Journal of Agrometeorology 23 (2) : 169-175 (June 2021)

Evaluation of linear and nonlinear models for temperature driven development of *Spodoptera litura* (Fabricius) on soybean crop

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ABSTRACT

The tobacco caterpillar, *Spodoptera litura*, a major pest of soybean in India is under surveillance in all soybean growing areas in Maharashtra in order to issue alerts to farmers and prevent economic losses. In this context, two linear models were fitted to developmental data of *S. litura* life stages reared on soybean at five constant temperatures *viz.* 15, 20, 25, 30 and 35°C through laboratory experiments. Optimum temperature for development (T_{opt}) and upper temperature threshold (T_{max}) were estimated from three nonlinear models by additionally including developmental response at >35°C. T_{opt} estimates for the total immature development were 34.5°C (Lactin-2), 33.7°C (Briere-1) and 33.2°C (Simplified Beta type function) while T_{max} estimates were in the range of 38 to 40°C. Application of a thermodynamic non-linear model (Optim SSI) gave estimate ofintrinsic optimum temperature (T_{φ}) for development of egg (28.3°C), larva (27.5°C) and pupal stage (30.3°C). The phenology model of *S. litura* on soybean based on estimated developmental threshold temperatures and thermal constants was validated using available field surveillance data to facilitate informed pest management decisions.

Key words: *Spodoptera litura*, threshold temperatures, degree days, phenology model

Spodoptera litura (Lepidoptera: Noctuidae) is an economically important pest on several crops and incidence of the pest often crosses economic threshold level on several field crops including soybean. Outbreak of *S. litura* on soybean has become a challenge for its management on soybean in India (Prasad *et al*., 2013).Temperature is a key factor for driving insect development (Pedigo 1989). Most studies on the developmental biology of *S. litura*on several hosts analyzed linear response to constant temperatures in the range of 15 to 40°C (Ranga Rao *et al*., 1989; Qin *et al*., 2002; Manimanjari *et al.,* 2014; Srinivasa Rao *et al*., 2014). The estimates of bioclimatic thresholds and constants are useful in phenology modelling and comparative analysis of different geographical populations. Phenology model of *S. litura* was validated with surveillance data from several locations in soybean growing areas to test its utility in predicting the timing of seasonal occurrence. Field application of the model makes it possible to issue pest alert advisories to soybean farmers for informed pest management decisions.

MATERIALS AND METHODS

Development studies at constant temperatures

Laboratory experiments were conducted using environmental growth chambers (MLR 350H and 351H, Sanyo, Japan). The insect culture was maintained on soybean foliage (most popular cultivar JS335) at 60 ± 5% relative humidity and photoperiod (14:10 L:D). Virgin pairs of adults were released on potted soybean plants for oviposition. Freshly laid 5 egg masses (between 250 to 500 eggs) were individually placed in Petri dishes (9 cm diameter) and were observed for hatching at constant temperatures at an increment of 5°Ci.e., 15, 20, 25, 30 and 35°C in separate experiments. Neonate larvae (0-12 h old) from each cohort of hatched egg mass were individually transferred on to fresh soybean foliage in Petri dishes and observed daily. Pupae were transferred to individual glass tubes to observe adult emergence. Each temperature treatment was repeated with another 25 larvae (5 larvae/ replication, 5 replications/temperature).In order to elicit non-linear development of *S. litura* life stages beyond 35°C, similar constant temperature experiments were

Table 1: Mathematical models used to describe the relationship between temperature and development rate for *S. litura*

Model and Equation	Model parameter	Reference
Campbell (Equation 1) $r(T) = a + bT$	r = rate of development T = ambient temperature (^{o}C) *a* = intercept *b* = slope	Campbell *et al.,* 1974
SSI linear model (Equation 2) $DT = k + T_{\min} D$	k= thermal constant in degree days (DD)	Ikemoto, 2005
Lactin-2 (Equation 3) $\frac{1}{D} = e^{\rho \times T} - e^{\left[\rho \times T_{\max} - \left((T_{\max} - T) \div \Delta\right)\right]} + \lambda$	*D* = the mean development duration in days ρ = the composite value for critical enzyme-catalyzed biochemical reactions as T increases to T_{opt} Δ = the difference between T_{opt} and T_{max} when thermal breakdown becomes the overriding influence λ = fitted coefficient that forces the nonlinear curve to intersect the *x*-axis and allows estimation of T_{min}	Lactin *et al*., 1995
Briere-1(Equation 4) $r(T) = aT(T - T_{\min})\sqrt{(T_{\max} - T)}$	T_{min}= lower temperature threshold at which development rate is zero T_{max}= upper temperature threshold at which development cease *a* =empirical constant	Briere *et al*., 1999
Simplified Beta (Equation 5) $r(T) = k \times [\alpha - (T/10)](T/10)^{\beta}$ $T_{opt} = \frac{10\alpha\beta}{1+\beta}$	*k*, α and β are model parameters T_{opt} = optimum temperature threshold at which development rate is maximal	Damos and Soultani, 2008
SSI non-linear model (Equation 6) $r(T) = \frac{\rho_\phi \frac{T}{T_\phi} \exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{T_\phi} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_L} - \frac{1}{T}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_H} - \frac{1}{T}\right)\right]}$	*T* = Absolute temperature, K (273.15K = 0°C) *R* = the universal gas constant (1.987 cal/deg/mol) ΔH_A= enthalpy of activation of the reaction that is catalyzed by the enzyme (cal/mol) ΔH_L= change in enthalpy associated with low-temperature inactivation of the enzyme (cal/mol) ΔH_H = change in enthalpy associated with high-temperature inactivation of the enzyme (cal/mol) T_L= temperature (K) at which the enzyme is half active and half low-temperature inactive (K) T_H= temperature (K) at which the enzyme is half active and half high-temperature inactive T_ϕ= intrinsic optimum temperature (K) at which probability of enzyme being in active state is maximal ρ_ϕ = the mean development rate at T_ϕ assuming no enzyme inactivation (days $^{-1}$)	Sharpe and DeMichele 1977; Schoolfield *et al.,* 1981; Shi *et al.,* 2011, 2012

performed between 36 to 40°C at one-degree increment. The pooled sample sizes of survivors that completed immature development from egg to adult emergence analyzed were as follows: 28 survivors at 15°C, 42 at 20°C, 38 at 25°C, 41 at 30°C, 37 at 35°C and 33 at 36°C.

Bioclimatic threshold and thermal constants

Development duration (days) of instars was converted to development rate (1/days) at each temperature. Linear and non-linear models were fitted to describe the rate of development of *S. litura* as a function of temperature to estimate bioclimatic development thresholds and thermal constants.

Statistical analyses

Linear regression was performed with mean developmental rate data using PROC REG to determine linear relationship between rate of developmental (1/*D*) and temperature (T) using equation 1 (Table 1) to obtain regression parameters (*a* and *b*).

Validation of degree-day model

Accumulated degree-days (ADDs) were calculated and compared between observed and predicted incidence of *S. litura* on soybean. Input start date was the observed first field incidence (bio-fix date) and accumulation till larval peak incidence in the rainy season of 2016 (June to October) from several field locations in four soybean growing districts in Maharashtra as part of the Crop Pest Surveillance and Advisory Project (CROPSAP) (http://mahaagriiqc.gov.in/cropsapadm/index.php). Estimated degree-days for completion of egg, larva and pupal stages were taken from our study while the estimate for pre-oviposition period (29 DD) was taken from Ranga Rao *et al*. (1989). Accumulated degree-days for one generation (larva to larva, 489 DD) from an observed start date were calculated using the degree day calculator from UCIPM website (http://ipm.ucanr.edu/WEATHER/index.html) opting for single sine horizontal cut-off method and providing threshold temperatures (T_{min} and T_{max}) as input values. Daily weather data (minimum and maximum temperatures) for different locations were sourced from nearest meteorological observatory for calculating ADD. Paired t-test was performed to compare predicted and observed ADDs for larval stage (bio-fix date to peak incidence). Timing of next generation egg stage (442 DD) was also aimed at to have forecast value in pest management advisories.

RESULTS AND DISCUSSION

Temperature markedly influenced development of life stages of *S. litura* on soybean (Fig 1). Developmental durations of egg, larva, pupa and total immature decreased linearly as temperature increased in the range of 20 to 35°C. Beyond 35°C, complete development from egg to adult emergence was observed only at 36°C but showed non-linear response for all life stages. Regression of developmental rate data in the linear temperature range (20-35°C) gave the estimates of lower developmental threshold temperature (T_{min}) and thermal constant (k) for all the life stages and total immature development (Table 2). The estimated lower developmental threshold temperature (T_{min}) for egg, larva, pupa and total immature life span of *S. litura* were 11.3, 11.7, 11.5 and 12.1°C with Campbell model, and 10.5, 11.2, 11.1 and 11.9°C with SSI linear model, respectively (Table 2). Similarly, thermal constants (k) were 46.9, 271.7, 141.0 and 448.4 DDs with Campbell model and 50.5, 284.7, 144.4 and 458.2 DDs with SSI linear model, respectively. Upper temperature threshold (T_{max}) estimates for life stages and total immature development obtained from Lactin-2, Briere-1 and Simplified beta type function were between 38.0 and 40.1°C. The estimated optimum temperature threshold (T_{opt}) for the total immature development was 34.5, 33.7 and 33.2 from Lactin-2, Briere-1 and Simplified Beta type function, respectively.

Nonlinear thermodynamic SSI model gave estimates of intrinsic optimum temperature (T_{φ}), which were 28.3°C for development of egg, 27.5°C for larva and 30.3°C for pupa. The estimated upper threshold temperatures (T_H) with SSI model were between 35.8 and 36.3°C for all life stages (Table 3).

Development at constant temperatures

Development of *S. litura* life stages were studied at constant temperatures on different host plants by several researchers. Studies on peanut (Ranga Rao *et al*., 1989; Srinivasa Rao *et al*., 2014), sunflower (Manimanjari *et al*., 2014) and cabbage (Qin *et al.,* 2002) addressed the developmental response of life stages at temperatures in the linear range only. In this paper, development of *S. litura* was attempted at higher temperatures (>35°C) and complete development was observed till 36°C, which showed a nonlinear response. We included developmental data of only surviving individuals that completed full immature development from egg to adult emergence in both linear and nonlinear modes. In

Table 2: Model parameter estimates for development of *S. litura* life stages*Description of parameters in Table 1

Model	Parameters*	Egg	Larva	Pupa	Total immature
Campbell	T_{min}	11.3 ± 1.26	11.7 ± 1.71	11.5 ± 0.57	12.1 ± 2.43
	K	46.9 ± 4.32	271.7 ± 34.94	141.0 ± 5.03	448.4 ± 70.97
	R^2	0.9752	0.9196	0.9975	0.9522
Linear SSI	T_{min}	10.5	11.2	11.1	11.9
	K	50.5	284.7	144.4	458.2
	R^2	0.9920	0.9555	0.9996	0.9918
Lactin-2	T_{opt}	34.5	35.6	35.9	34.5
	T_{max}	40.0	40.0	40.0	38.0
	R^2	0.9651	0.9512	0.9983	0.9546
Briere-1	T_{opt}	33.4	33.5	33.8	33.7
	T_{max}	40.0	40.0	40.0	40.0
	R^2	0.9446	0.9112	0.9691	0.9153
Simplified beta type function	T_{opt}	33.0	33.3	33.4	33.2
	T_{max}	40.0	40.1	40.1	40.0
	R^2	0.9446	0.9022	0.9477	0.9029

Table 3: Parameter estimates of non-linear thermodynamic SSI model for *S.litura* life stages

Parameter*	Egg	Larva	Pupa
T_φ (°C)	28.3	27.5	30.3
T_L (°C)	4.1	13.4	14.9
T_H (°C)	36.3	36.3	35.8
χ^2	0.00535	0.00397	0.00004
R^2	0.9920	0.9555	0.9996

* Description of parameters in Table 1

other studies, nonlinear response was observed at still higher temperatures of 37°C on peanut (Ranga Rao *et al.,* 1989). However, it is possible that these differences could be due to differences in experimental conditions.

Bioclimatic thresholds (T_{min}, T_{opt}, T_{max} and T_φ)

In our study, Campbell model using developmental rates in the linear range of 20 to 35°C gave T_{min} estimates between 11.3 and 11.7°C for all life stages. SSI linear model returned lower T_{min} values with better model fit statistics (R^2) (Table 2). However, Campbell model was selected as it returned comparable estimates of lower threshold temperature for initiation of development across life stages and also gave standard error estimates for number of degree-days required for completion of each life stage. The estimated degree-days from linear SSI model were within the standard error ranges of thermal constants for life stages estimated from the Campbell model and corroborated the thermal summation used in validation of the phenology model. Lower temperature threshold and thermal constants for development from constant temperature experiments are widely estimated using the simple linear model of Campbell (Padmavathi *et al*., 2013). Linear fit to developmental rate data of *S. litura* has been reported on peanut (Ranga Rao *et al*., 1989; Srinivasa Rao *et al*., 2014).

Three empirical models assessed the nonlinear relationship of development rate with temperature to estimate theoretical optimum temperature (T_{opt}) and upper threshold temperature (T_{max}). Theoretical estimates of T_{max} were similarly estimated by all three models at 40°C. However, best fit model estimates of T_{opt} for all life stages and total immature life span were obtained with Lactin-2 model based on higher coefficient of determination (R^2) (Table 2). T_{opt} values were closest to the observed fastest development rate at 35°C. Hence, Lactin-2 is preferred over the other two nonlinear models for giving biologically relevant estimates. Increased developmental time of *S. litura* life stages at 36°C

Table 4: Field validation of *S. litura* phenology model in crop season (June to October) during 2016 in Maharashtra

District	No. of locations	Biofix (date of first incidence)	Expected larval peak incidence		Observed larval peak incidence		Expected egg mass incidence	
			Date	Accumulated degree-days	Date	Accumulated degree-days	Date	Accumulated degree-days
Amravati	32	9 Aug	14 Sep	494.1	15 Sep	506.4	11 Sep	454.2
Washim	70	9 Aug	11 Sep	498.2	9 Sep	468.6	07 Sep	440.5
Parbhani	30	29 Aug	30 Sep	484.9	30 Sep	484.9	28 Sep	453.3
Akola	11	15 Aug	13 Sep	489.0	15 Sep	521.6	11 Sep	455.4

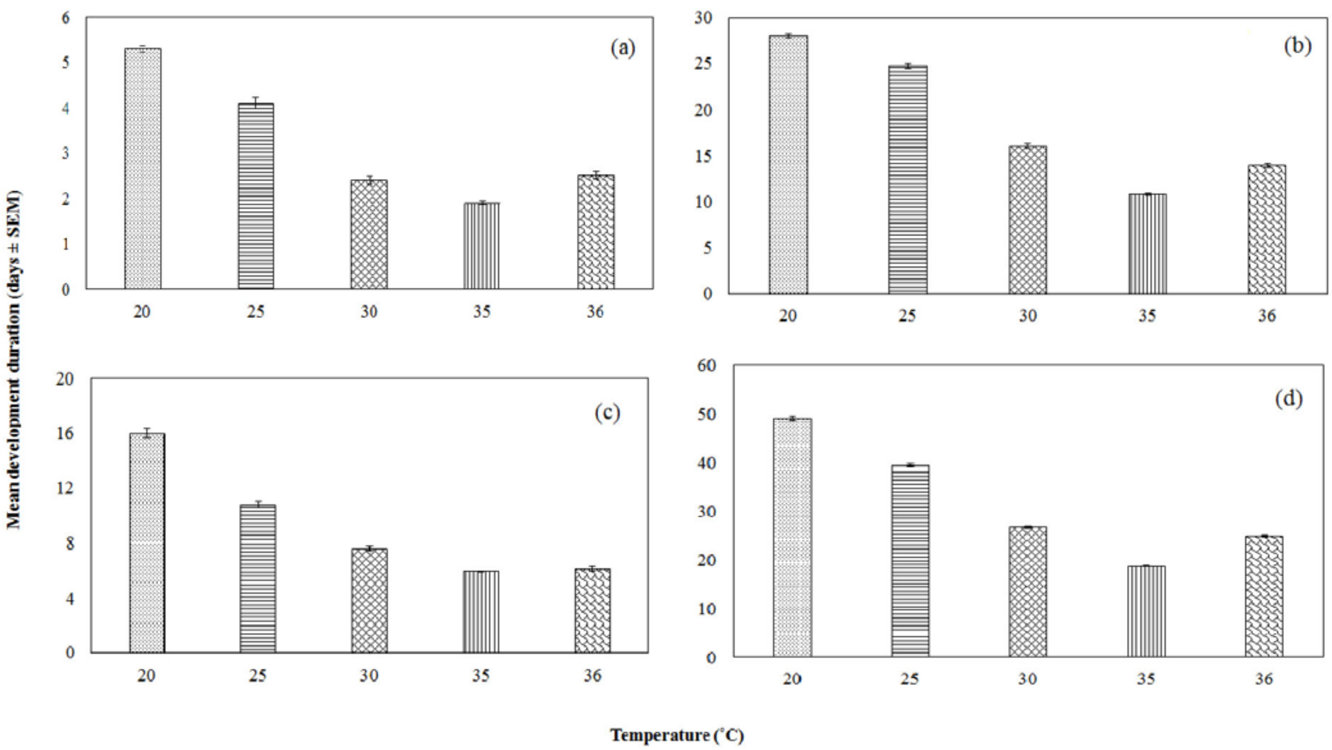

Fig 1: Temperature dependent development of *S. litura* life stages: (a) egg, (b) larva, (c) pupa, and (d) total immature life span

is probably explained by the best-fit estimates of T_H from the thermodynamic nonlinear SSI model. T_H is the temperature at which enzymes related to development are half-active and half-high temperature inactive (Shi *et al*., 2011) and probably explain the observed slower development rate. Values of T_H were lower than the upper lethal T_{max}, the temperature above which development ceases. Intrinsic optimum temperature (T_φ) estimated from thermodynamic SSI model indicated most favourable temperatures for maximal enzyme activity related to development of egg, larval and pupal stages of *S. litura* and also indicated the adaptation of a species to its thermal environment (Shi *et al*., 2012). Evaluation of linear and non-linear models explained the developmental responses (initiation, peak, decline and cessation) of *S. litura* life stages to a range of temperatures.

Field validation of phenology model

Validation of degree-day model was attempted for *S. litura* by comparing timing of predicted and observed phenological events using actual field pest surveillance data on soybean, which was employed previously in case of other pests (Blomefield and Gilimoee, 2014). Pest surveillance on soybean is implemented by State Department of Agriculture, Government of Maharashtra every season to provide pest alerts to farmers for timely pest management. First incidence of *S. litura* was observed between 9 and 29 August, 2016 at 143 locations spread across four soybean growing districts in Maharashtra. Pest scout data from weekly sampled fields (fixed fields over time) indicated peak larval incidence above the economic threshold level (ETL, >4 larvae/ m crop row at post flowering stage) (Vennila *et al*., 2016) between 9 and

30 September, 2016. Observed timing of larval incidence in next generation was not significantly different from predicted time of larval occurrence based on accumulated degree-days calculated from bio-fix dates in August ($t = 0.294$, $df = 3$, $P = 0.788$) (Table 4). Predicted timing of egg stage was 2 to 4 days prior when compared to the observed incidence of damaging larval stage across locations. Forecasts of egg stage of *S. litura* can assist more frequent surveillance at crucial times to provide pest alerts and prepare for management interventions (Javaid, 1990).

CONCLUSION

Bioclimatic parameter estimates from this study were useful in predicting the timing of *S. litura* on soybean in area-wide pest surveillance and issue of pest management advisories. Evaluation of both linear and nonlinear models and comparison of parameter estimates with other *S. litura* populations reported on other hosts was helpful in arriving at more precise estimates necessary for practical field application. Intrinsic optimum temperature threshold estimates from thermodynamic modelling for *S. litura* populations was not previously reported, which appears to be an important indicator of population development coinciding with peak crop damage when daily average temperatures approximate the threshold. However, temperature despite being a key driver of insect development, there are several other factors such as rainfall, humidity and regulation by natural enemies which are important as well in insect population dynamics under field conditions. Validation of phenology model with field surveillance data is one step forward in this direction. Development as a function of temperature reported in this study along with inputs from modelling of survival and growth of *S. litura* can be utilized in the development of more comprehensive simulation models for predicting potential geographical distribution, timing and abundance as reported for other pests. The results of this study can thus be applied in practice for informed decision making in pest surveillance projects currently being implemented on soybean in India.

ACKNOWLEDGEMENT

Optim SSI package in R-software was kindly provided by Dr Peijian Shi. Sharing of field data from CROPSAP project in Maharashtra is duly acknowledged.

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Received : August 2019 : Accepted : May 2021