Full paper

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Temperature dependent developmental biology and survival of *Spodoptera litura* life stages on soybean

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Abstract

The effect of temperature on development of different life stages of Spodoptera litura *(Fabricius) on soybean* (Glycine max *L.) was assessed under laboratory conditions in environmental growth chambers at six constant temperatures* viz., *15, 20, 25, 30, 35 and 36 ± 1 °C. Temperature had a pronounced effect on* S. litura *reared on soybean. Development was linear for immature life stages in the temperature range of 20 and 35°C. Developmental durations of different life stages decreased with increase in temperature till 35 °C. The decrease in duration for egg stage was from 10.7 to 1.9 days, for larva from 28.0 to 10.8 days, for pupa from 16.0 to 5.9 days and total immature development (egg to adult emergence) was from 49.0 to 18.7 days. At 36 °C, development durations increased for all life stages indicating non-linear relationship at higher temperatures. Completion of life cycle was affected at lower extreme temperature (15°C). Highest probability of survival was observed at 20 °C from Kaplan-Meier survival analysis. Oviposition period, fecundity and longevity were also influenced by temperature with peak fecundity at 25°C.*

Keywords: *Spodoptera litura*, soybean, developmental biology, survival

Introduction

Soybean, *Glycine max* (L.) Merrill, is an important seed legume crop, introduced in India 1970s. It is now a major crop with its cultivation expanded to over 10 m ha in the rainfed agro-ecosystem of the central and peninsular India. This brought about a shift in the cropping pattern in these areas and led to enhancement of cropping intensity with resultant increase in profitability to farmers. In recent years, insect pest outbreak on soybean is posing a challenge to soybean farmers (Prasad *et al.*, 2013). Tobacco cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae), is widely distributed in the tropics across Asia (India, China, Indonesia, Japan and Malaysia) and Oceania (Australia and Pacific island nations) (Kranz *et al.*, 1977). This insect pest causes economic damage to soybean and several other economically important crops such as cotton, peanut, tobacco, tomato, sunflower, seed legumes (*Vigna* spp.) and sweet potato (Venette *et al.*, 2003). Climate variability is often associated with fluctuations in insect populations (Bale *et al.*, 2002) and temperature among the environmental factors is considered as the key driver of insect development, survival and reproduction. Of the biological factors, host plant nutrition is known to influence various life cycle attributes of polyphagous species (Scriber and Slansky, 1981). In this paper, we report the developmental biology of different life stages of *S. litura* reared on soybean foliage at six constant temperatures in the range of 15 to 36 °C. This data on temperature driven biology of *S. litura* is useful in modelling the developmental rate, comparative analysis of different geographical populations and development of phenology models to predict the timing of seasonal occurrence of *S. litura* and to make informed decisions on the timing of insecticide applications or release of natural enemies to achieve its effective management.

Materials and methods

The study was conducted at the Central Research Institute for Dryland Agriculture (CRIDA), Hyderabad, India. Laboratory experiments were conducted using environmental growth chambers (MLR 350H and 351H, Sanyo, Japan). *S. litura* culture was maintained at 27±1 °C, 60±5% relative humidity and photoperiod (14:10 L: D) on soybean foliage (cultivar JS 335). Pairs of virgin adults were transferred to set experimental temperatures for oviposition on potted soybean plants.

Development studies at different temperatures

Freshly laid eggs in a cohort were exposed to constant temperatures of 15, 20, 25, 30, 35 and 36 °C in separate experiments. After hatch, neonate larvae (0-12 h old) were individually transferred onto fresh soybean foliage in Petri dishes (9 cm diameter). The larvae were observed daily. Presence of exuvia was noted to record moulting for determining instar durations. Survival rates were calculated based on the number at the start and end of each instar or stage. Pupae were transferred to individual glass tubes to observe for adult emergence and sexing. Development data for individuals that survived to adulthood was considered for analyses.

Statistical analysis

One-way analysis of variance (ANOVA) was performed to determine the effect of temperature on mean development durations and reproductive parameters of *S. litura* using PROC GLM in SAS 9.2 (Institute SAS 2009). Treatment means were separated using the Tukey-Kramer HSD (honestly significant difference) test at 5% level of significance.

Kaplan-Meier or Product limit analysis of the survival data for cumulative immature development to adulthood (egg to adult emergence) was carried out using PROC LIFE TEST. Point estimates of total immature development time and 95% confidence interval (days) of *S. litura* at 25th, 50th and 75th percentile for different constant temperatures were computed. Homogeneity in survival curves at 20, 25, 30, 35 and 36 °C was tested using Log-Rank and Wilcoxon tests.

Results and discussion

S. litura development was significantly influenced by temperatures between 15 to 36 °C (Table 1). Egg developmental duration decreased with increase in temperature from 10.7 days (15 °C) to 1.9 days (35° C), but increased to 2.5 days (36 °C) indicating a non-linear response at extreme temperature. Larval development showed a linear response of decreasing developmental durations of all the instars with increase in temperatures till 35 °C. Cumulative larval development of *S. litura* showed a non-linear response at 36 °C. At the lower temperature of 15 °C, *S. litura* larvae entered pupal stage but adult emergence was not observed. Pupal period varied from 16.0 to 5.9 days in the temperature range of 20 to 35 °C. Cumulative immature developmental duration to adulthood was longest at 20 °C (49.0 days) and shortest at 35 °C (18.7 days) with a non-linear response at 36 °C (25.0 days).

S. litura completed its development from egg to adult emergence at all temperatures except at 15 °C. The Kaplan-Meier survival curves for egg to adult stage followed by Log-Rank and Wilcoxon tests revealed that all survival curves at different temperatures were significantly different except the pair wise comparison between 30 and 36 °C. The expected median durations from Kaplan-Meier analysis were 49, 40, 26, 19 and 25 at 20, 25, 30, 35 and 36 °C, respectively (Table 2). Adult pre-oviposition period (emergence to start of egg laying), oviposition period (start to end of egg laying) and post-oviposition period (end of egg laying to mortality) were longest at 20 °C and decreased with increase in temperature with a non-liner response at 35 °C except oviposition period which was curtailed (Table 3). Fecundity parameters were highest at 25 °C with mean fecundity of 2189.7 eggs/female and a mean lifetime fecundity of 938.4 eggs/female/day with similar longevity of both females and males at this temperature (Table 3).

Table 1. Development duration in days (Mean ± SEM) of immature stages of *S. litura* at constant temperatures

Temperature (°C)	Sample size	Egg	Mean duration of larval instars I	II	III	IV	V	VI	Total larval duration	Pupal period	Total immature development duration
15	28	10.7 ± 0.12^{a}	14.0 ± 0.31^{a}	8.8 ± 0.25^{a}	9.8 ± 0.26^{a}	8.3 ± 0.40^{a}	9.9 ± 0.17^{a}	22.6 ± 0.50^{a}	73.3 ± 0.60^{a}	-	-
20	42	5.3 ± 0.07^{b}	6.0 ± 0.02^{b}	3.7 ± 0.08^{b}	3.8 ± 0.07^{b}	3.5 ± 0.13^{b}	3.5 ± 0.09^{b}	7.5 ± 0.12^{c}	28.0 ± 0.25^{b}	16.0 ± 0.32^{a}	49.0 ± 0.35^{a}
25	38	4.1 ± 0.12^{c}	3.6 ± 0.11^{c}	2.8 ± 0.10^{c}	2.7 ± 0.12^{c}	3.2 ± 0.11^{b}	4.0 ± 0.15^{b}	8.5 ± 0.19^{b}	24.7 ± 0.29^{c}	10.8 ± 0.21^{c}	39.5 ± 0.37^{b}
30	41	2.4 ± 0.08^{d}	2.0 ± 0.02^{d}	2.0 ± 0.00^{d}	1.0 ± 0.03^{e}	2.1 ± 0.05^{c}	2.5 ± 0.14^{c}	6.3 ± 0.19^{d}	16.0 ± 0.27^{d}	7.6 ± 0.16^{d}	26.7 ± 0.27^{c}
35	37	1.9 ± 0.04^{e}	2.1 ± 0.05^{d}	2.1 ± 0.06^{d}	1.2 ± 0.07^{de}	1.8 ± 0.07^{c}	2.6 ± 0.11^{c}	1.0 ± 0.03^{f}	10.8 ± 0.10^{f}	5.9 ± 0.07^{e}	18.7 ± 0.13^{e}
36	33	2.5 ± 0.09^{d}	2.0 ± 0.03^{d}	1.3 ± 0.09^{e}	1.6 ± 0.10^{d}	2.2 ± 0.09^{c}	2.1 ± 0.12^{c}	4.7 ± 0.17^{e}	13.9 ± 0.21^{e}	6.1 ± 0.20^{b}	25.0 ± 0.20^{d}
F		1158.02	1495.46	537.60	701.99	197.74	411.14	987.62	5074.50	389.63	1898.35
Df		5, 213	5, 213	5, 213	5, 213	5, 213	5, 213	5, 213	5, 213	4, 186	4, 186
P		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Means within a column followed by the same letter are not significantly different at $\alpha = 0.05$ (Tukey-Kramer test); - = no survivors

Table 2. Point estimates of total immature development time and 95% CI (day) of *S. litura* at 25th, 50th and 75th percentile estimated with Kaplan-Meier survival analysis for different constant temperatures

Temperature (±1°C)	Total immature development time (day)		
	25th percentile (LL, UL)	50th percentile (LL, UL)	75th percentile (LL, UL)
20	51 (49, 51)	49 (48, 49)	48 (46, 48)
25	41 (40, 42)	40 (39, 41)	38 (36, 39)
30	28 (27, 29)	26 (26, 27)	26 (25, 26)
35	19 (19, 20)	19 (18, 19)	18 (18, 19)
36	26 (25, 26)	25 (24, 25)	24 (24, 25)

LL and UL are the lower and upper limits of the 95% confidence interval

Temperature had a pronounced effect on *S. litura* reared on soybean with accelerated development at 35 °C, beyond which it was affected at 36 °C. Non-linear development response of *S. litura* observed at upper extreme temperature is in accordance with previous results reported in literature. A similar trend was observed with *S. litura* reared on groundnut (Ranga Rao *et al.*, 1989; Srinivasa Rao *et al.*, 2014), on cabbage (Qin *et al.*, 2002) and on sunflower (Manimanjari *et al.*, 2014). Also the response of various stages of *S. litura* to temperatures under constant laboratory conditions was similar to that under field conditions on groundnut (Ranga Rao *et al.*, 1989). The developmental effects observed for *S. litura* under diurnal temperature variation pattern as encountered in natural conditions were similar to the effects observed at the constant temperature of 25 °C (Fand *et al.*, 2015). Hence, developmental data generated under constant temperatures are useful in modelling and predicting pest abundance under field conditions as well. Host induced variation in developmental durations of *S. litura* immature stages at different constant temperatures is evident when compared with previous studies. Developmental durations were slightly longer when reared on tobacco (Xue *et al.*, 2010; Patil *et al.*, 2014). Peak fecundity of *S. litura* observed on soybean was at 25 °C while it was observed at 27 °C on soybean (Manimanjari *et al.*, 2014). Oviposition response of *S. litura* was influenced by temperature and appears to be the most important driver of field population dynamics across seasons. Hence, temperature dependent age-specific fecundity data of *S. litura* on different hosts is of pivotal importance for developing pest forecasting models (Fand *et al.*, 2015).

Kaplan-Meier survival curves also revealed decrease in survival time with increase in temperature up to 35 °C. Temperature is the most important environmental factor that influences insect development and survival. In this paper, constant temperature response experiments have been used to estimate parameters of phenology models to bring out the thermal differences in developmental times as experimented in previous studies with other insect pests (Prasad *et al.*, 2012, Padmavathi *et al.*, 2013 and Sreedevi *et al.*, 2013). Such a method was applied for forecasting of *Helicoverpa* populations in Australia (Zalucki and Furlong, 2005). Hence, the developmental, survival and reproductive data of *S. litura* on soybean provided in this study would be useful for developing forecast models, monitoring and planning control strategies on soybean and possibly in several other crops as well.

Table 3. Reproduction parameters of *S. litura* at constant temperatures

Temperature (±1°C)	Pre-oviposition period (day)	Oviposition period (day)	Post-oviposition period (day)	Mean fecundity/ female (no.)	Mean lifetime fecundity (no./ female/day)	Female longevity (day)	Male longevity	Sex Ratio
20	4.9 ± 0.79^{a} (16)	4.2 ± 0.67^{a} (16)	3.1 ± 0.70^{a} (16)	943.2 ± 96.6^{c} (16)	327.2 ± 33^{b} (16)	12.2 ± 0.97^{a} (16)	8.0 ± 0.82^{a} (17)	59.5
25	3.7 ± 1.26^{ab} (6)	2.7 ± 0.33^{a} (6)	1.7 ± 0.61^{a} (6)	2189.7 ± 528^{a} (6)	938.4 ± 143.3^{a} (6)	8.0 ± 1.63^{b} (6)	7.1 ± 0.59^{ab} (9)	75.0
30	1.2 ± 0.23^{b} (11)	2.6 ± 0.31^{a} (11)	1.2 ± 0.18^{a} (11)	1387.2 ± 188.8^{b} (11)	508.6 ± 48.1^{ab} (11)	5.0 ± 0.47^{b} (11)	5.2 ± 0.42^{b} (16)	61.0
35	3.0 ± 0.00 (1)	1.0 ± 0.00 (1)	2.0 ± 0.00 (1)	146 ± 0.00 (1)	146 ± 0.00 (1)	6.0 ± 0.00 (1)	7.7 ± 0.76^{ab} (11)	66.7
F	4.42	2.05	2.02	5.79	15.22	10.76	3.92	
df	3, 30	3, 30	3, 30	3, 30	3, 90	3, 30	3, 49	
P	0.0110	0.1274	0.1319	0.0029	<0.0001	<0.0001	0.0137	

Means within a column followed by the same letter are not significantly different at $\alpha = 0.05$ (Tukey-Kramer test); values in parantheses are sample sizes

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