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Past vegetation changes in the Brazilian Pantanal arboreal–grassy savanna ecotone by using carbon isotopes in the soil organic matter

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Abstract

Measurements of the organic carbon inventory, its stable isotopic composition and radiocarbon content were used to deduce vegetation history from two soil profiles in arboreal and grassy savanna ecotones in the Brazilian Pantanal. The Pantanal is a large floodplain area with grass-dominated lowlands subject to seasonal flooding, and arboreal savanna uplands which are only rarely flooded. Organic carbon inventories were lower in the grassy savanna site than in the upland arboreal savanna site, with carbon decreasing exponentially with depth from the surface in both profiles. Changes in ^{13}C of soil organic matter (SOM) with depth differed markedly between the two sites. Differences in surface SOM ^{13}C values reflect the change from C_3 to C_4 plants between the sites, as confirmed by measurements of ^{13}C of vegetation and the soil surface along a transect between the upland closed-canopy forest and lowland grassy savanna. Changes of ^{13}C in SOM with depth at both sites are larger than the 3–4 per mil increases expected from fractionation associated with organic matter decomposition. We interpret these as recording past changes in the relative abundance of C_3 and C_4 plants at these sites. Mass balances with ^{14}C and ^{13}C suggest that past vegetational changes from C_3 to C_4 plants in the grassy savanna, and in the deeper part of the arboreal savanna, occurred between 4600 and 11 400 BP, when major climatic changes were also observed in several places of the South American Continent. The change from C_4 to C_3, observed only in the upper part of the arboreal savanna, was much more recent (1400 BP), and was probably caused by a local change in the flooding regime.

Keywords: Brazil, Pantanal, radiocarbon, wetland, savanna, soil organic matter, stable carbon isotope, vegetation change

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Introduction

The Pantanal, with an area of *c.* 140 000 km^2, is one of the largest floodplains in the world. It is a large depression formed at the end of the Cretaceous and filled by sediments deposited mainly by the Paraguay river and its major tributaries, especially during the Quaternary (Moreira 1977; Moreira Franco & Pinheiro 1982; Ab'Saber 1988). It is located at the centre of South America, bordering the main physiographic zones of the continent, with the Amazon region to the north, the Cerrado to the east and the Chaco to the west. Due to the alternation of dry and wet climates that occurred at the end of the Pleistocene and during the Quaternary (Alvarenga *et al.* 1984), a mixed vegetation pattern was established, with species characteristic of the border areas (Amazon, Cerrado and Chaco) and with very few endemic species (Junk 1993). Drier periods also fostered the invasion of xeric species from the Caatinga of NE Brazil (Ab'Saber 1988). The distribution of the vegetation in the landscape is a function of the topography, which also governs the pattern of flooding. Consequently, small changes in the

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topography lead to a mosaic of habitats (Junk 1993), supporting numerous species of plants and animals, in one of the most biodiverse ecosystems of the world. The major vegetation type in the Pantanal is the savanna, in which different sub-units are established as a function of the local topography/hydrology (Loureiro *et al.* 1982). Plant communities may be classified based on the relative proportion of C_4 (grasses) and C_3 plants. The low-land areas are dominated by C_4 grasses forming the so-called grassy savanna. Higher elevation areas have an increasing proportion of C_3 plants with the progression from park savanna to open canopy arboreal savanna. Closed canopy arboreal savanna, formed almost exclusively by C_3 plants, dominates the highest elevations.

Spatial distributions of these vegetation are expected to be dynamic in a system like the Pantanal, both because of periodic flooding, and past climate changes.

In this paper we deduce present and past changes in the vegetation composition of a typical savanna of the south-eastern part of the Pantanal, using ^{13}C isotopic composition and radiocarbon dating of soil organic matter (SOM). The bases for the use of the ^{13}C technique are: (i) the isotopic composition of the SOM is similar to the isotopic composition of the vegetation cover from which it is derived, and (ii) there is a large difference in the isotopic composition of C_3 and C_4 plants (Vitorello *et al.* 1989; Martin *et al.* 1990; Ambrose & Sikes 1991; Mariotti & Peterschmitt 1994). Generally, the SOM in deeper layers of a soil is enriched in ^{13}C (Flexor & Volkoff 1977; Volkoff & Cerri 1987; Guillet *et al.* 1988; Desjardins *et al.* 1991). Depending on the degree of this enrichment two basic processes can explain the observed trends: (i) increases smaller than 3–4‰ are likely due to organic matter decomposition, which preferentially removes ^{12}C, enriching deeper, older soil layers in ^{13}C; and (ii) larger values are likely the result of changes from C_4 to C_3 vegetation. Radiocarbon dating is used here to identify past vegetation change.

We collected samples from soil pits dug in grass and in closed canopy arboreal savannas. Virtually no grasses were present in the arboreal savanna. The absence of significant change in the stable carbon isotopic composition with depth, for any of the pits, would indicate that the system has been stable for the period over which the soil has formed. This period is determined from the radiocarbon age of SOM in the profile. A ^{13}C enrichment with depth in the arboreal savanna, larger than the enrichment of 3–4‰ that typically results in decomposition, would indicate that the system evolved from a grassy savanna. Alternatively, a ^{13}C depletion with depth in the grassy savanna, would suggest that an arboreal savanna was present before being replaced by C_4 grassy savanna.

Material and methods

Study area

The Pantanal may be divided into 10 different geomorphological regions (Adamoli 1982). The Fazenda Nhumirim (18° 59'S and 56° 39'W), our sampling station, is situated in the Nhecolândia region. The climate of the region is classified Aw, after the Köppen system. The annual average temperature is 25° C, and the annual average rainfall is 1280 mm. The dry season extends from May to September and the rainy season from October to April. The soil was classified as *Areia Quartzoza* according to the Brazilian classification, equivalent to an Inceptisol in the American classification system.

The samples were collected in a typical savanna complex. Grassy savanna, formed almost exclusively by C_4 grasses, dominated the lower elevation terrain, which is periodically inundated. C_3 plants as a proportion of the vegetation increased with elevation, to the exclusively C_3 closed arboreal savanna, situated in higher terrain *c.* 1.5 m above the grassy savanna and so avoiding periodical flooding. Two soil sampling procedures were used. The first was a 950 m transect from the grassy to the arboreal savanna, where surface soil samples (0–20 cm) were collected every 50 m. The second was performed in soil pits dug in both the grassy and the arboreal savanna. Samples were collected at 5 cm intervals from the surface to 20 cm deep, and then at 10 cm intervals to the bottom of the pits (110 cm in the grassy savanna and 170 cm in the arboreal savanna). Following a botanical survey of the area (Pott *et al.* 1986) leaves from the most common plants in the grassy savanna, in the forest and in the border of the ecotone were collected for ^{13}C determination. In the arboreal savanna leaves were collected from the upper canopy (10–15 m) and also from the ground flora.

Analytical methods

Large roots and debris were separated from the soil using a 2 mm sieve. The sandy texture of the soil allowed manual separation of small roots by hand. Carbon concentrations were determined in a CHN analyser (Perkin Elmer, 2400 CHN). Sample treatment for isotope analysis was done through combustion with CuO in evacuated Pyrex tubes. Isotope measurements were performed with a Finnigan DELTA-E mass spectrometer fitted with double inlet and double collector systems. Results are expressed in $\delta^{13}C$ relative to the PDB standard, defined as:

$$\delta\,^{13}C = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \cdot 1000, \qquad (1)$$

where R_{sample} and $R_{standard}$ are the ratio ^{13}C:^{12}C of the sample and standard, respectively. Samples were analysed at least in duplicate with a maximum difference of 0.3 ‰ between replicates.

^{14}C activity was measured in an accelerator mass spectrometer at the Lawrence Livermore Laboratory, USA (Southon *et al.* 1992; Trumbore 1993). The conventional radiocarbon age, expressed as years before present (BP) ± standard-deviation, called Apparent Mean Residence Time (AMRT), was estimated using the following equation, assuming a ^{14}C half-life of 5568 years (Stuiver & Pearson 1986):

$$t = -8033 \cdot \ln \left[\frac{A_{\text{sample}}}{A_{\text{standard}}} \right], \quad (2)$$

where t is the radiocarbon age expressed in years BP, and A_{sample} and A_{standard} are the radiocarbon activity of the sample and standard, respectively.

For the ^{14}C mass balance presented in the Discussion section, the ^{14}C activity was expressed as $\Delta^{14}C$ per mil, estimated according to the following equation (Stuiver & Polach 1977):

$$\Delta^{14}C\,(‰) = \left(\frac{A_{\text{sample}}}{A_{\text{standard}}} - 1 \right) \cdot 1000, \quad (3)$$

Carbon stocks in soils were calculated by multiplying the respective concentrations by soil density and by soil depth. Soil density was calculated by collecting a mass of soil in a small cylinder of known volume. After drying to constant mass, the density was calculated.

Results

Soil organic carbon concentration and stock

Organic carbon concentrations were very low in both areas, and showed the typical decrease with depth. For any particular depth the concentration was higher in the arboreal than in the grassy savanna (Fig. 1). The higher carbon stocks in the arboreal savanna, resulted from a higher carbon concentration, since the soil densities from both areas were not significantly different. The carbon stock to 1 m depth was equal to 3.4 kgC m^{-2} in the arboreal savanna and equal to 2.0 kgC m^{-2} in the grassy savanna.

Carbon composition of plant species

The $\delta^{13}C$ values of the plant species collected along the transect are shown in Table 1. The dominant grass in the grassy savanna, *Elyonurus miticus*, showed a value typical of C_4 plants (–12.4 ‰). The trees from the border area showed an average $\delta^{13}C$ value of –28.8±0.9 ‰ (n = 10), which is significantly less negative than the average found in the upper canopy (–30.3±0.9 ‰, n = 11) and in the forest floor (–31.1±1.5 ‰, n = 6) vegetation. This enrichment was also present in the tropical environment (van der Merwe & Medina 1989; Sternberg *et al.* 1989; Kapos *et al.* 1993). The probable causes are, in order of importance, lower irradiance inside the forest, increasing the isotopic fractionation during photosynthesis, and to a minor extent, the use of isotopically depleted biogenic CO_2 (Farquhar *et al.* 1982; Schleser & Jayasekera 1985; Sternberg *et al.* 1989). Surprisingly, the difference between the upper canopy and ground flora of the arboreal savanna was not statistically different, as usually found in tropical forests (van der Merwe & Medina 1989; Martinelli *et al.* 1991). The small number of forest floor vegetation samples, together with the high variance of the data, may explain this lack of significance. Also, the arboreal savanna at this site was more open with only two strata, in comparison to forest of higher rainfall areas, with less potential for recycling of C within the canopy.

Carbon isotopic composition of soil organic matter along the transect

The variation of $\delta^{13}C$ along the transect followed the anticipated pattern: as the proportion of C_3 to C_4 plants increased, the values became more negative, reflecting the increasing contribution of C_3 derived organic matter in the SOM (Fig. 2). Two major changes were observed in the transect, the first after 350 m, where the $\delta^{13}C$ values dropped from −17 to −20 ‰, and the second at 600 m, where a drop from −20 to −27 ‰ occurred. These changes are the results of changes in vegetation cover. The first drop indicates the transition from grassy savanna to park savanna, and the second the transition from park to arboreal savanna.

The average $\delta^{13}C$ values for soil surface samples collected in the grassy savanna (–17.2±0.6 ‰, n = 7) are within the normal range for this type of vegetation cover. The average value of $\delta^{13}C$ found in the literature for samples collected from surface soils covered with C_4 grasses was –16.1±2.2 ‰ (Dzurec *et al.* 1985; Mondenesi *et al.* 1986; Schwartz *et al.* 1986; Volkoff & Cerri 1987; Martin *et al.* 1990; Desjardins *et al.* 1991; McPherson *et al.* 1993; Wang *et al.* 1993; Mariotti & Peterschmitt 1994; Trouvé *et al.* 1994).

Variation in carbon isotopic composition with soil depth and radiocarbon dating of the soil

The variations in $\delta^{13}C$ with depth, for both areas, were larger than the expected from fractionation during decomposition, suggesting that vegetation changes occurred in the past (Fig. 3). In the grassy savanna the $\delta^{13}C$ became progressively more negative with depth, suggesting that a progressive replacement of C_3 by C_4 plants had occurred.

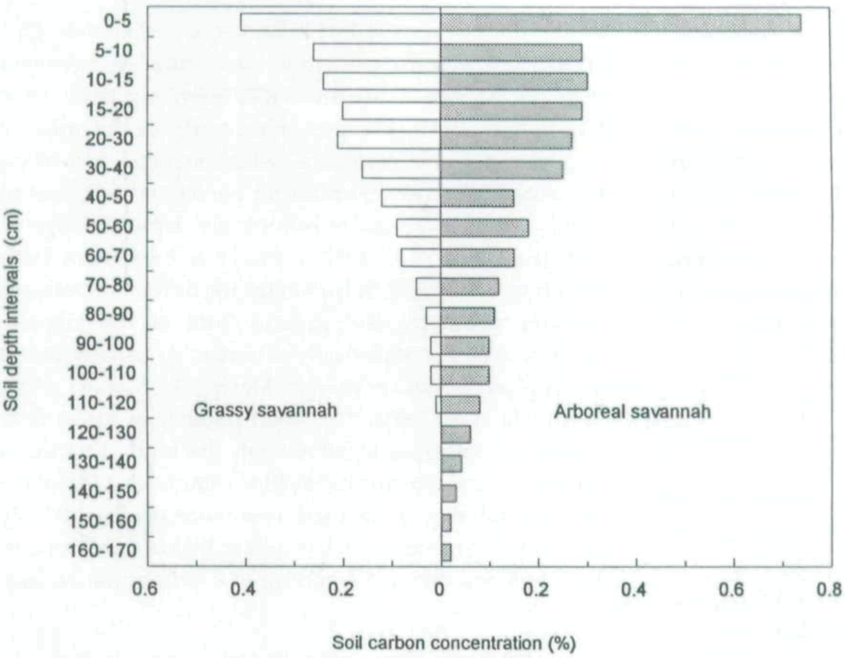

Fig. 1 Variation in the organic carbon concentration of soil organic matter with depth in the arboreal and grassy savanna soils.

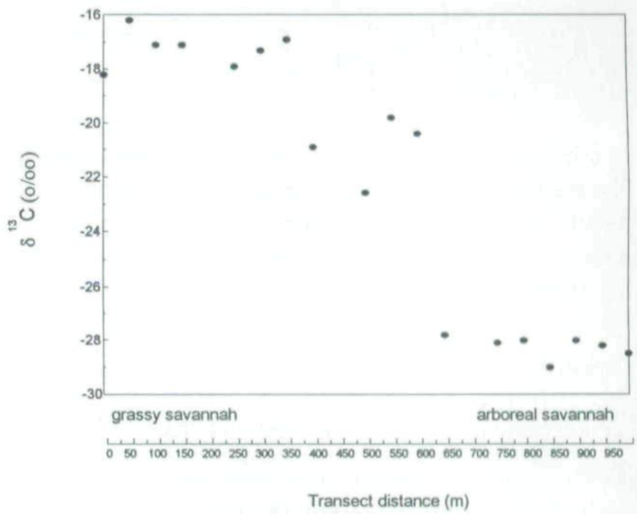

Fig. 2 Variation in $\delta^{13}C$ of surface SOM samples along a transect from grassy savanna (0 m) to arboreal savanna.

Table 1 $\delta^{13}C$ values of most common plant species (Pott *et al.* 1986) in the transect from grassy savanna to arboreal savanna.

Site	Species	$\delta^{13}C$
Grassy savanna	*Elyonurus miticus*	–12.4
Transition	*Curatella americana*	–29.4
	Cordia glabrata	–27.9
	Fagara hassleriana	–28.8
	Andira paniculata	–29.1
	Sapium haematospermum	–29.7
	Tabebuia caraiba	–26.5
	Simarouba versicolor	–28.8
	Caryocar brasiliense	–28.6
	Luehea panuculata	–29.2
	Byrsonima coccolobifolia	–29.7
Arboreal savanna	*Trichilia elegans*	–30.2
	T. elegans	–30.7
	Pouteria ramiflora	–31.7
	Copaifera martii	–31.1
	Sterculia striata	–28.9
	Vitex symosa	–33.8
	Attalea phalerata	–30.1
	Protium heptaphilum	–32.7
	Rhamnidium elaeocarpum	–30.4
	Ocotea suaneolens	–29.8
	Sapium haematospermum	–30.6
	Suilax sp.	–30.6
	Estronium fraxinifolium	–30.1
	Alibertia sessilis	–31.1
	Diospyrus hispida	–29.2
	Tabebuia roseo-alba	–29.4
	Magnaia pubescens	–29.9

The results were different for the arboreal savanna. From the soil surface to the 60–70 cm depth interval, the $\delta^{13}C$ became less negative, suggesting that C_4 vegetation had replaced the present vegetation. The value of −20 ‰ found at 60 cm depth is close to the average value found between 350 m and 650 m in the longitudinal transect, at the transition of grassy savanna to park savanna (Fig. 2). From the 60–70 cm depth interval to the bottom of the soil pit, $\delta^{13}C$ become progressively more negative; at 160–170 cm the $\delta^{13}C$ is similar to the value for the surface, indicating that C_3 plants had preceded the C_4 vegetation which formed the soil at 60–70 cm.

The AMRT of the soil organic matter was older in the

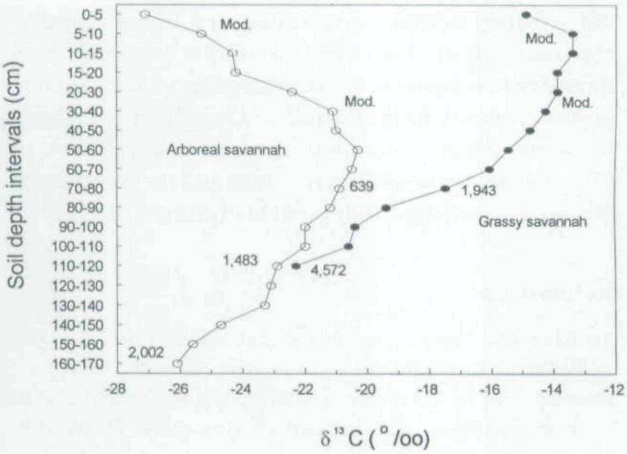

Fig. 3 Variation in $\delta^{13}C$ of SOM with depth in the arboreal and grassy savanna. Numbers indicate the AMRT expressed in years BP.

grassy savanna than in the arboreal savanna (Fig. 3). At 60–70 cm depth the SOM was 1940 ± 40 BP for the grassy savanna, and approximately three times younger (640 ± 40 BP) for the arboreal savanna. The same ratio was maintained at the 110–120 cm depth interval, with values of 4570 ± 40 BP for the arboreal and 1480 ± 50 BP for the grassy savanna. At the bottom of the arboreal savanna soil pit, the radiocarbon age was 2000 ± 40 BP (Fig. 3).

Discussion

The name *Pantanal* (swamp) may give a false impression of an area permanently flooded, with poorly drained soils promoting the accumulation of organic matter. Actually, most of the Pantanal is only seasonally flooded, and some areas, like the arboreal savannas, are only rarely flooded. In addition, the sandy texture of the soil facilitates good drainage. These, combined with the alternation between aerobic and anaerobic conditions which fosters organic matter decomposition (Lugo *et al.* 1990), are the most likely reasons for the observed low organic carbon concentration in both environments. The arboreal savanna soil showed higher carbon concentrations and stocks, probably reflecting higher carbon inputs from vegetation, and less frequent flooding events. However, compared to other soils, the carbon stock was much lower. For instance, *Areia Quartzoza* soils collected in the Amazon basin (Moraes 1991) showed a carbon stock approximately three times higher than the arboreal savanna.

The cause of vegetation changes in the past could be attributed either to changes in climate, or to a local change in the flooding regime. It is difficult to identify the exact cause of such changes. For instance, the chronology of past climate change in the Pantanal is not well understood (Ab'Saber 1988), although there is evidence of past climatic fluctuations, from drier to wet regimes and vice-versa, a couple of times during the Quaternary (Alvarenga *et al.* 1984). Obviously, a change caused by a climatic fluctuation would equally affect both areas, as they are adjacent to each other. For regions where the climate has become drier for a period, as in the Amazon, it is expected that the establishment of a C_4-rich vegetation is facilitated (van der Hammen 1974; Absy & van der Hammen 1976; Absy 1980; Markgraf 1989; Bush *et al.* 1990; Absy *et al.* 1991).

Soil organic matter is often modelled as a two- or three-component system, a mixture of more rapidly cycling fractions with turnover times ranging from less than one year to decades, and passive organic matter, with millennial or longer turnover times (Harrison *et al.* 1993; Jenkinson & Raynor 1977; O'Brien & Stout 1978; Parton *et al.* 1987; Schimel *et al.* 1994; Townsend *et al.* 1995; Trumbore 1993). Trumbore *et al.* (in press) have shown that this picture holds true even at depths > 1 m in tropical soils, as deep roots feed an active carbon cycle (turnover times of < 40 years) while the bulk of the carbon is in old, refractory organic carbon. Thus, the AMRT associated with a ^{14}C age, even in deep soils is most likely a mixture of decadal and faster cycling organic matter (with ^{14}C values $>$ Modern) and old, refractory carbon (with ^{14}C values substantially less than Modern). In a soil profile where vegetation has changed with time from C_3 to C_4-dominated plants, we assume that the ^{13}C changes in the SOM may be used as a measure of the minimum amount of rapidly cycling carbon (as these have adjusted to a new steady state within a century of conversion), and that residual ^{13}C-depleted carbon represents the passive carbon accumulated over millennia in the old vegetation regime. We used this approach to calculate the possible timing of vegetation change in this specific site of Pantanal. The change from arboreal savanna to grassy savanna (less negative $\delta^{13}C$ towards the soil surface) can be analysed on the results from the grassy savanna soil profile. We may assume that the carbon present at the 110–120 cm depth is a mixture of carbon of different ages: an *old carbon* fraction, originated from C_3 plants (AMRT $>$ 4572 BP, which is the estimated age at this depth interval in the grassy savanna profile), and a younger fraction derived from C_4 plants, added since the last vegetation change, and therefore with AMRT $<$ 4572 BP. Therefore, the *minimum AMRT* of the old C_3 carbon at the 110–120 cm would be *c.* 4572 BP, and no mixture would have taken place.

The maximum AMRT can be calculated through the following ^{14}C mass balance:

$$100\%\cdot(\Delta^{14}C_{soil\text{-}carbon}) = \%C_4\cdot(\Delta^{14}C_{new\text{-}carbon}) + \%C_3\cdot(\Delta^{14}C_{old\text{-}carbon}) \quad (4)$$

where $\Delta^{14}C_{soil\text{-}carbon}$ is the ^{14}C activity at the 110–120 cm soil depth interval in the grassy savanna profile (-435 ‰), $\Delta^{14}C_{new\text{-}carbon}$ is the ^{14}C activity of the new C_4 carbon, taken as the ^{14}C activity at the soil surface in the grassy savanna (+ 141 ‰), and $\Delta^{14}C_{old\text{-}carbon}$ is the ^{14}C activity of the old C_3 carbon that we want to estimate. The $\%C_4$ and $\%C_3$, the relative percentage of C_4 and C_3 carbon in the soil profile, were estimated by ^{13}C mass balance, through the following equation:

$$\%C_3 = \left(\frac{\delta\,^{13}C_{sample} - \delta^{13}C_{C_4}}{\delta^{13}C_{C_3} - \delta^{13}C_{C_4}}\right)100, \qquad (5)$$

where $\delta^{13}C_{sample}$ is the carbon isotopic composition of the soil at the 110–120 cm depth in the grassy savanna (–22.3‰), $\delta^{13}C_{C4}$ is the carbon isotopic composition of the C_4 material that is being added to the soil (–12.4 ‰, or the ^{13}C isotopic composition of the C_4 vegetation cover), and $\delta^{13}C_{C3}$ is the carbon isotopic composition of the C_3 material in the soil (–27.9 ‰, assumed to be 2 ‰ less negative than the average isotopic composition of C_3 plants,–29.9±1.4 ‰, $n = 29$). The proportion of C_4 plants is 100 -$\%C_3$.

Using (4) and (5) we calculated a maximum AMRT equal to 11 420 BP. Therefore, the vegetation change from arboreal to grassy savanna probably occurred between 4572 and 11 420 BP. The two major dry periods reported to have occurred in tropical and sub-tropical regions of South America were from 4000 to 5000 BP, and from 10 400 to 10 500 BP (Absy & van der Hammen 1976; Absy 1980; Absy *et al.* 1991; Servant *et al.* 1993), which agree with the range found in the Pantanal soil.

The same approach was used to estimate the timing of the change from grassy savanna to arboreal savanna, indicated by the results of the 50–60 cm depth interval in the arboreal savanna soil profile (Fig. 3). In this case, however, as the C_3 carbon increased 50–60 cm depth towards the soil surface, *old carbon* was assumed to be of C_4 origin, and new carbon of C_3 origin. In this case the data was analysed based on the results of the 30−40 cm depth interval in the arboreal savanna soil profile. The following values were used in (4): + 51 ‰ for $\delta^{14}C_{soil\text{-}carbon,}$ + 141 ‰ for $\delta^{14}C_{new\text{-}carbon}$, and $\delta^{14}C_{old\text{-}carbon}$ is the ^{14}C activity of the old C_4 carbon that we want to estimate. In (5), the same values of $\delta^{13}C$ for vegetation types were used, and the $\delta^{13}C$ of the soil samples at 50–60 cm depth interval was equal to –21.1 ‰ The *maximum AMRT* was then estimated to be equal to 1390 BP, suggesting that the change from grassy savanna to arboreal savanna was a recent local event.

In parallel with suggestions for other areas in the world (e.g. MacPerson *et al.* 1993), woodland is expanding over the grassland at this specific site of the Pantanal. However, we also observed that the highly dynamic characteristic of the flooding regime may cause large variations in the stable carbon isotopic composition, and in the radiocarbon age as well. Therefore, the results presented here should not be extrapolated to other areas of the Pantanal region, without further studies. Overall, the findings reveal the dynamic nature of the spatial distribution of C_3 and C_4 savanna sub-communities and the coincidence of vegetation change with periods of climate change.

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