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

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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, a region where any data are today available. This sequence, spanning the last 7000 cal. yr BP, shows that the vegetation response to this transitional climatic episode was neither abrupt nor really gradual. Forest degradation in this area is initially registered as early as 6100 cal. yr BP and modern savanna was definitely established at 3000 cal. yr BP and stabilized at 2400 cal. yr BP; but a slight forest regeneration episode is observed between 5200 and 4200 cal. yr BP. Moreover, in this area with modern high rainfall, increasing in the length of the dry season during the AHP termination, from 6100 cal. yr BP onward, has primarily controlled vegetation dynamics and above all the disappearance of a 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 episodes between climatic extremes such as the AHP termination might be different in timing, mode and amplitude according to the regional climate and hydrology 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 episodes 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 ecolog-

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ical threshold-pattern (Maslin, 2004; Jennerjahn et al., 2004; CCSP, 2009). In tropical Africa, the “African Humid Period” (AHP, de Menocal et al., 2000) termination is the last major environmental transition which has widely impacted the ecosystems. Palaeoclimatic syntheses of northern tropical Africa show evidence that this region dramatically dried out during the Middle Holocene (e.g., Jolly et al., 1998; Gasse, 2000; Hoelzmann et al., 2004; Lézine, 2009), involving complete dessication 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 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 savanna are evidenced (e.g., Vincens et al., 1999; Servant and Servant-Vildary, 2000; Bonnefille, 2007; Lézine, 2007) creating favorable 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 de Menocal et al. (2000) as very abrupt ca. 5500 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-Peroot, 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 of them have involved that strong vegetation-atmosphere feedbacks (i.e. biogeophysical feedback, Charney et al., 1975) may have amplified the abruptness of this transition (Clausen 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, ruling out such an explanation (Liu et al., 2007). More recently,

new multidisciplinary data from the eastern Sahara show that the AHP termination was gradual rather than abrupt suggesting a relatively weak biogeophysical feedback on climate (Kröpelin et al., 2008).

In this paper we present a new continuous palynological record from the Adamawa plateau, at 7° N in central Cameroon, recovering 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 savanna Soudanian region, could be a new key area for a better understanding of the AHP termination and related vegetation dynamics in northern tropical Africa. Indeed, in this phytogeographical region only one pollen sequence from Benin is today available (Salzmann and Hoelzmann, 2005) and another was obtained until today between 5° and 10° N.

2 Study site

Lake Mbalang (7°19' N, 13°44' E, 1110 m a.s.l.) is located 15 km East of Ngaoundéré town, in the eastern part of the Adamawa plateau belonging to the Cameroon Volcanic Line which extends south-west to the western Cameroon highlands until the Atlantic coastal plain and hosts numerous crater lakes (Fitton and Dunlop, 1985). With an area of 0.5 km² and a maximum depth of 52 m, it occupies the crater of a former volcano (maar) (Pourchet et al., 1991) (Fig. 1).

The Ngaoundéré region, with a mean altitude of 1100 m, is located under an altitudinal tropical climate transitional between the equatorial climate of southern Cameroon and the tropical soudano-sahelian climate of northern Cameroon (Génieux, 1958). According to its altitude, mean annual rainfall is high, 1500–1600 mm, and distributed only in one long season from April to October. The dry season, from November to March (5 months), is characterized by a great influence of continental North-East trade

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winds (Harmattan) from the Sahara desert involving low cloud cover. Such a distribution of rainfall is controlled primarily by the North-South movement of the Intertropical Convergence Zone (ITCZ) and its associated rainbelt over this region (Suchel, 1988; Leroux, 1983, 2001). Mean annual temperature is about 22–23 °C and evaporation about 1800 mm/year.

Lake Mbalang lies today in the wooded Sudanian savanna zone described in Cameroon by Letouzey (1968, 1985) as characterized by the presence of two main trees: *Daniella oliveri* (*Caesalpinaceae*) and *Lophira lanceolata* (*Ochnaceae*). It is located not more than 100 km of the most northerly patches of humid forest, this position providing a special opportunity to study the fluctuations of the northern boundary of the central African forest domain during the Holocene. In the frame of the ECOFIT program (CNRS-IRD-CEA), botanical inventories of tree species were performed in the Lake Mbalang area. They show the modern dominance of savanna species such as *Annona senegalensis*, *Piliostigma thonningii*, *Syzygium guineensis*, *Hymenocardia acida* ... associated around the lake with some forest species such as *Croton macrostachys*, *Khaya senegalensis* or forest pioneers such as *Harungana madagascariensis* (Tchot-soua, 2005).

3 Material and methods

Several 6 m long sediment cores were collected in 1998 (ECOFIT program) using a compressed-air Mackereth corer (Mackereth, 1969, 1979) in the deepest part of Lake Mbalang. The core studied in this paper, M4, was recovered in the northern part of the lake, under 44 m water depth. The cored sediments mostly consist of dark grey mud showing lamina at the base of the core, between 5,10 and 6 m, with two interbedded sand layers at 0.8–1 m and at 5.60–5.80 m (Ngos et al., 2008). Several studies have been carried out on this core (granulometry, mineralogy, magnetism, carbon content, diatoms). Some proxies were recently published (Ngos et al., 2008), others as diatoms are in progress (Nguetsop, in preparation). The chronology of the core M4 was estab-

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lished from four radiocarbon datings of total organic matter (TOM). Three dates were obtained using the accelerator mass spectrometry (AMS) method at the University of Kiel (Germany), 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) (Table 1). Using this set of ages, a linear depth-age model was established along the whole sequence using IntCal04 curve (Reimer et al., 2004) (Fig. 2).

Forty five samples were selected representing a mean resolution of ca. 150 years, then analysed for 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 African pollen morphology (e.g., Maley, 1970; Bonnefille, 1971a, b; Sowunmi 1973, 1995; A.P.L.F., 1974; Ybert, 1979; Bonnefille and Riollet, 1980; Salard-Cheboldaeff, 1980–1987, 1993) and photographs available on the African Pollen Database (APD) web site (2008). 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 (2008) 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 pre-

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sented 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 indeterminable 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.

Pollen zone M1 (7000–6100 cal. yr BP)

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

Pollen zone M2 (6100–5200 cal. yr BP)

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

Pollen zone M3 (5200–4200 cal. yr BP)

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

Pollen zone M4 (4200–3000 cal. yr BP)

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

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

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

4.2 Interpretations and discussion

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

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

20 A major feature of this sequence is the presence of a forested environment before 6100 cal. yr BP testified by the abundance of forest tree components and a very low representation of grasses and savanna 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 numerous regrowth or secondary forest

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trees, this forested environment had not a mature and so a stable character during this period.

The semi-deciduous facies of this forest was close, by its floristic composition, to the forest that is found today at the northern limit of the Guineo-Congolian forest massif in south central Cameroon, i.e. today at about 100 km southward of Lake Mbalang for the nearest patches, under rainfall of ca. 1500 mm/year with only a 3 months dry season and low cloud cover. 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 (Watrín et al., 2009). But, contrary to these dry regions, the scarcity of savanna elements around Lake Mbalang between 7000 and 6100 cal. yr BP testifies that the forest also largely extended on the plateau on well-drained soils. Such a feature was suggested from a long time by botanists such as Letouzey (1968) but without indication of timing. At the same moment, on 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, more than 50%, testify that the main regional formation was of savanna type, although a potential Tropical Seasonal Forest (TSFO) biome was reconstructed at 6000 cal. yr BP (Hély et al., 2009). Humid tree elements were probably only localized around the lake where they benefited from permanent fresh water (Salzmann, 2000; Salzmann et al., 2002).

Before 6100 cal. yr BP, the abundance of the sub-montane tree *Olea capensis* (14 to 30%) and above all its long persistence until 3000 cal. yr BP with significant frequencies (around 10%) is very peculiar to this region. Indeed, in the Tilla sequence *Olea capensis* (synonym of *Olea hochstetteri*) is present but only between 11 200 and 9500 cal. yr BP then becomes scarce (Salzmann, 2000; Salzmann et al., 2002). It has also been found westward in the pollen sequence from Lake Bosumtwi (Ghana) from 17 000 until 9500 cal. yr BP (Maley and Livingstone, 1983), and southward in the Bilanko depres-

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sion (Batéké plateau, Congo) ca. 12 500 cal. yr BP (Elenga et al., 1991). But on these sites, the maximum pollen frequencies are always lower than at Lake Mbalang and are exclusively recorded during the glacial/interglacial transition, so before the African Humid Period. Today on the Adamawa plateau the nearest population of *Olea capensis* is located only at 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 could have permitted a larger development and the maintain of *Olea capensis* near the site during the African Humid Period and its termination. It is excluded that pollen of *Olea capensis* was transported by rivers into the lake according that this crater lake has never had any inlet (Ngos et al., 2008).

Following this forested environment, a first slight degradation is observed between 6100 and 5200 cal. yr BP, marked by an increase of grasses testifying of local openings of the previous forest, and by the presence of *Pteridium aquilinum*, fern which is mainly present today in the herbaceous ecotone between forest and savanna, in forest clearings and other disturbed areas (Verdcourt, 2000). Then, forest locally regenerates until 4200 cal. yr BP, but it never reaches a so densely and continuous canopy than before 6100 cal. yr BP as indicated by the regular significant presence of grasses and the occurrence of local wooded savanna with *Hymenocardia* and *Hymenodictyon* as dominant elements. From 4200 cal. yr BP, savanna re-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 in which some elements are still present today, but also at the expense of the sub-montane forest which could have retreated at higher altitude such as on Mount Nganha (Letouzey, 1968). Ca. 3000 cal. yr BP, the savanna becomes for the first time the dominant formation in the landscape of the Lake Mbalang area and definitely persists from 2400 cal. yr BP until present day as testified by the constant high frequencies of grasses, more than 50% of the total pollen count. Such fluctuations between a forest and a savanna environment is also traduced by fluctuations in magnetic susceptibility and organic carbon content

of the sediments indicating after 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).

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

According to the modern distribution, climatic constraints and ecological thresholds of its main components, the presence of a semi-deciduous/sub-montane forested environment between 7000 and 6100 cal. yr BP on the eastern Adamawa plateau indicates that mean annual precipitations might have been at least similar than modern values (ca. 1500 mm/yr) or more probably higher, but in the two cases the length of the dry season was shorter than the modern one. Today in central Cameroon, semi-deciduous forest maintains and regenerates under annual rainfall of 1500 m/yr (Youta-Happi, 1998; Achoundong, 2000), but the main climatic parameter which might prevent such a dynamics is the length of the dry season which must not exceed 3 months without cloud cover (Hély et al., 2006; Lézine et al., 2009).

In tropical Africa, the yearly distribution of precipitation is mainly controlled by the north/south displacement of the ITCZ, a front that separates the dry N.E. 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 Northern Hemisphere summer (June to September) during which the regions located north of 4° N receive their maximum amount of precipitations but with an increasing 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 such fluctuations in the ITCZ position and its rainfall belt over northern tropical Africa during the Holocene, but they are primarily traduced by the local vegetation in terms of changes in rainfall seasonality. A northernmost position is evidenced during

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the Early Holocene allowing a long rainy season on the Adamawa plateau as attested by the presence of semi-deciduous/sub-montane forest until 6100 cal. yr BP. Then ITCZ shift southward attaining probably its modern position ca. 2400 cal. yr BP, enhancing progressively the influence of N.E. trade winds at the expense of that of the Atlantic monsoon on the Adamawa plateau and so increasing the length of the dry season until an exceeded physiological and ecological threshold around 4200 cal. yr BP when semi-deciduous forest no longer had the capacity to regenerate and was progressively replaced by modern savanna. Concerning the sub-montane elements and particularly *Olea capensis*, their retreat from the plateau is more abrupt at ca. 3000 cal. yr BP than for the semi-deciduous elements. This feature could be related to the synergic effect of increased rainfall seasonality and increased temperature mainly during the dry season.

Such a greater impact of rainfall seasonality than of mean annual amount on past tropical African vegetation changes was for the first time clearly demonstrated in south-eastern tropical Africa (7° 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). Lake Mbalang such as Lake Masoko are today located in areas with enough high rainfall to support semi-deciduous forest, but only a too long dry season (5 and 4 months, respectively) prevents such a modern botanical environment. Increased rainfall seasonality was also proposed in southern Cameroon, at Nyabessan swamp (2°15' N), to explain the shift between an evergreen forest to pioneer formations ca. 2500 cal. yr BP (Ngomanda et al., 2008) such as southward in Congo, at Lake Sinnda (3°50' S), but as early as 4200 cal. yr BP probably due to peculiar location of this site at the southern periphery of the Guineo-Congolian forest massif (Vincens et al., 1998). On the contrary, on many other sites from central Africa and from northern African sub-arid or arid regions, the main factor involved for vegetation changes during the Holocene was rather interpreted in terms of increase-decrease precipitation trends in response to enhancing or weakening of humid monsoon influence or inversely of dry N.E. trade winds according the study area (e.g., Vincens et al., 1999; Salzmann et al., 2002; Kröpelin et al.,

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2008; Lézine, 2009). In the same way, recent model simulations of the evolution of the northern tropical Africa 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).

5 Conclusions

Two major features are registered in the Lake Mbalang pollen sequence concerning the AHP termination. They are: (1) the timing and mode of the local vegetation response to this climatic event, and (2) the main climatic parameter responsible of the vegetation dynamics in this region.

(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 Adamawa plateau, the Lake Mbalang pollen sequence shows that this response was neither abrupt nor really gradual. Forest degradation in this area is initially registered as early as 6100 cal. yr BP and modern savanna was definitely established at 3000 cal. yr BP and stabilized at 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 yr, passing from a forested environment to an open savanna one. But, a striking feature during this period is that vegetation has not gradually adapted to this climatic change since a phase of slight forest regeneration occurs between 5200 and 4200 cal. yr BP. Thus, two steps of vegetation degradation are evidenced, the first one between 6100 and 5200 cal. yr BP and the second one between 4200 and 2400 cal. yr BP, with for this last one a gradual mode between 4200 and 3000 cal. yr BP and an accelerating one until 2400 cal. yr BP, this

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later episode been probably intensified by interferences with increasing human activities on the plateau. 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 Oya 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 degradation followed by a major change around 3000–2500 cal. yr BP (e.g., Vincens et al., 1999), but in most of the cases with a reversible pattern.

(2) The pollen sequence of Lake Mbalang evidences that increasing in the length of the dry season during the AHP termination, from 6100 cal. yr BP onward, has primarily controlled vegetation dynamics on the Adamawa plateau, according that modern and past rainfall amount could have been always sufficient to maintain forested environment.

The peculiar modern location of this site at mid-altitude and under higher annual rainfall amount relative to surrounding lowlands at the same latitude in West Africa, and its transitional position between the forest domain to the south and the savanna domain to the north, could have probably led to a more rapidly response of vegetation to register environmental changes at the AHP termination than sites located within the Guineo-Congolian forest massif. This clearly shows that the response of vegetation to climate change might be different in timing, mode and amplitude according to the regional climate and hydrology of the study sites, but also according the stability of vegetation before and during a climatic transitional episode. Meanwhile, the Mbalang pollen sequence is the first vegetation record obtained between 5 and 10° N and need to be in the future completed by other sequences on the Adamawa plateau which hosts numerous crater lakes and also in lowlands at the same latitude if appropriate sites exist.

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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 |
|----------|------------|--------------------------------|--------------------------------|---|
| TOM | 35 | 535 \pm 35 | 540 | 509/562 |
| TOM | 185 | 1796 \pm 31 | 1725 | 1688/1820 |
| TOM | 400 | 4023 \pm 29 | 4465 | 4421/4536 |
| TOM | 600 | 6400 \pm 70 | 7320 | 7234/7432 |

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

| Montane taxa | Evergreen forest taxa |
|--|---|
| <i>Ericaceae</i> undiff. | <i>Aidia</i> -type <i>micrantha</i> (<i>Rubiaceae</i>) |
| <i>Alchemilla</i> (<i>Rosaceae</i>) | <i>Alonia</i> -type <i>boonei</i> (<i>Apocynaceae</i>) |
| <i>Anagallis</i> (<i>Primulaceae</i>) | <i>Anthostema</i> -type (<i>Euphorbiaceae</i>) |
| <i>Anthospermum</i> (<i>Rubiaceae</i>) | <i>Argomuelleria macrophylla</i> -type (<i>Euphorbiaceae</i>) |
| <i>Galium</i> -type (<i>Rubiaceae</i>) | <i>Begonia</i> (<i>Begoniaceae</i>) |
| <i>Hagenia abyssinica</i> (<i>Rosaceae</i>) | <i>Caesalpiniaceae</i> undiff. |
| <i>Ilex mitis</i> (<i>Aquifoliaceae</i>) | <i>Cyathogyne</i> (<i>Euphorbiaceae</i>) |
| <i>Myrica</i> (<i>Myricaceae</i>) | <i>Dacryodes</i> -type (<i>Burseraceae</i>) |
| <i>Nuxia</i> -type <i>congesta</i> (<i>Loganiaceae</i>) | <i>Diospyros</i> (<i>Ebenaceae</i>) |
| <i>Olea capensis</i> -type (<i>Oleaceae</i>) | <i>Garcinia granulata</i> -type (<i>Clusiaceae</i>) |
| <i>Olea europaea</i> -type (<i>Oleaceae</i>) | <i>Hymenostegia</i> -type <i>pellegrinii</i> (<i>Caesalpiniaceae</i>) |
| <i>Podocarpus</i> (<i>Podocarpaceae</i>) | <i>Meliaceae</i> undiff. |
| <i>Polyscias fulva</i> -type (<i>Araliaceae</i>) | <i>Pancovia</i> -type <i>bijugata</i> (<i>Sapindaceae</i>) |
| <i>Prunus africana</i> -type (<i>Rosaceae</i>) | <i>Pausinystalia</i> -type <i>macroceras</i> (<i>Rubiaceae</i>) |
| <i>Rapanea melanophloeos</i> -type (<i>Myrsinaceae</i>) | <i>Petersianthus</i> -type <i>macrocarpus</i> (<i>Lecythidaceae</i>) |
| <i>Rubus pinnatus</i> -type (<i>Rosaceae</i>) | <i>Raphiostylis</i> (<i>Icacinaceae</i>) |
| <i>Rumex</i> (<i>Polygonaceae</i>) | <i>Santiria</i> -type <i>trimeria</i> (<i>Burseraceae</i>) |
| <i>Schefflera myriantha</i> -type (<i>Araliaceae</i>) | <i>Sapotaceae</i> undiff. |
| <i>Stoebe kilimandscharica</i> -type (<i>Asteraceae</i>) | <i>Sherbournia bignoniifolia</i> -type (<i>Rubiaceae</i>) |
| <i>Swertia</i> -type (<i>Gentianaceae</i>) | <i>Sorendeia</i> -type <i>juglandifolia</i> (<i>Anacardiaceae</i>) |
| | <i>Strombosia</i> -type (<i>Olacaceae</i>) |
| | <i>Vepris</i> -type (<i>Rutaceae</i>) |

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Table 2. Continued.

| | |
|---|---|
| Semi-deciduous forest taxa | <i>Piptadeniastrum-type africanum</i> (Mimosaceae) |
| <i>Alangium chinense</i> -type (Alangiaceae) | <i>Pycnanthus angolensis</i> -type (Myristicaceae) |
| <i>Anisotes</i> (Acanthaceae) | <i>Rauvolfia</i> (Apocynaceae) |
| <i>Antrocaryon</i> -type (Anacardiaceae) | <i>Serichostachys-type scandens</i> (Amaranthaceae) |
| <i>Campylospermum</i> (Ochnaceae) | <i>Sterculia</i> -type (Sterculiaceae) |
| <i>Carapa</i> -type <i>procera</i> (Meliaceae) | <i>Tabernaemontana</i> -type <i>crassa</i> (Apocynaceae) |
| <i>Ceiba pentandra</i> (Bombacaceae) | <i>Thymelaeaceae</i> undiff. |
| <i>Celtis</i> (Ulmaceae) | <i>Trilepisium</i> -type <i>madagascariensis</i> (Moraceae) |
| <i>Cola cordifolia</i> -type (Sterculiaceae) | <i>Triplochiton scleroxylon</i> -type (Sterculiaceae) |
| <i>Cordia platythyrsa</i> -type (Boraginaceae) | <i>Uncaria</i> -type <i>africana</i> (Rubiaceae) |
| <i>Detarium senegalense</i> -type (Caesalpiniaceae) | <i>Zanthoxylum</i> -type <i>gilletii</i> (Rutaceae) |
| <i>Funtumia</i> -type (Apocynaceae) | <i>Zanthoxylum</i> -type <i>zanthoxyloides</i> (Rutaceae) |
| <i>Ganophyllum</i> -type <i>giganteum</i> (Sapindaceae) | Swamp forest taxa |
| <i>Garcinia staudtii</i> -type (Clusiaceae) | <i>Aphania</i> -type <i>senegalensis</i> (Sapindaceae) |
| <i>Holoptelea grandis</i> (Ulmaceae) | <i>Bersama abyssinica</i> -type (Meliaceae) |
| <i>Hylodendron gabunense</i> (Caesalpiniaceae) | <i>Cleistanthus</i> -type <i>polystachyus</i> (Euphorbiaceae) |
| <i>Irvingia</i> -type <i>gabonensis</i> (Irvingiaceae) | <i>Cyathea manniana</i> -type (Cyatheaceae) |
| <i>Mallotus</i> -type <i>oppositifolius</i> (Euphorbiaceae) | <i>Guibourtia demeusei</i> -type (Caesalpiniaceae) |
| <i>Mansonia altissima</i> -type (Sterculiaceae) | <i>Klaineanthus gaboniae</i> (Euphorbiaceae) |
| <i>Mendoncia</i> (Acanthaceae) | <i>Pandanus</i> (Pandanaaceae) |
| <i>Milicia</i> -type <i>excelsa</i> (Moraceae) | <i>Phoenix reclinata</i> -type (Palmae) |
| <i>Moraceae</i> undiff. | <i>Raphia</i> (Palmae) |
| <i>Myrianthus</i> -type <i>arbores</i> (Moraceae) | <i>Symphonia globulifera</i> (Clusiaceae) |
| <i>Neoboutonia</i> -type <i>melleri</i> (Euphorbiaceae) | <i>Uapaca</i> (Euphorbiaceae) |
| <i>Oncinotis</i> -type (Apocynaceae) | |

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| | |
|--|--|
| Forest regrowth taxa | <i>Albizia</i> (Mimosaceae) |
| <i>Alchornea</i> (Euphorbiaceae) | Amaranthaceae/Chenopodiaceae undiff. |
| <i>Anthocleista</i> (Loganiaceae) | Anogeissus-type <i>leiocarpus</i> (Combretaceae) |
| <i>Asystasia gangetica</i> -type (Acanthaceae) | <i>Antidesma</i> -type <i>venosum</i> (Euphorbiaceae) |
| <i>Blighia</i> -type <i>unijugata</i> (Sapindaceae) | Apiaceae undiff. |
| <i>Bridelia ferruginea</i> -type (Euphorbiaceae) | Asteraceae undiff. |
| <i>Chaetacme aristata</i> (Ulmaceae) | <i>Bombax costatum</i> -type (Bombacaceae) |
| <i>Clausena anisata</i> (Rutaceae) | <i>Borassus</i> -type <i>aethiopum</i> (Palmae) |
| <i>Clematis</i> -type (Ranunculaceae) | Brassicaceae undiff. |
| <i>Dioscorea dumetorum</i> -type (Dioscoreaceae) | <i>Cassia</i> -type (Caesalpiniaceae) |
| <i>Elaeophorbia</i> -type (Euphorbiaceae) | <i>Cassia</i> -type <i>italica</i> (Caesalpiniaceae) |
| <i>Flabellaria</i> -type <i>paniculata</i> (Malpighiaceae) | <i>Cassia</i> -type <i>occidentalis</i> (Caesalpiniaceae) |
| <i>Flueggea virosa</i> (Euphorbiaceae) | <i>Celosia</i> -type <i>trigyna</i> (Amaranthaceae) |
| <i>Harungana madagascariensis</i> (Hypericaceae) | Chenopodiaceae undiff. |
| <i>Lygodium microphyllum</i> (Schizaeaceae) | Cichorieae undiff. |
| <i>Macaranga</i> -type (Euphorbiaceae) | <i>Cissampelos</i> -type <i>mucronata</i> (Menispermaceae) |
| <i>Margaritaria discoidea</i> (Euphorbiaceae) | <i>Cissus</i> -type <i>quadrangularis</i> (Vitaceae) |
| <i>Phaulopsis</i> -type <i>imbricata</i> (Acanthaceae) | <i>Combretum</i> -type <i>molle</i> (Combretaceae) |
| <i>Ricinus communis</i> (Euphorbiaceae) | Combretaceae undiff. |
| <i>Stephania</i> -type <i>abyssinica</i> (Menispermaceae) | <i>Commelina</i> -type <i>benghalensis</i> (Commelinaceae) |
| <i>Tacazzea</i> -type <i>apiculata</i> (Asclepiadaceae) | <i>Commiphora africana</i> -type (Burseraceae) |
| <i>Tetrapleura tetraptera</i> -type (Mimosaceae) | <i>Croton</i> -type (Euphorbiaceae) |
| <i>Tetrorchidium</i> (Euphorbiaceae) | Cucurbitaceae undiff. |
| <i>Trema</i> -type <i>orientalis</i> (Ulmaceae) | <i>Cussonia arborea</i> -type (Araliaceae) |
| Urticaceae undiff. | <i>Cyathula</i> -type <i>orthacantha</i> (Amaranthaceae) |
| Vernonieae undiff. | <i>Cyphostemma</i> -type <i>cyphopetalum</i> (Vitaceae) |
| <i>Virectaria</i> (Rubiaceae) | <i>Dichrostachys cinerea</i> -type (Mimosaceae) |
| Savanna taxa | <i>Dombeya</i> -type (Sterculiaceae) |
| <i>Acacia</i> groupe I (Mimosaceae) | <i>Ehretia</i> (Boraginaceae) |
| <i>Acacia</i> groupe III (Mimosaceae) | <i>Entada</i> -type (Mimosaceae) |
| <i>Acalypha</i> (Euphorbiaceae) | <i>Faidherbia</i> -type <i>albida</i> (Mimosaceae) |
| Acanthaceae undiff. | Gardenieae undiff. |
| <i>Achyranthes</i> -type <i>aspera</i> (Amaranthaceae) | <i>Grewia</i> -type (Tiliaceae) |
| <i>Acridocarpus</i> (Malpighiaceae) | <i>Guizotia</i> -type <i>abyssinica</i> (Asteraceae) |
| <i>Adansonia digitata</i> (Bombacaceae) | <i>Heliotropium steudneri</i> -type (Boraginaceae) |
| <i>Adenia venenata</i> -type (Passifloraceae) | <i>Hymenocardia</i> (Hymenocardiaceae) |
| <i>Aerva</i> -type <i>lanata</i> (Amaranthaceae) | <i>Hymenodictyon</i> -type <i>floribundum</i> (Rubiaceae) |
| <i>Aeschynomene</i> -type <i>baumii</i> (Fabaceae) | <i>Hypoestes</i> -type <i>aristata</i> (Acanthaceae) |
| | <i>Indigofera</i> (Fabaceae) |
| | <i>Ipomoea</i> -type (Convolvulaceae) |
| | <i>Isoberlinia</i> -type (Caesalpiniaceae) |

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Justicia-type *flava* (Acanthaceae)
Kedrostis-type (Cucurbitaceae)
Keetia-type *guelinzii* (Rubiaceae)
Kigelia africana (Bignoniaceae)
Kotschya africana-type (Fabaceae)
Lamiaceae undiff.
Lanena-type (Anacardiaceae)
Lantana-type *ukambensis* (Verbenaceae)
Lantana-type *viburnoides* (Verbenaceae)
Lepidagathis sericea-type (Acanthaceae)
Leucas-type (Lamiaceae)
Lophira lanceolata-type (Ochnaceae)
Macrosphyra-type (Rubiaceae)
Maesa lanceolata-type (Myrsinaceae)
Merremia-type *hederacea* (Convolvulaceae)
Micrococca-type *mercurialis* (Euphorbiaceae)
Mitracarpus villosus (Rubiaceae)
Mitragyna-type *inermis* (Rubiaceae)
Morelia senegalensis (Rubiaceae)
Parinari-type (Chrysobalanaceae)
Pavetta gardeniifolia-type (Rubiaceae)
Phyllanthus-type *nummulariifolius* (Euphorbiaceae)
Piliostigma thonningii-type (Caesalpiniaceae)
Poaceae undiff.
Protea-type (Proteaceae)
Psyrax schimperiana-type (Rubiaceae)
Pteridium-type *aquilinum* (Pteridaceae)
Shirakia-type *elliptica* (Euphorbiaceae)
Sida-type (Malvaceae)
Solanum-type (Solanaceae)
Spermacoe-type (Rubiaceae)
Syzygium-type *guineensis* (Myrtaceae)
Trichilia-type (Meliaceae)
Vangueria-type *madagascariensis* (Rubiaceae)
Zahna golungensis-type (Sapindaceae)

Ubiquitous taxa

Allophylus (Sapindaceae)
Apocynaceae undiff.
Celastraceae undiff.

Celastraceae/Hippocrateaceae undiff.
Combretaceae/Melastomataceae undiff.
Convolvulaceae undiff.
Euphorbiaceae undiff.
Fabaceae undiff.
Leguminosae undiff.
Ficus (Moraceae)
Lycopodiaceae undiff.
Monocotyledonae undiff.
Myrtaceae undiff.
Phyllanthus-type (Euphorbiaceae)
Rhamnaceae undiff.
Rubiaceae undiff.
Tapinanthus-type (Loranthaceae)
Tiliaceae undiff.
Pteridophyta undiff.

Aquatics

Crinum natans-type (Amaryllidaceae)
Cyperaceae undiff.
Eriocaulaceae undiff.
Heterotis-type *canescens* (Melastomataceae)
Hydrocotyle manii-type (Apiaceae)
Hygrophila (Acanthaceae)
Impatiens (Balsaminaceae)
Limnophyton-type *obtusifolium* (Alismataceae)
Melastomataceae undiff.
Mimosa pigra-type (Mimosaceae)
Nymphaea lotus-type (Nymphaeaceae)
Onagraceae undiff.
Polygonum senegalense-type (Polygonaceae)
Potamogeton thunbergii-type (Potamogetonaceae)
Stipularia africana-type (Rubiaceae)
Typha (Typhaceae)
Utricularia inflexa-type (Lentibulariaceae)

Cultivated taxa

Elaeis guineensis (Palmae)

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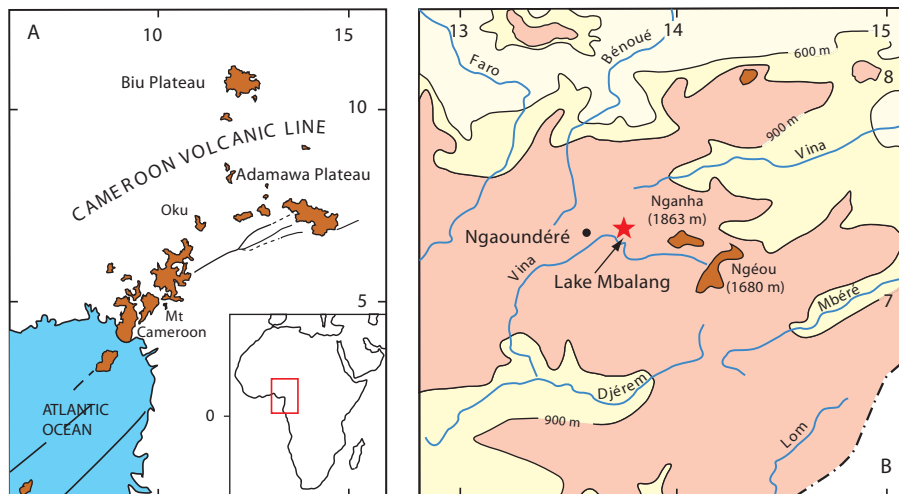
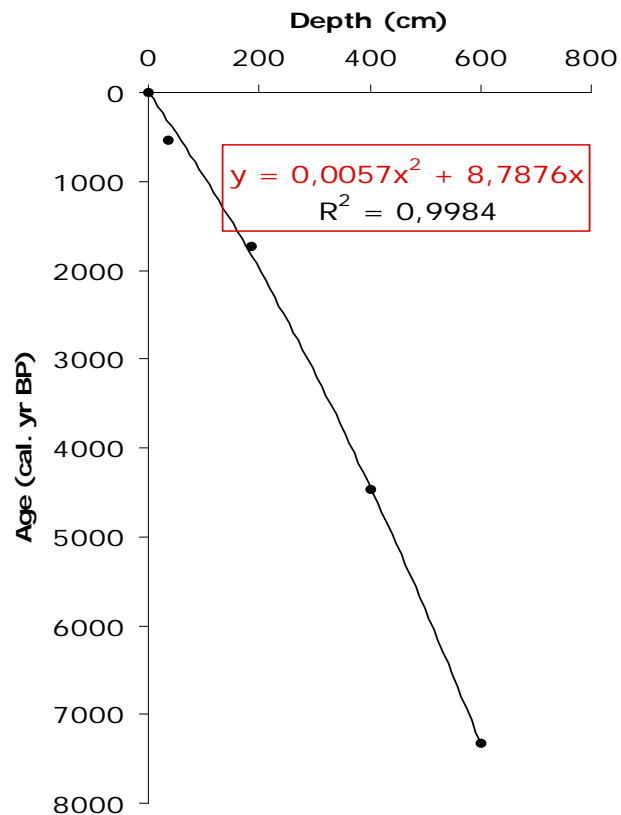


Fig. 1. (A): The Cameroon volcanic line; (B): Location of Lake Mbalang on the Adamawa plateau, central Cameroon.

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**Fig. 2.** Depth–age model of the core M4 of Lake Mbalang, Central Cameroon.[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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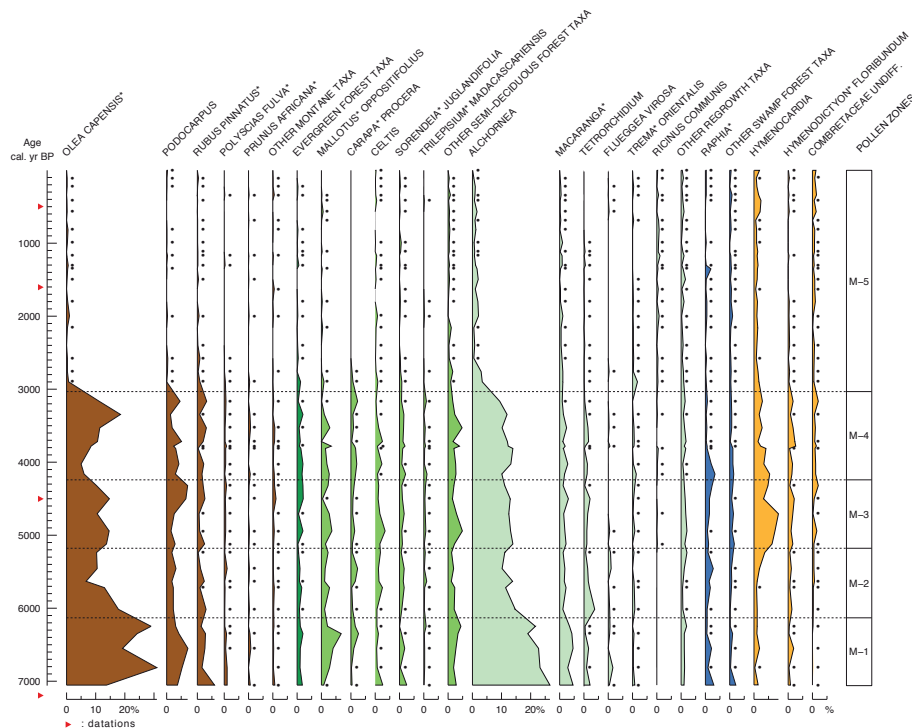


Fig. 3. The M4 pollen diagram for Lake Mbalang, Central Cameroon, showing relative percentages of selected taxa (the pollen sum includes all identified pollen and spore taxa, excluding Bryophyta and indeterminate grains).

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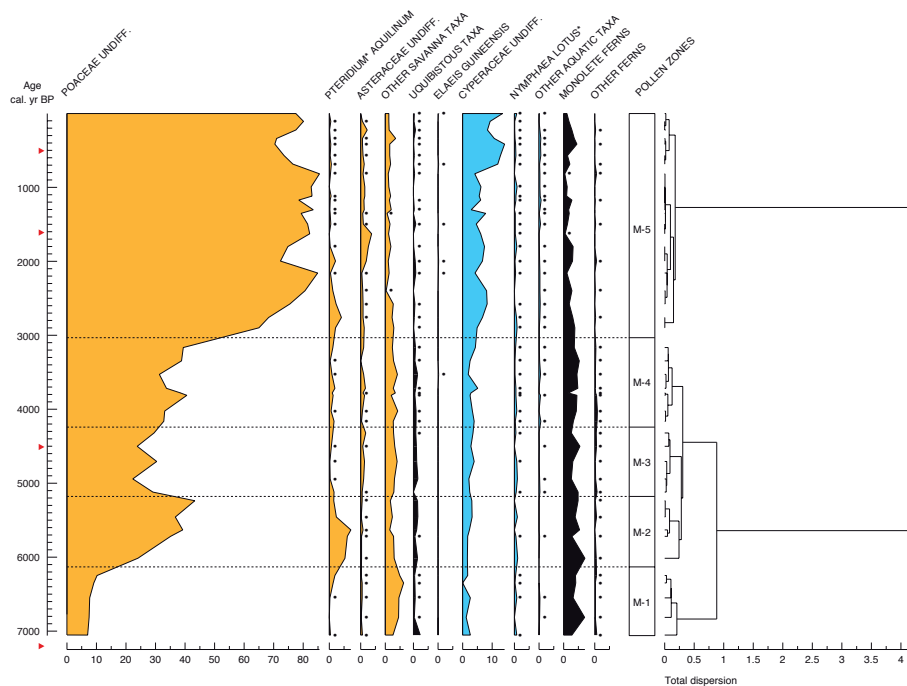


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