ABSTRACT. The question of forest refugia in Africa is briefly presented from a historical and evolutionary point of view. Main pollen evidence, which goes back to about 25-28,000 yr BP, is presented for two lakes situated in African lowland rain forest.

- The pollen data from Lake Bosumtwi (Ghana) show the disappearance of rain forest from ca. 28,000 to ca. 9000 yr BP. During this time interval the vegetation was a grassland of the montane type with sparse clumps of trees. There is synchronism between montane vegetation disappearance and rain forest reappearance. This phenomenon occurred abruptly between about 9000 and 8500 yr BP.

- In Lake Barombi Mbo (West Cameroon) the pollen data show clearly that from ca. 24,000 yr BP until recent time, rain forest persisted with limited variations, and thus, this area represents a refuge area. One also notes an extension of montane vegetation to low elevation which disappears near the beginning of Holocene time.

After a short synthesis of the palaeobiogeography of Afromontane vegetation, one discusses the palaeoclimatology. In the light of the present-day annual climate anomalies which relate mainly to sea surface temperature variations and upwelling of cold water in the Guinea Gulf, one points out the drying and cooling role of stratiform cloud cover, particularly during the time of fragmentation of the forest area. For the Ghananian rain forest one also discusses the weather types responsible for the forest extension after 9000 yr BP and during the major transgression of Bosumtwi lake during mid-Holocene time. One relates these two phenomena to the disappearance of the present-day summer "little dry season". The reappearance of this "little dry season" in late Holocene time, linked to the deterioration of the water budget, is probably responsible for the abrupt lacustrine regressions and also for the opening of the "Dahomey Gap".

1. INTRODUCTION. THE QUESTION OF FOREST REFUGIA

In the equatorial zone, the rain forest biome has long been considered
to be a quasi-fixed entity, sheltered from climatic fluctuations. In Africa, botanists such as Aubreville (1949, 1962) or Schnell (1950) and zoologists as Booth (1958), Moreau (1963, 1966) or Carcasson (1964) who described the large floristic and faunistic heterogeneity of this region, were among the first who came to the following conclusion: the forest biome had also undergone profound modifications. In the end, the continuation of research led to the hypothesis that during climatically unfavorable periods, the biological richness of the forest was conserved in refugia, privileged sectors where the climate would have remained favorable. The first schematic maps of forest refugia in equatorial Africa were published by Aubreville (1949, p. 66; 1962, p. 62).

Nevertheless, until recently, research on the question of forest refugia has increased, especially in South America, in the Amazon Forest (Prance, 1982; Whitmore et al., 1987), firstly in order to locate the position of refugia, secondly to study the speciation processes associated with the geographical isolation of refugia. Indeed, for many authors, the biologic richness of forest biome could at least partly be explained using the model of allopatric speciation (vicariance) (Haffer, 1982). However, according to the results of studies of animal and plant groups, the existence of refugia has been questioned because the proposed areas were not always superposed or had surfaces of different size (cf. examples given in Whitmore et al., 1987). Yet these authors consider that those differences could be linked mainly to the dynamics of each animal or plant group, without denying the refugia. Moreover, some authors, as Endler (1982), considering the African forest model, estimate that its biological richness could result uniquely from parapatric speciations. Indeed, the necessary isolation for the emergence of new species could be achieved only by the presence in this biome of numerous ecological niches (Fedorov, 1966; Richards, 1969; etc.). In refuting some of Endler's arguments (1982), Mayr and O'Hara (1986) re-affirmed evidence supporting allopatric speciation due to fragmentation of the African rain forest area.

All these authors finally estimate that the better arguments supporting the former existence of refugia and fragmentation of the rain forest area could be provided by pollen analyses on deposits from arid phases.

The first aim of this paper is to present the main pollen results answering this question. The second aim is to discuss the climatic conditions which led to fragmentation of the African rain forest into isolated refugia and later on to forest recolonization.

2. POLLEN ANALYSES IN AFRICAN RAIN FOREST

During the last few years, pollen analyses were carried out on upper Quaternary deposits from two lakes situated at low elevation in the lowland African rain forest: the Bosumtwi lake in Ghana and the Barombi Mbo lake in West Cameroon (Fig. 1).
2.1. Lake Bosumtwi in Ghana

This lake with a water level near 100m ASL (Above Sea Level) is situated in semi-deciduous rain forest that is characterized by the families of Ulmaceae, particularly with Celtis, and Sterculiaceae with Triplochiton and other genera (HALL et SWAINE, 1981). Climatically, this type of forest is adapted to a slightly less humid conditions than the evergreen type which will be presented below (§ 2.2). The semi-deciduous forest appears when the yearly number of "dry" months (rainfall below about 100mm) reach three. The two months of the "little dry season" in August and September (§ 4.2; Fig.9) are quasi rainless, but because the atmospheric humidity remains high, these two months must not be added (see the Gabon forest example, § 4.2) to the three months dry season of northern winter (December to February).

The core studied from Lake Bosumtwi, has a length of about 17m and reaches back to about 28,000 yr BP (Fig.2). The geological study of this core and outcrops of lacustrine deposits, permitted the reconstruction of the lacustrine fluctuations which were very distinct, with a maximum lake level in middle Holocene time and a very low lake level from about 20,000 to 15,000 yr BP (TALBOT et al., 1984; TALBOT et KELTS, 1986; MALEY, 1987).

The principal pollen results (MALEY et LIVINGSTONE, 1983; TALBOT et al., 1984; MALEY, 1987) (Fig.2 and 3) clearly show that before about 9000 yr BP, forest was not present in this region. Indeed, between the present and about 8500 yr BP arboreal pollen percentages oscillated from 75 to 85%, while before 9000 yr BP arboreal pollen percentages were generally below or close to 25%, except near the base of the core, where they were close to 50%. During the period between about 19,000 and 15,000 yr BP, arboreal pollen percentages reached minimum values of about 4 and 5%. At the same time trees had almost completely disappeared from the landscape and had been replaced by the herbaceous plants, essentially Gramineae and Cyperaceae which reached frequencies of 91 to 94%. Today such percentages of pollen grains from herbaceous and arboreal plants are common in the Sahelian zone (MALEY, 1981).

Other important evidence resulting from pollen analyses is the presence of a montane element in the period from the core base to its quasi disappearance around 8500 yr BP, near the time when the rain forest reappeared (Fig.3). This montane element includes the mountain olive, Olea hochstetteri, which today are only present 700 km westward, near 1200m ASL on the Hom Mountain in the Dan Massif of western Ivory Coast (SCHNELL, 1977). Eastward, the nearest modern location of this tree is in Nigeria on the Jos Plateau, and further eastward mainly in the mountains of the Cameroonian Ridge (LETOUZEY, 1968). Until about 8500 yr BP, the presence of a montane element at low elevation around the Bosumtwi lake, where the highest surrounding hills reach maximally elevations from 400 to 550m ASL, imply a lowering of the montane vegetation belt with minimally 600m. This corresponds to a temperature decrease of 3° to 4°C (MALEY et LIVINGSTONE, 1983) when applying a mean temperature gradient of 0.6°C for every 100m displacement of the vegetation belt (WALTER et BRECKLE, 1985) (§ 4.1). This temperature decrease has also been reached by...
Figure 3 - Lake Bosumtwi pollen analyses (J. MALEY). The chronology of the core is based on 15 radiocarbon dates (after TALBOT et al., 1984).

The presence of Pooidae flora below 550m altitude could involve an important decrease of temperature (TALBOT et al., 1984) which should be approximately 6°C, a value comparable to estimates from East Africa (§ 3).

Thus, before 9000 yr BP the forest was absent and it gave way to a mountain type grassland with sparse clumps of trees. Near the base of the core, dated about 27 - 28,000 yr BP, arboreal pollen percentages of about 50% are indicative of the presence of some kind of mountain forest. A remarkable feature is that the scattered trees in the open vegetation belonged in great majority to the semi-deciduous forest flora and not to the Sudano-Guinean savanna flora. Under modern conditions, only the Guinean montane grasslands of middle elevation (submontane belt) include isolated clumps of trees which, in addition to typical mountain species, contain a large set of species which are found from low elevations to the submontane belt (SCHNELL, 1977; LETOUZEY, 1968, 1985).

2.2. Lake Barombi Mbo in West Cameroon

Lake Barombi Mbo has a water level near 300m ASL and is situated in the lowland rain forest of West Cameroon (Fig.1). Around the lake two principal forest formations can be recognized in an area with about 10 km radius (RICHARDS, 1963; LETOUZEY, 1968, 1985; D. THOMAS, pers. commun.):
- The evergreen forest of Biafraan type is a richer variety of the Guineo-Congolan type. It spreads around the Bay of Biafra from east Nigeria to as far south as the boundary of Cameroon and Equatorial Guinea (LETOUZEY, 1985; WHITE, 1983). This forest type is characterized by its richness in Leguminosae, especially Caesalpiniaceae and is present when the dry season does not exceed two months.
- The semi-deciduous forest (§ 2.1) forms islets in the evergreen forest which remains largely dominant (LETOUZEY, 1985).

So far only the lower half of the longest core (BM-6: 23.50m, from the base to about 11,000 yr BP) has been studied in detail (28 samples spaced every 30 or 60 cm have been analyzed: BRENCAC, 1988; MALEY et al., 1988 (b), to be published). Samples at 2 or 3m intervals have also been studied from the upper part of the core (MALEY and BRENAC, 1987). Below 21m depth in the core, perturbed section interrupts the continuity of pollen spectra. However the dates obtained near the base and the pollen content (Fig.4) show that the lowermost part of the core is probably reversed (MALEY et al., 1988 (b) to be published).

The following principal results are to be noted (Fig.4):

Zone 1
From the base of the core (greater than 24,000 yr BP) to a level with an age of about 20,000 yr BP, pollen grains of Gramineae, Cyperaceae
Lake Barombi Mbo (West-Cameroon) Pollen Analyses of Late Pleistocene (P.BRENAC)

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Figure 4: Lake Barombi Mbo pollen analyses (P.BRENAC). (from BRENAC, 1988; MALEY et al., 1988,b, to be published).

Under modern conditions, the association of mountain taxa in combination with typical lowland evergreen forest flora is found in Cameroon, for example, on the hills' summits around Yaoundé (between 900 and 1200m ASL) (ACHOUNDONG, 1985). On the plain around these hills the forest is semi-deciduous, but on the hills' summits climate is more humid and cool because of the high frequency of clouds which favor this particular cloud forest association (BRENAC, 1988).

Zone II
Around 20,000 yr BP, a very sharp change occurs in the pollen spectra. Percentages of mountain olive pollen grains decrease to values of 5 to 15%. Forest taxa decrease as well, particularly Caesalpinioideae and Euphorbiaceae. Percentages of arboreal pollen grains oscillate around 40% until ca. 14,000 yr BP. During the same period, grass pollen grains increase to about 25%. It is the same for Cyperaceae and other aquatic plants.

These data are indications of a relatively dry and cool climate. The increase of Cyperaceae and shoreline plants is probably related to a lower water level, which is in accordance with a decrease in rainfall. By analogy with pollen analyses of modern samples of soils and lacustrine sediments (BRENAC,1988), the increase in herbaceous plants is indicative of the development of more open forest vegetation or the development of a mosaic pattern of forest and open formations.

Zone III
Between ca. 14,000 and 10,000 yr BP the forest taxa increase again, with percentages close to 60%. Among the tree taxa, some representatives of the semi-deciduous forest, such as Celtis, replace those of the evergreen forest present before 20,000 yr BP. One notes also pioneer forest taxa typical of secondary natural formations. Around the beginning of Holocene time, Gramineae percentages decrease to about 20%. In Zone III, percentages of mountain olive pollen increase again around 13,000 yr BP to disappear again near the beginning of Holocene (BRENAC, priv. commun.). One can conclude that this period was humid again, but not as cool as before 20,000 yr BP.

From about 10,000 yr BP to the present, the few data so far available show a relatively stable vegetation, dominated by semi-deciduous forest elements accompanied by many taxa of secondary natural formations (MALEY et BRENAC, 1987).

2.3. Conclusions
The pollen data presented here are particularly important because they...
show that during the last great arid phase, from about 20,000 to 14,000 yr BP, the rain forest disappeared in Ghana, particularly in the Bosumtwi sector, but persisted in West Cameroon. These conclusions have been associated with various biogeographic data obtained from studies on plants, birds, mammals, amphibians, butterflies, etc., from Cameroon and other parts of the forested zone, as well as palaeoclimatic data, in order to establish a new schematic map of lowland forest refugia in equatorial Africa during the last great arid phase, about 18,000 yr BP (Fig.1) (see MALEY, 1987, for a more detailed discussion). Another important result is the spread to low elevation of a montane element that are characterized by Olea hochstetteri. This indicates a temperature cooling which seems similar for the two sites studied.

3. PALAEOBIOGEOGRAPHY OF AFROMONTANE VEGETATION

To understand the problem of extension of montane vegetation to lowland, the modern composition of the African montane flora and fauna of middle altitudes from about 1000m to 3000m ASL must be recalled. Indeed, between the different mountain massifs of equatorial Africa, a great similarity has often been noted. For example, according to HALL (1973), the plant species common to Mount Cameroon and Eastern Africa are 53% for the montane forest and 49% for the montane grassland. In order to explain these similarities, some authors have assumed that during the Quaternary, the montane floras and faunas must have extended to the lowlands which facilitated migration between mountain massifs (MOREAU, 1966; WHITE, 1981; MALEY, 1987).

The extension of montane vegetation to lower elevation in Eastern Africa has been known for several decades, and for this reason temperatures are believed to have been 5' to 9°C lower (COETZEE, 1964; VAN ZINDEREN BAKKER et CLARK, 1962) and 7°C lower (HAMILTON, 1973, 1978; FLENLEY, 1979). Moreover, in southern Congo Republic (CARATINI et al., 1979; ELENGA et al., 1987) and in northern Angola (VAN ZINDEREN BAKKER et CLARK, 1962), several pollen analyses also clearly show extensions of montane vegetation to low elevation (MALEY, 1987).

The most important data has been obtained on the Plateaux Batéké, about 40 km north of Brazzaville, in a small depression near 600m ASL (ELENGA et al., 1987). The pollen analyses carried out on a short core show that from the base until around the beginning of Holocene time, the pollen spectra were dominated by Afromontane taxa; the pollen grains of Podocarpus milanjianus (syn. P. latifolius), Ilex mitis and Olea welwitschii (syn. O. hochstetteri, cf. TROUPIN, 1985) constituted about 60% of the pollen spectra, dominated by Podocarpus with about 50% (ELENGA et al., 1987).

Between the mountain massifs of Eastern Africa and Cameroon, several typical Afromontane taxa had been observed in various isolated stations (WHITE, 1981), on the southern rim of the Salza river catchment, and along the Guinea Gulf on the ridge of hills connecting Angola to Cameroon. For Podocarpus latifolius, there is a station near 700m ASL on the Congolese slope of Chaillu Mountain (MALEY et al., 1988) (a), to be published) and another about 900m ASL near the top of an isolated inselberg in south Cameroon, near the Gabon border (LETOUZEY, 1968). The cumulative evidence from these stations and the pollen data presented above show the pattern of a preferential junction way which could have operated intermittently during the Quaternary between East Africa and Angola, and subsequently expanded to the hill ridge of Mayombe, Chaillu, Monts de Cristal until eventually the Cameroon mountains (MALEY, 1987; MALEY et al. 1988 (a), to be published) (Fig.5).

4. PALAEOCLIMATOLOGY

4.1. Introduction. The hypothesis of lapse rate variation

During the Last Glacial Maximum (LGM) (about 18,000 yr BP) the extension of glaciers and vegetation belts to altitudes much lower than those of today are now widely accepted data (see for example the synthesis of FLENLEY, 1979). Many authors have tried to explain the temperature lowering which can be deduced from these data (generally between 5° and 9°C) with palaeoclimatic models (WEBSTER et STRETEN, 1978; WHITMORE et al., 1982; FLENLEY, 1984; RIND et al., 1982; FRENCH and FLENLEY, 1987; etc). The paper of WEBSTER and STRETEN (1978) is a good example of one of these essays. The authors (op. cit.) discuss about tropical Australasian palaeoclimates during the LGM, and like for tropical Africa, much of the data show a 6° to 8°C lowering of temperatures in New Guinea mountains. For the surrounding tropical oceans, the data from the CLIMAP Group (1976, 1981) suggest only a 2°C cooling or less. The value is similar for the seas around tropical Africa, except in a small sector of the Guinea Gulf where a 3°C cooling is indicated. WEBSTER and STRETEN (op. cit.) try to explain these opposite results from Australasia with several detailed palaeoclimatic reconstructions.

The principal hypothesis that is discussed in detail is the variation of the vertical lapse rate (WEBSTER et STRETEN, op. cit.). About this physical phenomenon, WALTER and BRENCKLE (1985, their Fig.120) used many temperature records from various mountain slopes in Venezuela to obtain a linear temperature elevation relationship, and from this relation calculated a vertical lapse rate of 0.57°C per 100m from sea level to 5000m. Using the temperature, recorded during vertical ascent in free atmosphere for several stations in Australia and New Guinea, WEBSTER and STRETEN (op. cit.) have shown that this value (about 0.6°C/100m) corresponds to the moist adiabatic lapse rate, but that in dry atmosphere the lapse rate is steeper and close to 0.8°C/100m. The principal point is that this dry atmosphere lapse rate fits quite well the palaeoclimatic data for the LGM. Because the climate was dry at about 18,000 yr BP, WHITMORE et al. (1982), FLENLEY (1984) and MORLEY and FLENLEY (1987), relying on this hypothesis, have estimated that the atmosphere was dry also at this time and, for this reason, had a steeper lapse rate. However WEBSTER and STRETEN (op cit...
Figure 5 - Distribution of the nine African regional mountain systems. I, West-African; II, Cameroon-Jos; III, Ethiopian; IV, Imatongs-Kenya-Uzambara; V, Rwenzori-Kivu; VI, Uluguru-Mlanje; VII, Chimanimani; VIII, Drakensberg; IX, Angolan. The black arrows schematically represent a possible migration path of Afromontane taxa from East Africa to Angola and subsequently via Cameroon to West Africa.

criticize this hypothesis because (op cit., p.305) the thermodynamics determining the atmospheric structure in the vertical are governed by strict physical laws. The vertical temperature profile are expected to be close to moist adiabatic even if the atmosphere were drier, as indicated by the winter temperature-height diagrams of Darwin, Cloncurry and Charleville. WEBSTER and STRETEN (op cit.) also expect similarity between the temperatures above the adjacent ocean regions and at corresponding levels on elevated terrain.

Additionally, in an important paper, KEND and PETER (1985) conclude (ibid., p.18) that at low latitudes the current lapse rate is consistently close to the moist adiabatic value and that, for this reason, the lapse rate would not have changed if sea-surface temperatures remained warm during the LGM.

Consequently an alternative hypothesis is necessary to explain the LGM data. The starting point of the alternative hypothesis presented here is that one observes today on some mountains a natural extension of mountain vegetation to lower elevations. The new hypothesis, which has been already formulated (MALEY et LIVINSTONE, 1983; MALEY, 1984, 1987), is based partly on the fact that ecologists studying present-day mountain conditions have demonstrated the primordial role played by the cloud covers and fogs (GRUBB et WHITMORE, 1966; BAYNTON, 1968: GRUBB, 1971, 1974, 1977).

4.2. Some present-day models of localized montane extensions to lower elevations

The montane biotopes appear generally above 1000m ASL; this limit forms a fundamental biological barrier which is characterized by changes in flora and fauna and also commonly by physionomical modifications (MOREAU, 1966; HOWARD, 1970; GRUBB, 1971, 1974; WHITMORE, 1975; LEIGH, 1975; BERNARD, 1979; etc.). However, one can locally observe the extension of normally montane faunas or floras to low elevation.

Outside of Africa, there are many examples of this phenomenon in the Antilles islands and around the Caribbean Sea (BAYNTON, 1968; HOWARD, 1970; etc.). In the northern tip of Colombia, SUGDEN (1982) describes a cloud forest on the Serrania de Macuira which attains a maximum elevation of 865m about 25 km inland from the coast. The slopes from about 500m to the summit are covered by a mountain forest formation. In the lowland the mean monthly temperature is 28°C and varies little throughout the year (SUGDEN, op cit.). At 500m ASL SUGDEN (op cit.) recorded a mean temperature of about 22.5°C and so, one obtains a temperature lowering of 5.5°C for 500m. Usually, with a lapse rate of 0.6°C/100m (see above § 4.1) one can calculate a temperature lowering of 3°C for an elevation of 500m. The extra 2.5°C of cooling must be related to the extensive cloud formation and fog which enshroud the summit.

Other examples exist on the Atlantic coast of Africa, but apparently, without temperature measurements. The hills of Freetown in Sierra Leone present one example. These hills rise from the sea to an elevation of about 900m ASL and, from 500m ASL upwards, they support a
set of montane plants (MORTON, 1968), such as *Olea hochstetteri* (HEPPER, 1963). Further to the east on the seaward south flank of Mount Cameroon, typical montane trees (THOMAS, 1966) and birds (SERLE, 1964) are found above 500m ASL. Further to the south on the Angola Escarpment, which rises above the sea to the level of the Plateau above 1000m, a cloud forest is found from 200 or 300m ASL with the implication that montane conditions already appear at this low elevation (EXELL et MENDONCA, 1937; AIRY-SHAW, 1947; WHITE et BERGER, 1978). Other examples exist in East Africa near the Indian Ocean on the Usambaras Mountains (MOREAU, 1935, 1938, 1966). All these occurrences show that this is a non-fortuitous ecological phenomenon which allows the extension of the climatic conditions normally found above 1000 to 1500m to lower elevations. The data presented above for the Serrania de Macuira in Colombia are an example of magnitude of temperature reduction in such environment.

Most authors who have considered this phenomenon have attributed it to persistency of cloud cover and fog which are particularly frequent on slopes facing the sea (AIRY-SHAW, 1947; MOREAU, 1966; SERLE, 1964; HOWARD, 1970; GRUBB, 1971; etc). The Angolan Escarpment is a particularly important model because it shows how the abundance of cloud cover depends directly on the low clouds coming from the sea where the cold Benguela current flows. HOFICH (1972) has shown how this current produces a thick mantle of stratiform clouds which influence greatly the climate of the neighboring continent by reducing the rainfall and lowering the temperature there.

### 4.3. The present day climatic role of upwelling and stratiform clouds

Recent research in the tropical Atlantic sector have shown that the interannual variability of the climate is related to enhancement or reduction of the annual cycle (HASTENRATH, 1984; NICHOLSON and ENTEKHABI, 1987). For example, HIRST and HASTENRATH (1983a, b), studying the variation of rainfall over the Zaïre river catchment, have found positive correlations between the evolution of the two principal rainy seasons and sea surface temperature (SST) off Angola. The periods with warmer (colder) SST are correlated with above (below) normal rainfalls. SST modulate rainfall by controlling moisture and stability in the lower atmosphere which are also related to cloudiness. But another positive correlation exist between upper air conditions and rainfall over the Zaïre catchment (HIRST et HASTENRATH, 1983a). Probably large scale atmospheric conditions influence both parameters (NICHOLSON et ENTEKHABI, 1987). In this way, SST variations and upwelling of cold waters (Fig.6) are indeed directly and remotely governed by the intensity of the winds which are related to the activity of the South Atlantic High (MERLE, 1980; HASTENRATH, 1984; SERVAIS et al., 1985; NICHOLSON et ENTEKHABI, 1987). This relation could account for the coherence of the interannual SST variations and particularly that of the upwelling throughout the Guinea Gulf, with particular years or periods having warmer (colder) sea surface waters (MERLE, 1980) (Fig.7). Such synchronicity on interannual scale amplifies

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**Figure 6** - Temperature distribution of surface water, surface water circulation and upwelling in the tropical Atlantic Ocean for July. The currents (from north to south): CC, Canary current; DNA, North Atlantic drift; CNE, North equatorial current; CCEM, North equatorial counter current; CEG, Current of Guinea; CSE, South equatorial current (equatorial upwelling); CCS, South equatorial counter current; DSA, South Atlantic drift; CB, Benguela current (from WAUTHY, 1983, fig.20A). The upwelling areas are shaded.
the impact of SST variations on the climate of the adjacent continent.

An example of this relation between SST and climate can be found during southern winter in the appearance of the "little dry season" (generally 2 months) in the rainforest north of the Guinea Gulf (DROCHON, 1976; BAKUN, 1978; HISARD, 1980) (Fig. 8, 9). This dry season, which is also the coldest period of the year (Fig. 9), depends directly on the presence in the lower troposphere of non-precipitating stratiform clouds, generated by the upwelling of cold waters at this time of the year (DROCHON, 1976). On the adjacent continent, the subsidence maintained aloft by the anticyclonic conditions spreading northward during southern winter explains the persistence of the stratiform clouds above the rainforest region (Fig. 8). East of the Guinea Gulf, closer to the equator, the impact of the upwelling is larger because the same chain of oceanic and atmospheric anomalies prevails during four months. This four month dry season in the regions of Gabon and Congo is characterized by a quasi-permanent and non-precipitating stratiform cloud cover which extends at least 800 to 1000 km inland and reduces temperature and evaporation and, as a consequence, maintains a moist atmosphere (SAINT-VILI, 1977). Without this atmospheric humidity a four month dry season would have resulted in a replacement of the forest by savanna.

The relation between this dry season of southern origin and the lowering of SST is very clear and is the most obvious phenomenon in the chain of atmospheric and oceanic anomalies. This conclusion is also supported by the observation that in some particular recent years (for example 1968 or 1984) warm waters persisted (Fig. 7) because the upwelling were weak or absent. This phenomenon is similar to the "El Nino" of the eastern Pacific Ocean (HISARD, 1980; MERLE, 1980). During the "warm" years this season was not dry whatever, but instead it was very wet with heavy rainfalls (HISARD, 1980; GUILLOT, 1985).

4.4. Major role of upwelling in the climatic changes of the rain forest region

The various present-day examples mentioned above (4.1 and 4.2) of the climatic action, either drying or (and) cooling of stratiform cloud covers, show that the generation of upwelling have a basic role in the climatic system (cf. FLOHN, 1982, 1983). The coherence of anomalies throughout the Guinea Gulf is the principal feature of this figure.

Figure 7 - Interannual sea surface temperatures (SST) anomalies for some successive years of the recent past in the Guinea Gulf (Figure adapted from MERLE, 1980).

Temperature anomalies
- Oblique shading: Positive anomalies ("warm waters")
- Large dots: Negative anomalies from 0 to 0.5°C (upwelling, "cold waters")
- Small dots: Large negative anomalies of more than 0.5°C (strong upwelling, "cold waters")

The recorded anomalies concern, from north to south:
- TEMA, a coastal locality, south of Ghana, and four marine areas (homogenized Nansen data, NOAA, Asheville, USA),
- Latitudinal strip of 10° longitude (0-10°W) between 4° and 5°N along the northern shore of the Guinea Gulf,
- North of Marsden square 300 (MS 300), an equatorial band 2° wide (equator - 2°S) between 6° and 10°W. This band corresponds to the equatorial upwelling area,
- The entire Marsden square 300 (MS 300) (0-10°W; 0-10°S),
- The entire Marsden square 371 (MS 371) (0-10°E; 10°S-20°S).

MERLE (1980) note that the choice of these areas has been mainly determined by the density and the quality of the data. The coherence of anomalies throughout the Guinea Gulf is the principal feature of this figure.

4.4.1. The last phase of maximum aridity, about 18,000 yr BP

In the tropical Atlantic Ocean and particularly in the Guinea Gulf, the reconstruction of SST by the assemblages of planktonic foraminifera and radiolarians shows that at about 18,000 yr BP the equatorial cold waters upwelling maintained a nearly constant position, and were 4°-8°C lower than those of the present southern winter (Fig. 10) (PRELL et al., 1976; MORLEY et al., 1979; MIX et al., 1986). Further, PRELL et al. (1976) have shown that during the southern summer (February), which
Figure 8 - Geographical distribution of southern winter dry season in equatorial Africa (adapted from LEROUX, 1983). The length of this dry season increases from about 2 months in the north (= "the little dry season") to more than 4 months a year southwards. Note in West Cameroon the absence of this dry season, replaced by a pluvial paroxysm.

Figure 9 - Diagram of seasonal climatic change in Abidjan (Ivory Coast), showing the succession of the main types of clouds (adapted from DROCHON 1976) and the principal elements of climate: rain, air temperature, evapotranspiration, and sea surface temperature (data from ORSTOM and ASECNA). The Adidjan station is representative of the western sector of the rain forest area.
is the season of warmest water, the surface temperatures were 3 degrees lower than today. This suggests that the upwelling of cold waters would have been a nearly year-round feature. From what we know from the present-day atmospheric phenomena related to upwelling, these data mean also a very powerful anticyclonic high pressure above the southern Atlantic associated with very strong trade winds. Indeed, research in this field has shown an important strengthening of trade winds around 18,000 yr BP (NEWELL et al., 1981). In conclusion the present-day interannual synchronism throughout the upwelling areas in the Guinea Gulf (equatorial and coastal) (Fig.7) means that in the past the SST variations have had a large climatic impact on the equatorial regions of Africa, mainly those covered today with rain forest. These phenomena and the action of stratiform cloud cover inland could explain (1) the aridification of the climate and the disappearance of large areas of rain forest and (2) the cooling effect of these quasi-permanent cloud covers and the accompanying extension of montane biotopes to lower elevations.

4.4.2. The abrupt change near 9000 years BP and the reappearance of the lowland rain forest

In West Africa, pollen evidence and other data from the Bosumtwi lake (§ 2.1) show that the near absence of forest and the extended spreading of montane vegetation to low elevations lasted until about 9000 yr BP. This coincided with important warming at higher latitudes in both hemispheres which began about 15,000 yr BP (LORIUS et al., 1979; BARD et al., 1987; SARNTHEIN et al., 1981). Pollen data (ROCHE, 1979; CATINI et al., 1979; M'BENEA-MUKA et ROCHE, 1980) and geological data (DE PLOEY, 1969; GIRESSE et LANFRANCHI, 1984; PEYROT et LANFRANCHI, 1984; RACHURA et al., 1986) from the Zaïre river catchment, the western Congo and southern Cameroon, show a comparable history of lowland rain forest reappearance. The foraminiferal data of PRELL et al. (1976) suggest that in the belt of equatorial upwelling, SST values at 9000 or 10,000 yr BP became close to those of the present. This change coincided with the rain forest reappearance and climate warming (disappearance of the montane element).

The increase in temperature from ca. 15,000 to 9000 yr BP affected mainly middle and high latitudes but in tropical regions and particularly in the African rain forest, the change was small. As explained above (§ 4.3), this phenomenon is probably related to the persistence of cold waters upwelling throughout the Guinea Gulf. The SST outside the upwelling areas increased (MIX et al., 1986), which provided more water vapor for the monsoon and resulted in more cloud covers inland and probably an increase in rainfall. At the time of the rain forest reappearance, the level of Bosumtwi lake was already very high above the present-day level (Fig.2,B). Since lower temperatures prevailed at that time (presence of montane vegetation until ca. 9000 yr BP), we could infer that the high lake level was partly caused by low evaporation rates, but also by increase in precipitation. These deductions indicate that the reappearance of the rain forest near 9000 yr BP was not solely dependent on rainfall and

Figure 10 - Sea surface temperatures estimates (August and February) according to transfer functions of foraminiferal assemblages in the north tropical Atlantic Ocean during the last glacial maximum, ca. 18,000 yr BP. Present-day values are provided for comparison (from PRELL et al., 1976, fig.11 and 12, in Geol. Soc. America Memoir, 145).
humidity, which were very sufficient several millennia before this date, but also on temperature and chiefly amount of sunshine. For this reason, we believe that the reappearance of the rain forest was mainly governed by the variations of cloud covers and cloud types.

One could estimate that between 15,000 and 9000 yr BP the present-day July-type weather with major rain produced by massive nimbostratus clouds (Fig.9), had progressively dominated each year during several months before July. Because we know that the lowland rain forests require large sunlight intensity during many months (LEIGH, 1975; WALTER et BRECKLE, 1985; etc), the reappearance of the rain forest could be due to a subtle balance between this July-type weather and the March to May-type weather which is characterized by longer periods of sunshine (Fig.9).

4.4.3. The Holocene period between about 9000 and 4000 years BP

The SST data for the Holocene of FRELL et al. (1976) are not sufficiently precise to detect and date temperature variations, but some other indirect data show that SST anomalies have had an important impact on the climate and the rain forest.

Near the coast of western Congo widespread savannas are presently found; however DECHAMPS et al. (1988) and SCHWARTZ et al. (to be published) have studied several extensive paleosols with in situ remains of numerous tree stumps which belong to a rain forest flora. Several tree stumps and also some samples of organic matter from the paleosols were radiocarbon dated. A first series of 10 samples were dated from about 6500 to 3300 yr BP and a second series of 3 samples were dated between 500 and 600 yr BP. Because the present-day savannas of this region are mainly related to a long dry season (MAKANY, 1964) which are caused by the cold water upwelling (SAINT-VIL, 1977) (§ 4.3), their replacement by rain forest was probably caused by a suppression or reduction of upwelling in this area.

Other data related to the upwelling suppression or reduction in the Gulf of Guinea during parts of Holocene time can be obtained by the study of the Bosumtwi lake sediments. Today, this lake is stratified with anoxic waters below about 10m, with a maximum water depth of about 80m (BEADLE, 1974), but almost each year an overturn of deep anoxic waters occurs. Because LIVINGSTONE (private commun.) counted about one lamination for one radiocarbon year in the core collected in the lake (Fig.2), the laminations of the sediment correspond to this yearly phenomenon. The overturn is mainly related to a lowering of air temperature in August and September which is induced by the non-precipitating stratiform cloud covers generated by the upwelling (§ 4.3) (Fig.9). This cooling also affects the water column which at this time becomes more or less homothermal (BEADLE, 1974). Because, at the same time, the wind stress from the southwesterlies is at its maximum, the instable waters are overturned (BEADLE, 1974; WHYTE, 1975). But for the core (Fig.2,A), a large part of the Holocene sediment is unlaminated and of sapropel type between about 9000 yr BP, when the rain forest reappeared, and about 3700 yr BP, when the laminations reappear suddenly (TALBOT et al., 1984). So, this unlaminated interval of the core and the high lake level of this period (at maximum 150m above present-day lake level) can be related to an absence or reduction of the "little dry season". Either an annual prolongation through August and September of the June-type weather (Fig.9) which is characterized by heavy precipitation from nimbostratus clouds, or the annual early start of the October-November-type weather (Fig.9) which dominates a large part of the rainy season, would explain these observations.

4.4.4. The regression of the lake Bosumtwi during late Holocene time

After 9000 yr BP, the present-day interruption of the rain forest area which is called the "Dahomey Gap" was probably absent, because of higher humidity (§ 4.4.3), and for biogeographical reasons (see the discussion in § 2.2). The Dahomey Gap probably appeared between 4000 and 3000 years ago, when lake Bosumtwi abruptly regressed. The abrupt regression of the lake, more than 120m, is dated at about 3700 yr BP which is the date of the sudden reappearance of the rain forest area (MALEY et LIVINGSTONE, 1983, and unpublished data: spectra have only very few pollen grains of Caesalpinioideae - characteristic of the evergreen forest type, see § 2.2 and BRENAC, 1988). Consequently one concludes that during this period the northern winter dry season had the same length as today, i.e. three months (December to February) (Fig.9). Present conditions in West Cameroon may be representative of those for the period 9000 yr BP to about 3700 yr BP in the Bosumtwi region and probably also for other parts of the African rain forest. In West Cameroon indeed, the three months from July to September represent the rainiest season of the year (Fig.8), and are described as a "pluviol paroxysm" by SCHUDEL (1972).

The abrupt regression of the lake, more than 120m, is dated at about 3700 yr BP which is the date of the sudden reappearance of the rain forest area (TALBOT et al., 1984), and is to be associated with the reappearance of the "little dry season" inland and to the upwelling of cold water in the Guinea Gulf. However the pollen data from this period show the persistence of the rain forest (Fig.2) and for biogeographical reasons (see the discussion in § 2.2 and BRENAC, 1988). Consequently one concludes that during this period the northern winter dry season had the same length as today, i.e. three months (December to February) (Fig.9). Present conditions in West Cameroon may be representative of those for the period 9000 yr BP to about 3700 yr BP in the Bosumtwi region and probably also for other parts of the African rain forest. In West Cameroon indeed, the three months from July to September represent the rainiest season of the year (Fig.8), and are described as a "pluviol paroxysm" by SCHUDEL (1972).
the lacustrine water budget that linked a rainfall decrease to a probable evaporation increase. If this rainfall decrease was distributed over the same number of months, then, provided the total precipitation does not reach values below 1200mm/year, rain forest could have remained, based on observations that today some northern parts of rain forest in Ghana and Ivory Coast receive yearly rainfall in this range (Fig.1). Thus, provided minima are not below 1200mm/year, the essential factor to maintain the rain forest in late Holocene time is good distribution of rainfall throughout the year, rather than the annual total.

5. CONCLUSIONS

After having briefly introduced the problem of rain forest refugia during the last glacial maximum and shown the pollen data which clearly demonstrate that the African rain forest area has been fragmented indeed and survived the glacial period in some refugia, one had attempted to reconstruct the weather types which may account for the recorded vegetation and lacustrine variations. Particular attention has been paid to the climatic reconstruction (1) during the phase of fragmentation of the rain forest belt and the extension of montane biotopes to lower elevation, (2) during the forest recolonization and its extension in early and middle Holocene time, and (3) the return to its present-day limits during the last four millennia and particularly the opening of the "Dahomey Gap". The latter phenomenon is probably related to a deterioration of the water budget, which is also responsible for the regressions of Lake Bosumtwi.

Many of these refugia have been formed and how were climatic conditions there, remains without precise answer. One of the major proposed refugia is located in West Cameroon (Fig.1) (MALEY, 1987), where today climatic conditions are atypical because this area experiences no "little dry season" during southern winter (Fig.8). For this reason the yearly rainfall is very high. This particularity could account for the survival of the tropical rain forest during dry periods. However, we see that there have been other refugia in which forest refugia have been experienced during colder periods, such as in Gabon and southern Cameroon. This suggests that other factors are necessary to explain the geographical position of refugia.

The study of climatic conditions of West Cameroon could provide the necessary informations to allow the development of a hypothesis. The exact reasons of the present-day July to September pluvial paroxysm of West Cameroon are not well understood (SUCHEL, 1972) and could be the result of several causes. It could be related first to the geographic position at the far end of the Guinea Gulf where today the SST seem to be unaffected by the upwelling phenomenon or to the presence of high mountains with possible orographic effects and strong dynamic lifting associated with upper air circulation.

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KEYWORDS


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REFERENCES


AUBREVILLE, A. 1962, Savanisation tropicale et glaciations quaternaires. Adansonia, 2,16-84.


FLOHN,H. 1986, Singular events and catastrophes now and in climatic history. Naturwissenschaften,73,136-149.


Diplôme d'Etudes Approfondies, Université d'Aix-Marseille II, pp.641-657.


MALEY, J. 1981, Etudes palynologiques dans le bassin du Tchad et
LUDLAM, F.H. 1966, Cumulus and cumulonimbus convection. u, 18,
LETOUZEY, R. 1985, Notice de la carte phytogeographique du Cameroun au
LETOUZEY, R. 1980, Note phytogeographiques sur les Palmiers du
LETOUZEY, R. 1968
LEIGH, E.G. 1975, Structure and climate in tropical rain forest.
KADOMURA, H., HIRAI, K., OGINO, T., TAMURA, T., OMI, G., HARUKI, M. et
HISARD, P. 1980, Observation de reponse de type 'El Nino' dans
HIRST, A.C. et HASTENRATH, S. 1986 (b), Palaeoclimatic evidence from
HIRST, A.C. et HASTENRATH, S. 1983 (b), Atmosphere-Ocean mechanisms of
HIRST, A.C. et HASTENRATH, S. 1986 (a), Diagnostic of hydrometeorological
HIRST, A.C. et HASTENRATH, S. 1983 (a), Diagnostics of hydrometeorological
HOPFICH, O. 1972, Die meteorologischen Wirkungen kalter Auftriebswasser-
KADOMURA, H., HIRAI, K., OGINO, T., TAMURA, T., OMI, G., HARUKI, M. et
M'BENZA-MUAKA et ROCHE, E. 1980, Exemple d'evolution paleoclimatique au
MIX, A.C., RUDDIMAN, W.F. et MCINTYRE, A. 1986, Late Quaternary palaeoceno-
graphy of the tropical Atlantic. 2: The seasonal cycle of sea surface temperatures, 0-20,000 years B.P. Palaeocenography, 1, 339-353.
MOREAU, R.E. 1935, A synecological study of Usambara, Tanganyika
Territory, with particular reference to birds. J. Ecology, 23, 1-43.


NEWELL, R.E., GOULD-STEWARD, S. and CHUNG, J.C. 1981, A possible interpretation of palaeoclimatic reconstructions for 18,000 BP for the region 60° N to 60° S, 60° W to 100° E. Palaeoecology of Africa, 13, 1-19.


*Océanographie tropicale*. OBSTOM, 19, 103-138.

WEBSTER, P.J. et STRETNEN, N.A. 1978, Late Quaternary Ice Age climates of 
tropical Australasia: interpretations and reconstructions. 

WHITE, F. 1978, The Afromontane region. in M.J.A. Werger (ed) 
*Biogeography and Ecology of southern Africa*, W. Junk, The Hague, 
2,469-513.

WHITE, F. 1981, The history of the Afromontane archipelago and the 

Memoir, 356 pp.

WHITE, F et WERGER, M.J. 1978, The Guineo-Congolian transition to 
southern Africa in M.J.A. Werger (ed) *Biogeography and Ecology of 

WHITMORE, T.C. 1975, Tropical rain forests of the Far East. Clarendon 
Press, Oxford.

WHITMORE, T.C., FLENLEY, J.R. et HARRIS, D.R. 1982, The tropics as the 

WHITMORE, T.C. et PRANCE, G.T. 1987, Biogeography and Quaternary History 

WHYTE, S.A. 1975, Distribution, trophic relationships and breeding 
habits of the fish populations in a tropical lake basin (Lake 