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Palaeogeography, Palaeoclimatology, Palaeoecology 136 (1997) 213–229

PALAEO

Phytoliths: indicators of grassland dynamics during the late Holocene in intertropical Africa

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Received 25 November 1996; received in revised form 8 April 1997; accepted 14 April 1997

Abstract

The reconstruction of African tropical grassland history during the late Holocene can be carried out using phytolith analysis. Fossil phytolith assemblages from Lake Guiers, in the Sahelian region of Senegal, and from Lake Sinnda, in the Guineo–Congolian region of Congo were investigated. The results are interpreted on the basis of modern phytolith assemblages from the same regions and compared to pollen data previously obtained. Tall or short grass associations are discriminated by their phytolith index Iph(%) = saddle/(cross + dumbel + saddle), while the density of shrubs and trees is indicated by relative proportions of the dicotyledon phytoliths.

The phytolith data emphasize that, in the Guineo–Congolian region around Lake Sinnda, the driest phase of the late Holocene occurred between 4000 and 1200 yr B.P., commencing with the opening of the dense forest and its replacement by a short grass savanna. From ca. 1000 yr B.P., wetter climatic conditions developed, as represented by the setting up of a tall grass savanna woodland. The modern shrub and tall grass savanna was developed ca. 700 yr B.P. In the Sahelian region around Lake Guiers, the driest phase occurred after about 2000 yr B.P. and has not been followed by moister conditions. A tall grass savanna woodland was gradually replaced by a shrub and short grass savanna which still occurs. A short period of development of swampy vegetation, which can be related to a lake level change, interrupted the semi-arid adaptation of the vegetation, between about 2000 yr B.P. and the present. © 1997 Elsevier Science B.V.

Keywords: phytoliths; tracers; paleoenvironment; Holocene; savannas

1. Introduction

Past vegetation reconstructions in intertropical Africa have mostly been based on pollen, charcoal, macroflora remains and carbon isotope data recorded in lacustrine and marine sediments and in soils. During the late Holocene, equatorial and North tropical Africa experienced large amplitude changes in the vegetation distribution, linked in the Northern Hemisphere tropics to variations in the Atlantic monsoon activity (Kutzbach and

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PII S0031-0182(97)00089-8

Street-Perrott, 1985). The climate experienced drier phases ca. 7500 yr B.P. and from ca. 2000 yr B.P. at Saharan and Sahelian latitudes (Servant-Vildary, 1978; Hillaire-Marcel et al., 1983; Ritchie et al., 1985; Ritchie and Haynes, 1987; Lézine, 1988, 1989; Lézine and Casanova, 1989; Petit-Marie, 1991; Ballouche and Neumann, 1995), and ca. 4000–3000 yr B.P. at equatorial latitudes (Talbot et al., 1984; Talbot and Kelts, 1986; Maley, 1992; Schwartz, 1992; Elenga et al., 1994; Vincens et al., submitted). These drier phases resulted in reduction of forests and a large extension of grasslands. However, the lack of precise pollen identification of species or subfamilies of Poaceae which constitute the main part of tropical grasslands strongly limits the reconstruction of tropical vegetation history. In particular, arid and humid grass associations cannot be discriminated through pollen and carbon isotope data.

Phytoliths are micrometric hydrated opal-A particles that precipitate in cells and/or between cells of living plant tissues. They are abundant in Poaceae where silicon ranges from less than 1% to more than 5% of the dry weight (Johnston et al., 1966; Jones and Handreck, 1967) and, unlike pollen, are well preserved under oxidizing conditions. Phytolith assemblage analysis can be used to identify past Poaceae subfamilies associations, as shown by numerous studies carried out in America (Fredlund, 1985; Kurmann, 1985; Bartolome and Klukkert, 1986; Piperno, 1988; Fredlund and Tieszen, 1994; Fisher et al., 1995; Piperno and Becker, 1996). δ^{13}C of organic carbon included in phytoliths have been analysed to distinguish C_4 from C_3 vegetations (Kelly et al., 1991). Phytolith assemblages recovered from marine sediments off west equatorial and tropical Africa, have been used as indexes of the continental aridity through the climatic cycles (Diester-Haas et al., 1973; Parmenter and Folger, 1974; Jansen et al., 1989). Although Palmer (1976) and Runge (1995) have considered the potential of phytoliths for African vegetation reconstruction, no paleoenvironmental study from phytolith assemblages have been made in intertropical Africa.

Here, we present phytolith data from lacustrine sediments recovered in the Sahelian and Guineo–Congolian phytogeographical regions (White, 1983) of West and Central Africa, in Senegal (Lake Guiers) and Congo (Lake Sinnda). The aim of this study is to determine the Holocene grassland history. Our results are interpreted on the basis of modern phytolith assemblages from the Sahelian, Sudanese and Guineo–Congolian regions, and discussed according to the fossil pollen data previously obtained from the same sites (Lézine, 1988; Lézine and Edorh, 1991; Vincens et al., 1994).

2. Environmental setting

Lake Guiers (16°15 N, 15°50 W) is located in the Sahelian region of Senegal (Fig. 1). It was fed by the Ferlo River during the Holocene, up to ca. 2000 yr B.P., and is now supplied by the Senegal River. The mean annual rainfall is 355 mm and the dry season is 8 months long. The lake is today surrounded by a discontinuous grassland mainly represented by the Poaeae subfamilies Chloridoideae (e.g. *Schoenefeldia gracilis*) and Arundinoideae (e.g. *Aristida funiculata* and *Aristida mutabilis*) and a minor proportion of Panicoideae (e.g. *Cenchrus biflorus*). Trees and shrubs (mainly *Acacia*) are scattered (Trochain, 1940). This grassland type is defined as a shrub steppe in the Yangambi nomenclature (C.S.A., 1956), the only system that describes with accuracy the different grasslands through continuity of the herbaceous cover, height of grasses and density of the ligneous elements.

However, the use of the term steppe remains controversial because it is better applied for cold grassland formations (Trochain, 1980; Menaut, 1983; White, 1983; Riou, 1995). Following the North American nomenclature, which distinguishes between short grass and tall grass prairies (Twiss, 1987; Fredlund and Tieszen, 1994), we propose to use the terms tall grass savanna and short grass savanna in place of savanna and steppe, respectively. Other patterns and terms of the Yangambi classification are followed. Thus, the vegetation surrounding the Lake Guiers is defined here as a shrub and short grass savanna.

Lake Sinnda (3°50S, 12°48E), is located in the Guineo–Congolian region of Congo, in the Niari

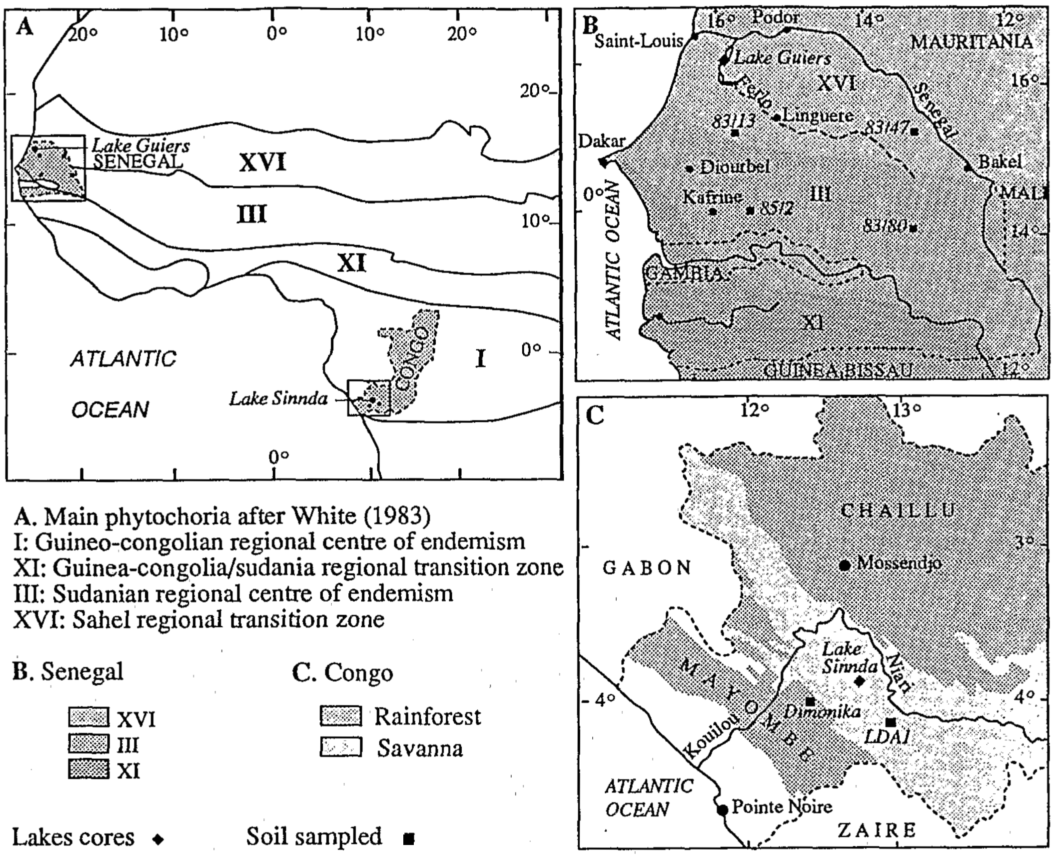

Fig. 1. Environment of the sites studied. (A) Main phytochoria after White (1983). (B) Senegal. (C) Congo.

Valley, surrounded by the forested Mayombe (to the southwest) and Chaillu (to the northeast) ranges (Fig. 1). The mean annual rainfall is about 1100 mm and the dry season is 5 months long. The whole Niari Valley is covered by continuous grasslands or shrub and tall grass savannas, dominated by the Panicoideae grass subfamily (e.g. *Hyparrhenia* or *Andropogon*) (Koechlin, 1961; Descoing, 1969). A local ring of forest occurs along the northern and southern banks of the lake.

3. Material and methods

3.1. Material

Sixteen samples of the upper 6.50 m of the core S2, taken from the southern part of the Lake Guiers (Senegal) (Lézine, 1988) and 17 samples of the core SN2 of 3.80 m length, taken from the western part of the Lake Sinnda (Congo) (Vincens et al., 1994) were analysed. The samples were 2–3 cm thick. The sampling ranges were narrowed at layers where some vegetation changes had been evidenced by pollen analysis. A sedimentary gap occurs in the core from Lake Sinnda between 0.82 and 0.77 m depth.

In order to interpret the fossil phytolith assemblages, modern materials were sampled on the soil surface or in the humic layer developed under four distinct plant associations. Soil samples are preferred to lacustrine surface sediments because they do not include a fluvial contribution. Soil samples thus permit an easier phytolith assemblage interpretation. The plant associations sampled were:

(1) The Sahelian shrub and short grass savanna

of Senegal. The grass community, dominated by the Chloridoideae subfamily, is similar to the botanical environment of Lake Guiers. Two samples of soil surface were collected at 15°20 N–13°20 W (sample 83/47) and at 15°10 N–15°40 W (sample 83/13) (Fig. 1).

(2) The Sudanian tree tall grass savanna of Senegal. The grass community is dominated by the Panicoideae (e.g. *Andropogon gayanus*), and Arundinoideae subfamilies (e.g. *Aristida longiflora*) (Trochain, 1940). The Chloridoideae one is absent. Two samples of soil surface were collected at 14°10 N–15°20 W (sample 85/2) and at 14°05 N–13°05 W (sample 83/80) (Fig. 1).

(3) The Guineo–Congolian tall grass savanna of the Niari Valley in Congo. One sample of the soil humic layer was collected at 4°01 S–13°07 E (sample LDA1) (Fig. 1).

(4) The Guineo–Congolian forest of Congo. West of the Niari Valley, the Mayombe range is covered by a mixed moist semi-evergreen rain forest (White, 1983). Under the continuous stand of trees, some monocotyledons are present including Palmae and C_3 grasses belonging to the Panicoideae or to the Bambusoideae subfamilies (e.g. *Commelinidium mayumbense*, *Puelia ciliata*, *Guaduella marantifolia* and *Oplismenus hirtellus*, Koechlin, 1962). One sample of *humic horizon* was collected at Dimonika, 4° S–12°30 E (sample F) (Fig. 1).

3.2. Phytolith extraction and counting

Between 20 and 2 g of dry soil or sediments were analysed. Phytoliths were extracted from the 2–50 µm fraction after granulometric separation, organic matter oxidation using H_2O_2, and densimetric separation in a $ZnBr_2$ solution with a density of 2.3 (Kelly, 1990; Fredlund and Tieszen, 1994). They were mounted on microscope slides in Canada Basalm. The extracted material includes phytoliths and diatoms. More than 200 phytoliths with a diameter greater than 5 µm were counted under the optical microscope, at × 600 magnification. They were classified into the following morphotype groups: (1) saddle; (2) dumbel and cross; (3) elongated, point and fan-shaped; (4) circular crenate; (5) circular rugose; (6) unclassified; and (7) cork cell-like morphotype (Fig. 2). Phytoliths were further examined under a Scanning Electron Microscope (SEM).

3.3. Phytolith taxonomy and assemblage analysis

Twiss et al. (1969) and Twiss (1992) proposed a morphological classification of phytoliths that is related to grass taxonomy: the morphology of phytoliths precipitated in short cells of the grass leave epidermis can be traced to three of the five grass subfamilies occurring in the world. These three subfamilies are the Festucoideae, Panicoideae and Chloridoideae. The two remaining subfamilies are the Bambusoideae and Arundinoideae (Watson et al., 1985). Grass genera belonging to a same grass subfamily often present the same photosynthetic pathway and suitability to a given environment: the C_3 Festucoideae subfamily requires cold, temperate or high elevation environments; the Panicoideae subfamily, composed of mixed C_4–C_3 tall grasses occurs in warm and wet environments; the Chloridoideae subfamily, composed of C_4 short grasses, occurs in warm and dry environments.

The saddle morphotype (Fig. 2a) is produced in large quantity by the Chloridoideae, and by some taxa of the Bambusoideae (C_3 genera) and Arundinoideae (mostly C_3 genera); The dumbel and cross morphotypes (Fig. 2b,c) are produced in large amounts but are not exclusive to the Panicoideae. They are also produced in smaller quantities by the Chloridoideae, Arundinoideae, Bambusoideae, and by *Stipa*; The dumbel, cross and saddle morphotypes are sometimes difficult to distinguish because of their orientation on the slide (Fig. 2d). The rectangular and circular morphotypes are produced in large amounts by the Festucoideae.

Both Arundinoideae and Bambusoideae subfamilies do not produce any distinctive morphotype but some dumbel, cross and small amounts of saddle morphotypes.

Phytoliths from the epidermal long specialized and bulliform cells of grass leaves are produced by the whole Poaceae family. They are elongated and smooth or spiny (Fig. 2f), point and fan-shaped (Fig. 2f) (Twiss et al., 1969; Twiss, 1992).

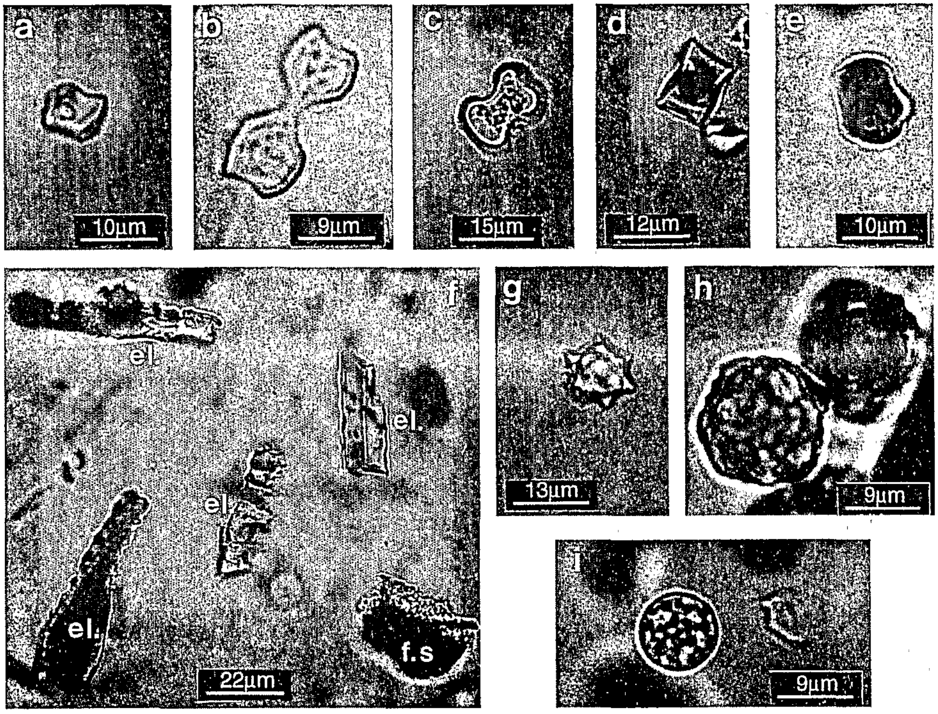

Fig. 2. Micro-photographs of the phytolith morphotypes distinguished in this study. (a) Saddle. (b) Dumbel. (c) Cross. (d) Another view of dumbel, cross or saddle morphotype. (e) Broken dumbel. (f) Elongated and fan-shaped. (g) Circular crenate. (h) Circular rugose. (i) Cork cell-like morphotype.

Other morphotypes with non-grass taxonomic value are identifiable: (1) the conical or hat-shaped morphotype is characteristic of the Cyperaceae (Le Cohu, 1973; Piperno, 1988; Hart, 1990; Ollendorf, 1987); (2) the circular crenate morphotype (Fig. 2g) is characteristic of the Palmae (Piperno, 1988); and (3) the circular rugous morphotype (Fig. 2h) is characteristic of dicotyledon sclerenchyma (Geis, 1973; Scurfield et al., 1974; Laroche, 1976; Welle, 1976; Bozarth, 1992). Lastly, the cork cell-like morphotype has no taxonomic value because it is produced by grasses and non-grasses (Fig. 2i) (Ellis, 1979).

This phytolith classification has been reviewed and criticized because of the multiplicity and the redundancy of many grass morphotypes (Rovner, 1971; Brown, 1986; Mulholland, 1989) which prevent the determination of plants on a species or genus level. However, Fredlund and Tieszen (1994) demonstrated by statistical analysis that investigations of the assemblages, in order to distinguish vegetation types are very sensitive to environmental change. In this study, discussions are based on phytolith assemblages and the related vegetation types.

4. Results and discussion

4.1. Modern phytolith assemblages (Fig. 3; Table 1)

Poaceae morphotypes represent more than 50% in the Guineo–Congolian shrub and tall grass savanna, more than 40% in the Sudanian tall grass savanna spectra and more than 30% in the Sahelian shrub and short grass savanna spectra. Tall grass and short grass phytolith assemblages are distinguished by the proportions of dumbel and cross morphotypes versus saddle morphotype; the ratio reaches 15 in the Guineo–Congolian grassland assemblage, 3 or 4 in the Sudanian grassland

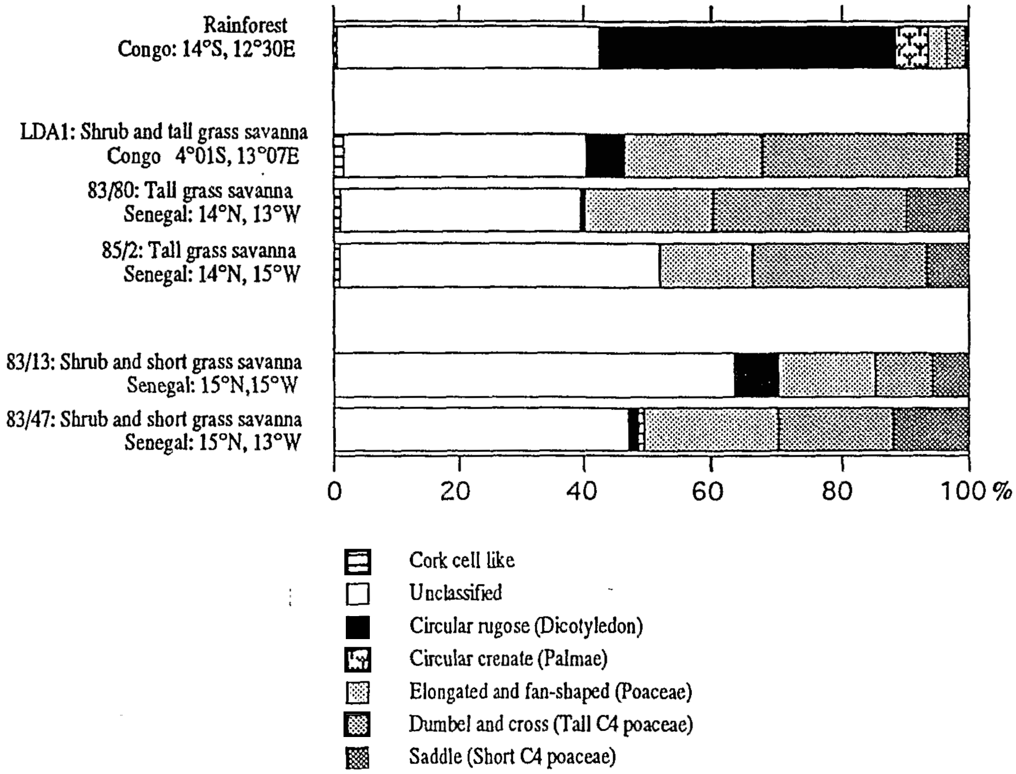

Fig. 3. Modern phytolith assemblages from the soil samples.

spectra, while it is only 1.5 in the Sahelian assemblages.

The ratio of circular rugose, the dicotyledon morphotype, versus Poaceae phytoliths is always lower than 1. The dicotyledon morphotype is 6% in the Guineo–Congolian tall grass savanna spectrum, ranges from 0% to 0.7% in the tall grass savanna assemblages and from 1.7% to 6.3% in the shrub and short grass savanna assemblages.

The dense forest phytolith assemblage is distinguished by a high amount of dicotyledon phytoliths (more than 40%) and a low amount of Poaceae (less than 7%). The related ratio of dicotyledon to Poaceae phytoliths is higher than 6. Among the Poaceae phytoliths, the dumbel and cross morphotypes represent 3% of the phytolith sum when the saddle morphotype accounts only for 0.5%. The circular crenate or Palmae morphotype reaches 6%.

In all the samples, unclassified phytoliths are abundant and represent at least 38% of the total count. Cork cell-like and circular crenate morphotypes are lacking or lower than 2%.

Grass communities with major tall C_4 Poaceae in the Guineo–Congolian and Sudanian savannas and with major short C_4 Poaceae in the Sahelian shrub and short grass savannas are clearly differentiated through their proportions of cross and dumbel versus saddle morphotypes.

The savannas spectra are also clearly differentiated from the dense forest spectrum by a ratio of dicotyledon versus Poaceae phytoliths lower than 1. The dicotyledon morphotype frequency gives information on the relative density of woody elements in each savanna type: trees or shrubs are scarce in the Sudanian tall grass savannas, more frequent in the Guineo–Congolian shrub and tall grass savanna and in the shrub and short grass savannas. These results are in agreement with the surrounded vegetation previously described. However, in addition to the circular rugose morphotype, dicotyledons produce other morphotypes

Table 1
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Sampl

Moder
Dimor
LDA1
83/80
85/2
83/13
83/47

Depth

Phytol
10.0
21.0
39.0
51.0
62.0
67.0
71.0
93.0
101.0
115.0
124.0
143.0
182.0
212.0
281.0
300.0
379.0
Phytol
4.5
24.5
50.0
75.0
100.0
125.0
150.0
175.0
200.0
225.0
250.0
300.0
360.0
375.0
500.0
650.0

[a] Elong
[b] Duml
[c] (Dico
[d] Iph (

Table 1
Abundance of the dicotyledon morphotype (circular rugose) and of the Poaceae morphotypes (elongated, point and fan-shaped, dumbel and cross, and saddle), in percent of the phytolith sum, ratio of the dicotyledon/Poaceae morphotypes and phytolith index (Diester-Haas et al., 1973) for the modern, Lake Sinnda and Lake Guiers phytolith assemblages

Sample	Circular rugose	Elongated[a]	Dumbel[b]	Saddle	(Dicot./Poa)[c]	Iph (%)[d]
Modern phytolith assemblages						
Dimonika	46.0	3.0	3.0	0.5	7.1	14.3
LDA1	6.0	21.0	30.5	2.0	0.1	6.2
83/80	0.7	20.1	29.9	9.9	0.0	24.8
85/2	0.0	14.0	27.1	6.8	0.0	20.0
83/13	6.3	14.9	9.0	5.9	0.2	39.4
83/47	1.7	20.4	17.9	12.1	0.0	40.3
Depth (cm)	Circular rugose	Elongated[a]	Dumbel[b]	Saddle	(Dicot./Poa)[c]	Iph (%)[d]
Phytolith assemblages from Lake Sinnda (Congo)						
10.0	8.3	12.5	20.8	2.1	0.2	9.1
21.0	5.5	17.4	11.0	2.8	0.2	20.0
39.0	11.9	20.5	15.1	1.8	0.3	10.8
51.0	18.0	16.0	8.7	0.0	0.7	0.0
62.0	21.5	20.6	13.6	2.3	0.6	14.7
67.0	10.0	18.5	20.5	2.5	0.2	10.9
71.0	5.7	18.9	21.4	6.9	0.1	24.4
93.0	48.8	5.4	0.8	0.0	7.9	0.0
101.0	36.0	6.8	0.0	0.0	5.3	
115.0	24.7	20.1	6.5	0.0	0.9	0.0
124.0	28.1	2.7	0.0	0.0	10.3	
143.0	62.6	1.4	0.5	0.0	33.0	0.0
182.0	82.4	0.0	0.5	0.0	159.0	0.0
212.0	64.2	2.4	0.6	0.0	21.2	0.0
281.0	60.0	0.6	0.6	0.0	46.5	0.0
300.0	59.6	1.2	0.0	0.0	51.0	
379.0	73.9	0.0	0.7	0.0	105.0	0.0
Phytolith assemblages from Lake Guiers (Senegal)						
4.5	1.5	17.8	10.9	8.0	0.0	42.3
24.5	1.1	10.9	12.0	9.8	0.0	45.0
50.0	2.6	13.5	13.1	5.3	0.1	28.8
75.0	3.1	19.1	14.8	15.4	0.1	51.0
100.0	0.8	14.3	11.0	4.3	0.0	28.1
125.0	19.6	3.6	6.7	0.1	1.9	1.3
150.0	7.2	3.6	5.0	1.4	0.7	21.9
175.0	11.6	12.8	7.0	1.7	0.5	19.5
200.0	5.1	9.0	9.0	0.0	0.3	0.0
225.0	19.8	4.2	10.4	3.6	1.1	25.7
250.0	16.0	8.9	5.9	1.8	1.0	23.4
300.0	19.1	9.9	8.6	1.2	1.0	12.2
360.0	1.6	13.7	18.5	6.0	0.0	24.5
375.0	5.9	0.0	0.0	0.0		
500.0	8.3	2.8	0.0	0.0	3.0	
650.0	7.7	0.0	0.0	0.0		

[a] Elongated = elongated, point and fan-shaped.
[b] Dumbel = cross and dumbel.
[c] (Dicot./Poa) = dicotyledon/Poaceae.
[d] Iph (%) = Phytolith index.

which are rapidly broken and dissolved in litter and soil (Alexandre et al., 1994, 1997). The stability of Poaceae phytoliths has not been studied until now, but their production in phytoliths is higher than the dicotyledon production (Jones and Handreck, 1967; Geis, 1973; Bartoli, 1983; Fredlund and Tieszen, 1994). Thus, phytolith analysis should underestimate the tree and/or shrub community density compared to the Poaceae density in savannas.

The dominance of trees in the dense forest is clearly indicated by the high frequency of dicotyledon phytoliths. The Palmae community is also well represented. The low percentage of the saddle morphotype, relative to the cross and dumbel morphotypes in the grass phytolith assemblage suggests that the Panicoideae and/or Bambusoideae grasses dominate. Indeed, the forest grasses belong to these two latter subfamilies. Comparison with the vegetation description shows that the forest formation is well discriminated by the phytolith assemblage.

In tropical areas, the extent of open vegetation, the high frequencies of fires, and the strength of northwesterly trade winds would favour eolian transportation of phytoliths in ash and dust (Fredlund and Tieszen, 1994). However, the local or regional Sahelian phytolith sources are likely to be better represented than long-distance Saharan sources which are poor in vegetation. Our results show that soil surfaces located more than 100 km apart, at the same latitude in Senegal (Fig. 2), indicate various tree or shrub proportions but close grass associations that are characteristic of the Sahelian phytogeographic region. About 100 km southward, soil surface samples from the same latitude also record various tree or shrub proportions but close grass assemblage characteristic of the Sudanian phytogeographic region. Each soil surface phytolith assemblage from Sahelian or Sudanian areas is therefore sensitive to the local vegetation, but is also connected to a zonal vegetation dominance.

In the equatorial area, the canopy prevents eolian and run-off transport. Consequently, the phytolith assemblage of the forest soil also reflects the local environment.

Diester-Haas et al. (1973) have defined a phytolith index (named here Iph) Iph(%) = saddle/(saddle + cross + dumbel) as a good indicator of aridity: Iph values higher than 40 characterize dry grasslands associated with arid phases in northern Sahara during the Pleistocene and Holocene (Fig. 4). Iph values have also been calculated from two other studies of vegetation changes in North America during modern (Kurmann, 1985), Pleistocene and Holocene periods (Fredlund and Tieszen, 1994) (Fig. 4). Iph values lower than 40–45% are characteristic of tall grass prairies whereas Iph values higher than 60% are characteristic of short grass prairies. These data suggest that Iph values of 40–45% could discriminate vegetation adapted to arid or humid conditions.

Our results indicate that the tall grass savanna assemblages LDA1, 83/80 and 85/2 show Iph values of 6%, 25% and 20%, whereas Iph values of the short grass savanna assemblages 83/13 and 83/47 are larger, reaching 40% and 39% (Fig. 4). Thus, a boundary Iph value of about 30% is suggested to characterize the grass associations in the areas studied (Fig. 4).

4.2. The late Quaternary phytolith assemblages

4.2.1. Lake Guiers assemblages

Three zones are distinguished within the phytolith sequence of Lake Guiers (Fig. 5; Table 1):

Zone 3 (6.50–3.70 m): the phytolith assemblage is widely dominated by the cork cell-like morphotype which represents more than 60% of the phytolith sum. Unclassified morphotypes range from 6% to 25%. The dicotyledon morphotype stabilizes around 8%, and the Poaceae phytoliths are nearly absent, except at 5.0 m where elongated, point and fan-shaped morphotypes represent about 3% of the phytolith sum. At this depth, the other Poaceae morphotypes are lacking.

Zone 2 (3.70–1.10 m): The cork cell-like morphotype abruptly becomes lower than 5%, while the Poaceae morphotypes proportion increases abruptly, ranging from 10% to 38%. Iph values of the grass assemblages remain less than 30% (Fig. 4). The dicotyledon morphotype increases also, ranging from 1% to 19%. Palmae phytoliths appear between 3 and 2.25 m and at 1.25 m, when

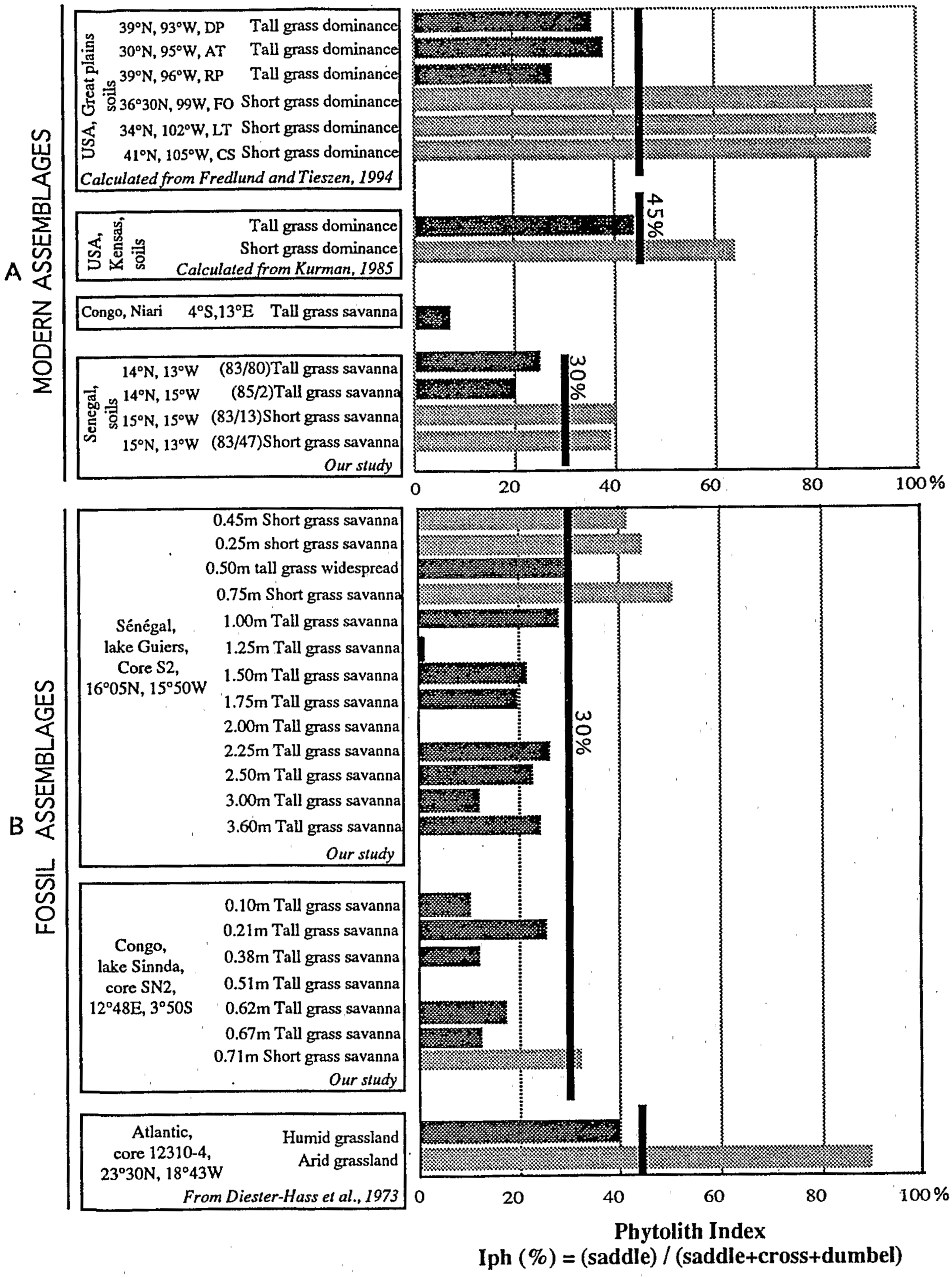

Fig. 4. Phytolith index Iph(%) = saddle/(saddle + cross + dumbel) (Diester-Haas et al., 1973), calculated from literature and from this study data. (A) Modern assemblages. (B) Fossil assemblages. The black vertical lines represent the Iph which separates tall grass and short grass savannas in each site.

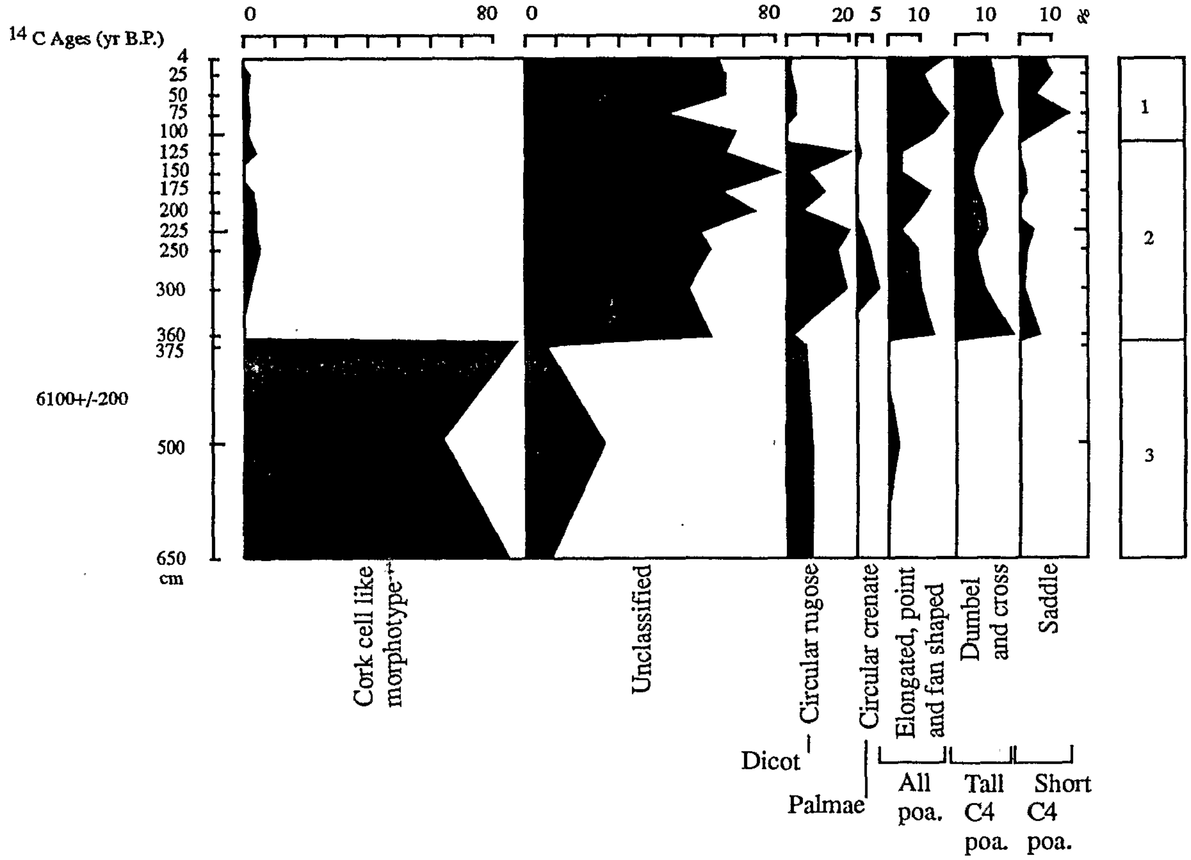

Fig. 5. Phytolith diagram for Lake Guiers (core S2). The abundance of each morphotype is expressed as a percentage of the phytolith sum. ^{14}C ages according to Lézine (1988) and Lézine (1989).

frequencies of dicotyledon morphotypes are the highest. At the bottom of this zone (3.60 m), the dicotyledon morphotype is a minimum, while the *Poaceae* morphotypes are maximum. The value of Iph is 24% (Fig. 4). Low frequencies of dicotyledon morphotypes also occur between 1.50 and 1.75 m, but the Poaceae phytolith assemblages do not show special features at these depths.

Zone 1 (1.10–0.04 m): The Poaceae phytoliths increase further, ranging from 27% to 48% of the phytolith sum. The Iph reaches values higher than 40%, except at 0.50 m where it is only 29%. Conversely, the Dicotyledon morphotypes drop in this zone, ranging from 1% to 3% up to the top of the core. Palmae phytoliths are absent or lower than 1%. Proportions of cork cell-like and of unclassified morphotypes are similar to those for *zone 2*.

Phytoliths in lacustrine sediments may have various origins. At present, the Senegal River and its tributaries would transport Sahelian and Sudanian elements into Lake Guiers. However, the phytolith assemblage from the top of the core is similar to that of the Sahelian soil surfaces assemblages 83/13 and 83/47, suggesting that the Sudanian contribution is poor. The Saharan contribution by the northwesterly winds would be also limited because of the scarcity of Saharan plants. The lacustrine shoreline vegetation would also provide phytoliths. Lacustrine vegetation is mainly made of Cyperaceae and of Poaceae belonging to the Panicoideae and Bambusoideae subfamilies.

However Cyperaceae conical morphotypes were not distinguished in the sediments. They could have been weathered and become unrecognizable. Lacustrine Poaceae which produce mainly the dumbel morphotype will be evident only if the surrounding grassland is a short grass savanna producing few dumbels. These observations illustrate that phytolith analysis is unsuitable for lacustrine vegetation reconstruction. Finally, in an ecoclimatic zonation context similar to the present one, the phytolith assemblages record the nearby vegetation changes, reflecting zonal vegetation changes. During more humid periods the contribution of northern elements to the lacustrine phytolith assemblages should be more significant, due to northwesterly winds. However, during these periods, the northern allochthonous pollen contribution to the lacustrine pollen spectra remained very low (Lézine, 1989). The density of phytoliths is higher than that of pollens, they are thus less susceptible to eolian transport over great distances. Therefore, the whole phytolith sequence from Lake Guiers may be interpreted as a local or regional paleoenvironmental record.

The main environmental changes around Lake Guiers reconstructed by pollen analysis are summarized as follow: from 6.50 to 3.70 m depth, a salt mangrove on the shores of the lake is indicated by the abundance of Rhizophora (Lézine, 1988; Fig. 6). From 3.70 to 1.25 m depth, the retreat of the mangrove and the widespread of Guinean and Sudanian elements in the watershed basin are recorded (Lézine, 1989). This transition can be related to a decrease of the marine influence in the Senegal River and to increased fluvial activity of the Ferlo River between 6.0 ka B.P. and 2.0 ka B.P. (Lézine, 1989). A Sahelian vegetation adapted to modern semi-arid conditions is recorded in the upper part of the pollen diagram (Lézine, 1988).

The phytolith diagram also records three successive vegetation types surrounding Lake Guiers from about 6000 yr B.P. until today. The vegetation changes are recorded at the same depths by phytolith and pollen analysis.

From 6.50 to 3.70 m (*zone 3*), phytolith assemblages do not exhibit any similarities with modern assemblages that have previously been studied: the low proportions of dicotyledon and grass phytoliths show that the vegetation cover surrounding Lake Guiers was neither a grassland nor a forest. We conclude that phytolith analysis cannot detect the mangrove recorded by pollen analysis, as already evidenced by Piperno (1988).

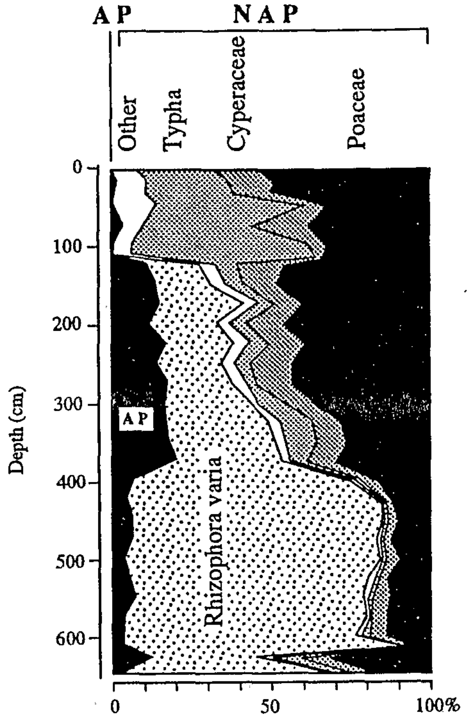

Fig. 6. Pollen diagram for Lake Guiers.

At 3.60 m (*zone 2*), the phytolith assemblage indicates a sudden increase in woody elements and a rapid spread of grasses. Up to 1.25 m depth, values of Iph lower than 30% characterize tall grass savanna. Woody elements representation in these phytolith assemblages is intermediate between those of modern tall grass savanna assemblages (85/2 and 83/80) and of forest assemblage. Thus, this vegetation was a tall grass savanna woodland, rapidly developed at the expense of the mangrove, after 6000 yr BP. The depths 3.60 m and 1.75–1.50 m evidence short periods of decline of the local woody community which have no correspondence in the pollen diagram (Fig. 6). These results further typify adaptation of the vegetation to Sudanian conditions.

Around 1.00 m depth (*zone 1*), phytolith spectra show a rapid decrease in the woody elements but a gradual development of the grass community dominated by short grasses. This zone indicates a period of gradual change from a tall grass savanna woodland to a shrub and short grass savanna similar to the modern one in the Sahelian region. This result differs from the pollen data which identify an abrupt appearance of modern semi-arid conditions (Lézine, 1988). The setting of the shrub and short grass savanna appears better connected to the spread of Sahelo–Saharan elements than to the spread of Sahelian elements mirrored by pollen spectra. This transition could have occurred around 2000 yr B.P., as suggested by Lézine (Lézine, 1988, 1989), and would have been synchronous with the development of modern semi-arid conditions, recorded elsewhere in the Sahel region (Chamley and Diester-Haas, 1982; Lézine, 1989; Lézine and Casanova, 1989). At 0.50 m depth, the phytolith assemblage records an expansion of tall grasses too brief to be interpreted in terms of regional vegetation change. This episode is probably due to a lake level change conducive to the development of swampy grasses belonging to the Bambusoideae subfamily (e.g. *Leersia hexandra*), and to the Panicoideae subfamily (e.g. *Jardineae congonensis*, *Vossia cuspidata*, *Echinocloa* and *Loudetia simplex*, Hutchinson and Dalziel, 1972). At this depth, pollen data show a decrease in arborescent taxa and an increase in the aquatic taxa, Cyperaceae and Typha (Fig. 6). Finally, the phytolith record reflects with accuracy the dynamics of the Sahelian vegetation around Lake Guiers.

To summarize, phytolith analysis of the core indicates the setting of a tall grass savanna woodland ca. 6000 yr B.P., and its progressive replacement by a shrub and short grass savanna (around 1 m depth). This shrub and short grass savanna occurs today. A short period of development of swampy vegetation must have interrupted this semi-arid adaptation of the vegetation.

4.2.2. *Lake Sinnda assemblages*

Three zones may be discriminated within the phytolith sequence of Lake Sinnda (Fig. 7; Table 1):

Zone 3 (3.79–1.30 m): The phytoliths are dominated by the circular rugose morphotype, with percentages ranging from 62% to 82%. The abundance of unclassified morphotypes is variable but never passes over 33%. The circular crenate morphotype is abundant between 3.79 and 2.81 m depth, ranging from 10% to 24% and decreases above. The Poaceae morphotypes are scarce, except at 2.12 m where they reach 2% of the phytolith sum.

Zone 2 (1.30–0.93 m): At 1.24 m, the circular rugose morphotype is half that in the lower zone (30%) and increases up to 50% at 0.93 m. The unclassified phytoliths follow an opposite tendency. The circular crenate morphotype never exceeds 6%. Poaceae phytoliths, mainly represented by elongated and fan-shape morphotypes, are more abundant than in the lower zone, but less than 7%, except at 1.15 m (20%). At this depth, dumbel phytoliths reach 7% of the phytolith sum, whereas the saddle morphotype remains absent.

Zone 1 (0.71–0.10 m): Through this zone, the Poaceae morphotypes become abundant, ranging from 31% to 47% of the phytolith sum. The Iph value equals 32% at the bottom (0.77 m), and remains lower than 30% upwards, with a minimum of 9% at 0.10 m (Fig. 4). The circular rugose morphotype abundance falls below 10%, except between 0.39 and 0.62 m.

Annual fires in the savannas should favour eolian and run-off transport towards the Niari Valley (Schwartz et al., submitted), screened by forested areas. In contrast, the transport of phytoliths by run-off towards the forested areas, should be limited in extent. It is therefore justifiable to interpret fossil assemblages from the core SN2 of Lake Sinnda in terms of vegetation changes in the Niari Valley, although the forested areas will be under-represented compared to the savanna ones, due to their lower production in silica.

The pollen sequence from Lake Sinnda indicates that savannas covering the Niari Valley today developed at the expense of semi-deciduous forests ca. 3000 yr B.P. These forests show a swampy character, indicated by the occurrence of the palm tree *Phoenix reclinata* at the base of the core between 5300 and 5000 yr B.P. They became more diversified later on, and a well marked semi-deciduous facies developed from 4000 yr B.P.,

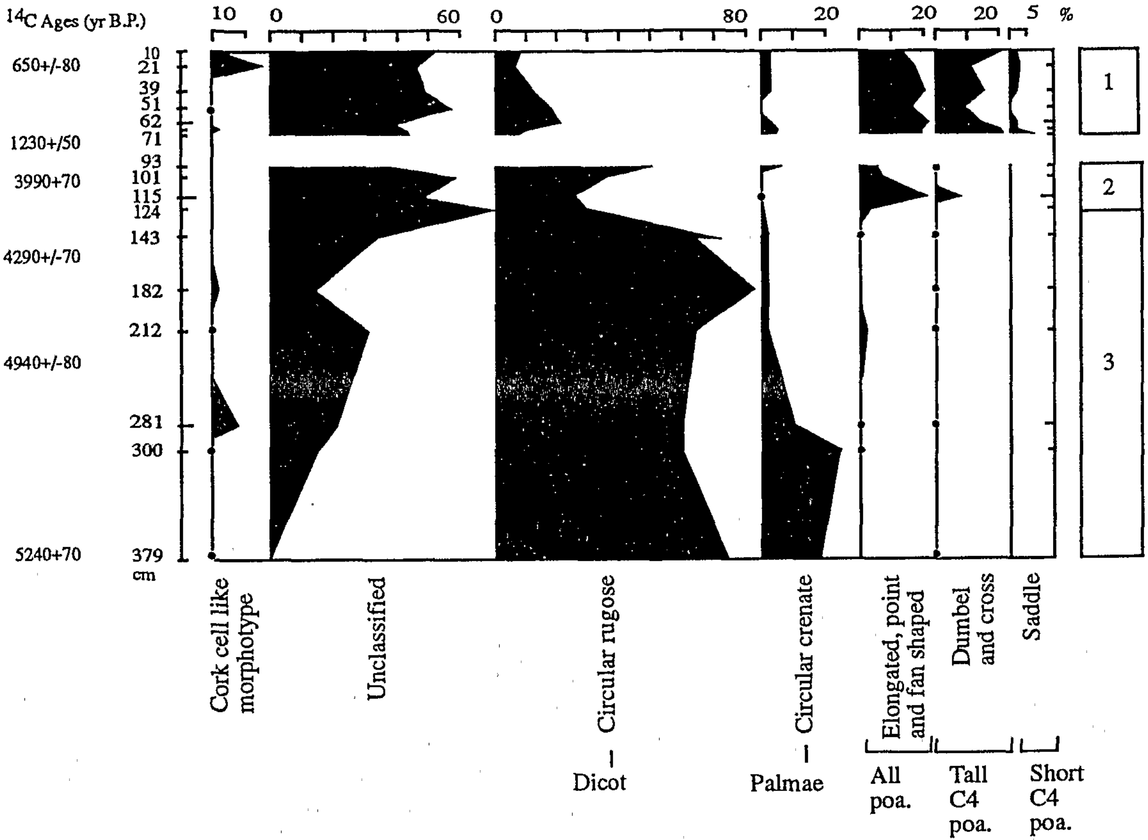

Fig. 7. Phytolith diagram for Lake Sinnda (Core SN2). The abundance of each morphotype is expressed as a percentage of the phytolith sum. ^{14}C ages according to Vincens et al. (1994).

which is indicated by the abundance of *Celtis* (Vincens et al., 1994, submi; Fig. 8).

The phytolith diagram clearly demonstrates that two major changes have occurred in the vegetation surrounding Lake Sinnda since 5000 yr B.P.:

Zone 3 characterizes two types of forest vegetation: (1) From 5240±70 yr B.P. until 4940±80 yr B.P. (3.79–2.12 m), a forested vegetation where grasses were scarce is indicated by the phytolith assemblages, which are dominated by the dicotyledon morphotype. The Palmae are more strongly represented than in the modern Mayombe forest. Their association with trees indicates a humid environment, which is also shown by the pollen record. (2) From 4940±80 yr B.P. (2.12 m), the Palmae decrease, whereas the Poaceae remain less abundant than in the present Mayombe forest until ca. 4000 yr B.P. (1.24 m).

Around 4000 yr B.P. (1.24 m, *zone 2*), an increase in grasses at the expense of the tree community is recorded. This phytolith sequence is not similar to any modern phytolith assemblage. The proportions of dicotyledon versus Poaceae phytoliths indicate vegetation type intermediate between a tall grass savanna woodland and a dense forest. The hypothesis of development of enclosed tall grass savannas and/or tall grass savanna woodland in the area of Lake Sinnda may be put forward. The opening of the forest occurred synchronously with the floristic change demonstrated by the development of *Celtis* in the pollen diagram (Fig. 8). This change might be connected

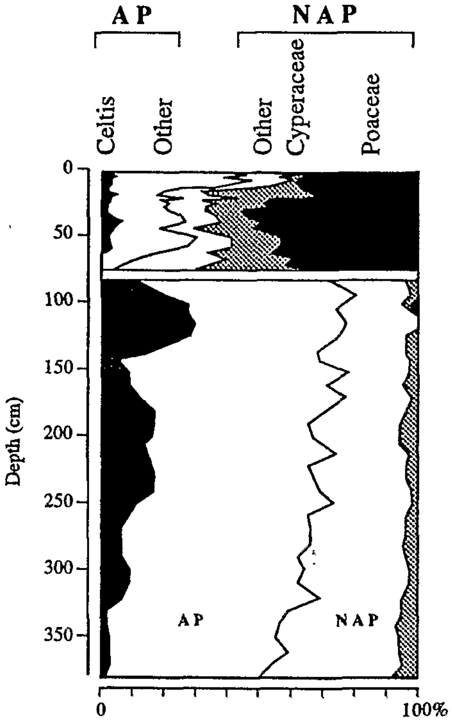

Fig. 8. Pollen diagram for Lake Sinnda.

to the beginning of drier climatic conditions. A decrease in the rainfall from ca. 5000 yr B.P. around Lake Sinnda has been evidenced by a decrease in detrital minerals flux recorded in core SN2 (Bertaux et al., submitted).

After the driest phase, leading to the complete drying up of the lake (between 0.93 and 0.71 m), phytolith analysis records a vegetation cover widely dominated by grasses (*zone 1*). At 1230±50 yr B.P. (0.71 m), just after the refilling of the lake, the vegetation that developed around the Lake Sinnda shows phytolith assemblages and Iph values close to those for the Sahelian shrub and short grass savanna but distinct from those characterizing the modern shrub and tall grass savanna of the Niari Valley. The expansion of short grasses adapted to dry conditions might be contemporaneous with the hydrological change leading to the sudden drop in the Niari discharge (Vincens et al., 1994). Phytolith analysis records the end of this semi-arid phase, characterized by a refilling of the lake that occurred before the semi-arid vegetation disappearance. Pollen data did not evidence this vegetation dynamic (Vincens et al., 1994; Fig. 8).

After 1230±50 yr B.P. (above 0.71 m), abundant tall grass development at the expense of short grasses displays the setting of more humid conditions. Comparison between modern and fossil phytolith assemblages, using Iph values and dicotyledon phytolith proportions, suggests the setting up of a tall grass savanna woodland after 1230±50 yr B.P., gradually replaced around ca. 700 yr B.P. (0.30 m) by a shrub or tree tall grass savanna surrounded the lake until today. Pollen data evidence show ca. 600 yr B.P. the development of a Cyperaceae swampy vegetation related to a decrease in the lake level (Vincens et al., submitted; Fig. 8). However, these data do not evidence the change in the local vegetation indicated by phytolith analysis for this period.

Previous studies have suggested that the driest phase of the late Holocene, conducive to the development of climate and vegetation close to the modern ones began from about 3000 yr B.P. over the Congo (Schwartz, 1992; Elenga et al., 1994; Vincens et al., 1994). However, new data indicate that a drying tendency began between ca. 5000 and ca. 4000 yr B.P. (Bertaux et al., submitted; Schwartz et al., submitted; Vincens et al., submitted). Phytolith analysis of Lake Sinnda sediments also argues for the development of drier conditions before ca. 4000 yr B.P. The arid phase reached a maximum between about 3900 and 1200 yr B.P. Wetter conditions occurred ca. 1000 yr B.P., while the modern environment was probably reached ca. 700 yr B.P.

5. Conclusion

Tropical grassland types are discriminated by phytolith assemblage analysis. Their wooded component density is recorded by the ratio of dicotyledon versus Poaceae phytoliths; their Poaceae associations are indicated by values of the phytolith index Iph. Tall grass savanna and short grass savanna are readily distinguished when this distinction cannot be made by pollen or δ^{13}C analysis. The phytolith sequences presented provide new indications of grassland evolution after 2000 yr

B.P. around Lake Guiers, and on forest opening dynamics and the replacement by semi-arid and then humid grasslands, between 4000 and 1000 yr B.P., in the Niari Valley (Congo).

Grassland dynamics in intertropical Africa are connected to arid and humid climate fluctuations and to later human impacts. These dynamics will be understood more clearly if modern and fossil phytolith assemblage analysis are widespread. Moreover, analysis of modern phytolith assemblages sampled along a north–south section in West Africa could evaluate the potential of Iph as a proxy data between phytolith assemblages and mean annual rainfall in this area.

Acknowledgements

This work was supported by the French programs PEGI, ECOFIT and GEOCIT (ORSTOM–CNRS). The authors would like to thank R.J. Gilkes for his helpful corrections.

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