Available online at www.sciencedirect.com
ScienceDirect
C. R. Geoscience 341 (2009) 656–670
Comptes Rendus Geoscience

External geophysics, climate and environment

Plant migration and plant communities at the time of the "green Sahara"

Julie Watrin [a,*], Anne-Marie Lézine [a], Christelle Hély [b]

Contributors[1]

[a] *UMR 1752 CNRS, CEA, Orme-des-Merisiers, laboratoire des sciences du climat et de l'environnement, 91191 Gif-sur-Yvette cedex, France*

[b] *CNRS, CDF, IRD, centre européen de recherche et d'enseignement des géosciences de l'environnement, université Aix-Marseille, BP 80, 13545 Aix-en-Provence cedex 04, France*

Received 24 October 2008; accepted after revision 19 June 2009
Available online 13 August 2009

Written on invitation of the Editorial Board

Abstract

Around 8500 cal years BP, at the time of the maximum of the African Humid Period, lakes and wetlands expanded in the present-day Sahara while large paleodrainages were formed or re-actived, in response to an orbitally-induced increase in monsoon rainfall. It has been suggested that the direct consequence of this increase in rainfall was the northward displacement of the Sahara/Sahel boundary, thought to have reached 23°N in central and eastern Africa. Here, we show a more complex situation characterized by an increase in biodiversity as the desert accommodated more humid-adapted species from tropical forests and wooded grasslands: tropical plant species now found some 400 to 500 km to the south probably entered the desert as gallery-forest formations along rivers and lakes where they benefited from permanent fresh water. At the same time, Saharan trees and shrubs persisted, giving rise to a vegetation that has no analogue today. In this article, we present distribution maps of selected plant species to show both the amplitude of the vegetation change compared to the present and the composition of the past plant communities. We also estimate the migration rate of tropical plant taxa to their northernmost position in the Sahara. This study is based on the use of several data sets: a data set of the modern plant distribution in northern Africa and a data set of modern and fossil pollen sites (from the African Pollen Database, http://fpd.mediasfrance.org/ and http://medias.obs-mip.fr/apd/). ***To cite this article: J. Watrin et al., C. R. Geoscience 341 (2009).***

© 2009 Published by Elsevier Masson SAS on behalf of Académie des sciences.

Résumé

Migration des plantes et composition des communautés floristiques pendant la période du « Sahara vert ». L'ensemble des données palynologiques et paléobotaniques disponibles en Afrique de l'Ouest montrent que d'importants changements phytogéographiques ont eu lieu dans le désert saharien pendant les derniers millénaires. Autour de 8500 ans cal BP, au moment du maximum de la période humide, de nombreux lacs et surfaces humides se sont formés dans cette région aujourd'hui désertique, en réponse à un renforcement de la mousson liée à un changement orbital. Suite à l'augmentation des précipitations, la végétation du

* Corresponding author.
E-mail address: julie.watrin@lsce.ipsl.fr (J. Watrin).

[1] P. Cour, A. Ballouche, D. Duzer, H. Elenga, A. Frédoux, P. Guinet, S. Jahns, H. Kadomura, J. Maley, A.-M. Mercuri, I.A. Pons, I. Reynaud-Farrera, J.C. Ritchie, U. Salzmann, E. Schulz, M.G. Tossou, A. Vincens, M.P. Waller.

1631-0713/$ – see front matter © 2009 Published by Elsevier Masson SAS on behalf of Académie des sciences.
doi:10.1016/j.crte.2009.06.007

Sahara s'est modifiée et ce changement a été interprété comme un déplacement vers le nord de la limite Sahara/Sahel, qui aurait atteint jusqu'à 23°N dans le Sahara central et oriental. Notre étude des données palynologiques suggère une situation plus complexe qu'un simple déplacement latitudinal des zones de végétation, avec la coexistence, dans la steppe désertique, de plantes caractéristiques des régions plus humides, allant du Sahel jusqu'aux savanes et forêts soudaniennes et guinéocongolaises. Les espèces tropicales (e.g. *Alchornea*, *Celtis*...), qui sont aujourd'hui localisées 400 à 500 km plus au sud, ont probablement migré vers le Sahara le long des paléodrainages réactivés et se sont développées le long des cours d'eau et des dépressions de la région, dans des formations de type forêts galeries. La présence à la même période d'arbres sahariens, tels que *Ziziphus, Salvadora* et *Tamarix*, suggèrent que la végétation était constituée de l'interpénétration d'écosystèmes secs et plus humides, formant ainsi un paysage sans analogue actuel. Dans cet article, nous présentons d'abord les vitesses de migration des plantes tropicales, en calculant leur déplacement depuis les régions équatoriales, où elles ont persisté pendant le Dernier Maximum Glaciaire, jusqu'à leur position la plus septentrionale enregistrée dans le Sahara. Elles varient, en fonction des espèces, de 300 à 400 m/an. Nous avons ensuite estimé la répartition de certaines espèces en fonction de la latitude et du temps (sur les 14 000 dernières années), afin de discuter (1) de l'amplitude du changement environnemental par rapport aux paysages actuels, et (2) de l'association des espèces à l'intérieur de cet écosystème particulier. Cette étude est basée sur l'utilisation de plusieurs bases de données : une base de données botaniques, regroupant la répartition des plantes actuelles sur l'Afrique de l'Ouest et les bases de données palynologiques actuelles et fossiles (issues de l'*African Pollen Database*). ***Pour citer cet article : J. Watrin et al., C. R. Geoscience 341 (2009).***
© 2009 Publié par Elsevier Masson SAS pour l'Académie des sciences.

Keywords: West Africa; Fossil pollen; Biodiversity; Migration rates; Holocene; Green Sahara

Mots clés : Afrique de l'Ouest ; Pollen fossile ; Biodiversité ; Vitesse de migration ; Holocène ; Sahara vert

1. Introduction

Fossil plant remains, such as leaf impression or charcoals of tropical trees in Holocene deposits from Sudan and northern Niger, several hundred kilometres north of their modern distribution [49,83], as well as widespread forest relicts from the edge of the Guineo-Congolian forest to the Saharan desert [36], provide evidence for the former expansion of tropical forest ecosystems in West Africa. This has been related to the orbitally-induced increase in Atlantic monsoon rains during the Early Holocene [6,31]. The forest-savanna ecotone may have been displaced north by 350 km compared to the present [1], while the northern limit of the Sudanian zone of woodlands and the Sahelian zone of wooded grasslands may have been displaced by at least 4° (450 km) [60]). In a review paper, Hoelzmann et al. [26] suggest that the boundary between steppes and wooded grasslands was situated around 20°N in western Sahara and 25°N in eastern Sahara, and that steppes expanded widely to 30°N during the mid-Holocene. Pollen data confirm that a significant number of tropical tree species were present in the Saharan region during the Holocene [38]. This period, marked by a strong environmental change, with a high number of lakes and wetlands and occurrence of tropical humid plants in a region that is nowadays arid, is called the ''green Sahara''. The tropical humid species however rarely exceed 1% in any of the pollen sequences from the Sahara, which remained dominated by grasses. That clearly points to a major issue regarding past vegetation and plant dynamics in response to climate change: can the environmental history of West Africa be summarized as the migration of existing vegetation zones, or have tropical species behaved individually? Could we, from the available paleodata, estimate the migration rates of the main tropical tree species recovered in the Holocene sediments from the Saharan desert? In this paper, we use the data set of well-dated pollen sites from the African Pollen Database (APD) to discuss vegetation dynamics, migration rates and plant community composition within the Sahara during the Holocene Humid Period.

2. Material and methods

2.1. Pollen and plant data

The set of fossil pollen data includes 73 terrestrial sites located between 4.3°S and 25.5°N in western Africa (Fig. 1; Table 1), with 28 sites from the modern Saharan desert, 19 sites from the Sahel, 10 sites from the Sudanian zone of dry forests and woodlands and 16 sites from the Guineo-Congolian zone of forests. In this article, we refer to different plant ecosystem types, using terms like steppe or wooded grassland: steppe refers to more or less open low herbaceous formations; wooded grassland refers to dense herbaceous formations including widespread trees and shrubs [82]. Given the truncated nature of most of the lacustrine sedimentary sequences not only in arid areas [36] but also near the equator [77], very few of these sites display

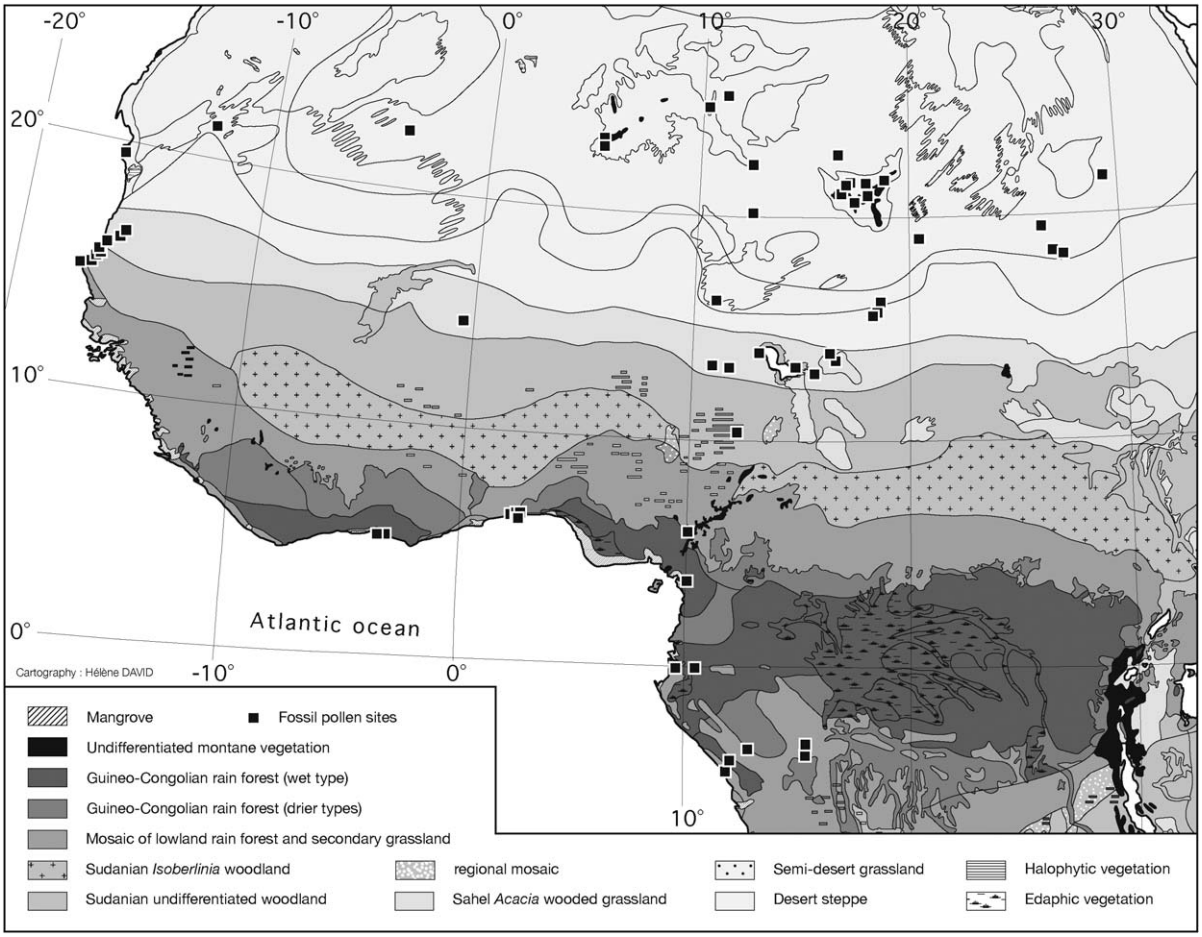

Fig. 1. Location of pollen sites in West and central Africa. Note the lack of data between 5 and 10°N. African vegetation map from [82].

Fig. 1. Localisation des sites polliniques en Afrique occidentale et centrale. Noter l'absence de données entre 5 et 10°N. Carte de végétation de l'Afrique tirée de [82].

a continuous Holocene sequence, with 27 of them having only one dated sample. The ^{14}C measurements were converted into calendar ages (cal years BP) using calibration from [4] and [52]. Age models were calculated by linear interpolation between two dated levels, taking into account sedimentary discontinuities and chronological uncertainties linked to the hard water effect [20].

After homogenization of the pollen nomenclature [79] and grouping of closest pollen types, a list of 476 pollen taxa was obtained including 261 trees, shrubs and lianas, 105 herbs and 109 undifferentiated pollen types. Thirty-three tree and shrub pollen taxa were selected on the basis that they were found in at least two pollen sites and are thought to indicate regional environmental conditions (Table 2, [38]). The present analysis focuses on a selection of 11 of them to illustrate the main plant distribution patterns in the Holocene Saharan region and to provide critical information for understanding vegetation dynamics in the tropics. Both pollen presence and percentage data are presented, the latter being calculated against a sum excluding indeterminable pollen grains.

As the determination of pollen is usually made at the genus or family levels, a given taxon may correspond to several plant species [79,81]. As a consequence, the list of all plants corresponding to each pollen taxon was established and the location of each individual plant record in West Africa was extracted from floras, botanical inventories or plant databases. Information from these different sources does not take into account the abundance of the species and the absence of a plant location point does not necessarily correspond to the absence of the species at that location [81]. Only the

Table 1
List of the pollen sites available in the African Pollen (APD) Database and located in the Sahara, in West Africa and near the central Atlantic coast.

Tableau 1
Liste des sites palynologiques disponibles dans l'*African Pollen Database* (APD) et localisés au Sahara, en Afrique occidentale et en Afrique centrale le long de la côte Atlantique.

Site Name (APD)	Longitude (decimal)	Latitude (decimal)	Altitude (Depth [m])	Country	Time interval		References
Amekni	5.52	22.79	1000	Algeria	7693		Guinet and Planque [24]
Taessa (Hoggar)	5.51	23.16	2150	Algeria	5661.5		Ballouche et al. [3]; Thinon et al. [74]; Pons and Quézel [50]
Dangbo	2.38	6.54	40	Benin	0	8371.3	Tossou [75]
Goho	2.58	6.44	35	Benin	887.4	7560	Tossou [75]
Lake Sélé	2.43	7.15	*NA*	Benin	274	8367	Salzmann and Hoelzmann [66]
Lake Nokoué	2.39	6.50	47	Benin	2330.7	8175.7	Tossou [75]
Yéviédié	2.38	6.54	53	Benin	1326.8	7926	Tossou [75]
Oursi	−0.49	14.66	290	Burkina Faso	0	3264.74	Ballouche and Neumann [2]
Lake Ossa [OW4]	10.75	3.80	8	Cameroon	28.7	5406.9	Reynaud-Farrera et al. [56]; Reynaud-Farrera [54,55]
Lake Ossa 1	10.02	3.78	8	Cameroon	15	635	Reynaud [53]; Reynaud-Farrera [54]
Shum Lake	10.05	5.85	1355	Cameroon	464	32420.44	Kadomura [32]
Bois de Bilanko [LH1]	15.35	−3.52	600	Congo	966.6	5467.3	Elenga [12]
Bois de Bilanko [LH3]	15.35	−3.52	600	Congo	2707.5	39380.5	Elenga [12]
Bois de Bilanko [LS3]	15.35	−3.52	600	Congo	12861		Elenga [12]; Elenga and Vincens [13]; Elenga et al. [14]
Coraf 1	11.85	−4.75	0	Congo	0	3506	Elenga [12]; Elenga and al. [15]
Coraf 2	11.85	−4.75	1	Congo	930	2978	Elenga [12]
Lake Kitina [KT3]	12.00	−4.27	120	Congo	200.9	6283	Elenga et al. [17]
Lake Sinnda [SN 2]	12.80	−3.84	128	Congo	450.9	6467	Vincens et al. [76]
Lake Sinnda [SN 3]	12.80	−3.84	128	Congo	0	4714.1	Vincens et al. [76]
Ngamakala 2	15.38	−4.08	400	Congo	495	23908.7	Elenga [12]
Ngamakala 4	15.38	−4.07	400	Congo	13178.8	28468.5	Elenga et al. [15]; Elenga et al. [16]
Songolo	11.86	−4.76	5	Congo	2761	7978	Fabing [19]; Elenga et al. [18]
Assinie	−3.32	5.13	0	Ivory Coast	8905		Frédoux and Tastet [22]; Frédoux [21]
IVCO3	−3.52	5.10	0	Ivory Coast	10979		Frédoux and Tastet [22]; Frédoux [21]
Messak Settafet	11.43	25.43	1100	Libya	4701.5		Schulz [71]
Uan Afuda Cave	10.50	24.87	922	Libya	8837	9307	Mercuri [46]
Uan Muhuggiag	10.50	24.83	915	Libya	4150	7697	Mercuri et al. [48]
Uan Tabu	10.52	24.86	915	Libya	4217	9745	Mercuri and Grandi [47]
Sebkha de Taoudenni	−4.00	22.67	120	Mali	6464.5		Cour and Duzer [8]
Baie de Saint Jean	−16.30	19.46	0	Mauritania	1777.5	3635	Lézine (unpublished)
Sebkha de Chemchane	−12.21	20.93	256	Mauritania	7590.5	9131.4	Lézine [34,37]; Lézine et al. [42]
Ari Koukouri 85	13.10	13.92	270	Niger	7249.5		Schulz [72]; Schulz et al. [73]
Ari Koukouri 88	13.10	13.92	270	Niger	5488	9617.4	Schulz [72]; Schulz et al. [73]
Nebenwadi - Enneri Achelouma 12	12.70	22.35	650	Niger	7805.5		Schulz [71]
Seguedine	12.78	20.16	412	Niger	8776.5		Baumhauer and Schulz [5]
Termit	11.07	16.20	450	Niger	9981		Schulz et al. [73]
Kaigama Oasis	11.56	13.25	300	Nigeria	3567.39	11111.93	Salzmann [62]; Salzmann and Waller [65]
Kajemarum Oasis	11.18	13.30	300	Nigeria	2844.68	11027.33	Holmes et al. [27]; Salzmann and Waller [65]; Salzmann [63]; Waller and Salzmann [80]
Kuluwu Oasis	11.55	13.21	330	Nigeria	4703.3	11405.6	Salzmann [62]; Salzmann and Waller [65]
Lake Bal	10.93	13.30	300	Nigeria	341.37	11905.13	Salzmann and Waller [65]; Holmes et al. [28]; Salzmann [63]; Waller and Salzmann [80]
Lake Tilla	12.11	10.38	690	Nigeria	247.85	13063.98	Salzmann [63,64]; Salzmann et al. [67]
Diogo 1	−16.80	15.26	8	Senegal	0	10826.47	Lézine [34,35]; Lézine and Chateauneuf [40]
Diogo 2	−16.80	15.26	8	Senegal	485.4	11412	Lézine [34,35]; Lézine and Chateauneuf [40]
Lake de Guiers 2	−15.91	16.11	0	Senegal	0	6702.66	Lézine [34,35]
Lake de Guiers 3	−15.91	16.11	0	Senegal	1121.1	6763.77	Lézine [34,35]
Lompoul	−16.71	15.35	3	Senegal	2007.6	10321.9	Lézine [34,35]; Lézine and Chateauneuf [40]
Potou	−16.50	15.75	11	Senegal	193.2	11399.2	Lézine [34,35]; Lézine and Chateauneuf [40]

Table 1 (*Continued*)

Site Name (APD)	Longitude (decimal)	Latitude (decimal)	Altitude (Depth [m])	Country	Time interval		References
Thiaye	−17.50	14.92	1	Senegal	5593.23	6371.44	Lézine [34]; Lézine et al. [41]; Chateauneuf et al. [7]
Touba Ndiaye 2	−16.86	15.16	6	Senegal	1208	12850	Lézine [34,35]; Lézine and Chateauneuf [40]
Bir Atrun	26.65	18.16	600	Sudan	6469.47	10228.53	Ritchie [57]; Ritchie and Haynes [60]
El Atrun	26.00	18.00	600	Sudan	10334		Jahns [30]
Oyo	26.45	19.30	510	Sudan	5186.9	10363	Ritchieet al. [61]; Ritchie [58]
Selima Oasis	29.30	21.36	270	Sudan	7643.18	11021.4	Ritchie and Haynes [60]; Haynes et al. [25]
Angéla-Kété	18.35	15.83	*NA*	Chad	25260.5		Maley [43]
Enneri Bardagué	16.91	21.41	*NA*	Chad	9294		Schulz [69,70]
Enneri Direnao	17.17	21.52	1135	Chad	8380		Schulz [69,70,71]
Enneri Tabi	17.05	21.33	*NA*	Chad	10523	12357	Schulz [71]
Fourtchiak Sud Ouest	18.27	15.95	*NA*	Chad	24516.5		Maley [43]
Kamala	15.00	14.00	*NA*	Chad	11783.5		Maley [43]
Kouka	15.51	13.11	283	Chad	11002		Maley [43]
Mandi	14.76	13.41	276	Chad	11352		Maley [43]
Mouskorbé	18.53	21.36	2600	Chad	7472.5	9443	Maley [43]
Nemra	18.55	16.30	*NA*	Chad	27000		Maley [43]
Ounianga	20.52	19.05	380	Chad	0	6033.5	Lézine (unpublished)
Tamarisken-Hügel - Bardagué	16.61	22.73	*NA*	Chad	1786		Schulz [71]
Tarso Yega	17.48	20.83	2200	Chad	7718.5		Maley [43]
Tarso Yega [Gavr I]	17.50	20.66	*NA*	Chad	8929.5		Schulz [69,70,71]
Tibesti Gabrong	17.10	21.75	*NA*	Chad	8948.5		Schulz [69,70,71]
Tjéri	16.50	13.73	275	Chad	565	10093.5	Maley [43,45]
Tjolumi	18.13	21.52	1115	Chad	6647		Schulz [69,70,71]; Gabriel [23]
Trou au Natron 688_690	16.50	20.00	1850	Chad	18188.5		Maley [43]
Trou au Natron Erg T63-64_Ka46	16.75	21.00	*NA*	Chad	15262.5		Schulz [71]
Yebbi Bou - Yebbigué [Gr A; Gr B]	18.03	20.86	1440	Chad	9136		Schulz [69,70,71]

occurrence of each plant species was considered to draw the modern distribution maps of plants corresponding to the selected pollen types.

2.2. Statistical analyses

Due to the wide geographical dispersion of pollen sites in West and central Africa, data are presented according to time and latitude, only. Two probability density functions [33,68] were calculated for each pollen taxon using respectively the distribution of pollen presence and the distribution of pollen percentages (Fig. 2B and C). Two probability thresholds were defined as the limit of the most probable occurrence of a pollen taxon in this spatiotemporal space: the 85% threshold displays the most similar contour compared to the limit of the presence whereas the 50% threshold points to the maximum of the distribution.

This probability space does not mean that the corresponding plants occupied the entire space during the past, but only that they may have occurred at this latitude. We used the same representation for the current distribution of plants to determine their probability density function over West Africa along longitude and latitude (Fig. 2A). All the analyses presented in this work were carried out using the open source R software[2].

3. Results: modern versus Holocene distribution of plants

3.1. Tropical humid plant types

The tropical humid pollen taxa include plant species with Guineo-Congolian, Guineo-Sudanian and Sudanian phytogeographical affinity. The modern distribution of tropical humid pollen types such as *Celtis*-type, *Alchornea*, *Syzygium*-type and *Piliostigma*, and their assigned climate spaces have been analyzed in detail in a previous study [81]. Except *Piliostigma*, which characterizes more open ecosystems of woodlands and wooded grasslands, all these tropical humid pollen types may occur in a wide range of wooded or forested

[2] http://www.r-project.org/.

Table 2
List of the tree pollen types present in at least two Saharan sites during the last 14,000 cal years BP. Taxa have been classified according to their phytogeographic affinity. Pollen types in italic in the table have been excluded as they represent too many plant species. The Temperate, Temperate-Mediterranean, Mediterranean-Montainous and Mediterranean pollen types have been excluded of further analyses, except Olea.

Tableau 2
Liste des types polliniques d'arbres présents dans au moins deux sites sahariens au cours des 14 000 ans. Les taxons sont classés en fonction de leur affinité phytogéographique.

Phytogeographic affinity	Family	Pollen type	Number of occurrences of each pollen type in the pollen sites located North of 18°N
Saharan-Mediterranean	*Rhamnaceae*	*Rhamnaceae undifferenciated*	*2*
Saharan-Mediterranean	Ephedraceae	Ephedra	19
Saharan	Polygonaceae	Calligonum polygonoides	6
Saharan	Boraginaceae	Moltkiopsis ciliata	7
Saharan	Salvadoraceae	Salvadora	10
Saharan	*Salvadoraceae*	*Salvadoraceae undiff.*	7
Saharan	Tamaricaceae	Tamarix	14
Saharan	Rhamnaceae	Ziziphus/Rhamnus	9
Tropical-Sahelian	Mimosaceae	Acacia	21
Tropical-Sahelian	Balanitaceae	Balanites	9
Tropical-Sahelian	Capparidaceae	Boscia/Cadaba	9
Tropical-Sahelian	Capparidaceae	Capparis	8
Tropical-Sahelian	Menispermaceae	Cocculus	5
Tropical-Sahelian	Burseraceae	Commiphora	7
Tropical-Sahelian	Capparidaceae	Maerua/Ritchiea	12
Tropical-Sahelian	Chenopodiaceae	Nucularia perrini	2
Tropical-Sahelian	Menispermaceae	Tinospora bakis-type	2
Tropical-Sudanian	Euphorbiaceae	Alchornea	3
Tropical-Sudanian	Palmae	Borassus/Hyphaene	3
Tropical-Sudanian	Ulmaceae	Celtis	11
Tropical-Sudanian	*Combretaceae*	*Combretaceae undiff.*	12
Tropical-Sudanian	Rubiaceae	Mitragyna-type inermis	2
Tropical-Sudanian	Myrtaceae	Eugenia/Syzygium	3
Tropical-Sudanian	Euphorbiaceae	Flueggea	3
Tropical-Sudanian	Anacardiaceae	Lannea/Sclerocarya	5
Tropical-Sudanian	Caesalpiniaceae	Piliostigma	4
Tropical-Sudanian	Anacardiaceae	Rhus/Antrocaryon/Pseudospondias	8
Tropical-Sudanian	Ebenaceae	Diospyros	1
Tropical-Sudanian	Hymenocardiaceae	Hymenocardia	1
Tropical-Sudanian	Euphorbiaceae	Macaranga/Mallotus/Mareya	1
Tropical-Sudanian	Palmae	Phoenix	2
Tropical-Sudanian	*Anacardiaceae*	*Anacardiaceae undiff.*	2
Tropical	*Mimosaceae*	*Mimosaceae undiff.*	*3*
Tropical	Moraceae	Ficus	5
Temperate	Betulaceae	Alnus	7
Temperate	Aceraceae	Acer	3
Temperate	Betulaceae	Betula	9
Temperate	Pinaceae	Cedrus	2
Temperate	Corylaceae	Ostrya/Carpinus orientalis-type	5
Temperate	Salicaceae	Populus	2
Temperate	Ulmaceae	Ulmus	3
Temperate	Tiliaceae	Tilia	5
Temperate-Mediterranean	Cupressaceae	Cupressaceae undiff.	5
Temperate-Mediterranean	Vitaceae	Vitis-type vinifera	2
Temperate-Mediterranean	Fabaceae	Ulex-type	3
Temperate-Mediterranean	Asparagaceae	Asparagus-genre	2
Mediterranean-Montainous	Oleaceae	Olea	10
Mediterranean-Montainous	Oleaceae	Oleaceae undiff.	5
Mediterranean-Montainous	Cupressaceae	Juniperus/Cupressus	10

Table 2 (*Continued*)

Phytogeographic affinity	Family	Pollen type	Number of occurrences of each pollen type in the pollen sites located North of 18°N
Mediterranean-Montainous	Ericaceae	Ericaceae undiff.	8
Mediterranean	Caesalpiniaceae	Ceratonia oreothauma	3
Mediterranean	Myrtaceae	Myrtus	3
Mediterranean	Apocynaceae	Nerium oleander	2
Mediterranean	Caesalpiniaceae	Cercis	2

habitats including swamp and gallery forests from the Guineo-Congolian to the Sahelian vegetation zones [78]. Their modern distribution in western Africa does not exceed 16–18°N to the north. Pollen grains from the corresponding species are found in Holocene sediments up to 20 to 25°N (Fig. 2B–D), i.e., 3° to 7°N of their northernmost present-day distribution (Fig. 2A). Moreover, probability density functions calculated from presence and percentage data confirm that the more humid plant types, *Alchornea, Celtis*-type and *Syzygium*-type, have been present near the equator in their current zone of distribution since 14,000 cal years BP [38]. Their penetration into areas currently under Sahelian and Saharan climates started roughly around 12,500 cal years BP, with specific taxa patterns: as a pioneer plant type, *Alchornea* expanded widely in the Early Holocene and reached its maximum abundance (27.9%) from 11,200 to 4600 cal years BP between 9° and 18°30′N, before its southward retreat during the Mid- to Late Holocene. *Celtis*-type also widely expanded throughout West Africa, but it remained of scattered occurrence with low abundance values (maximum = 4%). Its northernmost expansion occurred from 11,800 to 7600 cal years BP, spreading from 12° to 19°N. As compared to *Alchornea* and *Celtis*-type, the expansion of *Syzygium*-type within the Sahel and the Sahara was delayed by 1000 years (roughly 10,600 cal years BP), with its maximum abundance being recorded from 9400 to 2800 cal years BP between 9° and 19°N. *Piliostigma* displays a slightly different history since it has never been significantly present south of 10°N. During the Holocene, its maximum expansion occurred from 11,000 to 5500 cal years BP between 13° and 23°N (maximum = 2%).

3.2. Sahelian plant types

The modern Sahelian and Sahelo-Saharan wooded grasslands are characterized by the occurrence of *Acacia, Commiphora, Balanites*, *Salvadora* and *Boscia-Cadaba* pollen types [81]. During the Holocene, their northernmost occurrence was located up to 25°N in southern Libya, recording similar northward migration as the more humid Sudanian plant types. Probability density functions on pollen presence show that *Acacia* (maximum abundance of 12% reached at 22°N around 7800 cal years BP), *Balanites* (maximum abundance of 7.6% reached at 19°N around 3800 cal years BP) and *Salvadora* (maximum abundance of 20% reached at 21°N around 11,000 cal years BP) have expanded widely within the Saharan region since 12,000 cal years BP, while *Commiphora* and *Boscia-Cadaba* started their expansion roughly 500 to 1000 years later (with maximum percentages of 2.2% and 3.9%, respectively, reached at 19°N). While *Acacia* distribution remained relatively stable through time, *Commiphora, Balanites, Salvadora* and *Boscia-Cadaba* progressively retreated southward after 4500 cal years BP to reach their present-day position. Probability density functions from pollen percentages (Fig. 2C, 3.5 to 3.9) show that the more xeric plant types (*Salvadora* and *Boscia-Cadaba*) reached their maximum expansion earlier (11,500–11,000 cal years BP) than *Commiphora, Balanites* and *Acacia* for which the northernmost expansion successively occurred during a time interval spanning 8300 to 6300 cal years BP.

3.3. Saharan plant types

Calligonum and *Ephedra* are among the most ''arid'' types recovered in desert areas. They are currently found on sand dunes (e.g., ''grand erg'' in Algeria), up to the edge of the Mediterranean Sea to the north. *Ephedra* is also a characteristic component of mountain plant communities from the central Sahara. To the south, their area of distribution is delimited by the tropic of Cancer, except for one occurrence of *Calligonum* recorded at 18°N near Faya [51]. The Holocene distributions of these two plant types differs considerably from one another: *Ephedra* has been regularly present from 13,000 cal years BP to the present with a maximum density between 9000 and 5500 cal years BP (maximum abundance of 9.5% reached around 7500 cal years BP at 21°N), whereas the

expansion of *Calligonum* took place later, between 6000 and 2000 cal years BP (maximum of 5% reached at 25°N around 4200 cal years BP), with a southward expansion to roughly 20°N during the last four millennia.

4. Analysis: the migration rate of tropical plant types

Estimates of migration rates of tropical forest trees during their post-glacial northward movement is severely limited both by the scarcity of data, particularly between 5°S and 10°N, and by the incompleteness of the sedimentary records. Moreover, the Early Holocene period follows the Last Glacial Maximum at the end of the Late Pleistocene, which has been estimated as a period marked by a dry climate, related to the retreat of the tropical humid vegetation near the equator and the southern extension of the Sahara/Sahel boundary to 14°N [10,11,44]. The migration of the tropical humid plants in the Early-Mid Holocene probably started from the low latitudes of central Africa [1,38,39,84], but with the available fossil pollen data, we are only able to estimate the end of their progression, when they entered in the Sahara region. Taking into account the plant communities as a whole, Lézine [38] estimated that tropical plants entered the Saharan region roughly 7000 years after the onset of the Holocene Humid Period at 15,500 cal years BP. Here, we examine the first appearance of pollen grains from four selected tropical plant types and compare their migration rates and colonization patterns north of 10°N (Fig. 3):

- the first occurrence of *Celtis*-type in the Sahel is reported at Touba N'Diaye (15°10′N) at 12,450 cal years BP. It has also been registered at the same time at Tilla (10°23′ N). It was then reported at Selima (21°22′ N) at 10,700 cal years BP. Its northernmost occurrence was recorded in southern Libya at roughly 25°N between 9900–9500 cal years BP. Inferred migration rate estimates varied little around 400 m/year;
- *Syzygium*-type was present at Touba N'Diaye (15°10′N) as early as 12,850 cal years BP and at Tilla (10°23'N) 500 years later. Owing to age-model uncertainties at the base of the Touba N'Diaye series, the expansion of *Syzygium*-type was probably simultaneous at both sites. It was reported at Diogo (15°16′N) at 11,410 cal years BP, then at Chemchane (20°56′N) at 8900 cal years BP and at Taoudenni (22°6′N) at 6500 cal years BP. Inferred migration rate estimates varied from 600 m/year in the Sahel to 150 m/year in the Sahara;
- *Alchornea* appeared roughly simultaneously between 10°23′N (Tilla) and 14°02′N (Kamala) around 11,850–11,780 cal years BP. Then, it rapidly expanded to the west in the Niayes interdunes (15°–16°N) around 11,500–11,400 cal years BP. Its northernmost occurrence was first at el Atrun (18°10′N) at 10,330 cal years BP and then at Chemchane (20°56′N) at 8700 cal years BP. Inferred migration rate estimates averaged 505 m/year (460–570 m/year) in the Sahel and 200 m/year (235–195 m/year) in the Sahara;
- *Piliostigma's* northward movement started at 12,200 cal years BP at 10°23′N (Tilla). It reached the Manga region (Bal – 13°18′N) at 11,250 cal years BP before expanding widely throughout eastern Sahara, with its earliest occurrence dated from 10,360 cal years BP (Oyo – 19°15′N). Inferred migration rates estimates averaged from 340 m/year in the Sahel to 740 m/year in the Sahara.

These examples demonstrate that the northward progression of tropical trees throughout northern Africa did not follow a single trend: as pioneer plant types, *Alchornea*, *Piliostigma* and *Celtis*-type moved rapidly toward the northern tropic. The northward progression of *Syzygium*-type was comparatively slower. Mean values of migration rates presented here are only indicative, as they do not fully represent the real migration of the plants in the region, but only the probable northward migration estimated along latitudinal gradients from a limited number of pollen sites. Interestingly, they do not differ greatly from earlier pollen-based estimates of postglacial spread of temperate trees, such as the movement of spruce across northern America (200–376 m/year [9,59]) or northern Europe (500 m/year [29]).

5. Discussion: the "green Sahara"

Superimposed curves of probability density functions of all selected pollen types characteristic of the Sudanian, Sahelian and Saharan plant communities through time and latitude (Figs. 4 and 5) show that tropical humid plants started to expand northward since 12,000 cal years BP at 15°N and reached their maximum from 10,000 to 8000 cal years BP. They then remained present at this northernmost latitude until 5000 cal years BP, although they were more scattered at that time. Except for plants whose growth may have been favoured by soil humidity (*Syzygium*-type) and which may have persisted along rivers or fresh water bodies, all tropical humid taxa

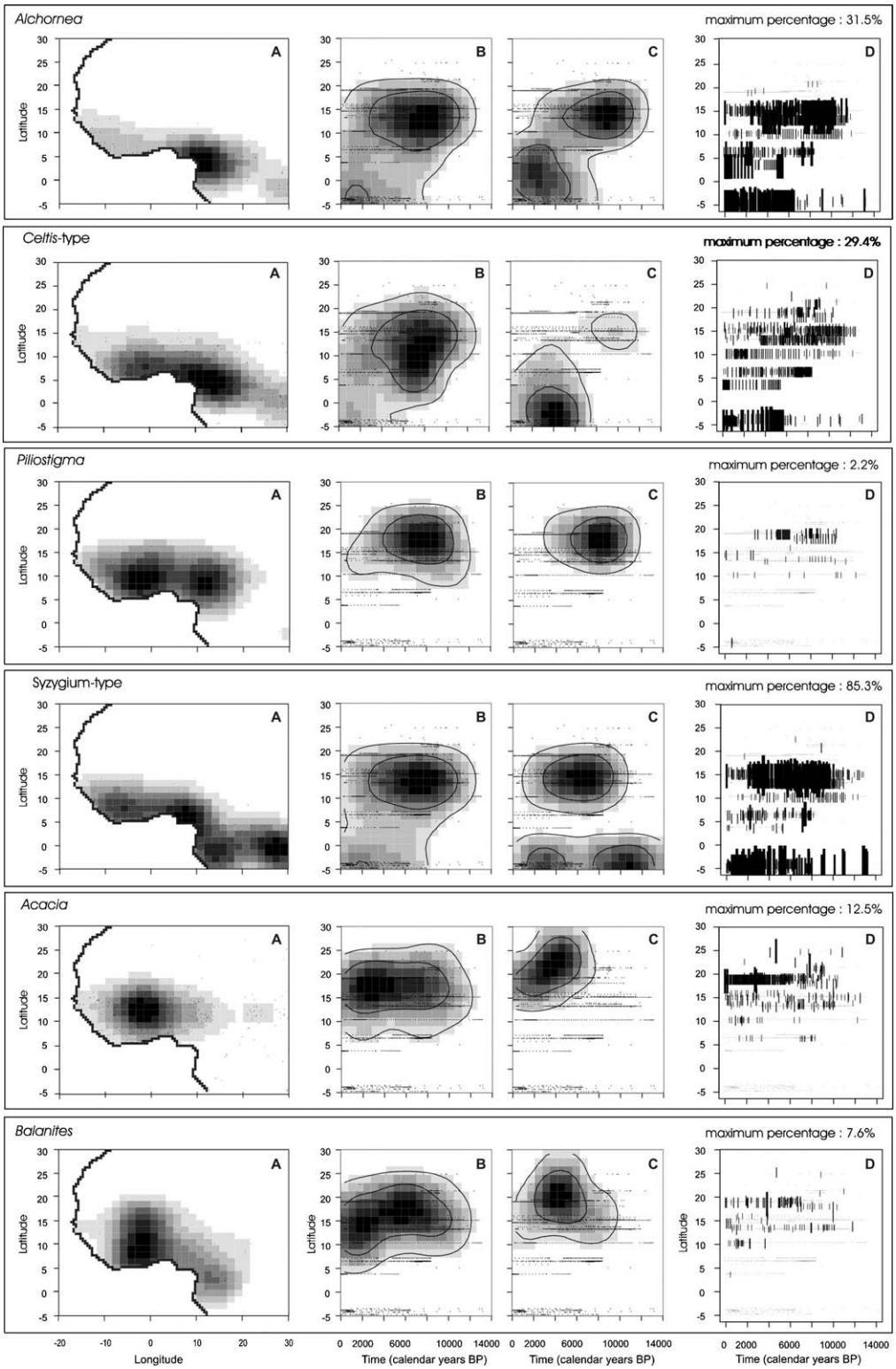

Fig. 2. Comparison between the latitudinal distribution of 11 selected fossil pollen taxa during the last 14,000 cal years BP and the present distribution of the corresponding plant taxa. **A**. Probability density functions established from the plant occurrences in West and central Africa. "**.**" symbolises each plant record. **B**. Probability density functions established from pollen taxon presence in the fossil assemblages. **C**. Probability

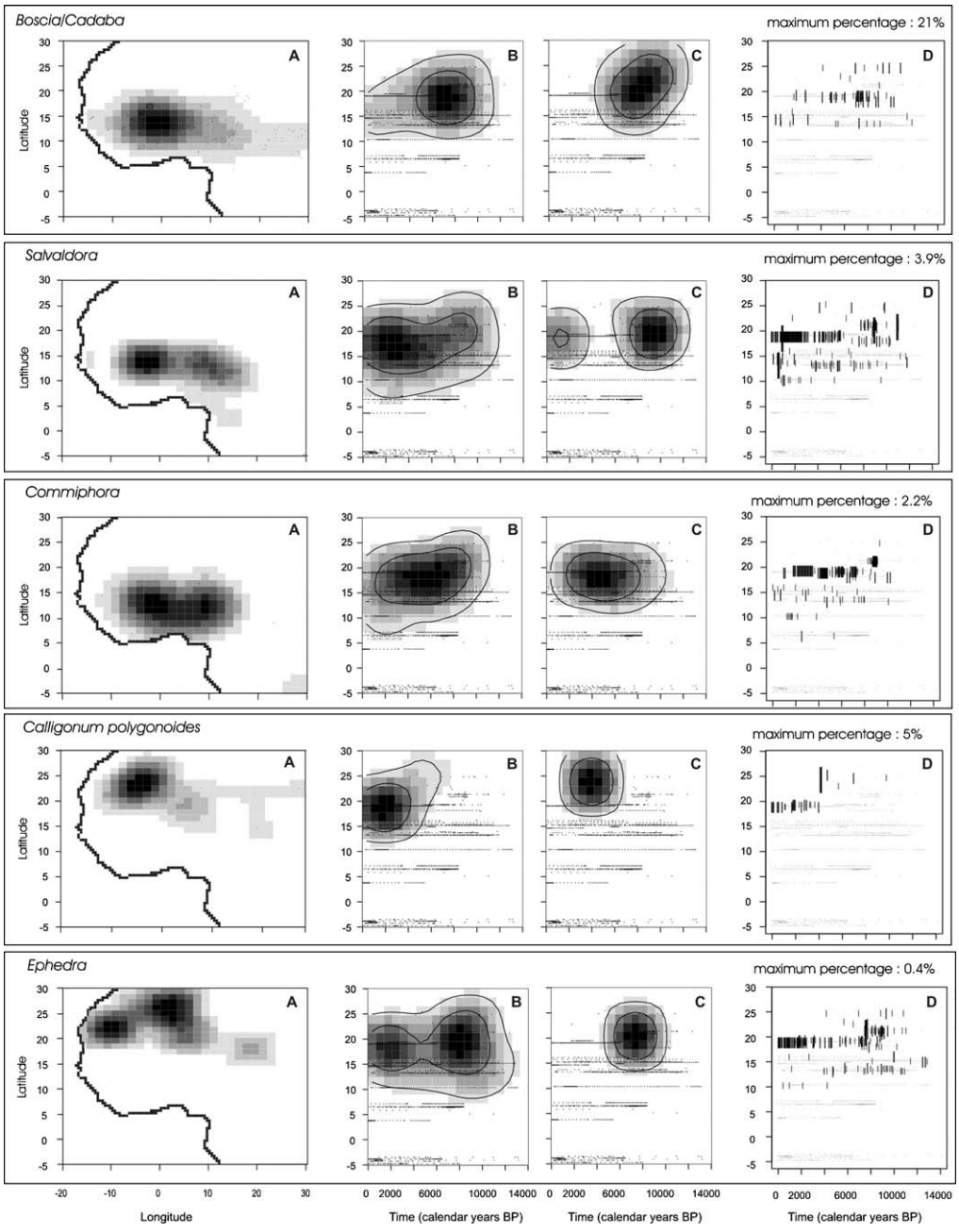

Fig. 2. (*Continued*).

density functions established from pollen percentages. **D**. Distribution of the pollen percentages of each taxon according to latitude and time. Size and thickness of the black lines are proportional to pollen percentages. The maximum percentage is indicated for each taxon.

Fig. 2. Comparaison entre la distribution latitudinale des 11 taxa sélectionnés dans cette étude au cours des derniers 14 000 ans et la répartition actuelle des plantes correspondantes. **A**. Densité de probabilité à partir de la présence des plantes en Afrique occidentale et centrale. Le « **.** » symbolise chaque présence de plante. **B**. Densité de probabilité à partir de la présence du pollen dans les assemblages fossiles en Afrique occidentale et centrale. **C**. Densité de probabilité à partir du pourcentage du pollen. **D**. Répartition des pourcentages polliniques de chaque taxon selon le temps et la latitude. La taille et l'épaisseur de chaque trait noir sont proportionnelles à la valeur du pourcentage. Le pourcentage maximum atteint par chaque taxon est indiqué.

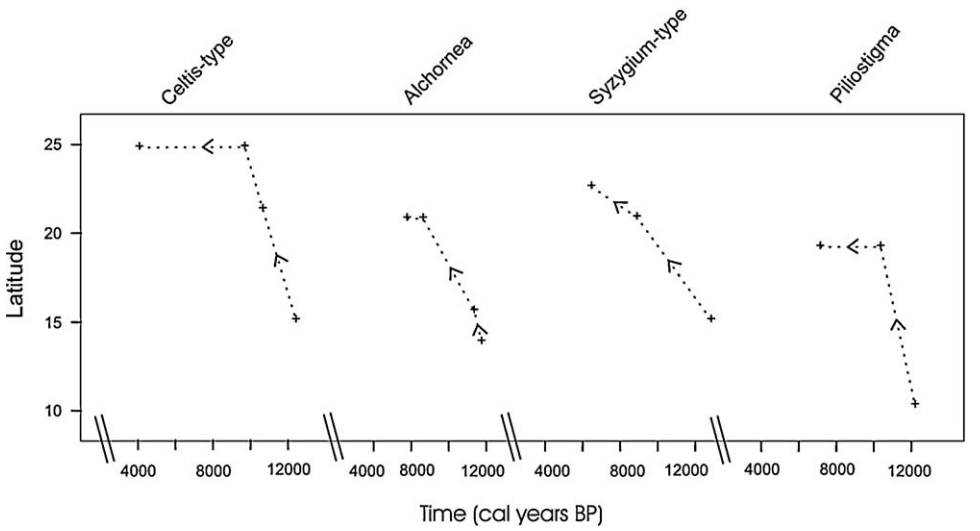

Fig. 3. Northward migration of the tropical pollen types. Pollen occurrences are represented with the "+" symbol, and the dashed line represents their estimated displacement. Pollen types have been ordered according to the date of first probable appearance at 20°N.

Fig. 3. Migration des types polliniques tropicaux en direction des latitudes sahariennes. La présence de chaque type est indiquée par une croix et la ligne interrompue figure son déplacement potentiel. Les types polliniques sont présentés en fonction de leur arrivée au-delà de 20°N.

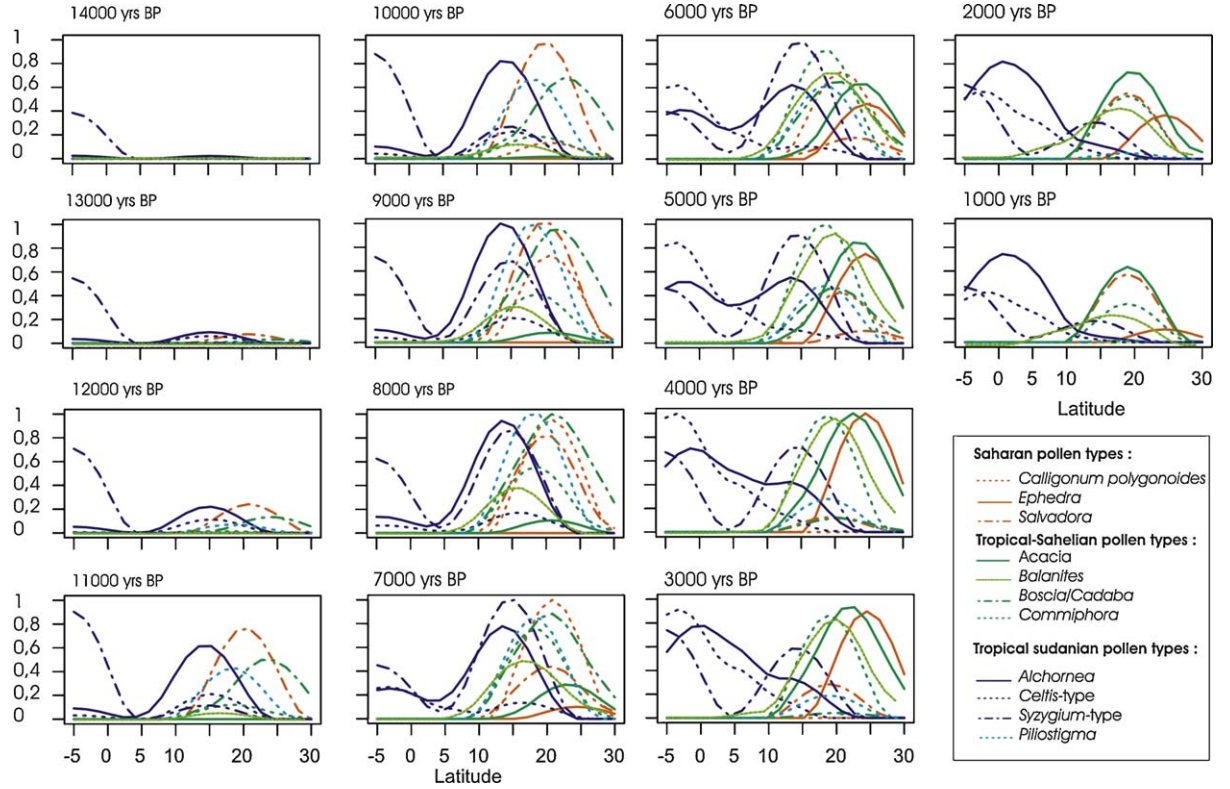

Fig. 4. Latitudinal distribution of selected pollen taxa from 14,000 to 1000 years BP. Curves show probability densities calculated from pollen percentages (normalised for each taxon and varying from 0 to 1).

Fig. 4. Répartition latitudinale des taxons sélectionnés dans notre étude de 14 000 à 1000 ans BP. Les courbes montrent les densités de probabilité calculée à partir du pourcentage pollinique (normalisées pour chaque taxon et variant entre 0 et 1).

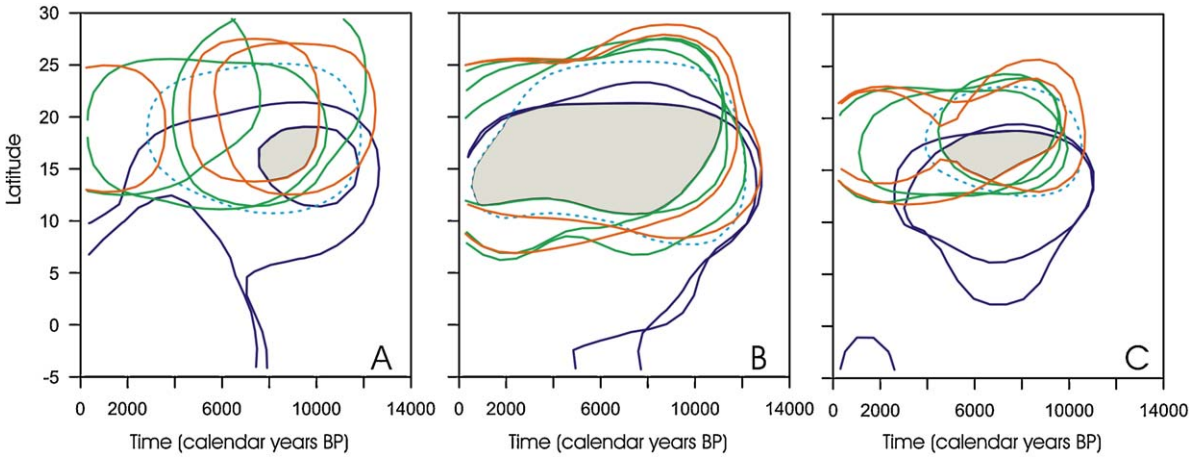

Fig. 5. Common space (in grey) occupied by tropical humid (Guineo-congolian and Sudanian), Sahelian and Saharan taxa. **A**. Probability density functions from the pollen percentages. The selected threshold, taken as the limit of the potential presence of the corresponding plants, corresponds to 85% of the total distribution of each taxon. **B**. Probability density functions from pollen presence (threshold = 85%). **C**. Probability density functions from pollen percentages (threshold = 50%).

Fig. 5. Espace commun (en gris) occupé par les taxons soudaniens, sahéliens et sahariens. **A**. Densité de probabilité calculée à partir du pourcentage pollinique. Le seuil sélectionné figurant la limite de la présence potentielle de la plante correspondante dans l'espace correspond à 58 % du total de la répartition de chaque taxon. **B**. Densité de probabilité calculée à partir de la présence du taxon (seul = 85 %). **C**. Densité de probabilité calculée à partir du pourcentage pollinique (seuil = 50 %).

retreated progressively south during the last 4000 years. During this latter period, *Alchornea* and *Celtis*-type density functions followed a similar decreasing trend, whereas *Piliostigma* maxima persisted in northern latitudes, confirming its adaptation to more xeric environmental conditions. Density probability functions for Saharan plant types (*Ephedra*) display an opposite trend with maxima reached at 25°N most of the time. Their southward expansion started from 7000 cal years BP and increased during the last 4000 years to reach 10–15°N. As expected, maxima of probability density functions for Sahelian and Sahelo-Saharian elements occur within an intermediate latitudinal range centred around 18°N. At this latitude, their maxima were reached from 11,000 to 8000 cal years BP; they then moved northward (ca 20°N) during the last 4000 years. *Acacia* displays a specific pattern since the highest values of probability density functions calculated from percentages arose between 6000 and 3000 cal years BP at 20–25°N. Probability densities calculated on pollen presence however did not confirm such northward progression.

This focus on individual plant species leads to a major conclusion: there is no evidence of one vegetation formation replacing another during the Holocene. Instead, all plants currently characteristic of distinct Saharan, Sahelian and Sudanian communities were able to occupy a common space ranging roughly between 12° and 20°N during the Holocene (Fig. 5B). The 85% probability threshold allows restriction of this common spatiotemporal space between 14° and 19°N from 10,000 to 7500 cal yrs BP (Fig. 5A) or 9500 to 4500 cal years BP (Fig. 5C) depending on the calculation method used. That suggests that the direct consequence of increased rainfall during the African Humid Period was an increase in biodiversity, since Saharan ecosystems accommodated more humid adapted plant types. For exemple, *Celtis*-type was among tropical humid taxa that did not form dense forest formations but were probably restricted to gallery forest formations along rivers and fresh water bodies. Our results lead us to question previous assumptions [26] according to which desert plant communities were absent from areas south of 30°N during the Mid-Holocene, and wooded grasslands extended to 25°N in central Africa. We observe here that plant species have responded individually to the climate change, leading to a complex floristic composition not analogue to the present vegetation. The same individual response, associated to unique plant associations, has been observed in temperate region during the last deglaciation, as suggested by the dissimilarity between fossil and modern pollen samples in North America [85].

6. Conclusions

It has been suggested that the direct consequence of the African Humid Period increase in rainfall was the northward displacement of the Sahara/Sahel boundary,

which is thought to have reached 23°N in central and eastern Africa. Our study shows that land-surface conditions in the Sahara formed a more complex situation characterized by an increase in biodiversity: plants of the present desert region accommodated more humid-adapted species from tropical forests and wooded grasslands. Tropical plant species, today found some 400 to 500 km southward, probably entered the desert as gallery-forest formations along rivers and lakes where they benefited from permanent fresh water. At the same time, Saharan trees and shrubs persisted, making a complex, ''no-analogue'' situation. This demonstrates that the vegetation history of the Sahara and the Sahel during the last few thousand of years has not merely been one of migration of the existing vegetation zones. Tropical plant types have intruded into the Saharan region at various rates, suggesting that they behaved individually rather than as a migrating community.

Acknowledgements

This work was supported by the French Centre national de la recherche scientifique (CNRS), Commissariat à l'énergie atomique (CEA) and Agence nationale de la recherche (ANR) through the ''Sahelp'' project. We thank the African Pollen Database contributors for allowing access to pollen data, H. David for drawings, J.-P. Cazet and F. Aptel for assistance. LSCE publication n° 4002.

References

[1] A. Aubréville, Contribution à la paléo-histoire des forêts d'Afrique tropicale, Société d'Éditions de Géographie maritime et coloniale, Paris, 1949.

[2] A. Ballouche, K. Neumann, A new contribution to the Holocene vegetation history of the West African Sahel: pollen from Oursi, Burkina Faso and charcoal from three sites in northeast Nigeria, Vegetation History and Archaeobotany 4 (1995) 31–39.

[3] A. Ballouche, M. Reille, M. Thinon, H.N. Barakat, M. Fontugne, La végétation holocène des montagnes du Sahara Central : une nouvelle conception, in: A. Le Thomas, E. Roche (Eds.), 2e symposium de Palynologie africaine, Publications occasionnelles du Centre international pour la formation et les échanges géologiques (CIFEG) 31, (1995), pp. 9–17.

[4] E. Bard, M. Arnold, B. Hamelin, N. Tisnérat-Laborde, G. Cabioch, Radiocarbon calibration by means of mass spectrometric $^{230}Th/^{234}U$ and ^{14}C ages of corals: an updated database including samples from Barbados, Mururoa and Tahiti, Radiocarbon 40 (3) (1998) 1085–1092.

[5] R. Baumhauer, E. Schulz, The Holocene lake of Seguedine, Kaouar, NE Niger, Palaoecology of Africa 16 (1984) 283–291.

[6] P. Braconnot, S. Joussaume, N. de Noblet, G. Ramstein, Mid-Holocene and Last Glacial Maximum African monsoon changes as simulated within the Paleoclimate Modelling Intercomparison Project, Global and Planetary Change 26 (2000) 51–66.

[7] J.J. Chateauneuf, H. Faure, A.M. Lézine, Facteurs contrôlant la genèse et la destruction des tourbes tropicales du littoral ouest-africain, Doc. BRGM 110 (1986) 77–91.

[8] P. Cour, D. Duzer, Persistance d'un climat hyperaride au Sahara Central et Méridional au cours de l´Holocène, Rev. de Géogr. Physique Géol. dyn. 18 (2–3) (1976) 175–198.

[9] P.A. Delcourt, H.R. Delcourt, Long-term forest dynamics in the temperate zone, Springer-Verlag, New York, 1987.

[10] L.M. Dupont, Marine palynology of interglacial-glacial transitions, in : G. Kukla, E. Went (Eds.), Start of a glacial, NATO ASI 13, Springer, Heidelberg, 1992, pp. 137–155.

[11] L.M. Dupont, H. Hooghiesmtra, The Saharan-Sahelian boundary during the Brunhes chron, Acta Botanica Neerlandica 38 (4) (1989) 405–415.

[12] H. Elenga, Végétation et climat du Congo depuis 24 000 ans B.P., Analyse palynologique de séquences sédimentaires du pays Batéké et du littoral, Thèse, université Aix-Marseille III, 1992, 238 pp.

[13] H. Elenga, A. Vincens, Paléoenvironnements quaternaires récents des plateaux Batéké (Congo) : étude palynologique des dépôts de la dépression du bois de Bilanko, in : R. Lanfranchi, D. Schwartz (Eds.), Paysages quaternaires de l'Afrique centrale Atlantique, Orstom, Paris, 1990, pp. 271–282.

[14] H. Elenga, A. Vincens, D. Schwartz, Présence d'éléments forestiers montagnards sur les Plateaux Batéké (Congo) au Pléistocène supérieur : nouvelles données palynologiques, Palaeoecology of Africa 21 (1991) 239–252.

[15] H. Elenga, D. Schwartz, A. Vincens, Changements climatiques et action anthropique sur le littoral congolais au cours de l'Holocène, Bull. Soc. géol. France 163 (1) (1992) 83–90.

[16] H. Elenga, D. Schwartz, A. Vincens, Pollen evidence of Late Quaternary vegetation and inferred climate changes in Congo, Palaeogeogr., Palaeoclimatol., Palaeoecol. 109 (1994) 345–356.

[17] H. Elenga, D. Schwartz, A. Vincens, J. Bertaux, C. de Namur, L. Martin, D. Wirrmann, M. Servant, Diagramme pollinique Holocène du lac Kitina (Congo) : mise en évidence de changements paléobotaniques et paléoclimatiques dans le massif forestier du Mayombe, C. R. Acad. Sci., Paris Ser.IIa 323 (1996) 403–410.

[18] H. Elenga, A. Vincens, D. Schwartz, A. Fabing, J. Bertaux, D. Wirrmann, L. Martin, M. Servant, Le marais estuarien de la Songolo (Sud Congo) à l'Holocène moyen et récent, Bull. Soc. géol. France 172 (3) (2001) 359–366.

[19] A. Fabing, Contribution à la connaissance des paléoenvironnements holocènes du Sud-Congo : étude par spectrométrie infrarouge de la carotte S2 (marais de la Songolo, Pointe Noire), Mémoire de Maîtrise de Géographie, Strasbourg University, 1995, 92 p.

[20] J.Ch. Fontes, F. Gasse, PALHYDAF (Paleohydrology in Africa) Program: objectives, methods, results, Palaeogeogr., Palaeoclimatol., Palaeoecol. 84 (1991) 191–215.

[21] A. Frédoux, Pollens et spores d'espèces actuelles et quaternaires de régions périlagunaires de Côte d'Ivoire, Thèse, université de Montpellier, 1978, 106 p.

[22] A. Frédoux, J.P. Tastet, Apport de la palynologie à la connaissance paléogéographique du littoral ivoirien entre 8 000 et 12 000 ans BP, in: 7th African Micropaleontological Colloquium, Ife-Ife, Nigeria, 1976, pp. 1–7.

[23] B. Gabriel, Zum ökologischen Wandel im Neolithikum der östlichen Zentralsahara, Berliner Geographische Abhandlungen 27 (1977) 111.

[24] P. Guinet, D. Planque, Résultats de l'analyse pollinique, in: G. Camps (Ed.), Amekni, Néolithique Ancien du Hoggar, Mémoires du Centre de Recherches anthropologiques, préhistoriques et ethnographiques, organisme de coopération scientifique en Algérie, Arts et métiers graphiques, Paris, 1969, pp. 186–188.

[25] C.V. Haynes, C.H. Eyles, L.A. Pavlish, J.C. Ritchie, M. Rybak, Holocene palaeoecology of the eastern Sahara; Selima Oasis, Quaternary Science Reviews 8 (1989) 109–136.

[26] P. Hoelzmann, D. Jolly, S.P. Harrison, F. Laarif, R. Bonnefille, H.J. Pachur, Mid-Holocene land-surface conditions in northern Africa and the Arabian Peninsula: A data set for the analysis of biogeophysical feedbacks in the climate system, Global Biogeochemical Cycles 12 (1) (1998) 35–52.

[27] J.A. Holmes, F.A. Street-Perrott, M. Allen, P. Fothergill, D. Harkness, D. Kroon, R.A. Perrott, Holocene palaeolimnology of Kajemarum Oasis, northern Nigeria: an isotopic study of ostracodes, autigenic carbonate and organic carbon, J. Geol. Soc. 154 (1997) 311–319.

[28] J.A. Holmes, M.J. Allen, F.A. Street-Perrott, M. Ivanovich, R.A. Perrott, M.P. Waller, Late Holocene palaeolimnology of Bal Lake, northern Nigeria, a multidisciplinary study, Palaeogeogr., Palaeoclimatol., Palaeoecol. 148 (1999) 169–185.

[29] B. Huntley, H.J.B. Birks, An atlas of past and present pollen maps for Europe: 0–13000 years ago, Cambridge Univ. Press, Cambridge, 1983.

[30] S. Jahns, A Holocene pollen diagram from El Atrun, northern Sudan, Vegetation History and Archaeobotany 4 (1995) 23–30.

[31] S. Joussaume, K.E. Taylor, P. Braconnot, J.F.B. Mitchell, J.E. Kutzbach, S.P. Harrison, I.C. Prentice, A.J. Broccoli, A. Abe-Ouchi, P.J. Bartlein, C. Bonfils, B. Dong, J. Guiot, K. Herterich, C.D. Hewitt, D. Jolly, J.W. Kim, A. Kislov, A. Kitoh, M.F. Loutre, V. Masson, B. McAvaney, N. McFarlane, N. de Noblet, W.R. Peltier, J.Y. Peterschmitt, D. Pollard, D. Rind, J.F. Royer, M.E. Schlesinger, J. Syktus, S. Thompson, P. Valdes, G. Vettoretti, R.S. Webb, U. Wyputta, Monsoon changes for 6000 years ago: Results of 18 simulations from the Paleoclimate Modeling Intercomparison Project (PMIP), Geophys. Res Lett. 26 (1999) 859–862.

[32] H. Kadomura, Origin of grassfields landscape in the West Cameroon Highlands, in : H. Kadomura, J. Kiyonaga (Eds.), Savannization Processes in Tropical Africa II, Tokyo Metropolitan University, Japan, 1994, pp. 47–85.

[33] N. Kühl, C. Gebhardt, T. Litt, A. Hense, Probability density functions as botanical-climatological transfer functions for climate reconstruction, Quaternary Research 58 (3) (2002) 381–392.

[34] A.M. Lézine, Paléoenvironnements végétaux d'Afrique Nord-Tropicale depuis 12 000 B.P. : analyse pollinique de séries sédimentaires continentales (Sénégal-Mauritanie), Thèse, Université Aix-Marseille II, 1987, 180 p.

[35] A.M. Lézine, Les variations de la couverture forestière mésophile d'Afrique occidentale au cours de l'Holocène, C. R. Acad. Sci., Paris Ser.II 307 (1988) 439–445.

[36] A.M. Lézine, Late Quaternary vegetation and climate of the Sahel, Quaternary Research 32 (1989) 317–334.

[37] A.M. Lézine, Chemchane, histoire d'une sebkha, Sécheresse 4 (1993) 25–30.

[38] A.M. Lézine, Pollen records, postglacial, in : A. Scott, Elias (Eds.), Encyclopaedia of Quaternary Sciences, Vol. 4, Elsevier, 2007, pp. 2682–2698.

[39] A.M. Lézine, J.P. Cazet, High-resolution pollen record from core KW31, Gulf of Guinea, documents the history of the lowland forests of West Equatorial Africa since 40,000 yr ago, Quaternary Research 64 (2005) 432–443.

[40] A.M. Lézine, J.J. Chateauneuf, Peat in the Niayes of Senegal: depositional environment and Holocene evolution, Journal of African Earth Sciences 12 (1991) 171–179.

[41] A.M. Lézine, S. Bieda, H. Faure, J.L. Saos, Étude palynologique et sédimentologique d'un milieu margino-littoral : la tourbière de Thiaye (Sénégal), Sci. géol. Bull. 38 (1) (1985) 79–89.

[42] A.M. Lézine, J. Casanova, C. Hillaire-Marcel, Across an Early Holocene humid phase in western Sahara: Pollen and isotope stratigraphy, Geology 18 (1990) 264–267.

[43] J. Maley, Études palynologiques dans le bassin du Tchad et paléoclimatologie de l'Afrique Nord-Tropicale de 30.000 ans à l'époque actuelle, Orstom, Paris, Travaux et Documents 129, 1981, 586 p.

[44] J. Maley, The African rain forest vegetation and palaeoenvironments during Late Quaternary, Climatic Change 19 (1991) 79–98.

[45] J. Maley, Le bassin du Tchad au Quaternaire recent : formations sédimentaires, paléoenvironnements et préhistoire. La question des paléotchads, in: A.M. Sémah, J. Renault-Miskovsky (Eds.), L'évolution de la végétation depuis deux millions d'années, Guides de la Préhistoire Mondiale, Éditions Errance, 2004, pp. 179–217.

[46] A.M. Mercuri, Palynological analysis of the Early Holocene sequence, in: The Uan Afuda cave, Hunter-Gatherer societies of Central Sahara. Arid Zone Archaeology, Monographs 1, ch. 8, Edizioni All'Insegna del Giglio, Firenze, 1999, pp. 149–253.

[47] A.M. Mercuri, G.T. Grandi, Palynological analyses of the Late Pleistocene, Early Holocene and Middle Holocene layers, in: E.A.A. Garcea (Ed.), Uan Tabu in the settlement history of the Libyan Sahara, Arid Zone Archaeology, Monographs 2, ch. 10, Edizioni All'Insegna del Giglio, Firenze, 2001, pp. 161–188.

[48] A.M. Mercuri, G.T. Grandi, G.T., M. Mariotti Lippi, M. Cremaschi, New pollen data from the Uan Muhuggiag rockshelter (Libyan Sahara, VII-IV millennia BP), in: M. Cremaschi, S. di Lernia (Eds.), Wadi Teshuinat - Palaeoenvironment and prehistory in south-western Fezzan (Libyan Sahara), Survey and excavations in the Tadrart Acacus, Erg Uan Kasa, Messak Settafet and Edeyen of Murzuq, 1990–1995, Edizioni All'Insegna del Giglio, Firenze, 1998, pp. 107–122.

[49] K. Neumann, Holocene Vegetation of the Eastern Sahara: Charcoal from Prehistoric sites, African Archaeological Review 7 (1989) 97–116.

[50] A. Pons, P. Quézel, Premières remarques sur l'étude palynologique d'un guano fossile du Hoggar, C. R. Acad. Sci., Paris 246 (1958) 2290–2292.

[51] P. Quézel, La végétation au Sahara. Du Tchad à la Mauritanie, Gustav Ficher Verlag, Stuttgart, 1965, 333 p.

[52] P.J. Reimer, M.G.L. Baillie, E. Bard, A. Bayliss, J.W. Beck, C. Bertrand, P.G. Blackwell, C.E. Buck, G. Burr, K.B. Cutler, P.E. Damon, R.L. Edwards, R.G. Fairbanks, M. Friedrich, T.P. Guilderson, K.A. Hughen, B. Kromer, F.G. McCormac, S. Manning, C. Bronk Ramsey, R.W. Reimer, S. Remmele, J.R. Southon, M. Stuiver, S. Talamo, F.W. Taylor, J. van der Plicht, C.E. Weyhenmeyer, Terrestrial Radiocarbon Age Calibration, 0–26 cal kyr BP, Radiocarbon 46 (2004) 1029–1058.

[53] I. Reynaud, Introduction à l'étude des relations Homme-Milieu naturel dans les forêts du Cameroun, Étude palynologique des sédiments du lac Ossa au cours des derniers siècles, Mém. de DEA, Université Montpellier II, France, 1991.

[54] I. Reynaud-Farrera, Histoire des paléoenvironnements forestiers du Sud-Cameroun à partir d'analyses palynologiques et statisti-

ques de dépôts Holocènes et actuels, Thèse, Université Montpellier II, 1995, 198 p.
[55] I. Reynaud-Farrera, Late Holocene vegetational changes in South-West Cameroon, in: H.N. Dalfes, G. Kukla, H. Weiss (eds), Climate change in the Third millennium BC climate change and old world collapse, Subseries I "Global Environmental Change", 1996, pp. 641–652.
[56] I. Reynaud-Farrera, J. Maley, D. Wirrmann, Végétation et climat dans les forêts du Sud-Ouest Cameroun depuis 4 770 ans BP : analyse pollinique des sédiments du Lac Ossa, C. R. Acad. Sci., Paris Ser. IIa 322 (1996) 749–755.
[57] J.C. Ritchie, A Holocene pollen record from Bir Atrun, Northwest Sudan, Pollen et Spores 29 (4) (1987) 391–410.
[58] J.C. Ritchie, Holocene pollen spectra from Oyo, northwestern Sudan: problems of interpretation in a hyperarid environment, The Holocene 4 (1) (1994) 9–15.
[59] J.C. Ritchie, G.M. MacDonald, The patterns of postglacial spread of white spruce, Journal of Biogeography 13 (1986) 527–540.
[60] J.C. Ritchie, C.V. Haynes, Holocene vegetation zonation in the eastern Sahara, Nature 330 (1987) 645–647.
[61] J.C. Ritchie, C.H. Eyles, C.V. Haynes, Sediment and pollen evidence for an Early to Mid-Holocene humid period in the Eastern Sahara, Nature 314 (1985) 352–355.
[62] U. Salzmann, Holocene vegetation history of Sahelian zone of NE-Nigeria: Preliminary results, Palaeoecol. Afr. 24 (1996) 103–114.
[63] U. Salzmann, Zur holozänen Vegetations- und Klimaentwicklung der westafrikanischen Savannen - Paläoökologische Untersuchungen in der Sahel- und Sudanzone NO-Nigerias, PhD Thesis, University of Wuerzburg, Frankfurt, 1999, 144 p.
[64] U. Salzmann, Are modern savannas degraded forests? - A Holocene pollen record from the Sudanian vegetation zone of NE Nigeria, Vegetation History and Archaebotany 9 (2000) 1–15.
[65] U. Salzmann, M. Waller, The Holocene vegetational history of the Nigerian Sahel based on multiple pollen profiles, Review of Palaeobotany and Palynology 100 (1998) 39–72.
[66] U. Salzmann, P. Hoelzmann, The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the Late Holocene, The Holocene 15 (2) (2005) 190–199.
[67] U. Salzmann, P. Hoelzmann, I. Morczinek, Late Quaternary climate and vegetation of the Sudanian zone of Northeast Nigeria, Quaternary Research 58 (2002) 73–83.
[68] C.A. Schölzel, Palaeoenvironmental transfer functions in a Bayesian framework with application to Holocene climate variability in the Near East, Universität Bonn, Bonn, 2005, 110 pp.
[69] E. Schulz, Zur quartären Vegetationsgeschichte der zentralen Sahara unter Berücksichtigung eigener pollenanalystischer Untersuchungen aus dem Tibesti-Gebirge, Staatsexamensarbeit FU Berlin, 1973.
[70] E. Schulz, Aktueller Pollenniederschlag in der zentralen Sahara und Interpretationsmöglichkeiten quartärer Pollenspektren, Palaeoecology of Africa 9 (1976) 8–14.
[71] E. Schulz, Zur Vegetation der östlichen zentralen Sahara und zu ihrer Entwicklung im Holozän, Würzburger Geographische Arbeiten 51, 1980, 194 p.
[72] E. Schulz, The southern limit of the Mediterranean vegetation in the Sahara during the Holocene, Historical Biology 9 (1994) 137–156.
[73] E. Schulz, S. Pomel, A. Abichou, U. Salzmann, Climate and man. Questions and answers from both sides of the Sahara, in: A. Le Thomas, E. Roche (Eds.), 2e symposium de palynologie africaine/2nd Symposium on African Palynology (Tervuren, Belgique, 6–10 mars 1995), Publications Occasionnelles du Centre International pour la Formation et les Echanges en Géosciences (CIFEG) 31, 1995, pp. 35–47.
[74] M. Thinon, A. Ballouche, M. Reille, Holocene vegetation of the Central Saharan Mountains: the end of a myth, The Holocene 6 (4) (1996) 457–462.
[75] M.G. Tossou, Recherche palynologique sur la végétation Holocène du Sud-Bénin (Afrique de l'Ouest), Thèse, Université de Lome (Togo), 2002, 133 p.
[76] A. Vincens, D. Schwartz, J. Bertaux, H. Elenga, C. de Namur, Late Holocene climatic changes in western Equatorial Africa inferred from pollen lake Sinnda, Southern Congo, Quaternary Research 50 (1998) 34–45.
[77] A. Vincens, D. Schwartz, H. Elenga, I. Reynaud-Farrera, A. Alexandre, J. Bertaux, A. Mariotti, L. Martin, D. Meunier, F. Nguetsop, M. Servant, S. Servant-Vildary, D. Wirrmann, Forest response to climate changes in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscape, J. Biogeogr. 26 (1999) 879–885.
[78] A. Vincens, L. Bremond, S. Brewer, G. Buchet, P. Dussouillez, Modern pollen-based biome reconstructions in East Africa expanded to southern Tanzania, Review of Palaeobotany and Palynology 140 (2006) 187–212., doi:10.1016/j.revpalbo.2006.04.003.
[79] A. Vincens, A.M. Lézine, G. Buchet, D. Lewden, A. Le Thomas, Contributors, African Pollen Database inventory of tree and shrub pollen types, Review of Palaeobotany and Palynology 145 (2007) 135–141., doi:10.1016/j.revpalbo.2006.09.004.
[80] M. Waller, U. Salzmann, Holocene vegetation changes in the Sahelian zone of NE Nigeria: The detection of anthropogenic activity, Palaeoecol. Africa 26 (1999) 85–102.
[81] J. Watrin, A.M. Lézine, K. Gajewski, A. Vincens, Pollen-Plant-Climate relationships in Sub-Saharan Africa, Journal of Biogeography 34 (2007) 489–499, doi:10.1111/j.1365-2699.2006.01626.x.
[82] F. White, La végétation de l'Afrique, Orstom, Unesco, Paris, 1983, 384p.
[83] G.E. Wickens, Quaternary plant fossils from the Jebel marra volcanic complex and their paleoclimatic interpretation, Palaeogeogr., Palaeoclimatol., Palaeoecol. 17 (2) (1975) 109–122.
[84] G.E. Wickens, Palaeobotanical speculations and Quaternary environments in the Sudan, in: M.A.J. Williams, D.A. Adamson, (Eds.), A Land between Two Niles, Quaternary geology and biology of the central Sudan, Balkema, Rotterdam, 1982, pp. 23–50.
[85] J.W. Williams, B.N. Shuman, T. Webb III, Dissimilarity Analyses of Late-Quarternary Vegetation and Climate in Eastern North America, Ecology 82 (12) (2001) 3346–3362.