Silicon accumulation in maize negatively impacts the feeding and life history traits of *Spodoptera exigua* Hübner

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Abstract:

Silicon (Si) accumulation in plant tissues helps alleviate abiotic and biotic stresses, including infestation by insect pests. Here, we tested the hypothesis that Si concentration in maize leaves negatively impacts *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae) with respect to: (i) feeding preferences; (ii) leaf digestion; and (iii) life history traits. We produced three groups of maize plants cultivated in a hydroponic system that had contrasting Si concentrations in their tissues (i.e., 0.21 ± 0.03, 4.45 ± 0.50 and 8.46 ± 0.61 g Si Kg^{-1} DW). In choice assays, fifth instars preferentially consumed leaves containing lower Si concentrations. In no choice-assays, we found that the approximate digestibility (AD) of larvae feeding on Si-enriched leaves was not affected. However, these larvae exhibited a 32% reduction in relative growth rates. Higher Si concentration in maize leaves extended larval development by three days; from 18.07 ± 0.29 when feeding on Si- diet to 21.39 ± 0.21 days on the Si++ enriched diet. Silicon also reduced larval survival by 18% and pupal weight by 20%. Our results confirm that Si supplementation in soil enhances the ability of plants to resist infestation with chewing insects, and should be considered as a viable option in the existing range of sustainable management practices.

Keywords: beet armyworm, *Zea mays*, silicon, herbivory, plant resistance, feeding preference, Noctuidae

Introduction

Silicon (Si) is among the most abundant elements in terrestrial environments. Plant tissues are no exception, as they contain up to 10% Si, depending on species accumulation ability (Epstein, 1994; Richmond & Sussman, 2003; Hodson *et al.*, 2005). While not considered essential for plant development, Si has been extensively studied for its action on plant growth, yield and quality (Etesami & Jeong, 2018; Guo-chao *et al.*, 2018). In addition, recent reports document the importance of Si uptake and accumulation on the ability of plants to alleviate abiotic and biotic stresses, including infestation by pests and infection by pathogens (Ma, 2004; Liang *et al.*, 2015; Reynolds *et al.*, 2016; Alhousari & Greger, 2018; de Tombeur *et al.*, 2020).

More precisely, Si increases the resistance of plants against insect herbivory via several mechanisms (Kvedaras *et al.*, 2007; Reynolds *et al.*, 2009). For instance, Si accumulates as amorphous hydrated silica (SiO_2. nH_2O), increasing the abrasiveness and hardness of plant tissue. Subsequently, it damages the mandibles and other oral parts of insects, as well as reducing the digestibility, palatability, and overall consumption of plants (Jeer *et al.*, 2017). Higher Si concentrations allow plants to develop silica-rich defensive structures, including trichomes or prickle cells (Andama *et al.*, 2020; Hall *et al.*, 2020). Si also impacts the nutritional quality of plants (Frew *et al.*, 2019). The biochemical responses of plants against insect infestation might also be promoted by Si (Rahman *et al.*, 2015). Plants characterized by high Si accumulation exhibit higher expressions of genes encoding for defensive enzymes, resulting in altered levels of defensive compounds (Gomes *et al.*, 2005; Rémus-Borel *et al.*, 2005; Yang *et al.*, 2017).

While integrated pest management strategies are emerging as a response to stricter regulations on insecticides, Si supplementation represents a possible alternative measure to limit damage from insect pests in several agricultural crops (Bakhat *et al.*, 2018; Leroy *et al.*, 2019; de Tombeur *et al.*, 2021). Evidence is accumulating on the beneficial role of Si supplements in various plant-pest associations. For instance, significant damage reduction by a stemborer (*Chilo suppresalis* Walker) and a leaf folder (*Cnaphalocris medinalis* Guenée) was observed in fields containing rice under Si amendment (Hou & Han, 2010; Han *et al.*, 2015). In field-grown sugarcane, Si treatment significantly reduced the proportion of stalks bored by *Eldana saccharina* Walker (Keeping *et al.*, 2013). The use of Si in controlling *Spodoptera* sp. populations has also received noticeable research interest. However, studies have mainly focused on *S. frugiperda* and *S. exempta* (to a lesser extent). Si accumulation in maize and cotton plants adversely affects the survival of *S. frugiperda* larvae *(*Goussain *et al.* 2002; Silva *et al.,* 2014). Si also affects the life history traits of *S. frugiperda*, including larval weight, adult longevity, and fertility (Nascimento *et al.,* 2014; Alvarenga *et al.,* 2017).

Here, we tested the hypothesis that Si concentration in maize leaves negatively impacts *Spodoptera exigua* Hübner with respect to: (i) feeding preferences; (ii) leaf digestion; and (iii) life history traits. We cultivated maize plants in a hydroponic system to produce three groups with different Si concentrations. The impact of Si in plant tissue on the ability of a plant to alleviate *S. exigua* Hübner (Lepidoptera: Noctuidae) damage has not been previously studied, despite its worldwide economic pest status (Zheng *et al*., 2011). Based on studies performed on other armyworms (i.e. *S. frugiperda* and *S. exempta*) (Massey & Hartley, 2006; Alvarenga *et al*., 2017), we hypothesized that higher Si assimilation in maize tissue would reduce the survival of pupae and larvae. We also expected other life history traits (including larval weight and pupal weight) to be reduced on plants with higher concentrations of Si. By demonstrating the positive impact of Si supplementation on the ability of maize plants to combat *S. exigua* infestations would expand the range of available options for sustainable control management.

Material and methods

Plant material and hydroponic system – Corn plants (*Zea mays* L. var Delprim) were used in all experiments (Delley Seeds and Plants, Delley, Switzerland). Seeds were germinated on paper towels moistened with distilled water in Petri dishes for three days under dark conditions at 23 °C. Seedlings were transplanted to rockwool substrate, inside a 20-litre plastic bucket containing water, and placed in a temperate chamber set at: 23 ± 2 °C (day), 19 ± 2 °C (night), 55-70% relative humidity (RH), and 300 $\mu mol.m^{-2}.s^{-1}$ light intensity. After four days, water was replaced by a commercial nutrient solution (HY-PRO© A&B, Bladel, Netherlands) [46.29 $mg.l^{-1}$ N; 23,94 $mg.l^{-1}$ P; 227.81 $mg.l^{-1}$ K; 115.12 $mg.l^{-1}$ Ca; 0.09 $mg.l^{-1}$ Cu; 38.79 $mg.l^{-1}$ Mg; 1.48 $mg.l^{-1}$ Fe; 0.15 $mg.l^{-1}$ Mn; 0.13 $mg.l^{-1}$ Zn; 3.71 $mg.l^{-1}$ Na]. Continuous aeration was maintained in the plastic bucket using an air pump. The seedlings were grown in quarter strength nutrient (diluted 4x) solution for two days, with the solution being gradually raised to full strength over one week to avoid osmotic shock. The nutrient solution was renewed every three days. The pH of the medium was adjusted to 5.5 ± 0.5 by adding 0.5 M $MgSO_4$. This addition also corrected the Mg/K ratio in the nutrient solution and prevented Mg deficiency in maize plants. One week after being cultivated in this nutrient solution, all plants were separated to one of the three Si concentrations: (a) control solution without Si addition, named Si- [0.05 mM Si]; (b) medium level of Si, named Si+ [0.6 mM Si]; (c) a highly-enriched solution, named Si++ [2.0 mM Si]. Si was supplied as monosilicic acid (H_4SiO_4) in the nutrient solution. The concentration of the Si+ solution was chosen according to the average concentration of Si found in soil (Epstein, 1994). The concentration of the Si++ solution was set according to the limit of saturation of silicic acid (> 2mM), at which point it precipitates as amorphous silica (Exley, 2015). The monosilicic acid solution was freshly prepared by dissolving sodium metasilicate in demineralized water, and passing the solution through cation-exchange resin (Amberlite© IR-120) (Cornelis *et al.*, 2010).

Insect rearing – Beet armyworm *S. exigua* eggs were purchased from Entocare Biological Control (Wageningen, Netherlands). After three days of incubation at 24 °C, first instars were transferred to an artificial diet (General purpose Lepidoptera, Frontier Scientific Services Agriculture, Newark, USA). The insects were reared at 24 ± 2 °C and 40–50% relative humidity, under a 18:6 (L:D) photoperiod.

Foliar Si content – Foliar Si content was determined on maize plants that were grown for 30 to 35 days in the hydroponic system (17-18 BBCH growth stage). All leaves were collected from one plant, dried at 50 °C for 72 h, ground in a plant shredder, and left for 24 h at 450 °C for calcination. One hundred milligrams of ash was melted at 1000 °C for 5 min in a graphite crucible containing 0.4 g Li-tetraborate and 1.6 g Li-metaborate (Chao & Sanzolone, 1992). The fusion bead was then dissolved in 10% HNO_3 before quantifying Si concentrations by ICP-OES. Five quantifications were performed per Si treatment, using different plants.

Effect of Si accumulation on the feeding preference of S. exigua – We aimed to evaluate the feeding preferences of *S. exigua* larvae in the presence of a piece of three maize leaves of contrasting Si concentrations. One entire maize leaf (5^{th} and 6^{th} leaf) was collected from each group of plants (Si-, Si+, Si++) using a pair of scissors. All three leaves were washed and cut in 5x3 cm pieces. One piece of each leaf was placed equidistantly in a glass Petri dish (20 cm diameter) containing a 1% agar-water layer. One caterpillar (third or fifth instar) was deposited in the centre of the Petri dish and the arena was sealed with PVC film. The assay was repeated 54 and 50 times, for third and fifth instars, respectively. All Petri dishes were placed in a dark room to prevent the effect of phototropism. Leaf area was recorded before caterpillar infestation after 48 h using ImageJ Software (Rasband 1997-2015). The consumed leaf area was calculated by subtraction (Nascimento et al. 2017). For most replicates, in each treatment, the piece of leaf was not entirely consumed. The replicate was removed if such case arose. The bioassay was conducted at 23 °C and 50% RH.

Effect of Si accumulation on the consumption and digestion of leaves by S. exigua – Fifth instars were removed from the artificial diet and starved for 24 h. They were then weighed before being placed in separate Petri dishes (9 cm diameter) and offered a piece of maize leaf (5x3 cm), like those used in the previous experiment. Larvae were allowed to feed for 72 h, and were then starved again for 24 h to allow the faeces to be evacuated, before being weighed again. All frass (excrement) was collected, dried and weighed. Leaves were renewed every day, and the remaining leaf material was dried at 50 °C and weighed. Relative growth rate (RGR) was calculated as mass gained (mg)/initial mass (mg) * time (days), over the three days of the experiment (Hall et al. 2020). We also evaluated Approximate digestibility (AD) as the weight of food ingested (mg dry mass) – weight of faeces (mg dry mass) / weight of food ingested (mg dry mass) * 100 (Massey & Hartley, 2009).

Effect of Si accumulation on the life history traits of S. exigua – Neonates were placed in separate Petri dishes (9 cm diameter) filled with a 1 % agar-water layer, and were fed *ad libitum* with 5x3 cm pieces of maize leaves cut from Si-, Si+ and Si++ plants. Insects were housed at 23 °C and 50 % RH. Leaves were changed every two days. Various life history traits were collected until adult emergence, including larval mortality, stage duration, larval size, larval weight, pupal mortality, pupal stage duration, pupal weight and sex-ratio of the pupae.

Statistical analyses – R studio software (v 1.2.1335) was used for all statistical analyses (R core team 2019). Data on Si content had to be square root transformed. Data on feeding preference with third and fifth instars, larval stage duration and pupal weight were transformed using (rn)transform function (GenAbel package). Data on RGR and the growth in size of larvae were not transformed. Data were transformed to obtain a normal distribution. Statistical analyses associated with the growth in size of larvae was carried out by comparing the slope of each line associated with the growth of each individual over time. Data were subjected to analysis of variance (ANOVA) and Tukey's post-hoc test ($\alpha = 0.05$). Data on larval survival, pupal survival and sex-ratio were subjected to generalised linear models (GLM), assuming a binomial distribution. We could not transform the data on the duration of the pupal stage and approximate digestibility (AD) to meet the requirements of the analysis of variance. Therefore, a Kruskal-Wallis test was used on these parameters.

Results

Foliar Si content – The Si content of leaves was dependent on the Si concentration of the nutrient solution ($F_{2,12}$ = 190.8; $P < 0.001$). We recorded the following mean silicon concentrations: 0.213 ± 0.030 g Kg^{-1}DW (Si-), 4.451 ± 0.498 g Kg^{-1}DW (Si+) and 8.459 ± 0.611 g Kg^{-1}DW (Si++) (mean ± SD). The means of all three concentrations significantly differing from each other (Tukey Post-Hoc test, $P < 0.05$).

Effect of Si accumulation on the feeding preferences of S. exigua – In choice assays, fifth instars preferentially consumed leaves with lower Si concentrations ($F_{2,159}$ = 11.23; $P < 0.001$) (Fig. 1 B). Instars consumed 33% more Si- leaf material compared to Si++ material. This difference was not observed for third instars ($F_{2,155}$ = 0.174; P = 0.841) (Fig. 1 A).

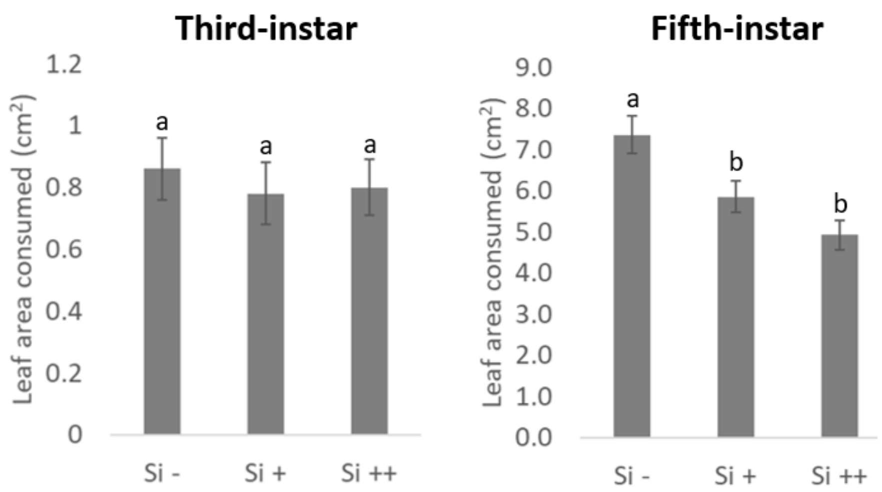

Fig. 1. Leaf area consumed by *S. exigua* third instar larvae (n=54) and fifth instar larvae (n = 50) in choice assays. Values are means ± SD. Different letters on bars indicate significant differences by Tukey's test ($p \leq 0.05$).

Effect of Si accumulation on the consumption and digestion of leaves by S. exigua – In the no-choice assays, the relative growth rate of instars was negatively impacted ($F_{2,89} = 10.14$; $P < 0.001$) (Fig. 2) Concerning food-utilization measurement, we found no significant difference between each Si treatment ($\chi^2 = 0.671$; df = 2, $P = 0.71$).

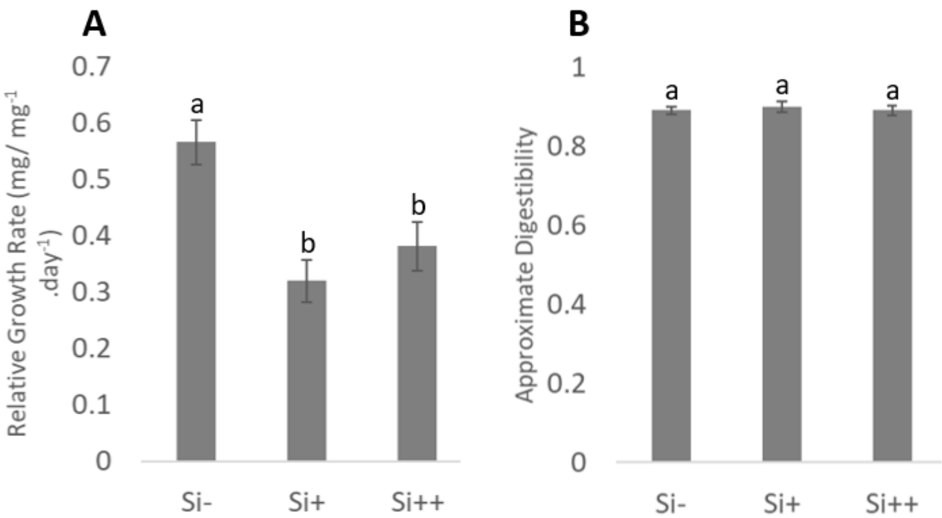

Fig. 2. Relative growth rate (A), Approximate digestibility (B) by S. exigua fifth instars (n = 30 per treatments). Values are means ± SD. Different letters on bars indicate no difference by Tukey's test ($p<0.05$).

Effect of Si accumulation on the life history traits of S. exigua – Si concentration in maize leaves impacted some of the recorded life history traits of *S. exigua*. We found that elevated Si concentrations extended the duration of larval development ($F_{2,65} = 34.84$; $P < 0.001$), leading to lighter pupae ($F_{2,65} = 8.51$; $P < 0.001$) (Tab. 1). While 58% of larvae survived under Si-, just 42% and 40% became pupae under Si+ and Si++ concentrations, respectively ($F_{2,147} = 2.62$; P

= 0.073). Si concentration in maize leaves significantly impacted the development of S. *exigua* larvae ($F_{2,74}$ = 12.74; P < 0.001) (Fig. 3). Differences were highlighted between Si- and Si+ treatments (P < 0.0001) and between Si- and Si++ treatments (P < 0.0001). The development of larvae exposed to Si+ and Si++ was not significantly different (P=0.743). We found that Si concentration did not impact the duration of the pupal stage (χ^2 = 0.216; df = 2, P = 0.89), nor the survival of pupae (F_2 = 0.093; P = 0.911), nor sex-ratio (F_2 = 0.415; P = 0.661).

Table 1. Impact of Si concentration in maize leaves on *S. exigua* life history traits. Different letters on means and percentages indicate significant differences

Si treatments	Larval stage duration (days)	Larval survival (%)	Pupal weight (g)	Pupal stage duration (days)	Pupal survival (%)	Sex ratio (M/F)
Si-	18.07 ± 0.29^{a}	58^{a}	75.54 ± 1.62^{a}	9.41 ± 0.14^{a}	76^{a}	0.94^{a}
Si+	20.67 ± 0.27^{b}	42^{a}	68.01 ± 3.35^{ab}	9.42 ± 0.21^{a}	81^{a}	0.75^{a}
Si++	21.39 ± 0.21^{b}	40^{a}	60.89 ± 2.69^{b}	9.57 ± 0.27^{a}	78^{a}	0.64^{a}

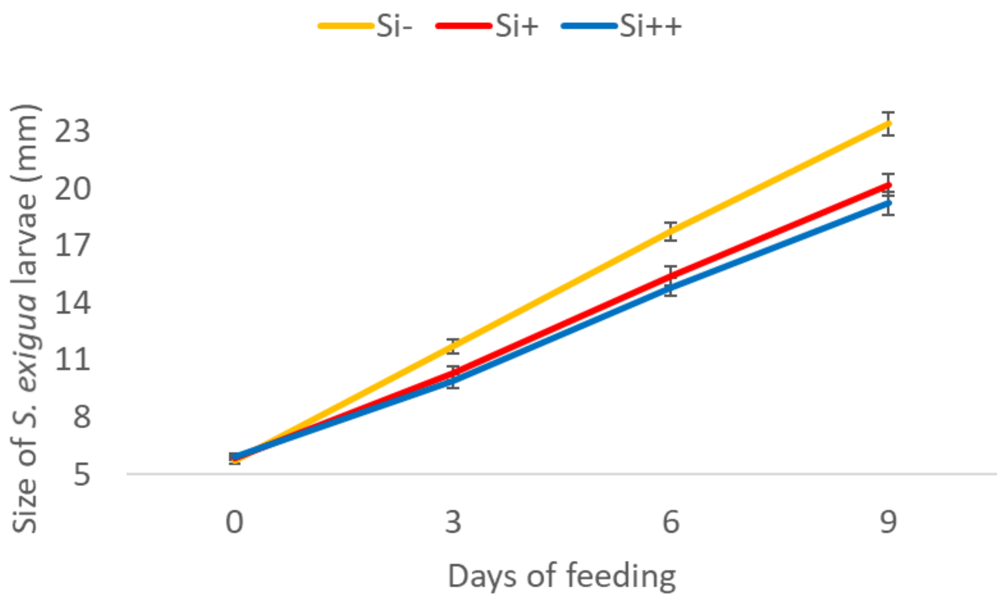

Fig. 3. *S. exigua* larvae size growth over the third instar (day 0 corresponds to the start of the third instar)

Discussion

Previous studies have shown that Si enhances the ability of plants to resist insect pests (Luyckx *et al*. 2017; Islam *et al.*, 2020; Johnson *et al*., 2020). In this study, we demonstrated that Si accumulation in maize plants negatively impacts some life history traits of *S. exigua*. High Si concentrations extended the duration of the larval stage and reduced pupal weight. We also found an 18% increase in larval mortality; however, this result was not supported statistically.

Pupal weight declined following exposure to plants containing Si, supporting a previous study on *S. exempta* (Massey & Hartley 2006). However, contrasting results were obtained for *S. frugiperda*. Some studies recorded mortality in *S. frugiperda* caterpillars fed with silicon-enriched diets, while other studies recorded no impact on life history traits (Silva *et al.*, 2014; Alvarenga *et al.*, 2017). Nascimento *et al.* (2017) found that Si addition to rice plants only reduced the weight of larvae and pupae. Nagaratna *et al.* (2021) observed that biological parameters of *S. frugiperda* such as larval weight and larval survival were negatively impacted by Si application. Si deposition as phytoliths within plant tissue is likely one of the main factors explaining the increased mortality of caterpillars. Phytoliths reduce the digestibility and palatability of plants by increasing rigidity and abrasiveness (Strömberg *et al.*, 2016). The other possible mechanism is linked to the biochemical response of plants against pests. There is increasing evidence that Si treatment alters the accumulation of various defensive compounds, including phytoalexins, phenolics and chlorogenic acid (Rémus-Borel *et al.*, 2005; Rahman *et al.*, 2015;Frew *et al.*, 2016; Wang *et al.*, 2021; de Tombeur *et al.*, 2021).

Unlike third instars, fifth instars preferentially consume maize leaves with low Si concentrations. Insects consuming phytolith-rich diets experience wear on the mandibles (Massey & Hartley, 2009), which could explain the selection of non-enriched leaves. Again, this conclusion is only partially supported by the published literature on *Spodoptera* (Massey *et al.*, 2006; Nascimento *et al.*, 2014). In our study, we regularly checked the content of the Petri dish, and we observed that all fifth instars tested all three pieces of leaves before preferentially feeding on the less Si-concentrated one. Our data suggest that Si acts as a feeding deterrent, and that fifth larvae are able to perceive this deterrent effect when feeding. However, this effect was not observed in third instars. Given their smaller size, it is possible that the quantity of leaf consumed was not sufficient to allow us to compare diets (third instars consumed 10 times less leaf mass than fifth instars).

Silica negatively impacts the digestibility of leaves by *S. exempta*, as demonstrated previously on various grass species (*Deschampsia caespitosa* L.; *Festuca ovina* L. and *Lolium perenne* L.) by Massey & Hartley (2009). The authors concluded that silica has a progressive impact with longer exposure time, indicating that herbivores cannot adapt to silica defences, and that they do not develop tolerance for silica with age. We also observed a reduction in the relative growth rate of *S. exigua* that fed, even for a short time, on high Si-enriched maize leaves. Whether this effect increases with exposure duration remains to be tested for *S. exigua*.

The effect of Si-accumulation in plant leaves on the life history traits of *Spodoptera* sp. in our study supported some existing studies and contrasted with others. Supporting previous studies, we found that several traits were not affected, including pupal stage duration, pupal survival, sex-ratio and approximate digestibility (AD). Thus, Si-stimulated defence mechanisms are not as efficient against *Spodoptera* spp. as other lepidopterans (Keeping & Meyer, 2013; Johnson *et al.*, 2020). To describe the underlying mechanisms, future studies should evaluate the levels of defensive compounds, focusing on the interplay between jasmonic acid (JA) (a phytohormone that regulates chemical defences against chewing insects) and Si accumulation (Johnson *et al.*, 2021; Waterman *et al*., 2021). Specifically, DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) has antifeedant effect on *S. exigua* (Rostás, 2007). As the feeding preferences of S. *exigua* are impacted by Si accumulation in maize leaves, future studies should investigate the impact of Si concentrations in leaves on the level of DIMBOA content.

Si concentrations of up to 0.85% were reached in our assays. These concentrations were similar to those used in previous studies (e.g. Johnson *et al.*, 2020), which also reported Si-stimulated herbivore resistance, except for in non-Poaceae species. The Si concentrations reached in the maize leaves in the current study were comparatively low to that found in other varieties of maize, with ranges of 1% to 2.5% (Ma *et al.*, 2001; Liang *et al.*, 2015). Thus, even higher Si concentrations could be added to maize, which would potentially enhance our results.

Our results confirmed that Si supplementation to the soil increases absorption by plants and the subsequent ability of plants to resist infestation with chewing insects. This approach should be considered among the diversity of available options of sustainable management practices for crop plants. However, future studies must focus on elucidating the mechanisms of action of Si on chewing insects. Also, field assays should be formulated to evaluate the beneficial role of Si through soil fertilization or by optimizing the Si biological cycle under outdoor conditions.

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Figures