

Millennial-scale climatic and vegetation changes in a northern Cerrado (Northeast, Brazil) since the Last Glacial Maximum

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Abstract

In the Southern Hemisphere, lacustrine sediments started to be deposited with the beginning of the deglaciation at ca 19,000 cal yr BP. At this time the region of Lake Caço was dominated by sparse and shrubby vegetation with dominance of steppic grasses in a poor sandy soil. The landscape did not present any ecological characteristics of a modern Cerrado. However single pollen grains of two Cerrado indicators, *Byrsonima* and *Mimosa*, suggest that some Cerrado species were able to survive under the prevailing arid climate, probably as small shrubs. After 15,500 cal yr BP, a sudden increase in the moisture rates is evidenced with the progressive expansion of rainforest showing successive dominance of various associations of taxa. The development of the forest stopped abruptly at the end of the Pleistocene between 12,800 and 11,000 cal yr BP, as attested by strong fires and the expansion of Poaceae. In the early Holocene an open landscape with a relatively high level of water in the lake preceded the progressive expansion of Cerrado species towards a denser forested landscape; fires are recorded from then on, resulting in the physiognomy of the Cerrado we know today. Late Pleistocene paleoenvironmental records from northern Brazil reflect the interplay between insolation forcing of two hemispheres with the local components represented by the interannual shift of the Inter Tropical Convergence Zone and the influence of seasonal equatorwards polar air incursions.

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1. Introduction

Recently published data from Northeastern Brazil (Nordeste) show strong teleconnections between atmospheric and oceanic circulation that enable us to distinguish two different climatic areas (Jennerjahn et al., 2004; Ledru et al., 2002; Wang et al., 2004). The first concerns the eastern coastal area which is subject to a winter rainy season created by the trajectory of the cold Benguela Current southward along the Brazilian coast; the second concerns the inland and northern part of the Nordeste which is subject to the Inter Tropical Convergence Zone

(ITCZ) seasonal shift and a summer rainy season (Fig. 1A and B). Marine (Jennerjahn et al., 2004), lacustrine (Ledru et al., 2002) and speleothem (Wang et al., 2004) data highlight differences, often out of phase, in signal expression depending on the location of the records. For instance a dry Younger Dryas (YD) climatic reversal is observed in north and inland Nordeste while a wet YD event is observed on the coast. This observation infers marked changes in seasonality during this climatic reversal with differences in signal expression depending on the location of the study area within the Nordeste region. Seasonal changes greatly influence the floristic composition of the tropical forest and also play a role in the dynamics and evolution of tropical biodiversity. This is why it is important to characterize the biome we are currently studying and to define the way it responded to climatic changes over time.

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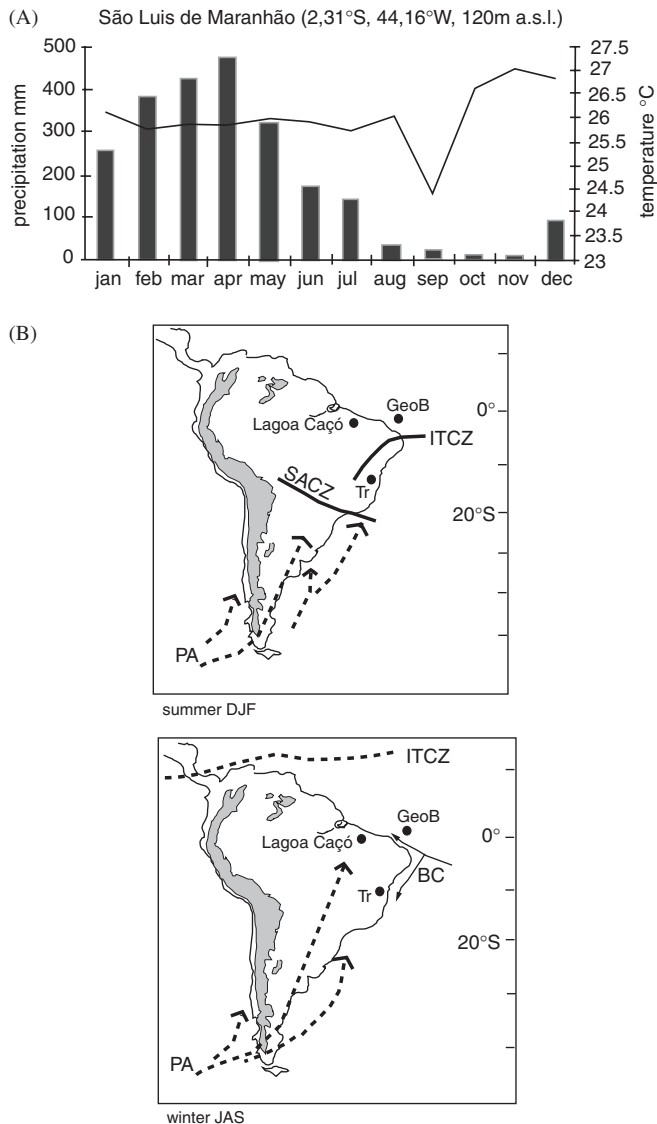


Fig. 1. (A) Climatic diagram of the city of São Luis (2°31'S, 44°16'W) the capital of Maranhão State. (B) Map of South America showing the respective austral winter and summer position of the Inter Tropical Convergence Zone and the South Atlantic Convergence Zone. Arrows indicate the trajectories of polar air advections. BC, Benguela Current; PA, polar advection; Tr, travertines from Wang et al. (2004), GeoB marine core from Jennerjahn et al. (2004).

The State of Maranhão in the Nordeste represents the northern Cerrado area within the six phytogeographic zones defined by Ratter (Ratter et al., 1996) and also the northern climatic region that is subject to a climate with summer rainfall and changes in the amplitude of ITCZ seasonal shifts. After Amazonia, the Cerrado represents the second largest biome in Brazil. It is composed of several mosaics of vegetation that are rich in endemic species. The surface area originally covered by Cerrado is estimated at 2 million km², or 22% of the Brazilian territory (Oliveira-Filho and Ratter, 2002). The floristic composition of a given area of Cerrado depends to a large extent on the

main neighboring ecosystem (Ratter et al., 1996; Oliveira-Filho and Ratter, 2002).

From rapid botanical inventories consisting in collecting different species in a delimited area for a period of no more than 30 mn, these authors were able to define six phytogeographical zones for the Cerrado biome: south, southeast, central, centerwest north and some patches of Cerrado inside the Amazonian rainforest. The mean annual precipitation, the length of the dry season and the mean winter temperature appear to be the main factors that separate these areas. The vegetation is extremely heterogenous as none of the 534 species identified was observed in all 96 study sites, and only 28 species were found at 50% or more of the sites. The Cerrado also has the highest variety of fruits in South America with regular production throughout the year. Archeological studies showed that during the last 12,000 yr BP, the populations of the central region of the Cerrado were subject to changes in their environment and consequently had to look for different kinds of food to survive.

Four different prehistoric periods are evidenced in the caves of Serranópolis, State of Goiás (Schmitz et al., 1989). The first or Paranaíba period, is related to the Itaparica tradition and dated between 11,000 and 8000 yr BP. Food remains attest to hunting of different types of animals such as capivaras, turtles, and fish from the surrounding rivers. Bones artifacts were mainly made from cervides. The environment was drier than today. During the second or Serranópolis period, the populations hunted and collected snails. This period dated between 8000 and 5500 yr BP and shows an increase in moisture rates. At the end of the Serranópolis period a sterile layer with no archeological content is observed. The third or Jataí period related to the Una tradition starts with layers covering eroded depositions. These layers contain remains of cultivated plants such as corn, peanut, various legumes and fruits from the Cerrado and riparian forest, as well as remains from hunting and snails. The Una tradition extended from the central Plateau to Rio de Janeiro at 2000 yr BP. The Tupiguarani tradition is evidenced in the surface layers of the caves and disappeared with European settlement. Pollen records from the central region also highlight an extremely arid event at mid-Holocene (Salgado-Labouriau et al., 1998). Here we present results obtained from the examination of lacustrine sediments, botanical surveys and soil isotopic analyses undertaken to characterize the evolution of this biome during the Late Quaternary. We compared our records with records in other Cerrado areas to discover how this biome responded to major climatic changes at different latitudes, and how the floristic composition of a biome can differ from one region to another depending on local climate changes.

2. Modern settings

Lake Caçó is an extended lake 3 km long and 0.5 km wide that occupies a small closed basin covering an area of

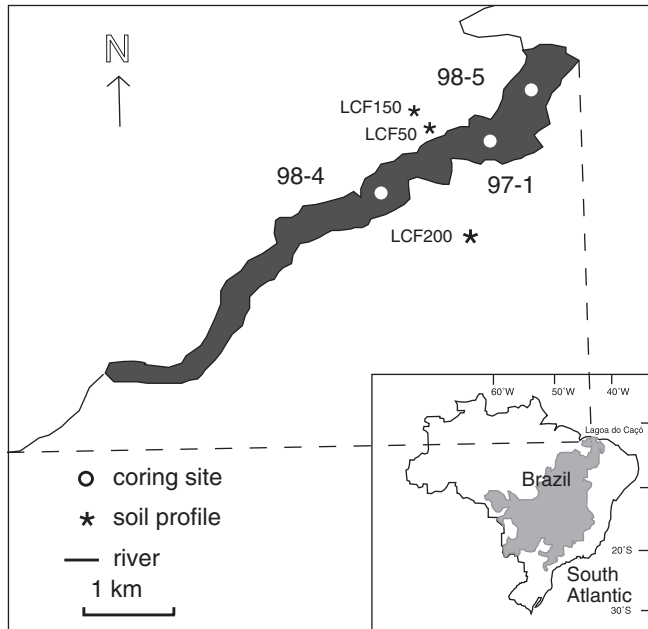


Fig. 2. Distribution of the biome Cerrado (in gray) and location of Lake Caço in Brazil. Map of the lake with location of the cores MA 97-1, MA 98-4 and MA 98-5 and of the soil profiles LCF 50, 150 and 200.

about 15 km² (Fig. 2). The modern-day vegetation in this area is diverse, from Restinga, the steppe vegetation typical of the coastal regions of Brazil, to Cerrado, consisting of woody savanna containing species from the Restinga growing on eolian sand, and finally gallery (riparian) forests containing Amazonian rainforest species. Botanical inventories were undertaken in all the different ecosystems from the lake to the coast covering a distance of ca 100 km in November 1998, at the end of the dry season, and in April 1999, at the end of the rainy season (Fig. 1). Material is available at the Herbarium of the Botanical Department of the University Federal of Paraná, in the city of Curitiba, Brazil. These inventories include the following species: (1) in the lake, the predominant aquatic species are *Nymphaea* sp., *Nymphoides* sp., *Sagittaria*, *Cabomba* and *Montrichardia linifera*. (2) The lake margins are occupied by herbaceous plants: Cyperaceae (*Eleocharis* sp.), Orchidaceae, and Eriocaulaceae, *Mauritia flexuosa*, a palm that forms large mixed colonies with *Xylopia* (Annonaceae) in seasonally flooded marshland, and trees from the gallery forest Melastomataceae, *Tapirira guianensis* (Anacardiaceae), *Vochysia tucanorum* (Vochysiaceae), *Cordia nodosa* (Boraginaceae), *Casearia* spp. (Flacourtiaceae), *Ficus* spp. (Moraceae) and *Picramnia* spp. (Simaroubaceae). (3) The Cerrado profiles vary with the density of the trees and include *Stryphnodendron adstringens* (Mimosaceae), *Parkia pendula* (Mimosaceae), *Qualea grandiflora* (Vochysiaceae), and *Curatella americana* (Dilleniaceae). (4) The coastal vegetation (Restinga) is observed on the dunes and includes small trees and shrubs (e.g., *Byrsonima* spp. (Malpighiaceae), *Copaifera* spp. (Caesalpiniaceae), *Hymenaea* sp. (Fabaceae), *Caryocar coriaceum* (Caryocaraceae) and

many Bromeliaceae; the dominant herbaceous plant being *Chamaecrista flexuosa* (Fabaceae). (5) The mangrove association on the coastal stretches is composed of *Rhizophora mangle* (Rhizophoraceae), *Avicennia nitida* (Verbenaceae), *Laguncularia flexuosa* (Combretaceae), and *Conocarpus erectus* (Combretaceae). The most representative families are Myrtaceae (16 species), Poaceae (10 species) Caesalpiniaceae (8 species), Fabaceae (7 species), Mimosaceae (7 species), Malpighiaceae (7 species), Annonaceae, Bignoniaceae and Rubiaceae (6 species) Arecaceae, Cyperaceae and Vochysiaceae (5 species), Asteraceae, Apocynaceae Clusiaceae and Malvaceae (4 species), Bromeliaceae, Chrysobalanaceae, Sapotaceae (3 species) followed by 34 families with 1 or 2 species.

A total of 31.4% of the plant species from this region are found in Cerrados in Central Brazil, and the correlation with gallery forest in Central Brazil (27.2%) is higher than with northern restingas (19.9%), while the correlation with Amazonian and Atlantic rainforests is low (10% and 14%, respectively). *Manilkara* sp. (Sapotaceae) is the dominant tree of the area and is common to the three types of vegetation, Cerrado, gallery forest and Restinga. In the rainforest, trees belonging to *Copaifera martii* (Caesalpiniaceae), *Platonia insignis* (Clusiaceae), *Anacardium occidentale* (Anacardiaceae) *Platonia martii* (Clusiaceae) and *Eschweilera ovata* (Lecythidaceae) grow to a height of 30 m while in the Lake Caço area they remain treelets (Table 1) (Ribeiro, 2002; Pessenda et al., 2004).

The area around Lake Caço has a mean annual precipitation of ~1400–1500 mm and a mean annual temperature of ~25 °C. Seasonal climate is controlled by the position of the ITCZ, or meteorological equator that divides the year into two main seasons: a rainy and a dry season (Fig. 1A and B). Variations in the position of the convergence zone are determined by the temperature gradient between the pole and the equator. Consequently, the convergence zone stays in the warmest hemisphere, i.e. in the northern hemisphere, when the winter temperature gradient between the Antarctic and the equator is the greatest, from June to September, and in the southern hemisphere when the winter temperature gradient between the Arctic and the equator is the greatest between December and March. This seasonal feature can change depending on the position of the South Atlantic Convergence Zone (SACZ) at mid-latitudes in Central Brazil. When the SACZ is present, at around 20 ± 3°S in latitude, moisture is transported from the equatorial Atlantic towards Amazonia with the help of the North-East trade winds and progressively channeled and incorporated into the SACZ in Central Brazil. When the SACZ is absent, the warm and moist equatorial air masses remain close to the coast, and polar advections from the south may be able to reach these low latitudes and cooler temperatures and heavy rainfalls occur. The interplay between these two convergence zones regulates precipitations and seasons in the northern part of the Nordeste (Fig. 1A and B) (Ledru et al., 2002).

Table 1
Main tree species in the Cerrado and riparian forest of Lake Caçó with their importance value index (IVI) (see explanation in the text)

Cerrado taxa	Cerrado IVI	Riparian forest taxa	Riparian forest IVI
<i>Plathymenia reticulata</i>	35	<i>Manilkara sp.</i>	56.2
Mimosoidae		Sapotaceae	
<i>Qualea parviflora</i>	31.8	<i>Platonia insignis</i>	35.4
Vochysiaceae		Clusiaceae	
<i>Parkia platycephala</i>	25.6	<i>Anacardium occidentale</i>	32.0
Mimosoidae		Anacardiaceae	
<i>Caryocar coriaceum</i>	24.0	<i>Copaifera martii</i>	17.3
Caryocaraceae		Caesalpinioideae	
<i>Stryphnodendron coriaceum</i>	21.4	<i>Protium sp.</i>	15.3
Mimosoidae		Proteaceae	
<i>Salvertia convalliaeriodora</i>	16.5	<i>Qualea parviflora</i>	15.1
Vochysiaceae		Vochysiaceae	

3. Material and methods

Three cores were collected in 1997 and 1998 in aluminium pipes 7 cm in diameter with a Vibracorer (Martin et al., 1995) at different locations in the lake and under 12 m of water (Fig. 2). Core 98-4 was located at the southernmost part of the lake near the entrance of a stream at a depth of 600 cm. Core 98-5 was drilled in the middle part of the lake where the seismic profile showed a sand accumulation at a depth of 810 cm, and core 97-1 in the northern part of the lake at a depth of 345 cm. Sediment samples were processed following standard palynological techniques (Faegri and Iversen, 1989). Pollen and spores were identified by comparison with a reference pollen collection of ~1000 taxa collected from various herbaria by M.-P. Ledru and published pollen floras (Colinvaux et al., 1999; Hooghiemstra, 1984; Markgraf and D'Antoni, 1978; Roubick and Moreno, 1991; Salgado-Labouriau, 1973). Non-pollen palynomorphs were identified according to van Geel (1976). Data are expressed as percentages of each taxon in relation to the sum of arboreal pollen (AP), non-arboreal pollen (NAP) and undetermined pollen grains, while pollen grains from aquatics and spores were excluded from the pollen sum. The relative percentages of spores and pollen grains from aquatics were calculated in relation to the total AP and NAP pollen sum. A pollen concentration diagram (pollen grains/gram of sediment) was also performed based on the method described by Cour (1974) which consists in measuring all the volumes and quantities during pollen extraction (Fig. 5). A chronologic framework for the sedimentary sequence was provided by conventional and accelerator mass spectrometer (AMS) radiocarbon dates (Table 2). Radiocarbon dates were calibrated into calendar years before present (Stuiver and Reimer, 1993).

Isotopic analyses of carbon were undertaken from soils in the area of Lake Caçó in order to study the changes in $\delta^{13}\text{C}$ of the humic material. Soil surface values of

$\delta^{13}\text{C}$ today range between -27.6‰ and -26.4‰ and characterize the vegetation cover of the area. The application of carbon isotopes in studies of vegetation dynamics is based on the variation in ^{13}C composition of C_3 and C_4 plants and its preservation in soil organic matter. ^{13}C values of C_3 plant species range from approximately -32‰ to -20‰ PDB, with a mean of -27‰ . In contrast, $\delta^{13}\text{C}$ of C_4 species range from -17‰ to -9‰ with a mean of -13‰ . Thus, C_3 and C_4 plant species have distinct $\delta^{13}\text{C}$ values and differ from each other by approximately 14‰ (Boutton, 1996). Botanical surveys have shown that crassulacean acid metabolism (CAM) plants, mainly consisted of succulent plants, are absent from the study area and thus cannot upset the measurement of $\delta^{13}\text{C}$ (Pessenda et al., 2005).

4. Results

4.1. Lithology of the cores

4.1.1. Core ma 97-1

Core MA 97-1 was drilled at a depth of 345 cm. The lowest 15 cm (Pollen zone VI in Fig. 4) were possibly contaminated by modern organic sediment during coring and were consequently not taken into consideration for this study. Two sedimentological units were distinguishable based on the color and the grain size of the sediment. In the upper 300 cm, the sediment was composed of black organic clay interbedded with a layer of sand between 238 and 250 cm. The unit from 300 to 310 cm was composed of gray clay with sand.

4.1.2. Cores ma 98-4 and ma 98-5

Core MA 98-4 was drilled at a depth of 700 cm and core MA 98-5 at a depth of 500 cm. Core MA 98-4 comprised 3 main units: the upper part was composed of black organic clay to a depth of 285 cm interbedded with gray clay and sand in the lowest part just above

Table 2
Radiocarbon ages of total organic matter from cores MA 97-1, MA 98-4 and MA 98-5

Age (^{14}C yr BP)	Depth (cm)	Lab number	Age range ^a (cal yr BP)	$\delta^{13}\text{C}$ (‰)
Core MA97-1				
3060 ± 50	18–23	Beta 110192	3370–3080	–27.7
3830 ± 60	31–32	AA 32146	4410–4000	–26.9
5090 ± 60	40–45	Beta 115180	5980–5660	–30.5
5580 ± 80	48–49	AA 32147	6520–6200	–28.1
6010 ± 50	68–70	AA33915	7010–6820	–27.4
7660 ± 50	95–100	Beta 110193	8540–8370	–28.3
9040 ± 90	118–120	AA 32148	10,040–9920	–30.3
9720 ± 50	135–140	Beta 110194	11,220–10, 880	–29.3
10,220 ± 40	150–151	AA 35584	12,400–11,740	–29.2
10,170 ± 40	158–160	AA 35585	12,360–11,630	–25.5
10,880 ± 50	172–174	Beta 110195	13,130–12, 650	–32
11,600 ± 120	178–180	AA 32149	13,910–13, 170	–31.9
12,640 ± 135	200–202	AA 32150	15,750–14, 180	–32.3
12,930 ± 90	215–218	Beta 115181	16,040–14, 480	–31.1
13,560 ± 185	241–242	AA 32151	16,920–15, 680	–30.1
15,400 ± 180	259–260	AA 32153	19,130–17, 740	–26.9
15,870 ± 60	275–277	Beta 110196	19,570–18, 370	–22.5
Core MA 98-4				
2650 ± 40	30–32	AA 41234	2890–2790	–28.6
7190 ± 90	90–92	AA 41232	8230–7840	–26.8
8980 ± 70	200–202	AA 41243	10,290–9940	–29.5
15,310 ± 100	336–338	AA 41235 (1)	18,980–17,790	–27.3
16,260 ± 280	432–434	AA 41236 (1)	20,340–18,590	–26.8
Core MA 98-5				
5130 ± 50	54–56	AA 49422	6040–5800	–28.5
12,010 ± 70	154–156	AA 49423	15,370–13,700	–31.7
11,047 ± 70	268–270	AA 49424	13,230–12,720	–25
14,760 ± 170	327–329	AA 49425	18,390–17,100	–24.2
15,260 ± 110	406–408	AA 49426	18,930–17,720	–24.4
15,380 ± 110	362–364	AA 49427	19,070–17,850	–24.1

Dates on samples with a (1) were obtained on vegetal remains only.

^aRange at two standard deviations with error multiplier of 1.0.

285 cm; the second unit was composed of gray clay with sand interbedded with several layers of sand between 285 and 432 cm; the lowest unit was composed of sand with organic clay and vegetal fragments to a depth of 570 cm. From 570 to 700 cm sand was recovered from the dunes with no organic content.

Core MA 98-5 comprised 3 main units: the upper unit was composed of black organic clay to a depth of 156 cm; the mid unit was composed of gray clay with sand between 409 and 156 cm, interbedded with sand layers, the thickest layer between 275 and 303 cm, and the lowest unit, between 409 and 500 cm, was composed of sand with organic clay.

Samples were collected at 2 cm intervals for pollen and non-pollen palynomorph analysis. The whole MA 97-1 core was analysed every 2 cm. In core MA 98-4, only the lower lithological units were analyzed every 4 cm to detail the end of the glaciation and the reinstallation of the vegetation after the Last Glacial Maximum (LGM) in this area. In core MA 98-5 we analyzed 41 samples every 4 cm to check if the vegetation changes detected in cores MA97-1 and MA 98-4 reflected a regional dynamic (Fig. 3).

4.2. Pollen and non-pollen palynomorphs

4.2.1. Ma 97-1

Based on changes in the proportions of AP we recognized 5 pollen zones in the simplified diagram numbered from V (the oldest) to I (the youngest) (see Fig. 4).

Pollen zone V extends from 310 to 250 cm with an estimated age of 20,000–17,000 cal yr BP and is characterized by low percentages of AP ranging from 18% to 50% with a peak of 85% at a depth of 258 cm. Among the main arboreal taxa we distinguished Mimosaceae (ranging from 2% to 12%) Myrtaceae (2–11%) followed by Melastomataceae/Combretaceae (0–2%) and *Byrsonima* (0.5–4%). Myrtaceae include taxa characteristic of forest regeneration and re-humidification of soils on lake margins (Marchant et al., 2002) that generally occur after a dry climatic event, while the three other taxa characterize Cerrado today. However the presence of *Richardia* (0.5–5%) together with the Cucurbitaceae *Ceratosanthes* (single pollen grain) evidence a dry prevailing climate at that time and AP

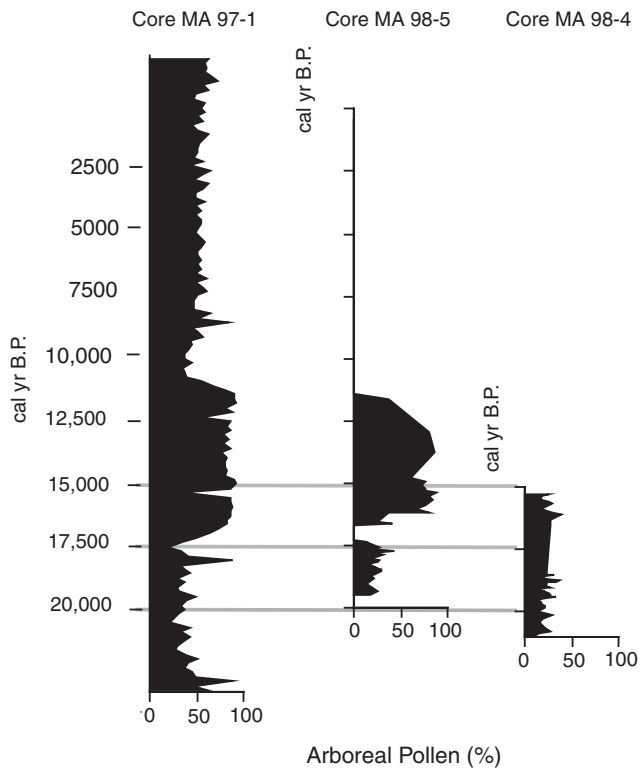


Fig. 3. Arboreal pollen frequency curves of cores MA 97-1, MA 98-4 and MA 98-5. Percentages are expressed in calendar ages along a linear time scale.

could represent treelets or bushes in a steppe environment. This dry environment was confirmed by the presence of *Borreria* (4–21%) and halophytic taxa (an association of two chenopods *Alternanthera* and *Gomphrena* that are herbaceous saline marsh plants) (1–12%). These taxa attest to fluctuating water levels in the lake while *Myriophyllum* (single grains in each sample) and *Botryococcus* (3–40%) attest to shallow waters and cool temperatures. The peak of 85% AP at a depth of 258–260 cm and an estimated age of 17,500 cal yr BP are due to a sharp increase in the percentage of Melastomataceae/Combretaceae (30%), Moraceae/Urticaceae (22%), *Myrsine* (6%) and *Didymopanax* (3.5%) together with a decrease in halophytes (0.5%) and *Borreria* (0.3%), which we interpreted to reflect an abrupt increase in both moisture rates and temperature. Among the non-pollen palynomorphs (Fig. 6), a high percentage of *Pleospora* sp., the presence of *Pediastrum*, low percentages of *Spirogyra* and *Mougeotia* and a peak of *Gieysztoria virgulifera* (Neorhabdocoela oocytes) are observed followed by the disappearance of *Pleospora* sp. at the end of this zone. At a depth of 280 cm the percentage of *Anthostomella fuegiana* reaches maximum together with high percentages of the algae *Botryococcus* and Zygnemataceae (*Spirogyra*) and some Neorhabdocoela such as *Micodalyellia armigera*. At a depth of 270 cm the disappearance of *Anthostomella fuegiana*, low rates of *Botryococcus*, a peak of *Pleospora* sp., two maxima for *Spirogyra* and the presence of *Mougeotia* are observed. *Pleospora* sp.

grows on dead plant remains and is linked with a dry environment; it is considered to be a good indicator for some Cyperaceae in the local vegetation (van Geel, 1976). As the two taxa *Pleospora* sp. and *Anthostomella fuegiana* are out of phase, we considered the latter to characterize moist edaphic conditions with the development of hygrophilous vegetation. Consequently, an increase in *Anthostomella fuegiana* at 280 cm is interpreted to indicate the presence of higher moisture rates in a meso-eutrophic environment (Haas, 1996). This change in local ecological conditions is also apparent in the pollen concentration diagram (Fig. 5) where an abrupt increase in the pollen concentration of up to 54,300 grains/g, attests to the dominance of Poaceae, Mimosaceae and Myrtaceae. In addition, high rates of *Pleospora* sp. (at 270 cm) are interpreted as indicating a shallow lake with eutrophic waters, while *Pleospora* sp. disappears and a more humid climate develops in this region (Haas, 1996; López Sáez et al., 1998).

The end of the glaciation and the beginning of the deglaciation are characterized by a steppe landscape with low levels of water in the lake and cool temperatures. Several abrupt changes in edaphic conditions indicate unstable local climatic conditions during this period.

Pollen zone IV extends between 251 and 173 cm with an estimated age of 17,000–12,800 cal yr BP. This pollen zone is characterized by high percentages of AP ranging from 75% to 90% attesting to marked changes in the environment. The detailed succession of the different dominant tree species is described in Ledru et al. (2001). Successive ecological associations are observed in this zone: first *Didymopanax* and *Byrsonima*, followed by Melastomataceae/Combretaceae and *Myrsine* and finally an increase in Moraceae, *Cecropia* and *Podocarpus*. These are light-tolerant, pioneer taxa and attest to the progressive installation of a dense forest around the lake. After the peak of *Podocarpus*, Myrtaceae becomes dominant while *Podocarpus* disappears. Two abrupt and brief changes in vegetation towards forest regression are recorded: the first at a depth of 222–224 cm, ~15,000 cal yr, shows 35% AP, and the second at 184–186 cm, ~13,500 cal yr, shows 52% AP. Both changes in arboreal cover are characterized by an increase in Mimosaceae (2%) *Borreria* (10% at 184 cm), Poaceae (35% at 222 cm, 41% at 184 cm) and *Botryococcus* (45% at 222 cm) and the appearance of a new taxon *Rhizophora* (6% at 184 cm). At 184–186 cm, during the second abrupt change, pollen concentration values (Fig. 5) increase sharply and are characterized by the presence of *Mauritia*, *Rhizophora* and Mimosaceae taxa; at the same time, the presence of the non-pollen palynomorphs (Fig. 6) *Coniochaeta* cf. *ligniaria*, type 359 and *Ustulina deusta*, indicators of stumps and dead roots of deciduous trees that form their usual habitat (López Sáez et al., 1998; van Geel, 1976; van Geel et al., 1981), confirm the drastic regression of the forest. The continuous presence of *Rivularia* type, a cyanobacteria indicator of deep running waters in a meso- to oligotrophic environment, of *Spirogyra*, *Mougeotia* and

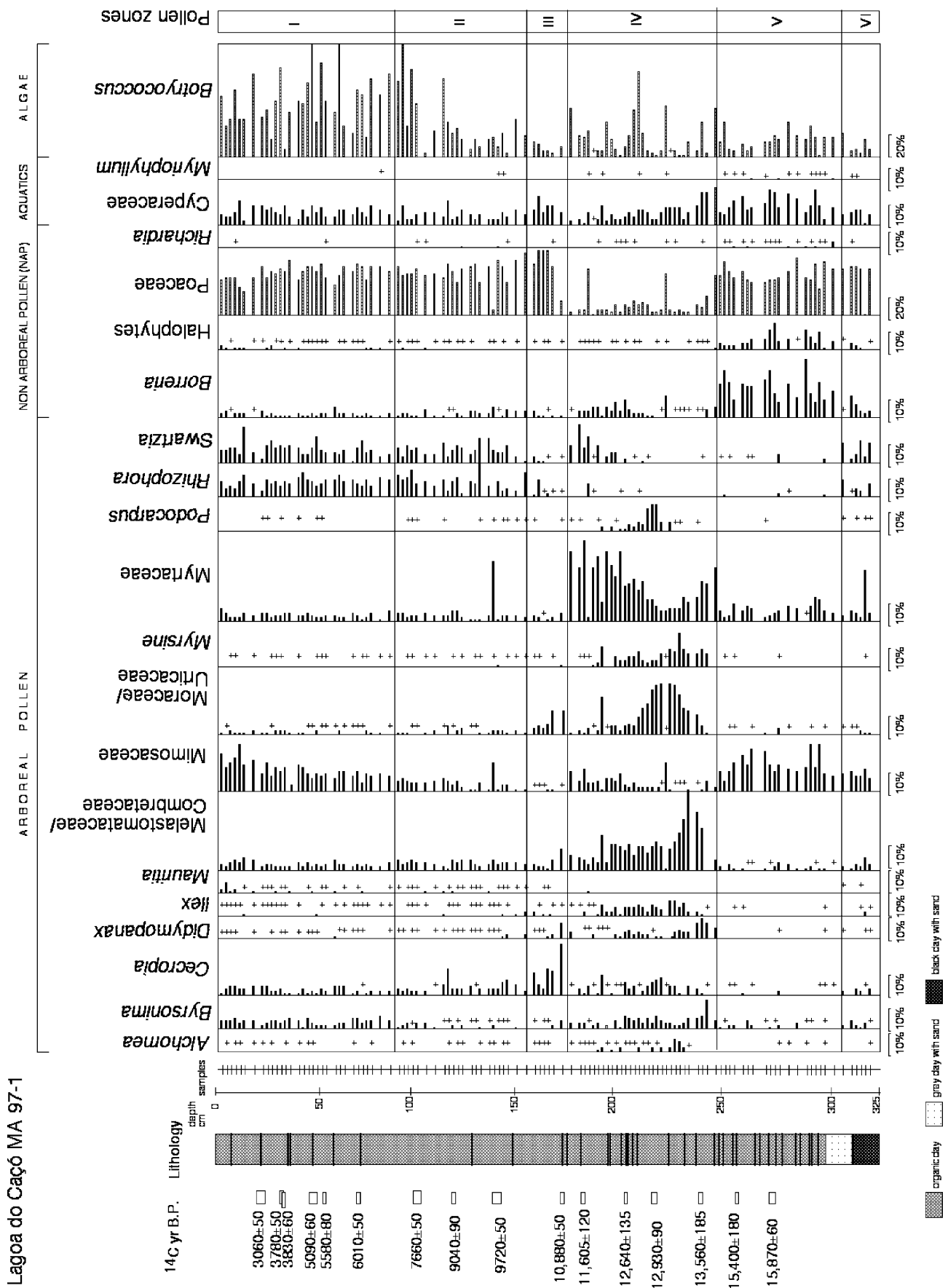


Fig. 4. Pollen percentage diagram of core MA 97-1 showing selected taxa. The pollen sum includes arboreal and non-arboreal pollen taxa. Values smaller than 1% are represented by the “+” sign.

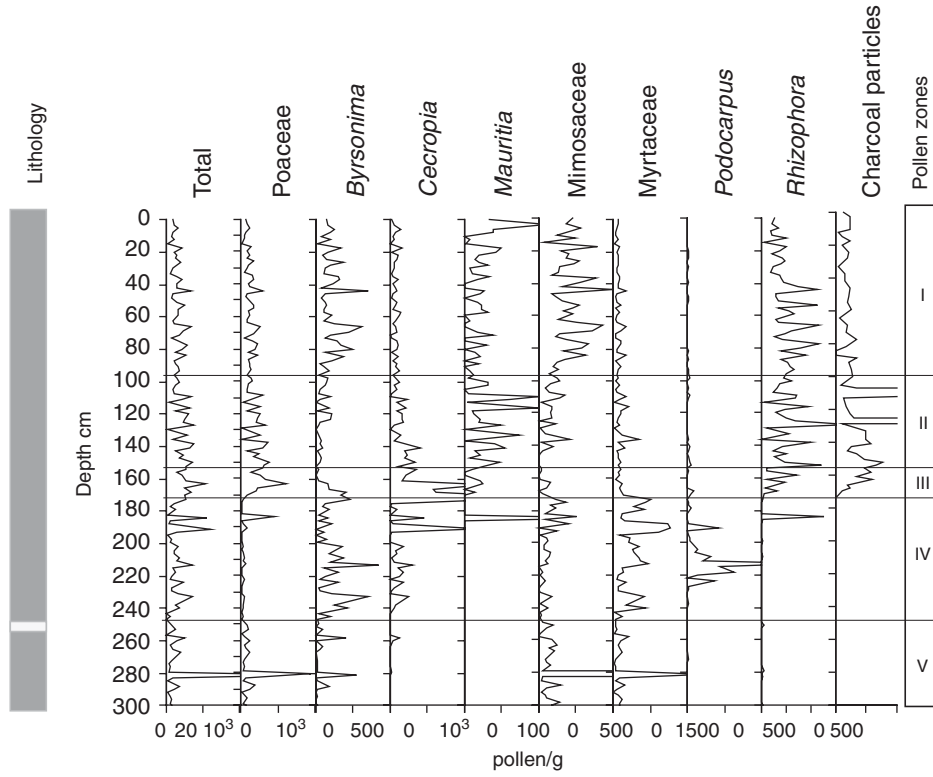


Fig. 5. Pollen concentration diagram of core MA 97-1 showing selected taxa.

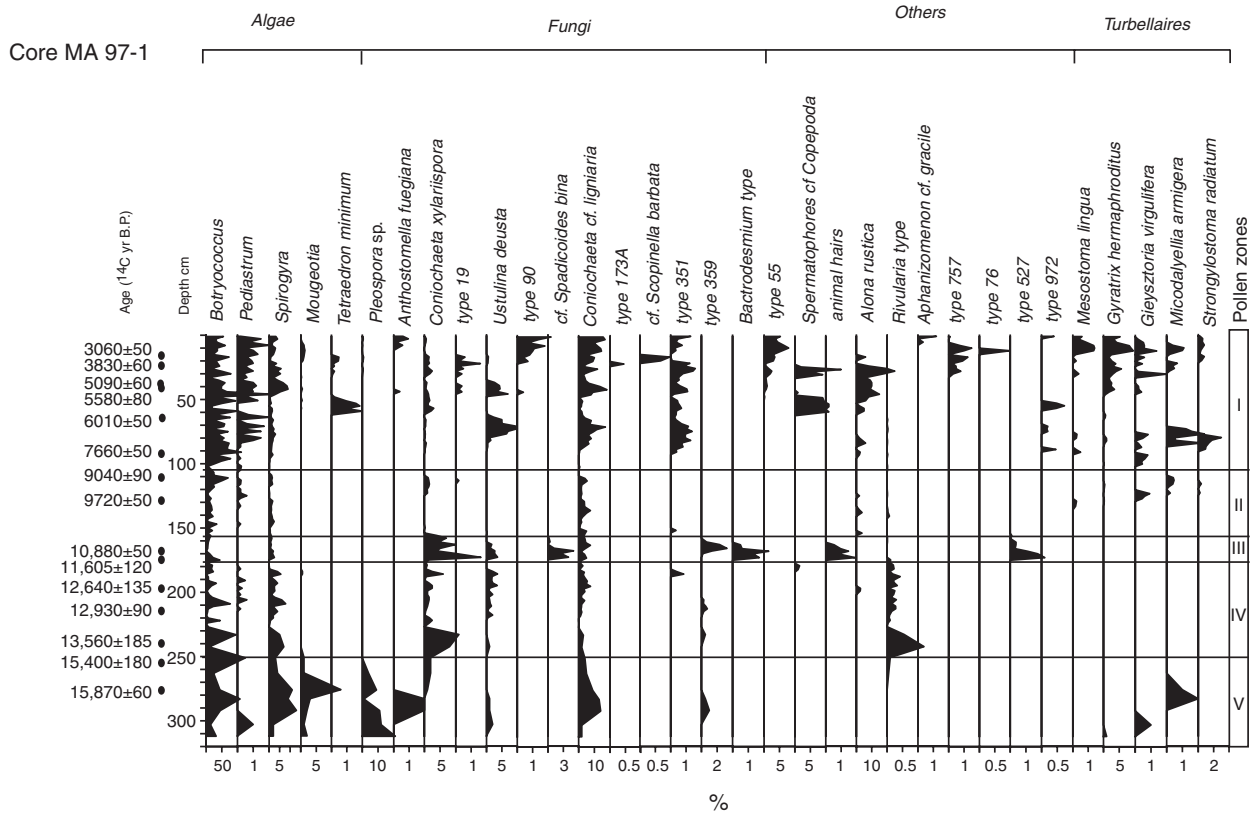


Fig. 6. Diagram of core MA 97-1 showing records of non-pollen palynomorphs. Values are percentages of the pollen sum.

Pediastrum, and more discontinuously of *Botryococcus*, are recorded throughout this zone.

The Lateglacial is characterized by the installation and the development of a dense moist forest with high water levels in the lake. Two regression phases towards open landscape are recorded during this period.

Pollen zone III extends between 172 and 154 cm with an estimated age of 12,800–11,000 cal yr BP and is characterized by the disappearance of the forest. The step corresponding to the decreasing concentration of ^{14}C in the atmosphere at that time is clearly visible in the radiocarbon dates with four dates between 11,600 and 10,220 ^{14}C yr BP within a 30 cm sediment deposition (Table 2) (Stuiver and Reimer, 1993). For a detailed description of this environmental change see Ledru et al. (2002). A sharp decline in the total percentage of AP (from 75% to 35% within a 100 yr time period) occurs and is replaced by an increase in Moraceae (from 2% to 23%) and *Cecropia* (from 0.5% to 23%) two pioneer species that provide evidence for the abrupt degradation of the previous dense moist forest. Micro particles of charcoal (Fig. 5) are also observed for the first time in the sediments of zone III attesting to frequent fires in the area. Among non-pollen palynomorphs (Fig. 6) we observe a decrease in the percentage of *Botryococcus*, *Spirogyra* and an even greater decrease in the *Pediastrum* and *Rivularia* type, as well as the presence of type 55 and *Coniochaeta* cf. *ligniaria*. This association is related to a locally meso-eutrophic environment with low water levels in the lake. *Coniochaeta xylariispora* and *Coniochaeta* cf. *ligniaria*, high percentages of cf. *Spadicoides bina*, type 359 and *Bactrodesmium* type are associated with strong fires; high percentages of *Ustulina deusta*, a non-pollen palynomorph common on stump butts and dead roots of deciduous trees deposited after forest burning are also apparent; Type 527 reflects a clay sedimentation environment (van Geel, 1976, van Geel et al., 1981, 1983a, 1986).

A drastic, short term but complete replacement of the dense moist forest by *Cecropia* and grasses associated with frequent fires characterize the general conditions of this period.

Pollen zone II extends from 153 to 105 cm with an estimated age of 11,000–8500 cal yr BP and is characterized by a stable percentage of AP of between 41% and 63%. The percentage of *Cecropia* is still high (0–11% with a mean value of 4%) and Poaceae becomes a dominant taxon (30–52%). New taxa such as *Mauritia* (single pollen grains) and *Rhizophora* (3–15%) appear. They attest to environmental conditions that are different from previous zones. *Mauritia* is a common palm tree of the Cerrado linked with seasonally inundated patches in the Cerrado and *Rhizophora* is a component of mangrove vegetation. The percentage (15%) of this species corresponds to the distance between the lake and the coast, i.e. ca 80 km, as the percentage of *Rhizophora* can reach more than 90% in modern samples collected on the surface of the mangrove (Behling, 1997). An abrupt change is apparent at 136 cm,

~10,500 cal yr BP characterized by lower percentages of Poaceae (7%) and *Rhizophora* (0%) and an increase in Myrtaceae (28%) and Mimosaceae (11%). We interpreted this as a short-term development of a dense riparian forest. The percentage of *Botryococcus*, *Pediastrum* and *Spirogyra* algae increase, and for the first time Spermatophores of *Copepoda* are observed in the sequence, suggesting the presence of open water (van Geel, 1976; van Geel and Middeldorp, 1988). *Rivularia* type increase and the appearance of the Neorhabdoceola oocytes (*Mesostoma lingua*, *Gyratrix hermaphroditus*, *Micodalyellia armigera*, *Gieystoria virgulifera* and *Strongylostoma radiatum*) suggests the presence of locally moister soils than before, as non-pollen palynomorphs that are characteristic of a dry-environment are not recorded (e.g. type 55). The high values detected for Neorhabdoceola could be the result of a rise in lake productivity due to inorganic and organogenic input to the lake, as attested by the subsequent blooming of *Pediastrum* species, *Botryococcus* species and Zygnemataceae (*Spirogyra*) (Haas, 1996).

After the destruction of the forest observed during the previous period, the composition of the vegetation did not reverse to a dense moist forest. Open vegetation, strong fires and the presence of some Cerrado species such as *Mauritia* attest to the establishment of a relatively seasonal climate with high water levels during this period.

Pollen zone I extends between 104 and 0 cm with an estimated age of 8500 cal yr BP to modern. AP progressively increases throughout zone I, with 48% at the base and 62% at the top. *Byrsonima* (1.5–5%), *Cecropia* (1–6%) Melastomataceae (1–6%) Myrtaceae (1–6%) *Rhizophora* (4.5–12%) and *Swartzia* (0–5%) represent a constant trend throughout the zone, while Mimosaceae increase progressively (2.5–17%). At the top of this zone, the percentages of *Mauritia* (5%), halophytes (4%) and *Botryococcus* (73%) increase and Moraceae (0.5–2%), Myrtaceae (3–6%), *Borreria* (1–3%) remain relatively high. Maxima of algae *Pediastrum*, *Botryococcus*, *Spirogyra*, *Mougeotia*, type 55, *Coniochaeta* cf. *ligniaria* and Neorhabdoceola, the presence of *Pleospora* sp., type 90, *Anthostomella fuegiana*, type 173A and *Aphanizomenon* cf. *gracile* are observed in the upper part of the zone (Fig. 6). Between 15 and 50 cm, spermatophores of *Copepoda* *Alonsa rustica*, *Tetraedron minimum* are also observed. These taxa are characteristic of lakes with a low pH and high water levels and indicate eu- to mesotrophic conditions of open fresh water (Bakker and van Smeerdijk, 1982; van Geel, 1976; van Geel et al., 1983b). *Aphanizomenon* cf. *gracile* are akinetes of cyanobacteria and are able to form dense populations (referred to as water blooms) under warm temperature conditions. They are considered as good indicators for meso- to eutrophic environments and are linked to the increased input of phosphates into the lake by man in modern times (van Geel et al., 1994; López Sáez et al., 2000). Types 19, 52, 757, 972 also show maxima in this zone but their ecological significance is not known yet (Fig. 6).

The wide range of non-pollen palynomorphs is characteristic of a eutrophic environment, with more organic-rich and shallower water than during the previous period. The Cerrado that started to develop in zone II now develops fully. Warm temperatures and an increase in moisture rates during the last centuries are modern features.

4.2.2. Core ma 98-4

Radiocarbon dates (Table 2) indicate that core MA 98-4 represents a more detailed post LGM recovery of the vegetation than in the other records. Consequently we analyzed the lowest 300 cm of sediment deposition between ca 21,000 and 17,000 cal yr BP. This section is characterized by low percentages of AP, between 5% and 20% (Fig. 7). Among the trees, we identified *Byrsonima* (0–5%), *Mimosa* (0–11%), *Myrtaceae* (0–9%), *Solanum* (0–4%), *Triplaris* (0–7.5%) and *Melastomataceae* (0–4%). Dominant herbs are *Borreria* (0–37.5%) and *Poaceae* (17–58%). A change in the aquatic taxa is evidenced at 427 cm by an increase in *Myriophyllum* (0–4%), the disappearance of *Alismataceae* (13–0%), and a decrease in *Cyperaceae* (from over 15% to less than 10%), while *Botryococcus* increase sharply up to 133%. Between 350 and 335 cm depth *Borreria* increase (33%) and *Richardia* (less than 1%) and *Botryococcus* (1.5%) decrease due to a drop in the previous water level.

The landscape was open with fewer trees and probably more bushes in a dry herbaceous vegetation cover. There is evidence of fluctuations in water levels from low to shallow (succession of aquatics and algae) and for a progressive increase in edaphic moisture (*Myrtaceae*).

4.2.3. Core ma 98-5

This core drilled at a depth of 439 cm was analyzed between 122 cm and the bottom of the core to check if the regional characteristics of the environmental changes detected in both cores 97-1 and 98-4 during the past 20,000 yr BP are also apparent in another part of the lake.

Two main zones could be distinguished separated by a sterile sand layer with no pollen content (Fig. 8). In the first zone, between 450 and 315 cm, the arboreal content is characterized by low percentages (13–30%) mainly comprising *Byrsonima* (0–4%) and *Myrtaceae* (1–7.5%). NAPs are mainly *Asteraceae* (0–6%), *Borreria* (7–55%), *Poaceae* (20–63%), *Gomphrena* (0–4.5%).

In the second zone, between 275 and 122 cm, after a brief fluctuation in the percentage of AP from 26% to 87%, the diversity and frequency of taxa increase: *Byrsonima* (0–7%), *Didymopanax* (0–10%), *Ilex* (0–6.5%), *Melastomataceae* (0–33%), *Moraceae* (0–22%), *Myrsine* (0–9.5%), *Myrtaceae* (6–25%), *Podocarpus* (0–6.5%). The peak of 6.5% of *Podocarpus* at 194 cm allows us to ignore the date of 11,000 ¹⁴C yr BP obtained at ca 260 cm since a similar a peak was dated at ca 12,000 ¹⁴C yr BP in core 97-1. The succession of the following tree taxa is observed: *Didymo-*

panax and *Byrsonima*, *Melastomataceae/Combretaceae* and *Myrsine* followed by an increase in *Moraceae* and *Cecropia* and *Podocarpus*. *Botryococcus* decrease attesting to an increase in the depth of the lake. The same pattern is observed in 97-1 between 17,000 and 12,800 cal yr BP (Ledru et al., 2001).

The first zone attests to an open landscape under dry environmental conditions and corresponds to zone V in core MA 97-1. The second zone confirms the progressive development of a dense moist forest during the lateglacial and corresponds to zone IV of the MA 97-1 pollen diagram.

The results obtained in the three cores MA 97-1, 98-4, and 98-5 show the same evolution of the environment during the last 20,000 yr and confirm the regional feature of the changes observed in percentages of pollen in the lacustrine sediments.

4.3. Changes in $\delta^{13}C$

Three profiles were analyzed 50 m from the edge of the lake (LCF 50), at 150 m (LCF 150) and at 200 m (LCF 200) to the south (Figs. 1 and 9). The soil profile 50 m from the edge of the lake does not show any changes in isotopic values while the two other profiles show a change at 180–190 cm depth with values of $\delta^{13}C$ of –21.5‰ in LCF 150 and of 21‰ at 140–150 cm depth in LCF200. We interpreted this as the presence of more open vegetation with the dominance of *C₄* plants at the time of this isotopic event. This change is estimated to have occurred between 9000 and ca 4000–3000 cal yr BP according to five ¹⁴C dates obtained in LCF 200. The presence of charcoals is attributed to fires during the same time interval (Fig. 5) (Pessenda et al., 2004, 2005).

5. Discussion

5.1. Evolution of the Cerrado at Lake Caço

Pollen, algae, spore and isotope contents of the cores and profiles analyzed from Lake Caço and surroundings attest to important changes in the floristic composition of the Cerrado. In the southern hemisphere warming started at ca 19,000 yr BP leading that of northern hemisphere by about 2000 yr (Clark et al., 2004; Grootes et al., 2001; Jouzel et al., 1995; Steig et al., 1999). The region of Lake Caço showed sparse and shrubby vegetation with dominance of steppic grasses and absence of trees in a poor sandy soil (Jacob et al., 2004) with numerous short-term fluctuations. This landscape does not present the characteristics of a Cerrado but indicates dry climatic conditions. However, single pollen grains of *Byrsonima* and *Mimosa* attest to their presence in this region and that they could survive under arid climates, most likely as shrubs. At the end of the LGM and the beginning of deglaciation, when sedimentation started in the lake, the vegetation was sparse and rare and mainly composed of dry herbs, *Gomphrena*,

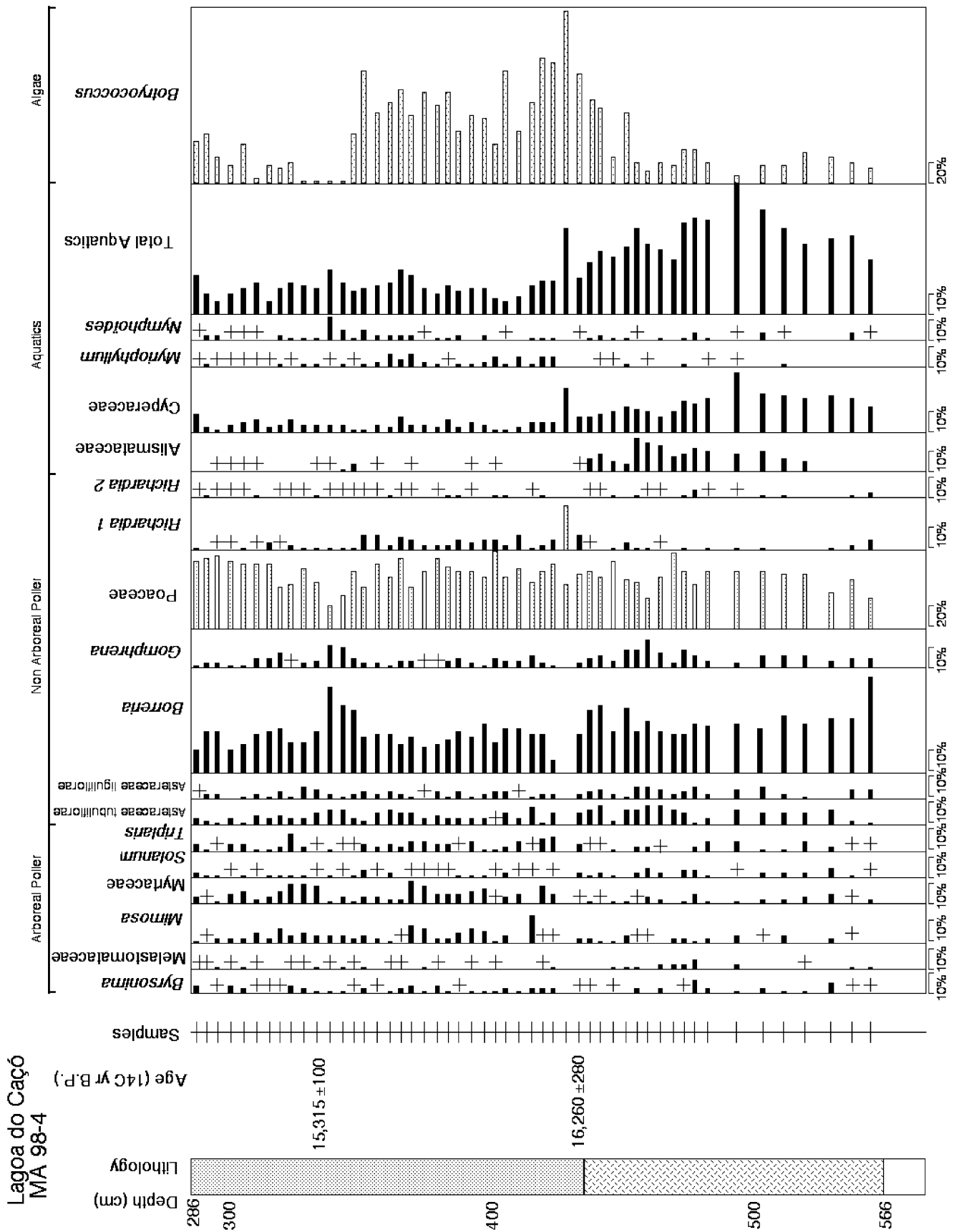


Fig. 7. Pollen percentages diagram of core MA 98-4 showing selected taxa. The pollen sum includes arboreal and non-arboreal pollen taxa. Values smaller than 1% are represented by the “+” sign.

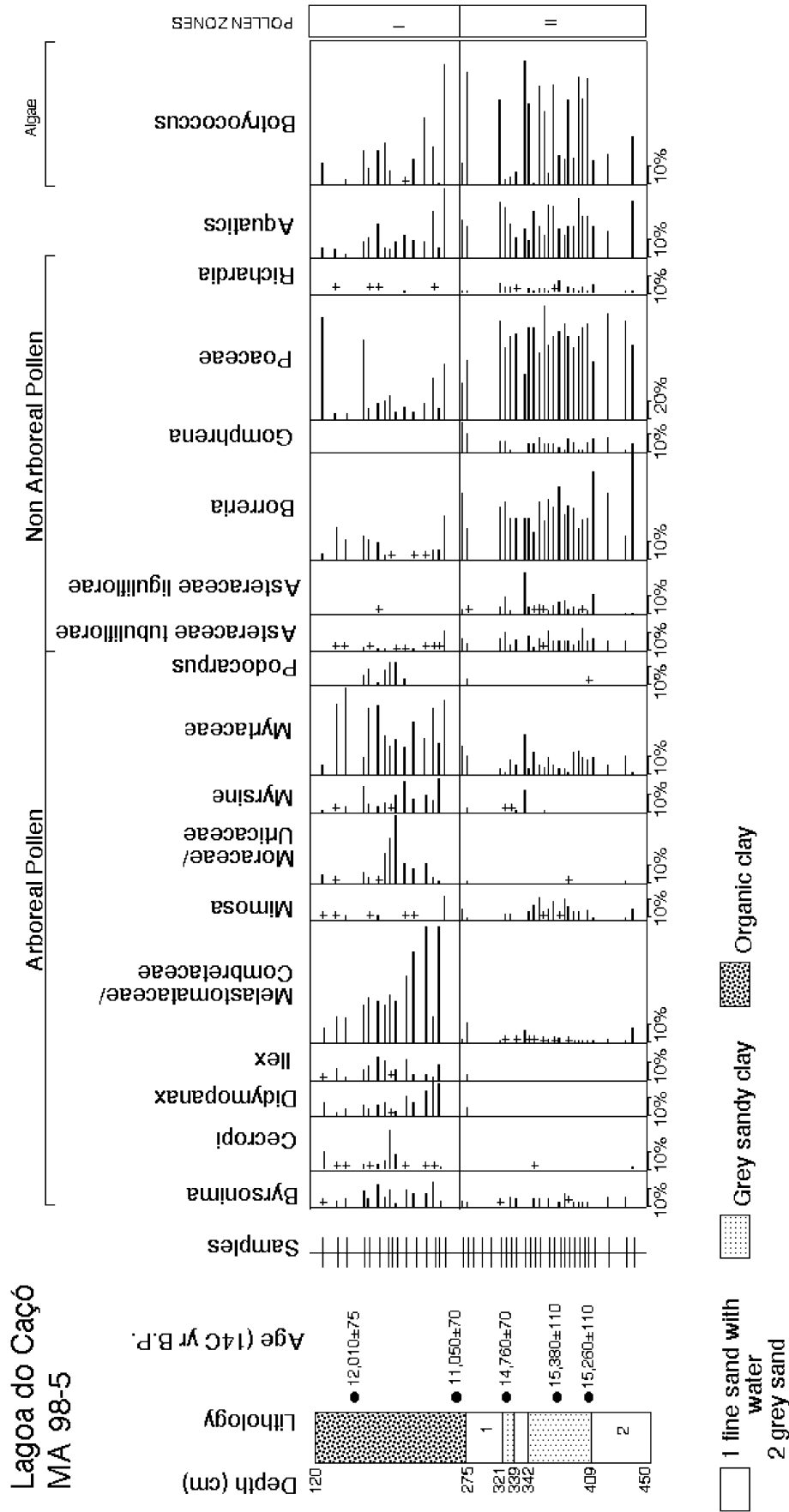


Fig. 8. Pollen percentage diagram of core MA 98-5 showing selected taxa. The pollen sum includes arboreal and non-arboreal pollen taxa. Values smaller than 1% are represented by the “+” sign.

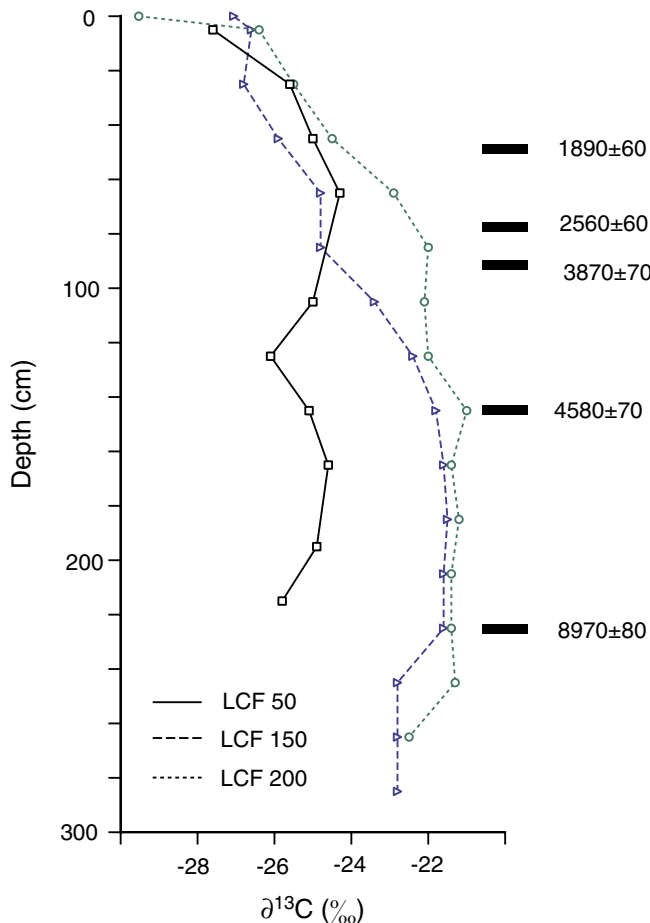


Fig. 9. $\delta^{13}\text{C}$ curves of the profiles LCF 50, LCF 150, LCF 200 and radiocarbon dates obtained from charcoals collected in LCF 200 trench, adapted from Pessenda et al. (2004).

Cyperaceae and Alismataceae, and shrubs such as *Ceratostyles* (Cucurbitaceae), *Richardia*, indicators of poor sandy soils in a dry climate. Cerrado was absent from the area although some of the main Cerrado taxa (*Byrsonima*, *Mimosa*) are represented by single pollen grains indicating that Cerrado taxa continued to be present in the form of some individual shrubs. Important taxa to consider are *Manilkara* and *Copaifera*, both trees common to the three vegetation types present today in the region of Lake Caço, Cerrado, Restinga and riparian forest. They are observed at Lake Caço since the beginning of the record, although in small numbers.

In Amazonia, at the same latitude as Lake Caço, the record of Carajas (6°S) shows that an expansion of *Byrsonima* occurred at least two times during the Last Glacial, which was interpreted as an indicator of a drier and more open landscape (Absy et al., 1991). However, this expansion of *Byrsonima* into Amazonia is not related to any of the three phases of the decrease in the percentage of AP (LGM, Lateglacial and mid Holocene for the latter) recorded in the pollen diagram (Ledru, 2002). Thus, we cannot infer an expansion of the Cerrado towards

Amazonia during glacial times. However we can infer the facility of *Byrsonima* and some other Cerrado taxa, such as *Myrsine*, to grow in association with other non-Cerrado species revealing the importance of this taxon when vegetation changes occur.

In northern Brazil, when humidity progressively increased after 17,000 calyr BP, the percentage of AP starts to increase mainly with an increase in *Byrsonima*, *Mimosa*, Myrtaceae and the presence of *Copaifera* and *Hymenea*, an assemblage of taxa that is characteristic of a Restinga. The percentage of Myrtaceae, an indicator for poorly drained soil, often increases when conditions suddenly become moister after a dry event. *Botryococcus*, which is observed at the base of all three cores, is associated with the presence of a shallow lake. Beside these local features, a major regional change is evidenced by the spread of the forest. This forest evolved from a forest dominated by pioneer-species towards a dense rain forest rich in *Podocarpus*, a conifer of the cloud forest (*Podocarpus lambertii*) that is widespread in southern Brazil today and is also found in refugia in northern Brazil (*P. sellowii*). This increase in *Podocarpus* is also evidenced in other records from northern Brazil thereby attesting to the spread of this species under favorable climatic conditions (Ledru et al., 2001). The development of a dense moist forest represents the main difference from the evolution of vegetation in Central Brazil, considered to be the main area for Cerrado today. In this region no forest installation was recorded during the Lateglacial (Barberi et al., 2000). Here the forest evolved from a forest with dominant-pioneer species to a dense rain forest and ended abruptly at the end of the Pleistocene.

The presence of *Rhizophora* since the beginning of the Holocene attests to the installation of the mangrove on the coast in the state of Maranhão after a rise in sea level. Its relatively low percentage (20%) compared to the 90% observed in records located inside the mangrove (Behling, 1997), attest to wind transportation from the coast to the lake, which corresponds to the direction the trade winds blow today.

During the early Holocene, summer insolation reached its lowest value in the southern hemisphere with warmer winters, colder summers and less precipitation than today (Martin et al 1997), ENSO was also weaker or absent (Rodbell et al., 1999). An open landscape expanded nearly throughout the southern tropics showing some hiatus in sedimentation (Ledru et al., 1998). At Lake Caço, all the Cerrado taxa are recorded since the beginning of the Holocene but at low rates. *Mauritia*, the main component of the swamp forest in the Cerrado, can be observed since the beginning of the Holocene attesting to an increase in available soil moisture. The high water level of the lake identified by sedimentological analysis (Sifeddine et al., 2003) that is reflected in the higher soil moisture availability in the region could be related to the rise in sea level that started at the beginning of the Holocene and continued until ~7000 yr BP (Milne et al., 2005). Fully

developed Cerrado is observed after 8000 yr BP when *Byrsonima* and *Mimosa* are widespread along with Poaceae. A sharp increase in *Botryococcus*, an alga that is an indicator of shallow lakes, followed by repeated changes in abundance attest to fluctuations in the level of the lake during the late Holocene due to a more seasonal climate. This is a general pattern observed in all neotropical savanna areas, Llanos in Colombia and Cerrados in Brazil, which became fully established after ~7000 yr BP (Behling and Hooghiemstra, 2001).

Fires in the Cerrado are characterized as surface fires that consume the fuel represented by the herbaceous layer. The vegetation comprising the herbaceous layer represents 94% of the fuel consumed during the fires and *Byrsonima* is fire resistant (Miranda et al., 2002). In northern Brazil, fires are evidenced after 12,000 yr BP when the herbaceous layer was fully established and Cerrado taxa started to expand.

5.2. Paleoclimatic inferences and comparison with other records

Late Pleistocene paleoenvironmental records from northern Brazil reflect the interplay between insolation forcing and local components represented by the inter-annual shift of the convergence zones (ITCZ and SACZ) and the influence of equatorwards polar air incursions during winter. At the time of the LGM, ice cores show that both southern and northern hemispheres had minima in temperatures. Consequently strong pole-equator temperature gradients on both sides of the equator were able to prevent large seasonal shifts of a weakened ITCZ. A dry climate and sparse open vegetation is observed at low latitudes. Further south, the diameter of the atmospheric circumpolar vortex increased and induced an increase in the intensity of the circulation: mid-latitude westerlies were able to extend northwards because of a weakened ITCZ and consequently the subtropical high shifted equatorward inducing changes in seasonal precipitation (Markgraf et al., 1992; Wainer et al., 2005). During the deglaciation, changes in insolation in Antarctica and Greenland resulted in the reorganization of the thermohaline circulation (Knorr and Lohmann, 2003) and rapid equatorward displacement of the polar air masses (Garreaud, 1999; Marengo et al., 1997). Two regional effects of changes in the global atmospheric circulation are recorded at Lake Caço during the Lateglacial. Both are characterized by a decrease in temperature although they express differences in signal expression. When the first abrupt climatic change occurred between 15,000 and 13,500 cal yr BP, it was related to the Antarctic cold reversal (ACR) when the southern hemisphere was cooler than the northern hemisphere. This event is also well recorded in ice cores from Antarctica and from the Andes (Blunier and Brook, 2001; Thompson et al., 1998). Today strong and frequent polar advections are able to reach low latitudes and influence the distribution of precipitation (Kousky, 1979). We infer the

same mechanism to explain the consequence of the ACR near the equator when semi-permanent atmospheric moisture enabled a forest of *Podocarpus* to expand instantly from its refugia while the ITCZ was maintained in a northern position in the warmest hemisphere. During the second abrupt climatic change that corresponds to the YD climatic reversal, temperatures in Greenland were lower than in the Antarctic (Blunier and Brook, 2001) and the northern hemisphere was consequently colder than the southern hemisphere. Polar advections were stronger in the northern hemisphere, reached tropical latitudes and prevented the seasonal northward shift of the ITCZ which was maintained in a southern position. This induced a drier and cooler climate in the tropics until 17°S in latitude (Ledru et al., 2002) and high moisture rates in northern Chile on the Pacific side (Nuñez et al., 2002) as well as the absence of a YD event further south in southern Patagonia (Markgraf, 1991). This short dry event drastically destroyed the moist forest and strong fires are evidenced at this time. This succession of abrupt climatic changes contributed to the expansion of the species of the Cerrado in this region which culminated during the Holocene. These abrupt changes reflect modifications in the thermal gradient between the pole and the equator that enable rapid shifts of polar air masses to low latitudes and changes in the seasonal shifts of the ITCZ and SACZ (Ledru, 2002; Ledru et al., 2001, 2002; Rind, 1998).

The precessional low that occurred at the beginning of the Holocene in the tropics is reflected in the out of phase response of the Central and South American lake levels. Precipitation maxima/minima are recorded on either side of a band located quite near the equator. South of this band lake levels reflect dry conditions associated with the early Holocene decrease in summer insolation, while north of the band the ITCZ remained stationary for some time and high moisture rates are evidenced (Haug et al., 2001; Mourguiart et al., 1998; Seltzer et al., 2000). At Lake Caço, the situation seems to lie between the two, as neither an increase in moisture rates nor an increase in aridity after the YD event is apparent. The expansion of the woody vegetation seems rather to be related to an increase in available soil moisture due to a rise in sea level. No major changes in vegetation cover are evidenced during the late Holocene while modern climatic conditions display a strong seasonal contrast.

6. Conclusion

The records obtained at Lake Caço provide evidence for important environmental changes since the beginning of deglaciation at low latitudes. These changes caused the installation of the Cerrado physiognomy and floristic composition that can be observed today. In addition, some Cerrado species, such as *Byrsonima* and *Myrsine*, are able to grow under different climatic conditions and different floristic associations which enable this biome to adapt to local environmental changes. This ability could be the

reason for the six different types of Cerrado defined by Ratter in 1996. Marked differences in the evolution of the climate within the six zones, e.g. between Central Brazil and Maranhão during the Lateglacial, are also assumed to explain these ecological differences.

Late Pleistocene paleoenvironmental records from northern Brazil reflect the interplay between insolation forcing of both hemispheres with the local components represented by the interannual shift of the ITCZ and the influence of equatorwards polar air incursions. Numerous abrupt and short climatic changes are recorded by the vegetation. One main change occurred between 15,000 and 13,500 yr BP and is characterized by forest expansion, and the second occurred between 12,800 and 11,000 yr BP and, is characterized by forest regression. The Holocene shows a markedly different evolution and is divided into two main periods: a relatively moist early Holocene due to a weak seasonal contrast during the low precession signal and the installation of a seasonally contrasted climate during the second half of the Holocene. This is different from the Central region of Brazil between 10 and 15°S, where marked mid Holocene aridity is evidenced by both pollen and archeological records. The absence of typical ENSO variations that are clearly apparent in other Holocene records from tropical South America (Martin et al., 1993; Rodbell et al., 1999; Stott et al., 2002) is attributed to the natural adaptation of the biome Cerrado to a contrasted seasonal climate, commonly a dry season lasting 5–6 months. This adaptation of the vegetation to long dry seasons and fires prevented the regional lacustrine sedimentation from being affected by interdecadal or inter-annual climatic changes at a time resolution of 50–70 yr per sample.

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