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THE AFRICAN RAIN FOREST VEGETATION AND PALAEOENVIRONMENTS DURING LATE QUATERNARY

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Abstract. This review paper presents first the main pollen results on the vegetation history of the rain forest during the late Quaternary.

– The Lake Bosumtwi record (Ghana) shows the disappearance of rain forest from the base of the core (ca. 28 000 yr BP) to ca. 9000 yr BP. During this time interval the vegetation was of montane type with sparse clumps of trees. There is synchronism between montane vegetation disappearance and rain forest reappearance. This phenomenon occurred abruptly around 9000 yr BP.

– The Lake Barombi Mbo record (West Cameroon) shows clearly that from ca. 24 000 yr BP until the present time, rain forest persisted with limited variations, and thus, this area represents a refuge area.

From these data and other, one concludes that Afromontane vegetation extended to lowland during cool and humid phases.

Other palaeoenvironmental data were obtained by diverse geological analyses of the lacustrine sediments. For Bosumtwi, the relatively precise reconstruction of lake-level fluctuations permitted several palaeoclimatic interpretations for the main Holocene phases.

For Barombi Mbo, the evolution of total organic carbon (TOC) and total nitrogen (TON) seems to be related mainly to temperature evolution. By comparison with present-day mountain environments, TOC and TON increase in cool environments, but decrease when warmth and humidity increase, as during Holocene time, because the recycling processes speed up in the topsoil. For the same period the alteration of the soils in the catchment produced a strong increase of kaolinite. All these change intervened ca. 9500 yr BP, which is a key date in tropical Africa.

In conclusion, climatic correlations between equatorial and dry north tropical Africa illustrate how changes in the forest block must have important effects on adjacent climatic zones.

1. Introduction

For reconstructing the vegetation and palaeoenvironments history of the equatorial zone of Africa and particularly that covered today by the rain forest, direct evidence is provided by palynological sources. Pollen analysis, when carried out on long sequences dated by radiocarbon, allows the reconstruction of the main vegetation changes over long time-scales.

Other environmental evidence is provided by various kinds of geological research (stratigraphical, sedimentological, geochemical, isotopic, etc.) on lacustrine deposits.

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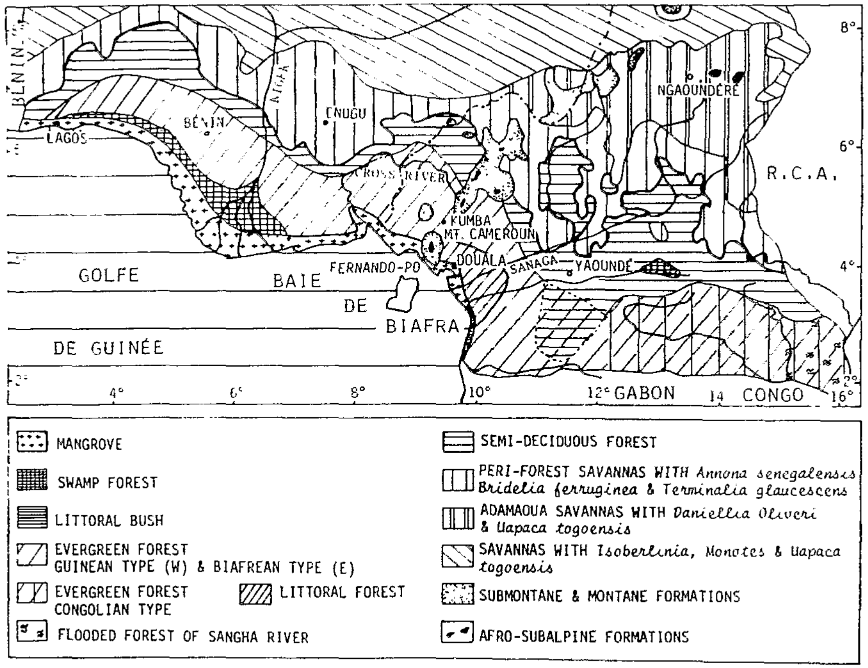

Fig. 1. Schematic map of the vegetation around the Baie of Biafra (from Maley *et al.*, 1990).

2. Pollen Analyses in African Rain Forest

Lakes inside or close to rain forests and yielding sequences favourable for pollen analysis have been investigated in Ghana (Maley and Livingstone, 1983; Maley, 1987, 1989), Cameroon (Maley and Brenac, 1987; Brenac, 1988; Maley, 1987, 1989) and Congo (Elenga, 1987).

Schematically the rain-forest vegetation of the Guineo-Congolian Region are constituted of two main types (White, 1983; Letouzey, 1968, 1985; Hall and Swaine, 1981) (cf. Figure 1):

– *the semi-deciduous rain forest*, which is characterized by a large number of trees who lose their leaves during some weeks in the course of the dry season. This type of forest appears when the yearly number of 'dry' months (rainfall below about 100 mm) reach three. Among the trees which reach the canopy, the dominant families are Ulmaceae, particularly with *Celtis*, and Sterculiaceae with *Triplochiton* and other genera.

– *the evergreen or semi-evergreen rain forest* is usually a richer variety of rain forest (except for some quasi mono-specific varieties). Climatically, this type of forest is adapted to slightly more humid conditions that the semi-deciduous type and usually this type is present when the dry season does not exceed two months (the soils also play an important role in the repartition of the forest types). This forest is characterized by its richness in Leguminosae, especially Caesalpiniaceae. Its maximum development is around the Baie of Biafra, from east Nigeria to Gabon (Figure 1); some large patches exist also more to the west, from Ghana to Liberia, and more to the east in the Zaïre-Congo basin.

2.1. *Lake Bosumtwi in Ghana*

This lake with a water level near 100 m ASL (above sea level) is situated in the lowland semi-deciduous rain forest and to the north from about 80 km of the present-day edge of the forest. The core studied from Lake Bosumtwi has a lengh of about 17 m and reaches back to about 28 000 yr BP (Figure 2).

The principal pollen results (Maley and Livingstone, 1983; Talbot *et al.*, 1984;

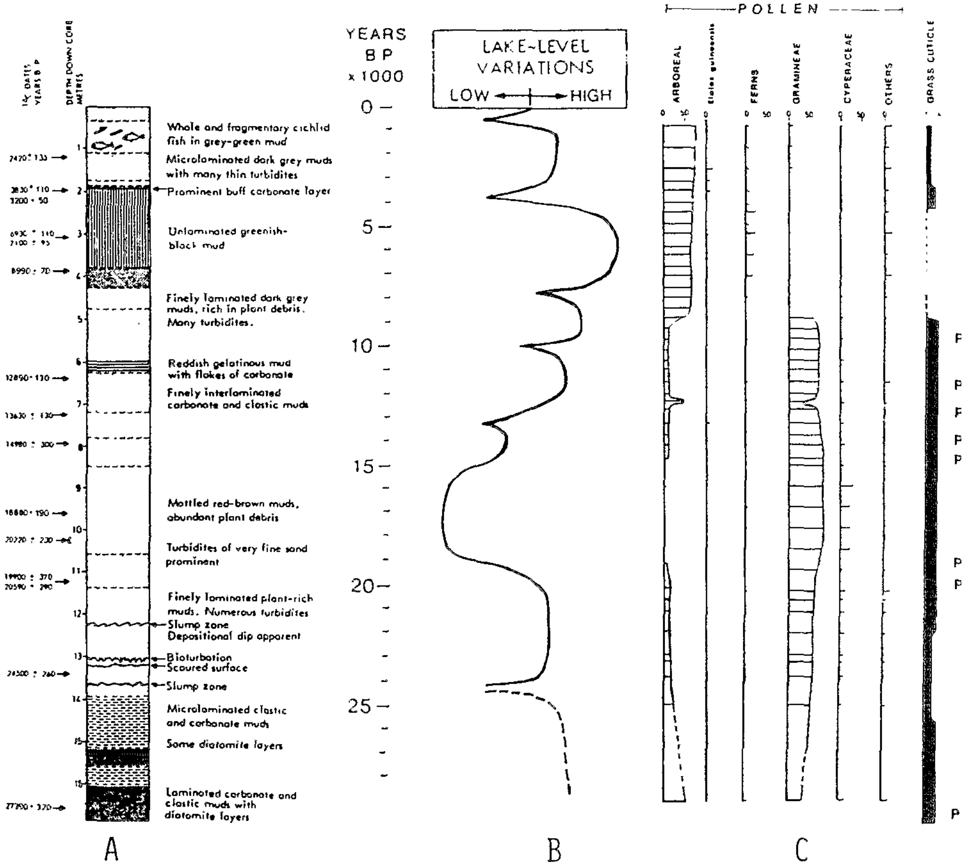

Fig. 2. Lake Bosumtwi in Ghana. (A) Stratigraphy of core B-7, from Talbot *et al.* (1984). (B) Lake-level variations adapted from Talbot and Kelts (1987); before about 15 000 yr BP the curve is modified by reference to pollen data (cf. Fig. 4). (C) Pollen data from Talbot *et al.* (1984) and Maley (1987). P – Cuticles of Pooideae (Afro-montane Gramineae) by Palmer, in Talbot *et al.* (1984).

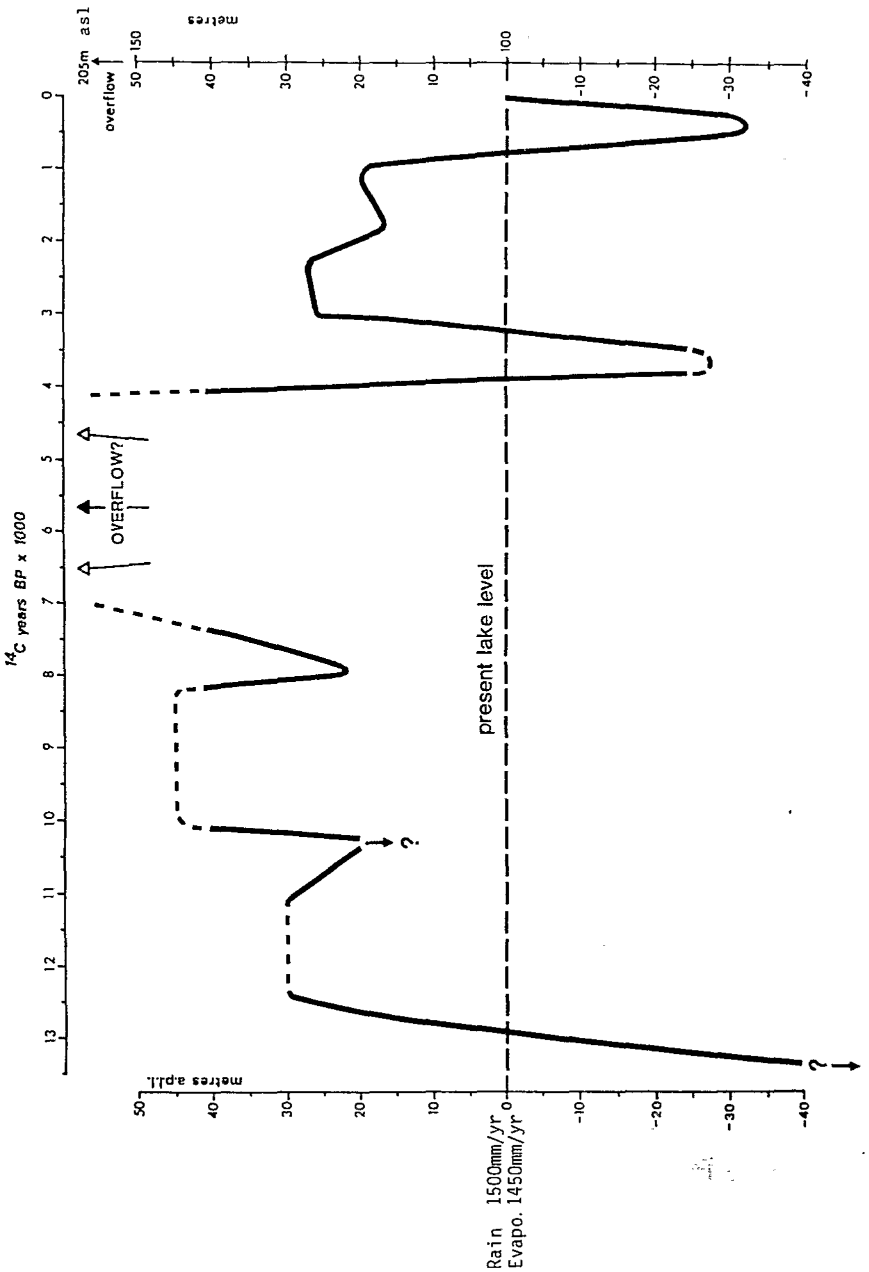

Fig. 3. Lake Bosumtwi level variations during late Pleistocene and Holocene time (Talbot *et al.*, 1984, Fig. 6); at left note the present-day values of rainfall and evaporation (from Talbot and Delibrias, 1977); metres a.p.l.l. = above present lake level; a.s.l. = above sea level.

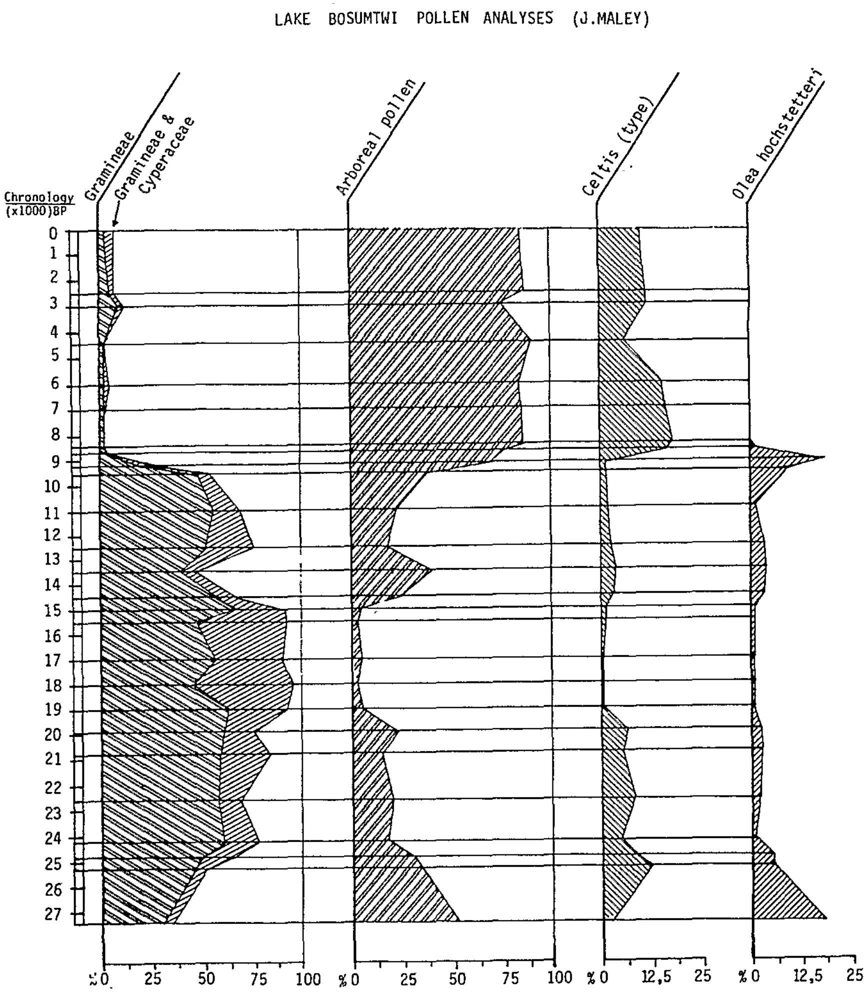

Fig. 4. Lake Bosumtwi pollen anlyses (J. Maley). The chronology of the core is based on 15 radiocarbon dates (after Talbot *et al.*, 1984).

Maley, 1987, 1989) (Figures 2 and 4) clearly show that before about 9000 yr BP, forest was not present in this region. The change was abrupt. Indeed, between the present and about 8500 yr BP arboreal pollen percentages oscillated from 75 to 85%, while before 9500 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 has been replaced by the herbaceous plants, essentially Gramineae and Cyperaceae, which reached frequencies of 91–94%. 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 from the core base to its quasi-disappearance around 9000 yr BP, near the time when the rain forest reappeared (Figure 4). This montane element includes the mountain olive, *Olea hochstetteri*, which today are only present 700 km westward, near 1200 m ASL on the Momy 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 9000 yr BP, the presence of a montane element at low elevation around the Bosumtwi lake, where the highest surrounding hills reach maximal elevations of from 400 to 550 m ASL, implies a lowering of the montane vegetation belt by minimally 600 m. This corresponds to a temperature decrease of 3–4 °C (Maley and Livingstone, 1983) when applying a mean temperature gradient of 0.6 °C for every 100 m displacement of the vegetation belt. This wet adiabatic lapse rate must be applied, even during the Last Arid Maximum ca. 18 000 yr BP, because the Tropical Atlantic Ocean remained relatively warm, except in the upwelling areas (Rind and Peteet, 1985; Maley, 1989). 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 27 000–28 000 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 300 m ASL with a maximum depth of 110 m and is situated in the lowland rain forest of West Cameroon (Figure 1). Around the lake, in an area with about 10 km radius, the dominant forest is the evergreen formation of Biafrean type, but there are also some islets of semi-deciduous forest within the evergreen forest, which remains largely dominant (Richards, 1963; Letouzey, 1968, 1985; D. Thomas, pers. commun.).

The following principal results are to be noted (Maley and Brenac, 1987; Maley, 1989; Brenac, 1988, and in preparation) (Figure 5):

– From the base of the core dated between 30 000 and 24 000 yr BP until ca. 20 000 yr BP, pollen of forest taxa is abundant with percentages from 60 to 75%. Among these, Caesalpiniaceae and Euphorbiaceae are particularly well represented. Two montane taxa are also relatively frequent in this section: the mountain olive, *Olea hochstetteri*, with percentages between 10 and 30%, and *Phoenix*

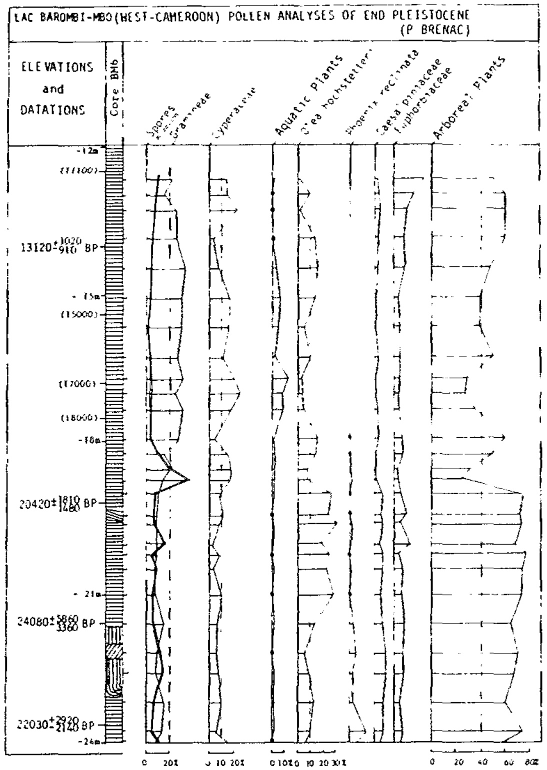

Fig. 5. Lake Barombi Mbo pollen analyses (P. Brenac) (from Brenac, 1988; Maley *et al.*, 1990).

reclinata (Palmae), which is found today in the Cameroon mountains frequently associated with *Olea hochstetteri* (Letouzey, 1978).

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 1200 m ASL) (Achoundong, 1985). On the plain around these hills the forest is semi-deciduous, but on the hills' summits the climate is more humid and cool because of the high frequency of clouds which favour this particular cloud-forest association.

Around 20 000 yr BP, a very sharp change occurs in the pollen spectra. Percentages of mountain olive pollen grains decrease to values of 5–15%. Forest taxa decrease as well, particularly Caesalpiniaceae 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, 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. This situation is very different from what we described from the Bosumtwi region, where we concluded to a complete disappearance of the forest.

After ca. 14 000 yr BP, the forest taxa increased again, with percentages reaching 60% near the beginning of Holocene time. 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%. Percentages of mountain olive pollen increase again around 13 000 yr BP to disappear near the beginning of the Holocene. One can conclude that the period 14 000–10 000 yr BP was humid again, but not as cool as before 20 000 yr BP.

From ca. 9500 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 and Brenac, 1987).

2.3. *Conclusions*

Previously, by comparing the present day biologic richness (plants, birds, mammals, amphibians, butterflies, etc.) of large parts of the West Cameroon rain forest with other parts of the African rain forest, several biogeographers have concluded with the hypothesis that during dry periods, such as during the Last Arid Maximum, an important refugium subsisted in West Cameroon. The pollen data presented here are particularly important because they confirm this hypothesis, showing that during the last great arid and cold 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 (Figure 6) (see a synthesis in Maley, 1987). Another important result is the spread to low elevation of a montane element characterized mainly by *Olea hochstetteri*. This indicates a temperature cooling which seems similar for the two sites studied, i.e. a decrease of ca. 3–4 °C. This result is similar to recent quantitative estimates obtained in East Africa indicating a decrease of 4 ± 2 °C (Bonnefille *et al.*, 1990).

3. Palaeobiogeography of Afromontane Vegetation

3.1. *The Extension of Montane Vegetation to Lowland*

To understand this question, the modern composition of the African montane flora and fauna of middle altitudes from about 1000 m to 3000 m 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 African are 53% for the

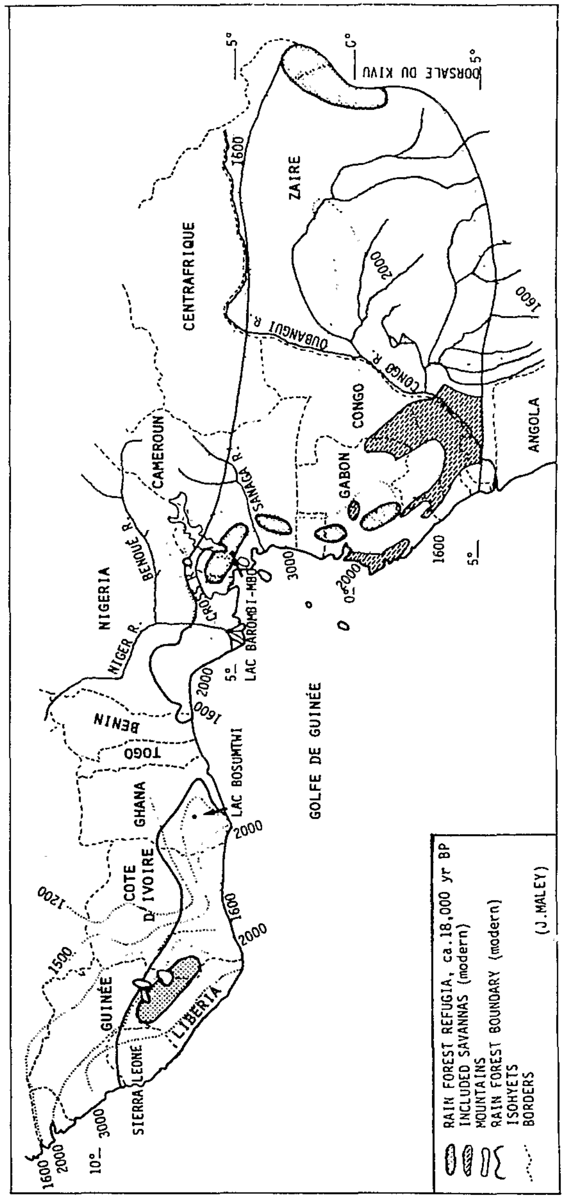

Fig. 6. Diagram of the main lowland rain forest refugia in equatorial Africa during maximum of the last great dry and cold period (about 18 000 yr BP) (from Maley, 1987, 1989). The modern conditions (forest boundary, included savannas and main isohyets) are adapted from White (1983, Fig. 5 and map).

montane forest and 49% for the montane grassland. In order to explain these similarities, many authors have assumed that during climatic changes and especially during colder periods of 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).

In equatorial East Africa the extension of montane belts to lower elevation has been known for several decades thanks to geological data on former glaciers and to palynological studies. The principal conclusions were a 5–9 °C lowering of the temperature during the last cold maximum phase (Coetzee, 1964; Van Zinderen Bakker and Coetzee, 1972; Hamilton, 1973, 1982; Flenley, 1979). Moreover, in other parts of equatorial Africa, such as northern Angola (Van Zinderen Bakker and Clark, 1962) and southern Congo Republic (Caratini and Giresse, 1979; Elenga, 1987), other pollen analyses have also clearly shown extensions of montane vegetations to low elevation (Maley, 1987, 1989). The most important data have been obtained on the Plateaux Batéké, about 40 km north of Brazzaville, in a small depression near 600 m ASL (Elenga, 1987). The pollen analyses carried out on a metre-long core show that from the base until around the beginning of Holocene time, the pollen spectra were dominated by Afromontane forest taxa; the pollen grains of *Podocarpus latifolius*, *Ilex mitis* and *Olea hochstetteri* constituted about 60% of the pollen spectra, dominated by *Podocarpus* with about 50%. This late Pleistocene lowland extension of mountain taxa implies a temperature lowering of 3–4 °C (Maley *et al.*, 1990).

3.2. *Possible Migrations of Afromontane Taxa*

Between the mountain massifs of East Africa and Cameroon, several typical Afromontane taxa had been observed in various isolated stations (White, 1981), on the southern rim of the Zaïre river catchment, and along the Guinea Gulf on the ridge of hills connecting Angola to Cameroon. For *Podocarpus latifolius*, there is a station near 700 m ASL on the Congolese slope of Chaillu Mountain (Maley *et al.*, 1990) and another at about 900 m 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 (3.1) show the pattern of a preferential junction way which could have operated intermittently during the Quaternary or even before, between East Africa and Angola, and subsequently expanded to the hill ridge of Mayombe, Chaillu, Monts de Cristal as far as the Cameroon mountains and eventually more to the west on the Guinea Ridge (western Ivory Coast and Guinea) (Figure 7) (Maley, 1987, 1989; Maley *et al.*, 1990). Today, *Podocarpus* no longer exists on the Guinea Ridge, but its former presence was recently discovered by large amounts of its pollen grain in a marine core offshore Ivory Coast (Fredoux and Tastet, 1988; Fredoux *et al.*, 1989). This pollen data show that the disappearance of this tree intervened near the very end of the Pleistocene.

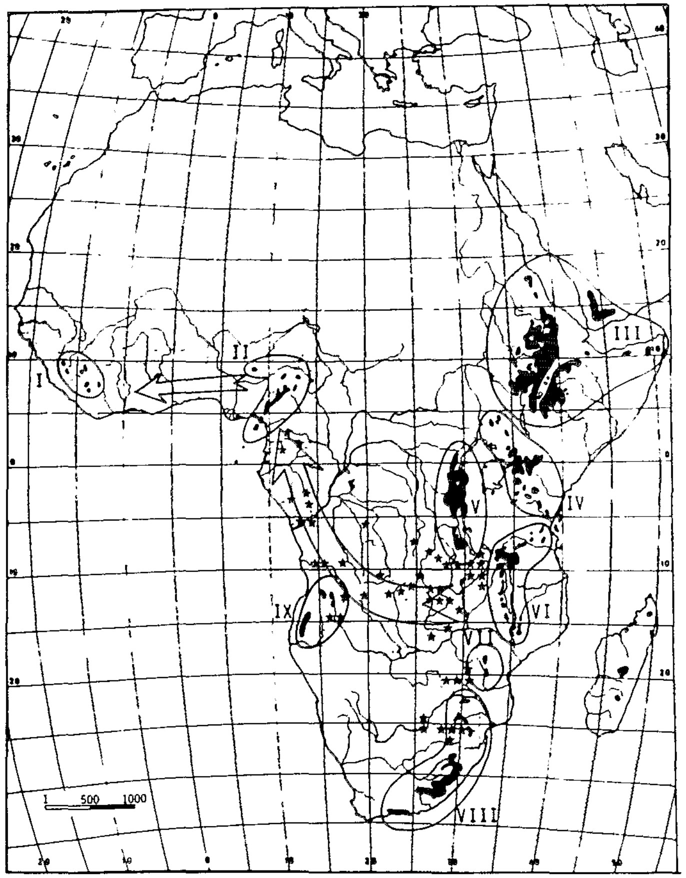

Fig. 7. Distribution of the nine African regional mountain systems. I, West-African; II, Cameroon-Jos; III, Ethiopian; IV, Imatongs-Kenya-Usambara; V, Ruwenzori-Kivu; VI, Uluguru-Mlanje; VII, Chimanimani; VIII, Drakensberg; IX, Angolan. The *stars* show many distant populations of Afromontane plant species outside the large mountain systems represented by *black areas* (adapted and completed from White, 1981). The *two arrows* schematically represent a possible migration path of Afromontane taxa from East Africa to Angola and subsequently via Cameroon to West Africa (adapted from Maley *et al.*, 1990).

4. Geological Data on Palaeoenvironments

4.1. *The Lacustrine Records*

4.1.1. *The Bosumtwi Lake, Ghana*

The geological study of the cores taken in the lake (mineralogy and geochemistry) and that of the numerous outcrops of lacustrine (beach levels, deltaic formations) and fluviatile deposits as well as palaeosoils on the catchment permitted the reconstruction of the lake-level fluctuations (Talbot and Delibrias, 1977; Talbot *et al.*, 1984; Talbot and Kelts, 1986). The lacustrine fluctuations were very distinct, with a maximum level in middle Holocene time and a very low level from about 20 000 to 14 000 yr BP (Figures 2 and 3) (Talbot and Delibrias, 1977; Talbot *et al.*, 1984; Talbot and Kelts, 1986; Maley, 1987, 1989). The sediments of the cores are for the most part laminated and of varve type; Livingstone (private commun.) counted about one lamination for one radiocarbon year. But *from ca. 9000 yr BP to ca. 3700 yr BP* (Figure 2) the sediment is unlaminated and of sapropel type (high organic content with 12–18% TOC – total organic content – in comparison to the laminated parts with ca. 8–12% TOC) (Talbot *et al.*, 1984; Talbot 1988).

Today, this lake is stratified with anoxic waters below about 10 m, with a maximum water depth of ca. 80 m (Beadle, 1974), but almost each year an overturn of deep anoxic waters occurs. Because the laminations are a yearly phenomenon, with great probability one can relate them to the yearly overturn of deep waters. Studies done on this phenomenon by Beadle (1974) and Whyte (1975) have shown that the overturn is mainly related to a lowering of air temperature in August and September, induced by the non-precipitating stratiform cloud covers generated by the upwelling of cold sea waters in the Gulf of Guinea and by the associated atmospheric phenomenons related to the southern winter (cf. Maley, 1987, 1989). This well-characterized season is called 'the little dry season', usually occurring during two months, August and September – in opposition to the great dry season from December to February (Figure 8). During 'the little dry season' the cooling of the air temperature also affects the water column, which becomes more or less homothermal. Because, at the same time, the wind stress from the southwesterlies is at its maximum, the instable waters are overturned (Beadle, 1974; Whyte, 1975). So, the unlaminated interval of the core, which also corresponds to the high lake level, can be related to an absence or reduction of the 'little dry season' and in consequence to the prolongation of the rainy season. One can speculate either an annual prolongation through August and September of the June-type weather (Figure 8), which is characterized by heavy precipitation from nimbostratus clouds, or the annual early start of the October–November-type weather (Figure 8), with numerous and typical towering cumuliform clouds, probably occurred. Because in West Africa fluviatile sediments generally show a transition from clay-type deposits to a more sandy type near 7000 yr BP ~~(section 4.3)~~ (Maley, 1981, p. 519; Maley, 1982, 1983), one is obliged to estimate that the June-type weather dominated until about 7000 yr BP and then the October–November-type weather dominated until about 3700 yr BP. The yearly rainfall was certainly higher than today (ca. 1520 mm), but, because the pollen data for this period exhibit no particular change, the composition of the forest must have remained of a semi-deciduous type (Maley and Livingstone, 1983, and unpublished data: spectra have only very few pollen grains of Caesalpiniaceae – characteristic of the evergreen forest type). Consequently one concludes that during this period the northern winter dry season had the same length as today, i.e. three months (December–February) (Figure 8). 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 and are described as a 'pluvial paroxysm' by Suchel (1972).

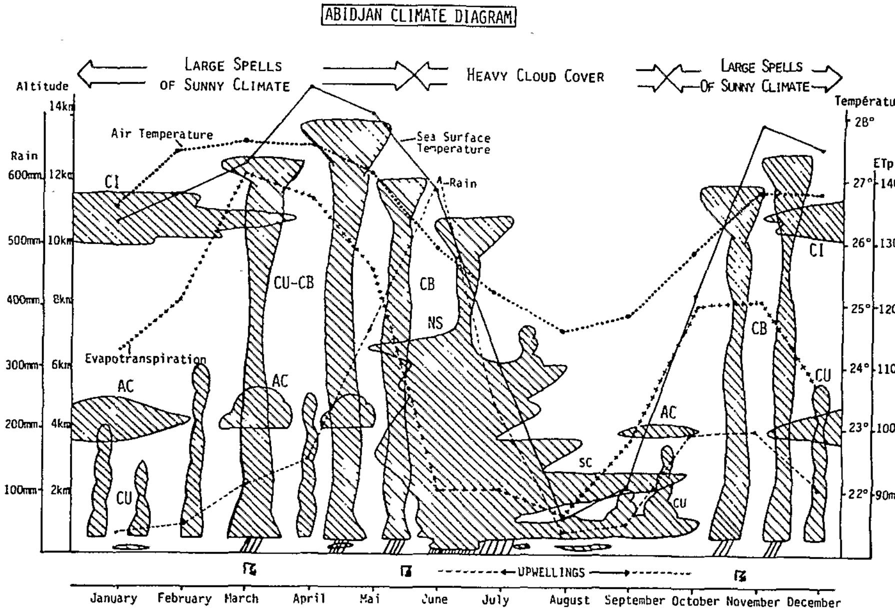

Fig. 8. Diagram of seasonal climatic change in Abidjan (Ivory Coast), showing the succession of the main types of clouds (adapted from Drochon, 1976) and the principal elements of climate: rain, air temperature, evapotranspiration and sea surface temperature (data from ORSTOM and ASECNA). The Abijdan station is representative of the western sector of the rain forest area (adapted from Maley, 1987, 1989).

After 9000 yr BP because of the large rainfall increase, and also because of biogeographical reasons (see discussion in Maley, 1987) the present-day interruption of the rain forest in Togo and Benin, which is called the 'Dahomey Gap' was probably absent, *an expansion of the rain forest largely outside its present-day limits* is very probable (cf. Maley, 1989).

The Dahomey Gap likely reappeared in late Holocene time, when Lake Bosumtwi abruptly regressed. Indeed, the abrupt regression of the lake, more than 120 m (Figure 3), is dated at about 3700 yr BP, which is the date of the sudden reappearance of the laminations (Talbot *et al.*, 1984). For the reasons explained above, this phenomenon must 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. In order to explain this, the present-day water budget of the lake, which is slightly positive (Figure 3; the average rainfall on the crater catchment is 1520 mm/yr with evaporation at only 1450 mm/yr – Talbot and Delibrias, 1977), must be considered. There is an average excess of 70 mm which explains the present-day transgressive phase of the lake, which has apparently been underway for several centuries (Figure 2), because a lacustrine minimum probably occurred in the 15th century AD (Maley, 1989b). This regression phase, like the one dated between 4000 and 3000 yr BP, was caused by a deterioration of the lacustrine water budget that linked 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 1200 mm/yr, 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 (cf. Figure 6). Thus, provided minima are not below 1200 mm/yr, 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.

4.1.2. *The Lake Barombi Mbo*

Though this lake is situated in the rain forest north of the Guinea Gulf (Figure 1) and at a latitude relatively similar to Lake Bosumtwi, it differs by several present-day characteristics:

- an active outlet meaning quite no level fluctuations;
- very stable stratification without yearly overturn;
- no 'little dry season' in August and September, but at the same time the maximum of the rainy season ('pluvial paroxysm' of Suchel, 1972). For this reason the climate there is much more humid than that of Bosumtwi region.

The main present-day limnologic characteristics of the Barombi Mbo were established by Kling (1987, 1988). Productivity of plankton biomass is low; this fact can be related to the quasi-absence of diatoms in the sediments studied. The sediments cored in the deepest part of the lake are laminated, and from field observations, one notes the disappearance of laminations above the depth of ca. 90 m. Laminations which frequently form a composite microsequence vary in thickness from less than 1 mm to 3 or 4 cm (Maley *et al.*, 1990; Giresse *et al.*, to be published). These microsequences commonly present

- a thin brown-to-black lower sublamina consisting of fine-grained quartz and flakes of mica. Fragments of microscopic organic debris are scattered within.
- an upper sublamina of mainly blue-to-greenish clay which near the top usually has tiny concretions of siderite.

The coarse lower unit indicates the deposition of flood detritus, versus the upper unit, which corresponds to quiet conditions with settling of essentially clayey fine particles from suspension. Development of the uppermost concretions of siderite expresses a slowing of the pace of sedimentation and a concentration of carbonate at the sediment-water interface, two conditions favourable to minerogenesis. By using the radiocarbon dates, the overall frequency of repetition of these laminae is defined as ca. 1/15 years; this frequency is comparable to various present-day large floody events in the intertropical African zone (Maley *et al.*, 1990; Giresse *et al.*, to be published).

Among the other geological results already obtained two concerning the palaeoenvironnements are important.

– The first one is related to organic geochemistry (Giresse *et al.*, to be published) (Figure 9). From Pleistocene to Holocene time the gradual increase in C/N ratio from around 15 to 13 for the present time is explained as a result of progressive degradation processes during diagenesis in the sediment; the short excursions of the curve correspond to coarse-grained layers with macroscopic lignin fragments. The values of total organic carbon (TOC) are around 8% in the Pleistocene layers and fall to around 5% in the Holocene layers. The total nitrogen (TON) are around 6% in the Pleistocene layers and fall to around 4–5% in the Holocene layers. The important point is that these changes intervened clearly at about 9500 yr BP, a key date in equatorial and tropical Africa.

– The second one is related to clay mineralogy (Giresse *et al.*, 1990). The analysis of the size fraction below 2 microns shows a general dominance of kaolinite (K) associated with illite (I) and common traces of mixed layer (I-Sm). The ratio K/I+I-Sm remains near 1 until the end of the Pleistocene and suddenly jumps to between 7 and 9 in Holocene time. The break in the curve intervenes again about 9500 yr BP, indicating that after this date the soil development in the catchment was more intensive and favoured greatly the formation of kaolinite, typical of the fersialitic soils which are today 2–3 m thick.

Concerning equatorial Africa we have already noted that, following the Last Arid Maximum, the rain forest expansion was at 9000 to 9500 yr BP quite completely achieved in the Bosumtwi and Barombi Mbo regions. Moreover it is also at this date that the mountain taxa, mainly *Olea hochstetteri*, disappeared from the lowland, indicating a warming of the climate. This temperature change, associated with increase of precipitation beginning around 12 000–13 000 yr BP, probably can explain most of the results reported above.

Indeed, several ecologists working on tropical lowland and mountain forest formations have done research about the mechanism 'forcing' the vegetations to change their composition and physiognomy between lowlands and mountains (see Grubb, 1971, 1977; Whitmore, 1975, chap. 16; Vitousek, 1984; Tanner, 1985). These authors have concluded that the lower temperatures on mountains act upon the plants not directly but indirectly through nutrient limitations, particularly for nitrogen and phosphorus.

– In mountain environments the temperature lowering allows the reduction of the alteration of organic matter (TOC) in the soils and its better conservation with thickening of the humus top soil. But at the same time humus accumulates larger quantity of nitrogen (TON). There is a slowing down of the recycling processes.

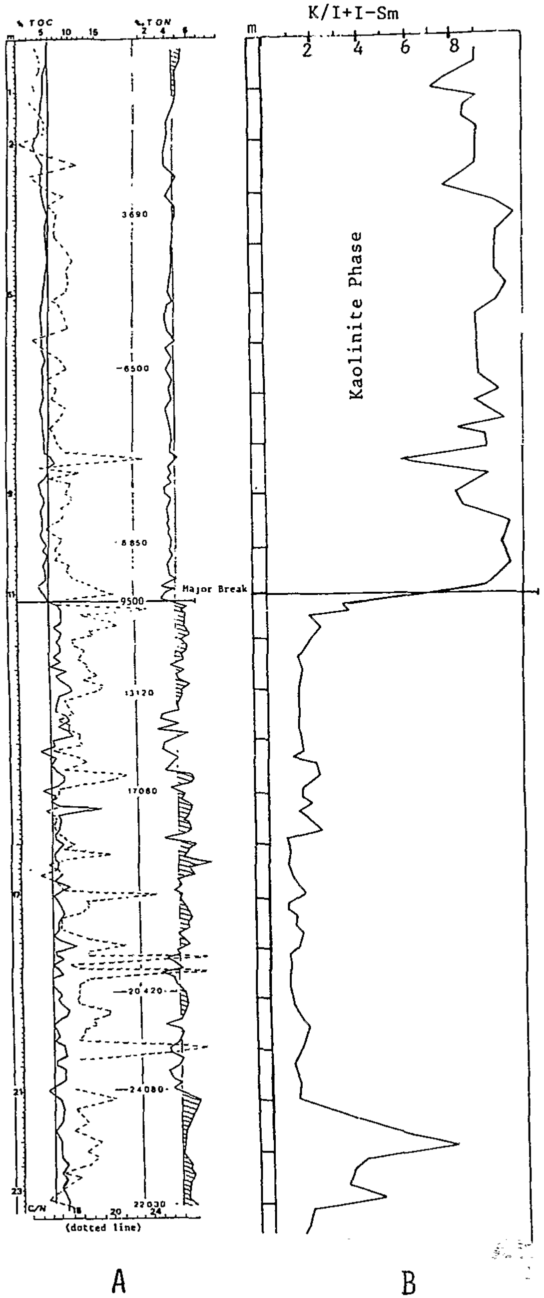

Fig. 9. Lake Barombi Mbo. (A) Log for the values of total organic carbon (TOC), total nitrogen (TON) and the ratio carbon to nitrogen (C/N) (Giresse *et al.*, 1990). (B) Log of X-ray diffraction mineralogy based on the maximum relative peak for quartz, kaolinite and clays (kaolinite, illite, smectite) according to the relation K/I+I–SM. The relative intensity of each peak is measured in centimetres (Giresse *et al.*, 1990).

These phenomena produce a shortage of mineral nutrients which leads to oligotrophic conditions (Whitmore, 1975).

– In lowland environments it is the opposite. Warmer and wetter conditions increase the alteration of organic matter and all the recycling processes are sped up, giving more nutrients to the plants, particularly nitrogen.

In the Barombi Mbo sediments the evolution of TOC and TON seems to reflect closely such phenomenons (Figure 9). Before 9500 yr BP, lower temperatures increased humus and nitrogen in the soils. The thicker humus topsoil gave more organic matter (TOC) with more nitrogen (TON) to the lacustrine sedimentation. After 9500 yr BP the climatic warming associated with more precipitations had the result of speeding up the pedologic phenomenons – confirmed by the large increase in the formation of kaolinite – and particularly of slowing down the influx of TOC and TON to the lacustrine sedimentation. The convergence of two independent data (pollen and organic matter analyses) confirm the extension of montane vegetation to the lowland in the region of Barombi Mbo.

The montane biotopes appear generally above 1000 m ASL; this limit forms a fundamental biological barrier which is characterized by changes in flora and fauna and also commonly by physiognomical modifications (Moreau, 1966; Grubb, 1971, 1977; Whitmore, 1975, chap. 16; Leigh, 1975; Bernardi, 1979). The ecologists who have demonstrated that all these changes are 'forced' by nutrient limitations have also shown that the cloud covers and fogs play an important ecological role in the montane biotopes (see particularly Grubb and Whitmore) and for this reason could explain

– some present-day localized extensions to low elevation of normally montane faunas or floras; the 'cloud forests' are related to this phenomenon;

– the extensions to lowland of montane faunas and floras during the cold periods of the Pleistocene (cf. Maley, 1987, 1989; Maley *et al.*, 1990).

5. Conclusion: Climatic Relations Between Equatorial and Dry North Tropical

In the course of the last twelve millennia, the main transgressive and regressive stages of the equatorial rain forest (13 000–12 000 yr BP, ca. 9500 yr BP, 7000–6500 yr BP, 4000–3500 yr BP) seem to correlate chronologically with the main lacustrine and vegetation phases in the dry north tropical Africa (Servant, 1973; Maley, 1981, 1982, 1983; Gasse *et al.*, 1990). With regard to the climatic mechanism involved, this correlation could indicate that the moisture-laden air of the monsoon, producing rain north of the forest right up to the central Sahara, derives not only directly from the Gulf of Guinea, but largely also from a recycling of the moisture already precipitated on the equatorial forest and then carried on by evapotranspiration. This recycling of moisture-laden air, probably multiple, has been demonstrated for the present period by isotopic analyses (Baudet and Laurenti, 1976; in process with the programme HAPEX-Niger); from this follows the system elaborated by Monteny (1986) and Monteny and Casenave (1989) and well illustrated by the detailed study of an annual cycle by Cadet and Nnoli (1987). For this reason every large change in the African forest block must have had important effects on adjacent climatic zones.

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