

DIAPAUSE INDUCTION IN *EPHESTIA ELUTELLA* (HÜBNER) AND *PLODIA INTERPUNCTELLA* (HÜBNER) (LEPIDOPTERA, PYRALIDAE) WITH A DAWN–DUSK LIGHTING SYSTEM

C. H. BELL and D. J. WALKER

Pest Infestation Control Laboratory, Ministry of Agriculture, Fisheries and Food, Slough, Bucks., England

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Abstract—The incidence of diapause in larvae of *Ephestia elutella* and *Plodia interpunctella* under two light systems operated by solar switches was observed at 25°C. Both switches gave progressively shortening daylength, as would be experienced from early July onwards at a latitude of 52°N. One of the light systems incorporated a device, which took 60 min to change to, or from, full light to near darkness, giving a dawn and a dusk with the photophase. The other was controlled directly by the time switch itself, without any extended periods of changing intensity.

Maximal percentages of *E. elutella* larvae entering diapause under the two systems were obtained with photoperiods half way through development of less than 13 hr 25 min and 13 hr 10 min respectively, measurements of photoperiod in the dawn–dusk system including the 1 hr dawn and 1 hr dusk. The mean critical photoperiod, here defined as that photoperiod giving half the maximum percentage of insects that enter diapause in response to photoperiod at a fixed temperature, was found to be 14 hr 15 min under the dawn–dusk system, and 14 hr 5 min under the other shortening daylength system. Comparison of the above results with the incidence of diapause under a series of fixed daylengths confirmed that the principal sensitive phase in *E. elutella* occurred early in the last larval instar.

Over 70 per cent emergence occurred in batches of *P. interpunctella* within 7 weeks of egg laying under all lighting conditions tested. Maximal percentages of larvae entered diapause after rearing in total darkness, continual light, or photoperiods of 13 hr or less. The sensitive phase occurred around 8 days after hatching at 25°C, and the mean critical photoperiod was found to be about 13 hr 15 min under both shortening daylength systems, and under fixed photoperiods. Photoperiods of over 13 hr, or increased temperature, appeared to inhibit diapause in *P. interpunctella*. Light intensities below 1 lux influenced diapause in both species.

1. INTRODUCTION

INSECTS in diapause usually show high tolerance to control measures. The Warehouse moth, *Ephestia elutella* (Hübner), is normally susceptible to fumigation with methyl bromide, but diapause renders it far more difficult to control. This species enters diapause as a fully fed larva (RICHARDS and WALOFF, 1946). Another storage moth that enters diapause in this stage is the Indian-meal moth, *Plodia interpunctella* (Hübner), (MICHELbacher, 1953; TSUJI, 1958; TZANAKAKIS, 1959), and in both species the incidence of diapause is influenced by daylength. Photoperiods of 12 hr or less increase the incidence of diapause in *P. interpunctella* (SARDESAI, 1968), while *E. elutella* is free from diapause in photoperiods of 15 hr or more and shows 100 per cent diapause in photoperiods of 13 hr or less (STRÜMPPEL, 1964).

Previous work on the induction of diapause in storage moths has utilized artificial lighting systems with fixed photoperiods controlled by a simple switch giving an abrupt

change between darkness and light. The object of the present work was to compare two systems giving progressively shorter daylengths, one of which gave a dawn and a dusk with the photophase, in order to find the minimum light intensity required for the determination of diapause in *E. elutella* and *P. interpunctella*. By comparing systems giving shortening daylengths with those giving fixed daylengths it was hoped to identify the sensitive phases, and to find the photoperiodic requirements for diapause in the two species.

2. MATERIALS AND METHODS

2.1 *The dawn-dusk system*

Experiments were conducted in a light proof room maintained at $25 \pm 0.1^\circ\text{C}$ and $70 \pm 3\%$ r.h. Under these conditions, the incidence of diapause is minimal in long daylength. Two cabinets were present in the room, each with an independently controlled lighting system. The operational lighting system of the room itself consisted of two 40-W bulbs placed 1 m apart and suspended 60 cm above a bench. Each bulb was enclosed in a 3 l. glass sweet jar, with a metal top provided with holes for the dissipation of heat. To achieve a quality of light as close as possible to that of natural daylight, the glass jars were covered with daylight blue acetate paper. A Venner solar time switch, linked with a light dimming unit, a low speed electric motor, and gears, provided a dawn and a dusk with the photophase. At the beginning of the cycle, the time switch started the motor and current through the bulb circuit increased until, after 1 hr, the bulbs had reached their maximum intensity. At this point, the motor switched off. At dusk the solar clock reversed the motor and the light decreased until, after 1 hr, it was at a minimum. The full photoperiod of the dawn-dusk system was thus 1 hr longer than the daylength for the date indicated on the solar time clock. The bulbs were never completely switched off and there was always a faint background illumination (intensity 0.3-0.4 lx) which served to screen any light escaping from the cabinets in the room and also to simulate starlight, moonlight and even street-lights which may be encountered under natural conditions.

The light system was calibrated using a Gossen Lunasix 3 light meter. Readings were taken at the bench surface every 5 min from maximum to minimum intensity. The procedure was repeated for the increase from minimum to maximum intensity. These readings were plotted on graphs (Fig. 1) from which the intensity of light at any point during the cycle could be estimated.

2.2 *The cabinet light units*

The external dimensions of each cabinet were $1.09 \times 0.51 \times 0.61$ m high. Illumination was provided by a warm-white 13-W tube on the ceiling of the cabinet, and was controlled by a time switch. Each cabinet was partially divided into two compartments by a transparent perspex sheet. The lower compartment contained the experimental material while the upper compartment was reserved for the strip light and, at one end, a Philips HR 3404 extractor fan to dissipate the heat produced. A 7.5 cm gap in the partition at the opposite end of the cabinet to the fan, and two rows of air inlet holes mounted below the fan in the lower compartment, ensured that air would first be drawn across the insect material and then across the lighting unit in its journey through the cabinet. Readings of temperature in the lower compartment were taken daily during the photophase. The cabinets were covered with black polythene sheeting to minimize light diffusing in or out. The light system of one cabinet was controlled by a Venner solar time clock which could give a

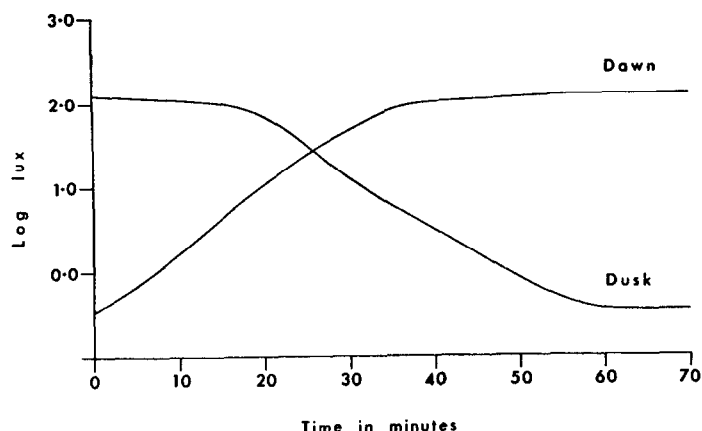


FIG. 1. Calibration of dawn-dusk lighting system. Increasing intensity—dawn; decreasing intensity—dusk.

progressively lengthening or shortening daylength, according to the date setting. The other cabinet was controlled by a fixed time clock so that any constant photoperiod could be selected. The extractor fans were automatically switched on with the lights.

2.3 Operation of light systems

The solar clocks of both systems were set to run from 1 July after the first batch of experimental material was prepared. Because overheating in the solar light cabinet caused by failure of the fan affected the results for *P. interpunctella*, a second run was performed over the range that was expected to include the critical photoperiod.

2.4 Source of insects

E. elutella was obtained from the Central Granary at Millwall, London, in July 1969. It was reared at the laboratory in an outbuilding with access to the external environment.

P. interpunctella was received in January 1971 from the Department of Agriculture for Scotland. The insects were obtained from a parcel of dandelion roots which arrived in Scotland, via England and Belgium in October 1970. After building up numbers at 25°C, the stock was transferred to the same room as *E. elutella* and, with the onset of winter, both species entered diapause.

2.5 Handling of insects

The food used for culturing comprised 10 parts by weight of wheatfeed, 2 parts of glycerol and 1 part of dried yeast, thoroughly mixed. The wheatfeed had previously been sterilized in covered trays in an oven for 2 hr at over 105°C, as a precaution against spores of *Bacillus thuringiensis*. Initially, cultures of both species of moth were established in large glass tanks measuring 0.28 × 0.22 × 0.41 m, containing a 2–3 cm layer (390 g) of food. To ensure a continuous supply of adults after the spring emergence in the tanks had declined, stock cultures were set up at 70% r.h. and 25°C by adding 50–100 moths to a sterilized 3 l. glass jar containing 130 g of food mix.

Supplies of *E. elutella* for diapause experiments were obtained solely from tanks which had overwintered. Adults were removed by suction into a 7.5×2.5 cm glass tube and were then anaesthetized with CO₂ before transfer for egg laying. *P. interpunctella* supplies were obtained from jars as tanks failed to produce sufficient adults for purposes other than culturing. In this case moths were anaesthetized and scooped from the parent culture.

Earlier work at this Laboratory established that in 7.5×2.5 cm tubes containing about 1.5 g of food mix as a layer 1.0–1.5 cm deep, larvae are sensitive to light intensities corresponding to those of the experimental systems. All tubes for experimental work were prepared in this fashion. To obtain 1st instar larvae for the tests, the following procedure was adopted. A piece of damp cotton wool was taped inside a 10 cm crystallizing dish. After anaesthetizing with CO₂, 30–40 insects were placed in a 11.5 cm hemispherical sieve. The 10 cm dish with drinking pad was attached to the sieve to confine the insects. The unit was then placed over a 12.5 cm crystallizing dish with a piece of black filter paper in the bottom so that eggs laid were clearly visible. The eggs of *E. elutella* started hatching after 6 days, and those of *P. interpunctella* after 4–5 days, at 25°C, 70% r.h. Young larvae were carefully picked up from the dish with a paintbrush and, as it was desired to expose as many insects as possible in a given space without incurring a second generation before the end of the experimental period, 2 larvae were added to each of the prepared tubes. These were then sealed with a numbered muslin square secured by a piece of polythene tubing. Generally, 72 tubes of each species were set up on the same day, half of which were put in boxes in the shortening daylength cabinet, and the other half in trays on the bench under the dawn–dusk system. This procedure was repeated each week. Additional batches were set up for work under total darkness and fixed photoperiods in the other cabinet.

2.6 Determination of results

Efforts were made to examine tubes daily from the time the first pupae were expected. All pupae and adults seen were recorded. After 6 weeks for *P. interpunctella* and 8 weeks for *E. elutella*, the tubes were carefully searched and a complete record was made of the stages found. Those larvae still remaining were assumed to be in diapause. Graphs of emergence were plotted, and for each batch the proportion of insects entering diapause, and the percentage mortality, were determined. The mean critical photoperiod, here defined as that length of illumination giving half the maximum percentage of insects that enter diapause in response to photoperiod at a fixed temperature, was found for each species from the results under constant photoperiods. The results obtained under the standard switch shortening daylength system, and under constant photoperiods, were compared to estimate the positions of the sensitive phases for *E. elutella* and *P. interpunctella*. It was assumed for this estimation that a similar percentage of insects would enter diapause if the sensitive phase experienced a particular photoperiod whether or not the photoperiod remained fixed throughout development. The performances of the standard and dawn–dusk shortening daylength systems were compared.

3. RESULTS

3.1 *Ephesia elutella*

The proportion of larvae entering diapause under fixed photoperiods was over 95 per cent at a daylength of 13 hr 30 min (see Table 1). No larvae entered diapause under a fixed photoperiod of 15 hr, and the mean critical photoperiod was just over 14 hr. When the

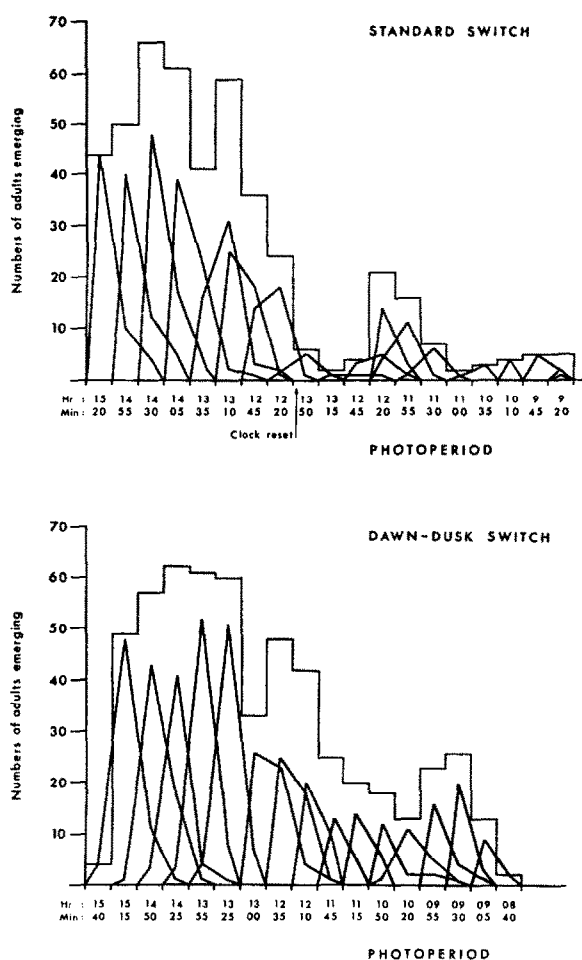


FIG. 2. Emergence of *Ephestia elutella* during 19 weeks under the standard shortening daylength system and during 17 weeks under the dawn-dusk shortening daylength system, showing the contribution of batches set up at weekly intervals.

weekly emergences under the standard and dawn-dusk shortening daylength systems were plotted against photoperiod (Fig. 2), the number of adults appearing was at first high. A sudden lowering of this number then occurred, followed by an increase in emergence before the expected progressive decline was observed. Under the dawn-dusk system, emergence only fell to about 40 per cent of the maximum possible, and remained fairly constant as photoperiods continued to shorten. Graphs plotted of the percentage of insects entering diapause in each separate batch against photoperiod at 3 weeks from egg laying are shown in Fig. 3. Equivalent numbers of larvae entered diapause under the standard switch shortening daylength system when photoperiods experienced by larvae 3 weeks from egg laying were compared with results obtained under fixed photoperiods. The mean critical photoperiods for the standard and dawn-dusk shortening daylength systems as obtained from Fig. 3, were 14 hr 5 min and 14 hr 15 min respectively, measurements of photoperiod fully including dawn and dusk.

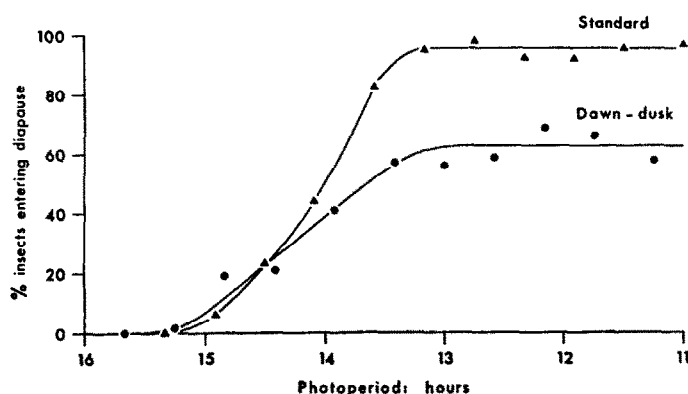


FIG. 3. Percentage of batches of *Ephestia elutella* larvae entering diapause against photoperiod at the sensitive phase (3 weeks after egg laying) under the standard and dawn-dusk shortening daylength systems.

3.2 *Plodia interpunctella*

The percentages of larvae failing to pupate when subsequent batches were exposed to the fixed and shortening daylength systems are set out in Tables 1-3. From fixed photoperiods a nominal value of 13 hr 15 min was obtained for the mean critical photoperiod, although no more than 30 per cent of any batch entered diapause in any of the conditions tested. Equivalent numbers of insects entered diapause under fixed and shortening daylength systems when photoperiods experienced by larvae 8 days old (2 weeks from egg laying) at 25°C, were considered.

The emergence of non-diapausing insects under the dawn-dusk system in photoperiods encouraging and photoperiods inhibiting diapause is compared in Fig. 4. Ninety per cent of the total emergence of non-diapausing insects from 5 batches with less than 5 per cent diapause occurred 31-38 days after egg laying while a similar proportion of non-diapausing insects from 4 batches with over 13 per cent diapause emerged 33-39 days after egg laying. The emergence of post-diapausing insects was extremely protracted. After 120 days emergence was still proceeding intermittently and about a third of those insects which had entered diapause had still not pupated.

TABLE 1. DIAPAUSE AND MORTALITY IN *Ephestia elutella* AND *Plodia interpunctella* UNDER FIXED PHOTOPERIODS AT 25°C (60-71 INSECTS PRESENT PER BATCH AT FINAL EXAMINATION)

Photoperiod (hr)	<i>E. elutella</i>		<i>P. interpunctella</i>	
	Mortality (%)	Diapause (%)	Mortality (%)	Diapause (%)
13	1.6	96.8	4.8	19.0
13.5	1.6	95.2	7.4	4.4
14	2.9	57.1	2.8	0
14.5	1.5	20.6	—	—
15	1.7	0	—	—
24	5.0	5.0	0	24.4
24 (at 0.3 lx)	6.7	31.1	—	—
0	4.8	45.2	8.2	29.5
Approximate mean critical photoperiod	14 hr 5 min		13 hr 15 min	

TABLE 2. RESULTS FOR *Plodia interpunctella* UNDER THE STANDARD SWITCH SHORTENING DAYLENGTH SYSTEM (64-72 INSECTS PRESENT PER BATCH AT FINAL EXAMINATION)

Maximum temperature during early development (°C)	Photoperiod at hatching (hr, min)	Photoperiod 6-8 days* after hatching (hr, min)	Mortality (%)	Alive and unpupated after 6 weeks (%)
26.0	15.45	15.20	0	0
26.0	15.20	14.50	0	0
26.0	14.50	14.25	4.5	0
26.0	14.25	14.00	8.4	0
26.0	14.00	13.30	2.9	1.4
26.5	13.30	13.05	7.4	1.5
26.5	13.05	12.45	1.5	10.3
27.5	12.40	12.20	0	1.5
Fan replaced	Clock reset	Clock reset		
25.5	14.05	13.30	1.5	0
25.5	13.35	13.00	3.2	26.9
25.5	13.05	12.35	1.6	21.3
25.5	12.40	12.10	3.2	24.9
25.5	12.15	11.45	1.4	15.9

* Depending on temperature.

TABLE 3. RESULTS FOR *Plodia interpunctella* UNDER THE DAWN-DUSK SHORTENING DAYLENGTH SYSTEM AT 25°C (66-72 INSECTS PRESENT PER BATCH AT FINAL EXAMINATION)

Photoperiod at hatching (hr, min)	Photoperiod 8 days after hatching (hr, min)	Mortality (%)	Alive and unpupated after 6 weeks (%)
16.25	15.55	0	0
16.00	15.30	1.5	0
15.35	15.05	0	4.4
15.10	14.40	6.9	0
14.45	14.15	1.4	0
14.20	13.45	0	1.4
13.50	13.20	0	10.6
13.25	12.55	0	23.4
12.55	12.25	0	26.6
12.30	12.00	4.5	24.2
12.05	11.35	1.4	13.9

4. DISCUSSION

The mean critical photoperiod for *E. elutella* was found to be 14 hr 5 min under fixed photoperiods, and when this photoperiod was examined in the standard switch shortening daylength system, the age of batches subsequently giving about 50 per cent of the maximum proportion of diapausing insects, was about 3 weeks. This point was taken as the sensitive phase, and at 25°C would correspond to the time of the last larval moult. Photoperiods

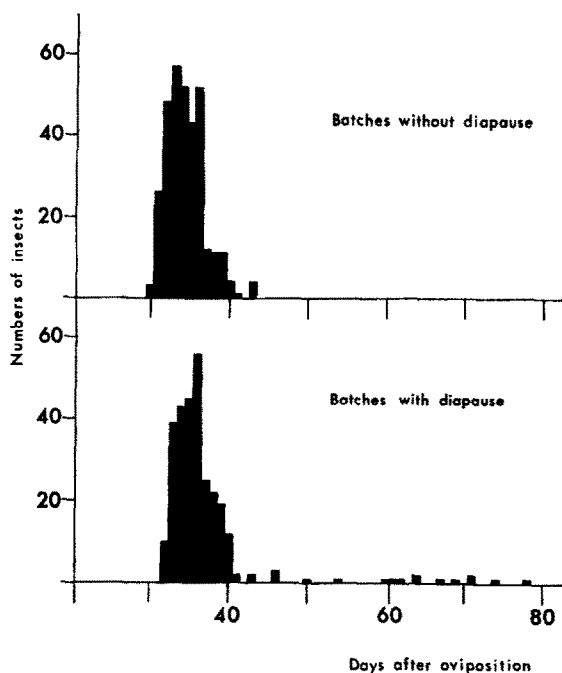


FIG. 4. Emergence of non-diapausing individuals from batches of *Plodia interpunctella* under photoperiods inhibiting, and photoperiods encouraging, diapause.

encouraging diapause also incited a delay in the emergence of non-diapausing insects. Figure 2 illustrates the dip observed in the emergence which corresponds to the threshold photoperiod for the incidence of diapause. The batch reaching the sensitive phase at this photoperiod showed a shift of several days in the time for peak emergence, although less than 20 per cent of the insects present in the batch entered diapause under both the standard and the dawn-dusk switch systems. Subsequent batches with higher proportions of diapausing insects continued to show the shift in emergence. The resurgence of emergence 3–4 weeks after resetting the clock of the standard switch system gave further evidence for a well-defined sensitive phase at age 3 weeks, as the total developmental time for non-diapausing *E. elutella* on wheatfeed mix at 25°C was found to be 6–7 weeks. STRÜMPEL (1964) obtained similar results for the photoperiodic control of diapause at about 25°C. He exposed batches of different ages to various fixed daylengths and found that the newly moulted 5th instar larva was the sensitive phase. He also observed a transition from 0 to 100 per cent diapause as photoperiods were decreased stepwise from 15 to 13 hr, which was the result of the present work on fixed photoperiods.

Under shortening daylength, transition from 0 to 100 per cent diapause occurred over a wider photoperiodic range than under fixed daylength. Variation in the time taken by individuals under shortening daylengths to arrive at the sensitive phase would account for the greater spread observed. Photoperiods required for equivalent percentages of insects entering diapause under the dawn-dusk switch system were only slightly longer than under the other shortening daylength system when measurements fully included the dawn and the dusk. It was concluded that nearly all of the dawn and dusk contributed to the photophase.

Assuming that similar threshold intensities during early dawn and late dusk form the boundaries of the photophase, then from Fig. 1, a light intensity of about 0.7 lx at the bench surface would be important in influencing diapause. The intensity experienced by insects inside glass tubes is likely to be even lower.

In *P. interpunctella*, using the same method as for *E. elutella*, the sensitive phase was found to occur around 8 days after hatching at 25°C. TSUJI (1963) working at 20°C found that the principal sensitive phase occurred during the 3rd and 4th larval instars. Figure 4 shows that, as with *E. elutella*, photoperiods enhancing diapause caused a slight delay in the emergence of non-diapausing insects. In groups with diapause, a long tail in the emergence pattern was observed, and it was difficult to divide the tail of the emergence of non-diapausing insects from the emergence of post-diapausing insects. Based on observations in the absence of diapause, the dividing line was set at 7 weeks.

Diapause occurred in the absence of photoperiodicity (Table 1) and results for continual light or total darkness resembled those obtained with photoperiods of 13 hr or less. It was concluded that in the stock selected for this work, photoperiods over 13 hr inhibit diapause at 25°C. TZANAKAKIS (1959) has also reported that light operates as an inhibiting agent for diapause in *P. interpunctella*. This statement is, however, at variance with the present results for continuous light. As the results from the standard and dawn-dusk shortening daylength systems (Tables 2 and 3) were closely comparable when measurements fully included the dawn and the dusk, low light intensities were effective in limiting diapause. Diapause in *P. interpunctella* was temperature dependent, as shown by the marked lowering of the percentage of insects entering diapause in the first run under the standard switch system where overheating occurred caused by failure of the fan. Temperature dependency would probably account for the limited proportion of insects entering diapause in any batch exposed at 25°C. The work of TSUJI (1958, 1963) and TZANAKAKIS (1959) has demonstrated the appearance of diapause in the life cycle of *P. interpunctella* at temperatures below 25°C, and the absence of diapause at 25°C or above.

With *E. elutella*, overheating in the reducing daylength cabinet occurred too late to upset results. Inhibition of diapause was, however, observed in the dawn-dusk system where the proportion of insects entering diapause in batches exposed to photoperiods well below the critical level was only about 60 per cent. This inhibition was probably caused by a response of some insects to the faint background illumination present during the dark part of the cycle, as with continuous illumination at 0.3 lx, the proportion of insects entering diapause was intermediate between the levels for continual darkness and continual illumination at 110 lx (see Table 1). WILDBOLZ and RIGGENBACH (1969) reported light intensities of 1–10 lx at the surface of infested apples to be effective in inducing diapause in *Carpocapsa pomonella* (L.), and estimated a 10–20 fold reduction of light intensity within the fruit. DE WILDE (1962) stated that the photoperiodic induction of diapause in insects is independent of intensity provided that a certain threshold is exceeded. He quoted thresholds ranging from 0.025 to 10 lx for various species, and concluded that twilight and even moonlight, which has an intensity of 0.1–0.5 lx, could contribute an effect in some cases.

The high sensitivity of *E. elutella* and *P. interpunctella* to low light intensity implies that dim light far into morning and evening twilight could be effective in limiting diapause. At the end of 'civil twilight' when the sun is 6° below the horizon, light intensity can be as high as 3.55 lx under good conditions (BECK, 1968). However the storage environment is one with limited access to outside light. The warehouse room described by RICHARDS and WALOFF (1946) with little access to daylight and with areas of near darkness is characteristic in this

respect. Photoperiodic stimuli available to insects even on the surface of stored produce are likely to be of low intensity. Furthermore, moth larvae are not found outside the food bulk until they are fully grown and enter the migratory phase. According to the present results, and those of STRÜMPER (1964), the sensitive phase occurs before feeding ceases and presumably photoperiodic stimuli would have to be received near the food surface rather than above it. In some situations it is clear that light intensities even at midday may barely be above the threshold level for response.

Diapause has been developed among temperate arthropods as an overwintering mechanism, and is closely linked to the natural environment. Stocks of relatively recent acquisition from the field, which had been maintained at the laboratory under natural climatic conditions, were therefore chosen for this work. In the storage environment, changes in microclimate are irregular as external variation is greatly buffered, and diapause serves more as a synchronizing mechanism for the spring emergence rather than as an overwintering device (HOWE, 1962). The high sensitivity of *E. elutella* and *P. interpunctella* larvae to light has enabled photoperiodic stimuli to remain of importance in the life cycle.

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