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Earthworms can increase mobility and bioavailability of silicon in soil

Nikolai Bityutskii*, Polina Kaidun, Kirill Yakkonen

Department of Agricultural Chemistry, Saint Petersburg State University, 7/9 Universitetskaya nab., Saint Petersburg, 199034, Russia

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ABSTRACT

Earthworms are one of the dominant groups of soil macro-invertebrates in many terrestrial ecosystems affecting nutrient cycling and plant growth. However, it is not well known how earthworms can influence availability of silicon (Si) as an element whose beneficial role in agricultural systems has been widely recognized. The objectives of this study were: (1) to determine the effect of earthworms on the mobility of Si in soil, and (2) to determine whether earthworm induced effects on Si mobility are of importance for the availability of Si to plants (*Cucumis sativus* L. and *Zea mays* L.). Two soils (a sandy loam soil and a sandy soil) with two levels of two independent treatments (±$CaCO_3$ and ± earthworms) were used. Concentrations of water-extractable Si and monosilicic acid ($Si(OH)_4$) in casts/soils and Si movement via xylem of plants were measured. Casts of earthworms – endogeic *Aporrectodea caliginosa* (Savigny) and anecic *Lumbricus terrestris* L., had generally higher amounts of water-extractable Si (by 2.0–12.0 times) and $Si(OH)_4$ (by 1.3–3.5 times) compared with bulk soils, irrespective of soil type and application of $CaCO_3$. Bioturbation of the sandy loam soil by living earthworms were generally of major importance in improving xylem translocation of Si from roots to shoots in cucumber and maize. The results highlight for the first time the importance of earthworms in plant acquisition of Si and biogeochemistry of Si.

1. Introduction

Silicon (Si) is the second most abundant element in the earth's crust (Epstein, 1999). Being an element of nearly all parent materials, Si is one of the basic components in most soils. Besides primary crystalline silicates and secondary silicates, Si also occurs as readily soluble Si pool (Matichenkov and Bocharnikova, 2001). Silicic acid ($H_4SiO_4^0$) is the main component of soil solutions, mostly as monomeric silicic acid at pH below 9 (Dietzel, 2000; Sommer et al., 2006), and plants absorb Si as the silicic acid (Pontigo et al., 2015). Complexes of Si with inorganic and organic compounds also occur in liquid phase of soil (Matichenkov and Bocharnikova, 2001).

Although Si is not yet listed among the essential elements for higher plants (Marschner, 1995), its beneficial role in agricultural systems has been widely recognized. Silicon has been reported to alleviate various biotic and abiotic stresses in many plant species (Ma, 2004; Hattori et al., 2005; Liang et al., 2007). Silicon is a structural component in plants. Epidermal cell walls impregnated with a firm layer of Si are effective barriers against water loss and fungal infections (Marschner, 1995). Grass leaf silicification is an inducible defense against herbivores (McNaughton and Tarrants, 1983). A pretreatment with Si primes plants to better respond to pathogen infections (Chain et al., 2009; Van Bockhaven et al., 2013). Over the past few years rapid progress has been made in elucidation of the mechanisms of how Si mediated metal excess (Li et al., 2008; Prabagar et al., 2011; Dragisic Maksimovic et al., 2012; Pontigo et al., 2015) and micronutrient deficiency (Gonzalo et al., 2013; Pavlovic et al., 2013; Bityutskii et al., 2014; Hernandez-Apaolaza, 2014). Very recently, the current knowledge inherent to the importance of Si nutrition for plants was summarized in a book (Liang et al., 2015). Silicon may also play a role in human physiology and metabolism, especially bone and connective tissue formation (Jugdaohsingh et al., 2004). Therefore, a provisional database for the Si content of foods has been reported (Powell et al., 2005). Despite the abundance of Si in soils, Si deficiency is recognized as a limiting factor for crop production, especially for Si-accumulating plants (Liang et al., 1994; Ma and Yamaji, 2006).

Earthworms are one of the abundant faunal groups in most terrestrial ecosystem affecting nutrient cycling of soil with relatively long-term benefits for plant nutrient acquisition (Edwards

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* Corresponding author.
E-mail addresses: n.bityutskii@spbu.ru (N. Bityutskii), polinakaydun@gmail.com (P. Kaidun), yakkonen@mail.ru (K. Yakkonen).

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and Bohlen, 1996; Blouin et al., 2013). Earthworms ingest large amount of material and modify both mineralization rate of soil organic matter (SOM) and availability of plant nutrients within casts and drilosphere (a part of the soil influenced by earthworm secretions). The mineralization processes are driven by microbial activity, however, the compositions and activities of microbial communities are strongly affected by earthworms (Scheu et al., 2002). It is generally thought that earthworms can enrich soils with available nitrogen (N) (Bityutskii et al., 2007; Eisenhauer and Scheu, 2008; Laossi et al., 2011; Van Groenigen et al., 2014), phosphorus (P) (Suarez et al., 2004), potassium (K), calcium (Ca) and magnesium (Mg) (Adejuyigbe et al., 2006; Jouquet et al., 2008) and some micronutrients (Wen et al., 2004; Bityutskii et al., 2012a). Contradictory results were also found when determining the importance of earthworms in nutrient mobility and bioavailability in soil (Bityutskii et al., 2012a; Clause et al., 2014). Whereas earthworms can induce mineralization of SOM and weathering of some minerals (Carpenter et al., 2007), limited information is available on how earthworms affect availability and uptake of Si in higher plants.

The objectives of this study were: (1) to determine the effect of earthworms on the mobility of Si in soil, and (2) to determine whether earthworms induced effects on Si mobility are of importance for the availability of Si to plants. In this study, it was hypothesized that earthworms can increase Si availability to higher plants.

2. Materials and methods

2.1. Study design

The experimental design included two experiments: experiment I where the Si mobility in cast/soil material was examined, and experiment II where the availability of Si to plants in soil bioturbated by earthworms was examined. Two earthworm species widely occurring in temperate regions were chosen. In experiment I two types of soil with different concentrations of soluble Si were used: a sandy loam soil and a sandy soil. Silicon bioavailability in calcareous soils is often low (Liang et al., 1994). To simulate conditions of calcareous soil calcium carbonate ($CaCO_3$) was added to a non-calcareous soil. Liming a moderately acid soil is, however, not directly analogous to a naturally calcareous soil.

The experimental design included two levels of two independent treatments (±$CaCO_3$ and ±earthworms). A detailed description of the experimental design has been reported most recently (Bityutskii et al., 2016). Briefly, fresh soils used in the +$CaCO_3$ treatments were mixed with $CaCO_3$ prior to the experiments (I and II) ± earthworms. Dried shoots of clover (*Trifolium pratense* L., 10 g kg^{-1}) was used as a food for earthworms and pre-incubated at 60% water holding capacity (WHC) for 1 week before the introduction of earthworms. Non-earthworm controls received the same clover inputs.

Experiment II was performed in two stages. The first stage was provided as a pre-incubation period (for 4 weeks) in the presence of living earthworms. The impact of *Aporrectodea caliginosa* (Savigny) on Si availability to plants was examined in 2012, whereas that of *Lumbricus terrestris* L. – in 2013. During the pre-incubation stage, an increase in Si mobility and availability induced by bioturbation of the soil by living earthworms was expected. At second stage of experiment II, the earthworms were removed from the soil and then plants (cucumber and maize) were grown for 4 weeks. In the sandy soil, after pre-incubation for 4 week earthworm mortality was observed. Therefore, plant performance induced by earthworms was only examined in the sandy loam soil where all earthworms survived.

2.2. Soil material

The two soils were collected from the humus layer of two different permanent grasslands near the Biological Research Institute of Saint Petersburg State University, Petergof, Russia (N 59° 53′ 36″; E 29° 49′ 48″). The sandy soil was a Umbric Albeluvisols soil and the sandy loam soil was a Anrthri-Umbri-Endogleic Luvisoil soil. Soil properties for these soils are tabulated in Table 1. For the $CaCO_3$ treatments, 50 g kg^{-1} dry soil of calcium in the form of fine powder was added to the soil. The pH in water (pH_w) was measured in a 1: 2.5 soil-water solution with a glass electrode. Total carbon (C) and total nitrogen (N) contents were determined by CHN-analyzer (model CHN-628, Leco Corporation, USA). Available P and K were measured in a 1:5 soil – 0.2 N HCl solution (Arinushkina, 1970). The proportions of sand (2–0.05 mm), silt (0.05–0.002 mm) and clay (<0.002 mm) of the soils were determined by laser diffraction particle size analyzer SALD-2201 (Shimadzu Corp., Japan).

2.3. Earthworms and their casts

We used the endogeic earthworms *Aporrectodea caliginosa* (Savigny) and the anecic earthworms *Lumbricus terrestris* (L.), which are commonly found in grassland ecosystems. Mature earthworms with an individual biomass without gut contents of 0.4 ± 0.1 g (*A. caliginosa*) and 3.5 ± 0.9 g (*L. terrestris*) were hand-selected.

The earthworm casts were collected (experiment I) and soil were pre-incubated (experiment II) as described previously (Bityutskii et al., 2016). Briefly, after voiding their guts on moist filter paper for 4 days, 12 individuals from a single species were added to each experimental soil and kept in the dark at room temperature (24 h). During the procedure the soil moisture was maintained at 60% WHC. Subsequently the earthworms were rinsed with distilled water and placed into Petri dishes (12 specimens per dish) and stored in the dark for 24 h. The soil samples without earthworms (control) were also placed into Petri dishes in amounts equivalent to amounts of earthworm casts (determined previously). Three independent experiments I were performed with the same results. During the pre-incubation stage of experiment II, three individuals from a single earthworm species were kept in 1 L plastic pot filled with 1 kg soil (dry weight) at room temperature in dark for 4 weeks. The moisture of soils was maintained at 60% WCH by daily watering.

2.4. Plant material and growth conditions

Three plants of cucumber (*Cucumis sativus* L., cv. Semcross) or maize (*Zea mays* L., cv. Uk23K1) were grown in each plastic pot filled with 1 kg soil (dry weight) after the pre-incubation stage of experiment II for 4 weeks. These species were selected because they are known as Si-accumulating plants (Liang et al., 2007; Wiese et al., 2007). Plants were grown in a room at the temperature regime of 24 ± 2 °C: 20 ± 2 °C (light: dark) with a day/night regime of 16/8 h, and photon flux density of 200 μmol m^{-2} s^{-1} at plant height. The plants were irrigated daily with distilled water to keep soil moisture of about 60% WHC.

2.5. Plant analysis

The xylem sap method is commonly used for evaluate availability of most nutrients in soil (Noguchi et al., 2005). The xylem sap was collected by a micropipette for 1 h after the stems were cut 2 cm above root base and after discarding of the exudates obtained during the first few minutes. Concentration of Si in freshly collected