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Changes of the forest-savanna boundary in Brazilian Amazonia during the Holocene revealed by stable isotope ratios of soil organic carbon

Received: 20 November 1995 / Accepted: 29 May 1996

Abstract The possibility of ecosystem boundary changes in northern Brazilian Amazonia during the Holocene period was investigated using soil organic carbon isotope ratios. Determination of past and present fluctuations of the forest-savanna boundary involved the measurement of natural ^{13}C isotope abundance, expressed as $\delta^{13}\text{C}$, in soil organic matter (SOM). SOM ^{13}C analyses and radiocarbon dating of charcoal fragments were carried out on samples derived from soil profiles taken along transects perpendicular to the ecotonal boundary. SOM $\delta^{13}\text{C}$ values in the upper soil horizons appeared to be in equilibrium with the overlying vegetation types and did not point to a movement of the boundary during the last decades. However, $\delta^{13}\text{C}$ values obtained from deeper savanna and forest soil layers indicated that the vegetation type has changed in the past. In current savanna soil profiles, we observed the presence of mid-Holocene charcoals derived from forest species: fire frequency at that time was probably greater, and more extensive savanna may have resulted. Isotope data and the presence of these charcoals thus suggest that the forest-savanna boundary has shifted significantly in the recent Holocene period, forest being more extensive during the early Holocene than today. During the middle Holocene, the forest could have strongly regressed, and fires appeared, with a maximum development of the savanna vegetation. At the beginning of the late Holocene, the forest may have invaded a part of this savanna, and fires occurred again.

Key words Soil organic matter · ^{13}C natural abundance · Forest-savanna boundary dynamics · Brazilian Amazonia · Paleoclimatic changes

Introduction

Palynological and geomorphological studies show that the tropical lowlands of South America have experienced vegetation changes during the late Quaternary (Servant et al. 1993). These studies suggest that the extent of tropical forest and savanna have varied greatly during this period, with changes in vegetation being predominantly controlled by ambient paleoclimatic variations (Servant et al. 1981; Bush et al. 1990; Van der Hammen 1991). Some results show that regional regressions of the forest coupled with modifications of the floristic composition have occurred in some areas of the Amazon basin as a consequence of previous drier climatic periods (Absy and Van der Hammen 1976; Liu and Colinvaux 1988; Absy et al. 1991).

At present, Roraima State (Brazilian Amazonia) and other parts of tropical South America are covered by a forest-savanna mosaic. The distribution of forest and savanna are not always correlated with geomorphologic, hydrologic and edaphic factors (Carneiro Filho 1993). The most likely hypothesis for the origin and present distribution of these mosaics is palaeoclimatic change; however, few data are available from this region of Amazonia.

The aim of this paper is to provide, through measurement of soil organic matter (SOM) natural ^{13}C abundance, direct geochemical evidence of the evolution of forest-savanna boundaries during the Holocene. SOM content under both vegetation types was also studied.

Materials and methods

Study site and sampling

The study was carried out in Roraima State, Brazil ($2^{\circ}52'\text{N}$ – $60^{\circ}32'\text{W}$; Fig. 1) at the northern limit of the Brazilian Amazon-

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ian forest. The climate is characterized by a mean annual temperature of 26.5° C and a mean annual rainfall of 1500 mm, 80% of which falls between April and October (Nimer 1989). The study area is located in a peneplain landscape recovered by a forest-savanna mosaic. The continuous savanna grass community is dominated by the genera *Arctida*, *Andropogon* and *Trachypogon* (Silva 1993), interspersed with trees, mainly *Curatella americana*, *Byrsonimia crassifolia* and *Bowdichia virgilioides*. Tropical semideciduous forest occurs at the savanna margin. This semideciduous forest is generally considered as a transitional state between the dense evergreen forest and the savanna (Radambrasil 1975).

Local soils have developed on Cenozoic continental sediments of the Boa Vista formation and are predominantly medium-textured oxisols. The main characteristics of these soils are shown in Table 1 and indicate that lower soil layers under both vegetation types are quite similar, having undergone the same ferrallitization process. On the other hand, the upper soil layers (0–40 cm) show some more important differences, with the savanna topsoil having a lower clay content and a stronger textural gradient than that of the forest. The cation exchange capacity and sum of exchangeable bases are slightly higher under the forest than the savanna system. Existing differentiation of topsoils seems to depend upon the type of vegetation.

In May 1992 and 1993, three transects (Tr I, Tr II, Tr III) 60 m apart, were laid out perpendicularly to the forest-savanna boundary at a site where the boundary was abruptly defined. The loca-

tion of the transects and sampling points are shown in Fig. 1. The transects (FSB on Fig. 1) were 140 m long extending from well within the forest, across the boundary and into the savanna. Six cores were taken from each transect: three from the forest soil, at 3, 15 and 70 m from the boundary and three from the savanna soil, at 3, 15 and 70 m from the boundary. Soils were sampled using a 6-cm-diameter auger, with cores varying in depth from 120 to 460 cm. The soil samples were then air-dried, sieved (2 mm), homogenized and ground to <200 µm. Forest litter was collected and fresh foliage was taken from the woody and herbaceous species of the savanna. This material was dried at 50° C and finely crushed using an electric mill. On the studied transects, three pits 150 cm long and 120 cm deep were dug, two in the savanna and one in the forest, in order to sample charcoals from the exposed profiles.

Two other profiles were sampled as references (Fig. 1): one under evergreen forest (Confiança, C on Fig. 1) located 50 km south of the forest-savanna boundary under investigation (2°25'N–60°40'W) and the other in a savanna zone (Agua Boa de Cima, ABC on Fig. 1) 5 km north-west of the study boundary (2°55'N–60°34'W). Both soils were sampled to a depth of 450 cm.

Analytical methods

The organic carbon and total nitrogen contents were determined by dry combustion in a Carlo Erba NA 1500 CHN elemental analyser. SOM isotope ratios were measured on a Fisons SIRA 10 Isotope Ratio Mass Spectrometer coupled with an elemental analyser (Girardin and Mariotti 1991). Carbon-13 natural abundance was expressed in δ units, by reference to the international standard PDB (Craig 1957), according to the following equation:

$$\delta^{13}\text{C} \text{‰} = \frac{[^{13}\text{C}/^{12}\text{C}]_{\text{sample}} - [^{13}\text{C}/^{12}\text{C}]_{\text{PDB}}}{[^{13}\text{C}/^{12}\text{C}]_{\text{PDB}}} \cdot 1000$$

Repeated δ¹³C measurements of a reference soil carefully ground and homogenized yielded a precision (1 σ, 8 aliquots) of 0.06‰. To minimize the effects of sample heterogeneity, all samples were ground, sieved and homogenized to <200 µm.

Radiocarbon measurements on charcoal samples distributed in the first metre of savanna soils were carried out by liquid scintillation counting (Balesdent and Guillet 1982) or by accelerator mass spectrometry. These charcoals are treated prior to ¹⁴C measurements in order to eliminate contaminants; after sorting out under a magnifying glass, they are cleaned by ultrasonics and sieved to eliminate particles <63 µm. They are then treated in a boiling alkaline solution (pH 10) for 1 h, rinsed, put in a boiling acid solution (pH 2) for 1 h and rinsed again.

Via the study of SOM isotope compositions, the natural difference in the stable carbon isotope composition of C₃ and C₄ plants (Bender 1971) provides an opportunity to assess vegetation changes in areas where forest (C₃) and tropical savanna grasses (C₄) coexist. Carbon isotope fractionation associated with photo-

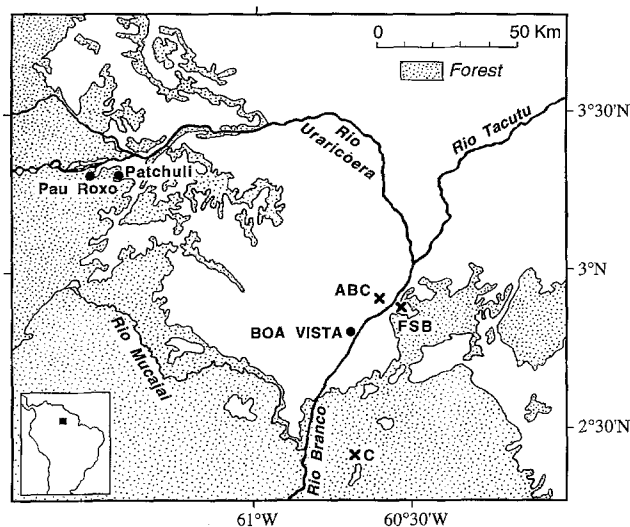
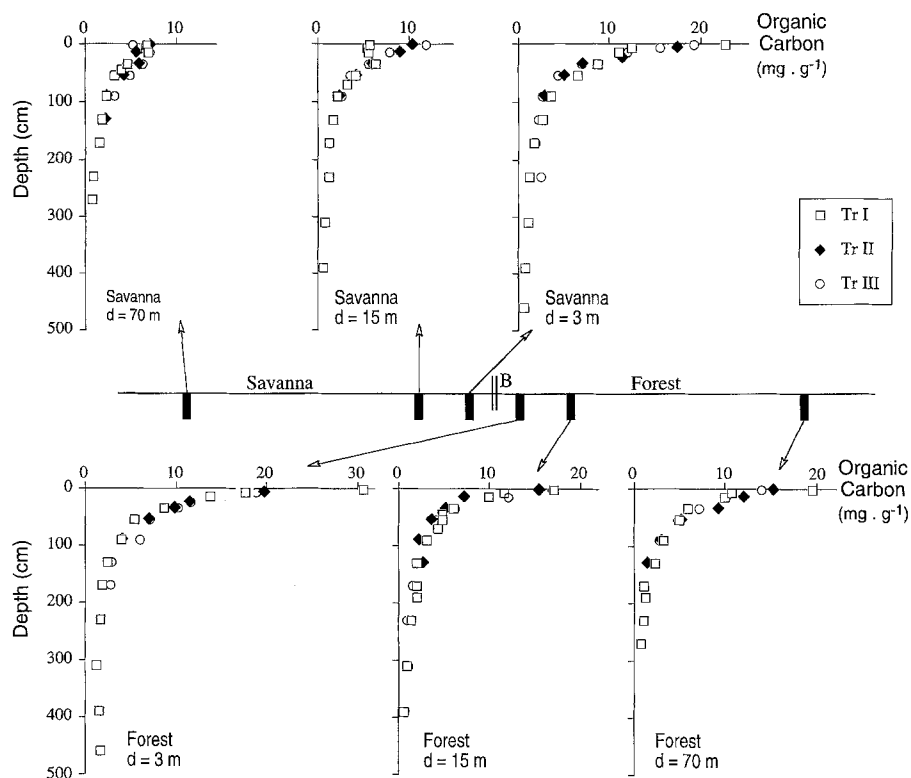


Fig. 1 Location map of the studied sites (ABC Agua Boa de Cima, C Confiança; FSB three transects on the forest-savanna boundary)

Table 1 Main analytical characteristics of soils from the study site (CEC cation exchange capacity)

Depth (cm)	Clay content (%)	pH (H ₂ O)	CEC (mEq 100 g ⁻¹)	Exchangeable bases (mEq 100 g ⁻¹)
Forest soil				
0–10	19.1	4.05	2.10	0.84
20–30	20.3	4.08	1.98	0.16
70–80	34.1	4.53	1.74	0.16
160–170	32.7	4.40	0.94	0.08
250–260	25.7	4.77	0.96	0.10
Savanna soil				
0–10	8.0	4.55	1.56	0.57
20–30	15.3	4.34	1.96	0.24
70–80	37.5	4.37	1.68	0.12
160–170	30.6	4.74	0.86	0.05
250–260	25.7	4.81	0.80	0.05

Fig. 2 Soil organic carbon content in the studied profiles of the three transects, Tr I, Tr II and Tr III [(*d* distance, in metres, between a given soil profile and the forest-savanna boundary) (*B*)]



synthesis is less in C_4 than in C_3 plants: $\delta^{13}C$ values of C_3 plants lie between -23 and -34‰ (average of -26‰) whereas for C_4 plants they range from -9 to -17‰ (average of -12‰). The isotope composition of SOM reflects that of the vegetation growing on the soil, except for a slight general increase of several ‰ with depth. This observed ^{13}C enrichment with depth can be explained as follows: (1) by an alteration with time of the isotope composition of the vegetation as a consequence of recent ^{13}C content variations in atmospheric CO_2 ; (2) differential preservation of ^{13}C -enriched SOM components could potentially account for the pattern of ^{13}C enrichment with depth: isotope differences up to 5‰ are reported between various biochemical components of plants, and (3) by isotope fractionation during SOM mineralization (for more details see Deines 1980; Balesdent et al. 1987; Nadelhoffer and Fry 1988; Mariotti 1991; Mariotti and Peterschmitt 1994). This enrichment, always $<4\text{‰}$, is not large enough to mask the 14‰ difference between C_3 and C_4 plant litter. Therefore, it is possible to determine, using the ^{13}C content of a SOM profile, if the C_3/C_4 composition of a plant community has changed in the past (Dzurec et al. 1985; DeLaune 1986; Schwartz et al. 1986; Guillet et al. 1988; Mariotti and Balesdent 1990; Ambrose and Sikes 1991; McPherson et al. 1993; Wang et al. 1993; Mariotti and Peterschmitt 1994).

Results

Distribution of organic carbon

Forest and savanna soil profiles showed significant differences in their total C contents (Fig. 2). The carbon concentration in the first few centimetres of the forest soil ranged from 14 to 20 mg g^{-1} . Then, the C concentration decreased abruptly but continuously, without any evidence of an organic palaeohorizon, ranging from 5.3 to 9.3 mg g^{-1} in the 30 to 40 cm layer. Below this level, the

C content decreased more slowly, but still continuously. In forest, near the savanna boundary (3 m), the C concentration was greater than 30 mg g^{-1} in the first centimetres and decreased to about 9 or 10 mg g^{-1} in the 30 to 40 cm layer. In the savanna soil, 15 and 70 m from the boundary, the C content of the upper 50 cm was clearly lower than that of the forest soil. Topsoil C concentrations ranged from 5.2 to 11.9 mg g^{-1} and at 35 cm decreased to 5 – 6 mg g^{-1} . Nearest to the forest boundary (3 m), the savanna soil C concentration was almost identical to that of the forest edge soil.

$\delta^{13}C$ of plant and litter materials

The $\delta^{13}C$ values of a mean bulk sample of forest litter components ranged from -30.2‰ for whole leaves to -28.3‰ for leaf fragments. Twig/branch fragments expressed an intermediate value of -29.1‰ . These values are typical of C_3 plants and similar to results obtained from another Amazonian forest litter (Desjardins et al. 1994). A mean bulk sample of savanna grasses presented a higher $\delta^{13}C$ value (-14.2‰) typical of C_4 plants, while savanna tree foliage expressed the low value of -29.6‰ more typical of C_3 plants.

Distribution of SOM $\delta^{13}C$

All forest soils have similar distribution profiles for the SOM $\delta^{13}C$, regardless of proximity to the savanna-forest boundary (Fig. 3). In the surface horizon (0 – 5 cm depth),

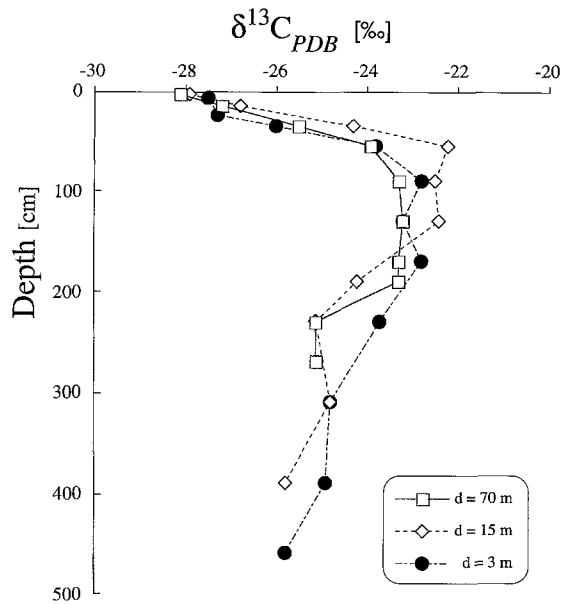


Fig. 3 Profiles of $\delta^{13}\text{C}$ in the soils under forest, at various distances (d) from the forest-savanna boundary. Up to 120 cm, each point represents the mean value for the three studied transects

the values ranged from -28.5 to -27.5‰ and then increased by $5\text{--}6\text{‰}$ to a depth of between 60 and 90 cm. The maximum $\delta^{13}\text{C}$ values ranged from -23.2 to -22.2‰ and remained relatively constant to about 2 m depth. In the lower parts of the soil profiles (2 to 4 m depth), the SOM $\delta^{13}\text{C}$ values decreased slightly, to -25.8‰ . Differences between individual transects are generally low (about 1‰).

Under savanna vegetation, the SOM $\delta^{13}\text{C}$ distribution in the upper soil profiles varied with distance from the boundary (Fig. 4). At 70 m from the boundary, topsoil $\delta^{13}\text{C}$ values ranged from -15.8 to -14.8‰ , typical of arboraceous savanna. Values increased slightly to 20–40 cm and then decreased abruptly between 40 and 130 cm. Below this depth, they continued to decrease slowly reaching values of -25 to -23‰ . The profile at 15 m from the forest boundary showed a similar topsoil ^{13}C distribution, with values being slightly more negative, ranging from -17.6 to -16.9‰ . Nearest the boundary (3 m), the upper soil layers showed a different $\delta^{13}\text{C}$ distribution. In the first few centimetres, the ^{13}C isotope composition of SOM was -23.9‰ , increasing sharply to -18.8‰ at 60 cm depth. Below 60 cm, the $\delta^{13}\text{C}$ distribution was almost the same as those of the other savanna profiles, decreasing to values of -25 to -24‰ .

In the reference soil, under evergreen forest (Confiança, C on Fig. 1) 50 km south of the study site, the SOM $\delta^{13}\text{C}$ distribution profile (Fig. 5) resembled that of the semideciduous forest soil (Fig. 3). From the topsoil to 60 cm depth, $\delta^{13}\text{C}$ increased from -28.3‰ to -23.9‰ and then decreased to -26.5‰ at 4 m depth. Except for the first few centimetres, $\delta^{13}\text{C}$ values were always slightly more negative than those for the semideciduous soil profiles.

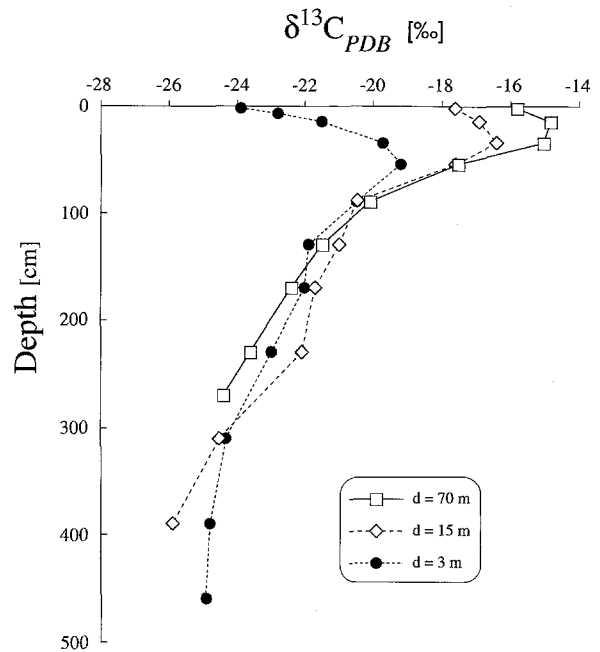


Fig. 4 Profiles of $\delta^{13}\text{C}$ in the soils under savanna, at various distances (d) from the forest-savanna boundary. Up to 120 cm, each point represents the mean value for the three studied transects

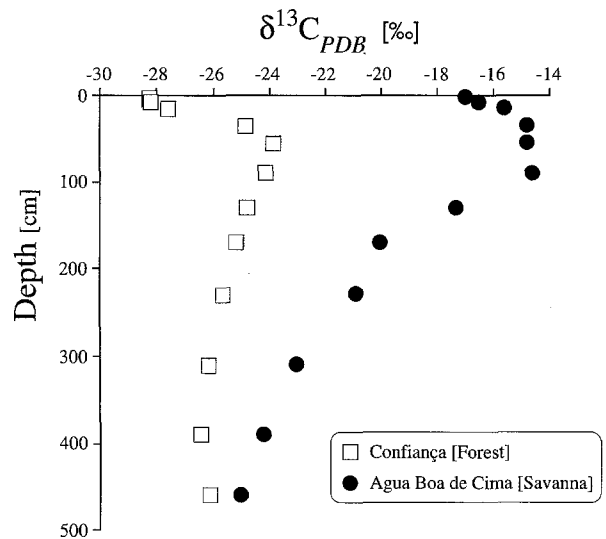


Fig. 5 $\delta^{13}\text{C}$ profiles in the reference soils, under savanna (Agua Boa de Cima) and forest (Confiança). See Fig. 1 for locations of the profiles

The reference savanna soil, located 5 km north-west of the studied transects (Agua Boa de Cima, ABC on Fig. 1), had surface horizon SOM $\delta^{13}\text{C}$ values (Fig. 5) similar to those of the study site savanna ($d=70$ m) profiles (Fig. 4). As with other savanna soils studied, $\delta^{13}\text{C}$ values remained almost constant (-14.8‰) between 30 and 100 cm and then decreased steadily to -25‰ at 460 cm.

Table 2 Charcoal origin and apparent radiocarbon age (determination of the origin of the charcoal was made by R. Dechamps, Musée Royal de l'Afrique Centrale, Tervuren, Belgique) (*for.* forest, *sav.* savanna)

	Depth (cm)	Species	Age (B.P.)
Forest soil	20	<i>Gutteria schomburgkiana</i> for.)	
	35	<i>Copaifera langsdorfii</i> (for.)	
	52	<i>Connarus</i> sp. (for. or sav.)	2750±60
Savanna soil pit 1	30	<i>Bauhinia</i> sp. (for.)	
	30	<i>Terminalia amazonica</i> (for.)	1790±60
	62	<i>Connarus</i> sp. (for. or sav.)	6540±30
	78	<i>Vitex</i> sp. (for. or sav.)	7630±70
Savanna soil pit 2	15	<i>Aspidosperma spruceanum</i> (for.)	
	34	<i>Terminalia amazonica</i> (for.)	
	34	<i>Cassia</i> sp. (for. or sav.)	
	40	<i>Terminalia amazonica</i> (for.)	3160±50
	45	<i>Peltogyne densiflora</i> (for.)	3230±60
	67	<i>Terminalia amazonica</i> (for.)	2780±60
	67	<i>Vitex</i> sp. (for. or sav.)	

¹⁴C dating of charcoal

Charcoal fragments were observed and sampled from pits dug in both savanna and forest soils. Fragments were more abundant in savanna than forest soils. A number of these fragments were radiocarbon dated (Table 2) leading to their classification into two age groups; one group with ages ranging from 1790 to 3230 years B.P. and the other from 6540 to 7630 years B.P.

Discussion

The carbon content and SOM distribution observed in the forest soil were similar to results obtained from most Amazonian oxisols (Volkoff and Cerri 1988). Soil organic carbon contents of the study site savanna soil are in the same range of values quoted by Askew et al. (1970), Eden (1974) and Ross et al. (1992) for other savanna regions of Amazonia. The lower C content of savanna compared to forest topsoil may be related to its lower clay content and smaller litter inputs. In most oxisols, SOM content is strongly correlated with soil texture (Feller et al. 1991). The savanna soil nearest to the boundary showed a higher C content than savanna soils further away, reflecting the influence of important litter inputs from the adjacent forest, and its greater clay content. Our results complement the review of Sanchez et al. (1982), who showed that soils under tropical forest vegetation generally have higher C contents in their uppermost layers than soils under tropical savanna vegetation.

The δ¹³C values measured in the topsoil of the forest soil at our study site are typical of C₃ vegetation, but the δ¹³C distribution pattern with depth did not reflect that observed in other Amazonian forest soils (Desjardins et al. 1991), where δ¹³C values increase steadily, 2.1–3.2‰, with depth (Fig. 6). A similar increase with depth was also observed in a number of other tropical and temperate forest soils (Goh et al. 1976; O'Brien and Stout 1978; Volkoff et al. 1982; Balesdent et al. 1987; Nadelhoffer and Fry 1988; Martin et al. 1990; Schwartz et al. 1992; Mariotti and Peterschmitt 1994), and may be

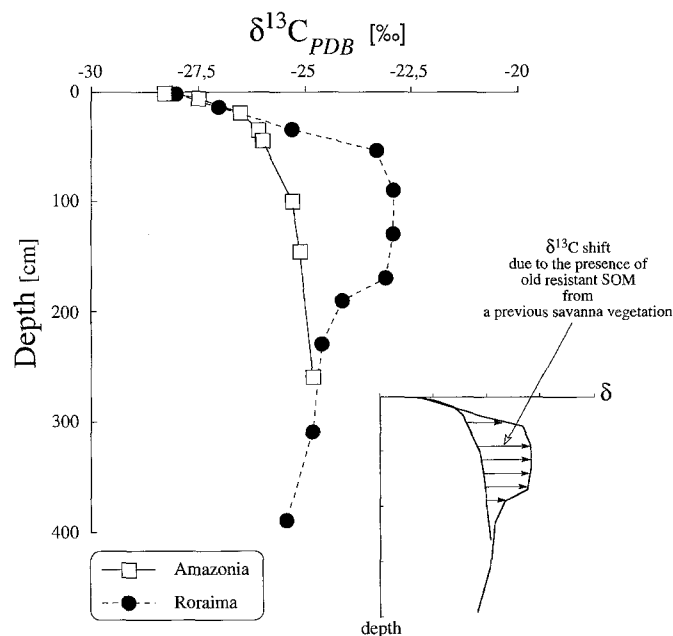


Fig. 6 Mean SOM ¹³C isotope composition in different forest soil profiles from the heart of Amazonia forest (□, Desjardins et al. 1991), compared to mean values obtained on forest soil profiles in Roraima State (●, present study)

considered a classic pattern for soils in which organic matter is in equilibrium with the C₃ vegetation cover.

In contrast, the Roraima forest soils showed a greater δ¹³C increase with depth (4.9–5.7‰) leading to less negative δ¹³C values at 50–200 cm depth (by about 2–2.5‰; the maximum value found was close to -23‰) than those generally observed in Amazonian forest soils. However, in the lower parts of the Roraima soils, δ¹³C values became more negative, reflecting the distribution pattern generally measured in the deeper horizons of other Amazonian forest soil profiles (Fig. 6).

The forest soils studied in Roraima were well-drained oxisols with a C content profile similar to those of most oxisols and ultisols of Amazonia (Desjardins et al. 1991). Thus it may be assumed that SOM decomposition and humification processes are similar in all of these

soils and cannot be responsible for the observed differences in ^{13}C profiles. Moreover, the organic C contents of these soils, decreasing continuously with depth, do not show any evidence of an organic palaeohorizon.

Changes in ^{13}C in these Roraima forest profiles, as compared to other Amazonian soils, coincide more or less with an increase in clay content. However, this mineralogical change cannot explain the ^{13}C differences between forest profiles for two reasons. First, other Amazonian profiles described by Desjardins et al. (1991) are utisols and oxisols showing, from profile to profile, very different clay contents, from <20 to 80% in surface horizons, and from 35 to 95% in deeper parts of the profile, without any significant difference in ^{13}C profiles. Moreover, in one of these profiles, a clay content increase from 18.5 to 41% can be observed with depth, with a $\delta^{13}\text{C}$ increase of <2‰ (from -28.5 to -26.7‰) (Desjardins et al. 1994), while in the present study, the clay content only varies from 19% in surface layers to 30% at 50–60 cm depth, with a more important increase of $\delta^{13}\text{C}$: from -28 to -23.3‰.

Second, evidence for heterogeneity in the ^{13}C abundance of SOM within organic separates exists, but particle size separates show, sometimes, only a very slight $\delta^{13}\text{C}$ increase with decreasing particle size. For example, Balesdent and Mariotti (1996) showed that finer fractions (<2 μm , in which clays are concentrated) of seven French soils in equilibrium with a C_3 vegetation are ^{13}C -enriched by only 1.2‰ relative to coarser organomineral fractions (sand and silt). Martin et al. (1990) observed no significant ^{13}C enrichment in particle size organic fractions in tropical soil under gallery forest in the Ivory Coast. Bonde et al. (1992) measured a roughly one unit increase in $\delta^{13}\text{C}$ from sand to clay size particles in forest oxisol near Piracicaba in southern Brazil (with a $\delta^{13}\text{C}$ of clay-associated SOM always <-25‰).

So, the very small ^{13}C -enriched value of clay-associated SOM compared to non-clay-associated SOM (when it exists) cannot explain the ^{13}C difference observed between forest profiles in our study.

The more probable explication for these $\delta^{13}\text{C}$ profiles is that, in the past, the savanna was more extensive than today, and the $\delta^{13}\text{C}$ values observed between 50 and 200 cm are due to the presence of a small amount of resistant organic matter derived from former savanna vegetation.

In the forest topsoils, both near to and at a distance from the boundary, $\delta^{13}\text{C}$ values are similarly typical of C_3 vegetation, indicating that at present, the forest is not invading the savanna. Mariotti and Peterschmitt (1994) and Schwartz (1991) have shown that when C_3 vegetation (forest) is invading C_4 vegetation (savanna), $\delta^{13}\text{C}$ values of the forest topsoil near to the boundary are intermediate between C_3 and C_4 -derived SOM, due to the persistence of C_4 -derived SOM. The sampled forest-savanna boundary of our study seems to be stable at present. It is possible that human activity, in particular yearly burning of the savanna for livestock farming, has induced this stability during recent decades.

The $\delta^{13}\text{C}$ values measured in the topsoil of the savanna furthest from the forest boundary were typical of an overlying vegetation dominated by C_4 plants. Nearest the forest-savanna boundary the influence of forest litter inputs is clear, $\delta^{13}\text{C}$ values being intermediate between C_3 and C_4 vegetation. In savanna soils, a slight decrease of $\delta^{13}\text{C}$ values with depth is commonly observed (Martin et al. 1990; Mariotti and Peterschmitt 1994). This decrease was sharp in savanna soils studied at Roraima, with $\delta^{13}\text{C}$ values observed in the deeper layers being similar to those observed under forest. A similar profile has been described by Schwartz et al. (1992) in a Congo savanna oxisol. The low $\delta^{13}\text{C}$ values measured at depth in the study savanna soil are a result of the conservation of old SOM originating from a previous forest vegetation. The frequent occurrence of charcoal in these soils indicates that this region has been subjected to some fire disturbance in the past. Most of the charcoals found in the soils presently under savanna vegetation are derived from forest tree species, thus confirming the isotope results. The distribution of charcoal ages with depth did not present a significant pattern. It is possible that animal activity has redistributed charcoal fragments and that burnt root material at lower levels is younger than upper-layer fragments. Charcoals dated from the middle to late Holocene, not directly related to human disturbance, have also been observed in the soils of northwestern and eastern Amazonia (Soubiès 1980; Saldarriaga and West 1986), results which are consistent with those of the present study.

A full development of tropical forest, in the south tropical zone of South America, occurred between 10000–9500 and 8000 years B.P. (Absy et al. 1991; Van der Hammen 1991; Servant et al. 1993). Even without ^{14}C dating, it is likely that the deep-layer savanna SOM can indicate the maximal forest extension of the past. Palynological and palaeolimnological studies in central Brazil and eastern Amazonia have shown that savannas appeared, with the development of a drier climate, beginning 8000 years B.P., reaching a maximum 6000–5000 years B.P. (Absy et al. 1991; Ledru 1992). It is likely that the present savannas appeared during this period. The existence, in the savanna soil, of charcoal derived from forest tree species dated 6000–7500 years B.P. supports this assumption. It is also possible that during this dry interval, savannas were more extensive than today. This could explain the $\delta^{13}\text{C}$ values observed in the Roraima forest soils between 50 and 200 cm depth (Fig. 6). During the transition between the middle Holocene and the present, the climate became more humid, but important climatic variability seems to have been at work leading to the regular occurrence of fires in South America (Servant et al. 1993). The presence of numerous charcoals, dated from 3230 to 1790 years B.P., confirms the role of such fires in forest-savanna dynamics during the late Holocene.

The data presented here support evidence of forest-savanna boundary fluctuations in the northern Brazilian Amazon during the Holocene period. The results are

consistent with other palaeoecological data obtained in various regions of the Amazon basin. However, further investigations in other forest-savanna boundaries within this region using ^{14}C analyses of both SOM and charcoals will be necessary in the future to confirm these results.

Acknowledgments We thank E.L. Sette Silva and R.I. Barbosa for assistance in the field and stimulating discussions; M. Servant, T.E. Cerling and anonymous reviewers for careful critical reading and helpful improvements of the manuscript; R. Dechamps for determining the origin of the charcoal and M. Grably for isotope laboratory assistance. We also thank INPA at Boa Vista for logistic support. This work was supported by the CNRS and the ECOFIT program from CNRS-ORSTOM.

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