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

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ABSTRACT

We investigated the variation of stable ($^{13}$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 $^{13}$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 C3 plants have remained the dominant vegetation cover. On the other hand, in forest soil profiles from Humaitá and Carolina sites, the enrichment was greater than 3.5%, indicating the influence of past C4 vegetation or a mixture of C3/C4 vegetation (woody savanna). The surface $^{13}$C values in the savanna profiles were 5–13% greater than the comparable forest profiles, indicating the influence of C4 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 $^{13}$C values throughout the profile, suggesting minor past changes in the vegetation composition. In profiles at Amapá, Roraima, Humaitá, and Carolina, $^{13}$C values decreased with depth from the surface and converged with comparable forest values, suggesting more woody savanna in the past than exists currently.

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 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, 1974, 1976, 1978, 1982; Sarmiento 1984; Andrade 1989; Trumbore 1993). The recognition of past vegetation changes is important for understanding the present and future sustainability of Amazonian ecosystems.
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 Colinhaux 1990, Bush et al. 1990, Ab'saber 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 Rondonia), 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 $^{813}$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 $^{813}$C signature of organic matter in soils (Desjardins et al. 1996, Martinelli et al. 1996, Neill et al. 1996, Bird & Pousai 1997).

**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 RADA MBRASIL (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 (RADA MBRASIL 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/Udix                    | Equatorial hot humid        | 2750          |
| Carolina   | Dystrophic quartz sands and lithic 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   | Lithic red-yellow podzols                                 | Ultisols                      | Equatorial hot humid        | 1750–2000     |
| Roraima    | Dystrophic yellow latosols and lateritic concretionary soils | Ustox/Udix                | Tropical hot subhumid       | 1500–1750     |

face δ13C 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 δ13C AND 14C 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 CO2 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 δ13C relative to the PDB standard in the conventional δ per mil notation as:

\[
\delta^{13}C = \frac{R_{\text{sample}} - R_{\text{std}}}{R_{\text{std}}} \times 1000,
\]

where R denotes the 13C:12C 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%0.

Radiocarbon analysis was performed on bulk soil organic matter samples collected in Amapá, Alter do Chão, Carolina, and Roraima profiles. 14C
Past Vegetation Changes in Amazon Savannas

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/kg in savannas soils, and from 0.48 to

| Site     | N (ind/ha) | BA (mm/ha) | Forest regional vegetation | Savanna regional vegetation |
|----------|------------|------------|---------------------------|-----------------------------|
| Amapá    | 250        | 4.16       | 0.22                      | 0.10                        |
| Roraima  | 190        | 1.47       | 0.26                      | 0.08                        |
| Humaitá  | 153        | 0.33       | 0.23                      | 0.06                        |
| Carolina | 195        | 2.37       | 0.18                      | 0.04                        |
| Parque   | 312        | 0.52       | 0.24                      | 0.04                        |
| Redenção | 282        | 2.74       | 0.10                      | 0.48                        |

TABLE 2. Regional vegetation type of savanna and forest according RADAMBRASIL project (1974). Physioecological information for savanna studies areas; N. is the number of individuals per hectare and BA is the basal area; data from Sampaio (1996). Soil chemical composition (SB) is the sum of bases in the surface soil for savannas and forests.
3.90 mmol/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/kg) by the RADAM- BRASIL project (Tognon 1997).

$^8^{13}$C VALUES OF LEAVES IN SAVANNAS AND FORESTS.—

The average $^8^{13}$C value of C$_4$ grass species found in the savannas was $-13.2 \pm 0.4\%$ ($N = 12$; Appendix 1). Leaves of C$_3$ tree species from the savannas had $^8^{13}$C values varying from $-21.5$ to $-33.4\%$ (Appendix 1) and the average value was $-29.0 \pm 1.7\%$ ($N = 195$). Variation among sites was small. The only statistically significant difference was the more negative average of foliar $^8^{13}$C found in Alter do Chão ($-30.3 \pm 1.5\%$; $N = 24$) in comparison with Carolina ($-28.2 \pm 1.4\%$; $N = 34$), Humaitá ($-28.9 \pm 1.5\%$; $N = 35$), and Parecis ($-28.5 \pm 1.7\%$; $N = 34$). The single largest difference between foliar $^8^{13}$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 *Salviera convallarioidora* that were collected at Carolina savanna.

$^8^{13}$C VALUES OF SURFACE SOIL ORGANIC MATTER.—

The $^8^{13}$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 $^8^{13}$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, $^8^{13}$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 $^8^{13}$C differences between two soil profiles (5%) were observed at Carolina, Humaitá, and Redenção (Table 3). The $^8^{13}$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 $^8^{13}$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 $^8^{13}$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).

DEPTH VARIABILITY IN $^8^{13}$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 $^8^{13}$C of
soil organic matter increases with depth in forests profiles. In this study, the changes in δ13C 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 δ13C values in the upper 5 cm of savanna profiles were 4–12‰ heavier than in comparable forest profiles, indicating the influence of C4 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 C4 material) than at Alter do Chão (−21.1 to −23.4‰). The savanna profiles at Alter do Chão had relatively constant δ13C values throughout the profile (Fig. 5). In the Chapada dos Parecis savanna profile, the δ13C values decreased ca 3.5‰ from the surface to ca 2 m depth. Below 2 m, the δ13C values increased by 3.4‰, becoming similar to values found at the soil surface. The δ13C of savanna profile values at Redenção increased ca 5% from the surface to the 140–150 cm soil layer. Below this layer the δ13C 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 δ13C at depths of 50 to 60 cm, with δ13C values below decreasing to converge with comparable forest values. Although each soil profile had particular changes in δ13C with depth, a common feature observed in Roraima, Humaitá, and Carolina profiles was that the δ13C values of soil organic matter of forest and savanna became similar with increasing depth, suggesting a dominance of C3 plants in the deepest layers of these profiles. The δ13C impoverishment with depth in the savanna profile of Amapá was not as high as observed in Roraima, Humaitá, and Carolina profiles. The δ13C values of deep soil organic matter in Amapá decreased to only −23% (compared to a forest value of −25‰), suggesting the presence of C4 organic matter even at depths of 4 m (Fig. 5).

14C 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 δ¹³C (‰) 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**

$^{813}$C VALUES OF LEAVES IN SAVANNAS AND FORESTS.—The average $^{813}$C value of C$_4$ grass found in the savannas ($-13.2\%$o) is higher (heavier) than the average value for C$_4$ plants found by Desjardins et al. (1996) at Roraima savannas ($-14.2\%$o) but lower (lighter) than the average value found by Pessenda. Gomes et al. (1998) at savannas in Rondônia ($-11.7\%$o). The $^{813}$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 $-11.7 \pm 0.9\%$ ($N = 102$). On the other hand, the average $^{813}$C value for C$_3$ plants of the savannas ($-29.0\%$o) was similar to values found by Desjardins et al. (1996) and Pessenda, Gomes et al. (1998) in tree leaves collected in Roraima ($-29.6\%$o) and Rondônia ($-29.0 \pm 1.8\%$o) savannas, respectively. As in the Brazilian Pantanal region (Victoria et al. 1995), the $^{813}$C values for tree leaves collected in savannas are enriched in $^{813}$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 $-32.1\%$o, ca $2\%$o more negative than tree leaves from savannas (Martinelli et al. 1998). The most probable cause for these differences is 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 $^{813}$C was greater than overall variation among different sites. Large intraspecies variation in $^{813}$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 $^{813}$C VALUES OF THE SOIL ORGANIC MATTER.—** Generally, forest soil profiles showed an enrichment of $^{813}$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 $^{813}$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 $^{813}$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 C₄ 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 C₃ stands were artificially replaced by C₄ vegetation (Vitorelli 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 δ¹³C 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 δ¹³C 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 δ¹³C variation with soil depth is the organic matter decomposition process, which favors the loss of ¹²C (Boutton 1996). Generally, it is accepted that up to a 3.5–4.0‰ isotopic enrichment in organic matter δ¹³C 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 & Peterschmit 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 C₄ vegetation. On the other hand, in savanna soils, an impoverishment of δ¹³C with depth may suggest the presence of relict organic matter derived from C₃ vegetation.

It is important to note that different rooting depths for trees and C₄ grasses may partly account for changes with soil depth in woody savanna, especially in Redenção, Roraima, and Alter do Chão, where the number of C₃ trees per hectare was high (Table 2). Most of the studies dealing with changes in δ¹³C 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 δ¹³C of roots were not in equilibrium with δ¹³C values of coexisting soil organic matter. The δ¹³C of roots in woodlands were ca. –25‰, while δ¹³C values of the soil organic matter varied from –24 to –17‰. The δ¹³C of roots in grasslands varied from –24 to –21‰ and δ¹³C 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 C₃ and C₄ roots.

The δ¹³C values observed in the forest soil profiles of Alter do Chão, Amapoté, and Roraima are in the range of the expected values for soils where C₃ plants have remained the dominant vegetation cover. In these profiles, the maximum δ¹³C 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 δ¹³C 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 C₄ vegetation, or a mixture of C₃ and C₄ 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 from surface values. In another forest profile in the same area but far from the forest–savanna boundary in Roraima, 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 δ¹³C distribution with depth in the Humaitá area. A transect of δ¹³C values from savanna to forest area indicated decreased contributions of C₄ 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
Absy Amapi, 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 δ13C signatures of organic matter in the deepest soil layers of savanna profiles appear to record more woody (C3) 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 δ13C savanna profile in Roraima clearly indicates a strong presence of C3 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 δ13C of soil organic matter of ca −21.0‰, which indicates a mixture of C3 and C4 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 studied in the Amazon, maximum δ13C values (higher proportion of C4 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 C4 grass population increased in areas with higher fire incidence, and the δ13C of the soil became higher, suggesting the increasing influence of C4 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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Past Vegetation Changes in Amazon Savannas

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

| Site          | $C_3$ Plant Species          | $\delta^{13}$C | Site          | $C_3$ Plant Species          | $\delta^{13}$C |
|---------------|-----------------------------|----------------|---------------|-----------------------------|----------------|
| Alter do Chaço| Bowdichia virgilioides      | -29.2          | H. speciosa   | -26.9                      |
|               | Byrsonima coccolobaifolia   | -27.9          | Kielmeyera coriacea | -26.6                  |
|               | B. crassifolia              | -28.5          | K. coriacea   | -26.2                      |
|               | Casearia jasmitensis        | -30.2          | Platyctenium reticulatum | -27.8              |
|               | Chamaecrista parviflora     | -30.6          | P. reticulata | -28.5                      |
|               | Chromelia parviflora        | -32.1          | Pouteria ramiiflora | -29.0                  |
|               | Decisa scriptosa           | -31.2          | P. ramiiflora | -27.9                      |
|               | Erythroxylum suberosum      | -29.5          | Pterodon pubescens | -28.1                  |
|               | Eugenia biflora            | -31.8          | P. pubescens  | -28.1                      |
|               | Galactia jussiaceae        | -28.8          | Qualea grandiflora | -27.4                 |
|               | Hiritelea racemosa         | -32.2          | Q. grandiflora | -28.4                      |
|               | Lachemisia pacari           | -28.6          | Q. parviflora | -28.2                      |
|               | Micenia albicans           | -30.1          | S. convallarioidora | -31.6              |
|               | M. fallax                  | -31.0          | T. aurea      | -27.8                      |
|               | Myrcia cf. obtusa          | -31.4          | T. ochracea   | -29.9                      |
|               | M. simiaica                | -30.1          | T. ochracea   | -29.1                      |
|               | Pouteria ramiiflora        | -31.5          | Xylopia aromatica | -30.4                |
|               | Pythichora barbiflora      | -31.4          | X. aromatica | -30.4                      |
|               | Qualea grandiflora         | -28.7          | X. aromatica | -30.4                      |
|               | Salveria convallarioidora  | -29.2          | Humaitá       | Anacardium cf. humile | -26.9        |
|               | Scelostobium paniculatum   | -31.3          | Andira cf. vermafíga | -28.0              |
|               | Icoryena formosa           | -28.9          | A. cf. vermafíga | -29.2                      |
|               | Xylopia aromatica          | -30.9          | A. cf. vermafíga | -27.1                      |
|               | Paspalum carinatum         | -13.7          | A. surinamensis | -27.9                      |
| Amapá         | Trachypogon plumosus       | -13.3          | A. surinamensis | -27.9                      |
|               | Aegipbila lbotzyana        | -29.6          | Bonyunia antonifíla | -31.4                |
|               | Bowdichia virgilioides     | -26.7          | Brosimum gauchichaudii | -29.2              |
|               | B. virgilioides            | -30.4          | Buchenavia capitata | -30.1                |
|               | Byrsonima crassifolia      | -30.2          | Carapa savannarum | -29.2                      |
|               | B. crassifolia             | -30.2          | Casearia sylvestris | -29.0                      |
|               | Curatella americana        | -28.7          | Cattchela acuminata | -31.0                |
|               | C. americana               | -30.2          | Guatteria foliosa | -30.4                      |
|               | Hancornia speciosa         | -29.6          | Hancornia speciosa | -29.2                      |
|               | H. speciosa                | -29.5          | Heisteria ovata | -32.3                      |
|               | Hypolysus cf. pulchrum     | -30.3          | Kielmeyera coriacea | -29.0                  |
|               | Hypolytrum sp             | -28.2          | L. pacari      | -28.9                      |
|               | Mesidurus lindaviana       | -31.4          | L. pacari      | -28.5                      |
|               | Pouteria ramiiflora        | -30.7          | Laxolamaria tesmamii | -27.0               |
|               | P. ramiflora               | -30.5          | Norantea guianensis | -27.3                      |
|               | Rauwolfa pentaphylla       | -28.4          | Parkia ultii  | -31.2                      |
|               | Roupala montana            | -28.8          | Physocalymma scaberrimum | -28.9              |
|               | R. montana                 | -31.0          | Qualea parviflora | -28.2                      |
|               | Salveria convallarioidora  | -27.8          | Q. parviflora  | -27.5                      |
|               | S. convallarioidora        | -28.5          | Roupala montana | -29.6                      |
|               | Scleria cypenina           | -25.7          | Salveria convallarioidora | -26.9              |
|               | Tracypogon plumosus        | -13.0          | Simarouba amara | -29.8                      |
| Carolina      | Agonandra brasiliensis     | -30.1          | Tabebuia aurea | -31.2                      |
|               | A. brasiliensis            | -28.5          | T. aurea      | -28.6                      |
|               | Andira chordata           | -26.7          | T. aurea      | -27.9                      |
|               | A. chordata               | -27.8          | Virola subessilis | -27.0                    |
|               | Bowdichia virgilioides     | -26.7          | Vochysta ferruginea | -28.0                  |
|               | B. virgilioides           | -28.1          | V. grandis   | -29.6                      |
|               | Byrsonima crassifolia     | -30.3          | V. sessiliflua | -29.1                      |
|               | B. crassifolia            | -29.8          | Xyridaceae sp. | -26.6                      |
|               | Cocoea paraeulis           | -29.0          | Leptocoryphium lanatum | -12.9              |
|               | Curatella americana       | -28.2          | Trachypogon spicatus | -13.4                 |
|               | C. americana              | -29.1          | P. Anacardium cf. humile | -30.0                |
|               | Cybistax antiphiylitica    | -28.2          | Andira cf. vermafíga | -29.7                      |
|               | C. antiphiylitica         | -26.3          | A. cf. vermafíga | -28.2                      |
|               | Hancornia speciosa       | -29.3          | Annona grandiflora | -29.5                      |
## APPENDIX 1. Continued.

| Site          | C₃ plant species    | δ¹³C  | Site          | C₃ plant species    | δ¹³C  |
|---------------|---------------------|-------|---------------|---------------------|-------|
| Bonyunia antonifolia | −30.3               |       | Rufgea erioloba | −28.8               |       |
| Buchenavia tomentosa  | −29.9               |       | Salvertia convallariodora | −30.1               |       |
| B. tomentosa      | −26.7               |       | S. convallariodora  | −30.5               |       |
| Byrsonima verbascifolia | −28.5               |       | Acomanthes steyermarkii | −28.1               |       |
| Caryocar brasiliense | −27.5               |       | Aegiphila thozyana  | −31.0               |       |
| Davilla elliptica  | −29.8               |       | Agonanda brasiliensis | −30.8               |       |
| Diploxyris hispida  | −30.0               |       | Anadenanthes peregrina | −29.3               |       |
| D. hispida        | −30.4               |       | Annona jahnii     | −33.4               |       |
| Emmetum nitens    | −28.0               |       | A. ovata         | −28.4               |       |
| Eriotheca gracileps| −27.7               |       | Aspidosperma multiflorum | −30.8               |       |
| Eschweileria 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 virgilioides | −29.0               |       |
| Mourtiri pusa     | −29.2               |       | B. crassifolia    | −30.7               |       |
| Myrcia cf. obtusa  | −33.2               |       | Casearia ulmifolia | −30.0               |       |
| Platyzomia reticulata| −27.5               |       | Chaetacrista 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               |       | Mourtiri apiranga  | −21.5               |       |
| Syrinx ferruginea  | −27.1               |       | Palicourea rigidula | −25.7               |       |
| Syngia petrae     | −27.4               |       | Paspalum lanceolatum | −26.8               |       |
| Tabebuia aurea     | −26.1               |       | Qualea parvisifolia | −29.2               |       |
| Virola subsessilis | −28.5               |       | Q. parvisifolia   | −31.0               |       |
| Vochysiia cinnamomea| −29.7               |       | Roupala montana   | −29.4               |       |
| V. rufa           | −28.9               |       | R. montana        | −28.2               |       |
| Streptopachys ramosa| −13.0               |       | Thrysia petrosa   | −30.1               |       |
| Redenção          |                    |       |                |                    |       |
| Bowdichia virgilioides | −29.6               |       | Trattinnickia rhoifolia | −27.7               |       |
| B. virgilioides   | −29.9               |       | T. rhoifolia     | −31.3               |       |
| Byrsonima crassifolia | −28.5               |       | Xylopia aromaticca | −29.7               |       |
| B. crassifolia    | −29.9               |       | X. aromaticca    | −31.3               |       |
| Calisthenia fasciculata | −29.3               |       | Andropogon fasciatus | −12.8               |       |
| Curatella americana| −28.3               |       | Andropogon sp.    | −13.1               |       |
| C. americana      | −26.9               |       | Andropogon sp.    | −13.4               |       |
| Kielmeyera latrophyon | −26.4               |       | Trachypogon spicatus | −13.8               |       |
| Pouteria ramiflora | −31.7               |       | T. spicatus      | −12.6               |       |
| P. ramiflora      | −30.6               |       |                |                    |       |