

Vegetation response to the “African Humid Period” termination in Central Cameroon (7° N) – new pollen insight from Lake Mbalang

A. Vincens¹, G. Buchet¹, M. Servant², and ECOFIT Mbalang collaborators*

¹Centre Européen de Recherche et d’Enseignement des Géosciences de l’Environnement, Université Aix-Marseille, UMR6635, CNRS, CDF, IRD, BP 80, 13545 Aix-en-Provence cedex 04, France

²IRD, 32 avenue Henri Ravagnat, 93143 Bondy cedex, France

*C. Barton, S. Ngos, F. Nguetsop, S. Servant-Vildary, and M. Tchotsoua

Received: 23 November 2009 – Published in Clim. Past Discuss.: 22 December 2009

Revised: 28 April 2010 – Accepted: 29 April 2010 – Published: 4 May 2010

Abstract. A new pollen sequence from the Lake Mbalang (7°19' N, 13°44' E, 1110 m.a.s.l.) located on the eastern Adamawa plateau, in Central Cameroon, is presented in this paper to analyze the Holocene African Humid Period (AHP) termination and related vegetation changes at 7° N in tropical Africa, completing an important transect for exploring shifts in the northern margin of the African Monsoon. This sequence, spanning the last 7000 cal yr BP, shows that the vegetation response to this transitional climatic period was marked by significant successional changes within the broad context of long-term aridification. Semi-deciduous/submontane forest retreat in this area is initially registered as early as ca. 6100 cal yr BP and modern savannah was definitely established at ca. 3000 cal yr BP and stabilized at ca. 2400 cal yr BP; but a slight forest regeneration episode is observed between ca. 5200 and ca. 4200 cal yr BP. In this area with modern high rainfall, increasing in the length of the dry season during the AHP termination linked to a contraction of the northern margin of the Intertropical Convergence Zone (ITCZ) from ca. 6100 cal yr BP onward, probably associated with decreasing in cloud cover and/or fog frequency, has primarily controlled vegetation dynamics and above all the disappearance of the forested environment on the Adamawa plateau. Compared to previous studies undertaken in northern tropical and Central Africa, this work clearly shows that the response of vegetation to transitional periods between climatic extremes such as the AHP termination might be

different in timing, mode and amplitude according to the regional climate of the study sites, but also according to the stability of vegetation before and during these climatic transitions.

1 Introduction

One of the major problems in understanding the climate history of tropical environments involves the correct assessment and the identification of processes associated with transitional periods between climatic extremes. This problem is often due to the paucity of well-preserved and reliable palaeoenvironmental records. But it can also be due to uncertainties and differences in timing and amplitude of responses of tropical ecosystems to climate change according to the proxies used and their specific ecological threshold-pattern (Maslin, 2004; Jennerjahn et al., 2004; CCSP, 2009). In tropical Africa, the “African Humid Period” (AHP; deMenocal et al., 2000) termination is the last major environmental transition which has widely impacted regional ecosystems. Palaeoclimatic syntheses of northern tropical Africa show evidence that this region dramatically dried out during the mid-Holocene (6000–3000 cal yr BP) (e.g. Jolly et al., 1998; Gasse, 2000; Hoelzmann et al., 2004; Lézine, 2009), involving complete desiccation of many lakes, definitive retreat of tropical tree species and large human displacement within the Sahara associated with cultural changes from sedentary human lacustrine-tradition toward mobile pastoralist-tradition (Kuper and Kröpelin, 2006). In Central Atlantic Africa, the impact of the AHP termination was not so drastic and



Correspondence to: A. Vincens
(Vincens@cerege.fr)

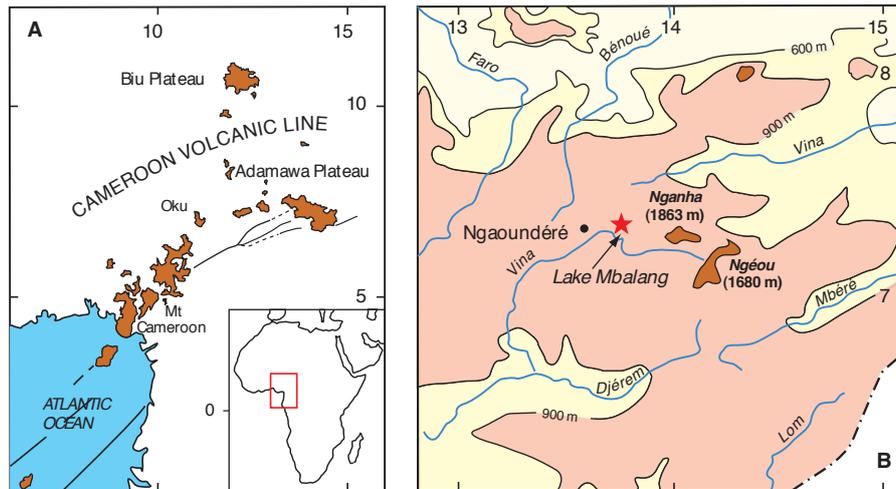


Fig. 1. (A): The Cameroon volcanic line; (B): Location of Lake Mbalang on the Adamawa plateau, Central Cameroon.

often reversible. Inside the forest massif, temporary change in the floristic composition toward more deciduous and/or secondary facies or local fragmentation of the forest including patches of savannah are evidenced (e.g. Vincens et al., 1999; Servant and Servant-Vildary, 2000; Bonnefille, 2007; Lézine, 2007) creating favourable conditions for farming and for expansion and migration of Bantu speaking populations (e.g. Schwartz, 1992; Eggert et al., 2006). But the timing, duration, mode and spatial pattern of the AHP termination are still a subject of debate.

The AHP termination, based on the analysis of a marine core off Mauritania, was identified by deMenocal et al. (2000) as very abrupt between 5700 and 5200 cal yr BP. Occurring within few decades to centuries, it was considered by these authors too rapid to be driven by a simple linear response to gradual insolation changes, known to be the main forcing of the African Monsoon (Kutzbach and Street-Perrott, 1985). This termination was widely investigated by climate modellers who tried to understand such an abrupt expression but no clear climate mechanisms fitting the palaeodata have emerged from these simulations. Some studies have concluded that strong vegetation-atmosphere feedbacks (i.e. biogeophysical feedback; Charney et al., 1975) may have amplified the abruptness of this transition (Claussen et al., 1999; Renssen et al., 2003), while others have rather shown that an abrupt change in vegetation may coincide with a gradual change in rainfall (Liu et al., 2007). More recently, new multiproxy data from the eastern Sahara show that the AHP termination was much more gradual suggesting a relatively weak biogeophysical feedback on climate and a simpler relationship with declining northern hemisphere insolation (Kröpelin et al., 2008).

In this paper we present a new continuous pollen record from the Adamawa plateau, at 7° N in Central Cameroon, recovering sediment spanning the last 7000 cal yr BP, which

well documents the response of the vegetation of this region to the AHP termination. This plateau, related to its transitional position in the northern part of the Guineo-Congolian mosaic of lowland rain forest and secondary grassland region (White, 1983), between the southern wet forested Guineo-Congolian region and the northern dry savannah Sudanian region, is a key area for a better understanding of this critical period in northern tropical Africa’s environmental history.

2 Study site

Lake Mbalang (7°19′17.53″ N, 13°44′18.73″ E, 1110 m a.s.l.) is located 15 km east of the town of Ngoundéré in Central Cameroon. This eastern region of the Adamawa plateau belongs to the Cameroon Volcanic Line which hosts numerous crater lakes and extends southwestward to the western Cameroon highlands and the Atlantic coastal plain (Fitton and Dunlop, 1985). The lake itself occupies the crater of a former volcano (maar) and has an area of 0.5 km² and a maximum depth of 52 m (Pourchet et al., 1991) (Fig. 1).

As a whole, the Ngoundéré region is situated under an altitudinal tropical climate transitional between the equatorial climate of southern Cameroon and the tropical sudano-sahelian climate of northern Cameroon (Génieux, 1958). As a function of its mean altitude of ca. 1100 m a.s.l., rainfall is high, 1500–1600 mm yr⁻¹, and mean annual temperature is about 22–23 °C. The precipitation is seasonally distributed in a single wet season from April to October. The dry season (<50 mm/month; Griffiths, 1972), is characterized by an increased influence of continental northeast trade winds (Harmattan) from the Sahara desert involving low mean annual cloud cover and fog frequencies less than 50 days/year (Suchel, 1988). Such a distribution of rainfall is controlled primarily by seasonal shifts of the Intertropical Convergence

Table 1. Radiocarbon chronology of core M4, Lake Mbalang, Central Cameroon.

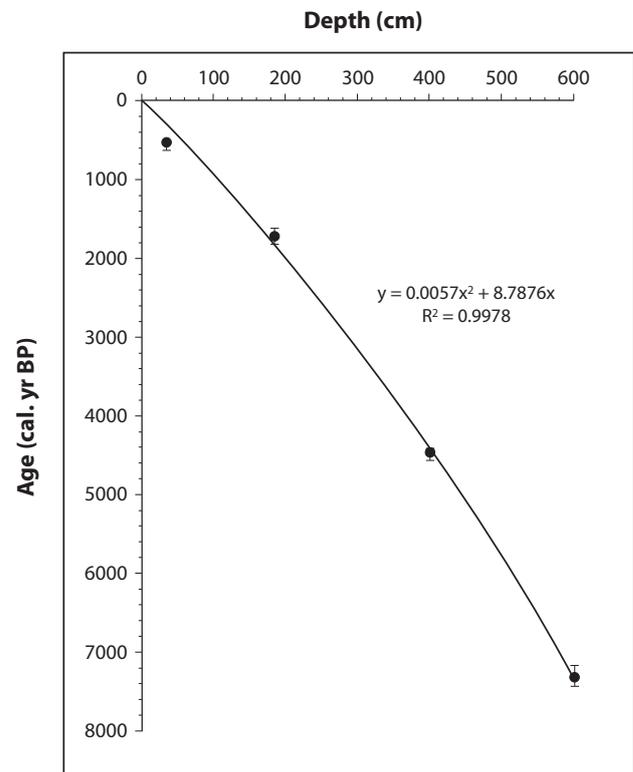
Material	Depth (cm)	¹⁴ C age [yr BP]	Calibrated age [cal yr BP]	Calibrated age 2-σ-error bounds	Relative area under distribution
TOM	35	535±35	540	509/562 594/635	0.69859 0.30141
TOM	185	1796±31	1725	1688/1820 1622/1671	0.82564 0.17436
TOM	400	4023±29	4465	4421/4536 4542/4549 4555/4568	0.94934 0.01545 0.0352
TOM	600	6400±70	7320	7234/7432 7173/7222	0.93552 0.06448

Zone (ITCZ) and its associated rain belt over this region (Suchel, 1988; Leroux, 1983, 2001).

Lake Mbalang lies today in the wooded Sudanian savannah zone described in Cameroon by Letouzey (1968, 1985) as being characterized by the presence of two main trees: *Daniella oliveri* (Caesalpiniaceae) and *Lophira lanceolata* (Ochnaceae). The proximity (ca. 100 km) of humid forests to the south provides an opportunity to study the fluctuations of the northern boundary of the Central African forest domain during the Holocene. In the framework of the “ECOSystèmes et paléocécosystèmes des Forêts InterTropicales” (ECOFIT) program, botanical inventories of tree species were performed in the Lake Mbalang area. They show the modern dominance of savannah species such as *Annona senegalensis*, *Piliostigma thonningii*, *Syzygium guineensis*, *Hymenocardia acida* around the lake as well as some forest species such as *Croton macrostachys*, *Khaya senegalensis* or forest pioneers such as *Harungana madagascariensis* (Tchotsoua, 2005).

3 Material and methods

Four 6 m long sediment cores were collected in 1998 from the deepest part of Lake Mbalang (ECOFIT program) using a compressed-air Mackereth corer (Mackereth, 1969, 1979). The core studied in this paper, M4, was recovered from the northern part of the lake, at a depth of 44 m. The cored sediments mostly consist of dark grey mud showing lamina between 5.10 and 6.0 m, and two interbedded sand layers at 0.8–1.0 m and at 5.6–5.8 m (Ngos et al., 2008). Several analyses have been carried out on this core (granulometry, mineralogy, magnetism, carbon content, diatoms). Some studies were recently published (Ngos et al., 2008), others, such as the diatoms, are in progress (Nguetsop, 2010). The chronology of the core M4 was established from four radiocarbon dates obtained on Total Organic Matter (TOM). Three dates were obtained using the Accelerator Mass Spectrometry (AMS) method at the University of Kiel (Germany),

**Fig. 2.** Depth-age model of the core M4 of Lake Mbalang, Central Cameroon.

the fourth one, at the base of the core, using the conventional method at the University of Lyon (France) (Ngos et al., 2008). In this paper, the calibration of radiocarbon dates into calendar age was made using the CALIB 5.0.1 software (Stuiver and Reimer, 1993) and the IntCal04 data (Reimer et al., 2004) (Table 1). Using this set of ages, a second-order polynomial depth-age model was established along the whole sequence (Fig. 2).

Forty-five samples, representing a mean resolution of ca. 150 years, were analysed for their pollen content. They were chemically treated following the classical method of Faegri and Iversen (1975). For each sample, at least 400 pollen grains and spores were counted. The identifications were based on the reference collection of some 7000 specimens at CEREGE, Aix-en-Provence, on specialised publications relevant to Central and West African pollen morphology (e.g. Maley, 1970; Sowunmi, 1973, 1995; A.P.L.F., 1974; Ybert, 1979; Salard-Cheboua, 1980–1987, 1993) and photographs available on the African Pollen Database (APD) web site (2010; <http://medias.obs-mip.fr/apd>). 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 (2010) for the others. The corresponding plant form-life and habitat of each pollen taxa identified were determined using West and Central African botanical literature (e.g. Hutchinson and Dalziel, 1954–1972; Flore du Cameroun, 1963–2001; Letouzey, 1968, 1985; Kahn, 1982; Lebrun and Stork, 2003, 2006) (Table 2).

4 Results

4.1 The Mbalang pollen diagram

Pollen preservation was good throughout the sequence, and the microflora was rich and well diversified, with a total of 237 taxa identified (Table 2). The results are presented in a pollen diagram (Fig. 3), which was drawn using the psimpoll 4.10 software program (Bennett, 2002). The relative percentages of each taxon or group of taxa are based on a pollen sum in which only Bryophyta (Anthocerotaceae) and indeterminate grains are excluded. Based on major fluctuations in the microfloristic composition, the pollen spectra were classified into five pollen zones (M-1 to M-5) using constrained cluster analysis by sum-of squares (CONISS; Grimm, 1987) from the psimpoll software program.

4.1.1 Pollen zone M1 (ca. 7000–ca. 6100 cal yr BP)

This zone is characterized by the maximum frequencies of regional arboreal pollen taxa recorded in the whole pollen sequence. Among sub-montane forest elements, *Olea capensis* is the dominant taxon associated with some *Podocarpus* and *Rubus pinnatus*-type. Lowland semi-deciduous (*Mallostus*-type *oppositifolius*, *Carapa*-type *procera* and *Celtis*) and regrowth (*Alchornea*, *Macaranga* and *Tetrorchidium*) forest elements are well represented. Savannah taxa are scarce, particularly grass pollen which display their minimum frequencies.

4.1.2 Pollen zone M2 (ca. 6100–ca. 5200 cal yr BP)

Grass pollen and *Pteridium*-type *aquilinum* spores increase significantly in this zone at the expense of regional arboreal taxa.

4.1.3 Pollen zone M3 (ca. 5200–ca. 4200 cal yr BP)

This zone shows a renewed increase in regional arboreal taxa, particularly those from lowland semi-deciduous forest and forest regrowth, but they never reach values higher than in pollen zone M1. Among local savannah trees, only *Hymenocardia* and *Hymenodictyon*-type *floribundum* display significant fluctuations. Grass pollen and *Pteridium*-type *aquilinum* spores decrease in abundance.

4.1.4 Pollen zone M4 (ca. 4200–ca. 3000 cal yr BP)

A slight increase in grass pollen is registered in this zone, mainly at the expense of the regional lowland semi-deciduous and regrowth forest taxa.

4.1.5 Pollen zone M5 (ca. 3000 cal yr BP–present day)

In this zone, the main feature is the regular increase in grass pollen until ca. 2400 cal yr BP associated with a new development of *Pteridium*-type *aquilinum* fern, which reach their maximum frequencies of the whole pollen sequence. Regional sub-montane forest taxa almost completely disappear ca. 3000 cal yr BP whereas lowland semi-deciduous and regrowth forest taxa decrease until ca. 2400 cal yr BP then stabilize to very low frequencies until present day. In this zone, the swamp taxon Cyperaceae shows slight indications of increased development.

4.2 Interpretations and discussion

4.2.1 Vegetation dynamics on the Adamawa plateau during the last 7000 cal yr BP

The pollen sequence from Lake Mbalang reflects vegetation changes on the eastern Adamawa plateau manifested by floristic, structural and palaeogeographic modifications during the last 7000 cal yr BP. Two environmental extremes are registered, a forest one between ca. 7000 and ca. 6100 cal yr BP and a savannah one after ca. 3000 cal yr BP, with a transitional period that corresponds in this region to the AHP termination.

A major feature of this sequence is the presence of a forested environment before ca. 6100 cal yr BP testified by the abundance of forest tree components and a very low representation of grasses and savannah trees. This forest had a complex floristic composition where both modern lowland semi-deciduous and sub-montane elements (mainly *Olea capensis*) are present. Modern lowland evergreen forest components are very scarce but according to the presence of

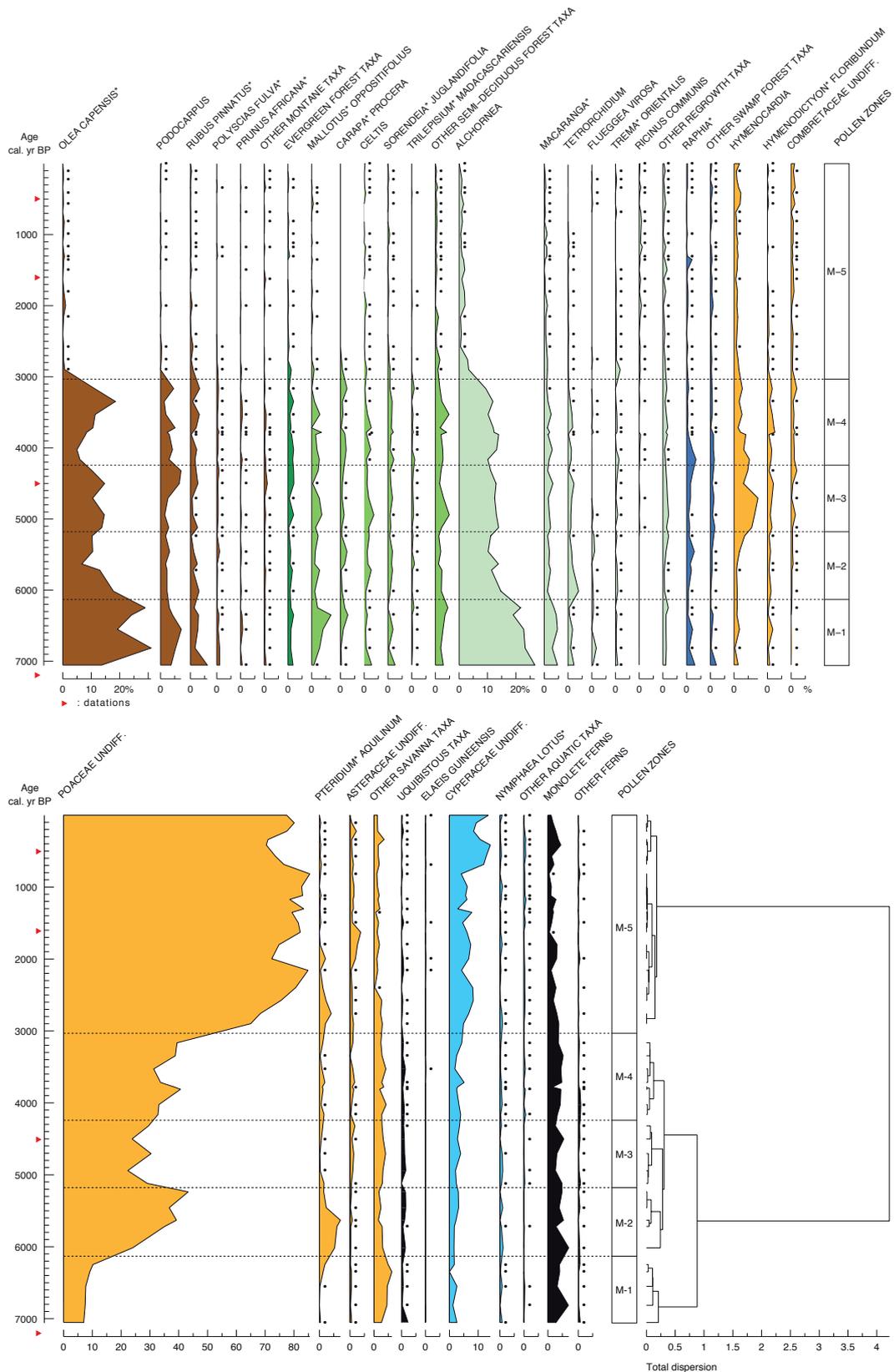


Fig. 3. The M4 pollen diagram for Lake Mbalang, Central Cameroon, showing relative percentages of selected taxa (the pollen sum includes all identified pollen and spore taxa, excluding Bryophyta and indeterminable grains. Dots are percentages <1).

Table 2. List of identified pollen taxa in core M4 from Lake Mbalang, Central Cameroon.

MONTANE TAXA
Ericaceae undiff.
<i>Alchemilla</i> (Rosaceae)
<i>Anagallis</i> (Primulaceae)
<i>Anthospermum</i> (Rubiaceae)
<i>Galium</i> -type (Rubiaceae)
<i>Hagenia abyssinica</i> (Rosaceae)
<i>Ilex mitis</i> (Aquifoliaceae)
<i>Myrica</i> (Myricaceae)
<i>Nuxia</i> -type <i>congesta</i> (Loganiaceae)
<i>Olea capensis</i> -type (Oleaceae)
<i>Olea europaea</i> -type (Oleaceae)
<i>Podocarpus</i> (Podocarpaceae)
<i>Polyscias fulva</i> -type (Araliaceae)
<i>Prunus africana</i> -type (Rosaceae)
<i>Rapanea melanophloeos</i> -type (Myrsinaceae)
<i>Rubus pinnatus</i> -type (Rosaceae)
<i>Rumex</i> (Polygonaceae)
<i>Schefflera myriantha</i> -type (Araliaceae)
<i>Stoebe kilimandscharica</i> -type (Asteraceae)
<i>Swertia</i> -type (Gentianaceae)
EVERGREEN FOREST TAXA
<i>Aidia</i> -type <i>micrantha</i> (Rubiaceae)
<i>Alstonia</i> -type <i>boonei</i> (Apocynaceae)
<i>Anthostema</i> -type (Euphorbiaceae)
<i>Argomuelleria macrophylla</i> -type (Euphorbiaceae)
<i>Begonia</i> (Begoniaceae)
Caesalpiniaceae undiff.
<i>Cyathogyne</i> (Euphorbiaceae)
<i>Dacryodes</i> -type (Burseraceae)
<i>Diospyros</i> (Ebenaceae)
<i>Garcinia granulata</i> -type (Clusiaceae)
<i>Hymenostegia</i> -type <i>pellegrinii</i> (Caesalpiniaceae)
Meliaceae undiff.
<i>Pancovia</i> -type <i>bijugata</i> (Sapindaceae)
<i>Pausinystalia</i> -type <i>macroceras</i> (Rubiaceae)
<i>Petersianthus</i> -type <i>macrocarpus</i> (Lecythidaceae)
<i>Raphiostylis</i> (Icacinaeae)
<i>Santiria</i> -type <i>trimera</i> (Burseraceae)
Sapotaceae undiff.
<i>Sherbournia bignoniifolia</i> -type (Rubiaceae)
<i>Sorendeia</i> -type <i>juglandifolia</i> (Anacardiaceae)
<i>Strombosia</i> -type (Olacaceae)
<i>Vepris</i> -type (Rutaceae)
SEMI-DECIDUOUS FOREST TAXA
<i>Alangium chinense</i> -type (Alangiaceae)
<i>Anisotes</i> (Acanthaceae)
<i>Antrocaryon</i> -type (Anacardiaceae)
<i>Campylospermum</i> (Ochnaceae)
<i>Carapa</i> -type <i>procera</i> (Meliaceae)
<i>Ceiba pentandra</i> (Bombacaceae)
<i>Celtis</i> (Ulmaceae)
<i>Cola cordifolia</i> -type (Sterculiaceae)
<i>Cordia platythyrsa</i> -type (Boraginaceae)

Table 2. Continued.

SEMI-DECIDUOUS FOREST TAXA (continued)
<i>Detarium senegalense</i> -type (Caesalpiniaceae)
<i>Funtumia</i> -type (Apocynaceae)
<i>Ganophyllum</i> -type <i>giganteum</i> (Sapindaceae)
<i>Garcinia staudtii</i> -type (Clusiaceae)
<i>Holoptelea grandis</i> (Ulmaceae)
<i>Hylodendron gabunense</i> (Caesalpiniaceae)
<i>Irvingia</i> -type <i>gabonensis</i> (Irvingiaceae)
<i>Mallotus</i> -type <i>oppositifolius</i> (Euphorbiaceae)
<i>Mansonia altissima</i> -type (Sterculiaceae)
<i>Mendoncia</i> (Acanthaceae)
<i>Milicia</i> -type <i>excelsa</i> (Moraceae)
Moraceae undiff.
<i>Myrianthus</i> -type <i>arboreus</i> (Moraceae)
<i>Neoboutonia</i> -type <i>melleri</i> (Euphorbiaceae)
<i>Oncinotis</i> -type (Apocynaceae)
<i>Piptadeniastrum</i> -type <i>africanum</i> (Mimosaceae)
<i>Pycnanthus angolensis</i> -type (Myristicaceae)
<i>Rauvolfia</i> (Apocynaceae)
<i>Serichostachys</i> -type <i>scandens</i> (Amaranthaceae)
<i>Sterculia</i> -type (Sterculiaceae)
<i>Tabernaemontana</i> -type <i>crassa</i> (Apocynaceae)
Thymelaeaceae undiff.
<i>Trilepisium</i> -type <i>madagascariensis</i> (Moraceae)
<i>Triplochiton scleroxylon</i> -type (Sterculiaceae)
<i>Uncaria</i> -type <i>africana</i> (Rubiaceae)
<i>Zanthoxylum</i> -type <i>gilletii</i> (Rutaceae)
<i>Zanthoxylum</i> -type <i>zanthoxyloides</i> (Rutaceae)
SWAMP FOREST TAXA
<i>Aphania</i> -type <i>senegalensis</i> (Sapindaceae)
<i>Bersama abyssinica</i> -type (Meliaceae)
<i>Cleistanthus</i> -type <i>polystachyus</i> (Euphorbiaceae)
<i>Cyathea manniana</i> -type (Cyatheaceae)
<i>Guibourtia demeusei</i> -type (Caesalpiniaceae)
<i>Klaineanthus gaboniae</i> (Euphorbiaceae)
<i>Pandanus</i> (Pandanaeae)
<i>Phoenix reclinata</i> -type (Palmae)
<i>Raphia</i> (Palmae)
<i>Symphonia globulifera</i> (Clusiaceae)
<i>Uapaca</i> (Euphorbiaceae)
FOREST REGROWTH TAXA
<i>Alchornea</i> (Euphorbiaceae)
<i>Anthocleista</i> (Loganiaceae)
<i>Asystasia gangetica</i> -type (Acanthaceae)
<i>Blighia</i> -type <i>unijugata</i> (Sapindaceae)
<i>Bridelia ferruginea</i> -type (Euphorbiaceae)
<i>Chaetacme aristata</i> (Ulmaceae)
<i>Clausena anisata</i> (Rutaceae)
<i>Clematis</i> -type (Ranunculaceae)
<i>Dioscorea dumetorum</i> -type (Dioscoreaceae)
<i>Elaeophorbia</i> -type (Euphorbiaceae)
<i>Flabellaria</i> -type <i>paniculata</i> (Malpighiaceae)
<i>Flueggea virosa</i> (Euphorbiaceae)
<i>Harungana madagascariensis</i> (Hypericaceae)
<i>Lygodium microphyllum</i> (Schizaeaceae)

Table 2. Continued.

FOREST REGROWTH TAXA (continued)
<i>Macaranga</i> -type (Euphorbiaceae)
<i>Margaritaria discoidea</i> (Euphorbiaceae)
<i>Phaulopsis</i> -type <i>imbricata</i> (Acanthaceae)
<i>Ricinus communis</i> (Euphorbiaceae)
<i>Stephania</i> -type <i>abyssinica</i> (Menispermaceae)
<i>Tacazzea</i> -type <i>apiculata</i> (Asclepiadaceae)
<i>Tetrapleura tetraptera</i> -type (Mimosaceae)
<i>Tetrorchidium</i> (Euphorbiaceae)
<i>Trema</i> -type <i>orientalis</i> (Ulmaceae)
Urticaceae undiff.
Vernonieae undiff.
<i>Virectaria</i> (Rubiaceae)
SAVANNA TAXA
<i>Acacia</i> groupe I (Mimosaceae)
<i>Acacia</i> groupe III (Mimosaceae)
<i>Acalypha</i> (Euphorbiaceae)
Acanthaceae undiff.
<i>Achyranthes</i> -type <i>aspera</i> (Amaranthaceae)
<i>Acridocarpus</i> (Malpighiaceae)
<i>Adansonia digitata</i> (Bombacaceae)
<i>Adenia venenata</i> -type (Passifloraceae)
<i>Aerva</i> -type <i>lanata</i> (Amaranthaceae)
<i>Aeschynomene</i> -type <i>baumii</i> (Fabaceae)
<i>Albizia</i> (Mimosaceae)
Amaranthaceae/Chenopodiaceae undiff.
<i>Anogeissus</i> -type <i>leiocarpus</i> (Combretaceae)
<i>Antidesma</i> -type <i>venosum</i> (Euphorbiaceae)
Apiaceae undiff.
Asteraceae undiff.
<i>Bombax costatum</i> -type (Bombacaceae)
<i>Borassus</i> -type <i>aethiopum</i> (Palmae)
Brassicaceae undiff.
<i>Cassia</i> -type (Caesalpiniaceae)
<i>Cassia</i> -type <i>italica</i> (Caesalpiniaceae)
<i>Cassia</i> -type <i>occidentalis</i> (Caesalpiniaceae)
<i>Celosia</i> -type <i>trigyna</i> (Amaranthaceae)
Chenopodiaceae undiff.
Cichorieae undiff.
<i>Cissampelos</i> -type <i>mucronata</i> (Menispermaceae)
<i>Cissus</i> -type <i>quadrangularis</i> (Vitaceae)
<i>Combretum</i> -type <i>molle</i> (Combretaceae)
Combretaceae undiff.
<i>Commelina</i> -type <i>benghalensis</i> (Commelinaceae)
<i>Commiphora africana</i> -type (Bursseraceae)
<i>Croton</i> -type (Euphorbiaceae)
Cucurbitaceae undiff.
<i>Cussonia arborea</i> -type (Araliaceae)
<i>Cyathula</i> -type <i>orthacantha</i> (Amaranthaceae)
<i>Cyphostemma</i> -type <i>cyphopetalum</i> (Vitaceae)
<i>Dichrostachys cinerea</i> -type (Mimosaceae)
<i>Dombeya</i> -type (Sterculiaceae)
<i>Ehretia</i> (Boraginaceae)
<i>Entada</i> -type (Mimosaceae)
<i>Faidherbia</i> -type <i>albida</i> (Mimosaceae)
Gardenieae undiff.

Table 2. Continued.

SAVANNA TAXA (continued)
<i>Grewia</i> -type (Tiliaceae)
<i>Guizotia</i> -type <i>abyssinica</i> (Asteraceae)
<i>Heliotropium steudneri</i> -type (Boraginaceae)
<i>Hymenocardia</i> (Hymenocardiaceae)
<i>Hymenodictyon</i> -type <i>floribundum</i> (Rubiaceae)
<i>Hypoestes</i> -type <i>aristata</i> (Acanthaceae)
<i>Indigofera</i> (Fabaceae)
<i>Ipomoea</i> -type (Convolvulaceae)
<i>Isobertinia</i> -type (Caesalpiniaceae)
<i>Justicia</i> -type <i>flava</i> (Acanthaceae)
<i>Kedrostis</i> -type (Cucurbitaceae)
<i>Keetia</i> -type <i>gueinzii</i> (Rubiaceae)
<i>Kigelia africana</i> (Bignoniaceae)
<i>Kotschya africana</i> -type (Fabaceae)
Lamiaceae undiff.
<i>Lansea</i> -type (Anacardiaceae)
<i>Lantana</i> -type <i>ukambensis</i> (Verbenaceae)
<i>Lantana</i> -type <i>viburnoides</i> (Verbenaceae)
<i>Lepidagathis sericea</i> -type (Acanthaceae)
<i>Leucas</i> -type (Lamiaceae)
<i>Lophira lanceolata</i> -type (Ochnaceae)
<i>Macrosphyra</i> -type (Rubiaceae)
<i>Maesa lanceolata</i> -type (Myrsinaceae)
<i>Merremia</i> -type <i>hederacea</i> (Convolvulaceae)
<i>Micrococca</i> -type <i>mercurialis</i> (Euphorbiaceae)
<i>Mitracarpus villosus</i> (Rubiaceae)
<i>Mitragyna</i> -type <i>inermis</i> (Rubiaceae)
<i>Morelia senegalensis</i> (Rubiaceae)
<i>Parinari</i> -type (Chrysobalanaceae)
<i>Pavetta gardeniifolia</i> -type (Rubiaceae)
<i>Phyllanthus</i> -type <i>nummulariifolius</i> (Euphorbiaceae)
<i>Piliostigma thonningii</i> -type (Caesalpiniaceae)
Poaceae undiff.
<i>Protea</i> -type (Proteaceae)
<i>Psyrax schimperiana</i> -type (Rubiaceae)
<i>Pteridium</i> -type <i>aquilinum</i> (Pteridaceae)
<i>Shirakia</i> -type <i>elliptica</i> (Euphorbiaceae)
<i>Sida</i> -type (Malvaceae)
<i>Solanum</i> -type (Solanaceae)
<i>Spermacoce</i> -type (Rubiaceae)
<i>Syzygium</i> -type <i>guineensis</i> (Myrtaceae)
<i>Trichilia</i> -type (Meliaceae)
<i>Vangueria</i> -type <i>madagascariensis</i> (Rubiaceae)
<i>Zahna golungensis</i> -type (Sapindaceae)
UBIQUISTOUS TAXA
<i>Allophylus</i> (Sapindaceae)
Apocynaceae undiff.
Celastraceae undiff.
Celastraceae/Hippocrateaceae undiff.
Combretaceae/Melastomataceae undiff.
Convolvulaceae undiff.
Euphorbiaceae undiff.
Fabaceae undiff.
<i>Ficus</i> (Moraceae)
Leguminosae undiff.

Table 2. Continued.

UBIQUISTOUS TAXA (continued)
Lycopodiaceae undiff.
Monocotyledonae undiff.
Myrtaceae undiff.
<i>Phyllanthus</i> -type (Euphorbiaceae)
Rhamnaceae undiff.
Rubiaceae undiff.
<i>Tapinanthus</i> -type (Loranthaceae)
Tiliaceae undiff.
Pteridophyta undiff.
AQUATICS
<i>Crinum natans</i> -type (Amaryllidaceae)
Cyperaceae undiff.
Eriocaulaceae undiff.
<i>Heterotis</i> -type <i>canescens</i> (Melastomataceae)
<i>Hydrocotyle manii</i> -type (Apiaceae)
<i>Hygrophila</i> (Acanthaceae)
<i>Impatiens</i> (Balsaminaceae)
<i>Limnophyton</i> -type <i>obtusifolium</i> (Alismataceae)
Melastomataceae undiff.
<i>Mimosa pigra</i> -type (Mimosaceae)
<i>Nymphaea lotus</i> -type (Nymphaeaceae)
Onagraceae undiff.
<i>Polygonum senegalense</i> -type (Polygonaceae)
<i>Potamogeton thunbergii</i> -type (Potamogetonaceae)
<i>Stipularia africana</i> -type (Rubiaceae)
<i>Typha</i> (Typhaceae)
<i>Utricularia inflexa</i> -type (Lentibulariaceae)
CULTIVATED TAXA
<i>Elaeis guineensis</i> (Palmae)

numerous regrowth or secondary forest trees, this forested environment is unlikely to have been either mature or stable during this period.

– The semi-deciduous forest facies

Before ca. 6100 cal yr BP, the semi-deciduous facies of this forest was closely related in terms of its floristic composition to the forest that is found today at the northern limit of the Guineo-Congolian forest massif in South Central Cameroon about 100 km southward of Lake Mbalang. Thus, a latitudinal shift of at least 100 km northward of the modern boundary of the Guineo-Congolian forest can be assumed during the African Humid Period. Modern lowland forest species probably first enter the Adamawa plateau at the beginning of this humid period as gallery formations along rivers such as it has been shown for tropical elements in Sahelian and Saharan regions (Watrin et al., 2009). But, contrary to these drier regions, the scarcity

of savannah elements and grasses around Lake Mbalang between ca. 7000 and ca. 6100 cal yr BP testifies that the forest also largely extended on the plateau on well-drained soils. Such a feature has long been suggested by botanists such as Letouzey (1968) but without an indication of the precise timing. At the same moment, around the closest pollen site of Lake Tilla, on the Biu plateau of northeastern Nigeria (10°23' N, 12°08' E, 690 m a.s.l.) (Fig. 1), Guineo-Congolian elements are present but high frequencies of grasses (>50%) indicate a dominance of savannah type vegetation, although a potential Tropical Seasonal Forest (TSFO) biome was reconstructed at ca. 6000 cal yr BP (Hély et al., 2009). Humid tree elements were probably only localized around the lake, however, where they benefited from permanent fresh water (Salzmann, 2000; Salzmann et al., 2002).

Following this semi-deciduous forested environment, a first slight deterioration is observed between ca. 6100 and ca. 5200 cal yr BP, marked by an increase of grasses testifying local openings in the forest, and by the presence of *Pteridium aquilinum*, a fern which is mainly present today in the herbaceous ecotone between forest and savannah, in forest clearings and other disturbed areas (Youta Happi, 1998; Verdcourt, 2000). The forest then locally regenerates until ca. 4200 cal yr BP, but as indicated by the regular significant presence of grasses and the occurrence of local wooded savannah with *Hymenocardia* and *Hymenodictyon*, it never reaches the density/continuity of pre-6100 cal yr BP. From ca. 4200 cal yr BP, savannah expands at the expense of the semi-deciduous forest which could have persisted only in the form of patches on well drained soils or in favourable edaphic environments such as ravines, where some elements are still present today (Letouzey, 1968). At approximately 3000 cal yr BP, the savannah becomes for the first time the dominant formation in the landscape of the Lake Mbalang area, and certainly characterises the vegetation from ca. 2400 cal yr BP onward as testified by the constant high frequencies of grass pollen (>50%). At the same time, herbaceous swamp formations dominated by Cyperaceae slightly develop on the shores of the lake.

– The sub-montane forest facies

Before ca. 6100 cal yr BP, the abundance of the sub-montane tree *Olea capensis* (14 to 30%) described by White (1983) as an ecological transgressor from upland to lowland areas, and above all its long persistence until ca. 3000 cal yr BP with significant frequencies (around 10%) is very peculiar to this region. Indeed, in the Lake Tilla sequence *Olea capensis* (synonym of *Olea hochstetteri*) is present, but only between ca. 11 200 and ca. 9500 cal yr BP before becoming scarce (Salzmann, 2000; Salzmann et al., 2002). It has also been found further north at Lake Chad (Maley, 1981) during the Last Glacial-Interglacial Transition (LGIT; ca. 18 000–11 500 cal yr BP), to the west in the pollen

sequence from Lake Bosumtwi (Ghana) from ca. 17 000 until ca. 9500 cal yr BP (Maley and Livingstone, 1983), and to the south at Lake Barombi Mbo before ca. 14 000 cal yr BP (Maley and Brenac, 1998) and in the Bilanko depression (Batéké plateau, Congo) ca. 12 500 cal yr BP (Elenga et al., 1991). At these sites, however, the maximum pollen frequencies are always lower than at Lake Mbalang, except at certain levels at Lake Barombi Mbo, and are mainly recorded during the glacial period and the LGIT, before the African Humid Period. Today, on the eastern Adamawa plateau the nearest population of *Olea capensis* is located 35 km east of Lake Mbalang, in ravine forests on Mount Nganha (7°22' N, 14°01' E, 1863 m) (Letouzey, 1968) (Fig. 1). Such a modern geographical proximity associated with the altitudinal position of Lake Mbalang ca. 1100 m a.s.l. could have allowed a large development and the persistence of *Olea capensis* near the site during the African Humid Period. It can be excluded that pollen of *Olea capensis* was transported by rivers because this crater lake has never had any inlet (Ngos et al., 2008). In return, related to their low frequencies, other montane taxa such as *Podocarpus* and *Rubus pinnatus* remained a part of the regional environment of the lake, the first one still occurring today on Mount Poli, 150 km northwest of Lake Mbalang (Letouzey, 1968).

From ca. 6100 to ca. 3000 cal yr BP, *Olea capensis* persists near Lake Mbalang, but it is less developed than during the early Holocene indicating a decline of the former population probably linked to unfavourable conditions to its regeneration. After ca. 3000 cal yr BP it rapidly retreats to higher altitude as shown by the modern population of *Olea capensis* on Mount Nganha which would constitute today a relictual station of a former and larger extension of this element on the Adamawa plateau. In Central Africa, such a recent rapid retreat of sub-montane and montane elements ca. 3000 cal yr BP, mainly *Olea capensis* and *Podocarpus*, has been previously observed in pollen sequences from mid-altitude at Bafounda swamp, 7 km to the north of Bafoussam in western Cameroon (Tamura, 1990), at Lake Barombi Mbo (Maley and Brenac, 1998) and also at lower altitude, near the coast at Lake Ossa (Reynaud-Farrera, 1995; Reynaud-Farrera et al., 1996).

4.2.2 Climate and importance of rainfall seasonality in vegetation dynamics on the eastern Adamawa plateau during the last 7000 cal yr BP

Today in south-central Cameroon, semi-deciduous forest maintains and regenerates under rainfall of 1500 mm yr⁻¹ (Letouzey, 1968; Suchel, 1988; Youta-Happi, 1998; Achoundong, 2000; Hély et al., 2006; Lézine et al., 2009), but the main climatic parameter which might prevent such a dynamic is the length of the dry season which must not exceed 3 months. Moreover, in this region mean annual cloud cover and fog frequencies (between 50 and 100 days/year) are slightly higher than on the Adamawa plateau (Suchel,

1988). Concerning *Olea capensis*, this sub-montane tree is found in transitional and upland dry forest, between 1000 and 2600 m a.s.l., receiving 1500–2500 mm yr⁻¹ of rainfall with a dry season equal to or less than 3 months. In western Cameroon, *Olea capensis* populations are found in areas where mean annual cloud cover is high and fog frequencies are generally more than 150 days/year, locally compensating for a reduction in rainfall. Temperatures are fairly constant throughout the year (White, 1981; Suchel, 1988; Maley and Elenga, 1993; Reynaud-Farrera, 1995; Orwa et al., 2009). According to the modern distribution, climatic constraints and ecological thresholds of its main components, the mixed semi-deciduous/sub-montane forested environment present between ca. 7000 and ca. 6100 cal yr BP on the eastern Adamawa plateau indicates that precipitation might have been at least similar to modern values or more probably higher, but in the two cases the length of the dry season was shorter than the modern one. Thereby, changes in rainfall seasonality, such as an increase of the dry season length, would have played the major role in the retreat of the forest during the AHP termination; a retreat probably more or less amplified by changes in cloud cover and fog frequencies.

In northern tropical Africa, the yearly distribution of precipitation is mainly controlled by the latitudinal displacement of the ITCZ, a boundary that separates the dry northeast trade winds from the humid Atlantic monsoon influence (Leroux, 1983; Nicholson, 2000). The core of the associated rain belt is located around 10° N during the boreal summer (June to September) when the regions located north of 4° N receive their maximum amounts of precipitation but with an increasingly long dry season from the south to the north. Numerous studies have shown that the position of the ITCZ had largely fluctuated during the Quaternary linked to insolation changes, but palaeodata have been essentially interpreted in terms of global hydrological changes (e.g. Gasse, 2000; Gasse et al., 2008; Hély et al., 2009). Our pollen sequence from Lake Mbalang registers fluctuations in the position of the northern margin of the ITCZ and the African Monsoon over northern tropical Africa during the Holocene. Considering that the amount of modern rainfall is sufficient to maintain a forest environment, however, the impact on local vegetation appears to have occurred as a result of changes in rainfall seasonality rather than in absolute amount. A northernmost position for the margin of the African Monsoon is evidenced between ca. 7000 and ca. 6100 cal yr BP allowing a long rainy season of at least nine months on the Adamawa plateau as attested by the presence of a semi-deciduous/sub-montane forest until ca. 6100 cal yr BP. Then the northern ITCZ margin shifts southward attaining probably its modern position between ca. 3000 and ca. 2400 cal yr BP, enhancing progressively the influence of northeast trade winds at the expense of the Atlantic monsoon on the Adamawa plateau, and so increasing the length of the dry season, from three to five months, until the physiological and ecological thresholds

of semi-deciduous forest and sub-montane forest were exceeded and they no longer had the capacity to regenerate, and were thus progressively replaced by savannah around 4200 cal yr BP and ca. 3000 cal yr BP, respectively.

Concerning the occurrence of the sub-montane forest element *Olea capensis* near Lake Mbalang and of *Podocarpus* and *Rubus* in the region until ca. 3000 cal yr BP, their rapid and synchronous retreat may perhaps be best understood in terms of changes in cloud cover and fog frequencies linked to changes in rainfall seasonality over the Adamawa plateau during the last 7000 cal yr BP. At Lake Ossa, even in low frequencies, the occurrence of *Olea capensis* and *Podocarpus* has been interpreted as reflecting a larger regional extension of these montane forest elements on the hills surrounding the lake during the Holocene up to ca. 3000 cal yr BP (Reynaud-Farrera, 1995; Reynaud-Farrera et al., 1996). These authors suggest that such a persistence of montane formations at mid-altitude in southwestern Cameroon would be linked to the combined effect of humid conditions and of more or less continuous seasonal development of clouds and fog related to the proximity of the Atlantic Ocean. Modern mid-altitude populations in this region would be only relictual formations persisting in areas with local cloud and mist development (White, 1981; Reynaud-Farrera, 1995). At Lake Mbalang, maximum extension of *Olea capensis* before ca. 6100 cal yr BP could be also explained by occurrence of higher seasonal cloud cover and/or fog during the maximum influence and intensity of the Atlantic monsoon over northern tropical Africa. The progressive southern shift of the northern margin of the ITCZ and the increasing influence of dry northeast trade winds from ca. 6100 cal yr BP onward would, as described above, have resulted in an increase in rainfall seasonality, but also a progressive reduction of clouds and/or fog over the plateau until ca. 3000 cal yr BP. This would have probably resulted in slightly increased temperatures, leading to the retreat of *Olea capensis* and its maintain only at higher altitudes.

The potential dominance of changes in rainfall seasonality as opposed to mean annual amount on past tropical African vegetation dynamics was for the first time clearly demonstrated in southeastern tropical Africa (9°20' S), at the Younger Dryas-Holocene climatic transition (ca. 11 700 cal yr BP) where semi-deciduous forest was definitely replaced by woodland in the Lake Masoko region (Garcin et al., 2007; Vincens et al., 2007). Today, Lake Mbalang similar to Lake Masoko is located in an area with enough high rainfall to support semi-deciduous forest, but with an excessively long dry season (5 and 4 months, respectively) which prevents its establishment. The role of increased rainfall seasonality was also proposed in southern Cameroon, at Nyabessan swamp (2°15' N), to explain the shift between an evergreen forest to secondary and pioneer formations ca. 2500 cal yr BP (Ngomanda et al., 2008). Similar shifts are observed in Congo, at Lake Sinnda (3°50' S) where evergreen forest was replaced by a semi-deciduous

one. At Sinnda, however, this shift is observed as early as ca. 4500 cal yr BP probably due to peculiar location of this site at the southern drier periphery of the Guineo-Congolian forest massif (Vincens et al., 1998). In contrast, at many other sites from Central Africa and northern African sub-arid or arid regions, the main factor involved for vegetation changes during the Holocene was rather interpreted in terms of increasing/decreasing annual precipitation trends in response to shifts in the relative influence of the African Monsoon and the dry northeast trades winds, depending on the study area (e.g. Vincens et al., 1999; Salzmann et al., 2002; Kröpelin et al., 2008; Lézine, 2009). In the same way, model simulations of the evolution of the northern tropical African climate-ecosystem for Holocene key periods (9500, 6000 and 4000 cal yr BP) were mainly analysed in terms of rainfall amount changes (e.g. Liu et al., 2007; Hély et al., 2009), even when modern biome sensitivity analyses in this region have shown that changes in vegetation composition and dynamics result both from competition for water between grasses and trees and from dry season length (Hély et al., 2006). More recently, Cassignat et al. (2009) using an equilibrium biosphere model to estimate the potential effect of a change in precipitation seasonality on equatorial African vegetation have shown the necessity of taking now into account seasonal changes in the hydrological balance, i.e. the length of the dry season, to reconstruct vegetation or to infer quantitative climate parameters from pollen.

5 Conclusions

Three major features are registered in the Lake Mbalang pollen sequence. They are: (1) the timing and mode of the local vegetation response to the AHP termination, (2) the main climatic parameter responsible for the vegetation dynamics in this region and (3) the local presence of the sub-montane *Olea capensis* tree during a large part of the Holocene.

- (1) Depending on the authors, the response of vegetation to the AHP termination in northern tropical Africa, based on vegetal remains analysis (pollen, charcoal), has been described as abrupt (e.g. Salzmann and Hoelzmann, 2005) or gradual (e.g. Neumann, 1989; Salzmann et al., 2002; Lézine, 2009). On the eastern Adamawa plateau, the Lake Mbalang pollen sequence shows that this response was marked by significant successional changes within the broad context of long-term aridification. Forest decline in this area is initially registered as early as ca. 6100 cal yr BP and modern savannah was definitely established at ca. 3000 cal yr BP and stabilized at ca. 2400 cal yr BP. This indicates that the local vegetation has reacted slowly to the AHP termination, i.e. during a period of about 3400 years, passing from a forested environment to an open savannah one. A striking feature during

this period, however, is that vegetation has not gradually adapted to this climatic change since a phase of slight forest regeneration occurs between ca. 5200 and ca. 4200 cal yr BP. Thus, two steps of vegetation change are evident, the first one between ca. 6100 and ca. 5200 cal yr BP and the second one between ca. 4200 and ca. 2400 cal yr BP, with for this last one a gradual mode between ca. 4200 and ca. 3000 cal yr BP and an accelerating one until ca. 2400 cal yr BP. Concerning this later episode, it has been probably intensified by interferences with increasing human activities on the plateau though no clear evidence is given in the pollen sequence. Such fluctuations between a forest and a savannah environment are also observed in fluctuations in magnetic susceptibility and organic carbon content of the sediments, indicating after ca. 6100 cal yr BP a progressive disappearance of a humic cover toward a complete denudation of ferrallitic soils present on the catchment ca. 3000 cal yr BP (Ngos et al., 2008).

Compared to other continuous pollen sequences from northern semi-arid and arid tropical Africa, the record of Lake Mbalang shows that the timing of vegetation change toward an irreversible ecological threshold ca. 4200 cal yr BP is similar to the one observed at Lake Tilla (northeastern Nigeria; Salzmann, 2000) and very close to that registered at Lake Yoa ca. 4300 cal yr BP (northern Chad, Lézine, 2009). It is also at this time that Guineo-Congolian forest, between 4° S and 5° N, locally undergoes a first slight perturbation (Vincens et al., 1998) followed by a major shift around 3000–2500 cal yr BP (e.g. Vincens et al., 1999), but in most of the cases with a reversible pattern. In southern tropical Africa, similar vegetation changes are registered during the AHP termination in Angola, 11°55' S. These data indicate the marked expansion of savannah at the expense of more wooded formations (woodland and montane forest) starting at ca. 3700 cal yr BP and reaching its maximum development after ca. 2000 cal yr BP (Dupont et al., 2008). Even further south, at Spitzkoppe in Namibia (21.8317° S), high-resolution stable carbon and nitrogen isotope records indicate also a period of marked aridity from ca. 3500 until ca. 300 cal yr BP (Chase et al., 2009). If some slight discrepancies can be observed in timing, mode and amplitude of vegetation response in the different Holocene records during the AHP termination, it is mainly due to location and peculiar environment of the study sites (cf. Marchant and Hooghiemstra, 2004), sometimes to poor chronological control, but also to the stability of the local vegetation during this climatic period (Vincens et al., 1999).

- (2) The pollen sequence of Lake Mbalang indicates that increases in the length of the dry season (from 3 to 5 months), during the AHP termination due to a southward shift of the northern margin of the ITCZ and

its rainfall belt over northern tropical Africa has been the primarily control on vegetation dynamics on the Adamawa plateau, as both modern and past rainfall amount have been always sufficient to maintain and regenerate a forested environment. Changes in rainfall seasonality would have also resulted in a decrease in seasonal cloud cover and fog frequency, slightly increasing temperatures and leading to the retreat of the sub-montane *Olea capensis* tree to higher altitude. Meanwhile, this shift of the northern margin of the ITCZ does not necessarily indicate a mean latitudinal shift of the equatorial trough as a whole since no anti-phasing of the climate and vegetation development in the northern and southern tropics is evident (Dupont et al., 2008; Chase et al., 2009). More likely, the amplitude of the yearly migration of the ITCZ got progressively less during the AHP termination.

- (3) As an expansion of *Olea capensis* is registered in several West and Central African sites during the last glacial period and the LGIT, one could suppose that this sub-montane transgressor tree could have been an important component of the vegetation on the eastern Adamawa plateau at this time. Compared to other sites, its continued presence during early Holocene would be related to the altitude of the plateau of ca. 1100 m a.s.l. and the associated favourable climatic conditions, such as a short dry season, occurrence of seasonal clouds and/or fog and slightly lower temperature. The modern presence of local patches of *Olea capensis* on Mount Nghanha would probably correspond to a relictual population of a former and larger expansion of this tree in Central Cameroon before the Holocene, such as probably modern local populations found northward on Mount Poli (8°20' N) or on the Mandara Plateau (12° N) in Central and Northern Cameroon, respectively (Letouzey, 1968). Such a hypothesis needs to be confirmed, however, by longer pollen sequences from this region.

Acknowledgements. This work is a contribution to the ECOFIT program (ECOsystemes et paléocöcosystemes des Forêts InterTropicales) financially supported by the CNRS (Centre National de la Recherche Scientifique), the IRD (Institut de Recherche pour le développement, ex. ORSTOM) and the CEA (Commissariat à l’Energie Atomique). The authors are indebted to the Cameroon authorities and institutions who have permitted and facilitated this research project. We also acknowledge Y. Garcin for assistance with the chronology, C. Vanbesien and J. J. Motte for drawing assistance, L. Dupont, A.-M. Lézine, J. Maley and an anonymous referee for constructive reviews, and B. Chase for comments and intensive language revision of the manuscript. After publication, the pollen data will be stored in the African Pollen Database (APD).

Edited by: V. Brovkin



The publication of this article is financed by CNRS-INSU.

References

- Achoundong, G.: Formation et évolution des recrûs sur savanes, in: *Dynamique à long terme des écosystèmes forestiers intertropicaux*, edited by: Servant, M. and Servant-Vildary, S., IRD, UNESCO, MAB, CNRS, Paris, 31–41, 2000.
- African Pollen Database: <http://medias.obs-mip.fr/apd>, last access: January 2010.
- A.P.L.F.: Pollen et spores d’Afrique tropicale: Travaux et Documents de Géographie Tropicale, 16, CNRS, Talence, France, 1974.
- Bennett, K. D.: Documentation for PSIMPOLL 4.10 and PSCOMB 1.03, C programs for plotting pollen diagrams and analysing pollen data, Quaternary Geology software, Uppsala University, <http://chrono.qub.ac.uk>, last access: September 2009, 2002.
- Bonnefille, R.: Rainforest responses to past climatic changes in tropical Africa, in: *Tropical rainforest responses to climate change*, edited by: Bush, M. D. and Flenley, J. R., Praxis Publishing, Chichester, 117–170, 2007.
- CCSP: Thresholds of climate change in ecosystems. A report by the US Climate Change Science Program and the Subcommittee of Global Change Research, US Geological Survey, Reston, VA, 2009.
- Charney, J. G., Stone, P. H., and Quirk, W. J.: Drought in Sahara – Biogeophysical Feedback Mechanism, *Science*, 187, 434–435, 1975.
- Chase, B. M., Meadows, M. E., Scott, L., Thomas, D. S. G., Marais, E., Sealy, J., and Reimer, P. J.: A record of rapid Holocene climate change preserved in hyrax middens from southwestern Africa, *Geology*, 37(8), 703–706, 2009.
- Claussen, M., Kubatzki, C., Brovkin, V., Ganopolski, A., Hoelzmann, P., and Pachur, H. J.: Simulation of an abrupt change in Saharan vegetation in the mid-Holocene, *Geophys. Res. Lett.*, 26, 2037–2040, 1999.
- deMenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L., and Yarusinsky, M.: Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing, *Quaternary Sci. Rev.*, 19, 347–361, 2000.
- Dupont, L. M., Behling, H., and Kim, J.-H.: Thirty thousand years of vegetation development and climate change in Angola (Ocean Drilling Program Site 1078), *Clim. Past*, 4, 107–124, doi:10.5194/cp-4-107-2008, 2008.
- Eggert, M. K. H., Höhn, A., Kahlheber, S., Meister, C., Neumann, K., and Sweizer, A.: Pits, graves and grains: archaeological and archaeobotanical research in southern Cameroon, *J. Afr. Archaeol.*, 4, 273–298, 2006.
- Elanga, H., Vincens, A., and Schwartz, D.: Présence d’éléments forestiers montagnards sur les plateaux Batéké (Congo) au Pléistocène supérieur, nouvelles données palynologiques, *Palaeoeco. A.*, 22, 239–252, 1991.
- Faegri, K. and Iversen, J.: Textbook of pollen analysis, 3th edition, Blackwell, Oxford, 295 pp., 1975.
- Fitton, J. G. and Dunlop, H. M.: The Cameroon line, West Africa, and its bearing on the origin of oceanic and continental alkali basalt, *Earth Planet. Sc. Lett.*, 72(1), 23–38, 1985.
- Flore du Cameroun: Museum National d’Histoire Naturelle, Paris, 1963–2001.
- Garcin, Y., Vincens, A., Williamson, D., Buchet, G., and Guiot, J.: Abrupt resumption of the African Monsoon at the Younger Dryas-Holocene climatic transition, *Quaternary Sci. Rev.*, 26, 690–704, doi:10.1016/j.quascirev.2006.10.014, 2007.
- Gasse, F.: Hydrological changes in the African tropics since the Last Glacial Maximum, *Quaternary Sci. Rev.*, 19, 189–211, 2000.
- Gasse, F., Chalié, F., Vincens, A., Williams, M. A. J., and Williamson, D.: Climatic patterns in equatorial and southern Africa from 30 000 to 10 000 years ago reconstructed from terrestrial and near-shore proxy data, *Quaternary Sci. Rev.*, 27, 2316–2340, doi:10.1016/j.quascirev.2008.08.27, 2008.
- Génieux, M.: Climatologie du Cameroun, in: *Atlas du Cameroun*, ORSTOM, France, 1958.
- Griffiths, J. F.: Climate of Africa, *World Survey of Climatology*, 10, Elsevier, Amsterdam, 1972.
- Grimm, E. C.: CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares, *Comput. Geosci.*, 13, 13–35, 1987.
- Gritti, E. S., Cassignat, C., Flores, O., Bonnefille, R., Chalié, F., Guiot, J., and Jolly, D.: Simulated effects of a seasonal precipitation change on the vegetation in tropical Africa, *Clim. Past*, 6, 169–178, doi:10.5194/cp-6-169-2010, 2010.
- Hély, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M., and Guiot, J.: Sensitivity of African biomes to changes in the precipitation regime, *Global Ecol. Biogeogr.*, 15, 258–270, 2006.
- Hély, C., Braconnot, P., Watrin, J., and Zheng, W.: Climate and vegetation: simulating the African humid period, *C. R. Geosci.*, 341(8–9), 671–688, doi:10.1016/j.crte.2009.07.002, 2009.
- Hoelzmann, P., Gasse, F., Dupont, L. M., Salzmann, U., Staubwasser, M., Leuchner, D. C., and Sirocko, F.: Palaeoenvironmental changes in the arid and subarid belt (Sahara-Sahel-Arabian Peninsula) from 150 ka to present, in: *Past Climate through Europe and Africa*, edited by: Battarbee, R. W., Gasse, F., and Stickley, C. S., Springer, Dordrecht, 219–256, 2004.
- Hutchinson, J. and Dalziel, J. M.: *Flora of West Tropical Africa*, Whitefriars, London, 1954–1972.
- Jennerjahn, T. C., Ittekkot, V., Arz, H. W., Behling, H., Patzold, J., and Wefer, G.: Asynchronous terrestrial and marine signals of climate change during Heinrich events, *Science*, 306, 2236–2239, 2004.
- Jolly, D., Harrison, S. P., Damnati, B., and Bonnefille, R.: Simulated climate and biomes of Africa during the Late Quaternary: Comparison with pollen and lake status data, *Quaternary Sci. Rev.*, 17, 629–657, 1998.
- Kahn, F.: La reconstitution de la forêt tropicale humide, Sud-Ouest de la Côte d’Ivoire, ORSTOM, Paris, mémoire 97, 148 pp., 1982.
- Kröpelin, S., Verschuren, D., Lézine, A.-M., Eggermont, H., Cocquyt, C., Francus, P., Cazet, J.-P., Fagot, M., Rumes, B., Russell, J. M., Conley, D. J., Schuster, M., von Suchodoletz, H., and

- Engstrom, D. R.: Climate-driven ecosystem succession in the Sahara: the last 6000 years, *Science*, 320, 765–768, 2008.
- Kuper, R. and Kröpelin, S.: Climate-controlled Holocene occupation in the Sahara: Motor of Africa’s evolution, *Science*, 313, 803–807, 2006.
- Kutzbach, J. E. and Street-Perrott, F. A.: Milankovitch forcing of fluctuations in the level of tropical Lakes from 18 to 0 Kyr BP, *Nature*, 317, 130–134, 1985.
- Lebrun, J.-P. and Stork, A. L.: Tropical African flowering plants. Ecology and distribution, Vol. 1: Annonaceae-Balanitaceae, Conservatoire et Jardin Botaniques, Genève, 796 pp., 2003.
- Lebrun, J.-P. and Stork, A. L.: Tropical African flowering plants. Ecology and distribution, Vol. 2: Euphorbiaceae-Dichapetalaceae, Conservatoire et Jardin Botaniques, Genève, 306 pp., 2006.
- Leroux, M.: Le climat de l’Afrique tropicale, Champion, Paris, 1983.
- Leroux, M.: The meteorology and climate of tropical Africa, Springer-Praxis, 2001.
- Letouzey, R.: Etude phytogéographique du Cameroun, Lechevalier, Paris, 1968.
- Letouzey, R.: Notice de la carte phytogéographique du Cameroun au 1: 500 000, Institut de la Carte Internationale de la Végétation, Toulouse, France, 1985.
- Lézine, A.-M.: Postglacial pollen records of Africa, in: *Encyclopaedia of Quaternary Sciences*, 4, Scott A. Elias, Elsevier, 2682–2698, 2007.
- Lézine, A.-M.: Timing of vegetation changes at the end of the Holocene Humid Period in desert areas at the northern edge of the Atlantic and Indian monsoon systems, *C. R. Géosci.*, 341(8–9), 750–759, doi:10.1016/j.crite.2009.01.001, 2009.
- Lézine, A.-M., Watrin, J., Vincens, A., Hély, C., and contributors: Are modern pollen data representative of West African vegetation?, *Rev. Palaeobot. Palyno.*, 156, 265–276, doi:10.1016/j.revpalbo.2009.02.001, 2009.
- Liu, Z., Wang, Y., Gallimore, R., Gasse, F., Johnson, T., deMenocal, P., Adkins, J., Notaro, M., Prentice, I. C., Kutzbach, J., Jacob, R., Behling, P., Wang, L., and Ong, E.: Simulating the transient evolution and abrupt change of Northern Africa atmosphere-ocean-terrestrial ecosystem in the Holocene, *Quaternary Sci. Rev.*, 26, 1818–1837, 2007.
- Mackereth, F. J. H.: A short core sampler for subaqueous deposits, *Limnol. Oceanogr.*, 14, 145–151, 1969.
- Mackereth, F. J. H.: Modifications to the Mackereth corer, *Limnol. Oceanogr.*, 24, 607–610, 1979.
- Maley, J.: Contribution à l’étude du bassin tchadien: atlas des pollens du Tchad, *Bull. Jardin Bot. Nat. Belgique*, 40, 29–48, 1970.
- Maley, J.: Etudes palynologiques dans le bassin du Tchad et paléoclimatologie de l’Afrique nord-tropicale de 30 000 ans à l’époque actuelle, *Travaux et Documents ORSTOM*, Paris, 129, 586 pp., 1981.
- Maley, J. and Livingstone, D. A.: Extension d’un élément montagnard dans le sud du Ghana (Afrique de l’Ouest) au Pléistocène supérieur et à l’Holocène inférieur: premières données polliniques, *C. R. Acad. Sci.*, 296(2), 1287–1292, 1983.
- Maley, J. and Elenga, H.: Le rôle des nuages dans l’évolution des paléoenvironnements montagnards de l’Afrique tropicale, *Veille Climatique Satellitaire*, 46, 51–63, 1993.
- Maley, J. and Brenac, P.: Vegetation dynamics, paleoenvironments and climatic changes in the forests of western Cameroon during the last 28 000 years B.P., *Rev. Palaeobot. Palyno.*, 99, 157–187, 1998.
- Marchant, R. A. and Hooghiemstra, H.: Rapid environmental change in African and South American tropics around 4000 years before present: a review, *Earth-Sci. Rev.*, 66, 217–260, 2004.
- Maslin, M.: Ecological versus climatic thresholds, *Science*, 306, 2197–2198, 2004.
- Neumann, K.: Holocene vegetation of Eastern Sahara: charcoal from prehistoric sites, *Afr. Archeol. Rev.*, 7, 97–116, 1989.
- Ngomanda, A., Neumann, K., Scheizer, A., and Maley, J.: Seasonality change and the third millennium BP rainforest crisis in southern Cameroon (Central Africa), *Quaternary Res.*, 71, 307–318, doi:10.1016/j.yqres.2008.12.002, 2008.
- Ngos, S., Siroko, F., Lehné, R., Giresse, P., and Servant, M.: The evolution of the Holocene palaeoenvironment of the Adamawa region of Cameroon: evidence from sediments from two crater lakes near Ngaoundéré, in: *Dynamics of forest ecosystems in Central Africa during the Holocene, Past-Present-Future*, edited by: Runge, J., Balkema, 103–120, 2008.
- Nicholson, S. E.: The nature of rainfall variability over Africa on time scales of decades to millennia, *Global Planet. Change*, 26, 137–158, 2000.
- Orwa, C., Mutua, A., Kindt, R., Jamnadass, R. and Anthony, S.: *Agroforestry Database: a tree reference and selection guide version 4.0*, <http://www.worldagroforestry.org>, last access: October 2009, 2009.
- Pourchet, M., Pinglot, J. F., Giresse, P., Ngos, S., Maley, J., Naah, E., and Pugno, J. C.: Programme sur les lacs à risque d’éruption gazeuse au Cameroun et en France, Evaluation des risques et tentative de prévision des éruptions gazeuses (résultats scientifiques), Ministère de l’Environnement, France, 1991.
- Reimer, P. J., Baillie, M. G. L., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Buck, C. E., Burr, G. S., Cutler, K. B., Damon, P. E., Edwards, R. L., Fairbanks, R. G., Friedrich, M., Guilderson, T. P., Herring, C., Hughen, K. A., Kromer, B., McCormac, G., Manning, S., Bronk Ramsey, C., Reimer, R. W., Remmele, S., Southon, J. R., Stuiver, M., Talamo, S., Taylor, F. W., van der Plicht, J., and Weyhenmeyer, C.: IntCal04 terrestrial radiocarbon age calibration, 26–0 cal kyr BP, *Radiocarbon*, 46, 1029–1058, 2004.
- Renssen, H., Brovkin, V., Fichefet, T., and Goosse, H.: Holocene climate instability during the termination of the African Humid Period, *Geophys. Res. Lett.*, 30, 1184, 2003.
- Reynaud-Farrera, I.: Histoire des paléoenvironnements forestiers du Sud-Cameroun à partir d’analyses palynologiques et statistiques de dépôts holocènes et actuels, Unpublished PhD thesis, University of Montpellier II, 198 pp., 1995.
- Reynaud-Farrera, I., Maley, J., and Wirmann, D.: Végétation et climat dans les forêts du sud-ouest Cameroun depuis 4770 ans B.P.: analyse pollinique des sédiments du lac Ossa, *C. R. Acad. Sci.*, 2a, 322, 749–755, 1996.
- Salard-Cheboldaëff, M.: Palynologie camerounaise, *Congrès national des Sociétés Savantes, Sciences*, 105(1), 233–247; 106(1), 125–136; 108(1), 117–129; 109(2), 19–35; 110(5), 231–248; 111(2), 59–80; 112(3), 47–63, 1980–1987.
- Salard-Cheboldaëff, M.: Palynologie Camerounaise, *Palynosciences*, 2, 189–208, 1993.

- Salzmann, U.: Are modern savannas degraded forests? A Holocene pollen record from the Sudanian vegetation zone of NE Nigeria, *Veg. Hist. Archaeobot.*, 9, 1–15, 2000.
- Salzmann, U., Hoelzmann, P., and Morczineck, I.: Late Quaternary climate and vegetation of the Sudanian zone of NE Nigeria, *Quaternary Res.*, 58, 73–83, 2002.
- Salzmann, U. and Hoelzmann, P.: The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the Late Holocene, *Holocene*, 15, 190–199, 2005.
- Schwartz, D.: Assèchement climatique vers 3000 B.P. et expansion Bantu en Afrique centrale atlantique: quelques réflexions, *B. Soc. Géol. Fr.*, 163(3), 353–361, 1992.
- Servant, M. and Servant-Vildary, S.: Dynamique à long terme des écosystèmes intertropicaux, IRD, UNESCO, MAB, CNRS, Paris, 2000.
- Sowunmi, M. A.: Pollen grains of Nigerian Plants, *Grana*, 13, 145–186, 1973.
- Sowunmi, M. A.: Pollen of Nigerian Plants, *Grana*, 34, 120–141, 1995.
- Stuiver, M. and Reimer, P. J.: Extended 14C database and revised CALIB 3.0 14C age calibration program, *Radiocarbon*, 35, 215–230, 1993.
- Suchel, J. B.: Les climats du Cameroun, Unpublished Thesis, University of Saint-Etienne, France, 1988.
- Tamura, T.: Late Quaternary landscape evolution in the West Cameroon Highlands and the Adamawa Plateau, in: *Paysages quaternaires de l’Afrique centrale atlantique*, edited by: Lanfranchi, R. and Schwartz, D., ORSTOM, France, 298–313, 1990.
- Tchotsoua, M.: Evolution récente des territoires de l’Adamaoua central. De la spatialisation à l’aide pour un développement maîtrisé, *Mémoire inédit*, 267 pp., 2005.
- Verdcourt, B.: Dennstaedtiaceae, in: *Flora of Tropical East Africa*, edited by: Beentje, H. J. and Smith, S. A. L., Balkema, 34 pp., 2000.
- Vincens, A., Schwartz, D., Bertaux, J., Elenga, H., and de Namur, C.: Late Holocene climatic changes in Western Equatorial Africa inferred from pollen from Lake Sinnda, southern Congo, *Quaternary Res.*, 50, 34–45, 1998.
- Vincens, A., Schwartz, D., Elenga, H., Reynaud-Farrera, I., Alexandre, A., Bertaux, J., Mariotti, A., Martin, L., Meunier, J.-D., Nguetsop, F., Servant, M., Servant-Vildary, S., and Wirmann, D.: Forest response to climate changes in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscapes, *J. Biogeogr.*, 26, 879–885, 1999.
- Vincens, A., Lézine, A.-M., Buchet, G., Lewden, D., Le Thomas, A., and contributors: African Pollen Database inventory of tree and shrub pollen types, *Rev. Palaeobot. Palyno.*, 145, 135–141, 2007.
- Vincens, A., Garcin, Y., and Buchet, G.: Influence of rainfall seasonality on African lowland vegetation during the Late Quaternary: Pollen evidence from Lake Masoko, Tanzania, *J. Biogeogr.*, 34, 1274–1288, doi:10.1111/j.1365-2699.2007.01698.x, 2007.
- Watrin, J., Lézine, A.-M., Hély, C., and contributors: Plant migration and plant communities at the time of the “green Sahara”, *C. R. Géosci.*, 341(8–9), 656–670, doi:10.1016/j.crte.2009.06.007, 2009.
- White, F.: The history of the Afromontane archipelago and the scientific need for its conservation, *Afr. J. Ecol.*, 19, 33–54, 1981.
- White, F.: *Vegetation of Africa*, UNESCO/AETFAT/UNSO, Paris, 356 pp., 1983.
- Ybert, J.-P.: *Atlas des pollens de Côte d’Ivoire*, Initiations-Documentations Techniques 40, ORSTOM, Paris, 1979.
- Youta Happi, J.: Arbres contre graminées, La lente invasion de la savane par la forêt au Centre-Cameroun, Unpublished PhD thesis, Université Paris IV, France, 237 pp., 1998.