

Impact of earthworms on soil Si availability and wheat Si concentration in low- and high-Si soils

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ABSTRACT

Silicon (Si) is a beneficial element known to increase growth and the stress resistance of plants, including resistance against drought. However, as with many other elements, only a small fraction of Si in soils is available for plant uptake. Plant-available Si originates either from the weathering of soil minerals or from the dissolution of phytoliths in plant litter. It is known that soil fauna plays a role in both processes that contribute to the availability of Si in the soil. However, very little is known about the interactions between the weathering of soil minerals and the dissolution of Si by earthworms from phytoliths and subsequent Si uptake by plants. In greenhouse pot experiments, this study investigated the effect of an epigeic earthworm species (*Dendrobaena veneta*) on Si availability and uptake by wheat (*Triticum aestivum*) grown in soils with high or low Si availability. In addition, Si-rich plant litter (wheat straw) was added to the topsoil in some treatments. The addition of plant litter significantly increased the available Si in the soil. Plant litter addition was positively correlated with the Si concentration in wheat in low-Si soil, but not in high-Si soil. Earthworms increased Si availability in soil and casts of the low-Si soil and partly of the high-Si soil, but not Si uptake by wheat. These results suggest that earthworms play an important role in regulating the Si status of soils and may influence Si uptake by plants, especially in soils with initially low Si content and when earthworm population densities are high.

1. Introduction

Silicon (Si) is the second most abundant element on the planet's surface after oxygen, accounting for almost 29 % of the mass of the Earth's crust (Wedepohl, 1995), but only a small fraction of Si is involved in biogeochemical cycling in soils (Conley, 2002). Silicon occurs in soils as part of minerals and as amorphous silica, which can be either minerogenic or biogenic in origin. Minerogenic amorphous silica is precipitated from dissolved Si, whereas biogenic Si is derived from plant material or from microbial and protozoic sources (Sommer et al., 2006; Struyf et al., 2009). The only form of Si available for plant uptake is Si in the form of orthosilicic acid (Si(OH)₄) (Casey et al., 2004), which is then deposited in plant tissues as hydrated amorphous silica, also known as opal phytolith (SiO₂.nH₂O) (Sangster and Hodson, 2007; Sharma et al., 2019). Although Si is not an essential nutrient for plants, it is often considered quasi-essential (Zargar et al., 2019) or beneficial

(Ma, 2004; Tripathi et al., 2016) because it improves plant growth and resilience under stress conditions, including drought (Wang et al., 2021). Wheat (Mayland et al., 1991) and rice (Ma et al., 2006) are examples of Si accumulation in crops, with Si concentrations in shoots ranging from 1 % to 3 % and occasionally reaching up to 10 % on a dry matter basis (Hodson et al., 2005; Yamaji et al., 2008). Deficiency of available Si in soil can lead to a decrease in productivity of crops such as rice (Savant et al., 1997), tomatoes (Miyake and Takahashi, 1978), and soybean (Miyake and Takahashi, 1985). In rice farming, Si is therefore routinely fertilized in highly weathered paddy soils (Datnoff et al., 1997; Ning et al., 2014). In wheat, Si is known to play an important role in defense against stress factors such as drought (Gong et al., 2003), salinity (Singh et al., 2022) and heavy metal toxicity (Wu et al., 2016). Given the drought risks faced by European crop production (Bindi and Olesen, 2011; Iglesias and Garrote, 2015; Tatar et al., 2016), increasing Si availability in the soil could be a way to increase drought resilience of

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wheat production, as the European Union is the main producer of this crop worldwide (Curtis and Halford, 2014). Thus, understanding the Si soil-plant cycle is important for future sustainable agricultural production.

Two main processes that contribute to Si availability in soil are the weathering of silicate minerals and the decomposition of Si-rich organic material, including plant litter. The role of soil macrobiota, such as earthworms, in the process of Si solubilization is potentially significant, although poorly studied. Earthworm activity could play an important role as they feed on plant litter and promote weathering of various minerals (Needham et al., 2004). A reduction in the grain size of quartz and K-feldspar after digestion and excretion by earthworms, even after only one day of incubation, has been reported (Suzuki et al., 2003). Earthworm-induced weathering of anorthite, biotite, smectite, and kaolinite was demonstrated in a four-month incubation experiment (Carpenter et al., 2007), but could not be confirmed under field conditions (Carpenter et al., 2008). Similarly, Liu et al. (2011) reported that earthworms (*Pheretima carnosus* (Kobayashi 1936)) accelerated the weathering of potassium-containing rocks such as feldspar, mica, dolomite, montmorillonite, kaolinite, and hornblende mixture. Hu et al. (2018) showed that the gut of earthworms (*Pheretima guillelmi* (Michaelsen 1895)) contains bacteria that promote the solubilization of silicate rock in addition to mechanical (Suzuki et al., 2003) and chemical (Carpenter et al., 2007) influences. Bitvitskii et al. (2016) demonstrated that the extractability of Si from earthworm casts (*Aporrectodea caliginosa* (Savigny, 1826) and *Lumbricus terrestris* (Linnaeus, 1758)) is higher than in soil that has not been ingested by earthworms. In that study, the passage of soil through earthworm guts led to an increase in the Si concentration in the xylem sap of cucumbers and maize. Georgiadis et al. (2019) showed that earthworms (*Octolasion cyaneum* (Savigny, 1826)) are able to solubilize Si from quartz, and Hu et al. (2018) demonstrated that bacteria isolated from earthworm guts are able to induce the release of Si from silicate minerals, leading to increased Si uptake by maize. In addition to mineral weathering, earthworms accelerate the decomposition of plant litter (Dechainea et al., 2005; Vidal et al., 2019) by fragmentation (Schulmann and Tiunov, 1999) and by promoting soil microbial activity (Edwards and Fletcher, 1988; Medina-Sauza et al., 2019). The decomposition of litter releases phytoliths into the soil, which increases the bioavailable Si pool in the soil (Senthilkumar et al., 2021). While the solubilization of Si from plant litter by earthworms has been demonstrated (Georgiadis et al., 2019), the effect of earthworms on Si uptake by plants has been investigated only sparsely so far.

The objective of the current study was to investigate the combined impact of earthworms and Si-rich plant litter on Si concentration in plants and to determine whether these effects differ in soils with different Si contents, since under natural conditions earthworms are expected to simultaneously solubilize Si from plant litter and soil minerals. Therefore, we wanted to find out (i) whether earthworms can solubilize Si from Si-rich plant litter and soil minerals, (ii) whether earthworm activity increases Si concentration in wheat shoots, and (iii) whether differences in soil Si concentration affect these interactions. Better knowledge of the Si cycling in agricultural soils will help to increase the resilience of crops under climate change with an increase in stress factors (Verma et al., 2020; Thakral et al., 2021).

2. Materials and methods

Two runs of a pot experiment were conducted in a greenhouse of BOKU University in Tulln, Lower Austria, Austria. The earthworm species *Dendrobaena veneta* (Rosa, 1886) and spring wheat (*Triticum aestivum* L., cv. Quintus) were used as experimental organisms. The experimental factors were soil Si level (high vs. low concentrations in CaCl₂-extractable Si (Si_{CaCl2})), earthworm addition (earthworms vs. no earthworms), and litter addition (addition of Si-rich plant litter vs. no litter). Each experimental run lasted for 16 weeks.

2.1. Soils

Soils from two sites in Lower Austria were collected in summer 2020 for experimental run 1 (soil batch 1) and spring 2021 for experimental run 2 (soil batch 2). The soils were selected based on their differences in Si_{CaCl2}, texture, type of land use, soil organic matter content and thus in favorability for earthworms. Soils were classified as “low-Si” and “high-Si” because they contained <20 mg kg⁻¹ and > 40 mg kg⁻¹ Si_{CaCl2}, respectively (Table 1) (Caubet et al., 2020). Total Si was determined using a Thermo Fisher Niton XL3t Handheld XRF Spectrometer (Institute of General and Analytical Chemistry, Montanuniversität Leoben, Leoben, Austria). The low-Si soil was collected from a grassland site, while the high-Si soil was collected from an arable site. The second experimental run was conducted to confirm the observations from the first, to take additional types of samples (casts), and to increase the number of observations.

2.2. Experimental plants

Wheat was selected because it is Si-accumulating, and one of the major cereal crops (Mayland et al., 1991). Seeds of spring wheat (*Triticum aestivum*, cv. Quintus, provided by the Institute of Plant Breeding, BOKU University, Austria) were surface-sterilized with 70 % ethanol for 3 min, rinsed with deionized water, disinfected with 1 % NaClO for 15 min, and rinsed with deionized water until the odor disappeared. Before sowing, seeds were pre-germinated on moist filter paper. Seven seeds were sown per pot (diameter 10 cm). After plant establishment, the number of plants was reduced to three per pot.

2.3. Earthworms

We used the earthworm species European nightcrawler (*Dendrobaena veneta*, also known as *Eisenia hortensis*) in this study. We added four similar-sized adult specimens to each pot (0.156 ± 0.025 g pot⁻¹, fresh mass (mean ± SD) in the first experimental run and 0.332 ± 0.082 g pot⁻¹ in the second run). This earthworm species was selected because it is an epigeic earthworm that lives at or near the soil surface and feeds on leaf litter or decaying roots (Domínguez, 2018) and therefore does not require a deep soil core. This species is also known to inhabit a wide range of habitats with sufficient layers of organic matter (Judas and Büchner, 1989; Yahyaabadi et al., 2018). Earthworms were obtained from a commercial worm farm (Superwurm, 52351 Düren, Germany;

Table 1
Characterization of the two experimental soils.

Location	Texture	pH _{CaCl2}	Si _{CaCl2}	Total Si †	CaCO ₃	TOC (Corg)
	g kg ⁻¹		mg kg ⁻¹	g kg ⁻¹	g kg ⁻¹	g kg ⁻¹
High-Si soil						
Zlabern	Sand:	7.36 ±	B1: 49.2	263	11.4 ±	13.3 ±
(48.705 N,	281	0.03	± 0.882		0.6	0.2
16.537 E)	Silt:		b			
	425		B2: 42.6			
	Clay:		± 1.45 a			
	295					
Low-Si soil						
Trauch	Sand:	7.19 ±	B1: 4.50	135	329 ±	107 ±
(47.846 N,	417	0.03	± 0.08 b		14.6	1.9
15.651 E)	Silt:		B2: 3.01			
	473		± 0.04 a			
	Clay:					
	180					

Data are means ± SD, n = 4. B1 - soil batch 1, B2 - soil batch 2. † - XRF measurements, n = 1, TOC (C_{org}) – total organic carbon, Si_{CaCl2}- CaCl₂-extractable Si. Different letters indicate significant differences between means according to the t-test.

www.superwurm.de.

2.4. Experimental setup

The experiment was conducted twice, with each repetition referred to as experimental run 1 (ER 1, between 28 June 2021 and 16 November 2021) and experimental run 2 (ER 2, between 23 November 2021 and 25 April 2022).

2.4.1. Experimental run 1

Custom-made plastic pots (10 cm diameter and 40 cm high) were used as experimental units. Ten cm high mesh barriers were placed around the upper rim of each experimental unit to prevent the earthworms from escaping. The pots were filled with either 2.5 kg of high- or 2 kg of low-Si soil respectively. Differences in the soil masses resulted from filling the pots to the same filling height (32 cm) and the inherently different bulk densities: 0.79 and 0.99 g cm⁻³ for low- and high-Si soils, respectively. Each pot was fertilized with N (115 mg kg⁻¹), P (100 mg kg⁻¹), and K (310 mg kg⁻¹) in liquid form prior to introducing the earthworms. Part of the pots received Si-rich wheat straw (22 mg g⁻¹ total Si, air dried and ground to ≤0.5 cm) as feeding material for the earthworms, with 10 g of litter mixed into the top 10 cm of soil at the beginning of the experiment (Li treatments) (Fig. 1). Each treatment consisted of four replicates and was conducted in a greenhouse cabinet. Air temperature during both experimental runs was 15–20 °C with a 14/10 h day-night cycle. This temperature range was chosen as a compromise between the earthworms' preference for lower (Amaroli et al., 2018) and the wheat plant preference for higher temperature (Porter and Gawith, 1999). The soil was incubated with earthworms and litter for 4 weeks at 75 % water-holding capacity before wheat was planted. Pots were irrigated with 0.01 mol L⁻¹ CaCl₂ solution to prevent soil silting. Individual treatments were designated as follows: W0 Li0 - control with no earthworms and no litter; W Li - both earthworm and litter addition; W Li0 - earthworm addition but no litter addition; W0 Li -

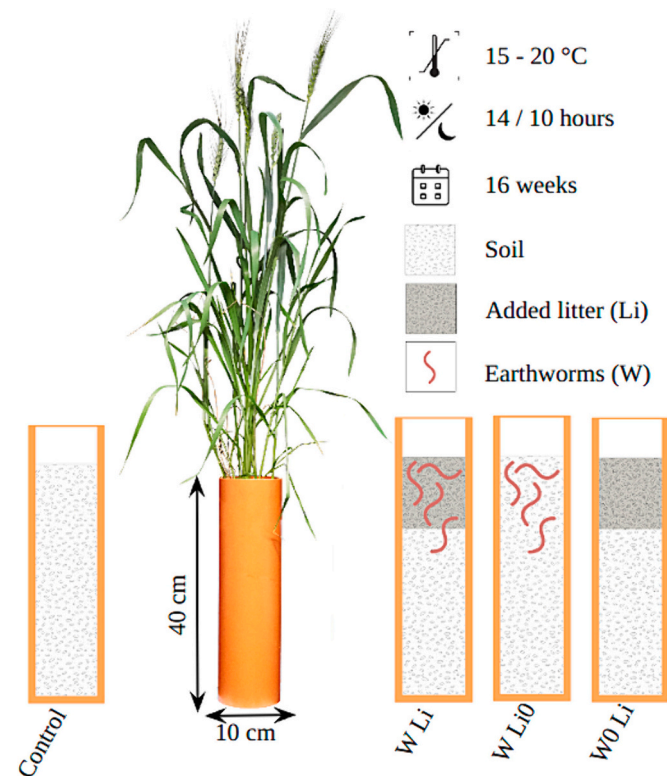


Fig. 1. Scheme of the experimental setup. Each pot represents a separate treatment.

no earthworms but with litter addition.

After 12 weeks of growth (16 weeks in total, including soil incubation), wheat plants were harvested at the late milk (BBCH 77) stage (Meier, 2018). The shoots were cut 2 cm above the soil surface and oven-dried in paper bags at 65 °C for 48 h before weighing. The top 10-cm-thick soil layer (including earthworm casts) was cut from the soil core. Roots and earthworms therein were removed. Earthworms were counted and weighed. Collected soil samples were air-dried in open plastic bags for one month and stored for further analysis. Earthworms in the soil below 10 cm were also retrieved, counted, weighed, and released into the wild.

2.4.2. Experimental run 2

The second experimental run was carried out in the same manner as the first one, with slight differences in soil characteristics (e.g., soil batch 2 was used instead of soil batch 1) and harvesting procedure (e.g., casts were collected from the top of the soil cores and analyzed separately). Both subsamples (casts and topsoil) were air-dried in open plastic bags and then sieved through a 2-mm sieve for further analysis of Si content. In addition, the irrigation procedure was slightly adjusted: watering was done more frequently and in smaller amounts to prevent the formation of cracks that had been observed in the high-Si soils in ER 1 due to the less frequent addition of larger amounts of water.

2.5. Determination of Si_{CaCl2} in soil and cast samples

In this study, the effect of earthworms and litter addition on Si availability was analyzed in soil samples collected in both experimental runs, and in earthworm casts collected in ER 2 only. When interpreting the Si_{CaCl2} concentrations in the soil samples, the difference in cast and soil collection procedures must be taken into account. Because casts in ER 1 were not separated from soil, these soil samples contain cast material; therefore, the Si_{CaCl2} concentrations in these samples is a combination of Si_{CaCl2} in soil and casts. In the following, these samples are referred to as soil_{cast+}. In ER 2, soil and cast samples were separated so that no cast material was mixed into the soil samples; for clarity, these samples are referred to as soil_{cast-}.

Extraction of Si from soil and casts followed the CaCl₂ method described by Haysom and Chapman (1975). This method was chosen as it has been shown to have a high correlation with plant Si concentration (Meirelles et al., 2022) and thus represents plant-available Si. Briefly, 3 g of air-dried sample, either soil or casts, sieved to ≤2 mm were placed into a 50 mL plastic vial. 30 mL of 0.01 mol L⁻¹ CaCl₂ were added and the vials were shaken on a plate shaker (80 rpm) for 16 h. The suspension was allowed to settle for 30 min and syringe-filtered through a 0.45 μm nylon filter. The filtrate was acidified to 2 % HNO₃ and analyzed for Si using ICP-OES (PerkinElmer Optima 8300 DV).

2.6. Determination of shoot Si content

Digestion was performed according to the method described by Kraska and Breitenbeck (2010). The oven-dried plant samples were first ground to a fine powder (<200 μm), and then 100 mg of material weighed into plastic vials. 80 μL of octyl alcohol (CH₃(CH₂)₇OH) was added to prevent foaming. 2 mL of 30 % H₂O₂ was added, and the vials were closed and incubated at 95 °C for 30 min. Subsequently, 4 mL of 50 % w/v NaOH was added, and the samples were incubated at 95 °C for another 5 h. Finally, the samples were diluted with ultrapure laboratory water to the final volume of 50 mL, resulting in a NaOH concentration of 1 mol L⁻¹. For analysis, the extracts were diluted to 0.2 mol L⁻¹ NaOH, and Si was measured on ICP-OES (PerkinElmer Optima 8300 DV).

2.7. Statistical analysis

To analyze and plot the data, Python (3.8.10) with the libraries Pandas (McKinney, 2010), Numpy (Harris et al., 2020) and Matplotlib

(Hunter, 2007) were used. A two-way ANOVA with type III sum of squares (Python package Scipy) was used to determine the impact of the experimental factors (earthworms, litter addition) and their interaction on the measured parameters. The fitness of data to ANOVA assumptions was confirmed by evaluation of the residuals: visual evaluation of QQ plots for normality, visual evaluation of scatter plots and Breusch-Pagan test for homoscedasticity. Tukey's HSD was used as a post-hoc test. To determine differences of means, Student's *t*-test was used. Statistical analysis of each experimental run was performed independently. Effects with $p \leq 0.05$ were considered statistically significantly different.

3. Results

3.1. Earthworm performance and survival

During the first experimental run in the low-Si soil, some mortality was observed among the earthworms. Dead earthworms found on the top of a column were replaced with specimens of similar weight. In the first experimental run, 82.8 % of the initial earthworm numbers, and in the second experimental run 172 % of the initial number of worms were recovered at harvest. The mean earthworm weight at the end of the experiment was $0.156 \pm 0.025 \text{ g pot}^{-1}$ (mean \pm SD) in the first experimental run and $0.159 \pm 0.035 \text{ g pot}^{-1}$ in the second experimental run. Wormlets were not considered in the biomass calculation.

3.2. Plant available Si in soil

Litter addition significantly increased $\text{Si}_{\text{CaCl}_2}$ in the soil in the low-Si

soils compared to the treatments without litter addition (Fig. 2A, B, Table 2). Si availability in soil also increased after the addition of litter compared to no-litter treatments in the high-Si soil in ER 1, but not in ER 2 (Fig. 2C, D, Table 2).

Earthworm effects were mainly observed in the casts. In both $\text{soil}_{\text{casts}^+}$ (ER 1) and in $\text{soil}_{\text{casts}^-}$ (ER 2), the presence of earthworms did not change Si availability when no litter was added (Fig. 2, Table 2). In the low-Si soil in ER 1 (Fig. 2A), the addition of litter combined with earthworm activity resulted in significantly higher Si availability compared to the treatment without litter addition (W0 Li), while in the

Table 2

Results of two-way ANOVA accounting for the effects of earthworms and litter addition on $\text{Si}_{\text{CaCl}_2}$ from the topsoil in the low-Si and high-Si soils.

	df		F		p-value	
	^a ER 1	^b ER 2	ER 1	ER 2	ER 1	ER 2
Low-Si soil						
Earthworms	1	1	0.321	0.414	0.584	0.532
Litter	1	1	74.8	1331	≤ 0.001	≤ 0.001
Earthworms \times Litter	1	1	3.76	4.69	0.078	0.051
High-Si soil						
Earthworms	1	1	0.061	3.94	0.809	0.073
Litter	1	1	8.54	2.43	0.013	0.148
Earthworms \times Litter	1	1	0.757	0.568	0.401	0.467

^a ER 1 - Experimental Run 1.

^b ER 2 - Experimental Run 2.

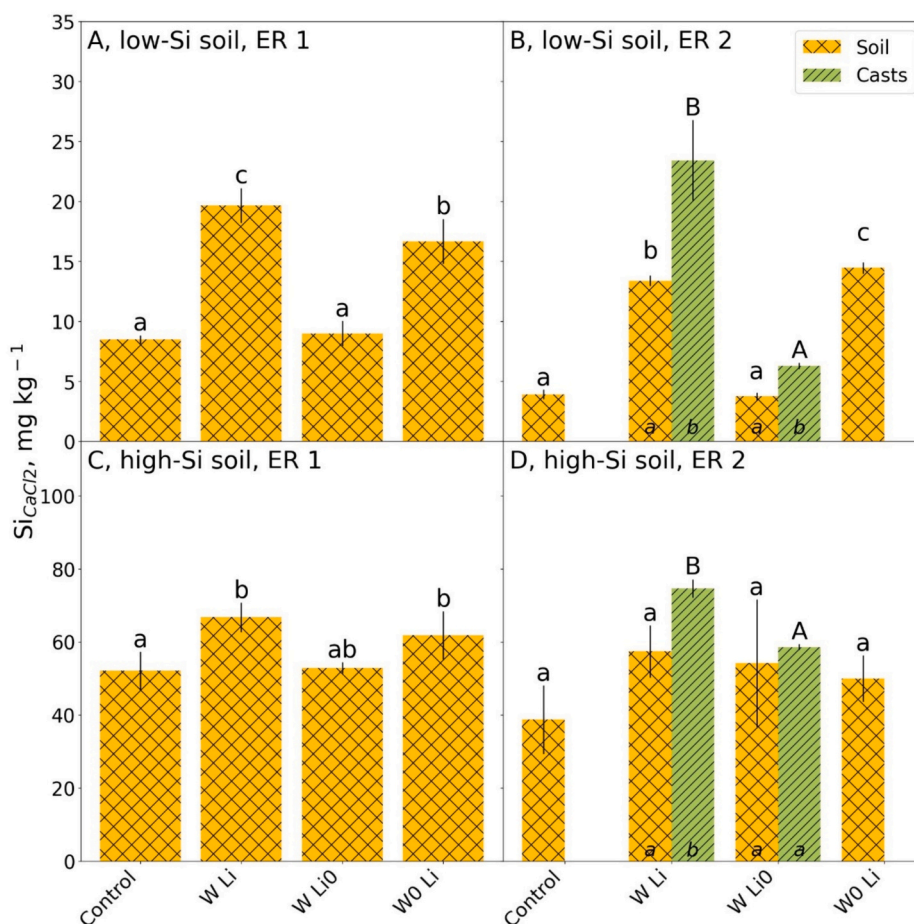


Fig. 2. $\text{Si}_{\text{CaCl}_2}$ from (A, C) $\text{soil}_{\text{casts}^+}$ and (B, D) $\text{soil}_{\text{casts}^-}$ and casts. A - low-Si soil first run, B - low-Si soil second run, C - high-Si soil first run, D - high-Si soil second run. Different letters indicate significant differences at $p \leq 0.05$ within runs. In the B and D panels, capital letters show differences between casts. Italic letters inside the bars show the differences between sample types (soil and casts) within the treatment. Error bars indicate the standard deviation of the mean.

ER 2, the opposite was observed: Si availability was significantly lower when earthworms were present (Fig. 2B).

Si availability in earthworm casts was only analyzed in the second experimental run. In the low-Si soil, Si availability in casts was significantly higher in both treatments with litter (W Li) and without litter (W Li0) than in the soil_{casts} of the respective treatments (Fig. 2B). However, a significant increase in Si availability in casts in the high-Si soil was observed after litter addition, but not in the absence of litter (Fig. 2C).

3.3. Shoot Si concentration

In both experimental runs in the low-Si soil (Fig. 3A, B), shoot Si concentrations of wheat plants were significantly higher after litter addition irrespective of earthworm presence compared to the control. According to a two-way ANOVA, earthworms had a significant effect on shoot Si concentrations in the first experimental run in the low Si soil. No such influence was observed in the second experimental run. A significant influence of litter was observed in both experimental runs (Table 3). In the high-Si soils (Fig. 3C, D, Table 3), shoot Si concentrations did not differ between treatments in either experimental run. Two-way ANOVA showed a significant effect of litter addition on plant Si uptake in the first experimental run (Table 3), however, Tukey's HSD test did not show any pairwise differences.

3.4. Correlation between soil Si_{CaCl2} and shoot Si concentration

In the low-Si soils, Si_{CaCl2} was significantly positively correlated with the plant Si concentration ($R^2 = 0.92$). In the high-Si soil, Si_{CaCl2} was not

Table 3

Results of 2-way ANOVA accounting for the effects of earthworms and litter addition on shoots Si concentration of wheat in the low-Si and high-Si soils.

	df		F		p-value	
	^a ER	^b ER	ER 1	ER 2	ER 1	ER 2
	1	2				
Low-Si soil						
Earthworms	1	1	5.33	≤0.001	0.044	0.991
Litter	1	1	130	32.7	≤0.001	≤0.001
Earthworms × Litter	1	1	0.054	0.053	0.820	0.822
High-Si soil						
Earthworms	1	1	0.121	0.416	0.734	0.531
Litter	1	1	9.29	0.110	0.010	0.919
Earthworms × Litter	1	1	0.806	0.046	0.387	0.835

^a ER 1 - Experimental Run 1.

^b ER 2 - Experimental Run 2.

correlated with the shoot Si concentration (Fig. 4).

4. Discussion

4.1. Effect of litter addition and earthworm activity on soil Si availability

4.1.1. Effect of litter on Si solubility

Our data indicate that the addition of phytolith-containing plant material can lead to a substantial increase in readily available Si in the

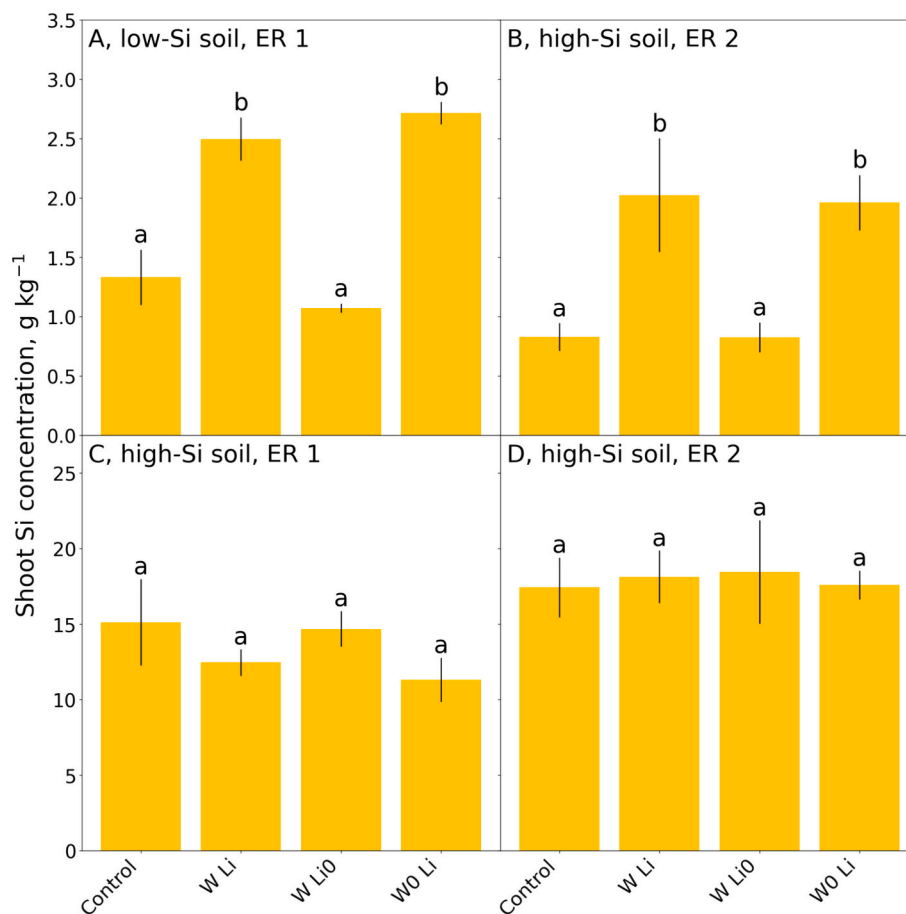


Fig. 3. Si concentration in shoots of the experimental wheat plants. A - first experimental run of the low-Si soil, B - second experimental run of the low-Si soil, C - first experimental run of the high-Si soil, and D - second experimental run of the high-Si soil. Different letters indicate significant differences at $p \leq 0.05$. Error bars indicate the standard deviation of the mean.

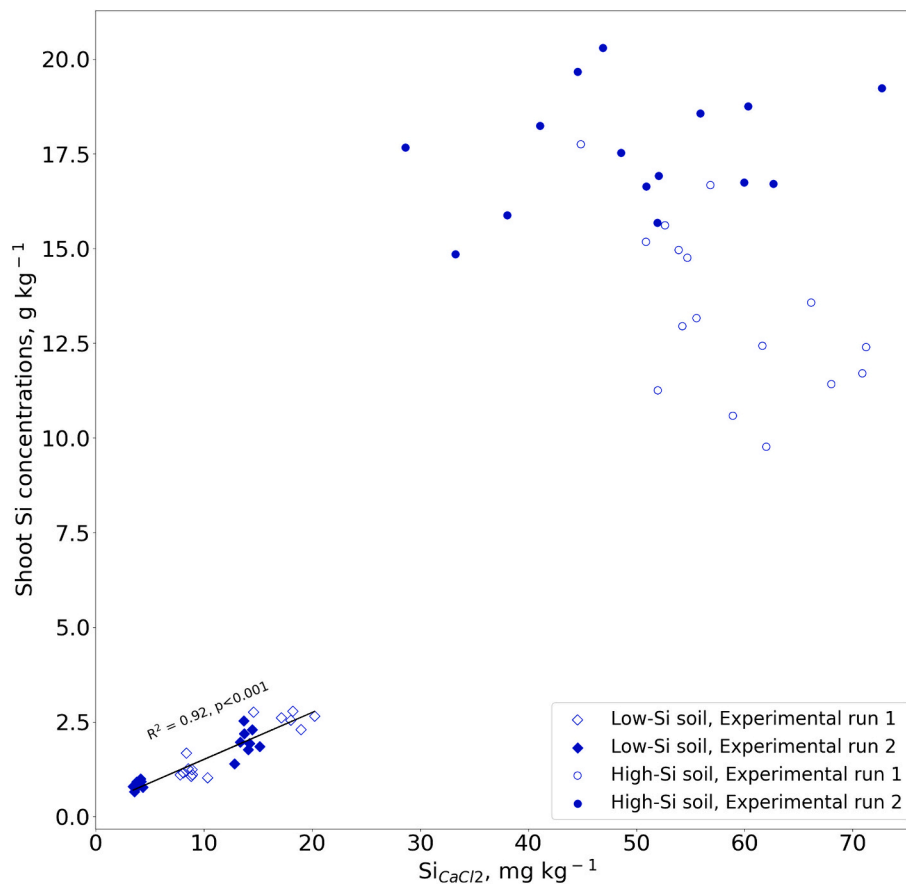


Fig. 4. Correlation between soil $\text{Si}_{\text{CaCl}_2}$ and shoot Si concentration in the low-Si and high-Si soils.

soil, especially in soils with initially low Si levels (Fig. 2). However, the effect of phytolith application might be lower in soils with high Si concentrations because the solubility of phytoliths is negatively affected by high $\text{Si}_{\text{CaCl}_2}$ concentrations, which could promote their stabilization (Marxen et al., 2016). Grinding the wheat straw and mixing it homogeneously into the topsoil layer in the present study likely increased the dissolution rate of phytoliths. Dissolution of Si from straw chopped to 1 cm size fragments was reportedly lower: Ma and Takahashi (1991) observed that only about 6% of the Si content of rice straw was released. In a long-term field experiment (1963–2018) in Germany, it was found that the regular incorporation of chopped straw in combination with NPK fertilization leads to a significant increase in $\text{Si}_{\text{CaCl}_2}$ in soil (Puppe et al., 2021). In contrast, Yang et al., 2020 found no correlation between the application of Si-rich straw and $\text{Si}_{\text{CaCl}_2}$ in a long-term field experiment (1982–2018) in China. However, both studies reported a significant increase in Si concentration in the plants due to the application of straw. In a pot experiment, the release of Si from fresh rice straw (2–7 cm length) after 5 days of incubation was observed and estimated that phytoliths take 50 days to completely dissolve at a constant dissolution rate, while an increase in $\text{Si}_{\text{CaCl}_2}$ in the soil solution was only observed in the first 25 days (Marxen et al., 2016). The results of the current study and that of Marxen et al. (2016) suggest that Si uptake from plant litter is higher when the litter is fresh or when it has been ground.

4.1.2. Si solubility in earthworm casts

The effects of earthworms on Si availability in the soil were most evident in the earthworm casts (Fig. 2B, D). The increase in $\text{Si}_{\text{CaCl}_2}$ concentration was higher in the treatments with litter addition than without litter addition, indicating that the ingestion of litter by earthworms contributes significantly to the dissolution of the contained phytoliths and releases large amounts of Si into the soil. Interestingly,

$\text{Si}_{\text{CaCl}_2}$ in casts of the low-Si soil was elevated even when no litter was added compared to the corresponding samples without casts, indicating that earthworms also release Si from autochthonous Si sources. The accelerated decomposition of organic matter by earthworms is a well-known process (Schulmann and Tiunov, 1999), which can increase the dissolution of contained phytoliths by exposing them directly to the surrounding solution (Marxen et al., 2016). Moreover, the gut passage of earthworms has been shown to fragment mineral soil particles (Suzuki et al., 2003) and accelerate mineral weathering (Carpenter et al., 2007). Although the release of Si from soil minerals was not measured in these studies, it can be assumed that these effects of earthworms on soil minerals contribute to increased Si solubility. In addition, Hu et al. (2018) demonstrated the ability of earthworm gut microbes to solubilize Si. An increase in soil pH due to gut passage, as reported by Horn et al. (2003), which could also contribute to Si solubilization, was not observed in the present study.

Taken together, the current data show that earthworms are able to solubilize Si from (i) phytoliths contained in freshly added plant litter as well as from soil, where Si can be solubilized from (ii) phytoliths contained in soil organic matter and (iii) soil minerals. These observations are consistent with reports of an increase in $\text{Si}_{\text{CaCl}_2}$ in casts compared to soil that was not ingested by earthworms, as it was solubilized from both soil minerals and wheat straw (Bityutskii et al., 2016; Georgiadis et al., 2019).

4.1.3. Si solubility in soil samples

In addition to the effects of Si solubilization in earthworm casts, slight earthworm-induced changes in Si solubility were observed in the soil samples collected in this experiment. It is important to note that these soil samples differ between the two experimental runs due to the difference in sampling, as soil samples from run 1 contain cast material,

while samples from run 2 do not. The small but significant increase in Si solubility in the low-Si soil with casts most likely reflects the Si-solubilizing effect of earthworms from litter phytoliths, although it is not as clear as in the cast samples analyzed in run 2. For the low-Si soil in run 2, the pattern was opposite to that observed in run 1. As a result, soil samples with cast material exhibited increased Si solubility, which increased the overall Si solubility of these samples. However, it is very likely that in soil samples without casts the overall undigested litter content was decreased due to the earthworm's feeding preference for litter-rich material (Neilson and Boag, 2003). Preferential consumption of litter may have resulted in a concentration of digested litter material in the casts, while reducing the amount of undigested litter in the remaining soil without casts (Lavelle, 1997). These two effects, (i) the preferential allocation of litter into casts in run 2 and (ii) the mixing of casts with soil in run 1, explain the different patterns of Si solubility in the soil samples on the low-Si soil in the two experimental runs.

The extent of cast production and therefore the impact of earthworm activity on Si solubilization is strongly related to earthworm population density, which in turn is related to the type of land use: intensive land use with frequent disturbances (e.g. tillage in arable farming) often leads to a decrease in earthworm populations (Didden, 2001; Spurgeon et al., 2013; Vazquez et al., 2019). Therefore, arable soils are usually less favorable habitats for earthworms than grasslands because of more frequent soil disturbance, but also because of their usually higher pH, as earthworms prefer soils in the pH range of 5.0–7.4 (Fabian et al., 2014; Singh et al., 2020). Silicon solubility is also known to be related to soil pH, as amorphous silica is well soluble and readily resupplies the $\text{Si}_{\text{CaCl}_2}$ pool in soils with neutral or slightly alkaline pH (Haynes, 2019, 2014). The $\text{Si}_{\text{CaCl}_2}$ content of arable soils has been reported to be usually above 20 mg kg^{-1} (Caubet et al., 2020, analysing ~2000 French soil samples), which is considered a threshold below which Si may be deficient for plants with a high Si demand. The Si levels in the soil can be positively affected by liming, as an increase in pH leads to an increase in $\text{Si}_{\text{CaCl}_2}$ due to the solubilization of amorphous silica (Haynes, 2019, 2014). For grasslands, which often have a lower soil pH, an average $\text{Si}_{\text{CaCl}_2}$ content of 9.8 g kg^{-1} was determined (Höhn et al., 2008, evaluating 20 German soil samples). Our own, unpublished data from 398 arable and grassland soil samples from north-east Austria also confirm generally lower $\text{Si}_{\text{CaCl}_2}$ content in grassland than in arable soils. Thus, the role of earthworms in Si cycling is expected to be higher in grasslands than in arable soils (Vazquez et al., 2019), not only because they are more favorable habitats for earthworms and have higher earthworm abundance (Köhler et al., 2014), but also because of their generally lower $\text{Si}_{\text{CaCl}_2}$ status.

4.2. Wheat Si uptake

In the low-Si soil, the Si concentration in shoots was mainly influenced by the addition of litter, but not by the presence of earthworms. In high-Si soil, the Si uptake of wheat was not altered by the experimental factors.

The Si concentration in the shoots of wheat plants grown in the low-Si soil was positively correlated with Si availability in the soil (Fig. 4). Although $\text{Si}_{\text{CaCl}_2}$ has previously been shown to correlate well with Si content in sugar cane (Meirelles et al., 2022), such a correlation has not been previously reported for wheat. Interestingly, a strong positive correlation was observed between $\text{Si}_{\text{CaCl}_2}$ and shoot Si concentrations in both batches of low-Si soil. However, no correlation was observed between $\text{Si}_{\text{CaCl}_2}$ and shoot Si in high-Si soil. Although only a limited number of studies on Si uptake by wheat are available, the studies by Gocke et al. (2013) and Rains et al. (2006) suggest that Si uptake by wheat is facilitated by LS11-like transporters (Montpetit et al., 2012) and thus can be regulated by the plant. The exact mechanism of LS11 regulation in wheat has not been studied, but in rice it depends on Si availability in the soil and is regulated by the Si status of the plant (Chaiwong et al., 2020; Ma et al., 2006). Si concentrations in wheat shoots are typically between 1 and 3 % (Hodson et al., 2005), which is

similar to the Si concentrations in the shoots observed in the high-Si soil in the current study (Fig. 3C, D).

The fact that the shoot Si concentration of the wheat plants in the low-Si soil correlated closely with the $\text{Si}_{\text{CaCl}_2}$ concentration and the very low shoot Si concentration (<0.5 %) indicates that Si uptake was limited by Si availability in this soil. This was not the case on the high-Si soil: in experimental run 2, shoot Si concentrations varied around an average of 1.79 %, while soil $\text{Si}_{\text{CaCl}_2}$ ranged from 30 to 75 mg kg^{-1} . In this experimental run, the water supply was unrestricted throughout the experiment on this soil, rendering it unlikely that the Si supply to the wheat roots limited Si uptake by the plant. The fact that shoot Si concentrations did not increase with $\text{Si}_{\text{CaCl}_2}$ indicates that the wheat may have accumulated Si at its maximum rate in the high-Si soil in experimental run 2. The average concentration in the wheat shoot was about 1.34 % in run 1 on the high-Si soil, which was significantly lower ($p < 0.001$) than in run 2, even though $\text{Si}_{\text{CaCl}_2}$ was higher in run 1 than in run 2. This was most likely due to the lower water content of the experimental soil in run 1 during limited periods of the experiment, which was caused by the less frequent irrigation. Although the plants showed no drought symptoms, the Si mass flow to the root surface was thereby reduced, explaining the lower Si uptake. This observation indicates that Si uptake by plant roots, like many other elements, is dependent on soil water availability. Therefore, for the potential benefits of plant Si accumulation during drought periods, as reported by several authors (Ahmad et al., 2016; Alzahrani et al., 2018; Bukhari et al., 2021), Si uptake is required prior to the occurrence of drought.

Our results suggest, though indirectly, that soil-dwelling invertebrates such as earthworms could play an important role in the accumulation of $\text{Si}_{\text{CaCl}_2}$ in the soil and consequently in the Si concentration in the shoot, given the right conditions (i.e. the initial Si status of the soil and a high population density). We expect a greater influence in soils characterized by high organic matter content and lower land use intensity (e.g., grasslands or pastures, organic farms), as those are more favorable for earthworms. The higher population density facilitates cast production and thus soil $\text{Si}_{\text{CaCl}_2}$ concentrations, which may be reflected in Si uptake by plants, especially when $\text{Si}_{\text{CaCl}_2}$ concentrations in the soil are initially low.

5. Conclusions

In this pot experiment, the role of an epigeic earthworm species (*D. veneta*) and its combination with wheat litter addition on Si availability in the soil and Si uptake by wheat was investigated. The Si concentrations in the shoots were well-correlated with the $\text{Si}_{\text{CaCl}_2}$ concentrations in soil with low Si content. In low-Si soils, an effect of both earthworms and litter was observed. The addition of litter had a significant effect on the $\text{Si}_{\text{CaCl}_2}$ concentration in the shoots. While the activity of *D. veneta* led to an increase in $\text{Si}_{\text{CaCl}_2}$ concentration in the casts due to the solubilization of Si from soil minerals and from the litter, this increase was not reflected in the Si concentration of the wheat shoots, probably due to the small total volume of casts compared to the total soil volume and the limited duration of the experiment. However, it can be assumed that the enhanced Si availability in casts will also contribute to higher Si concentrations in the plants in the long run. In soils with high Si content, the only observed effect was the increase of $\text{Si}_{\text{CaCl}_2}$ in the earthworm casts in the combined treatment with earthworms and plant litter.

CRedit authorship contribution statement

Dmytro Monoshyn: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Miriam C. Chibesa:** Formal analysis, Investigation, Writing – review & editing. **Markus Puschenreiter:** Conceptualization, Supervision, Writing – review & editing. **Johann G. Zaller:** Conceptualization, Supervision, Writing – review & editing. **Jakob Santner:** Conceptualization, Funding

acquisition, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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