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Fitness costs associated with spinetoram resistance in *Spodoptera frugiperda* is driven by host plants

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Abstract

Insecticide resistance is usually associated with fitness costs. The magnitude of the fitness costs is affected by environmental and ecological factors. Here, we explored how host plants could affect fitness costs associated with insecticide resistance. Initially, spinetoram-resistant and susceptible strains of *Spodoptera frugiperda* were selected using a F_2 screen from a population collected in São Desidério, Bahia State, Brazil. In addition to the RR and SS strains, fitness costs were also assessed for a heterozygous strain (RS). Life-history traits were evaluated to estimate population growth parameters of each strain feeding on corn, soybean, and cotton plants. The relative fitness of the RR strain was 1.06 higher compared to the SS strain on corn plants, while in soybean and cotton plants these values were 0.84 and 0.67 lower, respectively. The relative fitness of the RS strain was similar to the SS strain regardless of the host plant, suggesting a recessive fitness cost. No differences were found between the strains fed on corn plants. The larval development time was greater for the RR strain fed on soybean and cotton plants compared to the RS and SS strains. Low survival rate and fecundity of the RR strain were found when larvae fed on soybean and cotton plants. The results of this study showed that fitness costs of spinetoram resistance in *S. frugiperda* depend on the host plants that *S. frugiperda* larvae fed on. Such information can be used to design resistance management strategies considering the host plants of the agricultural landscape.

Keywords Fall armyworm · Spinosyns · Insect resistance management · Relative fitness

Key message

- The presence of fitness costs associated with resistance can be exploited in resistance management strategies.
- The host plant influences the fitness costs associated with spinetoram resistance in *S. frugiperda.*
- Information considering the host plants in an agricultural landscape is essential to design effective resistance management programs.

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Introduction

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae)*,* is recognized as one of the most important agriculturally damaging pests. Recently, the notoriety of this pest has increased because it has been reported as an invasive pest in many countries in Africa, Asia and Oceania (Goergen et al. 2016; Baloch et al. 2020; CABI 2021). *S. frugiperda* is a highly polyphagous pest with a wide range of host plant species (Montezano et al. 2018). The ability of this pest to explore different host plant species is one of the major factors in its success at colonizing new areas. The control of *S. frugiperda* relies mainly on the use of chemical insecticides, but the extensive use of this control tactic has resulted in resistance cases to many groups of insecticides (Diez-Rodríguez and Omoto 2001; Carvalho et al. 2013; Nascimento et al. 2016; Okuma et al. 2018; Bolzan et al. 2019; Lira et al. 2020; Muraro et al. 2021; Garlet et al. 2021a), challenging the management of this pest.

The spinosyns are broad-spectrum insecticides derived from the natural fermentation of *Saccharopolyspora spinosa* (Sparks et al. 2001). This group of insecticides is represented by two chemical molecules, spinosad and spinetoram, that act as allosteric modulators of the nicotinic acetylcholine receptor (Crouse et al. 2001; Salgado and Sparks 2010; Dripps et al. 2011). These insecticides have demonstrated high efficacy against many insect pests (Salgado and Sparks 2010; Dripps et al. 2011). However, some insect species have already shown resistance to spinosyns (Sparks et al. 2012; Mota-Sanchez and Wise 2021) including *S. frugiperda* with a resistance ratio > 890-fold in Brazil (Okuma et al. 2018; Lira et al. 2020). The high levels of resistance that *S. frugiperda* shows for spinosyns indicates an elevated risk of resistance evolution in this pest and an urgency in implementing insect resistance management strategies.

One of the main insect resistance management strategies is based on the assumption of fitness costs associated with resistance (Roush and McKenzie 1987; Gassmann et al. 2009; Kliot and Ghanim 2012). The fitness costs of insecticide resistance can be understood as a significant disadvantage of resistant individuals compared with their susceptible counterparts in the absence of insecticides (Kliot and Ghanim 2012). In general, fitness costs are associated with spinosyn resistance. A significant reduction in the survival rate to adulthood and a lower reproductive rate were found in a spinosad-resistant strain of *S. frugiperda* (Okuma et al. 2018). A fitness cost of spinosad resistance has also been reported for other pests such as *Chloridea virescens* (Fabricius) (Wyss et al. 2003), *Plutella xylostella* (Linnaeus) (Li et al. 2007b), *Helicoverpa armigera* (Hübner) (Wang et al. 2010), *Spodoptera litura* (Fabricius) (Rehan and Freed 2015), *Phenacoccus solenopsis* (Tinsley) (Afzal and Shad 2017) and *Ceratitis capitata* (Wiedemann) (Guillem-Amat et al. 2020). Spinetoram was introduced to the market more recently than spinosad, and so far only one study on the fitness costs associated with spinetoram resistance was reported in *Thrips hawaiiensis* (Morgan) (Fu et al. 2018); therefore, such information remains unknown for *S. frugiperda*.

The magnitude of fitness costs associated with insecticide resistance can be influenced by various environmental and ecological factors (Gassmann et al. 2009). Different host plant species and allelochemicals could play an important role in fitness costs (Carrière et al. 2004; Janmaat and Myers 2005; Bird and Akhurst 2007; Raymond et al. 2007, 2011; Wang et al. 2016; Chen et al. 2019; Santos-Amaya et al. 2022). The quality of the host plant can affect several insect development processes (Awmack and Leather 2002) and this is important for population increase and outbreaks of insect pests, especially those that can feed on a large range of host plants (Kennedy and Storer 2000; Sivakoff et al. 2013). Therefore, it is essential to understand the interaction

between the host plant and fitness costs associated with insecticide resistance to implement effective resistance management strategies.

Previous studies on the interaction between host plants and fitness costs have focused on Bt resistance (Janmaat and Myers 2005; Bird and Akhurst 2007; Raymond et al. 2007, 2011; Wang et al. 2016; Chen et al. 2019). To date, there is just one study conducted by Garlet et al. (2021b) exploring this interaction with chemical insecticide resistance. The recent documentation of spinosyn resistance in *S. frugiperda* (Okuma et al. 2018; Lira et al. 2020) and the broad host range of this pest provides us the unique opportunity to investigate the effect of different host plants on fitness costs associated with spinosyn resistance. Corn, soybean, and cotton are three of the most economically important crops in Brazil (Buainain et al. 2019), and their intensive cultivation offers an ideal scenario for the development of *S. frugiperda* populations throughout the year since this pest feeds on all three of those crops (Barros et al. 2010). In this context, we aimed to assess the fitness costs of spinetoram resistance in *S. frugiperda* by comparing several biological parameters and constructing fertility life tables for resistant, susceptible, and heterozygous strains feeding on plants of corn, soybean, and cotton plants. The findings of this study will contribute to the improvement of insecticide resistance management strategies of *S. frugiperda* and our understanding of how host plants can affect population growth in different agricultural landscapes.

Material and methods

Insect strains

The spinetoram-resistant strain (RR) of *S. frugiperda* was selected from a field population collected in São Desidério, Bahia State, in 2018. The F_2 screen method was used to obtain the resistant strain (Andow and Alstad 1998). To investigate the fitness cost of spinetoram resistance in strains with the same genetic background, a spinetoram susceptible strain (SS) was obtained from the same field population from which the resistant strain originated. The selection for susceptibility was conducted by establishing pair-mated adults from the field population. The larvae from the F_1 progeny of each couple were separated into two groups; one group was tested at the diagnostic concentration of 5.6 µg a.i. spinetoram/ml (sufficient to kill the susceptible individuals) (Lira et al. 2020) and the other group remained to establish the susceptible strain if the respective progeny had a 100% mortality. The SS strain was not exposed to any insecticide after its establishment in the laboratory. Both strains were reared on artificial diet (Kasten Jr et al. 1978). The heterozygous strain (RS) was obtained by crossing RR females and

SS males. Only one heterozygous strain was established because the inheritance pattern of spinosyn resistance in *S. frugiperda* is autosomal and both heterozygotes obtained from reciprocal crosses showed a similar mortality to spinosad and spinetoram (Okuma et al. 2018; Lira et al. 2020).

Concentration–response curves were performed to characterize the susceptibility of the SS and RR strains. In addition, a laboratory susceptible strain (SS-Lab), which was maintained in the laboratory for more than 25 years without the selection pressure of insecticides or Bt proteins, was used to validate the SS strain as a susceptible strain. Diet overlay bioassays were conducted in 24-well acrylic plates containing 1.25 ml of artificial diet in each well (1.9 cm^2 area). All strains were tested in eight logarithmically spaced concentrations (0.1 to 5.6 µg a.i. spinetoram/ml for the SS and SS-lab strains and from 180 to 5,600 µg a.i. spinetoram/ml for the RR strain). The different concentrations of spinetoram were obtained by diluting the formulated insecticide (Exalt® 120 g a.i./l) in distilled water with the addition of 0.1% (v/v) of the surfactant Triton X-100 (Sigma Aldrich Brasil Ltda). In each well, 30 µl of the insecticide solution was applied. One early third instar larva was infested in each well after the insecticide solution dried. Mortality was assessed after 48 h following the same criteria described by Lira et al. (2020), and larvae that did not show coordinated movement when prodded were considered dead.

Fitness costs assessment bioassays

Fitness costs associated with spinetoram resistance in *S. frugiperda* were investigated on corn, soybean, and cotton plants. Plants of non-Bt hybrid corn (3700 RR2), non-Bt soybean (95R51), and non-Bt cotton (FM 944GL) were cultivated in 12 l pots in a greenhouse. The SS and RR strains were reared for one generation on each host plant before the fitness costs bioassays to eliminate possible effects of changing the food source.

The bioassays were performed with leaves of corn from the V4 to V8 growth stages, leaves of soybean from V3 to V6, and leaves of cotton from the squaring phenological stage. The leaves of each plant were cut into pieces (approximately 4 cm^2) and placed over a gelled mixture of 2.5% agar-water in 16-well plastic trays (Advento do Brasil). One neonate (< 24 h old) from each strain was infested in each well and reared until the 6th instar. Then, the larvae were transferred to another 16-well plastic tray containing vermiculite and leaves of the respective host plants for development until the pupal stage. The leaves were changed every day. For each strain, 160 larvae were tested (10 replicates of 16 larvae) per host plant. The following parameters were evaluated: duration and survival rates of the egg, larval, pupal, and egg-adult periods; pupal weight; sex ratio; male and female longevity; durations of the periods of preoviposition,

oviposition, and postoviposition; fecundity; and fertility. To determine male and female longevity, duration of the preoviposition, oviposition, and postoviposition periods, fecundity, and fertility, 20 couples per strain were kept in PVC cages (10 cm diameter × 20 cm high) internally coated with paper for mating and oviposition. The adults were fed a 10% honey solution soaked into cotton. The embryonic period and survival were evaluated in 100 eggs of the second oviposition of each pair. All parameters were evaluated in daily observations. The bioassay trays and the insects were maintained in rearing rooms under controlled conditions of 25 ± 2 °C, 70% relative humidity and a photoperiod of 14:10 (L:D) h.

Statistical analysis

The mortality data of the concentration–response curves were fitted to a generalized linear model with a binomial distribution and probit as the link function. The LC$_{50}$s and the respective confidence intervals were estimated using the function *dose.p* in the MASS package (Venables and Ripley 2002).

The data from the fitness costs bioassays were analyzed using a generalized linear models (GLM) according to the distribution of the data. The pupal weight and fertility life table parameters data were fitted to a GLM with a Gaussian distribution; data on the development time of egg, larvae, pupae, and egg-adult period and the number of eggs were fitted to a GLM with a quasi-Poisson distribution; survival rates of egg, larvae, pupae, and the egg-adult period were fitted to a GLM with quasibinomial distribution. The fertility life table, which includes the net reproductive rate (total number of offspring that a female can produce during its lifetime-R_0), the mean length of a generation (mean time span between the birth of individuals of a generation and that of the next generation-T), the intrinsic rate of population increase (daily female offspring production per parental female-r_m), and the finite rate of population increase (multiplication factor of the original population size at each time period-λ), was estimated using the *lifetable.r* procedure (Maia et al. 2014). The parameters of the life table were calculated using the formulas described by Maia et al. (2000). The net reproductive rate was calculated as $R_0 = \sum lx.mx$, where *lx* is the probability of surviving to age x and *mx* is the mean number of female progeny per female of age x. The mean length of a generation was calculated as $T = \sum x.lx.mx / \sum lx.mx$. The intrinsic rate of population increase was calculated as $r_m = Ln(R_0)/T$ and the finite rate of population increase was calculated as $\lambda = e^{rm}$. The relative fitness was calculated by dividing the r_m values of the RR or RS strain by the r_m value of the SS strain as proposed by Bird et al. (2020). The goodness of fit for all data was verified using the *hnp* package (Moral et al. 2017). ANOVAs were performed to verify the effect of each factor (strain; host plant) and

their interaction using a GLM for each evaluated parameter, followed by a multiple pairwise comparison (Tukey's test) using the *lsmeans* package. All statistical analyses were performed in R Software (R Core Team 2020).

Results

Susceptibility of *Spodoptera frugiperda* strains to spinetoram

The SS and SS-Lab strains had a similar susceptibility to spinetoram (Table 1). The LC_{50} value of the SS strain was 1.0 μg ml^{-1}, while the SS-Lab strain presented a LC_{50} of 0.8 μg ml^{-1}, indicating a low variation of 1.2-fold. The LC_{50} value of the RR strain was 776.9 μg ml^{-1}, which results in a resistance ratio of 971.12-fold when compared to the SS-Lab strain and a resistance ratio of 776.9-fold when compared to the SS strain.

Survivorship of *Spodoptera frugiperda* strains on corn, soybean, and cotton plants

The effects of strain, host plant, and their interaction on the survivorship of the egg stage were not significant (F = 2.64, df = 2, 87, p = 0.07 for strain; F = 2.76, df = 2, 85, p = 0.06 for host plant; F = 2.11, df = 4, 81, p = 0.08 for the interaction).

A high survivorship of the egg stage (> 92%) was observed in all strains regardless the host plant (Fig. 1).

The larval stage was affected by strain, host plant and their interaction (F = 21.20, df = 2, 87, p < 0.05 for strain; F = 4.44, df = 2, 85, p < 0.05 for host plant; F = 12.24, df = 4, 81, p < 0.05 for the interaction). The SS and RS strains presented high survivorship (> 75%) on the three host plants and did not differ between them. A difference was observed in the survivorship of the larval stage of the RR strain on the different host plants. On corn plants, the RR strain had a larval survivorship of 90%, while on soybean and cotton plants the survivorship was 55% and 50.62%, respectively (Fig. 1).

No difference was observed in survivorship of the pupal stage among the SS, RS, and RR strains and among the three host plants evaluated (F = 2.10, df = 2, 87, p = 0.12 for strain; F = 1.19, df = 2, 85, p = 0.30 for host plant; F = 1.96, df = 4, 81, p = 0.10 for the interaction) (Fig. 1).

Development time of *Spodoptera frugiperda* strains on corn, soybean, and cotton plants

The effect of strain and the interaction between strain and host plant had significant effects on the duration of the egg stage (F = 8.60, df = 2, 87, p < 0.05 for strain; F = 10.20, df = 4, 81, p < 0.05 for the interaction). The effect of host plant was not significant (F = 2.04, df = 2, 85, p = 0.13). The duration of the egg stage ranged from 3 to 4 days in all

Table 1 Susceptibility of *Spodoptera frugiperda* strains to spinetoram

Strain	n[a]	Slope (± SE)	LC_{50} (CI 95%)[b]	χ^2	df[c]	RR[d]
SS-Lab	648	2.4 ± 0.2	0.8 (0.7–0.9)	9.1	5	–
SS	598	2.2 ± 0.2	1.0 (0.8–1.2)	8.1	5	1.2
RR	693	2.6 ± 0.2	776.9 (685.7–880.3)	9.8	5	971.12

[a]Number of larvae tested

[b]Lethal concentration (μg ml^{-1}) of applied insecticide solution that kills 50% of the individuals

[c]Degrees of freedom

[d]Resistance ratio: LC_{50} of the tested strain/LC_{50} of the susceptible reference strain

Fig. 1 Survival rates of different life stages of *Spodoptera frugiperda* strains on corn, soybean, and cotton plants. Bar height represents the mean of each treatment and error bars represent the standard error of the mean. Different lowercase letters indicate a significant difference between *S. frugiperda* strains on each host plant and uppercase letters indicate significant differences for the same strain on different host plants (Tukey's test, p < 0.05)
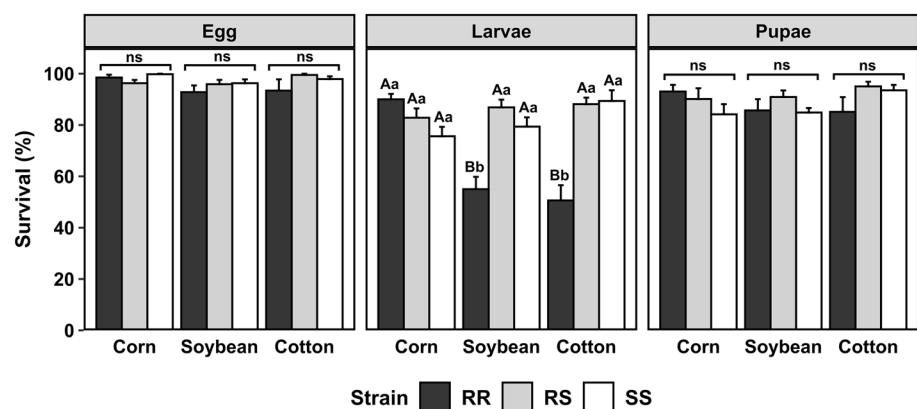
strains evaluated. A difference among the three strains was only observed on soybean and cotton plants (Fig. 2).

The duration of larval stage was affected by the strain, host plant, and their interaction ($F = 8.93$, df = 2, 87, $p < 0.05$ for strain; $F = 948.44$, df = 2, 85, $p < 0.05$ for host plant; $F = 22.19$, df = 4, 81, $p < 0.05$ for the interaction). The longest duration of the larval stage was observed when the strains were reared on cotton plants. On cotton, the RR strain presented a larval stage duration of 30.36 days, differing from the SS and RS strains, which had durations of 25.74 and 25.93 days, respectively. No difference was observed among the strains when they were reared on corn and soybean plants. The larval stage was 3.55–3.74 days longer on soybean plants compared to corn plants (Fig. 2).

The strain, host plant, and their interaction had significant effects on the duration of the pupal stage ($F = 5.72$, df = 2, 87, $p < 0.05$ for strain; $F = 107.86$, df = 2, 85, $p < 0.05$ for host plant; $F = 13.72$, df = 4, 81, $p < 0.05$ for the interaction). A difference among the strains in the duration of the pupal stage was observed only on cotton plants; the SS strain had the shortest pupal stage duration (9.93 days), differing from RS and RR, which had durations of 10.76 and 11.31 days, respectively. The longest pupal stage duration of the strains among the plants was observed on soybean plants, with a duration ranging from 11.67 to 11.88 days among the strains (Fig. 2).

Pupal weight and fecundity of *Spodoptera frugiperda* strains on corn, soybean, and cotton plants

The effects of strain, host plant, and their interaction had significant effects on pupal weight ($F = 14.05$, df = 2, 87, $p < 0.05$ for strain; $F = 52.57$, df = 2, 85, $p < 0.05$ for host plant; $F = 34.41$, df = 4, 81, $p < 0.05$ for the interaction). The

difference in pupal weight among the strains was observed on soybean and cotton plants. On soybean plants, the SS strain had a pupal weight of 188.23 mg, differing from the RS and RR strains, which had pupal weights of 202.96 and 207.36 mg, respectively. On cotton plants, the RR strain had the lowest pupal weight (158.77 mg), differing from the SS (197.82 mg) and RS (193.82 mg) strains (Fig. 3A).

The fecundity of *S. frugiperda* was affected by strain, host plant, and their interaction ($F = 9.38$, df = 2, 152, $p < 0.05$ for strain; $F = 11.63$, df = 2, 150, $p < 0.05$ for host plant; $F = 6.65$, df = 4, 146, $p < 0.05$ for the interaction). The number of total eggs laid per female did not differ among SS, RS, and RR strains on corn plants. However, a large reduction was observed in the number of eggs laid by the RR strain when it was reared on soybean and cotton plants. The SS and RS strains reared on soybean and cotton had similar fecundities with no significant difference between them (Fig. 3B).

Population growth parameters of *Spodoptera frugiperda* strains on corn, soybean, and cotton plants

Differences in population growth parameters were observed when the SS, RS, and RR strains were reared on corn, soybean, and cotton plants (Table 2). The net reproductive rate (R_0) was affected by strain, host plant, and their interaction ($F = 43.36$, df = 2, 154, $p < 0.05$ for strain; $F = 33.46$, df = 2, 152, $p < 0.05$ for host plant; $F = 20.04$, df = 4, 148, $p < 0.05$ for the interaction). The R_0 values of the SS, RS, and RR strains reared on corn ranged from 699.74 to 836.98, with no significant differences among them. A difference among strains was observed on soybean and cotton plants. When reared on soybean plants, the RR strain presented a R_0 value of 239.33 while the R_0 values of the SS and RS strains were 580.02 and 637.84, respectively. On cotton plants, the
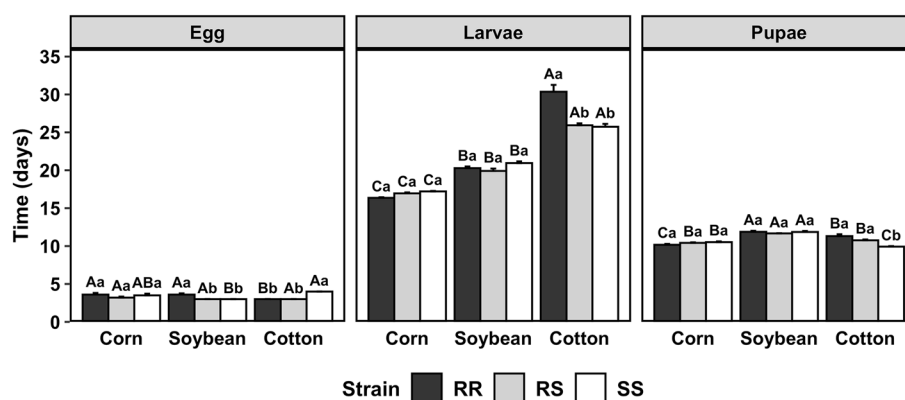

Fig. 2 Development time of different life stages of *Spodoptera frugiperda* strains on corn, soybean, and cotton plants. Bar height represents the means of each treatment and error bars represent the standard error of the mean. Different lowercase letters indicate a significant difference between *S. frugiperda* strains on each host plant and uppercase letters indicate significant differences for the same strain on different host plants (Tukey's test, $p < 0.05$)
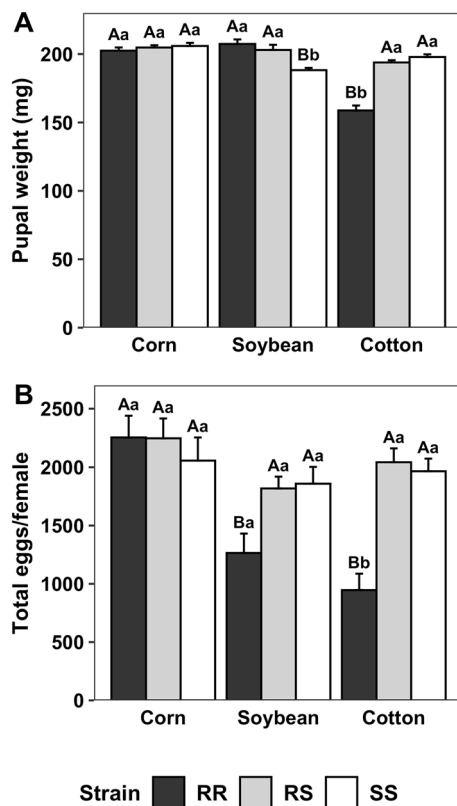
Fig. 3 Biological parameters of *Spodoptera frugiperda* strains reared on corn, soybean, and cotton plants: **A** Pupal weight and **B** Total number of eggs per female. Bar height represents the means of each treatment and error bars represent the standard error of the mean. Different lowercase letters indicate a significant difference between *S. frugiperda* strains on each host plant and uppercase letters indicate significant differences for the same strain on different host plants (Tukey's test, $p < 0.05$)

RR strain showed a R_0 value of 144.90, differing from the SS and RS strains, which showed R_0 values of 786.30 and 813.85, respectively.

The mean length of a generation (T) was affected by strain, host plant and their interaction ($F = 49.46$, df = 2, 154, $p < 0.05$ for strain; $F = 1431.17$, df = 2, 152, $p < 0.05$ for host plant; $F = 61.59$, df = 4, 148, $p < 0.05$ for the interaction). On corn plants, the duration of a generation was similar for the RR and RS strains (35.82 days), but it was significantly shorter when compared to the SS strain (37.37 days). No differences were verified in generation time between the RR (42.02 days) and SS (41.01 days) strains on soybean plants, however these two strains differed from the RS strain (39.98 days). The longest durations of generations of the SS, RS, and RR strains were observed on cotton plants. The mean length of a generation of the SS and RS strains on cotton plants were 44.53 and 44.44 days, respectively, differing from the RR strain, which presented a duration of 49.74 days.

The effects of strain, host plant, and their interaction had significant effects on the intrinsic rate of population increase (r_m) ($F = 98.84$, df = 2, 154, $p < 0.05$ for strain; $F = 448.49$, df = 2, 152, $p < 0.05$ for host plant; $F = 61.05$, df = 4, 148, $p < 0.05$ for the interaction) and on the finite rate of population increase ($F = 94.48$, df = 2, 154, $p < 0.05$ for strain; $F = 452.26$, df = 2, 152, $p < 0.05$ for host plant; $F = 58.95$, df = 4, 148, $p < 0.05$ for the interaction). On corn plants, the SS strain presented the lowest intrinsic rate of population increase (0.1753) differing from the RR (0.1874) and RS (0.1878) strains. While on soybean and cotton plants, the lowest r_m was observed in the RR strain, differing from the RS and SS strains. A similar pattern was verified for the finite rate of population increase (λ). The lowest finite rate of population increase was observed for the SS strain on corn, whereas the RR strain had the lowest finite rate of population increase on soybean and cotton plants. Differences in values of r_m and λ for the RS and RR strains were observed across the host plants; the highest values were observed on corn plants, followed by soybean and cotton, whereas no difference was observed in the SS strain for these two parameters on soybean and cotton plants.

Considering the relative fitness (w) of the SS strain as a reference ($w = 1$), the relative fitness for the RR and RS strains on corn plants were 1.06 and 1.07, respectively. A decrease in the relative fitness were observed for the RR strain on soybean plants ($w = 0.84$) and cotton ($w = 0.67$). However, the RS strain did not show any reduction in relative fitness when reared on soybean and cotton plants ($w > 1$ for both host plants). According to these results, the RR strain did not show a competitive disadvantage compared with the SS strain on corn plants. However, a reduction of the competitiveness of the RR strain was observed on soybean and cotton plants when compared to the SS strain. The RS strain did not demonstrate any disadvantages compared to the SS strain on the three host plants. This indicates that the fitness costs of spinetoram resistance in *S. frugiperda* are recessive independent of the host plant, since the fitness of the RS strain is similar to the fitness of the SS strain on the three host plants.

Discussion

In this study, we demonstrated the effects of host plants on fitness costs associated with spinetoram resistance in *S. frugiperda* through the comparison of different biological parameters using strains with same genetic backgrounds. The concentration–response curves estimated a high resistance ratio for the resistant strain of *S. frugiperda* to spinetoram used in this study. A similarly high resistance ratio has also been reported for this pest to spinosad and spinetoram by Okuma et al. (2018) and Lira et al. (2020). The spinosyn

Table 2 Population growth parameters of *Spodoptera frugiperda* strains reared on corn, soybean, and cotton plants

Population growth parameters	Strain	Host plant		
		Corn	Soybean	Cotton
Net reproductive Rate-R_0 (♀/♀)	RR	822.78 ± 36.23 Aa	239.33 ± 31.38 Bb	144.90 ± 20.62 Bb
	RS	836.98 ± 62.36 Aa	637.84 ± 35.00 Aa	813.85 ± 47.51 Aa
	SS	699.74 ± 67.56 ABa	580.02 ± 44.88 Ba	786.30 ± 43.28 Aa
Mean length of a Generation-T (days)	RR	35.82 ± 0.15 Cb	42.02 ± 0.29 Ba	49.74 ± 0.17 Aa
	RS	35.82 ± 0.20 Cb	39.98 ± 0.19 Bb	44.44 ± 0.05 Ab
	SS	37.37 ± 0.45 Ca	41.21 ± 0.19 Ba	44.53 ± 0.20 Ab
Intrinsic rate of population increase-r_m (♀/♀/day)	RR	0.1874 ± 0.001 Aa	0.1304 ± 0.003 Bb	0.1002 ± 0.003 Cb
	RS	0.1878 ± 0.002 Aa	0.1615 ± 0.001 Ba	0.1508 ± 0.001 Ca
	SS	0.1753 ± 0.003 Ab	0.1544 ± 0.002 Ba	0.1498 ± 0.001 Ba
Finite rate of population increase-λ (♀/♀/day)	RR	1.21 ± 0.001 Aa	1.14 ± 0.003 Bb	1.10 ± 0.003 Cb
	RS	1.21 ± 0.003 Aa	1.17 ± 0.002 Ba	1.16 ± 0.002 Ca
	SS	1.19 ± 0.003 Ab	1.16 ± 0.002 Ba	1.16 ± 0.002 Ba
Relative fitness (w)[a]	RR	1.06	0.84	0.67
	RS	1.07	1.04	1.01
	SS	1	1	1

Values represent means ± SE. Different lowercase letters indicate a significant difference between *S. frugiperda* strains on the same plants (columns) and uppercase letters indicates significant difference for the same strain on different plants (lines) (Tukey's test, $p < 0.05$)

[a]Relative fitness (w) = r_m (RR or RS strain)/r_m (SS strain)

insecticides are one of the chemical groups used to manage this pest in Brazil (Burtet et al. 2017). Thus, the increase in the number of highly resistant strains, selected in a short time, raises the hypothesis that the frequency of spinosyn resistance alleles in *S. frugiperda* populations in the field is rising, possibly due to an increase in the selection pressure exerted by these insecticides.

Fitness costs is one of the concepts that uphold enduring resistance management programs (Freeman et al. 2021). Our results showed that all strains (resistant, susceptible, and heterozygous) survived and completed their life cycles on corn, soybean, and cotton plants. Different patterns of development and life history traits were observed among the three evaluated host plants, indicating relevant fitness costs associated with spinetoram resistance in plants of soybean and cotton, but no significant fitness costs in corn plants. Different host plants can affect the magnitude of the fitness cost associated with insect resistance (Gassmann et al. 2009). Previous studies showed that plants of corn, soybean, and cotton affected the magnitude of fitness costs associated with Cry1F, chlorpyrifos and Cry1A.105 + Cry2Ab2 resistance in *S. frugiperda* (Jakka et al. 2014; Garlet et al. 2021b; Santos-Amaya et al. 2022). Similar results were also observed in other insect pest such as *H. armigera*, *P. xylostella* and *Trichoplusia ni* (Hübner) when feeding on different food sources (Bird and Akhurst 2007; Raymond et al. 2011; Wang et al. 2016). However, the fitness costs of Vip3A resistance in *S. frugiperda* was not evident on different host plants (Chen et al. 2019), suggesting that the magnitude of

fitness costs on different host plants is not always apparent, and it should be studied for each resistance case.

The variation in fitness costs on different host plants could be related to plant defense compounds and their nutritional quality that alters food conversion efficiency, which in turn can affect the development time and fecundity of insect pests (Awmack and Leather 2002). Although *S. frugiperda* is a highly polyphagous pest, corn and other grass plants appear to be the most suitable host plants for *S. frugiperda* (Barros et al. 2010; Silva et al. 2017). In our study we hypothesized that the slow development of *S. frugiperda* strains on soybean and cotton plants could be related to the secondary compounds of these plants. A study conducted by Peruca et al. (2018) demonstrated that secondary compounds of soybean plants impair the development of *S. frugiperda*. The lower fitness on cotton plants could be related to gossypol, a polyphenolic aldehyde, that affects larval development as demonstrated in Bt-resistant strains of *Pectinophora gossypiella* (Saunders) (Carrière et al. 2004, 2019; Williams et al. 2011).

Another hypothesis for the lower fitness of the RR strain on plants of soybean and cotton is the interaction between the resistance mechanisms of spinosyn resistance in *S. frugiperda* and the mechanisms of adaptation to the plant defense compounds of soybeans and cotton. Insects have to evolve different strategies to overcome plant secondary compounds. The main mechanism of insect adaptation to synthetic and natural xenobiotics is the increased metabolic capability of detoxification (Li et al. 2007a; Schuler 2011;

Feyereisen 2012; Heidel-Fischer and Vogel 2015; Lu et al. 2020; Vandenhole et al. 2020). Since the process of synthesizing detoxification enzymes is very costly, it demands an energy reallocation from other biological functions, resulting in a lower fitness (Kliot and Ghanim 2012). The spinosyns resistance mechanisms have been studied for several species of insect pests. Target site insensitivity has been associated with spinosyn resistance in most cases (Perry et al. 2007; Baxter et al. 2010; Hsu et al. 2012; Silva et al. 2016; Zimmer et al. 2016; Wan et al. 2018; Wang et al. 2020a, b; Zuo et al. 2020). However, some studies showed that metabolic detoxification enzymes could also be involved in spinosyn resistance (Wang et al. 2009; Sial et al. 2011; Rehan and Freed 2014). At the moment, the mechanism underlying spinosyn resistance in *S. frugiperda* is still unknown. Multi-omics approaches will be considered in our future studies in order to identify the molecular mechanism associated with spinosyn resistance in *S. frugiperda* and understand the interaction between the mechanism of insecticide resistance and the mechanism of host plant adaptation.

From a practical perspective, no significant fitness costs associated with spinetoram resistance on corn plants means that removing the selective pressure from the environment would not result in a decrease of spinetoram resistance allele frequency on corn plants since there is no competitive disadvantage between resistant and susceptible individuals. On the other hand, a negative impact was verified on the life history traits of the RR strain on soybean and cotton plants, which had a significant reduction in the survival and reproductive rates compared to the other strains. This information could be exploited to design effective resistance management strategies. For example, a seasonal removal of spinosyn insecticides in the control of *S. frugiperda* and an adoption of insecticides with different modes of action in a rotation scheme, or another control tactic, would aid in maintaining the resistance to spinetoram at low frequencies.

In conclusion, we showed that the rate of spinetoram resistance evolution in *S. frugiperda* might be dependent on the host plant. When feeding on corn plants, resistance may evolve more rapidly than when feeding on soybean and cotton plants. The shorter development time on corn plants increases the number of generations of the pest, consequently increasing the frequency of resistance alleles in the field. On soybean and cotton plants, the frequency of resistant individuals tends to be lower due to the presence of a fitness cost. Despite the competitive disadvantage of resistant individuals on soybean and cotton plants, an attention should be given to the heterozygous individuals because their performance is similar to the susceptible individuals regardless the host plant. The heterozygous individuals are the main carriers of resistance alleles and their competitiveness guarantees the permanence of resistance alleles in the field (Roush and Daly 1990). The information provided here supports the design of effective IRM strategies, highlighting the importance of not only the biological aspects of the pest, but also the host plants that are part of the agricultural system where the pests are found.

Author contributions

All authors conceived and designed the experiments; RHK, ASG, FEOP and JGR collected data; RHK performed the statistical analyses; all authors interpreted the results and wrote the manuscript.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Human or animal rights "This article does not contain any studies with human participants or animals performed by any of the authors."

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