

Influence of varying temperatures on the growth parameters of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Noctuidae; Lepidoptera)

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Abstract

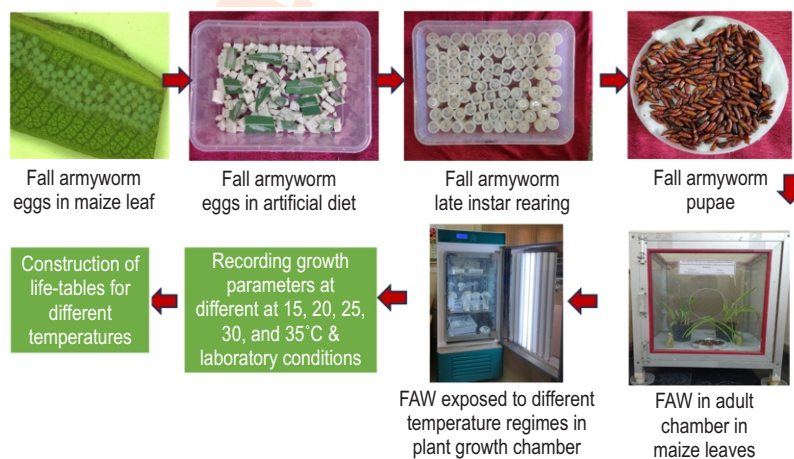
Aim: The research was undertaken to study the influence of varying temperature regimes on the growth parameters of invasive maize fall armyworm, *Spodoptera frugiperda* under controlled conditions.

Methodology: The life history and fitness parameters of the fall armyworm, *Spodoptera frugiperda*, were studied under laboratory conditions at different temperature regimes (15, 20, 25, 30, and 35 °C). The laboratory reared homogenous population was exposed to different temperature regimes and growth parameters were recorded at definite intervals.

Results: The results revealed that developmental time was longer at lower temperatures (20 °C) and shortened with increasing temperatures. The larval period was 22.98 days at 20 °C and 12.97 days at 35 °C. The maximum net reproductive rate (R_0) was observed at 30 °C (324.61) and the minimum at 20 °C (231.00). The intrinsic rate of natural increase (r_m) was positively correlated with temperature, and the maximum r_m was 0.238 individuals per female per day at 35 °C. The highest gross reproductive rate was recorded at 30 °C. The doubling time was 3.52, 3.29 and 2.91 days at 25 °C, 30 °C, and 35 °C, respectively.

Interpretation: These results suggest reduced fitness of *Spodoptera frugiperda* in the future scenario of global climate change with increasing temperatures.

Key words: Fall armyworm, Reproductive rate, *Spodoptera frugiperda*



Introduction

The initial detection of fall armyworm invasion beyond the borders of North America occurred in the Central and West Africa in 2016. By the end of 2017, the fall armyworm had spread to 44 sub-Saharan countries. Analysis by CABI during 2020 in twelve African nations revealed that fall armyworm (FAW) has the potential to cause maize losses ranging from \$2.5 billion to \$6.2 billion. In May 2018, the incidence of fall armyworm was documented in the maize fields of the University of Agricultural and Horticultural Science in Shivamogga, Karnataka, India. Following that, in June and July 2018, the occurrence was documented in the rural areas of Bangalore and south Karnataka, respectively (Kalleshwaraswamy et al., 2018a; Tippannavar et al., 2019). The presence of fall armyworm throughout India was recorded by the end of August 2019 (Suby et al., 2020). This indicates their adaptation to different climatic zones and their potential to inflict damage throughout the year. The ability of the FAW to ravage all stages of maize growth classifies it as a key maize pest (Navik et al., 2021), potential to cause severe damage to Indian maize farming during a brief invasion time.

The capacity of FAW to cause damage to over 300 host plants and its adaptability to many environmental conditions would enable it to survive in India. While it has been observed in several agroclimatic regions, this species has only spread to locations with a climate that closely matches its original range (Early et al., 2018). Swamy et al. (2018) observed that the 'R' strain was the most common in the fall armyworm populations found in maize fields in Andhra Pradesh, Madhya Pradesh, Tamil Nadu, Maharashtra, and Telangana. Nayyar et al. (2021) documented the occurrence of hybrid haplotypes between different strains of rice and corn in India. They also made predictions about the rapid growth of Indian fall armyworm population. Environmental factors have an impact on insect migrations, which determine the displacement patterns. Temperature is the primary environmental element that affects the pace of insect growth. Every insect has a certain temperature range that is most suitable for its growth and development. Any fluctuations in temperature will affect the rate of development, length of life cycle, and the ability of insects to survive (Howe and Linaweaver Jr., 1967).

The rate of insect growth is accelerated when the maximum and minimum temperatures fall within their ideal range (Mironidis and Savopoulou-Soultani, 2014). Temperature variations will impact the population dynamics of insects. Bale et al. (2002) showed that temperature has an impact on the behaviour, distribution, development, survival, and reproduction rates of insects. The temperature is the primary determinant that affects the composition of stem borer complexes in maize (Ntiri et al., 2016). Simmons (1993) found that the fall armyworm pupae, when exposed to 15 °C and 35 °C temperature, exhibited both poor survival rates and more deformities. This demonstrates that both higher and lower temperature ranges have an impact on the survival rate of the fall armyworm. In their field investigation, Nurzannah et al., 2020 observed that increase in rainfall had

positive correlation on FAW infestation in maize. Patel et al., 2020 found that rainfall, wind speed and minimum temperature contributed 49%, 60% and 70%, respectively, to fluctuation in *S. frugiperda* populations. A negative correlation was also observed by Nivetha et al. (2022) between temperature, rainfall and FAW infestation in India. Experiments involving the exposure of FAW to varied climatic conditions will give further insights about the effects of climate change on the prevalence and behaviour (Ahmad and Ibrahim, 2021). As an invasive insect pest, its ability to expand depends on its capability to overcome the weather extremes in the invaded areas. Among the different weather parameters, temperature is the most important factor. The present investigation aims to study the influence of extreme temperatures on the growth and development of FAW.

Materials and Methods

Insect cultures: *S. frugiperda* cultures maintained in the Insect Rearing Facility, Department of Agricultural Entomology, TNAU, Coimbatore for more than 20 generations was used in the present study. The purpose of using this homogeneous population was to eliminate the response variations in the experiments. In order to ensure that the homogeneous culture would continue to be viable, field collected populations were introduced into the laboratory cultures on an intermittent basis. Lablab bean and wheat germ based semisynthetic diet was used to rear the fall armyworm larvae (unpublished). The first three instar larvae were reared gregariously. The larvae of the late third to fourth instars were then transferred to individual plastic containers (30 x 40 x 40 mm). The lids of these containers were perforated to allow air to circulate through them. The artificial diet was changed periodically. Larval cultures were maintained at 28 ± 2 °C and a relative humidity of 70–80 %. The larvae, after pupation, were kept in adult emergence cages. The adult diet consisted of sugar and honey in 1:1 ratio, along with mineral supplements. Twenty-day-old maize seedlings were used as oviposition substrates and kept inside the oviposition chambers. The eggs were collected and transferred to transparent plastic boxes (17 x 11 x 5 cm) containing artificial diet.

Host plants: The maize seeds (Co HM 8) were sown in pots containing pot mixture of red soil, sand and vermicompost @1:1:0.5. Immediately after sowing, the pots were transferred to insect proof walk-in cages (8 x 8 x 6 feet) to avoid infestation by any pests and diseases. Need based irrigation was given to the potted plants. These plants were used as substrate for egg laying and kept inside the adult rearing cages. The maize plants (15–20 days) grown inside the rearing cages were used to rear the fall armyworm inside the plant growth chamber.

Life cycle studies under different temperature regime: The maize leaves were kept inside the adult rearing cage for oviposition, and the leaves were collected immediately after egg laying. The collected eggs were placed in the plant growth chamber (Make: Faithful Instrument Co., Ltd.) at different temperature regimes, viz., 15, 20, 25, 30, and 35 °C. Relative

humidity of 70–80% and a photoperiod of 14:8 was maintained in the plant growth chamber throughout the study period. For the individual temperature regime, the eggs were placed in a plastic container, and the number of eggs was counted by removing the hairs using a camel brush before being introduced into the plant growth chamber. Before the hatching of eggs, maize leaves were kept in the plastic container for feeding by the larvae. The maize leaves were changed daily by transferring the early instar larvae using a camel brush to avoid any contamination. The first three instar larvae were reared gregariously, and then they were transferred to individual plastic containers from the late third to early fourth instar to avoid cannibalism. After pupation, pupae were kept in small cages, and a 10% honey solution was provided for the feeding of adults. Biology and life table studies for laboratory conditions were carried out at 30 ± 2 °C and 70 ± 10 % relative humidity (Ashok et al., 2021; Du Plessis et al., 2020).

Data Collection: The parameters viz., fertility, mortality and survival rate were recorded at 24 hr. interval from the initiation of the experiment till the death of adults. Dead larvae and pupae were discarded daily. The observations on developmental time, total life cycle, fertility rate were taken to study the biology and life table of *S. frugiperda* under different temperature conditions.

Life table construction: The stage specific life tables for *S. frugiperda* were constructed by dividing the life cycle into distinct developmental stages viz., eggs, first instar, second instar, third instar, fourth instar, fifth instar, sixth instar, pupae and adult stage (Deevey 1947; Birch 1948). The parameters viz., pivotal age in days (X), survivors at beginning (l_x), number of individuals produced per female (m_x), number of individuals surviving at beginning of x (s_x), proportion dying during the age interval x to x+1 (d_x), rate of mortality during the age interval x to x+1 (q_x), mean expectation of life period for organisms (e_x) and reproductive expectation ($L_x m_x$) were calculated. The following parameters were calculated using the formulas described below

Net Reproductive rate (R_0)

$$R_0 = \sum_{x=\alpha}^{\beta} l_x m_x$$

Where, α = age of first reproduction; β = age of last reproduction and x = age in days

Intrinsic rate of increase (r_m)

$$\sum e^{-r_m x} l_x m_x = 1 \quad r_m = \log_x \frac{R_0}{T_c}$$

Finite rate of increase (λ)

$$\lambda = e^{r_m}$$

Generation time (T_c)

$$T_c = \log_e \frac{R_0}{T_m}$$

Gross Reproductive rate (GRR)

$$GRR = \sum m_x$$

Population Doubling time (t)

$$t = \frac{\ln 2}{r_m}$$

Survivorship curves

$$\text{Probability of survival (y)} = \frac{1}{1 + \exp\left(\frac{x-a}{b}\right)}$$

Where, a: day in which 50 per cent mortality recorded; b: Intercept and x: Age in days

Statistical Analysis: After the appropriate data transformation, differences in life history parameters were examined using analysis of variance (ANOVA). The Tukey's honestly significant difference (HSD) test was used to examine variations in developmental duration across various growth stages. The statistical study was carried out using SPSS version 20, IBM, Armonk, NY, USA.

Results and Discussion

Biology of *S. frugiperda* under different temperature regimes: The different temperature regimes (20 to 35 °C) showed significant differences in the life cycle of *S. frugiperda* (Table 1). The developmental time was longer at a lower temperature (20 °C) and shorter at a higher temperature (35 °C). The egg period was shorter at higher temperatures. The larval period was longer at 20 °C and shorter at 35 °C, which showed the influence of temperature. The 4th instar larvae took 4.17 days for development at 20 °C whereas at other temperatures, the 4th instar did not show much difference. The difference in larval duration between 35 °C and 20 °C was 10.01 days. The temperature also had an impact on the pupal development. The eggs get distorted and the colour of the eggs and pupa changed to black colour when reared at 35 °C. The order of *S. frugiperda* development at different temperatures was 20 °C > 25 °C > 30 °C > 35 °C, respectively. The average durations of the egg (2.11 days), larval (14.91 days), and pupal (9.41 days) stages observed in this study under controlled laboratory conditions support the conclusions of Kalleshwaraswamy et al. (2018b) and Kalyan et al. (2020).

The total incubation, larval and pupal period recorded by Kalleshwaraswamy et al. (2018b) were 2 – 3, 14 – 19 and 9 – 12 days, respectively. The length of pre-oviposition (3.85 days), oviposition (6.85 days), and post-oviposition (2.45 days) period in this laboratory study was much longer compared to the durations reported by Reddy et al. (2021), and Kalleshwaraswamy et al. (2018b). However, the mean oviposition period was similar to Reddy et al. (2021) and Kalleshwaraswamy et al. (2018b) findings. Basavaraj et al. (2018) in *H. armigera* and Ashok et al. (2021) reported that in *S. frugiperda*, female egg laying began on the 26th day of their pivotal age and lasted until 36th day, with the highest

Table 1: Biology of *S. frugiperda* *S. frugiperda* under different temperature regimes

Particulars	Laboratory condition		20 °C*		25 °C*		30 °C*		35 °C*	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
	(in days)									
Egg period	2.11 ± 0.29	2–3	3.06 ± 0.24 ^b	3-4	2.63 ± 0.21 ^b	2-3	2.24 ± 0.18 ^{ab}	2-3	1.67 ± 0.13 ^a	1-2
1 st Instar period	2.49 ± 0.26	2–3	4.37 ± 0.26 ^b	3-4	2.84 ± 0.17 ^a	2-3	2.61 ± 0.16 ^a	2-3	2.14 ± 0.13 ^a	2-3
2 nd Instar period	2.23 ± 0.42	2–3	3.74 ± 0.41 ^b	3-4	2.67 ± 0.29 ^{ab}	2-3	2.31 ± 0.25 ^a	2-3	1.85 ± 0.20 ^a	1-2
3 rd Instar period	2.14 ± 0.14	1–3	3.97 ± 0.15 ^b	3-5	2.39 ± 0.09 ^a	2-3	2.21 ± 0.09 ^a	1-3	2.06 ± 0.08 ^a	1-3
4 th Instar period	2.08 ± 0.25	1–3	4.17 ± 0.29 ^b	3-5	2.15 ± 0.15 ^a	1-3	2.15 ± 0.15 ^a	1-3	2.02 ± 0.14 ^a	1-3
5 th Instar period	2.03 ± 0.22	1–3	3.61 ± 0.23 ^b	3-4	2.12 ± 0.13 ^a	1-3	2.09 ± 0.13 ^a	1-3	1.97 ± 0.12 ^a	1-2
6 th Instar period	3.94 ± 0.70	3–4	3.12 ± 0.32 ^a	3-4	4.19 ± 0.43 ^a	4-5	3.97 ± 0.41 ^a	3-4	2.93 ± 0.30 ^a	2-3
Total larval period	14.91	10–19	22.98	18-26	16.36	12–20	17.58	10–19	12.97	8–16
Pupal period	9.41 ± 1.70	8–11	12.83 ± 1.34 ^b	11-13	10.27 ± 1.07 ^{ab}	9-12	9.98 ± 1.04 ^{ab}	8-11	7.64 ± 0.80 ^a	6-9
Adult period	12.53 ± 1.35	11–15	10.46 ± 0.65 ^a	8-12	13.06 ± 0.81 ^a	11-15	12.81 ± 0.79 ^a	11-15	11.40 ± 0.71 ^a	8-12
Total period	34.47 ± 4.47	28–36	43.78 ± 3.28 ^b	40-47	37.89 ± 2.84 ^{ab}	30-40	36.16 ± 2.71 ^{ab}	30-38	29.19 ± 2.19 ^a	27-31

* Mean values of three replications; Mean with different letters for different temperatures has significant differences (P < 0.05) (Tukey's test)

number of eggs being laid on the 28th day. He *et al.* (2021) recorded the survival rate of 0.79, 0.74 and 0.44 on rape, sunflower, and soybean, respectively, from egg development to mature larvae. The range of survival ratio and survival fraction in the present study was 0.00 – 0.83 and 0.73 – 0.98 respectively, across the temperatures and growth stages (Fig. 3, 4). Haung *et al.* (2021) recorded higher larval and pupal survival rates at higher temperatures (28 and 31 °C), which corroborate with the present findings.

Stage specific distribution at different temperatures: The different larval stage mortality responses varied in different temperature regimes (Fig. 1). The apparent mortality of eggs was lowest at 30 °C (Fig. 2). The third instar recorded the highest apparent mortality at 25 °C and the lowest in the sixth instar. Among the temperature regimes, the apparent mortality was lowest at 30°C, followed by 35 °C. The lowest apparent mortality of pupa was recorded at 30 °C. The highest mortality survival ratio was at 20 °C and the lowest at 30 °C (0.83 and 0.04) for larval stages (Fig. 3). Among all temperature regimes, the *S. frugiperda* larvae reared at 30 °C recorded the lowest mortality survival ratio across all larval instars. The sixth instar larva recorded the lowest survival ratio across all temperature regimes. At pupal stages also, 30°C recorded the lowest mortality survival ratio compared to other temperatures. Acharya *et al.* (2007) observed the lowest mortality rate in the later stages of larval development in *H. armigera*, whereas Shekhawat *et al.* (2018) reported similar results in *S. litura*.

The egg stage survival fraction increased up to 30°C and decreased at 35°C (Fig. 4). At 20 °C, the highest survival fraction was recorded in the sixth larval instar. The first and third instar larvae recorded the lowest survival fraction (0.66) and the sixth instar larvae recorded the highest survival fraction at 25 °C. The order of survival fraction of different larval stages at 25 °C was L1 = L3 > L4 > L2 > L5 > L6. The first instar recorded the lowest survival fraction at 30 and 35 °C. The sixth instar larvae at 30°C

and the second instar larvae at 20 °C recorded the highest and lowest survival fractions, respectively among all larval stages in different temperature regimes. The indispensable mortality also showed a similar trend as the apparent mortality and mortality ratio (Fig. 5). The different life stages recorded the highest survival proportion at 30 °C across all life stages (Fig. 6). The lowest survival proportions across all life stages were recorded at 20 and 25 °C. The duration of adult pre-oviposition, oviposition and adult lifespan for *S. frugiperda* that were raised on maize leaves were 5.5, 1.78, and 59.95 days at 20 °C, 1.83, 3.92, and 41.87 days at 25 °C, and 2.17, 2.61, and 26.1-days 30 °C, respectively (Chen *et al.*, 2022).

The present investigation recorded longer total life span contradicting to the above finding (Table 3). Exposing *S. frugiperda* to higher temperatures (30 °C) resulted in a decrease in the lifespan of adult insects that were fed with maize (Barfield *et al.*, 1978). The current study revealed that the lifespan of *S. frugiperda* reduces as the temperature rises. The results corroborate with the findings of Prasad *et al.* (2022), who observed a greater mean generation duration of 74.29 days at 15°C and a shorter mean generation time of 38.74 days at 30 °C. The present analysis did not find any notable variation in the duration of *S. frugiperda* oviposition at different temperatures. The age at which the final oviposition occurred was highest at a lower temperature of 20 °C and lowest at a higher temperature of 35 °C. These findings support the findings of Garcia *et al.*, 2018 and Chen *et al.*, 2022. The survivorship curve of *S. frugiperda* adheres to a type III curve (Fig. 7), which demonstrates that as the temperature rises, the survival rate of *S. frugiperda* declines. The survival probability of *S. frugiperda* varied between 30 and 47 days at various temperatures, as measured by Kaplan-Meier index (Fig. 8).

Impact of different temperatures on oviposition, adult longevity and lifespan of *S. frugiperda*: The age of first

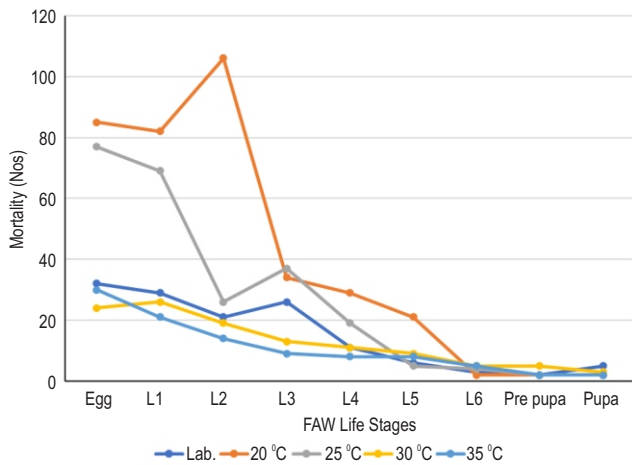


Fig. 1: Mortality of fall armyworm *S. frugiperda* at different temperature regimes.

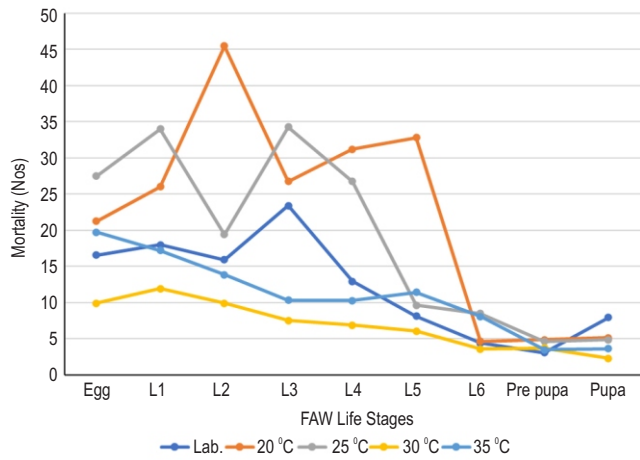


Fig. 2: Apparent Mortality of fall armyworm *S. frugiperda* at different temperature regimes.

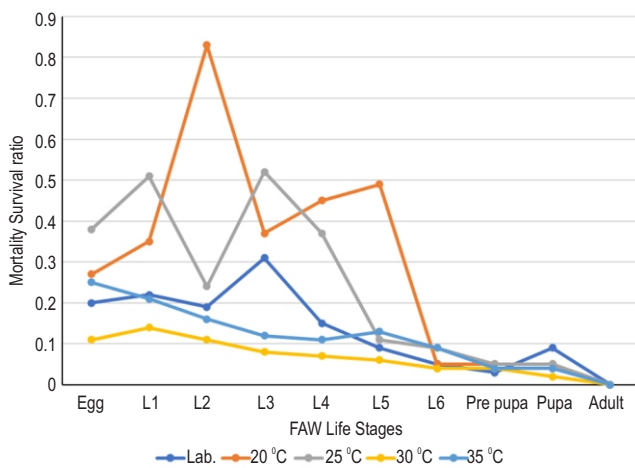


Fig. 3: Mortality survival ratio of fall armyworm *S. frugiperda* at different temperature regimes.

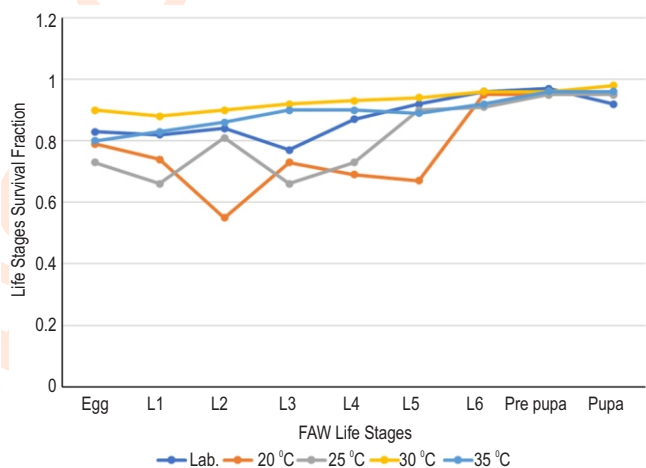


Fig. 4: Survival Fraction of fall armyworm *S. frugiperda* at different temperature regimes.

oviposition, age of last oviposition, and age of maximum oviposition decreased with an increase in temperature (Table 2). The length of the oviposition period doesn't change with an increase in temperature. The age of last oviposition was maximum (45 days) at the lowest temperature 20 °C and minimum (28 days) at the highest temperature 35 °C. The adult longevity decreased with increasing temperature (Table 3). The adult longevity was greater at 30 °C (11.85 days) and least at 35 °C (9.45 days). The order of impact of temperature on the longevity of male and female adults was 20 > 25 > 30 > 35 °C. The male and female lifespans were longest at 20 °C viz., 43.14 and 44.25 days. At 30 °C, the male and female completed their lifecycle in 33.45 and 34.63 days, whereas they required only 26.14 and 26.79

days at 35 °C. The difference within lifespan at temperatures between 20 and 35 °C for male and female adults was 17.00 and 17.46 days, respectively. This shows that adults have to spend more energy to complete their life cycle at a lower temperature than higher temperature. The lower temperature increased the longevity and lifespan of *S. frugiperda*, and at higher temperatures, they required a significantly lower number of days to complete their life cycle. Temperature has a significant impact on *S. frugiperda* life stages (Chen *et al.*, 2022). The average lifespan of *S. frugiperda* developmental stages varies significantly at 25, 30 and 35 °C (Ranaweera *et al.*, 2024). The duration of different larval stages exhibited an inverse relationship with temperature within the range of 18 to 30 °C (Garcia *et al.*,

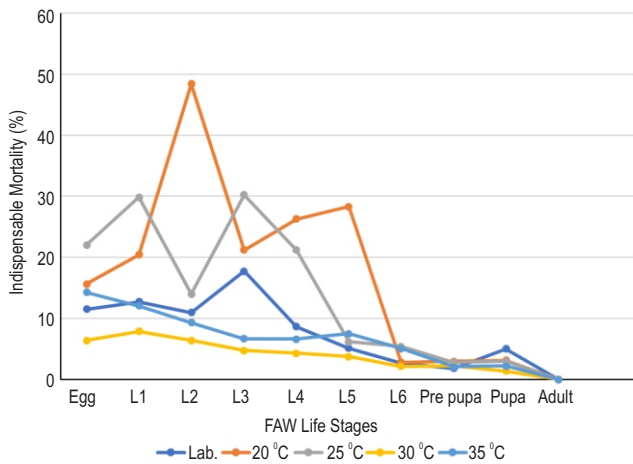


Fig. 5: Indispensable Mortality of fall armyworm *S. frugiperda* at different temperature regimes.

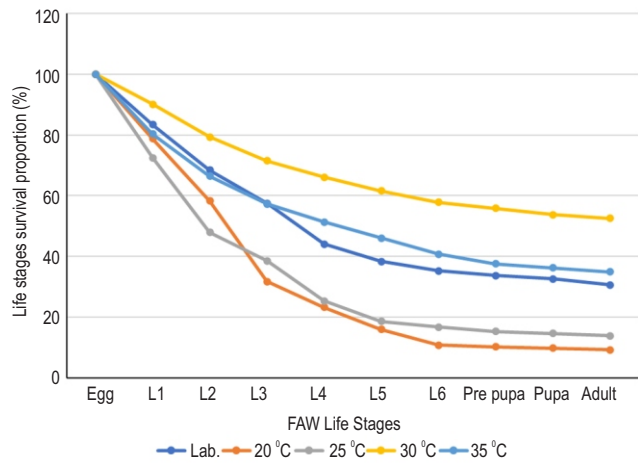


Fig. 6: Survival Proportion of fall armyworm *S. frugiperda* at different temperature regimes.

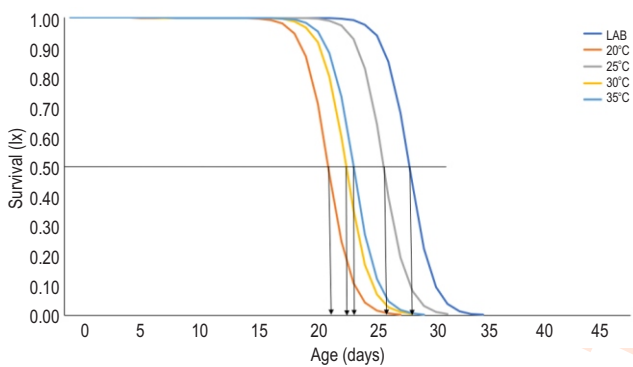


Fig. 7: Survivorship curves of fall armyworm *S. frugiperda* under different temperature conditions.

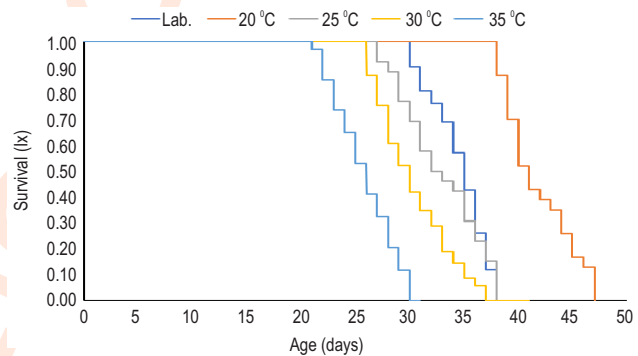


Fig. 8: Kaplan-Meier estimate of survival of *S. frugiperda* under different temperature conditions.

2018). The mean incubation, larval, and pupal durations for *S. frugiperda* were 13.2, 12.9 and 24.5 days at 14 °C and 2.0, 14.6, and 6.6 days at 30 °C, respectively (Garcia *et al.*, 2018). The larval (17.58 days) and pupal (12.97 days) periods were longer at 30 °C in the present investigation, contradicting to the above findings.

The current study found that the fall armyworm *S. frugiperda* was unable to successfully complete its life cycle at 15 °C. The fall armyworm, when raised at 15 °C, died either at the later larval stage or during the pupal stage. These results are consistent with the findings of Du Plessis *et al.* (2020) and contradict the findings of Garcia *et al.* (2018). Du Plessis *et al.* (2020) observed a death rate of 70 % in *S. frugiperda* at 18 °C. The current study found that the complete duration of the lifetime was 43.78 days at 20 °C and 29.19 days at 35 °C. The rise in temperature reduces the lifespan of *S. frugiperda* (Garcia *et al.*, 2018; Du Plessis *et al.*, 2020; Chander *et al.*, 2021). According to Barfield *et al.* (1978), the growth of *S. frugiperda* was slower at

18.3 °C, taking around 66.5 days of lifespan. Conversely, at 35 °C, the development was faster requiring only 18.3 days to complete life cycle. The *S. frugiperda* larvae, which were raised on maize tissues, had average growth durations of 3.3, 1.7, 1.5, 1.5, 2.7 and 3.7 days for the first, second, third, fourth, fifth, and sixth instars, respectively, at 25 °C (Hogg *et al.*, 1982). The present study found that the time it took for the larvae to develop through each of the six instars was as follows: 2.84, 2.67, 2.39, 2.15, 2.12 and 4.19 days at 25 °C. The duration of the sixth larval instar was longer than that of the previous instars in Hogg *et al.* (1982) and present investigation. The larvae raised on sweet corn kernels exhibited developmental periods of 3.0, 2.1, 2.0, 2.2, 2.3 and 3.4 days for the first to sixth instars at 26 °C (Du Plessis *et al.*, 2020). In the present investigation, the larvae reared at 25 °C recorded growth periods of 2.87, 2.68, 2.39, 2.15, 2.12 and 4.19 days for the first to sixth instars. Except for the sixth instar, the developmental periods of other instars corroborate with the findings of Du Plessis *et al.* (2020). Fall armyworm pupae that

Table 2: Life history characters related to oviposition of *S. frugiperda* under different temperature regimes

Parameters	Laboratory condition	Temperature*			
		20°C	25°C	30°C	35°C
Age of first oviposition(days)	27.00 ± 2.15	36.00 ± 2.25 ^b	26.00 ± 1.55 ^a	25.00 ± 2.56 ^a	19.00 ± 1.13 ^a
Age of 50 % oviposition (days)	29.50 ± 1.76	38.50 ± 3.94 ^{bc}	44.50 ± 4.84 ^c	27.00 ± 2.81 ^b	21.00 ± 2.28 ^a
Age of last oviposition (days)	36.00 ± 3.92	45.00 ± 4.69 ^b	36.00 ± 1.40 ^{ab}	35.00 ± 2.17 ^{ab}	28.00 ± 1.09 ^a
Age of maximum oviposition (days)	27.00 ± 1.05	36.00 ± 2.23 ^b	28.00 ± 1.93 ^{ab}	27.00 ± 2.02 ^{ab}	22.00 ± 1.52 ^a
Length of oviposition (days)	9.50 ± 0.66	10.00 ± 0.80 ^a	11.00 ± 0.69 ^a	11.00 ± 0.88 ^a	10.00 ± 0.63 ^a

* Mean values of three replications ± S.E.; Mean with different letters has significant differences (P < 0.05) (Tukey's test)

Table 3: Adult longevity and lifespan of *S. frugiperda* under laboratory and different temperature conditions

Parameters (Mean ± S.E)	Temperature*									
	Laboratory Condition		20°C		25°C		30°C		35°C	
	n	Mean	n	Mean	n	Mean	N	Mean	n	Mean
Male longevity	16	10.42 ± 0.83	14	10.26 ± 1.05 ^a	13	9.45 ± 0.65 ^a	58	9.12 ± 0.99 ^a	19	8.45 ± 0.50 ^a
Female longevity	42	12.71 ± 0.76	23	11.12 ± 1.16 ^a	26	10.85 ± 0.68 ^a	69	10.52 ± 0.41 ^a	34	9.36 ± 1.02 ^a
Male lifespan	16	36.23 ± 3.94	21	43.14 ± 3.43 ^b	13	34.89 ± 3.57 ^{ab}	58	33.45 ± 2.31 ^{ab}	19	26.14 ± 1.01 ^a
Female lifespan	42	35.36 ± 1.37	23	44.25 ± 2.64 ^b	26	35.74 ± 3.72 ^{ab}	69	34.63 ± 2.17 ^{ab}	34	26.79 ± 1.85 ^a
Adults longevity	58	12.43 ± 0.86	37	11.13 ± 1.21 ^a	39	10.42 ± 0.83 ^a	127	11.85 ± 1.21 ^a	53	9.45 ± 0.59 ^a
Total lifespan	58	34.47 ± 2.16	37	44.23 ± 1.72 ^b	39	35.42 ± 2.11 ^{ab}	127	35.36 ± 2.81 ^{ab}	53	27.41 ± 2.81 ^a

* Mean values of three replications ± S.E.; Mean with different letters has significant differences (P < 0.05) (Tukey's test)

were raised at 15 and 35 °C took 37.2 and 5.6 days, respectively, to complete their development (Simmons 1993). The pupal development of *S. litura* required 32.00 days at 18 °C and 8.00 days at 33 °C (Chander et al., 2021). Garcia et al. (2018) investigated the duration of pupal development at 18, 22, 26 and 30°C, which resulted in times of 24.5, 14.6, 9.6 and 6.6 days. Chen et al. (2022) found that the pupal development of *S. frugiperda* took 18.36, 21.47 and 21.53 days when the insects were fed with maize, sorghum, and coix seed at 20 °C. At a higher temperature (30 °C), the pupal development took 7.69, 8.87 and 7.48 days for the corresponding food sources. The results align with the current findings, indicating that higher temperatures led to a decrease in the length of the pupal stage. In the current study, the duration of the pupal stage at 20, 25, 30 and 35 °C was 12.83, 10.27, 9.98 and 7.64 days, respectively (Table 1).

Life history parameters of *S. frugiperda* under different temperature condition: The net reproductive rate (R_0), which measures the number of females in a generation, was seen to have a positive correlation with temperature rise (Table 4) up to 30 °C, but declined at 35 °C. The highest and lowest net reproduction rate (R_0) were recorded at 30 °C and 20 °C correspondingly. The intrinsic rate of natural increase (r_m) exhibited a positive correlation with the increase in temperature. The highest intrinsic rate of natural increase was 0.238 individuals per female per day at 35 °C. This rate was reduced to 0.211 and 0.197 individuals per female per day at 30 and 25 °C, respectively. The finite rate of

increase was 1.15 females per day at 20 °C. At 25, 30 and 35 °C, the number of individuals per female per day increased to 1.22, 1.23 and 1.27, respectively.

The gross reproductive rate, representing the number of individuals per female per life, was 397.11 at 20 °C (Table 4). The highest gross reproductive rate was recorded at 30 °C (652.85 off spring per individual). Life expectancy (e_x) of *S. frugiperda* increased with an increase in temperature; it was expected to live for 47 days at 20 °C and it decreased to 38, 37 and 30 days at 25, 30 and 35 °C. At 20 °C, the population doubling time was observed to be prolonged, whereas at 35 °C, it was shorter. The doubling time was 4.91 days at 20 °C and gradually decreased thereafter. At 25, 30 and 35 °C, the doubling time was 3.52, 3.29 and 2.91 days, respectively. It indicates that at high temperatures, the population of *S. frugiperda* would double in three days, while at low temperatures, it would double in five days. The net reproduction rate (R_0), intrinsic rate of natural increase (r_m), finite rate of rise (λ), and the estimated generation time (T_c) reported in this study were consistent with the reports of Ashok et al. (2021) and Chen et al. (2022) for *S. frugiperda*, as well as with the findings of Acharya et al. (2007) for *H. armigera*.

The net reproductive rate (R_0), gross reproductive rate (GRR), and weekly multiplication of population (A) exhibited an upward trend till reaching a temperature of 30 °C in the present investigation. However, at 35 °C, these rates declined. Prasad et

Table 4: Kinetics of the life history of *S. frugiperda* under different temperature regimes

Parameters (Mean ± SE)	Laboratory condition	20 °C	25 °C	30 °C	35 °C
Net reproductive rate (R_0) (female/female/lifetime)	433.33 ± 2.83	231.00 ± 1.70	286.54 ± 2.06	324.61 ± 1.86	181.18 ± 1.31
Intrinsic rate of natural increase (r) (individuals/individual/year)	0.203 ± 0.001	0.141 ± 0.0002	0.197 ± 0.0001	0.211 ± 0.0007	0.238 ± 0.001
Finite rate of increase (λ) (no./day)	1.22 ± 0.005	1.15 ± 0.009	1.22 ± 0.010	1.23 ± 0.013	1.27 ± 0.015
Mean generation time (T) (days)	29.93 ± 0.37	38.59 ± 0.48	28.71 ± 0.84	27.42 ± 0.59	21.86 ± 0.17
Approximate generation time (Tc) (days)	30.51 ± 0.38	38.98 ± 0.48	29.31 ± 0.86	27.96 ± 0.60	22.41 ± 0.18
Gross Reproductive rate (GRR) (no. of offspring / individual)	575.81 ± 7.18	397.11 ± 4.95	434.81 ± 12.80	652.858 ± 14.10	265.55 ± 2.16
Doubling time (DT) (days)	3.42 ± 0.04	4.91 ± 0.06	3.52 ± 0.10	3.29 ± 0.07	2.91 ± 0.02
Life expectancy (Ex) (days)	38 ± 0.47	47 ± 0.58	38 ± 1.11	37 ± 0.79	30 ± 0.24
Weekly multiplication of population (A) (times/week)	4.14 ± 0.05	2.68 ± 0.03	3.97 ± 0.11	4.38 ± 0.09	5.29 ± 0.04

al. (2022) documented a peak intrinsic rate of growth of 0.138 females per female per day, along with the shortest duration for population doubling of 4.9 days at 30 °C. A rise in temperature leads to a drop in the life table parameters, such as approximate generation time, doubling time, and life expectancy (Chen et al., 2022; Acharya et al., 2022; Ranaweera et al., 2024).

The influence of temperature on the growth and development of *S. frugiperda* was evident from the investigation. Though temperature extremes influenced the life span, the optimum temperatures of 25 and 30 °C did not exhibit an impact on the *S. frugiperda* life span. As the increase in temperature reduces the life cycle, the fall armyworm may adapt to the conditions and increase the damage. This study highlights the need for formulating management strategies in a challenging environment.

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References

- Acharya, M., H. Vyas, M. Gedia and P. Patel: Life table, intrinsic rate of increase and age-specific distribution of *Helicoverpa armigera* (Hübner) on cotton. *Ann. Plant Sci.*, **15**, 338–341 (2007).
- Acharya, R., M.J. Malekera, S.K. Dhungana, S.R. Sharma and K.Y. Lee: 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 (2022).
- Ahmad, S. and M. Ibrahim: Influence of meteorological factors on population dynamics of fall armyworm, *Spodoptera frugiperda*, Lepidoptera: Noctuidae and its varietal susceptibility to FAW. Proceedings of the 1st International Electronic Conference on Entomology, **68**, 10.3390/xxxx (2021).
- Ashok, K., V. Balasubramani, J. Kennedy, V. Geethalakshmi, P. Jeyakumar and N. Sathiah: Effect of elevated temperature on the population dynamics of fall armyworm, *Spodoptera frugiperda*. *J. Environ. Biol.*, **42**, 1098–1105 (2021).
- Bale, J.S., G.J. Masters, I.D. Hodkinson, C. Awmack, T.M. Bezemer, V.K. Brown, J. Butterfield, A. Buse, J.C. Coulson and J. Farrar: Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.*, **8**, 1–16 (2002).
- Barfield, C.S., E. Mitchell and E. Poeb: A temperature-dependent model for fall armyworm development. *Ann. Entomol. Soc. Am.*, **71**, 70–74 (1978).
- Basavaraj, K., M.I. Naik, K. Jagadish and Y. Shadakshari: Studies on age specific fecundity life tables for *Helicoverpa armigera* Hub., on sunflower (*Helianthus annuus* L.). *J. Entomol. Zool. Stud.*, **6**, 1364–1368 (2018).
- Birch, L. C.: The intrinsic rate of natural increase of an insect population. *J. Anim. Ecol.*, **17**, 15–26 (1948).
- Chander, S., M. Husain and G. Baradevanal: Thermal energy

- requirement for tobacco caterpillar *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) development on artificial diet. *J. Agric. Meteorol.*, **23**, 236–241 (2021).
- Chen Y.C., D.F. Chen, M.F. Yang and J.F. Liu: The effect of temperatures and hosts on the life cycle of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Insects*, **13**, 211 (2022).
- Deevey, E.S.: Life table for natural population of animals. *Q. Ver. Biol.*, **22**, 283–314 (1947).
- Du Plessis H., M.L. Schlemmer and M.L. Van den berg: The effect of temperature on the development of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Insects*, **11**, 228 pages (2020).
- Early, R., P. González-Moreno, S.T. Murphy and R. Day: Forecasting the global extent of invasion of the cereal pest *Spodoptera frugiperda*, the fall armyworm. *Neobiota*, **40**, 25-50 (2018).
- Garcia, A., W. Godoy, J. Thomas, R. Nagoshi and R. Meagher: Delimiting strategic zones for the development of fall armyworm (Lepidoptera: Noctuidae) on corn in the state of Florida. *J. Econ. Entomol.*, **111**, 120-126 (2018).
- He, L.M., T.L. Wang, Y.C. Chen, S.S. Ge, K.A. Wyckhuys and K.M. Wu: Larval diet affects development and reproduction of East Asian strain of the fall armyworm, *Spodoptera frugiperda*. *J. Integr. Agric.*, **20**, 736-744 (2021).
- Hogg, D.B., H.N. Pitre and R.E. Anderson: Assessment of early-season phenology of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Mississippi. *Environ. Entomol.*, **11**, 705-710 (1982).
- Howe, C.W. and F.P. Linaweaver Jr.: The impact of price on residential water demand and its relation to system design and price structure. *Water Resour. Res.*, **3**, 13-32 (1967).
- Huang, L.L., F.S. Xue, C. Chene, X. Guo, J.J. Tang, L. Zhong and H.M. He: Effects of temperature on life-history traits of the newly invasive fall armyworm, *Spodoptera frugiperda* in Southeast China. *EcolEvol.*, **11**, 5255–5264 (2021).
- Kalleshwaraswamy, C., R. Asokan, H.M. Swamy, M. Maruthi, H. Pavithra, K. Hegbe, S. Navi, S. Prabhu and G.E. Goergen: First report of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), an alien invasive pest on maize in India. *Pest Mgt. Horti. Ecosys.*, **24**, 23–29 (2018a).
- Kalleshwaraswamy, C., M. Maruthi and H. Pavithra: Biology of invasive fall army worm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) on maize. *Indian J. Entomol.*, **80**, 540-543 (2018b).
- Kalyan, D., M. Mahla, S.R. Babu, R. Kalyan and P. Swathi: Biological parameters of *Spodoptera frugiperda* (J.E. Smith) under laboratory conditions. *Int. J. Curr. Microbiol. Appl. Sci.*, **9**, 2972-2979 (2020).
- Mironidis, G. and M. Savopoulou-Soultani: Development, survivorship, and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) under constant and alternating temperatures. *Environ. Entomol.*, **37**, 16-28 (2014).
- Navik, O., A. Shylesha, J. Patil, T. Venkatesan, Y. Lalitha and T. Ashika: Damage, distribution and natural enemies of invasive fall armyworm *Spodoptera frugiperda* (J.E. Smith) under rainfed maize in Karnataka, India. *Crop Prot.*, **143**, 105536 (2021).
- Nayyar, N., R. Gracy, T. Ashika, G. Mohan, R. Swathi, M. Mohan, M. Chaudhary, N. Bakthavatsalam and T. Venkatesan: Population structure and genetic diversity of invasive fall armyworm after 2 years of introduction in India. *Sci. Rep.*, **11**, 1-12 (2021).
- Nivetha, T., G. Srinivasan, M. Shanthi, A. Gurusamy and S. Vellaikumar: Seasonal incidence and influence of weather factors on the incidence of *Spodoptera frugiperda* (J.E. Smith) on maize. *J. Pharm. Innov. J.*, **11**, 407–410 (2022).
- Ntiri, E.S., P.A. Calatayud, J. Van den berg, F. Schulthess and B.P. Le Ru: Influence of temperature on intra-and interspecific resource utilization within a community of lepidopteran maize stemborers. *PLoS One*, **11**, e0148735 (2016).
- Nurzannah, S.E., S.S. Girsang, M.A. Girsang and R. Effendi: Impact of climate change to fall armyworm attack on maize in Karo District, North Sumatera. IOP Conference Series: *Earth Environ. Sci.*, **484**, 012111 (2020).
- Patel, H.B. D.B. Sisodiya, K. Chavada and S.V. Sapteshvariya: Surveillance of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) Infesting Maize. *Int. J. Curr. Microbiol. App. Sci.*, **11**, 966-975 (2020).
- Prasad, T., M.S. Rao, K. Rao, S. Bal, Y. Muttapa, J. Choudhary and V. Singh: Temperature-based phenology model for predicting the present and future establishment and distribution of recently invasive *Spodoptera frugiperda* (J.E. Smith) in India. *Bull. Entomol. Res.*, **112**, 271-285 (2022).
- Ranaweera, G., A. Muhandiram, A. Kumara, M.B. Ayesmanthi, S.R. Sarathchandra and A.N.M. Mubarak: Association between temperature and life table development of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: noctuidae) under control condition. *Int. J. Trop. Insect Sci.*, **44**, 181–188 (2024).
- Reddy, N.A., Y. Saindane, C. Chaudhari and S. Landage: Biology of fall armyworm *Spodoptera frugiperda* (J.E. Smith) on maize under laboratory conditions. *J. Pharm. Innov.*, **10**, 1997-2001 (2021).
- Shekhawat, S.S., M.S. Ansari and M. Basri: Effect of host plants on life table parameters of *Spodoptera litura*. *Int. J. Pure Appl. Biosci.*, **6**, 324-332 (2018).
- Simmons, A.M.: Effects of constant and fluctuating temperatures and humidities on the survival of *Spodoptera frugiperda* pupae (Lepidoptera: Noctuidae). *Flor. Entomol.*, **76**, 333-340 (1993).
- Suby, S., P.L. Soujanya, P. Yadava, J. Patil, K. Subaharan, G.S. Prasad, K.S. Babu, S. Jat, K. Yathish and J. Vadassery: Invasion of fall armyworm (*Spodoptera frugiperda*) in India: nature, distribution, management and potential impact. *Curr. Sci.*, **119**, 44-51 (2020).
- Swamy, H., R. Asokan, C. Kalleshwaraswamy, Y. Prasad, M. Maruthi, P. Shashank, N.I. Devi, A. Surakasula, S. Adarsha and A. Srinivas: Prevalence of "R" strain and molecular diversity of fall army worm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in India. *Indian J. Entomol.*, **80**, 544-553 (2018).
- Tippannavar, P., C. Talekar, R. Mallapur, S. Kachapur, P. Salakinko and A. Harlapur: An outbreak of fall armyworm in Indian subcontinent: A new invasive pest on maize. *Maydica*, **64**, 10 pages (2019).