Quaternary International 434 (2017) 142–159

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Wood and bark phytoliths of West African woody plants

Lucia Veronica Collura*, Katharina Neumann

Goethe University, Institute of Archaeological Sciences, Dept. III: Pre- and Protohistory, Norbert-Wollheim-Platz 1, D-60629, Frankfurt am Main, Germany

ARTICLE INFO

Article history:
Available online 18 February 2016

Keywords:
Wood
Bark
Phytoliths
West Africa
Silica
Plant anatomy

ABSTRACT

Long-term wood anatomical research has shown that 10% of the world's trees and shrubs produce silica in their wood, but silica production in bark had never been systematically investigated. We present here the results of the first comprehensive study on phytoliths in bark and compare them with data on wood phytoliths. We studied 103 bark samples from 92 species and 35 wood samples from 31 species mainly distributed in the West African savannas, altogether representing 34 plant families. The presence of silica in >90% of the studied bark samples indicates that silica production in bark is much more common than in wood. We developed a classification with three anatomical and five morphological classes and recorded their abundance in the processed phytolith samples. With a few exceptions, the phytoliths of bark and wood belong to different classes and can be clearly distinguished from each other. Wood produces Globulars s.l. and Aggregates with their own shape independent from the cells in which they had been formed. In bark, unspecific Blockies and Silica particles/Accumulations are omnipresent while 31% of the species have specific morphotypes with consistent morphologies. These phytoliths reflect the anatomy of the cells and tissues and develop either through silification of the cell lumen or the cell walls. They belong to the anatomical classes Sclerenchyma (with two subclasses Fibres and Sclereids), Cork/Parenchyma, and Cork aerenchyma. Phytoliths in bark and wood have taxonomic relevance, but the distribution is uneven on different taxonomic levels. Some Urticalean Rosids, Bignoniaceae and Capparaceae develop diagnostic phytoliths in the bark. Wood and bark phytoliths can be identified in special archaeological and palaeoecological contexts, but because they are from vegetative tissues, redundancy with similar morphotypes from other plant organs and taxonomic groups has to be considered in mixed assemblages.

1. Introduction

When they decay, trees and shrubs produce phytoliths that are deposited in soils and sediments. Which morphotypes are representative for woody plants in forests, open woodlands and savannas and how the woody plant cover should be quantified is a matter of debate. In Africa, the density of the woody plant cover is usually assessed through calculation of the index D:P (dicotyledons = globular decorated vs. Poaceae short cell phytoliths, Alexandre et al., 1997; Barboni et al., 1999, 2007; Bremond et al., 2005, 2008; Neumann et al., 2009). The overall validity of the D:P for indicating tree cover densities has been questioned by Strömberg (2003, 2004). Besides globulars, Strömberg (2004) proposed silicified sclerenchyma from the leaves of tropical trees, Marantaceae and palm phytoliths, and short cells from Bambusoid grasses as indicators for forest. Neumann et al. (2009) and Garnier et al. (2013) used sclereids as additional representatives of the woody plant cover. In a study on phytolith assemblages in modern soils of Central African forests, Runge (1999) interpreted globulars and irregularly shaped phytoliths as forest indicators. Globulars, however, are widespread in different plant taxa and tissues, especially in monocots, e.g. the Zingiberales (Chen and Smith, 2013). The question arises: Which morphotypes are typical and diagnostic for the trees and shrubs themselves?

After their decay, dicotyledonous trees and shrubs deposit large amounts of phytoliths from leaves, wood and bark in the soil. Comparative studies on the phytoliths of modern woody dicots are essential for unambiguously assigning single morphotypes in an unknown assemblage to dicot leaves, wood and bark, and assessing redundancy between them and with other taxonomic groups. However, these studies are still rare, especially in Africa. Runge

* Corresponding author.
E-mail addresses: collura@stud.uni-frankfurt.de (L.V. Collura), k.neumann@em.uni-frankfurt.de (K. Neumann).

http://dx.doi.org/10.1016/j.quaint.2015.12.070
1040-6182/

(1996, 2000) investigated the leaf phytoliths of East African woody and herbaceous dicots, and Mercader et al. (2009) presented data on 90 woody species from the Miombo woodlands in Mozambique. While leaf phytoliths can be characterized by the presence of trichomes, epidermis fragments and special sclereids (Kondo and Peason, 1981; Postek, 1981; Baas et al., 1982), there is still much confusion on wood and bark phytoliths.

Because silica in wood can present problems in the handling of tropical timbers, phytoliths in wood have long since been recorded in the frame of wood anatomical research (e.g. Amos, 1952; Scurfield et al., 1974; Ter Welle, 1976a,b; Richter, 1980; Metcalfe and Chalk, 1983). The presence of silica is a useful diagnostic character in wood identification (InsideWood, 2004 onwards, http://insidewood.lib.ncsu.edu; Wheeler, 2011) and Ter Welle (1976a,b) distinguished between globular and aggregate silica bodies. In contrast to wood, it is almost completely unknown which phytoliths are produced in the bark.

A major problem of some comparative studies is that they do not treat wood and bark separately but as a unit, e.g. 'wood/bark' (Albert and Weiner, 2001), 'twig' (Iriarte and Paz, 2009), or 'stem' (Mercader et al., 2009). The lack of comparative data on the diagnostic morphotypes for the separation of wood and bark phytoliths hampers assessment of their redundancy in palaeoecological, archaeological and palaeoanthropological contexts when the distinction between wood and bark is a central point of the interpretation. A few examples may illustrate the dilemma. In a study of surface samples from soils in Olduvai Gorge/Tanzania, blocky parallelepipedal phytoliths were assigned to bark (Albert et al., 2006, Fig. 2h), but high percentages of this morphotype in soils could hardly be explained because the dominant vegetation in the area is an arid grassland with a very sparse tree cover. Were these phytoliths really from dicot bark? The use of wood and bark in prehistory and its role for human evolution is also an important issue. Wood phytoliths were reported on two 1.5 million year old Acheulean hand axes from Peninj/Tanzania, interpreted as wood working tools. The image of the 'phytoliths', however, does not show phytoliths, but polyhedral calcium oxalate crystals (Dominguez-Rodrigo et al., 2001, Fig. 2). In a recent study on phytoliths in the dental calculus of 2 million years old *Australopithecus sediba* (Malapa, South Africa), 'dicotyledon wood/bark' phytoliths were reported (Henry et al., 2012, Fig. 3b, and SOM Table 5), resulting in the interpretation that wood and bark were components of the diet of *Australopithecus sediba*. Because wood is not edible for humans, and bark is only consumed in boreal areas (Swetnam, 1984; Östlund et al., 2009), it is important to clarify if the phytoliths of the calculus can be unequivocally attributed to wood and/or bark, or if this is another case of redundancy with morphotypes from other origins.

Wood and bark constitute two functionally different components of the plant stem, being responsible for the water and nutrient transport respectively (Esau, 1965). Therefore differences in the cellular composition of the tissues should become manifest in the production of different phytolith morphotypes. In this paper we present the results of a study on wood and bark phytoliths from modern reference material mainly from West Africa. By treating wood and bark separately, we show that they produce clearly different phytolith assemblages. We also assess redundancy with phytoliths from other plant parts and taxonomic groups and eventually evaluate their taxonomic value and the reliability of identification of wood and bark phytoliths in different ecological and archaeological contexts.

Wood and bark are universal materials for numerous purposes in everyday life, e.g. as construction material, firewood, tools, ropes, textiles and containers. Identification of wood and bark phytoliths can open new perspectives for archaeology and palaeoanthropology because phytoliths are the final remnants of wood and bark long after their decay in the soil.

2. Material and methods

The wood reference collection in the Institute of Archaeological Sciences at Goethe University Frankfurt includes ca. 1200 wood samples, mainly from West and Central Africa. Most of them are backed up with corresponding herbarium specimens in the Herbarium Senckenbergianum (Frankfurt). 1123 anatomical slides of 795 species had been previously checked by K.N. and her collaborators in the course of wood anatomical studies, and 31 silica-containing species from 15 families had been identified for the West African savanna region. 35 corresponding wood samples were selected for phytolith extraction. For detecting patterns of silica production in the wood, the following species were represented by more than one specimen: *Lannea acida* (4) and *Trichilia emetica* (2). Species with no observable silica in the anatomical slides were not included in the study.

Numerous wood samples mostly from twigs collected by members of the Frankfurt team still had their bark adhering. Bark samples of 92 representative species from 34 plant families, including those with known silica in wood, were selected for phytolith extraction. The following species were represented by 2–3 samples each: *Acacia tortilis, A. nilotica, Alchornea cordifolia, Annona senegalensis, Boscia senegalensis, Capparis tomentosa*, *Ficus ingens*, *Kigelia africana, Parinari curatellifolia* and *Trema orientalis*. Every phytolith sample has a laboratory number (PHV), corresponding with the wood collection number. Plant family and species names follow The Plant List (http://www.theplantlist.org/). For species of the large Leguminosae family, the subfamily names Caesalpinioideae, Mimosoideae and Papilionoideae are indicated.

For phytolith extraction, we used a modified dry- and wet-ashing method after Piperno (2006). The bark samples were washed in Alconox® to remove contaminations. 1–4 g of dried plant material, first weighed to ±0.001g, was ashed in a muffle furnace at 500 °C for 8–12 h. For carbonate removal, the ash was treated with hydrochloric acid (HCl) for 10–15 min. at 95 °C, washed with destilled water and centrifuged at 3000–3800 rpm. For removal of organic substances, the sample was treated with nitric acid (HNO_3) and potassium chlorate (KlO_3) for 1–3 h, centrifuged, washed three times with ethanol 95%, centrifuged and dried. The resulting phytolith samples were placed in a small glass tube and weighed. Silica content is indicated as % of dry weight, as conventionally used in wood and phytolith studies (Amos, 1952; Pettersen, 1984; Piperno, 2006). For a few wood and bark samples no quantitative data were available because silica content was too low to be measured, or the samples had been processed before the beginning of this study.

After complete removal of water and ethanol with xylol, a small amount of the dried extracted sample was mounted on a microscope slide with Caedax. In a few cases immersion oil was used to enable 3D observation. We studied the slides with an optical light microscope Leica DMLS at magnifications of 200×, 400×, 630×; photos were taken with a camera Leica DFC 320. To better recognize the surface structure and decoration, we studied some samples with a scanning electron microscope Hitachi S4500. We worked with 5 KV and the lower detector. Images of the phytoliths were taken with the photo system and program of Point Electronic, DISS5.

Presence/absence of the different morphotype classes was noted in a semi-quantitative analysis. For assessing the abundance of the major morphotype classes in the bark samples, we used three categories after Iriarte and Paz (2009): (a) abundant, one or more in each image field; (c) common, one or more in each slide transect; (r) rare, on the order of one to three in each slide. For the Globulars