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Late Quaternary palaeoenvironments in the Lake Barombi Mbo (West Cameroon) deduced from pollen and carbon isotopes of organic matter

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ABSTRACT

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A sediment core, 23.5 m long, was recovered from a water depth of ca. 110 m in Lake Barombi Mbo, a maar crater of the Cameroon volcanic chain. This paper presents a carbon isotopic curve of organic matter linked to the main results of the pollen analysis. Interpretation of this carbon isotopic curve is simplified (1) because of the weak role played by the phytoplankton in the balance of the organic particle flux, and (2) because of the presumed absence of diagenetic alteration of the isotopic composition. The carbon isotopic curve exhibits an almost linear correlation with that of total grass pollen which form the main part of the C4 biomass. The major fluctuations of isotopic and pollen curves allow four main phases to be distinguished:

—from ca. 25,000 to 20,000 yr B.P., $\delta^{13}C$ values of −25 to −30‰ (PDB) are related to a forest environment associated with a montane floral element;

—from 20,000 to 13,000 yr B.P., the $\delta^{13}C$ values are between −23 and −28‰ and are linked to openings of landscape with a mosaic of forest and savanna and a fall of lake level with colonization of the shores by Cyperaceae and other aquatic plants;

—from 13,000 to 10,000 yr B.P., the forest extended again reaching a maximum density during the period from 9500 until 3000 yr B.P. and with an average $\delta^{13}C$ value of −32‰;

—a new dry phase occurred at around 2500–2000 yr B.P., with temporary openings in the forest, marked by a $\delta^{13}C$ excursion above −30‰, but during the last 2 millennia, the forest developed again with $\delta^{13}C$ values of −32‰.

Introduction

By comparing the present day biologic richness (plants, birds, mammals, amphibians, butterflies, etc) of large parts of the West Cameroon rain forest with other parts of the African rain forests, several biogeographers have concluded that during dry periods, such as during the Last Arid Maximum, an important refugium existed in West Cameroon. The Lake Barombi Mbo pollen record clearly shows that from ca. 24,000 yr B.P. until the present time, the rain forest persisted with limited variations, thus confirming that this region was a refuge area (Maley, 1991).

In the present study, we compare $\delta^{13}C$ variations in the bulk organic matter with the palynological record from a core collected in the central and deepest part of the lake. The results of multidisciplinary studies of sedimentological, palaeomagnetic and palynological records are published elsewhere (Giresse et al., 1991; Thouveny and Williamson, 1988; Maley and al., 1990; Brenac, 1988) or will be published. In the present paper, special emphasis will be placed on the compared response of ^{13}C indices and pollen.

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Plants have two types of photosynthetic pathways: one cycle in C3, called Calvin cycle, and one in C4, called Hatch and Slack cycle (Bender, 1968, 1971; Smith and Epstein, 1971). In lowland tropical regions most of the Gramineae, which are dominant in savanna areas, have a cycle in C4 with $\delta^{13}C$ values mainly between −12‰ and −16‰, while nearly all the equatorial rain forest trees have a pathway in C3 with $\delta^{13}C$ values from −26‰ to −36‰ (Livingstone and Clayton, 1980; Schwartz et al., 1986, 1992; Talbot and Livingstone, 1989; Medina and Minchin, 1980; Farquhar et al., 1989; Van der Merwe and Medina, 1989)(see p. 74). In this manner, $\delta^{13}C$ variations in the sediment organic matter can be explained by the change of vegetation cover, particularly with the substitution of open environments by forests. Because the productivity of plankton biomass is very low in this lake, which can be related to the near-absence of diatoms in the sediment studied, the $\delta^{13}C$ values mainly reflect the organic matter accumulated in the top soil (leaf litter and A1 humic horizon, mainly the upper 10 cm) and washed away in the lake by runoff (Stuiver, 1975; Talbot and Livingstone, 1989; Hillaire-Marcel et al., 1989). In addition, the carbon/nitrogen ratio was measured and Rock-Eval analyses were performed to complete the characterization of organic matter.

Setting

The Barombi Mbo (4°40'N–9°24'E), the largest lake in Cameroon (surface area 4.15 km^2), is situated in an explosive crater 1 Ma old and is located in the volcanic range of West Cameroon (Maley et al., 1990). One notable feature of this lake is an enlarged catchment created to the west by a second shallow and boxed-in crater (Dumort, 1968) (Fig. 1); a ferrallitic soil has developed on this enlarged catchment. The lake diameter is ca. 2 km, its altitude 301 m.a.s.l. (above sea level) and its maximum depth 110 m, with a mean of 68 m.

The lake level is stabilized by a natural spillway which has cut a subvertical gorge to the southeast. The lake has a bowl shaped morphology with a flat bottom and a narrowish littoral platform, except to the west where a deltaic zone has formed

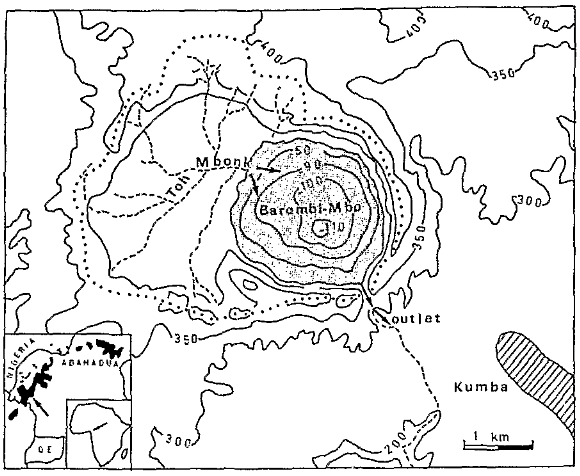


Fig. 1. Map of Lake Barombi Mbo area and bathymetry of the lake. At the right: Kumba city area; dotted line: lake catchment boundary.

at the inlet of a small river, the Toh-Mbok (Fig. 2). The lake exhibits a distinct thermal stratification with a thermocline oscillating during the year between −30 m in February (end of the dry season) and −40 m in September (maximum of the rainy season). This stratification leads to a strong stability which reaches 5784 J m^{-2} in June with a minimum of 3000 J m^{-2} in September (Kling, 1988b), this means that here the lowest values are greater than the highest ones reported by this author in other tropical lakes. For this reason an overturn is unlikely.

The transparency of Barombi Mbo (11 m estimated with the Secchi disk) is one of the highest in the Cameroon lakes. Surface water temperatures range between 28.6°C in February and 26.6°C in September, following closely the annual cycle of air temperature and insolation. Conductivity varies between 49.1 $\mu S\ cm^{-1}$ at the surface to 80.2 $\mu S\ cm^{-1}$ at depth: bicarbonate is the principal anion while the major cations are Si^{4+}(12.3–16.1 mg l^{-1} SiO_2), Ca^{2+}(2.6–7.5 mg l^{-1}), Mg^{2+}(2.5–2.6 mg l^{-1}), Na^{+}(2.3–2.6 mg l^{-1}) and K^{+}(1–1.2 mg l^{-1}) (Kling, 1987a,b).

Waters below −15 to −25 m are anoxic. The planktonic biomass is low and composed essentially of cladocerans and copepods (Kling, 1987a), allowing the growth of some cichlid fishes (Green et al., 1973). Diatoms are practically absent from

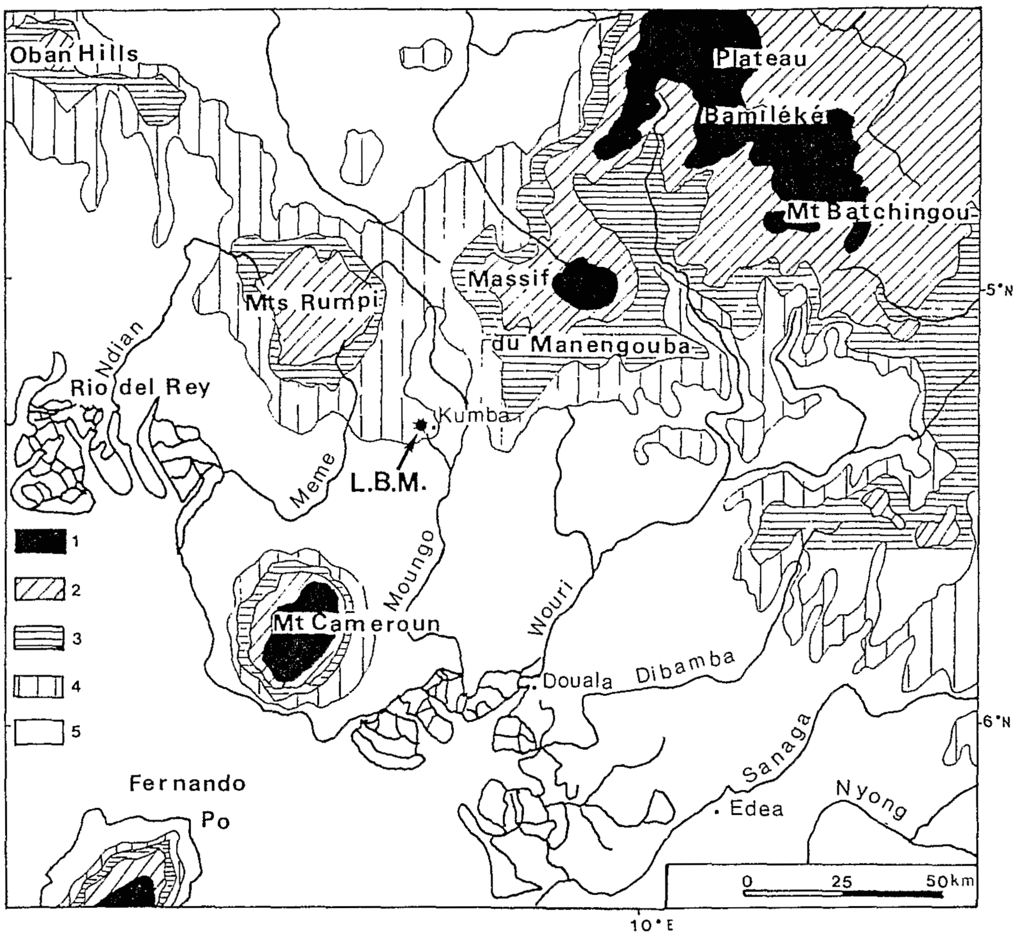


Fig. 2. Map of West Cameroon with position of lake Borombi Mbo (LBM). Altitudes, *1*= over 1500 m; *2*= 900–1500 m; *3*= 600–900 m; *4*= 300–600 m; *5*= 0–300 m.

the surface water and from the Quaternary sediments (Giresse et al., 1991); this near absence can be related to a nutrient deficiency, particularly phosphorus (cf. Kilham et al., 1986).

Methods

Several long cores (from 10 to 23 m) have been taken in this lake, particularly in the central zone, by a crew led by D.A. Livingstone as part of a cooperative program involving ORSTOM (France), Duke University (USA) and several Cameroon scientific Institutes of MESIRES (Maley et al., 1990). Later, short cores of about 1 m long, intended to analyze the secular sedimentary rhythms (Pourchet et al., 1988 and in prep.) were taken to complete the sampling.

The core studied (BM6) is situated in the central and deepest part (−110 m). A total of 15 radiocarbon datings (performed by Fournier in ORSTOM, Bondy: see Maley et al., 1990; Giresse et al., 1991) were done on this core. The greatest part was performed on the total sediment and some, by comparison, only on the carbon of the organic matter. The resulting chronological scale can be compared to the one based on paleomagnetism (Thouveny and Williamson, 1988; Williamson, 1991).

$^{13}C/^{12}C$ ratios of the total organic matter were measured in the Geotop Laboratory of l'Université du Québec à Montréal (Dir. C. Hillaire-Marcel) on samples taken each 10 cm except in some perturbed parts. Measurements were performed on samples decarbonated with dilute HCl ($0.1N$) agitated in an ultrasonic bath. The results are expressed as $\delta^{13}C$‰ with respect to the PDB standard, after the usual corrections (Craig, 1954)(Fig. 3A).

Each 30 cm, total organic carbon (TOC) was measured with a coulometer and total organic nitrogen (TON) was determined by the Kjeldahl method (Fig. 3A). Moreover, the Hydrogen Index was obtained by pyrolysis (Rock-Eval analyses, see Talbot and Livingstone, 1989) of 16 samples (about one sample for each core metre). The measurements were done by Michael Talbot, Geologisk Institutet, Bergen University (in litt., 1988). To support these data, smear slides of sediment were prepared for microscopic identification of organic particles, particularly abundant in brown sublaminae, and a semi-quantitative assessment of the principal components (wood, herbs or amorphous). Pollen assemblages were determined at intervals similar to those of $^{13}C/^{12}C$ measurements.

The main sedimentation conditions

Sedimentation is principally a result of recurrent floods of the Toh-Mbok which determine characteristic sequences in the lacustrine sediments: on the deltaic slope the deposits are mainly sandy (Giresse et al., 1991; Maley et al., 1990), beyond -80 to -90 m depth, in the central part of the basin, the sediment is laminated and each lamina is characterized by two different sedimentary facies:

—a lower, coarse, brown sublamina, with quartz and feldspathic grains, vegetal fragments and sponge spicules,

—an upper, light sublamina dominated by clay with disseminated microcrystals of siderite. Amorphous (ferrous or ferric) iron and siderite colour the sediment in blue or green. Sometimes yellow larger concretions of siderite are present at the top of the lamina, associated with a small proportion of vivianite (Giresse et al., 1991).

This sequence is interpreted as depending on the river floods, forming plumes of surface turbid waters which eventually settle more or less slowly. The overall frequency of repetition of laminae is, in the total section studied, on the order of about 15 yr (Giresse et al., 1991). This periodicity is close, or one multiple of magnitude (ca. 30 yr) or one lower multiple (ca. 8 yr), to that of the major floods of large African rivers for which there is a record of about one hundred years (Senegal, Niger, Chari, Congo-Zaire, cf. Probst and Tardy, 1987; Nile, cf. Quelennec, 1974; Sutcliffe and Knott, 1987). During periods of slow sedimentation between major floods, siderite precipitated within the upper clay-rich sublamina. Some darker microlaminae may be interlayered in the clayey sublamina, where they express the input of minor floods between two major floods (Giresse et al., 1991).

Above a discontinuity dated at about 21,000 yr B.P., the stratification continues regularly up to the top of the core. The $\delta^{13}C$ measurements reported here were done above this discontinuity. Millimetre to centimetre thick layers of volcanic ash are interstratified between ca. 18,000 and 10,000 yr B.P. (Maley et al., 1990; Cornen et al., 1992). Roughly the sedimentation rate from 20,000 to 14,000 years was slow (13–27 g cm^{-2} 10^{-3} yr); it speeded up particularly after 12,000 years (40–47 g cm^{-2} 10^{-3} yr), the clayey sublaminae becoming more important than the detrital brown sublaminae (Giresse et al., 1991). Later, during late Holocene time, the sedimentation rate slowed down again (<40 g cm^{-2} 10^{-3} yr).

Results

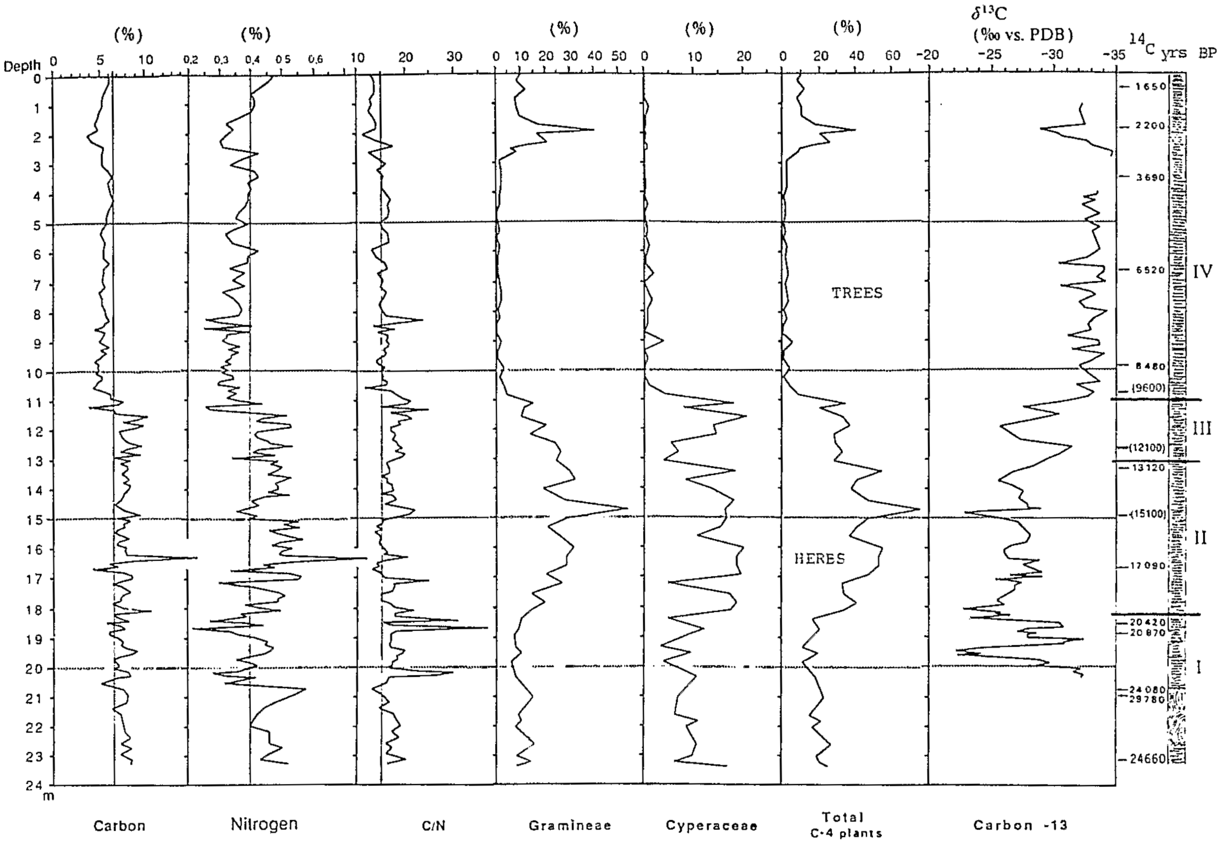
Vegetation history around the Lake Barombi Mbo from ca. 25,000 yr

The natural present day forest vegetation, within a radius of 10–20 km of the lake, is composed of two main formations (Letouzey, 1968, 1985):

— evergreen rain forest, of Biafrean type, widely dominant and characterized by its richness in Leguminosae,

—semi-deciduous rain forest, rich in Ulmaceae and Sterculiaceae, forming islets within the evergreen formation.

Several km^2 of relic savanna, with few trees, mainly the palm *Borassus aethiopum,* can be



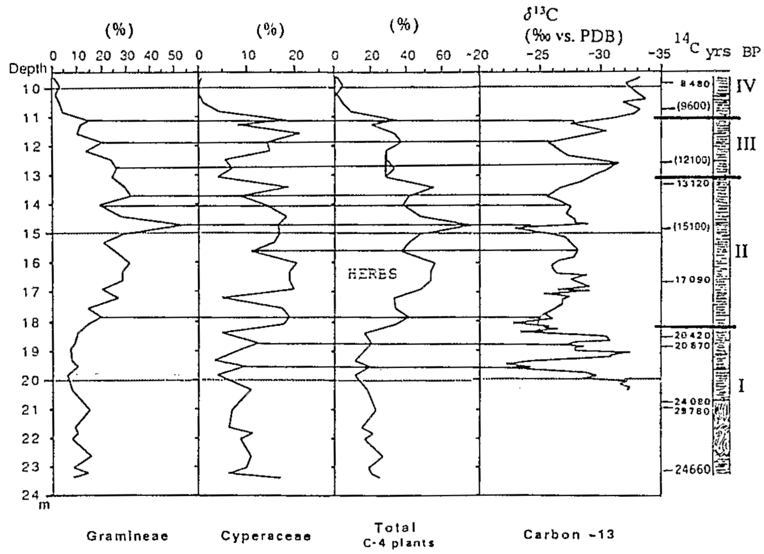


Fig. 3. Core BM 6 (− 110 m). A. From the left: depth (m); percentages of organic carbon and nitrogen; C/N ratio; curves of pollen percentages of Gramineae, Cyperaceae and total C4 plants which correspond to Non Arboreal Pollen (NAP or herbs) versus Arboreal Pollen (AP or trees); $\delta^{13}C$ PDB; at right the ages (mean values) from radiocarbon dating (from Giresse et al., 1991) and between brackets some interpolated ages; *I–IV* are the 4 zones distinguished for the carbon isotopic curve. B. Section between 10 and 20 m below the top (late Pleistocene): for selected parts correlations between the pollen curves and the $\delta^{13}C$ are shown (for some points there are short lag due to sampling).

observed at several points around the northeast foot of Mount Cameroon, ca. 60 km to the southeast of the lake (Letouzey, 1985).

The pollen analyses have been done in the BM6 core and some have already been published (Brenac, 1988; Maley and Brenac, 1987; Maley, 1991). Here we present the main results (relative percentages) with the curve of AP/NAP which shows the relative proportions of the total arboreal pollen versus total grass pollen (Figs. 3A and 6).

In this region most of the Gramineae are savanna species (Letouzey, 1968). Obervations on the present-day lacustrine environment show that hygrophilous Gramineae are uncommon (Brenac, 1988). As a whole, the relative importance of Gramineae pollen is a good indication of the vegetion, high Gramineae values reflecting relatively open vegetation (Maley, 1981; Vincens, 1982; Brenac, 1988). The study of pollen spectra shows that before 20,000 yr, Gramineae pollen frequencies are between 10 and 15%; thereafter they increase and range between 20 and 30% until about 12,500 yr, except one sample with 53% at ca. 15,100 yr B.P.; then they decrease again, with large variations, until the beginning of Holocene time. From 9500 to 3500 years the percentages are very low, nil to 1 or 2%. Another increase occurred after 3000 yr culminating between ca. 2500 and 2000 yr B.P. with values between 20 and 40%. After that, the percentages fall abruptly and during the last two millennia they vary between 7 and 11%. The present-day percentage is 7 %.

From these data, one can infer:

—before 20,000 yr B.P., a forest environment with a density comparable to the present, but associated with a montane element characterized by large amount of *Olea capensis* (syn. *O. hochstetteri*) pollen type; some present-day cloud forests exhibit a similar environment,

—between 20,000 and 14,000 yr, an opening of the landscape with a mosaic of patches of forest and savanna,

—after 14,000 yr the forest extended again and the reconquest was achieved in early Holocene time,

—from ca. 9500 yr until ca. 3000 yr B.P., the density of the forest was maximum,

—a new dry phase suddenly began around 2500 yr B.P. causing temporary openings in the rain forest during nearly 500 radiocarbon years (Maley, 1992).

—during the last 2 millennia the regional forest developed again and was close to the present-day state.

In other parts of the wet tropical zone a dry phase occurred near the beginning of Late Holocene time, as in Bosumtwi (Ghana) at 3700 yr B.P. (Talbot et al., 1984; Maley, 1991), but apparently not in the Barombi Mbo region. On the other hand the well marked dry phase which occurred here between 2500 and 2000 yr B.P. is very significant from Cameroon to Congo and East Africa (Maley, 1992).

The Cyperaceae are in great majority plants of aquatic environments, such as in Cameroon (Letouzey, 1968, 1985). Frequently, when a lake level falls or oscillates, muddy beaches appear which are quickly colonized by aquatic vegetation and particularly by Cyperaceae (Maley, 1972, 1981). At Barombi Mbo (Fig. 1) a large drowned shelf extends on the deltaic zone offshore the inlet of the Toh-Mbok and the aquatic vegetation can spread on this shelf during low stands of the lake. Before Holocene time, the variations of Cyperaceae pollen, positively correlated ($R = 0.648/n = 35$) with those of the pollen of other aquatic plants (mainly *Nymphaea*, *Typha*, *Utricularia*, *Potamogeton*), are related to slight variations in lake level.

In the section before 20,000 yr (Fig. 3A), the Cyperaceae pollen vary between 3 and 16%. After this time they increase with a maximum of 20% near 17,000 yr, they remain at 15–20% until the end of the Pleistocene, except around 12,000 yr with low percentages of 4–6%. At the beginning of Holocene time they disappear almost completely. The phase of maximum extension between ca. 20,000–10,000 yr B.P. was probably associated with slight falls of lake level, of no more than a few metres, interrupting from time to time the functioning of the outlet.

The Gramineae and Cyperacae pollen grains, to which the aquatic pollen are added, form the total of herbaceous plants. Among the Cyperaceae the C4 type is very dominant in tropical Africa (Raynal, 1972). The total of herbaceous plants here constitute the main C4 biomass, versus the total of tree pollen which constitute the main C3 biomass. In the tropics the C3 grass species (Pooideae) live only on the high mountains such as in East Africa, because of the reportedly higher frost sensitivity of C4 grasses (Ludlow, 1976). In altitudinal transects in Kenya and other African mountains, Tieszen et al. (1979) and Livingstone and Clayton (1980) found no C3 grass species below 2000 m and no C4 grass species above 3000 m (see pp. 73).

The terrigenous origin of the organic matter

The Hydrogen Index (HI) of the studied organic matter samples are between about 100 and 400, with an average close to 200. Such values are common for terrestrial plant remains and particularly wood remains and other ligno-cellulosic tissues. This result has been confirmed by microscopic examination of slides which have also shown the near absence of diatoms or other algae. Kling(1988) noted that the scarcity of zooplankton can be related to the scarcity of phytoplankton. These data show that the organic matter is almost entirely of terrigenous origin coming from the catchment, but relatively high values of HI also indicate that the organic matter is well preserved in bottom sediments.

Comparison of $\delta^{13}C$ variations and pollen relative values

In broad outline the carbon isotopic curve (Fig. 3,A) allows four main zones to be distinguished:

—from ca. 24,000 to 20,000 yr B.P., the curve, though somewhat irregular, exhibits values close to −25‰ or going under −30‰,

—from ca. 20,000 to 13,000 yr B.P., the concentrations in ^{13}C increase distinctly and the $\delta^{13}C$ range between −23 and −28‰,

—from ca. 13,000 to 10,000 yr B.P., there are large variations between −26 and −31‰

—from ca. 10,000 yr B.P. to the core top, the $\delta^{13}C$ values are again very low with an average of −32‰, except between ca. 2500 and 2000 yr B.P., with a distinct excursion above −30‰. Two hiatuses in the ^{13}C sampling must be noted, one between ca. 4000–3000 yr B.P. and the second corresponding to the last meter of the core top (the last measurement is dated at ca. 1800 yr B.P. by interpolation).

Before the Holocene forest extension $\delta^{13}C$ values exhibit an almost linear correlation ($R = 0.615$) with that of the total Gramineae and Cyperacae pollen which form the main C4 biomass (Figs. 3B and 4).

The maximum forest extension phase of early and middle Holocene time gives a relatively regular $\delta^{13}C$ of ca. −32‰, which is a very low value. Plants photosynthesizing via the C3 pathway are usually depleted in ^{13}C, particularly under tropical rain forest canopy (−22‰ up to −36‰) (Van der Merwe and Medina, 1989; Descolas-Gros and Fontugne, 1990) and up to −38‰ for plants growing in the ca. 20 cm zone above the ground (Blanc, 1989). In the case of the alluvial organic matter fraction of large rivers flowing through tropical rain forests (along which there are frequently large stands of aquatic vegetation, mainly of the C4 type), the $\delta^{13}C$ values are ca. −28‰ for the Congo–Zaïre river catchment (Mariotti et al., 1991), for the Amazon (Bird et al., 1991) and also for some forested areas of the Sanaga in south Cameroon (Bird, unpublished data; pers. comm.).

During the principal dry phase between 20,000 and 13,000 yr B.P. one observes a very distinct shifting of the curve towards higher values (average

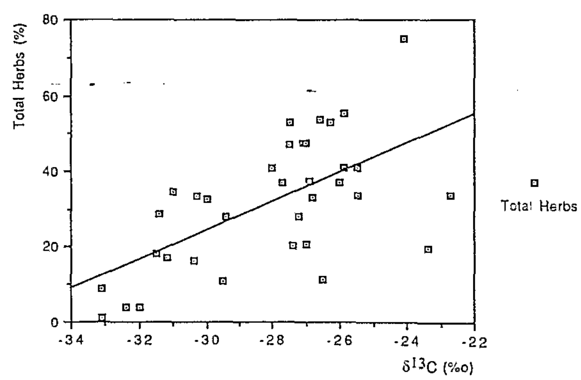


Fig. 4. Core BM 6 . Section between 10 and 20 m below the top. Relationship between total C4 grass pollen (total herbs) and $\delta^{13}C$ (point to point) is positively correlated ($R = 0.615$, $p < 0.001$, $n = 35$).

limit of typical forest isotopic values (−26 to −36‰). In the forest–savanna mosaic environment deduced from the pollen data (see p. 70), such a result is probably explained by the obvious dominance of forest areas over those of savanna type, characterized by the Gramineae, and also to the possibility that patches of savanna developed mainly outside the lake catchment. Nevertheless one sees here that the carbon isotopic curve suggests minimal spread of the savanna areas, confirming the presence of large forest refuges in this region during the last major arid phase.

In comparison, the pollen study carried out to the west, in the Guinean forest block, on the sediments of the Lake Bosumtwi in Ghana, has shown a forest disappearance in this region between ca. 19,000–15,000 yr B.P., with a total of tree pollen below 5% (Maley, 1991). Talbot and Johannessen (1992) have measured $\delta^{13}C$ of organic matter from the same core. The results confirm the pollen data. The forest period indicated by palynology between ca. 9500 yr B.P. and the present-day appears also very distinctly with an average $\delta^{13}C$ of −28‰, while the previous period without forest is characterized by $\delta^{13}C$ values of between −20 and −10‰, typical of very open environments where Gramineae are dominant.

In Lake Barombi Mbo, after a large negative spike bracketed between interpolated ages of ca. 13,000–12,000 yr B.P., the $\delta^{13}C$ curve exhibits two positive excursions which match two distinct positive spikes of C4 herbaceous plant pollen (Fig. 3A). These two successive positive $\delta^{13}C$ spikes, dry phase indicators, are dated by interpolation at ca. 11,200 and ca. 10,300 yr B.P. After that time the $\delta^{13}C$ curve reaches very negative values of −33‰ around 9800–9500 yr B.P., which marks the beginning of the last maximum and continuous forested phase. This phase persisted during Holocene time until the present day, interrupted only by the short but well marked dry phase between ca. 2500–2000 yr B.P. (Maley, 1992).

Between 20 and 18.5 m (ca. 21–20,000 yr B.P.) the carbon isotopic curve exhibits a negative anomaly which appears in neither the organic matter curve nor that of the C4 plant pollen. This interval corresponds to the end of a rain forest phase (see p. 70) and study of laminae microstructures from this core interval shows that brown lower sublaminae are particularly well developed (5–10 mm) and contain great quantities of vegetal forest remains, such as large leaf fragments and particularly many microscopic fragments of leaves, stems, wood and bark, which could explain this negative anomaly.

Relation between $\delta^{13}C$ values and the composition of accumulated organic matter

It has been suggested above (see p. 71) that the organic particle flux results essentially from terrigenous biomass. Lignin and cellulose, which are the dominant components of terrestrial higher plants, are nitrogen-poor. This allochthonous origin is indicated by the quite good correlation between carbon and nitrogen (Fig. 5). Organic nitrogen occurs preferentially in proteins and nucleic acids (Meybeck, 1982), which are abundant in lower plants such as aquatic phytoplankton. Because nitrogen is more labile than carbon, the C/N ratio is a good index of maturation, i.e. mineralization, of the organic matter. Autochthonous lacustrine organic matter is characterized by relatively low C/N ratios, typically < 10. Analyses from Barombi Mbo deposits give C/N values generally higher than 15, confirming the largely allochthonous origin of the organic matter.

The organic sedimentation can be schematically divided into two periods (Fig. 3A):

—before 10,000 yr B.P., total organic carbon (TOC) is close to 8% with ca. 16% of total organic matter (TOM), total organic nitrogen (TON) between 3.5 and 5.5% and the C/N ratio close to 17. The levels where the C/N ratio are above 24 intervene when the brown sublaminae (p. 68) are particularly thick and rich in lignitic fragments (wood, leave ribs, etc). Because lignin contains 50% more carbon than cellulose, these lignitic fragments have large effects on the total balance of $\delta^{13}C$ (Benner et al., 1987), especially when the catchment exhibits some savanna gaps rich in Gramineae.

—after 10,000 yr B.P., TOC decreases to 5–6% with ca. 10–12% of TOM and to 3–4% of TON; similarly, the C/N ratio decreases to 15, then to 13 during the last two millennia.

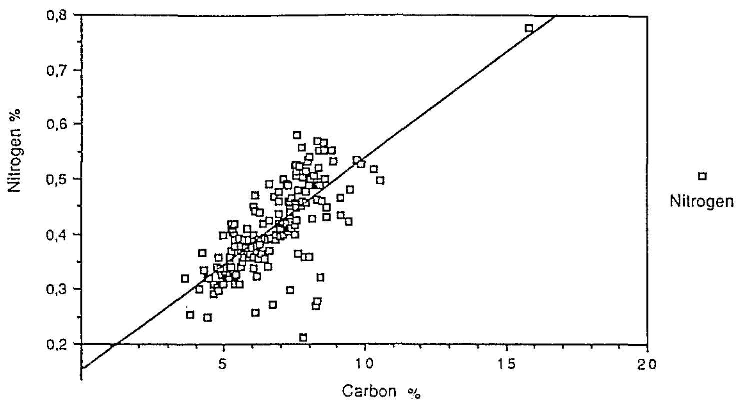


Fig. 5. Core BM 6 . Relationship between carbon (%) and nitrogen (%), positively correlated ($R = 0.741$, $p < 0.001$, $n = 174$).

The first period is correlated with a slowing down of the pedogenesis, during which few or no transformed minerals of the substratum, such as sheet silicates from the mica group, have been carried to the lake (Giresse et al., 1991). During this time, the litter or the A1 horizon are the main sources of organic matter; opening of the landscape promotes this important organic supply.

The second period saw an increase of ferrallitic pedogenesis which gave a large flux of kaolinitic clay particles (Giresse et al., 1991). A dense forest environment protected the A1–A2 horizons, the organic flux slowed down; smear slides have allowed to observe particularly low lignitic components. The organic matter is mainly colloidal and consists of amorphous matter.

Interpretations and discussion

(1) In relation to the temperature changes between the first period (before 10,000 yr B.P.), which was cooler and characterized by a vegetation including a montane element, and the second period, which was warmer and marked by the return of a lowland forest vegetation (Maley and Brenac, 1987; Brenac, 1988), complementary interpretations can be made (Maley, 1991). Considering that several ecologists working on tropical lowland and mountain forest formations have concluded that the lower temperatures on mountains do not act directly upon the plants, but indirectly through nutrient limitations, particularly for nitrogen and phosphorus (see Grubb, 1971, 1977; Whitmore, 1975; Vitousek, 1984; etc), one can conclude:

—in mountain environments the lower temperature reduces the alteration of organic matter in soils and permits better preservation with thickening of the humus top soils. But at the same time, humus retains larger quantities of nitrogen. There is a slowing down of the recycling processes. These phenomena lead to a shortage of mineral nutrients which results in oligotrophic conditions (Whitmore, 1975).

—in lowland environments the opposite occurs. Warmer and wetter conditions increase the alteration of organic matter and all the recycling processes are speeded up, giving more nutrients to the plants, particularly nitrogen.

In the Barombi Mbo catchment, during the first period, one assumes that the thicker humus topsoil (litter and A1 horizon) produced more organic matter (TOM) and nitrogen (TON) to the lacustrine sedimentation. During the second period pedologic phenomena were speeded up—confirmed by the large increase in the formation of kaolinite (Giresse et al., 1991)—with the result of a slowing down of the influx of TOC and TON to the lacustrine sediments.

(2) The generally low $\delta^{13}C$ values before 10,000 yr B.P. cannot be related to C3 grasses adapted to frost conditions (see p. 71), because the estimated mean temperature cooling in the lowland equatorial regions was less than 5°C (Maley, 1991). Even in the East African mountains, organic matter in

the deposits of Sacred Lake, which is located at 2350 m a.s.l. in the present-day moist montane forest of Mount Kenya, have for the coldest period (ca. 18,000–14,000 yr B.P.) $\delta^{13}C$ values of −14 to −16‰ (Street-Perrott et al., 1992 and pers. comm.), typical values of C4 grasses. This result will be discussed by these authors in a forthcoming paper, but concerning the palynology of this classical site, this result is in good agreement with the high grass pollen percentages of this period (Van Zinderen Bakker and Coetzee, 1988).

(3) In assuming that ^{13}C-depleted lacustrine plankton cannot significantly contribute to the bulk organic matter of the sediment (see pp. 71, 72), the unusually low ^{13}C content ($\delta^{13}C=$ ca. −33‰) of the organic matter between −10 and −5 m must be discussed. At first these low values can be interpreted as being of vegetative origin and related to C3 plants because in tropical rain forest the lower strata are depleted in ^{13}C (Medina and Minchin, 1980; Van der Merwe and Medina, 1989). For instance, in a laterite soil forest of Amazonia (soil similar to that of the Barombi Mbo catchment), the leaves of the upper canopy have $\delta^{13}C$ values from −27‰ to −30‰ and those near the forest floor, below 5 m, have significant lower values from −33‰ to −36‰ (Van der Merwe and Medina, 1989) up to −38‰ at ca. 20 cm above the ground (Blanc, 1989). The CO_2 content is higher near the forest floor as the result of soil respiration (roots and microrganisms of the litter): the CO2 emitted by this process is metabolized and depleted in ^{13}C before assimilation by the shade flora (Van der Merwe and Medina, 1989). Furthermore, in the lower strata of the forest, the decreasing solar irradiance due to shading also tends to give lower $\delta^{13}C$ values (Ehleringer et al., 1986). However, it seems improbable that all the leaves and other wood remains forming the litter and being partly incorporated in the humic top soil (A1 horizon) are derived only from the understorey: one part must be derived from the canopy where the $\delta^{13}C$ values are lighter. Therefore, to explain the low $\delta^{13}C$ values of the bulk sediment, one could suppose that a small part of it contains organic matter derived from methane-oxidising bacteria (Kelts and Talbot, 1990). However, because through time the anoxic conditions at depth in the lake remained constant, this process must have worked continuously with a $\delta^{13}C$ shift of about 2–3‰ over the whole core studied. This shift must be superimposed on the $\delta^{13}C$ variations induced by the vegetation changes on the catchment.

(4) There are several reasons to suppose that no other diagenetic process have modified the carbon isotopic composition of the sedimented organic matter in Lake Barombi Mbo:

(i) Neither % TOC, nor % TON decreases monotonically downcore; on the contrary there is evidence of higher values in the Pleistocene part of the core.

(ii) The C/N ratio is higher in the lower part of the core but without any systematic pattern: major excursions occur during very short stratigraphic intervals and some dramatic changes (higher values) are difficult to explain in term of diagenesis and, in several cases, they are directly related to concentrations of lignitic components.

(iii) Generally, % TOC and % TON are quite strongly correlated ($r=$ 0.741)(Fig. 5) indicating that both are present mainly as organically bound components. However, the graph shows that a small quantity of inorganically bound nitrogen is also present.

These considerations are in accord with a number of other studies where the $\delta^{13}C$ has been shown to reflect the composition of the primary organic matter and their isotopic signatures such as in a number of East African lakes (Talbot and Livingstone, 1989; Hillaire-Marcel et al., 1989) and Lake Bosumtwi (Talbot and Johannessen, 1992).

(5) Another form of alteration of $\delta^{13}C_{org.}$ might occur through bush fires and wood charcoal particles, but there is no evidence for such artefact either in the studied lake deposits or in the top soil of the catchment.

(6) We assume that the ^{13}C depletion related to methanogenesis is a constant process (see p. 74 (3)). Thus we infer that the ^{13}C content of bulk organic matter is mainly the result of an isotope mass balance reflecting the respective supplies of C4 and C3 organic matter. This mass balance is considered to be proportional to areas colonized by the respective plants because the release of organic matter is nearly comparable during the ca. 25,000 yr of this

core: the calculated accumulation rates of the bulk sediment is between 13 and 30 g cm^{-2} 10^{-3} yr in the Pleistocene and between 30 and 46 g cm^{-2} 10^{-3} yr in the Holocene (Giresse et al., 1991): but inversely the mean TOC content is lower during the Holocene (ca. 4–5%) than during the Pleistocene (ca. 7–8%).

(7) During the Pleistocene–Holocene transition (ca. 13,000–10,000 yr B.P.) the $\delta^{13}C$ curve exhibits two positive excursions which match two distinct spikes of C4 herbaceous plant pollen after a large negative spike. For this period the calculated accumulation rate based on dry weight appears to be between 20 and 30 g cm^{-2} 10^{-3} yr (Giresse et al., 1991). Based on the interpolated ages of the different events at the end of the Pleistocene, we interpret this large negative spike which indicates forest extension, and is dated at between ca. 13,000–12,000 yr B.P., as corresponding to Termination IA (Duplessy et al., 1981) dated from 14,500 to 11,500 yr B.P. (Fairbanks, 1989). Thus, the beginning of the forest phase at around 9800–9500 yr B.P. would correspond to Termination IB, which culminated at 9500 yr B.P. (Fairbanks, 1989). With these tentative correlations, the two positive excursions in between, which are dry phase indicators dated by interpolation at ca. 11,500–10,100 yr, could be linked to the Younger Dryas event (cf. Duplessy et al., 1981: Fairbanks, 1989), which was also apparently detected in other sites of equatorial Africa (i.e. Bosumtwi: Talbot and Johannessen, 1992 ; Mount Kenya: Perrott, 1992) (Figs. 3 and 6).

Conclusions

The interpretation of the carbon isotopic curve is simplified because of the insignificant role played by phytoplankton in the balance of organic particle flux. Thus, the biomass of phytoplanktonic origin which, in some cases according to Calvert and Fontugne (1987) is depleted in ^{13}C (up to −36‰), has not been considered here.

The parallel evolution between the isotopic curve and the arboreal versus grass pollen curve, such as the evolution of TOC, TON and C/N ratio, suggests the absence of any significant deformation of the isotopic signature. This conservative point of view has also been verified recently both in the oceanic realm (Calvert and Fontugne, 1987) and in the continental realm (Hedges and Van Geen, 1982; Cerling et al., 1989). Therefore, in the records of the last 25 millennia of Lake Barombi Mbo, one cannot find an impoverishment of ^{13}C by the more labile polysaccharid (cellulose, hemicellulose) diagenesis (Benner et al., 1987). In all cases, the average value of the Hydrogen Index close to 200 (see p. 71) indicates that a moderate mineralization of the organic matter has intervened during the first pedogenetic steps (mostly A1 horizon). Hence the isotopic composition appears to be a good indicator of the C3/C4 biomass ratio. Because of the almost permanent forest plant cover, there is no lag between the pollen signal and the $\delta^{13}C$ excursion like the lag of about 1500 years deduced in Lake Tanganyika (Hillaire-Marcel et al., 1989). Therefore, the carbon isotopic curve and the pollen

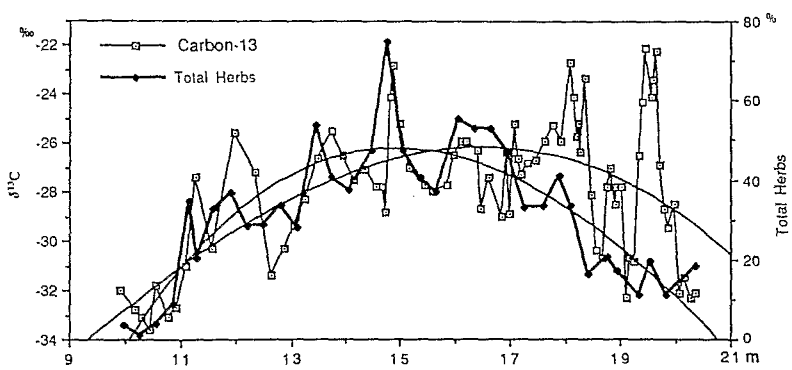


Fig. 6. Core BM 6. Section between 10 and 20 m below the top; polynomial curves (3th order) showing the principal trend for the curves of the total C4 grass pollen (total herbs) and $\delta^{13}C$.

curves allow the major fluctuations of the environment in the catchment to be recorded:

—from ca. 25,000 to 20,000 yr B.P. a forest environment with a montane component,

—from 20,000 to 13,000 yr B.P. opening of the landscape and a slight fall of the lake level with colonization by Cyperaceae and other aquatic plants,

—from 13,000 to 9500 yr B.P. a new extent of the forest with a dry phase at ca. 11,500–10,100 yr B.P. that could be linked to the Younger Dryas,

—a Holocene forest environment with temporary openings at around 2500–2000 yr B.P.

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