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Paleo-environmental change in Amazonian and African rainforest during the LGM

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Abstract

The paper provides new and comparative insight into the ecological history of the two largest continental tropical forest areas during the Last Glacial Maximum (LGM). The tropical forest regions are of particular interest because they present a large source of heat and have been shown to have significant impact on the extra tropical atmospheric circulation. They are also the most intense land-based convective centers. Thus, especially from the tropics paleoecological information is needed as benchmarks for climate modeling. The African data for LGM climates were published earlier including the reconstructed paleoprecipitation patterns deduced from SSTs.

The tropical South American LGM data were interpreted from pollen, geochemical, and $\delta^{18}O$ (stable oxygen isotope) data from Brazil and selected surrounding areas. The available terrestrial data are consistent with the SST derived precipitation data for the tropical forests in Brazil and for Africa. However, the impact of LGM climate extremes was less severe in the Amazon than in the Congo basin. The LGM humid forest area (including evergreen and semi-deciduous forest types) in Africa was probably reduced by 84%. In contrast, the Amazon humid forest area probably shrank to 54% of their present-day extension. Still, there are different interpretations with respect to the amount of reduction of the Amazon forest

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area during the LGM. Although direct information about LGM climates in Amazonia is still limited the more detailed map obtained in the present work, however, allows a more reliable characterization of the last glacial tropical environment than previously published for the Amazon region.

Keywords: Last Glacial Maximum; Climate history; Vegetation history; Rain forest; South America; Africa

Contents

1. Introduction

Climate, climate changes, and climate predictability have become increasingly more important within social and scientific discussions since 1990. Climate changes, induced naturally or by human activities, have direct implications on our environment and therefore on human society. The knowledge of an enhanced human influence on the atmosphere and the earth's climate since the beginning of the 20th century has led to global collaboration to analyze the dimension, the causes and the consequences of the anthropogenically induced climatic change (Houghton et al., 2001) in order to predict the possible implications on future climate developments. This also includes a better understanding of natural variability and stability of the climate system in general. In order to model the climate system of the earth, either forwards into the future or backwards into the past, it is necessary to understand the Earth's system, especially the interactions between atmosphere, biosphere and ocean.

In order to verify the ability of global circulation models (GCMs) to simulate the changes in regional cli- mate under different boundary conditions, key periods of the past were selected worldwide (COHMAP, 1988). The Last Glacial Maximum (LGM) (18,000 ± 1000 ^{14}C yr BP) and the mid-Holocene are the two key periods adopted by the Paleoclimate Modeling Intercomparison Project (PMIP-IGBP-PAGES) (Joussaume and Taylor, 1995). The LGM represents an experiment with enlarged ice sheets and low atmospheric CO_2. The mid-Holocene represents by contrast an orbital forcing experiment, with the perihelion in the northern summer/autumn and a greater-than-present axial tilt.

Paleoclimate model reconstructions failed for South America mainly because of the scarcity of modern climate data and the sparse regional coverage of paleoclimate data (Farreira et al., 1999; Prentice et al., 2000). Special focus of this paper is the regional development of vegetation and climate of the Amazon and adjacent areas during the LGM that is not represented in the models. Amazonia covers the largest continuous tropical lowland forest area. Tropical forests contain as much as 40% of the carbon stored in terrestrial biomes and are home for up to 90% of all living species (Ozanne et al., 2003). As the Amazon basin provides 20% of the total fresh water worldwide, a reliable reconstruction of the ecological conditions — prevailing under different climatic scenarios in the past — is essential in achieving major progress in environmental modeling.

As the number of well-dated paleoecological sites has increased considerably during the last few years, at least since the last COHMAP and BIOME (Prentice et al., 2000) evaluations, the paper provides a much needed update of past ecological conditions and climates within the South American tropics and subtropics for the last 21,000 years with special emphasis on the LGM. The main progress is in assessing paleoprecipitation at the different sites. The comparison with available data from the African tropical forest enables the description of similarities and differences in the development of the ecological conditions for the tropical continental zones.

2. Study regions

2.1. Amazonia

The Amazon region is of particular interest because it represents a large source of heat in the tropics and has been shown to have a significant impact on the extra tropical circulation; also it is the largest and most intense land-based convective center (Grimm and Silva Dias, 1995; Marengo and Nobre, 2001). During the Southern Hemisphere summer when convection is best developed, the Amazon basin is one of the wettest regions on Earth. Amazonia, of course is not isolated from the rest of the world and a global perspective is needed to understand the nature and causes of climatological anomalies in Amazonia and how they feed back to influence the global climate system. With a modern mean precipitation of 2.0–5.9 m/yr (Figueroa and Nobre, 1990; Marengo and Nobre, 2001), Amazonia's climate is likely to limit the environmental response to a precipitation change that would drastically alter the vegetation of the generally drier region of equatorial Africa (Anhuf, 2000). Nevertheless, an Amazonian "Dry Corridor" exists nowadays between Belém (1°28′S, 48°27′W) and Santarém (2°25′S, 54°42′W) with a mean annual precipitation below 1.75 m/yr (Figueroa and Nobre, 1990; Van der Hammen and Absy, 1994). But even this drier area is covered with evergreen and semi-deciduous forests today.

To describe the situation within the Amazon basin during the LGM we subdivide the region into five different areas. The northeastern Amazon covers the sector east of the "Dry Sector", the "Dry Sector" itself, the northwestern part of the Amazon (west of the dry sector and north of the equator), the central part (west of the Dry Corridor and between 0°N and 10°S, and the western and southwestern part (west of 70°W and south of 10°S). The modern natural vegetation distribution was adopted from the widely accepted IBGE system (Fig. 1) (Veloso et al., 1991).

Annual rainfall in northern South America varies greatly from less than 400 mm in Northeast Brazil and some parts of the Caribbean coast of South America to more than 3000 mm in the upper watershed of Rio Negro. Three centers of abundant rainfall in the Amazon basin can be identified. One is located in Northwest Amazonia, with more than 3600 mm per year. Another region with abundant rainfall is the central part of Amazonia around 5°S with 2400 mm per year. A third center is found in the northeastern area close to the mouth of the Amazon River near Belém, with more than 2800 mm per year. In the Rio Negro basin area, in northwestern Amazonia, the rainfall is abundant throughout the year reaching its maximum from April to June. In the central, the western and southwestern Amazon areas the rainy season is concentrated during the southern hemisphere summer (November–March/April) providing almost 80% of the total annual amount (Rao and Hada, 1990; Figueroa and Nobre, 1990; Marengo, 2003). The extremely high and localized values of precipitation in narrow strips along the eastern side of the Andean slopes are thought to be due to upslope condensation and a rain shadow effect on the lee side.

The coastal maximum is caused by nocturnal convergence between the trade wind and the land breeze (Marengo and Nobre, 2001). Today's dry sector in the eastern Amazon is related to the fact that as the sea breeze squall lines propagate to the West/Southwest, they travel over this region during the night, when the intensity of the system is at a relative minimum (Cohen et al., 1995). As the sun rises, the squall line intensity peaks up and heavier precipitation is expected to the West. The LGM displacement of the coast due to generally lower sea levels of the order of 120 m would have had a significant impact on the horizontal distribution of precipitation in view of this mechanism. Thus, the area directly influenced by the sea breeze climates would have been located 200 to 500 km to the Northeast.

The northeastern Amazon, the "Dry Sector", and the northwestern Amazon region as well as the northeastern Brazilian coast between Fernando de Noronha and Salvador receive a considerable part of their rain during the northern hemisphere summer (April to September) (Uaupés 50%, Belém 44%, Santarém 50%, Salvador 64%, and Recife/Olinda 73% (Ratisbona, 1976)). Although the timing of the annual cycle of rainfall is largely

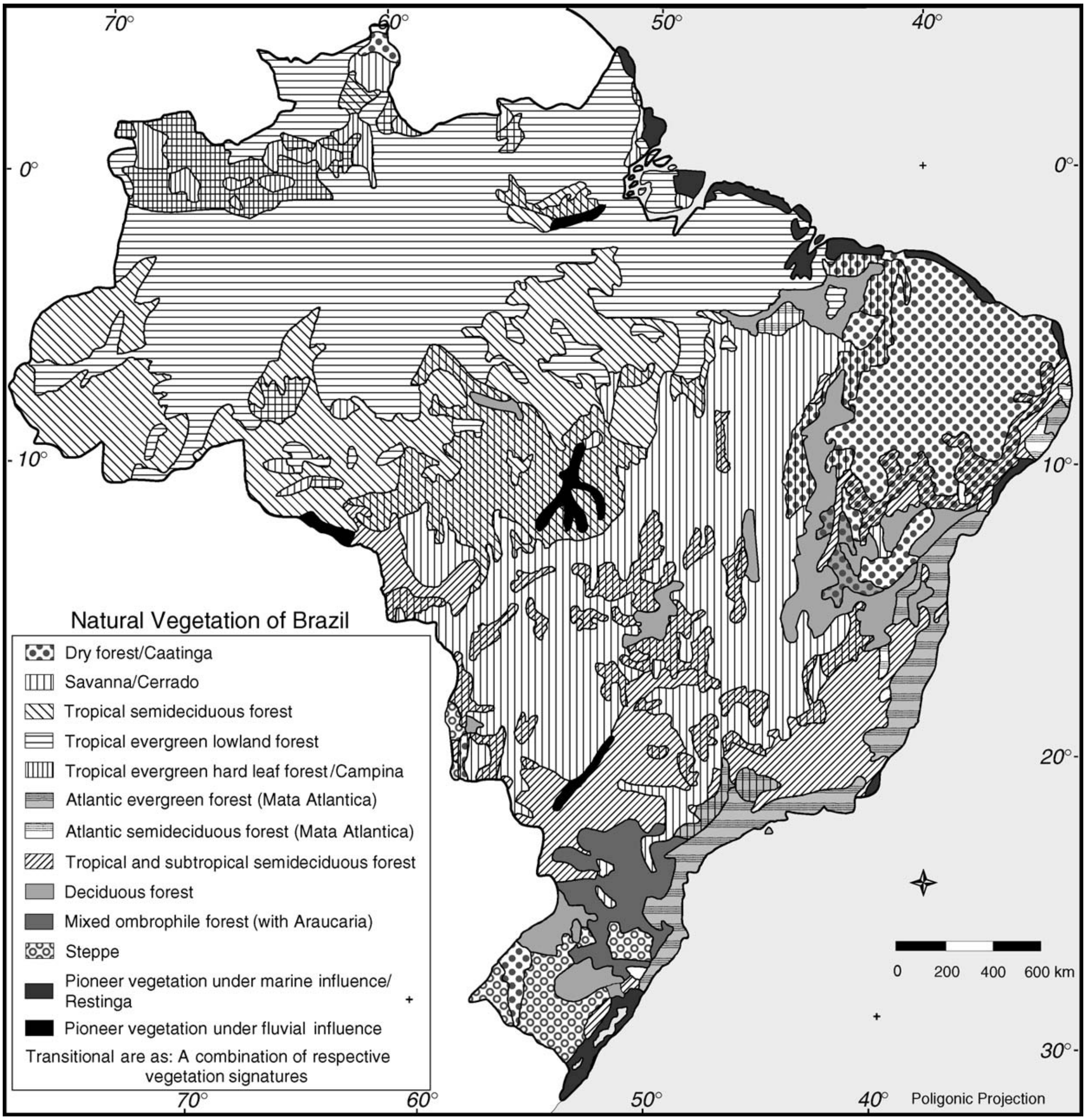

Fig. 1. Vegetation map of Brazil (adapted from IBGE, 1993).

controlled by the sun, rainfall in different parts of the basin is triggered by different rain producing mechanisms (Garreaud and Wallace, 1998; Fisch et al., 1998).

Regional water balances are calculated based on stream flow data, observed precipitation and evapotranspiration measurements. Studies on recycling of water in the hydrological cycle of the Amazon basin have been performed during the last two decades by Lettau et al. (1979), Salati (1987), Salati et al. (1979), Salati and Voce (1984), Salati et al. (2001), and Eltahir and Bras (1993). All of them indicate the active role of the evapotranspiration from the tropical forest in the regional hydrological cycle, although the latter study indicates a lesser role. The aerological estimates of the evapotranspiration over the eastern and central parts of the basin averaged 3 to 3.5 mm/day. The different estimates of moisture recycling in the Amazonia vary from 25% to 75% related to the percentage of total annual rainfall of the Amazon basin originating from water vapor import from the tropical Atlantic.

2.2. Congo basin

In contrast to the Amazon basin, the Congo basin receives lower annual precipitation, in general less than 2000 mm/yr (UNESCO, 1978). Higher rainfall, comparable to that of the western Andean ridge, are registered only in areas with considerable topographic relief like the east African ridge, the southern side of Mount Cameroon and along the Guinean Highlands between Greenville (5°01′N, 9°03′W) and Cape Palmas (4°25′N, 7°50′W). The amount of precipitation as well as the duration and the annual distribution of rainfall depends on the major water vapor sources for Africa, the South–East Atlantic along the west coast of Africa and the Indian Ocean along the east side of the continent.

In Africa, the humid tropical forests which dominate the floristic Guinea region, are subdivided into evergreen forests (Fig. 2), in which the annual dry season does not exceed two months, and into semi-deciduous forests with no more than three to four dry months (Anhuf, 2000). The Sudan region is dominated by dry forests and savannas, comparable to the Cerrado in South America. Most trees shed their leaves during the arid season when it lasts for more than four months.

The general atmospheric circulation over both equatorial areas is controlled by the seasonal movements of the ITCZ. Equatorial Africa consists of three main areas: the southern coast of west Africa between 5°N and 9°N, the Congo basin between 5°N and 6°S, and the equatorial east African highlands between 11°S and 14°N.

The large amounts of water vapor that maintain high rainfall quantities along the west African coast and within the Congo basin originate mainly from the southeastern Atlantic Ocean. However, rainfall totals in equatorial Africa are relatively modest compared to other equatorial regions within the tropics because the coastal areas adjacent to the Congo basin are often cooled by the Benguela current reducing the inflow of water vapor into the continent. The seasonal movements of the ITCZ create a major dry season during December, January, and February when dry northeasterly trade winds prevail over the region. When the ITCZ reaches its northernmost position in July and August a short dry season at the coast can sometimes be observed.

Generally exceptional low rainfall characterizes the equatorial region of east Africa. Two monsoon systems dominate the climate system. During the northern hemisphere winter (December to March) the dry northeastern monsoon passing over northeast Africa or the cool Somali current bringing mostly dry air masses into the equatorial region of the highlands. In spring, from March to June, the southwestern monsoon establishes resulting in the first "long" rainy season. During the ITCZ's northernmost position in July and August the equatorial east African highlands remain almost dry before the second "short" rainy season starts in October, lasting until the end of November, caused by the southward shift of the ITCZ.

West Africa and the Congo basin receive the water vapor from the east and southeast Atlantic when this is coolest (austral winter) and the water vapor pool of East Africa originates in the western Indian Ocean when it is warmest at the end of the austral summer.

3. The LGM in tropical South America

3.1. Amazon basin

The Amazon rainforest evolution during the glaciations of the Quaternary has been strongly debated during the last decade. The discussion — whether there was fragmentation of the forest or not — opened new ideas on how global climatic changes could impact the tropical rain forests. Two types of hypothesis emerged: 1) The Amazonian rain forest was fragmented in refugia islands or its areal extension remained relatively stable. 2) Its floristic composition was submitted to species re-associations because of connections with the Andean, Tepuyan, and Atlantic rainforest ecosystems. Both hypotheses came to the conclusion that the forest was different from the one we observe today and that it experienced transformations in distribution and floristic composition during the last glaciation. It also emphasized differences in the expression of the climatic signal between western and eastern Amazon basin (Colinvaux et al., 1996; Van der Hammen and Hooghiemstra, 2000; Colinvaux and De Oliveira, 2001; Van der Hammen, 2001; Haffer and Prance, 2001).

Only seven pollen records located in the Amazonian rain forest area including the Amazon fan date back to the last glacial maximum (Table 1): Katira (9°S, 63°W), Carajás (6°S, 50°W), Hill of Six Lakes (0°16′N, 66°4′W), Maicurú (0°30′S, 54°14′W), Laguna Bella Vista (13°37′S, 61°33′W), Laguna Chaplin (14°28′S, 61°04′W), ODP site 932 (5°13′N, 47°2′W (Absy et al., 1991; Van der Hammen and Absy, 1994; Siffedine et al., 2001; Colinvaux et al., 1996; Haberle and Maslin, 1999; Mayle et al., 2000; Santos et al., 2001; Colinvaux and De Oliveira, 2001; Bush et al., 2004).

A ^{14}C yr BP date of 18,500 at Katira is related to high frequencies of grass pollen and an almost total disappearance of arboreal pollen, while the ^{13}C values indicate the dominance of tropical grasses and colluvial

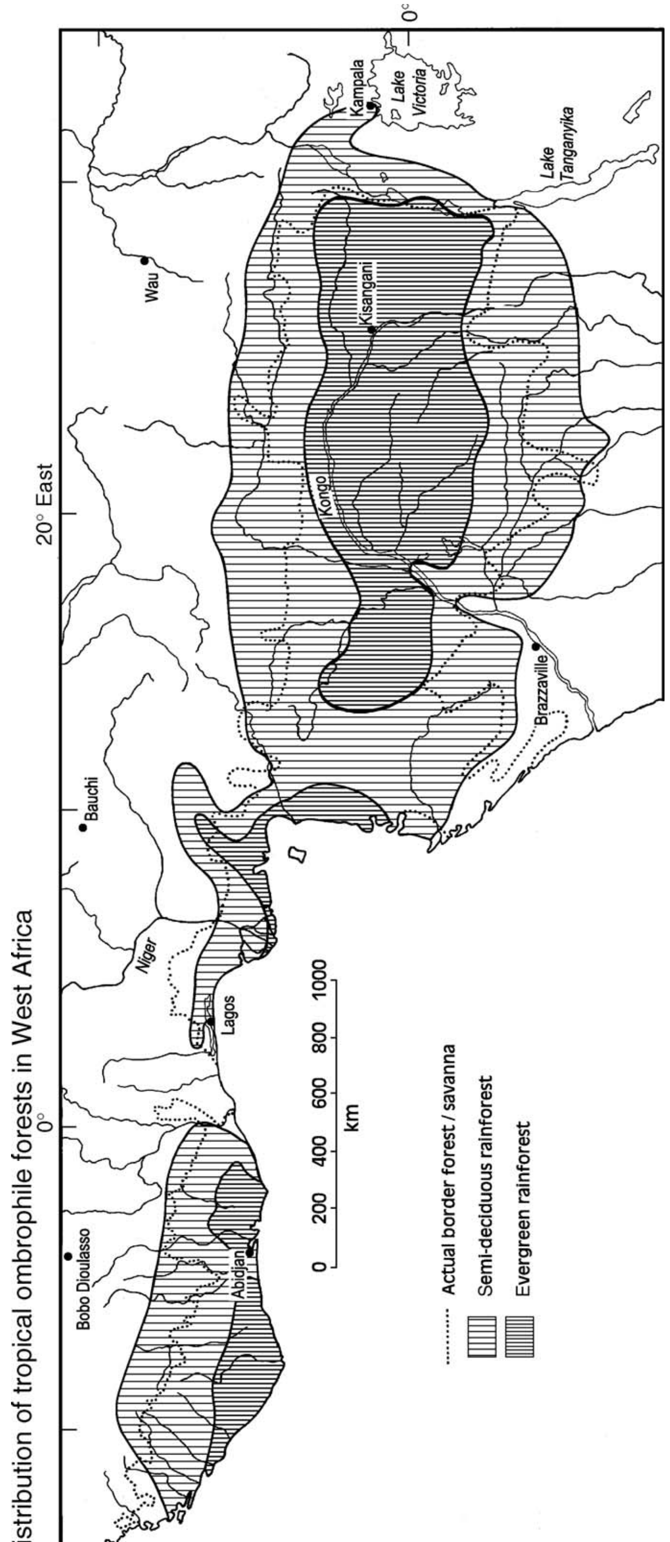

Fig. 2. Distribution of tropical humid forests in west Africa.

Table 1
Sites providing dated information of LGM ecological conditions based on pollen or plant macrofossil data within the Amazon Basin (01–08) and from the Amazon fan (09)

Number	Site	Location	Elevation (a.s.l.)	Actual climate	Actual vegetation	18 000 ^{14}C years BP climate	18 000 ^{14}C years BP vegetation	Reference
01	Laguna el Pinal (Colombia)	4°08′N/71°23′W	180	1200–2000 mm 4–5 dry months	Grass savanna and gallery forests with Mauritia palms	Less rainfall than today or longer dry season	savanna	Behling and Hooghiemstra, 1999
02	Lagoa Pata Lagoa Gragao Lagoa Verde (Seis Lagos)	0°16′N/66°41′W	250–300	>3000 mm no dry season	Tropical rainforest	5°C cooler, drier: Lake level decrease	Rainforest expansion of *Araucaria* + *Weinmannia*	Colinvaux et al., 1996, Santos et al., 2001, Bush et al., 2004
03	Maicuru	0°30′S/54°14′W	550	2000–2500 mm 3 months little rain	Forest	?	Hiatus	Colinvaux and De Oliveira, 2001
04	Carajas	6°20′S/50°25′W	700	1500–2000 mm 3 months little rain	Tropical rainforest, Edaphic savannas	>30% less rain	Hiatus Savanna expansion before and after	Absy et al., 1991, Sifeddine et al., 2001
05	Katira	9°S/63°W	<200	2000–2500 mm	Tropical rainforest	Very dry 1000–1500 mm	Dry grass savanna at 18 500 years B.P.	Van Der Hammen and Absym, 1994
06	Forest (46)	8°21′S/63°57′W	80–150	1800–3500 mm 3–4 months little rain	Forest	Wetter Cooler?	Forest	Freitas et al., 2001
07	Noel Kempff Laguna Bella Vista	13°37′S/61°33′W	210	1500 mm	Tropical rainforest/dry deciduous forest	?	Hiatus	Mayle et al., 2000
08	Noel Kempff Laguna Chaplin	14°28′S/61°04′W	210	1500 mm	Tropical rainforest/dry deciduous forest	?	Savanna	Mayle et al., 2000
09	ODP 932	5°13′N/47°2′W	–3334	~2700 mm (Belém) No dry season	Tropical rainforest (Belém)			Haberle and Maslin, 1999

sedimentation indicates even an incomplete vegetation cover (Absy and Van der Hammen, 1976; Van der Hammen and Absy, 1994). The Hill of Six Lakes has been intensively investigated since 1996 by Colinvaux and his colleagues showing that forest taxa dominated the vegetation cover also during the LGM (Bush et al., 2004). Mayle et al. (2000) report from Laguna Chaplin that savanna communities dominated the respective area continuously between 40,000 and 2240 ^{14}C yr BP. Haberle and Maslin (1999) published results from a deep-sea core from the Amazon fan covering the last 50,000 years. During the LGM the authors attested the lowest pollen concentration values within the whole time span, a significant increase of wind-transported pollen from Andean taxa like *Alnus* and *Podocarpus* but at the same time the pollen from Poaceae and Asteraceae remained low. The authors pointed out that no general change in Amazon ecosystems were detected but they also did not contradict to the possibility of a moderate extension of savanna ecosystems up to 32% of the entire catchment area. The respective core represents only a single late Quaternary fan record from the entire Amazon basin. Thus, it is advisable to be cautious in interpreting these data particularly when dating is based on an age model derived from $\delta^{18}O$ records and geomagnetic field excursion data.

All the following records show a hiatus in sedimentation between respectively 23,000 and 13,000 ^{14}C yr BP (Carajás), 30,000 and 16,000 ^{14}C yr BP or between 25,690 and 17,410 ^{14}C yr BP (Maicurú), and 38,600 and 11,030 ^{14}C yr BP (Laguna Bella Vista). This hiatus is associated with a lack of deposition of organic material during thousands of years (Ledru et al., 1998) and / or strong erosive conditions. Presence of tropical semi-deciduous dry forest at the Cerrado-rainforest boundary in northeastern Bolivia (Bella Vista: Mayle et al., 2000) was documented at ca. 30,000 yr BP after which a hiatus was recorded lasting until the beginning of the Holocene.

At Lagoa da Pata, geochemical analysis showed a sand layer intercalated by two organic-rich levels. This sandy facies with lower carbon and water content and high bulk density is interpreted to reflect sudden and torrential rains, typical of seasonal climates and different from today. After this probably drier episode, dated at ca. 18,000 ^{14}C yr BP, increase in lacustrine productivity associated to lake level rise is recorded documented by an increase in the chlorophyll derivates and the carbon flux. The C/N values dropped indicating an increase in algae organic matter contribution characteristic of open water. However, rainforest survived near Lagoa da Pata (Colinvaux et al., 1996) but possibly with more deciduous species (Van der Hammen and Hooghiemstra, 2000).

Analysis of Amazonian evaporation dependent vegetation and lakes also show a strong decrease in precipitation during the LGM, e.g. the tropical cloud forest of the Eastern Cordillera in Bolivia. Siberia, nowadays within the tropical cloud forest zone, is located at an altitude of 2920 m in Bolivia (17°50′S, 64°43′08″W) (Mourguiart and Ledru, 2003a). The LGM is represented by 2 m of sediment and 3 radiocarbon dates 23,660 ± 100, 21,900 ± 90, 19,150 ± 70 ^{14}C yr BP and shows low arboreal pollen frequencies, 4% to 10%, high quartz content to over 30% and low total organic carbon (TOC) of less than 0.5% suggested an open landscape and a dry, cold climate. More to the North, paleoenvironmental data from Lake Huiñamarca, is actually connected to L. Titicaca today as a sub-basin, (16°20′S, 68°57′45″W, at an altitude of 3810 m and under 19 m depth of water), with 4 radiocarbon dates (21,000 ± 260, 19,625 ± 220, 19,090 ± 200, 18,185 ± 180 ^{14}C yr BP) within 2 m of sediment deposition reveal low TOC values and high percentages for *Isoetes*, a submerged fern in oligotrophic waters, for *Valeriana*, a herb from mesic wetlands of the high Andes, and low algal frequencies (Mourguiart and Ledru, 2003a). Lake Huiñaimarca attests of at least a reduction of ~18 m of water which was not perceptible under 120 m depth of water in Lake Titicaca (Mourguiart and Ledru, 2003b). These data confirm a relatively low reduction in water level in the Andes of Bolivia compared to other regions of tropical South America.

3.2. Border and surrounding areas of the Brazilian Amazon basin

3.2.1. Cerrado-humid forest transitions

Carbon isotopes (^{12}C, ^{13}C, ^{14}C) of soil organic matter were used to evaluate and establish the chronology of past vegetation of patches of Cerrado surrounded by rainforest in the states of Rondônia and Amazonas. Large ranges in $\delta^{13}C$ values were observed from profiles obtained in the Cerrado area (−27‰ to −14‰) and in the forest (−26‰ to −19‰) reflecting changing distribution of ^{13}C-depleted C3 forest and ^{13}C-enriched C4 grassland vegetation. At the base of the soil profiles, between 17,000 and 9000 ^{14}C yr BP (km 46: 16,940 ± 140 ^{14}C yr BP), $\delta^{13}C$ values reflect C3 plants documenting presence of forest (Freitas et al., 2001). This corresponds to the edge of the predicted forest patch in the LGM vegetation map of Van der Hammen and Hooghiemstra (2000) and Van der Hammen (2001) and the corresponding savanna-forest gradient Katira–Porto Velho–Humaitá. $\delta^{13}C$ data also indicate that savanna grasses (C4 plants) have influenced significantly the composition of the vegetation reflecting drier climates after 9000 ^{14}C yr BP (Pessenda et al., 1998). However, the isotope analysis based on the humin fraction do not give any evidences as to which kind of forest persisted shortly after the LGM in that specific area of southern Amazonia.

3.2.2. Northern neotropical savannas: Llanos Orientales

The LGM in the Llanos Orientales in Colombia in the Laguna El Pinal region (4°08′N/70°23′W) was characterized by savanna vegetation and with very few woody taxa. The respective vegetation reflects the driest climatic conditions of the last 18,000 years (Behling and Hooghiemstra, 2001).

4. Summary of the results for Amazonia

From the pollen and few geochemical records in the Amazon basin including the Amazon fan that date back to the LGM we have clear indication of a cooler climate with average temperature 4.5±1 or 5±1 °C lower than that of today for the region and the northeastern Brazil (Stute et al., 1995; Van der Hammen and Hooghiemstra, 2000; Bush et al., 2001). This fact might be responsible for the appearance of mountainous species like *Alnus* and *Podocarpus* in lowland Amazonian forest sites including the Amazon fan during the LGM (Haberle and Maslin, 1999).

Other observational evidences around the Amazon basin are available to give indirect information about the climate in the Amazon region: Reconstructions of temperatures in the Andes between 4000 and 1500 m altitude above sea level (asl) have been presented by Van der Hammen and Hooghiemstra (2000). They found that the glacial lapse rate was 0.76 °C/100 m, 0.16 °C/100 m steeper than present day. However, temperature is one of the aspects to be considered with respect to the impact of changing climate on the vegetation in mountainous regions.

Precipitation within the tropics shows a characteristic vertical distribution as a function of height above sea level. The zone of maximum precipitation is generally not located in the tropical lowlands, but within the mountainous belt between 800 and 1500 m (asl). Above the level of maximum condensation precipitation decreases considerably and a much weaker second condensation level can be observed between 2700 and 3200 m within the tropical cloud forests belt (Lauer, 1989).

Thus, the pollen records from Siberia (2920 m) and Lake Huiñaimarca (3810 m) are of some help to reconstruct the tropical lowland vegetation. Before the LGM (40,000–29,000 ^{14}C yr BP) the vegetation at Siberia was dominated by an open forest with cloud forest elements. Between 28,000 and 17,000 ^{14}C yr BP the arboreal pollen decreased to 4–10%. After 16,000 ^{14}C yr BP, Siberia showed an increase of open forest-taxa again. Considering that the temperature decreases by 5 °C (Stute et al., 1995) the zone of maximum precipitation was lowered by up to 500–600 m due to the lowering of the respective condensation levels if precipitations were similar to the modern ones. The respective pollen record from Siberia represented an open landscape and a dry and cold climate during the LGM. The modern-day Andean cloud forest, provided that forest type had survived during the LGM, might have descended to a level of about 2000 m (asl) during that period according to the LGM cooling. Thus, one would expect Andean forest pollen, especially all wind-transported pollen types, to occur in the Siberia record, which would have been ca. 800 m above the proposed LGM Andean forest limit. However, Mourguiart and Ledru (2003b) did not find any pollen from this lower cloud forest.

In the analysis of the cores obtained between BR 319, km 46 north of Porto Velho (8°21′S, 63°57′W) to the South including Katira (less than a hundred kilometers further south), Laguna Bella Vista, and Laguna Chaplin (14°28′S, 61°04′W) a clear change in the LGM vegetation cover appears. The records show forest in northern Rondônia, savanna at Katira, a hiatus at Bella Vista but clear indication of savanna vegetation at the southernmost end at Laguna Chaplin of this transect.

Nevertheless, an inconsistent picture of the LGM vegetation conditions in the Amazon basin remains. The point of view that claims that the Amazon lowland forests were not replaced by savanna during the LGM (Colinvaux and De Oliveira, 2001; Bush et al., 2002; Haberle and Maslin, 1999) can no longer be supported by the data. On the other hand, data support the view that the Amazon evergreen forest border on the northern hemisphere was located probably about 200 km further south and that the same border on the southern hemisphere was located probably 300 km further north during the LGM (Van der Hammen and Hooghiemstra, 2000; Behling, 2002) The latter was also corroborated by paleovegetation simulations (Cowling et al., 2001).

5. Summary of results from Africa

The available African sites with dated paleoenvironmental information have been discussed in detail in Anhuf (2000). Only the general picture of the LGM environment in tropical Africa is summarized below (Table 2).

Table 2
Selected sites providing dated information of LGM ecological conditions for tropical Africa between 10°S and 20°N (for further information see Anhuf 2000)

Number	Site	Location	Elevation (m)	Dated Material	^{14}C years BP	Author
01	74 KL, Arabian Sea	14°19′N/57°20′E	−3416	Carbonates	20 580−1280 BP	Sirocko et al. (1991)
02	Lake Abhé, Ethiopia	11°15′N/42°00′E	240	Diatoms, SLC	17,100±400 BP 20,500±400 BP	Gasse (1977)
03	Sacred Lake, Mt. Kenya, Kenya	0°10′S/37°19′E	2400	P	15,695±70 BP 20,265±80 BP	Olago et al. (2000)
04	Lake Naivasha, Kenya	0°45′S/36°20′E	1890	SLC	12,270±180 BP 20,900±1700 BP	Maitima (1991)
05	Mt. Elgon - Laboot Swamp, Kenya	0°57′N/34°37′30″E	2880	P	13,776±80 BP 23,073±120 BP	Hamilton (1982)
06	Cherangani Hills, Kaisungor Swamp, Kenya	1°12′N/35°15′E	2900	P	17,000±300 BP	Coetzee (1967)
07	Karimu, Kenya	0°30′S/36°41′E	3040	P	17,900±150 BP 21,540±160 BP	Perrott and Street-Perrott (1982)
08	Pilkington Bay, Uganda	0°18′N/33°20′E	1134	P	14,730±200 BP	Kendall (1969)
09	Lake Mobutu, Uganda	1°50′N/31°10′E	619	P	14,700±260 BP 20,120±200 BP	Beuning et al. (1997)
10	Ahakagyezi (AH 2), Uganda	1°07′S/29°54′E	1830	P	15,640±110 BP 18,770±120 BP	Taylor (1990)
11	Sd-24 Lake Tanganyika, Tanzania	4°30′S/29°20′E	773	P	16,817±156 BP 32 328±894 BP	Vincens (1993)
12	Kamiranzowu Swamp, Rwanda	2°25′S/29°18′E	1950	P	15,745±150 BP 22,120±250 BP	Hamilton (1982)
13	K - Kuruyange, Burundi	3°28′S/29°34′E	2000	P	18,900±700 BP 21,500±1250 BP	Bonnefille and Chalié (2000)
14	Ijenda, Burundi	3°29′S/29°33′E	2150	P	21,870±470 BP	Roche and Bikwemu (1989)
15	Lake Chesi, Zambia	9°05′S/29°45′E	928	LF	12,500±550 BP 33,900±2000 BP	Stager (1988)
16	Walikale, Congo	1°15′S/27°50′E	662	P	17,650±1020 BP 18,310±860 BP	Runge (1996)
17	Hv 12945 Imbonga, Congo	0°42′7″S/19°43′5″E	20	P	19,920±765 BP	Preuss (1990)
18	Gama2 Ngamakala, Congo	4°18′S/15°14′E	400	P	16,300±140 BP 22,170±600 BP	Elenga et al. (1994)
19	GeoB1016 Southeast-Atlantic, Angola margin	11°46′S/11°40′5″E	−3410	P	12,000 cal. BP 24,100 cal. BP	Shi and Dupont (1997)
20	GeoB1023 Southeast-Atlantic, Angola margin	17°09′S/11°01′E	−1978	P	15,070±60 BP 17 890±80 BP	Shi et al. (1998)
21	KS 12 Gulf of Guinea	3°52′06″N/1°56′16″W	0	P	17,000 cal. BP 22,000 cal. BP	Lézine and Vergnaud-Grazzini, (1993)
22	BM6 Lake Barombi-Mbo, East Cameroon	4°39′N/9°24′E	300	P	20,240±1448 BP 22,030±2140 BP	Brenac (1988)
23	GIK16856 Gulf of Guinea, Niger Delta	4°48′N/3°24′E	−2860	P	18,300 cal. BP	Dupont and Weinelt (1996)
24	Lake Bosumtwi, Ghana	6°32′N/1°23′W	100	P	18,880±190 BP 20,220±230 BP	Talbot et al. (1984)
25	GIK16776 Atlantic, West Africa, Liberia	3°44′N/11°24′W	−4242	P	12,000 cal. BP 24,000 cal. BP	Jahns et al. (1998)
26	M.16017−2 Atlantic, North-West Africa	21°15′N/17°48′W	–	P	16,060±230 BP 20,060±300 BP	Hooghiemstra (1988)

Acronyms: P = Pollen, SLC = Sea Level Changes, LF = Limnic Fauna.

In the southeast of Ivory Coast, near the border to Ghana, only small relicts of the semi-deciduous rainforest existed during the LGM. Sediments of a marine core situated off the Ghanaian margin recorded the permanence of rain forest on the adjacent continent during the LGM (Lézine and Vergnaud-Grazzini, 1993). In contrast, this forest type remained in the western highlands of Guinea as well as in the area of Cape

Palmas, the southernmost peak in west Africa (Jahns et al., 1998). The topographic situation of the highlands of Guinea supported the existence of rather humid forest formations due to maximum rainfall during the LGM. Even reduced precipitation allowed the existence of a band of evergreen rainforests along the west African coast. Simultaneous conditions can also be found along the Niger Delta and even further to the east, around Douala and its hinterland which again allowed the existence of evergreen rainforests (Fig. 3) (Dupont and Weinelt, 1996).

In the central part of the Ivory Coast, as well as in the area of the "Dahomey Gap", very open dry forests or tree savannas with a high percentage of grasses almost reached the Guinean coast (Talbot et al., 1984; Maley, 1991). The area around Accra showed open tree savannas around 18,000 ^{14}C yr BP. Tree pollen was limited to 4–5%. These tree taxa however, did not originate from the Sudanian savannas, but mainly came from the area of semi-deciduous rainforests of the Guinean-Congolian forest belt north of the coast line (Fré- doux and Tastet, 1988; Dupont and Agwu, 1992).

There was only a very narrow strip east of Douala (Cameroon) reaching southward towards Port Gentil (Gabon) along the coast where evergreen forests survived (Brenac, 1988).

The major part of the Congo-Basin was dominated partly by open and partly by more dense dry forests. Rain forests persisted during the last 24,000 years around the "Mare de Ngamakala" and the southern "Batéké Plateau" NE of Brazzaville (Elenga, 1992; Elenga et al., 1994; Schwartz et al., 1995; Shi and Dupont, 1997; Shi et al., 1998). This record shows from 22,170 until 6500 ^{14}C yr BP an undiminished high amount of *Sapotaceae* and *Syzygium*, taxa from the evergreen and semi-deciduous African tropical rainforests. In addition, the δ^{13}C analyses of Congolian savannas, today covering more than 40% of the Congolian area — prove that these savannas developed only during the last 3000 years replacing former forests (Preuss, 1990). In the Bois de Bilanko (Batéké Plateau) at about 700 m, mountainous elements such as *Podocarpus*, *Olea hochstetteri* and *Ilex mitis*, record the presence of Afromontane forests during the LGM indicating that temperatures were about 5 °C lower than today (Elenga et al., 1994).

The generally dry highland with tree- and grass savannas was only interrupted by islands of dry montane forests. (Taylor, 1990; Vincens, 1993; Beuning et al., 1997). Merely along the edge of the Western Rift and northeast of Lake Victoria remains of semi-deciduous rainforests could be found during the LGM (Kendall, 1969; Runge, 1996).

Results from the east African high mountains show that the overall lowering of the vegetation belts during the LGM amounted to ±700 m in the dry high mountains, whereas in the humid high mountains it amounted to ±1000 m (Coetzee, 1967; Hamilton, 1982; Perrott and Street-Perrott, 1982; Maitima, 1991; Olago et al., 2000). The average vertical temperature gradient was 0.85 °C per 100 m for the former and 0.6 °C per 100 m for the latter. The lowering of temperatures during the LGM in East Africa amounted to 5–6 °C on average, which matches the reduction of the SST's in the western Indian Ocean between 0°N and 20°S and west of 50°E (Anhuf, 2000).

During the LGM the southern Saharan border was located at 15°N in Senegal and close to 14°N in the central part of today's Sudanian Zone, north of Kano/Nigeria (Anhuf, 1997). This northern frontier of the grass/shrub savanna in west Africa coincides with the southern border of moving sand dunes during the Pleistocene (Talbot, 1984), implying a southward shift of 3–4° latitude (Hooghiemstra, 1988).

6. Paleovegetation map of Amazonia and Africa

The present distribution of the natural vegetation in tropical South America and Africa is linked very closely to the climatic water-budget of the respective continents. The amount of precipitation as well as the duration and the intra-annual distribution of the rain depend on the condition of the most important water vapor sources for both continents, the tropical and southern Atlantic. Of minor importance are the water vapor sources from the Pacific and the Indian Ocean, respectively. In addition, intense moisture recycling from both tropical lowland forests, the Amazon and the Congo, can also provide an important source of moisture in this region (Salati, 1987). It is clear that in years with extreme warming in the tropical Pacific — typical of El Niño conditions — rainfall in the northern Amazon regions and Northeast Brazil would be lower than normal, and in some cases can even produce droughts, as in 1925–26, when extensive forest fires in Amazonia killed many rubber collectors (Meggers, 1994).

Pflaumann et al. (2003) have published SST reconstructions of the Atlantic ocean during the LGM. During northern glacial summer (May to September) along the equatorial Brazilian coast, between 4°N and 4°S, a distinct tongue of cool water (<18 °C) penetrated from the Southeast, originating in the Benguela Current off SW-Africa, and extended to the western Atlantic beyond 30°W. This implies a glacial increase of the southern trades (Marengo and Rogers, 2001), possibly a

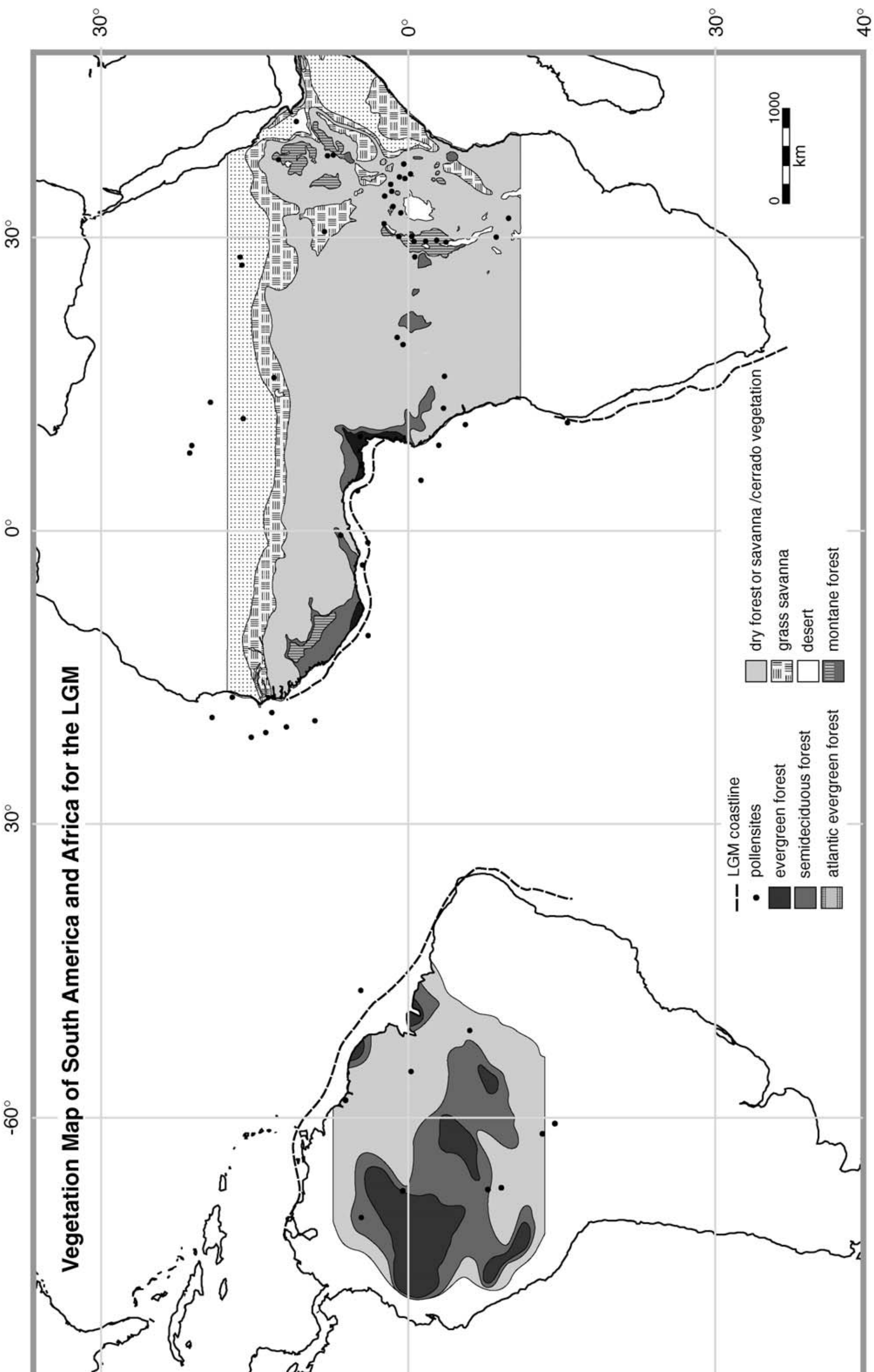

Fig. 3. Vegetation map of South America and Africa for the LGM.

result of the equator wards extended sea ice in the Southern Ocean (Amand, 2000; Gersonde et al., 2003). This cooling of the equatorial East Atlantic has large implications on the moisture balance of the "African and Brazilian Monsoons" and the respective continental humidity (Pflaumann et al., 2003). The temperature differences along the northern Brazilian coast (LGM minus modern) were 2–3 °C below the modern SST's.

The eastern Brazilian coast south of 10°S to 30°S has experienced only a minor SST decrease of about 1–2 °C (LGM minus modern)(Niebler et al., 2003). During LGM southern summer (November to March) the respective southern hemisphere SST's therefore were not much different from today during that season. The largest part of the Amazon basin (central, western and southwestern Amazon) did not suffer seriously from a decrease in water vapor transport into the continent (Baker et al., 2001b) while the northern part of the basin was influenced by a limited water vapor input from the Atlantic and the Caribbean during LGM northern summer. However, Mourguiat and Ledru (2003a,b) emphasized that due to LGM cooling within the Amazon basin the respective rainforest evapotranspiration decreased drastically supporting the picture of relatively drier Bolivian Amazon lowlands (Burbridge et al., 2004).

As today there are significant connections between the SST's and the precipitation system, such connections must have also existed during the LGM. They permit a reconstruction of the precipitation available during the LGM. Accordingly, the daily evaporation rates are about 4 mm over a 27 °C warm water body and 1 mm over a water body at 17–18 °C (Baumgartner and Reichel, 1975). Therefore, equatorial SST anomalies during northern glacial summer (between −8 °C in the eastern Atlantic and −2 to −3 °C in the western Atlantic) may have caused a precipitation decrease of up to 30% to 40% with a considerable amount of precipitation during northern summer within the areas of Uaupés, Belém, Santarém, Salvador, Recife/Olinda) and a decrease of about 20% at the stations with considerable amount of precipitation during southern summer (Manaus, Porto Velho, Cuiaba).

The detailed description of LGM precipitation over tropical Africa was published by Anhuf (2000). The results for Africa can be summarized as follows. The west African coast and the Congo basin north of the Equator received most of the precipitation during NH-summer. Due to the strong cooling of the eastern Atlantic during the LGM the total annual precipitation of the respective areas decreased by 30–40%. The east African highlands receiving the majority of rain during the austral summer were affected only by a minor annual precipitation decrease of up to 25% due to the less cool Indian Ocean during the austral summer (Hutson, 1980).

7. Discussion

7.1. Interpretation of the paleoecological conditions

Amazonia still has a scarcity of dated pollen records going back to the LGM. But the recently published data of Atlantic SSTs during the LGM (Pflaumann et al., 2003) enable a better insight into the potential climatic and even ecologic conditions in the Amazon forest area during that time. Based on the reconstructed LGM annual precipitation patterns the paleovegetation is reconstructed (Fig. 3). This approach has already been successfully applied for the LGM vegetation reconstruction of tropical Africa (Anhuf, 2000). Subsequently, the reconstructed vegetation cover is critically compared with the published pollen and geochemical data.

An earlier approach to reconstruct the possible vegetation pattern in the Amazon basin and surroundings during the LGM was published by Van der Hammen and Hooghiemstra (2000). These authors plotted all sites with paleodata on the present-day rainfall map of Amazonia published by Figueroa and Nobre (1990). The here presented map follows this approach, also assuming that no fundamental changes in the intra-annual distribution patterns of rainfall occurred during the LGM. But, based on the new LGM SST reconstructions in the Atlantic Ocean there probably was no general reduction of rainfall throughout the entire basin. Related to the intra-annual circulation pattern in the Amazon basin at least two different scenarios appear for the LGM precipitation patterns over the basin. During the NH-summer a significant rainfall reduction has to be assumed for the LGM due to the cooler tropical Atlantic during that season. An overall rainfall reduction of about 40% in comparison to the contemporary values was extrapolated for the northwestern, the "Dry Corridor" and the northeastern part of the Amazon basin comparable to the map by Van der Hammen and Hooghiemstra (2000). The central part (west of the "Dry Sector" and between 0°N and 10°S), the western, and southwestern part (west of 70°W and south of 10°S) probably experienced only a minor rainfall reduction due to the almost unchanged Austral summer SSTs of the tropical Atlantic during the LGM. Accordingly, in contrast to Van der Hammen and Hooghiemstra (2000) a general rainfall reduction of about 20% during the LGM austral summer is suggested for these respective regions in the Amazon basin. Thus, the most obvious difference in the present map from the earlier interpretations is the extension of the humid evergreen and semi deciduous forests.

All the findings from the published pollen and geochemical data agree with the reconstructed LGM map showing more open (probably dry forest or savanna like) vegetation in northern Amazonia (Bush et al., 2002). This also agrees with the postulated rainfall reductions, proposed by Van der Hammen and Hooghiemstra (2000). However, in our case this vegetation was restricted to the northeastern Amazon, the contemporary Amazonian "Dry Corridor" (Carajás), and the northwestern part of the Amazon basin, including dunes in several present-day savanna areas in Venezuela, Guyana, Colombia, and in the Rio Branco–Rio Negro area. Dunes, normally are or have been formed under dry climatic conditions as for example in the Sahelian zone of Africa (Talbot, 1984). Teeuw and Rhodes (2004) demonstrated that the Rio Branco–Rupununi dunes — probably formed just after the LGM — are active until today although the area receives an average annual rainfall of 1500 mm, 70–80% of which falls over a 4-months period.

The minor precipitation decrease in the western, central and southwestern parts of Amazonia of up to 20% is consistent with the survival of humid tropical forests in southern Amazonia (between Humaitá and Porto Velho) (Fig. 3), also confirmed along an ecosystem transect in the Amazon State between Humaitá and Lábrea (along BR 319). The whole area except the first 20 km west of Humaitá must have been covered with tropical forest during the LGM (Pessenda, *personal communication*). These results are also consistent with results from the Bolivian Altiplano, which receives maximum precipitation during austral summer today deriving from the tropical Atlantic ocean and advected across the Amazon basin, and which was characterized by a humid climate during the LGM (Baker et al., 2001a), but not with the results from Mourguiat and Ledru (2003a,b) who postulated a dry LGM and not with the results from Mayle et al. (2000) who inferred a dry and open vegetation in southern Amazonia at about 14°S. It has to be emphasized that the modern day tropical forests at Laguna Bella Vista and Laguna Chaplin are located in a climatic and ecological transition zone with only 1500 mm precipitation per year where Amazonian evergreen forests merge with dry forests and savannas (Mayle et al., 2000).

There is only one principle disagreement between the new map and the available pollen sites. The Katira data record for LGM requires a considerably higher rainfall reduction than 20% to explain the pollen data. Van der Hammen and Hooghiemstra (2000) have calculated a reduction of 50–60% necessary to explain the pollen data, although LGM in the Katira record includes only five pollen samples and therefore has to be taken with caution (Mayle et al., 2000).

Two scenarios can explain dry conditions in southern Amazonia and on the eastern Andean Cordillera. The drier LGM conditions can either be explained by stronger and more frequent polar air outbreaks (friagems) originating from the southwestern Pacific during the LGM. The advance of these cold air flows along the subtropical Andes into the tropical parts can also be observed nowadays affecting the west side of Brazil and Bolivia adjacent to the Andes (Marengo and Rogers, 2001). A different focus is the limited evapotranspiration from the humid tropical forests in the southwestern Amazon basin due to the pronounced temperature cooling that explain the absence of cloud forest pollen during the LGM at Siberia (Mourguiat and Ledru, 2003b).

However, the data show that we have a dry southern Amazonia and a dry eastern Cordillera and a relatively wet Altiplano during the LGM. This antagonism could be inferred by a reduction in summer moisture from the Atlantic inducing a decrease in precipitation and evapotranspiration over Amazonia and a northward shift of southern convective bands (westerlies) with stronger winter precipitations on the Altiplano reaching the latitude of Titicaca (Garreaud and Wallace, 1998; Vuille and Ammann, 1997; Wainer et al., 2005). The main aspect is that in contrast of today these two regions received distinctly different moisture sources during the LGM (Burbridge et al., 2004) — today both from the tropical Atlantic but during the LGM the Altiplano received a reasonable part of its precipitation through intensified snow precipitation originating from the Pacific (Vuille and Ammann, 1997; Wainer et al., 2005). This would also help to ex- plain that the Altiplano is today much drier than during the LGM although the Altiplano is and was characterized by a maximum austral summer insolation due to the precessional cycle today and during the LGM.

7.2. Intercomparison of the Amazon and the Congo basins

The LGM rainforest ecosystem in Brazil was restricted to four different areas imbedded in a continuous area of semi-deciduous forests. Despite of this, the evergreen forest areas were not really isolated hence semi-deciduous forests provide survival conditions for numerous rainforest taxa which is supported by a different species composition (Ledru et al., 2001). Only the probable coastal forest near Belém and in the State of Amapá near the border to Guyana could have been isolated from the Amazonian forest but experiences from Africa underline that transitions of forest taxa exist as well between ever- green and semi-deciduous forests as between semi-deciduous and dry forest types (Anhuf, 2000). Such transitions exist also among the tropical forest species within Brazil (Oliveira-Filho and Fontes, 2000).

In comparison to Africa where only really isolated forest relicts remained, the ecological conditions for the Amazon lowland forest in the central, western, and southwestern part were far less critical even during the LGM than today in Africa, because most tropical lowland forest areas in Africa experience a minimum of two dry months and average rainfall of a little more than 1800 mm/year (Anhuf, 1997). This unfavorable situation in the African lowlands is probably also responsible for the lowest species diversity of all tropical forest areas on earth (Richards, 1973). Apparently, even minor climate oscillations would have endangered the survival of tropical lowland forest taxa there in Africa.

Based on our reconstruction the tropical humid forest area (including evergreen and semi-deciduous forest types) in Africa was probably reduced by 84% (in comparison to the natural and by 74% to the contemporary vegetation cover derived from digital satellite images) during the LGM (Anhuf, 2000). In total, the humid forest area was reduced to 54% of their present-day extension in Amazonia (the evergreen tropical forest area in Brazil suffered probably a comparable reduction in extension (80%) while the area of semi-deciduous forests presumably increased by almost 60%). The remaining part (46%) probably was composed by transitional mosaics containing dry forests and savannas.

The new map depends on the accuracy of the present rainfall map and the correct evaluation and interpretation of the differences in the change in precipitation during the LGM and thus might change somewhat when more detailed data become available. This map also may help to conduct further paleoclimate and paleobotany research because it illustrates the most promising regions to enlarge our knowledge about the ecological conditions during the LGM in Amazonia and its surroundings (e.g. within the today's "Dry Corridor", the northeastern part and along the forest border in the states of Mato Grosso, Para, and Tocantins).

The validation of the map using available pollen spectra and geochemical data showed consistent results between the map and the data in Amazonia and tropical Africa (Anhuf, 2000). Therefore, good reasons exist to regard the multidisciplinary approach, at least in general, as a promising and overall reliable tool. Unfortunately there is still too little direct information on the vegetation of the LGM in order to validate the map as a whole. But one can say that a methodological approach has been found to get closer to the goal, nevertheless more coupled modeling is eligible.

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