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Does silica concentration and phytolith ultrastructure relate to phytolith hardness?

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Abstract

Grasses are an important part of the forage of many herbivorous mammals and their phytoliths have long been regarded as the most important agent of tooth wear. Recent work has challenged this "paradigm" in finding evidence 1. of native phytoliths to be much softer then tooth enamel and 2. indicating, that phytolith hardness is highly variable, 3. prone to methodology and 4. not easy to be related to habitat conditions. We conduct controlled silica-cultivations measuring SiO_2 content in the common forage grass *Themeda triandra*. Phytoliths are extracted natively, and nano-indentation values are measured. Phytolith hardness in *Themeda triandra* is found to be independent of silicate availability in the substrate. We further investigate the phytolith ultrastructure of *Hordeum vulgare* phytoliths. Phytoliths are shown to be an anisotropic composite of at least 3 components, silica bodies, inter-body matrix (both mineralised) and globular inclusions (likely non-mineralised). It can be argued, that indentation will be largely influenced by the heterogeneity of the structure and thus nano-indentation measurements will largely reflect the matrix and its mechanical properties but not necessarily the silicate bodies, which make up the vast majority of a phytolith.
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Keywords: Phytolith; Indentation; Ultrastructure; Material property; Silicate availability; Tooth wear

1. Introduction

Tooth morphology and tooth wear of herbivorous mammals has long been used for the interpretation of dietary behaviour and habitat reconstruction [1–4]. As grasses (Poaceae) constitute a significant proportion of the ingesta of many herbivorous mammals, their mineral inclusions (especially phytoliths) have long been assumed to be the main cause of tooth-wear [e. g. 5] and could be a powerful plant defense mechanism induced by herbivory [6–10] and do wear enamel [11]. This topic is highly discussed [12–15] and some studies, however, question this hypothesis because various methods of hardness tests indicating that opal phytoliths are softer then tooth enamel [16–20]. Lucas et al. [21] found the indentation hardness of enamel to be about 5 GPa, but significantly lower values were given for phytolits (0.9 GPa squash, 2.5 GPa grass), higher values for quartz dust. It is often assumed that external abrasives are the more important tooth wear agents in grazing mammals compared to phytoliths, because external abrasives are ingested in large amounts. Highest values for external abrasives from soil consumption are found for mammals with a grazing feeding behavior like in the domestic sheep in New Zealand which are showing peak soil intakes of 33% of daily dry matter intake (DMI, [22–25]). However, annual average soil intake values for sheep tend to range of 5–9% [22–26] and are comparable with other grazing ungulates (like the bison 6.8% [27]), grazing perissodactyles (like the feral horse 5%; [28]), while primary large African browsing species

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have soil intake rates below 5% faecal DMI with grazers tending to have higher values of 5.2–16.3% faecal DMI than browsers [29]. For internal abrasives like phytoliths such values are unknown. A thorough understanding of phytolith ultrastructure as well as their mechanical properties can be seen as a first step towards better comprehending their role during the mechanical disintegration of food particles.

Determining the mechanical properties of biogenic materials, such as opal phytoliths, is a challenging task. It is of high relevance in biotribolgical research requiring material testing on morphologically dissimilar biological particles involved in the wear process at nano-meter scale and is therefore of interest for many research disciplines like engineering, life sciences, veterinary medicine as well as anthropology, archaeology and palaeontology.

In general the amorphous mineral silica (opal) is commonly present in many plants and animals [30,31]. However, opal phytolith formation itself is poorly understood. In this pilot study, we use the term phytolith exclusively for silicate-containing plant bodies called opal-phytoliths. Former phytolith studies [5,16,18] provide little information about the origin of the plant material used and details of indentation measurements, which makes their results hard to compare. The only studies describing silicate uptake and phytolith ultrastructure and inferring on the process of phytolith formation are Kaufman, et al. [32], Kaufman, et al. [33], who describe the polymerization of silicate as follows: silicic acid is irreversibly formed to amorphous silicate gel (SiO_2*nH_2O), a non-crystalline product that has a hydrophobic SiO_2-molecule with corresponding hydrophilic OH groups at the surface. They present four levels of the silification process of phytoliths in *Avena sativa* L. In the interphase of intercalary meristem cells of an internode a sequence of long and short cells arises. The short cells can develop into a pair of silica and cork cell, stomata cells or trichomes. In the first stage of silification a short cell splits into a pair of cells, the future silica cell and the cork cell that initially appear morphologically similar. In the second stage, the two cells differentiate in size and shape. In the third stage, the nucleus of the future silica cell perishes and silicate is entering the final stage.

At the degradation of the nucleus, fibrillar elements arise from this and other cytoplasmic elements that spread through the cell lumen. The only remaining organelles are dark osmiophilic droplets, which are potentially derived from lipid droplets. Further, Kaufman, et al. [32] describe thickened cell walls forming around the cork and silica cell. The silica bodies now growing into the cell lumen of the silica cell are non-crystalline (containing 13.5% bound water) and are interpreted as silica gel. They grow along the fibrillar elements in parallel prism-like bodies [32].

1.1. Phytolith hardness and silicate concentration

If phytolith hardness would be only determined by the limited availability of silica cells produced by the apical meristem, one should assume that the silicate concentration available to plants in the soil had no effect on the hardness of phytoliths. The latter would then be independent of growth site and soil composition. Later in the ontogeny of a silica cell [32], barriers in its cytoplasma membrane account for a stop of further silica deposition in the cell. There is, however, good evidence, that once the apical meristem is removed (e.g. by feeding herbivores), resting mersitems are activated, which subsequently cause lateral growth including further silica deposition [34]. This growth pattern may account for the observation that pastures under high feeding pressure tend to show increased silica contents, which widely has been interpreted as a possible effect of animal-plant interaction causing increases in tooth wear [35]. In detail it has been shown the number, shape and distribution of Si-rich phytoliths and spines differ within and between different grass species and demonstrate that species also differ in their ability to change the deposition and distribution of these defenses in response to damage or increases in Si supply [9,36,37]. This would lead to an increased over all abrasiveness would thus be related to the proportion of silica phytoliths in ingesta, but would be independent of phytolith hardness. In a global sense, the evolution of herbivory may not be considered independent of phytolith hardness, because tooth abrasion is crucial to any vertebrate and to mammals in particular. A yet unsolved question is if phytolith hardness is independent of biogeographic parameters (such as silicate availability). If not so, we suggest that herbivore biogeography may have to be reconsidered as a result of differential abrasive impacts of herbivorous diets.

To test for a possible relationship between silicate concentration in the soil and the material properties of phytoliths, we determine the hardness of native opal phytoliths of *Themeda triandra* FORSSK. grown on a silicate-controlled cultivation with 10 and 100 mg SiO_2/L. The specific material properties of phytoliths are widely enigmatic, we chose to apply a standardised nano-indentation measurement (DIN EN ISO 145677) using the CSM-technique. This approach allows extracting material properties of the tested particles in a specific indentation depth and can therefore also reliably describe inhomogenous ultrastructures. We use *Themeda triandra* as a focal phytolith species because it is a common forage plant by a wide range of herbivorous mammals such as wildebeest, zebra [38–40], Grant's gazelle, Thomson's gazelle [40], zebu [38,40] and hartebeest [38].

Aside from nano-indentation measurements, the interpretation of phytolith biomechanical properties requires knowledge of phytolith-formation in silicate-accumulating plants, as well as ultrastructural information on phytoliths. A further aim of this pilot study is therefore to investigate the internal structure of phytoliths and improve the understanding of phytolith formation. We thus perform transmission electron microscopy (TEM) analyses of phytoliths of *Hordeum vulgare* L., which originate from a silicate-controlled cultivation (100 mg SiO_2/L). We choose *Hordeum vulgare* because it produces long-epidermal cell phytoliths particularly suitable for ultra thin sectioning because of their elongated morphology.

2. Material and methods

2.1. Silicate controlled cultivation and phytolith extraction

Silicate-controlled cultivations of *Themeda triandra* [red grass] with 10 and 100 mg SiO_2/L and *Hordeum vulgare* [barley] with

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