Vol. 13(3), pp. 26-34, July-September 2021 DOI: 10.5897/JEN2021.0268 Article Number: 858408267948 ISSN 2006-9855 Copyright ©2021 Author(s) retain the copyright of this article http://www.academicjournals.org/JEN



Journal of Entomology and Nematology

Full Length Research Paper

Do non-diapausing insects respond to different photoperiods: Spodoptera littoralis?

Esmat M. Hegazi^{1*}, Wedad E. Khafagi² and Essam Agamy³

¹Department of Applied Entomology, Faculty of Agriculture, Alexandria University, Alexandria, Egypt. ²Plant Protection Research Institute, Alexandria, Egypt. ³Department of Applied Entomology, Faculty of Agriculture, Cairo University, Giza, Egypt.

Received 13 June, 2021; Accepted 13 August, 2021

Photoperiod is a great factor in determining the developmental pattern (continued development vs. suspended development, this is, diapause) of many insect pests. The cotton leaf worm, Spodoptera littoralis (Boisd.) is non-diapaused insect. Knowledge about how developmental pathway of S. littoralis responds to photoperiod is necessary for mass rearing of the pest and its parasitoids and may suggest new control management. The present work was to investigate the effects of a range of photoperiods under different temperatures on the speed of development and the number of larval instars of S. littoralis in the laboratory conditions. The photoperiods (Light: Dark) 0L: 24D; 6L: 18D; 12L: 12D; 18L: 6D and 24L: 0D) of a constant temperature (15, 20, 25, or 30°C) affected the developmental speed, live fresh weight and number of instars of S. littoralis larvae. The day length demonstrated its greatest impact at 20°C, compared to lower (15°C) or higher temperatures (25 and 30°C). At 20°C, short photoperiod significantly accelerated the developmental pattern of both larval (by 14 days) and pupal stages (by 9 days), but long photoperiod slowed down the development. There was significant effect of photoperiod on the developmental time at 20°C, which decreased as the temperature, increased to 25, or 30°C. The occurrence of extra molt differed significantly among ranges of day lengths at constant rearing temperature. There was also an increased frequency of extra instars at low temperatures of different photoperiods. Extra instars were less common at high temperature (30°C). In summary, photoperiod had significant effects on the developmental durations of S. littoralis larvae, fresh pupal weight and number of larval instars.

Key words: Spodoptera littoralis, non-diapaused insect, photoperiodism, development time, number of larval instars.

INTRODUCTION

The cotton leafworm, *Spodoptera littoralis* (Boisd.), is a serious economic pest due to the damages it causes, and being difficult to control. The host range of *S. littoralis*

includes over 40 families, containing at least 87 economic species (Salama et al., 1970; Gerling, 1971). Among the most important host plants attacked by this insect in

*Corresponding author. E-mail: eshegazi@hotmail.com.

Author(s) agree that this article remain permanently open access under the terms of the <u>Creative Commons Attribution</u> <u>License 4.0 International License</u> Egypt are cotton and truck crops. It has been shown to reduce cotton yields by as much as 75% (Hosny and Issha, 1967). Damage on many crops arises from feeding by larvae, leading to complete stripping of the plants (Bishara, 1934). It occurs throughout Africa (e.g. Egypt, Algeria, Angola), Turkey, Spain, southern France, Southern Greece and northern Italy. It has been recorded many times in the UK (Campion et al., 1977). In, France and Greece, S. littoralis pupae have been seen in the soil after November. It is not established in the northern parts of Europe due to cooler temperatures and its guarantined pest status. The pest develops throughout the year, without undergoing diapaus (Sidibe and Lauge, 1977). Low winter temperatures are therefore an important limiting factor affecting the northerly distribution of this pest (Miller, 1976).

The minimum constant temperature for normal development in all stages is 13-14°C. Resistance to low temperatures, generally increases through the larval stages and is greatest in the pupal stage (Miller, 1977; Dahi, 2005). Sidibe and Lauge (1977), Baker and Miller (1974) and Ocete (1984) provided data on survival and development of S. littoralis at different temperatures. At 18°C, egg, larval and pupal stages last 9, 34 and 27 days, respectively. At 36°C, egg, larval and pupal stages decreased to 2, 10 and 8 days, respectively. Information on development on different host plants is given by Dimetry (1972), Harakly and Bishara (1974), Zoebelein (1977) and Badr et al. (1983). In Egypt, field studies carried out by Dimetry (1972), El-Shafei et al. (1981), Khalifa et al. (1982) indicated that six larval instars exist and there are six to seven overlapping generations of S. littoralis when feeding on cotton, and that there are three peak infestation periods. In the Middle East the leaf worm produces 7-10 annual generations (Gerling, 1971; Sidibe and Lauge, 1977).

Photoperiod is an importance greater factor in determining the developmental line (continued development vs. suspended development, that is, diapause) of many insect pests (Eizaguirre et al., 1994; Fantinou et al., 1995 López and Eizaguirre, 2019). effect of photoperiod Moreover, the on other developmental characteristics has also been determined (Lopez et al., 1995; Fantinou et al., 1996). However, data in the literature on the influence of photoperiod on life history parameters of non-diapaused insects, such as, S. littiralis or about other adaptations by which they synchronize their development with seasonal changes are little. The purpose of the present investigation was to study the effects of a range of photoperiods under different temperatures on the speed of development and the number of larval instars of S. littoralis larvae in the laboratory conditions. The obtained data may lead to more appropriate phenological models for evaluation of pest management methods and for population dynamics analysis. It can also contribute to an understanding of the

effects of weather conditions on S. littoralis phenology.

MATERIALS AND METHODS

The experiment was carried out in the biological control laboratory of Alexandria University, Egypt. The cotton leafworm S. littoralis was reared in mass culture on semi-artificial diet. The components of the diet were prepared and used as described by Hegazi (1976). To minimize genetic differences in developmental traits among test insects, regularly, fresh field-collected insects were made to eliminate the bad effects of inbreeding for the culture. For each trial, four cultures were established from a large egg mass, reared at 4 constant temperatures of 15, 20, 25 and 30 ± 1°C. Each temperature was combined with "L:D" 0:24, 6:18, 12:12, 18:6 or 24:0 and Relative Humidity of 65 ± 5%. Also, each treatment was carried out in three different rearing chambers. The hatched larvae were reared individually in petri-dishes (3.5 cm in diameter) (n = 30-35 larvae/rearing chamber x 4 trials/ day length). Larval instars were determined according to methods followed by Stavridis et al. (2004), Mironidis and Savopoulou-Soultani (2008).

The caterpillars were fed daily, with fresh diet available at all times (ad libidum). The daily procedures were food exchange, cleanings, record of deaths, and collection of cephalic capsules. The duration and number of instars were daily recorded. The pupae obtained were sexed using the Butt and Cantu (1962) technique and weighed with a precision scale with an approximation of 0.001 g. The development of the cotton leafworm was assessed by observing time for larval growth to pupation, larval weight, pupal developmental period, pupal weight.

The experiments were conducted in incubators (type Hann, Munden, Germany, Hegazi et al., 2017), equipped with six fluorescent 30-Watt cool white flurescent tube per cabinet. In all experiments, the light onset started at 5 am. The light intensity during photophase was approximately at 1270 foot candles. Light was measured with a Weston light meter (Model) (Weston Electrical Instrument Company, Newark, NJ). Some fans were used for cooling electronic equipment, operated during the light cycle to remove heat produced by lights. Variation of temperatures in rearing chambers was \pm 1°C. All incubators were located in a controlled rearing room. The results reported here only include those individuals that pass through six instars and successfully survived to eclosion.

Statistical analysis

Statistical analyses were conducted using SPSS 17.0. Differences in the durations of immature development between different treatments were compared using one way analysis of variance (ANOVA) followed by multiple comparisons analysis using Student's t-test.

RESULTS

The interactions between photoperiod and temperature in larval and pupal development on non-diapausing insect "*S. littoralis*", is shown in Tables 1 and 2. Table 1 shows the development time patterns in *S. littoralis* at low constant temperature (15 and 20 °C) under different photoperiods. The developmental period of males was less than that of females irrespective of temperature and photoperiodic conditions. Figure 1 shows that at 15°C, only short (6L:

	Photoperiod (L:D,h)							
Stage	0:24	6:18	12:12	18:6	24:0			
A: Temperature 15°C								
Egg	-	8.10 ± 0.02	-	8.20 ± 0.01	-			
First instar	-	9.28 ± 0.09	-	9.24 ± 0.20	-			
Second instar	-	8.36 ± 0.12	-	7.44 ± 0.18	-			
Third instar	-	8.50 ± 0.14	-	7.16 ± 0.17	-			
Fourth instar	-	7.84 ± 0.12	-	7.80 ± 0.40	-			
Fifth instar	-	10.12 ± 0.46	-	8.30 ± 0.40	-			
Sixth instar	-	12.60 ± 0.56	-	12.16 ± 0.64	-			
Larvae	-	56.70 ± 0.50^{a}	-	51.84 ± 0.13 ^b	-			
Pupa 👌	-	48.50 ± 1.90 ^a	-	39.7 ± 0.49^{b}	-			
Pupa ♀	-	42.90 ± 0.18^{a}	-	32.5 ± 0.37^{b}	-			
B: Temperature 20°C								
Egg	5.0 ± 0.01	4.50 ± 0.01	6.00 ± 0.10	6.00 ± 0.10	5.8 ± 0.20			
First instar	4.80 ± 0.14	3.48 ± 0.16	5.16 ± 0.07	5.12 ± 0.12	4.08 ± 0.08			
Second instar	3.20 ± 0.10	3.72 ± 0.12	4.28 ± 0.12	5.48 ± 0.20	3.48 ± 0.10			
Third instar	3.00 ± 0.10	2.52 ± 0.18	4.64 ± 0.15	4.44 ± 0.14	3.76 ± 0.18			
Fourth instar	3.30 ± 0.10	2.92 ± 0.17	5.00 ± 0.10	5.08 ± 0.14	4.00 ± 0.19			
Fifth instar	3.80 ± 0.10	3.36 ± 0.09	5.36 ±0.16	5.72 ± 0.23	4.36 ± 0.14			
Sixth instar	5.84 ± 0.10	5.12 ± 0.20	6.96 ± 0.30	8.24 ± 0.34	6.32 ± 0.19			
Larvae	24.00 ± 0.22 d	20.30 ± 0.50^{e}	31.30 ± 0.50^{b}	34.1 ± 0.40^{a}	$26.0 \pm 0.34^{\circ}$			
Pupa 👌	15.40 ± 0.20 b	15.10 ± 0.39 ^b	24.60 ± 0.20^{a}	24.80 ± 0.34^{a}	15.8 ± 0.30^{b}			
Ŷ	13.00 ± 0.21 c	13.10 ± 0.22 ^c	20.60 ± 0.52^{b}	22.00 ± 0.47^{a}	12.7 ± 0.15 [°]			

Table 1. Development time patterns in S. littoralis at low constant temperature and different photoperiods.

Means within a row followed by the same letter are not significantly different, (P < 0.01).

18D) and long (18L: 6D) photoperiods were tested. The developmental time for both larval and pupal stages was significantly longer ($t_{0.05} = 2.24$ for larvae; $t_{0.05} = 4.6$ for male pupae, $t_{0.05} = 2.1$ for female pupae) at short photoperiod compared to long photoperiodThe larval stage lasted 56.7 days at short photoperiod vs. 51.8 days at long photoperiod. At short photoperiod (6L: 18D) the developmental time of pupal stage lasted 48.5 days for male and 42.9 days for females vs 39.7 and 32.5 days for male and female at long day length(18L: 6D), respectively.

At 20°C, the results showed that photoperiods had significant effects on the developmental durations of the larval (F = 194.5; df = 4, 45; P < 0.05) and pupal (for male, F = 210.0; df = 4, 45; for female, F = 171.2; df = 4, 45; P < 0.05) stages of *S. littoralis* (Table 1). The short day length of 6L: 18D significantly accelerated the development of both the larval and pupal stages, while the long photoperiod (18L: 6D) slowed down the development, compared with other photo schedules. For instance the larval stage lasted 20.3 days at short photoperiod (18L: 6D).

At 25°C, the scenario was different at higher

temperatures, the continuous darkness (0L: 24D) significantly accelerated the development of both the larval (F = 13.05; df = 4, 45; P < 0.05) and pupal (for male, F = 10.1; df = 4, 45; for female, F = 13.39; df = 4, 45; P < 0.05) stages, while photoperiod of 12L: 12D significantly slowed down the development. The fastest development of the larvae lasted 16.5 vs 19.8 days, under continuous darkness and photoperiod of 12L: 12D, respectively (Table 2).

At 30°C, the developmental speed of the larval stage was significantly increased (F = 40.6; df = 4, 45; P < 0.05) at short photoperiod (11.4 days) compared to those of longest development at continuous photoperiod (14.2 days) (Table 2). Table 4 shows mean live weights of prepupal and pupal stages of *S. littoralis* at different photoperiods of different temperatures. The day length induced drastic changes in live weights of prepupal and pupal stages and it was temperature dependent. At 15°C, although short photoperiod (6L: 18D) slowed down the development of *S. littoralis* larvae, no significant differences in pupal weights were obtained at the long photoperiod (18L: 6D) or short photoperiod. At 20°C, there were significant differences (for male prepupae, F = 54.63; df = 4, 45; P < 0.05; for female pupae, F = 59.87;

	Photoperiod (L:D,h)							
Stage	0:24	6:18	12:12	18:6	24:0			
A: Temperature 25°C								
Egg	3.00 ± 0.04	3.00 ± 0.04	3.50 ± 0.03	3.60 ± 0.04	3.1 ± 0.20			
First instar	3.00 ± 0.00	3.80 ± 0.08	3.50 ± 0.10	3.2 ± 0.20	3.0 ± 0.00			
Second instar	2.08 ± 0.08	2.50 ± 0.11	2.80 ± 0.10	3.10 ± 0.20	2.12 ± 0.07			
Third instar	2.28 ± 0.10	2.28 ± 0.09	2.80 ± 0.13	2.36 ± 0.10	2.12 ± 0.07			
Fourth instar	2.20 ± 0.11	2.36 ± 0.09	2.90 ± 0.14	2.20 ± 0.10	2.2 ± 0.10			
Fifth instar	2.70 ± 0.13	3.12 ± 0.12	3.08 ± 0.13	2.60 ± 0.10	2.7 ± 0.12			
Sixth instar	4.20 ± 0.18	4.32 ± 0.09 b	4.70 ± 0.17	4.44 ± 0.02	4.76 ± 0.17			
Larvae	$16.50 \pm 0.30^{\circ}$	17.70 ± 0.21 ^a	19.80 ± 0.29^{a}	17.90 ± 0.36 ^b	$17.00 \pm 0.20^{\circ}$			
Pupa ♂	$10.00 \pm 0.10^{\circ}$	11.70 ± 0.15 ^b	12.20 ± 0.24^{a}	11.80 ± 0.13 ^{ab}	11.2 ± 0.13 ^c			
Pupa ♀	9.40 ± 0.16^{d}	10.30 ± 0.15^{b}	10.90 ± 0.10^{a}	$9.90 \pm 0.18^{\circ}$	10.3 ± 0.15^{b}			
B: Temperature 30 °C								
Egg	3.00 ± 0.10	3.00 ± 0.02	3.50 ± 0.20	3.60 ± 0.10	3.00 ± 0.10			
First instar	2.04 ± 0.04	2.04 ± 0.04	2.04 ± 0.04	2.12 ± 0.07	2.04 ± 0.04			
Second instar	1.76 ± 0.09	1.92 ± 0.08	1.84 ± 0.07	2.00 ± 0.08	2.36 ± 0.20			
Third instar	1.72 ± 0.09	1.80 ± 0.11	1.56 ± 0.10	1.64 ± 0.13	2.52 ± 0.17			
Fourth instar	1.64 ± 0.09	1.48 ± 0.11	1.56 ± 0.10	1.68 ± 0.14	1.64 ± 0.10			
Fifth instar	1.92 ± 0.08	1.88 ± 0.07	1.88 ± 0.07	2.04 ± 0.07	1.84 ± 0.09			
Sixth instar	3.60 ± 0.11	2.64 ± 0.13	2.92 ± 0.12	3.80 ± 0.20	3.88 ± 0.13			
Larvae	$12.64 \pm 0.17^{\circ}$	11.76 ± 0.17 ^e	11.96 ± 0.14 ^d	13.36 ± 0.39 ^b	14.24 ± 0.35^{a}			
Pupa ∂	7.70 ± 0.15^{a}	7.20 ± 0.13^{b}	7.20 ± 0.13^{b}	7.70 ± 0.20^{a}	7.1 ± 0.10^{b}			
Pupa ♀	6.50 ± 0.16^{bc}	$6.30 \pm 0.30^{\circ}$	$6.30 \pm 0.15^{\circ}$	7.10 ± 0.23^{a}	6.80 ± 0.20^{ab}			

Table 2. Development time patterns in S. littoralis at high constant temperature of different photoperiods.

Means within a row followed by the same letter are not significantly different, (P < 0.01).

df = 4, 45; P < 0.05) among live prepupal and pupal weights of S. littoralis developed from larvae reared under different photoperiods. The heaviest weights were for those reared under photo-schedules of (12L: 12D) and (18L: 6D).

Typically, S. littoralis has six larval instars, with developmental commitment to metamorphosis occurring in the 6th (late) instar. The results showed that S. littoralis larvae had substantial intraspecific variation in the number of larval instars when reared at different photoperiods of a constant temperature on a modified artificial diet. The occurrence of extra molt differed significantly among photoperiods under constant rearing temperature. Table 3 shows that 15°C, 56.4 and 30.0% of S. littoralis larvae developed extra instar (seventh) before pupation under short (6L: 18D) and long (18L: 6D) photoperiods ($t_{0.05}$ = 21.17), respectively. At 20°C, the larvae reared under (6L: 18D) and long (12L: 2D) photoperiods, showed the highest values (23 and 22%, in respect) of additional molts (F = 335.5; df = 4, 20; P < 0.05) compared to those reared under continuous darkness (0L: 24D) (0.0%), long (18L: 6D) (10.0%) and continuous photoperiod (24L: 0D) (8.1%). At 25°C, the larvae had significant (F = 246.7; df = 4, 20; P < 0.05) number of additional extra molt among different photoperiods. At 30° C, the frequency of individuals with extra instars significantly (F = 932.8; df = 4, 20; P < 0.05) decreased with increased rearing day length.

Figure 2 summarizes the effect of photoperiods (L: D, h) and constant temperature (°C) that accelerated (A, shortest duration) and slowed down (S, longest duration) the development larvae and pupae of *S. littoralis*. The photoperiod had significant effects on the developmental durations of *S. littoralis* larvae. The day length demonstrated its greatest impact at 20°C. At 20°C, short photoperiod significantly accelerated the developmental pattern of both larval (by 14 days) and pupal stages (by 9 days), but long photoperiod slowed down the development. The effect of photoperiod at 20°C decreased as the temperature increased to 25, or 30°C.

DISCUSSION

Detailed information of the insect life cycle and how it responds to environmental factors is the necessary for future events, and for developing successful control programs (Nylin, 2001; Bansode et al., 2016; Montezano



Figure 1. Mean durations (±SE) of larval stage $(1^{st} - 6^{th})$ of *S. littoralis* under different photoperiods of constant low 15 or 20°C (A); or high temperature 25 or 30°C (B). Bars with the same uppercase or lowercase letter are not significantly different (P > 0.05).

Table	3.	Effect	of	photoperiod	on	percentage	(mean	±	SE)	of	S.	littoralis	larvae	developed	an	extra	instar
before	pu	pation	•														

Photoperiod	Temperature (°C)							
(L:D,h)	15	20	25	30				
0:24	No data	00.00 ± 0.00^{D}	$8.30 \pm 0.00^{\circ}$	14.70 ± 0.90 ^A				
6 : 18	56.40 ± 2.30^{A}	23.00 ± 1.50 ^A	5.6 0± 1.20 ^D	6.73 ± 1.30 ^B				
12 : 12	No data	22.50 ± 0.90^{A}	9.30 ± 1.30 ^C	$0.00 \pm 0.00^{\circ}$				
18 : 6	30.00 ± 1.20 ^B	10.00 ± 1.20 ^B	17.8 0± 1.20 ^B	$0.00 \pm 0.00^{\circ}$				
24:0	No data	8.10 ± 2.20 ^C	19.10 ± 0.90^{A}	$0.00 \pm 0.00^{\circ}$				

For each temperature, means followed by different letters are significantly different from each other at P < 0.05.

Tamm (0C)	01.0.00	Photoperiod (L : D, H)							
Temp (°C)	Stage	0:24	6:18	12:12	18:6	24:0			
	Prepupa ♂	-	439.70±9.10 ^a	-	439.2±7.70 ^a	-			
15	Prepupa ♀	-	488.60±2.80 ^a	-	492.80±3.80 ^a	-			
	Pupa 🖒	-	394.99±7.80 ^a	-	401.70±7.60 ^a	-			
	Pupa ♀	-	437.20±11.90 ^a	-	436.3±11.20 ^a	-			
	Prepupa ♂	385.90±4.30 ^b	340.30±1.60 ^d	399.40±3.10 ^a	388.20±2.70 ^b	360.20±3.90 [°]			
00	Prepupa ♀	426.30±3.50 ^b	376.50±3.70 ^d	440.10±2.80 ^a	438.70±4.50 ^a	402.3±2.60 ^c			
20	Pupa ♂	339.60±7.30 ^c	337.60±6.50 ^c	378.10±4.10 ^b	391.97±5.50 ^a	341.3±6.90 ^c			
	Pupa ♀	353.60±5.50 ^d	397.40±4.40 ^b	425.40±2.40 ^a	414.90±4.60 ^a	376.5±4.80 ^d			
	Prepupa ♂	310.87±2.50 ^c	322.90±6.10 ^b	350.70±3.20 ^a	300.10±2.90 ^d	300.8±1.40 ^{cd}			
05	Prepupa ♀	366.80±3.00 ^d	415.40±3.10 ^a	390.20±3.40 ^b	299.70±3.20 ^e	336.1±7.70 ^c			
25	Pupa ♂	289.03±4.80 ^c	305.20±4.03 ^b	328.50±6.10 ^a	294.90±4.50 ^c	284.8±6.50 ^c			
	Pupa ♀	336.30±7.80 ^b	363.50±4.20 ^a	370.30±7.20 ^a	303.20±3.10 ^d	314.90±3.80 ^c			
30	Prepupa ♂	275.99±3.60 [°]	263.30±3.60 ^d	284.10±3.30 ^b	282.20±3.90 ^{bc}	292.10±4.40 ^ª			
	Prepupa ♀	305.10±2.98 ^b	299.98±4.10 ^b	310.50±2.99 ^b	300.90±3.50 ^b	352.96±4.80 ^a			
	Pupa ♂	253.40±0.80 ^b	246.50±1.40 ^c	265.40±0.93 ^b	265.40±1.00 ^a	262.6±1.40 ^a			
	Pupa ♀	282.60±2.60 ^c	291.10±2.50 ^b	283.70±1.80 ^{bc}	274.70±3.10 ^d	349.60±3.20 ^a			

Table 4. Mean live weights of prepupal and pupal stages of S. littoralis at different photoperiods of constant temperature.

Means within a row followed by the same letter are not significantly different, (P < 0.01).



□ Larval stage ■ Female pupal stage

Figure 2. Photoschedules (L: D, h) and constant temperature (°C) that accelerated (A, shortest duration) and slowed down (S, longest duration) the development of *S. littoralis*.

et al., 2019; Du Plessis et al., 2020, Papp et al., 2018). Many studies on the effects of photoperiod have been primarily concerned with diapause induction in insects (Mukai and Goto, 2016; He et al., 2017; Yamaguchi and

Goto, 2019; Saunders, 2020). Photoperiod is a main factor in determining the developmental line of many insect pests (Zohdy and Abou-Elela, 1975; Eizaguirre et al., 1994; Fantinou et al., 1995; Saunders, 2020; Poitou et al., 2020). However, data in the literature on the effect of photoperiod on life history parameters of nondiapaused insects are hard to find. Very little is known about photoperiodism in S. littoralis or about other adaptations by which they synchronize their development with seasonal changes. In a preceding investigation on the effect of different photoperiods on the relative speeds of the endo-developmental stages of Microplitis rufiventris wasp attacking S. littoralis larvae, Hegazi and Fuhrer (1985) found that the short day length (6L:18D) accelerated the development of M. rufiventris wasp larvae, while both of 18L:6D or 0L:24D slowed down the development. The results of the present study showed that photoperiod had significant effects on the developmental durations of S. littoralis larvae, fresh pupal weight and the number of larval instars. The effect was temperature dependent. At 15°C, the development was faster by 5 days for the larvae and 10 days for female pupae under long day length than under short one. At 20°C, different photoperiods significantly affected the larval duration, pupal weight and percentage of larvae that passed extra instar. For instance, the larval and pupal durations were shorter by 14 and 9 days at short photoperiod than those larvae reared under long photoperiod. It is not clear which factors can cause to come out such variability among the larval durations, and the involved physiological mechanisms.

It was reported that S. littoralis larvae had 6 larval instars (Salama and Shoukry, 1972). The present work showed that, photoperiod can influence the number of instars of this pest. The number of instars of S. littoralis was variable and 7 instars could be observed at rearing constant temperature under different ranges of photoperiods, where significant percentages of S. littoralis larvae developed through an extra instar before pupation. Baker and Miller (1974) reported similar observation on the effect of low temperatures in addition to the larval food "chrysanthemum" of S. littoralis larvae on producing extra instars. Duodu and Biney (1981) mentioned that S. littoralis larvae had an extra molt on some plants (cotton and Urena) of four tested food crops. Esperk et al. (2007), reported that the most common factors influencing insect instar number are photoperiod, temperature, humidity, food quantity and quality, injuries, inheritance and sex. Low temperature combined with short photoperiod induces slow development together with additional instars in several species (Ballmer and Pratt, 1989; Shintani and Ishikawa, 1997). Grossniklaus-Burgin et al., (1994), reported that nonparasitized S. littoralis pass through typical six larval instars. When parasitized by the egg-larval parasitoid Chelonus inanitus, they passed through five larval instars and entered metamorphosis precociously, and dig into the soil for pupation.

Juvenile hormone (JH) is vitally important in the control of insect development and reproduction (Pener and Shalom, 1987; Raabe, 1989; Nijhout, 1994). These JHs are secreted by a pair of glands in the head known as the corpora allata (Wigglesworth, 1940). JH has the power to maintain insects with larval characteristics that makes it possible for the continued growth of the larval form (Wigglesworth, 1964). Ecdysone is a steroid hormone secreted by prothoracic gland that, in its active form, stimulates metamorphosis and controls molting in insects. Nijhout and Williams (1974a, b) found that JH prevents secretion of the prothoracicotropic hormone (PTTH) by the brain of the late instar larvae of Munduca sexta. At the beginning of the periods of PTTH release is regulated by the photoperiod and it seems that the brain is needed as an initiator (Ciemiokr and Sehnalf, 1977; Matsuda, et al., 2017) for keeping in existence of the developmental rhythms. As shown from the above results, day length has significant effect on development, number of larval instars and live pupal weight. So, day length may influence insects' basic physiological processes, such as metabolic rates, as well as functions of the nervous and endocrine systems. The corpora allata and the prothoracic gland may be sensitive to day length changes at low temperature or the day length may affect JH biosynthesis at low temperature. The implication of the key present findings possibly could contribute to more appropriate phenological models for evaluation of pest management methods and for population dynamics analysis. It can also contribute to an understanding of the effects of weather conditions on S. littoralis phenology and better management strategy of the cotton leaf worm.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

The authors thank the five anonymous reviewers for constructive comments on the manuscript. The first author appreciate Alexander Von Humboldt Foundation for research equipment donation used in the present work and thank Miss Fedaa Y. for providing assistance in writing and cleaning the English. No funding was available to conduct this work.

REFERENCES

Badr NA, Moawad GM, Salem IEM (1983). Host plant shifting affects the biology of Spodoptera littoralis (Boisd.) (Lepidoptera: Noctuidae). Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent 48(2):369-374.

- Baker CRB, Miller GW (1974). Some effects of temperature and larval food on the development of Spodoptera littoralis (Boisd.) (Lep., Noctuidae). Bulletin of Entomological Research 63(3):495-511.
- Ballmer GR, Pratt GF (1989). Instar number and larval development in Lycaena phlaeas hypophlaeas (Boisduval) (Lycaenidae). Journal of the Lepidopterists' Society 43:59-65.
- Bansode SA, More VR, Zambare SP (2016). Effect of Different Constant Temperature on the Life Cycle of a Fly of Forensic Importance Lucilia cuprina. Entomology Ornithology and Herpetology 5:183.
- Bishara I (1934). The cotton worm Prodenia litura F. in Egypt. Bulletin de la Societe Entomologique d'Egypte 18:223-404.

Butt BA, Cantu E (1962). Sex determination of lepidopterous pupae. UDSA-ARS, pp. 33-75.

- Campion D, Bettany B, McGinnigle J, Taylor L (1977). The distribution and migration of Spodoptera littoralis (Boisduval) (Lepi-doptera: Noctuidae), in relation to meteorology on Cyprus, interpreted from maps of pheromone trap samples. Bulletin of Entomological Research 67(3):501-522.
- Ciemiokr E, Sehnalf C (1977). The role of neuro-endocrine system as a pacemaker of insect moulting cycle. Journal of Interdisciplinary Cycle Research 8(3-4):301-303.
- Dahi HF (2005). Egyptian cotton leafworm Spodoptera littoralis development on artificial diet in relation to heat unit requirements. The Third International Conference on IPM Role in Integrated Crop management and Impacts on Environment and Agricultural Products. Plant Protection Research Institute, ARC, Dokki, Giza, Egypt.

Dimetry NZ (1972). Further studies on the host plant preference of Spodoptera littoralis Boisd. (Lepid.,Noctuidae). Zeitschrift fur Angewandte Entomologie 71(4):350-355.

- Duodu YA, Biney FF (1981). Growth, food consumption and food utilization of Spodoptera littoralis (Boisduval) (Lepidoptera: Noctuidae) on four food-plants. Bulletin of Entomological Research 71(4):655-662.
- Du Plessis H, Schlemmer ML, Van den Berg J (2020). The Effect of Temperature on the Development of Spodoptera frugiperda (Lepidoptera: Noctuidae). Insects 11:228. https://doi.org/10.3390/insects11040228.
- El-Shafei SA, Isshak RR, Nasr ESA (1981). Seasonal abundance of the cotton leafworm moths, Spodoptera littoralis (Boisd.), in relation to the accumulated heat. Research Bulletin, Faculty of Agriculture, Ain Shams University, pp. 1613-1615.
- Eizaguirre M, Lopez C, Asin L, Albajes R (1994). Thermoperiodism, photoperiodism and sensitive stage in the diapause induction of Sesamia nonagrioides (Lepidoptera: Noctuidae). Journal of Insect Physiology 40(2):113-119.
- Esperk T, Tammaru T, Nylin S (2007). Intraspecific variability in number of larval instars in insects. Journal of Economic Entomology 100(3):627–645.
- Fantinou AA, Karandinos MG, Tsitsipis JA (1995). Diapause induction in the Sesamia nonagrioides (Lepidoptera: Noctuidae) effect of photoperiod and temperature. Environmental Entomology 24(6):1458-1466.
- Fantinou AA, Tsitsipis JA, Karandinos MG (1996). Effects of short- and long-photoperiods on growth and development of Sesamia nonagrioides (Lepidoptera: Noctuidae). Environmental Entomology 25(6):1337-1343.
- Grossniklaus-Burgin C, Wyler T, Pfister-Wilhelm R, Lanzrein B (1994). Biology and morphology of the parasitoid Chelonus inanitus (Braconidae, Hymenoptera) and effects on the development of its host Spodoptera littoralis (Noctuidae, Lepidoptera). Invertebrate Reproduction and Development 25(2):143-158.
- Gerling D (1971). Occurrence, abundance, and efficiency of some local parasitoids attacking Spodoptera littoralis in selected cotton fields in Israel. Annals of the Entomological Society of America 64(2):492-499.
- Harakly FA, Bishara SI (1974). Effect of nutrition on the biology of the cotton leafworm, Spodoptera littoralis (Boisd.), in Egypt (Lepidoptera: Noctuidae). Bulletin de la Societe Entomologique d'Egypte 58:25-30.

- He H, Chen C, Xiao H, Xue F (2017). Photoperiodic control of diapause induction in the zygaenid moth Thyrassia penangae involving day-length measurement. Research and Reports in Biology 8:1-5.
- Hegazi EM (1976). Further studies on certain natural enemies attacking the cotton leafworm in Alexandria region. Ph.D. thesis, Faculty of Agriculture, University of Alexandria, Alexandria, Egypt.
- Hegazi EM, Fuhrer E (1985). Instars of Microplitis rufiventris (Hym.; Braconidae) and their relative developmental speed under different photoperiods. Entomophaga 30:231-243.
- Hegazi E, Khafagi W, Aamer N (2017). Effects of photoperiod on the immature developmental time of Apanteles galleriae Wilkinson (Hymenoptera: Braconidae). Journal of Agricultural Science and Food Technology 3(1):1-6.
- Hosny MM, Isshak R (1967). New approaches to the ecology and control of three major cotton pests in U.A.R. Part 1: Factors stimulating the outbreaks of the cotton leafworm in U.A.R. and the principles of its prediction. U.A.R. Ministry of Agricultural Technical Bulletin 1:1-36.
- Khalifa A, Iss-hak RR, Foda ME (1982). Vertical and horizontal distribution of the Egyptian cotton leafworm egg masses in cotton fields in Egypt. Research Bulletin, Faculty of Agriculture, Ain Shams University pp. 1749-1756.

Lopez C, Eizaguirre M, Albajes R (1995). Diapause detection and

monitoring in the Mediterranean corn stalk borer. Physiological Entomology 20(4):330-336.

- López C, Eizaguirre M (2019). Diapause and biological cycle of Cydalima perspectalis (Walker) in the eastern Pyrenees. Journal of Applied Entomology 143(10)1096-1104.
- Matsuda N, Kanbe T, Akimoto SI, Numata H (2017). Transgenerational seasonal timer for suppression of sexual morph production in the pea aphid, Acyrthosiphon pisum. Journal of Insect Physiology 101:1–6.
- Miller GW (1976). Cold storage as a quarantine treatment to prevent the introduction of Spodoptera littoralis (Boisd.) into glasshouses in the UK. Journal of Plant Pathology 25(4):193-196.
- Miller GW (1977). Mortality of Spodoptera littoralis (Boisduval) (Lepidoptera: Noctuidae) at non-freezing temperatures. Bulletin of Entomological Research 67(1):143-152.
- Mironidis G, Savopoulou-Soulta M (2008). Development, Survivorship, and Reproduction of Helicoverpa armigera (Lepidoptera: Noctuidae) Under Constant and Alternating Temperatures. Environmental Entomology 37(1):16-28.
- Montezano D, Specht A, Sosa-Gómez DR Roque-Specht VF, de Paula-Moraes SV, Peterson JA, Hunt TE (2019). Developmental parameters of Spodoptera frugiperda (Lepidoptera: Noctuidae) immature stages under controlled and standardized conditions. Journal of Agricultural Science 11(8): 76-89.
- Mukai A, Goto SG (2016). The clock gene period is essential for the photoperiodic response in the jewel wasp Nasonia vitripennis (Hymenoptera: Pteromalidae). Applied Entomology and Zoology 51(2):185-194.
- Nijhout HF (1994). Insect hormones. Princeton University Press, Princeton.
- Nijhouth F, Williamsc M (1974a). The control of molting and metamorphosis in Manduca sexta (Lepidoptera): Growth of the last instar larvae and the decision to molt. Journal of Experimental Biology 61(2):481-491.
- Nijhouth F, Williamsc M (1974b). Control of molting and metamorphosis in the tobacco hornworm, Manduca sexta (L): cassation of juvenile hormone secretion as a trigger for pupation. Journal of Experimental Biology 61(2):493-501.
- Nylin S (2001). Life history perspectives on pest insects: What's the use? Austral Ecology 26(5):507-517.
- Ocete RE (1984). Study of the biological cycle of Spodoptera littoralis (Boisduval) at different temperatures. Graellsia 40:195-206.
- Papp V, Ladányi M, Vétek G (2018) Temperature-dependent development of Aproceros leucopoda (Hymenoptera:Argidae), an invasive pest of elms in Europe. Journal of Applied Entomology 142(6):589-597.
- Pener MP, Shalom U (1987). Endocrine manipulations, juvenile hormone and ontogenesis of male sexual behaviour in locusts. Insect

Biochemistry 17(7):1109-1113.

- Poitou L, Bras A, Pineau P, Lorme P, Roques A, Rousselet J, Auger-Rozenberg M-A, Laparie M (2020). Diapause Regulation in Newly Invaded Environments: Termination Timing Allows Matching Novel Climatic Constraints in the Box Tree Moth, Cydalima perspectalis (Lepidoptera: Crambidae). Insects 11(9):629.
- Raabe NJM (1989). Recent Developments in Insect Neurohormones. Plenum Press, New York.
- Salama HS, Dimetry NZ, Salem SA (1970). On the host preference and biology of the cotton leaf worm Spodoptera littoralis. Zeitschrift fur Angewandte Entomologie 67:261-266.
- Salama HS, Shoukry A (1972). Flight range of the moth of the cotton leafworm Spodoptera littoralis. Zeitschrift fuer Angewandte Entomologie 71(2):181-184.
- Saunders DS (2020). Dormancy, diapause and the role of the circadian system in insect photoperiodism. Annual Review of Entomology 65:373-389.
- Stavridis DG, Ipsilandis CG, Katarachias PC, Milonas PG, Ifoulis AA, Savopoulou-Soultani M (2004). Determination of Helicoverpa armigera (Lepidoptera: Noctuidae) larval instars and age based on head capsule width and larval weight. Entomologia Hellenica 15:53-61.
- Shintani Y, Ishikawa Y (1997). Effects of photoperiod and low temperature on diapause termination in the yellow-spotted longicorn beetle. Physiological Entomology 22:170-174. Sidibe B, Lauge G (1977). Effect of warm periods and of constant
- temperatures on some biological criteria in Spodoptera littoralis Boisduval (Lepidoptera: Noctuidae). Annales de la Societe Entomologique de France 13(2):369-379.
- Wigglesworth VB (1940). The determination of characters at metamorphosis in Rhodnius prolixus (Hemiptera). Journal of Experimental Biology 17(2):201-222.

- Wigglesworth VB (1964). The hormonal regulation of growth and reproduction in insects. Advances in Insect Physiology 2:247-336.
- Zoebelein G (1977). Practical experiences gained during twelve years of crop protection trials work in the Middle East and North Africa. Fourth report. The influence of different host plants on the development of the cotton leafworm Spodoptera littoralis (Boisd.) and on its response to insecticides. Pflanzenschutz-Nachrichten Bayer 30(2):164-212.
- Zohdy N, Abou-Elela R (1975). Effect of photperiod on the different developmental stages of Spodoptera littoralis" Zeitshcrift für Angwandte Entomologie 79:52-56.