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Millennial-scale changes in vegetation records from tropical Africa and South America during the last glacial

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ABSTRACT

To reconstruct the response of vegetation to abrupt climate changes during the last glacial we have compiled pollen records from the circum-Atlantic tropics between 23°N and 23°S from both marine and terrestrial sediment cores. Pollen data were grouped into mega-biomes to facilitate the comparison between the different records. Most tropical African records do not appear to register Dansgaard–Oeschger (D-O) variability, although there are vegetation changes during Heinrich Stadials (HS). There is a stronger signal of D-O and HS variability in the South American records. Records close to the modern northern and southern limits of the Intertropical Convergence Zone (ITCZ) show opposite trends in vegetation development during HS and D-O cycles. The pollen data from tropical South America corroborate the hypothesis of a southward shift in the migration pattern of the ITCZ and a reduction in the Atlantic Meridional Overturning Circulation (AMOC) during HS.

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1. Introduction

The last glacial (here 73.5–14.7 ka, see Sanchez Goñi and Harrison, [this issue](#)) was marked by large and abrupt climate variability in the form of Dansgaard–Oeschger (D-O) cycles and Heinrich Events (HE, e.g. Bond et al., 1997; Sarnthein et al., 2001). The D-O cycles registered in the Greenland ice cores are characterised by rapid warming followed by progressive cooling, with a timescale of ca 1500 years. The D-O cycles are thought to be related to a weakening of deep water formation in the North Atlantic by dilution of the surface waters through ice melt or other processes. Deepwater formation resumes as a response to the build-up of salty waters (e.g. Alley, 1998). Heinrich (1988) documented layers (Heinrich

layers) with high lithic fragment content that are associated with the abrupt occurrence of cold intervals (Heinrich Stadials: HS) at the end of some D-O cycles in the North Atlantic. It is thought that these cold intervals are triggered by iceberg discharges in the North Atlantic resulting in a reduction or possible shutdown of the Atlantic Meridional Overturning Circulation (AMOC) (e.g. Broecker et al., 1992; see also Sanchez Goñi and Harrison, [this issue](#)). However, recent studies (e.g. Hall et al., 2006) indicate that the collapse of the AMOC preceded the deposition of Heinrich layers and this suggests that Heinrich Events (HE) are a response to, rather than the cause of, AMOC collapse (Shaffer et al., 2004; Flückiger et al., 2006; Clark et al., 2007).

The North Atlantic HE and the Younger Dryas (YD) climatic perturbation have been shown to occur at a global scale (Voelker et al., 2002). The EPICA Community (2006) have shown a strict coupling between Greenland cold events and Antarctic warming, and thus corroborated the see–saw hypothesis (e.g. Crowley, 1992;

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Rühlemann et al., 1999). Although it appears that both D-O cycles and HE are registered globally, the response to these events varies geographically and the mechanisms behind them are still poorly understood although it is generally accepted that the strength of the AMOC plays an important role (e.g. Sarnthein et al., 1994; McManus et al., 2004; Clark et al., 2007).

There are two contrasting hypotheses concerning the behaviour of the tropics in relation to abrupt climate change. The first invokes changes in the tropical atmosphere–ocean dynamics as a cause of abrupt changes, and specifically argues that the decrease in water–vapour transport out of the tropical Atlantic during HS would lead to an increased net freshwater balance in the Atlantic affecting the density of ocean surface waters and the northward penetration of latent heat (e.g. Cane and Clement, 1999; Schmittner et al., 2000; Ivanochko et al., 2005). The second hypothesis attributes changes in the tropics to a slow-down of the AMOC, which might have been triggered by large iceberg discharges in the North Atlantic (e.g. Rahmstorf, 2002; Broecker, 2003).

The aim of this paper is to document vegetation changes in tropical Africa and South America, specifically focussing on intervals coincident with D-O cycles as registered in Greenland and HS as identified in the North Atlantic. The temporal definition for the last glacial, Marine Isotope Stage (MIS) 2, 3 and 4, and HS was taken from Sanchez Gofii and Harrison (this issue) and the chronological limits for D-O cycles follows the timings and durations given in Wolff et al. (this issue). By reviewing the existing low and high-resolution pollen data of tropical Africa and South America covering at least part of MIS 2, 3 and 4 (Table 1), we aim to document the impact (if any), timing and amplitude of rapid climate changes on the regional vegetation. Our synthesis provides the opportunity for a direct comparison of (1) sites situated north and south of the equator on the same continent, (2) responses of the tropical African and South American vegetation, and (3) pollen data with results of other terrestrial indicators. Our examination of vegetation records from the tropical regions of Africa and South America should enable us to test the plausibility of ideas that rapid climate changes are triggered by changes in the tropics or are a response to extra-tropical changes. Specifically, this synthesis allows us to test the hypothesis that abrupt climate change in the tropics is the result of shifts in the migration pattern of the ITCZ during the last glacial coupled with changes in the AMOC (e.g. Peterson et al., 2000; Mulitza et al., 2008).

The climate of the circum-Atlantic tropics today is strongly coupled to the latitudinal position of the ITCZ, a low pressure belt of warm, moist air surrounding the Earth near the equator (Ruddiman, 2001). Due to the strong linkage between variations in atmospheric and oceanic conditions the position of the ITCZ follows a seasonal cycle, with an abrupt shift from its northernmost position during boreal summer to its southernmost position during austral summer. These variations in the position of the ITCZ affect the rainfall distribution in equatorial and tropical regions, resulting in alternating wet and dry seasons (Fig. 1). Far from the equator the dry season (winter) is severe and the rainy season (summer) short; near the equator two short dry seasons occur (Ruddiman, 2001). The annual migration of the ITCZ is influenced by the distribution of land and ocean. Over the ocean the ITCZ is well defined by the combination of convergence of trade winds and subsequent convection and heavy rainfall. As a result moist air masses from the tropical Atlantic penetrate eastwards into the interior of the African continent during austral summer. In East Africa the penetration of the easterly flow is limited by the highlands. Over land, the meridional oscillation of the ITCZ across the equator responds to the seasonal insolation cycle and the near-surface convergence and convection become widely separated during the season of maximum excursion (northern- or southernmost ITCZ position).

Thus, the latitude of surface convergence between trades and monsoon over north-western Africa in August is around 18–20°N, whereas the latitude of the rainbelt (associated with convection) is about 10°N (Leroux, 1983; Nicholson, 2000). In South America during austral summer, when the ITCZ is located at its southernmost position, trade winds transport moisture from the equatorial Atlantic towards the Amazon basin causing the South American Summer Monsoon (Gan et al., 2004). These trade winds are channelled to the southeast to 20–23°S by the Andean Cordillera (Lenters and Cook, 1999). During the winter season the ITCZ moves to its northernmost position at ~10°N.

The vegetation distribution within the tropical regions is strongly affected by the length and the intensity of the dry season. However, it is not only the total amount of annual precipitation that is important, but also the seasonal distribution of rainfall. The presence or absence of a consistent cloud cover also influences the plant growth by limiting the solar radiation and the effective evapotranspiration. Additionally, the temperature has an effect on the evapotranspiration and therefore influences the moisture availability. In the tropics temperature alone rarely limits vegetation growth except in high mountain areas.

The present-day African vegetation around the equator consist of tropical forests including evergreen rainforest in the Congo basin and in the moist part of western Africa, to semi-evergreen and deciduous forest in northern Cameroon or southern Congo. North and south of the forest fringes there is a narrow belt of natural grass savannah. North of the xerophytic shrubland of the Sahel zone and along the coast of Namibia and southwest Angola desert vegetation occurs (White, 1983; see e.g. simulated vegetation distribution according to BIOME4; Kaplan et al., 2003). The modern South American vegetation is dominated in the north by savannah, evergreen and semi-evergreen broadleaf forest. In the east and southeast deciduous forest and woodland, savannah, xerophytic shrubland and warm-temperate mixed forest prevail (see e.g. simulated vegetation distribution according to BIOME4; Kaplan et al., 2003).

2. Chronology

The age models of most of the sediment records reviewed here were determined based on conventional, accelerator mass spectrometry (AMS) radiocarbon dating (Table 2). The chronology of some marine sequences off western and north-western Africa (Table 2) where radiocarbon dating is not feasible is based on peak-to-peak correlation of isotopic records (e.g. Lézine and Denèfle, 1997; Lézine et al., 2005). The age models of the Cariaco Basin sequence and the marine record off northeast Brazil (GeoB 3104-1) are based on a combination of radiocarbon dating and correlation with ice-core records. The original Cariaco records are aligned with the ²³⁰Th dated Hulu Cave speleothems (Wang et al., 2001; Hughen et al., 2006). In this review, however, we adapted the time scale to the Greenland Ice Core Chronology 2005 (GICC05) (Skinner, 2008; Wolff et al., this issue), aligning the steep drops in the reflectance curve of the Cariaco sediments with the start of Greenland Interstadials (GI). The time scale for the marine core GeoB 3104-1 (Jennerjahn et al., 2004) has also been adapted to the new GICC05 ages. The age model of the Colônia record is a combination of radiocarbon dates and tuning of the arboreal pollen record to precessional insolation fluctuations (Ledru et al., 2009). The age models of the Fúquene-2 and Fúquene-7C records are a combination of radiocarbon dates, frequency analysis in the depth domain, and tuning of the arboreal pollen record to the LR04 benthic oxygen isotope record (Lisiecky and Raymo, 2005; Bogotá-Angel et al., in review; Mommersteeg and Hooghiemstra, in review).

Table 1
Pollen records from Africa and South America covering at least part of MIS 4, 3 and 2.

Site name	Map Code	Record type	Lat. (°)	Long. (°)	Elevation (m)	Period covered	Interval (ka)	Sampling resolution (yr/sample)	Reference
Ngamakala Pond, Congo	1	terrestrial	-4.07	15.38	400	3–32 ka	10–15 15–24 24–29 29–32	>1000 470 >1000 270	Elonga et al., 1994
Barombi Mbo, Cameroon	2	terrestrial	4.51	9.40	300	0–32 ka	10–32	590	Maley and Brenac, 1998
Lake Bosumtwi, Ghana	3	terrestrial	6.50	-1.42	99	0–33 ka	10–33	>1000	Maley, 1991
Kashiru Bog, Burundi	4	terrestrial	-3.47	29.57	2240	0–40 ka	10–29 30–31	410 1000	Bonnefille and Riollet, 1988
Lake Rukwa, Tanzania	5	terrestrial	-8.42	32.72	793	0.3–21 ka	31–40 10–13 13–14 14–19 19–21	640 375 170 >1000 330	Vincens et al., 2005
Irunga, Tanzania	6	terrestrial	-7.82	35.91	2100	0–40 ka	poor age control	250	Mumbi et al., 2008
Lake Tanganyika	7	terrestrial	-8.50	30.85	773	9–25 ka	12–15 15–26 26–27 27–28 28–30 10–17 17–45	610 140 330 180 300 550	Vincens, 1991; Vincens et al., 1993
Lake Masoko, Tanzania	8	terrestrial	-9.33	33.75	840	4.4–45 ka	10–17 17–45	300 550	Vincens et al., 2007
Lake Malawi	9	terrestrial	-11.29	34.44	475	0–120 ka	10–60	>1000	Cohen et al., 2007
Lake Malawi, M86-18P	10	terrestrial	-11.22	34.42	470	10.5–45 ka	10.5–38 38–43	1000 200	DeBusk, 1998
Muchoya Swamp, Uganda	11	terrestrial	-1.17	29.48	2260	0–42 ka	poor age control	AH1 > 1000	Taylor, 1990; Morrison, 1968
Ahakagyezi Swamp, Uganda	12	terrestrial	-1.7	29.54	1830	0–26 ka	poor age control	AH2 ~ 1000	Taylor, 1990
Mubwindi Swamp, Uganda	13	terrestrial	-1.2	29.45	2000	2.5–43 ka	13–22	>1000	Marchant et al., 1997
off Cunene River Mouth, GeoB 1023	14	marine	-17.15	11.02	-1978	MIS 1–2	10–22	185	Shi et al., 1998
off Angola, ODP 1078	15	marine	-11.92	13.40	-426	MIS 1–3	22–27 27–32	140 830 280	Dupont et al., 2008
off Angola, GeoB 1016	16	marine	-11.77	11.68	-3411	MIS 1–8	27–32	280	Shi and Dupont, 1997
Congo deep-sea delta, GeoB 1008	17	marine	-6.59	10.32	-3124	MIS 1–6	MIS 1–6	>1000	Jahns, 1996
Congo deep-sea delta, T89-16	18	marine	-5.70	11.67	-824	MIS 1–3	MIS 1–3	>1000	Marret et al., 2001
Gulf of Guinea, GIK 16867	19	marine	-2.20	5.00	-3891	MIS 1–6	irregular sampling	>1000	Dupont et al., 1998
South of Niger River delta, KW 31	20	marine	3.52	5.57	-1181	MIS 1–3	10–15 15–17 21–25 30–40	200 670 500 670	Lézine and Cazet, 2005
West of Niger River delta, GIK 16856	21	marine	4.81	3.40	-2861	MIS 1–6	MIS 1–6	>1000	Dupont and Weinelt, 1996
off Ghana, KS 12	22	marine	3.87	-1.94	-2955	MIS 1–2	10–15 15–22	500 >1000	Lézine and Verghnaud-Grazzini, 1993
off Ivory Coast, KS 84-067	23	marine	4.12	-4.12	-3500	MIS 1–11	10–12	>1000	Fredoux and Tastet, 1993
off Ivory Coast, KS 84-063	24	marine	4.40	-4.18	-3135	MIS 1–2	10–12 13–14 14–19	220 330 450	Lézine et al., 1994; Lézine and Deneffe, 1997
off Liberia, GIK 16776	25	marine	3.74	-11.40	-4242	MIS 1–12	14–19	>1000	Jahns et al., 1998
Gulf of Guinea, GIK 16772	26	marine	-1.21	-11.96	-3913	MIS 1–8		>1000	Marret, 1994
off Sierra Leone, M30 (KL184)	27	marine	7.70	-14.39	-2330	MIS 2–4?		>1000	Agwu and Beug, 1982
off Guinea, GIK 16415	28	marine	9.57	-19.11	-3851	MIS 1–20		>1000	Dupont and Agwu, 1992
off Mauritania, V22-196	29	marine	15.83	-18.95	-3728	MIS 1–6		>1000	Lézine, 1991
off Mauritania, GIK 12329	30	marine	19.37	-19.93	-3320	MIS 1–6		>1000	Agwu and Beug, 1982
off Mauritania, ODP 658	31	marine	20.75	-18.58	-2263	MIS 1–17		>1000	Dupont et al., 1989
off Mauritania, GIK 16017	32	marine	21.25	-17.80	-812	MIS 1–2		>1000	Hooghiemstra, 1988

33	Lake Patzcuaro, Mexico	terrestrial	19.58	-101.58	2044	6–44 ka	28–40	> 1000	Watts and Bradbury, 1982
34	Lake Petén Itzá, Guatemala	terrestrial	16.92	-89.83			poor age control	> 1000	Bush et al., 2009
35	Lake Quexil, Guatemala	terrestrial	16.92	-89.82	110	8–43 ka?	10–19	80	Leyden et al., 1994
36	Lake Caco, North Brazil	terrestrial	-2.97	-43.42	120	0–19 ka		> 1000	Ledru et al., 2001
37	Salitre, Lake Campeste, Brazil	terrestrial	-9.00	-46.77	970	0–50 ka		> 1000	Ledru et al., 1996
38	Morro da Itapeva, Brazil	terrestrial	-22.78	-45.53	1850	0–35 ka		> 1000	Behling, 1997
39	Lake Pata, Brazil	terrestrial	0.16	-66.41	190	0 to >40 ka		> 1000	Colinvaux et al., 1996
40	Colônia, Brazil	terrestrial	-23.87	-46.71	900	0–130 ka	11–12	330	Ledru et al., 2009
							14–19	710	
							21–31	420	
							31–130	580	
41	Siberia, Bolivia	terrestrial	-17.83	-64.72	2920	0–50 ka	12–19	780	Mouguiart and Ledru, 2003
							23–50	750	
42	Constuelo, Peru	terrestrial	-13.95	-68.98	1360	0–48 ka		> 1000	Bush et al., 2004
43	Laguna La Compuerta, Peru	terrestrial	-7.30	-78.36	3950	0–33 ka		> 1000	Weng et al., 2006
44	Laguna Junín, Peru	terrestrial	-11	-76.17	4100	0 to >40 ka	10–15	330	Hansen et al., 1984
							15–26	920	
							26–40	> 1000	
45	Fúquene, Columbia	terrestrial	5.45	-73.46	2540	Fq-2: 0–42 ka	2–11	280	Van Geel and Van der Hammen, 1973;
							11–13	250	Mommersteeg, 1998;
							13–45	520	Mommersteeg
							2–3	250	and Hooghiemstra, in review
							4–6	> 1000	
							6–10	140	
							12–16	1000	
							16–21	220	
							21–22	1000	
							23–37	300	
							38–39	1000	
							39–85	410	
							9–15	500	Helmens et al., 1996
							15–23	670	
							23–24	140	
							24–30	1000	
							30–35	380	
46	La Laguna, Bogotá, Colombia	terrestrial	4.92	-74.03	2900	0–35 ka		> 1000	Burbridge et al., 2004;
								> 1000	Mayle et al., 2000, 2007
47	Laguna Chaplin, Bolivia	terrestrial	-14.28	-61.04	190	0–50 ka		> 1000	Burbridge et al., 2004;
								> 1000	Mayle et al., 2000, 2007
48	Laguna Bella Vista, Bolivia	terrestrial	-13.37	-61.33	200	0–50 ka		> 1000	Burbridge et al., 2004;
49	Lake Titicaca	terrestrial	-17.0	-67.0	3810	0–22 ka	13–22	~ 1000	Mayle et al., 2000, 2007
50	Cariaco Basin, Venezuela, MD 03–2622	marine	10.71	-65.17	-877	MIS 3–4		420	Paduano et al., 2003
									González et al., 2008;
51	off NE Brazil, GeoB 3104	marine	-3.67	-37.72	-767	MIS 1–3	10–18	670	González and Dupont, 2009
							21–40	> 1000	Behling et al., 2000
							41–50	900	
52	off NE Brazil, GeoB 3910-2	marine	-4.15	-36.21	-2362	MIS 2		125	Dupont et al., 2009
53	off SE Brazil, GeoB 3229	marine	-19.63	-38.72	-780	MIS 1–5		> 1000	Behling et al., 2002
54	off SE Brazil, GeoB 3203	marine	-21.62	-39.99	-1090	MIS 1–3		> 1000	Behling et al., 2002
54	off Amazon fan, ODP 932	marine	5.13	-47.18	-3334	MIS 1–3	9–11	330	Haberle and Maslin, 1999
							11–20	> 1000	
							20–40	> 1000	
							40–49	> 1000	

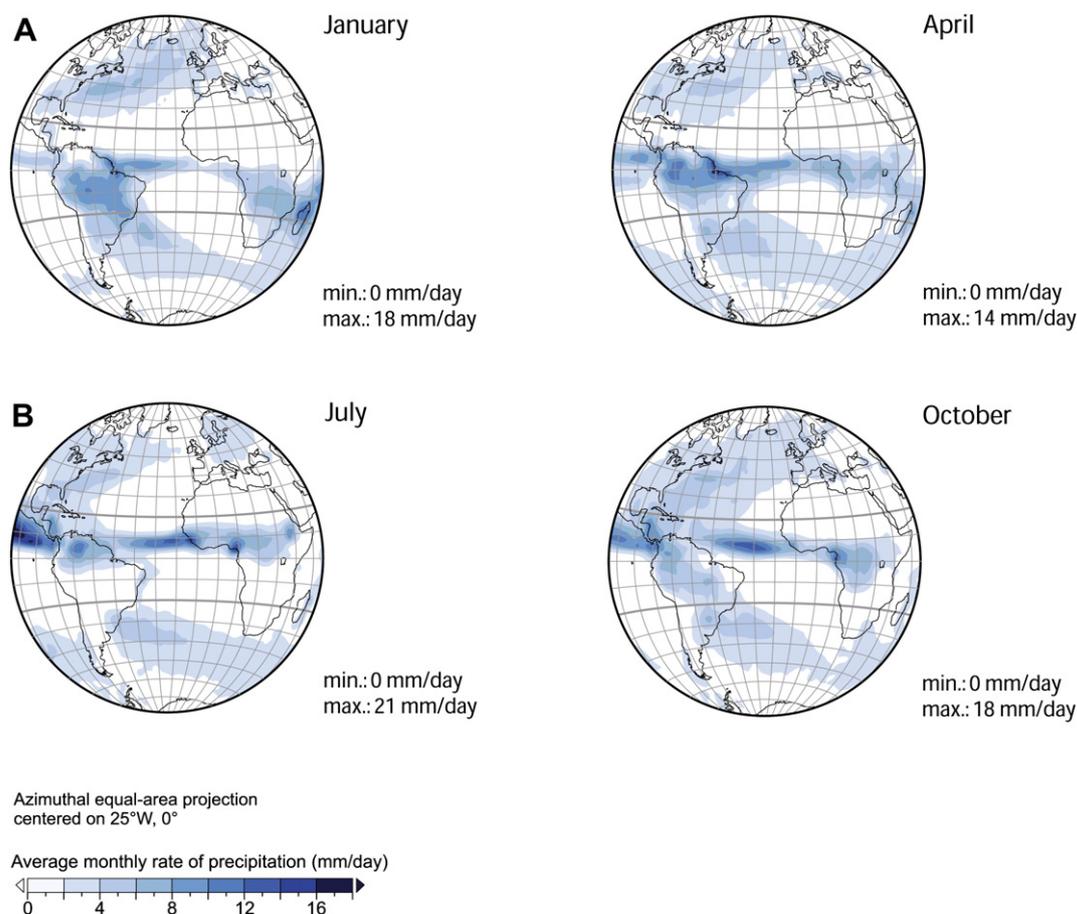


Fig. 1. Rate of precipitation over tropical Africa and South America, (A) austral summer (January, April) and (B) austral winter (July, October).

All of the records considered here have age models in calendar years. However, different calibration curves were used for the different records, which may increase the uncertainties in comparison between sites. Additionally, the age models of marine

sequences dated by the radiocarbon method include a marine reservoir age generally of 400 years which reflects the present-day global average (Hughen et al., 2004). In general, temporal and/or regional variations in reservoir ages are not taken into

Table 2
Chronological information for sites providing high-resolution pollen records from Africa and South America.

Site	Interval	Chronological control						
		AMS	¹⁴ C	U/Th	Other radiometric	Tephra	Varved	Tuning
<i>Africa</i>								
Kashiru Bog, Burundi	0–40 ka	9	15	–	–	–	–	–
Lake Tanganyika	9–25 ka	6 (core MPU-12)	1 (core MPU-11)	–	–	correlate MPU-11 and MPU-12	–	Diatom correlation
Lake Masoko, Tanzania	4.4–45 ka	18	–	–	–	–	–	–
Lake Malawi, M86–18P	10.5–45 ka	3	3	–	–	–	–	–
off Ivory Coast, KS 84-063	4–19 ka	–	–	–	–	–	–	Correlation with SU8118
Barombi Mbo, Cameroon	0–32 ka	–	12	–	–	–	–	–
off Angola, ODP 1078	0–30 ka	–	24	–	–	–	–	–
off Cunene River Mouth, GeoB 1023	0–22 ka	7	2	–	–	–	–	–
<i>South America</i>								
Cariaco Basin, Venezuela, MD 03-2622	26–68 ka	–	–	–	–	–	–	Reflectance curve correlation to ODP 1002
off NE Brazil, GeoB 3104	12–50 ka	12	–	–	–	–	–	–
off NE Brazil, GeoB 3910-2	11–23 ka	7	–	–	–	–	–	–
Lake Caçô, North Brazil	0–19 ka	17	–	–	–	–	–	–
Colônia, Brazil	0–130 ka	–	6	–	–	–	–	Comparison to speleothem tuning to precession
Siberia, Bolivia	0–50 ka	11	–	–	–	–	–	–
La Laguna, Bogotá, Colombia	0–35 ka	9	3	–	–	–	–	–
Fúquene-2, Columbia	0–42 ka	3	–	–	–	7	–	Orbital tuning
Fúquene-7C, Colombia	0–85 ka	7	–	–	–	–	–	Orbital tuning

consideration in dating marine cores because they are difficult to reconstruct (e.g. Bard et al., 1994) and, for pre-Holocene records are exceeded by the uncertainties in the radiocarbon dating (Fairbanks et al., 2005). Model simulations also show that temporal fluctuations in the marine reservoir age are less significant in the tropical Atlantic compared to the northern high-latitudes (Hughen et al., 2004; Franke et al., 2008).

3. Registration of abrupt climate variability in pollen records

We have reviewed pollen records from tropical Africa and South America spanning some part of the last glacial (Table 1, Fig. 2) to determine those that have the potential to document the vegetation response to abrupt climate variability. To be selected for further analysis, the sites had to cover at least part of MIS 2 and/or 3 and/or 4, with a temporal resolution better than 1000 years for a substantial part of the record, and sufficient age control to pinpoint millennial-scale changes. In addition, the pollen data had to be available. Only eight South American and eight African records met these criteria (Table 2). Two of these records are somewhat special cases. The Lake Malawi record (DeBusk, 1998) has a temporal resolution of 1000 years/sample for most of the record, but is included because the sample resolution is much better around the period including HS 4. Indeed, this record has the highest temporal resolution for the period associated with HS 4 of all African pollen records (Fig. 3). The marine record GeoB 3104 (Behling et al., 2000) has a comparatively low temporal resolution after ca 18 ka (Table 1) but provides significant insights into the vegetation development of NE Brazil (Fig. 4) which extends the record of the neighbouring shorter but high-resolution core GeoB 3910 (Dupont et al., 2009). We excluded core KW 31, located south of the Niger Delta (Lézine and Cazet, 2005), despite a sufficient time resolution due to substantial gaps in the pollen record (Table 1).

Differences in regional floras make it difficult to compare pollen records from different continents directly. To facilitate comparisons between sites, the vegetation records are summarized in terms of major vegetation types (or mega-biomes using the terminology of Harrison and Prentice, 2003, Table 3). This naturally involves a certain loss of information, but allow us to describe the main vegetation changes for each record (Figs. 3–6) in a consistent way. We assigned the pollen taxa to Plant Functional Types (PFTs) following Jolly et al. (1998) and Peyron et al. (2006) modified by Vincens et al. (2006) and Lebamba et al. (2009) for the African records, and after Marchant et al. (2009) for the South American records. The PFTs are then grouped into mega-biomes (Table 3) to allow direct comparison of the records (Figs. 3–6). In some cases, the response to millennial-scale climate variability is obscured by this rather coarse classification of the vegetation, particularly when this variability is expressed as within-biome fluctuations in species composition rather than between-biome transitions. Therefore, for each site, we have also selected a taxon that best illustrates the vegetation response to millennial-scale variability. In the descriptions of individual sites, we provide information on the original interpretation of the records, to emphasise the coherence between the original and simplified mega-biome data. We follow a slightly different approach for the pollen records from the Cariaco Basin (Fig. 5) and the Fúquene record (Fig. 6). In both cases, we have kept the original ecological grouping of pollen taxa. In the case of the Cariaco Basin pollen record (González et al., 2008), the grouping is based on the regional ecological preferences of every taxon for the Venezuelan flora. For the Fúquene record (Fig. 6), the grouping is based on the modern altitudinal zonation of vegetation in the Eastern Cordillera of Colombia (Van Geel and Van der Hammen, 1973; Mommersteeg, 1998; Mommersteeg and Hooghiemstra, in review).

3.1. Tropical Africa

The pollen record from Kashiru Swamp in east equatorial Africa (Bonnefille and Riollet, 1988; Bonnefille et al., 1992) provides a vegetation record over the past ca 50 ka (Tables 1 and 2). Between 50 ka and 40 ka the pollen record of the Kashiru site is characterised by high percentages of arboreal taxa (mainly warm-temperate mixed forest, tropical forest, Fig. 3), indicating a relatively wet climate. From 40 ka to the end of the deglaciation, the vegetation is more open with widespread grassland, mainly C₄ grasses, as well as savannah and xerophytic scrubland vegetation. An increase in temperate plants during this period suggests a lowering of the upper forest line as a consequence of cooler climate (Bonnefille and Riollet, 1988; Bonnefille and Chalié, 2000), although decreased atmospheric CO₂ during glacial times may have limited tree growth and favoured grass development (Jolly and Haxeltine, 1997; Harrison and Prentice, 2003). A short-term humid phase, characterised by lacustrine conditions and an expansion of *Podocarpus* forests (temperate-montane forest, Table 3, Fig. 3), occurred at about 24 ka and is followed immediately by forest development (Bonnefille and Riollet, 1988). Although of sufficient duration and time resolution, the Kashiru pollen sequence does not display D-O variability, but vegetation response to HS appears to have been recorded.

The pollen record from the Mpulungu sub-basin of southern Lake Tanganyika, east equatorial Africa (Fig. 3, Tables 1 and 2) (Vincens, 1991; Vincens et al., 1993) provides a record of vegetation changes during MIS 2. The pre- and post-Last Glacial Maximum (LGM) vegetation is dominated by grassland/dry shrubland and savannah/xerophytic scrubland vegetation (Fig. 3) with isolated patches of woodland and large swamp areas around the lake. During the LGM, tropical forest elements increased slightly whereas swamp taxa (see original diagram Vincens et al., 1993) are at their lowest abundance. The frequency of tropical forest taxa like *Brachystegia* and *Uapaca*-type *kirkiana* increased at the glacial/interglacial transition. A simultaneous decrease in Ericaceae (characteristic of grassland and dry shrubland, Table 3, Fig. 3) and an increase in drought-tolerant mountainous *Olea* and *Myrica* (characteristic of temperate-montane forest, Table 3) are interpreted as indicating an expansion of open dry forest or dry montane woodland on the uplands surrounding the basin (Vincens et al., 1993). The Mpulungu record is too short to show D-O cycles of MIS 3 and 4.

A high-resolution pollen record covering the period between 45 and 4.4 ka was obtained from Lake Masoko, southern Tanzania, east equatorial Africa (Fig. 3, Tables 1 and 2) and documents changes in the seasonal vegetation of the southern Miombo (Vincens et al., 2007). Miombo woodlands are a widespread and characteristic vegetation of the tropical forests of southern Africa dominated by species of *Brachystegia* (tropical forest and warm-temperate forest, Table 3, Fig. 3) (White, 1983). Between 42 and 23 ka the regional vegetation was dominated by savannah and xerophytic shrubland as well as grassland and dry shrubland (Fig. 3). In the original pollen diagram, the vegetation composition is basically expressed by high values of Poaceae (characteristic of savannah and xerophytic shrubland, grassland and dry shrubland, Table 3) and low values of local miombo woodland taxa (Vincens et al., 2007). Regrowth of forest occurred during the LGM with expansion of warm-temperate/mixed forest although grassy vegetation remained abundant. From the onset of the Bölling/Alleröd period (B/A) to the end of the YD there was a further increase in warm-temperate/mixed forest taxa. Although the original authors did not interpret the vegetation changes in terms of millennial-scale climate change, some vegetation changes might be a response to HS. The mountainous species *Olea* (characteristic of warm-temperate/mixed

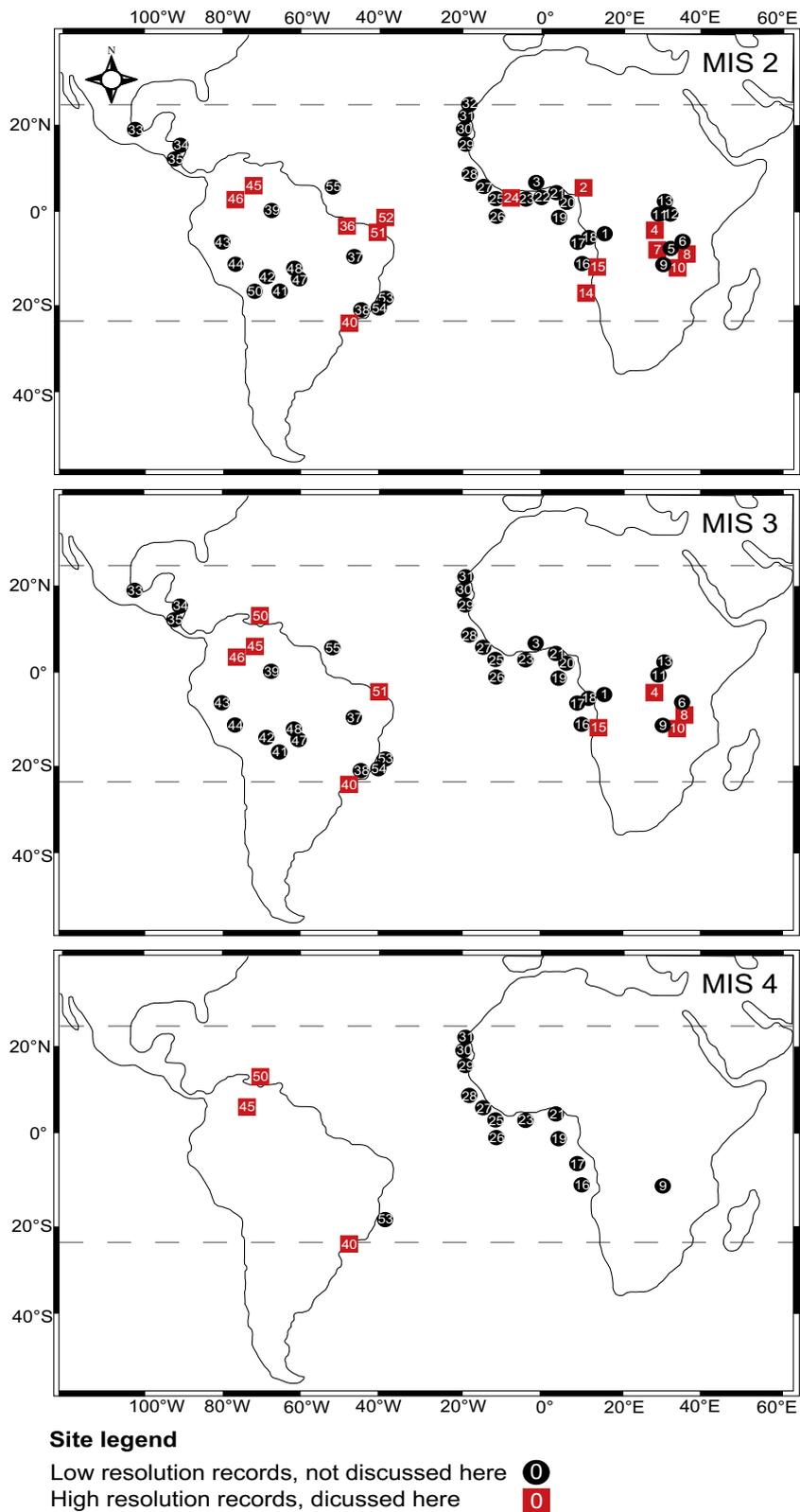


Fig. 2. Locations of high and low resolution pollen records during MIS 2, 3 and 4.

forest, temperate-montane forest, Table 3) is well represented between 45 and 40.2 ka and appears to increase following HS 4 and HS 1 (Fig. 3). However, there are no changes in the abundance of *Olea* associated with HS 2 and HS 3. Vincens et al. (2007)

interpreted the general expansion of *Olea* between 45 ka and 33 ka and between 16 ka and 14.1 ka as indicating reduced moisture availability compared to today, which might be a result of North Atlantic HS.

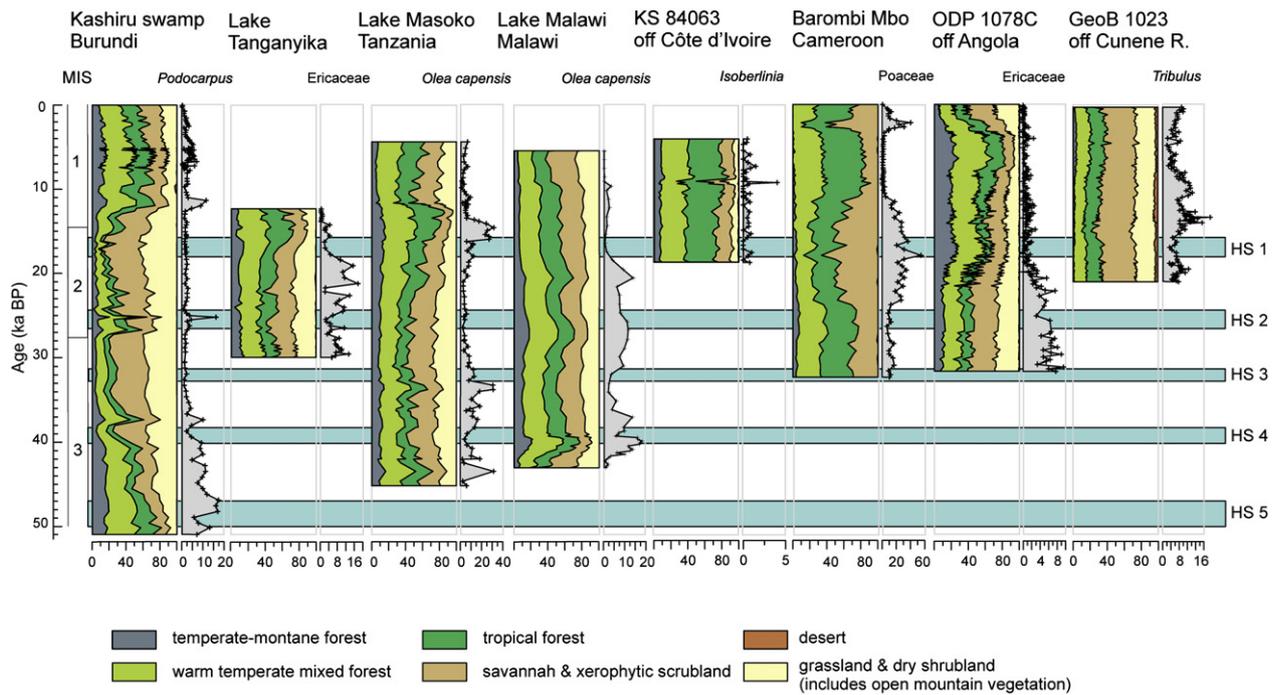


Fig. 3. Summary diagrams showing vegetation changes, using the biomisation scheme given in Table 3, for high-resolution sites from tropical Africa. An additional indicator pollen taxon is shown for each site. Fractions are expressed as percentages (X-axes).

The Lake Malawi record (core M86-18P) of DeBusk (1998) has a temporal resolution of about 1000 years/sample between 10.5 ka and 38 ka, and so is unsuitable for the detection of millennial-scale climate variability during this period. However, between 38 ka and 43 ka the record has a resolution of 200 years, and is therefore the

most detailed HS 4 record available for eastern Africa (Fig. 3, Tables 1 and 2). Prior to HS 4 the vegetation in the catchment of Lake Malawi is dominated by an open vegetation type composed of elements belonging to the biomes grassland and dry shrubland, and savannah and xerophytic scrubland (Fig. 3). At the same time pollen

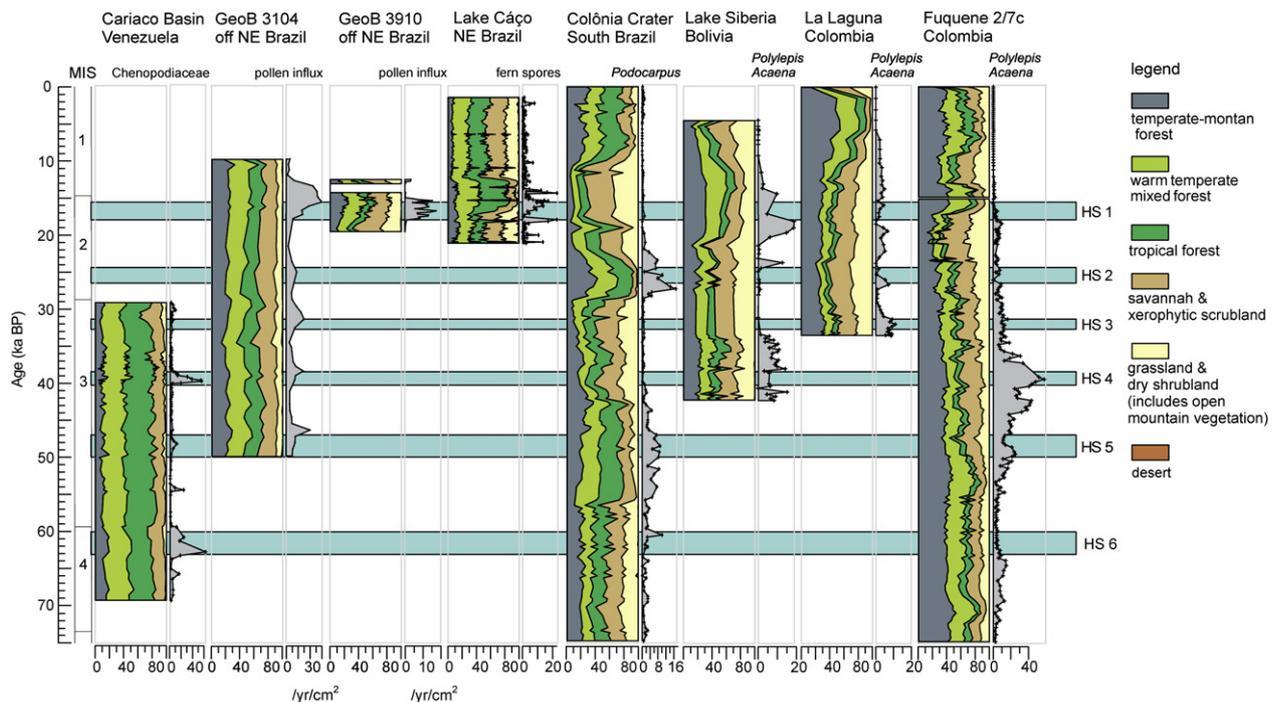


Fig. 4. Summary diagrams showing vegetation changes for South America using the biomisation scheme given in Table 3. The overlapping parts of the two Fúquene records are essentially the same. Here we have plotted the upper 15 ka of Fúquene-2 and the part 15–75 ka of Fúquene-7C. An additional indicator pollen taxon is shown for each site. Unless otherwise stated, fractions are expressed as percentages (X-axes).

Table 3
Definition of mega-biomes from Africa and South America in terms of major vegetation types, local vegetation names, and plant functional types (PFTs) and characteristic pollen taxa.

Mega-biome	Component biomes	Equivalent local vegetation names	Component PFTs	Characteristic pollen taxa
Temperate-montane forest	Cool temperate rain forest, Cool mixed forest	Temperate rain forest, Upper montane forest, High Andean forest, Cloud forest, Afromontane forest, temperate-montane dwarf forest, temperate rainforest	Tree fern, Temperate (spring-frost avoiding) cold-deciduous broad-leaved tree, Temperate (spring-frost tolerant) cold-deciduous broad-leaved tree, Temperate evergreen sclerophyll broad-leaved tree, Cool temperate evergreen needle-leaved tree, Temperate drought-intolerant forb, Herbs	<i>Podocarpus</i> , <i>Olea capensis</i> , <i>Myrica</i> , <i>Ploylepis-Acaena</i> , <i>Quercus</i>
Warm-temperate/mixed forest	Warm-temperate rain forest, Warm-temperate evergreen broad-leaved forest, Warm-temperate mixed forest	Lower montane forest, Sub-Andean forest, Upper Andean forest, Afromontane forest, temperate rainforest	Tree fern, Tropical wet evergreen broad-leaved tree, Tropical mesic drought-deciduous broad-leaved tree, Tropical xeric drought-deciduous broad-leaved tree, Warm-temperate evergreen needle-leaved tree, Warm-temperate evergreen broad-leaved tree, Temperate evergreen broad-leaved tree, Cool temperate evergreen needle-leaved tree, Cold evergreen needle-leaved tree, Temperate drought-intolerant forb	<i>Olea capensis</i>
Tropical forest	Tropical rain forest, Tropical seasonal forest, Tropical dry forest, Tropical dry forest	Amazonian forest, Atlantic forest, Guinean-Congolian rain forest, Guinean-Congolian deciduous forest, Zambebian forest, Lake Victoria Mosaic, Cerrado, Restinga, Cactus forest, Andean xerophytic bush,, Miombo woodland, tropical evergreen forest, tropical semi-deciduous forest, moist tropical forest	Tree fern, Tropical evergreen broad-leaved tree, Tropical wet evergreen broad-leaved tree, Tropical mesic evergreen broad-leaved tree, Tropical mesic drought-deciduous broad-leaved tree, Tropical xeric drought-deciduous broad-leaved tree, Tropical drought-intolerant forb, Wet/dry tropical lianas, Wet tropical herbs	<i>Brachystegia</i> , <i>Uapaca-type kirkiana</i> , <i>Isoberlinia</i> , <i>Mallotus</i>
Savannah and xerophytic shrubland	Tropical dry forest, Steppe, Savannah	Pampa, Caatinga, Steppes, Sudanian savannah, Somalia-Masai region, Zambebian savannah	Tropical xeric drought-deciduous broad-leaved tree, Drought-tolerant small-leaved low or high shrub, Eurythermic drought-adapted forb, Tropical arid drought-deciduous broad-leaved tree, Eurythermic drought-tolerant forb, Dry tropical herbs, Graminoid	Poaceae, <i>Tribulus</i> , Chenopodiaceae
Grassland and dry shrubland	Cool grass shrublands, Cool grasslands, Temperate xerophytic woods/shrub	Páramo, Grasspáramo, Subpáramo, Heather, Cushion Heather Afroalpine, tropical alpine grasslands	Temperate sclerophyll broad-leaved tree, Rosette or cushion forb, Eurythermic drought-adapted forb, Dry tropical herbs, Herbs, Graminoid	Poaceae, Ericaceae
Desert	Desert	Coastal desert, semi-desert	Desert shrubs, Eurythermic drought-adapted forb	

percentages of *Olea capensis* (characteristic of temperate-montane forest, Table 3) are at their minimum representing dry conditions on the surrounding highlands. Subsequently, the percentages of temperate-montane forests and warm-temperate/mixed forest start to increase with their maximum occurring in the beginning of HS 4. According to DeBusk (1998), temperate-montane forests expanded during this period whereas woodland was reduced in the area but still present. Another expansion of temperate-montane forests, with its main component being *Olea capensis*, appears to

correlate with the LGM, but is less strong than the expansion during HS 4 (Fig. 3). This forest expansion was interpreted by DeBusk (1998) as resulting from substantial cooling and an increase in effective moisture through decreased evaporation.

The pollen record of Lake Barombi Mbo, a large crater lake of 110 m maximum depth, provides a vegetation and climate record from western equatorial Africa covering the last 32 ka (Maley and Brenac, 1998). During the pre-LGM glacial period, the forest cover was rather similar to that of today with high values of tree pollen

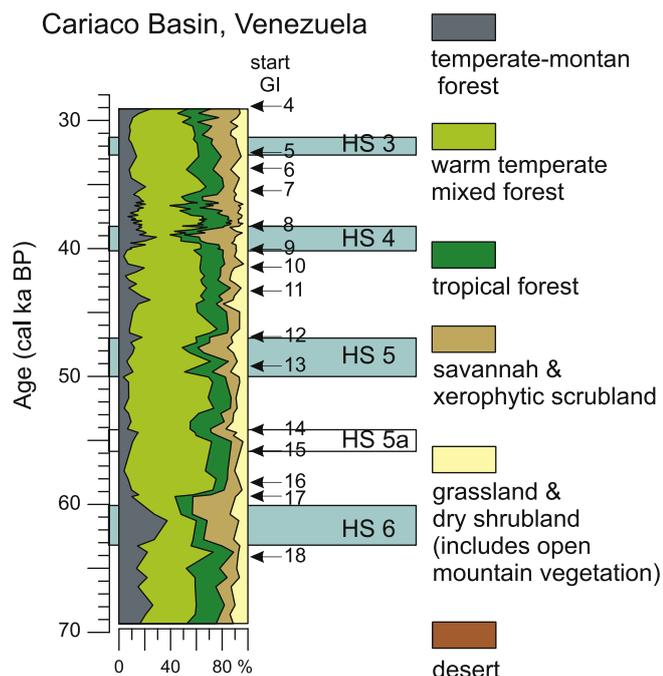


Fig. 5. An additional summary grouping is given for the record of the Cariaco Basin with montane forest elements, semi-deciduous trees of the tropical seasonal forest, evergreen trees of the tropical rain forest, savannah elements, and xerophytic shrubland after González et al. (2008). The Cariaco record hints at the existence of Dansgaard–Oeschger cycles. The start of each Greenland interstadial (GI, see also Wolff et al., this issue) is indicated by an arrow.

characteristic of tropical forest and warm-temperate/mixed forest (Fig. 3). *Olea capensis* (characteristic of warm-temperate/mixed forest, Table 3) reached maximum abundance during HS 2. The high abundance of this tree was interpreted as resulting from its extension on the crater walls close to the lake, and to indicate relatively cool conditions (Maley and Brenac, 1998). The interval spanning the LGM and HS 1 is marked by an abrupt increase in savannah and xerophytic scrubland vegetation (Fig. 3), as shown by high values of Poaceae (Table 3). Maximum values of Poaceae occur during HS 1 (Fig. 3). The LGM coincides with peaks of Cyperaceae which is considered to represent lowering of the lake level (Maley and Brenac, 1998). Cyperaceae percentages are not included in the reconstruction of tropical biomes since it is regarded as an aquatic taxon (e.g. Jolly et al., 1998). After a long transgressive phase between ca 18.5 and 14.7 ka, a final reduction in the abundance of forest taxa occurred during YD. The Barombi Mbo record (Fig. 3, Tables 1 and 2) does not show millennial-scale climate variability despite a mean temporal resolution of 600 years in the late Pleistocene. However, marked vegetation changes occur during periods that may be associated with HS 1 and HS 2.

The marine core from ODP Site 1078 C (Dupont and Behling, 2006; Dupont et al., 2008) provides a record of vegetation changes in tropical southwest Africa from 31.7 ka onwards (Fig. 3, Tables 1 and 2). During glacial times the vegetation in the source area (Angola and the southern Congo basin) was savannah and xerophytic scrubland, and grassland and dry shrubland (including open montane vegetation). Vegetation development in the sensitive high mountain areas during the last glacial (Fig. 3) is reflected by changes in the abundance of Ericaceae, a typical element of African alpine vegetation and an important constituent of grassland and dry shrubland (Table 3). The interval between 31.7 and 22 ka was generally characterised by open vegetation in the mountains, and an expansion of desert and

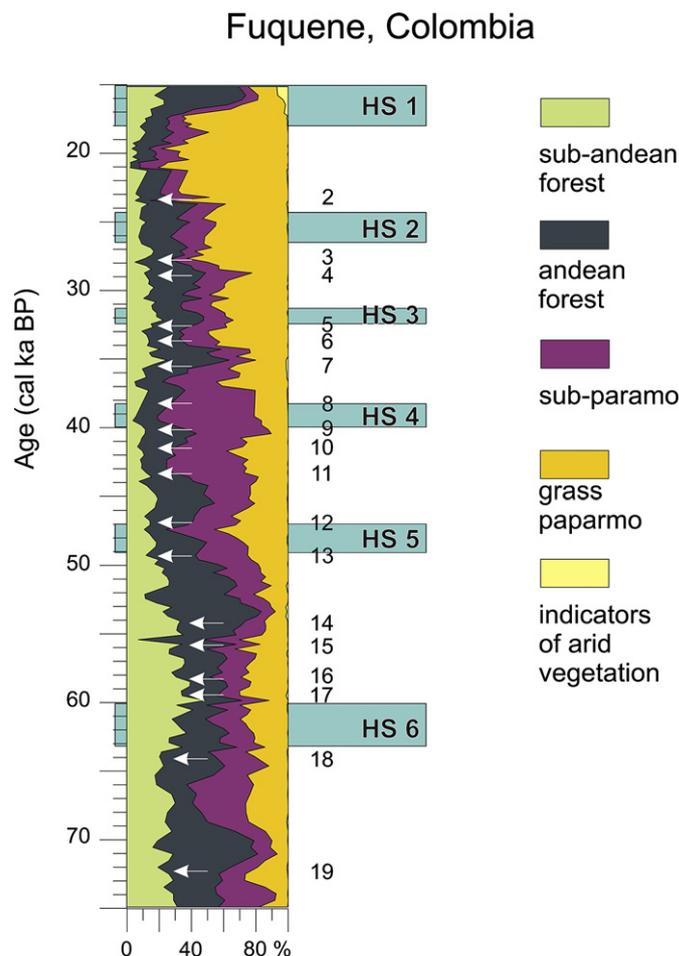


Fig. 6. An additional summary grouping is given for the Fúquene-7C record, in which the grouping is according the altitudinal vegetation zones in the Eastern Cordillera of the Andes. Increments of sub-Andean forest elements (green) are found in association with the Greenland Interstadials (numbers). Start of each interstadial (Wolff et al., this issue) is indicated by an arrow.

semi-desert vegetation in the lowlands. Between 22 and 19 ka temperate-montane forest became more extensive, as shown by increased abundance of the montane taxon *Podocarpus* (characteristic of temperate-montane forest, Table 3). Dupont et al. (2008) suggests that the increase in *Podocarpus* reflects an expansion of forest at intermediate altitude. In the lowlands, a simultaneous increase in tropical forests representatives like *Mallotus* indicates that rainforest became more widespread. The last deglaciation is dominated by *Podocarpus* pollen, corresponding in an expansion of temperate-montane forest, with a maximum occurrence during the HS 1 (Fig. 3). However, *Podocarpus* is a prolific pollen producer and the pollen is readily transported by wind; *Podocarpus* may therefore be over-represented in the pollen diagram. Nevertheless, its abundance in HS 1 suggests that *Podocarpus* forests were present locally. Simultaneously, low percentages of Ericaceae and grasses pollen indicate a reduction in grassland and dry shrubland. After HS 1, the percentages of lowland forest pollen (characteristic of tropical forest and warm-temperate/mixed forest) increased. The expansion of rainforest and warm-temperate/mixed forest is accompanied by a southward displacement of deserts and steppe (xerophytic shrubland, Table 3). Although the record has been analyzed in high-resolution and the time interval represented is sufficient, there are no indications of D-O variability. Only HS 1 clearly had an impact on the vegetation.

A marine sediment record (GeoB 1023-5) located in front of the mouth of the Cunene River off the coast of Namibia, tropical southwestern Africa, has been used to reconstruct vegetation changes on the adjacent continent for the past 21 ka (Tables 1 and 2, Fig. 3) (Shi et al., 1998). The vegetation of the pollen source area of GeoB 1023-5 (13–21°S, west of 24°E) is dominated by savannah and xerophytic shrubland, and grassland and dry shrubland throughout the whole record, with only minor changes in the vegetation composition (Fig. 3). However, variations in the pollen percentages of specific taxa indicate within-biome vegetation changes. High pollen percentages of the taxon *Tribulus* (characteristic of savannah and xerophytic shrubland, Table 3) indicate arid conditions during the LGM and subsequent to HS 1 (Fig. 3). High abundances of temperate taxa during the LGM in the original pollen data (Shi et al., 1998) suggests temperatures lower than today. An increase of grass pollen in association with low percentages of desert and semi-desert taxa and increasing values of dry forest/woodland taxa after the LGM, in the original pollen diagram, indicate increased temperatures and humidity. The timeframe covered by this record is too short to display D-O cycles. Moreover, the indications of vegetation changes associated with HS 1 are ambiguous, despite the high temporal resolution (185 years).

The pollen sequence from the deep-sea marine core KS84063 off the Ivory Coast, north-western equatorial Africa (Lézine et al., 1994; Lézine and Denèfle, 1997) only covers the timeframe from ~5 ka to 19 ka (Fig. 3, Tables 1 and 2) and consequently does not display D-O cycles. Although there are only small vegetation changes apparent in the biome diagram (Fig. 3), HS 1 and the YD are marked in Lézine et al. (1994) and Lézine and Denèfle (1997) by maximum pollen concentrations, Saharan dust input and the presence of Saharan desert taxa. Increased aridity during HS 1 is shown by the reduction in *Isobertinia* (Fig. 3), an important component of tropical forest in this region (Table 3). Moreover, Lézine et al. (1994) and Lézine and Denèfle (1997) show the sporadic occurrence of the Afromontane taxon *Podocarpus* (characteristic of temperate-montane forest, Table 3) which is usually restricted to the highlands further east. The authors suggested that during dry events, such as HS 1, lower temperatures were responsible for the extension of *Podocarpus* forest towards middle and low altitudes. In contrast, the occurrence of Saharan taxa originates from intensified meridional air-mass exchange. At the end of the deglaciation (~12 ka), *Podocarpus* forest retreated to its present-day altitudinal distribution.

3.2. Subtropical and tropical South America

The high-resolution pollen record of MD 03-2622 from the Cariaco Basin, off Venezuela, provides a record of changing environmental conditions during the period from 28 to 68 ka (Figs. 4 and 5, Tables 1 and 2) (González et al., 2008). Although sea-level changes have had an impact on this record (González and Dupont, 2009), the pollen diagram clearly shows the cold intervals associated with Greenland Stadials (GS) and with HS (González et al., 2008). The biome allocation procedure used for other South American records results in a rather bland representation of changes in Venezuelan vegetation in response to millennial-scale climate variability (Fig. 4). However, using the ecological groupings of González et al. (2008), Greenland Interstadials (GI) are obviously characterised by the expansion of tropical evergreen and semi-deciduous forests (Fig. 5) suggesting increased precipitation and river discharge. In contrast, GS show the opposite trend with the dominance of open vegetation (mainly savannah vegetation) and salt marsh taxa (e.g. Chenopodiaceae, Fig. 4, Table 3) indicating drier climatic conditions in the lowlands. Furthermore, enhanced orographic precipitation during GS promoted the expansion of montane forests (González et al., 2008). The reflection of HS in the

Cariaco Basin is a more extreme case of GS vegetation change, combined with the effects of increased sea-level that promotes the expansion of salt marshes and the succession of coastal vegetation (González and Dupont, 2009).

The GeoB 3104-1 core from the upper continental slope north-east of Fortaleza (Fig. 4, Tables 1 and 2) provides a vegetation record from northeastern Brazil reaching back over 50 ka (Behling et al., 2000). The neighbouring marine core GeoB 3910-2 (Fischer et al., 1996; Dupont et al., 2009) provides a high-resolution vegetation record covering HS 1, and thus complements the record from GeoB 3104-1. During the last glacial, there are only small changes in the biome diagram (Fig. 4): the vegetation composition was similar to the present day and characterised by dominance of caatinga (savannah and xerophytic shrubland, grassland and dry shrubland, Table 3) indicating semi-arid conditions. In the original pollen diagram (Behling et al., 2000; Jennerjahn et al., 2004), forest vegetation became more abundant during HS 1, HS 3, HS 4, and possibly HS 5 (although the dating of the lower part of the sequence is rather uncertain). A less-pronounced increase in forest occurred during HS 2. Forest expansion is interpreted as indicating wetter conditions, and is marked by increased pollen influx rates (Fig. 4).

Sediment core GeoB 3910-2 (Dupont et al., 2009), located offshore northeastern Brazil, supports the results of the neighbouring record GeoB 3104-1 (Behling et al., 2000) by providing a highly detailed vegetation history during the period including HS 1 (Fig. 4, Tables 1 and 2). At the beginning of HS 1, increased pollen influx (Fig. 4) suggests increased precipitation in the catchment area of GeoB 3910-2. However, Dupont et al. (2009) assume that the vegetation was still open, dominated by savannah and grassland vegetation, and the increased water supply results firstly in increased erosion. During the second part of HS 1 (16.6–14.9 ka) higher percentages of forest taxa (Fig. 4) imply a denser vegetation cover. In the original pollen diagram it is obvious that the diversity of trees increased significantly during the second part of HS 1 (Dupont et al., 2009). After HS 1, the vegetation gradually changes into a mixture of savannah and grassland comparable to the vegetation assemblage before 18 ka.

The pollen record from Lagoa do Caçó (Fig. 4, Tables 1 and 2) in northeastern Brazil (Ledru et al., 2001; Ledru et al., 2006) provides a detailed record of vegetation change during HS 1. Open grassland and savannah vegetation prevailed during the LGM, though at 17.5 ka an increase in fern spores marked the initial establishment of forests (Fig. 4). Dense moist forest was well established by 17 ka. Two brief intervals of forest decline occurred during the Lateglacial at 15 and 13.5 ka. The forest was destroyed at 12.8 ka, probably by fire, and the region was characterised by savannah and xerophytic scrubland vegetation during the Holocene (Ledru et al., 2006).

A long core from a peat bog in the impact crater Colônia near São Paulo, southeastern Brazil (Fig. 4, Tables 1 and 2) provides a vegetation record that covers a complete interglacial–glacial–interglacial cycle with sub-millennial temporal resolution for most of the sequence (Ledru et al., 2009). Here we only consider the last 75 ka of the Colônia pollen record (i.e. the last glacial as defined by Sanchez Goñi and Harrison, this issue). There are possible indications of D-O variability, particularly between 80 and 40 ka, indicated by higher arboreal pollen percentages. However, the age model relies on the assumption that forest growth is coupled to precession. The beginning of the glacial was characterised by a slight decrease in tree pollen frequencies but an increase in the frequency of *Podocarpus* (characteristic of temperate-montane forest, Table 3). Between 55.8 and 40.9 ka an expansion of tropical forests occurred in the pollen source area of the Colônia crater. The floristic composition was very similar to that observed during the interglacial. Another expansion of tropical forests occurred from 30 to 23 ka and was characterised by an assemblage of plant taxa that

might represent a temperate rainforest. During the periods from ca 40 to 30 ka, and from 23 to 12 ka, tropical forest was replaced by open vegetation dominated by grasses. The Atlantic forest, a regional type of tropical forest (Table 3) found in relatively wet climates, was considerably reduced during these dry episodes although small patches remaining in protected areas around the crater (Ledru et al., 2009). In general, the variations in the abundance of forest taxa seem to be correlated to precession and moisture availability. The floristic composition of the forest was different in each precession cycle attesting to varying climatic conditions and interference of high latitude climate change in this tropical region (Ledru et al., 2009).

The pollen record from the La Laguna depression (Helmens et al., 1996), located on the outer slopes of the Eastern Cordillera of Colombia west of the high plain of Bogotá, shows vegetation changes since 30 ka (Fig. 4, Tables 1 and 2). The pre-LGM period (before 25 ka) is characterised by relatively high proportions of grassland pollen and relatively low abundances of arboreal taxa, suggesting that the site was located in the grasspáramo (grassland and dry shrubland) vegetation zone. Helmens et al. (1996) recognized the occurrence of an interstadial period in the middle of the LGM (La Laguna Interstadial) from 23 to 20.5 ka. At this time glaciers retreated, extensive soil formation took place, and the upper Andean forest limit and mean annual temperature rose considerably. During the La Laguna Interstadial, grass pollen dominates the original diagram but pollen of *Polylepis-Acacena* (characteristic of temperate-montane forest, Table 3) is also well represented. In general, the LGM shows open grasspáramo conditions implying a lowering of the upper forest limit by 1100 m (early part of LGM) to 900 m (late LGM) and a drop in mean annual temperature (Helmens et al., 1996). Increasing percentages of *Polylepis-Acacena* pollen during the La Laguna Interstadial, indicate an expansion of temperate-montane dwarf forest. This forest type occurs at upper treeline, and thus the expansion indicates an upward shift of the upper forest limit resulting from higher temperatures (Fig. 4). Thus, the palynological data suggest that the La Laguna Interstadial warming event might be associated with the period between HS 1 and HS 2 (Fig. 4). Interstadial conditions are again registered during the Lateglacial, i.e. during the Guantiva Interstadial (Van Geel and Van der Hammen, 1973; Van der Hammen and Hooghiemstra, 1995; Van't Veer et al., 2000) at around 14 ka, when declining grass pollen percentages and increased arboreal pollen suggest slightly warmer temperatures than during the La Laguna Interstadial.

The pollen records of Fúquene-2 (Van Geel and Van der Hammen, 1973) and Fúquene-7C (Mommersteeg, 1998; Mommersteeg and Hooghiemstra, in review) come from Lake Fúquene, located at 2580 m in the Eastern Cordillera of Colombia. The lake lies ca 600 m below the present-day upper Andean forest (a type of warm-temperate/mixed forest) limit. The Fúquene-7C pollen record has a gap in the Lateglacial period, but the Fúquene-2 record provides good coverage for the last ca 15 ka (Figs. 4 and 6, Tables 1 and 2). Although the combined Fúquene records cover the last 85 ka, only the last 75 ka (corresponding to the glacial, see Sanchez Goñi and Harrison, this issue) are shown here (Figs. 4 and 6). The pollen record shows a series of interstadials which resulted in shifts in the relative importance of different biomes (Fig. 4); the interstadial intervals are even more clearly expressed in the original pollen record (Fig. 6). The trees *Polylepis-Acacena*, *Quercus*, and *Podocarpus* (all characteristic of the temperate-montane forest, Table 3) show considerable changes in abundance in response to millennial-scale climate variability. These taxa, *Quercus* in particular, are tolerant of a broad range of moisture conditions, thus the variability in arboreal taxa is assumed to reflect temperature change. The upper Andean forest limit (i.e. the transition between temperate-montane

forest and tropical alpine grasslands, páramo) occurs today at the ~13.5 °C annual isotherm. The pollen record indicates that this ecotonal boundary occurred at ca 2100 m (a decrease of >1000 m compared to its current elevation of ca 3180 m) during the LGM. During the warmest part of the Holocene, the boundary occurred at ca 3300 m (an increase of ca 150 m compared to its current elevation) during the warmest part of the Holocene. Such shifts, which are characteristic of the observed stadial–interstadial vegetation changes, imply temperature changes from ca 8 °C cooler to ca 1 °C warmer than today.

The 40 ka pollen record (Fig. 4, Tables 1 and 2) from a small, closed lake basin at 2920 m in the eastern Cordillera of Bolivia (Siberia: Mourguiart and Ledru, 2003) has a mean temporal resolution of about 750 years. Nevertheless, there are no obvious changes in vegetation in response to abrupt climate variations. From ca 40 to 29 ka, the vegetation was dominated by an open forest with cloud forest taxa (temperate-montane forest). According to Mourguiart and Ledru (2003) the low arboreal pollen percentages during the LGM suggest an open landscape, dry and cold climatic conditions, indicating a drastic lowering of moisture availability from the Amazonian region. Increasing percentages of *Polylepis-Acacena* (temperate-montane forest, Fig. 4) and the algae *Botryococcus* correspond to a short, rapid increase in moisture around 23 ka. Between 20 ka and 13 ka, a moist tropical forest developed. An initial increase in *Polylepis-Acacena* at 20 ka is attributed to an increase in moisture, immediately followed by the development of the moist tropical forest which can be attributed to an upslope shift of the upper forest limit and to more adiabatic moisture from the Amazonian Basin due to an increase in temperatures.

4. Discussion

4.1. Tropical Africa

There are eight records from tropical Africa, but only six of these include MIS 3. The longest record, from Kashiru swamp in Burundi, extends back to 50 ka. Most of these records show changes in vegetation in response to periods associated with Heinrich events (Tables 4 and 5). HS 1 is recorded in nearly all African records, but the nature of the vegetation response varies from site to site. The period including HS 2 is only covered by five of these records; in the case of the Lake Malawi record the time resolution is marginal. Pollen records that cover the time periods of HS 3 and 4 are available from just two East African records (Lake Masoko and Lake Malawi). Only the Kashiru swamp pollen record (Burundi) reaches back to 50 ka, and thus covers the period of HS 5. However, despite several of the records having sufficient temporal resolution during the end of MIS 3 and the first part of MIS 2, there is no indication of vegetation changes corresponding to D-O cycles in any of the African pollen records.

The evidence of D-O variability in other palaeoenvironmental records from tropical Africa is equivocal. Mulitza et al. (2008), for example, found no traces of D-O variability (although they do see prominent HS variability) in grain size records from a marine core off the mouth of the Senegal River. On the other hand, elemental Zr/Ti- and Si/Ti records from Lake Malawi, which reflect changing aeolian inputs and hence aridity, show changes related to both D-O cycles and HS (Brown et al., 2007). We suggest that the absence of D-O variability is a real phenomenon in north-western Africa, and that only the most marked climate changes corresponding to the HS were registered in the vegetation of tropical Africa.

Although there is no indication of vegetation changes in response to D-O warming events, there are changes related to HS. In general, the HS are marked by an increase in arboreal taxa, perhaps

Table 4
Summary of vegetation changes through D-O cycles at individual high-resolution sites from Africa and South America. Vegetation description follows Figs. 4 and 5 except for the Cariaco Basin (Fig. 5) and Fúquene (Fig. 6).

D-O cycle	Kashiru swamp	Lake Masoko	Colônia	Geob 3104	Cariaco Basin	Fúquene
D-O 1	temperate-montane forest, tropical forest	forest with Olea capensis	open grassland & dry shrubland, forest peaks at 12 and 19 ka	steppe, semi-desert forest, steppe	no data	subpáramo
D-O 2	grassland & dry shrubland, savannah & xerophytic shrubland little forest	warm-temperate mixed forest		steppe, semi-desert		Andean forest
D-O 3	temperate-montane forest, tropical forest	grassland & dry shrubland, savannah & xerophytic shrubland, little forest	temperate rainforest	forest?, steppe		Andean forest, grasspáramo
D-O 4	tropical forest, grassland & dry shrubland, savannah & xerophytic shrubland, little forest			steppe, semi-desert		
D-O 5	temperate-montane forest, tropical forest, grassland & dry shrubland, savannah & xerophytic shrubland, little forest	grassland & dry shrubland, savannah & xerophytic shrubland, little forest	tropical forest	forest, steppe	semi-deciduous forest, savannah, Montane forest semi-deciduous forest, savannah	Andean forest, grasspáramo
D-O 6	temperate-montane forest, tropical forest, grassland & dry shrubland, savannah & xerophytic shrubland, little forest	Grassland & dry shrubland, forest with Olea capensis	open grassland & dry shrubland	steppe, semi-desert		Andean forest
D-O 7	temperate-montane forest, tropical forest, grassland & dry shrubland, savannah & xerophytic shrubland, little forest					
D-O 8	temperate-montane forest, tropical forest, grassland & dry shrubland, savannah & xerophytic shrubland, little forest					
D-O 9	more forest		temperate rainforest	forest, steppe	semi-deciduous forest	grasspáramo
D-O 10	temperate-montane forest, less tropical forest, increasing savannah & xerophytic scrubland		grassland & dry shrubland, declining forest	steppe, semi-desert	evergreen & gallery forest, savannah, montane forest evergreen & gallery forest	subpáramo
D-O 11	temperate-montane forest, tropical forest	temperate-montane forest			montane forest semi-deciduous forest, evergreen & gallery forest	Andean forest, subpáramo
D-O 12	temperate-montane forest, tropical forest	no data	temperate rainforest	forest?, steppe	semi-deciduous forest	grasspáramo subpáramo
D-O 13	temperate-montane forest, tropical forest			steppe, semi-desert	montane forest semi-deciduous forest	Andean forest, subpáramo
D-O 14	no data			forest, steppe	semi-deciduous forest, savannah semi-deciduous forest	grasspáramo
D-O 15	no data			steppe, semi-desert	semi-deciduous forest, savannah	Andean forest, subpáramo
				no data	semi-deciduous forest, savannah	Andean forest
					semi-deciduous forest	sub-Andean forest

D-O 16	GS GI D-O warming	temperate- montane forest, savannah & xerophytic scubland
D-O 17	GS GI D-O warming GS (HS 6)	montane forest, savannah montane forest, evergreen & gallery forest no data
D-O 18	GI D-O warming	
D-O 19	GS GI D-O warming	subpáramo Andean forest

reflecting an increase in moisture availability. However, where multiple Heinrich events are registered at a site, the vegetation changes are not identical (Figs. 3 and 4). In general, in all the tropical African sites, the vegetation changes during HS are much less-pronounced than those registered in extra-tropical regions of the northern hemisphere (see e.g. Europe: Fletcher et al., this issue).

The absence of vegetation changes corresponding to HS 1 in the marine record off Ivory Coast is surprising because other palaeoclimatic indicators do show marked changes during this interval. The nearby marine record off the Senegal River mouth, for example, shows decreased river flow and increased aeolian dust during HS 1–5 (Mulitza et al., 2008). The magnetic grain size record of Lake Bosumtwi in Ghana also shows strong increases during HS 1, HS 2 and the YD (Peck et al., 2004). Peck et al. (2004) interpreted this as a result of increased aeolian dust input and increased erosion due to reduction in vegetation cover.

There is clearly a need for more records from tropical Africa, particularly from the northern equatorial tropics where there is no high-resolution pollen record at all. Furthermore, our interpretation of the existing records is limited by the rather low sample resolution of most cores and by our focus on vegetation changes at the mega-biome level in order to facilitate comparisons between sites and between regions. Despite these caveats, the existing records do show a vegetation response to HS variability and suggest that the response to rapid climate changes is not as strong in Africa as in other regions. The observed changes are consistent with the hypothesis that tropical climate changes are associated with a shift in the migration pattern of the ITCZ during HS due to reduction in the strength of the AMOC. The fact that the response is not as strong as that observed in extra-tropical regions is consistent with the idea of an attenuation of the North Atlantic climate signal into the tropical regions (e.g. Rahmstorf, 2002; Broecker, 2003). The fact that the magnitude of the response at a given site is not identical during each HS is unsurprising; the annual pattern of the ITCZ and the related Congolian Air Boundary is highly complicated over the African continent and it is unlikely that the behaviour of this system was consistent during different HS. The observed vegetation changes in tropical Africa are not consistent with the hypothesis that the circum-Atlantic tropics themselves play a key role in generating rapid climate changes. Although we have suggested a plausible climatic interpretation of the observed vegetation changes, there are a number of other influences including the effects of elevation, atmospheric CO₂, evaporation which are still poorly investigated and understood (e.g. Gasse et al., 2008).

4.2. Tropical South America

There are eight sites from South America with sufficiently high-resolution to record millennial-scale variability (Tables 4 and 5). The records from the northern (Cariaco Basin) and southern (Lagoa de Caçó, GeoB 3910) present-day limits of the ITCZ show that vegetation responds to both HS and to D-O variability. In the northern sites, lowland forests characterise GI while the vegetation becomes more open during GS. The opposite signal is found at the southern limit: vegetation cover increases during GS and becomes more open during GI. The records from Lake Caçó and GeoB 3910 even mimic the two phase internal structure of HS 1 (Ledru et al., 2001; Jennerjahn et al., 2004; Dupont et al., 2009). The opposition of vegetation changes at the northern and southern limits of the ITCZ support the hypothesis of a southward shift in the migration pattern of the ITCZ during HS (Martin et al., 1997; Peterson et al., 2000).

Records for southeast Brazil and western South America (Colônia, Lake Siberia, La Laguna, Lake Fúquene) do not seem to register rapid climate changes associated with D-O variability in

Table 5
Summary of inferred climate changes through D-O cycles at individual high-resolution sites from Africa and South America.

D-O cycle		Kashiru swamp	Lake Masoko	Colônia	GeoB 3104	Cariaco Basin	Fúquene
D-O 1	GS (YD) GI D-O warming	cool, moderately wet	moderately wet, short dry seasons	dry, wetter at 19 and 12 ka	moderately dry moderately wet	no data	moderately cool moderately cold, dry
D-O 2	GS (HS 1) GI D-O warming	cool and moderately dry, effects of low CO ₂	moderately wet		moderately dry		cold, dry cold
D-O 3	GS (HS 2) GI D-O warming	wet	cool and dry	wet	moderately wet? moderately dry		
D-O 4	GS GI D-O warming	cool and moderately dry, effects of low CO ₂					moderately cold
D-O 5	GS (HS 3) GI D-O warming			dry	moderately wet moderately dry	dry, cool very dry	
D-O 6	GS GI D-O warming		moderately dry and cool				
D-O 7	GS GI D-O warming					wet	warm
D-O 8	GS GI D-O warming	wet		moderately wet dry		wet, cool wet	cold, dry cool, dry
D-O 9	GS (HS 4) GI D-O warming	cool and increasingly drier, and/or effects of low CO ₂			moderately wet moderately dry	dry, cool very wet	
D-O 10	GS GI D-O warming						moderately cold, dry
D-O 11	GS GI D-O warming		moderately wet	wet		wet	cold, dry cool, dry
D-O 12	GS GI D-O warming		no data		moderately wet? moderately dry	cool wet	moderately cold, dry
D-O 13	GS (HS 5) GI D-O warming	cool, moderately wet			moderately wet moderately dry	dry wet	Cold, dry
D-O 14	GS GI D-O warming	no data			no data	moderately dry	moderately cool warm, wet
D-O 15	GS (HS 5a) GI D-O warming					wet	very warm, wet
D-O 16	GS GI D-O warming			moderately dry			
D-O 17	GS GI D-O warming						
D-O 18	GS (HS 6) GI D-O warming					dry, cool wet	
D-O 19	GS GI D-O warming					no data	cool, wet warm, wet

a consistent way. Changes in forest cover at Colônia are related to precessional variation rather than rapid climate change. Vegetation changes at the three high altitude sites (Lake Fúquene, La Laguna, and Lake Siberia) primarily reflect changes in temperature. At Lake Siberia, there are reductions in forest cover during HS, and traces of D-O variability in the abundance of trees from moist open forests between HS 4 and HS 3. D-O variability is reflected in the Lake Fúquene record by altitudinal shifts in the lower temperate-montane forest, which extends upslope during GI. Similarly, the La Laguna record indicates an upward shift in the Andean forest limit

resulting from increased temperatures following HS 2 and HS 1 which might also reflect traces of D-O variability.

5. Perspectives

This paper attempts to review and synthesise vegetation records from tropical Africa and South America covering the last glacial and to explore the response of the tropical vegetation to climate changes during a period characterised by millennial-scale climate variability and rapid warming events. Records from both continents

show vegetation response to HS; the response to D-O variability is more muted in tropical South America and absent from records from Africa. The records from northern South America show opposite responses in the northern and southern hemispheres, which support the hypothesis of a southward shift in the position of the ITCZ during HS. However, there are insufficient vegetation records from northern Africa to determine whether this pattern is mirrored on that continent.

There is a clear need for more, and higher-resolution, records from both regions. There is also an urgent need for improved dating of key records. The creation of age models independent of orbital-tuning techniques is required in order to be able to study leads and lags in the climate system. We have not included some key records from the Colombian Andes (e.g. Funza-1, Funza-2 and Fúquene-9C) because the existing age models are currently being reviewed.

It may not be possible to obtain high-quality records from terrestrial sites for some regions, either because of the lack of suitable basins or because recent climate conditions have prevented organic accumulation. An obvious example of this is the northern African tropics. An alternative is to make more use of pollen records from offshore marine cores. Not all such cores will provide a sufficiently high-resolution record to document rapid climate changes during the last glacial, but there are regions where this has proved possible and we have shown that such records can provide useful insights into the nature of the vegetation response to rapid climate changes. Marine records can be difficult to interpret because they record pollen coming from a very large source area, which may therefore include several different biomes (Dupont and Wypytta, 2003). Nevertheless, and again as we have shown here, it is possible to use such records to document latitudinal shifts in key biomes.

For comparison purposes, we have expressed the high-resolution pollen records from the African and South American tropics in terms of changes in major vegetation types (or mega-biomes) drawing on pre-existing schemes for converting pollen taxa to PFTs and PFTs to mega-biomes. However, the pre-existing schemes for Africa and South America are not mutually compatible, and our classification is to a large extent subjective. The data set of high-resolution pollen records produced through this synthesis exercise, in conjunction with the records from other regions (Fletcher et al., this issue; Jiménez-Moreno et al., this issue; Kershaw et al., in this volume; Takahara et al., this issue), will allow standard biomisation methods (see Prentice et al., 2000) to be applied in a globally consistent way to reconstruct global vegetation changes through the last glacial.

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