EFFECT OF HOST PLANTS ON THE BIOLOGY AND DIGESTIVE PHYSIOLOGY OF *Spodoptera frugiperda*

Shuxian Chen, Fan Yang, Min Fang, Ling Yao, Renwen Zheng and Qingfeng Tang

SUMMARY

Fall armyworm (Spodoptera frugiperda)*, a highly polyphagous lepidopteran pest, is impacting millions of hectares of maize crops and thereby posing a major threat to food security. Yet, up till present, limited research has been conducted on the biological determinants and digestive enzymes of* S. frugiperda *fed on different plants. Our results showed that there were differences in developmental duration, and body and pupal weight by statistical data. Individuals from F1 and F3 generations fed on* Zea mays *had the shortest development period, and the 10d weight (0.173mg, 0.177mg) and pupa weight (0.171mg, 0.193mg) were the heaviest, while the 10d weight (0.046mg, 0.054mg) and pupa weight (0.108mg, 0.138mg) were the lightest in those fed on* Eleusin indica *and* Triticum aestivum*, respectively. There were also significant differences in the digestive enzyme activities of* S. frugiperda *fed on four host plants. The trypsin activity, a-amylase activity, and lipase activity were the highest in F1 larvae fed on* Z. mays*. In F3 generation, trypsin activity had a high level in* Z. mays*, which was 856.26 folds higher than that in* Triticum aestivum*, which indicate digestive enzymes play key roles in helping* S. frugiperda *to adapt to the host plants. These findings provided a foundation for further understanding the role of digestive enzyme in* S. frugiperda *larvae in response to host plants.*

Introduction

Spodoptera frugiperda (fall armyworm), Lepidoptera Noctuidae, is a migratory pest that originates in tropical and subtropical America (Johnson, 1987; He *et al*., 2021). In recent years, the fall armyworm (FAW) has invaded Africa and Asia, which is impacting millions of hectares of maize and thereby posing a major threat to food security (Harrison *et al*., 2019; Early *et al*., 2018; Sun *et al*., 2021). *S. frugiperda* is present almost all year in China, the larval stage of FAW has a food preference for leaves and tender shoots, especially cultivated grasses, becoming a chewer of plant tissue and damaging 353 species, 227 genera, and 76 families of plants (Paredes-Sanchez *et al*., 2021), including economically important cereal crops such as maize, wheat, and sorghum (Early *et al*., 2018; Ingber *et al*., 2021). This polyphagous situation enhances FAW resistance against pesticides and provokes chemical insecticides have not been recommended for use (Bolzan *et al*., 2019; Lira *et al*., 2020). As a result, it is neccesary to understand how FAW adapt different host plants.

Insect herbivores need to acquire vital nutrients from their hosts plant, and the host plants also affect the performance of FAW, e.g. biology

KEYWORDS / Body Weight / Developmental Duration / Enzyme Activity / *Spodoptera frugiperda* /
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EFECTO DE LAS PLANTAS HUÉSPEDES SOBRE LA BIOLOGÍA Y LA FISIOLOGÍA DIGESTIVA DE *Spodoptera frugiperda*

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RESUMEN

El gusano cogollero (Spodoptera frugiperda)*, una plaga de lepidópteros muy polífagos, está afectando a millones de hectáreas de cultivos de maíz y por lo tanto, representa una gran amenaza para la seguridad alimentaria. Sin embargo, hasta el momento, se han realizado investigaciones limitadas sobre los determinantes biológicos y las enzimas digestivas de* S. frugiperda *alimentada con diferentes plantas. Los resultados mostraron que hubo diferencias en la duración del desarrollo y el peso corporal y pupal según los datos estadísticos. Los individuos de las generaciones F1 y F3 alimentados con* Zea mays *tuvieron el período de desarrollo más corto, y el peso a los 10d (0,173mg, 0,177mg) y el peso de pupa (0,171mg, 0,193mg) fueron los mayores, mientras que el peso a los 10d (0,046mg, 0,054mg) y el peso de pupa (0,108mg, 0,138mg) fueron menores para los alimentados con* Eleusin indica *y* Triticum aestivum*, respectivamente. También hubo diferencias significativas en las actividades de las enzimas digestivas de* S. frugiperda *alimentadas con cuatro plantas hospedantes. La actividad de tripsina, la a-amilasa y la actividad de lipasa fueron más altas en las larvas F1 alimentadas con* Z. mays*. En la generación F3, la actividad de la tripsina tuvo un alto nivel en* Z. mays*, que fue 856,26 veces mayor que en* Triticum aestivum*, lo que indica que las enzimas digestivas desempeñan un papel clave para ayudar a* S. frugiperda *a adaptarse a las plantas huésped. Estos hallazgos proporcionaron una base para comprender mejor el papel de la enzima digestiva en las larvas de* S. frugiperda *en respuesta a las plantas huésped.*

EFEITO DE PLANTAS HOSPEDEIRAS NA BIOLOGIA E FISIOLOGIA DIGESTIVA DE *Spodoptera frugiperda*

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RESUMO

A lagarta do cartucho (Spodoptera frugiperda)*, uma praga altamente polífaga de lepidópteros, está afetando milhões de hectares de plantações de milho e, portanto, representa uma grande ameaça à segurança alimentar. No entanto, até agora, têm sido realizadas pesquisas limitadas sobre os determinantes biológicos e enzimas digestivas de* S. frugiperda *alimentada com diferentes plantas. Os resultados mostraram que houve diferenças na duração do desenvolvimento e o peso corporal e pupal segundo os dados estatísticos. Os indivíduos das gerações F1 e F3 alimentados com* Zea mays*, tiveram o período de desenvolvimento menor, e o peso aos 10d (0,173mg, 0,177mg) e o peso pupal (0,171mg, 0,193mg) foram os maiores, enquanto que o peso aos 10d (0,046mg, 0,054mg) e o peso da pupa (0,108mg, 0,138mg) foram menores para os alimentados com* Eleusin indica *e* Triticum aestivum*, respectivamente. Também houve diferenças significativas nas atividades das enzimas digestivas de* S. frugiperda *alimentadas com quatro plantas hospedeiras. A atividade de tripsina, α-amilase e a atividade de lipase foram maiores nas larvas F1 alimentadas com* Z. mays*. Na geração F3, a atividade da tripsina teve nível alto em* Z. mays*, sendo 856,26 vezes maior do que em* Triticum aestivum*, o qual indica que as enzimas digestivas desempenham um papel chave para ajudar a* S. frugiperda *a se adaptar às plantas hospedeiras. Estes achados proporcionaram uma base para compreender melhor o papel da enzima digestiva nas larvas de* S. frugiperda *em resposta às plantas hospedeiras.*

and biometric characteristics (Gopalakrishnan and Kalia 2022), gene expression profiles (Silva-Brandao *et al*., 2017), oviposition preference (Guo *et al*., 2020), gut microbial community (Lv *et al*., 2021), pesticide resistance (Garlet *et al*., 2021). Meantime, digestive flexibility can help insects to adapt the noxious chemical-containing host plants. The gastrointestinal tract is the central organ for food digestion and absorption of nutrients. The digestive physiology of insects largely depends on a wide spectrum of digestive enzymes and a sophisticated detoxification system to use chemically diverse host plants as food sources (Veenstra *et al*., 1995; Zalucki *et al*., 2002; Borzoui *et al*., 2015). The gut digestive enzymes of herbivores are necessary for the host plant adaptation in response to the chemical composition of the food source (Singh *et al*., 2020). A previous study has evaluated the impact of corn and rice host plants on gut digestive enzymatic activity in *S. frugiperda* (Hafeez *et al*., 2021).

In this study, we evaluated under laboratory conditions the effect of four different hosts, *Zea mays* (maize), *Triticum aestivum* (wheat), *Eleusin indica* (Goosegrass), and *Veronica polita* (Speedwell) on the growth development and gut digestive enzymatic activity of FAW. The adaptation mechanism of *S. frugiperda* reared on different host plants for 3 generations was examined, as was the effects of the host plant diets on the digestive enzyme's activities in the FAW midgut. Our aim was to study the effects of host plants on the biological parameter of the FAW, which is closely related to the study of the biology and ecology of host insects, and to lay a foundation for studying the host plant adaptation mechanisms and identifing in the digestive system of insects against host plant chemical defenses.

Materials and Methods

Insects and plant material

Spodoptera frugiperda was reared from the Insect Molecular Ecology Laboratory of Anhui Agricultural University, Hefei, Anhui Province, China. The insects reared for three generations on maize, wheat, Goosegrass or Speedwell plants. Plant seeds were purchased from an agricultural company (ShouHe, China). Plants were grown to the level of 3–4 genuine leaves before being employed in the studies (Lv *et al*., 2021). They were housed in cages at a temperature of 25 ±3°C with a relative humidity of 70 ±10% and a photoperiod of 16h light, 8h dark.

Growth and Development of S. frugiperda *on different host plants*

Neonates were transferred to the rearing cage up to the third instar, 3rd larvae were put into a 12-well acrylic plates (each well 2cm in diameter and 1.5cm in depth) (Biosharp®, Labgic Technology Co., Ltd, China). FAWs raised with four kinds of host plants, the leaves were cutted into 1cm^2 and placed them in separate wells of the petri dish, larval development was observed and recorded daily, and the duration period and age recorded. The weight of 10th day (d) larvae (60 larvae for each diet) was determined, the pupae weighed 24h postpupation.

Digestive activity assay

Fifth instar latvae (2d after 4ecdysis) were selected, they were washed with physiological saline, wiped off the surface water, 3 larvae were collected in a 1.5mL centrifuge tube and were immediately frozen in liquid nitrogen and stored at -80°C until use. Digestive enzymes (a-amylase, lipase (LPS), trypsin) test kit purchased from Nanjing Jiancheng Bioengineering Institute. The samples were homogenized under ice condition, centrifuged at 2500rpm for 10min, and the supernatant was taken for measurement. The enzyme activity was determined according to the manufacturer's protocol, and a control containing no α-amylase, lipase, or trypsin extract with substrate was run simultaneously with reaction mixture. For a-amylase: 100µl (one percent of the supernatant) was added into 500µl substrate buffer preheated at 37°C for 5min. After mixing, the mixture was reacted in 37°C for 7.5min., 500µl iodine application solution and 3mL double steaming water were added into the mixture and the absorbance value was measured at 660nm. For lipase: 25µl (twenty percent of the sample) and 25µl of reagent 4 were added into to the test tube, absorb 2mL of substrate buffer preheated for 5min at 37°C, mix quickly and add the cuvette, and read the absorbance value at 420nm for 30s and 630s. For trypsin: 1µl (ten percent of the sample) was added to 1.5mL of trypsin substrate application solution preheated at 37°C for 5min. After mixing, the absorbance values at 30s and 1230s were read at 253nm in a 0.5cm light diameter quartz cubage. All experiments were set up with three biological replicates.

Statistical analysis

The test data is systematically counted by Excel, and the statistical results were analyzed by one-way ANOVA using SPSS 23.0 software (IBM, 2015). Duncan's new repolarization method was used to test and compare the differences between the treatments (p< 0.05).

Results

Effects of feeding on different host plants on the developmental duration

As shown in Table I and II, the developmental duration of *S. frugiperda* that reared on the four host plants had some difference in the F1 and F3 generations. During the early developmental stage of larvae (1st to 3th instar), the F1 generations of larvae that fed on maize was growing fastest compared to the other three populations, and the F3 generations of larvae reared on maize was shorter than the other three cohorts in 1st and 3th instar. During the late period (4th to 6th instar), the F1 and F3 generations of larvae fed on speedwell was developing slowest compared to other three populations, and the FAWs fed on maize had no significant difference compared to the two cohorts fed on goosegrass and wheat. Among the total larval stage, F1 and F3 generations of developmental period reared on maize is 15.267 ±0.135d and 14.733 ±0.082d respectively that showed the shortest developmental period, and the longest developmental period (15.933 ±0.235d and 17.733 ±0.230d) fed on speedwell. In the prepupa stage, the developmental duration of the larvae fed on wheat was significantly different from the larvae fed on the other three host plants, and it had the fastest growth rate, only 1.266 ±0.08din F1 generation. The prepupa duration of

TABLE I
DEVELOPMENT PERIOD OF THE FIRST GENERATION *Spodoptera Frugiperda* FED ON FOUR HOST PLANTS

Host plant	Development period (d)							
	1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar	prepupa	Larval duration
Zea mays	3.867±0.115b	2.000±0.001b	1.967±0.033b	2.000±0.001a	1.900±0.556a	1.833±0.118a	1.700±0.085b	15.267±0.135a
Triticum aestivum	4.133±0.346a	2.000±0.001b	2.000±0.001b	2.067±0.095a	2.133±0.104a	2.067±0.067a	1.266±0082c	15.667±0.138a
Eleusin indica	4.300±0.085a	2.100±0.056b	2.000±0.001b	1.300±0.085b	1.767±0.149a	1.883±0.097a	1.967±0.10a	15.267±0.225a
Veronica polita	4.400±0.090a	2.367±0.08a	2.167±0.069a	1.833±0.084a	1.767±0.104a	1.767±0.141a	1.633±0.089b	15.933±0.253a

Data marked with different letters in the same column indicate significant differences tested by Duncan's new multiple range test method (p<0.05). a, b, c: the letters for p-value.

TABLE II
DEVELOPMENT PERIOD OF THE THIRD GENERATION *Spodoptera Frugiperda* FED ON FOUR HOST PLANTS

Host plant	Development period (d)							
	1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar	prepupa	Larval duration
Zea mays	2.667±0.138c	3.333±0.138a	1.833±0.069b	2.000±0.001b	2.000±0.001b	1.900±0.056b	1.0000.001c	14.733±0.082d
Triticum aestivum	3.800±0.074b	2.4000.09c	2.400±0.091a	1.600±0.091c	1.600±0.090c	2.733±0.106a	1.267±0.082b	15.8000.305c
Eleusin indica	3.600±0.091b	2.700±0.085b	2.500±0.093a	2.100±0.056b	2.100±0.056b	2.000±0.083b	1.700±0.085a	16.700±0.322b
Veronica polita	4.200±0.074a	2.800±0.074b	2.367±0.102a	2.467±0.124a	2.467±0.124a	1.933±0.095b	1.500±0.093a	17.733±0.230a

Data marked with different letters in the same column indicate significant differences tested by Duncan's new multiple range test method (p<0.05). a, b, c: the letters for p-value.

FAWs fed on maize (1.000 ±0.001d) was shorter than the populations fed on speedwell (1.500 ±0.093d) and goosegrass (1.700 ±0.085d) in the F3 generation and had the shortest prepupa stage in the F3 generation.

The developmental duration of *S. frugiperda* fed on the same host plant also had certain difference between F1 and F3 generations (Figure 1). The developmental duration of the F3 generation fed on maize (14.733 ±0.082d) was longer than that of the F1 generation (15.267 ±0.135d). The larval developmental period of the F3 generation fed on speedwell (17.733 ±0.230d) and goosegrass (15.800 ±0.305d) was longer than F1 generation (15.933 ±0.253d, 15.267 ±0.225d respectively). There was no significant difference between the F1 and F3 generations fed on wheat.

Effects of feeding on different host plants on the body weight

In order to further understand the biological parameter of FAWs fed on different host plants, the body weight and pupa weight with significant differences between the four groups were compared. The F1 and F3 generations of *S. frugiperda* fed on maize in the figure showed the heaviest body weight and pupa weight, and the population reared on speedwell was lightest body and pupa weight in the both generations (Table III). The two different generations were also compared, the body weight of F1 and F3 generations of larvae fed on corn and speedwell were no significant difference between the F1 and F3 generations (Figure 2a). The pupa weight of all F3 generation were heavier than F1 generation that may demonstrate those insects gradually adapted to their host plants during the period (Figure 2b).

Effects of feeding on four kinds of host plants on digestive enzyme activity

According to the FAWs fed on four different host plants had the obvious differences in growth development, the digestive enzymes of FAWs larvae among each host group were analyzed. Some digestive enzymes were obtained for each host, including trypsin, α-amylase and lipase. The results showed that the activity of trypsin, α-amylase and lipase of the FAWs fed on maize were the highest in the F1 generation, which were 1570.172 ±33.766U·mg^{-1}prot, 0.016 ±0.001U·mg^{-1}prot and 53.301 ±4.296U·g^{-1}prot, respectively. The activities of digestive enzymes of the larvae fed on speedwell were the lowest. And the activities of the three enzymes in the larvae fed on corn were almost 4.83, 5.3 and 1.40 folds higher than those fed on speedwell (Table I). In the F3 generation, the trypsin activity of the larvae fed on the four host plants was diverse, the trypsin activity of corn was 856.26 folds than the wheat (Table V). The F1 generation of the three digestive enzymes fed on maize were all more abundant than the F3 generation, and the trypsin F1 generation was 2.4 times as much as that of the F3 generation. The activities of trypsin and lipase

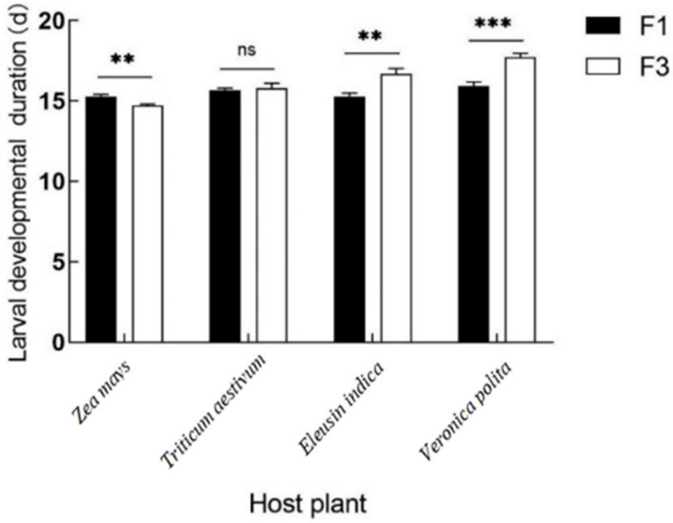

Figure 1. Effects of the same host plants on different generations of *Spodoptera frugiperda*. F1: first generation; F3: third generation; **: significantly different (p<0.01); ***: significantly different (p<0.001); ns: not significant.

TABLE III
EFFECT OF DIFFERENT GENERATION IN BODY AND PUPA WEIGHT *Spodoptera Frugiperda* FEEDING ON FOUR HOST PLANTS

Host plant	F1		F3	
	10 d Weight·mg^{-1}	Weight of pupa·mg^{-1}	10 d Weight·mg^{-1}	Weight of pupa·mg^{-1}
Zea mays	2.667±0.138c	3.333±0.138a	1.833±0.069b	2.000±0.001b
Triticum aestivum	3.800±0.074b	2.4000.09c	2.400±0.091a	1.600±0.091c
Eleusin indica	3.600±0.091b	2.700±0.085b	2.500±0.093a	2.100±0.056b
Veronica polita	4.200±0.074a	2.800±0.074b	2.367±0.102a	2.467±0.124a

Data marked with different letters in the same column indicate significant differences tested by Duncan's new multiple range test method (*p*<0.05). F1: first generation; F3: third generation; **: significantly different (p<0.01); ***: significantly different (p<0.001); ns: not significant.

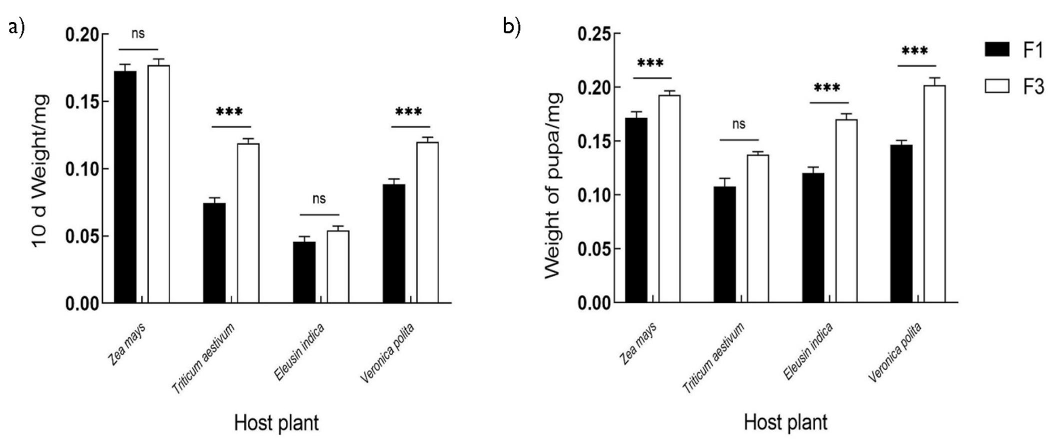

Figure 2. Effect of the same host plants in body and pupa weight *Spodoptera frugiperda* between different generations. F1: first generation; F3: third generation; ***: significantly different (p<0.001); ns: not significant.

TABLE IV
EFFECTS OF FOUR HOST PLANTS ON DIGESTIVE ENZYME ACTIVITIES IN THE FIRST GENERATION LARVAE OF *Spodoptera Frugiperda*

Host plant	Trypsin activity·(U·mg^{-1}prot)	a-amylase activity (U·mg^{-1}prot)	Lipase activity (U·mg^{-1}prot)
Zea mays	1570.172±33.766a	0.016±0.001a	53.301±4.296a
Triticum aestivum	1121.789±9.987c	0.0014±0.001b	49.853±2.148a
Eleusin indica	325.127±3.611d	0.003±0.001b	38.086±1.884b
Veronica polita	1470.261±45.312b	0.003±0.001b	54.127±3.049a

Data marked with different letters in the same column indicate significant differences tested by Duncan's new multiple range test method (p<0.05). a, b, c, d: the letters for p-value.

TABLE V
EFFECTS OF FOUR HOST PLANTS ON DIGESTIVE ENZYME ACTIVITIES IN THE THIRD GENERATION LARVAE OF *Spodoptera Frugiperda*

Host plant	Trypsin activity·(U·mg^{-1}prot)	a-amylase activity (U·mg^{-1}prot)	Lipase activity (U·mg^{-1}prot)
Zea mays	642.192±8.096a	0.0129±0.0009a	45.683±1.396bc
Triticum aestivum	0.750±0.059d	0.0056±0.0002c	48.636±0.228ab
Eleusin indica	457.986±33.648b	0.0109±0.0007b	51.064±0.572a
Veronica polita	365.352±6.806c	0.0044±0.0003c	44.275±1.186c

The data marked with different letters in the same column indicate significant differences tested by Duncan's new multiple range test method (p<0.05). a, b, c, d: the letters for p-value.

in F1 generation were higher than those in F3 generation when fed wheat and speedwell. The F1 generation of the three digestive enzymes fed on goosegrass were lower than the F3 generation (Figure 3a-c).

Discussion

As a kind of migratory pest, *S. frugiperda*, which can transfer a long distance, is ability to damage a lot of different host plants that is regarded to be an important factor influencing the population dynamics and population densities. So far, only a few studies have examined the digestive physiology of *S. frugiperda* and their interactions with different host plant species (Hafeez *et al*., 2021; Gopalakrishnan and Kalia 2022; Oliveira *et al*., 2013; Oliveira *et al*., 2022). In this study, we evaluated the growth parameter and digestive enzyme activity of FAW larvae fed on different host plants. The F1 developmental duration of FAW larvae fed on maize was 3.867d, 2.000d, 1.967d for 1st, 2nd, 3rd instar respectively that are shortest growing days compared to the other three populations in early stage, the F3 larval duration was only 14.733d that is also shortest, and their body had heaviest body including the 10d (0.173mg, 0.177mg) and pupa weight (0.171mg, 0.193mg). Those results that indicate FAW had a faster development time and higher growth rate compared with larvae fed other three host plants including maize, wheat, and goosegrass, which also illustrate maize is a high nutritious host for FAW development. FAW is ability to grow on lots of different host plants but prefers maize. Similarly, various studies have shown that the quality and quantity of food consumed by insects affect their host preferences and have an impact on their biology (Bentancourt *et al*., 2003; Cabezas *et al*., 2013; Silva *et al*., 2018; Su and Xia 2020). The larvae fed on speedwell had the longest developmental period, and lightest body weight. The results show that FAW fed on speedwell had a delay in the development and growth compared with larvae fed other three host plants, which also indicate speedwell is a less nutritious

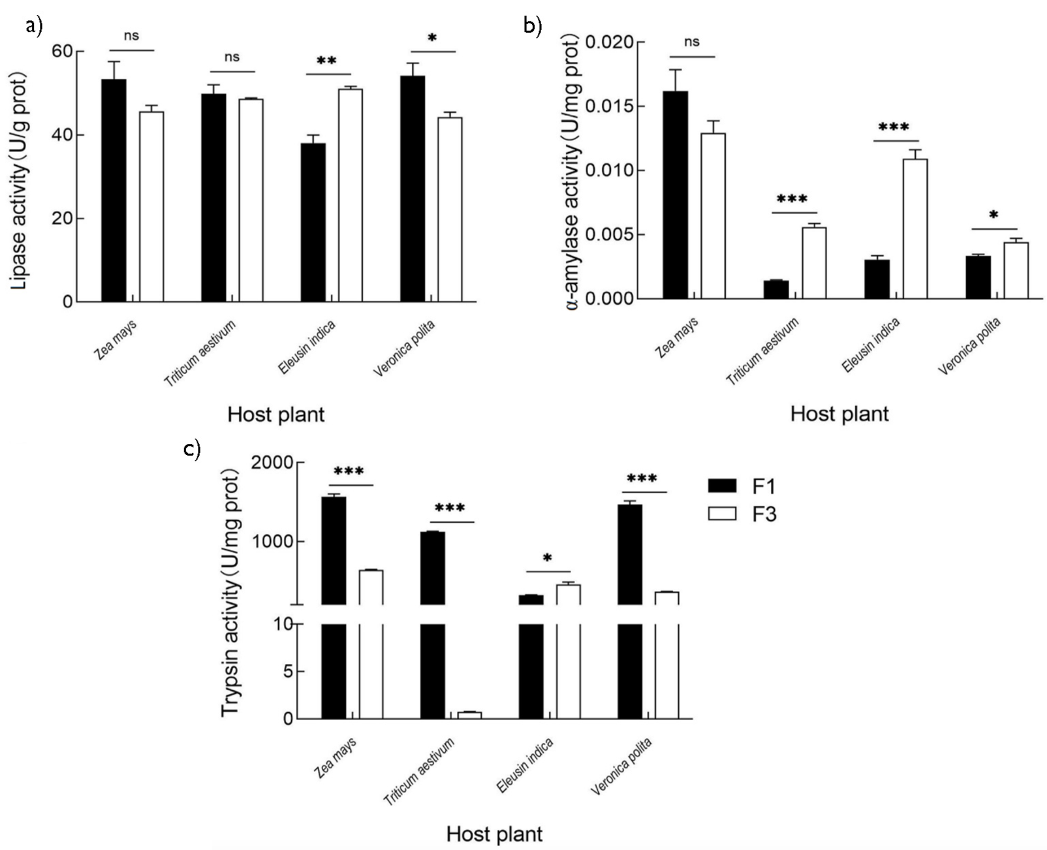

Figure 3. Effects of different generations on digestive enzymes and protective enzymes of *Spodoptera frugiperda*. F1: first generation; F3: third generation; *: significantly different (p<0.05); **: significantly different (p<0.01); ***: significantly different (p<0.001); ns: not significant.

host for FAW development. Speedwell maybe as the alternate host plant for its survival when it can not find other host plants. Some similar results have been reported that the longevity and body weight of *S. frugiperda* were significantly affected by low nutritious host plants, such as cotton and soybean (Hafeez *et al*., 2021). Those results would indicate corn is the best host plant for *S. frugiperda*, and the speedwell maybe have the resistance for FAWs. Nutritional factors in host speedwell might be a key reason for the longer developmental period compared with other plants, which imply the active components of speedwell has the great potential to be developed as a new botanic pesticide.

Phytophagous insects often depend on the effectiveness of their digestive physiology to feed on chemically diverse hosts as food sources, and some digestive enzymes with important functions can account for better adaptation to one host plant but not others (Zalucki *et al*., 2002; Wang *et al*., 2013; Oliveira *et al*., 2013; Borzoui *et al*., 2015). In our research, there were significant differences in the developmental process between preferred and alternate host plants. To elucidate the ability of *S. frugiperda* to adapt to host plant mechanisms, we evaluated the impact of primary and alternate host plants on digestive enzymatic activity, including trypsin, α-amylase and lipase. The results of the enzyme activity assay showed that all three digestive enzymes of the FAWs fed on maize were greatest, which indicated that trypsin, α-amylase and lipase play important roles in *S. frugiperda* host plant adaptation. Similar results were demonstrated trypsin was highly differentially regulated when *S. frugiperda* larvae fed on their primary plant and alternate host plant (Brioschi *et al*., 2007; Silva-Brandao *et al*., 2017; Hafeez *et al*., 2021). Recently, the effect of amylases on the adaptation of insects has been an increased focus, such as *Leptinotarsa decemlineata* amylases have been reported they are related to adapt to a variety of solanaceous plants (Ashouri and Farshbaf Pourabad 2021), and subsequent changes of amylases activity are responsible for grain damage in *Sitophilus granaries* (Ahmed *et al*., 2021). Lipase activity was enhanced in the population fed on corn, and inhibited the other three populations. Those results indicate lipases may play a crucial role in diets metabolism in *S. frugiperda*, which is consistent with its key role in fat metabolism (Jaeger and Reetz 1998, Gupta *et al*., 2004).

Our study provided an overview of the growth performance and the characteristics of digestive enzymes in *S. frugiperda* fed on different host plants. The results of the comparison analysis revealed significant differences in the duration, body weight and digestive enzyme activity between their primary plant and alternate host plant, indicating that diets have a significant impact on these changes. The analyses of enzyme activity are necessary in this study to show insect–host interactions and to provide a foundation for studying the functional annotation of enzyme content and host functional features, which is critical for a better understanding of the physiology of FAWs and the mechanisms responsible for the inhibitory potential of enzyme inhibitors. Dietary composition can have highly diverse effects on developmental parameters and enzymic responses. In our research, these findings were of great significance for the development and research of botanical pesticides against this serious insect pest based on the complex relationships between insects and host plants.

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