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Authors
Sanaiotti, TM
Martinelli, LA
Victoria, RL
et al.

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Past Vegetation Changes in Amazon Savannas Determined Using Carbon Isotopes of Soil Organic Matter[1]

T. M. Sanaiotti
Departamento de Ecologia, Instituto Nacional de Pesquisas da Amazônia, Manaus 69000-000, AM, Brazil

L. A. Martinelli[2], **R. L. Victoria**
Centro de Energia Nuclear na Agricultura, Av. Centenário 303, Piracicaba, 13416-000, SP, Brazil

S. E. Trumbore
Department of Earth System Science, University of California, Irvine, California 92697-3100, U.S.A.

and

P. B. Camargo
Centro de Energia Nuclear na Agricultura, Av. Centenário 303, Piracicaba, 13416-000, SP, Brazil

ABSTRACT

We investigated the variation of stable ($\delta^{13}C$) soil carbon isotopes in relation to depth in seven of the most important savanna areas to adjacent contiguous forests in the Amazon region. The $\delta^{13}C$ of bulk organic matter in all profiles from forested sites increased with soil depth. In forest profiles from Amapá, Alter do Chão, and Roraima, the enrichment was less than 3.5‰ between deeper soil and surface layers, suggesting that C_3 plants have remained the dominant vegetation cover. On the other hand, in forest soil profiles from Humaitá and Carolina sites, the $\delta^{13}C$ enrichment was greater than 3.5‰, indicating the influence of past C_4 vegetation or a mixture of C_3/C_4 vegetation (woody savanna). The surface $\delta^{13}C$ values in the savanna profiles were 5–13‰ greater than the comparable forest profiles, indicating the influence of C_4 vegetation. Two kinds of isotopic distribution were observed in deeper layers. The savanna profiles at Alter do Chão, Chapada dos Parecis, and Redenção had relatively constant $\delta^{13}C$ values throughout the profile, suggesting minor past changes in the vegetation composition. In profiles at Amapá, Roraima, Humaitá, and Carolina, $\delta^{13}C$ values decreased with depth from the surface and converged with comparable forest values, suggesting more woody savanna in the past than exists currently.

RESUMO

Nós investigamos neste estudo a variação em profundidade dos isótopos estáveis de carbono ($\delta^{13}C$) da matéria orgânica do solo (SOM) em sete áreas de savanas e florestas da região Amazônica. Os valores de $\delta^{13}C$ da SOM aumentaram com a profundidade do solo. Nos perfis em floresta do Amapá, Alter do Chão e Roraima o enriquecimento isotópico com a profundidade foi menor que 3,5‰, sugerindo que plantas do tipo C_3 foram sempre o tipo de vegetação dominante. Por outro lado, nos perfis em floresta de Humaitá e Carolina, o enriquecimento isotópico foi maior que 3,5‰, indicando a influência no passado de uma vegetação do tipo C_4, ou uma mistura de vegetação C_3/C_4 (savana lenhosa). Os valores de $\delta^{13}C$ na superfície do solo em savanas foram cerca de 5 a 13‰ maiores que os perfis em floresta, evidenciando a influência da vegetação C_4. Dois tipos de distribuição isotópica foram observados em camadas mais profundas. Nas savanas de Alter do Chão, Chapada dos Parecis e Redenção os valores $\delta^{13}C$ foram constantes ao longo do perfil do solo, sugerindo que não houveram mudanças significativas na vegetação. Nos perfis do Amapá, Roraima, Humaitá e Carolina, os valores de $\delta^{13}C$ diminuiram com a profundidade do solo, aproximando-se aos valores encontrados na floresta, sugerindo a existência no passado de uma savana mais lenhosa que a actual.

Key words: *Amazon; Brazil; carbon isotope; radiocarbon; savanna; tropical forest; vegetation change.*

THE AMAZON REGION IS OFTEN VIEWED AS A CONTINUOUS STAND of rain forest, but it contains patches of savanna vegetation. According to their geographical location, Amazonian savannas may be classified as either isolated or non-isolated. Isolated savannas are surrounded by rain forest, while non-isolated savannas are those located at the forest periphery. Non-isolated savannas include the northern border of the central Brazilian savannas, the Cerrado, which is the most extensive example of this vegetation type (Sarmiento 1984). Because of its importance as the second most extensive vegetation type in Amazonia, the origin of savannas has been debated for many years (Ducke & Black 1953, Egler 1960, Andrade-Lima 1966, Eiten 1972,

[1] Received 5 June 2000; revision accepted 17 July 2001.
[2] Corresponding author; e-mail: zebu@cena.usp.br

Brown & Ab'Saber 1979, Rizzini 1979, Irion 1982, Prance 1982, Kubitzki 1983, Sarmiento 1984, Bigarella and Ferreira 1985, Cole 1986, Sanaiotti 1996).

Several lines of evidence, including paleolimnological (van der Hammen 1972, Absy & van der Hammen 1976, van der Hammen 1983, Absy *et al.* 1991), paleofaunal (Rancy 1993), and the carbon isotopic composition of soil organic matter (Desjardins *et al.* 1996, Pessenda *et al.* 1996, Gouveia *et al.* 1997), suggest that the dynamics of expansion and contraction of savanna regions result from climatic fluctuations during the Quaternary period (Prance 1982, Sarmiento & Monasterio 1975). Several authors have pointed out that there were drier periods during the Pleistocene and the Holocene periods, when tropical forests were replaced by savanna-like vegetation having a predominance of grasses (van der Hammen 1974, Absy & van der Hammen 1976, Ab'Saber 1977, Absy 1980, Bigarella & Andrade-Lima 1982, Leyden 1985, Markgraf 1989, Bush and Colinvaux 1990, Bush *et al.* 1990, Absy *et al.* 1991, Markgraf 1991). The middle Holocene, from *ca* 6000 to 4000 years B.P., was identified as one of such drier periods in several places of South America, including the Amazon region (Absy 1980; Markgraf 1989; Servant *et al.* 1989; Absy *et al.* 1991; Ledru 1992, 1993; Servant *et al.* 1993). The presence of charcoal dated from *ca* 3900 to 1800 years B.P. found in the northern Amazon (Desjardins *et al.* 1996) suggests the occurrence of more recent climatic changes in that region as well as in other regions of Amazonia (Servant *et al.* 1993).

There are seven major savanna areas in the Amazon region; in two of them (Roraima and Rondônia), the past vegetation dynamics were investigated by using the carbon stable isotopic composition of soil organic matter (Desjardins *et al.* 1996, Gouveia *et al.* 1997, Pessenda, Gomes *et al.* 1998, Pessenda *et al.* 1998a). In both places, major vegetation changes occurred in the past; these studies inferred that savanna areas replaced forested areas of the early Holocene period during the middle Holocene.

In this study, we investigated whether or not similar vegetation changes occurred in other major savanna areas of the Amazon. We compared soil carbon isotopic composition and its variation with depth in seven of the most important savanna areas with nearby contiguous forests in the Amazon region. Since the main control of the $\delta^{13}C$ in soil organic matter is plant litter inputs, and C_3 plants (the dominant plants in forests) and C_4 plants (the dominant plants in the savannas) are isotopically distinct, it is possible to detect shifts in tropical forest zones to grassland (or vice versa) from the $\delta^{13}C$ signature of organic matter in soils (Desjardins *et al.* 1996, Martinelli *et al.* 1996, Neill *et al.* 1996, Bird & Pousai 1997).

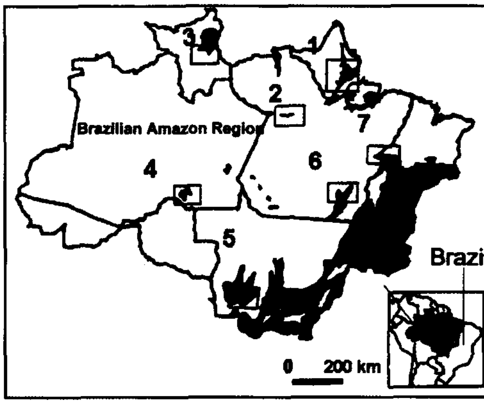

FIGURE 1. Brazilian Amazon basin showing the satellite image location of all study sites. Isolated savannas: (1) Amapá; (2) Alter do Chão; (3) Roraima; and (4) Humaitá. Non-isolated savannas: (5) Chapada dos Parecis; (6) Redenção; and (7) Carolina.

MATERIAL AND METHODS

SOIL SAMPLING.—Sampling locations for forest–savanna comparisons are identified in Figure 1. Four of these sites (Amapá, Alter do Chão, Humaitá, and Roraima) are "isolated" savanna pockets that are completely surrounded by forest, and three (Chapada dos Parecis, Redenção, and Carolina) are classified as non-isolated savannas. Soils in the sites generally showed a dystrophic character and with 1:1 clay type (Table 1). Climatic conditions were similar at all sites, most of them classified as equatorial hot humid (Nimer 1989). Rainfall varied from 1500 to 1750 mm in Roraima and Carolina up to 2750 mm in Amapá and Humaitá (Table 1). The regional vegetation type was very uniform for forest sites, tropical dense forest, following the classification of RADAMBRASIL (1974), or *terra firme* forest according to Pires and Prance (1985). The regional vegetation types of savanna sites were more diverse, varying from savanna park to open woody savannas (Table 2). The major difference between savanna park and open woody savannas is that in the latter type there is a higher number of trees (RADAMBRASIL 1974). The relative proportion of grasses (C_4) and trees (C_3) is important, since this proportion will directly affect the soil sur-

TABLE 1. *Soil types according to the Brazilian and USDA classification systems, climate, and annual rainfall in the study sites.*

Site	Soil type Brazilian classification	Soil type USDA soil taxonomy	Climate	Rainfall (mm)
Alter	Dystrophic yellow latosols and dystrophic quartz sands	Ustox/Quartzipsamments	Equatorial hot humid	1750–2000
Amapá	Dystrophic yellow latosols	Ustox/Udox	Equatorial hot humid	2750
Carolina	Dystrophic quartz sands and litholic soils	Quartzipsamments	Equatorial hot humid	1500–1750
Humaitá	Hydromorphic quartz sands and hydromorphic alic laterites	Tropaquods	Equatorial hot humid	2750
Parecis	Red-yellow latosols	Oxisols	Equatorial hot humid	1750–2000
Redenção	Litholic red-yellow podzols	Ultisols	Equatorial hot humid	1750–2000
Roraima	Dystrophic yellow latosols and lateritic concretionary soils	Ustox/Udox	Tropical hot subhumid	1500–1750

face $\delta^{13}C$ values. In order to better characterize such proportions, Table 2 shows the number of trees per hectare with diameter at breast height (DBH) greater than 5 cm (*N*) and also the basal area (BA/ha) in the savanna sampling sites (Sanaiotti 1996). *N* varied from 62 (Amapá) to 312 individuals per hectare (Redenção). The lowest BA was observed in Redenção and the highest in Alter do Chão (Table 2).

Soil cores were taken using a 4 m auger. In each study site, we sampled five depth intervals (0–0.05, 0.1–0.2, 0.5–0.6, 1.0–1.2, and 1.4–1.6 m) in two soil cores in the savanna and two in the surrounding or closest forest. We sampled just one of the two cores in the savanna from the soil depth interval 1.4–1.6 m to the bottom of the soil pit. In contrast, in the forest we continued depth sampling at the following intervals: 1.8–2.0, 2.2–2.4, 2.6–2.8, 3.0–3.2, 3.4–3.6, and 3.8–4.0 m. The exception was Parecis, where we sampled only in the savanna. The samples were air-dried and sieved (<2 mm) to remove roots. The forest and savanna core sites were chosen on flat ground in undisturbed vegetation well away from the present ecotone (savanna/forest boundary). The distance from the savanna/forest boundary to the area of the forest sampled varied from 0.2 to 23 km. In the case of the isolated savanna sites, we sampled close to the center of the savanna vegetation. As isolated savannas varied in size from several hectares to tens of square km, the distance from the ecotone boundary to the sampling location for savanna varied from 200 m to 40 km. Only the Chapada dos Parecis (Fig. 1) had no forest nearby.

PLANT SAMPLING.—Leaves of most common grass, shrub, and tree species were collected in savanna areas. Several leaves of each species were collected and pooled together to form one single sample. Leaves were air-dried and sieved for further isotopic determination.

SOIL ANALYSIS.—Soil texture was determined only in the deepest soil profiles by the pipette method (EMBRAPA 1997), and exchangeable Ca, Mg, and K were extracted by ion exchange resin (van Raij *et al.* 1986).

LABORATORY $\delta^{13}C$ AND ^{14}C ISOTOPE MEASUREMENTS.—A 10 g subsample of the sieved soil was combusted with CuO in sealed evacuated Pyrex tubes for 12 hours at 900°C. The resulting CO_2 was purified cryogenically and stable isotope measurements were made with a Micros 602E mass spectrometer (Finnegan Mat, Bremen, Germany) fitted with dual inlet and double collector systems. The results are expressed in $\delta^{13}C$ relative to the PDB standard in the conventional δ per mil notation as:

$$\delta^{13}C = \frac{R_{sample} - R_{std}}{R_{std}} \cdot 1000,$$

where R denotes the ^{13}C:^{12}C ratio of the sample and of the standard (std). All results represent the mean of at least two replicate analyses that differed by less than 0.3‰.

Radiocarbon analysis was performed on bulk soil organic matter samples collected in Amapá, Alter do Chão, Carolina, and Roraima profiles. ^{14}C

TABLE 2. *Regional vegetation type of savanna and forest according RADAMBRASIL project (1974). Phytosociological informations for savanna studies areas; N is the number of individuos per hectare and BA is the basal area; data from Sanaiotti (1996). Soil chemical composition (SB is the sum of bases in the surface soil) for savannas and forests soils.*

Site	Savanna regional vegetation	Type	N (ind./ha)	BA (m^2/ha)	SB-savanna ($mmol_c$/kg)	Forest regional vegetation	SB-forest ($mmol_c$/kg)
Alter	Savanna park	Isolated	250	4.16	0.22	Tropical dense forest	0.51
Amapá	Savanna park and open woody	Isolated	62	1.47	0.26	Tropical dense forest	0.48
Carolina	Savanna park	Non-isolated	190	3.14	0.33	Tropical dense forest	—
Humaitá	Savanna park	Isolated	153	1.45	0.23	Tropical dense forest	—
Parecis	Open woody savanna	Non-isolated	195	2.37	0.18	Tropical dense forest	—
Redenção	Savanna park and open woody	Non-isolated	312	0.52	0.24	Tropical dense forest	3.90
Roraima	Savanna park	Isolated	282	2.74	0.64	Tropical dense forest	3.44

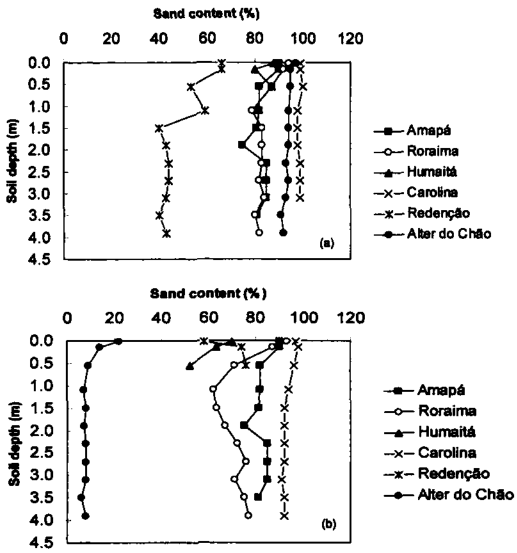

FIGURE 2. Variation in (a) sand content with depth in savanna and (b) forest soil profiles.

activity was measured in an accelerator mass spectrometer at the Lawrence Livermore Laboratory, Livermore, California (Trumbore 1993). The conventional radiocarbon age, expressed as years before present (B.P.) was estimated assuming a ^{14}C half-life of 5568 years.

RESULTS

SOIL CHARACTERIZATION.—The sand content of all savanna soils averaged higher than 50 percent, with all but the Redenção savanna profile having sand contents averaging more than 80 percent (Fig. 2). Forest soil profiles were generally lower in sand than in the savanna areas (Fig. 2), but still had average sand contents higher than 60 percent. The exception was the forest profile of Alter do Chão, which had an average sand content of only 10 percent. Therefore, with few exceptions, soils were predominantly sandy soils (Fig. 2). Textural changes with depth were observed mostly in forest soil profiles, which showed generally decreasing sand content with depth (Fig. 2B). The exception to this pattern was Redenção, where the opposite trend was observed (Fig. 2B).

At all sites, the soil chemical analyses indicated low pH and very low nutrient contents, as indicated by the low sum of exchangeable bases (Table 2). The pH varied from 4.4 to 5.1 (not shown) and sum of exchangeable bases (SB) from 0.18 to 0.64 $mmol_c$/kg in savannas soils, and from 0.48 to

3.90 $mmol_c$/kg in forest soils (Table 2). These values were below the average SB value of 184 profiles for Ultisols with different textures sampled in the Amazon basin (9.7 $mmol_c$/kg) by the RADAMBRASIL project (Tognon 1997).

$\delta^{13}C$ VALUES OF LEAVES IN SAVANNAS AND FORESTS.—The average $\delta^{13}C$ value of C_4 grass species found in the savannas was -13.2 ± 0.4‰ ($N = 12$; Appendix 1). Leaves of C_3 tree species from the savannas had $\delta^{13}C$ values varying from -21.5 to -33.4‰ (Appendix 1) and the average value was -29.0 ± 1.7‰ ($N = 195$). Variation among sites was small. The only statistically significant difference was the more negative average of foliar $\delta^{13}C$ found in Alter do Chão (-30.3 ± 1.5‰; $N = 24$) in comparison with Carolina (-28.2 ± 1.4‰; $N = 34$), Humaitá (-28.9 ± 1.5‰; $N = 35$), and Parecis (-28.5 ± 1.7‰; $N = 34$). The single largest difference between foliar $\delta^{13}C$ averages was 2.1‰, which was observed between Alter do Chão and Carolina. Some variability was found among leaves of individuals of the same species collected at the same site (Appendix 1). Most of this variability was smaller than 2‰. Leaves from individuals of the same species differed by less than 3‰, except in five cases. The largest single difference (5.3‰) was found between two individuals of *Salvertia convallariodora* that were collected at Carolina savanna.

$\delta^{13}C$ VALUES OF SURFACE SOIL ORGANIC MATTER.—The $\delta^{13}C$ values for surface forest soils (0–0.2 m) were similar among different sites and within sites. The minimum and the maximum values were -30.0 (Redenção) and -27.0‰ (Roraima), respectively. These values are within the range of -31.0 to -25.0‰ reported for similar forest surface soils (Fig. 3). Spatial variation in $\delta^{13}C$ values (both among different sites or within the same site) was greater for surface savanna soils than for surface forest soil samples. These larger variations observed in savannas appear to be common to other savanna areas of the world (Fig. 3) and probably are due to site-specific recent variations in the proportions and spatial distribution of C_3 and C_4 plants (Boutton *et al.* 1998). Among savannas, $\delta^{13}C$ values in organic matter ranged from a minimum of -26.5 (Redenção) to a maximum of -15.8‰ (Roraima; Table 3). Within savannas, the largest $\delta^{13}C$ differences between two soil profiles (5‰) were observed at Carolina, Humaitá, and Redenção (Table 3). The $\delta^{13}C$ difference between profiles within a savanna was smaller in the second depth interval (0.1–0.2 m) in relation to most surface samples (Table 3). There was a significant correlation between the density of C_3 individuals in savanna sampling sites (number of individuals per hectare) and the $\delta^{13}C$ values for surface (0–0.05 m) and subsurface (0.10–0.20 m) soil samples (Fig. 4). The density of C_3 individuals explained *ca* 50 percent of the variance in the $\delta^{13}C$ of surface soil samples from savanna sites. Excluding the Roraima sample, 85 percent of the variance in the 0.1–0.2 m layer can be explained by the density of C_3 individuals (Fig. 4).

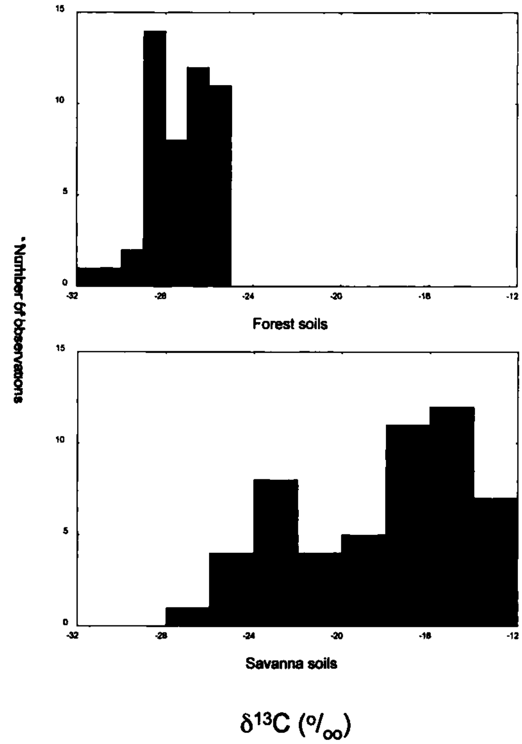

FIGURE 3. Histogram of $\delta^{13}C$ values for surface soil samples from the literature. Data from Volkoff *et al.* (1982), Mondenesi *et al.* (1986), Schwartz *et al.* (1986, 1996), Volkoff and Cerri (1987), Martin *et al.* (1990), Desjardins *et al.* (1991, 1996), Bird *et al.* (1992), Balesdent *et al.* (1993), McPherson *et al.* (1993), Valencia (1993), Mariotti and Petershcimitt (1994), Trouve *et al.* (1994), McClaran and McPherson (1995), Trumbore *et al.* (1995), Pessenda *et al.* (1996), Victoria *et al.* (1996) and Boutton *et al.* (1998).

DEPTH VARIABILITY IN $\delta^{13}C$ VALUES OF SOIL ORGANIC MATTER.—As several other studies have shown (Desjardins 1991, Balesdent *et al.* 1993, Desjardins *et al.* 1996, Martinelli *et al.* 1996, Gouveia *et al.* 1997, Pessenda, Gomes *et al.* 1998), the $\delta^{13}C$ of

TABLE 3. *$\delta^{13}C$ values of surface soils (0–0.05 and 0.1–0.2 m) in Amazon savanna areas and difference (Δ) between the $\delta^{13}C$ value of the first and second profiles collected in the same savanna.*

Site	Savanna 0–0.05 m	Savanna 0.1–0.2 m
Amapá	−16.0	−14.3
	−16.9	−14.6
Δ	0.9	0.3
Alter	−23.2	−21.6
	−23.6	−21.9
Δ	0.4	0.3
Carolina	−19.6	−18.4
	−24.9	−19.7
Δ	5.3	1.3
Humaitá	−18.1	−16.6
	−23.6	−21.2
Δ	5.4	4.6
Redenção	−22.0	−24.0
	−26.5	−24.2
Δ	4.5	0.2
Roraima	−15.8	−13.6
	−19.5	−14.6
Δ	3.7	1.0

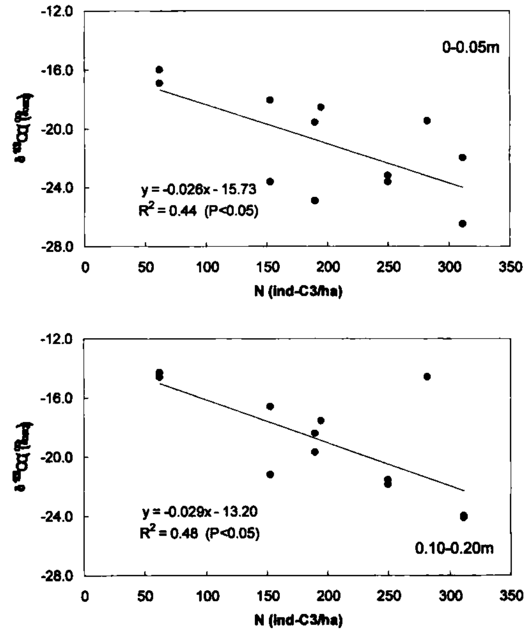

FIGURE 4. Correlations between number of C_3 individuals per hectare (*N*) and $\delta^{13}C$ of surface soil samples in savanna sites.

soil organic matter increases with depth in forests profiles. In this study, the changes in $\delta^{13}C$ values with soil depth can be divided into two groups: Alter do Chão, Amapá, and Roraima, where deeper portions of the soil organic matter (>1.5 m) showed little enrichment (<3.5‰) compared to surface layers in forests; and (2) a group represented by Humaitá, Carolina, and Redenção sites, where soil enrichment greater than 3.5‰ was observed with soil depth (Fig. 5).

As already discussed, organic matter $\delta^{13}C$ values in the upper 5 cm of savanna profiles were 4–12‰ heavier than in comparable forest profiles, indicating the influence of C_4 plant material (McPherson *et al.* 1993; Victoria *et al.* 1995; Boutton *et al.* 1998; Pessenda *et al.* 1998a, b). Less variation with depth was observed in Alter do Chão and Chapada dos Parecis. The isotopic shift from surface to deep layers at Chapada dos Parecis (−17.6 to −21.3‰) was relatively heavier (indicating greater influence of C_4 material) than at Alter do Chão (−21.1 to −23.4‰). The savanna profiles at Alter do Chão had relatively constant $\delta^{13}C$ values throughout the profile (Fig. 5). In the Chapada dos Parecis savanna profile, the $\delta^{13}C$ values decreased *ca* 3.5‰ from the surface to *ca* 2 m depth. Below 2 m, the $\delta^{13}C$ values increased by 3.4‰, becoming similar to values found at the soil surface. The $\delta^{13}C$ of savanna profile values at Redenção increased *ca* 5‰ from the surface to the 140–150 cm soil layer. Below this layer the $\delta^{13}C$ values decreased, reaching isotopic values similar to the ones found in shallower layers (Fig. 5). Other profiles (Amapá, Roraima, Humaitá, and Carolina) showed a maximum in $\delta^{13}C$ at depths of 50 to 60 cm, with $\delta^{13}C$ values below decreasing to converge with comparable forest values. Although each soil profile had particular changes in $\delta^{13}C$ with depth, a common feature observed in Roraima, Humaitá, and Carolina profiles was that the $\delta^{13}C$ values of soil organic matter of forest and savanna became similar with increasing depth, suggesting a dominance of C_3 plants in the deepest layers of these profiles. The $\delta^{13}C$ impoverishment with depth in the savanna profile of Amapá was not as high as observed in Roraima, Humaitá, and Carolina profiles. The $\delta^{13}C$ values of deep soil organic matter in Amapá decreased to only −23‰ (compared to a forest value of −25‰), suggesting the presence of C_4 organic matter even at depths of 4 m (Fig. 5).

^{14}C DATING OF SOIL ORGANIC MATTER.—The radiocarbon ages of bulk soil organic matter represent a mixture of younger and older carbon atoms and

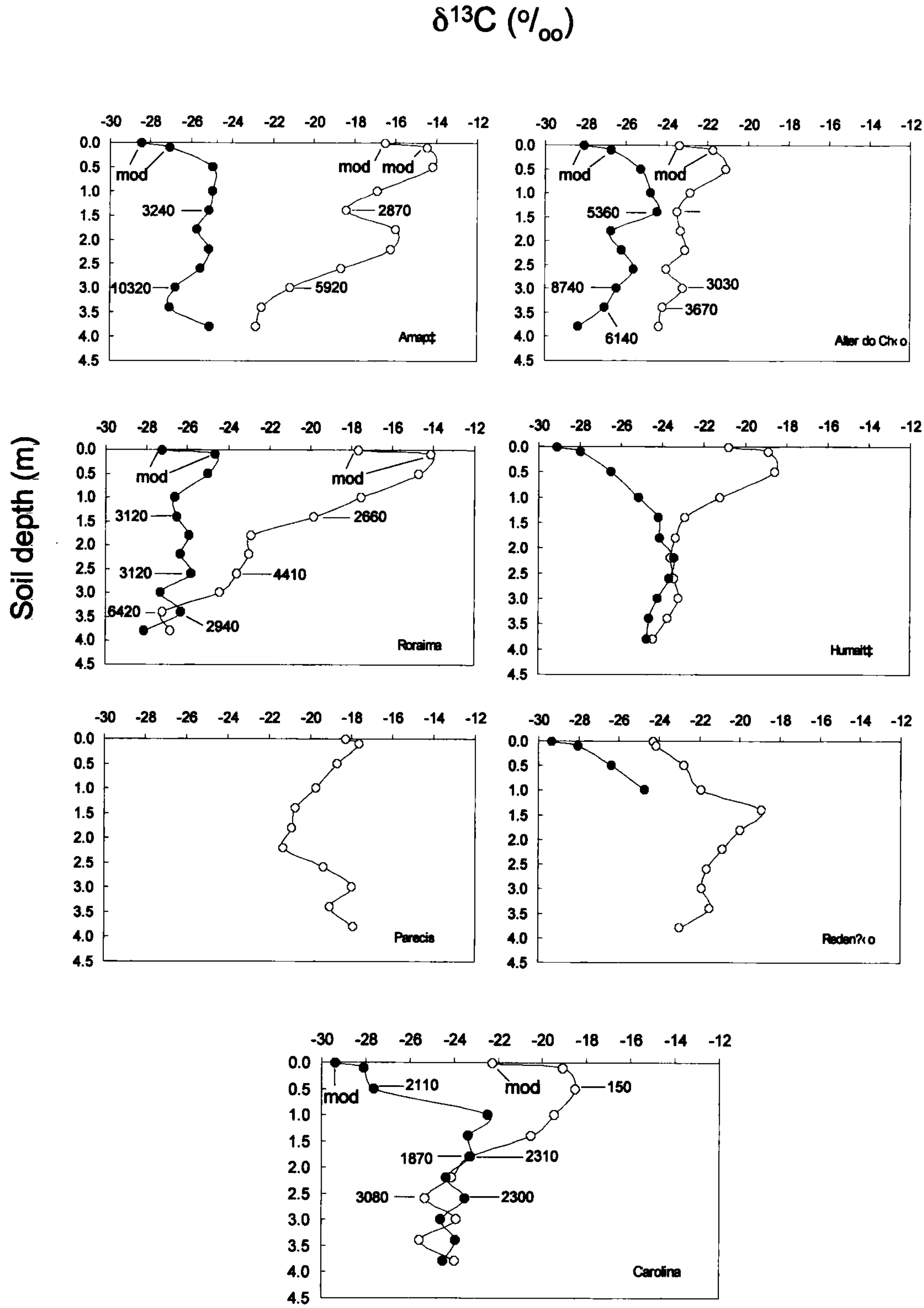

FIGURE 5. Depth variability of $\delta^{13}C$ (‰) values in savanna and contiguous forest soil profiles (average of two profiles). Full circles represent forest profiles and open circles represent savanna profiles. Bars represent standard errors. Numbers indicate radiocarbon age B.P.

consequently do not constitute an absolute age of soil organic matter. For example, radiocarbon dating of bulk soil organic matter was always younger than humin extracted from the same samples collected in soil profiles at Humaitá (Gouveia *et al.* 1997). The same trend was observed between bulk soil organic matter and charcoal (Pessenda, Gomes *et al.* 1998). Therefore, the interpretation of radiocarbon ages in terms of the mean age of organic matter in soil profiles must be undertaken with caution (Trumbore *et al.* 1995).

High values of radiocarbon (>Modern) reflect the incorporation of carbon fixed from the atmosphere since atomic weapons testing in the early 1960s, which nearly doubled the amount of ^{14}C in the atmosphere. This "bomb" ^{14}C signature is observed in the upper part of each soil profile (Fig. 5), indicating that the organic material in this layer is predominantly made up of constituents that cycle rapidly (decadal or shorter timescales; Trumbore *et al.* 1995). The ^{14}C content of bulk organic matter declines rapidly with depth in the soil, indicating that organic matter on average resides long enough for significant radioactive decay of radiocarbon (half-life = 5730 yr). The oldest organic matter was found at the bottom of the Amapá forest soil profile (*ca* 10,300 yr B.P.). The radiocarbon ages in the other profiles were generally less than in the Amapá profiles, and varied from *ca* 2300 to *ca* 6400 years B.P. in the deepest depths (Fig. 5). In Amapá and Alter do Chão, the radiocarbon ages were higher in the forest than in the savanna profiles. The opposite trend, however, was observed in Roraima, and practically no difference between forest and savanna was observed in Carolina.

DISCUSSION

$\delta^{13}C$ VALUES OF LEAVES IN SAVANNAS AND FORESTS.—The average $\delta^{13}C$ value of C_4 grass found in the savannas (−13.2‰) was higher (heavier) than the average value for C_4 plants found by Desjardins *et al.* (1996) at Roraima savannas (−14.2‰) but lower (lighter) than the average value found by Pessenda, Gomes *et al.* (1998) at savannas in Rondônia (−11.7‰). The $\delta^{13}C$ values of *ca* 100 C_4 plants analyzed from the herbarium of the Instituto Nacional de Pesquisas da Amazônia (INPA) ranged from −9.5 to −13.6‰ (Medina *et al.* 1999), with an average value of −11.7 ± 0.9‰ (N = 102). On the other hand, the average $\delta^{13}C$ value for C_3 plants of the savannas (−29.0‰) was similar to values found by Desjardins *et al.* (1996) and Pessenda, Gomes *et al.* (1998) in tree leaves collected in Roraima (−29.6‰) and Rondônia (−29.0 ± 1.8‰) savannas, respectively. As in the Brazilian Pantanal region (Victoria *et al.* 1995), the $\delta^{13}C$ values for tree leaves collected in savannas are enriched in $\delta^{13}C$ compared with leaves collected from trees in closed forests. For example, the average value of tree leaves collected in closed forest in Rondônia was equal to −32.1‰, *ca* 2‰ more negative than tree leaves from savannas (Martinelli *et al.* 1998). The most probable cause for these differences are increased incorporation of isotopically depleted CO_2 in forest tree leaves compared to savanna tree leaves (Sternberg *et al.* 1989, Kapos *et al.* 1993, Grace *et al.* 1995, Buchmann *et al.* 1996, Lloyd *et al.* 1996).

Intraspecies variation in leaf $\delta^{13}C$ was greater than overall variation among different sites. Large intraspecies variation in $\delta^{13}C$ is common (Walcroft *et al.* 1996, Berry *et al.* 1997, Martinelli *et al.* 1998), but its causes are difficult to identify. Characteristics such as leaf height, age, and position in the branch expose leaves to different light intensities, which can influence the photosynthetic rate, and consequently, leaf stable carbon isotopic composition (Farquhar *et al.* 1989).

SOURCES OF VARIABILITY IN $\delta^{13}C$ VALUES OF THE SOIL ORGANIC MATTER.—Generally, forest soil profiles showed an enrichment of $\delta^{13}C$ with depth throughout the profile (Fig. 5). Savanna soil profiles showed similar isotopic enrichment only to depths of 0.5 to 1 m, below which $\delta^{13}C$ values decreased in most of the profiles (Fig. 5). The magnitude of such isotopic changes varied, both in forest soil profiles and among savanna soil profiles. Several factors have been identified that cause isotopic changes with soil depth, including soil chemical composition and texture, organic matter decomposition processes, and past vegetation changes.

The sampled soils had similar chemical characteristics as expressed in terms of fertility, especially among savannas, where the sum of bases was very low. Therefore, chemical composition does not seem to be the major cause of isotopic changes found in soil profiles.

In forest stands, it has been observed that clay fractions are slightly enriched in $\delta^{13}C$, compared to coarser fractions of surface soil layers (Balesdent *et al.* 1993). For example, a difference of *ca* 4‰ was found between clay and sand fractions of a surface soil under tropical forest in southeast Brazil (Vitorello *et al.* 1989). Smaller enrichments were observed in surface soils of other regions in Brazil

(Desjardins *et al.* 1991), the Congo (Martin *et al.* 1990), and France (Balesdent *et al.* 1993). Even pure stands of native C_4 savannas showed a small enrichments (1–2‰) in fine compared to coarser fractions at the soil surface (Martin *et al.* 1990). On the other hand, in situations where C_3 stands were artificially replaced by C_4 vegetation (Vitorello *et al.* 1989, Desjardins *et al.* 1991) or vice versa (Balesdent *et al.* 1988, Martin *et al.* 1990), larger differences between fine and coarse soil factions have been observed (up to 10‰; Boutton *et al.* 1998). Among soil profiles that had changes in texture with depth, no significant change in the $\delta^{13}C$ of the bulk soil organic matter was observed in studies reported by Desjardins and collaborators (Desjardins *et al.* 1991, 1996). In our study, the same was true. In the few forest profiles that had depth changes of textural fractions, such as Roraima (Fig. 3), we could not detect any major change in $\delta^{13}C$ with depth (Fig. 5). Therefore, it seems that soil texture was not the main factor controlling the isotopic composition of soil organic matter.

Another possible cause of $\delta^{13}C$ variation with soil depth is the organic matter decomposition process, which favors the loss of ^{12}C (Boutton 1996). Generally, it is accepted that up to a 3.5–4.0‰ isotopic enrichment in organic matter $\delta^{13}C$ with depth in soils is due to decomposition processes (Mariotti & Peterschmitt 1994, Desjardins *et al.* 1996, Martinelli *et al.* 1996). Increases in the average radiocarbon age of organic matter with depth demonstrate that organic matter in deeper soils has been exposed longer to decomposition processes.

Vegetation changes in the past may be another important factor in explaining isotopic changes with soil depth (Schwartz *et al.* 1986; Volkoff & Cerri 1987; Martin *et al.* 1990; McPherson *et al.* 1993; Mariotti & Petershimitt 1994; Trouve *et al.* 1994; Desjardins *et al.* 1996; Martinelli *et al.* 1996; Schwartz *et al.* 1996; Victoria *et al.* 1996; Gouveia *et al.* 1997; Boutton *et al.* 1998; Pessenda, Gomes *et al.* 1998; Pessenda *et al.* 1998a, b; Roscoe *et al.* 2000). In forest soils, isotopic enrichment larger than 3.5–4.0‰ has been explained by the presence of remaining old C_4 vegetation. On the other hand, in savanna soils, an impoverishment of $\delta^{13}C$ with depth may suggest the presence of relict organic matter derived from C_3 vegetation.

It is important to note that different rooting depths for trees and C_4 grasses may partly account for changes with soil depth in woody savanna, especially in Redenção, Roraima, and Alter do Chão, where the number of C_3 trees per hectare was high (Table 2). Most of the studies dealing with changes in $\delta^{13}C$ with soil depth in savanna areas do not take into account the possible rooting effect on observed changes. One exception is the study conducted by Boutton *et al.* (1998) in a savanna area of south Texas. In that study, they found that $\delta^{13}C$ of roots were not in equilibrium with $\delta^{13}C$ values of coexisting soil organic matter. The $\delta^{13}C$ of roots in woodlands were *ca* −25‰, while $\delta^{13}C$ values of the soil organic matter varied from −24 to −17‰. The $\delta^{13}C$ of roots in grasslands varied from −24 to −21‰ and $\delta^{13}C$ values of soil organic matter varied from −16 to −20‰. Obviously, the results found by Boutton *et al.* (1998) cannot be extrapolated directly to our study areas. If the contribution of roots in our study is important, past climate changes may be overestimated or underestimated depending on the proportion of C_3 and C_4 roots.

The $\delta^{13}C$ values observed in the forest soil profiles of Alter do Chão, Amapá, and Roraima are in the range of the expected values for soils where C_3 plants have remained the dominant vegetation cover. In these profiles, the maximum $\delta^{13}C$ enrichment was *ca* 3‰ (Fig. 5). This trend was also shown for nine soil profiles collected at six forested sites not bordered by savannas in the central and southeast Amazon region (Desjardins *et al.* 1991, Valencia 1993, Trumbore *et al.* 1995, Martinelli *et al.* 1996). Enrichment in $\delta^{13}C$ values for forested sites greater than those that may reasonably be expected from decomposition processes, such as those found in Humaitá and Carolina profiles, have been interpreted as indicating the influence of past C_4 vegetation, or a mixture of C_3 and C_4 vegetation. Desjardins *et al.* (1996) found soil enrichment higher than 3.5‰ in forested sites at depths varying from 0.5 to 2.0 m in areas near the forest–savanna boundary in Roraima. Below 2 m depth, the enrichment predominantly observed was less than 3.5‰ different than surface values. In another forest profile in the same area but far from the forest–savanna boundary, the isotopic enrichment was greater than 3.5‰ only between 0.5 and 1.0 m depth. The latter site was similar to the study at Roraima, where an enrichment higher than 3.5‰ was observed only for the 0.1 to 0.2 m depth interval. Pessenda *et al.* (1998a) observed similar $\delta^{13}C$ distribution with depth in the Humaitá area. A transect of $\delta^{13}C$ values from savanna to forest area indicated decreased contributions of C_4 plant inputs toward the forest.

If we assume that past vegetation changes remain recorded in soil organic matter, it may be concluded that in the Alter do Chão and Chapada dos Parecis profiles appear not to have undergone major past changes in their vegetation cover, while major past vegetation changes are recorded in the Amapá, Roraima, Humaitá, Redenção, and Carolina profiles. Interestingly, among the sites where carbon isotopes indicate past vegetation changes, the degree and manner of change was different for each area (Fig. 5). The most common pattern is that the $\delta^{13}C$ signatures of organic matter in the deepest soil layers of savanna profiles appear to record more woody (C_3) vegetation than is present today. The same trend was found by earlier studies conducted in Roraima and Humaitá, especially in those profiles that were collected from the forest–savanna boundaries (Desjardins *et al.* 1996, Gouveia *et al.* 1997).

Radiocarbon dating of bulk soil organic matter does not allow us to infer with precision the chronology of past vegetation changes because it represents a mixture of younger and older material (Trumbore *et al.* 1995). For example, the bulk radiocarbon age may be influenced by factors such as soil texture, since clays tend to stabilize organic carbon in soils for a longer time than sands. Despite these complications, radiocarbon data can be used to roughly relate the timing of vegetation change with climatic events that occurred in the past. Paleoecological studies have suggested that a maximum in the proportion of grass pollen was found in the middle Holocene (6000–4000 yr B.P.; Absy *et al.* 1991, Ledru 1993, Servant *et al.* 1993). Desjardins *et al.* (1996) found charcoal with radiocarbon ages *ca* 6000–7000 years B.P. in Roraima savanna profiles, and according to them, those would be indirect evidence that present savannas were formed during that period. The radiocarbon ages in the deepest savanna profiles of our study are not old enough to support or reject this hypothesis (Fig. 5); however, at 3.4 to 3.6 m depth intervals, the $\delta^{13}C$ savanna profile in Roraima clearly indicates a strong presence of C_3 vegetation, and the radiocarbon age of the bulk soil organic matter was *ca* 6400 years B.P. Gouveia *et al.* (1997) found at 90 cm depth in Humaitá, humin dating 6000 years B.P. with a corresponding $\delta^{13}C$ of soil organic matter of *ca* −21.0‰, which indicates a mixture of C_3 and C_4 vegetation. Therefore, it could be that even a widespread event like the suggested climatic fluctuations during the Holocene period did not produce changes in vegetation distribution that were uniformly recorded in soil profiles. Probably other factors, such as microclimate, soil characteristics, root distribution, fire regime, and human actions, may have contributed to the composition of the vegetation cover in the forest–savanna ecotones of the Amazon. For example, based on charcoal dated from 3230 to 1790 years B.P., Desjardins *et al.* (1996) suggested that fires which occurred in the late Holocene period were a key process to define the forest–savanna dynamics in Roraima. In fact, in the majority of the savannas areas studied in the Amazon, maximum $\delta^{13}C$ values (higher proportion of C_4 plants) were found near the surface, and where radiocarbon dating was available, they have always indicated that this maximum occurred in the late Holocene (Desjardins *et al.* 1996, Gouveia *et al.* 1997, Pessenda, Gomes *et al.* 1998). In addition, Roscoe *et al.* (2000), working in a savanna area of central Brazil, showed that in a period of only *ca* 20 years, the C_4 grass population increased in areas with higher fire incidence, and the $\delta^{13}C$ of the soil became higher, suggesting the increasing influence of C_4 vegetation in the soil organic matter.

It is risky, based in only two soil profiles, to extrapolate our results to the entire savanna areas, since it has already been shown that major spatial variability can occur inside each savanna (Desjardins *et al.* 1996, Gouveia *et al.* 1997). Therefore, at least in the sites where soil samples were collected, we have concluded that five savannas (Amapá, Roraima, Humaitá, Redenção, and Carolina) of the Amazon region have experienced past vegetation changes during the Holocene period. Other studies have reached the same conclusion for the Roraima and Humaitá savannas (Desjardins *et al.* 1996, Gouveia *et al.* 1997, Pessenda, Gomes *et al.* 1998). On the other hand, in two other savanna areas (Alter do Chão and Parecis) it is likely that past vegetation changes were less pronounced. Several authors have suggested major climatic fluctuations during the Holocene period in South America, and the results showed above suggest that even widespread events did not produce uniform changes in vegetation distribution in the Amazon region.

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APPENDIX 1. *$\delta^{13}C$ (‰) values of C_3 and C_4 plant species collected in savanna areas.*

Site	C_3 plant species	$\delta^{13}C$
Alter do Chão	*Bowdichia virgilioides*	−29.2
	Byrsonima coccolobifolia	−27.9
	B. crassifolia	−28.5
	Casearia javitensis	−30.2
	Chamaecrista parviflora	−30.6
	Chomelia parviflora	−32.1
	Declieuxia fruticosa	−31.2
	Erythroxylum suberosum	−29.5
	Eugenia biflora	−31.8
	Galactia jussianea	−28.8
	Hirtella racemosa	−32.2
	Lafoensia pacari	−28.6
	Miconia albicans	−30.1
	M. fallax	−31.0
	Myrcia cf. *obtusa*	−31.4
	M. slvatica	−30.1
	Neea ovalifolia	−31.5
	Pouteria ramiflora	−31.8
	Psychotria barbiflora	−31.4
	Qualea grandiflora	−28.7
	Salvertia convallariodora	−29.2
	Sclerobium paniculatum	−31.3
	Tocoyena formosa	−28.9
	Xylopia aromatica	−30.9
	Paspalum carinatum	−13.7
	Trachypogon plumosus	−13.3
Amapá	*Aegiphila lhotzyana*	−29.6
	Bowdichia virgilioides	−26.7
	B. virgilioides	−30.4
	Byrsonima crassifolia	−30.2
	B. crassifolia	−30.2
	Curatella americana	−28.7
	C. americana	−30.2
	Hancornia speciosa	−29.6
	H. speciosa	−29.5
	Hypolytrum cf. *pulchrum*	−30.3
	Hypolytrum sp.	−28.2
	Mezilaurus lindaviana	−31.4
	Pouteria ramiflora	−30.7
	P. ramiflora	−30.5
	Rauvolfia pentaphylla	−28.4
	Roupala montana	−28.8
	R. montana	−31.0
	Salvertia convallariodora	−27.8
	S. convallariodora	−28.5
	Scleria cyperina	−25.7
	Trachypogon plumosus	−13.0
Carolina	*Agonandra brasiliensis*	−30.1
	A. brasiliensis	−28.5
	Andira chordata	−26.7
	A. chordata	−27.8
	Bowdichia virgilioides	−26.7
	B. virgilioides	−28.1
	Byrsonima crassifolia	−30.3
	B. crassifolia	−29.8
	Couepia paraensis	−29.0
	Curatella americana	−28.2
	C. americana	−29.1
	Cybistax antisiphyllitica	−28.2
	C. antisiphyllitica	−26.3
	Hancornia speciosa	−29.3
	H. speciosa	−26.9
	Kielmeyera coriacea	−26.6
	K. coriacea	−26.2
	Plathymenia reticulata	−27.8
	P. reticulata	−28.5
	Pouteria ramiflora	−29.0
	P. ramiflora	−27.9
	Pterodon pubescens	−28.1
	P. pubescens	−28.1
	Qualea grandiflora	−27.4
	Q. grandiflora	−28.4
	Q. parviflora	−28.2
	Salvertia convallariodora	−31.6
	S. convallariodora	−26.3
	Tabebuia aurea	−24.7
	T. aurea	−27.8
	T. ochracea	−29.9
	T. ochracea	−29.1
	Xylopia aromatica	−29.2
	X. aromatica	−30.4
Humaitá	*Anacardium* cf. *humile*	−26.9
	Andira cf. *vermifuga*	−28.0
	A. cf. *vermifuga*	−29.2
	A. cf. *vermifuga*	−27.1
	A. surinamensis	−27.9
	Antonia ovata	−29.6
	Bonyunia antoniifolia	−31.4
	Brosimum gaudichaudii	−29.2
	Buchenavia capitata	−30.1
	Caraipa savannarrum	−29.2
	Casearia sylvestris	−29.0
	Catthedra acuminata	−31.0
	Guatteria cf. *foliosa*	−30.4
	Hancornia speciosa	−29.2
	Heisteria ovata	−32.3
	Kielmeyera coriacea	−29.0
	Lafoensia pacari	−28.9
	L. pacari	−28.5
	Laxoplumeria teesmanii	−27.0
	Norantea guianensis	−27.3
	Parkia ulei	−31.2
	Physocalaymma scaberrimum	−28.9
	Qualea parviflora	−28.2
	Q. parviflora	−27.5
	Roupala montana	−29.6
	Salvertia convallariodora	−26.9
	Simarouba amara	−29.8
	Tabebuia aurea	−31.2
	T. aurea	−28.6
	T. aurea	−27.9
	Virola subsessilis	−27.0
	Vochysia ferruginea	−28.0
	V. grandis	−29.6
	V. sessilifolia	−29.1
	Xyridaceae sp.	−26.6
	Leptocoryphrium lanatum	−12.9
	Trachypogon spicatus	−13.4
Parecis	*Anacardium* cf. *humile*	−30.0
	Andira cf. *vermifuga*	−29.7
	A. cf. *vermifuga*	−28.2
	Annona grandiflora	−29.5

APPENDIX 1. *Continued.*

Site	C_3 plant species	$\delta^{13}C$	Site	C_3 plant species	$\delta^{13}C$
	Bonyunia antoniifolia	−30.3		*Rudgea erioloba*	−28.8
	Buchenavia tomentosa	−29.9		*Salvertia convallariodora*	−30.1
	B. tomentosa	−26.7		*S. convallariodora*	−30.5
	Byrsonima verbascifolia	−28.5	Roraima	*Acosmium steyermarkii*	−28.1
	Caryocar brasiliense	−27.5		*Aegiphila lhotzyana*	−31.0
	Davilla elliptica	−29.8		*Agonandra brasiliensis*	−30.8
	Diospyros hispida	−30.0		*Anadenanthera peregrina*	−29.3
	D. hispida	−30.4		*Annona jahnii*	−33.4
	Emmotum nitens	−28.0		*A. ovata*	−28.4
	Eriotheca gracileps	−27.7		*Aspidosperma multiflorum*	−30.8
	Eschweilera nana	−26.9		*A. multiflorum*	−28.9
	Himatanthus obovatus	−23.5		*Bowdichia virgilioides*	−29.4
	Kielmeyera coriacea	−26.2		*B. virgilioides*	−29.5
	K. rubriflora	−27.2		*Byrsonima crassifolia*	−29.0
	Mouriri pusa	−29.2		*B. crassifolia*	−30.7
	Myrcia cf. *obtusa*	−33.2		*Casearia ulmifolia*	−30.0
	Plathymenia reticulata	−27.5		*Chamaecrista desvauxii*	−31.3
	Qualea grandiflora	−26.5		*Cissampelos ovalifolia*	−29.4
	Q. grandiflora	−28.7		*C. ovalifolia*	−28.9
	Q. multiflora	−29.3		*Curatella americana*	−28.9
	Salvertia convallariodora	−28.9		*C. americana*	−27.1
	S. convallariodora	−28.0		*Erythroxylum* cf. *vernicosum*	−31.2
	Strychnos pseudoquina	−29.4		*Mouriri apiranga*	−21.5
	Styrax ferruginea	−27.1		*Palicourea rigida*	−25.7
	Syagrus petrae	−27.4		*Paspalum lanciflorum*	−26.8
	Tabebuia aurea	−26.1		*Qualea parviflora*	−29.2
	Virola subsessilis	−28.5		*Q. parviflora*	−31.0
	Vochysia cinnanomea	−29.7		*Roupala montana*	−29.4
	V. rufa	−28.9		*R. montana*	−28.2
	Streptostachys ramosa	−13.0		*Thrasya petrosa*	−30.1
Redenção	*Bowdichia virgilioides*	−29.6		*Trattinickia rhoifolia*	−27.7
	B. virgilioides	−29.9		*T. rhoifolia*	−31.3
	Byrsonima crassifolia	−28.5		*Xylopia aromatica*	−29.7
	B. crassifolia	−29.9		*X. aromatica*	−31.3
	Calisthene fasciculata	−29.3		*Andropogon fasciatus*	−12.8
	Curatella americana	−28.3		*Andropogon* sp.	−13.1
	C. americana	−26.9		*Andropogon* sp.	−13.4
	Kielmeyera latrophyton	−26.4		*Trachypogon spicatus*	−13.8
	Pouteria ramiflora	−31.7		*T. spicatus*	−12.6
	P. ramiflora	−30.6			