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Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondônia, Brazil

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Abstract Leaves of 208 trees were collected for isotopic analysis together with wood from 36 tree boles and 18 samples of fine litter from a *terra-firme* forest located at Samuel Ecological Reserve, Rondônia State, in the southwestern Amazon region. The range of $\delta^{13}C$ values in leaves was from −28 to −36‰, with an average (±1 SD) of −32.1 ± 1.5‰, which was more negative than the $\delta^{13}C$ values of bole samples (−28.4 ± 2.0‰) and fine litter (−28.7 ± 2.0‰). These values are within the range found for tropical and subtropical forests. Pooling the $\delta^{13}C$ values for leaf samples from trees of the same height gave averages which were positively correlated with plant height at a highly significant level, with a slope of 0.06 and an intercept of −33.3‰ and a correlation coefficient $r^2 = 0.70$ ($P < 0.001$).

Key words Amazon · Vegetation · Forest · Stable carbon isotope · Rondônia

Introduction

The abundance of stable carbon isotopes in plants of the C_3 group is controlled by environmental variables, such as the concentration of atmospheric CO_2 (ca) and its isotopic composition and by physiological factors, such as the CO_2 concentration inside the leaf intercellular space (ci), which in turn can be affected by environmental factors, such as light and water availability (Farquhar et al. 1982).

Tropical forest environments provide conditions promoting large variability in the carbon isotope composition of plant tissues, for several reasons: (1) a high number of plant species increasing the chances that genetic variability will affect carbon isotope composition, (2) strong variability in both CO_2 concentration and its isotopic composition due to the dilution of atmospheric CO_2 by isotopically depleted biogenic respired CO_2 (Sternberg et al. 1989; Grace et al. 1995; Buchmann et al. 1996; Lloyd et al. 1996), and (3) a gradient in light penetration inside the forest canopy (Ehleringer et al. 1986). With less light available for photosynthesis, the ratio of stomatal conductance to photosynthesis increases and the ci/ca ratio therefore, also rises (Farquhar et al. 1989). The isotopic fractionation resulting from limitation of light will produce plant organic matter depleted in ^{13}C and this effect is indistinguishable from the isotopic effect produced by the contribution of biogenic CO_2 for photosynthesis. As a consequence of the last two factors, the "canopy effect" is observed, where leaves become progressively isotopically depleted towards the forest floor (Medina and Minchin 1980; Schleser and Jayasekera 1985; Medina et al. 1986; van der Merwe and Medina 1989; Sternberg et al. 1989; Kapos et al. 1993; Kruijt et al. 1996).

Most of the studies on variability in stable carbon isotopes in tropical forest plants are limited to a few number of samples collected at several heights in order to establish a gradient between leaf height and stable carbon isotope composition. As tropical forests are very diverse systems in terms of biodiversity (number of tree species) and environmental conditions (e.g., light penetration), we decided to explore in more detail the stable carbon isotope composition variability in a patch of undisturbed tropical forest. The opportunity for such

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study came when EletroNorte (the electric company for the north region of Brazil) supported a 2-week field campaign in 1-ha transects of *terra-firme* located in the Samuel Ecological Reserve. The objectives of this campaign were to estimate biomass, characterize nutrient cycling in the site (Brown et al. 1995) and, as already mentioned, examine the stable carbon isotope composition of the vegetation. In this study, we determined the variability in stable carbon isotopes in 208 tree leaves, 57 tree boles, and 18 litter samples found in 1 ha of *terra-firme* forest at Samuel Ecological Reserve.

This extensive database offers the opportunity to explore several aspects of the carbon stable isotope composition of tropical plants.

Materials and methods

The study was conducted in an area of 20,000 ha within the Ecological Reserve of Samuel (8°45′ S, 63°23′ W), bordering the Samuel Hydroelectric Reservoir. The dominant upland forest type in the reserve is tropical moist forest (classification of Holdridge et al. 1971). In the RADAMBRASIL classification, the major forest type for this region at the 1:1,000,000 scale is open forest (*floresta aberta*) with the presence of palms and lianas (Departamento Nacional de Produção Mineral, Brazil 1978). Sampling was conducted in three subtransects, two (subtransects 1 and 2) with an area of 3,000 m^2 (10 m by 300 m) and the remainder (subtransect 3) 4,000 m^2 (10 m by 400 m), making a total of 1 ha study area. A total of 474 trees with a diameter at 1.35 m greater than 10 cm were mapped. These individuals belonged to approximately 220 species classified in 41 botanical families. From this total, leaves of 208 trees from approximately 100 species were collected for isotopic analysis. Several leaves from branches collected for botanical classification were sampled and formed a unique sample. Only leaves with a healthy aspect were collected, avoiding yellow to brownish leaves. Leaves were collected approximately in the middle and only on one side of the crown. During the field campaign, we measured two heights for trees: a total height that corresponds to the top of the crown and one that corresponds to approximately the middle of the crown. These latter heights are listed in Appendix 1 and 2 and were those used to correlate with leaf $\delta^{13}C$ values. We are aware that the ideal situation would have been to collect leaves from more than one height within the crown and from more than one side. However, we had just one climber, who, in 10 days, climbed and sampled 474 trees. Considering the logistic difficulties faced in a tropical forest, more accurate sampling would be virtually impossible during 2 weeks. It is appropriate to remember that Bassow and Bazzaz (1997) pointed out that sampling foliage from the top of trees in natural forests poses many logistical problems, and they concluded that such difficulties have been the main cause of small sample sizes in terms of number of trees in canopy research. Working within these restrictions, we selected 57 trees for bole samples among 474 trees. These trees were selected in order to encompass a broad range of height and diameter. Samples of wood from bole were taken using a tree auger. To avoid damaging the tree, the hole made with the auger was closed and the region was covered with a fungicide. The 1-ha transect was subdivided into 40 parcels of 250 m^2 each. From this total, we randomly choose 18 parcels where we sampled fine litter. In each parcel we collected litter inside a square of 1-m^2 that was placed in five positions in each parcel: in its four corners and in the center. These five subsamples were combined into one sample representative of that parcel. For more details about the study area and transect sampling refer to Brown et al. (1995).

Samples were combusted for 12 h with CuO in evacuated tubes at 550°C. Isotope measurements were performed with a Finnigan Delta-E mass spectrometer fitted with double-inlet and double-collector systems. Results are expressed in $\delta^{13}C$ relative to a PDB standard, defined as:

$$\delta^{13}C = (R_{\mathrm{sample}}/R_{\mathrm{std}}) - 1 * 1,000$$

where R_{sample} and R_{std} are the ratio ^{13}C:^{12}C of the sample and standard, respectively. Samples were analyzed at least in duplicate with a maximum difference of 0.2‰ between replicates.

The average values are followed by ±1 SD and by the number of samples used to compose that average. For differences among leaves, bole, and litter, we used the *t*-test for unequal variance with the STATISTICA package. For differences among families, we used ANCOVA blocking for height, also using the STATISTICA package.

Results and discussion

The $\delta^{13}C$ values of tree leaf samples at Samuel are shown in Appendix 1. The average $\delta^{13}C$ of leaves was −32.1 ± 1.5‰ ($n = 208$), which is significantly more negative ($P < 0.001$) than bole samples, with an average of −28.4 ± 1.8‰ ($n = 57$) and fine litter, averaging −28.7 ± 2.0‰ ($n = 18$). The box-whisker plot of $\delta^{13}C$ values for leaves, boles, and fine litter can be seen in Fig. 1. The range of values for leaves was from −36 to −28‰, which is within the range found for tropical and subtropical forests (Table 1). With the exception of one very negative value (−34.2‰), the $\delta^{13}C$ values in bole samples varied from −31.6 to −25.4‰, and in fine litter samples from −32.0 to −24.1‰ (Fig. 1). The heavier isotopic values found in boles in comparison to leaves is a common feature in plants, both from tropical systems (Medina et al. 1986, 1991) and from temperate regions (Francey et al. 1985; Leavitt and Long 1986). From the 57 trees sampled for wood, 33 also provided leaf $\delta^{13}C$ values. Comparing $\delta^{13}C$ values of leaves and wood samples from these trees, for only one tree was the isotope value for wood lighter than in the leaves. In this case, the bole was 0.85‰ lighter than the leaves. Excluding this exception, the smallest isotope enrichment observed between leaves and wood was 1.2‰ and the

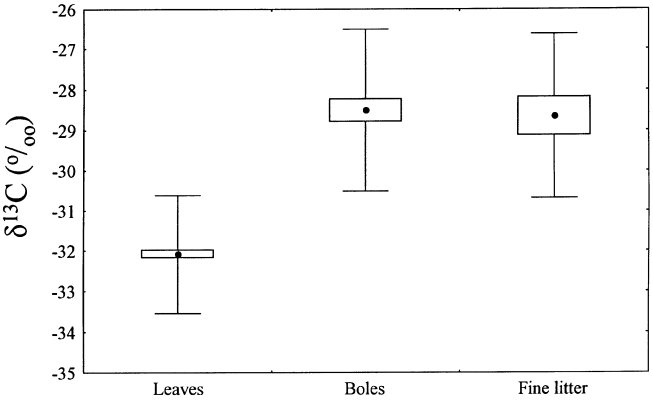

Fig. 1 Box-whisker plots of $\delta^{13}C$ values for leaves, boles, and fine litter. The *full circle* indicates the average values, *boxes* are the SEs of the average values, and *bars* represent 1 SD

Table 1 Average $\delta^{13}C$ (‰) values of tree leaves in distinct sites and types of forest

Site	Forest type	$\delta^{13}C$ (‰)	Reference
Rondônia (Brazil)	*Terra-firme*	−32.1	This study
S.C. do Rio Negro (Venezuela)	*Terra-firme*	−32.1	Media and Minchin (1980)
Amazon river (Brazil)	Várzea	−32.1	Martinelli et al. (1994)
Paracou (French Guiana)	*Terra-firme*	−32.1	Buchmann et al. (1997a)
Manaus (Brazil)	*Terra-firme*	−31.6	Ducatti et al. (1991)
Luquillo (Puerto Rico)	Tabonuco	−31.6	Medina et al. (1991)
Ding Hu Shan (China)	Monsoon	−31.1	Ehleringer et al. (1987)
Pantanal (Brazil)	Arboreal savanna	−30.9	Victoria et al. (1995)
Manaus (Brazil)	*Terra-firme*	−30.8	Kapos et al. (1993)
Luquillo (Puerto Rico)	Tabonuco	−30.7	Fischer and Tieszen (1995)
Luquillo (Puerto Rico)	Colorado	−30.5	Fischer and Tieszen (1995)
Hokaiddo (Japan)[a]	Broad-leaved trees	−29.5	Hanba et al. (1997)
Jülich (Germany)[a]	*Fagus sylvatica*	−29.0	Schleser (1992)
Utah (USA)[a]	*Pinus contorta* and *P. tremuloides*	−27.3	Buchmann et al. (1997b)
Prince and Thompson Albert (Canada)[a]	*P. mariana, P. banksina, P. tremuloides*	−26.9	Flanagan et al. (1996)

[a] Temperate sites

largest almost 9‰. The average enrichment was 4.2 ± 2.4‰ ($n = 33$).

There are two major explanations for isotopic differences between bole and leaf organic matter. Leavitt and Long (1986) hypothesized that respiratory effects cause this difference, suggesting that respiration releases isotopically light carbon. Thus, the remaining pool available for biomass production in the bole becomes isotopically heavier. Francey et al. (1985) hypothesized that the relative timing of carbohydrate export causes this difference between leaves and boles. Apart from differences among wood and leaf samples, $\delta^{13}C$ values of bole samples showed 6‰ variation. This variation may be caused in part by the so-called "canopy effect." In other words, the $\delta^{13}C$ value of wood samples would be related to tree height. Pooling the $\delta^{13}C$ values for wood samples of the same tree height gave averages which were positively correlated with plant height at a highly significant level, with a slope of 0.09 and an intercept of −30.5‰, and a correlation coefficient $r^2 = 91\%$ ($P < 0.001$). This correlation between tree height and $\delta^{13}C$ of wood implies that this tissues can also be used to test the "canopy effect" (Fig. 2). Since it is easier to sample wood than leaves in tropical forests, this may facilitate future sampling in forests. In contrast, Schleser (1992) did not find a significant correlation between wood and height in a 140-year-old *Fagus sylvatica* forest near Jülich, Germany. Schleser (1992) hypothesized that the CO_2 fixed by the leaves of the lower branches, which have lighter $\delta^{13}C$ values, does not supply a significant amount of carbon to the corresponding twigs and branches. Accordingly, the bole will receive carbon from the upper part of the tree, which has heavier $\delta^{13}C$ values. These heavier values would prevail all along the bole. The good correlation between $\delta^{13}C$ values of the wood in the boles and tree height in our samples, however, suggests that the same is not occurring in Samuel tropical forest. If future results confirm such a difference between tropical and temperate forests, this may indicate that different mechanisms of carbon transfer are operating in tropical and temperate trees.

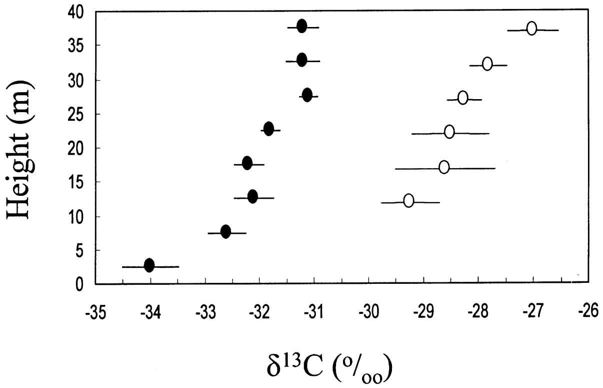

Fig. 2 Relationship between tree height classes and average $\delta^{13}C$ of leaves (●) and wood (○) from boles. Bars represent 1 SD

In general, the negative $\delta^{13}C$ values observed for tree leaves in part characterize an open system regarding the balance of stomatal conductance to photosynthesis (Farquhar et al. 1982). These negative values are determined by the higher ratios of stomatal conductance to photosynthesis, leading to high ci/ca ratios, that in turn lead to a higher fractionation in relation to the atmospheric CO_2 and consequently lower $\delta^{13}C$ values in relation to temperate systems (Table 1).

Some variability was observed among leaves of individuals of the same species collected at approximately the same height and near to each other. For instance, leaves of *Protium robustum* (tree numbers 424 and 444) differed by almost 3‰. A similar difference was also found for *Tachigalia paniculata* (tree numbers 305 and 314) and for *Pseudomedia laevis* (tree numbers 331 and 396). Such inter- and intra-species variation has been found elsewhere. Berry et al. (1997) found a variation of 4‰ among understory plants species in a *Pinus resinosa* plantation located south of Ottawa, Canada. They attributed such variability mainly to differences in CO_2 assimilation and conductance rates among the four species. Walcroft et al. (1996) found that the gas exchange of *Pinus radiata* foliage was affected by branch morphology. They found a variation of 3.8‰ between short and long *P. radiata* branches collected in New Zealand.

It is difficult to pinpoint causes for such variability since forest canopies are heterogeneous environments with regard to the light exposure of different leaves and, consequently, photosynthetic characteristics within the canopy (Lloyd et al. 1996; Bassow and Bazzaz 1997; Berry et al. 1997). Intra-specific differences caused by structural and compositional differences between leaves (Schleser and Jayasekera 1985; Hubick et al. 1986; Broadmeadow and Giffiths 1993), leaf age, and position in the crown (Gebauer and Schulze 1991) may play a role. The latter exposes leaves to different microclimates, and key environmental parameters like leaf-to-air vapor pressure (Farquhar et al. 1989) and light intensity (Ehleringer et al. 1986, 1987; Pearcy and Pfitsch 1991). The mutual effects of all these variables will determine the photosynthetic rate of a specific leaf which in turn will affect ci/ca that, together with the isotope ratio of source CO_2 is a dominant factor affecting variation in isotopic discrimination by C_3 plants (Hubick et al. 1988; Hanba et al. 1997).

Comparisons within species or even within genera were not possible with this dataset because tropical rain forests are characterized by high species diversity, with few individuals of the same species within a particular area. This makes statistical comparisons difficult, even for cases where there are enough individuals of the same species, since they tend to differ in height, precluding direct comparisons. However, there are a number of samples encompassing a broad range of heights within families. This is especially the case for four families: Burseraceae, Casealpinaceae, Lecythidaceae, and Moraceae. The average $\delta^{13}C$ of these families varies from −31.4 to −32.0‰, without any statistical difference among them, tested by ANCOVA blocking for height.

Pooling the $\delta^{13}C$ values for leaf samples of the same height gave averages which were positively correlated with plant height at a highly significant level, with a slope of 0.06 and an intercept of −33.3‰ and a correlation coefficient $r^2 = 70\%$ ($P < 0.001$). Previous studies did not have a sufficient sample number to permit the use of regressions, or to evaluate the variability in the data (Medina and Minchin 1980; Schleser and Jayasekera 1985; Medina et al. 1986; van der Merwe and Medina 1989; Sternberg et al. 1989; Kapos et al. 1993). Kruijt et al. (1996), also working in Rondonia State, at Reserva Jaru, also found a good correlation between $\delta^{13}C$ of leaves and height above the forest floor. They found a broader range of variation in $\delta^{13}C$ values with height than we found in Samuel. The most depleted average value in Samuel was −34.0‰, whereas in the Reserve Jaru, $\delta^{13}C$ values varied from −35.0 to −38.0‰ for the understory foliage. In Samuel, the most enriched average value was −31.0‰, while in Reserva Jaru, a $\delta^{13}C$ value of −29‰ was found at 30 m height.

Given that light penetration appears to be not only a function of height but also of forest structure, we found it useful to try to find a better relationship between leaf isotopic values and forest structure. Lieberman et al. (1989) noted that the simple dichotomy of forest structure into forest and gaps could be too simplistic. Indeed, the forest at any given geographic site in Samuel was once a gap sometime in the past few hundred years. Consequently, the forest can be considered a mosaic of tree patches recovering from gap disturbance. From this perspective, the light regime and relative contribution of CO_2 from the atmosphere overhead and from respiration on the ground is not only a function of the leaf height on a given tree but also of the distribution of trees around that tree. To estimate the effect of the surrounding taller trees on the local environment of sample trees, we used Lieberman et al.'s (1989) suggestion of calculating the sine of the vertical angles between surrounding taller trees and the sample tree. These sine values were then summed for taller trees in a 10-m radius of the sample to derive a G value for each tree sampled. Due to the narrow nature of the transect (10 m), these sample circles covered only between 50 and 61% of the transect; as a result, shading by taller trees outside the transect is not incorporated. Emergent trees have a G value of 0, while small trees often have G values above 10 (Table 2). The working hypothesis is that for trees of the same height, those with higher G values will have more negative $\delta^{13}C$ because the surrounding taller trees will impede penetration of overlying atmospheric air and the light intensity will be lower. This working hypothesis is based on the fact that Broadmeadow and Griffiths (1993) have shown that the stratification of CO_2 within the canopy is dependent on canopy formation, while more recently, Buchmann et al. (1996) have shown that stratification of

Table 2 Average $\delta^{13}C$ of leaves (‰) and average G values composed by tree height classes (m)

Height class	Aveage $\delta^{13}C$	Avearge G
3–5	−34.00	7.32
5–7	−32.48	5.33
7–9	−32.87	6.03
9–11	−32.14	4.41
11–13	−32.31	3.85
13–15	−31.94	4.16
15–17	−32.49	2.18
17–19	−31.99	2.23
19–21	−32.05	1.28
21–23	−31.86	1.28
23–25	−31.64	1.30
25–30	−31.13	0.57
30–40	−31.21	0.49

CO_2 within the canopy is also dependent on the stand structure and on the vegetation type.

Multiple linear regression with data from Table 2, using $\delta^{13}C$ values against height and G values yields $r^2 = 76\%$ ($P < 0.001$), which was not significantly higher than the r^2 found before. Therefore, G values do not help to explain the variability observed within the canopy. A variety of other mechanisms previously listed must also be playing a role in the variability of $\delta^{13}C$ values in tree leaves. But, more important, the "canopy effect" prevailed over a large number of different tree species, indicating that the $\delta^{13}C$ values of atmospheric CO_2 and light penetration within the forest canopy are the driving forces of the $\delta^{13}C$ values of tree leaves within forests.

In the introduction we listed three factors that can promote variability in $\delta^{13}C$ values in tropical forests. Bassow and Bazzaz (1997) have demonstrated that photosynthesis can vary among species and even within an individual tree in temperate forests. If this is also true for tropical forests, the high number of individuals per hectare and the high number of species would promote a highly variable environment in terms of photosynthesis, which in turn will affect the $\delta^{13}C$ values of the vegetation. In addition to variation in photosynthesis itself, it has been shown that the light gradient within the canopy and even among understory plants can be responsible for much of the variation in the $\delta^{13}C$ of tree leaves (Berry et al. 1997). This can help explain differences in $\delta^{13}C$ values of leaves collected at the same height. Both of these factors (photosynthesis and light) would affect the ci/ca ratio, which with the recycling of isotopically depleted CO_2 of biogenic origin is responsible for the $\delta^{13}C$ of the vegetation. The relative importance of these two attributes is still being debated (e.g., Lloyd et al. 1996; Sternberg 1997). Broadmeadow and Griffiths (1993) summarized the proportion of respiratory flux reassimilated by the understory vegetation from the literature – values varied from 8 to 26%.

An important feature found here was the good correlation between wood samples and tree height. Considering that canopy sampling is not trivial (Bassow and Bazzaz 1997), this fact may facilitate future research in this area.

Appendix 1 Tree height (m) and $\delta^{13}C$ values (‰) of leaves for species collected at Samuel Ecological Reserve, Rondônia

Tree	Species	Family	Height (m)	Leaf $\delta^{13}C$(‰)
1	*Parkia* cf. *nitida* Miq.	Leg-mimosaceae	12.0	−32.8
3	*Pouteria* sp.	Sapotaceae	17.5	−34.2
7	*Duroia macrophylla* Huber	Rubiaceae	9.0	−31.7
10	*Richardella* sp.	Sapotaceae	21.0	−31.5
11	*Maquira guianensis* Aubl.	Moraceae	12.5	−33.1
12	*Bauhinia forticata* Link	Leg-Caesalpiniaceae		−34.1
13	*Parkia* cf. *nitida* Miq.	Leg-Mimosaceae	24.0	−32.1
14	*Oxandra xylopoides* Diels	Annonaceae	22.7	−32.9
15	*Licania latifolia* Bth.	Chrysobalanaceae	13.5	−33.6
16	*Euterpe precatoria* Mart.	Palmae	14.0	−33.7
17	*Brosimum guianensis* (Aubl.) Huber	Moraceae	16.5	−32.0
18	*Pithecellobium racemosa* Ducke	Leg-Mimosaceae	16.5	−29.5
19	*Naucleopsis imitans* (Ducke) C.C. Berg	Moraceae	16.5	−32.4
26	*Eschweilera coriacea* (A.P.DC.) Mart. ex erg.	Lecythidaceae	10.7	−29.7
30	*Copaifera multijuga* Hayne	Leg-Caesalpiniaceae	33.3	−28.8
31	*Endopleura uchi* (Huber) Cuatr.	Humiriaceae	14.4	−31.4
33	*Copaifera* sp.	Leg-Caesalpiniaceae	28.3	−30.1
35	*Dodecastigma intergrifolium* (Lanj.) Lanj. & Sandw.	Euphorbiaceae	9.4	−32.0
37	*Dialium guianense* (Aubl.) Sandwith	Leg-Caesalpiniaceae	7.1	−32.9
39	*Rheedia* sp.	Guttiferae	10.1	−33.7
40	*Mouriri* sp.	Melastomataceae	11.1	−29.3
43	*Naucleopsis glabra* sp. *ruce*	Moraceae	15.3	−29.9
46	*Eschweilera* sp.	Lecythidaceae	18.2	−31.9
51	*Pseudomedia laevis* (R. & P.) Macbr.	Moraceae	23.6	−30.4
53	*Heliocostylis tomentosa* (P. & E.) Rusby	Moraceae	29.3	−28.8
58	*Protium* cf. *carnosum* A.C. Smith	Burseraceae	14.5	−32.3
61	*Tymatococcus amazonicus* P. & E.	Moraceae	15.8	−32.3
65	*Theobroma subincanum* Mart.	Sterculiaceae	18.0	−32.9
68	*Tymatococcus amazonicus* P. & E.	Moraceae	22.4	−31.9
76	*Pseuldomedia* sp.	Moraceae	19.9	−31.8
77	Undetermined	Myrtaceae	10.5	−32.7
82	*Bocageopsis multiflora* (Mart.) R.E. Fries	Annonaceae	24.8	−33.3
83	*Theobroma subincanum* Mart.	Sterculiaceae	3.5	−34.1
86	*Apeiba echinata* Gaertn.	Tiliaceae	14.8	−32.5
87	*Bocageopsis multiflora*	Annonaceae	22.3	−31.8
96	*Peltogyne* cf. *heterophylla* M.F. da Silva	Leg-Caesalpiniaceae	10.9	−31.6
98	*Tourouli guianensis* Aubl.	Quiinaceae	15.9	−31.6
104	*Peltogyne* cf. *heterophylla* M.F. da Silva	Leg-Caesalpiniaceae	28.1	−32.2
109	*Naucleopsis imitans* (Ducke) C.C. Berg	Moraceae	21.0	−33.2

Appendix 1 (contd.)

Tree	Species	Family	Height (m)	Leaf δ^{13}C(‰)
110	Undetermined	Moraceae	15.5	−32.0
111	*Minquartia guianensis* Aubl.	Olacaceae		−33.5
113	*Maquira calophylla* (P. & E.) C.C. Berg	Moraceae	21.0	−31.2
116	*Rauwola paraensis* Ducke	Apocynaceae	17.8	−28.6
117	*Brosimum guianensis* (Aubl.) Huber	Moraceae	11.3	−33.8
120	Undetermined	Icacinaceae	14.7	−31.6
125	*Naucleopsis imitans* (Ducke) C.C. Berg	Moraceae	16.4	−32.6
129	*Peltogyne prancei* M.F. da Silva	Leg-Caesalpiniaceae	15.9	−31.3
131	*Andira parviflora* Ducke	Leg-Papilionaceae	12.7	−33.1
133	*Cecropia* sp.	Moraceae	23.3	−34.5
135	*Coepia guianensis* Aubl.	Chrysobalanaceae	22.5	−33.1
143	*Amaioua corymbosa* H.B.K.	Rubiaceae	6.0	−31.4
151	*Eschweilera* sp.	Lecythidaceae	17.5	−32.2
152	*Micropholis* sp.	Sapotaceae	8.8	−31.7
157	*Sapotaceae* sp.	Sapotaceae	21.0	−32.5
161	*Eschweilera* sp.	Lecythidaceae	11.0	−31.4
169	*Brosimum mollis*	Moraceae	8.9	−31.6
171	*Grisma densiflora* sp. *ruce* ex Warm	Vochysiaceae	22.5	−30.2
179	*Pithecellobium cauliflorum* (illd) Bth	Leg-Mimosaceae	5.0	−34.5
180	*Malouetia tamaquirana*	Apocynaceae	19.0	−33.6
182	Undetermined	Apocynaceae	19.6	−34.1
186	*Lecythidaceae* sp.	Lecythidaceae	16.5	−31.6
189	*Heisteria* sp. *ruceana* Engl.	Olacaceae	14.1	−31.9
190	*Iryanthera* sp.	Myristicaceae	9.0	−32.3
196	*Licania micrantha* Miq.	Myrtaceae	16.5	−33.7
200	Undetermined	Chrysobalanaceae	10.5	−32.8
202	Undetermined	Palmae	15.9	−35.9
206	*Cordia ucayliensis* Johnston	Boraginaceae	19.1	−30.0
214	*Guarea pubescens*	Meliaceae	7.5	−32.1
218	*Protium opacum* Swart	Burseraceae	24.0	−31.9
221	*Amphirrox* cf. *latifolia* Mart.	Violaceae	17.1	−31.7
222	*Crepidosp. ermum* cf. *goudotiana* (Tul.) Tr. & Pl.	Burseraceae	15.0	−33.7
233	*Couratari* sp.	Lecythidaceae	33.5	−30.2
235	Undetermined	Moraceae	28.5	−30.1
237	*Cariniana decandra* Ducke	Lecythidaceae	34.0	−29.8
240	*Licania lata* Macbrid	Chrysobalanaceae	4.5	−33.5
243	*Leonia* cf. *crassa* Smith.	Violaceae	23.5	−32.5
244	*Pseudomedia laevis* (R. & P.) Macbr.	Moraceae	25.5	−31.0
250	*Inga* cf. *capitata* Willd	Leg-Mimosaceae	12.7	−32.9
254	*Tachigalia paniculata* Aubl.	Leg-Caesalpiniaceae	20.4	−31.9
255	*Quararibea muricata* Cuatr.	Bombacaceae	12.1	−33.3
256	*Lindackeria paludosa* Bth. ex Eichl.	Flacourtiaceae	12.7	−32.0
260	Undetermined	Lauraceae	18.3	−33.7
265	*Payparola* cf. *guianensis* Aubl.	Violaceae	15.5	−33.6
267	*Manilkara longiciliata* Ducke	Sapotaceae	13.4	−32.6
270	*Bombacopsis* cf. *nervosa* (Vitt.) A. Robyns	Bombacaceae	23.3	−28.0
271	*Micropholis* cf. *venuloso* (Mart. Eichl.) Pierre	Sapotaceae	11.7	−32.0
275	*Calophyllum* sp.	Guttiferae	12.0	−33.4
277	*Protium* cf. *krukofii* Swart	Burseraceae	22.3	−33.2
279	*Clarisa racemosa* R. et P.	Moraceae	26.2	−30.6
280	*Sterculia excelsa* Mart.	Sterculiaceae	12.2	−29.9
285	*Tavomita* sp.	Guttiferae	18.0	−31.0
286	Undetermined	Burseraceae	18.0	−32.3
294	*Metrodorea flavida rause*	Rutaceae	16.5	−33.2
299	*Diosp. yros subrolata* Hiern.	Ebenaceae	14.0	−31.5
300	*Hevea* cf. *brasiliensis* Muell. Arg.	Euphorbiaceae	18.8	−28.9
305	*Tachigalia paniculata* Aubl.	Leg-Caesalpiniaceae	24.0	−32.3
309	*Cordia ucayliensis* Johnston	Boraginaceae	12.0	−34.3
311	Undetermined	Hippocrateaceae	7.0	−33.3
312	*Astronium fraxinifolium* Schott	Anacardiaceae	9.0	−33.8
313	*Dacryoides* cf. *sclerophylla* Cuatr.	Burseraceae	18.3	−32.8
314	*Tachigalia paniculata* Aubl.	Leg-Caesalpiniaceae	20.5	−29.9
315	*Heliocostylis tomentosa* (P. & E.) Rusby	Moraceae	32.6	−30.4
317	*Inga* cf. *alba* Willd	Leg-Mimosaceae	14.1	−31.1
318	*Castiloa ulei* Warb	Moraceae	13.5	−28.3
321	Undetermined	Lauraceae	23.7	−32.1
322	*Eschweilera* sp.	Lecythidaceae	17.7	−33.1
324	*Socratea* cf. *exorrhiz* a (Mart.) Barb. Rodr.	Palmae	7.0	−32.0
327	Undetermined	Nyctaginaceae	16.5	−34.8

Appendix 1 (contd.)

Tree	Species	Family	Height (m)	Leaf $\delta^{13}C$(‰)
328	*Neea* sp.	Nyctaginaceae	16.5	−31.2
331	*Pseudomedia laevis* (R. & P.) Macbr.	Moraceae	16.9	−34.2
333	Undetermined	Lecythidaceae	9.2	−31.9
334	Undetermined	Leg-undetermined	15.0	−32.5
337	*Guatteria* sp.	Annonaceae	12.0	−31.8
338	*Trattinickia* sp.	Burseraceae	25.5	−31.7
339	*Protium* cf. *robustum* (Swart) Porter	Burseraceae	11.9	−32.9
342	*Amphirrox* cf. *latifolia* Mart.	Violaceae	8.0	−32.6
343	*Sorocea guillemiana* Guaud	Moraceae	15.9	−31.5
344	*Heliocostylis tomentosa* (P. & E.) Rusby	Moraceae	28.4	−28.8
345	*Pseudomedia laevis* (R. & P.) Macbr.	Moraceae	12.0	−31.1
346	*Eschweilera coriacea* (A.P.DC.) Mart. ex erg.	Lecythidaceae	15.5	−30.5
347	*Anacardium giganteum* Hanc. ex Engl.	Anacardiaceae	10.0	−32.5
348	*Euterpe precatoria* Mart.	Palmae		−29.5
349	*Eschweilera chartacea* Berg.	Lecythidaceae	10.0	−29.9
350	*Naucleopsis glabra* sp. *ruce*	Moraceae	11.0	−30.7
352	Undetermined	Lauraceae	18.0	−32.7
355	*Pseudomedia laevis* (R. & P.) Macbr.	Moraceae	33.0	−30.5
356	*Leonia* cf. *crassa* Smith.	Violaceae	20.8	−32.3
358	*Maquira calophylla* (P. & E.) C.C. Berg	Moraceae	12.7	−32.0
359	*Licania macrophylla* Bth.	Chrysobalanaceae	28.4	−33.2
362	*Crepidosp. ermum* cf. *goudotiana* (Tul.) Tr. & Pl.	Burseraceae	11.0	−32.1
363	*Grisma bicolor* Ducke	Vochysiaceae	14.0	−29.6
365	Undetermined	Burseraceae	15.1	−31.0
366	*Naucleospsis* sp.	Moraceae	21.1	−30.4
368	*Xylopia nitida* Dun.	Annonaceae	17.9	−32.5
374	*Tachigalia paniculata* Aubl.	Leg-Caesalpiniaceae	18.8	−29.6
375	*Asp. idosp. erma* sp.	Apocynaceae	11.0	−31.3
376	*Clarisa racemosa* R. et P.	Moraceae	14.0	−32.7
377	*Leonia* cf. *crassa* Smith.	Violaceae	14.1	−33.6
378	*Maquira guianensis* Aubl.	Moraceae	25.5	−30.9
379	*Brosimum guianensis* (Aubl.) Huber	Moraceae	24.6	−30.3
380	Undetermined	Hippocrateaceae	21.0	−34.1
385	*Guarea pubescens*	Meliaceae	8.0	−34.9
386	Undetermined	Lauraceae	18.8	−33.0
387	Undetermined	Sapotaceae	16.9	−34.9
388	*Tachigalia paniculata* Aubl.	Leg-Caesalpiniaceae		−32.0
390	Undetermined	Burseraceae	16.5	−32.4
391	*Sizigiopsis* sp.	Sapotaceae	41.3	−31.1
392	*Minquartia guianensis* Aubl.	Olacaceae	13.5	−31.0
393	*Tachigalia* sp.	Leg-Caesalpiniaceae	25.0	−31.7
394	*Tachigalia* sp.	Leg-Caesalpiniaceae	42.4	−30.7
395	*Neea* sp.	Nyctaginaceae	11.0	−34.8
396	*Pseudomedia laevis* (R. & P.) Macbr.	Moraceae	15.0	−31.0
399	*Compsoneura ulei* Warb.	Myristicaceae	11.9	−32.7
400	*Eschweilera coriacea* (A.P. DC.) Mart. ex erg.	Lecythidaceae	30.5	−34.3
401	Undetermined	Myrtaceae	15.3	−33.9
403	*Sloanea* cf. *rufa* Planch. ex Benth.	Euphorbiaceae	6.0	−34.3
404	*Neea* cf. *altissima* R. & E.	Nyctaginaceae	26.2	−31.8
406	*Protium* sp.	Burseraceae	30.9	−31.5
407	*Rheedia* sp.	Guttiferae	15.0	−33.5
408	*Symphonia globulifera* L.	Guttiferae	12.0	−32.9
410	*Protium* cf. *paniculatum* Engl. var *paniculatum*	Burseraceae	34.4	−31.4
411	*Pithecellobium racemosa* Ducke	Leg-Mimosaceae	12.8	−31.6
414	*Tetragastris* cf. *altissima* (Aubl.) Swart	Burseraceae	22.3	−32.2
415	*Tachigalia* sp.	Leg-Caesalpiniaceae	15.0	−32.1
416	*Eschweilera* sp.	Lecythidaceae	25.1	−32.3
418	*Protium* cf. *neglectum* Swart var. *robustum* Swart	Burseraceae	13.2	−31.0
419	*Tachigalia* sp.	Leg-Caesalpiniaceae	5.0	−32.8
420	*Virola pavonis* (A.D.C.) A.C. Smith	Myristicaceae	16.5	−33.5
421	*Guatteria* cf. *poeppigiana* Mart.	Annonaceae	22.3	−31.6
423	*Naucleopsis* sp.	Moraceae	18.9	−30.1
424	*Protium* cf. *robustum* (Swart) Porter	Burseraceae	17.1	−30.6
425	Undetermined	Leg-undetermined	26.5	−31.8
426	Undetermined	Leg-undetermined	26.5	−31.9
427	*Protium* cf. *paniculatum* Engl. var *paniculatum*	Burseraceae	12.0	−31.2
428	*Astrocaryum murumuru* Mart.	Palmae	4.0	−35.1
429	*Protium* cf. *aracouchini* (Aubl.) March	Burseraceae	16.5	−33.3
432	*Tachigalia* sp.	Leg-Caesalpiniaceae	23.1	−32.9

Appendix 1 (contd.)

Tree	Species	Family	Height (m)	Leaf δ^{13}C(‰)
433	*Sclerolobium* cf. *crysophyllum* P. & E.	Burseraceae	15.0	−32.2
434	*Maquira sclerophylla* (Ducke) Berg	Moraceae	14.0	−30.7
436	*Protium* cf. *paniculatum* Engl. var *paniculatum*	Burseraceae	17.6	−30.5
437	*Protium* sp.	Burseraceae	17.6	−31.5
438	*Virola pavonis* (A.D.C.) A.C. Smith	Myristicaceae	34.5	−32.8
439	Undetermined	Lauraceae	10.0	−33.8
441	*Tachigalia* sp.	Leg-Caesalpiniaceae	34.5	−31.0
442	*Eschweilera* sp.	Lecythidaceae	21.3	−31.3
443	*Protium opacum* Swart	Burseraceae	17.1	−32.9
444	*Protium* cf. *robustum* (Swart) Porter	Burseraceae	17.1	−33.4
446	*Metrodorea flavida rause*	Rutaceae	8.0	−32.6
447	*Metrodorea flavida rause*	Rutaceae	16.5	−32.0
450	*Neea* sp.	Nyctaginaceae	7.0	−31.4
451	*Protium* cf. *robustum* (Swart) Porter	Burseraceae	10.0	−31.7
454	*Cordia* sp. *rucei* Meaz.	Boraginaceae	8.0	−33.4
458	*Metrodorea flavida rause*	Rutaceae	8.0	−32.5
459	*Pseudomedia laevis* (R. & P.) Macbr.	Moraceae	8.0	−32.7
461	*Guatteria* cf. *poeppigiana* Mart.	Annonaceae	34.5	−32.6
462	*Ocotea* sp.	Lauraceae	40.7	−31.9
463	*Protium* cf. *robustum* (Swart) Porter	Burseraceae	13.7	−29.6
464	*Pithecellobium jupunba* (Willd) Urb.	Leg-Mimosaceae	24.6	−30.2
465	*Maquira sclerophylla* (Ducke) Berg	Moraceae	25.0	−30.8
466	*Neea* sp.	Nyctaginaceae	13.5	−34.7
467	Undetermined	Nonimiaceae	9.0	−34.1
471	*Licaria* sp.	Lauraceae	17.2	−34.1
473	*Minquartia guianensis* Aubl.	Olacaceae	25.1	−31.7
474	*Theobroma subincanum* Mart.	Sterculiaceae	18.0	−32.2
475	Undetermined	Moraceae	18.0	−31.8
476	Undetermined	Burseraceae	11.0	−33.8
477	*Bocageopsis* sp.	Annonaceae	9.0	−34.1
481	*Tachigalia* sp.	Leg-Caesalpiniaceae	18.0	−32.0

Appendix 2 Tree height (m) and δ^{13}C values (‰) of wood samples from boles for species collected at Samuel Ecological Reserve, Rondônia

Tree	Species	Height (m)	Wood δ^{13}C(‰)
1	*Parkia* cf. *nitida* Miq.	12.00	−29.1
2	Undetermined	17.50	−29.1
3	*Pouteria* sp.	17.50	−29.9
7	*Duroia macrophylla* Huber	9.00	−29.7
10	*Richardella* sp.	21.00	−29.9
11	*Maquira guianensis* Aubl.	12.50	−29.3
13	*Parkia* cf. *nitida* Miq.	24.00	−29.4
14	*Oxandra xylopoides* Diels	22.70	−30.3
15	*Licania latifolia* Bth.	13.50	−28.0
16	*Euterpe precatoria* Mart.	14.00	−31.2
17	*Brosimum guianensis* (Aubl.) Huber	16.50	−29.9
18	*Pithecellobium racemosa* Ducke	16.50	−28.3
19	*Naucleopsis imitans* (Ducke) C.C. Berg	16.50	−28.2
51	*Pseudomedia laevis* (R. & P.) Machbr.	23.60	−27.3
68	*Tymatococcus amazonicus* P. & E.	22.40	−26.5
82	*Bocageopsis multiflora* (Mart.) R.E. Fries	24.80	−25.5
109	*Naucleopsis imitans* (Ducke) C.C. Berg	21.00	−27.8
116	*Rauwolia paraensis* Ducke	17.80	−25.6
151	*Eschweilera* sp.	17.50	−29.0
193	*Eschweilera chartacea* Berg.	22.90	−28.9
202	Undetermined	15.90	−27.8
203	Undetermined	10.50	−31.0
204	Undetermined	18.75	−34.2
211	*Minquartia guianensis* Aubl.	14.30	−28.9
212	*Protium* sp.	29.00	−26.7
216	*Swartzia* cf. *ingiaefolia* Ducke	32.00	−26.0
218	*Protium opacum* Swart	24.00	−29.6
226	Undetermined	27.90	−29.0

Appendix 2 (contd.)

Tree	Species	Height (m)	Wood $\delta^{13}C$(‰)
228	*Apeiba echinata* Gaertn.	26.00	−31.5
233	*Couratari* sp.	33.50	−26.1
238	*Martiodendrum* sp.	39.60	−26.1
241	*Bagassa guianensis* Aubl.	31.50	−27.5
258	*Protium* cf. *robustum* (Swart) Porter	28.80	−25.8
268	*Protium* cf. *tenvifolium* (Engler) Engler	14.10	−27.0
270	*Bombacopsis* cf. *nervosa* (Vitt.) A. Robyns	23.30	−28.9
282	Undetermined	52.80	−26.4
286	Undetermined	18.00	−25.5
301	Undetermined	23.99	−30.6
303	*Pseudomedia laevis* (R. & P.) Macbr.	22.00	−27.4
310	*Anacardium giganteum* Hanc. ex Engl.	22.26	−26.8
315	*Heliocostylis tomentosa* (P. & E.) Rusby	32.60	−28.0
319	Undetermined	21.27	−30.0
354	*Brosimum guianensis* (Aubl.) Huber	43.50	−29.8
365	Undetermined	15.10	−27.8
372	*Swartzia* cf. *ingiaefolia* Ducke	18.80	−31.6
382	*Bertholletia excelsa* Humb. Bonpl.	46.58	−26.6
391	*Sizigiopsis* sp.	41.30	−26.3
400	*Eschweilera coriacea* (A.P.DC.) Mart. ex erg.	30.50	−29.6
409	Undetermined	49.50	−25.4
416	*Eschweilera* sp.	25.10	−28.9
421	*Guatteria* cf. *Poeppigiana* Mart.	22.30	−29.5
430	Undetermined	19.50	−25.7
438	*Virola pavonis* (A.D.C.) A.C. Smith	34.50	−29.5
445	*Apuleia molaris* Bth.	46.26	−27.7
461	*Guatteria* cf. *poeppigiana* Mart.	34.50	−28.4
475	Undetermined	18.00	−28.3
478	*Pseudomedia laevis* (R. & P.) Macbr.	28.67	−28.0

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