Taxonomic, ecological and palaeoecological significance of leaf phytoliths in West African grasses

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ABSTRACT

Grass short cell phytoliths (GSCP) are a valuable tool for the reconstruction of former grass-dominated ecosystems, especially in Africa. GSCP are highly diverse and most of them show affinities with certain taxonomic groups within the Poaceae. Taxonomic affiliation of the GSCP can be exploited for palaeoecology because many subfamilies, tribes and genera have specific ecological requirements. Finer classification of GSCP can improve the taxonomic resolution and palaeoecological reconstructions, but the numerous existing GSCP classification schemes have not been standardized yet, and are hardly comparable. It is therefore important to identify clearly defined morphotypes with taxonomic and ecological significance. We studied GSCP from 51 West African common grass species belonging to 32 genera, representing the entire ecological gradient from the Sahara to the Guinean savanna zones. We used 153 detailed GSCP morphotypes, considering variations in shape, size and 3D morphology, and eventually merged them into 20 supertypes. Correspondence analysis (CA) was applied to reveal correlations between morphotypes and taxonomic groups; ecological parameters were introduced as passive variables. In spite of redundancy among bilobates, crosses and saddles, the subfamilies Panicoideae, Aristidoideae, Chloridoideae and Ehrhartoideae can be clearly distinguished by their GSCP assemblages. Aristidoideae are characterized by very long bilobates with convex ends and very long shanks, Chloridoideae by squat saddles, Ehrhartoideae by scooped bilobates, and Panicoideae by *Stipa*-type bilobates and polylobates. The three Chloridoideae tribes can be separated, but not the panicoid tribes Paniceae and Andropogoneae. Rondels do not seem to have any taxonomic or ecological significance. Except for very long bilobates with very long shanks which are most common in xerophytic grasses, there is no direct correlation of certain morphotypes with the habitat requirements of the species. In the aquatic and mesophytic species, statistically significant GSCP rather mirror the taxonomic affiliation, e.g. the scooped bilobates in the aquatic *Oryza* species, or polylobates in mesophytic Panicoideae. The results of the Canonical CA for the detailed morphotypes and the merged supertypes are comparable. We conclude that the easily recognizable 20 supertypes are appropriate for future ecological and palaeoecological phytolith studies in Africa. For the supertypes of bilobates and crosses, the size of the particle and the length of the shank are important features whereas 3D morphology and the shape of the lobe ends can be neglected.

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1. Introduction

Grass-dominated vegetation formations, from treeless grasslands to densely wooded savannas, cover the largest part of the African continent. The development of these grasslands under changing climatic conditions is a key topic in palaeoecological studies and often related to questions of hominin evolution or the development of human land-use systems through time (Albert

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et al., 2006; Bamford et al., 2006; Neumann et al., 2009; Barboni et al., 2010; Albert and Bamford, 2012; Novello, 2012; Novello et al., 2012; Cordova, 2013; Garnier et al., 2013). Phytoliths are a valuable tool to study grassland changes, for two reasons: 1) Phytoliths as silica-bodies are extremely durable and can be preserved in ancient soils and sediments for millions of years (Strömberg, 2003, 2004; Strömberg et al., 2007); 2) phytoliths, especially those of grasses, offer a wealth of different shapes that can be used for identifying special vegetation types in the past (e.g. Alexandre et al., 1997; Fredlund and Tieszen, 1997; Barboni et a., 1999; Neumann et al., 2009; Novello et al., 2015). A major concern of phytolith studies in Africa, as in other regions of the world with grass-dominated ecosystems, is the search for diagnostic morphotypes that might be useful as discrete markers in the reconstruction of ancient vegetation.

The study of modern grass phytoliths is essential as a reference for interpreting the ecological or bioclimatic significance of phytolith assemblages in fossil samples. There are two approaches for the reconstruction of ancient vegetation through phytoliths. The first tries to identify characteristic morphotypes for certain taxonomic groups which can be correlated with ecological parameters, such as light and moisture requirements or photosynthetic pathway (e.g. Twiss, 1992; Piperno, 2006; Barboni and Bremond, 2009; Rossouw, 2009; Mercader et al., 2010). The second studies phytolith assemblages of modern soil surface samples and calibrates them in relation to vegetation types and environmental (especially climatic) factors (e.g. Fredlund and Tieszen, 1994, 1997; Barboni et al., 2007; Bremond et al., 2008a; Iriarte and Paz, 2009; Mercader et al., 2011; Cordova, 2013; Dickau et al., 2013). In Africa calibration of soil surface samples has led to the establishment of four indices characterizing woody vs. grass vegetation (D:P), temperature and rainfall gradients (Ic, Iph) and aridity (Fs) (Alexandre et al., 1997; Barboni et al., 1999, 2007; Bremond et al., 2005a,b, 2008b). In their study on phytoliths of the Lake Chad region, Novello (2012) and Novello et al. (2012) recently proposed three new indices for mesophytic, aquatic and xerophytic vegetation types.

Among the numerous morphotypes produced by grasses, the short-cell phytoliths (GSCP) are most meaningful whereas other phytoliths produced in the grass epidermis are usually less specific, e.g. elongates, bulliforms or trichomes (Piperno, 2006, pp. 35; exceptions are the dendritic elongates of the inflorescences which are useful for crop identification (Ball et al. in press) and as indicators for anthropogenic accumulation of grass inflorescences (Novello and Barboni, 2015). Based on the classification schemes of Twiss et al. (1969) and Mulholland (1989), seven major GSCP classes can be distinguished: Rondel, trapeziform, bilobate, cross, polylobate, trapeziform sinuate, and saddle (Barboni and Bremond, 2009). It has long been recognized that the Poaceae subfamilies produce different phytolith shapes; bilobates and crosses are especially common in Panicoideae, saddles in Chloridoideae and trapeziforms in Pooideae (Twiss et al., 1969; Brown, 1984; Piperno, 1988; Mulholland, 1989; Twiss, 1992; Piperno, 2006). However, in most cases the relationship between certain morphotypes and taxonomic groups is not exclusive, although sometimes suggested by names such as "Chloridoid class", "Panicoid class" etc. (Twiss et al., 1969; Runge, 1999; Gallego and Distel, 2004). Redundancy (i.e. the same morphotype occurs in several taxa) was already described in the first detailed grass phytolith studies by Brown (1984) and Mulholland (1989). For East African Poaceae, Barboni and Bremond (2009) have shown that bilobates occur in nine out of ten investigated grass subfamilies and saddles in six subfamilies. Thus redundancy decreases the potential of palaeoecological interpretation if only the major GSCP classes are considered.

Among the GSCP classes, redundancy can be reduced by applying a finer classification scheme, exploiting the numerous variations in shape, size, and 3D morphology. These criteria often permit discrimination below the subfamily level (Piperno, 2006, pp. 29). Studies on micromorphological characters in short cell phytoliths (e.g. length of the shank and shape of outer margin of the two lobes in bilobates) have demonstrated relationships between some morphotypes and taxonomic groups like tribes and genera (Lu and Liu, 2003b; Gallego and Distel, 2004; Fahmy, 2008; Barboni and Bremond, 2009). However, with finer classification systems the problem of multiplicity (i.e.one species produces several different morphotypes) becomes more pronounced: The more recognized morphotypes, the more subtle are the differentiating characters, thus complicating compatibility and reproducibility (Rovner, 1971). Therefore the question is legitimate which of the finer morphological variations can significantly contribute to improve taxonomic and ecological interpretations, and whether these variations can be unequivocally recognized by other phytolith researchers.

The main objective of this study is the identification of diagnostic GSCP which are taxonomically and ecologically relevant for the savanna grasses of West Africa, and the establishment of a reproducible classification scheme. We present detailed quantitative data on 51 grass species from 32 genera, using 153 GSCP morphotypes which were eventually merged into 20 easily recognizable supertypes. The studied species belong to four subfamilies (Aristidoideae, Ehrhartoideae, Chloridoideae and Panicoideae) and eight tribes (Aristideae, Oryzeae, Chlorideae, Cynodonteae, Eragrostideae, Andropogoneae, Paniceae and Tristachyideae), are widely distributed in West Africa and represent the entire ecological gradient from the Sahara to the Sudanian and Guinean savanna zones. They were selected because they are dominant or characteristic for the most common West African savanna vegetation types (Hepper, 1972; White, 1983; Hahn-Hadjali, 1998; Schmidt et al., 2011b), but they are also of interest beyond the regional context because sometimes their distribution area extends to the Zambezian zone in southern Africa or via the Middle East to South Asia. Finally we outline a way how to apply our findings to paleoenvironmental reconstructions.

2. Material and methods

2.1. Selection of samples and phytolith processing

Leaf blades were sampled from Poaceae specimens kept in the West Africa collection of the Herbarium Senckenbergianum (FR), Frankfurt am Main, Germany (Table 1). The herbarium specimens originate from Burkina Faso, Benin, Nigeria, and Niger. We selected leaf blades because they produce much more biomass than culms or inflorescenses and therefore contribute largely to the representative phytolith signal of the vegetation in soils and sediments. Most sub-Saharan grass species produce similar phytoliths in inflorescences and leaves (Novello and Barboni, 2015) so that the leave phytoliths can be regarded as representative for the species. Each species was represented by one herbarium specimen, except for *Pennisetum pedicellatum*, *Pennisetum polystachion*, *Andropogon fastigiatus*, *Brachiaria lata*, *Loudetia togoensis* and *Sorghum arundinaceum* which were represented each by two specimens.

Leaf blades were cut into small pieces, washed in distilled water, treated with Alconox, sonicated to remove dust and dirt and dried in a low temperature oven (100 C°) for 1 h. The dry material was ashed in ceramic crucibles in a muffle furnace at 500 C° for 4–5 h. The resulting ash was treated with hydrochloric acid (32%) to dissolve carbonates, washed in distilled water, and treated with concentrated nitric acid in a water bath (95 C°) for