

Pollen and spores in marine sediments from the East Atlantic.

A view from the ocean into the African continent.

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Abstract

Selected results of marine palynological studies for the West African region are presented. Emphasis is laid on the aeolian and fluvial transport of pollen grains from the continent to the ocean. The relative importance of transport processes from the continent to the ocean varies from region to region. Aeolian pollen transport to the Atlantic accounts for a major proportion of the pollen found in marine sediments off Northwest Africa. On the shelves along the Gulf of Guinea and the Angolan Basin, particularly in the vicinity of river mouths, pollen transport is predominantly fluvial.

NE-trade winds drift pollen from the southern Mediterranean and the northern Sahara southwest- and southwards. The African Easterly Jet transports pollen from the southern Sahara and the Sahel to the eastern Atlantic. As the southward trade-wind transport strongly increased during glacial stages, the westward African Easterly Jet transport stayed latitudinally stable.

A transect of cores from 30°N to 12°S covering the last 150 ka provides information of the vegetation history of the adjacent African continent. During glacial Stages 6 and 1, the Mediterranean forest strongly declined or disappeared completely from the southwest Mediterranean area and was replaced by an open steppe-like vegetation. The Saharan-Sahelian boundary migrated between 15°N (during Stages 6, 2 and Substage 5d) and 23°N (during Substage 5e). The rain forest was widespread during Stages 1 and 5, but strongly reduced during Stages 3 and 4 and especially during Stages 2 and 6 when open, grass-rich vegetation prevailed. Glacial rain forest refuges are found in the southwest of the Guinean mountains and along the eastern coast of the Gulf of Guinea. Miombo woodland expanded during Stage 5. Afromontane *Podocarpus* forests had their largest expansion during Substages 5d and 5b. *Podocarpus* did no longer occur in the Guinean mountains after Stage 5.

Introduction

Palynology investigates microfossils that resist drastic maceral treatment. Starting with the study of pollen and spores, the scope broadened when other entities, generally called palynomorphs, gained more and more attention. Palynomorphs can be fungal spores and

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small fructifications, polychaete jaws, extinct chitinozoans, animal and vegetable tissue fragments, as well as the more familiar algal cysts, spores, and pollen grains. The content of palynology is circumscribed by its techniques more than by the unity of the material studied (Jansonius & McGregor 1996).

It is thus not surprising that palynology has branched into various disciplines, of which the more important are briefly mentioned here. Knowledge of the morphology of pollen, spores, and algal cysts is essential. Several textbooks dedicate considerable sections to pollen and spore morphology (Moore et al. 1991; Nilsson & Pragowski 1992). While pollen morphologists often pursue taxonomic problems, palaeoclimatic and palaeoenvironmental studies are at the forefront of Quaternary palynology. Pollen analysis reconstructing former vegetation by means of the pollen grains it produced is a tool in palaeoecology as well as in plant geography (Faegri et al. 1989; Lang 1994). Pre-Quaternary palynology is strongly geologically orientated and covers biostratigraphic topics, palynofloras, and palaeoenvironments (Traverse 1988). Important contributions have been made to the study of plant evolution, particularly in the angiosperms (Muller 1970; Friis & Pedersen 1996) and the geographical and evolutionary development of dinoflagellates (Stover et al. 1996).

After the pioneering work of Iversen (1941), palynology - later in combination with archaeobotany - became well embedded in many archaeological studies (Behre 1986; Bryant & Holloway 1996). Melissopalynology, which examines the pollen content of honeys, is becoming increasingly important in monitoring the production, analysis, and sale of commercial honey (Jones & Bryant 1996). Aeropalynology investigates the pollen and spore content of the air and has prominent medical applications in hay-fever forecasting (O'Rourke 1996). In addition, modern pollen distribution studies form the base at the interpretation of the sedimentary record.

Pollen data derived from the deep-sea and lower continental slope sediments integrate palynological information over a large area, but often miss considerable detail. They are suitable for the investigation of large shifts in vegetation over long periods. In contrast, pollen data from terrestrial deposits give much more detailed information of local or regional vegetation patterns. Marine diagrams, however, cover often more than one climatic cycle which makes them suitable for tracing large-scale climatically-induced vegetation change. They normally have a firm stratigraphy provided, in the majority of cases, by oxygen isotope measurements on foraminifers from the same sediments. Careful interpretation of marine pollen diagrams places emphasis on transport and sedimentation processes, as these have a strong impact on the results. Marine pollen

data can be compared globally and are a valuable addition to other climate proxies. By their nature they allow a direct land-sea correlation. Pollen grains can also be used as tracers for the origin of organic matter (Wagner & Dupont, this volume)

Jan Muller was probably the first to link the pollen and spore distribution in marine surface sediment samples to the modern vegetation by his study sediments of the Orinoco delta (Muller 1959). In later years, numerous studies have used marine palynology as a tool in Quaternary palaeoclimatology. For instance, studies on Mediterranean sediments showed the influence of Nile discharge and monsoonal precipitation in tropical Africa on the circulation of the Mediterranean Sea (Rossignol-Strick 1983, 1985). Monsoonal variation as reflected by the vegetation of East Africa was studied by Van Campo et al. (1982, 1990) on cores from the Indian Ocean. Heusser & Morley (1985) and Heusser (1989) related the last glacial-interglacial vegetation history of Japan and Northeast Asia to the palaeoceanographic and palaeoclimatic change in the northwestern Pacific. Direct land-sea correlation of the pollen content in sediments from the northwestern Pacific with that of the adjacent continent elucidated the stratigraphical position of terrestrial pollen sequences of Stage 5 and older periods (Heusser & Shackleton 1979; Heusser & Heusser 1990). Other land-sea comparisons were carried out in Baffin Bay, where the combined study of pollen, spores, and dinoflagellate cysts provided data on the climatic and oceanographic history of eastern Canada (De Vernal & Hillaire-Marcel 1986; De Vernal et al. 1987; Hillaire-Marcel & De Vernal 1989). Changes in the composition of the vegetation on New Zealand during the last 350 ka reflecting regional climatic variation in concordance with global climatic change are represented in marine sediments of DSDP Site 594 (Heusser & Van de Geer 1994). The late Quaternary vegetation history of Indonesia, New Guinea, and northern Australia including the Sahul shelf during low sea-level stands was studied by Van der Kaars (1991) using marine piston cores from the eastern Indonesian seas.

In particular, the East Atlantic along the West African margin has been systematically investigated. Results of surface sediment samples (Hooghiemstra & Agwu 1986; Hooghiemstra et al. 1986; Dupont & Agwu 1991), of time slices (Hooghiemstra 1988a; Hooghiemstra et al. 1987), and of time series covering at least the glacial-interglacial transition on a transect of deep-sea cores from 37°N to 12°S (Caratini et al 1979; Rossignol-Strick & Duzer 1979; Agwu & Beug 1982; Hooghiemstra 1988b; Fredoux & Tastet 1988; Hooghiemstra & Agwu 1988; Dupont et al. 1989; Lézine & Hooghiemstra 1990; Lézine 1991; Bengo & Maley 1991; Lézine & Vergnaud-Grazzini 1993; Dupont & Agwu 1992; Hooghiemstra et al. 1992; Dupont & Weinelt 1996; Fredoux 1994; Marret &

Turon 1994; Jahns 1996; Jahns et al 1998; Shi & Dupont 1997; Dupont et al. 1998) have been published.

In this article, I will examine some aspects of marine palynology focussing on pollen data from the East Atlantic. I will not discuss the palynology of littoral or shelf sediments, because the proximity of the continent, the fluctuations in water table, and the differences in sedimentation regime would require a very different approach. Neither is an attempt made to give a review of previous work since that would surpass the scope of this paper.

In the interpretation of pollen data, several aspects must be taken into account: these include source and production of pollen grains, transport to the sea and through the water column, displacement by ocean currents, sedimentation processes, fossilisation and accumulation in the sediment. Production of pollen grains varies strongly between different species. After pollen and spores reach the sediments, they still can be displaced by sedimentological processes such as bioturbation or sediment movement. Embedded within very slowly accumulating sediments at great water depths, pollen and spores may decay if bottom waters over the site are rich in oxygen and therefore corrosive (Keil et al. 1994), or the pollen and spore content may become enriched by the dissolution of calcium out of the sediment.

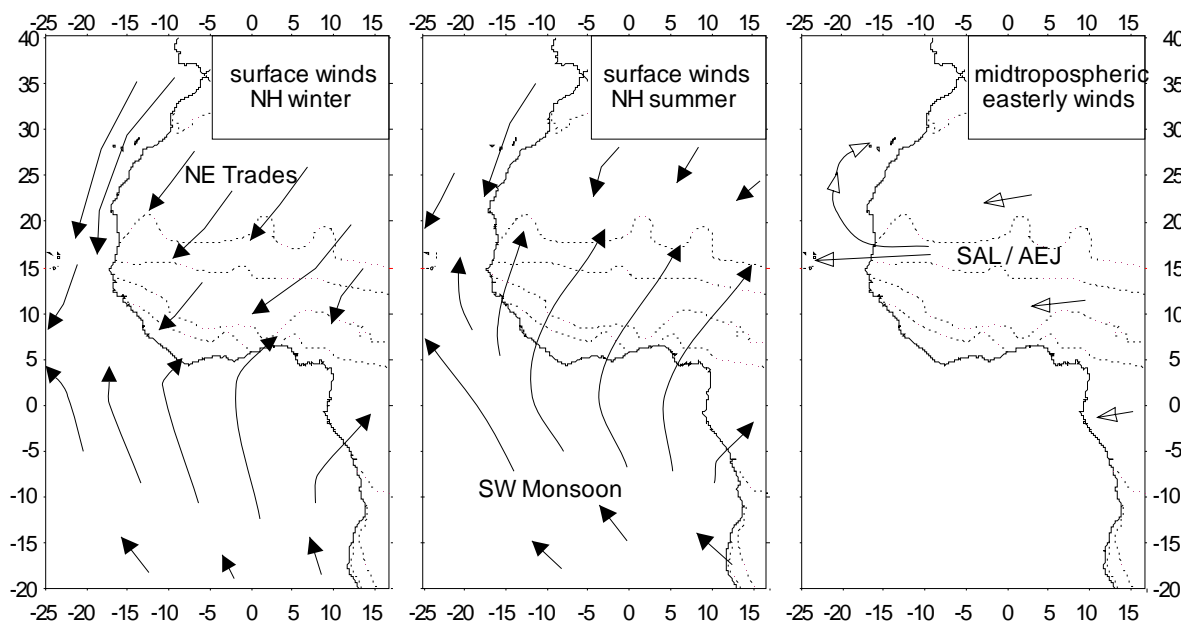


Fig. 1. Surface (left and middle) and midtropospheric (right) wind systems of West Africa. Boundaries between the main vegetation zones (named in Fig. 2) are stippled. SAL, Saharan Air Layer; AEJ, African Easterly Jet. After Leroux (1983) and Tiedemann et al. (1989).

Because pollen grains from marine sediments are typically transported over long distances, the evaluation of transport agents is always part of the interpretation of marine

pollen diagrams. The following sections give examples of different transport mechanisms as derived from palynological evidence of the East Atlantic.

Pollen transport

Transport of pollen and spores from their source areas to the marine sediments involves several steps. After pollen grains are released by the plants they disperse into the air and are transported by winds, or the grains fall into a lake or a river and are then carried by the river into the ocean. Aeolian transport of pollen and spores predominates in deep-sea sediments located far from the coast and along arid areas with no or small river discharge into the ocean (Heusser & Morley 1985; Hooghiemstra et al. 1986). In contrast to desert margins, fluvial transport of pollen and spores is especially high in the humid tropical areas. The role of fluvial transport has been shown by an increased pollen concentration in sediments sampled from the vicinity of river mouths (Muller 1959; Heusser & Balsam 1977; Davey & Rogers 1975; Heusser 1988; Bengo 1997).

Pollen that has eventually got into the upper layers of the ocean has to be transported down through the water column to the sea floor. Pollen grains are too small and too light to have an effective sink velocity by themselves. However, pollen is caught in larger aggregates - in faecal pellets or large filamental aggregates - that can have sink velocities of 100 m per day or more (Schrader 1971; Silver et al. 1978; Honjo 1980; Wefer 1991, 1993; Wefer & Fischer 1993). The transport through the water column is more efficient in areas with a high marine surface productivity where the incorporation of sporomorphs in the food chain is enhanced (Ratmeyer et al. 1998). The increased sink velocity reduces drifting by ocean currents. However, along continental slopes, strong boundary currents may displace pollen and spores (Heusser & Balsam 1985; Dupont & Agwu 1991).

Palynological studies on modern sediments of continental shelves reflect the influence of both river input and sorting of particles, whereby the sedimentation of pollen and spores can be compared to that of the medium to fine silt fraction, because of their size and density (Rossignol 1961; Davey 1971).

The relative importance of transport processes from the continent into the ocean varies from region to region. For the East Atlantic they involve, among others, trade-wind transport and mid-tropospheric wind transport (Fig. 1). Off the estuaries of large rivers and in delta areas, river transport predominates. Depending on the oceanographical situation, ocean currents may have some influence. I will give examples of wind transport of pollen

from North and Northwest Africa (by NE-trade winds and African Easterly Jet) and of river transport of pollen by the Niger.

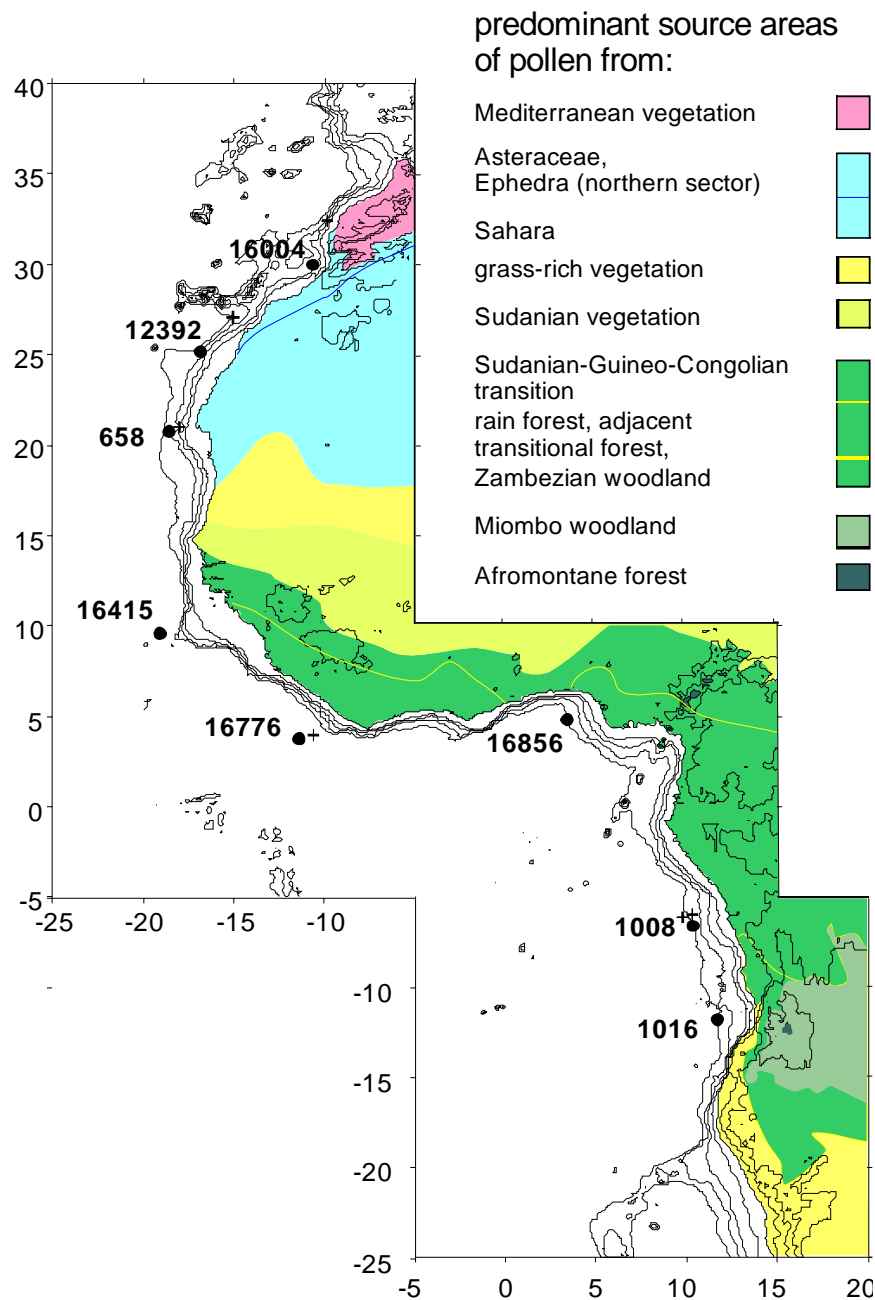


Fig. 2. Fossil sites and predominant pollen source areas. The natural Mediterranean vegetation is rich in oaks (deciduous and sclerophyllous) and pine. The majority of pollen from the Sahara are Chenopodiaceae-Amaranthaceae pollen. Pollen from *Ephedra* and Asteraceae (composites incl. *Artemisia*) originate mainly from the northern Sahara. Most of the grass pollen (Poaceae) north of the Equator are derived from the Sahel and probably from the Sudanian woodland and savanna, and south of the Equator from the Namib and the Kalahari. Grouped tropical forest pollen taxa are mainly derived from the Guineo-Congolian rain forest and its adjacent transitional forests, from the Sudanian woodland (northern sector), and from the Zambezian woodland (southern sector). The area of the Zambezian Miombo woodland is lighter shaded. Afromontane forests is found in Cameroon and Angola. Coastal mangrove swamps are not depicted. Phytogeographical units after White (1983). Isobaths at 2000, 1000, and 200 m. Contours at 500, 1000, and 1500 m.

NE trade-wind transport of pollen

Aeolian pollen transport to the Atlantic accounts for a major proportion of the pollen found in marine sediments off Northwest Africa. No large rivers discharge into the ocean from this arid part of the continent. The southward transport of pollen grains along the coast of Northwest Africa by the Canary Current is probably insignificant for two reasons: firstly, the transport of particles settling through the water column by surface currents to the south is counteracted by northbound undercurrents and secondly, particles settle fairly quickly to the ocean bottom (see above). Lithogenic flux analyses of sediment traps, set in the water column at 300 and 3000 m water depth at sites west of Cape Blanc and north of the Canary Islands, showed an efficient and fast downward transport of particulate matter. North of the Canary Islands, however, laterally advected material -probably originating from surface waters closer to the coast - was also trapped in the moorings at 300 m water depth (Ratmeyer et al. 1998).

The distribution of many pollen types, such as *Pinus*, *Artemisia*, other Asteraceae (composites), and *Ephedra*, in the modern marine surface sediments reflects the average course of the trajectory of the major wind belts (Hooghiemstra et al. 1986). The NE-trade winds over the East Atlantic originate from the northwestern fringe of the Sahara and blow basically parallel to the shore line (Leroux 1983). The average trajectory of the NE-trade winds over the Atlantic Ocean may reach 12°N in summer and as far south as 2°N in winter (Fig. 1). Hence, pollen from Mediterranean and North African trees and shrubs can be blown much further south by the NE-trade winds than the southernmost extension of their source areas (Fig. 2).

A major constituent in the pollen rain of Southwest Europe and North Africa is *Pinus* pollen. Pine trees are overrepresented in the pollen diagram because the trees produce more pollen grains than any other tree species from the Mediterranean forest, for instance *Quercus*, the oak tree. The aerodynamically well-equipped pine pollen is produced in large quantities, in particular from March to May, but pine pollen release continues at a lower level until up to July (Hooghiemstra et al. 1986; Rizzi Longo & Cristofolini 1987; Caramiello et al. 1990). Southward winds are dominant in Southwest Europe during the flowering period. Pine pollen grains showed up in a sediment trap moored in the vicinity of the Cape Verde Isles, where a maximum of pine pollen was found for the period between 21 March to 4 April 1993 and may be attributed to the spring bloom of pine trees in the western Mediterranean area (Agwu, unpublished results).

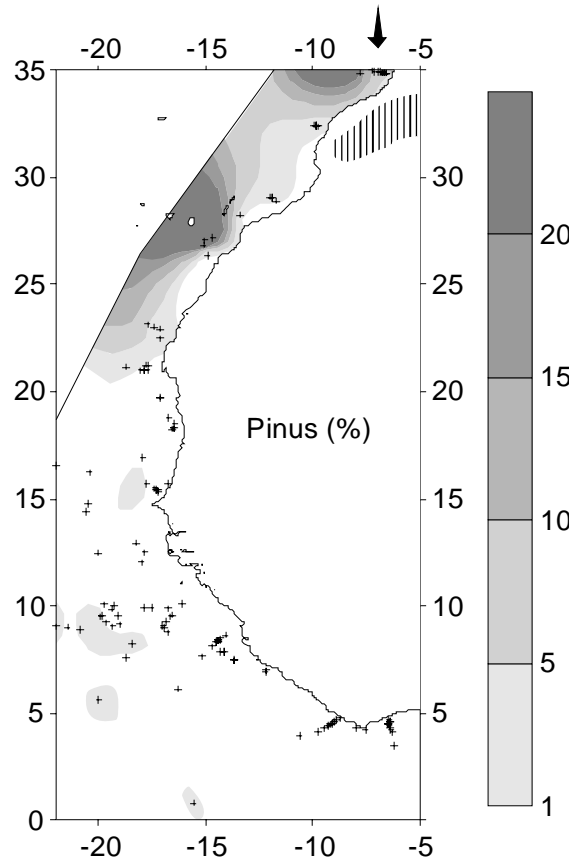


Fig. 3. *Pinus* pollen percentages (of total pollen) in surface sediment samples along the West African coast. The pine pollen source area on the African continent is hatched. Other source areas are in Europe (arrow) and on the Canary Islands. After Hooghiemstra et al. 1986.

Maximum representation of pine pollen in marine surface sediments West of North Africa is found at some distance from the coast, whereas percentages decrease coastwards. South of the Canary Islands, a secondary maximum is present, apparently representing the pine forests on those islands. Representation decreases southwards and isopol lines are roughly parallel to the coast (Hooghiemstra et al. 1986). The distribution pattern in the modern marine sediments matches the average wind flow pattern of the NE-trade winds (Fig. 3).

Ephedra pollen grains are also effectively downwind transported by the NE-trade winds. Species of *Ephedra* occur mainly in the northern and western Sahara, in the Saharan-Mediterranean transition zone, and in the drier parts of the Mediterranean (Knapp 1973; White 1983; Agwu & Beug 1982). *Ephedra major* grows in the Halfa steppe along the northern fringe of the Sahara (Knapp 1973; Quézel 1965, 1978). The distribution pattern of *Ephedra* pollen grains in marine surface sediments corresponds with the distribution of *Ephedra* on the continent. Low percentages in samples of lower latitudes attest downwind

transport by the NE-trade winds as far south as the equator (Fig. 4; Hooghiemstra et al. 1986).

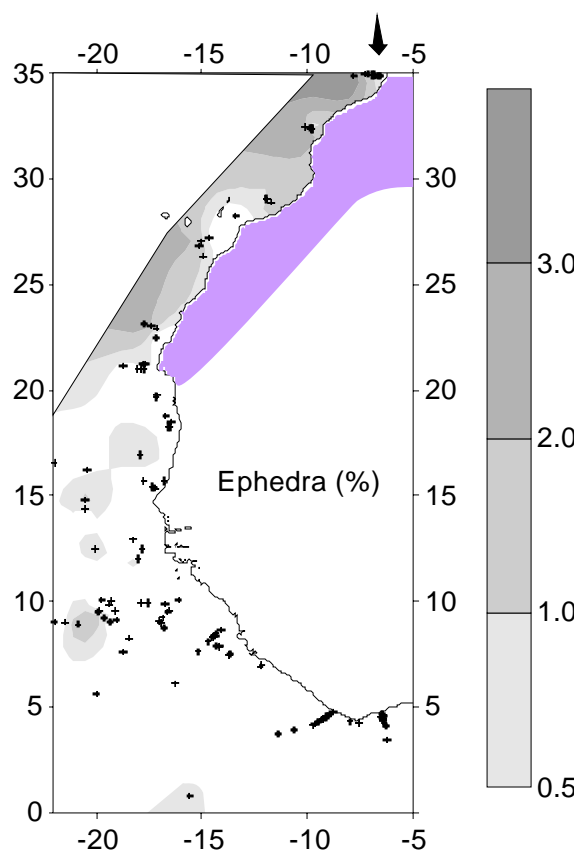


Fig. 4. *Ephedra* pollen percentages (of total pollen) in surface sediment samples along the West African coast. The source area of *Ephedra* pollen in Africa is denoted in violet. Other source areas are in Europe (arrow). After Hooghiemstra et al. 1986.

Compared to the modern situation, the distribution area of *Ephedra* on the continent strongly expanded during the Last Glacial Maximum (Hooghiemstra et al. 1987). The southernmost position of the desert is estimated to have been at 14°N during glacial maxima (Rossignol-Strick & Duzer 1979; Hooghiemstra 1988b; Hooghiemstra & Agwu 1988; Dupont 1993). Yet, an increase of *Ephedra* pollen in glacial stages is found in marine sediments at 9°N (Site GIK16415; Dupont & Agwu 1992). The *Ephedra* pollen percentage maxima at 9°N parallel those of the cores from Site GIK12392 at 21° (Agwu & Beug 1982) and ODP Site 658 at 25°N (Dupont et al. 1989). The maxima in the northern cores are interpreted as recording the enlargement of the distribution area of *Ephedra* on the continent during a glacial stage, whereas the southern core reflects the effective southward transport by enhanced NE trade-winds (Fig. 5; see Fig. 2 for core positions).

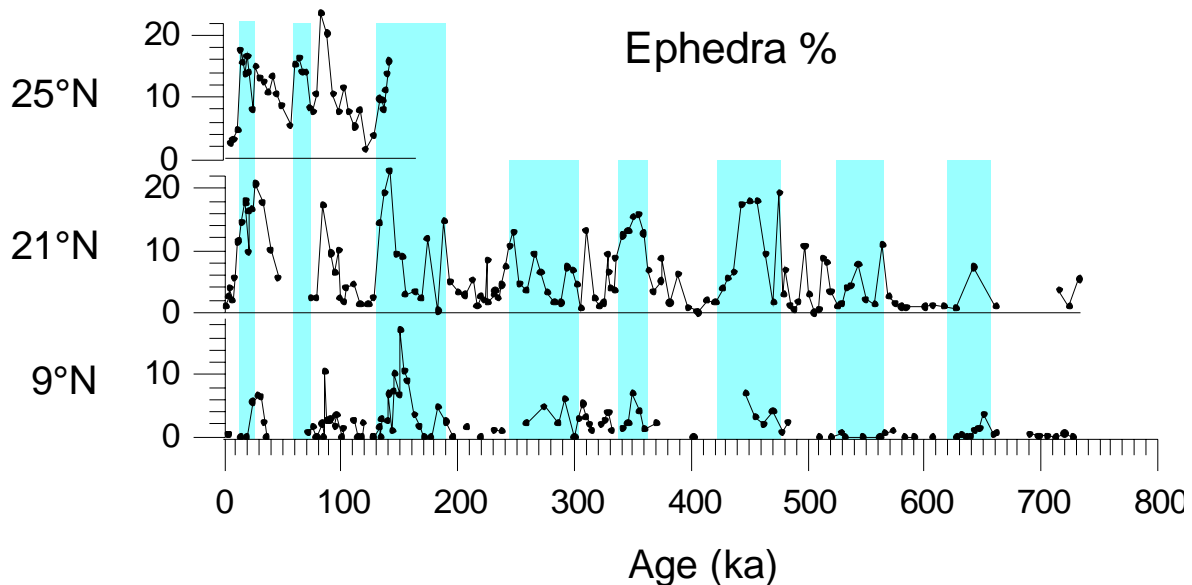


Fig. 5. *Ephedra* pollen percentages (of total pollen) of three late Quaternary sequences at different latitudes, GIK12392 at 25°N, ODP Site 658 at 21°N, and GIK16415 at 9°N. Glacial isotope stages are shaded.

Mid-tropospheric wind transport by the African Easterly Jet

Off West Africa, the lithogenic (siliciclastic) sediments are dominated by aeolian dust. The main transport of dust occurs in the Saharan Air Layer coupled to the zonal mid-tropospheric African Easterly Jet between 1000 and 5000 m altitude (Fig. 1). These dust outbreaks follow the temperature gradient linked to the Intertropical Convergence Zone (ITCZ), which today attains its northernmost position near 18°N during northern summer (Siedler 1980; Tetzlaff & Wolter 1980; Tetzlaff et al. 1989). Additional dust is supplied by the NE-trade winds below 1000 m altitude. The aeolian dust contribution to the East Atlantic was much increased up to 800 km offshore during the Last Glacial Maximum, but its centre showed almost no latitudinal shift to the south compared to today (Koopmann 1981; Sarnthein et al. 1981; Hooghiemstra et al. 1987).

The halophytic shrubs and herbs belonging to the families of Chenopodiaceae and Amaranthaceae have a wide distribution in the saline littoral zone of Northwest Africa and the extensive saline evaporation areas of the Sahara. Their flowers produce great quantities of pollen which is wind-dispersed. At the northern fringe of the Sahara the period of main pollen release lasts from November to April, but at the southern fringe from June to September. In these periods of the year, the NE-trade winds and the African Easterly Jet (AEJ), respectively, are the major wind systems. Furthermore, river systems are hardly present or totally absent in these areas.

Chenopodiaceae-Amaranthaceae (%)

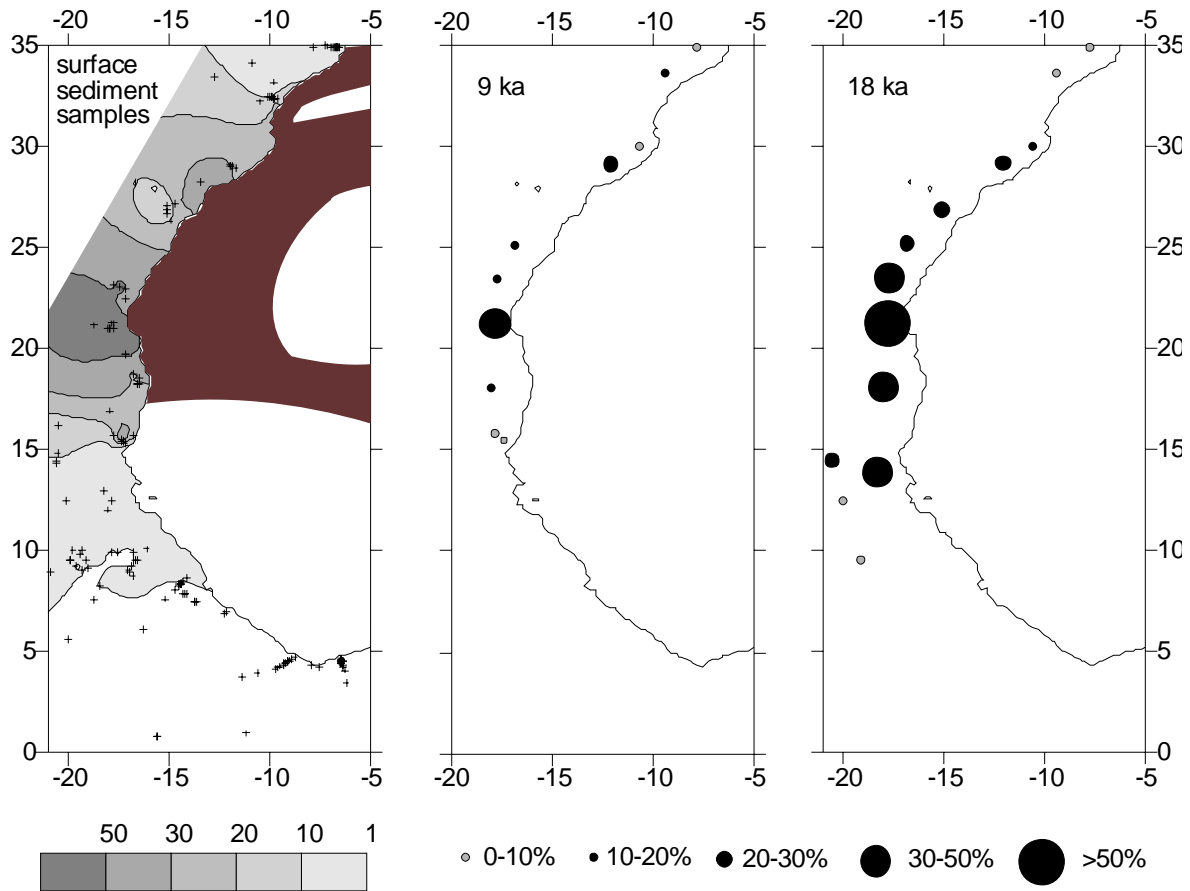


Fig. 6. Distribution of pollen of Chenopodiaceae-Amaranthaceae in percentages of total pollen for three different time slices, modern (surface sediment samples), Holocene climate optimum (9 ka uncalibrated), Last Glacial maximum (18 ka uncalibrated). Modern source areas of Chenopodiaceae-Amaranthaceae pollen are denoted in brown. After Hooghiemstra (1988a).

This explains why the distribution pattern of Chenopodiaceae-Amaranthaceae pollen in modern marine sediments matches the average wind flow pattern of those wind belts (Fig. 6; Hooghiemstra et al. 1986). The isopol maps of 9 and 18 ka show a latitudinal stationary area with a distinct pollen supply from the east by the AEJ, thus indicating that the belt with AEJ transport did not shift in latitude during the last glacial-interglacial transition and remained stationary at ca. 17-22°N (Hooghiemstra 1988a). On the basis of quartz accumulation rates from several ODP sites northwest of Africa, Tiedemann et al. (1989) concluded that the AEJ did not shift in latitude over the past 4 Ma, in spite of major climatic change. This wind belt thus forms a latitudinal stable and sensitive recorder of shifting vegetation zones (Dupont & Hooghiemstra 1989). The dominant pollen type in the marine sediments between 17° and 22°N is either Chenopodiaceae-Amaranthaceae or

grass depending on the type of vegetation growing between these latitudes on the adjacent continent, desert vegetation or savanna, respectively.

River transport of pollen

Palynological studies of sediments from the Cameroon shelf showed an abundance of river-borne pollen and spores (Bengo 1997). The composition of river-borne pollen spectra reflects the source area of the drainage basin of the river. Along the northern coast of the Gulf of Guinea, source areas of river-borne pollen from the numerous rivers partly coincide with those of pollen transported by the NE-trade winds blowing off the continent during boreal winter, when the ITZC is at its southernmost position. The SW-monsoon is not expected to bring much pollen from southern Africa because of its long trajectory over sea. Another possibility is transport by mid-tropospheric southeasterly and easterly winds that potentially could bring pollen from Central Africa (Wyputta pers. comm.). The distribution of pollen in the marine surface sediments reflects rather accurately the distribution of the forest on the adjacent continent indicating that the majority of pollen comes from the regions north and northeast of the Gulf of Guinea (Dupont & Agwu 1991).

Around the Niger delta, however, source areas of wind and water transported pollen have no complete overlap. The Niger river flows in a northeasterly direction from the Guinean mountains to Timbuktu, reaching 17°N before flowing southward in the direction of the Gulf of Guinea, thereby crossing several vegetation zones. Just south of 8°N, the Niger is joined by the Benue draining the Jos Plateau. The drainage area of the Niger thus includes the Sudanian, Sahelian, (and southern Saharan) vegetation zones as well as the Guineo-Congolian rain forests and the mangrove swamps of its delta.

Members of the grass family grow in various vegetation types all over the world. The abundance and diversity in the African savannas, however, makes this region a main source area for grass pollen. Grasses are most abundant between 12 and 19°N. This latitudinal zone includes the semi-desert grasslands, the Sahel *Acacia* wooded grasslands and the Sudanian wooded grasslands. Grasses also occur in the Sahara itself, but this source area is probably of lesser importance.

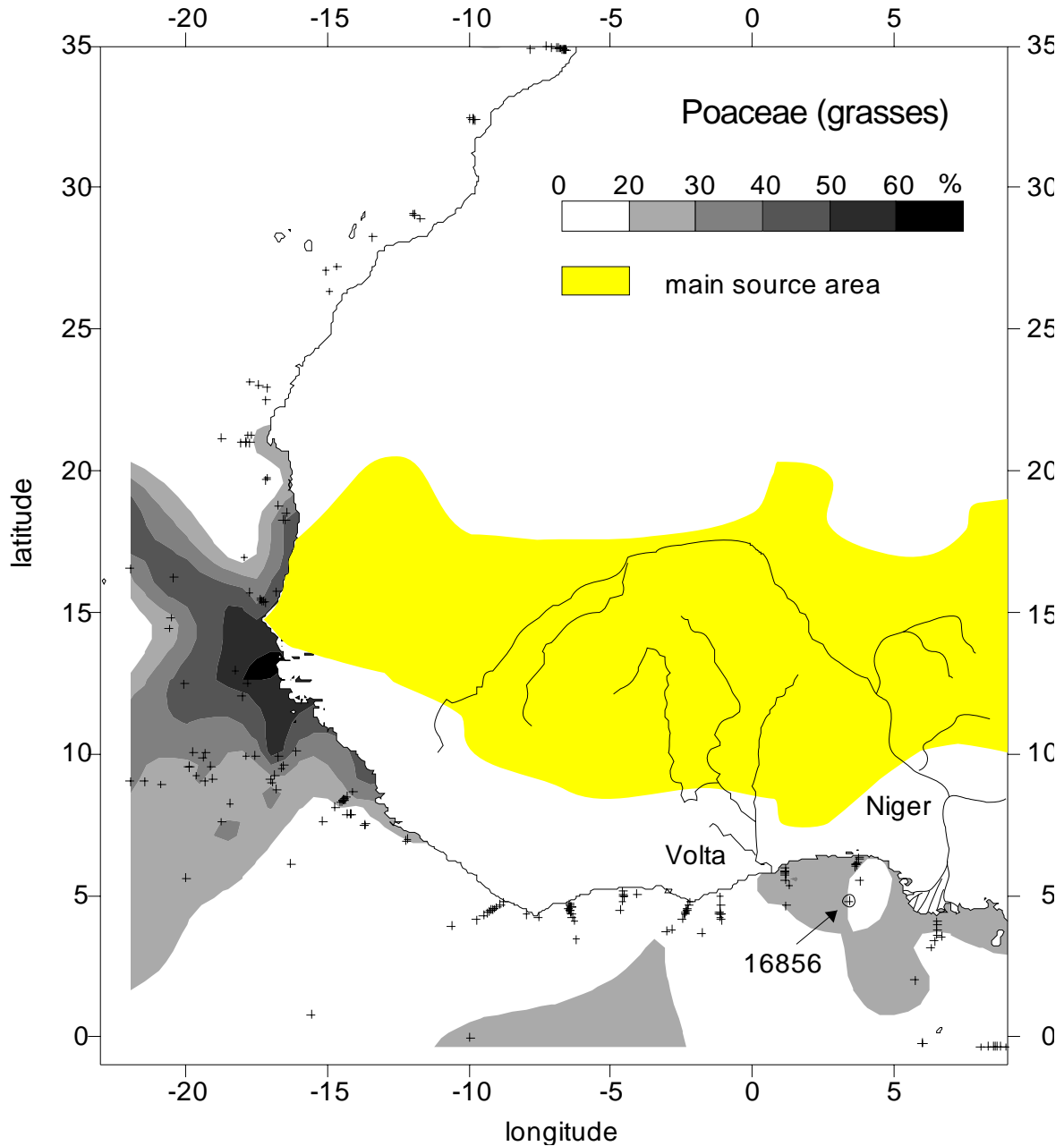


Fig. 7. Poaceae (grass) pollen percentages calculated on the sum of pollen minus *Rhizophora* from surface sediment samples from the Gulf of Guinea and the tropical NE Atlantic. Main source area of grass pollen is denoted in yellow.

The distribution pattern of Poaceae (grass) pollen in the marine sediments west of West Africa (Fig. 7) reflects the latitudes of the savanna to the open dry forest (Sahelian and Sudanian vegetation zones). Highest relative amounts of grass pollen are found west of the savanna area between 10 and 20°N with pollen percentages exceeding 30% (Dupont & Agwu 1991). The distinct change in percentages of Chenopodiaceae-Amaranthaceae and Poaceae pollen at 19°N clearly reflects the transition from Saharan desert to Sahelian grasslands (Lézine & Hooghiemstra 1990).

In a zone ranging from 8-12°N in Guinea to 4-8°N in Cameroon, the natural vegetation gradually changes from Sudanian wooded savanna to tropical rain forest. A savanna corridor, also called Togo or Dahomey Gap, reaches the coast in Togo and Benin and divides the Guineo-Congolian rain forest into a western and an eastern part. As a consequence, grass pollen percentages are much lower off the northern coast of the Gulf of Guinea. However, the areas south of the Niger delta and the Volta mouth form exceptions. Although the coastal mangrove swamps provide large amounts of *Rhizophora* pollen, grass pollen percentages rise up to 20% of the total. The high grass pollen percentages in this area are attributed, on the one hand, to represent the savanna and dry forest corridor reaching down to the coast in Togo and Benin, and on the other hand, to river transport. Surface samples from the central equatorial Atlantic are also comparatively rich in grass pollen. Those sediments, however, were sampled too far from the coast to include river-borne material (Westerhausen et al. 1993), but lay under the winter dust plume, which may bring grass pollen from the Sudanian savanna (see also Wagner & Dupont, this volume).

Confirmation of the importance of river transport in the case of grass pollen is found in the sediments of Site GIK16856. The 17 m long piston core from Site GIK16856 mostly consists of silty clay and clay. The stable isotope record of the planktonic foraminifer *Globigerinoides ruber* (white variety) covers the period back to late Stage 6. Sediments dated before 145 ka and between 122 and 125 ka do not contain foraminifera as the marine portion is strongly diluted by clastic sediments. Those sediments are also characterised by high sedimentation rates and the occurrence of colonies of the fresh-water algae *Pediastrum* and *Botryococcus*. During the periods before 142 ka, from 121 to 125 ka, and to a lesser extent from 100 to 105 ka, the deposition of fresh-water algae increased and the ratio between pollen and dinoflagellate cysts exceeded 0.75 (Fig. 8). Lack of foraminifera, occurrence of fresh-water algae, and reduced numbers of dinoflagellate cysts all indicate that the sediments mentioned above are strongly influenced by the Niger fresh-water discharge. Furthermore, only in those sediments did turbidity disturbances, sandy layers, and lenses appear. From the sedimentary record it is inferred that the modern position of the site outside the discharge gullies is only valid for the upper part of the core dated after 120 ka BP.

The change in sedimentation regime, however, gives a unique opportunity to study the influence of different discharge regimes on the pollen composition of the deep-sea sediments, especially the concentration of grass pollen grains (Fig. 8). Cyperaceae pollen also increases in the "fresh-water" sediments, whereas the concentration of other pollen

grains and of fern spores is relatively unaffected (Dupont & Weinelt 1996). The same can be said for cyperaceous pollen.

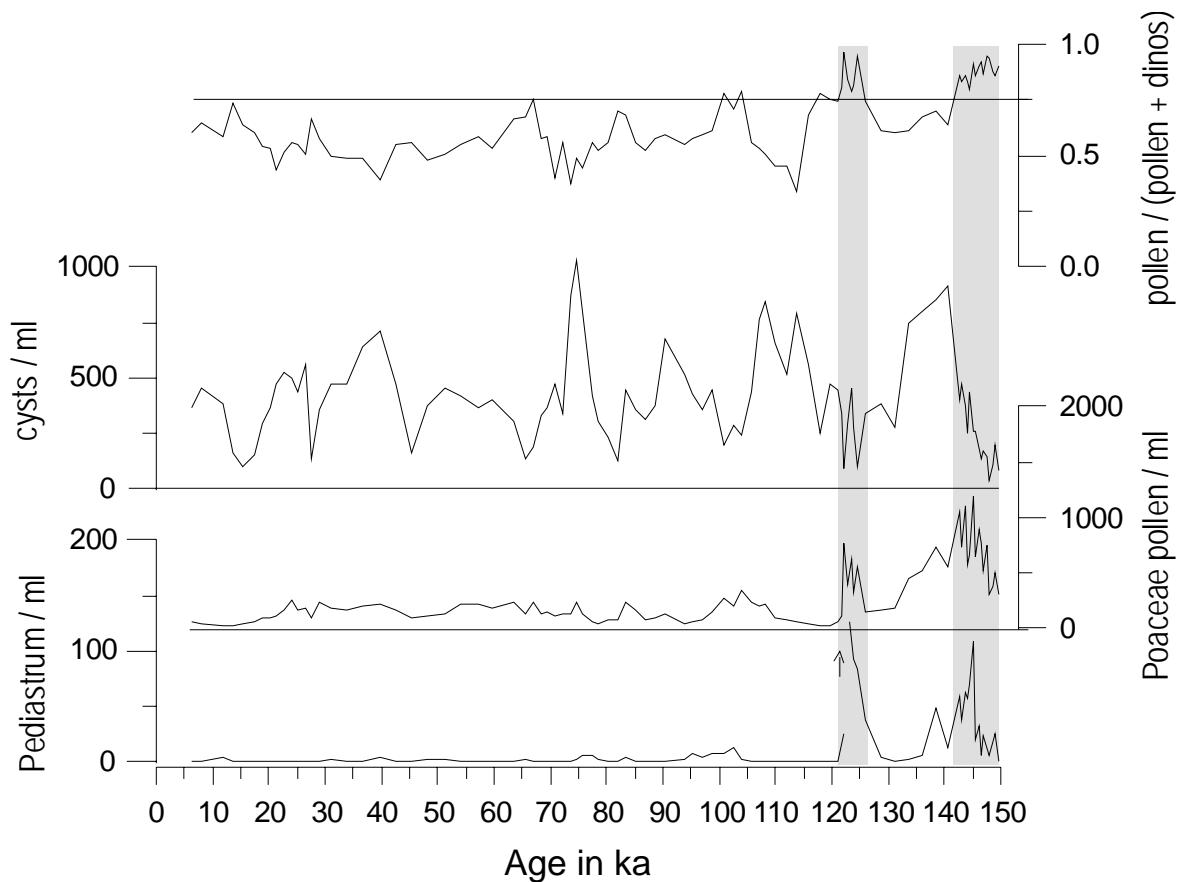


Fig. 8. Concentration values per ml of *Pediastrum* colonies (fresh-water algae), Poaceae (grass) pollen, dinoflagellate cysts, and the ratio of pollen to the total of pollen and dinoflagellate cysts plotted against time (after Dupont & Weinelt 1996). Data are from Site GIK16856 at 5°N 3°E (see Fig. 7).

A transect along the West African coast covering the last 150 ka

A transect of selected deep-sea sediment cores situated along the West African coast between 30°N and 12°S reflects the vegetation zones and their migration during the glacial-interglacial cycle since 150 ka. The transect covers modern latitudes of Mediterranean forest, Saharan-Mediterranean steppes, Saharan desert, Sahelian savanna, Sudanian savanna and dry open forest, Guinean-Congolian rain forest and adjacent transitional forest zones, and Zambezian vegetation including the Miombo woodland (Fig. 2). The modern northern boundary of the Namib desert lies just south of the southernmost core. Some indicator pollen types with their source areas and principal transport mechanisms are given in Table 1. The indicative value of certain pollen in

marine sediments is mainly derived from the modern distribution patterns in marine sediments (Hooghiemstra et al. 1986; Dupont & Agwu 1991).

Table 1: Indicator pollen types for marine sediments west of Africa with their main source areas (vegetation zones) and principal transport agents to the deep-sea.

Pollen taxon	vegetation zones ¹	transport ¹
<i>Pinus</i>	Mediterranean pine forest	NE-trade winds
<i>Quercus</i>	Mediterranean oak forests	NE-trade winds
<i>Artemisia</i>	Mediterranean-Saharan transitional steppes	NE-trade winds
<i>Ephedra</i>	Mediterranean-Saharan transitional steppes, northern Sahara	NE-trade winds
Chenopodiaceae-Amarantaceae	Saharan desert (halophytic vegetation)	AEJ, NE-trade winds
Poaceae	extreme values (>50%): Kalahari, Namib ² ; high values (>20%): Sahelian savanna, Sudanian savanna and dry open forest	SE-trade winds ² , rivers ³ , AEJ
<i>Alchornea</i>	rain forest	(January trades), rivers ⁴
<i>Rhizophora</i>	> 10%: mangroves	rivers, ocean currents
<i>Podocarpus</i>	Afromontane forest	mid-tropospheric winds, SE-trade winds
<i>Brachystegia</i>	Miombo woodland ²	SE-trade winds ²
Asteroidae (tubuliflorous composites)	Namib ² , Mediterranean, Sahara	SE-trade winds ² , NE-trade winds, AEJ

¹ After Hooghiemstra et al. (1986) and Dupont & Agwu (1991).

² After results from cores GeoB1008, GeoB1016, and GeoB1023 (Jahns 1996, Shi & Dupont 1997; Shi et al. submitted)

³ After Dupont & Weinelt (1996)

⁴ *Alchornea* trees often grow along water courses. As a result *Alchornea* pollen is well distributed on the continental shelf in the vicinity of the Sanaga river (Bengo 1997). River-borne *Alchornea* pollen grains are probably abundant in all those sediments sufficiently near the coast to receive fluvial sediment loads.

In addition to the pollen diagrams from each core, a pollen spectrum from a surface sample is shown (Fig. 9). Where we did not have a surface sediment sample from the same site as the core was taken, one as close as possible to the site was selected. Surface sediment samples mostly cover only the last few centuries. They can be compared to the modern vegetation, whereby the strong impact of agriculture and human occupation especially in the Mediterranean area, but also elsewhere, must be kept in mind.

Due to coring techniques, the top sediments are disturbed. As a consequence, the latest Holocene is missing in all cores and some of them even lack most of the Holocene. Sedimentary gaps exist in the sequence from ODP Site 658 including the lower part of

Stage 3 and Stage 4 (Tiedemann et al. 1989) and in GIK16415, Stages 3 and 4 are missing (Pflaumann 1986). Other gaps in the diagrams reflect sediments that are extremely poor in pollen or in the case of GIK16856 have turbiditic sediments. Stratigraphic and age control of the cores depend on the oxygen isotope stratigraphy (Winn et al. 1991; Pflaumann 1986; Tiedemann 1991; Dupont & Weinelt 1996; Schneider et al. 1995; Jahns et al. 1998).

GIK16004 (29°59'N 10°39'W)

The transect starts at 30°N just south of the Mediterranean vegetation zone and north of the Canary Islands. The Mediterranean forest in the Moroccan mountains includes, among others, several oak species, pine, ash, and cedar. Oak pollen dominates the arboreals in many terrestrial Holocene sequences (e.g. Ballouche 1986; Bernard & Reille 1987; Damblon 1991; Lamb et al. 1991). The transitional vegetation between the Mediterranean forest and the Sahara is formed by a steppe-like vegetation which is mainly represented by pollen from *Artemisia*, other composites, and *Ephedra*, and to a lesser extent by grass pollen from *Stipa* (Halfa grass).

The sediments of Site GIK16004 show high percentages of pine pollen (Hooghiemstra et al. 1992). Because of the large production of its aerodynamically well equipped pollen grains, pine is generally strongly over-represented in marine pollen diagrams. During the Last Interglacial (and the Holocene), the Mediterranean forest is mainly represented by *Quercus* (oak). The two surface sediment samples north of the site (32°N 10°W) show somewhat higher percentages of Mediterranean pollen, because of the samples' position nearer to its source area. They are otherwise comparable. The high percentages of pine pollen combined with very low ones for the other elements of the Mediterranean forest during Stages 6, 4, and 2 are probably a reflection of enhanced transport by the NE-trade winds rather than a record of increased distribution of pines because, in terrestrial diagrams of the High and Middle Atlas mountains, pollen percentages of pine during glacial times are low and those for *Artemisia* and Chenopodiaceae are high (Lamb et al. 1989, 1994).

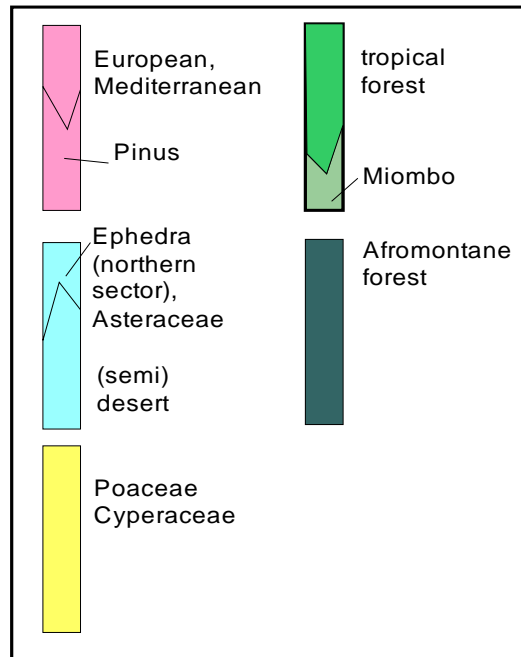
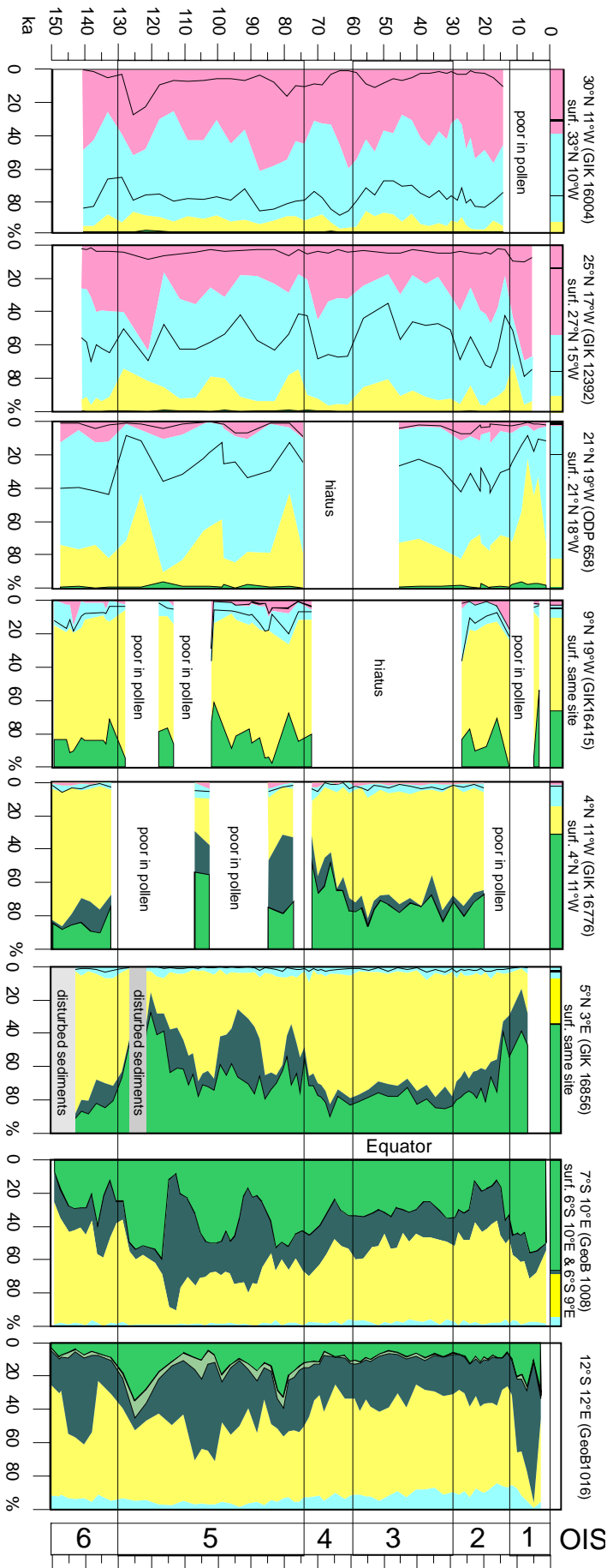


Fig. 9. Transect of seven pollen diagrams off the West African coast from 30°N to 12 °S covering the last 150 ka. Locality (see Fig. 2) and name of each site and the accompanying sediment surface sample are given in the heading. Pink = pollen from the European and Mediterranean vegetation zone, below the line *Pinus*; blue = pollen from the Sahara and the Mediterranean-Saharan transitional steppes (north of the Equator), above the line *Ephedra* and *Asteraceae*; south of the Equator, the blue pollen group mainly consists of composites that may have derived from the Kalahari; yellow = pollen from *Poaceae* (grasses) and *Cyperaceae*; green = pollen from the tropical forest (Sudanian, Guineo-Congolian, and Zambebian vegetation zones); dark green = pollen from the Afromontane forest (mainly *Podocarpus*). In the diagram of GeoB1016 (lowermost), pollen from the Zambebian Miombo woodland is denoted by a lighter shade, Oxygen Isotope Stages. Ages in ka on the vertical axis. Note X-axis runs from old (left) to young (right). For further explanations see text.

GIK12392 (25°10'N 16°51'W)

This core is situated south of the Canary islands. During interglacial periods, pine trees expanded on these islands, as indicated in the marine pollen diagram with prominent maxima of pine pollen in combination with low percentages of elements from the steppes (Agwu & Beug 1982). However, the pine pollen maxima in Stages 4 and 2 combined with high values of pollen from more arid areas (steppe and desert) indicate enhanced trade-wind transport (Hooghiemstra 1989).

The representation of the Moroccan Mediterranean forest is very low and probably insignificant in the diagram. Also, the representation of the Saharan-Mediterranean transitional steppes is considerably less than that off Morocco (GIK16004; 30°N). Increases in relative values of grasses and Cyperaceae during the "warm" periods of Stage 5 are probably attributable to a northward shift of the Sahelian savanna. Those pollen grains would have been transported by the northern branch of the AEJ as far north as 25°N. The relative amounts of Chenopodiaceae-Amaranthaceae pollen from the Sahara are larger than in the previous diagram with the exception of low values during the last Interglacial and the early Holocene reflecting a strongly reduced desert belt during interglacial stages.

The surface sediment sample is situated northeast of the core at 27°N 15°W. Pine pollen percentages are somewhat lower than in the early Holocene sample of the core at 25°N 17°W. The northeast position of the surface sediment sample is less favourable for the registration of trade-transported pine pollen from the Canary islands, which may explain the difference.

ODP Site 658 (20°45'N 18°35'W)

The next diagram in the section is only a small part of a much longer boring of ODP Leg 108 at Site 658. The complete sequence covers almost the complete Brunhes chron and large parts of the Pliocene (Tiedemann et al. 1989, Leroy & Dupont 1994). Here, I will only show the part covering the last 150 ka. Unfortunately, Stage 4 and the lower half of Stage 3 are not recorded due to a sedimentary hiatus. The pollen record consists mainly of either pollen from the desert or from the savanna. The location of the site is just north of the main outlet of the AEJ. The increase in pollen percentages of Poaceae and Cyperaceae during Stages 5 and 1 reflects a northward extension of the grass-rich Sahelian savanna. At this latitude, small amounts of pollen from the tropical forest - mostly elements from the Sudanian woodland - are also found (Dupont et al. 1989).

The influence of the NE-trade winds is registered by pollen types from the Mediterranean and the Mediterranean-Saharan transitional steppes (*Ephedra*, *Artemisia* and other composites), but their values in the pollen spectra of ODP Site 658 are lower compared to the other two diagrams previously discussed. Some increased pollen transport by the NE-trade winds is found in the cooler phases of Stage 5 and in Stage 2. The pollen percentages of the Mediterranean forest are very low during the warmer phases of Stage 5, Stages 3, and 1. Obviously, the expansion of that forest is not registered this far south (21°N). The surface sediment sample, located slightly to the east, shows much more pollen from the desert than the Holocene samples of ODP Site 658. It indicates an expansion of the Saharan desert in the later part of the Holocene as the result of aridification of the Sahara and Sahel after 3500 BP (Petit-Maire & Schulz 1981; Lézine 1989; Petit-Maire 1991). Increased human impact in the Sahel probably also contributed to the expansion of the desert southwards.

GIK16415 (9°34'N 19°6'W)

The next core, at 9°N, is very poor in pollen. Spores are more abundant probably reflecting the long distance to the shore. In surface sediment samples from the eastern Atlantic, a strong southward increasing gradient in the representation of fern spore percentages is found between 10 and 9°N, i.e. at the same latitude as the northern boundary of the Guinean rain forest. Therefore, the ratio between fern spores and grass pollen could be used to extract information of the latitudinal position of the northern rain forest boundary (Dupont & Agwu 1992). However, to compare the results of Site GIK16415 with the other cores, the spores are left out in the summary diagram in Fig.9. As a consequence, calculated sums are partly as low as 40 pollen which makes percentage representation hazardous. Results should only be taken as a rough estimate.

In all samples, pollen from Poaceae and Cyperaceae dominate. Although the Sudanian vegetation zone is rich in woody plants, their pollen production is much lower than that of many grasses and the forest element is under-represented in the pollen diagram. Reduced atmospheric circulation, especially reduced trade winds during Stages 5 and 1, is probably the main reason that hardly any pollen could be found in sediments of those ages. A sedimentary hiatus prevents a record of Stages 4 and 3.

Additional information is found in the literature (Lézine 1991). Between the latitudes of the southern Sahara boundary and the northern forest limit, core V22-196 (13°50'N 18°57'W, 3728 m water depth) west of Senegal shows the expansion of humid vegetation

(Sudanian and Sudano-Guinean elements) during periods dated between 140 and 118 ka (just before and during Substage 5e), 105 and 96 ka (Substage 5c), 92 and 73 ka (Substage 5a), 52 and 44 ka (early Stage 3), and at 12 ka. Increased trade-wind circulation is suggested for the period after 60 ka, especially after 40 ka reaching a maximum at 17 ka, when a maximum of pollen from the Sahara was registered (Lézine 1991).

GIK16776 (3°44'N 11°24'W)

Sediments of Site GIK16776 are also poor in pollen, but not so poor as those of GIK16415 (Jahns et al. 1998). The position of 16776 south of Liberia is more favourable for the reception of wind-blown pollen from West Africa. In winter, the NE-trade winds (January trades) blow off the continent when the ITCZ is at its southernmost position. The sparsity of pollen during Stages 5 and 1 probably reflects a reduction of the January trade-wind vigour. The core records a continuous presence of lowland rain forest southwest of the Guinean mountains even in Stages 6 and 2. Again, the under-representation of forest trees compared to Poaceae and Cyperaceae in the pollen diagram has to be taken into account.

Very interesting is the record of the Afromontane forest mostly represented by *Podocarpus* pollen grains. This conifer tree of the Afromontane forest no longer grows in West Africa (compare the surface sediment sample that was taken not far northeast of Site GIK16776). The modern westernmost occurrence of *Podocarpus* is in Cameroon and on the island of São Tomé. Large relative values of *Podocarpus* pollen grains were found at the end of Stage 6 and in the middle and end of Stage 5. Low pollen percentage values were found in Stages 4 to 2. Whilst low amounts of *Podocarpus* pollen grains may have been long-distance transported from the east or the south, the high percentages (up to 20%) testify that *Podocarpus* trees must have been growing in the Guinean mountains. It can be concluded that the latest occurrence of *Podocarpus* in the Guinean mountains was during Stage 5 and the tree disappeared at the beginning of Stage 4 (Dupont et al. 1996).

GIK16856 (4°48'N 3°24'E)

Site GIK16856 is located in the outer regions of the Niger fan south of Lagos. In contrast to the previously discussed cores, sediments of GIK16856 are rich in river-borne pollen (see discussion above). Preservation of the pollen was good indicating that little redeposited pollen reached the site. The source areas of the pollen at Site GIK16856 will

be mainly forest and savannas from Nigeria; but the Sahara, the Sahelian savanna, the vegetation of the Jos Plateau and the mountains of Cameroon probably also contributed to the pollen assemblages in the Niger fan sediments. These include pollen from *Podocarpus*, Poaceae, and Cyperaceae, and small amounts of pollen from the desert and semi-desert (Chenopodiaceae-Amaranthaceae, *Artemisia*, *Ephedra*). The record is good for the last 120 ka and that of the latest part of Stage 6 including Termination II (Dupont & Weinelt 1996).

During Stages 5 and 1, the lowland rain forest is represented by high pollen percentages exceeding 60%. A considerable proportion of the arboreal pollen is from *Alchornea*, a tree that is widespread and can be regarded as a pioneer (Reynaud-Farrera et al. 1996). Its large pollen production ensures good representation in the marine pollen diagram, much better than that of the numerous trees from the mature rain forest. Stage 3 shows low percentages of forest pollen as do Stages 6, 4, and 2. Pollen diagrams of the equatorial and south tropical eastern Atlantic show little differentiation between Stages 4 to 2 (Bengo & Maley 1991; Marret 1994; Jahns 1996; Shi & Dupont 1997).

The low representation of forest trees and the high pollen percentages of Poaceae and Cyperaceae during Stages 6, 4, 3, and 2 indicate that open forest and savanna vegetation types occupied much of the area along the northern coast of the Gulf of Guinea. Nowadays, the wooded savanna vegetation reaches the Gulf of Guinea in Togo and Benin, and westernmost Nigeria. During the last few centuries, the lowland rain forest in West Africa has been strongly reduced for agricultural purposes. A comparison of the pollen spectrum of the surface sample, which is from the same site as the core, with samples from glacial stages, however, indicates that the reduction of forest was much larger in glacial times.

Fluctuations in the percentages of *Podocarpus* are strong in Stage 5 and contemporaneous with those of core GeoB1008 at 7°S, which is described next. The large representation of *Podocarpus* indicates a spread of the Afromontane forest to lower altitudes during the cooler phases of Stage 5. Possible expansion areas are Cameroon and Congo (and south of it) and, perhaps, the Jos Plateau. The latter can only be verified by terrestrial pollen diagrams from that region. The extent of *Podocarpus* was limited during glacial Stages 6 and 2, probably as a result of aridity. The spread of *Podocarpus* probably indicates cooler climate and relative humid conditions. In the later part of Stage 5, the previously described record (GIK 16776) indicates a time shift in the representation of *Podocarpus* being high in the western Guinean area and low in the eastern area of Nigeria and Cameroon (Dupont et al. 1996).

A box core of the same site provides a surface sample and a modern pollen spectrum of Site GIK16867. In the surface sample *Podocarpus* is hardly represented, although a peak of pollen from that tree occurs in the early Holocene. The disappearance of *Podocarpus* pollen from terrestrial lowland sites in the east of Cameroon is dated between 2000 and 3000 years ago (Reynaud-Farrera et al. 1996; Maley & Brenac 1998).

GeoB1008 (6°36'S 10°19'E)

Site GeoB1008 is off the estuary of the Congo river and the majority of pollen and spores found here is of fluvial origin. Sediments are rich in pollen having their source areas in the huge Congo drainage basin. Rain forest grows east and north of the site, and the dry forest of the Zambezi vegetation zone is located east and south of it. The small amounts of pollen from *Artemisia* and other composites probably had their source area in the Namib and Kalahari deserts. Pollen from Poaceae and Cyperaceae may have derived from open swamps, but also from open vegetation types within the forested area.

To illustrate the mirrored sense of direction between south and north of the equator, I have drawn the diagram for this site and the next one, which both are located on the Southern Hemisphere, as in mirror images of those of the other sites, which are located on the Northern Hemisphere (Fig. 9). Representation of the forest is high during Stages 5 and 1 and lowest during Stages 6 and 2 (Jahns 1996). The division of Stage 5 into five periods is prominent, with the Afromontane forest expanding during the cooler intervals. This record, together with the previous and the next one, registers an expansion of the Afromontane *Podocarpus* forest that must have been considerable. *Podocarpus* pollen grains are also found in all other periods indicating that the tree has been growing in many places in highlands and mountains around the Congo basin. However, the surface sediment sample north of Site GeoB1008 is not rich in pollen and poor in *Podocarpus* grains indicating that, although the tree did not completely disappear, its occurrence has been strongly reduced in the later part of the Holocene (see above).

GeoB1016 (11°46'S 11°41'E)

The southernmost core in the transect is located off the coast of Angola in the trajectory of the SW-trade winds. The site is located at a distance of ca. 200 km from the nearest coast and about 250 km from the nearest river mouth. This core is rich in pollen, most of which

is probably wind-dispersed. A surface sediment sample SE of the site (12°S 12°E) was very poor in pollen and percentages can only be regarded as a rough estimate.

Most forest types of West Africa cannot be readily differentiated in the marine pollen diagrams, but the Miombo woodland forms an exception. Miombo woodland is a type of dry forest from the Zambebian vegetation zone on more elevated areas (White 1983). One of the main representatives of the Miombo woodland (*Brachystegia*) is well represented by its pollen, although not in large amounts. Pollen of accompanying trees in the Miombo forest are also found. In the Huambe mountains, *Podocarpus* trees are part of the Afromontane forest up to the present time. Poaceae pollen have their main source area in the Namib desert and the Kalahari Highveld area although grasses also grow in the open forest of the Zambebian vegetation zone.

Representation of the forest in the pollen diagram indicates that the rain forest extended farther southward during Substages 5e and 5a than in the Holocene. The Miombo woodland area increased during Substages 5e and 5c and other dry forest types expanded during Substages 5e, 5a, and 5c. The area of the Afromontane forest was probably quite small during Stage 5e, but expanded during the rest of Stage 5. Increased *Podocarpus* pollen percentages start at the beginning of Substage 5d, around 115 ka BP, in this and other sites of the tropical eastern Atlantic. A maximum of *Podocarpus* pollen percentages is found around the transition between Substages 5d and 5c. However, the representation of *Podocarpus* declines during that period at Sites GIK16856 and GeoB1008. *Podocarpus* pollen percentages show another maximum in the early to middle Holocene (Shi & Dupont 1997) but decline afterwards.

From 70 to 10 ka BP, high pollen percentages of Poaceae and increasing ones of tubuliflorous composites show a northward shift of the Namib desert. However, the maximum percentages of Poaceae never reach values as high as those found directly west of the Namib desert (Van Zinderen Bakker 1984). So, the northernmost position of the Namib probably did not cross the latitude of the site (12°S), although it came close at the end of Stage 2.

Concluding remarks

Palynological studies of marine sediments allow estimates as to the spatial changes in major vegetation zones in Africa over the last 150 ka. Information of the regional extension of phytogeographical units and the latitudinal position of vegetation zones during climatic cycles provides important clues about the climatic regime of the continent.

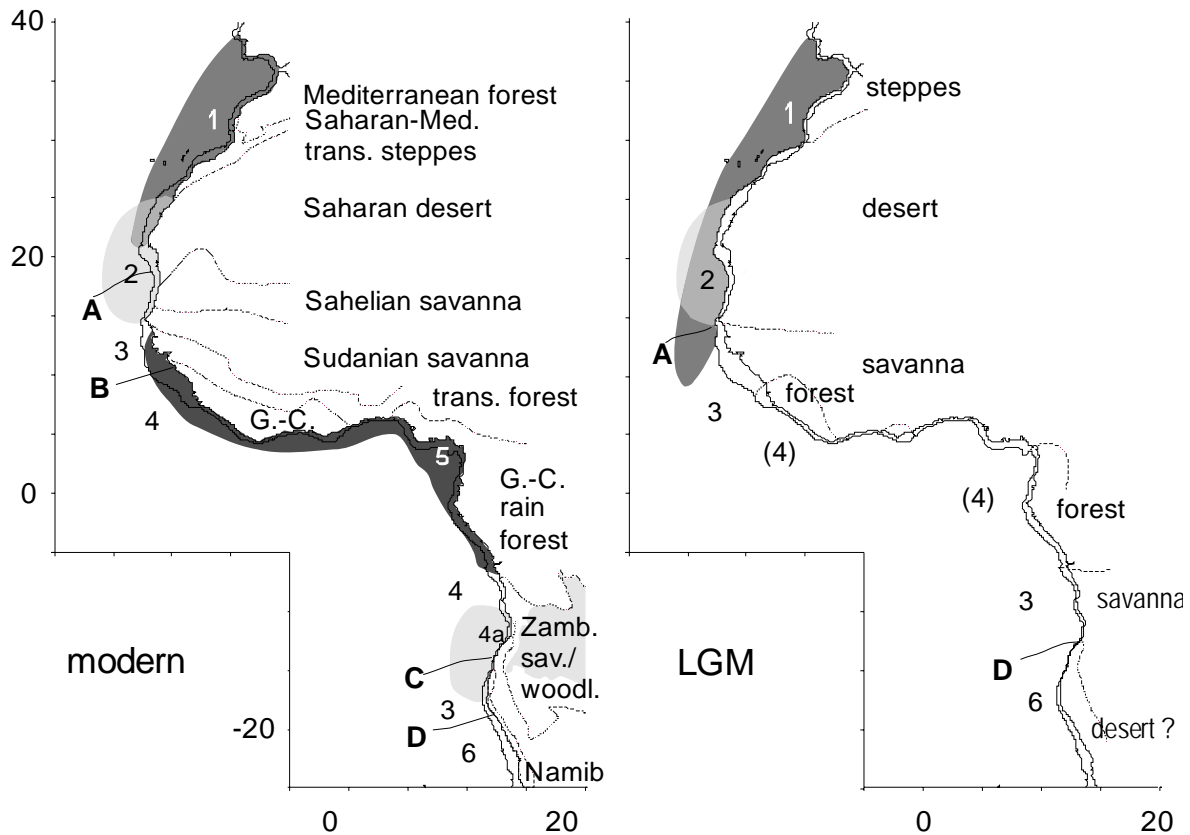


Fig. 10. Schematic representation of the pollen distribution areas in marine sediments off West Africa for present interglacial conditions (left) and for conditions of the Last Glacial Maximum (LGM, right). Med. forest = Mediterranean oak and pine forests; trans. forest = dry deciduous tropical forests and secondary grasslands from the transition between the Sudanian savanna (and woodland) and the Guineo-Congolian rain forest; G.-C. = Guineo-Congolian rain forest; Zamb. sav./woodl. = woodland and savanna from the Zambezi vegetation zone.

1 = area of marine sediments where pollen blown with the NE-trade winds from the Mediterranean area and the northern Sahara prevail; 2 = area with pollen predominantly from the southern Sahara and the Sahel mainly transported by the African Easterly Jet; 3 = area characterised by high percentages (>30%) of grass pollen; 4 = area with enhanced abundance of pollen from the tropical rain forest; 4a = area of enhanced values of *Brachystegia* pollen, characteristic of the Miombo woodland (shaded) of the Zambezi vegetation zone; 5 = *Rhizophora* pollen (from mangrove trees) exceeding 10%; 6 = pollen percentages of tubuliflorous composites exceeding 10%.

Between lines A and B and lines C and D (modern), and between line A and D (LGM), high grass pollen percentages indicate open grass-rich vegetation types prevailing on the adjacent continent. Whereas in modern sediments, the tropical rain forest and the mangrove forest are well represented (between lines B and C), both decline strongly during the LGM (see text).

Fig. 10 provides a schematic representation of vegetation and pollen distributions of the Last Glacial Maximum (LGM) compared to those of modern interglacial conditions. The LGM can be regarded as the most extreme time-slice in terms of reduction of rain forest and mangrove swamp areas. Other time-slices show distinctive

characteristics. For example, Stage 5 shows large variation in the extent of *Podocarpus*-rich Afromontane forest areas.

The natural Mediterranean vegetation consists mainly of Mediterranean oak forests (both sclerophyllous and deciduous) and conifer forests (dominated by pine and cedar). These communities strongly declined or disappeared completely from western Morocco during the LGM and were replaced by an open steppe-like vegetation with *Artemisia*, *Ephedra*, and *Chenopodiaceae*. The southward transport of pollen from the Mediterranean area and the northern Sahara strongly increases during the LGM (signature #1).

Pollen from the Sahara and the Sahel are effectively transported by the African Easterly Jet (signature #2). Although vegetation zones shift in latitude through the course of a climatic cycle, the latitudinal position of the African Easterly Jet is stable. The pollen load of this wind system depends on the vegetation growing between ca. 15 and 17°N. A northern position of the Saharan-Sahelian boundary results in increased abundance of grass pollen in marine sediments around 20°N, transported by the northern branch of the African Easterly Jet.

The representation of the modern savanna vegetation zones in the marine sediments is not differentiated as the high grass pollen content dominates over pollen from more specific elements. High grass pollen values (30-50% or higher; #3) include the area west of the Sahelian and Sudanian savanna zone (between line **A** and **B**) and the area west of the southern Zambebian woodland and the northern Kalahari shrubland (between line **C** and **D**). During the LGM, grass pollen percentages are high (>30%) in marine sediments between lines **A** and **D**, with exception of the northernmost Angola basin. They indicate the expansion of open vegetation types displacing denser forested ones.

Marine areas adjacent to tropical rain forests have a rich flora including pollen of many different trees from the tropical rain forest and the dry deciduous forest (#4). Because most of those trees produce little pollen, they are represented only in small numbers. An exception is *Alchornea*, which is a pioneer tree and, therefore, not growing in the denser parts of the rain forest. Nevertheless, its comparably large pollen production strongly improves the representation of the rain forest in marine sediments (between lines **B** and **C**). Pollen grains from *Rhizophora* are numerous (> 10%) along the coastal areas with mangrove swamps (signature #5). During the LGM, between lines **A** and **D**, the representation of the rain forest and the mangrove swamp dropped dramatically, although they did not completely disappear. Biogeographical evidence indicates rain forest refuge areas southwest of the Guinean mountains, along the coast in easternmost Ivory Coast, and west of the mountains in Cameroon, Gabon, and Congo (Sosef 1996).

The elevated area with Miombo woodland within the Zambezan vegetation zone is shaded in Fig. 10. The Miombo woodland is represented in the marine sediments by low but significant percentages of *Brachystegia* pollen (signature #4a). The representation of the Miombo woodland also strongly declines during the LGM.

South of the Zambezan vegetation zone, the Kalahari stretches far into southern Africa. Between the coastal Namib desert and the Zambezan woodland, transitional vegetation with elements from the Namib, Kalahari, and Zambezan phytogeographical units are found. South of line **D**, the representation of tubuliflorous composites in modern marine sediments increases and exceed 10%. New data indicate that during the LGM, pollen percentages of tubuliflorous composites increased considerably suggesting the impact of lower temperatures on the vegetation of southwestern Africa (Shi et al. submitted).

Results from marine and terrestrial palynology may be used to verify model reconstructions of the climate of Africa. Biome models could be used in this context as an intermediate between climate predictions and vegetation cover. A biome model translates temperature and rainfall data of direct measurements or those being generated by a general circulation model into terms of vegetation (biomes). Success of this strategy, however, depends on the accuracy of that translation, which is calibrated for the modern situation (Haxeltine & Prentice 1996).

As far as wind transport of pollen and spores is concerned, formalisation in a mathematical model would allow a quantification of wind-blown palynomorphs. Such a model compares the continental source areas and the pollen distribution in modern marine sediments using actual or modelled wind trajectories. Conversely, position and size of a pollen source area may be inferred from core data for specified time slices (Helbig unpublished). It could be a tool to objectively distinguish between pollen transport agents and may lead to a better understanding of vegetation shifts and climate.

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References

- Agwu COC, Beug HJ (1982) Palynological studies of marine sediments off the West African coast. "Meteor" Forsh Ergebn C 36: 1-30
- Ballouche A (1986) Paléoenvironnement de l'homme fossile holocène au Maroc. Aport de la Palynology. Thesis Université Bordeaux I: 134p
- Behre KE (1986) Anthropogenic indicators in pollen diagrams. Balkema, Rotterdam: 246p
- Bengo MD, Maley J (1991) Analyses des flux polliniques sur la marge sud du Golfe de Guinée depuis 135 000 ans. CR Acad Sci Paris t 313 Serie II: 843-849
- Bengo MD (1997) La sédimentation pollinique dans le Sud-Cameroun et sur la plateforme marine à l'époque actuelle et au Quaternaire récent: études des paléoenvironnements. Thesis Université Montpellier II (Languedoc): 220p
- Bernard J, Reille M (1987) Nouvelles analyses polliniques dans l'Atlas de Marrakech Maroc. Pollen et Spores 29: 225-240
- Bryant Jr VM, Holloway RG (1996) Chapter 23A. Archaeological palynology. In: Jansonius J, McGregor DC (eds) Palynology: principles and applications. AASP Foundation: vol 3, 913-917
- Caramiello R, Polini V, Siniscako C, Mecalli L (1990) A pollen calendar from Turin (1981-1988) with reference to geography and climate. Grana 29: 239-249
- Caratini C, Bellet J, Tissot C (1979) Étude microscopique de la matière organique: palynologie et palynofaciès. In: Arnould M, Pelet R Orgon 3 - Mauritanie Sénégal îles du cap-Vert - Octobre 1976. CNRS, Paris: 215-265
- Damblon F (1991) Contribution pollenanalytique a l'histoire des forêts de chene liège au Maroc: La subéraie de Krimda. Palaeoecology of Africa 22: 185-190
- Davey RJ (1971) Palynology and palaeo-environmental studies with special reference to the continental shelf sediments of South Africa. In: Farissacci (ed) Proceedings of the II planktonic conference Roma 1970 I: 331-347
- Davey RJ, Rogers J (1975) Palynomorph distribution in recent offshore sediments along two traverses off South West Africa. Mar Geol 18: 213-225
- De Vernal A, Hillaire-Marcel C (1986) Paléoenvironnements du Wisconsinien moyen dans l'Est du Canada par l'analyse palynologique et isotopique de sédiments océaniques et continentaux. Revue de Géologie et de Géographie Physique 27: 119-130
- De Vernal A, Hillaire-Marcel C, Aksu AE, Mudie JP (1987) Palynostratigraphy and chronostratigraphy of Baffin Bay deep sea cores: climatostratigraphic implications. Palaeogeogr Palaeoclimatol Palaeoecol 61: 97-105
- Dupont LM (1993) Vegetation zones in NW Africa during the Brunhes Chron reconstructed from marine palynological data. Quat Sci Rev 12: 189-202
- Dupont LM, Agwu COC (1991) Environmental control of pollen grain distribution patterns in the Gulf of Guinea and offshore NW-Africa. Geol Rundschau 80: 567-589
- Dupont LM, Agwu COC (1992) Latitudinal shifts of forest and savanna in NW Africa during the Brunhes chron: further marine palynological results from site M 16145 (9°N 19°W). Veget Hist Archaeobot 1: 163-175
- Dupont LM, Hooghiemstra H (1989) The Saharan-Sahelian boundary during the Brunhes chron. Act Bot Neerl 38: 405-415
- Dupont LM, Weinelt M (1996) Vegetation history of the savanna corridor between the Guinean and the Congolian rain forest during the last 150,000 years. Veget Hist Archaeobot 5: 273-292
- Dupont LM, Beug H-J, Stalling H, Tiedemann R (1989) First palynological results from ODP Site 658 at 21°N west off Africa: pollen as climate indicators. In: Ruddiman WF Sarinthein M et al. Proc ODP Sci Results 108. Ocean Drilling Program, College Station TX: 93-111
- Dupont LM, Shi N, Jahns S, Marret F (1996) Podocarpus in West Africa during the Late Pleistocene. Palaeoecology of Africa 24: 85-101
- Dupont LM, Marret F, Winn K (1998) Land-sea correlation by means of terrestrial and marine palynomorphs from the eastern Gulf of Guinea: phasing of SE trade winds and the ocean productivity. Palaeogeogr Palaeoclimatol Palaeoecol (in press).

- Faegri K, Kaland PE, Krzywinsky K (1989) Text book of pollen analysis by Knut Faegri and Johs. Iversen, 4th edition. John Wiley & Sons, Chichester: 328p
- Fredoux A (1994) Pollen analysis of a deep-sea core in the Gulf of Guinea: Vegetation and climatic changes during the last 225 000 years BP. *Palaeogeogr Palaeoclimatol Palaeoecol* 109: 317-330
- Fredoux A, Tastet J-P (1988) Stratigraphie pollinique et paléoclimatologie de la marge septentrionale du Golfe de Guinée depuis 200 000 ans. *Inst fr Pondichéry trav sci tech* 25: 175-183
- Friis EM, Pedersen KR (1996) Chapter 14B. Angiosperm pollen in situ in Cretaceous reproductive organs. In: Jansonius J, McGregor DC (eds) *Palynology: principles and applications*. AASP Foundation: vol 1, 409-426
- Haxeltine A, Prentice C (1996) BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochemical Cycles* 10, 693-709
- Heusser CJ, Heusser LE (1990) Long continental pollen sequence from Washington State (USA): correlation of upper levels with marine pollen-oxygen isotope stratigraphy through substage 5e. *Palaeogeogr Palaeoclimatol Palaeoecol* 79: 63-71
- Heusser LE (1988) Pollen distribution in marine sediments on the continental margin off northern California. *Mar Geol* 80: 131-147
- Heusser LE (1989) Northeast Asian climatic change over the last 140,000 years inferred from pollen in marine cores taken off the Pacific coast of Japan. In: Leinen M, Sarnthein M (eds) *Paleoclimatology and Paleometeorology: modern and past patterns of global atmospheric transport*. NATO ASI Series C 282. Kluwer, Dordrecht: 665-692
- Heusser LE, Balsam WL (1977) Pollen distribution in the northeast Pacific Ocean. *J Quat Res* 7: 45-62
- Heusser LE, Balsam WL (1985) Pollen sedimentation in the Northwest Atlantic: effect of the Western Boundary Undercurrent. *Mar Geol* 69: 149-153
- Heusser LE, Geer G van der (1994) Direct correlation of terrestrial and marine paleoclimatic records from four glacial-interglacial cycles - DSDP Site 594, Southwest Pacific. *Quat Sci Rev* 13: 273-282
- Heusser LE, Morley JJ (1985) Pollen and radiolarian records from deep-sea core RC14-103: climatic reconstructions of Northeast Japan and Northwest Pacific for the last 90,000 years. *J Quat Res* 24: 60-72
- Heusser LE, Shackleton NJ (1979) Direct marine-continental correlation: 150,000-year oxygen isotope-pollen record from the North Pacific. *Science* 204: 837-839
- Hillaire-Marcel C, De Vernal A (1989) Isotopic and palynological records of the late Pleistocene in eastern Canada and adjacent ocean basins. *Géographie physique et Quaternaire* 43: 263-290
- Honjo S (1980) Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. *J Mar Res* 38: 53-97
- Hooghiemstra H (1988a) Palynological records from northwest African marine sediments: a general outline of the interpretation of the pollen signal. *Phil Trans R Soc Lond B* 318: 431-449
- Hooghiemstra H (1988b) Changes of major wind belts and vegetation zones in NW Africa 20,000-5000 yr BP, as deduced from a marine pollen record near Cap Blanc. *Rev Palaeobot Palynol* 55: 101-140
- Hooghiemstra H (1989) Variations of the NW African trade wind regime during the last 140,000 years: changes in pollen flux evidenced by marine sediment records. In: Leinen M, Sarnthein M (eds) *Paleoclimatology and Paleometeorology: modern and past patterns of global atmospheric transport*. NATO ASI Series C, 282. Kluwer, Dordrecht: 733-770
- Hooghiemstra H, Agwu COC (1986) Distribution of palynomorphs in marine sediments: a record for seasonal wind patterns over NW Africa and adjacent Atlantic. *Geol Rundschau* 75: 81-95
- Hooghiemstra H, Agwu COC (1988) Changes in the vegetation and trade winds in equatorial Northwest Africa 140,000-70,000 yr BP as deduced from two marine pollen records. *Palaeogeogr Palaeoclimatol Palaeoecol* 66: 173-213

- Hooghiemstra H, Agwu COC, Beug H-J (1986) Pollen and spore distribution in recent marine sediments: a record of NW-African seasonal wind patterns and vegetation belts "Meteor" *Forsch Ergebn C* 40: 87-135
- Hooghiemstra H, Bechler A, Beug H-J (1987) Isopollen maps for 18,000 yr BP of the Atlantic offshore of Northwest Africa: evidence for palaeo-wind circulation. *Paleoceanography* 2: 561-582
- Hooghiemstra H, Stalling H, Agwu COC, Dupont LM (1992) Vegetational and climatic changes at the northern fringe of the Sahara 240,000-5000 years BP: Evidence from 4 marine pollen records located between Portugal and the Canary Islands. *Rev Palaeobot Palynol* 74: 1-53
- Iversen J (1941) Landnam i Danmarks stenalder. Danmarks Geologiske Undersøgelse, II Række 66: 1-68
- Jahns S (1996) Vegetation history and climate changes in West Equatorial Africa during the Late Pleistocene and Holocene based on a marine pollen diagram from the Congo fan. *Veget Hist Archaeobot* 5: 207-213
- Jahns S, Hüls M, Sarnthein M (1998) Palynological results from a marine core off Liberia (Site GIK16776) covering the last 400,000 years. *Rev Palaeobot Palynol* (in press)
- Jansonius J, McGregor DC (1996) Chapter 1. Introduction. In: Jansonius J, McGregor DC (eds) *Palynology: principles and applications*. AASP Foundation: vol 1, 1-10
- Jones GD, Bryant Jr VM (1996) Chapter 23D. Melissopalynology. In: Jansonius J, McGregor DC (eds) *Palynology: principles and applications*. AASP Foundation: vol 3, 933-938
- Kaars WA van der (1991) Palynology of eastern Indonesian marine piston-cores: A Late Quaternary vegetational and climatic record for Australasia. *Palaeogeogr Palaeoclimatol Palaeoecol* 85: 239-302
- Keil RG, Feng Sheng Hu, Tsamakis E, Hedges JI (1994) Pollen in marine sediments as an indicator of oxidation of organic matter. *Nature* 369: 639-641
- Koopmann B (1981) Sedimentation von Saharastaub im subtropischen Nordatlantik während der letzten 25.000 Jahre. "Meteor" *Forsch Ergebn C* 35: 23-59
- Knapp R (1973) *Die Vegetation von Afrika*. Fischer, Stuttgart: 626p
- Lamb HF, Eicher U, Switsur VR (1989) An 18,000-year record of vegetational lake-level and climatic change from the Middle Atlas Morocco. *J Biogeogr* 16: 65-74
- Lamb HF, Damblon F, Maxted RW (1991) Human impact on the vegetation of the Middle Atlas Morocco during the last 5000 years. *J Biogeogr* 18: 519-532
- Lamb HF, Duigan CA, Gee JHR, Kelts K, Lister G, Maxted RW, Merzouk A, Niessen F, Tahri M, Whittington RJ, Zearoual E (1994) Lacustrine sedimentation in a high-altitude semi-arid environment The palaeolimnological record of Lake Isli, High Atlas Morocco. In: Millington AC, Pye K (eds) *Environmental Change in Drylands: Biogeographical and Geomorphological Perspectives*. Wiley & Sons: 147-161
- Lang G (1994) *Quartäre Vegetationsgeschichte Europas*. Fischer, Jena: 462
- Leroux M (1983) *Le climat de L'Afrique tropicale (texte, atlas)*, Champion, Paris: 633p
- Leroy SAG, Dupont LM (1994) Development of vegetation and continental aridity in northwestern Africa during the Late Pliocene: the pollen record of ODP 658. *Palaeogeogr Palaeoclimatol Palaeoecol* 109: 295-316
- Lézine A-M (1989) Late Quaternary vegetation and climate of the Sahel. *J Quat Res* 32: 317-334
- Lézine A-M (1991) West African paleoclimates during the last climatic cycle inferred from an Atlantic Deep-Sea Pollen record. *J Quat Res* 35: 456-463
- Lézine A-M, Hooghiemstra H (1990) Land-sea comparisons during the last glacial-interglacial transition: pollen from west tropical Africa. *Palaeogeogr Palaeoclimatol Palaeoecol* 79: 313-331
- Lézine A-M, Vergnaud-Grazzini C (1993) Evidence of forest extension in West-Africa since 22,000 BP: A pollen record from eastern tropical Atlantic. *Quat Sci Rev* 12: 203-210
- Maley J, Brenac 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

- Marret F (1994) Evolution paléoclimatique et paléhydrologique de l'Atanique est-equatoriale et du proche continent au quaternaire terminal. Contribution palynologique (Kystes des dinoflagellés, pollen et spores) Thèse Université Bordeaux I: 271p
- Marret F, Turon JL (1994) Paleohydrology and paleoclimatology off Northwest Africa during the last glacial-interglacial transition and the Holocene: Palynological evidences. *Mar Geol*: 107-117
- Moore PD, Webb JA, Collinson ME (1991) Pollen analysis, 2nd edition. Blackwell, Oxford: 216p
- Muller J (1959) Palynology of recent Orinoco delta and shelf sediments: reports of the Orinoco shelf experiments. *Micropaleontology* 5: 1-32
- Muller J (1970) Palynological evidence on the early differentiation of angiosperms. *Biol Rev* 45: 417-450
- Nilsson S, Praglowski J (1992) Erdtman's handbook of palynology. Munksgaard, Copenhagen: 576p
- O'Rourke MK (1996) Chapter 23F, Medical palynology. In: Jansonius J, McGregor DC (eds) *Palynology: principles and applications*. AASP Foundation: vol 3, 945-955
- Petit-Maire N (ed) (1991) Paléoenvironnements du Sahara Lacs holocènes a Taoudenni (Mali). CNRS, Paris: 239p
- Petit-Maire N, Schulz E (1981) Data in Holocene vegetation in the Atlantic Sahara. *Palaeoecology of Africa* 13: 199-203
- Pflaumann U (1986) Sea-surface temperatures during the last 750,000 years in the eastern equatorial Atlantic: planktonic foraminiferal record of "Meteor"-cores 13519 13521 and 16415. "Meteor" *Forsch-Ergebn C* 40: 137-161
- Quézel P (1965) *La Végétation du Sahara, du Tchad à la Mauritanie*. Fischer, Stuttgart: 333p
- Quézel P (1978) Analysis of the Flora of Mediterranean and Saharan Africa. *Ann Missouri Bot Garden* 65: 479-534
- Ratmeyer V, Fischer G, Wefer G (1998) Lithogenic particle fluxes and grain size distributions in the deep ocean off NW Africa: implications for seasonal changes of aeolian dust transport and mass fluxes. *Deep-Sea Res* (in press)
- Reynauld-Farrera I, Maley J, Wirrmann D (1996) Végétation et climat dans les forêts du Sud-Ouest Cameroun depuis 4 770 ans BP: analyse pollinique des sédiments du Lac Ossa. *CR Acad Sci Paris t 322 Série II a*: 749-755
- Rizzi Longo L, Cristofolini G (1987) Airborne pollen sampling in Triest (Italy). *Grana* 26: 91-96
- Rosignol M (1961) Analyse pollinique de sédiments marins quaternaires en Israel 1. Sédiments récents. *Pollen et Spores* 3: 303-324
- Rosignol-Strick M (1983) African monsoons. An immediate climate response to orbital insolation. *Nature* 304: 46-49
- Rosignol-Strick M (1985) Mediterranean Quaternary sapropels an immediate response of the African monsoon to variation of insolation. *Palaeogeogr Palaeoclimatol Palaeoecol* 49: 237-263
- Rosignol-Strick M, Duzer D (1979) Late Quaternary pollen and dinoflagellate cysts in marine cores off West Africa. "Meteor" *Forsch Ergebn C* 30: 1-14
- Sarnthein M, Tetzlaff G, Koopmann B, Wolter K, Pflaumann U (1981) Glacial and interglacial wind regimes over the eastern subtropical Atlantic and North-West Africa. *Nature* 293: 193-196
- Schneider RR, Müller PJ, Ruhland G (1995) Late Quaternary surface circulation in the east equatorial South Atlantic: Evidence from alkenone sea surface temperatures. *Paleoceanography* 10: 197-219
- Schrader H-J (1971) Fecal pellets: role in sedimentation of pelagic diatoms. *Science* 174: 55-57
- Shi N, Dupont LM (1997) Vegetation and climate history of SW Africa: a marine palynological record of the last 300,000 years. *Veget Hist Archaeobot* 6: 117-131
- Shi N, Dupont LM, Beug HJ, Schneider R (submitted) Vegetation and climate changes during the last 21,000 yr in SW Africa - evidence from a high resolution marine palynological record. *Veget Hist Archaeobot*
- Siedler G (1980) Some implications of GATE results for Saharan dust transports across the Atlantic. *Palaeoecology of Africa* 12: 23-30

- Silver MW, Shanks AL, Trent JD (1978) Marine snow: microplankton habitat and source of small-scale patchiness in pelagic population. *Science* 201: 371-373
- Sosef MSM (1996) Begonias and African rain forest refuges: general aspects and recent progress. In: Maesen LJG van der, Burgt XM van der, Medenbach de Rooy JM van (eds) *The Biodiversity of African Plants*. Kluwer, Dordrecht: 602-611
- Stover LE, Brinkhuis H, Damassa SP, de Verteuil L, Helby RJ, Monteil E, Partridge AD, Powel AJ, Riding JB, Smelror M, Williams GL (1996) Chapter 19. Mesozoic-Tertiary dinoflagellates, acritarchs and prasinophytes. In: Jansonius J, McGregor DC (eds) *Palynology: principles and applications*. AASP Foundation: vol 2, 641-750
- Tetzlaff G, Wolter K (1980) Meteorological patterns and the transport of mineral dust from the North African continent. *Palaeoecology of Africa* 12: 31-42
- Tetzlaff G, Peters M, Janssen W, Adams LJ (1989) Aeolian dust transport in West Africa. In: Leinen M, Sarnthein M (eds) *Paleoclimatology and Paleometeorology: modern and past patterns of global atmospheric transport*. NATO ASI Series C 282. Kluwer, Dordrecht: 185-203
- Tiedemann R (1991) Acht Millionen Jahre Klimageschichte von Nordwest Afrika und Paläo-Ozeanographie des angrenzenden Atlantiks: Hochauflösende Zeitreihen von ODP-Sites 658-661. Thesis Universität Kiel: 127p
- Tiedemann R, Sarnthein M, Stein R (1989) Climatic changes in the western Sahara: aeolo-marine sediment record of the last 8 MY (ODP-Sites 657-661). In: Ruddiman WF, Sarnthein M et al. *Proc ODP Sci Results 108*. Ocean Drilling Program, College Station TX: 241-277
- Traverse A (1988) *Palaeopalynology*. Unwin Hyman, Boston: 600p
- Van Campo E, Duplessy JC, Rossignol-Strick M (1982) Climatic conditions deduced from a 150-kyr oxygen isotope-pollen record from the Arabian Sea. *Nature* 296: 56-59
- Van Campo E, Duplessy JC, Prell WL, Barratt N, Sabatier R (1990) Comparison of terrestrial and marine temperature estimates for the past 135 kyr off southeast Africa: A test for GCM simulations of paleoclimate. *Nature* 348: 209-212
- Wefer G (1991) Stofftransport zum Meeresboden: Eine Übersicht. *Naturwissenschaften* 78: 1-6
- Wefer G (1993) Formation and composition of marine particulates. In: Heinmann M (ed) *The Global Carbon Cycle*. Springer, Berlin: 505-530
- Wefer G, Fischer G (1993) Seasonal patterns of vertical particle flux in equatorial and coastal upwelling areas of the eastern Atlantic. *Deep-Sea Res* 40: 1613-1645
- Westerhausen L, Poynter J, Eglinton G, Erlenkeuser H, Sarnthein M (1993) Marine and terrigenous origin of OM in modern sediments of the equatorial East Atlantic: the ¹³C and molecular record. *Deep-Sea Res* 40: 1087-1121
- White F (1983) *The vegetation of Africa*. Natural Resources Research 20. UNESCO, Paris: 356p
- Winn K, Sarnthein M, Erlenkeuser H (1991) ¹⁸O Stratigraphy and Chronology of Kiel sediment cores from the East Atlantic. *Ber Geol-Paläontol Inst Kiel* 45: 100p
- Zinderen Bakker EM van (1984) Palynological evidence for Late Cenozoic arid conditions along the Namibia Coast from holes 532 and 530A Leg 75 Deep Sea Drilling Project. In: Hay WW, Sibuet J-C et al. *Initial Reports of the Deep Sea Drilling Project 75*. US Gov Printing Office, Washington DC: 763-768