Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years B.P.

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Abstract

The lake Barombi Mbo pollen record goes back to about 28,000 yr B.P. The pollen diagram based on 82 samples is subdivided into four main pollen zones. Zone I (ca. 28,000 to 20,000 yr B.P.) is characterized by relatively high frequencies of Caesalpiniaceae and also by a montane element with *Olea capensis*. The climate was cool and relatively wet. Zone II (ca. 20,000 to 10,000 yr B.P.). A sharp increase in Gramineae, the main non-arboreal land pollen taxon, began around 20,000 yr B.P. and lasted until 10,000 yr B.P. During this period the forest receded, giving way to a more open vegetation, but significant patches of forest (refuges) persisted in the area. This is confirmed by isotopic analyses ($\delta^{13}C$) of sedimentary detritic organic matter from the catchment. Until ca. 13,000 yr B.P. *Olea capensis* was well represented indicating a relatively cool climate. Between 13,000 and 12,000 yr B.P. a warming trend associated with a strong increase in precipitation occurred. After this an abrupt reduction in precipitation linked to an increase in seasonality, but without temperature lowering, intervened between ca. 11,500 and 10,400 yr B.P. This last phase corresponds partly to the Younger Dryas time period. Zone III (ca. 10,000 to 2800 yr B.P.). After ca. 10,400 yr B.P. the climate became very wet until ca. 3000 yr B.P. A sharp decrease in the Gramineae intervened at ca. 10,000 yr B.P.; from ca. 9500 to 3000 yr B.P. they remained very low, between 0 and 3%, and the forest trees reached their maximum extension. Most of the trees exhibited large variations with quasi-periods of around 1000 to mainly 2000 yr (ca. 2200 calendar years), which could be related to large sylvigenetic or successional cycles. In this zone the Caesalpiniaceae were relatively well represented, with a maximum extension between 4500 and 3000 yr B.P. *Podocarpus*, a typical tree of the montane stratiform cloud forests, exhibited very low frequencies before 10,000 yr B.P. but their relative increase during the early and middle Holocene can only be explained by its growth on distant mountains. Its maximum extension phase was roughly synchronous with that of Caesalpiniaceae. The climate was warm and wet, but cooler on the mountains. Zone IV (ca. 2800 yr B.P. to present time). Around 2800 yr B.P. a sharp increase in the Gramineae, peaking at 30 to 40% of total pollen between ca. 2500 and 2000 yr B.P., indicates a sudden phase of vegetation opening and forest retreat, accompanied by severe erosion. *Alchornea*, a typical pioneer taxon, increased rapidly at the same time to large frequencies because it develops abundantly in all the openings. *Elaeis guineensis*, originally a pioneer palm tree, follows the same pattern. The climate was warm, relatively dry, and linked to an increase of seasonality. After 2000 yr B.P. the Gramineae returned to low frequencies, around 10%, associated with a strong increase in trees, indicating that the forest expanded again but not to the same extent as in the early and middle Holocene. The climate was warm and relatively wet, rather similar to the present-day climate. © 1998 Elsevier Science B.V.

Keywords: western Cameroon; late Quaternary; African rain forest; vegetation dynamic; pollen analysis; palaeoenvironment; climatic changes; periodicities

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1. Introduction

The climatic conditions prevailing at present in the rain forest domain of the equatorial zone of Africa exhibit a gradient between a more humid zone near the Gulf of Guinea and less humid peripheral areas in the north and in the south. The most humid zone is characterized by an annual rainy season of ten to twelve months. In southern Cameroon this zone contains evergreen forests of two main types (Fig. 1). The first, the Biafrean Forest, is marked by the importance of Caesalpiniaceae. The second, the Atlantic Littoral Forest, extends in the littoral area and is particularly characterized by a paucity of Caesalpiniaceae. In the peripheral areas of the forest domain the annual precipitations are reduced to about nine months. This sector is characterized by the development of semi-deciduous forests with mainly

Ulmaceae and Sterculiaceae (Letouzey, 1968, 1985; White, 1983). In all types of rain forest numerous and diverse pioneer trees develop in all openings, whether natural or anthropogenic in origin.

In the areas presently covered by the most humid types of rain forest, botanists have found isolated spots with plant formations related to open environments and particularly to xeric vegetations, as in southern Cameroon at Nkolsia near Bipindi (Villiers, 1981; Letouzey, 1983) or in Monts de Cristal in Gabon (Reitsma et al., 1992). Such isolated spots have been interpreted by these authors as relics of former extensive xeric vegetations during dry periods. Stone lines existing at the base of numerous pedologic profiles give evidence that large areas in the present day forest regions had lost a large part of their wooded cover and that heavy erosion of the ground occurred several times during the late Quaternary
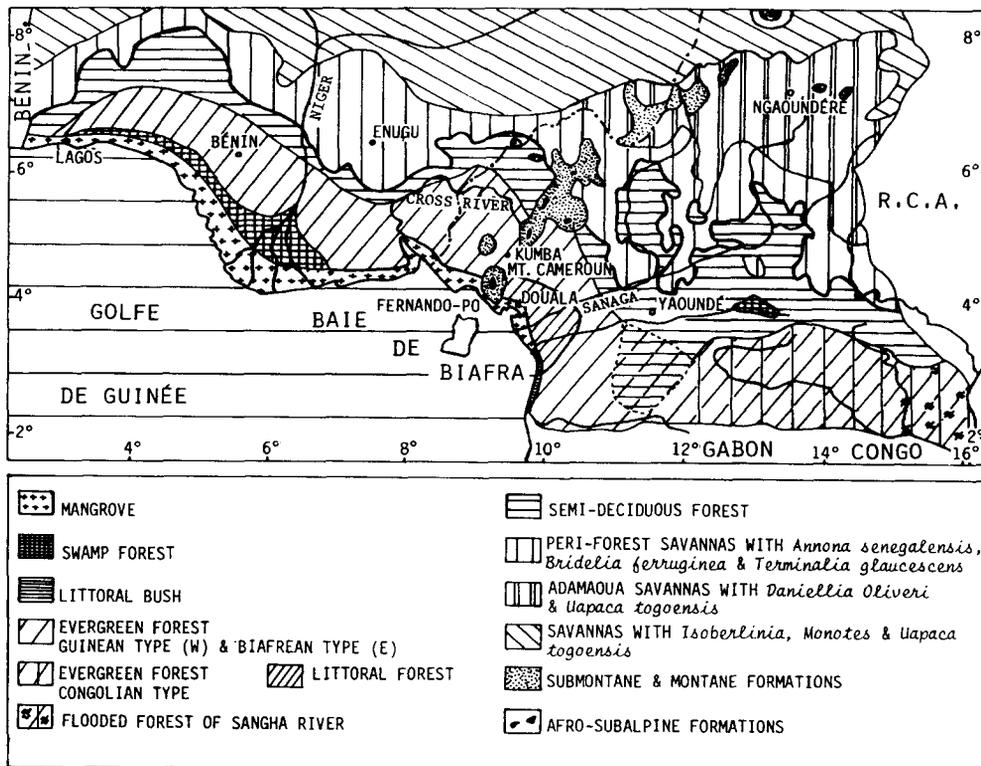
Fig. 1. Schematic map of vegetation along the Bay of Biafra (end of the Guinea Gulf), adapted mainly from Letouzey (1968) (from Maley et al., 1990a).

(Lanfranchi and Schwartz, 1991; Maley, 1996b). The study of fossil pollen accumulated in lacustrine sediments enables the history of the vegetation in the regions around these lakes to be determined, to date precisely former arid or more humid periods, and to document accurately fragmentation or extension phases of the African rain forest in the course of the late Quaternary (Maley, 1987, 1991, 1996a,b; Brenac, 1988; Vincens et al., 1994; Reynaud-Farrera et al., 1996; Elenga et al., 1996).

2. The Lake Barombi Mbo pollen record

2.1. Environmental setting. The main vegetation formations (Fig. 2)

Located 80 km from the sea at an altitude of ca. 300 m, lake Barombi Mbo is a 1 Myr old volcanic and explosive crater lake (Cornen et al., 1992). The lake has a diameter of ca. 2 km and a maximum depth of 110 m. The present day climate is of equatorial type with only two seasons (Suchel, 1972, 1988): one dry season of three months almost without rain from December to the end of February, and a long rainy season from March to November, culminating in four very wet months from July to October. The total annual precipitation is 2350 mm. The lake is surrounded by lowland evergreen rain forest with patches of semi-deciduous type (Letouzey, 1985). The edge of the largest patch is at ca. 20 km to the southwest and extends to the northern foot of Mount Cameroon which culminates at 4095 m (Fig. 2). From the north to the east of this mountain, Suchel (1988) described a rain shadow phenomenon which causes a large decrease in precipitation and particularly a reduction in the length of the rainy season, permitting the development of a semi-deciduous type of rain forest (Fig. 2). Adjacent to this forest the presence of several patches of natural savannas, characterized by *Borassus* palm trees (Fig. 2; Letouzey, 1978) indicates that the length of the rainy season is reduced to less than nine months (Suchel, 1988). The occurrence of some *Borassus* palm trees included in the rain forest near the edge of the savannas confirms that the peripheral forest is presently transgressing into these savannas

(Maley, 1990). In a region presently having a very wet climate these areas of natural savanna testify to a former dry period (Section 4.2.5; Maley, 1990). The present day Marantaceae open canopy forest which covers a large part of the western side of the mountain (Fig. 2; Letouzey, 1985; Maley, 1990), must be associated with a former, larger extension of open formations (Schwartz et al., 1997). In the large savanna area of the Lopé region in central Gabon, White (1995) and White et al. (1997) described similar formations to these of the western side of Mount Cameroun. At present all these open formations are in an active process of forest recolonization, illustrating a very general phenomenon of forest transgression in the African equatorial region (Maley, 1990; Servant, 1996).

The Atlantic Littoral Forest is presently situated in the littoral area around the Bay of Biafra (Fig. 1) but in several places it extends more inland. This forest is a degraded form of the evergreen forests (Section 4.2.3; Maley, 1990; Reynaud and Maley, 1994) and is characterized firstly by a strong regression of the Caesalpiniaceae and second by the development of *Lophira alata* and *Saccoglotis gabonensis* (Letouzey, 1968, 1985). The latter taxa are strong light demanders in their young phase of development, when they behave as pioneer trees.

Lake Barombi Mbo is located on a large undulating plain, between ca. 250 and 500 m in altitude, which is covered by lowland rain forests. Mount Cameroon is situated at ca. 35 km to the south, the Roumpi Hills (1765 m) ca. 20 km to the northwest and Mont Koupé (2050 m) at ca. 25 km to the northeast, this last one having a typical montane vegetation with *Podocarpus* (Section 4.2.1; Letouzey, 1985; Thomas, 1993; Cable, 1993).

2.2. The chronology of the sediments

The sedimentary geology, geochronology (^{14}C), isotopic geochemistry ($\delta^{13}C$) (Maley et al., 1990a; Giresse et al., 1991, 1994), volcanology (Cornen et al., 1992) and palaeomagnetism (Thouveny and Williamson, 1988) of the longest core (BM-6; 23.5 m), taken in the deepest part of the lake, have already been studied in detail.
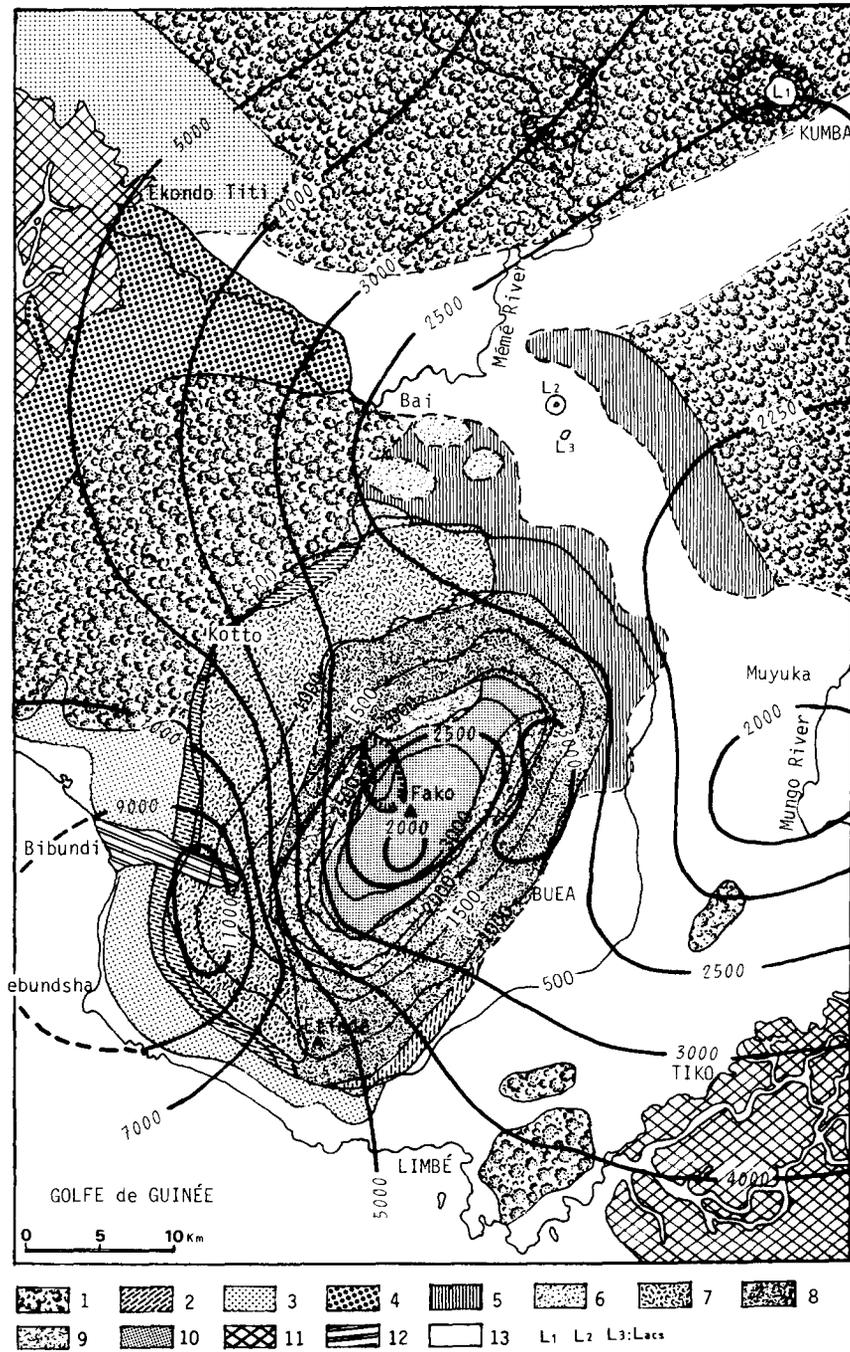
Fig. 2. Schematic map of vegetation from the Mount Cameroun (Fako, the summit at 4095 m) to the Lake Barombi Mbo area, adapted from Letouzey (1985). In superposition the main isohyets from 2000 to 11000 millimetres (adapted from Suchel, 1988) (from Maley, 1990). *1* = Evergreen Biafrean Forest with numerous Caesalpiniaceae; *2* and *3* = Evergreen transitional to Littoral Atlantic Forests poor in Caesalpiniaceae; *4* = Evergreen Littoral Atlantic Forests with rare Caesalpiniaceae; *5* = Semi-Deciduous Forest; *6* = Grass Savanna with few trees; *7* = Marantacae open canopy Forest (from altitude ca. 500 to 2000 m); *8* and *9* = Montane Rain Forests; *10* = Montane Grassland; *11* = Mangrove; *12* = recent lava flow with Pioneer Forest; *13* = plantations, villages and various anthropic vegetation. *L1* = Lake Barombi Mbo; *L2* = Lake Barombi Kotto; *L3* = Lake Mboandong.

Preliminary results of pollen analyses have been published (Brenac, 1988; Maley et al., 1990a; Giresse et al., 1994; Maley, 1996a).

The sediments are laminated, mainly composed of clay, rich in organic matter with 10 to 16% total organic carbon. Because of the very low productivity of the lake (oligotrophic) (Kling, 1988), the organic matter is largely allochthonous and comes from the catchment area (Giresse et al., 1994). The accumulation rate of the sediments was calculated from twelve radiocarbon determinations (Fig. 3; Giresse et al., 1991, 1994). The accumulation rate is regular from the top until ca. 24,000 yr

B.P., except for a change in rate around 10,000 yr B.P. (Fig. 3). Near the base of the core, below ca. 24,000 yr B.P., a section of 1.5 m is disturbed, probably by volcanic activity, but three radiocarbon dates from this section extend the chronology until ca. 27,500 yr B.P. (Giresse et al., 1991, 1994; Cornen et al., 1992). The calculated sedimentation rate, by interpolation, gives an age for the 82 pollen samples (Fig. 3). Each sample corresponds to 1 cm depth. Four to five samples were analyzed per thousand years for Holocene sediments, then three samples to 20,000 yr B.P. and two samples until the base.
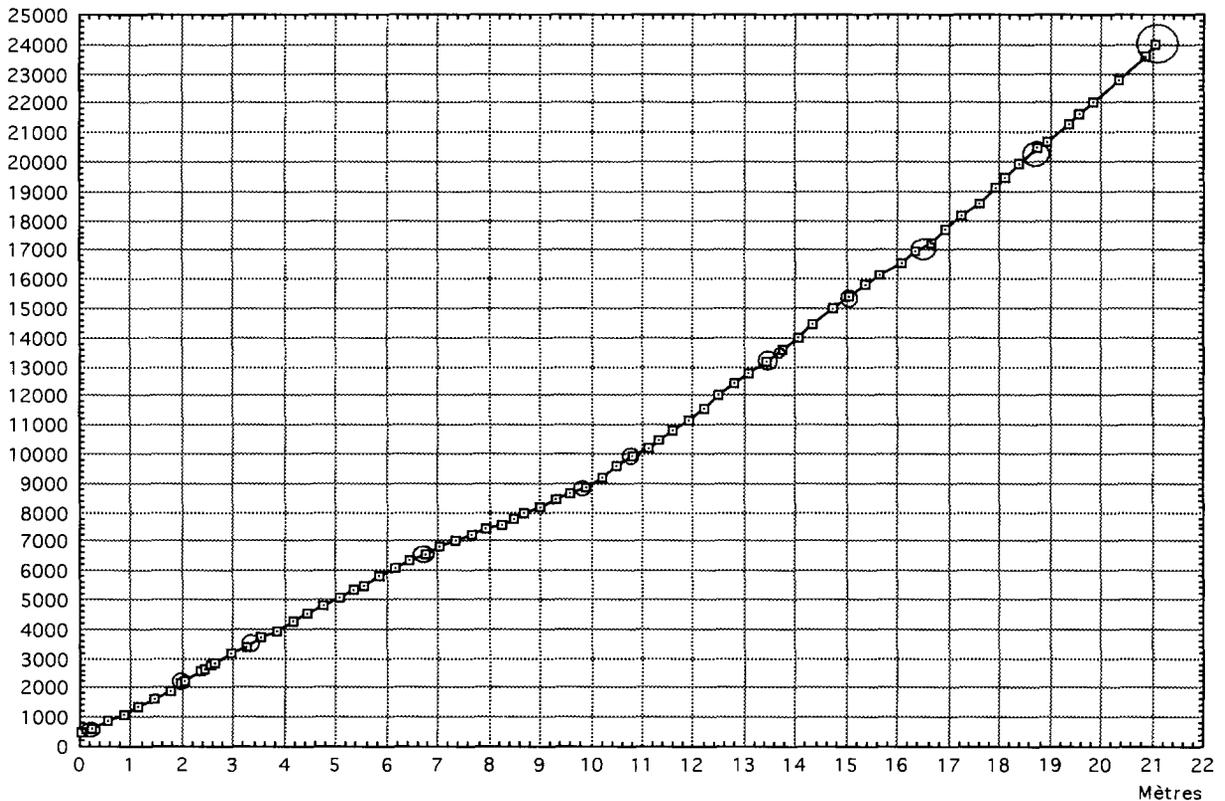
Fig. 3. The sediment accumulation rate in core BM-6 (lake Barombi Mbo) was calculated in using 12 radiocarbon datings (for more details see Giresse et al., 1991, 1994). The position of each pollen sample (1 cm depth) is shown by a point with a square. The position of each radiocarbon dating is shown by a circle which corresponds roughly to the size of the error margin, centred on the mean point of sampling. In abscissa, the levels in metres; in ordinate the interpolated dates (in B.P.) calculated with the following conventional radiocarbon datings performed in the ORSTOM Geochronological Laboratory, BONDY, France (code OBDY) (mean point of sampling level, dating and dating number); 0.25—770±100 B.P., OBDY 660; 2.05—2200±285 B.P., OBDY 146; 3.55—3690±315 B.P., OBDY 96; 6.75—6520±645 B.P., OBDY 263; 9.90—8690±475 B.P., OBDY 138; 10.80—9900±250 B.P., OBDY 751; 13.45—13,120±965 B.P., OBDY 61; 13.75—13,480±240 B.P., OBDY 757; 15.10—15,470±100 B.P., OBDY 811; 16.65—17,080±885 B.P., OBDY 266; 18.75—20,420±1500 B.P., OBDY 59; 21.05—24,080±3500 B.P., OBDY 58.

Table 1

List of the main pollen taxa from the upper Quaternary sediments of lake Barombi Mbo (core BM-6). The pollen type, t., groups several botanical genera. The vegetation formations are based mainly on Letouzey (1968, 1985)

1. Pioneer Forest	2. Semi-Deciduous Forest

Trees

Alchornea (Euphorbiaceae)
Allophylus (Sapindaceae)
Anthociesta (Loganiaceae)
Brucea (Simaroubaceae)
Ceiba pentandra (Bombacaceae)
Dalbergia (Papilionaceae)
Elaeis guineensis (Palmae)
Harungana madagascariensis (Hypericaceae)
Macaranga t. (Euphorbiaceae)
Mallotus t. (Euphorbiaceae)
Maprounea membranacea (Euphorbiaceae)
Margaritaria (Euphorbiaceae)
Musanga/Myrianthus (Moraceae)
Phyllanthus (Euphorbiaceae)
Pycanthus angolensis (Myristicaceae)
Ricinus communis (Euphorbiaceae)
Sapium (Euphorbiaceae)
Tetrorchidium (Euphorbiaceae)
Trema guineensis (Ulmaceae)
Zanthoxylum t. (Rutaceae)

Lianas

Acacia kamerunensis (Mimosaceae)
Adenia (Passifloraceae)
Ancistrophyllum (Palmae)
Calamus (Palmae)
Coccinia grandis (Cucurbitaceae)
Combretaceae
Eremosphatha (Palmae)
Tetracera (Dilleniaceae)

2. Semi-Deciduous Forest

Acridocarpus (Malpighiaceae)
Antiaris (Moraceae)
Blighia (Sapindaceae)
Bosqueia angolensis (Moraceae)
Canarium schwienfurthii (Burseraceae)
Ceiba pentandra (Bombacaceae)
Celtis (Ulmaceae)
Chaetacme aristata (Ulmaceae)
Combretaceae (cf. Terminalia)
Detarium macrocarpum (Caesalpiniaceae)
Discoglypremna caloneura (Euphorbiaceae)
Holoptelea grandis (Ulmaceae)
Lannea t. (Anacardiaceae)
Milicia excelsa (= *Chlorophora*) (Moraceae)
Nauclea (Rubiaceae)
Nesogordonia papaverifera (Sterculiaceae)

2. Semi-Deciduous Forest

Piptadeniastrum africanum (Mimosaceae)
Sterculia t. (Sterculiaceae)
Triplochiton scleroxylon (Sterculiaceae)

3. Biafrean and Evergreen Forest

Large trees
Afzelia (Caesalpiniaceae)
Anisophyllea (Rhizophoraceae)
Anopyxis klaineana (Rhizophoraceae)
Anthonotha (Caesalpiniaceae)
Antrocaryon (Anacaridiaceae)
Berlina t. (Ceasalpiniaceae)
Blighia (Sapindaceae)
Brachystegia (Caesalpiniaceae)
Caesalpniaceae (total)
Copaifera (Caesalpiniacea)
Cordia (Boraginaceae)
Cryptosepalum (Caesalpiniaceae)
Cynometra (Caesalpiniaceae)
Daniellia (Caesalpiniaceae)
Desbordesia glaucescens (Irvingiaceae)
Distemonanthus (Caesalpiniaceae)
Guibourtia (Caesalpiniaceae)
Hymenostegia (Caesalpiniaceae)
Irvingia (Irvingiaceae)
Julbernardia (Caesalpiniaceae)
Klainedoxa gabonensis (Irvingiaceae)
Lebruniodendron (Caesalpiniaceae)
Leonardoxa (Caesalpiniaceae)
Lophira (Ochnaceae)
Mezoneuron (Caesalpiniaceae)
Mitragyna t. (Rubiaceae)
Monopetalanthus (Caesalpiniaceae)
Oxystigma, cf. (Caesalpiniaceae)
Santiria (Burseraceae)
Sapotaceae
Scottelia (Flacourtiaceae)
Strombosia t. (Olacaceae)
Syzygium t. (Myrtaceae)
Tessmannia (Caesalpiniaceae)
Uapaca (Euphorbiaceae)

Lower strata
Aeschynomene (Papilionaceae)
Aidia t. (Rubiaceae)
Antidesma (Euphorbiaceae)
Baphia t. (Papilionaceae)
Bridelia t. (Euphorbiaceae)
Canthium t. (Rubiaceae)

Table 1 (*continued*)

3. Biafrean and Evergreen Forest	4. Montane Forest
Lower strata	Ericaceae
Cola t. (Sterculiaceae)	*Podocarpus* t. (Podocarpaceae)
Dialium (Caesalpiniaceae)	
Diospyros t. (Ebenaceae)	**5. Savanna tree**
Dracaena t. (Agavaceae)	
Drypetes t. (Euphorbiaceae)	*Borassus aethiopium* (Palmae)
Ficus (Moraceae)	
Flacourtiaceae (total)	**6. Herbs in forests**
Heisteria parviflora (Olacaceae)	
Homalium (Samydaceae)	*Acalypha* t. (Euphorbiaceae)
Ixora t. (Rubiaceae)	*Dorstenia* t. (Moraceae)
Klaineanthus (Euphorbiaceae)	*Justicia* t. (Acanthaceae)
Lasianthera africana (Icacinaceae)	Acanthaceae
Leptonychia (Sterculiaceae)	*Microdesmis puberula* (Euphorbiaceae)
Mesobotrya (Euphorbiaceae)	*Tragia* t. (Euphorbiaceae)
Pseudospondias (Anacardiaceae)	Urticaceae
Psychotria t. (Rubiaceae)	
Rhus t. (Anacardiaceae)	**7. Herbs in open formations**
Sabicea (Rubiaceae)	
Sorindeia t. (Anacardiaceae)	*Celosia* t. (Amaranthaceae)
Trichilia t. (Meliaceae)	*Alternanthera* (Amaranthaceae)
Trichoscypha (Anacardiaceae)	Amaranthaceae
	Compositae
Lianas	Gramineae
Apocynaceae	Liliaceae
Cissus t. (Ampelidaceae)	
Cnestis (Connaraceae)	**8. Aquatic and hygrophilous herbs**
Entada (Mimosaceae)	
Griffonia (Caesalpiniaceae)	*Ambrosia* (Compositae)
Hippocratea t. (Hippocrateaceae)	Commelinaceae
Iodes (Icacinaceae)	Cyperaceae
Mussaenda t. (Rubiaceae)	*Laurembergia* (Haloraghaceae)
Salacia t. (Hippocrateaceae)	*Limnophyton* t. (Alismataceae)
Tetracera t. (Dilleniaceae)	Nymphaeae (Nymphaeaeceae)
	Polygonum (Polygonaceae)
4. Montane Forest	*Potamogeton* (Potamogetonaceae)
	Typha (Typhaceae)
Ericaceae	*Utricularia* t. (Utriculariaceae)
Ilex (Aquifoliaceae)	Xyridaceae
Nuxia congesta (Loganiaceae)	
Olea capensis (= *O. hochstetteri*) (Oleaceae)	**9. Pteridophytes and hepathics**
Phoenix reclinata (Palmae)	
	(Spores, monolete and trilete)

2.3. Methods and pollen identification

The samples were treated by standard palynological techniques with the addition of the Lüber method for the most organic rich sediments (Faegri and Iversen, 1975). The identification of pollen was based on both the published pollen iconographies such as several Atlas for tropical Africa (Maley, 1970; Caratini et al., 1974; Ybert, 1979; Bonnefille and Riollet, 1980; Salard-Cheboldaeff, 1980, 1981, 1982) and pollen studies of families or genera with species living in tropical Africa (for instance, Graham and Barker, 1981; Ferguson, 1987), and the large pollen slide collection of the Montpellier Palynological Laboratory. The results are presented mainly as percentages of the pollen

sum which includes all the pollen counted in each sample, but excluding the damaged pollen grains and the spores (Pteridophytes and Hepatics). A separate figure is presented for the spores (Section 3.3) and for the pollen concentration and influx (Section 3.2). Undetermined pollen grains (never reaching 5%) are included in the pollen sum. For each sample approximately 200 to 250 pollen and spores were counted. A total of 274 different pollen taxa were determined. A list of the main pollen taxa (151) is presented in Table 1 with a phytogeographical classification based mainly on Letouzey (1968, 1985).

3. The palynological results

3.1. Modern pollen spectra in southern Cameroon

The need to investigate the present day pollen sedimentation is particularly relevant in tropical rain forests because of the very large species diversity and also the relative importance of the entomophilous pollen transport. In the forests of southern Cameroon two different studies have been undertaken.

The first, performed by Brenac (1988), concerns the study of modern samples taken in nine lakes situated in the forest domain of southern Cameroon, and two in savanna. Among the nine forest lakes, three are in the montane forests above 2000 m. In the six lowland forest lakes, the main pollen taxa belong, with decreasing importance, to Moraceae, Euphorbiaceae, Ulmaceae and Caesalpiniaceae. The last family is more important in forests of evergreen type, as are found around Barombi Mbo, and the Ulmaceae in forests of semi-deciduous type. The three best represented families have apparently more anemophilous taxa than the Caesalpiniaceae which have, by contrast, many entomophilous taxa. In general anemophilous taxa produce much more pollen than entomophilous ones. So one can infer from these results that even a low percentage of Caesalpiniaceae pollen indicates a relatively important presence of parent taxa. In the three montane lakes the main pollen taxa belong, with decreasing importance, to Euphorbiaceae, Moraceae and to montane taxa,

particularly Oleaceae (*Olea capensis*). The main interpretive difficulty at these sites is that the adjacent environments of these lakes are more or less perturbated by present day or recent anthropic activities leading to the development of pioneer taxa, particularly those of the Euphorbiaceae and Moraceae.

The second study performed by Reynaud-Farrera (1995), is an analysis of 50 samples of soil litter taken from plots situated in the different types of rain forest and from numerous localities of southern Cameroon. A similar study was conducted in one locality of northeastern Gabon, Makokou, by Jolly et al. (1996). The size of the plots was in general 20×20 m. The plants (trees and herbs) of each plot were carefully counted by experienced botanists. The comparison between the pollen spectra and the botanical inventories shows that for the dominant taxa, only about 50% are common. The reasons for this low similarity are multiple and complex (see Reynaud-Farrera, 1995). A statistical treatment by multivariate analysis was undertaken on the two sets of samples (pollen and plants). It appears that the picture given by a pollen spectrum is much more regional than that given by a botanical inventory limited to a small plot—even if this plot is representative of a relatively widespread formation. However, because the size of the source area is an important factor, a lake will receive pollen from a much larger area than from a small plot in a forested area (Prentice, 1985).

Another important conclusion obtained from these studies on present day pollen spectra is the advantage of grouping together several genera of the same family to form a new (super) taxon; this practice is frequently employed in palynology (for instance Gramineae, Cyperaceae, Compositae, Combretaceae, Amaranthaceae, etc.). Here, for instance, one uses only Amaranthaceae and not the classic association with Chenopodiaceae because in tropical regions the latter family lives only in dry and particularly salty soils, which do not exist in southern Cameroon. Several taxa which appear in an erratic way are grouped together by family: Commelinaceae (mainly hygrophilous herbs), Liliaceae, Sapotaceae, Flacourtiaceae, Caesalpiniaceae, etc. The

Caesalpiniaceae group together a large number of generic taxa (see Table 1), but because two of them, *Hymenostegia* and *Berlinia*, are present in numerous levels, their evolution is also presented separately. In the studies of Brenac (1988) and Reynaud-Farrera (1995), the grouping of Caesalpiniaceae proved to be very effective, not only for the present day but also during the late Quaternary (Section 4.2.2). Such a grouping procedure is also used by ecologists for several taxa which behave similarly (functional groupings) (Puig, 1995).

3.2. The pollen concentration and influx (Fig. 4)

The variations in pollen concentration (pollen/g) and pollen influx (pollen/g cm^{-2} yr^{-1}) respond to changes in vegetation and sedimentation; both are linked to climatic changes but with specific responses. The two curves are presented with the interpolated radiocarbon chronology link and in parallel with a calendar/calibrated (cal.) chronology (Section 2.2) because of their link with the sedimentation. These links probably explain why the main trends and spikes of these two pollen curves are roughly similar (Fig. 4). The lowest values were before 24,000 cal. yr B.P. during a forest period with a montane influence (see below). The first phase of large increases corresponded to the periods of abrupt changes between 24,000 and 10,500 cal yr B.P. (ca. 20,000 to 9500 ^{14}C yr B.P.) with high values between 24,000 and 17,500 cal. yr B.P. (ca. 20,000 to 15,000 ^{14}C yr B.P.) during the LGM (Last Glacial Maximum), which was also the period of maximum aridity. At this time the landscape of forest/savanna mosaic (see below) was characterized by an irregular erosion (Giresse et al., 1991, 1994), probably explaining the large oscillations of the curves. The main peak in the two curves intervened at the transition from Pleistocene to Holocene when the sedimentation rate changed abruptly (Fig. 4). This peak can be interpreted as a signal of an aggressive run-off when the rain forests cover was not yet complete. This particular pollen and sedimentation response can be dated roughly of the first part of the Younger Dryas time period (Section 5). Then, during the period of maximum forest extension

which began around 9500 yr B.P. (see below, pollen zone III), the pollen influx and concentration were relatively stable. Later, the two curves increased again during the relatively dry phase at the beginning of the late Holocene from ca. 2800 to 2000 yr B.P. (cal. and ^{14}C) (sub-zone IVa) and then remained with high values until the present day period.

3.3. The Barombi Mbo spore diagram (Fig. 5)

Before presentation of the pollen diagram, a special diagram is presented with the percentage values for the spores (Fig. 5). Here the basic sum includes all the pollen and spores counted, the damaged pollen and spores being excluded. In order to help the interpretation, the spore curve is presented in parallel with that of the Gramineae pollen (with a pollen sum excluding the spores). All the percentage results are presented with a radiocarbon chronology (Section 2.2 and Fig. 3).

Because the spores are relatively heavy particles, their frequencies are much higher during periods of increasing terrigenous influx (Poumot, 1989; Bengo, 1996). This explanation is largely appropriate to the main peaks of the curve around 20,000 yr B.P. and between 2500 and 2000 yr B.P. These two peaks are also obvious on the curves of pollen influx and concentration (Fig. 4), but the fact that the Pteridophytes are frequent in pioneer associations can partly explain these two main abrupt extension phases. One must note that the period of lowest spore frequencies is situated between ca. 19,000 and 10,000 yr B.P., a mainly dry period (Section 5). This probably indicates that the available humidity is also an important factor controlling the variation of the spores and the Pteridophytes. The fact that the amounts of spores were very low during the erosive phase which intervened during the Younger Dryas time period (Section 3.2) is an indication of some kind of dryness during this period (Section 5).

3.4. The Barombi Mbo pollen diagram and the pollen zonation (Fig. 6)

The diagram includes the 30 most frequent pollen taxa (Fig. 6). Four pollen zones can be distin-
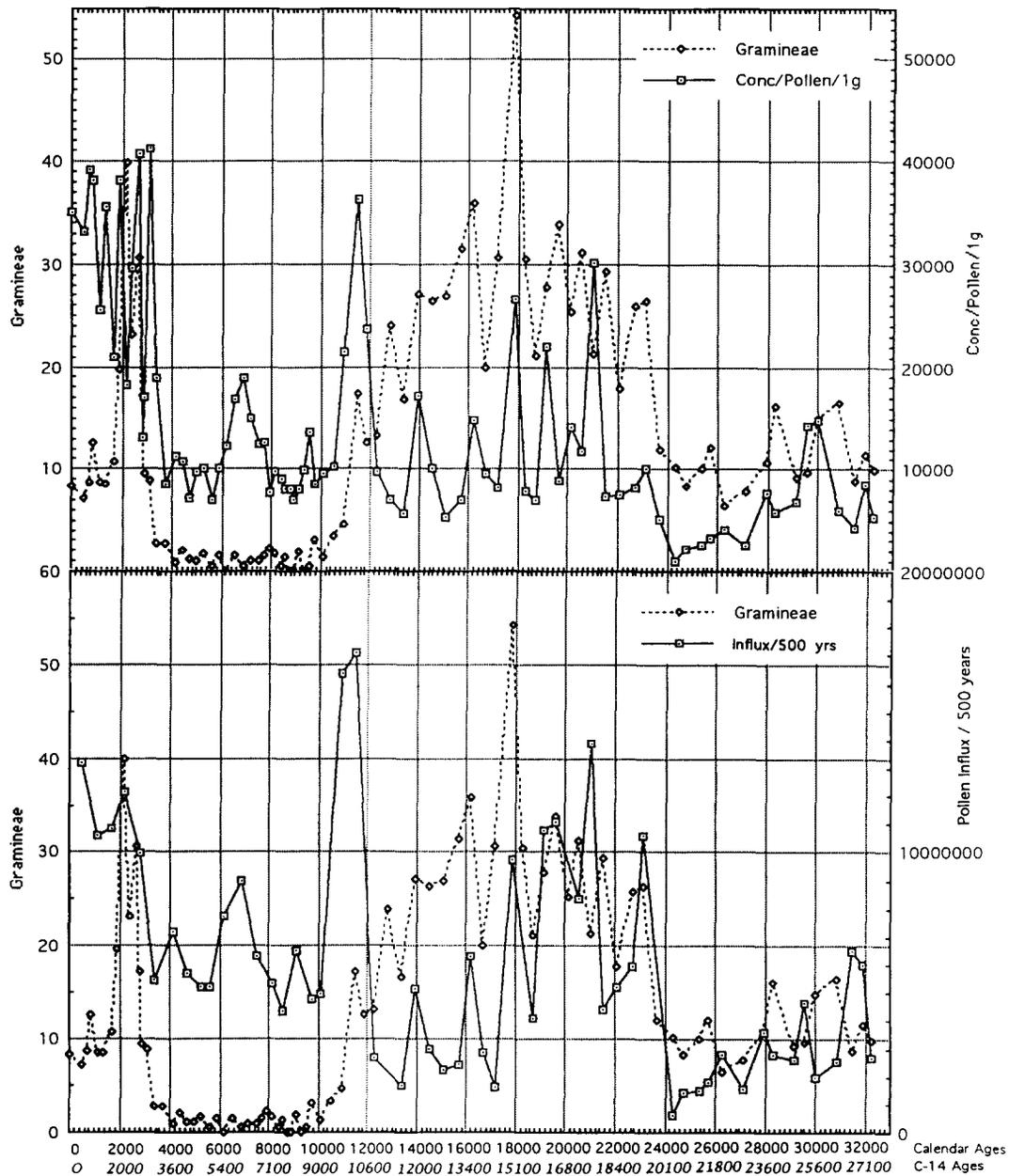
Fig. 4. The curves of pollen concentration (pollen/g) and pollen influx (pollen/g cm $^{-2}$ yr^{-1}) in the lake Barombi Mbo, core BM-6, with an interpolated radiocarbon chronology (Fig. 3) and a calendar/calibrated (cal.) chronology (section 2.2); in comparison, the Gramineae pollen diagram (dotted line, percentages).

guished mainly on the basis of the variation of terrestrial grass taxa versus arboreal taxa (i.e. roughly AP/NAP). The main and almost only terrestrial herb pollen in Gramineae (versus hygro-

philous herb pollen, mainly Cyperaceae, see Zone II), which in tropical regions is a good marker of open environments of the savanna types (Section 3.1; see also Bonnefille and Vincens, 1977).
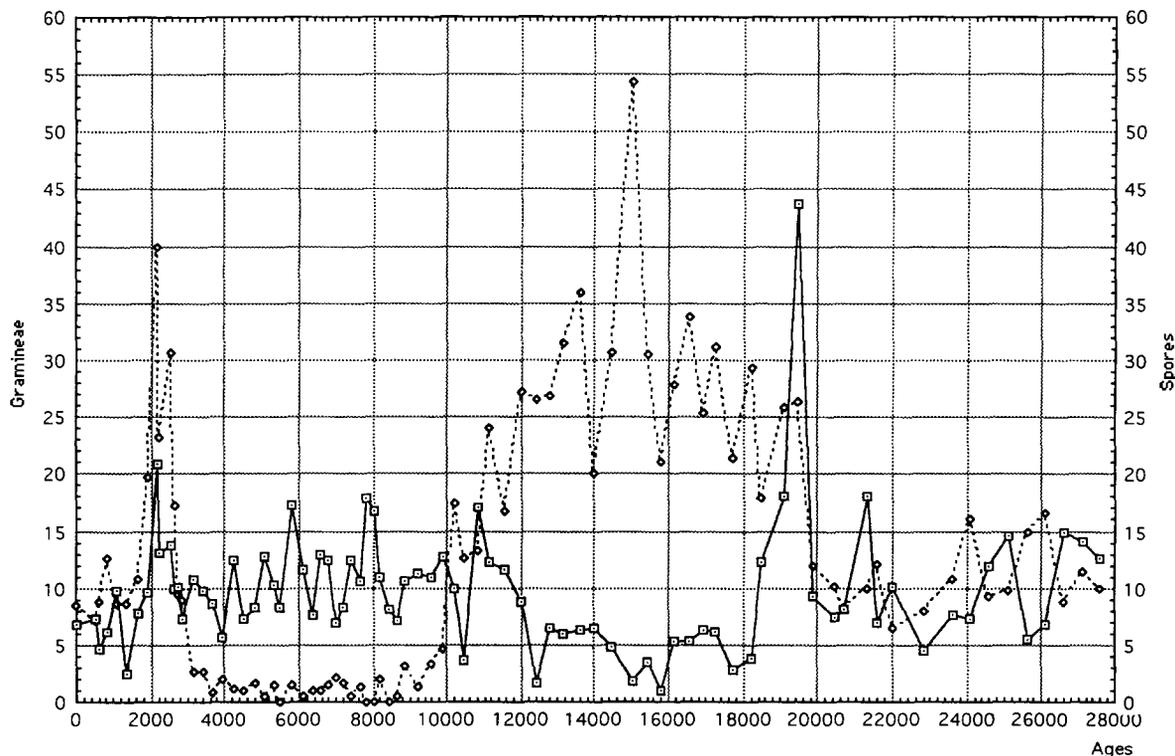
Fig. 5. The spore diagram (solid line, percentages) with an interpolated radiocarbon chronology (Fig. 3) in the lake Barombi Mbo, core BM-6; in comparison, the Gramineae pollen diagram (dotted line, percentages).

3.4.1. Pollen zone I (ca. 27,5000 to 20,000 yr B.P.)

This zone has almost the same pollen percentage of Gramineae (around 10 to 15%) as at the present time, probably indicating a similar regional forest cover. The two main other terrestrial herbaceous taxa are Compositae and Amaranthaceae. The former has frequencies between 0.5 and 1% and the latter between 1 and 2%, similar to the next zone. However, the Cyperaceae which is the main hygrophilous taxon, exhibits a mean frequency of 9.6% (today 0%) indicating a marshy environment in the western part of the catchment area.

The most important trees were Caesalpiniaceae with relatively high frequencies (average of 7.2% and extreme values of 4.6 to 10.5%) in comparison with the later Zones. Among the different genera included in this super-taxon the two most frequent are presented in the diagram. _Hymenostegia_ appears with a mean frequency of 2.1% and _Berlinia_ with 0.5% only. Almost all the tree pollen

taxa classified in Evergreen Formations exhibit relatively high frequencies in this Zone. _Strombosia_ had a mean frequency of 2.1%, similar or higher than in the Holocene (zones III and IV). Sapotaceae had a mean frequency of 1.4%, a few less than in the Holocene. Flacourtiaceae is present with a mean frequency of 0.3% and with a maximum value of 1.2%. Another important feature of this zone are the high frequencies of a montane element characterized mainly by _Olea capensis_ (syn. _O. hochstetteri_) with an average of 17.2% (extreme values of 7 to 35%) and also _Podocarpus_ but with low values (mean of 0.8%), a few more than in Zone II (0.4%), but much less than in Zone III (1.7%). In fact in this diagram the variation pattern of these two taxa are opposite (Section 4.2.1).

Several taxa classified in Semi-Deciduous Forest or as pioneer appear in this zone with relatively low frequencies in comparison with zones III and
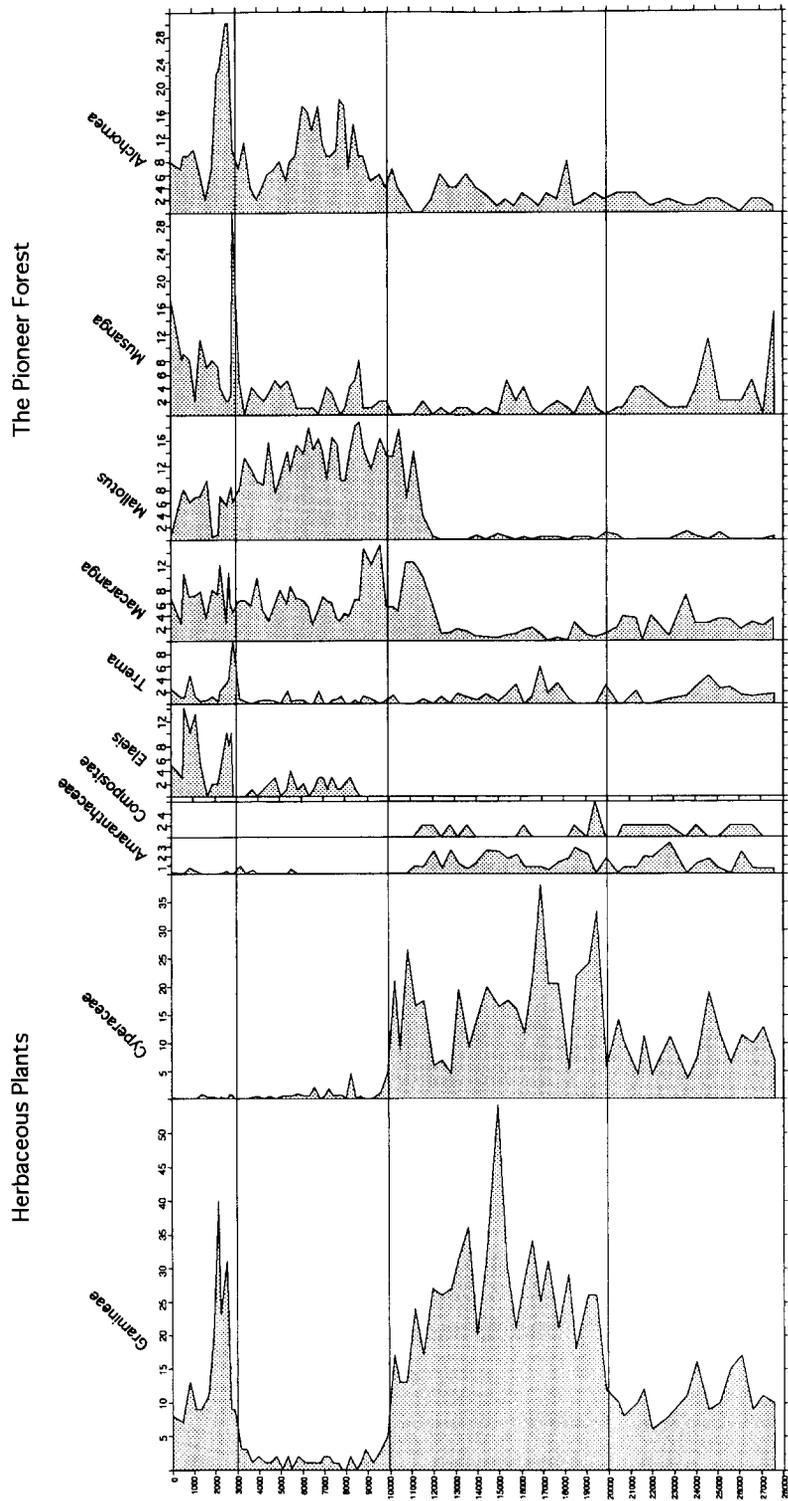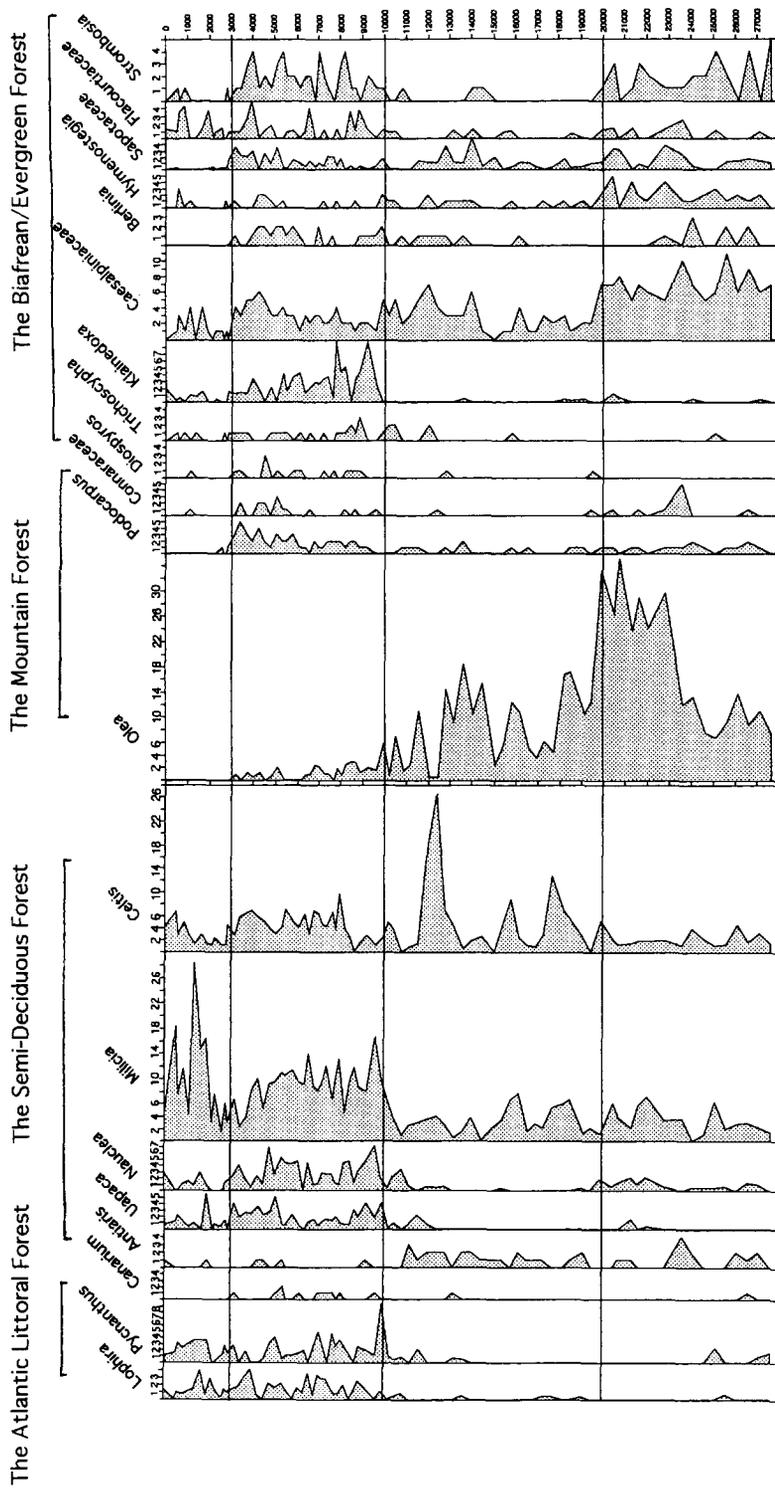
Fig. 6. The pollen diagram (percentages) of the main taxa with an interpolated radiocarbon chronology (years at left and right) (Fig. 3) in the lake Barombi Mbo, core BM-6; above, the percentage values for each pollen taxon. The pollen taxa are grouped following the main vegetation types or Formations (see Fig. 1, Table 1 and text).

IV (Holocene). For the semi-deciduous type taxa there are *Celtis* with a mean of 2%, *Milicia* with an average of 3.4%, *Nauclea* with an average of 1.6% between 22,000 and 21,000 yr B.P., *Antiaris* with three peaks of ca. 2% around 26.500 yr B.P., ca. 3% around 24,000 yr B.P. and 1.3% around 20,800 yr B.P. Among the seven pioneer taxa presented in the diagram, only two, *Musanga–Myrianthus* and *Trema*, show in this zone frequencies similar to the next zones and particularly to zone IV (late Holocene) where all these taxa were in great extension. These two taxa exhibit a large peak between 25,000 and 24,000 yr B.P. with 2.8 and 4.3% for *Trema* and 3.9 to 11.4% for *Musanga–Myrianthus*.

3.4.2. Pollen zone II (ca. 20,000 to 10,000 yr B.P.)

A sharp increase in the Gramineae began around 20,000 yr B.P. and lasted until 10,000 yr B.P. The frequencies oscillated between 20 and 35% except for an isolated maximum of 53% at 15,100 yr B.P. In this zone the forest receded, giving way to more open vegetation, but as the tree pollen oscillated around 50%, significant patches of forest survived in the area (Section 5). The main other terrestrial herbaceous taxon belongs to Amaranthaceae with frequencies between 2 and 3%. The Compositae were very low, less than 0.5%, except for an abrupt increase to 2.5% around 19,000 yr B.P. The Cyperaceae, the main hygrophilous taxon, were in great expansion in this zone whereas they disappeared almost completely during the Holocene. Between 20,000 and 16,000 yr B.P. the frequencies of Cyperaceae were between 5 and 20% with two maxima of 33% around 19,000 yr B.P. and 38% around 17,000 yr B.P. Then they regressed to a minimum of 4% around 12,800 yr B.P. and extended to a third maximum of 17 to 26% between ca. 11,500 and 10,200 yr B.P. The other hygrophilous taxa (Table 1) were positively correlated ($R = 0.648/n = 35$) with the variation in Cyperaceae; their mean frequency is 3%. They disappear almost completely between 12,800 and 11,500 yr B.P. and also in the following zones. The large variations of hygrophilous taxa in this zone are probably related to lacustrine oscillations (Section 4.2.8).

This zone can be split in two sub-zones, sub-zone IIa from 20,000 to 15,000 yr B.P. and sub-zone IIb from 15,000 to 10,000 yr B.P. In this zone the most frequent tree is *Olea capensis*, a montane forest element, with an average of 10.8% in sub-zone IIa and of 7.7% in sub-zone IIb (in comparison 1.1% in Zone III and 0% in Zone IV). *Podocarpus*, another important montane forest element, has a very low frequency in this zone, with an average of 0.4%. Amont the taxa belonging to evergreen formations the most important was Caesalpiniaceae which exhibits two phases, the first one in sub-zone IIa with an average of 1.8% (the extreme frequencies are 3.6 and 0.5%) and the second in sub-zone IIb with an average of 3.7% (the extreme frequencies are 6.5 and 1%). For the two most important taxa of this family, *Hymenostegia* appears regularly through this zone (frequencies of 0.4 to 1.2%) but *Berlinia* is absent until 16,500 yr B.P. and then present until the end of this zone with values of 0.4 to 1.4%. Because of the entomogamous behaviour of this family, these frequencies indicate a regular development even during the driest period between 20,000 and 15,000 yr B.P. Sapotaceae was also relatively frequent but with lower percentages, an average of 0.8% in sub-zone IIa and of 1.25% in sub-zone IIb. Several pioneer taxa were also relatively important in this zone with peaks around 18,000 yr B.P. for *Milicia*, *Trema* and *Alchornea* and around 16,000 yr B.P. for *Milicia*, *Musanga–Myrianthus*. Of particular interest are the abrupt variations of *Celtis* with large peaks of 12.7% at ca. 18,000 yr B.P., of 8.7% at ca. 16,000 yr B.P. and with the largest peak of 22.3% (average of two successive values of 26.4 and 18.1%) at 12,400 to 12,000 yr B.P. *Macaranga* was very rare (0.5 to 1.6%) in this zone except near the top with a very large and abrupt peak of 11.6% (three successive values of 10.2, 12.4 and 12.4%) between ca. 11,500 and 10,800 yr B.P. Moreover, several tree taxa which exhibit their maximum extension in Zone III and are very low in Zone II, begin their extension near the end of this zone, between 12,000 and 10,000 yr B.P., i.e. *Mallotus*, *Macaranga*, *Uapaca* and *Nauclea* (Fig. 8). *Antiaris* exhibits a positive trend with 0% at the beginning of this zone until the top where the frequency reaches a maximum of 3.3% at ca. 11,200 yr B.P. and after that an abrupt decrease from 10,700 to 10,000 yr B.P.

(Section 4.2.2); then in zones III and IV this taxon showed very low frequencies.

3.4.3. Pollen zone III (ca. 10,000 to 2800 yr B.P.)

A sharp synchronous decrease in Gramineae and Cyperaceae occurred at ca. 10,000 yr B.P. associated with an abrupt increase of almost all trees which reached maximum extension. This Zone is split into two sub-zones, sub-zone IIIa from 10,000 to 6000 yr B.P. and sub-zone IIIb from 6000 to 2800 yr B.P.

3.4.3.1. The Biafrean Forest.
The Caesalpiniaceae pollen exhibit two phases, the first one in sub-zone IIIa with relatively low frequencies (mean of 2.1%) and the second one in sub-zone IIIb with higher values of 3.9%. Concerning the two most important taxa of this family, *Hymenostegia* has a very low frequency in sub-zone IIIa with an average of 0.3%, whereas in sub-zone IIIb it exhibits a low peak with an average of 0.7%. *Berlinia* shows a low peak between ca. 10,000 and 8800 yr (mean of 1%) and then it disappears almost completely until the end of sub-zone IIIa. In sub-zone IIIb this taxon exhibits its largest peak (average of 1.2% with a maximum value of 2.4%). The Sapotaceae have low frequencies in sub-zone IIIa (average of 0.9%) and their largest peak in zone IIIb (average of 1.8%). The other important taxa of this forest are rather regularly present throughout this zone: *Strombosia* with an average of 1.7%, Connaraceae 0.5%, *Diospyros* 0.45%, Flacourtiaceae 0.6%, *Klainedoxa* 2.7% and *Trichoscypha* 0.65%. Moreover *Klainedoxa* shows a decreasing trend with a maximum frequency of 8.7% around 9200 yr B.P. until 1.3% at the end of this zone and 0% at the beginning of zone IV.

3.4.3.2. The Semi-Deciduous Forest.
The most typical taxon, *Celtis*, is rather regularly present throughout this zone with an average of 4.5%, except for low frequencies from 10,000 to 8500 yr B.P. (between 2 and 0%). *Nauclea* and *Uapaca* occur frequently in these forests and exhibit a similar development, e.g. an early start between 12,000 and 10,000 yr B.P., then an almost regular presence in this zone with an average of 3% for

Nauclea and 1.9% for *Uapaca. Canarium* is almost only present from ca. 8000 yr B.P. to the end of this zone with a low average of 0.4%. *Antiaris* occurs mostly only between 5400 and 3400 yr B.P. with a low average of 0.4%. Although *Milicia* is classified in these forests, its evolution is rather similar to that of most of the pioneer taxa because of its very large peak in zone IV. *Milicia* exhibits its largest extension in this zone with an average of 9.1%.

3.4.3.3. The Atlantic Littoral Forest.
Lophira, the main taxon of this forest, exhibits a rather regular presence with an average of 1.6% and two peaks (3 to 4%) around 7000 and 3000 yr B.P. *Pycnanthus*, after an early beginning around 11,500 yr B.P. and a large peak of 9.3% at ca. 9900 yr B.P., extends rather regularly with an average of 2%.

3.4.3.4. The Pioneer Forest.
In this pollen diagram the main characteristic of the pioneer taxa is their abrupt extension with large peaks. *Mallotus*, a typical pioneer taxon, exhibit an almost regular extension (average of 13.1%) with an early start around 11,500 yr B.P. but without abrupt peaks. Before 11,500 yr B.P. this taxon is nearly absent. *Macaranga*, another important pioneer, exhibits an early start around 12,000 yr B.P., then two large peaks (between 12 and 15%) until ca. 8000 yr B.P. and afterwards it extends rather regularly until the top of this zone with an average of 5.7%. *Alchornea* appears rather regularly throughout this diagram with very low frequencies in zone I (1.7%), a few more in zone II (3%), and disappearing between ca. 11,500 and 11,000 yr B.P. After an early start around 10,800 yr B.P. it extends in zone III until 16 to 18% between 8000 and 6000 yr B.P. and then it decreases regularly reaching 2.4% around 4000 yr B.P.; the average in this zone is 9.3%. *Trema* exhibits its lowest frequencies in this zone with an average of 0.5%. *Musanga/Myrianthus* after being at its lowest frequencies in zone II, is regularly present in this zone with an average of 2.5%.

3.4.3.5. The Montane Forest.
In this zone *Olea capensis* disappears progressively with an average

of 1.1%, whereas *Podocarpus* increases progressively with a mean of 1.2% in sub-zone IIIa and with a maximum extension in sub-zone IIIb with an average frequency of 2.5% and a maximum of 3.8% between 3700 and 3400 yr B.P. At the beginning of Zone IV, this taxon disappears abruptly.

3.4.4. Pollen zone IV (ca. 2800 yr B.P. to present day)

This zone is split into two sub-zones, sub-zone IVa between 2800 and 2000 yr B.P. and sub-zone IVb between 2000 yr B.P. and the present day. In sub-zone IVa all the taxa related to open environments and particularly pioneer taxa exhibit a very large and abrupt extension. The only herb taxon to follow such an expansion is Gramineae which increases abruptly to high frequencies between 2600 and 2100 yr B.P. (in comparison with an average of 1.4% in zone III).

3.4.4.1. The Biafrean Forest.
In the sub-zone IVa the Caesalpiniaceae taxa declined to very low frequencies with an average of 0.5% and in sub-zone IVb they exhibit large oscillations but with low frequencies (average of 1.6%); the present day value is very low with 0.15%. The most important taxon of this Family, *Berlinia*, disappears almost completely in this zone, whereas *Hymenostegia* is very low in sub-zone IVa but increases in sub-zone IVb (average of 0.6%) to a similar value as that in sub-zone IIIb, and is absent in the present day sample. The Sapotaceae disappears almost completely in this zone. The other important taxa of this forest regress or disappear almost completely in sub-zone IVa, most of them exhibiting a small increase in sub-zone IVb like Flacourtiaceae, *Klainedoxa*, *Diospyros* and *Trichoscypha*.

3.4.4.2. The Atlantic Littoral Forest.
Lophira decreases partly in sub-zone IVa but more than during short periods in zone III. There was a large peak between ca. 2200 and 1700 yr B.P. with a maximum of 3.8% (average of 2.8% in zone IV). *Pycanthus* decreases also partly in sub-zone IVa (average of 1%) but it exhibits a large extension in the sub-zone IVb with relatively high frequencies until the sub-actual (average of 3.8%).

3.4.4.3. The Semi-Deciduous Forest.
Celtis decreases to relatively low frequencies in sub-zone IVa (mean of 1.9%) and increases progressively in sub-zone IVb until the present day (mean of 2.9%). In sub-zone IVa *Nauclea* and *Antiaris* disappear almost completely, whereas *Uapaca* and *Milicia* decreases to low values (mean of 4% for *Milicia*). In sub-zone IVb *Nauclea* increases to low values (average of 1.4%), *Antiaris* disappears almost completely except for a low value of 1% in the present day sample, whereas *Uapaca* exhibits relatively large increases. *Uapaca* has a short peak at the very beginning of the sub-zone IVb (ca. 1900 yr B.P.) with a maximum of 5.5%. *Milicia* exhibits a very large increase in this sub-zone (average of 11.5%) and a particularly large peak between 1900 and 1300 yr B.P. with an average of 19.8%.

3.4.4.4. The Pioneer Forest.
Almost all the pioneer taxa exhibit large peaks in zone IV and most of them in the sub-zone IVa as for *Alchornea*, *Trema*, *Musanga/Myrianthus* and *Elaeis*. *Alchornea* has the largest peak in this sub-zone (average of 22.9% in comparison to an average of 5.2% in the preceding sub-zone IIIb). Then in the first part of sub-zone IVb it regresses strongly (average of 4.9%). *Trema*, being very low in zone III (average of 0.5%), exhibits a very large peak in the first part of sub-zone IVa (average of 7.3% for the first three levels). *Musanga/Myrianthus* shows a similar pattern with a regular low frequency in zone III (average of 2.5%) and a very large peak of 29.7% in the first level of sub-zone IVa. The average frequency of this taxon in zone IV (8.4%) is much higher than in zone III.

Elaeis, the last taxon of this group, presently usually classified as 'anthropic', existed in the past as a pioneer (Section 4.2.5). An important feature linking *Elaeis* to pioneer species is its very similar development, in the late Holocene, to the other pioneer taxa studied there, particularly *Alchornea*. Indeed *Elaeis* first appears near the beginning of the Holocene, almost at the same time as the rain forest completely reinvaded the region. *Elaeis* is present rather regularly throughout zone III with an average of 1.1%. It exhibits a large peak in sub-zone IVa (average of 5.8%) reaching a maximum frequency of 9.3% (average of three successive

levels between ca. 2750 and 2500 yr B.P.). This peak and the curve of *Elaeis* through the zone IV follow almost exactly the peak and the curve of *Alchornea*, only with lower values.

Mallotus exhibits very low frequencies at the end of sub-zone IVa and in the first level of sub-zone IVb (0.6%). This low frequency occurs at the end of a negative trend which began around 9000 yr B.P. For *Macaranga*, its curve oscillates to a greater extent in zone IV than in III and its mean frequency in zone IV (11.8%) is almost twice that observed in zone III (5.7%).

3.4.4.5. The Montane Forest. *Olea capensis* disappears at the very beginning of zone IV, as does *Podocarpus* but much more abruptly. In zone IVa the last few appearances of *Podocarpus* (0.5%) occurred between 2600 and 2300 yr B.P.

4. Interpretation and discussion

4.1. Introduction. The spatial and temporal complexity of the rain forest

In such a study the major question to be addressed is the nature of the coupling between climate variation and vegetation response (Ritchie, 1986). Until now this problem has been principally analyzed in North America and in Europe (Shugart, 1984; Overpeck et al., 1990; Campbell and McAndrews, 1993; etc.), but rarely in the tropical regions (Ritchie, 1995). The difficulty of this problem in the tropical rain forests is exacerbated by the large complexity which exists, particularly in the enormous species diversity which also explains the large gaps in knowledge of modern taxonomy and ecology (Puig, 1995; Riera, 1995). If the complexity of the rain forest is first related to the spatial multiplicity of levels of organization, it is expressed also by the multiplicity of the temporal scales which govern its functioning (Hallé et al., 1978; Whitmore, 1989; Riera, 1995; Pascal, 1995; Porter et al., 1996):

—between 10 and 100 years for the regeneration of 'cicatrization' of gaps due to tree falls;

—between 100 and 500 years (and more) for waves of colonization or succession of vegetation related to favourable climatic changes (Pascal, 1995; Loffeier and Favrichon, 1996);

—between 10 and 100 years for setback due to unfavourable climatic changes or 1 to 10 years for massive destruction due to large fires (see the recent example of Kalimatan in Borneo during the very dry year 1982–1983; Goldammer and Seibert, 1990).

The forest destruction can intervene for periods of less than a month to several years, whereas its reconstitution is a very slow and particularly complex process. This includes at least two formations succeeding one another. First a pioneer one, also called 'secondary', rapidly reconstitutes the canopy (10 to 50 years), then under the canopy a 'primary' formation (shade-tolerant) reconstitutes progressively (100 to 500 years or more) taking the place of the pioneer formation with which it will coexist for some time (Swaine and Hall, 1983; Whitmore, 1989; Maley, 1990; White et al., 1997). Most of the present day forests exhibit a mosaic pattern of at least two different formations (Letouzey, 1968, 1985; White, 1983; Maley, 1990). Because of this inertia or this phenomenon of delay, called 'hysteresis' by some ecologists who adopted a term coming from the physical sciences (Ritchie, 1986), it appears that the floristic composition of a forest massif is largely influenced by its history, which will also influence its later evolution. In some way the large tropical rain forests are partly fossil formations.

The results of pollen analysis from a permanent observatory like the lake Barombi Mbo, extending continuously from ca. 28,000 yr B.P. to the present, should provide precise documentation of the forest dynamics of the area.

4.2. Dynamism and trends in the vegetation of the Barombi Mbo region during the late Quaternary

In order to emphasize the trends, a smoothing technique by moving average or running means (Anderson, 1971) was applied to the pollen frequencies. This technique has already been applied by palynologists (f. ex. Ritchie, 1985). The use of three samples moving average would emphasize trends at the scale of millennia and also provide

evidence of peaks or abrupt changes. This smoothing was applied to all taxa depicted in the pollen diagram and are presented in Fig. 7Fig. 8. For many taxa (f. ex. Gramineae and most of the pioneers) the smoothing dampens short-term variations and only large peaks are emphasized.

4.2.1. The Montane Forest

The following summary of their phytogeography is prerequisite to understanding the history of the two main taxa, Olea capensis (syn. O. hochstetteri) and Podocarpus. Only the species Podocarpus latifolius grows in southern Cameroon (Letouzey, 1985) and also on several mountains of the central Atlantic region (Zaïre, Angola, Congo) (White, 1981; Maley et al., 1990b). The species Podocarpus gracilior grows only in East Africa (White, 1981). Another endemic species, Podocarpus mannii, is confined to the island Sao Tomé, ca. 300 km from Cameroon, where it probably differentiated long ago in Cretaceous period when the African and South American plates broke apart (cf. Maley, 1996b). In the mountains situated at distance from lake Barombi Mbo (Section 2.1) the nearest locality of Podocarpus latifolius is on the top of Mount Kupé (25 km northeast) and until now it has never been found on Mount Cameroun (35 km south) nor in the Roumpi Hills (20 km northwest) (Letouzey, 1985; Thomas, 1993; Cable, 1993).

Olea capensis grows on Mount Cameroun but not on Mount Kupé nor the Roumpi Hills. However, in southern Cameroon these two taxa are sometimes found on the same mountain, as on Mount Ngoro (1580 m) or Mount Oku (3010 m) (Letouzey, 1985). Concerning the present day ecology of these two mountain species, the data from Cameroon (Letouzey, 1968, 1985) and from different mountains of tropical Africa show that they grow mainly in cloud forests (Kerfoot, 1968; White, 1978, 1981) but Olea capensis in drier biotopes than Podocarpus latifolius (Bader, 1965; Coetzee, 1978; Hamilton and Perrott, 1981). This last feature can explain the opposite trend of the pollen curves of these two taxa. The clouds linked to these forests are low and of stratiform type, frequently becoming fogs (Kerfoot, 1968). These clouds usually give no rain or only drizzle but their relative permanence induces lowering of temperature (Maley and Elenga, 1993). The development of such montane vegetation is mainly linked to this cooling effect.

To explain the large pollen development of tropical montane taxa during cool phases, several palynologists estimated that their range extended into lowland areas as during the LGM (Van Zinderen Bakker and Coetzee, 1972, 1988; Flenley, 1979; White, 1981; Hamilton, 1982; Maley, 1987, 1989, 1996a). In the present day rain forest domain, diverse montane taxa sometimes exhibit residual extension to lowland areas, i.e. between 300 and 800 m, such as in southern Cameroon (Letouzey, 1968, 1985), Congo (Maley et al., 1990b; Maley and Elenga, 1993), Sierra Leone, Angola and also the island of Annobon (White, 1981, and pers. commun., 1983). Some taxa are more prone to extend to lowland areas and it is particularly the case for Olea capensis which White (1983) described as an 'ecological transgressor' from upland to lowland areas. However, all the present day lowland extensions of such upland transgressors correspond to relictual stations of probably former and larger extensions. These relictual stations can persist because at the present time they are associated with clouds or fog development (White, 1981; Maley, 1987, 1989, 1996a). For instance White (written commun., 10 August 1983) pointed out that on the island of Annobon, Olea capensis was found between the altitude of 300 and 500 m on one peak named 'Pico de Fogo' (peak of fog). Moreover in southern Cameroon the present day distribution of Podocarpus latifolius and Olea capensis (Letouzey, 1985) is directly related to high annual fog frequency (data and map of fog in Suchel, 1988; cf. Reynaud-Farrera, 1995). However, if the large frequencies of Olea capensis (average of ca. 17% in zone I and of ca. 11% of sub-zone IIa at the time of the LGM) can be explained by its growing at short distances from the lake, probably on the nearby hills culminating between 400 and 600 m (see similar extension in Ghana around the Bosumtwi lake, Maley and Livingstone, 1983; Maley, 1991), the very low frequency (<1%) of Podocarpus during the same period and then the relative increase during the early and middle Holocene (zone III) until a peak of 3.8% between 3700 and 3400 yr B.P., can only
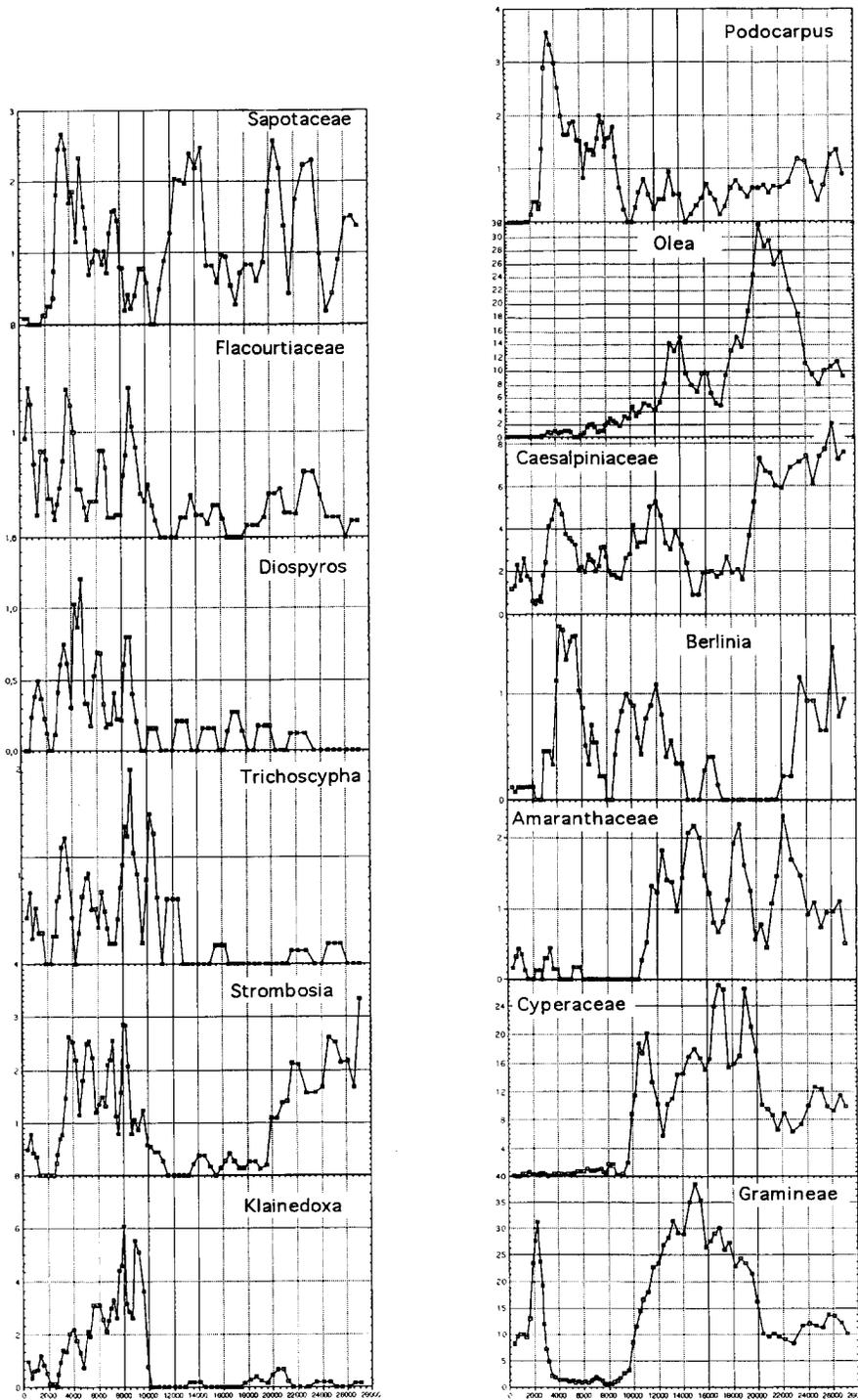
Fig. 7. Curves of the main trends and variations of the pollen taxa (3 samples moving average) with an interpolated radiocarbon chronology (Fig. 3) in the lake Barombi Mbo, core BM-6. The Biafrean/Evergreen Forest: Caesalpiniaceae, Sapotaceae, Flacourtiaceae, *Berlinia*, *Diospyros*, *Trichoscypha*, *Strombosia*, *Klainedoxa*. The Mountain Forest: *Podocarpus*, *Olea*. Herbaceous plants: Amaranthaceae, Cyperaceae, Gramineae.
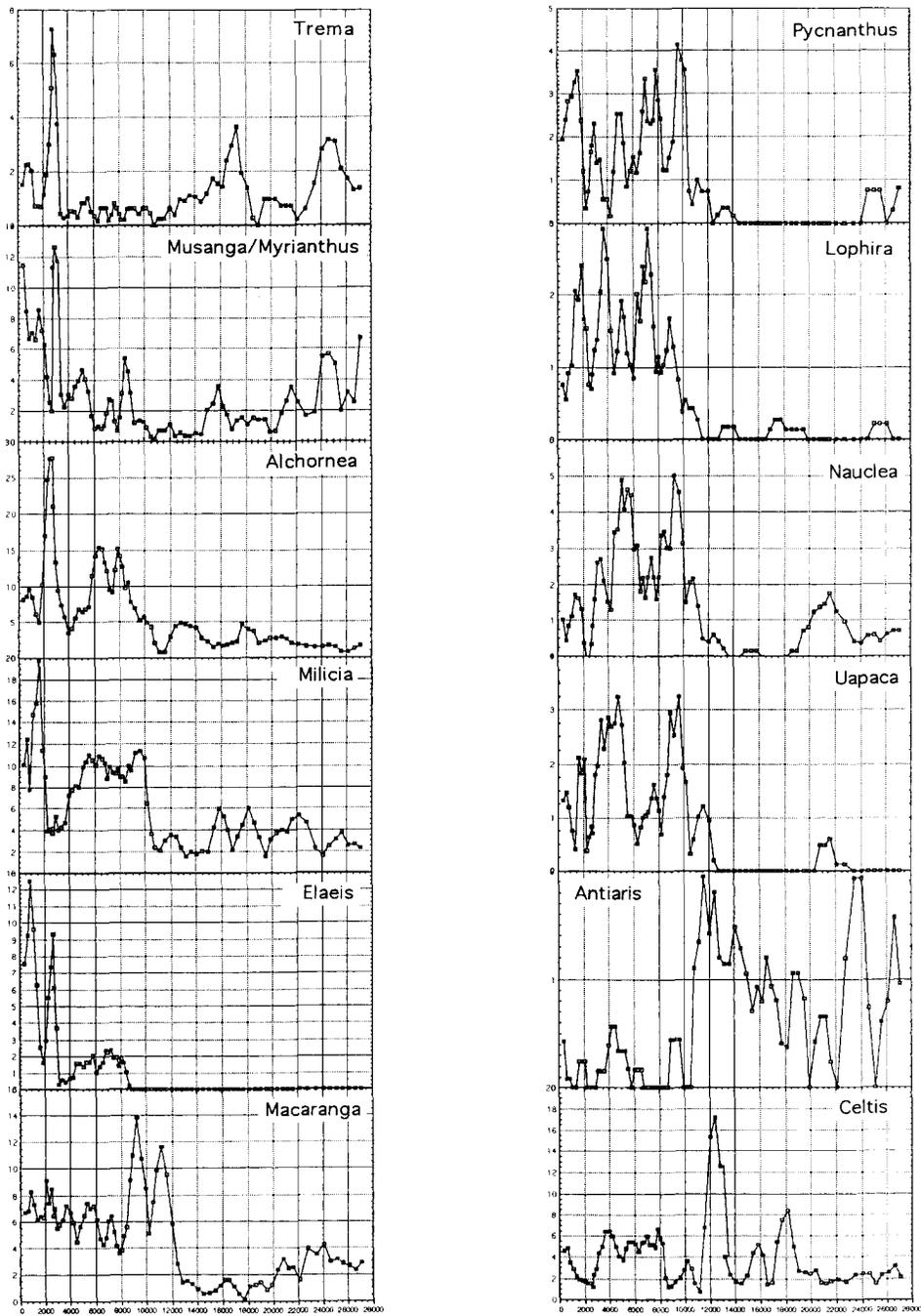
Fig. 8. Curves of the main trends and variations of the pollen taxa (3 samples moving average) with an interpolated radiocarbon chronology (Fig. 3) in the lake Barombi Mbo, core BM-6. The Pioneer Forest: *Trema, Musanga/Myrianthus, Alchornea, Milicia, Elaeis, Macaranga*. The Atlantic Littoral Forest: *Pycnanthus, Lophira*. The Semi-Deciduous Forest: *Nauclea, Uapaca, Antiaris, Celtis*.

be explained by its growing on distant mountains and probably Mount Kupé. Because the pollen of *Podocarpus* is well adapted to long distance dispersal, such an interpretation is compatible with these data. The relative increase of *Podocarpus* during early and middle Holocene, and particularly the important peak intervening between 3700 and 3400 yr B.P., can be explained by stratiform cloud development in Mount Kupé (Section 5; Maley, 1996a,b).

4.2.2. The Biafrean Evergreen Forest

The curve of the Caesalpiniaceae exhibits an alternation of periods with relatively high frequencies between ca. 27,000 and 20,000, between 15,000 and 10,000, and between 6000 and 3000 yr B.P., and periods with low frequencies between ca. 20,000 and 15,000, between 10,000 and 6000 yr B.P., and from 3000 yr B.P. to the present day. The lowest frequencies intervened between ca. 3000 and 2000 yr B.P. and also around 15,000 yr B.P. The curve of *Berlinia* follows the same general variation except for a period between 22,000 and 14,000 yr B.P., when it disappears almost completely. The variation of the pollen of *Hymenostegia*, in general much less frequent than that of *Berlinia*, produces a curve (not shown) almost opposite to that of *Berlinia*, particularly between 22,000 and 14,000 yr B.P. when it reaches relatively high frequencies.

Regarding the curve of the total pollen of Caesalpiniaceae, the relatively high frequencies before 20,000 yr B.P. probably correspond to a very large development of this family in the region around the lake. The relatively low development of the hygrophilous Cyperaceae before 20,000 yr B.P., in comparison to the important development between 20,000 and 10,000 yr B.P. (Section 4.2.8), probably indicates the extension on the catchment area of marshy and also riverine formations. The Caesalpiniaceae could have grown particularly in such riverine environments because in some regions of the present day African rain forest one observes large developments of many different species of Caesalpiniaceae in gallery forests as in Cameroon (Letouzey, 1985) or Gabon (White et al., 1997 and pers. commun.). The rather similar frequencies between 20,000 and 15,000 and

between 10,000 and 6000 yr B.P. can be interpreted by comparable importance and this family during the LGM period and the early to middle Holocene. This point could show that at the time of the LGM, the forest patches remaining in this region, partly also in reverine formations, and interpreted as Refugia (Section 5; Maley, 1987, 1989, 1996b; Giresse et al., 1994), were relatively rich in Caesalpiniaceae (cf. Rietkerk et al., 1995). Another interesting feature appears during early and middle Holocene with rather similar trends between the curve of Caesalpiniaceae and that of *Podocarpus* (Section 4.2.1). This feature could be related to the fact that certain evergreen lowland forests are also favoured by stratiform clouds and mist developments. Indeed today near the climatic boundary of such a formation, certain forests rich in Caesalpiniaceae, with frequently *Monopetalanthus*, are most likely to be found on hill tops [see instances in southern Cameroon (Letouzey, 1985; Achoundong, 1985) or in Congo and Gabon (Maley et al., 1990b)].

The curve of the Sapotaceae shows a general variation rather similar to that of the Caesalpiniaceae, except mainly before 24,000 yr and also between 11,000 and 10,000 yr B.P. Although the quasi periods of these two families have different time lengths, they are rather in phase. The very large periodicities of the curves of these two families, in comparison to the curves of the other taxa presented below, could be due to the fact that the Caesalpiniaceae and Sapotaceae group together a large number of taxa with partly different ecological requirement. The other pollen taxa frequent in evergreen formations (Flacourtiaceae, *Diospyros*, *Trichoscypha*, *Strombosia*, *Klainedoxa*) exhibit interesting quasi periodicities. Their frequencies are very low during the LGM continuing until the beginning of the Holocene, except *Trichoscypha*, which show an early start around 11,000 yr B.P. The Flacourtiaceae and particularly *Strombosia* show large developments before 20,000 yr B.P. During the Holocene, the curves of all these taxa exhibit quasi periods of roughly 2000 to 2200 radiocarbon years and sometimes between 2000 and 1000 yr for *Strombosia* and *Klainedoxa*. Most of the peaks and lows of these quasi periods do not occur at

the same time and their relative extension is also different. For these reasons one can interpret these features as large phases of succession or substitution of one taxon or group of taxa by another. So the pollen data of the lake Barombi Mbo confirm the hypotheses presented by several botanists concerning large sylvigenetic cycles, but with cycles apparently longer than estimated using present day botanical data (Section 4.1). Our data show that, in this region, the duration of these cycles is mostly of about 2000 to 2200 radiocarbon years which, for this period, corresponds to ca. 2200 to 2500 calendar years (Section 5). In a study of a pollen core from Burundi (East Africa) going back to ca. 12,000 yr B.P., Jolly (1993) presents evidence of rather regular lacustrine fluctuations with quasi periods of about 1300 yr. This last periodicity could be compared to that obtained for *Strombosia* and *Klainedoxa*. The causes of these different cycles or periods are diverse but the climatic changes, large or more discrete, probably play an important role, particularly for long temporal scales. For instance, proof is given by the fact that a major and synchronous low intervened in all these periodicities between ca. 2800 and 2000 yr B.P. at a time of a well defined climatic deterioration (relatively arid phase) (Maley, 1996a, 1997).

4.2.3. The Atlantic Littoral forest

The two main taxa of this type of forest, *Lophira* and *Pycnanthus*, exhibit pollen curves with quasi periods of roughly 2000 yr comparable to that of the evergreen taxa described above. In the forest domain, *Lophira* belongs to the species *alata*. In its young phase the ecological behaviour of *Lophira alata* is that of a light-demanding pioneer tree, but later when it reaches the canopy it can grow to very large size and live several centuries (Letouzey, 1968, 1985). However, no young tree can grow under the shade of the mature tree. The only possibility of regeneration of such a type of forest is its almost complete destruction. To explain the very large extension on almost all the Cameroon littoral area of this present day mature forest, with trees aged of 2 and 3 centuries, Letouzey (1968) estimated that it could result from a large and synchronous anthropic destruction 2 to 3 centuries ago. However, no archaeological data on this large

area sustain such a hypothesis but some abrupt palaeoclimatic disturbances seem to be a more plausible hypothesis (Reynaud and Maley, 1994). At the present time when a *Lophira alata* tree falls or is cut, *Pycnanthys angolensis*, another light-demanding pioneer tree, frequently grows in the gap, but hardly ever a *Lophira alata* tree (Letouzey, 1968, 1985) because this species is drought sensitive as a seedling (Swaine et al., 1997). Finally one can note that the temporal evolution of the pollen curve of these two trees during the Holocene is similar to that of the evergreen shade tolerant trees.

4.2.4. The Semi-Deciduous Forest

The forest taxa *Nauclea* and *Uapaca* occur frequently in this type of forest, and show large and rather similar quasi periodicities during the Holocene. The main period between ca. 10,000 and 4000 yr B.P. has a length of ca. 4000 to 4500 yr. These two curves also exhibit an early start between 12,000 and 10,000 yr B.P. Before 20,000 yr B.P. *Nauclea* also presents a low peak at around 22,000 yr B.P.

The curve of *Celtis*, an Ulmaceae taxon typical of this forest, exhibits three peaks between 20,000 and 10,000 yr B.P., a low one at 16,000 yr B.P., an intermediary at 18,000 yr B.P. and a very large one between 13,000 and 11,500 yr B.P. which culminated at ca. 12,200 yr B.P. These peaks probably correspond to abrupt pulses of this forest during colonization phases, particularly the last which intervened at the same time as the maximum extension of *Antiaris*. One will see below (Section 4.2.8) that a first major increase of precipitation culminated at ca. 12,200 yr B.P., before the beginning of the Holocene. So the major peaks of *Celtis* and *Antiaris* were probably linked to this humid pulse.

The curve of *Antiaris* is of particular interest because its major extension occurred before the Holocene. This curve presents first two large and abrupt peaks between 24,000 and 27,000 yr B.P., but its major extension occurred between 22,000 and 11,000 yr B.P. with a positive trend beginning with low frequencies between 22,000 and 20,000 yr B.P., and next extending progressively to a maximum between 12,200 and 11,500 yr B.P. and then decreasing abruptly to 0% around 10,500 yr B.P.

During the Holocene its frequency was nil or very low. The genus *Antiaris* has one species, *A. toxicaria*, with the sub-species *welwitschii* in West and Central Africa; this subspecies had two varieties, *welwitschii* and *africana* (Berg et al., 1985). The variety *welwitschii* grows only in wet forests but is uncommon and the variety *africana* lives in the driest forests and also in islands of forest included in savannas (Jones, 1963; Berg et al., 1985). The trend depicted there corresponds very probably to the variety *africana* implying that dry forests were present in this region during the LGM until about 11,000 yr B.P.

4.2.5. The Pioneer Forest

Almost all pioneer taxa presented in Fig. 8 do not exhibit quasi-periodicities as for most other taxa described above. With the exception of *Elaeis* (Section 4.2.6), which began to appear in the early Holocene, all the pioneer taxa are present from the base to the top of the diagram with rather regular frequencies, except several low peaks and one or two very large and abrupt peaks during the dry period situated between 2800 and 2000 yr B.P. (zone IVa). The main and abrupt peak of the *Milicia* curve occurred just after the end of this dry period and so just at the beginning of a new wet period. The latest peak of *Elaeis* intervened after that of *Milicia*, so these three successive peaks could be related to a classical succession. The fact that the major peak of *Milicia* intervened during a relatively wet phase, in contrast to the other pioneer tree described above, is comparable to the curve of *Celtis* which exhibits its major peak during another increase in precipitation (Section 4.2.4). This common behaviour shows that *Milicia*, as Letouzey (1968, 1985) estimated, belongs to the semi-deciduous forest. The behaviour of *Macaranga* is different but possibly closer to this second type because its two major peaks intervened during the large increases of rains in the early Holocene. From then until the present day the curve of *Macaranga* presents a rather regular succession of low peaks with quasi periods of about 2000 yr.

All the major peaks depicted by these curves illustrate the classic exponential plant population growth model which was described, for instance,

by Magri (1989) and Bennett (1990). These data also suggest that such exponential growths can occur during dry or wet periods, probably depending on the types of tree (either pioneer or from semi-deciduous forest) but also on the climatic characteristics of each period. Some present day studies on early successions in tropical forests show such exponential growth of population of pioneer trees (Swaine and Hall, 1983; Whitmore, 1989). Indeed if for any reason, part of a forest is cleared (chablis or larger gap), only a few species are able to grow quickly enough to fill the gap, explaining this exponential growth phenomenon. The climatic deterioration which lasted several centuries between ca. 2800 and 2000 yr B.P. was responsible for numerous large forest openings where the pioneer trees were able to extend into very large areas. The present day isolated patches of savanna at the north of the Mount Cameroun and also the very large areas of Maranthaceae open forest, on the western side of this mountain (Section 2.1; Fig. 2; Maley, 1990), are probably relics of this former extension, when they spread nearer to the lake Barombi Mbo. The same kind of conclusion was also reached by White (1995) and White et al. (1997) concerning large extensions during the same period of similar formations in the Lopé area, central Gabon.

4.2.6. Elaeis guineensis, the oil palm

The characteristic pollen of *Elaeis* belongs to the species *E. guineensis*, the oil palm. In order to interpret the pollen curve of *Elaeis guineensis*, one must first discuss the status of this palm tree. Usually today this palm is almost always associated with human activity, but it has been reported in some vegetal communities with natural status. In fact this palm tree belongs to the African forest vegetation (Maley, 1996a) and the oldest report of its pollen was in Eocene deposits near Konakry, Guinea (Zaklinskaya and Prokofyev, 1971). Later in some Miocene deposits of the Niger delta, its relative abundance already reached around 10% (Zeven, 1964). The oil palm was initially a pioneer tree living naturally near the periphery of the rain forest and in gaps. Indeed in western Cameroon in the northwestern part of the forest massif, between the altitudes of 500 and 800 m, from

Takamanda to Batibo and then to Fontem and Santchou, the botanist Letouzey (1978, 1985) described a forest belt, more than 150 km long (extending probably on the Obudu Plateau in eastern Nigeria), and 10 to 20 km wide, dominated by tall and numerous *Elaeis guineensis* (Fig. 9). This oil palm belt follows approximately the edge of the rain forest up to ca. 30 km inside. Letouzey (1978, 1985) considers this 'oil palm belt' as being a natural formation based on several criteria, particularly the absence of trees classically linked to Man and found in plantations. The large development of this palm tree in forests near the boundary with savanna where fire can occasionally spread, is linked to its resistance to fire, having no cambium and stem tissues protected by persistent woody leaf bases (Swaine, 1992), and to the fact that fire can enhance its seed germination (Swaine and Hall, 1986). So this forest belt close to the savanna could be compared to the 'Fire Zone' described in Ghana by Hall and Swaine (1981).
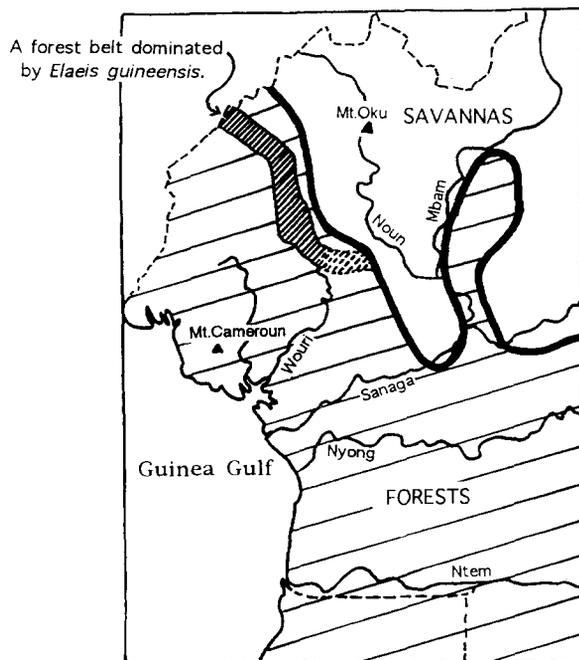
Fig. 9. An 'oil palm belt' near the edge of the rain forest in West Cameroon. This belt is formed by a high density of *Elaeis guineensis* reaching 20 to 25 m height in association with a mature forest of the semi-deciduous type (Letouzey, 1978).

In the Barombi Mbo diagram, *Elaeis guineensis* pollen first appeared with low percentages (ca. 1 to 3%) during the early Holocene at the same time as the first forest extension. Its first abrupt extension, reaching ca. 8 to 10%, occurred between ca. 2800 and 2400 yr B.P. and followed rather precisely, but with lower percentages, the peak of *Alchornea* pollen, another major pioneer tree (Section 4.2.5). Then the oil palm regressed to very low values around 2000 yr B.P. Finally a second and more important extension phase occurred between ca. 1500 and 700 yr B.P. with maximum values between ca. 10 and 13%, at the same time as a second peak of *Alchornea* and also during the major peak of *Milicia*. In the present day lacustrine sediment the frequency of the oil palm pollen is ca. 5%.

Because of the synchronous and abrupt extension of *Elaeis*, *Alchornea* and Gramineae pollen one can estimate that during the first *Elaeis* peak between ca. 2800 and 2400 yr B.P., the behaviour of the oil palm was exclusively natural and led to a very large development of this palm tree. It was during the following regression phase of *Elaeis*, between ca. 2300 and 2100 yr B.P., that the major Bantu invasion into the rain forest occurred (Schwartz, 1992; Oslisly and Fontugne, 1993; Oslisly, 1995), when these people probably collected nuts of the oil palm. It was shown that in traditional forest village, the natural regeneration of the oil palm is so prolific that there is no need for its plantation (Schnell, 1976). So when Bantu people clear a forest area, they protect several tree species growing naturally, as this palm. Domestication can intervene only with seed or seedling plantation associated to repeated selections (Schnell, 1976). One can hypothesize that the protection of this palm tree could have begun during the rarefaction phase of this taxon around 2000 yr B.P. and continued during its recent phase of development which culminated between ca. 1500 and 700 yr B.P. This phase was associated with the post 2000 yr B.P. new extension of the rain forest (Section 3.4; Zone IVb). In the lake Ossa near Edea (Reynaud-Farrera et al., 1996) and also in north Congo in the Nouabalé–Ndoki region (W. Fanjoy, pers. commun.) similar *Elaeis* peaks, between ca. 1700 and 1000 yr B.P., were also

recorded. In this context the 'oil palm belt' which presently extends near the edge of the rain forest in western Cameroon could be an example of a forest extension phase during which the oil palm could have been a major pioneer tree at the edge of the forest. During the last millennium, the wide extension of *Elaeis guineensis*, near the edge of the forest but also far inside, could have been a favourable factor of human population development.

However, more precise answers to these issues and particularly to the problem of the oil palm domestication, its way, its places and its time, will only be reached by new research associating palynologists, archaeologists, botanists, geneticians, geochemists, etc.

4.2.7. The grass vegetation

The main development period of grass vegetation, related mainly to the Gramineae, occurred before the Holocene and particularly during the LGM, and until ca. 10,000 yr B.P. However, as can be confirmed below (Section 5), the grass vegetation never dominated the forest. During the climatic deterioration between ca. 2800 and 2000 yr B.P. the Gramineae also exhibited an exponential development in association with the main pioneer trees (Section 4.2.5). This last grass vegetation development can be directly linked to savanna extension in the region (Section 2.1). This savanna extension resulted from a relatively dry climate due to increased seasonality (Section 5) but no data coming from the lacustrine sediment, particularly charcoal remains (Giresse et al., 1994), permit to estimate that this savanna extension was associated with large fires. The curve of Amaranthaceae (Section 3.1) extends at the same time as that of Gramineae and exhibits several large peaks with irregular periodicities, one of ca. 2500 yr and two of ca. 4000 yr.

4.2.8. The aquatic vegetation and the lake level variations

Frequently, when a lake level falls, muddy expanses appear which are quickly colonized by aquatic vegetation (Maley, 1972, 1981). At Barombi Mbo a large drowned shelf extends onto the deltaic zone offshore of the main inlet, 3 to

5 m below the present day surface (Giresse et al., 1994). The aquatic vegetation can then spread onto this shelf during low stands of the lake. Before the Holocene, the variations of the Cyperaceae pollen was positively correlated ($R = 0.648/n = 35$) with those of all other, though sparse aquatic taxa (mainly *Nymphaea*, *Typha*, *Utricularia*, *Potamogeton*) (Giresse et al., 1994). During wet phases, as during the present day, the water surplus is evacuated by the outlet and so the lake level variations are very small, but during dry periods due to rain decreases the lake level can fall below the outlet level. The large development of the Cyperaceae between 20,000 and 10,000 yr B.P. was probably related to the extension of aquatic vegetation onto the emerged shelf due to the lowering of the lake level. This lowering was probably of no more than five metres. As shown elsewhere, for instance for lake Chad (Maley, 1981, 1993) and for a pond in Burundi (Jolly, 1993), it is possible to use the pollen curve of Cyperaceae as a proxy of lake level variation. Between 20,000 and 14,000 yr B.P. the lake level was relatively low and the two maxima correspond with the lowest lake levels around 19,000 and 17,000 yr B.P. A first transgressive phase culminated around 12,200 yr B.P. and then the last major regression occurred culminating between ca. 11,500 and 10,400 yr B.P.

5. Conclusions. The palaeoenvironmental and climate changes

Several conclusions have already been published in previous publications (Brenac, 1988; Maley et al., 1990a; Maley, 1991, 1992, 1996a) and particularly one (Giresse et al., 1994) in which the main pollen record (curve of AP/NAP) was positively compared to the variation of carbon isotopes ($\delta^{13}C$) in the organic matter extracted from the lacustrine sediments. It was shown that this organic matter was almost completely detritic in origin and came from the litter and the humus top soil on the catchment (Giresse et al., 1994). The most important result concerns the main dry phase between 20,000 and 10,000 yr B.P. during which the $\delta^{13}C$ shifted towards lighter values (average of

−26‰ in comparison to −32‰ during the Holocene extension of the forest). However, the value of −26‰ is at the limit of typical forest isotopic values (−26 to −36‰) (Giresse et al., 1994). This result is explained in this region by the obvious dominance of forest areas over those of savanna type. This conclusion confirms, that during the LGM, large patches of forest interpreted as Refugia remained (Maley, 1987, 1989, 1996a,b; Giresse et al., 1994).

The curve of Cyperaceae (Fig. 7) which is linked to lake level variation (Section 4.2.8) is also related to variation of precipitation on the catchment. However, before the Holocene, the temperature lowering (see below) which also reduced the evaporation, partly counteracted the reduction of precipitation. One can conclude that the main reduction of precipitation occurred between 20,000 and 14,000 yr B.P. with two minima around 19,000 and 17,000 yr B.P. Then between ca. 13,000 and 12,000 yr B.P. a great increase of precipitation intervened, which was also related to the first warming trend near the end of the LGM (see below). So this period could correspond to an abrupt increase of the monsoon. Relatively high temperatures persisted later, particularly between ca. 11,500 and 10,400 yr B.P. when an abrupt and important reduction of precipitation occurred. During this period almost all pollen largely decreased except the pioneer tree *Macaranga*, which exhibited its first abrupt and very large extension. This dry phase dated between ca. 11,500 and 10,400 yr B.P. corresponds also to the first part of the Younger Dryas time period, dated between ca. 11,000 and 10,000 yr B.P. (Fairbanks, 1989; Gasse et al., 1990; Bonnefille et al., 1995). The lacustrine regression between ca. 11,500 and 10,400 yr B.P. could be due to an increase of the evaporation but primarily to a reduction in precipitation linked to an increase in seasonality with a particular lengthening of the annual dry period. The fact that the frequency of Cyperaceae was less than 1% in the samples situated in the dry period between ca. 2800 and 2000 yr B.P. indicates that no lacustrine regression was then registered. This important point probably indicates that this dry period was a response to a reduction in the length

of the rainy season, i.e. an increase in the seasonality, rather than a lower total of precipitation.

The discussion concerning the mountain forest and particularly the extension of the mountain taxon *Olea capensis* to the lowland and possibly onto the hills around the lake Barombi Mbo (Section 4.2.1) lead to the conclusion of a temperature cooling, particularly until ca. 13,000 yr B.P. The temperature lowering could be rather similar to that estimated with the same mountain taxon in the Bosumtwi region in Ghana, i.e. about 3°C (Maley and Livingstone, 1983; Maley, 1991), which also approximates the value estimated by statistical analyses in East Africa (Bonnefille et al., 1992). The large decrease of *Olea* occurring between ca. 13,000 and 12,000 yr B.P. was particularly linked to an important warming trend. The relatively high temperature persisted during the Younger Dryas time period (see above) and later during the early and middle Holocene. A similar result was obtained by Vincens et al. (1993) for the lake Tanganyika.

Concerning the pollen of the other montane taxon *Podocarpus* (Section 4.2.1), its relative increase during the early and middle Holocene and particularly its peak between 3700 and 3400 yr B.P. cannot be explained by a development of this tree in lowland near the lake but more probably by an increase on some mountains of this region, particularly on Mount Koupé (Section 4.2.1). A major peak of *Podocarpus* has also been found between ca. 4000 and 3000 yr B.P. in other pollen core analyses of southern Cameroon, such as that conducted in lakes Mboandong (Richards, 1986), Ossa (Reynaud-Farrera et al., 1996) and in the marine platform (Bengo, 1996), Another site in Congo, situated at Bilanko (altitude around 600 m) on the Batéké Plateau, 80 km north of Brazzaville, presents an important *Podocarpus* pollen record (Elenga et al., 1991; Elenga, 1992). However, the major extension phase, with a maximum frequency of 50%, occurred before the Holocene. If actually this *Podocarpus* peak occurred during the LGM (Elenga et al., 1991; Elenga, 1992), it is out of phase with that of southern Cameroon but it could be in phase with the *Olea* curve. Moreover, a low increase of the *Podocarpus* curve occurring near the top of the Bilanko core could tentatively be

linked to the early late Holocene peak recorded in southern Cameroon. A *Podocarpus* chronology comparable to that of this last region was also found in East Africa where, in some sites, a relative increases of *Podocarpus* pollen grains were observed during the early and middle Holocene and in many sites, a large peak or new increase was also dated around 3800/3500 yr B.P. (Coetzee, 1967; Perrott, 1982; Vincens et al., 1986; Tiercelin et al., 1987; Bonnefille and Riollet, 1988). This rather general *Podocarpus* extension in the wet equatorial zone of Africa around the early late Holocene was probably related to large increases of stratiform clouds (Maley, 1997). In the lowland forest areas this phenomenon lead probably to much more gentle rains (dominance of small rain drops, cf. Maley, 1982), which favoured also an important development of Caesalpiniaceae (Section 4.2.2) than before ca. 4000 yr B.P. Palaeoclimatic studies have shown that in the forest ares this general increase in stratiform clouds was particularly linked to an abrupt cooling of the sea surface temperature in the Guinea Gulf (Maley, 1995, 1996b, 1997; Maley and Elenga, 1993; Maley et al., 1997).

In the lake Barombi Mbo record, near the beginning of the dry period which followed around 2800 yr B.P., an abrupt diminution of the *Podocarpus* pollen occurred until their complete disappearance at ca. 2000 yr B.P. A similar feature was also observed in the other pollen sites of southern Cameroon cited above and in two other from northwestern Cameroon, the Bafounda depression at ca. 15 km northwest of Bafoussam (Tamura, 1986) and the lake Njupi of which the record begin around 2700 yr B.P. (Zogning et al., 1997). At present *Podocarpus latifolius* is very sparse near the summit of the Mount Koupé (Section 4.2.1; Letouzey, 1968; Thomas, 1993; Cable, 1993). From these results one can deduce that the increase of the seasonality between ca. 2800 and 2000 yr B.P. was probably linked to an abrupt reduction of stratiform clouds and at the same time to a large increase in cumuliform clouds. This last feature was linked to an abrupt warming of the sea surface temperature in the Gulf of Guinea (Maley, 1997; Maley et al., 1997). Other data show that this period was also characterized

by severe erosion which is also to be linked to the importance of cumuliform rains (Maley, 1981, 1982, 1992, 1997). After 2000 yr B.P. the new extension of the rain forest (Zone IVb) was probably linked to the return of a more balanced climate, possibly rather similar to that of the present day.

During the Holocene the appearance of large sylvigenetic cycles lasting mainly around 2000 to 2200 radiocarbon years, i.e. ca. 2200 to 2500 calendar years, could relate these phenomena to global climatic changes. Indeed such cycles were recorded in ice cores from Greenland (Dansgaard et al., 1984) and Antarctica (Benoist et al., 1982), in records from North Atlantic [i.e. the Dansgaard–Oeschger cycles during the last glacial (cf. Bond and Lotti, 1995) and during the Holocene (cf. Bond, 1995)], Indian and Pacific oceans (Magny, 1995), in the variations of lake levels or glaciers in Europe (Magny, 1993) and North America (Denton and Karlen, 1973; McKenzie and Eberli, 1987). Several of these authors link also these cycles of 2200 to 2500 calendar years to the main period of solar activity variation of ca. 2300 calendar years (Denton and Karlen, 1973; Stuiver et al., 1991; Magny, 1993, 1995).

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