**Climate
of the Past**

Palynological evidence for gradual vegetation and climate changes during the African Humid Period termination at 13° N from a Mega-Lake Chad sedimentary sequence

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Abstract. Located at the transition between the Saharan and Sahelian zones, at the center of one of the largest endorheic basins, Lake Chad is ideally located to record regional environmental changes that occurred in the past. However, until now, no Holocene archive was directly cored in this lake. In this paper, we present pollen data from the first sedimentary sequence collected in Lake Chad (13° N; 14° E; Sahel region). Dated between ca. 6700 and ca. 5000 cal yr BP, this record is continuous and encompasses part of the termination of the African Humid Period (AHP). Vegetation reconstructions are based on standard analyses of pollen diagrams and are strengthened by quantitative approaches. Potential biomes are reconstructed using the biomization method and mean annual precipitation (P_{ann}) is estimated using the modern analogues technique.

Results show that, between ca. 6700 and ca. 6050 cal yr BP, a vegetation close to humid woodland or humid savanna, including elements currently found further southward, thrived in the vicinity of the Mega-Lake Chad in place of the modern dry woodland, steppe and desert vegetation. At the same time, montane forest populations extended further southward on the Adamawa Plateau. The high abundance of lowland humid pollen taxa, particularly of *Uapaca*, is interpreted as the result of a northward migration of the corresponding plants during the AHP. This preferential zonal occurrence of these taxa in Lake Chad Basin (LCB) (rather than extrazonal) is driven by more humid local and regional climate conditions at this latitude, as shown by mean P_{ann} estimated values of ca. 800 (−400/+700) mm during this

period. However, we cannot rule out that an increase of the Chari–Logone inputs into the Mega-Lake Chad might have also contributed to control the abundance of these taxa. Changes in the structure and floristic composition of the vegetation towards more open and drier formations occurred after ca. 6050 cal yr BP, following a decrease in mean P_{ann} estimates to approximately 600 (−230/+600) mm. But, the constant significant presence of lowland humid taxa until ca. 5000 cal yr BP, contemporaneous with a slight increase in steppic taxa, demonstrates that at this date, the modern vegetation was not yet established in the vicinity of Lake Chad. Our data indicate that between ca. 6700 and ca. 5000 cal yr BP vegetation and climate changes must have occurred progressively, but that century-scale climate variability was superimposed on this long-term mid-Holocene drying trend as observed around ca. 6300 cal yr BP, where pollen data indicate more humid conditions.

1 Introduction

The most prominent environmental change experienced in northern Africa over the past 10 000 yr is the transition from the "green Sahara" to the present hyperarid desert that occurred during the mid-Holocene. Sedimentary records show that modern Sahel and part of the Sahara regions were moister during the early and mid-Holocene, between ca. 12 000 and ca. 5500 cal yr BP (see review in Gasse, 2000; Hoelzmann et al., 2004). During this period, known as the

African Humid Period (AHP), the Sahara landscape was largely vegetated with annual grasses, shrubs and small trees, some of them now located further south in tropical areas (e.g. Lézine, 1989, 2009; Jolly et al., 1998a; Hély et al., 2009; Watrin et al., 2009). Data sets of "lake status" that primarily reflect changes in the regional water budget (the balance of precipitation *minus* evaporation, P−E over the lake and its catchment) also indicate an enhancement of the annual P−E balance (Hoelzmann et al., 1998; Jolly et al., 1998b; Lézine et al., 2011). Geological records, supported by archaeological evidences (e.g. Kuper and Kröpelin, 2006), indicate that the Sahara/Sahel boundary that currently extends up to 18° N was shifted northward, at least as far north as 23° N (Jolly et al., 1998b), with influence of the western African monsoon recorded up to 27° N (Kuhlmann et al., 2004). This is supported by climate model simulations that have shown that, during this Holocene climatic "optimum" period, increase in Northern Hemisphere summer insolation, due to changes in earth's orbital parameters, enhanced the thermal contrast between land and sea surfaces, thereby increasing the African monsoon moisture supply to the Sahel and Sahara and shifting significantly northward the Intertropical Convergence Zone (ITCZ) and its associated rainfall belt (e.g. Kutzbach and Street-Perrott, 1985; Jousseaume et al., 1999). Positive feedbacks involving ocean and/or biophysical mechanisms may have increased the climate response to this orbital forcing by enhancing water advection and local moisture recycling (Kutzbach et al., 1996; Kutzbach and Liu, 1997; Braconnot et al., 1999). However, coupled atmosphere–ocean–continent climate models have failed to shift the African summer precipitation during early and mid-Holocene over northern Africa as far north as suggested by the paleodata (Sepulchre et al., 2009).

During the AHP termination corresponding to the onset of aridification of Sahara and Sahel regions, an inverse climatic scenario was proposed (Kutzbach and Street-Perrott, 1985). However, many questions related to this climatic transition that affected the African intertropical zone during the mid-Holocene are still unresolved. Concerning its timing and pace, oceanic records suggest that this transition might have started as early as ca. 5500 cal yr BP and was completed within a few hundred years (deMenocal et al., 2000; Kuhmann et al., 2004). Continental archives give a more complex picture, with pronounced differences in the timing and amplitude of hydrological and vegetation changes (e.g. Gasse, 2000; Hoelzmann et al. 2004). Owing to chronological uncertainties and low time resolution of most of these records, both regional climate variability and site-specific topographic and/or hydrogeological influences are often underestimated. The pace of the AHP transition, i.e. whether it was abrupt (e.g. deMenocal et al., 2000; Salzmann and Hoelzmann, 2005) or gradual (e.g. Salzmann et al., 2002; Kröpelin et al., 2008a; Vincens et al., 2010) is still the subject of intense debate (see, for example, the controversy between Brovkin and Claussen, 2008 and Kröpelin et al., 2008b).

Coupled atmosphere–ocean–vegetation climate model investigations suggest that positive feedbacks between vegetation cover and precipitation would have played a significant role in the collapse of vegetation in North Africa (Claussen et al., 1999; Renssen et al., 2003, 2006). Despite the scarcity of the data, the response of terrestrial ecosystems at the onset of this major climatic change seems to have occurred earlier in what is presently the northernmost and driest part of West Africa than in forested regions close to the equator (Vincens et al., 2010). This could be linked to instability or stability of the former vegetation communities in response to regional climate change and/or peculiar local edaphic conditions at each site during the AHP transition (e.g. Marchant and Hooghiemstra, 2004; Waller et al., 2007; Vincens et al., 2010). The most recent model that synchronously coupled northern Africa's climate–ecosystem in a global general circulation atmosphere–ocean–vegetation model also concludes that abrupt vegetation changes may be linked to nonlinear response of the vegetation to a precipitation threshold, rather than strong biogeophysical feedback (Liu et al., 2007). Moreover, a new and more complex view, supported by both climate-vegetation models and paleoecological observations, is now emerging: ecosystem changes at the AHP termination should have been significantly different between the western, central and eastern Sahara and Sahel areas, implying that mechanisms and feedbacks involved may have been likely diverse through the arid and sub-arid belt. But concerning its pace and in spite of coupled atmosphere-ocean-continent climate models investigations, no clear climate mechanism fitting the paleodata has emerged from these simulations (Claussen et al., 1999; Renssen et al., 2006; Liu et al., 2007).

The issues of whether ecosystem responses were abrupt or gradual and whether they were different from the west to the east of North Africa can only be resolved by means of new continuous terrestrial paleoecological records. In this Sahara and Sahel zone, the paucity of well-preserved and reliable continental records illustrating vegetation history at the end of the AHP is mainly due to major discontinuities and hiatus in lacustrine sequences due to wind deflation in a predominantly arid climate. The only continuous paleoecological sequence today available in the Sahara has been recovered at Lake Yoa, northern Chad (19° N; Kröpelin et al., 2008a; Lézine, 2009), a rare permanent lake even today. This record suggests a gradual aridification of the east-central Sahara at the end of AHP (Kropelin et al., 2008a), but its representativeness has been questioned (Brovkin and Claussen, 2008). In the central Sahel region, five pollen sequences have been obtained in the Manga Grasslands of northeastern Nigeria (13° N; Salzmann and Waller, 1998; Waller et al., 2007) (Fig. 1).

Notwithstanding the potential attractiveness of its location and the pioneer works carried out by Servant (1983) and Maley (1981) in the 1980s, Lake Chad and its Holocene sedimentary sequence did not receive the attention they merit and clearly deserve further investigation. With a drainage basin
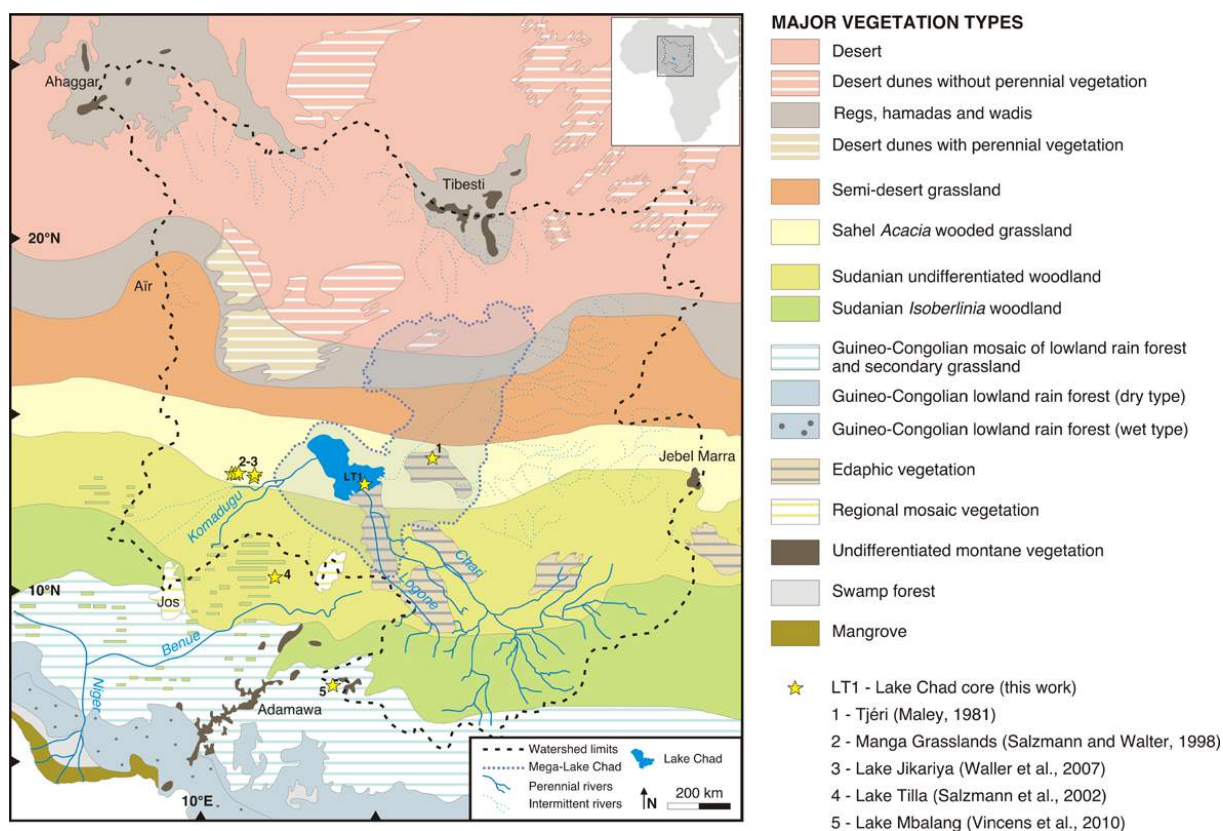
Fig. 1. Location map showing the Lake Chad Basin (LCB); the Holocene Mega-Lake Chad as reconstructed by Schuster et al. (2005) and the major modern vegetation types (from White, 1983). The modern Lake Chad is shown here at its largest extension reached during the past few decades.

that extends from 5° to 25° N and 8° to 28° E, Lake Chad is ideally situated to document at the regional scale paleoenvironmental changes that occurred during the Holocene in north-central Africa. Here we present the results of a palynological study performed on the first sedimentary core collected in Lake Chad. This one-meter-long sequence encompasses part of the mid-Holocene transition, and complements previous scarce data obtained by Maley (1981) on Holocene outcrops, particularly on the Tjéri site (Chad) (Fig. 1).

2 Study area

Lake Chad (ca. 13° N, ca. 14° E, ca. 280 m a.s.l. (above sea level)) is located in the Sahel region of north-central Africa, and extends over the territories of four countries: Chad, Niger, Nigeria and Cameroon. Its catchment, the Lake Chad Basin (LCB), is one of the world's largest endorheic basins, with an area of approximately 2.5 million km^2 (Fig. 1). It is divided into two sub-basins: the northern sub-basin presently desertic and extending far into the Sahara, and the southern sub-basin corresponding to the present-day active hydrological basin. The primary inflow into the lake comes from the Chari–Logone river system (95 % of water supply), which

drains southward into tropical humid areas and feeding Lake Chad today (Fig. 1). The remaining 5 % comes from the Komadugu river, which enters the northwestern part of the present-day lake and drains the southwestern part of the LCB (Komadugu River drainage basin ca. 120 000 km^2 according to SIEREM database from HSM Laboratory in Montpellier, France; Boyer et al., 2006), and precipitation falling on the lake itself (Olivry et al., 1996; Bader et al., 2011).

Lake Chad lies on an area of flat regional topography; therefore, changes in the hydrological budget lead to large fluctuation of its size (Olivry et al., 1996; Bader et al., 2011). Today, due to increased aridification, Lake Chad has a surface area of only ca. 12 000 km^2 and a mean depth comprised between 3 and 5 m. During past humid periods, sedimentological and paleontological evidences testify to the existence of giant water bodies. Although the occurrence of a Mega-Lake Chad during the Holocene has been questioned on the basis of neotectonic and sedimentological arguments (e.g. Durand, 1982), the paleolake might have reached an elevation of ca. 325 m a.s.l. during the AHP, corresponding to a maximal extension of 350 000 km^2 (Schuster et al., 2005; Leblanc et al., 2006a and b) (Fig. 1).

The climate over the LCB is under the influence of the Western African Monsoon (WAM). The rainfall regime is controlled by a combination of the Intertropical Convergence Zone (ITCZ) and the tropical rain belt that is linked to ascending air masses lying between the African easterly jet and Tropical easterly jet (Nicholson, 2009). The seasonal shift of the ITCZ controls the northernmost penetration of the WAM, but rainfalls linked directly to this zone of surface convergence remain generally low and affect only the southern Sahara and the northernmost Sahel. From November to March, the ITCZ is located far south of the basin and dominant continental northeast trade winds (Harmattan) induce extremely dry conditions. In April, the ITCZ starts to migrate north and the first precipitation occurs in May–June. Maximum rainfall occurs during July and August when the ITCZ is located in its northernmost position (ca. 20° N), then rapidly declines. Therefore, the climate in the largest part of the LCB is arid to semi-arid, with a long dry season that quickly increases in duration northwards. In the vicinity of Lake Chad, mean annual rainfall varies from ca. 500 mm in the south (N'Djamena meteorological station, Chad) to ca. 200 mm in the north (N'guigmi meteorological station, Niger) with a dry season of 9–10 months (Walter and Leith, 1960–1967; Olivry et al., 1996). Mean annual temperature is about 27 °C, with mean minima about 20.8 °C and mean maxima about 35.8 °C, and evaporation is about 2300 mm yr^{-1} (N'Djamena station; Olivry et al., 1996).

The vegetation in the LCB changes gradually according to latitude and water supply. The most humid communities occur in its southern part with Guineo–Congolian mosaic of lowland rainforest and secondary grassland, then replaced northwards by wet (*Isoberlinia* woodland) and dry (undifferentiated woodland) Sudanian formations. In its northern part, Sahel semi-desert grassland and Sahara desert vegetation are found (White, 1983) (Fig. 1). Today, Lake Chad lies in the Sahel *Acacia* wooded grassland zone described by White (1983). The vegetation is characterized by the presence of numerous woody spiny species of Mimosaceae (*A. seyal*, *A. sieberiana*, *A. nilotica, Faidherbia albida*) and Capparidaceae (*Maerua crassifolia*, *Boscia senegalensis*, *Capparis decidua*), associated with *Leptadenia pyrotechnica* (Asclepiadaceae), *Salvadora persica* (Salvadoraceae), *Commiphora africana* (Burseraceae) and *Balanites aegyptiaca* (Balanitaceae). The herbaceous layer, which does not reach 60 cm tall, is more or less continuous and dominated by annual Poaceae (Maley, 1972; White, 1983). Around the lake, swampy herbaceous formations are largely developed with abundant Cyperaceae.

3   Material and methods

Palynological results presented here were obtained from a one-meter sedimentary sequence (LT1 core; 13°0′29.8″ N, 14°35′51.1″ E), collected during a pilot coring operation

Fig. 2. Location of core LT1 (red circle; 13°0′29.8″ N, 14°35′51.1″ E) and modern pollen samples in Lake Chad and in the vicinity of the lake (blue circles are lacustrine or river sediment samples and yellow circles are surface soil samples). Images from Google Earth, 2011.

conducted in 2008 in the southern pool of Lake Chad (Fig. 2). The core was collected using a manual Wright piston corer (Wright et al., 1983) operated from an anchored boat. After drilling, the core was immediately shipped to France in 24 h and stored in a cold room at 5 °C. This core mostly consists of dark grey mud with some light grey plan-parallel laminations, especially in the upper 40 cm. Chronological control is based on six Accelerator Mass Spectrometry (AMS) ^{14}C measurements (Beta Analytic Inc., USA) performed on bulk organic matter (Table 1, Fig. 3). Calibration ages were obtained using CALIB 6.0 (Reimer et al., 2009), and the age of the studied samples was estimated by linear interpolation between adjacent dates (Fig. 3). ^{14}C data indicate that the LT1 core covers the period between ca. 6700 and ca. 5000 cal yr BP (Fig. 3) and thus encompasses part of the mid-Holocene transition. The constant sedimentation rate (0.5 mm yr^{-1} on average) as well as the absence of clear discontinuities and abrupt facies changes within the cored sediment sequence (except the top 5 cm) supports that sedimentation was continuous at the core location throughout the studied 1700-yr period. It is noteworthy that the top of the core shows a 3-cm-thick sloped layer which possibly represents reworked sediments (Fig. 3). This is substantiated by the radiocarbon age obtained for this material (3651 ± 80 cal yr BP at 1.5 cm depth) that very likely represents a mixing between more recent material and Holocene sediments. For this reason, the upper 5 cm deposits were not considered in this study. The upper part of the Holocene sequence may be truncated by wind deflation during drying phases of Lake Chad, which occurred since the desertification of the region (Maley, 1981). The last of these erosive events is likely to have occurred very recently as suggested by the quasi-lack of modern sediment. The drought that prevailed in the 1970s caused
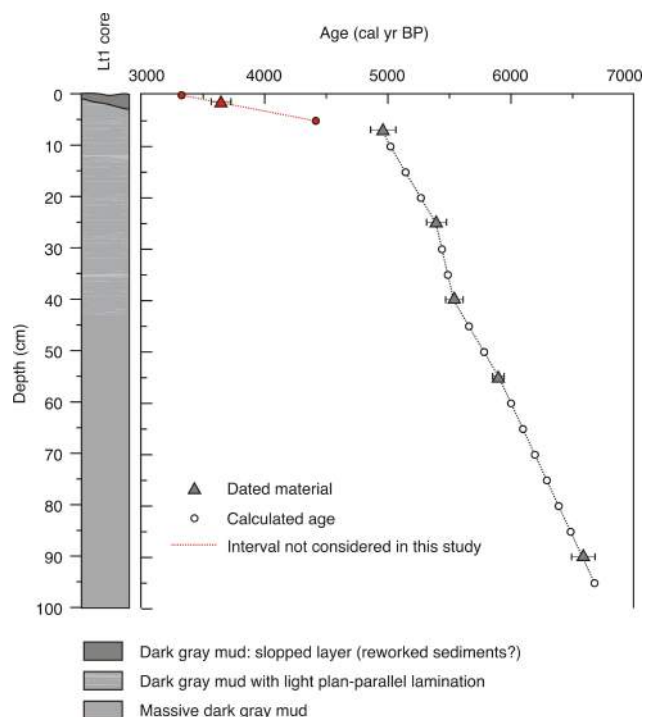
Fig. 3. Depth-age model of the core LT1, Lake Chad, based on six AMS-^{14}C measurements ages obtained on bulk organic matter. [14]C ages were calibrated using CALIB 6.0 (Reimer et al., 2009).

the drying of a large part of the southern pool of Lake Chad (Olivry et al., 1996), making aeolian erosion possible. This is in general agreement with ^{210}Pb analyses performed on LT1 core, which did not show any excess in ^{210}Pb at its top (Deschamps, personal communication, 2012). The absence of any unsupported ^{210}Pb at the sediment interface is likely due to fact that we failed to collect the very top of the sedimentary sequence by using a coring technique that is not specifically dedicated to sediment–water interface sampling. We also cannot rule out that wave action, due to windstorms that occurred frequently during the dry season, may cause remobilization and lacustrine erosion and transport of recent sediment. This mechanism may also explain locally the lack of modern sediment and thus of unsupported [210]Pb.

For pollen analyses, samples were taken every 5 cm throughout the studied sequence. This represents a mean time resolution of the data of ca. 90 yr. Samples were prepared using the standard method described by Faegri and Iversen (1975). For each sample, at least 350 pollen grains and spores were counted. Their identification was based on the reference collection available at CEREGE that contains some 7000 specimens, on specialized publications relevant to pollen morphology in dry African areas (e.g. Maley, 1970; Bonnefille and Riollet, 1980; El-Ghazali, 1993) as well as in wetter western and central African regions (e.g. Sowunmi, 1973, 1995; A.P.L.F., 1974; Ybert, 1979; Salard-Cheboldaeff, 1980–1987, 1993), and on photographs

available on the African Pollen Database web site (APD, 2010). The nomenclature of the pollen taxa was standardized following Vincens et al. (2007) for tree and shrub pollen types and the APD list of taxa (APD, 2010) for the others. The corresponding plant life-form and habitat of each identified pollen taxon were determined using western and central African botanical literature (e.g. Hutchinson and Dalziel, 1954–1972; Flore du Cameroun, 1963–2001; Letouzey, 1968, 1985; Lebrun and Stork, 2003, 2006, 2008a, b). On the pollen diagrams, taxa percentages were calculated using the total of pollen and spores counted, excluding only indeterminable grains (less than 5 % of the total count). In addition, a correspondence analysis (CA; Hill, 1974; ter Braak, 1985) was performed on the pollen data set using the package "VEGAN" developed in R open software (2012) (http://www.r-project.org/).b

Pollen-based biome reconstructions were carried out using the biomization method (Prentice et al., 1996), where pollen taxa are assigned to one or more plant functional types (PFTs) and PFTs are associated to one or more biomes. PFTs are groups of plants having similar responses to environmental factors and able to thrive together according to their physiological, phenological and bioclimatic characteristics (Smith et al., 1997). The method is based on the assumption that a pollen spectrum will have different degrees of affinity to different biomes that can be quantified by a simple algorithm (Marchant et al., 2009). The biome affinity scores are calculated based on the associated characteristic PFT scores and each pollen spectrum is assigned to the biome with which it has the greatest affinity (Prentice et al., 1996).

In this study, the biomization procedure was applied to the fossil pollen data set from core LT1 as well as to available modern pollen rain data around (soil samples) and inside (lacustrine sediments) Lake Chad (Maley, 1972; unpublished data CEREGE; see Fig. 2 for location). The modern data were used in order to establish a modern calibration and test the level of confidence of our taxa-PFT assignments, and to compare the reconstructed potential biomes along the core with the modern reconstructions. In the application of the biomization method on both modern and fossil pollen data, only native and "non-edaphic" pollen taxa have been considered, i.e. 128 among the 150 identified in the two data sets. Included among the "non-edaphic" pollen taxa, those from plants exclusively growing on well-drained soils, but also those for which a clear specific or generic identification is not possible and does not allow a differentiation between terrestrial and edaphic plants from which they are issued (e.g. species of *Uapaca*, *Alchornea*, *Syzygium* or genera of Combretaceae). The assignment of these taxa to PFTs is in line with the works of Lebamba et al. (2009a) and Lézine et al. (2009) in central and western Africa. Instead of considering only the dominant biome reconstructed, we proceed as Lebamba et al. (2012), taking all scores of potential biomes into account to evaluate the contribution of the different biomes in pollen record. The biome scores were

Table 1. Radiocarbon chronology of core LT1 from Lake Chad.

Laboratory code	Deph (cm)	Material	Conventional ^{14}C age (yr BP)	Calibrated age (cal yr BP)	Calibrated age (cal yr BP) – 2σ deviation	Relative areas under probability distribution
Beta-277995	1.5–2	bulk sediment	3420 ± 40	3651	3571–3732	0.83
Beta-277996	7.5–8	bulk sediment	4400 ± 40	4959	4857–5061	0.91
Beta-285575	25.5–26	bulk sediment	4660 ± 40	5391	5310–5471	0.95
Beta-267361	40–40.5	bulk sediment	4800 ± 40	5535	5465–5660	0.98
Beta-267362	55–55.5	bulk sediment	5140 ± 40	5903	5857–5950	0.58
Beta-267363	90–90.5	bulk sediment	5790 ± 20	6581	6486–6676	0.99

plotted along two oriented transects (NW–SE and N–S) for modern data and as a function of time for fossil data. The different biomes considered here are: WAMF (warm mixed-forest); TRFO (tropical rain forest); TSFO (tropical seasonal forest); TDFO (tropical dry forest); SAVA (savanna); STEP (steppe); DESE (desert).

Finally, transfer functions based on the modern analogues technique (Overpeck et al., 1985; Guiot, 1990; Guiot and de Vernal, 2007) were used to reconstruct mean annual rainfall values (P_{ann}) along core LT1. Our research used a modern pollen data set which includes 452 samples from western and central Africa originating from rain forest to desert vegetation (data set available in the African Pollen Database (2010) and complemented by data used in Lebamba et al., 2009a). The nomenclature of the pollen taxa was, as for our fossil data, standardized following Vincens et al. (2007) and the APD list of taxa (2010). As for the biomization method, we have considered only native and "non-edaphic" pollen taxa. Ultimately, 248 pollen taxa were considered.

The modern P_{ann} values were extracted at each pollen site from the FAO website database (2011) and interpolated from the three closest available meteorological stations. However, for the samples from Lake Chad (Maley, 1972), the P_{ann} values for the soil samples are those given by this author, and for the lacustrine samples the P_{ann} values are calculated based on precipitation time series (1932–1968) given by Olivry et al. (1996), since the samples analyzed by Maley (1972) were collected in 1968, during the rainfall surplus period in the Lake Chad region. The transfer function analysis was carried out using the package "BIOINDIC" developed in R open software. Error bars for each sample are defined by the P_{ann} variability among five modern best analogues, considering the uncertainty range given by the extreme driest and wettest analogues.

4 Results

4.1 Lake Chad pollen diagram

Pollen preservation was good along the whole core and 105 pollen taxa were identified (Table S1). On the basis of the correspondence analysis (CA) results that reveal the main variation in pollen assemblages, the pollen sequence was divided into two zones (Figs. 4 and S3).

4.1.1 Pollen zone I (ca. 6700 to ca. 6050 cal yr BP)

Zone I includes samples with negative values along CA axis 1 and covers the older part of the record (ca. 6700 to ca. 6050 cal yr BP). It is characterized by the maxima frequencies of total arboreal pollen (AP, mean value of 36 %), with an important contribution of *Uapaca* (16 to 26 %). Arboreal taxa such as *Alchornea* (0.5–3 %), Combretaceae (4.5–8 %) and *Syzygium* (0.3–1.4 %) are also well represented, although in lower frequencies. The Poaceae are always abundant with mean frequencies of about 40 %. Among local swampy/marshy herbaceous plants, the dominant taxon is Cyperaceae. In this zone, it displays its lowest frequencies recorded along the whole core between ca. 6500 and ca. 6200 cal yr BP (11.5 %). A peculiar feature of this zone is the regular and non-negligible frequencies of *Olea* (0.5–3 %), a sub-montane/montane forest component.

4.1.2 Pollen zone II (ca. 6050 to ca. 5000 cal yr BP)

This zone includes samples with positive values along CA axis 1 and encompasses the younger part of the LT1 core. Total AP significantly decreases (mean value of 26 %) mainly due to lower values of *Uapaca* (7.8–13.6 %), whereas other arboreal taxa frequencies remain relatively stable. Among herbaceous taxa, the Poaceae display similar values to zone I, but the Amaranthaceae/Chenopodiaceae (1.5–6.3 %) as well as the Asteraceae taxa (0.3–1.8 %) progressively increase. The Cyperaceae reach their highest frequencies of the sequence particularly between ca. 5500 and ca. 5000 cal yr BP (maximum of 26.9 %). *Olea* is present until ca. 5800 cal yr BP, after which its frequencies become negligible.
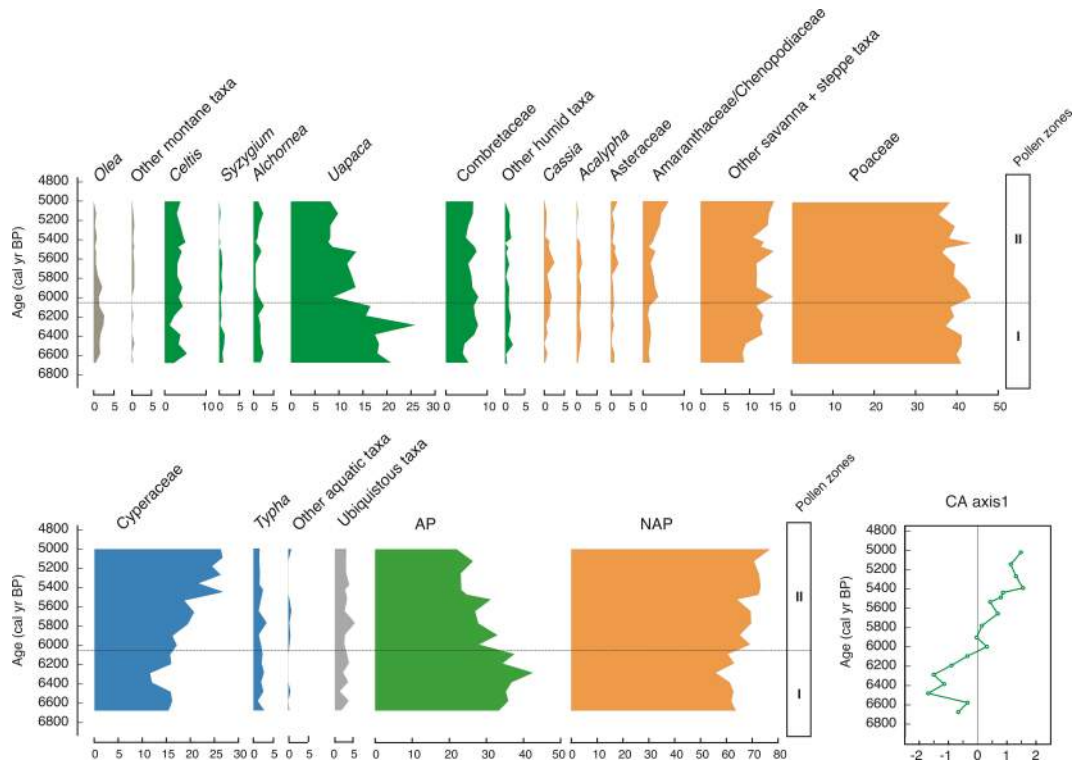
Fig. 4. Synthetic pollen diagram from core LT1, Lake Chad, showing relative percentages of selected taxa (the pollen sum includes all identified pollen and spore taxa, excluding indeterminable grains), and correspondence analysis (CA) performed on the pollen data set.

4.2 Biomization

4.2.1 Modern pollen data

When compared with the current vegetation at each sampled site, all the potential biomes are correctly reconstructed (Table 2 and Fig. 5). The driest biomes that characterized the vicinity of Lake Chad, i.e. SAVA (savanna), STEP (steppe) and DESE (desert), always display the highest scores. Among moister potential biomes, TDFO (tropical dry forest) has its highest scores in mud samples with direct influence of fluvial flood supply, i.e. in samples KK1 located in front of the Komadugu River delta, JM1 in front of the Chari–Logone Delta and "Chari" collected in the Chari River itself (Fig. 2). Similarly, TSFO (tropical seasonal forest), TRFO (tropical rain forest) and WAMF (warm mixed-forest) biomes, corresponding to the most distant vegetation communities from the lake, have their highest scores in the "Chari" river sample and slightly lower values in sample JM1. These data are consistent with the fact that the Chari and Logone rivers drain areas located further south and are occupied by humid forested communities, unlike the Komadugu river, which drains only part of the Sudanian woodland (Fig. 1). Occurrence of allochthonous pollen taxa from southern vegetation in lacustrine sediments is thus controlled by fluvial transport.
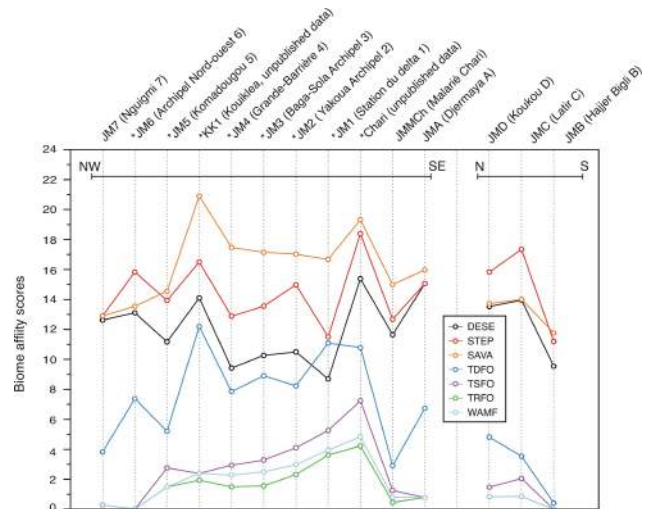

Fig. 5. Biome affinity scores derived from the modern data set, Lake Chad. Pollen counts are from Maley (1972) and from unpublished data (CEREGE). (DESE: desert; STEP: steppe; SAVA: savanna; TDFO: tropical dry forest; TSFO: tropical seasonal forest; TRFO: tropical rain forest; WAMF: warm mixed-forest).

Table 2. Modern samples characterization: coordinates (latitude and longitude), P_{ann} values (mm yr^{-1}), vegetation zone (White, 1983), local vegetation (Maley, 1972) and potential reconstructed biome (this paper).

Sample	Latitude	Longitude	P_{ann} (mm yr^{-1})	Vegetation zone (White, 1983)	Local vegetation	Potential reconstructed biome
JM7	14°19′48.00″ N	13°10′12.00″ E	226	Sahel *Acacia* wooded grassland	edaphic grassland	STEP
JM6	14°16′12.00″ N	13°34′48.00″ E	250	Sahel *Acacia* wooded grassland	lacustrine mud	STEP
JM5	13°41′60.00″ N	13°25′12.00″ E	265	Sahel *Acacia* wooded grassland	lacustrine mud	SAVA
KK1	13°48′50.80″ N	13°27′27.20″ E	250	Sahel *Acacia* wooded grassland	lacustrine mud	SAVA
JM4	13°22′48.00″ N	14°4′48.00″ E	350	Sahel *Acacia* wooded grassland	lacustrine mud	SAVA
JM3	13°30′0.00″ N	14°15′0.00″ E	340	Sahel *Acacia* wooded grassland	lacustrine mud	SAVA
JM2	13°25′12.00″ N	14°46′12.00″ E	327	Sahel *Acacia* wooded grassland	lacustrine mud	SAVA
JM1	13°1′48.00″ N	14°37′48.00″ E	450	Sahel *Acacia* wooded grassland and edaphic grassland	lacustrine mud	SAVA
Chari	12°38′23.40″ N	14°49′39.90″ E	500	Sahel *Acacia* wooded grassland and edaphic grassland	river mud	SAVA
JMMCH	12°30′0.00″ N	14°54′0.00″ E	600	Sahel *Acacia* wooded grassland and edaphic grassland	mosaic of edaphic grassland and Sahel *Acacia* savanna	SAVA
JMA	12°25′12.00″ N	15°4′48.00″ E	600	Sahel *Acacia* wooded grassland and edaphic grassland, close to the limits of Sudanian undifferentiated woodland	mosaic of edaphic grassland and Sahel *Acacia* savanna (Sahelian–Sudanian zone)	SAVA
JMD	13°49′48.00″ N	14°41′60.00″ E	300	Sahel *Acacia* wooded grassland	steppe	STEP
JMC	13°34′48.00″ N	14°46′48.00″ E	330	Sahel *Acacia* wooded grassland and edaphic grassland	edaphic grassland	STEP
JMB	12°46′12.00″ N	14°45′0.00″ E	500	Sahel *Acacia* wooded grassland and edaphic grassland	Sahel *Acacia* savanna	SAVA

4.2.2 Fossil pollen data

All along the LT1 sequence SAVA (savanna) is the dominant potential reconstructed biome (Fig. 6a). However, when all biome scores are considered, in order to identify the contribution of the different biomes along the pollen record, two important discrepancies are observed between results from fossil and modern data: (i) TDFO (tropical dry forest) and STEP (steppe) biome scores are very close in samples younger than ca. 6050 cal yr BP when in older samples higher scores of TDFO biome than STEP biome are observed, and (ii) DESE (desert) biome scores always have lower contributions than TDFO scores. In addition, it is noteworthy that the contributions of all reconstructed biomes younger than ca. 6050 cal yr BP are close to those observed in the modern sample JM1 in front of the Chari–Logone Delta.

However, all biome scores show the same positive trend from oldest to youngest samples (Fig. 6a), whereas an opposite trend between wooded and grassland biomes would be expected. The biome scores are based on the sum of the associated PFT scores. Because few pollen taxa are strictly assigned to a single PFT due to a limited level of identification to a genus or a species, numerous common taxa in-

fluence these scores. This is especially true for dry taxa that have a large ecological plasticity and can occur in tropical dry forest, savanna, steppe or desert. So, the reconstructed TDFO, SAVA, STEP and DESE biomes all display in our reconstructions a positive trend. However, if we consider the DESE, STEP and TDFO normalized by SAVA values, the ratio TDFO/SAVA is relatively constant while the ratios DESE/SAVA and STEP/SAVA show a strong increase after ca. 6050 cal yr BP (Fig. 6b). This would indicate a degradation of the vegetation toward drier and more open communities at this time.

4.3 P_{ann} reconstructions

Before proceeding to the reconstruction of P_{ann} on fossil samples, a calibration/validation was performed on the modern data set (Fig. 7). The 452 modern pollen spectra were split into two groups: the first one was used for calibration and the second one to verify the reliability of this calibration. The good correlation coefficient ($r = 0.71$) obtained between calibrated and observed values validates the use of this modern data set to reconstruct precipitation values from our fossil samples (Fig. 8). Nevertheless, the transfer function seems to underestimate low precipitation values
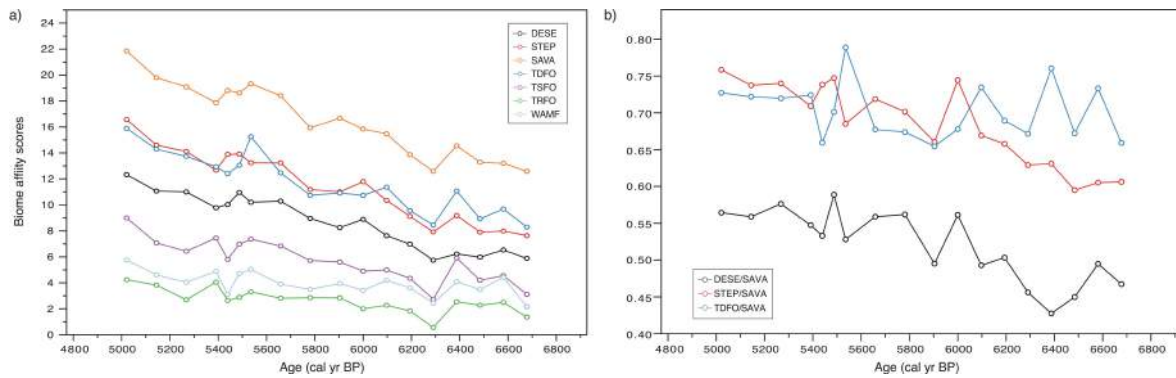
Fig. 6. Results from biomization method applied on fossil pollen data: **(a)** Biome affinity scores and **(b)** scores from drier biomes normalized by SAVA values, derived from the LT1 pollen data set, Lake Chad (DESE: desert; STEP: steppe; SAVA: savanna; TDFO: tropical dry forest; TSFO: tropical seasonal forest; TRFO: tropical rain forest; WAMF: warm mixed-forest).

($< 500\,\mathrm{mm\,yr^{-1}}$) and overestimate high precipitation values ($> 1500\,\mathrm{mm\,yr^{-1}}$; Fig. 8). It is noteworthy that only the lower bias may affect our record, i.e. the analogues of the post-6050 cal yr BP samples (see below).

The P_{ann} estimates calculated from LT1 samples are presented in Fig. 9 and Table S2. They show a general decreasing trend of mean P_{ann} between ca. 6700 and ca. 5000 cal yr BP. If a P_{ann} value of ca. 500 mm (Djamena meteorological station) is considered as modern reference in the southern part of Lake Chad, mean estimates, i.e. the average of P_{ann} in the five selected modern analogues with a weighting inverse to the distance between the fossil and modern spectra, are always reconstructed higher before ca. 6050 cal yr BP, particularly between ca. 6500 and ca. 6100 cal yr BP when mean P_{ann} values fluctuate between 730 and 1020 mm, with lower uncertainties of ca. 400 mm and upper ones of ca. 700 mm (Table S2a). The relatively high uncertainties, especially the upper ones, are due to the large difference of precipitation values between the five best analogues (1450 mm to 350 mm, relative to the wetter and dryer analogues, respectively). The higher frequencies of some taxa in LT1 core than in modern samples, as the case of *Uapaca*, would seem to be determinant in the selection of the best analogues. The two first selected ones are always either a sample from the wet Sudanian zone of Togo (TOG49) rich in *Uapaca* (25 %) (Edorh, 1986) or the sample JM1 from Lake Chad (2.7 %) (Table S2b). It can be noted that among the five selected best analogues none are from Gabon, though some pollen assemblages are rich in *Uapaca* (> 20 %; Lebamba et al., 2009b). This would indicate that the selection would be not only influenced by dominant taxa but also by the whole microfloristic association in the pollen assemblages. After ca. 6050 cal yr BP, P_{ann} estimates are more regular and closer to modern reference, with values between 490 and 660 mm (with lower uncertainties of about 230 mm and upper ones of about 600 mm), the two first major best modern analogues being samples from the southern part of Lake Chad (JM1 and
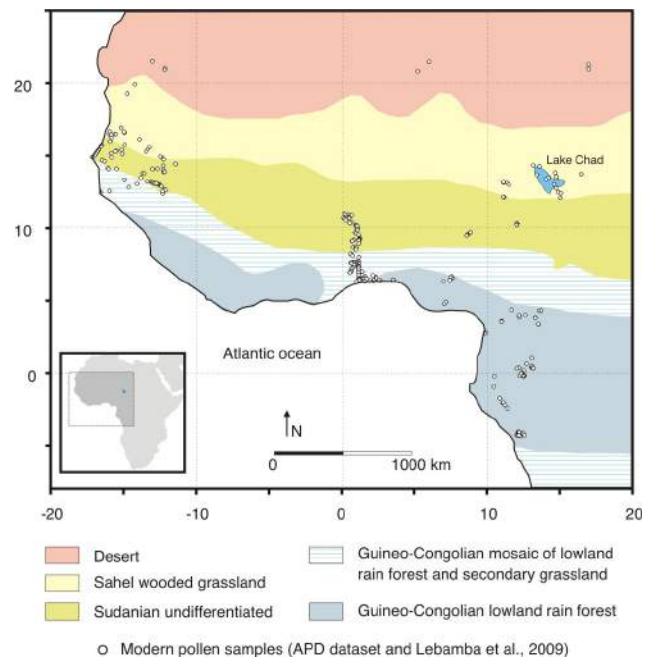

Fig. 7. Location of the modern pollen samples from West and central Africa used in the transfer function to reconstruct mean annual rainfall values (P_{ann}) along core LT1, Lake Chad.

JM3). As the P_{ann} estimates are always higher or very close to 500 mm, we may assume that there is no significant underestimation of annual precipitation over the period covered by the LT1 core by using our transfer functions.

Even if a clear trend toward drier conditions is observed in our reconstructions between ca. 6700 and ca. 5000 cal yr BP, with P_{ann} estimated values of ca. 800 mm and of ca. 600 mm before and after ca. 6050 cal yr BP respectively, our quantitative estimations show large error bars. These large uncertainties, however, remain close to those computed in previous works performed either in central Africa (Lebamba et
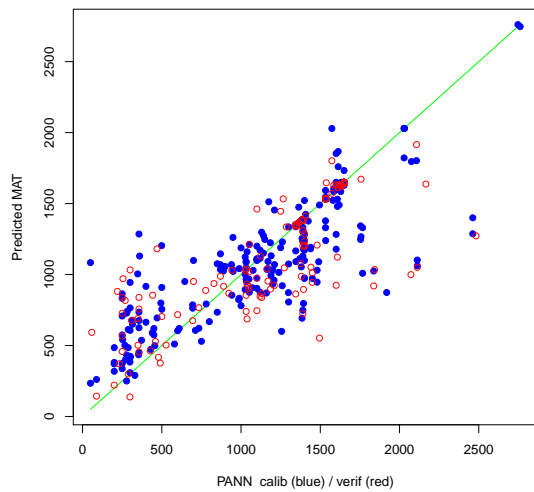
Fig. 8. Validation of the P_{ann} reconstructions performed on the modern pollen data set from West and central Africa.

Fig. 9. Reconstructed mean annual precipitation values (P_{ann}) for the period recorded in core LT1, Lake Chad, using modern analogues technique. Dashed line represents the modern precipitation value measured at the Djamena meteorological station, red line represents the error bars of the precipitation estimates.

al., 2012) or in central-east Africa (Bonnefille and Chalié, 2000). At least three hypotheses can be advanced to explain such large uncertainties: (a) the mid-Holocene vegetation in Lake Chad Basin (LCB) would have no best analogue in modern west and central African vegetation or, if such analogues have occurred, they have been largely modified by recent human impact; (b) the representativeness of the modern pollen database with respect to some types of vegetation which would seem to have empirically the best affinities with the mid-Holocene vegetation reconstructed in paleo-Lake Chad vicinity may be questioned. In this database, modern pollen assemblages from central African dry and humid Sudanian woodlands are under-represented, while modern pollen samples from north-central Guineo–Congolian mosaic of rain forest and secondary grassland are nearly missing (see Fig. 7); and/or (c) the composition of the modern pollen database used for our reconstructions would not be well adapted with regard to our purposes. Indeed, it mainly includes pollen assemblages from surface soils representing the modern pollen rain from a reduced area, while pollen assemblages from lacustrine sediments are more representative of pollen rain from a large panel of biomes (local, extra-local and regional), particularly in great lakes with as large a catchment as the LCB. In this case, the representativeness of the modern pollen database for quantitative reconstruction in a large-scale basin is questionable and it seems plausible that no best or very close modern analogue can be found in this database.

At this stage, it is impossible to target only one hypothesis among the three raised above. It is more probable that all of them have somehow biased our P_{ann} reconstructions and hence are responsible to the large error bars. As the closest analogues are usually acceptable and the following ones are taken by default, this enlarges the error bars but not really the median reconstruction.
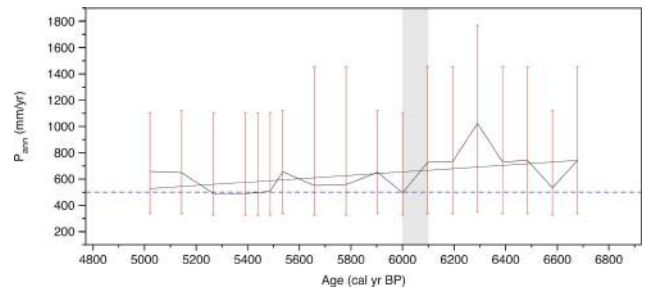
5　Interpretation and discussion

Pollen sedimentation in large lakes is complex, especially in those with high local river inflow and/or those where the rivers that feed the lake drain large areas occupied by several vegetation communities. Previous studies on modern pollen sedimentation undertaken in some East African great lakes, such as Lake Turkana (Vincens, 1984) or Lake Malawi (DeBusk, 1997), have shown that pollen distribution varies according to the location of the analyzed samples; regional pollen taxa are always most abundant in samples from deltaic zones while those from the center and/or shores of the lakes are dominated by more local taxa. This same pattern in pollen rain distribution has also been evidenced in modern Lake Chad by Maley's studies (1972, 1981), which indicate that rivers such as the Chari–Logone river system play the primary role in pollen transport over long distances, particularly for pollen issued from the southern wet Sudanian and Guineo–Congolian regions. It is important to note that our biomization results are consistent with this observation. Modern samples ("Chari" and "JM1") that are representative of sediments carried by the Chari–Logone system reflect biomes from the southern part of the basin (TSFO, TRFO and WAMF). Such pollen distribution and role of rivers in pollen input are important features that need to be taken into account in the interpretation of fossil pollen records from paleo-Lake Chad. Occurrences of allochthonous pollen taxa from southern biomes in lacustrine sediments are also likely to have been controlled in the past by fluvial transport.

It must also be considered that present-day configuration of Lake Chad is greatly different from its Holocene configuration. At that time, a giant body of water occupied the center of LCB depression. The paleo-Lake Chad had a larger latitudinal extension over northern areas today occupied by semi-desert grassland and desert, and southward over areas where dry Sudanian woodland is now found. The potential maximal extension (350 000 km^2) of Lake Chad was controlled by the Mayo Kebbi spillway, at 320–325 m a.s.l., where overflowing

lake waters could spill out towards the Gulf of Guinea, via the Benue River (Ghienne et al., 2002; Schuster et al., 2005; Leblanc et al., 2006a, b). During the Holocene, the hydrological budget might have also changed, leading to changes in the paleolake surface elevation that, due to the flat regional topography, would have resulted in large fluctuations of the paleolake size and its shoreline configuration through time. However, robust chronological constraints on paleoLake Chad elevation and surface-area variation through the Holocene remain scarce (see review in Leblanc et al., 2006a). Radiocarbon ages obtained by Schuster et al. (2005) on mollusk shells collected on ancient shorelines indicate that a highstand of the paleolake, at 325 m a.s.l. elevation, lasted until ca. 5300–ca. 4400 cal yr BP. There is no direct evidence of paleolake elevation before this period, but, on the basis of previous works (Maley, 1977; Gumnior and Thiemeyer, 2003), Schuster et al. (2005) suggest that this highstand episode could have started after ca. 7000 cal yr BP. Our pollen data, particularly the fluctuations in Cyperaceae frequencies (Fig. 4), plants that generally grow up around water bodies and can be considered as indicators of the extension or reduction of swampy/marshy environments, suggest that between ca. 6700 and ca. 5000 cal yr BP, the elevation and extent of the paleo-Lake Chad have been submitted to significant variations. According our data, the maximum surface area of Lake Chad, during the time period covered by LT1 sequence, should occur between ca. 6500 and ca. 6300 cal yr BP, when Cyperaceae pollen present their minima values (ca. 12 %), and a minimum surface area from ca. 5500 cal yr BP onward when Cyperaceae reach their maxima values (ca. 27 %). However, the occurrence of Cyperaceae pollen always lower in value than in the modern sample JM1 (61.4 %), a sample collected close to our sequence and considered as the best modern reference, indicates that the lake was always much larger than today. The absence of clear disconformities, abrupt facies changes and/or significant change in sedimentation rate in our sedimentary sequence can demonstrate that the sedimentation at the location of core LT1 was not directly affected by these surface elevations and extent changes of Mega-Lake Chad. However, these changes could have modified the distance of the fluvial sources during the studied period. Paleorivers draining the Tibesti and Ennedi uplands have been thought to be active during the AHP and fed the northern part of the paleolake (Maley, 2000; Schuster et al., 2005). These rivers seem too distant from the location of core LT1 to influence the pollen sedimentary signal (Fig. 1), so we may hypothesize that the LT1 sedimentary sequence mainly remained under the direct influence of the inflow of the Chari, Logone and Komadugu rivers as it is today.

According to the LT1 position, the most reliable modern pollen spectra for comparison with our fossil data are (i) the pollen spectrum JM1 in front of the modern Chari–Logone Delta and close to LT1 core (Fig. 2), which could be considered as the best modern reference for pollen sedimentation

in this lacustrine area, and (ii) the pollen spectra JM3 and JM4, also under the influence of Chari–Logone inputs, but located at a greater distance from the Chari–Logone Delta than JM1. The comparison between fossil and these modern data shows in LT1 sequence higher frequencies of numerous pollen taxa from plants that are not currently found in the vicinity of the lake. These taxa are all issued from humid vegetations today located far southward of Lake Chad and drained by the Chari–Logone river system. They more precisely correspond to (i) lowland south Sudanian and north Guineo–Congolian humid communities and (ii) to Afromontane communities (Fig. 1).

5.1 Taxa from lowland south Sudanian and north Guineo–Congolian humid communities

In the LT1 sequence, these humid communities are mainly represented by pollen of *Celtis*, *Alchornea*, *Uapaca* and Combretaceae (Fig. 4), with mean combined frequencies of 29 % between ca. 6700 and 6050 cal yr BP (Zone 1) and of 20 % after 6050 cal yr BP (Zone II), whereas in modern samples they never represent more than 6 % (JM1: 5.2 %; JM3: 3.6 % and JM4: 3.7 %). The most abundant taxon is *Uapaca*, whose mean frequencies in fossil spectra are of 20 % and of 10 %, before and after ca. 6050 cal yr BP (Figs. 4 and 10). In modern samples, it is lower than 3 % (JM1: 2.7 %; JM3: 1.9 % and JM4: 2.3 %). Three hypotheses can be put forward to explain such a variation in abundance of humid communities: (i) a higher influx of these southern lowland humid pollen taxa by the Chari and Logone rivers between 6700 and 5000 cal yr BP, and particularly between 6700 and 6050 cal yr BP; (ii) a closer localization of the Mega-Lake shoreline to these humid communities (Fig. 1); and (iii) a northward migration of these lowland humid plants which may have occupied large areas in the vicinity of the paleolake, perhaps as far as the modern Sahel zone (i.e., between 13 and 16° N) under more favorable regional climatic conditions during the AHP. To try to identify the most reliable hypothesis, it seems necessary to first discuss the modern distribution of these plants, mainly *Uapaca*, then the occurrence of these pollen in previously studied Holocene fossil sequences from Lake Chad and more broadly from northern Africa.

Today in West and Central Africa, most of *Uapaca* species occur in the Guineo–Congolian lowland rain forest region (wet type) (Fig. 1) and are mainly linked to more or less permanent swamp environments (Hutchinson and Dalziel, 1954–1972; White, 1983; Lebrun and Stork, 2006). This very humid forested region is currently not drained by the Chari–Logone river system (Fig. 1). It was probably also the case during the mid-Holocene, since only few pollen taxa that typify these communities are recorded in noticeable frequencies (more than 1 %) in fossil spectra. This feature was previously observed and discussed by Maley (1981) in the Tjéri pollen sequence and is also shown in our biome reconstructions by
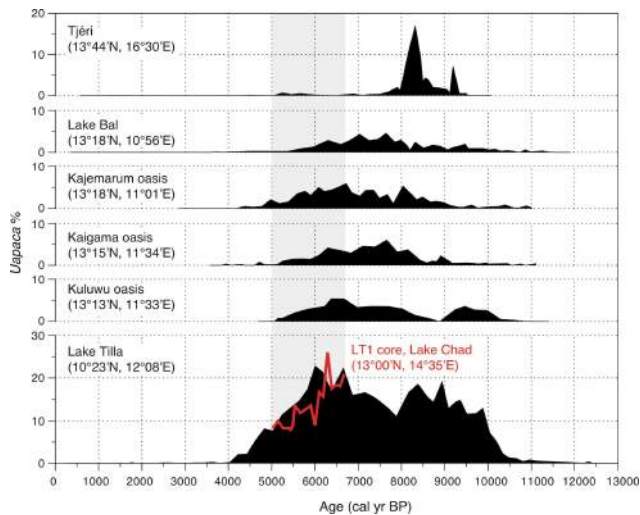
Fig. 10. Comparison between *Uapaca* frequencies from Tjéri (Maley, 1981), Lake Bal, Kajemarum, Kaigama and Kuluwu oases (Salzmann and Walter, 1998), Lake Tilla (Salzmann et al., 2002) and Lake Chad (this work). The grey band represents the time interval covered by LT1 core.

the lowest scores displayed by TRFO among all biomes considered (Fig. 6a). However, some *Uapaca* species are present in the wetter southern part of the Sudanian region (White, 1983; Lebrun and Stork, 2006) such as *Uapaca togoensis* in woodland and wooded savanna and *Uapaca heudelotii*, more often present near water or along fringing forest in savanna zone.

In the Holocene Tjéri pollen sequence (13°44′ N), located about 200 km northeast of the LT1 sequence in the present Sahel zone (Fig. 1), *Uapaca* pollen has been found between ca. 9600 and ca. 5200 cal yr BP (Maley, 1981). Higher frequencies than in modern samples (3 %) are registered only at ca. 9200 cal yr BP (7 %) and between ca. 8600 and ca. 8000 cal yr BP (10–17 %), so significantly earlier than in our sequence, and decreased to almost nothing at ca. 5200 cal yr BP (Fig. 10). At this period, the Tjéri site was likely submerged by the Mega-Lake Chad, and the presence of *Uapaca* pollen as well as other humid elements has been interpreted as related to an increase in river input from southern regions, i.e. through the Chari–Logone river system (Maley, 1981).

In the Manga Grasslands interdune depressions (northeastern Nigeria, 13° N), in the modern Sahel region, close to the northern boundary of the Sudanian region and at a similar latitude as Lake Chad (Fig. 1), *Uapaca* pollen was recorded with significant frequencies in five pollen sequences (Lake Bal, Kajemarum, Kaigama and Kuluwu oases (Salzmann and Waller, 1998) and Lake Jikariya (Waller et al., 2007)) between ca. 10 000 and ca. 3500 cal yr BP. In the four first sequences (raw data not being available for the Jikariya sequence), highest frequencies are registered from ca. 8000 to

ca. 6300 cal yr BP, with maximum of 4 %, 6 %, 6 % and 5 %, respectively (Fig. 10). On all these sites, *Uapaca* frequencies progressively decreased from ca. 5500 cal yr BP until ca. 3500 cal yr BP, disappearing after these dates. The authors have shown with their multiple pollen records that *Uapaca*, here considered as a "Guinean" element (vegetation type as defined by Keay, 1959, in Nigeria), migrated into the Sahel and colonized the dune depressions, then maintained during part of the Holocene as an extrazonal Guinean swamp forest element due to favorable local hydrological conditions, rather to be directly coupled to regional climate. At the same time, the presence of Sudanian humid elements (e.g. Combretaceae, *Detarium*) was interpreted as a colonization of the dune fields resulting from a more humid regional environment at this latitude.

At Lake Tilla (10°23′ N, 12°08′ E, 690 m, Biu Plateau), a crater lake in northeastern Nigeria, located south of the Manga Grasslands in the modern dry Sudanian undifferentiated woodland (Fig. 1), *Uapaca* pollen grains have been found in high frequencies (5 % to 22 %) between ca. 10 100 and ca. 4600 cal yr BP, with maxima values between ca. 6700 and ca. 6000 cal yr BP. After ca. 6000 cal yr BP, this taxon decreased then disappeared at ca. 4000 cal yr BP (Fig. 10). As in the Manga Grasslands, *Uapaca* has been interpreted as a "Guinean" extrazonal tree occurring in swamp forest fringing the lake (Salzmann et al., 2002).

It can be noted that in Holocene sediments from northern Sudan (El Atrun, 18° N), i.e. more than 2000 km north of the closest current populations, some pollen grains of *Uapaca* have been registered, but their presence on this site would have mainly resulted from a long distance wind transport (Jahns, 1995).

At Lake Chad, we suggest that the high presence of *Uapaca* pollen in our LT1 record would not be exclusively due to higher water discharge by the Chari–Logone river system. It can be also expected that local and regional floristic changes would have occurred, linked to a northward migration of humid plant species during the AHP into the modern dry Sudanian and Sahel parts of the LCB. These plants probably first entered in gallery forest formations along modern permanent rivers such as the Chari, Logone and Komadugu rivers (Fig. 1), but also along southern smaller rivers which were active during the AHP. Then, they dispersed on well-drained soils as observed northward (Watrin et al., 2009). The preferentially zonal distribution of *Uapaca* in the LCB as proposed here disagrees with an extrazonal presence of this tree, i.e. in local swamp forest, as previously interpreted at the same latitude in the Manga Grassfields (Salzmann and Waller, 1998; Waller et al., 2007) and southward at Lake Tilla (Salzmann et al., 2002). On the basis of our pollen data, we believe that such extrazonal formations would have preferentially established and maintained locally around small lakes or in dune depressions, mainly fed by groundwater inputs leading to a relatively stable surface elevation of water level, and so allowing favorable local conditions to support a

permanent swamp forested environment during humid periods such as the AHP. However, at Lake Chad, the local conditions should be different. Lake Chad occurs in a flat regional topography area and it is very sensitive to local and regional climate variations, implying large fluctuations of the lake surface and in the position of the shorelines as observed during the last decades. Thus, the presence of permanent swamp forest around the lake during at least 1700 yr is questionable. Such instability of paleo-Lake Chad surface can be testified in the time interval record in core LT1 by centennial fluctuations in Cyperaceae frequencies, representing phases of extension or reduction of swamp/marshy environments due to short time variations in lake level. Their lowest frequencies registered between ca. 6500 and ca. 6300 cal yr BP can be interpreted as corresponding to a maximum surface area of the paleolake during the whole period encompassed by LT1 core, i.e. to a high lake stand. This scenario is in agreement with the maxima of P_{ann} estimated values and would imply that the shorelines were, at this time, at their maximum distance to the LT1 core location. Thus, if *Uapaca* testified the occurrence of extrazonal swamp formations established around the paleolake, a similar and contemporaneous decrease in *Uapaca* and Cyperaceae frequencies would be expected. Nevertheless, an inverse trend in the frequencies of these two taxa is observed in our pollen sequence. This feature would indicate that *Uapaca* could not have occurred on the shorelines of paleo-Lake Chad in swamp formations as an extrazonal edaphic element, but preferentially in the vicinity of the paleolake as part of a zonal wooded savanna or woodland with Sudanian affinities.

Except this divergence, all Holocene pollen sequences from northern and north-central Africa are in agreement to demonstrate that a migration of humid plants during the AHP northward of their modern limit occurred during the AHP. This has been shown in the Sahara at Selima (21° N), Oyo (19° N) and El'Atrun (18° N) in northwestern Sudan (Ritchie et al., 1985; Ritchie and Haynes, 1987; Ritchie, 1994; Jahns, 1995), in the Ténéré Desert (19° N; Schulz, 1991), and more recently at Lake Yoa (19° N) in northern Chad (Lézine, 2009), with the presence of tropical Sahel and Sudanian plants species in this hyperarid region (Watrin et al., 2009). It can be also observed (i) in the Sahel region, in the Manga Grasslands (13° N), with the occurrence of humid "Guinean" and Sudanian trees in the depressions and on the dunefields, respectively (Salzmann and Waller, 1998; Waller et al., 2007); (ii) in the dry Sudanian zone, at Lake Tilla (10°23′ N), where vegetation has been interpreted as closely similar to modern vegetation occurring at the forest-savanna boundary about 350 km south of the lake (Salzmann et al., 2002); and (iii) in the Guinea-Congolia–Sudania transition zone (White, 1983), at Lake Mbalang (7° N), when the eastern part of the Adamawa Plateau was largely occupied by Guineo–Congolian semi-deciduous forest, now located more than 150 km southward (Vincens et al., 2010).

The onset of the decrease in *Uapaca* pollen ca. 6050 cal yr BP in the LT1 sequence was synchronous with that observed at Lake Tilla and in the Manga Grasslands (Fig. 10), and also with the onset of the decrease in semi-deciduous forest taxa at Mbalang on the Adamawa Plateau; however, it is two millennia later than in the Tjéri sequence. After ca. 6050 cal yr BP, *Uapaca* still displayed higher frequencies in LT1 sequence relative to modern values, which would indicate that the *Uapaca* retreat southward to its modern position was not complete by ca. 5000 cal yr BP, and must have resulted from a progressive process as previously suggested at Lake Tilla. This retreat would have been coupled to a progressive change toward drier conditions over the modern Sahel region as shown in our P_{ann} reconstructions, the onset of the decrease in P_{ann} occurring at about 6050 cal yr BP, with values after that date closer to modern ones (Fig. 9). Therefore, we cannot rule out that the decline in humid pollen taxa after 6050 cal yr BP was also partly caused by a contemporaneous decrease in input by the Chari–Logone river system related to a decrease in P_{ann} all over the southern basin. Decrease in P_{ann} and in river input would be moreover testified by a progressive increase in Cyperaceae, indicating an extension of marshy vegetation due to a lowering of Lake Chad water level, particularly after ca. 5500 cal yr BP. The progressive change in the floristic composition of the LCB vegetation would be confirmed by the slight and regular introduction of Sahel steppic taxa such as the Amaranthaceae/Chenopodiaceae (1.5 to 6.3 %) indicative of more open vegetation and local bare grounds (Fig. 4). Such vegetation change in the LCB is well reconstructed in our biomization, which shows TDFO potential biome displaying for the first time lower scores than STEP biome, but with still close values. After ca. 6050 cal yr BP, typical sub-desert and desert taxa (e.g. *Artemisia, Zygophyllum*) and taxa with a northern origin (Ericaceae) are present but always remain very scarce (only one or two grains) indicating that the Sahara desert zone was still far north as also suggested by Watrin et al. (2009). DESE biome scores are always lower than TDFO, STEP and SAVA (Fig. 6), contrary to reconstructions from modern pollen spectra (Fig. 5).

5.2 Taxa from Afromontane forest communities

Afromontane forest communities are mainly represented in our fossil spectra by *Olea*. This taxon displays non-negligible pollen frequencies (1.5–3 %) between ca. 6700 and ca. 5900 cal yr BP (Figs. 4 and 11) while it is absent from all modern samples (Maley, 1972). The interpretation of *Olea* presence in LT1 sequence is different to that of *Uapaca* and of other lowland humid plants. Indeed, *Olea* is a sub-montane/montane tree, and its modern and past distributions are more likely linked to altitude than latitude.

Today the closest *Olea* populations to Lake Chad (*Olea capensis*) are found above 1500 m altitude in north
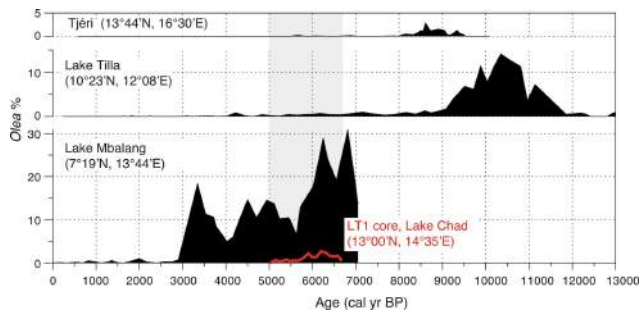
Fig. 11. Comparison between *Olea* frequencies from Tjéri (Maley, 1981), Lake Tilla (Salzmann et al, 2002), Lake Mbalang (Vincens et al., 2010) and Lake Chad (this work). The grey band represents the time interval covered by LT1 core.

and central Cameroon, on the Mandara Plateau (12° N), Mount Poli (8°20′ N) and Mount Nganha (7° N) (Letouzey, 1968); however, only this latter site, located on the Adamawa Plateau, belongs to LCB and is drained through a small river feeding the southwest of Logone river (Fig. 1). All these populations are currently degraded and persist only as relics. Northward, *Olea* communities (*Olea laperrinei*) that occur on Ahaggar, are completely absent from Tibesti, but recur on Aïr at the southern fringe of the Sahara. This species is also found eastward on the Jebel Marra (White, 1983) (Fig. 1).

In the Tjéri sequence (Chad), *Olea* has been found between ca. 9400 and ca. 8500 cal yr BP with frequencies close to those found in the LT1 record (1–2.3 %) (Maley, 1981) (Fig. 11). However, as observed with *Uapaca*, the highest frequencies and the onset of the decrease in *Olea* percentages are registered earlier in Tjéri than in LT1 record. More largely in West African sequences, presence of *Olea* pollen has been recorded in the Manga Grasslands (300 m altitude) but with very negligible frequencies (one or two grains), indicating its long distance transport (Salzmann and Waller, 1998; Waller et al., 2007). In the Lake Tilla sequence (700 m altitude), *Olea* is relatively well represented (maximum pollen frequencies of 14 %), but only between ca. 11 500 and ca. 9300 cal yr BP after which it largely decreases to very low values by ca. 8000 cal yr BP, and persists until ca. 4000 cal yr BP (Salzmann et al., 2002; Fig. 11). In the Mbalang sequence on the Adamawa Plateau (1100 m altitude), high frequencies of *Olea* (> 20 %) indicate that *Olea* populations were largely extended at mid-altitude between ca. 7000 and ca. 6100 cal yr BP, then retracted until ca. 3000 cal yr BP, when they probably only occupied their modern position on the Mount Nganha (Vincens et al., 2010). The persistence of *Olea* populations during a longer period at Mbalang compared to Lake Tilla is probably due to the higher altitude of the Adamawa Plateau compared to the Biu Plateau, and so to better climatic conditions during mid-Holocene for their local maintenance.

The presence of *Olea* pollen in LT1 sequence between ca. 6700 and ca. 5900 cal yr BP would be linked to a greater

extension of *Olea* populations at mid-altitude in the southern basin than present day. Pollen-based vegetation reconstructions from Mbalang (Vincens et al., 2010) show that *Olea* was an important component of the vegetation on the eastern part of Adamawa Plateau, which belongs to LCB. *Olea* decreased ca. 5900 cal yr BP onwards, follows a similar trend observed at Mbalang ca. 6100 cal yr BP, and would confirm its southern origin. On the Adamawa Plateau, influenced by peculiar climatic conditions due to its altitude, the retreat of *Olea* contemporaneous with the retreat of humid semi-deciduous forest components has been more linked to an increase in the length of the dry season than to change in the amount of mean annual rainfall (Vincens et al., 2010), whereas our reconstructions indicate a P_{ann} decrease in the Chad basin (Fig. 9). Low frequencies of *Olea* in LT1 sequence (also observed in the Tjéri record, but earlier) clearly indicate that Holocene populations of this tree have always occupied the southern regional environment of the Mega-Lake Chad; they were closer to the Mega-lake Chad than Guineo–Congolian humid elements, as shown by higher scores of WAMF biome, though with lower values than the TRFO biome (Fig. 6). Here, the presence of *Olea* pollen in fossil sediments, contrary to *Uapaca*, can be exclusively linked to river transport into the lake.

6 Conclusions

The LT1 pollen sequence from Lake Chad, though covering a short period of 1700 yr between ca. 6700 and ca. 5000 cal yr BP, provides new information concerning the vegetation in the LCB during part of the mid-Holocene. Our results, compared to modern data, show that during the recorded period:

1. The vegetation in the vicinity and in the regional environment of the lake was different in its structure and its floristic composition. Tree cover, as shown by higher frequencies of total arboreal taxa, would have been more extensive, maybe of woodland or humid savanna types, but the abundance of Poaceae indicates a largely discontinuous canopy. In its floristic composition, this vegetation would have included more humid tree plants such as *Uapaca*, *Alchornea*, Combretaceae, *Celtis* and *Syzygium* currently found southward in the LCB. Contrary to vegetation reconstructions proposed at similar or closed latitudes at Lake Tilla and in the Manga Grasslands, we have preferentially interpreted these humid plants as occurring in zonal vegetation than in extrazonal formations (i.e. as swamp forest elements on the shore line of paleo-Lake Chad) given that their pollen frequencies displayed an inverse trend to clear swamp/marshy taxa, mainly the Cyperaceae. In the regional environment, *Olea* populations were more extended at mid-altitude, mainly on the Adamawa Plateau in central Cameroon.

2. A change in vegetation is observed ca. 6050 cal yr BP. Lower frequencies of total arboreal pollen taxa than before (mainly of the *Uapaca* humid element, though its presence remains largely higher than present-day), contemporaneous with a slight development of drier Sahel taxa characteristic of bare grounds such as the Amaranthaceae/Chenopodiaceae, would suggest more open and drier formations around the lake. More locally swampy areas dominated by Cyperaceae developed, indicating a lowering of the lake level. At mid-altitude, *Olea* populations began to contract. This vegetation change in the Chad basin was related, as shown in our quantitative reconstructions, to a decrease in mean annual precipitation from a mean estimate of ca. 800 $(-400/+700)$ mm before ca. 6050 cal yr BP to approximately 600 $(-230/+600)$ mm onward, following a progressive drying trend. This change was observed at the same time and with the same gradual mode in the Manga Grasslands, at Lake Tilla and southward at Lake Mbalang, as evidenced at all sites by the concomitant progressive decrease of arboreal taxa and the increase of dryer taxa during this period.

   This progressive change in vegetation corresponds in West Africa to the AHP termination. This event was defined by deMenocal et al. (2000) on a marine record off the west coast of North Africa and based on an abrupt shift (within a few centuries) in dust content ca. 5500 cal yr BP. This shift has been attributed to an abrupt aridification and a collapse of vegetation cover in the southern Sahara region. As previously pointed out by Brovkin and Claussen (2008) and Holmes (2008), one has to be cautious in interpreting these dust records as unequivocally reflecting a decrease in vegetation cover. The abrupt change in the dust flux may also reflect a spread of the source area of the dust caused by lake desiccations. More recent data obtained on the same core (i.e. opal flux and alkenone) do not exhibit a collapse as abrupt as the dust flux but a rather gradual change from ca. 6000 to ca. 4000 cal yr BP (Adkins et al., 2006). Such pace and duration of the AHP termination are also suggested by Sahara and Sahel continental proxies, showing a progressive drying trend during the mid-Holocene, e.g. lake level status (Hoelzmann et al., 2004) or diatoms (Gasse, 2002), supporting our interpretations from pollen data.

3. The biomization approach used in this paper allows a more thorough and precise vegetation reconstruction by considering all scores of potential biomes. Such an approach was recently proposed in central Africa by Lebamba et al. (2012) and by Marchant et al. (2006) in South America. Indeed, if only the score of the dominant biome has been considered such as in Jolly et al. (1998a and b), Elenga et al. (2000), Hély et al. (2009) and Lebamba et al. (2009a), all fossil spectra would

have been reconstructed with the same biome, i.e. SAVA (savanna), thus indicating no change in vegetation in the LCB between ca. 6700 and ca. 5000 cal yr BP.

4. Our P_{ann} reconstructions exhibit for the period before ca. 6050 cal yr BP a mean annual estimate of ca. 800 $(-400/+700)$ mm in the Chad southern basin (ca. 13° N). According to the modern position of the 800 mm isohyet, at ca. 10–11° N (L'Hôte and Mahé, 1995), this value can suggest a migration of this isohyet ca. 200–300 km northward during mid-Holocene. Additionally, the modern occurrence in northern central Africa of dry and wet Sudanian woodlands, and more locally Guineo–Congolian mosaic of lowland rain forest and secondary grassland (Figs. 1 and 7), shows that these vegetation communities can occur under a mean annual precipitation of 800 mm, which would support our vegetation reconstruction. Likewise, for the mid-Holocene period, previous works based on pollen data have empirically estimated the position of the 400 mm isohyets at 19° N in the eastern Sahara (Ritchie and Haynes, 1987) and at 21° N in the western Sahara (Lézine, 1989), when its present position is about 14–16° N, representing a ca. 400 km northward shift of this isohyet, i.e. a migration roughly of the same magnitude than that proposed here.

   Moreover, our P_{ann} reconstructions, but also CA1 axis scores on the pollen diagram (Fig. 4) indicate that the period between ca. 6500 and ca. 6300 cal yr BP was the most humid period recorded in the LT1 pollen sequence. Because of the short period of time recovered by our record, however, we cannot propose the maximum extension of this episode during the early Holocene as suggested on some sites of the Manga Grasslands (Kajamorum and Kuluwu; Salzmann and Waller, 1998) or at Tilla (Salzmann et al., 2002). We can only hypothesize that it probably represents a prominent century-scale climate variability toward more humid conditions superimposed on a long-term mid-Holocene drying trend, also evidenced northward in the Lake Yoa record (Kröpelin et al., 2008a) and southward at Lake Mbalang (Vincens et al., 2010), and in agreement with simulations proposed by Renssen et al. (2003) showing climate instability during the AHP termination.

5. Fluctuations in surface area of the paleo-Lake Chad between ca. 6700 and ca. 5000 cal BP can be inferred from fluctuations in the pollen representation of the Cyperaceae. It appears that the maximum surface area of the paleo-Lake Chad would have occurred between ca. 6500 and ca. 6300 cal yr BP, when Cyperaceae pollen were at their minima values, the minimum surface area from ca. 5500 cal yr BP onward when Cyperaceae were at their maxima values; intermediate stages are observed between ca. 6700 and 6500 cal yr BP and

between ca. 6300 and ca. 5500 cal yr BP. These proposed lake-level fluctuations independently follow P_{ann} reconstruction changes, assuming that Cyperaceae do not intervene in our reconstructions, but are also contemporaneous to increase or decrease in humid southern tree components such as *Uapaca* (related to decrease/increase of river input and/or to regional climate changes). This shows that between ca. 6700 and ca. 5000 cal yr BP the water budget of Mega-Lake Chad was sensitive to precipitation variability, and that reduction in P_{ann} as inferred from pollen data before ca. 6500 cal yr BP and from ca. 6200 cal yr BP onward could have led to significant reductions in surface area and depth.

6. The time discrepancy between the vegetation change observed in LT1 data and the Tjéri record remains unresolved. While the retreat of humid elements from north-central African Sahel and Sudanian sites is roughly synchronous with that registered in the LT1 sequence, the Tjéri sequence records this change approximately 2000 yr earlier. This casts doubt on the Tjéri chronological framework that was established by assuming no discontinuity between the two available dates encompassing the end of the AHP. Another hypothesis would be that the Tjéri sequence would have been directly influenced by the fluvial input coming from rivers that drained the Tibesti and Ennedi mountains. If true, this sequence does not reflect vegetation changes in the southern part of the basin.

Much research remains to be done to document the vegetational response of ecosystems in north-central Africa to the succession of climatic events that occurred since the AHP and more generally since the last deglaciation. However, these first pollen results show the high potential of lacustrine archives of Lake Chad to record environmental changes at local and regional scales. They highlight the need to develop a higher resolution pollen data set spanning the entire Holocene. This also implies collecting more modern samples representative of the modern and recent vegetation around the lake to improve biomization and transfer function approaches. A more detailed and thorough study involving multiproxy quantification and ecosystem modelling will allow us to better understand the mid-Holocene climatic transition and will provide an original contribution to the current, still actively debated about the AHP termination and potential biophysical feedbacks that drive vegetation changes.

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