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Forecasting the occurrence of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on tomato crop: A non-linear model approach

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Abstract
The effect of various alternating temperatures on the development rate of immature stages of *H. armigera* (Hübner) on tomato crop was studied during 2013-14. Immature stages were exposed to multiple alternating temperatures (Max: Min˚C) varying from 25:10 to 30:16 ˚C. Development rates of all immature stages enhanced with the rise in alternating temperatures. Egg, larval, pupal, and total development rate of *H. armigera* were in the range of 0.24-0.34, 0.021-0.031, 0.043-0.077 and 0.013-0.021 d^{-1}, respectively. These development rates were fitted into three non-linear models *viz.* Lactin-2, Briere-1, and Briere-2 models which predicted favourable temperature ranges for *H. armigera* total immature period development that was 11.7-53.7 °C, 8.3-34.0 °C and 9.4-42.7 °C, respectively. Both Briere-1 and Briere-2 estimation for total immature period were better than Lactin-2. In contrast, Lactin-2 model was most reliable in estimating the favourable temperature range for all stages of *H. armigera* development. *H. armigera* attained maximum development rate at 35.4, 28.2 and 30.4 °C as per Lactin-2, Briere-1, and Briere-2 models, respectively. The present study is crucial in predicting the occurrence of *H. armigera* in the tomato field and will assist in the need-based application of control measures under integrated pest management.

Keywords: Alternating temperature, temperature-dependent-development, non-linear model, tomato, *Helicoverpa armigera*

1. Introduction
Solanum lycopersicum (L.) is one of the major vegetable crops grown around the world for processing and fresh market consumption [25]. It is required to be protected from several biotic constraints including insect pests. *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) is one of the major limiting factor in quality tomato production [11, 12]. The pest prefers to feed on the fruit of tomato plant [8]. In India, the avoidable yield losses caused by *H. armigera* on tomato are 31.5% [24] and under rising global temperatures more damage likely to occur due to increased food consumption [4]. Since, the northern Indian state, Punjab has experienced a steady rise in minimum temperature by 0.06 °C per year over the past four decades [13]. Consequently, increasing global temperatures in this region of the country may increase the number of generations, development rate and geographical range of *H. armigera* leading to greater damage [22]. Temperature is one of the most significant factors that can be utilized to ascertain the future incidence of insect pests by using modeling approach [16]. Temperature-dependent models analyze the impact of temperature on the geographical range, population dynamics, and management of insects [21]. Non-linear models describe the relationship between temperature and development rate of all immature stages of insect and predict lower, optimum and upper-temperature threshold [5, 23]. Insects exposed to alternating temperatures differ in their development rate as against constant temperatures [10]. It is customary to study the development of insect under alternating temperature as fluctuation in it emulate the diurnal temperature variation [18]. Hence, to prevent any inadvertent error in predicting the occurrence of the pest in the field, it is essential to undertake development studies under such temperatures. Keeping that in view, the present investigation was carried out under alternating temperatures using non-linear models to forecast the occurrence of *H. armigera* on tomato crop.

2. Materials and Methods

The present study was conducted during July 2013 to May 2014. Tomato was cultivated at the entomological Research Farm, Department of Entomology, Punjab Agricultural University, Ludhiana as per recommended package of practices [1]. Seeds of tomato genotype US-8502 (Ujjawal Seeds Pvt. Ltd, Delhi) were sown and raised in the medium size earthen pots and after that, transplanted in the field. No insecticides were applied to the crop for management of any insect pest. Larvae of *H. armigera* were collected from tomato field. All the larvae were reared in specimen tubes (37 X 50 mm) singly to establish the laboratory culture of the insect. The culture was maintained at a controlled temperature of 25±1 °C in the plant growth chamber. A semi-synthetic diet was used for larval rearing [2]. Sex of the pupae of *H. armigera* was identified morphologically [20] and kept separately before the emergence of adults. Single male and female adult pairs of *H. armigera* were transferred to the glass jar (30 x 20 cm) having moistened foam disc at the bottom. The top of the jar was covered with a muslin cloth, which was changed daily to obtain fresh eggs. A cotton swab dipped in a 10% sugar solution was hung in jars daily. The record of the time of oviposition by a female was maintained. The muslin cloth containing the eggs was kept in another glass jar (20 x 15 cm) at the base of which a moistened disc of foam was placed. These eggs were used for experimentation.

H. armigera immature stages were exposed to six alternating temperatures *viz.*25:10, 30:10, 25:13, 30:13, 25:16, and 30:16 °C inside digitally controlled growth chamber (PGW 40, Percival Scientific Company, USA). In the present study, every alternating temperature maintains constant maximum temperature (30 and 25°) for 14 hours, and after that, it fluctuated to constant minimum temperatures (10, 13 and 16 °C) for remaining hours in a day. Growth chamber also maintained a photoperiod of 14:10 (L: D) h at a constant relative humidity (65±5%). Alternating temperatures were converted to their respective means *viz.* 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) for the ease in establishing non-linear relationship between temperature and development rate. Freshly laid eggs taken from the laboratory culture were kept in Petri dishes @ 25 eggs per dish with four replications at every alternating temperature till hatching in the growth chamber. Neonates were transferred to specimen tubes containing leaf discs of 2 cm diameter of tomato genotype US-8502. After four days the larvae were reared singly over the small sized green fruit of tomato and kept till the pupal stage. Pupae were kept in the sterilized sand in battery jars (15cm X 10cm) @ one pupa per jar. The eggs kept the under every alternating temperature were examined after every 12 h to record the duration of egg stage. Larvae were examined daily until pupation for moulting to record larval duration. The pupae were similarly examined daily to record pupal duration.

2.1 Statistical analysis

Recorded durations under all alternating temperatures of all immature stages were converted to their respective development rates (1/duration of insect stage). The significant differences between treatment means with respect to development rates of egg, larval, pupal and total immature stage of *H. armigera* were analysed using post hoc, Tukey's HSD with SPSS 23.0 software (SPSS Inc., Chicago). Thereafter, the development rate values with their respective mean temperatures were fitted into three non-linear models (Table 1) *viz.* Lactin-2, Briere-1 and Briere-2 models [3, 14] using SPSS 16.0 software (SPSS, Chicago). These models yielded the values of various parameter estimates like lower threshold temperature (T_{min}), upper threshold temperature (T_{max}) and optimum threshold temperature (T_{opt}) of all the stages of *H. armigera*. Microsoft Excel was used to plot the curves of different models (Fig. 1-4). Empirical data assigned the starting parameters values of these models.

3. Results and Discussion

Table 2. provide the details of development rates of various stages of *H. armigera* affected by different alternating temperatures (Max: Min °C). Since a linear regression function cannot estimate T_{max} and T_{opt} [16] hence, efforts have been made in the present studies to employ three non-linear models viz. Lactin-2, Briere-1, and Briere-2 (Table 3-5; Fig.1-4) for their calculation. These models determine parameter estimates of all immature stages of *H. armigera* like T_{min}, T_{max}, T_{opt}, R^2, λ, and RSS whose values are provided in Table 3-4. Negative values of λ (Table 3) suggest good fit for the Lactin-2 model [14]. All the non-linear functions fitted very well owing to their high values of R^2 (R^2 >0.960) and low values of the residual sum of squares (RSS)

3.1 Egg stage

The development rate of egg of *H. armigera* did not increase noticeably when temperature increased from 25:10 to 25:13 °C and 30:10 to 30:13 °C (Table 2). However, development rate boosted with further increase in minimum temperature from 13 to 16 °C while keeping the maximum temperature (25 or 30 °C) constant. This suggest that a marginal rise in minimum temperature from 10 to 13 °C was insufficient to bring any impact in development rate of *H. armigera* eggs. Overall egg development rate expanded from 0.24 d^{-1}at 25:10 °C to 0.36 d^{-1} at 30:16 °C. Jallow and Masaya [11] observed the similar range of development rate of *H. armigera* egg which was 0.18 to 0.33 d^{-1} under increasing constant tempertature from 20 to 25 °C. Similar observations were recorded by Mironidis [18] with development rate elevating from 0.2 to 0.33 d^{-1} under fluctuating temperatures whose means rise from 17.5 to 25 °C. Alternating temperatures rising from 25:10 to 35:27.5 °C also affected the development rate of eggs to rise from 0.24 to 0.47d^{-1}. The present study regarding egg development rate of *H. armigera* was consistent with previous studies under constant, alternating and fluctuating temperatures. Subsequently, recorded development rates at every alternating temperature were fitted into three non-linear models. Lactin-2 model estimated T_{min}, T_{opt}, T_{max} for egg stage of *H. armigera* to be 12.2, 26.2 and 34.6 °C, respectively (Table 3; Fig. 1A). These values suggest that the development of eggs of *H. armigera* will begin from 12.2 °C and last up to 34.6 °C with achieving maximum development rate at 26.2 °C. Daily mean temperature moving below 12.2 °C and above 34.6 °C may be detrimental for eggs of *H. armigera*. Favourable temperature range estimated by both lactin-2 and Briere-2 (12.4 to 34 °C) is quiet close to each other. The Briere-2 model (Table 5; Fig. 1C) fitted well for egg stage among all the non-linear models owing to the lowest value of the residual sum of square (RSS= 5.38 X 10^{-7}) and comparatively higher value of the coefficient of determination (R^2=0.961). Previous studies under constant temperatures estimated T_{min} using linear models for egg of *H. armigera* to be in the range of 10.1 to 10.6 °C [26, 11, 19]. Mironidis and Savopoulou-Soultani [17] and Mironidis [18] used Lactin-2 model which predict T_{min} to be 2.3 °C and 8.7 °C under alternating and fluctuating temperatures, respectively. The prediction of T_{min} made by previous studies [11, 26, 17, 18] differed with the present study. This is probably due to the consideration of different kind of temperature fluctuation and model in the present study which presented different T_{min} results as against previous studies.

3.2 Larval stage

The larval development rate of *H. armigera* expanded drastically from 0.021 to 0.031 d^{-1} with rise in alternating temperature from 25:10 °C onwards (Table 2). However, the development rate remained uninfluenced by the changes in alternating temperature from 25:16 to 30:10 °C. Since development rate of *H. armigera* is linearly related with moderate temperatures [23] hence, similar mean temperatures calculated from alternating temperature 25:16 (21.25 °C) and 30:10 °C (21.67 °C) bound to have an insignificant impact on their development rates. Development rate of *H. armigera* reared on cotton leaves calculated from its duration values was in the range of 0.02 d^{-1} at 15 °C to 0.09 d^{-1} at 30 °C [26]. Tomato fed *H. armigera* recorded the development rate in the range 0.02 to 0.06 d^{-1} on increase of constant temperature from 16.4 to 25 °C [11]. Mironidis [18] under fluctuating temperatures observed development rates of artificial diet fed larvae of *H. armigera* to vary from 0.03 to 0.06 d^{-1} with increase in mean temperature from 17.5 to 25 °C. The rates recorded in the present study are consistent with those recorded under fluctuating temperature and tomato host. However, development rates of larvae of *H. armigera* also depend on the type of host they feed [11]. Furthermore, *H. armigera* larvae have registered lowest development rate on tomato as compared to other hosts [6, 15]. So, it can be infered that apart from temperature, host also affects the development rate of larvae of *H. armigera*. Lactin-2 model (Table 3) gave the good fit for the larval stage among all the three non-linear models due to lowest RSS (4.83 X 10^{-7}) and highest R^2 value (0.993). The predicted values of T_{min}, $T_{max,}$ and T_{opt} for larval stage of *H. armigera* were recorded as 10.8, 42.9 and 28.6 °C, respectively (Table 3; Fig. 2A). However, Briere-1 predicted (Table 4; Fig. 2B) significantly different favourable range (7.7 to 32 °C) from Briere-2 (9.4 to 38.5 °C) model (Table 5; Fig. 2C). Mironidis [18] used Lactin-2 model for estimation of favourable temperature range (6.5 to 34.9 °C) which was quiet close to the range estimated by Briere-1 model in our study. However, it differed from the Lactin-2 estimates of the present study. T_{opt} estimated (26 to 28.6 °C) using all non-linear models in the present study (Table 3-5) for larvae of *H. armigera* was not in agreement with T_{opt} values (39.3 and 32.2 °C) estimated by Mironidis and Savopoulou-Soultani [17] and Mironidis [18]. The differences in estimates can be explained by combined effect of different temperature types and artificial diet fed to the larvae of *H.armigera* in former studies. On the contrary, present study fed green tomato fruits to larvae of *H. armigera*. It is observed that larval developement rate of *H. armigera* is high on artificial diet than their natural host [8].

3.3 Pupal Stage

Development rate of pupae of *H. armigera* gained from 0.043 to 0.077 d^{-1} with subsequent rise in alternating temperatures (Table 2). Similar to egg stage, pupal development rate was unaffected by the increase in minimum temperature from 10 to 13 °C while keeping maximum temperature constant (25 or 30 °C). Jallow and Masaya [11] recorded development rate of *H. armigera* pupae under constant temperature to rise from 0.02 d^{-1}at 16.4 °C to 0.07 d^{-1} at 25 °C. Similarly Mironidis and Savopoulou-Soultani [17] under alternating temperatures observed 0.06 to 0.12 d^{-1} development rate. Mironidis [18] under fluctuating temperatures observed development rate to increase from 0.05 to 0.1 d^{-1}. The develop rate range in the present study (Table 2) was found to be in confirmity with these results of previous studies. The calculated development rates when subject to three non-linear models provided estimated values of favourable temperature range for pupal development. Lactin-2 predicted highest development rate (T_{opt}) at 39 °C with favourable range spanning from 11.3 to 40.8 °C (Table 3; Fig. 3A). This was found to be in agreement with the range (12.3 to 40 °C) recorded by Mironidis and Savopoulou-Soultani [17]. However, the estimated range (5.8 to 34.9 °C) for pupal development made by Mironidis [18] differed significantly with our results. Both Briere-1 and Briere-2 overestimated the T_{opt} and T_{max} values (Table 4,5; Fig 3B,3C) in the present study. The predicted values were unexpectedly higher than the normal well being of the insect. This suggests that both the Briere models were inappropriate in making favourable temperature range prediction for pupal development of *H. armigera*.

3.4 Total immature period

Rising alternating temperatures (25:10 to 30:16 °C) had a major impact on development rates of overall immature stage of *H. armigera* (Table 2). Even with the slight increase in mean temperature from 21.25 to 21.67 °C, a marked increase in development rate (0.017 to 0.018 d^{-1}) was observed. The developement rate surged from 0.013 to 0.021d^{-1} with rising alternating temperatures. Total development rate calculated from study of Wu *et al*. [26] were in the range of 0.008 to 0.04 d^{-1}. Mironidis and Savopoulou-Soultani [17] observed the development rate in the range of 0.02 to 0.04 d^{-1} under alternating temperatures. Similarly, under fluctuating temperatures development rates were ranged from 0.02 to 0.04 d^{-1} [18]. The rates recorded under present study deviated slightly from the previous studies. Liu *et al*. [15] and Dhandapani and Balasubramanian [6] recorded slowest development of *H. armigera* on tomato crop compared to other hosts. The development rate (0.028 d^{-1}) calculated from Liu *et al*. [15] study at 27 °C was close to the development rate recorded at 30:16 °C with 24.17 °C as mean in the present study. The effect of artificial diets were more pronounced in larval development rates which were also reflected in the total development rate as well. As the present study was carried out over tomato fruit hence, slow development rate was more evident. The development rate of the total immature period of *H. armigera* gave a good fit with all non-linear models (R^2 >0.990). However, among these models, Lactin-2 (Table 3) gave the good fit due to the low value of RSS (1.42 X 10^{-7}) and high value of R^2 (0.996). However, Lactin-2 model (Table 3; Fig 4A) overestimated the T_{max} value (53.7 °C) which was much higher than the values estimated by Briere-1 (34.0 °C) and Briere-2 (42.7 °C). The T_{min} value estimated by Lactin-2, Briere-1 and Briere-2 model was 11.7, 8.3 and 9.4 °C (Table 3-5; Fig. 4A,B,C). Noor-ul-Ane *et al*. [19] also predicted T_{min} using Lactin-2, Briere-1 and Briere-2 which were 12.1, 11.2 and 8.5. Both T_{min} value (11.7 and 9.4 °C) in our study was near to the similar estimate (8.5 °C) predicted by Noor-ul-Ane *et al*. [19] using Lactin-2 and Briere-2. However, under fluctuating temperatures Mironidis [18] recorded T_{min} estimates to be 7 °C. T_{opt} value (35.4 °C) estimted by Lactin-2 model was highest among all the non-linear models. The T_{opt} and T_{max} (24.7 and 29.0 °C, respectively) findings of the present study for total immature development using Briere-1 were lower than the similar estimates (28.2 and 34.5 °C, respectively) reported by Noor-ul-Ane *et al*. [19]. The T_{opt} estimates of both Briere-1 and Briere-2 (34.5 and 34.8 °C, respectively) in the present study were close to each other. The T_{max} (38.7 °C) estimates of the Briere-2 model were lower than the similar estimate calculated by Noor-ul-Ane *et al*. [19]. The difference in the estimates can be attributed to the use of alternating temperature in the present study instead of constant or fluctuating temperatures in the previous studies. Fantinou *et al*. [7] also observed lower values of different development threshold of various stages of *Sesamia nonagriodes* at alternating temperature than when they were exposed to constant temperatures.

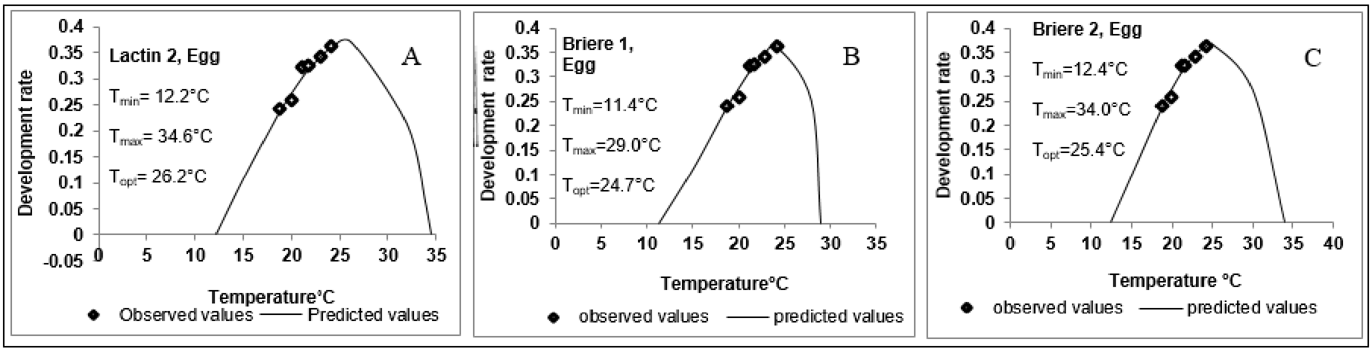

Fig 1: Relationship between temperature and rate of development of egg stage of *H. armigera* fitted into (A) Lactin-2, (B) Briere-1 and (C) Briere-2 models

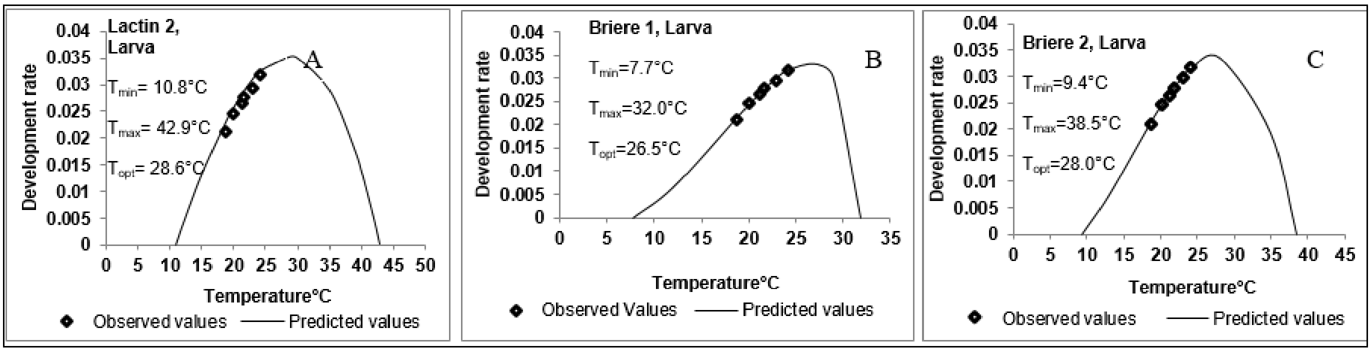

Fig 2: Relationship between temperature and rate of development of larval stage of *H. armigera* fitted into (A) Lactin-2, (B) Briere-1 and (C) Briere-2 models

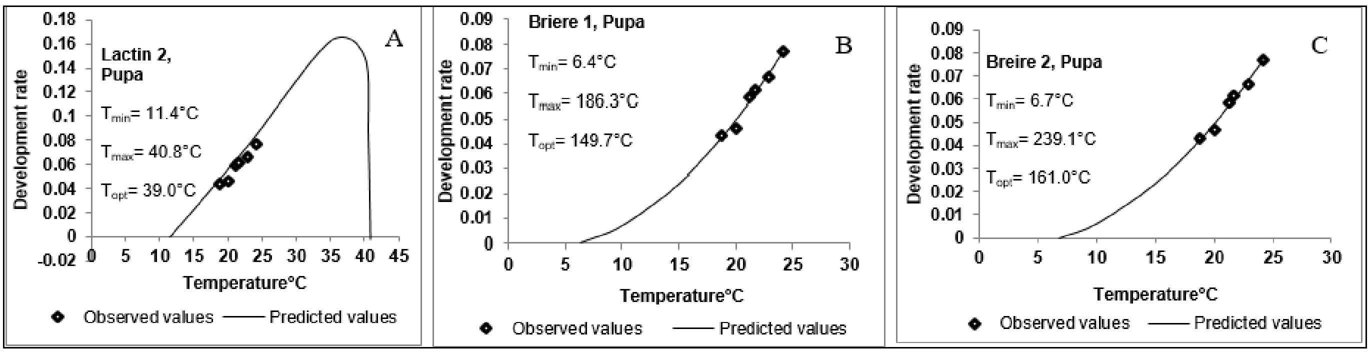

Fig 3: Relationship between temperature and rate of development of pupal stage of *H. armigera* fitted into (A) Lactin-2, (B) Briere-1 and (C) Briere-2 models

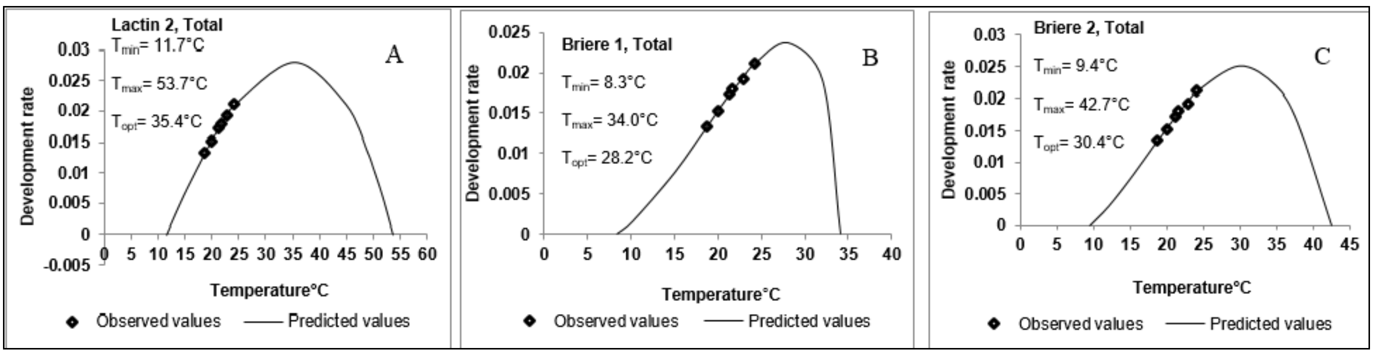

Fig 4: Relationship between temperature and rate of development of total immature life stages of *H. armigera* fitted into (A) Lactin-2, (B) Briere-1 and (C) Briere-2 models

Table 1: Selected temperature-dependent-development rate non-linear models

S.no	Non-linear models	Model name	Reference
1.	$Dr = e^{\rho T} - e^{\rho T_{max} - (T_{max} - T)/\Delta T} + \lambda$	Lactin-2	Lactin *et al.* (1995) [14]
2.	$Dr = aT(T - T_{min})\sqrt{T_{max} - T}$	Briere-1	Briere *et al.* (1999) [3]
3.	$Dr = aT(T - T_{min})\sqrt[m]{(T_{max} - T)}$	Briere-2	Briere *et al.* (1999) [3]

ρ is rate of increase to optimum temperature,"λ parameter that makes the curve intercept the x-axis,"
ΔT is difference between optimum and maximum temperature for development, T_{min} is minimum threshold temperature for *H. armigera* development, T_{max} is the maximum temperature for *H. armigera* development, T_{opt} is the temperature at which *H. armigera* development rate is highest, Dr is development rate of *H. armigera*

Table 3: The coefficients and measurable parameters of Lactin-2 non-linear model fitting to temperature dependent development rates of immature stages of *H. armigera* on tomato crop

Model type	Parameter estimates	Egg	Larva	Pupa	Total
Lactin-2	ρ	0.04	0.011	0.006	0.004
	ΔT	10.41	33.67	0.58	31.99
	$T_{max\ (parameter)}$	41.31	81.71	41.86	109.558
	λ	-1.33	-0.83	-1.071	-0.976
	T_{min}	12.2 °C	10.8 °C	11.4 °C	11.7 °C
	T_{opt}	26.2 °C	28.6 °C	39.0 °C	35.4 °C
	T_{max}	34.6 °C	42.9 °C	40.8 °C	53.7 °C
	R^2	0.959	0.993	0.979	0.996
	RSS	4.63×10^{-4}	4.83×10^{-7}	1.71×10^{-5}	1.42×10^{-7}

Table 2: Effect of various alternative temperatures on development rate (d^{-1}) of immature stages of *H. armigera*

Alternating Temperature* (Mean temp.) °C	Development rate (mean± SE)			
	Egg	Larva	Pupa	Total
25:10 (18.75)	0.24±0.001a	0.021±0.0002a	0.043±0.001a	0.013±0.0001a
25:13 (20.00)	0.26±0.004a	0.025±0.0003b	0.046±0.0002a	0.015±0.0001b
25:16 (21.25)	0.32±0.008b	0.027±0.0004c	0.058±0.0008b	0.017±0.0001c
30:10 (21.67)	0.33±0.003b	0.028±0.0002c	0.061±0.001b	0.018±0.0001d
30:13 (22.91)	0.34±0.002b	0.029±0.0005d	0.066±0.0006c	0.019±0.0002e
30:16 (24.17)	0.36±0.005c	0.031±0.0002e	0.077±0.0015d	0.021±0.0005f

Means within column followed by different letters are significantly different at $P < 0.05$ (Tukey's HSD Post Hoc test)
*These temperatures were maintained for 14:10 h along with L: D photoperiod

Table 4: The coefficients and measurable parameters of Briere-1 non-linear model fitting to temperature dependent development rates of immature stages of *H. armigera* on tomato crop

Model type	Parameter estimates	Egg	Larva	Pupa	Total
Briere-1	a	0.001	2.83×10^{-5}	1.40×10^{-5}	1.75×10^{-5}
	T_{min}	11.4	7.7 ˚C	6.4 ˚C	8.3 ˚C
	T_{opt}	24.7 ˚C	26.5 ˚C	149.7 ˚C	28.2 ˚C
	T_{max}	29.0 ˚C	32.0 ˚C	186.3 ˚C	34.0 ˚C
	R^2	0.962	0.991	0.980	0.996
	RSS	4.30×10^{-4}	5.85×10^{-7}	1.57×10^{-5}	1.49×10^{-7}

Table 5: The coefficients and measurable parameters of Briere-2 non-linear model fitting to temperature dependent development rates of immature stages of *H. armigera* on tomato crop

Model type	Parameter estimates	Egg	Larva	Pupa	Total
Briere-2	a	1.26×10^{-3}	1.31×10^{-4}	9.40×10^{-6}	6.62×10^{-5}
	T_{min}	12.4 ˚C	9.4 ˚C	6.7 ˚C	9.4 ˚C
	T_{opt}	25.4 ˚C	28.0 ˚C	161.0 ˚C	30.4 ˚C
	T_{max}	34.0 ˚C	38.5 ˚C	239.1 ˚C	42.7 ˚C
	m	9.74	21.46	11.08	20.66
	R^2	0.961	0.992	0.980	0.996
	RSS	5.38×10^{-7}	5.3×10^{-7}	1.58×10^{-5}	1.45×10^{-7}

4. Conclusion

The present study assessed the development rates of various immature stages of *H. armigera* under various alternating temperatures. Egg stage of *H. armigera* required drastic enhancement in minimum temperatures to improve their development rates significantly. Total immature stages were most sensitive to temperature change. As confirmed by previous reports, larvae registering slow development on tomato enhanced their rate with increasing alternating temperature. When development rates were subjected to various non-linear models, the favourable temperature range for insect development was predicted. Since *H. armigera* were exposed to alternating temperatures and fed natural host like tomato hence, their development rates likely to be different from the previous studies made under constant temperatures and artificial diet. Consequently, the prediction made by using non-linear models would also differ. Lactin-2 model prediction were more reliable for egg, larvae and pupal stages. Briere-1 and Briere-2 predicted total immature period estimates better than Lactin-2. To validate these favourable temperature development ranges, rearing of *H. armigera* immature stages under predicted temperature threshold values are required over the natural host.

5. Acknowledgment

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