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Threshold Temperatures and Thermal Requirements for the Development of *Spodoptera litura* (Lepidoptera: Noctuidae)

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ABSTRACT Developmental thresholds and thermal requirements for different stages of *Spodoptera litura* (F.) fed on groundnut leaves were determined under constant laboratory conditions and in the field. An average of 64 degree-days (DD) above a threshold of 8°C was required from oviposition to egg hatch, the larval period required 303 DD and pupal stage 155 DD above a 10°C threshold; females needed 29 DD above a 10.8°C threshold from emergence to oviposition. Fifth and sixth instars accounted for about 50% of the total larval requirement under laboratory and field conditions. The response of various stages of *S. litura* to temperatures under constant laboratory conditions was similar to that under field conditions. The upper developmental threshold temperature of all stages was 37°C; 40°C was lethal.

KEY WORDS Insecta, *Spodoptera litura*, threshold temperatures, thermal requirements

Spodoptera litura (F.) is an important pest of groundnut in Asia (Feakin 1973). In addition to groundnut, it is known to attack 112 cultivated plant species in different parts of its range and about 60 in India (Garad et al. 1984). Predicting the seasonal occurrence and abundance of any pest is essential for the accurate scheduling of control tactics. Such predictions require an understanding of the relationship between insect development rate and temperature. This relationship is often described in temperature-driven phenology models; the most widely used are based on degree-day summation which assumes a linear relationship between developmental rate and temperature over the "normal" range (Gregg 1981).

This paper describes experiments carried out to determine this relationship for *S. litura* fed on leaves of groundnut, *Arachis hypogaea* L. A comparison of the development rate under constant temperatures and in field temperatures has been made because there are instances where the fluctuating temperatures characteristic of field conditions induce development rates that are higher than those expected from laboratory studies carried out under constant temperature regimes (Hagstrum & Hagstrum 1970, Gregg 1981). Therefore, we ran a check over six successive generations under field conditions using rearing procedures similar to those employed in the laboratory.

Materials and Methods

The laboratory culture was started in 1985 from egg masses collected from groundnut fields at ICRISAT Center, Patancheru, Hyderabad, India. The culture was maintained at 24 ± 2°C, and the larvae were fed on groundnut leaves (TMV-2, Spanish bunch varieties). The number of days required for the development of each immature stage was determined at seven constant temperatures (15, 20, 25, 30, 35, 37, and 40°C (±1°C), in growth chambers with a 12:12 (L:D) photoperiod; the relative humidity was maintained at 75 ± 10%.

Egg development rate was evaluated by holding egg masses (6–18 h old) in Petri dishes (4.5 cm diameter). We recorded data from 41 (15°C), 42 (20°C), 44 (25°C), 46 (30°C), 50 (35°C), 25 (37°C), and 20 (40°C) egg masses, each containing 150–200 eggs. Larvae and pupae were held singly in transparent plastic cups (4.5 by 4 cm) and fed on excised groundnut leaves. Wet filter paper was provided to keep the leaf material fresh. Neonate larvae (<6 h old) were transferred to the leaves with a fine brush. The numbers of larvae and pupae in each temperature treatment were 22 (15°C), 33 (20°C), 36 (25°C), 56 (30°C), 55 (35°C), 18 (37°C), and 50 larvae and 25 pupae (40°C). Only individuals that survived to adulthood were included in the analysis. The instar determination was based on the head capsule width and the presence of molted cuticles. Because there was no difference in either the development period or the pupal weight between males and females, the data for both sexes were pooled. The stage of development was recorded daily once for larvae and pupae and twice daily for eggs.

Prepositional studies were conducted in plastic cages (30 cm high, 10 cm diameter) fitted on potted groundnut plants. Sucrose solution (10%) was provided for the moths during the ovipositional phase.

Field studies were conducted by placing eggs or neonate larvae (<12 h old) in individual rearing cups in a Stevenson screen under conditions identical (except for abiotic factors) to those used in laboratory studies. Six batches were reared in sequence from September 1985 to May 1986. Daily maximum and minimum temperatures in the Stevenson screen were recorded. The average monthly maximum–minimum temperatures for September, October, November, December, January, February, March, and April were 31–22, 29–18, 29–13, 29–13, 27–13, 30–17, 35–20, and 38–24°C, respectively. Daily observations of growth and development were taken of larvae, pupae, and preoviposition females; eggs were checked twice a day.

The degree-days (DD) required for different stages under field condition were calculated according to the thermal summation scheme of AliNiazee (1976):

$$DD = \frac{\text{Daily max} + \text{min temperature}}{2} - \text{threshold temperature}$$

Results and Discussion

The duration of the immature stages of *S. litura* decreased as temperature increased to 35°C (Table 1) There was no oviposition, egg hatch, or larval development–survival at 40°C. The upper threshold temperature for the development was between 37 and 40°C. Linear regression was used to calculate the developmental threshold (X intercept), and thermal requirement (inverse of the slope). As the rate of development at 37°C deviated from linearity, data for this temperature were not included in the analysis. The mean lower developmental threshold for eggs was 8.2°C (95% confidence limits, 4.1–12.2), for larvae 10°C (6.6–13.4), and for pupae 10.2°C (9.6–10.8). The adult during the preoviposition period had a slightly higher threshold of 10.8°C (7.5–14.1). There was no oviposition at 35 and 37°C. Development from egg to egg within the range 15–35°C (15–30°C for the preoviposition period required 551 DD using the appropriate lower threshold temperatures for each stage) (Table 2). Eggs, larvae, pupae, and preoviposition required 64, 303, 155, and 29 DD, which represent 12, 55, 28, and 5% of the total developmental period. Under laboratory conditions, first, second, third, fourth, fifth, and sixth instars required 14, 11, 12, 13, 15, and 35% of the total larval development time, respectively. These results are in agreement with the findings of Miyashita (1971) for this species feeding on an artificial diet at constant temperatures in Japan. However, in his experiments, the development of larvae and pupae was somewhat faster at constant fluctuating temperatures than at constant temperatures.

Table 1. Duration (days ± SE) of *S. litura* immature stages at constant temperatures

Stage	Temperature °C[a]					
	15	20	25	30	35	37
Egg	12.6 ± 0.2	5.0 ± 0.2	3.7 ± 0.1	2.9 ± 0.1	2.6 ± 0.1	2.7 ± 0.1
First instar	13.1 ± 0.5	3.0 ± 0.1	2.5 ± 0.1	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0
Second instar	11.1 ± 0.5	2.4 ± 0.1	2.6 ± 0.1	1.7 ± 0.1	1.6 ± 0.1	1.6 ± 0.2
Third instar	15.6 ± 1.4	2.8 ± 0.1	2.1 ± 0.1	1.5 ± 0.1	1.5 ± 0.1	1.8 ± 0.2
Fourth instar	16.5 ± 0.9	3.2 ± 0.2	2.4 ± 0.1	2.0 ± 0.1	1.1 ± 0.1	2.7 ± 0.2
Fifth instar	14.6 ± 1.1	4.3 ± 0.2	2.8 ± 0.1	2.5 ± 0.1	1.6 ± 0.1	2.1 ± 0.1
Sixth instar	23.6 ± 1.3	9.2 ± 0.1	7.6 ± 0.3	6.1 ± 0.2	4.6 ± 0.1	5.6 ± 0.2
Total for						
Larvae	94.5 ± 2.1	24.9 ± 0.4	19.9 ± 0.4	15.7 ± 0.2	12.4 ± 0.2	15.6 ± 0.2
Pupae	31.6 ± 1.0	17.2 ± 0.9	10.9 ± 0.3	8.1 ± 0.1	6.3 ± 0.1	7.3 ± 0.1
Preoviposition	6.3 ± 0.2	3.3 ± 0.2	1.6 ± 0.2	1.6 ± 0.2	—	—

[a] Photoperiod of 12:12 (L:D) and RH 75 ± 10% at all temperatures.

Table 2. Developmental thresholds and thermal requirements for *S. litura*

Stage	Lower developmental threshold temp (95% confidence limits)	Regression[a] equation	DD (95% confidence limits)	% Total thermal developmental period
Eggs	8.2 (4.1–12.2)	$-12.83 + 1.37x$, $r = 0.96$	64 (49–78)	12
Larvae	10.0 (6.6–13.4)	$-3.29 + 0.33x$, $r = 0.96$	303 (241–365)	55
Pupae	10.2 (9.6–10.8)	$-6.59 + 0.65x$, $r = 1.00$	155 (149–160)	28
Preoviposition	10.8 (7.5–14.1)	$-37.1 + 3.45x$, $r = 0.95$	29 (22–36)	5

[a] $y = a + bx$, calculated from data obtained when rearing at constant temperatures of 15, 20, 25, 30, and 35°C for egg, larva, and pupa, and rearing at 15, 20, 25, and 30°C for pre-oviposition period where y is the rate of development day (%), a is the intercept, b is the slope, and x is the temperature (°C)

Table 3. Thermal requirements (DD ± SE) of different stages of *S. litur* field conditions, 1985–86

Stages	Dates of egg hatch in different batches						Avg developmental period, days	% of total period
	3 Sept.	7 Oct.	13 Nov.	28 Dec.	10 Feb.	18 March		
Egg	50 ± 2.7	63 ± 1.6	68 ± 1.6	64 ± 1.3	56 ± 0.3	72 ± 1.0	62.0 ± 3.3	11.4
First instar	45 ± 1.1	64 ± 2.4	49 ± 0.7	33 ± 0.0	44 ± 0.7	69 ± 1.7	50.7 ± 5.5	17
Second instar	40 ± 2.2	31 ± 1.1	26 ± 0.8	32 ± 0.6	29 ± 0.9	53 ± 1.8	35.2 ± 4.0	12
Third instar	40 ± 2.4	34 ± 1.4	33 ± 1.8	23 ± 0.6	32 ± 1.2	34 ± 1.5	32.7 ± 2.3	11
Fourth instar	34 ± 1.3	44 ± 2.7	31 ± 1.8	42 ± 0.9	45 ± 1.5	38 ± 1.1	39.0 ± 2.3	13
Fifth instar	43 ± 1.9	47 ± 2.6	40 ± 2.2	36 ± 1.0	45 ± 1.5	42 ± 1.1	42.2 ± 1.6	15
Sixth instar	99 ± 2.2	89 ± 3.5	80 ± 1.8	99 ± 2.3	76 ± 1.4	108 ± 2.0	91.8 ± 5.0	32
Total for								
Larvae	301 ± 3.5	309 ± 3.5	259 ± 3.5	265 ± 2.3	268 ± 3.5	343 ± 2.5	290.8 ± 13.4	53.6
Pupae	159 ± 3.2	154 ± 3.2	161 ± 3.5	169 ± 2.4	151 ± 3.9	166 ± 2.1	160.0 ± 2.8	29.5
Preoviposition	42 ± 3.1	18 ± 2.53	23 ± 3.5	15 ± 1.21	33 ± 3.8	50 ± 4.6	30.2 ± 3.7	5.6
Total DD	552	544	511	513	508	631	543	—
Sample sizes								
Egg masses	32	10	10	15	15	17	—	—
Larvae–pupae	52	39	36	49	97	72	—	—
Females	10	10	12	10	10	12	—	—

There are conflicting reports on the number of larval instars of this species, the number varying from five to seven (Joshi & Ram Prasad 1975, Bhat & Bhattacharya 1978, Prasad & Bhattacharya 1980, Balasubramanian et al. 1985). We observed six instars under laboratory as well as field conditions.

Calculation of the thermal requirements in the field were based on low threshold temperatures of 8, 10, 10, and 11°C for egg, larva, pupa, and preoviposition, respectively, as derived from the laboratory study. In the field, the complete life cycle (egg to egg) needed an average of 543 DD (508–631). Eggs, larvae, pupae, and preoviposition required 11.4, 53.6, 29.5, and 5.6% of the total developmental period. The larval stage needed an average of 291 DD, whereas first, second, third, fourth, fifth, and sixth instars required 51, 35, 33, 39, 42, and 92 DD, respectively (Table 3). Egg development needed an average of 62 DD (range, 50–72 DD) and the larval period 291 DD (259–343) in different rearings. The mean DDs required by different stages were within the confidence limits obtained during laboratory tests, except for the pupal periods in December and March. During January (mean minimum temperature, 13°C), there were occasions when the night temperatures were 8.7°C, which is below the larval developmental threshold (10.0°C). During April, the maximum temperature reached 41°C (mean maximum temperature, 38°C), which is above the high temperature cutoff point. Because the December batch was at the pupal stage in January and the March batch in April, this slight prolongation could be because of the effects of temperatures below the threshold in January and excessively high temperatures in April. However, these studies clearly show that constant and fluctuating conditions have the same effect on the development of this species. Therefore, the laboratory data can be incorporated in our phenological models.

Usually the thermal requirements of the stages in an insect's life cycle vary; consequently, most phenological models consider different thresholds and thermal units. However, intrastage differences often are overlooked. Our results denote distinct differences in thermal requirements between larval instars. The application of these data will increase the precision of our models. Exposure of different stages to summer conditions (shade temperatures in April and May often exceed 40°C) resulted in high mortality (>95%), but no stage entered aestivation to overcome this unfavourable condition. Unpublished observations show no difference in the developmental rate of larvae feeding on excised leaves and intact plants.

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