g. Ciais et al., 1995; Fung et al., 1997; Tans et al., 1993). Thus, detailed isotopic information is needed to describe the terrestrial biospheric CO_2 exchange adequately. However, all current models use only one value for Δ_e across the globe, neglecting spatial and temporal variations, although a 3‰ difference between modeled and real ecosystem discrimination will result in a 20% change of the global carbon sink (Fung et al., 1997). Kaplan et al. (2002) modeled ecosystem discrimination for 26 different biomes, including three tropical forest types. Based on their equilibrium ecosystem model (BIOME4), ecosystem discrimination for evergreen broadleaf and semi-evergreen tropical forests averaged 22‰, about 2‰

larger than the mean Δ_e observed with field measurements (around 20‰; Table 6).

7. Conclusions

Our knowledge about the internal carbon dynamics of tropical forests and their contribution to the global carbon budget is still rather poor. Often, only a handful of datasets exists for any given research question, resulting in high uncertainties of whether or not an observed phenomenon reflects a general behavior of lowland tropical forests or rather a site-specific pattern caused by the interplay of the many environmental factors characteristic of a particular site. However, we found an outstanding similarity in the isotopic signatures of carbon pools and fluxes among a wide range of tropical forests in Central and South America, Asia and Australia. Despite temporal and spatial variations within any given site, carbon isotopic signatures showed similar trends worldwide. Thus, the French Guiana site, Paracou can well be considered a model ecosystem, representative for many lowland pristine forests globally.

Stable isotopes proved useful for many aspects that are relevant for the internal carbon dynamics of tropical ecosystems, ranging from the identification of major CO_2 sources within a canopy, to understanding the dominant controls of foliage and ecosystem gas exchange, to the partitioning of net ecosystem fluxes. However, the number of studies using stable isotopes is still rather small, and site selection for ecosystem studies has often been biased towards "ideal", undisturbed forests sites (Buchmann and Kaplan, 2001), leading to neglect of the effects of land use

change on these pristine forest sites. Filling this gap by studying these disturbed ecosystems will also benefit from using stable isotopes, not only in classical applications to determine the photosynthetic type of the dominant vegetation, but also to quantify the then changing contributions of different carbon fluxes to the overall ecosystem flux. Combining eddy covariance measurements of net ecosystem CO_2 exchange with ecophysiological measurements (Buchmann, 2002) and stable isotope analyses (Bowling et al., 1999a,b; Knohl et al., 2002) will probably be the most promising avenue in future ecosystem research. We strongly believe that determining the consequences of human impacts on these pristine forests will be the next challenging step in tropical ecology.

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