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Temperature-dependent Life History Traits of Fall Armyworm, *Spodoptera frugiperda*

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ABSTRACT

Background: A mid-May 2018 outbreak of fall armyworm (FAW) was witnessed in Karnataka and it then spread rapidly across the country, causing extensive damage to maize crop. It is ideally adapted to tropical and subtropical environments around the world. Temperature has a major role in synchronizing its invasion and life cycle since it does not go into diapause.

Methods: An investigation was conducted, to examine the life-history parameters of fall armyworm (FAW), *Spodoptera frugiperda* Smith fed with maize foliage at five different temperatures *viz.,*18, 20, 25, 30, 35 and 40±1°C, under 14 hr light and 10 hr dark cycle maintained inside a BOD incubator.

Result: Results revealed an inverse relation between developmental stages of eggs, larvae and pupae and growing temperatures, wherein the fastest growth occurred at 35°C and no development was observed at 40°C. Maximum percentage hatchability was noticed at 25°C (94.2%), while it decreased both at higher and lower temperatures. The larval developmental duration decreased from 34.08 days at 18°C to 10.06 days at 35°C. The duration of pupal development was also minimum at 35°C, taking 7.22 days. Adult longevity decreased linearly with an increase in temperature where females outlived males at all temperatures except at 18°C. The thermal constants for development were estimated at 45.92 (egg), 245.34 (larvae), 169.64 (pupae) and 466.06 degree days (total).

Key words: Degree-days, Development time, Fall armyworm, Lower thermal threshold, Thermal constant.

INTRODUCTION

Various species of insects inhabit diverse climates across different regions of the globe. The ongoing climate change process, particularly the increase in global temperatures, significantly influences multiple aspects of insect morpho physiology. Amongst these, several effects involve developmental processes, distribution patterns, population dynamics, life cycle alterations and mortality rates (Ashok *et al.,* 2021). During recent years, fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith), has become prevalent as an economically devastative pest worldwide. This species belongs to the Lepidoptera family, Noctuidae order and thrives mostly tropical and subtropical regions of United States. Initial studies of this pest focused on climates within the States; however, the pest has further spread, with evidence of its first occurrence in the African continent (Goergen *et al.,* 2016) and subsequently extended its reach to Asia (Keerthi *et al.,* 2023). Later, it invaded India and spread subsequently throughout the country, raising concerns due to its gregarious feeding behaviour and ability to consume a wide range of crop species (Sharanabasappa *et al.,* 2018; Ganiger *et al.,* 2018; Montezano *et al.,* 2019).

In case of ectotherms, environmental temperature is viewed as one of the most essential factors for phenotypic flexibility (Huang *et al.*, 2021), also influencing numerous life-history traits of insects. The degree of responsiveness to elevated temperatures is generally positive within an optimal thermal range, suggesting that higher temperatures increase metabolic rates and consequently promote growth, reduce development time and decrease adult size (Hance *et al.,* 2007). Organisms respond to thermal conditions for which degree days are calculated using average temperature. According to Prathima *et al.* (2023), growth and multiplication of FAW intensified with increase in both maximum and minimum temperatures. These thermal units are crucially important in the life cycle of insects, as they enable optimal heat for reproduction and development from eggs to adulthood (Begon *et al.,* 2006). Precise utilisation of these thermal units facilitates the accurate prediction of the development and growth of agriculturally important pests (Jin *et al.,* 2022). One of the most frequently employed methods in modelling insects, diseases and plants involves tracking the daily average temperature rise above a specific temperature or baseline temperature (Ashok *et al*., 2021). Moreover, the use of data from studies conducted on insect

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pest species under stable environmental conditions might be employed in forecasting the changes in development of these pests influenced by seasons/phenological periods, population dynamics and times at which control measures should be recommended. Objectives of the present study were to determine the developmental rate at constant temperature and to estimate the heat units (degree-days, °D) accumulated for the completion of each stage in *Spodoptera frugiperda*. This study also aimed at establishing a quantitative relationship among the °D required to develop from egg to adult.

MATERIALS AND METHODS

S. frugiperda larvae for the F0 generation were collected from a naturally infested maize field at SOA University's Agriculture Research Station in Khordha District, Odisha. They were reared individually in ventilated plastic containers (7.5×2.5 cm) with maize leaves as food under controlled laboratory conditions (26±1°C, 65±5% RH, 14L: 10D) during the year 2022-23. Containers were regularly cleaned and maize leaves replaced every 48 hours. After sex determination, pupae were moved to an oviposition cage (34×34×40 cm) with a cotton swab soaked in 5% honey solution for adult nutrition and two 30-day-old potted maize seedlings for egg-laying. The collected eggs were used for experiments. F1 eggs were divided into five groups of ~100 eggs each in Petri dishes, transferred to BOD incubators at 18, 20, 25, 30, 35 and 40±1°C. Eggs were monitored twice daily for hatching and unhatched eggs by the experiment's end were deemed non-viable. Number of eggs hatched, incubation period were observed and hatching percentages were calculated. Post-hatching, 100 larvae (20 per replicate) were moved to plastic vessels with maize leaf pieces in BOD incubators at the same temperatures. Larval development and mortality were observed daily from first to sixth instar using shed exuviae. The pre-pupal and pupal stadia were held together as one stadium, the pupal growth stage. Pupae were then checked daily for emergence of the adult moths, noting their duration of emergence. Adult males and females were then put together in mating cages for observation of their reproductive behaviour.

One-way ANOVA compared the means of the temperature treatments, maintaining the normality of distribution and homogeneity of variance assumptions. These assumptions had been checked by means of Shapiro-Wilk's test of normality and Levene's test of homogeneity of variance. Data analyses were performed with IBM SPSS version 28; post-hoc comparisons applied Tukey's HSD. A linear regression was done to determine the development rate of temperature (x) and development rate (y). For determination of threshold temperatures (t) and degree-days (k) for all stages, the equation developed by Campbell *et al.* (1974) was used. The lower temperature threshold was determined by setting y to 0 and solving for x in the regression equation.

$$y = a + bx$$

Where:
y = 1/days.
x = Temperature.
a = Intercept.
b = Slope.

The lower thermal threshold was derived as t = -a/b and the thermal constant (°D) as k = 1/b. Regression lines were plotted using mean values for describing the relation between temperature and development rate (1/days). These linear regression equations were used to derive t and k for each life stage.

$$°D = (T - Tb) \times D$$

Where:
T = The rearing temperature of the pest.
Tb = Minimum threshold or base temperature.
D = Number of days taken by the stage to complete the development at a constant temperature (T).

RESULTS AND DISCUSSION

Impact of temperature on developmental time, hatching, larval survivability and pupation

In this study, the egg, larval and pupal development duration, as well as adult longevity of *S. frugiperda*, inversely correlated with temperature. Egg incubation was notably affected by temperatures between 18°C and 35°C, with no hatching at 40°C. As temperatures rose, egg development shortened from 6.48 days at 18°C to 2.00 days at 35°C (Fig 1). Egg hatching rates increased from 18°C to 25°C then declined up to 35°C, with optimal hatchability at 25°C (94.2%) and 30°C (89.2%) (Fig 5). Larval development period decreased from 34.08 days (18°C) to 10.06 days (35°C) (Fig 2), with survival rates improving from 18°C to 30°C but dropping at 35°C. The highest larval survival was at 30°C (95%) and the lowest at 18°C (46%) (Fig 5). Pupal development spanned 30.64 days at 18°C, reducing to

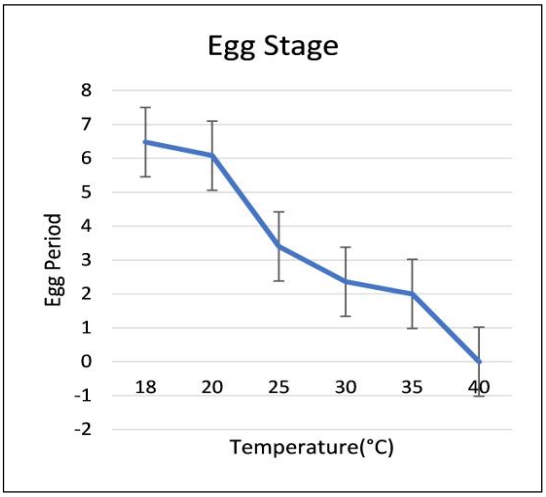


Fig 1: Egg period of *S. frugiperda* at different temperatures.

7.22 days at 35°C (Fig 3), showing a clear inverse relationship with temperature. The highest percent pupation was observed at 30°C (98.71%) and second highest at 25°C (97.14%) (Fig 5). The period from egg to adult emergence was longest at 18°C (71.20 days) and shortest at 35°C (19.44 days) (Fig 4). Adult longevity varied significantly with temperature, with females generally outliving males except at 18°C (females: 13.92 days, males: 13.94 days) (Fig 6). Adult longevity decreased with higher temperatures, with the shortest lifespans at 35°C (females: 7.92 days, males: 7.04 days).

Egg development times at 30 and 35°C were similar, aligning with Du Plessis *et al*. (2020), who found no significant difference between 30 and 32°C. The highest egg hatchability was at 25°C, followed by 30°C, indicating moderate to warm temperatures enhance viability. A significant drop in hatching success at 35°C suggests high temperatures cause physiological stress in embryos. Larval development time decreased as temperature increased from 18°C to 35°C, showing an inverse relationship. Rapid development at higher temperatures, a common insect adaptation, was paired with reduced larval survival rates at 35°C, aligning with Ashok *et al*. (2021), indicating higher temperatures increase metabolic demand, potentially overwhelming larvae (Malekera *et al.,* 2022). The total developmental period from egg to adult was longest at 18°C and shortest at 35°C, similar to Savadatti *et al*. (2023), who noted a lifecycle decrease from 47.78 to 20.34 days for males and 49.14 to 21.10 days for females as temperature rose from 18°C to 35°C. Rapid lifecycle completion at higher temperatures benefits *S. frugiperda* in warm regions, enabling multiple generations per season, but reduced survival rates indicate an upper limit to temperature's beneficial effects on population dynamics. Rising temperatures resulted in reduced adult lifespans, a common trend in insects. Shorter adult longevity at higher temperatures matches findings in *S. frugiperda*, where elevated temperatures accelerated metabolic rates and reduced lifespan (Day *et al.,* 2017). Female longevity generally exceeded male longevity except at 18°C, due to reproductive roles indicating enhanced resilience to temperature fluctuations. High thermal stress at 35°C reduced adult lifespan for both sexes, indicating elevated temperatures negatively impact physiological performance, leading to premature mortality, confirmed by Mironidis (2014), who found fluctuating temperatures significantly affected lifespan.

Determination of lower threshold temperature (t), thermal constant (k) and degree days (°D).

Fig 7 shows relationship between the temperature and development rate the immature stages of *S. frugiperda*. Mean values were used to calculate the regression lines

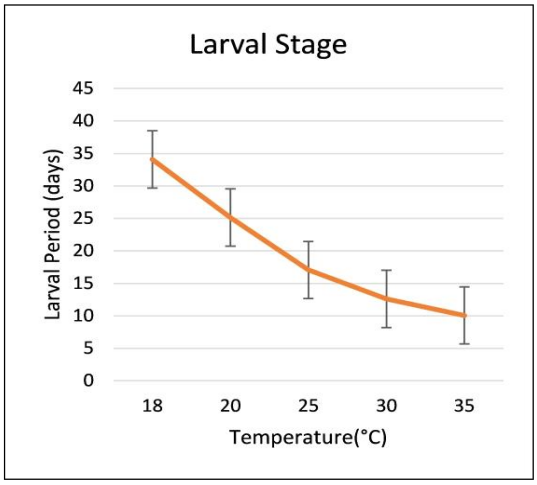


Fig 2: Larval period of *S. frugiperda* at different temperatures.

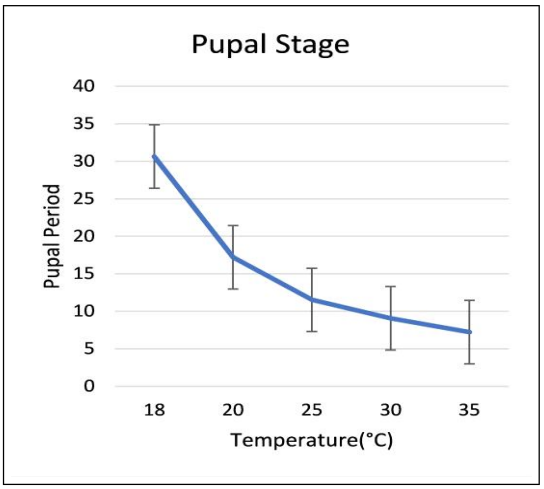


Fig 3: Pupal period of *S. frugiperda* at different temperatures.

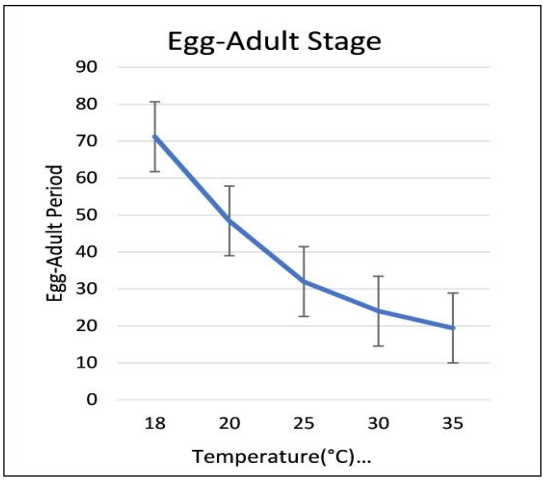


Fig 4: Egg to adult duration of *S. frugiperda* at different temperatures.

showing relationships between temperature and development rate expressed as 1/days. Linear regression equations describing these relationships, with estimates of thermal requirements, are given in Table 1. For egg development, the thermal constant (k) was determined to be 45.92, whilst for larval and pupal development, it was found to be 245.34 and 169.64, respectively. The lower thermal threshold (t) for the first instar larva was computed at 6.08°C, which is considered exceptionally low. At 18°C, the highest percent larval mortality of 54% was observed and the first instar larvae was highly susceptible. The linear regression analysis revealed that the minimum threshold temperature for development of egg and larvae were 11.49°C and 10.55°C respectively. Lower thermal threshold for the pupal stage was observed to be 11.11°C, while for the entire life cycle from egg to adult, it was found to be 10.92°C. The mean accumulated °D required for the completion of immature stages were determined to be 46.84, 245.80 and 173.53, for egg, larva and pupa, respectively, at varying temperatures from 18 to 35°C. The total degree days required for development of *S. frugiperda* from egg to adult was calculated as 466.06 (Table 2).

The effect of temperature on the development of *S. frugiperda* was examined through regression analysis and thermal requirements. Linear regression indicated a significant relationship (R^2= 0.963-0.995) between temperature and development rates for all the life stages of FAW. The lower thermal threshold for egg development was 11.49°C, with a thermal constant of 45.92 °D, slightly differed–from Prasad *et al.* (2022) who reported 12.10°C and Du Plessis *et al.* (2020) reported 13.01°C, may be due to regional or methodological variations. The larval development threshold was 10.55°C with a thermal constant of 245.34 °D, aligning with Silva *et al.* (2017) who reported that thresholds around 10°C and constants between 240-250 °D. The egg threshold is higher than the

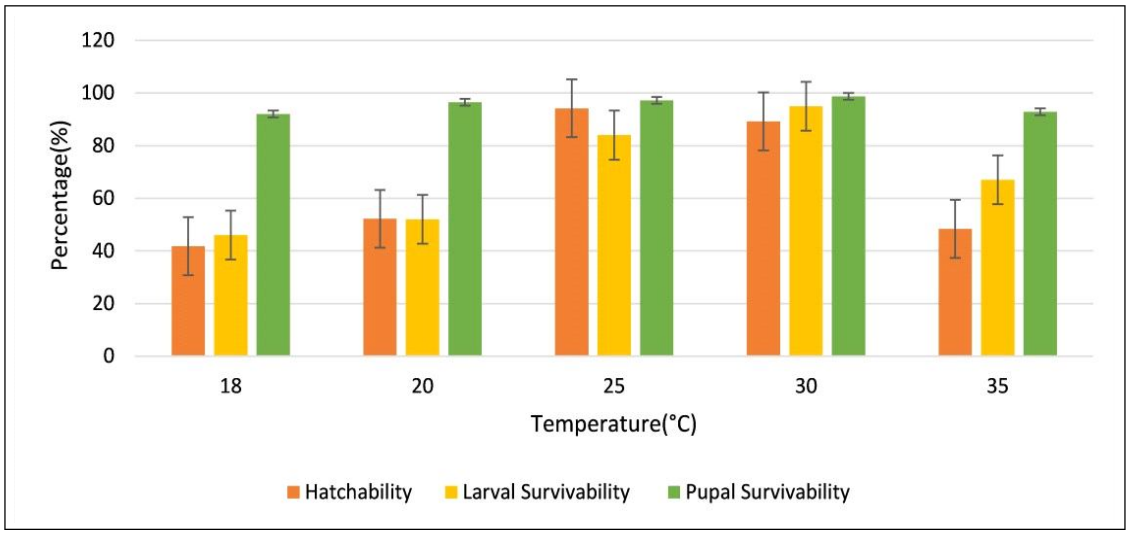


Fig 5: Egg hatching, larval and pupal survivability (%) of *S. frugiperda* at different temperatures.

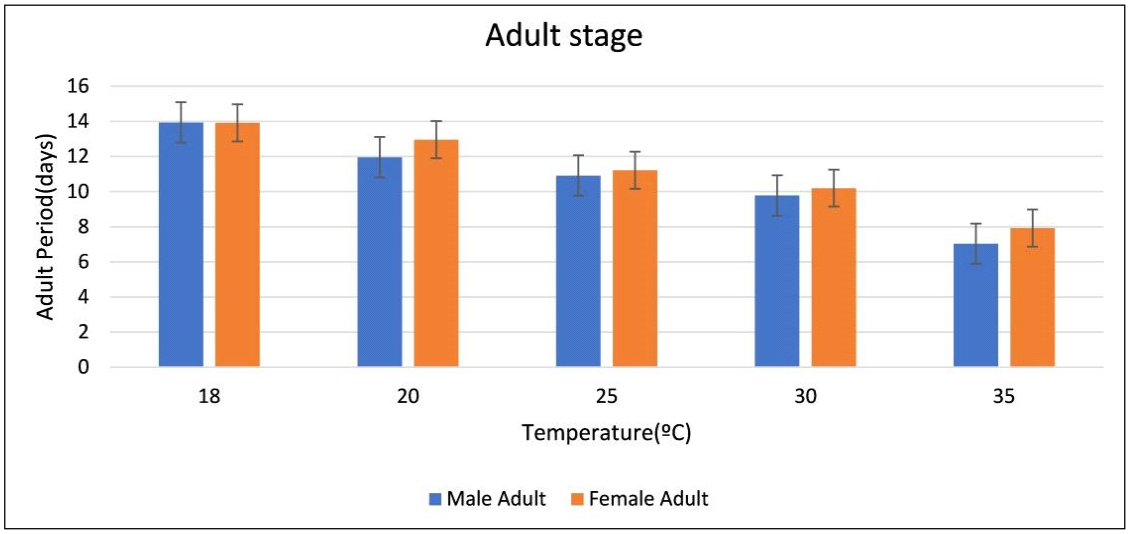


Fig 6: Adult longevity of *S. frugiperda* at different temperatures.

larval threshold, indicating eggs won't hatch at temperatures unsuitable for larvae (Du Plessis *et al.,* 2020). High larval mortality at 18°C likely results from early instar sensitivity to low temperatures, consistent with Reed *et al.* (2021). The pupal stage had a threshold of 11.11°C and a thermal constant of 169.64 °D, matching studies reporting thresholds near 11°C and constants around 170 °D (Sisay *et al.,* 2018). These findings suggest the pupal stage is highly conserved, serving as a reliable time-temperature model for developmental timelines. The total degree-days for FAW to complete the egg-to-adult stage was 466.06 °D, with a lower thermal threshold of 10.92°C, consistent with Nagoshi *et al*. (2020) who estimated 450-470 °D. Yan *et al.* (2022) also emphasized the importance of thermal thresholds for predicting future climate impacts on *S. frugiperda* survival and distribution.

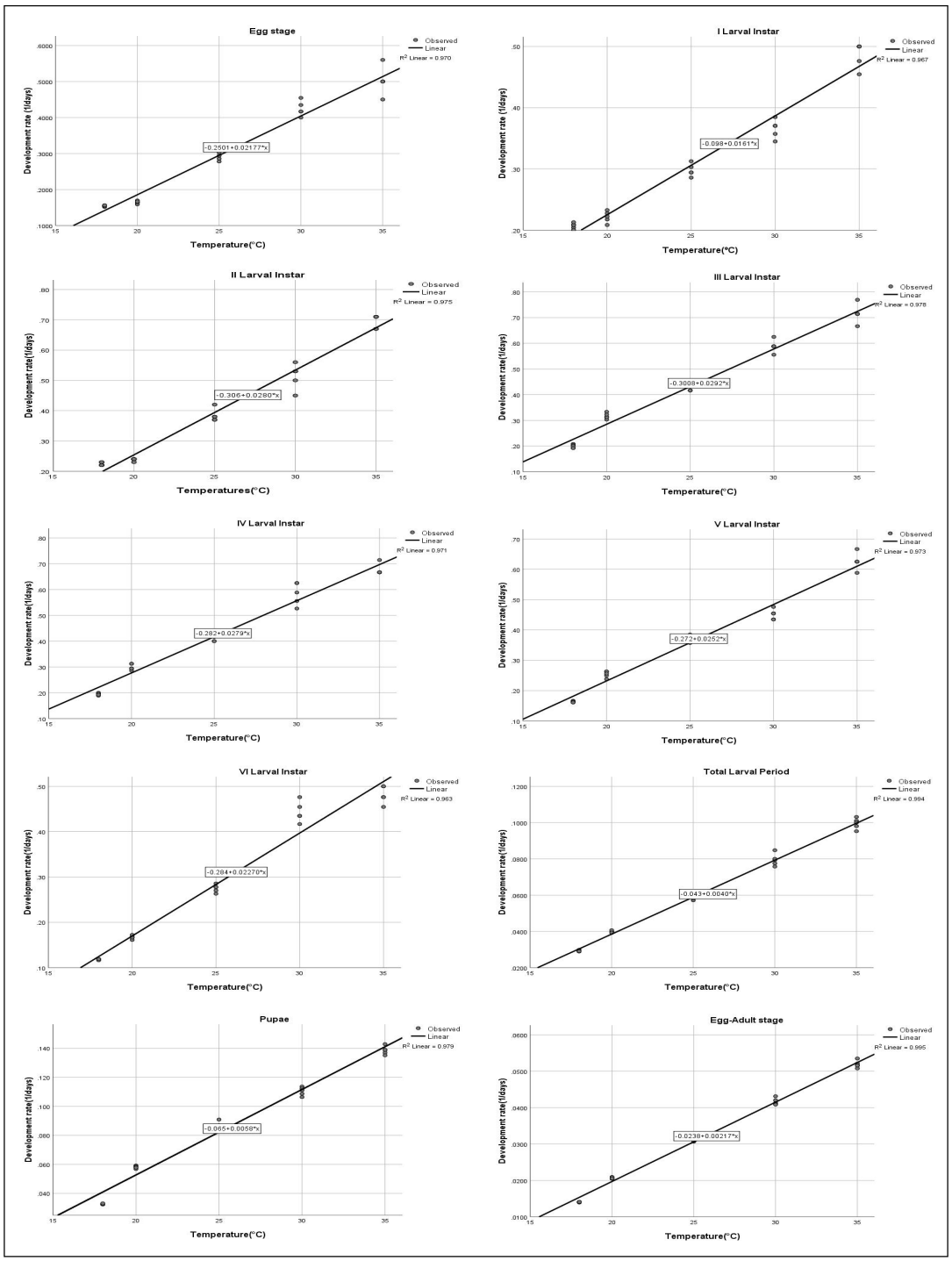


Fig 7: Relation between the development rate of *S. frugiperda* and rearing temperatures for all the life stages.

Table 1: Regression parameters describing relationship between rate of development and temperatures and thermal requirements for different life stages of *S. frugiperda*.

Developmental stages	Regression parameters				Thermal requirements	
	Equation	Slope±SE	Intercept±SE	R^2- Value	k=1/b	T=-a/b
Egg	y=0.021775x-0.2501	0.021775±0.001	0.2501±0.036	0.970	45.92	11.49
1st Instar	y=0.016163x-0.0982	0.016163±0.001	0.0982±0.016	0.967	61.87	6.08
2nd Instar	y=0.028036x-0.3068	0.028036±0.001	0.3068±0.024	0.975	35.67	10.94
3rd Instar	y=0.029290x-0.3008	0.029290±0.001	0.3008±0.023	0.978	34.14	10.27
4th Instar	y=0.027990x -0.2829	0.027990±0.001	0.2829±0.026	0.971	35.73	10.11
5th Instar	y=0.025249x-0.2727	0.025249±0.001	0.2727±0.023	0.973	39.61	10.80
6th Instar	y=0.022707x-0.2840	0.022707±0.001	0.2840±0.024	0.963	44.04	12.51
Larval Stage	y=0.004076x-0.0430	0.004076±0.000	0.0430±0.001	0.994	245.34	10.55
Pupa	y=0.005895x-0.0655	0.005895±0.0002	0.0655±0.005	0.979	169.64	11.11
Egg-Adult	y=0.002179x-0.0238	0.002179±0.000	0.0238±0.001	0.995	458.93	10.92

t= Estimated lower thermal threshold k= Estimated thermal requirement (degree days).

Table 2: Degree days for *S.frugiperda* under different constant temperatures.

Development stage	Degree-Days (°D)					
	18°C	20°C	25°C	30°C	35°C	Mean
Egg	42.18	51.74	45.93	43.68	50.78	46.84
1st Instar	57.69	62.92	63.57	65.54	59.58	61.86
2nd Instar	31.63	38.05	36.56	37.36	34.65	35.65
3rd Instar	38.80	30.75	34.76	33.54	34.62	34.49
4th Instar	40.55	33.03	36.03	34.21	36.84	36.13
5th Instar	44.06	36.25	38.06	42.62	38.72	39.94
6th Instar	46.56	44.79	45.46	39.53	46.78	44.62
Larval stage	253.90	237.57	246.52	245.07	245.97	245.80
Pupal stage	211.11	152.91	160.01	171.14	172.49	173.53
Egg-adult	504.09	443.52	452.83	460.22	469.67	466.06

CONCLUSION

Optimal conditions, in respect to development, range between 25-30°C under which the hatching of eggs and survival of larvae are maximum. This is in the range of between 18 and 35°C, beyond which the extreme temperatures drastically reduce the likelihood of viability and successful reproduction, hence increased mortality during development stages. Such results put into perspective the role temperature plays in effectively shaping both the life cycle and general population trend of the fall armyworm. These findings help in the anticipation of outbreaks regarding pest populations to face up to the challenges of a changing climate.

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Disclaimers

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Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article.

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