5

Rainforest responses to past climatic changes in tropical Africa

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5.1 INTRODUCTION

In Africa the lowland rain forest occurs under significantly drier conditions than in other continents, within an average precipitation of 1,600 to 2,000 mm/yr, although higher rainfall is observed around the Atlantic coast of Cameroon, Gabon, and in the Central Zaire Basin. Seasonal distribution of precipitation is far from being uniform (White, 1983). Variations in the duration of the dry season follow distance from the equator in both hemispheres and also along a west-to-east gradient. The Biafran Gulf is the only region where the minimum monthly precipitation value always exceeds the 50-mm threshold for the driest month, therefore experiencing no dry season. However, great annual rainfall variability is registered at most of the meteorological stations. Mean monthly temperatures remain constant. Inside the area occupied by the African rainforest, topography is not uniform. Low elevations are found in the coastal Atlantic plain, and in the Zaire Basin, that lie below 400 m. The undulating plateaus of Gabon and Cameroon, generally located between 600 and 800 m, can reach up to 1,500 m, whereas the eastern part of the Zaire Basin joins the slopes of high mountains above 2,000 m bordering the Rift in the Kivu region. Mount Cameroon exceeds 4,000 m in elevation.

The geographical distribution of plant species is complex (Richards, 1981). Relationships between geographical plant distribution and ecological variables—such as rainfall, available moisture, and seasonality—within the Guineo-Congolian domain are far from being well-established, although there are significant variations of these factors inside the areas occupied by rainforest. The only comprehensive review relies on the vegetation-mapping done for Africa. However, the classification of the different types (or variants after White, 1983) was difficult. This is partly because variation in floristic composition, physiognomy, and phenology is largely gradual and continuous (Aubreville, 1951). This chapter concerns the oriental part of the Guineo-Congolian domain, where the degree of endemism is high, representing 80% of the total 8,000

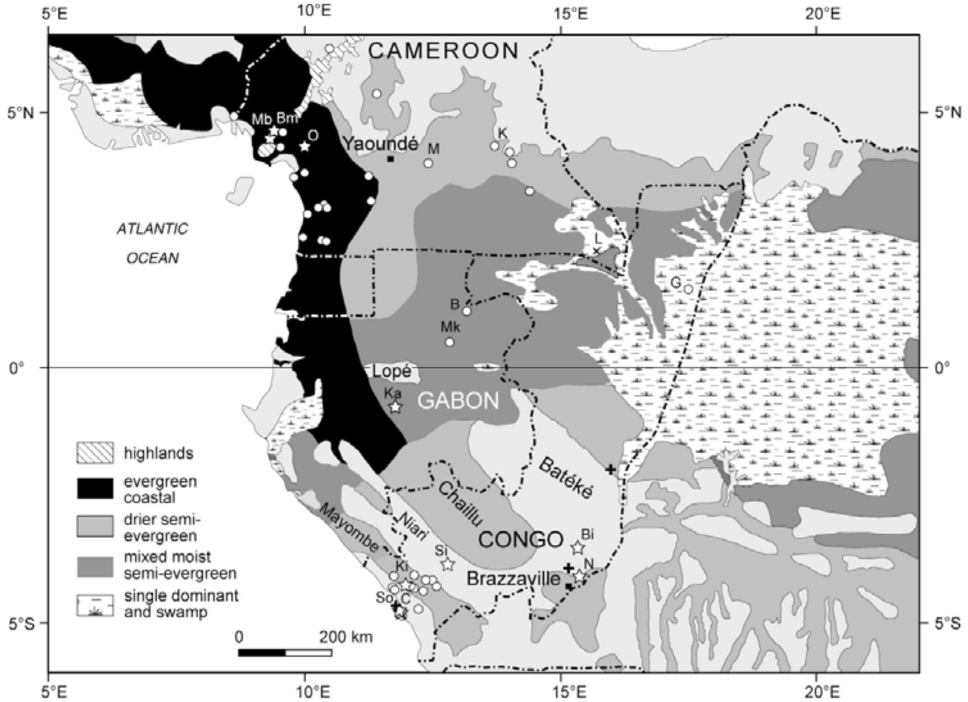

Figure 5.1. Distribution of different vegetation units within the Guineo-Congolian rainforest (6°S and 6°N) (after White 1983; Letouzey, 1965, 1985) with location of modern (○) and fossil pollen (*) and wood sites (+). Bm: Barombi Mbo; Mb: Mboandong, O: Ossa; M: Mengang; K: Kandara; L: Lobéké; B: Belinga; Mk: Makokou; G: Guibourtia; Ka: Kamalete; Bi: Bilanko; N: Ngamakala; Si: Sinnda; Ki: Kitina; C: Coraf; So: Songolo.

species and 25% of the genera, with the greatest number of endemic genera being found among the Leguminosae–Caesalpiniaceae. We present modern and fossil pollen data relating pollen and plant distribution within the present day and for the latest Quaternary (Figure 5.1).

5.2 VEGETATION UNITS WITHIN THE GUINEO-CONGOLIAN RAINFOREST

5.2.1 Hygrophilous coastal evergreen forest

Syn.: forêt biafréenne à Caesalpiniaceae (Letouzey, 1968), forêt dense humide sempervirente à Légumineuses (Aubreville, 1957–58), wet evergreen forest (Hall and Swaine, 1981).

The evergreen Guineo-Congolian wet forest is located between 2°S and 6°N in areas that receive 2,000 to 3,000 mm/yr rainfall, without or with a reduced dry season.

The atmospheric humidity is very high throughout the year. Most individuals of most tree species are evergreen and shed their leaves intermittently. *Lophira alata* (Ochnaceae) is one of the most abundant of the widespread taller trees, although it is not confined to this type. *Lophira alata* is light-demanding with drought-sensitive seedlings, with the potential to be a large tree that can live for several centuries. Historical remains (slave rings, pottery, charcoal, etc.) observed in excavations after deforestation for *Hevea* plantations and road cuttings indicate that such forest now occurs in areas that were cultivated perhaps a few centuries ago (Letouzey, 1968).

At its most typical sites, the hygrophilous coastal evergreen forest rainforest is rich in Caesalpinioideae, many of which are gregarious and include species of various genera such as *Anthonota*, *Brachystegia*, *Julbernardia*, *Berlinia*, *Monopetalanthus*, associated with *Cynometra hankie* (Caesalpiniaceae) and *Coula edulis* (Ochnaceae).

5.2.2 Mixed moist semi-evergreen

Syn.: forêt congolaise (Letouzey, 1968, 1985), forêt dense humide sempervirente à Légumineuses (Aubreville, 1957–58), forêts semi-caducifoliées sub équatoriales et guinéeennes (Lebrun and Gilbert, 1954).

Most Guineo-Congolian rainforest belongs to the mixed moist semi-evergreen type. It occurs on well-drained soils and covers most of the area at low elevation (600–700 m), throughout the region, comprising northeast Gabon, northern Congo, southeast Cameroon, and most of the Zaire Basin, except for the wettest and driest extremities. Mean annual rainfall is mostly between 1,600 and 2,000 mm and is well-distributed. The prevalent vegetation is moist semi-evergreen of mixed composition, and rich floristically. Some species are evergreen, but many are briefly deciduous. No detailed description of this type of forest exists except for the *Oxystigma oxyphyllum* (Caesalpiniaceae) and *Scorodophloeus zenkeri* (Caesalpiniodeae) association particularly significant in the Zaire Basin (Lebrun and Gilbert, 1954). Some of the most abundant emergent species—for example, *Canarium schweinfurthii* (Burseraceae), *Piptadeniastrum africanum* (Mimosoideae), *Ricinodendron heudelotii* (Euphorbiaceae), *Terminalia superba* (Combretaceae)—are also found in secondary forests of the dry peripheral semi-evergreen type. In Cameroon the forest of this type has few species of Caesalpiniaceae (except *Gilbertiodendron dewevrei* which can form pure stands), but includes large and tall *Baillonella toxisperma* (Sapotaceae) which exhibit no regeneration, suggesting that the over-mature forest is disintegrating, and being locally invaded by dry evergreen (semi-deciduous) forest (Letouzey, 1968).

5.2.3 Single-dominant moist evergreen and semi-evergreen

Several authors have described single-dominant forests which form isolated stands of a few hectares in extent inside the mixed moist semi-evergreen forest or islands which occur in a broad aureole surrounding the Zaire Basin (White, 1983). The upper stratum is formed by tall trees, usually 35–45 m high, that belong to a few or a single species (Evrard, 1968). Among the dominant species, *Gilbertiodendron dewevrei* (Caesalpiniaceae) from southeast Cameroon is normally completely evergreen, whereas the more widespread *Cynometra alexandrii* (Caesalpiniaceae) is irregularly deciduous. In Uganda, *Cynometra* trees, particularly abundant above 700–800 m, shed their leaves simultaneously, and *Julbernardia* (Caesalpiniaceae) inside the Zaire Basin is said to behave in a similar fashion. In the single-dominant moist evergreen forest, heliophitic trees are rare. Lianas and giant monocotyledonous herbs are poorly represented.

5.2.4 Drier peripheral semi-evergreen forest

Syn.: forêt dense humide semi-décidues de moyenne altitude (Letouzey, 1968), forêts semi-caducifoliées, forêts semi-décidues à Malvales et Ulmacées (Aubreville, 1957–58).

This type of forest extends geographically between the moist evergreen forest and occurs in the form of two bands running transversely across Africa to the north and south of the moister forests described above at the limit of areas occupied by savanna. They were called "peripheral" (White, 1983) and have a patchy distribution in the Lake Victoria basin. Rainfall is between 1,200 and 1,600 mm/yr, with a bimodal distribution. The dry season lasts 1 or 2 months during which relative humidity remains high. Mean annual temperatures range from 23.5 to 25°C. Most individuals of the commoner larger tree species are deciduous and lose their leaves during the dry season. But, any individual is deciduous for a few weeks only. This forest type has a distinct floristic composition and includes species virtually absent from the wetter types—such as *Afzelia africana* (Caesalpiniaceae), *Aningeria altissima* (Sapotaceae), *Cola gigantea* (Sterculiaceae). Some other species—such as *Celtis mildbraedi* and *C. zenkeri* (Ulmaceae), *Holoptolea grandis* (Ulmaceae), *Sterculia oblonga* (Sterculiaceae) that are important components of the dry peripheral semi-evergreen forest—also occur in mixed moist semi-evergreen forests. In Cameroon the "drier peripheral semi-evergreen forest" or forêt dense semi-decidue de moyenne altitude (Letouzey, 1968) is characterized by the dominance of *Cola*, *Sterculia*, *Celtis*, and *Holoptolea grandis*, together with *Piptadeniastrum africanum* (Mimosaceae), *Funtunia* (Apocynaceae), and *Polyalthia* (Annonaceae). *Terminalia superba* (Combretaceae) and *Triplochiton scleroxylon* (Sterculiaceae) are two rapidly growing, light-demanding, valuable timbers that can regenerate on abandoned farmland.

Besides the main four types of rainforest described above, there are different vegetation types that have also been mapped as separate units. Secondary forests, swamp forests, and a mosaic of forests and grasslands can be found in any of the four main types of forests described before (White, 1983).

5.2.5 Secondary rainforest

Outside the forest reserves, much of the remaining forest occurs on land that has been formerly cultivated and is therefore considered secondary. This regrowth contains abundant heliophytes and pioneers that grow quickly and have a short life; *Tetrorchidium* (Euphorbiaceae) and *Trema* (Ulmaceae) are characteristic, while *Musanga cecropioides* (Moraceae) is strictly Guineo-Congolian in distribution.

5.2.6 Swamp forest

Swamp forests, including riparian forest, occur throughout the Guineo-Congolian region wherever the conditions are suitable. These forests are floristically distinct, but have a similar appearance to rainforest with the tallest trees reaching 45 m in height. The main canopy, however, is irregular and open. Inside the clearings, climbing palms *Eremospatha* and *Calamus*, shrubs, and lianas fill the gap. Forest types with Marantaceae and *Gilbertiodendron* are located between the western side of the inundated wet evergreen forests and the mixed moist semi-evergreen forest (forêt congolaise).

5.2.7 Edaphic and secondary grasslands

On hydromorphic soils, edaphic grasslands surrounded by forest represent a transitory stage in the succession from aquatic vegetation to forest. The origin of such grassland patches is still controversial. They may be maintained by frequent fire, but they also occupy superficial soils on rocks that are periodically inundated (Koechlin, 1961). At its northern and southern limits, the Guineo-Congolian rainforest is burned at least once a year. A mosaic of patches of secondary grassland including scattered fire-resistant trees and secondary forest clumps locally replace the forest. In this situation, the mosaic can regenerate into forest. There are also patches of secondary grasslands inside the Guineo-Congolian region (Descoings, 1976), but most of them are distributed at the transition with the Sudanian zone in the north and with the Zambezian zone in the south. They show considerable local variation in floristic composition.

5.2.8 Transitional and Afromontane evergreen forests

In Cameroon, close to the border with Nigeria, Afromontane forests show a great resemblance to those from East Africa. Two distinct altitudinal horizons are distinguished. The lower, from 800 to 1,800 m, is characterised by *Podocarpus latifolius* (Podocarpaceae) (syn. *P. milanianus*) and is associated with *Olea capensis* (Oleaceae) (syn. *O. africana*). The upper, from 1,800 to 2,800 m, contains *P. latifolius* together with *Prunus africana* (Rosaceae), *Myrsine melanophloeos* (Myrsinaceae), and *Nuxia congesta* (syn. *Lachnopylis*, Loganiaceae). In eastern Zaire a transitional forest observed between 1,100 and 1,750 m includes tree species of the Afromontane forest among *Aningeria* (Sapotaceae), *Entandophragma* (Meliaceae), *Mitragyna* (Rubiaceae), and *Ocotea* (Lauraceae), associated with components of the lowland forest—such as *Cynometra alexandrii* (Caesalpiniaceae), *Pycnanthus angolensis* (Myristicaceae)—and some endemics, specific to the transitional forest. The species *Strombosia grandiflora* (Olacaceae), *Symphonia globulifera* (Olacaceae), *Uapaca guineense* (Euphorbiaceae), and *Parinari* sp. (Chrysobalanaceae) are ecological transgressors between lowland and Afromontane forests (White, 1983).

5.3 MODERN POLLEN RAIN STUDIES

No systematic study of modern pollen rain within the African rainforest has addressed the relationship between the distribution of vegetation types and climatic variables. Indeed, in equatorial Africa, this vegetation and climate pattern is very complex. The lack of ecological work and the long-standing, old belief of "equatorial climatic stability" might have discouraged such studies. New modern pollen rain data from tropical evergreen and deciduous forests of southwest India (Barboni *et al.*, 2003) should encourage them now. In India, the western coast supports many different types of forests under a single monsoonal regime, with a south-to-north increased gradient of rainfall, a west-to-east increase in dry season length (seasonality), and temperature decrease along highland slopes reaching up to 2,500 m in elevation. Ecological studies showed that these factors indeed influence the distribution of species and that of vegetation types, following the different bioclimatic regions (Pascal *et al.*, 1984). Modern pollen assemblages reproduce the pattern of bioclimatic regions and associated vegetation-mapped units. The results enable a clear distinction of the different types of forests and their associated pollen markers (Bonnefille *et al.*, 1999; Barboni and Bonnefille, 2001; Anupama *et al.*, 2000). In Africa, recent studies on modern pollen rain of the Guineo-Congolian region provides a first understanding of pollen production and markers of the different types within the rainforest. Many of the main types of vegetation (Figure 5.1) have now been sampled for modern pollen, although the mixed moist semi-evergreen forest of the Zaire Basin remains poorly documented. Detailed investigations were made in connection with floristic "relevés" in the evergreen rainforest of Cameroon and the semi-evergreen from southern Congo. Because different sampling procedures and different plot sizes were used by the various authors, and because original counts from Cameroon have not been included yet in the "African Pollen Data Base", it was not possible to provide a single synthetic diagram for the region's rainforest. Therefore, the presentation of the results on modern pollen studies will be organized according to geographical regions and vegetation-mapping units.

5.3.1 From coastal evergreen to drier semi-evergreen forests in Cameroon

In Cameroon, modern pollen rain studies mainly concern the evergreen and coastal hygrophilous forests ("biafréenne à Caesalpiniacées"), with a few samples collected within the mixed moist semi-evergreen "forêt congolaise" and the drier peripheral semi-evergreen ("forêt semi-caducifoliée") (Letouzey, 1968). Sampling for pollen analysis and counts of tree species over 5 cm in diameter were done within 20 × 20-m plots (Reynaud-Farrera 1995). The pollen counts of several plots have been used by the author to draw a diagram to compare plant (Figure 5.2a) and pollen frequencies of the different taxa (Figure 5.2b).

An interesting result from this work is that in all the samples collected inside forest plots, the ratio of arboreal pollen (AP)—including all trees and shrubs—calculated versus total pollen counts—excluding the spores—always exceeds 75% (Figure 5.2a). The samples showing the lowest AP values were collected in open vegetation areas such as at Kandara near the limit between the peripheral semi-evergreen and the forest/grassland mosaic. Because abundant tree or climber species among common tropical families—such as Annonaceae, Apocynaceae, Violaceae (except *Rinorea*), most Myristicaceae (except *Pycnanthus*), Chrysobalanaceae, Olacaceae (except *Strombosia*), Clusiaceae (except *Symphonia*), etc.—are not represented by their pollen, this was not expected *a priori*. A good correspondence between the total arboreal pollen and the tree coverage of the wet evergreen and semi-evergreen forests in Cameroon confirms results from other tropical regions in Africa (Bonnefille *et al.*, 1993). This interesting result shows that the classic distinction between arboreal pollen (AP) and non-arboreal pollen (NAP), used in the interpretation of pollen analysis from the temperate region, is also valid for palynology in the rainforest region. In the modern pollen study from Cameroon, the high number (279) of pollen taxa identified within the soil samples reflects the great floristic diversity of evergreen forests. Because of the strong heterogeneity in the spatial distribution of the tree species, the occurrence of many intermediate forest types, and the unavoidable bias between over- and under-representation of the pollen of many tropical families, a greater number of pollen samples, more evenly distributed within the different vegetation types, would have been advantageous. Nevertheless, despite evident discrepancies between vegetation cover and pollen representation, there is a certain degree of agreement between the listed plants within ecological plots and the pollen types found in the surface soil samples (Figure 5.2c). The pollen assemblages from the different forest types appear clearly distinct from each other, enabling one to recognize the different forest types. Joint occurrences of *Saccoglottis* and *Lophira*, together with "*Berlinia*-type" pollen including many Caesalpiniaceae, are good markers of the coastal Biafran forest, in agreement with the dominant trees. Pollen of *Irvingia* (Irvingiaceae), *Lophira*, *Diospyros* (Ebenaceae), and Sapotaceae (which might include *Baillonella toxisperma*, the pollen of which cannot be identified at the generic level), show highest representation in the mixed semi-evergreen "Congolese" forest. The *Pycnanthus* (Myristicaceae) and *Piptadeniastrum* (Mimosoideae) pollen association characterizes the dry evergreen (semi-deciduous) forest, although *Pycnanthus* alone can be abundant within the coastal Biafran forests. *Macaranga*, *Alchornea*, *Celtis*, and sometimes *Uapaca* tend to be over-represented in the pollen rain. The two pollen assemblages corresponding to the mountain forest are well-characterized by the association of *Podocarpus*, *Olea*, *Nuxia*, and Ericaceae pollen (Figure 5.2c).

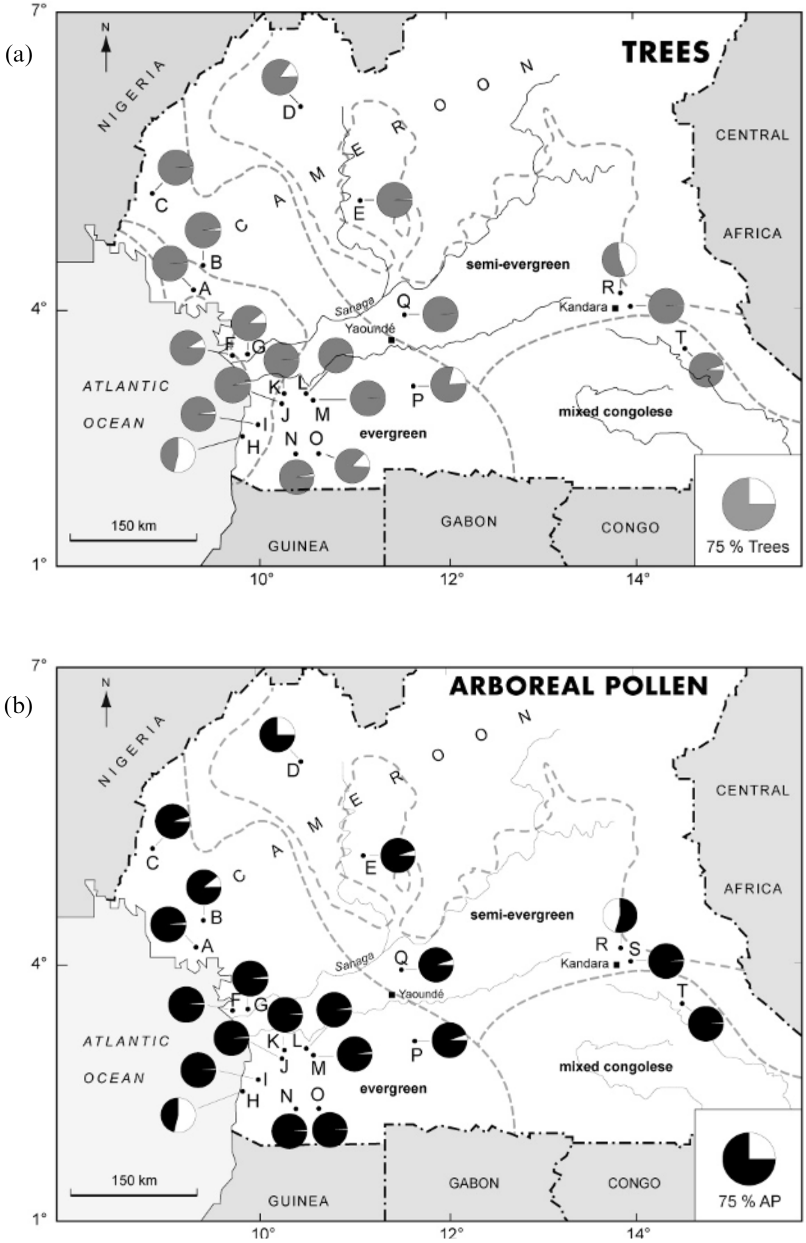

Figure 5.2. Modern pollen rain from coastal evergreen forests, mixed moist semi-evergreen, and drier semi-evergreen forests from Cameroon: (a) % of trees and shrubs among plants in the plots; (b) % of arboreal pollen in soil samples from the same plots. Some trees, identified in floristic counts, but not found as pollen are not illustrated here, such as the Marantaceae among the herbs, fern spores are not represented (% calculated versus pollen sum after excluding spores and Cyperaceae).

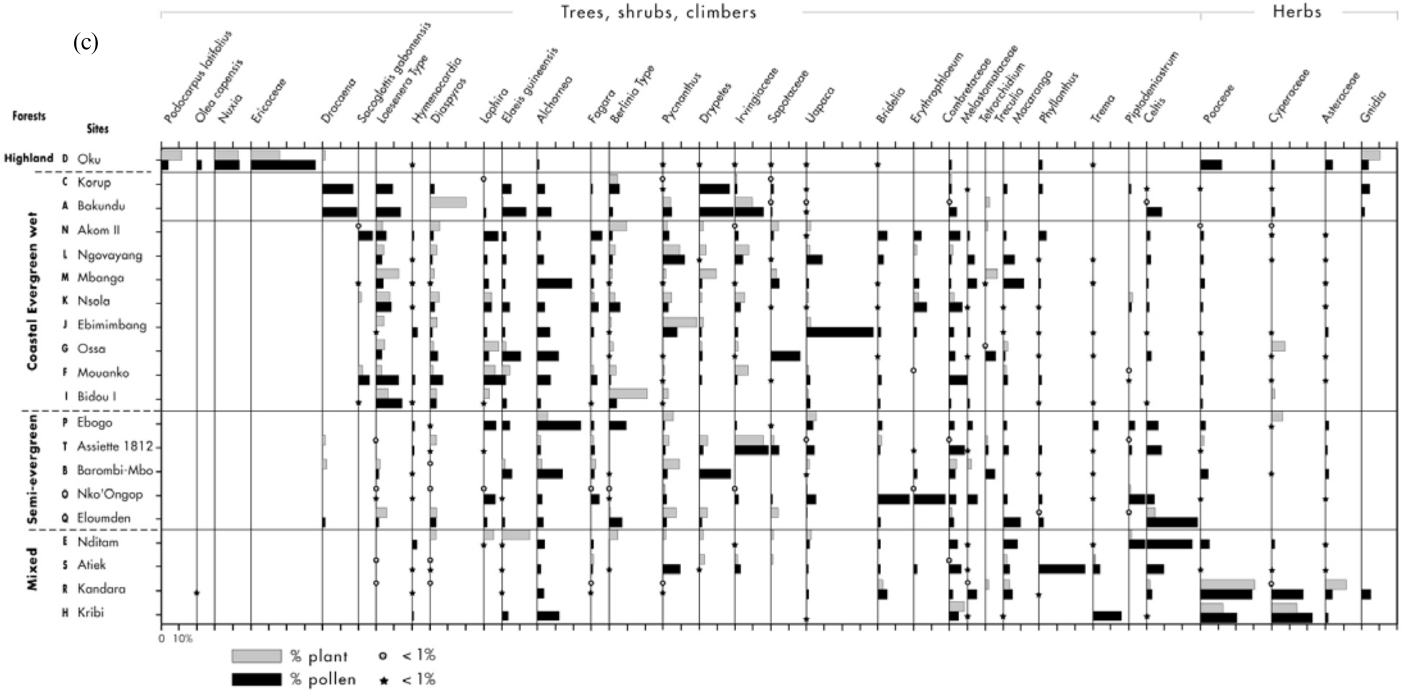

Figure 5.2 (*cont.*). (c) Distribution of relative frequencies of plant and pollen for the main taxa at pollen sampling sites as in (a) and (b) (after Reynaud-Farrera, 1995).

5.3.2 Mixed moist semi-evergreen forest

Mixed moist semi-evergreen forest was sampled in Central Gabon (Jolly *et al.*, 1996) during a preliminary palynological investigation in the forest reserves at Makokou (0°30′N, 12°50′) and Belinga (1°06′N, 13°10′E) (Figure 5.1). Located at 470 m elevation, near the Irvindo River, the Makokou forest is dominated by *Scorodophloeus zenkeri*, *Baphia*, *Dialium*, *Pancovia*, *Dichostemma glaucescens* among the Papilionaceae and *Polyalthia* among the Annonaceae (Caballe, 1986; Aubreville, 1967). Precipitation amounts to 1,500 to 1,700 mm/yr and mean annual temperature is over 24°C. At Makokou, various sampling strategies (line, diagonals, random, etc.) were tested to collect surface soil samples within 120 × 40 m forestry plots along a 1 km transect. No significant differences were shown between the pollen assemblages obtained with the different collecting methods. It was concluded that a random procedure represents the most parsimonious and the less time-consuming one. Random collection should certainly be made in regions where there is an urgent need to obtain modern pollen data within forests under threats of total disappearance. The pollen counts of 16 pollen assemblages from mixed moist semi-evergreen forest include 82 pollen taxa (Jolly *et al.*, 1996). The highest pollen frequencies come from Moraceae and Euphorbiaceae (mainly *Alchornea*), *Celtis*, Combretaceae, *Pausinystalia* (Rubiaceae), *Hymenostegia* (Caesalpiniaceae)—together with *Dacryodes* (Burseraceae) and *Pycnanthus* (Myristicaceae), which were not particularly well-represented in the vegetation. Pollen attributed to Papilionaceae has been counted but in much lesser abundance than the corresponding trees. High proportions of Urticaceae and *Macaranga* have been found within a plot located closer to the river, and were attributed to local disturbance. The pollen spectra from the mixed semi-evergreen forest at Makokou (Gabon) has some common taxa (*Celtis*, *Macaranga*, *Alchornea*, Combretaceae), with samples from Cameroon located in a forest intermediate between the evergreen Biafran and the semi-evergreen "Congolese". Interestingly, the Belinga pollen sample, located at higher elevation (950 m), contains significant percentages of *Syzygium* pollen. Although *Syzygium* has swamp species, this finding agrees with modern pollen data from highland forests of Ethiopia (Bonnefille *et al.*, 1993) and South India (Bonnefille *et al.*, 1999).

5.3.3 Drier peripheral semi-evergreen forest

5.3.3.1 North of the equator

Modern pollen data from the drier peripheral semi-evergreen forest (forêt semi-caducifoliées), which extends around the 4°N latitude between the mixed moist semi-evergreen and northern savanna, has been provided at two distinct sites: Mengang (east of Yaounde) and Kandara in Cameroon (Figure 5.1).

The Mengang forest station is located in an area receiving 1,600-mm/yr precipitation interrupted by two dry months (<50 mm)—December, January—and a minimum in July. Atmospheric pollen rain was captured in 1987 (April to October) by an aboveground framed trap, and the results presented at monthly intervals (Fredoux and Maley, 2000). They indicate that the greatest amount of pollen is produced by the forest trees (c. 90% of total counts), greatest monthly flux averaging 1,000 grains/m^3. Altogether, 118 tree taxa were identified distributed among 58 families. The Euphorbiaceae show the greatest diversity (21 taxa) and total 27% of the pollen counts dominated by Ulmaceae (33%) and Moraceae (26%). They are associated with Urticaceae (3%)—and Papilionaceae, Caesalpiniaceae, Mimosaceae, Anacardiaceae, Sterculiaceae, Rubiaceae, and Sapindaceae, each accounting for less than 1%. The greatest pollen producers indicated by flux calculations are *Macaranga* (1 to 1,000/m^3 maximum in May), *Celtis* (1 to 500/m^3 in April), *Musanga* (or *Myrianthus*) and Combretaceae (10 to 100/m^3). The amounts of *Pycnanthus*, *Trema*, Urticaceae, and Poaceae pollen are produced in much lower proportion (<1 to 10/m^3). Although established for 1 year, such discrepancies have to be remembered while interpreting fossil pollen results. It would have been most interesting to compare this distribution with parallel analysis of surface soil samples within the forest that provide an average of modern pollen rain over several years, minimizing monthly variations.

In southeastern Cameroon—east of Mengang (Figure 5.1), near the Kandara village (4°20′N, 13°43′E, 640 m)—the dry semi-evergreen forest encloses a few square kilometer area of shrub tall-grass savanna. The wet tropical climate is characterized by the same precipitation (1,600 mm/yr) and dry season, with mean annual temperature averaging 24°C. In this area the forest had expanded at a rate of 1 m/yr between 1951 and 1993 (Youta Happi, 1998; Achoundong *et al.* 2000), in agreement with observations made on aerial photographs in Cameroon (Letouzey, 1968). The forest succession begins with *Raphia monbuttorum* (Palmae) swamp along the Soukato River, followed by a semi-evergreen *Rinorea* (Violaceae) forest, a young *Albizia* forest, and a savanna–forest transition (ecotone) surrounding the savanna dominated by Panicoideae grasses with some *Albizia* clusters (Figure 5.3a). Associated with *Rinorea dentata* and *Rinorea batesii* (Achoundong *et al.*, 1996), the most abundant trees of the mature forest are *Triplochiton scleroxylon* (Sterculiaceae) and *Piptadeniastrum africanum* (Mimosaceae), good indicators of dry peripheral semi-evergreen forest (Letouzey, 1968). The young *Albizia* forest includes *Albizia adiantifolia* (Mimosaceae), *Funtumia elastica* (Apocynaceae), *Canthium* (Rubiaceae), *Tabernaemontana crassa* (Apocynaceae), *Sterculia rhinopetala* (Sterculiaceae), and *Myrianthus arboreus* (Moraceae). At Kandara, 26 surface soil samples collected in contiguous 20 × 30-m plots, along a 750-m transect across the succession (Figure 5.3a), provided modern pollen rain data. Each pollen sample consists of about 20 sub-samples randomly distributed (Vincens *et al.*, 2000). The relative frequencies of the most abundant ones among the 101 pollen taxa altogether identified are illustrated here (Figure 5.3c). All samples from the dry semi-evergreen forests register percentages of arboreal pollen (AP) ranging from 60 to 80%, in good correspondence with the canopy coverage estimated by field measurements of the leaf area index (Cournac *et al.*, 2002) and abundance of tree phytoliths counted in the same samples (Bremond *et al.*, 2005). The total AP drops abruptly to less than 10% in the nearby savanna, at less than 100 m from the forest limit, indicating very little transport from the forest into the savanna (Figure 5.3b). The pollen assemblages from this transect include some pollen of the trees characterizing dry peripheral semi-evergreen forest. These are *Celtis*, *Chaetachme*, *Holoptolea* among the Ulmaceae, *Triplochiton* (Sterculiaceae) associated with *Piptadeniastrum*

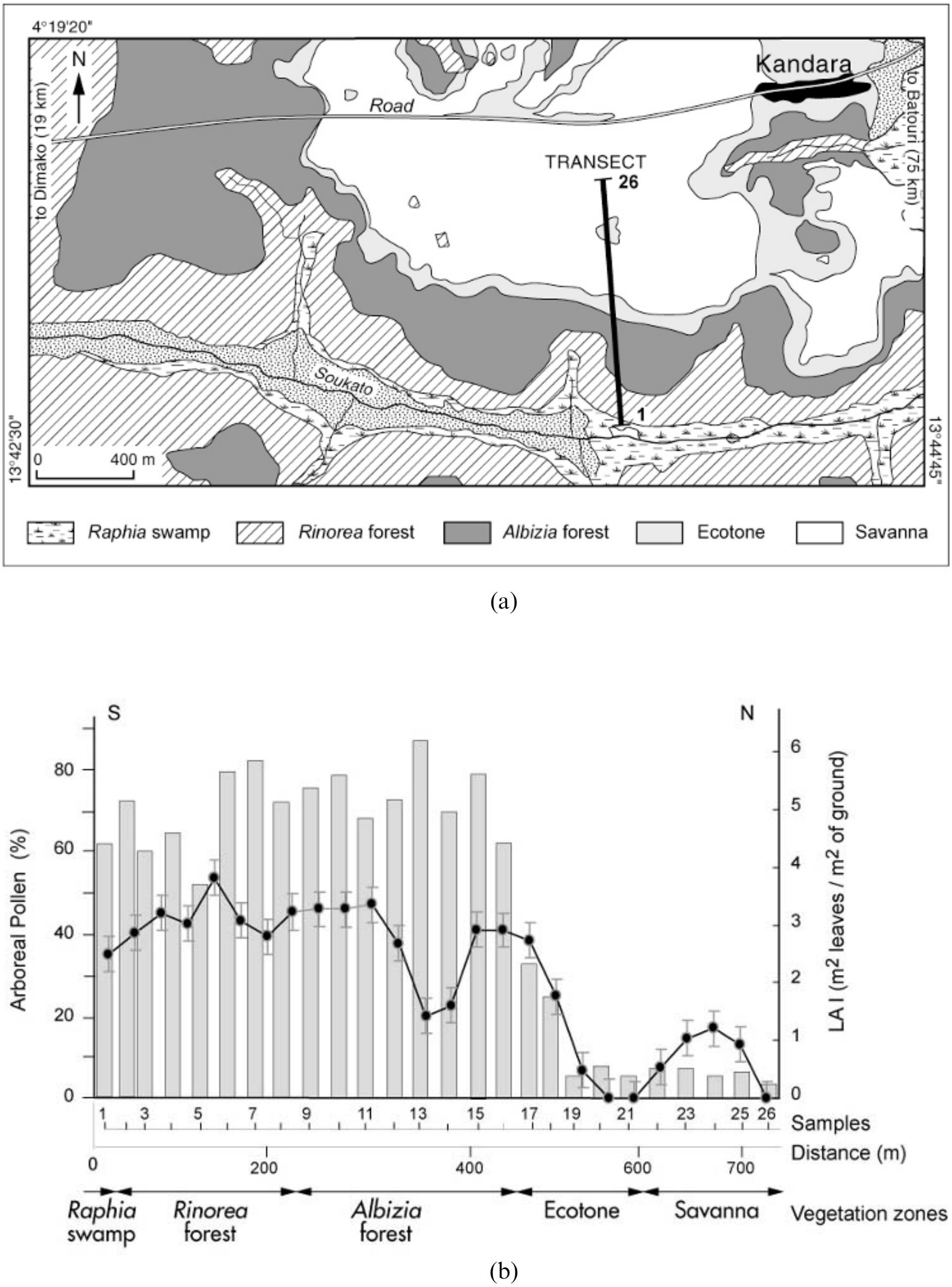

Figure 5.3. Modern pollen rain from the drier semi-evergreen forest in Cameroon, Kandara site: (a) location map of the studied transect (samples 1 to 26); (b) comparison between arboreal pollen and leaf area index (Cournac *et al.*, 2002). After Bremond *et al.*, 2005 and Vincens *et al.*, 2000.

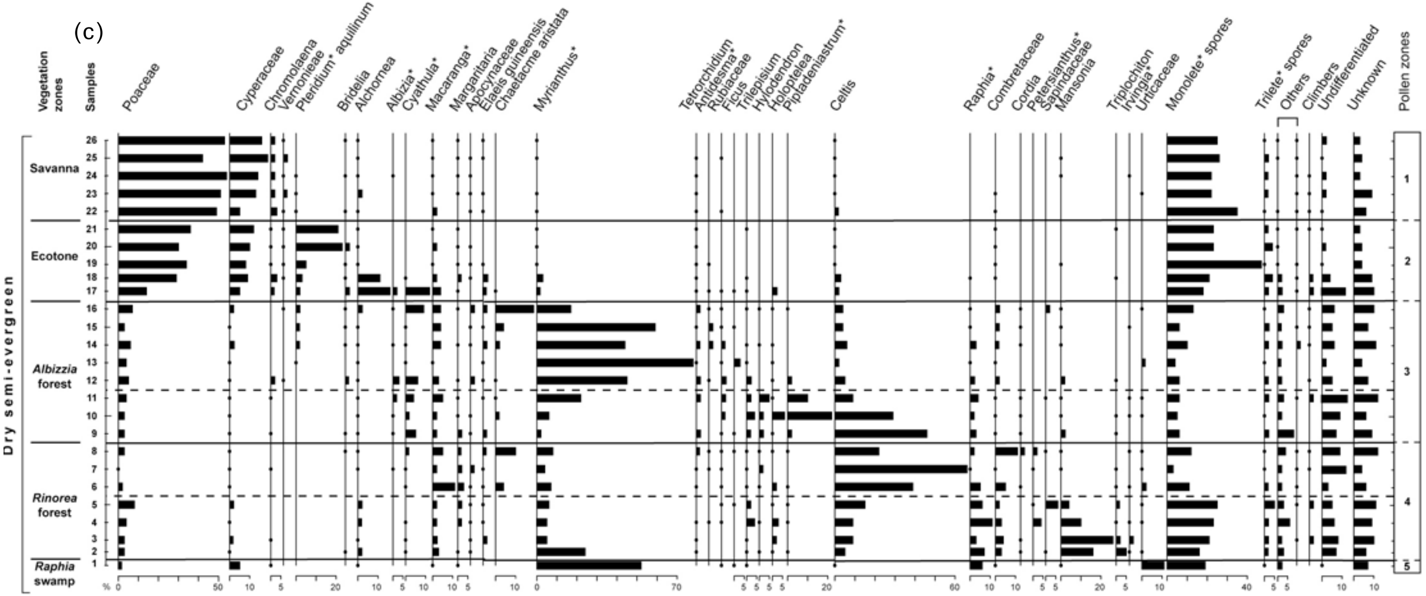

Figure 5.3. (c) Simplified pollen diagram (after Vincens *et al.*, 2000) (% calculated versus pollen sum including all identified taxa, Cyperaceae, and spores). * Denotes names representing the greatest probability for identification of pollen type, but for some pollen types other genera or species having the same pollen morphology cannot be excluded (pollen types <1%). Dots = pollen % < 1.

(Mimosaceae), *Margaritaria discoidea* (Apocynaceae) and Combretaceae. These taxa can be considered as good indicators of semi-evergreen forest under a seasonal climate, with a short dry season. However, and as expected, their pollen abundances do not exactly correspond to plant abundances in the vegetation cover. This is unavoidable due to differential pollen production. The soil samples from the *Albizia* forest contain a few grains of *Albizia* but are dominated by 50 to 70% *Myrianthus arboreus* (Moraceae). Near the contact with the savanna, *Chaetachme aristata* (Ulmaceae) dispersed more pollen (20%) than *Albizia* (5 to 10%) despite the latter being more strongly represented in the vegetation cover. *Tetrorchidium*, *Ficus*, *Trilepisium* (all Moraceae), *Antidesma* (Euphorbiaceae), Rubiaceae, and Sapindaceae are normal components of the semi-evergreen forest pollen rain. At contact with the *Rinorea* forest, *Piptadeniastrum* pollen was relatively abundant whereas none of the different species of *Rinorea* were recorded as pollen. *Raphia* pollen dominates near the swamp, which is also marked by an abundance of fern spores (*Pteridophytes monoletes*). At the northern end of the transect, close to the savanna, the abundance of *Pteridium aquilinum* spores indicates frequent burning. The pollen diagram illustrates the spatial colonization of a burnt savanna by a dry semi-evergreen forest. The succession starts with Moraceae, followed by *Celtis*, and then by Sterculiaceae/*Raphia*/Pteridophyta, following dry to wetter local conditions under climatic conditions favorable to the establishment of dry semi-evergreen forest. Although this succession might be valid only for the northern semi-evergreen forest region, the results improve our understanding of tropical rainforest dynamics in the past and should stimulate similar studies for other regions.

While there is some agreement among botanists that the forest dominated by shade-intolerant tree species established from relatively open conditions several hundred years ago, the origin of savanna "islands" in the semi-evergreen forest of southeast Cameroon still remains controversial. Analyses of opal phytolith assemblages from topsoil samples of the forests and the included savanna patches at Lobéke—2°17′N, 15°42′E, 300 to 700 m in elevation, south of Kandara (Figure 5.1) in a region receiving 1,600–1,700-mm/yr precipitation—suggest stable conditions with no evidence of recent disturbances, such as fire or logging (Runge and Fimbel, 1999). Elsewhere, evidence for recent invasion of forest into the savanna is also provided from soil organic carbon isotopic studies (Guillet *et al.*, 2001) whereas $\delta^{13}C$ of organic matter in soil profiles provides information on previous forest development in areas now occupied by savanna (Schwartz *et al.*, 1996). Constant re-organization of the distribution of forest and savanna patches at the limit of the drier semi- evergreen forest may be forced by the seasonal distribution of the rain through the year and variability in dry-season length. But, recent human deforestation has modified the pattern. Sorting out the respective effect of climate from that of human impact on modern vegetation deserves further thorough investigation.

5.3.3.2 South of the equator

The coastal semi-evergreen forest does not extend to southern Congo beyond 4°S latitude (White, 1983). Instead, a mosaic of forest–grassland occupies the Atlantic

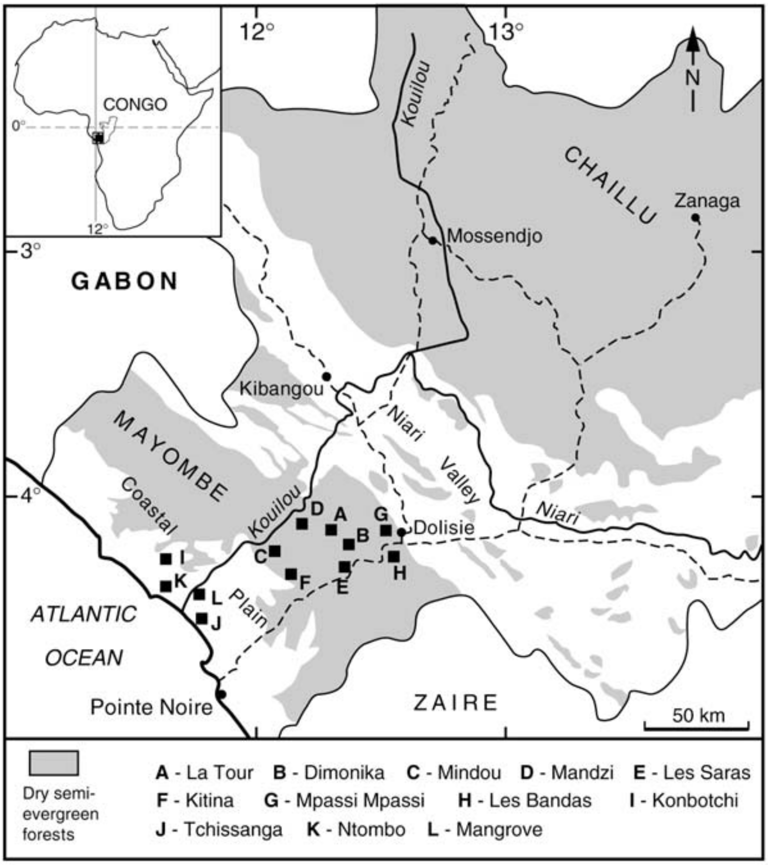

Figure 5.4. Location map of sites for floristic inventories and modern pollen surface soil samples collected within the semi-evergreen forests from Congo (after Elenga *et al.*, 2000a).

coast, receiving less than 1,100 mm/yr of rainfall and with temperatures averaging 18°C during the dry season. Several types of semi-evergreen forests are present further inland, in the Mayombe massif, which reaches 730 m maximum elevation and receives 1,400 to 1,600 mm/yr of precipitation. Botanical investigation was made at 12 geographical sites (A to L), distributed between 4°05′ to 4°50′S latitude and 11°45′ to 12°35′E longitude (Figure 5.1). Among the investigated sites, 8 are distributed in Mayombe and 4 correspond to the coastal plain (including the mangrove) (Figure 5.4). At each site, trees with a diameter at breast height >5 cm were counted within 20 × 100-m plots (Elenga *et al.*, 2000a). All the floristic inventories highlight the great number of tree species and the great spatial heterogeneity of their distribution. Out of a total of 620 individual trees, 352 species were identified, distributed among 47 botanical families. Of the represented tree species, the most important ones are Annonaceae (15 species), Euphorbiaceae (8 species), Caesalpiniaceae (7 species), Rubiaceae (6 species), followed by Burseraceae, Olacaceae, Sapotaceae, and Moraceae. Within all the studied plots, 110 species have tree frequencies >1%, but only 41 species were present in at least two sites where the average density of trees reached 120 individuals per 100 m^2 (Elenga *et al.*, 2000a). The forests of the Mayombe are remarkable for high floristic diversity and little overlap between tree composition at different localities. Correlation between floristic richness and climatic variables—such as insolation, water availability, or primary production—are now being explained by a new hypothesis. Palynological studies explore how such floristic diversity is reproduced in pollen assemblages extracted from 50 surface soil samples collected at the 12 sites where tree counts had been made (Figure 5.5).

5.3.4 Forests of the Mayombe

Within all the samples from the semi-evergreen forests of the Mayombe massif, c. 19 to 23 plant species make up more than 75% of the total tree counts. But, the dominant tree varies greatly within the 8 studied plots and the results of pollen analysis show that this dominance is not necessarily reproduced in the corresponding pollen assemblages. At La Tour (site A), *Treculia obovoidea* (Moraceae) represents 8.5% of the trees, but its pollen frequencies reach much higher percentages (30 to 60%) in all of the 10 pollen assemblages (Figure 5.5). Other trees—such as *Plagiostyles africana* (Euphorbiaceae), *Maranthes* (Chrysobalanaceae), *Irvingia*, *Uapaca* (Euphorbiaceae), common to the floristic list (Elenga *et al.*, 2000a, table 2) and the pollen diagram (Figure 5.5)—show similar percentages both as plants and pollen. *Strombosia* (Olacaceae) are under-represented by their pollen, whereas Annonaceae and Myristicaceae have not been found as pollen. At Dimonika (site B), 11 of the 22 most abundant trees have been recognized as pollen taxa. Among them, *Treculia obovoidea* (Moraceae), *Anisophyllea myriostricta* (Anisophyllaceae), *Trichoscypha* (Anacardiaceae), *Dacryodes* (Burseraceae), Caesalpiniaceae, and *Allanblachia* (Guttifereae) have significant percentages, both as plant and pollen. However, other genera among Burseraceae, Apocynaceae, Clusiaceae, and Annonaceae were found weakly or not represented by their pollen. At Mindou (site C), the most abundant trees—*Anthostema* (Euphorbiaceae, 13%), *Dialium* and *Guibourtia* (all Caesalpiniaceae totaling 22% trees)—are represented by significant pollen percentage values. *Syzygium*, not in the tree list, provided the greatest amount of pollen (20 to 50%) in samples 16 to 22 (Figure 5.5). The Mindou site, located on the humid western slopes of Mayombe, is close to the coastal forest. Proximity of *Syzygium* clumps in local swamps perhaps explains such high pollen percentages. At Mandzi (site D), of the most abundant trees—such as *Microdesmis* sp. (Pandanaceae 10%), *Grewia* (Tiliaceae 8%), and *Tessmania* sp. (Caesalpiniaceae 6%)—only *Grewia* is recorded by its pollen (2 to 5%). Other taxa—such as *Irvingia*, *Pancovia* (Sapindaceae), and *Aidia micrantha* (Rubiaceae)—have about the same representation both in trees and in pollen. However, associated pollen from *Piptadeniastrum*, *Calpocalyx* (Mimosaceae), *Dacryodes*/*Santiria*, *Ganophyllum* (Sapindaceae), *Fagara* (Rutaceae), *Macaranga* and *Elaeis* do not correspond to the listed trees at this site (Elenga *et al.*, 2000a, table 5.2), a discrepancy possibly explained by the fact that pollen origin may be found outside the sampled plots used for tree counts. At les Saras (site E), *Treculia*—an abundant tree

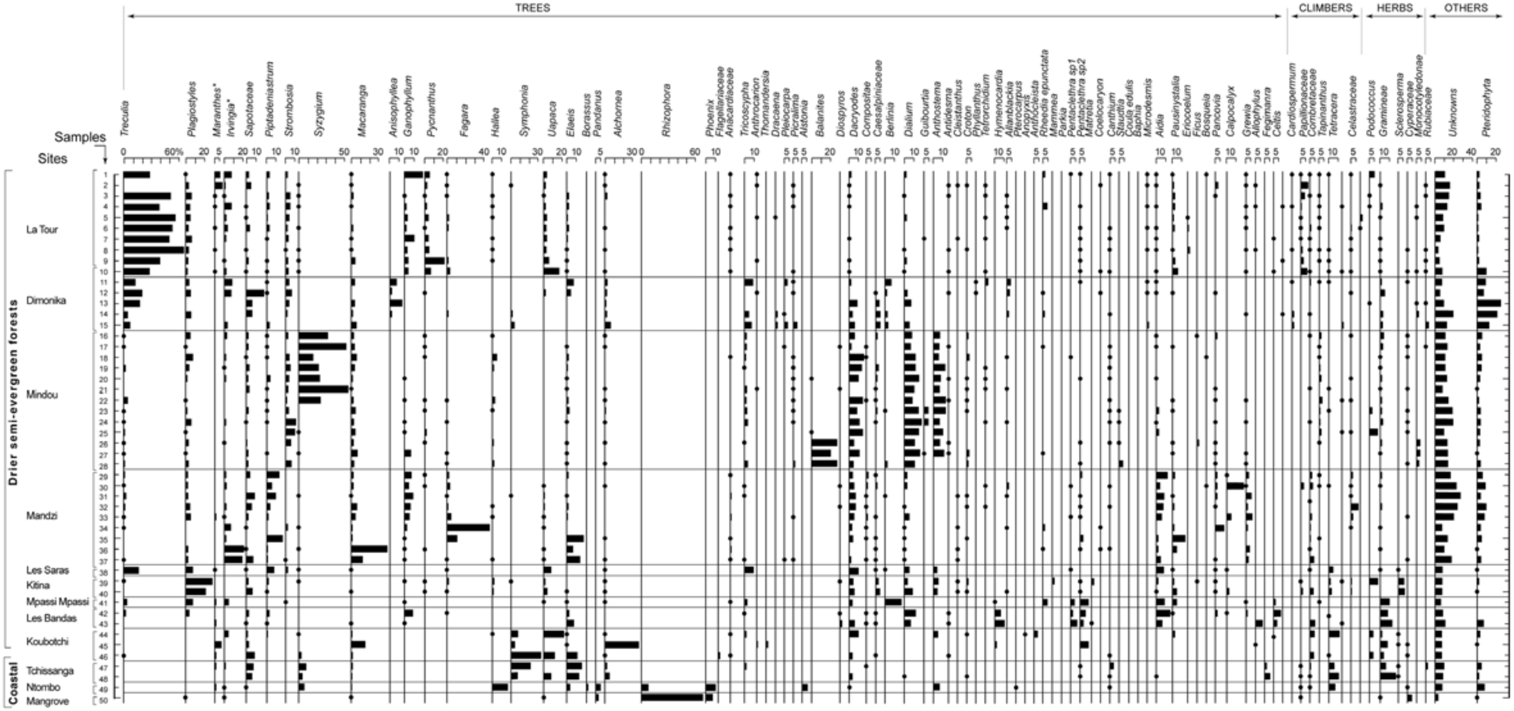

Figure 5.5. Frequencies of the main pollen taxa identified within modern soil surface samples from Southern Congo (after Elenga *et al.*, 2000a) (% calculated versus pollen sum including all identified taxa; Cyperaceae and Pteridophyta spores being unimportant, except at site B).

(12.6%)—is represented by similar pollen frequencies, whereas three species of Annonaceae (13.5% distributed between *Anonidium*, *Polyalthia*, and *Enantia*) are totally absent as pollen. At Kitina (site F, samples 39, 40), the dominant (12.4%) *Anthostema* trees (Euphorbiaceae) are recorded by pollen, but at much lower percentages (<5%). Other abundant trees—such as *Scytopetalum klaineanum* (8% Scytopetalaceae), *Ctenolophon englerianus* (6% Ctenolophonaceae), *Spathandra blackeoides* (6% Melastomataceae)—not identified during pollen analysis might correspond to unidentified pollen taxa, their pollen morphology not currently well-known (Figure 5.5). *Dialium* has about the same abundance (5%) both as plant and pollen. At Mpassi Mpassi (site G, sample 41), the two most abundant trees—*Hua gabonensis* (16% Huaceae) and *Pancovia* (7% Sapindaceae)—were not represented as pollen. *Pentaclethra* (Mimosoideae, 2 species, 5% trees) has the same representation as plant and as pollen, whereas the abundance of *Berlinia* pollen (20%) may correspond to another unknown Caesalpiniaceae pollen, since *Berlinia* was not in the list of counted trees. At les Bandas (site H), the dominant tree (56%) *Parkia* (Mimosaceae) was not found as pollen, whereas the diagram includes *Pentachlethra* pollen (10 %), which is clearly distinguishable from the polyad of *Parkia*. Except for *Dacryodes* and *Aidia* (Rubiaceae), both present in the plant record and in the pollen, there is not much overlapping of other common trees. Joint occurrences of pollen from *Allophyllus*, *Celtis*, *Hymenocardia*, and Combretaceae together with more Poaceae indicate much drier climatic conditions for sites located close to the drier Niari valley located in the rain shadow slope of the Mayombe massif.

5.3.5 Coastal forests

At Koubotchi (site I) the dominant (30% trees) forest component *Celocaryon preussii* (Myristicaceae) was not found as pollen, nor were *Xylopia aethiopica* (Annonaceae), *Carapa* (Meliaceae), *Staudia* (Myristicaceae), *Vitex* sp. (Verbenaceae). But the pollen representation of *Symphonia*, *Uapaca*, *Maranthes* (Chrysobalanaceae), *Pycnanthus* (Myristicaceae), and Sapotaceae correspond fairly well to the number of trees counted in the plot. Remarkably, *Macaranga* and *Alchornea* (<1.4% in the tree counts) are over-represented by significant pollen percentages (>20%), and *Tetracera* (Dilleniaceae) is also over-represented by its pollen (>10% pollen). At Tchissanga (site J), two pollen samples (47, 48) indicate pollen values for *Symphonia* and Sapotaceae, *Fegimanra* (Anacardiaceae), and *Syzygium* (Myrtaceae), that are also characteristic trees of the *Symphonia globulifera* forest in valleys of the coastal plain (Elenga *et al.*, 2000b). However, they lack the record of *Memecylon* (Melastomataceae) which accounted for 34% of the total number of trees in the same plot. At Ntombo (site K), *Anthostema* pollen (Euphorbiaceae) was found less abundant (5%) than in the tree cover dominated by *Anthostema aubryanum* (51%). But, there is good correspondence between the plant and pollen representation of *Syzygium guineensis*, *Hallea ciliata* (Rubiaceae), *Elaeis guineensis* (Palmae), and *Alstonia congensis* (Apocynaceae). *Tetracera* pollen (5%) was found, whereas this climber represents less than 1% in botanical inventories. This may indicate an over-representation of pollen from climbers, or an under-estimation of plant specimens, those with diameter lower than 5 cm not being counted. The mangrove (site L) is dominated by the abundance of *Rhizophora*, associated with *Phoenix* and *Pandanus*, also abundant plants in the plant cover.

In order to clarify the distribution of plants and pollen versus environmental factors, correspondence analysis done on all the samples compared the composition of the floristic inventories from lowland coastal forests with those of Mayombe mid-elevation forests. Indeed, there is a west/east increasing rainfall gradient from 1,100 to 1,600 mm/yr and an increased elevation between the coastal plain (sea level) and the Mayombe (700 m). But, the authors favoured an explanation involving different soil composition. They distinguished the pollen association of *Syzygium*, *Symphonia globulifera*, *Phoenix*, *Tetracera*, *Sclerosperma* (Arecaceae) as characterizing swamp forests (Elenga *et al.*, 2000b). However, differences in elevation and also strong variations in precipitation could partly explain the differences in floristic and pollen composition of the coastal and Mayombe forests. Variations in the amount of rainfall are not negligible. Moreover, during the dry season, the effect of clouds on evapo-transpiration (Maley and Elenga, 1993) and that of the Benguela Current induce cooler temperature in southern Congo (Maley, 1997).

In conclusion, the study on modern pollen rain from Congo shows that arboreal pollen percentages from 70 to 90% characterize samples collected under closed forest, lower values being found within disturbed forest. These high values are obtained despite the fact that important families—such as Annonaceae (all species), most Myristicaceae (except *Pycnanthus*), Chrysobalanaceae, Olacaceae (except *Strombosia*), Clusiaceae (except *Symphonia*), Apocynaceae, Meliaceae, Melastomataceae, etc.—were poorly documented in modern pollen rain. Well-diversified pollen assemblages from southern Congo document the floristic diversity of semi-evergreen forests south of the equator. Although there is no direct overlap between pollen and tree composition, pollen assemblages clearly distinguish the different types of forest that have produced them. Associated *Symphonia globulifera*, *Uapaca*, *Hallea*, *Dacryodes*, *Anthostema*, *Dialium*, *Plagiostyles*, and Sapotaceae, both in the vegetation and in the corresponding modern pollen rain, characterize the dry semi-evergreen forest of Mayombe. This is enough to appreciate that the semi-evergreen forests south of the equator appear palynologically distinct from the same vegetation unit mapped north of the equator in Cameroon (sites Q and E, Figure 5.2), including Kandara. Possible explanation for such differences may be searched for in the long-term geological history and (or) in the differential ecological requirements and threshold climatic limits of the various forest trees. More investigation on this line is needed.

5.3.6 Swamp forest

Preliminary information about modern pollen rain from the inundated evergreen swamp forests of Central Congo was provided by three samples collected within the *Guibourtia demeusii* (Caesalpiniaceae) dominated association. Located in the central Congo Basin below 400 m in elevation (1°34′N, 17°30′E), the area receives more than 1,600 mm/yr of precipitation with a very short dry season. The results show that arboreal pollen (AP) again ranges from 75 to 90%. Pollen assemblages are dominated by *Lophira* (up to 60% in one sample), followed by *Guibourtia*, *Alchornea*, *Macaranga*, *Uapaca*, Combretaceae, and *Myrianthus*, and a few pteridophyte spores. These pollen assemblages are different from those collected from the hygrophilous evergreen forest of Cameroon and from any types of the semi-evergreen drier peripheral forest (Elenga, 1992).

The pioneer studies summarized in this chapter represent significant progress in tropical modern pollen rain of Africa. First, they clearly demonstrate that a high proportion of tree pollen can identify forest cover. Second, they indicate that the main mapping vegetation units (evergreen, semi-evergreen, and mixed) as well as secondary subdivisions in the vegetation (from Cameroon and Congo) are characterized by different pollen assemblages. Third, there is partial overlap between pollen and plant representation. In conclusion, differences in pollen (taxa composition and abundance) can be used to recognize the vegetation units and sub-units within the Guineo-Congolian rainforest, despite the lack of pollen representation of some dominant trees. Although not covering continuous climatic gradients, the results discussed bear critical information for interpreting fossil pollen data from the region. Extracting individual or associated pollen markers for all the vegetation units within the rainforest, however, requires additional and more homogenously distributed samples before being statistically valid. A complete inventory of forest types is essential because of the high diversity of rainforests. Collecting along two distinct transects—one from south to north crossing the equator to address the climatic influence of the ITCZ (Haug *et al.*, 2001), the other from west to east, to address inland monsoon penetration—would be most valuable. This section has shown that modern pollen from the rainforest can be studied in the same way as other forests in the world. It is a long, but feasible task.

5.4 QUATERNARY HISTORY

Despite recent progress and new fossil pollen sequences obtained by coring swamps and lakes in Africa, it is not possible to reconstruct the Quaternary history of all the different forest units described in Section 5.2. Not all of them being documented yet, the presentation of fossil pollen records follows a chronological order, starting with the last glacial period, and then discussing the last 10,000 years of the Holocene. The list of sites where fossil pollen are available is given in Table 5.1 and Figure 5.1. Evidence for climate changes based upon other sources of information—such as lake sediments, paleosols, stable isotopic, phytoliths, diatoms—has been summarized in Battarbee *et al.* (2004).

5.4.1 Ice-age record

Marine sediments have provided pollen data related to vegetation change on the continent. These sequences have the great advantage of providing land–sea linkage on a straightforward isotopic chronology (Bengo and Maley, 1991; Dupont and Wienelt,

Table 5.1. List of fossil pollen sites located within the African lowland rainforest.

Sites	Coordinates	Elevation (m)	Rainfall (mm/yr)	Authors
Barombi Mbo	4°67′N, 09°40′E	300	2,400	Maley and Brenac (1998),
Mboandong	4°30′N, 09°20′E	120	2,400	Richards (1986)
Ossa (OW4)	3°40′N, 10°05′E	8	2,950	Reynaud-Farrera *et al.* (1996)
Kamalete	0°43′S, 11°46′E	350	1,500	Ngomanda *et al.* (2005)
Bilanko	3°31′S, 15°21′E	600	1,500	Elenga *et al.* (1991)
Sinnda	3°50′S, 12°48′E	130	1,100	Vincens *et al.* (1994, 1998)
Coraf	4°00′S, 11°00′E	0	1,260	Elenga *et al.* (1992)
Kitina	4°15′S, 11°59′E	150	1,500	Elenga *et al.* (1996)
Ngamakala	4°04′S, 15°23′E	400	1,300	Elenga *et al.* (1994)
Songolo	4°46′S, 11°52′E	5	1,260	Elenga *et al.* (2001)

1996; Dupont and Behling, 2006). Offshore transported pollen include taxa from different vegetation zones that are mixed together and can hardly be interpreted in terms of past expansion of each of the different forest types. Indeed, marine records are the only source of information for older geological time periods (see Chapter 1). Here, we will discuss the oldest continental evidence provided by lacustrine pollen sequences. Lake records span the last 30,000 years including part of the last glacial period (ice age) and its maximum in the Last Glacial Maximum (LGM).

The ice-age record for African tropical lowland forests is known from two sites: Barombi Mbo within a forested region of Cameroon (Maley and Brenac, 1998) and Ngamakala within secondary grassland nearby the Congo River (Elenga *et al.*,1994). A third record, from lake Bosumtwi, West Africa, remains poorly documented through a preliminary pollen diagram (Maley, 1991). Except for *Celtis*, *Olea* it does not contain any detail about the forest composition. Although the Bosumtwi record is informative about the lowland rainforest along the Guinean gulf, this review does not include it. A long core spanning the last 1.1 Myr was raised in 2003 and is still being analyzed. This record will be of immense significance to the reconstruction of West African paleoclimates.

5.4.1.1 Barombi Mbo, evergreen and semi-evergreen forests (Cameroon)

North of the equator, the small crater lake Barombi Mbo ("Mbo" means lake in the local language) (4°40′N, 9°24′E) is located 15 km north of Mount Cameroon and 50 km inland from the Atlantic coast. Core MB-6 recovered from the deepest part of the lake (Maley *et al.*, 1990) yields a remarkably complete record for the last 32,000 years (27 ^{14}C kyr BP), including the LGM. The lake is situated at low elevation (300 m a.s.l.) and presently surrounded by forest (Figure 5.6, see color section). The crater lies within the wide belt of lowland evergreen Biafran forest dominated by Caesalpiniaceae bordered by two large bands of semi-evergreen forest. Patches of semi-evergreen forest occupy areas under the rain shadow of Mount Cameroon, which causes a decrease in precipitation and a reduction in the length of the rainy season. Lying

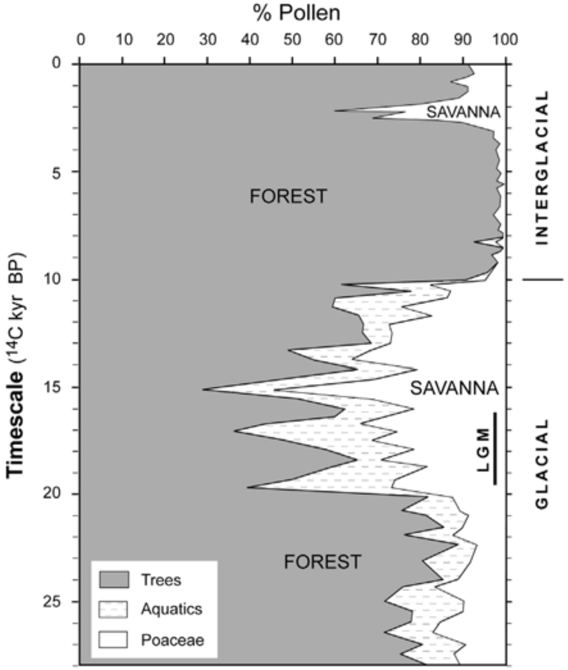

Figure 5.7. Synthetic pollen diagram from core BM-6, Lake Barombi Mbo, Cameroon, presented according to interpolated ^{14}C ages (after Maley and Brenac, 1998) (% calculated versus pollen sum including all identified taxa, excluding spores).

within Mount Cameroon's rainshadow, Barombi Mbo receives 2,350 mm/yr with a 3-month dry season from December to February. This relatively low rainfall contrasts with 9,000 mm/yr of windward (coastal) precipitation on the side of Mount Cameroon. The laminated sediments of the 23.5-m core were regularly deposited and present no hiatus, an exceptional situation for African lakes. Twelve AMS radiocarbon dates provide a reliable depth/age curve (Giresse *et al.*, 1991, 1994). In the pollen diagram each sample corresponds to a 1-cm thickness of sediment averaging c. 10 to 15 years of deposition. Pollen analyses were made at c. 200-yr intervals in the Holocene, and c. 300 yr in the glacial period (Maley and Brenac, 1998; Elenga *et al.*, 2004). All the results discussed here follow the ^{14}C chronology provided by the authors.

At Barombi Mbo, the curve of total arboreal pollen (Figure 5.7) provides a good average estimate of the forest cover surrounding the lake, although pollen deposition into the lake integrates a much larger basin. It clearly shows that, during the last glacial period—from 27 to 10^{14}C kyr BP (c. 32–11.5 kcal. yr BP)—the area around the lake remained forested. However, between 20 to 10^{14}C kyr BP (c. 24–11.5 kcal. yr BP) the tree cover was significantly reduced. Some fluctuations are depicted by the curve of total arboreal pollen, which would have been less marked if aquatics (sedges) had been eliminated from the pollen sum on which relative frequencies are calculated. High abundances of sedges (aquatics illustrated in Figure 5.7) coincide with the Last Glacial Maximum (LGM). Such peaks attest to enlarged herbaceous wetlands (including grass) that occupied emerged land on the shore line. A probable explanation for wetland expansion is falling lake levels in response to drier climatic conditions.

Glacial period and refuge hypothesis

Regarding the detailed pollen composition of the tree component, the last glacial period can be subdivided into two distinct phases (Figure 5.8). During the first phase from c. 32–24 kcal. yr BP, the total AP pollen (c. 80%) indicates a dense canopy cover (Figure 5.7) which remained fairly stable throughout and includes the highest frequencies (7 to 10%) of the Caesalpiniaceae evergreen component. Out of the 150 identified pollen taxa, 20 different genera are included in the Caesalpiniaceae curve (Maley and Brenac, 1998). As their pollen is normally under-represented in modern pollen rain (Reynaud-Farrera, 1995, and Section 5.3), the Caesalpiniaceae may have been a very important and diverse component within the forest at that time. Sapotaceae, a component of mature semi-evergreen forest (Elenga *et al.*, 2004), were also present (1 to 3%), together with other components of this subflora. Among markers of the mountain forest, *Podocarpus* pollen was found at such low frequencies (<1.5%) that it is unlikely that the trees occurred close to the lake. Today, *Podocarpus* is present on Mount Koupé (2,050 m) and its fossil occurrence could well be attributed to long-distance transport from this mountain. In marine cores *Podocarpus* pollen is quite abundant in sediment dating from the glacial period (Marret *et al.*, 1999). In contrast, *Olea* was recorded at higher pollen percentages (>10%) indicating that their trees may have been present near the lake. The *Olea* pollen curve shows a remarkable pattern through time. An increasing trend started at 24^{14}C kyr BP (28 kcal. yr BP), reaching a maximum (30%) at 20^{14}C kyr BP (24 kcal. yr BP), and then decreasing again to 5% at 17^{14}C kyr BP (c. 20 kcal. yr BP). From 24 kcal. yr BP to 20 kcal. yr BP, the decreasing trend of *Olea* pollen is in good correspondence with the 4,000-yr duration of the LGM chronozone placed between 23 kcal. yr BP and 19 kcal. yr BP on marine records (Mix *et al.*, 2001). Today, *Olea capensis* grows on Mount Cameroon at an elevation of 1,600 m and much higher, such as in cloud forest. Its abundance in the fossil pollen record has been explained by the impact of stratiform clouds and associated fogs produced by sea surface temperature cooling of the Atlantic (Maley, 1989; Maley and Elenga, 1993). That such processes may have played a role cannot be ruled out. Interestingly, the maximum of *Olea* percentages occurred slightly before the LGM and corresponds to the timing of the Dansgaard–Oeschger event 2 (DO2) and the last δ^{18}O maximum of the Antartica Byrd ice core (Mix *et al.*, 2001). The pollen/climate transfer function in East Africa indicates a glacial continental cooling of 3 ± 2°C in the tropical region (Bonnefille *et al.*, 1990, 1992; Vincens *et al.*, 1993)—a maximum value—since the effect of lower carbon dioxide content of the atmosphere could not be taken into account. Using the present day lapse rate, such an estimate corresponds to a 600-m shift in elevation, much less than the 1,300-m necessary lowering for *Olea* to reach the Barombi Mbo lowlands. Originally, tropical cooling was inferred from a significant shift in altitudinal distribution of vegetation zones on East African mountains (Flenley, 1979). The descent of vegetation on tropical mountains results from the

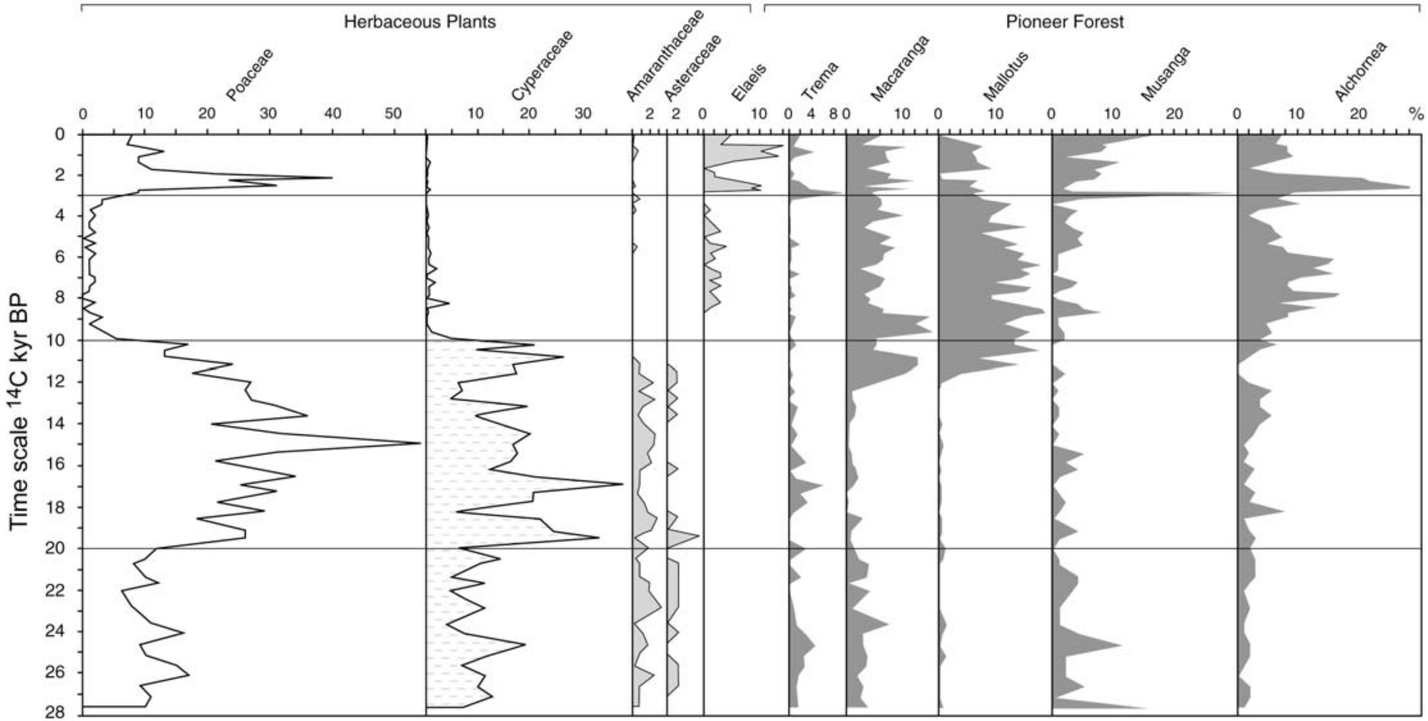

Figure 5.8(a). Detailed pollen diagram from core BM-6, Lake Barombi Mbo, Cameroon, presented according to interpolated ^{14}C ages: trees and shrubs (after Maley and Brenac, 1998) (% calculated versus pollen sum including all identified taxa, excluding spores).

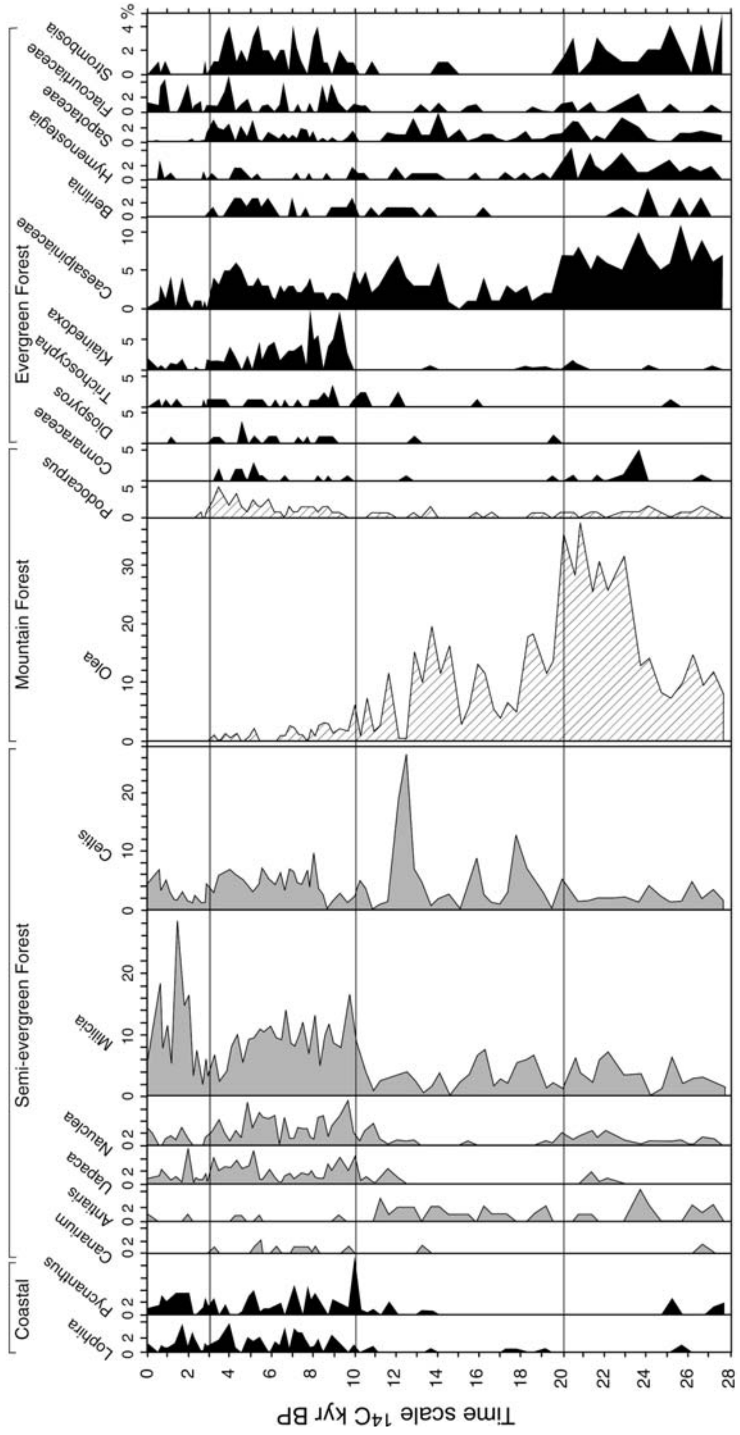

Figure 5.8(b). Detailed pollen diagram from core BM-6, Lake Barombi Mbo, Cameroon, presented according to interpolated ^{14}C ages: herbs (after Maley and Brenac, 1998) (% calculated versus pollen sum including all identified taxa, excluding spores).

associated effects of both decreasing temperature and rainfall. The Barombi Mbo record clearly demonstrates an individualistic movement of *Olea* into the lowland vegetation during glacial time. This cannot be forced by lower CO_2 concentration as it affected a tree which is a C_3 plant. Applying 3°C-cooling at the Barombi Mbo will lead to a value of 21°C ($24 - 3 = 21$°C) for mean annual temperature, a value above the 18°C threshold for tropical highland forests in India (Bonnefille *et al.*, 1999; Barboni and Bonnefille, 2001), and above the 15°C threshold used to define the tropical biome (Prentice *et al.*, 1992). Under such conditions, *Olea* could reach the lowland rainforest where other tropical trees remained. The pattern shown by the *Olea* curve in the Barombi Mbo fossil record provides a good example of how plants individualistically responded to climatic changes. Significant rainfall decrease, during glacial time at the equatorial latitude, was estimated around 20 to 30% of the present value (Bonnefille *et al.*, 1990; Bonnefille and Chalie, 2000). Applying this estimate at Barombi Mbo leaves enough precipitation (1,500 mm/yr) to maintain a forest cover, during the glacial period, prior to the LGM.

During the second phase of the glacial period (24–11.5 kcal.yr BP), total AP pollen dropped with decreasing abundance of typical Biafran evergreen forest taxa, whereas semi-evergreen components—such as *Celtis* and *Antiaris* (Moraceae)—become more abundant, although their pollen frequencies show large fluctuations. Lowland species of *Strombosia*, Flacourtiaceae, Sapotaceae, *Antiaris*, *Hymenostegia* (Caesalpiniaceae), *Berlinia*, and other Caesalpiniaceae are still present, but decreased significantly (Maley and Brenac, 1998). Isotopic studies from the same core point to an increased proportion of C_4 grasses, likely favored by low CO_2 concentration of the global atmosphere at that time (Giresse *et al.*, 1994). The increase in grass pollen does not overlap the *Olea* phase (29–22 kcal.yr BP), but follows it, becoming more abundant between 24 kcal.yr BP and 11.5 kcal.yr BP, synchronously with the increase in Cyperaceae (Figure 5.8). The different patterns of the Poaceae and the Cyperaceae curves may indicate that the peak of Poaceae is not related to subaquatic grasses, but rather come from open grassland inside the forest. Pollen/biome reconstruction at 22 kcal.yr BP emphasized the replacement of rainforest by a tropical seasonal forest (Elenga *et al.*, 2000c). However, during the minimum extent of forest which lasted 5,000 years (24–19 kcal.yr BP), two sharp increases in tree cover are observed. They attest that forest expanded significantly during glacial time, although fluctuations in tree pollen percentages would have been minimized by excluding Cyperaceae from the pollen sum in the calculation of relative percentages. The maximum of grass pollen associated with the greatest opening of the forest is dated at 18 kcal.yr BP, a radiocarbon date that fits Heinrich Event H1 (Mix *et al.*, 2001), and therefore occurred a long time after the LGM. If the peak of *Olea* registers the maximum cooling and the peak of grasses the maximum aridity, these were delayed by at least 5,000 years. Aridity and cooling were decoupled and a complex pattern of forest dynamics is evidenced during the glacial period when the climatic impact of the two Heinrich Events H1 and H2 affected the lowland rainforest at Barombi Mbo. Nevertheless, rainforest appears very sensitive to global climatic changes. While considering the high topography of Mount Cameroon and the high precipitation gradient, a great variety of climatic conditions must have prevailed in the region in the past, just as it does today. During glacial time, enough precipitation could have existed on the western slopes, allowing the persistence of evergreen forests there at the same time as semi-evergreen forests at Barombi Mbo, at the eastern base of Mount Cameroon. During glacial time, the coastal area expanded as sea level fell and offered new opportunities for new land occupation. Various forest refuges could have existed during glacial time and could be located on direct evidence by means of new palynological studies, rather than postulated on various hypotheses (Maley, 1996).

5.4.1.2 Ngamakala, savanna contact with semi-evergreen rainforest (Congo)

On the right bank of the Congo River, the small Ngamakala lake (4°04′S, 15°23′E, 400 m), is located at the southern end of the Bateke plateau (Figure 5.1) where mesophilous, hygrophytic forests are related to humid edaphic conditions (Descoing, 1960). The lake—1 km wide—is now covered by *Sphagnum* (Sphagnaceae) and clumps of trees of *Alstonia boonei* (Apocynaceae). It is surrounded by a wooded *Loudetia demeusei* (Poaceae) savanna, with *Pentaclethra* (Mimosoideae) new growth (Makany, 1976). The results of pollen analysis of a 160-cm core show that, from c. 30–17 kcal.yr BP, the fossil pollen sequence was dominated by Sapotaceae and *Syzygium* (Figure 5.9). With Fabaceae (Leguminosae) and *Canthium*, later identified among the unknown (Elenga *et al.*, 2004), percentages of tree pollen exceed 80%. This record clearly indicates a forested environment during the glacial period. This forest was developed on a swamp attested by the occurrence of aquatic plants—such as *Xyris*, *Laurembergia* and the floating *Nymphea*. The forest existing there during the last glacial period included significant Fabaceae with Combretaceae, *Alchornea*, *Campylospermum* (Ochnaceae), *Cleistanthus* (Euphorbiaceae), *Canthium*, and *Celtis*. Rare pollen of other trees—such as *Crudia gabonensis* (Caesalpinioideae), *Guibourtia*, and *Tetracera* (Dilleniaceae)—provide a link with modern surface samples of the central Congo Basin (Elenga *et al.*, 1994). But, except for *Celtis* and Sapotaceae, the glacial forest in southern Congo had no floristic resemblance to that documented at Barombi Mbo in Cameroon at the same time. More specifically, the Ngamakala record does not show any of the highland taxa pointing to cooler temperatures, such as observed in the Cameroon record. The swamp environment may not have been favorable to the growth of *Olea*, but the lack of *Podocarpus* is more surprising. If *Podocarpus* had been present at mid-elevation on the Bateke plateau, its abundant pollen would have been blown away, and at least a few grains found in the Ngamakala sediment. However, no valid conclusion can be drawn until another glacial sequence from southern Congo confirms it. As in the Cameroon record, variations within the relative abundance of the different trees are observed during the glacial period, although masked by abundant *Syzygium* and Sapotaceae. The Ngamakala core had a very low sedimentation rate with only an 80-cm thickness of sediment deposited during the glacial interval (from 29 kcal.yr BP to 17 kcal.yr BP), and conventional dating is not accurate enough. The time resolution interval between adjacent samples (350 years) is greater than that of Barombi Mbo and insufficient to address short-term climatic variability during the glacial period. At Ngamakala, no

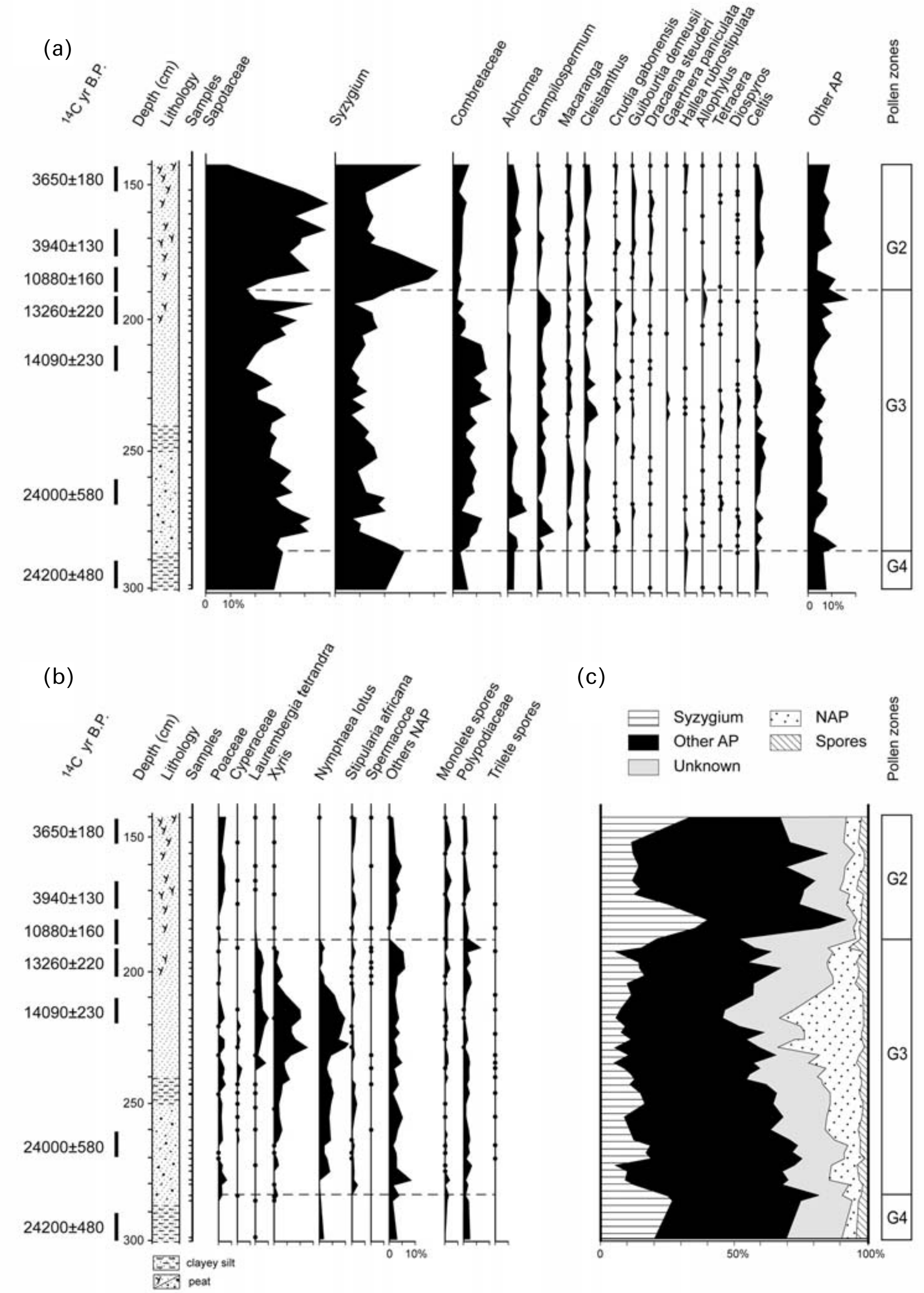

Figure 5.9. Simplified pollen diagram from Ngamakala, presented according to depth (Congo, after Elenga *et al.*, 1994): (a) arboreal and climber taxa; (b) herbaceous taxa; (c) synthetic diagram (% calculated versus pollen sum including all identified taxa, aquatics, and spores).

significant change at 24 kcal. yr BP is clearly identified in the pollen diagram, although postulated within a change of sediment. The minimum forest cover (60% AP) occurred at c. 17 kcal. yr BP when Sapotaceae and *Syzygium* decreased and Combretaceae reached their maximum relative abundance. Although the conventional dates of the Ngamakala core have a great experimental error, the minimum tree cover at Ngamakala appears synchronous with grass maximum frequencies at Barombi Mbo from which maximum aridity has been inferred. Simultaneous abundance of aquatic herbs, among which *Xyris* and *Nymphaea* dominate, may be explained by a water depth lower than 1 m. The Ngamakala record lacks evidence for cooler indicators, and therefore the decoupled effect of coolness and aridity during glacial time is not established yet for the southern tropics until further high-resolution pollen sequences are provided.

Past vegetation history of the rainforest during glacial time is only documented at two sites so far. It clearly indicates the persistence of two well-diversified rainforests of different composition on both sides of the equator.

5.4.1.3 Bateke plateau, savanna (Congo)

Bilanko

Located within the Bateke plateau (600–800 m), the Bilanko site (3°31′S, 15°21′E, 700 m) is a 10-km closed depression occupied by floating sedges and grass mats with

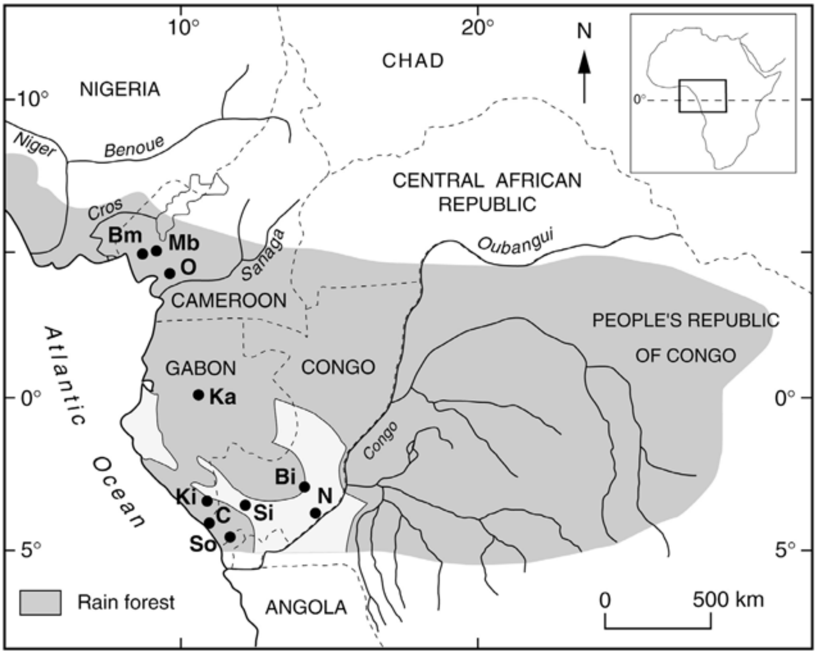

Figure 5.10. Location map of fossil pollen sites. Bm: Barombi Mbo; Mb: Mboandong; O: Ossa; Ka: Kamalete; N: Ngamaka; Si: Sinnda; Bi: Bilanko; Ki: Kitina; C: Coraf; So: Songolo.

abundant *Syzygium* (Figure 5.10). Shrub savanna vegetation occupies sandy soil in this region, characterized by 1,600-mm/yr rainfall, 4-month dry season and 4 to 6°C seasonal temperature range. The 60-cm short core, recovered from the 4 m thick peat deposit inside the depression, contained a wood fragment at the bottom that was dated at 10,850 ± 200 ^{14}C yr BP, the top part of the core not being dated. Although the pollen flora were fairly diverse (103 pollen taxa), the pollen sequence was dominated by *Syzygium* (90% of the total count) associated with a few dispersed forest trees of semi-deciduous forest. This indicated the development of a *Syzygium* swamp at Bilanko. The sediment of the core—yielding dated fossil wood—contained up to 30% *Podocarpus* pollen (Elenga *et al.*, 1991). *Podocarpus milanjianus* does not occur in the Congo Basin today, but it has been collected as isolated trees in the Chaillu Mountains, in Gabon, at the same elevation as Bilanko. Although its pollen can be transported over long distances, such high percentages imply the proximity of abundant trees nearby Bilanko, suggesting cooler temperatures during a time period corresponding to the Younger Dryas. Development of stratified low clouds has been proposed to explain occurrences of mountain plants in the lowlands (Maley and Elenga, 1993).

Bateke plateau

Macrobotanical remains have been identified from two glacial-aged sites (Figure 5.1) on the Bateke plateau (Dechamps *et al.*, 1988a). At Gaganlingolo, 17 km north of Brazzaville (3°55′S, 15°10′E) root specimens older than 30 ^{14}C kyr BP were tentatively attributed to several species of *Monopetalanthus* (Caesalpiniaceae), with *Grewia* (Tiliaceae) and *Pterocarpus* (Fabaceae). So many species of *Monopetalanthus* within a small area is surprising and brings into question the validity of specific identifications of this fossil wood. Nevertheless, the wood documents the presence of a forest in the Congo Basin during the last glacial period on the right bank of the Congo River, in a region now occupied by savanna. At Gambona (2°S, 16°E), a few hundred kilometers north, closer to the Congo Basin, wood remains of the same age yielded a more mixed assemblage including components of open woodland—such as *Nauclea latifolia* (Rubiaceae)—and evergreen forest components—such as *Detarium senegalense* (Caesalpiniaceae), *Connarus griffonianus* (Connaraceae), and *Brachystegia*.

The recovery of fossil wood at sites many kilometers apart attests to a certain geographical extension of the rainforest on land along the Congo River during the Last Glacial Maximum. Fossil wood of *Podocarpus* was not found in these terrestrial deposits dated prior to the Last Glacial Maximum, although its pollen was abundant in marine cores off the Congo coast (Jahns, 1996). Transported pollen from rainforest was indeed less important during the LGM than during stages 3 and 4 of the glacial period, but they showed their minimum percentages during stages 5b (90 kyr) and 5d (110 kyr) of the last interglacial, which cannot possibly be attributed to lower CO_2 content of the atmosphere.

5.4.2 Holocene record

In west Central Africa, the past history of lowland forests for the last 10,000 years is documented by a total of ten fossil pollen sequences located between 5°N and 5°S latitude (Figure 5.10). However, except for Barombi Mbo, most pollen records remain incomplete, discontinuous, and insufficiently well-dated. The persistence of rich, diversified forests until the last few thousand years, evidence for several drastic forest declines, use of oil palm accompanying (or not accompanying) Iron Age civilizations and the Bantu expansion in Africa will be discussed in this section.

5.4.2.1 Sites located north of the equator

Evergreen wet and semi-evergreen (Barombi Mbo, Cameroon)

The pollen sequence from the Barombi Mbo core, yielding a record for the last glacial period discussed above, also contains one of the most complete records for the last 10,000 years (Figure 5.8). In this sequence the maximum of tree density started around 11.5 kcal.yr BP and remained constant until 2.5 kcal.yr BP, with more than 90% AP indicating a dense tree canopy cover. *Olea* frequencies lower than 2% indicate that the tree had progressively disappeared from the surroundings of the lake since the beginning of the Holocene. Dominated by pioneer trees (*Mallotus*, *Macaranga*, *Musanga*, and *Alchornea*), and decreasing occurrences of *Antiaris*, the Holocene forest contained more Euphorbiaceae and fewer Caesalpiniaceae than the forest existing during the glacial period. The three types of forests occurring in the area today were already in place. The Biafran wet evergreen forest is attested by *Klainedoxa*, *Trichoscypha*, Connaraceae, the coastal by *Lophira/Saccoglottis* and *Pycnanthus*, the dry evergreen semi-evergreen by *Milicia*, *Celtis*, *Nauclea*, and *Uapaca*. The Biafran evergreen forest already existing during the glacial period appears more diversified during the Holocene with greater abundance of *Klainedoxa* (Irvingiaceae), *Trichoscypha* (Anacardiaceae), *Diospyros*, and Connaraceae. But, there were fewer Caesalpiniaceae altogether than between 31 kcal.yr BP and 24 kcal.yr BP. The forest succession started at 14.7 kcal.yr BP with abrupt increases of *Macaranga*, then *Mallotus*, followed by that of *Milicia* (Moraceae) which culminate around 11.5 kcal.yr BP. *Alchornea* reached its first peak at c. 9 kcal.yr BP. Such a progressive trend of forest took more than 2.5 kcal.yr BP to be fully established. Although it may have been triggered by increased monsoon rains, it cannot be qualified as an abrupt onset. Higher resolution pollen analysis for this interesting transition period would have allowed a valuable comparison with the fine-resolution isotopic record obtained on the same core (Giresse *et al.*, 1994). During the whole Holocene, several fluctuations in the pollen percentages of various components are depicted (Figure 5.8)—such as decreasing trends of *Klainedoxa*, *Mallotus*, and an increasing trend for *Musanga*. But, the c. 200-yr sampling interval of the pollen record remains too large to interpret these variations in terms of the vegetation dynamic under climatic variability attested by global changes. The strongest change depicted by the available data occurred around 3 kcal.yr BP when most components of the Biafran evergreen decreased or totally disappeared, while pioneers—such as *Musanga*—increased significantly. The sharp 40% peak of Poaceae attests to a short phase of open savanna around 2.5 kcal.yr BP. At that time, the increase in grass pollen was not accompanied by that of Cyperaceae, having almost disappeared during the Holocene when the lake was high and its shore immediately surrounded by forest. This is an indication that grasses may have developed inside forest openings rather than along the shoreline itself. To what extent this savanna phase is the result of human deforestation or of significant climatic aridity will be discussed later.

Ossa, hygrophilous evergreen forest (Cameroon)
The shallow Lake Ossa (7-m depth during wet season) is located a few kilometers to the west of the Sanaga River within the *Lophira/Saccoglottis* hygrophilous evergreen forest (Figure 5.10). *Elaeis guineense* and *Hevea brasiliensis* plantations have been recently established on the western shore line of the lake. The region is characterized by high rainfall—c. 3,000 mm/yr—with a long rainy season from March to November, followed by a short dry season from December to February (Nguestop *et al.*, 2004). Of the three cores recovered from Lake Ossa, one with a basal age of c. 10 kcal.yr BP shows reversed dates that indicate perturbed deposition, although the pollen attests to a well-diversified Caesalpiniaceae forest well-established around the lake since that date (Reynaud-Farrera, 1995). Another 5-m core OW 4 (3°48′N, 10°01′E, at 8 m a.s.l.), collected from the western side, provided an accurately dated pollen sequence for the last 5.5 kcal.yr BP. The pollen data include high percentages of sedges (Cyperaceae) reaching up to 50% of the total count, these perhaps due to the proximity of the river drainage, the shallowness of the lake, and associated land partially emerged during the dry season. The exclusion of Cyperaceae as well as that of fern spores from the total pollen sum for calculating percentages of other forest components is justified by the local context (Renaud-Farrera *et al.*, 1996). The Poaceae were kept in the pollen sum, although some may belong to local edaphic wetlands. Poaceae reached 15% at most and, except around 2.8 kyr BP, their stable percentages would not have strongly influenced variations in other elements (Figure 5.11).

The Ossa pollen diagram clearly indicates the persistence of an evergreen forest (AP percentages >75%) in the region throughout the last 5.5 kcal.yr BP. Forest composition around Lake Ossa differs significantly from that around Barombi during the same period (Renaud-Farrera *et al.*, 1996). Two distinct periods of forest development could be individualized, separated by an abrupt change at c. 2.85 kcal.yr BP, in surprisingly good correspondence with the limit between subboreal and subatlantic palynological subdivisions in Europe (Van Geel *et al.*, 1998). From 5.5 kcal.yr BP to 2.8 kcal.yr BP, forest composition is marked by the predominance of Caesalpiniaceae, Sapotaceae, and *Martretia* (Euphorbiaceae), associated with few *Lophira* and *Saccoglottis*, good markers of wet evergreen forest. Pollen input from highland forest is attested by minor percentages of *Podocarpus* and *Olea* (<5%), whereas the deciduous *Celtis*, *Holoptolea*, and *Piptadeniastrum* indicate a mixed semi-evergreen influence. From 2.8 kcal.yr BP to the last century, *Alchornea*, *Macaranga*, and then *Elaeis* increased significantly, while the evergreen components decreased. Although these taxa have been considered as pioneer heliophytics, it is unlikely that such strong changes in tree composition can be attributed to human impact. Earlier settlements in the Lake Ossa catchment have been dated at a much younger period, between 700 and 500 cal yr BP (Wirrmann and Elouga, 1998). From 5.5 kcal.yr BP to 2.8 kcal.yr BP, vegetation changes reflect climatic changes that may be looked for within the distribution pattern of the rainfall, rather than within its total

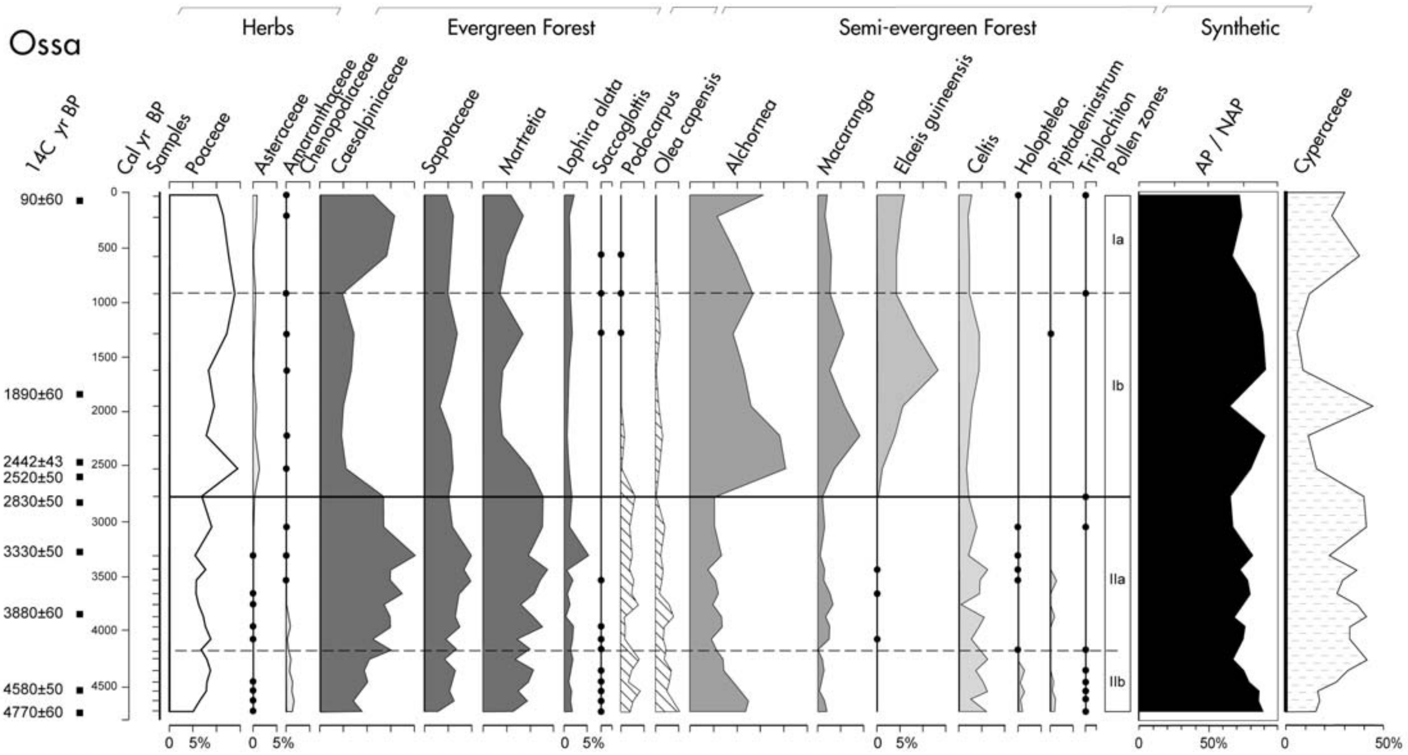

Figure 5.11. Simplified pollen diagram from Lake Ossa, Cameroon, presented according to calendar timescale (after Reynaud-Farrera *et al.*, 1996) (% calculated versus pollen sum including all the identified taxa, but excluding Cyperaceae plotted at the right-hand side of the diagram).

amount. Vegetation change appears in fairly good agreement with interpretation of the mineral composition of the sediment. High fluxes of orthoclase feldspar have been interpreted as an indication of higher precipitation than today (Wirmann *et al.*, 2001). However, a contradictory interpretation of less rainfall but high water level—indicating excess of precipitation versus evapo-transpiration—was supported by an hydrological model based upon diatom studies (Nguestop *et al.*, 2004). Interesting variability, documented by the 50-yr resolution of diatom analysis, is not depicted in the pollen diagram provided at c. 200-yr resolution only. Discrepancies in resolution prevents further comparison between the two indicators. Between 2.2 kcal.yr BP and 2 kcal.yr BP, complementary pollen counts (not illustrated here) showed another Poaceae increase synchronous with a significant input of Sahara dust that also contained allochthonous diatoms, attesting the stronger influence of north trade winds and subsequent drier conditions (Nguestop *et al.*, 2004).

The Caesalpiniaceae evergreen forest around Lake Ossa appears to have been re-established in its present composition c. 1,000 years ago. Although the wet evergreen forest was maintained, its pollen composition changed significantly throughout the last 5,000 years. To what extent such changes could be attributed to variability in the precipitation regime can be solved by performing finer resolution pollen analysis. This interesting, well-dated Lake Ossa sequence with its high deposition rate deserves further analysis.

Mboandong, evergreen wet and semi-evergreen (Cameroon)

From Lake Mboandong, (4°30′N, 9°20′E, 120 m a.s.l.) located close to Barombi Mbo (Figure 5.1), a 13 m long sediment core was recovered and provides a basal age of 6.8 kcal.yr BP (Richards, 1986). Although preliminary, the pollen diagram shows interesting highly diversified forest taxa throughout this period until the present day. Many tree pollen taxa have been identified, compared with just a few from herbaceous plants. The majority of pollen comes from components of the evergreen forest. High pollen percentages were from *Alchornea cordifolia*, an understorey tree, not specific to evergreen forest. Although there are indisputable variations in relative percentages from the Caesalpiniaceae, Euphorbiaceae, *Macaranga*, *Uapaca*, *Pycnanthus*, Moraceae, *Celtis*, *Lophira*, and *Uncaria* during the past 5,000 years, the author did not attribute them to ecological or climatic changes. The event recorded at c. 2.5 kcal.yr BP—interpreted as an indication of human impact—is discussed in Section 5.4.4 concerning the oil palm.

5.4.2.2 Sites located south of the equator

Coastal Congo, evergreen forest

The sandy coastal plain, north of Pointe Noire, is now occupied by a *Loudetia* (grass) savanna with *Manilkara lacera* (Sapotaceae). *In situ* fossil wood trunks with roots have been discovered included in a humic podzol bed (4°S, 11°45′E, Figure 5.1) that spans 7.4 kcal.yr BP to 4 kcal.yr BP (Schwartz *et al.*, 1990). The fossil wood specimens themselves have provided dates within the same time interval.Among the 117 collected specimens, a total of 20 species have been identified. These include *Saccoglottis gabonenesis*, *Agelaea* sp. (Connaraceae), and *Jundea* cf. *pinnata* (Connaraceae), *Uvariopsis angolana* (Annonaceae), *Cassipourea barteri*, *C.* sp. (Rhizophoraceae), *Dicranolepis* sp. (Thymeleaceae), *Dictyandra arborescens* (Rubiaceae), *Grewia* sp., *Neuropeltis acuminata* (Convolvulaceae), *Rinorea cf. gracilipes* (Violaceae), *Combretum* sp. (Combretaceae), *Rheedia* (Clusiaceae), and an unknown legume (possibly *Anthanota* according to Dechamps *et al.*, 1988b). Many species of *Monopetalanthus* (*M. microphyllus*, *M. pellegrinii*, *M. letestui*, and *M. durandii*), among the Caesalpiniaceae, indicate that a moist evergreen Caesalpiniaceae forest existed along the coastal plain for 3,000 years c. 6.8 kcal.yr BP to 3 kcal.yr BP. The forest was well-diversified and, according to the authors, resembles the evergreen forest described in Mount Cristal in Gabon. Fossil wood remains indicate that the moist evergreen coastal forest, now observed in Gabon, occurred 500 km south of its present southern limit between 7.4 kcal.yr BP and 3 kcal.yr BP, and therefore had a greater southern extension. The taphonomic conditions of the preserved fossil—such as standing trunks in the living position—tend to indicate that the Caesalpiniaceae forest had disappeared suddenly from the coastal region of Congo and that such disappearance was not due to human deforestation. The coastal Congo region receives 1,200 mm/yr of rainfall and experiences a 5-month dry season. There is a great contrast in seasonal temperature due to proximity of the cold oceanic upwelling offshore. The existence of a moist evergreen forest implies a greater rainfall (at least 2,000 mm/yr) or a shorter dry season. Its disappearance post-4 kcal.yr BP suggests strong changes in climatic or edaphic coastline conditions (Schwartz, 1992).

Two pollen sequences extracted from nearby depressions complete the Holocene vegetation history of southern Congo. The Coraf pollen sequence (4°15′S, 11°59′E, 150 m a.s.l.) located nearby the fossil wood site (Figure 5.10) was extracted from peat deposited inside a white sand horizon, and dated from 3 kyr to 950 yr BP. It documents a swamp forest progressively decreasing toward a modern savanna. The forest decrease was interrupted by a minor *Syzygium*/Combretaceae/*Tetracera* forest phase, dated around 1.4 kcal.yr BP. No sign of an abrupt forest decline around 2.5 kcal.yr BP was observed at Coraf, such as that in Cameroon, but the core was poorly sampled within that interval (Elenga *et al.*,1992). On the Atlantic coast, north of Pointe Noire, the Songolo pollen sequence S2 (4°45′, 11°51′E, 5 m a.s.l., 1,260-mm/yr rainfall)—dated to 7.5 kcal.yr BP at its base—indicates a well-developed *Rhizophora* mangrove, following the marine transgression at 10 kcal.yr BP. The mangrove was associated with a swamp forest dominated by *Symphonia globulifera*, *Hallea*, and *Uapaca*. Humid conditions required for the development of swamp forest are confirmed by $\delta^{13}C$ values on total organic matter. There are significant and well-dated changes depicted in the mineralogical analysis of this core. These have no equivalent in the pollen data illustrating the coastal swamp forest, but the resolution of the pollen study is too low. The swamp forest persisted until c. 3.6 kcal.yr BP, when sedges, palms, and ferns became dominant (Elenga *et al.*, 2001).

In summary, the coastal plain of southern Congo was occupied by two different types of forests: a highly diversified Caesalpiniaceae forest documented by fossil woods, and more localized swamp forests and mangrove documented by pollen evidence since at least c. 7 kcal.yr BP. The forests persisted until 3 kcal.yr BP, clearly attesting to higher humidity or precipitation than now between 7 kcal.yr BP and 3 kcal.yr BP. The pattern of forest disappearance from the area remains unsolved and variations in sea levels should be considered. The discrepancies in dating really preclude any synchronism in various changes as proposed for an environmental event occurring at 4 kyr (Marchant and Hooghiemstra, 2004). A rather more complicated pattern seems to emerge, which needs comparison of fossil data at the same resolution interval with firmly established short-term Holocene climatic variability. Nevertheless, coastal grassland in the Congo seems to have been established only after 3 kcal.yr BP, and was interrupted by a minor forest increase again at c. 1.4 kcal.yr BP.

Mayombe, evergreen transitional forests

Evergreen transitional forests dominated by Meliaceae, Fabaceae, and Irvingiaceae with a great diversity of representatives from other families occupy the Mayombe massif today (Descoings, 1976; Cusset, 1987). On the western slope of the Mayombe, Lake Kitina (4°15′S, 11°59′E, 150 m a.s.l.) is located in a valley which receives about 1,500 mm/yr of rainfall and experiences a 4-month dry season with heavy cloud cover. The lake is surrounded by swamp vegetation with *Cyperus papyrus*, *Anchomanes* (Araceae), ferns, and a few trees—such as *Alstonia* and *Alchornea*—followed by a swamp forest including *Uapaca*, *Santiria*, and *Memycelon*. A transitional semi-evergreen dry forest—with *Dacryodes*, *Klainedoxa gabonensis* (Ixonanthaceae), *Piptadenia* (Leguminosae), *Plagiostyles africana* (Euphorbiaceae), *Anthostema* (Euphorbiaceae), and Sapotaceae—is developed on slopes (Elenga *et al.*, 1996). The Holocene pollen record is dated 5,460 ± 70 yr BP at a 620-cm depth (Figure 5.12). From 5.5 to 2.7 ^{14}C kyr BP, the synthetic pollen diagram indicates two well-developed forest associations: one from dry land (*Dacryodes*, *Martretia*, and *Anopyxis* (Rhizophoraceae)), the other from swamp (*Syzygium*, *Hallea*, *Anthostema*). Between 2.7 and 1.3 ^{14}C kyr BP, four AMS dates within a 40-cm depth interval demonstrate a very low sedimentation rate (or perhaps a discontinuity). During that interval—which lasted almost 1.4 kyr—significant changes occurred. First, a sharp and important increase in dry land forest (40%) accompanied by a significant increase in amorphous silica (Bertaux *et al.*, 1996) shows that Lake Kitina partially dried out. The successive increase in pioneers (*Macaranga* and *Alchornea*), associated ferns, and Poaceae (c. 10%) indicates a greater extent of swampy conditions contemporaneous with the appearance of *Elaeis guineense*. Although these pollen changes appear depicted as an abrupt 2.7 ^{14}C kyr BP event, several episodes of reduced lake level are shown by the lithology (Figure 5.12). No detailed modifications of pollen taxa composition have been provided for documenting the effect of aridity on the composition of the forest. There is no evidence for human impact either (Elenga *et al.*, 1996). The return to humid conditions after 1.3 ^{14}C kyr BP is attested by swamp forest pollen rather than a decrease in dry land forest. But, pollen from dry land forest increased again at 0.5 ^{14}C kyr BP. The Kitina diagram clearly indicates that the composition of the Mayombe forest is recent—no older than 500 years at most.

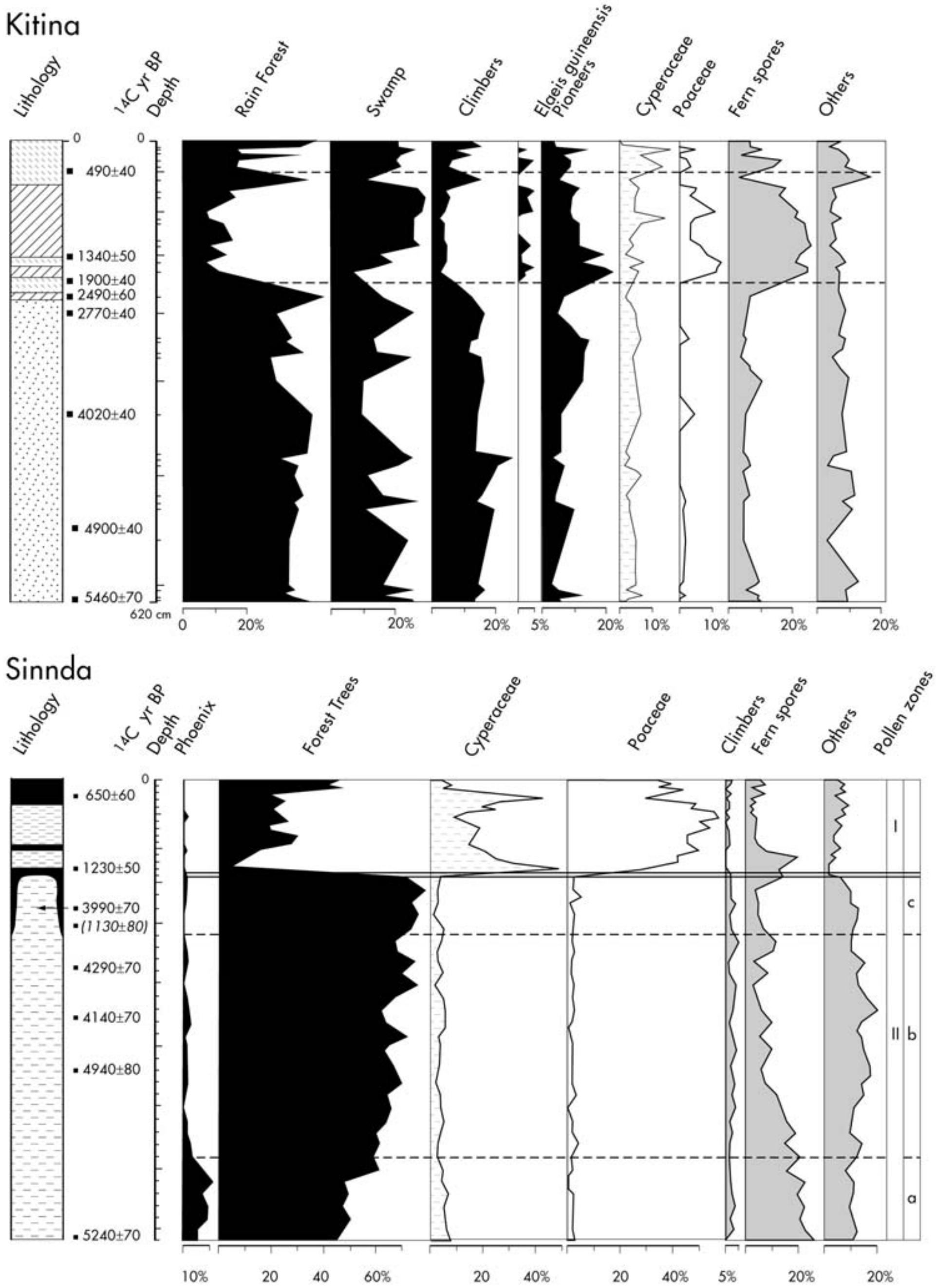

Figure 5.12. Simplified pollen diagrams from Lake Kitina (from Elenga *et al.*, 1996) and Sinnda, presented according to depth (after Vincens *et al.*, 1998) (% calculated versus pollen sum including all identified taxa, Cyperaceae, and spores).

Niari Valley, grasslands

The geographical location of Lake Sinnda (3°50′S, 12°48′E, 128 m a.s.l.)—inside a large band of wooded grassland separating the two massifs of Mayombe and Chaillu within the dry semi-evergreen forest to the south—is particularly interesting for addressing the origin of included grassland (Figure 5.10). Here, mean annual rainfall is about 1,100 mm/yr with a 5-month dry season from mid-May to mid-October. Two well-dated cores analyzed for both pollen (Vincens *et al.*, 1994) and phytoliths (Alexandre *et al.*, 1997) provide evidence for a well-diversified dense forest from 5,240 ± 70 to 3,990 ± 70 yr BP (Figure 5.12) with little impact of pollen from grasslands (Vincens *et al.*, 1998, Figure 5.4). Dominated by *Chlorophora* (Moraceae), *Alchornea*, *Celtis*, *Pausinystalia* (Rubiaceae), *Macaranga*, and *Lannea* (Anacardiaceae), and a great variety of taxa, the fossil pollen indicates a semi-evergreen (semi-deciduous forest). Noticeable changes occurred. *Phoenix*, *Myrianthus*, and ferns are well-represented before 5 ^{14}C kyr BP, whereas *Celtis*—associated with Caesalpiniaceae, Fabaceae, and many Euphorbiaceae—increased at about 4.5 ^{14}C kyr BP. But, the most obvious change observed at Sinnda is situated in the interval between c. 4 and 1.2 ^{14}C kyr BP when a strong gap is registered in the sedimentation of the core. After that gap, the pollen assemblages were dominated by grasses and sedges, evidencing greater development of marshes, now existing at the northeast end of the lake. The forest was considerably impoverished in taxa, although Ulmaceae (*Holoptolea*, *Trema*, and *Celtis*) and *Chlorophora* accompanied the *Alchornea* still present on the steep shores of the lake. The abrupt character of such a change results from a gap of more than 2,000 years, likely corresponding to an arid period when the 4 m deep Lake Sinnda dried out. Many forest trees disappeared during that interval. Although this is the most obvious post-4 kyr BP change observed in the region, the fact that the lake is shallow, located at the ecological limit for forest growth with a long dry season, and that the pollen percentages decreased abruptly at the discontinuity of the core maximize the impact of climatic change probably responsible for this pattern. Positive evidence for forest changes is missing. A second core in the central part of the lake contains black organic layers with abundant plant remains indicating that two subsequent drying phases occurred: one at 4.5 kyr BP followed by another post-1.7 ^{14}C kyr BP. An increase in tree forest taxa (AP $>$ 40%) at the upper part of the core dated 650 ± 60 yr BP points to a recovery of the forest nearby. The pollen curve of the possibly cultivated *Elaeis guineense* became significant only during the last 600 years, probably linked to possible settlement by Bantu-speaking proto-agricultural people (Schwartz, 1992). Charcoal dated 2,130 ± 70 yr BP, on the Bateke plateau, and 1,600 yr BP in Mayombe clearly support the long use of fire in the region (Schwartz *et al.*, 1990). A date of 1,350 ± 70 yr BP obtained on burned specimens of *Erythrophleum suaveloens* (Caesalpiniaceae)—a ubiquitous tree, used by local people for its toxic alkaloids and extracted from archeological sites—confirms human fire usage in Mayombe (Dechamps *et al.*, 1988b). From the Sinnda record itself, it cannot be exactly established when (between 4 and 1.2 ^{14}C kyr BP) the savanna spread in the Niari Valley, but grasslands are present once fire is introduced at c. 1.2 kcal.yr BP.

Close to the Congo River, grassland/semi-evergreen forests

Near the right bank of the Congo River three cores were recovered from the Ngamakala pond (4°04′S, 15°23′E, 400 m a.s.l.) which yielded records from the glacial period (see above). None of them yielded a complete Holocene sequence. In one core, there is only 20-cm sediment deposited between the two conventional radiocarbon dates of 10,880 ± 160 and 3,940 ± 130 yr BP (Elenga *et al.*, 1994). Their pollen content corresponds to a *Syzygium*/Sapotaceae swamp forest, but accurate age determination is not available. Another core provided a 1 m thick accumulation of peat deposited between c. 3 kyr and 1 kyr BP, attesting to the retreat of swamp forest at the expense of grasslands during that interval. A significant expansion of swamp *Syzygium* forest re-occupied the pond again at 930 ± 140 yr BP. Although far from being complete, the succession of forest associations nearby the Congo River emphasizes many successive steps of changes during the Holocene. Among those the opening of the forest at Ngamakala is sharply registered at c. 3.3^{14}C kyr BP. But, this cannot be considered synchronous with any of the events at 4 or 2.5^{14}C kyr BP previously discussed.

5.4.3 History of the rainforest during the last 5,000 years

During the last 5,000 years the evolution and dynamics of the rainforest forced by climatic changes appear rather complicated. Apparently, they do not depict the same pattern north and south of the equator, but the lower Holocene record is missing (or discontinuous) at all the sites except at Barombi Mbo in Cameroon. There, the depicted changes indicate significant climatic variability during the Holocene, but there is no clear identification of an "African humid period" prior to 6 kcal.yr BP. At most sites, negative evidence and lack of sedimentation during the early Holocene may attest to drier climatic conditions. Hence the status of rainforest existence at that time and composition remains unknown. The results summarized here firmly establish that evergreen and semi-evergreen rainforests persisted between 6 kcal.yr BP and c. 3 kcal.yr BP at all of the nine investigated sites. Slightly before or after 3 kcal.yr BP, major vegetation changes are documented (Vincens *et al.*, 1999). Because of discrepancies in the resolution of the analysis it is not clear, however, whether these changes reflect several short-term episodes of climatic variability at a millennial scale concerning seasonal distribution of rainfall, or a longer single event. One major vegetation change documented in Cameroonian sites is well-bracketed between c. 2.8 kcal.yr BP and 2.2 kcal.yr BP. Elsewhere, more attention needs to be paid to their chronological control (Russel *et al.*, 2003). Discrepancies in the stratigraphy, gaps in the sedimentation, different time resolutions of pollen data, as well as local climatic conditions relevant to length of the dry season, prevent the correlation of changes at all the sites within a single event. The proximity of a lake or rivers could maintain edaphic forests. Although reduction in the hydrological budget and lowering lake levels have been documented simultaneously by geological studies (Servant and Servant-Vildary, 2000), Upper Holocene aridity was not an irreversible climatic event.

Many sites indicate the return of wetter conditions during the last millennium, creating favorable conditions for new forest expansion again between 0.9 kcal.yr BP and 0.6 kcal.yr BP (Vincens *et al.*, 1996a, b; Elenga *et al.*, 2004).

On the other hand, the synchronous expansion of grasslands at c. 2.2 kcal.yr BP in lowlands, on the eastern side of Mount Cameroon, nearby lakes Barombi Mbo (Maley, 1992), Mboandong (Richards, 1986), and Ossa (Reynaud-Farrera, *et al.*, 1996) is in good correspondence with the Iron Age. But, whether such expansion was climatically controlled or human-induced does not reach a consensus among different specialists and remains a matter of speculation (Maley, 1992; Schwartz, 1992). High-resolution diatom analysis of the Ossa core provides new, interesting data for the climatic interpretation of the complexity of that event. In striking correspondence with the 2.7 kcal.yr BP North Atlantic cold event (Bond *et al.*, 1997), in Africa an increase in lake level and rainfall is bracketed by two strong amplitude shifts to drier conditions. The first was interpreted as a decrease in rainfall. The second lasted a few hundred years when decrease in water level and stronger input of allochthonous diatoms transported from Lake Chad indicate reinforced northern winds responsible for stronger aridity between 2.3 kcal.yr BP and 2 kcal.yr BP. The high-amplitude oscillations registered at Ossa suggest that a further high-resolution study of the nearby high-elevation Bambili lake (Stager and Anfang-Stutter, 1999) would be worthwhile. Synchronous vegetation change between a Caesalpiniaceae/*Lophira*-dominated forest before 2.5 kcal.yr BP replaced by an *Alchornea*/*Macaranga* open forest after 2.3 kcal.yr BP could well be explained by an increased length in the dry season and possible effect of low subsidence and storms following movement of the ITCZ (Nguestop *et al.*, 2004). Such an interesting hypothesis might receive more support when higher resolution pollen data have been obtained. An increased proportion of *Elaeis guineense* (oil palm) in the Ossa pollen record occurred simultaneously, which brings to the fore the fact that several dry episodes—also expressed at Kitina and Sinnda—created consecutive openings through the equatorial forest. These gaps offered a possible direct route for the Bantu migrations from Cameroon to the south.

5.4.4 The oil palm, evidence for human impact?

Evidence for human impact on past vegetation can come from the findings of abundant pollen from used or cultivated plants—such as *Dioscorea* (the yam), *Elaeis guineensis* (oil palm), and *Canarium schweinfurthii*, the last two producing fruits and seeds extensively used as a source of edible oil (Shaw, 1976). *Dioscorea* pollen has been identified in modern surface samples at the contact between the forest and the savanna at Kandara (Vincens, pers. commun.), but no evidence for its fossil pollen has been found, whereas fossil *Elaeis guineensis* has been reported at many sites. At Mboandong (Cameroon), a forest decrease associated with a significant grass increase, and followed by a well-marked increase in oil palm pollen (up to 20%) at 2.4 kcal.yr BP, has been interpreted as evidence for human impact on the basis that this date was close enough to that of the Nok archeological Iron Age site. It was suggested that forest clearance could be attributed to iron technology (Richards, 1986). But, in the pollen diagram opening of the forest occurred first. Pollen of

Canarium schweinfurthii, clearly distinguished from other Burseraceae—notably *Aucoumea* (Harley and Clarkson, 1999; Sowunmi, 1995)—was recorded at c. 5 kcal.yr BP, suggesting an earlier presence of humans nearby the fossil pollen site. Early evidence of oil palm pollen is known since the Tertiary in the Niger delta (Zeven, 1964), and was reported in Upper Pleistocene marine sediments offshore the Niger River (Dupont and Weinelt, 1996). However, it is only during the last 3,000 years that the proportion of *Elaeis guineensis* pollen reached significant values (up to 24%) in the Niger delta (Sowunmi, 1999). As a "palm belt", present day natural distribution of the oil palm follows the gulf of Guinea and largely penetrates inside the Congo Basin. *Elaeis guineensis* is an heliophytic pioneer species, also fire-resistant (Swaine, 1992), which occurs naturally in a great variety of habitats inside the rainforest including swamp and at its periphery (Letouzey, 1978). All these characteristics largely contribute to the difficulty of interpreting their fossil record. The pattern of occurrences and abundance of *Elaeis guineensis* pollen through time is not similar at all the investigated sites, and this led to controversial interpretation. In Ghana, archeological remains indicate an earliest use at 5.8 kcal.yr BP (Shaw, 1976), but its fossil pollen became abundant only after 3 kcal.yr BP in the Niger delta. The common pattern in the three Cameroon sites, starting with scattered *Elaeis guineensis* occurrences from c. 4 kcal.yr BP to 3 kcal.yr BP, followed by a significant increase at c. 2 kcal.yr BP (Richards, 1986; Reynaud Farrera *et al.*, 1996; Maley and Brenac, 1998) is remarkable. At Barombi Mbo the peak of oil palm pollen (2.9 kcal.yr BP to 2.4 kcal.yr BP) corresponds to the 2.75 kcal.yr BP crisis (Van Geel *et al.*,1998) or "dramatic forest decline". It occurs a few hundred years earlier than the peak of grasses (2.7 kcal.yr BP to 2.2 kcal.yr BP) and much earlier than the Bantu invasion (2.2 kcal.yr BP to 2 kcal.yr BP) (Schwartz, 1992; Maley, 2001). Therefore, *Elaeis guineensis* increased in response to increased aridity happening in the rainforest a few centuries before the spreading of oil palm by Bantu speakers. In contrast, several papers discussed the past record of *Elaeis guineensis* in West Africa (see Sowunmi, 1995 for an exhaustive literature), possibly enhanced by Bantu speakers (Schwartz, 1992; Maley, 2001). In Gabon, Neolithic populations had occupied the savanna of the Ogoué Valley since c. 3.7 kcal.yr BP and the main expansion of iron-smelting dates at c. 2.2 kcal.yr BP (Oslisly and Fontugne, 1993; Oslisly, 2001). Abundance of oil palm pollen happened at a coastal site around 3 kcal.yr BP, following forest reduction 1,000 years later. At Kamalete, inland, it is registered much later, during the warm medieval period from 1.2 kcal.yr BP to 0.3 kcal.yr BP. There, the oil palm phase is registered simultaneously within the pioneer forest phase, showing a significant peak at 0.9 kcal.yr BP, during a gap in human occupation (Ngomanda, in press). At the Songolo mangrove site (Congo coast line), scattered occurrences of *Elaeis guineensis* pollen have been found from 3.6 kcal.yr BP onward (Elenga *et al.*, 2001), but no significant increase has been observed until the last centuries, neither at Ngamakala and Bilanko nor Kitina and Sinnda (Vincens *et al.*, 1998). At inland sites, climatic conditions may have been too dry for the development of oil palm (Elenga *et al.*, 1996, 2001). Occurrences of oil palm are apparently associated with increased grass pollen or a more deciduous character of the forests (Vincens *et al.*, 1996a, b). But, their peaks in abundance are not synchronous events and the geographical distribution pattern through time is far from being spatially and geographically consistent. Our available knowledge can be summarized by the following conclusions. First, there was a greater evidence of oil palm pollen during the last 3,000 years over the Guineo-Congolian rainforest. Second, simultaneity of forest openings and use of oil palm by human populations is not demonstrated at all the sites with sufficiently accurate time control or fine-resolution interval. Third, geographical progression of the use of oil palm, following Bantu migration, remains to be demonstrated. The oil palm has a very short reproductive cycle, and it can indicate simultaneous use by humans following—by a few years—anthropogenic or natural forest perturbation. Fourth, proof of anthropologically enhanced modifications of the rainforest, prior to the last few centuries, has yet to be provided.

5.4.5 The last historical period (Gabon)

Important past vegetation changes inside the moist evergreen Guineo-Congolian rainforest have been evidenced in the historical period within core sediments obtained from Lake Kamalete in central Gabon (Ngomanda *et al.*, 2005). Within the forest of the Lopé National Park, Lake Kamalete is located inside a 60 km long strip of savanna interrupting the Maranthaceae forest, whereas the closed canopy forest stands at c. 20 km west of the lake (Figure 5.1). Situated at the end of a valley, not far from the Ogooué River, the shallow Lake Kamalete is surrounded by a mosaic of savanna and isolated fragments of Marantaceae forest. Sedges (Cyperaceae) and ferns colonize its shoreline (Figure 5.13, see color section). In this area, precipitation oscillates around 1,500 mm/yr, a low value for Gabon due to the rain shadow effect of the Cristal Mounts on the western side. But, present day meteorological values show great interannual variability related to variable timing and duration of the dry summer season (June to September) when the Inter Tropical Convergence Zone (ITCZ) moved to the northern hemisphere. During the dry season, dense cloud cover maintains high relative humidity and slightly lower temperature when sea surface temperature drops out.

A c. 4-m core recovered from Lake Kamalete (0°43′S, 11°46′E, 350 m a.s.l.) was dated by four conventional radiocarbon dates, providing a basal age of c. 1.3 kcal . yr BP. Fine-resolution pollen analysis of the order of one or two decades documents important past vegetation changes and detailed composition of the moist evergreen Guineo-Congolian rainforest (Ngomanda *et al.*, 2005). The original fossil pollen sequence includes 80 samples and counts of 124 identified pollen taxa. A simplified version is presented here (Figure 5.14).

In this context, fern spores, grasses, and sedges produced the highest quantities of pollen. Grass pollen percentages average 70% of the total pollen sum (after spores, aquatics, and sedges had been excluded) indicating persistence of a forest–savana mosaic at the site. Because significant pollen counts had been achieved at each level, a detailed diagram could be drawn for forest arboreal pollen (Figure 5.15).

Among palynologists it is assumed that pollen abundance is related to abundance of trees, rather than to direct yearly pollen production, although this might deserve consideration when 1-cm sampling represents 2 or 3 years of pollen deposition.

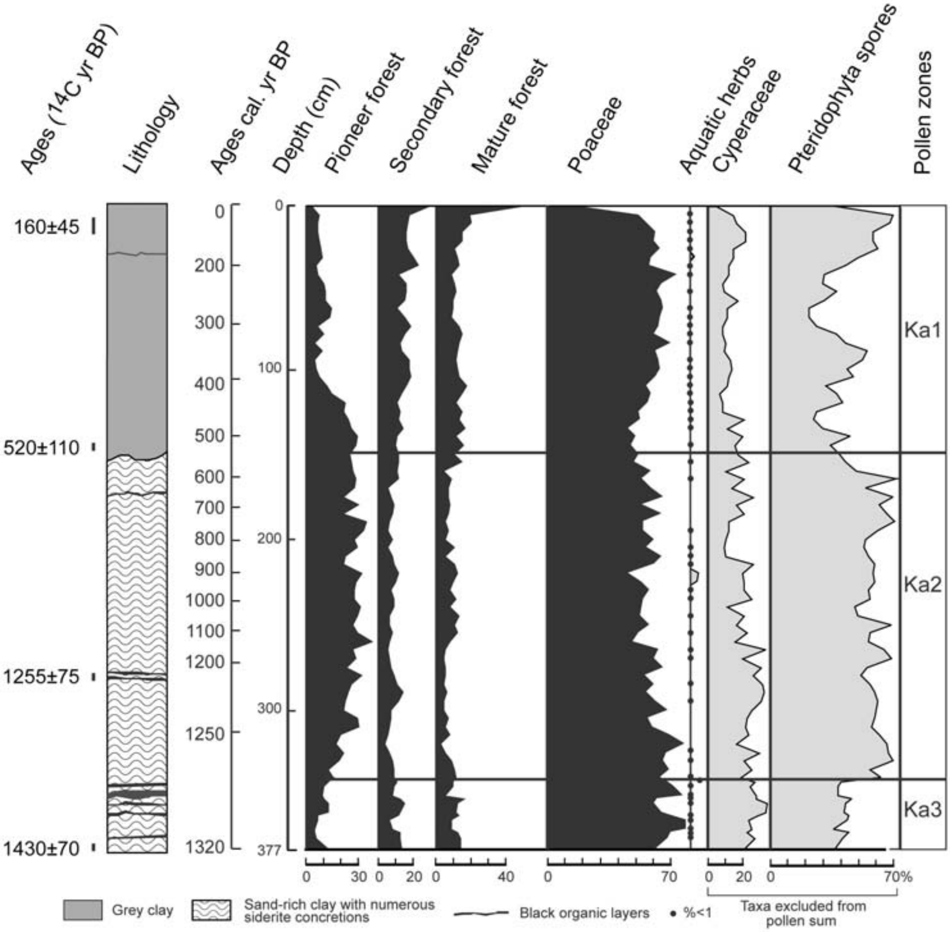

Figure 5.14. Synthetic pollen diagram from Kamalete, Gabon (after Ngomanda *et al*., 2005), presented according to depth with corresponding time scale (% calculated versus pollen sum including all identified taxa, Cyperaceae, and spores).

Significant changes in abundance and floristic composition of the regional forest occurred at Kamalete during the last c. 1.5 kcal . yr BP. Successive fluctuations in dominant taxa are documented by trends that lasted a few hundred years or more. Before c. 1325 to 1240 cal yr BP, the first forest phase includes high representation of *Cnestis* (Connaraceae), *Celtis*, *Bosqueia* (Moraceae), Caesalpiniaceae, and *Lophira alata* pollen. It ends rather abruptly, being replaced by a disturbed forest dominated by pollen from trees—such as *Tetrorchidium*, *Macaranga*, *Musanga*, *Alchornea*—that dominate in opening gaps within forests today, whereas mature forest trees simultaneously decrease. The disturbance phase lasted about 700 years (c. 1,250 to 550 cal yr BP) and may have been caused by stronger winds, changes in rainfall regime, or human impact. Indeed, Iron Age settlements occupied the Lopé region since

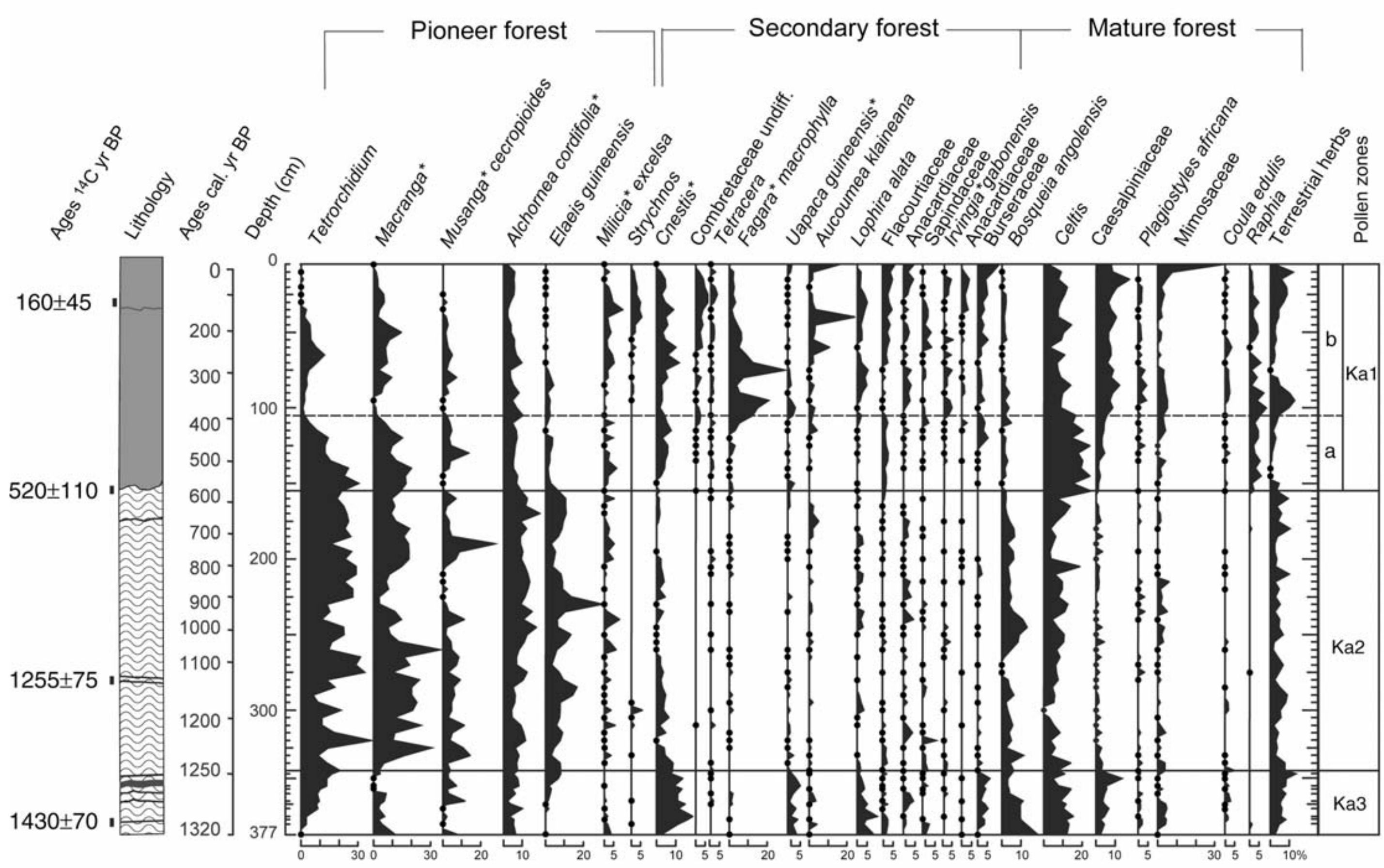

Figure 5.15. Detailed pollen diagram of the forest trees from Kamalete, Gabon (after Ngomanda *et al.*, 2005), presented as in Figure 5.12 (% calculated versus pollen sum after excluding Cyperaceae, spores, and Poaceae). Symbols for lithology as in Figure 5.12. * = pollen types < 1%.

2.6 kcal . yr BP—that is, long before the disturbed forest phase documented at Kamalete. But, from 1,400 to 800 yr BP the number of archeological sites in Gabon were fewer than before, a reduction attributed to a "population crash" (Oslisly, 2001). If there was any significant human impact on vegetation due to Iron Age population, one would expect it to be less important when the population was smaller than before or after. The opposite pattern being observed, Iron Age impact was considered not responsible for the observed disturbed forest (Ngomanda *et al.*, 2005). The period of maximum forest disturbance includes the time span of the "Medieval Warm Period" (MWP, 900–600 cal . yr BP), although the disturbed forest phase in Gabon (c. 1.25 kcal . yr BP to 550 cal . yr BP) started before the beginning of the MWP climatic anomaly. Well-known in the northern hemisphere (Bradley, 2000), the "Little Ice Age" (c. 600–200 cal . yr BP) that followed the MWP had a major effect on the evergreen forest of Gabon (Ngomanda *et al.*, in press), and is probably present in records from Cameroon (Nguetsop *et al.*, 2004), Congo (Elenga *et al.*, 1996), East Africa (Verschuren *et al.*, 2000), and Lake Victoria (Stager *et al.* 2005). In Gabon, a re-expansion of the forest took place at c. 550 cal . yr BP, after the disturbance phase. At this time *Celtis* and *Raphia* dominate, indicating a colonizing stage resembling the modern one described for Kandara (Vincens *et al.*, 2000). Two hundred years later, the site was both a "secondary forest" and a well-diversified mature forest occupied by *Lophira*, *Fagara* (Rutaceae), *Pycnanthus*, *Irvingia*, *Plagiostyles*, Caesalpiniaceae, and Burseraceae—bearing floristic affinities with the present day forest in the region (Jolly *et al.*, 1996). At Kamalete the "Little Ice Age" period was favorable for forest development. In Gabon the re-establishment of a well-diversified mature forest dates from 400 years at most. Since 250 years ago, *Aucoumea* pollen frequencies exhibit three sharp peaks, indicating significant recoveries after forest cutting for timber. We have already discussed that the origin of mature forest seems no older than a few hundred years, in strong contradiction with the long-standing belief of rainforest stability over time. Past hydrological changes across the equatorial tropics are partly explained by amplified shifts in mean latitude of the ITCZ (Haug *et al.* 2001). The sensitivity of the rainforest to short-term past climatic forcing is clearly demonstrated and suggests the great impact that greenhouse warming can have in the future.

5.5 CONCLUSIONS

For many decades, palynological studies in the tropics were limited by the lack of knowledge in tropical pollen morphology. Important reference collections of African tropical plants have been made in Durham (NC), Montpellier and Marseille (France), Germany, Nigeria (Africa), the United Kingdom, etc. Description of the pollen morphology for most common trees is available in several publications and pollen atlases (Maley, 1970; Bonnefille 1971a, b; Sowunmi, 1973, 1995; Caratini *et al.*, 1974; Bonnefille and Riollet, 1980; Salard-Cheboldaeff, 1980, 1981, 1982), from which some pollen photographs are now being included in the African Pollen Data Base. Therefore, pollen analysis in the African tropics is feasible, although it still requires lengthy training. The bias between pollen assemblages and plant associations will remain. But, interpretation of fossil data will be facilitated by modern pollen rain studies concerning many types of rainforest, encountered under different ecological conditions. Taxonomic composition and taxa frequencies of pollen assemblages can be used to characterize habitat types, despite the absence of pollen from important tropical families. Modern pollen assemblages help us to interpret tropical forest dynamics in the past, as forced by climatic changes. They have also been successfully used in elaborating a biome approach to modeling past global vegetation (Jolly *et al.*, 1998), the quality of which depends upon homogeneity in sampling and completeness along continuous climatic gradients. With the major threat of rainforest disappearance in mind, completing modern pollen data from all the African forests constitutes an urgent task.

Fossil pollen data from different vegetation types inside the Guineo-Congolian rainforest of the African continent—now available—document strong modifications in the floristic composition of both evergreen, semi-evergreen forests, and associated mixed types through time, the most important occurring during the last glacial maximum. Proof exists that rainforest persisted during glacial time, at two investigated sites, although it included more semi-evergreen taxa, a few highland taxa (*Olea* and *Podocarpus*) and was more open. Site-based maps of global vegetation at the LGM including Africa (Elenga *et al.*, 2000c) were used for a comparison between different vegetation models (Kohfeld and Harrison, 2000) addressing land surface feedbacks (Clausen, 1997) or the effect of lower CO_2 in global modelling. Although it has been generally considered that "tropical forests in Africa, Australia and Asia were partly replaced by more open vegetation" (Harrison and Prentice, 2003), the persistence of rainforest during the last glacial period, even when lower CO_2 content in the atmosphere was not favorable to tree growth, is clearly attested at two tropical sites located within the rainforest region. A greater extension of forest can even be postulated from abundant fossil wood remains.

Lowlands on the eastern side of Mount Cameroon and near the Congo River have been proved to be rainforest refuges during the LGM. Clearly, forest refuges were not geographical areas or spots bearing forests of similar composition to those of today, and there may have been many other refuges of different groups of species that remain to be found. Throughout the inter-tropical region ecological constraints related to hydrological constraints may have varied. Different species may have found refuge in different localities. Direct evidence can be provided by further research on fossil pollen or macrobotanical remains.

During the Holocene, significant variations in tree pollen assemblage percentages have also been observed at all the ten investigated sites presented in this chapter. These are not induced by variations in the CO_2 content of the atmosphere, which stayed fairly stable throughout this period. Replacement of dominant taxa or fluctuations in pollen abundance continuously occurred, suggesting the dynamic behavior and successive replacement and dominance within the rainforest forced by variations in the hydrological system. Some of these modifications reflect changes in the amount and distribution of rainfall in the tropics, a pattern determined by several causes not unanimously explained yet. Simultaneity of forest changes at different localities cannot be firmly established until homogeneity in resolution is reached and the lower Holocene is more fully documented at more than one site. A strong-amplitude century-scale arid/humid/arid oscillation in the interval 2.5 kcal.yr BP to 2 kcal.yr BP is only found north of the equator. This change corresponds fairly well to the Iron Age, but its reversal character seems to be reflecting natural climatic change rather than being attributed to human impact. Evidence for disturbed vegetation in Central Gabon during the warm medieval period, when the influence of the Iron Age decreased, is followed by a different forest composition from 600 to 200 cal yr BP when wetter conditions seem to have been a response to the "Little Ice Age". That the tropical world was not a stable environment in the past is now amply demonstrated. Permanent changes in ecological conditions may have triggered speciation leading to high floristic diversity. The great sensitivity of the rain forest to any short-term global climatic changes draws attention to the consequences of future climatic changes induced by the greenhouse effect on the rainforest. The modern composition of the different types of rainforests only dates from a few centuries or 1,000 years at most at all the investigated sites. This bears some consideration to rainforest conservation and biodiversity issues.

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