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Late Quaternary Vegetation Dynamics in the Southern Amazon Basin Inferred from Carbon Isotopes in Soil Organic Matter

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Carbon isotopes of soil organic matter (SOM) were used to evaluate and establish the chronology of the vegetation dynamics of an ecosystem presently composed of savannas surrounded by forests. The study was carried out on a 200-km transect along highway BR 319, on the border of Amazonas and Rondônia states, in southern Amazon, Brazil. Large ranges in δ^{13}C values were observed in SOM collected from profiles in the savanna (−27 to −14‰) and forest regions (−26 to −19‰), reflecting changing distribution of ^{13}C-depleted C$_3$ forest and ^{13}C-enriched C$_4$ savanna vegetation in response to climate change. These results indicate that from about 17,000 to 9000 ^{14}C yr B.P., the study area was covered by forest vegetation. Between approximately 9000 and 3000 ^{14}C yr B.P., savanna vegetation expanded at the expense of the forest. Although the expansion of savanna did not occur with the same intensity along the study transect, this process was very clearly registered by ^{13}C-enrichment in the SOM. Since 3000 ^{14}C yr B.P., the carbon isotope data suggest that forested regions have expanded. This study adds to the mounting evidence that extensive forested areas existed in the Amazon during the last glaciation and that savanna vegetation expanded in response to warm and dry conditions during the early to middle Holocene. © 2001 University of Washington.

Key Words: **carbon isotopes; soil organic matter; vegetation dynamics; climate change; last glaciation; Holocene; Amazonia; refugia.**

INTRODUCTION

The replacement of forest by savanna in the Amazon Basin during periods such as the last glaciation has been a controversial subject. Some investigations have suggested that this region may have formed forest "refugia" during cold glacial times, due to a dry climate (Haffer, 1969; Vanzolini, 1970; Vuilleumier, 1971; Brown and Ab' Saber, 1979; Van der Hammen and Absy, 1994). According to the "refugia hypothesis" (Haffer, 1969, 1997; Vanzolini, 1970), the forest and nonforest biomes changed continuously in distribution during the geologic past, breaking up into isolated blocks and again expanding and coalescing under the varying dry to humid climatic conditions of the Cenozoic Era. The combination of a developing complex geological structure and surface relief in peripheral regions of Amazonia (creating geographical rainfall gradients), together with the effect of

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global climatic fluctuations during the Cenozoic Era, are the basic factors underlining the refugia hypothesis. Thus, it has been proposed that during cold and dry climatic periods, extensive humid forests (the refuges) probably existed in fairly large regions of the Amazonian lowlands, where sufficient surface relief was present to create rainfall gradients (e.g., near the rising Andes, around the mountains of southern Venezuela and the Guianas, as well as in Rondônia state, southern Amazon, and in the hilly areas of Pará state, eastern Amazon) (Van der Hammen and Absy, 1994; Haffer, 1997). Open forests and gallery forests probably existed in the regions between the postulated forest refugia, where variously extensive wooded savannas may, at times, have dominated the landscape (Haffer, 1997). Others have suggested that changes in the thermal regime have been the major cause for vegetation changes in the Neotropics, although some areas with lower rainfall may have been more sensitive to vegetation change (Bush, 1996; Colinvaux *et al.*, 1996).

However, the possibility of savanna expansion into forested areas during the last glacial maximum (LGM) has received some criticism. It has been postulated that cold and wet conditions favored the development of typical Andean trees and not of savanna (Bush, 1996; Colinvaux *et al.*, 1996). Some evidence suggests that the tropical forest was widespread during the LGM (Colinvaux *et al.*, 1996; Haberle and Maslin, 1999) but varied in composition due to moderate nonuniform reductions in precipitation (Van der Hammen and Absy, 1994), as well as substantial cooling (Stute *et al.*, 1995). Vegetation changes (forest to savanna) during the Holocene, due to drier conditions, have also been documented (Haffer, 1969; Sifeddine *et al.*, 1994; Pessenda *et al.*, 1996b, 1998a, 1998b, 1998c).

The stable carbon isotope composition of soil organic matter (SOM) profiles has been instrumental in identifying the changing distribution of C_3 and C_4 plant communities in the Amazon basin (i.e., forest vs savanna vegetation, respectively) and elsewhere (e.g., Boutton, 1996; Pessenda *et al.*, 1996a, 1996b, 1998a). The typical carbon isotope values of C_3 photosynthetic-pathway plants range from -20 to -35‰, whereas values of C_4 photosynthetic-pathway plants range from -9 to -16‰. Thus, C_3 and C_4 plant species have distinct, nonoverlapping carbon isotope signatures (Boutton, 1996).

Here, we present the first long and regional SOM carbon isotope record of vegetation dynamics on the border of Amazonas and Rondônia states, southern Amazon, covering the last 17,000 ^{14}C years and spanning a 200-km transect across forest and savanna ecosystems. This study is part of a major research program carried out at the Center for Nuclear Energy in Agriculture (CENA), whose aim is to evaluate vegetation dynamics during the last 20,000 years in Brazil using carbon isotopes (Pessenda *et al.*, 1996b, 1998a, 1998b; 1998c; Gouveia *et al.*, 1999).

STUDY AREA

The climate of the region is characterized by a mean annual temperature of 26°C (the mean temperature during the coolest month is higher than 18°C) and irregular rainfall (1800 to 3500 mm/yr), with a dry season from June to September, when precipitation is less than 50 mm per month (Brasil, 1978). The altitude lies between 80 and 150 m.

Soil samples were collected on a 200-km transect along BR 319 in sites of savanna and tropical forest vegetation (Fig. 1, Table 1). The study transect is located between the coordinates 8°43′ S/63°58′ W (km 5) and 7°38′ S/63°04′ W (km 188), where natural forest/savanna vegetation boundaries are well defined.

A schematic diagram of the vegetation cover along the study transect is shown in Fig. 2. The savanna vegetation, called "Campos de Humaitá" (Brasil, 1978), is composed mainly of grasses and a few short (<8 m) trees. This ecosystem changes gradually in some places and abruptly in others to a tropical mesophitic open-canopy forest (known as *floresta de terra firme*) with palms. These forests surround the savannas, whose areas range from about 10 to 100 km^2.

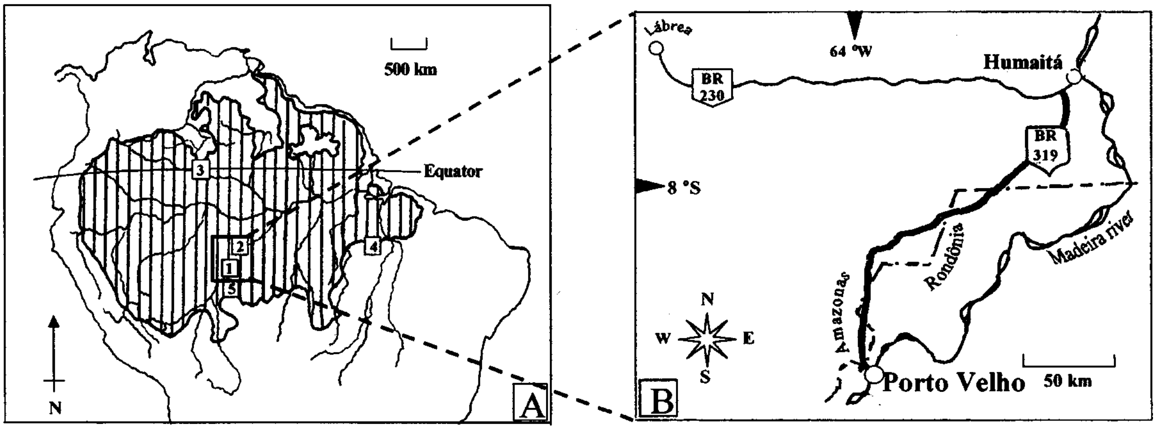

FIG. 1. (A) Map of northern South America showing Amazonia (shaded) (Shubart, 1983) and the localities (1) Porto Velho, (2) Humaitá, (3) Lago Pata, (4) Carajás, and (5) Katira. (B) Map showing the transect studied along BR 319, between Porto Velho (Rondônia state) and Humaitá (Amazonas state).

TABLE 1
Sites, Methods, Vegetation Types, and Geographic Coordinates of Soil Sampling

Site[a] (distance in km along BR 319)	Sampling method	Vegetation	Geographic coordinates
5	Drilling	Forest	8°43′ S/63°58′ W
46	Trench	Forest	8°21′ S/63°57′ W
68	Drilling	Forest	8°12′ S/63°53′ W
80	Drilling	Savanna	8°11′ S/63°49′ W
82	Drilling	Savanna	8°10′ S/63°48′ W
100	Drilling	Forest	8°06′ S/63°39′ W
111	Drilling	Forest	8°03′ S/63°31′ W
142	Trench	Forest	7°56′ S/63°20′ W
154	Drilling	Savanna	7°54′ S/63°18′ W
161	Drilling	Forest	7°50′ S/63°13′ W
172	Drilling	Savanna	7°47′ S/63°09′ W
178.5	Drilling	Forest	7°44′ S/63°06′ W
179	Drilling	Forest	7°43′ S/63°06′ W
188	Trench	Savanna	7°38′ S/63°04′ W

[a] These distances range from Porto Velho (RO) (km 0) to Humaitá (AM) (km 200) (Fig. 1), along BR 319.

METHODS

For discussion purposes, the soils are identified with (f) or (s) according to the vegetation cover (i.e., forest or savanna, respectively).

The soils were classified as Plintic Gley [km 80 (s), 82 (s), 154 (s), and 172(s)], Ferralitic Cambisol [km 5 (f), 46 (f), 100 (f), 111 (f), 142 (f), 161 (f), 178.5 (f), 179 (f), and 188 (s)], and Oxisol [km 68 (f)], according to American soil taxonomy. Soil samples were collected from trenches or with a hand-auger (Table 1).

From trenches, up to 5 kg of material was collected in 10-cm increments to a maximum depth of 300 cm. For δ^{13}C analysis, about 1 kg of soil or about 0.2 kg of hand-auger samples was sieved (5 mm) and dried at 50°C to a constant weight. Root fragments were discarded by hand picking. The dry samples were sieved again (210 μm) and any remaining debris was removed by flotation in 0.01 M hydrochloric acid and wet-sieved (210 μm). For ^{14}C analysis, the humin fraction was isolated using an acid–alkaline–acid treatment (Pessenda *et al.*, 1996a), dried to a constant weight, and sieved (210 μm).

The δ^{13}C analyses of modern vegetation were carried out on samples (leaves and branches) collected from a 10 × 100 m transect next to the trenches. The collected material was washed, dried at 50°C, ground, and analyzed. All species of plants inside the 10 × 100 m transect were identified.

Grain-size analyses were carried out at the Soil Science Department of the Escola Superior de Agricultura "Luiz de Queiroz," Piracicaba, Brazil. The results are expressed in percentages (%).

Carbon analyses of soils and plants (δ^{13}C, total C) were carried out at the Environmental Isotope Laboratory, University of Waterloo, Canada. Stable isotope results are expressed as δ^{13}C with respect to the PDB standard using the conventional δ (‰) notation,

$$\delta^{13}\mathrm{C}\ (‰) = [(\mathrm{R}_{\mathrm{sample}}/\mathrm{R}_{\mathrm{standard}}) - 1] \cdot 1000, \tag{1}$$

where $\mathrm{R}_{\mathrm{sample}}$ and $\mathrm{R}_{\mathrm{standard}}$ are the ^{13}C/^{12}C ratio of the sample and standard, respectively. Analytical precision is ±0.2‰.

The ^{14}C analyses of humin samples were carried out by AMS at Isotrace Laboratory, University of Toronto, Canada. Radiocarbon ages are expressed in ^{14}C yr B.P., normalized to a δ^{13}C value of −25‰ PDB.

RESULTS

Soil Properties and Total Organic Carbon Content

The grain-size analyses show that the clay content in the shallow parts of the soils is lower (20–30%) than in the deeper strata (32–56%) (Fig. 3). No clear difference was observed between the vegetation type and the soil clay content. The soils were classified as clayey or medium-clayey.

Total organic carbon contents of the studied soils are shown in Fig. 4. The carbon content data show a general decrease with depth, similar to that observed in other studies of the Amazon region (Pessenda *et al.*, 1998a, 1998b, 1998c). Values range from 3.39% in the shallow part of the soil to 0.05% in the deepest sampled levels. Soils of three profiles under savanna [km 80, 82, and 172] contain notably high carbon content in the upper 10 cm. Below 30 cm, similar carbon concentration was found in both savanna and forest profiles.

Soil Chronology

The radiocarbon dates are listed in Table 2. The radiocarbon data indicate increasing age with depth. Similar soil-age profiles have been reported in others parts of the Amazon basin and sites

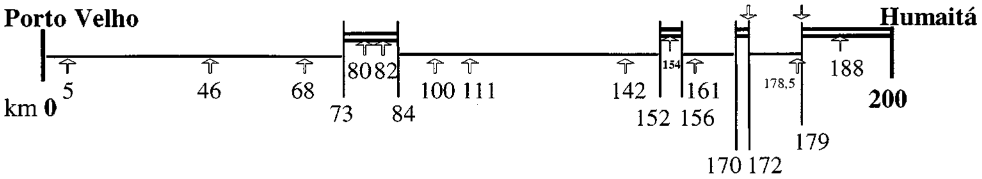

FIG. 2. Schematic diagram of the vegetation distribution and sample sites. Single lines, forest; double lines, savanna; arrows, sites of sample collection. Sample sites are identified by the distance along BR 319, from km 0 (Porto Velho) to km 200 (Humaitá).

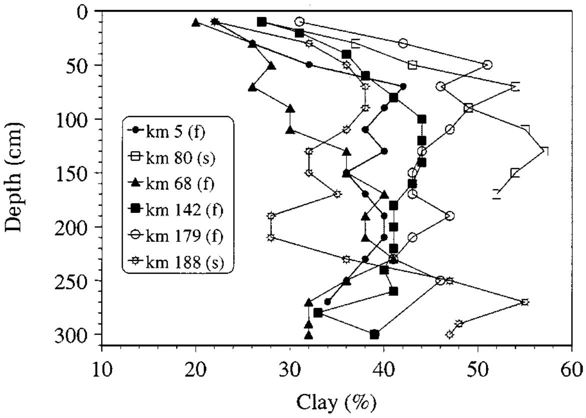

FIG. 3. Results of grain-size analyses.

TABLE 2
Results of Radiocarbon Dating (Humin Fraction)

Depth (cm)	Laboratory no. [km 46 (f)]	Age (^{14}C yr B.P.)	Laboratory no. [km 188 (s)]	Age (^{14}C yr B.P.)
30–40	TO-7734	1890 ± 50		
120–130	TO-7736	9590 ± 80	TO-7494	9170 ± 190
200–210	TO-7496	12,470 ± 110	TO-7737	12,060 ± 80
290–300	TO-7497	16,940 ± 140		

in Brazil (Pessenda *et al.*, 1996a, 1996b, 1998a, 1998b, 1998c; Gouveia *et al.*, 1997; Gouveia *et al.*, 1999). The radiocarbon data indicate that the soil profiles represent at least the last 17,000 ^{14}C yr B.P., approaching the LGM. This is the longest reported ^{14}C record for soils in the Amazon basin. Most of the reported soil profiles span the last 10,000 ^{14}C years (e.g., Pessenda *et al.*, 1996b, 1998a, 1998b, 1998c; Gouveia *et al.*, 1997), although older records describing vegetation changes during the last 40,000 ^{14}C years in the Amazon basin have been reported from lake sediments (Absy *et al.*, 1991; Sifeddine *et al.*, 1994; Van der Hammen and Absy, 1994; Colinvaux *et al.*, 1996) and marine sediments (Haberle and Maslin, 1999).

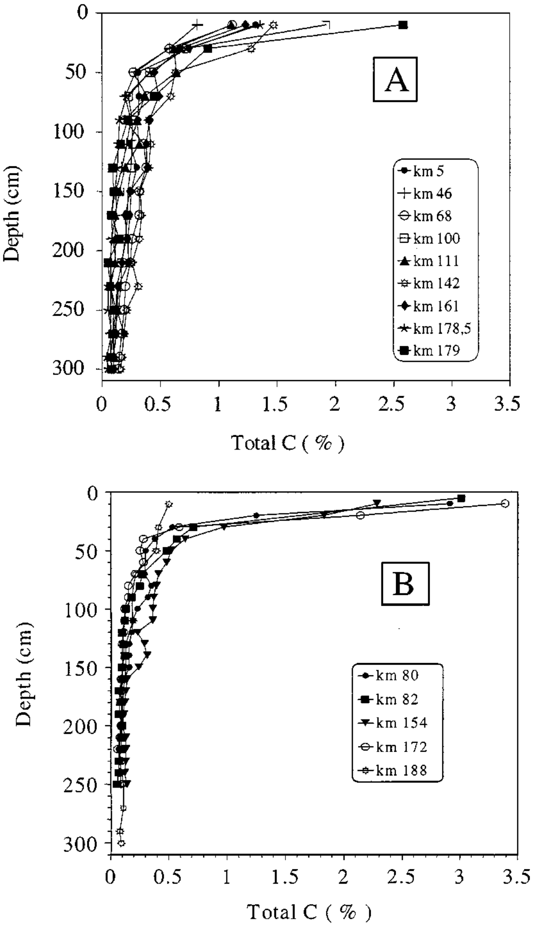

FIG. 4. (A) Total organic carbon content of the profiles under forest. (B) Total organic carbon content of the profiles under savanna.

Plant $\delta^{13}C$

Plant $\delta^{13}C$ data (Fig. 5) show that at km 188 (s), 13 (65%) of the identified species (not related to the biomass) have values ranging from −27.5 to −35.8‰ (typical of C_3 plants) and seven (35%) of the species have values ranging from −11.9 to −14.3‰ (representing C_4 vegetation). The most abundant species (related to the covering biomass) are Poaceae [Gramineae], like *Andropogon leucostachyus* ($\delta^{13}C$ −14.3‰), *Panicum* cf. *laxum* ($\delta^{13}C$ −12.5‰), and *Paspalum* cf. *multicaule* ($\delta^{13}C$ −12.9‰). These identifications are in agreement with Gottsberger and Morawetz (1986) and Janssen (1985). At the forest sites (km 46 and km 142), all 40 species (100%) present $\delta^{13}C$ values ranging from −26.2 to −38.0‰, including the Poaceae *Bambusa* sp. ($\delta^{13}C$ − 36.9), typical of C_3 plants. These results are in good agreement with other isotope studies of C_3 and C_4 plants (Ehleringer, 1991; Boutton *et al.*, 1996; Pearcy *et al.*, 1987; Ehleringer and Monson, 1993; Nordt *et al.*, 1994).

SOM $\delta^{13}C$

The SOM $\delta^{13}C$ results are presented in Figs. 6 and 7. The general analytic uncertainty of the values is ±0.2‰. The savanna soils show a wide range in isotopic composition that varies between −27 and −14‰. The lower parts of the profiles (300- to 150-cm depth) show the most ^{13}C-depleted values, ranging from −27.3‰ (at 250-cm depth; km 82) to −23.3 (at 220-cm depth; km 154). A trend toward ^{13}C-enriched values occurs between 150- and 30-cm depth in the savanna profiles, reaching values as high as −14.2‰ (km 154). This trend is reversed in the shallow part of the savanna profiles toward slightly more ^{13}C-depleted values (Fig. 6).

The soils at the forest sites also show large isotopic variations (−26 to −19‰). In the deepest interval (300–190 cm) $\delta^{13}C$ values range between −25 and −24‰. Similar to in the savanna profiles, a trend toward ^{13}C-enriched values occurs between

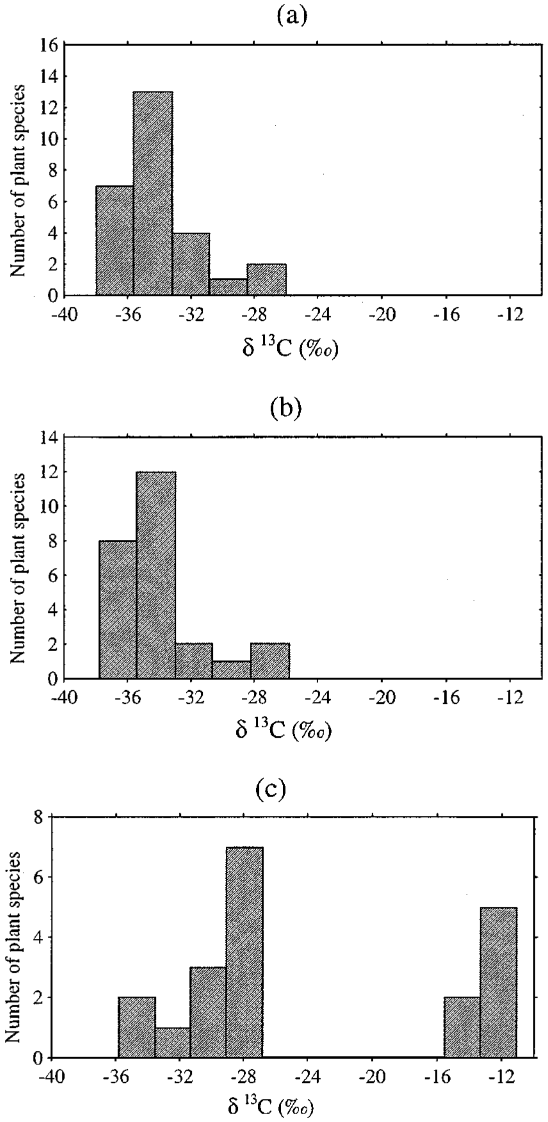

FIG. 5. The δ^{13}C range of the C_3 and C_4 plant species collected at: (a) km 46 (f); (b) km 142 (f); and (c) km 188 (s). The three sites have some common plant species.

190- and 40-cm depth in the forest profiles. This trend is more pronounced at sites km 68, km 100, and km 142, whereas no isotopic change is observed at site km 5 within this depth interval. The shallow parts of the forest profiles show a shift toward ^{13}C-depleted values (Fig. 7).

DISCUSSION

Soil Carbon Content and δ^{13}C Values in the Shallow Soils

The higher carbon content observed in the uppermost strata of some savanna soil profiles does not agree with data reported for other Amazonian soils (Desjardins *et al.*, 1996; Gouveia *et al.*, 1997). This may be related to the location of these savanna sites in depressions that are completely flooded during at least six months a year, causing accumulation of organic matter. As the savannas are surrounded by forest, the higher carbon content may be related to carbon transport from the forests during rain events (Pessenda, L. C. R., *et al.*, unpublished data).

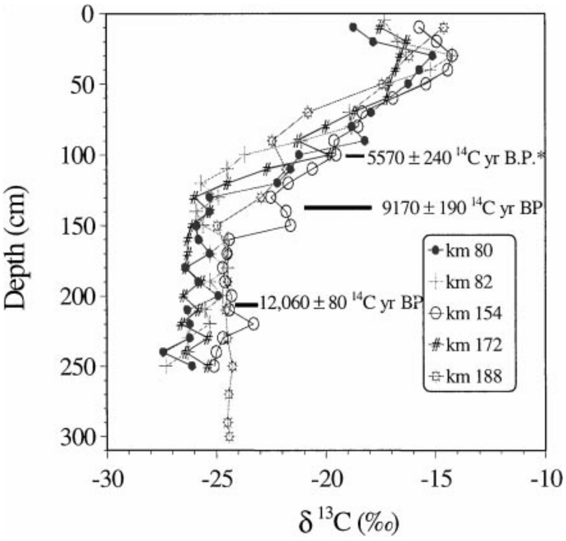

FIG. 6. The δ^{13}C and ^{14}C variation with depth at the savanna sites. Radiocarbon dates (^{14}C yr B.P.) are from the km 188 (s) site. The youngest date (marked with an asterisk) is from Pessenda *et al.* (1988a).

The high δ^{13}C value of $-14.6‰$ obtained in the soil surface layer (0–10 cm) at km 188 (s) likely best characterizes vegetation cover consisting of predominantly C_4 plants (Cerri *et al.*, 1985; Martin *et al.*, 1990). Notably, site km 188 (s) is located farthest from forest vegetation and is topographically high; thus it is not susceptible to carbon transport from surrounding areas. Lower δ^{13}C values in the shallow zones of soils from the others

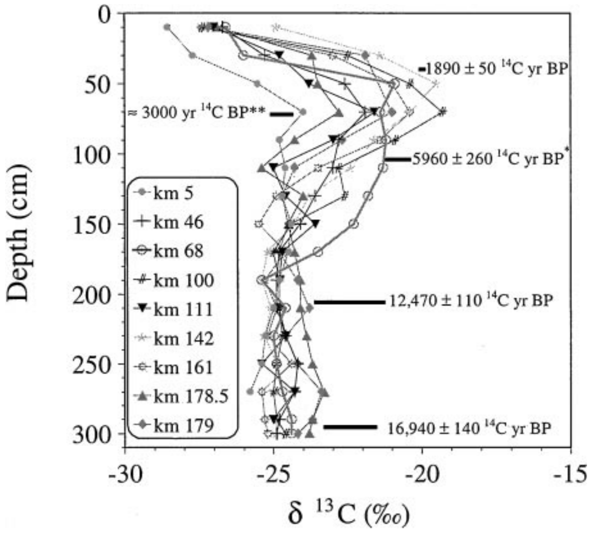

FIG. 7. The δ^{13}C and ^{14}C variation with depth, at the forest sites. Radiocarbon dates (^{14}C yr B.P.) are from the km 46 (f) site. The single asterisk marks a date obtained from Pessenda *et al.* (1998a), and the double asterisk marks an estimate obtained from Pessenda *et al.* (1998a).

savanna sites (−18.7‰ at km 80, −17.3‰ at km 82, −15.7‰ at 154 km, and −17.5‰ at km 172) reflect greater contributions of C_3 vegetation.

The $\delta^{13}C$ values in shallow levels of the forest soils (−24.9 to −28.6‰) are in good agreement with the $\delta^{13}C$ range of the present forest vegetation (−26.2 to −38.0‰).

SOM $\delta^{13}C$ and Vegetation Dynamics

In our interpretation of the SOM $\delta^{13}C$ profiles, we assume that variations smaller than 3‰ are associated with isotopic discrimination that can occur during organic matter decomposition and with variations in the carbon isotope composition of atmospheric CO_2 (Boutton, 1996). We infer that variations in excess of 4‰ have resulted from changes in plant community (Cerri *et al.*, 1985; Boutton, 1996; Desjardins *et al.*, 1996).

Thus, the low $\delta^{13}C$ values of −27.3 to −23.3‰ observed between 300 and 150 cm depth at the savanna sites are presumed to reflect SOM formed under forest vegetation. Similarly, the lower interval from 300- to 190-cm depth in the soils of forest sites show $\delta^{13}C$ values typical of SOM formed under forest (Schwartz *et al.*, 1986; Desjardins, *et al.*, 1996; Pessenda *et al.*, 1996a, 1998a, 1998b).

Substantial isotopic enrichment observed in the 150- to 30-cm depth interval in the savanna soils, and from about 190 to 70 cm in most of the forest sections, is likely related to an increase in the contribution of C_4 plant biomass due to savanna expansion. In the southern part of the transect, ^{13}C-enrichment is most pronounced in savanna soil profiles (km 80 and 82), reaching values as high as −14.2‰, and it becomes less evident in forested sections to the south and north, where the highest value is −19.3‰ (Fig. 8). These data suggest that savanna in this area expanded northward to at least km 111 and southward to at least km 46.

The trend toward ^{13}C-depleted values in the upper 70 cm in the forest soil profiles probably reflects a shift toward increasing influence of C_3 plants at the expense of declining savanna vegetation.

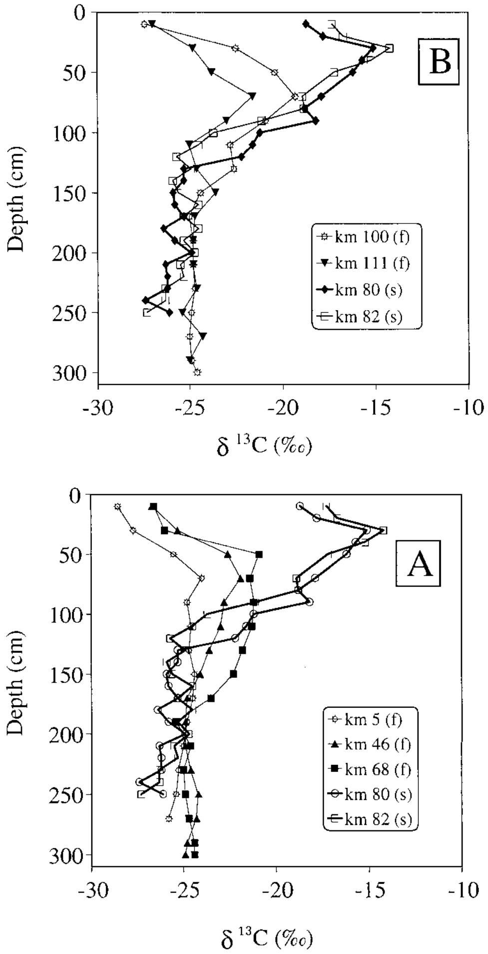

FIG. 8. SOM $\delta^{13}C$ profiles arranged (A) south and (B) north from the savanna at km 80 and km 82. The analytic uncertainty is ±0.2‰.

SOM $\delta^{13}C$ Data and the Palaeoclimatic Interpretation

The forest SOM in the lower level of the soil profiles was probably formed between 17,000 and 9000 ^{14}C yr B.P. based on radiocarbon dating of the km 46 (f) and km 188 (s) sites. Dominance of forest vegetation, during the last part of the last glaciation to the early Holocene, is consistent with other vegetation reconstructions (Colinvaux *et al.*, 1996; Haberle and Maslin, 1999). Other studies, however, have postulated that savanna expanded during the LGM until about 13,000 ^{14}C yr B.P. (Absy *et al.*, 1991; Sifeddine *et al.*, 1994; Van der Hammen and Absy, 1994). However, the Van der Hammen and Absy (1994) study was conducted from a single stratigraphic section at Katira Creek, located about 120 km to the south of Porto Velho in Rondônia. Based on limited information from organic matter dating 18,500 ^{14}C yr B.P. and a $\delta^{13}C$ value of −15.6‰, they suggested that Rondônia was covered by savanna vegetation during the LGM. Our study, carried out along a 200-km transect, strongly questions regional conclusions derived from a single locale in this area. Evidently, a uniform widespread vegetation change cannot be ascribed for the Amazon basin during the LGM. Indeed, recent analyses by Hooghiemstra and Van der Hammen (1998) suggest that a 40% reduction in precipitation will maintain a forest in the area studied by Colinvaux *et al.* (1996), whereas savanna vegetation will expand in the regions of Katira (Rondônia) and Carajás (Pará state).

In our study region, widespread savanna expansion does not appear to have been begun until ca. 9000 ^{14}C yr B.P., and it lasted until about 3000 ^{14}C yr B.P. This interpretation is similar to other documented forest-to-savanna vegetation changes in the Amazon basin during the early and middle Holocene (Sifeddine *et al.*, 1994; Desjardins *et al.*, 1996; Gouveia *et al.*, 1997; Pessenda *et al.*, 1998a, 1998b). However, some regions in the Amazon basin remained forested during the middle Holocene (Colinvaux *et al.*, 1996; Pessenda *et al.*, 1996b, 1998c), possibly reinforcing the refugia hypothesis. Some authors argue that savanna expansion did not occur on a regional scale, but rather was a much more localized (Martinelli *et al.*, 1996) and recent phenomenon (Sanaiotti, 1996).

Our results show forest expansion at the expense of savanna since about 3000 ^{14}C yr B.P. This vegetation pattern has also been documented near Humaitá-AM (Gouveia *et al.*, 1997; Pessenda *et al.*, 1998a). A similar study showed the advance of forest over savanna in Roraima in the northern Amazon (Desjardins *et al.*, 1996).

In view of C_3 and C_4 plant species dynamics, authors have established the dependence between the expansion of a C_4 dominant vegetation (savanna) at the expense of a C_3 dominant vegetation (tropical forest) and the presence of a climate with a significant proportion of annual precipitation occurring just prior to or during the warmest part of the growing season (Ehleringer and Monson, 1993; Boutton, 1996). In addition to the influence of the annual amount of precipitation and its seasonality, studies have indicated a temperature dependence in the C_4 and C_3 competitive interaction: C_4 species are better adapted to warmer (Guillet *et al.*, 1988; Ehleringer and Monson, 1993; Nordt *et al.*, 1994; Boutton, 1996), high-light-intensity (Osmond *et al.* 1982; Nordt *et al.*, 1994), and semiarid environments (Pearcy *et al.* 1987). Therefore, according to our study, the period 17,000–9000 ^{14}C yr B.P. appears to have been wetter and probably cooler. The expansion of the savanna between 9000 and 3000 ^{14}C yr B.P. suggests drier and probably warmer conditions than the previous period, during early and middle Holocene time. Martin *et al.* (1997) suggested a similar climate pattern for this region during the late Pleistocene. From 3000 ^{14}C yr B.P. to the present, expansion of C_3 vegetation (forest) suggests that suitably wetter conditions favored this change in the region.

It is well known that mechanisms other than climate are capable of inducing dramatic changes in vegetation, either through their direct effects or through interaction with climate. For example, grazing, fire, soil nutrients, and human activities can influence vegetation composition and inhibit the advance of C_3 woody plants (Nordt *et al.*, 1994). However, in our study we found no evidence of ancient human activity, grazing, or soil composition that could have led to savanna development. Fire is an important phenomenon at some sites in the studied region, and it may have been before. Probably its influence on vegetation dynamics was strongest, seeing that since 3000 ^{14}C yr B.P. forest vegetation expanded at the expense of the savanna. Considering that 250 km (taking in account the results obtained by Pessenda *et al.* (1998a) in a 50-km transect in the same region) is too large a distance for prehistoric human agricultural practice, we suggest that fire events probably were caused by some change of climate, such as a shift to drier and probably warmer conditions. The synchronous and similar vegetation changes in other regions of Amazonia reinforce this hypothesis.

CONCLUSIONS

This study presents the first long late Quaternary record of vegetation dynamics inferred from carbon isotope composition of SOM in the southern Amazon. Significant carbon isotope variations reflecting changes in vegetation were observed in 14 soil profiles collected along a 200-km transect that included forest and savanna sites. Three major vegetation phases were identified. These include (1) a forest phase between 17,000 and 9000 ^{14}C yr B.P., (2) savanna expansion between 9000 and 3000 ^{14}C yr B.P., and (3) forest expansion after 3000 ^{14}C yr B.P. Our study suggests that, in the region forest vegetation was not replaced by regional savanna expansion during the final part of the last glaciation as has been suggested by others studies, and brings into question the relationship between climate change and nonuniform vegetation response in the Amazon. Similarly, savanna expansion appears to have occurred during the dry and warm early and middle Holocene, although the regional significance of this vegetation change also remains uncertain in light of other studies indicating that forest vegetation was widespread during this interval. Further studies utilizing carbon isotope profiles in SOM at other forest–savanna ecotonal boundary regions may contribute to a more effective characterization of local versus regional vegetation response to past climate change in Amazonia.

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