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Western equatorial African forest-savanna mosaics: a legacy of late Holocene climatic change?

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Past vegetation and climate changes reconstructed using two pollen records from Lakes Maridor and Nguène, Gabon, provide new insights into the environmental history of western equatorial African rainforests during the last 4500 cal yr BP. The Lake Maridor pollen record indicates that the coastal savannas of western equatorial Africa did not exist during the mid-Holocene and instead the region was covered by evergreen rainforests. In the Lake Nguène pollen record, a rapid decline of hygrophilous evergreen rainforest occurred around 4000 cal yr BP, synchronously with grassland expansion around Lake Maridor. The establishment of coastal savannas in Gabon suggests decreasing humidity at the onset of the late Holocene. The marked reduction in evergreen rainforest and subsequent savanna expansion was associated with the colonization of secondary forests dominated by the palm, *Elaeis guineensis*, in the coastal region and the shrub, *Alchornea cordifolia*, further inland. A return to wetter climatic conditions from about 1400 cal yr BP led to the renewed spread of evergreen rainforest inland, whereas a forest-savanna mosaic still persists in the coastal region. There is no evidence to suggest that the major environmental changes observed are driven by human impact.

1 Introduction

In western equatorial Africa, the tropical lowland rainforest of Gabon is well known for its high biodiversity (Sosef, 1994). This part of the Guineo-Congolian rainforest (White, 1983) is today well conserved because of the absence of intensive agricultural activities, coupled with low population densities. However, although the Gabonese rainforest shows a relatively homogeneous aspect, it is perforated by grass-dominated savannas, most notably at its periphery in the coastal area, or within the forest block (e.g. the forest-savanna mosaic in the Middle Valley of Ogooué, see Fig. 1).

The origin and persistence of these savanna patches, typical of drier environments,

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remains controversial as at these equatorial latitudes, the current humid conditions favour rainforest development (Aubréville, 1967). A number of ecologists have assumed that the effects of recent human impact (e.g. cultivation, forest logging or savanna fires), can be extrapolated to explain the dynamics of the forest/savanna ecotone during the past few millennia (Fontes, 1978; White, 1992; King et al., 1997; White, 2001).

Indirect evidence for a climatic rather than an anthropogenic origin for these savannas is provided by regional palaeoclimatic data from Lakes Barombi-Mbo (Giresse et al., 1994; Maley and Brenac, 1998) and Ossa (Reynaud-Farrera et al., 1996; Wirmann et al., 2001; Nguetsop et al., 2004; Giresse et al., 2005) in Cameroon, and Lakes Sinnda (Vincens et al., 1998) and Kitina (Elenga et al., 1996) in the Congo, which are situated at the northern and southern limits of the Guineo-Congolian rainforest, respectively. Unlike the savannas formed during the coolest and driest conditions of the Last Glacial Maximum (Maley and Brenac, 1998), which were subsequently recovered by rainforest expansion, palaeoclimatological data indicate that the late-Holocene savannas correspond with a period of aridity and marked lake-level reduction. For example, Lake Sinnda became completely dry about 4000 yr BP (Vincens et al., 1998). This aridity produced a sudden contraction of rainforests, followed by a renewed expansion of savannas associated with secondary forests.

Archaeological findings for the same period indicate that Bantu-speaking peoples arrived in Central Africa synchronously as the widespread appearance of savannas and fragmented rainforests (Schwartz, 1992). It has been suggested that human migration from the grasslands of the Nigerian-Cameroonian border into central Africa at the onset of the late-Holocene was favoured by canopy openings in the dense rainforest. The band of small coastal savannas, which today run down from Equatorial Guinea through Gabon to the Congo, may even constitute part of the old migration route (Oslisly, 2001).

Here we present two new high-resolution pollen records from Gabon, spanning the late Holocene in order to determine the origin, timing and persistence of the forest-savanna mosaic on the coast and within the dense rainforest block inland.

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2 Regional setting

Lakes Nguène and Maridor are shallow lakes (~3 to 5 m depth) located in the western part of Gabon, at the same equatorial latitude, though in highly contrasting geomorphological and vegetational settings. Lake Nguène is situated on the southern slopes of the Cristal Mounts (0°12' S–10°28' E, 20 m a.s.l.), approximately 160 km from the northwest coast of Gabon (Fig. 1). This ancient fluvial depression of the Abanga River has an area of ~6 km², with large areas of the littoral zone covered by a dense swamp of Cyperaceae (*Cyperus papyrus*, *Killinga* sp., *Cyperus* sp., *Eleocharis* sp. etc...). In its northern part, the lake basin has an extensive floodplain, with abundant herbaceous plants (Asteraceae, Amaranthaceae, *Polygonum* sp., etc.), grasses (such as *Phragmites* sp. and *Echinochloa* sp.), as well as some flood-tolerant shrubs, particularly *Nauclea pobeguinii* and *Uapaca heudelotii*. On the waterlogged soils of sheltered lake shores, dense hygrophytic vegetation occurs, mainly dominated by shrubs of *Alchornea cordifolia*. The natural riparian vegetation of Lake Nguène is dominated by trees belonging to the Caesalpiniaceae family (*Anthonota macrophylla*, *Cynometra* sp., *Guibourtia* sp. etc.). Away from the lake, the Nguène region, located in one of the most species-rich areas of western equatorial Africa (Sosef, 1994), supports an evergreen rainforest dominated by *Aucoumea klaineana*, *Dacryodes büettneri* (Burs-
eraceae), *Desbordesia glaucescens* (Irvingiaceae), and *Monopetalanthus* sp. (Caesalpiniaceae) (Nicolas, 1977; Caballé and Fontes, 1978).

By contrast Lake Maridor (0°10' S–9°21' E) is located approximately 3 km from the coast of Gabon. The lake basin, maintained both by direct precipitation, small streams and probably by groundwater infiltration, has a surface area of about 0.25 km². Its shallow water is partly covered by macrophytes, while a marsh dominated by monocotyledonous herbs and Cyperaceae separate the lake basin from a small *Mitragyna ciliata* and *Uapaca guineensis* dominated swamp forest (Christy et al., 1990). This small wetland is surrounded by a forest-savanna mosaic with secondary forests rich in *Aucoumea klaineana* and low-diversity savannas, mostly consisting of grasses in

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the tribe Andropogoneae. These secondary forests have been suggested to result from human disturbance of the coastal mature evergreen rainforest, rich in *Aucoumea klaineana*, *Saccoglottis gabonensis* and *Erismadelphus exsul* (Nicolas, 1977; Caballé and Fontes, 1978; Christy et al., 1990), during the last few centuries, notably by logging. According to Christy et al. (1990), the mature evergreen rainforest today around Lake Maridor represents only 30% of the original forest cover.

Climatically, these two lakes lie in a humid part of Gabon, with mean annual rainfall ranging from 1916 mm at Lambaréné, 100 km south of Lake Nguène, to 2834 mm at Libreville 70 km north of Lake Maridor (period from 1953–1989). Precipitation is seasonal, with a wet season which lasts about nine months (September to May), interspersed by a “short dry season” centred on January with a distinct reduction in rainfall. Temperatures vary little throughout the year, with a range of 20–33°C; these are lowest during the major dry season (June to September), when cloud cover is almost constant, because of lower sea-surface temperatures in the Gulf of Guinea (Leroux, 1983). Similarly, mean relative humidity also varies little over the year and does not fall below 70%.

3 Materials and methods

Sediments were collected using a Vibracorer from the central part of Lakes Nguène and Maridor at 2 m water depth. Using a sampling strategy of 5 and 10 cm intervals, 55 samples were obtained from core NGUE1, and 58 from core MAR2. Pollen preparation followed the standard methodology (Faegri and Iversen, 1989). Identification was based on the reference collection at the Institut des Sciences de l'Évolution de Montpellier (Université Montpellier II), as well as published pollen images for tropical Africa (Assemien et al., 1974; Ybert, 1979; Bonnefille and Riollet, 1980). Pollen nomenclature follows the African Pollen database (<http://medias.obs-mip.fr/apd/>). Pollen percentages are based on a sum of at least 600 pollen grains and pteridophyte spores. However, to show a clear representation of the forest component, at least 250 terrestrial pollen

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grains were counted at each level, excluding Poaceae. These latter, as well as the local marshy herbaceous taxa (Cyperaceae, pteridophytes, *Nymphaea* etc.) are excluded from the pollen sum using to express pollen abundance of terrestrial taxa because their high pollen abundance masks the forest signal.

5 The chronology of the cores NGUE1 and MAR2 is based on radiocarbon ages determined by a gas proportional counter and AMS methods using samples of bulk organic matter (Table 1). These radiocarbon dates were converted to calendar years using the Calib rev. 5.0 program (Reimer et al., 2004), and a continuous chronology based on the stratigraphically consistent series of dates from each sequence was derived by
10 linear interpolation between the calibrated ages.

4 Age models and sedimentation rates

Of the 11 radiocarbon dates of the core NGUE1 10 dates are stratigraphically consistent, although two slight dating inversions can be noted. These inversed radiocarbon dates however confirm the neighbour date, 1630 ± 40 yr BP (at 105 cm) and 4430 ± 40 yr BP (at 375 cm) being close to 1600 ± 40 yr BP and 4110 ± 40 yr BP, respectively. Consider that the base of the core NGUE1 is dated to 4780 cal yr BP, two possible chronologies can be derived from the 11 radiocarbon ages of the core NGUE1 (Fig. 2). The first chronology (Fig. 2, dotted line) show a significant change in sedimentation rate through the gley-mud at 187 cm. However, this change in the accumulation rate is neither associated with change in the lithology of the core nor with significant variations of sand content, suggesting that it's not corresponded to regional environmental change. Thus, the 3310 ± 40 yr BP date, stratigraphically and sedimentologically anomalous, should be caused by allochthonous inputs or reworked organic matters. In contrast, the second chronology (Fig. 2, solid line), based on nine radiocarbon dates clearly show that changes in accumulation rates are systematically synchronous either with increasing sand content percent or with change in lithology of core. For example, between 2540 ± 40 yr BP and 2429 ± 40 yr BP, accumulation rate

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is very high (0.20 cm/yr) and contemporaneous to high sand content (between 2 and 6%) suggesting very an active erosive phase or a strong stream transport. For these stratigraphical and lithological arguments, the age-model illustrated by the solid line (Fig. 2a) has been retained.

5 The core MAR2 shows a sedimentary discontinuity around 405–400 cm with lack of A2 horizon of podzolic soil (Fig. 3), which point to a sediment hiatus with a chronological gap of several hundred years. This sediment hiatus, however, not appears in the MAR1 test-core, suggesting that the sediment break in the MAR2 core was not caused by the drying up of the lake Maridor. The 10 radiocarbon dates of Maridor cores indicate
10 a maximum age of ca. 4260 cal yr BP (Table 1), and similarly to core NGUE1, MAR2 core has two different age-models. The first chronology in dotted line is not consistent with lithology and sand content because it suggests a constant sedimentation rate between 4100 until 3460 ¹⁴C yr BP when the lithology and sand content show great variations. Even if the age-model illustrated by solid line show more variations which
15 are not very well correlated with stratigraphical change, we can assume that this one is closer to reality than the other one. The Other AMS date should be necessary to affine a robust chronology.

5 Nguène pollen record

A total of 121 pollen taxa were identified from the 55 samples of core NGUE1 and changes in the relative pollen abundance, reflecting the vegetation dynamics (Fig. 4).
20 Based on floristic changes of the forest component, three pollen zones characterizing the main successive stages have been visually defined.

Zone N3 (ca. 4590–3200 cal yr BP; 413–355 cm) is characterized by high pollen values of the families, Caesalpiniaceae (18–29%), Mimosaceae (11–18%) and Sapindaceae (5–16%). As many of the trees, commonly found in Gabon, belonging to the Caesalpiniaceae (e.g., *Monopetalanthus* spp., *Cynometra* spp., *Anthonota* spp.,
25 *Berlinia* spp., etc.), Mimosaceae (*Calpocalyx* spp., *Piptadeniastrum africana*, *Penta-*

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clethra spp., etc.) and Sapindaceae (*Eriocoelum* sp., *Chytranthus* sp., *Ganophyllum* sp., etc.), are characteristic of closed canopy rainforest (Aubréville, 1968; Fouilloy and Hallé, 1973; Villiers, 1989), these pollen assemblages indicate that dense stands of mature rainforest occupied the catchment area of Lake Nguène during the mid-Holocene.

However, a slight decline of Caesalpiniaceae between 4100 and 3200 cal yr BP (sub-zone N3b: 395–355 cm) is associated with high pollen values of Sapindaceae trees belonging to semi-deciduous rainforests (e.g. *Ganophyllum* sp, *Blighia*, sp, *Chytranthus* sp, etc), as well as with small amounts of *Pycnanthus angolensis* (~2%), *Trilepisium madagascariensis* (~3%) and *Aphania*-type (~3%). These later arboreal pollen taxa, also typical plant species of semi-deciduous rainforest too, are light-demanding species growing in old secondary evergreen rainforests. Then, this pollen assemblage suggests that, from 4100 cal yr BP the evergreen rainforest surrounding lake Nguène was progressively replaced by semi-deciduous rainforest.

Zone N2 (ca. 3200–1400 cal yr BP; 355–115 cm) indicates major changes occurred in both the marsh and rainforest pollen signal.

Between 3200 and 2400 cal yr BP (subzone N2c: 355–255 cm), arboreal pollen taxa characteristic of the mature rainforest are progressively replaced by pioneering shrubs, notably, *Alchornea cordifolia* (up to 60%) and *Elaeis guineensis* (~10%), which favour disturbed forest habitats (Maley and Chepstow-Lusty, 2001). In Guineo-Congolian wetlands, *Alchornea cordifolia* is a shrub which grows in well-drained lake shore soils, as well as open areas of fringing forest bordering the lower reaches of lowland rivers (Lebrun and Gilbert, 1954; Evrard, 1968; Schnell, 1976). This species, which can tolerate marked flooding regimes (Evrard, 1968), may gradually colonize swamp shorelines as the mean water-level lowers. Thus, an abrupt rise in *Alchornea cordifolia* pollen, following a corresponding decrease in Cyperaceae pollen, clearly indicates that dense stands of littoral vegetation progressively invaded the lake basin. The significant presence of *Elaeis guineensis* pollen, remaining remarkably constant (~10%) throughout zone N2, associated with *Tetrorchidium* pollen (~3%) and declining mature forest

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pollen taxa, indicate the creation of openings in the closed canopy forest surrounding the lake basin.

From 2400 to 2000 cal yr BP (sub-zone N2b: 255–175 cm), fern spores and grass pollen markedly increase, reaching maxima of 40% and 10% of the total pollen sum, respectively. Many of the marshy pteridophyte species found today around Lake Nguène are either epiphytic ferns in the surrounding *Cyperus papyrus* swamp, or terrestrial ferns invading the lake shores during dry season low-stands (personal observation). As fern spores were not identified beyond family level, a distinction was not established between epiphytic wetland and more terrestrial forms. Nevertheless, the rise in fern spores, associated with both a slow increase in grass pollen and declining Cyperaceae pollen abundance, suggests that lake-levels were low during this period. It is also notable that a rise in marshy herbaceous pollen taxa, following a significant decline in *Alchornea cordifolia*-type pollen, is accompanied by an increasing abundance of secondary forest pollen taxa (e.g., *Aphania*-type (~5%), *Lannea*-type (2–15%), Anacardiaceae (~5%), *Trilepisium madagascariensis* (~5%) and Flacourtiaceae (~3%)). However, Caesalpiniaceae and *Nauclea*-type pollen continue to maintain significant relative abundances (5–10%). This pollen assemblage suggests a closed canopy rainforest persisted, but with increasing fragmentation allowing secondary forest taxa to colonize the gaps.

Between 2000 and 1400 cal yr BP (Zone N2a: 175–115 cm) pteridophyte spores decline to <20%, followed by peaks in the riverine species, *Alchornea cordifolia* (>20%), *Morelia senegalensis* (>15%) and *Martretia quadricornis* (up to 54%). Pollen from mature evergreen rainforest, mainly Caesalpinaeae, as well as those from herbaceous marsh (i.e. Cyperaceae and Poaceae) are very scarce (<1%). In contrast, pollen from secondary forest and semi-deciduous rainforest taxa (e.g. *Aphania*-type, *Lannea*, Flacourtiaceae) are significant (~10%) This marked pollen assemblage indicate that maximal regression of the mature evergreen rainforest occurs between 2000 and 1400 cal yr BP, even if the distinctive alteration in sediments – showing that the grey gley-muds, typical of marshy environments are replaced by fine dark clayey-muds

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indicative of lake deposits (Makaya, 2005) – may suggest that rainfall became abundant.

Zone N1 (ca. 1400–20 cal yr BP; 115–5 cm): a detailed high-resolution description of this section of Nguène pollen diagram has yet been published and can be found in (Ngomanda et al., 2007). Here, we sub-divided the zone 1 in two sub-zones to facilitate interpretation.

Between 1400 and 950 cal yr BP (subzone N1b: 15–70 cm), pollen from herbaceous marsh and swamp tree taxa, particularly *Nauclea*-type (~5%) and *Macaranga*-type (~5–8%) increase significantly. This indicates that Lake Nguène became a truly lake, which supported both a well-developed swamp forest, dominated by *Nauclea*-type *pobeguinii*, as well as an herbaceous marsh. The similar percentages of Cyperaceae pollen and pteridophyte spores (40–50%) suggest recurring seasonal lake-level fluctuations. *Irvingia gabonensis*, Caesalpiniaceae and Mimosaceae appear with significant frequencies (>5%), while *Elaeis guineensis* pollen reaches its last high abundance, suggesting the end of evergreen rainforest disturbance.

From 950 to 20 cal yr BP (subzone N1a: 70–5 cm), *Nauclea*-type *pobeguinii* (5–10%), Mimosaceae (>5%) and Caesalpiniaceae (10–25%) continue to increase, associated with an abrupt decline of *Elaeis guineensis* pollen (<1%). This indicates a renewed spread of dense closed canopy rainforest around the catchment. The associated increase in *Nauclea* type (>10%) and *Uapaca* type (~5%) pollen suggests further expansion of swamp forest and probably higher lake levels.

6 Maridor pollen record

A total of 158 pollen and spore taxa were identified in the 58 samples analysed (Fig. 5). Changes in relative pollen abundance in the Maridor record, reflecting the vegetation dynamics suggest three major zones with a total of four subzones.

Pollen zone M3 (ca. 4265–3940 cal yr BP; 423–405 cm) is dominated by Caesalpiniaceae pollen (16–28%), an indicator of moist mature evergreen rainforest in the

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Guineo-Congolian region (Aubréville, 1968; White, 1983). Pollen from secondary forest taxa, mainly *Aucoumea klaineana*, *Sacoglottis gabonensis*, *Lophira alata* and Flacourtiaceae are significant (>5%), while pollen of grasses and pioneering shrubs (e.g., *Alchornea*-type, *Macaranga*, *Tetrorchidium*, *Elaeis guineensis*, etc.) and hygrophytic herbs (Cyperaceae, pteridophytes and aquatics) are scarce (<1%). Although *Aucoumea klaineana*, *Sacoglottis gabonensis* and *Lophira alata* are typical secondary forest taxa, they can still be dominant in mature evergreen rainforest (Nicolas, 1977; Caballé and Fontes, 1978). Hence, the pollen assemblage indicates that a closed canopy forest existed in the Maridor region. Evidence of high water levels is provided by Melastomataceae pollen attaining 30%, which is probably from *Dissotis congolensis*, a shrub that is found in swampy environments around the lake today (Christy et al., 1990).

Zone M2b (ca. 3460–2890 cal yr BP; 400–370 cm) is characterized by a major decline in the major closed canopy forest pollen taxa, notably Caesalpiniaceae, Sapindaceae and Mimosaceae, accompanied by a progressive increase in pollen from gap-colonisers (*Elaeis guineensis* (~1–50%), *Macaranga* (5–10%), *Alchornea*-type (5–10%)) indicating the colonisation of rainforest canopy openings. This rainforest disturbance is concomitant with a significant rise in grass pollen (up to 80%) and terrestrial herbaceous pollen (>15%) indicating savanna development, associated with significant peaks of *Holoptelea grandis* pollen (up to 10%). The presence of this deciduous tree (Letouzey, 1968; White, 1983) reinforces the evidence for drier environmental conditions occurring from ca. 3800 cal yr BP.

Zone M2a (ca. 2890–2280 cal yr BP; 370–180 cm) is particularly distinguished by a marked increase in pollen from *Elaeis guineensis* (25–50%), associated with the continued dominance of other gap-coloniser pollen taxa, *Alchornea*-type (10–20%) and *Macaranga* (10–25%). An increase in dry conditions is also indicated not only by the notable presence of savanna shrub pollen (such as *Crossopterix*-type), but even among the mature forest pollen taxa, *Celtis* (2–7%) and Sterculiaceae (2–5%), both characteristic of semi-deciduous forests (Letouzey, 1968; White, 1983). Cyperaceae pollen (up to 70%) and pteridophyte spores (up to 80%), as well as a decline in aquatic

herbs, indicate the development of herbaceous marshy vegetation. This vegetational change coincides with a lithological shift from podzolic soil to sand-rich clays, suggests the Maridor became a permanent lake.

In zone M1b (ca. 2280–1940 cal yr BP; 180–110 cm) pioneer forest pollen taxa, e.g., *Elaeis guineensis* (8–12%) and *Macaranga* (5–8%) significantly decline, and there is a marked increase in secondary forest pollen taxa (e.g., *Tetracera*, Flacourtiaceae, *Bosqueia angolensis* (Nicolas, 1977; Christy et al., 1990)). Concurrently, arboreal pollen taxa from the forest-savanna mosaic (e.g., *Lophira alata* and *Aucoumea klaineana*) expand; these species are today actively involved in the savanna colonisation in the absence of fire (White and Abernethy, 1997; White et al., 2000; White, 2001). Mature forest trees, mainly Caesalpiniaceae (~5%), Mimosaceae (~5%) and *Celtis* (2–11%) are also well-represented in the pollen assemblage, indicating that the rainforest was being progressively reconstituted. In addition, pollen from aquatic taxa (>5% of the total pollen sum) increase, associated with the marked rise of *Myrianthus*-type (>5%), *Uapaca*-type (5–10%) and Melastomataceae (4–17%) pollen, most probably from the swamp trees, present today, *Uapaca guineensis* and *Dissotis congolensis*, respectively. The concomitant decline of Cyperaceae pollen and fern spores suggests the significant regrowth of swampy environments around Lake Maridor.

In Sub-Zone M1a (ca. 1940–290 cal yr BP; 110–5 cm), pioneering tree pollen (e.g., *Elaeis guineensis* and *Macaranga*) pollen rise again. Although, this is interpreted as an expansion of pioneer forest, it was not associated with a decline of pollen from secondary forest (e.g., *Aucoumea klaineana*, *Tetracera*, etc.), swamp forest (*Uapaca guineensis*, Melastomataceae cf. *Dissotis congolensis* and *Raphia*), as well as mature rainforest (e.g., *Drypetes*, Caesalpiniaceae, Mimosaceae, *Plagiostyles africana*) taxa. These pollen assemblages reveal a picture of mixed rainforest types similar to the current complex landscape of forest-savanna mosaic. In addition to the importance of swampy environments around Lake Maridor, the high abundance of Cyperaceae pollen and pteridophyte spores suggest a mosaic of marshy-swampy vegetation.

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Pollen data from Lakes Nguène and Maridor clearly show that a well-developed moist rainforest existed around the lakes before 4200 cal yr BP, as Caesalpiniaceae, a major indicator of Guineo-Congolian moist evergreen rainforest (White, 1983) is abundant in the pollen assemblages. Similar regional vegetation reconstructions have been described from other palaeoecological records across western Equatorial and West tropical Africa. Notably, pollen records from Cameroon (at $\sim 2^\circ$ N of our sites) showed that a Biafrean-type rainforest, dominated by Caesalpiniaceae, existed around Lakes Barombi-Mbo (Maley and Brenac, 1998) and Ossa (Reynaud-Farrera et al., 1996) during the mid-Holocene. During the same period, a semi-evergreen rainforest surrounded the catchment of Lakes Sinnda (Vincens et al., 1998) and Kitina (Elenga et al., 1996) in southern Congo (\sim at 2° S of our sites), as well as the catchment of the Lakes Bosumtwi and Sélé in Ghana and Benin (Salzmann and Hoelzmann, 2005), respectively.

From 4000 cal yr BP, the contraction of moist evergreen rainforest suggests the onset of aridity during the late Holocene. This major vegetation change occurred progressively, starting first by change in the floristic composition of mature evergreen rainforest (as shown by the replacement of Caesalpiniaceae by semi-deciduous trees in pollen diagrams of Maridor and Nguène), following by expansion of savannas and/or open forest formations. These later reach their maxima between 2700 and 2400 cal yr BP. The widespread occurrence, at a subcontinental scale, of arid conditions about 4000 cal yr BP is attested by palaeoecological data from other sites across inter-tropical Africa (Marchant and Hooghiemstra, 2004). Central-East African pollen records clearly show that mountain forest openings occurred synchronously in the highlands of Burundi, Rwanda and Uganda around 3800 ^{14}C yr BP (Jolly et al., 1997). This arid event, which is also associated in the inter-tropical zone with lower lake-levels (Street and Grove, 1979; Russel et al., 2003) and riverine discharge in the Gulf of Guinea, resulted to a weakening of African monsoon system in response to cooling sea surface waters of eastern equatorial Atlantic (Weldeab et al., 2005; Weldeab et al.,

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2007).

Up until now, the late Holocene spread of savannas in west tropical Africa, in response to an arid event, has only been recorded in western equatorial Africa, after 3990 ± 70^{14} Cyr BP (4530–4400 cal yr BP) from pollen record of lake Sinnda located in the savanna area of southern Congo (Vincens et al., 1998). In West Africa, pollen data from Lake Sélé (Salzmann and Hoelzmann, 2005) showed that the Dahomey Gap, a savanna corridor interrupting the West African rainforest, was also established at the onset of the late Holocene, after 4500 cal yr BP, due to an abrupt drying event. However, because of a sedimentary hiatus observed between 4500 and 3400 cal yr BP in all cores of these lakes, the precise starting of the savanna spread in West and Central Africa is unknown. Taking into account the inherent uncertainties to radiocarbon ages of pollen record, it can be suggested that expansion of savannas in coastal region of Gabon occurred synchronously with the formation of Dahomey gap (Salzmann and Hoelzmann, 2005) and spread of savannas in the Niari valley (Vincens et al., 1998).

The spread of savannas in the Maridor region around 4000 cal yr BP, however, occurred as the level of lake increased, as shown both by the sharp rise of pollen from marsh communities, (e.g., Cyperaceae, aquatic herbs) and by the sedimentary changes, with the deposition of sand-clay, typical sediments of lake deposits (Giresse et al., 2009), following the podzolic soil. Different morphodynamic processes, operating within the lake basin due to climatic oscillations, may explain this apparent contradiction between lake-level fluctuations and vegetation change around Lake Maridor. From ca. 4300 cal yr BP and during a rather short episode (until to ~3900 BP), the bottom of the lake acted as a bottom valley: the strong stream transport within the drainage basin resulted in an accumulation of alluvial coarse deposit in bottom of lake. The subsequent emergence of these alluvial coarse sediments led to a podzolisation of the deposit. This strong stream transport, disturbing and breaking sediments, may also explain the sediment discontinuity (lack of the A2 horizon of podzolic soil) observed in the core MAR2, a view point reinforced by the fact that sediments of the core MAR2, rather those of MAR1, have been collected in the deeper part of lake, probably close to the

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drainage basin. Decrease of stream transport, due to decline of rainfall input, improved to the accumulated podzolised deposits to block the outflow around 4000 cal yr BP, allowing the formation of permanent open water.

In contrast to the Maridor record, pollen data from Lake Nguène show that the rain-forest perturbation around 4000 cal yr BP was not associated with the rise of pollen from grass and other plants indicative of savannas, a pattern of vegetation change which is also observed in other pollen records obtained within the dense rainforest block of western Equatorial Africa (Elenga et al., 1996; Reynaud-Farrera et al., 1996; Maley and Brenac, 1998). Nevertheless, there is evidence for the development of fern-dominated herbaceous wetlands in the Nguène area. This difference in the response of rainforests to similar climatic changes, may reflect the sensitivity of plants to site-specific environmental conditions, particularly soil types. Indeed, the arboreal species occupying the Lake Nguène catchment essentially grow in hydromorphic, and therefore well-saturated soils. However, the rainforests surrounding Lake Maridor are today established on poor soils, composed of sand to clayey-sands, with low saturation and a limited capacity to retain available water (Barret, 1983). Hence, it is likely that in the past, the hydromorphic soils, by maintaining sufficient water during drought periods, allowed rainforest trees of the Nguène region to cope during dry episodes. Meanwhile, arboreal species growing in the sand-rich clayey soils near the Gabonese coast were more vulnerable to shifts in the water balance.

It has also been suggested that the major expansion of *Elaeis guineensis*, coupled with a rise of grasses may be due to human agricultural activity (Maley, 1999; Maley and Chepstow-Lusty, 2001), as the recovery of pollen and macro-remains of this oil palm in palaeoecological records has often been used as an anthropogenic indicator (Clist, 1995; Oslisly, 1995; Oslisly, 1998; Oslisly, 2001; Assoko Ndong, 2002). This hypothesis is supported by the fact that in many Neolithic (4500–2500 cal yr BP) and Iron age (2400 cal BP to present) Gabonese archaeological sites, substantial amounts of palm nuts have been found in this region, suggesting the importance of this resource to humans during the late Holocene (Clist, 1995; Oslisly, 2001; Assoko Ndong,

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2002). However, no evidence for systematic cultivation of *Elaeis guineensis* in the re-
gion has been formerly demonstrated, although the Bantu are considered as farmers;
simply gathering palm nuts in secondary forests, naturally abundant in *E. guineensis*,
may easily explain its concentration in archaeological sites. Indeed, in other Holocene
5 sites from western equatorial Africa, pollen data clearly show that the expansion of
Elaeis guineensis always followed the widespread establishment of grassland savan-
nas (Elenga et al., 1992; Elenga et al., 1994) or temporary forest openings (Elenga et
al., 1996; Reynaud-Farrera et al., 1996; Maley and Brenac, 1998; Ngomanda et al.,
2005). It can be emphasized that the Lake Nguène vegetation record shows a signifi-
10 cant decrease in *E. guineensis* pollen during the last five centuries. This is exactly the
time interval when anthropogenic impact on rainforests (e.g., due to increasing human
population densities) would be expected to rise. In the absence of archaeological data
clearly demonstrating oil palm cultivation by the Bantu during the late Holocene, we as-
sume that the close synchronicity of its wide scale expansion during the late Holocene
15 in central Africa must have been caused by climatic-induced opening of the rainforest
as concluded in other studies (e.g. Maley, 1999).

8 Conclusions

Pollen data from Lakes Maridor and Nguène in Gabon show that hydrological changes
occurring over the past 4500 yr were the major driving force that controlled the dy-
namic of rainforest in this part of western equatorial Africa. They clearly evidence that
20 the current forest-savanna mosaics of the coastal region of Gabon established about
4000 cal yr BP, following a rapid climatic-induced deterioration of evergreen rainforest
which covered that region during the mid-Holocene.

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Table 1. Radiocarbon dates of bulk organic matter from cores MAR2 and NGUE1 of Lakes Maridor and Nguène, respectively. All radiocarbon dates were calibrated using the Calib rev. 5.0 program (Reimer et al., 2004).

Core Number	Depth (cm)	Materiel dated	Laboratory code	^{14}C age BP	Calendar age BP and range (2 σ)
Maridor-2	25	Bulk	BETA 195 417	1490±60	1360 (1299–1518)
	97	Bulk	BETA 206 438	3230±40	3435 (3377–3557)
	148	Bulk	BETA 195 416	2190±40	2226 (2113–2332)
	184	Bulk	BETA 206 439	3430±40	3725 (3582–3827)
	221	Bulk	BETA 202 480	3440±40	3728 (3612–3830)
	254	Bulk	BETA 206 440	2600±40	2540 (2508–2786)
	292	Bulk	BETA 202 481	4070±75	4620 (4419–4822)
	363	Bulk	BETA 206 441	2630±40	2810 (2714–2884)
	418	Plant macrofossil	GIF 11 619	3795±55	4200 (3991–4407)
Nguene-1	35	Bulk	BETA 195 415	430±40	492 (326–536)
	75	Bulk	BETA 195 414	990±40	845 (795–964)
	105	Bulk	BETA 195 413	1630±40	1512 (1410–1615)
	125	Bulk	GIF 11 618	1600±35	1442 (1406–1557)
	153	Bulk	BETA 202 478	1940±40	1896 (1815–1930)
	192	Bulk	BETA 202 479	3310±40	3526 (3449–3636)
	257	Bulk	UtC 13 545	2429±41	2425 (2351–2702)
	277	Bulk	BETA 206 442	2510±40	2550 (2458–2743)
	337	Bulk	BETA 195 412	2540±40	2720 (2488–2750)
	375	Bulk	BETA 206 443	4460±40	5127 (4960–5294)
	413	Bulk	BETA 189 989	4110±40	4590 (4453–4821)

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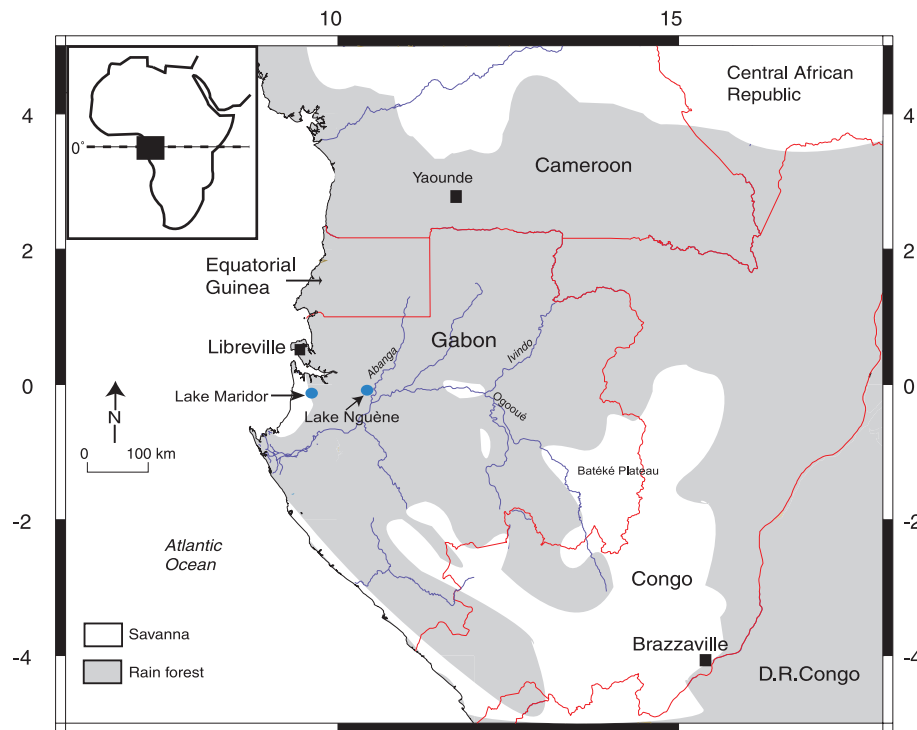


Fig. 1. Simplified vegetation map of Gabon in central Africa and location of Lakes Maridor and Nguène.

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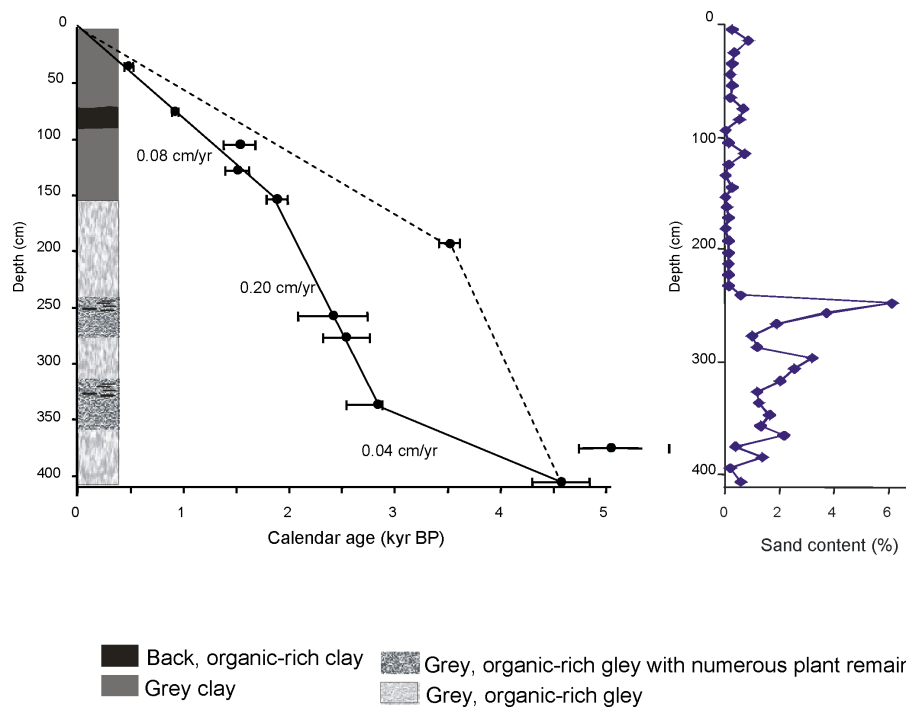


Fig. 2. Age-depth plot and sand content of core NGUE1. Sediment accumulation rates are based on linear interpolation of calibrated radiocarbon dates.

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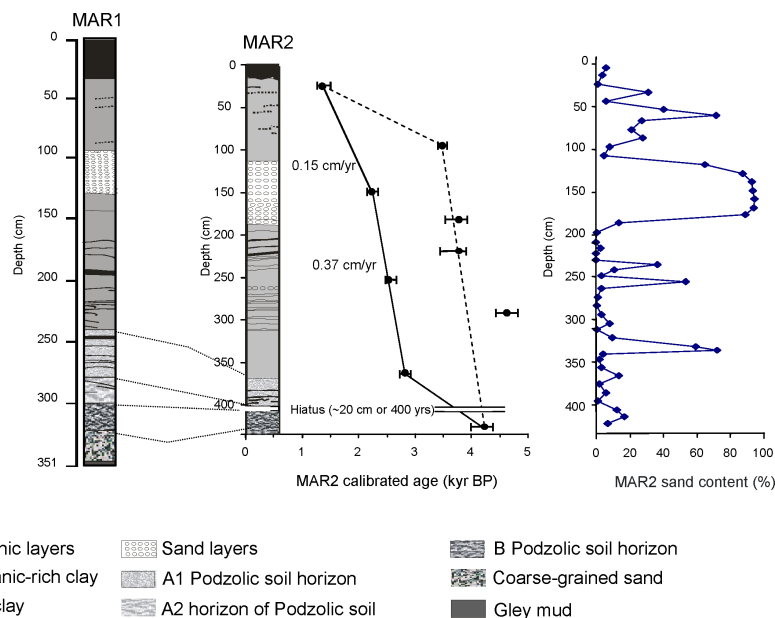


Fig. 3. Age-depth plot and sand content of core MAR2. Sediment accumulation rates are based on linear interpolation of calibrated radiocarbon dates.

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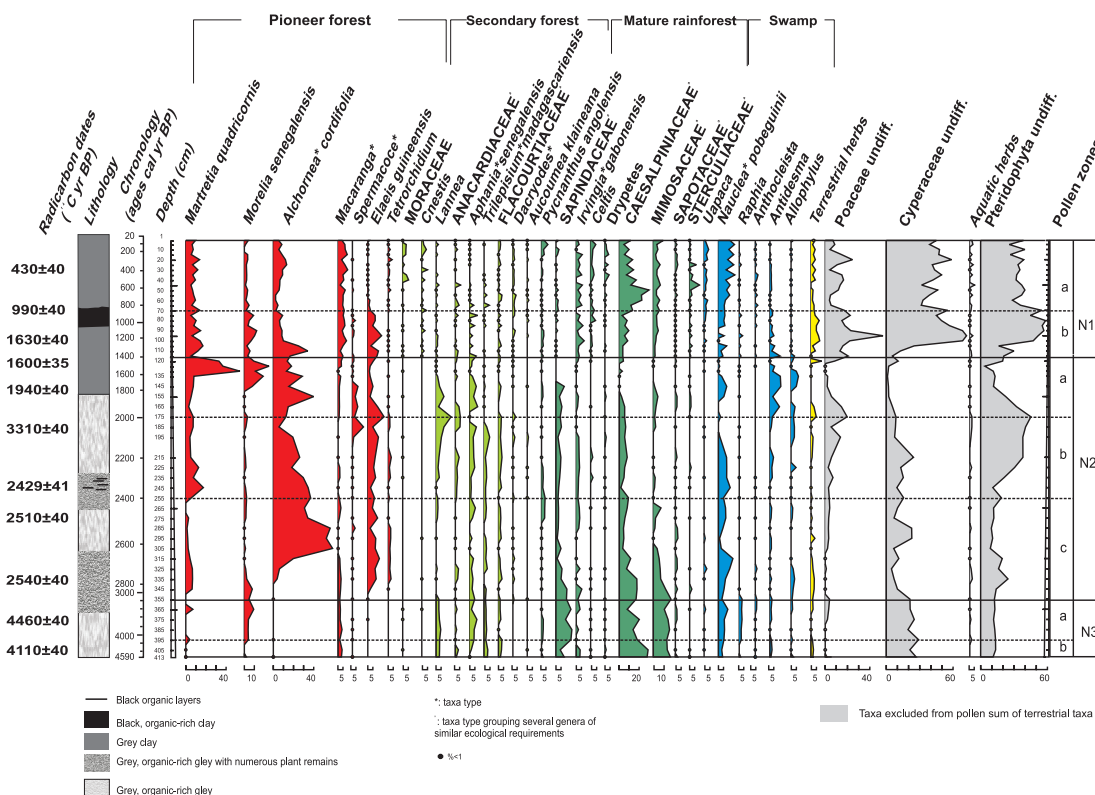


Fig. 4. Summary pollen diagram from Lake Nguène. The pollen sum of terrestrial taxa excludes pteridophyte spores, aquatic herbs, Cyperaceae and Poaceae pollen.

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