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Tropical Rain Forest and Climate Dynamics of the Atlantic Lowland, Southern Brazil, during the Late Quaternary

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Palynological analysis of a core from the Atlantic rain forest region in Brazil provides unprecedented insight into late Quaternary vegetational and climate dynamics within this southern tropical lowland. The 576-cm-long sediment core is from a former beach-ridge "valley," located 3 km inland from the Atlantic Ocean. Radiocarbon dates suggest that sediment deposition began prior to 35,000 ^{14}C yr B.P. Between ca. 37,500 and ca. 27,500 ^{14}C yr B.P. and during the last glacial maximum (LGM; ca. 27,500 to ca. 14,500 ^{14}C yr B.P.), the coastal rain forest was replaced by grassland and patches of cold-adapted forest. Tropical trees, such as *Alchornea*, Moraceae/Urticaceae, and Arecaceae, were almost completely absent during the LGM. Furthermore, their distributions were shifted at least 750 km further north, suggesting a cooling between 3°C and 7°C and a strengthening of Antarctic cold fronts during full-glacial times. A depauperate tropical rain forest developed as part of a successional sequence after ca. 12,300 ^{14}C yr B.P. There is no evidence that *Araucaria* trees occurred in the Atlantic lowland during glacial times. The rain forest was disturbed by marine incursions during the early Holocene period until ca. 6100 ^{14}C yr B.P., as indicated by the presence of microforaminifera. A closed Atlantic rain forest then developed at the study site.

Key Words: **Brazil; late Quaternary; pollen; tropical Atlantic rain forest; *Araucaria* forest; grassland.**

INTRODUCTION

Palynological studies from Catas Altas (755 m elevation, 20°05′S, in southeastern Brazil 43°22′W), at a distance of about 300 km from the Atlantic Ocean, indicate that glacial grassland and small areas of subtropical gallery forests were replaced by tropical semideciduous forest and cerrado (savanna, savanna forest to woodlands) (Behling and Lichte, 1997). Grasslands, which occur today in small patches in the southern Brazilian highlands, expanded at least 750 km northward during the recorded glacial period (ca. 18,000 to >48,000 ^{14}C yr B.P.). The vegetation reconstructions suggest a dry and cold climate with an average annual temperature reduction of 5°–7°C. Did these marked changes in climate, as documented from the lower elevations in the highlands, also affect the tropical rain forest of the Atlantic lowland? Estimated sea-surface temperatures (SSTs) for the western tropical South Atlantic Ocean show only a minor decrease in temperature (≤2°C) for the last glacial maximum (LGM; CLIMAP, 1981). Such a small change in temperature possibly had only minor consequences on the distribution of the lowland rain forest.

Paleoenvironmental data from the region of modern tropical Atlantic rain forest are only of Holocene age, and virtually nothing is known about glacial, especially full-glacial, conditions (Behling, 1995a, 1995b). The fragmentation of the Atlantic rain forest into relatively isolated "islands" during glacial times has been hypothesized in both zoo- and phytogeographic studies (e.g., Müller, 1973; Prance, 1982), but insufficient evidence exists to test this idea. It is also unknown whether *Araucaria* forests, which today occur in the southern highlands, occupied the Atlantic lowland. The modern occurrence of *Araucaria* on a few small isolated hills in the southern Atlantic lowland lends some support to the regional persistence of these trees during the last glaciation (Reitz and Klein, 1966). We present results of an investigation into past vegetation and climate in the southern Atlantic rain forest region, using pollen and radiocarbon analyses of recently discovered late Pleistocene deposits at Volta Velha, Santa Catarina, Brazil.

STUDY AREA

The study area (26°04′S, 48°38′W) lies within the Volta Velha biological reserve, which is part of the larger Mata Atlântica biosphere reserve. Volta Velha is located in the Itapoá district of northern Santa Catarina State (Fig. 1). The study area is only a

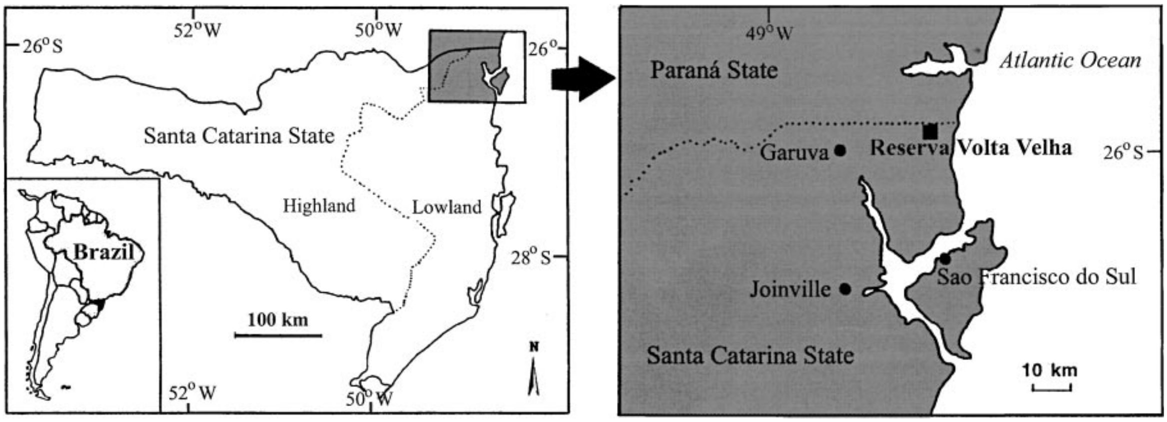

FIG. 1. Map of the Volta Velha Reserva and other localities mentioned in the text.

few meters above modern sea level and lies 3 km to the west of the Atlantic Ocean and 25 km to the east of the Serra do Mar Mountain. The topography is a flat to smoothly undulating coastal plain (0.5 and 5 m above modern sea level), that was formed by Quaternary sedimentary deposits of fluvial and marine origins (Martin *et al.*, 1988; Souza, 1999). Coastal beach ridges and small active and inactive river channels are also present. The coring site is part of a shallow basin, ca. 20 m wide and 100 m long. We refer to this landform as a former "beach-ridge valley."

The tropical Atlantic rain forest zone forms a 100 to 200-km-wide strip from Natal to Porto Alegre along the Brazilian coast (Klein, 1978; Por, 1992). A detailed floristic inventory was done on a 1-hectare plot adjacent to the coring site (Negrelle, 1995; Salimon and Negrelle, unpublished data). The plot includes 248 identified tree, shrub, and herb species (excluding epiphytes) from 50 families. *Tapirira guianensis* (Anacardiaceae), *Aparisthmium cordatum* (Euphorbiaceae), and *Ocotea acipahylla* (Lauraceae) are the dominant trees. The understory consists primarily of *Geonoma* spp., Melastomataceae (e.g., *Miconia chartaceae, Miconia hymenonervia, Ossaea sanguinea*), and Rubiaceae (e.g., *Psychotria* spp.). The results of a 1-year sample of modern pollen showed that tropical taxa common in the vegetation had high pollen abundances, whereas pollen from the more infequent plant types was rare (Behling *et al.*, 1997).

The study area experiences a warm, humid, tropical climate with no frost or annual dry season (Atlas de Santa Catarina, 1986; Nimer, 1986). The meteorological station at São Francisco do Sul (ca. 15 km to the south of the study area) has a mean annual rainfall of 1875 mm and a mean annual temperature of 21.4°C. Joinville station (ca. 30 km southwest of the study area) records values of 2171 mm and 20.3°C, respectively. The absolute minimum temperature is >1°C.

METHODS

Sampling and Pollen Analysis

The deepest portion of the basin was sampled using a Russian corer. The total length of the core, starting from the compact sandy base, is 580 cm. Stratigraphy of the core is given in Table 1. Sections of 50 cm length were extruded on site, wrapped in plastic film and aluminum foil, and stored under cool (ca. 8°C), dark conditions until sampling could be done. Eight bulk samples and one wood sample (70 cm core depth) were used for radiocarbon dating. An additional eight samples were dated by accelerator mass spectrometry (AMS) at the Van der Graaff Laboratory of the University of Utrecht and one sample through the conventional method by Beta Analytic (Table 2).

We took 58 subsamples (0.5 cm^3) at 5-cm, 10-cm, and 20-cm intervals for pollen analysis. All samples were processed following standard pollen analytical techniques (Faegri and Iverson, 1989). To determine the pollen concentration and pollen accumulation rate, one tablet containing exotic spores of *Lycopodium clavatum* was added to each sample. Pollen and spores were well preserved and a minimum of 300 pollen grains was counted for each sample. The total pollen sum includes herb, shrub, and tree taxa. Pollen identification was based on Behling's reference

TABLE 1
Stratigraphy of the Volta Velha Core

Depth (cm)	Description
0–14	Brown, relatively well-preserved organic material with plant remains and rootlets
14–105	Dark brown, decomposed organic material with plant remains and rootlets; 34–105 cm: less plant remains and fine sand
105–157	Black, highly decomposed organic material with a few plant remains and no rootlets; 145–157 cm: more compact
157–300	Black–dark gray organic-rich clay, fine sand, rare plant remains; 179–300 cm: greater clay component, compact
300–438	Dark gray fine sandy clay, less in organic material, rare plant remains
438–478	Black–dark gray organic rich clay, richer in clay and compact
478–576	Black, completely decomposed organic material
576–580	Sandy subsurface

TABLE 2
AMS and Conventional Radiocarbon Dates from Volta Velha Core

Lab number	Depth (cm)	Age (^{14}C yr B.P.)	^{13}C/^{12}C
UtC-5497	30	3816 ± 36	−29.6
UtC-5498	70 (wood)	3343 ± 38	−30.8
UtC-5499	180	6925 ± 44	−25.9
UtC-5500	280	7600 ± 60	−24.2
UtC-5501	380	7980 ± 50	−26.1
UtC-5502	430	7525 ± 44	−28.3
UtC-5503	480	12,330 ± 70	−26.4
UtC-5504	530	25,650 ± 170	−24.0
Beta-79120*	564–575	21,310 ± 160	−25.1

* Conventional radiocarbon date.

collection (containing about 2000 Brazilian species) and pollen morphological descriptions (Behling, 1993).

Calculations, cluster analysis, and illustration of the pollen and spore data were done using TILIA, TILIAGRAPH, and CONISS (Grimm, 1987). The pollen diagrams include individual percentages of the most abundant pollen and spore types (Fig. 2), total pollen concentration and accumulation rate (Fig. 3), and percentages of microforaminfera (Fig. 3). The zonation of the pollen record is based on changes in the pollen assemblages and the CONISS analysis.

RESULTS

Radiocarbon Data and Chronological Control

Radiocarbon dates provide the chronological control for the Volta Velha pollen record and indicate deposits of late Pleistocene and Holocene age. Reconstructed vegetational changes (see below) suggest that the AMS date of 25,650 ± 170 ^{14}C yr B.P. at 530 cm depth is probably correct, whereas the 21,310 ± 160 ^{14}C yr B.P. date is in error. Thus, the base of the core is seeiningly closer to the extrapolated age of 37,640 ^{14}C yr B.P. than to the radiocarbon age of 21,310 ^{14}C yr B.P. Radiocarbon dates from the late glaciation (480 cm) and early Holocene (430, 380, 280, and 180 cm) indicate that sedimentation was not continuous during this period. However, deposition most likely was continuous during the early to mid-Holocene (ca. 470–100 cm). The sedimentation rate was high during the early to mid-Holocene, while sedimentation was low or (probably) incomplete during the late Holocene. Radiocarbon dates at 564–575 cm, 430 cm, and 70 cm have been excluded from the age model which is a linear interpolation between radiocarbon date.

Volta Velha Pollen Diagram

Pollen assemblages in the Volta Velha core are diverse, with 178 pollen and spore types including 21 unknown types (Figs. 2 and 3). Six pollen zones were defined (Table 3). Pollen concentrations (grains/cm^3) and pollen accumulation rates (grains/cm^2/yr) vary greatly throughout the core, probably reflecting different

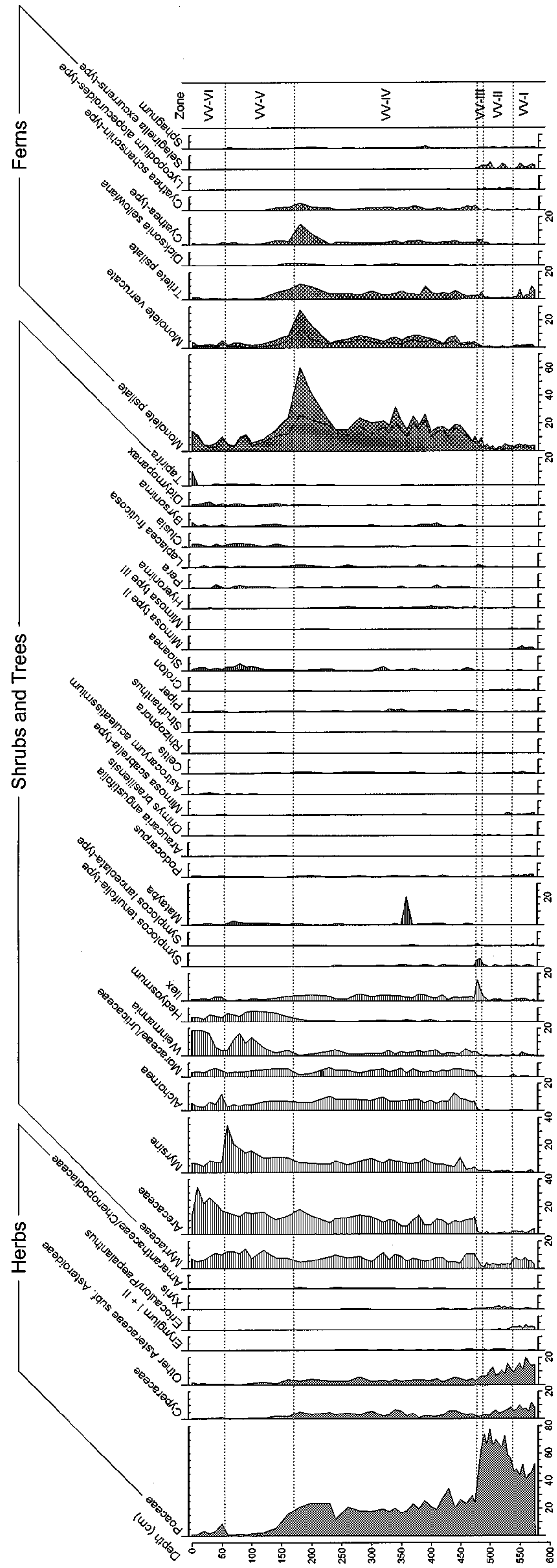

FIG. 2. Pollen percentage diagram of the major taxa from the Volta Velha core.

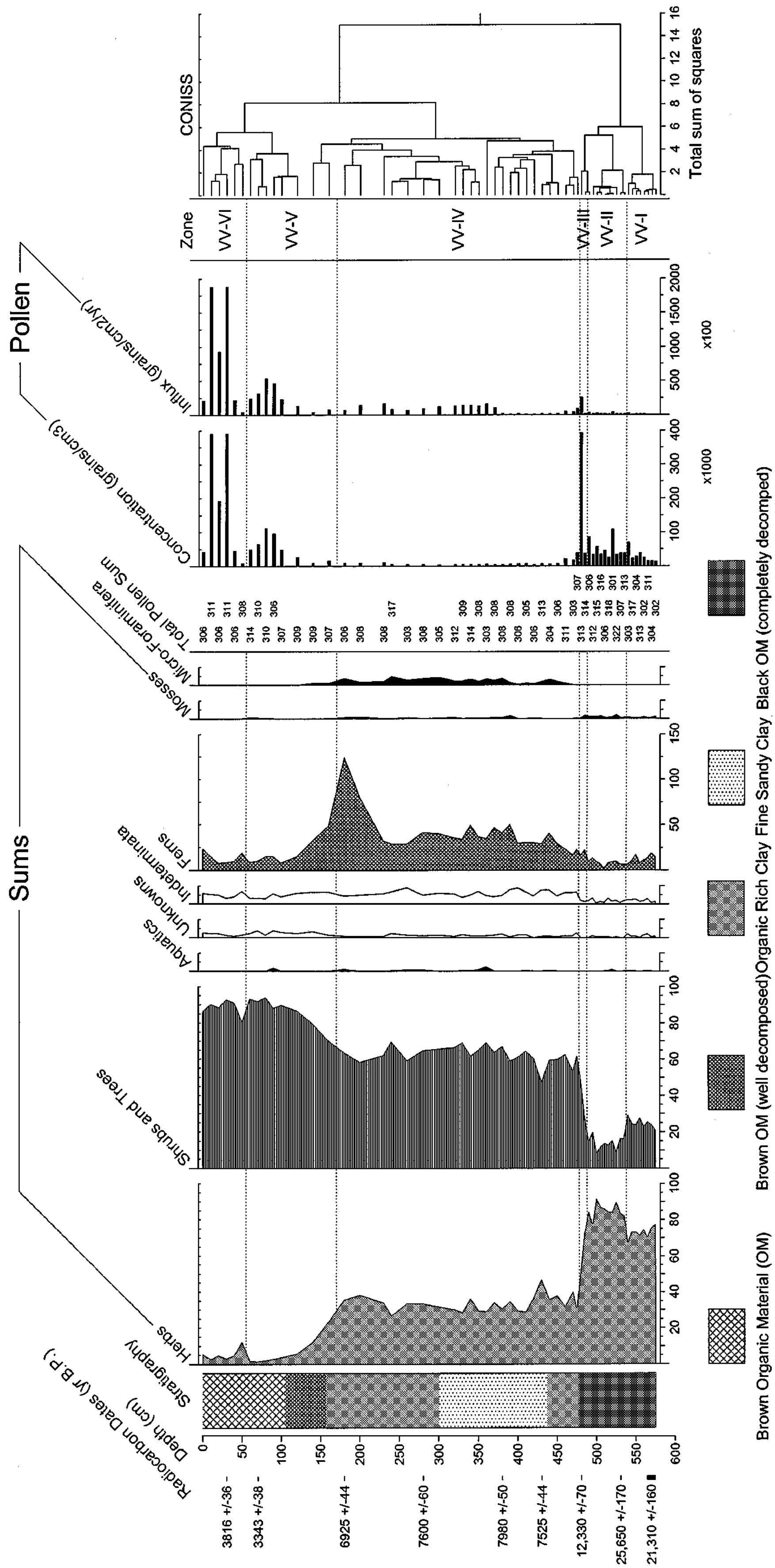

FIG. 3. Summary pollen diagram from Volta Velha, showing radiocarbon dates, stratigraphy, ecological groups, total pollen sums, pollen concentration, pollen accumulation, pollen zones, and the cluster analysis dendrogram.

TABLE 3
Pollen Zones Depth, Calculated Radiocarbon Ages, and Number of Pollen Samples in Each Pollen Zone of the Volta Velha Core

Zone	Depth (cm)	Age range (^{14}C yr B.P.)	No. of samples
VV-I	575–537.5	37,640–27,650	8
VV-II	537.5–487.5	27,650–14,328	10
VV-III	487.5–477.5	14,328–12,220	2
VV-IV	477.5–170	12,220–6720	24
VV-V	170–55	6720–4330	8
VV-VI	55–0	4330–3190 (or modern)	6

depositional environments. For example, particularly high pollen concentrations and accumulation rates are found in pollen zones VV-III and VV-V.

Pollen zone VV-I is characterized by a predominance of herb taxa (67–77%). Poaceae pollen (41–52%) dominates, followed by Asteraceae and Cyperaceae. Lesser types include *Eriocaulon/Paepalanthus* with a few grains each of *Eryngium, Xyris*, and *Moritzia dasiantha.* Shrub and tree pollen (21–29%) originate mostly from Myrtaceae and Melastomataceae. Pollen grains of Arecaceae, *Myrsine, Alchornea*, Moraceae/Urticaceae, *Weinmannia, Ilex, Symplocos tenuifolia*-type, *Podocarpus, Celtis*, and *Mimosa* II occur but are rare. A single pollen grain of *Araucaria angustifolia* was found. Pollen of *Mimosa* II and III occurs only in this zone. Percentages of fern spores are ca. 20%.

Herb pollen percentages (76–91%) are higher in zone VV-II than in zone VV-I. Pollen of shrubs and trees is low (8–19%). Among the herbs, Poaceae pollen (64–77%) retains high percentages, whereas Asteraceae and Cyperaceae decrease. Myrtaceae and Melastomataceae are the only arboreal taxa that remain relatively high. Percentages of all other shrubs and trees are represented only by single grains or are missing. Pollen grains of *Croton* occur only in zones VV-I and VV-II. Fern spores are slightly less well represented than in the previous zone.

Zone VV-III is characterized by a remarkable decrease in herb pollen (from 84 to 29%), especially of Poaceae (from 74 to 23%), and by an increase in shrub and tree pollen (from 14 to 62%), mostly of the *Symplocos tenuifolia*–type (maximum 6%, first part of the zone) and *Ilex* (maximum 15%, second part of the zone). Other arboreal taxa continue to show relatively low percentages. Fern spores increase, including the tree fern *Cyathea*.

Zone VV-IV is marked by low percentages of herb (27–46%) and high percentages of shrub and tree pollen (47–69%). Most arboreal taxa, such as Myrtaceae, Melastomataceae, Arecaceae, *Myrsine, Alchornea,* Moraceae/Urticaceae, *Weinmannia,* and *Ilex,* are well represented. Other taxa, such as *Symplocos tenuifolia*–type *Matayba* and *Podocarpus*, display lower percentages. Several types appear in this zone for the first time, including *Hedyosmum, Piper, Pera, Rhizophora, Struthanthus, Byrsonima*, and *Tapiria.* Fern spores have high percentages and increase markedly (maximum 124%) at the end of this zone. Marine microforaminifera are also found in the sediments.

Zone VV-V is characterized by another decrease of herb pollen (down to 1%) and by an increase of shrub and tree pollen (up to 94%). In particular, pollen percentages of *Myrsine* (maximum at the end of this zone), Arecaceae, *Weinmannia, Hedyosmum, Sloanea,* and *Clusia* increase. Fern spores are also higher during this zone. Microforaminifera are now rare or missing.

Zone VV-VI is marked by a slight increase in herb pollen, primarily at the beginning of the zone (maximum 12%). Among the group of shrubs and trees (80–93%), percentages of Arecaceae and *Weinmannia* pollen increase, while *Myrsine* pollen decreases.

INTERPRETATION AND DISCUSSION

Late Pleistocene and Holocene Depositional Environments

The beach-ridge valley was ca. 575 cm deeper than today at the time of initial organic deposition. During the last glacial maximum, Atlantic sea level was ca. 120 m lower than modern and the ocean was at least 100 km east of the site (modern distance is ca. 3 km). The beach-ridge valley probably was sufficiently moist to have allowed the accumulation and conservation of organic-rich material during the late Pleistocene. A lake never formed in the valley, however. The few aquatic pollen taxa (*Drosera, Utricularia, Ludwigia*) that were found in the core indicate moist but not fully hygric conditions. The organic-rich deposits also lack evidence of fluvial transport. Organic-rich clays fine sandy clays, and/or the presence of microforaminifera in the core document the occurrence of marine incursions into the beach-ridge valley during the early Holocene, suggesting close proximity of the Atlantic Ocean. These marine incursions possibly have disturbed and eroded portions of the late glacial to early Holocene record. No microforaminifera were found at 140 cm (i.e., younger than 6100 ^{14}C yr B.P.), indicating the end of marine incursions at the site. A sea level maximum of +3.5 to +4 m is reported from several localities along the east Brazilian coast during the mid-Holocene (e.g., Suguio *et al.*, 1985; Angulo and Lessa, 1997). The accumulation of organic material during the late Holocene (Zone VV-VI) was probably both slow and discontinuous.

Late Pleistocene Vegetational and Climate Dynamics

Pollen assemblages from the pre-LGM (ca. 37,500–ca. 27,500 ^{14}C yr B.P; Zone VV-I), and the LGM periods (ca. 27,500–ca. 14,500 ^{14}C yr B.P.; Zone VV-II) indicate a vegetation dominated by Poaceae. Asteraceae and *Eriocaulon/Paepalanthus, Eryngium, Xyris,* and *Moritzia dasiantha* also were relatively common. The pollen percentages are similar to those in Holocene records of the campos (grassland) vegetation from the highland in Santa Catarina (Behling, 1995a). *Moritzia dasiantha* currently grows only in the highlands. The Volta Velha data suggest that campos vegetation, perhaps with a floristic composition similar to modern, once occupied the lowlands. Today the campos is limited to elevations higher than 1000 m in the south Brazilian mountains.

The similarity of the LGM assemblage to modern spectra from the campos region in the highland of Santa Catarina (Table 4)

TABLE 4
Last Glacial Maximum Climate Estimates for Volta Velha Based on Comparison between Modern Climatic Conditions of Volta Velha, Santa Catarina (Site 1), and Pelotas (Site 2)[a]

Climate	Campos region in Santa Catarina (1)	Pelotas in Rio Grande do Sul (2)	Volta Velha	Climatic differences based on site 1/2
Average temperature	14 to 16°C	17.5°C	21.4°C	−5.4 to −7.4°C/−2.9°C
Minimum temperature	−4 to −8°C	−2.3°C	1°C	−5°C to −9°C/−3.3°C
Days of frost per year	20 to 30 days	5 days	0 days	20–30 days/5 days
Annual rainfall	1400 mm	1310 mm	1875 mm	−475 mm/−565 mm

[a] Modern climate datas from Nimer (1986) and Atlas de Santa Catarina (1986).

suggests that the average temperature was about 5.4° to 7.4°C lower than today at Volta Velha. The absolute minimum temperature may have been between −4° to −8°C, including ca. 20 to 30 days of frost. Annual precipitation perhaps was ca. 475 mm lower than present during the full glacial period.

The pollen results show that tropical trees typical of the modern Atlantic rain forest (such as *Alchornea*, Moraceae, and Arecaceae) were rare in the lowlands during the pre-LGM and almost absent during the LGM. Some tropical trees have their modern limits some hundreds of kilometers farther south. For example, the present-day range of *Alchornea* is to the Brazil and Uruguay border (Reitz *et al.*, 1983). Thus, tropical trees found at least 750 km to the north of their current southern distributional limit during the LGM. Using meteorological data from the Pelotas station (Table 4), average annual temperature was ca. 2.9°C lower during the full glacial period. The minimum temperature was ca. −2.3°C, including 5 days of frost. The annual rainfall would have been ca. 565 mm lower than today.

The relatively frequent occurrence of Myrtaceae and Melastomataceae and of rarer trees, such as *Podocarpus, Symplocos,* and *Ilex,* suggests the existence of cold-adapted subtropical forests in the lowland during the pre-LGM and the LGM. The high percentages of herb pollen indicate that only small areas of forest occupied the lowland, especially during the LGM. *Araucaria angustifolia* apparently did not grow in the Atlantic lowland because a single pollen grain was found for the entire glacial period. Pollen grains of *Mimosa* II and *Mimosa* III occurred only during the glacial periods.

The late-glacial record (Zone VV-III) at Volta Velha is probably incomplete. However, *Symplocos tenuifolia*–type and then *Ilex* reached maximum pollen percentages. This change happened somewhat before most of the tropical taxa reached higher values, indicating a stepwise change toward a warmer climate. These pollen results suggest the occurrence of a successional stage before the expansion and developement of the diverse tropical southern Atlantic rain forest of the early Holocene (Zone VV-IV).

Holocene Vegetational and Climate Dynamics

The composition of the Atlantic rain forest was relatively constant with only minor floristic fluctuations from the early Holocene (Zone VV-IV) until ca. 6700 ^{14}C yr B.P. Ferns, including some tree ferns, became frequent in the rain forest, suggesting a wetter climate than previously. Relatively high percentages of herb pollen (Poaceae, Cyperaceae, and Asteraceae) indicate that there was not complete forest cover during the early Holocene. Herb-dominated vegetation occurred near flooded lowlands, a result of possible marine incursions. A few levels with single grains of *Rhizophora* imply that mangrove vegetation was poorly developed near the study site. Today, local populations of *Rhizophora* can produce up to 80–90% of the total pollen sum (Behling *et al.*, 2001). Drier climatic conditions, as recorded in the highland (Behling, 1995a, 1997), may also have influenced the vegetation communities.

During the mid-Holocene (Zone VV-V), *Myrsine*, Arecaceae, W*einmannia, Hedyosmum, Sloanea,* and *Clusia* became more frequent in the rain forest. Wetter climatic conditions may have been the primary factor in altering the vegetational composition. With the marine regression (beginning of Zone VV-V) at about 6100 ^{14}C yr B.P., open areas became forested, forming a dense Atlantic rain forest.

During the late Holocene (Zone VV-VI) *Myrsine* was less frequent, while Arecaceae and W*einmannia* became more frequent. The higher occurrence of Poaceae pollen at the beginning of the zone may suggest some opening of the forest that perhaps reflects human activity. The increase of Arecacea perhaps indicates wetter climatic conditions. Modern pollen rain from the study area (Behling *et al.*, 1997) shows a relatively high average value of *Tapirira* (25%) and low average value of *Weinmannia* (1.6%). The uppermost core sample has 10% *Tapirira* and 18% *Weinmannia* pollen, suggesting that pollen from the modern Atlantic rain forest was not deposited in the uppermost core sediments.

CONCLUSION

The palynological results document the predominance of grassland-type vegetation during the late Pleistocene at the study area in the southern Atlantic lowland, where tropical rain forest currently exists. The late Pleistocene is sub divided into three distinct intervals. The pre-LGM (ca. 37,500 and ca. 27,500 ^{14}C yr B.P., zone VV-I) is characterized by grassland with a few stands of cold-adapted forests (e.g., Myrtaceae and Melastomataceae) and with rare occurrences of tropical trees (e.g., Arecaceae, *Alchornea,* and Moraceae/Urticaceae). The LGM (ca. 27,500 and ca. 14,500 ^{14}C yr B.P., zone VV-II) had widespread grassland with probably only a few small stands of cold-adapted forests and an almost complete absence of tropical trees. The late-glacial period (zone VV-III) was marked by an expansion of tropical shrubs and trees, including successional stages of *Symplocos* and *Ilex.*

The palynological data from the LGM suggest the widespread occurrence in the lowland of grassland (campos). This vegetation type is found today in some highland regions of Santa Catarina. Tropical trees, such as *Alchornea,* were dislocated at least 750 km to the north of their modern distributions. The tropical Atlantic rain forest was markedly reduced in both extent and diversity, especially during the full glacial period.

Comparing the modern climate of the campos region and Pelotas (southern limit of *Alchornea*) with that in the study region, we derive a 3° to 7°C lower average annual temperature for the LGM period. The minimum temperature was between −2° to −8°C, including 5 to 30 days of frost per year. The annual precipitation may have been about 500 mm lower than the present-day rainfall. A LGM cooling of at least 3° to 7°C is in disagreement with the 2°C lower sea-surface temperatures that were estimated for the western tropical South Atlantic Ocean (CLIMAP, 1981).

Pollen analytical data indicate that there were no *Araucaria angustifolia* trees in the study region during the late Pleistocene. However, other species that today are restricted to the highlands (e.g., *Moritzia dasiantha*) did expand into the lowlands.

Marine incursions affected the study site from the early Holocene until 6100 ^{14}C yr B.P. This marine influence is probably the primary reason the Atlantic rain forest was not completely closed. Marine incursions notwithstanding, mangroves remained poorly developed near the study site until modern times. Since the mid-Holocene, a dense Atlantic rain forest with abundant Myrtaceae, Arecaceae, Moraceae/Urticaceae, *Alchornea*, *Myrsine*, and *Weinmannia* has grown at the study site.

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