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The last 50,000 years in the Neotropics (Southern Brazil): evolution of vegetation and climate

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Abstract

In the "Lagoa Campestre" (Lake) of Salitre (19°S, 46°46′W, 970 m elev.), there are plant taxa belonging to many ecological groups that are encountered nowhere else at this latitude. Frequent incursions of polar advections causing cooling and humidity, a cool and foggy climate in the middle of the depression and warmer temperatures on the surrounding slopes help to maintain all these groups within a fairly restricted area. Late Pleistocene–Holocene climatic change has had a considerable impact on the flora and vegetation of Salitre. The pollen record of the 6 m deep core LC3 shows how cold forest trees such as *Araucaria angustifolia* and *Drimys brasiliensis,* semi-deciduous forest, halophytic plants and peat bog started to develop on this site. The initial period, between c. 50,000 and 40,000 yr B.P., was an arid phase not recorded in any other neotropical lowland site. It was followed by a period of high moisture levels (40,000 to 27,000 yr B.P.) with a maximum estimated at c. 35,000 yr B.P. The Late Glacial maximum is missing because of a gap in sedimentation. Humidity gradually increased during the Late Pleistocene, between 16,000 and 11,000 yr B.P. The early Holocene, 9500 to 5000 yr B.P., is characterized by a more marked seasonal pattern and higher temperatures, reaching a maximum c. 5000 yr B.P. The spread of semi-deciduous forest between 4000 and 3000 yr B.P. attests to a return of humidity. Comparison with the Serra Negra section (19°S, 46°45′–46′W, 1170 m elev.) not far from Salitre confirms the high moisture rates recorded at c. 35–40,000 yr B.P. (although temperatures were cooler at the altitude of Serra Negra, as is attested by the presence of *Araucaria* forest) and also confirms the strong impact of polar advections on the climate of Southeastern Brazil.

1. Introduction

Hypotheses concerning the development and evolution of present-day lowland vegetation in the Neotropics are based on two types of observation; firstly on present-day patterns of plant and animal distribution, and secondly on paleoenvironmental records. Analysis of speciation patterns in birds, plants, lizards and butterflies in the Amazonian forest region lead to the refuge hypothesis (Haffer, 1969; Prance, 1973; Vanzolini, 1973). According to this hypothesis, at some time in the past when climatic conditions were drastically different—during the Last Glacial Maximum—the rainforest

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area shrank, leaving only patches of forest surrounded by savanna. The second line of evidence comes from pollen records from various lowland sites in Ecuador (Bush et al., 1990), Panama (Bush and Colinvaux, 1990), Colombia (Van der Hammen et al., 1992a,b) and Brazil (Absy et al., 1991; Ledru, 1993; De Oliveira, 1992; De Oliveira and Colinvaux, in press). These records, many of which extend back to about 60,000 yr B.P., show a sequence of markedly different environments for the Middle Pleniglacial (65,000–26,000 yr B.P.), the Upper Pleniglacial (26,000–13,000 yr B.P.), the Late Glacial and the Holocene.

For the Middle Pleniglacial, a maximum extension of glaciers in the Eastern Cordillera of the Northern Andes is recorded, suggesting high effective rainfall (Van der Hammen, 1981). In the Amazonian lowland rainforest region the expansion of open vegetation with *Borreria*, *Cuphea* and Asteraceae suggest dry conditions at c. 60,000 yr B.P. and 40,000 yr B.P. (Van der Hammen et al., 1992a; Absy et al., 1991; Sifeddine et al., 1994a; 1994b). Open vegetation developed when precipitation rates were less than 2000 mm, while forests were maintained in areas where rainfall was above 2000 mm (Bush, 1994; Van der Hammen and Absy, 1994). Under these conditions, forests in sub-tropical areas on the fringes of Amazon basin, e.g. semi-deciduous forest where rainfall today is 1500–2000 mm/yr in southern Brazil, should have shrunk dramatically, to be replaced by savanna. But polar advections inducing incursions of cool, moist air and reducing the length of the dry season (Ledru, 1993) was able to maintain these forests in Middle Pleniglacial times, although semi-deciduous forest taxa were replaced by *Araucaria* forest taxa at Serra Negra (De Oliveira, 1992; De Oliveira and Colinvaux, in press). During the Last Glacial Maximum, many lowland records have sedimentological gaps, suggesting climatic conditions unfavourable for the persistence of lakes and bogs (Bush et al., 1990; Bush and Colinvaux, 1990; Absy et al., 1991; Ledru, 1993; Behling, 1993; De Oliveira and Colinvaux, in press). After 13,000 yr B.P., a "dry rain forest" with deciduous and evergreen trees spread throughout Amazonia (Ferreira Fernandes and Cleef, 1989), while throughout central Brazil a semi-deciduous forest expanded, with montane elements suggesting more humid climatic conditions than before. The Holocene is characterized by high effective rainfall interrupted by a short dry episode between 7000 and 4000 yr B.P., depending on latitude (Servant et al., 1989a,b; Martin et al., 1993). A progressive increase of the length of the dry season is recorded between 10,000 and 5000 yr B.P. (Ledru, 1993; Vicentini, 1993), while low temperatures persist at the beginning of the Holocene.

To further test the paleoenvironmental history of the Neotropical lowland forests, we set out below the results of the 6 m deep core LC3 collected at Lagoa Campestre de Salitre (or Salitre) (19°S lat., 46°45–46′W long., 980 m elev.), south of the Amazon basin on the Brazilian central plateau.

2. Present-day climate and vegetation

Salitre is located in an area influenced by the ITCZ (InterTropical Convergence Zone) (Fig. 1). In January, when the ITCZ is in its southernmost position, the convergence of winds induces strong precipitation in the Brazilian central plateau; in July, when the ITCZ moves north of the equator, only the lowland Amazon region remains wet. In the southern part of central Brazil, at a latitude of about 25°S, polar front incursions are frequent during the dry season and result in heavy precipitation. Summer frontal rains occur during the wet season and do not have the same impact on moisture conditions. Precipitation throughout the area averages 1500 mm and the dry season lasts 3–4 months. Mean winter temperatures range between 10 and 15°C (Ledru, 1993; Ledru et al., 1994).

The vegetation surrounding the site is composed of three elements: the swamp area (sites *1* and *2* on Fig. 2), the river valley (sites *3*, *6* and *7*) and the slopes of the depression (sites *4*, *5*, *6*). The swamp area is divided into peaty, marshy and flooded zones.

The depression, the "Lagoa" sensu stricto, is covered mainly by Cyperaceae. Other, less frequent herbs are *Paepalanthus* (Eriocaulaceae), *Xyris* (Xyridaceae), Polygalaceae, *Utricularia* (Lentibul

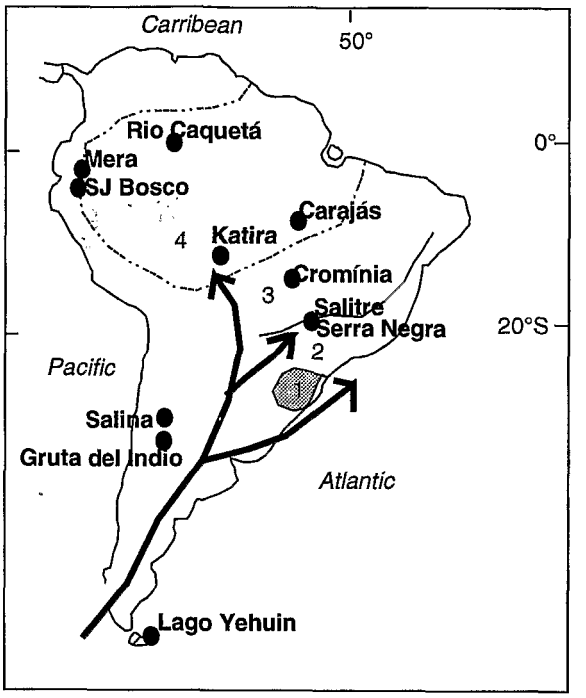

Fig. 1. Location of sites discussed in the text, position of the different Brazilian vegetation types. *1* = *Araucaria* forest; *2* = semi-deciduous forest; *3* = cerradão (wooded savanna); *4* = Amazonian rainforest, and trajectory of polar advections (arrows) through Brazil.

ariaceae), Orchidaceae (*Cynaeorchis arundimae* and *Cyrtopodium aff. paludicola*), Gesneriaceae, *Cuphea* sp. (Lythraceae), Lamiaceae, *Drosera* (Droseraceae), *Commelina* (Commelinaceae), Asteraceae, Asclepiadaceae, *Eryngium* (Apiaceae), *Borreria* (Rubiaceae), Mimosaceae, Bromeliaceae, Apocynaceae, Phytolaccaceae, *Sphagnum* moss and the clubmoss *Lycopodium*. On elevated, drier mounds (site *2* in Fig. 2) within the depression grow small trees and shrubs: *Drimys brasiliensis* (Winteraceae), *Microlicia* sp. (Melastomataceae), *Gaylussacia* sp. (Ericaceae) and treeferns (*Cyathea*). One recently burnt mound was covered by treeferns, suggesting a successional pattern.

Along the river draining the depression, there is a narrow belt of gallery forest (site *7* in Fig. 2); the right bank is mainly composed of Myrtaceae trees covered with *Tillandsia* (Bromeliaceae) and Orchidaceae. The Piperaceae genus *Peperomia* is found on rocks alongside the river. This part is seasonally flooded, as shown by the mud line on the trunks of the Myrtaceae trees up to about 50 cm above ground. The left bank is higher and is not seasonally flooded; tall trees grow there, such as *Gallesia* (Phytolaccaceae), and species in the families Fabaceae and Mimosaceae. Between the cerradão, or wooded savanna, (site *6*) and the gall ery forest grow *Drimys brasiliensis*, *Byrsonima* sp, Amaranthaceae and *Vochysia* sp. (Vochysiacae).

From the edge of the small pond (site 3) and towards deeper water grow aquatic plants such as *Podostema* (Podostemataceae), *Begonia* (Begoniaceae) and *Typha* (Typhaceae), accompanied by *Alchornia* sp. (Pontederiaceae), Poaceae, *Habenaria* sp. (Orchidaceae), Gesneriaceae, Commelinaceae, *Mandevilla* sp. (Apocynaceae), *Tibouchina* sp. (Melastomataceae), *Xyris* (Xyridaceae), Nymphaeaceae, Cyperaceae, Solanaceae and *Sida* sp. (Malvaceae).

The forest growing on the slopes is either cerradão (thickly wooded savanna in Brazil) (site 6) or mesophilic semi-deciduous forest (site 5) related

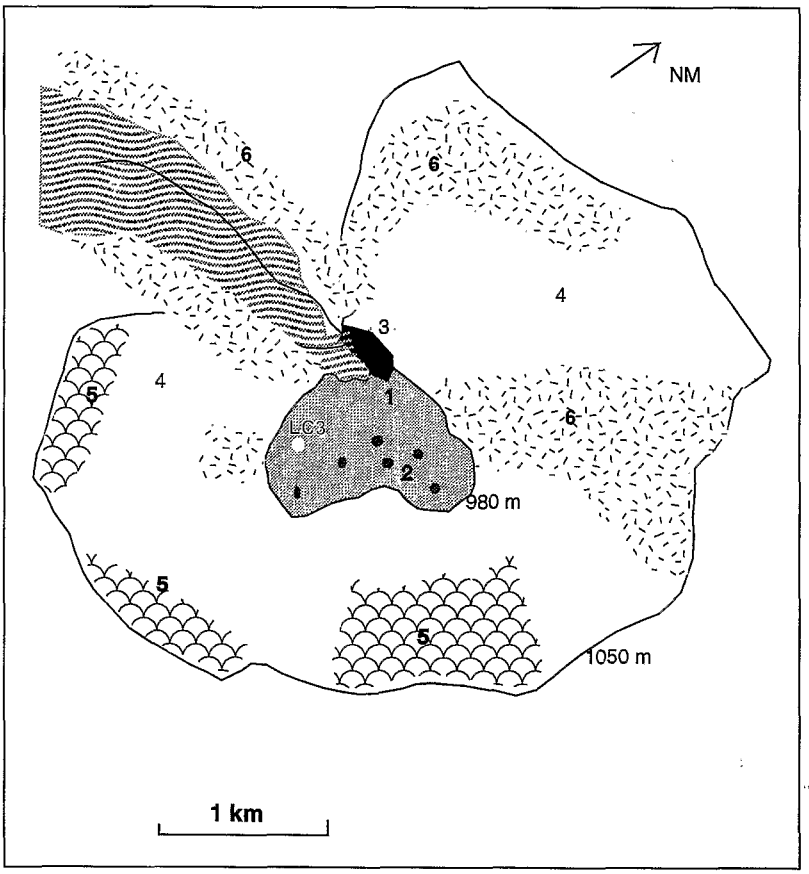

Fig. 2. Present-day vegetation distribution in the "Lagoa Campestre" depression at Salitre. *1* = swamp area with Cyperaceae, *2* = swamp area with Cyperaceae and mounds covered with *Drimys*, Ericaceae, Melastomataceae and *Cyathea*, *3* = flooded area with *Typha*, *4* = anthrogenic grasslands, *5* = semi-deciduous forest, *6* = dry forest (cerradão), *7* = gallery forest.

to specific edaphic conditions. The following taxa can be recognized, among others: *Clitoria* sp. (Fabaceae), *Leandra* sp., *Miconia* sp. (Melastomataceae), *Bauhinia* sp. (Fabaceae), *Copaifera l angsdorfii* (Caesalpiniaceae), *Xylopia aromatica* (Annonaceae), *Erythroxylon* sp. (Erythroxyl aceae), *Byrsonima* sp. (Malpighiaceae), *Rudgea viburnoides* (Rubiaceae), *Dalbergia mischolobium* (Fabaceae), *Andira* sp. (Fabaceae), *Stryphnodendron* sp. (Mimosaceae), *Cassia* sp. (Caesalpiniaceae), *Ocotea* sp. (Lauraceae), *Eugenia aurata* (Myrtaceae), *Cybistax antisyphilitica* (Bignoniaceae), *Jacaranda* sp. (Bignoniaceae), *Curatella* (Dilleniaceae) and many species in the Rubiaceae family.

All these taxa, including trees of the cerrado (wooded savanna) (*Byrsonima*, *Curatella*), semi-deciduous trees (*Copaifera langsdorfii*, etc), montane shrubs (*Drimys brasiliensis*), species of Orchidaceae found today in Patagonia (*Cynaeorchis arundimae*), taxa characteristic of peat bogs (*Sphagnum, Drosera)* and aquatics, occur within a restricted area, forming a vegetation mosaic. Several taxa, such as the Patagonian species of Orchidaceae and *Drimys brasiliensis*, are restricted to specific micro-climatic conditions where cool fog persists in the depression every morning until noon. The alternation of dry and wet seasons and local edaphic conditions determine the distribution of forest associations on the slopes.

Araucaria angustifolia trees grow in the area, though not as a forest formation as they do in the

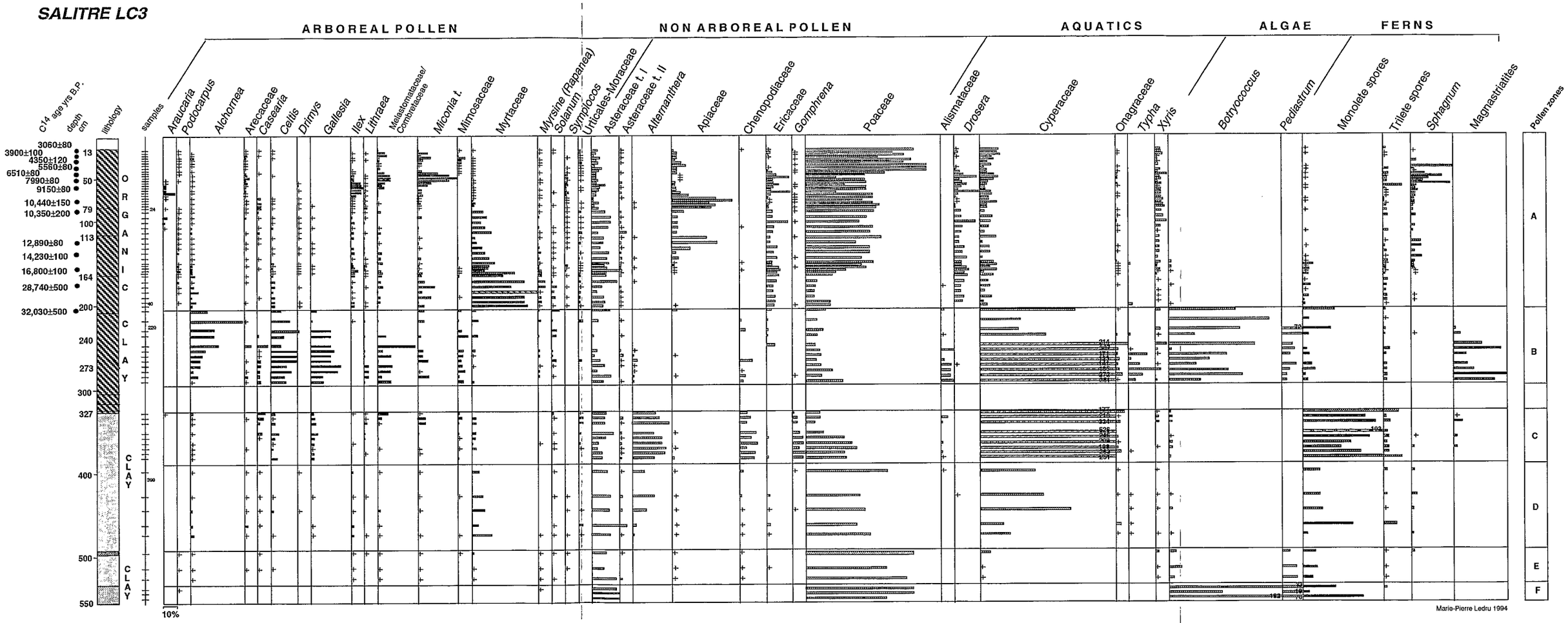

Fig. 3. Pollen percentage diagram with selected taxa of the core Salitre LC3. The pollen sum includes arboreal and non arboreal pollen taxa. Values smaller than 1% are represented by the "+" sign.

Serra da Mantiqueira (Central East Brazil) or the Paraná (South Brazil).

3. Material and methods

3.1. Material

Salitre is a 3.5 km wide depression located at 19°S and 46° 46′W, at an altitude of 980 m. It lies about 400 km to the west of Belo Horizonte, capital of the Minas Gerais state in Central Brazil. The highest point in the area is 1283 m. The depression lies at the centre of a 10 km wide, ultramorphic-alkaline cretaceous complex and is occupied by a 1 km wide peat bog called the "Lagoa Campestre". A 610 cm deep core (LC3) was drilled in 1988 by ORSTOM, using a vibracorer. Thick, loose lateritic soils cover the slopes of the depression, reaching an altitude of 1180 m at their highest point.

A detailed paleoenvironmental discussion of the upper 2 m of the Salitre core LC3, representing the last 30,000 years, has already been published (Ledru, 1993). Here we present the pollen diagram of the whole core and compare results with those from the 8 m deep core from the Serra Negra, only a few hundred meters from Salitre (De Oliveira, 1992; De Oliveira and Colinvaux, in press).

Three sedimentological units can be distinguished in the core on the basis of mineralogy and grain size characteristics (Fig. 3) (Soubiès et al., in prep.). The lowest unit (610–576 cm depth) is minerogenic, composed primarily of altered rock; the middle unit (576–327 cm depth) consists of sandy or silty, dark to light brown phosphatic clays with little organic matter (15–25%) and numerous tiny autochthonous phosphatic nodules (titanium and silicophosphates); and the uppermost, highly organic (50–85%) unit (327 cm to the top) is blackish brown to brown with few or no phosphatic nodules. Mineral matter is low at depths of 327–164 cm, but increases above, especially between 179 and 164 cm down. Quartz, ilmenite, anastase (perovskite pseudomorphs), crandallite family phosphate aggregates and kaolinite–gibbsite aggregates are the main detrital components of the sediments. Several discontinuities occur. These are between 494 and 498 cm in almost black sediment; between 315 and 303 cm in organic, dark colored clay with some sand; and, between 273 and 240 cm, a diagonal transition appears, without any change in color but with a shift to a lower vegetable fibre content. Between 273–240 and 209 cm, the sediment shows a high vegetable fibre content with longer (several cm long), larger elements. The sediments between 113 and 79 cm are more minerogenic than the over- and underlying sediments, but are still rich in organic matter (Soubiès et al., in prep.).

14 radiocarbon dates of the sediments were obtained to 204 cm down-core (32,030 ± 500 yr B.P.) (Ledru, 1993). Below this depth, we tried to correlate the recorded paleoclimatic events by comparison with other long sequences such as that from Serra Negra.

3.2. Methods

Samples were treated following the standard palynological techniques (Faegri and Iversen, 1975), applying the Lüber technique for the more organic part of the core using 50% HNO_3 solution and 10% KOH solution. The lower, more minerogenic unit, was treated with 70% HF hydrofluoric acid for 18 hours, followed by a 50% HCl treatment in a hot water bath and by a 10% KOH solution. Palynomorphs were separated using a $ZnCl_2$ solution of density 2 and mounted in glycerine for light microscopy analysis.

Pollen and spores were identified by comparison with our reference collection of about 600 Brazilian forest taxa and published pollen floras (Heusser, 1971; Salgado-Labouriau, 1973; Markgraf and D'Antoni, 1978; Hooghiemstra, 1984). At least 300 pollen grains were counted at each level. Pollen proportions of all taxa were calculated as a percentage of the pollen sum, including arboreal and non arboreal taxa. Aquatics, Cyperaceae, other wetland taxa and spore-producing taxa were excluded from the pollen sum. The frequencies of the principal pollens identified are plotted in Fig. 3. The list of all taxa identified from core LC3 is given in the Appendix.

4. Palynological results

4.1. Arboreal pollen and non arboreal pollen proportions

The Arboreal Pollen (AP) record shows the lowest frequencies in the lower part of the core, with less than 10% between 550 and 500 cm depth (Fig. 4). Between 500 and 400 cm, the AP percentage increases abruptly to 20% and continues to 360 cm. Myrtaceae taxa frequency remains at 10% thoughout these depths. Between 360 and 210 cm the AP count is high, reaching a peak of 90% between 260–220 cm. AP frequency declines to 20–30% above 220 cm. Myrtaceae become dominant above 210 cm, suggesting that forest composition has changed. From 210 cm to the top, AP frequency decreases to less than 30%, except

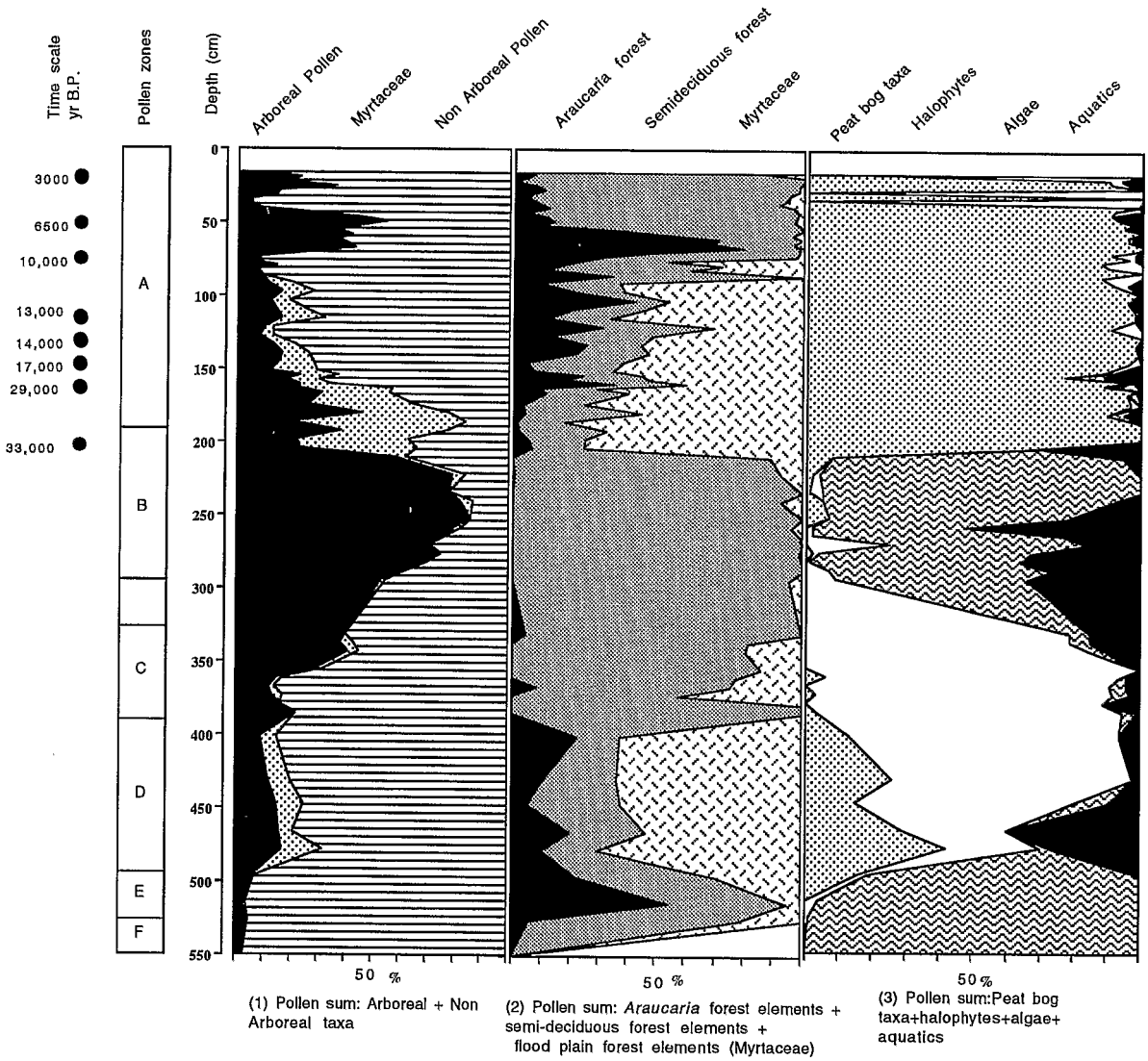

Fig. 4. Summary pollen diagrams of core Salitre LC3 showing changes in percentages of (1) Arboreal Pollen (AP), Myrtaceae and Non Arboreal Pollen (NAP), (2) *Araucaria* forest, semi-deciduous forest and Myrtaceae flood plain forest, (3) Peat bog taxa, halophytes, Algae and aquatics.

between 70 cm and 50 cm where it increases again to 50% (Ledru, 1993).

4.2. Description of the results

Based on changes in pollen proportions, 6 pollen zones could be distinguished, numbered from A (youngest) to F (oldest) (Fig. 3). Below 550 cm depth no pollen was recovered and from 600 to 576 cm the core is composed of altered rock.

Zone F extends from 550 to 532 cm and is characterized by low frequencies of arboreal pollen (0.5–3%). Asteraceae (18.5–28%) and Poaceae (69–79%) are dominant among the non-arboreal taxa. Wetland taxa are not represented but algae, *Botryococcus* (41.8–182%) and *Pediastrum* (18–76%) are abundant. This pollen assemblage is poor in taxa and indicates open, treeless vegetation surrounding a shallow pond with no fringe of aquatic vegetation. The low frequency of arboreal taxa indicates that trees were growing only at a distance. This suggests the presence of landscapes found today in central and northern Argentina, where the climate is cool and dry.

Zone E, extends from 532 to 494 cm and is characterized by the presence of a number of arboreal pollen taxa at low frequency (<1%) such as *Celtis*, Arecaceae, *Casearia, Ilex, Myrsine, Alchornea*, Myrtaceae, *Podocarpus* and Melastomataceae. The contribution of total arboreal pollen remains 4–7%. Among the non-arboreal pollen taxa, Poaceae and Asteraceae are still well represented but their frequencies are slightly lower than before, at 66–74% and 9–18% respectively. Chenopodiaceae appear with a less than 1% frequency. Most remarkable in this zone is the abrupt decrease in representation of the algae *Botryococcus* (4–8%) and *Pediastrum* (4–11%). A change in sediment color at 532 cm suggests a gap in the sediment sequence and this could explain the abrupt change in the frequency of algae. Although the regional vegetation was still open, the decline of algae and the appearance of semi-deciduous trees attests to low water levels and the existence of a few trees higher up on the slopes of the depression. The climate was probably more arid than before, with increased evaporation.

Zone D extends from 494 to 393 cm. Percentages of arboreal taxa are still low, but frequencies increase from 15 to 32%. The same arboreal taxa mentioned for zone E are represented; the increase in arboreal pollen is mainly due to an increase in Myrtaceae (5 to 15%) and *Ilex* (to 2%). Among the non-arboreal taxa, *Alternanthera* (Amaranthaceae) increase from 1 to 16%, and Cyperaceae from 17 to 67%. Onagraceae and *Typha* occur with frequencies of less than 1 to 3%. Algae are absent. This suggests that a Myrtaceae-dominated forest, characteristic of seasonally changing water levels, had started to grow in the depression. A Cyperaceae marsh now occupied the depression. The trend towards even more temperate climates inferred for the previous zone continues in zone D and evaporation has increased.

Zone C extends from 393 to 327 cm depth, ending with an abrupt lithological change at 327 cm. Arboreal pollen taxa continue to increase from 21% at the base to 55% at the top. They are mainly represented by *Casearia* (less than 1–6%), *Celtis* (less than 1–5%), *Gallesia* (2–6%), and Melastomataceae, which appear at 340 cm at the end of zone C, with a frequency of 2–6%. Myrtaceae continue, at 1–5%, as do Mimosaceae, at less than 1%. This zone is characterized by the expansion of semi-deciduous trees. *Araucaria* and *Drimys* are present only in a few samples, suggesting that they were probably growing at some distance from the site, at higher altitudes, e.g. in Serra Negra (De Oliveira, 1992). Herbaceous taxa are dominant and reach a peak of 86% at 365 cm depth, with *Alternanthera* accounting for 27%. After that, herbaceous taxa start to decrease to 1% at the top of this zone. At about 330 cm depth, Chenopodiaceae–Amaranthaceae (14%) also start to decrease in the last sample, *Gomphrena* (Amaranthaceae) reaching a maximum at the beginning of zone C, between 370 cm and 387 cm depth, before decreasing to less than 1%. Asteraceae remain well represented, as in zone D, at 7–16%. Poaceae decrease from frequencies of 37 to 6%, the minimum being reached at 341 cm. This zone is also characterized by large quantities of Cyperaceae (177–324%) and monolate fern spores (27–103%) until they decrease abruptly in the last sample, at 329 cm. It is interesting to note that the maxima for Cyperaceae (324%) and mono-

lete spores (103%) coincide with the minimum for Poaceae. Today they grow in competition in the Salitre depression. Other wetland taxa are not represented and/or frequencies continue low.

No sediment was recovered between 329 and 296 cm.

Zone B covers the section from 296 to 202 cm depth. Pollen frequencies in this zone continue the trends in Zone C, despite the missing samples in between. Arboreal frequencies continue to increase from 62% to a peak of 87% at 250 cm; they then decrease again to 63% at the end of pollen zone B. The principal tree is *Alchornea*, which increases from 1 to 38% at 220 cm, subsequently decreasing to 1% at the top of the zone; *Casearia* increases from 1 to 7% and then disappears above 236 cm; *Celtis* increases from 11 to 22%, showing a brief decline between 238 and 254 cm before reaching 22% again at 232 cm, and decreasing thereafter; *Gallesia* increases from 10 to 23% reaching a peak at 274 cm, and then decreases progressively to 1% at 202 cm; Melastomataceae increase from 2.5 to 28% at 262 cm and then decrease to 1%; Mimosaceae increase from 1 to 8% at 256 cm depth, then decrease and disappear at the top of the zone; Myrtaceae increase from less than 1 to 42% at the top of zone B (212–202 cm), while Arecaceae and *Lithraea* are represented at the beginning of zone B only. These tree taxa are semi-deciduous, and the presence of *Gallesia* is characteristic of a modern gallery forest environment (Ledru, 1991). These taxa were gradually replaced by a Myrtaceae forest which has been defined as a floodplain forest (Ledru, 1993).

Herbaceous taxa show a significant decrease. *Alternanthera* (1–0%) and Chenopodiaceae disappear, apart from two peaks at 238 cm (5%) and 274 cm (10%). Poaceae and Asteraceae are present, but their frequencies decline from 20 to 7% and from 14 to 10% respectively, with a minimum between 272 cm and 238 cm.

This zone is characterized by the appearance of aquatic taxa, with Alismataceae ranging between 2 and 9% (296–274 cm), *Typha* between 7 and 19% (296–274 cm), the algae *Botryococcus* between a minimum of 3% at 262 cm and a peak of 74% at 232 cm and *Pediastrum* from 0% at 274 cm to a peak of 73% at 238 cm. Both algae types disappear at 236 cm. The spores of Magnastriatites-type are often associated with moist periods (Morley, 1977). Monolete spores fluctuate between 0 and 23%.

Zone B shows the most humid conditions of the entire core.

Zone A, represents the core section between 202 cm and the top and is radiocarbon-dated at between 32,030 yr B.P. at the base and 3000 yr B.P. at the top. This part of the record has already been discussed by Ledru (1993). We would here like to stress the change occurring between zone B and zone A. It could correspond to a gap in sedimentation at 210 cm. Trees that were abundant prior to this sedimentologic change (*Gallesia, Celtis, Alchornea*) appear at low frequencies after the change. They are replaced by Myrtaceae, *Ilex, Podocarpus, Myrsine (Rapanea), Solanum* and *Symplocos*, taxa which are today associated with *Araucaria* forest and cooler climatic conditions. The mixture of taxa with different ecological implications indicates a new mosaïc pattern of vegetation including cool and temperate taxa. Open water with algae and aquatics (Alismataceae, *Typha*, etc.) disappears in this pollen zone. Peat bog vegetation including Ericaceae, Apiaceae, Poaceae and Cyperaceae rapidly spreads across the basin.

4.3. Summary diagrams

Forest composition

Taking only arboreal pollen (AP) taxa into account (Fig. 4), proportions of the forest taxa group were calculated as percentages of the following sum: Myrtaceae plus semi-deciduous forest taxa (*Alchornea, Casearia, Celtis, Gallesia*, Melastomataceae, *Miconia*-type, Mimosaceae) and *Araucaria* forest taxa (*Araucaria, Podocarpus, Symplocos, Ilex*). (Fig. 4). At the base of the core, where the total AP frequency is low, trees are represented by a combination of *Araucaria* forest taxa, semi-deciduous forest taxa and Myrtaceae. Myrtaceae taxa are high between 500 and 400 cm. Both *Araucaria* and Myrtaceae forest taxa are thereafter replaced by semi-deciduous forest taxa or gallery forest taxa which remain up to 202 cm. *Araucaria* forest has disappeared at 400 cm depth.

Between 202 and 100 cm, trees are represented by a mixture of *Araucaria* forest taxa, semi-deciduous taxa and Myrtaceae forest taxa, which remain dominant until the beginning of the Holocene (80 cm). During the Holocene, *Araucaria* forest is dominant initially but is later replaced by semi-deciduous forest. Myrtaceae flood plain vegetation becomes rare during the Holocene (less than 10%) and the forest composition begins to resemble today's vegetation, dominated by semi-deciduous forest taxa mixed with taxa from the *Araucaria* forest and the cerradão.

Local plants

The development of the local vegetation is reconstructed with the help of a main diagram with a pollen sum including algae (*Pediastrum, Botryococcus*), aquatics (Alismataceae, Onagraceae, *Typha*), halophytic taxa (Chenopodiaceae, *Alternanthera, Gomphrena*) and peat bog taxa (*Sphagnum*, Ericaceae, *Drosera*) (Fig. 4). Algae show high frequencies twice, first at the base of the core between 550 and 500 cm depth and a second time between 350 and 210 cm, reaching a peak between 250 and 210 cm. Peat bog taxa appear between 500 and 400 cm, at less than 40%. They become dominant (more than 90%) at 202 cm, dated 32,000 yr B.P. Halophytic taxa are dominant between 450 and 330 cm. Aquatic taxa are abundant above and below this section, i.e. between 500 and 450 cm and 350 and 250 cm. Changes in local vegetation in the basin are connected with changing water levels; abundant algae indicate times with relatively low lake levels, the presence of halophytes indicates periods of fluctuating water levels (seasonal precipitation) and peat bog taxa show when the basin was accumulating organically rich sediments.

5. Discussion

Most pre-Holocene plant assemblages in the tropics have no true modern analogues because present-day vegetation is the result of a complex bioclimatic evolution over time (Bonnefille et al., 1990). The base of the core, where algae, grasses and other herbs dominate, reflects a time when a lake existed in the depression, surrounded by treeless grassland (Zone F). This assemblage does not exist today in central Brazil; however, looking further afield for modern data, we have successfully interpreted the environmental changes occurring at Salitre in terms of climate.

For example, co-dominance of Poaceae and Asteraceae is characteristic of pollen assemblages from steppe-scrub vegetation in Patagonia, Argentina, between 39°S and 46°S (Schäbitz, 1994) in response to dry, cold conditions. Further south, at Lago Yehuin (54°20′S, 67°45′W), Markgraf (1983) has inferred an assemblage with 60% Poaceae and 20–30% herbs (mainly Asteraceae) as treeless grassland with very dry summers. The Poaceae–Asteraceae co-dominance is also recorded in Patagonia, in steppe-scrub vegetation with less than 500 mm mean annual precipitation occurring only in winter, long summer drought and cool temperatures (V. Markgraf, pers. comm., 1995). The local aquatic environment is characterized by high frequencies of algae, suggesting shallow water. Today's distribution of the chenopods in South America is restricted to lowland areas south of 30°S latitude in Argentina and Chile; they are not recorded in Brazil as native plants (Heywood, 1987). In Patagonia, halophytic plants, especially Chenopodiaceae–Amaranthaceae, form a belt surrounding shallow, fluctuating lakes (Schäbitz, 1994). In Gruta del Indio (Markgraf, 1983) the increase of saltflat vegetation indicators (Chenopodiaceae–Amaranthaceae) is connected with a decrease in precipitation leading to evaporation of open water in depressions. Vegetation on the playa near peat bog site Salina 2 (32°15′S, 69°20′W, 2000 m altitude) consists of saltflat plants (Chenopodiaceae–Amaranthaceae), while Poaceae grow on clayey ground above the fluctuating water level. This environment corresponds to an annual preciptation of 1000 mm (winter rains) and a mean annual temperature of 9°C (Markgraf, 1983).

In Salitre, after a transitional phase (zone E) where tree taxa begin to increase with semi-deciduous forest taxa and *Araucaria* forest taxa suggesting the development of forest in the region (Zone D), halophytic taxa and Cyperaceae expand their local range. Zones F–D are associated with semi-arid and arid cold climates; zone E is a

transition between F and D. The replacement of halophytic taxa by aquatic taxa in the next zone (Zone C) suggests more stable water levels, while the increase in semi-deciduous tree taxa indicates expanding semi-deciduous forest.

The expansion of the semi-deciduous forest starts in pollen zone C of core LC3 and suggests increased precipitation or a shorter dry season. In central Brazil, semi-deciduous forests are today related to a relatively temperate climate with mean winter temperatures of 10–15°C, about 1500 mm mean annual rainfall and a two-month dry season. As the spread of chenopods with Cyperaceae seems to indicate, water levels in the Lagoa Campestre depression were now more seasonal than before. In Zone B, between c. 40,000 and 33,000 yr B.P., the dominance of algae and tree taxa indicate stable water levels in the depression and dense semi-deciduous gallery forest in the surroundings. The upper part of zone B is radiocarbon dated at 32,030 yr B.P. ±500 (OBDY n°471). This period is characterized by a considerable increase in both precipitation and temperature. It is in fact the wettest period recorded at Salitre. The incursion of cold, moist air from the pole to the latitude of Salitre contributes to the increase in humidity, probably by reducing the length of the dry season.

A moist, cool episode has been detected between 43,000 and 31,000 yr B.P. at other South American sites as well: in Chili (Heusser, 1971) and in Panama (Bush and Colinvaux, 1990), in Brazil, at Cromínia (Vicentini, 1993), at Katira (Amazonia, Brazil) (Van der Hammen and Absy, 1994) and at Serra Negra (De Oliveira, 1993).

At Serra Negra, three periods of high moisture levels (called SN1, SN2 and SN4) alternate with more seasonal episodes (SN2 and SN3) (Fig. 5). Probably because Serra Negra, although quite close to Salitre, is markedly higher (980 m at Salitre versus 1170 m at Serra Negra), no periods of aridity have been recorded. However, based on the relative moisture changes, we suggest that SN1 to SN6 at Serra Negra are related to zones D and C at Salitre. The high moisture conditions are suggested by the presence of aquatic taxa and the extension of the *Araucaria* forest (which is not a species tolerant of dry seasons but needs cool temperatures and mean winter temperatures of less than 10°C to develop). Fluctuations in moisture conditions are more pronounced at Serra Negra than at Salitre. Between SN1 and SN3, moisture conditions have not reached their maximum since the *Araucaria* forest is not yet fully developed and lake levels are still fluctuating, as in zone D at Salitre when the semi-deciduous forest is spreading. SN4 from Serra Negra shows the highest moisture conditions and SN5, SN6 record a gradual decrease in *Araucaria* forest and the increase of Poaceae and aquatic taxa. At the end of SN6, *Araucaria* forest has completely disappeared. Radiocarbon dates show a gap in sediments at the top of SN6. As we know that this gap occurs after 31,000 yr B.P., it may be related to gaps detected in other records (Carajás, as e.g. Absy et al., 1991) and correspond to the Late Glacial Maximum, which Van der Hammen et al. (1992b) define as very arid in the tropical lowlands. In this case, the zones D and C and the SN1–SN6 moist, cold episodes correspond to the Middle Pleniglacial, between 65 and 26,000 yr B.P. (Fig. 5). The gallery forest around the depression at Salitre would have provided protection against evaporation during the more seasonal episodes recorded at Serra Negra (SN5–SN6).

Finally, in Zone A, the gallery forest disappears and Myrtaceae tree taxa increase, water levels fall and peat bog taxa increase. This is associated with the development of a seasonally inundated floodplain area between c. 33,000 and 28,000 yr B.P. After 17,000 yr B.P. the forest changed from an *Araucaria* dominated association to semi-deciduous forest, while peat formation continued in the depression. This indicates the onset of a climate similar to today's, characterized by a sharply-contrasted seasonal pattern. The Late Glacial (Zone A) at Salitre is characterized by a mixed semi-deciduous forest with cold montane elements, suggesting reduced precipitation and low temperatures (Ledru, 1993). Precipitation rates start to increase at c. 13,000 yr B.P. and seasonality increases during the Holocene.

6. Conclusions

Late Pleistocene climate change had a marked impact on both flora and vegetation in central

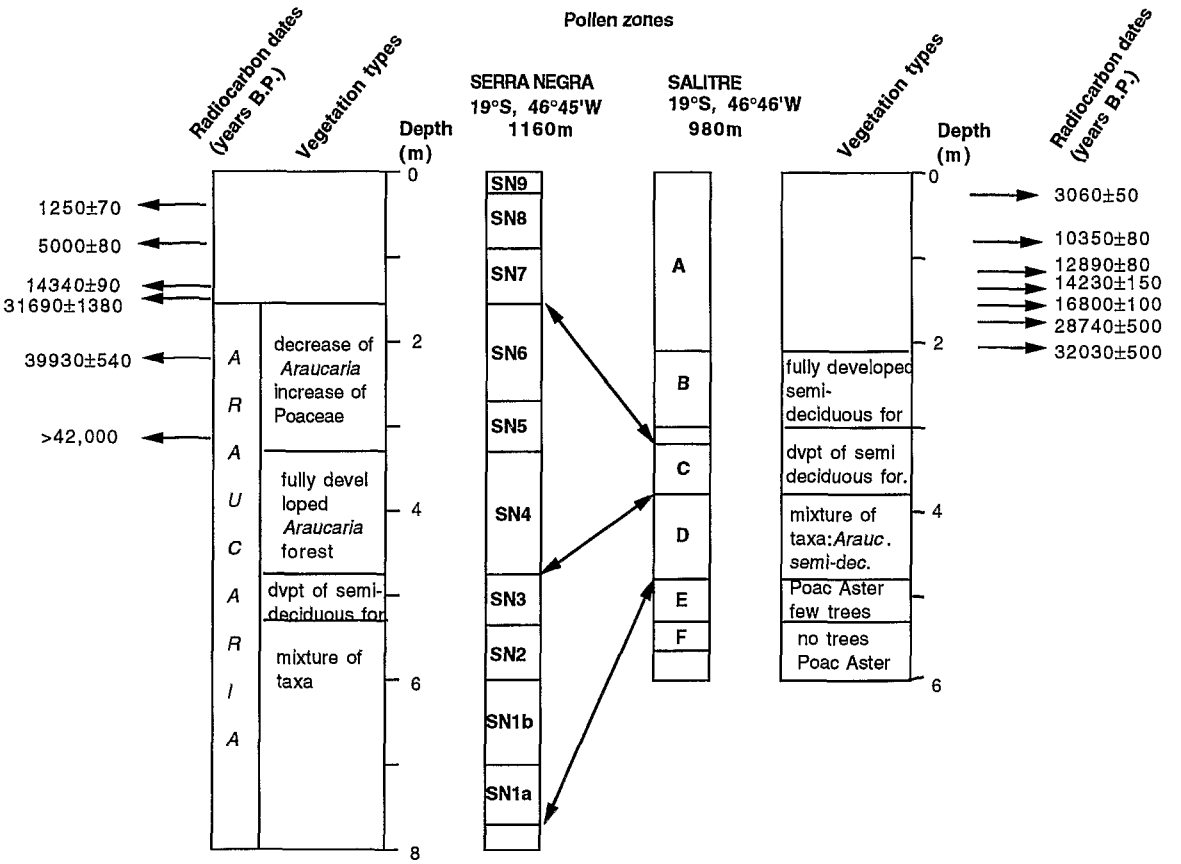

Fig. 5. Comparison of the pollen zones, vegetation zones and ^{14}C time control of Salitre and Serra Negra (after De Oliveira, 1992; De Oliveira and Colinvaux, in press) sediment cores over 30,000 yr B.P. (out of ^{14}C time control).

Brazil. The pollen record from the Salitre site shows a sequence of different climatic episodes.

(1) A cold, arid period c. 50,000 yr B.P. explains the modern-day presence at this latitude of one Patagonian orchid and some chenopods.

(2) A gradual increase in climatic humidity from 45,000 to 33,000 yr B.P., inferred from the increase in semi-deciduous tree taxa. During this period, cold-tolerant taxa such as *Drimys brasiliensis, Araucaria angustifolia* or the tree ferns *Cyathea* were still present in the Salitre area. Semi-deciduous tree taxa are represented by *Celtis, Copaifera, Gallesia,* and several Myrtaceae taxa. Today, these form small patches of forest above or within the depression. This association of cold-tolerant taxa with others that do not tolerate low temperatures (Brazil's semi-deciduous forest requires a two-month dry season and winter temperatures between 10 and 15°C) reached its maximum extent c. 35,000 yr B.P. At the same time, low water levels led to the development of various herbaceous plant associations, a dominant marshy vegetation with Poaceae, Cyperaceae and *Typha* and peat bog vegetation with *Drosera* and *Sphagnum*. This cool, moist episode is attributed to a northward displacement of the polar front of at least 5°, with an intensification of polar advections capable of maintaining the forests of the southern Amazon basin during Middle Pleniglacial times.

(3) Over the past 17,000 years, a rapid succession of different forest types are interpreted as reflecting rapid climate changes: Myrtaceae forest, a local forest which grows in flood plain areas, attests to

seasonal flooding; *Araucaria* forest attests to cold winter temperatures (less than 10°C) and high moisture rates (no dry season); semi-deciduous forest (characteristics mentioned above); cerradão (wooded savanna) characterizes a long dry season (4–5 months) and warm winter temperatures (above 15°C). These rapid climate changes are due to the impact of polar advections at the latitude of Salitre, mainly during the last 10,000 years. All these different forest types persist in small areas of the region to the present day. A progressive decrease in the intensity and frequency of the polar advections is associated with this warming of the climate.

Modern climate and relief conditions provide an explanation for the persistence of these different ecological groups; meteorological data indicate 1500–2000 mm mean annual rainfall, a four-month dry season and persistent fog every morning.

(4) This study also highlights the importance of analysing several cores from the same area. The LC3 core from Salitre and the Serra Negra core are two paleoclimatic records of comparable age from the same area. Pollen assemblage changes are not the same in the two cores, but interpretation of climatic history is compatible if one takes account of altitude, topography and sedimentology. Both records show a cold, moist episode between 40 and 30,000 yr B.P., but *Araucaria* is not recorded at Salitre owing to its lower altitude and consequently milder temperatures. Water levels in the two depressions are not synchronous, but this can be attributed to the impact of the local topography. Lastly, gaps in sedimentation at the two sites do not occur during the same periods.

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Appendix 1—List of all taxa determined in the LC3 core of Salitre

Arboreal pollen

ANACARDIACEAE
Alchornea
Anacardium
Astronium
Lithraea
APOCYNACEAE
AQUIFOLIACEAE
Ilex
ARALIACEAE
Didymopanax
ARAUCARIACEAE
Araucaria
ARECACEAE C1
ARECACEAE C3
ASTERACEAE
Mutisia
BIGNONIACEAE
Arrabidea
Jacaranda
Tabebuia
Tecoma
BOMBACACEAE
Chorisia
BORRAGINACEAE
BURSERACEAE
Protium
CAESALPINIACEAE
Apuleia type
Bauhinia
Copaifera
Myroxylon type
Cassia type
Sclerolobium
CARYOCARACEAE
Caryocar
CECROPIACEAE
Cecropia
CELASTRACEAE
Maytenus
Plenckia
CLETHRACEAE
Clethra
CHRYSOBALANACEAE
CHRYSOBALANACEAE
Licania
CLUSIACEAE
Vismia
CONNARACEAE
Connarus
CUNONIACEAE
Belangera
DILLENIACEAE
Curatella

EBENACEAE
Diospyros
ELAEOCARPACEAE
Sloanea
EUPHORBIACEAE
Julocroton
Longetia
Maprounea
Sapium
Sebastiana
FLACOURTIACEAE
Casearia
Lacistema
Xylosma
FABACEAE
Andira type
Erythrina
Poiretia
Pterodon type
FLACOURTIACEAE
Banara
LECYTHIDACEAE
Cariniana
LITHRACEAE
Laplacea
MALPIGHIACEAE
Heteropteris type
MELASTOMATACEAE/ COMBRETACEAE
MELASTOMATACEAE/ COMBRETACEAE
Miconia type
MELIACEAE/ SAPOTACEAE
MIMOSACEAE
MORACEAE
MORACEAE
Ficus
MYRSINACEAE
Myrsine (Rapanea)
MYRTACEAE
MYRTACEAE
Psidium
Campomanesia
NYCTAGINACEAE
Pisonia
MORACEAE
Ficus
PHYTOLACCACEAE
Gallesia
PROTEACEAE
Roupala
ROSACEAE
Prunus
RUBIACEAE
Bathysa
Chomelia
Coutarea
Ixora
Sabicea
RUTACEAE
Balfourodendron
SAPINDACEAE
Diatenopteryx
Matayba
Serjania
SAPOTACEAE
Chrysophyllum
Pouteria
SOLANACEAE
Cestrum
Solanum
STERCULIACEAE
Ayenia
STYRACACEAE
Styrax
SYMPLOCACEAE
Symplocos
ULMACEAE
Trema
RHAMNACEAE
RHAMNACEAE
Colubrina
RUTACEAE
Metrodorea
Zanthoxylum
ULMACEAE
Celtis
URTICALES
PODOCARPACEAE
Podocarpus
VOCHYSIACEAE
Qualea
Vochysia
WINTERACEAE
Drimys

Non arboreal pollen
ACANTHACEAE
Justicia
Ruellia
AMARANTHACEAE
Alternanthera
Gomphrena
APIACEAE
APOCYNACEAE
Peschiera
ASTERACEAE Tubuliflorae
ASTERACEAE Liguliflorae
ASTERACEAE
Ambrosia
Gochnatia
CARYOPHYLLACEAE
CHENOPODIACEAE/ AMARANTHACEAE
COMMELINACEAE
Commelina
CONVOLVULACEAE

ERICACEAE
EUPHORBIACEAE
Acalypha
Mabea
GENTIANACEAE
LAMIACEAE
LORANTHACEAE
LYTHRACEAE
Cuphea
PLANTAGINACEAE
Plantago
POACEAE
RANUNCULACEAE
Ranunculus
RUBIACEAE
Borreria

Aquatic taxa
ALISMATACEAE
ALISMATACEAE
Echinodorus
CYPERACEAE
DROSERACEAE
Drosera
ERIOCAULACEAE
HALORAGACEAE
Myriophyllum
LENTIBULARIACEAE
Lentibularia
ONAGRACEAE
POLYGALACEAE
POLYGONACEAE
Polygonum
SCROPHULARIACEAE
Buchnera
TYPHACEAE
Typha
XYRIDACEAE
Xyris

Algae
Botryococcus
Pediastrum

Ferns
Monoletes psilate
Monoletes (others)
Triletes psilate
Triletes (others)
Lycopodium type (=Triletes verrucate)
Polypodium type (=Monoletes verrucate)
Sphagnum
Magnastriatites type

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The last 50,000 years in the Neotropics (Southern Brazil): evolution of vegetation and climate

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