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The evolution of a tropical rainforest/grassland mosaic in southeastern Brazil since 28,000 ¹⁴C yr BP based on carbon isotopes and pollen records

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ABSTRACT

The lack of paleoecological records from the montane Atlantic Rainforest of coastal Brazil, a hotspot of biological diversity, has been a major obstacle to our understanding of the vegetational changes since the last glacial cycle. We present carbon isotope and pollen records to assess the impact of the glaciation on the native vegetation of the Serra do Mar rainforest in São Paulo, Brazil. From ca. 28,000 to ~22,000 ¹⁴C yr BP, a subtropical forest with conifer trees is indicative of cool and humid conditions. In agreement carbon isotopic data on soil organic matter suggest the presence of C₃ plants and perhaps C₄ plants from ~28,000 to ~19,000 ¹⁴C yr BP. The significant increase in the sedimentation rate and algal spores from ~19,450 to ~19,000 ¹⁴C yr BP. The significant increase in the sedimentation rate and algal spores from ~19,000 and ~15,600 ¹⁴C yr BP. From ~15,600 ¹⁴C yr BP to present there is a substantial increase in arboreal elements and herbs, indicating more humid and warmer climate. From ~19,000 to ~1000 ¹⁴C yr BP, δ^{13} C values indicated the predominance of C₃ plants. These results are in agreement with studies in speleothems of caves, which suggest humid conditions during the last glacial maximum.

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Introduction

The Brazilian Atlantic rainforest is one of the most diverse ecosystems on Earth (Morellato and Haddad, 2000; Oliveira-Filho and Fontes, 2000). Its remarkable diversity has been attributed to the presence of rich flora represented by unique physiological adaptations to unusual biophysical characteristics (Garcia, 2003). Despite its overwhelming biological importance, its environmental history is still poorly known. Paleoclimatic studies has been developed in the montane Atlantic rainforest of coastal Brazil during the Late Pleistocene and Holocene (Behling, 1995; Behling and Lichte, 1997; Behling 2007; Behling et al. 2007; Oliveira et al., 2008a, 2008b) and only one soil carbon isotope data covering the last glacial period is available (Saia et al., 2008). The carbon isotope approach allows us to understand the link between regional representation of past vegetational signals with climatic inferences, as it has been applied in regional studies extending from the Amazon basin to the southern region of Brazil (Boutton, 1996; Desjardins et al., 1996; Freitas et al., 2001; Gouveia et al., 2002; Pessenda et al., 1996a,b, 1998a,b, 2001, 2004a,b, 2005; Saia et al. 2008).

The application of carbon isotopes is based on the different ¹³C composition of C_3 (trees and grasses) and C_4 (grasses) plants and its preservation in the soil organic matter (SOM). The δ^{13} C values of C₃ plants vary from -32% to -20% PDB, with a mean of -27%. In contrast, δ^{13} C values of C₄ species range from -17% to -9%, with a mean of -13%. Thus, C₃ and C₄ plant species have distinct δ^{13} C values and differ from each other by approximately 14‰ (Boutton, 1996). In order to establish the chronology of the vegetation changes, it has been analyzed the humin fraction of the SOM by ¹⁴C technique (Pessenda et al., 1996a,b, 1998a,b, 2001, 2004a,b, 2005). Therefore, the carbon isotope approach can be used in the identification of changes in the distribution of C₃ and C₄ plant communities in the past, which are related to humid and drier paleoclimatic conditions, respectively. During the glacial times, carbon isotopes of SOM indicate the presence of C_3 and C_4 plants in southeastern Brazilian Atlantic forest (Saia et al. 2008), which could be associated with the presence of trees and C4 grasses, and also with C3 grasses, usually present in humid terrains.

Furthermore, one aspect that has garnered little attention in paleoenvironmental studies in Brazilian ecosystems is the influence of regional changes in moisture linked to a decrease in sea level of at least 100 m during the last glacial maximum (LGM) (Palma, 1984; Dawson, 1992; Salgado-Labouriau, 1994).

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This paper reports on the use of carbon isotopes in soils and peat samples, as well as pollen stratigraphy in a peat core, as tools for evaluating vegetation changes in the Atlantic Rainforest of the Serra do Mar State Park, Curucutu Nucleus, southeastern Brazil. This area is suitable for this study due to the presence of a peculiar tropical forest and a subtropical grassland vegetation mosaic. Unlike most opening vegetation, which typically comprise C_4 grasses, the study site contains a significant mixture of non-arboreal C_3 plants such as grasses and sedges, very well adapted to the local humid conditions maintained by air masses from the Atlantic Ocean.

Study area and vegetation

Curucutu is located in southeastern Brazil, at 23°56'S, 46°39'W (Fig. 1), approximately 20 km northern of the cities of Itanhaém and Mongagua in the southern coastal zone of São Paulo State, at an altitude ranging from 750 to 850 m and a mean annual precipitation in the range of 2000–3000 mm. The regional climate is temperate and wet, and is classified as Cfa according to the Köppen classification system (Serra, 1969).

The local climate is under the influence of wet air masses from the Atlantic Ocean and is characterized by warm and rainy summers and dry winters with mild temperatures. The annual average temperature is 19°C and the minimum and maximum annual average temperatures are 15°C and 24°C, respectively (Tarifa and Aramani, 2001).

The soil at the study site is classified as Dystropept, according to American Soil Taxonomy, USDA classification (Soil Survey Staff, 1999).

The vegetation contains a mosaic of cloud rainforest and a subtropical grassland called Campos, frequently covered by fog (Garcia, 2003; Garcia and Pirani, 2005). The landscape is formed by Campos limpos ("clean" grasslands, constituted of herbs and very small isolated trees), here called as grasslands or Campos sujos ("dirty" grasslands; herbs and disperses trees of about 3 m, density < 1000/ha and total basal area of 30000 cm²/ha), here called as arboreal grasslands (Goodland and Pollard, 1973). The dominant species in the grassland vegetation are the sedge Lagenocarpus rigido Nees (C3 plant) and the C3 grass Danthonia Montana; and the C₃ plants Clusia criuva, Tibouchina sellowiana and Asteraceae herbs are also abundant (Garcia and Pirani, 2005). The C₄ grasses Andropogon bicornis, Axonopus pressus, Paspalum polyphyllum, and Saccharum asperum are also present in the landscape. The five most abundant families in the cloud forest and in the arboreal grassland are Rubiaceae, Myrtaceae, Melastomataceae, Orchidaceae, and Asteraceae (Garcia and Pirani, 2005). In the last four decades Pinus elliottii, an exotic gymnospermous taxon typical of reforested areas has become a common invasive species of the grassland, as well as of the forested areas.

The peatland is located in a small depression basin of approximately 4000 m² with no influence of any modern drainage system. The forest/grassland mosaic vegetation is found in the surrounding area and in the coring site, located approximately in the center of the basin, C₃ grasses and sedges are dominant. Due to the high annual precipitation, during the rainy season a water column of up to ~0.5 m is found in the peatland.

Sampling and methods

Soil samples were collected in trenches or with a hand auger (Table 1) at nine locations including forested areas (FSM and AF), grassland (EG2) and arboreal grassland (EG, LN, AC, CER1, CER2, and PCN) vegetation (Fig. 1, Table 1).

In the trenches, samples up to 5 kg were collected in 10 cm depth intervals to a maximum depth of 400 cm. For 13 C analyses, approximately 0.5 kg of soil at the trenches and 0.2 kg of soil from the hand auger cores were collected. The samples were sieved (5 mm) and dried at 50°C to a constant weight. Root fragments were then discarded by

hand picking, small roots and rootlets separated by floating in 0.10 M HCl and the residue dried and sieved again (210 mm).

For ¹⁴C dating, soil samples collected at site CER2 received the conventional acid–alkaline–acid treatment (Pessenda et al., 1996b) for humin fraction extraction and were dried to a constant weight.

A 123-cm peat core was collected using a vibro-corer (Martin and Flexor, 1989) at a location identified as TU in Figure 1 and Table 1. The sediment color was classified according to Rock-Color chart (Goddard et al., 1984). A total of 20 peat samples containing 1 cm³ were collected in depth intervals that varied from 5 cm to 10 cm for pollen analyses with the exception of the first 8 cm which were sampled in 2 cm depth intervals to determine possible recent human interference on the landscape. A sampling depth interval of 2 cm was used for carbon isotopes analyses. Nine radiocarbon dates were obtained on peat samples by AMS and benzene synthesis liquid scintillation counting methods (Pessenda and Camargo, 1991). Pollen analysis followed the methodology described in Colinvaux et al. (1996), and included mineral removal with hot HF followed by acetolysis (9 parts acetic anhydride:1 part sulphuric acid). Pollen sums and percentages were based on counts that contained at least 300 non Poaceae grains in each sample in order to reduce the bias produced by this over-represented taxon. Pollen concentrations (grains/cm³) were determined by the addition of exotic *Lycopodium* clavatum spores (Stockmarr, 1971). All pollen and spore data were generated and represented graphically by the Tilia and TiliaGraph Software (Grimm, 1987, 1992).

Carbon analyses (total organic C, ¹³C) on peat samples were carried out at the Stable Isotope Laboratory of the Center for Nuclear Energy in Agriculture (CENA). Analyses of total organic C and ¹³C were carried out in the Environmental Isotope Laboratory of the University of Waterloo, Canada. Each soil sample was analyzed twice in both laboratories and the results represent the average of the measurements. Organic carbon is expressed as percentage of dry weight and ¹³C results are given as δ^{13} C with respect to PDB standard using the conventional δ (‰) notations:

$$\delta^{13}\mathsf{C}(\%) = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] 1000$$

where R_{sample} and R_{standard} are the ${}^{13}\text{C}/{}^{12}\text{C}$ ratios of the sample and standard, respectively. Analytical precision is $\pm 0.2\%$.

The ¹⁴C analyses on soil humin fraction were carried out by Accelerator Mass Spectrometry (AMS) at the Isotrace Laboratory of the University of Toronto, Canada. Radiocarbon ages are expressed as ¹⁴C yr (1 σ) BP (Before AD 1950) normalized to δ^{13} C of -25% PDB and in cal yr BP (Reimer et al., 2004). Calibrated ¹⁴C ages in cal yr BP (2 σ) are presented in Table 2; results and discussions are based on conventional ¹⁴C yr BP for the two oldest ¹⁴C dates (~28,000 and ~22,000 ¹⁴C yr BP), since they are out of the calibration range.

Due to the very low carbon content after the humin preparation of soil samples collected at 200 cm and 300 cm, it was not possible to obtain enough CO_2 for AMS dating.

Results

Textural sedimentary characterization and the ¹⁴C age

The 123 cm sediment core was characterized as a black clayey homogeneous material, with small vegetation fragments. No morphologic evidence of hiatus sedimentation was observed in the whole core.

The radiocarbon dates obtained on peat samples collected at site TU are presented in Table 2 and in Figure 7. The results showed an age profile ranging from 28,460 ¹⁴C yr BP at depth of 123–121 cm to 900 ¹⁴C yr BP at 8–6 cm. Relatively old carbon was found on the surface of the peat (900 ¹⁴C yr BP at 8–6 cm and 2510 ¹⁴C yr BP at 16–14 cm depth) suggesting a high rate of decomposition combined with a low rate of deposition (the C content of the peat is low compared to other



Figure 1. Map of Brazil showing the study site and the sampling points (see Table 1 for details) and structural map (right side) showing the Santos basin and Curutuctu nucleus, São Paulo State.

Table 1

Study sites, vegetation types, sampling method, and geographic coordinates in the Parque Estadual da Serra do Mar-Núcleo Curucutu

Cody site	Vegetation	Sampling method (m)	Geographic coordinates// altitude (m)
EG	Arboreal grassland	Drilling (4)	24°00'09"S/46°45'58"W/827
EG2	Grassland	Drilling (1)	24°00'09"S/46°45'58"W/827
FSM	Forest	Drilling (4)	23°59'46.01"S/46°46'1.05"W/804
LN	Arboreal grassland	Drilling (4)	23°59'11"S/46°45'14.3"W/792
AF	Forest	Trench (1.8)	23°59'14.4"S/46°44'25.2"W/804
AC	Arboreal grassland	Drilling (2)	23°59'14.4"S/46°44'25.2"W/804
CER1	Arboreal grassland	Drilling (4)	23°58'25"S/46°43'60"W/804
CER2	Arboreal grassland	Trench (3)	23°58'25"S/46°43'60"W/804
PCN	Arboreal grassland	Drilling (4)	23°59'0.05"S/46°42'9.91"W/797
TU	Forest/arboreal grassland	Drilling (1.23)	23°59'.09"S/46°44'45"W/770

EG-Embú-Guaçú; EG2-Embú-Guaçú 2; LN lado Norte; CER-Campo da Entrada da Reserva; AC-Alojamento/grassland; AF-Alojamento/Forest, FSM-Fazenda Santa Margarida, PCN-Ponto Central donúcleo, TU-peatland.

peatlands, implying loss of carbon by decomposition). A high rate of deposition seems to be observed at the interval of 52-34 cm represented by ¹⁴C dates of 19,500 and 19,000 ¹⁴C yr BP, respectively. A hiatus of almost 4000 yr is subsequently recorded in the interval of 34-32 cm (19,000–15,600 ¹⁴C yr BP); this could represent a major erosion event.

Table 3 presents the sedimentation rate in different depth intervals inferred from the uncalibrated radiocarbon ages (14 C yr BP) for the interval 28,460 to 22,780 14 C yr BP, since both dates are out of the calibration range, and from calibrated ages (cal yr BP) for the others. Sedimentation rates were similar (0.0083 cm yr⁻¹ and 0.0072 cm yr⁻¹, respectively) during the periods ~28,460 to ~22,780 14 C yr BP (123 cm to 76 cm depth) and 22,780 to 19,450 14 C yr BP (76 cm to 52 cm depth). From 23,670 to 22,010 cal yr BP (52 cm to 34 cm depth), the sedimentation rate increased significantly (~0.011 cm yr⁻¹), and increased progressively from 22,010 to 930 cal yr BP (depths of 34 cm to 8 cm depth).

Pollen analysis

The palynological content of the samples revealed the presence of 132 pollen taxa, of which 130 belong to the angiosperms and two to the gymnosperms (*Araucaria, Podocarpus*) as well as 20 pteridophytic spore taxa and five algal taxa belonging to Chlorophyta (green algae). Complete pollen data are given in four diagrams in Appendix A1, A2, A3, A4 whereas Figure 2 shows a summary percentage diagram of the arboreal and herbaceous pollen, pteridophytic and algal spores, divided into three pollen zones established by CONISS, a statistical package of the Tilia/TiliaGraph softwares (Grimm, 1987, 1992). The ages for each pollen zone have been interpolated from the available ¹⁴C dates shown on Table 2 and the characteristics of each one are given below.

Table 2

Radiocarbon dates from peat samples at TU site and from humin fraction in the soil depth at CER2 site

Laboratory number	Depth (cm)	Ages ($^{14}\mathrm{C}$ yr BP, 1 $\sigma)$	Ages (cal yr BP, 2σ)
CENA930	6-8	900 ± 75	680-930
TO12378	14-16	2510 ± 110	2340-2790
TO12379	24-26	8620 ± 120	9410-9950
CENA932	30-32	$13,750 \pm 150$	15,870-16,900
CENA933	32-34	$15,600 \pm 260$	18,480-19,430
CENA939	34-36	$19,000 \pm 280$	22,010-23,250
TO11920	50-52	$19,450 \pm 150$	22,630-23,670
TO12187	74–76	$22,780 \pm 170$	-
TO11920	121-123	$28,460 \pm 280$	-
TO 12188*	50-60	6090 ± 150	6630-7320
TO12189*	100-110	9840 ± 110	11,070-11,720

TO, Isotrace Laboratory, Toronto, Canada, CENA, ¹⁴C Laboratory, Centro de Energia Nuclear na Agricultura.

- Out of calibration range

Table 3

Sedimentation rates for the sediment interval

Interval (cm)	Sedimentation rates (cm yr $^{-1})/$ age intervals (cal yr BP, $2\sigma)$
16–08	0.00043/(2790-90)
26-16	0.0011/(9950-2790)
32–30	0.0008/(18,480-15,870)
34–32	0.0006/(22,010-18,480)
52-34	0.011/(23,670-22010)
76–52	0.0072/(22,780-19,450)**
123–76	0.0083/(28,460-22,780)**

** age intervals in ¹⁴C yr BP, 2o.

Zone 1 (123–65 cm; 28,460 ¹⁴C yr BP to ca. 20,000 ¹⁴C yr BP or ca. 24,000 cal yr BP)

This zone is characterized by the stable presence of forest (20–32% of the total sum) and grassland elements (82–67%). Aquatic herbs are represented by constant values of approximately 5%, whereas fern spores, with the exception of sample 108 cm, occur in values of approximately 25%. The most important aquatic elements found in this zone are Lentibulariaceae, Pontederiaceae, *Sagittaria–Echinodorus* and *Xyris*.

Among arboreal elements the most common taxa are *Alchornea*, *Araucaria*, Melastomataceae, Myrtaceae, *Podocarpus* and *Symplocos* with percentages ranging from 2% to 5%. In spite of their relatively low percentage values, these taxa are represented by significant concentrations, suggesting a relevant importance in the local vegetation. One example is *Araucaria*, which is found with concentration values ranging from 2000 to 6000 grains/cm³. Among the herbs the predominant taxa are Poaceae (50–60%) followed by Asteraceae (5%–15%) and Cyperaceae with percentage values varying from 5% to 15%. Tree ferns are represented by *Cyathea* (2%–10%) and *Dicksonia* (1%–2%) throughout this zone whereas native *Lycopodium* attains 20% in the basal samples. A peak of monolete psilate spores with affinity to Polypodiaceae reach a peak at 110 cm whereas monolete verrucate spores are well distributed (2%–10%) along the zone.

Zone 2 (65 cm-34 cm; ca. 24,000 cal yr BP to 19,000 ¹⁴C yr BP or ca. 23,000 cal yr BP)

This zone maintains basically the same proportion of arboreal and herbaceous pollen and presents an overall similarity with the previous zone in terms of floristic components with the exception of a few taxa such as *Cybianthus*, *Guapira*, and a slight increase in Melastomataceae. It also differs from zone 1 by the presence of *Vernonia* (1%–5%) and the more pronounced increase in *Debarya* and *Zygnema* algal spores.

Zone 3 (34–0 cm; ca. 23,000 cal yr BP to present)

This zone is markedly different from previous zones due to a sharp increase in the arboreal component which reaches 55% of the total pollen sum. The arboreal increase is more pronounced in *Cybianthus*, reaching a 15% peak, *llex* (5%–12%) and *Symplocos* (1%–5%). Another important feature of zone 3 is the pronounced increase in *Cyathea* tree ferns (5%–40%) and pteridophytes belonging to the monolete pislate and verrucate forms. This vegetational change is synchronous with *Debarya* and *Zygnema* algal spores and a very small contribution of aquatic herbs. From ~900 cal yr BP to the present, a decline in arboreal elements characterizes the pollen content, whereas modern and superficial samples show the presence of exotic *Pinus* for the first time in the record. Another important ecological characteristic of the most superficial samples, with ages younger than 900 cal yr BP is the increase of taxa associated with forest disturbance such as *Didymopanax* and *Cecropia*.

Age of humin fraction in soil

The radiocarbon dates obtained in the soil humin fraction of samples collected at site CER2 (Table 2, Fig. 4) show an age profile ranging from 9840 14 C yr BP at 110–100 cm (11720 to11070 cal yr BP) to 6090 14 C yr BP at 60–50 cm (7320 to 6630 cal yr BP), with a recovering



Figure 2. Summary percentage pollen diagram of selected arboreal taxa. Hatched areas correspond to 5× exaggeration. The CONISS dendrogram with the correspondent pollen zones is shown on right hand side.



Figure 3. Total organic carbon variation of soil samples with depth.

soil rate in ¹⁴C yr BP of ~0.009 cm yr⁻¹ and in cal yr BP of ~0.12 cm yr⁻¹, respectively. Considering a soil recovering rate in ¹⁴C yr BP for the remainder of the soil profile, we estimate that at around 200 cm and 300 cm soil depth, the ages should be in the range of ~18,000 and ~27,000 ¹⁴C yr BP, respectively. These ages are older than the results obtained in similar soil depths in distinct soil and locations in Brazil (Pessenda et al., 1996a,b; Pessenda et al., 1998a,b, 2004a,b, 2005).

Total organic carbon content

Total organic carbon contents in soils are shown in Figure 3. The carbon content data shows a general decrease with depth ranging from 10.4% in the shallow part of the soil to 0.01% in the deeper horizons. The highest value was obtained at FSM, probably due to organic material deposition from a dense forest and higher biomass content (Pessenda et al., 2004b).

δ^{13} C data on soil organic matter and of dominant C₃ and C₄ herbs

The δ^{13} C data on SOM are presented in Figures 4–6 and show a wide range of values between -27.5% and -23.6% for the surface samples



Figure 4. δ^{13} C variation and 14 C dating of SOM in one grassland and two arboreal grassland sampling points (eastern part of transect).



Figure 5. δ^{13} C variation and 14 C dating of SOM in four arboreal grassland sampling points (western part of transect).

of the nine (six arboreal grassland, one grassland and two forest) sampling points. These values indicate that the dominant vegetation type present in each sampling location, except in the forested sites, constitutes a mixture of trees and grasses, and primarily C_3 plants.

In the EG2 grassland site (Fig. 4) the δ^{13} C values show a trend changing from -26.7% in the deepest part of the profile toward more enriched values of -25.4% at the soil surface, indicating the predominance of C₃ plants at this location during the whole period under investigation.

In the EG site representing an arboreal grassland ecosystem, significant δ^{13} C variations of -22% and -25.5% are observed in the whole soil profile. The tendency toward more enriched δ^{13} C values is mainly observed below 100 cm, which represents the soil older than 10,000 ¹⁴C yr BP or ~12,000 cal yr BP. A similar pattern is observed in the other arboreal grassland site (LN), excepting the shallow soil profile that shows a trend toward more enriched δ^{13} C values compared to the EG location. The δ^{13} C values around -22% observed in these profiles suggested C₄ plants colonized part of the landscape during certain periods before 12,000 cal yr BP.

In the AC site representing an arboreal grassland (Fig. 5), the range of δ^{13} C values between -22.6% and -21.9% observed in the



Figure 6. δ^{13} C variation and 14 C dating of SOM in the forest sampling points.

soil depth range of 200 cm and 60 cm, representing soils older than 6000 ¹⁴C yr BP or ~7000 cal yr BP, show a mixture of C_3 and C_4 plants. From approximately 30 cm to the shallow layer the δ^{13} C values vary from -23.2% to -24.8%, characterizing the predominance of C₃ plants from the mid Holocene to the present. In the arboreal grassland site CER1 the values around -24.5%, observed in the whole soil profile (400 cm) to the surface, characterize the predominance of C₃ plants. In the arboreal grassland site CER2, the values oscillated between -22.8% and -24.5%, with most of the values around -23.5% until ~4000 ¹⁴ C yr BP or ~4500 cal yr BP; this indicates the predominance of C₃ plants on this location during most of history. A trend to more depleted δ^{13} C values is observed in the shallow part of the profile, confirming the predominance of C₃ plants during the late Holocene. In the arboreal grassland site PCN, the values varied from -19.1% to -23.0% in the interval 400 cm to 200 cm, suggesting a significant presence of C₄ plants and probably a mixture of C_3 and C_4 plants before $\sim\!18{,}000\ ^{14}\!C$ yr BP or ~21,000 cal yr BP. From 190 cm to the shallow layer the variation from -23.2% to -24.9% indicates that C₃ plants were well established from ~21,000 cal yr BP to the present.

The δ^{13} C values at forested site FSM varied from -23.7% at 400 cm to -25.1% in the surface soil sample (Fig. 6) and characterized the presence of C₃ plants in the whole profile. The enrichment of 1.4‰ is probably related to the isotopic fractionation of SOM decomposition as observed in other sites in southeastern Brazil (Gouveia et al., 2002; Pessenda et al., 1998a). In the forest site AF the δ^{13} C values varied from -22.3% at 170 cm to -24.7% at 130 cm, indicating a mixture of C₃ and C₄ plants (Pessenda et al., 2004b) with a probable predominance of C₃ plants before ~12,000 cal yr BP. From 120 cm to 40 cm an isotopic enrichment up to -22.4% occurs, which is indicative of more significant presence of C₄ plants from the early Holocene to mid Holocene. From 30 cm to the shallow layer a depletion of δ^{13} C up to -27.5% was observed, characterizing the predominance of C₃ plants in a more dense forest from the mid Holocene to the present.

The dominant species in the (arboreal) grassland vegetation as sedge (C_3 plant) *Lagenocarpus* rigido Nees (-27.4%) and the C_3 grass *Danthonia Montana* (-26.9%), as well as C_3 plants *Clusia criuva* (-30.7%), *Tibouchina sellowiana* (-28.7%) and Asteraceae herbs ($\sim -30\%$) were mainly found in the depressions of the study area, associated with the higher humidity (water accumulation) in such points. The C_4 grasses *Andropogon bicornis, Axonopus pressus, Paspalum polyphyllum*, and *Saccharum asperum*, with values around -13% were also present in the landscape, however predominantly found in the middle and top of the small hills, relatively far from more humid terrains.

Organic carbon and nitrogen, C/N values and δ^{13} C data of peat samples

The organic carbon content in peat samples shows values of 8.9% to 10.3% in the deeper part of the profile (123–106 cm). A trend toward higher values (between 15 and 20%) is subsequently observed in the depth interval 102–30 cm, changing to lower values as low as 8.7% between 28 and 10 cm, and reversing the trend to higher values toward the peat surface. The total organic nitrogen in the lower part of the core was 0.18%, and increased up to 1.42% at the shallow layer (Table 4).

The C/N values varied significantly in the whole profile, from ~49 at 123 cm to ~58 at 116 cm and ~53 at 40 cm, and decreased to ~16 in the shallow layer (Table 4 and Fig. 7). Overall, the carbon content is relatively low for sediments formed in a lagoon and a peatland and should be a reflection of productivity and decomposition. However, the carbon content can also be affected by the input of external inorganic sediments into the site. Most of the higher values should represent wetter conditions, and the trend to lower C values, observed in the middle Holocene, are indicative of drier conditions. The more recent trend to higher carbon content suggests the present wetter

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Total C, $\delta^{13}\text{C}\text{,}$ total N, and C/N values of peat samples

Depth (cm)	Total C (%)	Total N (%)	C/N	δ ¹³ C (%)
Litter	37.6	1.15	32.78	-29.3
0-2	22.9	1.42	16.13	-25.1
2–4	16.9	1.14	14.79	-25.1
4-6	16.6	1.05	15.80	-26.1
6–8	10.3	0.54	18.93	-26.7
8–10	8.7	0.44	19.64	-26.9
10-12	8.9	0.43	20.93	-26.7
12-14	8.1	0.34	23.60	- 27.2
14-16	7.1	0.27	26.10	-26.9
16-18	8.6	0.28 0.28	30.90	-27.1
18–20 20–22	7.9 7.5	0.28	28.55 30.09	- 27.4 - 27.5
20-22	9.0	0.30	30.05	-27.3 -25.7
24-26	10.4	0.33	31.96	-25.8
26-28	13.1	0.28	34.64	-25.7
28-30	15.1	0.43	34.92	-25.3
30-32	14.2	0.34	42.21	-25.2
32-34	15.3	0.32	47.73	-25.8
34-36	18.1	0.36	49.84	-25.4
36–38	19.1	0.45	42.68	-25.6
38-40	17.2	0.32	53.26	-25.1
40-42	18.3	0.35	52.00	-24.9
42-44	17.8	0.37	47.97	-24.5
44-46	20.8	0.40	52.59	-24.5
46-48	18.5	0.41	44.91	-24.8
48-50	20.0	0.47	42.98	-24.8
50-52	19.6	0.46	42.22	-25.1
52-54	19.9	0.49	40.33	-24.7
54-56	17.6	0.47	37.21	-24.5
56–58 58–60	18.4 15.9	0.44 0.39	41.54 40.86	-24.2 -24.3
60-62	15.5	0.39	40.40	-24.3 -24.3
62-64	12.5	0.41	30.41	-24.3 -23.7
64-66	16.2	0.40	40.16	-23.9
66–68	16.9	0.43	39.35	-23.9
68–70	17.8	0.44	40.24	-24.0
70–72	17.4	0.46	37.83	-23.7
72–74	19.4	0.51	38.21	-23.6
74–76	17.9	0.49	36.30	-23.3
76–78	19.5	0.48	40.86	-24.1
78–80	18.5	0.47	39.11	-24.3
80-82	16.6	0.45	36.94	-23.8
82-84	16.1	0.42	38.17	-23.9
84-86	15.1	0.41	37.26	-24.1
86-88	15.5	0.41	37.83	-23.7
88-90	15.7	0.41	37.95	-23.3
90–92 92–94	15.1 14.1	0.39 0.38	38.32 37.26	-23.6 -23.5
94–96	14.1	0.39	38.07	-23.3 -23.7
96-98	15.3	0.38	39.84	-23.1
98-100	13.9	0.35	39.94	-23.2
100-102	13.5	0.31	43.49	-23.3
102-104	13.1	0.31	42.64	-23.4
104-106	10.3	0.25	41.93	-23.4
106-108	9.9	-	-	-22.9
108–110	8.4	0.19	43.93	-22.9
110–112	9.1	0.18	50.78	-23.2
112–114	9.7	0.18	53.94	-22.9
114-116	10.6	0.18	57.48	-23.4
116-118	8.4	0.16	51.98	-23.2
118-120	8.7	0.22	39.92	-23.4
120-121	9.0	0.18	49.77	-23.8
121–123	8.9	0.18	48.98	-23.4

-Not determined.

condition. The very high C/N ratios values observed during the wetter periods are probably associated with the dominance of macrophytes during this period. The trend to lower C/N values might represent a change in plant communities in the wetland.

The isotopic values tend to be more enriched in the lower part of the profile (123–64 cm) with most of the δ^{13} C values around -23.5%, probably associated with the existence of in situ submerged macrophytes and C₃ plants. A trend toward more depleted δ^{13} C values is



Figure 7. Total organic C and N, C/N and δ^{13} C variation, and 14 C dating of peat samples from point TU.

observed in the higher part of the profile, reaching values as low as -27.2% and indicating a change in plant community that is present in the modern wetland (Table 4 and Fig. 7).

Discussion

Pollen analysis

In a recent analysis on pollen deposition in surface soils of a transitional Araucaria forest in Santo Antonio do Pinhal in the Atlantic Forest in São Paulo state, Garcia et al. (2004) found that the Araucaria was represented by 1.1% and 4700 grains/cm³. In the same forest, Podocarpus appears with 0.4% or 1800 grains/cm³. In contrast, the concentration of Araucaria and Podocarpus pollen found in the Curucutu core reach values between 125,000 and 17,000 and 4000 and 1500 grains/cm³, respectively. This comparison allows us to infer a physiognomy similar to that of an Araucaria forest for Curucutu from \sim 28,460 to \sim 22,780 ¹⁴C yr BP (zone 123–65 cm). The high Araucaria pollen concentration and the presence of Podocarpus, Myrsine, Symplocos, Weinmannia, Ericaceae, Melastomataceae, and Myrtaceae suggest a cold and humid forest in the peatland. The high percentage and concentration of Poaceae, in synchrony with the stable presence of aquatic herbs and algae, suggest a small lake or a swamp in the modern peatland location; partial components of those grasses are aquatic taxa and, therefore, C₃ grasses. The paleoenvironmental interpretation for zone 65–25 cm (<22,780 $^{14}\mathrm{C}$ yr BP to ~12,000 cal yr BP) indicates a forested landscape around the peat area, whereas the increase of algal spores suggests higher humidity levels. The presence of botanical elements such as Araucaria, Podocarpus, Weinmannia, found in other glacial sediments of the Late Quaternary of Brazil, clearly associated with cool climates, (De Oliveira et al. 2005; Colinvaux et al. 1996; Colinvaux and De Oliveira, 1999; Bush et al., 2004) suggests a significant temperature depression during the Late Glacial at Curucutu. The high percentage of Poaceae pollen is possibly explained by a larger contribution of C_3 grasses, which in turn could explain the reduction of arboreal elements in a lake with a significant water level.

With the decrease in water levels (zone 25–0 cm; ~12,000 cal yr BP to the present), the area of the peatland was taken over by forest at least ~900 cal yr BP From that time on, the widespread reduction of forest under humid climatic conditions can be attributed to anthropogenic impacts.

Peat, carbon isotopes and C/N values

The pollen data suggests that from ~28,460 ¹⁴C yr BP to ~19,450 ¹⁴C yr BP or ~23,000 cal yr BP a forest/grassland mosaic was present in Curucutu and that a small lake or a swamp existed at the modern peatland location. The isotopic δ^{13} C values of peat samples indicate an influence of macrophytes and C₃ trees and grasses present in and around the peatland during the same period. From ~23,000 cal yr BP to ~12,000 cal yr BP, the pollen data also indicates an increase of algal spores, suggesting increased humidity. From ~23,000 to ~19,000 ¹⁴C yr BP or ~22,750 cal yr BP, the highest sedimentation rate of 0.35 cm yr⁻¹ (Table 2) is recorded; this is probably associated with a very high humid period and thus reinforces the climatic interpretation of pollen analysis for Zone 2. A significant decrease in the sedimentation rate (~0.12 cm yr⁻¹), observed for the period of ~22,750 cal yr BP to ~13,750 ¹⁴C yr BP or ~16 400 cal yr BP, is interpreted as a loss of

material by the oxidation process related to a dry period, or to an erosional process caused by a humid period. Considering the previous very humid period, the second hypothesis seems more suitable and also emphasizes the presence of a probable sedimentation hiatus, because only 4 cm of material remained in the core in \sim 5250 14 C yr BP or ~6700 cal yr BP. The isotopic δ^{13} C values also agree with the pollen interpretation, since the gradual trend toward depleted δ^{13} C values indicates a more significant influence of C₃ plants in and around the peatland, probably associated with a humid period. High C/N values (>40 up to \sim 53), during this interval, are probably related to the presence of aquatic macrophytes found in shallow lakes. The presence of these plants, the most significant C source for the sediments when compared with the algae and the phytoplankton, reinforces the humid period hypothesis. After ~ 12,000 cal yr BP until the present, the reduction in algal spores, as well as in terrestrial and aquatic herbaceous pollen, may suggest a decrease in humidity, although a higher frequency of arboreal elements and pteridophytes indicates the expansion of rainforest during the Holocene. The disappearance of Araucaria after ~12,000 cal yr BP can be hypothesized as a consequence of Holocene warming. For the same period, the $\delta^{13}C$ data show the most depleted values in the whole core up to ~900 cal yr BP; this suggests a maximum C₃ plant influence in and around the peatland, eventually associated with a higher tree density and/or of C_3 grasses, and is in close agreement with the higher frequency of arboreal elements observed by pollen analysis. After ~900 cal yr BP until the present, the pollen results indicate a probable anthropogenic influence in the Curucutu area, where a decline in the arboreal elements and an increase of Pinus pollen was noticed, which is indicative of deforestation and substitution by exotic elements. Isotopic values around -26% and -25% probably indicate the dominance of C₃ plants. Considering the low contribution of aquatic herbs and algae and the absence of aquatic herbs in the interval from 8260 $^{14}\bar{C}$ yr BP or ~9700 cal yr BP to the present, the C/N values $(<\sim 32 \text{ to } \sim 15)$ found in the same period are probably related to the C influence from vascular plants, either grasses, shrubs, or trees (Meyers, 2003).

Carbon isotopes in SOM

Carbon isotope data in soil samples indicate that the forest/ grassland mosaic was present at Curucutu since ~27,000 ¹⁴C yr BP. The ¹³C data collected in the arboreal grassland sites PCN, LN, EG, CER1, and CER2 showed that the most significant presence of C₄ plants in the study site was observed in the period from ~27,000 ¹⁴C yr BP to ~21,000 cal yr BP. From ~21,000 cal yr BP to ~12,000 cal yr BP the ¹³C data showed the predominance of C₃ plants under a period more humid than previously, with probable mixture with C₄ plants in the arboreal grassland sites AC, CER1, CER2, and EG. From ~12,000 cal yr BP to the present, a predominance of C₃ plants was observed, except in CER1 where the data indicate a significant presence of C₄ plants.

The paleovegetation dynamics of the arboreal grassland ecotone (point AC) – forest (AF) (Fig. 1) can be illustrated considering the δ^{13} C data on SOM and ¹⁴C ages collected at the AF site (Fig. 6). In the period from ~21,000 cal yr BP to ~13,000 ¹⁴C yr BP or ~16,000 cal yr BP there was a significant depletion (~3‰), indicative of a probable forest expansion that could be associated with a humid period. Between ~16,000 cal yr BP to ~5700–4300 cal yr BP an enrichment of ~3‰ was recorded, probably indicating a tendency toward opening of the forest vegetation, and perhaps associated with a drier period and the presence of C₄ plants. After ~5700 to ~4500 cal yr BP until the present, the ¹³C data show a trend toward significantly depleted values (-22.5% to ~-27.5%), probably associated with a forest expansion and more humid climate.

The pollen and isotope techniques indicated similarities in the reconstruction of the paleoenvironment of Curucutu. The arboreal

grassland as well as the forest vegetation was present in the site since $\sim 28,000^{-14}$ C yr BP. The modern grassland vegetation in the forest domain of the Curucutu Atlantic Rainforest State Park probably has a natural origin, but appears to be represented less than in the past. The grass vegetation close to the mountain crests in altitudes around 750 m and 850 m, considered low for that vegetation type (Garcia, 2003), are probably reminiscent of a more open vegetation that in the past had a wider distribution and is now being naturally replaced by forest. Since ~900 cal yr BP to the present, the forest expansion has occurred in a less accelerated rhythm, probably due to anthropogenic influence.

Palaeoenvironmental history

The paleovegetation patterns inferred from carbon isotopes in SOM and pollen analysis in peats and sediments have also been documented in other regions of Brazil. Studies based on carbon isotopes in SOM which found evidence of the late Pleistocene dry phase (mixture of C_3 and C_4 plants) and the Holocene humid phases (predominance of C_3 plants) have been carried out in southern (Pessenda et al., 1996a) and southeastern Brazil (Pessenda et al., 1996a; Gouveia et al., 2002, Saia et al., 2008). Pollen analyses registered the presence of drier climatic conditions during the late Pleistocene and early Holocene in several sites of the areas in central (Ferraz-Vicentini, 1993; Ferraz-Vicentini and Salgado-Labouriau, 1996; Barberi, 2001), southeastern (Ledru, 1993; Ledru et al., 1996; Behling, 1995; Behling and Lichte, 1997; Behling et al., 1998) and southern (Roth & Lorscheitter, 1993; Neves and Lorscheitter, 1995; Lorscheitter and Mattoso, 1995; Behling, 1995; Behling and Lichte, 1997; Stevaux, 1994, 2000) in Brazil.

Carbon isotope data obtained in the southeastern Brazilian sites of Salitre (Minas Gerais State, ~850 km from the study site), Piracicaba (São Paulo state, ~250 km) and Jaguariúna (São Paulo state, ~170 km), and in Londrina (Paraná state, ~650 km) in southern Brazil, also show relationships with the present work. For instance, in the Salitre record, the occurrence of a mixture of C₃ and C₄ plants was verified since the early Holocene until ~1700 ¹⁴C yr BP. In Piracicaba, Jaguariúna and Londrina, significant presence of C₄ plants was observed since the late Pleistocene until early Holocene, indicating a climate drier than the present. From ~3000 ¹⁴C yr BP until the present, these studies indicate an expansion of the forest vegetation, suggestive of a more humid phase. In Botucatu and Anhembi (São Paulo state, ~350 km) (Gouveia et al., 2002) C₃ plants were dominant during the whole Holocene.

Pollen studies have recorded the presence of dry climatic conditions during the glacial period and the LGM, and more open vegetation (arboreal savanna) in distinct sites in Brazil. In Lagoa Bonita (Federal District, DF, ~1400 km), central region, semi-arid conditions with low temperatures are responsible for the regression of forest vegetation, and installation of erosive processes were observed by Barberi (2001). In the area of Águas Emendadas (DF), central region, dry phases from ~19,000-7000 ¹⁴C yr BP were recorded following humid climatic conditions from around 5600 ¹⁴C yr BP until the present (Salgado-Labouriau et al., 1998). In Botucatu (São Paulo state, ~350 km), from ~30,000 to 18,000 14 C yr BP cold and dry climatic conditions were recorded by Behling et al. (1998). In Catas Altas (Minas Gerais state, ~900 km), southeastern region, the landscape was dominated by large areas of grassland and small forested areas, reflecting a cold and dry climate during the last Glacial (Behling and Lichte, 1997) and the presence of an arid phase around \sim 27,000 ¹⁴C yr BP, with a maximum in 35,000 ¹⁴C yr BP in Salitre (Ledru, 1993; Ledru et al., 1996, 1998).

On the other hand, several sites within the Brazilian Amazonia (Bush et al. 2004; Colinvaux et al. 1996; Haberle, 1997), southeastern (Siqueira, 2006; Cruz et al., 2006, 2007; Wang et al., 2006; De Oliveira, 1992), and northeastern Brazil (Auler and Smart 2001;



Figure 8. Schematic representation for the landscape evolution around the coring site since ~28,000 ¹⁴C yr BP to the present.

Wang et al., 2004) indicate the presence of a wetter climate during the LGM. The climatic mechanisms for enhanced humidity during the last glacial period are mainly due to the influence of changing land-sea temperature contrasts on the atmospheric circulation patterns that control the South American summer monsoon (SASM) over South America (Cruz et al., 2007). The speleothem records from subtropical Brazil have indicated that periods of more abundant monsoonal rainfall are coinciding with high summer insolation phases on Milankovitch timescales (Cruz et al., 2006); with cold periods in the northern hemisphere during Heinrich events (Cruz et al., 2006; Wang et al., 2006); and between 70 and 17 ka during the marine oxygen isotope stages 4 to 2 (Cruz et al., 2007). Both factors positively affect the mean location and/or the convective activity of SASM, resulting in enhanced transport of moisture from the Amazon Basin into southeastern and southern Brazil because continental heating resulted from increased incoming of solar radiation or cooler sea surface temperatures in the northern tropical Atlantic, respectively.

The observed sedimentation gap in the peat core spanning from ~22,750 cal yr BP to ~15,000 ¹⁴C yr BP or ~18,000 cal yr BP suggests a reduction in the precipitation levels during this time compared with the prior period (~23,000 to ~22,750 cal yr BP), while the carbon isotopic data imply that the sufficient moisture maintained the forest/grassland mosaic, characterized by a mixture of C₃ and C₄ plants at Curucutu prior, during, and after the LGM.

Under reduced sea-level at the order of at least 100 m below present level (Dawson, 1992; Palma, 1984), the present São Paulo coastline had retreated at least 150 km eastwards due to the exposure of its shallow oceanic platform (Palma, 1984; Salgado-Labouriau, 1994) (Fig. 1). This phenomenon must have affected local humidity levels at Curucutu and it is possible that it may explain the lack of sedimentation at the peatland. It is reasonable to conclude that the impact of this significant displacement of the coastline would have been greater at Curucutu if other sources of humidity were not available. This hypothesis is supported by the climatic mechanism proposed by Da Cruz et al. (2006, 2007) and by pollen and mineralogical analyses at the Monte Verde site (Fig. 1) at the Mantiqueira Mountain chain, which is parallel to the Serra do Mar mountains where the Curucutu site is located. According to Siqueira (2006), the continuous Monte Verde record spanning the last 18,000 years shows undisturbed Atlantic Forest vegetation under continuously humid climates. It is very likely that higher humidity levels prevailing north of Curucutu were maintained by humid air masses originating in the Amazon basin. Figure 8 shows a schematic representation for the landscape evolution of the Curucutu landscape since the onset of its deposition based on the above discussed pollen and carbon isotope data.

Conclusions

Carbon isotopes and pollen data in peat samples and carbon isotopes of SOM collected at the Serra do Mar State Park-Curucutu Nucleus suggest an agreement in respect to the origin and the vegetation dynamics of the forest/grassland mosaic (mixture of C₃ and C₄ plants) since ~28,000 ¹⁴C yr BP. The present grassland islands within the forest domain of Curucutu are probably reminiscent of ancient and more open and widely distributed vegetation that was naturally substituted in the Late Holocene by forest vegetation, probably due to the presence of a more humid climate.

Despite the ocean retreat during the LGM, sufficient humidity to maintain the vegetational mosaic at Curucutu probably came from the Amazon basin, as proposed by Da Cruz et al. (2006, 2007).

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Appendix A

Appendix A1. Percentage pollen diagram of selected terrestrial elements.



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Appendix A4. Summary concentration (grains/cm³) diagram of pollen and spores categories.

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