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Palaeogeography, Palaeoclimatology, Palaeoecology 177 (2002) 19–27

PALAEO

www.elsevier.com/locate/palaeo

South and southeast Brazilian grasslands during Late Quaternary times: a synthesis

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Accepted 16 August 2001

Abstract

Fourteen pollen records from the south (S) and the southeast (SE) Brazilian regions have been synthesised. Late Glacial records from S Brazilian highlands document the predominance of grassland (campos) where today *Araucaria* forests occur. Records from SE Brazil show that during pre- and full-glacial times modern tropical semideciduous forest and cerrado (savanna to dry forest) were mostly replaced by grassland and some subtropical gallery forest. Modern montane *Araucaria* forests and cloud forests in SE Brazil were mostly replaced by grassland during pre- and full-glacial times. There is evidence that the modern tropical Atlantic rainforest in S Brazil was significantly reduced and replaced by cold-adapted forest taxa or grassland during glacial, especially during full-glacial times. The synthesis indicates that grasslands dominated the S and SE Brazilian landscape during the Late Pleistocene where today different forest ecosystems exist. Grassland extended over 750 km from S to SE Brazil from latitudes of about 28°/27° S to at least 20° S. These results indicate that climates in the region were markedly drier and 5–7°C cooler during glacial times. Antarctic cold fronts must have been much stronger and more frequent than today. Studies from S Brazil show that huge areas of Late Pleistocene campos vegetation were still found on the S Brazilian highlands during early and mid Holocene times, reflecting dry climatic conditions with an annual dry period of probably 3 months. Modern wet climatic conditions with no or only short dry periods were not established until the Late Holocene period when *Araucaria* forests replaced large areas of grassland vegetation after about 3000 ^{14}C yr B.P. and especially after 1500/1000 ^{14}C yr B.P.

Keywords: Late Quaternary; pollen analysis; grassland; palaeofire; palaeoclimate; southern Brazil

1. Introduction

The history of grassland ecosystems in South America, including Late Quaternary grassland distribution, its composition and biodiversity, and the role of fire and human impact has, to date, received little attention. Yet, spatial and temporal variations of subtropical and tropical grassland biomes, shifts of grassland/forest boundaries and changes in the composition of grassland vegetation are an important tool for reconstructing past climate changes. Knowledge of palaeograssland distribution may help to improve models of past vegetation and climate in subtropical and tropical regions.

A review of the Late Quaternary history of tropical South American savannas north and south of the Amazon is published in Behling

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0031-0182/02/$ – see front matter
PII: S0031-0182(01)00349-2

and Hooghiemstra (2001). The results show that during the full-glacial period, savannas both north and south of the equator expanded, reflecting markedly drier conditions. The Amazon rainforest area must have been reduced. In both hemispheres, climate started to become wetter during the Late Glacial period. During the early Holocene period (until ca. 6000–5000 ^{14}C yr B.P.) the distribution of savanna was much larger than during Late Holocene periods, documenting drier climatic conditions than during the Late Glacial and Late Holocene periods. The general synchrony of vegetational and climatic changes since the full-glacial, from savanna sites north and south of the equator, suggest that changes in the latitudinal migration of the inter-tropical convergence zone may have played an important role.

This paper provides a continued synthesis of the history of South American grasslands by reviewing the available pollen analytical studies from south (S) and southeast (SE) Brazil.

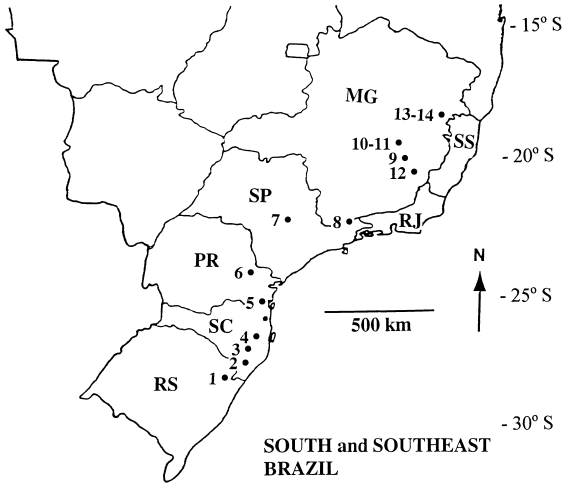

Fig. 1. Map showing the region of S Brazil with the location of the states RS, SC, PR and of SE Brazil with the states São Paulo (SP), Minas Gerais (MG), Rio de Janeiro (RJ) and Spirito Santo (SS), and the location of the available pollen records: (1) Fazenda do Pinto, (2) Serra do Rio Rastro, (3) Morro da Igreja, (4) Serra da Boa Vista, (5) Volta Velha, (6) Serra Campos Gerais, (7) Botucatú, (8) Morro de Itapeva, (9) Catas Altas, (10) Lago dos Olhos, (11) Lagoa Santa, (12) Lago Silvana, (13) Lagoa Nova and (14) Lago do Pires.

2. Modern environmental setting

2.1. Study region

The region of S Brazil comprises the states of Rio Grande do Sul (RS), Santa Catarina (SC), and Paraná (PR), and SE Brazil includes São Paulo, Minas Gerais, Rio de Janeiro and Spirito Santo (Fig. 1). The main topographic features that characterise the landscape of S and SE Brazil are the southern lowlands of RS (<500 m above sea level (a.s.l.)) forming a small 100–200-km-broad strip along the Atlantic coast, and the S and SE Brazilian highlands (between 500 and 1200 m a.s.l.). Higher-elevation mountains (>1200 m a.s.l.) are formed by the Serra Geral in S Brazil and continue northeastwards through the Serra do Mar. Also in SE Brazil is the Serra da Mantiqueira, a second inland mountain range located inland of the Serra do Mar.

2.2. Modern vegetation and climate

The modern potential natural vegetation cover in S and SE Brazil includes primary forest ecosystems such as the tropical Atlantic rainforest, the *Araucaria* forest, the semideciduous forest and the cerradão (dense woodland) (Fig. 2).

The Atlantic rainforest occurs in S and SE Brazil as a 100–250-km small belt in the coastal lowlands along the Atlantic Ocean, and on the coastal eastern slopes of the Serra Geral and Serra do Mar mountains. Frost-sensitive tropical Atlantic rainforests reach their limit in the southern region of SC state (Klein, 1978; Por, 1992). The climate is warm and humid without any or only a short dry period of less than 2 months. The annual precipitation ranges from 1250 to 2000 mm and is over 2000 mm in the higher mountains. The average annual temperature is between 17 and 24°C (Nimer, 1989).

Subtropical *Araucaria* forest is found on the S Brazilian highlands between latitudes 24 and 30° S (1000–1400 m elevation), and in SE Brazil in small isolated areas between 18 and 24° S (1400–1800 m elevation) (Hueck, 1953). The climate is temperate and humid without pronounced dry periods. The average annual precipitation is

between 1400 and 2200 mm. *Araucaria angustifolia* itself requires a minimum of 1400 mm annual rainfall without a marked annual dry season (Hueck, 1966). The average annual temperature ranges mainly between 12 and 18°C. Nights in cold winters may have temperatures of −4 to −8°C in the upper region of the Serra Geral (Nimer, 1989).

The tropical semideciduous forest (about 20–30 m tall) is found further inland in SE Brazil, in regions with an annual dry season between 3 and 5 months and an annual rainfall between 1000 and 1500 mm. The average annual temperature is between 20 and 26°C.

Cerrado (tropical savanna which includes several physiogenomic vegetation types) is distributed primarily in central Brazil, but is also found in the northern part of SE Brazil. A few isolated patches of cerrado occur in the area of semideciduous forest in SE Brazil (Hueck, 1956). The average annual precipitation in most of the cerrado region is between 1000 and 1750 mm, the average annual temperature is between 20 and 26°C, and the length of the dry season is between 5 and 6 months (Nimer, 1989).

The distribution of these S and SE Brazilian vegetation types is dictated by the South Atlantic Anticyclone. This semi-permanent high-pressure system transports moist tropical oceanic air masses inland in an easterly and northeasterly direction during the whole year. Additionally, the annual variation of the inter-tropical convergence zone (ITCZ) causes high rainfall in SE Brazil during the summer months (October–March) and a low rainfall-induced dry season from April to September. There is a decrease of the annual dry season from about 6 months in northwestern SE Brazil to about 3 months south and east of SE Brazil. Advections of Antarctic cold fronts produce strong rainfall when they meet tropical air masses. This occurs mainly in the regions of S and southern SE Brazil. One consequence is that these regions have little or no marked dry season (Nimer, 1989; Hastenrath, 1991).

2.3. Modern grasslands

Modern potential natural grasslands in S and SE Brazil, including campos, campos de altitude, and cerrado, are much smaller in area than forest biomes (Fig. 2). The subtropical grassland, which is called in Brazil campos, is found in the lowlands of the southernmost region of RS (Fig. 1). This grassland type is similar to the pampa grassland, which occurs mainly in Uruguay and Argentina.

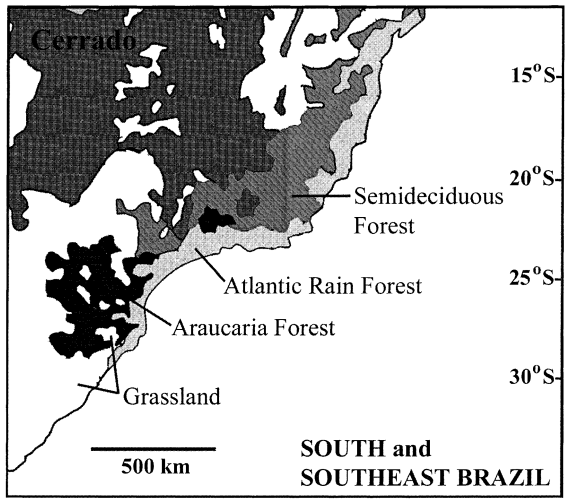

Fig. 2. Geographical distribution of modern major S and SE Brazilian vegetation types (adapted after Seibert, 1996).

Campos is also found on the S Brazilian highlands, especially in the states of RS and SC. Patches of these species-rich grasslands often form a mosaic with *Araucaria* forests. Campos is differentiated into campos limpo ('clean grassland'), which contains a predominance of herbs of the Poaceae, Cyperaceae and Asteraceae family, and campos sujo ('dirty grassland'), which in addition to grasses and sedges contains shrubs, primary of the families Asteraceae (*Baccharis gaudichaudiana*, *B. uncinella*) and Apiaceae (*Eryngium* sp.) (Klein, 1978). Both types of campos include a high number of different herb species (Klein, 1979; Rambo, 1957).

Campos de altitude (high elevation grasslands) grow on mountains, at elevations above 1600 m in S Brazil and above 1800 m in SE Brazil. This grassland contains species of the Poaceae and Cyperaceae families, but also includes small shrubs of Melastomataceae, Ericaceae, Eriocaulaceae, Asteraceae and Verbenaceae (Safford, 1999a,b).

Table 1
List of pollen records from S and SE Brazil, including location, elevation, radiocarbon range and references of the analysed profiles

State	Name	Modern local vegetation	Coordinates	Elevation (m)	Age (^{14}C yr B.P.)	Reference
S Brazil						
RS	Fazenda do Pinto	campos[a]	29°24′ S, 50°34′ W	900	0–6 750	Behling et al., 2001
SC	Serra do Rio Rastro	campos[a]	28°23′ S, 49°33′ W	1 420	1 000–11 210	Behling, 1995a
SC	Morro da Igreja	campos de altitude[a]	28°11′ S, 49°52′ W	1 800	0–10 200	Behling, 1995a
SC	Serra da Boa Vista	campos[a]	27°42′ S, 49°09′ W	1 160	0–14 000	Behling, 1995a
PR	Volta Velha	Atlantic rainforest	26°04′ S, 48°38′ W	5	0–25 650	Behling and Negrelle, 2001
PR	Serra Campos Gerais	campos[a]	24°40′ S, 50°13′ W	1 200	0–12 500	Behling, 1997b
SE Brazil						
SP	Botucatú	semideciduous forest	22°48′ S, 48°23′ W	770	ca. 18 000–30 000	Behling et al., 1998
SP	Morro de Itapeva	campos de altitude[a]	22°47′ S, 45°32′ W	1 850	0?–35 000	Behling, 1997a
MG	Catas Altas	semideciduous forest	20°05′ S, 43°22′ W	755	ca. 18 000– > 48 000	Behling and Lichte, 1997
MG	Lago dos Olhos	semideciduous forest	19°38′ S, 43°54′ W	730	0–19 000	De Oliveira, 1992
MG	Lagoa Santa	semideciduous forest	19°38′ S, 43°54′ W	730	0–6 200	Parizzi et al., 1998
MG	Lagoa Silvana	semideciduous forest	19°31′ S, 42°25′ W	ca. 250	0–ca. 10 200	Rodriges-Filho et al., 2002
MG	Lagoa Nova	semideciduous forest	17°58′ S, 42°12′ W	390	100–10 020	Behling, unpubl. data
MG	Lago do Pires	semideciduous forest	17°57′ S, 42°13′ W	390	0–9 700	Behling, 1995b

[a] With *Araucaria* forest.

Campos de altitude is rich in endemic species and occurs on several mountain peaks in S and SE Brazil (Ferrão and Soares, 1989).

The grass-dominated tropical savanna formations in SE Brazil, all included within cerrado, range from tropical grasslands (campo limpo), to grasslands with small shrubs and occasionally small trees (campo sujo), open or closed low-tree and or -scrub woodlands (campo cerrado), to tree and scrub woodland with 2–5 m tall trees and an open tree canopy (cerrado, in the strict sense) (Eiten, 1972, 1982). Grass layers of different densities are found in these cerrado types. Fires occur frequently in the cerrado vegetation.

The modern forest and grassland biomes of S and SE Brazil are strongly influenced by human activity. Forest clearance and the transformation of the landscape by agriculture and pasture have markedly changed the original vegetation. Only a few small natural grassland areas remain in S and SE Brazil.

3. Methods and available pollen records

Pollen analysis of Late Quaternary peat, lake or other organic deposits is one important tool to reconstruct the history of grasslands. Grass and sedge pollen in conjunction with pollen from other components of the grassland species allow identification of grassland communities. The site specifics and the pollen proportions of the local vegetation, including the vegetation of the peat bog or the lake margin, has to be taken into account when reconstructing the palaeovegetation of the study region. Further, the abundance of carbonised particles in the studied sediment core provide data on the past fire frequency. Frequent fire may indicate an open landscape covered by grassland.

Table 1 lists available pollen records relevant for regional palaeograssland reconstruction in S and SE Brazil, including information of the location, elevation, radiocarbon age range of the

studied deposits and references. Fazenda do Pinto, Serra do Rio Rastro, Morro da Igreja, Serra da Boa Vista and Serra Campos Gerais are small peat bogs (between 300 and 2000 m^2) in the campos and *Araucaria* forest region on the S Brazilian highlands (Figs. 1 and 2). Volta Velha samples come from organic-rich deposits in a old beach-ridge 'valley' that is located in the coastal lowland of the tropical Atlantic rainforest region. The studied organic rich deposits of small head-water areas from Botucatú and Catas Altas are located in the semideciduous forest region of the SE Brazilian highlands. The pollen record Morro de Itapeva is from a small peat bog in the Campos Jordão mountain region, which is part of the Serra da Mantiquera. The modern vegetation of this mountain area is *Araucaria* forest and campos de altitude. Lago do Pires is a small lowland lake in the semideciduous forest zone. The proportion of local pollen from the peat bog, head-water area or lake-shore vegetation of all of these sites is low, because of the very small area of the collecting basins.

In Fig. 3, summary pollen diagrams from four selected sites representative of the different regions in S and SE Brazil show the pollen sum of the different ecological groups. For the extended pollen records, see the original publications (Table 1).

4. Palaeograsslands in S and SE Brazil during the Late Quaternary

4.1. Late Glacial period in S Brazil

The Serra da Boa Vista pollen record from the S Brazilian highland extends back to 14 000 ^{14}C yr B.P. and indicates the predominance of campos vegetation during the Late Glacial period, where today *Araucaria* forests would dominate (Behling, 1995a). Other records, which span at least part of the last glacial period, show also the predominance of campos vegetation. Extensive areas with campos vegetation coupled with rare occurrences of *Araucaria* forest trees, suggest a cold climate with strong frosts and minimum temperatures below −10°C. An average annual temperature depression for the Late Glacial period in the range of 3–5°C is possible. A charcoal record from the S Brazilian highlands indicates that fire was relatively rare in the campos vegetation of Serra Campos Gerais during the Late Glacial period (Behling, 1997a). The lower frequency of fire suggested by this record may indicate that this period was wetter than the early Holocene period and/or that first humans may not yet arrived in this region.

The 26 000 ^{14}C yr B.P. pollen record from the Volta Velha forest reserve, located in the southern Atlantic lowland (near the border between the states of SC and PR) documents that grassland and cold-adapted forests occurred in the southern tropical Atlantic rainforest region during full-glacial times (Fig. 1; Behling and Negrelle, 2001). During the last glacial maximum (LGM) period in particular, grasslands were abundant in the coastal lowland and on the exposed continental shelf, while tropical trees (e.g. *Alchornea*, palm trees) were almost absent. Grasslands and cold-adapted forest replaced the tropical Atlantic rainforest. Tropical forest must have been shifted at least 500 km further north, indicating a cooling of about 3–7°C for the LGM (Behling and Negrelle, 2001). After 12 300 ^{14}C yr B.P., tropical rainforests replaced these cool grassland communities.

4.2. Last glacial period in SE Brazil

The pollen records from Botucatú and Catas Altas cover a period between 30 000 and ca. 18 000 ^{14}C yr B.P. and between $>48\,000$ and ca. 18 000 ^{14}C yr B.P., respectively. These records indicate an almost treeless, Late Pleistocene landscape of grassland vegetation where today tropical semideciduous forest exists. Abundant charcoal suggests frequent fires at that time. Only very few stands of subtropical *Araucaria* forest trees occurred along water courses with sufficient moisture. *A. angustifolia* and *Podocarpus* were absent (Botucatú) or rare (Catas Altas). The mostly treeless landscape reflects cold and dry climatic conditions. The calculated average annual palaeotemperature was at least 5–7°C lower than today (Behling and Lichte, 1997).

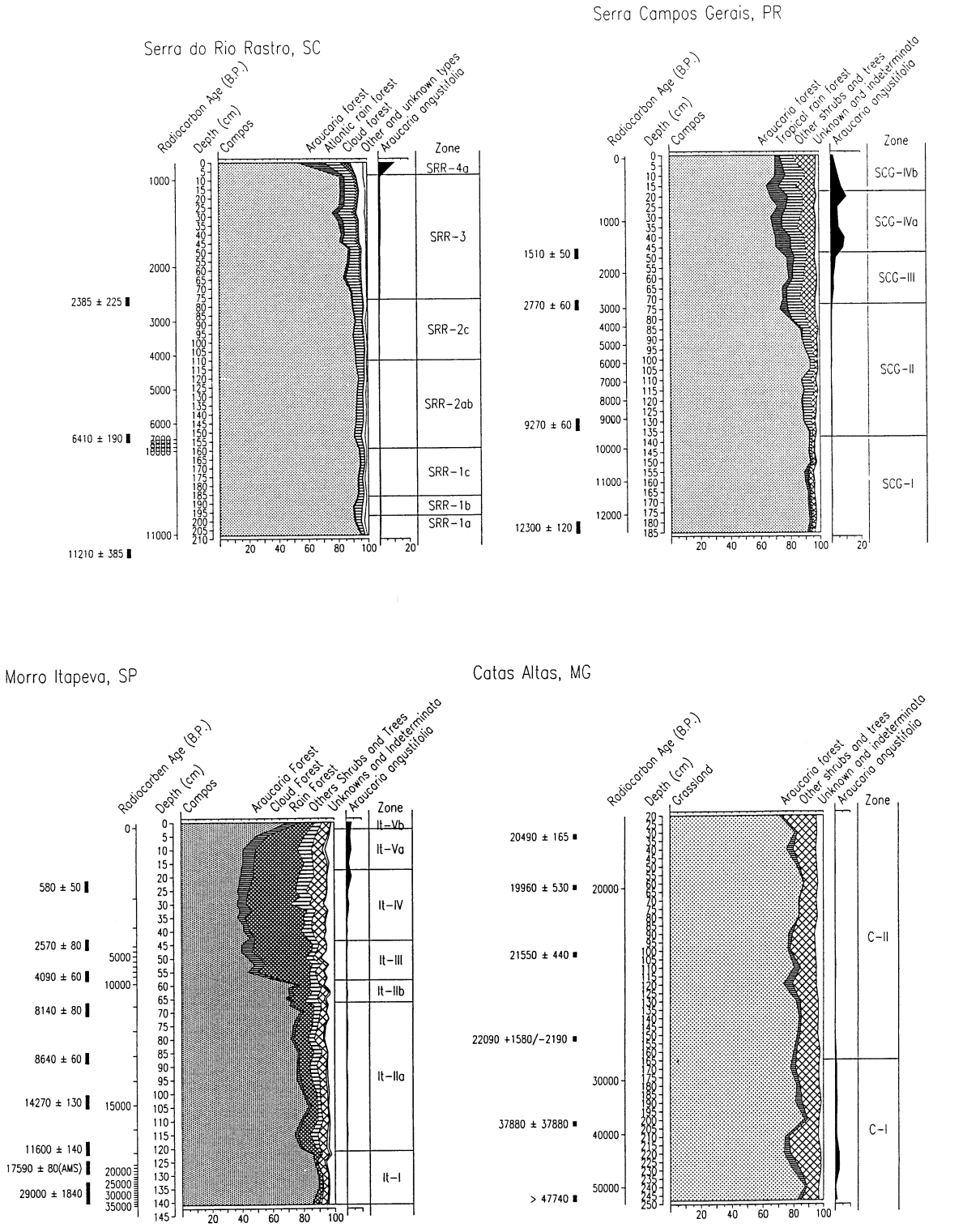

Fig. 3. Summary diagrams of four selected sites, Serra do Rio Rastro (Behling, 1995a), Serra Campos Gerais (Behling, 1997b), Morro de Itapeva (Behling, 1997a) and Catas Altas (Behling and Lichte, 1997) from S and SE Brazil.

Pollen data from Morro de Itapeva (1850 m elevation) show that during the last glacial period, from about 35 000 to 17 000 ^{14}C yr B.P., the Campos do Jordão highland region was treeless and covered by high-elevation grassland, reflecting a cold and dry climate. Between 17 000 and 10 000 ^{14}C yr B.P., *Araucaria* forest, cloud forest and Atlantic rainforest species expanded into the mountain regions, but were still rare and probably grew mostly at lower elevations. This vegetational change indicates a somewhat warmer Late Glacial climate than during full-glacial times (Behling, 1997b).

Abundant palaeofires may have markedly influenced the floristic composition of the grassland communities in SE Brazil. In addition, the pollen diversity of herb taxa in the SE Brazilian grasslands during the glacial period was relatively low, compared to the modern campos vegetation in S Brazil.

4.3. Holocene period in S Brazil

The pollen analytical results from Fazenda do Pinto (RS), Serra do Rio Rastro, Morro da Igreja, Serra da Boa Vista (SC), and Serra do Campos Gerais (PR) show that huge areas of campos vegetation continued to dominate the landscape of the S Brazil highlands during early and mid-Holocene times. This vegetation reflects warm and dry climates with an annual dry season of probably about 3 months (Behling, 1997b). Initial expansion of *Araucaria* forests started from gallery forests along the rivers about 3000 ^{14}C yr B.P., and indicates a somewhat wetter climate than the early and mid-Holocene. A pronounced expansion of *Araucaria* forests on the highlands, replacing the campos vegetation, is found in RS and SC after 1000 ^{14}C yr B.P. and in PR (Serra Campos Gerais) after 1500 ^{14}C yr B.P. This Late Holocene period is apparently characterised by a very humid climate without a marked annual dry period as is found today on the S Brazilian highlands. Today, *Araucaria* forest is expanding under natural conditions (e.g. Klein, 1960; Rambo, 1956, 1960).

4.4. Holocene period in SE Brazil

Few publications describe the Holocene vegetation and climate history of SE Brazil (e.g. De Oliveira, 1992; Behling, 1995b; Parizzi et al., 1998). The record from Lago do Pires (390 m elevation), located in the semideciduous forest region of the Atlantic lowland, indicates cerrado (campo cerrado with a dense grass layer) in the study region during the early Holocene period until 5500 ^{14}C yr B.P. Palaeofires were frequent. Subsequently, semideciduous forest expanded markedly and replaced the remaining cerrado. Similar vegetational changes are also recorded from Lagoa Santa, Lago dos Olhos, Lagoa Silvana, and Lagoa Nova. Larger areas of cerrado during the early Holocene period reflect a drier climate with a long annual dry season of 5–6 months. The relatively wettest Holocene period occurred in the last 1000 yr, as inferred from the Lago do Pires record (Behling, 1995b). During this time, only semideciduous forests were found and fires were very rare.

5. Discussion, conclusions and outlook

The review of 14 S and SE Brazilian pollen records shows that during Late Glacial times large areas of the southern highlands were primarily covered by subtropical grassland. The records indicate that subtropical grassland vegetation, which is found today as natural patches on the highlands in S Brazil (especially in SC), expanded from S Brazil over more than 750 km to SE Brazil, from latitudes of about 28°/27°S to at least 20°S. Also, the southern coastal lowland rainforest was mostly replaced by grassland and cold-adapted forest during the pre- and full-glacial period. Thus, grasslands were the major biomes in southern Brazil during the last glacial period where different forest biomes exist at present. The Antarctic cold fronts must have been much stronger, more frequent and displaced further North during glacial times. The average annual temperature was about 5–7°C cooler than today.

Due to the colder climatic conditions, the frost-sensitive cerrado vegetation must have also shifted further north where frosts were rare or absent (Silberbauer-Gottsberger et al., 1977).

Charcoal records indicate palaeofires were frequent in the SE Brazilian grasslands, while fires were probably rare in S Brazil during glacial times, as shown from the Serra Campos Gerais record. This may be related to even drier Late Pleistocene conditions in SE Brazil than in S Brazil. The ITCZ may have migrated seasonally within a narrow band at that time, reducing precipitation and enhancing seasonality in SE Brazil (Behling and Hooghiemstra, 2001). More palaeofire records from S Brazil are required to confirm this observation.

During the Late Glacial period, subtropical grassland in the northern region of the SE Brazilian highlands was replaced by tropical cerrado vegetation related to the warmer climatic conditions. In addition, cerrado expanded eastwards during the Late Glacial period and occurred also in the Atlantic lowlands. During the early Holocene, the area of cerrado vegetation in SE Brazil was markedly larger than during the Late Holocene period. Since around 5500 ^{14}C yr B.P. and especially after 1000 ^{14}C yr B.P., cerrado was replaced by semideciduous forest due to the shorter annual dry season and wetter climatic conditions. Isolated patches of cerrado occur at present in the area of semideciduous forest in southern SE Brazil (Hueck, 1956). This suggests that they may be remnants of a farther-southward distribution area during the early Holocene period. Although during the early and mid Holocene period SE Brazilian grasslands were replaced by cerrado and semideciduous forests, Late Pleistocene grassland still remained on the highlands in S Brazil. This vegetation remained due to a climate marked by low precipitation and a long annual dry period, probably up to 3 months in length in this region at this time (Behling, 1997a). Only during the Late Holocene period, after about 3000 ^{14}C yr B.P., did *Araucaria* forests expanded into the campos. The strongest expansion of *Araucaria* forest occurred during the last 1000 yr in SC and during the last 1500 yr in PR. During the Late Holocene period and especially over the last 1000/1500 yr, the climate has changed to wet conditions without long dry periods.

The synthesis of the southern Brazilian records documents dry full-glacial climatic conditions as summarised from the pollen records from the savannas south and north of the Amazon. Early Holocene dry conditions are also found in the S and SE Brazilian regions. The change to wetter climatic conditions started around 6000–5000 ^{14}C yr B.P. in SE Brazil and even later, around 3000 yr B.P., in S Brazil. The wettest Holocene period in S and SE Brazil (Lago do Pires), is the last 1000 yr, but a similar Late Holocene wet period is not found clearly in the equatorial regions. The differences in the chronology of vegetation shifts are still unclear and have to be analysed in detail. While the ITCZ plays a central role in the equatorial tropics, the annual movement of the ITCZ plays only a minor part in S Brazilian climate. Instead, in S Brazil, the Antarctic cold fronts are important. The system of Antarctic cold fronts may have changed during the Late Holocene period.

Despite the increased number of available pollen records, the history of the S and SE Brazilian grassland biota is still little-known. There are large regions, such as the southern regions of RS or the western part of the S Brazilian highlands, where no pollen records exist. Additional pollen records from the existing 'white spots' are important for modelling of palaeovegetation such as the BIOME-projects. An interesting question for palaeoclimatic research is also to know exactly how far to the North grasslands expanded during glacial times, especially during the LGM period. This may provide a precise-palaeotemperature reconstruction. Studies of carbon isotope ratios, indicating changes in C_3 and C_4 grass distribution, of fossil phytolith assemblages and of grass epidermal fragments during the Late Quaternary would greatly enhance our understanding of palaeograssland distribution and floristic composition in southern Brazil. Investigation of past pollen diversity may also serve as a tool to study changes on past grassland diversity. Multivariate analysis of fossil pollen may provide additional insight to past dynamics of subtropical and tropical grass-dominated biomes. More detailed stud-

ies of past fire frequencies may yield better understanding of the role of fire in grassland ecosystems.

Acknowledgements

The reviewers Kristina Beuning, Vera Markgraf and Sarah E. Metcalfe are thanked for providing constructive reviews. The 'Deutsche Forschungsgemeinschaft (DFG)' is acknowledged for the support while preparing this paper.

References

Behling, H., 1995a. Investigations into the Late Pleistocene and Holocene history of vegetation and climate in Santa Catarina (S Brazil). Veg. Hist. Archaeobot. 4, 127–152.

Behling, H., 1995b. A high resolution Holocene pollen record from Lago do Pires, SE Brazil: Vegetation, climate and fire history. J. Paleolimnol. 14, 253–268.

Behling, H., 1997a. Late Quaternary vegetation, climate and fire history in the *Araucaria* forest and campos region from Serra Campos Gerais (Paraná), S Brazil. Rev. Palaeobot. Palynol. 97, 109–121.

Behling, H., 1997b. Late Quaternary vegetation, climate and fire history from the tropical mountain region of Morro de Itapeva, SE Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 129, 407–422.

Behling, H., Bauermann, S.G., Neves, P.C., 2001. Holocene environmental changes from the São Francisco de Paula region, southern Brazil. J. South Am. Earth Sci., 14, 631–639.

Behling, H., Hooghiemstra, H., 2001. Neotropical savanna environments in space and time: Late Quaternary interhemispheric comparisons. In: Markgraf, V. (Ed.), Interhemispheric Climate Linkages. Academic Press, pp. 307–323.

Behling, H., Lichte, M., 1997. Evidence of dry and cold climatic conditions at glacial times in tropical southeastern Brazil. Quat. Res. 48, 348–358.

Behling, H., Negrelle, R.R.B, 2001. Late Quaternary tropical rain forest and climate dynamics from the Atlantic lowland in southern Brazil. Quat. Res., 56, 383–389.

Behling, H., Lichte, M., Miklos, A.W., 1998. Evidence of a forest free landscape under dry and cold climatic conditions during the last glacial maximum in the Botucatú region (São Paulo State), southeast Brazil. Quat. South Am. Antarct. Penins. 11, 99–110.

De Oliveira, P.E., 1992. A palynological record of late Quaternary vegetational and climatic change in southeastern Brazil. Ph.D. Thesis, The Ohio State University, Columbus, OH, 238 pp.

Eiten, G., 1972. The cerrado vegetation of Brazil. Bot. Rev. 38, 205–341.

Eiten, G., 1982. Brazilian 'savannas'. In: Huntley, B.J., Walker, B.H. (Eds.), Ecology of Tropical Savannas. Ecological Studies 42. Springer, Berlin, pp. 25–47.

Ferrão, C., Soares, J.P.M., 1989. Campos de altitude. Editora Index, Rio de Janeiro, 159 pp.

Hastenrath, S., 1991. Climate Dynamics of the Tropics. Kluwer Academic Publishers, Dordrecht, 488 pp.

Hueck, K., 1953. Distribuição e habitat natural do Pinheiro do Paraná (*Araucaria angustifolia*). Bolm. Fac. Filos. Ciênc. Univ. São Paulo, Bot. 10, 1–24.

Hueck, K., 1956. Die Ursprünglichkeit der brasilianischen 'Campos cerrados' und neue Beobachtungen an ihrer Südgrenze. Erdkunde 11, 193–203.

Hueck, K., 1966. Die Wälder Südamerikas. Fischer, Stuttgart, 422 pp.

Klein, R.M., 1978. Mapa fitogeográfico do estado de Santa Catarina. Flora Ilustrada Catarinense.

Klein, R.M., 1979. Ecologia da flora e vegetação do Vale Itajai. Sellowia 31, 1–164.

Klein, R.M., 1960. O aspeto dinâmico do pinheiro brasileiro. Sellowia 12, 17–44.

Nimer, E., 1989. Climatologia do Brasil. IBGE, Rio de Janeiro, 421 pp.

Parizzi, M.G., Salgado-Labouriau, M.L., Kohler, H.C., 1998. Genesis and environmental history of Lagoa Santa, southeastern Brazil. Holocene 8, 311–321.

Por, F.D., 1992. Sooretama the Atlantic rain forest of Brazil. SPB Academic Publishing bv, The Hague, 130 pp.

Rambo, B., 1956. A flora fanerogâmica dos Aparados riograndenses. Sellowia 7, 235–298.

Rambo, B., 1957. Regenwald und Kamp in Rio Grande do Sul. Sellowia 8, 257–298.

Rambo, B., 1960. Die Südgrenze des brasilianischen Regenwaldes. Pesqui. Bot. 8, 1–41.

Rodriges-Filho, S., Behling, H., Irion, G., Müller, G., 2002. Evidence for late formation as a response to an inferred Holocene climatic transition in Brazil. Quaternary Research 57, 1–7.

Safford, H.D., 1999a. Brazilian Páramos I. An introduction to the physical environment and vegetation of the campos de altitude. J. Biogeogr. 26, 693–712.

Safford, H.D., 1999b. Brazilian Páramos II. Macro- and mesoclimate of the campos de altitude and affinities with high mountain climates of the tropical Andes and Costa Rica. J. Biogeogr. 26, 713–737.

Seibert, P., 1996. Farbatlas Südamerika: Landschaft und Vegetation. Stuttgart, Ulmer, 288 pp.

Silberbauer-Gottsberger, I., Morawetz, W., Gottsberger, G., 1977. Frost damage of cerrado plants in Botucatu. Biotropica 9, 253–261.