Biologia (2026) 81:69
https://doi.org/10.1007/s11756-026-02140-5

ORIGINAL ARTICLE

# Simulation of the temperature-dependent developmental response of the invasive fall armyworm *Spodoptera frugiperda* via phenology modeling

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Received: 1 February 2024 / Accepted: 14 January 2026 / Published online: 17 February 2026


## Abstract

The fall armyworm (FAW), *Spodoptera frugiperda*, is a highly destructive and invasive polyphagous pest that originated in tropical America and has rapidly spread to several regions across the globe. In this study FAW rearing experiments were conducted under five constant-temperature conditions (15 – 35 °C) to construct a temperature-based phenology model. Non-linear mathematical equations of biological significance were applied to describe temperature-dependent life processes, and the precision and reliability of the model were validated using stochastic simulations along with real-time daily temperature data from different regions of India. The lower developmental thresholds for egg, larva, and pupa were estimated at 11.25 °C, 13.89 °C, and 12.06 °C, respectively, while their degree-day requirements were 64.5, 208.3, and 101.8. Application of the Sharpe–De Michele model revealed the upper developmental thresholds as 41.2 °C (egg), 44.6 °C (larva), and 34.7 °C (pupa), derived from temperature-dependent development rates. Stochastic modeling of life table parameters indicated that FAW development, survival, and reproduction are most favorable at 25 – 32 °C. These findings are critical for understanding FAW seasonal dynamics, particularly moth emergence, oviposition, egg hatching, and larval activity. The developed phenology model provides valuable insights for pest management by predicting key developmental events and can guide the timing of monitoring efforts using pheromone traps, the release of biocontrol agents, and the judicious application of insecticides. This approach strengthens integrated pest management strategies and supports sustainable control of FAW under diverse agro-climatic conditions.

**Keywords** FAW · Temperature · Thermal units · Lower and upper thresholds · Life table parameters · Phenology model

## Introduction

The fall armyworm (FAW), scientifically known as *Spodoptera frugiperda* (J.E. Smith, 1797), is an invasive alien pest that poses a substantial threat to global food security, predominantly for crops such as maize (*Zea mays*). FAW is a highly adaptable and polyphagous insect that originated in America but has spread to various regions around the world. This insatiable pest has caused widespread harm to over 350 plant species across 76 distinct families, including numerous economically important crops such as sorghum (*Sorghum bicolor*), rice (*Oryza sativa*), and various millet varieties. Additionally, FAW has a wide-ranging appetite because it affects various weed species (Montzeno et al. 2018; Jaba et al. 2020a, 2021).

The fall armyworm (FAW) is known for its migratory and sporadic nature, with adult moths capable of nighttime flights covering distances exceeding 100 km (Johnson 1987). According to Fonseca et al. (2019), FAW is a highly destructive, omnivorous pest that thrives in subtropical and tropical regions, exhibiting impressive adaptability to a diverse array of temperatures and geographical conditions. During the larval stages, both young and late-stage larvae exhibit a preference for feeding on the tender portions of whorl

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leaves. FAW neonates, in particular, engage in scraping and skeletonizing the leaves, leaving behind a distinct silvery, transparent membrane. As crops mature, larvae tend to favor feeding on corn cobs (Jaba et al. 2020a).

The fall armyworm (FAW) has a significant economic impact because of its aggressive encroachment into crucial agricultural regions, driven by its high reproductive rate, migratory ability, and ecological adaptability. FAW was initially identified in West and Central Africa in Early 2016 (Goergen et al. 2016), followed by incursions into India in mid-2018 (Sharan Basappa et al. 2018) and into China in Early 2019 (Yang et al. 2019). Presently, FAW has expanded its reach to more than 20 states across India (Naganna et al. 2020), wreaking havoc on various crops, including cotton, sorghum, rice, sugarcane, pearl millet, and maize (Suby et al. 2020).

CABI estimates suggest that if left unchecked, FAW could lead to maize production losses ranging from 4.1 to 17.7 million tonnes per year in 12 maize-producing countries, translating to an annual economic loss of US$ 1,088-4,661 million (CABI 2020). In India Farmers are using two rounds of insecticide sprays during the initial stages of the crop, and the cost of plant protection measures increased after its invasion to southern India in mid-2018 (Deshmukh et al. 2021). However, recent outbreaks of the fall armyworm have been reported in various northern Indian locations, including Jabalpur, Dhar, and Indore districts in Madhya Pradesh (Vishwakarma et al. 2020), Banswara and Dungarpur districts in southern Rajasthan (Babu et al. 2019), the Biswanath district in Assam (Sarma et al. 2022), the Palampur district in Himachal Pradesh (Sharma and Sharma 2020), and the Nainital district in Uttarakhand (Paschapur et al. 2021). These occurrences indicate the rapid geographical expansion of FAW into diverse habitats. The factors that influence the developmental response and population dynamics of this invasive pest must be recognized.

The prevalence of insect pests is subject to a multitude of environmental conditions, among which temperature is one of the most pivotal factors, driving phenotypic plasticity in ectotherms and exerting a profound influence on various aspects of insect life. Insects are ectothermic creatures, and their body temperature is contingent upon ambient conditions. Temperature represents a fundamental abiotic factor that significantly affects insect survival and reproductive rates and, consequently, plays a substantial role in shaping these pest's demographic characteristics (Gilbert and Raworth 1996). This knowledge is instrumental for comprehending population dynamics, developmental rates, and seasonal occurrences (Fand et al. 2014, 2015, 2021; Peddu et al. 2020).

Temperature fluctuations can exert both unmediated and incidental effects on FAW distribution, physiology and flying capabilities. These effects can be immediate or indirectly manifest through host plants and antagonistic species (Du Plessis et al. 2020). Understanding how temperature affects the growth, development, and regeneration of FAW is important to understand its possible distribution (Early et al. 2018), seasonal migration, and population changes in the context of expected global climate change. This knowledge is invaluable for implementing targeted pest management strategies tailored to specific agroclimatic zones (Fand et al 2014, 2015, 2021). Insects have specific heat unit requirements quantified in degree days for advancing from one life stage to the next. Understanding the relationship between insect development and temperature is pivotal in predicting their seasonal presence and population dynamics. The ability of an insect to adapt and develop at variable temperatures is a vital for thriving in diverse climates, whether tropical, subtropical, or temperate. Many studies have been conducted in a laboratory setting at constant temperatures to better understand how temperature affects the biology of FAW development, and these studies resulted in reasonably accurate estimates of developmental rates and threshold temperatures via linear degree-day models.

The application of accumulated heat unit-based degree-day models has proven to be a significant tool for evaluating the phenology of both insects and crops, anticipating the timing of insect activity, and executing, early interventions for effective pest management. Previous temperature-dependent biological studies of FAW (Du Plessis 2020; Yan et al. 2022; Prasad et al. 2022) have focused primarily on the lower temperature threshold (LTT) while often neglecting the upper temperature threshold (UTT). However, for precise predictions of pest activity in response to temperature variations both LTT and UTT must be considered (Dhaliwal et al. 1991; Fand et al. 2021). The inclusion of UTT significantly enhances the prediction accuracy. A thorough understanding of an insect's thermal requirements is instrumental in assessing its current geographical range and forecasting its potential distribution (Cammell and Knight 1992; Macro et al. 1997). Earlier studies on FAW in India have focused primarily on various aspects, including its biology (Keerthi et al. 2021), insecticide resistance (Deshmukh et al. 2020; Yainna et al. 2021), species diversity, and seasonal incidence (Kumar et al. 2020; Reddy et al. 2020; Pradeep et al. 2022). Although Prasad et al. (2022) examined the response of FAW to constant temperatures in laboratory settings, they did not explore the changes in FAW population dynamics via real-time temperature data from different regions of India. A critical step in assessing the accuracy and applicability of the model is conducting a multilocation validation of the phenology model.

In light of the existing research gaps, our present study was designed to address the significant shortcomings in estimating both upper and lower developmental thresholds and simulating the population dynamics of FAW across various geographical locations. For the development and validation of our model, we used Insect Life Cycle modeling

software (Version 3.0) developed by the International Potato Centre in Lima, Peru (Tonnang et al. 2013). Researchers and practitioners can accurately predict critical life events in FAW, including egg hatching, larval development, and pupation, using temperature-dependent developmental response models (Dixon et al. 2009). This information can be invaluable in fine-tuning pest management strategies to align with the observed pest development. The insights generated by this study have the ability to inform the development of effective management strategies for FAW, particularly in the context of changing climate scenarios.

## Materials and methods

The experiment was conducted at the Insect Rearing and Bio-Assay Research Laboratory of the International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India. The laboratory is situated at 17.51° N latitude and 78.27° E longitude, with an altitude of 522 m. The experiment was conducted at five different constant temperatures:15, 20, 27, 32 and 35 °C for the temperature—dependent life table study. A biological incubator manufactured by Percival (USA) was used for this purpose. Throughout the experiment, the photo period was set at 14 h of light and 10 h of darkness (L:D), and the relative humidity was maintained at 70 ± 5%.

### Stock culture maintenance procedures

In 2018, fully grown fall armyworm (FAW) larvae were collected from maize (variety: TA5144) and sorghum (variety: Swarna) fields at an experimental farm located at the International Crops Research Institute for Semi-Arid Tropics (ICRISAT) in Hyderabad, India, in 2018. Artificial Diet Standardization: The biology of the pest was investigated using three different crop-based artificial diets to standardize artificial diets for FAW, as documented by Jaba et al. (2020a). Among these diets, the sorghum-based artificial diet resulted in the shortest life cycle duration and greater fecundity. Consequently, this sorghum-based diet was chosen for continued rearing of FAW, as presented in Sect. 2.1.1. This process ensured the maintenance and propagation of a stable FAW culture for research and experimentation.

### Preparation of the artificial diet

The artificial diet for rearing FAW larvae was prepared following the method described by Jaba et al. (2020a). The specific components used in the formulation of this artificial diet are detailed below (Table 1).

The ingredients of Fraction A were weighed, and the sorghum leaf powder was separately soaked in 1210 ml of hot water. The soaked sorghum leaf powder was mixed with the other ingredients in Fraction A for 3 min. The agar−agar mixture was boiled in 1210 ml of water. The agar−agar mixture was allowed to cool to 50 °C. Fractions A and B containing cooled agar−agar, were combined, formaldehyde was added, and the mixture was stirred for 3 min. The prepared diet was poured into sterilized plastic trays and allowed to solidify under laminar airflow. The rearing process involved the following steps: Neonates to 2nd instars were reared in plastic cups smeared with the artificial diet. Subsequently they were transferred to six-well trays, each containing 2.5 $cm^2$ pieces of the diet, and reared until pupation. Pupae were separated by sex (males and females) following the methods outlined by Sharanbasappa et al. (2018). Pupae were placed in custom-made pupal jars (13 × 11 cm) with perforated lids, and a suitable environment for pupation was created by placing vermiculite at the bottom. All emerging adults were obtained individually in small glass vials. Adult FAWs were paired in wooden oviposition cages measuring 30 × 30 × 30 cm, with each cage containing ten females and ten males. They were provided with a 10% sucrose solution as a food source for adults. Small pieces of blotting paper were hung inside the

**Table 1** Composition of artificial diet for *Spodoptera frugiperda*

| Diet composition | Quantity |
|---|---|
| Fraction – A | |
| Ascorbic acid | 7.5 g |
| Bavistin | 1.0 g |
| Chickpea flour | 265.0 g |
| Formaldehyde | 5.0 ml |
| Sorghum leaf powder | 75 g |
| Methyl p hydroxy benzoate | 6.0 g |
| Multivitamin capsules – Glaxo smith kline (GSK) | 2 capsules<br>Each capsule contains<br>Vit-A—5000 IU<br>Vit D—400 IU<br>Vit E- 15 mg<br>Vit B1- 5 mg<br>Vit B2- 5 mg<br>Vit B3- 45 mg<br>Vit B5- 5 mg<br>Vit B6- 2 mg<br>Vit B9- 1000 mcg<br>Vit B12- 5 mcg<br>Vit C- 75 mg |
| Sorbic acid | 3.9 g |
| Vitamin E – Evion | 5 capsules<br>Each capsule contains 400 mg of Vit E |
| Water | 1210.0 ml |
| Yeast | 68.0 g |
| Fraction – B | |
| Agar | 38.0 g |
| Water | 1210.0 ml |

cages to serve as oviposition substrates. Fresh egg masses were collected daily and used for the experiments. This technique allows for the controlled rearing of FAW, facilitating research and experimentation on this insect species.

## Data collection at constant temperatures

This study assessed the impact of five distinct constant temperatures on the growth, development, and life cycle of the fall armyworm (FAW), encompassing all stages from egg to adult. To ensure controlled conditions, all individuals were placed in temperature-controlled incubation chambers, specifically the Percival 1241VL model from Percival Scientific USA. The selected temperatures for testing were 15 °C, 20 °C, 27 °C, 32 °C, and 35 °C, each with five replications. The environmental conditions in the chambers were set to 70 ± 5% relative humidity and a photo period of 14 h of light and 12 h of darkness (L:D). The incubators were equipped with the necessary mechanisms to precisely control the temperature and humidity levels. The various FAW life stages were carefully assessed at each of the specified test temperatures. The methodology for evaluating these life stages is as follows:

Egg. Medium-sized egg masses containing, approximately 200–230 eggs collected from the FAW stock colony. Each egg mass was placed in a plastic container within the growth chambers at the specified test temperatures. Ten replicates were maintained for each test temperature. The egg hatchings at each test temperature were recorded daily.

Larval stage. Freshly emerged neonate FAWs from the stock colony were positioned in plastic cups coated with an artificial diet, and were raised until they reached the 2nd instar. The plants were subsequently transferred to six-well insect breeding dishes, with each cell having dimensions of 2 cm in depth and 3.5 cm in diameter. Each sample contained 7 ml of diet. A total of 200 larvae were placed in these breeding dishes for each test temperature and kept inside the incubators. Observations included recording the developmental time, larval mortality, and number of pupae. These records were retained daily for each replicate at different test temperatures.

Pupae. Newly developed pupae that were less than 24 h old were selected from the FAW stock colony. For each replication, a sample of 200 pupae was separated into four batches, with each batch comprising 50 pupae. These pupae were housed in a pupal container measuring 13 × 11 cm, featuring perforations on the upper lid. All the pupae were subjected to various test temperatures within the incubators. Daily records were maintained for the period of the pupal stage, and the number of adult moths that emerged at each test temperature was determined.

Adult stage. Thirty pairs of newly emerged adult FAWs, each less than 16 h old, were collected from the FAW stock colony. These adults were paired off and placed pairwise in small mating cages made of Mylar plastic (18 × 14 cm). The adult moths received nourishment with a 10% sucrose solution through absorbent cotton. Blotting paper served as the substrate for oviposition. The longevity of each male and female adult was recorded at the respective test temperatures. In cases where a male adult died prematurely, replacement male adults were introduced to ensure optimal mating and fertility. This detailed methodology allowed for comprehensive assessments of FAW development and life cycle characteristics under various temperature conditions.

## Model parametrization

### Estimation of immature development and adult senescence times

To describe the distribution of immature development times, three different distribution models, i.e., probit, logit, and cloglog, were fitted to the experimental data. On the basis of Akaike's information criterion (Akaike 1973), a well-known goodness-of-fit indicator and coefficient of determination ($R^2$), the log model provided the best fit to describe the variability in the developmental times of immature stages and senescence times of adult stages of FAW at various constant temperatures.

The mathematical expression of the C LogLog distribution function (Tonnang et al. 2013) is as given below.

$$F(x) = 1 - \exp(-\exp(ai + b\ \ln x)) \quad (1)$$

where F(x) is the probability of completing development at time x, lnx is the natural logarithm of the days observed, a is the intercept corresponding to temperature i, and b is the common slope of the regression model.

### Estimation of the developmental rates

The developmental rates of FAW immature life stages at different test temperatures were estimated by taking the inverse of the development times (1/d) of the respective life stages. Nonlinearity was observed in egg, larval, and pupal development at temperatures above 35 °C. As a result, these temperatures were eliminated to fit a linear model to the data on egg and larval development, and the data were fitted for the remaining temperatures. For the pupal development rate test temperatures ranging from 15 °C to 35 °C were used. The following formula for a linear regression model was fitted to estimate the temperature-dependent development rates. (Campbell et al. 1974).

$$r(T) = a + bT \tag{2}$$

where r (T) is the rate of development (days$^{-1}$) at temperature T °C, and 'a' and 'b' represent the intercepts and slopes of the equation, respectively.

Owing to the poor predictability of the linear model at high temperatures, the nonlinear Sharpe and Demichelle model (Sharpe and DeMichele 1977) to estimate the developmental rates of eggs, larvae, and pupae using the following mathematical equation:

$$r(T) = \frac{p \cdot \frac{T}{T_0} \cdot e^{\left[\frac{\Delta H_A}{R}\left(\frac{1}{T_0} - \frac{1}{T}\right)\right]}}{1 + e^{\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_L} - \frac{1}{T}\right)\right]} + e^{\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_H} - \frac{1}{T}\right)\right]}} \tag{3}$$

In the given equation, r (T) indicates the rate of development at temperature T (in Kelvin), R is the universal gas constant (1.987 cal degree-1 mol-1), and p denotes the rate of development at the optimal temperature. To calculate the temperature (in Kelvin) without considering any enzyme deactivation, we need to know the enthalpy of activation (ΔHa) for the reaction catalyzed by the enzyme (in calories per mole), the change in enthalpy at high temperature (ΔHh) (in calories per mole), and the high temperature (Th) at which the enzyme is half active.

## Temperature-dependent mortality for immature life stages and adult senescence

The mortality rate was estimated by subtracting the cumulative frequency of surviving individuals at each test temperature from 1. The relationship between temperature and mortality in the early life stages of FAW was assessed using the Wang model (Wang et al. 1982)

$$m(T) = 1 - \frac{H}{e^{\left(\left(1+e^{\left(\frac{T-T_{ppp}}{B_i}\right)}\right)\left(1+e^{\left(\frac{T_{pp}-T}{B_{ij}}\right)}\right)^*\right)}} \tag{4}$$

where m(T) represents the rate of mortality at temperature T (°C); $T_{opt}$ is the optimum temperature (°C) for cohort survival; and B and H represent the fitted parameters of the equation, respectively.

A simple exponential model was fitted to establish the associations between the senescence of both male and female FAW adults and test temperatures. The following mathematical expression of a simple exponential model was used.

$$r(T) = sy^* e^{b(T - T_b)} \tag{5}$$

where r (T) represents the development rate at temperature T (°C), e is the natural exponential, and b (T) and T b are the parameters to be estimated.

### Fecundity and age-specific oviposition

The oviposition was modeled via three temperature-dependent functions: temperature-dependent total fecundity, age-related oviposition frequency, and age-specific adult survival. Total fecundity refers to the cumulative number of eggs produced by each female of the fall armyworm (FAW) throughout her lifespan. The following formula for the Wang model was fitted to fecundity.

$$m(T) = 1 - \frac{H}{e^{\left(\left(1+e^{\left(\frac{T-T_{ppp}}{B_i}\right)}\right)\left(1+e^{\left(\frac{T_{pp}-T}{B_{ij}}\right)}\right)^*\right)}} \tag{6}$$

where m (T) is the total number of eggs laid by a female adult in the total life span at a given temperature T (°C); B and H are the model fitted parameters; and $T_{opt}$ is the temperature optimum at the maximum number of eggs laid by the cohort.

A gamma function was fitted to describe the age-specific fecundity rate of FAW females at different constant temperatures (Mack et al. 1987; Sporleder et al. 2004)

$$f(T) = \frac{1}{b^a * \mathrm{X}(a)} x^{a-1} e^{-\left(\frac{T}{b}\right)} \tag{7}$$

where f(T) is the cumulative oviposition frequency at temperature T; X is the normalized age of females expressed as a ratio of age in days and mean survival time; and a and b are the fitted equation parameters.

### Simulation of the lifetable parameters

The stochastic simulation tool in ILCYM software was used to estimate various life table parameters, viz., the gross reproductive rate (GRR), net reproductive rate (R0), mean generation time (T), intrinsic rate of natural increase (rm), finite rate of increase (l), and doubling time (Dt) of FAW. The cohort updating and rate summation approach (Curry et al. 1978) was used to perform the simulations. The projected life table parameters were derived based on the phenology model developed for FAW at five different constant temperatures ranging from 15 to 35 °C, with ten repetitions each. Random number generation between 0 and 1 was used to determine the sex of the emerging adults. The temperature and age of the ovipositing female did not significantly affect the proportion of females in the offspring. Hence, for the simulation of population growth rates, a constant female rate of 0.5 for the progeny was assumed when the life table parameters were estimated. The initial number of eggs was set to 100 for the simulations to start at each of the test temperatures.

(a) Net reproductive rate ($R_o$)

$$R_o = \frac{\text{Fecundity} \times \text{Immature survival}}{\text{Female rate in the progeny}} \tag{8}$$

(b) Generation length in days (T)

$$T = \left(\frac{1}{d1}\right) + \left(\frac{1}{d2}\right) + \left(\frac{1}{d3}\right) + \left(\frac{1}{d4}\right) + \left[\left(\frac{1}{sf}\right) \times \mathrm{TR}_{50}\%\right] \quad (9)$$

where d1, d2, and d3 represent the median development rates for immature life stages of FAW, especially for egg, larva and pupa, respectively; the variable sf represents the mean survival rate of the female; and TR 50% represents the age at which females reach 50% of their total oviposition.

(c) Intrinsic rate of increase

$$(\mathrm{r}_m) = \frac{\ln(\mathrm{R}_0)}{T} \quad (10)$$

(d) Finite rate of increase

$$(\lambda) = \exp(r_m) \quad (11)$$

(e) Doubling time

$$(\mathrm{Dt}) = \frac{\ln(2)}{\mathrm{r}_m} \quad (12)$$

## Modeling tools and statistical analysis

The model builder tool in Insect Life Cycle Modeling (ILCYM) software version 4.0 (International Potato Centre, Lima, Peru) was utilized for estimating the temperature-dependent development of FAW at constant temperatures ranging from 15 to 35 °C. The ILCYM is free and open-source software with three main components: model builder, validation and simulation, population analysis and risk mapping. The 'model builder' includes a number of linear and nonlinear models for calculating temperature-dependent life processes in insects. The investigation employed the model builder' component to estimate life functions that are dependent on temperature. The "validation and simulation" component was utilized to stimulate the life table parameters. Several mathematical linear and nonlinear equations were fitted to the data via the 'model builder' module to estimate the temperature-dependent distributions of development times, rates of development, survival, and reproduction. This study assessed the mean development period and cumulative frequency of survival for each life stage of FAW at different constant temperatures. The development rates of immature life stages were calculated at different test temperatures by calculating the inverse of the development times (1/d) of the corresponding life stages. The estimation of the best appropriate models for development time, development rate, mortality, longevity, and fecundity across several life stages was conducted via widely known signs of goodness of fit, such as the AIC (Akaike's information criterion), which was proposed by Akaike in 1973. The coefficient of determination ($R^2$), analysis of variance (ANOVA) and least significant difference (LSD) were used as postadhoc tests, and the significance was tested at the $p < 0.05$ level with probability thresholds and hypothesis testing (Fisher 1953).

### Model validation

Life table parameters were estimated at variable temperatures within the temperature range of 15 °C to 35 °C to validate the phenology model (Fand et al. 2014; Peddu et al. 2020). The simulation approach used in ILCYM software (Tonnang et al. 2013) requires daily minimum and maximum temperature data as inputs. The data for the period 2020–2022 collected from Automatic Weather Stations at five locations, viz., Mahabubnagar and Sangareddy (Telangana State), Nandyala (Andhra Pradesh State), and Kalburgi and Raichur (Karnataka State), were used in stochastic simulations at fluctuating temperatures. The diurnal temperature variability was accounted via a time step length of 15 min. For half-day temperature predictions, a cosine function was used, and the temperature-dependent life table parameters of FAW were calculated for each 15-min time step. The equation used for predicting the temperatures for the first half-day is given below (Kroschel et al. 2013).

$$\mathrm{Ti} = \frac{(\mathrm{Max} - \mathrm{Min})}{2} \times \cos\left(\frac{\times(\mathrm{i} - 0.5)}{48}\right) + \frac{(\mathrm{Min} + \mathrm{Max})}{2} \quad (13)$$

where Ti is the temperature (°C) of time step i (i = 1, 2, 3,…48) and Min and Max are the daily minimum and maximum temperatures, respectively.

Subsequently, the aforementioned approach was replicated to calculate temperatures for the latter half of the day by utilizing the minimum temperature of the following day in the equation. This process was then continued for the remaining duration. The life table parameters were simulated stochastically (Curry et al. 1978) and compared with the observed values obtained in constant-temperature experiments.

# Results

## Development times of immature and adult survival of FAW

The results of the duration of development indicated that FAW individuals were able to develop within the evaluated range of temperatures (15–35 °C). Slight distortion and dwindling of larval bodies were observed at 35 °C.

The duration of immature development and adult lifespan decreased with increasing temperature. The development time rapidly decreased at 35 °C (Table 2, Fig. 1). The observed mean development times for immature stages were lower at 15 °C (egg: 14 ± 0.15 days, larva: 53 ± 0.10 days, and pupa: 32 ± 0.19 days) and greater at 35 °C (egg: 3 ± 0.00 days, larva: 9 ± 0.14 days, and pupa: 8 ± 0.12 days). The mean senescence time of adults decreased linearly from low to high across the evaluated range of temperatures (15 °C female: 32 ± 0.11) male: 26 ± 0.12; 35 °C: female: 7 ± 0.06; male: 6 ± 0.07). The developmental periods of the FAW life stages observed at different test temperatures were in reasonably good agreement with those predicted by the model. The data were well represented by fitting the complementary log function, which captured the variations in the durations of immature stage development and the survival times of adult stage FAW (Table 3). The R2 values ranged from 0.94, with a slope of 39.35 ± 2.47 for the larval stage, to 0.99 for both the egg stage and the adult female stage, with slopes of 11.42 ± 0.70 and 41.70 ± 4.73, respectively.

## Immature development rate at different test temperatures

The linear model reasonably estimated the developmental rates for eggs, larvae, and pupae at temperatures of 15, 20, 27, 32, and 35 °C (ANOVA egg: df = 1,3; F = 117.5, R2 = 0.97, $p < 0.0017$; larva: df = 1,3: F = 15.80; $R^2 = 0.84$; $p < 0.028$; pupa: df = 1,3; F = 81.58, $R^2 = 0.96$, $p < 0.0029$) (Table 4). The three-parameter version of Sharpe and De-Michelle provided the best fit for temperature-dependent egg development (ANOVA: df = 6,8; F = 73.68; $R^2 = 0.98$; AIC = −5.84; $p < 0.001$). The larval development rate was fitted by a nine-parameter version of the Sharpe and De-Michelle model (ANOVA: df = 3,11; F = 113.7; $R^2 = 0.96$; AIC = −20.13; $p < 0.001$). Pupal development was fitted by the sixth parameter version of Sharpe and Demichelle (ANOVA: df = 4,10; F = 168.0; $R^2 = 0.98$; AIC = −21.19; $p < 0.001$). The linear increase in the rate of egg development decreased above 40 °C, indicating that there was no egg development above this temperature. The larval development was linear up to 44.65 °C, indicating a well-fitted curve, which declined sharply thereafter to reach the absicia stage. The graph fitted for pupal development was nonlinear, indicating that the pupal development rate increased with increasing temperature. The lower threshold temperatures (LTTs) for the development of FAW eggs, larvae, and pupae, taken as the ratios of intercepts and slopes (a/b) of the linear regression, were 11.25, 13.89 and 12.06, respectively. Similarly, the thermal constants expressed in degrees (DDs) and obtained by taking the inverse of the slopes of linear regression for the development of eggs, larvae and pupae were 64.51, 208.3, and 181.8, respectively. The upper thermal thresholds (UTTs) predicted for immature stages of FAW were 41.22 °C (egg), 44.65 °C (larva), and 34.69 °C for pupae. Similarly, the optimum temperatures ($T_0$) predicted by the model for immature development rates were 27 °C for eggs, 32.7 °C for larvae, and 25 °C for pupae (Table 5, Fig. 2).

## Temperature-dependent survival of immature stages

Egg survival was lowest at 27 °C (39.3%) and highest at 35 °C (79.0%). Larval and pupal survival rates were lower at 27 °C (53.25%) and higher at 35 °C (66%). The highest mortality rates were observed in both the larval (79.0%) and pupal (87.0%) stages were observed at 35 °C. Test temperatures below 20 °C and above 32 °C resulted in the highest mortality among the immature stages, whereas

**Table 2** Mean developmental time of immatures stages of *Spodoptera frugiperda* at different constant temperatures

| Temperature °C | Development time (days) ± SE | | | | | | Senescence (days) ± SE | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Egg | | Larva | | Pupa | | Female | | Male | |
| | Observed | Predicted | Observed | Predicted | Observed | Predicted | Observed | Predicted | Observed | Predicted |
| 15 | 14 (0.15) | 13.12 (0.11) | 53 (0.10) | 52.02 (0.09) | 32 (0.19) | 31.48 (0.11) | 32 (0.11) | 31.66 (0.08) | 26 (0.12) | 25.65 (0.09) |
| 20 | 8 (0.10) | 7.75 (0.07) | 46 (0.15) | 45.67 (0.11) | 25 (0.28) | 24.94 (0.11) | 28 (0.15) | 27.31 (0.08) | 21 (0.11) | 20.66 (0.08) |
| 27 | 5 (0.07) | 4.57 (0.05) | 22 (0.09) | 21.16 (0.06) | 12 (0.09) | 11.62 (0.06) | 12 (0.07) | 11.03 (0.05) | 11 (0.10) | 10.58 (0.05) |
| 32 | 4 (0.05) | 3.16 (0.04) | 14 (0.10) | 13.64 (0.04) | 10 (0.07) | 9.06 (0.05) | 11 (0.07) | 10.09 (0.04) | 10 (0.11) | 9.76 (0.05) |
| 35 | 3 (0.00) | 2.54 (0.00) | 9 (0.14) | 8.05 (0.05) | 8 (0.12) | 7.05 (0.05) | 7 (0.06) | 6.8 (0.04) | 6 (0.07) | 5.05 (0.04) |

Numbers in parenthesis are standard errors

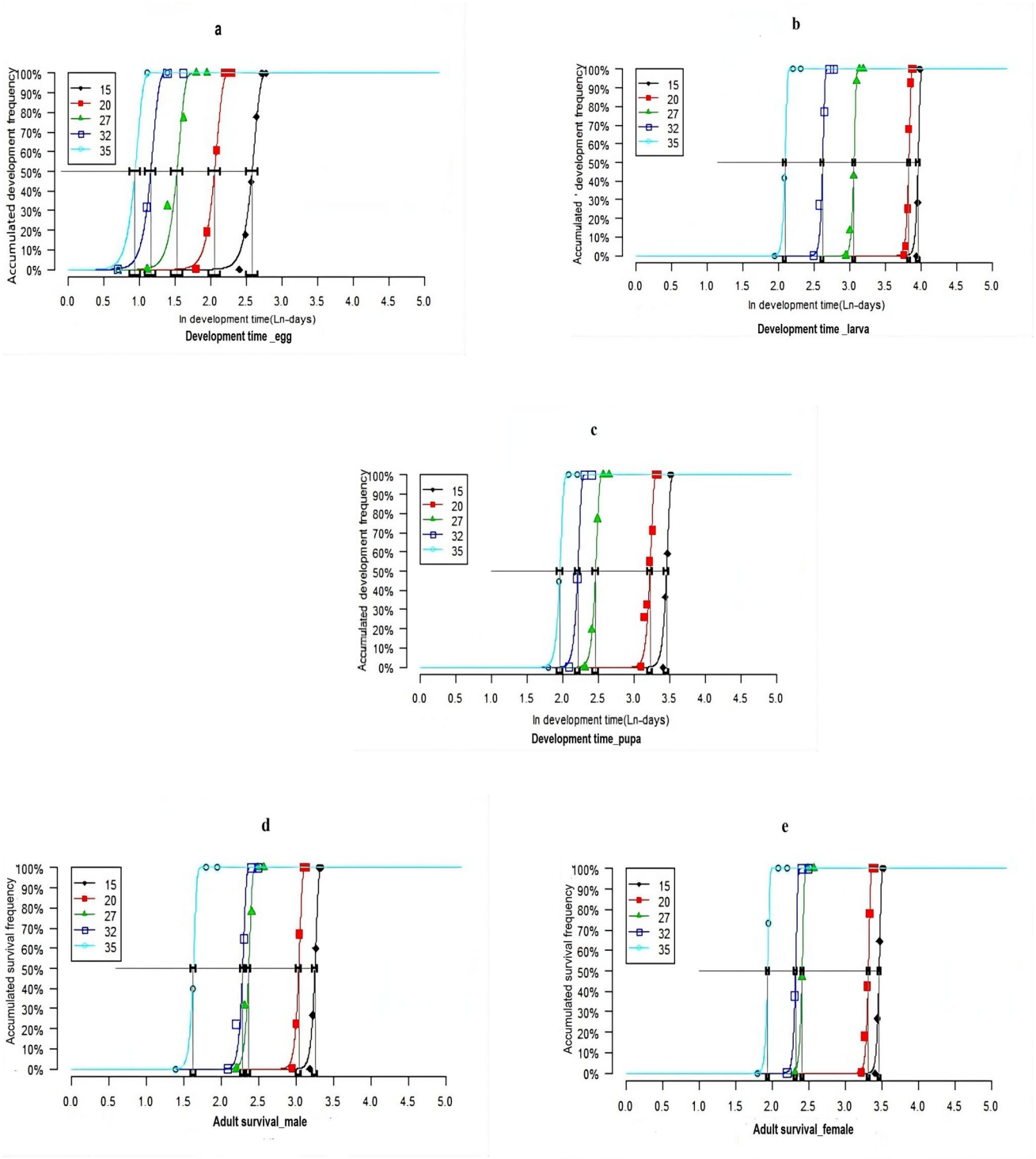


**Fig. 1** Temperature-dependent development time for different stages of *Spodoptera frugiperda* at various constant temperatures; Fitted model Clog log for all the stages: egg (**a**), larva (**b**), pupa (**c**), male (**d**), female (**e**)

**Table 3** Estimated parameters of cumulative distribution function fitted to normalized development time frequencies for immature stages and survival time for adult survival stages of *Spodoptera frugiperda*, senescence (fitted function: clog log for all stages)

| Life stages | Intercepts "a" for temperature ($^0$C) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 15 | 20 | 27 | 32 | 35 | Slope (b) | AIC | $R^2$ |
| Egg | −29.77 (1.83) | −23.76 (1.46) | −17.73 (1.10) | −13.53 (0.79) | −11.01 (0.84) | 11.42 (0.70) | 92.36 | 0.99 |
| Larva | −155.89 (9.80) | −150.67 (9.47) | −120.48 (7.57) | −120.48 (7.57) | −82.46 (5.15) | 39.35 (2.47) | 113.97 | 0.94 |
| Pupa | −85.56 (6.69) | −79.82 (6.23) | −60.96 (4.75) | −54.80 (4.21) | −48.62 (3.76) | 24.70 (1.93) | 85.74 | 0.97 |
| Male | −87.55 (6.08) | −81.73 (5.67) | −63.77 (4.44) | −61.60 (4.27) | −43.92 (3.01) | 26.8 (1.86) | 97.60 | 0.97 |
| Female | −144.45 (12.04) | −138.30 (11.52) | −100.48 (8.33) | −96.78 (8.0) | −80.87 (6.7) | 41.70 (4.73) | 63.53 | 0.99 |

Numbers in parenthesis are standard errors

**Table 4** Development rate fitted for all the immature stages of *Spodoptera frugiperda*—linear model

| Life stages | a | B | T (min) | DD | $R^2$ | F | Df | *p* |
|---|---|---|---|---|---|---|---|---|
| Egg | −0.1744 (0.038) | 0.0155 (0.001) | 11.25 | 64.51 | 0.97 | 117.5 | 1,3 | 0.001 |
| Larva | −0.0667 (0.032) | 0.0048 (0.001) | 13.89 | 208.3 | 0.84 | 15.80 | 1,3 | 0.028 |
| Pupa | −0.0603 (0.016) | 0.0055 (0.000) | 12.06 | 181.8 | 0.96 | 81.58 | 1,3 | 0.002 |

Numbers in parenthesis are standard errors

**Table 5** Estimated parameters of the non-Linear model fitted to the development rates of immature stages of *Spodoptera frugiperda*

| Life stages | Fitted model: Sharpe & De Michele, model 3 for egg stage, model 9 for larva and model 3 for pupa | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | P | $T_0$ | $H_a$ | $H_h$ | $T_h$ | $T_1$ | AIC | $R^2$ | F | Df | *p* |
| Egg | 0.2188 (0.04) | 300.0 (0.00) | 12808.72 (0.00) | 522831.2 (0.00) | 314.22 (0.00) | 287.54 (0.42)) | −5.8400 | 0.98 | 73.68 | 6,8 | 0.00 |
| Larvae | 0.0898 | 305.7 (0.49) | 20597.70 (1689.72) | 1083779.7 (0) | 317.65 (0) | - | −20.1340 | 0.96 | 113.7 | 3,11 | 0.00 |
| Pupa | 0.1052 (0.012) | 298.0 (0.00) | 17369.62 (0.02) | 11591.71 (0.00) | 307.69 (4.12) | - | −21.1940 | 0.98 | 168.0 | 4,10 | 0.00 |

Numbers in parenthesis are standard errors

temperatures between 20 °C and 35 °C were more conducive to the growth of the FAW immature stages. The four-parameter version of the Wang model (Wang-7) was determined to be the most accurate fit for temperature-dependent mortality in all immature stages (Table 6, Fig. 3): egg, larva, and pupa. These findings provide significant insights into the impact of temperature on FAW survival and development., i.e., egg (ANOVA for egg: df = 3,1; F = 19.60; AIC = 10.83; $R^2 = 0.98$; $p < 0.16$), larva (ANOVA for larva: df = 3,1; F = 1038; AIC = 31.27; $R^2 = 0.99$; $p < 0.02$), and pupa (ANOVA for pupa: df = 1,3; F = 57.02; AIC = 22.15; $R^2 = 0.99$; $p < 0.09$) of FAW. The optimum temperatures predicted by the model for better survival of eggs, larvae, and pupae were 33.12, 31.32, and 32.89 °C, respectively.

## Temperature-dependent adult survival

Males had lower survival rates than females, regardless of temperature. The adult survival rates were greater at lower temperatures (15 °C) and lower at higher temperatures (32 °C). Within the evaluated range of temperatures, the survival rate of adult females increased linearly as the temperature rose. Male and female adult FAWs had lifespans ranging from 6 to 32 days when exposed to constant temperatures between 15 °C and 35 °C (Table 7, Fig. 4). The exponential model was determined to be a good fit for describing temperature-dependent adult survival. For male survival, the model indicated a base temperature of 14.02 °C, whereas for female survival, the base temperature was 11.80 °C. These findings provide vital information on the impact of temperature on the survival and

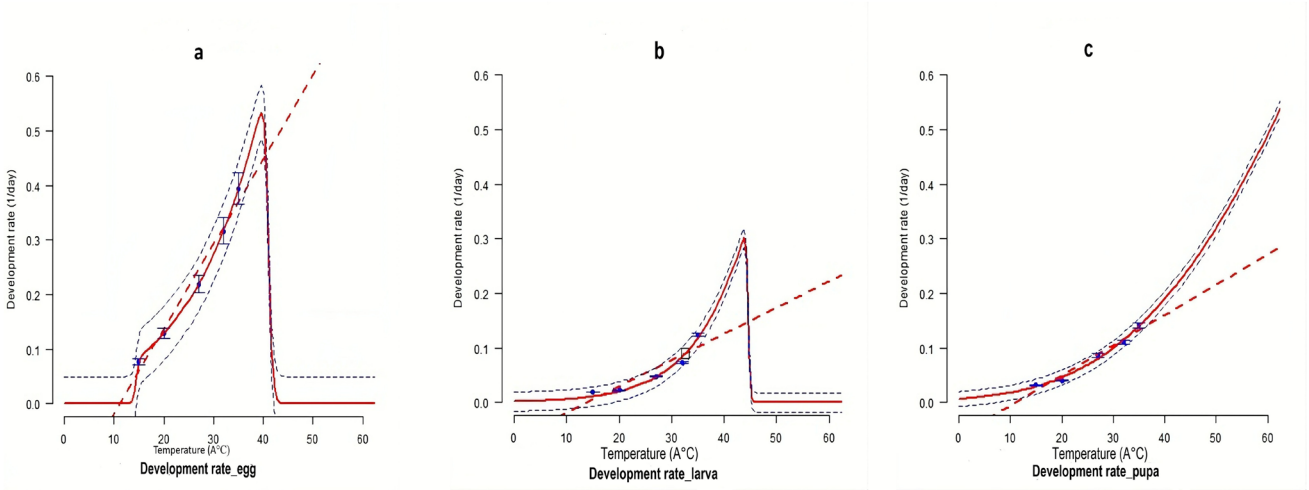


**Fig. 2** Temperature dependent developmental rates (1/d) for immature stages of *Spodoptera frugiperda*: Fitted model Sharp and Demichele for all the stages. The bold solid line is the selected model output and dashed lines above and below represents the upper and lower confidence bands. Bars represent standard deviation of the mean: development rate_ egg **(a)**, development rate_ larva **(b)**, development rate_ pupa **(c)**

**Table 6** Estimated parameters of non-Linear model fitted to mortality rate for immature life stages of *Spodoptera frugiperda.* Fitted model: Wang model 7

| Life stages | Parameters | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Egg | $T_{opt}$ | B1 | $B_h$ | H | AIC | $R^2$ | F | Df | *p* |
| | 33.12 (0.47) | 26.37 (4.48) | 1.21 (0.27) | 8.20 (0.84) | −10.83 | 0.98 | 19.60 | 3,1 | 0.16 |
| Larvae | 31.32 (0.11) | 16.72 (0.36) | 1.59 (0.07) | 7.91 (0.13) | −31.27 | 0.99 | 1038.3 | 3,1 | 0.02 |
| Pupae | 32.89 (0.34) | 22.19 (1.89) | 1.72 (0.24) | 5.30 (0.31) | −22.15 | 0.99 | 57.02 | 3,1 | 0.09 |

Numbers in parenthesis are standard errors

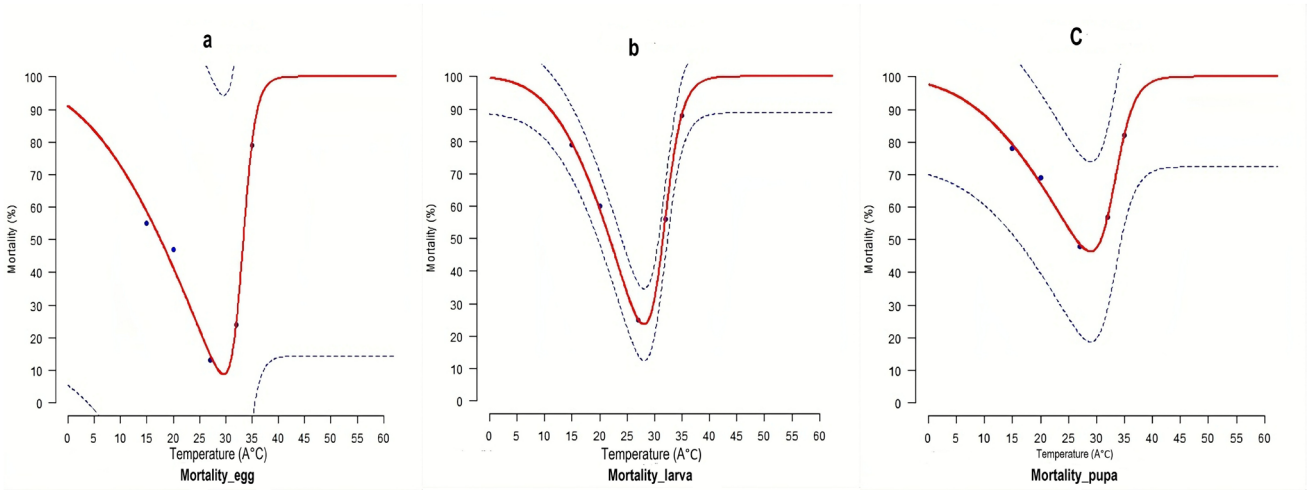


**Fig. 3** Temperature dependent mortality rates for immature stages of *Spodoptera frugiperda*: Fitted model: Wang 7 for all total oviposition and relative oviposition was fitted by Gamma model. The upper and lower confidence intervals of the model are indicated: mortality egg **(a)**, mortality larva **(b)**, mortality pupa **(c)**

longevity of male and female FAW adults. (ANOVA for males: df = 2,2; F = 8.54; AIC = 17.810; $R^2 = 0.89$; $p < 0.10$) (ANOVA for females: df = 2,2; F = 18.6; AIC = −24.339; $R^2 = 0.94$; $p < 0.05$). The base temperature for male survival is 14.02 °C, whereas for female survival, it is 11.80 °C.

## Temperature-dependent reproduction

Female FAWs produced eggs only at temperatures ranging from 20 to 35 °C. Increasing temperatures shorten the life span of female's and reduce their reproductive capacity. The duration of the preoviposition phase ranged from 2 to 13 days, and the post oviposition duration ranged from 1 to 4 days. Female FAWs deposited the fewest eggs (24.40) at a temperature of 20 °C, whereas the highest number of eggs (385.6) were laid at a temperature of 32 °C. No oviposition was observed at the minimum test temperature of 15 °C. The temperature-dependent reproduction of FAW was described via the four-parameter version of the Wang 7 model. These findings provide valuable insights into influence of temperature on the reproductive behavior, longevity, and egg production of female FAWs (Table 8) (ANOVA: df = 3,1; F = 5214.1; $R^2 = 0.99$; AIC = 46.961; $p < 0.010$). The favorable temperature range for oviposition was predicted to be 27–32 °C, and the optimum temperature required for oviposition was 31.89 °C. The gamma function describes the relationship between the cumulative oviposition rate and the age of the females. (ANOVA: df = 1,130; F = 2374.7; $R^2 = 0.94$; AIC = −273.60; $p < 0.001$). At the physiological age of 0.56 days, the female had completed 50% oviposition (Table 9; Fig. 5).

## Life table parameters at constant and simulated temperatures

Temperatures ranging from 25 °C to 32 °C were found to be most favorable for FAW development, survival, and reproduction. The population of FAW reached its peak net reproductive rate, ranging from 182.9 to 434.8 females per generation within this specific temperature range. The highest total fecundity, which reached between 961.2 and 1966.1 individuals per female per generation, was likely

**Table 7** Estimated parameters of non-Linear function fitted to mean senescence rates of adult of *Spodoptera frugiperda*. Fitted Model: Exponential model

| Life stages | Parameters | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | $T_b$ | B | $S_y$ | AIC | $R^2$ | F | DF | *p* |
| Female | 11.80 (0.0) | 0.07 (0.01) | 0.023 (0.00) | −24.339 | 0.94 | 18.6 | 2,2 | 0.05 |
| Male | 14.02 (0.00) | 0.09 (0.02) | 0.026 (0.014) | −17.810 | 0.89 | 8.54 | 2,2 | 0.10 |

Numbers in parenthesis are standard errors

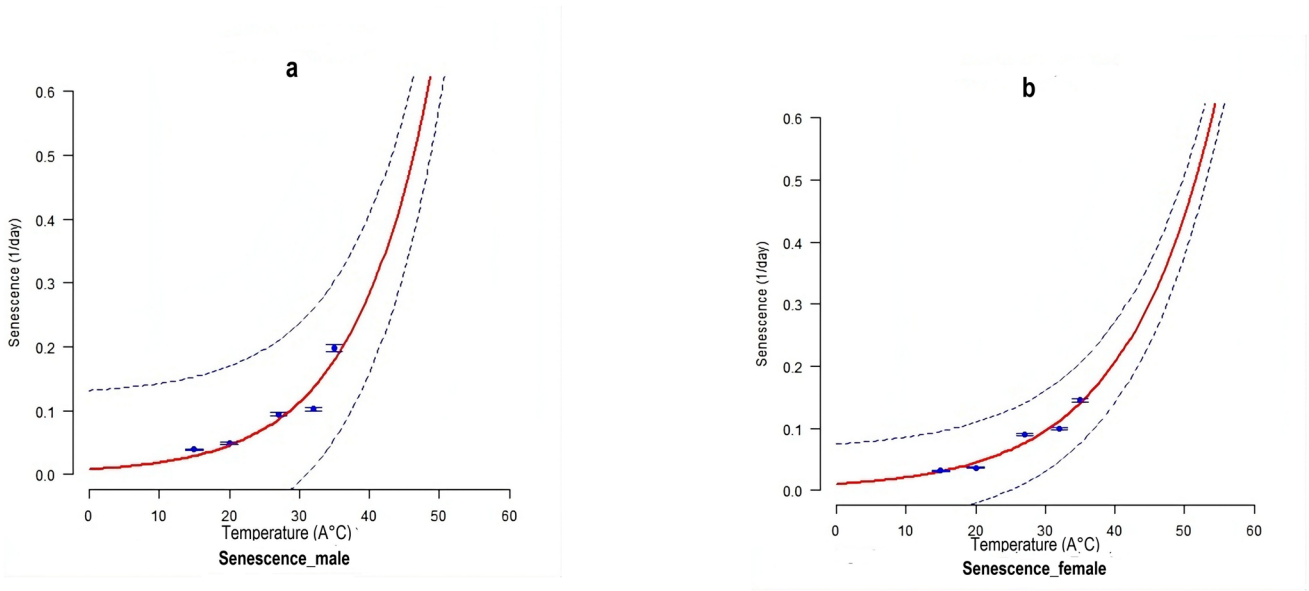


**Fig. 4** Temperature–dependent senescence rates (1/day) for adults of *Spodoptera frugiperda*. Fitted curves: Exponential model for both sexes. The upper and lower 95% confidence intervals of the model are indicated: senescence_ male **(a)**, senescence_female **(b)**

**Table 8** Estimated parameters of non-Linear models fitted to temperature-dependent reproduction of *Spodoptera frugiperda* fitted model: Wang 7

| T (Opt) | b1 | Bh | H | AIC | $R^2$ | F | Df | *p* |
|---|---|---|---|---|---|---|---|---|
| 31.89 (0.02) | 8.92 (0.06) | 1.18 (0.02) | −42,593.6 (0.02) | 46.96 | 0.99 | 5214.1 | 3,1 | 0.01 |

Numbers in parenthesis are standard errors

**Table 9** Cumulative oviposition rate of *Spodoptera frugiperda*, Fitted Model: Gamma

| a | B | AIC | $R^2$ | F | DF | *p* |
|---|---|---|---|---|---|---|
| 11.44 (1.70) | 20.42 (3.07) | −273.6020 | 0.94 | 2374.7 | 1,130 | 0.00 |

Numbers in parenthesis are standard errors

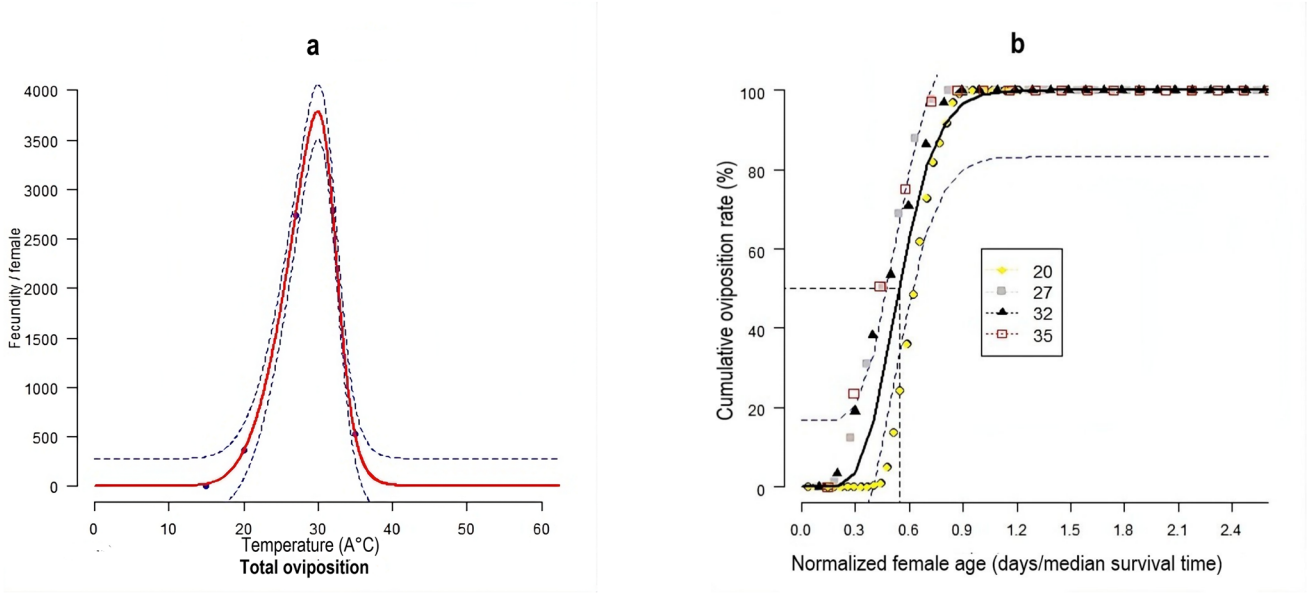


**Fig. 5** Temperature dependent reproduction of *Spodoptera frugiperda*. Total egg production curve fitted function: Wang7 **(a)**; Age related oviposition rate, fitted curve: Gamma distribution function **(b)**. The upper and lower 95% confidence intervals of the model are indicated. The dots are observed data points

observed at temperatures between 25 °C and 32 °C. The mean generation time substantially decreased with increasing temperature, ranging from 162.8 days at 15 °C to 28.2 days at 32 °C. The maximum finite rate of increase, between 1.14 and 1.21 females per female per day, and the shortest doubling time, ranging from 3.6 to 7.1 days, were observed at temperatures between 27 °C and 35 °C. These findings illustrate the critical role of temperature in shaping the life table parameters and population dynamics of FAW, with temperatures between 25 °C and 32 °C being most conducive for their development and reproduction. (Table 10; Fig. 6).

## Validation of life table parameters

The life table simulations were conducted using real-time daily temperature data from five distinct weather stations, which provided reasonably accurate predictions of the life table parameters for FAW at designated locations, including Mahabubnagar, Sangareddy, Nandyal, Kalburgi, and Raichur (Table 10). The life table characteristics derived through these simulations closely resembled those obtained from laboratory studies conducted at constant temperatures of 25 °C –27 °C. This implies that real-time temperature data acquired from various locations can effectively predict the life table parameters

**Table 10** Intrinsic rate of natural increase (rm), net reproductive rate (Ro), gross reproductive rate (GRR), mean generation time (T, in days), finite rate of increase (λ) and doubling time (Dt, in days) of *Spodoptera frugiperda* as mean (±SE) estimated for constant and real time fluctuating daily temperatures, when reared on artificial diets in laboratory

| Life table parameter | Constant temperatures in the laboratory | | | | | | | | Simulations using real-time daily temperatures from weather stations | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 15°c | 18 °c | 20 °c | 23 °c | 25 °c | 27 °c | 30 °c | 32 °c | 35°c | 38°c | Mahabubnagar | Sangareddy | Nandyal | Kalburgi | Raichur |
| $r_m$ | −0.005 (0.00) | 0.01 (0.03) | 0.03 (0.00) | 0.07 (0.00) | 0.10 (0.00) | 0.13 c (0.00) | 0.19 (0.00) | 0.18 (0.01) | - | - | 0.10 | 0.08 | 0.10 | 0.10 | 0.09 |
| $R_0$ | 0.048 (0.03) | 4.09 (1.10) | 12.23 (3.00) | 81.46 (13.9) | 197.6 (17.5) | 434.8 c (74.9) | 629.5 (40.4) | 182.95 (50.2) | - | - | 174.9 | 117.8 | 168.3 | 147.6 | 102.9 |
| GRR | 4.8 (3.0) | 76.6 (7.9) | 195.2 (14.4) | 551.7 (55.8) | 961.2 (78.3) | 1492.6b (120.0) | 1966.1 (64.8) | 1522.3 (255.4) | - | - | 779.6 | 962.9 | 1036.2 | 1014.9 | 769.8 |
| T | 162.83 (32.5) | 112.35 (1.05) | 90.68 (0.57) | 66.59 (0.22) | 54.26 (0.26) | 44.6abc (0.24) | 33.94 (0.07) | 28.2 (0.20) | - | - | 52.7 | 59.8 | 49.9 | 47.7 | 51.9 |
| λ | 0.39 (0.24) | 1.01 (0.00) | 1.03 (0.00) | 1.07 (0.00) | 1.01 (0.00) | 1.14 (0.00) | 1.21 (0.00) | 1.20 (0.01) | - | - | 1.10 | 1.08 | 1.11 | 1.11 | 1.09 |
| $D_t$ | 20.5 (12.6) | 79.1 (21.5) | 26.70 (1.90) | 10.71 (0.46) | 7.15 (0.14) | 5.21 (0.14) | 3.66 (0.04) | 3.90 (0.19) | - | - | 7.1 | 8.7 | 6.7 | 6.6 | 7.7 |

Numbers in parentheses are the standard error

of FAW under field conditions, further supporting the importance of temperature in influencing the population dynamics of this pest.

## Discussion

The results of the present study, which focused on the temperature-dependent growth of FAW reared on artificial food in a controlled laboratory environment, highlight the significant effect of temperature on the growth and development of this invasive pest. The primary goal of this research was to employ phenology modeling to investigate and reproduce the temperature-dependent developmental responses exhibited by the fall armyworm. This research aims to offer unique insights into how temperature affects the life cycle and population dynamics of this pest, which can have significant ramifications for pest management and agricultural practices. We explored the effects of temperature on the growth, survival, and population dynamics of the pest by integrating temperature data from various geographic sites, laboratory tests, and mathematical modeling.

The temperature-dependent population growth potential of FAW was assessed via rate summation and cohort update methods, with constant temperatures ranging from 15 to 35 °C. (Curry et al. 1978). Additionally, the outcomes were verified by stochastically modeling the life table parameters under a range of temperature conditions via real-time meteorological information gathered from various places. Our findings showed that FAW could survive at all of the measured constant temperatures between 15 °C and 32 °C, although growth was greatest at 25 °C to 32 °C. Additionally, we discovered that FAW females were incapable of producing eggs at a constant temperature of 15 °C, rendering it unfeasible to evaluate the reproductive fitness of FAW at that temperature. The results of this investigation were more in line with those of earlier researchers, Milano et al. (2008), who also noted that oviposition did not occur at temperatures of 10 °C or 15 °C. Another similar species, *Spodoptera litura* (Fabricius, 1775) has also been shown to exhibit low-temperature suppression of oviposition (Rao et al. 1989; Fand et al. 2015). Our results contradict the findings of Prasad et al. (2022), who observed FAW oviposition at a temperature of 15 °C. In this study, we examined the impact of a regime of constant temperatures between 15 and 35 °C on the growth, development, survival, and reproduction of FAW, considering both the UTT and LTT during the pest's entire life cycle. The egg development period was eight days at a temperature of 20 °C and three days at a temperature of 35 °C. The development period for larvae was 46 days at a temperature of 20 °C and nine days at a temperature of 35 °C. The length of the immature development times was in line with previous studies by Ali et al. (1990), Lu et al. (2019), Duplesis et al. (2020), Huang et al. (2021), and Malekara et al. (2022), who reported that

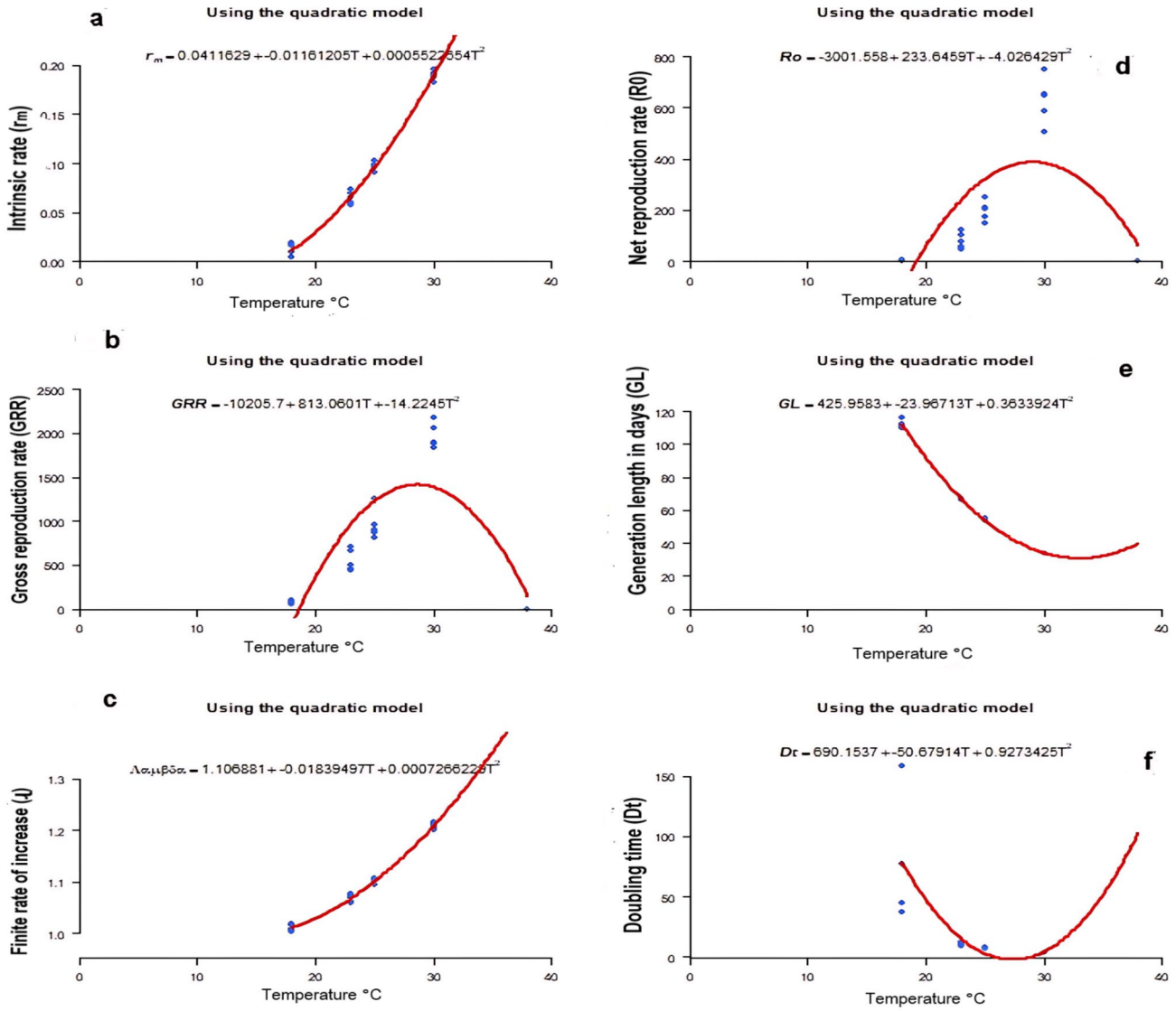


**Fig. 6** Life table parameter of *Spodoptera frugiperda* estimated at six constant temperatures. Intrinsic rate of natural increase **(a)**, net reproduction rate **(b)**, gross reproductive rate **(c)**, mean generation time **(d)**, finite rate of increase **(e)**, and doubling time **(f)**

the immature stages of FAW developed more quickly as temperatures rose. The lower developmental threshold for the egg stage of 11.25 °C was reasonably similar to the results of earlier researchers, Prasad et al. (2022) and Du Plesis et al. (2020), who reported LTTs in the range of 12.1 °C –13.0 °C. The LTTs for larval development (12.88 °C) were equivalent to those reported by Lu et al. (2019). The LTT for pupal development (12.06 °C) was closely related to the findings of Dahi et al. (2020) (14.05 °C).

The variation in the LTTs reported in the present study and those of earlier researchers may be due to variations in rearing circumstances and larval food (natural or artificial diet) (He et al. 2021). The upper thermal thresholds for eggs, larvae and pupae were 41.24, 44.65, and 34.69 °C, respectively. The present findings largely conform with those of Maino et al. (2021). In addition to the LTT and UTT, we have estimated the optimum temperature for various immature stages by fitting nonlinear functions for greater accuracy. The estimated heat unit requirement (DD) of 64.51 for egg development was relatively similar to the findings of Barfield et al. (1978) and Dahi et al. (2020). The DD requirement for larval development (208.3 DD) estimated in the present study slightly deviated from the findings of Ashok et al. (2021) (237.38 DD). The degree-days for completion of pupal development (181.8 DD) are partially in agreement with the value of 184.4 DD reported by earlier researchers

(Ashok et al. 2022; Parra et al. 2022). The total number of thermal units required for FAW life cycle completion (454.61 DD) was supported by the report of Malekara et al. (2022) (490 DD). However, our results are in direct opposition to the findings of Lee et al. (2022) and Garica et al. (2019). The contrast includes estimates between 285.30 and 320.10 DD at the lower end of the present findings.

Substantial differences were observed in the temperature-dependent survival of immature stages at different test temperatures. Egg survival was impacted below 20 °C, whereas continuous temperatures of 27 °C above 32 °C were more advantageous for larval and pupal survival. Similar trends in immature survivorship were confirmed by Sparks (1979), Capinera (2001), and Duplesis et al. (2020) confirmed similar trends in immature survivorship. Furthermore, an insect's fitness and ability to feed affect its survival rate. Because insects are raised on artificial diets, which are influenced by the temperature of the environment, larval feeding decreases. (Simmon 1993; Murua and Virla 2004) Pupal mortality of FAW was greater at 35 °C and 15 °C and was highest at 32 °C. The summer months in India may be particularly hot because FAW pupates in the field at a depth of 2–8 cm below the soil surface, making it susceptible to daily temperature changes (Lugin Bill 1928). This aligns with the time of year when crops are cultivated and the FAW infection of various host crops. Compared with other pests, the FAW has advantages in terms of growth and survival because its pupae can survive and develop in soil at high temperatures.

The duration of females decreased by 3–4 times at continuous temperatures of 15–35 °C, which may have been due to a decrease in the number of insects in the generative phase. Temperature has a significant effect on the FAW fecundity and cumulative oviposition rate. While no oviposition was noted at 15 °C, oviposition was observed in the range of 20 °C –35 °C. At 32 °C, egg production peaked at 2786 eggs per female, and it significantly decreased at 20 °C and 35 °C. This suggests that the incidence of the ideal temperature influences FAW appropriateness more than other factors. Ashok et al. (2021) reported a similar pattern in the temperature-dependent FAW fecundity by observing a greater fecundity at 34 °C. Huang et al. (2021) and Yan et al. (2022) reported similar findings. Our study solely examined the influence of temperature on the fertility of FAW when raised on an artificial diet; hence, the total number of eggs laid by females was slightly lower than that of Heo et al. (2022). This can be explained by the variable oviposition response of FAW when raised on an artificial diet (Chen et al. 2022). The main factor in insect reproductive biology that affects population variation is oviposition. In-depth knowledge of temperature dependent, age-specific fecundity is needed to create prediction models (Wagner et al. 1984). Our study only discusses the effect of temperature on the fecundity of FAW reared on an artificial diet. Fecundity is affected by several of biotic and abiotic factors, including the quality and quantity of food, the host used in the diet, light intensity, and relative humidity (Jaba et al. 2020b; He et al. 2021; Chen et al. 2022). Temperature thresholds and thermal requirements reveal the physiological reaction of the fall armyworm to temperature, which can be used to estimate the population dynamics of these insects under various climatic situations. The effects of constant temperatures on the life table parameters of FAW have been reported by various researchers (Sarkar et al. 2021; Sabra et al. 2022; Prasad et al. 2022; Malekara et al. 2022; Hong et al.2022; Ranaweera et al. 2024). Our findings on constant temperature simulations of FAW life table parameters are in line with most of these studies. Ranaweera et al. (2024) obtained slightly higher values for FAW life table parameters at constant temperatures between 25 °C and 32 °C. These disparities appear to be attributable mostly to variations from the specified submodel for immature stage development and mortality, as well as overall fecundity per female, which are considered the most variable elements (Fand et al. 2015). In addition, an artificial diet with various ingredients used as host material adds further variability in lifecycle, fecundity, and developmental durations. The general divergence between our results and those reported by earlier researchers may be due to a variation in the model chosen.

The created phenology model predicts the timing and length of important life stages, such as egg hatching, larval development, and pupation, across a range of temperature regimes. Additionally, we used real-time weather station data to simulate the FAW population dynamics in various regions of India at varying temperatures. These simulations accurately predicted the lifetable parameters for FAW at all the test locations, including Mahabubnagar, Sangareddy, Nandyal, Kalburgi, and Raichur. The effects of steady temperatures between 25 °C and 27 °C were simulated by treating daily temperature variations. The temperature-based phenology model of FAW given here may produce reasonably accurate results for life table simulations because of its sensitivity to even small fluctuations in daily temperature.

These multilocation simulations enhanced the model's usefulness in estimating prospective FAW population increase in various agro ecological context which were not covered by earlier investigations.

## Conclusion

This study revealed that temperature has a major effect on growth, development, and reproduction of FAW. The lower and higher temperature thresholds prevented FAW from developing, reproducing, and surviving. FAW grows best at 27 °C, and as the temperature increases, so does the rate of growth. A temperature-dependent phenology model that

accurately depicts the temperature-dependent growth of the pest was developed utilizing thermal thresholds, and heat units were calculated via several mathematical models and simulated life table parameters from different geographical regions in India. The results of these experiments will help us better understand the phenological patterns and temperature-dependent response of FAW. The knowledge gathered from this research will be used to develop proactive and targeted management measures that consider how temperature affects the population dynamics of this devastating pest. To enhance national-level pest risk assessment and track the possible spread of FAW, the data offered here may be relevant.

**Acknowledgements** The authors would like to thank Mr Suraj Prashad Mishra Senior Officer, Mr. Rajendra Kumar and Mr. Ramana, research technicians at ICRISAT, for their assistance in conducting the experiments.

**Author contributions** J.J. and BF conceived and designed the experiments; J.K. and S.K. performed the experiments; JK and BF analyzed the data; J.K. wrote the first draft paper; J.J. provided financial support; JJ and BF revised and provided additional technical inputs. All the authors have read and agreed to the published version of the manuscript.

**Funding** This research was partially funded by the ICAR-ICRISAT, CGIAR-Plant Health Initiative & CGIAR-GLDC programme.

**Data availability** The datasets generated and/or analyzed during the current study are available from the corresponding author, based on request will share the same.

## Declarations

**Conflict of interest** The authors declare that they have no conflicts of interest.

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