

Abstract

Located at the transition between the Saharian and Sahelian zones, at the center of one of the largest endoreic basins, the Lake Chad is ideally located to record regional environmental changes that occurred in the past. However, until now, no continuous archive from Lake Chad covering the Holocene has been studied. In this paper, we present pollen data from the first Holocene sedimentary sequence collected in Lake Chad (13° N; 14° E; Sahel region). Dated between ca. 6700 and ca. 5000 cal yr BP, this record encompasses the termination of the African Humid Period (AHP). Vegetational reconstructions are based on standard analyses of the pollen diagrams and are strengthened by quantitative approaches. Potential biomes that occurred at that time around Mega-Lake Chad are reconstructed using the biomization method and mean annual precipitation 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 much further southward, thrived in the vicinity and/or the extra-local environment of the Mega-Lake Chad in place of the modern steppe, dry woodland and desert vegetation observed today. At the same time, montane forest populations extended further southward on the Adamawa plateau. This vegetation distribution is supported by biome reconstructions as well as by mean annual precipitation estimates of ca. 800 (–400/+700) mm for the period. The high abundance of lowland humid pollen taxa is interpreted as the result of a northward migration of the corresponding plants during the AHP driven by more favorable climatic conditions. Our interpretation in favor of a regional vegetation response to climatic changes is supported by other pollen data from several Northwestern African records. However, we cannot rule out that an increase of Chari-Logone inputs into the Mega-Lake Chad due to variations in hydrological regime might have contributed to the higher abundance of lowland humid pollen taxa observed in the mid-Holocene sedimentary sequence. Changes in the structure and floristic composition of the vegetation towards more open and drier formations occurred after ca. 6050 cal yr BP. This is also

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evidenced by a decrease in mean annual precipitation estimates to approximately 600 (–230/+600) mm. This change corresponds to the onset of the AHP termination. The constant presence of lowland humid taxa until ca. 5000 cal yr BP, even if displaying a slight decrease, contemporaneous with an increase in steppic taxa, demonstrates that at ca. 5000 cal yr BP the modern vegetation was not yet established in the vicinity of Lake Chad. Our data indicate that vegetational change during this period must have occurred progressively, at least over 1000 yr, and are inconsistent with an abrupt aridification and a collapse of the vegetation cover in the East-Central Saharan and Sahelian regions at the AHP termination.

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, ca. 6000–5500 yr ago. 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. Jolly et al., 1998a; Hély et al., 2009; Lézine, 1989, 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 (Jolly et al., 1998b). Geological records, supported by archaeological evidence (e.g. Kuper et Kropelin, 2006), indicate that the present 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 the influence of the Western African monsoon being recorded up to 27° N (Kuhlmann et al., 2004). This is substantiated by simulations with climatic models that have shown that, during this Holocene

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climatic “optimum” period, increases 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 inter-tropical convergence zone (ITCZ) and its associated rainfall belt (e.g. Kutzbach and Street-Perrott, 1985). Positive feedbacks involving ocean and/or biophysical mechanisms may have increased the climate response to this orbital forcing by enhancing water advection and local recycling of precipitation (Braconnot et al., 1999; Kutzbach et al., 1996; Kutzbach and Liu, 1997). However, coupled atmosphere-ocean-continent climate models have failed to shift the African summer precipitation during the early and mid-Holocene over Northern Africa as far north as suggested by the paleodata (Sepulchre et al., 2009).

During the AHP termination and the onset of aridification of the Sahara and the Sahel regions, an inverse climatic scenario was proposed (Kutzbach and Street-Perrott, 1985). But, many questions related to this climatic transition that affected the African inter-tropical 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. 5.5 kyr and was completed within few hundred years (deMenocal et al., 2000; Kuhmann et al., 2004). Continental archives give a more complex picture, with pronounced differences in the apparent timing and amplitude of hydrological and vegetational changes inferred from individual records (Gasse, 2000; Hoelzmann et al., 2004). Regardless the chronological uncertainties and low time resolution of most of these records, this underscores both regional variability in climate change and site-specific topographic or hydrogeological influences. In particular, the issue of 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., 2008; Vincens et al., 2010) is still the subject of intense debate (see, for example, the controversy between Brovkin and Claussen, 2008; Kropelin et al., 2008). Coupled atmosphere-ocean-vegetation climate model investigations suggest that positive feedbacks between vegetation cover and precipitation played a significant role in the rapid collapse of vegetation in North

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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 the presently northern 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 different vegetation communities in response to local conditions (precipitation) during the AHP transition (e.g. Marchant and Hooghiemstra, 2004; Vincens et al., 2010). The most recent state-of-the-art model that synchronously coupled transient simulation of the evolution of the Northern Africa climate-ecosystem in a global general circulation ocean-atmosphere-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, 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 palaeodata 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 Saharian and Sahelian 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., 2008; 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., 2008), but its representativeness

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2011). Today, due to increased aridification, Lake Chad has a surface area of only ca. 2500 km² and a mean depth comprised between 3 and 5 m. During past humid periods, sedimentological and palaeontological evidence 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 (see Durand, 1982), the Holocene paleolake might have reached a surface area of more than 350 000 km² during the AHP (Schuster et al., 2005; Leblanc et al., 2006a, 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 inter-tropical 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 continental northeast trade winds (Harmattan) are dominant, causing the region to be extremely dry. 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 (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 and evaporation about 2300 mm yr⁻¹ (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 northwards wet (*Isobertinia* woodland) and dry (undifferentiated woodland) Sudanian formations. In its northern part,

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Sahelian semi-desert grassland then Saharian desertic 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 species dominated by the Mimosaceae (*A. seyal*, *A. sieberiana*, *A. nilotica*, *Faidherbia albida*.) and the Capparidaceae (*Maerua crassifolia*, *Boscia senegalensis*, *Capparis decidua*. . .), associated with *Leptadenia pyrotechnica* (Asclepiadaceae), *Salvadora persica* (Salvadoraceae), *Commiphora africana* (Burseraceae), *Balanites aegyptiaca* (Balanitaceae). The herbaceous layer, which does not reach 60 cm, is more or less continuous and is dominated by annual Poaceae (Maley, 1972; White, 1983). Around the lake, swampy herbaceous formations are largely developed and dominated by Cyperaceae.

3 Material and methods

Palynological results presented here were obtained from a 1-m sedimentary sequence (LT1 core; 13° 0' 29.8" N, 14° 35' 51.1" E), collected during a pilot coring operation conducted in 2008 in the southern pool of the Lake Chad (Fig. 2). This core mostly consists of dark grey mud with some light grey plan-parallel lamination, especially in the upper 40 cm. Chronological control is based on six Accelerator Mass Spectrometry (AMS) ¹⁴C measurements (Beta Analytic Inc., USA) performed on the 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 two dates (Fig. 3). ¹⁴C data indicate that the LT1 core covers the period between ca. 6700 and ca. 5000 calyrBP (Fig. 3) and thus encompasses the mid-Holocene transition. The sedimentation rate (mean of 0.5 mm yr⁻¹) is quite constant over the period. It is noteworthy that the top of the core shows a sloped layer, 3 cm thick, which possibly represents reworked sediments (Fig. 3). This is substantiated by the radiocarbon age obtained for the material collected at the top of the core (3651 calyrBP at 1.5 cm depth) that very likely represents a mixing between modern and Holocene sediments. For this reason,

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these upper 5 cm deposits were not considered in this article. The upper part of the Holocene sequence may be truncated by wind deflation during drying phases of Lake Chad, which have 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. This is suggested by ^{210}Pb analyses performed on LT1 core, which did not show any excess in ^{210}Pb at its top (Deschamps, personal communication). The drought that prevailed in the 1970s caused the drying of a large part of the southern pool of Lake Chad (Olivry et al., 1996), making aeolian erosion possible.

For pollen analyses, samples were taken every 5 cm throughout the studied sequence. This sampling represents a mean time resolution of ca. 90 yr between two samples. 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. Identification of pollen grains was based on the reference collection available at CEREGE that contains some 7000 specimens, on specialised 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-Chebouldaef, 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 form-life and habitat of each identified pollen taxa 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, 2003–2008). On the pollen diagram, taxa percentages were calculated using the total of pollen and spores counted, excluding only the 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 (<http://www.r-project.org/>).

annual rainfall values (P_{ann}) along core LT1. Our research used the modern pollen dataset, which includes 452 samples from Western and Central Africa originating from rain forest to desert vegetation (dataset available in the African Pollen Database (2010) and was complemented by data used in Lebamba et al. (2009). 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 removed all marshy and aquatic herbs and shrubs, swamp trees, anthropogenic taxa and ferns that have no significance for quantitative climatic reconstructions. 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 samples collected inside the lake, the P_{ann} values are calculated based on precipitation time-series (1932–1968) given by Olivry et al. (1996), since the samples analysed 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 bar for each sample is 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. After standardization to the nomenclature adopted here (Vincens et al., 2007), 105 pollen taxa were identified (Table S1). On the basis of the correspondence analysis (CA) results that reflect the main

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variations in pollen assemblage composition, the pollen sequence was divided into two zones (Fig. 4).

4.1.1 Pollen zone I (ca. 6700 to ca. 6050 calyrBP)

Zone I, which includes samples with negative values along CA axis 1, covers the older part of the record (ca. 6700 to ca. 6050 calyrBP). 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%), Combrretaceae (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/aquatic plants, the dominant taxon is Cyperaceae but, in this zone, it displays its lowest frequencies (maximum 17%) recorded along the whole core. 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 calyrBP)

This zone includes samples with positive values along CA axis 1 and encompasses the younger part of the LT1 core. Total arboreal pollen (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 taxa 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 taxa reach their highest frequencies of the sequence (maximum of 26.7%). *Olea* is present until ca. 5800 calyrBP, after which its frequencies become negligible.

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important discrepancies are observed between results from fossil and modern data: (i) TDFO (tropical dry forest) and STEP (steppe) biome scores are very close, mainly in samples after 6050 calyrBP (Zone II), and (ii) DESE (desert) biome scores always have lower contributions than TDFO scores. In addition, the analyses of biome scores vs. time show another important modification in the pollen assemblage, occurring at ca. 6050 calyrBP. Samples older than 6050 calyrBP (Zone I) show higher scores of TDFO biome than the STEP biome, then an inverse trend is observed onwards (Zone II), where the contributions of all reconstructed biomes are close to those observed in the modern sample JM1 front of the Chari-Logone delta.

However, all biome affinity scores show the same positive trend from oldest to youngest samples (Fig. 6a), whereas an opposite trend between forest and grassland biomes would be expected. The biome affinity scores are based on the sum of the associated PFT scores. Because few pollen taxa are strictly assigned to a single PFT, a kernel of common taxa influences these biome 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 savanna biome shares steppic and tropical dry forest taxa, which all contribute to the positive trend of these three biomes. 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 6050 yrBP (Fig. 6b). This indicates an aridification of the vegetation.

4.3 P_{ann} reconstructions

Before proceeding to the reconstruction of P_{ann} on fossil samples, a calibration/validation was performed on the modern dataset (Fig. 7). The 452 modern pollen spectra were split into two groups: the first one was used for the calibration and the second one to verify the reliability of the calibration. The good correlation coefficient ($r = 0.71$) obtained between calibrated and observed values validates the use of this modern dataset to reconstruct precipitation values from our fossil samples (Fig. 8). Nevertheless, the transfer function seems to underestimate low precipitation values

(<500 mm yr^{-1}) and overestimate the high precipitation values (>1500 mm yr^{-1} ; see Fig. 8). It is noteworthy that only the lower bias may affect our record, i.e. the analogues of the post-5500 yrBP samples (see below).

The P_{ann} estimates calculated from LT1 samples are presented on Fig. 9 and Table S2. They show a global trend toward a decrease of P_{ann} between ca. 6700 and ca. 5000 calyrBP. If a P_{ann} value of ca. 500 mm (Djamena meteorological station) is considered as the modern reference in the southern part of Lake Chad, higher estimates are always reconstructed before ca. 6050 calyrBP, particularly between ca. 6500 and ca. 6100 calyrBP when P_{ann} values fluctuate between 730 and 1020 mm with lower uncertainties of about 400 mm and upper ones of about 700 mm (Table S2a). The relatively high uncertainties, especially the upper ones, are due to the large difference of precipitation values between the five analogues (1450 mm to 350 mm, relative to the wetter and dryer analogues, respectively). The P_{ann} reconstruction is the average of these analogues with a weighting inverse to the distance between the fossil and the modern spectra and the confidence interval is provided by the difference between the extreme wet/dry analogues. The high frequencies of some taxa found in LT1 core that are present in much lower frequencies in modern samples around the lake, as the case of *Uapaca*, seem to be determinant in the choice of the best analogue. The two first selected best modern analogues 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 (Table S2b). After ca. 6050 calyrBP, P_{ann} estimates are more regular and closer to modern references, 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 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 based on the modern analogues technique. So, uncertainties are overestimated and a better estimate will be only possible after collecting more samples representative of the lake modern vegetation.

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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 Logone-Chari river system play the primary role in pollen transport through 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. 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, 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 in paleolake 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 also must 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 BLC depression. The paleolake Chad had a larger latitudinal extension over northern areas today occupied by semi-desert grassland and desert, and southward over areas where dry Sudanian undifferentiated woodland is now found. But its shoreline never reached the most modern humid formations found south of 10° N (Fig. 1). The potential maximal extension (350 000 km²) of the Lake Chad was controlled by the Mayo Kebbi spillway, at 320–325 m b.s.l. (meter below sea level), where overflowing

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lake waters could spill out towards the Gulf of Guinea, via the Benue River (Ghienne et al., 2002; Leblanc et al., 2006; Schuster et al., 2005). During the Holocene, the hydrological budget might have also changed, leading to changes in the paleolake height 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 height/expanse fluctuation through the Holocene remain scarce (see review in Leblanc et al., 2006). 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 b.s.l. elevation, lasted at least the 5.3–4.4 kyr cal BP. There is no direct constraint on paleolake elevation before this period, but, on the basis of previous work, Schuster et al. (2005) suggest that this highstand episode started at 7000 kyr.

This means that during the period covered by the LT1 sequence, the height and extent of the paleolake Chad very likely remained quite constant and near its maximal Holocene extent. Therefore, we may argue that the sedimentation at the location of core LT1 was not affected by variation in the distance of the fluvial sources during that period. The respective delta of the Chari and Logone Rivers were however far from their present location (between 200–300 km southward). 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 sedimentary signal (Fig. 1). We may also hypothesize that the LT1 sedimentary sequence 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 the pollen spectrum JM1 in front of the modern Chari-Logone delta and close to LT1 core (Fig. 4), which could be considered as the modern reference for pollen sedimentation in this lacustrine area; and the pollen spectra JM3 and JM4, also under the influence of Chari-Logone inputs, but located at a larger distance from the Chari-Logone delta than JM1. This empirical choice is supported by our

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climatic quantitative reconstructions for which these three samples have been preferentially selected as best analogues (Table S2b).

The comparison between fossil and modern data shows higher frequencies of numerous pollen taxa, of plants that are not currently found in the vicinity of the lake, in LT1 sequence. These taxa are all issued from humid vegetations today located far southward of Lake Chad and drained by the Chari-Logone river system, but which have been closer to the Mega-Lake during the Holocene. 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. 3), with mean total frequencies of 29 % between ca. 6700 and 6050 calyrBP (Zone 1) and of 20 % after 6050 calyrBP (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 calyrBP, (Figs. 3 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: (1) a higher influx of these southern lowland humid pollen taxa by the Chari and Logone rivers between 6700 and 5000 calyrBP, and particularly between 6700 and 6050 calBP; (2) a closer localization of the Mega-Lake shoreline to these humid communities (Fig. 1) and (3) 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 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,

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mainly *Uapaca* in this article, then the occurrence of their pollen in previously studied Holocene fossil sequences from Lake Chad and more broadly from Northern Africa.

Today in West and Central Africa, the majority 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 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 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 wooded savanna and *Uapaca heudelotii*, more often present near water or along fringing forest in savanna zone.

In the Holocene pollen sequence of Tjéri (13° 44' N), located about 200 km north-east of the LT1 sequence in the present Sahel zone (Fig. 1), and at a probably similar distance to the influence of the Chari-Logone river system, *Uapaca* pollen has been found between ca. 9600 and ca. 5200 calyrBP (Maley, 1981). Higher frequencies than in modern samples (3%) are registered only at ca. 9200 calyrBP (7%) and between ca. 8600 and ca. 8000 calyrBP (10–17%), so significantly earlier than in our sequence, and decreased to almost nothing at ca. 5200 calyrBP (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 only interpreted as related to an increase in river input from southern regions (Maley, 1981).

In the Manga Grasslands (Northeastern Nigeria, 13° N), in the modern Sahel region, close to the northern boundary of the Sudanian region, at a similar latitude than Lake Chad (Fig. 1), *Uapaca* pollen was recorded in four pollen sequences (Lake Bal, Kajemarum, Kaigama and Kuluwu oases) between ca. 10 000 and ca. 3500 calyrBP

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(Fig. 10). Highest frequencies are registered from ca. 7600 to ca. 6300 calyrBP, with maximum of 4 %, 6 %, 6 % and 5 %, respectively. On these sites, *Uapaca* frequencies progressively decrease from ca. 5500 calyrBP until ca. 3500 calyrBP then completely disappear. These sites are interdune depressions without river input and the presence of *Uapaca*, considered a “Guinean” element (as defined by Keay, 1959, in Nigeria), has been interpreted more as an extrazonal occurrence due to favorable local hydrological conditions (swamp tree) than as a migration of this element as far north as the Manga Grasslands (Salzmann and Waller, 1998). However, no hypothesis was proposed to explain how this plant could have reached such sites and then thrived, while other humid Sudanian elements present at the same time were interpreted as occupying the well-drained zones around these depressions as result of their northward migration.

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 calyrBP, with maxima values between ca. 6700 and ca. 6000 calyrBP. After ca. 6000 calyrBP, this taxon decreased then disappeared at ca. 4000 calyrBP (Fig. 10). As in the Manga Grasslands, *Uapaca* has been interpreted as a “Guinean” swamp forest element fringing the lake (Salzmann et al., 2002). Nevertheless, in the absence of specific determination it cannot be excluded that this tree could have occurred on well-drained soils on the Biu Plateau among other humid Sudanian elements as in the Manga Grasslands. 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 to a wind transport (Jahns, 1995).

All these data indicate that during the Holocene, the maxima of *Uapaca* pollen frequencies are always registered before ca. 6000 calyrBP, regardless the hydrological context of the sites (Fig. 10). Thus, the high presence of *Uapaca* pollen in our LT1 record would not be exclusively due to higher water discharge by the Chari-Logone

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river system, or to the greater proximity of the Mega-Lake shoreline to *Uapaca* populations. Indeed, sites such as Lake Tilla (a crater lake) and the Manga Grasslands (interdune lake or oases mainly fed by groundwater) have a reduced catchment with minor surficial water inflow and no direct input from southern humid regions where *Uapaca* are currently present. It is more probable that in the Chad basin, and more largely in West and Central Africa, local and regional floristic changes in vegetation would have occurred, linked to a northward migration of more humid plants during the AHP, in this case into modern dry Sudanian and Sahel regions. Such migration of humid plants during the AHP northward of their modern limit is now well demonstrated in Northern Africa. It 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; Schlulz, 1991), and more recently at Lake Yoa (19° N) in Northern Chad (Lézine, 2009), with the introduction and expansion of tropical Sahel and Sudanian plants species in this hyperarid region (Watrin et al., 2009). This northward migration of humid communities can be observed (i) in the Sahel region, in the Manga Grasslands (13° N), with the occurrence of humid Sudanian trees on the dune-fields (Salzmann and Waller, 1998); (ii) in the dry Sudanian zone, at Lake Tilla (10° 23' N), where mid-Holocene vegetation has been interpreted as closely similar to the modern Guineo-Congolian mosaic of lowland rain forest and grassland (referred to in this paper as “dense Southern Guinean savannas”, Keay, 1959) 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 retreat of *Uapaca* ca. 6050 calyrBP 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 retreat of semi-deciduous forest plants at Mbalang on the Adamawa plateau; however, it is two millennia later than in the Tjéri sequence. After

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ca. 6050 calyrBP, *Uapaca* still displayed higher frequencies in LT1 sequence relative to modern values, which could indicate that the *Uapaca* retreat southward to its modern position was not complete until ca. 5000 calyrBP, and must have resulted from a progressive process as previously suggested at Lake Tilla. In our P_{ann} reconstruction, the onset of the decrease in mean annual precipitation occurred at about 6050 calyrBP. After that date, P_{ann} reach values closer to modern ones (Fig. 9). Therefore, we cannot rule out that the decline in humid pollen taxa after 6050 calyrBP in LT1 core is in part caused by a contemporaneous decrease in input by the Logone-Chari river system related to a decrease in P_{ann} all over the southern basin. The progressive change in the floristic composition of the LCB vegetation would be confirmed by the slight and regular reintroduction 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 is also registered in our biome reconstructions, which show TDFO potential biome displaying for the first time lower scores than STEP biome, but still close in values. After ca. 6050 calyrBP, typical sub-desert and desert taxa (e.g. *Artemisia*, *Zygophyllum*) and taxa with a northern origin (Ericaceae) 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 reconstructions support this hypothesis with scores 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 calyrBP (Figs. 4 and 11) while it is absent from all modern samples (Maley, 1972). The interpretation of *Olea* presence in LT1 sequence is quite 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.

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Today the closest *Olea* populations to Lake Chad (*Olea capensis*) are found above 1500 m altitude in North and Central Cameroon, on the Mandara Plateau (12° N), the Mount Poli (8° 20' N) and the 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 south-west of Logone river (Fig. 1). All these populations are currently degraded and persist only as relicts. Northward, *Olea* communities (*Olea laperrinei*) occur on Ahaggar, are completely absent from Tibesti, but recur on Air 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 with frequencies close (1 to 2.3 %) to those found in LT1 record between ca. 9400 and ca. 8500 calyrBP (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 extra-regional origin (Salzmann and Waller, 1998). 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 calyrBP after which it largely decreases until ca. 4000 calyrBP (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 calyrBP, then retracted until ca. 3000 calyrBP, 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 calyrBP 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, 2010) show that *Olea* was an important component of the vegetation on the eastern part of Adamawa plateau, which belongs to LCB. The *Olea* decrease ca. 5900 calyrBP onwards follows a similar trend to that observed at Mbalang ca. 6100 calyrBP 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 the 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 regional environment of the Mega-Lake Chad. This is confirmed by reconstructions of WAMF biome, which display very low scores in both fossil and modern samples (Figs. 5 and 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 calyrBP, provides new information concerning the vegetation in the LCB during the mid-Holocene. Our results, compared to modern data, show that during the recorded period:

(1) The vegetation in the vicinity and in the extra-local 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 indicate 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

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found southward in the LCB, many of them found at the same time and same latitude in the Manga Grasslands. 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 calyrBP. 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, probably 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 calyrBP 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 related to a climate fluctuation corresponds in West Africa to the African Humid Period termination. This event was defined by de Menocal 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 calyrBP. 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), one has to be cautious in interpreting these dust records univocally as 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 calyrBP (Adkins et al., 2006). Such pace and duration of the AHP termination are also suggested

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by Sahara and Sahel continental proxies, showing a progressive drying trend after the mid-Holocene, e.g. lake level status (Hoelzmann et al., 2004) or diatoms (Gasse, 2002), supporting our interpretations from pollen data for this event.

(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, b), Elenga et al. (2000), Hely et al. (2009) and Lebamba et al. (2009), all fossil spectra would have been reconstructed with the same biome, i.e. SAVA (savanna), thus indicating no change in vegetation in the LCB basin between ca. 6700 and ca. 6050 calyrBP.

(4) Our P_{ann} reconstructions exhibit for the period before ca. 6050 calyrBP 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.

(5) 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

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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 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 Tchad to record environmental changes at local and regional scales in LCB. They highlight the need to develop a higher resolution pollen dataset 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 modeling will allow us to better understand the mid-Holocene climatic transition and will provide an original contribution to the still active debate about the AHP termination and potential biophysical feedbacks that drive vegetation changes.

Supplementary material related to this article is available online at:

<http://www.clim-past-discuss.net/8/2321/2012/cpd-8-2321-2012-supplement.pdf>.

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

Laboratory code	Depth (cm)	Material	Conventional ^{14}C age (yr BP)	Calibrated age (cal yr BP)	Calibrated age (cal yr BP) 2s 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

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Table 2. Modern samples characterization: Pann values (mmyr^{-1}), vegetation zone (White, 1983), local vegetation (Maley, 1972) and potential reconstructed biome (this paper).

Sample	P_{ann} (mmyr^{-1})	Vegetation zone (White, 1983)	Local vegetation	Potential reconstructed biome
JM7	226	Sahel <i>Acacia</i> wooded grassland	edaphic grassland	STEP
JM6	250	Sahel <i>Acacia</i> wooded grassland	lacustrine mud	STEP
JM5	265	Sahel <i>Acacia</i> wooded grassland	lacustrine mud	SAVA
KK1	250	Sahel <i>Acacia</i> wooded grassland	lacustrine mud	SAVA
JM4	350	Sahel <i>Acacia</i> wooded grassland	lacustrine mud	SAVA
JM3	340	Sahel <i>Acacia</i> wooded grassland	lacustrine mud	SAVA
JM2	327	Sahel <i>Acacia</i> wooded grassland	lacustrine mud	SAVA
JM1	450	Sahel <i>Acacia</i> wooded grassland and edaphic grassland	lacustrine mud	SAVA
Chari	500	Sahel <i>Acacia</i> wooded grassland and edaphic grassland	river mud	SAVA
JMMCH	600	Sahel <i>Acacia</i> wooded grassland and edaphic grassland	mosaic of edaphic grassland and Sahel <i>Acacia</i> savanna	SAVA
JMA	600	Sahel <i>Acacia</i> wooded grassland and edaphic grassland, close to the limits of sudanien undifferentiated woodland	mosaic of edaphic grassland and Sahel <i>Acacia</i> savanna (Sahelian-Sudanian zone)	SAVA
JMD	300	Sahel <i>Acacia</i> wooded grassland	steppe	STEP
JMC	330	Sahel <i>Acacia</i> wooded grassland and edaphic grassland	edaphic grassland	STEP
JMB	500	Sahel <i>Acacia</i> wooded grassland and edaphic grassland	Sahel <i>Acacia</i> savanna	SAVA

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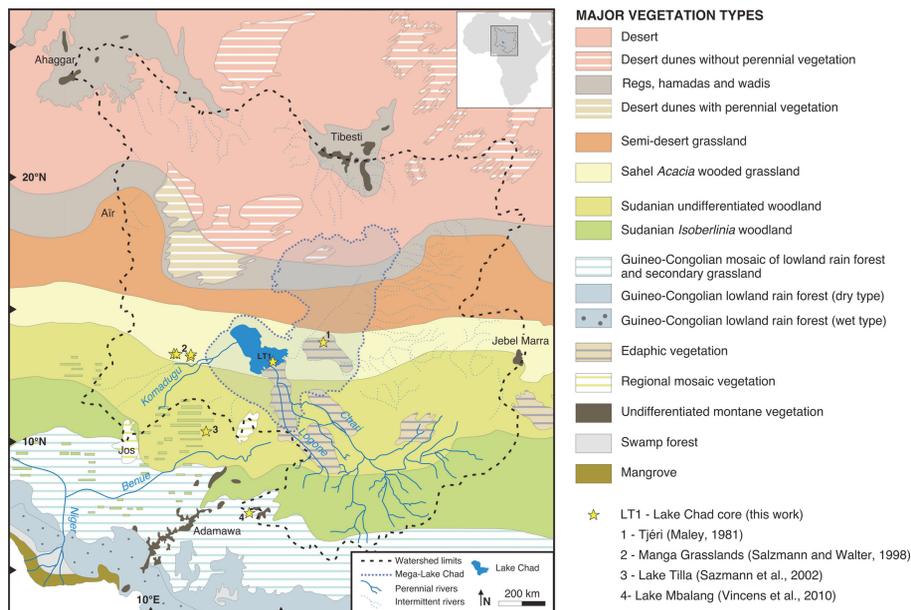


Fig. 1. Location map showing the Lake Chad Basin (LCB); the Holocene Mega-Lake Chad as reconstructed by Schuster et al. (2005) and the major modern vegetation types from White (1983). The modern Lake Chad is shown here at its largest extension reached during the past few decades.

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Fig. 2. Location of core LT1 (red circle; $13^{\circ} 0' 29.8''$ N, $14^{\circ} 35' 51.1''$ 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).

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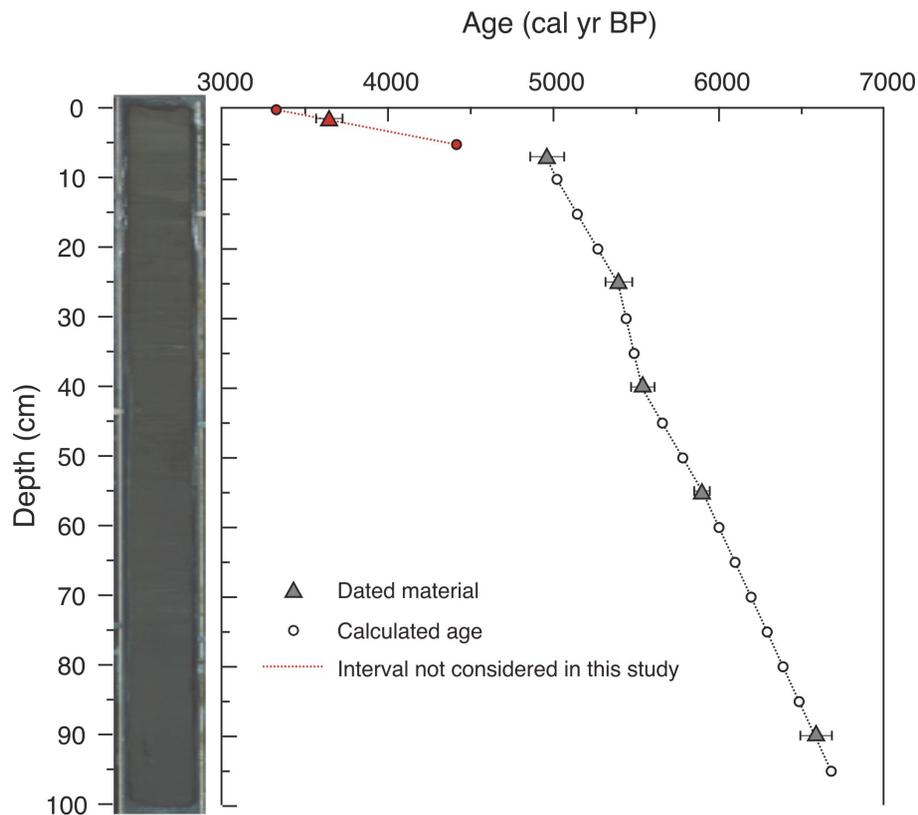


Fig. 3. Depth-age model of the core LT1, Lake Chad, based on six AMS- ^{14}C measurements ages obtained on bulk organic matter. ^{14}C ages were calibrated using CALIB 6.0 (Reimer et al., 2009).

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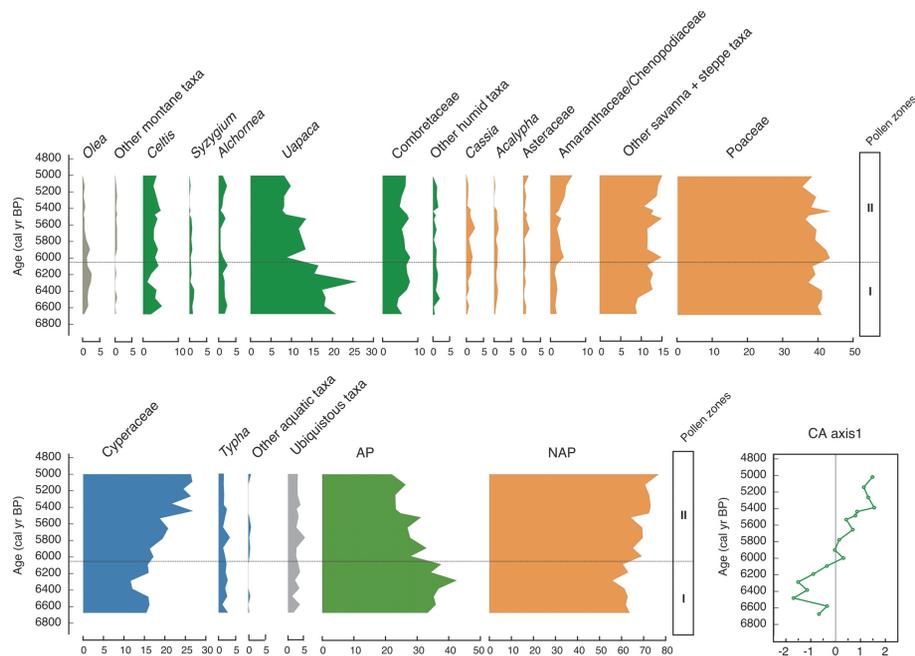


Fig. 4. Lake Chad (core LT1) synthetic pollen diagram showing relative percentages of selected taxa (the pollen sum includes all identified pollen and spore taxa, excluding indeterminate grains), and correspondence analysis (CA) performed on the pollen dataset.

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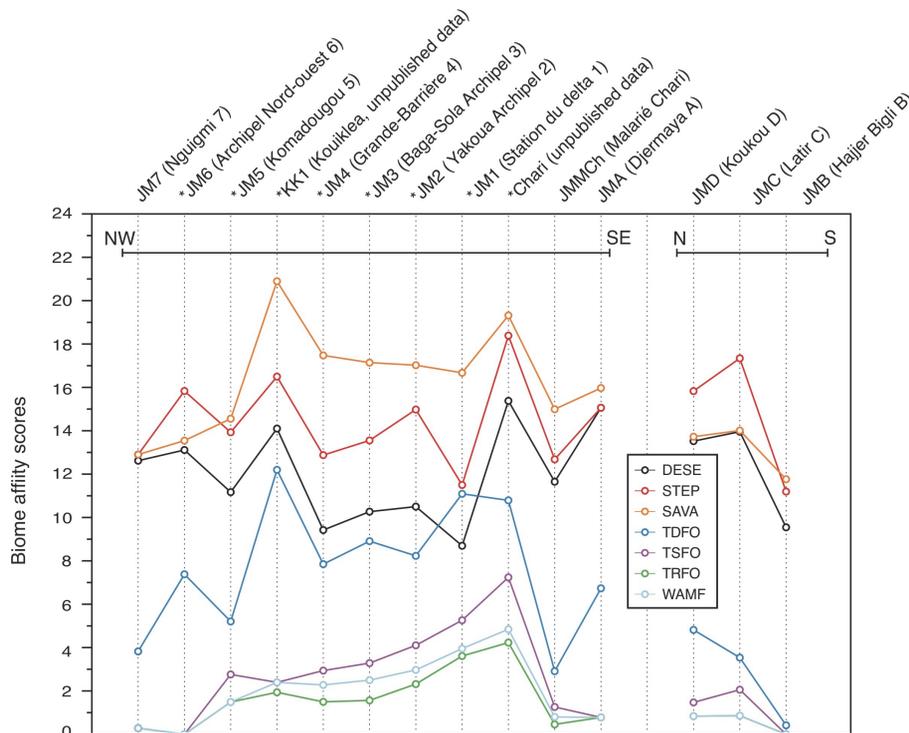


Fig. 5. Biome affinity scores derived from the modern dataset, Lake Chad. Pollen counts are from Maley (1972) and from unpublished data (CEREGE). DESE: desert; STEP: steppe; SAVA: savanna; TDFO: tropical dry forest; TSFO: tropical seasonal forest; TRFO: tropical rain forest; WAMF: warm mixed-forest.

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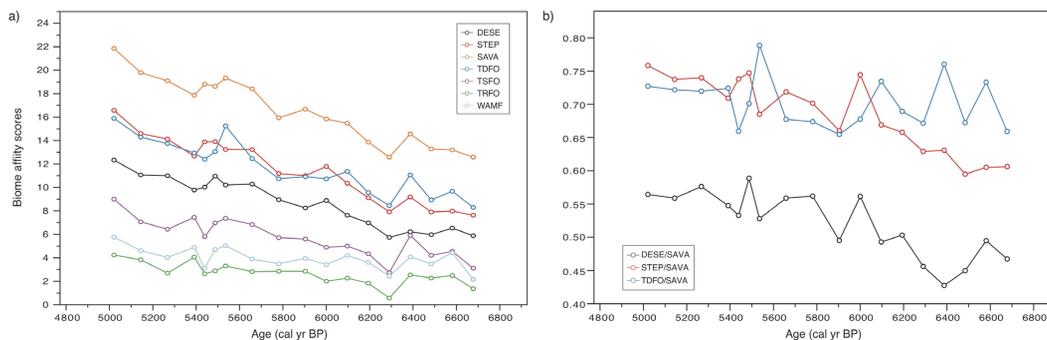


Fig. 6. Results from biomization method applied on fossil pollen data: **(a)** Biome affinity scores and **(b)** scores from drier biomes normalized by SAVA values, derived from the LT1 pollen dataset, Lake Chad (DESE: desert; STEP: steppe; SAVA: savanna; TDFO: tropical dry forest; TSFO: tropical seasonal forest; TRFO: tropical rain forest; WAMF: warm mixed-forest).

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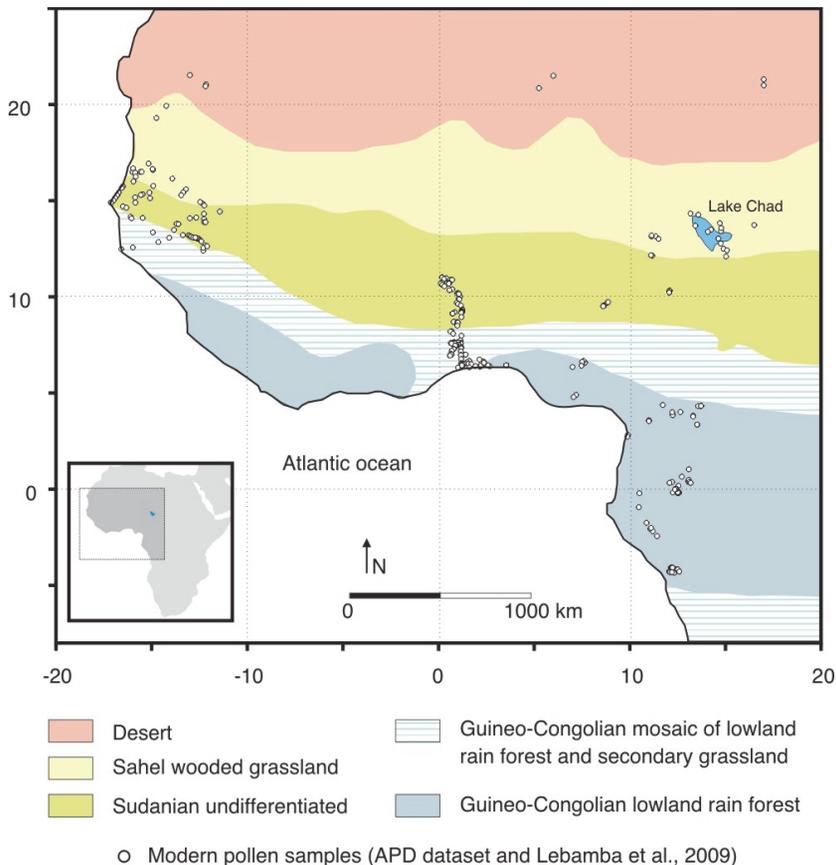


Fig. 7. Location of the modern pollen samples used in the transfer function to reconstruct mean annual rainfall values (P_{ann}) along core LT1, Lake Chad.

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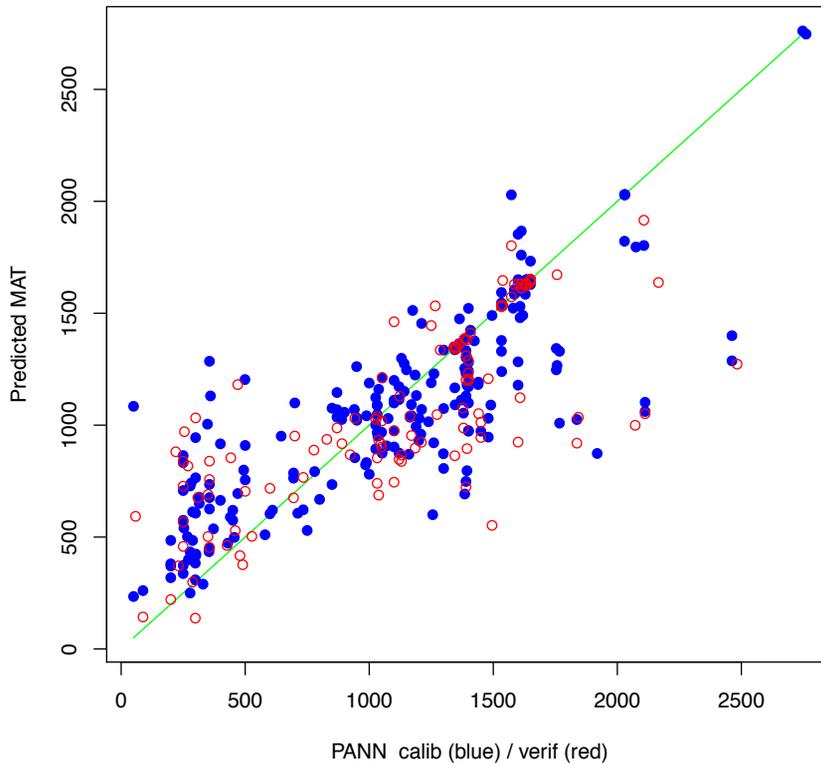


Fig. 8. Validation of the P_{ann} reconstructions performed on the modern pollen dataset from West and Central Africa.

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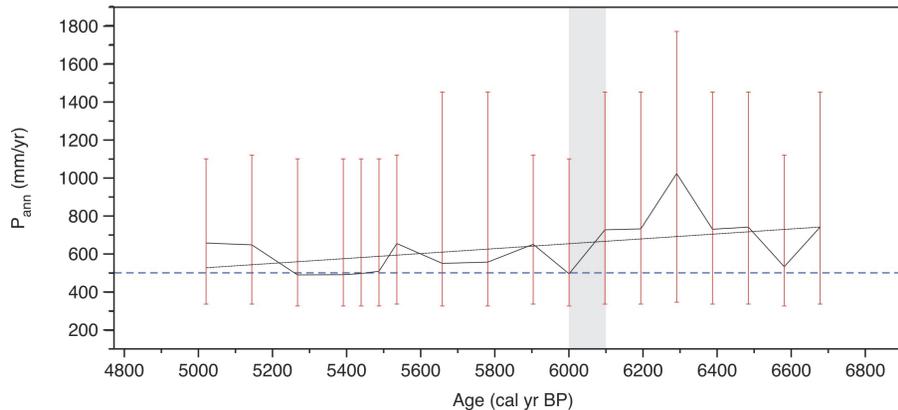


Fig. 9. Reconstructed mean annual precipitation values (P_{ann}) for the period recorded in core LT1, Lake Chad, using modern analogues technique. Dashed line represents the modern precipitation value measured at the Djamena meteorological station, red line represents the error bar of the precipitation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

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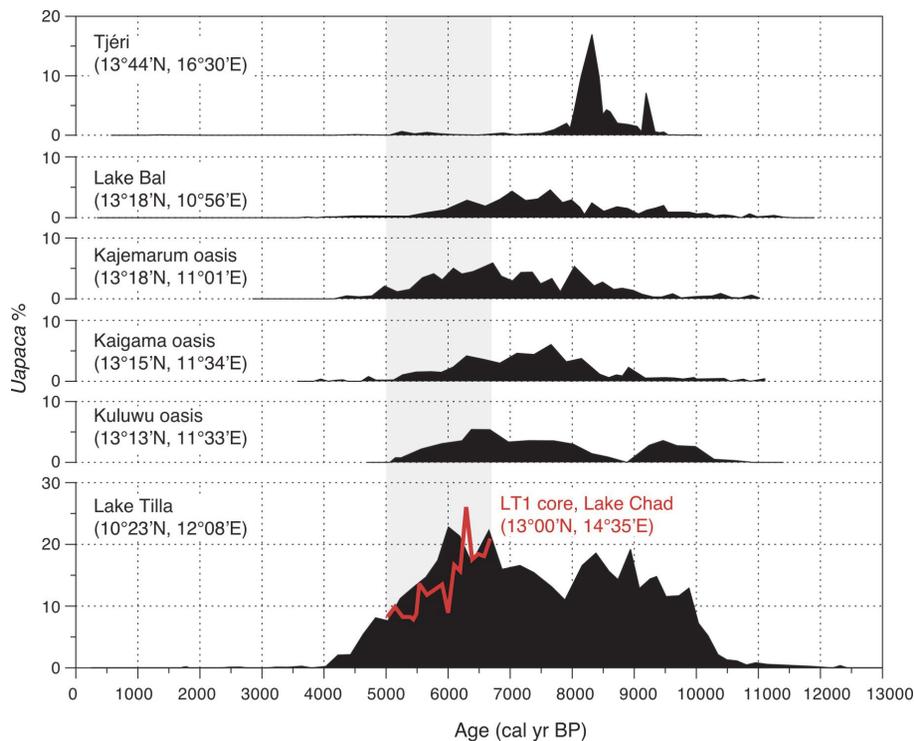


Fig. 10. Comparison between *Uapaca* frequencies from Tjéri (Maley, 1981), Lake Bal, Kajemarum, Kaigama and Kuluwu oases (Salzmann and Walter, 1998), Lake Tilla (Salzmann et al., 2002) and Lake Chad (this work). The grey band represents the time interval covered by LT1 core.

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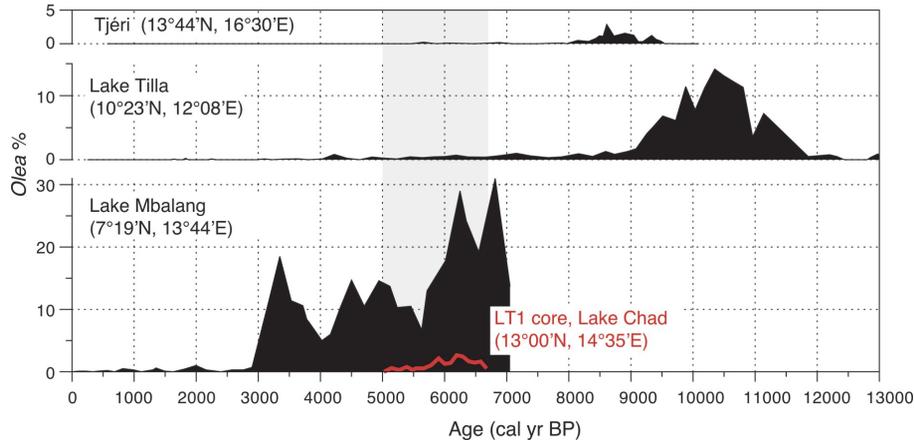


Fig. 11. Comparison between *Olea* frequencies from Tjéri (Maley, 1981), Lake Tilla (Salzmann et al., 2002), Lake Mbalang (Vincens et al., 2010) and Lake Chad (this work). The grey band represents the time interval covered by LT1 core.

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