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LATE PLEISTOCENE/HOLOCENE ENVIRONMENTAL HISTORY OF THE SOUTHERN BRAZILIAN PANTANAL WETLANDS

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Abstract: This study presents paleolimnological records from two lakes denominated locally as Lagoa Negra and Lagoa Castelo (Pantanal Brazilian Wetland), using sediment cores. The sediment core was dated using ^{14}C geochronologies and samples were analyzed for bulk density, grain size, organic matter, carbonate, phosphorus, carbon and nitrogen elemental and isotopic composition ($\delta^{13}C$ and $\delta^{15}N$), sedimentary pigments and sponge spicules. Pollen and diatoms remains were analyzed only in Lagoa Negra because they were scanty and poorly preserved in Lagoa Castelo core. Paleolimnological and palynological records were used with the objective to gain a better understanding of the environmental history of the Pantanal during the last 21,000 cal yrs BP (calibrated years Before Present). The different phases in the development of the lakes were based on the palynological analysis of Lagoa Negra core (CONISS analysis) used as a proxy key. The Lagoa Negra core indicates than the late Pleistocene (~21,000 to 12,200 cal yrs BP) was marked by strong river-lake connectivity (~21,000-19,000 cal yrs BP and ~13,000-12,200 cal yrs BP) and with regression of the Paraguay River between ~19,000-13,000 cal yrs BP. The emergence of the gallery forest in the early to mid-Holocene (~12,200 to 8500 cal yrs BP) indicates wetter conditions, similar to the present. In such conditions began the development of Lagoa Negra, from ~11,500 cal yrs BP, with the deposition of fine organic-rich sediments. In the mid to late Holocene (8500 cal yrs BP to present) the connectivity with the river was reduced or lost completely, between ~8200 and 6500 cal yrs BP (Lagoa Negra). The semi-closed Lagoa Castelo reduced connectivity with the Paraguay River only about 6500 cal yrs BP, when abruptly occurs the transition to deposition of organic sediments. A reactivation of the river-lakes interaction was detected after this period, although not as intense as in the early Holocene.

Keywords: floodplain lakes; isotopic geochemistry; Paleoecology; Paleolimnology; sedimentary organic matter.

INTRODUCTION

The Pantanal Wetland of Central Brazil is one of the largest wetlands in the world and despite its overwhelming importance for the central South American biota, very little is known about its environmental history during the late Quaternary. The Pantanal system, located between 16-22º S and 55º-58º W, has approximately 135,000 - 200,000 km² (Godoi-Filho 1986). This wetland contains four important South American phytogeographic influences such as the Cerrado and the Chaco woodlands, the Amazon and the Atlantic Rainforests (Adámoli 1982).

Referred to as the largest intracratonic Quaternary sedimentary basin of Brazil (Shiraiwa 1994), the Pantanal region occupies the floodplains of the Upper Paraguay River Basin, where one of its most important geographical features is the presence of many lakes differing among each other by their origin, topographical features and their relationship with the large local river systems. Many of these lakes, located within the alluvial fan of the Taquari River, also known as the Nhecolândia Pantanal, are generally ephemeral and smaller than 1 km² in diameter (Tricart 1982). However, large permanent lakes such as Lagoas Negra and Castelo, located at the shores of the Paraguay River, can be found in the region (Figure 1). Ab'Sáber (1988) suggests that the Pantanal is a legacy of late Pleistocene environmental changes. According to the author, the late Pleistocene climate of the Pantanal region was drier than the present, with torrential rains in the rainy season. As a result, the Pantanal consists of alluvial fans of its main rivers, the largest and most important of which is the Taquari fan, which extends onto a 50,000 km² area (Braun 1977).

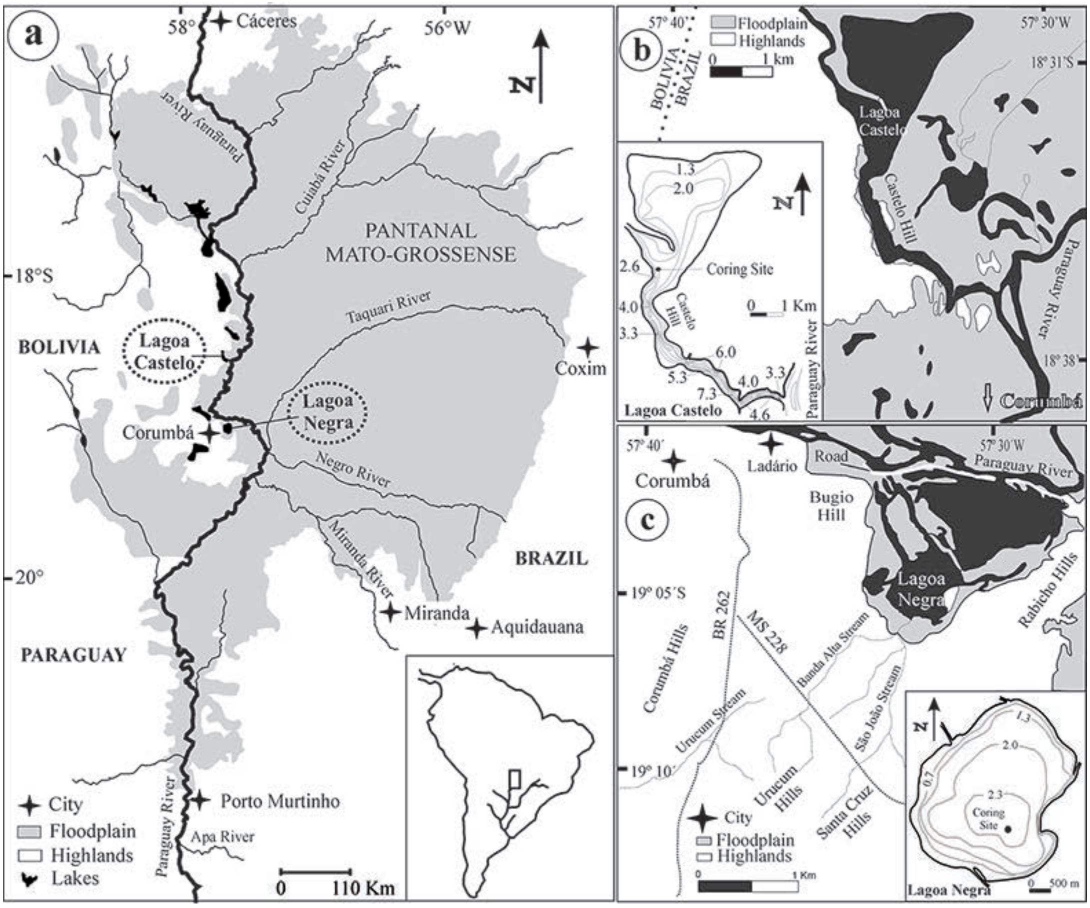

Figure 1. Location of Lagoa Negra and Lagoa Castelo in the Pantanal wetland, Brazil (a). Detailed map and bathymetry of Lagoa Castelo (b) and Lagoa Negra (c), with the location of the sediment cores described in this study.

Recent late Quaternary paleolimnological studies have focused mainly on great lakes hydrologically-connected to the Paraguay River (especially in Lagoa Gaíva, also called Laguna La Gaiba on the Bolivian side of the lake), in the international boundary Bolivia-Brazil (Whitney *et al.* 2011, McGlue *et al.* 2012, Whitney & Mayle 2012, Metcalfe *et al.* 2014) and hydrologically closed small lakes in the southern Pantanal Wetlands, Nhecolândia Pantanal (McGlue *et al.* 2017, Becker *et al.* 2018, Guerreiro *et al.* 2018). These studies used multi-proxy paleolimnological (especially sponge spicule, *Pediastrum* and diatom paleoecology) and palynological records and provided evidence that the Pantanal was drier during the last glacial period than during the Holocene. They also concluded that drought affected the Pantanal in the early to mid-Holocene and a shift to wetter conditions began in the late Holocene.

The aim of this study was to reconstruct the paleoenvironmental history of the Lagoas Negra and Castelo, since 21,000 cal yrs BP by means of ^{14}C dating, sedimentological and geochemical characteristics (especially C/N ratio, ^{13}C and ^{15}N compositions) as well as biological remains analyses (pollen, diatoms and sponge spicules) in sediment cores. The paper provides the first well-dated continuous sedimentary records of late Quaternary, obtained from Lagoas Negra and Castelo. The paleoenvironmental information of both Quaternary sedimentary records were amplified in relation to previously published data (Bezerra & Mozeto 2008).

MATERIAL AND METHODS

Study area

The Lagoas Negra (19°04’ S, 57°31’ W) and Castelo (18°32’ S, 57°34’ W) are located in the municipality of Corumbá, Mato Grosso do Sul state, on the west edge of the Brazilian Pantanal Wetland (Figure 1). Both lakes are connected with extensive floodplains periodically inundated by the overflow of the Paraguay River. Bathymetric data were collected in December 1995, low water period (Bezerra 1999) and indicated that the lakes are small (< 20 km^2) and shallow (< 7.3 m) (Figure 1). The Lagoa Castelo has a low ion concentration with pH and conductivity values ranging between 6.2-6.9 and 47-87 µS/cm, respectively (Calheiros & Hamilton 1998). Data collected in Lagoa Negra water in 2001-2002 showed that the pH is slightly alkaline (6.9-8.3) and the electrical conductivity ranged between 140 and 240 µS/cm (M. A. O. Bezerra, unpublished data). The altitude is ~85 m a.s.l and the lakes are surrounded by hills, some of which reach up to 1000 m. The local climate is warm and humid with temperatures frequently above 27°C. Mean annual rainfall is slightly above 2000 mm at the northern boundary of the Paraguay River Basin and falls to 800 mm in the south and west (Collischonn *et al.* 2001). In these conditions, the discharge of the Paraguay River is mainly due to precipitation in the upper part of the basin, which contributes with 70% of the water that raises the level of the river in the region of the studied lakes (Adámoli 1986). The floods in the studied area occur approximately three months after the rainfall maxima due to the slow passage of the flooding waters throughout the Pantanal, because of its flat relief (Valverde 1972). Highest flood levels occur between the months of April and July, corresponding to the period of lower local rainfall (Figure 2).

Data collection and analysis

A vibro-coring sampler was used to recover two sediment cores from Lagoa Negra (LN95/L1 core, 2.3 m water depth) and Lagoa Castelo (LC95/L1 core, 2.6 m water depth). The cores LN95/L1 (272 cm) and LC95/L1 (350 cm) were collected during a low water period in December 1995. Bulk density was calculated as dry mass (dried at 105ºC) divided by wet sediment volume (Håkanson & Jansson 1983).

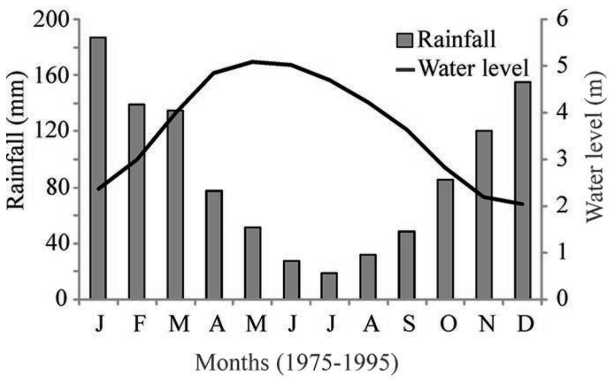

Figure 2. Rainfall (Instituto Nacional de Meteorologia, municipality of Corumbá, Brazil) and water level of Paraguay River (Brazilian Navy District, municipality of Ladário, Brazil), mean monthly of the years 1975-1995.

Samples for grain size analysis were pre-treated using 30% H_2O_2 to remove organic matter. To prevent flocculation, 5% sodium hexametaphosphate was added to each sample. After mechanical agitation, the analyses were carried out using the sieve and pipet method (Suguio 1973). Total organic matter (TOM) content and carbonate were estimated through loss-on-ignition at 550ºC and 1000ºC, respectively (Dean 1974).

Conventional ^{14}C ages were carried out at the Environmental Isotope Laboratory of the University of Waterloo, Canada and the analyses by Accelerator Mass Spectrometry (AMS) were carried out at the IsoTrace Laboratory of the University of Toronto, Canada. The ^{14}C data are here reported as radiocarbon ages yrs BP normalized to a $\delta^{13}C$ value of -25‰ (Stuiver & Polach 1977). The ages were expressed into calibrated years (cal yrs BP, 2σ probability) using the IntCal13 calibration curve (Reimer *et al.* 2013). An age model was derived by fitting a cubic-spline curve through the calibrated dates. All samples received acid-wash pretreatments to remove possible carbonates prior to organic elemental and isotopic measurements. The sediment accumulation rate was calculated by multiplying the sedimentation rate (mm yr^{-1}) by bulk density (g cm^{-3}) (Turcq *et al.* 2002).

Analyses of total organic carbon (TOC), total nitrogen (TN) and stable isotopic ($\delta^{13}C$ and $\delta^{15}N$) were carried out at the Environmental Isotope Laboratory of the University of Waterloo, using a Carlo Erba EA attached to a VG Isochrone Isotope Ratios Mass Spectrometer. The ^{13}C and ^{15}N data were expressed in per mil (‰) relative to atmospheric air and Vienna PeeDee Belemnite (VPDB), respectively. The total phosphorus (TP) concentrations were determined after combustion of 0.2 g of dry sediment at 550°C. The burning residue was digested with 25 ml 1N HCl at 105ºC and an aliquot of the extract was subjected to the Murphy and Riley colorimetric method (Andersen 1976). Sedimentary pigments were extracted from 2.5 g of wet sediment in 90% acetone (Swain 1985). The sedimentary pigment concentrations were expressed as chlorophyll derivatives (CD) and given as standard absorbance units per gram of TOM as suggested by Vallentyne (1955).

The analyses of palynomorphs and diatoms were performed only in the LN95/L1 core due to poor preservation of such structures in the LC95/L1 core. Standard palynological analyses were conducted in 23 samples from the LN95/L1 core following the chemical treatment described in Faegri & Iversen (1989) and Colinvaux *et al.* (1999). Residues were later washed with concentrated glacial acetic acid, followed by washes with absolute ethanol. Palynomorphs found in the residues were stained with an alcoholic safranin solution and later dispersed in glycerine. Permanent slides were made by mounting the residues on a glass coverslip, sealed with paraffin. Pollen and spores were identified using a Leitz Otholux II photomicroscope (400x-1000x). Identifications were based on the modern pollen reference collection housed at the Micropaleontology Laboratory of the Institute of Geosciences of the University of São Paulo, which contains approximately 5000 tropical American taxa as well as by the use of published pollen floras (Markgraf & D'Antoni 1978, Colinvaux *et al.* 1999). Palynological profiles were graphed with the Tilia/TiliaGraph software and pollen zones were established after running cluster analysis for stratigraphically constrained samples using the CONISS software (Grimm 1987).

Identification of diatom and counting of diatoms and spicules were performed in 35 samples from the LN95/L1 core and prepared following the standard method proposed by Battarbee (1986). Sediment samples were treated with H_2O_2 to remove all organic components and then rinsed with distilled water. Diluted aliquots of the residue were dried onto glass coverslips, and the coverslips were mounted onto slides with Permount and analyzed under oil immersion (1000x). Several transects along each coverslip were examined until at least 300 specimens were counted per sample. In order to avoid overestimation, only valves and spicules contained over 50% of the surface were counted. Diatom taxa were identified following Barber & Haworth (1981), Round *et al.* (1990), Bicudo & Menezes (2006) as well as the assistance of diatom researchers of the Institute of Botany of the state of São Paulo. Relative abundances of each taxon were calculated from the total sum of counted valves only for samples with valves count > 300. The qualitative analysis of spicules was performed in 28 samples of the LN95/L1 core, and in five samples selected from the LC95/L1 core. The samples were treated with nitric acid and aliquots were evaporated at room temperature onto coverslips, and the coverslips were mounted onto slides with Entellan following the method proposed by Volkmer-Ribeiro & Turcq (1996) aiming the taxonomic identification of sponge spicules.

RESULTS

Lithostratigraphy, bulk density, TOM, and ^{14}C chronology

The stratigraphy reveals that the base of the core LN95/L1 (between 272 and 165 cm) is composed of silt/clay sediments intercalated with two distinct sandy units (Figure 3). These sediments are characterized by high bulk density (> 1.5 g cm^{-3}), low water content (< 28%) and low values of TOM (< 4%). The core-top samples (above 165 cm) are composed primarily of darker and more compact silt/clay sediments, which are characterized by lower bulk density, high water content and much higher content of TOM. The TOM concentrations showed an increasing trend reaching a value of 17.7% at a depth of 73 cm and the concentrations decreased toward the topmost samples. The sediment profile of core LC95/L1 reveals sandy sediments (fine sand) with some peaks of 80% of the sand fraction in the base of the core, between 350 and 110 cm (Figure 4). In this interval, the sediments are characterized by high-density values (> 1.2 g cm^{-3}), low water content (< 21%) and very low content of TOM (< 4%). Above 110 cm depth, a clear abrupt sedimentary change was observed as TOM increases and reaches 24.3% at 96 cm depth. This unit is characterized by lower density values and higher water content than the base of the core. Both cores contain a low content of carbonate with an average of 1.4%.

The age-depth model constructed based on six (LN95/L1 core) and seven (LC95/L1 core) radiocarbon dates indicates a basal age of the cores of ~21,000 cal yrs BP (Table 1; Figure 5). The average sedimentary rate of the cores was 0.2 mm yr^{1} ranging from 0.1 to 0.6 mm yr^{1}. The sediment accumulation rates ranged from 75-477 g m^{-2} yr^{1} (LN95/L1 core) to 77-599 g m^{-2} yr^{1} (LC95/L1 core) (Figures 3 and 4). The highest rates occurred between ~12,000 to 6500 cal yrs BP and ~1000 cal yrs BP to the present.

Elemental analyses, stable C and N isotope and sedimentary pigments

The lower concentrations of TOC (< 0.3%) in the base of the cores limits the analysis of these parameters (Figures 6 and 7). The concentration of TOC varied from 0.1 to 7.6% (LN95/L1 core) and 0.1 to 11.6% (LC95/L1 core). The data for both cores showed the highest TOC value at ~6500 cal yrs BP and a decreasing trend reaching ~2% at the top of the cores. The average carbon accumulation rate was 2.7 g m^{-2} yr^{1} (LN95/L1 core) and 3.4 g m^{-2} yr^{1} (LC95/L1 core), ranging from 0.2 to 12.3 g m^{-2} yr^{1}. The concentrations of TN ranged from 0.02 to 0.96% and C/N ratio varied from 12 to 24, between the sediment cores. TP concentrations vary between 0.01 and 0.5 mg/g of dry sediment in the cores. The lowest TP concentrations were observed between ~10,000 and 1000 cal yrs BP in the LN95/L1 core and below ~3200 cal yrs BP in the core LC95/L1.

The $\delta^{13}C$ data in the LN95/L1 core showed an enrichment trend from -24‰ to values as high as -18 around 6500 cal yrs BP (Figure 6). Then, a decreasing trend toward more depleted $\delta^{13}C$ values reaching values as -28 is observed in the core-top samples. The $\delta^{13}C$ data varied between -24 and -27‰ in the sediments from core LC95/L1 (Figure 7). The $\delta^{15}N$ values varied between -0.6 and 3.6 in both cores (Figures 6 and 7). The CD concentration varied between 0.1 and 2.3 units/g TOM and from ~6500 cal yrs BP to present, the sedimentary pigment profiles showed a progressive increase to the top of the core, in both lakes (Figures 6 and 7).

Pollen analysis

Pollen counts in Lagoa Negra sediments are restricted to the Holocene due to the absence of palynomorphs in the sediments of the Pleistocene age. The Holocene sediments, in general, contained well-preserved pollen, spores and other palynomorphs. Out of the 23 samples examined, six samples were sterile. The results of the Coniss cluster analysis suggest three pollen zones, which are displayed in all pollen diagrams (Figure 8). The pollen zone 3 (272-201 cm; ~21,000 to 12,200 cal yrs BP) is devoid of pollen and other palynomorphs. Pollen zone 2 (201-110 cm; ~12,200 to 8500 cal yrs BP) is marked by an increase in the relative abundance of arboreal pollen, dominated by the *Anacardium*/*Tapirira* type (4-20%), with Apocynaceae, *Astrocaryum*, *Cecropia*, Leguminosae

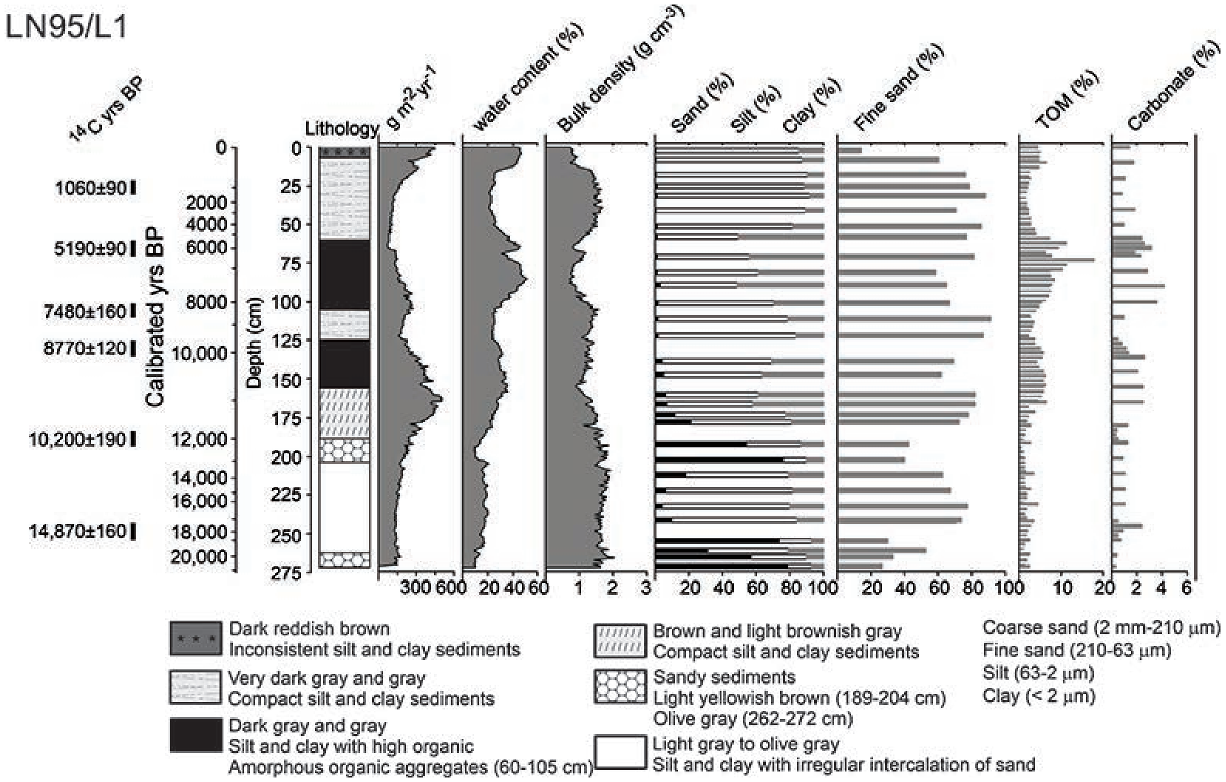

Figure 3. Geochronology, lithologic units, sediment accumulation rates (g m^{-2} yr^{-1}), water content, bulk density, grain size (including % of fine sand in total sand fraction), TOM (total organic matter), and carbonate diagram of the core LN95/L1, Lagoa Negra, Brazil.

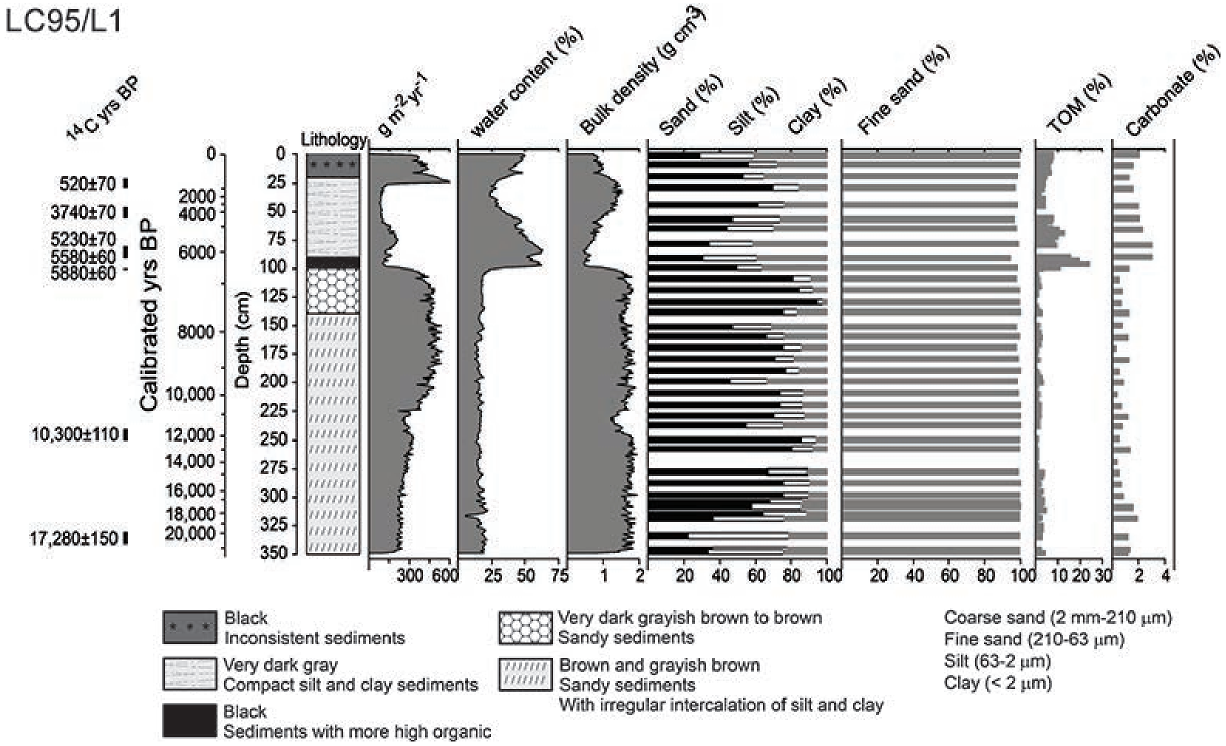

Figure 4. Geochronology, lithologic units, sediment accumulation rates (g m^{-2} yr^{-1}), water content, bulk density, grain size (including % of fine sand in total sand fraction), TOM (total organic matter), and carbonate diagram of the core LC95/L1, Lagoa Castelo, Brazil.

Table 1. Radiocarbon age determinations for the sediment cores LN95/L1 (Lagoa Negra) and LC95/L1 (Lagoa Castelo), from the Pantanal Wetland, Brazil. Dating method: [a]Liquid scintillation counting, [b]Accelerator mass spectrometry, - = not available

Core depth (cm)	Lab. number	^{14}C age (yrs BP)	Median Calibrated age (cal yrs BP)	$\delta^{13}C$ (‰) VPDB	Dated materials
LN95/L1					
21-30	WAT-4036[a]	1060 ± 90	980	-26.3	TOC
60-70	WAT-2967[a]	5190 ± 90	5960	-19.3	TOC
101-110	WAT-4037[a]	7480 ± 160	8280	-25.0	TOC
125-135	WAT-2975[a]	8770 ± 120	9850	-23.4	TOC
181-191	WAT-2976[a]	10,200 ± 190	11,900	-23.4	TOC
243-254	TO-6178[b]	14,870 ± 160	18,090	-22.9	TOC
LC95/L1					
21-30	WAT-4038[a]	520 ± 70	550	-26.2	TOC
46-56	WAT-3039[a]	3740 ± 70	4100	-26.3	TOC
80-90	WAT-3049[a]	5230 ± 70	6010	-25.7	TOC
90-91	TO-7096[b]	5580 ± 60	6380	-23.5	Wood fragments
100-101	TO-7097[b]	5880 ± 60	6700	-28.5	Wood fragments
239-249	TO-6180[b]	10,300 ± 110	12,100	-	TOC
336-346	TO-6181[b]	17,280 ± 150	20,850	-	TOC

(indet.), Palmae (Arecaceae), *Rapanea* (*Myrsine*), all with less than 4% of the total pollen sum, indicative of dense gallery forests of the tropical rainforest domain (Colinvaux *et al.* 1999, Garcia *et al.* 2004) (Figures 8 and 9). This trend in the arboreal component is synchronous with an increase in Cyperaceae (11-32%), aquatic herbs, together with grasses (Poaceae), with 34 to 43% of the total pollen sum, Compositae (Asteraceae) varying from 3 to 5% and with aquatic macrophytic taxa, represented by 5 to 10% of the total sum, such as *Myriophyllum*, *Ludwigia*, *Polygonum* and Pontederiaceae (Figure 10). Pollen zone 1 (110-0 cm; ~8500 cal yrs BP to present) is initially characterized by highly fluctuating percentages of algae spores and aquatic pollen grains together with continuously increasing values of Cyperaceae, reaching a maximum of 59% with consequent reduction of arboreal pollen (Figures 8 and 10). The modern vegetation pattern is established especially after ~6500 cal yrs BP as indicated by an expansion of arboreal and shrub taxa, although in low percentages, producing a pollen signal composed, in addition to *Anacardium*/*Tapirira*, of *Mimosa* (< 11%), *Cassia* (< 3%), *Mauritia* (< 10%), Palmae (6%), *Sebastiania* (< 5%) and Urticaceae/Moraceae (< 3%) (Figure 9). Such change is also mirrored in the fluctuating arboreal pollen curve (11-32%) (Figure 8). The increased contribution of taxa associated with herbaceous aquatic vegetation in the Middle Holocene, dominated by Cyperaceae and Poaceae is suggestive of an extensive opening of flooding habitats in the fluvial system (Figures 8 and 10).

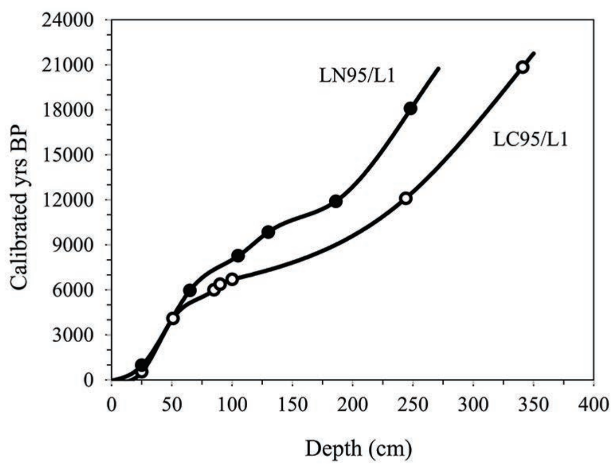

Figure 5. Age-depth curves for the core LN95/L1 (Lagoa Negra) and LC95/L1 (Lagoa Castelo).

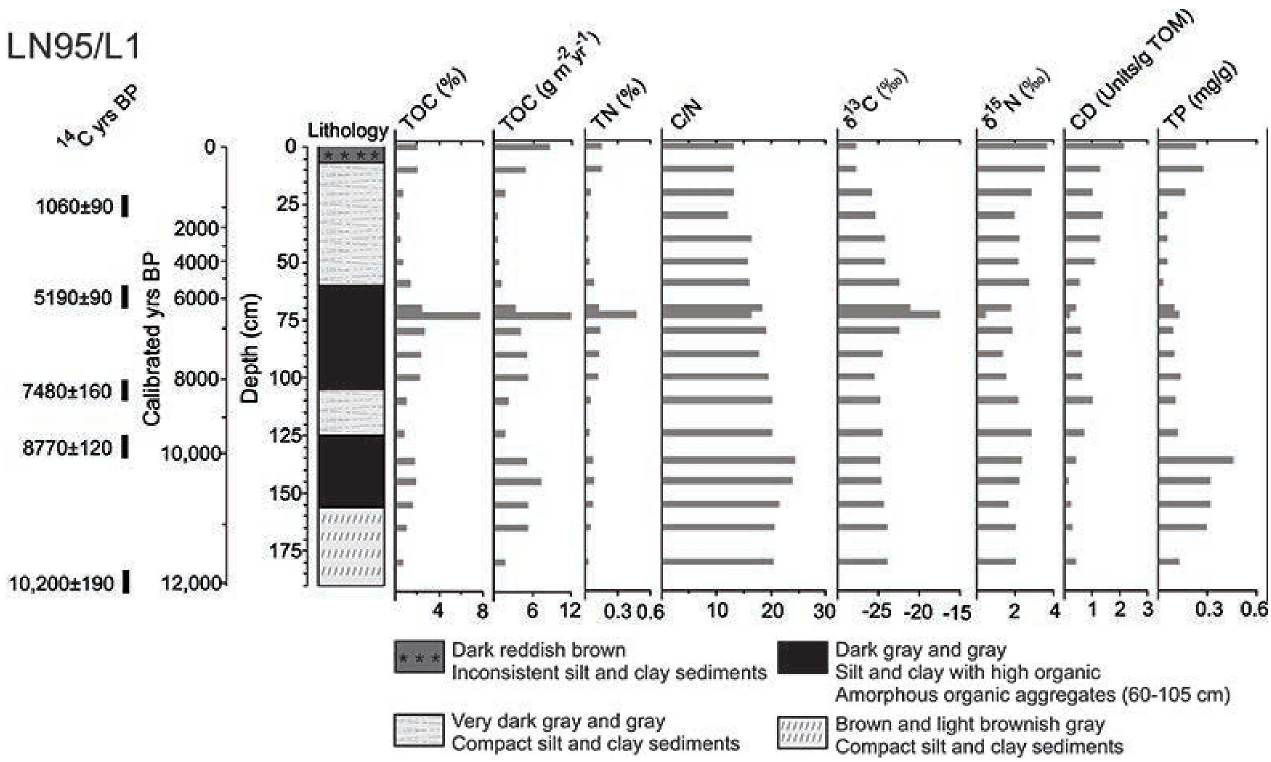

Figure 6. Geochronology, lithologic units, total organic carbon (TOC), total nitrogen (TN), C/N ratio, $\delta^{13}C$ and $\delta^{15}N$ composition, CD (chlorophyll derivatives expressed in standard absorbance units) and total phosphorus (TP) diagram of the core LN95/L1, Lagoa Negra. The concentrations of TOC below 180 cm were very low (< 0.3%), not allowing the analysis of the ratios C/N, $\delta^{13}C$, $\delta^{15}N$ and CD. The concentrations of TP below these depths were < 0.2 mg/g.

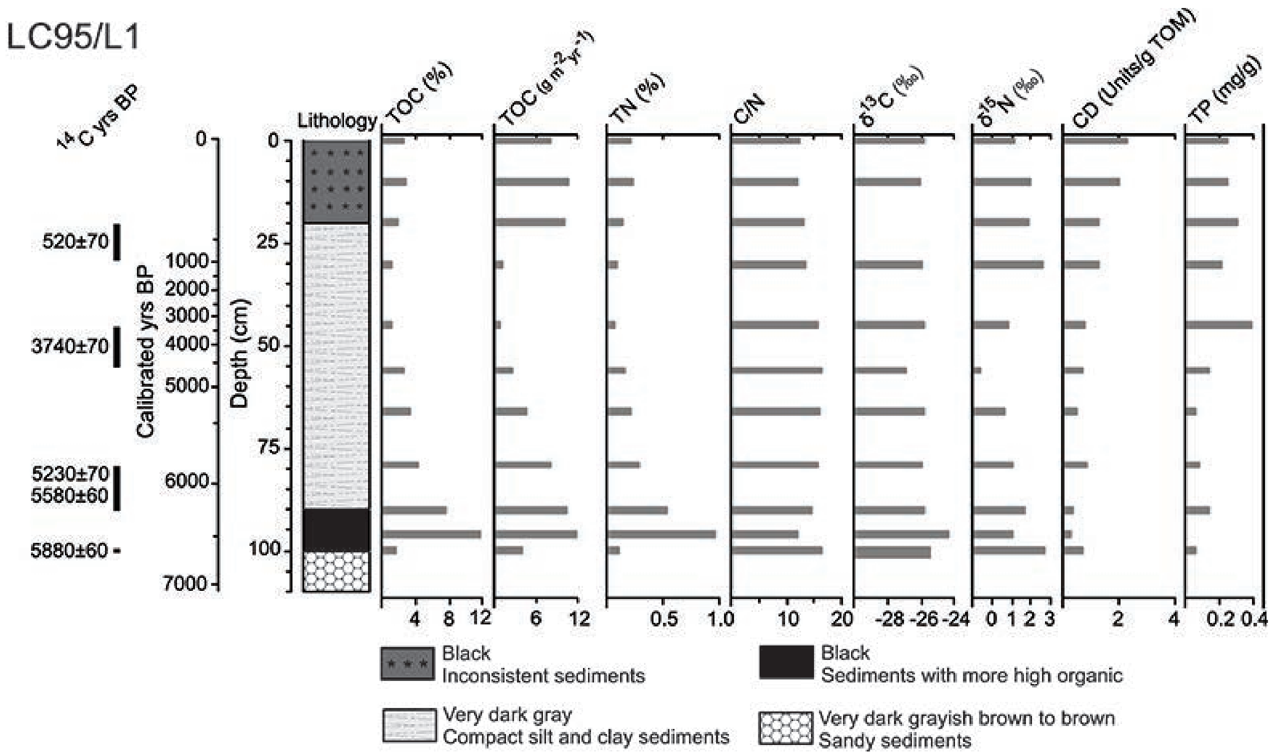

Figure 7. Geochronology, lithologic units, total organic carbon (TOC), total nitrogen (TN), C/N ratio, $\delta^{13}C$ and $\delta^{15}N$ composition, CD (chlorophyll derivatives expressed in standard absorbance units) and total phosphorus (TP) diagram of the core LC95/L1, Lagoa Castelo. The concentrations of TOC below 180 cm were very low (< 0.3%), not allowing the analysis of the ratios C/N, $\delta^{13}C$, $\delta^{15}N$ and CD. The concentrations of TP below these depths were < 0.2 mg/g.

The Coniss cluster dendrogram shows that the pollen compositions after ~6500 cal yrs BP are more similar to each other than to previous pollen floras, thus indicating a stabilizing trend of the local vegetation towards present-day patterns. This condition is best seen in the arboreal curve after ~6200 cal yrs BP and this is indicated by an increase in the diversity of pollen grains belonging to tropical forest taxa followed by a slight decline afterwards (Figure 9). During this time of forest reduction towards the present, there is a shift in the dominance in the aquatic vegetation, which becomes dominated by Cyperaceae, *Ludwigia*, *Polygonum* and *Myriophyllum* (Figure 10). In this regard, core-top pollen spectra contrast to those of the early Holocene when grasses dominated the assemblage as opposed to a present-day dominance of aquatic sedges in the wetlands.

Diatom and spicules analyses

In the LC95/L1 core, diatoms were absent or rare. Systematic diatom analysis and sponge spicules counts were performed only in the LN95/L1 core (Figures 11 and 12). Samples selected for identification of sponges evidenced six species in the sediments of the cores, including *Corvoheteromeyenia australis*, *Corvospongilla seckti*, *Oncosclera navicella*, *Radiospongilla amazonensis*, *Trochospongilla paulula*, and *Trochospongilla repens*. Diatoms are represented by 15 genera and at least 27 species in the sediments of the LN95/L1 core (Figure 12). The zoning of the diatom and spicule diagram was based on the palynological analysis (Figure 8). The zone 3 (272-201 cm; ~21,000 to 12,200 cal yrs BP) marks the onset of sponge spicules accumulation, what is characterized by rare and broken spicules (Figure 11). In this time interval, two samples of the LC95/L1 core were analyzed and showed spicules belonging to *C. seckti*, *O. navicella*, and *T. repens*. In zone 2 (201-110 cm; ~12,200 to 8500 cal yrs BP) there is a substantial increase of spicules and the diatoms were rare or absent. In contrast, zone 1 (110-0 cm; ~8500 cal yrs BP to present) is characterized by the presence of both spicules and diatoms, which are found abundantly and well-preserved between ~8200 and 6500 cal yrs BP (Figure 11). During this interval of time, a lentic

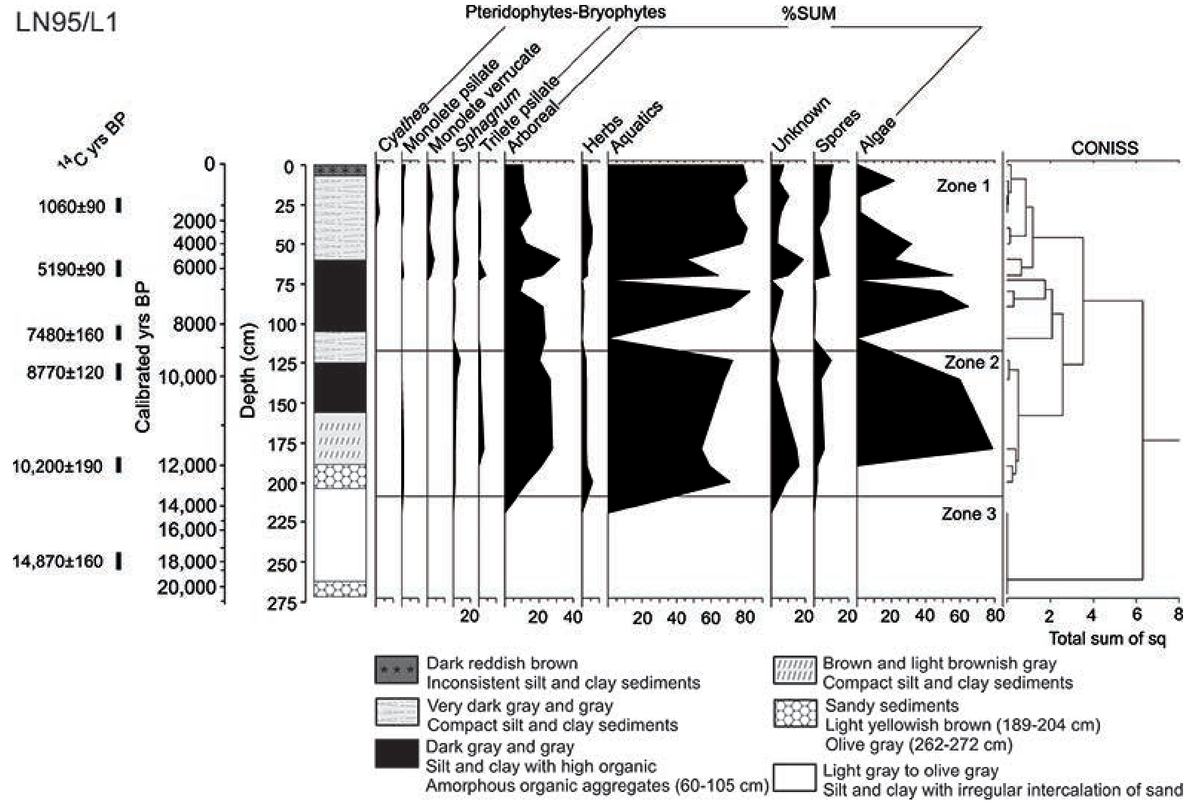

Figure 8. Percentage palynomorph diagram of the core LN95/L1, showing geochronology, lithologic units, percentage of spores (pteridophytes and bryophytes), total palynomorph sum, pollen phases and the cluster analysis (CONISS).

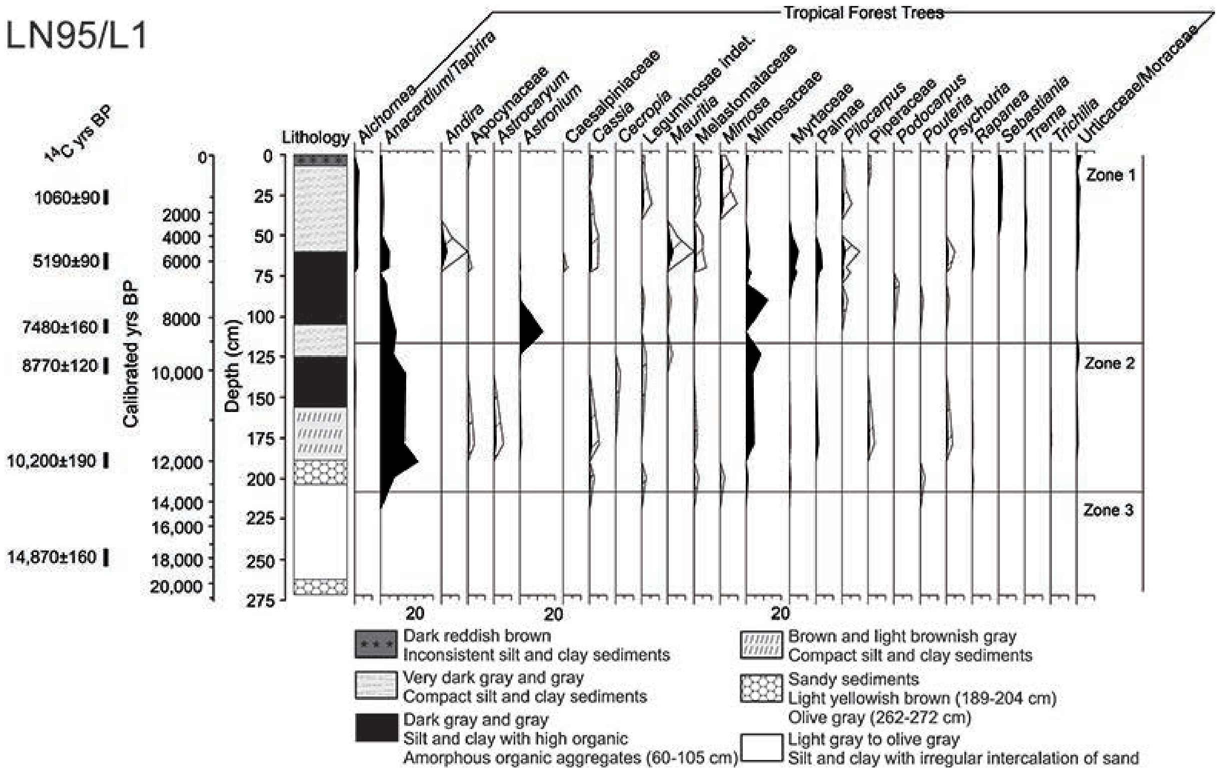

Figure 9. Pollen diagram of the core LN95/L1 (Lagoa Negra), showing geochronology, lithologic units, arboreal pollen percentage and pollen phases.

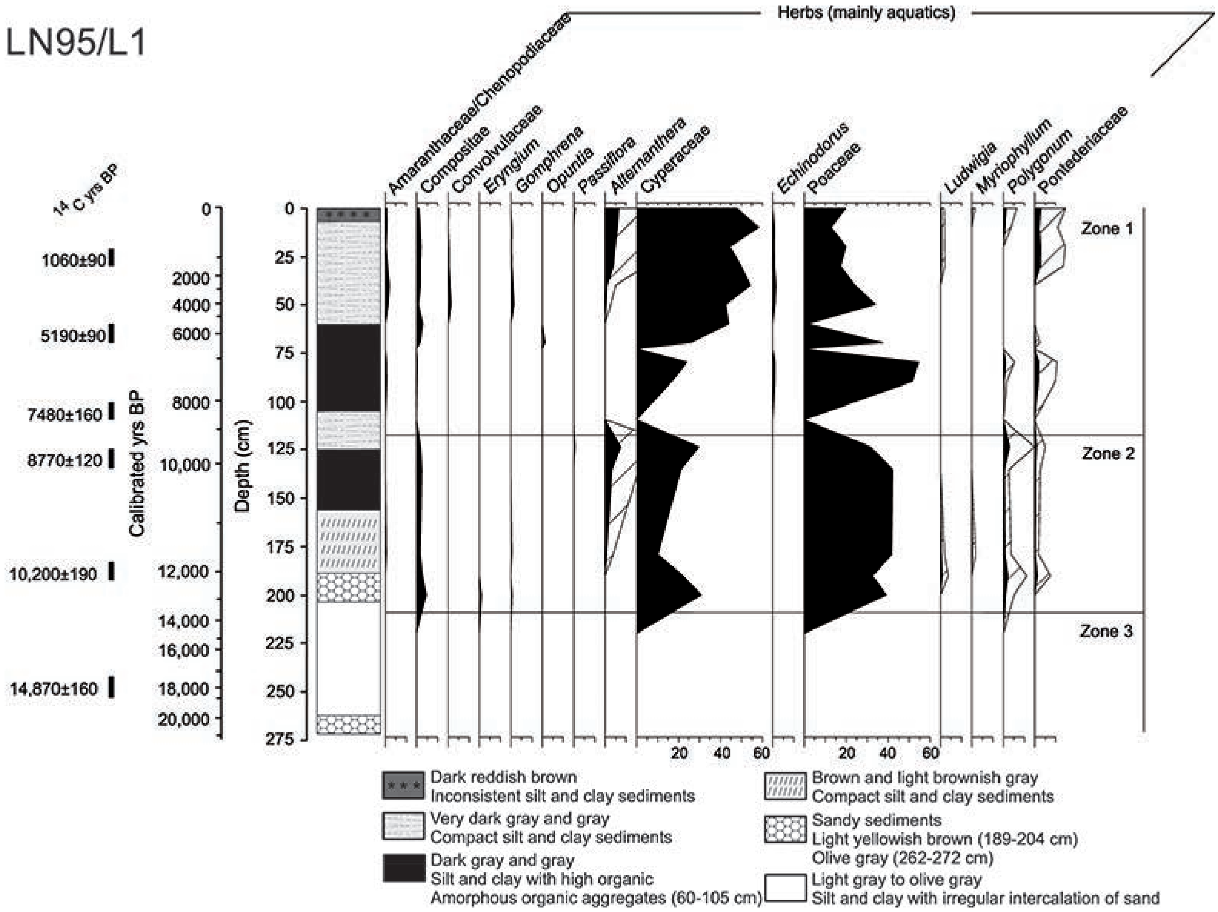

Figure 10. Pollen diagram of the core LN95/L1 (Lagoa Negra), showing geochronology, lithologic units, herbs pollen percentage and pollen phases.

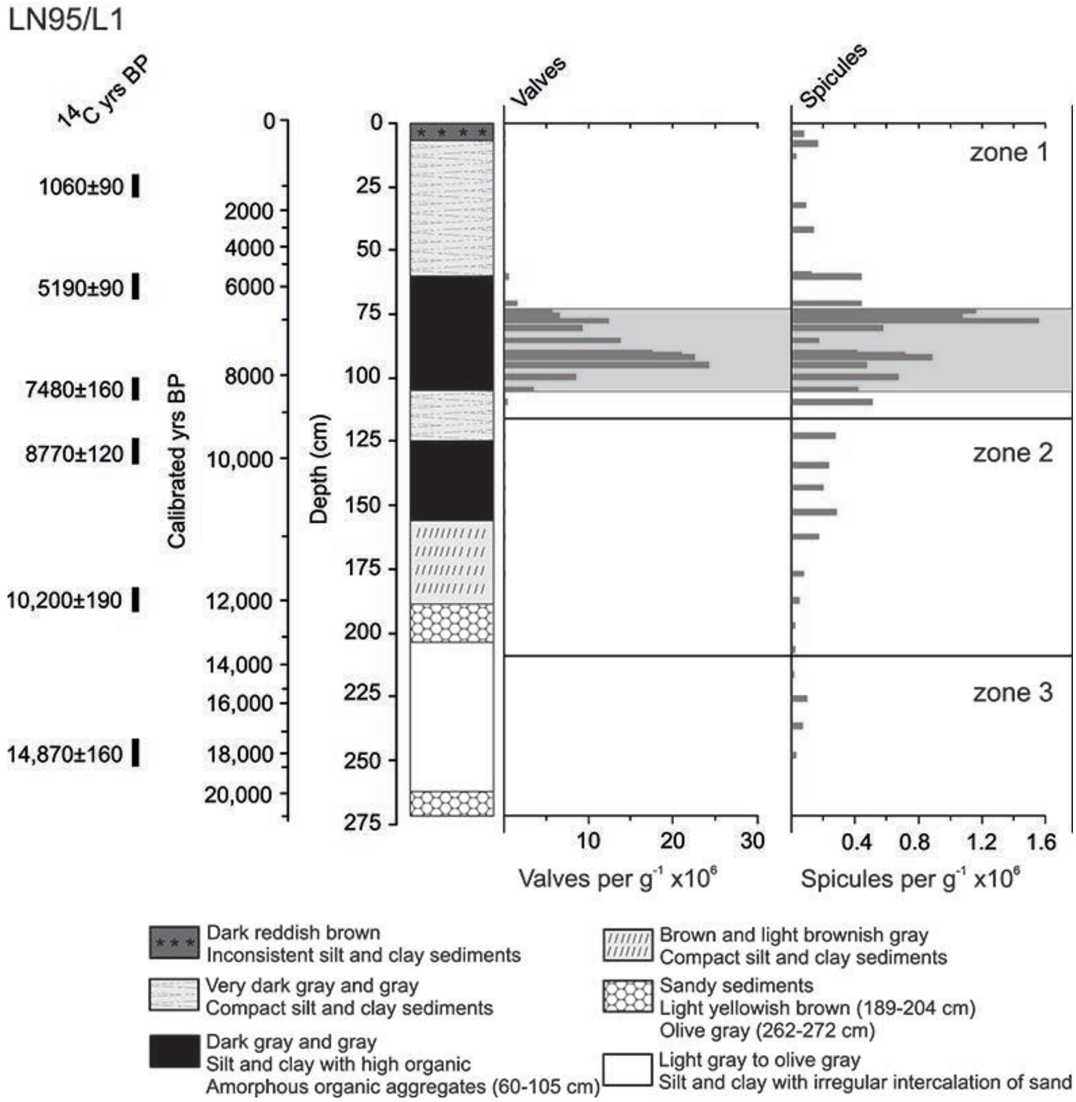

Figure 11. Diatom and spicules diagram of the core LN95/L1 (Lagoa Negra), showing geochronology, lithologic units, diatom ($x10^6$ valves g^{-1} dry weight sediment) and spicules concentrations ($x10^6$ spicules g^{-1} dry weight sediment).

community of sponges occurred with unbroken microscleres of *C. australis*, besides gemoscleres of *R. amazonensis* and *T. paulula*. The same species of sponges were identified in sediment samples at the top of the LC95/L1 core, representing modern species. The diatom assemblage is dominated by the planktonic taxon *Aulacoseira ambigua* (> 90-97%) which populated the lake between ~8200 and 7000 cal yrs BP (Figure 12). Diatom valves were more abundant between 91 and 93 cm (~7600 cal yrs BP) with the presence of large valves of *Pinnularia neomajor*. In a short interval of time between ~7000 and 6500 cal yrs BP a marked reduction is noted in the abundance of planktonic species *A. ambigua* (< 40%) followed by an increase of the periphytic taxa *Achnanthes oblongella* (< 10%), *Encyonema silesiacum* (30-43%), *Gomphonema gracile* (< 9%), *Nitzschia* sp. (< 7%) and *Staurosira construens* (< 10%). From ~6500 cal yrs BP to the present, the diatoms disappear from the record whereas sponge spicules decrease sharply in abundance, thus reaching concentration values similar to those of samples of Pleistocene age.

DISCUSSION

Late Pleistocene (~21,000-12,200 cal yrs BP)

Possibly turbulence conditions were unfavorable to the preservation of diatoms and palynomorphs, on the base of the cores (connectivity river-lake). The rare sponge spicules with uncompleted growth, in these sediments, are strong indication that these

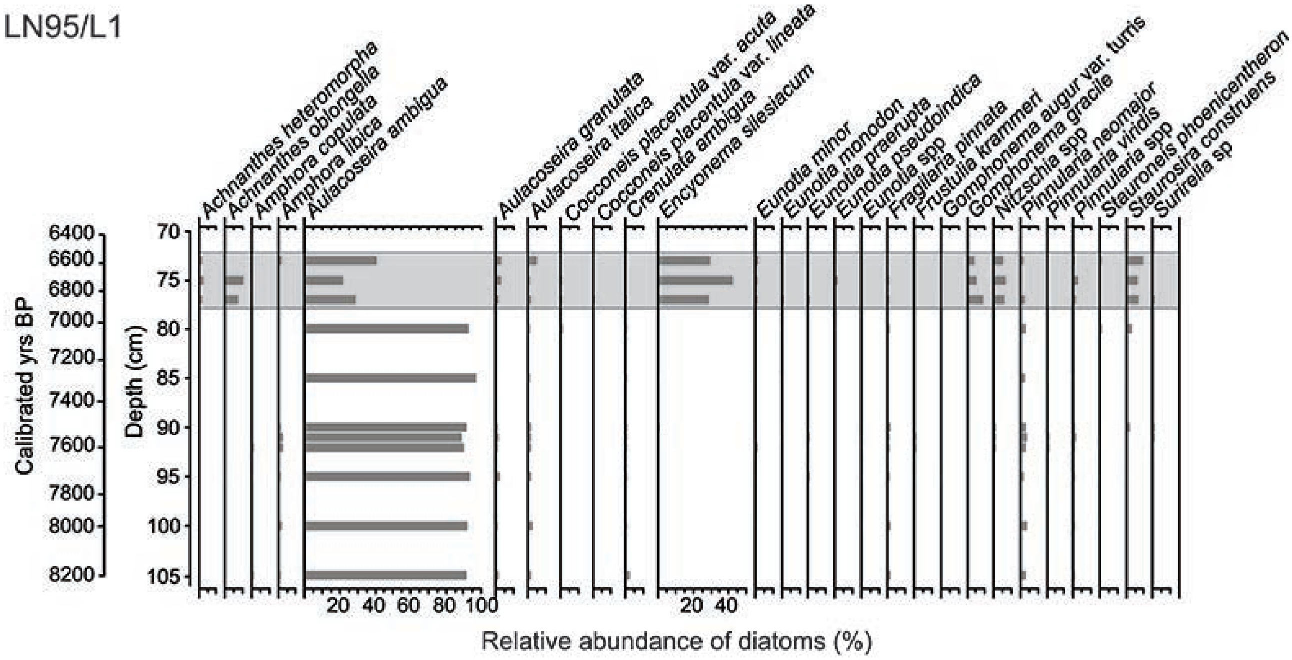

Figure 12. Diatom diagram of the core LN95/L1 (Lagoa Negra), showing geochronology and relative abundance (%) of diatom taxa (73-106 cm), indicating period with domain of periphytic diatoms (shaded area in gray).

sponges did not live in the site or that they were possibly transported by floods. The occurrence of many spicules of *O. navicella*, *T. repens* and *C. seckti*, identified in sediments of the LC95/L1 core, corroborates the evidence of the strong influence of the Paraguay River, in both lakes. These sponges encrust the rocky bottoms of South American rivers, producing closed, hard, spicular networks. Their gemmules are set at the under part of the crusts, firmly soldered to the substrate and in *T. repens* and *C. seckti* protected by an extra spicular capsule. The three species stand strong water currents and friction with river sediment loads. Their extensive crusts may extend over sand and pebbles, contributing to the fixation of the river natural bottom. This same sponge community was seen living and was sampled from rocky substrates at Manso River, downstream the Manso Hydroelectric Power Plant (Batista & Volkmer-Ribeiro 2002). This river is a contributor to the upper Cuiabá River and thus to the left margin of the Paraguay River itself. Therefore, as evidenced in Lagoa Negra core, the late Pleistocene (~21,000-12,200 cal yrs BP) was hydrologically variable, with regression of the Paraguay River between ~19,000-13,000 cal yrs BP (silt/clay sediments) and two phases marked by deposition of sandy sediments suggesting strong river-lake connectivity (~21,000-19,000 cal yrs BP and ~13,000-12,200 cal yrs BP) (Figure 3). Metcalfe *et al.* (2014), infers that Lagoa Gaíva was quite shallow but with periodic flooding at about 24,500 to 12,200 cal yrs BP. These data corroborate the information produced in the present study, contrary to the drier climate conditions at Lagoa Gaíva between 45,000 and 12,200 yrs BP suggested by Whitney *et al.* (2011).

Early to mid-Holocene (~12,200-8500 cal yrs BP)

The palynomorphs of the LN95/L1 core indicate that the transition to the Holocene was wetter, similar to the present, with the establishment of gallery forests and floodplain starting at ~12,200 cal yrs BP. The wetter conditions and deposition of large loads of fluvial sediments must have led the construction of the alluvial dykes between the Paraguay River and the lakes, allowing the establishment of gallery forests and reducing river-lake interaction. In such conditions begins the development of Lagoa Negra, from ~11,500 cal yrs BP, with the deposition of fine organic-rich sediments. An abrupt change with rising water level at about 12,200 cal yrs BP marks the onset of the wetter Holocene conditions at the Lagoa Gaíva (Whitney *et al.* 2011, Metcalfe *et al.* 2014).

Mid- to late Holocene (~8500 cal yrs BP to present)

In the interval of time between ~8200 and 6500 cal yrs BP the connectivity river-lake was reduced or lost completely, establishing the lacustrine system. Between ~8200 and 7000 cal yrs BP the sediments of Lagoa Negra were dominated by the planktonic diatom *A. ambigua*, an indicator that the lake was deeper. Whitney *et al.* (2011) analyzed the modern diatom assemblages of the surface-sediment samples across Lagoa Gaíva (Pantanal Wetland) and noted that the deeper areas were clearly dominated by *A. ambigua*. The lentic conditions are also evidenced by the preservation of fine and delicate sponges spicules (*C. australis*, *T. paulula* and *R. amazonensis*). The three taxa of sponges and particularly *T. paulula* were also abundant in the island embayments at the inner delta at the head of the Guaiba River (Rio Grande do Sul state), adhering to macrophytic stands and subjected to seasonal floodings (Tavares *et al.* 2003). More recently, *T. paulula* was sampled encrusting the riparian forest at Malheiros Lake of the Paraguay River itself, Pantanal of Mato Grosso (Marostega *et al.* 2013).

In the brief interval between ~7000 and 6500 cal yrs BP, periphytic diatom species are dominant on the plankton, suggesting a decline in lake level. The data are corroborated with the reduction of diatoms and increased concentrations of sponge spicules. The lowering of the lake level allows for expansion of the macrophytic vegetation and thus also of support under shade for the sponges besides offering higher concentrations of silicon and an organically enriched environment. All such condition favors the abundance of sponges (Volkmer-Ribeiro *et al.* 1998) whilst the increase in turbidity is detrimental to diatoms that require light for photosynthetic activities. Organic sediments were deposited in this interval of time in both lakes. In Lagoa Castelo the transition to organic sediments occurred abruptly at ~6500 cal yrs BP. The deposition of organic sediments and reduction of the sandy fraction suggest the onset of the lake development, with reduced river-lake interaction. This change was preceded by a strong energy event characterized by the deposition of sandy sediments (> 80% sand fraction), possibly associated with river-lake interactions, in return moisture. The event was not recorded in sediments of Lagoa Negra and is inferred to be due to the protection of the alluvial dyke built in the previous period.

At ~6500 cal yrs BP the semi-closed lakes, due to reduced river-lake connectivity, are more productive and populated by aquatic macrophytes. Lagoa Castelo continues to deposit sandy sediments such as modern Lagoa Castelo, suggesting greater river-lake connectivity than Lagoa Negra. The ^{13}C enriched sediments, the highest rates of TOC accumulation, and the presence of abundant and well-preserved spicules and diatoms (LN95/L1 core) evidence higher lake productivity. It is suggested that ^{13}C-enriched sediments reflect high aquatic productivity and the expansion of C_4 aquatic macrophytes among the Cyperaceae and Poaceae (dominant in the palynological record). In highly productive lakes, the DIC (dissolved inorganic carbon), the carbon source for aquatic plants, tends toward more enriched ^{13}C values (Aravena *et al.* 1992). The $\delta^{13}C$ values for C_3 plants globally range between -37‰ and -20‰ (average -28.5‰), while the $\delta^{13}C$ values for C_4 plants range from -15‰ to -9‰ (average -13‰) (Deines 1980, Kohn 2010). The likely existence of ^{13}C enriched aquatic plants in the past has been supported by isotope data in modern aquatic plants, collected in the Lagoas Negra and Castelo and their respective floodplain (Bezerra, 1999). According to the author, Poaceae and Cyperaceae species showed $\delta^{13}C$ values ranging between -14.3 to -11.1‰, such as some: *Andropogon bicornis* (-12.4‰), *Echinochloa polystachya* (-11.1‰), *Imperata tenuis* (-14.3‰), *Paspalum repens* (-11.9‰) and *Cyperus giganteus* (-12.1‰). The mentioned species grow extensively as large floating mats in the modern Pantanal Wetlands. The higher C/N ratios (> 15) and low concentration in CD and TP are strong indicators that the aquatic macrophytes were the main source of sedimentary organic matter. The phytoplankton has atomic C/N ratio < 10, whereas vascular land plants have C/N ratios ≥ 20 (Meyers 1994). Analyses of modern aquatic macrophytes from both basins yielded an average C/N ratio of 36 (C_3 and C_4 plants; Bezerra 1999). The organic matter depleted in CD and TP suggests a diluting effect by a predominantly non-planktonic organic deposition, impoverished in chlorophyll compounds. Kenney *et al.* (2002) relate low concentrations of TP with a greater contribution of aquatic macrophytes and higher concentrations of TP with greater contribution of phytoplankton in sediment cores collected in five shallow lakes in Florida.

Modern morphometric parameters of the studied lakes allow inferring that the river-lake complete isolation and reduction in local rainfall would easily provoke the dry-up process of these water bodies. However, high TOM contents in the sediments, preservation of siliceous structures and palynomorphs allow to infer that, at ~6500 cal yrs BP, the lakes did not completely dry. With such isolation, the pollen signal is likely to lose the arboreal component present in the riverine forests and be characterized primarily by the herbs growing on the autochthonous floating mats of Cyperaceae and Poaceae. From this analysis, it is postulated that river-lake isolation occurred during the mid-Holocene by a reduction in river discharge and the lakes were maintained by local precipitation.

There is widespread evidence that during the transition from the early to mid-Holocene (~8000 to 4000 yrs BP) climatic conditions in tropical South America was significantly drier than present (Baker *et al.* 2001). Archaeological and paleoenvironmental data suggest that dryness events constitute a major cause of depopulated or altogether abandoned in vast areas of Central Brazil during the mid-Holocene (Araujo *et al.* 2005). In the Pantanal, archaeological studies recorded the earliest human occupation (~8200 yrs BP) in elevated areas on the banks of the Paraguay River and new records of human presence occur only from ~5500 yrs BP, in the floodplain (Schmitz *et al.* 1998, Peixoto 2003). Schmitz *et al.* (1998) suggest that during the cultural hiatus, between ~8000 to 5500 yrs BP, human groups inhabited elevated areas near large rivers, in the Pantanal Wetland. These data are suggestive that the floodplain did not present favorable conditions for human occupation. Whitney *et al.* (2011) inferred that dry event between ~ 10,000 and 3000 yrs BP allowed the expansion of tropical dry forest in Lagoa Gaíva. McGlue *et al.* (2012) documented hiatus in sedimentation in Lagoa Gaíva (~5300 to 2600 cal yrs BP) and desiccation in Lagoa Mandioré (~4700 cal yrs BP) as an episode of regional dryness.

The transition to late Holocene occurred with a drastic reduction in the sediment accumulation rate, in both cores, and in the concentrations of sponge spicules and diatoms in the core LN95/L1. The TOC accumulation rates are negligible between ~6500 to 1000 cal yrs BP, suggesting a return of the influence of the river on the lakes but without violent discharges as observed in the early Holocene. The most recent pollen spectra are dissimilar to those at ~6500 cal yrs BP. It is possible that this zonation reflects higher humidity in late Holocene when compared with the mid-Holocene. A wetter climate in the late Holocene and increased level of Lagoa Gaíva were observed from ~2600 cal yrs BP (McGlue *et al.* 2012) and from ~4400 yrs BP (Whitney & Mayle 2012). In Mato Grosso do Sul state, stalagmite began to grow around ~4000 yrs BP when the climate became more humid during the late Holocene (Bertaux *et al.* 2002).

Archaeological investigations indicate that human groups occupied densely the floodplain from ~5500 yrs BP (Schmitz *et al.* 1998, Peixoto 2003). The oldest archaeological site in the floodplain (~5500 yrs BP) is located in modern shores of Lagoa Negra and the zooarchaeological material consists predominantly of remnants of fish and aquatic molluscs (Peixoto 2003). The data suggest the existence of Lagoa Negra and floodplain since the beginning of the occupation. Most interesting is the fact that entire fragments with gemmules of the sponge *Drulia browni* were detected in all the cauxi pottery sherds (precolonial potters between ~2600 and 1200 yrs BP) resulting from local production close to an archaeological site located near Lagoa Castelo (Volkmer-Ribeiro *apud* Peixoto 2003). The authors conclude that the large amount of whole gemmules indicates that the sponges were collected and applied as antiplastic in the clay for archaeological pottery production. This sponge was recently seen to form conspicuous specimens encrusting the branches and trunks of the Paraguay River flooded forest at Malheiros Lake (Marostega *et al.* 2013). As this sponge forms hard siliceous spheres strongly sticking to branches and trunks of the riparian vegetation reached by the high flood waters, their spicules would eventually appear in the lake sediments only if a riparian forest was at the place. Contrary to the interpretations of McGlue *et al.* (2012), the species *O. navicella* and *C. seckti* were not identified in the cauxi pottery sherds and they would not be because the cauxi artisans intentionally gathered sponges which formed those remarkable silicious masses sticking to the seasonally flooded forests, as particurlaly *D. browni* (Linné 1928, Gomes 2002, Volkmer-Ribeiro & Viana 2006) and not the ones forming crusts on the river permanently submerged rocky bottoms such as *O. navicella* and *C. seckti*.

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