Age-stage, two-sex life table analysis of *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) reared on maize and kidney bean

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**Abstract**

**Background:** *Spodoptera frugiperda* (JE Smith), or fall armyworm, is one of major migratory agricultural pests with a wide range of hosts. The effect of different hosts (maize and kidney bean) on the growth and reproduction of *S. frugiperda* were investigated using the age-stage, two-sex life table method.

**Results:** The results showed that *S. frugiperda* could complete its entire life cycle on both hosts, albeit with significantly different development and reproduction. The durations of larval and pupal development were significantly prolonged whereas adult lifespan was shortened on kidney bean compared to maize. The differences of survival rates at each instar, prepupal and pupal stages between the two hosts were not statistically significant. The total preoviposition period was longer on kidney bean than that on maize (42.05 vs 39.04 days), but there was no difference in the oviposition rate (64.77 on kidney bean vs 62.48 on maize). The differences of net reproductive rate, intrinsic rate of increase and finite rate of increase were nonsignificant, while the mean generation time on kidney bean (42.05 days) was significantly longer than that on maize (40.92 days).

**Conclusions:** The results indicate that *S. frugiperda* can grow and reproduce normally on both hosts, although maize is more suitable. Nonetheless, the data show that this pest is harmful when the population density is high or when the preferred host is scarce.

**Keywords:** *Spodoptera frugiperda*, Life table, Maize, Kidney bean, Reproduction

**Background**

The fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) is one of the important worldwide pests that is native to the tropical and subtropical Americas [1]. It was rated as one of the top 10 out of 1187 arthropod pests by the Centre for Agriculture and Biosciences International in the 2017 “State of the World’s Plants” report because of its perniciousness and invasiveness [2]. The inherently superior biological characteristics of *S. frugiperda* such as high fecundity, strong migratory ability, and wide range of hosts contribute to its invasiveness [3]. In the last 3 years, it has invaded 47 African countries, 18 Asian countries, and Australia [4]. *Spodoptera frugiperda* was first detected in Africa in January 2016 and rapidly spread to sub-Saharan Africa [5, 6]. *Spodoptera frugiperda* was first monitored in Jiangcheng County, Yunnan Province, in January 2019 and was reported as invasive species [7]. By December 31, 2019,
S. frugiperda had spread to 1524 counties in 26 provinces in China [8]. Since S. frugiperda can feed on more than 350 plants of 76 families such as Gramineae, Compositae, and Leguminosae, it is more prone to outbreaks [9]. Two sympatric host-plant strains have been identified: the “maize (C-) strain” that mostly feeds on maize (Zea mays), cotton (Gossypium hirsutum), and sorghum (Sorghum bicolor), and the “rice (R-) strain” that is primarily associated with rice (Oryza sativa) and various pasture grasses [10]. The population of S. frugiperda that invaded China is thought to have originated as the offspring of a hybrid group of R-strain female and C-strain male parents [11]. The nuclear genome of the C-strain has occupied a dominant position in the long-term evolutionary process, which has led to the emergence of a unique C-strain that has caused extensive damage to maize, sugarcane, sorghum [12]. In the absence of preferred hosts, the C-strain also feeds on other plants [13–15].

Kidney bean (Phaseolus vulgaris) is a host plant of the C-strain that is rich in nutrients [16]. China is one of the main producers of kidney bean, with the largest cultivation area, highest average yield and total output in the world [17]. Thus, S. frugiperda can cause considerable damage to kidney bean when there are no other suitable hosts. Clarifying the factors that influence the adaptation of pests to different hosts can provide insight into pest dynamics in the field, which can promote the timely adoption of prevention and control strategies [18].

This study aims to explore the suitability of S. frugiperda on kidney bean compared to maize (its preferred host) and determine whether the new C-strain of S. frugiperda has a potential damage risk on kidney bean. So, the development and reproduction of S. frugiperda on maize and kidney bean were compared using the age-stage, two-sex life table method to assess the threat posed by the new C-strain to kidney bean production in China. Our results also provide a theoretical basis for investigating host adaptation mechanisms of S. frugiperda, which can guide future pest control strategies.

Materials and methods

Insect

The original S. frugiperda colony was collected from maize in Guizhou, China, and transferred to a climate-controlled room (Temperature: 25 °C ± 1 °C, relative humidity: 70 ± 5%, light/dark cycle: 14:10-h, Ningbo Jiangnan Instrument Factory, Ningbo, China) in the laboratory, and were used to establish a laboratory colony. Fall armyworm larvae were reared on fresh maize leaves until the pupal stage while adults were fed with a 10% honey solution. All S. frugiperda stages were kept and isolated in plastic containers.

Hosts

Maize plants (Qingqing 300 variety; Guizhou Qinnong-gyuan Agricultural Development Co, Guiyang, China) were grown in a greenhouse under the above-described conditions at the Institute of Entomology, Guizhou University, China. Seeds were sown in pots (diameter of 12 cm, height of 10 cm) with nutrient soil and plants were watered once daily.

Kidney bean plants (Jinshulu variety; Shengnong Seed Company, Xinji, China) were planted in a climate chamber under the above-described conditions. The specific method refers to Liu et al. [19]. Healthy, undamaged kidney bean plants with two leaves were collected for experiments. No pesticides were applied to both crops and no pest damage was observed.

Methods

In order to evaluate the development and reproduction of S. frugiperda on different host plants, 20 adult couples (mated 3 days after emergence) were randomly selected from the laboratory population and placed in a 50 cm × 50 cm cage, fed with a 10% honey solution. After 12 h, all broods were collected and individual eggs were gently transferred with a brush to a 12-hole transparent storage box (23 × 15 cm) with a small compartment (5.5 × 5 cm) (10 eggs were randomly placed into compartments per insect box, respectively) and each compartment was regarded as an independent space. Four 12-hole transparent storage boxes with fresh corn or kidney bean leaves were prepared for each host and three replicates per host were conducted. The developmental stage and survival from the first instar to adult was observed at 9:00 am daily. Fresh maize and kidney bean leaves were replaced daily. All boxes were kept separately in climate chamber under the above-described conditions.

After pupation for 3 days, S. frugiperda was weighed and transferred to a round plastic box (upper and lower mouth diameters of 6 and 5 cm, respectively, with a height of 3 cm). After emergence, the adults fed with a 10% honey solution. S. frugiperda feeding on the same host was paired with one male and one female in a disposable plastic cup (upper and lower mouth diameters of 9.5 and 7.3 cm, respectively, and with a height of 5.5 cm) for observation and recording. The oviposition of female was accurately recorded every day until died. The egg stage of the offspring was observed every morning at 9:00 am and was replaced the egg stage of parent generation, and hatched larvae were fed to adulthood and the ratio of females was recorded.
Construction of the age-stage, two-sex life table
According to the age-stage, two-sex life table principle [20, 21] and method [22–25], the following parameters were calculated and the age-stage, two-sex life tables of *S. frugiperda* on the two hosts were established:

1. Adult pre-oviposition period (APOP): the period between the emergence of an adult female until initiate of first oviposition. Total pre-oviposition period (TPOP): the time interval from birth to the beginning of oviposition) [26, 27].

2. Age-stage-specific survival rates (*S*): the probability that a newborn egg will survive to age *x* and stage *j*:
   \[ S_{xj} = \frac{n_{xj}}{n_{o1}}. \]

3. Age-specific survival rate (*l*): the probability that a newborn egg will survive to age *x*:
   \[ l_x = \sum_{j=1}^{m} S_{xj}, \]
   where *m* is the number of stages.

4. Age-stage-specific fecundity (*f*): the number of hatched eggs produced by female adult at age *x*.

5. Age-specific fecundity (*m*): the number of eggs per individual at age *x*:
   \[ m_x = \frac{\sum_{j=1}^{m} S_{xj} f_{xj}}{\sum_{j=1}^{m} S_{xj}}. \]

6. Age-specific maternity (*l*): the product of *l* and *m*.

7. Age-stage-specific life expectancy (*e*): the time that an individual of age *x* and stage *y* is expected to live:
   \[ e_{xj} = \sum_{i=1}^{m} \sum_{j=1}^{m} S'_{ij}, \]
   where *S'$_{ij}$* is the probability that an individual of age *x* and stage *y* will survive to age *i* and stage *j*.

8. Age-stage-specific reproductive value (*V*): the contribution of individuals of age *x* and stage *y* to the future population:
   \[ v_{xj} = \frac{e^{r(x+1)}}{S_{xj}} \sum_{i=x}^{n} e^{-r(i+1)} \sum_{j=y}^{m} S'_{ij}. \]

9. Intrinsic rate of increase (*r*):
   \[ \sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1. \]

10. Finite rate of increase (*λ*):
    \[ \lambda = e^r. \]

11. Net reproductive rate (*R₀*):
    \[ R_0 = \sum_{x=0}^{\infty} l_x m_x. \]

12. Mean generation time (*T*):
    \[ T = \frac{\ln R_0}{r}. \]

Data analysis
TWSEX-MSChart 2020 software (http://140.120.197.173/Ecology/prod02.htm) was used to calculate each parameter; the standard errors were determined by bootstrapping with 100,000 repetitions. SigmaPlot v12.5 software (Systat Software, San Jose, CA, USA) was used to plot the figures, and TWSEX-MSChart software was used to evaluate the statistical significance of the observed differences. Differences between groups were evaluated by paired bootstrapping, with *P* < 0.05 considered statistically significant; Student’s *t*-value, degrees of freedom, eggs laid per female per day, pupal weight and survival rate (analyzed after arcsine square root transformation, formula: ARSIN(SQRT(A1*180/3.1415926)) at each stage before emergence were analyzed by SPSS version 22.0 (SPSS Inc., Chicago, IL, USA).

Results
Development time of each stage of *S. frugiperda*
The effect of host plants on the duration of each developmental stage of *S. frugiperda* is shown in Table 1. *S. frugiperda* could complete its entire life cycle on maize and kidney bean. The 1st, 2nd, 5th, and 6th instar larval and pupal stages were significantly longer on kidney bean compared to maize (*t* = −7.782; *p* < 0.01; *t* = −8.803; *p* < 0.01; *t* = −11.824; *p* < 0.01; *t* = −10.242; *p* < 0.01, respectively), and the total duration of the egg and larval stage was 22.56 days on kidney bean, which was significantly longer than 19.04 days on maize (*t* = −13.397; *p* < 0.01). However, adult longevity was significantly shorter on kidney bean than that on maize (females: 14.76 vs 16.15 days; males: 14.95 vs 16.25 days) (*t* = 2.191; *p* = 0.034; respectively). The differences were nonsignificant in the duration of the 3rd and 4th instar larval and prepupal stages between two hosts (*t* = 1.59; *p* = 0.114; *t* = 0.176; *p* = 0.860; respectively).
Table 1 Duration of each developmental stage of Spodoptera frugiperda on maize and kidney bean

| Duration, days  | Maize         | Kidney bean |
|----------------|---------------|-------------|
| Egg            | 3.40±0.06     | 3.43±0.05   |
| 1st instar     | 2.54±0.05*    | 3.15±0.06   |
| 2nd instar     | 2.50±0.05*    | 3.19±0.06   |
| 3rd instar     | 1.88±0.07     | 1.74±0.06   |
| 4th instar     | 2.50±0.06     | 2.49±0.06   |
| 5th instar     | 2.70±0.07*    | 3.96±0.08   |
| 6th instar     | 3.57±0.07*    | 4.68±0.08   |
| Egg + larva    | 19.04±0.10*   | 22.56±0.22  |
| Prepupa        | 2.20±0.07     | 2.13±0.06   |
| Pupa           | 12.04±0.10*   | 13.07±0.15  |
| Female adult   | 16.15±0.51*   | 14.76±0.36  |
| Male adult     | 16.25±0.38*   | 14.95±0.18  |

The data in the table are mean values ± SE
*Means P < 0.05 (paired bootstrap test)

Table 2 Survival rate at each stage of Spodoptera frugiperda before emergence on maize and kidney bean

| Survival rate, %  | Maize       | Kidney bean |
|-------------------|-------------|-------------|
| Egg               | 100.00±0.00 | 100.00±0.00 |
| 1st instar        | 96.67±1.67  | 95.00±2.89  |
| 2nd instar        | 98.25±1.75  | 91.26±2.28  |
| 3rd instar        | 99.17±0.83  | 98.09±0.83  |
| 4th instar        | 94.76±1.42  | 90.35±1.42  |
| 5th instar        | 91.64±3.18  | 90.23±1.77  |
| 6th instar        | 96.05±2.59  | 95.14±2.59  |
| Prepupa           | 97.85±1.08  | 100.00±0.00 |
| Pupa              | 92.36±2.97  | 95.00±1.08  |

The data in the table are mean values ± SE
*Means P < 0.05 (paired Student’s t-test)

Survival rate of S. frugiperda at each stage before emergence

Survival rates at immature stages of S. frugiperda on the two hosts are shown in Table 2. The differences of survival rates at each instar, prepupal and pupal stages between the two hosts were not statistically significant.

Reproduction and pupal weight

APOP did not differ significantly between S. frugiperda adults fed maize and kidney bean (Table 3); however, TPOP was shorter for the former (39.04 vs 42.05 days) (t = -3.556; p < 0.01). There was no difference in the oviposition rate (OR) (64.77 on kidney bean vs 62.48 on maize) (t = -0.248; p = 0.805) and female ratio of offspring (0.50 on kidney bean vs 0.51 on maize). Additionally, the pupal weight of S. frugiperda on maize was significantly higher than that on kidney bean (t = 5.031; P < 0.01).

Population parameters

The r and λ values of S. frugiperda populations were >0 and >1, respectively, for both maize and kidney bean (Table 4), indicating that the S. frugiperda were able to survive on the two hosts. The differences of R₀, r and λ were nonsignificant on the two hosts. On the other hand, T was longer on kidney bean than that on maize (42.05 vs 40.92 days, P < 0.01).

Survival rate

Sxj of S. frugiperda on maize and kidney bean are shown in Fig. 1. The values differed across developmental stages, which was attributable to variable growth rates among individuals. Spodoptera frugiperda completed the larval stage at 23 days and emerged at 29 days on maize compared to 28 and 33 days, respectively, on kidney bean. However, there were no differences in the survival of
adults between two hosts (59 days for both). This result suggested that it was significantly delayed for the development of *S. frugiperda* on kidney bean. The *S*$_x$ of *S. frugiperda* males and females from egg to adult were 0.425 and 0.2833, respectively, on maize, and 0.3083 and 0.3167, respectively, on kidney bean, representing statistically significant differences according to the host for both sexes.

**Population survival rate and fecundity**

Figure 2 shows the influence of hosts on the survival rate and fecundity of *S. frugiperda*: $l_x$,$f_x$,$m_x$, and $l_x^*m_x$. $l_x$ on maize and kidney bean showed a downward trend with increasing age; based on the estimated values, the death of the last adult on both hosts occurred at 59 days. $f_x$, $m_x$, and $l_x^*m_x$ reached maximum values at 41 days, on maize (101.3235, 40.5294, and 28.7083, respectively), and at 42 days on kidney bean plants (72.4474, 36.7067 and 22.9417, respectively); each of these maxima were all lower compared to maize. Thus, a diet of maize was more conducive to the development and reproduction of *S. frugiperda*. Additionally, the fluctuations in the fecundity curve were suggest that the emergence and oviposition of *S. frugiperda* did not occur at specific ages.

**Life expectancy**

The value of $e_{x_0}$ showed a downward trend on both maize and kidney bean, with maximum average longevity values of 39.5833 and 38.3 days, respectively, at age 0 ($e_{0x}$) (Fig. 3). The value of $e_{x_0}$ was lower on kidney bean than on maize in the first 8 days but the trend was reversed thereafter, indicating that *S. frugiperda* developed more slowly on kidney bean.
Reproduction value

\(v_{xj}\) of \(S.\ frugiperda\) feeding maize and kidney bean at age zero \((v_{0,1})\) was 1.1392 and 1.1253, respectively, which were both close to \(\lambda\) (Fig. 4). The peak value of the \(v_{xj}\) curve showed an upward trend with advancing age and developmental stage, with the highest value at 36 days on maize (412.9524) and at 39 days on kidney bean (360.6198). The highest \(v_{xj}\) was in female adults reared on maize.

Discussion

The differences of nutrient content in host plants have big influence on the life cycle of herbivorous insects and affect the changing trend of their populations [26, 28–32], including those of \(S.\ frugiperda\) [33–36]. In this study, we found that the development and fecundity of \(S.\ frugiperda\) were affected by host species. The durations of larval and pupal stage were longer for \(S.\ frugiperda\) reared on kidney bean; moreover, adult longevity and fecundity were reduced compared to \(S.\ frugiperda\) fed maize.

The development of insects generally depends on the quality of the diet in the first few instars, which was different among the host [37]; a longer larva-to-adult period is thought to reflect a compensatory response in larvae to a low-quality diet [38]. Xu et al. [39] reported that the development time of the larval stage was prolonged and survival rate declined when \(S.\ frugiperda\) were fed tobacco (a non-preferred host) instead of maize, which was consistent with our findings. However, the final larval mortality rate on tobacco was 85.5%, which was higher than the 32.5% that we observed on kidney bean. This might be attributable to differences in the principal materials or secondary metabolites in the leaves of the two plants [40].

The \(r\) represents the growth potential of insect populations; a larger value reflects more rapid development [41, 42]. The differences of \(R_0\), \(r\) and \(\lambda\) were nonsignificant on
the two hosts, whereas the value of $T$ was higher for *S. frugiperda* fed kidney bean compared to maize. Based on these parameters, maize was found to be more conducive to *S. frugiperda* growth and development than kidney bean. But other studies found that the population parameter values of *S. frugiperda* were lower on maize than on three triticeae crops [43], which may be related to diet quality and feeding conditions [38].

In addition, it was also found in this study that there were non-reproductive females on both host plants, and the ratio of non-reproductive females/total females was 8/34 (maize) and 16/38 (kidney bean). This phenomenon was most likely due to unsuccessful mating and were reported by other researchers [44, 45]. But the mechanism of the generation of non-reproductive female and the increase in the number of non-reproductive female is still unclear, and further research is needed.

**Conclusion**

Although our results indicate that kidney bean is a less suitable host than maize, it still supported the full life cycle of *S. frugiperda* and is thus vulnerable to damage by this pest, especially if *S. frugiperda* populations optimize the utilization of kidney bean as a food source under conditions of high population density and food scarcity.

Therefore, the occurrence of *S. frugiperda* on crops should be closely monitored in the future. Additionally, clarifying the mechanisms and factors associated with adaptation to a kidney bean diet can provide a basis for predicting and controlling the growth of *S. frugiperda* populations.

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**Authors’ contributions**

WX performed the experiments, analyzed data, and wrote the article. JRZ and CXH designed the experiments and revised the manuscript. QJY, DYL and GZ collected the original *S. frugiperda* colony and established a laboratory colony. YMZ analyzed data. WBY guided the use of Sigmaplot v12.5 software. CL and CXH designed the experiments and revised the manuscript. QJY, DYL and GZ WX performed the experiments, analyzed data, and wrote the article. JRZ and CXH designed the experiments and revised the manuscript.

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**Availability of data and materials**

The datasets used and/or analyzed during the study are available from the corresponding author on reasonable request.

**Declarations**

**Ethics approval and consent to participate**

Not applicable.

**Consent for publication**

The authors consent for publication.

**Competing interests**

The authors declare that the research has no competing interests.

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