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ORIGINAL ARTICLE

Definition of grassland biomes from phytoliths in West Africa

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ABSTRACT

Aim In order to enhance the effectiveness of comparisons between modelled and empirical data for present and past vegetation, it is important to improve the characterization of tropical grass-dominated biomes reconstructed from fossil tracers. This study presents a method for assigning phytolith assemblages to tropical grass-dominated biomes, with the objective of offering a new tool for combining pollen and phytolith data in the reconstruction of tropical biomes.

Location The West African latitudinal transect studied here extends from 12° N (southern Senegal) to 23° N (southern Mauritania), passing through the Guinean, Sudanian, Sahelian and Saharan bioclimatic zones.

Methods Modern phytolith assemblages were extracted from 59 soil surface samples taken throughout the study area and allocated, *a priori*, to three current biomes: (1) desert C_4 grassland, (2) short grass savanna, and (3) tall grass savanna. Five out of nine phytolith types identified were used as predictors in a discriminant analysis (with calibration and validation steps) for assigning phytolith assemblages to biomes. In addition, 74 modern pollen spectra from the West African transect, acquired from the African Pollen Database (http://medias.obs-mip.fr/apd), were processed by the biomization method. This mathematical procedure involves assigning palynological taxa to one or more plant functional types, which represent broad classes of plants. The plant functional types, in turn, are combined to define biomes following a specific set of algorithms and rules. The resulting maps of the phytolith biomes thus derived were compared with maps of pollen biomes and of contemporary ecosystem classes.

Results In the calibration and validation steps, 91.5% and up to 83%, respectively, of the phytolith samples were assigned to the correct biome. The short grass savanna and tall grass savanna biomes were assigned with similar accuracy by both the phytolith and pollen biomization methods, but the phytolith method gave substantially superior results for the desert C_4 grassland biome, providing seven out of seven correct assignments, compared with just one out of four by pollen biomization. Comparisons between an existing ecosystem map and the maps created from phytolith estimation showed close correspondence for desert C_4 grassland, short grass savanna and tall grass savanna, the latter providing correct assignments in 88, 62 and 91% of cases, respectively.

Main conclusions The phytolith discriminant analysis method presented here accurately estimates three C_4 grass-dominated biomes that are widespread in West Africa. Complementarities between the phytolith method and pollen biomization are highlighted. Combining complementary phytolith and pollen data would provide more accurate assignments of C_4 grass-dominated biomes than pollen biomization alone.

Keywords
Arid environments, biome, C_4 grasses, classification, grassland, phytolith, pollen, tropical grassland, West Africa.

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INTRODUCTION

Global vegetation models provide a means for translating the outputs from climate models into maps of potential vegetation distribution in present, past and future climate scenarios (Prentice *et al.*, 1992; Haxeltine & Prentice, 1996). One type of output from such models is assignment to biomes, which may be defined as macro-scale landscape types classified according to the predominant vegetation characterized by its adaptation to the corresponding environment (Campbell, 1996). The simplest vegetation models are based on bioclimatic indicators linked to climatic variables affecting specific aspects of plant growth or survival. These indicators, when appropriately selected, can be used to estimate the locations and potential shifts of biome limits in response to past or future climate changes (Cramer, 2002). Thus, biome models can be coupled with climatic models to estimate the distribution of past biomes (Prentice *et al.*, 1992). The validity of these simulations may be assessed by comparisons with the distribution of biomes reconstructed from proxy data. To this end, the biomization method (Prentice *et al.*, 1996, 2000) reconstructs biomes from pollen data by assigning pollen taxa to one or more plant functional types (PFTs; broad classes of plants defined by stature, leaf form, phenology and bioclimatic factors) and by considering biomes as combinations of several PFTs (Jolly *et al.*, 1998). This method has proven very efficient for the reconstruction of forest biomes. However, in the absence of precise pollen identification of Poaceae species and subfamilies, grass-dominated biomes, which are the most widespread modern continental biomes (Bond *et al.*, 2005), are not accurately characterized by pollen data. For instance, the two steppic PFTs (warm grasses/shrubs and cool grasses/shrubs) defined by Prentice *et al.* (1992), although distinguished in Europe (Tarasov *et al.*, 1999), cannot be reconstructed properly in the intertropical area from modern pollen data (Jolly *et al.*, 1998). Samples collected in the steppe biome (dry tropical grassland) are often incorrectly assigned by the biomization method to the savanna biome (wet tropical grassland), the tropical xerophytic woods/scrub biome or the temperate xerophytic woods/scrub biome (Jolly *et al.*, 1998). This lack of precision is a cause of particular concern when attempting to reconstruct vegetation during the last glacial period, when grass-dominated biomes were even more widespread than at present.

One potentially useful method for reconstructing grassland biomes is based on analysis of phytoliths, amorphous silica particles that precipitate in and/or between the cells of living plant tissues. Because of redundancy and multiplicity in phytolith production (Fredlund & Tieszen, 1994), often one phytolith type cannot be related to one plant taxon. However, at a broader level, there are several notable advantages in the use of phytolith assemblages for reconstructing vegetation types, particularly for estimating biomes. Phytolith assemblages can be used successfully to discriminate current intertropical grassland types and forests of low elevation, through variations in phytolith type abundances associated with variations in dominant grass subfamilies and tree-cover density (Bremond *et al.*, 2005a, 2008; Barboni *et al.*, 2007). Several authors (e.g. Alexandre *et al.*, 1997; Scott, 2002; Abrantes, 2003) have also reconstructed paleovegetation changes in the intertropical area using fossil phytolith assemblages. In addition, recent studies present quantitative calibration of the relationships between intertropical grass phytolith assemblages and climatic parameters (Prebble *et al.*, 2002; Bremond *et al.*, 2005b; Lu *et al.*, 2006). Results of these studies suggest that, as fossil phytolith remains are recoverable in significant quantities from various kinds of soil, as well as marine and continental sediments, phytolith analyses could make significant contributions to the accurate reconstruction of global grassland types and their related bioclimatic constraints. Furthermore, the complementary use of phytolith and pollen data (the latter being most efficient for reconstructing forest types) could offer interesting opportunities for developing a better understanding of global vegetation and climate dynamics.

The objective of the study presented here was to develop a new tool for combining pollen and phytolith data in the analysis of vegetation in intertropical areas. We present a discriminant analysis procedure that allows biomes estimated from modern phytolith data to be compared with those estimated from pollen data using the biomization method (Prentice *et al.*, 1992). Consistencies and inconsistencies between the biomes indicated by the two methods are discussed, and an attempt is made to evaluate estimated West African vegetation types with respect to the ecosystem groups described by Olson (1994a,b).

MATERIALS AND METHODS

The West African latitudinal transect studied here ranges between 12° N (southern Senegal) and 23° N (southern Mauritania). The climatic zoning (Table 1) is characterized from south to north by a decrease in mean annual rainfall from 1300 to 100 mm and a concomitant increase in the duration of the dry season from 5 to > 9 months. The mean temperature of the coldest month ranges from 19°C in the south to 25°C in the north, and the mean temperature of the warmest month is between 30 and 31°C throughout the study area.

The sampled transect passes through four vegetation zones (Fig. 1): the Guinean, Sudanian, Sahelian and Saharan zones. Table 1 presents, for each zone, a description of the vegetation physiognomy after White (1983); a summary of the dominant grass subfamilies after Wyk (1979), Lézine (1987) and Le Houérou (1993); and associated climatic boundaries after Leemans & Cramer (1991) and the Office Météo du Sénégal (Centre de Suivi Ecologique, 2000). On the basis of this information, three current biomes have been outlined (Table 1): (1) the desert C_4 grassland biome, characteristic of the Saharan zone, dominated by shrub and short grass savannas with annual and perennial C_4 grasses; (2) the short grass savanna biome, characteristic of the Sahelian zone, composed of shrub and tree grass savannas dominated by

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Table 1 Phytolith samples used for the West African calibration and validation sets: location of sampled sites, number of samples, coordinates, AET/PET* and annual rainfall after Leemans & Cramer (1991) and the Office Météo du Sénégal (Centre de Suivi Ecologique, 2000), vegetation zones after White (1983), dominant grasses (Wyk, 1979; Lézine, 1987; Le Houérou, 1993) and current biomes.

Sampled sites	No. samples	Longitudes	Latitudes	Mean altitude (m)	Mean AET/PET	Mean annual rainfall (mm)	Vegetation zones	Vegetation types	Dominant grasses	Current biomes
West Africa (Mauritania)	7	12°09′–14°05′ W	19°56′–21°32′ N	265	0.06	100	Saharan	Semi-desert grassland and shrubland. Desert dunes with perennial, regs, hamadas and wadis	Perennial Panicoideae (*Panicum turgidum*), annual Arundinoideae (*Aristida*)	Desert C_4 grassland
West Africa (Senegal)	24	12°15′–16°00′ W	14°45′–17°00′ N	41	0.24	360	Sahelian	Acacia wooded grassland and deciduous bushland	Annual Chloridoideae (*Schoenefeldia, Aristida, Eragrostis*)	Short grass savanna
West Africa (Senegal)	25	12°11′–16°35′ W	12°24′–14°43′ N	59	0.38	778	Sudanian	Woodland	Annual and perennial Panicoideae and Arundinoideae (*Andropogon, Cenchrus, Aristida*)	Tall grass savanna
West Africa (Senegal)	3	12°20′–14°57′ W	12°26′–12°58′ N	16	0.4	966	Guinean	Mosaic of lowland rain forest and secondary grassland	Perennial Panicoideae (*Hypparenia*)	Tall grass savanna

*AET/PET, ratio of annual actual evapotranspiration to annual potential evapotranspiration.

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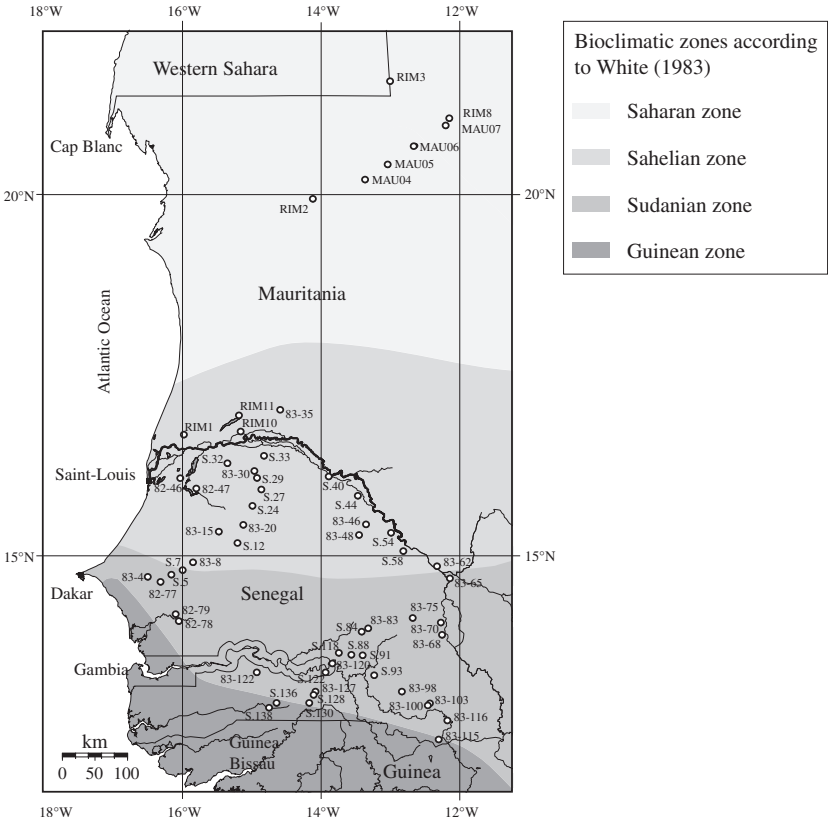

Figure 1 Location of the sampled sites across four bioclimatic zones in West Africa (after White, 1983).

annual C_4 grasses; and (3) the tall grass savanna biome, widespread in the Sudanian and Northern Guinean zones, consisting of both woodlands and tree and tall grass savannas dominated by perennial C_4 grasses.

Phytoliths

Modern phytolith assemblages were extracted from soil surface samples collected from 59 sites between 1987 and 1995 (Lézine *et al.*, 1995) in various vegetation zones and current biomes in West Africa (Fig. 1; Table 1). At each site, individual subsamples were collected randomly over 100 m^2 from the humic horizon when present, or from the surface of the regolith in dry areas. In all cases, the litter was removed from the sampled material.

The method used for extracting phytoliths (following Kelly, 1990) involved: (1) grinding, (2) dissolution of carbonates, (3) reduction and removal of iron oxides, (4) oxidation of organic matter, (5) sieving at 60 μm, checking for the absence of phytoliths in the > 60 μm fraction, (6) removal of clay, and (7) densimetric separation of phytoliths in a dense solution of $ZnBr_2$ ($d = 2.3$).

Phytolith assemblages, based on the relative abundances of nine phytolith types in each sample, have been described by Bremond *et al.* (2005b). Nine types of phytolith were counted in the assemblages and, of these, five were used as predictors in a discriminant analysis in order to assign each phytolith assemblage to its biome of origin. These five phytolith types were selected, *a priori*, as their relative abundance in the assemblages reflected a vegetation characteristic (Bremond *et al.*, 2005b) that could be used to discriminate between phytolith biomes. The terms used follow the International Code for Phytolith Nomenclature (ICPN) according to Madella *et al.* (2005), and common names previously used by Bremond *et al.* (2005b) are given in brackets. The five selected phytolith types were: (1) Globular granulate (rough spherical), (2) parallelepipedal and cuneiform bulliform cells (fan-shaped), (3) bilobate short cell (dumbbell), (4) cross, and (5) saddle. Type 1 is produced by the wood of tropical trees and shrubs (Kondo *et al.*, 1994), and its abundance (relative to that of short cells' phytoliths from grasses) reflects the density of tree cover (Bremond *et al.*, 2005a; Barboni *et al.*, 2007). Type 2 is produced in the bulliform cells of grasses. The outer epidermal walls of these cells contract when the leaf is dehydrated (due to increases in transpiration and/or the duration of water stress), promoting leaf-rolling (O'Toole & Cruz, 1980; Hsiao *et al.*, 1984). This, in turn, leads to silica saturation and precipitation. The more grasses transpire and/or suffer water stress, the more silicified bulliform cells they produce (Bremond *et al.*, 2005b). Types 3 and 4 occur primarily in the Panicoideae subfamily (Twiss *et al.*, 1969; Mulholland, 1989; Fredlund & Tieszen, 1994; Kondo *et al.*, 1994), which is dominated by tall C_4 grasses adapted to warm climates in sites with readily available soil moisture (Sage *et al.*, 1999). Type 5 is relatively abundant in the Chloridoideae grass subfamily (Twiss *et al.*, 1969; Mulholland, 1989; Fredlund &

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Tieszen, 1994; Kondo *et al.*, 1994), a group of short C_4 grasses adapted to warm and dry climates at sites with little available soil moisture (Sage *et al.*, 1999).

The following four phytolith types, although components of the phytolith assemblages, were excluded from the discriminant analysis for the reasons outlined below. First, the papillae cell (ICPN name) or cone-shaped (Bremond *et al.*, 2005b) type is characteristic of Cyperaceae (sedges) (Kondo *et al.*, 1994; Wallis, 2003). However, because this type fragments and dissolves rapidly, its relative abundance in soils and sediments is not proportional to the abundance of sedges (Alexandre *et al.*, 1997). Second, the globular psilate (ICPN name) or smooth spherical (Bremond *et al.*, 2005b). This type appears to have several origins (Kondo *et al.*, 1994; Piperno, 2006), and has no clear taxonomic significance. Third, the globular echinate (ICPN name) or crenate spherical (Bremond *et al.*, 2005b) is produced by Palmae (Piperno, 2006). However, as palms can be adapted to various climatic conditions, this type is not helpful for distinguishing among intertropical biomes. Fourth, the acicular hair cell (ICPN name) or point-shaped (in Bremond *et al.*, 2005b) type is produced by all the grasses, and no relationship has been demonstrated between its relative abundance and either climate or vegetation parameters.

After allocating, *a priori*, each of the 59 phytolith assemblages to one of the three current biomes previously outlined (Table 1), a factorial discriminant analysis (Venables & Ripley, 2002) was run using the five phytolith types as predictors to assign one of the three biomes as a result of a discriminant linear function. In this (calibration) step, the resulting biomes were referred to as phytolith biomes. The discriminant linear functions were characterized by coefficients associated with the five phytolith variables. Each coefficient was calculated to minimize the variance of the samples (phytolith assemblages) within groups (phytolith biomes) and to maximize the variance between the group centroids.

The validity of the discriminant analysis was checked through bootstrapping analysis with 100 iterations (validation step) using the function 'lda' provided by the R software (http://www.r-project.org). The data set, comprising 59 assemblages, was randomly sampled. The sampled observations were then used to recalibrate the discriminant functions, while the remaining observations were used to verify them. Percentages and confidence intervals of well classified dependent and independent observations were calculated, and the results presented as 2.5th, 50th and 97.5th percentiles.

Pollen

Seventy-four modern pollen spectra from the West African study area (for details see Peyron, 1999) were accessed online through the African Pollen Database (http://medias.obs-mip.fr/apd) and assigned to pollen biomes using the biomization method (Prentice *et al.*, 1996), which classifies the plant taxa represented in pollen assemblages into a small number of PFTs. As a biome is defined as a combination of PFTs potentially present within it (Prentice *et al.*, 1992), it is possible to construct a taxon vs. biome matrix indicating which taxa may occur in which biome(s). This matrix can then be used to calculate affinity values between each pollen assemblage and each biome. The biome assigned is the one with the highest affinity value. In this study, assigned pollen biomes were identified using PPPbase software (Goeury & Guiot, 1996), which generates affinity scores for PFTs for each pollen assemblage. The calculation is based on the sum of the square roots of pollen percentages using all the pollen grains (excluding aquatics, ferns and exotic taxa) present in the pollen assemblages. The sum of the scores of the PFTs included in each biome provides a biome score. Lastly, a biome is assigned according to the highest affinity score obtained at each site. This biomization method was applied to African pollen data first by Jolly *et al.* (1998) and later by Peyron *et al.* (2000) and Vincens *et al.* (2006).

RESULTS

Phytolith biomes

Calibration step

Table 2 presents the coefficients calculated for the five phytolith types and for each of the three discriminant functions (one per phytolith biome). Assemblages were correctly assigned to biomes for 54 out of 59 samples (91.5% correct assignments). However, the five erroneous assignments need to be explained. Edaphic conditions may, at a local scale, control the intensity of water stress and the distributions of grass subfamilies (which may differ from their regional distributions). Samples RIM 1 and 82–47 (Fig. 1), belonging to the short grass savanna biome but assigned to the tall grass savanna biome, may actually represent a local predominance of Panicoideae (tall) grasses in contrast to the zonal dominance of Chloridoideae (short) grasses. For example, the 82–47 sampling site is located in the Ferlo river valley, where humid

Table 2 Results of the discriminant analysis run for the 59 phytolith assemblages (calibration step).

Current biomes	Desert C_4 grassland	Short grass savanna	Tall grass savanna
Variables (phytolith types)	(12%)	(41%)	(47%)
Globular granulate	3.1713	3.739	3.949
Parallepipedal and cuneiform bulliform cells	3.5291	3.915	3.915
Bilobate short cell	2.2149	2.527	2.649
Cross	2.8684	3.277	3.676
Saddle	2.5961	3.366	2.834
Constant	−96.1819	−125.038	−126.996

Coefficients are calculated for the five phytolith types and for each of the three discriminant functions (one per phytolith biome). Percentages represent the proportions of samples per current biome.

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edaphic conditions may have favoured the local predominance of tall grasses in the riparian vegetation. In contrast, S7 (Fig. 1) was assigned to the desert C_4 grassland biome rather than the tall grass savanna biome, on account of the high proportion of parallelepipedal and cuneiform bulliform cells in the assemblage, while S-136 (Fig. 1) was assigned to the short grass savanna biome instead of the tall grass savanna biome. These samples may have originated from a grassy patch that was subject to high local water stress and/or high transpiration rates. Furthermore, erroneous assignments may be related to the location of some sampling sites in the transition area between two bioclimatic zones. While the boundaries between the different zones in this study are defined according to White (1983), transition areas represent a macro-scale continuum of grassland types, and some samples obtained from these areas may have been assigned incorrectly. For instance, S5 (Fig. 1), located at the transition of the Sudanian and Sahelian zones, may have been wrongly defined as part of the tall grass savanna biome.

Validation step

The results of the bootstrapping analysis are summarized in Table 3. The first matrix presents the classification of the samples (as percentages) for the new calibration set, while the second presents the independent verification set after bootstrapping. The results of this validation step support those obtained by the calibration step: 92.5% (95% confidence interval (CI) = 83, 98.4) of the calibration samples and up to 83.1% (95% CI = 68.8, 95) of the verification samples were correctly assigned to biomes.

Comparison between estimated phytolith and pollen biomes

Maps of pollen and phytolith biomes, estimated for the West African samples, are displayed in Fig. 2. The seven samples from the Saharan zone were accurately assigned to the phytolith desert C_4 grassland biome by the phytolith method, whereas three of the four samples from the desert biome were erroneously assigned to the steppe biome by the pollen biomization method. Twenty-two of 24 samples from the Sahelian zone were correctly assigned to the short grass savanna biome by the phytolith method, while 27 of the 34 samples were correctly assigned to the steppe biome by pollen biomization. Samples from the Sudanian zone or the northern Guinean zone were mainly correctly assigned either to the tall grass savanna biome by the phytolith method (25 out of 28 samples) or to the savanna biome and tropical xerophytic woods/scrub biome by the pollen biomization (20 and 8, respectively, out of the 34 samples).

DISCUSSION

Comparison between estimated phytolith biomes and contemporary ecosystem classes

The Global Land Cover Characteristics Database, derived from satellite data (Loveland *et al.*, 2000; http://edcdaac.usgs.gov/glcc/af_int.html), provides the basis for several thematic maps including Olson's (1994a,b) Global Ecosystems maps. Comparisons between biome maps estimated by pollen biomization and the Global Ecosystems maps have frequently been made (Jolly *et al.*, 1998; Hély *et al.*, 2006; Vincens *et al.*, 2006). In this study, in order to confirm that the phytolith method was adequate for characterizing present West African vegetation types, the phytolith sites were projected onto the West African section of the Global Ecosystems map using MapInfo software (Fig 2c). Table 4 displays the quantitative results of this projection, confirming that the distribution of the desert C_4 grassland phytolith biome was in close agreement with the occurrence of bare desert (88% correct assignments). The short grass savanna phytolith biome corresponded to the combined distributions of hot and mild grasses and shrubs

Table 3 Validity of the discriminant analysis checked through bootstrapping analysis with 100 iterations (validation step).

	Phytolith biomes			Well classified Phytolith biomes			Total of well classified Phytolith biomes*		
Current biomes	Desert C_4 grassland	Short grass savanna	Tall grass savanna	2.5th	50th	97.5th†	2.5th	50th	97.5th
Calibration									
Desert C_4 grassland	**100**	0	0	66.7	100	100			
Short grass savanna	0	**92**	8	78.5	94.4	100	83	92.5	98.4
Tall grass savanna	3	7	**90**	78.9	91.7	100			
Verification									
Desert C_4 grassland	**86**	14	0	50	100	100			
Short grass savanna	8	**79**	13	50	78.9	100	68.8	83.1	95
Tall grass savanna	4	11	**86**	65.1	84	100			

Percentages of well classified phytolith assemblages (phytolith biomes) were obtained after calibrating and verifying the discriminant functions.
*Calculated for each bootstrap simulation by summing the number of well classified observations in each group (taking into account the group's size).
†2.5th, 50th and 97.5th percentiles (median and 95% CI) are deduced from the vector summing the well classified simulated observations.

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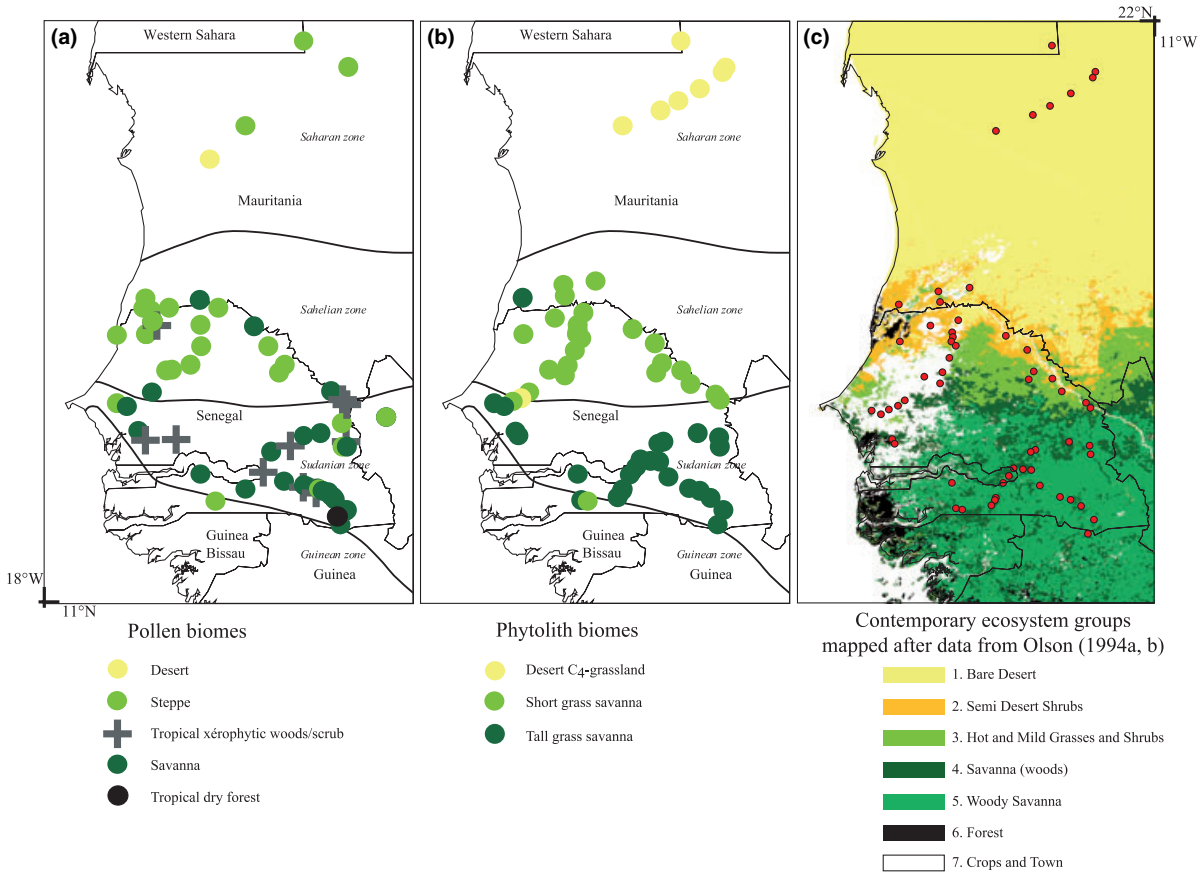

Figure 2 (a) Assignment of the samples to pollen biomes (Peyron *et al.*, 2000). (b) Assignment of the samples to phytolith biomes (this study). (c) Contemporary ecosystem classes, modified after Olson (1994a,b). Olson's ecosystem classes (16 in this study area) were combined and reduced to seven groups representing more than 94% of the area.

Table 4 Quantitative results of the projection of the 59 sites for which phytolith biomes were estimated onto the ecosystem map derived from Olson (1994a,b).

Phytolith biomes	Bare desert	Hot and mild grasses and shrubs	Semi-desert shrub	Woody savanna	Savanna (woods)	Mangrove	Broadleaf crops	Crops and town	Inland water
Desert C_4 grassland	**88**	1	0	0	0	0	11	0	0
Short grass savanna	13	**35**	**27**	4	6	0	8	5	3
Tall grass savanna	0	1	4	**56**	**35**	1	3	0	0

For each site, consideration was given to the ecosystem class represented in the grid cell (1×1 km^2) in which it is located, as well as the ecosystem class from the contiguous cells (3×3 km^2), in order to take into account the imprecision of some site coordinates. Values are percentages of grid cells of each ecosystem class in each estimated phytolith biome.

and semi-desert shrub (62% correct assignments), while the tall grass savanna phytolith biome corresponded closely to the occurrence of woody savanna and savanna (woods) (91% correct assignments).

Comparisons between the phytolith method and pollen biomization

The pollen biomization method was relatively unreliable for characterizing the desert biome, and the phytolith discriminant analysis appeared to be more powerful for identifying the desert C_4 grassland biome. This difference can be attributed to the fact that phytolith assemblages effectively characterize the grass cover when non-grass taxa are scarce, and indicate the duration or intensity of the water stress to which the grass is subjected. The reliability of phytoliths for characterizing the desert biome is particularly interesting as phytoliths, in contrast to pollen, are well preserved in oxidizing environments.

Both the phytolith discriminant analysis and the pollen biomization method reliably distinguished between tall grass

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savanna and short grass savanna biomes, although the phytolith method correctly assigned a higher percentage of samples of these kinds.

CONCLUSIONS

The phytolith discriminant analysis procedure presented here accurately identified three C_4 grass-dominated biomes that are widespread in West Africa: the desert C_4 grassland, the short grass savanna and the tall grass savanna biomes. This was tested by statistical validation and by comparing maps of estimated phytolith biomes and contemporary ecosystem classes.

The success of this first study in defining a method for constructing phytolith biomes highlights the potential value of phytolith analysis in the description of vegetation types. In particular, it is suggested that future studies should be aimed at defining new phytolith discriminant functions for tropical biomes with various tree cover densities (e.g. tree and tall grass savanna, tree and short grass savanna, tropical dry forest, tropical dense forest) or with C_3 grass components. The applicability of the calibrated functions to phytolith assemblages from other tropical areas should also be examined. The present study suggests that phytolith data may be used to complement pollen data in attempts to identify tropical biomes according to the following two procedures. First, as in this study, phytolith and pollen biomes can be defined for the same vegetation types and, following Cheddadi *et al.* (1997), who used a combination of pollen and lake-level data, the assignment of samples to given biomes by the biomization method can be considered to be validated if they are in agreement with the biomes estimated by the phytolith method. Second, a combination of phytolith and pollen data could be used to define new discriminant functions (biomes) using both phytolith indices (Bremond *et al.*, 2005b) and PFT scores as discriminant variables. These developments should improve the reliability of reconstructions of tropical grass-dominated biomes from fossil records, and enhance the effectiveness of model/empirical data comparisons for both past and present systems.

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