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Effect of elevated co$_2$ and temperatures on thermal requirement and thermal constants of beet armyworm, *Spodoptera exigua* (Noctuidae: Lepidoptera) on chickpea

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Abstract
The objective of this study was to examine the development of beet armyworm, *Spodoptera exigua* (Noctuidae: Lepidoptera) at six temperatures (20, 25, 27, 30, 33 and 35 °C) and to estimate temperature thresholds and thermal constants for the forecasting models based on heat accumulation units, which could be developed for use in forecasting. The developmental periods of different stages of *S. exigua* were reduced with increases in temperature from 20 to 35 °C under both ambient and elevated CO_2 conditions. The lower development threshold for egg, larva, pupa, adult and total development period required 11.57, 10.72, 9.05, 6.97 and 10.24 ^{o}C under *e*CO_2 conditions, whereas it was 11.61, 10.43, 10.49, 6.15 and 9.83 ^{o}C under *a*CO_2 conditions, respectively. The thermal requirement of *S. exigua* from egg to adult (total development period) was found to be 588.24 degree days under *e*CO_2 conditions as against 555.56 degree days under *a*CO_2 conditions. These estimated temperature thresholds and degree days can be predict the occurrence, number of generations and population dynamics of *S. exigua*.

Keywords: *Spodoptera exigua*, temperature thresholds, thermal constant, degree days, forecasting models and population dynamics

Introduction

Beet armyworm (*Spodoptera exigua* Hubner) (Noctuidae: Lepidoptera) possesses wide distribution, polyphagous, strong migration ability and high temperature suitability. It was reported as an important folivorous pest of numerous cultivated crops including cotton, tomato, celery, cabbage, onion and alfalfa in India [14]. Recently the infestation of *S. exigua* is noticed at significant levels in different states of South India and is gaining major insect pest status on chickpea.

The changes in temperature and CO_2 concentration can influence the growth and development of insect pests and in turn influence population dynamics and their status. Among the climatic factors, temperature is the most important, as it has profound influence on the development and survival of insects. The rate of insect development is affected by the temperature to which insects are exposed [2]. Numerous studies have shown that the annual average temperature of the earth will increase 1 °C by 2025 and the probable rise in temperature by the end of the century is expected to reach 3 °C [15]. Temperature influences the developmental rate of insects significantly and has direct effects, whereas the effect of *e*CO_2 is host-mediated and indirect. It is well known that development rate of insects increases with temperature up to certain levels beyond which they usually decrease [19]. Insects require a certain amount of heat units (degree days) to develop from one life stage to the other stage. Quantification of the relationship between insect development and temperature is useful to predict the seasonal occurrence and population dynamics of the insects. The ability of an insect to develop at different temperatures is an important adaptation to survive under various climatic conditions (tropical, subtropical, and temperate).

So far, there is no published report from India on the effect of constant temperatures on *S. exigua*. Hence, in the present study, developmental periods of different stages of *S. exigua* were examined at six constant temperatures and two CO_2 conditions to estimate the temperature thresholds and thermal requirements, which would be useful in developing models for predicting its distribution and abundance.

Materials and Methods
Maintenance of *Spodoptera exigua* Culture
The stock culture (neonate larvae) of *S. exigua* was obtained from the nearby chickpea crop fields, Rajendranagar, Hyderabad. The culture of *S. exigua* was maintained at optimum temperature of 27 ± 1 ºC and 75 ± 5% RH in the insectory of Entomology section, CRIDA, Hyderabad. The larvae were reared on chickpea leaves for one generation (from egg to egg) to obtain bulk population for further experimentation. Light intensity of 30, 000 Lx being provided by 26 W florescent bulb was maintained inside the chamber during the 14 hours light period with relative humidity of 60% (day) and 70% (night). Insects were reared in growth chambers (I 36LL; Percival Scientific, Inc. Perry, USA) under set conditions of 27±1 ºC, 60-70% relative humidity with a photoperiod ratio of 14: 10 (14 hours of light: 10 hours of dark). The light and illumination is provided through fluorescent lamps horizontally mounted in pairs above each shelf. Programming and control of the lighting were done *via* the Intellus Ultra real time controller. Air circulation inside the chamber was maintained from a specifically designed air diffuser. Each chamber was maintained with a desired level of CO_2 concentrations (*e*CO_2 - 500 ppm and *a*CO_2 - 380 ppm). The CO_2 concentrations were automatically monitored and controlled by using Intellus Ultra Controller. The foliage obtained from chickpea plants grown in open top chambers (OTC) from respective CO_2 conditions was used for insect feeding trails in these growth chambers

Experiments on life tables were conducted at temperatures of 20, 25, 27, 30, 33 and 35 °C both in ambient CO_2 (*a*CO_2; 380 ± 25 ppm) and elevated CO_2 (*e*CO_2; 550 ± 25 ppm) conditions. In order to construct life tables, a group of newly laid eggs of *S. exigua* were placed on a piece of wet filter paper in petridish (75 x 10 mm). These petridishes were maintained at six different temperatures (20, 25, 27, 30, 33 and 35 ± 0.5 ºC) at 75 ± 5% relative humidity (RH) and 14L: 10D hour's photoperiod in CO_2 growth chambers. After egg hatching, the egg period was recorded at different temperatures under both CO_2 conditions. Freshly hatched neonates (thirty) were collected and experimental trials were initiated. Freshly hatched thirty neonates were reared individually in petridishes (75 x 10 mm) till the adult stage. Larvae were fed with fresh chickpea foliage collected from the plants grown in OTCs at two CO_2 levels *i.e.*, *e*CO_2 and *a*CO_2. The data on durations of egg, larval, pupal and adult and total development periods (TDP) at each temperature under *e*CO_2 and *a*CO_2 conditions were recorded.

Calculation of lower temperature thresholds and thermal constants
Quantification of the relationship between insect development and temperature is useful to predict the seasonal occurrence and population dynamics of the insects. The degree day model (thermal summation model) was used to estimate the linear relationship between temperature and the rate of development of insect pests [2]. The reciprocal of developmental period for each stage was calculated to obtain the development rate (1/day) at each temperature. Development threshold and thermal constant were determined by regressing development rate on temperature. Thermal constant is estimated as per the formula given below

Thermal constant (K) = $(T - T_0) \times D$

Where, T - Temperature at which insect species is reared

T_o - Development threshold temperature

D - Duration of development

K was estimated as reciprocal of regression coefficient (b) between development rate and temperature. K = 1/ b. T_o was determined as ratio of regression intercept 'a' and 'b' $T_0 = -a / b$. The life table parameters were estimated for *e*CO_2 and *a*CO_2 separately at above mentioned six temperatures and were plotted against the tested temperatures to compare the lower threshold temperatures and thermal constant under both *e*CO_2 and *a*CO_2 conditions.

Results and Discussion
Durations of different growth stages of *S. exigua*
The durations of different growth stages *S. exigua* were significantly affected by temperatures and CO_2 concentrations. The results pertaining to the variation in durations of egg, larva, pupa and adult stages of *S. exigua* on chickpea at six temperatures of 20, 25, 27, 30, 33 and 35 °C and the two test CO_2 conditions *viz*, ambient CO_2 (*a*CO_2; 380 ± 25 ppm) and elevated CO_2 (*e*CO_2; 550 ± 25 ppm) are presented in Table 1.

The durations of egg (5.20 to 2.00 days), larva (24.60 to 9.45 days), pupa (15.45 to 5.60 days), adult (11.50 to 5.40 days) and total developmental periods (56.75 to 22.45 days) decreased from 20 to 35 °C temperature under *e*CO_2 conditions. Similar trend of reduction of durations of egg (5.40 to 2.00 days), larva (22.70 to 9.05 days), pupa (14.85 to 5.40 days), adult (11.90 to 5.70 days) and total developmental periods (54.85 to 22.15 days) with increasing temperature was noticed under *a*CO_2 conditions. Although the egg, larval and pupal durations was shorter under *a*CO_2 than *e*CO_2 conditions, the duration of adult was more under *a*CO_2 compared to that of *e*CO_2 conditions across the temperatures.

Temperature is the most important and critical abiotic factor exerting profound influence on growth and development of insects. The effects of temperature on insects are species specific. Increase in temperature will have a greater effect on insects than the rising CO_2 concentrations [6]. The reduction of duration of an insect occurs with increasing temperature [18] and similar trend of reduction of duration was observed in the results as well. The present results are in conformity with the findings of Manimanjari *et al* [8]., who reported that the reduction in durations of egg, larva, pupa, adult and total development period of *S. litura* was observed with increase in temperature under both *e*CO_2 and *a*CO_2 conditions. Mean developmental time of egg (7.61 to 3.32 days), larva (29.8 to 12.87 days), pupa (16.46 to 7.93 days), adult (5.33 to 3.67 days) and total development period (59.2 to 27.8 days) decreased from 20 to 35 ºC temperature under *e*CO_2 conditions. Similarly under *a*CO_2 conditions, the development period for egg (7.53 to 3.68 days), larva (27.60 to 13.13 days), pupa (16.80 to 6.66 days), adult (7.0 to 2.6 days) and total development period (58.93 to 26.06 days) from 20 to 35 ºC. Similar results have been reported by Srinivasa Rao *et al* [16], who reported that the reduction in durations of egg, larva, pupa, adult and total development period of *S. litura* with increase in temperature under both *e*CO_2 and *a*CO_2 conditions. Karimi-Malati *et al* [7]. reported that the egg period decreased with increasing temperature and varied from 5 days at 20 °C to 2 days at 30 and 33 °C and the development time of the immature stages ranged from 41.63 to 14.5 days at 20 °C and 33 °C, respectively. The total developmental time for *S. exigua* at 25 - 26 °C has been reported to be 20.2–26.4 days [4], 24.71–33.2 days [12] and 21.63–27.22 days [3] on different host plants. Similar decrease in development period with an increase in constant temperatures was reported in case of other lepidopteran insect pests like *Cnaphalocrocis medinalis* Guenee [10] and *Elasmopalpus lignosellus* Zeller [5].

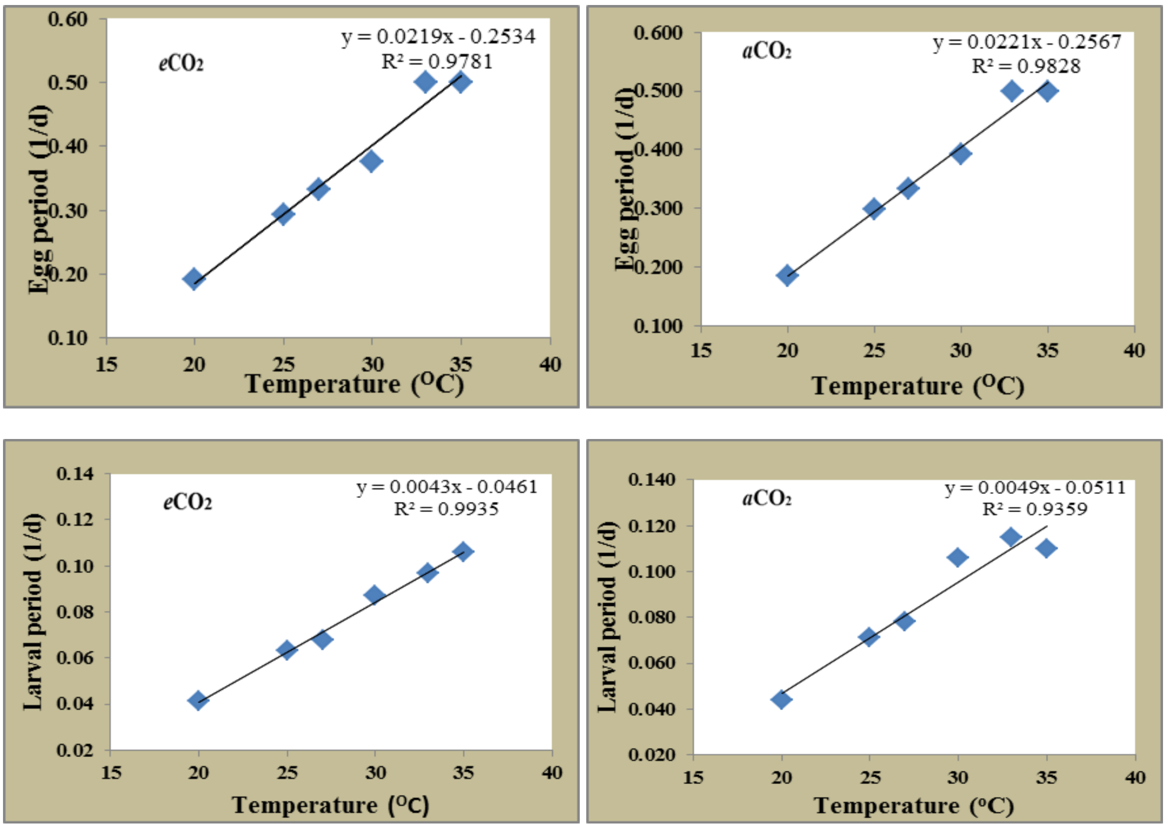
Lower threshold temperatures and thermal constants of *S. exigua*

Linear regression model was used to calculate the lower temperature threshold and thermal constant are presented in Fig 1a & 1b. The development rate of each stage of insect was regressed on temperature and linear regression equations are depicted in the Table 2. The linear regression equations of development rate with temperature under *e*CO_2 conditions indicated significant multiple coefficient of determination for egg (y = 0.0219x - 0.2534, R^2 = 0.9780), larva (y = 0.0043x-0.0461, R^2 = 0.9935), pupa (y = 0.0066x - 0.0597, R^2 = 0.9280), adult (y = 0.0060x - 0.0418, R^2 = 0.8977) and total development period (y = 0.0017x- 0.0174, R^2 = 0.9928). Similarly the linear regression equations for different stages of *S. exigua* under *a*CO_2 indicated significant multiple coefficient of determination for egg (y = 0.0221x - 0.2567, R^2 = 0.9828), larva (y = 0.0049x- 0.0551, R^2 = 0.9359), pupa (y =0.0075x - 0.0787, R^2 = 0.9895), adult (y = 0.0054x - 0.0332, R^2 = 0.8656) and total development period (y = 0.0018x - 0.0177, R^2 = 0.9980).

The lower development threshold for egg, larva, pupa, adult and total development period required 11.57, 10.72, 9.05, 6.97 and 10.24 ºC under *e*CO_2, whereas it was 11.61, 10.43, 10.49, 6.15 and 9.83 ºC under *a*CO_2 conditions, respectively. The thermal requirement of *S. exigua* from egg to adult (total development period) was found to be 588.24 degree days under *e*CO_2 conditions as against 555.56 degree days under *a*CO_2 conditions. Egg, larva, pupa and adult stages required 45.25, 204.08, 133.33 and 185.18 degree days under *e*CO_2 conditions as against 45.25, 204.08, 133.33 and 185.18 degree days under *a*CO_2 conditions respectively. Thus, the thermal requirements for larva and pupa were more under *e*CO_2 conditions compared with *a*CO_2 conditions.

The rate of insect development is affected by the temperature to which insects are exposed. Insects require a certain amount of heat units (degree days) to develop from one life stage to the other [1]. The thermal requirement of *S. exigua* from egg to egg (within the range of 20-35 °C) was higher (538.50 degree days) under *e*CO_2 conditions than that of *a*CO_2 conditions (494.51 degree days). These higher thermal requirements might be due to feeding on low nutritious chickpea foliage obtained from *e*CO_2 conditions. It was suggested that the thermal constant is influenced not only by the temperature but also by the host plant quality [9]. The estimated temperature thresholds and thermal constants are useful in the prediction of population peaks [17] and the present data will be relevant in future climate change scenarios to understand the distribution and abundance of insect pest.

Thermal constant provides better prediction of insect development than developmental period. Depending upon temperature and development threshold, heat units are accumulated until fulfilment of thermal constant requirement, which indicates completion of insect life cycle (or) a development stage [13]. Present results are in agreement with the results of Karimi-Malati *et al* [7], who reported that the lower development thresholds for egg, larva, pupa and total development periods of *S. exigua* were 11.65, 12.41, 12.98 and 12.98 °C, respectively. The thermal requirement of eggs, larvae, pupa and immature stages were 40.16, 174.83, 106.38 and 294.99 degree days estimated by using linear regression model. Similar results were reported by Srinivasa Rao *et al* [16] under *e*CO_2 and *a*CO_2 conditions, who reported that the mean lower temperature thresholds for egg, larva, pupa and pre-oviposition of *S. litura* were 9.55, 10.14, 13.18 and 6.7 ºC under *e*CO_2 conditions, whereas it was 8.16, 11.92, 14.5 and 7.81 ºC under *a*CO_2 conditions, respectively. The thermal requirement of *S. litura* from egg to egg was found to be 538.50 degree days under *e*CO_2 conditions as against 494.51 degree days under *a*CO_2 conditions. Similarly, Rangarao *et al* [11] reported lower threshold temperatures and thermal constant for the development of *S. litura* and observed that an average of 64 degree days above a threshold of 8 °C was required from oviposition to egg hatch; the larval stage required 303 degree days and pupal stage required 155 degree days above a 10 °C threshold temperature.



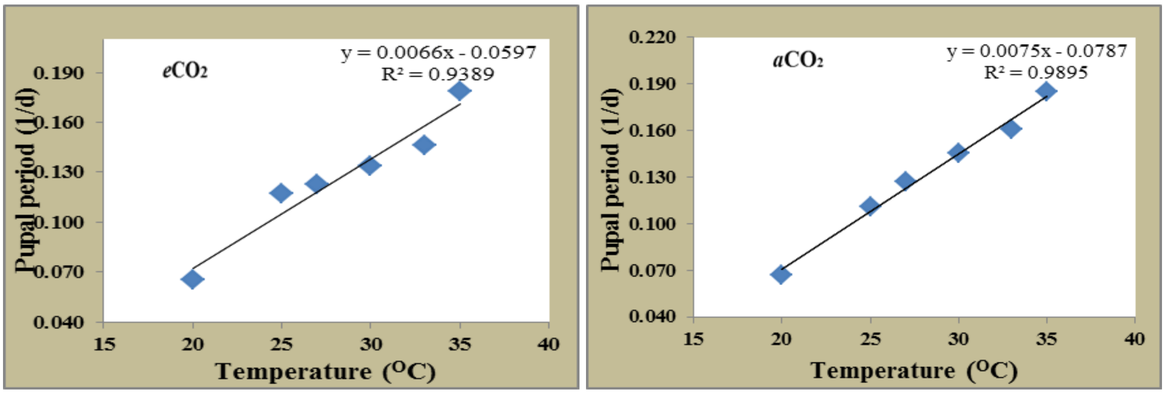


Fig 1a: Regression analysis between temperatures and development rate to determine lower temperature threshold and thermal constant for egg, larval and pupal stages of *S. exigua* on chickpea under elevatedCO_2 and ambient CO_2 conditions

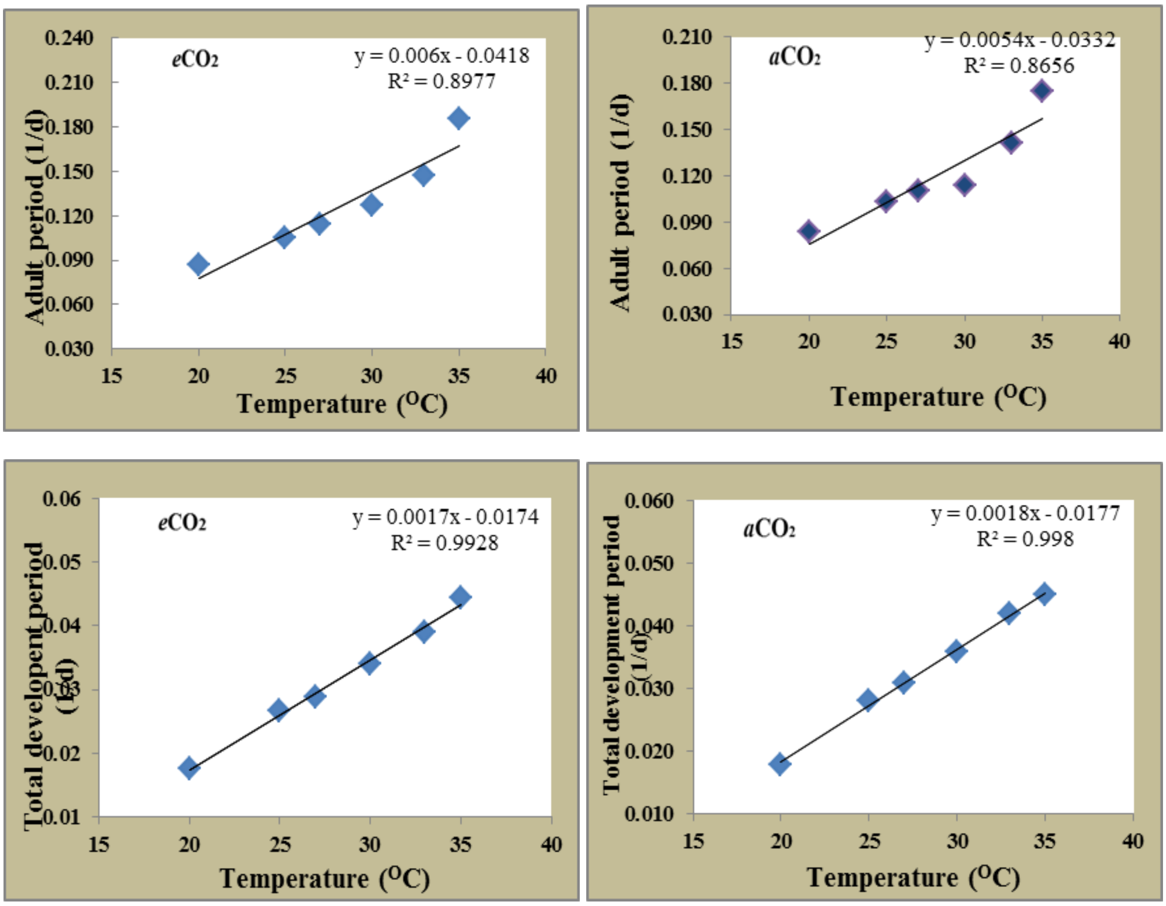


Fig 1b: Regression analysis between temperatures and development rate to determine lower temperature threshold and thermal constant for adult and total development periods of *S. exigua* on chickpea under *e*CO_2 and *a*CO_2 conditions

Table 1: Effect of elevated temperatures and CO_2 concentrations on the duration of different growth stages of *S. exigua* on chickpea

Temp (°C)	Egg period (days)		Larval period (days)		Pupal period (days)		Adult period (days)		Total development period (days)	
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2
20	5.40 ± 0.51	5.20 ± 0.51	22.70 ± 0.75	24.60 ± 0.75	14.85 ±1.41	15.45 ± 1.41	11.90 ± 0.72	11.50 ± 0.72	54.85 ± 2.01	56.75 ± 2.01
25	3.35 ± 0.49	3.40 ± 0.50	14.05 ± 0.69	15.95 ± 0.67	9.00 ± 0.73	8.55 ± 0.61	9.70 ± 0.77	9.50 ± 0.92	36.10 ± 1.29	37.40 ± 1.23
27	3.00 ± 0.00	3.00 ± 0.00	12.80 ± 0.41	14.80 ± 0.50	7.85 ± 0.88	8.10 ± 0.79	9.10 ± 0.75	8.80 ± 0.79	32.75 ± 1.16	34.85 ± 1.23
30	2.55 ± 0.51	2.65 ± 0.49	9.45 ± 0.51	11.50 ± 0.94	7.05 ± 1.28	7.45 ± 0.69	8.75 ± 0.75	7.85 ± 0.64	27.80 ± 1.70	29.35 ± 1.09
33	2.00 ± 0.00	2.00 ± 0.00	8.70 ± 0.80	10.30 ± 0.66	6.20 ± 0.95	6.85 ± 0.88	7.10 ± 0.83	6.80 ± 0.79	24.00 ± 1.70	25.95 ± 1.10
35	2.00 ± 0.00	2.00 ± 0.00	9.05 ± 0.69	9.45 ± 0.51	5.40 ± 0.68	5.60 ± 0.68	5.70 ± 0.75	5.40 ±0.66	22.15 ± 1.27	22.45± 0.95
F test	0.72^{NS}		8.67**		2.43**		1.18^{NS}		2.56**	
S.Em ±	0.10		0.23		0.27		0.24		0.43	
CD	NS		0.46		0.53		NS		0.86	
CV (%)	11.41		6.61		11.65		9.43		5.06	

All values are mean ± standard deviation
**Significant @ 5% level of significance (P = 0.05)
NS = Non-significant

Table 2: Effect of elevated CO_2 on lower temperature thresholds and thermal constants of each developmental stage of *S. exigua* on chickpea

Development stage	Regression Equation		R^2 value		Lower Temperature Threshold (T_0=a/b) (°C)		Thermal constant (K=1/b) (Degree Days-DD)	
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2
Egg	y = 0.0221x - 0.2567	y = 0.0219x - 0.2534	0.9828	0.978	11.61	11.57	45.25	45.66
Larva	y = 0.0049x - 0.0551	y = 0.0043x - 0.0461	0.9359	0.9935	10.43	10.72	204.08	232.56
Pupa	y = 0.0075x - 0.0787	y = 0.0066x - 0.0597	0.9895	0.9280	10.49	9.05	133.33	151.52
Adult	y = 0.0054x - 0.0332	y = 0.0060x - 0.0418	0.8656	0.8977	6.15	6.97	185.18	166.67
TDP	y = 0.0018x - 0.0177	y = 0.0017x - 0.0174	0.9980	0.9928	9.83	10.24	555.56	588.24

Parameters estimated by plotting developmental rates (y=1/D, D=developmental duration) against temperatures (x)
TDP- Total Developmental Period

Conclusion

In conclusions, this study indicated the growth and development of *S. exigua* were significantly influenced by temperature and CO_2 concentrations. Both lower and higher temperatures inhibited the development of insect pest and the ideal conditions for the growth of the pest are 25-27 °C temperature. This study provides the biological response of *S. exigua* to a wide range of temperatures to predict its population dynamics under filed conditions. The thermal requirements and degree days are used to forecast accurately the occurrence of different stages of *S. exigua* in chickpea crop and enable us to choose the best time for controlling this pest with greater precision.

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