



Short communication

Dynamics and drivers of the protozoic Si pool along a 10-year chronosequence of initial ecosystem states

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ABSTRACT

The size and dynamics of biogenic silicon (BSi) pools influence silicon (Si) fluxes from terrestrial to aquatic ecosystems. The research focus up to now was on the role of plants in Si cycling. In recent studies on old forests annual biosilicification rates of idiosomic testate amoebae (i.e. TA producing self-secreted silica shells) were shown to be of the order of Si uptake by trees. However, no comparable data exist for initial ecosystems. We analyzed the protozoic BSi pool (idiosomic TA), corresponding annual biosilicification rates and readily available and amorphous Si fractions along a 10-year chronosequence in a post-mining landscape in Brandenburg, Germany.

Idiosomic Si pools ranged from 3 to 680 g Si ha⁻¹ and were about 3–4 times higher at vegetated compared to uncovered spots. They increased significantly with age and were related to temporal development of soil chemical properties. The calculation of annual biosilicification resulted in maxima between 2 and 16 kg Si ha⁻¹ with rates always higher at vegetated spots. Our results showed that the BSi pool of idiosomic TA is built up rapidly during the initial phases of ecosystem development and is strongly linked to plant growth. Furthermore, our findings highlight the importance of TA for Si cycling in young artificial ecosystems.

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1. Introduction

On a global scale the silicon (Si) cycle is connected to the C cycle by C-occlusion within phytoliths (e.g. Parr and Sullivan, 2011), weathering processes and fluxes of dissolved Si (DSi) from terrestrial to aquatic ecosystems, where it influences diatom production (Sommer et al., 2006; Struyf and Conley, 2012). DSi mainly originates from weathering of silicate minerals and dissolution of amorphous silica (ASi) of pedogenic and biogenic origin (Cornelis et al., 2011; Sauer et al., 2006). Biogenic silica (BSi) as the main component of the ASi pool is produced by several aquatic and terrestrial

organisms forming BSi pools (Clarke, 2003; Ehrlich et al., 2010). In terrestrial ecosystems BSi pools can be separated into phytogenic, microbial and protozoic Si pools influencing Si fluxes of DSi into aquatic systems (Sommer et al., 2006). While many publications on the phytogenic pool (phytoliths) highlight its importance for Si cycling (e.g. Bartoli, 1983; Carey and Fulweiler, 2012; Cornelis et al., 2014), little is known about microbial and protozoic Si pools (Aoki et al., 2007; Clarke, 2003; Wilkinson, 2008).

In soils the protozoic Si pool is represented by idiosomic testate amoebae (TA). TA are unicellular eukaryotes building up populations up to several millions of individuals per square metre even at young recultivated sites promoting the colonization by plants and animals (Hodkinson et al., 2002; Wanner and Dunger, 2001; Wanner et al., 2008). Generally, protozoa including TA form the base of the food web of heterotrophic eukaryotes in soil ecosystems and enhance decomposition (Foissner, 1999), which is of vital importance for nutrient cycling needed for a successful ecosystem development after restoration (Bradshaw and Hüttl, 2001).

TA are protected by a shell (test), which can be proteinaceous or agglutinated: agglutinated shells are either built from foreign

Abbreviations: DSi, dissolved Si; ASi, amorphous silica; Si_{Tiron}, Tiron extractable Si; BSi, biogenic silica; TA, testate amoebae; C_t, total carbon; N_t, total nitrogen; TIC, total inorganic carbon; SOC, soil organic carbon; Si_{CaCl2}, readily available, calcium chloride extractable Si; FEM, fine earth mass.

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materials (so-called xenosomes, e.g. mineral particles) or endogenous self-synthesized calcareous or siliceous platelets (so-called idiosomes) (Meisterfeld, 2002a,b). They evolved independently in the orders Euglyphida (Rhizaria; idiosomic shells) and Arcellinida (Amoebozoa; mainly proteinaceous and xenosomic shells) (Adl et al., 2012; Meisterfeld, 2002a,b). They have been used as model organisms and sensitive bioindicators in many ecological studies (e.g. Foissner, 1999; Wanner et al., 2008), but only few researchers focused on Si cycling yet (Aoki et al., 2007; Wilkinson, 2008). Sommer et al. (2013) recently analyzed Si cycling in a forested ecosystem including phytogenic and protozoic BSi pools. They found a relatively small protozoic Si pool in comparison to the phytogenic one. However, annual biosilicification of microscopic TA reached 50% of Si uptake of plants (beech, 35 kg Si ha⁻¹). Further on, Sommer et al. (2013) concluded that the BSi pool generally cannot be assumed to be in steady state at decadal time scales and concluded transient states should be studied. One option to quantify non-stationary BSi pool development is the chronosequence approach.

We studied idiosomic Si pools in differently aged initial states of artificial catchments in a post-mining landscape. These sites are well-suited landscape labs for studies of early ecosystem development (Gerwin et al., 2009). Due to the fact that at initial ecosystem states TA belong to the first colonizing organisms (see e.g. Wanner and Elmer, 2009) we hypothesized that the BSi pool represented by idiosomic TA is already significant in the beginning of ecosystem development influencing Si cycling. Age- and vegetation-related changes during pedogenesis should be reflected in soil parameters and idiosomic Si pool size. The aims of our work were (i) to quantify the protozoic Si pool (incl. annual biosilicification) and its contribution to the ASi fraction in soils of initial ecosystem states and (ii) to identify interactions of the protozoic Si pool with soil-related drivers (e.g. Si(OH)₄ as a source for synthesis of idiosomes) at vegetated and uncovered spots.

2. Materials and methods

2.1. Sites and sampling

The artificial catchments “Chicken Creek” (51°36′18″ N, 14°15′58″ E) and “Neuer Lugteich” (51°35′50″ N, 14°17′22″ E) are part of a post-mining landscape located in the active mining area “Welzow-South” (lignite open-cast mining, 150 km south-east of Berlin) in the state of Brandenburg, Germany (Kendzia et al., 2008; Russell et al., 2010). Climate is characterized by an average air temperature of 9.3 °C with an annual precipitation of 559 mm comprising data from 1971 to 2000 (Gerwin et al., 2009). The construction of “Chicken Creek” was completed in 2005 (time zero). In 2008 a small area west of the catchment was restored to time zero (removal of the upper 20 cm of soil) for additional experimental plots. Construction of the study site “Neuer Lugteich” was finished in 2001. Soils classify as Protic Arenosol (Calcaric, Transportic) or Haplic Arenosol (Hyperochric, Transportic) depending on site age (WRB, 2006). Detailed site descriptions and construction information of the catchment areas “Chicken Creek” and “Neuer Lugteich” can be found in Gerwin et al. (2009) and Kendzia et al. (2008), respectively. All samples were taken from Quaternary substrate at 3- and 5- (“Chicken Creek”) and 10-year-old (“Neuer Lugteich”) spots representing a chronosequence. Samples (20 cm × 20 cm × 5 cm; subdivided in two compartments: 0–2.5 and 2.5–5 cm depth) were taken at randomly chosen spots within an area of approx. 25 m². Vegetated (cov) and uncovered (unc) spots were sampled in four field replicates each to analyze possible impacts of vegetation (3 cov: *Tussilago farfara* and *Trifolium arvense*;

5 cov: *Corynephorus canescens* and *T. arvense*) on idiosomic Si pools. At “Neuer Lugteich” almost the whole surface was vegetated with biogenic crusts, Poales and several shrubs, which is why only vegetated spots (10 cov) were sampled. Samples were taken in May 2010 (5 unc, 5 cov), May 2011 (10 cov) and August 2011 (3 unc, 3 cov).

2.2. Soil analyses

Soil samples (total $n=40$) were air dried and sieved (2 mm). For soil analysis only fine earth (<2 mm) was used. Soil suspensions in 0.01 M CaCl₂ (soil:solution ratio = 1:5) were used for measurements of soil pH with a glass electrode. Total carbon (C_t) and nitrogen (N_t) contents were determined by dry combustion using an elemental analyzer and contents of total inorganic carbon (TIC) were measured with a multiphase analyzer. Soil organic carbon (SOC) contents were calculated by subtraction (C_t – TIC) and C:N ratios were calculated by division (SOC:N_t). For extraction of the readily available (mainly Si(OH)₄) Si fraction (Si_{CaCl₂}) and the ASi fraction (Si_{Tiron}) we followed the description in Höhn et al. (2008). Mass densities (g m⁻²) were calculated considering thickness of soil compartments (2.5 cm), bulk densities (g cm⁻³) and skeleton contents (>2 mm) and were summed up for upper 5 cm of soil (Sommer et al., 2002). All results except for pH were converted to an oven-dry basis (105 °C).

2.3. Testate amoeba analyses

Samples (total $n=40$) were taken and analyzed as described in Sommer et al. (2013) using stained (aniline blue) aqueous soil (125 mg each) suspensions received from serial dilution (Wanner, 1999). Within the order Euglyphida we differentiated between idiosomic taxa with known silica contents per shell published by Aoki et al. (2007). Summarizing these data we calculated Si ($M=28.085$ g mol⁻¹) contents (pg shell⁻¹, below given in parentheses) from SiO₂ contents ($M=60.08$ g mol⁻¹) by simple multiplication (SiO₂ content × 28/60 = Si content) for 9 taxa: *Assulina muscorum* (750), *Corythion dubium* (580), *Euglypha spec.* (720), *Euglypha rotunda/laevis* (420), *Euglypha strigosa* (1420), *Tracheleuglypha dentata* (750), *Trinema complanatum* (500), *Trinema enchelys* (770) and *Trinema lineare* (360). Indistinctly idiosomic shells or other silica platelet-synthesizing taxa (e.g. *Valkanovia elegans*) were recorded as “idiosomic amoebae” with an averaged Si content of 700 pg per shell (mean of the 9 taxa above). Individual density of TA (ind. cm⁻²) was calculated from dry weight density of TA (ind. g⁻¹ dry mass (dm)) considering bulk density (g cm⁻³) and thickness (2.5 cm) of soil compartments. Idiosomic Si pool (BSi_{TA}; g ha⁻¹) was calculated per soil compartment using the following formula:

$$\text{BSi}_{\text{TA}} = (N_i \times \text{Si}_i \times \rho_b \times t \times 10^{-4}) \quad (1)$$

where N_i is the density of idiosomic individuals (living plus dead amoebae; ind. g⁻¹ dm), Si_i is the corresponding Si content (pg shell⁻¹), ρ_b is the bulk density (g cm⁻³) and t is the thickness per soil compartment (2.5 cm). In contrast, for estimation of annual biosilicification only living idiosomic amoebae (ind. g⁻¹ dm) were considered for N_i in Eq. (1) due to their ability of reproduction. After calculation steps as described in Eq. (1) results were multiplied with 13 and 90 (TA generations per year; Foissner, 1999) for minimal and maximal annual biosilicification, respectively. For the upper 5 cm of soil the results of the superimposed soil compartments were added up. For scanning electron microscopy TA were taken from soil suspensions by micromanipulation, washed in dist. H₂O and placed on clean cover slips. After air drying cover slips were stuck on aluminium-stubs equipped with adhesive tabs.

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