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RESEARCH

Silicon Application Enhances Sugarcane Growth by Impairing the Development of Larval Sugarcane Borer

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Abstract
Sugarcane borer, *Diatraea saccharalis*, is one of the main insect pests of sugarcane fields, and it has been mainly managed by the use of chemical or biological controls. Considering the benefits of Silicon (Si) fertilization against pests, it was assessed the development of sugarcane borer larvae and sugarcane growth with and without Si. A greenhouse experiment was conducted using a factorial design (2×2) with 10 repetitions. Two commercial sugarcane varieties were evaluated: SP80-3280 and IAC91-1099, which have, respectively, susceptibility, and intermediate resistance to *D. saccharalis*. Si was applied in soil in an equivalent rate of 800 kg of Si ha^{-1}. Before herbivory, Si increased stalk diameter and plant height in both varieties, and number of leaves and leaf width were only increased in IAC91-1099. After 20 days of herbivory, Si increased stalk diameter in both varieties and plant height in IAC91-1099, but decreased the number of leaves and leaf width in SP80-3280. Larval *D. saccharalis* showed a reduced weight and a greater index for mandible abrasion after feeding Si-treated plants independently of variety. No influence of Si-treated plants was found in immunological parameters of larvae (total number of hemocytes, cell viability, encapsulation capability, lysozyme active). The activity of phenol oxidase, an immunological and stress marker for insects, was greater in larval *D. saccharalis* fed with IAC 91-1099, independently of Si. In conclusion, Si application improved sugarcane growth of IAC91-1099 and impaired the development of larval *D. saccharalis* in both sugarcane varieties.

Keywords *Diatraea saccharalis* · Plant resistance · Plant tolerance · Abiotic elicitor · Potassium silicate

1 Introduction

The sugarcane borer, *Diatraea saccharalis* (Fabricius, 1794) (Lepidoptera: Crambidae), is a major pest of sugarcane, *Saccharum* spp. (Poaceae) [1–3]. Sugarcane borer feeding causes direct and indirect damage through stalk consumption and opportunistic infections with phytopathogenic fungi in the galleries opened by larvae [4]. Damage caused by *D. saccharalis* also includes decreases ranging from 50 to 70% in the sucrose content in the stalk juice [5].

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Management of the sugarcane borer is based on chemical [6] and biological [7] controls or the introduction of transgenic [8] or conventional [9] sugarcane resistant plants. Chemical control using synthetic molecules or biological control using commercial formulations of *Bacillus thuringiensis* Berliner based on spray applications is hampered by the endophytic habit of the larvae [10]. Despite the success of biological control with natural enemies such as the larval parasitoid *Cotesia flavipes* Cameron, 1891 (Hymenoptera: Braconidae) or the egg parasitoid *Trichogramma galloi* Zucchi, 1988 (Hymenoptera: Trichogrammatidae), biological control agents are not available for the entire sugarcane area [7] and the efficiency of parasitism varies with environmental conditions [11]. Complete plant resistance to the sugarcane borer is limited to transgenic events, as most commercial varieties are susceptible to the sugarcane borer [9].

The study and definition of complementary control methods to those currently available are desirable for inclusion in Integrated Pest Management (IPM) programs

[12–14]. The application of silicon (Si) can be considered a viable alternative, especially when applied to grasses (Poaceae), due to their high capacity to accumulate this element in the plant [15, 16]. Although Si is not considered an essential element for plant growth, the application of Si promotes increased plant growth, chlorophyll contents, and provided hardened and erect leaves, resulting in greater light interception, and consequently, a higher photosynthetic rate of plant. In addition, Si helps increase plant resistance to biotic and abiotic stresses [17–20].

Increased resistance to herbivores induced by Si application have been reported in sugarcane, such as reduction of stalk gallery size and reduced body mass of the stalk borer *Eldana saccharina* Walker, 1865 (Lepidoptera: Pyralidae) [21], increased mortality and duration of the nymphal phase of root spittlebug [22], and reduced incidence of *D. saccharalis* [23]. In addition, Si also resulted in reduction of the weight of *Spodoptera frugiperda* (J.E. Smith, 1797) (Lepidoptera: Noctuidae) caterpillars fed on maize plants fertilized with Si [24].

Another way to assess the negative effects of Si over herbivore insects would analyzing their immune system [25]. The insect immune system consists of structural barriers and active responses against xenobiotic "foreign to live" elements that enter the haemocoel. When these barriers are overwhelmed, the invaders are exposed to the cellular and humoral mechanisms of the defense system [26]. The exposure of the insect to foreign elements can induce various immune responses that stimulate the production of hemocytes, which are responsible for cell encapsulation and constitute the final barrier of the insect defense system [26–28]. Silicon has already been reported in the literature to interfere with the immune system of *Helicoverpa armigera* (Hübner, [1808]) (Lepidoptera: Noctuidae), in which caterpillars fed on silicon-fertilized grasses showed higher activities phenol oxidase and total phenol oxidase [25].

This study investigated whether management of the sugarcane borer with plant resistance could be improved with Si fertilization applied in soil by enhancing sugarcane growth as well the responses of sugarcane to biotic stresses. The responses of two sugarcane varieties with and without Si application in terms of growth were assessed before and after herbivory of *D. saccharalis*. The effects of Si application in sugarcane over larval *D. saccharalis* were assessed in terms of larval weight and mandibular abrasion. In addition, considering that food type could modulate the immune system of lepidopteran herbivores [29, 30], immune-related parameters such as phenol oxidase and lysozyme activities, total number of hemocytes, hemocyte viability and cell encapsulation of sugarcane borer fed with Si-treated sugarcane plants were assessed to better understand the effects of Si-fertilized sugarcane plants *D. saccharalis* larvae.

2 Materials and Methods

2.1 Plants

Sugarcane variety SP80-3280 (Sugarcane Technology Center-CTC) was chosen because it is susceptible to *D. saccharalis* and is also widely used in breeding programs and studies of sugarcane genome, transgenesis and transcriptomics [31–33]. IAC91-1099 (intermediate resistance to *D. saccharalis*, Agronomic Institute-IAC) was selected because it showed reduced infestation levels in plant crop [5].

2.2 Soil Characteristics and Experimental Procedure

The initial chemical characteristic of samples of Typic Quartzipsamment soil showed: $pHCaCl_2 = 4.6$; organic matter = 16 g dm^{-3}; P = 6.0 mg dm^{-3}; Ca, Mg, and K = 6, 3, and 0,6 $mmol_c$ dm^{-3} respectively; cation exchange capacity (CEC) = 26.7 $mmol_c$ dm^{-3}; basis saturation (SB) = 33%; and aluminum saturation = 24%.

Soil samples were collected from 0 to 20 cm depth in an area of native vegetation, and they were air-dried, and sifted through a 4-mm screen. Before filling the plastic pots, soil samples (2.5 kg) were homogenized inside plastic bags with rate equivalent to 1000 kg ha^{-1} of lime (Ca = 214 g kg^{-1} Ca; Mg = 126 g kg^{-1} Mg; PRNT = 100%) and maintained under 80% soil field capacity for 30 days. Lime quantity was calculated in function of soil analysis to increase the base saturation until 70%, according to the recommendations of [34] for sugarcane.

Sugarcane stalks with single-budded setts of SP80-3280 and IAC91-1099 varieties were planted in plastic trays containing commercial substrate Carolina Soil (Carolina Soil do Brasil Ltda., Vera Cruz, RS, Brazil) at May 02, 2021. Thirty days after planting, pre-sprouted plants were transferred to plastic pots (3 L) containing the soil treated with lime. A geotextile drainage fabric (Bidim, 105 g m^{-2}) was placed at the inner bottom of the pots to avoid nutrient leaching.

The planting fertilization with N, P and K was done with the equivalent of 60 kg ha^{-1} of N as ammonium sulphate, 180 kg ha^{-1} of P_2O_5 as simple superphosphate, 100 kg ha^{-1} of K_2O as potassium chloride, according to [35]. After 30 days, superficial fertilization with N and K took place with same rates in the planting fertilization.

Si was applied in soil using a solution containing 100 mL of a water and 2.4 mL of liquid potassium silicate (12% Si 12% K_2O, Fertisilício, Ineous®). This solution was applied at 3, 7 and 9 weeks after transplanting of sugarcane in pots. The three applications amounted equivalent

to 800 kg ha^{-1} Si, as already applied in sugarcane pot experiments with potassium silicate by [19] for sugarcane experiment. After Si solution application, 50 mL of water were added to each pot. When Si solution was applied in the Si treatments pots, control pots (-Si) were watered with 150 mL in order to provide the same quantity of water applied in the Si treatments. During the experiments manual irrigation was made equally in all pots to maintain 100% of soil field capacity.

2.3 Plant Evaluation Before Herbivory

Plant assessments were made in 10 replicates of each treatment after 26 days of Si application. Plant height was measured from the ground to the insertion of the top visible dewlap (TVD), and leaf width was measured in the central part of the same leaf. The number of fully expanded leaves from soil to TVD was counted and stalk diameter was measured. In addition, the chlorophyll index in TVD was measured using SPAD-502 (Konica Minolta Sensing).

2.4 Herbivory and Evaluation of Plant and Larvae Development

On the same day as the plant evaluation before herbivory, plants were infested with *D. saccharalis* larvae. The neonates *D. saccharalis* were obtained from insects fed with artificial diet [36] in a biofactory located in São Paulo state, Brazil (21◦21′ 23″S, 48◦3′ 48″W). Three 3rd instar *D. saccharalis* were transferred to each sugarcane plant exposed to the Si or control treatments.

Twenty days after infestation, stalk diameter, plant height, number of leaves, leaf width, and chlorophyll index in TVD of sugarcane plants were evaluated as indicated above. The larvae were then collected from inside the stalk and weighed. Larval mandible abrasion was measured after dissecting the mandibles under a stereoscope using forceps and ophthalmic scissors. Mandibles were transferred to a microscope slide and covered with glycerin and a coverslip. The mandibles were photographed under a microscope and the distance between the base of the mandible until the apex of the second tooth and the distance between the apex of the second tooth until its sclerotized base were measured using the software ImageJ 1.53k (National Institute of Health, USA). The distances were measured in both mandibles of each insect and the mandible abrasion indexes (MAI). The calculation of the mandible wear index was performed using Eqs. (1), (2) and (3) adapted from [37] (Supp 3).

$$ID = \frac{LD \times 100}{LT} \quad (1)$$

$$IM = 100 - ID \quad (2)$$

$$IUM = 10 \times \frac{ID}{IM} \quad (3)$$

Where ID is the tooth width index, LD is the tooth width, LT is the total width, IM is the jaw width index, and IUM is the jaw use index. So that the data could be in the same proportion, that is, the higher the jaw use index, the greater the wear, we used Eq. (4) to calculate the jaw wear index (WI).

$$WI = 10 - IUM \quad (4)$$

2.5 Collection of Hemolymph Plasma from *Diatraea saccharalis* Larvae

Hemolymphs from larvae fed for 20 days with sugarcane varieties amended or not with Si were collected after cutting a larval proleg. Each replicate consisted of hemolymphs extravasated from 2 larvae. Each repetition was composed by hemolymphs extravasated from 2 larvae. Samples (ca. 30 µL) were centrifuged (1,000 g; 2 min; 4 °C) and the supernatants (hemolymph plasma) were used for measuring the activities of phenol oxidase and lysozyme activities.

2.6 Phenol Oxidase and Lysozyme Activities in Hemolymph Plasma of *D. saccharalis* Larvae

Phenol oxidase (PO) activity was measured by incubating 198 µL of substrate (5 mM L-Dopa, 10 mM sodium cacodylate, 5 mM $CaCl_2$, pH 7.0) with 2 µL of hemolymph plasma in a 96-well microplate. The microplate was incubated at 30 °C in a microplate spectrophotometer (MultiSkan Sky, Thermo Scientific, Waltham, MA, USA) and absorbance readings were taken at 490 nm in 30 s intervals for 2 h. The linear phase showing increase in absorbance values was used to calculate PO activity. One unit (U) of PO activity was defined as the amount of PO required to increase 0.001 units of absorbance at 490 nm per minute. Each treatment was replicated 5 times using the hemolymph of 2 larvae per replicate.

Lysozyme activity was measured by the incubation of 98 µL of 0.015% w/v suspension of *Micrococcus lysodeikticus* (Sigma-Aldrich, St. Louis, MI, USA) prepared in 0.05 M potassium phosphate buffer (pH 6.4) with 2 µL of hemolymph plasma in a 96-well microplate. The microplate was incubated at 30 °C in a microplate spectrophotometer and absorbance measures were taken at 450 nm in 40 s intervals for 2 h. The linear phase showing decrease in absorbance values was used to calculate lysozyme activity. One unit (U) of lysozyme activity was defined as the amount of lysozyme required to decrease 0.0001 units of absorbance at 450 nm

per minute. Each treatment was replicated 5 times using the hemolymph of 2 larvae per replicate.

2.7 Cellular Immune Measurements in the Hemolymph of *D. saccharalis* Larvae

Hemolymphs from *D. saccharalis* (30 µL) larvae fed the sugarcane varieties with or without Si were collected as described for hemolymph plasma collection except for the centrifugation step. Hemolymphs were diluted 10-fold in phosphate-buffered saline (PBS), homogenized by pipetting and 20 µL of diluted hemolymph samples were transferred to a Neubauer chamber (HBG® 9020-01) for total hemocyte count (THC) under a phase contrast microscope (Zeiss® Axio Imager A2; 40x objective lens). The number of hemocytes was counted in four quadrants and the number of hemocytes per µL of hemolymph was estimated using the formula: Hemocytes μL^{-1} = [(∑number of hemocytes × dilution × 10.000)/∑quadrants]/1000 [38].

Hemocyte viability was assessed using Trypan Blue (Sigma-Aldrich, St. Louis, MI, USA). Hemolymph was collected and 10 µL of hemolymph was diluted in 40 µL of PBS and mixed with 50 µL of Trypan Blue reagent. This solution was placed on a microscope slide, covered with a coverslip and observed under a light microscope (Zeiss® Axio Imager A2; 40x objective lens). Cell viability was estimated as described in [39].

Cellular encapsulation was evaluated by incubating 30 µL of *D. saccharalis* larval hemolymph with 40 µL of InsectXpress™ (Lonza Group, Basel, Switzerland) insect cell culture medium and 20 µL of an aqueous suspension containing 0.1% (w/v) Sephadex A-25 beads in a 500 µL Eppendorf tube. Samples were kept at room temperature and for 2 h at 100 rpm to allow the hemocytes to encapsulate the Sephadex beads. Five classes of hemocyte encapsulation were defined according to the thickness of cells around the beads observed under a phase contrast microscope [40–43]. Class I = beads containing up to 10 hemocytes attached; class II = beads containing from 10 to 50 hemocytes attached; Class III = beads covered with more than 50 hemocytes forming a hemocyte capsule with up to 3 layers of hemocytes; Class IV = beads covered with a hemocyte capsule with more than 3 layers but thinner than the diameter of the bead; Class V = beads covered with an hemocyte capsule thicker than the diameter of the bead. The encapsulation index (EI) was calculated using the formula EI = [(Σ defined classes/Σ number of encapsulated beads evaluated) × 100] /5 [44].

2.8 Statistical Analysis

The experiment was conducted in a completely randomized 2 × 2 factorial design (2 commercial sugarcane varieties x 2 Si conditions) with 10 repetitions. For plant attributes, each repetition consisted of one plant of each variety exposed or not to Si. For larval attributes, each repetition consisted of one or two insects fed with each variety exposed or not to Si. Data was analyzed to observe normal distribution (Cramer-von Mises test, $\alpha = 0.05$) and homoscedasticity (Bartlett test, $\alpha = 0.05$). Data meeting these assumptions were analyzed by two-way ANOVA ($\alpha = 0.05$). Statistics were performed using R software 4.0.3 [45].

3 Results

3.1 Development of Sugarcane Before Herbivory

Before herbivory, no interaction between the factors Si and sugarcane variety was observed for stalk diameter ($F_{1,39} = 0.50$; $P = 0.49$). However, independently of the variety ($F_{1,39} = 3.68$; P = 0.06) plants fertilized with Si showed 20.21% increase in stalk diameter (1.39 ± 0.06 cm) compared to control plants (1.11 ± 0.08 cm) (Fig. 1A).

Plant height was influenced by sugarcane variety ($F_{1,39} = 28.07$; $P < 0.001$), being SP80-3280 plants (1.82 ± 0.02 m) higher than IAC91-1099 plants (1.59 ± 0.03 m). Plant height was also influenced by the application of Si ($F_{1,39} = 5.37$; $P = 0.03$), and, independently of sugarcane variety, Si fertilized plants were higher (1.75 ± 0.03 m) than control plants (1.66 ± 0.04 m). No interaction of Si application with sugarcane variety was observed for plant height ($F_{1,39} = 2.51$; $P = 0.12$) (Fig. 1B).

An interaction between Si application and sugarcane variety was observed for leaf number ($F_{1,39} = 4.97$; $P = 0.03$). In control plants, leaf number was higher in SP80-3280 plants (11.4 ± 0.34 leaves per plant) than in IAC91-1099 plants (10.2 ± 0.36 leaves per plant). However, an increased number of leaves similar to that observed in SP80-3280 plants fertilized or not with Si was only observed in IAC91-1099 plants fertilized with Si (11.4 ± 0.45 leaves per plant) (Fig. 1C).

Similar to that observed for leaf number, an interaction between Si application and sugarcane variety was observed for leaf width ($F_{1,39} = 12.24$; $P = 0.001$). In non-Si fertilized plants, leaf width of SP80-3280 plants (3.34 ± 0.11 cm) was higher than that observed in IAC91-1099 plants (2.56 ± 0.13 cm). However, increased leaf width similar to that observed in SP80-3280 plants fertilized or not with Si was only observed in IAC91-1099 plants fertilized with Si (3.39 ± 014 cm) (Fig. 1D). In addition, chlorophyll index (SPAD value) was not influenced by Si, sugarcane varieties or the interaction between these factors ($F_{1,39} = 0.0681$; $P = 0.7956$) (Suppl Table 1). Chlorophyll indexes before herbivory ranged from 35.22 to 38.21.

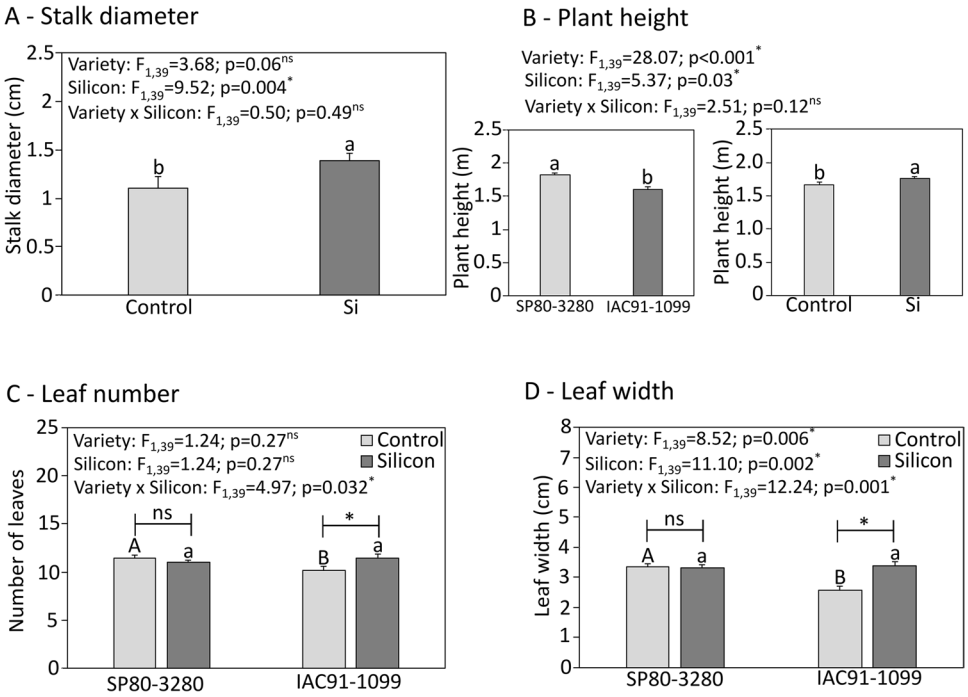

Fig. 1 Development of sugarcane varieties SP80-3280 and IAC91-1099 fertilized or not with Si before herbivory by larval *Diatraea saccharalis*. **A** Stalk diameter (cm). **B** Plant height (m). **C** Leaf number per plant. **D** Leaf width (cm). Different uppercase letters above bars indicate significant differences among sugarcane varieties not fertilized with Si (control plants). Different lower-case letters above bars indicate significant differences among sugarcane varieties fertilized with Si. * and ns above the bars indicate, respectively, significant or not significant differences among the same sugarcane variety fertilized or not with Si

3.2 Development of Sugarcane After Herbivory

Si fertilization also resulted in increased stalk diameter of sugarcane plants after herbivory ($F_{1,39} = 13.70$; $P < 0.001$). For both sugarcane varieties, stalk diameter was greater in Si-fertilized plants (1.96 ± 0.09 cm) than in non-fertilized plants (1.53 ± 0.07 cm) (Fig. 2A).

An interaction between Si application and sugarcane varieties was observed for plant height after herbivory ($F_{1,39} = 11.09$; $P = 0.002$). Plant height was smaller in the non-Si fertilized variety IAC91-1099 (1.65 ± 0.06 cm) when compared to the non-Si fertilized variety SP80-3280 (1.88 ± 0.04 cm). Si application did not change the plant height of SP80-3280 plants after herbivory ($1.86.5 \pm 2.23$ cm). However, plant

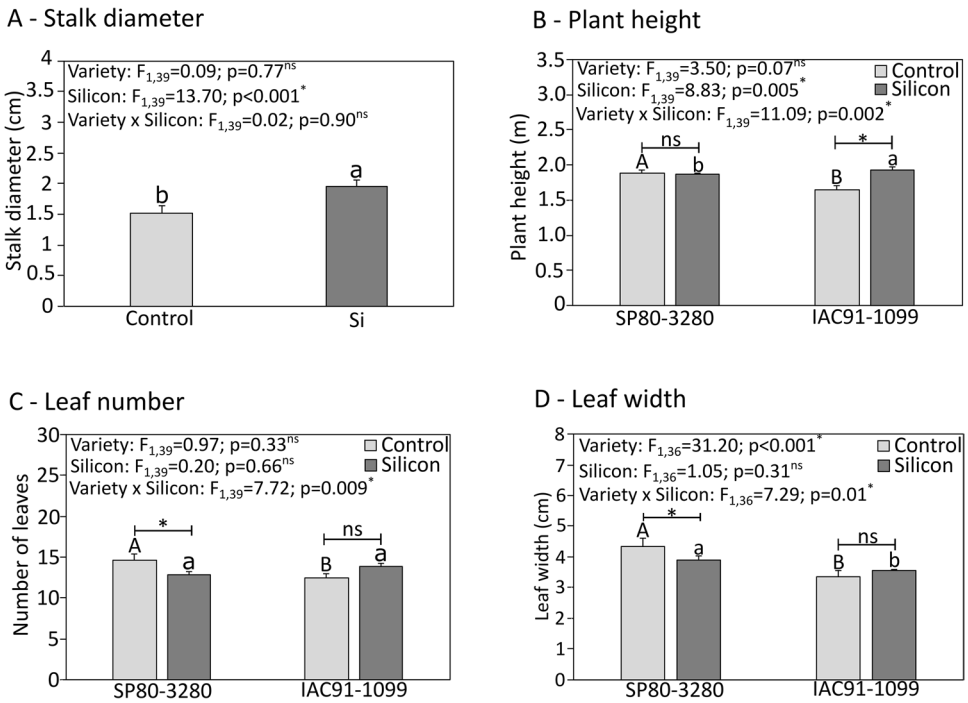

Fig. 2 Development of sugarcane varieties SP80-3280 and IAC91-1099 fertilized or not with Si after herbivory by larval *Diatraea saccharalis*. A - Stalk diameter (cm). B - Plant height (m). C - Leaf number per plant. D - Leaf width (cm). Different uppercase letters above bars indicate significant differences among sugarcane varieties not fertilized with Si (control plants). Different lower-case letters above bars indicate significant differences among sugarcane varieties fertilized with Si. * and ns above the bars indicate, respectively, significant or not significant differences among the same sugarcane variety fertilized or not with Si

height of Si-fertilized IAC91-1099 plants (1.93 ± 0.04 cm) was greater than that of non-Si fertilized IAC91-1099 or Si-fertilized SP80-3280 plants (Fig. 2B).

The number of leaves per plant after herbivory was also influenced by the interaction between Si and sugarcane varieties ($F_{1,39} = 7.72$; $P = 0.009$). The number of leaves in SP80-3280 plants without Si (14.6 ± 0.81 leaves per plant) was higher than in IAC90-1099 without Si (12.5 ± 0.40 leaves per plant). Compared to the respective control plants, the number of leaves was reduced in Si-treated SP80-3280 plants (12.8 ± 0.47 leaves per plant), while the number of leaves was maintained in Si-treated IAC90-1099 plants (13.8 ± 0.47 leaves per plant). In Si-treated plants, the number of leaves in SP80-3280 plants was the same as in IAC90-1099 plants (Fig. 2C).

After herbivory, an interaction between Si application and sugarcane varieties was also observed for the leaf width ($F_{1,39} = 7.29$; $P = 0.01$). In non-Si treated plants, leaf width values were higher in SP80-3280 (4.35 ± 0.27 cm) compared to IAC90-1099 (3.37 ± 0.20 cm). Compared to the respective control plants, leaf width was reduced in SP80-3280 plants treated with Si (3.91 ± 0.14 cm), while leaf width was maintained the same in IAC90-1099 plants (3.55 ± 0.03 cm). In Si-treated plants, leaf width was greater in SP80-3280 plants than in IAC90-1099 plants (Fig. 2D). Chlorophyll index (SPAD value) was not influenced by Si, sugarcane varieties or the interaction between these factors ($F_{1,39} =$ 0,717; $P = 0.403$) (Suppl Table 2). Chlorophyll indexes in sugarcane plants after herbivory ranged from 34.27 to 37.87.

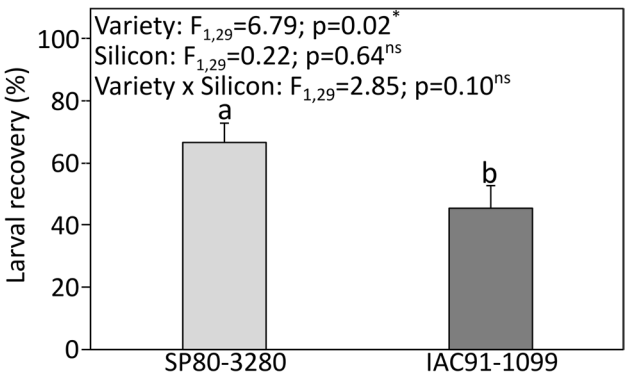

Fig. 3 Recovery of *Diatraea saccharalis* larvae after 20 days in Si-treated and control sugarcane varieties SP80-3280 and IAC91-1099. Different lower-case letters above bars (SEM) indicate significant differences among sugarcane varieties ($P < 0.05$)

3.3 Development of *D. saccharalis* Larvae

Si application and the interaction between sugarcane varieties and Si did not influence larval recovery of *D. saccharalis* after 20 days they were transferred to sugarcane plants (Two-way Anova, $p \geq 0.05$). Independently of Si application, larval recovery was higher in the variety SP80-3280 (66.67 ± 6.80%) than in variety IAC91-1099 (45.24 ± 4.43%) (Fig. 3).

The weight of *D. saccharalis* larvae was not influenced by sugarcane varieties or by the interaction of the factors Si and sugarcane variety (Two-way Anova, $p \geq 0.05$), only by the application of Si ($F_{1,27} = 4.84$; $P = 0.038$). Compared to the weight attained by larvae fed with control plants (60.7 ± 6.1 mg per larva), larval weight was reduced by approximately 36% when *D. saccharalis* larvae were fed with Si-treated plants of SP80-3280 or IAC91-1099 (38.8 ± 7.4 mg per larva) (Fig. 4A). Furthermore, mandibular abrasion of *D. saccharalis* was not influenced by sugarcane varieties or by the interaction of the factors Si and sugarcane variety (Two-way Anova, $p \geq 0.05$), only by Si application ($F_{1,32} = 13.94$; $P < 0.001$). The highest indexes of mandibular abrasion were observed in larvae fed with Si-treated plants of both varieties (8.43 ± 0.18) compared to indexes of mandibular abrasion observed in larvae fed with control plants (7.77 ± 0.08) (Fig. 4B).

3.4 Immune Responses of *D. saccharalis* Larvae

Phenol oxidase activity in the hemolymph of *D. saccharalis* larvae was not influenced by Si application or by the interaction of the factors Si and sugarcane variety (two-way ANOVA, $p > 0.05$). Phenol oxidase activity was influenced only by the sugarcane varieties ($F_{1,17} = 15.40$; $P = 0.002$), since the activity of phenol oxidase in the hemolymph of larvae fed with IAC91-1099 plants (3.42 ± 0.66 U μL^{-1} of hemolymph) was higher than that observed in larvae fed

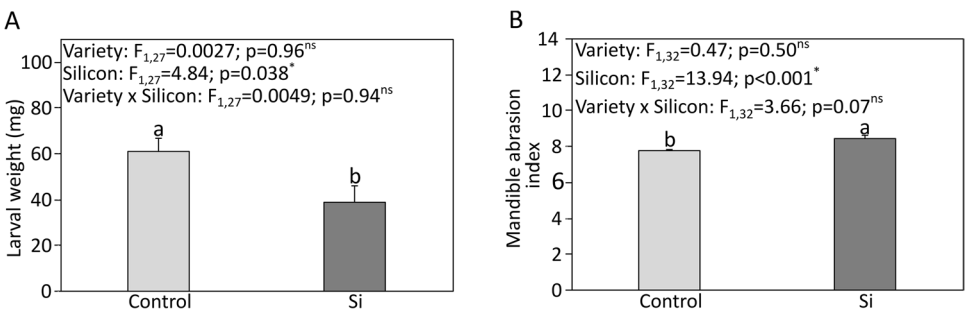

Fig. 4 Larval weight (mg) (**A**) and mandible abrasion index (**B**) of *Diatraea saccharalis* larvae fed with Si-treated (Si) and control sugarcane varieties SP80-3280 and IAC91-1099. Different lower-case letters above bars (SEM) indicate significant differences among sugarcane plants fertilized or not (Control) with Si ($P < 0.05$)

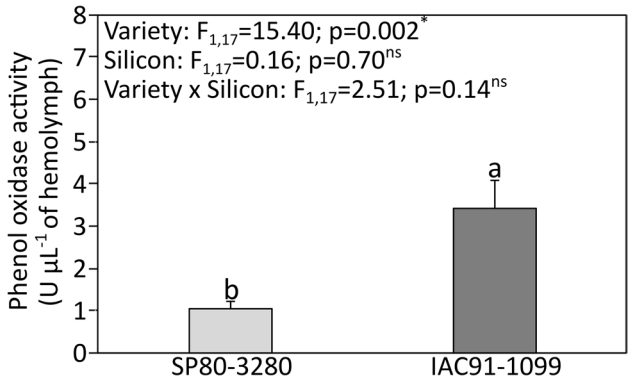

Fig. 5 Phenol oxidase activity in the hemolymph of larval *Diatraea saccharalis* (U μL^{-1} of hemolymph) fed with Si-treated sugarcane varieties SP80-3280 and IAC91-1099. Different lower-case letters above bars (SEM) indicate significant differences among sugarcane varieties ($P < 0.05$)

with SP80-3280 plants (1.03 ± 0.19 U μL^{-1} of hemolymph) (Fig. 5).

Lysozyme activity (12.08 U μL^{-1} of hemolymph) was not influenced by Si application, sugarcane varieties or the interaction between these factors (Two-way Anova, $P > 0.05$). Cellular immune responses of *D. saccharalis* larvae were not influenced by Si application, sugarcane varieties or by the interaction between these factors (two-way Anova, $P > 0.05$). Independent of Si application or sugarcane variety, total hemocyte count was measured in 19.044 cells μL^{-1} of hemolymph, cell viability in 99.6%, and cell encapsulation index of 37.

4 Discussion

This study showed that the application of Si improved the development of the evaluated sugarcane varieties resulting mainly in increased stalk diameter. Before herbivory by *D. saccharalis* larvae, the benefits of Si were more evident for IAC91-1099 for leaf number and leaf width. After herbivory, the development of sugarcane varieties was still benefited by Si application, also observed mainly by the increased stalk diameter in both varieties fertilized with Si. Improvements of Si application on plant physiology and development under ideal conditions or under biotic or abiotic stresses have also been reported in previous studies [46, 47] and greater biomass in Poaceae plants, including sugarcane, fertilized with Si sources have also been shown [23, 48–51].

Regarding the effects of herbivory, Si application, independent of the variety, benefited sugarcane plants against herbivory, as already shown by [52]. In the present study, it was observed that consumption of Si-fertilized sugarcane plants of both varieties reduced the larval weight and increased the index of mandible abrasion of *D. saccharalis*. Si fertilization has been recognized as a stimulator of plant resistance to herbivory [53] mainly by altering morphological aspects of plants such as tissues hardness [54, 55] or plant biochemical composition [56].

The accumulation of Si in plants confers resistance to herbivore attack through physical and mechanical barriers [54, 55, 57]. The deposition of silica in the epidermal cells of the thatch increases its hardness and abrasiveness, providing a mechanical barrier to the penetration of *D. saccharalis* larvae into the thatch of early-stage plants [58, 59]. Considering that Si accumulates in the stalk of sugarcane plants [35, 60], i.e. the feeding site of *D. saccharalis* larvae, increased tissue hardiness may had impaired the feeding of larvae through increasing mandible abrasion as observed for *Spodoptera* spp. larvae fed with Si-fertilized maize plants [24, 37, 61, 62] and for *Chilo infuscatellus* Snellen, 1890 (Lepidoptera: Crambidae) fed with Si-fertilized sugarcane plants [63]. Despite the reduction of damage by Si fertilization have already been reported for other herbivores in sugarcane [17, 57, 64], including *D. saccharalis* [23], this study is the second in the literature to demonstrate the effect of silicon on the larval performance of *D. saccharalis*. Previously, [65], reported that there was no effect of silicon on the larval weight of *D. saccharalis*, differing from our results.

This study also showed that Si application was not involved in alterations of the activity of phenol oxidase in the hemolymph of *D. saccharalis* larvae. These results are in agreement with [66], who also found similar results when studying a soil dwelling herbivore interacting with sugarcane and Si. However, [25] observed increased values of phenol oxidase activity in the hemolymph of *H. armigera* larvae fed on the Si-fertilized model grass *Brachypodium distachyon*

Despite Si did not result in changes of phenol oxidase activity in the hemolymph of larval *D. saccharalis*, the activity of this enzyme was greater in larvae fed with IAC91-1099 plants than in those fed with SP80-3280 plants. These results and a reduced rate of permanency of larvae in IAC91-1099 plants suggest that IAC91-1099 as less suitable plant for larval *D. saccharalis*, confirming [5]. Increased phenol oxidase activities in insects under stress are reported [67–70], suggesting, independently of Si application, an increased fitness cost for *D. saccharalis* larvae to develop consuming IAC91-1099 plants when compared to SP80-3280 plants. It is worth noting that, different to that observed in the susceptible variety SP80-3280, increased plant height observed only in IAC91-1099 with the application of silicon suggest that this sugarcane variety presents a specific tolerance mechanism induced by the application of silicon, capable of compensating for the damage suffered by herbivory with greater growth and vegetative development. [53] have already demonstrated that Si can promote tolerance to herbivory in grass species capable of accumulating high levels of Si. In the same study,

the authors observed greater aerial biomass of Si-fertilized wheat plants under herbivory conditions.

Regarding the Integrated Pest Management (IPM), it would be hypothesized that herbivores immune-activated by the consumption of resistant or tolerant plants might impair the development of a parasitoid. Considering the importance of the parasitoid *C. flavipes* for the management of *D. saccharalis* [7], it is noteworthy evaluate the possible impacts of *D. saccharalis* with increased phenol oxidase activity over the parasitism success of *C. flavipes*. However, these effects may be null or minimum given that *D. saccharalis* larvae with increased values for phenol oxidase activity stimulated by exposition to *B. thuringiensis* were still susceptible to parasitism by *C. flavipes* without noticeable impacts over the development of the parasitoid [27]. Moreover, field evaluation of Si-fertilized sugarcane plants also indicated compatibility of Si-fertilized plants with the use of *C. flavipes* for the management of *D. saccharalis* [65]. Additionally, other immune responses that could also impact parasitism success, i.e. cellular and lysozyme activity, were not altered by the consumption of Si-fertilized sugarcane plants or by the sugarcane varieties evaluated in the present study as also observed by [25].

The analysis of the caterpillars' digestive system will also be essential to better answer some questions about the interaction of Si in the insect's biochemical pathways, in order to identify the influence of Si on some enzymes responsible for protein absorption and whether there is any relationship with the lower gain of larval weight.

The results obtained in the present study suggest that Si could act as an inducer of resistance in sugarcane to *D. saccharalis*, affecting its larval performance and also improving the morphological aspects of sugarcane plants. These effects can be seen directly in the insect, in which the application of silicon reduced the weight of the larvae and led to greater wear and tear on the lower jaw. Another interesting finding of the study is that Si also acted as an inducer of tolerance mechanisms in the plants, where Si fertilization led to a larger stalk diameter and a greater plant height. These effects were more pronounced in the resistant genotype IAC-91-1099. These data are important to understand the effects provided by the application of Si and to use it as a complementary tactic into IPM of *D. saccharalis* in sugarcane.

5 Conclusion

Si acts as an inducer of resistance in sugarcane against *D. saccharalis* and contributes to the plant's growth and development. Therefore, Si can be used as a component to enhance sugarcane productivity and mitigate the adverse effects of *D. saccharalis* larvae in sugarcane fields.

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Author Contributions A.C.G.S. planned, designed, and carried out the experiments, analyzed and interpreted the data, and was responsible for the manuscript preparation, C.P.G.P., A.L.Z.S., and S.S.F. carried out the experiment, and took the biometric measurements, and contributed to writing the latest version of the manuscript, M.S.C. and G.D.R. planned, designed, interpreted the data, and contributed to writing the manuscript.

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Data Availability Not applicable.

Code Availability Not applicable.

Declarations

Research Involving Human Participants and or Animals The authors declare this study does not contain studies with human participants or animals.

Consent to Participate All authors give their consent for participate of this paper.

Consent for Publication All authors give their consent for submission and publishing this paper.

Competing Interests The authors declare no competing interests.

Conflict of Interest The authors declare that there is no conflict of interest.

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