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High-resolution vegetation history of West Africa during the last 145 ka [★]Mathieu Dalibard^{a, *}, Speranta-Maria Popescu^a, Jean Maley^b, François Baudin^{c, d},
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Abstract:

The essential characteristics of the vegetation dynamics of tropical Africa remain only partially known. This study assesses the succession of vegetation-types over Central Africa during the last two glacial/interglacial cycles. Analysis of core KZai 02, which contains pollen from the Zaire River watershed (latitudes 9°N–13°S), allows the investigation of long-term patterns of plant ecosystem development and their climatic causes. Core KZai 02 (18.20 m long) was recovered from 6°24.20'S/9°54.10'E in the uppermost axial edifice of the Zaire deep sea fan. The chronology of this sedimentary archive was established using nanofossils and correlations of pollen and total organic carbon signals with the nearby core GeoB1008. The pollen record indicates that: (i) glacials (MIS 6, 4, 2) are marked by the development of afro-montane (*Podocarpus*) forest at high altitudes when central basin lowlands were occupied by *Cyperaceae* marshes and savannah; (ii) during interglacials (MIS 1, 5) lowland forests were developed, marked by the successive expansion of pioneer, warm-temperate, rain forests, and mangrove indicating sea-level rise; (iii) glacial-interglacial transitions (MIS 6/5, 2/1) display similar vegetation dynamics. The strong evidence of afro-montane forest and the opening of the vegetation during glacials suggest a reduced latitudinal distribution of rainfall by the strengthening of the trade wind system. West African monsoon systems were enhanced during interglacials, allowing the progressive development of lowland forests. The development of rain and pioneer forests during glacial Heinrich stadials suggests an enhancement of water availability in tropical Africa associated with these high latitude events. However, no augmentation of wind activity, described by previous studies, is evidenced by our pollen record. Similar vegetation successions during glacial/interglacial transitions suggest the diachronous and stepped intervention of CO₂ (emphasizing the influence of temperature on plant ecosystems) and water availability.

Keywords : Central Africa ; Climate ; Environmental parameters ; Late Pleistocene ; Pollen ; Vegetation dynamics

1. Introduction

Tropical environments contain some of the richest ecosystems on Earth but the mechanisms that control their dynamics are still not fully understood. To predict the future evolution of these environments, further studies are needed to link the vegetation response to climate forcing and explore the underlying processes. Thus, the development of high-resolution ecosystem reconstructions represents a necessary step towards a better understanding of the past dynamics of the vegetation. Such paleovegetation records will constitute an essential input for models that take into consideration vegetation/climate coupling.

African phytogeography is tightly correlated with the InterTropical Convergence Zone (ITCZ) and its associated precipitation. West Equatorial Africa is particularly suited to the reconstruction of past vegetation dynamics because it displays a complete set of the regional plant ecosystems that cover the Zaire/Congo River watershed (between 9°N and 13°S; Fig. 1). Central African vegetation, which develops according both to latitude and altitude, has been directly impacted by climate changes and has responded through successive replacements. Interglacials are marked by the development of forested environments, whereas glacials are characterized by the expansion of Cyperaceae marshes at the center of the Zaire Basin, with the north and south surrounded by savannah (Dupont *et al.*, 2000; Olago, 2001). Several pollen studies have already been undertaken in Central Africa (e.g., Maley and Brenac, 1987, 1998; Médus *et al.*, 1988; Vincens *et al.*, 1991; Elenga *et al.*, 1991, 1994; Ssemanda and Vincens, 1993; Maley, 1996; Salzmann, 2000), but the records are often scarce and do not benefit from a long temporal extent. Marine pollen records allow continuous reconstructions over longer time-intervals (Bengo and Maley, 1991; Lézine and Vergnaud Grazzini, 1993; Frédoux, 1994; Jahns, 1996; Jahns *et al.*, 1998; Dupont *et al.*, 1998, 2000; Marret *et al.*, 1999; Lézine *et al.*, 2005). They provide pollen floras that represent the dominant vegetation features of a wide region, without the disturbance exerted by local ecosystems on continental pollen records. These marine studies have emphasized the dominant control of precipitation on African plant ecosystems. Moreover, the results have highlighted the late Pleistocene dynamics of the West African monsoon (WAM) system, indicating rainfall decrease and trade-wind enhancement during glacials, and conversely during interglacials. They are associated with south- and northward shifts of the ITCZ, respectively. Yet, these fluctuations

in precipitation cannot completely explain the vegetation signal reconstructed by these pollen records.

The rainfall front associated with the ITCZ interacts with several parameters that may affect the various plant ecosystems. Temperature variations are usually considered a minor influence on African vegetation (Wyputta and McAveney, 2001). In tropical areas, cooling episodes are balanced by a negative feedback resulting from reduced evaporation due to a decrease in tropical rainforest representation. It reduces latent heat loss, thereby leading to relatively warmer surface temperatures (Weijers *et al.*, 2007). However, the moisture availability, driven by thermic gradients between tropical/subtropical (Schefuss *et al.*, 2005) and oceanic/continental (Weijers *et al.*, 2007) areas, impacts the precipitation distribution and consequently the phytogeography. Additionally, temperature fluctuations emphasize the CO₂ impact on the African plant ecosystems according to Jolly and Haxeltine (1997), Street-Perrot *et al.* (1997) and Wu *et al.* (2007). It appears that C₃ plants, including almost all trees and shrubs, are disadvantaged when atmospheric CO₂ concentration is low (Idso, 1989; Ehleringer *et al.*, 1991) in comparison to savannah grasses and Cyperaceae marshes (Osmond *et al.*, 1982). Nonetheless, the influence of these other environmental parameters, or of their combined effects, on the different plant ecosystems remains poorly documented.

For a better understanding of the past dynamics of the African vegetation in response to fluctuations in these parameters, high resolution records spanning several successive glacial and interglacials are needed. Transitions are of particular interest because the substitution of plant ecosystems during these major environmental changes may highlight the impact of climate changes on the regional vegetation. The last transition is already well documented by existing pollen records, but most of these do not extend further than the Last Glacial Maximum (LGM). There is a clear lack of studies reconstructing environmental changes in the area over longer time periods. For that purpose, the core KZai 02 has been analysed for its pollen content. The studied material was chosen for its potential to yield a long paleoclimatic record at high-resolution due to its location in front of the Zaire/Congo River mouth, and was expected to be particularly fruitful in capturing the pollen diversity, as indicated by a previous pollen study of the nearby core GeoB 1008 (Jahns, 1996). This study aims to accurately reconstruct successions of flora over the Central Africa in order to improve understanding of the continental environmental parameters in Central Africa under the influence of Late Pleistocene glacial/interglacial oscillations.

2. Modern atmospheric/oceanic coupled circulations

In the tropical Atlantic, the climate is driven by variations in annual insolation resulting in complex ocean/atmosphere interactive dynamics. The convergence of Hadley cells towards low latitudes are expressed by the trade wind systems that keep the margins of the tropical zone relatively dry because evaporation is higher than precipitation. The meeting of the South East and the North East trades concentrates humidity near the Equator, generating a precipitation front associated to the ITCZ (Hastenrath, 1992). Over the ocean and at high altitudes, this rain-inducing structure is vertically oriented around equatorial latitudes. However, it inclines over lower-altitude land due to the contrast of physical properties between warm and arid continental and cold and humid marine air masses (Leroux, 1993). In West Africa, after passing the Equator (between 2°N and 5°N), the SE trades change direction. Charged with oceanic humidity they meet the dry NE trades becoming the SW monsoon. This lower atmospheric wind field controls the surface ocean circulation. The SE trades drive the Benguela Current (BC), a cold northward offshore flow following the SW African coast. It divides into two branches, the main branch (Benguela Ocean Current, BOC) continuing offshore towards the northwest with the other branch (Benguela Coastal Current, BCC) moving northward along the coast (Peterson and Stramma, 1991). The BOC constitutes the southern part of the cyclonic gyre circulation of the eastern South Atlantic. The northern subdivision of this large system is composed of the east-directed water masses of the South Equatorial Counter-Current (SECC); it conveys warm equatorial water southward via the Angola Current (AC) (Gordon and Bosley, 1991). North of 15°S, the wind-stress-driven BCC declines, allowing this cold current to meet the south-directed warm AC. The meeting of these heterogeneous water masses generates a front called the Angola Benguela Front (ABF). The offshore-directed component of the Trade wind system and the coastal driven currents induce upwelling zones along the Guinean Gulf coasts (Herbland *et al.*, 1983). Fluctuations in trade wind intensity over the year regulate the quantity of cold North Atlantic Deep Water advected (Bearman/Open University, 1989). This complex system controls sea surface temperatures (SSTs), and hence evaporation of the Guinean Gulf. Several studies have noted the strong influence of SSTs on the location and intensity of the ITCZ through oceanic moisture export (Camberlin *et al.*, 2001; Schefuss *et al.*, 2005; Weijers *et al.*, 2007). Thus, the ITCZ latitudinal position fluctuates during the year, influenced by atmospheric and oceanic parameters. Over the Guinean Gulf and the western region of the African continent, these interactions define the West African monsoon (WAM) system. The annual migration of the

ITCZ leads to a strong seasonality driven by disparity in rainfalls (Hastenrath, 1988). The desert margins receive precipitation only at the height of summer, whereas equatorial regions are exposed to rainfall all year round. Latitudes in between experience a precipitation regime marked by two maxima.

3. From pollen record to Present-day vegetation

African vegetation shows a symmetrical pattern across the Equator (White, 1983), controlled by rainfall seasonality (Fig. 1). The Guinea-Congo area is covered by rain forest, surrounded to the north and south by warm-temperate forests, pioneer forests and savannahs. Three other more or less azonal vegetation-types can be identified in addition to the latitudinal types: afro-montane forest on massifs, mangrove on the coastline, and hygrophilous ecosystems along rivers and lakes.

Rain forest constitutes the main vegetation type of the Guineo-Congolian zone, located between 10°N and 5°S. This area receives high precipitation (1600 to 2000 mm per year) but records weak thermal amplitudes over the year (from 22° to 34°C). It mainly comprises evergreen rain forest. Despite the high plant diversity of this biome, its representation in pollen records is weak because many tree species are entomophilous, producing low quantities of pollen (Hooghiemstra *et al.*, 2006; Hooghiemstra and Agwu, 1986, 1988; Maley and Brenac, 1998; Dupont and Wyputta, 2003). Previous pollen records from Central Africa indicate the presence of undifferentiated Apocynaceae, Fabaceae Caesalpinoideae, Sapotaceae, *Entada*, *Martretia*, *Piptadeniastrum*, and *Rhus*.

Bordering the Guineo-Congolian area to the north and south, a “warm-temperate forest” develops under a more pronounced seasonality. Precipitation weakens but still remains high (900-1500 mm per year), while annual temperatures decrease (18°-28°C). This peripheral forest is also described as “semi-evergreen” because most of its arboreal species lose their leaves during a marked dry season of about 3 months. Its most representative taxa in marine sediment pollen records are Sterculiaceae, *Celtis*, *Hymenodictyon*, and *Nauclea*.

Pioneer forest represents a recovery state of the forested environment after an ecological perturbation. It corresponds to a transition between grass and woody environments and comprises taxa with weak forest ecological requirements such as *Alchornea*, *Cnestis*, *Syzygium*, and undifferentiated Rutaceae.

Savannah, represented by open dry vegetation, consists mainly of grasslands with dry forests. It covers two zones to the north and south of the Central Africa woody environments,

from Senegal to Ethiopia and from South Angola to Namibia, respectively. These areas are characterized by relatively low rainfall (from 1,000 to < 500 mm per year) and a long dry season of 4 months and more. Bush fires are also frequent during the dry season (Maley, 2012). Taxa from the grassy savannah are dominant over woody taxa in offshore pollen records. Asteraceae, Lamiaceae, Poaceae and Fabaceae Papilionoideae are the most representative families.

Described by White (1983) as a center of split endemism, the afro-montane forest biome (based on *Podocarpus*) covers the area east of the Zaire/Congo watershed and high altitudes of Angola and Cameroon. Owing to its morphology, *Podocarpus* pollen is dispersed effectively by wind and occurs with high relative abundance in pollen records of cooler periods (Dupont and Wypytta, 2003; Dupont *et al.*, 2007). In marine pollen records, *Podocarpus* is mainly associated with *Ilex*, *Olea*, and *Protea* (Dupont *et al.*, 2000).

Mangrove ecosystems are characteristic of tropical coastal environments. Their development is not only correlated to climatic variations but also depends on marine currents and responds to changes in sea level. The West African mangrove ecosystem is poorly diversified (White, 1983) and its representation in marine sediments almost exclusively comprises two taxa: *Rhizophora* living on foreground coastal locations, and *Avicennia* which develops further inland (Schnell, 1976, 1977; Thanikaimoni, 1987). Mangrove pollen is weakly represented in marine sediments and is usually related to episodes of sea-level changes (Kim *et al.*, 2005; Scourse *et al.*, 2005).

Hygrophilous plants represent the vegetation of lake shores and river banks (White, 1983), and are dominated by Cyperaceae associated with *Typha*, *Nymphaea*, *Polygonum*, *Aeschynomene*, *Mimosa*, *Sesbania*, etc. The location of these plants is generally advantageous for the input of their pollen into the ocean by the fluvial network (Hooghiemstra *et al.*, 1986; Hooghiemstra and Agwu, 1988).

Pollen can be transported from its source areas into marine sediments by several processes, including winds or, if it falls into a river or lake, by the river system into the ocean. Studies of surface samples from the eastern Atlantic Ocean along the African coasts indicate that wind-blown pollen predominates in sediments located far offshore and along arid areas with little or no river discharge into the ocean (Melia, 1984; Hooghiemstra *et al.*, 1986). Conversely, fluvial transport becomes prominent in humid tropical areas in the vicinity of river mouths (Davey and Rogers, 1975; Bengo, 1997). However, the proportion of river-borne particles strongly declines beyond the continental margin (Lutze *et al.*, 1988; Knaack, 1990),

except where the detrital material is channelled by turbidity currents such as along the submarine canyons of the Zaire River (Giresse *et al.*, 1981). Ocean currents do not seem to significantly influence pollen distribution patterns, due to the high sinking velocity of pollen grains and other particles through the water column (Fischer and Wefer, 1996). It is therefore assumed that a good correspondence exists between the latitudinal distribution of the African vegetation groups inland and their pollen representation in marine sediments (Hooghiemstra *et al.*, 2006; Dupont *et al.*, 2007).

4. Material and methods

The 1820 cm-long section was cored by the R/V Atalante (ZaiAngo 2 cruise, 2001) at 6°24.20'S, 9°54.10'E at a water depth of 3417 m (Fig. 1). The sediments are hemipelagic, draping the turbiditic channels and levees abandoned at 210 ka (Savoye *et al.*, 2009 and references therein). Recent turbiditic activity is restricted to the narrow strip along the presently active submarine channel (Babonneau *et al.*, 2002). The studied sediments have mostly been transported by rivers (Zaire network; Giresse *et al.*, 1981). Some additional transport may have occurred through aeolian input by the mid-tropospheric easterly winds (Dupont *et al.*, 2000), although these winds originate from approximately the same source as the Congo River with probably more input from the southern part of the watershed.

Pollen was extracted from *ca.* 20 grams (dry weight) of sediment after the following processing: 1) 200 ml of cold HCl (30%) for 24 hours; 2) 100 ml of cold HF (70%) for 24 hours; and 3) 200 ml of cold HCl (30%) for 6 hours. Residues were concentrated using ZnCl₂ (density 2.0) and sieved at 10 µm before mounting within glycerol. The sampling resolution of the uppermost 1455 cm of the core is every 5 cm and lower at its base.

Pollen grains were initially located at ×250 magnification, and identified at ×1000. A total of 229 samples contained sufficient pollen for vegetation reconstruction. Botanical identification was based on detailed morphological analysis supported by comparison with modern pollen from: (i) the Montpellier collection; (ii) the African Database (<http://medias3.mediasfrance.org/apd/>); and (iii) specialized literature (Lobreau *et al.*, 1969; Guers, 1970; Maley, 1970; Association des Palynologues de Langue Française, 1974; Ybert, 1979; Thanikaimoni, 1987; Bonnefille and Riollet, 1980). Counting was performed until a minimum pollen sum (excluding spores, reworked and unidentified pollen grains) of 150 was reached. Results are displayed in detailed and synthetic pollen diagrams (Fig. 2).

Total Organic Carbon (TOC) values were obtained using a LECO IR-212 analyser on 262 samples at 5 cm intervals between 600 and 1400 cm, and at 10 cm intervals over the rest of the core. Assuming that all carbonate is pure calcite or aragonite, the TOC percentage is taken as the difference between total carbon and carbonate carbon. Precision for calcium carbonate and total carbon are $\pm 0.5\%$ and $\pm 0.1\%$, respectively.

5. Results

5.1. Pollen flora and palynostratigraphy of core KZai 02

We identified 327 taxa from the 229 samples and grouped them according to the present-day ecological requirements of plants (Schnell, 1976, 1977; White, 1983; Appendix A). Visual inspection of significant variations in the relative abundance of the most common taxa, such as *Rhizophora* (mangrove), *Podocarpus* (afromontane vegetation), Poaceae (savannah) and Cyperaceae (humid environments), allow the characterization of 11 pollen zones from the bottom (P11) to the top (P1) of the core (Fig. 2).

Zone P11 (1449-1665.5 cm) is characterized by the strong dominance of aquatic taxa (Cyperaceae: up to 57%). They progressively decrease down to 30%, substituted by other groups such as mangrove, rain and pioneer forests (*Rhizophora* and *Avicennia*: 10%; Fabaceae Caesalpinoideae: 7%; *Alchornea*: 7%), reaching a maximum at the end of zone P11.

Zone P10 (1449-1374 cm) begins with a rapid augmentation of Cyperaceae and *Podocarpus* (to 32% and 26%, respectively). While the afromontane proportion remains high through P10, aquatic ecosystem signal decreases briefly in the middle of this interval. Mangrove and pioneer forest strongly decline through this zone.

Zone P9 (1374-1161 cm) starts with high values of Poaceae and Fabaceae Papilionoideae (total: 13-30%) after which savannah shows no significant variations. This zone is characterized by a coeval rapid decrease in *Podocarpus*, whose proportion in the pollen signal then remains low until the topmost part of P9. High values of Rhizophoraceae (around 13%) characterize this zone with an initial maximum. Increases in forest components, with the exception of afromontane elements, tend to follow mangrove representatives. Components of the low-altitude forests rise to 40-50%. Rain forest and warm-temperate forest indicators increase to 33% and 10%, respectively.

Zone P8 (1161-1068 cm) starts with an increase in afromontane elements led by two peaks of *Podocarpus*, the most important reaching 65%. These maxima alternate with a brief increase in Cyperaceae up to 19%. From the lowermost part of the zone, decreases in pollen

grains from savannah and rain forest are recorded, quickly followed by that of pioneer (*Alchornea*) and warm-temperate (*Nauclea/Hymenodictyon*) taxa.

Zone P7 (1068-968 cm) presents increases in all groups except the afro-montane group, which records a strong reduction from 31% to less than 6%, and Cyperaceae that display fluctuations at low values. Lowland trees reach a total higher than 40% in the mid-zone. As in zone P9, mangrove elements slightly increase but only to 8%. While pioneer and warm-temperate taxa decrease during the second half of zone P7, savannah, rain forest and aquatic taxa become dominant.

Zone P6 (968-885 cm) includes the most prominent peak of *Podocarpus* (68%), consistent with a fall in mangrove and lowland forest representatives. High values of Poaceae end this interval, leading to savannah rise, and preceding an important decrease in *Podocarpus*.

Zone P5 (885-778 cm) begins with a brief increase in Cyperaceae (around 25%) while afro-montane elements decrease strongly. Then, the percentage of aquatic taxa lowers while that of taxa of savannah and lowland forests increases up to 20% and 48%, respectively. Rhizophoraceae present some peaks but as a whole the mangrove group does not show a significant increase (peak at 8%).

Zone P4 (778-663 cm) starts with a decrease in elements of mangrove and rain forest, followed by successive falls of those of the warm-temperate and pioneer forests. *Podocarpus* shows two peaks (26 and 22%) in the middle of the zone interrupted by a maximum in Cyperaceae up to 32%.

Zone P3 (663-253 cm) displays at its base a decrease in rain forest elements mainly marked by the Fabaceae Caesalpinoideae (from 13 to 4%). This decrease is followed by distinct increase in pioneer elements (the Rutaceae, reaching 8%). This group maintains high values but exhibits important fluctuations during the entire zone. A prevalence of lowland forest taxa falls in the mid-zone, coinciding with peaks of Cyperaceae (22%) and *Podocarpus* (29%). After this maximum the signal of this afro-montane taxon decreases towards the end of the interval.

Zone P2 (253-105 cm) starts with a peak of the afro-montane genus *Podocarpus* up to 34%. The hygrophilous group reaches a maximum (36%), followed by Poaceae (21%). These two groups decrease towards the end of the zone while the representation of pioneer forest (especially Rutaceae) and then the warm-temperate forest (especially Sterculiaceae) display successive increases. Mangrove representation starts to rise during this interval.

Zone P1 (105-0 cm) is characterized by a maximum reached by *Rhizophora* at 21%, its abundance then decreasing until the top. Tropical rain taxa replace the warm-temperate ones as the most represented lowland forest groups and maintain a strong signal (higher than 20%) with scattered increases. The low-altitude forest signal weakens in the mid-zone, which correlates with an increase in *Podocarpus* and the hygrophilous group to 19 and 11%, respectively. The Poaceae signal fluctuates with a peak (up to 14%) at the topmost part of the core.

5.2. Chronological calibration of the KZai 02 core

Except for some samples at the base of the core, the carbonate content of KZai 02 sediments is low due to an important siliciclastic flux and abundance of organic matter. Consequently, the core cannot be dated using the usual oxygen isotope stratigraphy. Accordingly, the only possibility to chronologically calibrate the KZai 02 core lies in a reliable stratigraphic correlation with the nearby core GeoB1008 which benefits from a robust oxygen isotope record (Schneider, 1991). For this purpose, we first evaluated the temporal extent of core KZai 02, using nannofossils for the base of the core and radiocarbon dating its top.

We have examined nannofossils in 10 samples from the lowermost core section (1820-1360 cm). The biostratigraphic markers *Emiliana huxleyi* and *Gephyrocapsa* spp. were continuously recorded for the interval 1620-1360 cm (Fig. 3). *Emiliana huxleyi* indicates an age younger than 291–289 ka (lowest occurrence: Raffi *et al.*, 2006). The abundance of *Gephyrocapsa caribbeanica* indicates that the studied samples predate the *Gephyrocapsa caribbeanica/Emiliana huxleyi* cross-over (82-63 ka: Raffi *et al.*, 2006). Accordingly, the base of the core (1820-1360 cm; Fig. 3) corresponds to the NN21 calcareous nannoplankton Zone (Martini, 1971) and can be placed somewhere between 291 and 63 ka, which fits the proposed age of the axial edifice of the Zaire deep sea fan (Droz *et al.*, 2003). A radiocarbon age at $13,020 \pm 70$ years BP (Poz-34447; 14,453-15,216 Cal years BP, using Marine09 calibration curve; Reimer *et al.*, 2009) dates the top of the core at 179 cm. It was obtained on *Globigerinoides ruber* and *G. sacculifer* using 1.5 SDH-Pelletron Model “Compact Carbon AMS” ser. no. 003 (Poznan Radiocarbon Laboratory).

The nannofossil analysis provides a maximum stratigraphic extent for the core whereas the radiocarbon date gives a temporal point of reference. In addition, two signals, the ‘*Podocarpus/Podocarpus* + Rain forest’ pollen ratio and the TOC, have been used to

accurately compare cores KZai 02 and GeoB1008. The palynostratigraphy of KZai 02 is similar to that of GeoB1008 (Jahns, 1996), but at a significantly higher resolution, making pollen zones more apparent and allowing reliable climatostratigraphic relationships to be established between these two records (Fig. 3). Correspondence is also supported by strong agreement between the TOC curves, with wiggle-matching attesting to the similar sedimentary archives for the two cores (Fig. 3). It allows the calibration of KZai 02 core from MIS 6 to MIS 1, *i.e.*, from about 145 ka to present, in agreement with the chronology estimated from nannofossils. In this way, each pollen zone, which has a robust climatic background, can be directly correlated with a Marine Isotope Stage (Fig. 3).

The resulting chronologic calibration can be matched with the depth curve (Fig. 4). According to this curve, sediment input from the Zaire River recorded no significant fluctuations during the time interval covered by our study. Considering the chronologic calibration, the average resolution of the pollen record corresponds to one sample every 500 years for the uppermost part of the core and a rather longer duration between samples at its base.

6. Discussion

The high-resolution pollen record of KZai 02 details the successions of plant ecosystems in Central Africa over the past 145 ka (Fig. 5). These successions, especially at glacial/interglacial transitions, allow the assessment of environmental parameters that influence vegetation dynamics. To understand the climatic patterns involved in the observed sequence of plant ecosystem replacements, our pollen record was compared to several other proxies. As presented by Schneider *et al.* (1997) for the proximal GeoB1008 core, the TOC curve reflects paleoproductivity and in that peculiar location may be linked to upwelling intensity and therefore approximately correlated to southeast trade wind intensity (Schneider *et al.*, 1997). Pollen and TOC records from the KZai 02 core have been plotted against the Vostock ice core CO₂ record from Antarctica (Petit *et al.*, 1999) in order to explore the impact of this parameter on the plant ecosystems represented in our pollen record. To investigate the influence of temperature fluctuations on these vegetation groups we compared our signal to marine and continental temperature reconstructions. Three records were selected to test the effect of latitudinal and ocean/land thermic gradients on regional climate and the associated vegetation response. For Guinean Gulf SSTs, we selected the record of the nearby core GeoB1008 (Schneider *et al.*, 1996). Aside from its correlated chronology with the KZai 02

core, core GeoB1008 provides a summarized overview of the thermal impact of the different tropical East Atlantic water masses (Van Bennekom and Berger, 1984; Peterson and Stramma, 1991). The SST record of the GeoB1008 core (Schneider *et al.*, 1995) illustrates temperature fluctuations in the Southern Atlantic. Unfortunately, continental temperature reconstructions for intertropical Africa are scarce and hindered by relatively short temporal extents. For continental temperature fluctuations we selected the Congo Basin Mean Air Temperature (MAT) signal presented by Weijers *et al.* (2007), covering the last 25 ka. Fluctuations in precipitation intensity are given by the West African Monsoon (WAM) signal of Weldeab *et al.* (2007). This dataset is correlated to the summer insolation curve at 15°N (Berger and Loutre, 1991) and the summer Latitudinal Insolation Gradients (LIG) 60°-30°N (Davis and Brewer, 2009) implied in the monsoon system intensity and its poleward progression through its control on thermic gradient, respectively, as suggested by Davis and Brewer (2009).

6.1. Vegetation changes in Central Africa unrolled with respect to Marine Isotope Stratigraphy

6.1.1. MIS 6 (Zones P11 and P10)

In the KZai 02 core, the lowermost record of MIS 6 (Zone P11) is characterized by an important incidence of Cyperaceae and Poaceae (Figs. 2, 5) suggesting a significant opening of the vegetation over Central Africa. It indicates rather dry conditions. It probably results from a limited humidity export from the ocean inland due to reduced evaporation. This assumption is in agreement with the lowering of SSTs in the Guinea Gulf (Schneider *et al.*, 1996). Such conditions prevented the development of forests in lowlands, restricting them to refuge areas along riverbanks (Colin *et al.*, 1991; Maley, 1996). Marshes replaced them while the north and south marginal regions dried up, resulting in savannah expansion, as also proposed by Dupont *et al.* (2000). The coeval development of both dry and humid environments supports concentrated rainfall over Central Africa, which was probably more effective over mountains, compressed by the Northeast and Southeast trade wind system. The highest Cyperaceae extent matches a maximum in the summer insolation and a minimum in the summer LIG, supporting the assumption of Davis and Brewer (2009) that this orbital configuration induced an intensification of rainfall and a reduced latitudinal extent of the West African monsoon system, confined by southeast and northeast trade wind systems. The synchronous productivity enhancement, shown by the TOC signal, strengthens this hypothesis

and is consistent with previous studies (Shi *et al.*, 2001; Zabel *et al.*, 2001). This boosted atmospheric circulation associated with the relatively cool climate characterizing this MIS, and increased atmospheric circulation as represented by the SST signal (Fig. 5), should be fitted to a strong representation of afro-montane forests in our record. However, the KZai 02 pollen signal indicates a reduced extent of this ecosystem over Central Africa. The open vegetation during this interval may be inferred by the low atmospheric CO₂ concentration (Fig. 4). Such an assumption fits with the results of Jolly and Haxeltine (1997), Street-Perrot *et al.* (1997), and Wu *et al.* (2007) that emphasize how greatly forested environments, notably *Podocarpus* forests, are disadvantaged when CO₂ concentrations decrease.

The vegetation of MIS 6 can therefore be elucidated. It is not only characterized by the narrowing of lowland forests, replaced by Cyperaceae marshes. It combined with a shift of savannah fringes towards the central Zaire Basin (Dupont *et al.*, 2000 and references therein) and the maintenance of afro-montane forests, strongly reduced by the low atmospheric CO₂ concentration. These conditions did not continue for the whole interval. The slight development of rain and pioneer forests at the beginning and end of MIS 6 suggests climatic fluctuations, in agreement with Jahns (1996). Variations in temperature associated with changes in precipitation patterns could be implicated (Fig. 5).

Substage 6.1 (Zone P10), ending MIS 6, is characterized by a rapid increase in *Podocarpus* (Fig. 2). A trade wind enhancement may explain this pattern in vegetation dynamics and is consistent with the peak displayed by the productivity signal during this interval. However the TOC values reached during substage 6.1 are no different from those within MIS 6, so another parameter must be involved. The coeval rise of atmospheric CO₂ concentration represents a reliable candidate (Jolly and Haxeltine, 1997; Street-Perrot *et al.*, 1997; Wu *et al.*, 2007). According to the summer LIG and insolation, substage 6.1 corresponds also to an enhancement in rainfall intensity and a poleward extension of the precipitation area (Davis and Brewer, 2009). Such conditions should lead to an expansion of lowland forests. However, their signal in core KZai 02 displays a slight decrease during the first step of this glacial/interglacial transition (Fig. 5). The temperature parameter could be responsible: delayed temperature rise could prevent the development of lowland forests, even with an increase in atmospheric CO₂ concentration. However, despite an interruption of temperature rise just before substage 6.1, the SST signal displays a progressive increase (Fig.5; Schneider *et al.*, 1996). The warming could be delayed over land, although we lack continental temperature data for this termination to reinforce this hypothesis. Hence,

Cyperaceae marshes represent the main lowland ecosystem while afro-montane forest expands from massifs during this interval. This peculiar succession of ecosystems displayed by the KZai 02 record suggests a stepped intervention of temperature, CO₂ and water availability fluctuations on African vegetation dynamics at transition II.

6.1.2. MIS 5 (Zones P9 to P5)

The expansion of mangrove, almost exclusively indicated by *Rhizophora*, marks the onset of MIS 5 in core KZai 02 (Fig. 5), in agreement with other regional pollen records (Frédoux, 1994; Jahns, 1996; Shi and Dupont, 1997). It correlates with a sea-level rise in response to Northern Hemisphere ice-cap melting (Shackleton, 1987).

At the beginning of the interstadial of substage 5.5 (Zone P9), a brief expansion of savannahs, dominated by Poaceae, points to a relative dry phase probably due to the delayed WAM enhancement following the summer insolation oscillation (Fig. 5). Such expansion of the bordered dry savannah indicates strong seasonality in the precipitation regime. This short episode is followed by a progressive development of ecosystems requiring wetter conditions: pioneer, warm-temperate and then rain forests whose climax occurred at the end of this interstadial, the optimum of MIS 5.5 (Fig. 5). The gradual expansion of lowland forests is led by the inception of interglacial conditions. Maximum levels are reached in temperature, CO₂, WAM intensity and extent of latitudinal oscillation (Schneider *et al.*, 1997; Gingele *et al.*, 1998; Lézine *et al.*, 2005, Weldeab *et al.*, 2007). This assumption is consistent with: (i) the spread of lowland forests, as indicated by intertropical Africa records (Dupont *et al.*, 2000), and (ii) the orbital configuration (Fig. 5).

Following this, the vegetation signal becomes dominated by afro-montane forest that spread from highlands to plains, where it competed with other forest assemblages and partly replaced them (Fig. 5). This interval (Zone P8) corresponds to the substage 5d. This is in agreement with numerous pollen records of the region, where this interstadial is expressed by *Podocarpus* shifting from mountains (Bengo and Maley, 1991; Frédéric, 1994; Jahns *et al.*, 1998; Dupont *et al.*, 2000). Schefuß *et al.* (2003) linked this vegetation pattern to tropical SST fluctuations, an assumption supported by the coeval spread of afro-montane forest and the STT signal of Schneider *et al.* (1996) (Fig. 5). However, the high proportion of this group in our record is most likely partially the expression of trade-wind strengthening when considering the wind dispersion of *Podocarpus* pollen. This hypothesis is consistent with the rise in the TOC signal for the duration of this interstadial and with the results of Hooghiemstra and

Agwu (1988) and Flores *et al.* (2000) on pollen influx and wind-transported biosiliceous particles, respectively. Savannah extent displays limited reduction suggesting that the overlapping of dry fringes on the Zaire/Congo watershed decreased. An opposite trend should be expected regarding the diminution of WAM intensity and poleward progression but is probably concealed by the over-representation of *Podocarpus* (Fig. 5).

During interstadial 5.3 (Zone P7), the spread of lowland forests at the expense of afromontane forest indicates an increase in temperature, consistent with the Guinea Gulf SSTs signal (Schneider *et al.*, 1996), along with rainfall enhancement, suggesting a reinforced monsoon activity (Weldeab *et al.*, 2007). The orbital configuration is in agreement with the intensification of precipitation through a maximum reached by summer insolation. The rising LIG during MIS 5.3 suggests a progressive increase in the latitudinal extent of ITCZ oscillations according to Davis and Brewer (2009), reflected by increasingly pronounced rainfall seasonality. This climatic pattern is consistent with the increase in lowland forests and savannah representation in our record while the development of Poaceae remains low. It indicates that during interstadial 5.3 the wooded savannah covered the poleward fringe of the Zaire watershed while warm-temperate and rain forests occupied the equatorial area of Central Africa.

The vegetation pattern during interstadial 5.2 (Zone P6) is similar to that of 5.4, indicating comparable climatic conditions. Many studies of the region show similar results (Bengo and Maley, 1991; Frédoux, 1994; Jahns *et al.*, 1998; Dupont *et al.*, 2000). However, the representation of savannah and Poaceae experienced a more pronounced decrease at the beginning of this interval, while afromontane forest representation is highest. This episode coincides with a low WAM activity (Weldeab *et al.*, 2007) matching a minimum in summer insolation (Fig. 5). Unlike the interstadial 5.4, the summer LIG seems to influence significantly the poleward progression of the ITCZ according to Davis and Brewer (2009). Thus, the savannah and Poaceae decline may point to the expansion of areas affected by precipitation, and so restricting the overlap of the savannah domain over the Zaire watershed. During the second half of interstadial 5.2, *Podocarpus* forest dominance is replaced by that of open savannah (with a significant representation of Poaceae) and rain forest. Considering studies by Jolly and Haxeltine (1997), Street-Perrot *et al.* (1997) and Wu *et al.* (2007), the low atmospheric CO₂ can explain the relative opening of the vegetation.

Interstadial 5.1 (Zone P5) corresponds to a new episode of West African monsoon enhancement (Weldeab *et al.*, 2007). The rise in temperature and precipitation (Fig. 5) led to

the restriction of the afro-montane forest to the advantage of Cyperaceae marshes followed by lowland forests. The low CO₂ level at the beginning of this interstadial may explain the expansion of aquatic ecosystems quickly replaced by lowland forest while the atmospheric CO₂ rate rose.

6.1.3. MIS 4 (Zone P4)

In core KZai 02, the onset of MIS 4 is characterized by a reduced representation of rain forest followed by a decline of warm-temperate and then pioneer forests (Fig. 5). It suggests a progressive installation of glacial conditions, as reflected by a gradual disappearance of lowland forests as shown by other records (e.g., Dupont *et al.*, 2000; Whiting Blome *et al.*, 2012). These vegetation ecosystems are replaced by afro-montane forest at the beginning of MIS 4. Representation of that group in the core KZai 02 pollen signal may imply an enhancement of the trade wind system, consistent with the TOC signal (Fig. 5) and results from numerous studies (Hooghiemstra and Agwu, 1988; Flores *et al.*, 2000; Shi *et al.*, 2001; Zabel *et al.*, 2001). The reduction in temperature and carbon dioxide levels associated with the rising West African monsoon intensity and reduced poleward progression led to the rapid installation of Cyperaceae marshes during the middle of MIS 4 (Fig. 5). However, unlike MIS 6, aquatic ecosystems expansion was stopped while Poaceae expanded, a vegetation pattern also observed by Jahns *et al.* (1998) and interpreted as suggesting the progressive establishment of drier conditions. This brief savannah spread is replaced, at the very end of MIS 4, by the development of rain forest probably linked to a reinforced monsoon associated with slightly higher CO₂ levels (Fig. 5). So, except for a short reduction coeval with the peak in Cyperaceae marsh development, lowland forests did not contract as significantly as during MIS 6, as also observed by Jahns *et al.* (1998). This pattern may be attributed to a limited temperature drop as indicated by the SST curve (Fig. 5).

6.1.4. MIS 3 (Zone P3)

The MIS 3 vegetation record displays important fluctuations, and major trends are evident. The beginning of this interval, MIS 3.3, is marked by the good representation of pioneer, warm-temperate taxa while those of rain forests slightly decline (Fig. 5). Lowland forests did not achieve their maximum range as in MIS 5.5, and domination by Zaire/Congo Basin vegetation is shared with Cyperaceae marshes. The relatively cool temperatures during this MIS, associated with low CO₂ levels (Fig. 5), may have prevented the complete

expansion of a lowland forest over the watershed. Cyperaceae marsh expansion is synchronous with that of savannah in core KZai 02 (Fig. 5) and in the pollen signals of Jahns *et al.* (1998). This vegetation pattern suggests a compression of the ITCZ leading to a convergence of the dry open environment fringes towards the centre of the basin where marshes and lowland forests expanded. This interpretation supports conclusions of Davis and Brewer (2009), who associated low values of summer LIG and a maximum reached by summer insolation (Fig. 5) with a reduced poleward progression of precipitation and a WAM enhancement, respectively.

A reduction in monsoon strength during the middle of MIS 3 (MIS 3.2) led to conditions unsuitable for maintaining aquatic ecosystems and rain forest, which were partly replaced by less water-dependent savannah, pioneer and warm-temperate forests (Fig. 5). An episode in which lowland forests and wooded savannah were substituted by afro-montane forests and Cyperaceae marshes followed. If the high frequency of *Podocarpus* reflects a strengthening of the wind system, in agreement with the KZai 02 TOC signal and results from Flores *et al.* (2000) and Shi *et al.* (2001), this will indicate trade-wind enhancement during the middle part of MIS 3. The coeval spread of aquatic ecosystems is less expected. Indeed this interval, characterized by a slight rise in WAM activity and temperatures (Fig. 5), should represent suitable conditions for the spread of lowland forests. But our record indicates the opposite behavior of such forests, with the strong reduction of pioneer and warm-temperate forests and, to a lesser extent, of rain forest. We may suppose that the temperature rise, overstepping increases in rainfall and humidity availability, induces a decrease in effective moisture through increased evaporation. It should lead to a drying up of lowlands, consistent with the decrease observed in pioneer, warm-temperate and rain forests, while massifs remained humid and suitable for afro-montane forest expansion.

MIS 3.1, the last interval of MIS 3, is characterized by an enhanced monsoon system while the latitudinal progression of the ITCZ is reduced due to maximum summer insolation but low LIG, respectively, according to Davis and Brewer (2009) (Fig. 5). Therefore, the climatic pattern is not represented in the WAM signal probably because of the northern position of the core studied by Weldeab *et al.* (2007). However the center of the Zaire/Congo Basin must have received important precipitation, allowing the development of pioneer and rain forests, even when its margins became drier and suitable for the spread of savannah (Fig. 5). As for the first step of MIS 3, the expansion of lowland forests did not reach a climax and the vegetation signal was partially occupied by Cyperaceae marshes. The decrease in

temperatures at the end of this interval could have limited the expansion of rain, warm-temperate and pioneer forests.

6.1.5. MIS 2 (Zone P2)

The beginning of MIS 2 in our pollen record of core KZai 02 displays the lowest mangrove values, indicating a low sea level in agreement with other records in the area (Dupont *et al.*, 2000). This episode is accompanied by a significant and rapid development of afro-montane forest synchronous with an opening of the vegetation (Maley and Brenac, 1998; Shi *et al.*, 1998; Olago, 2001, Thevenon *et al.*, 2002) at the expense of the most thermophilous taxa (Maley, 1996; Dupont *et al.*, 2000) corresponding to the Last Glacial Maximum (LGM) (Fig. 5). Abundant *Podocarpus* representation is also revealed by this study as in many other sites scattered over tropical Africa (*e.g.*, Caratini and Giresse, 1979; Bengo and Maley, 1991; Marret *et al.*, 1999). It could be referred to an intensification of the wind system (Shi *et al.*, 2001) in agreement with our productivity signal (Fig. 5). This episode is also characterized by low atmospheric CO₂ levels, low continental and oceanic temperatures, and a reduced WAM activity. The reduced coeval land-sea thermal gradient (equivalent marine and continental temperatures) may have enhanced the continental aridity by preventing the incursion of moist air masses over the Zaire/Congo Basin (Weijers *et al.*, 2007).

Despite similar environmental conditions, the plant ecosystems pattern is different between MIS 6 and the beginning of MIS 2. The low temperatures and CO₂ levels should have led to a wider opening of the vegetation (Osmond *et al.*, 1982; Idso, 1989; Ehleringer *et al.*, 1991). This distinctive vegetation pattern may be attributed to a stronger reduction of water availability during the LGM. If the LIG along these two intervals displays comparable values, the summer insolation curves are antagonistic. According to Davis and Brewer (2009), these episodes are both characterized by reduced poleward progression of the WAM system, but with enhanced precipitation intensity for MIS 6. These climate settings may explain the wider expansion of Cyperaceae marshes during the penultimate glacial while during MIS 2, rainfalls concentrated on massifs. The rapid regression of afro-montane forest in our signal is coeval with a productivity drop (Fig. 5) and testifies to the wind-associated representation of *Podocarpus* in the marine pollen signal. Cyperaceae marshes succeeded as the main vegetation. The coeval negative land-sea temperature gradient, relatively cool continent and warm sea, resulting in a generally off-land air flow and thus preventing marine moist air to

flow onto the continent, may explain the inability of forest environments to expand. Marshes progressively regressed due to precipitation, CO₂ level and temperature increases (Fig. 5) enabling lowland forested ecosystems to spread, as also observed in numerous other studies (e.g., Jahns, 1996; Maley, 1996; Marret *et al.*, 1999). Deglaciation was interrupted by a brief decrease in WAM activity (Fig. 5), corresponding to the Younger Dryas, and was marked by the spread of savannah in many records (e.g., Maley, 1991; Ssemanda and Vincens, 1993; Shi *et al.*, 1998; Lézine *et al.*, 2005; Lézine and Cazet, 2005; Marret *et al.*, 2008), including the present one. It indicates an important seasonality in the precipitation regime. This episode is followed by the spread of lowland forests (pioneer, warm-temperate and then rain forest) indicating the progressive establishment of interglacial conditions characterized by enhanced rainfall.

6.1.6. MIS 1 (Zone P1)

A rapid and important rise of mangrove in the KZai 02 pollen record marks the onset of MIS 1 and evidences a sea-level rise (Dupont *et al.* 2000). Two main phases, the African Humid Period and the Late Holocene, characterize the climate history of this interglacial in the region and correspond to variations in latitudinal distribution and intensity of precipitation (Gasse, 2000). These episodes are not revealed in the KZai 02 pollen record, possibly because of the wide geographic area covered by our pollen assemblages and the counterbalanced regional environmental influences. However, a short rise in *Podocarpus* and savannah representation possibly corresponds to one of the unstable climatic events of the Holocene described by Gasse (2000). Reduced WAM and lowered temperatures are recorded during this episode (Fig. 5) and may have induced the savannah expansion displayed by our record. However, precipitation must have remained sufficient on massifs to explain the maximum reached in afro-montane forest representation. The establishment of the present-day vegetation followed this brief climatic episode. MIS 1 is well-documented (e.g., Lézine and Casanova, 1989; Lézine and Vergnaud Grazzini, 1993; Ssemmanda and Vincens, 1993; Maley and Brenac, 1998; Dupont *et al.*, 2000; Olago, 2001; Marret *et al.*, 2006) and will not be further discussed in this paper.

6.2. Influence of Heinrich Events on tropical African vegetation

The glacial/interglacial trend is interrupted by shorter climatic events. Heinrich events (HEs; Heinrich, 1988; Bond *et al.*, 1997), although attenuated at low latitudes, are recorded in

the intertropical climate dynamic (Jullien *et al.*, 2007, Weldeab *et al.*, 2007) and influence African plant distribution (Hessler *et al.*, 2010, Harrison and Sanchez-Goñi, 2010). No unambiguously reproducible pattern in the vegetation dynamic of tropical Africa arises from our record. Hessler *et al.* (2010) has already underlined the inconsistency of plant ecosystem responses to the different HEs between several scattered records. Even if the vast area covered by our study may blur a potential general reaction of the vegetation to these climatic pulses, some tendencies may be highlighted.

The spread of lowland forests is synchronous with most of HEs, suggesting rising humidity (Fig. 6). This interpretation is consistent with the decrease in the less hygrophilous savannah group, notwithstanding a greater variability in their behavior in response to these events. Thus, our record is in agreement with the conclusions of Hessler *et al.* (2010) who linked increased arboreal taxa in several sites scattered over Africa with enhanced moisture availability. However, if these events correspond to enhanced WAM intensity based on our record, we cannot unequivocally link them to ITCZ latitudinal fluctuations. According to Jullien *et al.* (2007), these high-latitude climatic pulses triggered a southward shift of the ITCZ. So, considering the presence of afro-montane forests over the Cameroon highlands and the wind-driven dispersion of *Podocarpus* pollen, we could expect a more pronounced response of this group to HEs. Yet, except for HE 6, these events are characterized by reductions in afro-montane forest representation in our record (Fig. 6). Accordingly, the variability of responses suggests fluctuations in the impact of the different HEs on low-latitude atmospheric circulation over the African continent.

Our record thus suggests an inconsistency in HE impact on African low-latitude climates and consequently on vegetation. H6 seems to be a special case. During this event, the dynamics of most of the plant ecosystems display trends opposite to those observed during the other HEs (Fig. 6). Our inability to associate a vegetation pattern with these climatic pulses pinpoints the need to develop high-resolution records covering the last glacial periods in tropical Africa. Such data should help to decipher the influence of the ITCZ on African intertropical climate variations linked to HEs. Moreover, the implication of other parameters could be investigated, such as atmospheric CO₂ concentration or evapo-transpiration impact, as suggested by Hessler *et al.* (2010).

6.3. Environmental changes at climatic transitions

The KZai 02 pollen record presents an undeniable similarity in the succession of vegetation types during the last glacial/interglacial transitions, MIS 6/5 and 2/1, respectively (Fig. 5). Late glacials are marked by an important representation of afro-montane forest, almost exclusively characterized by *Podocarpus* (Figs. 2, 5), supporting an atmospheric circulation strengthening also proposed by Shi *et al.* (2001). This peak of high-altitude elements is followed by an opening of the vegetation. Cyperaceae succeeded as the main vegetation type, being rapidly replaced by savannah. Afterwards, conditions apparently became suitable for the expansion of lowland (pioneer, warm-temperate, rain) forests restricting savannahs.

The mechanism of the last deglaciation and its impact on vegetation are well-documented but the MIS 6/5 transition is not completely deciphered. During MIS 2, the replacement of afro-montane forest by open vegetation in African pollen diagrams may be inferred as a reduction of the wind-stress in the intertropical area associated with the fall in atmospheric CO₂ concentration, emphasizing the temperature influence on ecosystems according to Jolly and Haxeltine (1997), Street-Perrot *et al.* (1997) and Wu *et al.* (2007). A temporary negative land-sea temperature gradient leading to an off-shore air flow that prevents marine moist air from flowing onto the continent may have been involved in the expansion of Cyperaceae marshes and savannahs. The following enhancement of the WAM system (Weldeab *et al.*, 2007; Gasse *et al.*, 2008) led to the progressive installation of the lowland forests. The gradual rise in water availability over tropical Africa was interrupted by the dry event of the Younger Dryas, marked by the spread of savannah in many records (Lézine *et al.*, 2005; Lézine and Cazet, 2005; Gasse *et al.*, 2008; Marret *et al.*, 2008) including the present one. Thus, concentration in atmospheric CO₂ and its impact on temperature control over flora triggered changes in plant ecosystems, while a delayed increase in rainfalls achieved the transition leading to climax of the interglacial indicated by maximum expansion of the rain forest. These results are consistent with those of Sinninghe Damsté *et al.* (2011) for equatorial East Africa. The similar vegetation successions from glacial to interglacial conditions that we observe in Central Africa suggest that: (i) the MIS 2/1 and 6/5 transitions are both characterized by a time-lag between at least two parameters controlling plant distributions, *i.e.*, increase in CO₂ and/or temperature *vs.* humidity, and (ii) the MIS 6/5 transition presents distinct climatic steps in vegetation dynamics.

An increasing number of studies evidence the asynchronous relationship between Antarctic and Greenland climate on millennial time-scales (Sowers and Blender, 1995;

Blunier *et al.*, 1998; Blunier and Brook, 2001; Shulmeister *et al.*, 2006; Shakun and Carlson, 2010). Through its position astride the Equator, the Zaire/Congo Basin is under the influence of both northern and southern highest latitudes. Thus, the time-lag in the various environmental parameters revealed by our study may express the shared control of both hemispheres on intertropical climate. Bianchi and Gersonde (2002) and Shulmeister *et al.* (2006) proposed that the two last glacial/interglacial transitions are characterized by southern high-latitude cold reversals impacting the global climate. These events, affecting the atmosphere/ocean CO₂ exchange system (Stephens and Keeling, 2000), may explain the observed transition from afro-montane ecosystems to open vegetation. The following spread of savannah at glacial/interglacial transitions, coeval with the Younger Dryas for Transition I, is consistent with an increased seasonality linked to an amplified extension of ITCZ latitudinal fluctuations (Garcin *et al.*, 2007). Thus, conditions may be inferred for a maximum LIG (Davis and Brewer, 2009) and thermohaline circulation modifications impacting the tropical SSTs and associated oceanic moisture export over intertropical Africa. The following development of lowland forests could be inferred as a WAM enhancement with increased rainfall indicating the inception of interglacial climax conditions. So, if water availability remains an important factor, our data suggest that high-latitude Atlantic SSTs, considering their impact on atmospheric CO₂ concentration and global temperature, must be equally taken into account when dealing with vegetation distribution in Africa.

During the MIS 5-4 progression, a decrease in humidity is indicated by declining lowland forests. This led to the installation of open savannah, marked by increased Poaceae in the core KZai 02 (Fig. 5). However a complete reversal in vegetation dynamics, as during the glacial/interglacial transitions, is not observed. The spread of afro-montane forests and Cyperaceae marshes occurred at the MIS 5/4 transition and preceded the drying up of the area. This difference in vegetation dynamics implies interfering diverse parameters and/or time-lags in their respective effects.

7. Conclusion

To date, the study of the pollen in core KZai 02 constitutes the most detailed contribution towards the reconstruction of vegetation dynamics in Central Africa over the last 145 kyrs. In addition to describing the major successions of past plant ecosystems, this study has focused on the climatic parameters involved. The major trends of Late Pleistocene African vegetation are evidenced in the KZai 02 pollen record. Glacials (MIS 6, 4, 3, 2)

resulted in the development of grassy environments, whereas interglacials (MIS 5, 1) were dominated by forests. Our high-resolution record details the vegetation succession for the last 145 ka and shows peculiar patterns such as the distinctive steps in MIS 3 and dissimilarities between the two last glacial periods. To investigate the environmental parameters controlling the plant ecosystems, pollen signals are correlated to indicators of trade winds, WAM, CO₂ levels, and to orbital forcing. This confirms the strong influence of water availability on African vegetation but also indicates that temperature and CO₂ levels must be equally taken into consideration when dealing with African vegetation. During glacials, reduced precipitation and temperatures associated with low CO₂ levels led to an opening of the vegetation. This occurs with a strengthening of the wind system as testified by the rise of *Podocarpus* pollen in our signal. A rise in temperature, CO₂ and WAM activity during interglacials drove the expansion of lowland forests over tropical Africa at the expense of savannah and Cyperaceae marshes.

The response of African plant ecosystems to short glacial climatic pulses displays various patterns. For most of the HEs, the development of lowland forests, either rain or pioneer forests, are recorded suggesting increased water availability over the Zaire/Congo Basin. No systematic increase in the air-dispersed *Podocarpus* pollen is evidenced during these episodes. Thus, our observations do not support a modification of the ITCZ fluctuations and their associated wind-system as proposed by other studies.

Special attention was paid to glacial/interglacial transitions where vegetation dynamics provides further information on the forcing climatic parameters. A similar succession of vegetation was observed during the MIS 6/5 and 2/1 transitions. Replacement of afro-montane forests by Cyperaceae marshes and savannah, and then lowland forests suggests the influence of at least two factors. Moisture availability is regarded as an important parameter for vegetation dynamics in tropical Africa. Other factors (CO₂ and/or temperature) must be considered when trying to explain these peculiar replacements. Interglacial/glacial transitions, however, do not show a recognizable pattern. Further high-resolution studies are needed to fully explore the factors controlling vegetation dynamics during these episodes.

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Appendix A. Supplementary information

Supplementary information (list of pollen taxa recorded in core KZai 02) associated with this article can be found, in the online version, at:

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Figure captions

Figure 1. Simplified vegetation map of Africa, modified from White (1983), with outline of the watershed of the Zaire River network (black thick line) and location of the core KZai 02. 1, Mangrove; 2, Pioneer forest; 3, Warm-temperate forest; 4, Rain forest; 5, Aquatic ecosystems; 6, Savannah; 7, Afromontane forest; 8, Mediterranean ecosystems; 9, Desert. Positions of the InterTropical Convergence Zone (ITCZ) during the boreal winter and boreal summer are indicated by grey dotted lines (from Leroux, 1983; Ngomanda *et al.*, 2009).

Figure 2. Core KZai 02: lithology, detailed and synthetic pollen diagrams and resulting zonation. Lithology: A, Laminated clay; B, Silty clay; C, Clay without internal structure; D, Clay with sigmoidal structure; E, Bioturbation; F: Shell; G, Fluid release structure. Pollen diagram: percentages are calculated on the total pollen sum. Synthetic pollen diagram where elements of the following vegetation types are grouped: 1, Mangrove; 2, Pioneer forest; 3, Warm-temperate forest; 4, Rain forest; 5, Aquatic ecosystems; 6, Savannah; 7, Afromontane forest.

Figure 3. Correlation of proxies: core KZai 02 vs. core GeoB1008 vs. ice core from Dome C. Core KZai 02: simplified synthetic pollen diagram and TOC curve (with location of radiocarbon age and nannofossil data) plotted with depth. Core GeoB1008: simplified synthetic pollen diagram (Jahns, 1996; Dupont *et al.*, 2000), TOC curve (Gingele *et al.*, 1998), and $\delta^{18}\text{O}$ (Schneider *et al.*, 1995) curve. Ice core from Dome C (EPICA Community Members, 2004): δD curve and MIS.

Figure 4. Age model of KZai 02 core.

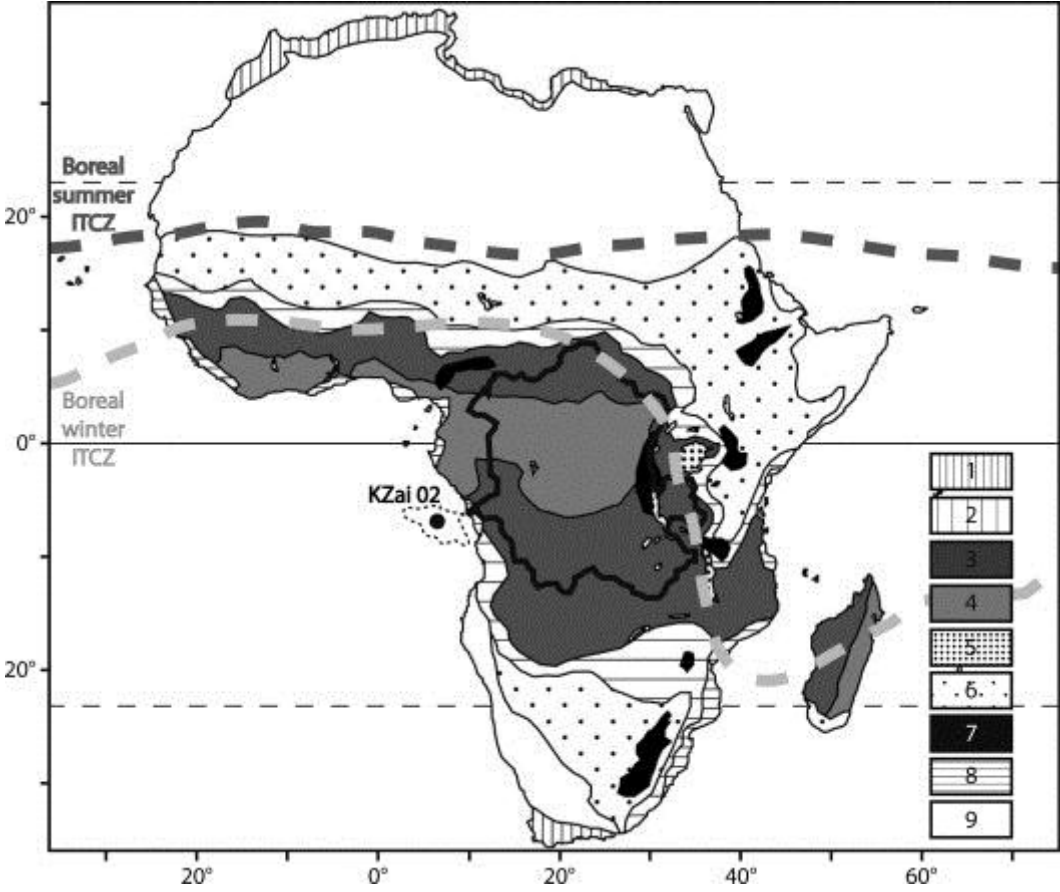
Figure 5. Semi-detailed pollen diagram of the core KZai 02 correlated to TOC curve (as productivity signal), Vostok CO_2 level (Petit *et al.*, 1999), Guinea Gulf SSTs (Schneider *et al.*, 1997), Congo Mean Annual Temperature (Weijers *et al.*, 2007), Ba/Ca ratio (Weldeab *et al.*, 2007; as a WAM system activity signal), summer insolation curve at 15°N (Berger & Loutre, 1991), and summer LIG $60^\circ\text{-}30^\circ\text{N}$ (Davis & Brewer, 2009).

Figure 6. Impact of Heinrich events (grey lines) on West African vegetation groups during the Last Glacial. Semi-detailed pollen diagram of core KZai 02 correlated to TOC curve (as productivity signal), Guinea Gulf SSTs (Schneider *et al.*, 1997), Congo Mean Annual Temperature (Weijers *et al.*, 2007), and Ba/Ca ratio (Weldeab *et al.*, 2007; as a WAM system activity signal).

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Figures

Figure 1



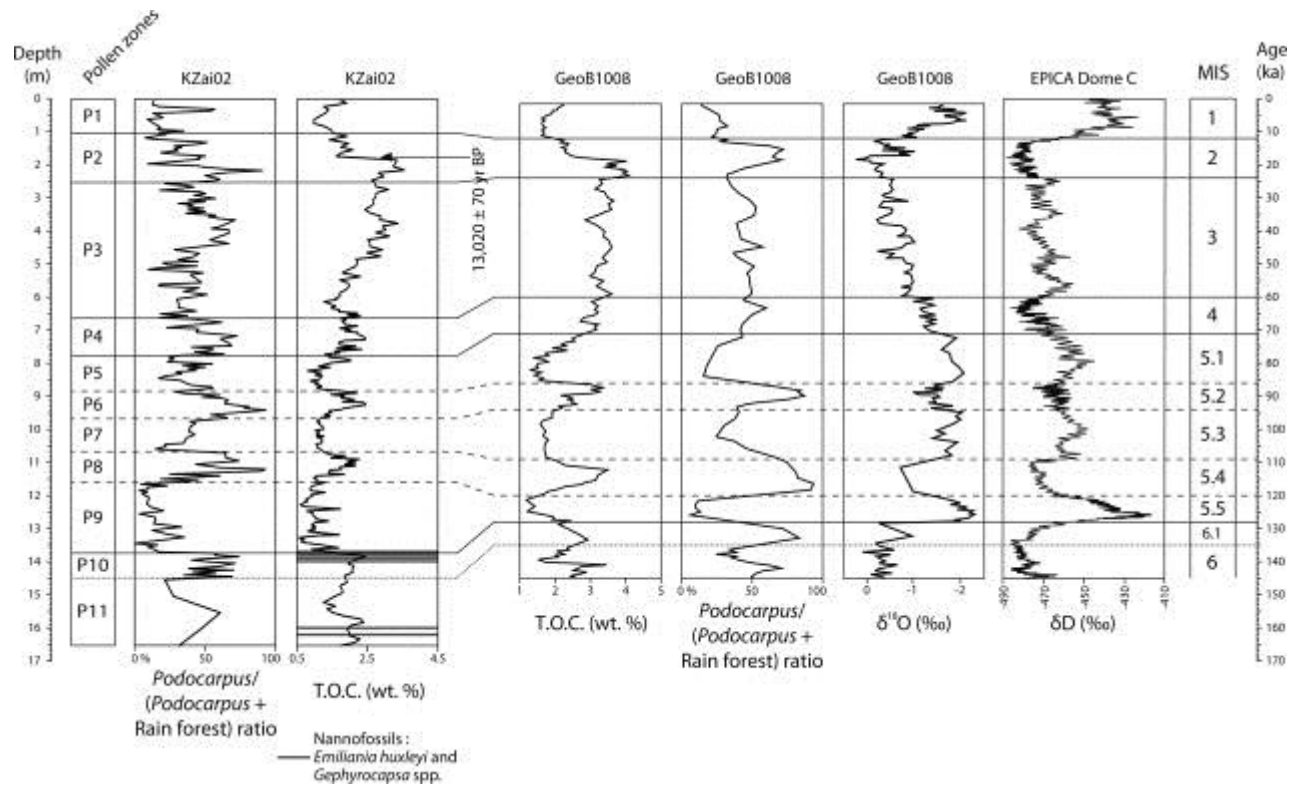
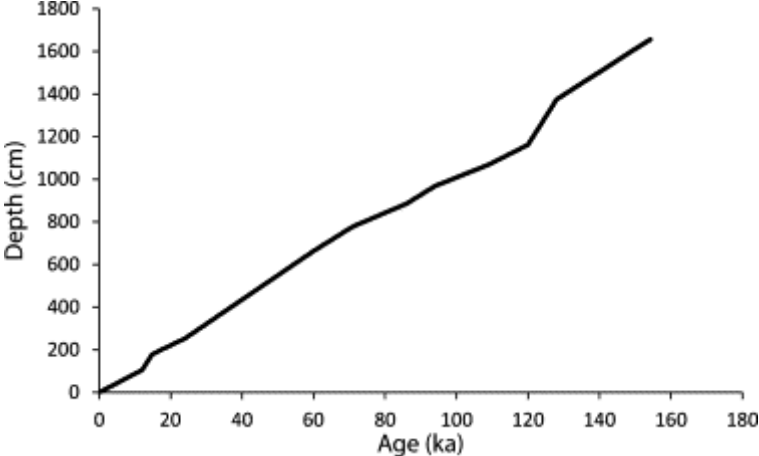


Figure 3

Figure 4



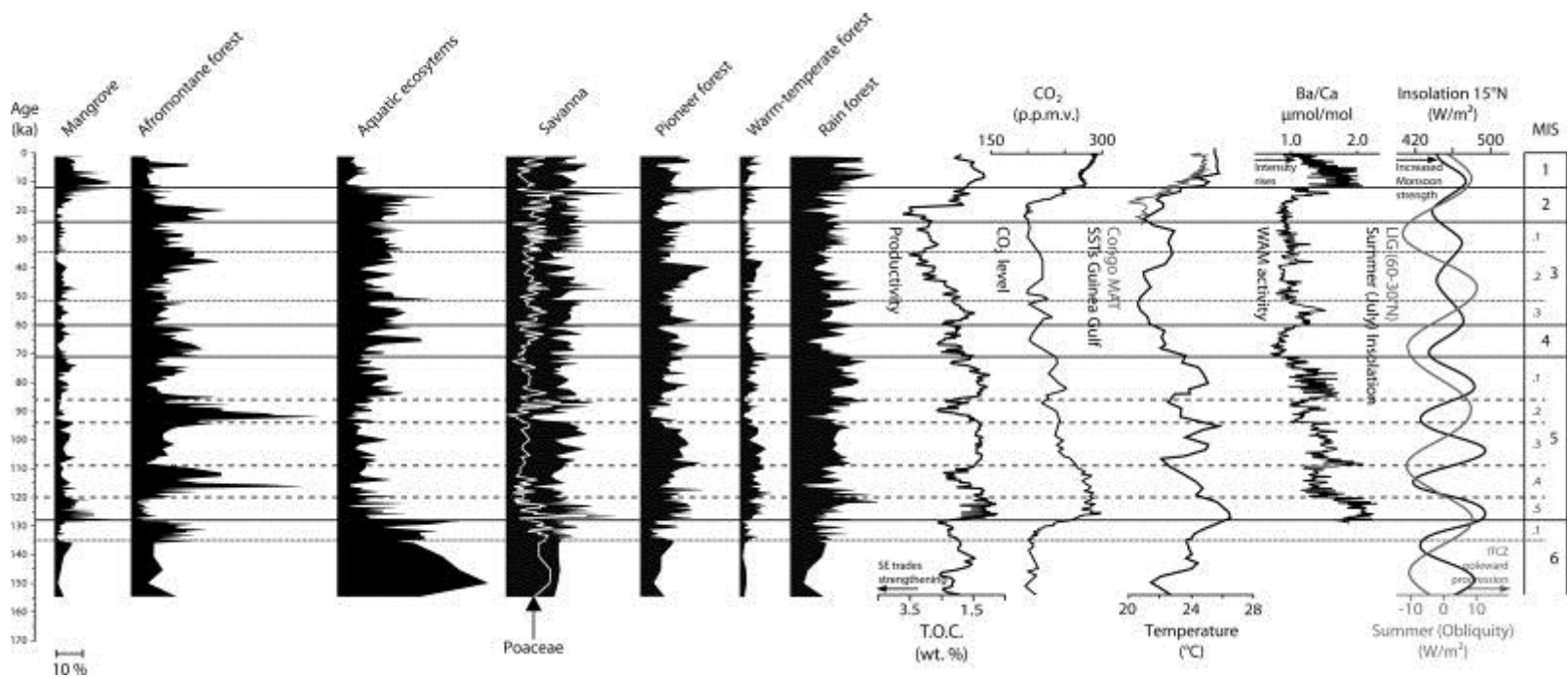


Figure 5

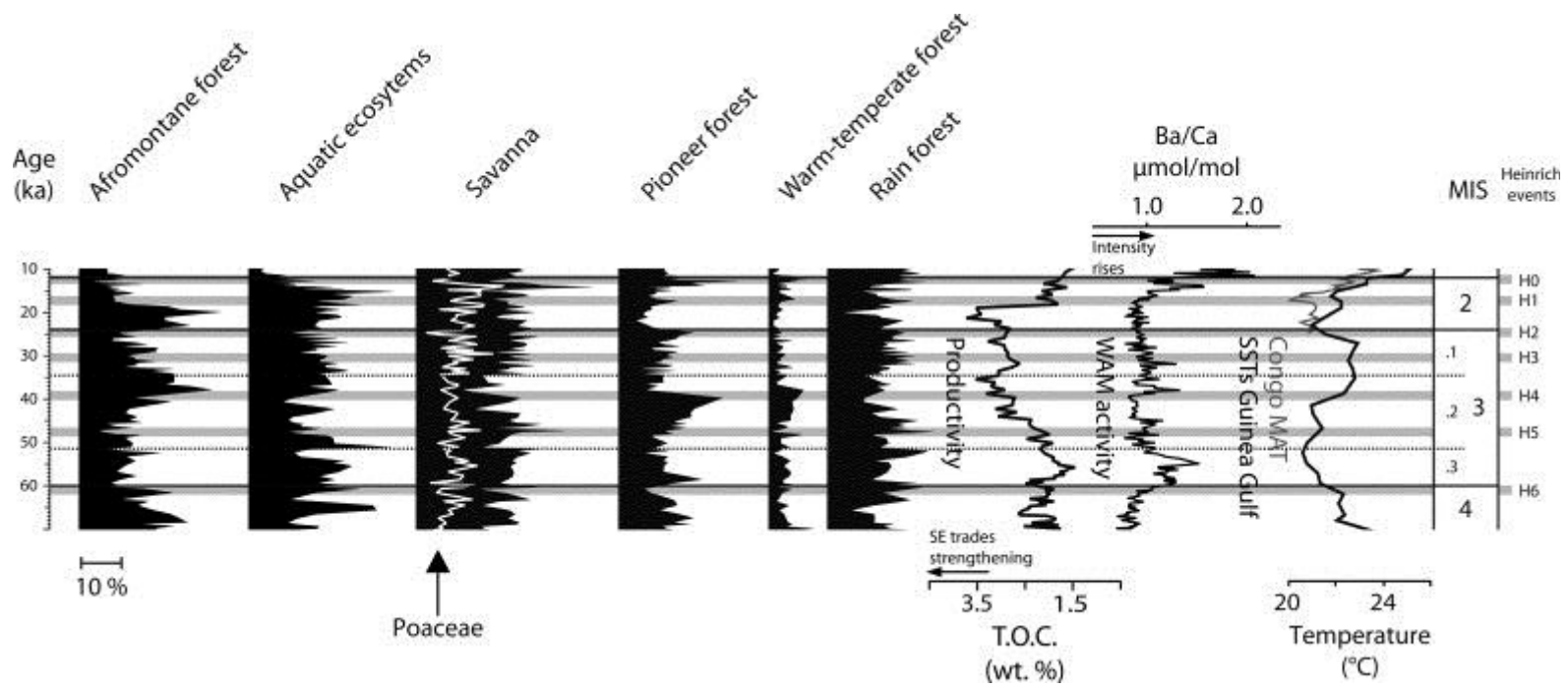


Figure 6