

Late Quaternary palynology in marine sediments: A synthesis of the understanding of pollen distribution patterns in the NW African setting

Henry Hooghiemstra^{a,*}, Anne-Marie Lézine^b, Suzanne A.G. Leroy^c,
Lydie Dupont^d, Fabienne Marret^e

^aDepartment of Paleocology and Landscape Ecology, Institute for Biodiversity and Ecosystem Dynamics, Kruislaan 318, 1098 SM Amsterdam, The Netherlands

^bLaboratoire des Sciences du Climat et de l'Environnement, UMR 1572 du CNRS, CEA-Orme des Merisiers, F-91191 Gif-sur-Yvette cedex, France

^cDepartment of Geography and Earth Sciences, Brunel University, Kingston Lane, UB8 3PH, Uxbridge, UK

^dDepartment of Geosciences, University of Bremen, P.O. Box 330440, Bremen D-28334, Germany

^eSchool of Ocean Sciences, University of Wales, Bangor, Menai Bridge, Anglesey, LL59 5AM, UK

Available online 19 January 2006

Abstract

After a review of the first steps in marine palynology, we show that the understanding of the northwest African setting is crucial to evaluate the potential of marine palynological studies elsewhere. We studied distribution patterns of pollen grains in recent marine sediments off NW Africa and were able to clearly relate patterns to modern pollen source areas (vegetation belts) and operating transport systems (wind belts and ocean currents). In particular patterns of *Quercus*, *Artemisia*, Chenopodiaceae–Amaranthaceae, *Ephedra*, Gramineae, and wet forest trees are very indicative of the position of the vegetation belts on the adjacent continent. Aeolian pollen transport is carried out by the northeast trade winds and the African Easterly Jet (AEJ). In the rain forest belt transport of pollen and fern spores also occurs by rivers. A detailed comparison between recent pollen rain samples from terrestrial and marine sites between 21 and 12°N showed that the latitudinal range of vegetation belts is clearly reflected in the pollen samples of both environments. A migration of the southern border of the Sahara is reflected by the changing ratio between Chenopodiaceae–Amaranthaceae pollen from the desert and Gramineae pollen from the savannah belt.

Distribution patterns of pollen for 9000 and 18,000 ¹⁴C yr BP (last glacial maximum) time-slices, based on pollen records from eleven marine cores between Portugal and the Gulf of Guinea show significant latitudinal migrations of vegetation belts, but a stable position of the main wind trajectories. The AEJ had a stable position around 21°N. The belt with trade winds had a stable position from Morocco southwards. Changing vigour of the trade winds is clearly reflected by the patterns of isopollen contours and by changes in pollen influx records.

© 2005 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

1.1. Early studies of pollen in marine sediments

Marine palynology developed in the oil industry where it became a successful biostratigraphic tool (e.g. Kuyl et al.,

1955; Muller 1959; Germeraad et al., 1968). With the initiation of the Deep Sea Drilling Project (DSDP) in the 1960s the potential of palynological analysis was explored in Quaternary sediments. Early cruises were held in the western Atlantic Ocean off USA. The pollen content in these marine sediments was poor and first papers in DSDP volumes reported marine palynology was disappointing (Groot and Groot, 1966; Groot, 1971). This might have explained why marine palynologists were seldom involved in cruises. Further exploration of pollen in marine sediments as a proxy to reconstruct past environments of adjacent continents was hardly explored any more in following DSDP cruises. Only a few colleagues continued

Abbreviations: AEJ African Easterly Jet; BP Before Present; DSDP Deep Sea Drilling Project; ITCZ Inter Tropical Convergence Zone; ka 1000 years; LGM Last Glacial Maximum; Ma million years; MIS Marine Isotope Stage; ODP Ocean Drilling Project; SAL Saharan Air Layer; ¹⁴C yr BP uncalibrated radiocarbon years before present.

*Corresponding author. Tel.: +31 20 525 7857; fax: +31 20 525 7832.

E-mail address: hooghiemstra@science.uva.nl (H. Hooghiemstra).

the exploration of pollen in marine sediments, such as Heusser in the eastern Pacific Ocean off California (e.g. Heusser and Balsam, 1977; Heusser and Shackleton, 1979; Heusser, 1983), S. van der Kaars in the area between Indonesia and Australia (e.g. Van der Kaars, 1991; Van der Kaars et al., 2000) and Suc in the Mediterranean Sea (Suc, 1984). These authors obtained significant results, such as a correlation of terrestrial and marine records of palaeoclimate change, and palaeogeographical maps of the last glacial maximum (LGM) coastlines and biome distributions in the area of Australia and Indonesia.

1.2. General context

Pollen grains are transported either by wind, or by water currents to the ocean, and when in the water column they sink to the ocean floor where they become incorporated in surface sediments. In a chosen study area the potential for recognisable pollen source areas, pollen transport systems by wind and water currents, possible perturbations by seasonality in pollen production and/or pollen transport, and mechanisms of how pollen grains sink in the water column and are incorporated in the surface sediments should be evaluated to assess the potential of pollen and spore analysis in marine sediments.

In general, lake sediments show pollen concentration values of 10,000 to 1,000,000 grains cm^{-3} . Pollen concentrations in marine sediments may vary between 10 and 5000 grains cm^{-3} . Preparation of large sample volumes may compensate for low pollen concentrations in sediments. Sample volumes from lacustrine sediments often vary between 0.5 and 1 cm^3 while sample volumes from marine cores often are 5 cm^3 , occasionally reaching up to 20 cm^3 . There is little evidence to compare the effect of bioturbation in superficial sediments on ocean floors and on the bottom of lakes. In general, samples for pollen analysis are collected at maximum 1 cm distance along lacustrine cores; only when thinner laminations are present, samples may be closer spaced. In marine cores, samples are often spaced not closer than 10 cm along the core.

Available methods for pollen preparation of marine sediment samples were already available in the early 1950s (e.g. Muller, 1959) and did not differ significantly from the methods used more recently (e.g. Faegri and Iversen, 1964; Kummel and Raup, 1965; Tschudy and Scott, 1969; Moore et al., 1991; Bennett and Willis, 2001). Different traditions can be observed in the chemicals used: concentrated HF is often used to prepare pollen samples from marine sediments in order to eliminate silicates, while the acetolysis mixture (HNO_3 and H_2SO_4) is often used for preparation of samples from lake sediments and peat to eliminate cellulose. This difference in methodology is not obligatory: good experience has been obtained by applying the acetolysis method of Faegri and Iversen (1964) in combination with a heavy liquid separation (to eliminate silicates) on marine sediments.

Coming back to the area where first DSDP efforts were made in the early 1960s, it is obvious that available sample preparation techniques cannot explain the poor results. In eastern North America vegetation belts (pollen source areas) are oriented north–south. As a consequence, offshore sediments in the western Atlantic Ocean potentially receive pollen from few biomes. This setting offers few possibilities to link pollen assemblages to well-defined source areas. Considering potential transport systems in this area we observe that pollen transport by water currents (rivers) leads at the best to a number of point sources that show pollen spectra in which the biomes crossed along the path of the river are mixed (Leroy, 1992). Potential aeolian pollen transport neither offers a promising setting as surface winds hardly form a connection between inland biomes and pollen trapping sediments offshore. Therefore, the location of pollen producing biomes, the available systems to transport pollen, and marine sediments potentially able to receive pollen do not match well. With today's knowledge is it comprehensible why marine palynology undertaken in the western North Atlantic Ocean led to disappointing results. On the contrary, in the northwest African area and adjacent Eastern Atlantic Ocean this configuration offers a very favourable setting. Palynological textbooks adopted premature conclusions such as “marine deposits are, on the whole, rather disappointing from the point of view of pollen analysis” (Faegri and Iversen, 1964) and further research was not stimulated.

1.3. Aims of this paper

In this paper, we discuss the mechanisms operating in the northwest African area relevant to the interpretation of distribution patterns of pollen and spores in marine surface sediments. Also reconstructed distribution patterns for 9000 ^{14}C yr BP and 18,000 ^{14}C yr BP (LGM) are shown and discussed. Selected aspects were earlier published in a variety of journals. In this paper, we have collated figures that illustrate operating mechanisms and clarify how to interpret the pollen signal in marine sediments in terms of environmental and climate change. We conclude this paper with a set of observations and recommendations that might form a basis to evaluate the potential of marine palynological studies elsewhere.

2. Modern vegetation distribution, wind systems, and ocean currents

In northwest Africa the main vegetation belts are oriented east–west and have a strong link to north–south gradients in precipitation (Fig. 1). From north to south the main vegetation belts are: the Mediterranean *Quercus*-dominated forest, the *Artemisia*-dominated steppe belt, the desert vegetation of the Sahara in which *Chenopodiaceae*–*Amaranthaceae* are important, the Gramineae-dominated Sahelian vegetation belt (savannah), the Sudanian vegetation belt, the Guinean vegetation belt, and the belt of

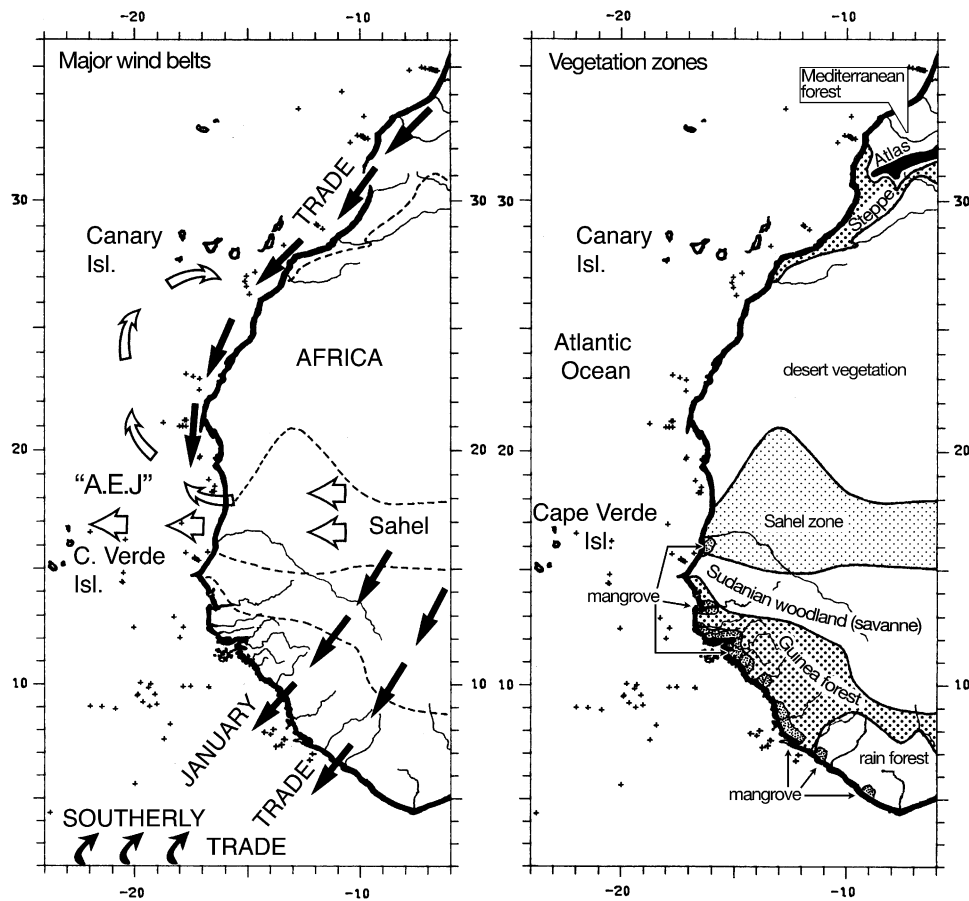


Fig. 1. Left: major wind belts: solid arrows indicate surface winds between 0 and 1000 m (NE trades, January trades, southerly trades (= northeast monsoon); open arrows indicate zonal winds at ca. 3000 m altitude (African Easterly Jet); dotted lines indicate boundaries of vegetation belts; crosses indicate sample stations of modern pollen rain. Right: modern vegetation zones of NW Africa; from north to south: Mediterranean vegetation (*Quercus* dominated); steppe vegetation (*Artemisia* dominated); desert vegetation (*Chenopodiaceae*–*Amaranthaceae* dominated); Sahelian vegetation (grass dominated); Sudanian woodland and savannah; Guinean forest; rain forest. Small dotted areas along the coast indicate mangrove vegetation (modified after Hooghiemstra et al., 1986).

tropical rainforest adjacent to the Gulf of Guinea (White, 1983). All these vegetation belts have a distinct floral composition and can be recognised by their characteristic pollen assemblages (Gajewski et al., 2002). As modern vegetation belts in northwest Africa are limited to some degrees of latitude (Fig. 1), the source area of pollen grains in the sediments found offshore can be identified with significant precision. It is evident that pollen grains identified at the generic level provide a more accurate source area than pollen grains identified at the family level only. Along the coast where rivers pour fresh water in the Atlantic Ocean, *Rhizophora* mangrove vegetation occurs (at present-day north to the River Senegal; a much degraded *Avicennia* mangrove is still present in the Banc d'Arguin, 20°N, but now in the absence of a flowing river).

The main wind systems are the northwest trade winds and the southeast monsoon (Fig. 1). Both are surface wind systems mainly blowing between 1000 m and the surface. Both wind systems meet at the meteorological Equator or, the Inter-Tropical Convergence Zone (ITCZ). The ITCZ migrates in an annual cycle between ca. 21°N in July to ca. 4°N in January. As a consequence moisture-laden-

monsoon winds reach far to the north in July bringing rain to sub-Saharan vegetation, and dry trade winds reach far to the south in January causing the dry season in the sub-Saharan area.

A wind system operating at higher elevation (ca. 3000–5000 m) is the African Easterly Jet (AEJ), also named as the Saharan Air layer (SAL). This wind system collects dust and pollen in the present-day southern Sahara and Sahel belts and is transporting all particles westwards. Above the Atlantic Ocean a part of this dust continues its trajectory westwards and finally reaches the Caribbean area; another part of the AEJ turns to the north when the air masses move around the high-pressure belt located above the northern Sahara. This wind vector transports dust and pollen in the direction of the Canary Islands and operates mainly from June to September.

3. Pollen transport

During the 1990s, numerous studies came out elucidating much of the horizontal transport of dust and pollen to the ocean and the vertical transport of particles through the

water column. Satellite imagery dramatically showed the large amounts of dust blown from the continent over the North Atlantic Ocean (Swap et al., 1996; Prospero et al., 2002). Using modelled wind trajectories, sources of dust and pollen could be better related to the distribution patterns of pollen in the marine sediments of the eastern North Atlantic Ocean (Chiapello et al., 1997; Wyputta and Grieger, 1999). Major dust sources were identified in the Sahel, the southern and central Sahara, and the northern and western Sahara.

Snapshots of the pollen content in the air over the ocean have been provided by filter studies (Melia, 1984; Calleja et al., 1993). The major part of the pollen load in the surface atmosphere along the West African coast is freshly emitted although remobilisation of settled pollen with dust storms also may occur (Calleja et al., 1993). A sediment trap study off Cap Blanc by Romero et al. (2003) records the continental input of both the trade wind system and the AEJ, which show large interannual variability in the flux of pollen, fresh water diatoms, and phytoliths.

Although pollen grains have little weight, they gradually sink through the atmosphere to the sea surface, or are washed out of the atmosphere by rains and enter the water column of the Atlantic Ocean. Marine organisms living in the surface waters (filter feeders) consume sinking debris (including pollen grains) and produce faecal pellets which have a greater sinking velocity in the water column. Particle aggregation due to turbulence in the water column may also participate to a better sedimentation of pollen grains (Jones et al., 1998). Sediment traps at different water depths indicate rapid sinking velocities of faecal pellets and other aggregates enabling organic and lithogenic particles to reach the seafloor within 10 days to 1 month (Neuer et al., 1997; Ratmeyer et al., 1999a). However, differences in vertical particle transport between three different locations in the eastern North Atlantic Ocean have been recorded. In the area off Cape Blanc, sinking velocities are highest and the composition of the flux of particles show no alterations between upper and lower sediment traps. North of the

Canary Islands, advected material from the coastal region enriches the lower water masses with organic material and also the vertical sediment transport in the region of the Cape Verde Island is more complicated by the horizontal transport of particles in the deep ocean (Neuer et al., 1997; Ratmeyer et al., 1999a, b). In our study area offshore of northwest Africa, during vertical sinking the aggregates with pollen grains will be transported southward by the Canary Current, northward by the Counter Current, and finally southward again by the Bottom Current. Most essential is that the location where a pollen grain enters the water column is close to the location on the ocean floor where the same pollen grain is incorporated in the surface sediments (Fig. 2). In other words, the distribution pattern of pollen grains in the air above the sea surface is reflected in the sediments on the ocean floor to a high degree (Hooghiemstra, 1996). In particular the study by Melia (1984) supported this mechanism: during his cruise he collected pollen samples from the air as well as from the ocean floor sediments. Distribution patterns and/or positions of maximum concentrations were very similar (Fig. 3; Hooghiemstra, 1996). Even seasonality was reflected in his data: at 21°N Melia did not observe a high supply of desert pollen to the Atlantic Ocean: indeed his cruise was held in February when the AEJ is not operating.

4. Modern distribution patterns and modern pollen source areas

In the following section, we show for a number of taxa the present-day vegetation distribution in northwest Africa and on the Iberian Peninsula, and the distribution pattern of its pollen in the marine surface sediments. The latter pattern is based on pollen analysis of 110 surface sediment samples between 33 and 3°N. The abundance in each sample is expressed as a percentage of the total pollen spectrum and patterns are obtained by connecting points with a similar percentage (isopollen contours) (Hooghiemstra and Agwu, 1986; Hooghiemstra et al., 1986; Dupont

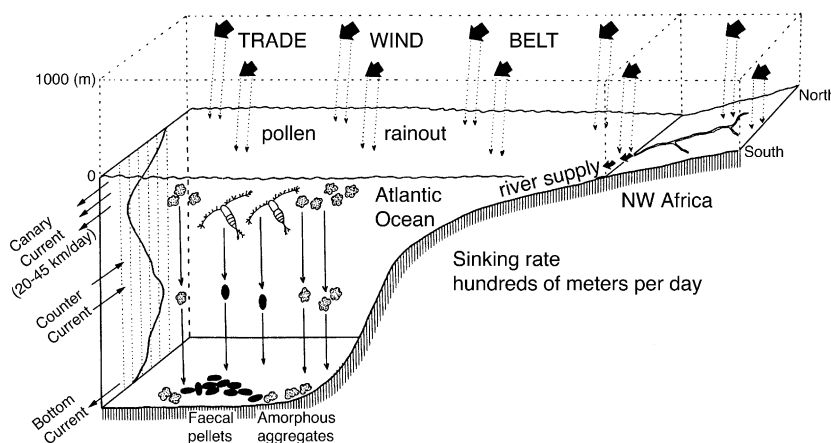


Fig. 2. Model of pollen transport from the northwest African continent to offshore marine sediments. Explanation in the text (after Hooghiemstra, 1996).

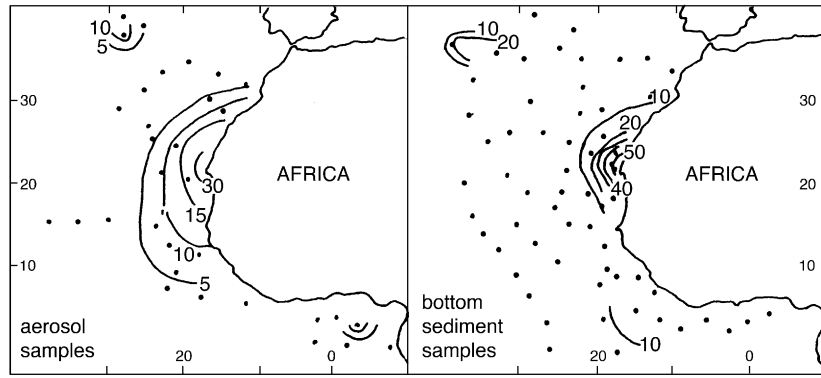


Fig. 3. Distribution of Chenopodiaceae–Amaranthaceae pollen (isopercentage contours are shown) in aerosol samples and bottom sediment samples off the coast of NW Africa (redrawn after Melia (1984); From Hooghiemstra 1996).

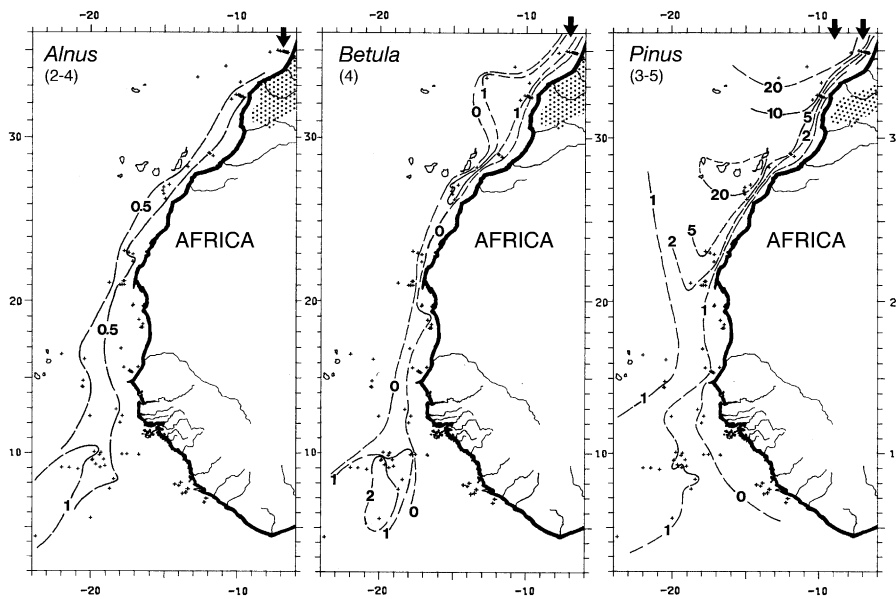


Fig. 4. Distribution maps of pollen in recent surface sediments in the Atlantic off NW Africa of *Alnus*, *Betula* and *Pinus*. Representation is expressed as a percentage of all pollen (isopollen lines). General legend for Figs. 4–8: bold dots = main pollen source area; thin dots = area of secondary importance; arrows = pollen supply from areas outside the map; crosses = marine sample stations; numbers in brackets = months of main pollen production and transport (1–12 stands for January to December) (modified after Hooghiemstra et al., 1986).

and Agwu, 1991). Fig. 4 shows distribution patterns for *Alnus*, *Betula* and *Pinus*, all from trees with a source area in the Mediterranean region. Maximum representation of pollen in marine surface sediments clearly echoes the source area: the operating trade winds form the connection between both patterns. *Pinus* shows high percentages decreasing with distance; the pine forest on the Canary Islands are re-loading the air masses with pollen and isopollen contours show higher values immediately south of the Canary Islands. Further south decreasing percentages show that the air gradually is also cleaned from *Pinus* pollen. Other studies report a very long residence time of *Pinus* pollen in the air (e.g. Traverse and Ginsburg, 1966), but our results show a distribution pattern undoubtedly related to source area, transporting wind system, and

distance. Fig. 5 shows the distribution patterns for *Quercus*, *Olea* and *Artemisia*. *Quercus* and *Olea* are elements from the Mediterranean vegetation belt and show a direct relationship between source area and transport by the trade winds. *Artemisia* is the dominating element in the zone with steppe vegetation and isopollen contours evidently show how trade winds transport pollen out of the source area. Fig. 6 shows the distribution patterns for *Calligonum*, *Ephedra* and Gramineae. *Calligonum* and *Ephedra* reflect desert vegetation and isopollen contours are unmistakably related to the source area. Gramineae show highest percentages in marine sediments offshore the belt with grass-dominated herbaceous vegetation (Sahel zone) and isopollen contours are characteristic of the latitudinal position of this vegetation belt. Fig. 7 shows the

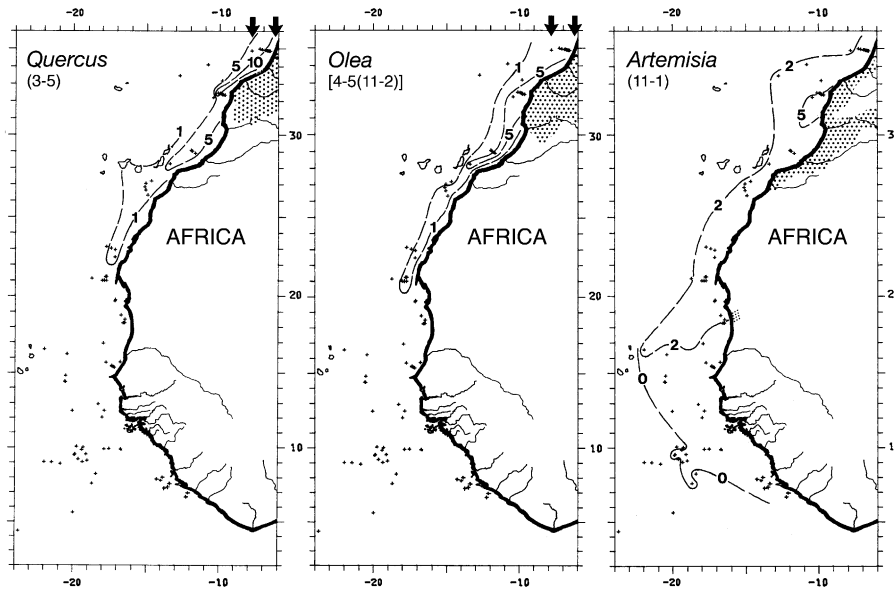


Fig. 5. Distribution maps of pollen in recent surface sediments in the Atlantic off NW Africa of *Quercus*, *Olea* and *Artemisia*. Representation is expressed as a percentage of all pollen (isopollen lines). For legend see caption of Fig. 4 (modified after Hooghiemstra et al., 1986).

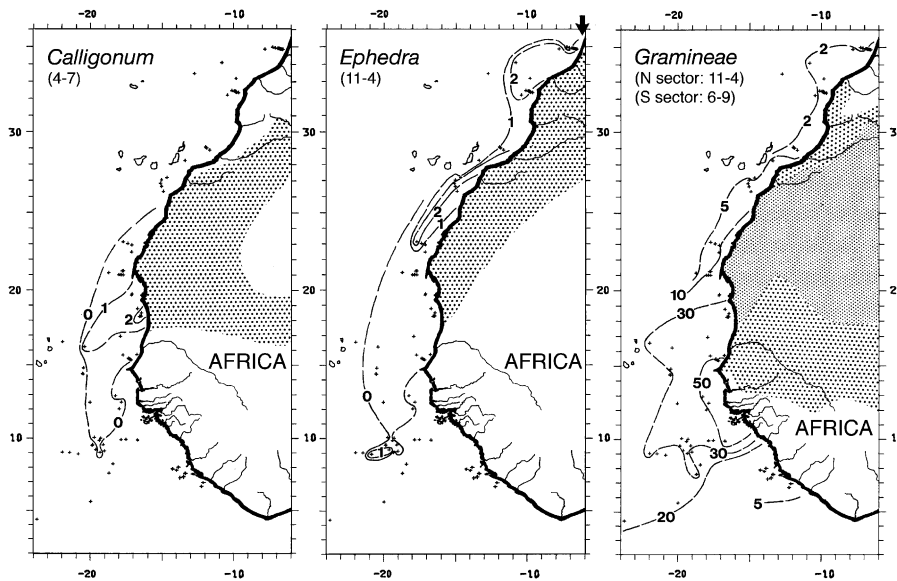


Fig. 6. Distribution maps of pollen in recent surface sediments in the Atlantic off NW Africa of *Calligonum*, *Ephedra* and Gramineae. Representation is expressed as a percentage of all pollen (isopollen lines). For legend see caption of Fig. 4 (modified after Hooghiemstra et al., 1986).

distribution patterns for Chenopodiaceae–Amaranthaceae, *Combretum* and *Mitracarpus*. Chenopodiaceae–Amaranthaceae in the northern coastal area produce pollen between November and April and trade winds clearly transport pollen southwards. Chenopodiaceae–Amaranthaceae in the Sahara flower between July and September when the AEJ prevails. In the south, around 8°N, isopollen contours show a rapid decrease of percentages and here the average position of the ITCZ-related rain belt is reflected: all pollen grains are washed out of the air (also shown by *Pinus*). *Combretum* and *Mitracarpus* have their source areas from the Sahel–Sudanian zones southwards

and flower between November and May. Isopollen contours visibly reflect boreal winter pollen transport when trade winds blow across the Sahara far to the south (January position of the ITCZ) and even occasionally bringing dust into the Gulf of Guinea by the January Trades. Fig. 8 shows the distribution patterns for *Alchornea*, *Elaeis* and fern spores. Distribution patterns of *Alchornea* and *Elaeis* unmistakably reflect the position of the wet forest belt; its northern limit in particular is very sharply demarcated. The distribution pattern of fern spores also closely reflects the location of wet forest. Ferns are abundant as epiphytes in gallery forest along rivers and

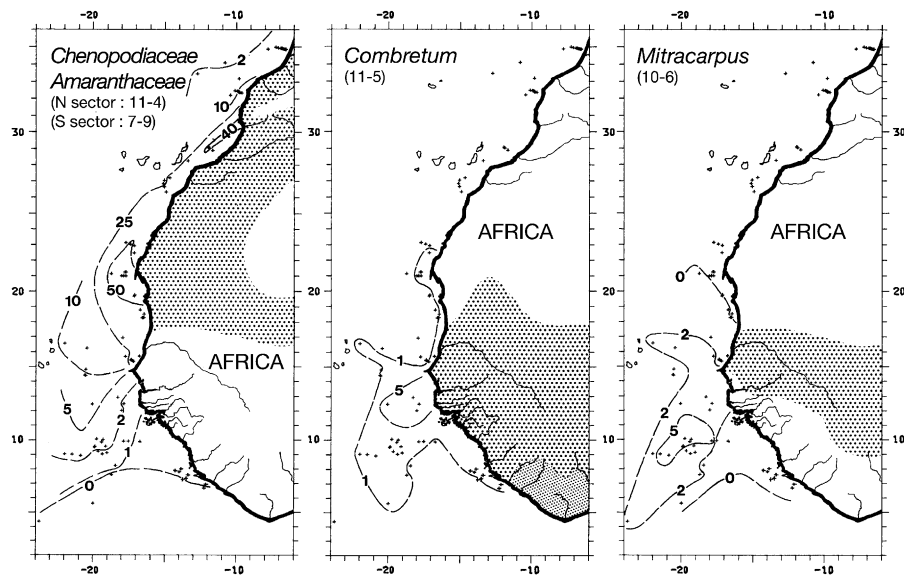


Fig. 7. Distribution maps of pollen in recent surface sediments in the Atlantic off NW Africa of *Chenopodiaceae–Amaranthaceae*, *Combretum* and *Mitracarpus*. Representation is expressed as a percentage of all pollen (isopollen lines). For legend see caption of Fig. 4 (modified after Hooghiemstra et al., 1986).

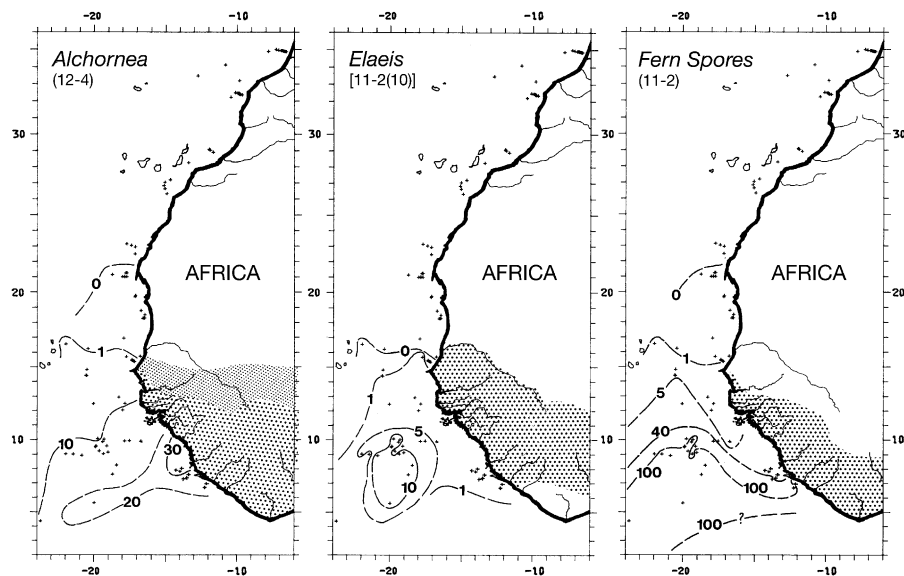


Fig. 8. Distribution maps of pollen in recent surface sediments in the Atlantic off NW Africa of *Alchornea*, *Elaeis* and fern spores. Representation is expressed as a percentage of all pollen (isopollen lines). For legend see caption of Fig. 4 (modified after Hooghiemstra et al., 1986).

often are able to shed their spores directly into the water. Distribution patterns of different spore types (Hooghiemstra et al., 1986), and also of the pattern of total spores (shown in this paper) do not depict the average position of the ITCZ and strongly suggest fern spores are mainly transported by water currents.

5. Comparison of modern distribution patterns in terrestrial and marine sediments

In the previous section we have clarified the relationship between a modern pollen source area (vegetation belt), the

main season of pollen production (flowering period), the setting of transport mechanisms at that time of the year (seasonality in climate), and the distribution of pollen in marine surface sediments. For selected taxa the close relationship between source area, transporting wind system, and resulting distribution pattern in marine sediments is shown (Hooghiemstra et al., 1986; Dupont and Agwu, 1991).

In this section we make a comparison between two data sets of recent pollen rain samples: one from the continent and another from the eastern Atlantic Ocean. We will verify to which degree successive vegetation belts on the

continent are reflected by their pollen in the marine sediments (Lézine and Hooghiemstra, 1990).

In the following section we will reverse the relationship demonstrated in the previous section: when the pollen distribution in marine sediments for a selected time-slice is reconstructed, the geographical position of the concerning vegetation belt can be deduced, provided the transporting system operating during that time-slice is also known.

Recent pollen rain data from surface soil sediments in coastal northwest Africa between 12 and 21°N, and recent pollen rain data from surface sediments collected from the ocean floor between similar latitudes (Fig. 9) allowed comparison of pollen distribution patterns on land and in the surface marine sediments. Fig. 10 shows the modern pollen representation in terrestrial soil surface samples of six different vegetation belts along a north–south transect from 21 to 12°N. Maximum values are found at latitudes where the concerned vegetation is dominant. There are sharp transitions between the ecological groups that indicate that mostly locally produced pollen is not transported over large distances. A similar data set from marine surface sediments is presented (Fig. 11). The modern pollen representation of the same vegetation belts is also found at latitudes where the concerned vegetation occurs. As expected, transitions are less sharp as pollen

transport to the marine sediments dilutes the clear patterns seen in Fig. 10. Fig. 12 shows the representation of individual taxa in the marine surface sediments between 21 and 12°N. Most salient is the transition from Chenopodiaceae–Amaranthaceae-dominated pollen spectra at latitudes north of 19°N to Gramineae-dominated pollen spectra at latitudes south of 19°N. On the continent the transition from Chenopodiaceae–Amaranthaceae-dominated desert vegetation to grass-dominated Sahel vegetation is also at ca. 19°N. Thus, the southern border of the Sahara can be identified from the ratio between Chenopodiaceae–Amaranthaceae pollen versus Gramineae pollen. This is an important observation and provides an elegant mechanism to document migrations of the southern border of the Sahara.

Migrations were reconstructed from core ODP Site 658 spanning the last 0.7 Ma and located at the latitude where today the Saharan vegetation belt is transitional to the Sahelian vegetation belt (Fig. 13; Dupont and Hooghiemstra, 1989). The same principles were applied to the interpretation of the part of the core spanning 3.7 to 1.7 Ma (Leroy and Dupont, 1994). Modern pollen transported to this location is mainly supplied by the AEJ and collected in the modern southern Sahara and northern Sahel. When the Sahara expands very far to the south (e.g. during the LGM), the AEJ is mainly collecting

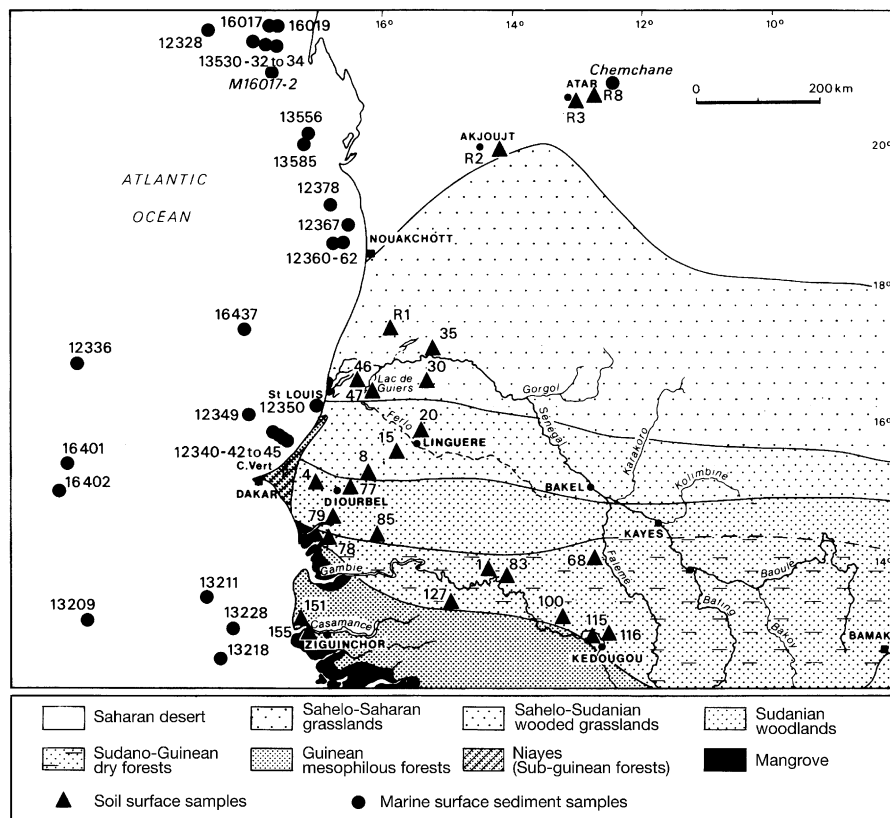


Fig. 9. Vegetation belts in NW Africa and locations of recent pollen rain samples on the continent and in the offshore Atlantic Ocean (modified after Lézine and Hooghiemstra, 1990).

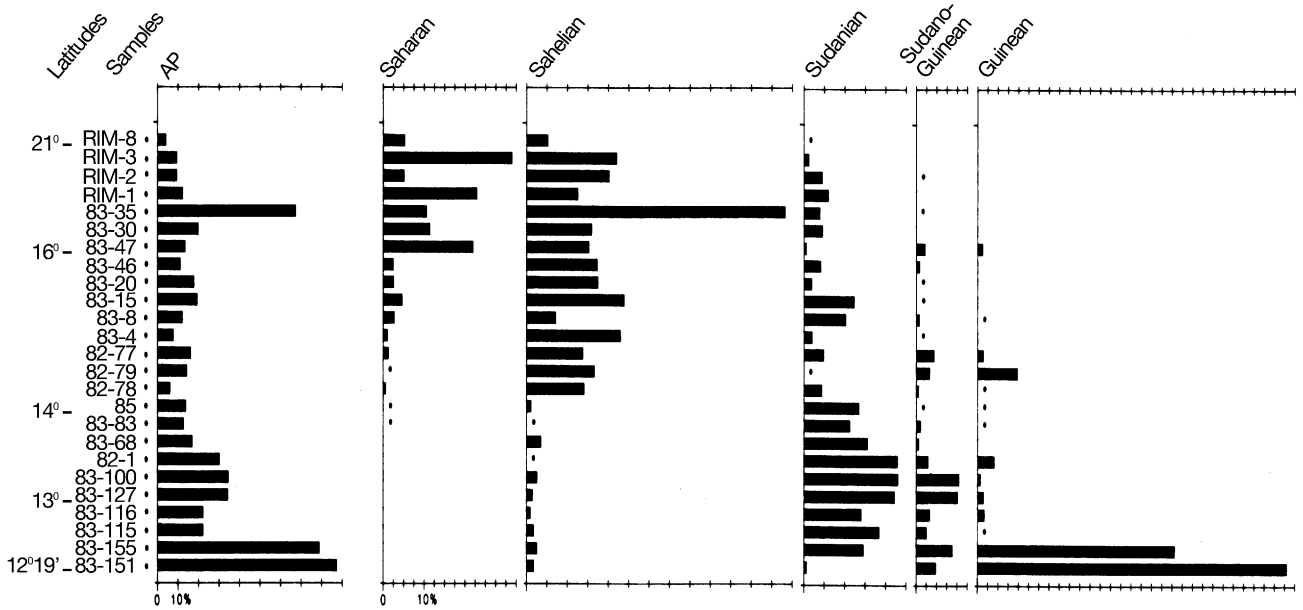


Fig. 10. Distribution of modern pollen rain in NW Africa from surface soil samples along a transect from 12 to 21°N. Taxa are categorised in five different vegetation belts, and total Arboreal Pollen (modified after Lézine and Hooghiemstra, 1990).

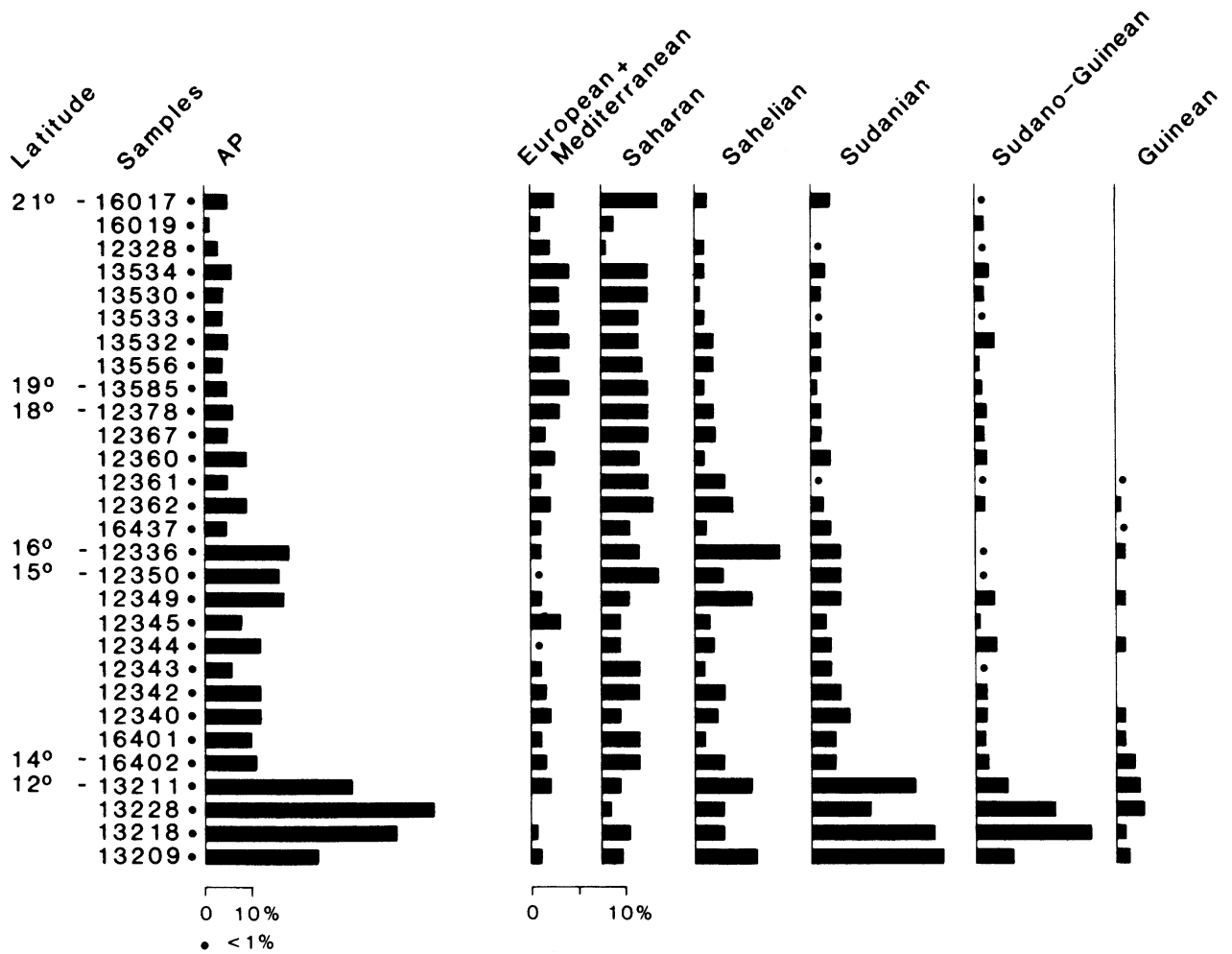


Fig. 11. Distribution of modern pollen rain in NW Africa from surface sediment samples from the ocean floor along a transect from 12 to 21°N. Taxa are categorised in six different vegetation belts, and total Arboreal Pollen (modified after Lézine and Hooghiemstra, 1990).

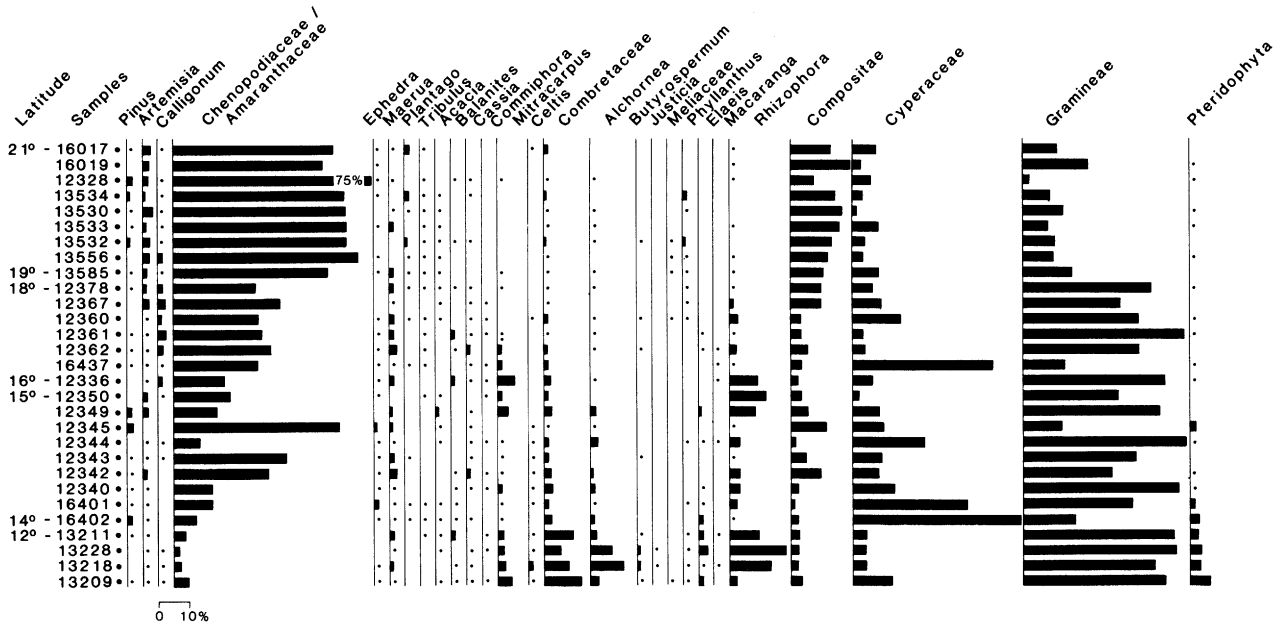


Fig. 12. Distribution of modern pollen rain in NW Africa from surface sediment samples from the ocean floor along a transect from 12 to 21°N. Representation is shown per taxon. Note the high representation of Gramineae in the south and Chenopodiaceae–Amaranthaceae in the north (modified after Lézine and Hooghiemstra, 1990).

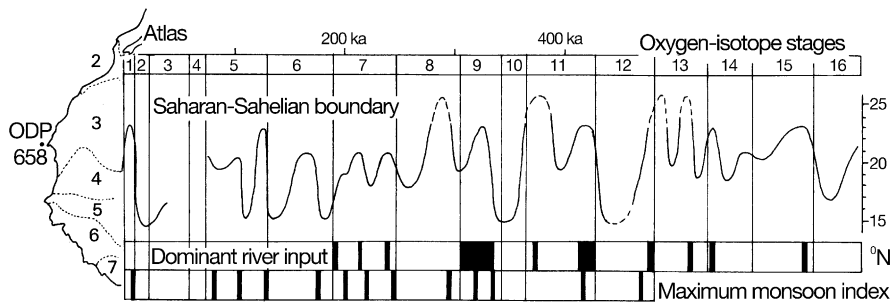


Fig. 13. Estimated latitudinal migrations of the Saharan–Sahelian boundary based on pollen data (ratio Chenopodiaceae–Amaranthaceae vs. Gramineae; see text) of ODP Site 658. Migrations are shown on a linear time scale along the marine isotope stratigraphy (MIS). Estimated period of fluvial discharge from the central Sahara is recorded by high clay content in ODP Site 658 and periods with a high-monsoon index, giving rise to Mediterranean sapropels, are indicated. Modern vegetation distribution is shown at the left: 2 = steppe zone; 3 = Sahara; 4 = Sahel; 5 = Sudanian woodlands; 6 = Guinean forest; 7 = rain forest (modified after Dupont and Hooghiemstra, 1989).

Chenopodiaceae–Amaranthaceae pollen. In case the Sahara is very restricted to the north, the latitudes where the AEJ is collecting its dust and pollen load is mainly covered by grassy vegetation. This was the case during the early Holocene ca. 9000 ¹⁴Cyr BP, the period of the ‘Green Sahara’, when moisture bringing monsoon winds penetrated Africa very far northwards, i.e. a northward migration of the ITCZ). We reconstructed migrations over 9° of latitude during the last 0.7Ma showing that the Sahara is a very dynamic desert at its southern border. In this reconstruction we have assumed that the AEJ has a stable position and does not migrate latitudinally. Some evidence of this is given in the next section.

6. Distribution patterns of past time-slices document stable positions of wind belts

In this section, we address the question how distribution patterns have changed in the past. From 11 well-dated marine cores located on a transect between Portugal (37°N) and the Gulf of Guinea (5°N), pollen spectra from selected time-slices of the past have been collected (Hooghiemstra et al., 1987; Hooghiemstra, 1988b). We show the patterns of pollen distribution for 18,000 ¹⁴Cyr BP (LGM), and for 9000 ¹⁴Cyr BP (one of the wettest episodes in Saharan Africa during the last glacial–interglacial cycle). For comparison we repeat the distribution pattern for the

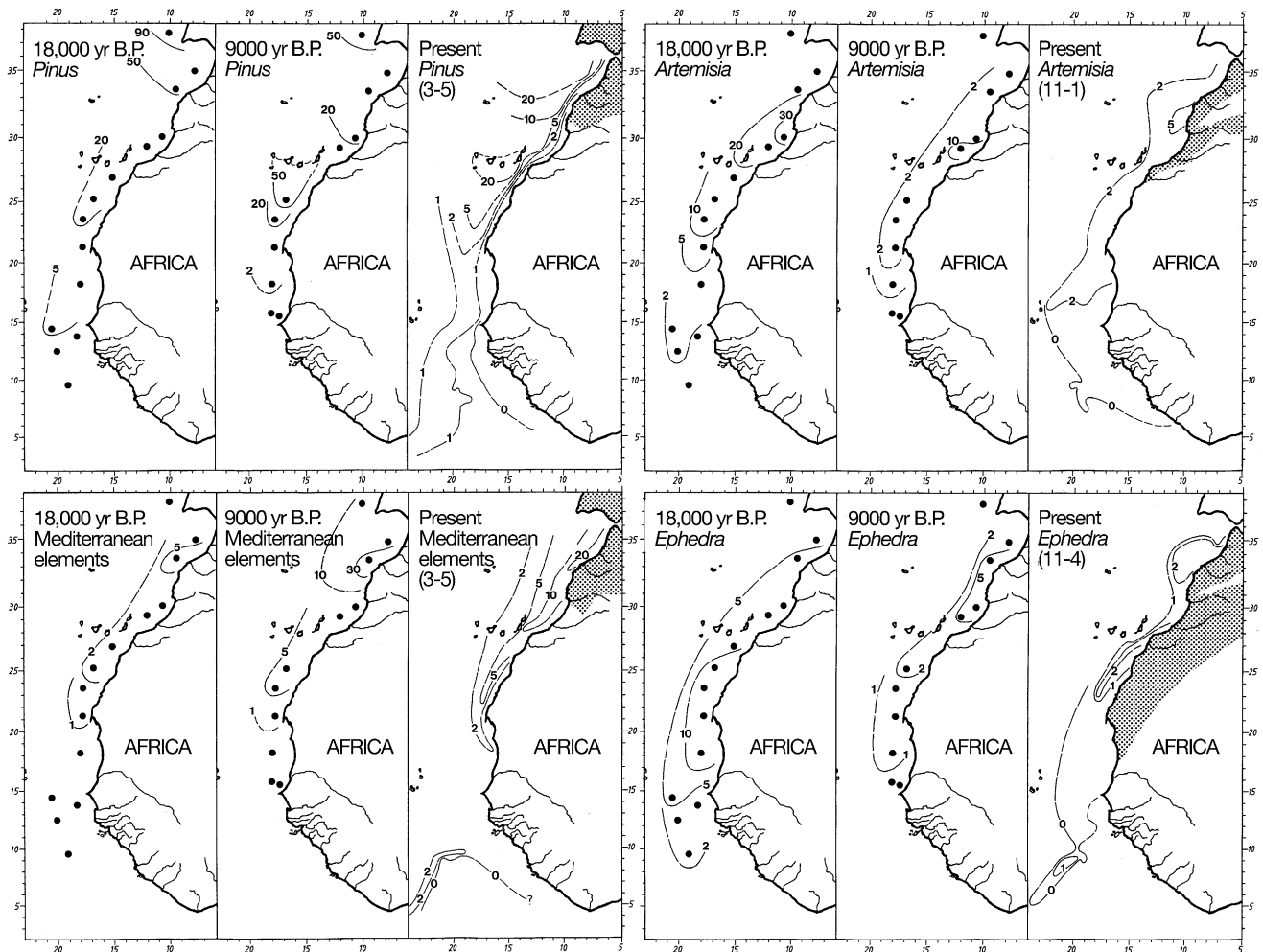


Fig. 14. Distribution maps for 18,000 ^{14}C yr BP, 9000 ^{14}C yr BP and present-day for *Pinus*, Mediterranean elements, *Artemisia* and *Ephedra*. Representation is expressed as a percentage of all pollen (isopollen contours). Months of the flowering season (pollen production) is indicated in the 'present' map (1–12 stands for January–December) (modified after Hooghiemstra, 1988b).

recent time. Fig. 14 shows the 18–9–0 ka BP triplets for *Pinus*, Mediterranean elements, *Artemisia* and *Ephedra*. During the LGM, a *Pinus*-wooded steppe on the Iberian Peninsula produced large amounts of pollen (up to 90% of the pollen spectrum). Isopollen contours with lower values lie far to the south pointing to vigorous trade wind transport. The 9 ka and recent patterns show less efficient pollen transport to the south suggesting the trade winds were less vigorous. The effect of the *Pinus* forests on the Canary Islands is clear: air masses passing over these islands are re-loaded with *Pinus* pollen reflected by isopollen contours with higher percentages immediately south of the Canary Islands.

The maps for Mediterranean elements show isopollen contours that reflect trade wind transport. The Mediterranean vegetation was almost absent during the LGM; this is clearly reflected by the low values (5% isopollen contour) compared to the values reflecting present-day conditions (20% isopollen contour). High values of *Artemisia* during the LGM (up to 30%) show the steppe belt was wider during that time. Isopollen contours with low values have a

very southern position, suggesting *Artemisia* pollen was transported by trade winds much more vigorous than today. Steppe vegetation diminished rapidly in the early Holocene and present-day values (up to 5%) reflect *Artemisia* vegetation in the coastal area of Morocco as well as in the narrow steppe belt at the northern border of the Sahara. *Ephedra* is characteristic of dry (saline) soils and present-day vegetation is represented with isopollen contours up to 2%. During the LGM isopollen contours reached up to 10% between 17 and 26°N and reflect abundant desert vegetation in a large part of NW Africa.

Fig. 15 shows the triplets for Chenopodiaceae–Amaranthaceae, Gramineae, elements of the tropical wet forest, and the 'trade wind indicators'. Most important in the distribution maps of the Chenopodiaceae–Amaranthaceae is the stable position of the maximum isopollen contour (40–50% values) around 21°N showing that the AEJ wind belt had a stable position over the last glacial to interglacial transition. This is the best evidence to illustrate the validity of the mechanism we used in the previous section to reconstruct the latitudinal migration of the southern

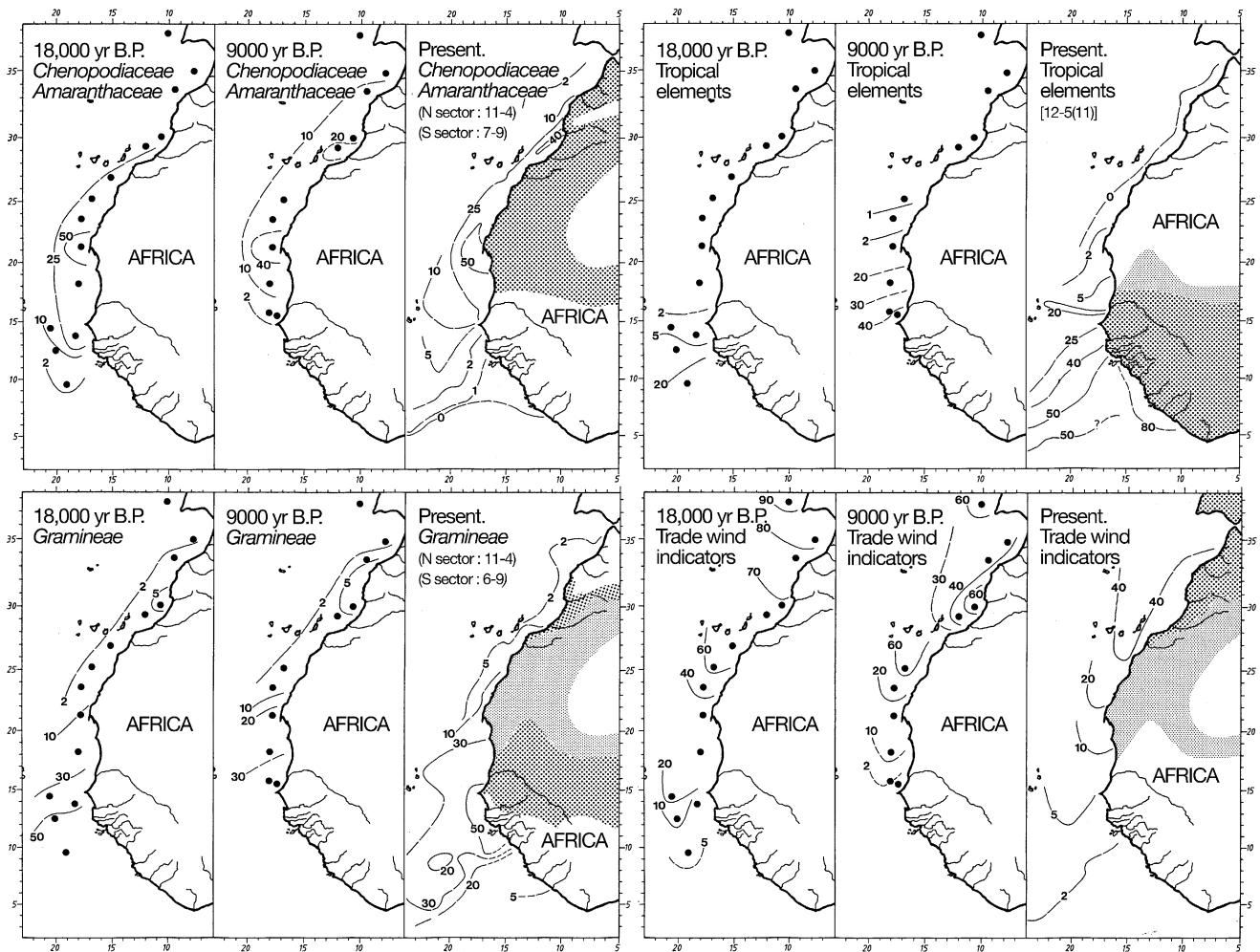


Fig. 15. Distribution maps for 18,000 ^{14}C yr BP, 9000 ^{14}C yr BP and present-day for Chenopodiaceae–Amaranthaceae, Gramineae, elements of the tropical wet forest, and the ‘trade wind indicators’ (*Alnus*, *Betula*, *Pinus*). Representation is expressed as a percentage of all pollen (isopollen contours). Months of the flowering season (pollen production) is indicated in the ‘present’ map (1–12 stands for January–December) (modified after Hooghiemstra, 1988b).

border of the Sahara. Isopollen contours reach similar values (25%) during the LGM and present-day when desert vegetation was widespread. The period of the ‘Green Sahara’ ca. 9000 ^{14}C yr BP is well reflected in the offshore sediments by low pollen percentages (10% isopollen contour). Thus, the distribution pattern of Chenopodiaceae–Amaranthaceae is very informative: in the northern sector trade wind transport is reflected, around 21°N AEJ transport is reflected, and the rapid decrease of pollen south of 10°N locates the average position of the ITCZ, an area where rains frequently wash pollen out of the atmosphere.

Maps of the Gramineae are not very conclusive about possible migrations or expansion of the belt with grass-dominated herbaceous vegetation. Values of isopollen contours show little variation through time. The low number of available deep-sea cores is probably responsible. The triplet of tropical elements shows a more northern position of the 20% and 40% isopollen contours at 9000 ^{14}C yr BP and a more southern position of the 20%

isopollen contour at the LGM. This is indicative of a narrower desert belt 9000 ^{14}C yr BP and a more expanded Sahara at the LGM: this is supported by much terrestrial evidence (e.g. Hooghiemstra et al., 1992 and references therein).

The group of ‘trade wind indicators’ (Fig. 15) consist of taxa whose distribution was always limited to the area north of the Sahara (*Alnus*, *Betula*, *Pinus*). The maps show by isopollen contours how far this pollen was transported southward by the trade winds. We observe, during the LGM, high pollen production on the Iberian Peninsula (isopollen contours up to 90% offshore) and efficient transport of that pollen to the south (compare the latitudes of the 20% isopollen contour at the LGM and at present-day). This triplet of maps clearly shows that trade winds blew with much more vigour southwards during the LGM. It also shows that trade winds originated in northernmost Africa: this is in contrast with the reconstructions of Nicholson and Flohn (1980) who claimed that the trade wind belt had migrated southward in response to the

southward migration of the belt with westerlies, at present-day blowing at central European latitudes. The LGM distribution pattern of *Pinus* clearly shows that northernmost Africa cannot be located in the belt of westerlies as all isopollen contours show directions in accordance with the present-day flow pattern of the trade winds.

A further analysis was made of changes in intensity of the trade winds during the last 140,000 years (Hooghiemstra, 1989). For each core the pollen influx record of several taxa (a.o. *Pinus*, *Artemisia* and trade ‘wind indicators’) was calculated and plotted along the transect from Portugal to the Gulf of Guinea. It was obvious that trade wind intensity changed significantly: periods of high intensity occurred during the relatively cold periods of Marine Isotope Stage 6 (MIS 6), and further during MIS 5d, MIS 5b, MIS 4, and during the period from 40,000 to 10,000 ¹⁴Cyr BP in particular. Pollen-based changes in trade wind intensity were supported by evidence from sediment fractions (see Hooghiemstra (1989) and references therein).

From the triplets of distribution maps it was concluded that the geographical position of the trade wind belt was stable in time, but the position of isopollen contours and pollen influx records show that the intensity fluctuated. Since the LGM the trajectory of the AEJ has had a stable position around 21°N (based on the stable position of maximum values of isopollen contours). With respect to migrations of vegetation belts the triplets of distribution patterns indicated for the LGM: an abundant presence of *Pinus* in the steppes on the Iberian Peninsula, an almost absence of Mediterranean vegetation, a wide *Artemisia*-dominated steppe belt at the northern border of the Sahara, a maximum north–south extension of the desert (*Ephedra*-based), and a more southern position of the savannah belt and the belt with wet tropical forest.

7. Changing distribution patterns cause downcore changes in marine pollen records

In the previous sections we learned how pollen is transported from the source area to the marine sediments in the different climatological and environmental settings at 18,000 ¹⁴Cyr BP (LGM), at 9000 ¹⁴Cyr BP, and at present-day. This understanding forms the basis of the interpretation of downcore changes in the marine pollen records offshore northwest Africa. It is evident that northwest Africa is an almost ideal place on Earth to study such relationships.

Since the LGM northwest Africa experienced significant vegetation change. The main driving force was the changing precipitation patterns, related to migration of the ITCZ. In the area between Australia and Indonesia Van der Kaars (1991) showed that changing sea-level stands were the main trigger for large-scale vegetation change. LGM sea-level stands at ca. 120 m below the present level exposed large areas and caused significant changes in the distribution patterns of the main vegetation types. One of the objectives of this paper was to become

familiar with operating mechanisms in order to better evaluate other potential study areas. We believe that within the development of a research project a fair prediction can be made of the potential of a selected site to give answers to clearly specified research questions.

Interpretation of downcore changes of pollen records from marine cores is out of the scope of this paper. However, there are many studies available that show how our understanding of distribution patterns of pollen in marine sediments is applied to reconstruct changing environments on the African continent. For the area from the Canary Islands northward (ca. 28 to 38°N) we mention the paper by Hooghiemstra et al. (1992). For the area between the Canary Islands and the Gulf of Guinea (ca. 8 to 28°N) we mention the papers by Agwu and Beug (1982), Dupont and Beug (1991), Hooghiemstra (1988a), Leroy and Dupont (1994), Lézine et al. (1995), Lézine and Deneffe (1997) and Marret and Turon (1994).

Studies were extended along the west African coast southward and showed that also in the equatorial belt (ca. 10°N to 10°S) meaningful interpretation of marine pollen records was possible (Caratini et al., 1987; Hooghiemstra and Agwu, 1988; Dupont and Agwu, 1992; Lézine and Vergnaud-Grazzini, 1993; Lézine and Le Thomas, 1995; Jahns, 1996; Dupont and Weinelt, 1996; Dupont et al., 1998, 2000; Jahns et al., 1998; Marret et al., 2001). In this latitudinal interval pollen transport by water currents plays an important role. Studies were extended to the area offshore southern Africa (ca. 10 to 30°S) where aeolian pollen transport is more important again than pollen transport by water currents. The setting of wind belts in southern Africa and offshore the eastern Atlantic Ocean is less pronounced compared to northwest Africa. Moreover, in the south winds more commonly blow landward, instead of transporting dust and pollen from the continent into the Atlantic. Notwithstanding this environmental setting, significant changes in the vegetation of southern Africa were carefully documented (Ning and Dupont, 1987; Shi et al., 1998, 2000, 2001; Dupont and Yputta, 2003).

8. General conclusions

- Analysis of pollen in marine cores offers the possibility to make a direct comparison between changes on the continent and in the ocean.
- In areas where meaningful results might be expected pollen analysis of marine cores should be a standard component of multi-proxy analysis.
- Pollen supply to offshore sediments by rivers leads to coastal point-sources; pollen distribution patterns in marine sediments reflect dilution patterns of point sources rather than reflecting the position of biomes in the hinterland.
- Conclusions that pollen grains of *Pinus* have a very long residence time in the atmosphere as well as in the water column (Traverse and Ginsburg, 1966) and are

an almost omni-present and information lacking taxon, are not substantiated by our study. In the NW African area transport distance of *Pinus* pollen grains is limited, distribution patterns are meaningful and related to wind trajectories and gravitational clearing of the atmosphere, and point sources (pine forests of the Canary Islands) clearly re-load the pollen content of passing air parcels.

- In areas with significant seasonality in the climate system, the month of main flowering should be identified and compared to the average wind directions of the same period, before distribution patterns are interpreted.
- Preferably, a comparison between terrestrial and marine modern pollen rain samples should be made in order to verify to which degree distribution patterns reflect actual vegetation belts.
- In case time control of sediment cores is sufficient, pollen influx records are very helpful to assess changes in vigour of the transporting wind system.
- Northwest Africa offers an almost ideal setting to study relationships: vegetation belts organised along a north–south gradient, wind systems parallel (trade winds) and perpendicular (AEJ) to the vegetation gradient, and a system of ocean currents that assure the point where pollen grains enter the water column is close to the point where the same pollen grain is incorporated in the sediments on the ocean floor.
- It is hypothesized that if the DSDP had started their explorative work offshore northwest Africa, pollen analysis of marine sediments possibly had obtained a more productive position in palaeoceanography.

Acknowledgements

This research was carried out at the University of Göttingen. We thank H.-J. Beug and E. Gröger (Göttingen), M. Sarnthein (Geological Institute, Kiel), G. Tetzlaff (Meteorological Institute, Hanover) for support and productive cooperation. The 'Institut für Palynologie und Quartärwissenschaften' in Göttingen formed the stimulating nucleus of a successful line in palaeoclimatology. Recent participation in an ICSU/IGCP 490 field conference in Mauritania (organised by S. Leroy), and a PAGES Workshop in Kenya (organised by D. Olago), provided the stimulus and energy to write this synthesis. Jan van Arkel (Amsterdam) is thanked for support with the preparation of the figures. This paper is dedicated to professors Hans-Jürgen Beug and Eberhart Gröger, who provided in their laboratory so many opportunities to be trained in marine palynology.

References

Agwu, C.O.C., Beug, H.-J., 1982. Palynological studies of marine sediments off the West African coast. *Meteor. Forschungs. Ergebnisse C* 36, 1–30.

- Bennett, K.D., Willis, K.J., 2001. Pollen. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments, Terrestrial, Algal, and Silicicous Indicators*, vol. 3. Kluwer, Dordrecht, The Netherlands, pp. 5–32.
- Calleja, M., Rossignol-Strick, M., Duzer, D., 1993. Atmospheric pollen content off West Africa. *Review of Palaeobotany and Palynology* 79, 335–368.
- Caratini, C., Tastet, J.-P., Tissot, C., Frédoux, A., 1987. Sédimentation palynologique actuelle sur le plateau continental du Cote d'Ivoire. *Mémoire et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier*, pp. 17–100.
- Chiappello, I., Bergametti, G., Chatenet, B., Bousquet, P., Dulac, F., Santos Soares, E., 1997. Origins of African dust transported over the northeastern tropical Atlantic. *Journal of Geophysical Research* 102 (D12), 13701–13709.
- Dupont, L., Agwu, C.O.C., 1991. Environmental control of pollen grain distribution patterns in the Gulf of Guinea and offshore NW Africa. *Geologische Rundschau* 80, 567–589.
- Dupont, L., Agwu, C.O.C., 1992. Latitudinal shifts of forest and savanna in NW Africa during the Brunhes chron: further marine palynological results from site M 16415 (9°19'W). *Vegetation History and Archaeobotany* 1, 163–175.
- Dupont, L., Beug, H.-J., 1991. Marine palynological studies off NW Africa. *Palaeoecology of Africa* 22, 135–155.
- Dupont, L., Weinelt, M., 1996. Vegetation history of the savanna corridor between the Guinean and the Congolian rain forest during the last 150,000 years. *Vegetation History and Archaeobotany* 5, 273–292.
- Dupont, L., Wyputta, U., 2003. Reconstructing pathways of aeolian pollen transport to the marine sediments along the coastline of SW Africa. *Quaternary Science Reviews* 22, 157–174.
- Dupont, L.M., Hooghiemstra, H., 1989. The Saharan–Sahelian boundary during the Brunhes chron. *Acta Botanica Neerlandica* 38, 405–415.
- Dupont, L.M., Marret, F., Winn, K., 1998. Land-sea correlation by means of terrestrial and marine palynomorphs from the equatorial East Atlantic: phasing of SE trade winds and the oceanic productivity. *Palaeogeography Palaeoclimatology Palaeoecology* 142, 51–84.
- Dupont, L.M., Jahns, S., Marret, F., Shi, N., 2000. Vegetation change in equatorial West Africa: time-slices for the last 150 ka. *Palaeogeography Palaeoclimatology Palaeoecology* 155, 95–122.
- Fægri, K., Iversen, J., 1964. *Textbook of Pollen Analysis*. Munksgaard, Copenhagen 237pp.
- Gajewski, K., Lézine, A.-M., Vincens, A., Delestan, A., Sawada, M., APD Members, 2002. Modern climate-vegetation-pollen relations in Africa and adjacent areas. *Quaternary Science Reviews*, 21, 1611–1631.
- Germeraad, J.H., Hopping, C.A., Muller, J., 1968. Palynology of Tertiary sediments from tropical areas. *Review of Palaeobotany and Palynology* 6, 189–348.
- Groot, J.J., 1971. Distribution of pollen and spores in the oceans. In: Funnell, B.M., Riedel, W.R. (Eds.), 1967. *The micropaleontology of oceans*. In: *Proceedings of the Symposium on Micropalaeontology of Marine Bottom Sediments*, Cambridge, UK, September 1967, pp. 359–360.
- Groot, J.J., Groot, C.R., 1966. Marine palynology: possibilities, limitations, problems. *Marine Geology* 4, 387–395.
- Heusser, L.E., 1983. Contemporary pollen distribution in coastal California and Oregon. *Palynology* 7, 19–42.
- Heusser, L.E., Balsam, W.L., 1977. Pollen distribution in the northeast Pacific Ocean. *Quaternary Research* 7, 45–62.
- Heusser, L.E., Shackleton, N.J., 1979. Direct marine-continental correlation: 150,000-year oxygen isotope-pollen record from the North Pacific. *Science* 204, 837–839.
- Hooghiemstra, H., 1988a. 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. *Review of Palaeobotany and Palynology* 55, 101–140.
- Hooghiemstra, H., 1988b. Palynological records from northwest African marine sediments: a general outline of the interpretation of the pollen

- signal. Philosophical Transactions Royal Society London B 318, 431–449.
- 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, Kluwer, Dordrecht, pp. 733–770.
- Hooghiemstra, H., 1996. Aspects of Neogene-Quaternary environmental and climatic change in equatorial and Saharan Africa. *Palaeoecology of Africa* 24, 115–132.
- Hooghiemstra, H., Agwu, C.O.C., 1986. Distribution of palynomorphs in marine sediments: a record for seasonal wind patterns over NW Africa and adjacent Atlantic. *Geologische Rundschau* 75, 81–95.
- Hooghiemstra, H., Agwu, C.O.C., 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. *Palaeogeography Palaeoclimatology Palaeoecology* 66, 173–213.
- Hooghiemstra, H., Agwu, C.O.C., Beug, H.-J., 1986. Pollen and spore distribution in recent marine sediments: a record of NW-African seasonal wind patterns and vegetation belts. 'Meteor' Forschungs Ergebnisse, Reihe C 40, 87–135.
- Hooghiemstra, H., Bechler, A., Beug, H.-J., 1987. Isopollen maps for 18,000 years BP of the Atlantic offshore of northwest Africa: evidence for paleowind circulation. *Paleoceanography* 2, 561–582.
- Hooghiemstra, H., Stalling, H., Agwu, C.O.C., Dupont, L.M., 1992. Vegetational and climatic changes at the northern fringe of the Sahara 250,000–5,000 years BP: evidence from 4 marine pollen records located between Portugal and Canary Islands. *Review of Palaeobotany and Palynology* 74, 1–53.
- 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. *Vegetation History and Archaeobotany* 5, 207–213.
- Jahns, S., Hüls, M., Sarnthein, M., 1998. Vegetation and climate history of west equatorial Africa based on a marine pollen record off Liberia (site GIK 16776) covering the last 400,000 years. *Review of Palaeobotany and Palynology* 102, 277–288.
- Jones, S.E., Jago, C.F., Bale, A.J., Chapman, D., Howland, R., Jackson, J., 1998. Aggregation and resuspension of suspended particulate matter at seasonally stratified site in the southern North Sea: physical and biological controls. *Continental Shelf Research* 18, 1283–1310.
- Kummel, B., Raup, D. (Eds.), 1965. *Handbook of Paleontological Techniques*. Freeman, San Francisco, USA, 852pp.
- Kuyl, O.S., Muller, J., Waterbolk, H.T., 1955. The application of palynology to oil geology with reference to western Venezuela. *Geologie en Mijnbouw* 17, 49–76.
- Leroy, S., 1992. Palynological evidence of *Azolla nilotica* Dec. in recent Holocene of eastern Nile Delta, and its environment. *Vegetation History and Archaeobotany* 1, 43–52.
- Leroy, S., Dupont, L., 1994. Development of vegetation and continental aridity in northwestern Africa during the Late Pliocene: the pollen record of ODP Site 658. *Palaeogeography Palaeoclimatology Palaeoecology* 109, 295–316.
- Lézine, A.-M., Deneffe, M., 1997. Enhanced anticyclonic circulation in the eastern North Atlantic during cold intervals of the last deglaciation inferred from deep-sea pollen records. *Geology* 25, 119–122.
- Lézine, A.M., Hooghiemstra, H., 1990. Land-sea comparisons during the last glacial–interglacial transition: pollen records from West Tropical Africa. *Palaeogeography Palaeoclimatology Palaeoecology* 79, 313–331.
- Lézine, A.-M., Le Thomas, A., 1995. Histoire du massif forestier ivoirien au cours de la dernière déglaciation. 2e Symposium Palynologie Africaine, CIFEG, Publication a Occasional 31, 73–87.
- Lézine, A.-M., Vergnaud-Grazzini, C., 1993. Evidence of forest extension in West Africa since 22,000 BP: a pollen record from the Eastern Tropical Atlantic. *Quaternary Science Reviews* 12, 203–210.
- Lézine, A.-M., Turon, J.-L., Buchet, G., 1995. Pollen analysis off Senegal: evolution of the coastal environment during the last deglaciation. *Journal of Quaternary Science* 10, 95–102.
- Marret, F., Turon, J.-L., 1994. Paleohydrology and paleoclimatology off northwest Africa during the last glacial–interglacial transition and the Holocene: palynological evidences. *Marine Geology* 118, 107–117.
- Marret, F., Scourse, J., Versteegh, G., Jansen, J.H.F., Schneider, R., 2001. Integrated marine and terrestrial evidence for abrupt Congo River palaeodischarge fluctuations during the last deglaciation. *Journal of Quaternary Science* 16, 761–766.
- Melia, M.B., 1984. The distribution and relationship between palynomorphs and aerosols and deep-sea sediments off the coast of northwest Africa. *Marine Geology* 58, 345–371.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*, second ed. Blackwell, Oxford, UK 216pp.
- Muller, J., 1959. Palynology of recent Orinoco delta and shelf sediments. *Micropaleontology* 5, 1–32.
- Neuer, S., Ratmeyer, V., Davenport, R., Fischer, G., Wefer, G., 1997. Deep water particle flux in the Canary Island region: seasonal trends in relation to long-term satellite pigment data and lateral sources. *Deep-Sea Research I* 44, 1451–1466.
- Nicholson, S.E., Flohn, H., 1980. African environmental and climatic changes and the general atmospheric circulation in Late Pleistocene and Holocene. *Climatic Change* 2, 313–348.
- Ning, S., Dupont, L.M., 1987. Vegetation and climate history of southwest Africa: a marine palynological record of the last 300,000 years. *Vegetation History and Archaeobotany* 6, 117–131.
- Prospero, J.M., Ginoux, P., Torres, O., Nicholson, S.E., Gill, T.E., 2002. Environmental characterization of global sources of atmospheric soil dust identified with the Nimbus 7 Total Ozone Mapping Spectrometer (TOMS) absorbing aerosol product. *Reviews of Geophysics* 40, 31.
- Ratmeyer, V., Fischer, G., Wefer, G., 1999a. Lithogenic particle fluxes and grain size distributions in the deep ocean off northwest Africa: implications for seasonal changes of aeolian dust input and downward transport. *Deep-Sea Research I* 46, 1289–1337.
- Ratmeyer, V., Balzer, W., Bergametti, G., Chiapello, I., Fischer, G., Wyputta, U., 1999b. Seasonal impact of mineral dust on deep-ocean particle flux in the eastern subtropical Atlantic Ocean. *Marine Geology* 159, 241–252.
- Romero, O.E., Dupont, L., Wyputta, U., Jahns, S., Wefer, G., 2003. Temporal variability of fluxes of eolian-transported freshwater diatoms, phytoliths, and pollen grains off Cape Blanc as reflection of land–atmosphere–ocean interactions in northwest Africa. *Journal of Geophysical Research* 108 (C5), 3153–3164.
- Shi, N., Dupont, L.M., Beug, H.-J., Schneider, R., 1998. Vegetation and climate changes during the last 21,000 years in SW Africa based on a marine pollen record. *Vegetation History and Archaeobotany* 7, 127–140.
- Shi, N., Dupont, L.M., Beug, H.-J., Schneider, R., 2000. Correlation between vegetation in southwestern Africa and upwelling in the last 21,000 years. *Quaternary Research* 54, 72–80.
- Shi, N., Schneider, S., Beug, H.-J., Dupont, L.M., 2001. Southeast trade wind variations during the last 135 kyr: evidence from pollen spectra in eastern South Atlantic sediments. *Earth and Planetary Science Letters* 187, 311–321.
- Suc, J.-P., 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* 307, 429–432.
- Swap, R., Ulanski, S., Cobbett, M., Garstang, M., 1996. Temporal and spatial characteristics of Saharan dust outbreaks. *Journal of Geophysical Research* 101 (D2), 4205–4220.
- Traverse, A., Ginsburg, R.N., 1966. Palynology of the surface sediments of Great Bahamas Bank, as related to water movement and sedimentation. *Marine Geology* 4, 417–459.
- Tschudy, R.H., Scott, R.A., 1969. *Aspects of Palynology*. Wiley-Interscience, New York, USA 510pp.
- Van der Kaars, W.A., 1991. Palynology of eastern Indonesian marine piston-cores: a Late-Quaternary vegetational and climatic record for

- Australasia. *Palaeogeography Palaeoclimatology Palaeoecology* 85, 239–302.
- Van der Kaars, W.A., Wang, X., Kershaw, P., Guichard, F., Setiabudi, D.A., 2000. A Late Quaternary palaeoecological record from the Banda Sea, Indonesia: apperns of vegetation, climate and biomass burning in Indonesia and northern Australia. *Palaeogeography Palaeoclimatology Palaeoecology* 155, 135–153.
- White, F., 1983. The vegetation of Africa. A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. Unesco, Paris, 356pp (with 3 maps).
- Wyputta, U., Grieger, B., 1999. Comparison of eastern Atlantic atmospheric trajectories for present day and last glacial maximum. *Palaeogeography Palaeoclimatology Palaeoecology* 146, 53–66.