International Journal of Tropical Insect Science (2021) 41:2851–2865
https://doi.org/10.1007/s42690-021-00467-x

ORIGINAL RESEARCH ARTICLE

Fecundity and life-table parameters of *Helicoverpa armigera* (Hübner) (*Lepidoptera: Noctuidae*) on tomato crop under alternating temperature regimes: implications for pest monitoring in sub-tropical India

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Received: 21 July 2020 / Accepted: 4 February 2021 / Published online: 15 February 2021

Abstract
Constant temperatures influencing the biological traits of *Helicoverpa armigera* (Hübner) is widely documented. However, information was lacking on impact of alternating temperatures on population growth of *H. armigera* on tomato crop. The impact of 6 different alternating temperatures (ATs) viz. 25:10, 25:13, 25:16, 30:10, 30:13, 30:16°C were studied on its life table parameters on tomato crop inside the climatic chamber. Only 7–13% eggs of *H. armigera* developed successfully into their respective adults under treated ATs. The immature development period and mean generation time shortened by 36.7 and 35.7%, respectively with enhancement in AT from 25:10–30:16°C. ATs viz. 25:13, 25:16 and 30:10°C favoured the higher oviposition (554.83–625 eggs/female) of female *H. armigera*. Fitting closely to observed values, the total fecundity (TF) model predicted 21.0°C as the favourable temperature for maximum fecundity (591.3 eggs /female). Under 30:10°C, *H. armigera* attained maximum intrinsic (0.05635 day^{-1}) and finite rate of increase (1.0579 day^{-1}) on tomato crop. The methodology involving law of effective accumulated temperatures estimated that *H. armigera* may complete 2 generations in a tomato growing season. These results can assist in planning sustainable pest management modules in preventing potential pest outbreaks and associated economic losses.

Keywords Life table · Insect generation · Fecundity · Intrinsic rate of increase · Alternating temperature

Introduction

Tomato, *Solanum lycopersicon* is a commercially important vegetable crop for table consumption and food processing industries around the world. The production of premium quality tomato fruits requires air temperature in the range of 20–27°C during a growing season (Nicola et al. 2009). However, biotic stress involving several insect pests, diseases and weeds compromises its production and quality (Lange and Bronson 1981).

Tomato fruit worm, *Helicoverpa armigera* (Hübner) (*Lepidoptera: Noctuidae*) is an economically important insect pest of tomato crop, reported from across Asia, Africa, Australia, Europe and South America (Zalucki et al. 1986; Nyambo 1988; Jallow and Matsumura 2001; Garcia 2006; Pratissoli et al. 2015). *H. armigera* larvae prefer feeding on economically important reproductive structures of tomato plants (Rajapakse and Walter 2007), and cause economic losses by boring into fruits and eating away their inner contents (Garcia 2006; Cunningham and Zalucki 2014). Yield losses of up to 80% had been recorded on it (Tewari and Krishna Moorthy 1984; Wakil et al. 2010; Singh et al. 2017). The extensively migrating females of *H. armigera* also possess high reproductive ability and prefer to lay eggs singly on leaves of tomato plants during the mild winter season having wider diurnal temperature variation (Fitt 1989, Jallow et al. 2001; Zitsanza et al. 2006; Rajapakse and Walter 2007; Khokhar et al. 2019).

Pesticides are applied indiscriminately in response to damaging *H. armigera* larval population, which results in unsafe residues in tomato fruits, environmental pollution and killing of their natural enemies (Romeis and Shanower 1996). On the contrary, for timely implementation of

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eco-friendly and sustainable measures, information on favourable temperature regimes for high fecundity of *H. armigera* females on tomato crop can be useful. This information can prevent potential outbreak of *H. armigera* on tomato crop through release of egg parasitoids and applying entomopathogens.

Based on the knowledge of temperature dependent insect survival and fecundity, life tables can be developed to forecast the favourable environments for its population growth (Birch 1948). In the event of temperature rise, *H. armigera* is anticipated to get favourable environments, which may lead to expansion of their geographical distribution, reduced generation time, higher number of generations per cropping season resulting in colossal yield losses (Parmesan et al. 1999; Bale et al. 2002; Karban and Strauss, 2004; Sharma et al. 2010; Jaworski and Hilszczański 2013). Previously, several development and life table studies of *H. armigera* had been carried out under a range of constant temperatures on different hosts including tomato (Dhandapani and Balasubramanian 1980; Sharma and Chaudhary 1988, Mohite et al. 2011; Liu et al. 2004; Bartekova and Prasclika 2006; Mironidis and Savopoulou-Soultani 2008; Jallow and Matsumura 2001; Gomes et al. 2017) with few studies involved rearing of *H. armigera* larvae on artificial diet under alternating and fluctuating temperatures (Mironidis and Savopoulou-Soultani 2008; Mironidis 2014). The daily temperature variation occurring in the field involves fluctuation in temperatures from maximum to minimum temperature and vice-versa. In addition, daily temperature variation found close resemblance to alternating temperature (AT) regimes, which can be set in the climatic chambers (Mironidis 2014; Colinet et al. 2015). Therefore, to understand the impact of diurnal temperature variation on insect biology in the field, it was felt customary to study insect biology and reproductive parameters under range of alternating temperatures in the climatic chambers. Moreover, many previous relevant studies had reported the effects of constant temperatures differing from mean of alternating temperatures on account of development rate, thermal constant and life table parameters of many insects, including *H. armigera* (Hagstrum and Milliken 1991; Liu et al. 1995; Mironidis and Savopoulou-Soultani 2008; Colinet et al. 2015). Furthermore, these parameters of *H. armigera* also differed when reared on different hosts (Dhandapani and Balasubramanian 1980; Liu et al. 2004; Gomes et al. 2017). Therefore, field-level forecasting of temperature dependent population growth of *H. armigera* on tomato crop based on studies considering gradient of constant temperatures and artificial diet or hosts other than tomato for larval rearing can be exaggerated and misleading. The correct prediction of pest phenology and population growth of insect can only be made when temperature dependent life table studies of an insect in the laboratory considers environmental settings of natural pest incidence like natural hosts and fluctuating temperatures (Colinet et al. 2015; Abarca et al. 2018). However, no information was available so far that studied the impact of alternating temperature on biological and life table parameters of tomato feeding *H. armigera*. The temperature dependent life table parameters of pest can reveal favourable temperatures for its population growth and can also assist in taking timely, need-based and eco-friendly pest control measures (Birch 1948; Nylin 2001; Ramalho et al. 2015). The attempt was made to understand the influence of alternating temperatures on life table parameters of tomato feeding *H. armigera*. The aim of this study was to establish the favourable temperatures for population build up of *H. armigera* on tomato crop so that growers can be forewarned on pest outbreaks. In addition, the role of rising ambient temperatures on growth of *H. armigera* population on tomato crop can also be known. Eventually, appropriate and timely pest control measures can be deployed to avoid impending pest outbreaks and resulting economic losses.

Material and methods

Raising of tomato crop

The tomato crop was cultivated during February to May 2014 by following standard agronomic practices (PAU 2018) at the Entomological Research Farm, Department of Entomology, Punjab Agricultural University, Ludhiana, India. The seeds of tomato genotype US-8502 (Ujjawal Seeds Pvt. Ltd, Delhi) were obtained from the local market, Ludhiana and raised in the medium size earthen pots (Diameter: 20 cm; Height: 30 cm) and there after transplanted in the field during February 2014. No insecticides were applied on growing tomato plants during the experiment.

Mass production of *H. armigera* eggs

Laboratory culture of *H. armigera* was established in one of the cabinets of walk-in-type climatic chamber unit (PGW 40, Percival Scientific Company, USA) at Department of Entomology, Punjab Agricultural University, Ludhiana. Larvae of *H. armigera* were collected from the tomato field and were used to establish the laboratory culture of the insect. The larvae were identified as *H. armigera* based on the morphological features such as longitudinal bands which is interspersed light and dark areas including light whitish band on spiracular area (Fig. 1c). All the larvae were reared in specimen tubes (37 X 50 mm) singly and the culture was maintained at controlled temperature of 25 ± 1°C with 65 ± 5% RH and a photoperiod of 14:10 (L: D) h. A semi-synthetic diet was used for larval rearing (Armes et al.

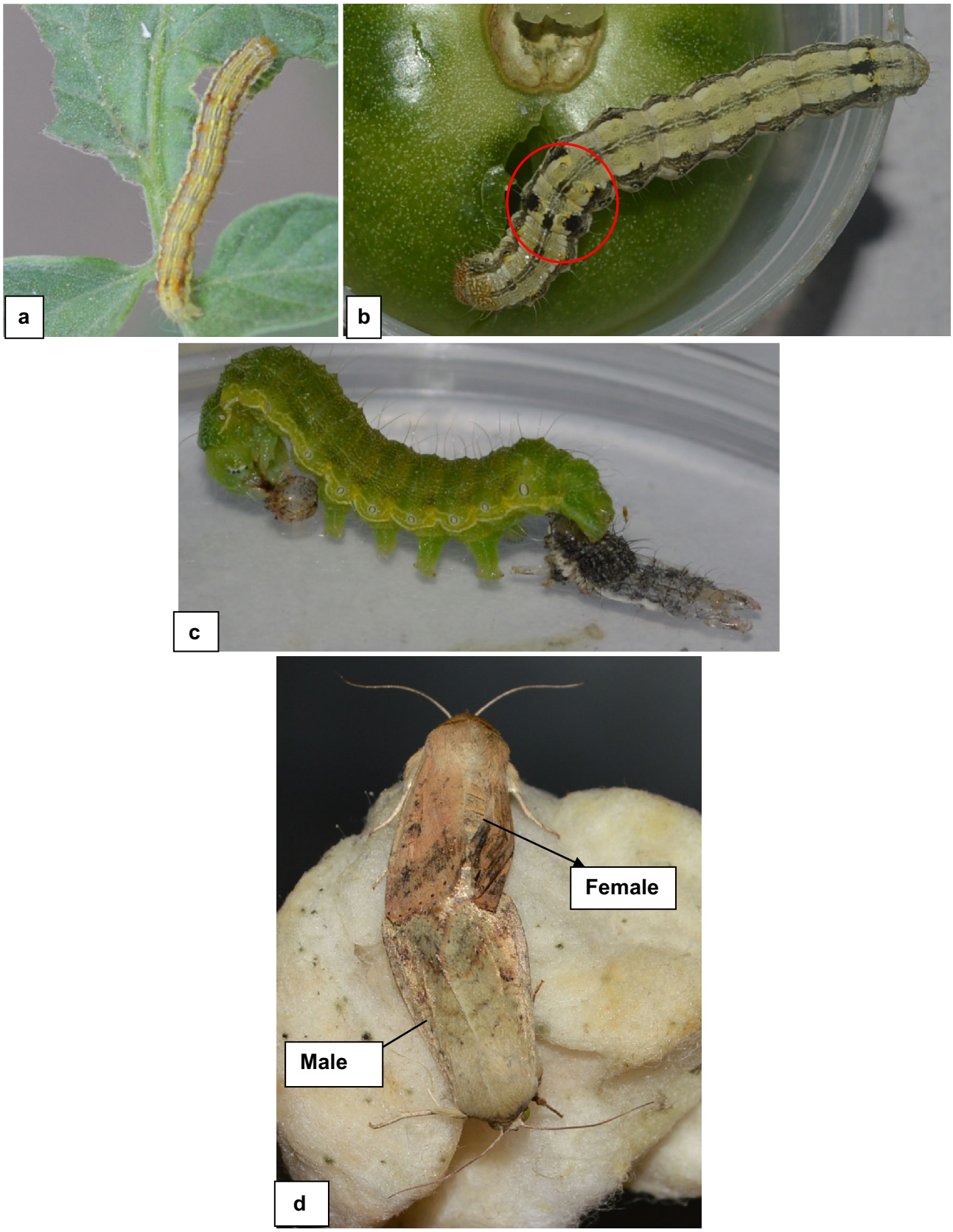

Fig. 1 **a** Third instar *H. armigera* larva feeding on tomato leaves **b** Fifth instar larva having characteristic morphological feature under red circle feeding on tomato fruit **c** moulting *H. armigera* larva **d** Adult mating pair of *H. armigera*

1992). *H. armigera* pupae were sorted out morphologically as per Quieroz-Santos et al. (2018) before the emergence of adults. A single adult pair of *H. armigera* was transferred to oviposition chamber made from a simple earthen pot with a hole at the bottom and placed on the plastic tub containing water (Arora and Battu 1996). The top of the pot was covered with a muslin cloth, which was changed daily to obtain fresh eggs. Cotton swab dipped in a 10% sugar solution was hung in containers daily. A small quantity of water was added every day to the plastic tub to maintain water level in the pot. Extreme sanitary conditions were maintained and 0.025% sodium hypochlorite solution was used for surface sterilization of eggs of *H. armigera* laid on muslin cloth (Rabindra et al. 1997). Date and time of oviposition by female adult was recorded. The muslin cloth containing the eggs was kept in a glass container (20 cm × 15 cm) at the base of which a moistened disc of foam was placed. These eggs were used for further experiments.

Experimental set up

The experiments related to immature stage development time, survival, adult longevity, and female oviposition of tomato fed *H. armigera* were performed inside another cabinet of climatic chamber unit which can be pre-set for temperature alternation (PGW 40, Percival Scientific Company, USA) at Department of Entomology, Punjab Agricultural University, Ludhiana. A total of 6 alternating temperatures (ATs) were selected as treatments viz. 25:10, 30:10, 25:13, 30:13, 25:16, 30:16°C under a photoperiod of 14:10 (L:D) h at a constant relative humidity (65 ± 5%). In the present study, every AT can be understood as constant maximum temperature (30 and 25°) maintained for 14 h, and thereafter, it fluctuated to constant minimum temperatures (10, 13 and 16°C) for remaining hours in a day. The transition from maximum to minimum temperature and vice-versa took 5–10 min in the chamber (Square wave form). The mean temperatures were calculated from the ATs which were 18.75°C (25:10 °C), 20.00°C (25:13°C), 21.25°C (25:16°C), 21.67°C (30:10°C), 22.91°C (30:13°C), 24.91°C (30:16°C). Consequently, the increasing order sequence of ATs can be assigned as 25:10 < 25:13 < 25:16 < 30:10 < 30:13 < 30:16°C.

Experiment and observation

Under every AT, freshly laid eggs (12 h old) were taken from the laboratory culture and kept along with muslin cloth pieces in the Petri dishes (100 × 15 mm) 25 eggs per dish with four replications till hatching. Survived neonates were transferred singly using camel hairbrush to individual specimen tube (37 X 50 mm) containing fresh leaf discs of 2 cm diameter of tomato genotype US-8502 and were continually fed with leaves till the completion of second instar. The third instar larvae were offered leaves (Fig. 1a) and pea sized green fruit of tomato for feeding and kept singly till the pupal stage (Fig. 1b). Changing of larval instars was recognised from removal of exuvia and head capsule (Fig. 1c). Newly formed pupae were kept on sterilized sand in battery containers (15 cm X 10 cm) at one pupa per container. The containers were covered with muslin cloth to prevent the escape of newly emerged adults. The eggs kept under each AT were examined after every 12 h to record the duration and number of eggs hatched (Egg hatchability). Neonates emerging from hatched eggs, were kept singly on leaf discs and counted daily until the completion of larval stage. Similarly, larvae were counted daily until pupation to record larval survival% on tomato flower and fruit. Pupae were also counted daily for number of adults emerged. Finally, total survival % was estimated from number of adults emerging from the cohort of 25 eggs. Mean durations of egg, larva and pupa were recorded separately and added to get total immature period. Apart from pupal characters, sexes of the adults were identified (Fig. 1d) based on the colour of adult moths (Quieroz-Santos et al. 2018). Under every alternating temperature, sex ratio was estimated on the basis of emergence of number ofmale and female adults from the pupae. These adults were released in pairs separately in the glass containers (15 × 10 cm) at 1 pair per container for mating and laying eggs. Cotton swab dipped in a solution of the adult diet as described earlier was hung in containers daily. The containers were covered with muslin cloth and fastened with rubber band. Oviposition, total fecundity (Total eggs laid per female) of *H. armigera* females were estimated by daily observing muslin cloth for oviposition of eggs from the time of adult release till their death. Female longevity calculated from the day of female emergence till its death. Likewise, male longevity was also recorded from the time of adult release till their mortality. The daily record of number of eggs laid for each female under every alternating temperature was maintained.

Development of life table parameters

Six age-stage two-sexlife tables of *H. armigera* on tomato crop representing effect of every alternating temperature were developed (Chi 1988; Chi and Liu 1985). The age-stage specific survival rates were also evaluated (Huang and Chi 2012). The parameters such as Net reproductive rate (R_o), Mean generation time (T), Intrinsic rate of increase (r_m) and Finite rate of increase (λ) were determined using formulae given below (Carey 1993), Eqs. 1, 2, 3, 4

$$R_0 = \sum_{x=0}^{i} l_x m_x \quad (1)$$

$$T = Log_e(R_0)/r_m \tag{2}$$

$$r_m = \sum_{x=0}^{i} e^{-r_m x} l_x m_x \tag{3}$$

$$\lambda = e^{r_m} \tag{4}$$

r_m was calculated using iterative and trial and error method as described by Portilla et al. (2014). Here specific age x is indexed from 0 to i , l_x is age-specific survival rate, and m_x is female specific fecundity.

Model-based analysis

The fecundity (eggs/female) of *H. armigera* was fitted against experimental mean temperature to describe their relationship using total fecundity model (Kim and Lee 2003). Eq. 5

$$F(T) = a.exp^{\left[1+\frac{b-T}{k}-exp^{\frac{b-T}{k}}\right]} \tag{5}$$

where, F(T) is the number of total eggs produced by a female during her entire life span at temperature (T), a is the maximum reproductive capacity, b is the temperature at which maximum reproduction occurs, and k is the fitted constant. The values of parameters were estimated using Table curve 2D (Jandel Scientific 1996). The maximum and minimum threshold temperature for total fecundity was evaluated by interpolating and extrapolating the predicted values to upper and lower temperature values where total fecundity becomes zero.

Predicting number of generations of *H. armigera* on tomato crop

Predicting number of generations of *H. armigera* in Ludhiana (30.9010° N, 75.8573° E), North Western region of India during tomato season (February to May) required the following parameters: 1) Historical mean monthly data of the Ludhiana which was accessed free of cost from https://weather.com/en-IN/weather/monthly/l/INXX0193:1:IN (Ludhiana weather 2014) 2) Effective accumulated temperature of insect and total effective accumulated temperature of Ludhiana region 3) Minimum threshold temperature of *H. armigera*. Both 2 and 3 were calculated using formulae used by Li et al. (2013) which is given below (Eq. 6).

$$T = C + KV \tag{6}$$

$$\mathrm{C} = \frac{\sum \mathrm{v}^2 \sum \mathrm{T} - \sum \mathrm{V} \sum \mathrm{VT}}{\mathrm{n} \sum \mathrm{V}^2 - (\sum \mathrm{V})^2} \tag{7}$$

$$\mathrm{K} = \frac{\mathrm{n} \sum \mathrm{VT} - \sum \mathrm{V} \sum \mathrm{T}}{\mathrm{n} \sum \mathrm{V}^2 - (\sum \mathrm{V})^2} \tag{8}$$

where T is the temperature, V is the development rate of *H. armigera* generation, n is the sample number or treatments, C is the minimum temperature threshold and K is effective accumulative temperature of the insect. The total effective accumulative temperature during tomato growing season (February-May) of Ludhiana region in Punjab State of India was calculated keeping in view, C as the base temperature. The number of generations of *H. armigera* completed during tomato growing season can be calculated using a step-wise protocol described below.

Step 1: Calculate values of C and K as given above in the Eqs. 7 and 8.

Step 2: Get monthly maximum and minimum temperature of a region (For example, Ludhiana, Punjab) from data repository or agrometeorological observatory.

Step 3: Evaluate monthly average temperatures from maximum and minimum temperatures.

Step 4: Multiply number of days in a month with average temperature of that month to get month wise gross accumulated temperature (GAT).

Step 5: Multiply minimum threshold temperature of insect, C with number of days in a month to get gross accumulated temperature of insect (GAI).

Step 6: Monthly effective accumulated temperature (EAT) can be calculated by subtracting GAI from GAT.

Step 7: To arrive at EAT values of tomato season, take a sum of EAT of all months (February-May) covering the tomato crop season.

Step 8: Finally, using Eq. 9, number of insect generation can be estimated.

$$Number\ of\ insect\ generation = \frac{Total\ effective\ accumulated\ temperature}{effective\ accumulated\ temperature\ of\ insect} \tag{9}$$

Statistical analysis

The recorded data of *H. armigera* related to survival % and immature stage development were tested for normality using Shapiro–Wilk test (SPSS 23.0 2015) before subjecting them to statistical analysis. Bothtotal immature duration, and total immature survival were subjected to one-way ANOVA using SPSS 23.0. Significant differences between treatment means for these aspects were analysed through Tukey's HSD post hoc test ($P < 0.05$). Male and female longevity, oviposition days, fecundity and life table parameters were subjected to

Table 1 Effect of various alternating temperatures on development duration and survival of immature stage of *H. armigera* reared on tomato crop at constant relative humidity (65 ± 5%)

Alternating Temperature °C	Initial number of eggs (n)**	Adults Emerged Out of 100 eggs	Total immature stage (mean ± SE)	
			Survival (%)	Duration (days)
25:10 (18.75 °C)*	25 × 4 = 100	9	9.0a ± 1.91a	74.7 ± 0.97a
25:13 (20.00 °C)	25 × 4 = 100	13	13.0a ± 1.0a	65.9 ± 0.49b
25:16 (21.25 °C)	25 × 4 = 100	10	10.0a ± 2.58a	57.9 ± 0.38c
30:10 (21.67 °C)	25 × 4 = 100	11	11.0a ± 1.91a	55.5 ± 0.49c
30:13 (22.91 °C)	25 × 4 = 100	8	8.0a ± 0.0a	51.9 ± 0.68d
30:16 (24.17 °C)	25 × 4 = 100	7	7.0a ± 1.91a	47.3 ± 0.13e
Df			5, 23	5, 23
F			1.500	288.617
P			0.239	0.000

Means within column followed by different lowercase letters are significantly different at $P < 0.05$ (Tukey's HSD Post Hoc test)

*Figures in parentheses represent mean of alternating temperature; **4 replications each of 25 eggs were taken initially for experimentation

bootstrapping program contained in TWOSEX-MS Chart program Version 2020 which can be accessed through https://140.120.197.173/Ecology/ (National Chung Hsing University) to get 100,000 resamplings, which were further subjected to paired bootstrapping to get significant difference between means using confidence interval difference. Means and standard error values of Male and female longevity, oviposition period, fecundity,R_o, T, r^m, and λ of specific alternating temperature were evaluated throughTWOSEX-MS Chart program. Microsoft excel was used to create graphs.This program simplified the complicated nature of life table parameter estimation.

Results

Development and survival of immature stage of *H. armigera*

Only 7–13% of *H. armigera* eggs developed to adults at all experimental ATs with no significant difference between the treated ATs (F = 1.50; df = 5, 23; P = 0.239) suggesting equal impact of all ATs on immature stage survival of insect. 13 adults emerged from 100 eggs in the sex ratio of 7 male and 6 female under 25:13°C alternating temperature (Table 1; Table 2). Moreover, Male adults emerged in slightly more than female in five ATs, except 30:13°C.

Table 2 Matrix indicating percent decrease in immature stage duration with increase in alternating temperature

	25:10 (18.75 °C)	25:13 (20.00 °C)	25:16 (21.25 °C)	30:10 (21.67 °C)	30:13 (22.91 °C)	30:16 (24.17 °C)
25:10 (18.75 °C)*	0.0	11.8	22.5	25.7	30.5	36.7
25:13 (20.00 °C)		0.0	12.1	15.8	21.2	28.2
25:16 (21.25 °C)			0.0	4.1	10.4	18.3
30:10 (21.67 °C)				0.0	6.5	14.8
30:13 (22.91 °C)					0.0	8.9
30:16 (24.17 °C)						0.0

*Figures in parentheses represent mean of alternating temperature

Total immature duration decreased (F = 288.617; df = 5,23; P = 0.000) by 36.7% (74.7–47.3 days) with enhancement of AT from 25:10–30:16°C (Table 1; Table 2). Furthermore, the shortening of immature duration of *H. armigera* by 18.3–25.7% (Table 2; compare 25:10–30:10; 25:13–30:13; 25:16–30:16°C) was witnessed with 5°C increase in maximum temperature. Similarly, enhancement in minimum temperature by 6°C (compare 25:10–25:16; 30:10–30:16) reduced the immature duration in the range of 14.8–22.5%. The results presented here provide additional information of effect of rising maximum and minimum temperatures on immature duration of *H. armigera* reared on tomato.

Longevity and fecundity

The male longevity decreased significantly from 9.29 days at 25:10°C to 6.75 days at 30:16°C (P < 0.001) (Table 3). Oviposition period of female *H. armigera* varied in the range of 4.33–5.75 days and shortened significantly under influence of increasing ATs (P < 0.001). Female of *H. armigera* expanded its longevity significantly (P < 0.001) to 10.25 days at 25:10°C from 7.00 days attained under 30:16°C. Female of *H. armigera* during oviposition period laid maximum number of eggs (625 eggs/female) under 30:10°C and maintained similar fecundity level under 25:13 and 25:16°C (Table 3). Conversely, female fecundity decreased significantly (P < 0.001) under 25:10, 30:13 and 30:16°C. Therefore, among all the tested ATs, only 25:13, 25:16 and 30:10°C favoured the tomato reared females to lay higher number of eggs.

Table 4 Estimated parameter values (value ± SE) of total fecundity model of *H. armigera* fed on tomato crop

Fecudity model	Parameters	Estimated values
	Maximum fecundity (a)	591.3 ± 42.2 eggs
	Temperature for maximum fecundity (b)	21.0 ± 0.26 °C
	k	2.5 ± 0.38
	Temperature range for fecundity (graphically)	15.3–39.5 °C
	R^2	0.82

The observed fecundity level of *H. armigera* females were also substantiated by total fecundity model based prediction of parameters (Table 4; Fig. 4). The model prediction fitted strongly ($R^2 = 0.82$) to the observed fecundity of *H. armigera*. Furthermore, model predicted the ambient mean temperature of 21°C for maximum *H. armigera* fecundity (591 eggs/female). Interestingly, the predicted 21°C found to be fairly close to the mean of ATs viz. 25:13 (20.00°C), 25:16 (21.25°C) and 30:10°C (21.67°C), where vigorous egg laying was observed. In addition, the model also predicted 15.3–39.5 °C (Table 4, Fig. 2) as the maximum to minimum temperature range for egg laying on tomato crop. Figure 3(a–f) illustrates the influence of different ATs on the age-specific fecundity (m_x) and survivorship (l_x) of *H. armigera* females. High fecundity in the range of 60.1–82.73 female eggs/ female/ day were witnessed on 4th and 5th day of female longevity under 25:13, 25:16 and 30:10°C having mean temperature

Table 3 Effect of various alternating temperatures on adult longevity and fecundity of *H. armigera* reared on tomato crop in a growth chamber at constant relative humidity (65 ± 5%)

Alternating Temperature°C	Sex Ratio (Male:Female)	Longevity in days (Mean ± SE)			Fecundity (eggs/female)
		Male	Female		
			Oviposition period	Total	
25:10 (18.75 °C)**	5:4	9.29 ± 0.29a	5.75 ± 0.25a	10.25 ± 0.85a	352.25 ± 53.73a
25:13 (20.00 °C)	7:6	9.20 ± 0.20a	4.83 ± 0.31b	8.50 ± 0.34a	554.83 ± 16.44b
25:16 (21.25 °C)	6:4	7.83 ± 0.17b	4.75 ± 0.25b	8.00 ± 0.41ab	562.75 ± 64.95b
30:10 (21.67 °C)	6:5	7.67 ± 0.21bc	4.8 ± 0.20b	8.00 ± 0.32ab	625.00 ± 114.21b
30:13 (22.91 °C)	4:4	7.00 ± 0.00c	4.5 ± 0.29b	7.75 ± 0.25ab	393.25 ± 17.06a
30:16 (24.17 °C)	4:3	6.75 ± 0.253c	4.33 ± 0.33b	7.00 ± 0.58b	397.33 ± 28.99a
P		0.000	0.000	0.000	0.000

Means within column followed by different letters are significantly different by using paired bootstrap test based on the difference of confidence intervals; Standard errors were calculated using 100,000 bootstrap resamplings

*Figures in parentheses represent mean of alternating temperature

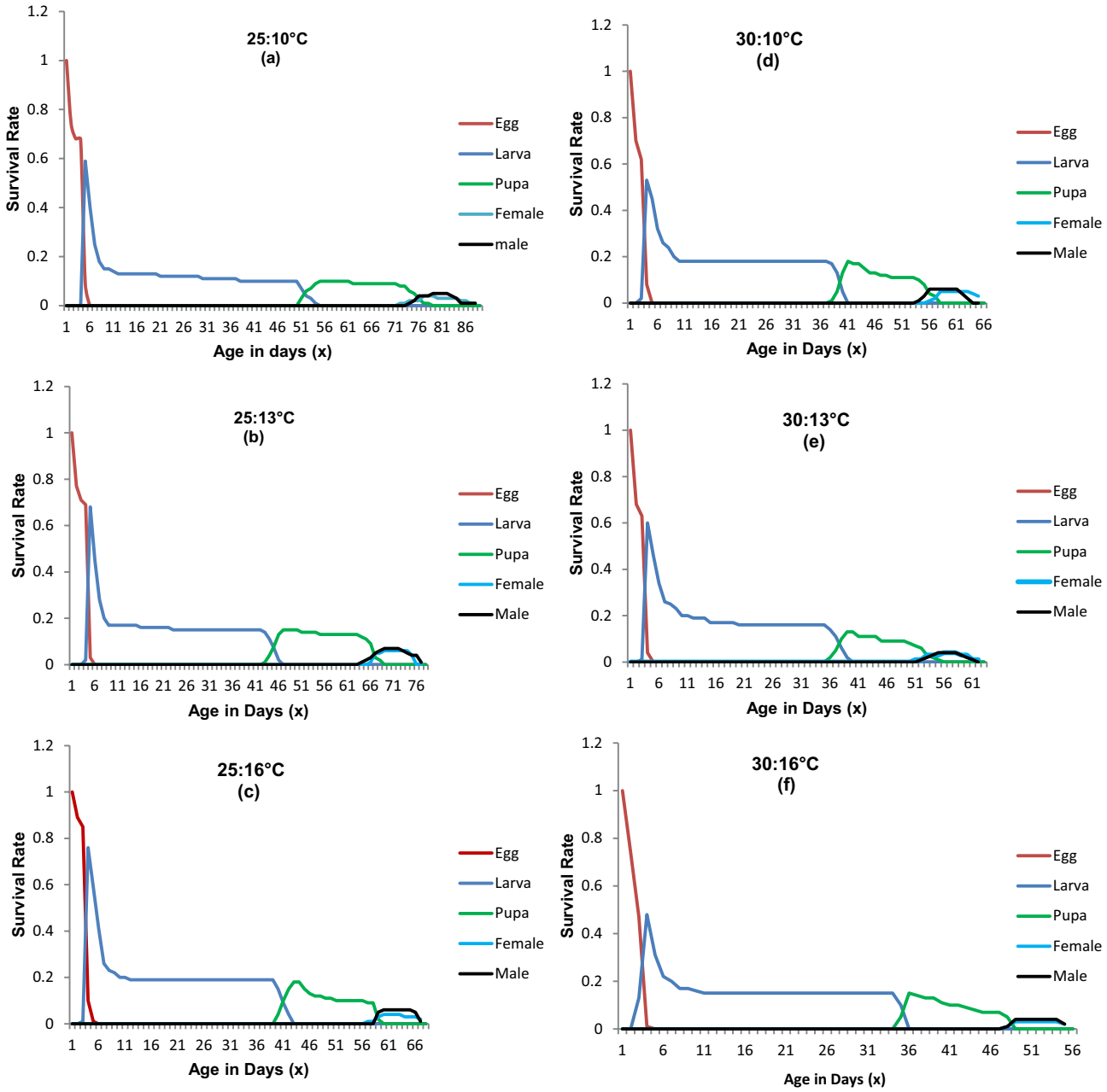

Fig. 2 (**a-f**) Influence of different alternating temperatures on age-specific survival rate (lx) and age-specific fertility (mx) of the *H. armigera* on tomato crop

of 20.0, 21.25 and 21.67°C, respectively (Fig. 3b–d). On the other hand, their corresponding values (35.5–65.57 female eggs/female) recorded under 25:10, 30:13 and 30:16 were lower (Fig. 1a, e and f). In addition, during the fecundity period, female of *H. armigera* had the higher l_x under all treated ATs. These results clearly indicated that ATs viz. 25:13, 25:16 and 30:10°C, were the most preferred temperature regimes for fecundity and survival of *H. armigera* females on tomato crop.

Life table parameters

The influence of ATs on life table parameters of *H. armigera* is summarized in Table 5. Net reproductive rate (R_o) represents multiplication in the population of the species in each generation under optimum conditions (Odum and Barrett 1971). No impact of different ATs was observed on R_o of *H. armigera* females as the values remained at par in the range of 14.09–33.29 offsprings/

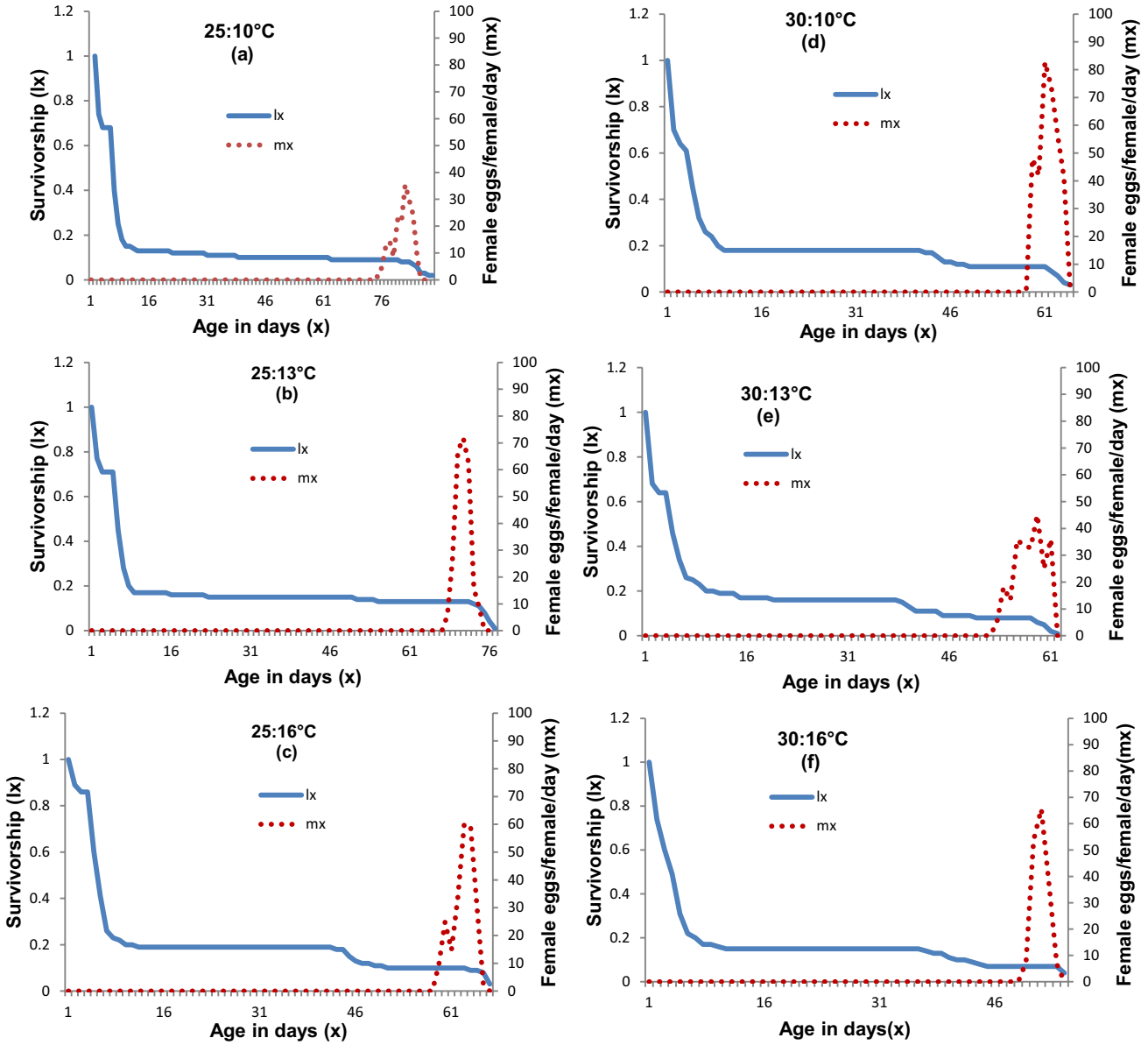

Fig. 3 (**a-f**) Influence of different alternating temperatures on age-stage survival rate of the *H. armigera* on tomato crop

individual. ($P > 0.05$). Under influence of 25:10°C, *H. armigera* took 80.68 days to complete whole generation while under higher AT (30:16°C), mean generation time (T) reduced significantly ($P < 0.001$) to 51.87 days. T values reduced by 22.3% with increase in minimum temperature of 6°C (Table 6; Compare 25:10–25:16°C) while 24.3% reduction in T values was recorded with enhancement in minimum temperature by 5°C (compare 25:10–30:10°C). Intrinsic rate of increase is the population growth or increase in the population of species when the environment is not limiting (Southwood 1978). *H. armigera* value for r_m was 0.03279 at 25:10°C day^{-1} which increased significantly to maximum level of 0.05635 under 30:10°C ($P < 0.001$). The finite rate of increase (λ) increased significantly from 1.033 day^{-1} at 25:10 to 1.0579 day^{-1} at 30:10°C ($P < 0.001$). The effective accumulated temperature (EAT) model predicted 8.74°C and 797.59 ^{O}D as the lower threshold temperature limit and accumulated degree days, respectively for development of *H. armigera* (Table 7 and 8). Applying the aforementioned lower threshold temperature and degree day values along with historical temperature data of Ludhiana region of Punjab (30.9010° N, 75.8573° E) during tomato growing months, 2.3 generations of *H. armigera* were evaluated to attack tomato crop. Thus, these results clearly indicate that 30:10°C is the most favourable AT for survival, oviposition

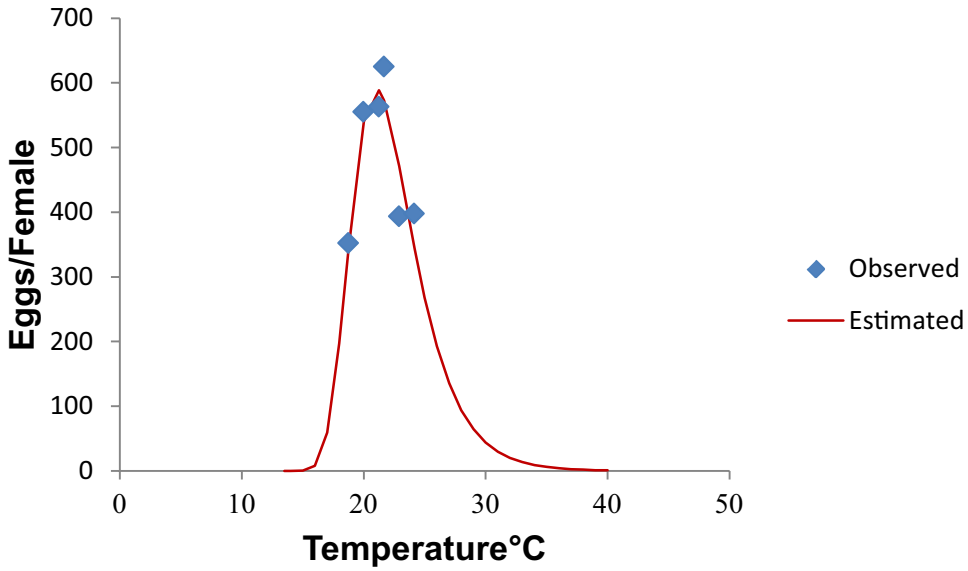

Fig. 4 Relationship between eggs laid per female adult of *H. armigera* and temperature using total fecundity model

and population growth of *H. armigera*. The survival rates of egg and pupa were lowest under 30:16°C and highest under 25:16 and 25:10°C, respectively while larval survival rates were equally influenced by all the ATs (Fig. 2).

Discussion

The treated ATs (25:10–30:16°C) considered in this study were fairly equivalent to the maximum and minimum temperatures recorded by Garg and Cheema (2011) and Khokhar et al. (2019) during tomato crop season in Ludhiana and Hisar region of India (North Western India), respectively. Therefore, it is expected that diurnally varying temperature experienced by *H. armigera* in the field would be similar to the experimental ATs undertaken in this study. The treated ATs exhibited varied temperature amplitudes with maximum being ± 20°C (30:10°C) and minimum as ± 9°C (25:16°C). On the contrary, their mean temperatures were close ranged with only 5.4°C gap from lowest (18.75°C) to highest mean temperature (24.17°C). However, striking differences in immature duration (Table 1) was observed within this gap. Already, several reports had recorded the shortening of immature stage duration of *H. armigera* on different hosts like chickpea, cotton, tomato and artificial diet with increasing constant temperatures (Sharma and Chaudhary 1988; Wu et al. 1993; Jallow and

Table 5 Effect of various alternating temperatures on fertility life table parameters of *H. armigera* reared on tomato crop in a growth chamber

Alternating Temperature°C	Life Table Parameters (Mean ± SE)			
	R_0 (offspring/individual)	T (days)	r_m (day^{-1})	λ (day^{-1})
25:10 (18.75 °C)**	14.09 ± 7.20a	80.68 ± 11.93a	0.03279 ± 0.008a	1.033 ± 0.15a
25:13 (20.00 °C)	33.29 ± 13.23a	70.87 ± 3.79a	0.04946 ± 0.007b	1.050 ± 0.06b
25:16 (21.25 °C)	22.51 ± 11.27a	62.66 ± 8.57bc	0.04969 ± 0.010b	1.0509 ± 0.14b
30:10 (21.67 °C)	31.25 ± 14.59a	61.07 ± 5.59bc	0.05635 ± 0.010b	1.0579 ± 0.10b
30:13 (22.91 °C)	15.73 ± 7.96a	57.15 ± 10.24c	0.04822 ± 0.012ab	1.0494 ± 0.19ab
30:16 (24.17 °C)	11.92 ± 6.92a	51.87 ± 12.78c	0.04777 ± 0.015b	1.0489 ± 0.25ab
P	> 0.05	0.000	0.000	0.000

Means within column followed by different letters are significantly different by using paired bootstrap test based on the difference of confidence intervals; Standard errors were calculated using 100,000 bootstrap resamplings

*Figures in parentheses represent mean of alternating temperature

Table 6 Matrix indicating percent decrease in mean generation time (T) with increase in alternating temperature

	25:10 (18.75 °C)	25:13 (20.00 °C)	25:16 (21.25 °C)	30:10 (21.67 °C)	30:13 (22.91 °C)	30:16 (24.17 °C)
25:10 (18.75 °C)*	0.0	12.2	22.3	24.3	29.2	35.7
25:13 (20.00 °C)		0.0	11.6	13.81	19.4	26.8
25:16 (21.25 °C)			0.0	2.5	8.8	17.2
30:10 (21.67 °C)				0.0	6.4	15.1
30:13 (22.91 °C)					0.0	9.2
30:16 (24.17 °C)						0.0

*Figures in parentheses represent mean of alternating temperature

Matsumura 2001; Mironidis and Savopoulou-Soultani 2008; Mironidis 2014). However, relatively varied mean immature duration was observed in *H. armigera* immature stages when raised on different hosts (Liu et al. 2004; Gomes et al. 2017). Secondly, the studies concerning influence of ATs and associated temperature amplitudes on development, survival, oviposition and life table parameters of insect pests developing on their natural hosts are few. The artificial diet raised *H. armigera*, when subjected to increasing alternating/fluctuating temperatures resulted in shortening of their immature duration (Mironidis and Savopoulou-Soultani 2008; Mironidis 2014). The present study, which forms the first report in elucidating the effects of rise in AT on *H. armigera* feeding on tomato also registered the linear relationship with increasing ATs. Rising temperature stimulates the activation of metabolic enzymes of *piokilothermic* insects, which in turn improve the development rate of *H. armigera* with increasing temperatures, leading to early completion of immature stages (Zuo et al. 2012; Colinet et al. 2015). Furthermore, besides temperature, the host plant also plays an important role in determining total development period and survival (Jallow and Matsumura 2001; Liu et al. 2004; Abarca et al. 2018). Previous investigations also pointed that tomato is an unsuitable host in relation to other hosts for immature stage survival of *H. armigera* due to low immature survival and elongated immature duration (Dhandapani and Balasubramanian 1980; Liu et al. 2004; Hemati et al. 2012). Larval stages possessed poor to moderate survivability in the range of 18.5–58% on tomato crop resulting in only fewer neonates developing successfully into adults (Casimero et al. 2000; Jallow et al. 2001; Liu et al. 2004). In addition, tomato fruits possess secondary compound like ortho-hydroxy phenols which have antibiotic properties against tomato feeding *H. armigera* larvae (Banerjee and Kalloo 1989; Selvanarayanan and Naryanasami 2006). In our study, the larvae of *H. armigera* reared on tomato could not tolerate the fluctuating ATs, which resulted in its poor immature stage survival (Fig. 2). The cabbage reared larvae of *Plutella xylostella* failed to tolerate the wide temperature amplitude of ± 10 and 12°C, and suffered high mortality (Xing et al. 2019). Higher total immature duration may, in turn, increase generation time and likely to reduce number of generations in a cropping season (Liu et al. 2007).

Table 7 Calculation of functions related to law of effective accumulated temperature equations

mean temperature °C of treatment	Development rate of a generation (V)	V^2	VT
18.75	0.012	0.00015	0.23
20.00	0.014	0.00020	0.28
21.25	0.016	0.00025	0.34
21.67	0.016	0.00027	0.35
22.91	0.017	0.00031	0.40
24.17	0.019	0.00037	0.47
$\sum T = 128.75$	$\sum V = 0.096$	$\sum V^2 = 0.00155$	$\sum VT = 2.08$

n = 6; C = 8.74 °C; K = 797.59 degree days

The range of female longevity of *H. armigera* on tomato crop in our results (Table 3) was in near agreement with similar observation recorded by previous studies (Liu et al. 2004; Saifuraie-Parizi et al. 2014). When subjected to increasing ATs, reduction in *H. armigera* oviposition period was observed on tomato crop (Table 3). Similar to our results, decrease in oviposition period, male and female longevity was noticed in artificial diet raised *H. armigera* with increase in mean of fluctuating temperatures and constant temperatures (Mironidis 2014; Noor-ul-Ane et al. 2018). The range of total fecundity (Table 3) of *H. armigera* on tomato crop reported in

Table 8 Historical monthly temperature data of Ludhiana, Punjab (source: Ludhiana weather (2014) https://weather.com/en-IN/weather/monthly/l/INXX0193:1:IN) and estimation of insect generation during tomato growing months

Month	Maximum temperature	Minimum temperature	Average temperature	Effective Monthly Degree days	Effective tomato season (Feb-May) degree days* = 1729.2
January	18.9	6.7	12.8	125.9	*H. armigera* degree days** = 797.6
February	21.0	8.6	14.8	168.3	
March	26.0	12.8	19.4	330.5	Number of generations of *H. armigera* completed in a tomato season*** = 2.3 generations
April	34.6	18.8	26.7	538.8	
May	38.8	23.3	31.1	691.6	
June	39.6	26.2	32.9	724.8	
July	34.9	26.1	30.5	674.6	
August	32.9	24.8	28.9	623.4	
September	33.4	23.4	28.4	589.8	
October	32.0	17.7	24.9	499.4	
November	26.4	11.6	19.0	307.8	
December	20.7	7.4	14.05	164.6	

*Effective tomato season degree days calculated using protocol (Material and methods section); **Calculated using eq. (7); ***Calculated using eq. (8)

this study is similar to other studies (Jallow et al. 2001; Liu et al. 2004; Saifuraie-Pairizi et al. 2014). A trend of improving fecundity was witnessed with enhancement of ATs from 25:10–30:10°C but declined with further increase in ATs to 30:16°C. The temperatures ranged from 25:13 to 30:10°C can be considered as optimum range for overall female fecundity of *H. armigera*. Moreover, these temperatures are similar in terms of mean value of temperature. However, we observed the highest female total fecundity at 30:10°C despite having widest temperature amplitude of ± 20°C. The cotton boll fed female of *H. armigera* was more fecund in the moderate temperature range of 20–30°C in comparison to the extreme cold and hot temperatures (Wu et al. 1993). In contrast to previous studies (Mironidis and Savopoulou-Soultani 2008; Mironidis 2014; Noor-ul-Ane et al. 2018) which recorded highest fecundity at mean temperature of 25°C, present study had recorded robust fecundity of *H. armigera* under mean temperature of 20–21°C. The model prediction of 21°C as favourable temperature for maximum female fecundity was in full compliance with observed results.

The survival and fecundity values of insect is also reflected in life table parameters like net reproductive rate (R_o), intrinsic rate of increase (r_m) and finite rate of increase (Southwood 1978; Portilla et al. 2014). The range of R_o values (14.09–33.29 offspring/individual) of *H. armigera* in our study was slightly higher than that recorded (9.5 offspring/individual) by Liu et al. (2004) at 27°C. However, it was consistent with wide R_o range (7.8–113.9 offspring/individual) reported by Safuraie-Parizi et al. (2014) on some tomato cultivars at 25°C. Earlier studies on artificial diet observed vigorous R_o values (383.04–977.6 offspring/indiviual) in *H. armigera* at 25°C (Mironidis 2014; Noor-ul-Ane et al. 2018). In contrast, our study on tomato crop recorded maximum R_o (33.29 offspring/individual) at alternating temperature of 30:10°C having mean 21.67°C. It shows the clear reflection of the diet-related differences appeared in reproductive rate. Secondly, under wide temperature amplitude of ± 20°C (30:10°C), the lower immature survival was offset and compensated by robust oviposition leading to improved net reproductive rate. The mean generation time (T) is the period between birth of offspring and parents (Krebs 1972). The present study recorded declining T values with increasing mean of ATs. T values of cotton fed *H. armigera* also reduced with increasing constant temperatures (Wu et al. 1993). Although, artificial diet based *H. armigera* studies have recorded shorter T values but followed the similar trend of decreasing T with increasing temperatures (Mironidis 2014; Noor-ul-Ane et al. 2018). The shorter T can be attributed to shorter immature development time which in turn depends on suitability of host (Van Lantern and Noldus 1990). Mironidis (2014) and Noor-ul-Ane et al. (2018) observed highest r_m at 27.5°C (0.170 day^{-1}) and 30°C (0.40 day^{-1}), respectively as against our experiment conducted at 30:10°C (0.05635 day^{-1}). On tomato crop, Saifuraie-Parizi et al. (2014) record of r_m (0.0410–0.0660 day^{-1}) on few cultivars of tomato, which was found consistent to the range of r_m (0.0332–0.0591 day^{-1}) recorded in our study. The comparison of monthly

meteorological data involving maximum and minimum temperatures (Table 5) with fecundity model results (Table 2) indicates March as vital month for population growth of *H. armigera.* The population dynamics field study of *H. armigera* on tomato crop recorded maximum mean egg count (4.6 eggs/ plant) during March and April months in North Western region of India (Khokhar et al. 2019). In addition, the temperature variation similar to 30:10°C exists in North Western India during March month. The number of generations calculated in this study was based on the law effective accumulative temperature which also undertook natural host and ATs into consideration. Earlier, Mohammed et al. (1999) predicted 4 generations of artificial diet reared *H. armigera* in Japan using gradient of constant temperatures. The prediction (Table 5) made in the present investigation with regard to generations clearly suggest that generations number tend to increase with decrease in generation time. So, it can said that if average global temperature rises insects will have shorter generation time and crops will in turn receive repeated attacks due to increased number of generations. Among the range of ATs tested, maximum potential of population growth of *H. armigera* was recorded under 25:13, 25:16 and 30:10°C due to prolific oviposition. The increasing ATs from 25:10 to 25:13°C (3°C rise in minimum temperature) had resulted in sporadic increase in r_m values, which can produce major *H. armigera* outbreak in tomato crop. It is this information, which was missing in all previous tomato based *H. armigera* studies. We also witnessed that *H. armigera* performed better on many parameters at 30:10°C which means wider temperature variation did not lead to population retardation on tomato crop. Such temperature regime occurs during March in the North Western part of India region hence, close monitoring of the pest before this month is suggested. Previous studies took fluctuating or alternating temperatures into consideration with the assumption that they better simulate the influence of diurnal temperature variation on insects than constant temperatures (Wada and Kobayashi 1980; Foley 1981; Xiuzhen et al. 1993; Liu et al. 1995; Fand et al. 2015), but in nature other biotic factors like natural enemies and abiotic factors like soil temperature, relative humidity can also have influence on life table parameters of insect (Foley 1981; Wu et al. 1993). Hence, there is need to fill this information gap to precisely predict any pest outbreak. Finally, we expect the empirical observation of the present study to help in developing region specific model-based pest risk maps that will help in close monitoring of temperature-dependent fluctuation in *H. armigera* population on tomato crop in different regions of the world. Further, it will assist in forewarning the growers about the upcoming threats of pest outbreaks in the light of ambient temperature fluctuation.

Conclusion

The life table parameter investigation for *H. armigera* on tomato crop revealed that alternating temperature 25:10, 30:13 and 30:16 is unfavourable to ovipositing *H. armigera* females that may result in poor population build up and lesser incidence. Such unfavourable temperature regimes occur most of the time of the year except between February-May in Northern plains of India. Therefore, these temperature regimes occurring during tomato crop cultivation can lessen the incidence of *H. armigera* and in turn leads to lesser reliance on harmful pesticides. Also, the estimation of favourable temperatures for population growth of *H. armigera* on tomato crop in March can help pest managers to timely release biocontrol agents before minor incidence of pest turns into outbreak.

Acknowledgment Authors express gratefulness to Indian Council of Agricultural Research (ICAR), New Delhi for providing junior research fellowship (ICAR-JRF).The help redendered by Prof. Dr. Hsin Chi of National Chung Hsing University, Republic of China in analysing life table parameters is also acknowledged.

Declarations

Conflict of Interest Authors express no conflict of interest.

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