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RESEARCH

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Fitness of the fall armyworm *Spodoptera frugiperda* to a new host plant, banana (*Musa nana* Lour.)

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Abstract

Background: The fall armyworm *Spodoptera frugiperda* is a highly destructive agricultural pest that primarily damages maize in China. However, there were no reports of *S. frugiperda* damage to banana until it was observed on bananas in the wild. This suggested that banana crops may be potential hosts of the pest. To clarify the fitness and potential impact of *S. frugiperda* on banana, this study analysed the survival and development of *S. frugiperda* fed on bananas in the laboratory and constructed age-stage and two-sex life tables.

Results: Larvae of *S. frugiperda* fed on bananas completed their life cycles and produced fertile offspring, but the larvae had eight instars and presented longer developmental duration, slower population growth, and lower body weight than maize-fed larvae. Furthermore, the banana-fed *S. frugiperda* had longer adult longevity and preoviposition periods than the maize-fed larvae, while the opposite tendency was observed for oviposition days and egg production. Based on age-stage and two-sex life tables, the survival probability at each stage of *S. frugiperda* fed on bananas was lower than that of maize-fed larvae, and banana-fed *S. frugiperda* showed lower reproductive capacity.

Conclusions: Although banana is not an ideal host for the fall armyworm, it may be colonized by the species in situations in which the population density is high or the preferred host is scarce. Therefore, it is essential to prevent the pest from transferring to bananas and thereby increasing the number of sources of outbreaks.

Keywords: Polyphagous pest, Host adaptation, Maize, Life table, Host shifts

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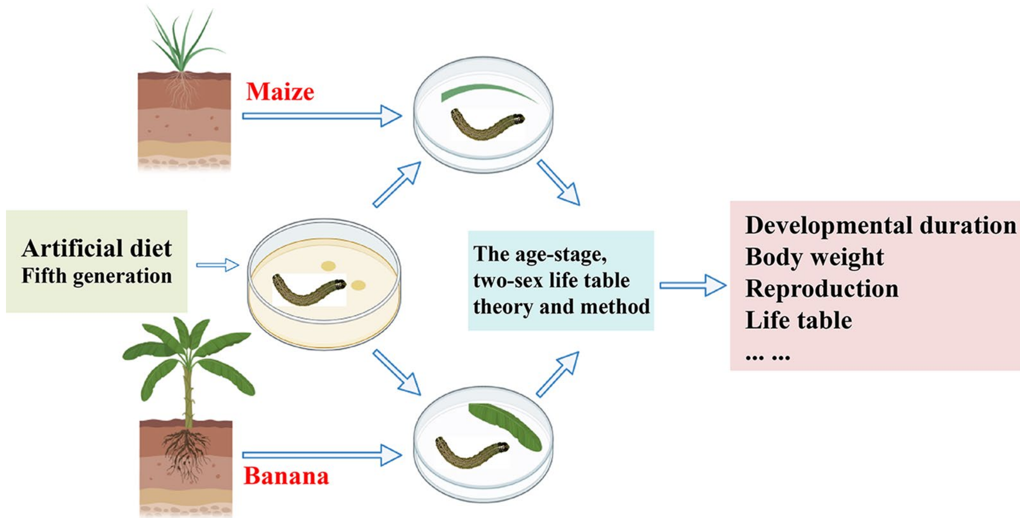
Graphical Abstract



Background

The fall armyworm *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is a worldwide agricultural pest native to the tropics and subtropics of the Western Hemisphere [1]. It is a highly polyphagous moth that reportedly attacks over 350 hosts across 76 plant families, including Poaceae (106 species), Asteraceae (31 species) and Fabaceae (31 species) [2]. *S. frugiperda* can migrate over long distances. In 2016, invasion of Africa by *S. frugiperda* was reported; this was the first time this species was found outside its origin [3], and in May 2018 it was found in Asia [4]. Since then, *S. frugiperda* has spread to 47 African nations and 18 Asian countries, and now to Australia, where it poses a serious threat to crops [5]. In addition, feeding by *S. frugiperda* larvae can introduce saprophytic and pathogenic fungi, leading to infestation of crops and grains and resulting in significant preharvest losses and loss of grain quality [6–8].

S. frugiperda adults and larvae were first detected in China on December 11, 2018, and January 11, 2019 [9, 10], and it was confirmed that they belonged to a corn strain through gene fragment sequencing analysis [11]. The corn strain *S. frugiperda* prefers to attack maize (*Zea mays*) during its process of spreading [12]. According to a survey conducted in 2019, maize accounts for 98.6% of the total area of crops damaged by *S. frugiperda* in China [13]. Furthermore, feeding on maize appears to be more beneficial for *S. frugiperda* development and population growth than feeding on other crops such as rice (*Oryza sativa*), potato (*Saccharum officinarum*), wheat (*Triticum aestivum*) and soybean (*Glycine max*) [14–17]. On June 26, 2019, *S. frugiperda* larvae were observed feeding on bananas in Wuming District (23° 9′ 42.69″ N, 108° 16′ 44.13″ E), Nanning City, Guangxi, P. R. China (see Additional file 1, 2, 3). As a strategic crop for food security, bananas are highly valued for their nutritional quality [18–20] and are grown in more than 100 countries and regions around the world [21]. Bananas are also the most traded and consumed fruit internationally and are a major source of economic growth and income in many rural areas, creating jobs and providing foreign exchange value for many countries [22].

Factors that contribute to fluctuation of pest populations in the field include population density, reproductive rate, climatic conditions, and the abundance of natural enemies; the quality, availability, distribution and preference of the pest for alternate hosts also play an important role [23–27]. Food limitations play a key role in controlling insect populations since herbivore life history traits are influenced by host-plant characteristics [28]. For instance, an insect's body size can be affected by the quality of its host plant, thereby determining life history parameters such as survival, longevity and fecundity [29, 30]. The presence of immature individuals of a species on any crop does not necessarily imply that the plant was a host for the insect [31].

Life tables are widely used as research tools in insect population ecology and pest management [32]. Compared with the traditional life table, the age-stage and two-sex life table not only takes into account the variability in developmental duration among individuals of both sexes, but also integrates the changes in the developmental speed changes of all stages in the form of stage distribution; thus, it can accurately describe the instar differentiation of insects and the generational overlap of populations [33–36]. Elucidating how well pests are adapted to different hosts can provide insights into pest dynamics in the field and thereby facilitate the timely adoption of prevention and control strategies [37]. It is essential to explore whether *S. frugiperda* feeding on bananas can develop to maturity and acquire the ability to produce fertile offspring. Therefore, in this study the survival and development of *S. frugiperda* on banana and maize were compared using age-stage and two-sex life tables with the goal of clarifying the adaptability of the species to banana. The study was designed to provide information on potential threats and risks to banana production, analyse the population source, and monitor and forecast *S. frugiperda* infestation of banana.

Materials and methods

Host plants

The test plant cultivars used in this study were banana variety (Williams B6; Guangxi Rural Export-oriented Economic Development Co., Ltd., Guangxi, China) and maize hybrid (Mei Yu Jia Tian Nuo No. 3; Hainan Lvchuan Seedling Co., Ltd., Hainan, China). Banana and maize were grown under field conditions without the use of pesticides. Maize seedlings at the three-leaf stage and newly developed banana leaves were used in the experiments.

Insect culture

S. frugiperda larvae at the 4^{th}–6^{th} instar were collected from maize fields in Shuangdou Village (22° 52′ 47.27″N, 109° 14′ 14.85″ E) in Jiaoyi Township, Hengzhou City, Guangxi, P. R. China on June 6, 2020. The larvae were reared in 11.5-cm diameter plastic petri dishes and fed an artificial diet [38]. The dishes containing the larvae were kept in an artificial climate chamber at 25 ± 2 °C, 75 ± 5% RH and 14 h L:10 h D photoperiod until pupation occurred. The newly emerged moths were paired (one female and one male) and introduced in plastic cups (11.5 cm in diameter and 15.5 cm in height) and fed with a 10% honey solution supplied through a small cotton wick. Eggs were collected daily and deposited in plastic petri dishes (9 cm diameter) until the emergence of the neonate larvae. Newly hatched larvae of the fifth generation raised on artificial diets were used in the following experiments.

Life history traits study

Three hundred newly hatched larvae were randomly selected and reared individually in plastic petri dishes (11.5 cm in diameter) on banana leaves or maize leaves (control) in the artificial climate chamber described above until pupation. Survival was checked daily, and larval instars were determined by checking for moulted exoskeletons. The larvae on the first day of each instar and the pupae on the second day were weighed with an electronic balance (JJ224BF; Changshu Shuangjie Testing Instrument Factory, Jiangsu, China).

The methods used to culture adults and eggs were the same as stated above. The longevity and reproduction, including the number of progeny eggs and their hatching, of each *S. frugiperda* adult were recorded.

Construction and analysis of the age-stage, two-sex life table

Life tables of *S. frugiperda* were constructed and analysed based on the age-stage, two-sex life table theory and method [33, 34] using the TWOSEX-MSChart program [39].

The age-stage survival rate (S_{xj}), is the probability that a newly hatched individual will survive to age x and stage j, and age-stage specific fecundity (f_{xj}) is the number of fertile eggs produced by the female adult at age x. These parameters accurately represent the biological characteristics of *S. frugiperda* [40]. The age-specific survival rate (l_x) was calculated as

$$l_x = \sum_{j=1}^{m} S_{xj},$$

where m is the number of stages. If all individuals of age x are included, this value expresses the age-specific fecundity (m_x) of the total population:

$$m_x = \frac{\sum_{j=1}^{m} S_{xj} f_{xj}}{\sum_{j=1}^{m} S_{xj}}.$$

The net reproductive rate (R_o) is defined as the total number of progeny that a female produces during her lifetime and is calculated as

$$R_o = \sum_{x=0}^{\infty} l_x m_x.$$

The intrinsic rate of increase (r) is an important indicator of population characteristics. When the population is in an unrestricted environment and the age structure of the population is stable, r is the instantaneous growth rate of the population. r was calculated using the iterative bisection method with age indexed from zero, as in [35, 41]:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1.$$

Table 1 Effects of banana and maize on developmental duration, body weight of *S. frugiperda*

Developmental stage	Developmental duration (d)		Body weight (mg)	
	Banana	Maize	Banana	Maize
1st instar larva	4.42 ± 0.06*	2.12 ± 0.03	0.53 ± 0.01	0.54 ± 0.02
2nd instar larva	5.40 ± 0.06*	2.35 ± 0.04	3.75 ± 0.13	9.46 ± 0.40*
3rd instar larva	6.56 ± 0.11*	2.33 ± 0.03	12.50 ± 0.25	29.96 ± 0.53*
4th Instar larva	6.12 ± 0.10*	2.71 ± 0.05	37.29 ± 0.71	67.14 ± 1.47*
5th instar larva	7.87 ± 0.09*	4.46 ± 0.04	137.95 ± 2.06	181.12 ± 3.02*
6th instar larva	8.62 ± 0.10*	4.96 ± 0.05	276.57 ± 4.15	496.08 ± 10.23*
7th instar larva	11.27 ± 0.14	—	377.67 ± 4.94	—
8th instar larva	14.71 ± 0.21	—	453.56 ± 7.03	—
Larva	64.94 ± 0.35*	18.93 ± 0.07	—	—
Pre-pupa	2.38 ± 0.06*	1.58 ± 0.04	—	—
Pupa	11.91 ± 0.12*	11.50 ± 0.08	132.02 ± 2.72	242.01 ± 23.87*
Progeny egg	2.84 ± 0.05	2.76 ± 0.04	—	—

Mean ± (SE) follow by asterisk indicates significant differences in the same row of data for the same index ($P < 0.05$, *U*-test) and short horizontal line indicates that no data is available

The finite rate of increase (λ) is the theoretical value that represents the growth of the population per unit time; it is measured as e^r [42]:

$$\lambda = e^{r}.$$

The mean generation time (T) is defined as the amount of time a population requires to increase its size R_0-fold as time approaches infinity and the population achieves a stable age-stage distribution. The mean generation time is calculated as:

$$T = \frac{\ln R_0}{r}.$$

Statistical analysis

The Mann–Whitney U test (U test) was used to identify differences between groups of *S. frugiperda* with respect to duration of development, body weight, female and male longevity, preoviposition period, oviposition days and eggs per female. Differences in adult sex ratios were compared using a nonparametric test (binomial test). The life table parameters were calculated using TWOSEX-MSChart software and the results were plotted using GraphPad Prism 8.0.1 (GraphPad Software Inc., San Diego, CA, USA). A probability level of $P < 0.05$ was accepted as statistically significant. All statistical analyses were performed using SPSS 26.0 (IBM Corp., Chicago, IL, USA).

Results

Developmental duration and body weight of *S. frugiperda*

S. frugiperda completed its life cycle by feeding on bananas (Table 1). Maize-fed larvae had six instars, while banana-fed larvae had eight instars. The developmental durations of the 7th and 8th instar larvae fed on bananas were 11.27 ± 0.14 days and 14.71 ± 0.21 days, respectively. The developmental duration of each larval instar, prepupal and pupal stage of *S. frugiperda* fed on bananas was significantly longer than that of the control (1st, $Z = -20.832$, $P < 0.001$; 2nd, $Z = -19.652$, $P < 0.001$; 3rd, $Z = -19.133$, $P < 0.001$; 4th, $Z = -18.542$, $P < 0.001$; 5th, $Z = -18.288$, $P < 0.001$; 6th, $Z = -17.255$, $P < 0.001$; prepupa, $Z = -9.991$, $P < 0.001$; pupa, $Z = -2.663$, $P = 0.008$). The larvae fed on bananas had a developmental duration of 64.94 ± 0.35 days, 3.43 times longer than

Table 2 Effects of banana and maize on reproduction of *S. frugiperda*

Host plant	Sex ratio (♀: ♂)	Female longevity (d)	Male longevity (d)	Pre-oviposition period (d)	Oviposition Days	Fecundity (eggs per female)
Banana	1: 0.95	9.93 ± 0.49 *	9.07 ± 0.37 *	2.87 ± 0.17 *	1.97 ± 0.14	392.23 ± 27.02
Maize	1: 1.08	8.07 ± 0.18	7.95 ± 0.20	1.63 ± 0.07	3.13 ± 0.08 *	875.79 ± 29.21 *
Statistical analysis	$P_{Banana} = 0.909$, $P_{Maize} = 0.615$	$Z = -3.591$, $P < 0.001$	$Z = -2.163$, $P = 0.031$	$Z = -6.316$, $P < 0.001$	$Z = -6.055$, $P < 0.001$	$Z = -7.472$, $P < 0.001$

Mean ± (SE) follow by asterisk indicates significant differences in the same column of data ($P < 0.05$, *U*-test)

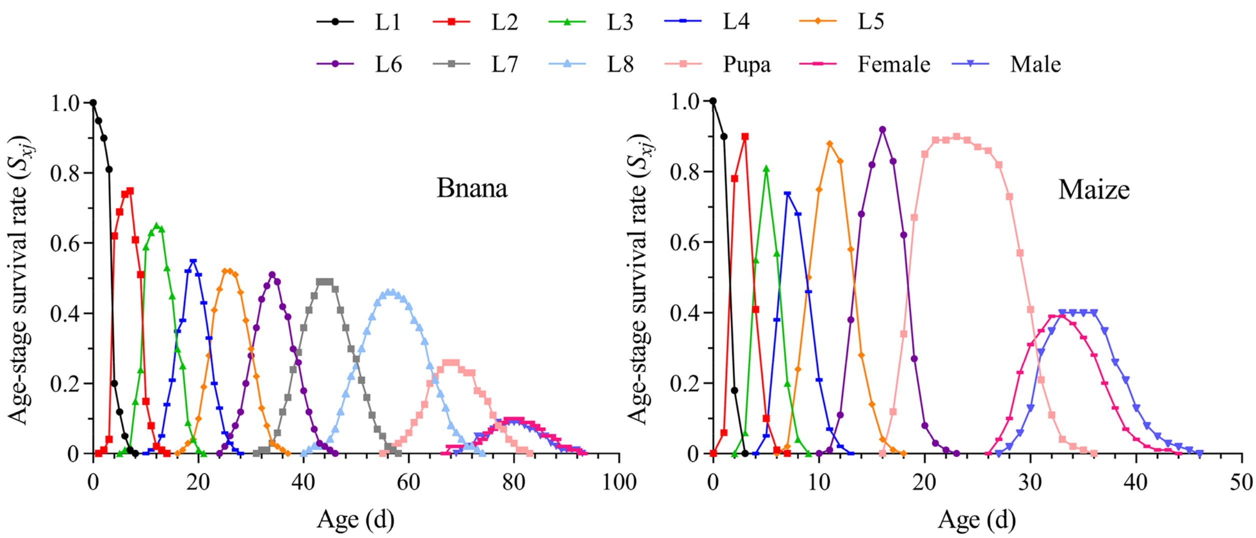


Fig. 1 Effects of banana and maize on age-stage survival rate (S_{xj}) of *S. frugiperda*. L1, L2, L3, L4, L5, L6, L7 and L8 represent 1st, 2nd, 3rd, 4th, 5th, 6th, 7th and 8th instar larvae, respectively

that of the control larvae (18.93 ± 0.07 d). There was no significant difference in the hatching periods of the two groups of progeny eggs ($Z = -1.292$, $P = 0.197$).

The difference in the body weights of 1st instar larvae fed maize and banana was not statistically significant ($Z = -0.551$, $P = 0.582$) (Table 1). However, the body weights of 2nd to 6th instar banana-fed larvae were significantly lower than those of maize-fed larvae (2nd, $Z = -10.694$, $P < 0.001$; 3rd, $Z = -11.526$, $P < 0.001$; 4th, $Z = -11.008$, $P < 0.001$; 5th, $Z = -10.374$, $P < 0.001$; 6th, $Z = -10.490$, $P < 0.001$). Interestingly, the 8th instar larvae fed bananas weighed less (453.56 ± 7.03 mg) than 6th instar larvae fed maize (496.08 ± 10.23 mg). The average pupal weight of the individuals reared on maize (242.01 ± 23.87 mg) was significantly greater than that of the individuals reared on banana (132.02 ± 2.72 mg); it was 1.83 times that of the banana group ($Z = -11.012$, $P < 0.001$).

Reproduction of *S. frugiperda*

There was no significant difference in the sex ratios of the two populations reared on banana and maize. The female longevity, male longevity and preoviposition period of *S. frugiperda* in the banana-fed populations were significantly longer than those in the controls, while oviposition

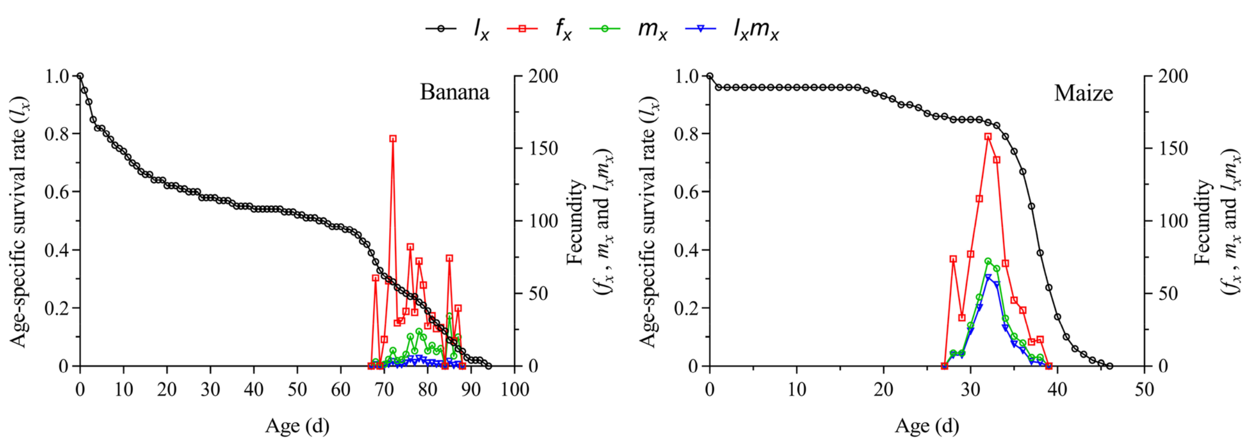


Fig. 2 Effects of banana and maize on age-specific survival rate (l_x), age-stage specific fecundity (f_x), age-specific fecundity (m_x) and l_xm_x of *S. frugiperda*

days and the number of eggs laid per female in banana-fed populations were significantly lower than those in controls (Table 2).

Life table

The age-stage survival rate (S_{xj}) is the probability that a newborn larva will survive to age x while in stage j (Fig. 1). Significant overlaps between stages were observed under both crops. The banana-fed populations of *S. frugiperda* completed the larval stage on Day 74, the pupal stage on Day 83, and eclosion on Day 68, while the corresponding times for the maize-fed populations were Day 23, 36 and 27, respectively. The S_{xj} that a newly hatched larva fed on maize would survive to the pupal stage was 0.90, considerably higher than that for larvae fed on banana (0.26). The S_{xj} values of *S. frugiperda* females and males from first instar larva to adult were 0.10 and 0.09, respectively, for larvae fed on banana and 0.39 and 0.40, respectively, for larvae fed on maize.

The age-specific survival rate l_x is the probability that a newly hatched larva will survive to age x; because this parameter includes all individuals of the cohort and ignores stage differentiation, the l_x curve is a simplified version of the S_{xj} curve (Fig. 2). Higher peaks of age-stage specific fecundity (f_x), age-specific fecundity (m_x), and $l_x m_x$ were observed in *S. frugiperda* reared on maize than in *S. frugiperda* reared on banana. The maize-reared populations of *S. frugiperda* oviposited from Day 28 to the end of Day 39, and the banana-reared populations of *S. frugiperda* oviposited from Day 68 to the end of Day 88. Most of the females of in the maize-reared populations laid eggs on Days 31–33, while those in the banana-reared populations had multiple irregular oviposition peaks during the breeding period. The highest f_x peak of females reared on banana occurred on Day 72, and the mean fecundity was 156.50 eggs, while the highest f_x peak of females reared on maize occurred on Day 32, and the mean fecundity was 158.02 eggs.

Life table parameters

The net reproductive rate (R_o) of *S. frugiperda* reared on maize was 253.98 progeny per female, much higher than that of *S. frugiperda* reared on banana (39.22 progeny per female) (Table 3). The intrinsic rate of increase (r) and the finite rate of increase (λ) for *S. frugiperda* reared on banana were 0.05 d^{-1} and 1.05 d^{-1}, respectively, lower than those for *S. frugiperda* reared on maize ($r = 0.17\ d^{-1}$, $\lambda = 1.18\ d^{-1}$). The r and λ values for both groups were greater than 0 and greater than 1, respectively, indicating that *S. frugiperda* can complete generational proliferation whether feeding on banana or maize. The λ values of the banana-fed populations and maize-fed populations of *S. frugiperda* were 1.05 d^{-1} and 1.18 d^{-1}, respectively, indicating that the two populations grew continuously and geometrically at rates of 1.05-fold and 1.18-fold per day, respectively, under these conditions. On the other hand, the mean generation time (T) of the banana-fed populations ($T = 78.48$ d) of *S. frugiperda* was 2.38 times longer than that of the maize-fed populations ($T = 33.03$ d).

Table 3 Effects of banana and maize on life table parameters of *S. frugiperda*

Host plant	Net reproductive rate R_0	Mean generation time T (d)	Intrinsic rate of increase r (d^{-1})	Finite rate of increase λ (d^{-1})
Banana	39.22	78.48	0.05	1.05
Maize	253.98	33.03	0.17	1.18

Discussion

Herbivorous insects can generally complete their entire life cycles (egg to adult) on a host plant that can be considered an alternative host. *S. frugiperda* has been reported to damage a variety of plants [2, 38, 43]. Some plant species may support the complete development of *S. frugiperda*. For example, this pest can complete its life cycle on maize, sugarcane (*Saccharum officinarum*), rice (*Oryza sativa*), potato, cotton (*Gossypium* spp.), and amaranth (*Amaranthus viridis*) [44–50]. However, other plant species may not support complete development of *S. frugiperda* but may still be used by larvae or adults for feeding and laying eggs. For example, although damage to cabbage (*Brassica oleracea*), maranta (*Maranta arundinacea*), and coix (*Coix lacryma-jobi*) has been reported, no evidence that *S. frugiperda* can complete its life cycle on these plants [51–53]. The results of current study showed that *S. frugiperda* can complete its life cycle on banana plants, suggesting that banana is an alternative host plant for this insect pest.

Since *S. frugiperda* larvae were first observed to damage bananas in this study, and the larvae used in the study were either hatched on bananas or transferred from weeds of the family Gramineae, such as *Eleusine indica*, *Setaria viridis* and *Digitaria sanguinalis* [54, 55]. In Guangxi, spring maize is planted in early February, and it enters the late growth or harvest period in June. At this time, autumn maize and fresh maize were not yet been sown [56]. It may be that the absence of an ideal host causes female moths to lay their eggs on more numerous and occasional hosts, such as the perennial herb banana, rather than on their preferred host, but their larvae are underfed on the occasional hosts. Nevertheless, the presence of even a few surviving larvae can ensure the presence of some individuals on the occasional hosts until the population increases in the next growing season of the preferred crop. In addition, the abundance of natural enemies on some host plants may also cause females to lay eggs on less nutritious hosts to better protect their offspring [57, 58]. However, whether deposition of eggs on bananas by female *S. frugiperda* protects their offspring from predation or parasitization by natural enemies needs further study.

Undoubtedly, differences in the type of food consumed have a great impact on the growth and development of herbivorous insect larvae and on the reproduction of adults even under the same environmental conditions, and this in turn affects the change trend of the entire insect population [30, 59]. Although our results show that banana is an alternative host plant for *S. frugiperda*, we found that *S. frugiperda* feeding on bananas have a longer ontogeny cycle and lower survival and fecundity than maize-fed *S. frugiperda*. This finding indicates that although banana plants supply *S. frugiperda* with the nutrients required to complete its entire life cycle, growth on banana is not conducive to optimal development of its population.

A number of studies have reported that *S. frugiperda* has six larval instars [15, 17, 37, 48, 50]. However, the present study identified up to eight larval instars, and He et al. [17, 60] also reported a similar result. To date, no other study of *S. frugiperda* has shown this phenomenon, but there are examples showing a similar occurrence of eight instars in other species, including *Malacosoma disstria* [61], *S. exigua* [62] and *Chilo suppressalis* [63].

Notably, our findings indicated that although the sex ratios of in the banana- and maize-reared populations did not differ significantly, the females and males in the banana-reared population lived significantly longer than those in the maize-reared population and that the females in the maize-reared populations had shorter preoviposition periods, more oviposition days, and higher fecundity. Previous studies have shown that the opportunity to reproduce closely related to longevity; therefore, decreased longevity in response to current reproductive efforts was used to estimate the costs of reproduction [64]. For example, the parasitic wasp *Itoplectis naranyae* has a shortened lifespan after parasitizing its hosts, suggesting that parasitization has reproductive costs in terms of egg production [65]. It is also possible that nutritional restriction is responsible for this difference. For instance, in the case of complete feeding, Grandison et al. [66] found that the addition of amino acids increased fecundity and shortened longevity in flies.

Conclusions

In conclusion, bananas are alternative but not ideal hosts of *S. frugiperda* compared to maize. Even so, in situations in which the population density is too high or the preferred host is scarce, it is still critical to prevent *S. frugiperda* from transferring to bananas and thereby increasing the number of sources of outbreak. On the other hand, larval instars of *S. frugiperda* reared on banana had longer developmental times than those reared on maize. These findings may be applied to the design of a comprehensive integrated pest management strategy and may help explain the rapid expansion of this polyphagous species across different areas in China. Our results show that banana can serve as an alternative host for *S. frugiperda* during the maize harvest or during off-season planting.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40538-022-00341-z.

Additional file 1. The damage of *Spodoptera frugiperda* to bananas.

Additional file 2. *Spodoptera frugiperda* larvae on bananas.

Additional file 3. The oviposition site of *Spodoptera frugiperda* to bananas.

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Author contributions

SCZ contributed to experimental work, data analysis, and writing the article. YXQ established *S. frugiperda* laboratory colonies and recorded experimental data. XYW directed the experiments and edited the original draft. WL and XLZ designed experiments and performed project administration, supervision, review, and editing of the original draft. All authors read and approved the final manuscript.

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Availability of data and materials

A reasonable request to the corresponding author can gain access to the data that support this study's findings. The data are not publicly accessible due to ethical and privacy considerations.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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