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Do phytoliths play an antiherbivory role in southwest Asian Asteraceae species and to what extent?

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ABSTRACT

Phytoliths (silica bodies) occur in Poaceae species in large numbers and have been shown to have antiherbivory roles. However, phytoliths occur also in many other taxa in much smaller numbers, which raises the question of the extent of both their potential and actual antiherbivory role in these taxa. In order to address the question of their potential antiherbivory role, we sampled 20 wild-growing southwest Asian species of the family Asteraceae, species of which have a much lower phytolith concentrations than Poaceae taxa. We studied the potential positive effect of grazing on phytolith formation and the possible tendency of plants to have higher concentrations of such defence structures in their reproductive organs. We sampled plants from populations of 12 non-spiny and eight spiny species growing in un-grazed and grazed plots in seven sites along a large rainfall gradient (80–900 mm mean annual) in Israel, a region known for its long and intensive grazing history. The study included 21 pairs of un-grazed and grazed plants from 16 of these 20 species. In addition, ten populations of eight species were sampled in order to examine whether phytolith concentrations in the reproductive organs are higher than in vegetative organs. We did not find consistently higher phytolith concentrations in grazed plants compared to un-grazed plants of the same species and habitat (15 species), and in 12 out of 21 pairs of un-grazed and grazed plants (from 15 species) we even found higher phytolith concentrations in un-grazed plants, a phenomenon which was more common in the more arid sites. Phytolith concentrations in inflorescences are commonly (6 out of the 8 species) lower than in the rest of the shoot. We conclude that the antiherbivory potential of phytoliths in the southwest Asian Asteraceae as a group is much smaller than in the Poaceae.

Introduction

Phytoliths are tiny bodies of amorphous silica, detectable by light microscopy, deposited either inside or in association with plant cells, thus shaped with some or even strong similarity to the shapes of their cells of origin. Phytoliths in Poaceae species occur in large numbers (hundreds of thousands to tens of millions per gram plant dry matter) and are the main form of silica in most plant species in which they occur (Piperno, 2006). Silica and phytoliths play multiple roles in Poaceae species, alleviating both abiotic and biotic stresses, such as water deficit, extreme high and low temperatures, heavy metal toxicity, salinity and herbivory (Cooke and Leishman, 2011; Epstein, 1999; Guntzer et al., 2012; Ma, 2004; Ma and Yamaji, 2008; Piperno, 2006). Invertebrate (Reynolds et al., 2009) and small vertebrate (Massey and Hartley, 2006) herbivores have been shown to be negatively affected by plant silica. These effects include abrasion of mouth parts of invertebrates and teeth of mammals (e.g., Kaiser et al., 2013; Massey and Hartley, 2006; Mihlbachler et al., 2011), reduced digestibility caused by phytoliths (e.g., Hunt et al., 2008), nutritional effects of both phytoliths and soluble silica (e.g., Massey and Hartley, 2009) and attracting natural enemies of herbivorous insects induced by soluble silica (Kvedaras et al., 2010). Accordingly, many herbivores prefer plants with lower silica and phytolith concentrations when given the choice between plants from the same or closely related species of the Poaceae under controlled conditions (Massey et al., 2007a,b; Van-Soest, 2006). The little available evidence gathered so far indicates that phytoliths have similar although less prominent effects on larger herbivores such as deer and cattle (Hunt et al., 2008; Soininen et al., 2013).

In contrast to Poaceae, species of many other plant families usually have much lower phytolith concentrations, usually not

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exceeding tens of thousands of phytoliths per gram dry matter (e.g., Piperno, 2006; Tsartsidou et al., 2007), and it is thus uncertain whether phytoliths play a significant antiherbivory role in these taxa as well. One key issue is that phytoliths are most likely a quantitative defence mechanism, and are therefore expected to have a lower antiherbivory function as phytolith concentrations decrease. Nonetheless, since studies of the defensive role of phytoliths so far have focused on the Poaceae (to the best of our knowledge, there is no study of non-Poaceae species), only a limited range of phytolith and silica concentrations has been discussed so far. Moreover, the range of phytolith concentrations in Poaceae species is closer to the higher end of the phytolith/silica concentrations spectrum found in plants, and there are practically no data about the defensive potential of phytoliths along most of this spectrum. We therefore do not know whether the anti-herbivory function of phytoliths simply declines with decreasing phytolith concentrations, or whether a threshold exists under which phytoliths have no defensive function. In order to investigate this question, we have studied whether Asteraceae species from a region with a very long history of grazing and with varying phytolith concentrations follow defence-related patterns as those previously observed in the more phytolith-rich Poaceae.

The Asteraceae is one of the largest and most diverse plant family (Bremer, 1994), consisting in the flora of southwest Asia of hundreds of both spiny and non-spiny species (Feinbrun-Dothan and Danin, 1991; Ronel and Lev-Yadun, 2012; Ronel et al., 2009). Phytolith concentrations in Asteraceae are low compared to Poaceae, as it is the case also in many other phytolith-poor plant families (Katz et al., 2013; Piperno, 2006; Tsartsidou et al., 2007; Wallis, 2003). In a previous study, we found that phytolith concentrations in the Asteraceae range between almost zero and several tens of thousands of phytoliths per g dry matter (Katz et al., 2013), compared to hundreds of thousands to tens of millions per g dry matter in the Poaceae. Therefore, the Asteraceae complement the lower range of phytolith concentrations in higher plants and are suitable for our study.

We focused our study on 20 wild Asteraceae species (about 7% of the Asteraceae species in the flora of Israel), providing one of the largest studies of potential phytolith functions in terms of species number. Our study is composed of two parts, as detailed below. We studied the potential positive effect of grazing on phytolith formation and the possible tendency of plants to have higher concentrations in their reproductive organs of these structures that potentially function as defence against herbivory. Both phenomena were previously observed with respect to phytoliths of Poaceae. We therefore suggest that if these phenomena are also found to characterise the Asteraceae species, then phytoliths have an antiherbivory function in these species.

The effect of grazing on phytolith formation in Asteraceae

Brizuela et al. (1986) observed that silica concentrations in naturally growing Poaceae species are negatively correlated to the distance from colonies of prairie dogs (*Cynomys ludovicianus*; Rodentia), the main small mammalian herbivore species in their study area. Cid et al. (1989) suggested that selection against silica-low plants on one hand and induced response to herbivore damage on the other are the main causes of this phenomenon. Massey et al. (2008) showed a cyclic reciprocal relationship between grass silica concentration and vole (*Microtus agrestis* L., Rodentia) population size, which implies negative effects of high silica concentrations on voles and grazing-induced natural selection for silica-rich grasses. Induction of increased silicification by herbivory in the Poaceae is well documented (Massey et al., 2007b, 2008, 2009; McNaughton and Tarrants, 1983; McNaughton et al., 1985), but the level of induced silicification varies according to the identity of the herbivores (Massey et al., 2007b; Soininen et al., 2013) and plant genotypes (Garbuzov et al., 2011; Melzer et al., 2010; Soininen et al., 2013).

Recently, Soininen et al. (2013) studied the differences in phytolith concentrations in eight naturally growing Poaceae species with and without the presence of a large mammalian herbivore (*Rangifer tarandus* L., Artiodactyla). They found that the grazed plants did not always have higher silica concentrations than the un-grazed plants, and even found lower silica concentrations in grazed compared to ungrazed *Avenella flexuosa* L., one of the species with relatively lower silica concentrations in their study. These results further imply that the effect of herbivory on phytolith formation is more common in species with relatively greater silica accumulation capabilities. We therefore hypothesise that if

Table 1
Site descriptions (see map in Fig. 1). (a) Principal study sites. Mean annual rainfall was interpolated from nearby Israeli Meteorological Service stations (http://www.ims.gov.il): for Har Tsiv'on from Har-Kna'anand Mitspe-Harashim stations and for Sayeret Shaked Park from Be'er-Sheva station. Ramat-Hanadiv has its own station (http://www.ramatahanadiv-edu.org.il/weather). (b) Soil type and silica availability in the four principal sites, as well as in the sites in which plants were sampled to compare reproductive and vegetative parts. The number of samples per soil type is five.

(a)

Site	Year	Har Tsiv'on	Ramat-Hanadiv	Sayeret Shaked	Mitspe-Ramon
Location		33°10′ N, 35°15′ E	32°30′ N, 34°57′ E	31°15′ N, 34°39′ E	30°36′ N, 34°45′ E
Elevation (m above sea level)		850	120	200	800
Mean annual rainfall (mm)		~900	533	206	~80
Rainfall in sampling year (mm)	2010			180	<80
	2011			140	
	2012	740	530	140	
	2013		510	180	
Studied grazing herbivores		Cattle	Goat/sheep	Goat/sheep	Goat/sheep

(b)

Site	Soil type	FAO classification	Soil silica availability (mg Si g^{-1} soil, ±SD)
Har Tsiv'on	Terra Rossa	Eutric/Vetric Cambisol	0.557 (±0.063)
Ramat-Hanadiv	Terra Rossa	Eutric/Vetric Cambisol	0.701 (±0.090)
Neve-Yam	Nazaz	Eutric Planosol	0.253 (±0.120)
Binyamina	Hamra	Chromic Luvisol	0.116 (±0.015)
Caesarea	Sand dune	Albic Arenosol	0.026 (±0.005)
Sayeret Shaked	Loess	Calcaric Fluvisol	0.162 (±0.055)
Mitspe-Ramon	Loess	Calcaric Fluvisol	0.179 (±0.038)