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Trans-generational effects of spinetoram on biological traits of *Spodoptera frugiperda*

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ABSTRACT

Spodoptera frugiperda (J.E. Smith) is the invasive pest of maize (*Zea mays* L.) and spinetoram is the novel insecticide used mainly against lepidopteran pests. The experiment was conducted during 2022, 2023 and 2024 at ICAR-Indian Agricultural Research Institute, New Delhi to comprehend the sub-lethal and trans-generational effects of spinetoram (Delegate® 11.7% SC) at LC_{10} and LC_{25} against *S. frugiperda*. The leaf dip bioassay findings indicated that spinetoram exhibited notable toxicity with the LC_{50} of 0.157 ppm. Exposure of sub-lethal doses of spinetoram on parental generation (F_0) revealed that there are trans-generational deleterious effects on biology and lifetable parameters of *S. frugiperda* where the adverse effects were significantly hampering in the F_0 and F_1 whereas the F_2 generation was found to be free of it. LC_{10} and LC_{25} of spinetoram significantly diminished biological attributes including rate of pupation, adult hatching, fecundity, longevity of adult, weight of larval and pupa and concurrently increased deformed adults and the duration of the larval and pupal stages. The lifetable parameters such as net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ) were decreased significantly in F_0 and F_1 generations. Moreover, these sub-lethal doses of spinetoram had significant decreased nutritional indices and considerably increased detoxification enzymatic activities like C-P450 and GST. It is inferred that, spinetoram exerted deleterious sub-lethal and trans-generational effects on the *S. frugiperda* population by impairing its survival, development and reproduction.

Keywords: C- P450, GST, Leaf-dip bioassay

Fall armyworm [*Spodoptera frugiperda* (J.E. Smith)] is an invasive lepidopteran pest native to north America and is now widespread across the globe (Nagoshi *et al.* 2012). Its invasion in India was intially reported by Sharanabasappa *et al.* (2018) and later it spread quickly to other regions in India. It has been reported to feed at least on 353 spp. across 76 plant families, *S. frugiperda* primarly damages major families such Poaceae (106) followed by Asteraceae (31) and Fabaceae (31) and others of immense agricultural importance however it shows a distinct preference for poaceae (Montezano *et al.* 2018). From the date of establishment, farmers predominantly depend on chemical insecticides, as non-chemical control methods alone often fail to sufficiently prevent economic losses (Deshmukh *et al.* 2021). The formidable challenges are the high migration ability, prolific reproduction rate, rapid evolution of insecticide resistance, and the high physiological and behavioural adaptability exhibited by the pest (Paredes *et al.* 2021). Spinetoram, an insecticide from the spinosyn class (IRAC Group 5), acts as a nicotinic acetylcholine receptor allosteric modulator (IRAC 2023). In comparison to traditional insecticides, it demonstrates superior efficacy and a greater insecticidal diversity against various groups of insects (Tamilselvan *et al.* 2021). Along with lethal effects, it is important to consider sub-lethal effects when choosing an insecticide.as it alters an insect's growth, development, feeding, fecundity, population dynamics and biochemical activities. Various groups of insecticides have different effects on targeted insect pests when applied at sub-lethal doses. Insecticides such as imidacloropid have shown to enhance the reproductive potential of target pests at sub lethal concentrations (Ullah *et al.* 2019). Conversely, other investigations have reported that adult fecundity and survival rates tend to decrease when subjected to sub-lethal doses of insecticides (Xu *et al.* 2016). The evident contradictions in these studies highlight the critical importance of studying the sub-lethal effects of insecticides. While the acute lethal effects of spinetoram on test-insect have been thoroughly investigated, Hence, in a comprehensive study, it is essential to consider not only the biology of the pest but also the sub-lethal and trans-generational effects of spinetoram on the feeding indices, demographic traits and detoxification enzymes of the target insect (Quan *et al.* 2016). This study has explored the lethal,

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sub-lethal, and trans-generational effects of spinetoram on test-insect.

MATERIALS AND METHODS

The experiment was conducted during 2022, 2023 and 2024 at ICAR-Indian Agricultural Research Institute, New Delhi. *S. frugiperda* larvae were acquired from unsprayed maize field of ICAR-Indian Agricultural Research Institute, New Delhi. Colonies were sustained in a rearing chamber at 27 ± 1°C and 70 ± 5% RH and photoperiod L/D = 16 h/8 h, respectively. The larvae were maintained in petri dishes (4.5 mm × 1.5 mm) individually and provided with fresh maize leaves on daily basis. The pupae were kept in clean containers until the adult emergence. The adults were paired and kept in separate mating jars. To facilitate proper egg laying adults were provided with 10% honey solution. Eggs hatched within 2–3 days and the larvae that emerged were fed tender maize leaves until they reached in to the third instar.

Bioassay: The spinetoram formulation (Delegate® 11.7% SC) employed in this research was sourced from Dow Agro Sciences India Pvt. Ltd. Bioassays were executed with freshly emerged third-instar larvae utilizing the validated leaf-dip protocol (IRAC 2009). Maize leaf bits of (5 cm × 4 cm) size were cut, and plunged for 20 sec into various spinetoram concentrations. Followed by 2 h air-drying interval, leaf sections were placed within petri dish on a moistened filter paper. Larvae were starved for 4 h prior to their introduction into the petri dish containing insecticide-treated leaf sections. First preliminary broad range doses were used to determine a suitable concentration range that resulted in mortality rates ranging from 10–90% and utilizing this mortality dose data testing concentrations (5–6 concentrations) were refined which was used to generate final mortality data. Individual larvae were released in to petri dish. Every treatment encompassed three replications, each incorporating ten larvae. The observations on larval mortality were taken 48 h post-exposure.

Sub-lethal effects on F_0 generation: LC_{10} and LC_{25} concentrations of spinetoram were determined using bioassay results. Maize leaves were immersed in sub-lethal concentrations of spinetoram for 20 sec, while a simultaneous untreated control was held concurrently. Each petri dish received thirty third-instar larvae, which were placed individually, each containing a treated leaf bit along with filter paper at the base and kept for 48 h. Eight replications were provided for each treatment. The surviving larvae were given maize leaves till they pupated. Upon emergence, pair of female and male moths was released in a glass jar and were daily fecundity was recorded. The biological parameters like pupal survival (%), adult emergence (%), malformed adults (%), females (%), larval period, pupal period, weight of larval and pupal stages, longevity of male and female adults and reproductive ability were recorded daily.

Trans-generational effects on F_1 and F_2 generation: To investigate the trans-generational impacts of spinetoram on F_1 traits, a total of 100 larvae from every treatment in F_0 generation were collected and each larva was kept in individual petri dish, and was supplied with insecticide-free fresh maize leaves, under the identical laboratory conditions as outlined earlier. Assessments were documented in a manner similar to the F_0 generation.

Life table studies: To comprehend the changes in population dynamics of insect pests under insecticidal treatments, it is important to consider life table parameters. Employing methodologies established by (Birch 1948, Chi *et al.* 1985) the ensuing life table attributes encompassing the net reproductive rate (R_0), the intrinsic rate of increase (r), the finite rate of increase (λ), and the mean generation time (T) were computed for F_0, F_1 and F_2 generations.

Nutritional parameters: To analyze the nutritional indices of test-insect, daily observations were taken including initial and final weights of leaves, the weight of fecal matter, the weight of larvae at various instars, and the duration of each instar using a digital electronic analytical balance. To study the food utilization patterns and assimilation of FAW larvae, several development indices including Rate of Growth (GR), Index of Consumption (CI), Efficiency of Conversion of Ingested Food (ECI), Approximate Digestibility (AD) and Efficiency of Conversion of Digested Food (ECD) were computed for larvae across different treatments taken in the experimentation by using the methodologies outlined by (Farrar *et al.* 1989, Mahapatro *et al.* 1999).

$$CI = \frac{\text{Fresh weight of food consumed}}{\text{Duration of feeding period} \times \text{Mean fresh weight of larvae duriung feeding period}}$$

$$GR = \frac{\text{Fresh weight gain of larvae during feeding period}}{\text{Duration of feeding period} \times \text{Mean fresh weight of larvae during feeding period}}$$

$$ECI = \frac{\text{Fresh weight gain of larvae during feeding period}}{\text{Fresh weight of food consumed}} \times 100$$

$$ECD = \frac{\text{Fresh weight gain of larvae during feeding period}}{\text{Fresh weight of food consumed} - \text{Fresh weight of excreta}} \times 100$$

$$AD = \frac{\text{Fresh weight of food consumed} - \text{Fresh weight of excreta}}{\text{Fresh weight gain of food consumed}} \times 100$$

Detoxification enzymes: After 48 h of exposure, the midguts of 23rd instar FAW larvae were dissected and afterwards blended in ice-cold phosphate buffer 100 mM concentration adjusted to *p*H 7.0 with 20% glycerol, and 1 mM each of Ethylene Diamine Tetra Acetic acid (EDTA), phenylthiourea (PTU), phenyl methyl sulfonyl fluoride (PMSF) using a mortar and pestle. The produced homogenate was in turn swirled at 10,000 revolutions/min for 15 min at a temperature of 4°C, the liquid fraction was leveraged for the appraisal of Glutathione-S-transferase (GST), Cytochrome P450, and Carboxylesterase (CarE). (Kranthi 2005).

Carboxylesterase (CarE) activity: It was examined by employing 1 mM α-naphthyl acetate as the substrate

material. A standard curve using 1-naphthol was prepared. The reaction mixture (250 µl) comprised 25 µl of sodium phosphate buffer (0.1 M, adjusted to *p*H 6.0), along with 25 µl of the enzyme source and 200 µl of the substrate solution (1 mM). The specific activity of the Car E enzyme was assessed at 25°C using a Bio Tek microplate reader for 10 min, with readings taken every minute at 450 nm wavelength (Kranthi 2005).

Glutathione S-transferase (GST) activity: It was appraised using Glutathione reduced (GSH) and 1-chloro-2, 4-dinitrobenzene (CDNB) as substrates. The reaction mixture (300 µl) comprised 100 µl of the enzyme source, 100 µl of CDNB solution (0.4 mM) along with 100 µl of GSH solution (4 mM). GST activity was measured at 25°C using a Bio Tek microplate reader for 10 min, with readings taken every minute at 340 nm wavelength (Habig *et al.* 1974).

Cytochrome P450 monooxygenase activity: It was evaluated using 4-nitroanisole (p-NA) as the substrate the reaction mixture consisted of 100 µl of p-NA (8 mM concentration), 10 µl of NADPH (6 mM concentration), and 90 µl of the enzyme preparation. This mixture was then fostered at 34°C in an aerobic environment for 30 min. C-P450 activity was measured at 25°C using a Bio Tek microplate reader for 10 min, with readings taken every minute at 405 nm wavelength (Kranthi 2005).

Statistical analysis: The estimate of lethal and sub-lethal concentrations at 95% confidence level was computed by log-dose probit analysis employing software Poloplus 2.0 (LeOra Software Petluma, CA). For the analysis of *S. frugiperda* life table data, the age-stage, two-sex life table approach (Chi and Liu 1985, Chi 1988) was employed with TWOSEX-MS Chart computer program (Chi 2018). Using SPSS version 2.0 (SPSS; IBM S PSS, Armonk, New York, USA) the biology, consumption indices and life table data were statistically analysed. Parametric data underwent one-way ANOVA, and mean separation was carried out using Tukey's HSD test at $P<0.05$.

RESULTS AND DISCUSSION

Bioassay: After 48 h leaf dip bioassay, LC_{50} for spinetoram in *S. frugiperda* was 0.157 ppm (Table 1). The same concentration-mortality response line was used to generate LC_{10} (0.042 ppm) and LC_{25} (0.074 ppm) values (Table 1). Similar findings were documented by Kumar *et al.* (2022) that spinetoram as an effective insecticide against *S. frugiperda*.

Sub-lethal effects on biology: In F_0 generation all parameters under the investigation exhibited significant detrimental effects when exposed to sub lethal doses (LC_{10} and LC_{25}) (Table 2). The parameters those exhibited reduction were pupation (44–49%), adult emergence (12–18%), larval weight (28–39%), pupal weight (21–34%), fecundity (46–53%), male longevity (0.78–1.09 days) and female longevity (1.96–2.28 days) (Table 2). Meanwhile, parameters those showed significant increase was the larval period (0.93–1.23 days) and pupal period (0.57–0.74 day) and deformed adult (9.86–16.37%) (Table 2). But interestingly the sub-lethal doses of spinetoram did not affect female ratios. In the F_1 generation, there were significant decrease in pupation (10–20%), adult emergence (5–8%), larval weight (15–22%), pupal weight (11–17%) and fecundity (18–25%) (Table 2) at the LC_{10} and LC_{25} concentration. In the F_2 generation, the adverse effects were weakened and fecundity was at par with the control.

The extended larval and pupal duration might be because of the energy tradeoff taking place when under insecticide stress i.e. spinetoram treated larvae are required to allocate more resources to detoxification instead of development, resulting in a significantly prolonged development period compared to the control. Similarly, sub lethal concentration of emamectin benzoate and chlorantranaliprole has already reported to have deleterious effects on developmental duration of test-insect (Liu *et al.* 2022). The reduction in larval weights was owing to the decline in food ingestion required for ideal larval growth and the diminished recovery efficiency of spinetoram-treated larvae (Tamilselvan *et al.* 2021) noted a considerable reduction in the pupation, adult emergence, larval and pupal weight and a concurrent rise in the occurrence of adults with wing deformities in both the F_0 and F_1 generations of *Plutella xylostella* when subjected to the sub-lethal doses of spinetoram. The diminished fecundity could be explained by the adverse effects of spinetoram influencing the ovaries of female adults Liu *et al.* (2022) observed lower fecundity in *S. frugiperda* exposed to low concentrations of emamectin benzoate.

Trans-generational effects on life table: The significant decreases were noted in the net reproductive rate (R_0), intrinsic rate of increase (r), and finite rate of increase (λ) at both LC_{10} and LC_{25} concentration compared to control in F_0 and F_1 generation (Table 3), however, spinetoram augment the mean generation interval of *S. frugiperda* for about 2.62 days (LC_{25}) to 2.28 days (LC_{10}) in F_0 generation (Table 3). In F_2 generation there was no substantial differences between treatment and control. A similar trend was reported in *P. xylostella* when it was treated with a sub-lethal concentration of spinetoram (Tamilselvan *et al.* 2021).

Table 1 Toxicological effects of spinetoram on third instar larvae of *S. frugiperda*

Insecticide	LC_{10} (95% FL) ppm	LC_{25} (95% FL) ppm	LC_{50} (95% FL) ppm	n	Slope ± SE	x^2(df)
Spineotoram	0.042 (0.028-0.055)	0.074 (0.056-0.087)	0.157 (0.091-0.187)	260	2.485 ± 0.340	3.513(3)

FL, Fiducial limit; SE, Standard error; χ2 [at P= 0.05, df = 3], 7.81.

Table 2 Impact of sub-lethal concentrations of spinetoram on the biology of the F_0 generation of *S. frugiperda*, as well as the transgenerational effects of spinetoram exposure in F_0 *S. frugiperda* on the biological development of the F_1 and F_2 generations

Treatment	Pupation (%)	Adult emergence (%)	Deformed adults (%)	Female (%)	Larval duration (days)	Larval weight (mg)	Pupal duration (days)	Pupal weight (mg)	Female longevity (days)	Male longevity (days)	Fecundity (eggs/♀)
F_0 Generation											
Control	74.72 ± 0.88^{b}	89.46 ± 0.49^{b}	3.38 ± 0.51^{b}	56.57 ± 0.31^{a}	15.32 ± 0.74^{a}	522.25 ± 11.56^{b}	8.75 ± 0.16^{b}	188.34 ± 2.68^{b}	10.61 ± 0.18^{b}	8.62 ± 0.12^{b}	938.25 ± 21.81^{b}
LC_{10}	41.50 ± 1.71^{a}	78.51 ± 2.58^{a}	13.24 ± 1.30^{a}	54.78 ± 2.34^{a}	16.55 ± 1.03^{b}	373.51 ± 8.64^{a}	9.49 ± 0.31^{a}	147.12 ± 3.56^{a}	8.65 ± 0.26^{a}	7.53 ± 0.18^{a}	488.62 ± 12.34^{a}
LC_{25}	37.38 ± 3.37^{a}	72.86 ± 1.33^{a}	19.75 ± 0.49^{a}	54.65 ± 2.42^{a}	16.25 ± 0.77^{b}	317.27 ± 7.22^{a}	9.32 ± 0.24^{a}	123.93 ± 2.81^{a}	8.33 ± 0.22^{a}	7.84 ± 0.37^{a}	424.37 ± 9.45^{a}
F_1 Generation											
Control	76.27 ± 0.56^{c}	91.45 ± 0.33^{b}	2.03 ± 0.12^{b}	55.42 ± 1.23^{a}	15.17 ± 0.22^{a}	537.23 ± 6.23^{b}	8.48 ± 0.12^{a}	187.71 ± 2.32^{b}	10.34 ± 0.16^{b}	8.77 ± 0.11^{a}	979.31 ± 18.81^{c}
LC_{10}	70.56 ± 2.22^{b}	87.73 ± 4.09^{a}	3.56 ± 0.35^{b}	53.41 ± 0.78^{a}	15.98 ± 0.51^{a}	452.45 ± 9.35^{a}	8.68 ± 0.18^{a}	165.2 ± 4.76^{a}	9.89 ± 0.17^{ab}	8.38 ± 0.13^{a}	727.91 ± 11.34^{b}
LC_{25}	61.23 ± 1.34^{a}	83.24 ± 3.16^{a}	6.82 ± 1.33^{a}	54.73 ± 0.31^{a}	15.65 ± 0.36^{a}	418.24 ± 12.31^{a}	8.75 ± 0.46^{a}	154.4 ± 4.32^{a}	9.35 ± 0.19^{a}	8.52 ± 0.26^{a}	793.23 ± 8.45^{a}
F_2 Generation											
Control	78.34 ± 0.67^{a}	90.54 ± 0.32^{b}	1.22 ± 0.80^{a}	55.57 ± 0.43^{a}	15.21 ± 0.16^{a}	524.28 ± 11.23^{b}	8.37 ± 0.15^{a}	189.98 ± 3.24^{b}	10.76 ± 0.13^{a}	8.67 ± 0.18^{a}	984.45 ± 17.23^{b}
LC_{10}	75.54 ± 3.28^{a}	88.78 ± 2.56^{a}	2.07 ± 0.12^{a}	54.69 ± 2.56^{a}	15.32 ± 0.29^{a}	512.39 ± 9.27^{a}	8.21 ± 0.27^{a}	181.54 ± 2.76^{a}	10.47 ± 0.34^{a}	8.58 ± 0.14^{a}	923.27 ± 16.35^{a}
LC_{25}	74.48 ± 2.37^{a}	86.49 ± 3.23^{a}	1.98 ± 0.76^{a}	54.98 ± 2.13^{a}	15.26 ± 0.29^{a}	502.34 ± 9.64^{a}	8.43 ± 0.32^{a}	182.29 ± 2.48^{a}	10.37 ± 0.28^{a}	8.62 ± 0.16^{a}	967.18 ± 17.23^{b}

All values are mean ± SE. In a column, if means are followed by different letters, it indicates a significant difference between them (P = 0.05 Tukey's HSD Test).

Table 3 Impacts of sub-lethal concentrations of spinetoram on life-table parameters of F_0 generation of *S. frugiperda* and transgenerational impacts of spinetoram applied to F_0 *S. frugiperda* on the life-table attributes of F_1 and F_2 generation

Treatment	R (day^{-1})	λ (day^{-1})	R_0 (Offspring/Individual)	T (days)
F_0 Generation				
Control	0.214±0.001^{b}	1.191±0.006^{b}	260.841±21.713^{c}	31.931±0.215^{b}
LC_{10}	0.153±0.004^{a}	1.137±0.006^{a}	156.364±17.501^{b}	34.213 ±0.301^{a}
LC_{25}	0.142±0.005^{a}	1.132±0.007^{a}	132.637 ± 11.627^{a}	34.560±0. 259^{a}
F_1 Generation				
Control	0.216±0.003^{b}	1.194±0.007^{b}	271.503±20.434^{b}	31.611±0.215^{a}
LC_{10}	0.196±0.005^{a}	1.179±0.007^{a}	235.136±16.132^{a}	32.132±0.259^{a}
LC_{25}	0.198±0.006^{a}	1.174±0.006^{a}	247.771± 14.276^{a}	32.534±0.232^{a}
F_2 Generation				
Control	0.219±0.003^{a}	1.197±0.005^{a}	274.329±19.324^{a}	31.263±0.345^{a}
LC_{10}	0.217±0.006^{a}	1.182±0.005^{a}	266.234±15.678^{a}	31.872±0.298^{a}
LC_{25}	0.214±0.006^{a}	1.188±0.007^{a}	269.402±13.543^{a}	31.597±0.243^{a}

All values are mean ± SE. In a column, if means are followed by different letters, it indicates a significant difference between them. (P=0.05 Tukey's HSD Test). R, The intrinstic rate of increase (d$^{-1)}$; λ, The finite rate of increase (d^{-1}); R_0, Net reproductive rate (Offspring/Individual); T, Mean generation time (days).

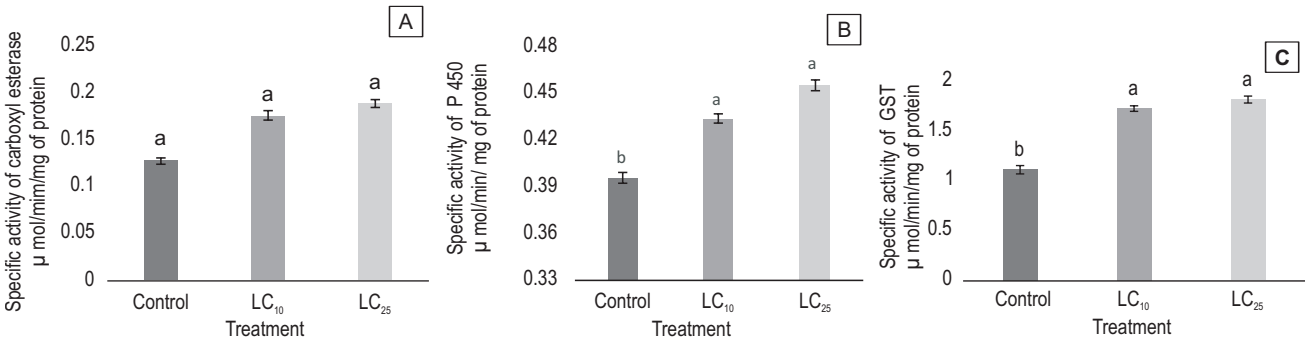

Fig. 1 Comparison of specific activity (A) CarE; (B) C-P450; and (C) GST in *S. frugiperda* larva population on LC_{10} and LC_{25} spinetoram treatments and control. Bar and error bar indicates Mean + SEM, respectively.

Nutritional indices: The feeding behaviour of third-instar larvae of *S. frugiperda* was drastically diminished up on consumption of spinetoram treated maize leaves. Specifically, CI (2.94±0.42) and GR (0.17±0.07 g) at LC_{25} were reduced significantly (Supplementary Table 1). The reduction of CI and GR in spinetoram treated larvae suggests that the food was incompatible with the insect and may work as an inhibitor; as a result, the treated larvae might not secure the necessary nutrition for standard growth. In contrast, AD exhibited a significant elevation at LC_{10} (76.79±0.31%) and LC_{25} (79.21±0.38%) (Supplementary Table 1). Similar detrimental effects were documented on another lepidopteran pest *Agrotis ipsilon* on sub-lethal exposure of cyantraniliprole (Xu *et al.* 2016).

Detoxification enzyme assays: Specific activity of GST was found to be significantly higher in LC_{25} treated *S. frugiperda* larvae (1.828 µMol/min/mg of protein) compared to the control (1.121 µMol/min/mg of protein) (Fig. 1). Specific activity of C-P450 also following same trend (0.434 µMol/min/mg of protein) (Fig. 1), interestingly there was no associated change in specific activity of carboxyl esterase that is its activity was on par with control and lower doses of spinetoram. Similar results were obtained on *P. xylostella* detoxification enzymes on sublethal exposure of Fulxametamide (Gope *et al.* 2022).

In conclusion, the results illustrated that sublethal doses of spinetoram extend the duration of both the larval and pupal periods, while adversely affecting survival, adult lifespan, and reproductive capacity in *S. frugiperda*. Moreover, it hinders the population parameters and nutritional indices of *S. frugiperda*. Beyond its direct lethal impact, certain larvae may come in contact with sublethal doses in field application, our results suggested that the spinetoram negatively affects biological traits, demographic traits and consumption indices and detoxification activities of *S. frugiperda*. Apart from this it also possesses a deleterious trans-generational capable of suppressing the F_1 and F_2 progeny of *S. frugiperda*. Spinetoram offers significant advantages, making it a promising option for widespread application in crop production. In field conditions, insects are often exposed to sublethal concentrations of insecticides over extended periods. Thus, both lethal and sublethal effects must be taken into account when formulating pest management strategies. By doing so, the frequency of pesticide applications can be reduced, minimizing the total amount of pesticides used and, consequently, lowering environmental pollution. This study serves as a valuable reference for farmers in the rational use of pesticides and offers a theoretical basis for minimizing or avoiding their side effects. Future studies should emphasize the sublethal effects of different botanicals and entomopathogens to enhance their incorporation into Integrated Pest Management (IPM) programmes.

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