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Potential of Silicon to Improve Biological Control of Fall Armyworm, *Spodoptera frugiperda* on Maize

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Abstract: Silicon (Si) accumulation in plants confers a mechanical barrier to insect herbivory and may alter plant chemistry to increase the attraction of natural enemies to host insect herbivores on Si−treated plants. The fall armyworm (FAW), *Spodoptera frugiperda*, is a major insect pest of grain crops, including maize (*Zea mays* L.). This study examined whether Si supplementation alters maize volatile compounds that mediate host location in *Euthyrhynchus floridanus*, a generalist predator of FAW. A four-arm olfactometer was used to test the olfactory preference of nymphs and adults of *E. floridanus* to the odor of maize leaf materials from plants that were; Si−treated and infested, Si−treated without infestation, Si−deprived and infested, and Si−deprived without infestation. The probabilities of individual insects choosing between the four treatments were estimated using a multinomial generalized linear mixed model. There were no statistical differences in the olfactory preference of *E. floridanus* between Si−treated and Si−deprived maize leaf materials. However, the median estimate showed that nymphs were almost twice likely to be attracted to Si−supplemented leaf material, indicating a potential positive effect of Si. However, a more robust follow-up study is needed to further assess the impact of Si on *E. floridanus*.

Keywords: silicon; biocontrol; fall armyworm; maize; *Euthyrhynchus floridanus*; volatile compounds

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1. Introduction

The fall armyworm (FAW) *Spodoptera frugiperda*) (J.E Smith) (Lepidoptera: Noctuidae) is a pest of economic importance to maize (*Zea mays* L.) [1,2]. It is a highly polyphagous insect native to North and South America, where it breeds all year round in tropical and subtropical regions [3]. Moths are active at night, and females lay their eggs on the leaves, silk, developing kernels, and ears of maize [4]. The resulting larvae feed and develop on the different parts of the plant, severely impacting both vegetative and grain production [5]. Application of synthetic chemical insecticides, such as Radiant, Tracer, Karate, Ampligo, and Malathion, are among the commonly used products to control FAW [6]. However, overreliance on insecticides may cause target organisms to be resistant to certain active ingredients and therefore reduce their efficacy [7]. It is also widely accepted that synthetic chemical insecticides can have negative impacts on human health and the environment if not sustainably used within an integrated pest management (IPM) framework [8]. Consequently, there is a growing need for more sustainable options for the management of FAW on maize, and improving the efficacy of biological control agents (i.e., parasitoids and predators) is one avenue that could be explored [9].

Biological control is an ecologically based approach to pest management that involves the use of one organism (i.e., natural enemy) to control another (i.e., pest) [10]. Owing to the environmental and human health risks associated with the use of synthetic pesticides [8], biological control has become an increasingly important component of IPM [11]. Fall armyworm natural enemies, such as parasitoids and predators, have been recorded in many parts of the world [6,12]. The Florida predatory stink bug *Euthyrhynchus floridanus* (L.) (Heteroptera: Pentatomidae) is a generalist predator of FAW native to North America (Florida) [13]. It feeds on a diverse range of crop pest species, including larvae of Coleoptera and Lepidoptera, and it has been used as a model predator for FAW [13]. Attracting and retaining populations of *E. floridanus* is likely to improve the biological control of FAW on maize crops under open field conditions [14].

Silicon (Si) is the second most abundant element in the earth's crust after oxygen [15]. Silicic acid (Si(OH)4) is a water-soluble form of Si commonly found in the soil solution at pH < 9 [16]. Plant roots absorb Si in the form of monosilicic acid and are transported through the transpiration stream to vegetative parts [17]. During transportation through the plant, monosilicic acid is polymerized and deposited in the vegetative parts (i.e., leaves, stems, and hulls) as a silica gel [18]. Agricultural crops in the grass family (Poaceae), including maize, are regarded as high accumulators of Si [19]. Although not regarded as an essential element for plant growth, there is an increasing volume of research suggesting the importance of Si in plant defense against insect pests [20,21].

Silicon enhances plant resistance against insect herbivory mainly through physical and chemical mechanisms [22]. The physical resistance mechanism is facilitated by the deposition of Si in the plant tissues (i.e., foliage, spines, and trichomes), thereby forming a physical barrier to insects [23]. Previous research has demonstrated that Si−enriched plant tissues are highly abrasive and rigid, making it difficult for an insect to chew and digest [20]. A study by [24], for example, showed increased mortality and mandibular wear in FAW larvae reared on Si−treated maize plants. Similarly, feeding on Si−treated maize plants resulted in a six-fold increase in mortality of neonates and a two-fold reduction in weight gain of third-instar FAW larvae compared to those on Si−deprived plants [20]. Briefly stated, these studies suggest that tissue hardness and reduced digestibility may be among the primary resistance mechanisms against chewing insect pests on Si−treated plants. The chemical resistance mechanism is mediated by the ability of Si to amplify or alter the blend of volatile plant defense compounds emitted during insect herbivory [25]. Volatile defense compounds often act as deterrents or attractants of insect pests and thus may be exploited as host location cues by predators and parasitoids of herbivory insects [26,27]. For example, a study on cucumber (*Cucumis sativus*) showed that the application of Si increased the attraction of a generalist predator (*Dicranolaius bellulus* Guerin-Meneville) (Coleoptera: Melyridae) to plants infested by (*Helicoverpa armigera* Hübner) (Lepidoptera: Noctuidae) [27]. Using olfactometer bioassays, [20] also showed that herbivore-induced plant volatiles (HIPVs) produced by Si−treated maize plants were more attractive to a generalist FAW predator (*Orius insidiosus* Say) (Hemiptera: Anthocoridae), compared to odor from Si−deprived plants.

Based on this potential of Si for attracting natural enemies of insect pests, it was hypothesized that treating maize plants with silicon would improve the biological control of FAW. Therefore, the aim of this study was to evaluate if soil application of Si to maize could increase the attraction of E. floridanus to FAW−infested plants.

2. Materials and Methods

2.1. Study Site

This study was carried out at the Center for Biological Control, College of Agriculture and Food Sciences, Florida A&M University, Tallahassee, FL, USA.

2.2. Insect Culture

A colony of FAW was initiated from egg masses that were collected from an existing culture maintained at the Center for Biological Control laboratory. Egg masses were packed in Ziploc bags and placed in a growth chamber with temperature, humidity, and photoperiod set at 25 ± 2 °C, 40–60%, and 13L:11D, respectively, until larval eclosion (3–4 days). An artificial diet for FAW was prepared by mixing diet (dry formulation) (Multiple Species diet, Southland Products, Inc., Lake Village, AR, USA) with boiling water and linseed oil (ingredient ratio: 174.19 g diet/1000 mL water/2.85 mL linseed oil) using an electronic blender. The diet mix was blended for 3–4 min and immediately poured into plastic cups (Volume ~30 mL) under a laminar flow. Each plastic cup contained about 10 g of prepared artificial diet and was left on the laminar flow to cool for 30 min. Using a camel hair brush, neonate larvae were placed singly into each of the plastic cups. The cups were immediately closed and taken to the rearing room. During the rearing process, temperature, relative humidity, and photoperiod were also maintained at 25 ± 2 °C, 40–60%, and 13L:11D, respectively. Larvae were reared on an artificial diet until they reached 3rd–4th instars, when they were used to infest maize leaves for olfactometer bioassays. All the adults and nymphs of *E. floridanus* used in this experiment were collected from a culture maintained at the United States Department of Agriculture (USDA)–Agricultural Research Service (ARS), Center for Medical, Agricultural and Veterinary Entomology, Tallahassee, FL, USA.

2.3. Plant Growth and Silicon Supplementation

Hybrid maize seed cv. DeKalb (Monsanto, Felda, FL, USA) was planted in a greenhouse, singly in plastic pots containing 1 kg of potting soil (Smart Naturals, Happy Frog potting soil, FoxFarm Soil, and Fertilizer Co., Arcata, CA, USA). Plants were arranged into 2 batches of 30 plants; Si−treated, each drenched with 200 mL of 16 g/L potassium silicate (AgSiL H16®, PQ Corporation, Valley Forge, PA, USA), and control-Si−deprived plants, drenched with 200 mL of 7.5 g/L potassium chloride. Control plants were treated with potassium chloride in order to balance the amounts of potassium across treatments. Each pot was placed on a plastic plate to trap and allow subsequent uptake of the drained Si or potassium chloride solution. Potassium silicate and potassium chloride were applied twice, at 1 week after plant emergence and the final application 1 week later. Plants were irrigated with tap water every 2–3 days. Data of water analysis at Florida A&M University showed that the water contained about 1.5 mg/L of Si.

2.4. Plant Silicon Analysis

A separate set of plants with the same levels of treatments (as described above) was maintained in the greenhouse to confirm if Si−treated plants accumulated adequate amounts of Si compared to control plants. One week after the final application, leaves were cut off from plants, put in paper bags, and later dried in an oven at 60 °C for 72 h. Dry leaves were ground using a grinder (Mixer Mill MM 400, Verder Scientific, Newtown, PA, USA). The ground leaf samples were sent to the University of Florida (Analytical Research Laboratory, Gainesville, FL, USA) for silicon content analysis using a method similar to that of [28].

2.5. Olfactory Response of *E. floridanus* to Silicon-Treated Plants

One week following the final application of Si, when plants were 4 weeks old, leaves from each batch of plants (treatment or control) were cut into 5 cm sections and placed onto Petri dishes. Four treatments were prepared: (1) Si−treated and infested (Si+FAW+), (2) Si−treated without infestation (Si+FAW−), (3) Si−deprived and infested (Si−FAW+), and (4) Si−deprived without infestation (Si−FAW−). In order to achieve infestation, 10 larvae (3rd–4th instar) of the FAW were placed into Petri dishes containing maize leaves and allowed to feed for 24 h. Petri dishes were maintained in the insect rearing room at 25 ± 2 °C, 40–60% RH, and 13L:11D until the leaves were used for olfactometer bioassays.

A four-arm olfactometer (Analytical Research Systems, Gainesville, FL, USA) (Figure 1) was used to test the olfactory attraction of *E. floridanus* to odor from four treatments. Three to four pieces of leaves from each treatment were placed into an odor chamber of the olfactometer. The airflow was set at 8 L/h during the bioassays, and the temperature ranged between 22 and 25 °C during the day between 10:00 am and 5:00 pm. The olfactometer arena and odor chambers were rinsed with 85% ethanol and dried in an oven at 50 °C for 1 h. Five adult insects or 10 nymphs were introduced at a time into the inlet adaptor of the olfactometer. For adult *E. floridanus*, each treatment was replicated 5 times, while 3 replicates were performed for nymphs, giving a total of 100 adults and 120 nymphs tested. A choice was recorded after 10 min when the insect entered the arm or odor chamber of the olfactometer. The 10 min duration of bioassay was adopted based on results of preliminary experiments showing that this was the minimum time it took for insects to enter the olfactometer arena and choose a treatment arm.

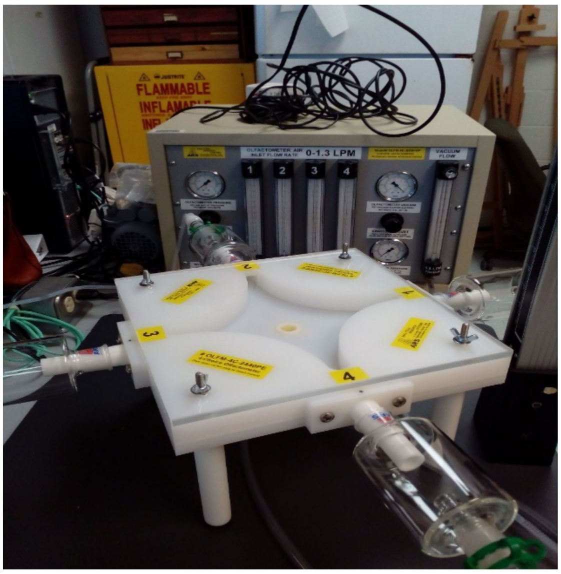

Figure 1. A four-arm olfactometer used to test the olfactory response of *E. floridanus* to odor from maize leaf materials.

2.6. Statistical Analysis

A Welch two-sample t-test was used to test for differences in the amounts of Si accumulated in plant tissue between Si−deprived and Si−supplemented plants. A multinomial generalized linear mixed model was fit to the *E. floridanus* olfactory response data. The model estimates the probabilities of an individual insect choosing between five different outcomes. Each individual insect could have either entered one of the four olfactometer arms or not responded; therefore, the probability of those five outcomes was constrained to sum to 1. No response was coded as the reference level in the model. We included a fixed effect of age (nymph or adult) and a random intercept for each replicate nested within each age. The random variation of runs within replicates was accounted for by the overall model residuals. The model assumes a multinomial response distribution with a logit link function. We fit the multinomial mixed-effects model in a Bayesian framework. We assigned normal prior distributions with mu = 0 and sigma = 3 to the fixed-effect parameters and Student's *t* prior distributions with mu = 0, sigma = 2.5, and nu = 3 to the intercept and random-effect variance parameters. We sampled the posterior distribution with four Markov chains, each for 2000 warmup and 1000 post-warmup iterations. We assessed model convergence by ensuring that the R-hat statistic was less than 1.01 for all parameters. We extracted the posterior probabilities of response for each treatment and the contrasts between each pair of treatments from the fitted model object. The pairwise treatment contrast is a ratio of the probability of attraction of two treatments; a value of

1 indicates the equal probability of attraction to either treatment. We calculated medians, 66%, and 95% quantile credible intervals for each probability and contrast. In addition, we took a contrast between the average of both Si+ and both Si− treatments to assess whether there was an overall difference in the attractiveness of plant material with and without the Si treatment. Finally, we calculated the Bayes factor (BF) for each fixed-effect parameter in the model to assess the strength of evidence that the posterior distributions differed from the prior distributions centered at zero.

3. Results

3.1. Plant Silicon Analysis

Analysis of maize plant leaves for Si content indicated that plants treated with Si accumulated more Si in their tissue compared to control plants (Figure 2) (t = −8.42; *d.f.* = 2.02; p = 0.013).

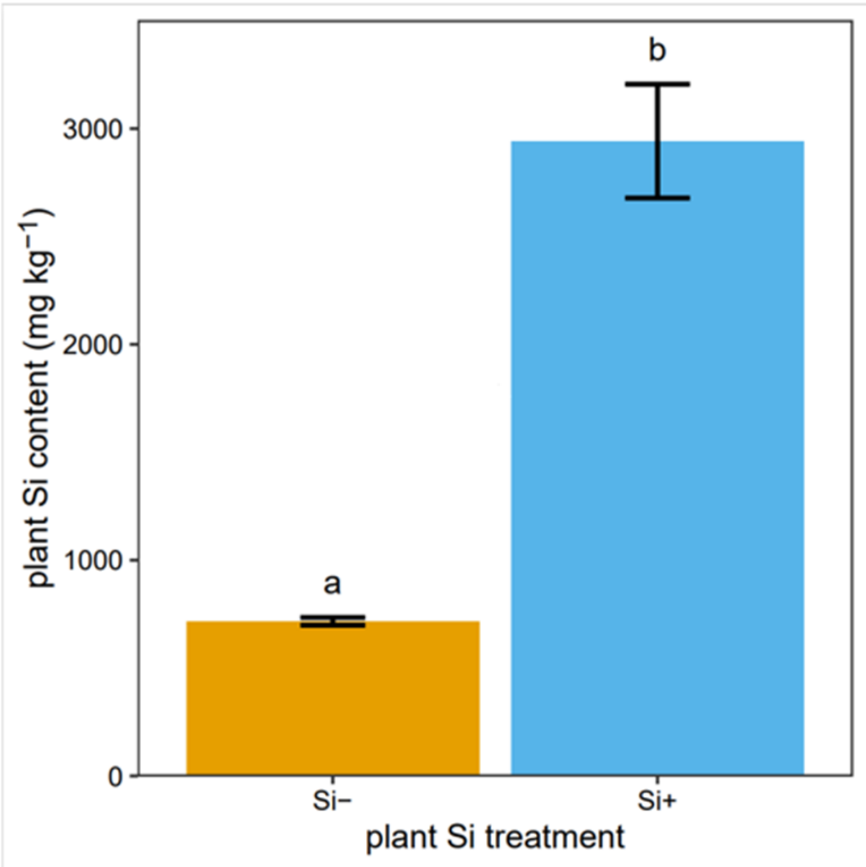

Figure 2. Silicon (Si) content in maize leaf tissue 1 week following application. Si−(orange bar) = silicon deprived plants treated with potassium chloride; Si+ (blue bar) = silicon supplemented plants treated with potassium silicate. N = 3, error bars = standard error. Silicon content between Si− and Si+ is significantly different (t = −8.42, p = 0.013). Letters 'a' and 'b' indicate significant differences between the bars.

3.2. Olfactory Response of *E. floridanus* to Silicon-Treated Plants

We did not observe evidence for the relative difference in attraction of adult or immature (3rd–4th instar nymph) *E. floridanus* to odor from plants subjected to any of the four treatments. The posterior estimate of the probability of attraction of adult insects to plant material from the Si+/FAW+ treatment was 0.142 with 95% credible interval (CI) [0.053, 0.284], Si+/FAW− was 0.220 [0.098, 0.380], Si−/FAW− was 0.094 [0.016, 0.345], and Si−/FAW+ was 0.166 [0.041, 0.433]. For nymphs, the modeled probability of attraction to

Si+/FAW+ was 0.138 [0.058, 0.281], Si+/FAW− was 0.141 [0.061, 0.258], Si−/FAW− was 0.058 [0.008, 0.253], and Si−/FAW+ was 0.078 [0.015, 0.245] (Figure 3).

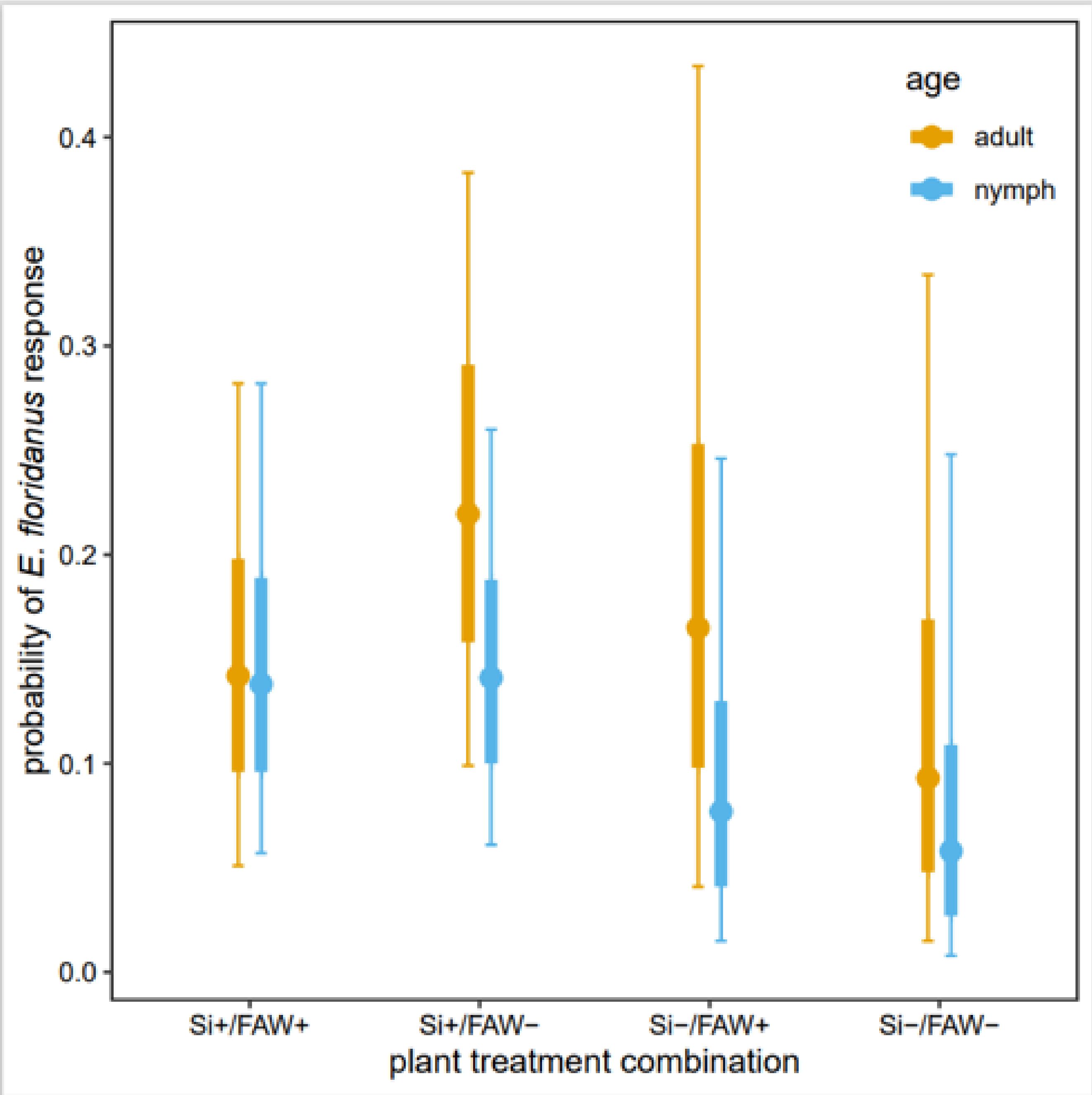

Figure 3. Posterior estimates of the probability of response by adult (orange points and bars) and nymph (blue) of *E. floridanus* to each of the four treatments. Median estimates are indicated with points; thick error bars represent 66% quantile credible intervals, and thin error bars represent 95% quantile credible intervals. FAW = fall armyworm; Si+FAW+ = silicon-treated and infested; Si+FAW− = silicon-treated without infestation; Si−FAW+ = silicon deprived and infested; Si−FAW− = silicon deprived without infestation.

When comparing treatments' attractivenesses, the 95% credible intervals for the relative preferences contain 1 in all cases (Table 1), and the BFs for all parameters were no greater than 1.27 (Table 2), indicating no evidence that the posterior distribution differed from the prior expectation of no effect. We also did not find any evidence that the odor of the plant material treated with Si was more attractive overall than material not treated with Si for either adults or nymphs; again, the 95% credible intervals for the relative preferences contain 1 (Table 2).

Table 1. Pairwise treatment contrasts (relative preferences) for all pairs of treatments for adults and nymphs and for Si+ and Si− overall. Median posterior estimates of relative preference are given, along with the lower and upper bounds of the 95% and 66% credible intervals.

	Contrast	Relative Preference	95% Credible Interval	66% Credible Interval
Adult	Si+/FAW+ vs. Si+/FAW−	0.645	0.199, 1.982	0.387, 1.053
	Si+/FAW+ vs. Si−/FAW−	1.514	0.263, 11.138	0.707, 3.34
	Si+/FAW+ vs. Si−/FAW+	0.862	0.173, 4.352	0.439, 1.714
	Si+/FAW− vs. Si−/FAW−	2.332	0.439, 16.143	1.11, 5.144
	Si+/FAW− vs. Si−/FAW+	1.348	0.315, 6.709	0.725, 2.541
	Si−/FAW− vs. Si−/FAW+	0.574	0.063, 4.635	0.229, 1.436
	Si+ vs. Si−, overall	1.337	0.385, 4.067	0.789, 2.273
Nymph	Si+/FAW+ vs. Si+/FAW−	0.981	0.331, 3.001	0.585, 1.619
	Si+/FAW+ vs. Si−/FAW−	2.4	0.373, 19.626	1.071, 5.65
	Si+/FAW+ vs. Si−/FAW+	1.746	0.367, 11.357	0.91, 3.733
	Si+/FAW− vs. Si−/FAW−	2.44	0.401, 19.7	1.117, 5.63
	Si+/FAW− vs. Si−/FAW+	1.797	0.394, 11.625	0.923, 3.765
	Si−/FAW− vs. Si−/FAW+	0.749	0.071, 7.421	0.271, 1.98
	Si+ vs. Si−, overall	1.933	0.496, 6.714	1.127, 3.385

Si+ = silicon supplemented plants; Si− = silicon deprived plants; FAW+ = fall armyworm infested plants; FAW− = plants not infested by fall armyworm.

Table 2. Bayes factors (BF) associated with the fixed-effect parameters for each treatment. BF < 3 indicates no evidence for a difference from the prior expectation of no treatment effect, and BF < 1 indicates evidence against an effect.

	Treatment	Bayes Factor
Adult	Si+/FAW+	1.157
	Si+/FAW−	0.220
	Si−/FAW−	1.272
	Si−/FAW+	0.482
Nymph	Si+/FAW+	0.337
	Si+/FAW−	0.992
	Si−/FAW−	0.648
	Si−/FAW+	1.026

Si+ = silicon supplemented plants; Si− = silicon deprived plants; FAW+ = fall armyworm infested plants; FAW− = plants not infested by fall armyworm.

4. Discussion

Silicon content analysis of maize plants used for the olfactometer bioassays indicated that Si content more than tripled in treated plants compared to Si−deprived plants. This finding provided evidence that plant leaves that were subjected to olfactometer bioassays had accumulated sufficient amounts of Si compared to control plants. Although Si uptake in most plants is facilitated by insect herbivory [29], this study clearly indicated that maize has a capacity to accumulate Si within a relatively shorter period of time (~14 days), even in the absence of plant damage or insect herbivory. This is consistent with previous studies suggesting that cereal crops (Poaceae) are high accumulators of silicon due to the presence of efficient Si transporter genes in the plants [30].

The olfactory response of nymphs and adult *E. floridanus* to maize plants treated with Si was observed during a 10 min olfactometer bioassay. While there was no statistical difference in the olfactory response of *E. floridanus* between Si−treated and Si−deprived maize plants, results from this study indicated the potential of increasing attraction of particularly nymphs of *E. floridanus* to Si−supplemented plants: the median estimate indicated that nymphs were almost twice as likely to be attracted to Si−supplemented leaf material, although this estimate was highly uncertain (relative preference 1.933, 95% credible interval [0.496, 6.714]; Table 1). When plants are attacked by herbivory insects, they defend themselves indirectly by producing volatile defense compounds, which attract and guide natural enemies such as predators and parasitoids to host insects [31,32]. Studies have shown that Si supplementation in plants regulates the jasmonate pathway resulting in the production of volatile compounds that are more attractive to natural enemies [21,25]. We, therefore, assume that the slight increase in olfactory preference of *E. floridanus* nymphs for Si−treated and FAW−infested maize plants could have been due to a change in plant volatiles resulting from Si application [25]. This observation is similar to that of [20], who showed that HIPVs from Si−supplemented maize plants were more attractive to the FAW generalist predator (*O. insidiosus*) compared to odor from Si−deprived plants. Results from this study suggest that Si supplementation may benefit *E. floridanus* nymphs in search of FAW larvae on maize plants.

Since the current study is preliminary, a more robust follow-up study with adequate replication of treatments is needed to further assess the impact of Si supplementation on the attraction of *E. floridanus* to FAW−infested maize plants. Since Si−treated and control plants were raised in the same greenhouse, there could have been a chance of '*cross-talk*' between the plants, which may have elicited the production of defense chemicals in control plants. It is well established that volatile compounds produced by herbivore-infested plants could trigger defense responses in nearby plants against future insect attacks [33]. It would, therefore, be useful in future studies to consider complete isolation of Si treatments (i.e., use of separate greenhouses) to reduce the effect of cross-talk.

Results from this study are promising and provide insights that could help to optimize the biological control efficiency of natural enemies of FAW under field conditions. Future studies should consider identifying volatile compounds associated with Si−treated maize plants as well as testing their attractiveness to a range of natural enemies of FAW. The effect of Si supplementation on the volatile compounds used by FAW females to locate maize plants for oviposition [34,35] is equally another interesting aspect to investigate in the future.

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