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Grass inflorescence phytoliths of useful species and wild cereals from sub-Saharan Africa

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ABSTRACT

Dendritic phytoliths that precipitate in grass inflorescences are often used in archaeology to trace the use of cereals (i.e. grasses harvested for their edible grain) and their domestication by early human societies. High amounts of these morphotypes are sometimes interpreted in terms of cereal accumulation in archaeological contexts. In sub-Saharan Africa, few cereals were domesticated during the mid-Holocene, but many wild grasses are still largely harvested by modern societies for food. The harvesting of wild cereals is also considered as one of the first stages toward early grass domestication. To evaluate how well dendritic phytoliths and/or other phytoliths produced in the grass inflorescences could help trace the use of wild cereal grains in sub-Saharan Africa, we analyzed the phytolith content of 67 African species (including 20 wild cereals), and 56 modern soils. We used test-value analysis and ANOVA to evaluate how well grass inflorescences could be distinguished from leaf/culm parts based on their phytolith content. We also measured the abundances of these phytoliths in natural soils from sub-Saharan Africa to provide a benchmark percentage abundance above which anthropogenic accumulation may be suspected in archaeological deposits. Our results confirm that, although rondel type phytoliths are abundant, only the dendritic phytolith morphotype is exclusive to the grass inflorescences. Yet, dendritic phytoliths do not occur in all species. They happen to be most frequent and found in greatest abundance (>34% relative to total phytolith count) in Panicoideae grasses (Sehima ischaemoides, Sorghastrum stipoides, and Sorghum purpureo-sericeum), and in one Eragrostideae species (Eragrostis squamata), which are not considered cereals. Inflorescences of the wild African cereals studied here do not happen to be particularly rich in dendritics (<7% in average). Finally, dendritics are rare in modern natural soils (<1% relative to total phytolith count, <3% relative to sum of grass silica short cells plus dendritics), even under stands of rich dendritic producers. We conclude that dendritic phytoliths may be used for tracing remarkable deposits of grass inflorescences at archaeological sites in sub-Saharan Africa, but are not exclusive to domesticated or wild cereals. Abundances of dendritics >>3% relative to sum of grass silica short cell phytoliths plus dendritics are likely to indicate anthropogenic accumulation of grass inflorescences. Yet, the absence or low abundance of dendritic phytoliths in archaeological deposits may not always indicate the absence of anthropogenic accumulation of grass inflorescence material.

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1. Introduction

Phytoliths are used to elucidate plant phylogeny (e.g. Prasad et al., 2011; Strömberg, 2011), to study past vegetation dynamics and paleoenvironments (e.g. Coe et al., 2014; Garnier et al., 2013; Miller et al., 2012), and as paleovegetation and paleoclimate

* Corresponding author. *E-mail address:* novelloalice@gmail.com (A. Novello). proxies (e.g. Aleman et al., 2012; Novello et al., 2012; Strömberg et al., 2007; Bremond et al., 2012; Fredlund and Tieszen, 1997). Phytoliths are also used in archaeology to infer early human living environments (e.g. Barboni et al., 2010; Rossouw and Scott, 2011; WoldeGabriel et al., 2009) and diet (e.g. Power et al., 2014; Henry et al., 2014), as well as early agriculture (e.g. Pearsall et al., 2003; Rosen and Weiner, 1994; Zhao and Piperno, 2000).

At archaeological sites, there is a particular interest in using grass phytoliths preserved in deposits to document past human activities integrating Poaceae species as primary resources (Albert et al.,







2008; Cabanes et al., 2010; Harvey and Fuller, 2005; Iriarte et al., 2010; Madella et al., 2013; Mercader, 2009; Portillo et al., 2010). For instance, grass phytoliths are largely searched for to study the first stages of cereal domestication (Lu et al., 2009; Pearsall et al., 2003; Ranere et al., 2009; Zhao and Piperno, 2000), early associated farming practices (e.g. irrigation) (Rosen and Weiner, 1994), and different processing (e.g. harvesting, threshing, storage, and pounding) that precede grass consumption (Harvey and Fuller, 2005). The multi-potentiality of grass phytoliths is linked to the fact that silica deposition occurs in roots, culms, leaves, and inflorescences, and in different types of cells (e.g. Parry and Smithson, 1964; Piperno, 2006), offering a large range of morphotypes to explore for paleoenvironmental and archaeological perspectives.

Particularly interesting for archaeology, Rosen (1992) observed that culm (straw) and husks (inflorescences bracts) of grasses produce different cell patterns that allow determining plant parts. Grass culm epidermis has basically the same cell pattern as leaves; they are characterized by "long-cells, short-cells and stomata aligned in longitudinal strips ... long-cells are narrow (ca 5-10 microns in width), with side walls that are smooth or slightly sinuous ... Papillae are absent". Grass husks (inflorescence bracts comprising glumes, lemmas and paleas) "include comparatively wide long-cells (ca 15-20 microns) ... pronounced sinuosity of the long-cell walls" (leading to the characteristic elongate dendritic types), "... often very thick long-cell walls and numerous papillae with elaborate ornamentations". Yet, her observations do not mention bulliform cells and hairs in culms, and prickles, hairs, stomata, and short cells that abundantly produce "hats" (i.e. rondel type phytoliths, ICPN, Madella et al., 2005) in husks (Parry and Smithson, 1966). To our knowledge, the phytolith type redundancy between grass culms/leaves, on the one hand, and grass inflorescences, in the other hand, has been explored (e.g. Albert et al., 2008; Mulholland, 1989; Parry and Smithson, 1966; Rosen, 1992), but never statistically demonstrated.

Bio-archeologists have largely investigated the inflorescence phytolith signal of the Pooideae as this subfamily of grasses includes several cereals: rye (Secale), barleys (Hordeum), wheat (Triticum), and oats (Avena) species, which early domestication is associated with the Fertile Crescent in the Near East 12000 to 9000 years BP (Harlan, 1971; Larson et al., 2014). To provide taxonomical identification of these cereal species, Ball and colleagues developed a morphometric approach applied to the dendritic phytoliths and to the silicified tissues of the grass inflorescences (Ball et al., 1999, Ball et al., 2009; Portillo et al., 2006). A morphometric approach was also successfully applied to the double-peaked glume phytoliths produced by Oryza species to distinguish domesticated rice (Oryza sativa) from wild Oryza species in Asia (e.g. Zhao et al., 1998). Conversely, few phytolith studies have dealt with early grass domestication in Africa (Fahmy, 2008; Fahmy and Magnavita, 2006; Radomski and Neumann. 2011).

Plant domestication in Africa occurred during the middle Holocene between 8200 and 4200 years BP in three key regions: the West African savannas in the Sahel, the Sudanic savannas, and the Ethiopian plateau (e.g. Fuller and Hildebrand, 2013). Cereals that were domesticated are pearl millet (*Pennisetum glaucum*), fonio (*Digitaria exilis*), black fonio (*Digitaria iburua*), and African rice (*Oryza glaberrima*) in the Sahel, sorghum (*Sorghum bicolor*) in the Sudanic savannas, and tef (*Eragrostis tef*), finger millet (*Eleusine coracana*), and Ethiopian oat (*Avena abyssinica*) in the Ethiopian plateau (see review in Larson et al., 2014). Domestication was a long and complex process, which involved ecological, biological, and human cultural factors, and which lead to morphological and phenological changes collectively referred to as the domestication syndrome (Purugganan and Fuller, 2009). The domestication syndrome "is defined by a wide variety of traits that, depending on the species, may include: a reduced ability to disperse seeds without human intervention, reduction in physical and chemical defenses, reduction in unproductive side-shoots, reduction in seed dormancy, bigger seeds, more predictable and synchronous germination, and in some seed-propagated species, bigger and more inflorescences. (...) Recent genetic and archaeological research, however, has demonstrated that "not all of these traits arose at the same time in either plants or animals" (Larson et al., 2014). Because phytoliths in grass inflorescences can contribute to reinforce the toughness of the glume, their greater abundance in the Pooideae cereals may be a response to increased seed mass during domestication. To our knowledge, however, the relationship between seed mass and silicon content of inflorescences of domesticated versus wild cereals has never been tested.

Botanical studies of crops and their sister taxa are necessary to assess what differences have evolved between domesticated and wild plants (Fuller and Hildebrand, 2013). To date, few phytolith studies applied to research on cereal domestication and agriculture in Africa have done so. Radomski and Neumann (2011) showed that some cereal genera, e.g. *Oryza, Digitaria,* and *Sorghum,* produce remarkable phytolith assemblages in their inflorescences, but the difference between wild and domesticated subspecies of African rice, pearl millet, and sorghum cannot be determined so far. They suggest that these taxa can still be identified in the archaeological record based on their phytolith assemblages. However, given the phytolith type redundancy in grasses from the same group e.g. the Panicoideae, these cereal species could easily be mistaken with other grass species producing the same phytolith assemblages. More studies, notably on wild cereals are therefore needed.

In the Sahel, wild grass cereals were harvested by nomadic tribes before domestication (de Wet, 2009). Even today wild grass cereals represent a valuable supplemental food source in many areas where agriculture is poorly developed and/or when products from crops are insufficient (Harlan, 2009). Numerous wild grass cereals, e.g. *Brachiaria deflexa* (Guinea millet), *Panicum laetum* (wild fonio), and *Oryza longistamina* (wild rice), are still harvested from natural stands by local populations for food in the Sahel. Other useful grasses, e.g. *Andropogon gayanus* are harvested for forage, fiber, medicinal uses, etc. (Table 1) (PROTA4U).

Plant species other than those belonging to the grass (Poaceae) family (e.g. quinoa) are often considered as cereals based on the fact that their seed is harvested for human consumption (FAO, 2015). In this paper, however, we follow the *sensu stricto* definition of "cereals" i.e. species exclusively of the Poaceae (grass) family, whose caryopsis (grain, seed) is harvested and used for food by humans. Wild grass cereals are harvested from natural stands. Their caryopsis are not (or cannot be) planted or sown for next year's harvest, on the contrary to domesticated grass cereals.

In order to contribute to making phytoliths a valuable tool to further explore early use of cereals in sub-Saharan Africa, we provide here a thorough analysis of the phytolith content of 67 African grass species, which include 20 wild cereals and 47 other useful species in the Sahel. First we evaluate the potential for phytoliths to characterize grass inflorescences, and then we evaluate how abundant these inflorescence phytoliths need to be in archaeological deposits to confidently infer anthropogenic accumulation of grass inflorescences.

2. Material and methods

2.1. Modern grass and surface soil samples

We analyzed 67 non-domesticated grass species, which occurrence in Sahelian and Sudanian savannas is largely documented (César and Lebrun, 2003; Poilecot, 1999). Among these species, 57 Download English Version:

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