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ORIGINAL PAPER

Silicon reduces slug feeding on wheat seedlings

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Abstract Slugs are a serious pest of cereal crops, and recent emphasis in slug pest management has shifted from solely chemical towards integrated approaches. The objective of the present research was to test if boosted silicon (Si) and calcium (Ca) levels in wheat seedlings can reduce slug grazing. Laboratory experiments were conducted in which wheat seedlings were grown firstly, with soluble Si and Ca (with and without additional mineral N) or secondly, with six levels of soluble Si, and consumption of leave sections by the field slug (*Deroceras reticulatum*) was measured. Boosted foliar Si concentrations reduced consumption significantly ($P < 0.001$) compared to an untreated control and Ca treatments in a no-choice setting; a similar trend ($P < 0.10$), but with a higher variability, was observed in a simultaneous choice setting. It is shown for the first time that increasing the nominal Si concentration of treatment solutions in a geometric series (from 0 to 6 g sodium metasilicate nonahydrate l^{-1}) translated into a logarithmic increase in foliar Si concentrations (from 5.0 to 19.4 g Si kg^{-1} dry weight). When these leaves were offered simultaneously (choice setting), wheat leaves containing less than 10 g Si kg^{-1} were consumed preferentially by *D. reticulatum* ($P < 0.001$), suggesting that Si concentrations as low as 1 % leaf dry weight may be effective at reducing grazing by slugs. It is concluded that boosting Si levels in cereals has potential as a novel tool in crop protection against pest slugs and snails. Various open research questions to advance this tool are identified.

Keywords Cereals · Crop protection · Gastropoda · Plant defences · Poaceae · Pest management

Introduction

Terrestrial slugs (Gastropoda) are serious pests of agricultural and horticultural crops worldwide. Slugs attack various field crops, including cereals, oilseed rape, potatoes, soybean, sugar beet, forages and vegetables (Godan 1983; South 1992). Among cereals, newly sown wheat is highly vulnerable to slug damage (Glen and Moens 2002; Port and Port 1986). In the United Kingdom, for example, 22 % of winter wheat crops may suffer slug damage with associated yield losses in the region of 5 %, if affected areas are left untreated with chemical molluscicides (ADAS 2010). Similarly, slug damage may reduce wheat yields by 8–24 % within Australian cropping systems (Murray et al. 2013). Slug damage to wheat can occur by hollowing of the recently drilled seeds and also by grazing on and shredding of the leaves of seedlings after emergence, with a risk of seedling death up to about tillering (Glen and Moens 2002; South 1992).

Conventional slug pest management in field crops has primarily been based on chemical methods with metaldehyde and methiocarb as active ingredients (South 1992; Glen and Moens 2002). For instance, in the above mentioned UK survey (ADAS 2010) covering 1998–2008, between 8 and 28 % of the total wheat crop area were treated with these chemical molluscicides. However, more recently, environmental concerns

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associated with molluscicidal chemicals have shifted the emphasis towards integrated approaches that combine cultural tactics (e.g. choice of crop/cultivar, rotations, soil tillage, residue management) with monitoring, chemical control and natural enemy conservation (Douglas and Tooker 2012). Excellent progress has also been achieved in biological control with parasitic nematodes, but its large-scale commercial use in arable crops is unlikely (Howlett 2012).

One mechanism that can confer protection to plants against herbivores is the incorporation of silicon (Si) into plant tissues (Epstein 2009; Guntzer et al. 2012; Snyder et al. 2006). This phenomenon is well-documented for various grasses and mammalian (Cotterill et al. 2007) as well as chewing insect pests (Reynolds et al. 2009), and it is often implied as a possible plant defence against molluscan pests (e.g. Barlow et al. 2013). Yet, only one study has explicitly tested the effects of a boosted Si level (in rice leaves) on slug feeding (Wadham and Wynn Parry 1981). Furthermore, calcium (Ca) is another abundant mineral element that can, when deposited as calcium oxalate, protect plants from herbivorous animals including chewing insects (Franceschi and Nakata 2005; Park et al. 2009), but its effect on slugs has not been tested.

The objectives of this research were (1) to compare the effects of Si and Ca amendments, with or without additional mineral N, on slug grazing on wheat seedling leaves; and (2) to assess the effects of different soluble Si concentrations in irrigation water on Si concentrations in wheat leaves and the subsequent Si impacts on slugs grazing. A series of short, related laboratory experiments is reported.

Materials and methods

Plants

Spring wheat (*Triticum aestivum* L.) var. Raffles was used. Raffles is an early maturing British variety listed since 2000 in the Spring Cereal Recommended List of the Irish Department of Agriculture, Food and the Marine. Cleaned but untreated seeds were used.

Commercial John Innes No. 2 potting-on compost (Westland Horticulture Ltd., Dungannon, County Tyrone, Northern Ireland) served as growing medium. Containing about 45 % peat, this compost has a pH of 6 and a medium nutrient content. About 800 g (fresh weight) of compost was filled into plastic trays (20 cm by 15 cm by 6 cm high) with drainage holes. About 60 wheat seeds were planted randomly (1 cm deep) per tray. Planted trays were placed indoors, beside a window in a heated laboratory, and given 250 ml of tap water every second or third day until treatments were commenced. A pH meter was used to measure the pH (in distilled water) of the potting compost (10 g per tray) before planting and at harvest of wheat seedlings. Seedlings were harvested for feeding experiments about 25 days after emergence (2 or 3 leaves unfolded).

Treatments: Si, Ca and N

First, a no-choice and a choice experiments were conducted to compare the effects of Si and Ca amendments, with or without additional mineral N, on slug grazing on wheat seedling leaves. The five fertilisation treatments for producing wheat seedlings were as follows:

1) Control (no chemical amendments).
2) Silicon (sodium metasilicate nonahydrate [$Na_2O_3Si \cdot 9H_2O$], 3.04 g l^{-1}; 98 % pure chemical, Sigma-Aldrich).
3) Silicon as above plus nitrogen (urea [$CO(NH_2)_2$], 0.6 g l^{-1}).
4) Calcium (calcium carbonate [$CaCO_3$], 24 g l^{-1}).
5) Calcium as above plus nitrogen (urea [$CO(NH_2)_2$], 0.6 g l^{-1}).

The Si concentration in irrigation solutions (3.04 g compound l^{-1} tap water, equivalent to 300 ppm Si) for use on compost was between 4 and 6 times higher than that used in hydroponic systems in previous studies (Wadham and Wynn Parry 1981; Cid et al. 1990; Massey and Hartley 2009). The total N and Ca applications per plant tray were equivalent to agronomic field rates of 50 kg N ha^{-1} and 2,000 kg $CaCO_3$ ha^{-1}. Chemical treatments were applied as solutions 5 times over 10 days, starting about 15 days after wheat emergence. The control trays received tap water. Each of the five treatments was applied to three replicate plant trays, each placed in a larger foil tray to prevent leakage and cross-contamination.

Treatments: Si levels

Second, an experiment was conducted to assess the effects of different Si concentrations in irrigation water on Si concentrations in wheat leaves and their impact on slugs grazing in a choice setting. Wheat seedlings were grown under similar conditions as described above, but using 18 smaller plant pots (9-cm diameter) for six treatments of increasing Si concentrations: (1) control, (2) 0.38 g l^{-1}, (3) 0.76 g l^{-1}, (4) 1.52 g l^{-1}, (5) 3.04 g l^{-1}, and (6) 6.08 g l^{-1}. These concentrations refer to the mass of sodium metasilicate nonahydrate ($Na_2O_3Si \cdot 9H_2O$) and represent a geometric series with 3.04 g compound l^{-1} tap water (300 ppm Si) used in the first experiments, as a higher-end reference point. Six seedlings were grown per pot and treated five times over a 10-day period.

Slugs

Experiments were conducted in March 2012. Grey field slugs, *D. reticulatum* (Müller) (Gastropoda: Agriolimacidae), were collected manually from an amenity grassland area in Shankill, Co. Dublin. In preparation of each experiment, slugs were kept without food on moist tissue paper for 24 h and then weighed individually and placed in Petri dishes (9-cm diameter) lined with filterpaper (Whatman No. 1) that was saturated with distilled water. As a control of hydration status, slugs were weighed before and after all experiments lasting between 24 and 72 h, but weights did not change. All feeding experiments were performed in an incubator, in the dark, at 17 °C.

No-choice experiment

A no-choice experiment was conducted to assess feeding by *D. reticulatum* on wheat seedling leaves produced with one of the five treatments with Si or Ca amendments, with or without additional N: control, Si, Si + N, Ca, Ca + N. Randomly selected leaf strips (weighing close to 200 mg) from the different treatments were placed in Petri dishes lined with saturated filter paper, with only one treatment per dish. Starved, weighed slugs were introduced individually and their feeding assessed over three consecutive 24-h periods. After each 24-h period, remaining leaf strips were removed and weighed, and new strips of known weight introduced. Six replicate dishes were set up per treatment, but in order to reduce variability due to injured or otherwise completely inactive individual slugs, the dish with the lowest feeding activity (mostly none at all) in each treatment was excluded from statistical analysis ($n = 5$).

Choice experiments

Two choice experiments were conducted. In the first choice experiment, individual *D. reticulatum* could select from one of five leaves, representing treatments with Si or Ca amendments, with or without additional N, in the same dish. Petri dishes were set up as described and single, 2-cm-long leaf strips (weighing about 20 mg each) were weighed and fixed onto the filter paper with coloured pins, each colour representing a different treatment for identification: control, Si, Si + N, Ca, and Ca + N. Starved *D. reticulatum* were introduced and allowed to feed for 48 h; then, mass loss was recorded for each leaf strip. Ten replicate dishes were set up, but one dish with no feeding activity was excluded from statistical analysis ($n = 9$).

The second choice experiment tested the effects of different Si concentrations in wheat leaves on grazing by *D. reticulatum*. Leaves of wheat from the six Si treatments were cut into 1-cm strips (about 10 mg each), weighed and fixed onto the filter paper with coloured pins for identification. Starved *D. reticulatum* were introduced and allowed to feed for 24 h; then, mass loss was recorded for each leaf strip. Nineteen replicate dishes were set up, but one with no feeding activity was excluded from statistical analysis ($n = 18$).

Slug-free controls

Additional controls of leaves under identical conditions but without slugs were included in all experimental runs in order to assess changes in leave weight that may occur without the consumer being present (termed ‘autogenetic changes’ by Roa 1992). Water contents of wheat leaves from Si, Ca and N treatments were also measured once by oven-drying at 60 °C for 24 h.

Chemical analysis of wheat leaves

Wheat leaf samples were dried at 60 °C for 24 h and pulverized using a Retsch Mixer Mill with steel containers and balls. Total carbon (C) and nitrogen (N) contents were measured in the first experiment with Si, Ca and N treatments, with one pooled sample per treatment, by dry combustion using an Exeter Analytical CE 440 elemental analyser. Si concentrations of leaves were measured on one pooled sample per treatment in the first experiment, and on one replicate sample per wheat growing pot ($n = 3$ per treatment) in the second experiment with increasing Si concentrations.

Si analysis: dry ashing and alkaline fusion

Fifty mg dry plant powder were placed in a nickel (Ni) crucible and fitted with a corresponding Ni lid. The crucibles were placed in a muffle furnace at 550 °C for a minimum of 4 h and afterwards allowed to cool overnight. Then, about 2 g of anhydrous granular NaOH were added to each crucible, and crucibles were returned to the muffle furnace set to 500 °C for 1.5 h. After cooling, 10 ml of deionised water was added to each crucible to dissolve the fused contents and left overnight. The content of crucibles was transferred to polypropylene beakers where excess NaOH was neutralised using

4 M HCl. Finally, the solution was transferred to 100 ml polypropylene volumetric flasks and brought to volume using deionised water.

Si analysis: colourimetry

The amount of Si present in the solution was measured using the Heteropoly Blue method (Eaton et al. 1995). First, 5 ml of the solution was transferred to 15 ml centrifuge tubes, and 0.1 ml of 4 M HCl and 0.2 ml of ammonium molybdate reagent (10 g $(NH_4)_6Mo_7O_{24}\cdot 4H_2O$ in 100 ml deionised water, pH adjusted to 8 with silica free NaOH) were added to each tube and mixed well. After 5 min, 0.2 ml of oxalic acid (7.5 g $H_2C_2O_4\cdot H_2O$ dissolved in deionised water) was added and mixed thoroughly. The sample was allowed to stand for at least 2 min but no more than 15 min. After this, 0.2 ml of the reducing agent (0.5 g of *p*-methylaminophenol and 0.58 g sodium sulphite [Na_2SO_3] in 50 ml deionised water) were added. The sample was mixed thoroughly and the concentration was measured after 5 min using a spectrophotometer (Helios, Unicam Instruments, Cambridge) set at 650 nm. New reagents were prepared every 7–10 days, and the use of glassware was eliminated wherever possible to reduce the risk of Si contamination.

Statistical analyses

The no-choice experiment, with Si, Ca and N amendments and slug feeding assessed over three consecutive 24-h periods, was analysed with Repeated Measures ANOVA and Scheffé's multiple comparisons. By contrast, the two other feeding assays were multiple-choice feeding experiments, with simultaneous assessments of different foods exposed to the same consumer animal, which require an analysis accounting for the fact that such measurements are not independent (Roa 1992; Lockwood 1998). Therefore, the two food choice assays were analysed as multivariate mean comparisons using Hotelling's T^2 statistic calculated from proportional consumption data for each food type and slug, as outlined by Lockwood (1998).

To allow for comparisons with published consumption data, feeding results are shown as absolute, standardised feeding rates (i.e. mg leaf consumed per g slug biomass), rather than proportional consumption data employed in the statistical analysis. Standardised feeding rates account for differently sized slugs used (Godan 1983) and were calculated for each dish by dividing the amount consumed by the slug (mg fresh weight) by the weight of the slug (g live biomass). Effects of nominal Si concentration of treatment solutions on measured Si concentrations of wheat seedling leaves were visualised by regression analysis, fitting a logarithmic curve. All statistical analyses were computed using SPSS Statistics version 20 (IBM Corporation, New York). Results are reported as mean and standard error.

Results

Leaf composition in Si, Ca and N treatments

Total N contents in wheat leaves from these young seedlings were very high in agronomic terms (Bergmann 1992), ranging from 5.2 to 5.9 % in treatments without additional mineral N, with somewhat elevated values of 6.2 and 6.4 % in Si and Ca treatments with additional N. Correspondingly, C:N ratios were higher in treatments without N (6.0–6.3) than in Si and Ca treatments with additional N (5.3 and 5.5). Foliar Si concentrations were several times higher in the treatments receiving soluble Si (17.2 and 14.9 g kg^{-1} in the Si treatments without and with additional N, respectively) compared to treatments without soluble Si (2.3–4.5 g kg^{-1}). Water contents of leaves were similar across treatments (89–94 %).

The pH of the compost at harvest was significantly elevated (ANOVA $F_{4,10} = 61.75$, $P < 0.001$, Scheffé's $P < 0.01$) in all four Si and Ca treatments (7.04 ± 0.06) compared to the control (5.96 ± 0.07).

No-choice feeding with Si, Ca and N treatments

In a no-choice situation, *D. reticulatum* consumed much less wheat from the two treatments receiving soluble Si compared to the control and Ca treatments (Fig. 1). Repeated measures ANOVA showed that treatments (between-subject factor) had highly significant effects ($F_{4,20} = 17.87$, $P < 0.001$) on consumption measured over three consecutive 24-h periods. Slugs consumed significantly less leaf biomass within both Si treatments in comparison to the untreated control and the Ca addition treatments (Scheffé's, $P < 0.05$). For example, average consumption (in mg g^{-1} 24 h^{-1}) was 17.4 ± 9.3 in the Si treatment and 67.1 ± 16.4 in the control (see Fig. 1). Consumption in the Ca treatment was the highest (114.7 ± 15.8), but this was not significantly different from the control (Scheffé's $P = 0.11$). Importantly for subsequent feeding experiments, neither Time nor Time × Treatment interactions (Within-subject factors) were

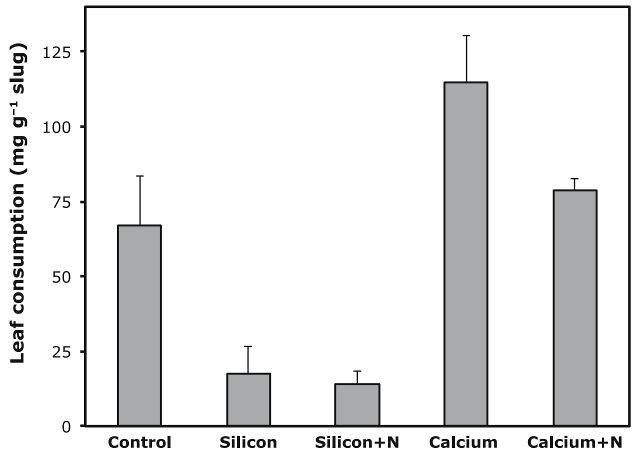

Fig. 1 Effects of Si and Ca treatments, with or without additional N, on the average consumption [in mg (leaf fresh weight) g^{-1} slug biomass per 24 h] of wheat leaves by *D. reticulatum* in a **no-choice** setting measured over three consecutive 24-h periods ($n = 5$, means + standard error)

significant in repeated measures ANOVA ($F_{adj.} < 1.00$, $P > 0.10$), suggesting that the observed treatment effects on slug consumption were the same in each 24-h period.

Leave strips incubated in slug-free control dishes increased by just 0.9 % in weight on average per 24 h (range 0.6–2.6 %).

Choice feeding with Si, Ca and N treatments

In the multiple-choice feeding situation, *D. reticulatum* also tended to consume less wheat from the two treatments receiving soluble Si compared to the control and Ca treatments (Fig. 2). However, the difference in the proportional consumption for each food type was only marginally significant statistically (Hotelling's $T^2 = 29.80$, $F_{4,5} = 4.66$, $P = 0.061$).

Leave strips were much smaller in this experiment (about 20 mg); when incubated in slug-free control dishes, they increased in weight by 18.9 % ± 6.3 on average in 48 h. This likely contributed to variability and also means fresh weight consumption data (Fig. 2) are underestimates.

Experimental manipulation of foliar Si levels

The experimental manipulation of wheat foliar Si concentration by means of watering with sodium metasilicate solutions was successful (Fig. 3). Increasing the nominal Si concentration of treatment solutions in a geometric series (from 0 to 6.08 g $Na_2O_3Si{\cdot}9H_2O$ l^{-1}) translated into a logarithmic increase in foliar Si concentrations (from 5.0 ± 0.1 to 19.4 ± 0.8 g Si kg^{-1} dry weight). The coefficient of determination of this relationship was $r^2 = 0.91$ (details in legend to Fig. 3).

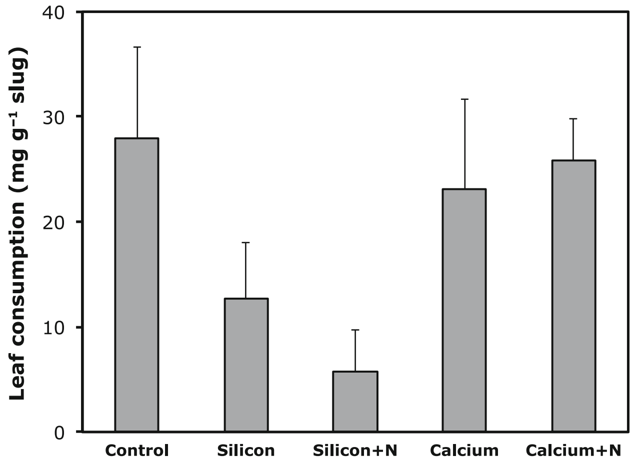

Fig. 2 Effects of Si and Ca treatments, with or without additional N, on the consumption [in mg (leaf fresh weight) g^{-1} slug biomass per 48 h] of wheat leaves by *D. reticulatum* in a **choice** setting ($n = 9$, means + standard error)

Choice feeding in relation to foliar Si concentrations

In the multiple-choice feeding situation with manipulated Si levels, the difference in the proportional consumption of offered wheat leaves with different Si concentrations was statistically highly significant (Hotelling's $T^2 = 160.51$, $F_{5,13} = 24.55$, $P < 0.001$). *D. reticulatum* consumed about 25 mg g^{-1} in 24 h from the control and the lowest Si treatment leaves, about half of that figure from leaves with intermediate Si levels, and just 4 mg g^{-1} from leaves with the highest Si level (Fig. 4). Expressed as proportional consumption of the slugs' total consumption, only wheat leaves containing less than 10 g Si kg^{-1} dry weight (control and the lowest Si treatment with 0.38 g $Na_2O_3Si{\cdot}9H_2O$ l^{-1}) were consumed preferentially (0.30 and 0.26 of total), whereas consumption of leaves containing more than 10 g Si kg^{-1} accounted for between 0.14 and 0.05 of total. Slug-free controls were not included in this experiment.

Discussion

All potential crop protection strategies against slugs are deserving further research. The knowledge gap addressed in the present work was the effect of Si and Ca levels in wheat on slug feeding. Overall, these preliminary experiments under controlled conditions yielded positive results for Si. Boosted foliar Si concentrations reduced wheat leaf consumption by *D. reticulatum* significantly (by 74 %) compared to an untreated control in a no-choice setting; similar trends, but higher variability, were observed in choice settings. These findings extend the results obtained on rice leaves by Wadham and Wynn Parry (1981). Furthermore, the present research has, for the first time,

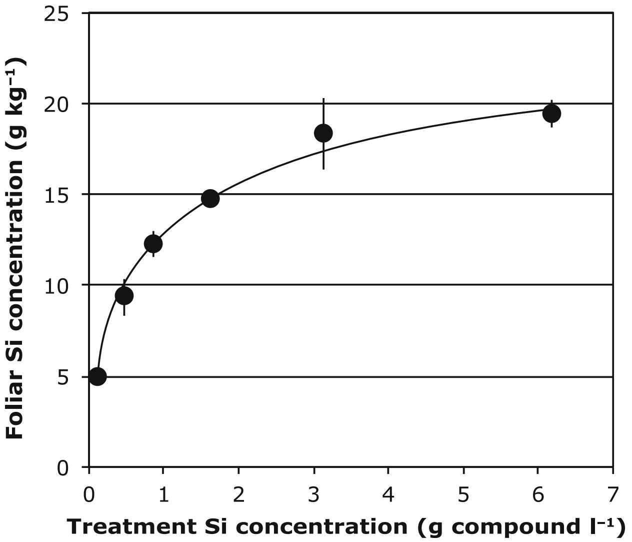

Fig. 3 Effect of nominal Si concentration of treatment solutions (Si_s, in g [$Na_2O_3Si \cdot 9H_2O$] l^{-1}) on the measured Si concentration of wheat seedling leaves (Si_w, in g Si kg^{-1} dry weight). Si_s data are plotted as +0.1 to fit the curve shown: $Si_w = 3.708*\ln(Si_s) + 13.035$ ($r = 0.954$, $F = 151.0$, $P < 0.001$, $n = 3$ for each concentration)

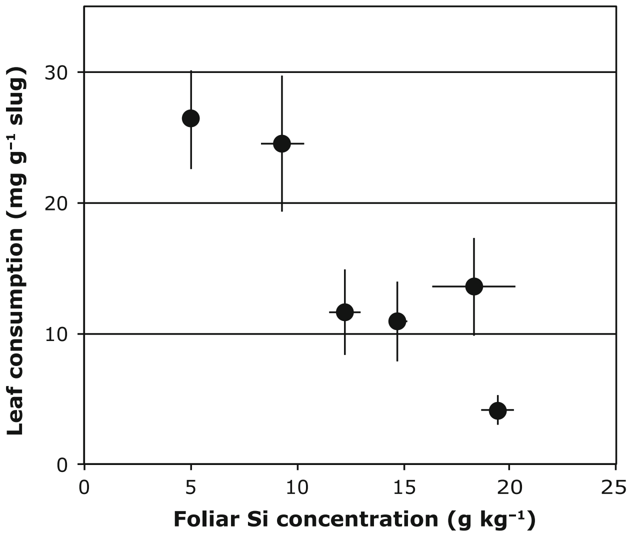

Fig. 4 Relationship between measured Si concentration of wheat seedling leaves (in g Si kg^{-1} dry weight) and leaf consumption [in mg (leaf fresh weight) g^{-1} slug biomass per 24 h] by *D. reticulatum* in a choice setting (mean ± standard error, $n = 3$ for Si data, $n = 18$ for consumption data)

experimentally generated a range in Si contents in cereal foliage and tested how different contents affect gastropod herbivory.

The boosted Si concentrations achieved here in wheat seedlings (from ≤ 0.5 % Si in controls to almost 2 % in Si treatments) were comparable to those reported from other experiments. For instance, Gocke et al. (2013) reported maximum Si concentrations of about 2–2.5 % in wheat seedlings that had been grown on various artificial substrates for 7 to 28 days. Garbuzov et al. (2011) reported somewhat higher Si concentrations of about 2.5–3.5 % in 6-month old *Poa* and *Lolium* species fed high-concentrate sodium silicate solutions. Wadham and Wynn Parry (1981) did not measure Si in their rice-feeding experiment, but data presented here (Fig. 4) suggest that Si concentrations as low as 1 % leaf dry weight may be effective at reducing grazing by slugs.

High foliar Si contents in grasses creates an abrasiveness that can contribute to mandible wear in chewing insects (Massey and Hartley 2009; Reynolds et al. 2009). It may be that this ‘abrasiveness’ has a similar effect on the gastropod radula, unmineralized chitinous teeth of which can wear down, but the radula is being replaced constantly (South 1992). High Si contents can also affect the digestive system in mammals (Cotterill et al. 2007), and it may be that Si particles known as phytoliths deposited in plant cell walls (Guntzer et al. 2012) exert similar effects on gastropod intestines. Wadham and Wynn Parry’s (1981) results were generally ascribed to mechanical deterrence or increase in leaf hardness (South 1992; Speiser 2001). However, exact mechanisms in which Si may interfere with feeding and digestion in slugs are not known and thus require further research.

Two other nutrients that potentially affect slug feeding were tested here, Ca and N. First, calcium oxalate provides defence against chewing insects in many plant taxa (Franceschi and Nakata 2005; Park et al. 2009), and it can accumulate in several tropical grass species (Rahman and Kawamura 2011). However, providing soluble Ca to wheat seedlings in the present experiments did not have a significant effect on slug consumption (it marginally increased no-choice consumption, but foliar Ca contents were not measured to inform a detailed interpretation). Second, foliar N concentrations are likely to control gastropod food choices because N is generally seen as a limiting nutrient (South 1992; Speiser 2001). The mineral N fertiliser treatment did probably not have significant effects on feeding by *D. reticulatum* in the present experiments because leaf N concentrations in wheat seedlings grown in commercial compost without additional N (5.2–5.9 %) were at the higher end typical for cereal seedlings (Bergmann 1992).

While the form of Si used in experiments (sodium metasilicate) is very effective, different, more economical Si sources are required for agricultural settings. Potential sources include various Si-rich crop residues (e.g. rice) and industrial byproducts (e.g. slag) (Reynolds et al. 2009; Snyder et al. 2006); their usefulness for conferring Si-based protection of crops against gastropod pests needs to be researched. Indeed, it has been argued recently

(Vandevenne et al. 2012) that the high level of Si export from agricultural ecosystems worldwide may create a global depletion of Si stocks in such systems and hence a potential loss of Si functions, including natural protection of crops against herbivorous pests.

Whilst the present work focused on a pest slug species, the findings reinforce the need to quantify Si effects in mollusc–plant interaction. For instance, Allan and Crawley (2011) showed in exclusion experiments on English grassland that molluscs can act as drivers of plant community composition. Working on Californian grasslands, Motheral and Orrock (2010) surmised that significant differences in feeding by snails (*Helix aspersa*) on different grass species reflect factors, such as Si content, affecting palatability. Similarly, Barlow et al. (2013) discussed Si as a potential factor determining seedling acceptability to *D. reticulatum* in the context of seedling recruitment in grassland restoration plant communities. In the light of present findings, further research into the role of Si in the feeding ecology of terrestrial gastropods is warranted.

In conclusion, these preliminary laboratory experiments suggest that boosted foliar Si concentrations in wheat seedlings can reduce slug consumption and that foliar Si concentrations can be manipulated through application of soluble Si sources. This approach has potential as a novel tool in crop protection against pest slugs and snails. Among the research questions that need to be addressed to develop this tool are the mechanisms by which Si interferes with slug feeding, the foliar Si concentrations that elicit significant feeding reduction under different environmental conditions, and the usefulness of Si-rich sources for agricultural settings in terms of economic viability and environmental acceptability.

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