

Biological Parameters and Fertility Life Table of *Spodoptera frugiperda* in Different Host Plants

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Abstract

This work evaluated the biology and life table parameters of susceptible populations (Sus) of *Spodoptera frugiperda* to insecticides and Bt proteins, in conventional maize, Bt YieldGard VT PRO™ (Cry1A.105/Cry2Ab) and PowerCore™ (Cry1A.105/Cry2Ab/Cry1F), millet and sorghum to better feeding behavior in this population. The following parameters were assessed: width of the cephalic capsule, duration and viability of larval, pupal and egg stages, pupal weight, sex ratio, adult longevity, pre-oviposition and oviposition period and daily fecundity. The larval diet affected most of the parameters analyzed, with the exception of adult longevity and the period of embryonic development. The sus population completed its development in all hosts except in the VT PRO™ and PowerCore™ technologies. Non-Bt maize (87.50%) had higher larval viability, with larvae pupating nearly twice as fast (14,364 days) than sorghum (22,663 days) and millet (25,153 days), with the lowest viability (25.63%) and longest larval stage observed in millet. The pre-oviposition period was significantly shorter in maize (2.2 days) and longer in millet (6.5 days). Females fed on maize (1872.3) also showed higher total fertility than sorghum (671.0) and millet (405.0). Our results suggest that millet is the least suitable host for the development of this population. Although maize is considered the preferred host, *S. frugiperda* was able to complete its development in most of the tested hosts, indicating that sorghum and millet, plants commonly cultivated in the main producing regions of Brazil, can sustain susceptible populations in the field, although not as productively as maize and can act as a reservoir for the pest between seasons.

Keywords: fall armyworm, life table, host plant, biology, sorghum, millet

1. Introduction

The Fall armyworm, *Spodoptera frugiperda* (Smith, 1797) (Lepidoptera: Noctuidae) is a polyphagous insect that can feed on the leaves, stems and reproductive structures of more than 350 plant species belonging to 76 different families (Montezano et al., 2018). Infestations of the species are commonly reported in wild and cultivated grasses of the Poacea family, such as maize (*Zea mays* L.), rice (*Oryza sativa* L.), sorghum (*Sorghum bicolor* L.) and sugarcane (*Saccharum officinarum* L.), but also in other broadleaf crops such as cotton (*Gossypium hirsutum* L.) and soybeans (*Glycine max* L.) (Machado et al., 2020). Since 2016 when *S. frugiperda* was first detected in Africa, it has become a significant economic pest in the continent, causing substantial losses in maize and sorghum and has the potential to damage other crops such as forage grasses (Day et al., 2017; Rwomushana et al., 2018). The fall armyworm is now present in 44 African countries (Rwomushana et al., 2018). In China, infestations of *S. frugiperda* have reached more than one million hectares of agricultural land, mainly affecting maize, sugar cane, sorghum, millet, peanuts, rice, potato and wheat plantations, which comprise about 99.98% of total crop production affected by the fall armyworm (Jiang et al., 2019).

The Food and Agriculture Organization (FAO) estimates that Brazil alone spends US\$600 million per year on infestation control (Wild, 2017). In Brazil, the overlap of cultivated hosts (maize, cotton, and soybean) and the widespread availability of concurrent alternative hosts allow *S. frugiperda* populations to remain in the field for successive generations (up to 6) throughout the year (Barros et al., 2010). Likewise, sowing in areas close to different crops with different phenology, such as soybean, corn and cotton grown in the summer, and cover crops,

such as millet in the off-season, may favor the larval movement of *S. frugiperda* between crops (Nagoshi, 2009; Malaquias et al., 2020). If oviposition and early development take place in host plants suitable for development, later instars are able to move in mass to cultivated hosts, thus maximizing the potential for damage (Montezano et al., 2018). This bioecological and feeding behavior may allow *S. frugiperda* to build and maintain populations outside the primary growing season or outside the growing areas, contributing to the constant permanence of the pest in the field and functioning as a natural reservoir of the pest (Arends et al., 2021).

The adoption of genetically modified plants expressing insecticidal proteins from *Bacillus thuringiensis* Berliner (Bt) is currently the most efficient control method available for pest management (Okumura et al., 2013; Waquil et al., 2013). However, resistance evolved rapidly in field pest populations, with reports of control failure and resistance to various Bt proteins expressed in maize and cotton plants (Cry1F, Cry1Ab, and Cry1A.105) (Farias et al., 2014; Omoto et al., 2016). Selection for resistance occurs almost exclusively in maize and Bt cotton. Moths of *S. frugiperda* that complete the biological cycle in maize disperse and infest other cultivated and uncultivated host plants such as oats (*Avena stringosa* S.), brachiaria (*Urochloa decumbens* S.), gherkin (*Lotus corniculatus* L.) and even weeds such as amaranthus (*Amaranthus* sp.) and sedge (*Cyperus rotundus* L.) (Dias et al., 2016; Montezano et al., 2018; Malaquias et al., 2020). Among them are also cotton in the flowering stage, soybean, millet (*Pennisetum americanum* L.) and sorghum (Sá et al., 2009; Dias et al., 2016; Oliveira et al., 2019).

Thus this study aimed to evaluate the biology and life table parameters of *S. frugiperda* in 5 different food sources (conventional maize—non-Bt), Bt maize YieldGard VT PRO™ (Cry1A.105/Cry2Ab), PowerCore™ (Cry1A.105/Cry2Ab/Cry1F), millet and sorghum, to better understand their feeding behavior in hosts that are commonly cultivated in tropical and subtropical regions worldwide. In Integrated Pest Management (IPM) programs, biology and fertility life table studies are of great importance for understanding the population dynamics of a species, since it allows an integrated view of the biological characteristics of a population under specific environmental conditions (Coppel & Mertins, 1977).

2. Method

2.1 Insects

In this study, a susceptible population of *S. frugiperda* established in the laboratory for more than 30 generations on the artificial diet of Karsten et al. (1978) was used, this population is free of selection pressure by chemical insecticides and Bt proteins. A 10% honey solution (v v⁻¹) was used for feeding the adults. The moths were kept in cylindrical PVC cages (24.0 cm high × 14.5 cm in diameter), covered internally with newsprint as a substrate for oviposition and closed at the top with voile fabric.

2.2 Host Plants

Bt maize YieldGard VT PRO™ (Cry1A.105/Cry2Ab), PowerCore™ (Cry1A.105/Cry2Ab/Cry1F), non-Bt maize (cultivar BM 3051) and sorghum (cultivar Candy Graze MT) were sown in 20 L pots, filled with soil and kept in a greenhouse until the V3 stage (40 days after emergence) in which the leaves were used in the bioassays. As for millet (cultivar ANm 38), they were sown in plastic trays (30.0 × 20.0 × 6.00 cm) and when the leaves were approximately 10–20 cm in height (≈ 30 days) they were removed and used in the experiments. All host varieties are commercially cultivated in Brazil.

2.3 Biology Parameters and Life Table of *Spodoptera frugiperda* in Different Host Plants

The experiments were carried out at the Entomology Laboratory of the Brazilian Agricultural Research Corporation (Embrapa) Center for Temperate Climate-Lowlands Experimental Station (ETB) located in the city of Capão do Leão, state of Rio Grande do Sul, Brazil. The tests were conducted under controlled conditions (25±2 °C, 70±10% RH and photoperiod of 14h10 [L:D]). For each host, 120 neonatal larvae (< 24 hours of age) were individually transferred to 16-cell plastic trays (2.8 × 4.1 × 1.6 cm) (B16-Biossupply). The larvae were fed daily with leaflets (≈ 5 cm in diameter) from their respective hosts until they reached the pupal stage when they stopped feeding. In addition, the width of the cephalic capsule of 30 larvae was checked daily until the pupal stage, to determine the number of instars using a micrometric lens attached to a stereoscopic microscope (LEICA®). After 24-hour of pupation, pupae were weighed and sexed according to Butt and Cantu (1962). The pupae were kept individually in glass tubes (2.5 × 8.0 cm) with a piece (1 cm) of moistened filter paper until the adults emerged. After emergence, twenty couples of *S. frugiperda* (with a maximum of 48 hours of age) from each host were placed in PVC cages (10 cm in diameter × 20 cm in height) covered with recycled sulphite paper (oviposition substrate) and closed at the top with voile. The adults were fed daily with 10% honey solution until the insects died. The eggs were removed daily and counted using a stereoscopic microscope. In order to

determine the duration and viability of the egg phase, the second posture of each couple was kept in glass tubes (2.5 × 8.0 cm) containing moistened paper until the larvae hatched. The biological parameters evaluated during the immature phase were width (cm) of the cephalic capsule, duration (days) and viability (%) of the larval and pupal stages, weight (g) of 24-hour pupae and sex ratio. In the adult phase, the longevity (days) of adults, pre-oviposition and oviposition period and daily fecundity were determined. The experimental design was completely randomized, with 8 replicates per host, with 15 larvae per replicate (n = 120).

2.4 Data Analysis

The biological parameters (embryonic, larval, pupal and adult stages, pre-oviposition period, daily fertility and pupae weight) were evaluated for normality by the Shapiro-Wilk test and homoscedasticity by Hartley and Bartlett, means were compared by the Tukey's test, at 5% probability, using the GraphPad Prism 9.0 software. The graphical method was used to determine the number of instars, the hypotheses were formulated and tested in the linear model of Dyer's rule, using the MOBAE Software, based on confidence intervals, whose constant ratio was defined as 1.53. When growth peaks were observed in the measurements, it was suggested that there was a change in the instar of larvae. Survivorship, development, and reproduction data were used to estimate fertility life table parameters, including mean length of a generation (T), net reproductive rate (Ro; average number of female offspring that would be born to a cohort of females), and intrinsic rate of population increase (rm; daily production of females per parental female). The parameters of the fertility life table were obtained using the jackknife technique applying the "lifetable.sas" procedure developed by Maia et al. (2000) in SAS® 9.1 (SAS Institute 2011).

3. Results

The susceptible population of *Spodoptera frugiperda* completed its biological cycle in all evaluated hosts, except in Bt YieldGard VT PRO™ and PowerCore™ maize technologies, where there were no surviving larvae. There was no significant difference in the embryonic period among the tested hosts, but the egg survival rate was higher in maize (83.45%) and lower in millet (18.16%). Although the larval stage was significantly shorter in non-Bt maize (14,364 days) larvae had 4 instars in millet and sorghum and 5 instars in maize (Figure 1) however the instar change occurred faster in maize with greater frequency of larvae with larger cephalic capsules. Compared with larvae fed on sorghum (61.25%) and millet (25.63%) leaves, non-Bt maize (87.50%) (P < 0.0001) showed higher larval viability (Table 1). The pupal period for sorghum (12,213 days) and millet (11,533 days) was longer than for non-Bt maize (9,507 days). However, pupal weight and viability were higher in non-Bt maize (96.42%), which showed a shorter pupal development time than in sorghum and millet, respectively (P < 0.0001). Millet was the host that provided the highest proportion of females in relation to males (sex ratio) (0.64) when compared to maize (0.51) and sorghum (0.49) (Table 2). The pre-oviposition period of adults was also longer in millet, which was reflected in total fertility, with maize-restricted females showing higher fertility than sorghum (P < 0.0001) and millet (P < 0.00001) (Table 2). When evaluating adult longevity, there was no significant difference in duration (days) of longevity in males (P = 0.6192) and females (P = .8176) (Table 3).

Table 1. Duration (days) and viability (%) of each developmental stage of *Spodoptera frugiperda* fed on different hosts plants

Hosts	Larva		Pupa		Egg	
	Duration* (days)	Viability (%)	Duration* (days)	Viability (%)	Duration* (days)	Viability (%)
Maize non Bt	14.364±0.101 c	87.50±a	9.507±0.075 b	96.42 a	3.523±0.131 a	83.45 a
Sorghum	22.663±0.294 b	61.25 b	12.213±0.202 a	76.53 b	3.692±0.398 a	18.16 c
Millet	25.153±0.851 a	25.63 c	11.533±0.359 a	52.50 c	4.000±1.000 a	30.04 b

Note. * Means±SE. An analysis of variance ANOVA (Tukey at P < 0.05) was performed for each biological parameter between hosts. Group of columns with the same letters do not show significant differences between them.

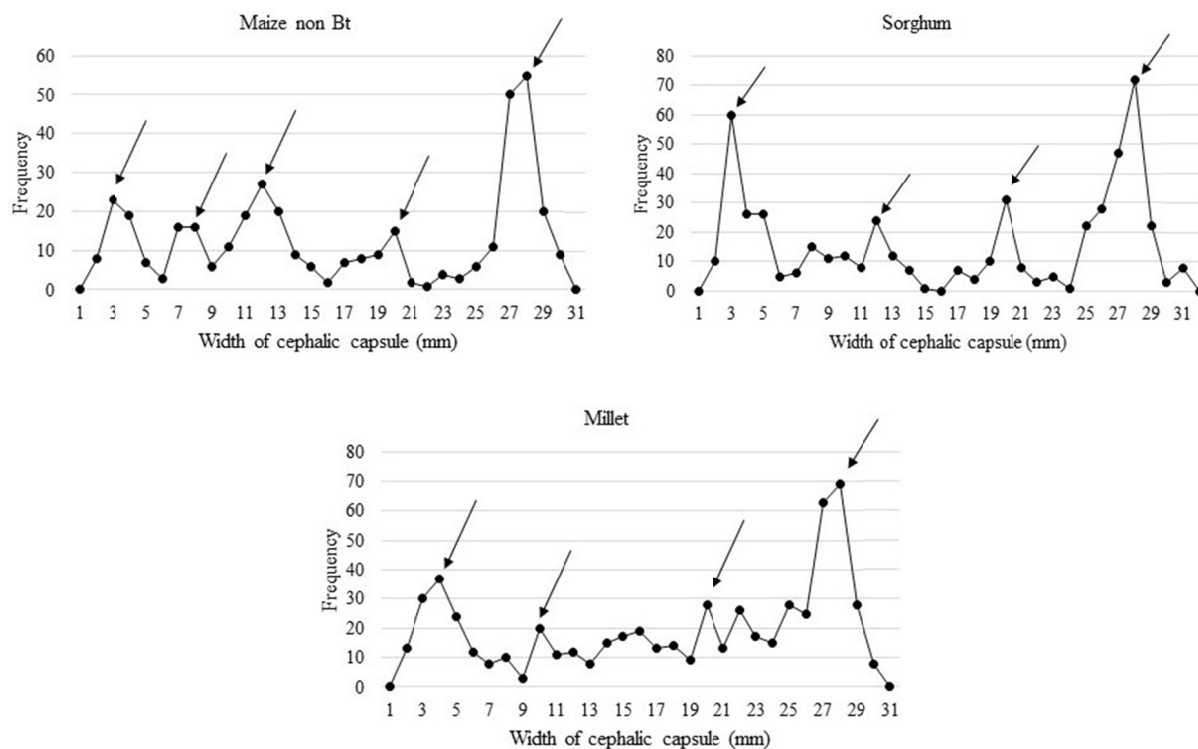


Figure 1. Frequency distribution of the sizes of cephalic capsules during the larval stage of *S. frugiperda* fed on (A) non-Bt maize, (B) sorghum, and (C) millet

Table 2. Biological parameters of *Spodoptera frugiperda* fed on non-Bt maize, sorghum, and millet

Biological Parameters*	Hosts		
	Maize non-Bt	Sorghum	Millet
Pupal weight (g)	0.18±0.0 a	0.14±0.0 b	1.3±0.05 b
Sex rate (♀/♀+♂)	0.51	0.49	0.64
Longevity ♂ (days)	13.9±0.8 a	13.4±0.9 a	13.3±4.0 a
Longevity ♀(days)	13.7±1.0 a	13.0±0.8 a	11.0±1.4 a
Pre-oviposition (days)	2.2±0.1 c	4.0±0.3 b	6.5±0.3 a
Total fertility	1872.3±110.6 a	671.0±50.0 b	405.0±112.7 b

Note. * Means±SE. An analysis of variance ANOVA (Tukey at P < 0.05) was performed for each biological parameter between hosts. The same letters within a line do not show significant differences between them.

The high reproductive capacity verified in maize reflected positively on the fertility life table and in all the evaluated biological parameters, the values of the net reproduction rate (Ro) indicated that in maize *S. frugiperda* has a high capacity to generate female offspring (Table 3). Sorghum and millet showed the greatest increase in the duration of each generation (T) ~50.15 days and 50.81 days, respectively. In addition, they produced less than ~30.74 and ~8.05 females/emerged female/generation (Ro), while progeny survivors in non Bt maize produced approximately 662.44 females/female in ~38.89 days. The female progeny of millet and sorghum survivors showed a natural population increase rate (rm) of less than 0.041 and 0.068 respectively, indicating that approximately 25 to 40% less capacity for population increase when compared to non-Bt maize.

Table 3. Fertility life table of *Spodoptera frugiperda* fed on non-Bt maize, sorghum and millet

Biological Parameters	Hosts		
	Maize non-Bt	Sorghum	Millet
T (days)	38.89±5.11 a	50.15±4.11 b	50.81±3.12 b
R ₀ (♀/♀)	662.44±32.9 a	30.74±1.40 b	8.05±1.12 c
r _m (♀/♀*day)	0.167±0.003 a	0.068±0.002 b	0.041±0.003 b
Λ	1.075±0.002	1.030±0001	1.017±0.002

Note. ^aT = mean length of a generation (d); R₀ = net reproductive rate (females per female per generation); and r_m = intrinsic rate of population increase (per day).

^bMeans±SE followed by the same letter in each line are not significantly different (t-test for pairwise group comparisons, P > 0.05).

4. Discussion

In Brazil, millet and forage sorghum are used for pasture and soil cover, mainly in no-tillage systems and in rotation with soybean and maize increasing their importance in the midwest and southeastern regions of the country (Sá et al., 2009; Barros et al., 2010; Assis et al., 2018). The present study evaluated the biological and life table parameters of *S. frugiperda* susceptible to Bt plants to maize, millet and forage sorghum. The suitability of a given host plant for development can be assessed by processing different fitness traits or life table parameters (egg survival, developmental rate, pupal weight) (Moreau et al., 2006). Significant differences in survival and developmental time of *S. frugiperda* were observed among the three host plants. Millet and sorghum-fed larvae showed lower survival rates and slower developmental rates compared with maize-fed larvae. Compared with sorghum and non-Bt maize, millet had lower larval and pupae survival and prolonged larval and pre-oviposition periods, suggesting that millet is the least suitable host for the development of this population. According to Boregas et al. (2013) generally shorter larval stages indicate better host adaptation to insect development as cycles are completed faster and the number of generations increase.

Similar results were observed by Dias et al. (2016) where when compared to maize and other cover crops, the survival of *S. frugiperda* larvae and the biomass of pupae were lower in millet. The larvae development period in this host was also extended ~26 days more than in maize. The changes in the biological parameters of *S. frugiperda* were related to the amount of nitrogen available in the leaves, which was 3.16% in millet and 6.12% in maize. According to Dias et al. (2016), and Panizzi et al. (2009) among the constituent elements of plants, nitrogen is considered the most important in terms of insect nutrition, as it is involved in all metabolic processes. In terms of quantity and quality available, nitrogen often limits insect growth and fecundity and can also impact larval survival and pupae biomass.

Hence, the results in this study may be due to problems associated with nutrient ingestion, digestion and assimilation, or a combination of physical and chemical characteristics of the plant, such as secondary anti-herbivore compounds (*i.e.*, phenolic and alkaloid compounds), leaf tenacity and lower protein content (Veenstra et al., 1995; Silva et al., 2017). This can delay larval development and reduce weight gain and survival (Awmack & Leather, 2002). Thus, the increased duration of the larval stage can be explained as a compensatory measure by which larvae “recover” when feeding on a lower quality host and are able to pupate and gain higher body weight. Based on the “slow growth-high mortality” hypothesis of Benrey and Denno (1997), this resource can be used in IPM programs, such as by increasing the time of contact with beneficial arthropods or insect pathogens, as this helps reduce pest levels to below levels and will not result in economic losses from pollution, ecosystem damage or loss to producers.

He et al. (2021), and Sá et al. (2009) also reported median values of biological variables for *S. frugiperda* feeding on sorghum plants. It is important to remember that within the same species, significant differences in the biological parameters of *S. frugiperda* were found between the growing seasons of the cultivar and the tested host. Barros et al. (2010) for example, observed high survival rates and reduced larval period in maize and millet, as well as Boregas et al. (2013), where the biological variables of *S. frugiperda* studied in general did not differ significantly between maize, millet, grain sorghum and wild sorghum with the exception of the larval period and pupae biomass, which were affected by the host species and the season of cultivation.

The findings indicate that non-Bt maize can significantly increase larval survival and pupal biomass, in addition to decreasing development time. The general nutritional status and fitness of larvae is reflected in pupal stage characteristics such as pupation rate, cycle length, and biomass (Oliveira et al., 2019). In this study, the pupae

were heavier and the most fertile females were from non-Bt maize. According to Bernardi et al. (2014), even when larvae were exposed to negative factors such as *B. thuringiensis* protein-expressing plants, noted differences between *S. frugiperda* pupae weight and egg production, with heavier pupae leading to higher fertility in females.

Differences in overall fertility may be related to feeding at the immature stage, when most Lepidoptera feed heavily in the larval stage and adults have almost all the nutrients they need to reproduce. Feeding indirectly affects the maturation process and sexual activity activates the endocrine system. This affects oviposition behavior (Awmack & Leather, 2002). Furthermore, for some insects, the intake of protein sources is crucial for the activation of this endocrine system, as it is directly related to oocyte production (Wheeler, 1996; Papaj, 2000; Panizzi & Parra, 2009).

Although maize is considered the preferred host, the susceptible population was able to complete its development in all tested hosts, indicating that sorghum and millet can sustain pest populations in the field, although not as productively as maize and can function as a reservoir between seasons (Sá et al., 2009). For example, using millet as a cover crop could serve as a winter host for *S. frugiperda* to build populations from which it can colonize major summer crops such as maize, soybean and cotton that make up the landscape of major Brazilian producing regions. Consequently, *S. frugiperda* can find suitable hosts throughout the year, and since temperature and availability of food resources are not factors limiting development or survival, it is expected that this highly polyphagous species will be able to produce successive generations, thus maximizing economic losses.

However, our experiments suggest that millet and sorghum have the potential to reduce this population density by prolonging development time and increasing larval mortality. Furthermore, these alternative cover crops are much less attractive to *S. frugiperda* larvae and adults, thus limiting the density of this pest in the absence of maize (Meagher et al., 2004). Reducing endogenous populations of *S. frugiperda* in cover crops can reduce density and delay subsequent infestation of maize crops while hindering migration. Although a potentially effective and cost-effective means of cultural control, further research is needed to determine the impact of cover crops on fall armyworm population dynamics and therefore the potential impact of changes in cover crop selection. In particular, it is necessary to determine the extent to which various cover crops serve as refuge for armyworm populations throughout the seasons, especially during periods when maize is not available (Meagher et al., 2004).

Our results indicate that the success of controlling *S. frugiperda* will depend on monitoring populations between cropping systems during and between seasons, considering the plant species used for intercropping and for cover crops in no-tillage systems. The migration of *S. frugiperda* between crops can have a serious impact on the management of this pest, especially considering that insecticides and mainly Bt plants can be used simultaneously on adjacent crops in the same landscape. Life table and biology studies of different populations can allow the development of integrated pest management strategies with diverse mortality factors, rather than just relying on large-scale use of unique control tactics (He et al., 2021).

5. Conclusion

This study provides new information on the biology and life table of *S. frugiperda* susceptible to Bt and insecticides on maize, millet and sorghum, commonly cultivated hosts in tropical and subtropical regions of the world. Although maize is the preferred host, our results show that *S. frugiperda* can successfully survive and reproduce in millet and sorghum under conditions where temperature is not a limiting factor. However, the observed differences in biology and life tables between these hosts suggest that millet and sorghum may reduce pest population densities. These responses varied across studies, suggesting that factors such as population origin and cultivars tested may affect these parameters. Further research is needed to determine the impact of cover and rotation/succession crops on fall armyworm population dynamics and therefore the potential impact of changes in crop selection. In particular, it is necessary to determine the extent to which these crops serve as refuge for armyworm populations throughout the seasons, especially during periods when maize is not available. Considering the importance of these grasses in Brazil and that they can play an essential role in FAW population performance, it would be necessary to initiate field studies on populations responsible for the colonization of maize crops and FAW dispersal patterns and the factors that govern them.

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