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

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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 richness, 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 middle 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, 2004; Gasse, 2000; Kröpelin et al., 2008; 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 (*pdf*s) 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, each migrating 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.

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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 northwestern Africa during the Holocene. Unlike Watrin et al. (2009), who focused their study on a 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). Pollen taxa have been grouped into four main phytogeographical groups (Guineo–Congolian, Sudanian, Sahelian, and Saharan, respectively) in order to show the broad-scale changes in the vegetation distribution through time.

2 Material and methods

2.1 Study area and paleo-data sets

In order to focus on the Atlantic monsoon, the study area has been restricted to the 10–28° N region (Fig. 1), and areas north of 30° N subject to the dominant influence of Mediterranean depressions during winter have been avoided. Fossil pollen samples from 48 sites belonging to the studied region (Table S1 in the Supplement) 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 (the Western Sahara in northeastern Mauritania, and the Eastern Sahara in both eastern Libya and eastern Chad). However, 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 phytogeographical affinities (sensu White, 1983) and biodiversity indexes

All pollen taxa were classified according to the phytogeographical affinities (Table S2 in the Supplement) of their source plants (Vincens et al., 2007) and four groups were analyzed: (1) the Guineo–Congolian group, mainly composed of humid (semi-deciduous or evergreen) forest taxa growing under 1500 mm annual rainfall or more today (Trochain, 1940; White, 1983), (2) the Sudanian group, primarily composed of dry forest, woodlands, and wooded savanna taxa (500–1500 mm year^{-1}), (3) the Sahelian group, composed of grassland or wooded grassland taxa (150–500 mm year^{-1}), and finally (4) the Saharan group, composed of steppe and

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

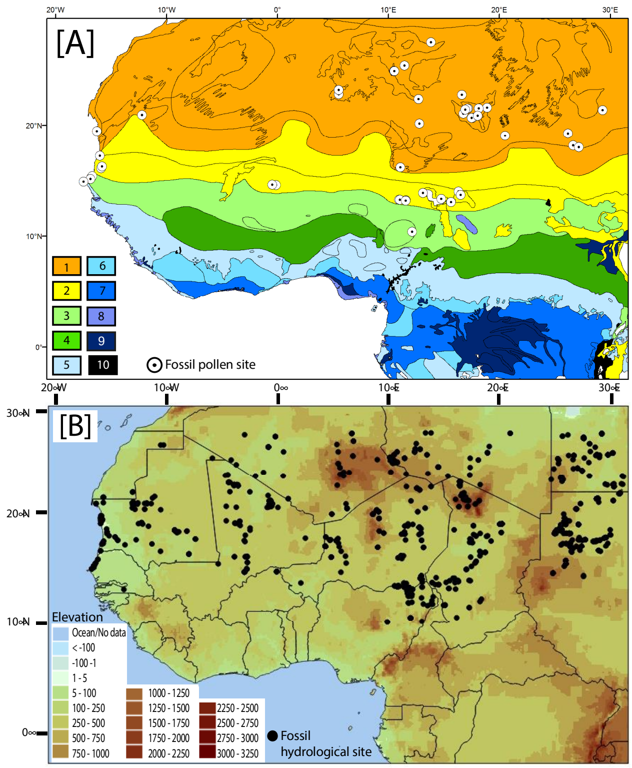

Fig. 1. Location of West African sites over the study area. **(A)** Fossil pollen sites (white circles) extracted from the African Pollen Database (http://apd.sedoo.fr/apd/accueil.htm) with the distribution of modern phytogeographical zones and associated biomes (adapted from White, 1983) as follows: desert steppe (1), Sahel acacia wooded grassland (2), Sudanian undifferentiated woodland (3), Sudanian *Isoberlina* woodland (4), mosaic of lowland rain forest and secondary grassland (5), Guineo–Congolian rain forest dry types (6), Guineo–Congolian rain forest wet types (7), mangrove (8), edaphic vegetation (9), and undiferentiated montane vegetation (10). **(B)** Fossil hydrological sites (black circles) from Lézine et al. (2011a) on elevation (m a.s.l.) background. It is worth noting that modern phytogeographical zones of Guineo–Congolian forests and Sudanian woodlands and savannas are far more south than the southernmost hydrological and pollen fossil sample.

desert taxa (< 150 mm year^{-1}) and presented here for information only (Table S2 in the Supplement). 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). It is worth noting that there are only four exclusive taxa in the Sahelian group (Table S2 in the Supplement). Given the uncertainties due to the heterogeneity of the data sets (Watrin et al., 2009; Lézine et al., 2011a), we have focused our study on the long-term evolution of the vegetation using a 500- or 1000-year time interval from 15 cal ka BP to the present. We have also 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 years. In parallel, we used the R Ash library (Gebhardt, 2009) to compute the probability density function (*pdf*) (Kühl et al., 2002) of each data set (pollen and hydrology, respectively). To proceed, records of a given data set were first split into bins to configure a two-dimensional (time and latitude) space. Then, the default Ash package setting with a five-bin window was used to compute the presence record distribution within such a spatio–temporal space. All statistical analyses were performed using the open source R software (R Development Core Team, 2007).

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 taxa 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 they 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 toward southern latitudes after 7.5 cal ka BP, with a slower rate after 4.5 cal ka BP. Meanwhile, the core area of the Sudanian group resisted longer and Sudanian taxa only started to retreat southward after 2.5 cal ka BP. The distribution of the Sahelian group differed strongly from the two others, with a stable core area centered at 19° N since the middle Holocene (Fig. 2). The maximum extent of this group clearly follows the maximum extent of lacustrine area during 6000 years (from 11 to 5 cal ka BP), with a rapid northern expansion until 9 cal ka BP followed by a stable period of 1500 years, then a southern retreat starting from 7.5 cal ka BP onward. The slower rate of the retreat recorded after 5 cal ka BP is likely a statistical artefact due to the presence of a single sample (site #8, see Table S1 in the Supplement). Despite such spatio–temporal bias toward the end of the Holocene, our results clearly show that Sahelian taxa were always present in the whole Sahara and Sahel during the Holocene.

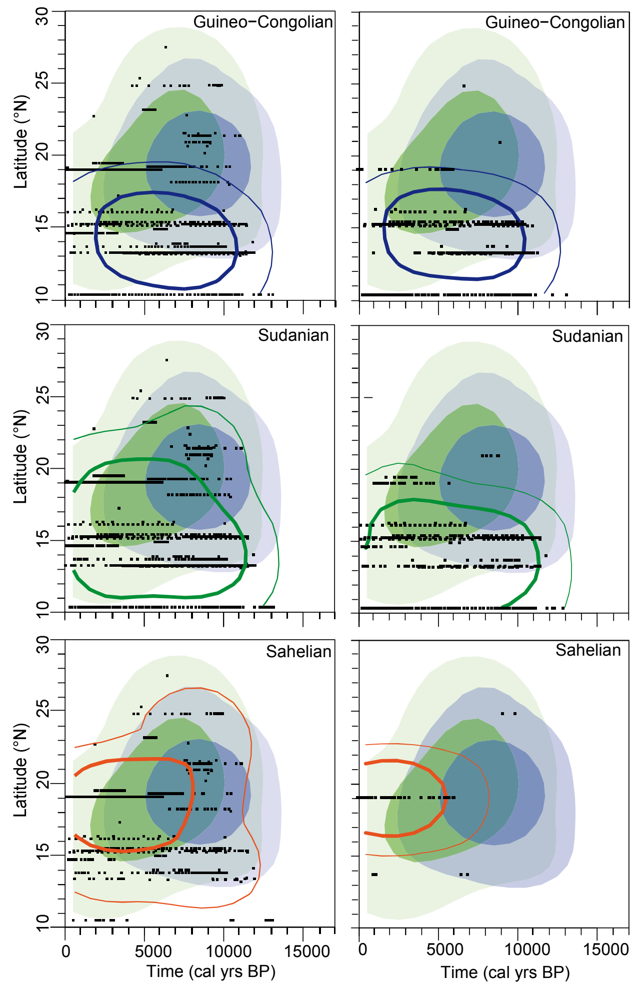

Fig. 2. Spatio–temporal changes (in latitude and millennia) in pollen taxa presences within the Guineo–Congolian, Sudanian, and Sahelian groups during the Holocene using probability density functions (Kühl et al., 2002). Left panels give spatio–temporal distributions based on non-exclusive taxa, while right ones give distributions computed with only exclusive taxa. Bold line stands for the 0.5 isoprobability delineating the core zone in which 50 % of the samples are the most concentrated (maximum presence). Similarly, the thin line is the 0.85 isoprobability delineating the maximum extent zone in which 85 % of the samples are included (Lézine et al., 2011a). Black dots are representative of pollen samples referenced in latitude and time. Blue and green probability density functions refer to lacustrine and palustrine distribution through time, respectively, with dark areas reflecting core zones (0.5 isoprobability computed on paleohydrological data), while light areas refer to the maximum extent (from Lézine et al., 2011a).

The core area of both the lacustrine and palustrine hydrological records closely matches the maximum extent of the non-exclusive Sudanian group (Fig. 2). This shows that the widespread expansion of freshwater bodies throughout the now arid and semi-arid areas of northern Africa during the AHP took place under a seasonal climate. Sudanian elements were able to survive in association with wetter elements (Guineo–Congolian) south of 24° N and in association with drier elements (Sahelian) 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. S1 in the Supplement): 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 Guineo–Congolian groups (Fig. 2) confirmed earlier observations on the co-occurrence of plants during the early to middle Holocene (2009) that occupy distinct distribution areas today (Watrin et al., 2007). The dramatic expansion of the Sahelian taxa from the middle 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 richness changes (Fig. 3) points to long-term trends, which are likely related to climate change. The regional analysis shows overall temporal trends in all latitudinal zones such as (i) the rapid increase in both richness and abundance of all groups in the early Holocene (13–11 cal ka BP), signalling the African monsoon onset and intensification, (ii) rapid changes but with vegetation recovery over the 10–6 cal ka BP period, signalling the optimum of the African Humid Period, (iii) the simultaneous abrupt changes around 4.5 cal ka BP, likely signalling the termination of the monsoon intensification, with different trends among zones and among groups. South of 15° N, Sahelian taxa were of minor importance compared to the dominance of tropical humid taxa. Sudanian and Guineo–Gongolian taxa displayed similar trends from the early Holocene until 4.5 cal ka BP, with mainly higher richness in Sudanian taxa, but a higher abundance in Guineo–Congolian taxa. After 4.5 cal ka BP, the Sudanian group kept a stable richness but became more abundant than the Guineo–Congolian group that declined dramatically both in terms of richness and abundance. This trend is particularly acute for the last millennium, reflecting the overall aridification 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 displayed overall similar trends as the lower latitudes before 4.5 cal ka BP. Conversely, after 4.5 cal ka BP, both Sudanian and Guineo–Congolian groups became richer and more abundant than before (from 20 to ∼50 % increase), at least during the subsequent two millennia, after

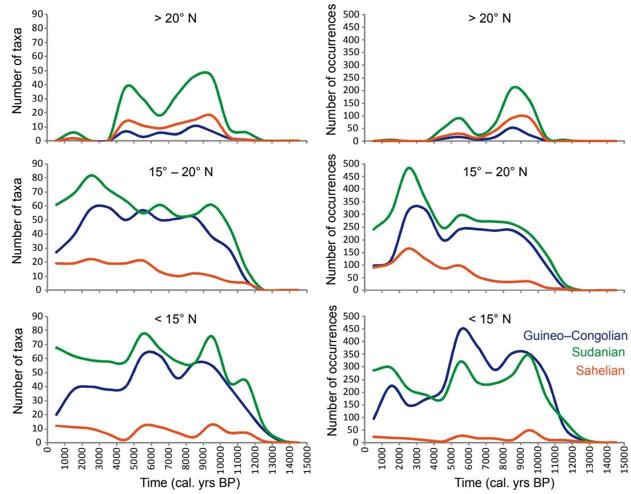

Fig. 3. Change in biodiversity within the Guineo–Congolian, Sudanian, and Sahelian groups (including exclusive and non-exclusive taxa) as a function of time in the three latitudinal zones: < 15° N, 15–20° N, > 20° N, with the richness (number of taxa) on the left and their abundance (occurrences) on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

which they strongly declined toward their current conditions. North of 20° N, Sudanian taxa dominated the early to middle 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. In this northernmost zone, a first abrupt decrease occurred at 6.5 cal ka BP, followed by a short recovery before the final relapse initiated at 4.5 cal ka BP.

Considering the number of exclusive Guineo–Congolian and Sudanian taxa in the three latitudinal zones (Fig. 4), three main observations can be made: (i) in the belt > 20° N, both types of exclusive taxa appeared only during the AHP maximum; (ii) the number of Sudanian taxa was higher south of 15° N than between 15 and 20° N during the early and middle Holocene; and (iii) the Guineo–Congolian taxa were twice as numerous between 15 and 20° N compared to the southern latitudes. Surprisingly, 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 wide 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 regional 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

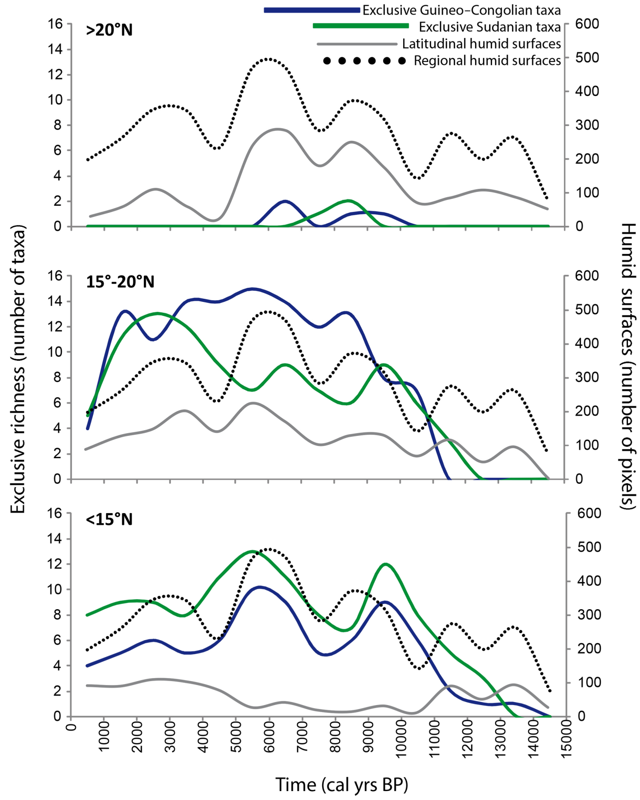

Fig. 4. Variation in the number of exclusive Guineo–Congolian and Sudanian pollen taxa compared to paleohydrological changes during the Holocene for each latitudinal zone and the entire studied area. Humid surfaces refer to the maximum extents of lacustrine and palustrine conditions estimated from the 0.85 isoprobability space at each 1000-year time interval. See Lézine et al. (2011a) for a discussion on the representativeness of humid surfaces.

along rivers and/or in the immediate vicinity of lakes and wetlands, allowing for tropical humid plants to coexist with plants of drier phytogeographical affinities growing in the surrounding areas. A more complex situation is observed over the 15–20° N latitudinal belt. 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 richness of this group was not only dependent upon soil water availability but that it found, in this 15–20° N belt, the best environmental conditions for their expansion. We suggest that the distribution and richness of these exclusive taxa during the AHP likely reflect 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 at the southernmost latitudes, explaining the prevalence of Sudanian taxa south of 15° N and the apparent reduced extent of humid surfaces 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 suggests 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.net/10/681/2014/cp-10-681-2014-supplement.pdf.

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