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Influence of the local environment on lacustrine sedimentary phytolith records

Julie C. Aleman^{a,b,c,*}, Sandrine Canal-Subitani^{a,b}, Charly Favier^d, Laurent Bremond^{a,b}

^a Centre for Bio-Archaeology and Ecology (UMR5059|CNRS, Université Montpellier 2, EPHE), Montpellier, France

^b Paleoenvironments and Chronoecology (PALECO, EPHE), École Pratique des Hautes Études, Montpellier, France

^c Centre for Forest Research, UQAM, Montréal, Canada

^d Institut des Sciences de l'Evolution (UMR5554|CNRS, Université Montpellier 2, IRD), Montpellier, France

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ABSTRACT

Fossil phytolith assemblages from soils and lake sediments are widely used to reconstruct past vegetation patterns and dynamics, especially in tropical environments where a phytolith index has been quantitatively calibrated to estimate tree cover. Most calibration studies have focused on comparing phytolith assemblages in modern soil with the present aboveground vegetation. However, little is known about phytolith taphonomy and the representativeness of phytolith assemblages and indices in lake sediments. The aim of this study is to improve the understanding of the composition of phytolith assemblages and their influx into recent lake sediments by comparing them with local land cover assessments. This study focused on three lakes in the Central African Republic located in savanna, forest-savanna mosaic, and forest. It appears that the local environment surrounding the lake was critical for interpreting current and past assemblages, and the ratio of dicotyledon to Poaceae diagnostic phytoliths (the D/P index). The presence of a riparian forest in an open environment had no impact on phytolith assemblages or the D/P index, which instead reflected both the local and regional landscapes. Conversely, contributions from a marsh, if present in a forested environment, completely dominated the phytolith records, which consequently reflected only the local environment of the lake. A high correlation between the Poaceae phytoliths influxes and the charcoal accumulation rates for the two lakes surrounded by a riparian forest has also been found. This finding, which was associated with a high proportion of burned Poaceae phytoliths, provides evidence that Poaceae phytoliths are mainly transported by wind in ash clouds produced by fires.

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1. Introduction

Long-term ecological records from lake sediments are important for understanding responses of vegetation to climate change and anthropogenic pressure (e.g., Willis et al., 2010), especially in tropical and inter-tropical environments. Indeed, in these areas other sedimentary archives are rare (e.g. terrestrial soil profiles, loess or temporary swamps, Piperno and Becker, 1996; Runge, 1999; Albert et al., 2006; McMichael et al., 2012; Dickau et al., 2013) and generally do not allow continuous recording, contrary to lacustrine archives where most of paleoenvironmental studies are conducted (e.g., Piperno, 1993; Bush et al., 2007; Nelson et al., 2012; Colombaroli et al., 2014). In particular, lake sediments have helped determine the respective roles of climate and fire in initiating and maintaining savannas (Vincens et al., 1999; Gillson, 2004; Rull, 2009), and the impact of past climate change on the resilience of savannas (Gillson and Ekblom, 2009; Ekblom and Gillson, 2010) and forests (Brncic et al., 2007; Brncic et al., 2009). Savanna ecosystems are characterized by the co-dominance of trees and grasses (Scholes and Archer, 1997). Thus, tree cover is a key factor to consider when studying both savanna and forest ecosystems (Hirota et al., 2011). The relative importance of drivers that determine the structure of savannas is still under debate (e.g., Sankaran et al., 2005; Staver et al., 2011) and would benefit from further understanding of past interactions between tree cover and its potential drivers (e.g., climate, fire, herbivory, soil, land use), especially in forest–savanna mosaics areas (Iriarte et al., 2012).

Several paleo-environmental proxies are available to study past tree cover (Aleman et al., 2012). For pollen analysis, the ratio of arboreal to non-arboreal pollen provides qualitative information about tree cover and distinguishes between wooded and more open ecosystems (Liu et al., 1999; Vincens et al., 2000). However, pollen is associated with long distance dispersal (Nathan, 2006) and represents a regional signal of the vegetation around the lake (Sugita, 1994; Sugita et al., 1999). A commonly used indicator of the relative abundance of trees and grasses in tropical environments is the δ^{13} C value of soil organic matter, which reflects the relative contributions to carbon fixation of the C₃ and C₄ photosynthetic pathways used by tropical trees and grasses, respectively (Boutton et al., 1998; Kelly et al., 1998; Gillson et al., 2004; Coe et al., In press). However, this proxy is rarely used in lakes as a vegetation

^{*} Corresponding author at: Centre for Forest Research, UQAM, Montréal, Canada. *E-mail address:* julie.aleman@gmail.com (J.C. Aleman).

proxy due to the multiple origins of lacustrine organic matter (allochtonous and autochtonous, e.g., Cole et al., 2002; Nguetsop et al., 2004). Phytoliths are increasingly used, especially in tropical environments where diagnostic phytoliths are produced by many tropical families (Pearsall, 2000; Piperno, 2006) and have proven to be very accurate in quantitatively reconstructing the cover of woody plants (Bremond et al., 2005a; Aleman et al., 2012) and the histories of tropical ecosystems (Alexandre et al., 1997; Boyd et al., 1998; Barboni et al., 1999; Neumann et al., 2009; Dickau et al., 2013; Whitney et al., 2013). Phytolith deposition and accumulation are associated with the decomposition of local vegetation (Piperno, 2006), thus examination of phytoliths can provide valuable complementary information to pollen analysis.

A problem is that modern assemblages used to calibrate past records are from soils (Fredlund and Tieszen, 1994; Piperno and Becker, 1996; Alexandre et al., 1997; Runge, 1999; Aleman et al., 2012) or fresh plants (Albert et al., 2006; Novello et al., 2012) rather than directly from recent lake sediments. Furthermore, factors affecting signals from current vegetation in sedimentary phytoliths in lake sediments have not yet been elucidated. Thus, imperfectly understood differences in the taphonomic processes (production, transportation, deposition and potential degradation of the bioproxies) between soil and lake sediments could complicate attempts to extrapolate calibration assemblages and phytolith indices from one material to the other (e.g. Aleman et al., 2012). Assessing the taphonomic signature of phytoliths contained in lacustrine deposits would be of great interest for paleoenvironmental studies. For example, Aleman et al. (2013a) showed that the direct environment around a lake can influence the mode of deposition of particles in recent sedimentary charcoal records. To explore the processes in more detail, the impact of the lake shoreline environment on phytolith assemblages and indices (notably the ratio of dicotyledon to Poaceae diagnostic phytoliths, D/P index) was investigated, using recent sedimentary records from three lakes in savanna, forest-savanna mosaic, and forest environments in central Africa. The relationships between the local environment of the lakes and the representativeness, transport and mode of deposition, of their phytolith assemblages were studied and the D/P index was then compared to land cover changes around each lake from 1974 to 2005.

2. Material and methods

2.1. Study sites

The sediments of three lakes, situated in savanna (Lake Gbali, 4°49′ 07″N, 18°15′46″E), forest–savanna mosaic (Lake Doukoulou, 4°15′10″ N, 18°25′25″E), and forest (Lake Nguengué, 3°45′40″N, 18°07′19″E) in the Central African Republic (Fig. 1), were studied. The climate around Lakes Gbali and Doukoulou is tropical with ~1500 mm annual precipitation. The 4-month dry season from November to February is followed by an 8-month long wet season, (Bangui weather station, Hijmans et al., 2009). Lake Nguengué experiences a shorter dry season (December–February) and is wetter with an average rainfall of 1738 mm (1982–2007, Boukoko Meteorological station, A. Ougou, personal communication, 2008).

The three lakes are of various sizes (2, 36 and 14 ha for Lakes Gbali, Doukoulou and Nguengué, respectively), but all are shallow (2.00-2.35 m depth at the time of sampling) with a gently sloping bottom. Lake Gbali is bordered by a 200-m wide riparian forest mainly composed of Hallea stipulosa (DC.) Leroy and some Raphia vinifera P. Beauv. The woody savanna vegetation that surrounds the riparian forest is composed of the dominant grass Imperata cylindrica (L.) Raeusch., associated with Cenchrus polystachios (L.) Morrone and Hyparrhenia diplandra (Hack.) Stapf., and a woody cover of typical fire-resistant trees: Daniellia oliveri (Rolfe) Hutch. and Dalz., Terminalia schimeriana Hochst., Prosopis africana (Guill. & Perr.) Taub., Hymenocardia acida Tul., Piliostigma thonningii (Schumach.) Milne-Redh., Sarcocephalus latifolius (Sm.) E.A. Bruce, Annona senegalensis Pers. and Crossopteryx febrifuga (Afzel. ex G.Don) Benth. The lake is situated at around 400 m from a road and 1 km from a village, so some parts of the landscape burn at least once a year during the dry season (Aleman et al., 2013a).

Lake Doukoulou is surrounded by an extensive zone dominated by Poaceae with a gradient of *Vetiveria zizanioides*, *Imperata cylindrica* and *Pennisetum purpureum* from the lake edge towards a mosaic of dense savanna (herb layer of *I. cylindrica*, *V. zizanioides* L. Nash and *P. purpureum* Shumach.; woody layer of *P. thonningii*, *Erythrina sigmoidea* Hua, *Vitex doniana* Sweet., *Terminalia glaucescens* and very sparse *D. oliveri*, *Albizia zygia* (DC.) J.F.Macbr.) and very degraded forest including *Terminalia superba* Engl. & Diels, *Cola lateritia* K. Schum., *Pycnanthus angolensis* (Welw.) Warb. and the alien invasive



Fig. 1. Location of the three lakes and distribution of the major African vegetation types (from White (1983)) in the Central African Republic.

Chromolaena odorata (L.) R.M. King & H. Rob. This lake is surrounded by lots of fields and situated at around 500 m from a road and 1 km from a village, so the landscape is situated within a 5 km-radius from the lake burn at least once a year during the dry season (Aleman et al., 2013a).

Lake Nguengué is within a wide riparian forest composed of *Alstonia boonei* De Wild. with some *H. stipulosa* and *Raphia farinifera* (Gaertn.) Hyl. The surrounding mature semi-evergreen forest — with *Celtis tessmannii* Rendle, *Trilepisium madagascariense* D.C., *Pentaclethra macrophylla* Benth., *Pouteria altissima* (A.Chev.) Baehni, *Triplochiton scleroxylon* K. Schum., *Macaranga barteri* Müll.Arg., *Myrianthus arboreus* P. Beauv. — is impacted by humans as evidenced by ruderal trees (*Elaeis guineensis* Jacq., *P. angolensis*, *Musanga cecropioides* R.Br.). There are open patches of fields and pastures within the forest matrix of ~0.5 ha to 1 ha (the closest patches are located 300 m from the lake). Moreover, a village is situated at around 1 km from the lake. Thus, some of the open patches burn once a year (Aleman et al., 2013a).

The landscape around the three lakes is flat (maximum of 110 m of elevation gradient within 10 km around each lake), so it was not possible to compute the size of the catchment area. The water supply for the three lakes is mainly by run-off.

2.2. Sampling and sediment dating

Cores of the topmost water-saturated sediments were extracted in December 2010 using a Kajak-Brinkhurst sampler in the center of each lake. In Lakes Gbali, Doukoulou and Nguengué, 12, 12 and 14 samples were taken from core depths of 42, 20 and 36 cm, respectively for phytolith extraction (see depth sampling in Fig. 5). The sediments, mostly organic, were dated based on radioactive cosmogenic tracer analysis of ⁷Be (half-life = 53.22 days) and ²¹⁰Pb (half-life = 22.3 years) (Appleby and Oldfieldz, 1992). The age-depth models are fully described in Aleman et al. (2013a) (Fig. S1 in Appendix 1). In order to study sediment compaction with depth, the dry weight of the three cores was measured each centimeter.

2.3. Phytolith extraction and counting

Phytoliths were extracted from 5 g sediment samples using the following protocol (Aleman et al., 2013b): (1) deflocculation of the sediment with NaPO₃, (2) dissolution of carbonates using HCl, (3) oxidation of organic matter with H₂O₂, (4) reduction and removal of iron oxides, (5) removal of clay by gravity, (6) drying of the residue with ethanol and (7) densimetric separation of phytoliths in a dense solution of $ZnBr_2$ (d > 2.3). Before drying the phytolith solution, silica microspheres were added to determine the phytolith concentration and influx (Aleman et al., 2013b). The recovered fraction was mounted on microscope slides on glycerin for 3D observation and phytoliths were counted at 600× magnification. Sufficient items (microspheres and the most frequent phytolith morphotype with taxonomic significance) were counted to reach an estimate of the total phytolith concentration with a precision of at least $\pm 15\%$, as described in Aleman et al. (2013b). A total of 350 to 1000 diagnostic phytoliths were counted per sample for a minimum count of 200 grass silica short cells (GSSC) to minimize analytic and statistical errors (Aleman et al., 2013b). Only phytoliths with diameters larger than 5 µm were counted and classified. Phytolith diagrams were then prepared with the TILIA program (Grimm, 1993).

For GSSC and woody dicotyledon phytoliths, dark opaque phytoliths – potentially burned specimens resulting from the burning of occluded organic material (Parr, 2006; Piperno, 2006) – were differentiated from light and colored translucent ones that occur naturally in some plants. Charcoal accumulation rates in number (CHAR_n, #.cm⁻²·yr⁻¹) are from Aleman et al. (2013a), and presented for comparison with phytolith influxes. W/L ratios correspond to the width-to-lentgh ratio of charcoal particles, and have been proven to be a good proxy for changes in fuel type (Aleman et al., 2013a).

2.4. Phytolith classification and indices

Phytoliths were described according to their three dimensional shape and classified (Table S1) following the international code of phytolith nomenclature (Madella et al., 2005) and based on the classification schemes of Twiss et al. (1969) and Twiss (1992), augmented by information presented by Scurfield et al. (1974), Piperno (1988, 2006), Mulholland (1989), Fredlund and Tieszen (1994), Kondo et al. (1994), Alexandre et al. (1997), Piperno and Pearsall (1998), Barboni et al. (2005b), Albert et al. (2006), Bremond et al. (2008a), Gu et al. (2008), Barboni and Bremond (2009), Iriarte and Paz (2009), Neumann et al. (2009), Eichhorn et al. (2010), Novello et al. (2012) and Garnier et al. (2013). The morphotypes identified in this study were grouped into four categories:

- (1) Grass silica short cells (GSSC, Fig. 2A) are produced by Poaceae (Mulholland and Rapp, 1992). Among the GSSCs, the bilobates (Fig. 2Aa-d), polylobates (Fig. 2Ag) and crosses (Fig. 2Ae-f) are mainly produced by the Panicoideae subfamily (Twiss et al., 1969; Mulholland, 1989; Fredlund and Tieszen, 1994; Kondo et al., 1994), which are C₄ grasses adapted to warm and humid climate. The saddle type (Fig. 2Al) occurs dominantly in the Chloridoideae subfamily (Twiss et al., 1969; Mulholland, 1989; Fredlund and Tieszen, 1994; Kondo et al., 1994), C₄ grasses adapted to a warm and dry climate. The rondel type, corresponding to the pooid type defined by Twiss et al. (1969) and the conical, keeled and pyramidal types from Fredlund and Tieszen (1994), include conical (Fig. 2Ah), conical bilobate (Fig. 2Ai-j), conical trilobate and conical quadrilobate (Fig. 2Ak) morphotypes (Table S1). The trapeziform short cell type (Table S1) (Twiss et al., 1969; Mulholland, 1989; Fredlund and Tieszen, 1994; Kondo et al., 1994) comprises trapeziform, trapeziform bilobate (Fig. 2Am), trapeziform trilobate and trapeziform quadrilobate (Fig. 2An) morphotypes. The rondel and trapeziform short cell types are produced not only by the Pooideae subfamily (C₃, high elevation grasses), but also by the other subfamilies (Barboni and Bremond, 2009).
- (2) The woody dicotyledon category is composed of globular granulate (Fig. 2Ba) (Scurfield et al., 1974; Kondo et al., 1994; Alexandre et al., 1997; Bremond et al., 2005a), globular decorated (Fig. 2Bb–e) (Runge, 1999; Piperno, 2006; Neumann et al., 2009; Novello et al., 2012), sclereid (Fig. 2Bg) (Runge, 1999; Mercader et al., 2000; Neumann et al., 2009), blocky faceted (Fig. 2Bf) (Runge, 1999; Mercader et al., 2009; Neumann et al., 2009) and blocky granulate morphotypes (Table S1) (Mercader et al., 2009).
- (3) In this study, two family-specific morphotypes were described. Three papillae types were identified (Fig. 2Cb-e, Table S1) (Runge, 1999; Albert et al., 2006; Gu et al., 2008; Novello et al., 2012), produced by Cyperaceae (Kondo et al., 1994) mainly occurring in wetlands. The globular echinate morphotype (Fig. 2Ca) is produced by palms (Arecaceae) (Kondo et al., 1994; Runge, 1999).
- (4) The last category includes the non-diagnostic morphotypes (Table S1): globular smooth, elongated (Fig. 2Cj-k), tabular (Fig. 2Ci and m) and blocky types (Fig. 2Cf-h).

For each sample the Iph index was computed, i.e. the ratio of Chloridoideae (saddle type) to the sum of Chloridoideae and Panicoideae (saddle, cross and bilobate) phytoliths, which indicates the dominance of short-grass or tall-grass savanna (Bremond et al., 2008a). The D/P index (ratio of woody dicotyledon to Poaceae phytoliths) was also calculated. To facilitate comparison of the results with those of other studies, this index was computed as the ratio of globular granulate and decorated phytoliths to the GSSC (Bremond et al., 2008b). The transformation ln(D/P + 1) was calculated for each



Fig. 2. Phytolith morphotypes found in samples from the three lakes. (A) GSSC morphotypes: (a) bilobate long, (b) bilobate short, (c) burned bilobate short within burned organic mater, (d) burned bilobate short, (e–f) cross, (g) polylobate, (h) rondel, (i–j) conical bilobate, (k) conical quadrilobate, (l) short saddle, (m) trapeziform bilobate, (n) trapeziform quadrilobate. (B) Woody dicotyledon morphotypes: (a) globular granulate, (b–e) globular decorated indiff., (f) blocky faceted, (g) sclereid. (C) Other morphotypes: (a) globular echinate (Arecaceae), (b–e) Papillae (Cyperaceae), (f) point-shaped, (g) bulliform cell, (h) blocky smooth, (i) tabular crenate, (j) tracheid, (k) elongate smooth, (l) elongate triangular psilate, (m) tabular thick. (D) Image of a microsphere inside a diatom. The scale bar in each case is 10 µm.

sample, which has been proven to be linearly correlated with the Leaf Area Index, a good indicator of vegetation structure (Aleman et al., 2012).

2.5. Land cover analysis

To assess recent changes in land cover, Landsat Multispectral Scanner (MSS; 68 m × 83 m pixel resolution) and Thematic Mapper (TM, 30 m pixel resolution) images collected in January 1974, December 1984, December 1994, January 1995, and February 1999, and SPOT 5 images (2.5 m pixel resolution) from December 2005 were analyzed. Two land cover types were identified: closed vegetation (forest), and open landscapes that have similar spectral signatures (savanna, fields and pastures). These two vegetation classes were expected to produce different phytolith assemblages. To quantify land cover changes in the area covered by each image and around each lake, the percentages of forested pixels within different distances from the lake centre (1 to 10 km) were computed. Then, the land cover around each lake (maps in Fig. S2 in Appendix 2 and in Aleman et al. (2013a)) was compared with the corresponding phytolith tree cover index.

2.6. Statistical analysis

The phytolith assemblages of the three lakes were compared by Principal Component Analysis (PCA), using FactoMineR in R (version 2.15.3, R Development Core Team, 2012). Only the most frequent morphotypes were represented on PCA graphs (Fig. 6). To study the relationships between the phytolith influxes and charcoal accumulation rate time series, a cross-correlation analysis was performed, using the 'ccf function in R (R Development Core Team, 2012). Autocorrelation and cross-correlation functions are useful for analyzing the joint behavior of two time series (Shumway and Stoffer, 2011). The cross correlation between the two time series describes the normalized cross covariance function and enabled to determine time delay between the two signals.

3. Results

3.1. Sediment compaction and phytolith influx

The dry matter concentration along the core, which illustrates the compaction of sediments with depth, differed among the three lakes (Fig. 3A–C). For Lakes Doukoulou and Nguengué, the concentration increased until the bottom of the core with a plateau at 6–10 cm and 5–12 cm, respectively, for the two lakes. For Lake Gbali, dry matter concentration stabilized at a depth of approximately 20 cm depth and remained constant at further depths.

Total phytolith concentration increased with depth following the same pattern as dry matter in the three cores (Fig. S3). Total phytolith influxes differed among the three lakes (Fig. 3D–F) and were highest



Fig. 3. Variation in dry matter concentration with depth in cores from Lakes Gbali (A), Doukoulou (B), and Nguengué (C), and phytolith influxes over time for Lakes Gbali (D), Doukoulou (E), and Nguengué (F). In D, E and F, phytolith influxes are for grass silica short cells (\bullet), globular granulate and decorated morphotypes (\star), Arecaceae (\checkmark) and other woody dicotyledons (–) expressed as phytoliths.cm⁻²·yr⁻¹ and for the charcoal accumulation rate (CHAR_n, $_{\bigcirc}$) as particles.cm⁻²·yr⁻¹.

in Lake Doukoulou, except between 1990 and 2010 when they were highest in Lake Nguengué.

For Lake Gbali, GSSC and woody dicotyledon influxes had parallel trends, along with the globular echinate morphotype, diagnostic of Arecaceae, after 1950 (Fig. 3D). Phytolith influxes and charcoal accumulation rates both decreased after 2000. For Lake Doukoulou, GSSC, woody dicotyledon and Arecaceae phytolith influxes had parallel trends along the entire core (Fig. 3E). From ~1990 there was an abrupt decrease of all phytolith influxes until ~2006, when influxes increased again. Charcoal accumulation rates exhibited the same trend, with a peak in ~1990 and a decrease until ~2005, followed by another increase. For Lake Nguengué, there was little variation in phytolith influxes except after 2000 when a peak in all phytolith influxes was followed by a decrease (Fig. 3F). All phytolith morphotypes had the same trend, along with the charcoal accumulation rates, which had an earlier increase in the 1950s. Influxes of all phytoliths were consistently higher in Lake Doukoulou until 1990. Phytolith influxes were higher in Lake Nguengué in the 2000s.

3.2. Phytolith assemblages and indices

The globular echinate morphotype dominated signals in the Lake Gbali core (accounting for >50% of all phytoliths, except in the two deepest samples) along with lobate morphotypes (>20%, Fig. 4A), especially bilobate and cross morphotypes (Fig. S4a–c). The elongated morphotypes were also well represented with over 8% of all phytoliths. The proportions of burned GSSC and woody dicotyledon phytoliths were both high (over 15% and 12%, respectively). The D/P index was stable at <0.25, and the Iph index was characteristic of a tall grass savanna (<40%, Fig. 5). The woody dicotyledon assemblage in Lake

Gbali was dominated by globular granulate and blocky faceted morphotypes (Fig. S4g-k).

The phytolith signals in Lake Doukoulou were dominated by rondel (>18%) and echinate (>15%) morphotypes, with papillae (>11%) and elongated (>7%) morphotypes also well represented (Fig. 4B). The percentage of burned GSSC was very low (<6%) compared to the percentage of burned woody dicotyledon phytoliths (>17%). The D/P index was also low along the entire sequence (<0.4), with an increase at 20 cm where it reached 0.6. The Iph index was characteristic of a tall grass savanna (<40%, Fig. 5).

Globular granulate (>30%) and echinate (21%) morphotypes dominated the assemblage in Lake Nguengué (Fig. 4C). Elongated morphotypes were also well represented in the signal (5–23%, Fig. 4C). The percentage of GSSC that were burned was high (>10%), but the percentage of woody dicotyledon phytoliths that were burned was low (<10%). The D/P index was very high with values reaching 11 and always >3.

There were no notable differences in the assemblages with depth along the three cores (Fig. 4), except for the relatively low proportions of echinate and elongated morphotypes in the two deepest samples from Lake Gbali and relatively high proportion of GSSC that were burned in the 25 cm depth sample from Lake Nguengué. Nevertheless, the assemblages strongly differed among the three lakes.

3.3. Assemblages' signature within each lake

The three lakes were well discriminated by the phytolith morphotypes: the first two axes of the PCA explained 68% of the variance (Fig. 6). Lake Gbali was differentiated by high frequencies of globular echinate and blocky morphotypes, along with bilobate morphotype and high percentages of burned woody dicotyledons.



Fig. 4. Phytolith diagrams, the ratio of dicotyledon to Poaceae diagnostic phytoliths (D/P), the ratio of Chloridoideae to the sum of Chloridoideae and Panicoideae phytoliths (Iph), the charcoal accumulation rate (CHAR_n in $\#.cm^{-2} \cdot yr^{-1}$) and the width-to-length ratio of charcoal particles (W/L) in samples from Lakes Gbali (A), Doukoulou (B), and Nguengué (C). Abundances lower than 1% are represented by dots. Percentages in brackets are the relative percentages for each phytoliths groups, averaged for each lake sequence.



Fig. 5. Characteristics of phytoliths from all samples of Lakes Gbali, Doukoulou, and Nguengué. (a) Ratios of dicotyledon to Poaceae diagnostic phytoliths (D/P index), (b) ratios of Chloridoideae to the sum of Chloridoideae and Panicoideae phytoliths (Iph index, as percentages), (c) proportions of burned grass silica short cells (GSSC) phytoliths, (d) proportions of burned woody dicotyledon phytoliths (D). Different letters indicate means that are significantly different based on a Kruskal–Wallis test.

Lake Doukoulou was mainly characterized by trapeziform short cells, and rondel and papillae forms, as also highlighted in a comparison of the morphotype abundances among the three lakes (Fig. S4). Lake Nguengué was well described by globular granulate and decorated morphotypes, which are characteristic of a forest environment. High proportions (>10%) of burned GSSC were features of Lakes Gbali and Nguengué distinguishing them from Lake Doukoulou, which had low proportions (<5%, Fig. 5). Lakes Gbali and Nguengué had the highest

and the lowest proportions of burned woody dicotyledon phytoliths, respectively.

3.4. Correlation between phytolith and charcoal influxes

The cross-correlation analysis showed that GSSC influxes and charcoal accumulation rates were significantly correlated for Lakes Gbali and Nguengué (autocorrelation function coefficient > 0.3 and 0.4,



Fig. 6. Ordination diagrams of the phytolith morphotypes from the Principal Component Analysis of samples from Lakes Gbali (GBL), Doukoulou (DKL), and Nguengué (NGG). Axes 1 and 2 explained 39.4% and 28.9% of the variance, respectively. In the variables factor map (A), the arrows represent different types of phytoliths (D = woody dicotyledons, GSSC = grass silica short cells). Numbers in the individual factor map (B) indicate samples depth taken from the three lakes.



Fig. 7. Results of the cross-correlation analysis: autocorrelation function coefficients (ACFs) between GSSC influxes and charcoal accumulation rates for Lakes Gbali (A), Doukoulou (B), and Nguengué (C). Vertical bars correspond to computed ACF at each lag time, and dashed lines correspond to the minimum ACF value for a significant autocorrelation between the two time series.

respectively, Fig. 7). Moreover, the lag time between the two time series was centered on zero. For Lake Doukoulou, the autocorrelation function coefficient reached high values (0.4), but the correlations were not significant and no temporal pattern in the relationship between phytolith and charcoal influxes was detected (Fig. 7).

3.5. Effect of land cover on the phytolith tree cover index

For Lake Gbali, $\ln(D/P + 1)$ values were low (<0.25) but with some variation (Fig. 8A). From 1990, the general increase in the percentage of forested land around the lake seems to match the increase in the D/P index. Recently the D/P index has been decreasing, but land cover values were not available to confirm this trend. For Lake Doukoulou, $\ln(D/P + 1)$ was low with values <0.3. The surrounding landscape was dramatically opened, from forest to a more open landscape starting between 1980 and 1990 (Fig. 8B), during a time when $\ln(D/P + 1)$ was stable. For Lake Nguengué, $\ln(D/P + 1)$ values were high (>1.5, thus there were 3.5 times more woody dicotyledon than Poaceae phytoliths, Fig. 8C). The ln(D/P + 1)index increased slightly from 1960 to 2006 (reaching 2.5), then decreased abruptly in 2009, and increased again in 2010. However, these values correspond to only one year of accumulation (2010-2011), and averaging their values resulted in a $\ln(D/P + 1)$ index of 1.7 (i.e., 4.5 times more woody dicotyledon phytoliths). The landscape around Lake Nguengué developed from a closed forest to a more degraded forest with open patches since ~1950 (Aleman et al., 2013a).

4. Discussion

To explore effects of the lakes' local environment on phytolith assemblages, the phytolith content of recent sediments in cores extracted from three lakes surrounded by different environments was investigated. More specifically, their assemblages in terms of total numbers of phytoliths and influxes, and both Iph and D/P indices, were compared with charcoal accumulation rates and recent landscape history. Indeed, in contrast to phytolith assemblages and the D/P index in soil record, which provide relatively direct records of standing vegetation (Piperno and Becker, 1996; Runge, 1999; Bremond et al., 2005a; Aleman et al., 2012), various taphonomic processes affect lake sediment records that must be considered when interpreting them. These processes correspond to the stages of production, transport, deposition and conservation of a bio-proxy in a sedimentary archive (Efremov, 1940).

4.1. Taphonomy and associated biases

First, the differential production of phytolith morphotypes by plants can introduce a bias in the assemblages by over or under-representing some of them. For example, the phytolith assemblage in Lake Gbali was dominated by the Arecaceae morphotype (>40%) even though Arecaceae plants constituted only 5% of the riparian forest and were not part of the savanna matrix. The globular echinate phytoliths (Arecaceae) were the third most important morphotype of the total assemblage (~20%) for Lake Doukoulou; they were detected in the



Fig. 8. Transformed ratios of woody dicotyledon to Poaceae diagnostic phytoliths $\ln(D/P + 1)$, which are linearly correlated to the vegetation structure, and proportions of forested land (% forest pixels) at indicated times in the surroundings $-1(\bigcirc, 2(\times), 3(\lor), 4(*), 5(\oiint, 7(*)$ and $10(\diamond)$ km from the centers - of Lakes Gbali (A), Doukoulou (B), and Nguengué (C).

botanical survey of the swampy area, but not in the savanna landscape. For Lake Nguengué, the globular echinate phytoliths that dominated the total phytolith assemblage were likely from palm trees that were detected in the riparian forest surrounding the lake but not in the forest matrix. Palm trees are known to produce phytoliths abundantly (Pearsall, 2000; Piperno, 2006), and thus are expected to be overrepresented in assemblages. For example, Bremond et al. (2005a) found that Arecaceae morphotypes could represent up to 40% of the assemblage due to their presence in the surrounding forest, even if no palm trees were present within 10 m.

Second, transport and deposition of phytoliths can vary between the lakes or the sedimentary archives. In this study, it has been found higher percentages of burned GSSC deposited in Lakes Gbali and Nguengué, both lakes surrounded by riparian forest, than in Lake Doukoulou, along with positive correlations between GSSC influxes and charcoal accumulation rates for these two lakes. These findings clearly indicate strong transportation of GSSC with charcoal particles in ash clouds from further away (Clark et al., 1998). Eolian transport of phytoliths in ash and dust is important in open environments (Fredlund and Tieszen, 1994; Piperno, 2006) as in Lake Gbali surroundings. High proportions of burned grass and woody dicotyledon phytoliths in Lake Gbali probably originated from stems of burned tree seedlings or leaves of deciduous savanna trees (Bond and Keeley, 2005; Gignoux et al., 2009). Aerial transport must be the main transportation mode for GSSC and woody dicotyledon phytoliths into this lake. Indeed, in the case of direct deposition from the local environment (i.e. the 200-m wide riparian forest) the phytolith signal would be a forest one, whereas the assemblage corresponded to a savanna environment. In the degraded forest surrounding Lake Nguengué, the open patches of field and pastures burned almost every year (Aleman et al., 2013a), and GSSC phytoliths may have been transported by wind with charcoal particles. Nevertheless, GSSC constitute only ~7.2% of the total assemblage in Lake Nguengué, confirming that aerial transport is not dominant in closed environment (Piperno, 2006). Thus, woody dicotyledon phytoliths (~45% of the total assemblage) mostly originated from the local woody vegetation surrounding the lake (Kealhofer and Penny, 1998; Piperno, 2006). In the Lake Doukoulou samples, there were very few burned phytoliths indicating that eolian transportation was not the main mode of deposition. Instead, the phytoliths in this lake were probably mainly deposited by direct run off, as Aleman et al. (2013a) evidenced for charcoal particles deposition, and the phytolith assemblages likely reflect the local environment. Thus, higher GSSC phytolith influxes for Lake Doukoulou than the two other lakes may indicate this different mode of transportation, as well as a surrounding ecosystem that produces more grass phytoliths (Pearsall, 2000; Piperno, 2006). A further factor that should be considered is that Lakes Gbali and Nguengué are surrounded by riparian forest, which acts as a physical filter for charcoal particles (Aleman et al., 2013a) and thus may also trap other airborne particles (notably phytoliths). Identifying the main transportation mode of phytoliths in lakes may enable to point out their source area, which is crucial information to interpret assemblages and indices.

4.2. Ecological interpretation of assemblages and indices

For Lake Gbali, the assemblage was dominated by GSSC phytoliths, especially bilobate and cross morphotypes, which is consistent with tallgrass savanna (Iph index < 40%: Bremond et al., 2008a) dominated by Panicoideae. The woody dicotyledon assemblage was nevertheless dominated by blocky faceted and granulate morphotypes, along with globular granulate morphotypes. Mercader et al. (2009) found large quantities of such blocky morphotypes in the Miombo woodlands of Mozambique. The blocky morphotypes in Lake Gbali could have been produced by riparian forest (Runge, 1999; Mercader et al., 2000). Surprisingly, there were few blocky and sclereid morphotypes in Lake Nguengué assemblage, although they have previously been found in tropical forest soils (Runge, 1999). These morphotypes may not be sufficiently well preserved in soil to reach the lake, or perhaps they were not produced in our area. Therefore, using these morphotypes to record an environmental change or discriminate between environments in tropical areas is not straightforward, especially since their morphology is neither clearly described nor easy to recognize. The tree cover index for Lake Gbali was consistent with open savanna (Bremond et al., 2005a; Neumann et al., 2009; Aleman et al., 2012). The large riparian forest around the lake did not mask the savanna landscape signal, probably due to the high production of phytoliths by Poaceae (Piperno, 2006) from the savanna, the low production by riparian forest trees and the aerial transportation of phytoliths. Similar patterns have been previously noted in several locations (Pearsall, 2000), including Lake Sinnda in Congo, using phytolith data acquired by Alexandre et al. (1997) and estimations of past tree cover in the surroundings by Aleman et al. (2012). The signature of phytoliths from riparian forest remains unclear. Hallea trees were present around Lakes Gbali and Sinnda (Vincens et al., 1998), suggesting that this genus may produce few globular phytoliths, but the characteristics of phytoliths produced by other tree species that are physiologically adapted to standing water (if any) are unknown. Thus, the phytolith signal of Lake Gbali is extralocal and records the savanna landscape.

The assemblage in Lake Doukoulou was highly discriminated by rondel, trapeziform and papillae morphotypes, with GSSC dominating the total assemblage. High proportions of papillae morphotypes are characteristic of the presence of Cyperaceae (Piperno, 2006) found in the swamp around the lake. Globular granulate and decorated morphotypes dominated the woody dicotyledon assemblage, which is consistent with the presence of forest around the lake (Runge, 1999; Strömberg, 2004). Rondel and trapeziform short cell types of phytoliths are not subfamily specific, but are mainly produced by the Pooideae (Twiss et al., 1969) that contains mostly C₃ grasses. This result is puzzling since Lake Doukoulou is situated in an area dominated by Panicoideae C₄ grasses (I. cylindrica, V. zizanioides and P. purpureum). Borba-Roschel et al. (2006) suggested that rondel-concave morphotypes could be produced by Rhynchospora emaciata, a Cyperaceae. However, we extracted phytoliths from R. emaciata, V. zizanioides, Cyperus flabelliformia and Nymphaea lotus L. and found no rondel types. Therefore, the grass species that produced the rondel phytoliths is still unknown. Regarding the D/P index, despite an abrupt change in the landscape around Lake Doukoulou, it remained low along its entire sequence. Low D/P values (<1) before ~1990 while the area around the lake was still forested can be explained by the large Poaceaedominated marsh around the lake that probably released many more phytoliths directly into it than the surrounding forest (Fredlund and Tieszen, 1994). Such "edge" effects are very important for long-term reconstruction studies; for example, in Lake Doukoulou, the D/P index indicates a savanna whereas the landscape around the lake was actually forested. In this case, the phytolith signature corresponds to the lakeshore environment, which was characterized by a combination of Cyperaceae and Poaceae. Clearly, phytolith assemblages and indices need to be interpreted cautiously, taking into account the phytoliths source area. In the case of Lake Doukoulou, the phytoliths are mainly deposited by direct run-off into the lake and the signal corresponds to the very local environment of the lake, and does not reflect the surrounding landscape. Influxes can bring important information, which was not recorded by the assemblage neither the D/P index. Indeed, the change in land cover matched an abrupt decrease in influxes of GSSC, woody dicotyledons and Arecaceae phytoliths. These reductions are difficult to interpret, but a possible explanation is that a decrease in the swamp area around the lake led to the decrease in GSSC and Arecaceae phytolith influxes, while deforestation led to the decrease in the woody dicotyledon phytolith influx.

For Lake Nguengué, globular granulate and decorated morphotypes, which are characteristic of tropical forest trees (Runge, 1999; Piperno, 2006; Neumann et al., 2009), dominated the total phytolith assemblage.

Among the few GSSC recorded (~7.2%), the bilobate and cross morphotypes were the most abundant, which is consistent with Panicoideae grasses from the open patches of the degraded forest. The elongated types were present in all three lakes, making it difficult to identify their origin from grasses or trees (Runge, 1999; Novello et al., 2012; Garnier et al., 2013). The D/P index did not record small open patches of fields and pastures that have been created by disturbance from anthropogenic activities since ~1950 (Aleman et al., 2013a), although recent lower values may be starting to reflect these changes. This is probably because most of phytoliths originate from the local environment of the lake. Nevertheless, changes in D/P > 1 are difficult to interpret, and the D/P index in Lake Nguengué exceeded 6, beyond values in existing calibrations between the D/P and vegetation structure indices (Bremond et al., 2005a; Aleman et al., 2012).

5. Conclusion

The results of this study have shown that to interpret lacustrine phytoliths records, taphonomical processes, especially production, transport and deposition, must be considered since they indicate the main phytoliths source area. Indeed, the local environment surrounding a lake can strongly affect its phytolith assemblage and the representativeness of its phytolith indices. The presence of an area with abundant Poaceae, which are high phytoliths producers, in the immediate surroundings of a lake can lead to a "super-local" signal that is distinct from the local and regional landscape signals. In contrast, regional signals may not be hidden by a riparian forest surrounding a lake situated in an open environment, due to high phytolith production by Poaceae and low production by riparian trees (Pearsall, 2000; Piperno, 2006). The woody dicotyledon signal from the riparian forest of Lake Gbali was not "super-local" since it has been shown that burned savanna made important contributions to these phytoliths. Moreover, when interpreting ecological significance of phytoliths, it is highly preferred to analyze the entire phytolith assemblage as a whole rather than taxa by taxa because of the variations in phytolith production by plants. For example, in Lake Doukoulou, the rondel and trapeziform short cell types that have been identified are not associated with the trapeziform polylobate type (Bremond et al., 2008b; Barboni and Bremond, 2009) so it cannot be concluded that the Lake Doukoulou environment contained C₃ Poaceae. The use of phytolith assemblages from recent lacustrine sediments of a core are crucial to help interpreting long-term assemblages because they reveal valuable information about taphonomic processes, compared to soil assemblages from the catchment area or region.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.palaeo.2014.08.030.

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