CHAPTER 5

Timing and nature of the end of the African Humid Period in the Sahel: Insight from pollen data

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ABSTRACT: Pollen, spores, and algae from a 4m-long sediment core at the Mboro-Baobab site (15°8′58.49″N, 16°54′34.37″W), in the Niayes region of Senegal were used to provide a record of the end of the African Humid Period (AHP) in the western Sahel. We show that the drying of the Mboro-Baobab landscape was gradual, starting from 3750 cal yr BP then culminating at 1300 cal yr BP. In contrast, the response of the lake system and the gallery forest developed in two main phases: the sharp decline of tropical humid forest elements at 3200 cal yr BP followed by the almost complete collapse of the gallery forests at 2500 cal yr BP. Our results are consistent with those from the central Sahel, which show a gradual transition from the AHP to the modern landscape.

5.1 INTRODUCTION

At the end of the African Humid Period (AHP), tropical North Africa experienced a major environmental crisis. The southward displacement of the desert margin (Kuper and Kröpelin 2006) with the related loss in biodiversity (Hély *et al.* 2014; Watrin *et al.* 2009) along with the decline of wetlands (Lézine *et al.* 2011) had dramatic consequences for human populations through a decline in population density, cultural adaptations with the development of pastoralism and migrations toward the main rivers (Nile, Senegal, Niger) (Manning and Timpson 2014 and references therein) and the Equatorial forest block (Lézine *et al.* 2013). How long was this transition from a "green Sahara" to the hyper-arid desert of today? This question remains largely unanswered, as the number of palaeorecords with adequate temporal resolution and age control is low and often contradictory. Based on marine records, deMenocal *et al.* (2000) showed that an abrupt increase in dust transport to the ocean between 5579 and 5299 cal yr BP marked the end of the AHP in the Saharan desert. Studies in the central Sahara suggested that the modern desert was definitely established at 2700 cal yr BP after a period of gradual drying likely originating from the mid-Holocene and intensifying at 4300 cal yr BP (Kröpelin *et al.* 2008; Lézine *et al.* 2011; Lécuyer *et al.* 2016).

In the Sahel, interdunal depressions of Senegal and Nigeria provided detailed records of environmental change during the AHP (Lézine 1988; 1989; Salzmann and Waller 1998; Waller *et al.* 2007). The presence of a water table near the surface favored the development of forest galleries along water bodies. However, pollen studies suggest a contrasted situation: in Senegal, an abrupt change *c*. 2500 cal yr BP, interpreted as the crossing of a biological threshold, brought about the destruction of the forests and the decline of tropical humid elements (Lézine 1989).

In Nigeria, the modern vegetation was established earlier, c. 3300 cal yr BP (Salzmann and Waller 1998). However, new data from Jikaryia Lake (Waller et al. 2007) suggest that "rather than a single abrupt event, Late Holocene aridification appears to have occurred progressively" from 4700 cal yr BP onward. Here we present a new and high-resolution pollen record from Mboro-Baobab in the "Niayes" coastal region of Senegal (15°8′58.49″N, 16°54′34.37″W). We focus on the period between 4300 cal yr BP (the base of the Mboro-Baobab pollen sequence) and the last millennium, which has been the subject of a separate publication (Lézine et al. 2019). Our goal is to determine whether the transition from AHP to the present was abrupt or gradual in this area, to discuss the turnover of species and the response times of forest trees to changes in hydrological conditions.

5.2 GENERAL SETTING

Niayes are interdunal depressions with accumulations of organic sediments, formed between linear fixed and partially fixed coastal dune ridges, located along the Atlantic coast between 15° N and 16° N, at roughly 17° W. The mean annual rainfall (369 mm) is characteristic of the Sahel, but in response to local soil moisture conditions, the depressions support an array of plant communities that include an azonal extension north of Guinean humid forests and Sudanian dry forests and wooded grasslands (Trochain 1940) (Figure 1A).

The Mboro-Baobab depression is located 2.3 km from the seashore west of the Mboro paleoriver (Figure 1B), at the edge of the central zone of the Niayes where the sub-surface aquifer is the most developed (Putallaz, 1964). The Mboro-Baobab depression is 570 m long and 310 m wide. To the south, it is covered with vegetation and partially exploited for agricultural purposes.

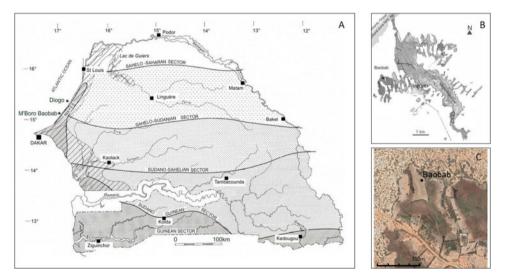


Figure 1. (A) vegetation map of Senegal from Trochain (1940) showing the azonal position of the Niayes along the Atlantic Ocean, north of the Dakar peninsula. Trochain described the vegetation of the Niayes as belonging to a "sub-Guinean domain" owing to its strong relation with the Guinean (rain) forests today found in the Casamance region, south of Senegal. (B) Location map of the Mboro-Baobab interdunal depression west of the Mboro paleoriver channel. In gray, inundated sectors (ORSTOM 1962). (C) Satellite image showing the Mboro-Baobab depression surrounded by dunes fields covered with Sahelian vegetation. The localization of the core in the northern part of the depression is shown.

Its northern part is an open water basin of 270 m by 90 m wide and 0.4 m maximum depth (Figure 1C). Mboro-Baobab is currently filled by brackish waters and occasionally desiccated.

5.3 MATERIAL AND METHODS

A 4 m long core was collected near the northeastern shore of the open water basin using a manual Russian corer (Jowsey 1966) in 2016 (Lézine et al. 2019). It was divided into 8 sections of 50 cm each. The sediment consists of homogeneous organic clay. Samples (1 cm³ each) were taken at 5 cm intervals for pollen and non-pollen palynomorphs (NPP = freshwater algae (*Pediastrum*, Botryococcus, Coelastrum, Scenedesmus, Tetraedron and undifferentiated fungi) analyses, They were processed using the standard HF method described by Faegri and Iversen (1977). Pollen identification was based on the reference slide and photo collections of the LOCEAN laboratory and the Musée National d'Histoire Naturelle in Paris as well as on pollen atlases of tropical African flora from e.g. Maley (1970), APLF (1974), Ybert (1979) and Bonnefille and Riollet (1980). Pollen nomenclature, which follows the standard defined by the African Pollen Database (Vincens et al. 2007), was based on Lebrun and Stork (1991-2015). The pollen spectra was composed of 105 taxa among which 57 trees, shrubs, lianas and palms, 21 herbs, 16 undifferentiated (trees, shrubs or herbs), 7 aguatics and 4 ferns (Table 1). Pollen taxa have been grouped according to the phytogeographical affinity of the parent plants following Trochain (1940) and White (1983) (Table 1).

Table 1. Mboro-Baobab pollen taxa. A: trees: AL: tree/lianas: L: lianas: I: undifferentiated: N: herbs: Ng: aquatics. Nomenclature from the African Pollen Database. According to Vincens et al. (2007) a "type" is added to the name of the taxon (1) to the genus when several plant genera display similar pollen morphology. The species name can be added in case of monospecificity or when the species is dominant or characteristic in the study area (2) to the species when, the genus being clearly identified, several species can be concerned. SH: Saharan. SL: Sahelian; SU: Sudanian; GU: Guinean.

Family	Taxon	Life form	SH	SL	SU	GU
ACANTHACEAE	Hygrophila	N			X	
	Justicia-type	I		X	X	
	Justicia-type flava	N		X	X	
AMARANTHACEAE	Achyranthes-type aspera	N	Х	Х		
	Aerva-type lanata	N	X	X		
	Alternanthera	N	X	X		
	Amaranthaceae undiff.	I	X	X		
	Celosia-type trigyna	N	X	X		
	Chenopodium-type	N	X	X	X	
	Gomphrena	N	X	X		
	Suaeda	I	X	X		
ANACARDIACEAE	Anacardiaceae undiff.	A			X	X
	Lannea-type	A		X	X	X
APIACEAE	Apiaceae undiff.	I		х	X	

(continued)

Table 1. Continued.

	Table 1. Continued.					
Family	Taxon	Life form	SH	SL	SU	GU
APOCYNACEAE	Apocynaceae undiff. Tabernaemontana	I AL	X	X	X X	х
ARECACEAE	Elaeis guineensis Phoenix reclinata-type	PA PA	x	x	x	X X
ASCLEPIADACEAE	Gymnema	AL	X			
ASTERACEAE	Asteraceae undiff. Centaurea-type perrottetii Cichorieae undiff.	I N I	X X X	X X X	x x	
BOMBACACEAE	Adansonia digitata	A			X	х
BURSERACEAE	Commiphora africana-type	A		X	X	
CAESALPINIACEAE	Detarium senegalense	A			X	X
CAPPARACEAE	Capparis fascicularis-type Cleome-type gynandra	AL N	X	X X	X	
CARYOPHYLLACEAE	Caryophyllaceae undiff. Cerastium-type Polycarpaea-type Polycarpon-type	I N N N	x x x x	x x x x	x x	X
CASUARINACEAE	Casuarina equisetifolia-type	A				
CELASTRACEAE	Celastraceae undiff. Salacia	AL AL	X	X	X X	X
CHRYSOBALANACEAE	Chrysobalanus/Parinari	A			X	х
COMBRETACEAE	Combretaceae undiff.	A		X	X	X
COMMELINACEAE	Commelina-type benghalensis Commelina-type forskalaei	N N	X	X X	X	X
CONVOLVULACEAE	Convolvulus-type Ipomoea-type	N I	X X	X X	X X	
CYPERACEAE	Cyperaceae undiff.	Nq				
DILLENIACEAE	Tetracera	AL			X	х
EBENACEAE	Diospyros Ebenaceae undiff.	A A			X	Х
EPHEDRACEAE	Ephedra	AL	Х			

(continued)

Table 1. Continued.

	_	Life	_	_		
Family	Taxon	form	SH	SL	SU	GU
EUPHORBIACEAE	Acalypha	I			X	X
	Alchornea	A			X	X
	Anthostema-type	A				X
	Antidesma-type Bridelia-type	A A			X	X
	Erythrococca-type	A			X X	X X
	Hymenocardia	A		X	X	X
	Macaranga-type	A		••	X	X
	Mallotus-type	A			X	X
	Uapaca	A			X	X
FABACEAE	Aeschynomene	I			X	х
HALORRHAGACEAE	Laurembergia tetrandra	Nq				
LAMIACEAE	Basilicum-type polystachyon	N			X	
LORANTHACEAE	Tapinanthus-type	L		X	х	Х
MALVACEAE	Hibiscus	I	X	Х	х	
MELIACEAE	Khaya-type senegalensis	A				х
MENISPERMACEAE	Cissampelos-type	AL			х	Х
	Cocculus	L	X	X	X	
	Tinospora bakis	L	X	X	X	
MIMOSACEAE	Acacia	AL	X	x x		
	Prosopis-type africana	A		X	X	X
MORACEAE	Ficus	A		х	Х	
	Musanga-type	A		X	X	X
	Myrianthus-type	A				X
MYRTACEAE	Syzygium-type guineense	A			X	X
NYMPHAEACEAE	Nymphaea	Nq				
OCHNACEAE	Lophira	A			X	X
ONAGRACEAE	Ludwigia-type ascendens	Nq				
POACEAE	Poaceae undiff.	N	X	X	X	х
POLYGALACEAE	Polygala-type	I	X	X	X	
POLYGONACEAE	Polygonum senegalense	Nq				
POTAMOGETONACEAE	Potamogeton	Nq				

(continued)

Table 1. Continued.

Family	Taxon	Life form	SH	SL	SU	GU
RANUNCULACEAE	Clematis-type	AL	Х	Х	Х	
RUBIACEAE	Leptactina	A				X
	Hymenodictyon-type	A			X	X
	Ixora-type	A			X	X
	Mitracarpus villosus	N		X	X	
	Mitragyna-type inermis	A		X	X	X
	Morelia senegalensis	A		X	X	X
	Pavetta	AL			X	X
	Rubiaceae undiff.	I	X	X	X	X
	Spermacoce-type radiata	N		X	X	
RUTACEAE	Zanthoxylum-type zanthoxyloides	A			X	X
SALVADORACEAE	Salvadora persica-type	A	X	X		
SAPINDACEAE	Allophylus	AL		Х	X	X
	Paullinia pinnata	L			X	X
	Sapindaceae undiff.	AL		X	X	X
SAPOTACEAE	Sapotaceae undiff.	AL		Х	х	X
	Vitellaria-type paradoxa	Α				X
SOLANACEAE	Solanum-type	I	Х	X	X	
STERCULIACEAE	Dombeya-type	A			Х	X
TAMARICACEAE	Tamarix	A	х	X		
TILIACEAE	Triumfetta-type	I		X	X	
ТҮРНАСЕАЕ	Турһа	Nq				
ULMACEAE	Celtis	A		X	X	X
ZYGOPHYLLACEAE	Tribulus	N	X	X		

Data are presented as percentages and influx values (number of grains/cm²/year) and diagrams are drawn using Tilia and CONISS (Grimm 1991). Pollen percentages were calculated against a sum excluding aquatics and ferns, the percentages of which were calculated separately against a sum including all the pollen grains and fern spores counted. Algae and fungi percentages were calculated against the sum of NPP. Correspondence statistical analyses (CA) were performed on the raw pollen counts using the Package 'Rcmdr/FactoMinR' (Husson *et al.* 2020).

An age model was derived from three Accelerator Mass Spectrometry (AMS) radiocarbon dates and an additional control point given by the first occurrence of *Casuarina equisetifolia* pollen grains, the parent trees of which were planted in 1948 along the coast (Ndiaye *et al.* 1993), using the Bacon age-depth modeling (Blaauw and Christen 2011) from calibrated ¹⁴C ages (Reimer *et al.* 2013) (Table 2).

Lab.	Mean depth (cm)	Nature	Radiocarbon Age BP	Error	δ ¹³ C	Age cal yr BP
49827 49828	0 30.5 99.5 299.5	Date of coring Casuarina pollen Bulk sediment Bulk sediment	580 3265	30 30	-22.40‰ -28.60‰	-66 -2 604 3496
49829	399.5	Bulk sediment	3865	30	-29.10%	4298

Table 2. Mboro-Baobab ages. Radiocarbon dating (99.5 cm, 299.5 cm, and 399.5 cm) was conducted at UMS-ARTEMIS AMS Facilities (France). At 30.5 cm downcore, the first appearance of Casuarina equisetifolia pollen grains provide a date of 1948 CE. The age of the surface is that of coring (from Lézine et al. 2019).

5.4 POLLEN DIAGRAM

Based on the variations in percentages of the main pollen taxa and NPP types, four zones corresponding to the main phases of landscape evolution over the last 4300 years can be distinguished. Zones 3 and 4 were presented in detail in Lézine et al. (2019, Figure 2).

5.4.1 Zone 1A: 4300 – 3700 cal yr BP

Guinean tree taxa such as Mallotus (3%), Zanthoxylum (2.4%), Uapaca (2.5%), Alchornea (15%) and Macaranga (11%) characterized this zone. Lakeshore populations are reduced with Typha percentages less than 1%.

Among the NPPs, *Pediastrum* and *Coelastrum* are largely dominant with percentages that can reach values above 80% for Pediastrum and 30% for Coelastrum.

5.4.2 Zone 1B: 3700 – 3050 cal yr BP

There is little change from the previous zone. However, the forest taxa listed above decreased significantly (e.g. *Uapaca* (0.3%)). Other tree taxa such as *Lannea* (1.2%) and *Mitragyna* (1.2%) increased, along with taxa from lakeshore populations, Syzygium (7.2%) and Elaeis (1.2%). Upland herbaceous taxa, such as Amaranthaceae and Aerva, which were occasionally present in zone 1A, also increased. However, their percentages remained low (less than 1.5%).

Among the NPPs, this zone is characterized by the rapid development of *Tetraedron*, which reached up to 80% reflecting the onset of the lake level lowering.

5.4.3 Zone 2A: 3050 – 1600 cal yr BP

This zone is characterized by the sharp increase in Typha percentages (15%) and the more gradual increase of Cyperaceae (22.8%) showing the development of reed swamp populations around the lake. Among the trees, Mallotus or Uapaca gradually decrease to less than 0.5%, whereas Alchornea increased (16.5%). Dry herbaceous taxa, such as Mitracarpus and Spermacoce, already present previously, increased with percentages up to 4%.

NPP are characterized by the progressive increase in the percentages of *Botrycoccus*, (maximum = 17%).

5.4.4 Zone 2B: 1600 – 700 cal yr BP

Cyperaceae (23%) then *Elaeis* (2.6%) increased in this zone. Some tree taxa of Guinean affinity (Mallotus, Anthostema, Zanthoxylum, Celtis) or wetlands decreased or even disappeared

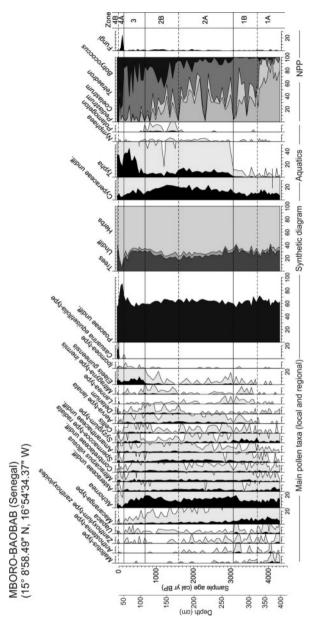


Figure 2. Figure showing from left to right, a simplified diagram of pollen percentages for Mboro-Baobab (Senegal). Black shading shows selected taxa. Light-gray shading shows the same results, multiplied by 10 for highlighting. On the right, the main NPP (Algae and Fungi) are shown.

almost completely, while others were stable (Alchornea 19%) or even increased (Detarium 2.1%, Mitragyna 1.6%). Typha percentages decreased significantly (5%) while another aquatic plant, Potamogeton (1.9%), appeared.

Among the NPPs, Tetraedron and Botryococcus continued to increase until reaching 85% and 47%, respectively.

5.4.5 Zone 3: 700 – 129 cal vr BP

Alchornea and Elaeis dominated this zone though following an opposite trend. Elaeis reached its highest value (12%) while Alchornea decreased steadily (minimum at 4.5%). Syzygium remained well represented (2%). Among read swamp populations, Typha increased remarkably, up to 35% and Cyperaceae decreased (7%). NPPs were dominated by *Tetraedron* (up to 90%) and Botryococcus (up to 60%).

5.4.6 Zone 4A: 129 -14 cal yr BP

This zone is characterized by the massive increase in Poaceae (90%) and the correlative decrease in Typha (17%). The percentages of Elaeis remained at the level reached in the previous area (7%). Botryococcus almost exclusively dominated the algae assemblage. This zone is also characterized by the noticeable presence of fungi.

5.4.7 Zone 4B: 14 cal vr BP - Modern

This zone differs from the previous one by the appearance of Casuarina equisetifolia, which reaches up to 16%. Poaceae decreased to 55%, in contrast to Typha, which increased to values above 30%. Botryococcus totally dominated the assemblages of algae.

5.5 ENVIRONMENTAL RECONSTRUCTION AND DISCUSSION

5.5.1 The decline in tropical humid plant taxa

Figure 3 is the graphical representation of a correspondence analysis using the microfossil assemblages for the environmental evolution of the Mboro-Baobab area. Three groups of taxa emerge from this analysis. The first is dominated by tropical humid (Guinean) tree taxa (e.g. Dictyandra, Macaranga, Mallotus, Syzygium, Uapaca), the second group is a mixture of taxa from trees and herbs of drier, Sudanian, phytogeographical affinity or having a wide spatial distribution (e.g. Alchornea, Asteraceae, Celtis, Mitracarpus). The third group is dominated by herbs found today in dry places in the Sahara and Sahel (e.g. Aerva lanata, Tribulus, Amaranthaceae). Only few trees are found in this group (e.g. Acacia, Adansonia digitata).

The most striking result of the analysis of these groups is the major environmental change revealed at 3200 cal yr BP (Figure 4A). The most humid tree taxa (group 1) which dominated earlier in the record, and particularly around 3875 cal yr BP (Figure 4B), dramatically declined in favor of drier plant taxa (group 2). This decline continued into the late Holocene in two main stages respectively around 2500 and 1300 cal yr BP. Contrasting with this step-like evolution of forest diversity, the regional, dry elements (group 3) exhibit a slow increasing trend starting from 3700 cal yr BP and peaking around 1600-1300 cal yr BP.

5.5.2 Changes in the hydrological regime

The 3200 cal yr BP event closely matches a major change in the hydrological regime (Figure 4C): changes in the algal community show that the lowering of the water level was initiated as soon as 3750 cal yr BP (cf. expansion of Tetraedron, Figure 2). At 3200 cal yr BP, the development of the oligotrophic algae Botryococcus (Figure 2 and 4C) mark the reduction in nutrient supply due to increasingly dry conditions, which culminated during the last millennium. The strong decline in the freshwater algae Pediastrum and Coelastrum, followed by the development of Typha populations, confirms this major change in the hydrological regime and the lowering of the lake level.

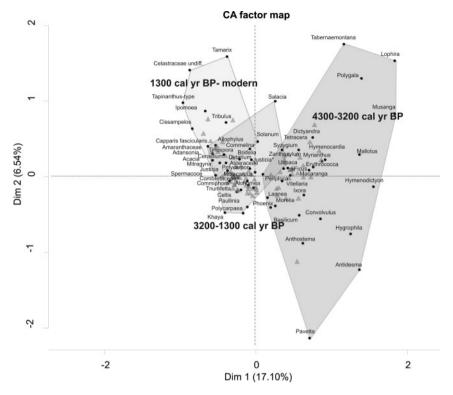


Figure 3. Correspondence analyses on the Mboro-Baobab pollen counts allowing distinction of tree main groups of taxa according to a decreasing humidity gradient. These groups define three periods (in bold).

5.5.3 Timing of the end of the AHP in the Sahel

Earlier work by Lézine (1988, 1989) in the Niaves suggested the sudden disappearance of the gallery forests around 2500 cal yr BP as illustrated at Diogo, only a few kilometers north of Mboro (Figure 1A). Diogo illustrates the magnitude of this environmental crisis by showing the drop in the water level allowing for the development of a Cyperaceae swamp contemporaneous with the collapse of most of the trees, which established during the AHP (Figure 5). Only swamp forest (Syzygium) and pioneer (Alchornea) trees were able to persist in a context of increased dry conditions (Braconnot et al. 2019).

Our Mboro-Baobab record does not show such an abrupt shift from a humid to a dry environment. The tree cover (AP%, cf. Lézine et al., this issue) was never highly developed, probably due to the distal position of the site with respect to the core of the Niaye groundwater system (Diogo) (Putallaz 1962) and seems to have only slightly varied over the last 4300 years (Figure 2). Forest composition however strongly changed. Guinean taxa underwent a clear phase of expansion centered at 3875 cal yr BP. A similar phase of development of tropical trees is seen at Jikariya (Waller et al. 2007) in the Manga grasslands of northern Nigeria between 3800 and 3500 cal yr BP that points to the regional character of this short phase of forest recovery. At Mboro-Baobab, this forest phase ended rapidly with steppic conditions increasing as soon as 3750 cal yr BP. Interestingly, this increase in aridity did not have an immediate effect on the composition of the forest gallery but probably only on its density. It is only at 3200 cal yr BP that the replacement of the wettest forest elements by forest taxa more adapted to drier climatic

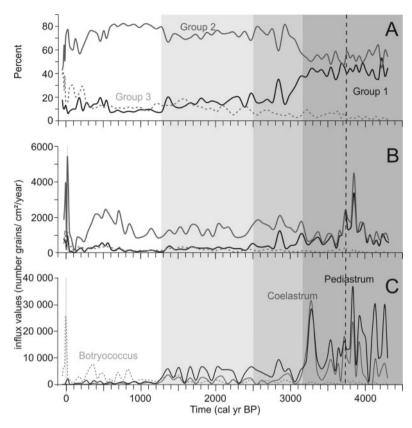


Figure 4. Summary of the evolution of the environment at Mboro-Baobab over the last 4300 years. (A) Percentages of the three groups of pollen taxa revealed by the CA statistical analysis; (B) influx values of these groups; (C) influx values of the algae Pediatrum, Coelastrum and Botryococcus. The gray bars (from dark to light) show the progressive decline of the most humid elements. The dotted line shows the onset of dryness in a still humid context. Note that curves are superimposed and not cumulative.

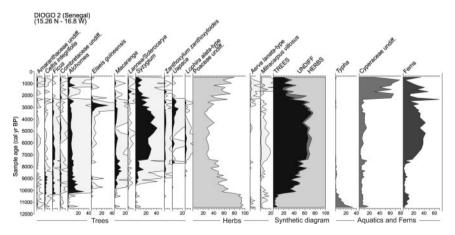


Figure 5. Percentage pollen diagram of main taxa from Diogo in the Niaye area of Senegal (Lézine 1988).

conditions occurred. This replacement was not as abrupt as at Diogo but its amplitude was not negligible as shown by the decrease in percentages of group 1 by about 10% (Figure 4A). Taking into account the chronological uncertainties between sites, our Mboro-Baobab record closely fits with that of Jikaryia, which dates the decline of tropical humid trees at 3150 cal yr BP.

5.6 CONCLUSION

As already noted by Waller et al. (2007), significant differences in the timing and amplitude of similar events may occur in pollen records from the same region. The size of the sites and their location with respect to groundwater availability are among the parameters that can influence the local response of plants to climate change in terms of amplitude and timing. Compared to the other Niaye sites (Lézine 1988) Mboro-Baobab contains the most complete and detailed record of the end of the AHP. Despite its location on the edge of the wettest zone of the Niayes region, where the forest gallery was only poorly developed, it has undergone profound environmental changes allowing distinction of the successive phases in the establishment of the modern landscape. The drying of the Mboro-Baobab landscape was gradual, starting from 3750 cal yr BP then culminating at 1300 cal yr BP. In contrast, a major shift in the lake system and the forest diversity occurred at 3200 cal yr BP, marked by the lowering of the water level and the sharp decline of the tropical humid forest elements. The species turnover initiated at that time continued up to 2500 cal yr BP. Our results are consistent with those obtained in the central Sahel, which place the end of AHP between 3300 and 3150 cal yr BP depending on the site (Salzmann and Waller 1998; Waller et al. 2007). According to our study, the end of AHP (i.e. the retreat of the most humid elements from the gallery forests of the Niayes region) lasted about 700 years between 3200 and 2500 cal vr BP. The duration of this transition period was likely favored by the presence of a water table close to the surface, which was able to maintain humid conditions for several centuries after the major event of 3200 cal yr BP.

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