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Forest response to climate changes in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscapes

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Abstract

This review paper synthesizes the recent published palaeoecological results obtained in Atlantic Equatorial Africa (ECOFIT program) on the history of forest ecosystems and inferred climate changes during the past 4000 years. Evidence are mainly provided by pollen analysis carried out at nine sites from Congo, Cameroon and Ghana, locally supported by macroflora remains, phytoliths, diatoms, $\delta^{13}C$ and mineralogical data.

At all the sites, except Lake Bosumtwi (Ghana), following a large expansion of rain and mesophilous forests until 3000 years BP, a major change is registered, affecting floristic composition, structure and geographical distribution. According to the hydrological sensitivity of the different sites, local openings of the forests with development of heliophilous formations and/or isolated enclosed savannas are observed at the most humid sites; complete disappearance of forested formations at the driest. The agreement between pollen records, hydrological and hydrobiological data definitely demonstrates that an arid event has been the primary driving factor of this change and is responsable for the main features of the modern landscapes in Atlantic Equatorial Africa. Moreover, the most recent palaeoecological data obtained in Congo (Lake Sinnda), indicate that this Late Holocene increasing aridity was of longer duration, from 4000 to 1300 years BP, and more progressive than previously inferred. A new expansion of forests is locally detected *c.* 900–600 BP despite increased human impact.

Keywords

Pollen, multi proxydata, forest, climate, Atlantic Equatorial Africa, Late Holocene.

Until the last three decades, extremely little was known of the past history of the tropical lowland forest formations. Thereby, these forests have been longer considered as the most stable ecosystems of the Earth and their great floristic diversity has been often interpreted in terms of persistence or of very slow change through time compared to drier vegetation types. Based on recent palaeoecological studies carried out from 1970 onwards, the Equatorial forests are now believed to have been the subject of drastic modifications (floristic, structural and palaeogeographical ones) in response to global climatic changes.

During the Quaternary, African lowland forests, like Amazonian ones (Bush *et al.*, 1990; Servant *et al.*, 1993; Van der Hammen & Absy, 1994; Turq *et al.*, 1996; Colinvaux, 1997), have been largely affected by long time-scale duration and large amplitude climatic fluctuations. Thus, the dry and cold period of the Last Glacial Maximum led to their fragmentation, to the isolation of forested communities in refugia and to the presence of montane biotopes in the lowlands

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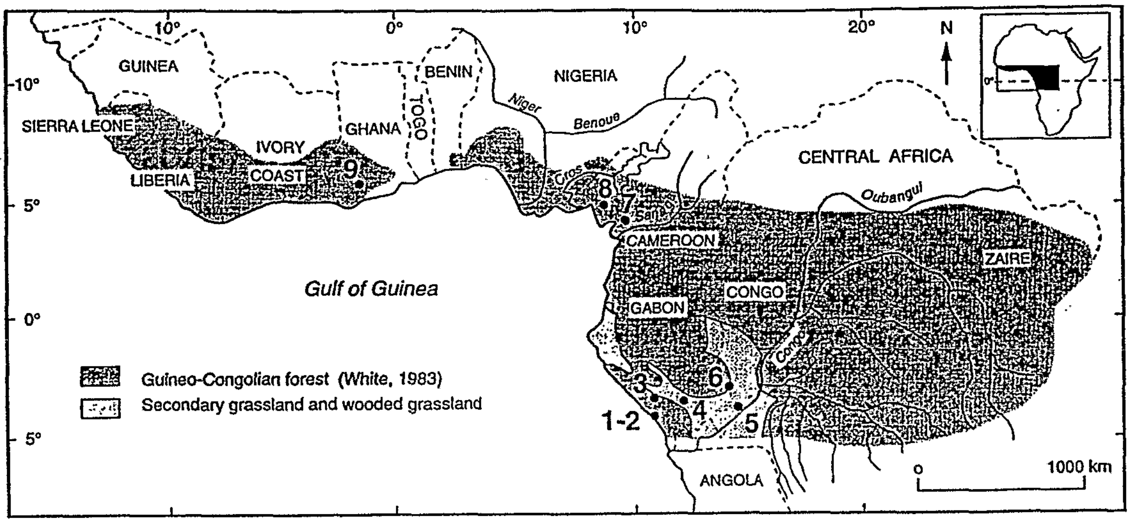

Figure 1 Location map of the pollen sites inside the Guineo-Congolian phytogeographical region as defined by White (1983): 1, Songolo; 2, Coraf; 3, Kitina; 4, Sinnda; 5, Ngamakala; 6, Bilanko; 7, Ossa; 8, Barombi Mbo; 9, Bosumtwi.

(Maley, 1987, 1989, 1991, 1996; Elenga *et al.*, 1991; Elenga, 1992; Maley & Elenga, 1993). These forests have also suffered of shorter climatic events, such as this which took place during the last 4000 years BP (Maley, 1991, 1992; Elenga *et al.*, 1992, 1994, 1996; Elenga, 1992; Vincens *et al.*, 1994, 1996a, 1996b, 1998; Reynaud-Farrera, 1995, 1997; Reynaud-Farrera *et al.*, 1996; Maley & Brénac, 1998).

This paper summarizes the recent published Late Holocene palaeoecological researches carried out in Atlantic Equatorial Africa, mostly relevant to the ECOFIT program (CNRS-ORSTOM). For the purpose of the reconstruction of past vegetation patterns, the synthesis will be based primarily on palynological sources from nine sites, a method which is still widely used for such a work. The interpretations will be completed, on some sites, by sedimentological, limnological and phytoliths results proceeding from the same sedimentary sequences, or, on some others, by macroflora remains and $\delta^{13}C$ data obtained in their vicinity.

THE POLLEN SITES STUDIED

The available well radiocarbon dated palynological sequences, recovered by coring in lakes or swampy depressions, come from three African Atlantic Equatorial regions (Fig. 1 and Table 1). They are, from the South to the North, the following.

The Congo with: (a) the Coraf and Songolo sites located on the littoral, today occupied by short grass-savannas with locally swampy herbaceous or dense arboreal formations (Makany, 1963; Elenga *et al.*, 1992; Elenga, 1992; in preparation); (b) the lake Kitina, on the western escarpment of the Mayombe Massif, inside the semideciduous forest (Cusset, 1987; Elenga *et al.*, 1996); (c) the lake Sinnda, in the Niari valley today covered by tall grass-savannas with locally more or less well developed patches of remained semideciduous forest (Koechlin, 1961; Vincens *et al.*, 1994, 1998); (d) the Ngamakala and Bilanko sites, two swampy arboreal depressions, located on the Bateke plateaus occupied by grass or wooded savannas (Descoings, 1960; Makany, 1976; Schwartz, 1988; Elenga, 1992; Elenga *et al.*, 1994).

Table 1 The pollen sites from Atlantic Equatorial Africa. Geographical location and mean annual rainfall values.

Sites	Latitude	Longitude	Altitude	Mean annual rainfall
1 Songolo	4°45′S	11°51′E	5 m	1260 mm
2 Coraf	4°S	11°E	0 m	1260 mm
3 Kitina	4°15′S	11°59′E	150 m	1500 mm
4 Sinnda	3°50′S	12°48′E	128 m	1100 mm
5 Ngamakala	4°04′S	15°23′E	400 m	1300 mm
6 Bilanko	3°31′S	15°21′E	600 m	1500 mm
7 Ossa	3°48′N	9°61′E	8 m	2950 mm
8 Barombi Mbo	4°40′N	9°24′E	300 m	2400 mm
9 Bosumtwi	6°30′N	1°25′W	100 m	1550 mm

The Cameroon with: (a) the lake Ossa, inside the Atlantic littoral forest with *Sacoglottis gabonensis* and *Lophira alata* (Letouzey, 1968, 1985; Reynaud & Maley, 1994; Reynaud-Farrera, 1995, 1997; Reynaud-Farrera *et al.*, 1996); (b) the lake Barombi Mbo, located inside the Biafrean evergreen forest with numerous Caesalpiniaceae (Brénac, 1989; Maley, 1991, 1996; Maley & Brénac, 1998).

The Ghana, with the lake Bosumtwi whose basin is occupied by semideciduous forest (Hall & Swaine, 1981; Maley, 1987, 1989, 1996).

According to the sites, the time resolution of the pollen data ranges from 20 to 300 years, except at lake Bosumtwi where only four samples were analysed for the past 4000 years.

SYNTHESIS AND INTERPRETATION OF THE DATA

The synthesis proposed for the last 4000 years BP in Atlantic Equatorial Africa is given in Fig. 2. The studied sites and their

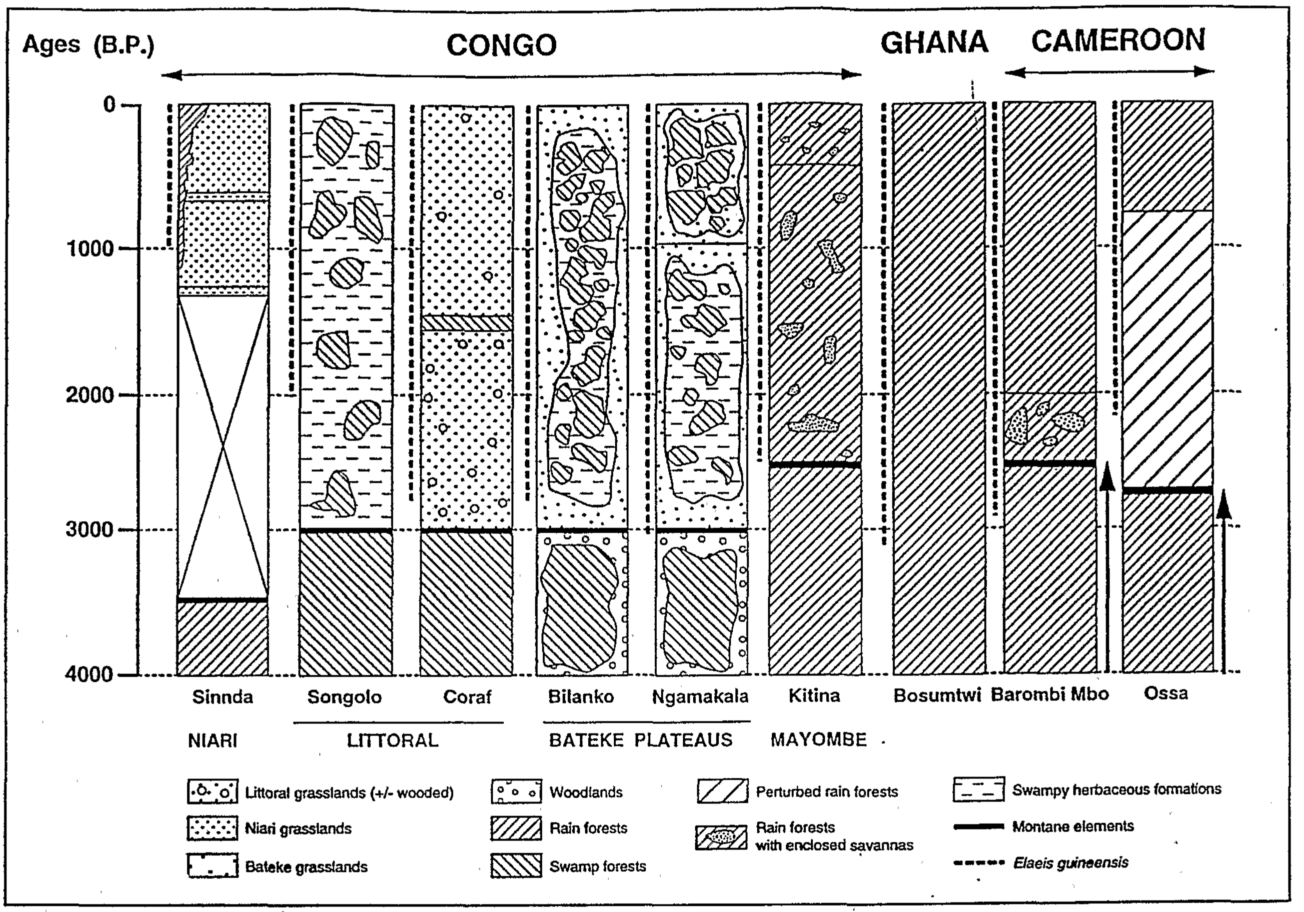

Figure 2 Synthesis of the pollen and macroflora remains data from Atlantic Equatorial Africa and vegetation reconstruction during the past 4000 years.

vegetation reconstruction are arranged, from the right to the left, according to the modern mean annual rainfall values registered near each site (Table 1), from the driest site (Sinnda) to the most humid one (Ossa). The timescale was extrapolated from non calibrated ages obtained along the different sequences. The list of these ages can be found in Maley (1989), Giresse *et al.* (1994), Elenga (1992), Elenga *et al.* (1992, 1994, 1996), Vincens *et al.* (1994, 1998), Reynaud-Farrera (1995) and Maley & Brénac (1998).

This synthesis clearly shows that between 4000 and 3500 years BP, all the sites were occupied by forested communities. These forests were of two main types.

- Mainland forests are found, with a semideciduous facies well developed at Sinnda (Congo) and Bosumtwi (Ghana) as testified by the abundance of *Celtis*. Around the lakes Ossa and Barombi Mbo (Cameroon), forests of Briafrean type dominated by Caesalpiniaceae are present. At Kitina, *Anopyxix*, *Martretia*, *Dacryodes* are well developed in the environment of this site, with locally fringing arboreal swamp formations with *Hallea*, *Anthostema* and *Syzygium*.
- Dense swamp forests occur on hydromorphic soils, such as on the congolese littoral, with abundance of *Symphonia globulifera*, *Hallea* and *Uapaca* on the Songolo site, or of *Syzygium* at Coraf. In this region, pollen data are completed by macroflora remains (wood and tap-roots) of *Monopetalanthus* (*microphyllus* dominant), *Sacoglottis gabonensis* and *Jaundea pinnata* recovered at Coraf and southward at Loango (Dechamps *et al.*, 1988a; Schwartz *et al.*, 1990).

In the hydromorphic depressions of the Bateke plateaus, *Syzygium* is largely developed on the Bilanko site, associated with numerous Sapotaceae at Ngamakala. Concerning the vegetation which occupied the Bateke plateaus, macroflora remains indicate the occurrence of woodlands during this period (Dechamps *et al.*, 1988b).

Centered around 3000–2500 years BP, a major vegetation change is registered, which has not the same pattern according to the sites.

On the modern most humid sites, forests persist but a fragmentation of these forests is observed and isolated enclosed savannas develop. This change is clearly shown on the Kitina and Barombi Mbo sites, at *c.* 2500 years BP, where Gramineae become abundant in the pollen diagrams, synchronous, at Kitina, with an expansion of swampy and heliophilous arboreal taxa such as *Pandanus*, *Raphia*, *Macaranga*, *Alchornea*. Around the lake Ossa, a vegetational deterioration is registered

c. 2700 years BP, marked by the substitution of the primary forest by a colonizing one rich in pioneer species (*Alchornea*, *Macaranga*). Only the forests which occurred around the lake Bosumtwi do not seem to be affected by such a change. But, this site would need more detailed palynological studies (higher time resolution of the data) to confirm this persistence.

On the modern driest sites, the former forested environment completely disappears with, synchronously extension of open formations of savanna type around the lake Sinnda (Niari valley), or of more or less wooded grasslands on the Coraf site (littoral).

In the hydromorphic depressions, a fragmentation of the swampy forests is demonstrated with, at the same time, expansion of hygrophytic herbaceous formations dominated by Cyperaceae and *Raphia* at Songolo (littoral), by Cyperaceae, *Stipularia africana*, *Laurembergia tetrandra* and *Xyris* at Ngamakala and Bilanko on the Bateke plateaus. On this last site, palynological data coupled with $\delta^{13}C$ measures on the same core, clearly show that the development of Gramineae observed in the pollen diagram is not local but corresponds to the extension of open grasslands on the plateaus (^{13}C data from Mariotti non published in Elenga, 1992).

During the last millenium, a new expansion of forest communities is registered on the sites where these formations had never completly disappeared c. 3000–2500 years BP. Thus, at Ossa, Biafrean and Atlantic littoral rainforests re-extend from 700 years BP onward; at Kitina, a progressive reforestation of the enclosed savannas and a decrease of heliophilous elements take place c. 500 years BP; at Ngamakala, swampy forests become progressively more developed from 900 years BP. Around Sinnda, only a local ring of forest along the margins of the lake expends from 650 years BP. Only the data from the Barombi Mbo site indicate an earlier reforestation dated c. 2000 years BP.

DISCUSSION

The synthesis of the data clearly shows that the African Atlantic Equatorial forests, occurring between 4°S and 7°N, and largely extended during the Middle Holocene, have been subject of important floristic, structural and palaeogeographical modifications during the last 4000 years BP. The main vegetation change centred around 3000–2500 BP is registered on all the sites where high time resolution of the data was available, indicating the great intensity and the large geographical impact of this event.

It is now clear that this major change in the forest communities is linked to an arid event, as far as, at the same time, some lakes such as Sinnda completely dried up between 3800 and 1300 years BP (Vincens *et al*., 1994, 1998; Bertaux *et al*., 1996), or such as Bosumtwi and Ossa registered a low lake level c. 3700 and c. 3200 years BP, respectively (Talbot *et al*., 1984; Talbot & Johannessen, 1992; Nguetsop & Servant-Vildary, 1996; Servant-Vildary *et al*., 1996; Nguetsop, 1997). So, human impact as early as 3000 BP can be excluded as a primary reason why forests opened or were replaced by grasslands.

As shown above, this change had not the same pattern and was not synchronous according to the sites. These differential responses can be explained in terms of the former local stability (or fragility) of forests on each site before 3000 BP, stability (or fragility) being mainly governed by local climatic and edaphic conditions (Baumgartner, 1978; Richards, 1981).

On the present driest sites such as Sinnda, climatic and edaphic conditions prevented the persistence of forested ecosystems during this arid event, related with annual rainfall certainly below the minimum values for their survival and low water availability in the soils (Schwartz *et al*., 1995). Such critical conditions led to the complete disappearance of forests in this area between 3800 and 1300 years BP, just after a first major modification of their floristic composition towards a well marked semideciduous facies c. 4200 years BP (Vincens *et al*., 1998). The same evidence is registered on the Bateke plateaus c. 3000 years BP where woodlands were replaced by open formations rich in Gramineae (Schwartz *et al*., 1995, 1996a). Nevertheless, under such critical climatic conditions, some patches of forested formations have locally maintained themselves, particularly in hydromorphic depressions (Ngamakala and Bilanko on the Bateke plateaus, and Songolo on the littoral) where, during this arid event, permanent soil moisture could have compensated for a deficit in rainfall.

On sites where climatic conditions remained above or near the minimum rainfall values for the survival of forests, such as Kitina, Ossa and Barombi Mbo, no drastic and irreversible perturbations are observed. Forests persisted with only local openings after 2700 years BP (development of heliophilous formations or of enclosed savannas). Near the two last sites, the persistence of humid forests rich in Caesalpiniaceae until 2700 and 2500 years BP, respectively, has been linked to the occurrence of stratiform clouds and permanent fogs over this region (Maley & Elenga, 1993).

In addition to pollen data, some other palaeoecological studies have been carried out on the same sedimentary sequences, with similar time resolution. The most recent results obtained agree with the vegetation reconstruction and the climatic interpretation proposed above. They also point to a longer (from 4200 to 1300 years BP) and less abrupt change toward aridity than previously proposed in this part of Africa (Elenga, 1992; Maley, 1992; Schwartz, 1992), with a maximum probably centred around 3000–2500 BP. At Sinnda, when pollen data show a major change to semideciduous trees in the forests surrounding the lake c. 4200 years BP, phytoliths analyses demonstrate a first occurrence of Gramineae which indicates a beginning of fragmentation of the forests with, certainly, development of isolated enclosed savannas (Alexandre *et al*., 1996, 1997; Vincens *et al*., 1998). Mineralogical studies carried out on this same site show, from 4300 years BP, a decrease of quartz and kaolinite contents and an increase of calcite and talc interpreted as a progressive reduction of rainfall (Bertaux *et al*., 1996). At the same time and with the same climatic interpretation, a decrease of quartz and kaolinite fluxes and of siderite precipitation is registered at Kitina (Bertaux *et al*., 1996; Elenga *et al*., 1996) but no major perturbation of the local forests is still observed until 2500 years BP linked to their relative former stability on this site.

The refilling of lake Sinnda after 1300 years BP and the recent expansion of the forests observed around the lakes Kitina (*c.* 500 BP) and Ossa (*c.* 700 BP), and in the Ngamakala depression (*c.* 900 BP), despite increased human impact as shown by the appearance and development of *Elaeis guineensis* (oil palm), confirms the re-establisment of more humid conditions over Atlantic Equatorial Africa during the last millenium. Increased rainfall is also testified from 600 to 500 BP onwards on the Congolese littoral by the resumption of erosion (Sitou *et al.*, 1996). On the least favourable sites, Sinnda and Coraf, the development of open grasslands and their maintenance until today are the result of three main successional and/or cumulative factors: climatic stress, low available water capacity of the soils, and, more recently, fires set by people (Schwartz *et al.*, 1995; 1996a).

Within this recent humid period, a brief drought was registered at Sinnda *c.* 650 BP, within the interval spanned by the Little Ice Age, as evidenced by a large extension of marsh linked to a short drop in the lake level (Vincens *et al.*, 1998). But, without a time resolution of the data on the forested sites as high as at Sinnda (20 years in the upper part of the core), one cannot infer for the moment the impact of this climatic event on the forests.

CONCLUSION

In Atlantic Equatorial Africa, the agreement between pollen records, macroflora remains, phytoliths, isotopic, hydrological and hydrobiological data definitely demonstrates that climate has been the primary driving factor in the evolution of forests during the last 4000 years BP. It is now clear that the great floristic, structural and palaeogeographical perturbations which have affected these forests are mainly linked to an arid event centred around 3000–2500 BP, but of longer time-scale duration than the one previously proposed, from 4200 to 1300 years BP. This event is responsable to the main features of the modern vegetational landscapes in this region, particularly occurrence of secondary open grasslands in some areas and of enclosed savannas inside the forests.

Such an increasing aridity during the Late Holocene associated with major vegetation changes has been previously observed in other parts of tropical Africa (Servant & Servant-Vildary, 1980; Bonnefille *et al.*, 1991; Taylor, 1992; Ssemmanda & Vincens, 1993; Vincens, 1993; Jolly *et al.*, 1994; Yan & Petit-Maire, 1994) but also in other tropical regions such as India (Bryson & Swain, 1981; Swain *et al.*, 1983; Caratini *et al.*, 1994) or Tibet (Gasse *et al.*, 1996). The regional pattern and the contemporaneity of these records are now a strong argument against an extensive anthropogenic deforestation at this time.

During the last millenium, rehumidication and forest advance despite human interferences are also clearly registered in the data. This pattern continued onwards as shown by historical and ecological results obtained on savanna-forest boundaries in Ivory Coast, Central Africa, Congo and Cameroon (Gautier, 1989; Boulvert, 1990; Schwartz *et al.*, 1996b; Youta Happi, 1998) despite rainfall markedly below normal during the past decades in West Africa (Nicholson, 1994).

After all, such a synthesis now clearly demonstates that research into climate change/past vegetation during the Holocene in Atlantic Equatorial Africa needs to resolve timescales shorter than have been previously explored (100 years or less) to lead to more precise and realistic comparisons between sites.

REFERENCES

Alexandre, A., Meunier, J. D., Lezine, A. M., Vincens, A. & Schwartz, D. (1997) Phytoliths: indicators of grassland dynamics during the late Holocene in intertropical Africa. *Palaeogeogr. Palaeoclim. Palaeoecol.*136, 213–229.

Alexandre, A., Meunier, J. D., Vincens, A., Soubies, F. & Pironon, J. (1996) Les phytolithes, marqueurs paléogéographiques. *Dynamique à long terme des écosystèmes forestiers intertropicaux*, pp. 37–38. CNRS-ORSTOM, Bondy.

Baumgartner, A. (1978) Tropical forests and the biosphere. *Tropical forest ecosystems*, pp. 33–60. UNESCO, Paris.

Bertaux, J., Sifeddine, A., Schwartz, D., Vincens, A. & Elenga, H. (1996) Enregistrement sédimentologique de la phase sèche d'Afrique équatoriale c. 3000 BP par la spectrométrie IR dans les lacs Sinnda et Kitina (Sud-Congo). *Dynamique à long terme des écosystèmes forestiers intertropicaux*, pp. 213–215. CNRS-ORSTOM, Bondy.

Bonnefille, R., Riollet, G. & Buchet, G. (1991) Nouvelle séquence pollinique d'une tourbière de la crête Zaïre-Nil (Burundi). *Rev. Palaeobot. Palynol.* 67, 315–330.

Boulvert, Y. (1990) Avancée ou recul de la forêt centrafricaine. Changements climatiques, influence de l'homme et notamment des feux. *Paysages Quaternaires de l'Afrique Centrale Atlantique* (ed. by R. Lanfranchi and D. Schwartz), pp. 353–366. ORSTOM, Paris.

Brénac, P. (1989) Analyse palynologique du lac Barombi Mbo: histoire de la forêt tropicale humide et du climat dans les 30 000 dernières années. *Symposium Association des Palynologues de Langue Française*, Orléans, Sept. 1989.

Bryson, R.A. & Swain, A.M. (1981) Holocene variations of monsoon rainfall in Rajasthan. *Quat. Res.* 16, 135–145.

Bush, M. B., Colinvaux, P. A., Wiermann, M.C., Piperno, D. R. & Liu, K. B. (1990) Late Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. *Quat. Res.* 34, 330–345.

Caratini, C., Bentaleb, I., Fontugne, M., Morzadec-Kerfourn, M. T., Pascal, J. P. & Tissot, C. (1994) A less humid climate since ca. 3500 yr B.P. from marine cores off Karwar, western India. *Palaeogeogr. Palaeocliml. Palaeoecol.* 109, 371–384.

Colinvaux, P. (1997) *The ice-age Amazon and the problem of diversity*, pp.7–30. NWO/Huygenslezing, Netherlands Organization for Scientific Research NWO, The Hague.

Cusset, G. (1987) *La flore et la végétation du Mayombe congolais. Etat des connaissances.* UNESCO, Paris.

Dechamps, R., Lanfranchi, R., Le Cocq, A. & Schwartz, D. (1988b) Reconstitution d'environnements quaternaires par l'étude de macrorestes végétaux (Pays Bateke, R.P. du Congo). *Palaeogeogr. Palaeoclim. Palaeoecol.* 66, 33–44.

Dechamps, R., Lanfranchi, R. & Schwartz, D. (1988a) Découverte d'une flore forestière mi-holocène (5800–3100 B.P.) conservée in situ sur le littoral ponténégrin (R.P. du Congo). *C. R. Acad. Sci. Paris, Serie 2*, 306, 615–618.

Descoings, B. (1960) *Les steppes loussékés de la zone de Gabouka (Plateau Batéké, République Congo-Brazzaville).* ORSTOM Brazzaville.

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.

Elenga, H., Schwartz, D. & Vincens, A. (1992) Changements climatiques et action anthropique sur le littoral congolais au cours de l'Holocène. *Bull. Soc. Géol. Fr.* 163, 83–90.

Elenga, H., Schwartz, D. & Vincens, A. (1994) Pollen evidence of Late Quaternary vegetation and inferred climate changes in Congo. *Palaeogeogr. Palaeoclim. Palaeoecol.* 109, 345–356.

Elenga, H., Schwartz, D., Vincens, A., Bertaux, J., de Namur, C., Martin, L., Wirrmann, D. & Servant, M. (1996) Diagramme pollinique holocène du lac Kitina (Congo): mise en évidence de changements paléobotaniques et paléoclimatiques dans le massif forestier du Mayombe. *C. R. Acad. Sci. Paris, Série 2a,* 323, 403–410.

Elenga, H., Vincens, A. & Schwartz, D. (1991) Présence d'éléments forestiers montagnards sur les plateaux Batéké (Congo) au cours du Pléistocène supérieur. Nouvelles données palynologiques. *Palaeoecol. Africa,* 22, 239–252.

Gasse, F., Fontes, J. C., Van Campo, E. & Wei, K. (1996) Holocene environmental changes in Bangong Co basin (Western Tibet). Part 4: Discussion and conclusions. *Palaeogeogr. Palaeoclim. Palaeoecol.* 120, 79–92.

Gautier, L. (1989) Contact forêt-savane en Côte d'Ivoire centrale: évolution de la surface forestière de la réserve de Lamto (sud du V-Baoulé). *Bull. Soc. Bot. Fr.* 136, 85–92.

Giresse, P., Maley, J. & Brénac, P. (1994) Late Quaternary palaeoenvironments in the lake Barombi Mbo (West Cameroon) deduced from pollen and carbon isotopes of organic matter. *Palaeogeogr. Palaeoclim. Palaeoecol.* 107, 65–78.

Hall, J.B. & Swaine, M.D. (1981) *Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation in Ghana.* Dr W. Junk, The Hague.

Jolly, D., Bonnefille, R. & Roux, M. (1994) Numerical interpretation of a high resolution Holocene pollen record from Burundi. *Palaeogeogr. Palaeoclim. Palaeoecol.* 109, 357–370.

Koechlin, J. (1961) *La végétation des savanes dans le Sud de la République du Congo.* Mémoire de l'ORSTOM, Paris.

Letouzey, R. (1968) *Etude phytogéographique du Cameroun.* Lechevalier, Paris.

Letouzey, R. (1985) *Notice de la carte phytogéographique du Cameroun au 1: 500 000.* IRA Yaoundé et Inst. Cart. Intern. Végétation, Toulouse.

Makany, L. (1963) Contribution à l'étude de la végétation côtière du Congo-Brazzaville. Unpublished Thesis, University Paris XI.

Makany, L. (1976) *Végétation des plateaux Téké.* Travaux Université Brazzaville.

Maley, J. (1987) Fragmentation de la forêt dense humide africaine et extension des biotopes montagnards au Quaternaire récent: nouvelles données polliniques et chronologiques. Implications paléoclimatiques et biogéographiques. *Palaeoecol. Africa,* 18, 307–334.

Maley, J. (1989) Late Quaternary climatic changes in the African rain forest: forest refugia and the major role of sea surface temperature variations. *Paleoclimatology and paleometeorology: modern and past patterns of global atmospheric transport* (ed. by M. Leinen and M. Sarnthein), pp. 585–616. NATO Advanced Sc. Inst. Series, C, Math. & Phys. Sc., 282. Kluwer, Dordrecht.

Maley, J. (1991) The African rain forest vegetation and palaeoenvironments during late Quaternary. *Climatic Change,* 19, 79–98.

Maley, J. (1992) Commentaire à la note de D. Schwartz: Mise en évidence d'une péjoration climatique entre ca. 2500 et 2000 ans B.P. en Afrique tropicale humide. *Bull. Soc. Géol. Fr.* 163, 363–365.

Maley, J. (1996) The African rain-forest – main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Essays on the ecology of the Guinea-Congo rain forest* (ed. by I. J. Alexander, I. J. *et al.*). *Proc. R. Soc. Edinb.* B, 104, 31–73.

Maley, J. & Brénac, P. (1998) Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years B.P. *Rev. Palaeobot. Palynol.* 99, 157–187.

Maley, J. & Elenga, H. (1993) Le rôle des nuages dans l'évolution des paléoenvironnements montagnards de l'Afrique Tropicale. *Veille Climatique Satellitaire,* 46, 51–63.

Nguetsop, V.F. (1997) *Evolution des environnements de l'Ouest Cameroun depuis 6000 ans d'après l'étude des diatomées actuelles et fossiles dans le lac Ossa. Implications paléoclimatiques.* Unpublished Thesis, Museum National d'Histoire Naturelle, Paris.

Nguetsop, V.F. & Servant-Vildary, S. (1996) Variations hydrologiques du lac Ossa (Ouest Cameroun) au cours des 5000 dernières années à partir de l'étude des diatomées. *Dynamique à long terme des écosystèmes forestiers intertropicaux.* CNRS-ORSTOM, Bondy.

Nicholson, S.E. (1994) Recent rainfall fluctuations in Africa and their relationship to past conditions over the continent. *Holocene,* 4, 121–131.

Reynaud, I. & Maley, J. (1994) Histoire récente d'une formation forestière du Sud-Ouest-Cameroun à partir de l'analyse pollinique. *C. R. Acad. Sci. Paris, Sci. Vie,* 317, 575–580.

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.

Reynaud-Farrera, I. (1997) Late Holocene vegetational changes in South-West Cameroon. *Third Millennium BC climate change and Old world collapse* (ed. by H. N. Dalfes *et al*), NATO ASI serie I: Global Environmental Change, 49, 641–652. Springer-Verlag, Berlin.

Reynaud-Farrera, I., Maley, J. & Wirrmann, D. (1996) Végétation et climat dans les forêts du Sud-Ouest Cameroun depuis 4770 ans B.P. analyse pollinique des sédiments du lac Ossa. *C. R. Acad. Sci. Paris, Série 2a,* 322, 749–755.

Richards, P.W. (1981) *The tropical rain forest. An ecological study.* Cambridge University Press, Cambridge.

Schwartz, D. (1988) *Histoire d'un paysage: le lousseke. Paléoenvironnements quaternaires et podzolisation sur sables Bateke (quarante derniers millénaires, région de Brazzaville, R.P. du Congo).* Collection Etudes et Thèses. ORSTOM, Paris.

Schwartz, D. (1992) Assèchement climatique vers 3000 B.P. et expansion Bantu en Afrique centrale atlantique: quelques réflexions. *Bull. Soc. Géol. Fr.* 163, 353–361.

Schwartz, D., de Foresta, H., Mariotti, A., Balesdent, J., Massimba, J. P. & Girardin, C. (1996b) 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.

Schwartz, D., Dechamps, R., Elenga, H., Lanfranchi, R., Mariotti, A. & Vincens, A. (1995) Les savanes du Congo: une végétation spécifique de l'Holocène supérieur. Actes 2° Symposium de Palynologie Africaine, Tervuren, Belgique, *Publ. occas. CIFEG 1995/31,* Orléans, 99–108.

Schwartz, D., Dechamps, R., Elenga, H., Mariotti, A. & Vincens, A. (1996a) Les savanes d'Afrique Centrale: des écosystèmes à l'origine complexe, spécifiques de l'Holocène supérieur. *Dynamique à long terme des écosystèmes forestiers intertropicaux.* CNRS-ORSTOM, Bondy.

Schwartz, D., Guillet, B. & Dechamps, R. (1990) Etude de deux flores forestières mi-holocène (6000–3000 BP) et subactuelle (500 BP) conservées in situ sur le littoral pontenegrin (Congo). *Paysages Quaternaires de l'Afrique Centrale Atlantique* (ed. by R. Lanfranchi and D. Schwartz), pp. 283–297. ORSTOM, Paris.

Servant, M., Maley, J., Turq, B., Absy, M. L., Brenac, P., Fournier, M. & Ledru, M. P. (1993) Tropical forest changes during the Late Quaternary in African and South American lowlands. *Global Planetary Change,* 7, 25–40.

Servant, M. & Servant-Vildary, S. (1980) L'environnement quaternaire du bassin du Tchad. *The Sahara and the Nile* (ed. by M. A. J. Williams and H. Faure), pp. 133–162. Balkema, Rotterdam.

Servant-Vildary, S., Nguetsop, F., Roux, M., Reynaud-Farrera, I., Servant, M. & Wirmann, D. (1996) Relations statistiques diatomées/milieux aquatiques et application à l'estimation des paléo-niveaux lacustres. *Dynamique à long terme des écosystèmes forestiers intertropicaux*, pp. 93–94.CNRS-ORSTOM, Bondy.

Sitou, L., Schwartz, D., Mietton, M. & Tchicaya, J. (1996) Histoire et dynamique actuelle des cirques d'érosion du littoral d'Afrique centrale. Une étude de cas: les cirques du littoral ponténégrin (Congo). *Dynamique à long terme des écosystèmes forestiers intertropicaux*, pp. 187–191.CNRS-ORSTOM, Bondy.

Ssemmanda, I. & Vincens, A. (1993) Végétation et climat dans le basin du lac Albert (Ouganda, Zaïre) depuis 13 000 ans B.P.: apport de la palynologie. *C. R. Acad. Sci. Paris, Série 2*, 316, 561–567.

Swain, A. M., Kutzbach, J. E. & Hastenrath, S. (1983) Estimates of Holocene precipitation for Rajasthan, India, based on pollen and lake-level data. *Quat. Res.* 19, 1–17.

Talbot, M.R. & Johannessen, T. (1992) A high resolution palaeoclimatic record for the last 27,500 years in tropical West Africa from the carbon and nitrogen isotopic composition of lacustrine organic matter. *Earth Planet. Sci. Letts*, 110, 23–37.

Talbot, M. R., Livingstone, D. A., Palmer, P. G., Maley, J., Melack, J. M., Delibrias, G. & Gulliksen, S. (1984) Preliminary results from sediment cores from lake Bosumtwi, Ghana. *Palaeoecol. Afr.* 16, 173–192.

Taylor, D. (1992) Pollen evidence from Muchoya swamp, Rukiga Highlands (Uganda), for abrupt changes in vegetation during the last ca. 21,000 years. *Bull. Soc. Géol. Fr.* 163, 77–82.

Turq, B., Vincens, A., Absy, M. L., Bertaux, J., Ledru, M. P., Servant, M., Sifeddine, A., Ybert, J. P., Elenga, H., Maley, J. & Schwartz, D. (1996) Evolution des forêts tropicales d'Amérique du Sud et d'Afrique Centrale Atlantique à l'échelle des 20 000 dernières années. *Dynamique à long terme des écosystèmes forestiers intertropicaux*, pp. 277–280. CNRS-ORSTOM, Bondy,

Van der Hammen, T. & Absy, M.L. (1994) Amazonia during the Last Glacial. *Palaeogeogr. Palaeoclim. Palaeoecol.* 109, 247–261.

Vincens, A. (1993) Nouvelle séquence pollinique du lac Tanganyika: 30,000 ans d'histoire botanique et climatique du bassin Nord. *Rev. Palaeobot. Palynol.* 78, 381–394.

Vincens, A., Alexandre, A., Bertaux, J., Dechamps, R., Elenga, H., Maley, J., Mariotti, A., Meunier, J. D., Nguetsop, F., Reynaud-Farrera, I., Schwartz, D. & Servant-Vildary, S. (1996b) Evolution de la forêt tropicale en Afrique Equatoriale Atlantique durant les 4000 dernières années et héritage sur les paysages végétaux actuels. *Dynamique à long terme des écosystèmes forestiers intertropicaux*, pp. 287–289. CNRS-ORSTOM, Bondy.

Vincens, A., Buchet, G., Elenga, H., Fournier, M., Martin, L., de Namur, C., Schwartz, D., Servant, M. & Wirrmann, D. (1994) Changement majeur de la végétation du lac Sinnda (vallée du Niari, Sud-Congo) consécutif à l'assèchement climatique holocène supérieur: apport de la palynologie. *C. R. Acad. Sci. Paris, Serie 2*, 318, 1521–1526.

Vincens A., Elenga, H., Schwartz, D., de Namur, C., Bertaux, J., Fournier, M. & Dechamps, R. (1996a) Histoire des écosystèmes forestiers du Sud-Congo depuis 6000 ans. *Dynamique à long terme des écosystèmes forestiers intertropicaux*, pp. 291–294.CNRS-ORSTOM, Bondy.

Vincens, A., Schwartz, D., Bertaux, J., Elenga, H. & de Namur, C. (1998) Late Holocene climatic changes in Western Equatorial Africa inferred from pollen from lake Sinnda, Southern Congo. *Quat. Res.* 50, 34–45.

White, F. (1983) *The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa.* UNESCO, Paris.

Yan, Z. & Petit-Maire, N. (1994) The last 140 ka in the Afro-Asian arid/semi-arid transitional zone. *Palaeogeogr. Palaeoclim. Palaeoecol.* 110, 217–233.

Youta Happi (1998) *Arbres contre graminées; la lente invasion de la savane par la forêt au Centre-Cameroun.* Unpublished Thesis, Université Paris IV.

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