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Performance of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) Fed on Six Host Plants: Potential Risks to Mid-high Latitude Crops in China

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Abstract

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is a polyphggous and widespread insect pest. In the study, the biological characteristics and nutritional indices of *S. frugiperda* fed on six crops, namely corn, sorghum, wheat, soybean, peanut, and cotton, were investigated under laboratory conditions. These crops are cultivated mainly in the mid-high latitude of China. Results showed that *S. frugiperda* was able to develop and reproduce on all six tested plants. Larvae reared on corn exhibited a significant shorter larval and pupal duration, higher pupal weight, and higher fecundity, which were 16.2 d, 8.9 d, 0.248 g, and 979.4 eggs per female, respectively. The host plant significantly affected relative growth, consumption, and metabolic rates, as well as other nutritional indices. Biology and nutritional indexes suggested that corn was the most suitable host. Besides, peanut, sorghum, and wheat have also been shown to be the suitable hosts for *S. frugiperda*. Although cotton and soybean were found to be less adequate, high larval and pupal survivors recorded on cotton and soybean leaves have indicated that damage may occur in these plants. This work reveals the damage risk of potential hosts of *S. frugiperda*, lays the foundation for the design of pest management strategies.

Keywords: fall armyworm, *Spodoptera frugiperda*, biology, nutritional index, food consumption

1. Introduction

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), is an important polyphagous pest native to tropical and subtropical regions of the Americas (Sparks, 1979; Nagoshi et al., 2017). It is widely distributed throughout the United States, Puerto Rico, Mexico, Brazil, and Argentina (Clark et al., 2007). In January 2016, *S. frugiperda* was detected in western Africa (Goergen et al., 2016; Nagoshi et al., 2018). In May 2018, this pest was discovered in southwest India (Sharanabasappa et al., 2018). In January 2019, *S. frugiperda* was first observed in Yunnan Province, southwest of China, and subsequently invaded 26 different provinces except for Xinjiang, Qinghai, and northeastern China (Guo et al., 2018; Jing et al., 2020). So far, *S. frugiperda* has been confirmed in eastern and southern Asian countries (Sun et al., 2019; Li et al., 2020).

S. frugiperda is commonly referred as the corn (C) strain, and the rice (R) strain (Quisenberry, 1991; Nagoshi & Meagher, 2004). The caterpillars of *S. frugiperda* can damage over 350 plant species, causing severe yield losses in many economic crops, especially corn (*Zea mays* L.), rice (*Oryza sativa* L.), soybean (*Glycine max* (L.) Merrill) and cotton (*Gossypium hirsutum* L.) (Nagoshi, 2009; Bueno et al., 2011; Montezano et al., 2018; Guo et al., 2020). This pest causes damage on corn with average losses of 26.6% in Ghana and 35% in Zambia (Day et al., 2017), and reduced grain yields of up to 55% and annual losses of US $ 400 million (Lima et al., 2010).

Necessary biological studies on the consumption and utilization of different host plants are essential to address the effects of the nutritional composition of different plants on the pest (Scriber & Slansky, 1981; Barros et al., 2010). Host plants can affect the life history of insects in many ways, including development, survivorship, reproduction, and longevity (House, 1961; Meagher & Nagoshi, 2004). The food ingested by insect herbivores undergoes digestion, and the energy transformed it into body substance. The investigation on the utilization of host by insect becomes significant as it gives indirect measurements of relative susceptibilities and attributes of the host plant to insect performance and infestation (Slansky, 1990).

Studies on food utilization and consumption of insect are critical in understanding the interaction between insects and plants and also in helping to plan pest management strategies by providing estimates of potential economic losses (Ramalho et al., 2011) and improving insect mass rearing techniques (Souza et al., 2001; Busato et al., 2002). Recently, numerous researches on biology and nutrition have been carried out. The focus of these studies was based on different varieties of the same crop (Naseri et al., 2010; Rosa-Cancino et al., 2016; Barcelos et al., 2019), genetically-modified plants (Ramalho et al., 2011; Sousa et al., 2016), or artificial diets (Pinto et al., 2019; Truzi et al. 2019). Less research compared the life parameters among different hosts. Field surveys found that *S. frugiperda* caused damage on corn, wheat, sorghum, and peanut in China (Jiang et al., 2019). Though the infestation was not detected on soybean and cotton in China at present, *S. frugiperda* is becoming an important pest to cotton and soybean, which were grown on a large scale in the Brazilian Cerrado (Barros et al., 2010).

Therefore, this study aimed to assess the biology and nutrient indices of *S. frugiperda* larvae feeding on corn, soybean, sorghum (*Sorghum bicolor* (L.) Moench), wheat (*Triticum aestivum* L.), peanut (*Arachis hypogaea* L.) and cotton, which were the most important economic crops in China, in order to reveal the damage risk of potential hosts of *S. frugiperda*.

2. Methods

2.1 Insect Stocks

A colony of *S. frugiperda* was initially collected and identified from a corn field in Mangshi, Yunnan Province, China, and maintained in the laboratory for five to six generations. They were reared under laboratory-controlled conditions (temperature of 26±1 °C, relative humidity of 60±10%, photoperiod of 16 h light/8 h dark) and fed on a regular artificial diet.

2.2 Plant Material

For the treatments, leaves of corn (‘Zhengdan 958’ cultivar), sorghum (‘Liaoza 11’ cultivar), wheat (‘Zhongmai 9’ cultivar), soybean (‘Wandou 28’ cultivar), peanut (‘Zhonghua 5’ cultivar), and cotton (‘Shiyuan 321’ cultivar) were used. About 30 seeds were sown in a plastic pot (L 60 × W 50 × H 50 cm) and cultivated in a greenhouse (24.0±1 °C, 50-70% (RH) and photoperiod 16:8 h (L:D). When plants grew up to three or four leaves fully expanded, they were used for larvae rearing.

2.3 Biological Parameters Assay

Experiments were carried out in environmental chambers (Heraeus Group, HPS 500, Germany) under controlled conditions (26±1 °C, 60±10% RH and hours of photoperiod, 16 L:8 D). The newly hatched larvae (< 24 h) were selected and placed individually in Petri dishes (6 cm diameter × 1.5 cm height). Leaf discs (about 1 cm in diameter) from each host plant were offered as food sources for larvae and replaced on a daily basis to avoid excessive water loss. There were six replicates for each crop and 60 larvae per treatment to record the data of larval and pupal stage.

After the emergence of the adults, one pair of male and female moths, which had emerged on the same day, were moved to a transparent cylindrical PVC cage (15 cm diameter × 30 cm height). The cage was lined with a paper sheet to collect eggs, and the top was covered with double-deck gauze to avoid adult escape. Adults were fed with a 10% honey-water mixture on a piece of soaked cotton packed inside a Petri dishes. There were 20 replicates (20 PVC cages) for each treatment.

The following biological parameters were evaluated: larval duration, larval survivorship, pupal duration, pupal weight at 24 h, pupal survivorship, the female fecundity (eggs/female), and longevity of male and female adults.

2.4 Nutritional Indices Assay

Since the first-third instar larvae of *S. frugiperda* are too light to weigh, fourth instar larvae were weighed precisely to investigate the effects of different host plants on the nutritional physiology of *S. frugiperda*. Experiments were carried out in environmental chambers (Heraeus Group, HPS 500, Germany) under controlled conditions (26±1 °C, 60±10% RH and hours of photoperiod, 16 L:8 D).

Newly hatched larvae (< 24 h) were maintained on leaves of each host plant up to the fourth instar stage. Then, the fourth instar larvae (< 12 h) were selected, without feeding for 24 h to clear the intestinal tract, and weighed by using an analytical balance (Shimadzu/Toledo AY220) accurate to 0.0001 grams. Twenty larvae were used for each host plant (independent replicates). The larvae were individually isolated in Petri dishes (6 cm diameter × 1.5 cm height) lined with moistened filter paper and fed plant leaves of a single landrace on three consecutive days. Host leaves were replaced daily. After the experiment, the larvae, remaining leaves, feces were separated, weighed, and dried in an oven at 60 °C for 72 h until reaching a constant weight and then were weighed. At the same time, fresh and dry weights of 10 larvae were recorded to obtain the correction factor for initial dry weight. The water loss of the host leaf was calculated similarly to the water loss of the larvae.

From these data the weights were obtained: food ingested (I), feces (F), larvae weight gain (B), larvae mean weight (C), and the duration of feeding time (T). Then the nutritional indices were calculated as follows: food metabolized (M = (I – F) – B), the relative growth rate (RGR = B/(C × T)), the relative consumption rate (RCR = I/(C × T)), the relative metabolic rate (RMR = M/(C × T)), the efficiency of conversion of ingested food (ECI = (B/I) × 100) and digested food (ECD = (B/(I – F)) × 100), the approximate digestibility (AD = ((I – F)/I) × 100), weight of the assimilated food (I – F) (Waldbauer, 1968; Scriber & Slansky, 1981).

2.5 Statistical Analysis

Effects of host plants on biological characteristics (duration, pupae weight, survival, female fecundity, and adult longevity) of *S. frugiperda* were analyzed with one-way analysis of variance using the generalized linear model (PROC GLM, SAS V9.4) (Zhao et al., 2014). Prior to analysis, all data were checked for normality and homogeneity of variances using the Kolmogorov-Smirnov (Kolmogorov, 1933; Smirnov, 1939) and Levene's test (Levene, 1960). The percentage survivorship was normalized using the transformation y = arsine $(x/100)^{1/2}$. Nutritional parameters were subjected to one-way ANOVA using the *F*-test (Fite et al., 2018). Treatment differences among means were compared using Tukey's multiple range tests. Statistical analyses were performed using SAS software (SAS Institute Inc., Cary, NC, USA). Graphs were generated using GraphPad Prism 5.0 (GraphPad Software, Inc., San Diego, CA). All data are calculated as Means±standard error.

3. Results

3.1 Growth and Development

The host plant had a significant impact on the growth and development of *S. frugiperda*. The larval duration was the shortest for *S. frugiperda* fed on corn leaves, and longest on peanut and soybean, while the other treatments did not differ between themselves ($F_{5,320} = 27.72$, $P < 0.001$, Figure 1). The larval duration was 2.9, 3.6, 5.1, 4.5, and 4.0 days shorter for corn when compared to the larval duration fed on sorghum, wheat, peanut, soybean, and cotton, respectively. The pupal duration was shorter when *S. frugiperda* fed on grasses (corn, sorghum, and wheat) than those fed on soybean, peanut, and cotton ($F_{5,319} = 7.76$, $P < 0.001$; Figure 1).

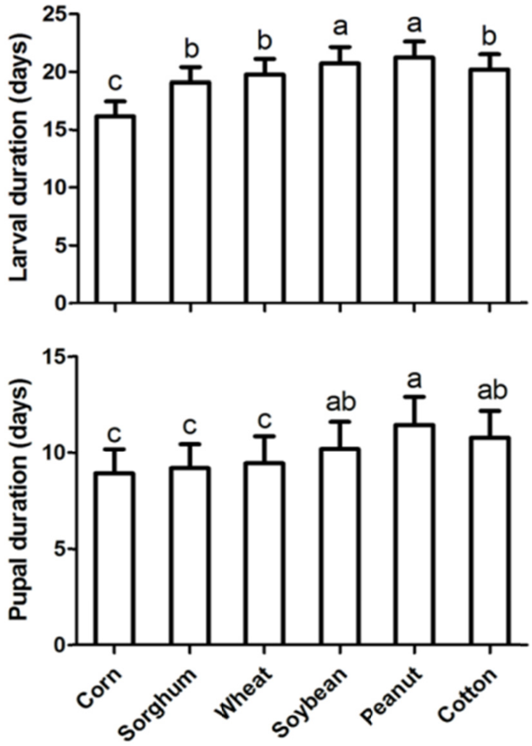

Figure 1. Larval and pupal duration (Mean±SE) of *Spodoptera frugiperda* fed on six different host plants

Note. Different letters indicate significant differences ($P < 0.05$) by using Tukey's multiple range tests, the same as below.

The pupal weight was also significantly affected by the host plant ($F_{5,319} = 9.30$, $P < 0.001$; Figure 2). The peanut and corn possessed the highest pupal weight among the treatments, which was 0.253 and 0.248 g, respectively. The lowest pupal weight was observed when larvae fed on cotton, which was about 0.200 g.

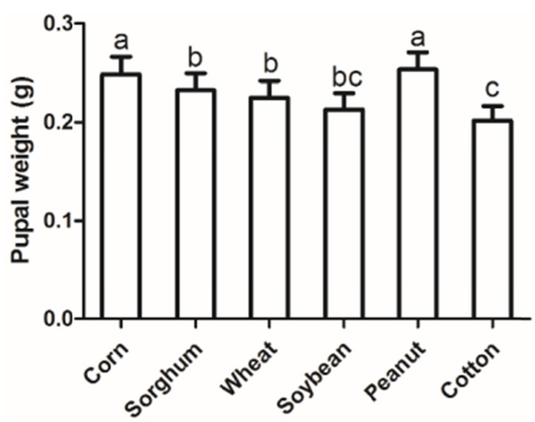

Figure 2. Pupal weight (Mean±SE) of *Spodoptera frugiperda* fed on six different host plants

Survivors of *S. frugiperda* larvae and pupae fed on six plants ranged from 87% to 95%, 90% to 96%, respectively, and no significant difference was foundbetween treatments ($P > 0.05$, Figure 3).

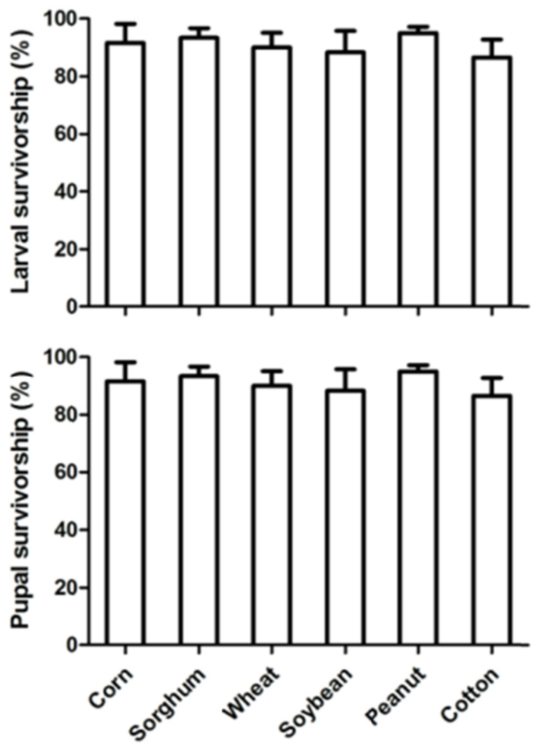

Figure 3. Larval survivorship and pupal survivorship (Mean±SE) of *Spodoptera frugiperda* fed on six different host plants.

Although there were no significant difference in female ($F_{5,114}$ = 0.86, P = 0.322) and male longevity ($F_{5,114}$ = 0.54, P = 0.645), the longevity of female was about 1.5 days longer than male adult (Figure 4).The number of eggs per female was significant influenced by host plant ($F_{5,114}$ = 21.25, P < 0.001). Higher amounts of eggs/female were found in peanut and corn, reaching around 1000 eggs/female. The fecundity was significantly lower for females reared on cotton, which was 683 eggs/female (Figure 5).

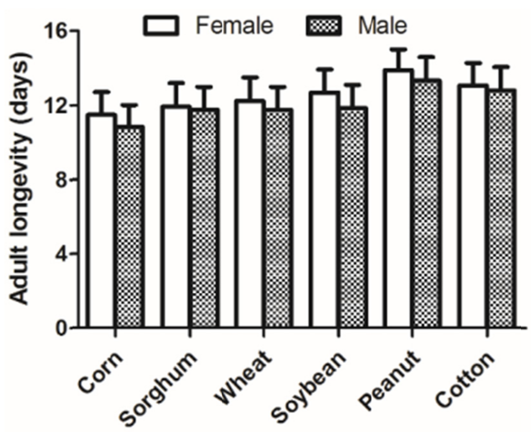

Figure 4. Female and male adult longevity (Mean±SE) of *Spodoptera frugiperda* fed on six different host plants

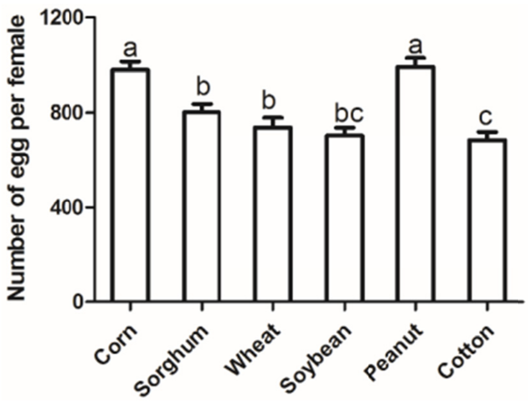

Figure 5. Number of eggs per female (Mean±SE) of *Spodoptera frugiperda* fed on six different host plants

3.2 Food Intake, Utilization, Metabolization and Assimilation

Host plant significantly affect food intake, utilization, metabolization and assimilation by *S. frugiperda* larvae. The weight gain ($F_{5,114} = 10.43$, $P < 0.001$), food consumption ($F_{5,114} = 22.18$, $P < 0.001$) and feces production ($F_{5,114} = 29.92$, $P < 0.001$) of *S. frugiperda* larvae fed on grasses (corn, sorghum, and wheat) were significant higher than soybean and cotton (Figure 6).

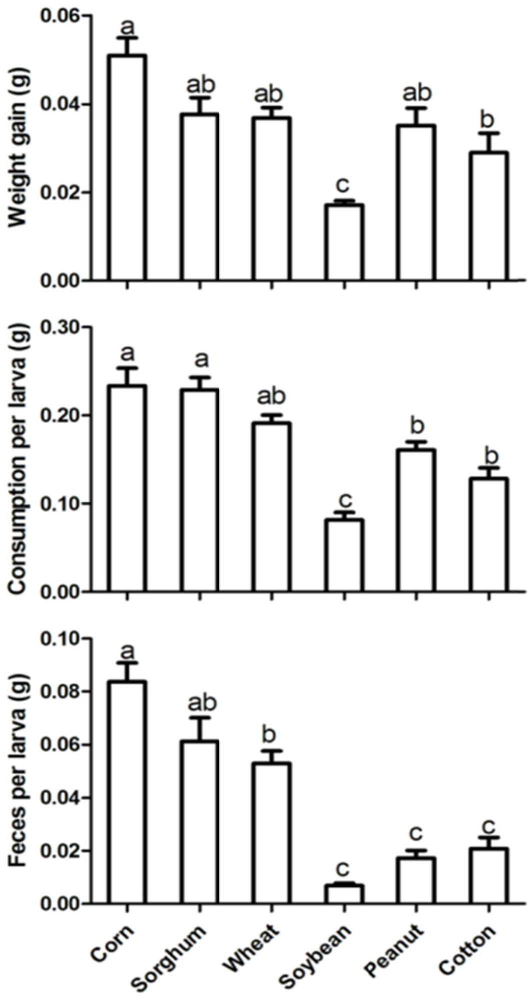

Figure 6. Mean (±SE) of weight gain, consumption, and feces per larva by *Spodoptera frugiperda* fed on six host plants

The food metabolized ($F_{5,114}$ = 6.48, P < 0.001) and assimilated ($F_{5,114}$ = 10.06, P < 0.001) by *S. frugiperda* larvae were significant different between host plants. Metabolized food per larva was the lowest (0.06 dry weight) when larvae were fed on soybean. Similarly, larvae assimilated less soybean leaves (0.08 g dry weight) than larvae fed on other host plants (Figure 7).

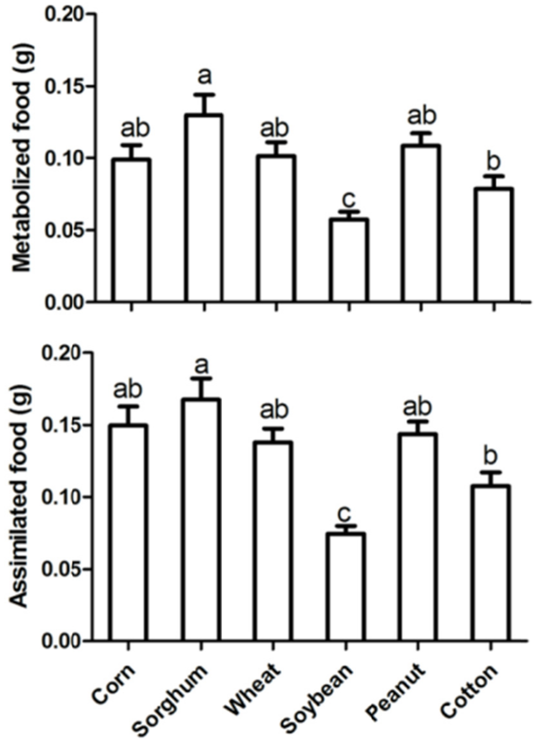

Figure 7. Mean (± SE) of food metabolized and assimilated of *Spodoptera frugiperda* larvae fed on six host plants

3.3 Nutritional Indices

The nutritional indices of *S. frugiperda* larvae were significantly influenced by host plants (Table 1, P < 0.05 in all cases). The values of RGR, RCR, RMR, ECI, and ECD were significantly higher in corn, peanut and sorghum, and lower in soybean and cotton. The highest value of AD was found in corn, which was 87.8%, and the lowest value of AD was observed in heat, peanut and cotton, which was 84.3%, 84.6%, and 84.9%, respectively.

Table 1. Nutritional indices for *Spodoptera frugiperda* larvae fed on six host plants

Parameter	Host plants						$F_{5,114}$
	Corn	Sorghum	Wheat	Soybean	Peanut	Cotton	
RGR(g/g/day)	0.39±0.02a	0.34±0.03b	0.32±0.02bc	0.30±0.02c	0.35±0.02b	0.29±0.03c	2.65
RCR(g/g/day)	1.63±0.09a	1.58±0.13ab	1.52±0.11ab	1.41±0.15b	1.60±0.17a	1.38±0.13b	2.54
RMR(g/g/day)	1.08±0.12ab	1.19±0.13a	0.99±0.14ab	0.73±0.06b	1.22±0.16a	0.87±0.09b	3.02
ECI (%)	23.62±1.86a	21.53±2.01ab	21.27±1.67ab	20.85±1.36b	22.13±2.07a	20.98±3.11b	2.26
ECD (%)	26.91±2.72a	25.09±1.61ab	25.24±2.68ab	24.13±3.69b	26.17±3.34a	24.72±3.18b	2.84
AD (%)	87.77±2.93a	85.81±3.43ab	84.27±2.64b	86.41±1.22ab	84.56±1.56b	84.87±1.39b	27.93

Note. All data are calculated in g dry weight.

Data in the table are represented as Mean±SE. Means in the same row followed by different letters are significantly different (P < 0.05).

4. Discussion

The development of insects mainly depends on food quality (Barros et al., 2010). Therefore, the performance of insects are strongly influenced by the host plant (Bavaresco et al., 2004; Koussoroplis & Wacker, 2016; McCormick et al., 2019). By comparing the biological characteristics, food consumption and utilization of *S. frugiperda* larvae fed on six different crops mainly cultivated in the mid-high latitude of China, significant differences were identified.

In the study, the development of *S. frugiperda* fed on corn was similar to the observations of Sharanabasappa et al. (2018), who reported that the larval period, pupal period, male adult longevity, female adult longevity, fecundity were 15.9 d, 10.5 d, 8.2 d, 10.8 d and 1064.8 eggs per female, respectively. *S. frugiperda* larvae reared on corn leaves exhibited a shorter developmental time in the larval and pupal stage, heavier pupal weight, and higher amounts of eggs per female than other tested plants. Our results were consistent with previous research that *S. frugiperda* larvae fed on corn performed better than on cotton or soybean (Buntin, 1986; Nagoshi et al., 2007). Compared to corn, *S. frugiperda* larvae fed on cotton and soybean were adversely affected with extended larval duration and reduced pupal weight (Silva et al., 2017).

Considering the plants tested, the number of eggs produced per female was significantly lower on cotton than corn and soybean. In contrast, the longevity of females reared on cotton was shorter than that of females reared on corn and soybean (Barros et al., 2010). In the present study, the fecundity of *S. frugiperda* fed on cotton was 683 eggs per female, significantly lower than that fed on corn, which was about 979 eggs per female. However, the longevity of females reared on cotton, corn and soybean was about 13.0 d, 11.9 d, 12.7 d, respectively, which showed no significant differences between treatments.

The host plant significantly affected food consumption and utilization of *S. frugiperda* larvae. In the study, *S. frugiperda* larvae fed on soybean and cotton leaves had lower values of food consumption, feces production, and weight gain, together with lower values of RCR, RMR, RGR, and AD. This is probably due to decreased consumption of food, resulting in reduced production of feces and low weight gain, leading to the lower efficiency of food assimilation and subsequent conversion to body mass (Slansky & Scriber, 1985; Giongo et al., 2015).

Among nutritional indices, ECI is the efficiency of an insect's ability to utilize the food ingested into growth, and ECD is the efficiency of conversion of digested food into growth (Nathan et al., 2005). Change in ECI and ECD reflects the conversion rates of food ingested and digested into body biomass (Abdel-Rahman & Al-Mozini, 2007). In the present experiment, *S. frugiperda* larvae fed on cotton and soybean had lower values of ECI and ECD, which suggested that these larvae were unable to convert digested food into biomass efficiently. These findings indicated that cotton and soybean leaves were likely containing some toxic compounds that inhibit *S. frugiperda*'s growth (Fite et al., 2018).

In the current experiment, *S. frugiperda* larvae fed on corn had higher nutritional indices than other hosts, which is consistent with the view of the previous study that corn could increase the consumption and nutrition of this pest (Pinto et al., 2019). The shorter larval and pupal period, the faster life cycle, the heavier pupal weight and the higher nutritional indices of *S. frugiperda* were recorded on corn compared to other host plants, indicating that corn was the most suitable host for *S. frugiperda* development. Studies of *S. frugiperda* populations showed that the crop-specific severity of *S. frugiperda* infestations is associated with host-related strains and, as a result, the corn is the preferred host plant for corn strain of *S. frugiperda* (Pashley et al., 1985; Meagher & Nagoshi, 2004). Besides, this kind of plant might provide the best blend and balanced nutrition for insect development, including carbohydrates, amino acids, trace elements, fatty acids, vitamins, water, etc (Behmer, 2009).

The lower performance of *S. frugiperda* larvae feeding on cotton and soybean leaves have some possible explanation. Secondary compounds in cotton leaves, such as gossypol that confers resistance to herbivores, slows the development of larvae and reduces weight gain (Montandon et al., 1987; Farrar & Ridgway, 2000; Hoover et al., 2000). Soybean has inducible phytoalexin glyceollin, which plays a role in insect resistance. These toxic substances posed an antifedent activity against the specific herbivorous insect. The plant protected itself against pests by creating a toxic environment at the cellular level (Fischer et al., 1990). An extended duration of the larval phase is considered as a compensatory strategy when food is not suitable for their development so that they remain a more extended period feeding to form active pupae and adults (Smith & Collier, 2005).

Likewise, nutritional indices also used to study ingestion, digestion, assimilation, and food conversion of other Lepidopteran larvae, such as *Helicoverpa armigera* (Naseri et al., 2010; Fite et al., 2018; Truzi et al., 2019). Although the nutritional parameter varied in different species, larval instars, and feeding times, it was crucial to determine the fitness of insects. The development, survival and fecundity of the insect were affected by the different nutritive values of crops which could influence the immigration, emigration, even population dynamics of the target insect pest. Therefore, knowledge of nutritional indices in conjunction with biological studies may contribute to an understanding of the physiological basis of insect response to host plants, which is essential for the development of integrated pest management programs.

5. Conclusions

In conclusion, *S. frugiperda* was able to develop and reproduce on all six host plants. Biology and nutritional indexes suggested that corn was the most suitable host. Besides, peanut, sorghum and wheat have also been shown to be the appropriate host species for growth and development of *S. frugiperda.* Although cotton and soybean were found to be less adequate, high larvae and pupal survivors recorded on cotton and soybean leaves have indicated that damage could also occur in these plants. Future work should focus on the long-term interaction and evolution between the pest and plant, such as the plant suitability and/or resistance to the target insect pest. Further data collection from different sites would help to estimate the host range, potential economic losses and design an effective pest management strategies for *S. frugiperda*.

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