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Temperature Effects on the Development of Life Stages of Fall Armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) on Maize

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

The effect of temperature on the development of different life stages of *Spodoptera frugiperda* on maize was assessed at the Centre for Agro Climatic Studies, University of Agricultural Sciences, Raichur at five different constant temperatures *viz*., 18, 22, 26, 30, and 32°C with a constant relative humidity 65 ± 5% for all the temperatures under growth chambers conditions. Over the temperature studied, the duration of different life stages decreased with a rise in temperature from 18 to 32°C. Where, the duration of the egg stage reduced from 6.00 days (1°C) to 2.00 days (32°C); for the larva from 31.50 to 10.10 days and for the pupae from 30.86 to 6.0 days. The temperature ranges of 26 to 30°C were found to be favourable for growth and development whereas the temperature extremities of 18 and 32°C were not favourable for the growth and development of fall armyworm; at 18°C there was no eclosion and at 32°C there was eclosion of adults but mortality occurred within an hour. The linear regression studies revealed that lower developmental threshold temperatures of 11.50, 11.49, 13.90, and 20.13 and corresponding thermal constants of 43, 236, 149, and 494 degree days were recorded for the incubation period, larval period, pupal period and total life cycle respectively in order. The present study revealed that the upper threshold of 32°C and a lower threshold of 18° C were detrimental to the development of fall armyworm life stages. These estimated thermal thresholds and degree days might be used to predict the fall armyworm activity in the field for devising strategies to manage fall armyworms effectively.

Keywords: Biology of fall armyworm; degree days; lower thresholds; upper threshold; temperature.

1. INTRODUCTION

“The fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), was first reported in Africa” (Keerthi et al .2021). “A large area of South and Southeast Asia is highly suitable for the year-round occurrence of the fall armyworm. There are also important invasion routes from Africa into different countries in this region. The pest spread to various areas in 2018 and 2019 and was reported from India, Thailand, Myanmar, China, the Republic of Korea, Japan, the Philippines, Indonesia, and also in Australia. Pest biology, distribution, and abundance are influenced by the relationship between temperature and the development rate [1]. Since the development of insects occurs within a specific temperature range, a temperature change will, therefore, influence the development rate, the duration of the life cycle, and, survival. An increase in ambient temperature to near the thermal optimum of insects causes an increase in their metabolism and, therefore, also their activity”. (Keerthi et al. 2021) As such the temperature might have a direct impact on the life cycle of FAW. Theoretically, the thermal optimum is defined as the temperature at which a species thrives well in terms of growth, reproduction, and survival. When the maximum and minimum temperatures are within the species' optimum it promotes, insects’ growth and development [2]. Further, the length and number of each instar that larvae go through before reaching adulthood are influenced by temperature. Moreover, the relationship between temperature and development rate has a huge impact on pest biology, distribution, and abundance. Increased ambient temperature near the thermal optimum of insects causes an increase in metabolic activities [3].

From an ecological perspective, life tables are useful resources for evaluating, predicting, and comprehending insect population development rates. However, recent publications have focused on revealing the impact of FAW in selected specific temperatures, though the impact of various temperatures has not been revealed [4,5]. Owing to such limitations, our present study was conducted to evaluate the life tables of FAW on selected three different temperature regimes under laboratory conditions.

2. MATERIALS AND METHODS

Response of S. *frugiperda* eggs to different temperatures were assessed by exposing them to five constant temperatures *viz.*, 18, 22, 26, 30, and 32 °C each temperature regime was studied as a separate experiment. *S*. *frugiperda* egg masses were collected from the stock culture and placed in Petri plates (9 cm diameter) consisting of moist filter paper sealed with parafilm. Each egg mass having 100 eggs from the same cohort was observed at a time to determine the development time. The Petri plates with eggs were placed in environmental chambers maintained at different constant temperatures. The eggs were observed daily to determine the hatching rates and development time at each constant temperature. After hatching, larvae from each treatment were collected and shifted to separate vials with fresh leaves of maize until pupation. Vials were checked every day until the larvae pupated. Moulting periods and dead larvae were recorded daily to determine the developmental periods and survival rates at each life stage. Survival rates were calculated based on the number at the beginning and end of each stage. After pupation, pupae were transferred to individual vials to observe adult emergence [6].

2.1 Calculation of Lower Temperature Thresholds and Thermal Constants

"The relationships between temperature (x) and the development rate (y) were determined by using simple linear regression analysis. The lower threshold temperature (t) and the number of degree-days (k) required to complete the development of each stage, were calculated using the equations provided by" [7]. The lower threshold temperature was estimated by setting y = 0 and solving x for the regression equation, y = a + bx, where y = 1/days, x = temperature, a = intercept, and b = slope. The lower temperature threshold was calculated as t = -a/b and the thermal constant for development in the number of degree-days (D): k = 1/b.

The relationship between temperature and the development rate of different larval instars of *S. frugiperda* is illustrated in Fig. 1. Means were used to generating regression lines that described the relationships between temperature and the development rate (1/days). Linear regression equations describing these relationships and calculated lower temperature threshold (t) and the number of degree-days (D) for each life stage are given in Table 2.

2.2 Data Analysis

Data were compared using one-way ANOVA procedure and the means were separated by Tukey post hoc test using IBM SPSS (version 21). Graphical expression created using IBM SPSS (version 21) and Microsoft Excel (version 2010).

The means of developmental period (by stage and instar) and temperature was analysed following one-way ANOVA.

Degree days were also calculated by using

Degree days (°D) = (T - Tb) × Days to develop

T is the temperature at which the pest was reared

Tb is the minimum threshold or base temperature

3. RESULTS

The present findings revealed that the incubation period of *S. frugiperda* was significantly influenced by temperature between 18°C to 32°C (Table 1). The egg developmental period was found to decrease with an increase in temperature from 6.00 days (18°C) to 2.00 days (32°C). At 22°C the incubation period recorded was 4.30 days whereas, it was 3.00 days at 26°C. The incubation period of 2.4 days was recorded at 30°C which did not differ significantly from 32°C (2.00) days. There were significant differences in the incubation periods at different treatments of 18, 22, and 26°C except for 30 and 32°C, there is a non-significant difference. The relationship between temperature and the development rate of the egg period of *S. frugiperda* at different constant temperatures is illustrated in (Fig. 1). Percent egg hatching varied from 30-96 percent at different constant temperatures with minimum hatching at 18 °C and maximum hatching at 26°C.

The mean developmental time of eggs decreased from 9.51 days at 18°C to 3.10 days at 34°C at 34°C, but increased to 3.58 days at 35°C, indicating a non-linear response at extreme temperatures was reported by Padmavathi et al*.,* 2014.

Gayathri et al., 2016 reported that the egg developmental stage of *Spodoptera litura* on Soybean decreased from increasing temperature from 10.71 days at 15°C to 1.9 days at 35°C temperature which is in line with the present study.

Although there was egg development at 32°C neonates died due to exposure to high temperatures. The mean developmental time of eggs varied from 6 days at 18°C to 2 days at 32°C indicating linear response to increasing temperatures. The present findings are in line with an earlier study by Gayathri et al. (2021) who reported mean developmental period of *Helicoverpa armigera* (Hubner) eggs decreased with an increase in temperature 10.7 days (at 15°C) to1.9 days (at 35°C). Similarly, Du Plessis et al. [2] documented a mean incubation period of 6.38 days at 18°C and 2.00 days at 32°C in fall armyworm when reared on maize.

The total larval development period was inversely related to a temperature between 18°C to 32°C. Larval development showed a linear response of decreasing developmental durations for all the instars with an increase in temperature (Fig. 2). The total larval development period was inversely related to a temperature between 18°C and 32°C as given in Table 1, statistically significant differences were recorded between the mean larval duration at the five different constant temperatures were observed. In general, the developmental duration of the *S. frugiperda* larvae decreased with the increasing constant temperature from 18°C (31.50 days) to 32°C (10.10 days). The larval duration of 20.66, 17.02, and 13.06 days was recorded at 22, 26, and 30°C, respectively. All instars of the fall armyworm showed a similar trend where larval development decreased with an increase in temperature. Fall armyworm completed its development at all temperatures from 26-30°C but did not well develop at 18, 22, and 32°C.

The development of pupa was also inversely related to temperature. The pupal period varied from 30.86 days (at 18°C) to 6 days (at 32°C). A pupal period of 8.42 days was recorded at 26°C followed by 7.00 days at 30°C. At 22°C the pupal period was 12.60 days (Table .1). The pre-pupa and pupa developed were deformed at 32°C and the adults that emerged were feeble with deformed wings. The present results are in with Du Plessis et al*.,* 2022 where the pupal development of *S. frugiperda where* pupal development time ranged between 7.82 and 30.70 days at 32 and 18°C which is in a similar range in our present studies 6 days to 30.86 days at 32 and 18°C, whereas he also reported that pupa of *S. frugiperda* survived at 10 even up to although no moths emerged from pupa.

The male longevity varied significantly among different constant temperatures from 18°C to 32°C. The male adult longevity of 7.44 days at 22°C followed by 7.36 days at 26°C and 4.30 days at 30°C. At 32°C, the adult longevity was just a day. The female longevity of 8.80 days was recorded at 22°C followed by 8.08 days at 26°C and 5.30 days at 30°C. The female longevity was one day at 32°C. The present findings are by Dahi et al*.* [7] where the pupal period of *S. frugiperda* decreases with a rise in temperature from 22.5 days at 20°C to 7.7 days at 30°C.

The total life cycle of *S. frugiperda* was 49.14 and 47.78 days at 22°C, 38.02 and 37.30 days at 26°C, 29.06 and 28.06 days at 30°C and 21.10 and 20.34 days for females and males respectively in order at 32°C. There was no eclosion recorded at 18°C and the temperature was not found to be suitable for *S. frugiperda* eclosion. The temperature of 32°C was found to be harmful to the growth and development of fall armyworm; the adults emerged at this temperature where feasible with wing deformity and died within one hour of emergence. There was no mating recorded at 18, 22, and 32°C.

3.1 Thermal Units

Table 2 and Fig. 2 indicated that a lower temperature threshold of development (t_0) and average thermal units in degree-days (dd's) were required for the completion of the development of *S. frugiperda* stages. It was 11.50°C and 42.90 dd's for the egg stage. Data in Table 2 and Fig. 1 indicated that the lower threshold of development (t_0) and average degree-days (dd's) required for the completion of development for *S. frugiperda* larval stage, it was 11.49°C and 234.52 dd's. The lower threshold of development (t_0) and average degree-days (dd's) required for the completion of development for *S. frugiperda* larval stage was 13.91°C and 148.86 dd's and lower threshold of development (t_0) and average degree-days (dd's) required for the completion of development for *S. frugiperda* larval stage, it was 20.13°C and 424.66 dd's Table 3 and Fig. 2).

The degree day requirements to complete the egg stage at 18, 22, 26, 30, and 32°C were 39.00, 45.15, 44.95, 44.40, and 41.00 dd's respectively. And for six larval instars, 53.84, 32.16, 24.11, 35.36, 38.87, and 30.15 dd's, respectively were required to complete the larval stages at 18°C. In total, the larvae of *S. frugiperda* required 214.3 degree days to complete their development at 18°C (Table 3). The degree day accumulated to complete the first, second, third, fourth, fifth, and sixth-instar larvae were 53.64, 30.07, 22.70, 33.23, 37.69, and 41.03 dd's, respectively at 32 °C. In total, the larvae of *S. frugiperda* required 187.54 degree days to complete their development at 32 °C (Table 3). The lower threshold of development (t_0) and average degree-days (dd's) required for the completion of development for *S. frugiperda* pupal stage was 13.91°C and 148.86 dd's and the lower threshold of development (t_0) and average degree-days (dd's) required for the completion of development for *S. frugiperda* larval stage, it was 20.13°C and 424.66 dd's (Table 3 and Fig. 2).

Table 1. Mean development time for different life stages of *Spodoptera frugiperda* on maize

Temp. regimes (°C)	Biological parameters of *S. frugiperda* at different constant temperatures (Mean ± SE)															
	Egg Period (Days)	**Egg Hatchability (%)**	**I instar**	**II instar**	**III instar**	**IV instar**	**V instar**	**VI Instar**	**Total Larval Period (Days)**	**Larval Mortality (%)**	**Pre Pupal Period (Days)**	**Pupal Period (Days)**	**Adult male longevity (Days)**	**Adult female longevity (Days)**	**Total life cycle Male**	**Total life cycle Female**
18	6.00 ± 0.03^{a}	30	4.22 ± 0.04^{a}	4.27 ± 0.05^{a}	4.95 ± 0.06^{a}	5.17 ± 0.04^{a}	5.58± 0.05^{a}	6.67 ± 0.05^{a}	31.50 ± 0.01^{a}	60	4.00 ± 0.00^{a}	30.86 ± 0.01^{a}	-	-	-	-
22	4.30 ± 0.04^{b}	52	4.00 ± 0.00^{b}	3.01 ± 0.05^{b}	2.57 ± 0.07^{c}	2.69 ± 0.05^{b}	3.41± 0.10^{b}	5.00 ± 0.05^{b}	20.66 ± 0.01^{b}	40	2.78 ± 0.04^{b}	12.60 ± 0.01^{b}	7.44 ± 0.07^{a}	8.80 ± 0.04^{a}	47.78 ± 0.08	49.14± 0.06
26	3.00 ± 0.00^{c}	96	3.00 ± 0.00^{c}	2.47 ± 0.05^{c}	2.55 ± 0.05^{c}	2.78 ± 0.04^{b}	3.00 ± 0.00^{c}	3.02 ± 0.03^{c}	17.02 ± 0.02^{c}	16	1.50 ± 0.05^{c}	8.42 ± 0.02^{c}	7.36 ± 0.05^{b}	8.08 ± 0.07^{b}	37.30 ± 0.05	38.02± 0.05
30	2.40 ± 0.05^{e}	90	2.90 ± 0.03^{d}	2.28 ± 0.05^{d}	1.68 ± 0.05 ^{d}	1.68 ± 0.05^{d}	2.20 ± 0.04^{d}	2.15 ± 0.00^{d}	13.06± 0.01^{d}	22	1.30 ± 0.05^{d}	7.00 ± 0.02^{d}	4.30 ± 0.07^{c}	5.30 ± 0.05^{c}	28.06 ± 0.07	29.06± 0.07
32	2.00 ± 0.00^{d}	44	2.00 ± 0.00^{e}	1.40 ± 0.05^{e}	1.16 ± 0.04^{e}	1.60 ± 0.05^{e}	1.80 ± 0.06^{e}	2.03 ± 0.04^{e}	10.10± 0.01^{e}	30	1.24 ± 0.04^{e}	6.00 ± 0.02^{e}	1.00 ± 0.00^{d}	1.00 ± 0.00^{d}	20.34 ± 2.03	21.10± 2.11
SEm(±)	0.13	-	0.02	0.01	0.01	0.01	0.01	0.02	0.04	-	0.03	0.05	0.06	0.07	0.03	0.05
CD (1%)	0.54	-	0.08	0.04	0.03	0.04	0.04	0.07	0.15	-	0.12	0.21	0.24	0.28	0.12	0.16
CV(%)	8.39	-	2.79	1.36	0.89	1.30	1.26	1.79	0.45	-	2.98	0.89	6.71	6.85	5.11	6.14

'' indicates no eclosion was observed at that temperature, Number of eggs taken=100, Number of larvae taken=100*
SE = Standard Error
SEm = Standard error of mean
CD = Critical difference
CV= Coefficient of variation

Table 2. Linear regression between the development rate and temperature for different developmental stages of *S. frugiperda*

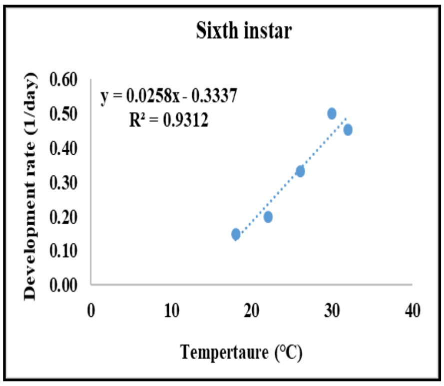
Development Stages	Regression model	K ± SE	t ± SE	R^2-Value
Egg	y = 0.0233x - 0.2683	42.90 ± 0.02	11.50 ± 0.03	R^2 = 0.98
I instar	y = 0.0163x - 0.0845	61.83 ± 0.05	5.18 ± 0.02	R^2 = 0.80
II instar	y = 0.028x - 0.2945	36.03 ± 0.05	10.52 ± 0.03	R^2 = 0.79
III instar	y = 0.0361x - 0.4721	28.51 ± 0.07	13.08 ± 0.02	R^2 = 0.75
IV instar	y = 0.0301x - 0.3381	33.59 ± 0.07	11.23 ± 0.03	R^2 = 0.95
V instar	y = 0.0249x - 0.2754	40.54 ± 0.06	11.06 ± 0.03	R^2 = 0.96
VI instar	y = 0.0258x - 0.3337	37.59 ± 0.06	13.35 ± 0.02	R^2 = 0.93
Total larval period	y = 0.0045x - 0.0517	234.52 ± 0.03	11.49 ± 0.02	R^2 = 0.96
Pupa	y = 0.0092x - 0.1277	148.86 ± 0.07	13.91 ± 0.01	R^2 = 0.99
Total life cycle	y = 0.0014x - 0.0056	494.12 ± 0.08	20.13 ± 0.05	R^2 = 0.96

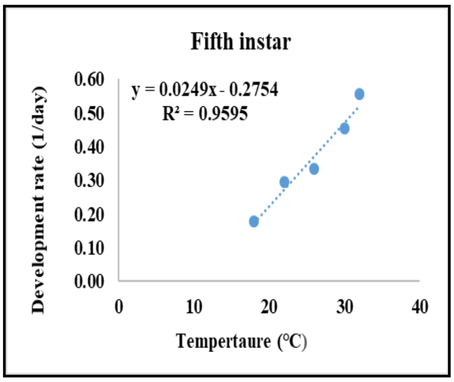
t = Estimated lower temperature threshold
K = Estimated thermal unit's in degree-days

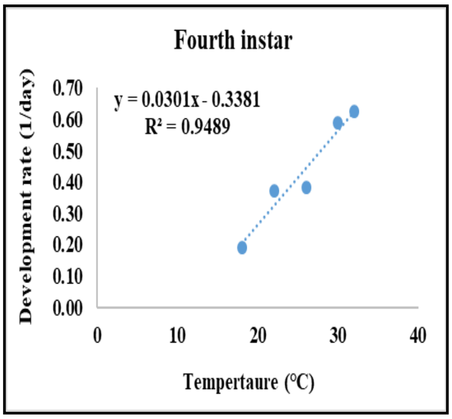
Table 3. Accumulated degree days for *S. frugiperda* under different constant temperatures

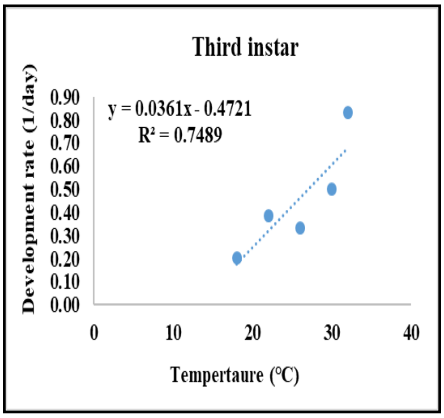
Stage	Degree-days(˚D)							
	18 ˚C	22 ˚C	26 ˚C	30 ˚C	32 ˚C	SEm (±)	CD (1%)	CV (%)
Egg	39.00^{e}	45.15^{a}	44.95^{b}	44.40^{c}	41.00^{d}	0.12	0.49	0.63
I instar	53.84^{a}	67.28^{b}	62.46^{c}	71.98^{a}	53.64^{d}	0.23	0.91	0.81
II instar	32.16^{d}	34.44^{c}	38.70^{b}	44.80^{a}	30.07^{e}	0.29	1.18	1.79
III instar	24.11^{c}	23.19^{d}	38.76^{a}	33.84^{b}	22.70^{d}	0.15	0.60	1.17
IV instar	35.36^{c}	29.07^{d}	38.40^{b}	31.90^{a}	33.23^{a}	0.18	0.70	1.07
V instar	38.87^{c}	37.19^{e}	44.82^{a}	41.69^{b}	37.69^{d}	0.13	0.54	0.74
VI instar	30.15^{e}	43.25^{a}	37.95^{c}	35.60^{d}	41.03^{b}	0.11	0.45	0.66
Larval stage	214.13^{c}	211.88^{d}	240.24^{a}	237.39^{b}	187.54^{e}	0.31	1.26	0.32
Pupal	124.99^{a}	101.93^{d}	101.80^{d}	112.63^{b}	108.54^{c}	0.20	0.79	0.40
Adult	0.00^{e}	15.52^{c}	44.03^{b}	52.61^{a}	11.87^{d}	0.01	0.05	0.61
Total life cycle	378.29^{c}	374.48^{d}	468.97^{a}	447.03^{b}	348.95^{e}	-	-	-

Values mentioned in vertical rows are the number of heat units required to complete each stage at that particular constant temperature.
Degree days (˚D) = (T - Tb) × Days to develop
T is the temperature at which the pest was reared
Tb is the minimum threshold or base temperature









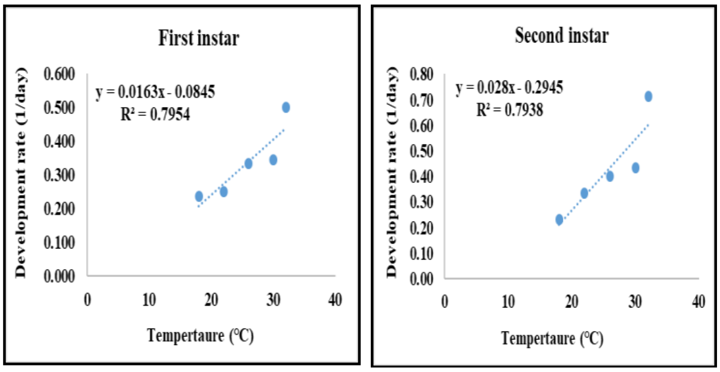


Fig. 1. The relationship between *S. frugiperda* development rates and rearing temperature for larval instars one to six

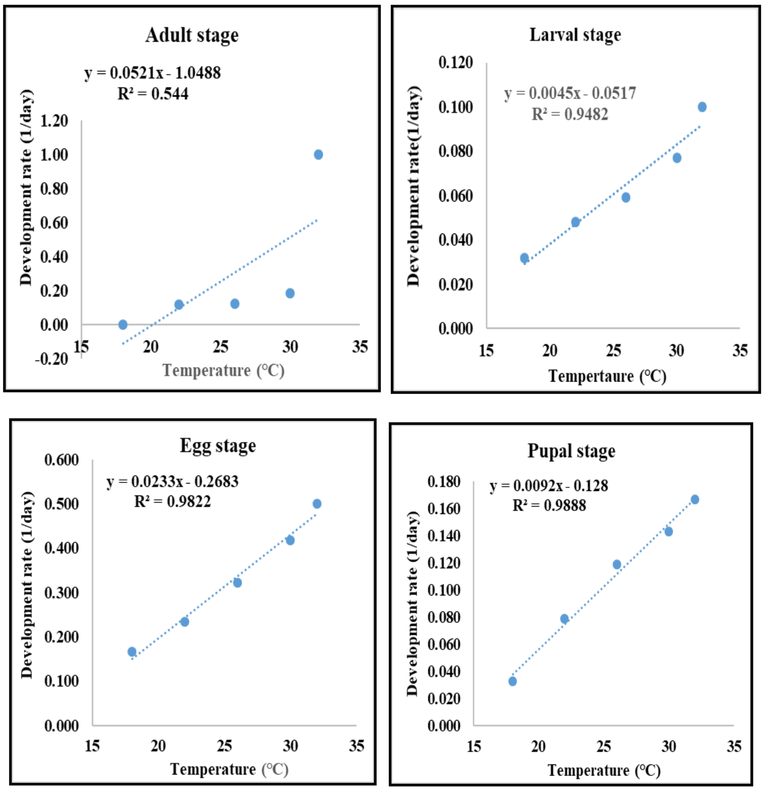


Fig. 2. The relationship between *S. frugiperda* development rates and rearing temperature for each stage

4. DISCUSSION

The relationship between temperature and the development rate of the egg period of *S. frugiperda* at different constant temperatures is illustrated in Fig. Per cent egg hatching varied from 30-96 per cent at different constant temperatures with minimum hatching at 18°C and maximum hatching at 26°C (Table 2). The present findings are in line with a study made by Gayathri et al. (2021) who reported mean developmental period of *Spodoptera litura* eggs decreased with an increase in temperature from 10.7 days (15°C) to 1.9 days (35°C). Similarly, Du Plessis et al. [2] documented a mean incubation period of 6.38 days at 18°C and 2.00 days at 32°C in fall armyworm when reared on maize.

The larval mortality was highest at 18°C with 60 per cent indicating that a constant temperature of 18°C was not suitable for the development of *S. frugiperda* larvae. The lowest larval mortality occurred at 26°C with 16 percent (Table 2 and Fig. 2). Our results are following Du Plessis et al. [2] who published that the most favourable temperature for the development and survival of *S. frugiperda* reared on maize was 26°C. At 32°C duration of developmental stages was significantly shorter than at lower temperatures, but larval mortality was high (Fig. 2).

The present findings are per the results of Du Plessis et al. [2] where they reported the lower thresholds for egg, larva, pupa, egg to adult were 13.01,12.12,13.06 and 12.57°C, respectively and the degree days required are 35.73,202.66,150.29 and 390.41 dd's, respectively. The present results are closely corroborated with the findings of Dahi et al. [7] who documented the estimated lower threshold for egg, larva, pupa, and egg to adult was 15.79,10.39,14.05, and 12.49°C respectively. The number of degree days required for each stage was 30,10.99,14.05 and 527.3 dd's, respectively. Pavithra et al. (2022) studied the impact of five different temperatures on the growth and development of tomato leaf miner, *Tuta absoluta* where they reported that egg, larval and pupal decreased with an increase in temperature (10 to 40°C) and the duration of egg to adult was shorter at 32 and longer at 18°C [8-10].

"Knowledge of the temperature thresholds of insects is important for predicting their potential distribution. The respective developmental stages have specific temperature requirements, which are important for survival in specific environments. The threshold temperatures determined in this study can be used to refine existing models estimating the areas suitable for crop cultivation to which *S. frugiperda* can migrate from its overwintering sites as well as areas with suitable environmental conditions for persistent occurrence" [7].

5. CONCLUSION

The optimal range for egg, larval and egg-to-adult development of *S. frugiperda* was between The minimum temperature threshold for egg development was 11.50°C, and that for larvae and pupae was 20.13 and, 13.91°C, respectively. This indicates that *S. frugiperda* populations will not develop and persist in geographical regions where temperatures decrease to below these levels.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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