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Holocene changes in African vegetation: tradeoff between climate and water availability

C. Hély[1], **A.-M. Lézine**[2], **and APD contributors**

[1]PALECO, CBAE, UMR5059 – CNRS-EPHE-Université Montpellier 2, Institut de Botanique, 163 rue Auguste Broussonnet, 34090 Montpellier, France
[2]LOCEAN, UMR7159 – CNRS-IRD-Université Pierre et Marie Curie-MNHN, Institut Pierre Simon Laplace, Boîte 100 – 4, place Jussieu 75252 Paris Cedex 05, France

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Correspondence to: C. Hély (christelle.hely-alleaume@univ-montp2.fr)

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Abstract

Although past climate change is well documented in West Africa through instrumental records, modeling activities, and paleo-data, little is known about regional-scale ecosystem vulnerability and long term impacts of climate on plant distribution and biodiversity. Here we use paleohydrological and paleobotanical data to discuss the relation between available surface water, monsoon rainfall and vegetation distribution in West Africa during the Holocene. The individual patterns of plant migration or community shifts in latitude are explained by differences among tolerance limits of species to rainfall amount and seasonality. Using the probability density function methodology, we show here that the widespread development of lakes, wetlands and rivers at the time of the "Green Sahara" played an additional role in forming a network of topographically defined water availability allowing for tropical plants to migrate north from 15 to 24° N (reached ca. 9 cal ka BP). The analysis of the spatio-temporal changes in biodiversity, through both pollen occurrence and diversity, shows that the core of the tropical rainbelt associated with the Intertropical Convergence Zone was centered at 15–20° N during the early Holocene wet period with comparatively drier/more seasonal climate conditions south of 15° N.

1 Introduction

During the early to mid-Holocene, the so-called "African Humid Period" (de Menocal et al., 2000), parts of the now hyper-arid Sahara were vegetated (e.g. Hoelzmann et al., 1998) and inhabited by humans (Kuper and Kröpelin, 2006). A dense fluvial network developed (Drake et al., 2011), and lakes and wetlands, now mostly desiccated, were widespread (Street and Grove, 1976; Hoelzmann et al., 1998; Kröpelin et al., 2008; Gasse, 2000; Lézine et al., 2011a). Climate simulations from general circulation models have highlighted the role of land surface conditions including vegetation cover and open water surfaces, and their feedbacks (Claussen and Gayler, 1997; Hoelzmann et al., 1998; Krinner et al., 2012) in amplifying the influence of orbital forcing on precipitation changes and the establishment of a so-called "Green Sahara". Using probability density functions (pdfs) performed on dated paleohydrological records, Lézine et al. (2011a) have shown that paleolakes related to increased monsoon rainfall during the Holocene extended up to 28° N, while the maximum expansion of lacustrine conditions occurred at 8.5 cal ka BP (between 12 and 5 cal ka BP) and reached roughly 25° N. Subsequently, with the dessication of this system from 7.5 cal ka BP onward, shallow water bodies and swamps became more prevalent between 16 and 23° N. Using a similar statistical approach, Watrin et al. (2009) have shown that tropical plant taxa may have migrated north by 5 to 7° latitude compared to their modern distribution in response to increased monsoon rainfall. Instead of having moved as communities in response to climate change (Hoelzmann et al., 1998), they appear to have behaved independently, migrating each at its own speed. The consequence of this was the relatively diverse vegetation assemblages characterized by the co-occurrence of species whose ranges do not overlap today.

In this paper, we use two distinct sets of paleodata (hydrological and pollen data) to examine the links between vegetation distribution, and changes in surface hydrology and rainfall in north-western Africa during the Holocene. Unlike Watrin et al. (2009) who focused their study on few selected taxa, we use here the complete set of pollen data from the African Pollen Database, as well as recently published pollen records (Lézine et al., 2011b). Three main pollen groups are analyzed: (1) the Guineo–Congolian group, mainly composed of humid (semi-deciduous or evergreen) forest taxa that grow under 1500 mm annual rainfall or more, (2) the Sudanian group, primarily composed of dry forest and savanna taxa (500–1500 mm) and (3) the Sahelian group, mainly composed of grassland or wooded grasslands taxa (150–500 mm) (Trochain, 1940; White, 1983). The Saharan group is only presented for information (Table B1). Due to the high diversity of plant species that share the same pollen morpho-type in tropical regions (Vincens et al., 2007), two broad categories are considered here: the "non exclusive" taxa whose tolerance may encompass several phytogeographical entities, and that are

classified according to the most humid phytogeographical entity they may refer to. This category includes both pollen grains corresponding to plants with a wide ecological range and/or plants displaying pollen morphology not easily identifiable at an optical view (e.g. *Combretum*-type including other genera and species of mostly Sudanian but also Sahelian and Guineo–Congolian phytogeographical affinities, Vincens et al., 2007). The second category concerns the "exclusive" taxa whose plant species are exclusively found in a given group, (e.g. *Anthocleista* is strictly Guineo–Congolian, Vincens et al., 2007). Given the uncertainties due to the heterogeneity of the data sets (Lézine et al., 2011a; Watrin et al., 2009), we have focused our study on the long-term evolution of the vegetation using a 500 or 1000 yr time interval from 15 cal ka BP to the present.

2 Material and methods

2.1 Study area and paleo-datasets

In order to focus on the Atlantic monsoon, the study area has been restricted to the 10–28° N region (Fig. 1) to avoid areas north of 30° N submitted to dominant influence of Mediterranean depressions during winter. Fossil pollen samples from 48 sites belonging to the studied region (Table A1) were extracted from the African Pollen Database[1] and from Lézine et al. (2011b). Such extraction included approximately 820 samples representative of the last 15 kyr BP, among which 22 sites reported only one date. These pollen data were compared to 1515 paleohydrological records already published by Lézine et al. (2011a) and stored at the NOAA paleoclimatology data center. It is clear from their geographic distribution that the scarcity of pollen sites could induce more bias in the data analysis as compared to the analysis performed using hydrological data that are far more numerous and cover almost the entire area except two regions. However,

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[1] http://apd.sedoo.fr/apd/accueil.htm

the pollen data used are the only ones available that have been checked by specialists and included in the African Pollen Database.

2.2 Analysis of pollen taxa ecological affinities and biodiversity indexes

All pollen taxa were classified according to the ecological affinities (Table B1) of their source plants (Vincens et al., 2007). We focused on three main groups: Guineo–Congolian representative of tropical humid (semi-deciduous or evergreen) forests, Sudanian representative of tropical dry forests, woodlands, and wooded savannas and Sahelian representative of semi-arid savannas and grasslands. Taxa belonging to the Saharan group are provided for information (Table B1). In parallel, we have checked all the pollen taxa corresponding to these groups in order to discuss biodiversity issues in terms of richness (number of taxa) and abundance as we have calculated their occurrence within each time interval of 500 or 1000 yr. Pollen and hydrological data were analyzed statistically using probability density functions (Kühl et al., 2002) on pollen/hydrological record presences. All statistical analyses were performed using the open source R software (R Development Core Team, 2007), with the Ash library (Gebhardt, 2009) for the *pdf* computation.

3 Results and discussion

Both non-exclusive and exclusive Guineo–Congolian groups displayed a similar Holocene distribution with a core area never exceeding 18° N and a maximum potential extension reaching 20° N, the occurrence of Guineo–Congolian plants being statistically insignificant north of this latitude (Fig. 2). Conversely, two clearly different patterns characterized the Sudanian group. Exclusive Sudanian taxa occupied a core area roughly similar to that of the Guineo–Congolian group except that it started earlier and continued toward the present at 14–16° N, whereas non-exclusive taxa covered a much larger region (Fig. 2). Their maximum potential extension reached 25° N during the

Early-Holocene, then gradually moved to more southern latitudes after 4 cal ka BP. The distribution of the Sahelian group strongly differed from the two others with a core area clearly centered at 19° N starting from Mid-Holocene and reinforced after 5.5 cal ka BP (Fig. 2). However, the maximum extent of this group clearly shows that Sahelian taxa were always present in the whole Sahara and Sahel during the Holocene.

The core area of both the lacustrine and palustrine hydrological records closely matches the maximum extent of the Sudanian group (Fig. 2). This shows that the widespread expansion of fresh-water bodies throughout the now arid and semi-arid areas of northern Africa during the AHP took place under a seasonal climate. Tropical elements were able to survive in association with wetter elements south of 24° N and in association with drier elements north of this latitude up to 28° N, i.e. roughly 6° N of their modern distribution (Watrin et al., 2009). Three broad latitudinal eco-climatic entities can be distinguished beyond the omnipresence of Saharan taxa (Fig. C1): latitudes north of 25° N were unequivocally dominated by Sahelian and Saharan elements throughout the Holocene. Between 20 and 25° N, the co-occurrence of Sudanian and Sahelian groups defined a typically “Sahelo–Sudanian” vegetational sector (Trochain, 1940). Then, south of 20° N the three phytogeographical groups cohabited with the clear dominance of the two tropical humid ones. This overall configuration and particularly the almost perfect superimposition of the exclusive Sudanian and the Guineo–Congolian groups (Fig. 2) confirmed earlier observations on the co-occurrence of plants during Early- to Mid-Holocene (Watrin et al., 2009) that occupy distinct distribution areas today (Watrin et al., 2007). The dramatic expansion of the Sahelian taxa from the mid-Holocene onwards was concomitant with the drying of most freshwater lakes throughout the Sahara and Sahel and clearly responded to the progressive aridification.

The timing of diversity changes (Fig. 3) points to long-term trends, which are likely related to climate change. South of 15° N, Sahelian taxa were of minor importance compared to the dominace of tropical humid taxa. Sudanian and Guineo–Gonolian taxa displayed similar trends in Early-Holocene, but with a clear dominance of Guineo–Congolian taxa. Then, after 6 cal ka BP, their trends diverged with Sudanian elements remaining stable to the present both in terms of diversity and occurrence, while the Guineo–Conoglian declined dramatically. This trend is particularly acute for the last millennium, reflecting the overall aridification of the most humid components of the tropical forest environment. Between 15 and 20° N, the Sahelian taxa progressively increased since the Early-Holocene, recording the drying of the regional environment. The number of Guineo–Congolian and Sudanian taxa display similar trends compared to the lower latitudes except that Sudanian elements significantly increased in Late-Holocene instead of remaining stable. North of 20° N, Sudanian taxa dominated the Early to Mid-Holocene vegetation, especially at 8.5 cal ka BP, when the maximum northward migration of tropical plants in the Sahara was recorded. During this period, Guineo–Congolian taxa were present but scarce.

Considering the number of exclusive Guineo–Congolian and Sudanian taxa in the three latitudinal zones (Fig. 4), two main observations can be made: the number of Sudanian taxa was higher south of 15° N than between 15 and 20° N during Early- and Mid-Holocene; and the Guineo–Congolian taxa were twice as numerous between 15 and 20° N compared to the southern latitudes. These distributions suggest a different rainfall pattern in comparison with the modern one with a more seasonal climate south of 15° N than between 15 and 20° N. Changes in these exclusive taxa through time, compared to the reconstructed wet surfaces (Lézine et al., 2011a) give additional information while emphasizing the role of soil water and rainfall in the enhanced expansion of tropical plants in West Africa during the Holocene. South of 15° N, exclusive Guineo–Congolian and Sudanian taxa display peaks in phase with the maximum extent of lakes and wetlands at 9, 6 and 3 cal ka BP. A similar distribution is observed north of 20° N, with the difference that the tropical humid taxa were comparatively rare and definitively disappeared after roughly 5.5 cal ka BP. The most likely hypothesis of this strong relation between plants and open surface waters is that tropical humid gallery forests developed along rivers and in the immediate vicinity of lakes and wetlands, allowing for tropical humid plants to coexist with plants with drier phytogeographical

affinities growing in the surrounding area. A more complex situation is observed over the 15–20° N region. If the number of exclusive Sudanian taxa is clearly related to the maximum presence of lakes and wetlands, this is not the case for the Guineo–Congolian taxa, which largely dominated with no major fluctuations during the 8.5–3.5 cal ka BP time interval. This suggests that the diversity of this group was not only dependent upon soil water availability. The Guineo–Congolian taxa found the best environmental conditions for their expansion in the 15–20° N region. We suggest that the distribution and diversity of these exclusive taxa during the AHP likely reflects the northward shift of the core of the tropical rain belt compared to nowadays with a mean position between 15 and 20° N over Northwestern Africa. This shift would be due to the increased upper-level divergence that would move the main convergence cells and the associated rainfall belt northward (Texier et al., 1997). This implied a relative drying in southernmost latitudes, explaining the prevalence of Sudanian taxa south of 15° N.

4 Conclusions

According to our study, soil water availability played a major role in the northward migration of tropical plants during the AHP with Sudanian and Guineo–Congolian trees using river banks as migration paths to enter drier (semi-desert, desert) environments. Its consequence was the setting of a mosaic-like environment and the biodiversity increase with the co-occurrence of plants whose ranges do not overlap today. A tropical seasonal climate characterized the Sahara and Sahel during the AHP. However, the distribution of the exclusive tropical humid (Guineo–Congolian) taxa clearly shows that the core of the rain belt was centered over the 15–20° N latitudinal region leaving the southernmost latitudes under comparatively drier conditions. The southern retreat of the rain belt from the Late-Holocene onward induced the aridification of the Sahel and the Sahara, and drove the regional establishment of taxa in their present-day latitudinal distribution.

Supplementary material related to this article is available online at http://www.clim-past-discuss.net/9/6397/2013/cpd-9-6397-2013-supplement.pdf.

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Table A1. Characteristics of the West African sites from which fossil pollen assemblages have been extracted (African Pollen Database).

Site ID	Site Name	Latitude (° N)	Longitude (° E)	Elevation (m a.s.l.)	Country	Time range (yr BP)	References
1	AMEKNI	22.7850	5.5183	1000	Algeria	7663	Guinet and Planque (1969)
2	TAESSA	23.1667	5.5167	2150	Algeria	4919–5661	Ballouche et al. (1995); Thinon et al. (1996)
3	BILGOY [Enneri Dirennao]	21.5183	17.1717	1135	Chad	8381	Schulz (1973, 1980)
4	KAMALA	14.0333	16.3167	420	Chad	11 784	Maley (1981)
5	KOUKA	13.1000	15.6333	283	Chad	11 002	Maley (1981)
6	MANDI	13.3833	14.7500	276	Chad	11 352	Maley (1981)
7	MOUSKORBE	21.5833	18.8833	2600	Chad	7473–9443	Maley (1981)
8	KA26	22.7333	16.6217	N/A	Chad	1780	Schulz (1980)
9	TARSO YEGA	20.6667	17.5833	2200	Chad	7718	Maley (1981)
10	TJERI	13.7333	16.5000	275	Chad	565–10 094	Maley (1981, 2004)
11	TJOLUMI	21.5167	18.1333	1115	Chad	6647	Schulz (1973, 1980)
12	TROU AU NATRON	21.0500	16.7500	1850	Chad	18 188	Maley (1981)
13	Baie de Saint Jean	19.4707	−16.3012	0	Mauritania	1778–3635	Lézine, A. M., unpublished data
14	Chemchane 1	20.9333	−12.2167	256	Mauritania	7590–9131	Lézine (1987, 1993); Lézine et al. (1990)
15	SEGUEDINE	20.1667	12.7833	412	Niger	8777	Baumhauer and Schulz (1984)
16	TERMIT	16.2000	11.0667	450	Niger	9981	Schulz et al. (1995)
17	ARI KOUKOURI	13.9167	13.1000	270	Niger	5488–9617	Schulz et al. (1995)
18	ARI KOUKOURI 85	13.9167	13.1000	270	Niger	7250	Schulz et al. (1995)
19	Nebenwadi – Enneri Achelouma [Profil XII]	22.3500	12.7000	650	Niger	7806	Schulz (1980)
20	SETTAFET	25.3500	11.4333	1100	Libyan Arab Jamahiriya	4710	Schulz (1980)
21	Uan Afuda Cave	24.8678	10.5003	922	Libyan Arab Jamahiriya	8836–9835	Mercuri (1999)
22	Uan Muhuggiag	24.8387	10.5078	915	Libyan Arab Jamahiriya	4496–7758	Mercuri et al. (1998)
23	Uan Tabu	24.8558	10.5237	915	Libyan Arab Jamahiriya	4218–9933	Mercuri and Trevisan Grandi (2001)
24	Shati	27.5000	13.8333	305	Libyan Arab Jamahiriya	6350	Delibrias et al. (1982)
25	BAL	13.3042	10.9430	300	Nigeria	341–11 905	Salzmann and Waller (1998); Salzmann (1999)
26	KAIGAMA	13.2510	11.5675	330	Nigeria	3567–11 112	Salzmann (1996); Salzmann and Waller (1998)
27	KAJEMARUM	13.3030	11.0240	300	Nigeria	2845–11 027	Salzmann and Waller (1998)
28	KULUWU	13.2170	11.5505	330	Nigeria	4703–11 406	Salzmann and Waller (1998)
29	TILLA	10.3907	12.1245	690	Nigeria	248–13 064	Salzmann (2000); Salzmann et al. (2002)
30	DIOGO 1	15.2667	−16.8000	8	Senegal	9990	Lézine (1987)
31	DIOGO 2	15.2667	−16.8000	8	Senegal	450–11 412	Lézine (1988b)
32	GUIERS 02	16.1167	−15.9167	0	Senegal	162–6703	Lézine (1988a)
33	GUIERS 03	16.2833	−15.8333	1	Senegal	1121–6764	Lézine (1988a)
34	LOMPOUL	15.4167	−16.7167	3	Senegal	2008–10 309	Lézine (1987, 1988b; Lézine and Chateauneuf (1991)
35	POTOU	15.1667	−16.8667	11	Senegal	193–11 399	Lézine (1987, 1988b; Lézine and Chateauneuf (1991)
36	TIGUENT	17.25	−16.0166	N/A	Mauritania	3342	Medus and Barbey (1979)
37	KISSI (BS6)	14.6183	−0.1367	280	Burkina Faso	567	Ballouche (1998)
38	OURSI	14.6528	−0.4860	290	Burkina Faso	52–3265	Ballouche and Neumann (1995)
39	BIR ATRUN	18.1667	26.6500	600	Sudan	6469–10 229	Ritchie and Haynes (1987); Ritchie (1987)
40	EL ATRUN	18.0167	27.1500	600	Sudan	10 334	Jahns (1995)

Table A1. Continued.

Site ID	Site Name	Latitude (° N)	Longitude (° E)	Elevation (m a.s.l.)	Country	Time range (yr BP)	References
41	OYO	19.2560	26.1747	510	Sudan	5187–10 363	Ritchie et al. (1985); Ritchie (1994)
42	SELIMA	21.3667	29.3060	270	Sudan	7643–11 021	Ritchie and Haynes (1987); Haynes et al. (1989)
43	THIAYE	14.9167	−17.5000	1	Senegal	5593–6371	Lézine (1987); Lézine et al. (1985)
44	GABRONG [Enneri Dirennao] GABR)	21.5000	17.1167	1115	Chad	8945	Schulz (1980)
45	TARSO YEGA GAVRILOVIC GAVR 1)	20.6667	17.5000	2000	Chad	8930	Schulz (1980)
46	Enneri Bardague [JAMT36]	21.4167	16.9167	N/A	Chad	9294	Schulz (1980)
47	YEBBI [GRA]	20.8667	18.0383	1440	Chad	9136	Schulz (1980)
48	YOA	19.05	20.5166	380	Chad	0–6034	Kröpelin et al. (2008); Lézine (2009); Lézine et al. (2011b)

Table B1. Classification of pollen taxa into Saharan Sahelian, Sudanian, and/or Guineo–Congolian groups according to the ecological affinities of the species they represent. A pollen taxon is considered as exclusive to a given group when it presents ecological affinities with only this group. The taxa nomenclature is from the African Pollen Database (Vincens et al., 2007) and respects the original determination provided by authors.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Acanthus-type	x			
Afraegle-type *paniculata*	x			
Ammannia-type	x			
Anthocleista	x			
Anthostema-type	x			
Anthostema-type *senegalense*	x			
Brachystegia	x			
Caesalpinia-type	x			
Chrysobalanus icaco/Parinari	x			
Connaraceae undiff.	x			
Dodonaea	x			
Dodonaea viscosa-type	x			
Dombeya-type *buettneri*	x			
Dombeya-type *quinqueseta*	x			
Elaeis guineensis	x			
Eremospatha	x			
Erythrococca-type *africana*	x			
Garcinia	x			
Harungana	x			
Harungana madagascariensis-type	x			
Hewittia-type *scandens*	x			
Landolphia-type	x			
Lophira alata-type	x			
Mallotus-type	x			
Meliaceae undiff.	x			
Millettia-type	x			
Myrianthus-type	x			
Myrianthus-type *serratus*	x			
Naucleae undiff.	x			
Nauclea-type	x			
Pancovia-type	x			
Pancovia-type *bijuga*	x			
Sorindeia-type *juglandifolia*	x			
Thunbergia	x			
Treculia	x			
Treculia africana-type	x			
Trema-type *orientalis*	x			
Vitellaria-type *paradoxa*	x			
Vitex-type	x			
Acalypha	x	x		
Adansonia digitata	x	x		
Afzelia africana-type	x	x		
Alchornea	x	x		
Alchornea cordifolia-type	x	x		
Anacardiaceae undiff.	x	x		
Annonaceae undiff.	x	x		
Antidesma-type	x	x		
Antidesma-type *venosum*	x	x		

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Aphania-type *senegalensis*	x	x		
Araliaceae undiff.	x	x		
Blighia	x	x		
Blighia sapida-type	x	x		
Bombax	x	x		
Bridelia ferruginea-type	x	x		
Bridelia micrantha-type	x	x		
Bridelia-type	x	x		
Bridelia-type *scleroneura*	x	x		
Burkea africana	x	x		
Caperonia	x	x		
Caperonia serrata-type	x	x		
Cardiospermum halicacabum-type	x	x		
Catunaregam-type *nilotica*	x	x		
Ceiba pentandra	x	x		
Cissampelos-type	x	x		
Clusiaceae undiff.	x	x		
Cochlospermum	x	x		
Cola cordifolia-type	x	x		
Combretaceae undiff.	x	x		
Cordia africana-type	x	x		
Cynometra-type	x	x		
Desmodium	x	x		
Detarium	x	x		
Dialium	x	x		
Dialium guineense-type	x	x		
Diospyros	x	x		
Dombeya-type	x	x		
Erythrococca-type	x	x		
Eugenia-type	x	x		
Gardenia-type	x	x		
Gardenia-type *imperialis*	x	x		
Haematostaphis-type *barteri*	x	x		
Hallea-type	x	x		
Hallea-type *stipulosa*	x	x		
Irvingiaceae undiff.	x	x		
Ixora-type	x	x		
Ixora-type *brachypoda*	x	x		
Jasminum	x	x		
Khaya-type	x	x		
Lophira	x	x		
Macaranga-type	x	x		
Manilkara-type	x	x		
Monechma-type *ciliatum*	x	x		
Monotes kerstingii-type	x	x		
Mussaenda	x	x		
Ormocarpum-type	x	x		
Parinari-type	x	x		
Parkia	x	x		
Paullinia pinnata	x	x		
Pseudospondias-type *microcarpa*	x	x		
Raphia	x	x		
Salacia senegalensis-type	x	x		
Schrebera arborea-type	x	x		
Stereospermum-type	x	x		
Syzygium-type	x	x		

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Syzygium-type *guineense*	x	x		
Tabernaemontana	x	x		
Teclea-type	x	x		
Tetracera	x	x		
Tetracera alnifolia-type	x	x		
Uapaca	x	x		
Verbenaceae undiff.	x	x		
Vitex-type *doniana*	x	x		
Ximenia	x	x		
Ximenia americana-type	x	x		
Zanthoxylum-type	x	x		
Zanthoxylum-type *zanthoxyloides*	x	x		
Albizia-type	x	x	x	
Allophylus	x	x	x	
Allophylus africanus-type	x	x	x	
Celtis	x	x	x	
Combretum-type	x	x	x	
Dalechampia	x	x	x	
Dichrostachys	x	x	x	
Gnidia-type	x	x	x	
Hemizygia bracteosa-type	x	x	x	
Hymenocardia	x	x	x	
Hymenocardia acida-type	x	x	x	
Mitragyna-type *inermis*	x	x	x	
Morelia senegalensis	x	x	x	
Musanga-type	x	x	x	
Piliostigma reticulatum-type	x	x	x	
Pseudocedrela kotschyi	x	x	x	
Pterocarpus-type	x	x	x	
Sapindaceae undiff.	x	x	x	
Tapinanthus-type	x	x	x	
Acanthaceae undiff.	x	x	x	x
Apocynaceae undiff.	x	x	x	x
Asteraceae undiff.	x	x	x	x
Caesalpiniaceae unfiff.x	x	x	x	x
Campanulaceae unfiff.x	x	x	x	x
Euphorbiaceae unfiff.x	x	x	x	x
Farsetia	x	x	x	x
Lippia-type	x	x	x	x
Mimosaceae unfiff.x	x	x	x	x
Moraceae unfiff.x	x	x	x	x
Myrtaceae unfiff.x	x	x	x	x
Phoenix	x	x	x	x
Phoenix reclinata-type	x	x	x	x
Rubiaceae unfiff.x	x	x	x	x
Rutaceae unfiff.x	x	x	x	x
Sapotaceae unfiff.x	x	x	x	x
Acalypha ciliata-type		x		
Acalypha crenata-type		x		
Adansonia		x		
Alysicarpus		x		
Basilicum-type *polystachyon*		x		
Borassus/Hyphaene		x		
Capparis tomentosa-type		x		
Cayratia-type		x		
Cissus		x		

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Clerodendrum		x		
Combretum-type *molle*		x		
Crossopteryx febrifuga		x		
Cussonia		x		
Entada/Prosopis		x		
Entada-type		x		
Eriosema-type		x		
Flueggea virosa-type		x		
Hygrophila		x		
Isoberlinia-type		x		
Kedrostis		x		
Lannea/Sclerocarya		x		
Maytenus		x		
Micrococca-type *mercurialis*		x		
Oxalis		x		
Pavetta		x		
Pentodon-type *pentandrus*		x		
Rhus-type *longipes*		x		
Salacia		x		
Sida		x		
Sopubia-type *parviflora*		x		
Spondias monbin-type		x		
Sterculia-type		x		
Sterculia-type *setigera*		x		
Strychnos		x		
Tacazzea-type *apiculata*		x		
Tacca leontopetaloides		x		
Vernonia perrottetii-type		x		
Vernonia-type *galamensis*		x		
Vigna-type		x		
Zornia		x		
Acacia ehrenbergiana-type		x	x	
Acacia gummifera-type		x	x	
Acacia nilotica-type		x	x	
Acacia polyacantha-type		x	x	
Acacia senegal-type		x	x	
Acacia tortilis-type		x	x	
Adenium obesum-type		x	x	
Aeschynomene		x	x	
Asystasia gangetica-type		x	x	
Bauhinia		x	x	
Bauhinia rufescens-type		x	x	
Boscia-type *angustifolia*		x	x	
Boscia-type *senegalensis*		x	x	
Boswellia-type		x	x	
Capparis fascicularis-type		x	x	
Capparis sepiaria-type		x	x	
Carissa edulis-type		x	x	
Cassia-type *occidentalis*		x	x	
Celosia argentea-type		x	x	
Celosia-type		x	x	
Celosia-type *trigyna*		x	x	
Celtis toka-type		x	x	
Centaurea-type *perrottetii*		x	x	
Cissampelos-type *mucronata*		x	x	
Combretaceae/Melastomataceae undiff.		x	x	

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Combretum-type *aculeatum*		x	x	
Combretum-type *glutinosum*		x	x	
Combretum-type *paniculatum*		x	x	
Commiphora		x	x	
Commiphora africana-type		x	x	
Cordia		x	x	
Cynoglossum-type		x	x	
Dichrostachys cinerea-type		x	x	
Erythrina		x	x	
Flueggea		x	x	
Gomphrena		x	x	
Indeterminable		x	x	
Justicia striata-type		x	x	
Justicia-type *flava*		x	x	
Lannea-type		x	x	
Lannea-type *acida*		x	x	
Lobelia		x	x	
Maytenus senegalensis-type		x	x	
Mitracarpus villosus		x	x	
Ocimum-type		x	x	
Phyllanthus-type		x	x	
Phyllanthus-type *amarus*		x	x	
Phyllanthus-type *fraternus*		x	x	
Phyllanthus-type *maderaspatensis*		x	x	
Phyllanthus-type *reticulatus*		x	x	
Piliostigma		x	x	
Pluchea		x	x	
Prosopis-type *africana*		x	x	
Spermacoce-type		x	x	
Spermacoce-type *chaetocephala*		x	x	
Spermacoce-type *radiata*		x	x	
Triumfetta-type		x	x	
Waltheria		x	x	
Acacia		x	x	x
Acacia seyal-type		x	x	x
Achyranthes-type *aspera*		x	x	x
Amaranthaceae unfiff.		x	x	x
Amaranthaceae/Chenopodiaceae undiff.		x	x	x
Apiaceae unfiff.		x	x	x
Asclepiadaceae unfiff.		x	x	x
Asparagus		x	x	x
Balanites		x	x	x
Balanites aegyptiaca-type		x	x	x
Barleria		x	x	x
Blepharis-type		x	x	x
Boerhavia-type		x	x	x
Boscia-type		x	x	x
Boscia-type *salicifolia*		x	x	x
Cadaba-type		x	x	x
Cadaba-type *farinosa*		x	x	x
Cadaba-type *glandulosa*		x	x	x
Capparidaceae unfiff.		x	x	x
Capparis		x	x	x
Capparis decidua-type		x	x	x
Caryophyllaceae unfiff.		x	x	x
Cassia-type		x	x	x

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Celastraceae unfiff.		x	x	x
Chenopodiaceae unfiff.		x	x	x
Chenopodium-type		x	x	x
Chrozophora		x	x	x
Citrullus		x	x	x
Clematis-type		x	x	x
Clematis-type *hirsuta*		x	x	x
Cleome brachycarpa-type		x	x	x
Cleome-type		x	x	x
Cleome-type *gynandra*		x	x	x
Clutia		x	x	x
Coccinia		x	x	x
Cocculus		x	x	x
Cocculus pendulus-type		x	x	x
Commelinaceae unfiff.		x	x	x
Commelina-type		x	x	x
Commelina-type *benghalensis*		x	x	x
Convolvulaceae unfiff.		x	x	x
Convolvulus-type		x	x	x
Corchorus-type		x	x	x
Cotula-type *anthemoides*		x	x	x
Crassula		x	x	x
Crateva adansonii		x	x	x
Crotalaria		x	x	x
Croton/Jatropha		x	x	x
Croton-type		x	x	x
Cucumis		x	x	x
Cuscuta-type		x	x	x
Euphorbia-type		x	x	x
Faidherbia albida		x	x	x
Ficus		x	x	x
Gentianaceae unfiff.		x	x	x
Geraniaceae unfiff.		x	x	x
Grewia-type		x	x	x
Heliotropium		x	x	x
Heliotropium strigosum-type		x	x	x
Hibiscus		x	x	x
Hypericum		x	x	x
Hyphaene-type		x	x	x
Indigofera		x	x	x
Kohautia		x	x	x
Lamiaceae unfiff.		x	x	x
Lotus arabicus-type		x	x	x
Maerua/Ritchiea		x	x	x
Maerua-type		x	x	x
Maerua-type *crassifolia*		x	x	x
Malvaceae unfiff.		x	x	x
Menispermaceae unfiff.		x	x	x
Mentha-type		x	x	x
Merremia-type		x	x	x
Monsonia		x	x	x
Nyctaginaceae unfiff.		x	x	x
Oldenlandia-type		x	x	x
Palmae unfiff.		x	x	x
Pavonia		x	x	x
Peristrophe-type		x	x	x

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Poaceae unfiff.		x	x	x
Polycarpaea-type		x	x	x
Polycarpon-type		x	x	x
Polycarpon-type *prostratum*		x	x	x
Ranunculaceae unfiff.		x	x	x
Rhamnaceae unfiff.		x	x	x
Rhus-type		x	x	x
Rhynchosia-type		x	x	x
Ricinus communis		x	x	x
Ruellia		x	x	x
Rumex		x	x	x
Salix		x	x	x
Salvadora		x	x	x
Salvadora persica-type		x	x	x
Salvadoraceae unfiff.		x	x	x
Sesbania		x	x	x
Solanaceae unfiff.		x	x	x
Solanum-type		x	x	x
Tamarindus-type *indica*		x	x	x
Tephrosia		x	x	x
Thymelaeaceae unfiff.		x	x	x
Tiliaceae unfiff.		x	x	x
Tinospora bakis-type		x	x	x
Trichodesma		x	x	x
Trichodesma africanum-type		x	x	x
Vahlia		x	x	x
Zygophyllaceae unfiff.		x	x	x
Cayratia-type *ibuensis*			x	
Guiera senegalensis			x	
Lamiaceae type 6 (exine type *Leucas*)			x	
Saxifraga hederifolia			x	
Abutilon			x	x
Aerva-type *javanica*			x	x
Aerva-type *lanata*			x	x
Aizoaceae unfiff.			x	x
Alternanthera			x	x
Ambrosia-type *maritima*			x	x
Arnebia hispidissima-type			x	x
Brassicaceae unfiff.			x	x
Cassia-type *italica*			x	x
Centaurea-type *senegalensis*			x	x
Chascanum			x	x
Cichorieae unfiff.			x	x
Cirsium			x	x
Cleome-type *arabica*			x	x
Cleome-type *monophylla*			x	x
Cleome-type *scaposa*			x	x
Commicarpus-type			x	x
Cynareae unfiff.			x	x
Euphorbia-type *hirta*			x	x
Galium-type			x	x
Helichrysum-type			x	x
Hyphaene-type *thebaïca*			x	x
Ipomoea-type			x	x
Lactuceae unfiff.			x	x
Lathyrus/Vicia			x	x

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Leucas-type			x	x
Limeum			x	x
Luffa-type			x	x
Lythraceae unfiff.			x	x
Nucularia perrini			x	x
Phyla-type *nodiflora*			x	x
Plantago lanceolata-type			x	x
Polygala-type			x	x
Psilotrichum-type			x	x
Psoralea			x	x
Pulicaria			x	x
Resedaceae unfiff.			x	x
Suaeda			x	x
Tamarix			x	x
Tamarix senegalensis-type			x	x
Tribulus			x	x
Tribulus terrestris-type			x	x
Veronica			x	x
Zygophyllum			x	x
Aerva-type				x
Aizoon canariense-type				x
Allium				x
Amaranthus-type				x
Anchusa-type				x
Anthyllis-type				x
Armeria-type				x
Artemisia				x
Asphodelus				x
Asphodelus-type *tenuifolius*				x
Astragalus-type				x
Atractylis-type				x
Boraginaceae unfiff.				x
Calligonum polygonoides				x
Campanula-type				x
Carduus-type				x
Caylusea-type				x
Centaurea-type				x
Chrozophora brocchiana-type				x
Cistaceae unfiff.				x
Cistanche				x
Cistus				x
Cleome-type *brachycarpa*				x
Cleome-type *chrysantha*				x
Cleome-type *parvipetala*				x
Commelina-type *forskalaei*				x
Corchorus-type *fascicularis*				x
Cornulaca monacantha-type				x
Cornulaca/Aerva				x
Cotula-type				x
Cressa-type *cretica*				x
Cucumis dispaceus-type				x
Cucurbitaceae unfiff.				x
Cupressaceae unfiff.				x
Cupressus-type				x
Cynomorium coccineum				x
Daucus-type				x

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Echium				x
Echium plantagineum-type				x
Ephedra				x
Ephedra alata-type				x
Ephedra distachya-type				x
Ephedra fragilis-type				x
Ephedra major-type				x
Ericaceae unfiff.				x
Erica-type				x
Erica-type *arborea*				x
Erodium				x
Fabaceae unfiff.				x
Fagonia				x
Genista-type				x
Gisekia pharnacioides-type				x
Grewia-type *villosa*				x
Helianthemum				x
Hyosciamus muticus-type				x
Hyoscyamus				x
Hyoscyamus niger-type				x
Inula-type				x
Juncus				x
Knautia				x
Launaea-type *taraxacifolia*				x
Lavandula-type				x
Leguminosae unfiff.				x
Limeum viscosum-type				x
Limonium-type				x
Limonium-type *humile*				x
Lotus				x
Medicago laciniata				x
Moltkiopsis ciliata				x
Myrtus-type				x
Myrtus-type *nivellei*				x
Nerium oleander				x
Neurada procumbens				x
Nitraria retusa				x
Olea				x
Olea europaea-type				x
Olea lapperrinei-type				x
Oleaceae unfiff.				x
Ornithogalum-type				x
Orobanche aegyptiaca-type				x
Pancratium-type				x
Panicum				x
Paronychia				x
Peganum				x
Pentzia monodiana-type				x
Peristrophe-type *paniculata*				x
Pistacia				x
Pistacia atlantica-type				x
Plantago				x
Plantago afra-type				x
Plantago amplexicaulis-type				x
Plantago ciliata-type				x
Plumbaginaceae unfiff.				x

Table B1. Continued.

Taxon Name [APD]	Guineo–Congolian	Sudanian	Sahelian	Saharan
Polygonaceae unfiff.				x
Polygonum persicaria-type				x
Polygonum plebeium-type				x
Ranunculus-type				x
Rhamnus-type				x
Rhus-type *tripartita*				x
Rosaceae unfiff.				x
Rumex vesicarius-type				x
Ruta montana-type				x
Salix ledermannii-type				x
Sclerocephalus arabicus				x
Scrophulariaceae unfiff.				x
Scrophularia-type *arguta*				x
Silene-type				x
Silene-type *lynesii*				x
Solanum-type *nigrum*				x
Spergula-type				x
Teucrium				x
Urticaceae unfiff.				x
Warionia-type				x
Zaleya-type *pentandra*				x
Zilla spinosa				x
Ziziphus-type				x
Ziziphus-type *mauritiana*				x

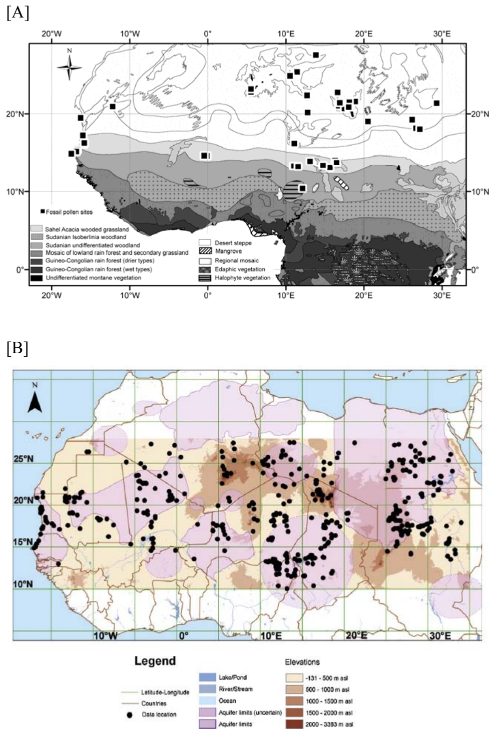

Fig. 1. Location of Western African sites over study area. **(A)** Fossil pollen samples (black squares) extracted from the African Pollen Database (http://apd.sedoo.fr/apd/accueil.htm) with the distribution of modern biomes (adapted from White, 1983) as background, and **(B)** fossil paleohydrological samples (black circles) from Lézine et al. (2011a).

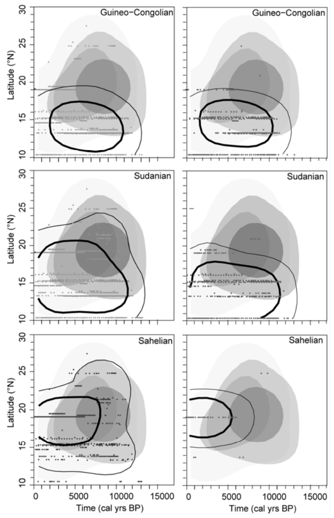

Fig. 2. Spatio-temporal changes (in latitude and millennia) in pollen taxa presences within the Guineo–Congolian, Sudanian, and Sahelian groups during the Holocene using probability density functions (Kühl et al., 2002). The left panel gives spatio-temporal distribution based on non-exclusive taxa, while the right panel gives distributions computed with only exclusive taxa. Bold line in each graph stands for the 0.5 isoprobability that delineates the core zone in which 50 % of the samples are the most concentrated (maximum presence). Similarly, thin line is the 0.85 isoprobability line delineating the maximum extent zone in which 85 % of the samples are included (Lézine et al., 2011a). Grey dots are representative of pollen samples referenced in latitude and time. Grey probability density functions in the background of each graph show the lacustrine (dark) and the palustrine (light) extent through time; the darker area reflecting the core zone (0.5 isoprobability computed on paleohydrological data), while the lighter area refers to the maximum extent (0.85 isoprobability) (from Lézine et al., 2011a).

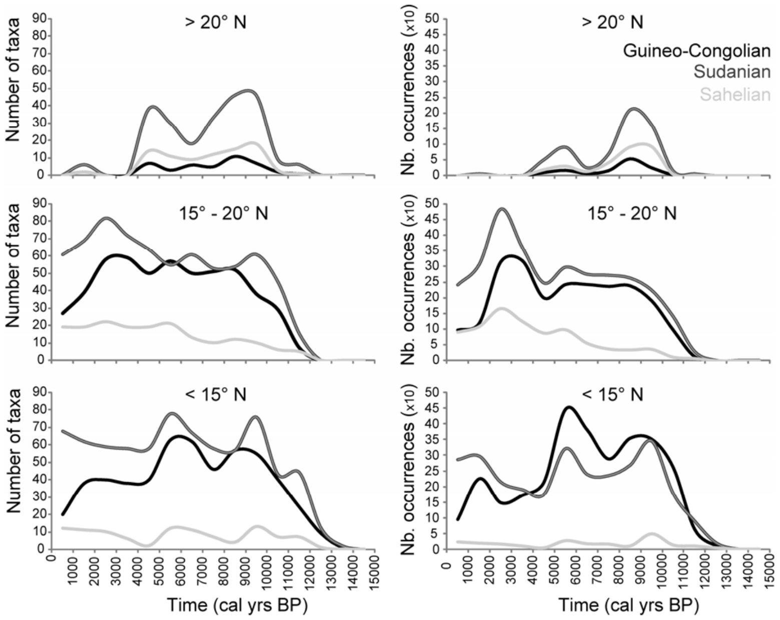

Fig. 3. Change in biodiversity within the Guineo–Congolian, Sudanian, and Sahelian groups (including exclusive and non exclusive taxa) as a function of time in the three latitudinal zones: < 15° N, 15–20° N, > 20° N, with the richness (number of taxa) on the left and their abundance (occurrences) on the right.

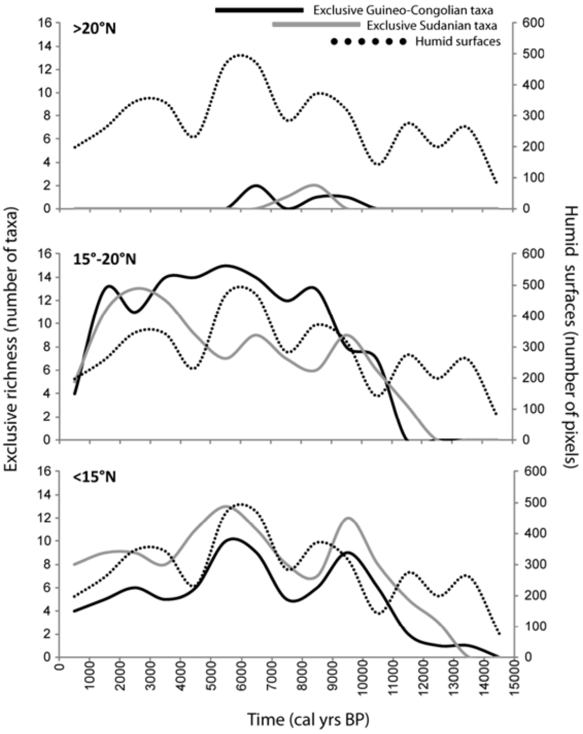

Fig. 4. Variation in the number of exclusive Guineo–Congolian (black line) and Sudanian (grey line) pollen taxa compared to paleohydrological changes during the Holocene for the entire studied area (dotted line). Humid surfaces refer to the maximum extent of humid conditions estimated from the 0.85 isoprobability space at each 1000 yr time interval.

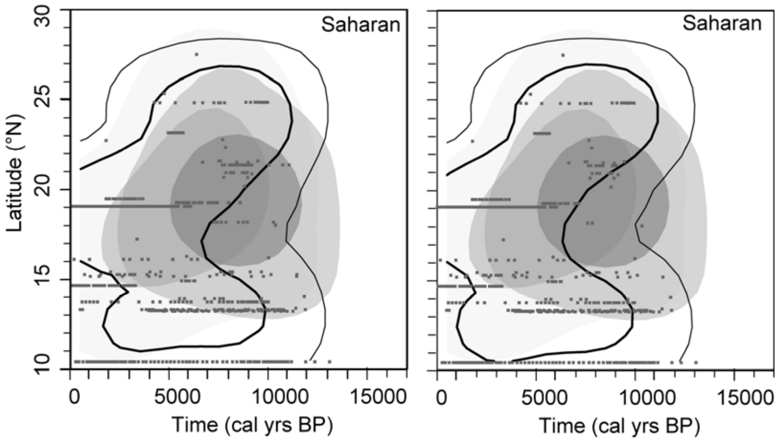

Fig. C1. Spatio-temporal changes (in latitude and millennia) in pollen taxa presences within the Saharan group during the Holocene using probability density functions (Kühl et al., 2002). As for Fig. 1 in the main text, the left panel gives spatio-temporal distribution based on non-exclusive taxa, while the right panel reports gives distributions computed with only exclusive taxa. Bold line in each graph stands for the 0.5 isoprobability that delineates the core zone in which 50 % of the samples are the most concentrated (maximum presence). Similarly, thin line is the 0.85 isoprobability line delineating the maximum extent zone in which 85 % of the samples are included (Lézine et al., 2011a). Grey dots are representative of pollen samples referenced in latitude and time. Grey probability density functions in the background of each graph show the lacustrine (dark) and the palustrine (light) extents through time (Lézine et al., 2011a); the darker area reflecting the core zone (0.5 isoprobability computed on paleohydrological data), while the lighter area refers to the maximum extent (0.85 isoprobability).