INDUCTION OF DIAPAUSE IN *ERIOISCHIA BRASSICAE* BOUCHÉ (DIPT., ANTHOMYIIDAE)

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INTRODUCTION

A culture of cabbage rootfly (*Erioischia brassicae*) has been maintained for 4 years in a heated glasshouse at Wellesbourne. During this period a series of generations could be reared between late March and September, the pupal stage of each generation occupying 16–20 days. In the autumn and winter, however, breeding was interrupted because the pupal stage of generations reared during this period was prolonged to between 60 and 200 days.

Under field conditions in southern England the rootfly passes through three generations in a year; in the first two the pupal stage normally occupies 2 weeks, whilst in the third (autumn) generation the pupae remain dormant over the winter. The stage then lasts about 200 days and gives rise to flies in the spring of the following year.

The occurrence of a dormant period, similar to the natural overwintering condition, in pupae raised and kept in a heated glasshouse suggests that these pupae were in a state of diapause induced by variations of the environment other than temperature. The work of Lees (1955) and others indicated that daylength during development was a factor which might influence the time spent in the pupal stage.

METHODS OF CULTURE

The procedure used for culturing cabbage rootfly was briefly as follows. The eggs were collected from a cage containing the adult flies and were placed in their natural oviposition site on the soil around the base of the experimental host plants. Young actively growing turnips were used as hosts, successive batches of plants being raised in pots throughout the year. After 3 or 4 days the eggs hatched and the young larvae started to feed on the root cortex.

The turnips were grown in a heated glasshouse in which there was a daily cycle of temperature between approximately 10° and 20° C. throughout the year, although in summer the upper limit was occasionally exceeded. The larvae fed on the turnips for about 4 weeks, and when fully developed left the root to pupate in the soil. Within a week of their formation the pupae were washed out of the soil and put into gauze-topped glass jars half filled with damp vermiculite. The jars were stored at 20° C. and the flies that emerged into the upper part of the jars were removed each day.

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OBSERVATIONS ON THE CULTURE RECORDS

The emergence of the flies was recorded from more than forty experimental generations reared in this way. Fig. 1 shows the emergence curves of seven representative populations. They may be divided into two primary groupings according to the length of the emergence period. Group A (two curves) have a short pupal period and a high percentage emergence, whilst group B (three curves) have a long pupal period and a low percentage emergence. The two remaining curves were intermediate in both respects.

The low percentage emergence within the group B populations was a result of the prolonged and continuous storage of the pupae at a temperature of 20° C. If such

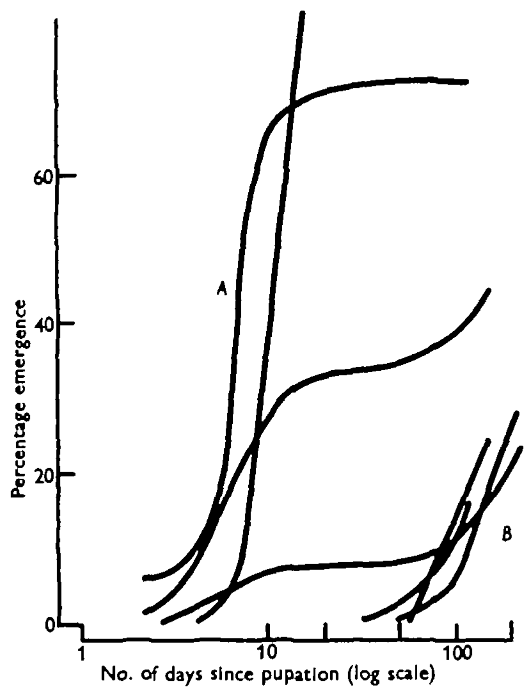

Fig. 1. Emergence curves of culture populations of pupae showing short and long and intermediate pupal stages.

pupae were given 6 weeks' cold treatment at 4° C. during storage, then about 60% of the population emerged.

Group A curves are typical of populations reared in the spring and summer, and group B of those raised in the autumn and winter. The intermediate type of curve occurred with populations raised in early spring and early autumn. When the proportion of individuals in each generation which enter into a prolonged pupal stage is plotted against the time of year during which development occurred, the continuous nature of the annual changes of this proportion can be seen. This effect is shown graphically in Fig. 2, each population being represented by a thick horizontal line starting at the time when the eggs were placed on the turnips and ending with the time when the pupae were washed out from the pot soil. The upper abscissa of Fig. 2 gives the annual cycle of daylength to show that the change over from long to short pupal periods occurs in generations which have their larval development when the daylengths are the same. From this culture data it can be calculated that half the individuals of a generation would have gone into a prolonged pupal stage if the larval stage developed during a period when the mean time between sunrise and sunset was just over 14 hr.

These observations suggest that the prolonged pupal stage may be a facultative diapause induced by the daylength at some stage of the larval development.

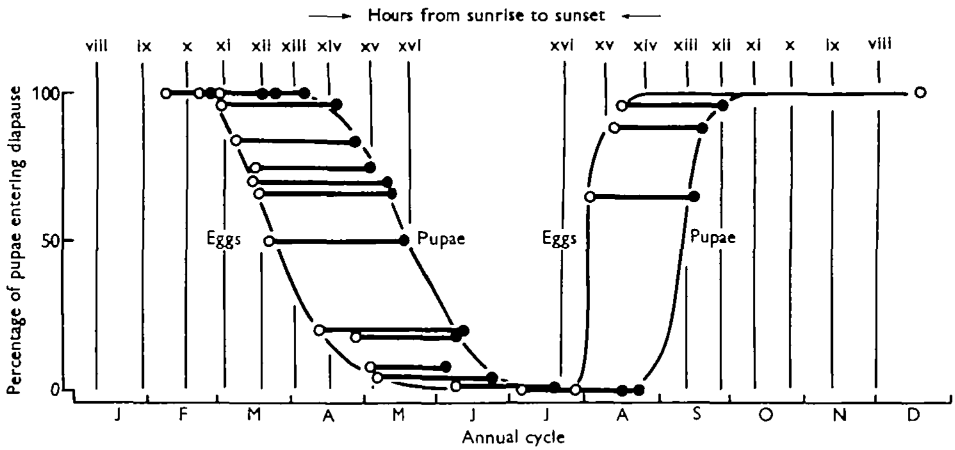

Fig. 2. Proportion of individuals entering a prolonged pupal stage compared with the time of year when development of the larvae took place. Key: ○, times when eggs were placed on plants; ●, times when pupae were collected.

DEMONSTRATION OF DAYLENGTH AS A STIMULUS TO DIAPAUSE

To investigate further the action of daylength during the larval stage on the occurrence of pupal diapause, and to determine whether the perceptive period is confined to a shorter time than the whole developmental period, the following experiment was carried out. Two daylength treatments were used: (*a*) normal daylength, which increased from 12 to 13·5 hr. during the experiment, as the short day, and (*b*) this normal daylength supplemented throughout the night by a 500 W. mercury vapour lamp giving 250 f.c. at the plant, as the long day.

A group of thirty eggs was placed around each of twelve turnip plants which were at a similar stage of growth. The schedule of the combinations of short-day and long-day treatments given to each plant is shown in Table 1. From the table it will be seen that the percentage of pupae which entered diapause varied greatly with the treatments. The proportion of diapausing pupae was progressively reduced as the number of long days increased and long days at the beginning of larval development were much more effective than long days towards the end of the larval stage (compare plants 5 and 6 with plants 8 and 9). Long days of 24 hr. light tend to prevent diapause as long as a certain proportion occur during the first 4 weeks of larval life. As few as 7 long days appear to be sufficient to prevent the majority of the pupae from going into diapause.

Table 1. *The effect of different combinations of short- and long-day treatments on the proportion of* Erioischia brassicae *individuals entering a prolonged pupal stage*

Plant	Schedule	Proportion of diapausing pupae (%)	No. of pupae obtained
1	39 long days, 0 short days	20	15
2	36 long days, 3 short days	0	10
3	28 long days, 10 short days	0	13
4	21 long days, 17 short days	23	17
5	14 long days, 24 short days	13	16
6	7 long days, 32 short days	15	13
7	42 short days, 0 long days	88	18
8	35 short days, 9 long days	100	21
9	28 short days, 16 long days	100	17
10	21 short days, 23 long days	79	14
11	14 short days, 31 long days	25	12
12	7 short days, 38 long days	4	23

THE SITE OF PHOTORECEPTION

As its common name implies, the larval stages of *E. brassicae* feed below ground level. The existence of this habit in an insect responding to daylength immediately raises the question of the site of photoreception.

The eggs are laid near the soil surface around the host plant and could therefore receive a light stimulus. However, since the eggs only take about 4 days to hatch in the glasshouse conditions the minor occurrence of diapause in the pupae from plants 11 and 12 shown in Table 1 seems to exclude this possibility.

The larvae on hatching from the eggs move rapidly below ground to the root system of the host plant, where the chance of their receiving a daylength stimulus seems remote (see Baumgartner, 1953). When reared on turnips the light may reach the insects through the tissues of the swollen root (cf. *Grapholitha*, Dickson, 1949). Measurements on the absorption of light by turnip tissue of the material used suggest that on the average only 0·6 % of the light incident on the plant surface would have reached a feeding larva.

To investigate the site of photoreception the following experiment was designed. The tops of plant pots, in which turnips had been grown in daylengths of 8 hr., were covered by two thicknesses of opaque black cloth drawn tightly around the upstanding leaf pedicels. In this way the light was prevented from reaching both the soil and the swollen root surface.

Groups of thirty eggs, collected within 12 hr. of being laid, were placed around each of these plants and around each of similar plants without covers. Pairs of plants, one covered except for the leaves and the other with both the soil and the swollen root exposed, were given one of the following light-treatments.

(*a*) 24 hr. light (11 hr. daylight, supplemented throughout the 24 hr. with a mercury vapour lamp giving 250 f.c.), allowing the plants to grow normally.

(*b*) 24 hr. light (11 hr. daylight, supplemented by 100 W. tungsten lamp giving about one-tenth of the light of the mercury vapour lamp used in (*a*)).

(*c*) 8 hr. daylight and 16 hr. darkness.

(*d*) 8 hr. daylight and 16 hr. darkness during the time when the larvae were developing on the plants, but prior to the eggs being placed on them, the plants were pretreated for 10 days with 24 hr. light as in treatment (*a*) above.

Table 2. *Comparisons of the proportions of diapausing pupae reared from larvae subjected to different light treatments*

Plants	Daylength: Pretreatment	Daylength: Treatment	Proportion of diapausing pupae* (%): Plants with covers	Proportion of diapausing pupae* (%): Plants without covers
Pair (*a*)	8 hr. day	24 hr. day + (250 f.c.)	22	33
Pair (*b*)	8 hr. day	24 hr. day + (20 f.c.)	8	19
Pair (*c*)	8 hr. day	8 hr. day	100	100
Pair (*d*)	24 hr. day + (250 f.c.)	8 hr. day	93	50

* The numbers of pupae used to obtain these proportions varied from 9 to 25.

The results of this experiment, expressed as the proportions of the pupae that went into diapause, are shown in Table 2. All the insects reared in the short days of treatment (*c*) went into diapause, whilst those subjected to long days showed significant reductions of the amount of diapause. The presence of the opaque covers made little difference to the proportion of insects responding to a direct long-day stimulus, even when dim lighting was used. This result indicates that the plant was acting as the photoreceptor for the insects feeding on it.

The simplest hypothesis would seem to be that a change in the chemical composition of the plant, associated with the long daylength, is the stimulus detected by the insect feeding on the root. The idea of a change in the composition of the plant would seem to be supported by the results of treatment (*d*). Here, the pretreatment of the plant with 10 long days gave indications of a change in the plant sufficiently stable to be passed on to insects starting to feed about 4 days after the plant had been returned to a short-day treatment. A pretreatment effect may account for the stronger response to the long-day stimulus when this was given before the short days in the experiment shown in Table 1.

Whilst a daylength-perceiving role of the host plant would appear logical in the timing mechanism of a root-feeding insect, the exclusion of a plant effect in *Diataraxia* (Way & Hopkins, 1950) and in *Metatetranychus* (Lees, 1953) suggests that such a mechanism may be unusual.

SUMMARY

1. The overwintering resting stage of the cabbage rootfly (*Erioischia brassicae*) is a facultative diapause in the pupal instar.

2. The induction of the diapause takes place during larval development and appears to be governed by changes in the daylength operating through the host plant.

3. It is suggested that the daylength stimulus is passed on to the insect by way of a change in the composition of its food, and this hypothesis is supported by the finding that a long-day stimulus remains apparent to feeding insects after the host plant has been removed to short-day treatments.

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