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Pollen-rain–vegetation relationships along a forest–savanna transect in southeastern Cameroon

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Abstract

Modern soil and litter samples from southeastern Cameroon, collected along a continuous forest–savanna transect were analysed for pollen content to define modern pollen–vegetation relationships. The pollen results, completed and compared with botanical inventories, leaf area index and basal area measurements performed in the same area, clearly registered the physiognomy, the main floristic composition and floral richness of the two sampled ecosystems. Distortions were observed between sampled vegetations and their pollen rain, related to important differences in pollen production and dispersal of plant species: this is a general feature in many tropical regions. The pollen data in the area studied reflected well the recent transgression of forest versus savanna. This permitted us to define inside the forest ecosystem more successional vegetation communities than the botanical surveys allowed. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: calibration; Cameroon; modern pollen spectra; palynology; vegetation communities

1. Introduction

In Africa, until recently, the study of modern pollen deposition has been largely used to provide modern references for quantitative reconstructions of biomes (Jolly et al., 1998, 2000; Elenga et al., 2000) and climatic parameters (Peyron, 1999; Peyron et al., 2000) at key periods of the Quaternary (6000 and 18 000 ^{14}C B.P.), or along continuous temporal sequences (Bonnefille et al., 1992; Chalié, 1992; Vincens et al., 1993). Pollen sampling was generally made under stable and mature formations, without anthropogenic influences, representative of the main vegetation types occurring today in Africa (White, 1983). In some regions, long pollen transects have been established (e.g. Ybert, 1975; Bonnefille and Riollet, 1987; Lézine and Hooghiemstra, 1990; Bonnefille et al., 1993; Vincens et al., 1997), but they were always discontinuous, i.e. without relations and interferences between sampled vegetation types.

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This paper presents the most recent palynological research carried out in southeastern Cameroon, in the Kandara area, as part of the ECOFIT program (CNRS–ORSTOM). The work is based on pollen analyses of soil and litter samples collected along a continuous transect representative of the recent dynamics (recent centuries) between forest and savanna. Replacement of savanna by forest has been demonstrated in many regions of Central Atlantic Africa. For example, in Ivory Coast and in Congo, long-term experiments and models have shown that, during recent centuries, forests have been transgressive owing to climatic conditions favourable to their expansion and that savanna vegetation is today mainly maintained by the dual effects of fires and water stress in soils (Schwartz et al., 1986, 1996; Menaut et al., 1990). In Cameroon, more precisely in the Kandara area, the recent researches undertaken by Achoundong et al. (1996, 2000), Kamgang Beyala et al. (1996), Kamgang Kabeyene Beyala (1998) and Youta Happi (1998), have also clearly demonstrated that the forest is today spreading over the savanna, with occurrence of several successional stages of colonization.

This work attempts to characterize by palynological methods the recent dynamics of the Kandara forest, and to identify the modern pollen rain in vegetation types that reflects successional stages of colonization of savanna by forest. A comparison with local botanical data and with leaf area index (LAI) and basal area measurements is shown.

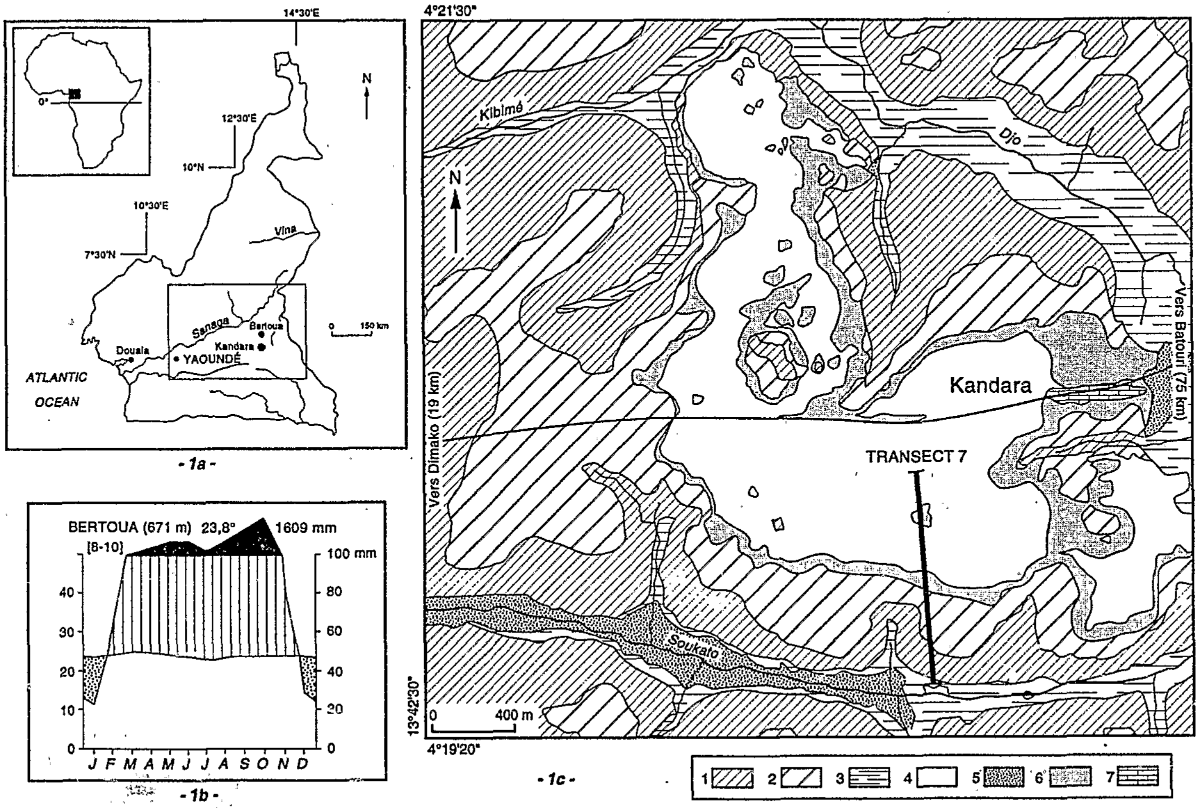

Fig. 1. (a) Location map of the Kandara area in Cameroon; (b) meteorological data registered at the Bertoua station [from Walter and Lieth (1960)]; (c) location of the transect 7 in the Kandara area and main vegetational communities [1: *Rinorea* forest; 2: *Albizia* forest; 3: *Raphia* swamp; 4: *Albizia* savanna; 5: herbaceous swamp; 6: recent transgessive forest (1951–1993); 7: village; from Youta Happi (1998)].

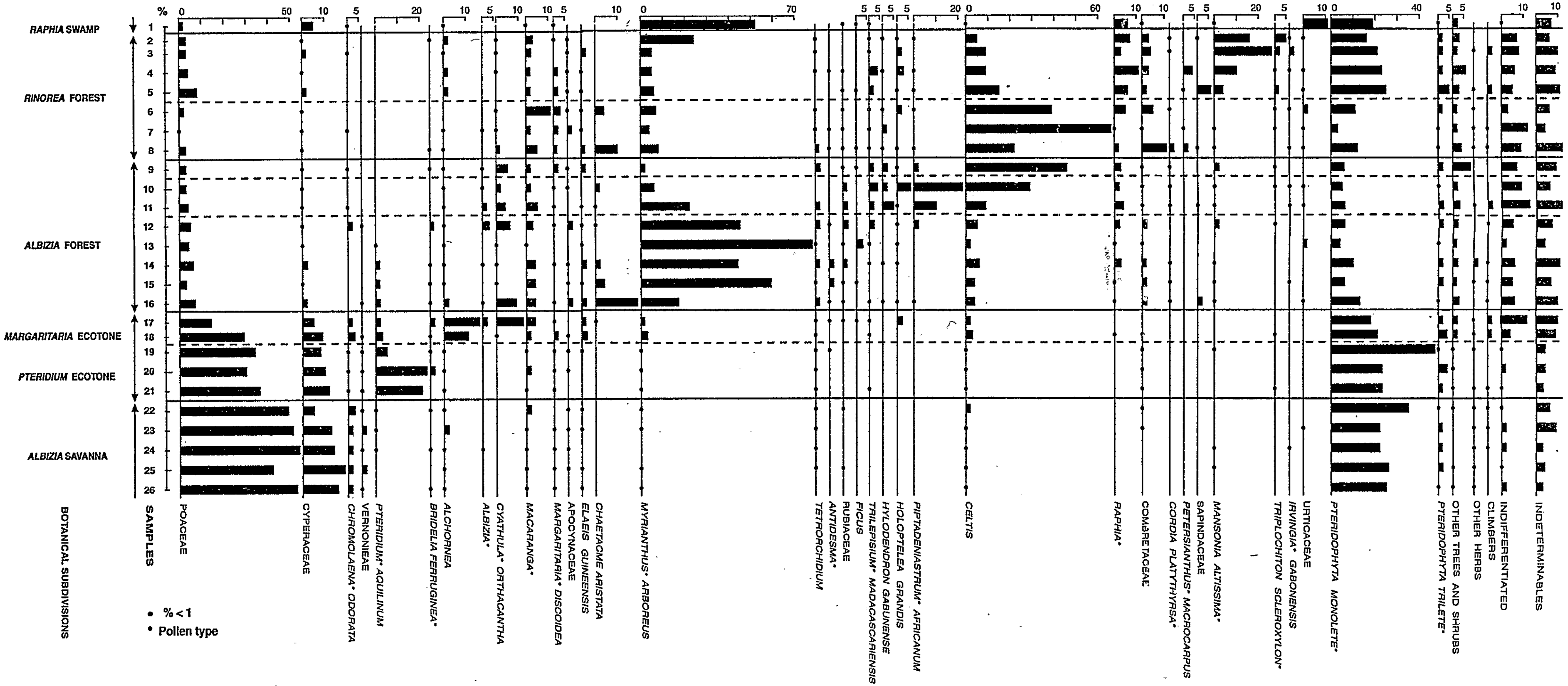

Fig. 2. Simplified diagram of modern pollen spectra from the Kandara area, southeastern Cameroon. The pollen sum includes all identified taxa, excluding damaged grains.

2. General setting

The Kandara site studied (4°20′N, 13°43′E) is located in the southeastern part of Cameroon, south of the town of Bertoua, at an altitude of 640 m (Fig. 1a). The climate of this area is defined by Suchel (1988) as of Cameroonian type, characterized by mean annual precipitation of about 1600 mm with a short dry season from December to January ($P<50$ mm/month), and a mean annual temperature of 23.8°C (Bertoua meteorological station; Fig. 1b).

This region is occupied today by a forest–savanna mosaic consisting of a mixture of semi-deciduous forest and savanna belonging to the Guineo-Congolian phytogeographical region (Letouzey, 1968; White, 1983). The Kandara site is characterized by the presence of a tall grass savanna enclosed in semi-deciduous forested formations (Fig. 1c). Detailed botanical studies made by Achoundong et al. (1996, 2000) and Youta Happi (1998) along several transects show a succession of five main formations from the north to the south, namely: (1) a tall grass savanna with *Imperata cylindrica* rich in *Albizia* (*Albizia adianthifolia* and *Albizia zygia* dominant); (2) an ecotone with a high frequency of *Pteridium aquilinum*, *Aframomum latifolium*, *Chromolaena odorata*, *Margaritaria discoidea*, and *Antidesma venosum*; (3) a young *Albizia* forest with as dominant trees *A. adianthifolia*, *Funtumia elastica*, *Canthium* sp., *Tabernaemontana crassa*, *Sterculia rhinopetala* and *Myrianthus arboreus*; (4) a mature *Rinorea* forest with abundant *Triplochiton scleroxylon*, *Piptadeniastrum africanum*, *Rinorea dentata* and *Rinorea batesii*; (5) at the southernmost part of the transects, along the Soukato river (Fig. 1c), swampy formations with the dominant arboreal component found being *Raphia*.

3. Material and methods

The modern pollen samples analysed in this study have been collected on 26 contiguous plots located along a 750 m transect (transect 7, Fig. 1c) cutting through the savanna (north), the ecotone and the forest until the *Raphia* swamp (south) and crossing the forest–savanna boundary at right angles. Each pollen sample consists of 20–30 subsamples (1 cm^3) of surface soil or litter mixed together, collected randomly within each plot of 30×10 m^2 in size. Samples 2 (10×10 m^2, *Raphia* swamp–mature forest boundary) and 18 (15×10 m^2, forest–savanna boundary) were of a different size. Some plots located in the *Albizia* forest (10, 13 and 16) had suffered from recent local clearance affecting only the understory.

At the laboratory, the samples were sieved with a 200 μm sieve in order to eliminate the coarse particles and 10 to 15 g of the finest sediment was analysed. Chemical treatment follows the classical method of Faegri and Iversen (1964): dissolution of the carbonates and silicate with diluted HCl (10%) and cold HF (70%) respectively; removing colloidal silica with warm diluted HCl and destruction of humic acid by dilution in KOH (10%) solution. After several centrifugations and rinsing in distilled water, the final residue was coloured by safranin and diluted in glycerin. A small fraction of this residue was mounted for microscopic observation.

Pollen was counted and identified at 250 × and 1000 × magnifications. At least 450 pollen grains were counted for each sample. The identifications were based on the reference collection of some 7000 specimens present in the CEREGE, Aix-en-Provence, and on specialized publications relevant to African pollen morphology (e.g. for the Cameroon or adjacent countries: Sowunmi, 1973, 1995; A.P.L.F., 1974; Ybert, 1979;Salard-Cheboldaeff, 1982, 1983, 1984, 1986, 1987).

Results are presented as pollen diagrams (Figs. 2 and 3), which were drawn using the GPAL3 program (Goeury, 1988). The vertical axis represents the location of the samples along the transect 7. The horizontal axis indicates the relative percentages of the main pollen taxa (Fig. 2) or groups of taxa (Fig. 3). For the calculation of these percentages, only damaged grains have been excluded from the pollen sum.

Parallel to the pollen sampling, LAI measurements were performed every 15 m along the transect, using a photoresistor with fish-eye optics. The method is based on the Beer–Lambert law and gives a result with a typical error of ±0.2 (Cournac et al., 2000). The LAI is the cumulative leaf area above ground per unit of soil surface expressed in

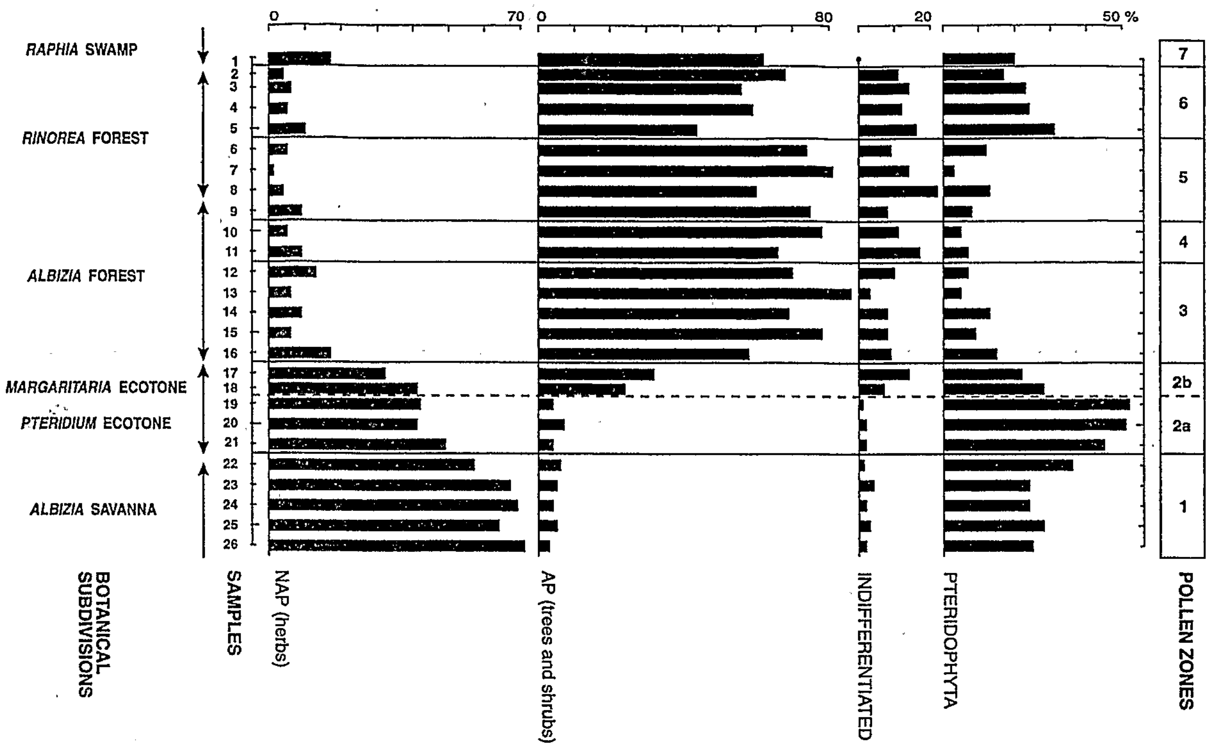

Fig. 3. Synthetic diagram of modern pollen spectra from the Kandara area, southeastern Cameroon, showing the main groups of taxa lumped according to the physiognomy of the producing plants.

square metres of leaves per square metre of ground. An LAI transect is a synthetic descriptor of a forest: the averaged signal is strongly correlated to the photosynthetic and water exchange characteristics of the canopy, while the fluctuations yield indications on the variations in canopy structure.

4. Results

Pollen conservation was good in all the samples analysed and the microflora was rich and well diversified. A total of 101 taxa has been identified (Table 1). The pollen diagram (Fig. 2) shows the 35 most abundant taxa that are considered as the most important ones in the interpretation of the data. Seven main pollen zones can be distinguished, which reflect clearly the vegetation types sampled. The boundaries between these zones were established on the basis of significant changes in the proportion of the major taxa.

From the savanna (north) to the *Raphia* swamp (south), the seven pollen zones are listed below.

4.1. Pollen zone 1 (samples 26 to 22)

The pollen spectra are dominated by the Poaceae (50%) associated with some Asteraceae tubuliflorae, *Chromolaena*-type *odorata* (<5%) and liguliflorae (Vernonieae-type). Pteridophyta (monolete-type) and Cyperaceae are relatively abundant. Among arboreal taxa (total <10%), only *Alchornea*, *Macaranga*-type (including some *Mallotus*) and *Celtis* originating from the forest or the ecotone and transported by wind are present with >1%. *Albizia* is represented in one sample (24) with only one grain.

4.2. Pollen zone 2 (samples 21 to 17)

Two different pollen assemblages were found, which allows us to define two pollen subzones.

4.2.1. Subzone 2a (samples 21 to 19)

Except taxa previously abundant in zone 1, the pollen assemblages are characterized by a high representation of fern spores of *Pteridium*-type *aquilinum*. Poaceae are significantly less abundant (30%) and arboreal taxa are always <10%.

4.2.2. Subzone 2b (samples 18 and 17)

Arboreal taxa are represented with frequencies > 25%. The main taxon is *Alchornea* (>10%) associated with some *Bridelia ferruginea*-type (including *Bridelia micrantha*) and *Macaranga*-type. *Albizia* is found with frequencies >1%. Pteridophyta (monolete-type) and Cyperaceae are well represented. Poaceae progressively decrease (<30%).

4.3. Pollen zone 3 (samples 16 to 12)

This zone registers high percentages of arboreal pollen (AP; 70%) and low percentages of herbaceous taxa, particularly of Poaceae (<10%). The dominant taxon is *Myrianthus*-type *arboreus* (including *Musanga cecropioides*) with more than 50% in samples 15 to 12. *Antidesma*-type, *Ficus*, Apocynaceae and *Albizia* have low representation. *Chaetacme aristata* shows significant frequencies (20%) in sample 16.

4.4. Pollen zone 4 (samples 11 and 10)

This zone does not show dominant taxa. *Piptadeniastrum*-type *africanum* is abundant (10 to 20%) associated with some *Hylodendron gabunense* and *Holoptelea grandis*. The gradual decrease of *Myrianthus*-type *arboreus* and the progressive increase of *Celtis* seem to represent a transition between zone 3 and zone 5.

4.5. Pollen zone 5 (samples 9 to 6)

Arboreal pollen is abundant and *Celtis* is dominant (20 to 65%). *Macaranga*-type is well represented associated with some *Margaritaria*-type *discoidea*, Combretaceae (*Terminalia superba*-type) and *Cordia platythyrsa*-type (including *Cordia africana*).

4.6. Pollen zone 6 (samples 5 to 2)

The main characteristic of this zone is the occurrence of Sterculiaceae belonging to the species *Mansonia altissima*-type and *Triplochiton scleroxylon*-type. One grain of *Cola cordifolia*-type was found. Irvingiaceae (*Irvingia*-type *gabonensis* including *Desbordesia* and *Klainedoxa*) and *Petersianthus*-type *macrocarpus* (including *Barringtonia racemosa*) are also present but in low percentages. Representation of Pteridophyta (monolete-type), *Myrianthus*-type *arboreus* and *Raphia*-type is higher than in previous zones.

4.7. Pollen zone 7 (sample 1)

This zone is characterized by high frequencies of *Myrianthus*-type *arboreus* (50%) associated with *Raphia*-type (7%). Among the herbaceous taxa, Urticaceae and Cyperaceae are present in significant percentages (10% and 5%, respectively). Ferns (monolete-type) are also well represented (20%).

5. Interpretation and discussion

Many results from the Kandara transect mainly agree with previous studies carried out in Central Atlantic Africa in similar environments (e.g. Ybert, 1975; Elenga, 1992; Reynaud-Farrera, 1995; Elenga et al., 1996; Jolly et al., 1996).

In the two main ecosystems crossed by the transect, savanna and forest, the spectra clearly register the pollen rain at a local scale. Few pollen grains are found outside their producing community. In the savanna plots, some forest AP grains (i.e. *Myrianthus*-type *arboreus*, *Tetrorchidium*, *Mansonia altissima*-type, etc.) supplied by wind are found, but they never reached significant frequencies (<1%), except for *Celtis*. The local savanna taxa (mainly herbs such as Poaceae, Cyperaceae, Pteridophyta monolete-type) were always dominant. Inside the forest plots, where the dense structure of the canopy inhibits the entry of pollen of well-dispersed regional taxa, the same pattern is observed. No marker of savanna is found. Although Poaceae are found regularly in this ecosystem, they only represent between 1 and

Table 1
List of identified pollen taxa in the modern soil and litter samples from the Kandara area, southeastern Cameroon.Taxa in bold are shown in the pollen diagram of Fig. 2: ([1], trees and shrubs (A.P.); [2], herbs (N.A.P.); [3], climbers; [4], undifferentiated taxa)

ACANTHACEAE	Acanthaceae [4]
	Asystasia gangetica-type [2]
	Mendoncia [1]
AMARANTHACEAE	**_Cyathula_-type _orthacantha_** [2]
AMARANTHACEAE/CHENOPODIACEAE	Amaranthaceae/Chenopodiaceae [2]
ANACARDIACEAE	*Lannea*-type [1]
APOCYNACEAE	*Alstonia*-type *boonei* [1]
	Funtumia-type [1]
	Oncynotis-type [3]
	Rauvolfia [1]
	Tabernaemontana-type [1]
ARALIACEAE	*Polyscias fulva*-type [1]
ASTERACEAE	**_Chromolaena_-type _odorata_** [2]
	Vernonieae [4]
BOMBACACEAE	*Ceiba pentandra* [1]
BORAGINACEAE	**_Cordia platythyrsa_-type** [1]
	Ehretia [1]
CAESALPINIACEAE	Caesalpiniaceae [1)
	Guibourtia-type *demeusei* [1]
	Hylodendron gabunense [1]
CELASTRACEAE/HIPPOCRATEACEAE	Celastraceae/Hippocrateaceae [1]
CHENOPODIACEAE	Chenopodiaceae [2]
CHRYSOBALANACEAE	*Chrysobalanus*-type *icaco* [1]
COMBRETACEAE	**Combretaceae** [4]
COMBRETACEAE/MELASTOMATACEAE	Combretaceae/Melastomataceae [4]
CONVOLVULACEAE	Convolvulaceae [2]
CYPERACEAE	**Cyperaceae** [2]
EBENACEAE	*Diospyros* [1]
EUPHORBIACEAE	Euphorbiaceae [4]
	Alchornea [1]
	Antidesma-type [1]
	Bridelia ferruginea-type [1]
	Cleistanthus-type *polystachyus* [1]
	Croton-type [1]
	Cyathogyne-type [1]
	Elaeophorbia-type [4]
	Macaranga-type [1]
	Mallotus-type *oppositifolius* [1]
	Margaritaria-type _discoidea_ [1]
	Tetrorchidium [1]
	Uapaca guineensis-type [1]
FABACEAE	Fabaceae [4]
GUTTIFERAE	*Harungana madagascariensis*-type [1]
HYMENOCARDIACEAE	*Hymenocardia* [1]
IRVINGIACEAE	**_Irvingia_-type _gabonensis_** [1]
LABIATAE	Labiatae [2]
LECYTHIDACEAE	**_Petersianthus_-type _macrocarpus_** [1]
LEGUMINOSAE	Leguminosae [4]
LOGANIACEAE	*Anthocleista* [1]
MALPIGHIACEAE	*Acridocarpus* [3]

Table 1 (*continued*).)

MALVACEAE	*Ipomoea*-type [2]
MELASTOMATACEAE	Melastomataceae [2]
MELIACEAE	Meliaceae [1]
	Trichilia-type [1]
MIMOSACEAE	*Acacia* groupe I [4]
	Acacia groupe III [4]
	Albizia [1]
	Entada-type [4]
	Piptadeniastrum*-type *africanum [1]
MONOCOTYLEDONAE	Monocotyledonae [4]
MORACEAE	***Ficus*** [1]
	Myrianthus*-type *arboreus [1]
	Trilepisium*-type *madagascariensis [1]
MYRISTICACEAE	*Pycnanthus angolensis*-type [1]
MYRTACEAE	*Syzygium*-type [1]
OCHNACEAE	*Campylospermum* [1]
OLACACEAE	*Strombosia*-type [1]
PALMAE	***Elaeis guineensis*** [1]
	Phoenix reclinata-type [1]
	***Raphia*-type** [1]
PANDANACEAE	Pandanus [1]
POACEAE	**Poaceae** [2]
RANUNCULACEAE	*Clematis*-type [3]
RHAMNACEAE	Rhamnaceae [1]
RUBIACEAE	Rubiaceae [4]
	Aidia-type *micrantha* [1]
	Macrosphyra-type [1]
	Pausinystalia-type *macroceras* [1]
	Psydrax subcordata-type [1]
	Sherbournia bignoniifolia-type [1]
	Spermacoce-type [2]
RUTACEAE	*Zanthoxylum*-type [1]
SAPINDACEAE	*Allophylus* [1]
SAPOTACEAE	Sapotaceae [1]
STERCULIACEAE	*Cola cordifolia*-type [1]
	Mansonia altissima-type [1]
	Triplochiton scleroxylon-type [1]
THYMELAEACEAE	Thymelaeaceae [1]
TILIACEAE	Tiliaceae [4]
	Grewia-type [4]
ULMACEAE	***Celtis*** [1]
	Chaetacme aristata [1]
	Holoptelea grandis [1]
UMBELLIFERAE	Umbelliferae [2]
URTICACEAE	**Urticaceae** [2]
VITACEAE	*Cissus*-type *quadrangularis* [4]
PTERIDOPHYTA	***Pteridium*-type *aquilinum***
	Lygodium macrophyllum
	monolete-type
	trilete-type
ANTHOCEROTACEAE	Anthocerotaceae

10%, values which are similar to those registered in Ivory Coast by Ybert (1975). However, one cannot conclude whether grass pollen is exclusively of local source areas in the forest or partly originated from the savanna because of the lack of qualitative and quantitative botanical surveys of the forest undergrowth.

The density of the canopy trees is clearly evidenced by the distribution of the AP frequencies (Fig. 3). The highest values (>50%) are always registered in forest communities, the lowest ones (<10%) in savanna, with intermediate values (mean of 30%) at the savanna–forest transition (plots 17 and 18) where the youngest stage of the forest colonization occurs. However, on the basis of these AP values alone no distinction can be made between *Albizia* forest and *Rinorea* forest, although *Albizia* forest has numerous openings in the upper strata due to recent settlement, as shown by tree basal area measurements performed along transect 7 (Fig. 4) (Youta Happi, 1998; Achoundong et al., 2000). Moreover, no decrease in AP frequencies due to local clearances is observed in the forest represented by plots 10, 13 and 16. The canopy always appears closed, and no savanna or ecotone species colonize the openings (Fig. 2). In fact, these cleared patches are very recent and only the understory of the *Albizia* forest has been locally affected.

Compared with the pollen data, the LAI measurements performed along the same transect show very similar trends (Fig. 4). The highest values of LAI (>2.5) were always obtained from sites inside the forest, the lowest ones (zero) in savanna. We noted an abrupt decrease inside the youngest stage of the forest colonization, which registers well at Kandara the sharp boundary between the dense and the open ecosystems (Youta Happi, 1998). The main differences are observed under the *Albizia* cluster occurring in the savanna (plot 22) where the LAI is about 1.5, basal area values increase, though AP is very scarce, particularly *Albizia*, and in plot 13 where the local clearance of the forest is well marked by a great decrease of LAI.

The short and rapid fluctuations registered in the LAI transect, compared with the relative homogeneity of the AP frequencies inside the forest ecosystem, are mainly related to the spatial scale of the measurement used in the two methods. The LAI measures are made at a given point, whereas pollen samples are representative of a vegetation averaged over a minimum area of about 300 m^2.

The highest richness in pollen taxa (>33) was always registered in forest sites, except for plot 13 where *Myrianthus*-type *arboreus* is over-represented, masking therefore the other taxa in spite of a high pollen count (Fig. 5). The lowest diversity in pollen taxa (<26) is always found at sites in open formations, such as the savanna and the youngest part of the ecotone, but also locally in the *Raphia* swamp.

Inside the forest ecosystem, richness in pollen taxa is as inefficient as AP frequencies to differentiate the *Albizia* forest from the *Rinorea* forest, contrary to botanical data (Achoundong et al., 2000). Identical values are registered in the two formations, showing that the floristic diversity of the Kandara forest is poorly reflected in pollen assemblages.

The two samples corresponding to the oldest part of the ecotone (plots 17 and 18), and so to the youngest stage of the forest colonization, register intermediate values.

Numerous discrepancies between representation of taxa in the local stands of vegetation and in the pollen spectra are observed. Indeed, many of the plants that are considered by the botanists as markers of the main communities occurring along the transect (Achoundong et al., 2000) are not represented by their pollen grains or are found only in low percentages in the spectra. This is the case of *Albizia* inside the savanna, even under *Albizia* clusters such as plot 22, and inside the *Albizia* forest, and of *Rinorea* inside the *Rinorea* forest. Concerning *Margaritaria discoidea*, a marker of the oldest part of the ecotone, this species is present under this community but is not the dominant pollen taxa. It has been found with more significant percentages in the oldest part of the *Albizia* forest and the youngest part of the *Rinorea* forest (Fig. 2).

The same discrepancy is observed for some other common plants, such as: *Chromolaena odorata* (a recently introduced and invading Asteraceae; de Rouw, 1991) and *Aframomum*

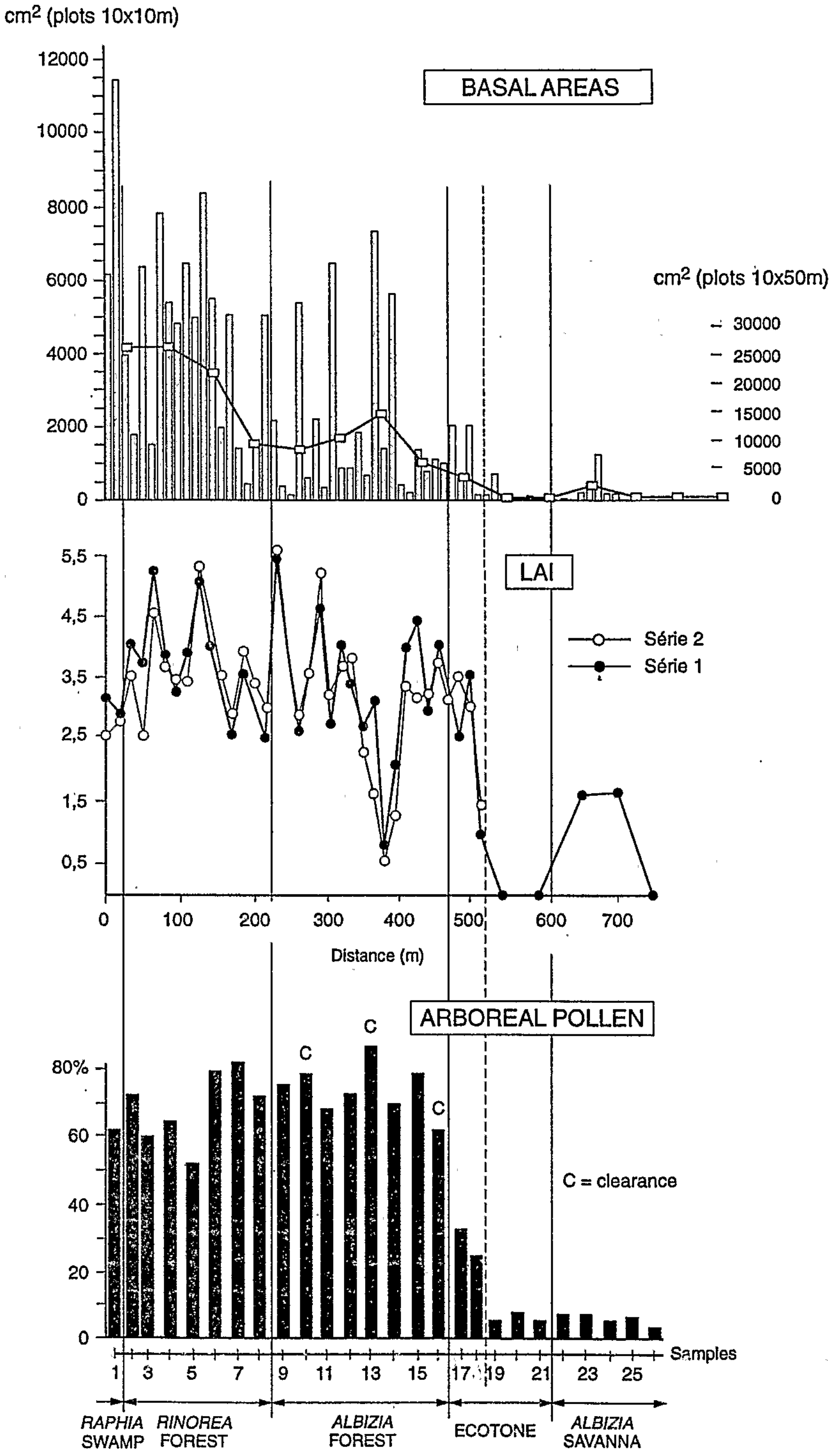

Fig. 4. Comparison between percentages of AP and LAI and basal area [from Youta Happi (1998)] measurements along transect 7 in the Kandara area, southeastern Cameroon.

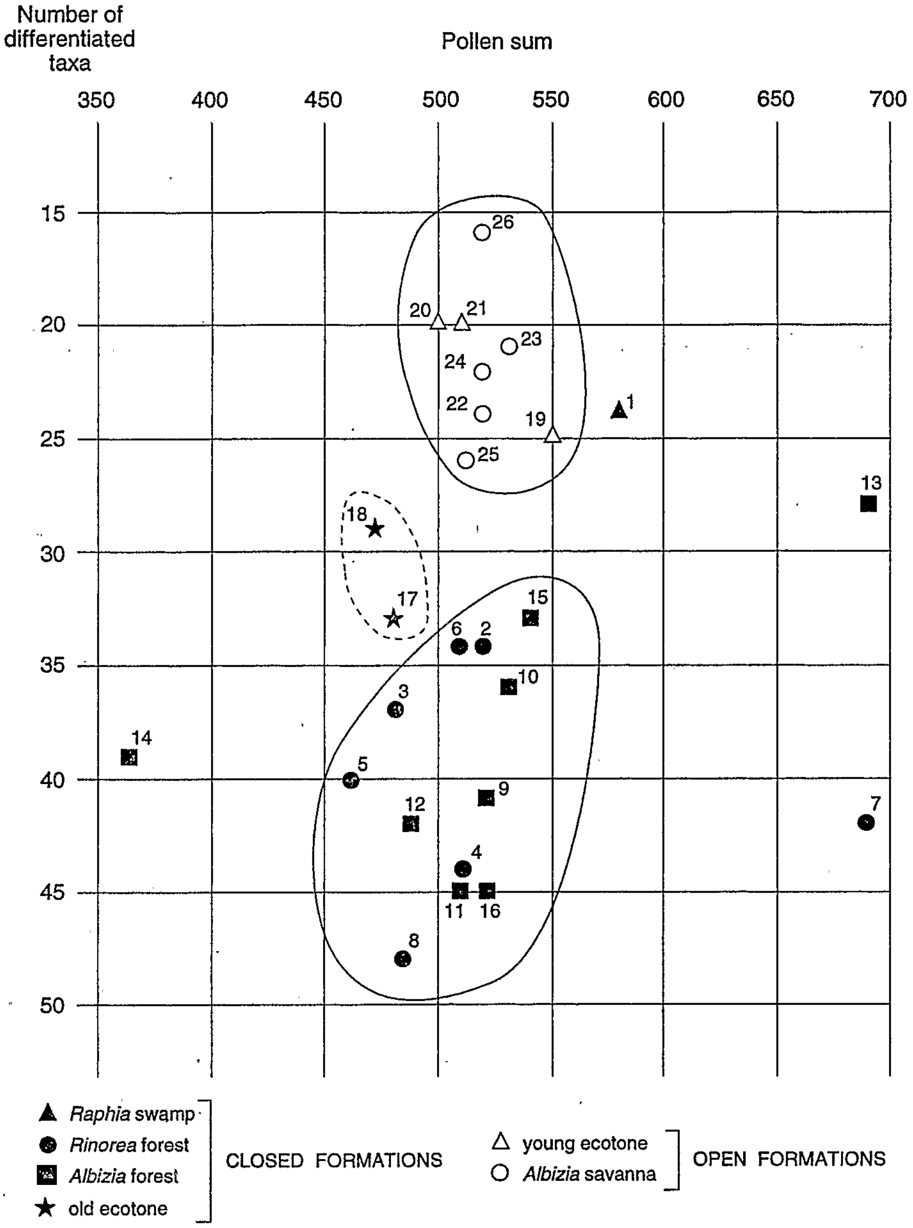

Fig. 5. Pollen taxa richness in the modern pollen spectra from the Kandara area, southeastern Cameroon, related to the pollen sum.

(Zingiberaceae), abundant in the savanna and in the ecotone; Apocynaceae (*Funtumia*, *Tabernaemontana*), *Sterculia* and *Canthium* in the *Albizia* forest; *Trichilia*, *Cola*, *Amphimas*, *Duboscia*, *Desplatsia* and *Parkia* in the *Rinorea* forest.

On the other hand, some pollen taxa with significant frequencies in the spectra do not always belong to genera or families defined as the most abundant in the sampled formations (Fig. 2). These taxa are as follows:

- the Cyperaceae and ferns (monolete-type) inside the savanna. These plants are generally considered as markers of humid and/or swampy formations, but some genera or species can also be found in open grasslands (Kornas, 1993).

- *Pteridium aquilinum* is a fern that, in the youngest part of the ecotone, excludes the grasses by competition and, consequently, protects the forest from fire (Youta Happi, 1998). The same is true for the recently introduced *Chromolaena odorata*.
- *Alchornea* is a typical pioneer and heliophilous element, common in the oldest part of the ecotone.
- *Chaetacme aristata* and *Myrianthus arboreus*, in the youngest part of the *Albizia* forest. These two species are generally considered by botanists as markers of the youngest stage of the forest colonization (Achoundong et al., 2000).
- *Celtis*, in the oldest part of the *Albizia* forest and the youngest part of the *Rinorea* forest, is a good marker of semi-deciduous forests (Letouzey, 1968).
- In the oldest part of the *Rinorea* forest, numerous Sterculiaceae, mainly *Mansonia* and *Triplochiton*, are semi-deciduous trees character-

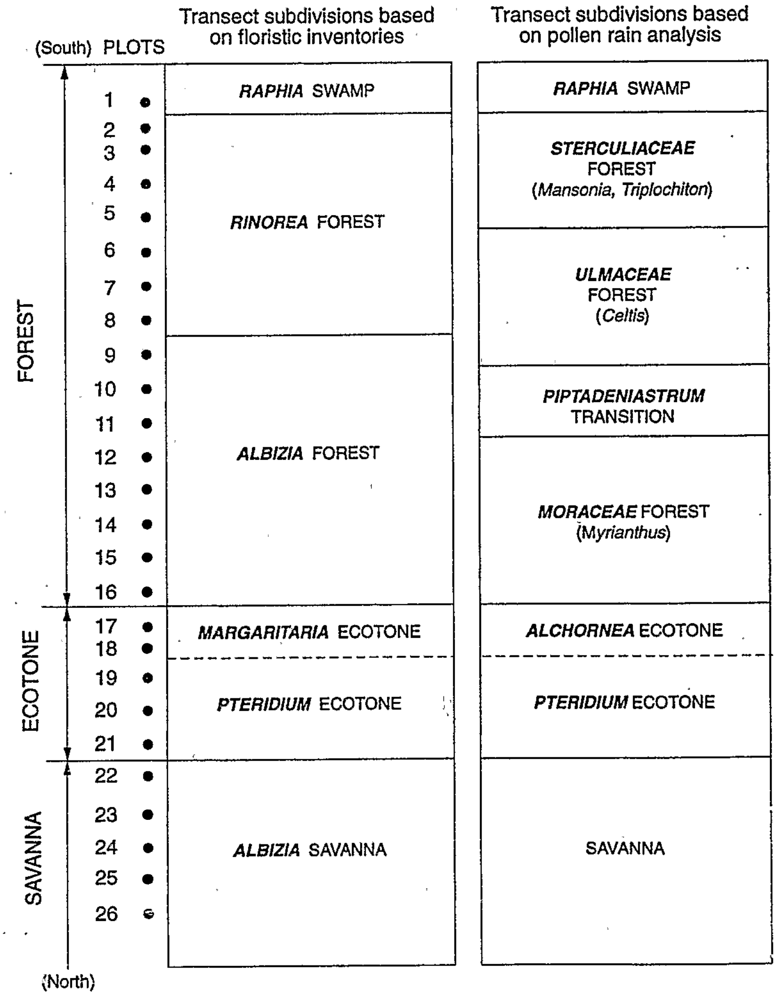

Fig. 6. Subdivisions along transect 7 in the Kandara area based on floristic inventories (left) and pollen rain analysis (right). Note that forest communities are classified with more detail when pollen rain data are used.

istic of the final stage of the development of forest in an area that was previously covered by savanna (Letouzey, 1968).

These differences between sampled vegetation and its pollen rain are mainly linked to important differences in pollen production and pollen dispersal of plant species. Some previous studies undertaken in tropical Africa have shown such a large difference between anemophilous and entomophilous plants, mainly those concerning the quantitative relationships between pollen and vegetation (Reynaud-Farrera, 1995; Elenga et al., 1996). They have shown that entomophilous plants, generally dominant in forests, produce considerably less pollen than anemophilous ones and their pollen is not well dispersed. But these distortions can also be related to the method used in the botanical surveys. Indeed, the inventories made in the Kandara area are not exhaustive and concerned only trees of more 3 cm in diameter at breast height (DBH), whereas herbs and small trees and shrubs were not considered at all.

The main botanical subdivisions and their spatial boundaries proposed by Achoundong et al. (2000) were also identified in the pollen transect. However, in this study we propose to define and/or redefine these subdivisions in order that they can be used in the future for palaeoenvironmental reconstructions in the Kandara area. As shown in Fig. 6, the main palynological redefinitions concern the *Albizia* and the *Rinorea* forests, where the pollen data register more successional vegetation communities. In this ecosystem, four palynological facies, each corresponding to a stage of the forest colonization, are well defined and they are, from the youngest to the oldest: a Moraceae (*Myrianthus*) forest; a transitional formation with *Piptadeniastrum*; an Ulmaceae (*Celtis*) forest; a Sterculiaceae (*Triplochiton* and *Mansonia*) forest.

6. Conclusion

This transect study shows good relationships between the pollen rain and the vegetation, i.e. the spatial distribution, the structure and the floristic richness of savanna and forest. However, pollen assemblages do reflect with some distortion the floral composition of the sampled vegetation.

In spite of this distortion, this study led us to define the botanical subdivisions proposed at Kandara and to characterize the main successional stages of colonization of the forest on savanna. The pollen–vegetation relationships evidenced could serve as a calibration tool for future palaeoenvironmental reconstructions from pollen records obtained in this area.

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After publication, the pollen data will be stored in the African Pollen Database (APD) managed by the INCO CEE project and the UNESCO PICG 431.

References

Achoundong, G., Youta Happi, J., Bonvallot, J., Guillet, B., 1996. Formation et évolution des recrus sur savanes. In: Symposium 'Dynamique à Long Terme des Écosystèmes Forestiers Intertropicaux'. CNRS–ORSTOM, Bondy, pp. 115–119.

Achoundong, G., Youta Happi, J., Guillet, B., Bonvallot, J., Kamgang Belaya, V., 2000. Formation et évolution des recrus sur savanes. In: Servant-Vildary, S., Servant, M. (Eds.), Dynamique à long terme des écosystèmes forestiers intertropicaux. UNESCO, Paris, in press.

A.P.L.F., 1974. Pollen et spores d'Afrique tropicale. Travaux et Documents de Géographie Tropicale. CEGET–CNRS, Bordeaux. 282 pp.

Bonnefille, R., Riollet, G., 1987. The Kashiru pollen sequence (Burundi). Palaeoclimatic implications for the last 40,000 yr B.P. in Tropical Africa. Quaternary Research 30, 19–35.

Bonnefille, R., Chalié, F., Guiot, J., Vincens, A., 1992. Quantitative estimates of full glacial temperatures in equatorial Africa from palynological data. Climate Dynamics 6, 251–257.

Bonnefille, R., Buchet, G., Friis, G., Ensermu Kelbessa, Mohammed, U., 1993. Modern pollen rain on an altitudinal range of forests and woodlands in South West Ethiopia. Opera Botanica 121, 71–84.

Chalié, F., 1992. Paléoclimatologie quantitative en Afrique orientale depuis 40 000 ans. Pollen et statistiques. Unpublished Thesis, University Aix-Marseille III, 160 pp.

Cournac, L., Dubois, M.A., Chave, J., Riera, B., 2000. Fast determination of light avaibility and Leaf Area Index in tropical forests. Journal of Tropical Ecology. submitted for publication.

de Rouw, A., 1991. The invasion of *Chromolaena odorata* (L.) King and Robinson (ex *Eupatorium odoratum*) and competition with the native flora, in a rain forest zone, south-west Côte d'Ivoire. Journal of Biogeography 18, 13–23.

Elenga, H., 1992. Végétation et climat du Congo depuis 24 000 ans B.P. Analyse palynologique de séquences sédimentaires du Pays Bateke et du littoral. Unpublished Thesis, University Aix-Marseille III, 238 pp.

Elenga, H., de Namur, C., Roux, M., 1996. Etude des relations pollen–végétation dans le Mayombe congolais d'après les analyses statistiques. In: Symposium 'Dynamique à Long Terme des Écosystèmes Forestiers Intertropicaux'. CNRS–ORSTOM, Bondy, pp. 59–62.

Elenga, H., Peyron, O., Bonnefille, R., Prentice, I.C., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V., Bottema, S., Buchet, G., de Beaulieu, J.L., Hamilton, A.C., Maley, J., Marchant, R., Perez-Obiol, R., Reille, M., Riollet, G., Scott, L., Straka, H., Taylor, D., Van Campo, E., Vincens, A., Laarif, F., Jonson, H., 2000. Pollen-based biome reconstruction for southern Europe and Africa 18,000 years ago. Journal of Biogeography. in press.

Faegri, K., Iversen, J., 1964. Text Book of Pollen Analysis. second ed., Munksgaard, Copenhagen.

Goeury, C., 1988. Acquisition, gestion et représentation des données de l'analyse pollinique sur micro-ordinateur. Institut Français de Pondichéry, Travaux Section Sciences et Techniques 25, 405–416.

Jolly, D., Bonnefille, R., Burq, S., Roux, M., 1996. Représentation pollinique de la forêt dense humide du Gabon tests statistiques. Comptes Rendus de l'Académie des Sciences, Paris 322, IIa, 63–70.

Jolly, D., Prentice, I.C., Bonnefille, R., Ballouche, A., Bengo, M., Brenac, P., Buchet, G., Burney, D., Cazet, J.P., Cheddadi, R., Edorh, T., Elenga, H., Elmoutaki, S., Guiot, J., Laarif, F., Lamb, H., Lezine, A.M., Maley, J., Muaka-Mbenza, Peyron, O., Reille, M., Reynaud-Farrera, I., Riollet, G., Ritchie, J.C., Roche, E., Scott, L., Ssemmanda, I., Straka, H., Mohammed, U., Van Campo, E., Sikiminywa Vilimumbalo, Vincens, A., Waller, M., 1998. Biome reconstruction from pollen and plant macrofossil data for Africa and Arabian peninsula at 0 and 6 ka. Journal of Biogeography 25, 1007–1027.

Jolly, D., Prentice, I.C., Guiot, J., Bengo, M., Bonnefille, R., Brenac, P., Buchet, G., Edorh, T., Elenga, H., Lezine, A.M., Maley, J., Reynaud-Farrera, I., Riollet, G., Vincens, A., 2000. Reconstruction des biomes à partir des données polliniques actuelles d'Afrique de l'Ouest. Revue de Géographie Physique et Quaternaire. in press.

Kamgang Beyala, V., Ekodeck, G.E., Achoundong, G., 1996. Essai d'interprétation de la dynamique de la mosaïque forestière dans la zone de contact forêt/savane du Sud-Est Cameroun. In: Symposium 'Dynamique à Long Terme des Écosystèmes Forestiers Intertropicaux'. CNRS–ORSTOM, Bondy, p. 155.

Kamgang Kabeyene Beyala, V., 1998. Evolution supergène des roches et incidences phytogéographiques; cas du contact forêt–savane du Sud-Est Cameroun. Unpublished Thesis, University of Yaoundé I, Cameroun.

Kornas, J., 1993. The significance of historical factors and ecological preference in the distribution of African pteridophytes. Journal of Biogeography 20, 281–286.

Letouzey, R., 1968. Etude Phytogéographique du Cameroun. Lechevalier, Paris. 511 pp.

Lézine, A.M., Hoogheimstra, H., 1990. Land-sea comparisons during the last glacial–interglacial transition, pollen records from West Tropical Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 79, 313–331.

Menaut, J.C., Gignoux, J., Prado, C., Clobert, J., 1990. Tree community dynamics in a humid savanna of the Côte-d'Ivoire: modelling the effects of fire and competition with grass and neighbours. Journal of Biogeography 17, 471–481.

Peyron, O., 1999. Le climat de l'Europe et de l'Afrique au dernier maximum glaciaire et à l'Holocène moyen: nouvelle méthode de quantification à partir de données polliniques et comparaison avec les modèles climatiques. Unpublished Thesis, University Aix-Marseille II.

Peyron, O., Jolly, D., Bonnefille, R., Vincens, A., Guiot, J., 2000. The climate of East Africa from pollen data, 6000 years ago. Quaternary Research. in press.

Reynaud-Farrera, I., 1995. Histoire des paléoenvironnements forestiers du Sud-Cameroun à partir d'analyses palynologiques et statistiques de dépôts holocènes et actuels. Unpublished Thesis, University Montpellier II, 230 pp.

Salard-Cheboldaeff, M., 1982. Palynologie camerounaise. III. Grains de pollen de la forêt dense humide de basse et moyenne altitude. 107° Congrès national des Sociétés savantes, Brest. Sér. Sciences 1, 127–141.

Salard-Cheboldaeff, M., 1983. Palynologie camerounaise. IV. Grains de pollen de la forêt dense humide de moyenne altitude. 108° Congrès national des Sociétés savantes, Grenoble. Sér. Sciences 1, 117–129.

Salard-Cheboldaeff, M., 1984. Palynologie camerounaise. V Grains de pollen de la forêt dense humide semi-caducifoliée de moyenne altitude. 109° Congrès national des Sociétés savantes, Dijon. Sér. Sciences 1, 19–35.

Salard-Cheboldaeff, M., 1986. Palynologie camerounaise. VII. Grains de pollen des savanes arbustives et arborées, voire boisées, de l'Adamaoua. 11° Congrès national des Sociétés savantes, Poitiers. Sér. Sciences 2, 59–80.

Salard-Cheboldaeff, M., 1987. Palynologie camerounaise. VII. Grains de pollen des savanes boisées et forêts claires sèches. 12° Congrès national des Sociétés savantes, Lyon. Sér. Sciences 3, 47–63.

Schwartz, D., Mariotti, A., Lanfranchi, R., Guillet, B., 1986. $^{13}C/^{12}C$ ratios of soil organic matter as indicators of vegetation changes in the Congo. Geoderma 39, 97–103.

Schwartz, D., de Foresta, H., Mariotti, A., Balesdent, J., Massimba, J.P., Girardin, C., 1996. Present dynamics of the savanna-forest boundary in the Congolese Mayombe: a pedological, botanical and isotopic (^{13}C and ^{14}C) study. Oecologia 106, 516–524.

Sowunmi, M.A., 1973. Pollen grains of Nigerian plants. I Woody species. Grana 13, 145–186.

Sowunmi, M.A., 1995. Pollen of Nigerian plants. II Woody species. Grana 34, 120–141.

Suchel, J.B., 1988. Les climats du Cameroun. Unpublished Thesis, University of Saint-Etienne.

Vincens, A., Chalié, F., Bonnefile, R., Guiot, J., Tiercelin, J.J., 1993. Pollen-derived rainfall and temperature estimates from lake Tanganyika and their implication for Late Pleistocene water levels. Quaternary Research 40, 343–350.

Vincens, A., Ssemmanda, I., Roux, M., Jolly, D., 1997. Study of the modern pollen rain in Western Uganda with a numerical approach. Review of Palaeobotany and Palynology 96, 145–168.

Walter, H., Lieth, H., 1960. 1967. Klimadiagramm-Weltatlas. Fisher, Jena.

White, F., 1983. The Vegetation of Africa. A Descriptive Memoire to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa. UNESCO, Paris.

Ybert, J.P., 1975. Emissions polliniques actuelles dans la zone de contact forêt-savane en Côte d'Ivoire. Bulletin de la Société Botanique de France, Collection Palynologie 122, 251–265.

Ybert, J.P., 1979. Atlas de pollens de Côte d'Ivoire. ORSTOM, Initiations-Documentations techniques, 40, 40 pp.

Youta Happi, J., 1998. Arbres contre graminées: la lente invasion de la savane par la forêt au Centre-Cameroun. Unpublished Thesis, University Paris IV, 237 pp.