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Article abstract

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EVOLUTION OF THE WEST AFRICAN MANGROVE DURING THE LATE QUATERNARY: A REVIEW

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ABSTRACT The review of pollen data on mangrove pollen deposition in modern and late Quaternary sediments of West Africa points to two distinct signals linked to the sedimentary environment concerned. Along the littoral and on the slope of the continental shelf, mangrove peat deposits recording more than 40% of *Rhizophora* percentages reflect the postglacial sea-level rise and give evidence for the associated paleogeographical modifications (*e.g.* during the Nouakchottian transgression). Deep oceanic records show that the mangrove was present along the West African coasts during the Late Glacial Maximum reflecting local conditions of fresh water input and sea surface temperatures not as low as previously suggested. Mangrove developed after 12 500 BP as far north as 21°N; its maximum extension was recorded *ca.* 9500 BP reflecting the enhanced monsoon circulation over West Africa.

RÉSUMÉ *Évolution de la mangrove ouest africaine au Quaternaire récent.* La revue des données concernant la sédimentation pollinique des taxons de mangrove dans les sédiments actuels et quaternaires récents d'Afrique occidentale met en évidence la différence du signal enregistré selon qu'il s'agit de sédiments littoraux ou de sédiments marins profonds. Le long du littoral et sur les pentes du plateau continental, les tourbes de mangrove contenant des pourcentages de pollen de *Rhizophora* supérieurs à 40 % de la somme pollinique totale enregistrent très clairement les différentes étapes de la remontée postglaciaire du niveau marin et donnent la mesure des modifications paléogéographiques associées (comme par exemple lors de la transgression du Nouakchottien, il y a 5500 ans BP). Les sédiments marins profonds indiquent que la mangrove était présente, bien que réduite, le long des côtes ouest africaines lors du dernier maximum glaciaire indiquant la permanence de conditions locales d'apport d'eau douce et des températures de surface de l'océan proche moins basses que précédemment indiquées. La mangrove se développe dès 12 500 BP et s'étend probablement jusqu'à 21°N; son extension maximale a été atteinte il y a 9500 ans BP en réponse à l'augmentation des pluies de mousson atlantique au-dessus de l'Afrique nord-occidentale.

ZUSAMMENFASSUNG *Entwicklung der westafrikanischen Mangrove während des späten Quartärs : Ein Überblick.* Die Überprüfung von Pollen-Daten von Mangrove-Pollenablagerungen in gegenwärtigen und Spät-Quartär-Sedimenten Westafrikas weist zwei unterschiedliche Signale auf, je nach der betreffenden Sediment-Umgebung. Entlang der Küste und an den Hängen des Kontinentalplateaus spiegeln Mangrove-Torf-Ablagerungen, die über 40 % Rhizophera-Anteile enthalten, die postglaziale Anhebung des Meeresspiegels und belegen die damit verbundenen paleogeographischen Veränderungen (z.B. während der Nouakchottian-Transgression). Tiefseebelege zeigen, dass die Mangrove entlang der westafrikanischen Küsten im späten glazialen Maximum vorhanden war, und dass die lokalen Bedingungen für Süsswasserzufuhr und Meeresoberflächentemperaturen nicht so niedrig waren, wie zuvor angenommen. Die Mangrove entwickelte sich nach 12 500 v.u.Z. und breitete sich nördlich bis 21°N aus ; ihre maximale Ausbreitung ist um etwa 9500 v.u.Z. belegt und spiegelt die verstärkte Monsun-Zirkulation über West-Afrika.

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INTRODUCTION

Mangrove pollen grains, mainly *Rhizophora* from late Quaternary sediments are considered generally as good stratigraphical markers of sea-level fluctuations (Ellison, 1989). Moreover, some authors have suggested that mangrove development was related to such specific climatic parameters as important rainfall, responsible for fresh water occurrence (from rivers or ground waters) and sea-surface temperatures above 24°C (Van Campo, 1983). In West Africa, pollen data from late Quaternary mangroves are discontinuous owing primarily to the irregular, often truncated nature of the related nearshore sediments (Lézine, 1987). Recent data on long, well calibrated and continuous sequences from deep oceanic sediments collected at a short distance from the coasts (Rossignol-Strick and Duzer, 1979; Hooghiemstra, 1988; Lézine and Vergnaud-Grazzini, 1993; Lézine *et al.*, 1994, 1995) fill the gap in the record of the mangrove history during the last glacial-deglacial transition. I present here a review of studies on mangrove pollen deposition in (sub-)recent and Pleistocene sediments to discuss the different signals recorded in both littoral and deep-sea records.

THE MODERN FEATURES

A) GEOGRAPHICAL CONTEXT

Mangrove occurs in the intertidal coastal plains of West Africa between 12°30'S and 19°50'N (Fig. 1). Its optimal development is attained under rainforest climate (mean annual *rainfall = more than 1200 mm year*$^{-1}$), *out of direct influence* of swell and sea-water currents, at the mouths of large rivers such as the Niger, where it benefits from both dilute sea-water and large muddy areas (Marius, 1985). Sea surface temperatures average 25°C (*e.g.* mini 24°C, maxi 38°C off Lagos) (Diop and Barrusseau, 1994) in the Gulf of Guinea and decrease toward the north to 23°C off Senegal (min. 18°C, max. 28°C) in relation with local "coastal" upwelling, while salinity averages 30 to 35‰ all along the coast except for more equatorial areas as in Cameroun where values below 20‰ are recorded.

West african mangrove populations are mainly composed of *Rhizophora, Avicennia, Laguncularia*, and *Conocarpus* (White, 1983). These genera are mostly distributed according to a gradient in water depth (frequency and duration of flooding by sea-water) and salinity. The consistency of the soil (sandy or clayey) also plays a non-negligible role. *Rhizophora racemosa, R. harrisonii, R. mangle* occur at the outer edge of the mangrove on muds, and may support intertidal variations of 4 m amplitude (Trochain, 1980). Behind the *Rhizophora* zone, the zone of *Avicennia germinans* and *Paspalum vaginatum,* associated with *Laguncularia racemosa, Conocarpus erectus,* and locally with *Pandanus candelabrum* and *Acrostichum aureum,* lies on sandbanks, in irregularly submerged areas. The back-mangrove, characterized by high salt concentrations is composed of herbaceous plants such as *Sesuvium portulacastrurn* and *Philoxerus vermicularis.*

The most widespread genera, *Rhizophora* reaches its northern limits at the mouth of the Senegal River near 16°N latitude (Adam, 1965) (mean annual rainfall = *ca.* 300 mm year^{-1}), whereas *Avicennia*, which is adapted to highly saline conditions, extends up to Tidra in Mauritania at 19°50'N (White, 1983) (<100 mm year –1), probably as relict population.

B) MODERN POLLEN DEPOSITION

The mangrove association recorded in pollen spectra from modern littoral or oceanic sediments is mainly represented by *Rhizophora,* the high percentages of which are closely linked to the high pollen productivity of the source plants

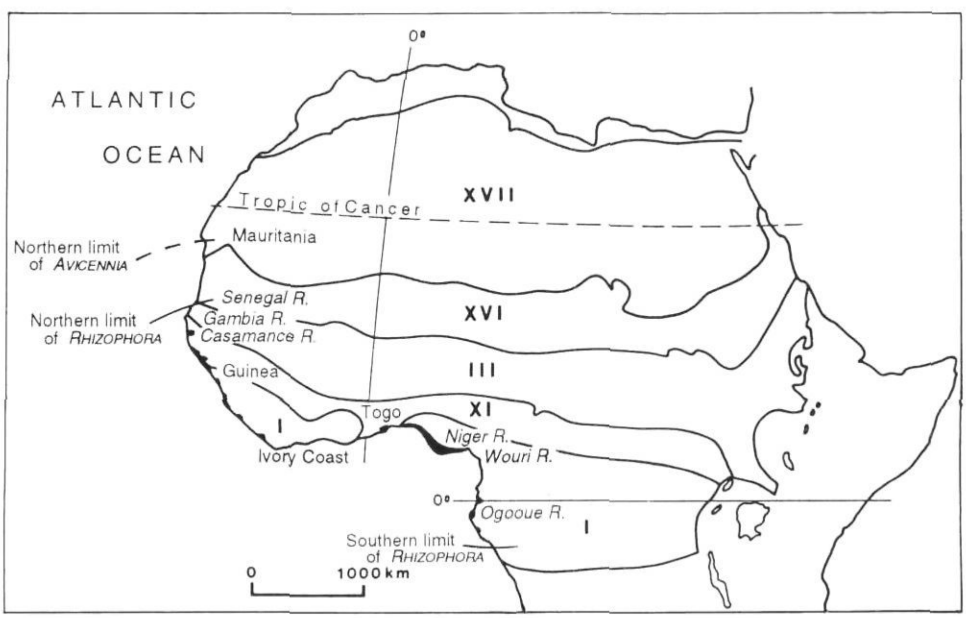

FIGURE 1. Distribution of *Rhizophora* and *Avicennia* in West Africa (adapted from Muller and Caratini,1977, and White, 1983). Roman numbers refer to the vegetation zonation described by White inluding from south to north: I: Guineo-Congolian centre of endemism; XI: Guineo-Congolian/ Sudanian transition zone; III: Sudanian centre of endemism; XVI: Sahelian transition zone; XVII: Saharan transition zone. Extent of mangroves is figured in black.

Répartition actuelle de Rhizophora *et* Avicennia *en Afrique occidentale (adapté de Muller et Caratini, 1977, et White,1983). Les chiffres romains réfèrent à la zonation de la végétation de White, avec du sud vers le nord : I : centre d'endémisme guinéo-congolais ; XI : zone de transition guinéo-congolaise/soudanienne ; XVII : zone de transition du Sahara. La mangrove apparaît en noir.*

(Muller, 1959) and the predominantly anemophilous dispersion of their pollen grains (Tomlison *et al.*, 1979)

Rhizophora represents between 70 and 90% of the total pollen sum in soil surface sediment samples from well developed mangroves at the mouth of the Ogooué (Aoutin, 1967), Wouri (Boyé *et al.*, 1974), Niger (Sowunmi, 1981) and Casamance rivers (Tissot *et al.*, 1983), and remain high (46%) in a sample from a restricted formation located south of the Senegal River delta (Lézine, 1988; Lézine and Hooghiemstra, 1990). It rapidly decreases with the distance: only 0,3% of *Rhizophora* pollen are recorded in the rear-mangrove from Togo (Edorh, 1986); in the Wouri estuary, *Rhizophora* decreases upstream from 90 to 5% in soil samples from the adjacent emerged area, and downstream to 30%; it may also be absent from some samples. In pollen spectra from the degraded formations of Lagune Adjin in the Ivory Coast (Frédoux, 1978), *Rhizophora* is often absent, and represents a maximum of only 30% in one sample.

In spite of its anemophilous mode of dispersal, the occurrence of *Rhizophora* pollen in the nearby ocean seems to be primarily linked to river inputs: *Rhizophora* is absent from the aerosol samples from the Gulf of Guinea (Melia, 1984) and represents only 1,9% in samples from atmospheric traps collected off the coast of Senegal and Gambia (Caratini and Cour, 1980). Additional aerosol samples from the eastern Atlantic (Calleja *et al.*, 1993) record a scattered occurrence of *Rhizophora* pollen, the highest percentages of which, reached between latitudes 4° and 12°30'N, being no higher than 5 and 12%. In contrast, pollen transport of *Rhizophora* by the Senegal River in bottom sediment samples is notable as far upstream as 250 km (5%) and up to 400 km seaward into the Atlantic (9%) (Lézine and Hooghiemstra, 1990). The highest *Rhizophora* percentages are recorded in sediments collected at a short distance from the coast off the source areas in Sierra Leone between 6 and 10°N latitude (Hooghiemstra and Agwu, 1986) (60%). They represent more than 30% in the Gulf of Guinea, off the well developed *Rhizophora* formation of the Niger delta (Dupont and Agwu, 1991), whereas they average only 6% (0-19%) off the Ivory Coast (Caratini *et al.*, 1987), where the corresponding formation are strongly reduced. Toward the north, *Rhizophora* percentages decrease to 18 and 12% off the less important mangrove extensions of the Casamance, Gambia and Senegal rivers (Hooghiemstra and Agwu, 1986). The percentages rapidly decrease seaward to 2% off Sierra Leone, and to 5% in the Gulf of Guinea (Melia, 1984).

Other specific mangrove taxa such as *Avicennia* and *Acrostichum aureum* are rare in soil and bottom sediment samples, even in those from the corresponding vegetation associations. When present, they reach a maximum value of 2% of the total pollen sum, as recorded in samples from the Ivory Coast (Frédoux, 1978; Caratini *et al.* , 1987) and from the Wouri (Boyé *et al.*, 1974) and Ogooué (Aoutin, 1967) rivers. Finally, owing to the homogenous character of their pollen morphology, it does not seem possible to distinguish *Laguncularia* and *Conocarpus* from the other Combretaceae pollen, even though the small size of *Conocarpus* (less than 15 µm) (Guers, 1970) can be indicative.

THE LATE QUATERNARY RECORD

a) THE GEOLOGICAL CONTEXT: THE LATE QUATERNARY SEA-LEVEL FLUCTUATIONS

Sea-level fluctuations along the West African continental shelf since the Last Glacial Maximum (LGM) have been described from shells, beach and littoral peat deposits (Pirazzoli, 1991). Although the associated radiocarbon dating probably needs more accurate calibration (Bard *et al.*, 1990), these deposits suggest that the sea level during the LGM was −110 m (Mc Master *et al.*, 1970) or −102 m (Einsele *et al.*, 1977) below the present level, which agrees with more recent estimates based on $\delta^{18}O$ measurements on planktonic foraminifera from two Eastern Atlantic deep-sea cores (Bard *et al.* 1989). The postglacial sea-level rise was rapid in spite of probable slowdowns recorded notably between 15 and 11 ka (*e.g.* Martin and Delibrias, 1972; Delibrias, 1974), and then also around 8 ka. The present level was reached *ca.* 6,5 ka (Faure *et al.*, 1980) and then experienced minor fluctuations: two transgressive episodes of about 1 or 2 m above the present level have been recognized in the northern sector, along the coasts of Senegal and Mauritania around 5,5 ka, the Nouakchottian (Elouard, 1968), then around 3 ka, the Tafolian (Hébrard, 1972) (Fig. 2).

b) THE REGIONAL RECORD OF PAST CLIMATIC VARIATIONS

Late Quaternary paleoclimatic reconstructions for West Africa deduced from continental and oceanic records have demonstrated the great sensitivity of the tropical and equatorial ecosystems to changes in rainfall and temperature. These have been clearly related to general circulation mechanisms (COHMAP, 1988) and particularly to changes in the North Atlantic SST field (DeMenocal and Rind, 1993).

At the onset of the deglaciation *ca.* 14 ka BP, pollen data indicate that some montane forests components lowered by 500 m or more in Equatorial West Africa, recording a substantial cooling, the estimation of which varies according to the authors between 2 and 6°C (Maley, 1991; Elenga *et al.*, 1991; Elenga, 1992). At the same time, the southward displacement, down to 10°N latitude of lowland open vegetations such as *Acacia* woodlands or wooded grasslands (Aubréville, 1949), the considerable extension of the Saharan desert (Sarnthein, 1978), together with the local degradation of the equatorial forest (Maley and Livingstone, 1983; Lézine and Le Thomas, 1995) point to dry conditions that have been related to enhanced continental trade wind circulation (Leroux, 1990). This was also responsible for the large amount of both dust removed from extensive denuded areas (Kolla *et al.*, 1979) or from dried lakes (Pokras and Mix, 1985) and pollen grains from Saharan and Sahelian ecoclimatic zones (Lézine *et al.*, 1994; Hoghiemstra 1988; 1989) and transported to the ocean. The humidity increased since *ca.* 12,5 ka as shown by the first discharges of the Niger and Senegal rivers recorded in the Atlantic (Pastouret *et al.*, 1978, Sarnthein *et al.*, 1982) to a maximum registered around 9-8,5 ka leading for the northward displacement of forests, 400-500 km from their modern position, the reduction of desert areas and

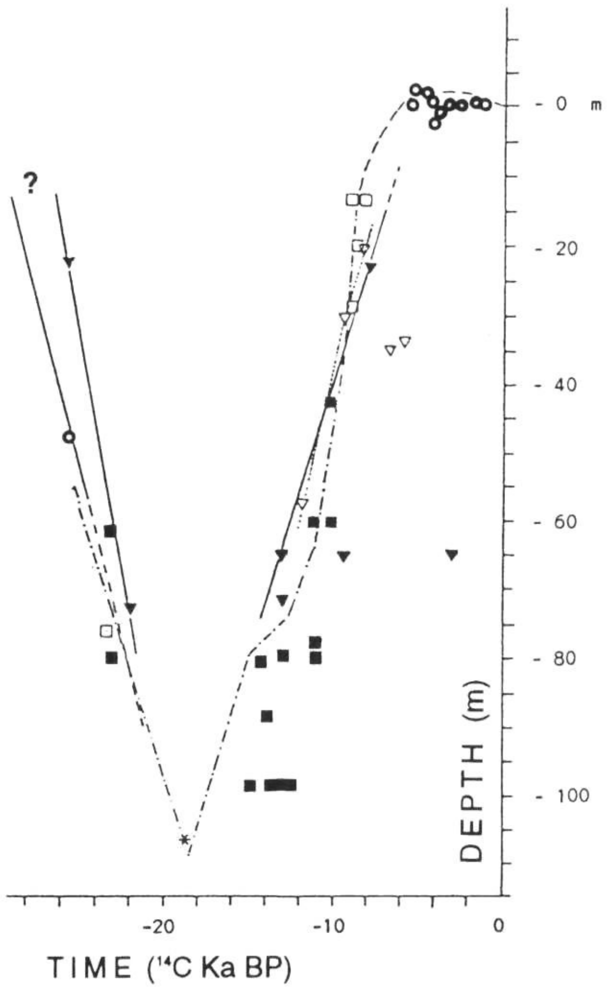

FIGURE 2. Schematic curve of late Quaternary sea-level fluctuations after Faure and Elouard (1967) (white circle), Mc Master *et al.* (1970) (star), Martin and Delibrias (1972) (black square), Delibrias (1974) (white square), Einsele *et al.* (1977) (black triangle), Pinson-Mouillot (1980) (white triangle).

Schéma des variations du niveau de la mer au Quaternaire récent le long de la côte ouest africaine d'après Faure et Elouard (1967) (cercle vide), Mc Master et al. *(1970) (astérisque), Martin et Delibrias (1972) (carré noir), Delibrias (1974) (carré vide), Einsele* et al. *(1977) (triangle noir), Pinson-Mouillot (1980) (triangle vide).*

widespread lake extension (Lézine and Casanova, 1989; Petit-Maire and Riser, 1981). This climate amelioration since 12,5 ka was clearly linked to the enhanced Atlantic monsoon circulation (COHMAP, 1988). However several short periods of return of dry conditions are recorded during the glacial-deglacial transition, such as that probably coeval with the Younger Dryas chronozone centered near 10,3 ka and marked by low lake-levels and inputs of dust and pollen to the ocean as important as those recorded at the onset of the deglaciation (Gasse *et al.*, 1990; Lézine *et al.*, 1994; 1995). The middle and late Holocene was humid, characterized by the widespread development of Sudanian vegetation associations probably reflecting the appearance of a well marked dry season. Episodes of dryness were recorded, notably *ca.* 7,5 ka (Lamb *et al.,* 1995), while the modern climate conditions were definitively established at 2 ka (Lézine and Casanova, 1989).

Mean annual sea surface temperatures (Mix *et al.*, 1986) remained high in the Gulf of Guinea since the Last Glacial Maximum, above 25°C and peaked at 26-27°C near 6 ka BP. Off North West Africa however, the influence of the Canaries Current and the regional upwelling induced the persistence of cool water (<16°C) until 8 ka, which is corroborated by recent dinoflagellate cyst studies carried out off Morocco near 34°N (Marret and Turon, 1994). The coastal upwelling decreased southward: off Senegal, near 15-16°N, the dinoflagellate cyst assemblages from the Late Glacial Maximum did not record noticeable changes compared to the modern situation (Lézine *et al.*, 1995), suggesting that the glacial-deglacial sea surface temperature difference previously estimated around 6°C in this area (Ericson *et al.*, 1956) was certainly overestimated.

c) THE POLLEN DATA

1) The littoral sediments and near-shore marine records

The abundance of mangrove pollen records from littoral and near-shore sediments suggests a former extension of *Rhizophora* populations along the West African coasts. However, the irregular and often truncated nature of the sediments in such specific environments does not permit a continuous record of the mangrove history during the last deglaciation but gives "windows" on detailed episodes primarily linked to the sea-level fluctuations (Fig. 3).

The earliest evidence of mangrove is given by the analysis of a peat layer from core A10 (5°08'N, 4°21'W) recovered on the slope of the continental shelf of Ivory Coast. Assémien *et al.* (1970) do not specify the exact percentages reached by mangrove pollen taxa but note the predominance of *Rhizophora* in the pollen spectra and interprete the data as recording the occurrence of a well developed mangrove –60 m below the present level at 11 900±125 BP. In core N-110Z off Senegal (15°17'N, 16°56'W) pollen and sedimentological studies indicate that mangrove was present -51/-52 m below the present level near 11 500 BP; however, *Rhizophora* percentages do not exceed 36% in this core, suggesting that mangrove did not reach a large extension near the core site. *Rhizophora* reached *ca.* 92% in a peat layer recovered at –38 m from core IVCO 3 (5°06'N, 3°31'W) dated from 9625±125 BP (Frédoux and Tastet, 1976). The other littoral deposits described as mangrove deposits in this area but containing only few mangrove pollen grains (less than 20%) (Frédoux and Tastet, 1976; Frédoux, 1977) have not been taken into account in this study.

A more continuous record of mangrove occurrence is given by the Keur Marsal pollen sequence from the rear-delta of the Senegal River (16°32'N, 16°15'W) (Médus and Monteillet, 1981): twelve levels taken at 1 to 4 m intervals through a long section of 34 m dated between 9920±180 and 4360±110 BP yielded percentages varying from 0,3 to about 70%. However, the irregular nature of the sedimentation in such a fluviatile environment and the paucity of studied levels do not permit to precise the chronology of the mangrove evolution in this

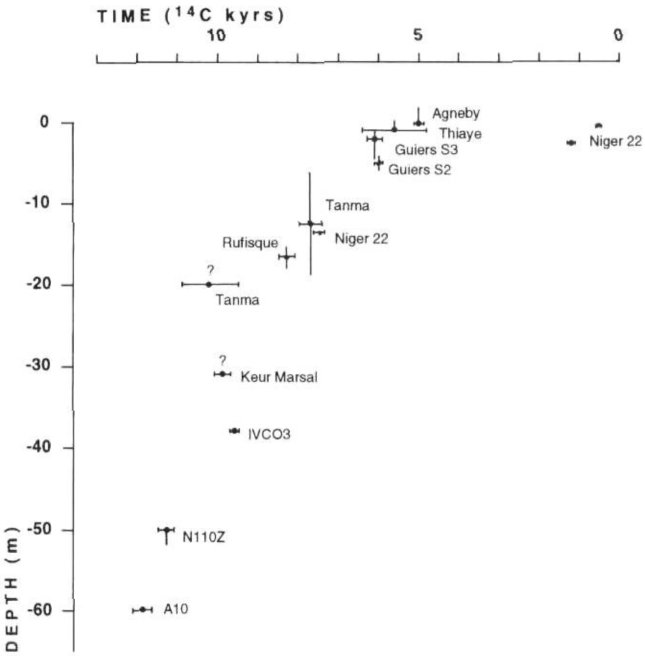

FIGURE 3. ^{14}C measurements on littoral and near-shore mangrove deposits of North West Africa figured versus depth (below present sea-level and time and recording the postglacial sea-level rise. The measurements correspond to samples characterized by significant *Rhizophora* percentages (around 40% or more). Question marks indicate doubtful samples either because of their age or because of their pollen content.

Datations au ^{14}C des dépôts littoraux (tourbes de mangrove) selon la profondeur (sous le niveau marin actuel) et le temps. Les datations correspondent aux échantillons contenant un pourcentage suffisant de grains de pollen de Rhizophora *(autour de 40 % et plus). Les points d'interrogation indiquent les échantillons douteux soit en raison de la qualité des datations, soit en raison de leur contenu pollinique.*

area. At Tanma (14°55'N, 17°30'W) (Médus *et al.*, 1981; Médus, 1984) several sedimentary sequences studied for pollen and sedimentological analyses suggest two successive phases of mangrove extension linked to probable slowdowns in the sea-level transgression and characterized by high accumulation rates. The best recorded phase is dated from *ca.* 7800 BP between –12 and –19 m depth in core 3 and between –15 and –7 m in core 4. This may indicate the position of the sea-level at a depth averaging –10 m below the present level (see discussion *in* Lézine, 1985). The earlier phase recorded at –28/–20 m depth and centered near 10 000 BP seems to be more questionable, taking into account the low quality of the ^{14}C measurements (Lézine, 1985). In Rufisque Bay, core 40-S52, recovered at –15 m water depth (14°37'N, 17°13'W) (Dumon *et al.*, 1977), records the continuous occurrence of *Rhizophora* pollen with high percentages (60 to 80%) through the two upper metres of the core, which indicates a local mangrove extension *ca.* 8100 BP related to the position of the sea-level *ca.* –15 m below the present level.

The latest, well documented episode of large mangrove extension depicted from near-shore and littoral sediments is that related to the Nouakchottian transgression: *Rhizophora* pollen percentages reached 85% in the corresponding levels (between –6.5 m and –3.95 m downcore) from core Guiers S2 (16°07'N, 15°55'W) taken east of the Senegal River delta (Lézine, 1988). This indicates, according to modern pollen transport and deposition patterns, that *Rhizophora* populations developed near the shore of the Guiers Lake, about 150 km east of the present coast-line. In addition, the Nouakchottian levels from the Bogué record (16°35'N, 14°17'W) recovered in the Senegal river bed (Michel and Assémien, 1970) show the coeval extension of the marine influence 500 km upstream with a maximum of 19-34% of *Rhizophora* pollen.

Similarly, the Nouakchottian is recorded in the peaty depression of Thiaye in Senegal (14°56',N 17°29'W) (Lézine *et al.*, 1985), where sediments between –2 and –0.5 m depth dated between 6400 and 4800 BP contain a large amount of *Rhizophora* (58 to 80%), as well as in the Agneby swamp of the Ivory Coast (5°20'N, 4°15'W) (Assémien, 1971): in the latter site, *Rhizophora* is associated with *Avicenia* and *Acrostichum,* the highest percentages of which are reached at a depth of *ca.* –2 m. In both cases, pollen data indicate the development of littoral populations inland, 7 to 20 km from the present shore line, and the position of the sea-level close to the present one.

These data point to the widespread Holocene extension of the mangrove in West Africa, notably at the northern edge of its modern area of distribution, in Senegal (Fig. 4, Table I). This is confirmed by the pollen records from the fresh-water interdunal depressions of the Niaye area located behind the Atlantic coastal strand between 14°55'N and 15°45'N (Lézine, 1987) and from core N-110Z (Lézine *et al.*, 1995) which show evidence of continuous input of *Rhizophora* pollen from 12 000 to 2000 BP. Mangrove developed at the mouth of the large rivers such as the Senegal and Casamance rivers (at Tobor and Balingor, Tissot *et al.*, 1983) as well as in paleovalley (Tanma Lake-Thiaye) and in protected areas (Rufisque Bay) where it is nowadays absent. These, together with other mangrove deposits along the slope of the continental shelf off the Ivory Coast and at the mouth of the Niger River (Sowunmi, 1981) give evidence for the former sea-level position. Uncertainties illustrated by the large error barres in Figure 3 are related to the specificity of the mangrove sedimentation characterized by high accumulation rates, such as in the Niger delta (around 2 mm year^{-1}; Sowunmi, 1981), notably during

TABLE I

Littoral deposits sites of Senegal

Site	Lat., Long.	References
Guiers S2	16°07'N, 15°55'W	Lézine A.M. (1988).
Keur Marsal	16°32'N, 16°15'W	Médus and Monteillet (1981)
N110-Z	15°17'N, 16°56'W	Pison-Mouillot (1981) Lézine *et al.* (1995)
Tanma 1-4	14°55'N, 17°30'W	Médus *et al.* (1981) Médus (1984)
Thiaye	14°56'N, 17°29'W	Lézine *et al.* (1985)
Bay of Rufisque	14°37'N, 17°13'W	Dumon *et al.* (1977)
Balingor/Tobor	~12°40'N, 16°30'W	Tissot *et al.* (1983)

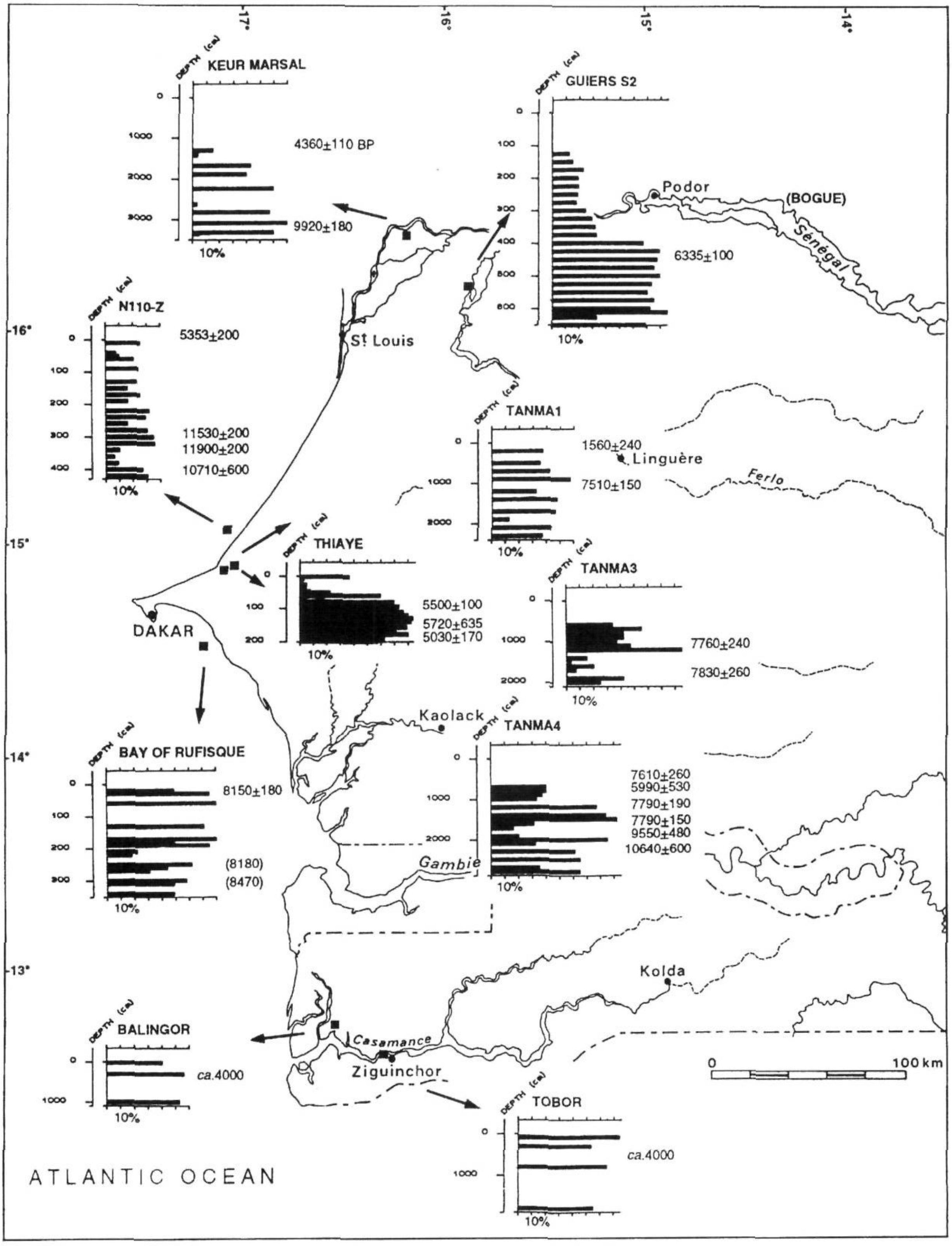

FIGURE 4. Pollen representation of the genus *Rhizophora* in the littoral deposits of Senegal. Each diagram corresponds to a studied site. From left to right are figured the depth (in centimetres), the percentages of *Rhizophora* calculated against the total pollen sum per sample and the ^{14}C apparent ages as indicated in the literature.

Représentation pollinique du genre Rhizophora *dans les sédiments littoraux du Sénégal. Chaque diagramme correspond à un site étudié. Sont représentés, de gauche à droite, la profondeur (en centimètres), les pourcentages de* Rhizophora *calculés sur le total des grains de pollen comptés par échantillon et les âges au ^{14}C apparents, tels qu'indiqués dans la littérature.*

phases of sea-level stabilization such as at Tanma and the lack of precision of the chronology in ancient litterature which does not necessary take into account the fluctuations of the atmospheric ^{14}C during the period studied (Suess, 1970).

2) The deep-sea records (fig. 5, table II)

Percentages of *Rhizophora* in deep oceanic records from 4°N to 16°N exhibit similar trends: Core M-12345-5 (Rossignol-Strick and Duzer, 1979) recovered off Senegal at 15°28'N and 17°21'W shows a maximum of 40% at 145 cm downcore dated from the beginning of the Holocene ca. 9500 BP (Sarnthein *et al.*, 1982). Then, percentages decrease toward the top to 6%. Levels below 145 cm, dated from the Late Glacial Maximum contain low percentages, often less than 1%. A similar peak of *Rhizophora* at levels dated from 9500-10 000 BP is recorded in the Gulf of Guinea, in cores KS-84063 (4°23'N, 4°11'W) with percentages reaching 38% at 380 cm downcore (Lézine and Le Thomas, 1995) and KS-12 (3°52'N, 1°56'W) with 40% at 95 cm (Lézine and Vergnaud-Grazzini, 1993). In these cores, however, percentages of

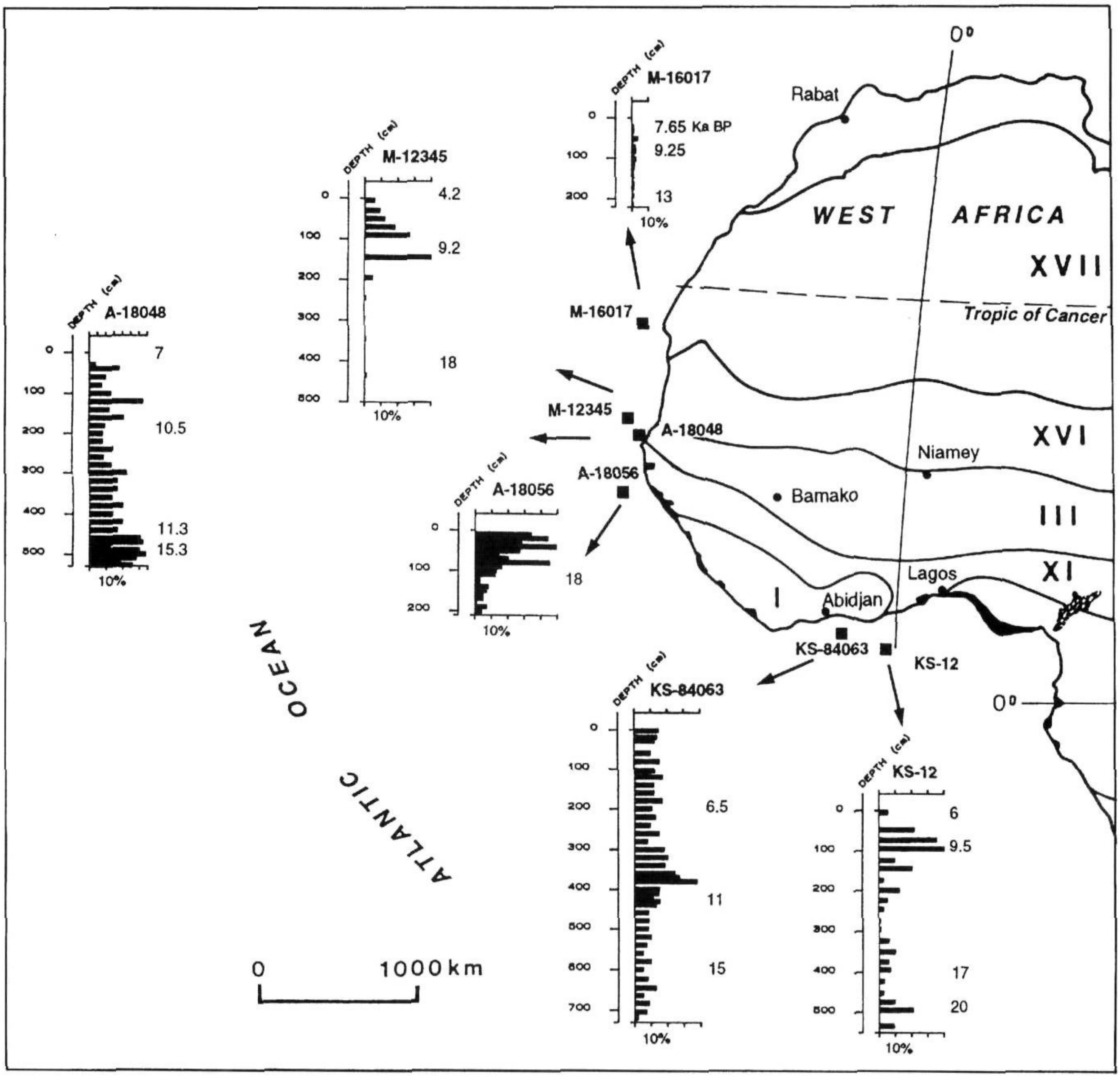

FIGURE 5. Pollen representation of the genus *Rhizophora* in deep-sea sediments off North West Africa (see Fig. 4 for caption). Except for core A180-48, the ^{14}C ages are inferred from the isotopic curve for each sequence studied. In the vegetation map of West Africa drawn after White (1983) (see Fig. 1), the doted area represents the montane vegetation of Cameroon highlands.

Représentation pollinique du genre Rhizophora *dans les sédiments marins profonds au large de l'Afrique nord tropicale (voir la légende à la fig. 4). Les âges sont déduits des courbes isotopiques, sauf pour la carotte A180-48. Sur la carte de végétation dessinée d'après White (1983) (voir la fig. 1), la végétation de montagne (monts Cameroun) apparaît en pointillé.*

TABLE II

Cores in deep-sea sediments off North West Africa

Core	Lat., Long.	Reference
M-16017	21°15'N, 17°48'W	Hooghiemstra (1988)
M-12345-5	15°28'N, 17°21'W	Rossignol-Strick and Duzer (1979) Sarnthein *et al.* (1982)
A-18048	15°19'N, 18°06'W	Ericson *et al.* (1956) Lézine *et al.* (1995)
A-18056	12°14'N, 17°46'W	CLIMAP (1976)
KS-84063	4°23'N, 4°11'W	Lézine *et al.* (1994) Lézine and Le Thomas (1995)
KS-12	3°52'N, 1°56'W	Lézine and Vergnaud-Grazzini (1993)

Rhizophora remained significant at levels dated from the Late Glacial Maximum and increased during deglacial times, between 2 and 15% in KS-84063, and between 1 and 13% in KS-12. Core A-18056 recovered off the Casamance River delta (12°14'N, 17°46'W) exhibits a similar trend with percentages from 3% at the onset of deglaciation to 49% at the beginning of the Holocene; uncertainties remain, however, owing to the lack of precise chronology in this core.

Mangrove pollen is also regularly present, with percentages between 4 and 32%, in core A-18048, recovered near the bottom of the submarine Canyon of Cayar at the foot of the continental shelf off Senegal (15°19'N, 18°06'W). The different pattern of *Rhizophora* occurrence recorded through this core, compared to those described above, is due to the irregular sedimentation rate varying from 0.04 cm yr^{-1} during the Holocene to 0.27 cm yr^{-1} during the deglaciation (Lézine *et al.*, 1995), linked to the core site.

North of the modern boundary of *Rhizophora* distribution, core M-16017-2 (21°15'N, 17°48'W) (Hooghiemstra, 1988) records continuous occurrence of *Rhizophora* pollen through a sequence dated between *ca.*13 000 and 5000 BP, with maximum percentages reached at levels dated between 9500 and 8500 BP. Even though percentages do not exceed 2% in this core, they may indicate pollen transport from the nearby littoral and correspond to the mangrove that nowadays remains only as a relict population near Cap Blanc. Owing to the main eolian path predominantly of NE-SW direction in this area, it seems difficult to link the occurrence of *Rhizophora* pollen at this latitude to the mangrove formations of the Senegal River delta located 5° of latitude to the south.

CONCLUSION

Pollen records reported here suggest a wide extension of the mangrove along the West African coast up to 21°N testifying to climate conditions wetter than today from at least 13 000-12 000 BP to *ca.* 2000 BP. Comparison between near-shore and deep oceanic data points to distinct signals:

1) The near-shore pollen assemblages, interpreted according to the modern deposition pattern of *Rhizophora* pollen, record the extension of the mangrove linked to the sea-level transgression: the curve of sea-level rise deduced from these data fit well into the general context of global sea-level variations during the last deglaciation even though the associated ^{14}C measurements need more acurate calibration. The mangrove occupied large flat areas along rivers and paleorivers banks. It also occurred in less favourable areas. The best recorded phase of mangrove development corresponded to a low amplitude sea-level rise of +1 or 2 m above the present level near 5500 BP. The regional climate at this time was however of Sudanian character, dominated by a well marked dry season (Lézine, 1989).

2) The deep oceanic sequences show that the mangrove was strongly reduced during the Late Glacial Maximum at nowadays Sahelian latitudes (16°N) but never disappeared southward, from the Gulf of Guinea, which indicates the persistence of both fresh-water occurrence near the littoral in spite of the regional drought and compatible oceanic conditions regarding notably sea surface temperatures.

During the glacial-deglacial transition, pollen signal of mangrove development in deep-sea sediments agrees well with the first evidences of increased Senegal and Niger river discharges to the ocean dated from 12 500 BP in response to the enhanced Atlantic monsoon circulation over West Africa. The *Rhizophora* peak at *ca.* 10 000-9500 BP represents a specific deep-sea pollen signal, since it has not been recorded in near-shore and littoral deposits. It illustrates the first regional response of the tropical vegetation to the global climatic amelioration during the last deglaciation.

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