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Forest-savannah dynamics on the Adamawa plateau (Central Cameroon) during the "African humid period" termination: A new high-resolution pollen record from Lake Tizong

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ABSTRACT

Due to its transitional position, located between the Guineo-Congolian rain forest and the Sudanian savannah, the Adamawa plateau of central Cameroon is ideally situated to record how forest and savannah composition and distribution responded to changes in climate and human interactions during the Holocene. We present a 4000-yr old pollen sequence derived from the Lake Tizong sediments (7°15′N, 13°35′E, 1160 m a.s.l) analysed at high-resolution (50 year intervals) that extends from the end of the African Humid Period to the present day. The last 4000 years represents a critical period for understanding the environmental history of the region as it covers the period when people started to have strong impact on the surrounding ecosystems. The pollen sequence distinguishes two short-duration forested phases that lasted between ca. 3900 and 3000 cal yr BP, and ca. 1900 and 1450 cal yr BP; these were against a backdrop of overall forest degradation from the mid-Holocene. A critical ecological threshold occurred around 3000 cal yr BP when Poaceae reached higher percentages than forest taxa, and savannah was established until the present day with a brief expansion of lowland semi-deciduous forest, dominated by *Myrianthus arboreus*-type, between ca. 1000 and 700 cal. yr BP. Although, human impacts and climatic factors driving vegetation change are difficult to differentiate, the late Holocene on the Adamawa plateau was characterized by a variable climate that resulted in significant vegetation transitions.

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1. Introduction

Understanding the processes and mechanisms driving ecosystem change in the tropics are subjects of increasing debate. Ecologists continue to discuss if modern forests, savannahs and grasslands respond linearly to precipitation gradients, aridity, fire disturbance and grazing pressure, or if they respond more rapidly, shifting from one ecosystem state to another (Gillson and Hoffman, 2007; Rucina et al., 2010). A growing body of evidence suggests the transition between different ecosystem states are nonlinear with instabilities governed by feedbacks at local, regional or global scales (Favier et al., 2012; Hirota et al., 2011; Mayer and Khalyani, 2011). Field observations, coupled with remote sensing techniques and modeling studies, have shown that savannah ecosystems are becoming more woody, even transitioning to forest during the last decades (Marchant, 2010; Midgley and Bond, 2015). The reasons for this rapid transition are complex: decreasing human disturbances, a rise of atmospheric CO_2 and local climate change have all been invoked to explain forest expansion with progressive coalescence of tree cover in savannah systems (Youta Happi, 1998; Achoundong, 2000; Favier et al., 2004a, 2004b; Gillson and Marchant, 2014). A forest expansion rate of 20 to 100 m yr^{-1} (i.e. between 20 and 100 km per millennium) has been estimated with a suggestion that this rate would have been faster over the Holocene (Kahn, 1982; Schwartz et al., 1996; Youta Happi, 1998; Delègue et al., 2001; Guillet et al., 2001; Favier et al., 2004b). Studies carried out in Kandara (Cameroon) and along the Congolese littoral zone show that through altering the fire regime and cultivating the understorey there has been reduced forest expansion regardless of favorable environmental conditions.

Broad scale changes in tree cover from the mid Holocene are quite well documented and the general patterns of change appear robust. From 6100 to 3000 cal yr BP, forests were replaced by savannahs near the equator (Vincens et al., 1999, 2010) whereas grasslands expanded at northern latitudes as the Sahara expanded (Hoelzmann et al., 2004; Watrin et al., 2009; Hély and Lézine, 2014). A phase of rapid environmental change, and associated ecosystem response, took place within a few centuries (Lézine et al., 2013a) that was part of a wider pan-tropical environmental shift centered around 4000 years cal yr BP (Vincens et al., 1999; Marchant and Hooghiemstra, 2004). Our understanding of forest decline is much more contested in the late Holocene: in the Guineo-Congolian lowlands a decline of mesic forest occurred ca. 3000–2500 cal yr BP as the savannah extent increased around Lake Barombi Mbo (Maley and Brenac, 1998; Lebamba et al., 2012), Lake Nguène (Giresse et al., 2008), Lake Sinnda in Congo (Vincens et al., 1994, 1998) and Lake Kitina (Elenga et al., 1996). What is lacking in our broad understanding of these late Holocene forest transitions is detail on the structure, composition and timing of ecosystem shifts. This paper presents a fine-scale reconstruction of forest and savannah dynamics in response to environmental shifts following the end of the African Humid period as recorded within sediments extracted from Lake Tizong located on the Adamawa plateau, Cameroon. The eastern Adamawa plateau, at the boundary between the Guineo-Congolian rain forest to the south, and the Sudanian savannah to the north, is ideally situated to record environmental changes linked to monsoon-driven rainfall fluctuations in the past due to the climatically sensitive nature of the location.

2. Environmental setting

Lake Tizong (7°15′N; 13°35′E, 1160 m a.s.l.) is located 8 km south of Ngaoundéré in central Cameroon (Fig. 1). This region of the Adamawa plateau belongs to the Cameroon Volcanic Line characterized by numerous lakes extending east of the Central African Republic and southwestward to the western Cameroon Highlands and the Atlantic coastal plain (Fig. 1). Lake Tizong extends over 0.8 km^2 and has a maximum water depth of 48 m (Pourchet et al., 1991). The Lake Tizong watershed extends to about 1.8 km^2 and is an ancient volcanic crater reaching 1260 m altitude. The region is located at the transition between the humid equatorial climate to the south and the tropical dry Sudano-Sahelian climate to the north that is influenced by the Adamawa plateau (Génieux, 1958). Mean annual rainfall is 1500–1600 mm yr^{-1} distributed during a continuous rainy season from April to October (Olivry, 1986). A dry season (with rainfall of <50 mm) occurs from November to March when there is increased influence of continental northeast trade winds (Suchel, 1998). The seasonal rainfall distribution is controlled by north-south migration of the Intertropical Convergence Zone (ITCZ) and its associated rain belt over this region (Suchel, 1998; Leroux, 1983, 2001). Mean annual temperature varies between 23 °C and 26 °C.

The Adamawa plateau is characterized by a highly diverse plant communities due to in part to its late Quaternary climate history (Olivry, 1986). The modern dominant biome is a wooded savannah (Letouzey, 1968, 1985; White, 1983) although combined anthropogenic pressures today (including fire, cultivation and grazing) have led to its degradation to more open herbaceous vegetation in-turn inducing increased soil erosion (Bille, 1965; Boutrais, 1974). Guineo-Congolian semi-deciduous forests ("bois de ravins", Aubréville, 1948) dissect the Adamawa plateau along permanently humid valleys. Sub-montane/montane trees (e.g. *Olea*) occur in ravines from around 1700 m on Mount Nganha (Letouzey, 1968, 1985) in restricted areas where locally humid edaphic conditions compensate for rainfall deficit during the dry season. Inside the Lake Tizong crater, the vegetation is dominated by savannah species such as *Annona senegalensis, Antidesma venosum, Bridelia ferruginea, Cussonia barteri, Entada africana, Lannea kerstingii, Maytenus senegalensis* and *Terminalia glaucescens. Sterculia tragacantha*, a semi-deciduous forest species, is also occasionally present (Tchotsoua, 2005).

3. Material and methods

A 6 m long core (T2) was recovered using a Mackereth corer (Mackereth, 1969, 1979) from the deepest part of Lake Tizong in 1998 through the ECOFIT program (IRD-CNRS-CEA). The sediment consists of dark grey homogeneous mud with fine sandy lamina. Three volcanic rich layers were identified at 582–586, 164–160 and 152–140 cm (Ngos and Giresse, 2011). The chronology was based on six radiocarbon dates obtained from organic matter; five of these are accelerator mass spectrometry (AMS) radiocarbon measurements provided by UMS-ARTEMIS (Ngos and Giresse, 2011). Calibration of the radiocarbon dates was done using CALIB 6.0.1 software (Stuiver and Reimer, 1993) and Intcal05 data (Reimer et al., 2004) (Table 1): using these ages a linear age model was constructed that indicates the Lake Tizong sediment sequence extends back to 4000 cal yr BP (Fig. 2).

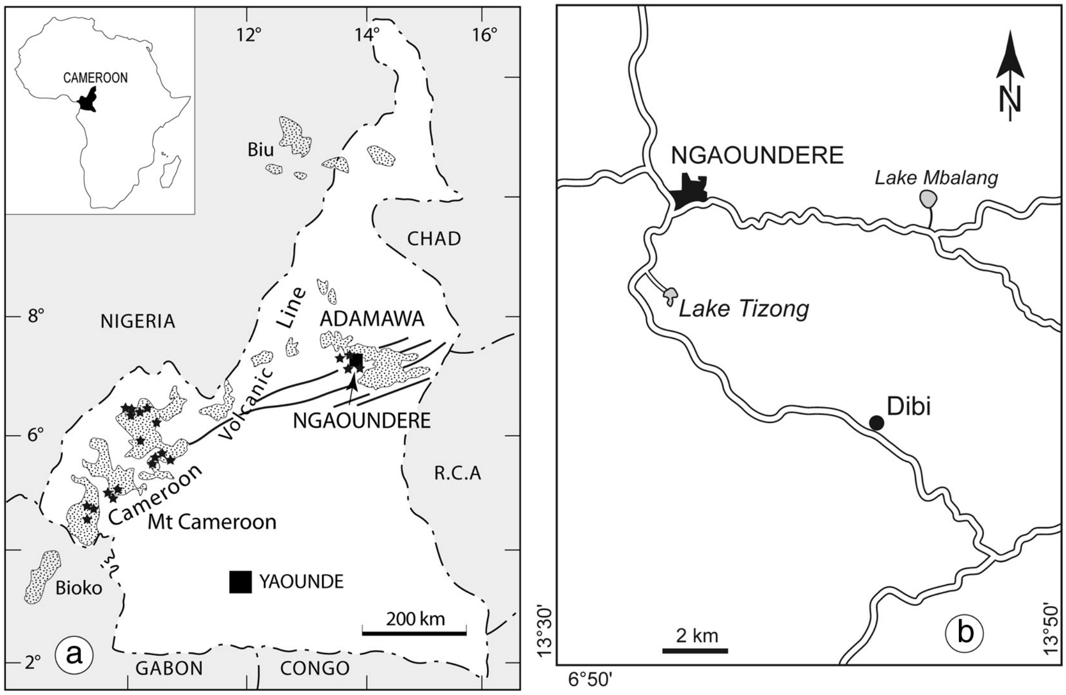

Fig. 1. (a): The Cameroon volcanic line and location of the Adamawa plateau in Cameroon; (b) location of Lake Tizong in the Ngaoundéré area, central Cameroon.

Seventy samples were analysed for pollen content from the sedimentary sequence with a sampling interval representing a mean time resolution of ca. 50 years. Samples were processed following the standard HF method (Faegri and Iversen, 1975). Pollen grains were identified using the reference collection at CEREGE (Aix-en-Provence, France), specialized publications relevant to Central and West African pollen morphology (e.g. Maley, 1970; Sowunmi, 1973, 1995; Caratini and Guinet, 1974; Ybert, 1979; Salard-Cheboldaeff, 1980-1987, 1993) and electronic photographs from the African pollen Database (APD, 2012). 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, 2012). The corresponding plant form-life and habitat of each identified pollen taxon were determined using Central African and West African botanical literature (e.g. Hutchinson and Dalziel, 1954–1972; Flore du Cameroun, 1962; Letouzey, 1968, 1985; Kahn, 1982; Lebrun and Stork, 2010). Pollen percentages were calculated based on a sum of at least 450 pollen grains and spores that excluded indeterminable pollen grains and Bryophyta spores (Fig. 3).

The biomization method, as described by Prentice et al. (1992, 1996) and applied several times in western Africa on sedimentary sequences including at Lake Barombi Mbo (Lebamba et al., 2012) and Lake Chad (Amaral et al., 2013), is based on the Plant Functional Type (PFT) concept (Smith et al., 1997). The principal steps of this methodology are: (1) Depending on the growth form of the possible parent plant each pollen taxon is assigned to one or several PFTs (groups of plants having the same ecological requirements, physiological characteristics, stature, leaf-form and climatic thresholds) to obtain a Taxa-PFTs matrix; (2) the PFTs are associated with one or several biomes; and (3) the scores of each PFT and biome in each pollen spectrum are calculated. In this paper, the assignment of taxa to PFTs is in line with the works of Lebamba et al. (2009) and Lézine (2009) in central and western Africa. The biomes considered here are Warm Mixed Forest (WAMF), Tropical Rain Forest (TRFO), Tropical Seasonal Forest (TSFO), Tropical Dry Forest (TDFO) and Savannah (SAVA).

4. Results

4.1. Lake Tizong pollen diagram

The pollen assemblages display a high taxonomic diversity with a total of 140 identified taxa (Table 2 and Fig. 3). The pollen diagram was drawn using the Psimpoll 4.10 software program (Bennett, 2012). Based on the major fluctuations composition, the pollen spectra were classified into four pollen zones (T-1 to T-4) using constrained cluster analysis by sum-of-squares (CONISS; Grimm, 1987) within the Psimpoll software program. The four pollen zones are characterized as follows.

Table 1
Radiocarbon chronology of core T2, Lake Tizong, central Cameroon. The symbol *indicates date published in Ngos et al., 2008; Ngos and Giresse, 2011.

Material	Depth (cm)	^{14}C age [yr BP]	Calibrated age [cal yr]	Calibrated age 2-σ-errors bounds	Relative area under distribution	Laboratory number
Total organic matter (TOM)	50	545 ± 30	538	515/562	0.64	SacA 19776
				594/635	0.31	
Total organic matter (TOM)	90	1040 ± 30*	1096	918/1001	0.02	Poznan University
				1031/1051	0.07	
Total organic matter (TOM)	123	1610 ± 30	1484	1412/1556	1	SacA 19777
Total organic matter (TOM)	316	2550 ± 30	2720.5	2498/2596	0.31	SacA 19779
				2612/2638	0.177	
				2692/2749	0.509	
Total organic matter (TOM)	501	3315 ± 35	3548.5	3462/3635	1	SacA 19781
Total organic matter (TOM)	600	3780 ± 50*	4105	3983/4297	0.973	
				4329/4352	0.02	Poznan University
				4371/4382	0.02	

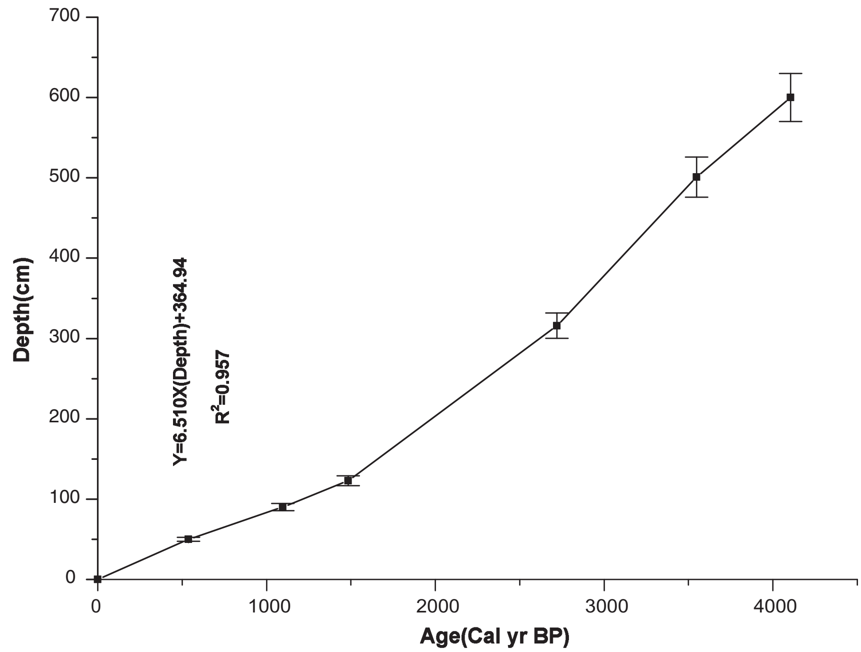

Fig. 2. Depth-age model for core T2 from Lake Tizong, central Cameroon.

4.2. Pollen zone T-1; 587.5–362 cm (ca. 4000 – ca. 3000 cal yr BP)

This zone is characterized by the highest abundance of arboreal pollen taxa, particularly between ca. 3600 and 3000 cal yr BP. The main taxa are *Podocarpus*, (5–8%), *Olea* (5–10%) and *Rubus pinnatus*-type (1–5%) associated with scarce *Schefflera*, corresponding to trees that currently occurring sub-montane/montane forests. Other forest elements such as *Celtis* (1–5%), *Mallotus oppositifolius*-type (1–4%) and *Trilepisium madagascariensis*-type (1–4%), characteristic of lowland semi-deciduous forests also present in association with evergreen forest taxa (10%) (*Sorindeia juglandifolia*-type, Sapotaceae) and forest pioneers, mainly *Alchornea* (10–13%) and *Tetrorchidium* (<1%). In addition, the savannah taxa continuously occur (5–10%), with Poaceae-type (45–55%) particularly abundant at the base of this zone. Cyperaceae pollen, derived from lake shore plant communities, account for (8%) together with swamp forest taxa increase through the zone (0–5%).

4.3. Pollen zone T-2; 362–194 cm (ca. 3000–ca. 1900 cal yr BP)

This zone is characterized by a general decrease of all the tree taxa. Poaceae undiff, which is an indicator of open and/or degraded vegetation, largely dominate (70–80%) together swamp taxa Cyperaceae (10%).

4.4. Pollen zone T-3; 194–141 cm (ca. 1900–ca. 1450 cal yr BP)

This zone is characterized by a slight increase in arboreal pollen taxa relative to Pollen zone T-2, e.g. *Rubus pinnatus*-type (2–4%), *Podocarpus* (2–5%) and *Olea* (3–6%); all derived from the montane forest, *Sorindeia juglandifolia*-type (1–3%) from the lowland evergreen forest and *Alchornea* (8–10%) from the pioneer forest. Semi-deciduous forest taxa percentages remain relatively stable with values averaging 4 to 5%. Savannah trees record a slight increase (10–11%), particularly *Hymenocardia* that reaches noticeable percentages (4–5%). Poaceae (50–60%) is characterized by a significant decrease whereas no change is observed in lake shore communities (9–10%).

4.5. Pollen zone T-4; 141–5 cm (ca. 1450 cal yr BP–present-day)

From ca. 1450 cal yr BP onwards, forest taxa percentages largely decrease whatever their origin. Among semi-deciduous forest taxa, only *Myrianthus arboreus*-type (2–7%) displays significant percentages between ca. 1000 and ca. 700 cal yr BP. In contrast, the savannah taxon *Hymenocardia* becomes more common and is regularly present throughout this zone. Poaceae (80–85%) increases to reach the maximum percentages recorded through the whole sequence. Cyperaceae (11%) increases only during the last two centuries.

4.6. Biomization

The reconstruction of down-core biomes (Fig. 4) shows that savannahs dominated the whole period from 4000 cal yr BP through to the present-day where the importance of savannahs within the landscape regularly increased from the base of the core to the top of the sequence. All the other reconstructed biomes (tropical rain forest, tropical seasonal forest, tropical dry forest and warm mixed forest) were of minor importance, and even the most mesic biomes completely disappeared during the time interval from 3000 to 2400 cal yr BP before increasing from 2000 cal yr BP to the present day. The dominant savannah biome is followed by the biomes TSFO and TDFO, whose Plants Functional Types (PFT) are dominated by taxa such as *Bridelia ferruginea*, *Hyminocardia*, *Myrianthus*, *Trema*-type, *Moraceae* and *Macaranga*; taxa all found within wooded savannah: the current Lake Tizong catchment is characterized by wooded savannah dominated by taxa such as *Bridelia ferruginea*, *Hyminocardia*, *Sterculia tragacantha*, *Terminalia glaucescens* and *Trema*-type (Tchotsoua, 2005).

5. Discussion

5.1. Chronology and development of the depth-age model

The linear model used in this study appears to be robust with sediment accumulation rates of about 57 cm year^{-1}. This model (Fig. 2) suggests that no major event has affected the sedimentation rate in the Lake Tizong catchment over the last 4000 years. Contrary to earlier studies (Ngos and Giresse, 2011; Nguetsop et al., 2013), we suggest that

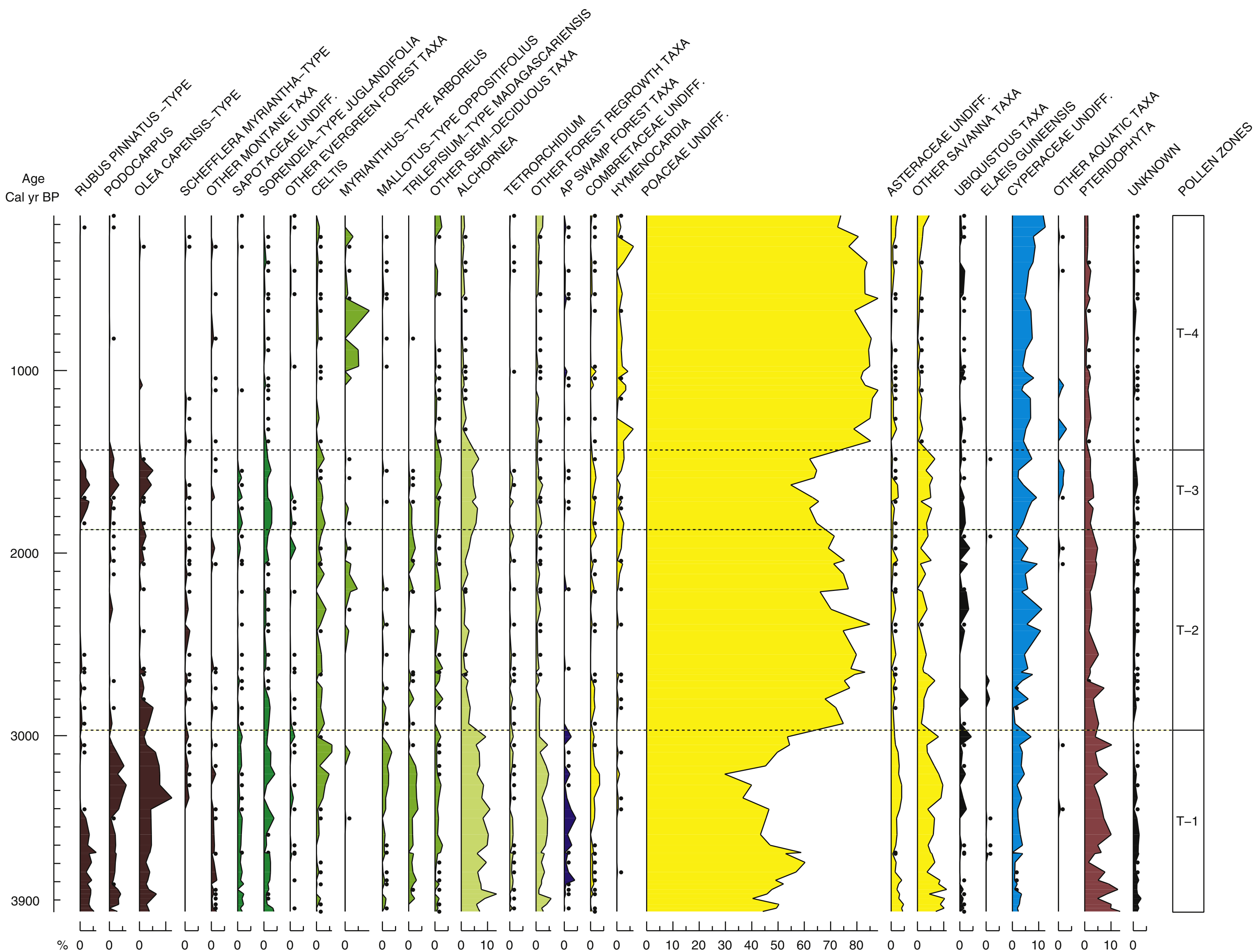

Fig. 3. Pollen diagram from T2 core from Lake Tizong, central Cameroon, showing relative percentages of selected taxa (the pollen sum includes all identified pollen and spore taxa, excluding Bryophyta and indeterminable grains. Dots represent percentages <1.)

Table 2
List of identified pollen taxa in core T2, Lake Tizong, central Cameroon,

Family	Taxa
Acanthaceae	Mimulopsis-type
Acanthaceae	Anisotes
Acanthaceae	Acanthaceae undiff.
Acanthaceae	Justicia-type flava
Alangiaceae	Alangium chinense
Amaranthaceae	Achyranthes-type aspera
Amaranthaceae	Aerva-type lanata
Amaranthaceae	Cyathula-type orthacantha
Amaranthaceae/Chenopodiaceae	Amaranthaceae/Chenopodiaceae undiff.
Anacardiaceae	Sorendeia-type juglandifolia
Anacardiaceae	Ozoroa-type
Anacardiaceae	Lannea-type
Apocynaceae	Alstonia-type boonei
Apocynaceae	Rauvolfia
Apocynaceae	Apocynaceae undiff.
Araliaceae	Polyscias fulva-type
Araliaceae	Schefflera myriantha-type
Asclepiadaceae	Tacazzea-type apiculata
Asteraceae	Vernonieae undiff.
Asteraceae	Asteraceae undiff.
Balanitaceae	Balanites
Bombacaceae	*Ceiba pentandra*
Bombacaceae	Bombax costatum-type
Boraginaceae	Cordia platythyrsa-type
Boraginaceae	Heliotropium steudneri-type
Burseraceae	Commiphora africana-type
Caesalpiniaceae	Cassia-type
Caesalpiniaceae	Cassia-type italica
Caesalpiniaceae	Isoberlinia-type
Caesalpiniaceae	Caesalpiniaceae undiff.
Campanulaceae	Wahlenbergia-type
Caryophyllaceae	Caryophyllaceae undiff.
Celastraceae	Celastraceae undiff.
Celastraceae/Hippocrateaceae	Celastraceae/Hippocrateaceae undiff.
Chrysobalanaceae	Parinari-type
Clusiaceae	Garcinia granulata-type
Combretaceae	Anogeissus-type leiocarpus
Combretaceae	Combretaceae undiff.
Combretaceae	Combretum-type molle
Combretaceae/Melastomataceae	Combretaceae/Melastomataceae undiff.
Commelinaceae	Commelina-type benghalensis
Cucurbitaceae	Cucurbitaceae undiff.
Cyperaceae	Cyperaceae undiff.
Ebenaceae	Diospyros
Euphorbiaceae	Mallotus-type oppositifolius
Euphorbiaceae	Alchornea
Euphorbiaceae	Antidesma-type venosum
Euphorbiaceae	Bridelia ferruginea-type
Euphorbiaceae	Elaeophorbia-type
Euphorbiaceae	*Flueggea virosa*
Euphorbiaceae	Macaranga-type
Euphorbiaceae	Margaritaria discoidea
Euphorbiaceae	*Ricinus communis*
Euphorbiaceae	Tetrorchidium
Euphorbiaceae	Acalypha
Euphorbiaceae	Croton-type
Euphorbiaceae	Phyllanthus-type nummulariifolius
Euphorbiaceae	Klaineanthus gaboniae
Euphorbiaceae	Uapaca
Euphorbiaceae	Euphorbiaceae undiff.
Euphorbiaceae	Phyllanthus-type
Fabaceae	Aeschynomene-type baumii
Fabaceae	Indigofera
Fabaceae	Fabaceae undiff.
Flacourtiaceae	Scottelia-type
Hymenocardiaceae	Hymenocardia
Hypericaceae	Harungana madagascariensis
Icacinaceae	Raphiostylis
Icacinaceae	Iodes
Irvingiaceae	Irvingia-type gabonensis
Lamiaceae	Lamiaceae undiff.
Lamiaceae	Leucas-type
Loganiaceae	Anthocleista
Loranthaceae	Tapinanthus-type
Meliaceae	Ekebergia-type capensis

Table 2 (*continued*)

Family	Taxa
Meliaceae	Bersama abyssinica-type
Meliaceae	Carapa-type procera
Meliaceae	Meliaceae undiff.
Meliaceae	Trichilia-type
Mimosaceae	Piptadeniastrum-type africanum
Mimosaceae	Tetrapleura tetraptera-type
Mimosaceae	Acacia groupe I
Mimosaceae	Acacia groupe III
Mimosaceae	Entada-type
Moraceae	Moraceae undiff.
Moraceae	Myrianthus-type arboreus
Moraceae	Trilepisium-type madagascariensis
Moraceae	Ficus
Myricaceae	Myrica
Myristicaceae	Pycnanthus angolensis-type
Myrtaceae	Myrtaceae undiff.
Nymphaeaceae	Nymphaea lotus-type
Ochnaceae	Campylospermum
Ochnaceae	Lophira lanceolata-type
Oleaceae	Olea capensis-type
Oleaceae	Olea europaea-type
Palmae	Borassus-type aethiopum
Palmae	Raphia
Palmae	*Elaeis guineensis*
Poaceae	Poceae undiff.,
Podocarpaceae	Podocarpus
Proteaceae	Protea-type
Pteridophyta	*Lygodium microphyllum*
Pteridophyta	Pteridium-type aquilinum
Pteridophyta	Pteridophyta undiff.
Ranunculaceae	Clematis-type
Rosaceae	Hagenia abyssinica
Rosaceae	Rubus pinnatus-type
Rubiaceae	Anthospermum
Rubiaceae	Pausinystalia-type macroceras
Rubiaceae	Gardenieae undiff.
Rubiaceae	Hymenodictyon-type floribundum
Rubiaceae	Mitragyna-type inermis
Rubiaceae	Morelia senegalensis
Rubiaceae	Pavetta gardeniifolia-type
Rubiaceae	Psydrax schimperiana-type
Rubiaceae	Rubiaceae undiff.
Rutaceae	Vepris-type
Rutaceae	Zanthoxylum-type gilletii
Sapindaceae	Pancovia-type bijugata
Sapindaceae	Ganophyllum-type giganteum
Sapindaceae	Blighia-type unijugata
Sapindaceae	*Paullinia pinnata*
Sapindaceae	Zahna golungensis-type
Sapotaceae	Sapotaceae undiff.
Solanaceae	Withania-type somnifera
Sterculiaceae	Dombeya-type
Sterculiaceae	Mansonia altissima-type
Sterculiaceae	Sterculia-type
Sterculiaceae	Triplochiton scleroxylon-type
Thymelaeaceae	Thymelaeaceae undiff.
Tiliaceae	Grewia-type
Ulmaceae	Celtis
Ulmaceae	Holoptelea grandis
Ulmaceae	Chaetacme aristata
Ulmaceae	Trema-type orientalis
Verbenaceae	Vitex-type
Vitaceae	Cissus-type qudrangularis
Vitaceae	Cyphostemma-type cyphopetalum

there was no significant drying of the lake or volcanic event in the catchment that resulted in disturbance of the sediment deposition. Indeed, Ngos et al. (2008) showed that the sedimentary sequence of a nearby core (Tizong T2) was homogeneous with only some thin strips of dark limestone and some sand micro-beds that are of volcanic origin.

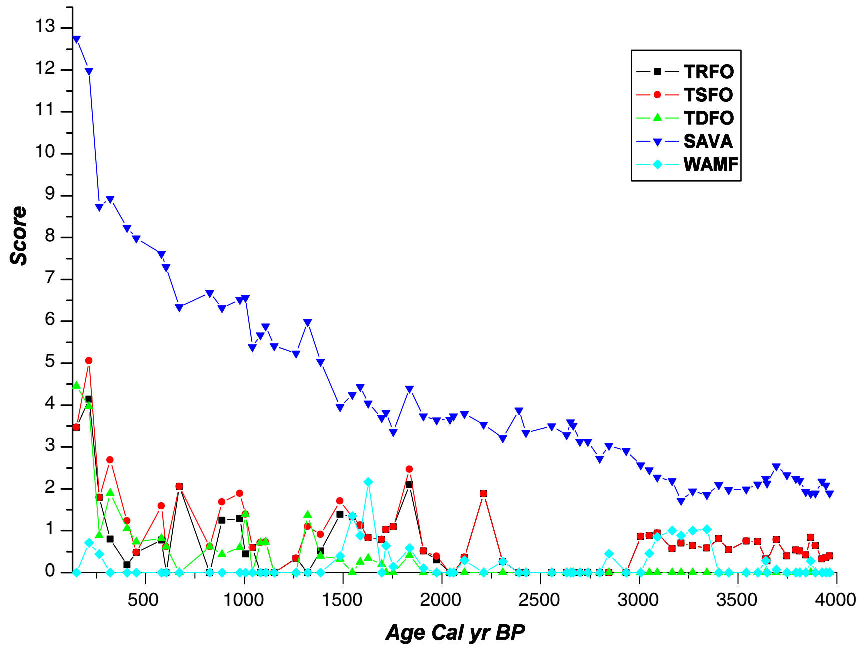

Fig. 4. Reconstructed potential biomes along the Tizong (T2) pollen sequence. TRFO (Tropical Rain Forest), TSFO (Tropical Seasonal Forest), TDFO (Tropical Dry Forest), WAMF (Warm Mixed Forest), SAVA (Savannah).

5.2. The timing of vegetation changes

There are four main periods of vegetation change within the Lake Tizong catchment

5.2.1. Between ca. 4000 and ca. 3000 cal yr BP

The regional vegetation within the Lake Tizong catchment was a mosaic containing sub-montane/montane forest, lowland semi-deciduous forest and savannah elements. The abundance of Poaceae in the pollen record is similar to that observed in the nearby Lake Mbalang (Fig. 5) during the same time interval (Vincens et al., 2010). After this 'warning signal', there is a decrease in forest pollen frequencies during three successive short-lived phases (mean of 50%, 35% and 19% over ca. 900, 600 and 450 years, respectively (Fig. 5) that indicate that forest has never been able to fully recover and that the successive forest phases were progressively reduced in density or extent. In the same way, a critical ecological versus climatic threshold (Maslin, 2004) or a so-called "tipping point" (Scheffer et al., 2009; Drake and Griffen, 2010) could have occurred ca. 3200 cal yr BP when for the last time in the Tizong and Mbalang records forest taxa and Poaceae reached similar frequencies of 40%, last experienced during the "warning signal" ca. 5600 cal yr BP (Scheffer et al., 2009) (Fig. 5). Mesic forests expanded up to 3000 cal yr BP with some characteristic WAMF trees, such as *Olea* and *Podocarpus*, and some TSFO trees, including *Celtis*, *Mallotus oppositifolius*-type and *Trilepisium madagascariensis*-type. WAMF elements are surprisingly more developed at Tizong compared to Mbalang, that are located a few kilometers apart, suggesting the presence of a forest micro-refuge near Lake Tizong (Richards, 1963).

5.2.2. Between ca. 3000 and ca. 1900 cal yr BP

Forests (TRFO, TSFO, WAMF) declined significantly at 3000 cal yr BP as grassland expanded (Fig. 4). This event occurred within a relatively short time interval (<400 years) comparable to that observed in the Cameroon Highlands (Lézine et al., 2013b). However, some humid elements of TSFO persisted within the Lake Tizong catchment after 3000 cal yr BP, particularly *Celtis* and *Myrianthus arboreus*-type. The preservation of these elements characteristic of semi-deciduous forests (Letouzey, 1968) attest to their ability resist to water stress as they lose their leaves during dry periods as a survival strategy. This event closely matches the reduced extent of tropical forest ecosystems throughout the northern tropics (Vincens et al., 1999) as tropical trees retreated from the Sahara and the Sahel (e.g. Hoelzmann et al., 2004; Watrin et al., 2009; Hély and Lézine, 2014). In some sites in the Guineo-Congolian lowlands, the decline of mesic forest occurred somewhat later ca. 3000–2500 cal yr BP such as the savannah increase around Lake Barombi Mbo (Maley and Brenac, 1998; Lebamba et al., 2012), Nguène (Giresse et al., 2008), Lake Sinnda in Congo (Vincens et al., 1994, 1998) and Lake Kitina (Elenga et al., 1996) whereas secondary forest trees expanded around Lake Mboandong (Richards, 1986), Lake Ossa (Reynaud-Farrera et al., 1996) and Nyabessam swamp in Cameroon (Ngomanda et al., 2009) at 2400 cal yr BP. In the Cameroonian uplands a forest collapse was recorded ca. 3300 cal yr BP at Lake Bambili, then forest was never able to fully recover with only subsequent minor phases of re-growth between 1600 and 800 cal yr BP (Assi-Kaudjhis et al., 2008; Lézine et al., 2013a) coeval with the discrete phase of montane forest regrowth at Lake Tizong detailed below.

5.2.3. Between ca. 1900 and ca. 1450 cal yr BP

A discrete phase of forest development is recorded within the Lake Tizong catchment between ca. 1900 and ca. 1450 cal yr BP that was characterized by an increase in WAMF elements (*Olea*, *Podocarpus* and *Rubus pinnatus*-type) in association with lowland evergreen trees and taxa of forest regrowth such as *Alchornea*. The phase of forest regrowth was coeval with volcanic eruptions detected ca. 1700 cal yr BP and between ca. 1550 and ca. 1450 cal yr BP (Ngos et al., 2008; Ngos and Giresse, 2011). Our pollen data suggest that this volcanic activity did not significantly affect the regional flora. An erosive event has also been suggested during this time interval (Nguetsop et al., 2013) that is not supported by our pollen data as the discrete expansion of montane forest recorded at Lake Tizong during this time fits into the broader context of forest expansion across the Adamawa plateau and the Cameroon Volcanic Line.

5.2.4. From ca. 1450 cal yr BP to the present

A savannah landscape was established in the Lake Tizong catchment, and also more widely in the eastern Adamawa plateau (Vincens et al., 2010). Only one single forest taxon (*Myrianthus arboreus*-type) still

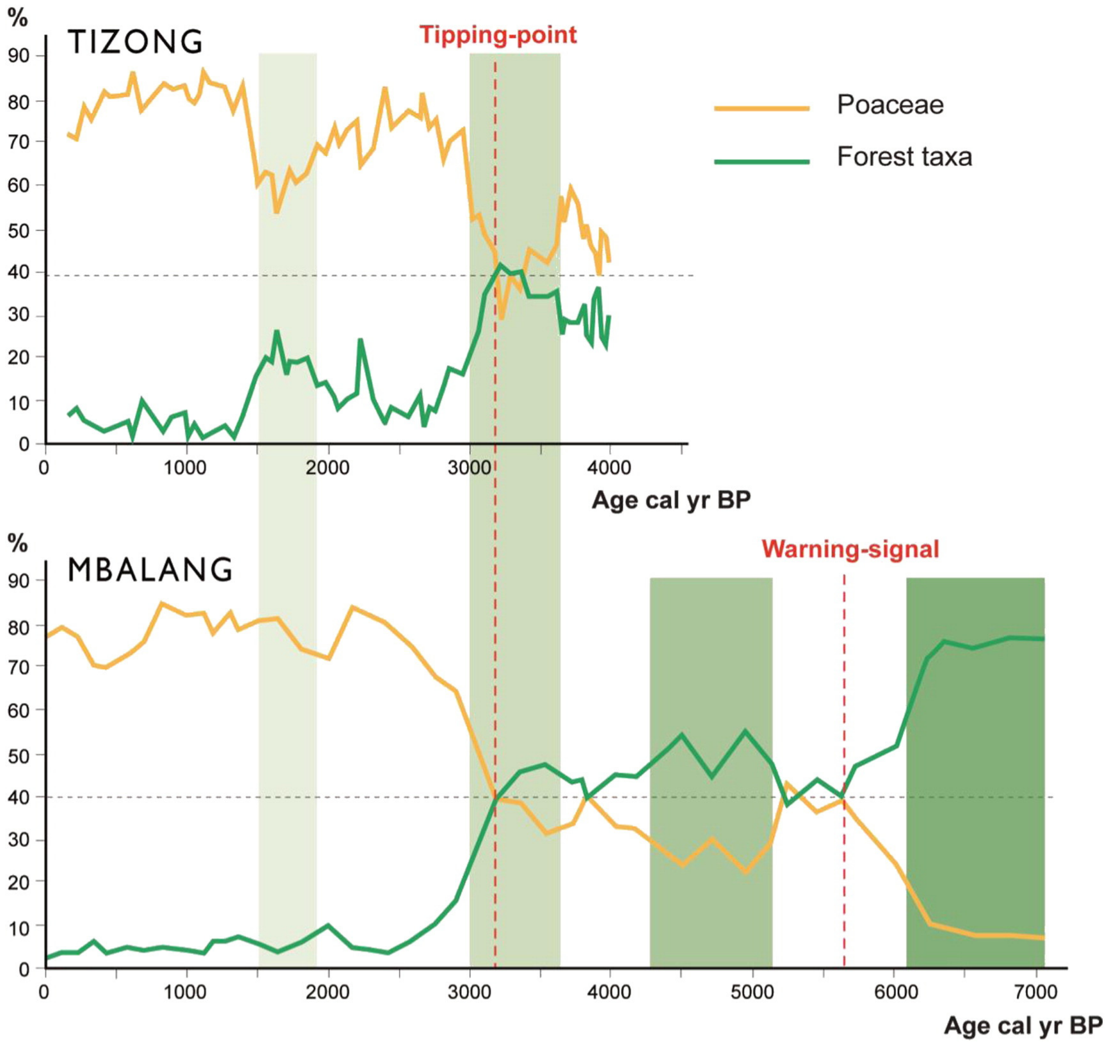

Fig. 5. Representation of total forest taxa versus Poaceae pollen frequencies in the Lake Tizong (T2) pollen sequence (this paper) and the Lake Mbalang (Vincens et al., 2010) sequences. Decreasing green indicates progressive decrease of forest in time and space.

displayed significant presence between ca. 1000 and 700 cal yr BP; this is a highly pollen productive tree of lowland semi-deciduous forest (Vincens et al., 2000), and although the evidence suggest that *Myrianthus* trees persisted in the Lake Tizong catchment they may not have been that common. In addition, some other forest elements were still present on the shores of some lakes on the Adamawa plateau, i.e. *Croton macrostachys* and *Sterculia tragacantha* at Lakes Tizong and Mbalang, or *Celtis africana* and *Lannea nigritana* at Lake Tabéré (Tchotsoua, 2005). At the same time, the sedimentation rate increased, possibly indicative of an increase in soil erosion linked to the degradation of vegetation. Anthropogenic pressures driven by human activities such as agricultural, livestock and metallurgy practices have occurred from the mid-Holocene in western and Central African savannah regions (e.g. Harlan et al., 1976; Sowunmi, 1985; Zangato and Holl, 2010) although there is no evidence of anthropogenic activity in the current pollen sequence, possibly because of the difficulties to differentiate cereals from other members of the Poaceae family based on pollen morphology.

5.3. Climatic inference

The continuous increase of the savannah biome from 4000 cal yr BP to the present day clearly indicates the progressive spread of dry conditions on the Adamawa plateau. However, the presence of forest elements from 4000 to ca. 3000 cal yr BP suggests that relatively local mesic conditions persisted. This result agrees with diatom studies on the same samples that show the lake level was high during this period (Nguetsop et al., 2013). The mosaic-like character of the regional ecosystem with abundant grasses and the presence of WAMF elements (*Olea*, *Piniathus*-type, *Podocarpus* and *Rubus*) within the forest, even as restricted populations, is indicative of a seasonal climate. A well-established dry season on the Adamawa plateau during the mid-Holocene would result from a southward shift of the northern margin of the ITCZ and the associated rainfall belt over northern tropical Africa (Ngomanda et al., 2009; Vincens et al., 2010). This shift does not necessarily indicate a latitudinal shift of the equatorial trough to the south but more probably indicates reduced amplitude in the annual migration of the ITCZ over tropical Africa (Dupont et al., 2008; Chase et al., 2009; Vincens et al., 2010). This supports the general evolution of hydro-climatic conditions over Northern Africa that shows the progressive replacement of deep freshwater lakes by swamps and wetlands from 7500 cal yr BP onward (Lézine et al., 2011). The disappearance of all the forest biomes from 3000 to 2400 cal yr BP suggests a short period of marked aridity which matches the phase of lake level instability recorded at Lakes Tizong and Ossa (Nguetsop et al., 2004; Nguetsop et al., 2013) between about 2650 and 2050 cal yr BP. Van Geel et al. (1998) indicate this arid period was driven by decreased solar activity that engendered a decrease in the production of ozone in the stratosphere (Harvey, 1980). Such a reduction in solar activity would also decrease the annual migration of the Hadley Cell, resulting in a weakened monsoon.

5.4. Environmental change

5.4.1. The end of the Holocene forest phase

Fig. 5 shows that the Lake Tizong record corroborates the general evolution of the ecosystems on the Adamawa plateau described by Vincens et al. (2010). In the Lake Mbalang catchment this was characterized by two successive phases of forest change; a first phase recorded about 6100 cal yr BP, the second phase from 3000 cal yr BP. Tree populations were probably restricted to small refuges in local permanent humid zones (valleys and lake shores) where edaphic conditions would have compensated for a deficit in rainfall while the dry season collapsed. These two successive phases are typified by a loss of about 40% of arboreal pollen types occurring within centuries. However, some semi-deciduous forest trees never disappeared from the area and persisted to the present day contrary to the montane forest taxa that declined from 3000 cal yr BP at Lake Mbalang and again from 1450 cal yr BP at Lake Tizong to reach their present-day distribution in Mount Poli, several hundred kilometers northwest of the lakes (Letouzey, 1968). The two sites from the Adamawa plateau agree well with that previously observed upward at Lake Bambili. In both cases the forest collapsed abruptly within centuries, at 3300 cal yr BP at Lake Bambili and at 3000 cal yr BP on the Adamawa plateau.

5.4.2. The last three millennia

Our biome reconstruction points to two contradictory trends: the progressive increase of the savannah biome which abruptly accelerated over the last 2500 years and the reappearance of forest mesic biomes which increased toward the top of the sequence after an interruption of about 900 years (from 1500 to 600 cal yr BP). The increase of the savannah biome may reflect the enhanced aridity that characterized the end of the Holocene Humid Period, leading to the expansion of grasslands at the expense of forest cover (deMenocal et al., 2000). However, diatom data (Nguetsop et al., 2011, 2013) suggest that the level of lakes Tizong and Mbalang where high during the last two millennia that would have facilitated the reappearance of forest around the lakes. Anthropogenic activity would also have played a role in the evolution of the landscape in the Adamawa plateau; human-induced forest disturbance has been extensively recorded from the lowlands. For example, at Lake Kamalète (Gabon) Ngomanda et al. (2007) showed a disturbance trend around 1250–520 cal yr BP with secondary forest dominated by pioneer taxa such as *Elaeis*, *Macaranga*, *Musanga* and *Tetrochidium* although it is suggested this could have been driven by a climatic cooling period coeval with the Medieval Warm Period rather than anthropogenic pressures. Indeed, diatom data from Lake Ossa (Nguetsop et al., 2004) record an arid phase between 1300 and 600 cal yr BP that was associated with a decrease in rainfall responsible for the establishment of secondary forest in southwestern Cameroon (Reynaud-Farrera et al., 1996). In addition, in western Congo, the pollen data and diatom data from Lake Kitina (Elenga et al., 1996) show the persistence of the open areas between 1340 and 490 cal yr BP, which corresponds to the arid environment. However, increased burning from 1250 cal yr BP through to the present day (Brncic et al., 2009) has been observed in the Congo Basin which suggest increased human pressure to the natural environment. Furthermore, at Lake Sinnda a drastic decline in tree taxa was observed from 1200 to 500 cal yr BP as savannah, dominated by Cyperaceae, Poaceae and Pteridophyta, is attributed to anthropogenic factors (Elenga et al., 1992; Elenga et al., 2001). On the Adamawa plateau, the oldest archaeological evidence indicative of the potential human influence on vegetation change through Iron production activities in this region dates back to ca. 4000 cal yr BP (Zangato and Holl, 2010). Edible plant remains have been found in archaeological levels dated from 4000 to ca 2000 cal yr BP (Lézine et al., 2013b). From ca. 3000 to 2000 cal yr BP onward it cannot be excluded that increased human activities through iron smelting and agricultural practices did not play a significant role in forest decline and/or degradation toward more heliophilous vegetation associations observed in the pollen record.

6. Conclusions

This study emphasises the importance of sedimentary sequences from the crater lakes on the Adamawa plateau to understand regional ecosystem change during the Holocene. The Lake Tizong sedimentary sequence, sampled at high resolution (50 years), allows us to characterize the different vegetation structure and dynamics that occurred during the Holocene. There were two main different forest stages between 3900 and 2900 cal yr BP and 1900–1450 cal yr BP that clearly confirm that the degradation of forest between 3000 cal yr BP and about 2000 cal yr BP observed in many sites in Central Africa that was not abrupt but rather a gradual progression. According to these data, it appears that this region, at the transition between the Guineo-Congolian rain forest to the south and the Sudanian savannah to the north, is a key area in northern Central Africa to understand the environmental history of these two forest formations. More high-resolution investigations and abstraction of longer sedimentary sequences gathered from crater lakes are needed to understand the clearly complex ecosystem history of the region. Particularly, understanding the interactions between human and climatic factors that affect forest composition and distribution on the Adamawa plateau should be a focal target of such future studies.

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(Adapted from Nguetsop et al., 2011)

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