Silicon
https://doi.org/10.1007/s12633-020-00901-8

ORIGINAL PAPER

Effect of Silicon and Plant Growth Regulators on the Biology and Fitness of Fall Armyworm, *Spodoptera frugiperda,* a Recently Invaded Pest of Maize in India

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Received: 29 October 2020 / Accepted: 14 December 2020

Abstract
Silicon (Si) and Plant growth regulators (PGR's) are known to induce resistance against various insect pests. A study was conducted to determine the effect of Si and PGR's on biology and induced resistance in maize against recently invaded fall armyworm (FAW), *Spodoptera frugiperda.* Different foliar silicic acid (FSA), gibberellic acid (GA_3) and jasmonic acid (JA) at different concentrations and combinations were evaluated. The larvae fed on plants treated with FSA, FSA + GA_3 and jasmonic acid exhibited lower larval, pre-pupal and pupal weight, whereas no effect of gibberellic acid alone on these parameters. Application of FSA at 2 ml $L^{-1}$and GA_3 0.5 mg $plant^{-1}$ significantly decreased the larval weight (18.38 mg at 5th day, 219.35 mg at 10th day), pre-pupal weight (168.64 mg), pupal weight (158.22 mg) and larval survival (70.00%), fecundity (500.20 eggs/female) and fertility (62.68%). Male longevity was decreased by all the treatments except with the application of GA_3 and JA and female longevity was unaffected by JA. The biological parameters of *S. frugiperda* were negatively correlated with increase in Si, phenols and tannins and potassium concentration in leaves. The study conclusively demonstrated significant negative effect on various biological parameters of FAW when plants were treated with Si and PGR's.

Keywords Exogenous application · Foliar silicic acid · GA_3 · JA · Induced resistance

1 Introduction

Fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) an invasive pest, causing huge damage to maize in different states of India. It was reported in India on maize during May 2018 [57] and now widespread throughout India. FAW is native to Americas found in many countries namely USA, Brazil, Canada, Argentina [12, 48]. FAW was first reported in African countries in 2016 [18] and now it is widespread in Asian countries [39], causing economic losses in different crops like maize, soybean, cotton, beans [40, 46], rice, other grasses and number of weeds [38]. Since its introduction in India, various management strategies are being evaluated to reduce its damage. One of the areas which could be employed for FAW management in India is induced host plant resistance.

Throughout the world, research interest has increased in host plant resistance and on chemical elicitors to stimulate host plant defence against insect pests [7, 23]. Many of these defences are regulated by signalling pathways of plants in which plant growth regulators and other amendments have central roles. Plants produce a wide variety of hormones; exogenous application of some of the PGRs induces defence in plants to several biotic and abiotic stresses. They also interfere in the biology of insects, thus reducing growth and development.

Silicon is the second most abundant element in soil and comprises ~28% (wt/wt) of earth's crust [17]. Although Si is non essential element for the majority of plants, the beneficial effects of this element on plant growth, development, stress resistance and defence mechanism against insect pest and diseases have been well documented in many plant species.

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Foliar application of silicon has been shown to influence plant growth, yield and silicon content of different crops such as rice [14, 44], finger millet [52], wheat [54], soybean [58] sugar beet [3], control pest and disease in rice [8, 50, 61], soybean [51, 13], grape [6], coffee [33], cucumber [32] and tomato [29] and induce resistance to abiotic stress in crops like rice [64], wheat [53] potato [45] and soybean [31]. It is now well established that Si enhances plant resistance and reduces plant damage caused by pathogens, insect and non-insect pests [35]. The application of silicon increases resistance in plants in two ways; one is by physical resistance and second is by chemical defence. However, the effect of application of silicic acid needs to be evaluated against FAW.

Fall armyworm is a recently invaded pest so that various strategies need to be developed for its management in India. Chemical insecticides are known to be often hazardous to many life forms within the natural environment and affect plant productivity. To preserve the plants productivity and maintain the ecological balance, it is important to understand the host plant resistance and its utilization for pest management. The aim of present study is to evaluate the effect of exogenous application of foliar silicic acid (FSA) [as a source of Si], gibberellic acid (GA_3) and jasmonic acid (JA) [as plant growth regulators] on the biology and fitness of *S. frugiperda.* These treatments known to affect the biochemical contents thereby induce resistance in plants. Hence studies were made to analyse the phenols, tannins, silicon and potassium content of the plants to understand the relationship between biology and induced resistance against *S. frugiperda* due to the foliar application of silicic acid and PGR's.

2 Materials and Method

2.1 Experimental Details

Experiment was conducted under laboratory condition at College of Agriculture, Navile, Shivamogga, during 2019–20. The laboratory culture was maintained by field collected eggs and larvae of different instars which were reared in laboratory with maize plants grown in green house in the pots (4 l capacity). The culture was maintained on commercial grown maize variety P3550 (Pioneer) in growth chamber with temperature of 25 ± 1 °C, RH 80% and light 14 L:10 D. Treatments composed of various plant growth regulators and silicic acid were sprayed to the plants grown in pots. A pot consisted single maize plant and each treatment consisted 30 plants in replications. Potting mixture consisted of red loamy soil mixed with compost having uniform NPK and Si (57.05%) contents. The treatment details are as follows; T1- Foliar silicic acid* (Rexil India Pvt. Ltd. Bangalore) @ 2 ml L^{-1}; T2- Foliar silicic acid @ 4 ml L^{-1}; T3- Gibberlic acid (ProGibb 40% WSG; ValentBiosceinces Corp, Libertyville, IL 60048, USA) @ 0.3 mg $plant^{-1}$; T4- Gibberlic acid @ 0.5 mg $plant^{-1}$; T5 - Jasmonic Acid** (Sigma Aldrich Cat: J2500) @ 2 ml L^{-1} (2 mM solution); T6 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.3 mg plant-^{1}; T7 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.5 mg $plant^{-1}$; and T8- Control (No application). For application of foliar silicilic acid and gibberlic acid, initially, the quantity of solution required to spray 30 plants was calibrated using water spray. Then required quantity of chemical [FSA @ 2 or 4 ml L^{-1} and GA @ 0.3 or 0.5 mg $plant^{-1}$] for 30 plants was mixed with water and sprayed thoroughly drenching on all the above ground parts of the plant. Same method was followed for combined application of FSA and GA. However, for jasmonic acid spray, 25.2 mg of commercial formulation was dissolved in 60 ml of water along with 1 ml ethanol and sprayed on all the parts of the plant using fine mist sprayer (Urban King®).

Foliar silicic acid and PGR's such as GA_3 and 2 mM solution of JA were sprayed three times at 15, 25 and 35 days after sowing of maize grown in green house using a 2-L manual sprayer.

2.2 Effect of Si and PGRs on the Biology

The first instar larvae (freshly emerged one day old) from laboratory culture were placed individually on the circular insect breeding dish (Himedia, 90 × 40 mm dia). Individual larvae were fed with leaves (two discs of 5 cm dia.) of treated plants from 10 days after first spray so that within 35–40 days of plant age the larval duration should be completed. Leaf discs were replaced daily with fresh leaf discs till the pupation. Leaf discs were taken from mid region of a leaf and same leaf was not repeated for feeding again. Five replications were carried out on each treatment consisting of 10 larvae each, thus forming 50 larvae per treatment. Observations recorded at different interval include, larval weight (at 5th and 10th day), duration (in days from egg hatching to the day of pupation), survival (%) and prepupal weight (just before pupation), papal weight, pupal duration, pupal survival (%), sex ratio of emerged adults, fecundity of female, fertility and adult longevity.

2.3 Si and PGR's Induced Resistance in Maize against *S. frugiperda*

Samples from fully opened leaves were collected from the plants on 10th day following first and subsequent application each time at 25th, 35th and 45th day (days at which maximum incidence is generally found in field condition and also biology takes on an average of 15 days). Silicon, phenols, tannin and potassium contents were analyzed by following standard procedures such as Silicon [47], phenols [34], tannins [9] and potassium [25]. The pooled mean of these three intervals were compared across the treatments and correlated with biological parameters of *S. frugiperda*.

2.4 Statistical Analysis

All the experimental data were transformed with arc sign when the data was in per cent and square root (x + 0.5) when in counts before analysis. Data then were subjected to analysis of variance (ANOVA) and treatments were compared by Tukey's test ($p = 0.05$) when ANOVA was significant. Pearson's linear correlations were performed between data of biochemical and nutrients content and biological parameters of *S. frugiperda*. Pearson's linear correlation was performed to know the effect of silicon and PGR's on the biological parameters of fall armyworm (FAW). The statistical analysis was performed in SPSS software (Version 16.0).

3 Results

3.1 Effect on FAW Biology

The mean larval weights of both five days old and ten days old larvae were significantly affected by the application of FSA, FSA + GA_3 and JA whereas unaffected by GA_3 alone (Table 1). On 5th day the lowest mean larval weight was recorded for FSA at 2 ml/plant + GA_3 at 0.5 mg plant^{-1} (18.38 mg) and FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1} (18.46 mg). This was followed by FSA at 4 ml L^{-1} (19.75 mg), FSA at 2 ml L^{-1} (19.96 mg) and JA (20.88 mg/plant). The maximum larval weight was recorded in control and GA_3 at 0.5 mg plant-1 which were on par with GA_3 at 0.3 mg per plant (Table 1). Similarly, the larval weight at 10th day was followed same trend as 5th day with lowest mean larval weight was recorded for FSA at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} (219.35 mg) and FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1} (219.92 mg). The maximum larval weight was recorded in control which was on par with GA_3 at 0.3 mg plant-1and GA_3 at 0.5 mg plant^{-1} (Table 1).

No significant difference was observed with respect to mean larval duration between control and larvae fed on plant treated with silicon and plant growth regulators (Table 1). However, there was a significant effect of silicon and PGR's on larval survival with the lowest per cent larval survival recorded with the application of FSA + GA_3 (70% larval survival). All the treatments differed significantly from untreated control which recorded the highest of 90% larval survival (Table 1).

The mean pre-pupal and pupal weight was significantly affected by silicon and JA (Table 1). The lowest mean prepupal weight was recorded for FSA at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} (168.64 mg) which was on par with FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1}(169.05 mg). This was followed by FSA (2 and 4 ml L^{-1}) and JA. The maximum

Table 1 Mean larval weight, duration and survival and pre pupal weight, pupal weight, duration and survival (mean ± SE) of *Spodoptera frugiperda* fed on maize plant treated with silicon and plant growth regulators

Tr. No.	Larval weight (mg)		Larval duration (days)^{ns}	Larval survival (%)	Pre-pupal weight (mg)	Pupal weight (mg)	Pupal duration (days)^{ns}	Pupal survival (%)^{ns}
	At 5th days	At 10th days						
T_1	19.96 ± 0.20^b	263.04 ± 1.61^b	14.46 ± 0.21^a	76.00 (60.78 ± 1.63)^{bc}	202.41 ± 1.75^c	190.91 ± 1.61^c	7.40 ± 0.10^a	87.14 (78.32 ± 4.7)^a
T_2	19.75 ± 0.16^b	256.04 ± 13.53^b	14.37 ± 0.34^a	76.00 (60.78 ± 1.63)^{bc}	200.24 ± 0.32^c	186.98 ± 1.39^c	7.63 ± 0.22^a	86.78 (68.69 ± 0.37)^a
T_3	24.04 ± 0.20^a	314.04 ± 2.24^a	14.67 ± 0.31^a	82.00 (65.06 ± 1.63)^b	236.32 ± 0.73^a	226.56 ± 0.85^a	7.50 ± 0.16^a	90.28 (73.68 ± 4.09)^a
T_4	24.06 ± 0.12^a	314.80 ± 2.01^a	14.36 ± 0.21^a	82.00 (65.06 ± 1.63)^b	237.78 ± 0.82^a	227.20 ± 0.54^a	7.66 ± 0.16^a	88.33 (70.04 ± 0.30)^a
T_5	20.88 ± 0.55^b	271.46 ± 7.91^b	14.42 ± 0.23^a	82.00 (65.06 ± 1.62)^b	216.09 ± 0.84^b	206.92 ± 2.07^b	7.64 ± 0.09^a	90.56 (73.93 ± 4.03)^a
T_6	18.46 ± 0.19^c	219.92 ± 3.55^c	14.75 ± 0.06^a	70.00 (56.79 ± 0.00)^c	169.05 ± 0.30^d	158.34 ± 0.54^d	7.67 ± 0.14^a	85.71 (70.21 ± 5.32)^a
T_7	18.38 ± 0.12^c	219.34 ± 3.48^c	14.05 ± 0.13^a	70.00 (56.79 ± 0.00)^c	168.64 ± 1.06^d	158.22 ± 0.65^d	7.43 ± 0.09^a	82.85 (65.78 ± 2.02)^a
T_8	24.06 ± 0.27a	314.98 ± 5.04^a	14.97 ± 0.23^a	90.00s (71.57 ± 0.00)^a	237.94 ± 0.56^a	227.25 ± 1.05^a	7.70 ± 0.22^a	93.34 (70.27 ± 4.99)^a
F	90.19	41.89	1.488	14.906	927.594	581.777	0.558	1.028
P	<0.001	<0.001	0.207	<0.001	<0.001	<0.001	0.784	0.431

Figures in the parentheses are arc sine transformed values; Mean values followed by different letters are significantly different by Tukey's test ($P \le 0.05$); ns – non significant; Note: T1- Foliar silicic acid@ 2 ml L^{-1} ; T2- Foliar silicic acid @ 4 ml L^{-1} ; T3- Gibberlic acid @ 0.3 mg plant^{-1} ; T4- Gibberlic acid @ 0.5 mg plant^{-1} ; T5 - Jasmonic Acid @ 2 ml L^{-1} (2 mM solution); T6 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.3 mg plant-^{1} ; T7 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.5 mg plant^{-1} ; and T8- Control (No application) pre-pupal weight was recorded in control (237.94 mg) which was on par with GA_3.

The lowest mean pupal weight was recorded for FSA at 2 ml/plant + GA_3 at 0.5 mg plant^{-1} (158.22 mg) and was on par with FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1} (158.34 mg). This was followed by FSA at 4 ml L^{-1} (186.98 mg) it was on par with FSA at 2 ml L^{-1} (190.91 mg) and JA (206.92 mg). The maximum pupal weight was recorded in control (227.25 mg) which was on par with GA_3 (Table 1). There was no significant difference observed in mean pupal duration and pupal survival among the treatments and control (Table 1).

The significant effects of silicon and PGR's on adult parameters of *S. frugiperda* were observed except for the sex ratio. Male longevity decreased by 34.79% in FSA at 4 ml L^{-1}, 33.83% in FSA at 2 ml L^{-1}. This was followed by 22.31% in FSA at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} and 21.81 in FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1}. GA_3 and JA were on par with control (Table 2).

Female longevity was 16.23% shorter in FSA at 4 ml plant^{-1}, 15.79% in FSA at 2 ml L^{-1}. This was followed by 10.21% for adult female emerged from larvae fed on plant treated with both FSA at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} and 10.12% for FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1}. This was followed by 7.33% for GA_3 at 0.5 mg plant^{-1} and this was on par with GA_3 at 0.3 mg plant^{-1} (6.54%) whereas JA was on par with control (Table 2).

Fecundity was decreased about 57.36% for FSA at 2 ml/plant + GA_3 at 0.5 mg plant^{-1} and this was on par with FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1} (55.15%). Application of FSA also decreased the fecundity (46.85% for FSA at 4 ml L^{-1}, 46.13% for at 2 ml L^{-1}). Further, this was followed by GA_3 at 0.5 mg plant^{-1} 34.08% which was on par with GA_3 at 0.3 mg plant^{-1} (33.37%) and 18.33% in JA. Fecundity was more in untreated control and it was significantly differed from other treatments (Table 2). Similarly, fertility was also significantly affected by silicon and PGRs. The least fertility was recorded FSA at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} (62.68%) which was on par with FSA at 2 ml L^{-1} + GA_3 at mg plant^{-1} (64.50%). There was no significant effect of silicon and PGR's on the sex ratio of *S. frugiperda* (Table 2).

3.2 Induced Resistance in Maize against *S. frugiperda*

3.2.1 Silicon, Phenols, Tannins and Potassium Content in Maize as Influenced by FSA and PGR's

Significantly higher mean Si content was found in plants treated with foliar silicic acid (FSA) at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} (3.10%) and FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1} (3.09%). However, application of FSA alone at 2 and 4 ml L^{-1} recorded 2.48 and 2.47 per cent Si, respectively and significantly very low amount of Si (1.39%) was recorded in untreated control (Fig. 1). While, the Si content in PGR's treated (both GA and JA) was on par with untreated control.

The pooled mean of phenol content in maize plant was significantly influenced by the application of Si and PGR's. Significantly higher mean phenol content was found in plants treated with foliar silicic acid (FSA) at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} (4.26 μg/g) and FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1} (4.25 μg /g). The lowest phenol was for JA (3.74 μg /g) followed by GA_3 at 0.3 mg plant^{-1} (3.83 μg /g) and GA_3 at 0.5 mg plant^{-1} (3.87 μg /g). The phenol content in untreated control was 3.66 mg/g, which was significantly lower than other treatments (fig. 2).

Significant difference was observed in tannin content between control and plant treated with Si and PGRs. Significantly higher mean tannin content was found in plants treated with foliar silicic acid (FSA) at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} (2.97 μg /g) and FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1} (2.95 μg /g). The lowest tannin was for JA (1.93 mg/g) followed by GA_3 at 0.3 mg plant^{-1} (2.05 μg /g) and GA_3 at 0.5 mg plant^{-1} (2.07 μg /g). The phenol content in untreated control was 1.69 μg /g which is significantly lower than other treatments (Fig. 2).

There was a significant increase in the K content with the application of FSA and combination of FSA + GA3. The highest K content was recorded with the application of FSA at 2 ml L^{-1} + GA_3 at 0.5 mg plant^{-1} (1.65%), FSA at 2 ml L^{-1} + GA_3 at 0.3 mg plant^{-1} (1.67%) which was on par with FSA (at 2 and 4 ml L^{-1}). The treatments with GA_3 and JA are on par with untreated control (Fig. 3).

3.3 Correlation between Leaf Si and *S. frugiperda* Biological Parameters

There was a significant negative correlation between silicon content and larval weight at five days (r = −0.91**) and ten days (r = −0.93**), pre pupal weight (0.96**) and pupal weight (r = −0.97**), larval survival (r = −0.92**), pupal survival (0.88**), fecundity (r = −0.84**), fertility (r = −0.88) and male longevity (r = −0.78*). Non significant negative correlation with, female longevity (r = −0.68) larval duration (r = −0.36), sex ratio (r = −0.67), pupal duration (r = −0.38) (Figs. 4 and 5). By these findings, it was clear that Si content was more for FSA+ GA_3 compared to FSA alone.

4 Discussion

The foliar application of FSA, PGR's such as GA_3 and JA adversely affected the larval development and biology of *S. frugiperda* fed on treated maize plants. The possible reasons for such encouraging results are discussed hereunder.

Table 2 Mean adult longevity, fecundity, fertility and sex ratio (mean ± SE) of *Spodoptera frugiperda* fed on maize plant treated with silicon and plant growth regulators

Tr. No.	Adult longevity (days) $N = 10$ each				Fecundity[#] N = 10	% Reduction over control	Fertility (%)	Sex ratio (F:M)[ns]
	Male	% Reduction over control	Female	% Reduction over control				
T_1	6.22 ± 0.25[c]	33.83	9.65 ± 0.09[c]	15.79	632.00 (25.15 ± 0.24)[d]	46.13	71.12 (57.52 ± 0.86)[cd]	1: 0.70 ± 0.30[a]
T_2	6.13 ± 0.24[c]	34.79	9.60 ± 0.10[c]	16.23	623.60 (24.98 ± 0.14)[d]	46.85	70.77 (57.32 ± 1.14)[cd]	1: 0.73 ± 0.17[a]
T_3	8.76 ± 0.16[a]	6.81	10.71 ± 0.08[b]	6.54	781.60 (27.96 ± 0.09)[c]	33.37	78.60 (62.46 ± 0.59)[bc]	1: 0.75 ± 0.00[a]
T_4	8.65 ± 0.17[a]	7.98	10.62 ± 0.10[b]	7.33	773.40 (27.82 ± 0.09)[c]	34.08	77.94 (62.05 ± 1.13)[bc]	1: 0.70 ± 0.30[a]
T_5	9.27 ± 0.07[a]	1.38	11.33 ± 0.13[a]	1.13	958.20 (30.94 ± 0.57)[b]	18.33	82.66 (65.76 ± 2.46)[b]	1: 0.72 ± 0.30[a]
T_6	7.35 ± 0.13[b]	21.81	10.30 ± 0.03[b]	10.12	526.20 (22.95 ± 0.12)[e]	55.15	64.50 (53.44 ± 0.78)[d]	1: 0.60 ± 0.61[a]
T_7	7.30 ± 0.12[b]	22.34	10.29 ± 0.1[b]	10.21	500.20 (22.35 ± 0.53)[e]	57.36	62.68 (52.50 ± 0.91)[d]	1: 0.60 ± 0.67[a]
T_8	9.40 ± 0.16[a]	–	11.46 ± 0.10[a]	–	1173.20 (34.26 ± 0.04)[a]	–	94.20 (76.26 ± 1.20)[a]	1: 0.66 ± 0.37[a]
F	56.909		40.769		183.668		37.421	2.137
P	<0.001		<0.001		<0.001		<0.001	0.068

Figures in the parentheses are arc sine transformed values; Mean values followed by different letters are significantly different by Tukey's test ($P \leq 0.05$); ns – non significant; # mean of number of eggs laid by ten females in each treatment; Note: T1- Foliar silicic acid@ 2 ml L^{-1} ; T2- Foliar silicic acid @ 4 ml L^{-1} ; T3- Gibberlic acid @ 0.3 mg $plant^{-1}$; T4- Gibberlic acid @ 0.5 mg $plant^{-1}$; T5 - Jasmonic Acid @ 2 ml L^{-1} (2 mM solution); T6 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.3 mg plant-[1] ; T7 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.5 mg $plant^{-1}$; and T8- Control (No application)

4.1 Effect of Si and PGR's on Biological Parameters of *S. frugiperda*

Foliar silicic acid application to maize plants adversely affected the larval growth. GA_3 alone had no influence on mean larval weight but when it was applied with FSA, there was a decrease in mean larval weight (Table 1). Silicon is known to reduce the larval weight of *S. frugiperda* [41] and *Eldana saccharina* Walker [30]. Reduction in larval weight due to Si application helps to reduce the feeding injury to plants under field condition. However, there was no significant effect of GA_3 on the larval weight of *S. frugiperda* on maize.

No significant effect on larval duration was observed by any of the treatments in the present study (Table 1) as

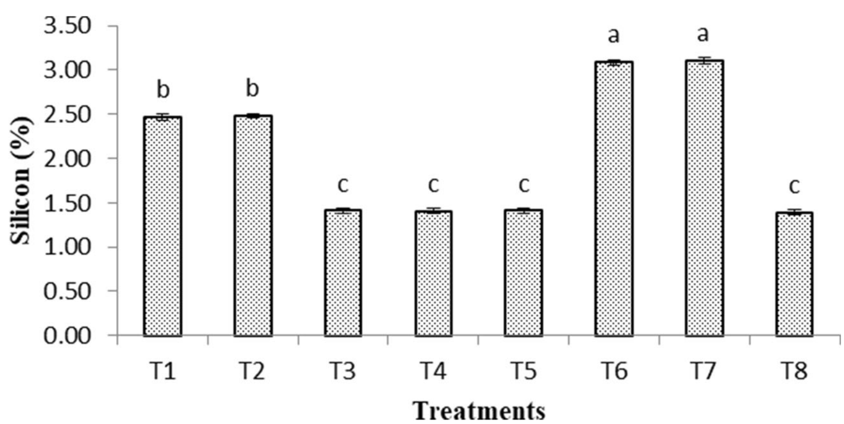

Fig. 1 Mean (±SE) of the leaf silicon content of maize treated with silicic acid and plant growth regulators. Different letters on bars indicate significant difference by Tukey's test ($p \leq 0.05$). Vertical bars (±) indicate SEs of the means. Note: T1- Foliar silicic acid@ 2 ml L^{-1}; T2- Foliar silicic acid @ 4 ml L^{-1}; T3- Gibberlic acid @ 0.3 mg $plant^{-1}$; T4- Gibberlic acid @ 0.5 mg $plant^{-1}$; T5 - Jasmonic Acid @ 2 ml L^{-1}(2 mM solution); T6 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.3 mg plant-[1]; T7 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.5 mg $plant^{-1}$; and T8- Control (No application)

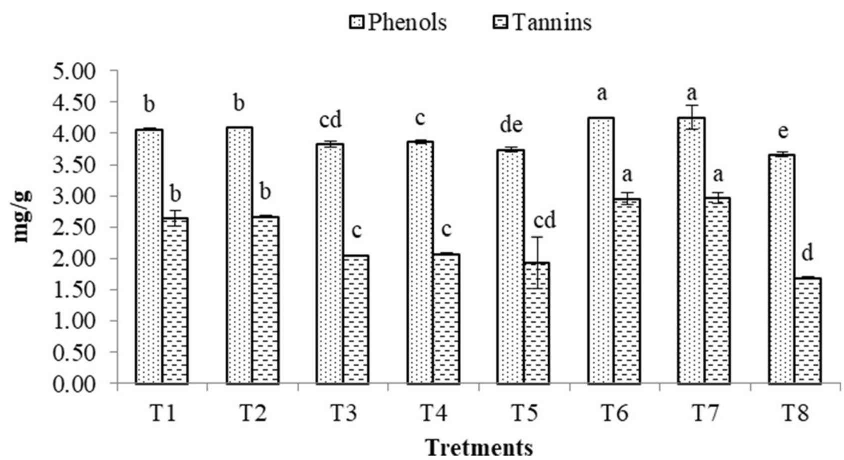

Fig. 2 Mean (±SE) of the phenol and tannin content of maize treated with silicic acid and plant growth regulators. Different letters on bars indicate significant difference by Tukey's test ($p \leq 0.05$). Vertical bars (±) indicate SEs of the means. Note: T1- Foliar silicic acid@ 2 ml L^{-1}; T2- Foliar silicic acid @ 4 ml L^{-1}; T3- Gibberlic acid @ 0.3 mg $plant^{-1}$; T4-Gibberlic acid @ 0.5 mg $plant^{-1}$; T5 - Jasmonic Acid @ 2 ml L^{-1}(2 mM solution); T6 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.3 mg plant-[1]; T7 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.5 mg $plant^{-1}$; and T8- Control (No application)

demonstrated [2] and Si had no influence on the larval duration of *S. frugiperda* on rice [41]. However there was a reduction in larval survival due to application of silicon and PGR's indicating negative impact on FAW biology (Table 1). The negative effect of exogenous application of Si on larval development of *S. frugiperda* might have resulted from the accumulation of Si in the plant cell walls that increased the rigidity of leaf tissues and enhanced synthesis of secondary defensive compounds such as tannins and phenols.

Similarly, feeding of leaves treated with JA significantly reduced the larval weight and survival but there was no effect on larval duration (Table 1). The exogenous application of JA was known to stimulate resistance to various insects in varieties of plants. JA reduced the final larval weight and survival of *S. frugiperda* feeding on cotton [37]. Similarly, it reduced the larval weight of *S. frugiperda* on soybean [21] and rice [60]. The elevated levels of terpenoid aldehydes due to exogenous application of JA [37] might be the reason for slow development and high mortality of *S. frugiperda*.

There was a significant reduction in the pre-pupal and pupal weight of *S. frugiperda* (Table 1) due to feeding on leaves treated with Si and JA. Previously it was reported that larvae of *S. frugiperda* showed lower pupal weight when fed on Si treated rice plants [41] and cotton plants [59]. GA_3 had no influence on pre-pupal and pupal weight, whereas JA reduced the pre-pupal and pupal weight (Table 1).

Silicon and PGR's had no influence on pupal duration and survival (Table 1). Previously it was reported that silicon had no effect on pupal duration and survival of *S. frugiperda* on rice [41]. Similarly, no influence of silicon and GA_3 on pupal

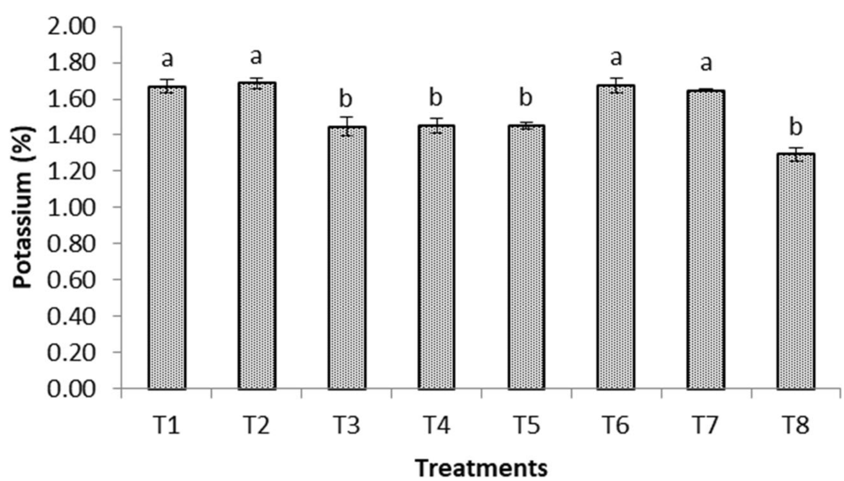

Fig. 3 Mean (±SE) of the potassium content content of maize treated with silicic acid, plant growth regulators. Different letters on bars indicate significant difference by Tukey's test ($p \leq 0.05$). Vertical bars (±) indicate SEs of the means. Note: T1- Foliar silicic acid@ 2 ml L^{-1}; T2- Foliar silicic acid @ 4 ml L^{-1}; T3- Gibberlic acid @ 0.3 mg $plant^{-1}$; T4-Gibberlic acid @ 0.5 mg $plant^{-1}$; T5 - Jasmonic Acid @ 2 ml L^{-1}(2 mM solution); T6 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.3 mg plant-[1]; T7 - Foliar silicic acid + Gibberlic acid @ 2 ml L^{-1} + 0.5 mg $plant^{-1}$; and T8- Control (No application)

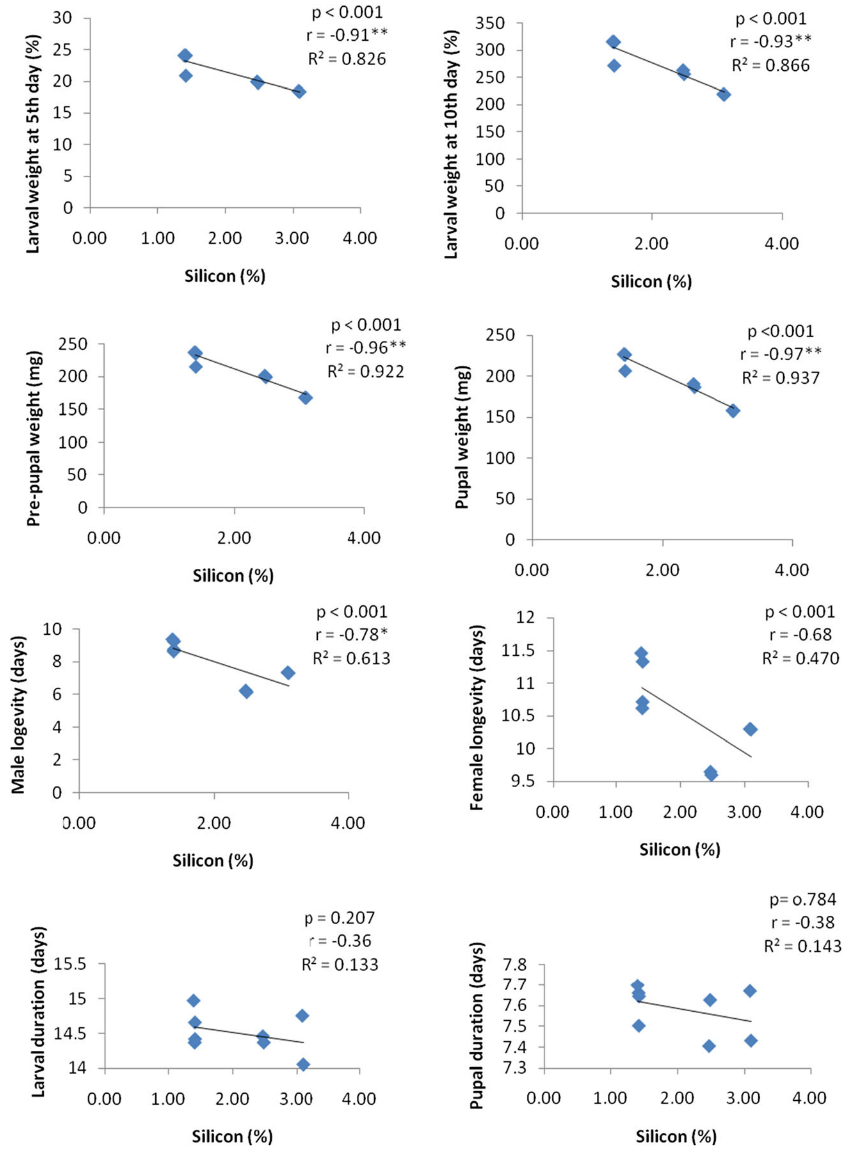

Fig. 4 Pearson's correlation between maize silicon content and biological parameters of *Spodoptera frugiperda* Larval weight (mg), pre-pupal weight (mg), pupal weight (mg), larval and pupal duaration (days) and adult longevity (days). Correlation coefficient (r), coefficient of determination (R^2), p value as shown. $N = 8$; ** Correlation is significant at the 0.01 level; Table r value at $p = 0.01$ is 0.834; *Correlation is significant at the 0.05 level; Table r value at $p = 0.05$ is 0.707

duration and survival were observed on maize plants [2] and application of GA_3 had no influence on the pupal duration of *S. obliqua* [22].

The significant impact of Si source and PGR's (GA_3 and JA) was reduced fecundity and fertility of females, where as male longevity was declined only by Si and female longevity declined by both Si and GA_3 (Table 2). The reason for this variation across sex needs further investigation. However, the results are encouraging as the reduction in female longevity always contributes to reduction in population under field condition.

The effect of Si and GA_3 on adult longevity was studied in many insect pests. The adult males and females of *S. frugiperda* fed with leaves from silica treated rice plants exhibited lower longevity [41]. Similarly, the application of sodium silicate to wheat plant decreased the longevity of the green aphid, *Schizaphis graminum* (Rondani) [4]. The adult longevity of *G. mellonella* [63] and *B. cucurbitae* [28] was decreased by GA_3 treatment. In *Pimpla turionellae* (L.) male longevity significantly reduced, whereas females lived longer comparing to control and other treatments [63]. While, JA had no effect on the adult longevity of *S. frugiperda* in present study (Table 2). In contrast, adult longevity of wolfberry aphid on wolfberry seedlings [20] and brown planthopper, *Nilaparvata lugens* Stal on rice [55] was reduced with JA treatment.

It has been previously demonstrated that silicon known to reduce fertility and fecundity of *S. frugiperda* on maize plants [2]. Similarly, silicon application on rice plants reduced the female fecundity and egg viability of *S. frugiperda* [41] and Nilaparvata lugens' [24]. Similarly, adult males and females of *S. frugiperda* derived from larvae fed with cotton plants treated with Si laid less number of eggs [59]. By reducing the female fecundity, silicon acted as a resistance inducer against *Myzus persicae* (Sulzer) in potato [19].

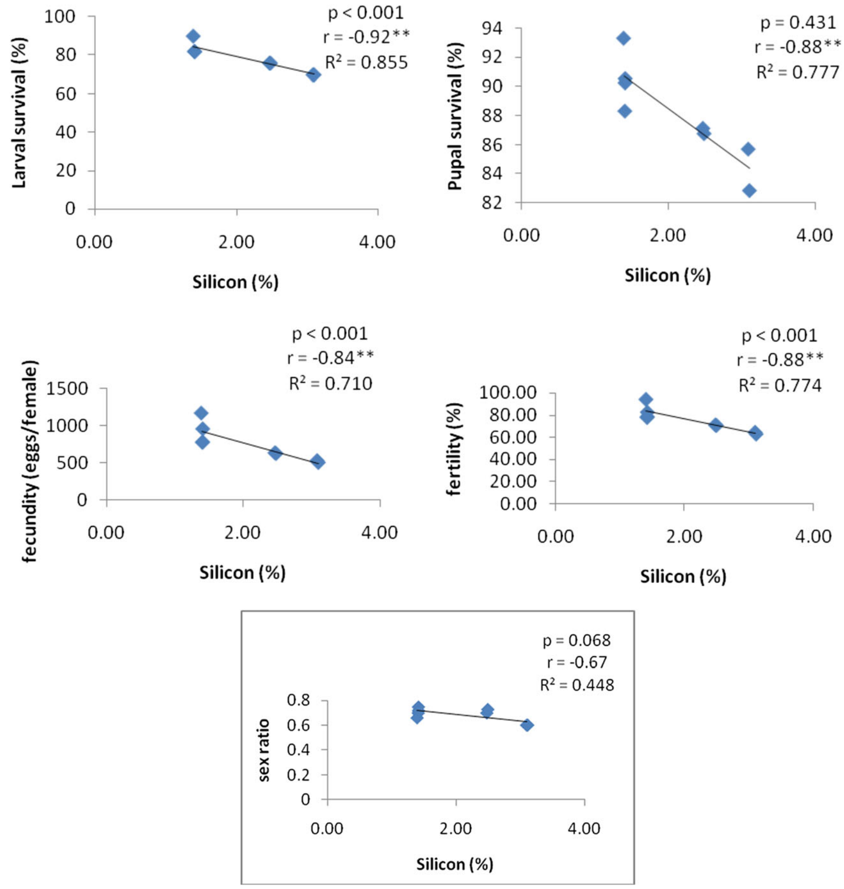

Fig. 5 Pearson's correlation between maize silicon content and biological parameters of *Spodoptera frugiperda* larval and pupal survival (%),fecundity (eggs/female), fertility (%) and sex ratio. Correlation coefficient (r), coefficient of determination (R^2), p value as shown. . N = 8; ** Correlation is significant at the 0.01 level; Table r value at p = 0.01 is 0.834; *Correlation is significant at the 0.05 level; Table r value at p = 0.05 is 0.707

This detrimental effect of silicon on fecundity and fertility and adult longevity in the present study might be due to the accumulation of silicon in plants, which can activate and increase the production of defence metabolites [62]. Increased Silicon content in leaf tissue may prevent the ingestion of a sufficient amount of nutrients and water by larvae [43] and caused the physiological changes and negatively affected the fitness of *S. frugiperda.* Therefore, this sub-lethal effect of Si on *S. frugiperda* development may decrease the reproductive potential.

GA_3 and JA were known to reduce the fecundity and fertility of many insects. The greater reduction in fecundity and fertility of female *Bactrocera cucurbitae* was observed when freshly emerged (0–1 day old) male and female adults were treated with GA_3 [28]. Similarly, GA_3 applied to an adult female during the pre-ovipositional phase significantly reduced both fecundity and fertility of *Locusta* migratoria [1]. The fecundity of *Helicoverpa armigera* [56], folivore Pacific spider mite, *Tetranychus pacificus* McGregor and root-feeding grape phylloxera, *Daktulosphaira vitifoliae* Fitch [42] was decreased by GA_3.

JA application reduced the preference and performance of herbivores [5] and also responsible for the production of certain secondary metabolites such as phenols and tannins which act as a repellent to herbivores [26, 27]. These secondary metabolites might be responsible to decrease the survival and reproduction of the *S. frugiperda.* Similarly, GA_3 also increased the secondary metabolites, which may be the reason for decreased fecundity and fertility of *S. frugiperda.* There was no effect on the sex ratio of FAW by silicon and PGR's (Table 2). In support of our studies, there was no significant effect on the sex ratio of FAW fed on rice plants treated with silicon [41].

4.2 Induced Resistance in Maize against *S. frugiperda*

Any changes in nutritional parameters in the host plant can directly affect the survival and biological parameters of the phytophagous insect. In the present study, the content of leaf Si, phenols and tannins were increased by the application of FSA and PGR's. This negatively affected the biological parameters of *S. frugiperda*.

4.2.1 Influence of FSA and PGR's on Silicon (Si), Phenol, Tannin and Potassium (K) Content of Maize

The foliar applied silicic acid increased the Si content in maize leaves, while PGR's had no significant influence on Si (Fig. 1). Similarly, in plants treated with FSA + GA_3, Si content was higher compared to FSA alone. It may be because of increased accumulation of Si in leaves, which makes them harder and interfere in feeding [15]. The increased leaf Si content in rice caused a negative effect on *S. frugiperda* development [41].

In the present study, the content of phenols and tannins in maize leaves had increased significantly after the application of Si and PGR's (Fig. 2). This may be due to induced gene expression of enzymes of the secondary metabolic pathway, involved in the synthesis of phenols and tannins [49]. Previously, it was proved that Si application to wheat plant increased total phenols and tannins and thus increased the resistance to aphids *Sitobion avenae* (Fabricius) [65]. Similarly, jasmonic acid (JA) lowered the gypsy moth growth on American chestnut by increasing the tannin content [11] and it was also known to increase phenols in plants [36]. The increased phenol and tannin contents induced the resistance to rice pests [10]. Similar observations were recorded in the present study with increased phenol and tannin contents due to the application of Si and PGR's.

In the present study, the application of FSA and FSA + GA_3 increased the K concentration in leaves. Silicon fertilization is known to increase the nutrient uptake (N, P, K, Ca, Mg, Fe, Mn and Zn) by melon plants [16]. Similarly, the increased K content in maize leaves caused a decrease in pupal weight, survival and fecundity of *Eldana saccharina* and *Sesamia calamistis* [15].

5 Conclusion

The present study proved that Si and PGR's (GA_3 and JA) induced resistance in plants against recently invaded FAW, *S. frugiperda*. Laboratory study proved a significant negative effect on various biological parameters of the FAW. Application of Foliar silicic acid 2 ml L^{-1} + GA_3 0.5 mg $plant^{-1}$ was found to significantly decrease all the biological parameters of *S. frugiperda.* Further studies are necessary to understand the effect of exogenous application of Si under field condition and field incidence of invasive FAW for better exploitation of host plant induced resistance.

Acknowledgments Authors thank Dr. M. Hanumanthappa, Director of Research, UAHS, Shivamogga-577 204 for encouragement and facilities. The facilities generated under DST-FIST in Department of Entomology, UAHS is also acknowledged.

Funding Statement The authors thank UAHS, Shivamogga for SRP grants to the first author.

Author Contributions W. Nagaratna, C.M. Kalleshwaraswamy: Rearing test insects, conducted experiment and statistical analysis.

C.M. Kalleshwaraswamy, N. B. Prakash, Sharanabasappa: Planned the design and experiment.

B.C. Dhananjaya and N. B. Prakash: Analysed soil and plant samples.

Data Availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Compliance with Ethical Standards The insects used were pests of the maize crop and investigation is helpful for its management and is compliance with the ethical standards.

Conflict of Interest The authors declare no conflict of interest.

Consent to Participate Not applicable. The insects used were pests of the crop and investigation is helpful for its management.

Consent for Publication Not applicable.

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