*Bulletin of Entomological Research*

**cambridge.org/ber**

## Research Paper

**Cite this article:** Sharma S, Sharma PL, Sharma P, Verma SC, Sharma N, Sharma P (2024). Demographic analysis and biotic potential of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) on pea. *Bulletin of Entomological Research* 1–10. https://doi.org/10.1017/S0007485324000312

Received: 19 January 2024
Revised: 10 April 2024
Accepted: 11 May 2024

**Keywords:**
fall armyworm; pea; population parameters; population projection; two-sex life table

**Corresponding author:**
Prajjval Sharma;
Email: sharmaprajjval@gmail.com



# Demographic analysis and biotic potential of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) on pea

Shubham Sharma, Prem Lal Sharma, Prajjval Sharma, Subhash Chander Verma, Nidhi Sharma and Priyanka Sharma

Department of Entomology, Dr YS Parmar University of Horticulture and Forestry, Solan, HP 173230, India

**Abstract**

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is a highly destructive polyphagous pest that primarily damages maize. Maize is considered a most versatile crop for growing intercrops due to the wide row it needs. Maize–pea intercropping is preferred by small and marginal farmers worldwide due to various advantages including higher yield and improved economic benefits. However, the success of this intercropping system may be hampered if pea could sustain the FAW population. Thus, to clarify the fitness and potential effect of *S. frugiperda* on pea, we analysed the survival and development of *S. frugiperda* fed on pea leaves in the laboratory and constructed age-stage and two-sex life tables. Results showed that FAW successfully completed its life cycle when fed on pea and produced fertile offspring. The pre-adult duration was significantly higher on pea than maize. The net reproductive rate, intrinsic and finite rate of population increase on pea (135.06 offspring per individual, 0.12 offspring per individual per day and 1.13 times per day) were all significantly different from those on maize (417.64 offspring per individual, 0.19 offspring per individual per day and 1.21 times per day). The probability of survival of *S. frugiperda* at each stage was lower when fed on pea leaves than that of maize-fed larvae. Due to the overlapping growth periods of the maize and pea, *S. frugiperda* can easily proliferate throughout the year by shifting between adjacent crops. Thus, this study revealed the adaptability of *S. frugiperda* for pea and provides the foundation for further assessment of FAW risk to other inter-crops.

## Introduction

The fall armyworm (FAW), *Spodoptera frugiperda*, formerly known as *Laphygma frugiperda* (Smith and Abbott), is a serious pest of maize native to tropical and subtropical regions of the Americas since 1797 (Goergen *et al*., 2016; Rwomushana, 2019). However, in 2016, it invaded Africa and abruptly advanced throughout most African countries and later in Asia. In India, this alarming pest was detected first time in 2018 in Karnataka and has now been spread to almost all the maize-growing states (Sharanabasappa *et al*., 2018). According to a preliminary calculation, FAW was expected to affect about 170,000 ha of maize crops in ten Indian states (Sangomla and Kukreti, 2023). The prolificacy of *S. frugiperda* (egg masses usually contain hundreds of eggs) and its potentiality to emigrate long distances are the two peculiar traits that facilitated it to invade more than 80 countries worldwide (Wu *et al*., 2022).

FAW is known to infest more than 353 plants belonging to 76 different families; mostly under Poaceae followed by Asteraceae and Fabaceae (Montezano *et al*., 2018), implicating that polyphagy can enable it to develop or sustain populations outside of the primary cropping areas or cropping season imparting larger pest pressure. This wider host range of FAW in comparison to other congeneric species like *Spodoptera cosmioides* (Walker), *Spodoptera eridania* (Stoll), *Spodoptera albula* (Walker) and *Spodoptera dolichos* (Fabricius) (Montezano *et al*., 2014; Specht and Roque-Specht, 2016) has entitled it to the distinction of an invasive species. Although FAW larvae have a decided preference for grasses such as maize and sorghum (its main hosts), various other crops including weeds are also attacked. *Spodoptera frugiperda* has been reported to feed in large numbers on the leaves, stems and reproductive parts of *Solanum lycopersicum* Mill. (Tietz, 1972), *Capsicum annum* L. (Casmuz *et al*., 2010), *Brassica oleracea* var. *capitata* L., *Zingiber officinale* Roscoe, *Citrus sinensis* L. Osbeck, *Prunus persica* L. Batsch, *Fragaria ananassa* Duchesne, *Abelmoschus esculentus* L. Moench, *Solanum tuberosum* L. etc. (Rwomushana, 2019). The potential of FAW to sustain on both crop and non-crop plants including weeds enables it to maintain the population year-round (Montezano *et al*., 2018).

India is a tropical country that favours rapid reproduction and multiplication of FAW. The peak activity period of FAW is from July to September in India, thus becoming a major threat to the *Kharif* maize crop. To escape excess rainfalls and higher incidence of insects in *Kharif* season, maize is also cultivated in *Rabi* season in different parts of the country. However, various studies have reported cold hardiness in stages of FAW resulting in damage to winter crops which in turn can empower FAW to sustain throughout the year (Zhang *et al.*, 2021; Vatanparast and Park, 2022; Qi *et al.*, 2024). Consequently, when *Kharif* maize is absent, FAW being a polyphagous pest may shift to crops in succession after *Kharif* maize or to other inter-crops. Maize–pea intercropping is widely practiced worldwide including India, due to the complementary use of N sources by intercropping with legumes (Aulakh, 2020). However, information on the host susceptibility of *S. frugiperda* to companion plants like pea in the intercropping system and crops grown in succession is lacking. Such knowledge is requisite to assess the biotic potential of *S. frugiperda* on different crops at risk. Life tables provide comprehensive information on the insect population dynamics and their fitness by including all life-history parameters and reproduction of both sexes (Huang *et al.*, 2017; Chen *et al.*, 2020). In this study, we assessed the life table data of FAW reared on pea and analysed the population fitness. Our research aimed to provide comprehensive knowledge about the FAW population growth and possible damage to pea with the objective of providing helpful information for the application of fruitful FAW management tactics in the newly FAW-invaded agricultural ecosystems.

## Materials and methods

### Insect

FAW larvae were field-collected in Experimental Farm, Department of Entomology Dr YS Parmar University and Forestry, Nauni, Solan, Himachal Pradesh, India (1275 m amsl; 31.28°N; 76.94°E), and reared in the laboratory at 25 ± 0.5°C, 70 ± 5% RH and 14L:10D photoperiod. The pest was raised on the respective host for one generation before being used in the experiments.

### Host plant raising

Maize (*Zea mays* L. var. Early Composite) and pea (*Pisum sativum* var. *sativum* L. var. Azad P-1) plants were grown as per the standard package of practices at the experimental farm of the Department of Entomology. Due to the different growth cycles of plant species, 25-day-old maize and 35-day-old pea leaves were used to feed *S. frugiperda* larvae.

### Larval feeding trials

The trials were performed in Biological Control Research Laboratory of the Department of Entomology, Dr YS Parmar University and Forestry, Nauni, Solan, Himachal Pradesh, India at 25 ± 0.5°C, 70 ± 5% RH and 14L:10D photoperiod. Newly emerged adults obtained from mass culture were paired and placed in separate plastic cylindrical containers covered with nylon mesh on one side (150 × 150). Ten egg masses (one from each container) laid on host leaves within 24 h period were randomly selected. Ten eggs were then randomly picked from each egg mass. The neonate larvae hatched from selected 100 eggs were reared individually on the test host plants in Petri plates (100 mm). Petri plates with fresh leaves were changed daily to ensure sufficient food for larvae. The larval development and survival were recorded until death, pupation or pupal emergence. Newly eclosed adults were kept in pairs in plastic cylindrical containers (1L) covered on one side with nylon mesh (150 × 150). All adults were fed daily with 30% (v/v) honey solution in cotton swabs. FAW adults that mated successfully included 20 pairs that were fed with maize, and 14 pairs that were fed with pea. Each pair was offered with host leaves as a substrate for oviposition. Observations on the duration of different developmental stages, adult longevity, pre-oviposition and oviposition periods, fecundity and sex ratio were recorded.

### Life table analysis

Life tables of *S. frugiperda* reared on maize and pea leaves were constructed and analysed based on the age-stage, two-sex life table theory using the TWOSEX-MSChart program (Chi, 2022b).

The age-stage survival rate ($s_{xj}$, probability that a newly laid egg can survive to age $x$ and stage $j$) and age-stage specific fecundity ($f_{xj}$, number of eggs produced by female adult at age $x$) were computed. These parameters accurately illustrate the biological characteristics of *S. frugiperda.* The age-specific survival rate ($l_x$) and age-specific fecundity ($m_x$) were calculated as:

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

$$m_x = \frac{\sum_{j=1}^{m} s_{xj} f_{xj}}{l_x}$$

where $m$ is the number of stages.

The gross reproductive rate ($GRR$) was calculated as:

$$GRR = \sum_{x=0}^{\infty} m_x$$

The net reproductive rate ($R_0$), defined as the rate of multiplication of the population in a generation, represented in terms of number of offspring produced per generation was calculated as summation of the product of $l_x$ and $m_x$, i.e.

$$R_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{m} s_{xj} f_{xj}$$

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

The true intrinsic rate of increase ($r$) is the number of offspring produced by an individual in a day (offspring per individual per day) and was calculated by using the Lotka–Euler equation:

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

The mean generation time ($T$) is defined as the time period required by a population to increase to $R_0$-fold of its size as time approaches infinity and population settles down to a stable age-stage distribution and was calculated by:

$$T = \frac{lnR_0}{r}$$

https://doi.org/10.1017/S0007485324000312 Published online by Cambridge University Press

The finite rate of increase ($\lambda$) is the rate of multiplication of population in a day (times per day) and was calculated as:

$$\lambda = e^r$$

The doubling time ($DT$), the time required by a population to double its size, was calculated by the formula:

$$DT = \frac{ln2}{r}$$

Age-stage-specific life expectancy ($e_{xj}$) is the time that an individual of age $x$ and stage $j$ is predicted to live. It was calculated by the formula:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{m} s'_{iy}$$

where, $s'_{iy}$ = probability that an individual of age $x$ and stage $j$ can survive to age $i$ and stage $y$ assuming $s'_{xj} = 1$.

Age-specific reproductive value ($v_{xj}$), the contribution of an individual of age $x$ and stage $j$ to the future population, was calculated by the formula:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{m} s'_{iy} f_{iy}$$

The life table parameters for the two host treatments were estimated using the bootstrap technique with 100,000 resampled data for calculating the means and standard error of population parameters. The differences in population parameters, development duration and reproductive values among host plants were compared using the paired bootstrap test in the program of TWOSEX-MSChart ($P < 0.05$).

### *Population projection of* Spodoptera frugiperda

The life table data for *S. frugiperda* reared on maize and pea were used to project the population growth and its uncertainty to elucidate the predicted population size using the computer program TIMING-MSChart (Chi, 2022a). The population growth for 200 days was projected for an initial population of ten eggs. The results of the 100,000 bootstrap sampling of the intrinsic rate of increase ($r$) obtained in the previous section were sorted to find the 2.5th and 97.5th percentiles of the sorted bootstrap samples. We then utilised the bootstrap life table samples that generated the 2.5th and 97.5th percentiles of the intrinsic rate of increase ($r$) to project the population growth. The results indicate the confidence interval of the population.

## Results

### *Developmental biology, reproduction and life table of* Spodoptera frugiperda

*Spodoptera frugiperda* successfully completed its life cycle by feeding on pea leaves. The developmental duration of each larval instar, prepupal and pupal stage of *S. frugiperda* fed on pea leaves was significantly longer than that on maize leaves (table 1). The female longevity, male longevity and adult preoviposition period (APOP) were significantly higher on maize than on pea. The mean fecundity of *S. frugiperda* on maize (1265.58 eggs per female) and pea (710.84 eggs per female) was significantly different (table 2). The survival rate from egg stage to adult female and male was 33 and 20% on maize, and 19 and 14% on pea, with a sex ratio of 1.65:1 and 1.36:1, respectively (table 2; fig. 1).

The age-stage-specific survival rate ($s_{xj}$) of *S. frugiperda* is shown in fig. 1. Due to the variation in developmental rates

**Table 1.** Developmental biology of *Spodoptera frugiperda* on maize and pea

| Stage | *N* | Maize (day) | *N* | Pea (day) |
|---|---|---|---|---|
| Egg | 100 | 2.00 ± 0.00 | 100 | 2.00 ± 0.00 |
| 1st larval instar | 100 | $2.22 \pm 0.06^a$ | 100 | $2.90 \pm 0.08^b$ |
| 2nd larval instar | 83 | $1.92 \pm 0.07^a$ | 84 | $2.81 \pm 0.08^b$ |
| 3rd larval instar | 72 | $2.28 \pm 0.06^a$ | 70 | $2.97 \pm 0.09^b$ |
| 4th larval instar | 65 | $2.24 \pm 0.05^a$ | 59 | $2.94 \pm 0.09^b$ |
| 5th larval instar | 62 | $2.44 \pm 0.06^a$ | 50 | $3.91 \pm 0.11^b$ |
| 6th larval instar | 61 | $3.48 \pm 0.07^a$ | 45 | $4.69 \pm 0.07^b$ |
| Pre-pupa | 60 | $2.46 \pm 0.07^a$ | 42 | $3.36 \pm 0.08^b$ |
| Pupa | 57 | $9.17 \pm 0.28^a$ | 39 | $10.94 \pm 0.28^b$ |
| Pre-adult | 57 | $28.15 \pm 0.43^a$ | 39 | $36.43 \pm 0.28^b$ |
| Adult female longevity | 33 | $12.55 \pm 0.17^a$ | 19 | $9.79 \pm 0.19^b$ |
| Adult male longevity | 20 | $9.35 \pm 0.21^a$ | 14 | $7.29 \pm 0.22^b$ |
| Adult preoviposition period (APOP) | 33 | $3.58 \pm 0.16^a$ | 19 | $4.00 \pm 0.13^b$ |
| Total preoviposition period (TPOP) | 33 | $29.73 \pm 0.29^a$ | 19 | $39.32 \pm 0.31^b$ |
| Oviposition days | 33 | $5.06 \pm 0.27^a$ | 19 | $3.95 \pm 0.18^b$ |

Means in the row with different alphabetical superscript differ significantly by the paired bootstrap test ($P < 0.05$).

**Table 2.** Population growth parameters of *Spodoptera frugiperda* on maize and pea

| Parameter | Maize | Pea |
|---|---|---|
| Fecundity (eggs per female) | $1265.58 \pm 57.3^a$ | $710.84 \pm 31.36^b$ |
| Gross reproductive rate (*GRR*) (offspring per individual) | $799.48 \pm 93.52^a$ | $455.2 \pm 73.87^b$ |
| Net reproductive rate ($R_0$) (offspring per individual) | $417.64 \pm 62.38^a$ | $135.06 \pm 28.42^b$ |
| Intrinsic rate of increase ($r$) (offspring per individual per day) | $0.19 \pm 0.01^a$ | $0.12 \pm 0.01^b$ |
| Finite rate of increase ($\lambda$) (times per day) | $1.21 \pm 0.01^a$ | $1.13 \pm 0.01^b$ |
| Mean generation time ($T$) (days) | $32.14 \pm 0.29^a$ | $41.5 \pm 0.33^b$ |
| Doubling time ($DT$) (days) | $3.69 \pm 0.10^a$ | $5.86 \pm 0.28^b$ |
| Sex ratio (female:male) | 1.65:1 | 1.36:1 |

Means in the row with different alphabetical superscript differ significantly by the paired bootstrap test ($P < 0.05$).

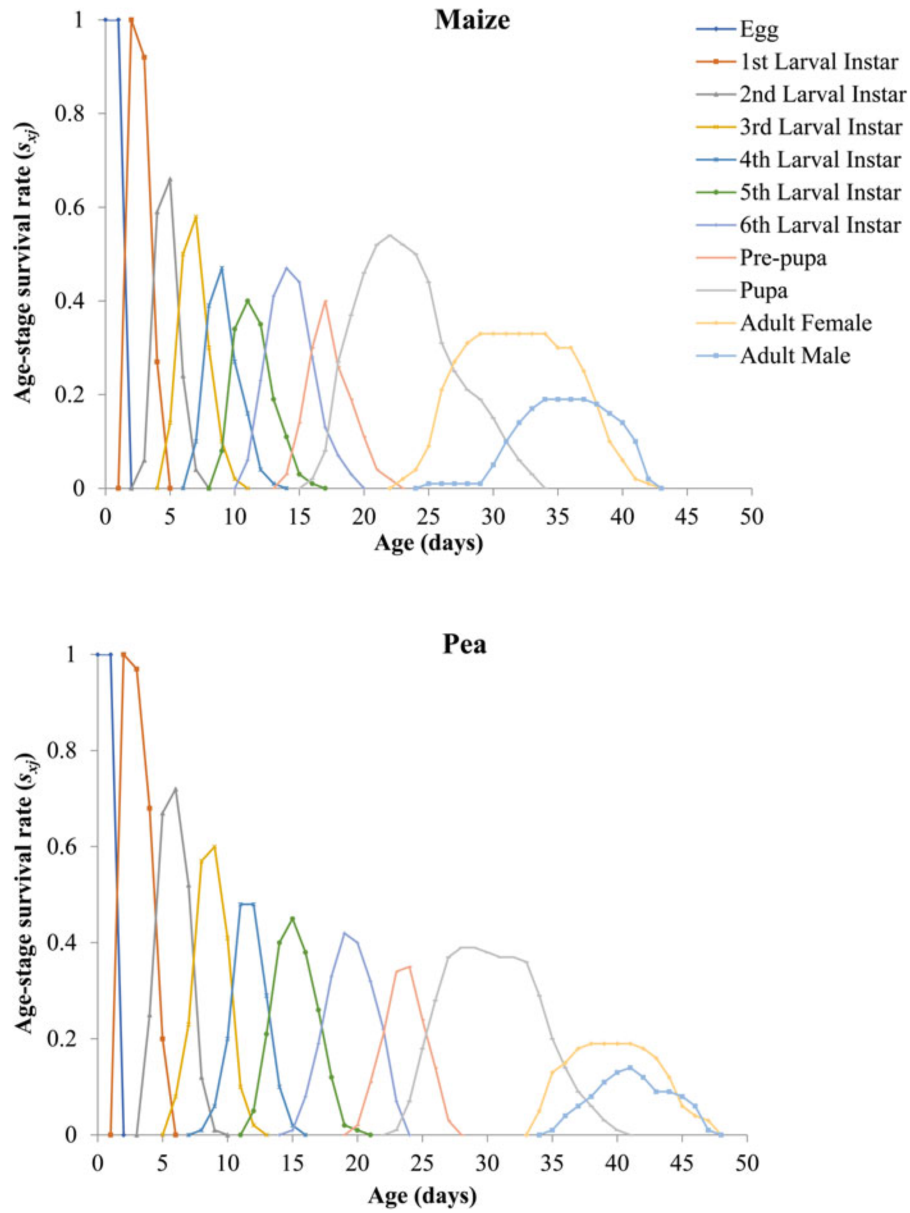


**Figure 1.** Age-stage-specific survival rate ($s_{xj}$) of the *Spodoptera frugiperda* reared on maize and pea.

among individuals as well as between sexes, there was overlapping between different stages. The survival rate of the sixth larval instar and pupa was much higher on maize (61 and 57%, respectively) than on pea (45 and 39%, respectively). The number of eggs laid by adult female at age $x$ is shown as $f_x$ in fig. 2. The $f_x$ of *S. frugiperda* fed on maize and pea increased initially before declining, and peaked on the 31st and 41st days, respectively. The curve of $l_x$ is a simplified version of the curves of $s_{xj}$. The $l_x$ curve of *S. frugiperda* fed on maize significantly decreased from 35th day, and its survival rate decreased to zero by 43rd day, whereas the age-specific survival rate of *S. frugiperda* fed on pea leaves dropped rapidly from 42nd day, and by 48th day, it had dropped to zero (fig. 2).

The age-stage-specific life expectancy ($e_{xj}$) explains the future expected life duration of an individual of age $x$ and stage $j$ (fig. 3). The life expectancies of newly laid eggs ($e_{01}$) were 25.01 and 23.04 days on maize and pea, respectively. The $e_{xj}$ of adult females fell from 15.70 on maize to 11.11 days on pea, while the maximum $e_{xj}$ of adult males, 15.74 days, was observed on maize, but decreased to 10.21 days on pea (fig. 3).

The reproductive value ($v_{xj}$) shows the contribution of an individual of age $x$ and stage $j$ to the future population (fig. 4). After the emergence of adult females of *S. frugiperda* at 23 and 34 days on maize and pea, the $v_{xj}$ jumped to 280.79 and 330.06 eggs, respectively, while the peak $v_{xj}$ occurred at 29 days (728.41 eggs) and 38 days (514.88 eggs) on maize and pea, respectively. The duration of $v_{xj}$ of female adults was 16 days on maize whereas it was 12 days on pea (fig. 4).

### *Population parameters of* Spodoptera frugiperda

The population growth parameters of *S. frugiperda* were significantly influenced by the host plant. The net reproductive rate ($R_0$) of FAW reared on maize (417.64 offspring per individual) was significantly higher than that of FAW reared on pea (135.06 offspring per individual). Feeding on maize achieved

https://doi.org/10.1017/S0007485324000312 Published online by Cambridge University Press

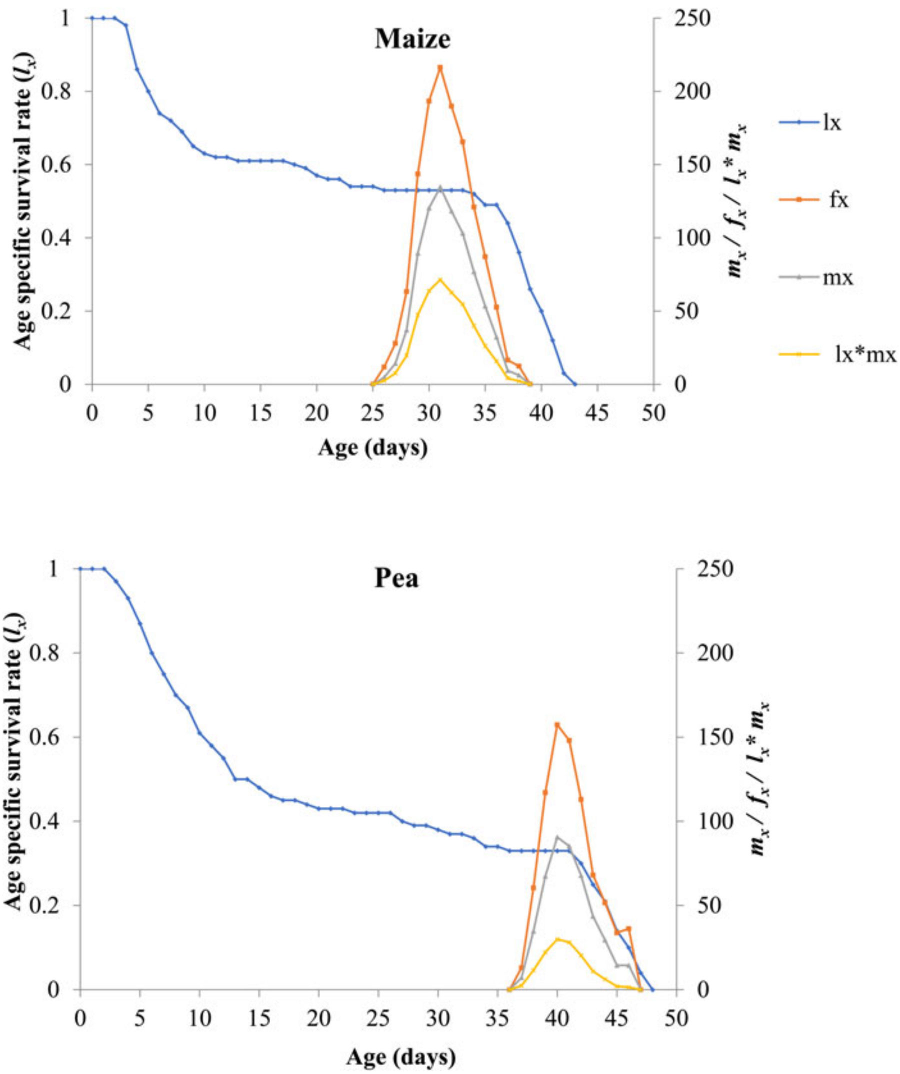


**Figure 2.** Age-specific survival rate ($l_x$), female age-specific fecundity ($f_x$), age-specific fecundity of the total population ($m_x$) and age-specific maternity ($l_xm_x$) of the *Spodoptera frugiperda* reared on maize and pea.

higher values of intrinsic rate of increase ($r$), finite rate of increase ($\lambda$) than feeding on pea (table 2). Since the $r$ and $\lambda$ values on both crops were greater than 0 and 1, respectively, it implies that *S. frugiperda* can successfully sustain its population both on maize and pea. The $\lambda$ values of the pea-fed populations and maize-fed populations of *S. frugiperda* indicate that the two populations grew continuously and geometrically at the rates of 1.13- and 1.21-fold per day, respectively. Contrarily, the mean generation time ($T$) of pea-fed populations (41.5 days) was 1.29 times that of maize-fed populations (31.14 days). The doubling time ($DT$) was significantly longer when FAW was fed on pea, while the gross reproductive rate ($GRR$) was significantly higher on maize (799.48 offspring per individual) than pea (455.2 offspring per individual) (table 2).

### *Population projection of* Spodoptera frugiperda

The population projection showed that *S. frugiperda* reared on maize would grow faster than on pea (fig. 5). In the simulation period of 200 days, the total population size on log scale was higher on maize (16.53), than on pea (9.96). Beginning with ten eggs, the population fed on maize was expected to go through six generations, while five generations on pea. As the age-stage, two-sex life table can express the stage differentiation; the development of each life stage can be noticed (fig. 6). Figure 7 describes the growth and dynamics of each life stage of *S. frugiperda* in a logarithmic scale. The positive rate demonstrates an increase of a stage from time $t$ to $t+1$, and the negative rate indicates a decrease in stage size. The intrinsic rate of increase ($r$) displays the multiplication potential of a population under ideal conditions when the population approaches stable age-stage distribution. The curves of the stage-specific growth rates of *S. frugiperda* raised on maize leaves approached the intrinsic rate of increase in 200 days. Alternatively, the population growths of *S. frugiperda* on maize and pea were highly uncertain; this could be attributed to variations in developmental speed and fertility among individuals. The variability of population growth was projected by using life tables from the 2.5th and 97.5th percentiles of the intrinsic rate of increase (fig. 5).

## Discussion

Nutrition has a major role in the development of insect herbivores, and the resources acquired during development translate to resource allocation among key life history traits throughout an individual's life (Nestel *et al.*, 2016). Larval-derived dietary

https://doi.org/10.1017/S0007485324000312 Published online by Cambridge University Press

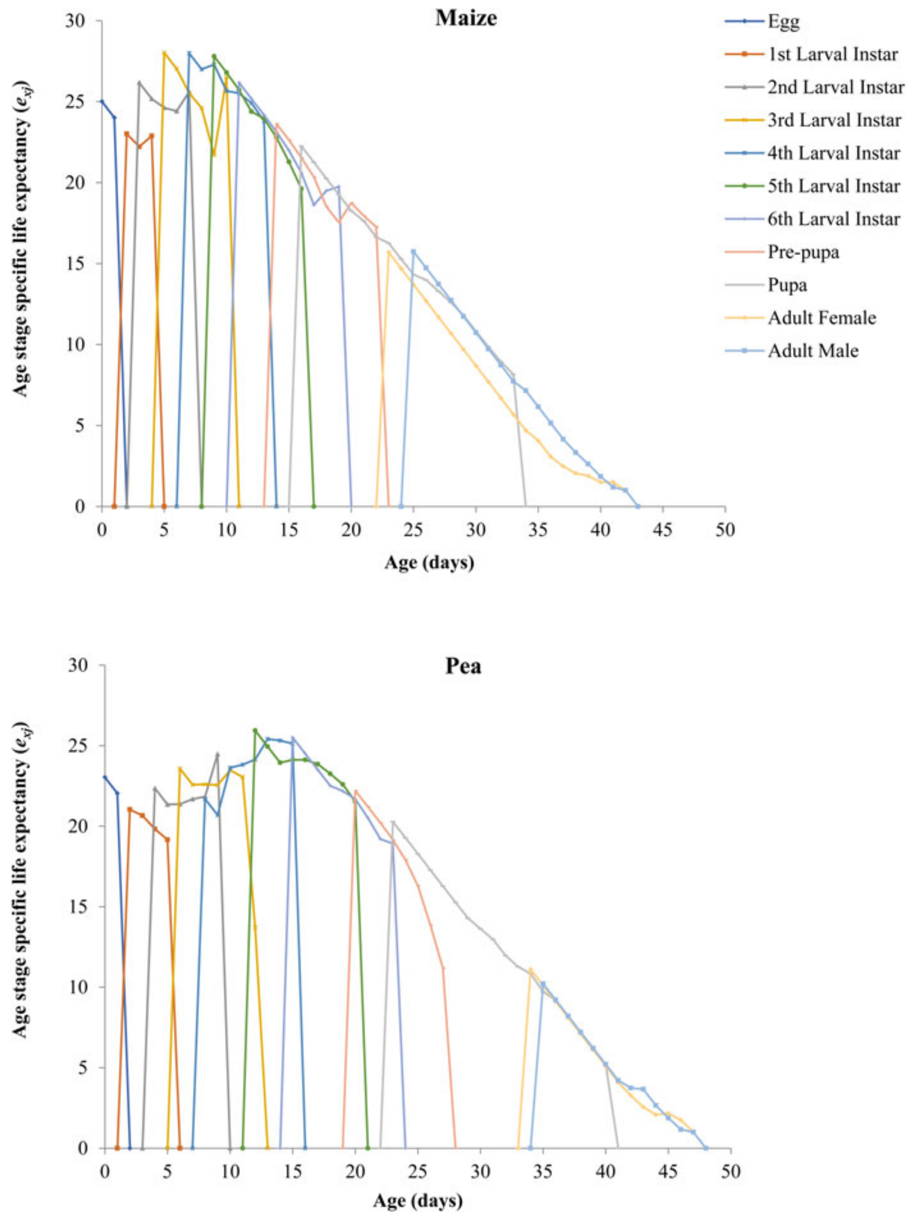


**Figure 3.** Age-stage-specific life expectancy ($e_{xj}$) of the *Spodoptera frugiperda* reared on maize and pea.

reserves are crucial in affecting insects' adult fitness (Salgado and Saastamoinen, 2019). Because of the diversified range of hosts, many pests including FAW are successfully flourishing not only during the crop development period but also over the off-season (Moraes *et al*., 2020). As FAW has been reported to damage a variety of plants, only certain plant species can support its complete development, e.g. maize, sorghum, sugarcane, potato, cotton etc. (Barros *et al*., 2010; Maruthadurai and Ramesh, 2020; Zhou *et al*., 2022) while other plant species may not support complete development of *S. frugiperda* but may still be utilised by larvae or adults for feeding and oviposition, e.g. cabbage, eggplant and Coix (Liu *et al*., 2019; Zou and Yang, 2019; Zhou *et al*., 2020). The results of the present study revealed that *S. frugiperda* can complete its life cycle on pea, suggesting that pea is an alternative host plant for this insect.

The longer developmental duration, higher survival rate, higher fecundity and other population growth parameters of FAW on maize observed in the present study suggest that maize is a highly susceptible host plant compared to pea. However, the biotic potential of *S. frugiperda* noted on pea in the present study corroborates with previous studies carried out on its favoured hosts. For instance, the larval duration of FAW reared on pea leaves (20.36 days) is similar to that reported when reared on sorghum (19.4 days), soybean (16.65 days), tomato (21.23 days) and cotton (22.81 days) (Wang *et al*., 2020; He *et al*., 2021; Li-hong *et al*., 2021). This varying offspring performance of FAW can be due to the differences in larval food utilisation efficiency. El-Shennawy *et al*. (2022) also recorded a low larval mortality, high growth rate and fast development time of FAW when reared on pea indicating that nutritional contents of pea are suitable for its growth and development. The female adult longevity of *S. frugiperda* in the present study is 9.79 days on pea which is comparable with that reported when raised on soybean (9.33 days) (Wang *et al*., 2020). Certainly, differences in the type of food ingested have a major impact on the development of herbivorous insect larvae and on the reproduction of adults even under

https://doi.org/10.1017/S0007485324000312 Published online by Cambridge University Press

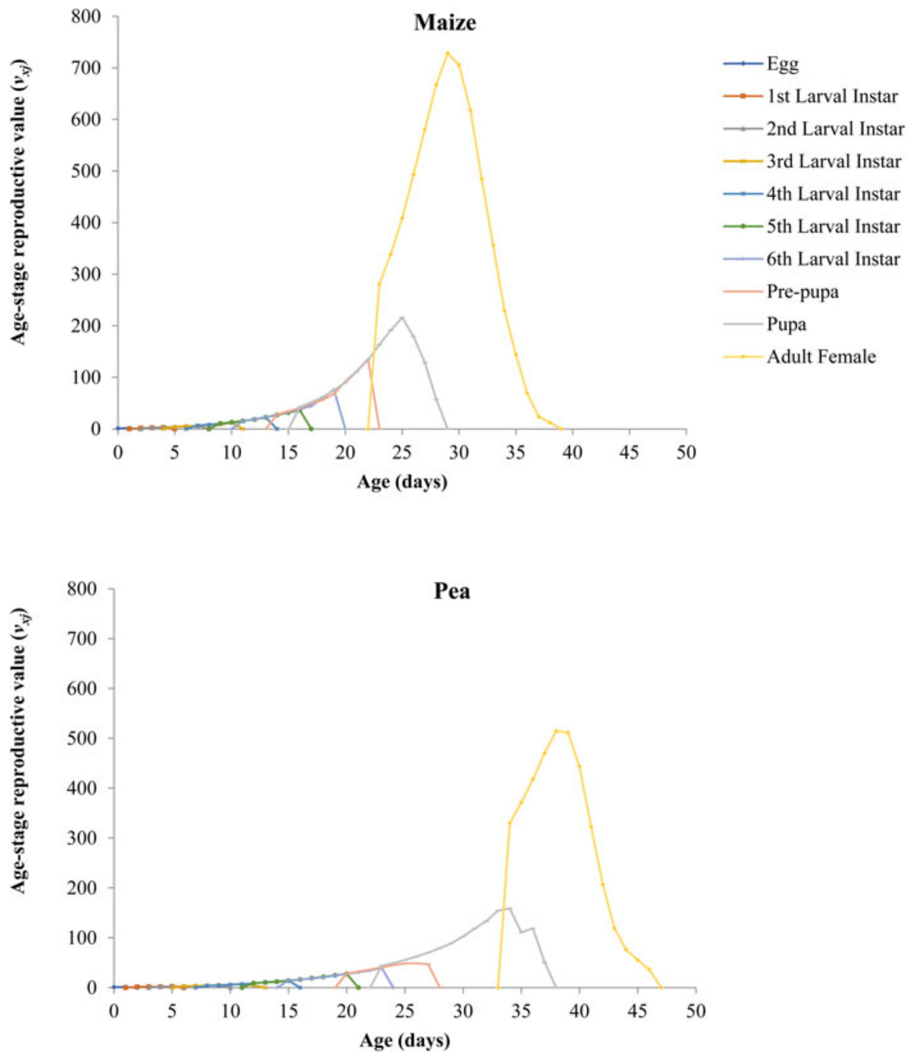


**Figure 4.** Age-stage-specific reproductive value ($v_{xj}$) of the *Spodoptera frugiperda* reared on maize and pea.

the similar conditions, which in turn governs the change trend of the entire insect population. When reared on pea leaves, FAW females started oviposition after 4 days of emergence and continued to oviposit for 3.95 days. However, Wang *et al.* (2020) reported an APOP of 2.89 days and 7.22 oviposition days when reared on maize. The fecundity of *S. frugiperda* reared

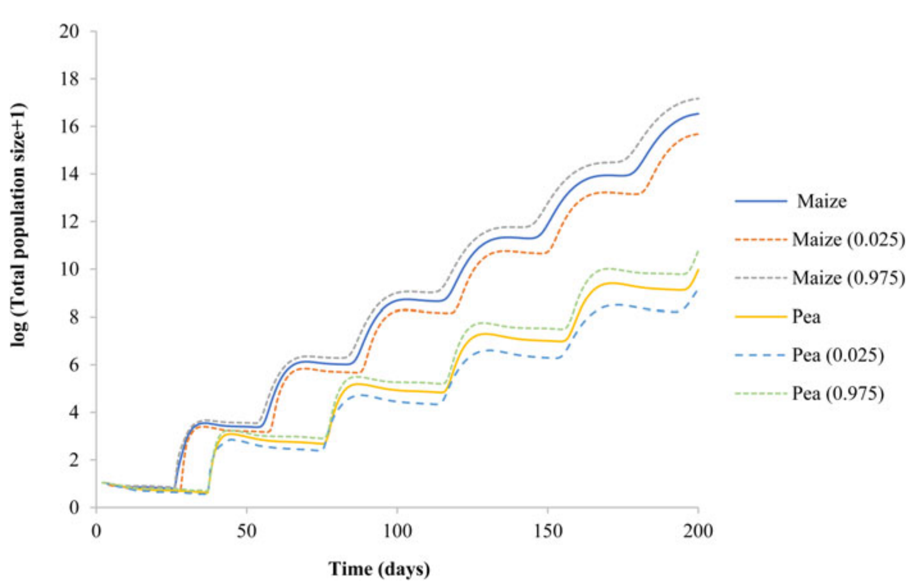


**Figure 5.** Total population size of the *Spodoptera frugiperda* projected by using life tables of 0.975 and 0.025 percentiles of intrinsic rate on increase (*r*) on maize and pea with an initial population of ten eggs.

https://doi.org/10.1017/S0007485324000312 Published online by Cambridge University Press

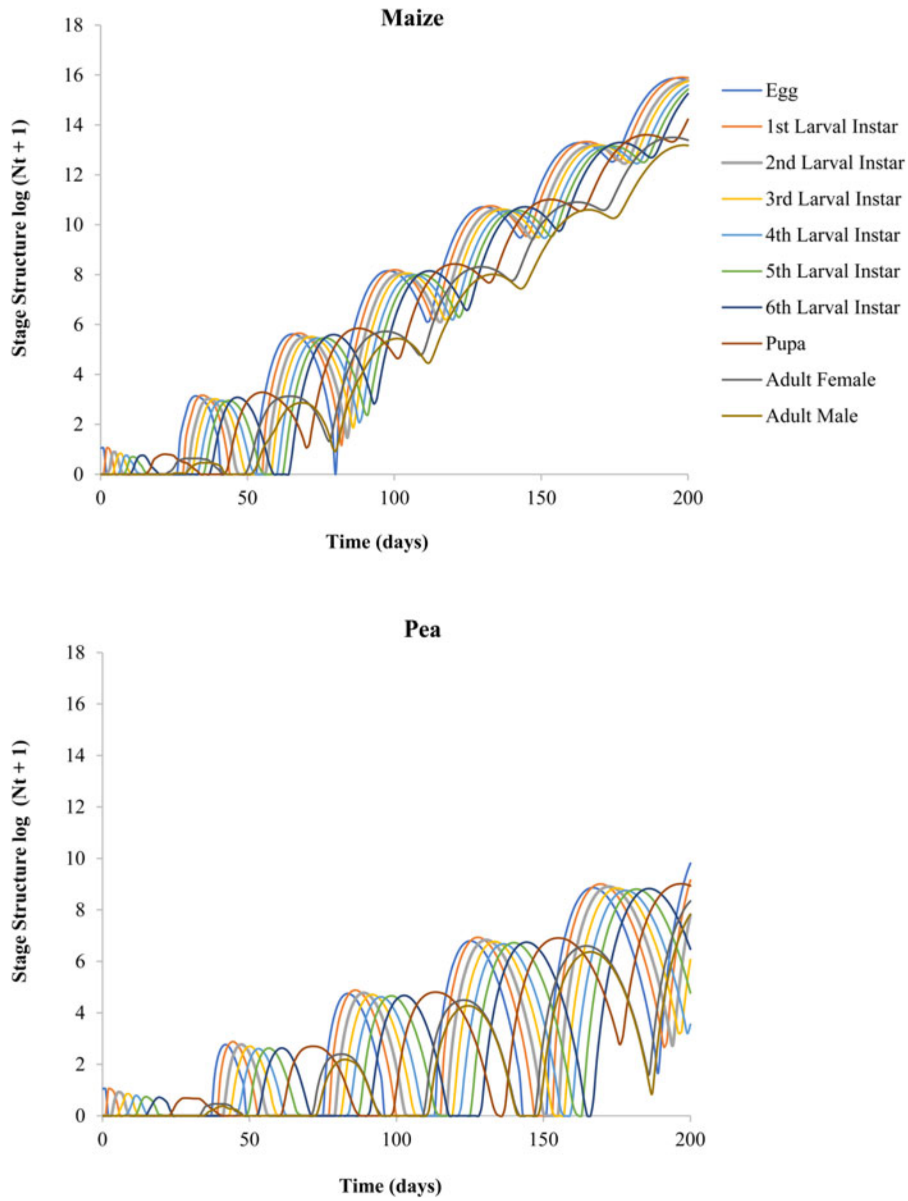


**Figure 6.** Population projection of *Spodoptera frugiperda* reared on maize and pea with an initial population of ten eggs.

on pea in the present study was 710.84 eggs per female which is in accordance with that reported when fed with maize leaves (955.62 eggs per female), rice leaves (590.77 eggs per female) (Acharya *et al*., 2022) and cotton leaves (803.51 eggs per female) (Wang *et al*., 2020). Similarly, El-Shennawy *et al*. (2022) reported a fecundity of 880.67 eggs per female when reared on pea. The population growth parameters of *S. frugiperda* recorded in pea are similar to the previous studies, on its preferred hosts. The net reproductive rate of FAW on maize was recorded to be 134.43 offspring per individual (He *et al*., 2021), 114.59 offspring per individual, 172.23 offspring per individual at 20 and 25°C, respectively (Chen *et al*., 2022), which are in line with the present study (135.06 offspring per individual). The $r$ and $\lambda$ of the FAW in the current study were greater than 0 and 1, respectively, which indicates that pea could also be a potential host crop for this pest.

Population projections drawn on the basis of life table rates display the stage structure and damage potential of a pest population. As intercropping maize with legumes including pea is a common practice, when egg masses are laid by *S. frugiperda* on maize, their offspring can transfer to adjacent legume fields. Although the early larval development of FAW occurs on maize, later instars are capable of moving to legume fields after attacking maize. Furthermore, the damage to peas in a maize/pea intercropping system may be more severe than that in single cropping systems of peas, as per the observations of damage in a sugarcane–maize intercropping system (Tai *et al*., 2019). Davidson-Lowe *et al*. (2021) studied the performance and behaviour of FAW larvae on maize grown after different cover crops including pea. FAW larvae oriented more frequently towards maize plants grown in soil after radish and pea cover crops and had 90.4% higher weight when fed on maize grown after pea than triticale. Additionally, the emission of volatile organic compounds and total soil inorganic nitrogen was highest in maize plants grown after pea; resulting in attraction of FAW larvae to maize plants grown after pea. Various other studies have also shown the positive correlation between nitrogen availability and volatile terpene emissions leading to increased herbivore attractiveness to plants grown under

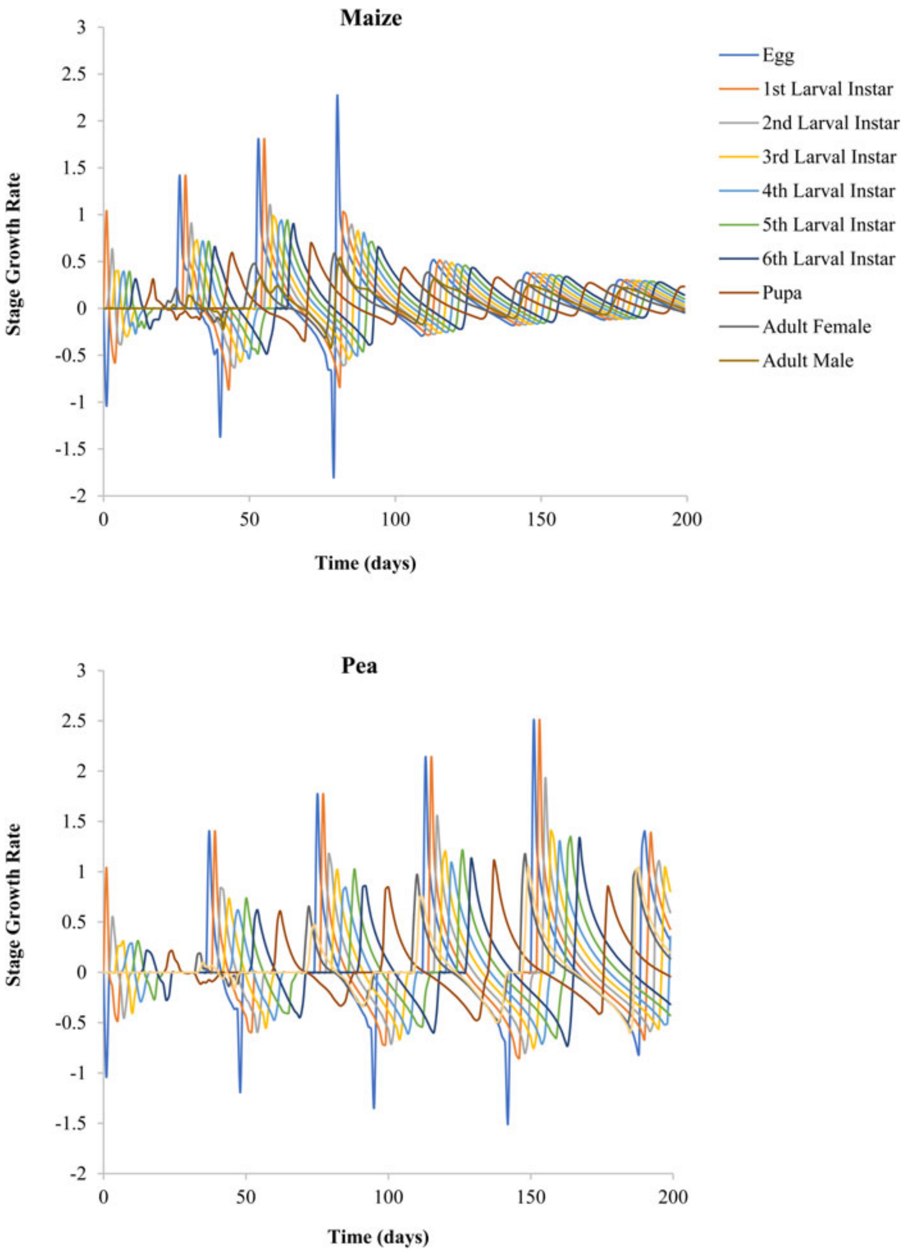


**Figure 7.** Stage growth rate of *Spodoptera frugiperda* reared on maize and pea with an initial population of ten eggs.

increased nitrogen availability (Ormeño *et al.*, 2011; Ormeño and Fernandez, 2012).

In India, *Rabi* maize has emerged as an important crop in the non-traditional areas widely planted in October–November, and pea is also planted in October–December as sole or inter-crop, resulting in an overlap of these crops. Moreover, many other suitable host plants, e.g. soybean, sorghum, rice, vegetable crops, etc., are commonly grown in India all year round. The presence of these alternate hosts could be the reason for *S. frugiperda* outbreaks occurring annually in maize fields. Assessing the impact of different host plant species on the bio-ecology of insect pests is critical for their management. The high population growth potential of *S. frugiperda* on pea observed in this study showed the suitability of this pest in sustaining FAW population. As shown in the present study, life table studies provide the most extensive understanding of the stage differentiation, reproduction and survival of pest populations. These findings provide a strong scientific foundation for formulating an effective and timely integrated pest management programme for managing *S. frugiperda*.

**Data availability.** The datasets created during and/or examined during the current study are available from the corresponding author on reasonable request.

**Author contributions.** Shubham Sharma: writing, investigation and methodology; Prem Lal Sharma: supervision and editing; Prajjval Sharma: investigation, writing – review and data analysis; Subhash Chander Verma: supervision and editing; Nidhi Sharma: supervision and formal analysis; Priyanka Sharma: formal analysis. All authors have read and approved the final manuscript.

**Financial support.** Not applicable.

**Competing interests.** The authors declare that they have no conflict of interest.

**Ethics approval and consent to participate.** This research did not involve any human participants and/or animals, other than the *Spodoptera frugiperda*.

## References


**Acharya R, Malekera MJ, Dhungana SK, Sharma SR and Lee KY** (2022) Impact of rice and potato host plants is higher on the reproduction than growth of corn strain fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Insects* **13**, 256.

**Aulakh G** (2020) Studies on intercropping of maize (*Zea mays* L.) with pea (*Pisum sativum* L.) genotype. *Indian Journal of Ecology* **46**, 354–357.

**Barros EM, Torres JB, Ruberson JR and Oliveira MD** (2010) Development of *Spodoptera frugiperda* on different hosts and damage to reproductive structures in cotton. *Entomologia Experimentalis et Applicata* **137**, 237–245.

**Casmuz A, Juarez ML, Socias MG, Murua MG, Prieto S, Medina S and Gastaminza WE** (2010) Revision de loshospederos del gusanocogollero del maiz, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Revista de La Sociedad Entomologica Argentina* **69**, 209–231.

**Chen Y, Guo J, Gao Z, He K, Bai S, Zhang T and Wang Z** (2020) Performance of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) fed on six host plants: potential risks to mid-high latitude crops in China. *Journal of Agricultural Science* **12**, 16.

**Chen YC, Chen DF, Yang MF and Liu JF** (2022) The effect of temperatures and hosts on the life cycle of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Insects* **13**, 211.

**Chi H** (2022a) *Timing-MS Chart: Computer Program for Population Projection Based on Age-Stage, Two-Sex Life Table*. Taichung, Taiwan: National Chung Hsing University, http://140.120.197.173/Ecology/ Accessed 20 October 2023.

**Chi H** (2022b) *TWOSEX-MS Chart: A Computer Program for the Age-Stage, Two-Sex Life Table Analysis*. Taichung, Taiwan: National Chung Hsing University, http://140.120.197.173/Ecology/Download/ Twosex-MSChart.zip Accessed 20 October 2023.

**Davidson-Lowe E, Ray S, Murrell E, Kaye J and Ali JG** (2021) Cover crop soil legacies alter phytochemistry and resistance to fall armyworm (Lepidoptera: Noctuidae) in maize. *Environmental Entomology* **50**, 958–967.

**El-Shennawy RM, Sabra IM and Kandil MAA** (2022) Biology and growth index of fall army armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reared on different host plants. *Asian Journal of Advances in Research* **5**, 904–912.

**Goergen G, Kumar PL, Sankung SB, Togola A and Tamo M** (2016) First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in west and central Africa. *PLoS ONE* **11**, e0165632.

**He LM, Wang TL, Chen YC, Ge SS, Wyckhuys KAG and Wu KM** (2021) Larval diet affects development and reproduction of East Asian strain of the fall armyworm, *Spodoptera frugiperda*. *Journal of Integrative Agriculture* **20**, 736–744.

**Huang H-W, Chi H and Smith CL** (2017) Linking demography and consumption of *Henosepilachna vigintioctopunctata* (Coleoptera: Coccinellidae) fed on *Solanum photeinocarpum* (Solanales: Solanaceae): with a new method to project the uncertainty of population growth and consumption. *Journal of Economic Entomology* **111**, 1–9.

**Li-Hong W, Cao Z, Gui-Yun L, Xi-Bin Y, Zhi-Yan W, Hong L and Chao-Xing Y** (2021) Fitness of fall armyworm, *Spodoptera frugiperda* to three solanaceous vegetables. *Journal of Integrative Agriculture* **20**, 755–763.

**Liu YQ, Wang XQ and Zhong YW** (2019) Fall armyworm *Spodoptera frugiperda* feeding on cabbage in Zhejiang. *Plant Protection* **45**, 90–91.

**Maruthadurai R and Ramesh R** (2020) Occurrence, damage pattern and biology of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) on fodder crops and green amaranth in Goa, India. *Phytoparasitica* **48**, 15–23.

**Montezano DG, Specht A and Bbarros NM** (2014) Immature stages of the armyworm, *Spodoptera eridania*: developmental parameters and host plants. *Journal of Insect Science* **238**, 1–11.

**Montezano DG, Specht A, Sosa-Gomez DR, Roque-Specht VF, Sousa-Silva JC, Paula-Moraes SV, Peterson JA and Hunt J** (2018) Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. *African Entomology* **26**, 286–300.

**Moraes T, Ferreira Da Silva A, Leite N, Karam D and Mendes S** (2020) Survival and development of Fall Armyworm (Lepidoptera: Noctuidae) in weeds during the off-season. *Florida Entomologist* **103**, 288–292.

**Nestel D, Papadopoulos NT, Pascacio-Villafan C, Righini N, Altuzar-Molina AR and Aluja M** (2016) Resource allocation and compensation during development in holometabolous insects. *Journal of Insect Physiology* **95**, 78–88.

**Ormeño E and Fernandez C** (2012) Effect of soil nutrient on production and diversity of volatile terpenoids from plants. *Current Bioactive Compounds* **8**, 71–79.

**Ormeño E, Goldstein A and Niinemets Ü** (2011) Extracting and trapping biogenic volatile organic compounds stored in plant species. Trends in Analytical Chemistry: TRAC **30**, 978–989.

**Qi XW, Hong L, Chen J and Liang YY** (2024) Fitness and cold tolerance of *Spodoptera frugiperda* fed on corn and two winter crops. *Journal of Applied Entomology* **148**, 49–56.

**Rwomushana I** (2019) *Spodoptera frugiperda* (fall armyworm). Invasive Species Compendium, CABI. https://doi.org/10.1079/ISC.29810.20203373913

**Salgado AL and Saastamoinen M** (2019) Developmental stage-dependent response and preference for host plant quality in an insect herbivore. *Animal Behaviour* **150**, 27–38.

**Sangomla A and Kukreti I** (2023) Fall armyworm attack: the damage done. Available at https://www.downtoearth.org.in/coverage/agriculture/fall-armyworm-attack-the-damage-done-63445

**Sharanabasappa, Kalleshwaraswamy CM, Asokan R, Mahadeva, Swamv HMM, Maruthi MS, Pavithra HB, Hegde K, Navi S, Prabhu ST and Goergen G** (2018) First report of the fall armyworm, *Spodoptera frugiperda* (J E Smith) (Lepidoptera: Noctuidae), an alien invasive pest on maize in India. *Pest Management in Horticultural Ecosystems* **24**, 23–29.

**Specht A and Roque-Specht VF** (2016) Immature stages of *Spodoptera cosmioides* (Lepidoptera: Noctuidae): developmental parameters and host plants. *Zoologia* **33**, e20160053. https://doi.org/10.1590/s1984-4689zool-20160053

**Tai HK, Guo JF, Yang SC, Zhang F, Liu J, Yang YQ, Song M, Xia YG, He K, Lin QX and Wang ZY** (2019) Biological characteristics and damage symptoms of fall armyworm, *Spodoptera frugiperda*, on sugarcane in Dehong preference of Yunnan Province. *Plant Protection* **45**, 75–79.

**Tietz HM** (1972) An index to the described life histories, early stages and hosts of the macro Lepidoptera of the continental United States and Canada. *Journal of the New York Entomological Society* **81**, 120–121.

**Vatanparast M and Park Y** (2022) Cold tolerance strategies of the fall armyworm, *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae). *Scientific Reports* **12**, 4129.

**Wang W, He P, Zhang Y, Liu T, Jing X and Zhang S** (2020) The population growth of *Spodoptera frugiperda* on six cash crop species and implications for its occurrence and damage potential in China. *Insects* **11**, 639. https://doi.org/10.3390/insects11090639

**Wu F, Zhang L, Liu Y, Cheng Y, Su J, Sappington TW and Jiang X** (2022) Population development, fecundity, and flight of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reared on three green manure crops: implications for an ecologically based pest management approach in China. *Journal of Economic Entomology* **115**, 124–132.

**Zhang DD, Zhao S, Wu QL, Li Y and Wu KM** (2021) Cold hardiness of the invasive fall armyworm, *Spodoptera frugiperda* in China. *Journal of Integrative Agriculture* **20**, 764–771.

**Zhou SC, Li SB, Su RR, Wang XY, Zheng XL and Lu W** (2020) Preliminary report on the damage of *Spodoptera frugiperda* on *Maranta arundinacea* in Guangxi. *Plant Protection* **46**, 209–211.

**Zhou S, Qin Y, Wang X, Zheng X and Lu W** (2022) Fitness of the fall armyworm *Spodoptera frugiperda* to a new host plant, banana (*Musa nana* Lour.). *Chemical and Biological Technologies in Agriculture* **9**, 78. https://doi.org/10.1186/s40538-022-00341-z

**Zou CH and Yang JJ** (2019) *Spodoptera frugiperda* harms Coix. *China Plant Protection* **39**, 47.