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Plant succession in a forest on the Lower Northeast Slope of Serra Geral, Rio Grande do Sul, and Holocene palaeoenvironments, Southern Brazil

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RESUMO – (Sucessão vegetal em uma floresta da Encosta Inferior do Nordeste da Serra Geral, Rio Grande do Sul, e os paleoambientes do Holoceno, Sul do Brasil). O estudo de sucessão vegetal permite obter informações sobre a dinâmica da vegetação de uma região e, portanto, compreender melhor os ecossistemas da atualidade e suas tendências naturais. Com este objetivo foi feito um estudo de sucessão vegetal, com base em Palinologia, em um perfil sedimentar do interior de uma floresta paludosa, porção baixa da Encosta Inferior do Nordeste da Serra Geral, Rio Grande do Sul. As amostras foram tratadas com HCl, HF, KOH e acetólise e as lâminas montadas em gelatina-glicerinada. Para cada amostra foi contado um número mínimo de 500 grãos de pólen + esporos de pteridófitos e briófitos, com uma contagem paralela dos demais palinomorfos. Os programas Tilia e Tilia Graph foram usados na confecção dos diagramas de porcentagem e concentração. Foram obtidas três datações por ^{14}C. Os resultados apontam um corpo lacustre no começo do Holoceno (± 9.800 anos AP), que dá origem a um pântano herbáceo por hidrossere. O início da primeira colonização do pântano por plantas arbóreas parece ter ocorrido há cerca de 8.800 anos AP, com a contribuição de espécies tropicais da Planície Costeira, através de uma migração leste-oeste. Segue uma fase seca, entre 7.000-5.000 anos AP, caracterizada por indicadores de campo seco. O segundo desenvolvimento florestal inicia há cerca de 5.000 anos AP, resultando na atual mata e na migração oeste-leste de espécies tropicais dos terrenos baixos mais interiorizados, como este, para a re-colonização da Planície Costeira, após a última regressão marinha.

Palavras-chave: Palinologia, paleoecologia, migração de plantas, Quaternário, América do Sul

ABSTRACT – (Plant succession in a forest on the Lower Northeast Slope of Serra Geral, Rio Grande do Sul, and Holocene palaeoenvironments, Southern Brazil). The study of plant succession provides information on vegetation dynamics of a region and, therefore, improves our understanding of the natural trends of present ecosystems. With this objective, plant succession based on palynology of a sediment profile in a swamp forest was studied on the Lower Northeast Slope of Serra Geral, Rio Grande do Sul. Samples were treated with HCl, HF, KOH and acetolysis; slides were mounted in glycerol-jelly. For each sample a minimum of 500 grains of pollen + pteridophyte and bryophyte spores was counted and other palynomorphs were counted in parallel. Tilia and Tilia Graph software were used to construct percentage and concentration diagrams, with three ^{14}C datings. The results show a local water reservoir in the beginning of the Holocene (± 9800 yrs. BP), creating a herbaceous plant marsh by hydrosere. The initial colonization of the marsh by trees occurred about 8800 yrs. BP, with tropical species from the Coastal Plain migrating in an east-west direction. Afterwards, there was a dry phase between 7000-5000 yrs. BP. The second appearance of regional tree species began at about 5000 yrs. BP, resulting in the present forest and in the west-east migration of tropical species from interior lowlands, like this one, to re-colonize the coast after the last marine regression.

Key words: Palynology, palaeoecology, plant migration, Quaternary, South America

Introduction

In Rio Grande do Sul, an analysis of the present flora shows migratory routes of the Atlantic rain forest *stricto sensu* (Mata Atlântica), probably through Torres Municipality, migrating to the south along the Coastal Plain and to the west over lowlands of the Central Depression and the lower northeastern slopes of the Serra Geral (Rambo 1950). This east-west migration is evidenced by the existence today of typical species from this tropical forest in regions near the coast, gradually decreasing in number towards the west (Baptista 1967; Budke *et al.* 2004). However, the historical processes involved in this migration and their chronology are not studied by current flora analysis.

The Rio Grande do Sul Coastal Plain and adjacent lowlands are also being studied by sediment palynology, focusing on vegetation and climate history, especially

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of the last 10000 years. These studies have contributed to a better understanding of the dynamics of this vegetation over time (Cordeiro & Lorscheitter 1994; Grala & Lorscheitter 2001; Lorscheitter 1997; 2003; Lorscheitter & Dillenburg 1998; Neves & Lorscheitter 1995; 1997; Prieto *et al.* 1999). A synthesis of these studies (Lorscheitter 2003) indicates the presence of Atlantic rain forest (*stricto sensu*) components dispersed along the Coastal Plain at the beginning of the Holocene (10000-8000 yrs. BP), the negative influence of Holocene marine transgression on coastal vegetation (8000-4000 yrs. BP) and the important role of plants from the adjacent lowlands in the re-colonization of the coast, after the last marine regression (4000-2000 yrs. BP). The site farthest inland reached by these studies is located in Guaíba Municipality, in the Rio Grande do Sul Central Depression (30º11'21"S - 51º22'47"W). Information on lowlands farther inland, like those at the base of Serra Geral slopes, is still lacking.

This paper aims to obtain data on the vegetation and climate of the last millennia on the Lower Northeast Slope of Serra Geral, Rio Grande do Sul, between the Taquari and Caí rivers. This will complement palynological studies from the lowlands, starting on the Coastal Plain. Plant succession was studied using palynology of a sediment profile in a swamp forest in Serra Velha, Brochier Municipality (29º36'22"S - 51º38'55"W, Fig. 1). The results were compared to the events of the same age already detected for the Coastal Plain and the Central Depression. Preliminary information on the Serra Velha study was presented by Grala & Lorscheitter (2001).

The forest – The swamp semi-deciduous forest is located at an altitude of 50 m with a subtropical regional climate, mean annual temperature over 18 ºC and annual rainfall between 1500 and 1700 mm (Moreno 1961).

It is composed of species that are widespread in Rio Grande do Sul, as well as species from the rain forest of the Paraná-Uruguai River Basin, such as *Trichilia claussenii* C. DC, and of Atlantic tropical east-west migratory species such as *Faramea marginata* Cham, *Mollinedia elegans* Tul, and *Piper corcovadensis* (Miq.) C. DC. It is also possible to find species from Central Brazil, such as *Erythrina crista-galli* L., *Calliandra tweediei* Benth and flora that has migrated from the Rio Grande do Sul northwest region, such as *Salix humboldtiana* Willd (Rambo 1954). Many epiphytes, mainly Bromeliaceae and Orchidaceae, occur inside the forest. Pteridophytes such as *Blechnum brasiliense* Desv., *Pleopeltis angusta* Humb. & Bonpl. ex Willd., *Polypodium polypodioides* (L.) Watt and *Niphidium rufosquamatum* Lellinger are also abundant. A thick layer of decomposed leaves covers the forest floor. Agricultural activities surround this forest.

Material and methods

The 512-centimeters-deep sedimentary profile was collected in the forest with a Hiller Sampler, from which the 40 samples for palynological analysis were taken (at intervals of ca. 10 cm). The standard chemical treatment was performed (Faegri & Iversen 1989), adding *Lycopodium clavatum* tablets (Stockmarr

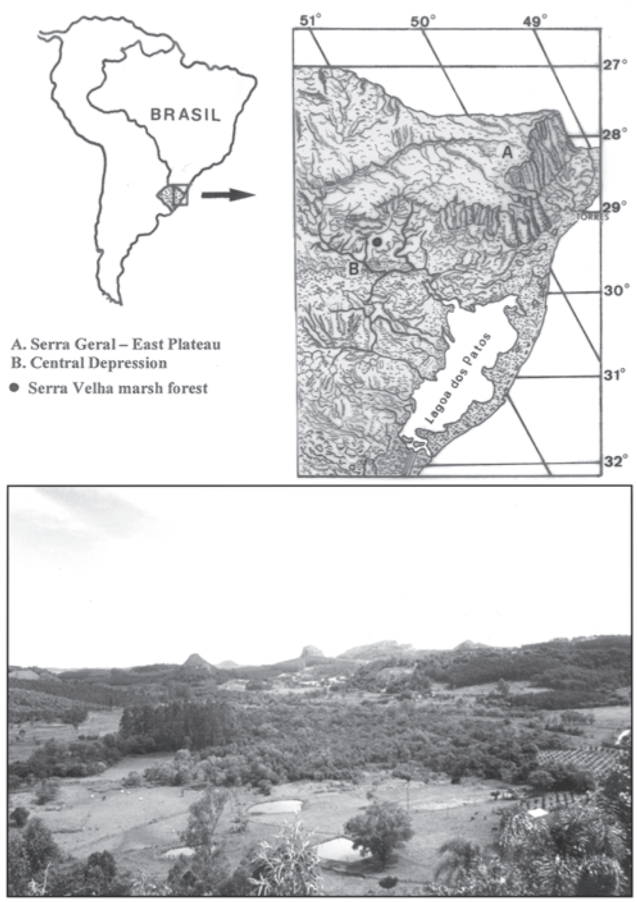

Figure 1. Above: Rio Grande do Sul and the Northeast relief, with the location of the swamp forest of Serra Velha, Brochier Municipality (on left Taquari River, on right Caí River). Below: overall view of the region, showing the swamp forest and sandstone elevations in the background.

1971) to calculate palynomorph concentration/cm^3 of fresh sediment and using HCl, HF, KOH and acetolysis, as well as filtering through a 250 µm net. The slides were mounted in glycerol-jelly. Botanical identification of the grains was based on the Palynology Laboratory reference collection (Botany Department, Federal University of Rio Grande do Sul). Unidentified grains were classified by morphology. The word "type" was used when a precise identification was impossible. A minimum number of 500 pollen grains + pteridophyte and bryophyte spores and 100 previously added *Lycopodium clavatum* exotic spores (for concentration analysis) were counted for each sample, leaving out other palynomorphs, which were counted in parallel. Counting sufficiency was monitored by saturation curves.

Tilia and Tilia Graph software were used to construct the diagrams. Cluster analysis was performed by CONISS (Grimm 1987).

Focusing on palaeoenvironment study, all the counted palynomorphs were grouped as in Tab. 1 (grassland - field, forest, water reservoir, herbaceous plant marsh, indeterminate environment and fungi) and included in the analysis. For angiosperms, gymnosperms, pteridophytes and bryophytes, the percentage of each taxon was calculated using the total of these four groups. For the other palynomorphs, the percentage of each taxon was calculated using the total of the four groups + the group in question. Grassland (field), forest, water reservoir, herbaceous plant marsh and fungi indicators were included in the diagrams. The group of indeterminate environment grains, although included in the frequencies, does not appear in diagrams. Composite diagrams, with total percentage of the forest × grassland (field) indicators and the forest × herbaceous plant marsh indicators were also presented. The cluster analysis is showed in percentage diagrams. The concentration diagrams included only taxa with a minimum of 5000 grains/cm^3 of fresh sediment in at least one sample of sedimentary profile. In percentage and concentration diagrams the sum of a group includes all their components. The diagrams of fungi show only the main components. Profile lithology is included in the analysis. Three ^{14}C

Table 1. Palynomorphs found in the sedimentary profile counts of Serra Velha swamp forest, Brochier Municipality, Rio Grande do Sul, Brazil.

Groups	Pollen, spores and other palynomorphs
Grassland (Field)	*Alternanthera* Forssk., *Amaranthus* L.- Chenopodiaceae type, *Baccharis* L. type, Caryophyllaceae, *Cuphea carunculata* Koehne, *Ephedra tweediana* Fisch. & C.A. Mey., *Galianthe angustifolia* (Cham. & Schltdl.) E.L. Cabral, *Gnaphalium* L. type, *Gomphrena* L., *Plantago* L., Poaceae, *Polygala* L., *Valeriana eichleriana* (C. Muell.) Graebn., *Verbena* L., *Vernonia* Schreb. type.
Forest	*Acacia* Mill., *Acacia* Mill. type, *Adiantopsis* Fee type, *Alchornea triplinervia* (Spreng.) Müll, Arg., *Allophylus edulis* (St. Hill.) Radlk. ex Warm., Anacardiaceae, *Anemia* Sw., *Anemia phyllitidis* (L.) Sw., *Asplenium* L., *Cecropia* Loefl., *Celtis* L. type, *Chrysophyllum* L. type, Cyatheaceae, *Daphnopsis racemosa* Griseb., *Dicksonia sellowiana* Hook., *Dryopteris* Adans. type, *Erythrina* L. type, *Ilex* L., *Marattia* laevis Smith, Meliaceae type, *Microgramma vacciniifolia* (Langsd. & Fisch.) Copel. type, *Myrsine* L., Myrtaceae, *Paraptadenia rigida* (Benth.) Brenan, *Phrygilanthus* Eichler., *Polypodium* L. type, *Pteris*, *Roupala* Aubl. type, Sapindaceae, *Syagrus* Mart. type, *Trema micrantha* (L.) Blume, Urticales.
Water reservoir	Alismataceae, *Debarya* (De Bary) Wittrock, *Isoetes* L., *Mougeotia* C.A. Agardh, *Pseudoschizea rubina* Rossignol ex Christopher, *Regnellidium diphyllum* Lindm., *Spirogyra* Link, *Zygnema* C.A. Agardh.
Herbaceous plant marsh	*Anthoceros* L. Emend. Prosk. 1, *Anthoceros* L. Emend. Prosk. 2, *Blechnum* L. type, Cyperaceae, Eriocaulaceae, *Eryngium* L., Hepaticae type, *Osmunda* L., *Phaeoceros laevis* (L.) Prosk., *Riccia* (Mich.) L. type, *Selaginella marginata* (Humb. & Bonpl. ex Willd.) Spring., *Sphagnum* (Dill.) Hedwig, *Typha* L.
Indeterminateenvironments	Hepaticae type, Lamiaceae, Liliaceae type, Malpighiaceae, Malvaceae, Melastomataceae, *Mimosa* L. 1, *Mimosa* L. 2, *Mimosa* L. série Lepidotae, Monolete 1, Monolete 2, Other bryophytes, Other pteridophytes, Other monoletes, Other triletes, Other tricolporates, Pantoporates, *Polygonum* L., *Relbunium* (Endl.) Hock. F. type, Rosaceae type, Rubiaceae, Scrophulariaceae type, Stephanoporates, Tetracolpates, Tetracolporates, Tricolpates, Tricolporate 1, Tricolporate 2, Triporates, *Valeriana* L., *Vicia* L. type.
Fungi	*Athelia* Pers. type, *Gaeumannomyces caricis* J. Walker type, *Gelasinospora adjuncta* Cain, *Gelasinospora* cf. *reticulispora* (Greis & Greiss-Dengler) C. & M. Moreau, *Glomus* Tus. & C. Tus., Hyphae, Indeterminate spores, *Microthyrium* Desm. type., Spore 1, Spore 2, Spore 3, *Tetraploa aristata* Berk. & Br.

dates from Beta Analytic Inc., Florida, U.S.A. establish the chronology.

Results

Four zones were identified in the palynological diagrams, according to the distinct intervals of the sedimentary profile:

Zone I (depth: 512-430 cm): dark-clay-sediments, with a slight trace of very fine-grained sand; ^{14}C age of 9800 ± 90 yrs. BP (Beta 154709, 506 cm depth, sequence base); interval estimated age of 9800-8800 yrs. BP. The lower portion of the zone has very low pollen concentration. Grassland indicators are better represented than those of the forest in the percentage and concentration diagrams, mainly the Poaceae and *Baccharis* type. The *Amaranthus*-Chenopodiaceae type, *Gomphrena*, *Cuphea carunculata* Koehne, *Galianthe angustifolia* (Cham. & Schltdl.) E.L. Cabral, *Valeriana eichleriana* (C. Muell.) Graebn., *Plantago* and *Vernonia* are scarcer. Among the forest indicators are Myrtaceae, *Alchornea triplinervia* (Spreng.) Müll, Arg., Urticales, Anacardiaceae, Cyatheaceae, *Trema micrantha* (L.) Blume, *Anemia phyllitidis* (L.) Sw., *Microgramma vacciniifolia* (Langsd. & Fisch.) Copel. type, *Celtis* type, *Roupala* type, *Anemia*, *Pteris* (Fig. 2-3). *Isoetes* and algae indicate an aquatic environment. Among the herbaceous plant marsh indicators are *Osmunda*, *Blechnum* type, Cyperaceae and *Phaeoceros laevis* (L.) Prosk. (Fig. 2-3). The forest has a very low frequency in the composite diagrams, when compared to the grassland or herbaceous plant marsh components (Fig. 2). Fungi indicators show a very low concentration (Fig. 4). The pollen assemblage becomes more numerous towards the end of the zone. This zone coincides with the inferior cluster of the dendrogram (Fig. 2).

Zone II (depth: 430-302 cm): dark-clay-sediments with a slight trace of very fine-grained sand, smaller than that of zone I.; ^{14}C age of 7280 ± 60 yrs. BP (Beta 151165, 317 cm depth); interval estimated age of 8800-7000 yrs. BP. This zone is characterized by a great increase of grassland, forest, water reservoir, herbaceous plant marsh and fungi indicators (Fig. 2-4). The frequencies are high in the lower portion of the zone, falling sharply afterwards, especially in the concentration diagrams. Among the aquatic indicators *Isoetes* and algae are generally in evidence, as well as *Osmunda*, *Blechnum* type, Cyperaceae and *Phaeoceros laevis* (L.) Prosk. in the herbaceous plant marsh indicators. The greatest concentration of grains is found in the sum of the grassland indicators (Fig. 3). In the forest × grassland composite diagram, the forest components are slightly better represented than before, decreasing towards the end of the zone. In the forest × herbaceous plant marsh composite diagram, the high frequency of the herbaceous plant marsh indicators shows no major change (Fig. 2). The greatest concentration of fungi indicators is found in this zone. Most of the zone is in agreement with the second cluster of the dendrogram (Fig. 2).

Zone III (depth: 302-248 cm): dark-clay-sediments with very fine, scarce sand, which disappears in the upper portion of the zone; interval estimated age of 7000-5000 yrs. BP. The zone is characterized mainly by a great reduction in pollen and spore frequency, as clearly seen in the concentration sum of grassland, forest, water reservoir and herbaceous plant marsh indicators (Fig. 3). Grassland indicators predominate over those of the forest, which are very scarce. *Amaranthus*-Chenopodiaceae type stand out in percentage and concentration in the grassland pollen, thus reaching the highest profile frequency for this type (Fig. 2-3). *Osmunda*, *Blechnum* type and Cyperaceae stand out among herbaceous plant marsh indicators. In the composite diagrams there is an increase in the percentage of grassland and herbaceous plant marsh indicators over those of the forest (Fig. 2). The fungi indicators are greatly reduced in this zone, especially in the concentration diagrams (Fig. 4). The third dendrogram cluster corresponds to this zone (Fig. 2).

Zone IV (depth: 248-0 cm): dark-clay-sediments rich in organic matter, with no sand; ^{14}C age of 3730 ± 60 yrs. BP (Beta 192341, 199 cm depth); interval estimated age of 5000 yrs. BP - Present. A rise in the percentage and concentration frequency of forest indicators is evidenced in the beginning of the zone. This frequency increases greatly towards the top (Fig. 2-3). Forest indicators have higher concentrations than those of the grassland and herbaceous plant marsh in the upper portion of the zone (Fig. 3). At the top, however, there is a sudden tree component retraction. The best represented forest indicators in this zone are Myrtaceae, *Alchornea triplinervia* (Spreng.) Müll, Arg., and Urticales, together with a higher number of other tree pollen, in contrast to the previous zones. In the upper portion of this zone there is the greatest part of the forest indicators of the whole profile, many with an increase in frequency, showing the greatest pollen diversity of all the zones (the same for indeterminate

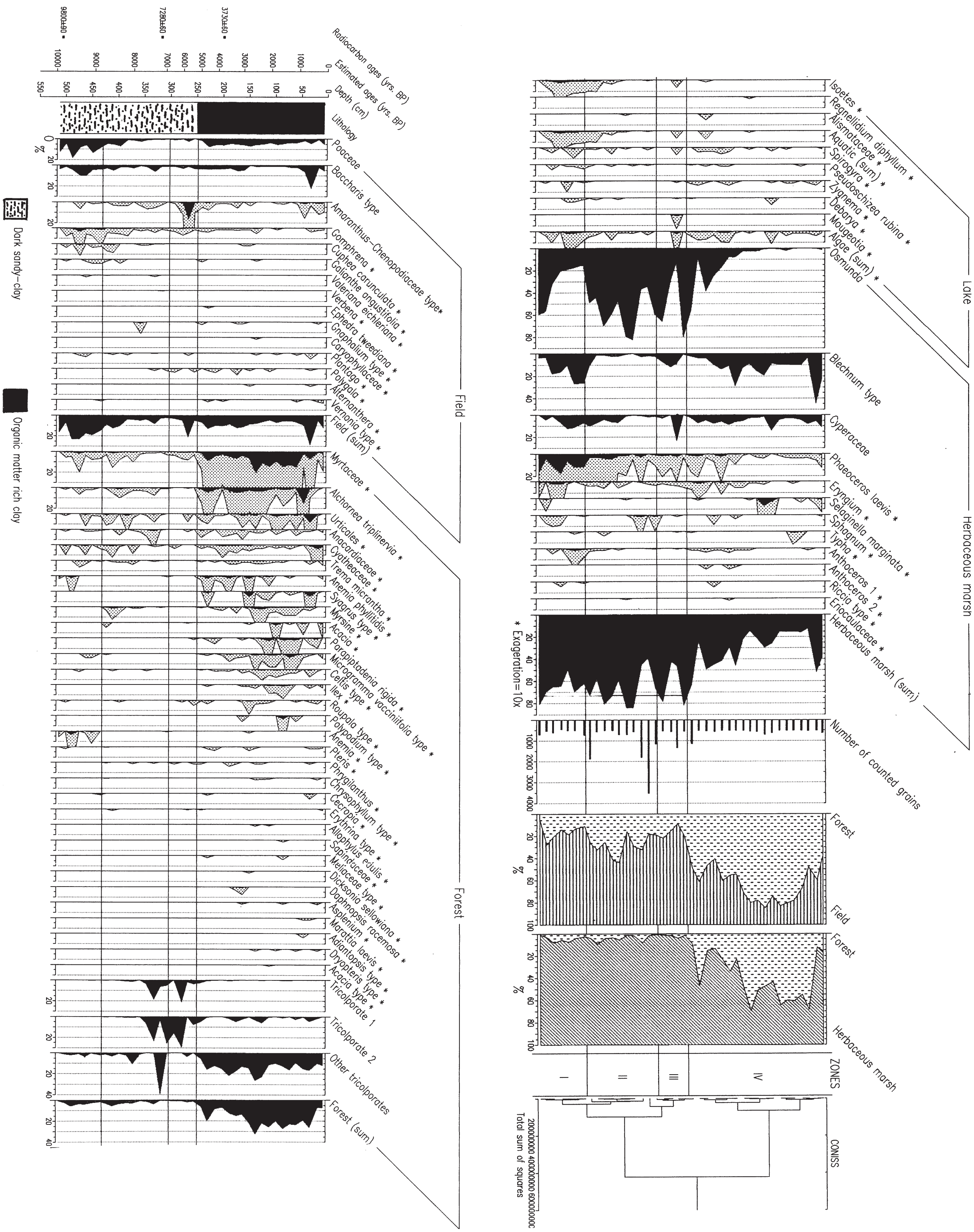

Figure 2. Palynological percentage diagrams for the sedimentary profile from the Serra Velha swamp forest, including all individual indicators of grassland (field), forest, water reservoir and herbaceous plant marsh, sum of each group, composite diagrams, zones and dendrogram.

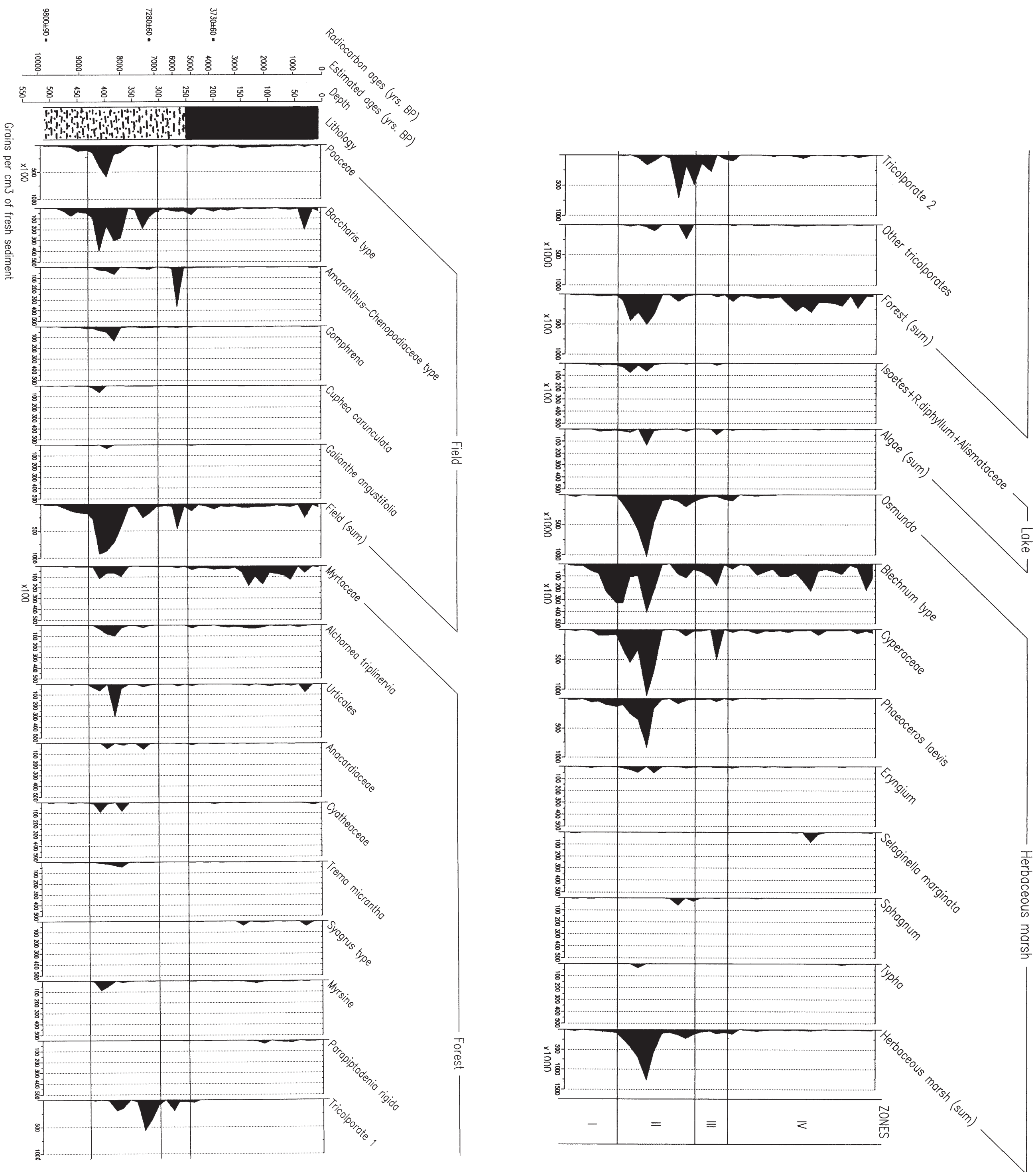

Figure 3. Palynological concentration diagrams for the sedimentary profile from the Serra Velha swamp forest, including the main individual indicators (taxa with a minimum of 5000 grains/cm[3] of fresh sediment in at least one sample). Grassland (field), forest, water reservoir and herbaceous plant marsh, sum of each group and zones.

environment indicators, not showed in diagrams). In contrast, grassland indicators have low frequencies, except in the portion near the top, where the *Baccharis* type is relevant. Aquatic indicators are very rare. The herbaceous plant marsh components generally show a sharp decline towards the top of the percentage diagrams (Fig. 2) and are scarce in the concentration diagrams (Fig. 3). The most important indicators of this environment in the zone are *Osmunda*, *Blechnum* type and Cyperaceae. In the composite diagrams there is a great increase of forest indicators compared to grassland and herbaceous plant marsh components (Fig. 2). The fungal spores increase greatly in the percentage diagrams (Fig. 4). *Glomus* and hyphae are more frequent towards the upper portion of the zone

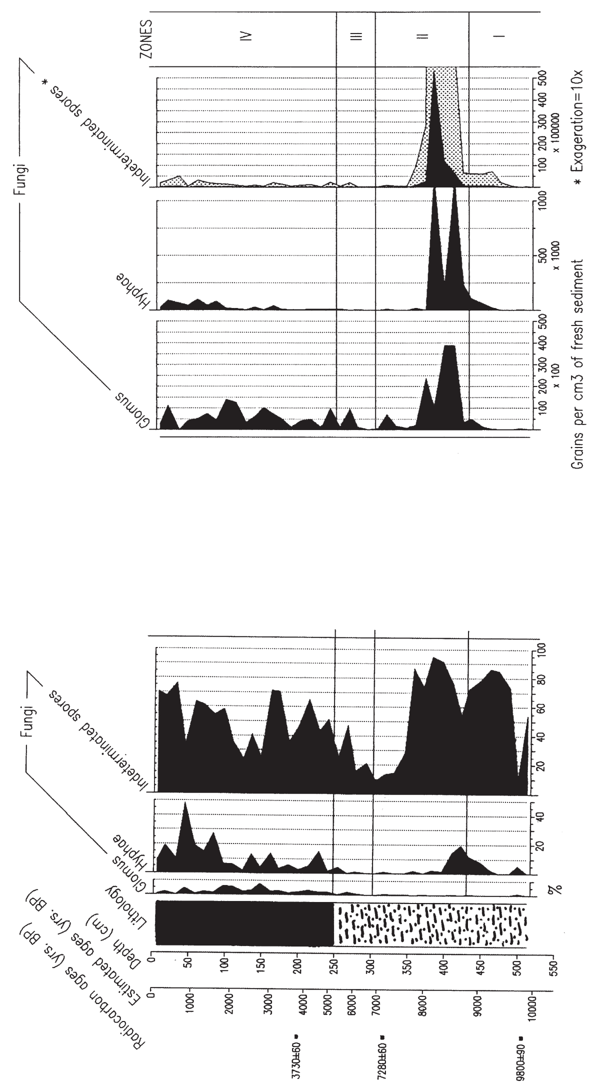

Figure 4. Palynological summarized percentage and concentration diagrams of fungi for the sedimentary profile from the Serra Velha swamp forest, including the main indicators (concentration: taxa with a minimum of 5000 grains/cm^3 of fresh sediment in at least one sample) and zones.

in the concentration diagrams (Fig. 4). The two last dendrogram clusters correspond to this zone (Fig. 2).

Discussion

The data shows the following phases in local and regional environments:

9800-8800 yrs. BP (Zone I): about 9800 yrs. BP the data indicate the existence of a water reservoir at the site of the present swamp forest (*Isoetes* and algae in the lower portion of Zone I, Fig. 2-3). The regional vegetation seems to be made up of a sparse grassland (scarce pollen from plants such as Poaceae and *Baccharis* type) with scattered trees or trees distant from this place (rare arboreal pollen). These data show a landscape that is still compatible with a semi-arid climate, indicating a delay in vegetation response to the improved climate at the beginning of the Holocene, since the end of the last Pleistocene glacial stage should have been semi-arid in Southern Brazil (Lorscheitter & Romero 1985; Roth & Lorscheitter 1993; Neves & Lorscheitter 1995; Behling *et al.* 2004).

The response of local vegetation to the great rise in temperature, humidity and rainfall at the beginning of the Holocene (± 10000 yrs. BP, Berglund 1986) seems to occur a little later, around 9000 yrs. BP, according to a rapid filling of the water reservoir, which gave rise to a herbaceous plant marsh (increase in aquatic indicators and a great increase in *Blechnum* type, Cyperaceae and *Phaeoceros laevis* (L.) Prosk. concentrations in the upper portion of Zone I, Fig. 3). Therefore, the data suggest plant succession by hydrosere. In the regional vegetation, grassland and forest are now a little more evident than in the previous phase. Part of the grassland indicators (especially Poaceae) can also be related to the local herbaceous plant marsh.

8800-7000 yrs. BP (Zone II): as the herbaceous plant marsh grows on the former water reservoir, dense arboreal vegetation seems to grow vigorously on the margin or close to the reservoir in this phase (high concentration of arboreal pollen indicators in zone II, especially in the lower portion, Fig. 3). The development of local soil, possibly involving mycorrhizal activities, coincides with forest formation (high *Glomus* concentration, as well as other fungal spores and hyphae in the lower portion of Zone II, Fig. 4). The grassland regional vegetation is also growing (high pollen concentration of Poaceae and *Baccharis* type, Fig. 3). Therefore, the data indicate an increase in temperature and humidity in the region during this phase of the early Holocene. Moreover, the Atlantic rain forest (*stricto sensu*) components seem to occur close to the marsh about 8800 yrs. BP, having migrated in an east-west direction from the Coastal Plain in the early Holocene (unmistakable presence of *Cecropia* pollen in the lower portion of Zone II, Fig. 2). This result corroborates that of Lorscheitter (2003), who mentions Atlantic rain forest (*stricto sensu*) components for the Coastal Plain and the adjacent areas since the beginning of the Holocene. Today, *Cecropia glaziovi* Snethl. and *Cecropia. pachystachya* Trec. are characteristic of this tropical migratory route (Rambo 1950). Possibly due to reduced humidity, a retraction of the local and regional vegetation towards 7000 yrs. BP is observed (reduction in most of the pollen content in the upper portion of Zone II, Fig. 2-3).

7000-5000 yrs. BP (Zone III): a great decline in the regional and local vegetation seems to occur, indicating the beginning of a dry, hot climate phase (a high overall frequency reduction of most pollen indicators in the percentage and concentration diagrams of Zone III, Fig. 2-3). The herbaceous plant marsh and forest vegetation retract, while a dry grassland environment species expand (a high increase of *Amaranthus*-Chenopodiaceae type frequencies, the greatest percentage and concentration - Zone III, Fig. 2-3). It is possible that the environmental alterations of this phase are not only climatic, but somehow related to human presence, as indicated by records in the region since the early Holocene (Ribeiro *et al.* 1989). Moreover, among *Amaranthus* and Chenopodiaceae there are weedy species that grow in disturbed environments, compatible with anthropogenic activities. However, these environmental alterations should be better investigated because it seems rather improbable that primitive man could have changed the environment so drastically.

5000 yrs. BP - Present (Zone IV): from about 5000 yrs. BP onwards, humidity increase and high temperatures seem to promote a great expansion of forest over marsh, reaching a maximum between 3000-500 yrs. BP (composite diagram of forest × herbaceous plant marsh, Zone IV, Fig. 2). Again, soil development and mycorrhizal activities seem to be evident (increase in the frequency of *Glomus*, other fungal spores and hyphae in general, Zone IV, Fig. 4). The marsh occupation by tree species gave rise to the present swamp forest (according to the percentage and concentration diagrams, Zone IV, Fig. 2-3), with a clear retraction in the last 500 yrs. BP (registered in the top sample of the sedimentary profile, according to an abrupt rise of the percentage and concentration of *Baccharis* type). This last, wide Serra Velha forest expansion over the marsh had already been detected by Grala & Lorscheitter (2001) beginning from approximately 6000 yrs. BP. However, new ^{14}C dating allowed us to recalculate the onset of this last forest expansion to about 5000 yrs. BP. From this age on, pioneer arboreal components appear in the formation (Myrtaceae, *Alchornea triplinervia* (Spreng.) Müll, Arg., *Trema micrantha* (L.) Blume, *Celtis* type and Urticales pollen, with an almost constant presence - Zone IV, Fig. 2).

The wealth of species from Serra Velha forest, observed at present, was not totally registered in the diagrams. This is probably due to the impossibility of determining part of the tricolporate grains, very similar and common among the arboreal pollen, or to the entomophily found in several species. It is also probable that the majority of pollen and spores from indeterminate environments belong to species from the swamp forest, since they are more related to this phase. This is the case, for instance, of the Liliaceae type, which can include several monosulcate grains from the inner forest, such as Liliaceae, Iridaceae, Smilacaceae and Arecaceae.

The presence of *Ilex* from about 5000 yrs. BP (lower portion of Zone IV, Fig. 2) deserved more detailed research due to the existence of the genus in *Araucaria* forests with others, characteristic of the Coastal Plain today. Due to the impossibility of identifying species by pollen morphology, an indirect distinction attempt was performed, using habitat. Among *Ilex* species mentioned for Rio Grande do Sul (Edwin & Reitz 1967; Klein 1972; Rambo 1950) the only one mentioned as typical from swamp forest is *Ilex pseudobuxus* Reiss. According to Rambo (1950), this species is also among those characteristic of the tropical migratory route from the Coastal Plain onwards. Therefore, *Ilex pseudobuxus* Reiss pollen would be another typical indicator, besides *Cecropia*, of the east-west Atlantic rain forest (*stricto sensu*) migration during the Holocene, to the studied region.

Ephedra tweediana Fisch. & C.A. Mey. evidence, also around 5000 yrs. BP for the regional grassland (lower portion of Zone IV, Fig. 2), indicates a wider distribution compared to the present. This species belongs to the Andes migration contingent, which penetrates into southern Rio Grande do Sul from Argentina (Rambo 1954), with present distribution restricted to the Coastal Plain to 30ºS latitude.

Comparing the results of this study to palynological results already obtained from the Coastal Plain and the Central Depression of Rio Grande do Sul (Lorscheitter 2003), we see that Serra Velha's present swamp forest is one of the oldest (last expansion about 5000 yrs. BP). This certainly happened because increased temperature and humidity during the Holocene promoted forest expansion over interior lowlands like this one. On the contrary, high temperatures caused extensive marine transgression on the Coastal Plain, reaching a maximum between 5000-4000 yrs. BP, with vegetation destruction. Only when the sea regressed and desalinization occurred, after 4000 yrs. BP, was the Coastal Plain re-colonized by west-east tropical rain forest species migration from interior lowlands, like this one. These results coincide with those of Villwock *et al.* (1986) and Villwock & Tomazelli (1998) on the geological history of Rio Grande do Sul Coastal Plain.

With the exception of the drier climate phase, between 7000-5000 yrs. BP, palynological results show an overall moderate climate on the lower parts of the Lower Northeast Slope of Serra Geral during the Holocene, according to results already obtained for Rio Grande do Sul Coastal Plain (Lorscheitter 2003) and for other sites in South and Southeast Brazil (Behling *et al.* 2001; Ybert *et al.* 2001; 2003). According to Martin *et al.* (1992) the constant humidity in South Brazil during the last 5000 years is probably due to *El Niño*-like conditions. On the Lower Northeast Slope of Serra Geral more humid phases, in a hot climate, resulted in the expansion of forests in the lower portions, forming mosaics with the grasslands. This variegated landscape is compatible with primitive human records, especially from the Umbu Tradition, from the Pre-Ceramic period (Prous 1991), widely active in the region since 11000 yrs. BP. The phytofaunistic evidence of human occupation of this region, related to eating habits, was investigated in 20 caves (Ribeiro *et al.* 1989), being compatible with overall high temperatures and humid climate, according to palynological data. Several gastropod shells, one of the most important kinds of primitive human food in the region, were found in the caves, besides *Syagrus romanzoffiana* (Cham) Glassman seeds (between 11000-1000 yrs. BP, burnt and fragmented) and remains of eggs from the large grassland bird *Rhea americana* L. (Ema), indicating human movement to the grassland area. After 6000 yrs. BP, freshwater bivalves (*Diplodon*), found today in Caí and Jacui tributaries, are present in the caves, coinciding with the last forest expansion detected by palynological data. In the same phase, there is a modification in the typology of hunting instruments, indicating an increase in the capture of small animals (Ribeiro 1993).

The results indicate a local water reservoir and a semi-arid regional climate at the end of the last Pleistocene glacial stage. A great change in climate in the beginning of the Holocene, about 10000 yrs. BP, to a more humid and warmer climate, apparently initiated the hydrosere which generated the current forest. Plant succession continued during the Holocene in an overall hot, humid climate, though with changes in regional humidity which influenced this succession. The occurrence of Atlantic rain forest (*stricto sensu*) components at about 8800 and 5000 yrs. BP shows tropical species migration in an east-west direction since the beginning of the Holocene.

The hot, humid climate of the Holocene with more rainfall seems to have determined a variegated regional landscape, with forest and grassland mosaics, compatible with the intense human activity registered in archaeological sites. Only one dry climate phase was found (between 7000-5000 yrs. BP). Phases with higher humidity were more favorable to forest expansions in this region, such as between 8800-7000 yrs. BP and from 5000 yrs. BP onwards. This last expansion of the swamp forest is much older than the present forests already studied on the Rio Grande do Sul Coastal Plain. It is probable, therefore, that the forests farther from the coast, like this one, contributed with a contingent of tropical species to colonize the Coastal Plain after the last marine regression, from 4000 yrs. BP onwards, but now in a west-east migration.

The results show the importance of the water reservoirs as generators of forests in a hot, humid climate, with long periods of rain, such as the one from the northeastern portion of Rio Grande do Sul in the far south of Brazil.

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