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Palynological evidence for climatic and oceanic variability off NW Africa during the late Holocene

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ABSTRACT

Pollen and organic-walled dinoflagellate cyst assemblages from core GeoB 9503-5 retrieved from the mud-belt (~50 m water depth) off the Senegal River mouth have been analyzed to reconstruct short-term palaeoceanographic and palaeoenvironmental changes in subtropical NW Africa during the time interval from ca. 4200 to 1200 cal yr BP. Our study emphasizes significant coeval changes in continental and oceanic environments in and off Senegal and shows that initial dry conditions were followed by a strong and rapid increase in humidity between ca. 2900 and 2500 cal yr BP. After ca. 2500 cal yr BP, the environment slowly became drier again as indicated by slight increases in Sahelian savannah and desert elements in the pollen record. Around ca. 2200 cal yr BP, this relatively dry period ended with periodic pulses of high terrigenous contributions and strong fluctuations in fern spore and river plume dinoflagellate cyst percentages as well as in the fluxes of pollen, dinoflagellate cysts, fresh-water algae and plant cuticles, suggesting “episodic flash flood” events of the Senegal River. The driest phase developed after about 2100 cal yr BP.

Introduction

Climatic variability has severe consequences for the human populations of West Africa. Most recently, the Sahel drought from the late sixties to early eighties of the last century caused famine and socio-economic decline (e.g., Nicholson, 2000). Recent studies from tropical and subtropical West Africa suggest that increasing humidity during the early to mid-Holocene was followed by an abrupt onset of aridity around 5500 cal yr BP (deMenocal et al., 2000) and by several dry climatic events between ca. 4500 and 2000 cal yr BP characterized by lowered water tables and precipitation (Lézine and Chateauneuf, 1991; Maley and Brenac, 1998; Salzmann and Waller, 1998; Salzmann et al., 2002; Marchant and Hooghiemstra, 2004). These climatic fluctuations detected in several palaeoecological sites have been related to global climatic changes (Maley and Brenac, 1998; Gasse, 2000; Salzmann et al., 2002). A number of studies suggest a close relationship between changes in ocean conditions and changes in African precipitation (Lamb et al., 1995; Schefuβ et al., 2005; Weldeab et al., 2005; Mulitza et al., 2008).

To obtain insight into this relationship, a combined study of terrestrial palynomorphs (pollen and spores) and organic-walled dinoflagellate cysts (dinocysts) enables the recognition of simultaneous changes in both oceanic and atmospheric conditions and offers the opportunity to establish direct land-sea correlations of terrestrial and marine palaeoenvironmental changes (Hooghiemstra, 1988b; Hooghiemstra et al., 2006). In this paper, we present an integrated description and interpretation of late Holocene high-resolution pollen and dinocyst records derived from a marine core from the mud-belt deposited on the inner shelf off Senegal near the mouth of the Senegal River.

Environmental setting

Regional climate

The climate of NW Africa is controlled mainly by the West African monsoon circulation with intense precipitation in summer and dry conditions in winter (Hsu and Wallace, 1976) caused by the seasonal movement of the Intertropical Convergence Zone (ITCZ). The ITCZ migrates between about 2°N and 12°N over the eastern Atlantic Ocean and 8°N and 24°N over the continent (Nicholson and Grist, 2003). Its northern position from July to September is some ten degrees of latitude north of the summer rainfall maximum. The latter is known as the tropical rain belt and produces most of the rainfall in NW Africa (Nicholson and Grist, 2003). Its southern position from December to February produces dry conditions in the study area associated with dry continental trade winds blowing almost parallel to the NW African coast. Another main wind system is the Saharan Air Layer (SAL) related to the African Easterly Jet (AEJ), a mid-tropospheric zonal

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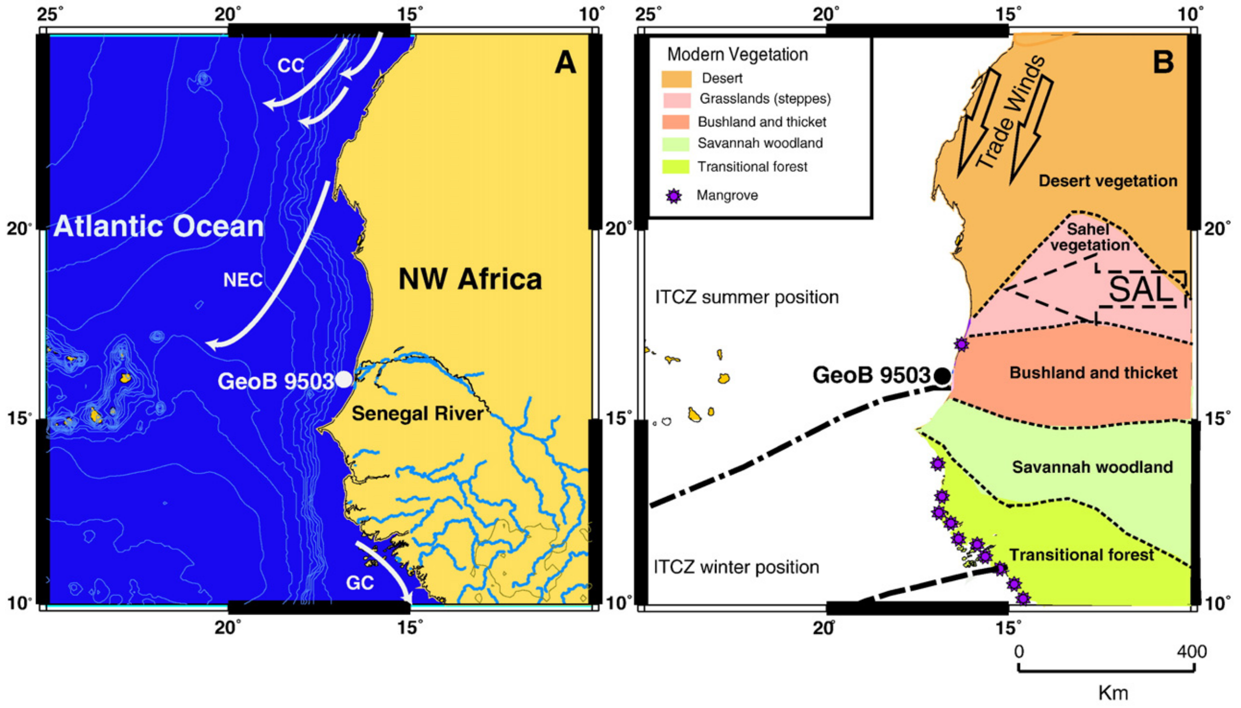

Figure 1. (A) Location map of marine core GeoB 9503-5 with major hydrographic systems and surface oceanic currents: CC: Canary Currents, NEC: North Equatorial Current, GC: Guinea Current (after Sarnthein et al., 1982 and Mittelstaedt, 1991). (B) Simplified phytogeography and biomes (after White, 1983) with main wind belts (Saharan Air Layer (SAL) and trade winds). The dashed lines indicate the present-day boreal summer (dash-dotted line) and boreal winter (dashed line) positions of the Intertropical Convergence Zone (ITCZ).

wind system occurring at higher altitudes (1500–5500 m) (Prospero, 1990). It is responsible for transporting dust and pollen offshore from the Sahara and Sahel belt to the Atlantic Ocean (Prospero and Nees, 1986; Prospero et al., 2002; Colarco et al., 2003) (Fig. 1).

Oceanic circulation

The tropical East Atlantic off NW Africa is influenced by several oceanic currents that are controlled by the prevailing wind systems (Fig. 1A). The dominant surface-water current is the Canary Current (CC), the easternmost branch of the Azores Current. The CC flows southwestward along the NW African coast as far south as Senegal where it turns westward to join the Atlantic North Equatorial Current (Mittelstaedt, 1991).

The alongshore flow is associated with upwelling when the position of the subtropical high pressure system strengthens the North East (NE) Trade Winds in boreal winter (Nykjaer and Van Camp, 1994). Filaments and eddies (Johnson and Stevens, 2000) entrain cool, upwelled nutrient-rich water from the coast and transport it up to several hundred km offshore (Mittelstaedt, 1991). The enhanced biological activity in these nutrient-rich waters is documented by diatoms, coccolitophores (Nave et al., 2001), dinocysts (Margalef, 1973), and planktonic foraminifera (Meggers et al., 2002).

At the core site, sea surface temperatures (SST) range from 23 to 29°C. The sea surface salinities range from 34.8 to 35.6 psu (WOA, 2001). Salinities are lower near the coast than offshore due to the fresh-water input from the Senegal River.

Senegal River

The 1790-km-long Senegal River, located between 10°20′–17°00′ N and 8°00′–16°30′ W, is one of the most active drainage systems of NW Africa. The total area of the Senegal River basin is about 419,650 km^2 (World Resources Institute, 2003). The river's flow regime is characterized by a high-water season from July to October with a peak flow generally occurring in late September and early October (Gac and Kane, 1986), while from November to June the discharge of the Senegal River drops, allowing seawater to penetrate the reduced river channel over a distance of approximately 250 km inland (Gac et al., 1985). The average water discharge at the last downstream point immediately landward of the estuary is 641 m^3/s, and the annual sediment load delivered to the Atlantic Ocean is $\sim 2 \times 109$ kg (Gac and Kane, 1986). Satellite images of the chlorophyll-*a* concentrations of the sea surface during boreal summer indicate that the plume of the Senegal River extends approximately 10 km offshore (http://reason.gsfc.nasa.gov).

Vegetation and pollen transport

The main vegetation belts in NW Africa reflect the north–south precipitation gradient (Fig. 1B). They range from Mediterranean vegetation containing trees and shrubs to the tropical rainforest along the Gulf of Guinea. In between, we find, from north to south, the steppes of the semi-desert area of the western Atlas region, desert vegetation of the Sahara, semi-desert grassland and shrubland of Sahelian (dry savannah) vegetation, and the Sudanian savannah zone (White, 1983). Coastal vegetation is represented by mangrove, occurring in estuaries and near the river mouths (White, 1983). The distribution of mangrove depends on water salinity, river runoff, and humidity (Blasco, 1984). Today, mangroves are well-developed off the Casamance and Gambia River mouths and the Saloum delta (Spalding et al., 1997). Their abundances decrease near the mouth of the Senegal River (Hooghiemstra and Agwu, 1986).

In the NW African region, aeolian transport of pollen is mainly dependent on the two dominant wind systems, the NE trade winds and the SAL (Hooghiemstra and Agwu, 1986; Hooghiemstra and Agwu, 1986). The Senegal River, on the other hand, is the most important fluvial source of pollen and other terrestrial particles in the study area. Hooghiemstra et al. (2006) suggests that offshore of NW Africa, the distribution of pollen over the ocean surface is reflected in the marine sediments without substantial displacement by marine

Table 1
Radiocarbon age dates and calibrated ages (the mode of the calibrated age ranges) used to construct the age model for marine core GeoB 9503-5.

Core depth (cm)	Lab code	^{14}C age ± 1σ error (yr BP)	1σ calendar age ranges	Calibrated age (cal yr BP)
20	KIA 28454	1675 ± 30	1225–1383 BP	1240
70	KIA 29768	1870 ± 30	1327–1383 BP	1355
140	KIA 29767	2310 ± 30	1824–1883 BP	1855
213	KIA 28452	2555 ± 30	2113–2158 BP	2140
320	KIA 29766	2665 ± 30	2205–2232 BP	2210
410	KIA 29765	2740 ± 30	2335–2358 BP	2350
529	KIA 28451	2925 ± 30	2540–2592 BP	2550
600	KIA 29764	2965 ± 30	2710–2748 BP	2730
700	KIA 29763	3600 ± 30	3391–3445 BP	3420
780	KIA 28450	4140 ± 35	4079–4150 BP	4110

Calibrated ages were estimated using CALIB 5.0.2 and are based on the Intcal04 calibration curve (Reimer et al. 2004; Stuiver et al. 2005).

currents. We therefore assume that no large-scale transport has displaced the palynomorphs and terrigenous material while sinking through the water column.

Materials and methods

We studied the marine sediment core GeoB 9503-5, recovered from the Senegal mud-belt off the mouth of Senegal River at ~50 m water depth (16°03.99′ N, 16°39.15′ W) during R/V *Meteor* cruise M65-1 (Mulitza et al., 2006). The 791-cm-long core consists of homogenous dark olive green mud with shell fragments. The core does not include the upper sediments, which are likely to have been lost during the coring procedure.

Radiocarbon dating

Ten AMS radiocarbon dates from bivalve shells were obtained at the Leibniz-Laboratory for Radiometric Dating and Stable Isotope Research in Kiel University. Radiocarbon dates were converted to 1σ calendar age ranges with the CALIB 5.0.2 software (Stuiver and Reimer, 2005) using the Intcal04 calibration curve (Reimer et al. 2004), with a constant reservoir correction of 400 yr (Bard, 1988; Bard et al., 2000). Sediment ages between dated core depths were calculated by linear interpolation between the mode of the calibrated age ranges (Table 1).

Palynological processing

Fifty-six samples were taken at 10- to 20-cm intervals along the core and processed according to standard palynological preparation procedures (Faegri and Iversen, 1989). A volume of 1 cm^3 of sediment was decalcified with diluted HCl (10%) and treated with HF (40%) to remove silicates. One tablet of exotic *Lycopodium* marker (10,679 ± 426 spores/tablet) was added to each sample during the decalcification process in order to calculate palynomorph concentrations. After neutralization and rinsing, the samples were sieved through an 8-μm mesh size sieve using an ultrasonic bath (5 min) to disintegrate lumps of organic matter. The residue was concentrated by centrifuging for 8 min at 3500 rotations per minute and resuspended in 1 ml of water. A 40- to 60-μl aliquot was mounted on a slide using glycerine jelly and sealed with nail polish. One to four slides per sample were counted under a light microscope at 400× and 1000× magnification to a minimum of 100 pollen grains (including herbs, shrubs, trees and aquatics) and 200 dinocysts when possible.

The nomenclature of the identified dinocysts was based on published morphological descriptions and the cyst nomenclature follows de Vernal et al. (1997), Zonneveld (1997), Marret and Zonneveld (2003), and Fensome and Williams (2004).

Pollen grains were identified following Vincens et al. (2007) and Bonnefille and Riollet (1980). Besides dinocysts and pollen, other palynomorphs, such as fern spores, plant cuticles and fresh-water algae (*Botryococcus*, *Cosmarium*, *Pediastrum*, *Scenedesmus* and *Staurastrum*) were also counted.

Table 2
List of the identified Dinoflagelate cyst species in marine core GeoB 9503-5.

Cyst name	Motile affinity	Grouping
Lingulodinium machaerophorum	*Lingulodinium polyedrum*	*L. machaerophorum*, *L. machaerophorum* var. short processes
Gonyaulacaceae family		
Cyst of *Pentapharsodinium dalei*	*Pentapharsodinium dalei*	
Polysphaeridium zoharyi	*Pyrodinium bahamense*	
Operculodinium israelianum	*? Protoceratium* sp.	
Operculodinium centrocarpum	*Protoceratium reticulatum*	*O. centrocarpum* and *O. centrocarpum* var. short processes.
Spiniferites mirabilis	*Gonyaulax spinifera*	*S. mirabilis* and *S. hypercanthus*
Spiniferites bentorii	*Gonyaulax digitale*	
Spiniferites pachydermus	*Gonyaulax spinifera*	
Spiniferites ramosus	*Gonyaulax* sp.	
Spiniferites spp.	*Gonyaulax* sp.	*S. bulloideus*, *S. membranaceus* and *S.* Spp.
Peridineaceae family		
Brigantedinium spp.		Cyst of *Protoperidinium* spp., cyst of *Diplopelta symetrica*, *Votadinium calvum*, *Votadinium spinosum*, *Stelladinium stellatum*, *Dubridinium* spp., cysts of *Protoperidinium americanum*, *Bitectatodinium* spp. and *Zygabikodinium lenticulatum*
Xandarodinium xanthum	*Protoperidinium divaricatum*	
Quinquecuspis concreta	*? Protoperidinium leone*	
Bitectatodinium spongium		
Lejeunecysta oliva	Unknown	
Selenopemphix quanta	*Protoperidinium conicum*	
Selenopemphix nephroides	*Protoperidinium subinerme*	
Trinovantedinium applanatum	*Protoperidinium pentagonum*	
Echinidinium granulatum	Unknown	
Echinidinium spp.	Unknown	*E. delicatum*, *E. aculeatum* and *E.* spp
Echinidinium transparantum	Unknown	*E. zonneveldii* and *E. transparantum*
Cysts of *Protoperidinium monospinum*		
Polykrikaceae family		
Cysts of *Polykrikos kofoidii*	*Polykrikos kofoidii*	Cyst of *P. kofoidii* and cyst of *P. schwarzii*
Pyrophacaceae family		
Tuberculodinium vancampoae	*Pyrophacus steinii*	

(Nomenclature after Marret and Zonneveld, 2003).

Pollen abundances are expressed as percentages of total pollen; spores are expressed as percentages of total pollen and spores. Dinocyst abundances are expressed as percentages of total cysts.

Statistical methods

A Detrended Correspondence Analysis (DCA) was carried out to quantify trends in the species distributions. It showed that the dataset had a linear character, validating the application of multivariate ordination technique principal component analysis (PCA) (ter Braak and Smilauer, 1998). In order to establish a grouping of dinocyst species based on their ecological preferences and to explore the consistency of the proposed zonings of the records, we performed the PCA on the relative abundances of all dinocyst species and on the 56 samples (ter Braak and Smilauer, 1998). Species occurring in abundances of less than 1% were grouped as indicated in Table 2. The groupings of dinocyst taxa provided by PCA were further refined using the results of a modern-calibration study based on the regional distribution of dinocyst assemblages in surface sediments off West Africa (Bouimetarhan et al., 2009).

Results

Age model

Radiocarbon dates from 10 samples ranging between 20 and 780 cm core depth are presented in Table 1. The time period represented by core GeoB 9503-5 ranges from approximately 4200 to 1200 cal yr BP (Fig. 2). Maximum sedimentation rates of 1.53 cm/yr occurred at the time period between ca. 2200 and 2100 cal yr BP and a minimum of 0.16 cm/yr is recorded between ca. 4200 and 3400 cal yr BP.

Dinocyst and pollen records

A total of 40 dinocyst taxa and 32 pollen taxa were identified (Tables 2 and 3). Dinocyst concentrations from core GeoB 9503-5 range between 600 and 45,800 cysts/cm^3 and their accumulation rates vary between 300 and 8300 cysts/cm^2/yr. Pollen concentrations range between 700 and 7800 grains/cm^3 and their accumulation rates fluctuate from 200 to 3800 grains/cm^2/yr, reaching maximum values at ca. 2160 cal yr BP (251 cm). Based on contemporaneous changes in the dinocyst and pollen records, we distinguish five zones (Fig. 3).

Zone A: (ca. 4200–2900 cal yr BP, 790–630 cm, 11 samples)

Dinoflagellate assemblages are dominated by heterotrophic species, accounting for up to 59% of the assemblage, such as cysts of *Protoperidinium monospinum*, *Selenopemphix quanta*, *Selenopemphix nephroides*, *Brigantedinium* spp., and *Echinidinium transparantum*.

Table 3
List of the identified pollen taxa in marine core GeoB 9503-5.

- Mangrove
  - *Rhizophora*
- Rivers and swamps
  - *Typha*
- Sahelian Savannah
  - Cyperaceae
  - Poaceae
- Salt marsh
  - Amaranthaceae/Chenopodiaceae
- Semi-desert
  - Asteroideae
- *Artemisia*
- Trees and shrubs
- European/Mediterranean
  - *Olea*
  - *Pinus*
  - *Clematis*-type
  - *Fraxinus*
- Sahelian elements
  - *Mitracarpus*
  - *Acacia*
  - *Ziziphus*-type
  - *Boscia*
  - *Borreria*
- Sudanian elements
  - *Butyrospemum* (Sapotaceae)
  - *Piliostigma* (Caesalpiniaceae)
  - Pterocarpus (Fabaceae)
  - *Vernonia*-type (Asteraceae)
  - *Indigofera*-type
  - *Tamarindus*
  - *Cuviera*
- Guinean forest
  - Annonaceae
  - *Stereospermum*-type (Bignoniaceae)
  - *Phoenix*-type (Palmae)
  - *Uapaca*
  - *Psydrax* type *subcordatum* (Rubiaceae)
- Other elements
  - *Euphorbia*
  - Rubiaceae spp.
  - *Galium*

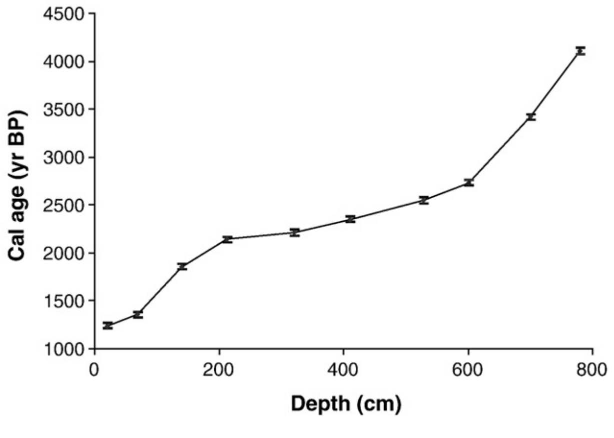

Figure 2. Calibrated age-depth graph for core GeoB 9503-5 (error bars indicate the ± 1σ error [cal yr BP]).

Pollen concentrations reach maximum values in this interval (~7800 grains/cm^3). The pollen assemblages are dominated by Poaceae (grasses) reaching 82% in association with *Rhizophora* (mangrove) of which percentages fluctuate between 2 and 17% reaching their maximum in this record at ca. 4030 cal yr BP (781 cm). Conversely, Cyperaceae, Amaranthaceae/Chenopodiaceae (Cheno-Am; representatives of salt-marshes), and Asteroideae (Compositae Tubuliflorae) occur at low values. This interval shows minimum values of Sahelian elements such as *Acacia* (2%) and *Mitracarpus* (5%) as well as fern spores, fresh-water algae and plant cuticles.

Zone B: (ca. 2900–2500 cal yr BP, 630–500 cm, 9 samples)

The main feature of this time interval is the abrupt increase of dinocyst concentrations and accumulation rates. Dinocyst assemblages are characterized by a marked shift from heterotrophic to phototrophic dominated association accounting for 83% of the assemblage. Percentages of *Spiniferites mirabilis* (12%) and *Spiniferites ramosus* (7%) reach their highest values along with *Trinovantedinium appelanatum* (8%), cysts of *Pentaspharsodinium dalei* (5%), and *Tuberculodinium vancampoae* (3%). *Polysphaeridium zoharyi* and *Operculodinium centrocarpum* with reduced process lengths occur in low percentages.

Pollen concentrations decrease markedly in this zone. The pollen assemblage shows a slight increase of Cyperaceae pollen (19%) along with *Acacia* (5%), *Mitracarpus* (6%), *Typha* (7%), and Cheno-Am (9%). Within this time interval, *Rhizophora* pollen decreases to a minimum value of 1.8% and similarly, Asteroideae pollen decreases to 1% at ca. 2630 cal yr BP (561 cm). In contrast, the fluxes of total fresh water algae and plant cuticles increase to a maximum value of 120/cm^2/yr and 2700/cm^2/yr, respectively. Fern spores increase considerably up to 18%.

Zone C: (ca. 2500–2230 cal yr BP, 500–330 cm, 12 samples)

Both the accumulation rates and concentrations of dinocysts decrease substantially in this interval. The dinocyst assemblage is dominated by heterotrophic species (61%) such as cysts of *P. monospinum* (20%), *S. quanta* (19%), and *Brigantedinium* spp. (17%).

The total pollen fluxes and concentrations increase gradually to 2100 grains/cm^2/yr and 3200 grains/cm^3, respectively. Although the Poaceae are still the dominant group, their percentages do not exceed

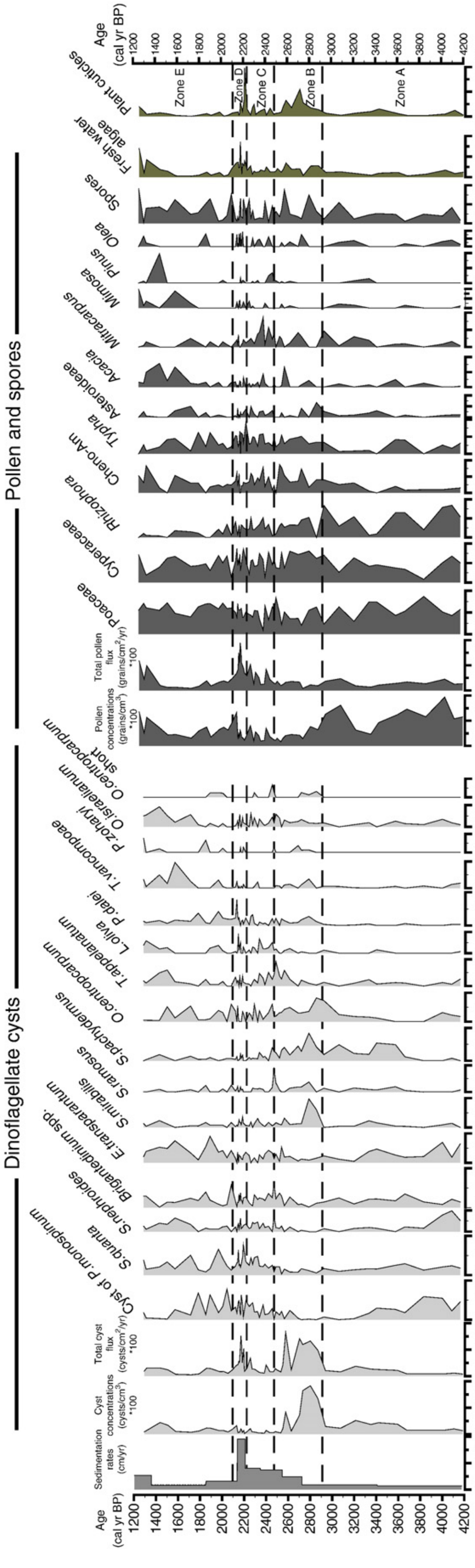

Figure 3. Integrated palynological data from marine sediment core GeoB 9503-5 showing sedimentation rates, concentrations and accumulation rates (fluxes) of dinocysts and pollen, relative abundances of main dinocyst and pollen taxa as well as percentages of spores and fluxes of fresh-water algae and plant cuticles are also presented in the diagram. The palynological data are subdivided into five zones indicated by the dashed lines. Dinocyst percentages are expressed on the total of counted cysts. Pollen abundances are calculated as percentages of the sum of total pollen including trees, shrubs and aquatic pollen. Spore percentages are calculated relative to the sum of pollen and spores fresh-water algae and plant cuticle are expressed as fluxes (number/cm^2/yr).

70% and decrease to 36% at ca. 2380 cal yr BP (431 cm). The percentages of Cyperaceae pollen vary from 4 to 19%. During this time interval, *Typha* pollen decrease to 3% at ca. 2470 cal yr BP (481 cm) with an intermediate increase reaching 7% at ca. 2390 cal yr BP (431 cm). Abundances of semi-desert elements such as Asteroideae pollen increase to 3% along with Sahelian elements such as *Mitracarpus* (11%). Conversely, Cheno-Am and *Rhizophora* pollen show low percentages. Relative abundances of *Olea* pollen do not exceed 1% in this interval, whereas *Pinus* pollen percentages reach 3% at ca. 2470 cal yr BP (481 cm). Spore percentages decrease significantly together with the total fresh water algae and plant cuticle fluxes.

Zone D: (ca. 2230–2130 cal yr BP, 330–210 cm, 10 samples)

The salient feature of this zone is the rapid increase in sedimentation rates and the strong fluctuations in the fluxes of pollen, spores, dinocysts, fresh-water algae, and plant cuticles (Fig. 3). Cysts of *P. monospinum*, *S. quanta*, and *Brigantedinium* spp. still dominate the dinocyst assemblages in association with *T. appelanatum*, *L. oliva*, and *P. dalei*.

The pollen assemblages are dominated by Poaceae (72%) and Cyperaceae (21%). *Typha* occur at high values (10%) reaching the highest percentage in the record while Cheno-Am percentages decrease to a minimum value of 2%. The abundances of Sahelian elements, including *Mitracarpus* and *Acacia*, decrease abruptly. Percentages of fern spores increase to 13% at ca. 2170 cal yr BP (271 cm). Similarly, fluxes of plant cuticles as well as total fresh-water algae increase markedly in this interval.

Zone E: (ca. 2130–1240 cal yr BP, 210–20 cm, 14 samples)

This zone is characterized by abrupt decreases in sedimentation rate, fluxes and concentrations of dinocysts and pollen, and abundances of fern spores. The dinocyst assemblages are dominated by heterotrophic species such as cyst of *P. monospinum* (26%), *S. quanta* (27%), and *Brigantedinium* spp. (9%).

Poaceae pollen abundances slightly increase to 73%, whereas *Rhizophora* pollen (1%) and *Mitracarpus* (2%) exhibit their lowest percentages along the core. Percentages of Cyperaceae remain stable in this time interval. *Pinus* pollen is present in three samples, at ca. 2000 cal yr BP (181 cm), 1430 cal yr BP (81 cm) and ca. 1280 cal yr BP (41 cm). Fluxes of fresh-water algae and plant cuticles decrease considerably compared to the previous zone. After ca. 1500 cal yr BP, fluxes and concentrations of dinocysts and pollen show a small increase together with spores and fresh-water algae. During this time interval, the pollen assemblages show an increase in abundances of Cheno-Am (9%), *Acacia* (6%), *Mimosa* (4%), and Asteroideae (3%).

Principal component analysis (PCA)

Based on the PCA analysis of the 56 samples using the relative abundances of individual dinoflagellate and pollen taxa, three distinct clusters of samples can be distinguished. The first cluster comprises samples from 2900 to 2500 cal yr BP (zone B) that are ordinated at the most positive side of the first axis. Samples deposited from 2200 to 2100 cal yr BP (zone D) are grouped in a second cluster at the positive sides of the first and the second axes. All the other samples that have been assigned to Zones A, C, and E are ordinated at the negative sides of both the first and the second PCA axes (Fig. 4A).

Based on the PCA results of individual dinoflagellate taxa percentages, four groups of dinoflagellate species with comparable distribution can be distinguished (Fig. 4B).

Group 1: Shelf association

S. mirabilis, *S. ramosus*, *Spiniferites* spp., *S. pachydermus*, *S. bentorii*, and *O. centrocarpum*. These species are grouped on the most positive side of the first PCA axis.

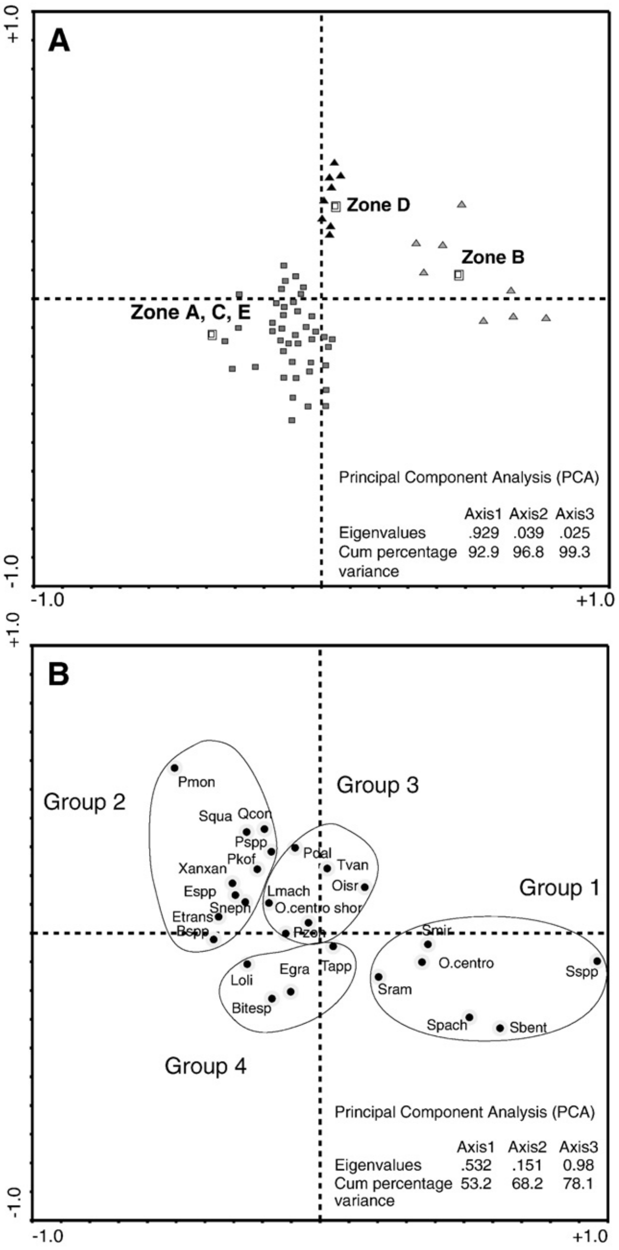

Figure 4. (A) PCA ordination plot of the 56 samples from core GeoB 9503-5. Light grey triangles stand for the zone B samples, dark triangles for the zone D samples, and grey rectangles denote the zones A, C, and E. (B) PCA ordination plot of individual dinoflagellate species (>1%) from core GeoB 9503-5. Group1: Smir: *Spiniferites mirabilis*, Sspp: *Spiniferites* spp., Sbent: *Spiniferites bentorii*, Spach: *Spiniferites pachydermus*, Sram: *Spiniferites ramosus*, O.centro: *Operculodinium centrocarpum*. Group2: Pmon: cysts of *Protoperidinium monospinum*, Squa: *Selenopemphix quanta*, Qcon: *Quinquecuspis concreta*, Pspp. cysts of *Protoperidinium* spp., Xanxan: *Xandarodinium xanthum*, Pkof: cysts of *Polykrikos kofoidii*, Espp: *Echinidinium* spp., Sneph: *Selenopemphix nephroides*, Etrans: *Echinidinium transparantum*, Bspp: *Brigantedinium* spp. Group3: Pdal: cysts of *Pentapharsodinium dalei*, Tvan: *Tuberculodinium vancampoae*, Oisr: *Operculodinium israelianum*, Lmach: *Lingulodinium machaerophorum*, O.centro shor: *Operculodinium centrocarpum* short, Pzoh: *Polysphaeridium zoharyi*. Group 4: Tapp: *Trinovantedinium applanatum*, Egra: *Echinidinium granulatum*, Loli: *Lejeunecysta oliva*, Bitesp: *Bitectatodinium spongium*.

Group 2: Upwelling association

Brigantedinium spp., *E. transparantum*, *Echinidinium* spp., cysts of *P. monospinum*, *Protoperidinium* spp., cysts of *P. kofoidii*, *Q. concreta*, *S. nephroides*, *S. quanta*, and *X. xanthum*. These species are ordinated at the positive side of the second PCA axis and the negative side of the first axis.

Group 3: Lagoon assemblage

L. machaerophorum, *P. dalei*, *P. zoharyi*, *O. centrocarpum* with short processes, *O. israelianum*, and *T. vancampoae*. This group includes species that are ordinated at the positive side of the second PCA axis.

Group 4: River plume assemblage

E. granulatum, *T. appelanatum*, *L. oliva*, and *B. spongium*. These species are ordinated at the negative side of the second PCA axis.

The composition of the dinocyst groups provided by PCA shows, to a large extent, similar patterns as the regional distribution of dinocyst assemblages in surface sediments off West Africa (Bouimetarhan et al., 2009). The species forming group1 in PCA are found in modern shelf sediments where nutrient concentrations are relatively high (Bouimetarhan et al., 2009). As result we can consider this association as indicative of nutrient-rich waters in shelf areas. Species that constitute group 2 have their highest relative abundances in areas characterized by high productivity such as upwelling regions (e.g., Marret and Zonneveld, 2003; Holzwarth et al., 2007). In modern sediments off West Africa, these species have been used as indicators for nutrient-rich waters linked to the seasonal upwelling in the study area (Bouimetarhan et al., 2009). The dinocyst assemblage of group 3 includes species that are typically known from lagoon areas and/or regions where large changes in sea-surface salinities (SSS) can occur (Marret and Zonneveld, 2003). Therefore, these species can be described as a lagoon assemblage in the present study.

Species of group 4 classically occur in high relative abundances in modern sediments of regions influenced by river discharge waters (Zonneveld and Jurkschat, 1999; Marret and Zonneveld, 2003; Holzwarth et al., 2007). This association has been used as an indicator for river outflow in modern sediments off West Africa (Bouimetarhan et al., 2009).

Discussion

Use of dinocysts for environmental reconstruction

Organic-walled dinocyst associations can be related to environmental conditions in surface waters such as nutrient availability, turbulence, sea-surface temperature, and sea-surface salinity. Consequently, they form a valuable tool for palaeoclimatic and palaeoceanographic reconstructions (Marret and de Vernal, 1997; Rochon at al., 1999; Marret and Zonneveld, 2003, Bouimetarhan et al., 2009). However, this only holds when species-selective degradation processes under aerobic conditions have not altered the association post-depositionally (e.g., Zonneveld, 1997; Zonneveld et al., 2001, 2007; Hopkins and McCarthy, 2002; Versteegh and Zonneveld, 2002). At our study site, sedimentation rates and primary production in the surface waters are high. This results in low oxygen concentrations in pore waters and a quick burial of organic matter. We therefore expect that the cyst associations at this site have not been significantly altered by degradation processes and can trustworthily be used to document changes in past oceanic conditions. This combined study of dinocysts and terrestrial palynomorphs such as pollen and pteridophyte spores, suitable for assessing changes in vegetation cover and/or transport mechanisms (wind strength and river discharge), will enable the recognition of co-occurring changes in both terrestrial and marine environments.

Late Holocene changes in oceanic and terrestrial environments

Relatively dry conditions between ca. 4200 and 2900 cal yr BP are indicated by the considerable representation of Sahelian savannah (Poaceae and Cyperaceae) as well as the presence of semi-desert elements, such as Asteroideae (Fig. 5). Additional evidence for dry conditions is provided by the low amount of fern spores as well as the low fluxes of fresh-water algae and plant cuticles, which are indicative of low river output. Confirmation for low river discharge is provided by the low dinocyst concentrations; the total cyst production of dinoflagellates is positively related to the nutrient and terrigenous element availability in the upper waters (e.g., Zonneveld and Brummer, 2000; Zonneveld et al., 2007; Bouimetarhan et al., 2009). Low dinocyst concentrations suggest therefore reduced marine productivity induced by low nutrient input from the Senegal River. The high *Rhizophora* pollen abundance in this time period reflects the expansion of mangrove vegetation along the Senegal River caused by reduced fresh-water flow and subsequent increased marine influence that would have allowed mangroves to extend considerably into the estuary despite the relatively dry conditions on the continent (Lézine and Casanova, 1989). An alternative explanation for high *Rhizophora* values would be efficient transport by the Senegal River (Dupont and

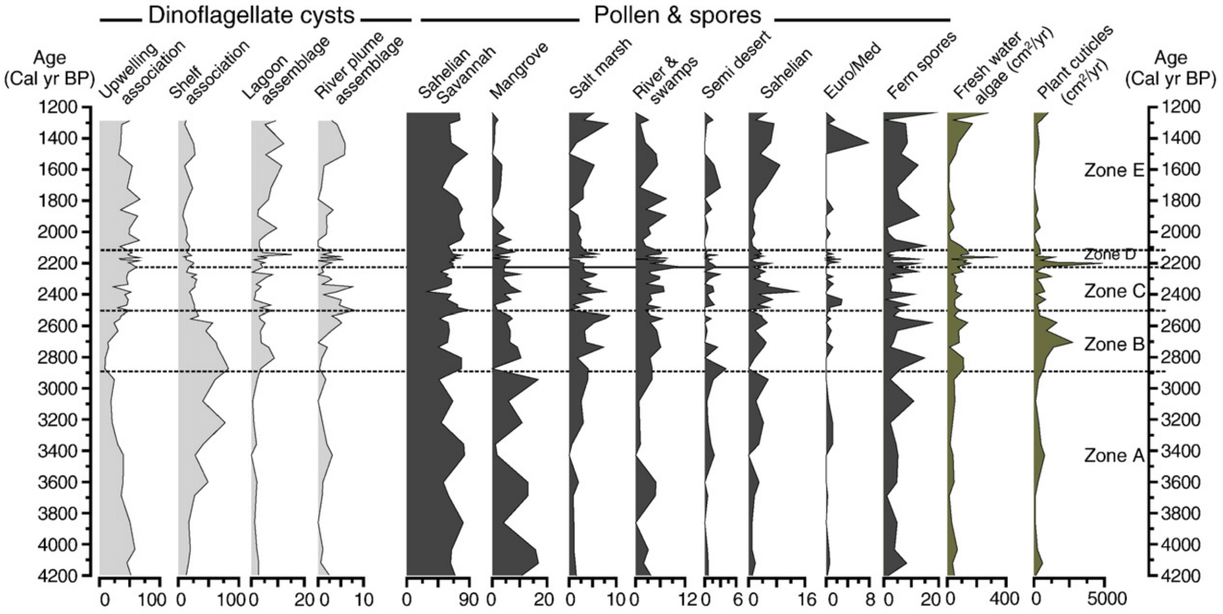

Figure 5. Relative abundances of dinocyst and pollen groups from core GeoB 9503-5.

Agwu, 1991; Lézine et al., 1995; Lézine, 1996). This would, however, require locally wetter conditions and continuous input of fresh water for which no evidence exists.

Supporting evidence for dry conditions at this time has been reported from subtropical NW Africa in the Cap Blanc region (Mauritania). A general trend towards increased aridity culminated in an abrupt change towards drier conditions at the end of the "African humid period" at ca. 5500 cal yr BP (e.g., deMenocal et al., 2000). Other evidence for dry conditions between ca. 4500 and 2000 cal yr BP comes from the late Holocene hydrographical and sedimentological records where significant lake-level declines from sites in western Sahel have been observed (e.g., Servant and Servant-Vildary, 1980; Lézine, 1989; Lézine and Casanova, 1989; Salzmann and Waller, 1998; Salzmann et al., 2002). In addition, in the Sahel of Nigeria (Salzmann and Waller, 1998) and Burkina Faso (Ballouche and Neumann, 1995) the establishment of modern vegetation characterized by Sahelian vegetation and degraded shrubland occurred between ca. 3500 and 3000 cal yr BP along with a distinct decrease of lake levels (Salzmann et al., 2002).

Between ca. 2900 and 2500 cal yr BP, the sudden increase of dinocyst fluxes and concentrations as well as the marked increase of cysts from the river-plume assemblage reflect enhanced Senegal River runoff that supplied large amounts of terrigenous material and nutrients to the surface waters. Enhanced Senegal River discharge is moreover evidenced by the significant increase in shelf-association species preferring warm and nutrient-rich conditions of neritic environments (Rochon et al., 1999; Bouimetarhan et al., 2009). In addition, high fluxes of plant cuticles and fresh-water algae as well as fern spore and *Typha* swamp elements indicate moister continental conditions and higher fluvial discharge.

We interpret these features as an indication of more humid conditions that we refer to as a "little humid phase" (LHP). This interval is characterized by increased runoff from the Senegal River, possibly related to higher monsoonal precipitation. Such an increase of precipitation rates could have been caused by the migration of the tropical rain belt towards the north. Our data suggest significant climate variability in the Senegal area between ca. 2900 and 2500 cal yr BP, a period that is generally considered as rather stable and dry. The earlier dry phase reported in previous studies (Lézine, 1989; Lézine and Casanova, 1989; Maley and Brenac, 1998; Salzmann and Waller, 1998; Salzmann et al., 2002) obviously ended with wetter conditions around 2900 cal yr BP. The LHP has not previously been recorded in any other palaeohydrological or palaeoenvironmental data from tropical and subtropical West Africa. The lack of evidence for the LHP in other records may be attributable to lower sampling resolution or subregional climatic variability.

From ca. 2500 to 2200 cal yr BP, the total accumulation rates and concentrations of dinocysts decrease substantially. Dinocyst records reveal a marked shift from the river plume and phototrophic/shelf associations to the upwelling association. In parallel, the pollen data indicate a dramatic decrease of fern spores and plant cuticles as well as low values of fresh-water algae. These changes were most likely related to changes in atmospheric and/or oceanic conditions adjacent to the Senegal River mouth, suggesting a reduced discharge of fresh water and inefficient transport by the Senegal River. Additionally, *Mitracarpus* pollen originating in the southern Sahelian and Sudanian zone is well represented during this period, indicating strong aeolian transport by the NE trades (Hooghiemstra and Agwu, 1986; Hooghiemstra et al., 1988a). We therefore interpret this interval as being characterized by lower sediment discharge from the Senegal River and an increase in trade wind strength. The increase in the abundance of dinocysts of the upwelling association may reflect a response to increasing nutrient availability in the surface waters caused by regional wind-induced upwelling.

These findings are in agreement with the results from a study in the rain forest of western Cameroon, where an abrupt opening of the vegetation took place at 2500 cal yr BP, indicating a climatic change toward dry conditions followed by a return to wetter climates after ca. 2200 cal yr BP (Maley and Brenac, 1998). In addition, archeological data indicate the appearance of large settlements on the Senegal delta after ca. 2500 cal yr BP. It is argued that people moved farther to the south during times when the Sahelian climate became drier (McIntosh and McIntosh, 1983; McIntosh, 2006). This migration can likely be related to the fact that the drying Senegal delta allowed agricultural activity in previously flooded plains (McIntosh, 1999).

Between ca. 2200 and 2100 cal yr BP, a rapid increase of sedimentation rates and strong fluctuations in percentages of fern spores and dinocysts from the river-plume assemblage, as well as in the total accumulation rates of pollen, dinocysts, fresh-water algae, and plant cuticles, indicate large environmental changes in the Senegal area. Wind-induced upwelling may have been associated with strong river discharge, suggesting that the previous dry phase ended with periodic pulses of terrigenous material, which could be caused by episodic flash-flood events of the Senegal River. These events might have been climatically induced through strengthening of the monsoon system in relation to the northward migration of the tropical rain belt, causing torrential rain and flooding in the catchment area of the Senegal River and supplying large amounts of terrigenous material. Another possible cause for increased terrigenous sediment load in the river would be the intensification of agriculture by the human population established on the Senegal delta after ca. 2500 cal yr BP, which could have aggravated erosion in the area (McIntosh, 1999).

After ca. 2100 cal yr BP, the sudden decrease in sedimentation rates, fluxes of dinocysts, pollen, fresh-water algae and plant cuticles as well as the increase in Sahelian savannah elements suggest lower discharge of the Senegal River under more arid conditions. At around 1800 cal yr BP, pollen assemblages show a strong occurrence of Saharan (Asteroideae) and Sahelian elements (*Acacia, Mimosa*). In addition, pollen from *Pinus* and *Olea*, which likely originated in North Africa and South-West Europe, exhibit high percentages indicating a strong increase in trade wind strength. The simultaneous decline of mangrove pollen at ca. 1800 cal yr BP can be interpreted as lower discharge of the Senegal River. Alternatively, this signal may also be related to human activities on the Senegal delta after 2500 cal yr BP (McIntosh, 1999). Our results corroborate the findings of Alexandre et al. (1997) who report phytolith evidence from Lake Guiers in the Sahelian region that shows the development of the driest phase at ca. 2100 cal yr BP. In western Senegal, Lézine (1988, 1989) shows that a second major change affected the Sahel after ca. 2000 cal yr BP and led to a rapid degradation of the vegetation and establishment of the modern semi-arid environment in the present Sahelian zone. These changes are clearly recorded in our core but not before ca. 1800 cal yr BP.

After ca. 1500 cal yr BP, our record shows a small increase in fluxes and concentrations of dinocysts and pollen as well as in abundances of river plume dinocyst assemblage. These observations could be interpreted as a shift toward wetter conditions. However, since the record ends at 1200 cal yr BP this may only be verified in another high-resolution record that covers the last 2000 yr.

Conclusion

Changes in the assemblages, concentrations, and fluxes of pollen and dinocysts in marine sediment core GeoB 9503-5 were observed for the time period ca. 4200–1200 cal yr BP, providing insights into past climatic, hydrologic, and oceanic conditions. Our study emphasizes significant coeval changes in continental moisture conditions and oceanic environmental changes in and off Senegal. Initial dry conditions between ca. 4200 and 2900 cal yr BP were followed by somewhat moister conditions we refer to as the "little humid phase". This phase was characterized by stronger fluvial transport and, by inference, greater monsoonal humidity between ca. 2900 and 2500 cal yr BP, which was likely caused by latitudinal migration of the tropical rain belt towards the north. Our data show decreasing Senegal River runoff and increasing Sahelian winds between ca. 2500 and 2200 cal yr BP reflecting a trend towards drier conditions. Around ca. 2200 cal yr BP, this relatively dry period ended with periodic pulses of high terrigenous contributions and strong fluctuations in fern spore and river plume dinocyst percentages and in the total accumulation rates of pollen, dinocysts, fresh-water algae, and plant cuticles. We suggest that these fluctuations were caused by episodic flash flood events of the Senegal River between ca. 2200 and 2100 cal yr BP. Our results show that the LHP and interval of episodic flash floods on the Senegal River interrupt the general climatic trend of increasing aridity in NW Africa that began in the mid-Holocene (deMenocal et al., 2000).

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