



ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 152 (1999) 319–337

PALAEO

Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: the fossil dunes of the middle São Francisco River

Paulo E. De Oliveira^{a,b,*}, Alcina Magnólia Franca Barreto^a, Kenitiro Suguio^a

^a Departamento de Estratigrafia e Paleontologia (DPE), Instituto de Geociências, Universidade de São Paulo, Caixa Postal 11348, São Paulo, SP 05422-970, Brazil

^b Department of Botany, The Field Museum of Natural History, Roosevelt Rd. at Lake Shore Drive, Chicago, IL 60605, USA

Received 2 February 1998; revised version received 14 January 1999; accepted 9 February 1999

Abstract

Palynological studies of a peat-bog sequence, with a basal date of $10,990 \pm 80$ yr B.P., provide a history of vegetational and climatic changes in the Icatu River Valley located inside a large system of stabilized sand dunes at the middle São Francisco River at $10^{\circ}24'S$, $43^{\circ}13'W$ in northeastern Brazil. The present day vegetation of the valley is 'vereda' a *Mauritia vinifera* palm swamp forest bordered by a narrow strip of semi-deciduous tropical forest. The adjacent dunes are stabilized by arboreal caatinga and cerrado vegetation in some areas. The palynological profile of the Saquinho locality within this valley was divided into five pollen zones: Zone SA1 (10,990–10,540 yr B.P.) contains pollen of taxa found in present Amazonian and Atlantic forests, as well as from montane taxa, thus suggesting very humid climatic conditions synchronous with more reduced temperatures. Zone SA2 (10,540–6790 yr B.P.) has pollen spectra from a vegetation type dominated by *Mauritia*, suggesting progressive warming and high humidity levels. The period between 8920 and 8910 yr B.P. has rapid sedimentation rate, few thermoluminescence (TL) dates, pronounced increase of *Mauritia* and *Ilex* pollen suggesting a very moist climate. From 8910 to 6790 yr B.P. there is a progressive decline in forest taxa and a gradual increase of caatinga and cerrado taxa on the landscape. Zone SA3 (6790–ca. 6230 yr B.P.) does not contain palynomorphs, possibly indicating semi-arid conditions. Zone SA4 (ca. 6230–ca. 4535 yr B.P.) marks the return of mosaic vegetation composed of gallery forest, cerrado and caatinga taxa indicating moister climatic conditions. A marked decline in moisture levels characterizes the period between 4240 yr B.P. and Present, as suggested by an increase in caatinga and cerrado species and a decline in gallery forest taxa. Zone SA5 (ca. 4535 yr B.P.–Present) establishes the present vegetational and climatic pattern of the Icatu River Valley. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: caatinga; palynology; thermoluminescence; Brazil; Bahia; Holocene; dunes

1. Introduction

Palaeovegetation and palaeoclimates of the Late Pleistocene and Holocene of semi-arid northeast-

ern Brazil remain unknown despite great advances in palaeoecological studies on the Quaternary of Brazil in the last decade. One of the main obstacles to the development of palaeoecological studies in northeastern Brazil is linked to the difficulty in locating permanent lake basins or unoxidized peat-bog sediments within the present caatinga forest phyto-

* Corresponding author. Fax: +55-11-78443810; E-mail: bjd@bragnet.com.br

geographical domain in semi-arid regions. Understanding late Quaternary biotic and abiotic changes in northeastern Brazil is fundamental for the test of biogeographical hypotheses such as the hypothesized former connection between the Amazonian and Atlantic rainforests (De Andrade-Lima, 1966; Cartelle and Hartwig, 1996). Palaeoecological profiles from a caatinga region are also fundamental to the understanding of Late Pleistocene tropical cooling reported by various authors and of climatic effects possibly related to the El Niño/Southern Oscillation

(ENSO) phenomenon (sensu Kousky et al., 1984) and to northward displacements of the Intertropical Convergence Zone (ITCZ).

2. The study site

2.1. Geographical setting

The fossil sand dunefields of the middle São Francisco River (Fig. 1), referred to as “The Little Sahara

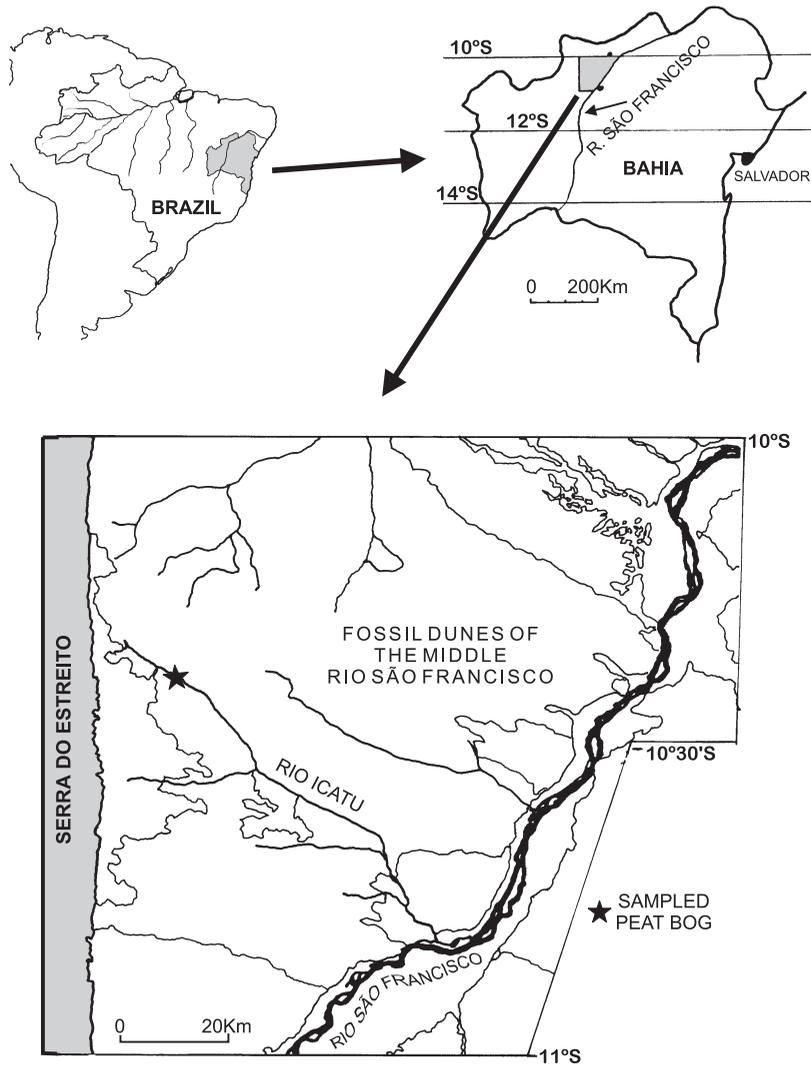


Fig. 1. Study site location in relation to the drainage system of the western section of the middle São Francisco River sand dunefield system. Site of sediment collection is indicated by the star sign.

along the São Francisco River” by Williams (1925), has an area of ca. 7000 km² located between the towns of Barra and Pilão Arcado in Bahia, north-eastern Brazil, between the latitudes 10°00′–11°00′S and longitudes 42°30′–43°20′W (Barreto, 1996). The dunes are dissected by various ephemeral drainages. The Icatu River, the only permanent river of the Rio São Francisco in this region, runs through a valley ca. 400 m wide where moist peat-bog sediments were collected for palynological analysis (Fig. 1). The Icatu River originates at the foothills of the Serra do Estreito, which is a narrow, long mountain strip averaging 800 m elevation, and the westernmost limit of the sand dunefields ca. 50 km from the study site.

2.2. Climate

The climate of the Icatu River Valley according to the Köppen system is classified as BShw, hot, semi-arid, with a dry season of 7–8 months. Rainfall is concentrated in the summer months (October–March) and annual precipitation ranges from 400 to 800 mm. Mean temperature of the coldest month is higher than 18°C and annual mean temperatures are not higher than 27°C (Nimer, 1977, 1989). Present precipitation rates at the studied site result from the interplay between the Intertropical Convergence Zone (ITCZ), and the permanent high pressure system centered in northeastern Brazil (Nimer, 1989). Rains generated by the ITCZ generally reach the studied site in late summer (March–April) resulting from its seasonal shifts. These rains account for most of the precipitation in the northeastern Brazilian caatinga region lying between the latitudes of 2 and 10°S (Nimer, 1977). Incursion of polar air and frontal rains into the studied area occur infrequently, and are restricted to unusually cold winters (Nimer, 1977, 1989).

2.3. Vegetation

The vegetation of the Bahian fossil dunefield system is composed of different types of caatinga vegetation, e.g. arboreal, shrub and hyperxerophytic caatinga, stabilizing the dunes (Barreto, 1996). Caatinga is defined in Brazil as a xerophytic vegetation type containing essentially spiny deciduous

trees and shrubs in association with succulent plants, cacti and bromeliads (Kuhlmann, 1977). Arboreal caatinga is characterized by a three-layered system: an arboreal layer 8–10 m in height, a perennial spiny scrub layer and a seasonal herb layer dominated by grasses. Arboreal genera typically found in this caatinga type are *Astronium* (Anacardiaceae), *Schinopsis* (Anacardiaceae), *Chorisia* and *Cavanillesia* (Bombacaceae), *Caesalpinia* (Caesalpiniaceae), *Cnidoscopus* (Euphorbiaceae). Hyperxerophytic caatinga refers to an open thorn-scrub vegetation with varying plant densities composed particularly of *Calliandra parviflora*, *Caesalpinia microphylla* (Caesalpiniaceae), species of *Jatropha* and *Cnidoscopus* (Euphorbiaceae), various cacti (*Cereus*, *Melocactus*, *Opuntia*, *Pilocereus*), spiny bromeliads (e.g. *Bromelia laciniosa*) and other drought-adapted taxa (Kuhlmann, 1977). A gallery forest, containing species presently found in semi-deciduous and deciduous dry forests is found as a narrow strip bordering the river. *Mauritia vinifera* palm swamp forests (veredas) are found in the waterlogged peat sediments and the adjacent sand dunes are stabilized by caatinga vegetation. Scattered islands of cerrado (savanna) found in some areas of the dunefields contain the arboreal taxa *Caryocar* (Caryocaraceae), *Byrsonima* (Malpighiaceae), *Cassia* (Caesalpiniaceae), *Piptadenia* (Mimosaceae), *Kielmeyera* (Clusiaceae), *Lafoensia* (Lythraceae), among many other taxa. Peat-bog vegetation consists mainly of Gramineae, Cyperaceae and aquatic herbs like *Borreria* (Rubiaceae), *Eriocaulon* (Eriocaulaceae), *Drosera* (Droseraceae), *Ludwigia* (Onagraceae). The macrophytes *Nymphaea* (Nymphaeaceae), *Pontederia* (Pontederiaceae) and *Isoetes* (Isoetaceae) occur mainly at the edge of the Icatu River.

2.4. Drainage and pollen source

The Icatu River at 480 m elevation (Fig. 1), drains a small watershed at the foot of the Serra do Estreito (860 m elevation), at the western edge of the sand dunefield. The pollen source lies therefore within the caatinga region of this watershed. Pollen is not only derived from the caatinga and gallery forests vegetation of this valley but also likely to come from the present caatingas of the Serra do Estreito. Therefore, the pollen accumulated in the Icatu River valley peat

bogs can be used as indicators of regional vegetational changes, for it is not representing exclusively autochthonous sources.

3. Materials and methods

3.1. Sediment coring, ^{14}C and pollen analysis

A 3.29 m long core was collected from the Icatu River Valley (Fig. 1) with a modified Livingston piston sampler (Colinvaux, 1993). Coring was carried out at a locality known as Saquinho at 10°24'S, 43°13'W. Sediments were sampled at 10 cm intervals for palynological analyses, following protocols for pollen extraction described in Moore et al. (1991) and Faegri and Iversen (1989): silicate removal with hydrofluoric acid; humic acid removal and dispersion of organic matter by 10% potassium hydroxide; acetolysis (9 parts acetic anhydride:1 part sulfuric acid). Two to three *Lycopodium clavatum* tablets were added to the sediment samples to calculate pollen concentration (Stockmarr, 1971). Final residues were stained with 2% alcoholic safranin. Carbonized (charcoal) particles larger than 20 μm were counted in each sample and a total pollen/carbonized particles ratio (Berglund, 1986) was used to infer relative palaeofire activity. Pollen percentages and concentrations were calculated based on total pollen sums of at least 300 grains per level, excluding pteridophytic and algal spores. In a few samples with poor pollen preservation, at least 200 grains were counted. Pollen percentage and concentration diagrams were prepared using the Tilia and Tiliagraph computer programs. Six sediment samples were sent to Beta Analytic Inc (USA) for ^{14}C dating.

3.2. Thermoluminescence studies

A total of 43 sand samples were collected over the entire sand dunefield system, in depths ranging from 0.30 to 3 m. At 3 m depth loose sediments collapsed the hole and prevented further penetration. These samples were protected from sunlight immediately after collection, and treated following the methodology described in Ichikawa (1965). The sands were initially sieved to obtain the 0.088–

0.180 mm fraction and later treated with acids to remove alpha radiation from the TL signal as well as to eliminate less resistant minerals. Heavy minerals were eliminated by the bromoform flotation technique, yielding only quartz grains for thermoluminescence (TL) dating. Samples were irradiated, at room temperature, with ^{60}Co at the Institute of Nuclear Energy (IPEN/CNEN-SP) of the University of São Paulo. A Harshaw 2000^A photo multiplier, without filter, and with a warming rate of 7.8°C/s, yielded TL readings. Accumulated TL dose was determined following Prószyńska et al. (1985). Local annual doses of natural radiation were determined by a Germanium detector, specific for low doses, at the Dating Laboratory of the University of Education in Nara, Japan. TL methodology used here is detailed in Barreto (1996) and Barreto et al. (1997).

4. Results and interpretation

4.1. Stratigraphy and ^{14}C dating

Cored sediments are composed primarily of black organic peat (Munsell Color Chart 10 YR2/1), from the top to 340 cm depth, where a sharp sedimentary boundary occurs between peat and white eolian sands. Radiocarbon dates of the six sediment samples from the Icatu River Valley (Saquinho peat bog) are given in Table 1.

4.2. Palynological results

The analyzed sediment samples contained well preserved pollen, spores and other palynomorphs. Depth levels 98.5, 133.5, 199.5, 304.5, 309.5 and 314.5 cm have not yielded enough pollen for statistical analyses and have been excluded from the palynological profile. The total pollen sum in each sample depth is shown in Fig. 5. The percentage diagrams of pollen grains belonging to taxa typically found in tropical forests, caatinga and cerrado vegetations are given in Figs. 2 and 3, respectively. In order to improve palaeological interpretations of the pollen spectra of caatinga taxa, these were divided into two separate categories, i.e. caatinga taxa, those restricted to this vegetation type, and caatinga/cerrado taxa, those known to occur in both

Table 1
Radiocarbon chronology of the Icatu River Valley sediment samples

Laboratory No.	Locality	Depth (cm)	Age (yr B.P.)	$^{13}\text{C}/^{12}\text{C}$	Corrected age (yr B.P.)
Beta 97254	Saquinho	143.5–148.5	4240 ± 70	–25 00	4240 ± 70
Beta 97255	Saquinho	214.5–215.5	6790 ± 80	–25 00	6790 ± 80
Beta 97256	Saquinho	264.5–269.5	8910 ± 80	–25 00	8910 ± 80
Beta 97257	Saquinho	279.5–284.5	8920 ± 120	–25 00	8920 ± 120
Beta 97258	Saquinho	316.5–321.5	10540 ± 80	–25 00	10540 ± 80
Beta 89265	Saquinho	324.5–329.0	11040 ± 80	–28 00	10990 ± 80

vegetation types. The occurrence of all pollen taxa, found in the analysis, in the different vegetation types of Brazil is shown in Table 3. Fig. 4 shows the percentage diagram of pollen taxa that are not restricted to the above vegetation types and are known to occur in other tropical phytogeographical domains in Brazil. The percentage pollen diagram depicted in Fig. 5 contains profiles of montane taxa, other selected herbaceous plants, selected indeterminate grains and pteridophytic spores (ferns), total sum of trees, herbs and unknowns. Number of grains counted in each level are shown next to profiles of the total pollen sum. The results of a stratigraphically constrained cluster analysis of the palynological data by CONISS (Grimm, 1987) are also shown in Fig. 5. Fig. 6 shows a summary diagram of all caatinga, caatinga/cerrado taxa, montane taxa, pollen concentration and charcoal particles (>20 µm). A total of five pollen zones was identified by the cluster analysis.

4.2.1. Zone SA 1 (10,990–10,540 yr B.P.)

This pollen zone has the highest pollen concentration values in the entire sequence, reaching over 90,000 grains/cm³ of sediment. It is probable that the high pollen concentration values found in SA1 reflect a large and well drained watershed under a climate conducive to a dense forest cover. Similar high pollen concentration values have been found at Lake Kumpaka in Ecuador and were attributed to the size of a well drained watershed covered only by amazonian rainforest (Liu and Colinvaux, 1988).

The zone is characterized by the absence of *Mauritia* and by the presence of humid tropical forest taxa e.g. *Palmae* (<5%), *Alchornea* (ca. 5%), *Cecropia* (<5%), *Ilex* (5–9%), *Melastomataceae* (4–12%) and *Myrtaceae* (4–11%). Some arboreal taxa

known to occur in lowland Amazonian and Atlantic rainforests in Brazil e.g. *Cecropia*, *Cedrela*, *Pouteria*, *Protium*, *Simarouba*, *Symphonia* and *Trichilia* (Jolly, 1976; Veloso et al., 1991; Lorenzi, 1992; Colinvaux et al., 1996) have their occurrence restricted to this zone with values <5%. Arboreal montane taxa and typical components of pollen spectra of glacial age (Ledru, 1991, 1992; De Oliveira, 1992; Colinvaux et al., 1996; Ledru et al., 1996), e.g. *Rapanea*, *Ericaceae*, *Hedyosmum*, *Humiria*, appear in this zone with values ranging from <5 to 22%. Herbarium collections both at the Field Museum of Natural History and at the New York Botanical Garden, as well as botanical surveys by the Radambrasil project (Radambrasil Project Members, 1976) indicate that *Humiria* is found in forests with altitudes over 1000 m in northwestern Brazilian Amazonia, while *Ericaceae*, *Rapanea* and *Hedyosmum* are distinctly montane taxa in the Atlantic rainforests of southeastern Brazil (Andrade and Lamberti, 1965; Jolly, 1976; Schultz, 1985). The montane occurrences of *Rapanea* and *Hedyosmum* are also documented by Van der Hammen (1979) in Colombia and by Gentry (1993) in northwestern Amazonia. These taxa are also presently found in the high elevation forests of the Chapada Diamantina, within the caatinga domain of Bahia (Stannard, 1995). Pollen of *Zanthoxylum*, a genus of trees of the Brazilian Atlantic rainforest known to have one species found mainly in upper elevation forests (Lorenzi, 1992) is restricted to this and the following pollen zone. Aquatic taxa are found in this zone with values <1% and are represented by *Sagittaria* (Alismataceae) and *Lentibulariaceae*. Some caatinga taxa, e.g. *Arrabidaea* (Bignoniaceae), *Bromelia*, *Cereus* (Cactaceae), *Caryocar* (Caryocaraceae), *Chamaesyce* (Euphorbiaceae), *Cuphea*

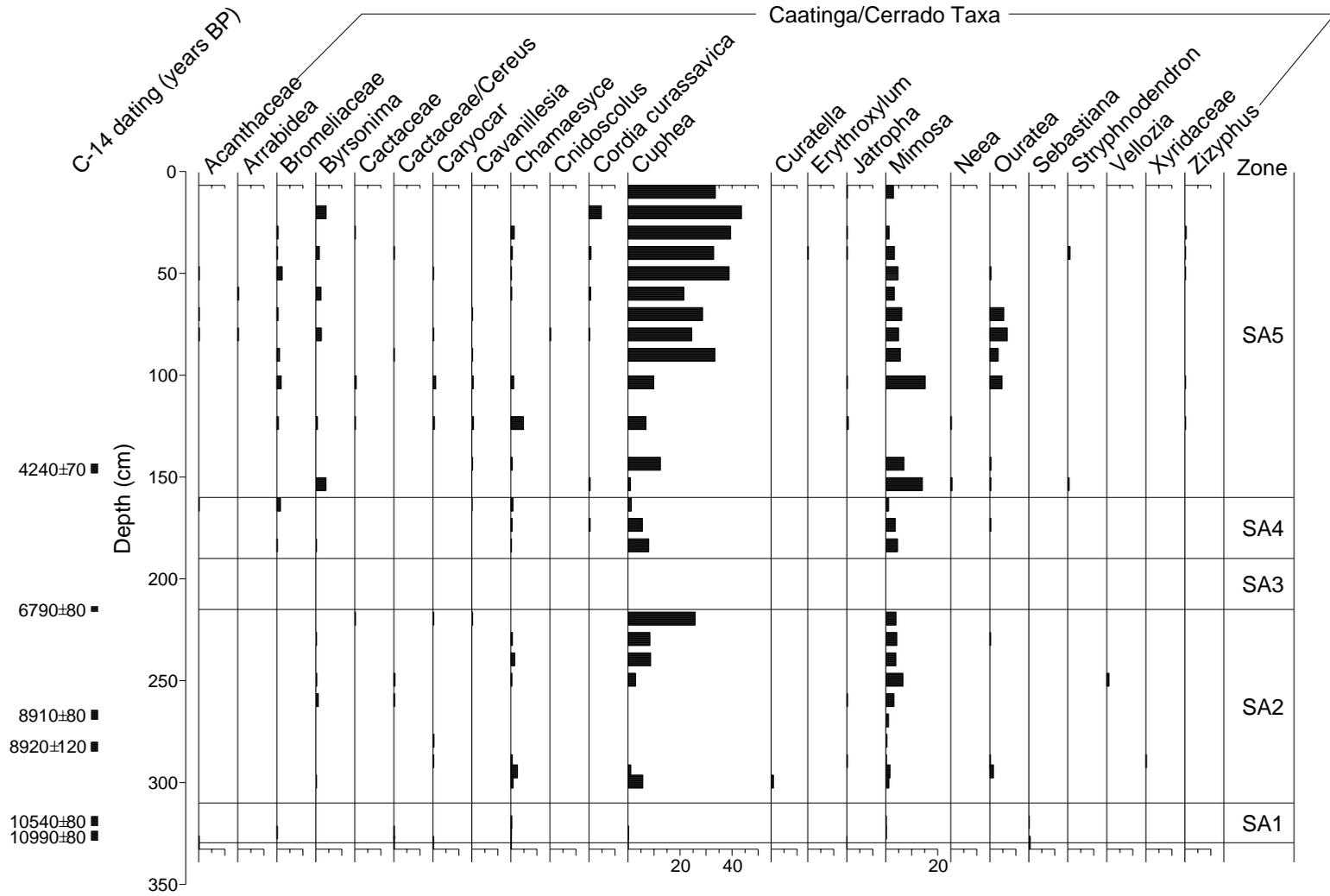


Fig. 3. Percentage pollen diagram of caatinga/cerrado taxa.

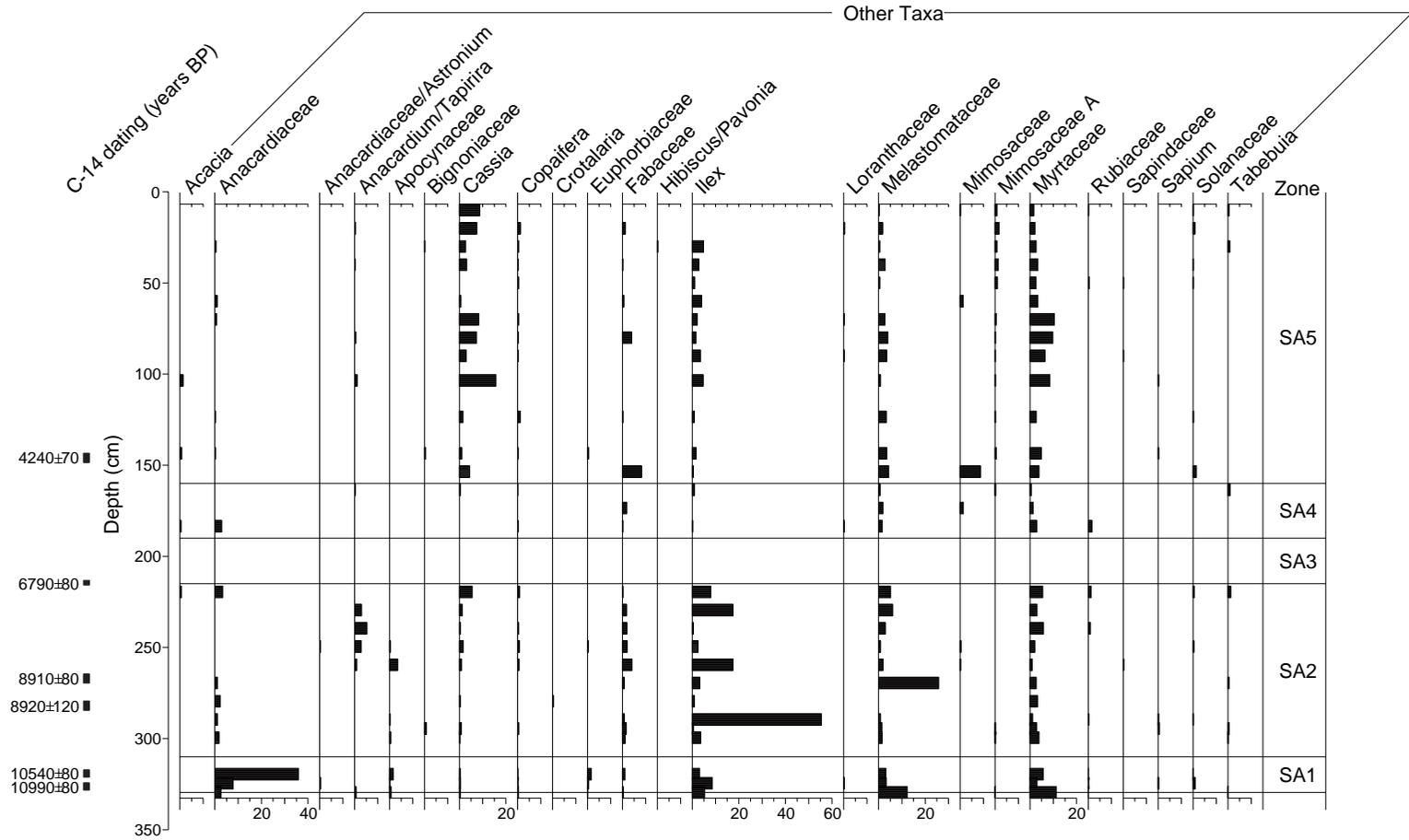


Fig. 4. Percentage pollen diagram of taxa known to occur in several tropical phytogeographical domains in Brazil, and here represented as 'other taxa'.

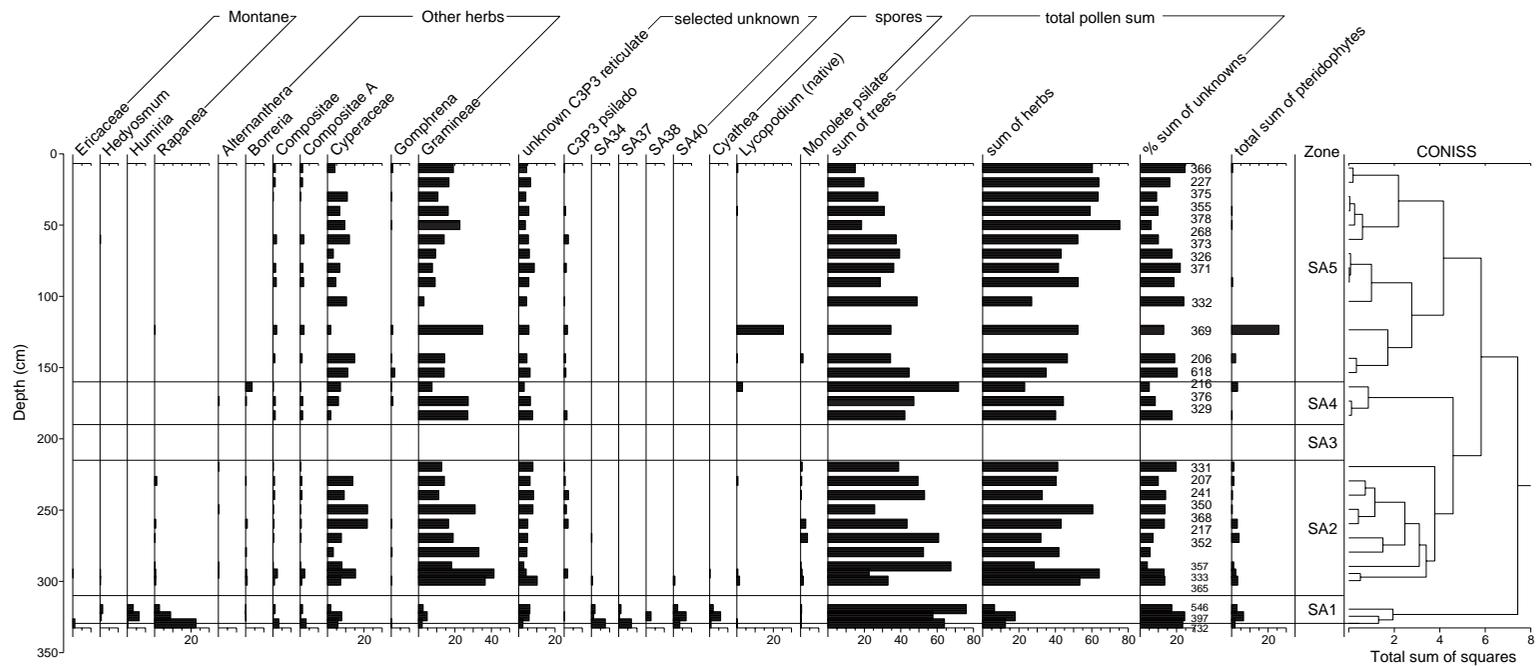


Fig. 5. Percentage pollen diagram showing profiles of montane taxa, other herbs, selected unknown grains, selected pteridophytic spores (ferns), total pollen sum showing sum of trees, herbs and unknowns, followed by the number of grains counted in each sample, total percent sum of pteridophytes and the CONISS dendrogram.

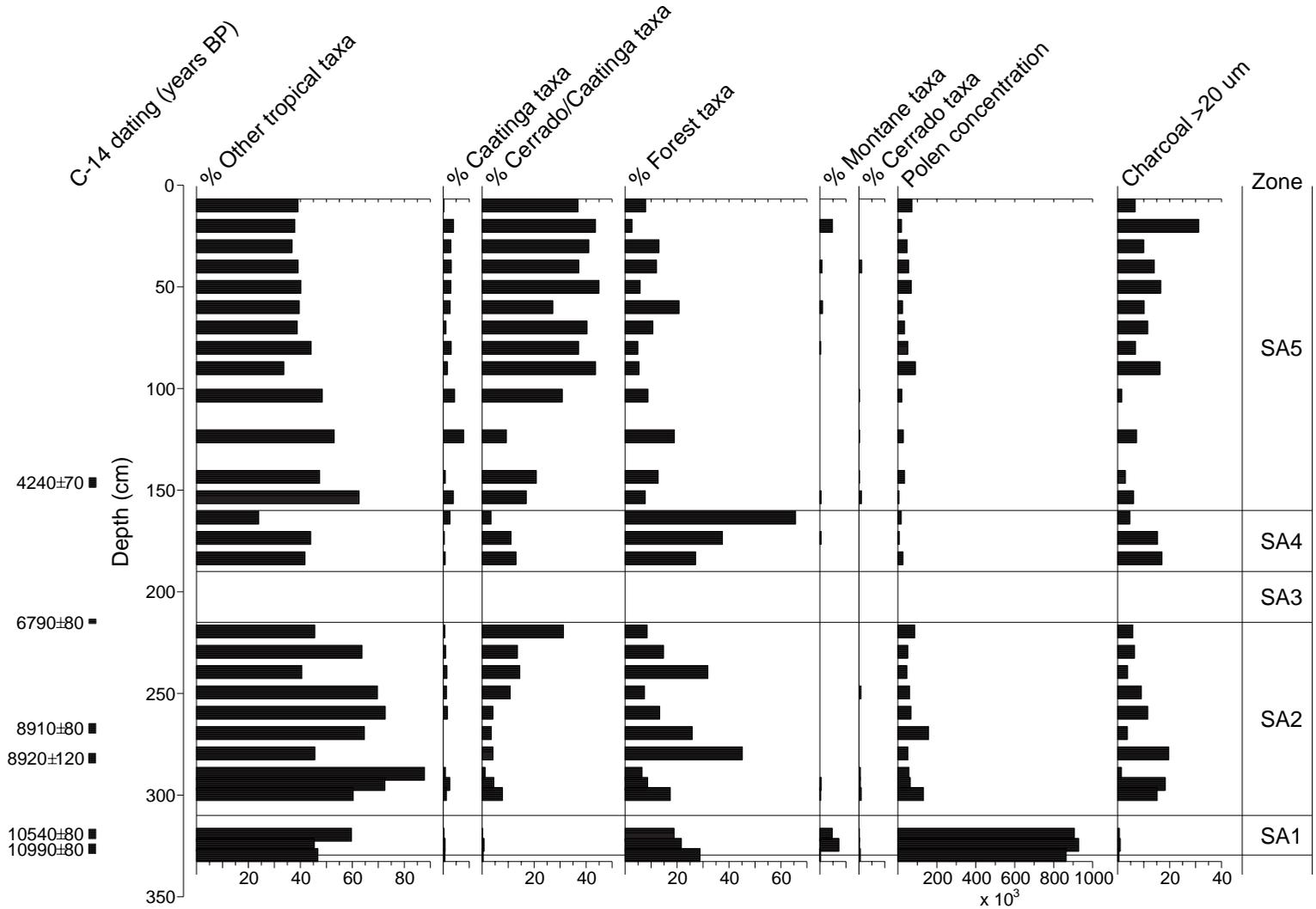


Fig. 6. Summary diagram of all caatinga, caatinga/cerrado, forest and montane taxa, pollen concentration and charcoal particles (>20 μm).

(Lythraceae), *Jatropha* (Euphorbiaceae) and *Mimosa* (Mimosaceae) are present with values <1%. Pterodophytic spores encountered in this zone belong mainly to *Cyathea*, a genus of Amazonian and Atlantic montane forest tree ferns, and to Polypodiaceae (Andrade and Lamberti, 1965; Jolly, 1976). *Cyathea* is typically associated with cool and moist montane conditions (Steyermark, 1979; Schultz, 1985). This zone is also characterized by a low frequency of dune activation as indicated by a low number of TL dates available (Barreto, 1996; Barreto et al., 1997) for the time interval of zone SA1.

4.2.2. Zone SA 2 (10,540–ca. 6790 yr B.P.)

While montane arboreal pollen and pollen of Amazonian/Atlantic forest taxa decline in abundance in this zone, the basal sample of this zone contains 35% Anacardiaceae pollen (arboreal). In this zone *Mauritia* pollen appears for the first time in the record, together with other arboreal taxa such as *Alchornea*, *Pterocarpus*, Urticaceae/Moraceae. There is a marked increase, at the onset of this zone, in grass (Gramineae = Poaceae) and sedge (Cyperaceae) pollen followed by an increase in caatinga and cerrado taxa, e.g., *Byrsonima*, *Chamaesyce*, *Cuphea*, *Curatella*, *Mimosa* and *Ouratea* towards the end of SA2. This suggests an increase in scattered semi-arid vegetation as closed gallery forest dwindles at the upper samples of this zone. Increased aridity at the end of SA2 is also supported by an increase in carbonized particles (Fig. 6), despite the relative low number of thermoluminescence dates obtained by Barreto (1996) for the time interval of this pollen zone.

The period between 8920 and 8910 yr B.P. differs from the earlier stages of this zone by the conspicuous increase in *Ilex* and *Mauritia*. The latter taxon is found with values ranging from 3.7 to 44%. Radiocarbon dates and the pollen spectra found are consistent with high sedimentation rates, probably under a warm and humid climate. From 8910 to 6790 yr B.P. there is a pronounced decline of *Mauritia* (from 22.5 to 0.6%), Melastomataceae, and other forest taxa simultaneously with an increase in *Cuphea* (up to 26%) *Mimosa* (up to 10%) and in other caatinga taxa. Number of carbonized particles in zone SA2 is somewhat constant but low.

4.2.3. Zone SA 3 (6790–ca. 6230 yr B.P.)

Pollen poor zone. The few grains encountered were invariably deteriorated. The end date of this zone has an interpolated age.

4.2.4. Zone SA 4 (ca. 6230–ca. 4535 yr B.P.)

This zone is initially characterized by oscillating and alternating vegetational types as suggested by an increase in tropical forest taxa and a decline of caatinga and cerrado taxa marked by the decrease of *Cuphea* from 8 to 1%. The arboreal maximum in this zone is related to another significant increase in *Mauritia* pollen, reaching 63% of the pollen sum at 163 cm depth. This maximum is immediately followed by a progressive increase of caatinga and cerrado taxa and a drastic decline in *Mauritia* pollen to 2%, prior to 4240 yr B.P.

4.2.5. Zone SA 5 (ca. 4535 yr B.P.–Present)

Pollen spectra from 4240 yr B.P. to Present mark the onset of the present day climatic and vegetational patterns found in the studied region. This zone is initially characterized by the presence of pollen-poor sediments, at depths of 123.5, 113.5 and 98 cm. These levels alternate with pollen-rich layers indicating a progressive decline of *Mauritia*, *Mimosa* and stable percentages of *Cuphea* (5–10%). In the upper sediments of the record, *Cuphea* dominates the pollen spectra by reaching 45–50% of the pollen sums. Other taxa that make up the pollen spectra of the final phase of SA 7 are *Cassia*, *Ilex*, Melastomataceae, Myrtaceae, *Mimosa* and *Byrsonima*, clearly suggesting a pronounced tendency towards a caatinga and cerrado expansion at the expense of gallery forest. A significant increase of carbonized particles occurs in the sediments together with the increase in cerrado/caatinga taxa.

4.3. Thermoluminescence results and discussion

TL dates obtained for the sand dune sediments range from 28,000 to 900 yr B.P. (Barreto, 1996) are shown in Table 2. The results indicate discontinuous and intense eolian activity phases throughout the Holocene in localized areas of the sand dunefield system (Barreto, 1996). The remarkable decrease in dune activation from 10,500 to 9000 yr B.P. is in direct agreement with the pollen data, which sug-

Table 2
Thermoluminescence dating

Sample ID	Depth (cm)	Weathering level	Mean diam.	Text. classes (No.)	Fine sed. (%)	TL date (yr B.P.)	¹⁴ C (yr B.P.)
B-1	30–50	low	FS	4	1.18	1200	
B-5	30–50	low	FS	4	1.13	2200	
S-1	30–50	low	MS	3		2500	
S-2	30–50	low	FS	3		5000	
S-3	150	low	FS	5	1.98	27000	
S-4	30–50	low	FS	3		2800	
S-8	30–50	low	FS	5	1.23	2000	
S-10	30–50	low	FS	3	0.88	6200	
S-13	30–50	low	FS	4	1.28	2400	
S-14	30–50	low	MS	3	0.26	3700	
P-1	30–50	low	MS	3		2400	
P-2	30–50	moderate	MS	3		3400	
P-4	30–50	low	MS	4		5300	
P-5	30–50	low	MS	4		900	
P-9	30–50	moderate	FS	3		4000	
P-10	30–50	low	FS	3		1700	
P-11	30–50	moderate	FS	3	0.64	7700	
P-12	30–50	moderate	FS	3	0.48	11000	
P-14	30–50	low	FS	3	1	6600	
P-17	30–50	moderate	FS	34	1.39	3300	
P-18	30–50	moderate	FS	3	0.6	7500	
P-19	70–90	moderate	FS	3	0.5	2800	
P-23	30–50	moderate	FS	4		12000	
I-17	70–90	low	FS	3	0.07	1800	1600
I-18	80–90	low	FS	3	0.21	4000	
I-19	80–90	moderate	FS	4	0.39	4500	
I-20	80–90	moderate	FS	4	0.75	12000	
I21-0.5	50	low	FS	4	0.37	2900	
I21-1.5	150	low	FS			8200	3310
I21-3.0	300	low	FS			9000	
I-23	100	low	FS	3	0.96	3300	
I-24	200	low	FS			3600	
SAQ	340	peat	FS	3	0.1	10700	10990
SAQ	390	peat	FS			14400	
UMB	100	peat	FS			1900	2190
S-5	30–50	low	FS		0.28	7800	
S-7	30–50	low	FS	5	1.15	2700	
S-12	30–50	low	FS	4	0.37	1800	
B-7	30–50	low	FS	3	0.43	3300	
B-8	30–50	moderate	FS	3	0.68	28000	
B-15	30–50	low	FS	4	0.4	10500	
I-8	70–90	moderate	MS	4	1.34	6300	
I-14	80–90	moderate	FS	4	1.19	13900	

Size classes of sands shown on the mean diameter column of the sands were based on the classification of Shepard (1954) where FS = fine sand and MS = moderate size grains.

gests high moisture levels, and expansion of humid vegetation in the Icatu River Valley. The increase in dune activation registered by TL dating between 4500 and 1700 yr B.P. is also supported by pollen

analysis indicating expansion of semi-arid vegetation in the studied area. It is likely that the recent reduction in dune activation in the studied area is a consequence of dune stabilization by the closing

Table 3

List of identified pollen and spore taxa and their grouping according to vegetational types

<i>Acacia</i> — CA, CE, TF	<i>Humiria</i> — TF, MT
<i>Acalypha</i> — mostly TF; some in CE	<i>Ilex</i> — CE, TF, MT
Acanthaceae/ <i>Stendandrium</i> — CA	<i>Inga</i> — TF
<i>Alchornea</i> — TF	<i>Jatropha</i> — CA
<i>Alternanthera</i> — H — cosmopolitan	Lentibulariaceae — cosmopolitan
Anacardiaceae — CE, CA, TF	Loranthaceae — CA, CE, TF, MT
<i>Anacardium/Tapirira</i> — CE, TF	<i>Ludwigia</i> — H
Apocynaceae — CA, CE, TF	<i>Luehea</i> — TF, occasionally in CE
<i>Arrabidaea</i> — CA, CE	<i>Mabea</i> — CE, TF
<i>Astronium</i> — CE, TF	<i>Machaerium</i> — TF; occasionally in CE
Bignoniaceae — CA, CE, TF	<i>Macrocarpea</i> — TF
<i>Borreria</i> — H — cosmopolitan	Malvaceae — CA, CE, TF
<i>Bromelia</i> — CA, CE, TF	Melastomataceae — CA, CE, TF, MT
Bromeliaceae — CA	Mimosaceae — CA, CE, TF
<i>Byrsonima</i> — CA, CE	<i>Mimosa</i> — CA, CE, also TF in other biomes
Cactaceae — CA	Monolete psilate — H, CE, TF, MT
<i>Caryocar</i> — CA, CE, also TF in Amazonia, Atlantic Forest	Myrtaceae — CE, CA, TF, MT
<i>Cassia</i> — CA, CE, TF	<i>Neea</i> — CE
<i>Cavanillesia</i> — CA, CE	<i>Nymphaea</i> — H — cosmopolitan
<i>Cecropia</i> — mostly TF, some in CE	<i>Ouratea</i> — CA, CE
<i>Celtis</i> — TF	Palmae — TF, a few taxa occur in CE
<i>Cedrella</i> — TF	<i>Passiflora</i> — CA, CE, TF
<i>Cereus</i> — CA, CE	Piperaceae — TF
<i>Chamaesyce</i> — CA	<i>Plenckia</i> — TF
Clusiaceae/ <i>Calophyllum</i> — TF	<i>Polygala</i> — H — cosmopolitan
<i>Cnidocolus</i> — CA	<i>Pontederia</i> — H
<i>Combretum</i> — TF	<i>Pouteria</i> — TF
Compositae (Asteraceae) — HE	<i>Protium</i> — TF
<i>Copaifera</i> — CE, TF	<i>Pterocarpus/Sclerobium</i> — TF
<i>Cordia</i> — TF	<i>Rapanea (Myrsine)</i> — TF, MT
<i>Cordia curassavica</i> — CA	Rubiaceae — CA, TF, MT
<i>Crotalaria</i> — CE, TF	Rutaceae — TF
<i>Cuphea</i> — CA; also H in other biomes	Rutaceae/ <i>Eisenbeckia</i> — TF
<i>Curatella</i> — CE	<i>Sagittaria</i> — H
<i>Cyathea/Cyatheaceae</i> — MT	Sapindaceae — CA, CE, TF
<i>Dioclea</i> — TF	<i>Sapium</i> — CE, TF
<i>Drosera</i> — H	<i>Sebastiana</i> — CE
Ericaceae — MT	<i>Serjania</i> — TF
<i>Eriocaulon</i> — here CA; also in CE and H in mountains of northeastern Amazonia	<i>Simarouba</i> — TF
<i>Erythroxyllum</i> — CE	Solanaceae — CA, CE, TF
Euphorbiaceae — CA, CE, TF	<i>Stryphnodendron</i> — CE
Fabaceae — CA, CE, TF	<i>Symphonia</i> — TF
<i>Forsteronia</i> — TF	<i>Tabebuia</i> — CA, CE, TF, MF
<i>Gomphrena</i> — H, HE	<i>Trichillia</i> — TF
Gramineae (Poaceae) — H, HE	Umbelliferae — CA, CE, TF
<i>Hedyosmum</i> — MT	Urticaceae/Moraceae — mainly TF, also CE
<i>Hibiscus</i> — CE, TF	<i>Vellozia</i> — CE
<i>Hippocratea</i> — TF	Xyridaceae — CE
<i>Hymenaea</i> — TF; occasionally in CE	<i>Zanthoxylum</i> — TF
<i>Hyptis</i> — H, HE	<i>Zizyphus</i> — CA (<i>Z. joazeiro</i>); TF

CA = caatinga; CE = cerrado; TF = tropical forest; MT = montane tropical forest; H = aquatic herbs; HE = herbs, based on Jolly (1976), Croat (1978), Flenley (1979), Van der Hammen (1979), Schultz (1985), De Oliveira (1992), Gentry (1993), Colinvaux et al. (1996), Behling (1997), on botanical surveys by Radambrasil and on plant collections at the Field Museum of Natural History in Chicago and those at the New York Botanical Garden, New York, USA.

of the sandy terrain by the modern dense/arboreal caatinga vegetation.

5. Discussion

5.1. Climate and vegetation of the Late Pleistocene of the Icatu River Valley: testing of climatic and biogeographical hypotheses

5.1.1. Late Pleistocene cooling

The palynological profiles of the Icatu River peat sediments, representing the first palynological records available for the late Quaternary of a caatinga region in Brazil, suggest five main changes in vegetation and climate during the last 11,000 years. The final Pleistocene (10,990–ca. 10,000 yr B.P.) was characterized by climatic conditions which do not prevail in the present climate of the studied region. A significant increase in moisture levels and lowered temperatures allowed the expansion of a taxonomically rich tropical gallery forest within the Icatu River Valley. It is likely that montane pollen, found in the Icatu River Valley sediments during this period, came from the Serra do Estreito (860 m elevation) when temperatures were significantly lower than at present. A 5°C temperature depression during the Last Glacial Maximum was reported by Stute et al. (1995) after an extensive study of palaeoaquifers in northeastern Brazil. Widespread tropical 5°C cooling has also been reported for the Late Pleistocene of western Brazilian Amazonia (Colinvaux et al., 1996), the Amazon River delta (Behling, 1996), southeastern (De Oliveira, 1992) and southern Brazil (Behling, 1997). Palynological evidence from southeastern Brazil (Ledru, 1991, 1992; De Oliveira, 1992; Ledru et al., 1996) point to a more active role of the Atlantic Polar Front during the Late Glacial, bringing more rains and strongly reducing annual average temperatures in this region, thus favoring expansion of *Araucaria* forests in areas presently covered by cerrado vegetation. It is possible that the Late Pleistocene cooling of the Icatu River Valley region could have been associated with a northward displacement of this frontal system during the late Quaternary, but more records from the caatinga region will be necessary to test this hypothesis.

5.1.2. Former connection of Amazonian and Atlantic forests

This hypothesis was first suggested by floristic disjunctions revealed by studies of humid forests enclaves in high elevations within the semi-arid region of the caatinga phytogeographical domain by De Andrade-Lima (1966) and Rizzini (1967). The first author listed 388 Amazonian forest species and the second 277 genera which are shared between the two distinct modern phytogeographical regions. Some forest tree taxa, such as *Cedrela*, *Chrysophyllum*, *Hedyosmum*, *Humiria*, *Pouteria*, *Protium*, *Symphonia* and *Simarouba* are presently found in Amazonian and Atlantic rainforests, although *Symphonia* is a typical amazonian taxon. *Simarouba* and *Humiria* are more common in Amazonian forests (Radambrasil Project Members, 1976; Lorenzi, 1992). The presence of amazonian taxa in forest enclaves in northeastern Brazil was first noticed by Ducke (1953) and Ducke and Black (1954). Fig. 7 shows the hypothetical coastal route (route A) of migration of forest taxa, from the Atlantic Forest to Amazonia (and vice-versa).

The present palynological analysis strongly suggests that these taxa had already successfully migrated to the Icatu River valley by ca. 10,500 yr B.P. It is very likely that the migration of Amazonian taxa into the Atlantic forest, and vice-versa, could have taken place during various humid phases of the Pleistocene or even earlier. This migration was possibly facilitated by a former and much larger network of gallery forests that is likely to have existed in central Brazil (Oliveira-Filho and Ratter, 1995). Support for this hypothesis comes also from the work of Meave et al. (1991) which suggested that tropical gallery forests could have maintained a large part of the South American tropical forest biodiversity during adverse climatic conditions of the Pleistocene. Former expansion of tropical forest in the Icatu River Valley (10°50'S) is also supported by megafaunal studies conducted by Cartelle and Hartwig (1996) and Hartwig and Cartelle (1996) in a cave within the modern caatinga region, of Bahia, at 10°09'S latitude, roughly equivalent to that of the present studied area. Their discovery of a complete skeleton of a large-bodied *Protopithecus* primate of presumably Pleistocene age provided another source of data suggesting the former existence of tropi-

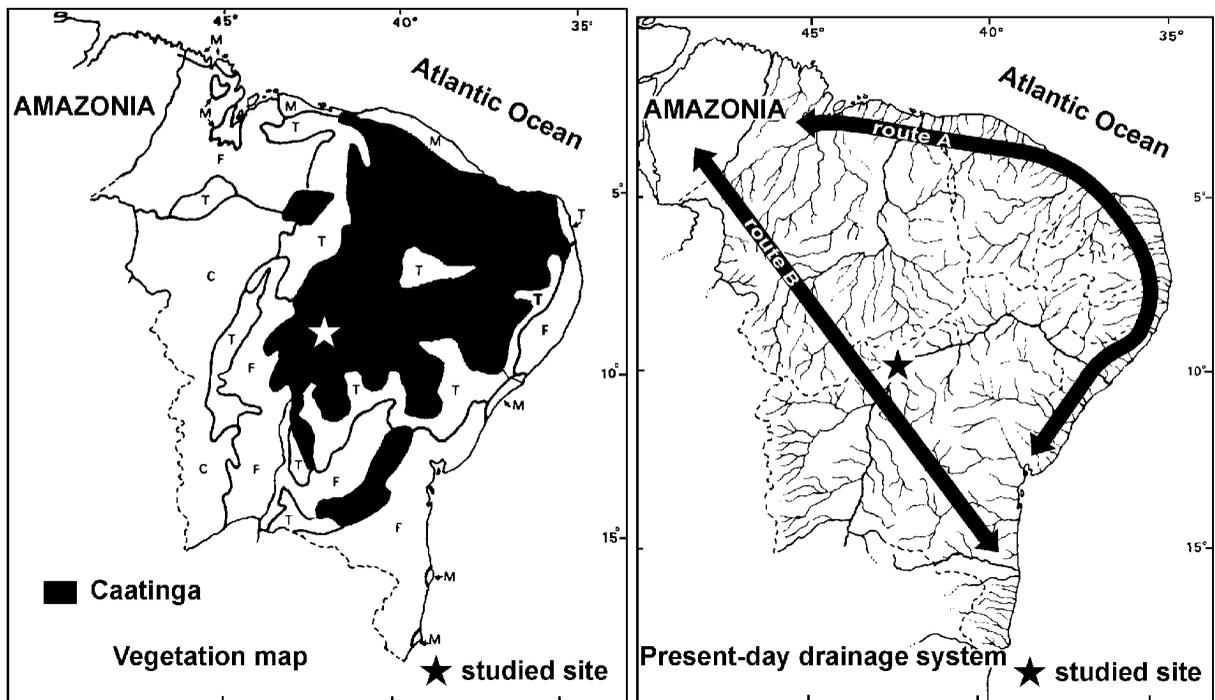


Fig. 7. Vegetation (left) and present-day drainage system maps of northeastern Brazil (right), showing possible migration routes for tropical forest taxa in the Quaternary. Modified from Coimbra-Filho and Câmara (1996). Route A is supported by botanical data (Ducke, 1953; Ducke and Black, 1954; De Andrade-Lima, 1966; Rizzini, 1967) whereas Route B is supported by the palynological record from the Icatu River Valley, botanical data from the Chapada da Diamantina and by paleontological data (Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996). The caatinga vegetation nuclear area is represented by the black area, other vegetation types are indicated by *F* = Atlantic Forest, *M* = coastal successional vegetation under marine/fluvial influence, *T* = transitional tropical forest (semi-deciduous), and *C* = cerrado.

cal forests in areas presently covered by caatinga vegetation (Cartelle and Hartwig, 1996). Since the onset of the Holocene, the climate of the Icatu River Valley has become progressively more arid. The modern day floristic pattern found at the Chapada da Diamantina, Bahia, a mountain chain reaching 10°S latitude within the caatinga domain in Bahia (Stanard, 1995) supports this hypothesis. Additional support comes also from the rare disjunct occurrence of high elevation Atlantic rainforest taxa such as *Podocarpus lambertii*, *Podocarpus sellowii*, *Drimys brasiliensis*, *Hedyosmum brasiliense*, *Ilex theezans*, *Ilex paraguariensis* (Andrade and Lamberti, 1965; Jolly, 1976; Schultz, 1985; Lorenzi, 1992) on the inselberg tops of semi-arid Bahia reported by De Andrade-Lima (1966, 1982) and by various herbarium collections (Field Museum and New York Botanical Garden). Therefore, the present botanical data

unequivocally support the former existence of a forest corridor into this phytogeographical province. Route B, in Fig. 7, indicates a hypothesized continental route of migration from and to Amazonia, of rain forest taxa, which is supported by the palynological record of the Icatu River Valley, botanical and palaeontological data.

5.2. Climatic and vegetational changes during the Holocene

Tropical forest taxa are well represented throughout the Holocene of the studied area. During the early Holocene the Icatu River Valley landscape was especially dominated by gallery forest taxa from 10,060 to 6790 yr B.P., which correlates in part with the time of occurrence of gallery forest at Lago do Pires (17°S) in northeastern portion of the State of

Minas Gerais, Brazil from 8810 to 7500 yr B.P. (Behling, 1995). From 8910 to 6790 yr B.P. the pollen spectra are characterized by tropical forest taxa, although there is a progressive tendency towards more arid conditions, which appear to reach a climax between 6790 and 6230 yr B.P. This arid phase appears to be synchronous with a similar dry interval in central Brazil. The disappearance of *Mauritia vinifera* from the pollen profiles and henceforth from the landscape at Cromínia, State of Goiás (Ferraz-Vicentini, 1994; Salgado-Labouriau et al., 1996) and Águas Emendadas in Brasília between 7500 and 7000 yr B.P. (Barberi-Ribeiro, 1994) has been attributed to a marked reduction in precipitation levels in central Brazil. The absence of preserved pollen grains from 6790 yr B.P. and the extrapolated date of 6230 yr B.P. at the Icatu Valley could be explained by the occurrence of former drier climates and/or oxidizing conditions of the sediments. This scenario is supported by the climatic evidence provided by the Lagoa do Pires record where a return to a drier climate and increased fire frequencies were reported from 7500 and 5530 yr B.P. (Behling, 1995).

From ca. 6230 to ca. 4240 yr B.P., the vegetation and the climate of the studied area were characterized by various oscillations in the abundance of taxa belonging to different plant formations. One of such climatic oscillation is represented by an increase of *Mauritia* pollen at 163.5 cm depth (ca. 4886 yr B.P.) suggesting a short-lived return to moist climate. This pattern, however, changed immediately after 4240 yr B.P., when caatinga and cerrado pollen become persistently more abundant in the diagrams.

5.3. Middle Holocene climatic asymmetry between the fossil dunefield system of the middle São Francisco river and southeastern/central Brazil

From 11,000 to ca. 5000 yr B.P., the palaeoclimatic interpretations derived from the palynological history of the Icatu River Valley are supported by palaeoecological records from southeastern (Ledru, 1991, 1992; De Oliveira, 1992; Ledru et al., 1996), and central Brazil (Ferraz-Vicentini, 1994; Barberi-Ribeiro, 1994; Salgado-Labouriau et al., 1996). However, after 4000 yr B.P. climatic trends begin to differ in these regions. For example, at Lagoa dos Olhos (19°38'S; De Oliveira, 1992) and at adjacent

Lagoa Santa (Parizzi, 1994), the period after 4000 yr B.P. is characterized by high lake levels. At Serra Negra and Salitre (18°00'–19°00'S), in southeastern Brazil, a moist climate is recorded from 5000 to 4000 yr B.P. (Ledru, 1991; De Oliveira, 1992; Ledru et al., 1996). In central Brazil, *Mauritia* palm forests, indicative of present day (semi-humid) climate, are found in the pollen records from Cromínia (Ferraz-Vicentini, 1994; Salgado-Labouriau et al., 1996) and from Águas Emendadas (Barberi-Ribeiro, 1994) from 7500 yr B.P. onwards. Therefore, as the climate of southeastern and central Brazil became moist, the climate in the caatinga region of the middle Rio São Francisco started a trend towards aridity after 4000 yr B.P. This late Holocene arid interval is supported by the palynological evidence, i.e., a significant increase in pollen percentage and concentration values of caatinga and cerrado plants on its landscape. This mid-Holocene climatic scenario is supported by a total of 22 thermoluminescence samples of eolian dune sands, which yielded dates ranging from 4000 to 1000 yr B.P., thus suggesting a significant increase in reworking of sands in wind-activated dunes, under a semi-arid climate, during that time interval (Barreto, 1996).

5.4. El Niño-like events and displacement of the intertropical convergence zone

Only in some years, the present day climate of the São Francisco River sand dunefields is directly affected by the Polar Frontal System. Its climate is more affected by the South Atlantic Anticyclone and the yearly southward migration of the Intertropical Convergence Zone (Nimer, 1977; Nimer, 1989). However, during El Niño-like climatic phenomena, the Atlantic Polar Front incursion into the South American continent is blocked at the 25°00'S latitude (Kousky et al., 1984). This blockage of cooler polar air triggers an increase in precipitation in southern and southeastern Brazil. Because the polar frontal system becomes stationary in the south, a decrease in precipitation levels, brought about by a reduction of frontal rains, occurs in northern and northeastern (El Niño Southern Oscillation) Brazil (Kousky et al., 1984). Although former ENSO signals are not easily detected in palaeoclimatic studies, late Holocene dry episodes attributed to ENSO-like conditions were re-

ported at Carajás, eastern Brazilian Amazonia, the Rio Doce Delta and the Brazilian coast (Absy et al., 1991; Martin and Suguio, 1992; Martin et al., 1993). An El Niño-related drying phase, reported at Carajás between 7500 and 3000 yr B.P., is simultaneous with maximum drying in the Icatu River Valley (6790–ca. 6000 yr B.P.). However, the greatest expansion of caatinga on the sand dune fields (4200 yr B.P.–Present) and dune activation (4000–1700 yr B.P.) are not synchronous with the Carajás record, but with two ENSO-like events (1300 and 2300 yr B.P.), reported for the late Holocene of the Rio Doce Valley (Martin and Suguio, 1992). An alternative hypotheses for increased late Holocene aridity in the sand dune fields region especially from 8910 to 6230 yr B.P. and from 4240 yr B.P. to Present, invokes a northward displacement of the ITCZ climatic system. Palaeoclimatic records from the Caribbean region support a northward displacement of the ITCZ, especially from 8200 to 2500 yr B.P., when high lake levels and moister climates prevailed at Lake Miragoane in Haiti (Curtis and Hodell, 1993). Palaeoecological records from Lake La Yeguada in central Panama (8°27'N, 80°51'W) suggest warm climate and rising lake levels prevailing from ca. 6500 to 2000 yr B.P. (Bush et al., 1992). Wet conditions also prevailed in the Yucatan peninsula between 7100 and 3100 yr B.P. and from 3310 to 1785 yr B.P. (Hodell et al., 1991, 1995). More studies in semi-arid northeastern Brazil are required for a more thoroughly understanding as well as testing of this opposing climatic pattern between this region and southeastern/central Brazil during the Holocene, as well as the role of ENSO events and the suggested Holocene northward displacement of the ITCZ.

6. Conclusions

The following conclusions on the vegetational and climatic history of the Icatu River Valley can be drawn based on the palynological records:

(1) Five distinct vegetational and climatic changes have been reported during the last 11,000 yr at the studied site.

(2) The Late Pleistocene climate of the presently semi-arid São Francisco River sand dune fields was

more humid than present, favoring the occurrence of gallery forests within the Icatu River Valley.

(3) Some of the forest tree taxa of the Icatu River Valley Late Pleistocene forests are presently restricted to Amazonian and Atlantic rainforests of Brazil, thus providing direct evidence for past connections between the Amazonian and Atlantic forest realms. Such conclusion is supported by Late Pleistocene megafaunal primate remains found within the caatinga region of Bahia, at the same latitude of the studied site and by botanical data on disjunct forest elements on the Chapada Diamantina.

(4) Caatinga vegetation taxa, although not abundant, always occurred on the Icatu River Valley landscape during the Holocene. The present climatic and vegetational patterns of the studied area were only established after 4240 yr B.P. Dune activation suggested by TL studies and fire frequencies inferred from charcoal fragments, were greatly increased after 4240 yr B.P.

(5) The palaeoclimatic results of the studied area are in agreement with the Late Pleistocene to mid-Holocene palaeoecological and palaeoclimatic records from southeastern and central Brazil. An opposing climatic pattern of that found for southern and central Brazil, characterizes the climate of the studied region after ca. 5000 yr B.P. This opposing climatic signal is possibly related to increased ENSO-like phenomena, coupled or not to a northward displacement of the Intertropical Convergence Zone.

Acknowledgements

The authors thank Dr. Peter Crane and the staff of the Herbarium of the Field Museum of Natural History in Chicago, USA and Dr. Douglas Daly, The New York Botanical Garden, for access to their plant collections during the development of this research. Thanks are also due to Dr. Paul Colinvaux, Woods Hole Marine Biology Laboratory for supporting the laboratory phase of this research through NSF grant ATM-9528280. De Oliveira was supported in Brazil by CNPq visiting professor's scholarship (Processo 300526/95-4 NV). Field work was financed by FAPESP, The State of São Paulo Research Foundation, through a grant to Dr. Kenitiro Suguio and Dr.

Alcina M.F. Barreto. We also thank Dr. Vera Markgraf, INSTAAR, University of Colorado, USA, and Dr. Marie Pierre Ledru, ORSTOM Bondy, France, for reviewing the manuscript and providing the authors with important comments and suggestions. An unknown reviewer has provided the authors with very useful suggestions which improved the overall quality of the manuscript.

References

- Absy, M.L., Cleef, A., Fournier, M., Martin, L., Servant, M., Sifeddine, A., Ferreira da Silva, M., Soubies, F., Suguio, K., Turcq, B., Van der Hammen, T., 1991. Misé en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de l'Amazonie au cours des 60000 dernières années. Première comparaison avec d'autres régions tropicales. C. R. Acad. Sci. Paris Sér. II 312, 673–678.
- Andrade, M.A.B., Lambert, A., 1965. A Vegetação. In: Azevedo, A. (Ed.), A Baixada Santista—Aspectos Geográficos, Vol. I. Univ. de São Paulo, pp. 151–179.
- Barberi-Ribeiro, M., 1994. Paleovegetação e Paleoclima no Quaternário Tardio da Vereda de Águas Emendadas, DF. MS. Thesis, Univ. Brasília.
- Barreto, A.M.F., 1996. Interpretação Paleoambiental do Sistema de Dunas Fixas do Médio Rio São Francisco, Bahia. Ph.D. Thesis, Univ. São Paulo, São Paulo.
- Barreto, A.M.F., Tatum, S.H., Suguio, K., Nagatomo, T., Watanabe, S., 1997. O Quaternário Tardio no Sistema de Dunas Fixadas do Médio Rio São Francisco (Bahia) datado pelo Método da Termoluminescência. VI Congresso da Associação de Estudos do Quaternário e Reunião sobre o Quaternário da América do Sul, Universidade Federal do Paraná, Curitiba, Expanded Abstract Vol., pp. 171–175.
- Behling, H., 1995. A high resolution Holocene pollen record from Lago do Pires, SE Brazil: vegetation, climate and fire history. J. Paleolimnol. 14, 253–268.
- Behling, H., 1996. First report on new evidence for the occurrence of *Podocarpus* and possible human presence at the mouth of the Amazon during the Late-glacial. Veg. Hist. Archaeol. 5, 241–246.
- Behling, H., 1997. Late Quaternary vegetation, climate and fire history of the *Araucaria* forest and campos region from Serra Campos Gerais Paraná State (South Brazil). Rev. Palaeobot. Palynol. 97, 109–121.
- Berglund, B.E., 1986. Pollen analysis and pollen diagrams. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology, pp. 455–484.
- Bush, M., Piperno, D.R., Colinvaux, P., De Oliveira, P.E., Krisek, L., Miller, M.C., Rowe, W.E., 1992. A 14,300-yr paleoecological profile of a lowland lake in Panama. Ecol. Monogr. 62 (2), 251–275.
- Cartelle, C., Hartwig, W.C., 1996. Macacos sul-americanos: os-
 sos que são um verdadeiro tesouro. Ciênc. Hoje 21 (125), 31–36.
- Coimbra-Filho, A.F., Câmara, I.G., 1996. Os Limites Originais do Bioma Mata Atlântica na Região Nordeste do Brasil. Fundação Brasileira para a Conservação da Natureza-FBCN, 86 pp.
- Colinvaux, P.A., 1993. Ecology, 2. Wiley, 688 pp.
- Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from Lowland Amazonia: forest and cooling in glacial times. Science 274, 85–88.
- Croat, T., 1978. Flora of Barro Colorado. Stanford Univ. Press, 943 pp.
- Curtis, J., Hodell, D.A., 1993. An isotopic and trace element study of ostracods from lake Miragoane, Haiti: A 10,500 year record of paleosalinity and paleotemperature changes in the Caribbean. Climate change in continental isotopic records. Geophys. Monogr. 78, 135–152.
- De Andrade-Lima, D., 1966. Contribuição ao estudo do paralelismo da flora amazônica-nordestina. Inst. Agr. Pernambuco. N. S. Bol. Téc. 19, 3–30.
- De Andrade-Lima, D., 1982. Dry forest refuges in neotropical Brazil. In: Prance, G.T. (Ed.), Biological Diversification in the Tropics. Columbia Univ. Press, New York, NY, pp. 245–251.
- De Oliveira, P.E., 1992. A palynological record of late Quaternary vegetational and climatic change in southeastern Brazil. Ph.D. Thesis, Ohio State Univ., Columbus, OH.
- Ducke, A., 1953. As leguminosas de Pernambuco e Paraíba. Mem. Inst. Oswaldo Cruz 51 (4), 417–461.
- Ducke, A., Black, G.A., 1954. Notas sobre a fitogeografia da Amazônia Brasileira. Bol. Tecn. Inst. Agron. Norte 29, 3–62.
- Fægri, K., Iversen, J., 1989. A Textbook of Pollen Analysis, 4 ed. Wiley, New York, NY.
- Ferraz-Vicentini, K.R., 1994. Análise Palinológica de uma Vereda em Cromínia, GO. MS. Thesis, Univ. Brasília.
- Flenley, J., 1979. The Equatorial Rain Forest: A Geological History. Butterworths, London, Boston, 162 pp.
- Gentry, A., 1993. A field guide to the families and genera of woody plants of northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa. Conservation International, Washington, DC, 895 pp.
- Grimm, E.C., 1987. CONISS: A Fortran 77 program for stratigraphically constrained cluster analysis by the method of the incremental sum of squares. Pergamon J. 13, 13–35.
- Hartwig, W.C., Cartelle, C., 1996. A complete skeleton of the giant South American primate *Protopithecus*. Nature 381, 307–311.
- Hodell, D.A., Curtis, J.H., Jones, G.A., Higuera-Gundy, A., Brenner, M., Bindford, M.W., Dorsey, K.T., 1991. Reconstruction of Caribbean climate change over the past 10,500 years. Nature 352, 790–793.
- Hodell, D.A., Curtis, J.H., Brenner, M., 1995. Possible role of climate in the collapse of Classic Maya civilization. Nature 375, 391–394.
- Ichikawa, Y., 1965. Dating of ancient ceramics by thermoluminescence. Bull. Inst. Chem. Res. 43, 1–6.

- Jolly, A.B., 1976. Botânica: introdução à taxonomia vegetal. Companhia Editora Nacional, 777 pp.
- Kousky, V.E., Kagano, M.T., Cavalcanti, I.F.A., 1984. A review of the Southern Oscillation: oceanic-atmospheric circulation changes and related rainfall anomalies. *Tellus* 36A, 490–504.
- Kuhlmann, E., 1977. A Vegetação. In: *Geografia do Brasil-Região Nordeste*. Vol. 2. IBGE, Rio de Janeiro, pp. 85–110.
- Ledru, M.P., 1991. Etude de la pluie pollinique actuelle des forêts du Brésil central: climat, végétation, application à l'étude de l'évolution paléoclimatique des 30.000 dernières années. Ph.D. Thesis, Museum of Natural History, Paris.
- Ledru, M.P., 1992. Late Quaternary Environmental Changes in Central Brazil. *Quat. Res.* 39, 90–98.
- Ledru, M.P., Braga, P.I.S., Soubiès, F., Fournier, M., Martin, L., Suguio, K., Turcq, B., 1996. The last 50,000 years in the Neotropics (Southern Brazil): evolution of vegetation and climate. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 123, 239–257.
- Liu, K.-B., Colinvaux, P.A., 1988. A 5200-year history of Amazon Rain Forest. *J. Biogeogr.* 15, 231–248.
- Lorenzi, H., 1992. Árvores Brasileiras. Manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Plantarum, Nova Odessa, SP.
- Martin, L., Suguio, K., 1992. Variation of coastal dynamics during the last 7,000 years recorded in beach-ridge plains associated with river mouths: example from the central Brazilian coast. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 99, 119–160.
- Martin, L., Fournier, M., Mourguiart, P., Sifeddine, A., Turcq, B., Absy, M.L., Flexor, J.-M., 1993. Southern oscillation signal in South American paleoclimatic data of the last 7000 years. *Quat. Res.* 39, 338–346.
- Meave, J., Kellman, M., MacDougall, A., Rosales, J., 1991. Riparian habitats as tropical refugia. *Global Ecol. Biogeogr. Lett.* 1, 69–76.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*. Blackwell, Oxford, 216 pp.
- Nimer, E., 1977. Clima. In: *Geografia do Brasil — Região Nordeste*. Vol 2. IBGE, Rio de Janeiro.
- Nimer, E., 1989. *Climatologia do Brasil*. IBGE, Rio de Janeiro, 421 pp.
- Oliveira-Filho, A.T., Ratter, J.A., 1995. A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. *Edinburgh J. Bot.* 52 (2), 195–203.
- Parizzi, M.G., 1994. A gênese e a dinâmica da Lagoa Santa com base em estudos palinológicos, geomorfológicos e biológicos de sua bacia. MS. Diss., Univ. Federal de Minas Gerais, 55 pp.
- Prószyńska, H., Stanska, P.W., Prószyński, M., 1985. Thermoluminescence dating of partially bleached sediments by the regeneration method. *Quat. Sci. Rev.* 7, 265–271.
- Radambrazil Project Members, 1976. Folha NA., 19. Pico da Neblina. Vol. 11. Departamento Nacional de Produção Mineral, 374 pp.
- Rizzini, C.T., 1967. Delimitação, caracterização e relações da flora silvestre hileiana. *Atlas Simp. Biota Amazônica* 4 (Botânica), pp. 13–36.
- Salgado-Labouriau, M.L., Vicentini, K.R.F., Barberi, M., Parizzi, M.G., 1996. A dry climatic event during the Late Quaternary of Tropical Brazil. IX Int. Palynol. Congr., Houston, TX (abstract).
- Schultz, A., 1985. *Introdução à Botânica Sistemática*. Univ. Fed. Rio G. Sul., NBS, Vol. I, 414 pp., Vol. II, 295 pp.
- Shepard, F.P., 1954. Nomenclature based on sand-silt-clay ratios. *J. Sediment. Petrol.* 24 (3), 151–158.
- Stannard, B.L. (Ed.), 1995. *Flora of the Pico das Almas-Chapada Diamantina — Bahia, Brazil*. Royal Botanic Gardens, Kew, 853 pp.
- Steyermark, J.A., 1979. Plant refuge and dispersal centres in Venezuela: their relict and endemic element. In: Larsen, K., Holm-Nielsen, L.B. (Eds.), *Tropical Botany*. Academic Press, London, pp. 185–221.
- Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13, 615–621.
- Stute, M., Forster, M., Frischkorn, H., Serejo, A., Clark, J.F., Schlosser, P., Broecker, W.S., Bonani, G., 1995. Cooling of Tropical Brazil (5°C) during the last Glacial Maximum. *Science* 269, 379–383.
- Van der Hammen, T., 1979. History of flora, vegetation and climate in the Colombian Cordillera Oriental during the last five million years. In: Larsen, K., Holm-Nielsen, L.B. (Eds.), *Tropical Botany*. Academic Press, London, pp. 25–32.
- Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C.A., 1991. *Classificação da Vegetação Brasileira, adaptada a um Sistema Universal*. IBGE, Rio de Janeiro, 123 pp.
- Williams, H.E., 1925. Notas geológicas e econômicas sobre o Vale do Rio São Francisco. *Bol. Serv. Geol. Mineral.* 12, 56 pp.