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Interspecific variability of $\delta^{13}\text{C}$ among trees in rainforests of French Guiana: functional groups and canopy integration

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Abstract The interspecific variability of sunlit leaf carbon isotope composition ($\delta^{13}\text{C}$), an indicator of leaf intrinsic water-use efficiency (WUE, CO_2 assimilation rate/leaf conductance for water vapour), was investigated in canopy trees of three lowland rainforest stands in French Guiana, differing in floristic composition and in soil drainage characteristics, but subjected to similar climatic conditions. We sampled leaves with a rifle from 406 trees in total, representing 102 species. Eighteen species were common to the three stands. Mean species $\delta^{13}\text{C}$ varied over a 6.0‰ range within each stand, corresponding to WUE varying over about a threefold range. Species occurring in at least two stands displayed remarkably stable $\delta^{13}\text{C}$ values, suggesting a close genetic control of species $\delta^{13}\text{C}$. Marked differences in species $\delta^{13}\text{C}$ values were found with respect to: (1) the leaf phenology pattern (average $\delta^{13}\text{C}=-29.7\text{‰}$ and -31.0‰ in deciduous-leaved and evergreen-leaved species, respectively), and (2) different types of shade tolerance defined by features reflecting the plasticity of growth dynamics with respect to contrasting light conditions. Heliophilic species exhibited more negative $\delta^{13}\text{C}$ values (average $\delta^{13}\text{C}=-30.5\text{‰}$) (i.e. lower WUE) than hemitolerant species (-29.3‰). However, tolerant species (-31.4‰) displayed even more negative $\delta^{13}\text{C}$ values than heliophilic ones. We could not provide a straightforward ecophysiological interpretation of this result. The negative relationship found between species $\delta^{13}\text{C}$ and midday leaf water potential (Ψ_{wm}) suggests

that low $\delta^{13}\text{C}$ is associated with high whole tree leaf specific hydraulic conductance. Canopy carbon isotope discrimination (Δ_A) calculated from the basal area-weighted integral of the species $\delta^{13}\text{C}$ values was similar in the three stands (average $\Delta_A=23.1\text{‰}$), despite differences in stand species composition and soil drainage type, reflecting the similar proportions of the three different shade-tolerance types among stands.

Key words Tropical rainforest · ^{13}C · Interspecific diversity · Functional grouping · Canopy carbon isotope discrimination

Introduction

Tropical rainforests are characterised by the co-existence of a multitude of tree species. More than 1300 tree species with a diameter at breast height (DBH) higher than 10 cm have been identified by botanists in French Guiana (Riéra et al. 1989; Sabatier and Prévost 1990; D. Sabatier and M.F. Prévost, unpublished data). Studies on the ecophysiological diversity of tropical rainforest tree species remain scarce and have concentrated only on a small number of species, which were mostly chosen based on light adaptation features (Bazzaz and Pickett 1980; Doley et al. 1988; Huc and Guehl 1989; Roberts et al. 1990; Alexandre 1991; Meinzer et al. 1993; Huc et al. 1994; Koch et al. 1994; Hogan et al. 1995; Guehl et al. 1998; Bonal et al., in press).

Plant carbon isotope composition ($\delta^{13}\text{C}$) measures allow the assessment of ecophysiological traits and their differences among tree species. Leaf $\delta^{13}\text{C}$ is related to the time-integrated intrinsic water-use efficiency (WUE), defined as the ratio of leaf area based rate of CO_2 assimilation (A) to stomatal conductance for water vapour (g_s) (Farquhar et al. 1982). Even though leaf $\delta^{13}\text{C}$ is greatly affected by environmental factors, namely light penetration in the canopy and vertical gradients of canopy air $\delta^{13}\text{C}$ (Medina and Minchin 1980; Sternberg et al. 1989; Van der Merwe and Medina 1989; Buchmann et al.

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1997), species effects have been found among tropical rainforest trees (Huc et al. 1994; Buchmann et al. 1997; Guehl et al. 1998; Martinelli et al. 1998). The $\delta^{13}\text{C}$ approach is therefore ideal for addressing functional diversity in complex forest ecosystems, and for distinguishing functional groups of species (Brooks et al. 1997).

Huc et al. (1994) used the $\delta^{13}\text{C}$ approach to compare the ecophysiological characteristics of pioneer species and late-stage forest species growing under similar conditions in plantations. They found that pioneer species had lower $\delta^{13}\text{C}$ values than late-stage ones, i.e. lower WUE. Pioneer species also presented higher A , g_s , leaf transpiration rate, midday leaf water potential (Ψ_{wm}) and hydraulic conductance than late-stage species. More recently, however, in a study including 18 species in a rainforest of French Guiana, Guehl et al. (1998) found that some very abundant shade-tolerant canopy late-stage species presented lower $\delta^{13}\text{C}$ values than pioneer species. This does not conform with the simple paradigm of pioneer/late stage or heliophilic/shade-tolerant dichotomy. Validation of this result over a larger number of species is necessary.

Leaf phenology (deciduous-leaved vs evergreen-leaved) is another trait that has been found to be associated with contrasting species leaf $\delta^{13}\text{C}$ values in forest ecosystems. In dry tropical conditions, shallow-rooted deciduous-leaved species displayed less negative $\delta^{13}\text{C}$ than the deeply rooted evergreen-leaved ones (Sobrado and Ehleringer 1997). In contrast, in a Mediterranean macchia ecosystem, Valentini et al. (1992) found most negative $\delta^{13}\text{C}$ values for the deeply rooted deciduous-leaved species. Such an assessment has not been carried out for tropical rainforests so far, even though the pattern of leaf phenology of major species is known (for French Guiana, see Loubry 1994; D. Sabatier, personal communication). In tropical rainforests, numerous deciduous-leaved species occur. However, they display distinct seasonal patterns of leaf fall, the drought-deciduous one being only a particular case. Species occurring in lowland rainforests in French Guiana are also characterised by differences in their geographical range of distribution, from French Guiana exclusively to a wide distribution in the wet and dry neotropical zone, as shown by the data compiled in the floras (Flora of the Guianas; Flora Neotropica). Whether such differences in geographical distribution are associated with differences in $\delta^{13}\text{C}$ is an important question.

Functional grouping of species based on ecophysiological characteristics (Chapin et al. 1996; Brooks et al. 1997) has become a necessary step to the understanding and modelling of the functioning of complex ecosystems such as the tropical rainforest (Lloyd and Farquhar 1994; Lacroix and Abbadie 1998). The knowledge of whole canopy carbon isotope discrimination (Δ_A) – defined roughly as the difference between atmospheric $\delta^{13}\text{C}$ and the CO_2 assimilation weighted average leaf $\delta^{13}\text{C}$ of the different species in the canopy (Lloyd and Farquhar 1994) – is critical for our understanding of the global carbon budget and our ability to model carbon fluxes at

the earth scale. Lloyd and Farquhar (1994) attempted to model the role of the different ecosystems on the earth in the global carbon cycle on the basis of Δ_A estimates for these ecosystems. For the tropical rainforest ecosystem, the Δ_A value used in the model was derived from leaf gas exchange studies performed on a reduced number of species, which did not take into account the interspecific $\delta^{13}\text{C}$ diversity of this ecosystem (Guehl et al. 1998; Martinelli et al. 1998). Furthermore, tropical rainforests are characterised by spatial gradients of floristic composition and soil characteristics (Lescure and Boulet 1985; Sabatier and Prévost 1990; Sabatier et al. 1997). We wonder if these factors affect Δ_A .

The objectives of this study were:

1. To assess the variability of sunlit leaf $\delta^{13}\text{C}$ for a large number of canopy tree species. Is leaf $\delta^{13}\text{C}$ for a given species stable over sites differing in overall stand floristic composition or in soil conditions? Only sites under similar climatic conditions were considered.
2. To assess whether interspecific differences in $\delta^{13}\text{C}$ are associated: (1) with traits like shade tolerance or the leaf phenology pattern, (2) with the type of distribution of the species in South America (e.g. extension towards the dry tropics), and/or (3) merely with the taxonomic position of the species. Based on these characteristics, is it possible to define a simple grouping of species (Tilman 1988) taking account of the variability of $\delta^{13}\text{C}$ among species?
3. To provide an ecophysiological interpretation of the variability in species $\delta^{13}\text{C}$. Does the variability in $\delta^{13}\text{C}$ among species, and also among possible functional groups of species, relate to differences in hydraulic traits assessed by predawn (Ψ_{wp}) and midday (Ψ_{wm}) leaf water potential measurements?
4. To estimate canopy carbon isotope discrimination (Δ_A) by the integration of leaf $\delta^{13}\text{C}$ values over the different species constituting the canopy. Do spatial gradients in stand floristic composition or in soil drainage characteristics modulate Δ_A under similar climatic conditions?

Species were selected as representative: (1) of the canopy of three lowland forest stands differing in floristic composition and in soil drainage characteristics, including also a large number of rare species, (2) of the different light adaptation strategies, (3) of the different leaf phenology patterns. Since our aim was also to spatially integrate the tree $\delta^{13}\text{C}$ values, we sampled intensively the three stands and recorded all tree co-ordinates.

Materials and methods

Sampling sites

This study was carried out in the tropical rainforest of French Guiana in two areas differing in floristic composition. The St-Elie site is located in the ECEREX research zone (Sarraillh 1984) (5°18'N; 53°30'W); the Paracou site is located in the experimental forest zone of Paracou described by Bariteau and Geoffroy (1989),

on the concession of "CIRAD-forêt" (5°20'N, 52°50'W). Soils in both sites are oxisols with a ferrallitic cover developed over a Precambrian metamorphic rock (Boulet 1990). The climate is characterised by a long dry season from mid-August to the end of November and a short dry season in February/March. Mean annual rainfall (1986–1993) is 2.9 and 3.0 m in Paracou and St-Elie, respectively. Average annual temperature is 25.8°C. Leaf area index is close to 8 in both forests (A. Granier, personal communication) and average canopy height is 30 m.

In St-Elie, two untouched 1-ha stands differing in soil drainage characteristics were chosen among the stands described by Sabatier et al. (1997). Stand St-Elie DVD is characterised by a deep vertical soil drainage, down to several meters depth. Stand St-Elie SLD has mainly a superficial lateral soil drainage, with apparition of a "dry to the touch" character at a depth of less than 1.2 m (Guehl 1984). Sabatier et al. (1997) found that such differences in soil features have a strong influence on the forest community. In Paracou, one untouched 1.25-ha stand with mostly deep vertical soil drainage characteristics was studied.

In each stand, all trees with a DBH higher than 10 cm were inventoried, identified, and named following the Checklist of the Plants of the Guianas (Bogdan et al. 1997). Three main families (out of a total of 38 in Paracou and 50 in St-Elie) represent about 50.0% of the trees in each stand. In Paracou, the Lecythidaceae, the Caesalpiniaceae and the Chrysobalanaceae families represent 18.5, 13.2 and 10.1%, respectively (D. Sabatier and J.F. Molineau, unpublished data). For both stands in St-Elie, the first two families are the Lecythidaceae (28.5% for St-Elie DVD and 30.6% for St-Elie SLD) and the Caesalpiniaceae (9.6% for St-Elie DVD and 17.0% for St-Elie SLD), but the next family is the Euphorbiaceae in St-Elie DVD (6.4%) and the Chrysobalanaceae in St-Elie SLD (7.1%).

Trees were selected according to the three following criteria:

1. Relative abundance in the stand. At least 3 – and up to 11 – trees per species were selected for the 20 main species in each stand. Furthermore, one or two trees per species were selected for sparse species.
2. Social status of the trees in the canopy. Mainly trees reaching the top of the canopy were considered. Additionally, few trees per stands belonging to the sub-canopy, but growing in large canopy gaps, and thus having sunlit leaves, were selected.
3. To cover a wide range of taxa with consideration of species present in the three stands.

The second criterion was strictly respected, since it has been demonstrated that vertical gradients in leaf $\delta^{13}\text{C}$ will occur due to light attenuation and gradients in canopy air carbon isotope composition ($\delta^{13}\text{C}_{\text{air}}$) (Medina and Minchin 1980; Medina et al. 1991; Buchmann et al. 1997).

We sampled 187 trees representing 64 species in Paracou, 106 trees representing 46 species in St-Elie DVD and 115 trees representing 54 species in St-Elie SLD (Appendix 1, Fig. 1). One hundred and two species were sampled in total. Twenty-eight species were common to St-Elie DVD and St-Elie SLD; 18 species were common to the 3 stands. The species considered in our sampling procedure represented 81.2, 67.7, and 83.3% of the total stand basal area in Paracou, St-Elie DVD and St-Elie SLD, respectively. Tree height was measured in Paracou using a laser dendrometer (Ledha Geo, Jenoptik laser, Jena, Germany). The DBH of each tree was recorded in the three stands.

Leaf sampling, elemental and isotopic analyses

Leaves were sampled in 1998 in the short dry season in Paracou and in the long dry season in St-Elie. Ten to fifteen fully expanded, sunlit leaves per selected tree were shot down using a rifle. Leaves were oven-dried at 70°C for 48 h and finely ground. A sub-sample of 1 mg of leaf powdered material was combusted and analysed for C and N elemental concentration and for ^{13}C composition using an isotope ratio mass spectrometer (Delta S, Finnigan MAT, Bremen, Germany) at the stable isotope facility of INRA Nancy. Carbon isotope composition ($\delta^{13}\text{C}$) was calculated as:

$$\delta^{13}\text{C}(\text{‰}) = \frac{R_{\text{sa}} - R_{\text{st}}}{R_{\text{st}}} 1000,$$

where R_{sa} and R_{st} are the $^{13}\text{C}/^{12}\text{C}$ ratio in the sample and in the conventional Pee Dee Belemnite standard, respectively. Since only sunlit leaves were sampled, atmospheric CO_2 concentration (C_a) and carbon isotope composition ($\delta^{13}\text{C}_a$) can be considered as constant (Buchmann et al. 1997) ($C_a=358$ ppm; $\delta^{13}\text{C}_a=-7.85\text{‰}$; Buchmann et al. 1997). Therefore, leaf $\delta^{13}\text{C}$ is negatively and linearly related to the time-integrated ratio of intercellular to ambient CO_2 concentration (C_i/C_a) and positively related to the time-integrated leaf intrinsic water-use efficiency ($\text{WUE}=A/g_s$) (Farquhar et al. 1982):

$$\begin{aligned} \delta^{13}\text{C} &\approx \delta^{13}\text{C}_a - \left(a + (b - a) \frac{C_i}{C_a} \right) \\ &= \delta^{13}\text{C}_a - \left(a + (b - a) \left(1 - \frac{1.6\text{WUE}}{C_a} \right) \right). \end{aligned}$$

Leaf water potential

Leaf water potential was measured using a pressure bomb (PMS Instruments Model 1000, Corvallis, Ore.) (Scholander et al. 1965) in the two St-Elie stands in the 1998 long dry season and in the 1999 long wet season. Predawn (Ψ_{wp}) and midday (Ψ_{wmp} , 1100–1330 hours) leaf water potentials were measured on two fully expanded, sunlit leaves per tree that were shot down on one to three trees per species. All leaf water potential measurements were conducted on bright days. Species were selected based on previous studies (Guehl et al. 1998; D. Bonal and J.M. Guehl, unpublished data) in order to cover a wide range of leaf $\delta^{13}\text{C}$ values. All selected trees occupied a dominant position in the canopy. Leaf water potential measurements were performed on the same trees in the wet and the dry season on 27 species in St-Elie DVD and on 18 species in St-Elie SLD, 8 species being common to the 2 stands.

Integration of $\delta^{13}\text{C}$ at canopy level

To estimate canopy carbon isotope discrimination (Δ_A) in the three stands, we were not able to assess the CO_2 assimilation weighted average leaf $\delta^{13}\text{C}$ of the different species in the canopy (Lloyd and Farquhar 1994). We assumed a proportional relationship between basal area and CO_2 assimilation of the different species and calculated a basal area weighted Δ_A as:

$$\Delta_A = \frac{\delta^{13}\text{C}_{\text{air}} - \frac{\sum_{i=1}^n (\delta^{13}\text{C}_i \text{BA}_i)}{\sum_{i=1}^n \text{BA}_i}}{1000 + \frac{\sum_{i=1}^n (\delta^{13}\text{C}_i \text{BA}_i)}{\sum_{i=1}^n \text{BA}_i}} 1000,$$

where n is the number of species in the stand considered in this study, $\delta^{13}\text{C}_i$ is the average $\delta^{13}\text{C}$ value of species i in the stand, and BA_i is the basal area of species i in the stand. Assuming the assimilation of the understorey trees to be negligible in the canopy assimilation, we only considered trees with $\text{DBH} > 20$ cm for the Δ_A calculation.

Species characteristics

Species were grouped according to their light adaptation features assessed on the basis of growth dynamics observations made in Paracou on established trees, either in the pristine cover or in response to microclimatic changes induced by thinning of various intensities (Favrichon 1994). Within one group, species are characterised by similar growth response patterns to light conditions in

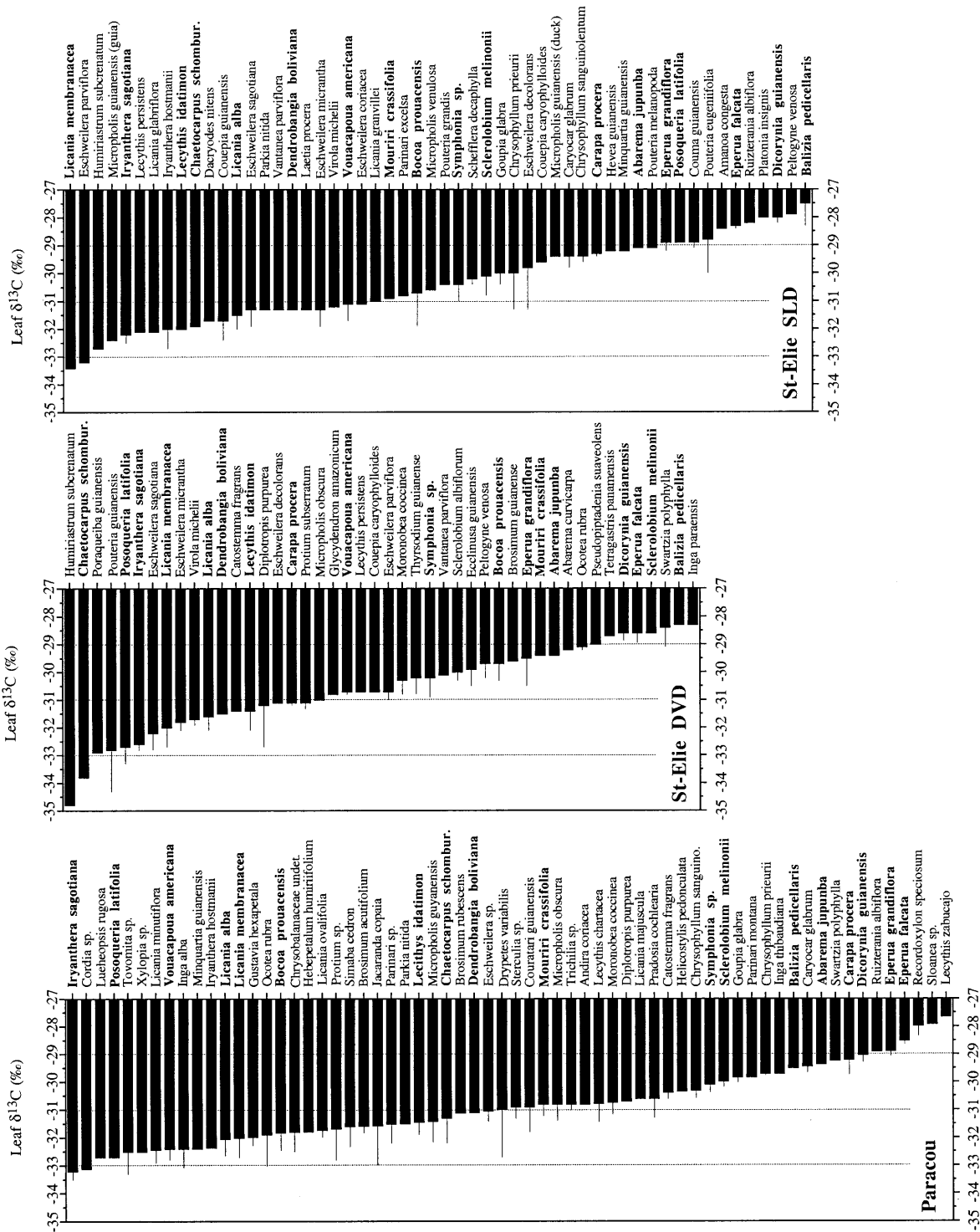


Fig. 1 Carbon isotope composition ($\delta^{13}C$) of fully sunlit leaves of a range of species growing in the three studied stands. The species were ordered according to the $\delta^{13}C$ values (average species values ± 1 SE) observed within each stand. The 18 species common to the 3 stands are indicated in *bold*

the sub-adult and adult stage. More precisely, this classification is based on the following characteristics of trees with DBH > 10 cm: (1) species mean DBH, (2) absolute radial growth rate in the different diameter classes both in control undisturbed plots and in thinned plots in Paracou, (3) mortality, and (4) recruitment (i.e. accession rate to the 10-cm DBH class) in the control and thinned plots. According to these criteria, three groups were distinguished:

1. Species reaching the upper canopy, but able to establish and reproduce under shade, with low growth rates in all DBH classes. These species were interpreted by Favrichon (1994) as shade-tolerant (T) species.
2. Species able to tolerate low light levels for seedling establishment but needing high light levels to reproduce once in the canopy. These species are characterised by high growth rates; they display higher growth rates in the higher DBH classes and were interpreted as hemitolerant (HT) species. Hemitolerance denotes here shade tolerance at the juvenile state and absence of tolerance in mature trees. Many species within this group are potentially emergent (i.e. with tree crowns above the canopy).
3. Species needing openings in the forest to establish and reproduce, with high growth rates and displaying higher growth rates in lower diameter classes, interpreted as heliophilic (H) species.

Species not studied by Favrichon (1994) were classified according to Bena (1960). It must be emphasised that only trees that had access to full sun were considered in this study. Short-lived heliophilic, as well as lower canopy and understory shade-tolerant species, were not included. Species were also grouped according to their pattern of leaf phenology (deciduous-leaved/evergreen-leaved) (Loubry 1994; D. Sabatier, unpublished data) or to their range of distribution in tropical South America (1 Guianas; 2 Guianas+northeastern Amazonia; 3 Guianas+Amazon; 4 Amazon to Panama; 5 Tropical South America) (Flora Neotropica) (Appendix 1).

Statistical analysis

Statistical analyses were performed using SAS/STAT procedures (SAS Institute 1989). Analyses of variance were used to detect any effect of species, shade-tolerance characteristics, area of distribution or leaf phenology characteristics on $\delta^{13}\text{C}$. These analyses were followed by a Duncan test ($P < 0.05$) to compare the mean $\delta^{13}\text{C}$ values among the different groups. A regression was performed to detect any relationship between leaf $\delta^{13}\text{C}$ and tree diameter, leaf nitrogen concentration or midday or predawn leaf water potential. In order to disentangle the intrinsic species effect from the diameter effect on $\delta^{13}\text{C}$, a covariance analysis was performed. Finally, a Pearson's correlation analysis among the stands on leaf $\delta^{13}\text{C}$ values corrected for unique nil diameter obtained from the covariance analysis was performed, in order to compare the ranking of the 18 species which were common to the 3 stands, or the ranking of the 28 species which were common to the 2 stands in St-Elie. These corrected values were calculated only for the purpose of the covariance analysis.

Results

Interspecific differences in leaf $\delta^{13}\text{C}$ and relationships with tree diameter

In each stand, a high interspecific variability in species leaf $\delta^{13}\text{C}$ values was observed ($P < 0.001$) (Appendix 1, Fig. 1). Mean $\delta^{13}\text{C}$ values ranged from -33.2 to -27.6‰ in Paracou, from -34.8 to -28.2‰ in St-Elie DVD and from -33.4 to -27.5‰ in St-Elie SLD, with continuous values between the extremes (Fig. 1). Mean species diameter ranged from 12.4 to 54.0 cm in Paracou, from 14.2 to 97.0 cm in St-Elie DVD and from 10.7 to 105.0 cm in St-Elie SLD (data not shown).

In the three stands, leaf $\delta^{13}\text{C}$ values were positively related to tree diameter ($P < 0.001$), even though the R^2 values were quite low (0.20, 0.23, and 0.20 for Paracou, St-Elie DVD and St-Elie SLD, respectively). The covariance analysis performed to disentangle the intrinsic species effect from the diameter effect on $\delta^{13}\text{C}$ yielded distinct results among the stands (Table 1). In the two St-Elie stands, the variability of $\delta^{13}\text{C}$ was accounted for by the species effect only, whereas in Paracou, both factors affected $\delta^{13}\text{C}$ independently, even though the slope of the $\delta^{13}\text{C}$ versus diameter was low (0.039‰ cm^{-1}). To account for this slight diameter effect in Paracou, estimated Y -axis intercepts were considered for comparing species. These calculated values were related to the measured ones by a close linear relationship ($\delta^{13}\text{C}_{\text{corrected}} = 0.82 \delta^{13}\text{C}_{\text{measured}} - 6.48$; $R^2 = 0.82$, $P < 0.001$), the variation span of the Y -axis intercepts (data not shown) being sim-

Table 1 Degrees of freedom (df), coefficient of correlation (R^2) and significance levels (P -value) from covariance analysis between leaf $\delta^{13}\text{C}$ and tree diameter or species in canopy tree species growing in three natural stands in French Guiana. The two stands in St-Elie differ in soil drainage type: DVD deep vertical drainage; SLD superficial lateral drainage (Sabatier et al. 1997)

Stand	Source of variation	df	R^2	P -value
St-Elie DVD	Diameter	1	0.76	0.55
	Species	45		<0.001
St-Elie SLD	Diameter	1	0.78	0.27
	Species	53		<0.001
Paracou	Diameter	1	0.72	<0.001
	Species	63		<0.001

ilar to that of the measured ones (i.e. 5.6%). In Paracou (no measurements made in St-Elie) species $\delta^{13}\text{C}$ values were significantly correlated with tree height ($R^2 = 0.23$, $P < 0.001$).

The range of species leaf N concentration values was similar in the three stands ($7\text{--}31 \text{ mg g}^{-1}$) (Appendix 1). Within legumes, there was no significant difference in leaf N concentration between N-fixing species and non-fixing species. Mean species leaf $\delta^{13}\text{C}$ values were slightly related to leaf N concentration values in St-Elie DVD stand ($R^2 = 0.22$; $P = 0.03$), whereas no significant relationship was found between these variables in the two other stands (data not shown).

In the three stands, $\delta^{13}\text{C}$ values and tree diameter were significantly different among the three groups of shade tolerance (Table 2). Hemitolerant species displayed less negative leaf $\delta^{13}\text{C}$ values than heliophilic and shade-tolerant species in the three stands. Heliophilic species were characterised by less negative $\delta^{13}\text{C}$ values than shade-tolerant species in Paracou and St-Elie DVD stand, but not in St-Elie SLD stand. Mean tree diameter of tolerant species was similar to that of the heliophilic species and was smaller than that of hemitolerant species (Table 2). The mean diameter differed between heliophilic and hemitolerant species in St-Elie DVD only. Leaf $\delta^{13}\text{C}$ was more negative in evergreen-leaved than in deciduous-leaved species in the three stands (average difference = 1.3‰) (Table 2). There was no significant difference in $\delta^{13}\text{C}$ among the five different geographic groups of species distribution (Table 2). In the three stands, $\delta^{13}\text{C}$ values differed significantly among families ($P = 0.001$).

Ranking of species $\delta^{13}\text{C}$ among stands

Eighteen species were common to the three stands (Appendix 1, Fig. 1). The average species $\delta^{13}\text{C}$ values were significantly correlated among the three stands (Table 3), reflecting a consistent overall ranking of species. Fur-

Table 2 Mean leaf $\delta^{13}\text{C}$ values (± 1 SE) of canopy tree species growing in three natural stands in French Guiana. The two stands in St-Elie differ in soil drainage type: *DVD* deep vertical drainage; *SLD* superficial lateral drainage. Species were grouped according to their tolerance to shade (tolerant, hemitolerant, heliophilic), or to their range of distribution in South America (1 Guianas; 2 Guianas+northeastern Amazon; 3 Guianas+Amazon; 4 Amazon to Panama; 5 Tropical South America), or to their pattern of leaf phenology (deciduous-leaved; evergreen-leaved). Additionally, mean tree DBH (± 1 SE) for each shade-tolerance group in the three stands is represented. For each group and in each stand, an ANOVA was performed to test the group effect on $\delta^{13}\text{C}$ or DBH (*P*-value). For each group and in each stand, mean values not sharing common letters are significantly different (Duncan's Multiple Range test, $P < 0.05$)

	Paracou	St-Elie DVD	St-Elie SLD
Leaf carbon isotope composition ($\delta^{13}\text{C}$)			
Shade tolerance	$P < 0.001$	$P < 0.001$	$P < 0.001$
Tolerant	-31.6 ± 0.1^c	-31.4 ± 0.2^c	-30.9 ± 0.2^b
Hemitolerant	-29.7 ± 0.2^a	-29.3 ± 0.2^a	-29.0 ± 0.2^a
Heliophilic	-30.6 ± 0.3^b	-30.7 ± 0.4^b	-30.3 ± 0.2^b
Area of distribution	$P = 0.12$	$P = 0.12$	$P = 0.49$
1	-31.1 ± 0.2	-30.4 ± 0.3	-30.4 ± 0.4
2	-31.0 ± 0.2	-30.9 ± 0.2	-30.1 ± 0.3
3	-31.4 ± 0.4	-30.4 ± 0.4	-29.7 ± 0.6
4	-30.8 ± 0.4	-29.1 ± 0.7	-30.7 ± 0.4
5	-30.2 ± 0.3	-30.8 ± 0.5	-29.8 ± 0.2
Leaf phenology	$P < 0.001$	$P < 0.001$	$P < 0.001$
Deciduous	-30.3 ± 0.2^a	-29.7 ± 0.2^a	-29.0 ± 0.2^a
Evergreen	-31.2 ± 0.1^b	-31.1 ± 0.2^b	-30.6 ± 0.2^b
Tree diameter			
Shade tolerance	$P < 0.001$	$P < 0.001$	$P < 0.001$
Tolerant	28.1 ± 1.2^b	33.4 ± 1.7^b	34.4 ± 1.8^b
Hemitolerant	36.9 ± 2.4^a	55.7 ± 4.5^a	50.3 ± 4.0^a
Heliophilic	31.6 ± 2.5^{ab}	40.5 ± 6.2^b	43.5 ± 4.6^{ab}

Table 3 Pearson correlation coefficients (*R*) and significance levels (*P*-value) from a correlation analysis performed on the leaf $\delta^{13}\text{C}$ values of 18 species common to 3 natural stands in French Guiana, and on 28 species common to the 2 St-Elie stands. The two stands in St-Elie differ in soil drainage type: *DVD* deep vertical drainage; *SLD* superficial lateral drainage. Correlation analysis was performed on estimated leaf $\delta^{13}\text{C}$ values corresponding to the *Y*-axis intercepts for the diameter effect in the covariance analysis presented in Table 1

	St-Elie DVD	St-Elie SLD	Paracou
18 common species			
St-Elie DVD	<i>R</i> 1.00		
	<i>P</i> -value 0.00		
St-Elie SLD	<i>R</i> 0.63	1.00	
	<i>P</i> -value < 0.01	0.00	
Paracou	<i>R</i> 0.65	0.80	1.00
	<i>P</i> -value < 0.01	< 0.01	0.00
28 common species			
St-Elie DVD	<i>R</i> 1.00		
	<i>P</i> -value 0.00		
St-Elie SLD	<i>R</i> 0.62	1.00	
	<i>P</i> -value < 0.01	0.00	

Furthermore, the species $\delta^{13}\text{C}$ values did not significantly differ among the three stands, except in *Carapa procera* (Appendix 1). Among the nine species that were represented in two stands with at least two trees sampled by stand, only *Chrysophyllum sanguinolentum* displayed $\delta^{13}\text{C}$ values that differed significantly between stands (Appendix 1). There was no overall significant effect of the type of drainage on $\delta^{13}\text{C}$ for the 28 species which were common to the St-Elie DVD and St-Elie SLD stands (Table 3).

Relationships between leaf $\delta^{13}\text{C}$ and leaf water potential

Within each stand, there was a close relationship between the midday leaf water potential (Ψ_{wm}) values observed in the different species in the wet and in the dry seasons ($R^2 = 0.62$ and 0.78 in St-Elie DVD and St-Elie SLD, respectively). There was no significant seasonal effect on Ψ_{wm} . Therefore, we pooled the data from the dry and wet seasons within each species (Fig. 2). Average species Ψ_{wm} ranged from -0.4 to -3.2 MPa in St-Elie DVD and from -0.4 to -2.8 MPa in St-Elie SLD (Fig. 2). There was a close relationship between Ψ_{wm} values measured in the two stands (eight species only). Predawn leaf water potential values ranged from -0.2 to -0.7 MPa for both seasons (data not shown). Extremely high Ψ_{wm} values were found in the three species belonging to the Myristicaceae (Fig. 2, Appendix 1). Additional Ψ_{wm} measurements performed on other Myristicaceae species occurring in French Guiana (*Virola sebifera*, *V. surinamensis*, *Ostepхлоem platyspermum*) yielded values all higher than -0.4 MPa (data not shown).

In both stands, a negative relationship ($P = 0.001$) was found between leaf $\delta^{13}\text{C}$ and Ψ_{wm} , even though the data displayed an important scatter (Fig. 2), mainly due to the distinct position of the hemitolerant and tolerant species in the overall relationship. For those species common to the two stands, the position of the data in the $\delta^{13}\text{C}$ versus Ψ_{wm} relationship was similar. Predawn water potential values (St-Elie DVD) were not related to $\delta^{13}\text{C}$ (data not shown).

$\delta^{13}\text{C}$ distribution and carbon isotope discrimination at canopy level (Δ_A)

The distributions of the frequency of species by $\delta^{13}\text{C}$ classes were roughly monomodal (modal $\delta^{13}\text{C} = -31.0\text{‰}$) (Fig. 3a-c). The distribution of total basal area (all sampled species pooled) by $\delta^{13}\text{C}$ classes in Paracou was also monomodal (modal $\delta^{13}\text{C} = -31.0\text{‰}$). In contrast, the distributions were bimodal in both St-Elie stands (Fig. 3d-f): a first mode corresponded to that of Paracou and a second mode was displayed at -29.0‰ . This second mode, as well as the basal area corresponding to $\delta^{13}\text{C}$ values higher than -30.0‰ in Paracou, was composed mostly of hemitolerant species (Fig. 3d-f), which represent a high basal area with only a small number of species (Appendix 1,

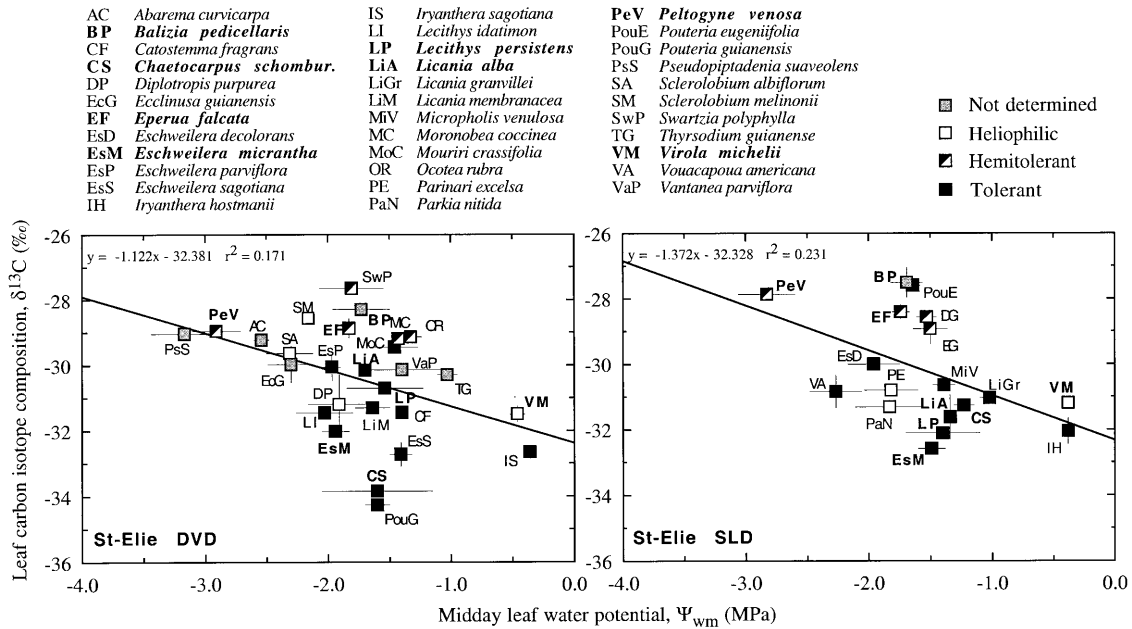


Fig. 2 Relationships between midday leaf water potential (Ψ_{wm}) and sunlit leaf ($\delta^{13}C$) for the season average species values (± 1 SE) in the two St-Elie stands. The regression lines correspond to significant correlation ($P < 0.01$). The types of shade tolerance of the different species (Favrichon 1994) have been represented. The eight species common to the two stands are indicated in *bold*

Fig. 3a-c). The first mode of the basal area distribution was almost entirely constituted by the numerous tolerant species. Heliophilic species represented only a small proportion of the total basal area, despite the large number of species.

The calculated Δ_A values were 23.6, 23.0 and 22.6 ‰ in Paracou, St-Elie DVD and St-Elie SLD, respectively.

Discussion

Interspecific variability in leaf $\delta^{13}C$

We found a high variability of sunlit leaf $\delta^{13}C$ among tropical rainforest canopy tree species. Mean species $\delta^{13}C$ values varied over a ca. 6‰ range within each stand and over a 7.3‰ range (–34.8 to –27.5‰) when pooling the three stands. This variability is higher than the range found in a previous study in French Guiana including only 18 species (4.5‰) (Guehl et al. 1998). Martinelli et al. (1998) assessed the interspecific variability of tree leaves $\delta^{13}C$ in an Amazonian rainforest in Rondônia (Brazil), considering both upper and lower canopy trees. They found an overall range of variability of 7.1‰ for the average species $\delta^{13}C$ values. Considering only upper canopy trees (total height > 25 m), this range was 5.5‰ (from –34.3 to –28.8‰), which is remarkably consistent with our results.

Even though we only sampled mature, sunlit leaves in order to minimise canopy effects (Buchmann et al. 1997; Martinelli et al. 1998), leaf $\delta^{13}C$ was related

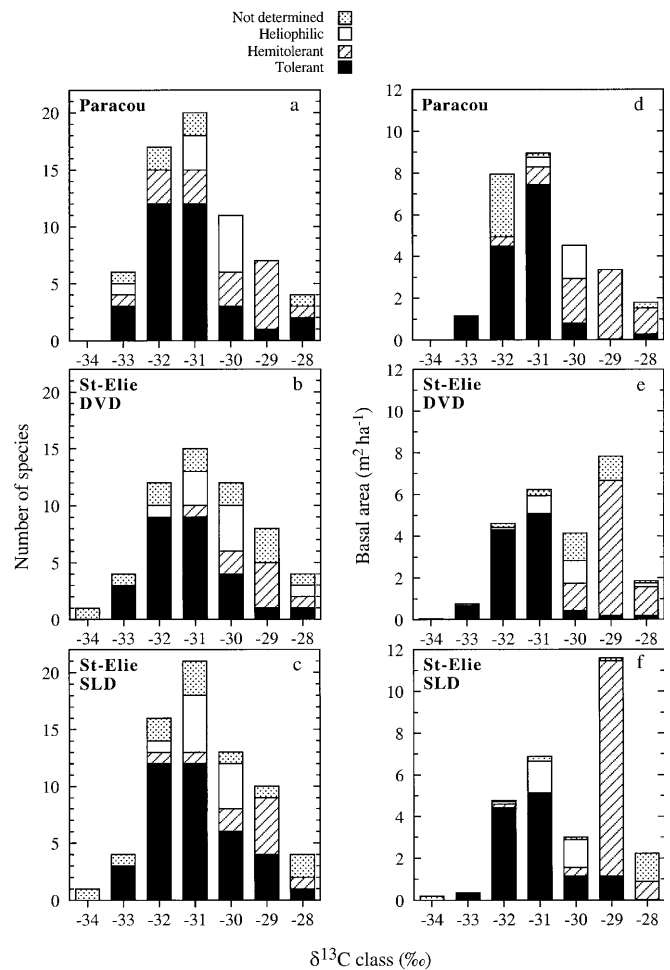


Fig. 3 Frequency distributions of the number of species (a-c) and the corresponding basal area values (d-f) by $\delta^{13}C$ classes. The shade tolerance types of the different species are distinguished according to Favrichon (1994)

to tree diameter (Table 1). In the two St-Elie stands, this relationship was entirely accounted for by the species effect, whereas in Paracou a slight diameter effect was expressed, independently of the species effect (Table 1). This intrinsic diameter effect observed in Paracou, which was also associated with a tree height effect, might reflect a microclimatic effect on leaf gas exchange (C_i/C_a) and thus on leaf $\delta^{13}\text{C}$. Trees of the low-diameter classes were more abundant in Paracou than in the two St-Elie stands. This led us to sample more trees in the 15- to 35-cm-diameter classes in Paracou as compared to St-Elie (Table 2). These trees might be subject to more lateral shading from the surrounding taller trees in the morning and in the afternoon, even though they are fully sunlit at midday. Taking account of this diameter effect resulted in negligible effects on the ranking of the species for the $\delta^{13}\text{C}$ values in Paracou.

Despite differences in topography and soil conditions, and differences in background floristic composition among the three stands, species occurring in at least two stands displayed remarkably stable $\delta^{13}\text{C}$ values (Table 3, Appendix 1). These results suggest a predominant genetic control of species $\delta^{13}\text{C}$ under the similar climatic conditions prevailing in the three stands. The absence of modulation of species $\delta^{13}\text{C}$ by the soil characteristics in St-Elie, together with the fact that stand species composition was affected (Sabatier et al. 1997), suggest that effects of extreme and rare climatic conditions (e.g. severe drought) – rather than average conditions – play a predominant role in community adjustments to soil conditions through differential species mortality and/or recruitment.

Functional grouping of species

Marked differences in species $\delta^{13}\text{C}$ values were found with respect to the different types of shade tolerance (Table 2). However, the ranking of the $\delta^{13}\text{C}$ values for these different types was not consistent with the gradient of shade tolerance. Heliophilic species indeed exhibited more negative $\delta^{13}\text{C}$ values (i.e. lower intrinsic water-use efficiency) than hemitolerant species, which is in agreement with the “gambler” (i.e. resource waster) ecological strategy proposed by Oldeman and van Dijk (1991), leading to the ability of heliophilics to rapidly dominate neighbours. However, tolerant species displayed even more negative $\delta^{13}\text{C}$ values than heliophilic species, confirming our expectations and first results obtained on a reduced set of species in Paracou (Guehl et al. 1998). Clearly, there are two distinct groups among the late-stage species (heliophilic ones excluded) based on the $\delta^{13}\text{C}$ values, in remarkable correspondence with Favrichon’s hemitolerant and tolerant groups (Fig. 3). Tolerant species are able to grow in understory conditions where light is the main limiting factor. It might be suggested that the extremely negative $\delta^{13}\text{C}$ found in this group is associated with high g_s (Bonal et al., in press), allowing maximised carbon assimilation

under low light (Givnish 1988). Low light-saturated A values may also explain the low leaf $\delta^{13}\text{C}$. It is noteworthy that this trait was maintained for trees reaching the upper canopy. The hemitolerant group encompasses most emergent species – and is characterised on average by higher DBH values than the tolerant group (Table 2) – whereas emergent species are not included in the tolerant group (Favrichon 1994). High WUE in the former group may be considered as an adaptive trait to the high evaporative demand prevailing in the emerging tree crowns.

Evergreen-leaved species displayed more negative $\delta^{13}\text{C}$ values than deciduous-leaved ones. Sobrado and Ehleringer (1997) found similar results in a tropical dry forest. Because, in wet tropical conditions, the drought-deciduous type is only one among different deciduous patterns (Loubry 1994), differences in phenology can not yet be clearly interpreted from an ecological or ecophysiological point of view. The association found here between $\delta^{13}\text{C}$ and phenology patterns remains to be elucidated. However, we found to some extent an association between shade-tolerance types and phenology patterns: most hemitolerant species are deciduous (11 out of 17), whereas heliophilic or tolerant species are mainly evergreen (14 out of 18 and 37 out of 53, respectively). Our results clearly point to the absence of association between the gradients in $\delta^{13}\text{C}$ values and the area of distribution of the species. Particularly, there was no peculiar $\delta^{13}\text{C}$ characteristic for those species extending towards the dry tropics.

Interestingly, differences among species in $\delta^{13}\text{C}$, and their shade-tolerance type, were associated with their taxonomic situation, at least for the four main families represented in the study stands: Caesalpiniaceae (average $\delta^{13}\text{C} = -29.5\text{‰}$) mainly encompass hemitolerant species with least negative $\delta^{13}\text{C}$; Chrysobalanaceae (-31.8‰), Euphorbiaceae (-31.4‰) and Lecythidaceae (-31.2‰) mainly encompass shade-tolerant species with low $\delta^{13}\text{C}$. Heliophilic species are included in numerous families which are less represented and displayed mostly intermediate $\delta^{13}\text{C}$.

Ecophysiological interpretation of the interspecific variability in $\delta^{13}\text{C}$

According to the classical two-step model of carbon isotope discrimination during photosynthesis (Farquhar et al. 1982), the range of about 6.0‰ we observed between species would correspond to a difference of 85 $\mu\text{mol mol}^{-1}$ in average C_i and to A/g_s ranging from 28 to 82 $\mu\text{mol mol}^{-1}$.

Leaf N concentrations varied over a fourfold range among species (Appendix 1), highest values being observed in legumes (Caesalpiniaceae, Fabaceae, Mimosaceae), as already found by Roggy et al. (1999). However, neither the ability for symbiotic nitrogen fixation, nor leaf N concentration were clearly related to leaf $\delta^{13}\text{C}$, confirming previous studies made in Paracou (Guehl et al. 1998).

Midday leaf water potential differed markedly among the species with consistency over the two sites (Fig. 2) and the two seasons. One major result of this study consists of the negative relationships found between average species leaf $\delta^{13}\text{C}$ values and Ψ_{wm} (Fig. 2). These results confirm previous observations made on a reduced number of species growing in monospecific plantations near Paracou (Huc et al. 1994; Bonal et al., in press). To our knowledge, such relationships have not been described in other wet tropical forests so far. Ehleringer et al. (1991) found a negative relationship between $\delta^{13}\text{C}$ and Ψ_{wm} among desert species, which they attributed to differences in the access to summer rains. In a tropical dry forest in Venezuela, Sobrado and Ehleringer (1997) found a negative relationship between $\delta^{13}\text{C}$ and Ψ_{wm} , which they attributed to differences in the depth of the rooting system. In our study, Ψ_{wp} values remained high (> -0.7 MPa) in all species, even though soil water depletion occurred in the upper soil layer in the dry season (Guehl 1984; Bonal et al., in press). This might explain the lack of relationship between $\delta^{13}\text{C}$ and Ψ_{wp} . Since there was no pronounced difference in Ψ_{wm} between the dry and the wet season in either stand, the low Ψ_{wm} values found in some species, and the high differences in Ψ_{wm} among species, were not induced by differential species responses to soil drought. Furthermore, Ψ_{wm} values of species growing in St-Elie stands and in a nearby 15-year-old plantation were similar, and in this plantation, the range of Ψ_{wm} values for 21 tropical rainforest canopy tree species was similar to that in the natural forest (-2.8 to -0.3 MPa) (Bonal et al., in press; D. Bonal and J.M. Guehl, unpublished data). Therefore, the observed Ψ_{wm} values can be considered as reflecting intrinsic species characteristics.

A theoretical background to analyse interspecific differences in $\delta^{13}\text{C}$ and in Ψ_{wm} is provided by the study by Panek (1996). According to Panek's equations, the negative relationship we found between $\delta^{13}\text{C}$ and Ψ_{wm} can only be accounted for by a positive relationship between $\delta^{13}\text{C}$ and A/K_L , where K_L denotes the whole tree leaf specific hydraulic conductance (i.e. the whole tree hydraulic conductance divided by the tree leaf area). Indeed, results available from ecophysiological studies performed on seven heliophilic or hemitolerant species in French Guiana differing in leaf $\delta^{13}\text{C}$ values clearly show that low $\delta^{13}\text{C}$ values are associated with high A and very high g_s and calculated K_L (Huc et al. 1994; Bonal et al., in press). For a given range of Ψ_{wm} values, shade-tolerant species clearly displayed lower $\delta^{13}\text{C}$ values than hemitolerant species (Fig. 2). Whether this reflects lower A – or higher K_L – in the former group is still unclear.

Canopy carbon isotope discrimination (Δ_A)

The rainforest in French Guiana is characterised by important geographic gradients in floristic composition due to

soil, climatic and historical factors (Lescure and Boulet 1985; Sabatier and Prévost 1990; Charles-Dominique et al. 1998). We analysed here the effects of such gradients on Δ_A under common climatic conditions by: (1) comparing stands differing in the most represented families, and (2) comparing two stands with different soil water drainage types. Sabatier et al. (1997) have shown that forest communities are affected by the latter factor for the abundance of major species. Despite the large differences in floristic composition among the stands (see basal areas in Appendix 1) and the high interspecific variability in $\delta^{13}\text{C}$, Δ_A values were similar in the three stands. This result is to be associated with the similar distribution of the different shade-tolerance groups, which correspond to distinct $\delta^{13}\text{C}$ values, in the three stands. This shows that in these highly diverse communities, the substitutions among species occur in such a way as to maintain the relative importance of the different $\delta^{13}\text{C}$ -contrasted groups and ultimately to maintain Δ_A almost stable. Whether the stability of Δ_A found here for three stands 30 km apart holds in the more contrasting climatic conditions and floristic gradients encountered at larger scale (Guiana, Amazonia, dry tropical forests) is an important question. Schulze et al. (1998) found a stability of community average carbon isotope discrimination in forests along rainfall gradient in northern Australia. The mechanisms underlying such adjustments and their ecological implications (niche differentiation for the capture of resources, response to perturbations?) remain unknown.

Our calculated Δ_A values (on average 23.1‰) were about 5.0‰ higher than the values estimated by Lloyd and Farquhar (1994) for tropical rainforests inferred from gas exchange data of a reduced number of species. Hemitolerant and tolerant species constitute the predominant groups in the studied stands (Fig. 3). The high Δ_A found in our study can clearly be attributed to the importance of the tolerant group comprising species with extremely negative $\delta^{13}\text{C}$. Direct and careful estimations of Δ_A made in the different types of ecosystems at the surface of the globe will improve the relevance of bottom-up approaches of the global carbon cycle based on the integration of Δ_A values over the different vegetation types (Lloyd and Farquhar 1994). However, Δ_A refers only to the canopy component of the whole ecosystem carbon isotope discrimination and does not incorporate the contribution of plant and soil respiration. The model of ecosystem carbon isotope discrimination (Δ_e) proposed by Buchmann et al. (1997) includes all these components. Buchmann et al. (1997) provided an estimate of 20.4‰ for Δ_e in the Paracou forest. The difference between the two approaches ($\Delta_A - \Delta_e = 2.7$ ‰) shows the necessity of further researches aimed at assessing the factors influencing both estimates, as discussed in detail by Buchmann et al. (1997).

In conclusion, we found an extremely high interspecific variability in sunlit leaf $\delta^{13}\text{C}$ among canopy trees, the range of variations being similar to that found over broad climatic gradients (Schulze et al. 1998) or among distinct life forms within communities (Brooks et al. 1997), in other types of forests. Even though this variability seems

to be at least partly driven by differences in hydraulic features among species, its precise ecophysiological basis, as well as its ecological implications (e.g. niche differentiation for water acquisition) largely remain to be elucidated. We found an interesting association between species $\delta^{13}\text{C}$, a trait related to leaf gas exchange regulation, and features reflecting the plasticity of growth dynamics with respect to contrasting light conditions. To our knowledge, this association constitutes a first validation, for rainforests, of the concept of functional types of species (Grime 1977; Tilman 1988), stating a unique grouping of species with respect to various functional traits. We could provide here a clear confirmation of the existence of two distinct groups within the non-heliophilic late-stage species (Favrichon 1994), as well as elements for the functional

characterisation of these groups. An expression of the association between species $\delta^{13}\text{C}$ and the type of shade tolerance, at the integrated canopy level, consisted in the fact that, despite the differences in species composition, similar proportions of the different shade-tolerance types among stands were accompanied by similar Δ_A values.

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Appendix 1

Shade-tolerance characteristics (*H* heliophilic; *HT* hemitolerant; *T* tolerant) according to Favrichon (1994), leaf phenology pattern (*D* deciduous-leaved; *E* evergreen-leaved) (Loubry 1994; D. Sabatier, personal communication) and area of distribution in tropical South America (*1* Guianas; *2* Guianas+northeastern Amazon; *3* Guianas+Amazon; *4* Amazon to Panama; *5* Tropical South America) (Flora Neotropica) of tree species growing in three stands (Paracou, St-Elie DVD, St-Elie SLD) in the tropical rainforest of

French Guiana. The two stands in St-Elie differ in soil drainage type: *DVD* deep vertical drainage; *SLD* superficial lateral drainage (Sabatier et al. 1997). Species total basal area ($\text{m}^2 \text{ha}^{-1}$) is reported. For each sampled species and in each stand, leaf $\delta^{13}\text{C}$ values (‰) and nitrogen concentration (mg g^{-1}) are reported. Average species values (± 1 SEM) within sites were 0.50‰ for $\delta^{13}\text{C}$ and 1.5 mg g^{-1} for N concentration. For each species, leaf $\delta^{13}\text{C}$ or nitrogen concentrations of species common to at least two stands were compared. The number of trees sampled per species and per stand ranged from 1 to 11 (*F* symbiotic nitrogen fixation; Guehl et al. 1998; Roggy et al. 1999)

FAMILY				Basal area ($\text{m}^2 \text{ha}^{-1}$)			$\delta^{13}\text{C}$ (‰)				Leaf N concentration (mg g^{-1})				
	Species	Shade tolerance	Phenology	Area	Paracou	St-Elie DVD	St-Elie SLD	Paracou	St-Elie DVD	St-Elie SLD	P	Paracou	St-Elie DVD	St-Elie SLD	P
ANACARDIACEAE															
<i>Thyrsodium guianense</i>	–	E	1	–	0.37	–	–	–30.2	–	–	–	12	–	–	–
ANNONACEAE															
<i>Xylopia sp.</i>	H	E	2	0.05	–	–	–32.5	–	–	–	–	14	–	–	–
APOCYNACEAE															
<i>Couma guianensis</i>	T	D	2	0.05	–	0.23	–	–	–28.9	–	–	–	15	–	–
ARALIACEAE															
<i>Schefflera decaphylla</i>	H	E	2	–	0.02	0.28	–	–	–30.2	–	–	–	8	–	–
BIGNONIACEAE															
<i>Jacaranda copaia</i>	H	E	5	0.08	0.10	0.11	–31.6	–	–	–	–	18	–	–	–
BOMBACACEAE															
<i>Catostemma fragrans</i>	T	D	2	0.06	0.04	–	–30.4	–31.4	–	ns	–	12	15	–	*
BORAGINACEAE															
<i>Cordia sp.</i>	–	–	1	0.03	–	0.02	–33.1	–	–	–	–	18	–	–	–
BURSERACEAE															
<i>Dacryodes nitens</i>	–	E	1	–	0.17	0.05	–	–	–31.7	–	–	–	11	–	–
<i>Protium sp.</i>	–	E	–	0.09	0.04	0.01	–31.7	–	–	–	–	11	–	–	–
<i>Protium subserratum</i>	T	E	2	–	0.21	–	–	–31.1	–	–	–	–	13	–	–
<i>Tetragastris panamensis</i>	T	E	4	–	0.18	0.03	–	–28.7	–	–	–	–	10	–	–

Appendix (continued)

FAMILY				Basal area (m ² ha ⁻¹)			δ ¹³ C (‰)				Leaf N concentration (mg g ⁻¹)				
	Species	Shade tolerance	Phenology	Area	Paracou	St-Elie DVD	St-Elie SLD	Paracou	St-Elie DVD	St-Elie SLD	P	Paracou	St-Elie DVD	St-Elie SLD	P
CAESALPINIACEAE															
<i>Bocoa prouacensis</i>	T	E	1	0.33	0.22	0.11	-31.8	-29.7	-30.7	ns	25	20	22	ns	
<i>Dicorynia guianensis</i>	HT	D	2	0.94	0.60	1.16	-29.0	-28.6	-28.0	ns	20	18	21	ns	
<i>Eperua falcata</i>	HT	D	2	0.66	1.50	5.42	-28.5	-28.6	-28.3	ns	16	20	18	*	
<i>E. grandiflora</i>	HT	E	1	1.33	1.46	2.58	-28.9	-29.5	-28.9	ns	12	12	15	ns	
<i>Peltogyne venosa</i>	HT	D	3	-	2.90	0.37	-	-29.7	-27.9	ns	-	16	17	ns	
<i>Recordoxylon 2 venosa</i>	HT	D	1	1.23	-	-	-28.0	-	-	-	20	-	-	-	
<i>Sclerobium albiflorum</i> ^F	H	E	1	-	0.55	-	-	-30.0	-	-	-	29	-	-	
<i>S. melinonii</i> ^F	H	E	-	0.33	0.44	0.21	-30.0	-28.6	-30.1	ns	25	23	31	ns	
<i>Swartzia polyphylla</i> ^F	HT	D	4	0.04	1.39	-	-29.2	-28.4	-	-	27	22	-	-	
<i>Vouacapoua americana</i>	T	D	2	1.66	0.33	0.80	-32.4	-30.7	-31.1	ns	21	21	23	ns	
CARYOCARACEAE															
<i>Caryocar glabrum</i>	HT	D	5	0.52	-	0.12	-29.4	-	-29.4	ns	11	-	20	ns	
CELASTRACEAE															
<i>Goupia glabra</i>	H	E	4	0.50	-	0.62	-29.9	-	-30.0	ns	17	-	14	ns	
CHRYSOBALANACEAE															
<i>Couepia caryophylloides</i>	T	E	-	-	0.20	0.05	-	-30.7	-29.6	-	-	17	15	-	
<i>C. guianensis</i>	HT	E	-	-	-	0.17	-	-	-31.7	-	-	-	13	-	
<i>Licania alba</i>	T	E	1	0.40	0.79	1.24	-32.1	-31.6	-31.5	ns	12(1)	7(2)	11	ns	
<i>L. glabriflora</i>	T	-	4	-	-	0.09	-	-	-32.1	-	-	-	14	-	
<i>L. granvillei</i>	T	E	4	-	-	0.14	-	-	-31.0	-	-	-	6	-	
<i>L. membranacea</i>	T	E	3	0.38	0.30	0.01	-32.0	-32.0	-33.4	ns	11	17	13	*	
<i>L. ovalifolia</i>	T	E	1	0.16	-	0.01	-31.8	-	-	-	11	-	-	-	
<i>Licania sp. 1</i>	T	-	2	0.25	-	-	-30.6	-	-	-	12	-	-	-	
<i>Licania sp. 2</i>	T	-	2	0.42	-	-	-32.5	-	-	-	12	-	-	-	
<i>Parinari excelsa</i>	H	E	3	-	-	0.57	-	-	-30.8	-	-	-	12	-	
<i>P. montana</i>	H	E	5	0.23	-	-	-29.8	-	-	-	15	-	-	-	
<i>Parinari sp.</i>	H	E	5	0.25	-	-	-31.5	-	-	-	14	-	-	-	
<i>Undetermined</i>	-	-	-	3.31	-	-	-31.8	-	-	-	12	-	-	-	
CLUSIACEAE															
<i>Moronobea coccinea</i>	HT	D	1	0.29	0.84	-	-30.8	-30.3	-	ns	12	14	-	ns	
<i>Platonia insignis</i>	HT	D	2	-	-	0.87	-	-	-28.0	-	-	-	10	-	
<i>Symphonia sp.</i>	HT	E	5	0.96	0.47	0.28	-30.1	-30.2	-30.4	ns	14	15	15	ns	
<i>Tovomita sp.</i>	T	E	-	0.52	0.04	0.01	-32.5	-	-	-	16	-	-	-	
ELAEOCARPACEAE															
<i>Sloanea sp.</i>	T	D	-	0.05	0.18	0.01	-27.9	-	-	-	28	-	-	-	
EUPHORBIACEAE															
<i>Amanoa congesta</i>	-	E	2	-	-	0.49	-	-	-28.4	-	-	-	11	-	
<i>Chaetocarpus schomburg.</i>	T	E	1	0.73	0.02	0.27	-31.3	-33.8	-31.9	ns	10	11	9	*	
<i>Drypetes variabilis</i>	T	E	2	0.12	-	0.02	-31.0	-	-	-	26	-	-	-	
<i>Glycydendron amazoni.</i>	-	D	2	-	0.05	0.03	-	-30.8	-	-	-	21	-	-	
<i>Hevea guianensis</i>	T	D	2	-	-	0.03	-	-	-29.2	-	-	-	23	-	

Appendix (continued)

FAMILY				Basal area (m ² ha ⁻¹)			δ ¹³ C (‰)				Leaf N concentration (mg g ⁻¹)				
	Species	Shade tolerance	Phenology	Area	Paracou	St-Elie DVD	St-Elie SLD	Paracou	St-Elie DVD	St-Elie SLD	P	Paracou	St-Elie DVD	St-Elie SLD	P
FABACEAE															
<i>Andira coriacea</i> ^F	HT	D	1	0.03	–	–	–30.8	–	–	–	–	18	–	–	–
<i>Diplostropis purpurea</i> ^F	H	E	2	0.15	0.03	–	–30.7	–31.2	–	ns	–	19	20	–	ns
FLACOURTIACEAE															
<i>Laetia procera</i>	H	E	4	–	–	0.27	–	–	–31.3	–	–	–	–	19	–
HUGONIACEAE															
<i>Hebepetalum humiriifoli.</i>	T	E	2	0.03	0.15	0.02	–31.8	–	–	–	–	17	–	–	–
HUMIRIACEAE															
<i>Humiriastrum subcrenat.</i>	–	E	–	–	0.03	0.20	–	–34.8	–32.7	–	–	–	9	10	–
<i>Vantanea parviflora</i>	–	E	–	–	0.23	0.10	–	–30.1	–31.3	–	–	–	10	9	–
ICACINACEAE															
<i>Dendrobanxia boliviana</i>	T	E	–	0.08	0.04	0.07	–31.1	–31.5	–31.3	–	–	16	13	15	–
<i>Poraqueiba guianensis</i>	–	E	–	–	0.08	–	–	–32.9	–	–	–	–	11	–	–
LAURACEAE															
<i>Ocotea rubra</i>	HT	E	2	0.22	0.01	–	–31.9	–29.1	–	ns	–	14	18	–	ns
LECYTHIDACEAE															
<i>Couratari guianensis</i>	T	D	4	0.13	–	–	–30.9	–	–	–	–	19	–	–	–
<i>Eschweilera coriacea</i>	T	E	4	–	–	0.04	–	–	–31.1	–	–	–	–	20	–
<i>E. decolorans</i>	T	E	3	–	0.06	0.37	–	–31.1	–29.8	ns	–	–	21	22	ns
<i>E. micrantha</i>	T	E	2	–	2.34	1.02	–	–31.8	–31.3	ns	–	–	22	17	*
<i>E. parviflora</i>	T	E	1	–	1.78	0.02	–	–30.7	–33.2	ns	–	–	20	18	ns
<i>E. sagotiana</i>	T	E	2	–	0.10	0.87	–	–32.2	–31.3	–	–	–	15	15	–
<i>Eschweilera sp.</i>	T	E	–	2.17	–	–	–31.0	–	–	–	–	–	–	–	–
<i>Gustavia hexapetala</i>	T	E	3	0.25	0.02	0.01	–32.0	–	–	–	–	21	–	–	–
<i>Lecythis c hartacea</i>	T	–	2	0.47	–	–	–30.8	–	–	–	–	23	–	–	–
<i>L. zabucajo</i>	T	D	2	0.23	–	–	–27.7	–	–	–	–	15	–	–	–
<i>L. idatimon</i>	T	D	2	1.77	1.87	1.97	–31.5	–31.4	–32.0	ns	–	18	15	13	ns
<i>L. persistens</i>	T	E	2	–	0.25	1.19	–	–30.7	–32.1	–	–	–	17	14	–
MELASTOMATAACEAE															
<i>Mouriri crassifolia</i>	T	E	2	0.65	0.16	0.25	–30.9	–29.4	–30.9	ns	–	13	10	4	ns
MELIACEAE															
<i>Carapa procera</i>	H	E	5	0.47	0.07	0.22	–29.2	–31.1	–29.3	*	–	14	15	14	ns
<i>Trichilia sp.</i>	–	E	–	0.12	–	–	–30.8	–	–	–	–	17	–	–	–
MIMOSACEAE															
<i>Abarema curvicarpa</i>	–	D	–	–	0.34	–	–	–29.2	–	–	–	–	24	–	–
<i>A. jupunba</i> ^F	–	D	5	0.23	0.06	0.13	–29.4	–29.4	–29.1	–	–	18	20	19	–
<i>Balizia pedicellaris</i> ^F	–	D	–	0.28	0.11	0.86	–29.5	–28.3	–27.5	ns	–	23	24	18	ns
<i>Inga alba</i> ^F	H	D	3	0.13	–	–	–32.4	–	–	–	–	21	–	–	–
<i>I. paraensis</i> ^F	H	–	–	–	0.18	–	–	–28.3	–	–	–	–	29	–	–
<i>I. thibaudiana</i> ^F	H	S	3	0.08	–	–	–29.7	–	–	–	–	23	–	–	–
<i>Parkia nitida</i>	H	D	4	0.12	0.01	0.28	–31.5	–	–31.3	–	–	18	–	20	–
<i>Pseudopiptadenia suaveol.</i>	–	D	–	–	0.77	–	–	–29.0	–	–	–	–	30	–	–

Appendix (continued)

FAMILY	Species	Shade tolerance	Phenology	Area	Basal area (m ² ha ⁻¹)			δ ¹³ C (‰)				Leaf N concentration (mg g ⁻¹)			
					Paracou	St-Elie DVD	St-Elie SLD	Paracou	St-Elie DVD	St-Elie SLD	P	Paracou	St-Elie DVD	St-Elie SLD	P
MORACEAE															
	<i>Brosimum acutifolium</i>	T	D	2	0.19	–	–	–31.6	–	–	–	18	–	–	–
	<i>B. guianense</i>	T	E	5	–	0.13	0.01	–	–29.6	–	–	–	11	–	–
	<i>B. rubescens</i>	T	E	5	0.12	–	0.05	–31.1	–	–	–	12	–	–	–
	<i>Helicostylis pedunculata</i>	T	E	–	0.07	0.05	–	–30.3	–	–	–	14	–	–	–
MYRISTICACEAE															
	<i>Iryanthera hostmanii</i>	T	E	2	0.09	–	0.03	–32.4	–	–32.0	ns	20	–	15	*
	<i>I. sagotiana</i>	T	E	2	0.39	0.37	0.30	–33.2	–32.6	–32.2	ns	16	12	14	ns
	<i>Virola michelii</i>	H	E	2	–	0.83	0.36	–	–31.7	–31.2	ns	–	20	12	ns
OLACACEAE															
	<i>Minuartia guianensis</i>	–	E	5	0.75	–	0.08	–32.4	–	–29.2	–	18	–	22	–
RUBIACEAE															
	<i>Posoqueria latifolia</i>	T	E	–	0.05	0.25	0.04	–32.7	–32.7	–28.9	ns	12	12	12	ns
SAPOTACEAE															
	<i>Chrysophyllum prieurii</i>	T	D	5	0.16	–	0.15	–29.7	–	–30.0	ns	19	–	19	ns
	<i>C. sanguino.</i>	T	E	3	0.57	–	0.38	–30.3	–	–29.4	*	12	–	11	ns
	<i>Ecclinusa guianensis</i>	–	–	3	–	0.96	0.13	–	–29.9	–	–	–	14	–	–
	<i>Micropholis guianensis</i>	T	E	4	0.08	–	0.26	–31.4	–	–29.4	ns	14	–	16	ns
	<i>M. guianensis</i> ^b	T	E	4	–	–	0.52	–	–	–32.4	–	–	–	15	–
	<i>M. obscura</i>	T	E	4	0.58	0.48	–	–30.8	–31.0	–	ns	13	13	–	ns
	<i>M. venulosa</i>	T	E	5	–	–	0.43	–	–	–30.6	–	–	–	14	–
	<i>Pouteria eugeniifolia</i>	T	E	3	–	–	0.86	–	–	–28.8	–	–	–	8	–
	<i>P. grandis</i>	T	E	1	–	–	0.18	–	–	–30.4	–	–	–	13	–
	<i>P. guianensis</i>	T	E	5	–	0.26	–	–	–32.8	–	–	–	15	–	–
	<i>P. melanopoda</i>	HT	E	1	–	–	0.08	–	–	–29.1	–	–	–	21	–
	<i>Pradosia cochlearia</i>	T	D	2	1.03	–	–	–30.6	–	–	–	14	–	–	–
SIMAROUBACEAE															
	<i>Simaba cedron</i>	T	E	–	0.14	–	–	–31.6	–	–	–	21	–	–	–
STERCULIACEAE															
	<i>Sterculia sp.</i>	H	–	2	0.21	–	0.04	–30.8	–	–	–	15	–	–	–
TILIACEAE															
	<i>Lueheopsis rugosa</i>	HT	D	1	0.03	–	–	–32.7	–	–	–	15	–	–	–
VOCHYSIACEAE															
	<i>Ruizterania albiflora</i>	HT	D	2	0.11	–	0.80	–28.9	–	–28.2	–	14	–	14	–

*P<0.05; ns not significant

^a Subsp. *duckeana*^b Subsp. *guianensis*

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