

Characterization of Priming, Induced Resistance, and Tolerance to *Spodoptera Frugiperda* by Silicon Fertilization in Maize Genotypes

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Abstract

Fall armyworm (FAW) *Spodoptera frugiperda* is considered the main defoliating insect pest of maize in many countries. Silicon (Si) applied to plants has been shown to increase the resistance to insects, especially in grasses such as maize. This study characterized the effects of Si fertilization regarding priming, induced resistance, and tolerance to FAW in a landrace variety and hybrid of maize. Si was applied in soil of potted-plants as H_4SiO_4 at 2 t ha^{-1} when maize plants were at V2 stage, and when they reached V3 two FAW neonates were infested in the plants whorls. Plants at V4 were reinfested with a 4th-instar larva that was kept feeding until V5 stage. Concentrations of H_2O_2 and malondialdehyde were used as proxies of injury and oxidative stress, and activities of antioxidant enzymes were related to Si-induced responses on plants growth, and FAW injury and performance. As main results, there was reduced FAW injury and larval weight gain in Si-treated plants subjected to herbivory. Greater root dry mass was observed in the landrace variety with Si and without herbivory. Landrace plants showed higher shoot weights than the hybrid under FAW infestation. Si-fertilized plants showed higher H_2O_2 concentrations. The highest peroxidase activities occurred in Si-treated plants without herbivory, and the catalase and superoxide dismutase activities were highest in Si-treated plants without herbivory or herbivory-injured plants without Si. These results are important for characterizing the Si-induced defense effects in maize to FAW, which can benefit the strategic use of Si in integrated pest management.

Key Message

- *Spodoptera frugiperda* is a polyphagous pest that threatens food security in many countries.
- Plants of maize landrace and hybrid were fertilized with Si to characterize triggered defense responses regarding induced resistance, priming, and tolerance to insect herbivory.
- Si effects on insect performance, plant growth, and antioxidant enzyme activities were more specific to maize landrace and varied in conditions with and without herbivory.
- Si primed chemical defenses in landrace maize that were potentiated by induction of resistance following insect herbivory.

Introduction

Fall armyworm (FAW) *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is considered the main insect pest of maize crop in Brazil (Cruz et al. 2008; Lima Júnior 2012; Eghrari et al. 2021). In recent years, it has become a new invasive species in West and Central Africa, where the first outbreaks were recorded in early 2016; the presence of distinct haplotypes collected from maize samples in Nigeria and São Tomé suggests FAW introduction to the African continent. This pest has also been reported more recently in Asian countries (Goergen et al. 2016; Shylesha et al. 2018; Jing et al. 2019; Zhang et al. 2019). The losses in crop yields due to FAW herbivory in these countries vary from 8.3 to 20.6 tons per year (Goergen et al. 2016; Day et al. 2017). Thus, FAW has become a pest that threatens food security in many developing countries worldwide and requires cost-effective control strategies.

Silicon (Si) is an element that is naturally present in soil, mostly in non-assimilable forms, but to a lesser extent found in the form of silicic acid (H_4SiO_4) (Epstein 1994). Although Si is not considered an essential nutrient for plants development, when Si is available in the soil solution as H_4SiO_4 it can be easily absorbed by the roots, playing an important role in plants growth, nutrition, and mechanical resistance to fungal diseases, insect herbivory, and the chemical conditions of the medium (Epstein 1994; Ma and Yamaji 2006; Kvedaras et al. 2007; Reynolds et al. 2016). Plants fertilized with Si show enhanced resistance against chewing insects, including FAW larvae (Goussain et al. 2002; Alvarenga et al. 2017; Oliveira et al. 2017; Nascimento et al. 2017), due to silicification (SiO_2) of the plant cell wall, increasing its rigidity and making it difficult for insects to feed on the plants tissues (Datnoff et al. 2001). In addition to this mechanical/morphological effect in fertilized plants, Si can elicit the increase in activities of enzymes and metabolites involved in plant chemical defense (Dixon et al. 1994; Fawe et al. 2001; Gomes et al. 2005). Due to the negative effects of Si on insects, plants fertilization with Si can be considered a viable alternative in the integrated management of insect pests with economic importance such as FAW (Oliveira et al. 2017; Nascimento et al. 2017).

Resistance mechanisms of plants act in response to various types of stress to which they are constantly exposed, whether biotic or abiotic (Walters and Heil 2007; Borges et al. 2017). The resistance mechanisms are classified as constitutive or induced depending on when they are constantly expressed in the plant or are triggered only after a stress condition, respectively (Borges et al. 2017). Production of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), due to stresses experienced by plants, for example insect herbivory, activates a series of defensive physiological processes, where antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) are highly important in maintaining the balance of ROS and plant cell homeostasis. Antioxidant enzymes were reported to be more activated in plants fertilized with Si (Yang et al. 2017).

Among the mechanisms of induced resistance, priming consists of the activation of immune memory or a readiness state in stressed plants. Priming is a process in which there is a preparation of plants defense responses, which allows them to act more quickly and efficiently in response to future threats (Frost et al. 2008). After the first sign of stress, the challenged plant recognizes and stores this information and prepares itself if it is subjected to further stress (Martinez-Medina et al. 2016; Borges et al. 2017). Thus, plant induced defense responses, including both priming and induced resistance, are conditioned upon an initial stress stimulus. They represent a type of immune memory, allowing the plant to use the stored stress information by changing the coding of resistance genes for keeping their defense mechanisms activated to deal with upcoming attack (Mauch-Mani et al. 2017).

Tolerance is another plant defense category against insect herbivory (Stenberg and Muola, 2017). Tolerance is defined as the ability of plants to withstand injury caused by insects without their growth and production being significantly affected (Peterson et al. 2017). Moreover, tolerance poses no negative effect on the biology or feeding and oviposition behavior of insects, and overall involves the expression of plant traits and physiological processes that confer the ability to mitigate the negative impact caused by pest injury (Chen et al. 2015). Such tolerance mechanisms are those that have influence on plants

photosynthesis and other physiological processes, such as growth, phenology, and reallocation and use of stored nutrients and photoassimilates (Strauss and Agrawal 1999; Stowe et al. 2000; Tiffin 2000). Tolerance has been recognized by some authors as a defense category apart from resistance (Stout 2013; Stenberg and Muola 2017) because of the distinct mechanisms participating in plant defense to insect herbivory, and this novel classification is thought to benefit the use of plant resistance in applied research and integrated pest management (Stout 2013). Johnson et al. (2019) reported for the first time that Si fertilization to wheat induced tolerance to herbivory by *Helicoverpa amirgera*, in which plants growth were overcompensated in the Si-fertilized insect-infested condition, in expense of resistance that was not induced.

Si fertilization can favor plants growth and development (Epstein 1994). Plants fertilized with Si have higher chlorophyll contents and leaves that are more rigid and erect, which favor greater light interception inside the canopy and consequently higher photosynthetic rates (Marschner 1995; Nascimento et al. 2017). The beneficial effects provided by Si on plants growth are more evidenced under stress situations, whereas the effects of fertilization in unstressed plants are reported to be neutral (Coskun et al. 2018). According to aforementioned effects of Si fertilization on plant growth and insect performance, there is debate about the actual plant defense responses promoted by Si, raising questions of whether the effects are in the form of: (i) induced resistance, a condition where fertilized plants have higher level of resistance owing to the application of Si itself; or (ii) priming, where induced defense responses are activated at higher levels only after a first attack by an insect in Si-fertilized plants (Walters et al. 2014; Nascimento et al. 2017). Another emerging possibility is that (iii) Si fertilization induces greater vigor and tolerance to plants, promoting greater vegetative growth under insect herbivory. It is also hypothesized that a mixed defensive response involving all these effects in Si-fertilized plants may occur (Johnson et al. 2019).

Maize is a grass species that has high capacity to accumulate Si (Marschener 1995; Epstein 1999). Although some studies have demonstrated Si-induced resistance to FAW (Goussain et al. 2002; Alvarenga et al. 2017; Oliveira et al. 2017), none of them dissected whether the defensive responses triggered by Si are related to priming or induction of resistance per se, and whether Si can induce tolerance to insect herbivory in different maize genotypes, which have variable levels of genetic diversity as being more or less improved by conventional breeding, as the landrace varieties and hybrids. Better understanding the effects of induced resistance, priming, and tolerance may help shed light on the characterization of the specific plant defense responses elicited by Si. This knowledge will certainly aid in the development of strategies of Si application in integrated pest management to mitigate damage caused by FAW in maize crops especially in developing countries where the pest is considered a food security threat. Therefore, this study characterized the effects of Si fertilization on priming, induced resistance, and tolerance to FAW in a hybrid and landrace variety of maize.

Materials And Methods

Location of the experiment

The experiment was conducted under greenhouse and laboratory conditions in the Laboratory of Plant Resistance and Integrated Pest Management, Department of Entomology, Federal University of Lavras (UFLA), in Lavras, Minas Gerais, Brazil. In the laboratory the assays were conducted under controlled environmental conditions (26 ± 2 °C; $70 \pm 10\%$ RH; 12L:12D h) and in the greenhouse under controlled temperature (25 ± 2 °C) and ambient light.

FAW larvae

Larvae of FAW used in the experiment were obtained from a rearing colony established in the laboratory. To establish the colony, larvae were collected from maize fields in an experimental area of UFLA and brought to the laboratory. Larvae of the colony were fed an artificial diet and adults were fed a 10% honey solution, according to the methods of Greene et al. (1976). The insects were kept in a climate-controlled room at 28 ± 2 °C, $70 \pm 10\%$ RH, and 12L:12D-h photoperiod.

Treatments and experimental design

The experiment was set up in a $2 \times 2 \times 2$ factorial scheme (with or without Si \times with or without herbivory \times hybrid or landrace variety) in a completely randomized design, which formed eight treatments. Twenty plants were prepared for each treatment and maintained in a greenhouse, as described in the next section. Thus, the three factors evaluated in this study (Si fertilization, herbivory, and maize genotype) were combined in the following treatments: T1) landrace variety, with Si, with herbivory; T2) landrace variety, with Si, without herbivory; T3) landrace variety, without Si, with herbivory; T4) landrace variety, without Si, without herbivory; T5) hybrid, with Si, with herbivory; T6) hybrid, with Si, without herbivory; T7) hybrid, without Si, with herbivory; T8) hybrid, without Si, without herbivory.

Experiment conduction

Maize seeds were sown in 3-L pots filled with a mixture of soil (dark red latosol), cattle manure, and Tropstrato substrate (4:1:1). Soil analysis was performed and fertilization calculations were done following the recommendations for the use of correctives and fertilizers (Ribeiro et al. 1999). Thus, the soil was fertilized with 180 g of dolomitic limestone and 732 g of NPK (8-28-16), which were incorporated into the soil preparation. For the micronutrients, a solution was prepared with 1.95 g of magnesium sulfate, 0.65 g of potassium chloride, 1.77 g of urea, 0.012 g of boric acid, 0.017 g of zinc sulfate, and 1.5 g of monoammonium phosphate (MAP) fertilizer, which was applied at 30 mL per pot immediately after sowing. Every 15 days, the plants were fertilized with 30 mL of Hoagland and Arnon nutrient solution. Two maize seeds were sown per pot, and after 10 days of emergence of plants, they were thinned to one plant per pot. The maize seeds were of the landrace variety Amarelão and the conventional non-Bt hybrid SHS4070. The plants were irrigated whenever necessary.

The dose of SiO₂ (1% silicic acid solution) (Vetec fine chemical, Duque de Caxias, Brazil) used was proportional to 2 t ha⁻¹ (Alvarenga et al. 2017) – equivalent to 2.76 g of diluted SiO₂ in 276 mL of distilled water – which was applied to each pot in the treatments assigned to receive Si application. The application of silicic acid solution was made in the pot around the plants at V2 stage (Magalhães et al. 2002), simulating a drench application (Supplementary 1).

When the plants reached V3 stage, two FAW neonates obtained from the rearing colony were infested inside the whorl of maize plants with the aid of a fine paintbrush in the groups of plants submitted to herbivory. After 7 days, V4-stage plants of each treatment were reinfested with a 4th-instar larva of FAW. Next, when the plants reached V5 they were divided into four groups to evaluate the following parameters: (i) FAW larval performance; (ii) shoot and root dry weights, height, relative chlorophyll index, and leaf Si content; (iii) activity of the antioxidant enzymes SOD, CAT, and APX, and concentrations of hydrogen peroxide (H₂O₂) and malondialdehyde (MDA); and (iv) FAW injury on the plants. These steps are described in detail in the following sections.

Evaluation of FAW larval performance in the laboratory

To evaluate the larval performance of FAW, the two youngest leaves of each treated plant were detached from the sheath and taken to the laboratory where leaf sections (5 × 3 cm) were prepared with the aid of scissors. Two leaf sections were prepared on each side of the midrib of each maize leaf; one leaf section was transferred to Petri dishes (5 cm diameter) to perform the assay, and the other leaf section was used as an aliquot. One neonate larva (<24 h old) was confined to each dish, which was allowed to feed on the leaf section for 5 days. The dishes were lined with paper towels moistened with distilled water and were kept in a climatized room with temperature at 25 ± 2 °C, relative humidity of 60 ± 10%, and a 12L:12D-h photoperiod. For each treatment, five plants were used as replicates, and each replicate consisted of four dishes with leaf sections of the same plant and containing one larva per dish. In total, 20 experimental units (dishes) were used for each treatment.

Five days after setting up the bioassay, FAW larvae weight and leaf consumption were evaluated. For this purpose, we inspected whether the larvae were alive or dead by gently poking them with a fine paintbrush. Live larvae were removed from the Petri dishes, and were starved for ~3 h to ensure that midgut of each larva was void. The larvae were dried at 60 °C for 48 h in an oven and then weighed with the aid of a precision analytical balance (AG200, GEHAKA, São Paulo, Brazil). To measure leaf consumption, the remaining leaf sections and the respective aliquots were dried in an oven at 60 °C for 48 h (TE-394/2, TECNAL, Piracicaba, Brazil) and then weighed. Leaf consumption by larvae was calculated by subtracting the dry weight of remaining leaf sections after larvae feeding from the dry weight of intact aliquot leaf sections.

Evaluation of plant growth and leaf Si concentration

Five plants of each treatment were used as replicates for assessment of growth parameters of maize plants, and three plants of each treatment were used as replicates for the analysis of leaf Si concentration. Plant height was measured before and after larval infestation, i.e., when the plants were at V3 and V4 stages, respectively. The height of plants was evaluated with the aid of a ruler, from the soil surface to the insertion of the uppermost leaf in the sheath of plants. The relative chlorophyll content was read using a SPAD-502 portable chlorophyll meter (Konica Minolta Sensing, Inc, TECNAL, Piracicaba, Brazil). This reading was taken on each of the two youngest leaves of the plants, and the mean of the readings was used for statistical analysis.

To determine the shoot and root dry weights, the V4-stage maize plants were carefully removed from the pots with moist soil and cut near the soil surface so that they were separated into the shoot and root sections. Each part of the plants was packed in paper bags, dried in a forced-circulation oven at 60 °C for 72 h, and then weighed on a balance. Next, the plant fractions were ground to a fine powder in a blender, packed in paper bags, and sent for determination of Si concentrations in the Department of Soils of UFLA. The leaf analysis of Si was performed as described by Korndörfer et al. (2004).

Evaluation of oxidative stress and antioxidant enzyme activities

Analysis of the activities of the enzymes SOD, CAT, and APX were performed to verify the antioxidant effect of Si application in the presence and absence of FAW herbivory in maize plants of the landrace variety and hybrid. In addition to the enzyme activities, the concentrations of H₂O₂ and MAD were evaluated as indicators of injury and oxidative stress in the plants. Five plants from each treatment were used as replicates, and the two youngest leaves of the plants were taken for chemical analysis. The leaves were carefully detached from plants at the sheath, stored in aluminum foil envelopes, wrapped in a plastic bag, and placed in a Styrofoam box with liquid nitrogen. Samples were taken to the Plant Physiology Sector, Department of Biology of UFLA, and stored in a freezer at -80°C until analysis.

The extraction method for the analysis of SOD, CAT, and APX activities was based on the protocol of Biemelt et al. (1998). For the enzymatic analyses, SOD activity was evaluated as described by Giannopolitis and Ries (1977); CAT activity was evaluated as described by Havir and McHale (1987); and APX activity was determined according to the protocol of Nakano and Asada (1981). The H₂O₂ content was quantified as proposed by Velikova et al. (2000), and the lipid peroxidation level was measured in terms of the MDA concentration using the thiobarbituric acid reaction (Buege and Aust 1978). The H₂O₂ and MDA analyses were performed in duplicates, and the enzymatic analyses were performed in triplicates.

Evaluation of FAW injury on maize plants in the greenhouse

The same procedures of Si and herbivory treatments were applied to maize landrace and hybrid plants in the greenhouse as previously. To determine the injury caused by FAW on potted-maize plants, V4-stage plants were reinfested with a 4th-instar larva. The larvae were weighed before infestation and remained feeding on the plants for 7 days. Next, the plants were carefully inspected for FAW injury, and larvae were removed from the plants, placed in Petri dishes, and taken to the laboratory, where they were weighed on a precision scale (Supplementary 2). The plants were visually rated for FAW injury, receiving scores from 1 to 9 according to the Davis scale (Davis et al. 1992).

Statistical analysis

Data obtained in the experiment were subjected to exploratory analysis for normality of residuals and homogeneity of variances and were then subjected to three-way ANOVA to verify the main effects of Si application, herbivory, maize genotype, and all their interactions. Means of the treatments were compared by Tukey's test ($\alpha = 0.05$) when the ANOVA was significant. The analyses were performed in R software (R Development Core Team, 2014). The values of all statistical analyses are presented (Supplementary 3).

Results

Evaluation of FAW larval performance in the laboratory

In the laboratory bioassay, there were no significant effects of treatments on the biomass of FAW larvae ($P > 0.05$). The relative consumption rate (RCR) of the larvae was significantly affected by the maize genotype \times Si interaction ($F_{1,32} = 5.88$; $P = 0.0212$). Larvae RCR was higher in the hybrid when there was no Si application (Figure 1). When Si was applied, there was no difference in the RCR between the maize genotypes. The efficiency of conversion of ingested food (ECI) of the larvae was not significantly affected ($P > 0.05$) by treatments.

Evaluation of plant growth and leaf Si concentration

The root dry weight showed a significant interaction of maize genotype \times Si \times herbivory ($F_{1,32} = 4.27$; $P = 0.0469$). The highest root mass was observed in the landrace variety with Si application and without herbivory, and it was significantly lower when this maize genotype was under Si application and herbivory conditions (Table 1). In the maize hybrid, the root dry mass was slightly higher when there was no Si application and no herbivory than under the condition without Si and with herbivory. For the shoot dry mass, there was a significant effect of the maize genotype \times herbivory interaction ($F_{1,32} = 10.26$; $P = 0.0031$). Plants of the landrace variety had a higher shoot dry mass than the hybrid only when the plants were infested with FAW (Figure 2a).

The relative chlorophyll index measured before larvae infestation was significantly affected by the interaction of maize genotype \times Si ($F_{1,32} = 5.73$; $P = 0.0227$). The chlorophyll index was higher in the

hybrid without Si application than in the fertilized treatment. This effect was not observed in the landrace variety (Figure 2b). The chlorophyll index measured after larvae infestation showed no significant effects ($P > 0.05$) of the treatments (data not shown).

The height of maize plants before infestation showed a significant effect of the maize genotype \times Si interaction ($F_{1,32} = 3.07$; $P = 0.0313$). Plants height before infestation was higher in the landrace variety than the hybrid only in the condition without Si (Figure 2c). The greatest plants height after herbivory was observed in the landrace variety (Figure 2d; $F_{1,32} = 8.38$; $P = 0.0068$), as previously expected since landrace varieties have agronomic characteristics genetically different from those of hybrids.

The Si content that was absorbed by the roots and accumulated in the shoots of maize plants did not differ between infested and non-infested plants with Si fertilization (Figure 2e; $F_{1,32} = 7.45$; $P = 0.0149$). However, when the plants were not fertilized, the highest leaf Si content was observed when FAW herbivory occurred. In the absence of herbivory, maize plants accumulated higher Si contents when fertilized.

Evaluation of oxidative stress and antioxidant enzyme activities

The concentrations of H_2O_2 were higher when Si was applied to plants in the absence of herbivory (Figure 3; $F_{1,32} = 9.99$; $P = 0.0034$). When there was no Si application, the H_2O_2 concentrations were similar between the conditions with and without herbivory, although there was some variation in the data likely due to the intensity of injury by FAW larvae, which tended to be greater in infested plants. This demonstrates that applied Si itself is recognized by the plant as a stress condition, which leads to increased concentrations of H_2O_2 in the leaf tissues.

There was a significant effect of the maize genotype \times Si \times herbivory interaction ($F_{1,32} = 4.68$; $P = 0.0380$) on lipid peroxidation, as measured by the MDA concentration. The highest MDA concentrations were observed in the hybrid without Si application and without herbivory (Table 2). MDA concentration was significantly different in the hybrid with vs. without Si; the effect was greater when there was no Si application in the absence of herbivory or when there were both Si application and herbivory.

In the landrace variety, APX activity was higher in the Si-without herbivory condition (Table 3; $F_{1,32} = 6.36$; $P = 0.0169$). This is similar to what have occurred with H_2O_2 , where Si application itself increased the H_2O_2 concentrations (Figure 3). The enzymatic activity of APX was higher in the hybrid when there was no Si application and no herbivory (Table 3).

The enzymatic activity of CAT was higher in the hybrid when there was no Si application and no herbivory (Table 4; $F_{1,32} = 11.03$; $P = 0.0022$). In the presence of herbivory, CAT activity in the hybrid was higher with Si application. In the landrace variety, higher CAT activity occurred when there was no Si application

in the presence of herbivory or when there was Si application in the absence of herbivory. In this maize genotype, both herbivory and Si treatments signaled stress conditions to the plants, increasing the enzymatic activity of CAT.

SOD activity was higher in the landrace variety without Si application and with FAW herbivory (Table 5; $F_{1,32} = 5.14$; $P = 0.0303$). The enzymatic activity was also higher in the landrace variety when the plants were Si-fertilized in the absence of herbivory.

Evaluation of FAW injury on maize plants in the greenhouse

There was a significant effect of the maize genotype \times Si \times herbivory interaction on the larval weight gain of FAW infesting potted-plants in the greenhouse (Table 6; $F_{1,32} = 26.71$; $P < 0.0001$). The larval weight gain was lower in plants of the landrace variety treated with Si and subjected to herbivory. In the absence of herbivory, the greatest larval weight gain of FAW occurred in the hybrid without Si. The effect of herbivory in the hybrid was very different under the two Si conditions: the weights of larvae were higher with Si application in the presence of herbivory or without Si application and without herbivory.

For the FAW injury on the plants, there were significant effects of the Si \times herbivory interaction (Figure 4a; $F_{1,32} = 4.32$; $P = 0.0457$). The injury scores were lower in Si-fertilized plants subjected to herbivory than in plants without Si application and with herbivory. Plants that did not experience herbivory showed lower injury scores than those subjected to herbivory under both Si conditions. The landrace variety exhibited lower injury than the hybrid (Figure 4b; $F_{1,32} = 8.04$; $P = 0.0080$).

Discussion

Our results showed that defense responses to FAW were increased in maize plants by Si fertilization, which partially interacted with the effects of herbivory and were more specific to the landrace variety. Greater root growth was observed in Si-fertilized landrace plants in the absence of herbivory, while in the hybrid greater root growth occurred in the absence of both Si and herbivory, which was correlated with higher chlorophyll index. In turn, landrace maize plants fertilized with Si and subjected to herbivory showed lower weight gain of FAW larvae and less injury, in exchange for a lower plant height. Such effects indicate that there was a specific priming effect in the landrace variety by Si application followed by induction of resistance with FAW herbivory. In addition, the landrace variety is naturally more resistant and tolerant to FAW than the hybrid of maize, as evidenced by the lower injury and higher shoot biomass and plant height after larval infestation.

The lowest weight gain of FAW larvae occurred in plants of the landrace variety only when herbivory took place after Si application. The lower larval weight gain may have occurred because the larvae fed less on the landrace variety due to resistance induced by attacked plants under Si fertilization, which resulted in reduced injury to the plants. These results suggest that the effects primed by Si fertilization were

triggered by subsequent herbivory, slowing the growth of infesting FAW larvae and reducing the injury to the landrace variety due to increased deterrence. Based on these results, we hypothesize that the landrace variety has specific resistance mechanisms, such as genes that encode Si transporter proteins in the roots, since the effects were observed only in this maize genotype that has broader genetic variability due to less intensified breeding for agronomic traits. Lsi1 and Lsi2 transporters of Si have been found in the roots of rice, maize, wheat, and pumpkin. Lsi6 is an intervascular transport protein that plays a role in Si discharge from the xylem to leaf tissues. No external transport proteins have been reported in the leaves (Yamaji and M, 2009; Reynolds et al. 2016).

Analysis of leaf Si concentrations indicated that Si applied in the soil led to greater accumulation in the shoots of maize plants, with no significant difference of herbivory in Si leaf concentration; in the absence of Si fertilization though, maize plants accumulated more Si when FAW herbivory occurred than when there was no herbivory. This suggests that Si applied to soil was absorbed by maize roots, transported to the aerial part of plants, and deposited in the leaves; under the herbivory stress condition, even without Si supplementation the plants absorbed Si to aid in induced resistance to insect attack, since the element is naturally present in soil (Epstein 1994). Previous studies have shown an increase in leaf Si concentration in maize plants fertilized with Si (Gossain et al. 2002; Alvarenga et al. 2017; Pereira 2018). Studies with other grass species have also highlighted the higher Si accumulation in the leaves of fertilized plants. For instance, Nascimento et al. (2017) and Vilela et al. (2014) found higher levels of Si in rice and sugarcane leaves fertilized with Si, respectively.

Other studies have demonstrated the Si-induced resistance to FAW in different grass species other than maize. Nascimento et al. (2017) found lower larval weight of FAW fed rice leaves fertilized with Si via the soil. Nogueira et al. (2018) also found a lower weight of FAW larvae fed leaves of rice plants treated with Si. In contrast to effects of Si-induced resistance to insects, information is lacking on Si interaction with insect herbivory to increase tolerance in plants. Jhonson et al. (2019) showed an increase in the shoot biomass of wheat plants fertilized with Si under herbivory compared to those that were fertilized but did not undergo herbivory, suggesting that insect attack could not reduce the shoot biomass in Si-fertilized plants. In the present study, the highest shoot dry mass was observed in the landrace variety when there was herbivory, which suggests that landrace plants activated tolerance mechanisms to compensate for injury caused by FAW, resulting in greater vegetative growth of the plants. The study of Jhonson et al. (2019) was pioneering in showing that Si can also elicit induction of plant tolerance to insect herbivory in grass species.

The jasmonic acid (JA) signaling pathway plays an important role in mediating the defense responses of plants against chewing herbivorous insects. After being attacked, the plant recognizes the molecular patterns associated with the herbivores and mounts a defense response. Ye et al. (2013) showed that there is a strong interaction between Si and the JA signaling pathway as Si-fertilized rice plants increased the defense levels mediated by this phytohormone and acted as a priming agent against larvae herbivory. The authors also found increased activities of defense enzymes and proteins, greater induction of transcripts encoding proteins involved in JA signaling, and greater phytohormone accumulation after

insect attack (Ye et al. 2013). According to Hall et al. (2019), when plants are fertilized with Si and later attacked by herbivores, the induction of JA production occurs more rapidly due to the priming effect triggered by Si application.

Based on the results obtained herein, Si application itself increased H_2O_2 concentrations in the leaves of fertilized maize plants, signaling a stress condition (Fester and Hause 2005). Hydrogen peroxide is one of the main ROS produced by plants under stress conditions that stimulates reactions leading to the expression of defense genes, which protect the plants from future attacks by pathogens and insects (Torres 2010). At low concentrations, H_2O_2 acts as a signaling molecule of plant defenses (Maffei et al. 2007). However, it is difficult to estimate the threshold between a high and low H_2O_2 concentration that can be compared with the values obtained in our study that could help understand the correlation between its concentrations and the plant defense responses. Future studies are warranted on this topic to give insight on the plant signaling processes mediated by H_2O_2 following Si fertilization and the interaction with insect herbivory. The present study is the second in the literature to demonstrate an increase in H_2O_2 concentrations upon Si application. Yang et al. (2017) first reported an increase in H_2O_2 concentrations in rice plants fertilized with Si.

The results allowed us to conclude that Si did not act per se as an inducer of resistance in maize to FAW. Such effects can be inferred from the results observed in the insect performance, where only under the condition of Si fertilization followed by insect herbivory was there a reduction in FAW larval weight gain in plants of the landrace variety. This was probably due to greater deterrence induced by landrace maize to infesting larvae in the plants previously primed by Si fertilization, since there was also less injury caused by FAW on the plants under this condition, indicating lower larval weight gain due to reduced feeding on plants. This is the first study dissecting the effects of priming from induction of resistance promoted by Si fertilization to insect herbivory.

Previous studies conducted with Si and FAW in maize plants only evaluated the effects of the fertilization, without testing the interactive effect with herbivory (Goussain et al. 2002; Alvarenga et al. 2017; Oliveira et al. 2017). Although in these studies the authors claimed that Si successfully induced resistance to FAW, the negative effects recorded on experimental insects were only slight, without affecting the immature development of FAW, which is the biological phase that causes injury to host plants. This suggests that the beneficial effects promoted by Si fertilization depend on the interaction with insect herbivory. This finding agrees with Coskun et al. (2018) that compiled information from the literature and concluded that the majority of positive effects with Si application were observed in stressed plants, whereas the fertilization in unstressed plants has shown to provide no additive effects. In recent studies by Oliveira et al. (2020) and Sampaio et al. (2020) that evaluated Si application to wheat and sorghum plants on the performance of aphids species, respectively, the negative effects of the fertilization per se on the insects were only modest.

Plants can respond to the presence of insect herbivores in a complex way, where priming and induced resistance can occur together, minimizing the energy costs of mounting a defense to the biotic stress

(Frost et al. 2008). Thus, it is more likely that Si acts as a primer than an inducer of resistance itself, leading to the expression of induced resistance only when the plant is under substantial stress, in this case insect herbivory (Dixon et al. 1994; Fawe et al. 2001; Reynolds et al. 2009; Alhousari and Greger 2018). In the present study, H₂O₂ production in the leaves by Si fertilization played an important role in priming defense in the landrace maize against FAW herbivory. Molecular, biochemical, and physiological traits associated with the phenotype can be used to evaluate defense priming in plants (Balmer et al. 2015; Martinez-Medina et al. 2016; Mauch-Mani et al. 2017), and measuring the concentrations of H₂O₂ produced upon application of resistance elicitors seems to be a reliable biochemical marker to dissect the effects of priming and induced resistance.

The landrace variety of maize showed higher APX activity when Si was applied in the absence of FAW herbivory, which indicates that Si played an important role in ROS scavenging by increasing the activities of antioxidant metabolism. The highest CAT and SOD activities in the landrace variety occurred in contrasting conditions where only one type of treatment was applied, i.e. when there was no Si application and presence of herbivory or when there was Si application without herbivory. The greater enzyme activities may have resulted in higher plant shoot biomass, so the increased activities in response to FAW herbivory may have contributed to ROS scavenging, thus resulting in greater tolerance in plants of the landrace variety.

In the study by Yang et al. (2017), there was an increase in CAT and SOD activities in Si-fertilized rice plants under insect herbivory, so that Si delayed the decrease in the enzyme activities under infestation condition. Contrasting results were found by Torabi et al. (2005) that observed that SOD activity increased when Si was applied to rice plants, but CAT and APX activities were decreased. In addition, Si was reported to increase plant tolerance to abiotic stress through improvement of antioxidant metabolism, as demonstrated by Gong et al. (2005) and Shi et al. (2014; 2016), in which Si fertilization increased tolerance in tomato and wheat plants subjected to water stress by increasing the enzymatic activities of SOD and CAT. Jhonson et al. (2019) first demonstrated that Si induced tolerance in wheat by promoting overcompensation in plants growth under insect herbivory. Therefore, there is evidence that Si fertilization can increase tolerance to both biotic and abiotic stress conditions by upregulating the activities of antioxidant metabolism in plant species classified as Si-accumulators.

The highest enzymatic activities of CAT and APX in the maize hybrid were observed in the conditions without Si application and without herbivory. Higher concentrations of MDA and greater larval weights of FAW were also observed under these conditions. Because the effects depended on the maize genotype, higher activities of the antioxidant enzymes served to remove excess ROS from the cells to reduce oxidative stress in the hybrid plants due to possible abiotic stress provided by the experimental conditions in the greenhouse. For example, the lesser availability of nutrients to the plants grown in pots may have been an influential factor, since maize hybrids are usually bred to respond to higher levels of macronutrient fertilization for high yields (Amorim and Souza 2005).

The increase in lipid peroxidation by ROS results in increased concentrations of MDA, one of the main products of lipid peroxidation of cell membranes, which indicates oxidative damage to these structures (Corbineau et al. 2002). MDA is used as one of the main proxies of oxidative stress in plants (Yang et al. 2017). Therefore, the results of the present study indicate that Si fertilization reduces MDA concentrations in maize plants under herbivory stress condition, reducing oxidative damage to plant cells. Ma et al. (2016) also concluded that Si decreased lipid peroxidation in fertilized plants. The results of our study along with data in the literature agree with the hypothesis that Si fertilization improves plants antioxidant metabolism, especially the increased activities of antioxidant enzymes, contributing to reducing ROS levels that would ultimately cause oxidative damage to stressed plants.

The antioxidant enzymes SOD, CAT, and APX are the main enzymes involved in plant tolerance to oxidative stress. Plants that express high antioxidant enzyme activities can more efficiently eliminate excess ROS, which protects the cellular components from the toxic effects of ROS produced under stress situations, and consequently the plants experience less oxidative damage, allowing them to tolerate the stress (Caverzan et al. 2016). In general, the results of the present study showed that increase in the activities of antioxidant enzymes occurred independently among plants fertilized with Si or subjected to herbivory, and that the responses of antioxidant enzyme activities were probably due to the sequence of events in methodology used here, i.e. first application of Si and then larval infestation, and time at which samples were collected for chemical analysis.

In the larval performance bioassay with FAW, the same effects as in the greenhouse experiment were not observed, and there were no significant differences in leaf consumption and larvae biomass for the landrace variety in the laboratory. In the hybrid there was lower leaf consumption rate and lower larval weight gain in the laboratory and greenhouse experiments, respectively. Differences in the effects between experiments were due to the methods used. The presence of FAW larvae feeding on the plants in the greenhouse was essential for the induced defense responses to occur in a more dynamic and effective way; in turn, in the lab bioassay we most likely observed the predetermined effects of the Si fertilization. These effects may be due to the mechanical barrier formed in the leaves by deposition of Si and polymerization as SiO_2 (Ma and Yamaji 2006). Thus, the methods used in the greenhouse are more appropriate for experiments aimed at evaluating the Si-induced defense effects in plants to insect herbivory.

Although Si is not classified as an essential nutrient for plants development, this element can interact with plant defense signaling pathways by regulating various physiological activities under biotic and abiotic stress conditions, attenuating oxidative stress caused by increased ROS production (Ye et al. 2013). The results of the present study demonstrate that the defense effects provided by Si probably cannot be characterized as induction of resistance, since the application of Si per se did not induce resistance in maize plants. Thus, we suggest a more appropriate term to be used in scientific literature of integrated pest management for Si in function of the negative effects it promotes on insects feeding and development via plants fertilization as “resistance elicitor” (Souza and Boiça Júnior 2019), which broadly encompasses the defense effects of both priming and induced resistance.

Another interesting result was the biostimulant effect of Si in the landrace variety under fertilization in the absence of herbivory, which resulted in higher root growth of the plants. Biostimulatory effects of Si have been reported (Van Oosten et al. 2017). “Biostimulant” is a term recently adopted by the scientific community and industry to characterize chemical and microbial compounds that improve the nutritional efficiency, tolerance to abiotic stresses, and crop quality traits, regardless of nutrient content (Du Jardin 2015; Yakhin et al. 2017). Thus, biostimulants are compounds that act in the metabolic and defense signaling pathways of plants. In the present study, the biostimulant effect provided by Si was genotype-dependent and occurred only when there was no concomitant herbivory. Vargas-Hernandez et al. (2017) suggest that some compounds play the roles of both resistance elicitor and biostimulant, depending on the doses used, which resembles an hormesis-like effect, a subject that deserves future in-depth investigation for Si (Abreu et al. 2021).

Molecular analyses will also be needed to better answer important questions on Si interactions with plant metabolic and defense signaling pathways, such as which genes are up- and down-regulated upon Si fertilization, and which transporters are present in the roots of different plant genotypes, so that desired effects can be potentiated in integrated pest management by using plants that were previously bred to better respond to Si fertilization and induce higher levels of resistance or tolerance to insect herbivory. Another interesting issue to be addressed is whether priming in Si-fertilized plants can be passed on to the produced seeds, i.e., whether the activation effect of epigenetic defenses are transgenerational. The results obtained in this study are important for characterizing the induced defense effects provided by Si fertilization and encouraging its use in a more appropriate way in integrated pest management. The implementation of Si fertilization to maize plants could contribute to the management of FAW both in countries where it is native and in the regions of the world the pest was recently established.

Declarations

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Conflicts of interest

There are no conflicts of interest.

Availability of data and material

Data transparency and originality.

Author contribution statement

All authors conceived and designed the study. LF conducted the experiment, analyzed the data, and wrote the manuscript. KE helped with part of the data collection. BS and KE assisted in writing and revising the manuscript. AB developed and provided the corn hybrids. All authors read and approved the manuscript.

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Tables

Table 1 Effects of maize genotype × Si × herbivory interaction on root dry mass (g) of maize plants

Genotype	+Herbivory		-Herbivory	
	+Si	-Si	+Si	-Si
Landrace	3.46 ± 0.15 Aa	3.65 ± 0.26 Aa	6.57 ± 0.10 Aa*	3.26 ± 0.39 Ab
Hybrid	4.06 ± 0.58 Aa	4.39 ± 0.54 Aa	4.69 ± 0.64 Ba	4.71 ± 0.33 Aa*

Means followed by the same uppercase letters in columns and lowercase letters in rows are significantly different by Tukey's test ($P < 0.05$). * indicates a significant difference between herbivory events.

Table 2 Effects of maize genotype × Si × herbivory interaction on lipid peroxidation (mmol MDA mg FW⁻¹)

Genotype	+Herbivory		-Herbivory	
	+Si	-Si	+Si	-Si
Landrace	132.69 ± 27.53 Aa	55.00 ± 50.84 Aa	100.77 ± 67.44 Aa	69.61 ± 27.77 Ba
Hybrid	262.31 ± 36.38 Aa*	159.61 ± 35.14 Aa	72.31 ± 45.40 Ab	391.92 ± 129.86 Aa*

Means followed by the same uppercase letters in columns and lowercase letters in rows are significantly different by Tukey's test ($P < 0.05$). * indicates a significant difference between herbivory events.

Table 3 Effects of maize genotype × Si × herbivory interaction on APX activity ($\mu\text{M AsA min}^{-1} \text{mg}^{-1} \text{FW}$)

Genotype	+Herbivory		-Herbivory	
	+Si	-Si	+Si	-Si
Landrace	4.48 ± 0.76 Aa	4.20 ± 0.89 Aa	6.65 ± 1.27 Aa	1.65 ± 0.48 Bb
Hybrid	4.29 ± 0.63 Aa	3.68 ± 0.56 Aa	4.77 ± 0.57 Aa	5.76 ± 1.42 Aa

Means followed by the same uppercase letters in columns and lowercase letters in rows are significantly different by Tukey's test ($P < 0.05$)

Table 4 Effects of maize genotype × Si × herbivory interaction on CAT activity ($\mu\text{mol H}_2\text{O}_2 \text{min}^{-1} \text{mg}^{-1} \text{FW}$)

Genotype	+Herbivory		-Herbivory	
	+Si	-Si	+Si	-Si
Landrace	0.54 ± 0.05 Bb	1.22 ± 0.42 Aa	1.00 ± 0.07 Aa	0.76 ± 0.18 Ba
Hybrid	1.29 ± 0.16 Aa	1.07 ± 0.12 Aa	1.36 ± 0.16 Ab	2.00 ± 0.09 Aa*

Means followed by the same uppercase letters in columns and lowercase letters in rows are significantly different by Tukey's test ($P < 0.05$). * indicates a significant difference between herbivory events

Table 5 Effects of maize genotype × Si × herbivory interaction on SOD activity ($\text{U SOD min}^{-1} \text{mg}^{-1} \text{FW}$)

Genotype	+Herbivory		-Herbivory	
	+Si	-Si	+Si	-Si
Landrace	0.26 ± 0.00 Ab	0.29 ± 0.00 Aa	0.29 ± 0.00 Aa*	0.28 ± 0.00 Aa
Hybrid	0.28 ± 0.00 Aa	0.27 ± 0.00 Ba	0.28 ± 0.00 Aa	0.27 ± 0.00 Aa

Means followed by the same uppercase letters in columns and lowercase letters in rows are significantly different by Tukey's test ($P < 0.05$). * indicates a significant difference between herbivory events

Table 6 Effects of maize genotype × Si × herbivory interaction on larvae biomass (mg) of *S. frugiperda*

Genotype	+Herbivory		-Herbivory	
	+Si	-Si	+Si	-Si
Landrace	82.53 ± 5.30 Bb	135.26 ± 16.03 Ba	108.53 ± 5.22 Ba	104.66 ± 0.35 Ba
Hybrid	243.76 ± 8.54 Aa*	198.36 ± 3.40 Ab	185.03 ± 9.34 Ab	234.66 ± 19.41 Aa*

Means followed by the same uppercase letters in columns and lowercase letters in rows are significantly different by Tukey's test ($P < 0.05$). * indicates a significant difference between herbivory events

Figures

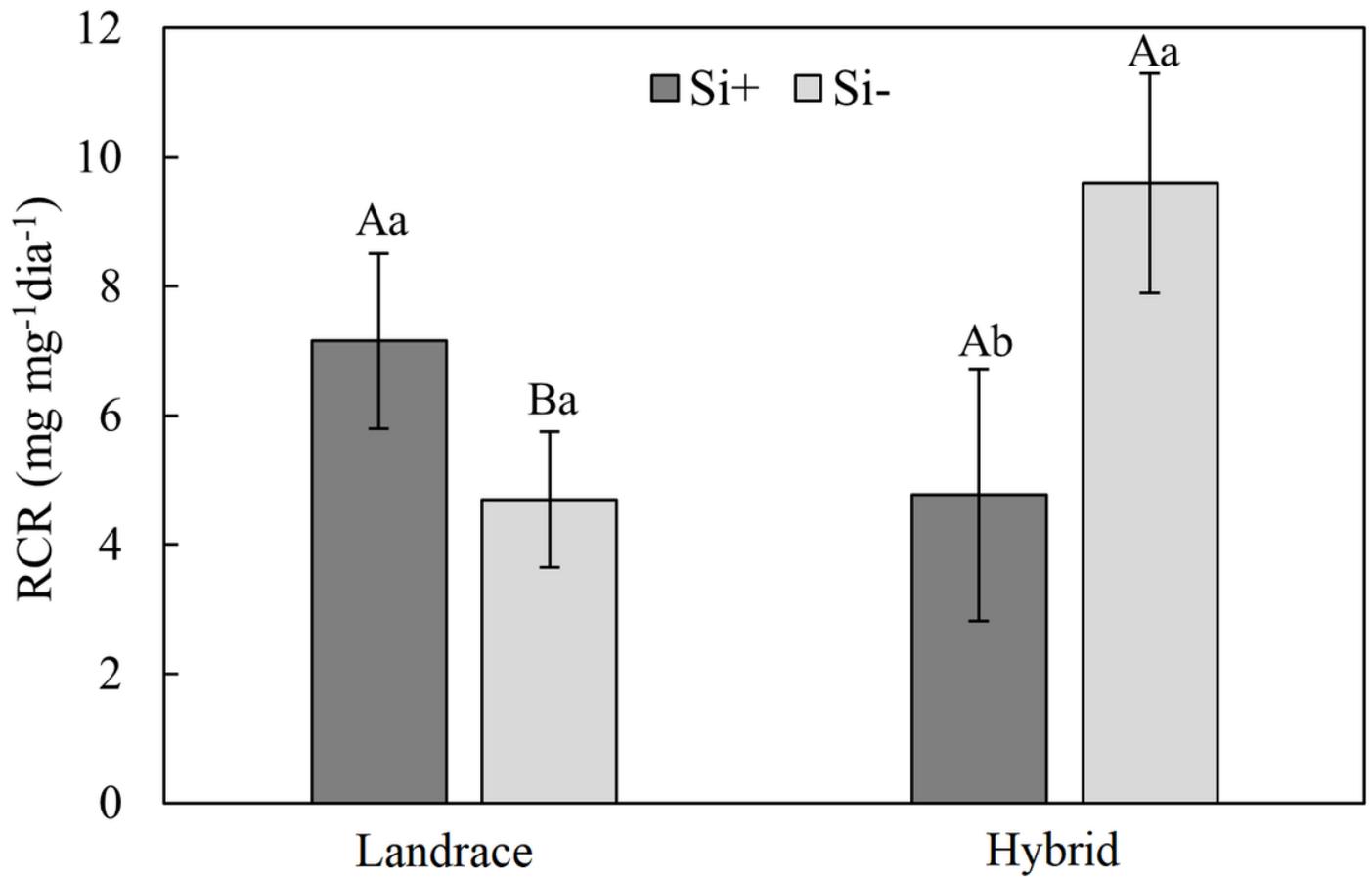


Figure 1

Effects of maize genotype × Si interaction on the relative consumption rate (RCR) of *Spodoptera frugiperda* larvae. Different uppercase letters between genotypes and lowercase letters within the genotype denote significant differences ($P < 0.05$).

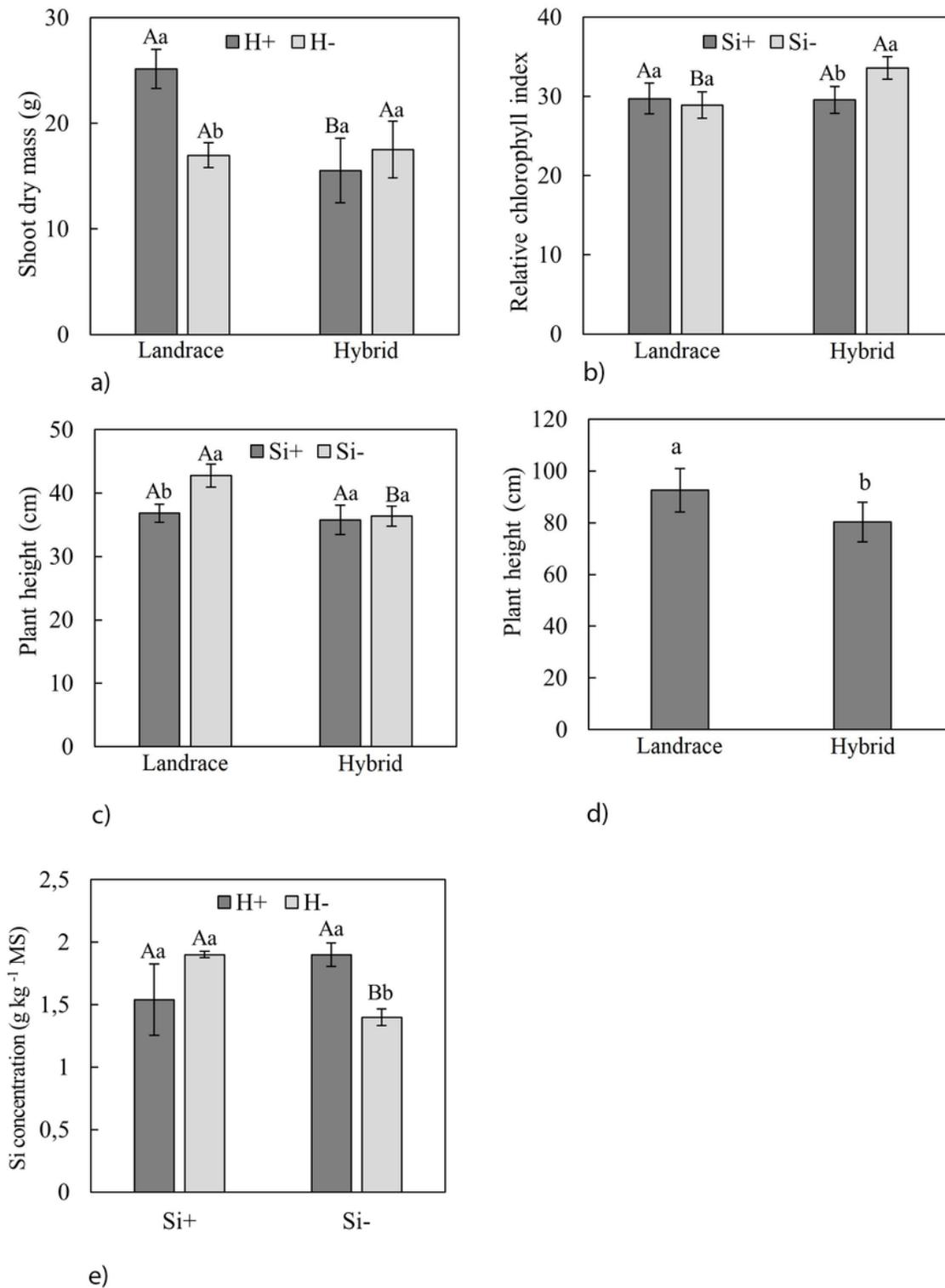


Figure 2

a Effects of maize genotype × herbivory by *S. frugiperda* interaction on shoot dry mass of plants; b Effects of maize genotype × Si interaction on relative chlorophyll index before infestation; c Effects of maize genotype × Si interaction on plant height before infestation.; d Effects of maize genotype on plant height after infestation; e Effects of Si × herbivory interaction on Si concentration in the shoot of plants

Different uppercase letters between genotypes and lowercase letters within the genotype denote significant differences ($P < 0.05$)

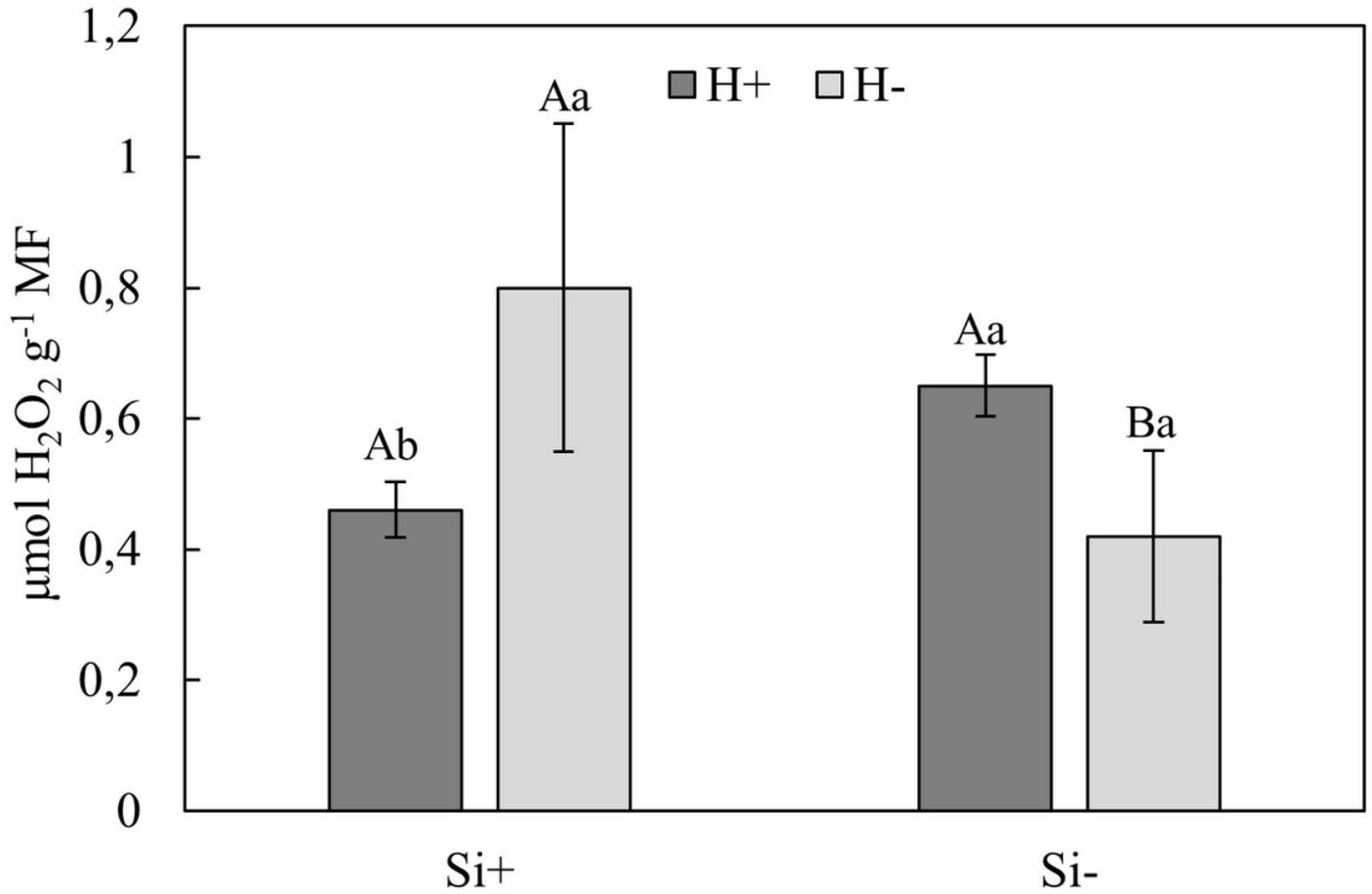


Figure 3

Effects of the Si × herbivory interaction on concentration of hydrogen peroxide (H₂O₂) Different uppercase letters between genotypes and lowercase letters within the genotype denote significant differences ($P < 0.05$).

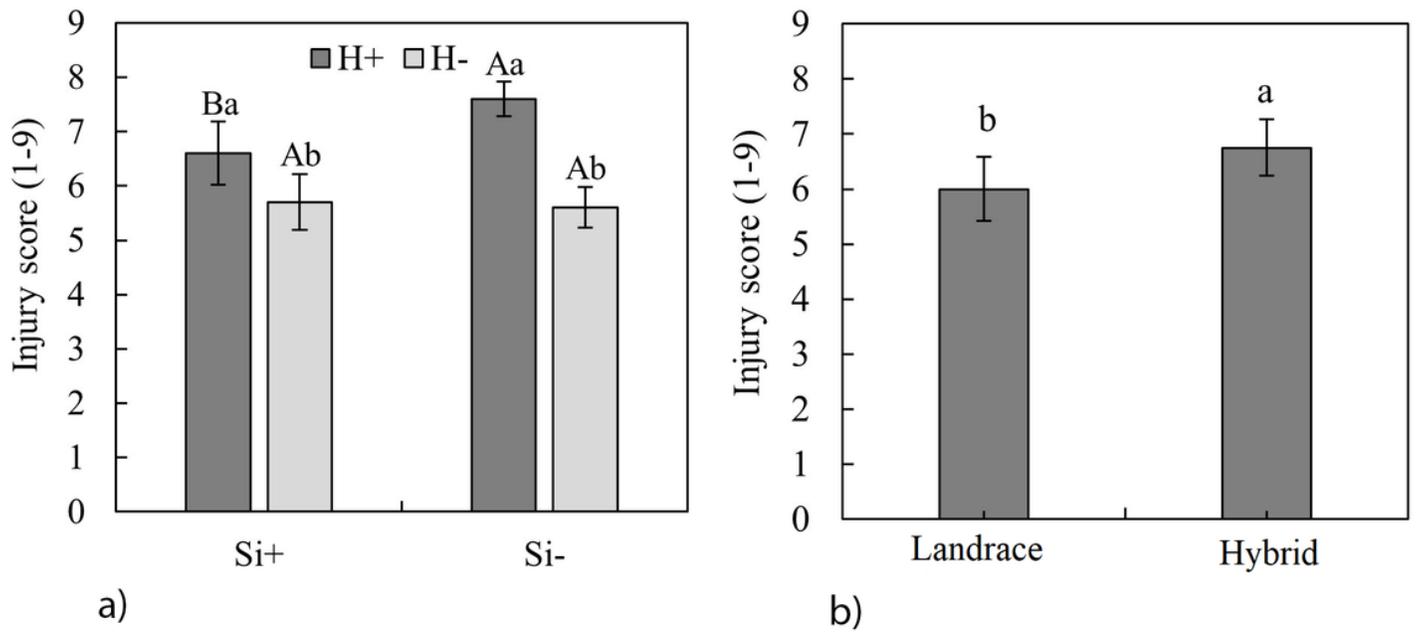


Figure 4

a Effects of the Si x herbivory interaction on the injury score of *Spodoptera frugiperda* larvae in maize genotypes. b Effect of maize genotype on the injury score of *Spodoptera frugiperda* larvae. Different uppercase letters between genotypes and lowercase letters within the genotype denote significant differences ($P < 0.05$)

Supplementary Files

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