CHAPTER 5

The Impact of Arid Phases on the African Rain Forest Through Geological History

Jean Maley **✕**

There were great variations in paleoenvironment and vegetation in the African tropics toward the end of the Neogene. These can be explained by global temperature changes, particularly the cooling phase that occurred at the same time as Antarctic and Arctic glacial advances (Maley 1980, 1996a, 1996b). Pollen in the sediments of the Niger delta reflects changes in the rain forest and adjacent savannas during this period (Poumot 1989; Morley and Richards 1993). Analysis of pollen in sediments suggests that several important extensions of savanna vegetation, associated with reductions of the extent of the rain forest, occurred at the end of the Miocene, between 8 and 5 million years ago. There is evidence of similar changes in east Africa (Harris 1993, based on the paleofauna). This period was characterized by large and rapid eustatic fluctuations directly associated with variations of polar ice extent (Haq et al. 1987). However, near the Gulf of Guinea (Poumot 1989; Morley and Richards 1993), as well as in east Africa (Bonnefille 1983), the main change occurred around 2.5 million years ago, at the same time as the first large Arctic glacial advance. In fact, all the large glacial advances in the Arctic—including the last one, which culminated around 18,000 B.P.—have

had major impacts on humid tropical Africa (Maley 1996a, 1996b).

During the Pliocene and Pleistocene, changes in marine $\delta^{18}O$ show a progressive increase in the amplitude of glacial variations. Two main stages occurred, the first around 2.5 million years ago and the second about 800,000 years ago (Ruddiman et al. 1989), when there was a strong increase of climatic variability, characterized by stronger cooling phases with a periodicity of 100,000 years (Start and Prell 1984). Pollen data based on marine records in the Gulf of Guinea (covering the past 250,000 years) and lacustrine records in forest areas (covering the past 25,000 years) demonstrate the impact of these variations on vegetation at the end of the Quaternary. There was a maximum reduction of the rain forest between 20,000 and 15,000 B.P. (Maley 1996a). Indirect information about certain aspects of the history and dynamics of the rain forest can also be obtained from the modern biogeography of various groups of animals and plants (Hamilton 1976; Maley 1987; Colyn 1987, 1991; Sosef 1994).

Climate is highly dependent on latitude, the distribution of continents, and especially regional geographical factors (mountains, depressions, and so on), all of which were rela-

tively stable during the period of interest (the end of the Neogene). Therefore, climatic changes in the past probably affected particular regions repeatedly in similar ways. This means that during arid phases, fragmentation of the forest must have reoccurred numerous times, especially over the past 800,000 years. Various sedimentary and micropaleontological recordings in the Gulf of Guinea demonstrate that cyclic worldwide climatic events have repeatedly had a marked impact on the African equatorial zone (Prell et al. 1976; Jansen et al. 1984, 1986; Ruddiman et al. 1989; Bonifay and Giresse 1992). Therefore, the end of the most recent climatic cycle, from 25,000 B.P. to the present, for which abundant data exist, could provide a model for the main fluctuations that have affected the African rain forest over the past 800,000 years. The two extremes of this model are (1) a phase of maximum fragmentation, when forest cover was at a minimum, and (2) a phase of maximum extension, which peaked between approximately 9,000 and 4,000 B.P. Furthermore, the intermediary periods, before and after each of these phases, are characterized by a number of phases of regression and recolonization (Maley 1996a). This suggests that during 80–90% of the past 800,000 years the African rain forest was less extensive and more fragmented than at present.

Fragmentation of the Rain Forest

The study of paleoenvironments and their variations has often indicated phases of intense aridity. Stone lines that are found at the base of numerous soil profiles indicate that during several periods of the upper Pleistocene, extensive areas that are currently forested lost a large part of their tree cover and severe soil erosion occurred, especially between 70,000 and 40,000 B.P., as well as at the very end of the Pleistocene (Lanfranchi and Schwartz 1991; Maley 1993, 1996b; Runge 1997).

The study of fossil pollen, preserved in

lacustrine sediments accumulated regularly over millennia, can be used to reconstitute the history of vegetation around the lakes. This technique has yielded important insights into the fragmentation of the forest. Pollen analyses at Lake Bosumtwi (Ghana) have demonstrated the regional disappearance of the forest from about 19,000 to 15,000 B.P. (Maley 1987, 1989, 1991). In contrast, pollen analyses at Lake Barombi Mbo have demonstrated that forest persisted in this region of west Cameroon between 20,000 and 15,000 B.P. (figure 5.1; see also Maley 1987, 1991; Brenac 1988; Giresse et al. 1994; Maley and Brenac 1998a).

The fragmentation of the forest block during arid periods resulted in the extension of various plant assemblages from more or less xeric habitats into the zone currently occupied by rain forest. This is clearly demonstrated by pollen analyses for the last arid maximum (18,000 B.P.) in the two aforementioned locations: in Bosumtwi the pollen of taxa from open environments completely dominated at that time, whereas at Barombi Mbo these taxa increased considerably, although they almost never dominated. Today, relics of xeric vegetation persist in isolated refuges where unfavorable soil or local climatic conditions have prevented recovery of moist rain forest, as on Mount Nimba (Ivory Coast and Guinea) (Schnell 1952), in the Crystal Mountains (Gabon) (Reitsma et al. 1992), or even in the large savanna enclave of La Lopé, in central Gabon (Aubréville 1967; White 1992). On the large rocky hill of Nkoltsia, near Bipindi in southeastern Cameroon, Villiers (1981) described a prairie of cactiform Euphorbiaceae and a low, open forest with numerous *Julbernardia letouzeyi*, which both he and Letouzey (1983) associate with the southern zambezian dry forest type.

Pollen analyses undertaken at Bosumtwi and Barombi Mbo, both located in lowland parts of equatorial Africa below 500 m altitude,
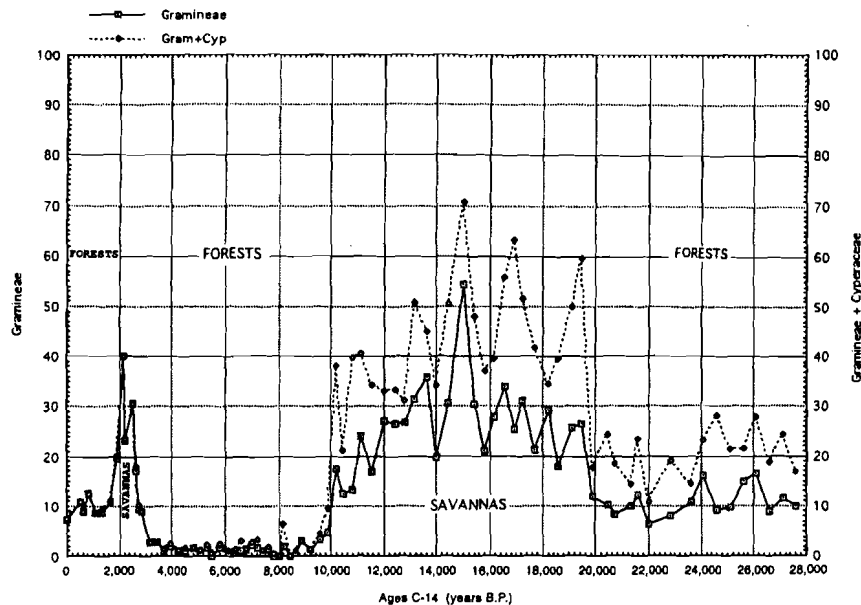
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Figure 5.1. Variation in savannas and forests in western Cameroon during the recent Quaternary reconstituted from analysis of pollen in sediments of Lake Barombi Mbo, near Kumba (Maley and Brenac 1998a). A core about 23 m long was taken from this crater lake, located at about 300 m altitude in lowland rain forest about 40 km northeast of Mount Cameroon and 60 km from the sea. Pollen analyses were undertaken on 82 samples, 12 of which were radiocarbon dated to establish the chronology of the core (Maley and Brenac 1998a). The figure shows relative changes in tree pollen compared to pollen from grasses (unbroken line). The dotted line represents the percentage of Cyperaceae pollen added to that for Gramineae. The Gramineae pollen are almost exclusively from herbaceous plants found on well-drained soils, characteristic of open savanna vegetation. The Cyperaceae are mostly aquatic. This figure allows us to depict the different phases of forest and savanna expansion over the past 28,000 years. We can see that from 28,000 to c. 20,000 B.P. forest cover was similar to that seen today (the percentages are similar). From 20,000 to 10,000 B.P., during the last major global and regional cold period, the climate was much drier, resulting in replacement of forest by savanna vegetation. However, in the Barombi Mbo region grass pollen remained at about 30–40% and never dominated tree pollen. This suggests that the landscape at the time was a forest-savanna mosaic in which forests were more widespread. This has been confirmed by an analysis of carbon isotopes (Giresse et al. 1994). This landscape probably corresponds to the forest refuges thought to have occurred in equatorial Africa during this period (Maley 1996a; Sosef 1994). From c. 9,500 to 2,800 B.P. forest was at its most dominant; between 2,800 and 2,000 B.P. there was a brief and intense period of forest retreat and savanna expansion. This climatic pejoration was probably due to increased seasonality associated with a shorter rainy season (see text). Finally, forests have expanded from about 2,000 B.P. up to the present.

have demonstrated that a montane forest taxon, Olea capensis (syn. Olea hochstetteri), extended into the lowlands before the Holocene. Furthermore, this species and two other montane forest taxa, Podocarpus cf. latifolius and Ilex mitis, extended into the lowlands on the Batéké Plateau north of Brazzaville before the Holocene and possibly before 20,000 B.P. (Elenga et al. 1991, 1992, 1994; Maley and Elenga 1993). As is the case for xeric vegetation, refuges of montane vegetation, with Olea capensis and Podocarpus latifolius, can still be found today at low altitudes (see White 1981). The largest stand located was at Kouyi, between 600 and 700 m altitude on an old ironcrust plateau in the Massif du Chaillu in Congo, which is very unfavorable for the growth of rain forest (Maley et al. 1990b). These montane extensions at low altitudes can be explained only as relics of periods in the past when decreased temperatures occurred during certain arid phases, especially the one that culminated around 18,000 B.P., when temperature was estimated to be 3–4°C below the present yearly mean (Maley and Livingstone 1983; Maley 1987, 1989, 1991, 1996a; Maley and Elenga 1993). Studies in the mountains of east Africa have demonstrated similar values (Bonnefille et al. 1992; Vincens et al. 1993). Thus, the entire zone currently occupied by rain forest has experienced extensive changes in the environment and vegetation in the past.

Biogeography and History of the African Rain Forest: The Refuge Debate

Current climatic conditions in the equatorial region covered by rain forest are relatively homogeneous with respect to average temperature and humidity, although there is a gradient between a more humid zone near the Gulf of Guinea, with some extensions toward the central part of the Congo Basin, and a somewhat less humid peripheral zone in the north and south. The principal vegetation formation in the most humid zone is evergreen rain forest,

characterized by the predominance of Caesalpiniaceae, whereas the peripheral zone is mostly semi-deciduous forests dominated by Ulmaceae and Sterculiaceae (White 1983; Maley 1990).

This general pattern has numerous exceptions that can be analyzed from a historical viewpoint. In the most humid zone the distribution of species is not homogeneous, and it is particularly noteworthy that the main biogeographic gaps are not systematically located where important gaps occur at present, either for climatic or for geographic reasons (large rivers, mountain chains, and so one). The best example and the one that has been most studied is the Dahomey interval, where Sudanian savannas extend all the way to the sea and interrupt the western forest block for approximately 200 km in Togo and Benin. In fact, this gap seems to play only a minor role in the distribution of typical forest plants (Léonard 1965; Brenan 1978; White 1979), small mammals (Robbins 1978; Grubb 1982), birds (Moreau 1963, 1966; Crowe and Crowe 1982), batrachians (Amiet 1987), or insects (Carcasson 1964; Lachaise et al. 1988). These data show that the distribution limits of few forest species occur at the Dahomey interval. The most significant gap in the Guineo-Congolian forest block occurs in eastern Nigeria along the Cross River. As a result, Brenan (1978) distinguished the vegetation of the Guinean Domain, to the west of the Cross River, and the Congolian Domain, to the east (figure 5.2). Thus, there seems to be no direct relationship between the magnitude of these geographical gaps and their biogeographical impact. The geographical gap formed by the Cross River is minute compared to the scope of the biogeographical phenomenon, while the inverse holds for the Dahomey interval. This is why most of the authors who have discussed these questions have suggested that the biogeographical gap of the Cross River, like other less important gaps, might be
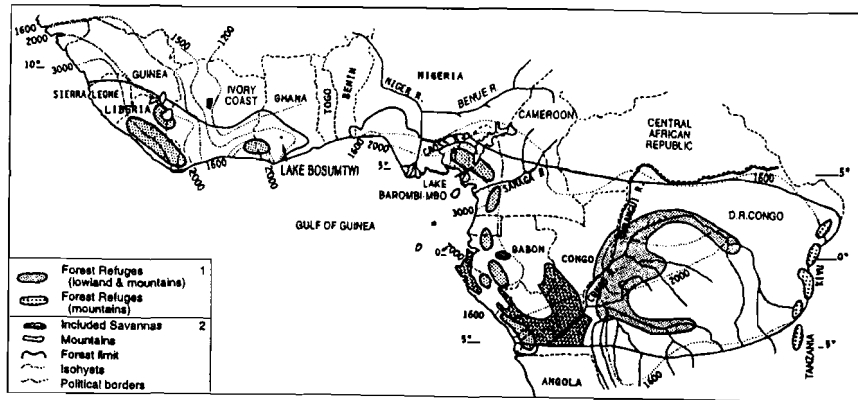
Figure 5.2. Schematic map of the African forest refuges during the last maximum arid phase (around 18,000 B.P.), according to various authors mentioned in the text. *Key to inset:* (1) c. 18,000 B.P.; (2) present-day environment. Figure adapted from Maley 1987, figure 1, and completed following Van Rompaey (1993) for the western forest block, Sosef (1994) for Gabon and west Congo, and Colyn (1987, 1991) for the Congo basin.

the result of previous fragmentations of the forest block as a result of past climatic changes (see Maley 1987, 1989, 1996a, 1996b).

Biogeographers who have studied the present distribution of wildlife in the African forest have concluded that four main sectors have high biodiversity, meaning that they are richer in species and endemic taxa than others.

- The richest sector is that which comprises the evergreen Biafran forest (close to the Bay of Biafra in the Gulf of Guinea). This extends from the Cross River to the Sanaga and, farther south, includes part of the forest of southwest Cameroon, the west of Gabon, and the Chaillu and Mayombe mountains in Gabon and western Congo (Aubréville 1968; Letouzey 1968, 1985; Brenan 1978; White 1983; Breteler 1990; Sosef 1994). In the east of Nigeria, Biafran extensions run all the way to the Niger delta (Hall 1981).
- A less rich sector is located at the western limit of the forest block. It consists of a

large part of the forests to the south of the Guinea Ridge, Liberia, and the far west of the Ivory Coast (Guillaumet 1967; Van Rompaey 1993). The southwestern forests of Ghana and adjacent parts of the Ivory Coast are also notable for the presence of various endemics (Hall and Swaine 1981; Swaine and Hall 1986).

- Two sectors in the Congo Basin have been identified on the basis of their relative richness, particularly for endemic mammals (especially simian primates; see Kingdon 1980; Grubb 1982; Colyn 1987, 1991; Colyn et al. 1991) and vascular plants (Ndjélé 1988). The first sector is located in the central part of the basin, mainly to the east of the large river, and the second, a mostly mountainous sector, is on the eastern side of the basin bordering the Kivu-Tanganyika Rift.

Most biogeographers conclude that this high biodiversity and endemism can be explained by the fact that these regions have been little

affected, if at all, by arid phases and that they represent "refuges" for forest biotopes. Schematic maps of the supposed refuges have been published by various authors (see figure 5.2): Aubréville (1949, 1962), Moreau (1969), Hamilton (1976), Mayr and O'Hara (1986), Maley (1987), Sosef (1994), Rietkerk et al. (1995), and, for the Congo Basin, Grubb (1982) and Colyn (1987, 1991). The large central refuge was riparian, associated with the permanent fluviatile flux of the Congo River and its main tributaries (Giresse et al. 1982). This refuge is thought to have resulted not from regional climatic conditions but from conditions in its distant headwaters, particularly on the eastern ridge bordering the rift. Research by Colyn (1987, 1991) has shown that this region also contained refuges of mountain forests. This hypothesis seems to be confirmed by the botanical data of Ndjélé (1988) and by pollen analyses undertaken at Lake Mobutu in Uganda (Sowunmi 1991), and in Burundi (Bonnefille and Riollet 1988). These mountain forest refuges seem to have benefited from conditions typical of the cloud forest (see Maley and Elenga 1993).

As far as the locations of refuges are concerned, the study by Sosef (1991, 1994) of two sections of African begonias is particularly important and commendable. The forty-six species and subspecies of begonias included in the study are strictly limited to non-riparian rain forest environments, at low altitude of the Guineo-Congolian Domain. They are fragile plants that live only in very shady forest understory. The great majority are endemic to a few very small areas. A phylogenetic tree was established by modern cladistic methods. Then, by combining the cladogram with distribution records, Sosef obtained a historical hierarchy of the areas where these begonias occur at present. On the basis of this analysis Sosef (1994:116–121) conjectured: "During the last glacial era (18,000 years BP), they will

have survived almost exclusively in the refuges." Because the seeds are subject to very limited dispersal and these begonias sprout only at the base of the mother plants, Sosef (1994:117) concluded: "The location of the former refuges may be deduced from their present-day distribution." The areas of these refuges concur with those that had already been proposed by Maley (1987) for the Cameroon-Gabon sector, adding two new refuge areas, a very small one in the Doudou Mountains on the western edge of the Massif du Chaillu, and another larger one in Mayombe in western Congo (Sosef 1994). Because these plants do not live in riparian environments (gallery forests), it is logical that Sosef's map (1994) does not include refuges toward the center of the Congo Basin, identified by Colyn's (1987, 1991) study of forest monkeys, which do occur in gallery forests.

The work of the ethnologist Serge Bahuchet (1993, esp. fig. 6) is also relevant to discussions about refuges. He concluded that the pygmies of Central Africa were affected by the arid phase that peaked around 18,000 B.P., because their tribes fall into three main groups that correspond to the principal refuges of (from west to east) south Cameroon/Gabon, the central Congo Basin, and the eastern Congo Basin.

Refuges and Speciation

Although various data are consistent with the fragmentation of the forest block and the maintenance of refuges during the most arid periods, there is much debate about the role played by these successive isolations (in refuges) in the appearance of new species or subspecies. Two principal lines of thought emerge. One, expressed by a minority, more or less refutes the idea that speciation is linked to fragmentation and isolation of forest biotopes. The other, on the contrary, suggests that these isolations are the origin of a great number of taxa. Many publications have discussed these issues; here I mention some that represent all or part of the

issue (Endler 1982; Haffer 1982, 1993; Mayr and O'Hara 1986; White 1993).

Mayr and O'Hara (1986) argue that modern biogeographical gaps in the African rain forest are not spread spatially (when the sampling unit is small enough) but are limited to restricted areas, such as the Cross River gap. They believe that this evidence refutes Endler's (1982) hypothesis that these isolations resulted only in parapatric speciation (in areas that were partially linked) and that either the diversity and the great number of ecological niches in forest environments (see Richards 1969) or ecotones between forest and savanna (trees: Aubréville 1949; birds: Smith et al. 1997) or between lowland and upland formations (Gentry 1989) would generate sufficient isolation for the emergence of new species. However, it seems that the two explanations—speciation in environments isolated ecologically (niches) and speciation in geographically isolated environments (vicariance)—especially under the effect of arid phases, are not incompatible and indeed seem to complement each other (see Haffer 1982; Blandin 1987; Gentry 1989; Smith et al. 1997).

Given the problems of dating the appearance of different forest taxa, it is difficult to come to any conclusions in this debate about speciation. Yet it is interesting to note that many studies have resulted in reliable hypotheses about the appearance of the main genera of leguminous plants, especially the Caesalpiniaceae. The fact that numerous genera and species of leguminous plants are common throughout the humid African forests, including the relict rain forests bordering the Indian Ocean (in the Zanzibar-Inhambane area), clearly shows that they were once linked in a large area of continuous distribution (Aubréville 1968; White 1993; Van Rompaey and Oldeman 1996). Polhill et al. (1981) suggest that numerous genera of Mimosoideae and Caesalpiniaceae, which live in the African rain forest, date back to the beginning of the Tertiary (Paleogene, from 65 to 23 million

years ago). In fact, palynological studies have revealed that various present-day leguminous forest plants can be associated with taxa from the Eocene, Oligocene, and Miocene (Guinet et al. 1987; Salard-Cheboldaeff and Dejax 1991). This indicates that they persisted through the arid phases of the end of the Neogene and the Quaternary (Maley 1996a), although numerous taxa must have disappeared during these arid phases.

The high species richness of the African rain forest can be explained by, on one hand, the conservation of a large stock of genera and species going back to the beginning of the Tertiary or even, for some, to the separation of the continent of Gondwana during the upper Cretaceous. Persistence of the same forest blocks during the most arid phases would favor the conservation of very ancient taxa. On the other hand, the species richness could be explained by the later fragmentation of a large forest block that had its origins in the Paleogene (Maley 1996a).

This phenomenon of repeated fragmentation, with refuges always in the same location, could explain the numerous endemic species or genera. If one compares Cowan and Polhill's (1981) catalogue for the four main forest sectors with high biodiversity of Caesalpiniaceae with Van Rompaey's (1993, app. 1) list of large trees found in the forests of southeast Liberia and southwest Ivory Coast (the presumed zone of the western refuge), it appears that from a total of forty-three to forty-five Caesalpiniaceae, twenty-three to twenty-five (53–55%) are endemic. Because arid to very arid periods have occurred in equatorial latitudes since the end of the Neogene, it seems that at least some of these endemic taxa go back to that era. The greater prevalence of climatic cycles associated with phases of high aridity over the past 800,000 years could also have resulted in further evolution of new taxa.

It seems that for genetic (or for other still unknown) reasons, some taxa or groups of taxa

develop faster than others at certain moments of their geological history (see, for example, the difference between the ammonites, a dynamic group, and the nautilus, a closely related group that has been very stable). Studies suggest this is the case for begonias and monkeys in the African forests. Indeed, Sosef (1994), for the begonias, and Colyn (1987, 1991), for the monkeys of the Congo Basin, came to the conclusion that new species and subspecies may have appeared in the refuges resulting from the most recent arid phase. Genetic research using modern techniques to test these ideas should be considered a priority.

Fragmentation of the Tropical Rain Forests During Warm Interglacial Periods

COMPARISON BETWEEN EQUATORIAL AFRICA AND AMAZONIA

Palynological and sedimentological studies carried out over the past decade on sediments from various lakes in the forest zones of Amazonia and Africa provide important evidence about the evolution of vegetation and the paleoenvironments during the upper Quaternary. A comparison of the evolution of these two forest blocks shows that between 15,000 and 20,000 B.P. a phase of high aridity occurred along with a synchronous regression of the forest in Africa (see earlier discussion) and Amazonia (Absy et al. 1991; Servant et al. 1993; Van der Hammen and Absy 1994). From about 15,000 years ago phases of recolonization began in both the Amazonian and African forest blocks; the forests in both regions are presumed to have totally reestablished at the same time, around the beginning of the Holocene (c. 9,500 B.P.; Sifeddine et al. 1994). After that, while the forest in Africa was maintained or expanding (Maley 1991, 1996a), there appears to have been a new regression of part of the Amazonian forest from about 8,000 B.P. This was especially marked at Carajas, the region at the

southeast periphery of the forest block, which at present is less humid than the rest of the forest (Absy et al. 1991; Servant et al. 1993) and where the regression reached its peak around 5,000 B.P. In Ecuador, however, in the more humid piedmont region in the Andes, the forest existed from 7,000 B.P. onward (the base of the core was studied by Bush and Colinvaux [1988]). The Amazonian forest around Carajas recolonized to reach limits near the present ones about 3,700 B.P., although there were some fluctuations (Sifeddine et al. 1994). Evidence from sediments has shown that the regression of the forest in the Carajas region was characterized by the development of *Piper*, a pioneer forest taxon, and a great abundance of fine carbonized plant debris, demonstrating that fire played a role in the creation of openings in the forest (Absy et al. 1991; Martin et al. 1993; Sifeddine et al. 1994).

Remarkably, at the time the Amazonian forest had again reached an extension close to the present-day one, at c. 3,700 B.P., rainfall declined abruptly in the western part of the African forest block, as shown by a dramatic 120 m regression of Lake Bosumtwi in Ghana (Talbot et al. 1984). The forest around this lake was not directly affected, but the peripheral forests retreated, especially in present-day Benin and Togo, forming a new gap (the Dahomey interval, or Dahomey Gap) in the forest strip north of the Gulf of Guinea (Maley 1991). In the central part of the forest block, pollen data from lakes in Cameroon (for Barombi Mbo, see Maley 1992; Giresse et al. 1994; for Mboandong, see Richards 1986; for Ossa, see Reynaud-Farrera et al. 1996; for Njupi, see Zogning et al. 1997), western Congo (Elenga et al. 1992, 1994; Schwartz 1992), southeastern Uganda (Taylor 1990), and the region north of Lake Tanganyika (Vincens 1993) demonstrate that a pronounced decline of forest pollen types occurred relative to those from open environments (mainly Gramineae), starting around 3,000–2,800 B.P. and peaking around

2,500–2,000 B.P. (Maley 1992, 1997; Maley and Brenac 1998a; see also figure 5.1).

In the eastern part of the Guineo-Congolian Domain, similar data have been obtained in Ituri, a forest sector in the northeast Congo Basin (T. Hart and J. Hart, pers. comm.; Hart et al. 1996). Identification and dating of charcoal (R. Deschamps, pers. comm.) from the upper part of the soil in the region of Epulu, located more than 100 km from the present forest-savanna boundary, has demonstrated that over the past 2,500 years there have been frequent fires, which have burned forest trees. Furthermore, the charcoal of two trees typical of savanna environments was found to occur there between c. 2,500 and 2,000 B.P. (Hart et al. 1996).

Runge (1995, 1997) studied soil profiles between Osokari and Walikale along the road from Kisangani to Bukavu to the south of Epulu. Fossil tree trunks were found in the saprolite below the main "stone line" which gave radiocarbon dates of 17,000–18,000 B.P. By comparing these data with those obtained in the deep-sea fan (delta) of the Congo river (Giresse et al. 1982), one can conclude that this stone line probably formed during another major arid phase at the end of the Pleistocene, around 11,000 B.P. (Maley 1996b; Maley and Brenac 1998a). Runge (1995, 1997) described another detrital and coarse layer containing charcoal dated to 2,000 B.P., similar to a layer observed in western Congo at Kakamoeka in the Mayombe (Maley and Giresse 1998).

Pollen and sedimentological data from other parts of tropical Africa confirm that the aforementioned facts are not isolated, and demonstrate that a phase of generalized aridification affected the majority of the African tropics, starting around or a little after 3,000 B.P. and culminating between 2,500 and 2,000 B.P. This arid phase affected the savannas of the Sahelian zone (Chad and Senegal: Maley 1981; Lézine 1989) and the more southern woody savannas of Cameroon and Nigeria, and is associated with intensive erosion. The term "climatic pejoration" is often used to describe this arid phase, because it seems to have resulted from a more marked seasonality of rainfall, probably due to an increase in squall lines (large cumuliform clouds) to the detriment of other types of rain (that is, mainly "monsoon" rains) associated with a hot, evaporating atmosphere (see Maley 1981, 1982, 1997; Maley and Elenga 1993; Maley et al., in press). As a result of this increase in squall lines there was probably a reduction in the length of the rainy season but probably not in the amount of annual precipitation (see Maley and Brenac 1998a; Maley et al., in press). Such phenomena have been observed in certain recent years (for instance, in 1983) and have been linked to large variations of sea-surface temperatures in the Gulf of Guinea (Suchel 1988; Mahé and Citeau 1993; Maley and Elenga 1993; Maley 1997).

The available sedimentological and pollen data for the end of this climatic pejoration, about 2,000 years ago, show that a humid climate re-established in tropical Africa and that rain forest vegetation recovered. However, this recovery was very slow relative to the speed at which the forest retreated between 2,800 and 2,000 B.P., and the recovery was associated with large fluctuations and setbacks (Maley and Brenac 1998a).

The intense erosion that occurred during the climatic pejoration resulted in the deposition of coarse sediments constituting the base of a "low terrace" in valley bottoms (Unit 1 below). This terrace has been observed in the woody savannas of the Chad Basin as well as in the forest zone of south Cameroon, Gabon, Congo, and DR Congo (Maley 1981, 1992; Maley and Brenac 1998b). During the past two millennia there has been further accumulation in the low terrace, which can be divided into four units (for more details, see Maley and Brenac 1998b):

1. Basal unit consisting of very coarse sediments (c. 2,800–2,000 B.P.)
2. Fine sediments frequently containing fossil wood and charcoal (c. 2,000–1,200 B.P.)
3. More sandy sediments frequently eroding Unit 2 (c. 1,200–800 B.P.)
4. Fine to sandy sediments (c. 800 B.P. to recent centuries)

A new phase of erosion intervened in recent centuries which became particularly strong at the beginning of the twentieth century (Maley 1981).

THE ROLE OF FIRE

The role played by fire, especially in the forest, must have been important during the climatic pejoration discussed above. The situation in Africa was probably similar to the the situation in Carajas, Amazonia, described earlier. At present, fires started by humans sweep the peripheral savannas but do not penetrate the forest edge (Swaine 1992). They are stopped by the dense, low vegetation (lianas, ferns, and shrubs) that occurs along the forest edge and remains green during the dry season (Spichiger and Pamard 1973). However, in unusually arid years, when the dry season is extended, fires can penetrate the peripheral semi-deciduous forests. Hall and Swaine (1981) and Swaine (1992) describe a "fire zone" in Ghana, where fires penetrate forests adjacent to savannas approximately every fifteen years. In 1983 there were many reports of an exceptional propagation of forest fires in the Ivory Coast (Bertault 1990), Ghana (Hawthorne 1991; Swaine 1992), and the Nyong valley of Cameroon (Amougou 1986). Contemporary examples of spontaneous fires under similar conditions occurred in Borneo during the very dry El Niño year of 1982–1983, when fires raged through normally fire-resistant humid evergreen forest (Goldammer and Seibert 1990). Nevertheless, the propagation of fires within the African forest block is an uncommon phenomenon, as is the case for natural fires started in the forest by lightning, which generally remain confined (for example, Tutin et al. [1994] observed a *Pterocarpus soyauxii*, 40 m high, which burned in a forest in central Gabon).

In the rare event when a fire affects part of the forest, forest regeneration is rapid (assuming that no other fire occurs during the following months or years; see Swaine 1992), with a characteristic phase when large monocotyledons belonging to the Marantaceae and Zingiberaceae dominate, smothering pioneer trees, which are much reduced in density (De Foresta 1990; White, this volume, chapter 11). This stage corresponds to "clear forests" (forests with open canopy and few mature trees), which have been described by various authors and which sometimes cover considerable areas, as in Lopé (in Gabon), northern Congo, and the extreme east of Cameroon (see Letouzey 1968, 1985; Maley 1990). It has been suggested that the development of these "Marantaceae forests" reflects the passage of forest fires (Swaine 1992). However, these clear forests also develop naturally during the recolonization of savannas by the forest, as in Lopé, Gabon (White 1992, 1995, and this volume, chapter 11) or in the Mayombe, Congo (De Foresta 1990). The large areas of peripheral savannas that presently surround the forest block in the north and the south, almost without interruption, and which are characterized by very low density of savanna trees (Letouzey 1968, 1985; White 1983), might be the consequence of successive retreats of the forest block during the climatic pejoration that occurred in the late Holocene, between c. 3,700 and 2,000 B.P. (Maley et al., in press). The frequent occurrence of fires during this period, especially between 2,500 and 2,000 B.P. and also later in eastern DR Congo (see above) and in central Gabon (see Oslisly, this volume), may have destroyed the young regenerating forest dominated by the Marantaceae, Zingiberaceae,

and pioneer trees, and thus could explain the occurrence of grass savannas observed today, where typical savanna trees seem to have had difficulty becoming established because of the frequency of fires.

Whereas fire destroys forests more or less instantaneously, their recovery over vast areas is a slow process. Wherever accurate observations have been made at the periphery of the African forest, recolonization of savannas has been shown to be under way, particularly since the beginning of the twentieth century (Maley 1990). This phenomenon has surprised observers in that it takes place despite the annual propagation of fires started by humans, and, even more astonishing, traditional agricultural practices and livestock passages further this phenomenon by removing vegetation cover and hence limiting the propagation and the intensity of fires. These processes have been well documented over the past forty years in the V-Baoulé, Ivory Coast (see Miège 1966; Spichiger and Pamard 1973; Blanc-Pamard and Peltre 1984; Gautier 1990), and more recently in the Lopé Reserve (White 1995) and in Odzala at the northern end of the Bateke Plateau (Dowsett-Lemaire 1996). In Cameroon south of the Adamaoua, the process was described in detail by the highly experienced botanist Letouzey (1968, 1985). The phenomenon of forest colonization, which he observed over more than forty years, occurs mainly in fallow areas after abandonment of the fields by the farmers, without an intermediary stage of savanna vegetation, as has often been suggested. In effect, temporary agricultural occupation promotes forest development in certain regions. This phenomenon of afforestation of savannas can be seen clearly by comparing several sets of aerial photographs and satellite images and occurs over a large area of up to one million hectares south of Adamaoua, in the basins of the Kadei, Lom-Pangar-Djerem, and Ndjim-Mbam-Noun-Kim (Letouzey 1985; see

also Youta-Happi 1998). A comparable large forest extension also occurred in Central African Republic around Bangassou (TREES Project 1998). In conclusion, it appears that in the twentieth century the tropical forests still had a considerable dynamism. Thus it is reasonable to suggest that the extensive peripheral band of semi-deciduous forest in southern Cameroon has developed over the past two millennia as a result of establishment and development of pioneer forest formations.

Humans and the Changes In the Environment

The possible role of humans in forest retreat or fragmentation through the Holocene must be considered (here I shall discuss only Africa). During the upper Quaternary, groups of pygmies seem to have wandered throughout the African forest, but because of their lifestyle and their low numbers, they leave almost no trace (Bahuchet 1993). In contrast, Bantu farmers have cultivation practices that modify vegetation locally (the slash-and-burn method), and they may leave various archaeological traces (stone or iron tools, or pottery). Therefore, it is important to know how long the forest block of central Africa has been inhabited by farmers, following its recovery at the beginning of the Holocene. In a synthesis of the archaeology of the central Congo Basin, Eggert (1992, 1993) states that the oldest pottery level, the Imbonga Horizon, occurred between approximately 2,500 and 2,000 B.P. Further to the west, in coastal regions of Gabon, remains of settlements associated with archaeological remains of the Neolithic kind appeared as early as 4,000–5,000 B.P. (Clist 1990; Oslisly and Peyrot 1992; Oslisly and Fontugne 1993). However, the first period of relatively high density of settlements in Gabon occurred later and corresponds with the introduction of iron technology, probably by Bantu, starting approximately 2,500 B.P. (Oslisly and Peyrot 1992; Oslisly and Fontugne 1993; see also Oslisly, this volume).

Schwartz (1992) reviewed archaeological evidence for the region comprising south Cameroon, Gabon, and the forests of western Congo. He found evidence that metallurgy spread to all the areas between Yaoundé and Pointe-Noire (1,000 km) between approximately 2,250 and 2,100 B.P. Such a rapid spread of this new technology over the course of one or two centuries seems incompatible with the presence of dense, uninterrupted forest cover (Schwartz 1992). Schwartz hypothesized that the rapid spread of Bantu peoples carrying iron would have been possible only if there had been multiple openings in the forest block as a result of paleoclimatic changes during the late Holocene. The climatic pejoration described above, which affected all of central Africa and which culminated between 2,500 and 2,000 B.P., corresponds well with the period of iron expansion and also with the first pottery level (the Imbonga Horizon) in the central Congo Basin (Eggert 1993). Thus, it can be assumed that the numerous openings and regressions of the forest caused by this unfavorable climatic phase, which was also associated with the frequent occurrence of forest fires, might have favored and even caused this migration of the Bantus. However, from approximately 2,000 B.P. onward, when the climate became humid again, the available data show that the forest recovered even though the Bantu continued to live in the African forest and to practice their agricultural techniques.

Several pollen analyses have demonstrated that the period spanning the last two to three millennia was also characterized by increased abundance of the oil palm (*Elaeis guineensis*) (Elenga et al. 1992; Vincens 1993; Reynaud-Farrera et al. 1996; Bengo 1996; White et al. 1996; Zogning et al 1997; Maley and Brenac 1998a, 1998b; Maley and Giresse 1998; Maley, in press; J. M. Fay, pers. comm.). The oil palm is an indigenous tree whose typical pollen has been identified in deposits dating to the Eocene in

Guinea/Konakry and then to the Miocene from Senegal to Nigeria and Uganda (Maley and Brenac 1998a, 1998b). During the Holocene a first large extension phase occurred between approximately 2,800 and 2,200 B.P., with a second culminating between approximately 1,200 and 700 B.P. These two main extension phases were associated with large disturbances within the rain forest initiated by climatic changes that were linked to erosive phenomena. The two extension phases were a result of the pioneer nature of the oil palm, which becomes abundant in the forest-savanna mosaic and in regenerating forests (Letouzey 1968; Swaine and Hall 1986). Although the oil palm is extensively used by African peoples, there is little or no tradition of cultivation of this species (Zeven 1967; Eggert 1993). Instead, bunches of palm nuts are collected from naturally occurring palm stands, which may be managed to some extent by clearing of the understory (see Haxaire 1996). While collecting bunches of palm fruits, humans accidentally drop seeds, hence contributing to the regeneration of the oil palm, which is always prolific, and to the welfare of various species of animals (chimpanzees, tauracos, parrots, rats, and so on; see Schnell 1952). The true domestication of the oil palm is a recent phenomenon (Zeven 1972). Hence, it seems safe to conclude that the traditional exploitation of the oil palm corresponds to a "proto-culture" closely resembling the hunter-gatherer society of modern pygmies. It seems safe to suggest that the natural periods of expansion of the oil palm over the past three millennia were particularly favorable for the human populations who later undertook the Bantu migration in west central Africa.

The aridity of the climate during a period of global cooling was the main reason for the large forest fragmentations between 15,000 and 20,000 B.P. The forest retreats and fragmentations that occurred in Amazonia and in Africa during different periods of the Holocene, a rel-

atively warm period, are also of climatic origin, but in several areas the propagation of large fires must have speeded up this process. In the African forest block, the last extensive regression seems to have occurred between 2,500 and 2,000 B.P., when deep openings appeared particularly in areas with the highest climatic variability. It is possible that the fragmentation of the forest block in the Cameroon-Gabon-Congo region provoked some of the Bantu migrations. The mosaic aspect of the present-day forests of Congolian type (characterized by a mixture of evergreen and semi-decidu-ous forests) and even of some evergreen Biafran formations, like those in Cameroon (see Letouzey 1985; Maley 1990), probably date back to the late Holocene and may be linked to these phenomena. Climatic trends that were out of phase in Africa and Amazonia during the Holocene were linked to fluctuations of sea-surface temperatures (Maley 1989, 1991, 1995, 1997; Fontaine and Bigot 1993), to the zonal atmospheric circulation of Walker type (see Flohn 1984, 1986), and especially to phenom-ena of the El Niño type in the Pacific and trop-ical Atlantic Oceans (Martin et al. 1993; Maley 1997; Maley et al., in press).

Climatological models of global warming during the twenty-first century (see Stager, this volume) predict that a 4°C rise in global air temperature would result in a 30% increase in evaporation with only 12% more rain in inland parts of tropical Africa (Rind 1995). This could lead to the catastrophic retreat and destruction of the African rain forest, as occurred between 2,800 and 2,000 B.P., during a warm climatic phase that is thought to have resulted in a large increase in convective rainfall, particularly in equatorial Africa (see the earlier discussion and Maley 1997; Maley et al., in press).

The devastation of vast areas of dense for-est in Indonesia and Amazonia during the sum-mer of 1998 are thought largely to be the result of a very strong El Niño climatic event result-ing from unusually warm sea-surface tempera-tures. A similar strong El Niño event occurred in 1983. Unusual climatic conditions associ-ated with these two El Niño events resulted in reduced rainfall and, in particular, an extended dry season, which allowed savanna fires to pen-etrate deeply into the forest, causing consider-able damage. Such savanna fires are generally blocked at the forest edge by a community of pioneer and lianescent plant species. In unusu-ally dry years these plants perish, and in some places fires penetrate the forest edge and burn into the dry leaf litter in the forest understory. Observations in Indonesia and in Ghana (see Hawthorne 1991; Swaine 1992) have shown that areas that have been subject to commercial logging are particularly susceptible to fire at these times. It is therefore a priority for conser-vationists and forest managers alike to under-take further studies of the fire risk in logged forests and to evaluate the possibility of leaving unlogged areas to act as natural firebreaks within blocks of logged forest (see also the rec-ommendations in Stager, this volume).

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