CHAPTER 6

Changes in the West African landscape at the end of the African Humid Period

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ABSTRACT: Existing pollen datasets from northern Africa stored in the African Pollen Database were used to assess changes in landscape physiognomy at the end of the African Humid Period (AHP) from 5000 cal yr BP to the present using arboreal pollen percentages. The thirty-six sites available were used to map changes in arboreal cover at a sub-continental scale. Based on their location in present-day forested and non-forested areas and their relatively higher temporal resolution eight of them were selected to examine the timing and amplitude of the vegetation response in more detail, and particularly in the Sahel. In spite of low pollen production and dispersal of many tropical plants, which lead to the under representation of most of the trees relative to their abundance in the landscape, we were able to distinguish the geographical pattern and timing of vegetation changes. The landscape response to the end of the AHP was far from homogeneous particularly in the Sahel where a clear east-west gradient of changing tree cover is indicated with the central Sahel being notably species poor. In areas where forests were well developed during the AHP, i.e. in the south and west, the establishment of the modern landscape was abrupt with a threshold crossed between 3300 and 2500 cal yr BP according to local conditions. Elsewhere in northern Africa the switch from tree (C_3) to grass (C_4) dominated landscapes occurred more gradually during the same period. This review shows that the timing of the ecosystem response at the end of the AHP was remarkably synchronous throughout northern Africa.

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6.1 INTRODUCTION

Reconstructing vegetation changes in tropical North Africa during the Holocene and understanding how the landscape has evolved from a 'humid' state characterized by the development of numerous lakes and wetlands into the today's hyper-arid desert continues to be the subject of extensive research (e.g. Dallmeyer *et al.* 2020; Krinner *et al.* 2012; Lézine *et al.* 2011; Shanahan *et al.* 2015). Pollen data have been successfully used to assess biodiversity changes that occurred during the African Humid Period (AHP) (deMenocal *et al.* 2000) such as the penetration of tropical trees into the Sahara and the Sahel at its onset or their retreat at its termination (e.g. Hély *et al.* 2014 and references therein). Pollen data are however extremely complex and changes in plant cover and related land-surface albedo remain difficult to be quantified. A large part of this complexity is due to the uneven geographical distribution of the data, difficulties in establishing robust chronologies, and the incomplete and/or discontinuous nature of the sedimentary series (Watrin *et al.* 2009). The desiccation of the ancient Saharan lakes and the deflation of exposed lacustrine deposits, still continuing today, have eroded lake sediments and considerably hampered the preservation of pollen grains. Therefore, preserved sediments provide limited time windows mainly concentrated in wettest periods. Only a single, continuous, sequence covering a time interval from the end of the AHP to the present is available for the entire Sahara (Lézine *et al.* 2011). Continuous pollen series with high temporal resolution are however more numerous to the south, from the Sahel to the Congo basin (e.g. Lézine *et al.* 2013a; Maley and Brenac 1998; Ngomanda *et al.* 2009; Salzmann *et al.* 2002; Vincens *et al.* 2010; Waller *et al.* 2007).

Differences in pollen production and dispersal between tropical plants means that interpretation of vegetation cover within the landscape from ancient pollen records is further complicate, especially in the driest regions. Most of the trees have a low pollen productivity, disperse pollen entomophilously, and are thus under-represented in the pollen spectra (Ritchie 1995). While the presence of tree pollen, even a single grain, may be indicative of the presence of the corresponding plants (Watrin *et al.*, 2006), it is extremely difficult given the current state of knowledge, to quantify the importance of these trees in the landscape. Therefore, the timing and magnitude of the environmental change related to the end of the AHP remains poorly documented.

Here we use a simple index: the percentage of tree pollen (AP %) from selected high resolution pollen records from both continental and marine environments in northern Africa, from 5° to 19°N, in order to characterize the environmental change at the end of the AHP. This index is commonly used to qualitatively evaluate woody cover in temperate regions where most of the tree species are wind-pollinated. Our goal is to discuss how well this index can be applied to northern Africa, given the particularities of the pollen production and dissemination syndromes of tropical tree species.

6.2 ENVIRONMENTAL SETTING

The climatic features of northern Africa are related to the Atlantic monsoon circulation and the seasonal migration of the Intertropical Convergence Zone (ITCZ). In January, the monsoons' influence is confined to the periphery of the Gulf of Guinea and the northernmost areas are subject to the hot, dry continental trade winds. In July, the ITCZ reaches its northernmost position at 22°N allowing moist monsoon air to extend over north tropical Africa up to the southern fringe of the Sahara.

The progressive decrease of the monsoon influence and related rainfall on the continent is correlated with the latitudinal distribution of the vegetation. Five major floristic regions can be delineated from south to north: Guineo-Congolian forests of different types (evergreen and semi-evergreen forests) and secondary wooded grasslands (mean annual rainfall more than 1200 mm), Sudanian dry forests and wooded grasslands (1500–500 mm yr^{-1}), Sahelian wooded grasslands
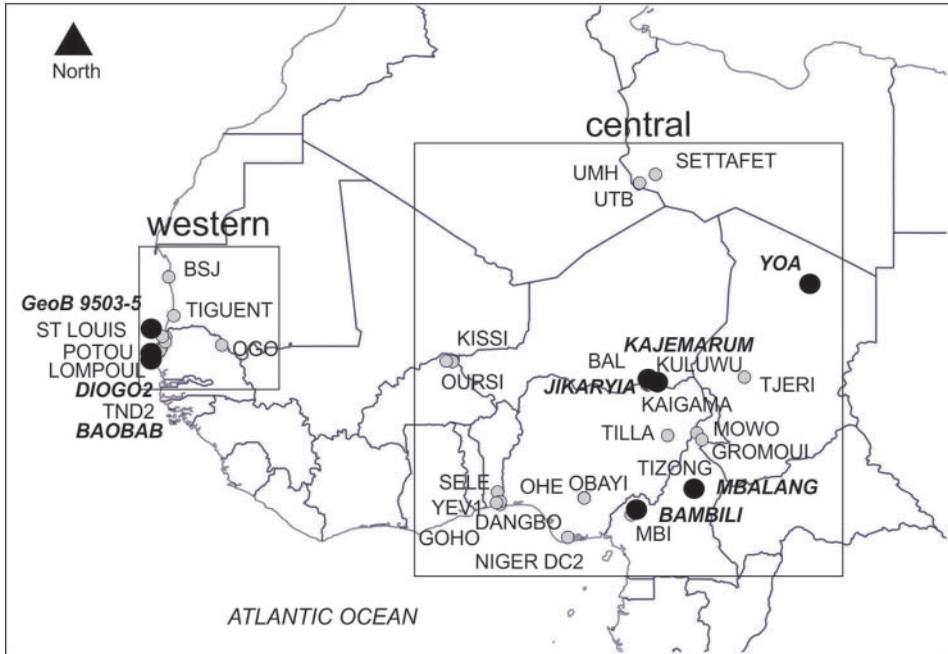
Figure 1. Location map of the Holocene pollen sites used in this study (Table 1). In bold and italic, pollen sites detailed in the text (Figure 3). Boxes define the two sectors shown in Figure 5.

and grasslands (500–100 mm yr^{-1}) and Saharan steppes (less than 100 mm yr^{-1}) (White 1983) (Figure 1). In addition, Afromontane forests occur in the Cameroon Volcanic Line between roughly 1800–2300 m asl (annual rainfall: 2000 mm yr^{-1}; mean temperature: 18 °C) bordered at upper elevations by Afroalpine grasslands and at lower elevations by sub-montane forests and wooded grasslands.

Along the coast, mangrove forests expand at the mouth of rivers where they benefit from both brackish waters and large muddy areas. Their optimal growth is attained under a rain forest climate but two main components expand northward along the coast of West Africa: *Rhizophora racemosa* reaches its northern limit at the mouth of the Senegal River near 16°N and *Avicennia germinans* extends up to Tidra at 19°50 N.

6.3 DATA USED

In this study, we use all the available Holocene pollen data from northern Africa stored in the African Pollen Database (APD) (Figure 1; Table 1). We focus on changes in landscape physiognomy, i.e. the shift from a C$_3$ plant dominated landscape to a C$_4$ plant dominated one at the end of the AHP. Therefore, pollen records from equatorial lowland forests (e.g. Elenga *et al.* 1994, 1996; Reynaud-Farrera *et al.* 1996) were excluded, since the impact of the environmental crisis, which occurred at the end of the AHP in the Congo Basin, was more a change in forest composition and density than the replacement of lowland forests by grasslands or wooded grasslands (Vincens *et al.* 1999). The dataset consists of 36 sites among which seven continental (Bambili, Mbalang, Diogo, Mboro-Baobab, Kajemarum, Jikaryia, Yoa) and one marine (GeoB 9503-5) pollen records have been selected in order to characterize the evolution of the landscape in the

Table 1. List of the pollen sites used in this study according to latitude from north to south in the two sectors defined in this study. In bold and italic = selected sites, see black dots on Figure 1.

Site name	Latitude	Longitude	Altitude (m asl)	Country	Time frame (cal yr BP)	Reference
			Central sector			
SETTAFET	25.35	11.43	1100	Libya	5000	Schulz (1980)
UAN TABU [UTB]	24.86	10.52	915	Libya	4000–4250	Mercuri, and Grandi (2001)
UAN MUHUGGIAG [UMH]	24.84	10.51	915	Libya	4000–4250	Mercuri *et al.* (1998)
YOA	19.03	20.31	380	Chad	0–5000	Lézine *et al.* (2011)
OURSI	14.65	−0.49	290	Burkina Faso	0–3500	Ballouche and Neumann (1995)
KISSI	14.62	−0.14	280	Burkina Faso	500–750	Ballouche (1997)
TJERI	13.73	16.50	275	Chad	500–4750	Maley (2004)
JIKARYIA	13.31	11.08	343	Nigeria	0–5000	Waller *et al.* (2007)
BAL	13.30	10.94	300	Nigeria	250–5000	Salzmann and Waller (1998)
KAJEMARUM	13.30	11.02	300	Nigeria	2750–5000	Salzmann and Waller (1998)
KAIGAMA	13.25	11.57	330	Nigeria	3500–5000	Salzmann and Waller (1998)
KULUWU	13.22	11.55	330	Nigeria	4750–5000	Salzmann and Waller (1998)
MOWO	10.60	13.99	574	Cameroon	500–750	Delneuf and Médus (1997)
TILLA	10.39	12.12	690	Nigeria	0–5000	Salzmann *et al.* (2002)
GROMOUI	10.32	14.32	430	Cameroon	1000–1250	Delneuf and Médus (1997)
MBALANG	7.32	13.73	1110	Cameroon	0–5000	Vincens *et al.* (2010)
TIZONG	7.25	13.58	1160	Cameroon	0–4000	Lebamba *et al.* (2016)
LAC SELE	7.15	2.43	11	Benin	0–5000	Salzmann and Hoelzmann (2005)
OBAYI	6.82	7.37	550	Nigeria	1750–2000	Njokuocha (2012)
OHE POND	6.80	7.37	1502	Nigeria	1250–1500	Njokuocha and Akaegbobi (2014)

(*Continued*)

Table 1. *Continued.*

Site name	Latitude	Longitude	Altitude (m asl)	Country	Time frame (cal yr BP)	Reference
DANGBO	6.60	2.59	40	Benin	0–5000	Tossou (2002)
YÉVIÉDIÉ	6.53	2.37	53	Benin	1250–5000	Tossou (2002)
GOHO	6.44	2.57	35	Benin	750–4750	Tossou (2002)
MBI	6.08	10.35	2018	Cameroon	0–5000	Lézine *et al.* (2021)
BAMBILI 1	5.94	10.24	2273	Cameroon	0–5000	Lézine *et al.* (2013a)
NIGER DELTA [DC2]	4.55	6.43	0	Nigeria	500–3750	Sowunmi (1981)
Western sector						
BAIE SAINT JEAN [BSJ]	19.47	−16.30	1	Mauritania	1750–3750	Unpublished (Lézine A.M.)
TIGUENT	17.25	−16.02	8	Mauritania	3000–3250	Médus and Barbey (1979)
GeoB 9503-5	16.07	−16.65	−50	Atlantic Ocean	1500–4250	Bouimetharhan *et al.* (2009)
ST LOUIS	16.03	−16.48	2	Senegal	0–1000	Fofana *et al.* (2020)
POTOU	15.75	−16.50	11	Senegal	0–5000	Lézine (1988)
OGO [OS2]	15.57	−13.28	15	Senegal	750–1000	Feller *et al.* (1981)
LOMPOUL	15.42	−16.72	3	Senegal	2000–5000	Lézine (1988)
DIOGO 2	15.27	−16.80	8	Senegal	250–5000	Lézine (1988)
TOUBA N'DIAYE 2 [TND2]	15.17	−16.87	6	Senegal	1000–5000	Lézine (1988)
MBORO-BAOBAB	15.15	−16.91	4	Senegal	0–4500	Lemonnier and Lézine (this volume)

two main vegetation types which expanded in northern Africa during the AHP: (i) continuous forests in the Cameroon Highlands, and (ii) gallery forests around water bodies in the Sahara and Sahel within a dry, open regional environment. The whole dataset was then used to map landscape changes at a sub-continental scale.

The chronology is given in calendar years BP (cal yr BP) after conversion of ^{14}C dates to calendar age according to Stuiver *et al.* (2020). The age models were retrieved from the published articles or from the APD (i.e. based on linear interpolation between the dated samples) taking into account possible discontinuities in sediment deposition. Arboreal pollen types (AP) include trees, shrubs, palms and lianas. Undifferentiated pollen types (UP) include taxa corresponding to plants with various life forms (trees, shrubs, lianas or herbs) and taxa determined at a low taxonomic level, typically the family level (Vincens *et al.* 2007). Percentages are calculated against a sum of total pollen excluding those of aquatics (including Cyperaceae), cultivated and Mediterranean plant types.

6.4 POLLINATION SYNDROMES OF THE TROPICAL PLANTS

The pollination syndromes of the families represented at the seven selected sites (Table 2) are derived from Watson and Dallwitz (1992) and the gymnosperm database (www.conifers.org). This reveals the major challenge of representing landscapes from pollen data in northern Africa. Most of the families present in our pollen records are entomophilous or zoophilous (mainly cheiropterophilous and ornithophilous), whereas 16% are anemophilous or entomophilous and only 5% are strictly anemophilous. Most of the entomophilous/zoophilous plants produce small amounts of pollen, which may be exceptionally large. As a result, they are under-represented (e.g. *Adansonia*) or rarely (e.g. *Isoberlinia, Daniellia*) represented in the pollen assemblages (Watrin *et al.*, 2006). In contrast, members of the Poaceae family, which is exclusively anemophilous, produce large quantities of pollen, and therefore largely dominate the pollen assemblages, particularly those derived from wooded grasslands and grasslands. Taking into account these specifications and the difficulties of measuring the quantity of pollen grains produced by the plants, the most widely used method for describing the pollen signature of the modern vegetation in terms of diversity, biomes or vegetation types is that of surface samples, either from soil, mosses or pollen traps. This method has been successfully developed in tropical Africa since Hedberg (1954). Gajewski *et al.* (2002) have validated the APD dataset, which covers all of sub-Saharan Africa.

6.5 POLLEN REPRESENTATION OF THE MODERN LANDSCAPE

In northern Africa the pollen-plant and pollen-biome relationships have been extensively studied (e.g. Lézine *et al.* 2009; Watrin *et al.* 2007 and references therein). These studies have identified the pollen signature of common plants and biomes along latitudinal (Lézine *et al.* 2009) or altitudinal gradients (Verlhac *et al.* 2018) in order to provide the basis for reliable vegetation reconstructions in the past and for quantitative estimates of climate parameters from pollen data. However, the physiognomy of the vegetation is only rarely addressed (Lézine and Hooghiemstra 1990; Vincens *et al.* 2000). Based on arboreal pollen percentages (AP%) and undifferentiated pollen percentages (UP%), Figure 2A shows that the two extreme vegetation types along a south-north transect in northern Africa, the Guineo-Congolian forest in the south and the desert steppe in the north, are easily identified (Lézine and Hooghiemstra 1990). The Guineo-Congolian forest is represented by AP higher than 80% and UP lower than 8% while the desert steppe is represented by AP lower than 10%. In desert steppe, UP (mainly herbs, sub-shrubs or shrubs from the Amaranthaceae, Brassicaceae, Caryophyllaceae, Asteraceae families) values are exceptionally high, representing more than 50%. While AP% consistently range between 20% and 50% in the Sudanian dry forests of southern Senegal, they strongly vary between 5 and 35% in the Sahelian woodlands and wooded grasslands, making the pollen signature of the tree cover in these grass-dominated landscapes difficult to detect. The difficulty in detecting tree cover is mainly due to the uneven distribution of the trees within the landscape. This is particularly the case in the transition zone between forest and desert where trees are mostly concentrated along rivers and wetlands (Trochain 1940; White 1983). In addition, these vegetation formations share numerous tree species, the distribution of which is denser in the woodlands and sparser in the wooded grasslands (e.g. Combretaceae, *Acacia*). The characteristics of their pollen production and dispersal hampers any reliable reconstruction of vegetation types.

In the Equatorial regions, the forest-wooded grassland transect of Kandara (Vincens *et al.* 2000) shows AP higher than 60% in the forest. AP dramatically decrease to less than 10% in the adjacent wooded grassland and the transition between the two is typified by intermediate values (45%) (Figure 2B). However, as stated by the authors, the different kind of forests (*Albizia* forest and *Rinorea* forest) cannot be distinguished, and no decrease in AP% is observed in the forest

Table 2. List of the families encountered in the Holocene pollen sites used in this study (Table 1) and included in the pollen sum with their pollination syndromes (after Watson and Dallwitz (1992) and the gymnosperm database (www.conifers.org)).

Family	Pollination system	Family	Pollination system
Acanthaceae	entomophilous	Liliaceae	entomophilous
Aizoaceae	entomophilous	Lobeliaceae	entomophilous
Alangiaceae	entomophilous	Loganiaceae	entomophilous
Amaranthaceae	entomophilous	Loranthaceae	entomophilous, or ornithophilous
Anacardiaceae	entomophilous	Lythraceae	entomophilous
Annonaceae	entomophilous	Malpighiaceae	entomophilous
Apiaceae	entomophilous	Malvaceae	entomophilous
Apocynaceae	entomophilous	Melastomataceae	entomophilous, or ornithophilous, or cheiropterophilous
Aquifoliaceae	entomophilous	Meliaceae	entomophilous (usually)
Araliaceae	entomophilous	Melianthaceae	entomophilous, or ornithophilous
Asclepiadaceae	entomophilous	Menispermaceae	unknown
Asparagaceae	entomophilous	Mimosaceae	entomophilous, or ornithophilous, or cheiropterophilous, or anemophilous
Asteraceae	entomophilous (mostly), or anemophilous	Moraceae	anemophilous, or entomophilous
Balanitaceae	entomophilous (mostly), or anemophilous	Myricaceae	anemophilous
Balsaminaceae	entomophilous	Myristicaceae	entomophilous
Begoniaceae	entomophilous	Myrsinaceae	entomophilous
Bignoniaceae	entomophilous, or ornithophilous, or cheiropterophilous	Myrtaceae	entomophilous, or ornithophilous
Bombacaceae	cheiropterophilous	Nyctagynaceae	entomophilous
Boraginaceae	entomophilous	Ochnaceae	entomophilous
Brassicaceae	anemophilous, or entomophilous	Olacaceae	entomophilous
Buddleyaceae	entomophilous, or ornithophilous	Oleaceae	anemophilous (mostly), or entomophilous
Burseraceae	entomophilous	Orobanchaceae	entomophilous
Caesalpiniaceae	entomophilous;	Palmae	entomophilous (mostly), or anemophilous
Campanulaceae	entomophilous	Pandanaceae	anemophilous (mostly), or entomophilous, or ornithophilous, or cheiropterophilous
Capparidaceae	entomophilous	Passifloraceae	entomophilous

(*Continued*)

Table 2. *Continued.*

Family	Pollination system	Family	Pollination system
Caryophyllaceae	entomophilous	Phyllanthaceae	entomophilous
Casuarinaceae	anemophilous	Plantaginaceae	anemophilous, or anemophilous and entomophilous
Celastraceae	entomophilous	Poaceae	anemophilous (exclusively)
Chrysobalanaceae	entomophilous, or cheiropterophilous	Podocarpaceae	anemophilous
Clusiaceae	entomophilous, or ornithophilous	Polygalaceae	entomophilous
Cochlospermaceae	entomophilous	Polygonaceae	anemophilous, or entomophilous
Combretaceae	entomophilous, or ornithophilous	Primulaceae	entomophilous
Commelinaceae	entomophilous	Proteaceae	entomophilous, or ornithophilous, or cheiropterophilous (?), or by unusual means (notably by small marsupials and rodents)
Connaraceae	autogamous or entomophilous	Ranunculaceae	anemophilous, or entomophilous
Convolvulaceae	entomophilous	Resedaceae	entomophilous
Crassulaceae	entomophilous	Rhamnaceae	entomophilous
Cucurbitaceae	entomophilous	Rhizophoraceae	anemophilous, or entomophilous
Cupressaceae	anemophilous	Rosaceae	anemophilous (occasionally), or entomophilous (usually)
Dichapetalaceae	entomophilous	Rubiaceae	entomophilous
Dilleniaceae	entomophilous	Rutaceae	entomophilous
Dioscoreaceae	entomophilous	Salicaceae	anemophilous, or entomophilous
Dipsacaceae	entomophilous	Salvadoraceae	entomophilous
Ebenaceae	entomophilous	Sapindaceae	entomophilous
Ephedraceae	anemophilous, or entomophilous	Sapotaceae	entomophilous
Ericaceae	entomophilous (usually?)	Scrophulariaceae	entomophilous, or ornithophilous
Euphorbiaceae	entomophilous	Simaroubaceae	entomophilous, or ornithophilous
Fabaceae	entomophilous, or ornithophilous, or cheiropterophilous	Solanaceae	entomophilous
Flacourtiaceae	entomophilous	Sphenocleaceae	entomophilous
Gentianaceae	entomophilous	Sterculiaceae	entomophilous

(*Continued*)

Table 2. *Continued.*

Family	Pollination system	Family	Pollination system
Geraniaceae	entomophilous	Tamaricaceae	entomophilous, or anemophilous
Gesneriaceae	entomophilous, or ornithophilous, or cheiropterophilous	Thymeleaceae	entomophilous
Hippocrateaceae	entomophilous	Tiliaceae	enthomophilous
Hymenocardiaceae	entomophilous (mostly), or anemophilous	Tribulaceae	entomophilous
Hypericaceae	entomophilous	Ulmaceae	entomophilous
Icacinaceae	entomophilous	Urticaceae	anemophilous
Irvingiaceae	entomophilous	Verbenaceae	entomophilous
Lamiaceae	entomophilous or ornithophilous	Vitaceae	entomophilous (mostly), or anemophilous
Lecythidaceae	entomophilous	Zygophyllaceae	entomophilous
Portulaceae	entomophilous		
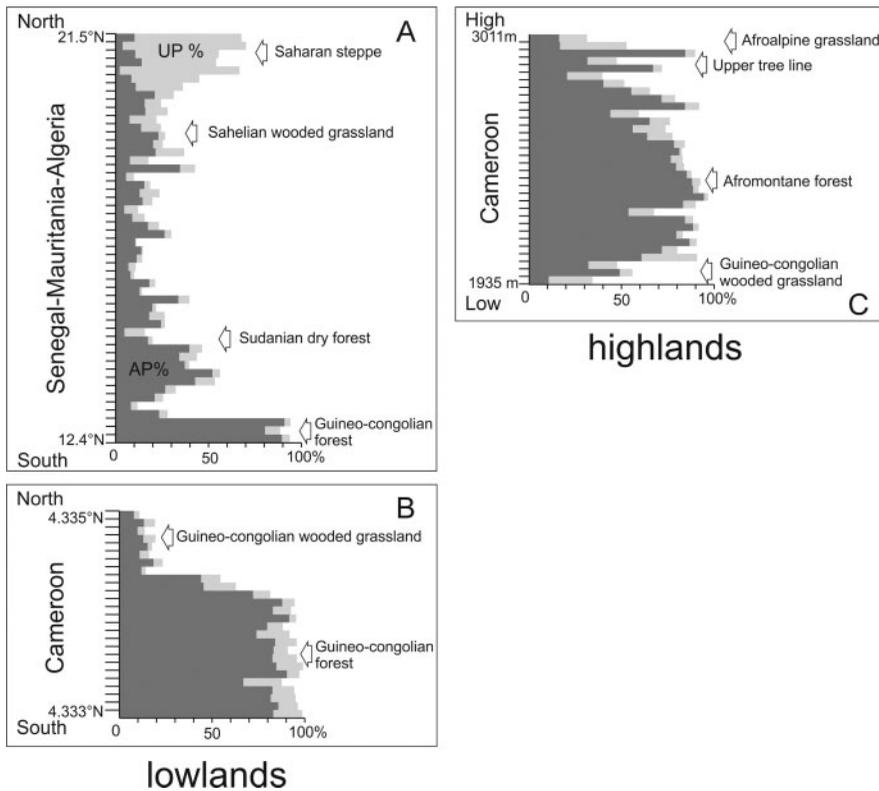
Figure 2. Modern pollen deposition in three different sectors of northern Africa: (A): a South-North transect in Senegal-Mauritania-Algeria (Lézine and Hooghiemstra 1990), (B): the Kandara forest-savanna transect in Southern Cameroon (Vincens *et al.* 2000), and (C): an altitudinal transect in the Cameroon highlands (Verlhac *et al.* 2018). Percentages calculated against a sum excluding fern spores, aquatics and Cyperaceae pollen. Dark grey: AP%. Light grey: UP%.
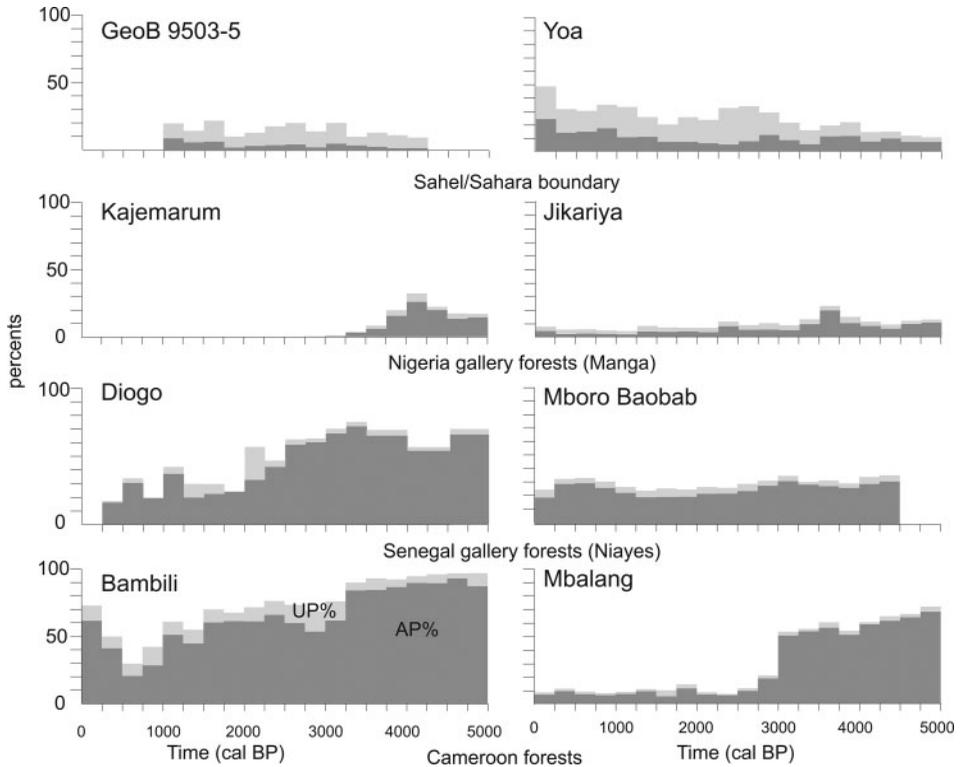
Figure 3. Percentages of Arboreal (AP) and Undifferentiated pollen types (UP) in selected sites from northern Africa from 5000 cal yr BP to the present. In order to facilitate the comparison between sites, data are averaged by 250-years' time bins.

gaps linked to recent settlements. A slightly different pattern is observed in the montane forests Cameroon (Figure 2C; Verlhac *et al.* 2018). As expected, AP reach high values, up to 90%, within the forest. However, they strongly vary, reflecting the highly heterogeneous forest cover (Momo Solefack 2009) (Figure 2C). This is particularly the case at higher elevations where the trees are irregularly distributed and the upper tree line is often patchy due to marked topography. Afroalpine grasslands at the top of the mountains and wooded grasslands below the forest block show AP averaging 15% and 10%, respectively.

6.6 THE HOLOCENE POLLEN SEQUENCES

Vincens *et al.* (1999) first reviewed the equatorial forest response at the end of the AHP. They showed that the lowland forests changed in nature from rain or swamp forests to woodlands or secondary forests characterized by an increase in light demanding trees. While the timing of this change is remarkably coherent in the lowlands of Cameroon at around 2400 cal yr BP (Lézine *et al.* 2013b and reference therein), it varies in Congo within a time interval from 3800 and 1800 cal yr BP according to local hydrological conditions (Vincens *et al.* 1999). In mountain areas, a clear signal of forest disruption occurred at 3300–3000 cal yr BP (Figure 3): AP values abruptly fell from 50 to 9% in the Adamawa plateaus (Mbalang) and then remained below 11% up to the present day. At higher elevations (Bambili), AP decreases from 84% to 54% at 3300 cal yr
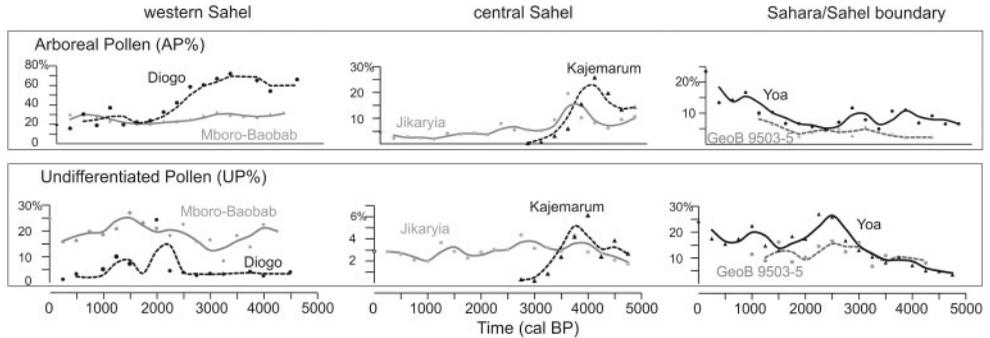
Figure 4. Arboreal pollen percentage (AP%) and undifferentiated pollen percentage (UP%) from selected sites from the Sahara and the Sahel. Dashed lines show the second order running average.

BP and then remained at this level up to 2500 cal yr BP. AP subsequently increased again to a maximum of 65% indicating a later forested phase, albeit less developed compared to that of the AHP. This second phase of forest development ended during the last millennium.

In the Sahel, the pollen diagrams testify to a contrasting situation: in the west, near the Atlantic coast, AP% were remarkably high during the Holocene forest phase indicating dense gallery forests in the coastal region (Diogo). AP decreased from 72% to 19% between 3250 and 1250 cal yr BP through a well-marked threshold at 2500 BP characterized by a drop of about 20%. In the same region however, Mboro-Baobab did not record such an evolution and AP values displayed rather constant percentages during the last 5000 years, only slightly fluctuating between 30 and 20%. In the central Sahel, AP never reached percentages as high as those recorded in the west, even during the AHP reflecting poorly developed gallery forests around water bodies. The maximum of AP at Kajemarum and Jikaryia in the Manga region of northern Nigeria did not exceed 26% and 19%, respectively. At Kajemarum, AP definitively disappeared at 3000 cal yr BP. At Jikaryia, the transition between the Holocene and the present landscape was less contrasted though a slight decrease in AP% was observed at the same time. At the Sahara/Sahel transition (Yoa, GeoB 95013-5) AP were constantly less than 23% during the AHP. At Yoa, the retreat of tropical plant species (e.g. *Celtis, Piliostigma, Grewia*) and the establishment of desert conditions at the end of the AHP occurred in two phases at 4700 and 2700 cal yr BP, respectively (Lézine *et al.* 2011). This transition occurred in a context of poorly developed tree cover and is therefore not reflected by our AP index. Interestingly, AP% slightly increased during the last few centuries which may reflect increased anthropogenic influence, for instance the establishment of palm tree plantations at Yoa (Lézine *et al.* 2011), or the occurrence of episodic humid events in the Senegal River Basin (Bouimetarhan *et al.* 2009). In order to refine the timing and structure of the end of the AHP in the Sahel, we plotted the undifferentiated pollen types (UP) (Figure 4) that are especially abundant in the most arid regions as shown in the modern samples (Figure 2). Three sectors of the Sahara and the Sahel emerge from the examination of UP %: at the Sahara/Sahel boundary, the UP % gradually increased from 5000 cal yr BP (or even before) to the present with a peak at 2700 cal yr BP. A roughly similar trend is observed in the Central Sahel. Here they were present from 4000 cal yr BP and then remained constant throughout the last millennia. In contrast, UP % increased much later, since 2700 cal yr BP in the western Sahel.

6.7 DISCUSSION

Our study illustrates one of the major problems of tropical palynology: can the abundance of trees and grasses in the landscape be described using a simple index: the percentage of arboreal

pollen? Open landscapes dominate in Africa today between 30°S and 30°N with the exception of the equatorial mangrove, and afromontane forests. These open landscapes are of various types, ranging from dry forests, to woodlands, wooded grasslands and grasslands (White 1983). The particularities of pollen production and dispersal of tropical plants mean that trees are often under-represented in pollen spectra, making distinction between these types of vegetation difficult. Based on the modern samples (Figure 2), we have considered three AP% categories to characterize the late Holocene landscape of northern Africa (Figures 5 and 6): (i) AP higher than 45% corresponding to a dense tree cover, (ii) AP lower than 15% indicating grass-dominated landscapes, and (iii) intermediate values ($15 < AP < 45\%$), secondary/dry forests. Figure 5 shows that dense forest stands remained developed in mangroves along the coast of the Gulf of Guinea, in the western Sahel and in the Cameroon highlands well after the establishment of xeric conditions at the end of the AHP. Surprisingly, it suggests that there was no transition from forested to open landscapes from south to north throughout northern Africa with open landscapes dominating largely from 5000 to *c*. 3000 cal yr BP north of 10°N. The absence of intermediate tree cover between forests and open landscapes is likely an artefact due to the difficulties evoked in distinguishing woodlands from wooded grasslands and grasslands. While different kinds of open environments are difficult to infer from AP%, it is even more difficult to derive related climatic factors. For instance, modern AP% are higher at Yoa in the Saharan steppe, where the annual rainfall does not exceed 7 mm (23%) than at Mbalang in the Sudanian wooded grassland, where it averages 1500–1600 mm (6.5%). Environmental reconstructions in such grass-dominated landscapes are thus particularly challenging and new methodological approaches such as those developed by Sugita (2007) are crucial for a better estimation of regional vegetation proportions (See Gaillard *et al.*, this volume). Despite this major limitation and the purely qualitative aspect of our approach, two key results emerge from our review (6.7.1 and following).

6.7.1 Abrupt forest collapses or gradual establishment of xeric conditions?

In densely forested areas from western Sahel (Diogo) and the Cameroon Highlands (Bambili, Mbalang), AP% permits identification of the tipping points between forested and non-forested (or less-forested) states that occurred at times, varying according to altitude and hydrological conditions, between 3300 and 2500 cal yr BP (Figure 3). However, the determination is only qualitative since the evaluation of its magnitude depends mainly on the pollen productivity and dispersion of tropical trees (see Gaillard *et al.*, this volume). Abrupt forest collapse most certainly originated from the middle Holocene, when an increased seasonality in rainfall was established (Vincens *et al.* 2010). At Bambili, the progressive destabilization of the forest is thought to have originated from the '8.2 event', which could thus be considered as the 'early warning signal' (Lenton 2011) of the environmental crisis that took place several millennia later, at 3300 cal yr BP (Lézine *et al.* 2013a). Unlike these sites, where a threshold was abruptly crossed leading to the collapse of the forests, the establishment of an open landscape at the end of the AHP was gradual (Figure 4); tree cover decreased gradually in already arid areas, particularly in the central Sahel. This supports the interpretations by Kröpelin *et al.* (2008) that the transition to xeric conditions at the end of the AHP was a gradual one. Consequently, pollen data from the Sahel do not support the earlier hypotheses of an abrupt environmental change at the end of the AHP as proposed by de Menocal *et al.* (2000).

6.7.2 A complex pattern of environmental change

Changes in distribution of trees across the landscape was not merely latitudinal following a south-north gradient of decreasing precipitation (Figure 5). The most striking feature is the difference between the central and western Sahel. We therefore consider two separate transects, one along the west coast and the other in central northern Africa. Forests widely developed in the west.
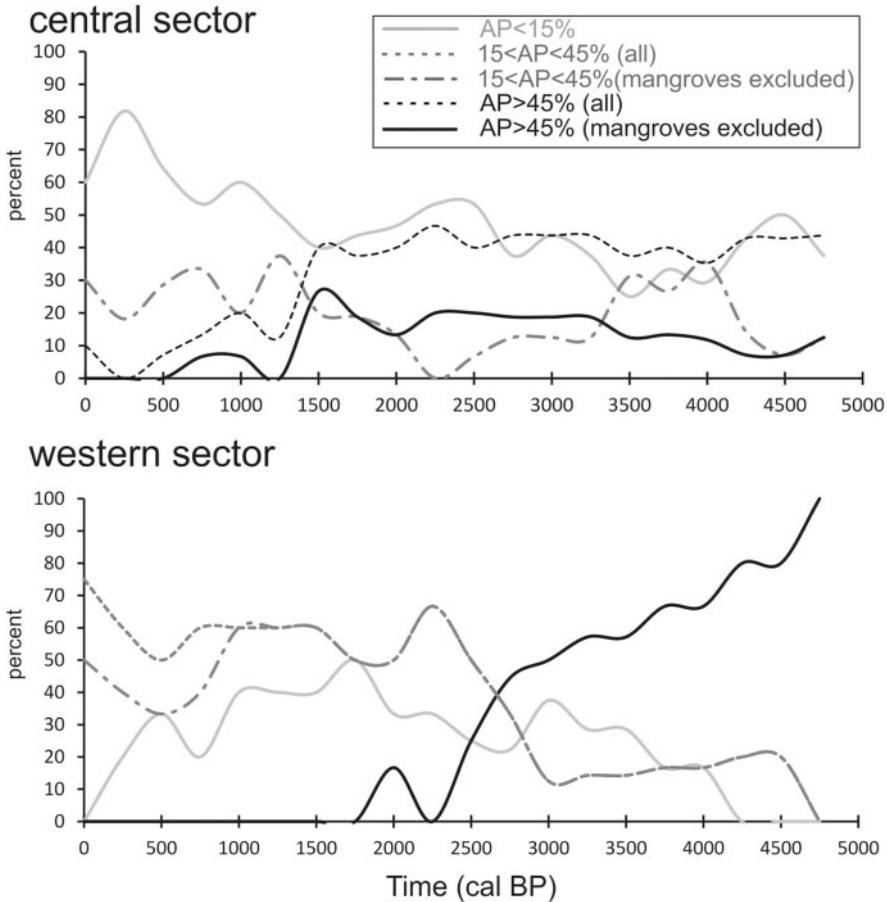
Figure 5. (A) Spatial distribution of tree pollen percentages from 5000 cal yr BP to the present in northern Africa. Three categories are considered with AP > 45% showing dense tree cover, 15 < AP < 45% intermediate tree cover and AP < 15% sparse tree cover. (B) Patterns of tree cover change according to latitude in the two sectors defined in Figure 1. The selected sites are indicated on the left column by a box.

Figure 6. Timing of landscape change in the western (on the left) and central (on the right) sectors of northern Africa. The curves show the number of sites in the categories defined by AP% in northern Africa (AP = O, AP < 15%, 15 < AP < 45%, >45%). Data are expressed in per cent of the total of sites present in each time bin (cf. Figure 5B).

Their expansion reached approximately 16°N, i.e. the mouth of the Senegal River. In contrast, forests only occurred along the coast and in the highlands in central Africa. Trees were rare north of 10°N in the Sahel, except during a time interval spanning from 4500 to 3500 cal yr BP in the Manga region (13°N) and in the central Saharan massifs in southern Libya (25°N) where they slightly increased (Figures 5 and 6).

Despite the limited number of sites in both sectors clear patterns can be discerned. In the western sector, the major change in forest cover occurred from 3000 to 2250 cal yr BP. This is shown by the opposing trends between the number of sites with AP values above 45%, which were gradually decreasing in number and those with AP values ranging from 15 to 45%, which were gradually increasing. Sparse tree cover became gradually commoner over the western sector from 4250 cal yr BP with the modern landscape composed of woodlands and wooded grasslands being definitively established after 1750 cal yr BP. Unlike the western sector, sites with sparse tree cover dominated the central sector throughout the last 5000 years. The number of such sites progressively increased in two phases respectively dated 3500 and 1500 cal yr BP. Sites with

dense tree cover were restricted to the Cameroon Highlands and the mangrove areas along the Gulf of Guinea. In both sectors, they declined from 1500 cal yr BP onwards. The most striking result of our study is the behaviour of sites with intermediate tree cover. As already noted, trees increased in the Manga sector of the Sahel around 3800 cal yr BP due to the recovery of tropical taxa during a short wet phase (Waller *et al.* 2007). After 3500 cal yr BP, trees disappeared from the Manga sector. Elsewhere in the central sector of northern Africa, the number of sites with intermediate and sparse tree cover increased from 2250 cal yr BP onwards.

6.8 CONCLUSIONS

Reconstructing vegetation cover from AP% is highly challenging, particularly given the predominantly open vegetation types that are widely distributed in northern Africa from the Sudanian dry forests to the Sahelian wooded grasslands and Saharan grasslands. Despite this caveat, our review shows that the landscape response to the end of the AHP was far from homogeneous particularly in the Sahel where a clear east-west gradient of tree cover change is indicated, the central Sahel being notably poor in tree species as shown for instance in the Lake Chad (Tjeri) and the Niger bend (Oursi, Kissi) areas. In areas where forests were well developed during the AHP, i.e. in the south and west, the establishment of the modern landscape was abrupt with a threshold crossed between 3300 and 2500 cal yr BP according to local conditions. Elsewhere in northern Africa the switch from tree (C_3) to grass (C_4) dominated landscapes occurred at approximately the same time, but more gradually. This review allows the timing of the ecosystem response at the end of the AHP be identified, which was remarkably synchronous throughout northern Africa, in contrast to hydrological data, which suggest a time transgressive end to the AHP (Shanahan *et al.* 2015).

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