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THE INFLUENCE OF PHOTOPERIOD ON THE LIFE-CYCLE OF *ECTOMYELOIS CERATONIAE* (ZELLER) (LEPIDOPTERA: PYRALIDAE)

P. D. COX

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(*First received* 23 *March* 1977 *and in final form* 21 *June* 1979)

Abstract—Diapause in fully grown larvae of *Ectomyelois ceratoniae* was induced by low temperature and short photoperiods. When larvae were reared at 30°C, 70% r.h. there was no diapause in a light regime of 12 hr light followed by 12 hr darkness (12L/12D), and only 20% entered a weak diapause in continuous darkness. However, at 20°C, 70% r.h. there was no diapause in 16L/8D but almost all larvae entered diapause in 12L/12D. At 20°C diapause delayed adult emergence by an average of 111 days, compared with about 50 days at 30°C. Survival to adult at 30°C was 75% or more at most photoperiods, but at 12L/12D and 13L/11D it was less than 50%. At 20°C survival was about 70% at the two photoperiods tested.

A slight effect of photoperiod on non-diapause growth rates was observed. Above 16 hr light longer photoperiods reduced the mean developmental period from egg hatch to adult emergence, by 4 days at 20L/4D and 6 days at 24L/0D.

The significance of diapause in this species in relation to its potential as a pest is discussed.

INTRODUCTION

In the Mediterranean region, Southern Russia and some areas of Africa, America and Western Australia, *Ectomyelois ceratoniae* (Zeller) attacks fruit on the tree. It is particularly important on carobs and ASHMAN (1968) reported that it oviposits on unripe pods, the damage done to these making them vulnerable to attack after harvest by *Ephestia calidella* (Guenée), *E. figulilella* (Gregson), *E. cautella* (Walker), *Oryzaephilus surinamensis* (L.), *O. mercator* (Fauv.) and *Lasioderma serricorne* (F.). The carob moth also infests these and other products, especially dried fruit, nuts and seeds, in storage.

The importance of photoperiod on the life-cycle has been demonstrated for two of the *Ephestia* species that attack stored carobs, *E. calidella* and *E. figulilella* (COX, 1975), fully fed larvae of both entering diapause when the daily duration of light is 13 hr or less. The object of the present study was to determine if photoperiod also influenced the development of *Ectomyelois ceratoniae*.

METHODS

Rearing method

The original cultures were prepared from eggs provided by Dr. S. Gothilf (Israel Institute for Biological Research, Tel-Aviv). *Ectomyelois ceratoniae* is not so easy to rear in the laboratory as the *Ephestia* spp. The major difficulty is to ensure that the adults mate and lay fertile eggs. This problem was solved by constructing a special oviposition cage in which there was forced movement of air and by simulating dawn and dusk in the breeding room. The rearing technique and precautions taken to prevent infection of moths by pathogens, such as *Bacillus thuringiensis* (Berliner) were described in detail by COX (1976). Larvae were reared on a mixture of 87 g soya bean meal, 87 g sucrose and 26 g water in a glass jar. Cultures were kept at 30 ± 1°C and 70 ± 5% r.h. in a light regime of 16 hr light followed by 8 hr darkness (16L/8D).

Experimental conditions and equipment

All experiments were carried out in special light-proof cabinets (35 cm^3) made of wood and hardboard with a hinged door on one side. Each was equipped with a thermostat, heater unit and electric fan. A Venerette 24 hr time-switch attached to a Mazda white 6W miniature fluorescent tube was installed in each cabinet to control the duration of the light period. Darkness in the cabinets was timed to coincide with natural darkness as far as practical, but to ensure that no extraneous artificial light entered a cabinet, layers of thick black polythene sheeting were wrapped round each one. The cabinets were kept in light-proof rooms maintained at 25°C or 15°C, the temperatures in the cabinets being maintained 5°C higher at 30°C or 20°C each $\pm$ 1°C. Humidity was controlled at 70 $\pm$ 5% r.h. in desiccators using potassium hydroxide solutions of appropriate specific gravity (SOLOMON, 1951). At 30°C, a series of six light regimes was used: continuous light (24L/0D), 20 hr of light alternated with 4 hr of darkness (20L/4D), 16 hr light and 8 hr darkness (16L/8D), 13 hr light and 11 hr darkness (13L/11D), 12 hr light and 12 hr darkness (12L/12D) and continuous darkness (0L/24D). The last was maintained for 54 days after which the larvae were exposed to light for short periods whilst observations were made. At 20°C, two light regimes were used: 16L/8D and 12L/12D.

A food mixture comprising 8 parts by weight of wheatfeed, 2 parts of glycerol, 2 parts of glucose and 1 part of yeast was prepared and kept in thin layers at 70% r.h. and the relevant temperature for 2 weeks before use. Batches of about 50 eggs were collected and kept, each in a petri dish of 10 cm dia. in the various light regimes at 30 $\pm$ 1°C and 70% r.h. Upon hatching each larva was placed singly on 4 g of food that had been compressed to a depth of 2.5 cm in a 7.5 $\times$ 2.5 cm glass tube. Each freshly hatched larva was transferred to the tube on a fine squirrel-hair paint brush, and then the tube closed with a fine-mesh cloth held in place with a 1 cm length of polythene tubing. Thirty tubes were set up at each light regime.

Every tube regularly exposed to light was examined briefly during the light periods for signs that the large mature larva had ceased to feed and was commencing the construction of its silk-lined emergence tunnel leading to the surface of the food. This is a signal that pupation is about to begin and will be followed by adult emergence in about 5 days at 30°C or 13 days at 20°C. When these signs were observed the tubes were examined daily and when an adult emerged, its weight, sex and the date were all recorded. These operations were usually done some 12–18 hr after emergence, as adults generally emerge at the start of the dark period. At this stage, any larva that delayed pupation was assumed to be in diapause. It was examined only twice a week until it pupated and then daily until the adult appeared.

The tubes initially kept in continuous darkness were examined after 54 days when the larvae should either have pupated or entered diapause. Thereafter they were examined at intervals of 4 weeks. This procedure ensured that the larvae received no light before diapause was initiated and little afterwards.

Recognition of diapause

As with *Ephestia calidella* and *E. figulilella* (Cox, 1975) there is no satisfactory morphological criterion for recognising larval diapause in *Ectomyelois ceratoniae*. Therefore the delayed pupation of the fully fed larva must be accepted as a sign of diapause. Generally there is only a short period between the end of feeding and the start of pupation. However, some larvae that cease feeding do not pupate for many weeks, and when this delay is considerable, there can be no question that they are in diapause. Occasionally, however, the delay is intermediate in length and some arbitrary method must be employed to define diapause. Accordingly, individuals that emerge as adults more than 80 days after egg hatch at 20°C or more than 50 days at 30°C are considered to have been in diapause. These figures were chosen by rounding up the longest period to adult emergence in photoperiods in which diapause was absent (Fig. 1), namely 71 days at 20°C and 49 days at 30°C. The chosen periods also meet the criterion that the minimum delay to pupation attributable to diapause exceeded by at least three times the mean

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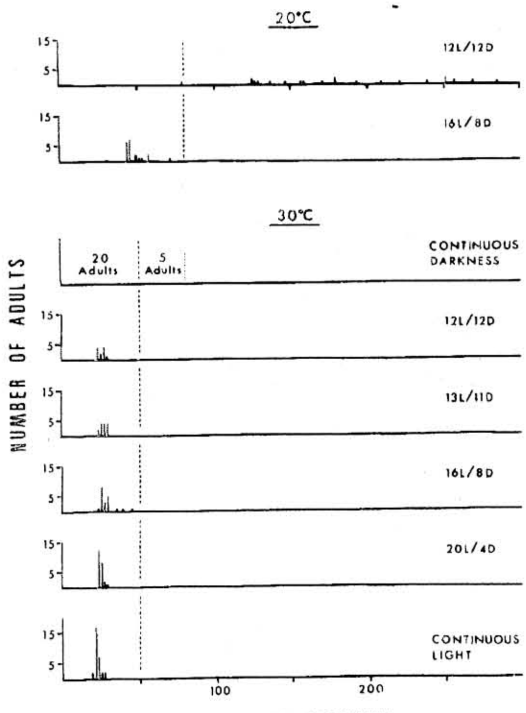

FIG. 1. Effect of photoperiod on development of *Ectomyelois ceratoniae* from egg hatch to adult emergence at 30°C and 20°C., 70% r.h. The dotted line indicates division between adults emerging from diapause and non-diapause larvae.

delay for individuals in photoperiods at which diapause was absent. These were 9 days at 20°C and 2 days at 30°C. All larvae defined as in diapause were examined for signs of disease because pathogens can retard development, but none was found.

RESULTS

Influence of photoperiod at 30°C

Diapause was detected at 30°C only in continuous darkness. Five out of the 25 larvae to reach the adult stage entered diapause (Table 1), and all of these emerged within 80 days of egg-hatch (Fig. 1). Survival was good at most photoperiods, 23 or more out of 30, but at 12L/12D with 11 adults and 13L/11D with 14 it was less than 50%. Most of the

TABLE 1. INFLUENCE OF PHOTOPERIOD AND TEMPERATURE ON THE NUMBERS OF *Ectomyelois ceratoniae* OUT OF 30 EMERGING AND ENTERING DIAPAUSE, ON THE DEVELOPMENTAL PERIOD FROM EGG HATCH TO ADULT EMERGENCE AND ON THE WEIGHTS OF ADULTS

Photoperiod	No. of adults emerging	Mean developmental period (days)	♂ adult weight (mg) No.	Mean	Range	♀ adult weight (mg) No.	Mean	Range
30°C								
(Non-diapause) 24L/0D	30	23	11	19.9	16.9–23.4	19	28.1	21.0–34.9
(Non-diapause) 20L/4D	23	25	12	21.5	18.4–25.4	11	31.2	27.6–34.8
(Non-diapause) 16L/8D	20	29	7	18.8	15.6–24.2	13	26.6	23.4–29.4
(Non-diapause) 13L/11D	14	27	4	20.1	18.9–21.0	10	30.5	28.5–32.0
(Non-diapause) 12L/12D	11	26	5	21.1	20.3–21.8	6	28.6	26.6–31.9
(Non-diapause) 0L/24D	20	—	13	—	—	7	—	—
(Diapause) 0L/24D	5	—	2	—	—	3	—	—
20°C								
(Non-diapause) 16L/8D	20	49	12	23.3	20.8–26.4	8	30.8	28.2–36.7
(Non-diapause) 12L/12D	1	79	—	—	—	1	19.1	—
(Diapause) 12L/12D	20	190	8	19.8	14.3–26.4	12	35.7	23.4–47.4

mortality was presumably in the early instars because remains of dead larvae were rarely found. All 30 larvae reached the adult stage in continuous light and development was most rapid in these conditions. Development was slower at 16L/8D than in both longer and shorter periods of light, and the adults obtained weighed least at this photoperiod. The heaviest adults were obtained at a photoperiod of 20L/4D. The differences between the mean weights of females at 20L/4D and 16L/8D as determined by an analysis of variance and t-test were highly significant at the 0.001 level, although male weight differences were not.

Influence of photoperiod at 20°C

In a light regime of 12L/12D at 20°C, 20 out of 21 larvae surviving to the adult stage entered diapause, and did not become adult until 126 to 287 days after egg hatch (Fig. 1). On average, diapause delayed adult emergence by 111 days as compared with about 50 days at 30°C in continuous darkness. No diapause was detected among the 20 adults emerging at 16L/8D photoperiod (Table 1). Survival was about 70% at both photoperiods.

No consistent influence was exerted by diapause on final weight. Some of the females emerging after diapause were considerably heavier than any not entering diapause. The heaviest male after diapause was as heavy as that not entering diapause. Overall, the mean weight of diapausing individuals was lower for males and greater for females than those of individuals not experiencing diapause.

DISCUSSION

In the experiments described above there was no diapause at 30°C in a light regime of 12L/12D, and only 20% of larvae entered diapause in continuous darkness. Even these emerged within 80 days of egg hatch, so it is probable that this species enters diapause naturally only at lower temperatures. At 20°C there was no diapause in 16L/8D but almost all larvae entered diapause in 12L/12D and remained in it for 80 days or more. Thus, 20°C, 12L/12D initiates diapause, and in Cyprus, the country of origin of this stock of *E. ceratoniae*, daylengths including civil twilight fall to about 12 hr and mean temperatures to about 20°C by the middle of October (ASHMAN, *et al*, 1974). In Israel GOTHILF (1970) observed that no larvae of this species pupated in carobs kept out of doors during the winter, and adults seldom emerged after the end of November. Larvae spent the winter in the pods of carobs and on the ornamental tree, *Acacia farnesiana* (L.) Willd. Temperatures fell to about 10°C midwinter but when they rose in the spring, larvae pupated and adults emerged in the second half of April. A similar cessation of pupation and adult emergence has been noted for this species in Western Australia where it feeds in almonds (MICHAEL, 1966), and in Southern Russia where it attacks withered and fallen fruit (KRASIL'NIKOVA, 1966). Thus, diapause is widespread in this species and enables the larva to survive the winter when temperatures are low. Adult emergence is thus delayed until fresh food on which females can lay eggs is available, and until temperatures are high enough to enable eggs to hatch. Thus, in laboratory experiments eggs failed to hatch at 20°C and below (Cox, 1976).

In the experiments at 20°C 12L/12D, the mean period spent in diapause was 111 days or about 4 months. Under natural winter conditions in Cyprus, temperatures are lower than this, falling to 10°C or less, and pupation is delayed until the end of April when the temperature reaches 20°C. Daylengths do not reach 12L/12D until March or 14L/10D until April. In earlier work (Cox, 1975) I found that long photoperiods hastened the termination of diapause in Cyprus strains of *Ephestia calidella* and *E. figulilella*, and reduced the subsequent range of adult emergence. BELL (1976b) observed that in *Plodia interpunctella* (Hübner), another phycitine associated with stored products, temperature rises or periods at low temperatures also hastened diapause termination. Thus, the longer days of Spring and the rising temperatures after the cold winter can be expected to break diapause in *Ectomyelois ceratoniae* and stimulate the emergence of adults at the end of April as noted by GOTHILF (1970).

mortality was presumably in the early instars because remains of dead larvae were rarely found. All 30 larvae reached the adult stage in continuous light and development was most rapid in these conditions. Development was slower at 16L/8D than in both longer and shorter periods of light, and the adults obtained weighed least at this photoperiod. The heaviest adults were obtained at a photoperiod of 20L/4D. The differences between the mean weights of females at 20L/4D and 16L/8D as determined by an analysis of variance and *t*-test were highly significant at the 0.001 level, although male weight differences were not.

Influence of photoperiod at 20°C

In a light regime of 12L/12D at 20°C, 20 out of 21 larvae surviving to the adult stage entered diapause, and did not become adult until 126 to 287 days after egg hatch (Fig. 1). On average, diapause delayed adult emergence by 111 days as compared with about 50 days at 30°C in continuous darkness. No diapause was detected among the 20 adults emerging at 16L/8D photoperiod (Table 1). Survival was about 70% at both photoperiods.

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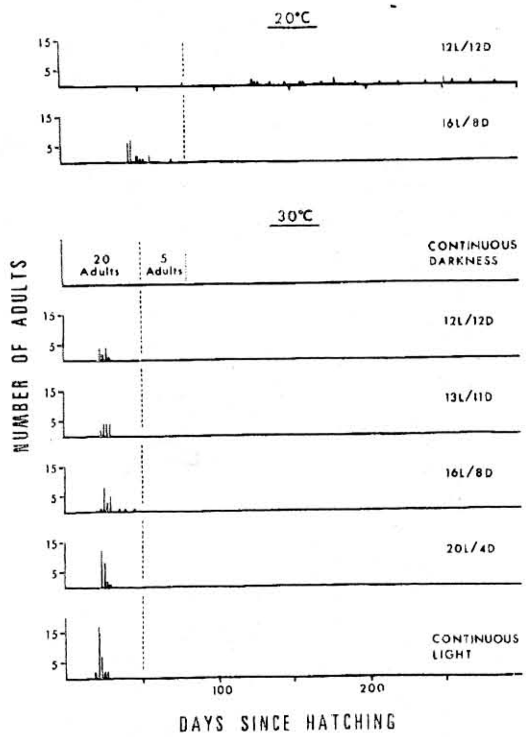

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No consistent influence was exerted by diapause on final weight. Some of the females emerging after diapause were considerably heavier than any not entering diapause. The heaviest male after diapause was as heavy as that not entering diapause. Overall, the mean weight of diapausing individuals was lower for males and greater for females than those of individuals not experiencing diapause.

DISCUSSION

In the experiments described above there was no diapause at 30°C in a light regime of 12L/12D, and only 20% of larvae entered diapause in continuous darkness. Even these emerged within 80 days of egg hatch, so it is probable that this species enters diapause naturally only at lower temperatures. At 20°C there was no diapause in 16L/8D but almost all larvae entered diapause in 12L/12D and remained in it for 80 days or more. Thus, 20°C, 12L/12D initiates diapause, and in Cyprus, the country of origin of this stock of *E. ceratoniae*, daylengths including civil twilight fall to about 12 hr and mean temperatures to about 20°C by the middle of October (ASHMAN, *et al*, 1974). In Israel GOTHILF (1970) observed that no larvae of this species pupated in carobs kept out of doors during the winter, and adults seldom emerged after the end of November. Larvae spent the winter in the pods of carobs and on the ornamental tree, *Acacia farnesiana* (L.) Willd. Temperatures fell to about 10°C midwinter but when they rose in the spring, larvae pupated and adults emerged in the second half of April. A similar cessation of pupation and adult emergence has been noted for this species in Western Australia where it feeds in almonds (MICHAEL, 1966), and in Southern Russia where it attacks withered and fallen fruit (KRASIL'NIKOVA, 1966). Thus, diapause is widespread in this species and enables the larva to survive the winter when temperatures are low. Adult emergence is thus delayed until fresh food on which females can lay eggs is available, and until temperatures are high enough to enable eggs to hatch. Thus, in laboratory experiments eggs failed to hatch at 20°C and below (Cox, 1976).

In the experiments at 20°C 12L/12D, the mean period spent in diapause was 111 days or about 4 months. Under natural winter conditions in Cyprus, temperatures are lower than this, falling to 10°C or less, and pupation is delayed until the end of April when the temperature reaches 20°C. Daylengths do not reach 12L/12D until March or 14L/10D until April. In earlier work (Cox, 1975) I found that long photoperiods hastened the termination of diapause in Cyprus strains of *Ephestia calidella* and *E. figulilella*, and reduced the subsequent range of adult emergence. BELL (1976b) observed that in *Plodia interpunctella* (Hübner), another phycitine associated with stored products, temperature rises or periods at low temperatures also hastened diapause termination. Thus, the longer days of Spring and the rising temperatures after the cold winter can be expected to break diapause in *Ectomyelois ceratoniae* and stimulate the emergence of adults at the end of April as noted by GOTHILF (1970).

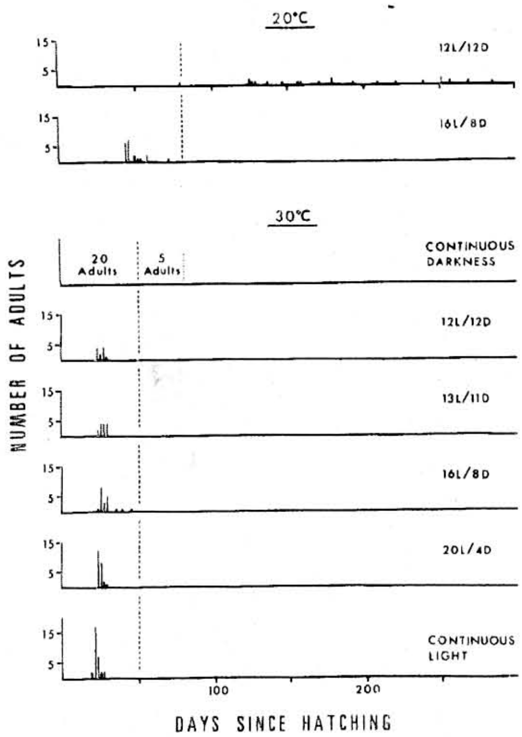

FIG. 1. Effect of photoperiod on development of *Ectomyelois ceratoniae* from egg hatch to adult emergence at 30°C and 20°C., 70% r.h. The dotted line indicates division between adults emerging from diapause and non-diapause larvae.

delay for individuals in photoperiods at which diapause was absent. These were 9 days at 20°C and 2 days at 30°C. All larvae defined as in diapause were examined for signs of disease because pathogens can retard development, but none was found.

RESULTS

Influence of photoperiod at 30°C

Diapause was detected at 30°C only in continuous darkness. Five out of the 25 larvae to reach the adult stage entered diapause (Table 1), and all of these emerged within 80 days of egg-hatch (Fig. 1). Survival was good at most photoperiods, 23 or more out of 30, but at 12L/12D with 11 adults and 13L/11D with 14 it was less than 50%. Most of the

TABLE 1. INFLUENCE OF PHOTOPERIOD AND TEMPERATURE ON THE NUMBERS OF *Ectomyelois ceratoniae* OUT OF 30 EMERGING AND ENTERING DIAPAUSE, ON THE DEVELOPMENTAL PERIOD FROM EGG HATCH TO ADULT EMERGENCE AND ON THE WEIGHTS OF ADULTS

Photoperiod	No. of adults emerging	Mean developmental period (days)	♂ adult weight (mg) No.	Mean	Range	♀ adult weight (mg) No.	Mean	Range
30°C								
(Non-diapause) 24L/0D	30	23	11	19.9	16.9–23.4	19	28.1	21.0–34.9
(Non-diapause) 20L/4D	23	25	12	21.5	18.4–25.4	11	31.2	27.6–34.8
(Non-diapause) 16L/8D	20	29	7	18.8	15.6–24.2	13	26.6	23.4–29.4
(Non-diapause) 13L/11D	14	27	4	20.1	18.9–21.0	10	30.5	28.5–32.0
(Non-diapause) 12L/12D	11	26	5	21.1	20.3–21.8	6	28.6	26.6–31.9
(Non-diapause) 0L/24D	20	—	13	—	—	7	—	—
(Diapause) 0L/24D	5	—	2	—	—	3	—	—
20°C								
(Non-diapause) 16L/8D	20	49	12	23.3	20.8–26.4	8	30.8	28.2–36.7
(Non-diapause) 12L/12D	1	79	—	—	—	1	19.1	—
(Diapause) 12L/12D	20	190	8	19.8	14.3–26.4	12	35.7	23.4–47.4

At first sight, the fact that larvae develop inside almonds, carobs and acacia pods casts doubt on photoperiod as the trigger for diapause induction, because very little light penetrates the tough pods and shells beneath which the larvae feed and pupate. However, most of the pods and shells infested by over-wintering larvae are damaged by other insects or by splitting. This has been recorded for carobs in Israel by GOTHILF (1970) and in Cyprus by ASHMAN *et al.*, (1974), for almonds in Australia by MICHAEL (1968) and in Israel by CALDERON *et al.*, (1969), and for a wide variety of fruit in Russia by KRASIL'NIKOVA (1966). Mature larvae will also bore exit holes in the shell or pod to facilitate adult emergence. In these ways it is likely that sufficient light can reach the larvae to induce and terminate diapause, particularly when it is remembered that in other phycitids it is the older instars that are sensitive to photoperiodic induction of diapause. For example, in *Ephestia elutella* (Hübner) and *P. interpunctella* (Hübner) the sensitive phase occurs at about the time of the fourth larval moult, larvae being able to enter diapause in response to light intensities of less than 1 lux (BELL, 1976a).

The presence of a winter diapause in *Ectomyelois ceratoniae* could account for some of the apparent failures reported by ASHMAN, *et al.*, (1974) to control this species in Cyprus carob stores during the autumn with dichlorvos strips. For example, they estimated the adult population of *Ephestia cautella* in a treated warehouse to be only 7% of that in an untreated one, whereas the parallel comparisons for *E. calidella*, *E. figulilella* and *Ectomyelois ceratoniae* exceeded 40%. Of these species, only *Ephestia cautella* does not enter diapause as a larva in Cyprus (COX, 1975) and thus it is the only species to yield the adults that are killed by the dichlorvos vapour.

As well as the ability of different photoperiods to regulate diapause, a slight effect on non-diapausing growth rates was also observed. Thus, above 16 hr light, longer photoperiods reduced the mean developmental period from egg hatch to adult emergence. The 6 days difference in mean developmental period at 16L/8D and 24L/0D was significant ($P < 0.001$, *t*-test after analysis of variance). At 13L/11D and 12L/12D survival to the adult stage was less than 50% and the reduced sample size probably accounts for the variation of 2–3 days in their mean compared to that at 16L/8D. A similar effect of long photoperiod was noted by DANILEVSKI (1961) in the noctuid *Agrotis occulata* which grew more slowly at 12L/12D than at 24L/0D.

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