





Increase in foliar silicon content reduces defoliation by *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) in maize

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ABSTRACT: The effect of silicon (Si) on fitness and leaf consumption of the fall armyworm (FAW), *Spodoptera frugiperda* (Smith), has been observed in the laboratory, but the effects of Si on damage or defoliation reduction have not yet been determined under field conditions. Here, we evaluated the effects of amendment of soil with Si on defoliation by FAW and crop yield in maize. Two field experiments were carried out, with four doses of Si and a control (no Si amendment). Experiment #1 evaluated 150, 300, 450, and 600 kg of total Si·ha⁻¹, with natural or manual infestation with FAW eggs, while Experiment #2 tested 600, 800, 1,000 and 1,200 kg of total Si·ha⁻¹, with natural or manual infestation with FAW larvae. Defoliation reduction was observed with Si increasing in both Experiments #1 and #2. However, reduction was not observed in all evaluations, and it was dependent of infestation (natural and manual) and the time since manual infestation. Reduction in defoliation began at 600 kg Si·ha⁻¹. In contrast, plant Si content increased linearly with increasing soil Si application. No effect of Si application was observed on maize kernel yield. The increase in leaf Si content reduced FAW defoliation, but it did not affect maize yield from 600 to 1,200 kg·ha⁻¹ of Si. Amendment of soil with Si can be used as a strategy to optimize integrated pest management of FAW in maize.

Key words: fall armyworm, induced resistance, silicate fertilization.

INTRODUCTION

Silicon (Si) is absorbed by plants as silicic acid through transmembrane channel proteins and it is polymerized in plant tissue as inorganic amorphous oxide phytoliths (SiO₂) (Deshmukh and Belanger 2016; Imtiaz et al. 2016; Bakhat et al. 2018). The resistance induced in plants to pathogens and insects is among the major benefits of Si amendments. The enhanced plant resistance results from the deposition of SiO₂ in plant tissues, which forms a mechanical barrier and increases vegetable tissue stiffness, the production of Si-induced defensive chemicals compounds, such as defense enzymes and substances that lower tissue digestibility (Hartley et al. 2015; Reynolds et al. 2016; Luyckx et al. 2017; Hall et al. 2020), and enhanced attraction and improvement of the fitness of natural enemies (Kvedaras et al. 2010; Liu et al. 2017; Oliveira et al. 2020; Sampaio et al. 2020). Silicon supplementation thus provides an alternative method of control for insect populations, one that is compatible with other pest management practices in several crops, mostly in the Poaceae (Liang et al. 2015).

Even though Si is the second most abundant element in the earth's crust (27.7%) (Bakhat et al. 2018) and represents up to 45% of soil composition (Currie and Perry 2007), Si levels available to plants are low (Liang et al. 2007), mainly because Si is most often found in crystalline form in insoluble minerals. Some crops can respond to Si amendments, particularly in soils with low availability of this element (< 8 mg Si per kg soil) (Korndörfer et al. 1999). Agriculture fertilization with Si is

based on the application of soluble forms, such as calcium, magnesium, or potassium silicates. These silicates have a range of origins, which influences different aspects of various amendments' performance, especially in relation to supplying Si to plants. Therefore, more information is needed to clarify if silicate application adds sufficient Si to the soil to promote plant resistance to pests or pathogens without jeopardizing crop yield (Pereira et al. 2004).

The fall armyworm (FAW), *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae), is a major economic pest of maize (*Zea mays* L.), cotton, sorghum, and a variety of agricultural grasses and vegetable crops throughout the Western Hemisphere (Nagoshi et al. 2015) and, recently, in Africa (Goergen et al. 2016) and Asia (Sharanabasappa et al. 2018; Guo et al. 2019). The FAW feeds on more than three hundred plant species (Montezano et al. 2018), including those used as cover crops in no-tillage systems, such as species of *Urochloa* (Dias et al. 2016), increasing FAW infestation levels in intensive agricultural systems in which two or three crops are harvested each year.

Planting of *Bacillus thuringiensis* (Bt) maize has been the major strategy adopted for FAW management (Waquil et al. 2016); however, there have been reports of resistance to Bt proteins (Farias et al. 2014; Omoto et al. 2016). The aggressiveness of FAW and some control failures in Bt maize have created a need for more complex management strategies for this pest (Fatoretto et al. 2017) and increased the importance of different control methods, such as resistance induced by Si supplementation.

In this context, laboratory and greenhouse studies have shown a fitness reduction in FAW fed on Si treated plants (Goussain et al. 2002; Neri et al. 2005; González et al. 2015; Alvarenga et al. 2017; Nascimento et al. 2018). However, no evidence is available so far to show that the FAW resistance induced by Si fertilization occurs in field-grown maize, despite its being observed under laboratory conditions (Neri et al. 2009; Antunes et al. 2010).

To fill this knowledge gap, we evaluated the effect of soil Si fertilization on defoliation by FAW and maize yield under field conditions, to determine which calcium and magnesium silicate doses supply sufficient Si to the soil to reduce defoliation by FAW larvae without reducing crop yield.

MATERIAL AND METHODS

Experiment location

Two field experiments (Experiment #1 and Experiment #2) were carried out to evaluate the effect of Si on maize defoliation by FAW and on yield at the Capim Branco Experimental Farm, of the Universidade Federal de Uberlândia, Uberlândia, Minas Gerais state (18°52'55.66'S and 48°20'28.21'W), Brazil, at 805 meters above sea level. The climate in the region is classified as Aw, by Köppen's method, with tropical hot and humid summer and dry winter, average annual temperature of 21.5°C and 1,479 mm average annual rainfall (Rolim et al. 2007).

Soil character, preparation, and fertilization

The soil was classified as Rhodic Acrudox soil (Soil Survey Staff 1999), with a clay texture (50% clay), pH 5.3 in water, and low Si content (5.5 mg·kg⁻¹ soil), which favors responses to silicate fertilization (Korndörfer et al. 1999).

Soil was prepared by plowing once and harrowing twice. Si was manually applied, for both experiments, 30 days before sowing, using calcium and magnesium silicate, in the form of the commercial product Agrosilício Plus[®] (10.5% total Si, 4.8% soluble Si, 35% CaO, and 10% MgO). Dolomitic lime Ercal[®] (37-38% CaO, and 8-10% MgO) was also applied, based on the silicate dose used, so that both experimental units received the same amount of calcium and magnesium. Thus, the total amount of Agrosilício Plus[®] varied from 1,500 to 6,000 kg·ha⁻¹ in Experiment #1 (low dose Si application: 0, 150, 300, 450 and 600 kg total Si·ha⁻¹) and from 6,000 to 12,000 kg·ha⁻¹ in Experiment #2 (high dose Si fertilization: 0, 600, 800, 1,000 or 1,200 kg total Si·ha⁻¹), and the total amount of dolomitic lime used in Experiment #1 was 6,000, 4,500, 3,000, 1,500 and 0 kg·ha⁻¹, respectively for 0, 150, 300, 450 and 600 kg total Si·ha⁻¹, and in Experiment #2 it was 12,000, 6,000, 4,000, 2,000 and 0 kg·ha⁻¹, respectively, for 0, 600, 800, 1,000 or 1,200 kg total Si·ha⁻¹. To ensure uniform delivery of Si in both experiments, either calcium and magnesium silicate or dolomitic lime were incorporated into the soil using hoes and rakes until the Si, or lime was completely mixed into the soil in each experimental unit.

Experimental protocol

Experiment #1 was carried out from December 2016 to April 2017. Experiment #2 was carried out from December 2017 to April 2018. The two experiments were carried out in adjacent areas, 15 m apart. Both experiments used a randomized block design with a 5×2 factorial design (five silicon levels \times with or without manual infestation by FAW), each treatment with four replications. Each experimental unit consisted of six 5-m-long rows, spaced 0.50 m apart, for a total of 15 m². The area used for evaluation was the two central rows, excluding 1 m at each end of the rows, for a total of 3 m².

Maize hybrids DKB 390RR2 and DKB 4600RR2, both resistant to glyphosate, were used in Experiments #1 and #2, respectively. Experiment #1 was sown on December 3, 2016 and Experiment #2 on December 20, 2018. Sowing was done manually at a depth of 3-4 cm, with 23 seeds per row (5 m long). Seven days after emergence, the maize was thinned to 60,000 plants·ha⁻¹, leaving the most vigorous seedlings.

The first fertilization was done at sowing, with 350 kg·ha⁻¹ of fertilizer (NPK at 6-28-16). The second fertilization was done 18 days after sowing (DAS), in the V4 growth stage (four completely developed leaves), with 150 kg·ha⁻¹ of urea + 72 kg·ha⁻¹ of potassium chloride, and the third was with urea at 100 kg·ha⁻¹, 13 days after the second fertilization in the V8 growth stage (eight completely developed leaves).

Weed control was done during the experiment with glyphosate (Roundup® WG, Monsanto, São José dos Campos, SP, Brazil) at 2.5 kg·ha⁻¹, 15 days before sowing and 21 days after maize germination. Leaf diseases were controlled by spraying azoxystrobin + flutriafol (Authority®, FMC Química do Brasil, Campinas, SP, Brazil) at 0.50 L·ha⁻¹. Plots received overhead irrigation in Experiment #2 due to variation in rainfall between years.

Half of all plots (both with or without Si applications) were manually infested with FAW eggs (Experiment #1) or larvae (Experiment #2). In the other half of the plots, no FAW eggs or larvae were added, and chemical pesticides were used against natural infestations of FAW. Both infestation of plants with FAW and application of insecticides were done 30 DAS, when maize was at the V8 growth stage (eight completely developed leaves). For Experiment #1, the whorls of each of the 30 plants in the two central rows of each plot were manually infested with egg masses each containing an average of approximately 500 eggs nearly ready to hatch. For Experiment #2, the FAW larvae were reared on artificial diet until the third instar and then used to infest the plants, adding three larvae per plant. The insect eggs were supplied by Empresa Brasileira de Pesquisa Agropecuária (Embrapa) Milho e Sorgo, from Sete Lagoas, Minas Gerais state. Non-infested plots (with natural infestations of FAW) were sprayed with the insecticide thiamethoxam+lambda-cyhalothrin (Engeo Pleno®, Syngenta, Paulínia, SP, Brazil) at 250 mL·ha⁻¹ to reduced natural FAW infestations. The insecticide was delivered directly into the corn whorls to ensure efficiency and reduce drift.

Damage caused by FAW infestation was evaluated using the visual scale (0-5) proposed by Carvalho (1970)³, in which 0 is no defoliation of the whorl and 5 is complete destruction of the whorl by FAW. This scale was chosen due to its consistency in evaluating defoliation by FAW (Farinelli and Fornasieri Filho 2006; Mendes et al. 2008). Defoliation evaluation was done on 19 plants per plot in Experiment #1 and 20 plants per plot in Experiment #2. A previous evaluation (pre-trial assessment) was done to assess natural FAW infestation before the standardized infestation at 29 DAS. Subsequently, defoliation by FAW was evaluated five, ten, and 15 days after infestation (DAI), i.e., 35, 40, and 45 DAS, respectively.

Foliar or shoot Si content and crop productivity

In Experiment #1, we assessed the levels of plant Si enrichment as the foliar silicon content. In Experiment #2, plant enrichment with Si was assessed as the shoot Si levels. For Si foliar content analysis (Experiment #1), the first leaf below the maize ear was collected from 10 plants in the evaluation area of each plot eight days after tasseling. The leaves were divided into thirds and the middle third had the midrib removed along with any lesion caused by disease. For shoot Si analysis (Experiment #2), shoots were collected from all plants in the 2-m row of the area used for evaluations in each plot at harvest. Subsequently, the leaf sections or shoots were placed in paper bags and dried at 60-65°C until at constant weight, then ground and taken for analysis of Si content in the Fertilizer Laboratory at the Universidade Federal de Uberlândia, according to Korndörfer et al. (2004).

³ Carvalho, R. L. P. (1970). Danos, flutuação da população, controle e comportamento de *Spodoptera frugiperda* (J. E. Smith, 1797) e susceptibilidade de diferentes cultivares de milho, em condições de campo. PhD Thesis, Piracicaba, ESALQ/USP.

Kernel yield ($\text{kg}\cdot\text{ha}^{-1}$) was estimated by measuring the area of the plots for all experiments (at approximately 140 DAS). All ears were harvested, threshed and weighed, and kernel moisture levels were determined. Kernel weight was then corrected to 13% moisture.

Data analyses

Data from both experiments, i.e., on defoliation levels of whorls per plant at each evaluation data (previous, 5, 10 and 15 DAI), on leaf or shoot Si levels, and on kernel yield, were tested for normality by Shapiro-Wilk test and for homogeneity of variances by Levene's test, both at 5% probability. Two-way analysis of variance (ANOVA) was used for analysis of both experiments, considering FAW infestation (manual and natural), Si doses, and their interactions as independent variables. Defoliation data (Experiment #1) and shoot Si content (Experiment #2) were transformed to either square roots (Experiment #1) or $\arcsin[\sqrt{\times/100}]$ (Experiment #2) to meet the assumption of normality. Regression analysis was done for the effect of Si dose, while the effect of FAW infestation (manual or natural) was compared with F tests. All analyses were performed with 5% probability.

RESULTS

Experiment #1: defoliation at low dose Si application

In Experiment #1, no interaction was observed for the factors dose and FAW infestation in the pre-trial assessment ($F = 0.746$; $df = 4,27$; $P = 0.5689$), nor at five DAI ($F = 1.477$; $df = 4,27$; $P = 0.2368$). Defoliation was not affected by Si dose ($F = 1.286$; $df = 4,27$; $P = 0.3003$) nor by infestation method ($F = 3.322$; $df = 1,27$; $P = 0.0795$) in the pre-trial assessment since this evaluation was done before infestation with FAW. It indicates that natural infestation by FAW was homogeneous among the treatments. However, greater defoliation was observed at 5 DAI in plants manually infested with FAW ($F = 7.636$; $df = 1,27$; $P = 0.0102$) (Table 1). Also, the effect of Si in reducing defoliation was observed at five DAI, in both plots with manual and natural FAW infestations ($F = 3.891$; $df = 4,27$; $P = 0.0127$), and the data were best fit by a quadratic model, showing a trend of reduced defoliation at the Si dose of $600 \text{ kg}\cdot\text{ha}^{-1}$ (Fig. 1).

Table 1. Maize defoliation rates (average \pm SE) under field conditions in Experiment #1 (December 2016 to April 2017), with different silicon doses ($\text{kg}\cdot\text{ha}^{-1}$) applied to the soil, with natural infestation before and after manual infestation with 500 eggs of *Spodoptera frugiperda* per plant, according to the scale of Carvalho (1970), in which 0 is a whorl with no defoliation and 5 is a completely defoliated whorl. Capim Branco Experimental Farm, Uberlândia, Minas Gerais state, Brazil*.

Evaluation	Silicon doses ($\text{kg}\cdot\text{ha}^{-1}$)	Infestation type		Average \pm SE
		Manual	Natural	
Previous	0	2.28 \pm 0.33	2.11 \pm 0.10	2.19 \pm 1.16A
	150	2.53 \pm 0.31	1.91 \pm 0.22	2.22 \pm 0.21A
	300	2.26 \pm 0.27	1.76 \pm 0.41	2.01 \pm 0.24A
	450	2.00 \pm 0.25	1.71 \pm 0.35	1.86 \pm 0.21A
	600	1.68 \pm 0.17	1.83 \pm 0.17	1.77 \pm 0.11A
	Average \pm SE	2.15 \pm 0.13a	1.86 \pm 0.11a	CV = 2.74%
5 DAI	0	1.95 \pm 0.37	1.29 \pm 0.34	--
	150	2.92 \pm 0.34	2.21 \pm 0.49	--
	300	2.22 \pm 0.34	1.32 \pm 0.49	--
	450	2.01 \pm 0.25	1.37 \pm 0.47	--
	600	1.17 \pm 0.27	1.46 \pm 0.17	--
	Average \pm SE	2.06 \pm 0.17a	1.53 \pm 0.18b	CV = 18.32%
10 DAI	0	1.72 \pm 0.25a	0.86 \pm 0.24b	--
	150	2.61 \pm 0.18a	1.92 \pm 0.41a	--
	300	1.95 \pm 0.36a	1.05 \pm 0.37b	--
	450	1.80 \pm 1.17a	1.24 \pm 0.29a	--
	600	0.67 \pm 0.14a	1.20 \pm 0.18a	--
		--	--	CV = 18.25%

continue...

Table 1. Continuation...

Evaluation	Silicon doses (kg·ha ⁻¹)	Infestation type		Average ± SE
		Manual	Natural	
15 DAI	0	1.70 ± 0.25a	0.89 ± 0.30b	--
	150	2.24 ± 0.17a	1.62 ± 0.38a	--
	300	1.70 ± 0.24a	0.71 ± 0.32b	--
	450	1.63 ± 0.24a	1.07 ± 0.21a	--
	600	0.67 ± 0.12a	1.05 ± 0.14a	--
		--	--	CV = 18.72%

*Averages followed by different letters, capital in the column and small case in the rows, differ by the F test at 5% probability; previous: one day before manual infestation; DAI: days after manual infestation; CV: coefficient of variation; SE: standard error.

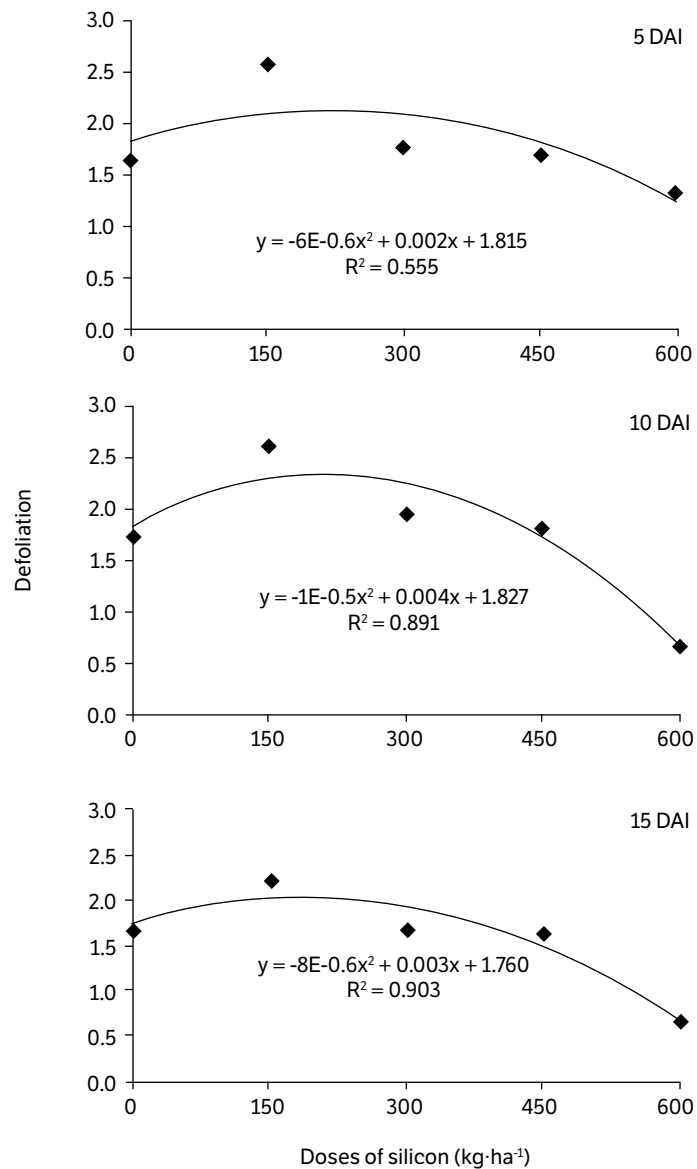


Figure 1. Defoliation ratings of Experiment #1 at five, ten and 15 days after manual infestation (DAI) with *Spodoptera frugiperda* in maize with different silicon doses (kg·ha⁻¹) applied via soil, under field conditions. Uberlândia, Minas Gerais state, Brazil, December 2016-April 2017*.

DAI: days after manual infestation; 5 DAI: average of natural and manual infestations; 10 and 15 DAI: average of manual infestation; *according to the scale of Carvalho (1970), in which 0 is a whorl with no defoliation and 5 is a completely consumed whorl.

A significant interaction was observed for Si dose and infestation method for FAW defoliation at 10 DAI ($F = 3.404$; $df = 4,27$; $P = 0.0223$) and at 15 DAI ($F = 3.427$; $df = 4,27$; $P = 0.0217$). Greater defoliation of manually infested plants was observed in the non-fertilized treatment and at $300 \text{ kg}\cdot\text{ha}^{-1}$, both at ten DAI ($F = 6.678$; $df = 1,27$; $P = 0.0007$) and at 15 DAI ($F = 5.120$; $df = 1,27$; $P = 0.0033$), while at the other Si doses ($150, 450, \text{ or } 600 \text{ kg}\cdot\text{ha}^{-1}$) no differences in the level of defoliation were observed between the FAW-infestation modes (Table 1).

There was no effect of Si on defoliation levels in naturally infested plots at ten DAI ($F = 2.557$; $df = 4,27$; $P = 0.0611$) or 15 DAI ($F = 2.642$; $df = 4,27$; $P = 0.0550$). However, Si reduced FAW defoliation in the manually infested plots at ten DAI ($F = 6.678$; $df = 4,27$; $P = 0.0007$) and at 15 DAI ($F = 5.120$; $df = 4,27$; $P = 0.0033$). Trends in defoliation fit a quadratic model, with observable reductions in defoliation begun at $600 \text{ kg}\cdot\text{ha}^{-1}$ (Fig. 1).

Experiment #2: defoliation at high dose Si application

In Experiment #2, no interaction was observed between Si dose and FAW infestation method in the pre-trial assessment ($F = 0.213$; $df = 4,27$; $P = 0.9288$), nor at the five DAI ($F = 0.343$; $df = 4,27$; $P = 0.8466$) or ten DAI ($F = 1.228$; $df = 4,27$; $P = 0.3223$) evaluations. Also, in the pre-trial assessment, defoliation was not affected by either Si dose ($F = 0.607$; $df = 4,27$; $P = 0.6612$) or infestation method ($F = 0.014$; $df = 1,27$; $P = 0.9057$).

Defoliation was not affected by Si dose at five DAI ($F = 0.402$; $df = 4,27$; $P = 0.8056$) or ten DAI ($F = 1.935$; $df = 4,27$; $P = 0.1333$); however, defoliation was higher in plants infested manually with FAW than in those that were naturally infested, at both five DAI ($F = 149.028$; $df = 1,27$; $P < 0.0001$) and ten DAI ($F = 174.915$; $df = 1,27$; $P < 0.0001$) (Table 2).

Table 2. Maize defoliation rates (average \pm SE) under field conditions in Experiment #2 (December 2017 to April 2018), with different silicon doses ($\text{kg}\cdot\text{ha}^{-1}$) applied to the soil, with natural infestation before and after manual infestation with three larvae of *Spodoptera frugiperda* per plant, according to the scale of Carvalho (1970), in which 0 is a whorl with no defoliation and 5 is a completely defoliated whorl. Capim Branco Experimental Farm, Uberlândia, Minas Gerais state, Brazil*.

Evaluation	Silicon doses ($\text{kg}\cdot\text{ha}^{-1}$)	Infestation type		Average \pm SE
		Manual	Natural	
Previous	0	1.68 \pm 0.19	1.73 \pm 0.10	1.70 \pm 0.10A
	600	1.84 \pm 0.11	1.78 \pm 0.17	1.81 \pm 0.10A
	800	1.63 \pm 0.20	1.73 \pm 0.12	1.68 \pm 0.11A
	1,000	1.90 \pm 0.05	1.80 \pm 0.11	1.85 \pm 0.61A
	1,200	1.71 \pm 0.17	1.78 \pm 0.15	1.74 \pm 0.11A
	Average \pm SE	1.75 \pm 0.07a	1.76 \pm 0.05a	CV = 15.06%
5 DAI	0	2.89 \pm 0.17	1.83 \pm 0.08	2.36 \pm 0.22A
	600	2.99 \pm 0.17	1.84 \pm 0.09	2.41 \pm 0.24A
	800	2.81 \pm 0.10	1.89 \pm 0.08	2.35 \pm 0.19A
	1,000	3.06 \pm 0.12	1.85 \pm 0.06	2.46 \pm 0.24A
	1,200	2.89 \pm 0.27	1.69 \pm 0.12	2.28 \pm 0.27A
	Average \pm SE	2.93 \pm 0.07a	1.82 \pm 0.04b	CV = 12.12%
10 DAI	0	3.53 \pm 0.14	1.89 \pm 0.07	2.71 \pm 0.29A
	600	3.45 \pm 0.15	2.25 \pm 0.14	2.95 \pm 0.29A
	800	3.33 \pm 0.14	2.01 \pm 0.05	2.68 \pm 0.26A
	1,000	3.35 \pm 0.13	1.99 \pm 0.04	2.67 \pm 0.27A
	1,200	3.10 \pm 0.14	1.96 \pm 0.02	2.53 \pm 0.23A
	Average \pm SE	3.35 \pm 0.06a	2.06 \pm 0.03b	CV = 11.42%
15 DAI	0	3.88 \pm 0.11a	2.03 \pm 0.72b	--
	600	2.78 \pm 0.06a	1.66 \pm 0.07b	--
	800	2.00 \pm 0.11a	1.81 \pm 0.09a	--
	1,000	2.19 \pm 0.08a	1.56 \pm 0.12b	--
	1,200	1.84 \pm 0.06a	1.45 \pm 0.18b	--

*Averages followed by different letters, capital in the column and small case in the rows, differ by the F test at 5% probability; previous: one day before manual infestation; DAI: days after manual infestation; CV: coefficient of variation; SE: standard error.

An interaction was observed between Si dose and FAW infestation method at 15 DAI ($F = 21.322$; $df = 4,27$; $P < 0.0001$). An effect of Si of reducing defoliation was observed at 15 DAI, both in manual ($F = 66.145$; $df = 4,27$; $P < 0.0001$) and natural ($F = 4.842$; $df = 4,27$; $P = 0.0044$) FAW infestations ($F = 3.891$; $df = 4,27$; $P = 0.0127$), using a linear and quadratic model for natural and manual infestations, respectively, with a trend of decreased defoliation with increased Si in the soil (Fig. 2). Defoliation was not affected by infestation method at $800 \text{ kg}\cdot\text{ha}^{-1}$ of Si ($F = 1.693$; $df = 1,27$; $P = 0.2042$); however, higher levels of defoliation were observed on plants that were manually infested than on those with natural infestations of FAW in plots without Si ($F = 164.839$; $df = 1,27$; $P < 0.0001$) and in plots with 600 ($F = 59.610$; $df = 1,27$; $P < 0.0001$), 1,000 ($F = 18.814$; $df = 1,27$; $P = 0.0002$), or 1,200 ($F = 7.232$; $df = 1,27$; $P = 0.0121$) $\text{kg}\cdot\text{ha}^{-1}$ of Si (Table 2).

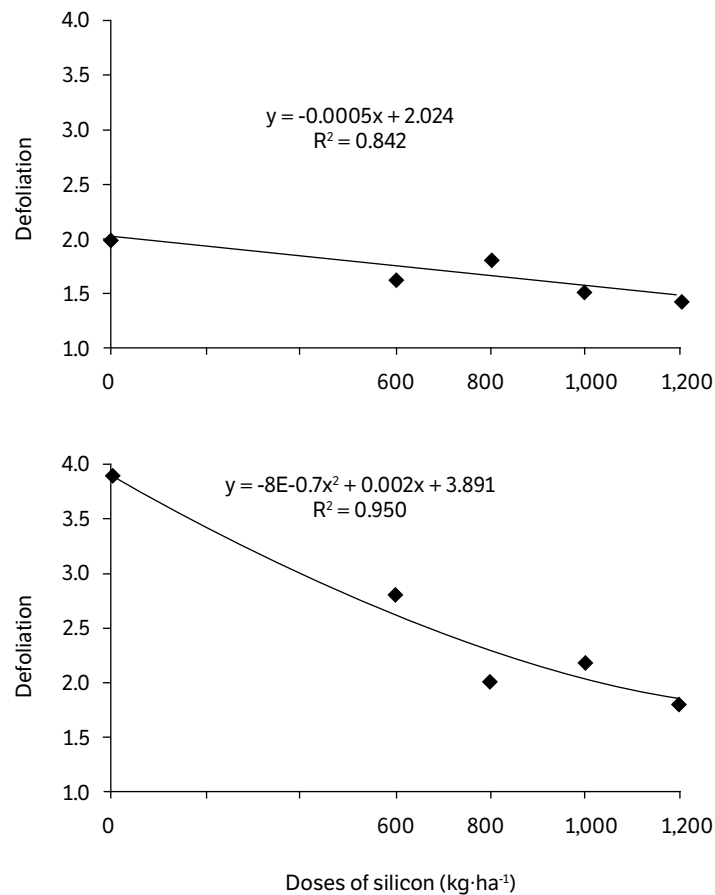


Figure 2. Defoliation ratings of Experiment #2 at 15 days with natural and after manual infestation of *Spodoptera frugiperda* in maize with different silicon doses ($\text{kg}\cdot\text{ha}^{-1}$) applied via soil, under field conditions. Uberlândia, Minas Gerais state, Brazil, December 2016-April 2017*.

*According to the scale of Carvalho (1970), in which 0 is a whorl with no defoliation and 5 is a completely consumed whorl.

Foliar and stock Si content and maize yield

In Experiment #1, no significant interaction was found between Si dose and FAW infestation method for leaf Si content ($F = 1.396$; $df = 4,27$; $P = 0.2618$). There was no effect of FAW infestation method on plant Si content ($F = 2.797$; $df = 1,27$; $P = 0.1060$). However, significant effects were found for leaf Si content as a function of soil fertilization with silicate ($F = 3.811$; $df = 4,27$; $P = 0.0139$). Leaf Si content increased linearly with increasing application rates, and, for each kilogram

of Si applied to the soil, there was an increase of 0.05% in leaf Si levels, with a minimum of 1.22% Si in the non-fertilized plants (Fig 2).

In Experiment #2, no interaction was observed between Si application rate and FAW infestation method for plant Si content ($F = 0.152$; $df = 4,27$; $P = 0.9604$). There was no effect of FAW infestation method on plant Si content ($F = 2.350$; $df = 1,27$; $P = 0.1369$); however, significant effects were found for plant Si content as a function of soil fertilization with silicate ($F = 3.083$; $df = 4,27$; $P = 0.0326$). Plant Si content increased linearly with increasing doses and, for each kilogram of Si applied to the soil, an increase of 0.02% plant Si was observed, with a minimum of 0.53% Si in the non-fertilized treatment (Fig. 3). Silicon content in Experiment #2 had absolute values smaller than those in Experiment #1 (Figure 3), since the analysis was done with the shoots in the former, and with leaves in the latter, and plant stalks usually accumulate less Si than the leaves do.

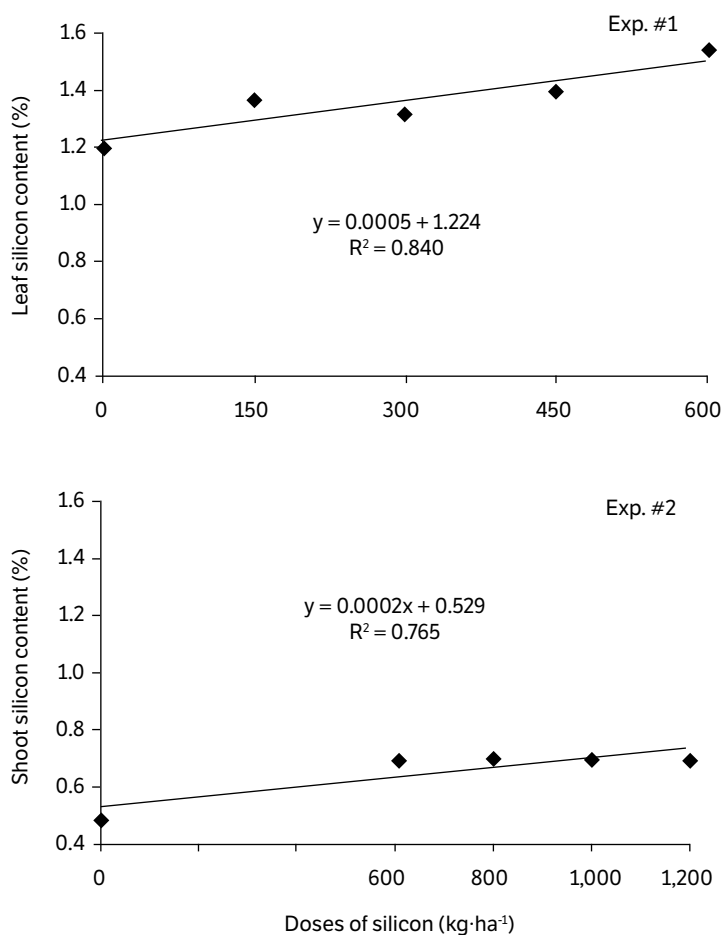


Figure 3. Leaf (Experiment #1) and shoot (Experiment #2) silicon content in maize plants as a function of different doses of silicon applied via soil, under field conditions. Uberlândia, Minas Gerais state, Brazil, December 2016-April 2017 (Experiment #1) and December 2017-April 2018 (Experiment #2).

For maize yield, there was no interaction between Si dose and FAW infestation method in Experiment #1 ($F = 1.531$; $df = 4,27$; $P = 0.7132$) or Experiment #2 ($F = 0.448$; $df = 4,27$; $P = 0.7732$), and yield was not affected by the Si fertilization rate (Experiment #1: $F = 1.904$; $df = 4,27$; $P = 0.1231$; Experiment #2: $F = 1.007$; $df = 4,27$; $P = 0.4212$) or by FAW infestation method (Experiment #1: $F = 1.310$; $df = 1,27$; $P = 0.2582$; Experiment #2: $F = 0.057$; $df = 1,27$; $P = 0.8139$) (Table 3).

Table 3. Maize productivity (average \pm SE) under field conditions in Experiment #1 (December 2016 to April 2017) and Experiment #2 (December 2017 to April 2018) with different silicon doses ($\text{kg}\cdot\text{ha}^{-1}$) applied to the soil, with natural or manual infestation of *Spodoptera frugiperda*. Capim Branco Experimental Farm, Uberlândia, Minas Gerais state, Brazil*.

Productivity Experiment #1 ($\text{kg}\cdot\text{ha}^{-1}$)			
Silicon doses ($\text{kg}\cdot\text{ha}^{-1}$)	Manual	Natural	Average \pm SE
0	8,661.8 \pm 598.7	9,013.9 \pm 1,200.5	8,837.83 \pm 654.5A
150	8,955.1 \pm 397.0	8,823.5 \pm 378.9	8,889.27 \pm 254.9A
300	9,504.0 \pm 572.10	9,764.4 \pm 610.9	9,634.18 \pm 390.6A
450	8,864.6 \pm 621.9	8,712.8 \pm 176.6	8,788.73 \pm 850.4A
600	9,598.9 \pm 812.0	10,729.8 \pm 648.7	10,164.34 \pm 526.4A
Average \pm SE	9,116.9 \pm 258.5a	9,408.9 \pm 325.8a	CV = 13.84%
Productivity Experiment #2 ($\text{kg}\cdot\text{ha}^{-1}$)			
Silicon doses ($\text{kg}\cdot\text{ha}^{-1}$)	Manual	Natural	Average \pm SE
0	15,423.9 \pm 1,568.2	16,321.4 \pm 904.4	15,872.7 \pm 855.0A
600	14,784.2 \pm 546.3	15,269.0 \pm 1,486.0	15,026.6 \pm 738.6A
800	14,835.0 \pm 457.3	13,775.3 \pm 712.4	14,305.1 \pm 440.1A
1,000	14,267.6 \pm 1,382.5	15,588.4 \pm 251.9	14,928.0 \pm 696.7A
1,200	16,682.7 \pm 1,229.8	15,874.7 \pm 1,744.3	16,278.7 \pm 999.7A
Average \pm SE	15,198.7 \pm 487.7a	15,365.8 \pm 499.3a	CV = 14.59%

*Averages followed by different letters, capital in the column and small case in the rows, differ by the F test at 5% probability; CV: coefficient of variation; SE: standard error.

DISCUSSION

The addition of Si to the soil resulted in an increase in leaf content of this element, which may have induced resistance in maize plants and reduced defoliation by FAW in both experiments. While reduced defoliation by FAW was not observed in all evaluations, defoliation was dependent on the type of infestation (natural and manual) and the time after manual infestation. For example, defoliation in natural infestations was reduced in soils with low Si doses (Experiment #1) only at five DAI, while high doses of Si (Experiment #2) reduced defoliation in natural infestation of FAW only at 15 DAI. Meanwhile, defoliation from manual infestations was reduced by Si application in all evaluations in Experiment #1 and at 15 DAI in Experiment #2. Despite Experiment #1 and Experiment #2 having several differences in methodology and employing different maize hybrids, Si application reduced defoliation by FAW in both natural and manual infestations in both experiments.

Soil fertilization with Si can induce plant resistance due to its accumulation as amorphous silica in epidermal cells, xylem vessels or intracellular spaces, forming a mechanical barrier that increases vegetable tissue stiffness (Marschner 1995; Goussain et al. 2002; Reynolds et al. 2016; Liu et al. 2017; Wang et al. 2017). This accumulation can change the morphology of specialized defense structures in leaves (Hall et al. 2020) and therefore limits herbivore access to nitrogen and other nutrients in plant tissues. Si-induced effects may also damage the digestive tract of caterpillars and reduce their feeding (Bakhat et al. 2018).

In addition, Si induces the activation of defensive enzymes (Gomes et al. 2005; Hartley et al. 2015; Bakhat et al. 2018) and flavonoids (Manivannan and Ahn 2017), as well as playing a role in the production in plant sap of substances with low digestibility, negatively affecting insect herbivore biology (Korndörfer et al. 2011).

Increased insect resistance in Poaceae plants fertilized with Si has been observed by several authors (Moraes et al. 2004; Gomes et al. 2005; Moraes et al. 2005; Antunes et al. 2010; Dias et al. 2014; Boer et al. 2019; Hall et al. 2020). Jeer et al. (2017) observed lower damage from the caterpillar *Scirpophaga incertulas* (Walker) in vegetative and reproductive stages of rice plants fertilized with Si. Moreover, caterpillar mandibles that were collected from Si-fertilized plants were damaged, and the gut mesentery of these insects showed ruptured peritrophic membranes.

Studies under laboratory and greenhouse conditions have shown evidence of reduced FAW fitness after Si application. For instance, FAW fed on Si-fertilized rice plants, ate less, and had lower survival rates (Nascimento et al. 2014; Nascimento

et al. 2018), lower larval and pupal weights, and lower fertility and egg viability (Nascimento et al. 2018). In addition, FAW fed with Si-treated maize leaves showed greater cannibalism among second instar larvae, increased mandible wear in all instars (Goussain et al. 2002), and lower consumption of leaf area (Goussain et al. 2002; Neri et al. 2005; González et al. 2015). Despite results of many laboratory studies that suggest that Si has potential to reduce damage from FAW, no field evidence of Si-promoted resistance against FAW has been found in maize in previous studies (Neri et al. 2009; Antunes et al. 2010). The reduced defoliation in maize fertilized with Si that we found in this study could have been due to effects on the caterpillars, as observed by other authors under controlled conditions.

Si doses in this study below 600 kg·ha⁻¹ (6,000 kg·ha⁻¹ of calcium and magnesium silicate) had no effect on FAW-caused defoliation, while doses from 600 to 1,200 kg·ha⁻¹ of Si (12,000 kg·ha⁻¹ of calcium and magnesium silicate) reduced defoliation without any loss of maize yield, which is critical since the Si source used must allow the use of a Si dose high enough to reduce insect injury without affecting crop yield. In the case of calcium silicate, doses of 5,000 kg·ha⁻¹, when used in sugarcane, increased yield, while reducing attack by *Eldana saccharina* Walker (Keeping and Meyer 2003). In contrast, for maize, Boer et al. (2019) found that Si at 600 kg·ha⁻¹ (= 6,000 kg·ha⁻¹ of calcium and magnesium silicate) reduced infestations of *Rhopalosiphum maidis* (L.), but had no effect, neither positive nor negative, on maize yield. It demonstrates that Si can be used effectively in maize, and that induced resistance is a management strategy that can be combined with other control methods, optimizing integrated pest management of FAW and other pests.

CONCLUSION

Under our test conditions, soil fertilization with Si increased Si leaf or stock content in maize and promoted plant resistance against attack by FAW under field conditions. Si doses from 600 to 1,200 kg·ha⁻¹ reduced FAW defoliation without affecting maize yield.

AUTHORS' CONTRIBUTION

Methodology: Sampaio, M. V., Celotto, F. J., Mendes, S. M. and Pereira, H. S.; **Funding Acquisition:** Sampaio, M. V., Celotto, F. J., Mendes, S. M. and Pereira, H. S.; **Investigation:** Perdomo, D. N., Rodrigues, A. A. R., De Lima, D. T., Rezende, G. F. and Pereira, H. S.; **Writing – Original Draft:** Perdomo, D. N. and Sampaio, M. V.; **Writing – Review and Editing:** Perdomo, D. N., De Lima, D. T., Rezende, G. F. and Rodrigues, A. A. R.

DATA AVAILABILITY STATEMENT

All dataset were generated and analyzed in the current study.

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