The effect of different light regimes on the induction of diapause in the cabbage maggot, Hylemyia brassicae Bouché (Diptera: Anthomyiidae).

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ABSTRACT

Photophases of 8 to 12 hours induce diapause in the cabbage maggot, Hylemyia brassicae Bouché and the sensitive stage is the larva. The pupa is the responsive stage and the size of a pupa has no effect on the incidence of diapause at 21.1°C. At this temperature, the critical daylength is 14 hours and diapause is inhibited by continuous illumination and by darkness.

With respect to prevention of diapause, wavelengths in the violet (395mμ), blue (460mμ), blue-green (495mμ), and the short-wave infrared (1750mμ) regions of the spectrum are photoperiodically active, while wavelengths between 500mμ and 600mμ, that is, green (525mμ), yellow (570mμ), and orange (600mμ) and those below 395mμ (ultraviolet, 330mμ) and near infrared (800mμ) are less efficient. The red (675mμ) and visible light (400-750mμ) are totally inactive. There seems to be a heating effect and a threshold of sensitivity at the short-wave infrared region (1750mμ).

These results have been used in an interpretation of the life cycle and the phenology of the insect.

EFFECT OF LIGHT ON *HYLEMYIA BRASSICAE* BOUCHE

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M. Sc.

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by

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I. INTRODUCTION

The effect of daylight or photoperiod in the regulation of the rhythmic activity of organisms was first demonstrated in plants (Garner and Allard, 1920) and later on in arthropods (Marcovitch, 1924) and in birds and mammals (Rowan, 1926). The geographical distribution, seasonal activity, growth form, metabolism, and the behaviour of the animal are all influenced by the diel rhythm of photoperiod. The environmental photoperiod provides a rhythm of light energy which, superimposed on the internal biological rhythm of animals, allows them to have an activity pattern which makes them nocturnal, diurnal or crepuscular (Bunning, 1964). In addition to these daily or "circadian" rhythms many animals have a seasonal rhythm so that the seasonal biology of many temperate insects is timed to synchronise with the seasons of the year. They may produce two or more generations under favourable climatic conditions, but only one generation in areas where the summers are very short. In either case, the insect species overwinters in a state of hibernation known as "diapause" which is induced by the environmental conditions to which the population is exposed.

Photoperiod is one of the environmental factors that governs the onset of diapause in the cabbage maggot, Hylemyia

brassicae (Bouché) (Hughes, 1960; Zabirov, 1961; McLeod and Driscoll, 1967; and Read, 1968a). Indeed, it would hardly be surprising if photoperiod proved to be the major diapause inducing factor, since this adaptation undoubtedly confers a stabilizing influence on the life cycle in the environment where other significant climatic factors, such as, temperature, and humidity are subjected to much variation (Danilveskii, 1965).

Photoperiodic induction of diapause involves the reception of light by the insect and this process is dependent on the wavelengths of the impinging light, the habit and the habitat of the insect species and the photoreceptors of the insect. Knowledge of the response to light of this soil dwelling species may contribute to the understanding of the ecological significance of photoperiod and also to the physiological analysis of the photodynamic processes involved in this response.

Callahan (1965A) suggested that cryptic animals may sense the photophase by being sensitive to the infrared part of the electromagnetic spectrum, as visible light (400-700mμ) is quickly filtered out by barriers such as soil.

With this in mind, a quantitative study of the effect of different light regimes on the induction of diapause in H. brassicae was initiated at Macdonald College, of McGill University, in 1967.

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The object was to determine in the laboratory, at a constant temperature, humidity, and light energy, the part of the light spectrum which suppresses diapause in the cabbage maggot, that is, the region which is photoperiodically active.

Preliminary tests, reported in Section I, were made to determine the effect of photoperiod on the egg, larval, and the pupal stages. Similar experiments were conducted to determine the pupal period of non-diapausing pupae in order to establish a time after which pupae that failed to emerge would be classified as "diapausing".

Other experiments were performed to determine the effect of temperature, crowding of the larvae, and maternal influence on diapause induction in the cabbage maggot.

As a prerequisite of the spectral studies, a study of the influence of different lengths of light period on diapause induction was undertaken (Section II). Section III deals with the spectral response of the cabbage maggot with respect to diapause induction.

H. brassicae was chosen for this study because it has been found to have a pupal diapause in the seasonal cycle which is induced by a short daylength (less than 12 hours of light per day) at an approrpriate temperature (15° - 25°C). The larvae are the sensitive stage and live in the soil (Hughes, 1960; Zabirov, 1961; Missonier, 1963; Zohren, 1968), and are useful for initial studies

for a future project of wider scope, on the effect of solar radiation on subterranean anthropods.

This thesis is a report on the results of the above experiments and on the interpretation and the significance of the data obtained.

In the present discussion, the term photoperiod is used in the sense of Beck (1968) and refers to the total cycle composed of a period of light and a period of dark. The period of light within the photoperiod is termed photophase and the dark portion is referred to as the scotophase.

II. REVIEW OF LITERATURE

A. Historical Aspect

Hylemyia brassicae Bouché 1834 has been known to occur in all temperate regions of the world as a pest of crucifers in varying degree of severity (Miles, 1956; Hughes, 1960; Zabirov, 1961; Stepanova, 1962; Missonier, 1963; Coaker and Wright, 1963; Davis and McEwen, 1966; Priore, 1966; Coaker, 1967 and Zohren, 1968).

It is not known exactly when H. brassicae reached Canada but it is reported to have been imported from Europe (Fletcher, 1885). It was first found in Canada around Montreal in 1875 (Couper, 1875). It was noticed as a pest around Vancouver Island and in Ontario, and Fletcher (1885) found out that it destroyed about 25% of the cauliflower in these localities. Prevalent in certain parts of Ontario and along the St. Lawrence River as early as 1875 (Couper, 1875; Fletcher, 1885), it was found to be destructive in New Brunswick, Prince Edward Island and in parts of Saskatchewan and Alberta between 1900 and 1902 (Fletcher, 1901; 1902; Gregson, 1902). Its spread throughout the country followed closely the cultivation of cruciferous crops introduced into these areas and in a little over 50 years, it had spread over the greater

part of Canada (Slinglerland, 1894; Schoene, 1916).

In Canada, it is considered to be one of the most serious pests on vegetables due in part to its development of resistance to the cyclodiene insecticides (Read, 1956; 1965a; 1965c; McLeod, 1964; Allen;1965; Harris and Svec, 1966; Read & Brown, 1966; and Ritchot, 1968, 1969).

Early life history and biology studies were carried out by a number of workers due to the importance of this insect as a pest of cauliflower (Hewitt, 1911; Gibson and Treherne, 1916; Schoene, 1916; Caesar, 1922, Brittain, 1927; Vasina, 1927; and Nikitina,1938). Recently, many authors have detailed the bionomics and described various methods and techniques for establishing cultures in the field, laboratory and greenhouse, (Miles, 1951; 1952; 1953; 1954; 1956a; 1956b; Sherwood and Pond, 1954; Foott, 1954, Read, 1956; 1960; 1962; 1965a; Read and Welch, 1960; Swailes, 1961; 1963; 1967; Forbes, 1962; Doane and Chapman, 1964a; 1964b; Harris and Svec, 1966; Traynier, 1965; 1967a; 1967b; and Zohren,1968, Ritchot, 1968, 1969).

Studies in voltinism have demonstrated that the number of generations per year depends upon the geographical distribution of the species. Partially univoltine strains are found in the northern parts of the Soviet Union (USSR) where the winters are very severe (Stepanova, 1962). In more southerly zones and in Canada, there are

two or three generations in a year (Caesar, 1922; Brittain, 1927; Vasina, 1927; Forbes, 1962; Stepanova, 1962; Allen, 1965 and Ritchot, 1968, 1969), while in Europe, United States of America (US) and the more southerly countries with less severe winters, three or more generations per year are found (Miles, 1954; 1956a; Stepanova, 1962; Coaker and Wright, 1963; Whitcomb and Garland, 1964; Priore, 1966; and Coaker, 1967).

Some of the early workers believed that H. brassicae overwintered in the larval form (Fletcher, 1885; Gibson and Treherne, 1915), others thought that it did so in the adult stage (Schoene, 1916; Nikitina, 1938). A third group maintained that the pupal stage was the overwintering form (Hewitt, 1911; Treherne, 1915; and Vasina, 1927). It is now confirmed that the diapausing pupae of H. brassicae is the overwintering stage (Hughes, 1960; Zabirov, 1961; Stepanova, 1962; Missonier, 1963; Zohren, 1968; and Richot, 1969).

B. Life Cycle

The biology of the cabbage maggot has been studied by various workers both in the field and in the laboratory (Slingerland, 1894; Hewitt, 1911, Gibson and Treherne, 1916; Schoene, 1916; Caesar, 1922, Brittain, 1927; Vasina, 1927; Smith, 1927, Vodinskaya, 1928; Nikitina, 1938; Fulton, 1943; de Wilde, 1947; Miles, 1951; 1952; 1953, 1954; 1956a; 1956b; Foott, 1954; Sherwood and Pond, 1954; Read, 1956; 1958; 1960; 1962; 1965a; Swailes, 1957; 1961; 1963; Auclair, Cartier, Hudon, Lafrance, and Perron, 1958; Hughes, 1959; Read and Welch, 1960; Forbes, 1962; Doane and Chapman, 1964a; 1964b; Berte, Decraemer, and Gillard, 1965; Allen, 1965; Traynier, 1965; 1967a; 1967b; Harris and Svec, 1966; Varis, 1967; Ritchot, 1968; 1969; Zohren, 1968).

In Canada, two or three generations have been found under natural conditions with a partial third or fourth generation in which the insect overwinters as a pupa.

In southern Alberta and southern Ontario, adult emergence from overwintering pupae begins in early May with a peak in late May and early June. There is a continuous emergence of the adults and the second peak occurs about mid-July. Oviposition of the overwintering generation starts about a week after the first emergence of the adults and lasts until early July with a

peak in the first two weeks of June (Gibson and Treherne, 1916; Caesar, 1922, Foott, 1954; Swailes, 1957; 1961; 1963; Allen, 1965).

In these provinces the summer generation starts to emerge in early August and continues emerging until late August with a peak in mid-August. The peak of egg production is between mid-August and mid-September. At infestation level an average of 430 eggs may be found per plant (Foott, 1954; Swailes, 1963).

In British Columbia, eggs are laid in late April or early May with a peak in May. Then mid-June to mid-July for the summer generation. The egg laying peak for the third generation occurs in mid-August to mid-September (Gibson and Treherne, 1916; Forbes, 1962).

In Prince Edward Island, two generations are generally found (Read, 1956; 1958). Flies begin to emerge from over-wintered pupae in mid-June in sandy soil areas and late July in heavier soils giving an emergence period which extends over a period of six weeks. The larval period of the first generation in the sandy soils extends from late June to mid-September with a peak at the end of July.

The second generation larval period starts in late July and early August and continues until early October with a peak of

larval numbers in the last two weeks of September. The third generation larval peak occurs in late September to mid-October. In clay soils, only one generation is found with a partial second at which the insects overwinter. The adults emerge from overwintering pupae in late July and the first generation larval period extends from early August to the end of September with a peak at the end of September.

In Nova Scotia, two generations occur. Eggs laid by adults from overwintered pupae appear in mid-May and continue until mid-August (Brittain, 1927). Two generations are also found in Manitoba with the first adults from overwintering pupae emerging at the end of June (Allen, 1965).

In Quebec, Ritchot (1968) pointed out that there were three generations in a year with the pupae of the third generation overwintering. There is, however, a possible partial fourth generation.

In the laboratory, a single generation is completed in 40-60 days at a rearing temperature of 20°C. Mating has been observed to occur in the mornings between 08.00 and 11.00 hours (Zohren, 1968) and egg laying starts four to six days after emergence (Schoene, 1916; Foott, 1954, Read, 1960; Swailes, 1961; Harris and Svec, 1966; Zohren, 1968, Ritchot, 1969).

At the same average temperature of 20°C, the number

of eggs laid by a single female has been variable. Brittain (1927) reported 103 eggs from one female fly and 20 to 50 mature eggs from dissected females from the field. Swailes (1961) also reported an average of 78 eggs per female ranging from four to 165, while Read (1965a) found that each female fly laid 20 to 25 eggs in 24 hours. A single female fly may lay an average of 371 eggs over a period of 66 days, and normally four to five eggs are laid by an adult female in one day and even less if the soil is very wet (Harris and Svec, 1966). Dry soil or sand has no effect on oviposition, but if the eggs are left on the soil for a long period of time, they tend to dry out and fail to hatch (Zohren, 1968). When flies of the same age are used, oviposition is frequently interrupted by three-day intervals (Zohren, 1968) and in the absence of an oviposition attractant, the females hold their eggs for about seven days after which the eggs are laid indiscriminately around the cages (Read, 1965a).

The incubation period varies between three to six days with an average of four days according to the rearing temperature (de Wilde, 1947; Swailes, 1957; 1963; Hughes and Salter, 1959; Read, 1965a; Harris and Svec, 1966; Varis, 1967; Zohren, 1968).

According to de Wilde (1947), the incubation period was between 2.5 to three days at temperatures of 23° to 25°C., and Swailes (1957) found that eggs could not survive for an hour at 42°C but

hatched after 2.7 days at a temperature of 25°C and after 12 days at 10°C; the maximum hatching of 94% or more was obtained at 10°C to 25°C. (Swailes, 1963). The minimum threshold temperature for egg development was found to be 7.2°C (Hughes and Salter, 1959). About 80% of the eggs hatched after two to four days with a mean of 75 hours at 20°C (Read, 1965a; Zohren, 1968) and according to Harris and Svec (1966) about 90 to 100% of the eggs hatched after one to two days at 25°C, and two days at 23°C. In the northern part of Finland with severe weather conditions, the incubation period was found to vary between three to six days in the field (Varis, 1967).

The rate of egg hatching and the life span of the first instars depend on the soil moisture as these either fail to hatch or die from dessication (Swailes, 1957; Read, 1965a;). At least 15% soil moisture is required for the survival of the first instars (Read, 1965a).

The larval stage extends for a period of 18 to 22 days with a prepupal period of three to five days at which the insect is inactive at a temperature of 20°C. (Read, 1965a; Harris and Svec, 1966). At a rearing temperature of 25°C, the average pupal period is about 15 days and is 30 days at 15°C (Zabirov, 1961).

About 70 to 100% of the pupae emerge into adults 6 to 20 days after pupation under 16-hour rearing photophase and a

temperature of 20°C. (Zabirov, 1961, Missonier, 1963; Read, 1965a; 1965b; Harris and Svec, 1966; Zohren, 1968). Temperatues above 22°C have been found to cause aestivation and those below 15°C induce diapause (Missonier, 1963; Read, 1965b).

Longevity of the adults has been shown to be about 29 days for the females and 19 days for the males at a temperature of 21.1°-23.9°C (Foott, 1954). Harris and Svec (1966) showed that the average life span of a female was 42.6 days and that of the male was 32.6 days at 18.9°-22.2°C. Some females have been found to live as long as 63 days at 21.1°C (Schoene, 1916; Miles, 1951) and even more than three months at 20°C (Vodinskaya, 1928). An average age for an unmated female was 9.5 days as compared with 22.2 days for mated female at a temperature of 18.3°-23.9°C. (Swailes, 1961).

C. Aspects of Diapause

1. Ecological significance of diapause

The significance of diapause to the arthropod has been emphasized by many workers (Andrewartha, 1952; Lees, 1955; 1959; de Wilde, 1962; Danilveskii, 1965; Wigglesworth, 1965; Beck, 1968). In these animals, diapause is a mechanism for withstanding harsh climatic conditions, that is, the diapause stage is usually an overwintering stage. Correlated with this, the diapause stage is frequently cold hardy, resistant to dessication, and often a non-feeding stage. However, Danilveskii (1965) points out that not only does diapause ensure survival through an unfavourable season, but it also determines the constancy of the life cycles and the synchronization of the developmental stages with the seasons of the year to which the insect is well adapted.

2. Diapause determination

The induction of diapause in arthropods is influenced by environmental factors and it takes place at a particular stage in the life cycle of the species before the onset of the unfavourable season of the year. (Andrewartha, 1952; Lees, 1955; Danilveskii, 1965). The stage of development in which diapause occurs varies in different insect species; some diapause in the egg stage while others diapause during the larval, pupal, or the adult stages.

In the cabbage maggot, the larval stage has been found to be the sensitive stage, that is, the stage which is influenced by the environment; diapause being induced when the larvae are exposed to short daylengths (12-hour or less photophases). The responsive stage, that is, the stage which demonstrates the diapause phenomenon is the pupa, and this is insensitive to photoperiod (Hughes, 1960; Zabirov, 1961; Stepanova, 1962; Missonier, 1963; Read, 1968a). Missonier (1963) reported that there was an accumulative effect of the environment on the sensitive stage which began at the third instar stage and terminated at the end of pupal histolysis. When a certain minimum quantity of induction stimulus has been received, even during only part of this sensitive stage, diapause is induced. Once the insects are induced to diapause they must undergo a period of diapause development. Hughes (1960) found that long days at the beginning of the larval development were much more effective than long days towards the end of the larval stage in averting diapause. As few as 7 long days were sufficient to prevent the majority of the pupae from going into diapause.

Diapause is genetically determined (Lees, 1955; Harvey, 1957; 1961; Apple and Beck, 1961; de Wilde, 1962; Danilveskii, 1965; Barry and Adkisson, 1966; Beck, 1968), and is under the immediate control of the neuroendocrine system. During diapause,

neither the prothoracotropic hormone nor the juvenile hormone is secreted and in the absence of these hormones, the prothoracic glands cannot produce ecdysone and the insect's growth and differentiation are stopped (Morohoshi, 1959; Schneiderman and Gilbert, 1959; 1964; Harvey, 1962; Lees, 1963; McLeod and Beck, 1963; Williams, 1963; Beck, 1964; Williams and Adkisson, 1964a; 1964b; Siew, 1965a; 1965b; Engleman, 1968).

There is no visual means of telling when the insect has entered diapause. In the cabbage maggot, however, the pupae which do not enter into diapause emerge as adults in 6 to 25 days, depending upon the ambient temperature (between 18° and 22.5°C) while those in diapause take 3 to 6 months or more to emerge both in the field and in the laboratory (Miles, 1956b; Coaker and Wright, 1963; Missonier, 1963; Read, 1965b; 1968a; Harris and Svec, 1966; McLeod and Driscoll, 1967; Zohren, 1968).

Diapause, however, that takes place in the adult stage, may be expressed by the failure to show reproductive activity (Lees, 1955, de Wilde and Bonga, 1958; Brazzel and Newson, 1959; Hardwood and Halfhill, 1964; Beards and Strong, 1966). In the immature stages, diapause is manifested by reduced growth and development (Beck and Havec, 1960; Harvey, 1962; Beck and Alexander, 1964; Beck, 1968; Ring, 1968). Pupal diapause is characterized by reduction in metabolic rate, cessation of adult

development, decrease in water content, and resistance to water loss by transpiration (Mansingh and Smallman, 1966; 1967; Wellso and Adkisson, 1966; Brokway and Schneiderman, 1967; MacLeod, 1967; Beck, 1968).

A facultative diapause is normally found in the cabbage maggot, that is, a diapause that may or may not be manifested in a given individual or population depending on the environmental conditions prevailing during the critical stages of the insects' development. However, a strictly univoltine strain, that is, a strain with obligatory diapause where every individual of every generation undergoes diapause as part of its life history, arising from hereditary constitution of the species, is found in the northern parts of the Soviet Union (Stepanova, 1962).

D. Influence of the Environment on Diapause Inductions

The environmental factors that induce diapause in insects are photoperiod, temperature, diet, relative humidity and the age of the parent insect (Lees, 1959; de Wilde, 1962; Harvey, 1962; Danilveskii, 1965; and Beck, 1968).

1. Photoperiod

Of all these factors which are involved in the induction of diapause in arthropods, daylength has been proven to be the most important, although its effect may be modified or completely obliterated by some of the above factors; Dnintjir, and Mook, 1959; Beck and Hanec, 1960; Hughes, 1960; Zabirov, 1961; Adkisson, Bell, and Wellso, 1963; Beck, 1964; William and Adkisson, 1964b; Danilveskii, 1965; Wellso and Adkisson, 1966; Dehn, 1967; Engelman, 1968; Prokopy, 1968). The cabbage root maggot is a "long day" insect as it enters a state of diapause when the daylength is less than 12 hours (Hughes, 1960; Zabirov, 1961; Stepanova, 1962; McLeod, 1965; Read, 1965b; 1968a; McLeod and Driscoll, 1967). Zabirov (1961) found that in Leningrad the critical daylength, that is, the daylength inducing diapause in 50% of the population, lies between 15 and 16 hours of light, thus the critical daylength is 15 hours and 30 minutes at 21°C. Hughes (1960) in England, calculated that half the individuals of a generation in the

field would have entered into prolonged pupal (diapause) stage if the larval stage developed during a period when the mean time between sunrise and sunset was just over 14 hours. That is, the critical daylength was calculated to be 14 hours. "Short day" insects, on the other hand, are those that would enter diapause if subjected to more than 12 hours of daylight. Daylength is the most important environmental factor influencing diapause in H. brassicae, (Hughes, 1960; McLeod, 1965; McLeod and Driscoll, 1967), for it is the only environmental factor that changes with mathematical precision being not at all affected by changes in the weather and climate, but only by changes in latitude and the seasons of the year (Danilveskii, 1965; Beck, 1968).

Hughes (1960) reported that facultative diapause in H. brassicae was induced by the changes in the daylength and that the proportion of diapausing pupae was progressively reduced as the number of long days increased. Populations reared in the spring and summer in the field when the daylength was between 14 hours (April) and 17 hours (July) had a high percentage of emergence (60% after 10 days) while those raised in the autumn and winter with daylengths of 13 hours in September and 8 hours in January had a long pupal period (diapause) and a low percentage of emergence, 20% after 100 days at 20°C. He postulated that the daylength stimulus was passed on to the insect by means of a change in the

chemical composition of the host plant which was detected by the insect when feeding on it; but did indicate that 0.6% of the light incident on the host plant surface would reach a feeding larva. The following treatments were given to the larvae:

(a) 24 hour light (11 hour daylight supplemented by a mercury vapour lamp giving 250 foot-candles)

(b) 24 hour light (11 hour daylight supplemented by 100 watt tungsten lamp giving 25 foot-candles)

(c) 8 hour daylight and 16 hour darkness

(d) 8 hour daylight and 16 hour darkness when the larvae were developing, but the plants were pre-treated for 10 days with 24 hours of light as in (a).

One batch of each treatment was covered with black cloth to prevent light reaching the soil and plant. With (a) treatment, covered plants gave 22% diapause as against 33% in uncovered ones. Treatment (b) had 8% in uncovered plants and 19% in covered ones while treatment (c) had 100% diapause in both treatments. Treatment (d) gave 93% in covered and 50% in uncovered plants.

Zabirov (1961) claimed that the larvae of the cabbage root maggots responded directly to the light stimulus and not to the stimulus received through the host plant.

McLeod (1965) in a summarized form reported that diapause in the root maggot was induced by an 8-hour photophase at 15°C and that non-diapausing pupae were produced at 22.5°C under 16-hour photophase.

McLeod and Driscoll (1967) showed that although short daylength (12 hours photophase) induced diapause, the photoperiodic effect was manifest only between 20° and 22.5°C. They found that at rearing temperatures of 15° and 25°C and a photoperiod of 16 hours photophase, the percentage emergence was 0% and 46% respectively, whereas at 20° and 22.5°C the percentage of emergence was 98% and 96% respectively. Under 12 hour photophase, emergence at 15°C and 25°C was 4% and 35% respectively as against 22% and 35% obtained at 20° and 22.5°C respectively.

Zabirov (1961) also showed that the photoperiodic effect could be seen at the temperatures where maximum growth occurred, that is, between 18° and 25°C. He observed that at a larval rearing temperature of 18°C, 9% of the pupae diapaused under 24 hours light, as against 92.6% under short day regime of 12 hours of light. At 21° and 25°C, under 24 hours of light, 24% and 40% diapausing pupae were obtained and 92% and 90% with 12 hours of light respectively. At 12°C, the percentage of diapausing pupae at both light regimes was 100%. He concluded that photoperiodic reaction governed the beginning of diapause in the cabbage

root maggot.

Stepanova (1962) and Danilveskii (1965) explained that voltinism depended mainly on the photoperiodic conditions in the range of the optimum growth temperatures and outside these optimum temperature limits, diapause depended on temperature. Danilveskii concluded that the effect of temperature was negligible as the photoperiodic reaction that induced diapause was manifest at the optimum range of temperatures for growth.

Beck (1962; 1968) reported that diapause induction in insects depended upon the actual number of hours of the photoperiodic phase and that the scotophase duration was more critical than the photophase. This indicated that insects responded to actual or absolute daylight rather than changes in the daylength. In an experiment using the European corn borer, Ostrinia nubilalis, (Hübner) scotophases of 17 hours in a 24-hour photoperiod at 30°C were systematically interrupted by a one-hour light period. Above 90% diapause was associated with 12 hours uninterrupted dark. When the interrupting light occurred after either eight or six hours of darkness, less than 5% diapause occurred, and after two or four hours of dark, an hour of light was followed by 14 or 12 hours dark, 50% diapause incidence was obtained.

Similar results have been reported by Ring (1967a; 1967b) for the larvae of Lucilia caesar L. which were sensitive

to changes in the absolute length of the photophase during all instars, and the females did not respond to the intrinsic rate of changes in the photoperiod but to the absolute length of the light and the dark phases. He found out that transference of the larvae from long day (20 hours of light) to short day (12 hours of light) during the first instar resulted in a mean increase of 72% in diapause rate in experimental groups over control groups. This value became progressively smaller with increasing age of the larvae at the time of transfer, being 48% in the second instar and only 5% in the third instar. Removal from short day to long day in the first instar resulted in a 44% decrease in the diapause rate, in the second instar a 28% decrease, and in the third instar a similar 28% decrease but the age at transference did not seem to be so critical.

With the female flies, Ring (1967b) found that at a constant temperature of 22°C and a photophase of 18 hours, there was no diapause incidence and also when the photophase was decreased from 20-1/2 hours to 19 hours, there was complete absence of diapause. A regular decrease of 10 minutes per day from 18 hours to 14 hours showed that after 6 weeks 90% diapause occurred in the 14-hour flies, 96% in the 14-1/2-hour, and 15% in the 16-1/2-hour flies. Above this photophase, no diapause incidence was recorded.

Beck (1962) found that although the scotophase was far more critical than the photophase, the temperature during the scotophase was important for diapause induction. He found that diapause induction in the European corn borer involved a scotophasic temperature sensitivity. Low temperatures of 21°C during the 9 hour scotophase caused 96% diapause incidence, whereas the low temperatures during the light phase produced 16% diapause, equal to the control of total darkness. Low temperatures of 21°C during nine hours of 16 hour photophase and high temperatures of 31°C during the scotophase resulted in only 15% diapause.

Although photoperiod has been found to induce diapause in the cabbage root maggot, its effects has been observed to be variable. Missonier (1963) found that photoperiod acted over a narrow range, 8 to 12-hour photophases. He observed that at a rearing temperature of 25°C, under continuous darkness, 4-hour, 8-hour, 12-hour and 16-hour photophases, 91%, 74%, 94%, and 99%, 99% emergence occurred respectively. At 10°C, only 9%, 5%, 0%, and 2%, 11% emergence were obtained under similar photophases. However, at 20°C, 99% emergence occurred under continuous darkness, 96% and 100% under 4- and 16-hour photophases respectively; 8-hour photophase gave 1% and 12-hour photophase resulted in no diapause incidence.

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2. Light Intensity and Spectral Response

The effect of different light intensities and quality of light in the induction of diapause in the H. brassicae has not been determined. Read (1965b; 1968b) speculated that light intensity may play an important role in the photoperiodic induction of diapause in the H. brassicae. He observed that when the flies were subjected to 10 hours of summer daylight with temperatures held close to 21.1°C none of the pupae entered diapause, whereas all pupae reared under 'similar conditions' in December and January entered a long-term diapause.

Observations on light intensities have shown that very low energies are effective for the prevention of diapause in certain arthropods. This has also been suggested by Zabirov (1961) and Stepanova (1962) for H. brassicae. Such soil inhabiting forms have been found to detect the light intensity of their outside surroundings by displaying a very low threshold sensitivity. (Danilveskii, 1965; Beck, 1968). Soil inhabiting insects, such as the larvae of the cutworm, Tryphaena pronuba L, have been found to have a threshold of sensitivity of 0.5 lux (Madge, 1964a). Similar lower threshold sensitivity has been found in wireworms, Agriotes lineatus, and A. obscurus, by Falconer (1944). They are sensitive to illumination as weak as 0.05 to 0.1 meter-candles respectively.

Kogure (1933) found that silkworm eggs responded to light of 0.1 lux and that the early instars were also sensitive to incident light of about 0.1 lux. The threshold intensity for photoperiodic response in the Colorado beetle, Leptinotarsa decemlineata Say, was found to be below 0.1 lux (0.4 ergs/cm^2/sec) (de Wilde and Bonga, 1958). Above this intensity value, however, they found that the responses increased with the intensity until above 5 lux when they remained more or less constant, that is, further increase had no effect. Paris and Jenner (1959) reported a similar extreme sensitivity in the larvae of Metriocnemus knabi, which reacted to light intensity of 0.0025 foot-candles.

Beck (1968), however, pointed out that the threshold light intensity required for diapause induction in insects is usually found between 5 and 25 lux (0.5-2 foot candles). Danilveskii (1965) found out that Acronycta rumicis needed about 5 lux to show any photoperiodic effect. The Oriental fruit moth, Laspeyresia (=Grapholitha) molesta (Busck) has been found to have a threshold for photoperiodic reaction of 32 lux (3 foot-candles) (Dickson (1949). Lees (1953) found that the threshold for diapause induction in the spider mite, Metatetranychus ulmi Koch., was about 10 lux.

The response to different wave lengths of light has been observed for a number of insects. However, most of the effective

wavelengths seem to lie between about 400 and 500mμ with wavelengths above 600mμ not effective. Kogure (1933) found that under the influence of violet-blue light rays, 350 - 510mμ, the adults of silkworm laid about 98% diapausing eggs, while with approximately the same intensity, the adults obtained under orange-yellow and red light (over 550mμ) gave the same results as those obtained under total darkness, about 3 - 8% diapausing eggs. The silkworm is a short day insect.

Dickson (1949) exposed the larvae of the Oriental fruit moth, a long day insect, to a temperature of 24°C and 12 hours of light per day with filtered light during their feeding period. He showed that the wavelengths from approximately 400mμ-580mμ (a range from violet to yellow) gave 87% - 99% diapause in the prepupae. A low incidence of diapause occurred at 660mμ (red) and neither ultraviolet (below 400mμ) nor infrared (1400mμ) had any inducing effect. He concluded that the wavelengths from approximately 400-580mμ were photoperiodically active as the response at these wavelengths was equal to 12-hour photophase of unfiltered light.

Williams, Adkisson, and Walcott (1965) found that in the oak silkworm the photoperiodic signal was conveyed by the direct action of violet, blue, and blue-green light (398-508mμ) on

the brain itself. They exposed diapausing pupae to unfiltered light for eight hours and then placed them so that they received filtered light during the final eight hours of a daily 16-hour photophase at 25°C. Diapause was terminated (100% development) by all pupae exposed to violet, blue, and blue-green light (398-508mμ). A similar emergence occurred in the control series given 16 hours of unfiltered light. 100% and 90% diapause occurred at yellow (580mμ) and red light (640mμ) respectively.

The range below 400mμ and above 600mμ may, however, be effective in the photoperiodic response in other insects. Lees (1953) indicated that the range from near ultraviolet to blue-green (365mμ -500mμ) had a photoperiodic effect, averting diapause in M. ulmi, with the maximum effect in the blue region (about 425mμ) the range from yellow to infrared had the same effect as short day-length, allowing diapause. He found out that above 580mμ with a peak of 700mμ and above 530 (650mμ peak), 100% diapause incidence was obtained. Under spectral wavelengths of 480 - 600mμ (540mμ peak), 350 - 500mμ (425mμ peak), 300 - 390mμ (365 peak), no diapause incidence was recorded when the highest relative energy was used.

On the other hand, de Wilde and Bonga (1958) reported that the Colorado beetle, L. decemlineata, was sensitive to filtered

light (423mμ - 675mμ) but not infrared (above 700mμ). Under long day conditions (16 hours) with filtered light between 423mμ and 675mμ, only about 30% of the beetles went into diapause. At a maximum transmission of 423mμ, 33% of the beetles entered diapause, 4% diapause occurred at 480mμ, 19% occurred at 560mμ and 31% occurred at 675mμ. With light filtered to remove wavelengths below 700mμ, 87% diapause incidence occurred.

Harris, Lloyd, Lane, and Burt, (1967) found that the region most effective for suppressing diapause in the boll weevil was between 400 - 665mμ and the region 359-390mμ and 670 - 1000mμ were less effective. They exposed the weevils to 11 hours unfiltered light and 2 hours extension of filtered light and obtained 19.3% diapause incidence at a spectral range of 400 - 475mμ, 17.1% at 485-560mμ, 16.1% at 525 - 570mμ and 18.5% at 580 - 665mμ which is not significantly different from the diapause suppressing light regime of 13 hours unfiltered light (15.6%). Percentages of diapause at regions of 350 - 390mμ and 670 - 1000mμ were 23.0 and 28.2 respectively which showed no significant difference between these and a diapause inducing regime of 11 hours of light (33.3% diapause).

Callahan (1965a) argued that due to the fact that infrared frequencies could penetrate many natural substances such as wood, it should be considered fully in induction of diapause in arthropods. He showed that with a 100-watt incandescent light bulb, more than

80% of the output fell from the near to far infrared.

3. Temperature

Temperature has been found to act in two ways in the induction of diapause in the cabbage maggot, H. brassicae, depending on whether the temperature is constant or fluctuating through a daily rhythm (Zabirov, 1961; Missonier, 1963; Read, 1965b; Harris and Svec, 1966; McLeod and Driscoll, 1967).

Constant temperatures may bring about differences in the critical daylength and cause a shift in the periods of diapause induction in the field (Zabirov, 1961). Zabirov found that a 5°C temperature difference (from 20° - 25°C holding temperature of the larvae) caused a one hour shift of the critical daylength. At 20°C, the critical daylength was found to be at 15 hours of light while at 25°C, it was at a 16-hour photophase.

Missonier (1963) and Read (1965b) observed that diapause induction in the cabbage maggot did not depend upon the daily variation of the temperature but on the mean daily temperature. Missionier reared the eggs and the larvae under different daily thermoperiods. Two basal temperatures of 10°C and 25°C were used for 8-hour and 16-hour photophases for the rest of the day (16 or 8-hour photophase); the larvae were placed in groups at different temperatures (T) 2°, 8°, 10°, 15°, 20°, 25°, and 30°C.

After pupal formation, the pupae from each group were divided into two groups, one submitted to 20°, the other to 25°C.

The results obtained in the mean temperatures under which the larvae were reared were identical to those obtained at constant temperatures. At a pupal holding temperature of 20°C, the pupae from rearing temperatures of 25° + 10° at 16-hour photophase (mean rearing temperature of 20°C) showed no diapause as compared with similar no diapause incidence at a constant temperature of 20°C. At a rearing temperature of 25° + 10°C (mean of 15°C, 16-hour photophase), 97% diapause incidence was obtained while at a constant rearing temperature of 15°C, 16-hour photophase, 100% diapause pupae were recorded.

Read (1965b) found that when the larvae were reared at constant temperatures of 15.6°, 18.3°, or 21.1°C under 10-hour photophase, 98% of the resultant pupae entered into diapause whereas fluctuating the larval rearing temperature between 10° and 18.3°C and 18.3° and 21.1°C under similar photophase resulted in a slightly lower (90% and 85% respectively) but not significantly different percentage of diapausing pupae.

Missonier (1963) found that daily variations of temperature between 3° and 25°C affected the development of the larvae of the cabbage maggot. However, entry into diapause was found to be

determined by the quantity of heat received during the larval period, that is, the summation of temperature. Missonier showed that H. brassicae required about 300 deg.-days for complete development (from egg to adult). Coaker and Wright (1963) also found that in England, morphogenesis was completed at a constant temperature after an accumulation of about 368 deg.-days above 7.2°C.

However, the rate of the larval development depended on the temperature; the lower the rate of development, the higher the incidence of diapause (Missonier, 1963). He reared the larvae at mean temperatures of 10° and 20°C under 8-hour and 16-hour photophases. The rates of larval development at 10°C were 1.7 and 2.13 for 16-hour and 8-hour photophases respectively, where the rate of development was calculated as the reciprocal of the developmental time in days. 100% diapause was obtained under both photophases.

At a rearing temperature of 20°C, rates of development were 4.2 for 16-hour and 3.1 for 8-hour photophase, both photophases gave 0% and 100% diapause respectively.

High temperatures have been found to inhibit pupal development of the cabbage maggot but immediately these pupae are returned to a lower temperature, they emerge (Missonier, 1963;).

Missonier found that high temperatures stopped development and this reaction was well realized at temperatures above 22°C. He used the term "aestivation" to describe these pupae as they emerged immediately they were put at a lower temperature. Aestivation is thus a dormant state which is a direct response to deleterious physical factors and is terminated immediately after the cessation of these unfavourable conditions. He reported that the percentage of pupae that aestivated at a holding temperature of 30°C was 88, 91% at 25°C and 16% at 20°C when the larvae were reared at 20°C and 16-hour photophase.

This important factor, according to Read (1968a) was not recognized by Hughes (1960), Zabirov (1961), Stepanova (1962), Coaker and Wright (1963), McLeod and Driscoll (1967) or himself (1960; 1962; 1963; 1965b) some of whom used the word "diapause" to describe these pupae. (Zabirov, 1961; Read, 1965b; McLeod and Driscoll, 1967).

Zabirov (1961) observed that in the first generation, 5% of the pupae entered diapause when the larvae were held at 18°C and 98% "diapaused" at a rearing temperature of 28°C. Both treatments received 24-hour photophase. Similar results were reported by Read (1965b). He found that with pupae produced from larvae reared at 20°C when held at temperatures of 22.8°, 23.9°, and 26.7°C,

only 2-3% emergence occurred after 12 months but when the pupae were held at 19.4°C, 45.4% emergence occurred after 6 months as compared with less than 1.0% at the higher temperatures. The larvae were reared under 10-hour photophase.

Harris and Svec (1966) found that high temperatures at above 21.7°C most pupae failed to emerge. They observed that in pupae obtained from larvae reared at 20°C under 18-hour photophase, 18% "diapaused" (pupae) at 21.7°C, 87% at 25.6°C, and 0.0% at 18.9°C. When these non emerged pupae were subjected to a lower temperature of 18.9°C, 100% emergence occurred. McLeod and Driscoll (1967) also reported that 54% and 100% 'diapause' pupae were obtained at rearing temperatures of 25° and 27.5°C respectively but pointed out that these pupae emerged when they were placed at lower temperatures.

4. The Interaction of photoperiod and temperature

Zabirov (1961) and Read (1968) suggested that both photoperiod and temperature were responsible for diapause induction in the cabbage maggot. Zabirov reported that as the temperature or the photoperiod decreased, the percentage of diapausing pupae increased, both in the field and in the laboratory. At 18°C, the percentage of diapausing pupae obtained in the laboratory under 12 hours of light was 96.2% as against 9.0% at

24 hours of light. In the field, 100% diapausing pupae were obtained when the day light was 14 hours 12 minutes and the soil temperature at a depth of 5-10cm was 18°C. However, at a temperature of 12°C, 100% diapause was obtained under both 12-hour and 24-hour photophases in the laboratory.

Read (1968a) found that all pupae went into diapause if the puparia were subjected to a temperature of 5°C for 72 hours after the flies, eggs, and the larvae had been held at a temperature of 14°C, with 12 hours photophase or if the eggs and the larvae were reared in total darkness. The pupae did not diapause without the short period at 5°C. A similar situation occurred at rearing temperatures of 17°C and 18°C but the percentage entering diapause after the cold treatment was not quite so high. He also (1965b, 1968b) suggested light intensity as a possible factor in diapause induction but there is no work published on this.

Temperature has been shown to modify or nullify the photoperiodic effect inducing diapause in the cabbage root maggot. Zabirov (1961) found that there was a gradual increase in the number of diapausing individuals as the rearing temperature was lowered and this was more pronounced under short-day conditions. However, under low temperature conditions (12°C), diapause induction was found to be independent of the daylength. He found that at 25°C, 40% of the pupae entered diapause under longday

conditions, that is, 24 hours of light and 90% diapaused under 12 hours of light. Only 9% diapause incidence was recorded at 18°C, 24 hours of light and 96.2% under short-day of 12 hours of light. At 12°C, 100% diapausing pupae were obtained at both 12 hours and 24 hours of light. Similar results were reported by McLeod and Driscoll (1967). They found out that at a temperature of 15°C, 100% diapause and 96% diapause incidence occurred when the larvae were reared under 16 hours and 12 hours of light, respectively. At 20°C and 12 hours of daylight, 78% of the pupae entered diapause and 2% diapause incidence was obtained at the same temperature and 16-hour photophase.

Missonier (1963) found that when the larvae were exposed to a photophase of 8 hours at temperatures of 10° and 15°C, 100% of the pupae entered diapause whereas at 25°C only 9% diapausing pupae were obtained under similar photoperiodic conditions. Harris and Svec (1966) reared the larvae at a day temperature of 22.2°C (18 hours) and a night temperature of 18.9°C (8 hours). The resulting pupae were held at 16-hour photophase; at 7.8°, 13.3°, 18.9°, and 16.9°C; the percentages of diapause were 100%, 56%, 0% and 20% respectively.

5. Other factors

Relative Humidity, diet, and the age of the parents are considered to be of minor importance in the induction of diapause in the cabbage maggot (Stepanova, 1962; Missonier, 1963). The effect of Relative Humidity has not been studied in detail but Stepanova and Missonier speculated that it might not have any effect in diapause induction due to the endophytic type of life of the larvae.

Missonier (1963) seems to be the only worker who has done some preliminary tests on the effect of diet. He found that diet modified the action of photoperiod. At 20° C under 16-hour photophase, he observed that when the larvae were reared on fresh turnips, 86% of the pupae emerged whereas on old turnips only 25% of the pupae emerged into adults under similar photophase. He found that the age of the parents or the conditions which the parents have undergone have no effect on the incidence of diapause in their progeny.

E. Light Penetration into Soil

Apart from the adult flies, all stages of the cabbage maggot are spent in the top 10cm of the soil, feeding on the roots of cruciferous plants. They may use the soil for pupation to protect themselves from frost (Kuhnelt, 1961; Kevan, 1968).

The larvae, which are sensitive to daylength, live mainly inside the cruciferous roots where no light or little light may reach. Such soil inhabiting forms, however, have been shown to detect very low light intensities in their surroundings (Falconer, 1944; Madge, 1964a; Danilveskii, 1965; Beck, 1968).

Solar radiation incident on the earth's surface may not immediately be absorbed or reflected and may penetrate to considerable depth. Penetration, however, in most soils, is very low and depends on the wavelength of the incident light and the size of the soil particles (Baumgartner, 1953; Geiger, 1965 and Sellers, 1967). Thermal conductivity is highest for a soil containing absorbent quartz and least for soils rich in organic matter, and increases with increasing moisture content since water replaces air in the soil pore spaces. Penetrated light warms or serves to illuminate the soil's interior (Baumgartner, 1953).

For the sun, the maximum emission is near 500mμ, which is in the visible portion of the electromagnetic spectrum

(Johnson, 1963; Sellers, 1967), and almost 99% of the sun's radiation is contained in the wavelengths ranging from 150-4000mμ. Of this, 9% is in the ultraviolet (less than 400mμ), 45% is in the visible portion (400-740mμ) and 46% in the infrared (above 740mμ) (Sellers, 1967).

Most soils absorb energy in the ultraviolet portion of the spectrum and scatter and reflect it at longer wavelengths. With increasing depth in the soil and as far as sunlight penetrates, less of the radiation is in the short wavelengths (blue) and more in the longer wavelengths (red) (Baumgartner, 1953; Geiger, 1965; and Sellers, 1967). Baumgartner (1953) showed that the proportion of light of a wavelength of 800mμ (farthest red) increases 15-fold after four reflections. Visible light in the soil is, therefore, mainly in the red part of the spectrum.

Sauberer (1957) observed that blue light (470mμ) was reduced to 0.01% of its surface intensity at a depth of 1.8mm in wet sand. At the same depth, orange light (630mμ) was reduced to 0.1% of its surface intensity.

High absorption in the ultraviolet takes place in the atmpsphere due to ozone and molecular oxygen, thus essentially, none reaches the ground (Sellers, 1967). This has been shown to be of advantage for soil dwelling insects as they are very susceptible to ultraviolet light and are heavily injured by it; high absorption helps

them to live close to the soil surface (Baumgartner, 1953).

Penetration of light has also been demonstrated to depend on the size of the soil particles. The coarser the grains, the more light penetrates (Baumgartner, 1953; Geiger, 1965; and Sellers, 1967). In coarse sand with grain size of 4-6mm Baumgartner found that 1/1000 of the outside light penetrated to a depth of 20mm, where half of the penetrating light was absorbed. In fine sand of grain size 0.1 -0.5mm, 1/1000 of the light reached a depth of about 2mm. With the coarse sand, 3% of the penetrating light remained in the layers between 10mm and 12mm.

Geiger (1965) cited Kohn who observed that at a depth of 0.5mm the illumination in a powdered soil was equivalent to moonlight, whereas employing loam he observed that considerable light was present at 10mm.

F. Perception of Light by Arthropods

The mode of light perception of soil arthropods has not yet been explained. Kuhnelt (1961) suggested that soil animals had reduced light receptors, which were compensated for by a better development of touch-sensitive organs.

The larvae of dipterous flies received their light through stemmata situated in the head (Snodgrass, 1935; Dethier, 1963; Wigglesworth, 1965). The whole body surface of most of these larvae also seems to be sensitive to light (Dethier, 1963).

In other insects, light has been shown to be perceived through direct action on the brain (Lees, 1955; 1963; William and Adkisson, 1964a; Williams, Adkisson, and Walcott, 1965). Lees (1955) stated that photoperiodic reception may be situated in the epidermis of larvae or light may penetrate the integument and affect the nervous system. Lees (1963) postulated that in the apterous aphid, Megoura viciae Buckton, the endocrine centre is switched on by 'long' but not 'short' photophases. The light receptor with its pigment system, is located in the brain.

Williams and Adkisson (1964a) showed that light acted directly on the pupal brain of the Oak silkworm to control the secretion of the brain hormone. Williams et al (1965) concluded that the photoperiodic signal is conveyed by the direct action of

violet, blue, and blue-green light (398-508mμ) on the brain of the Oak silkworm. They speculated that a pink brain pigmentation may be involved in the absorption of these effective wavelengths. The light may penetrate the cuticle to act on the brain.

Grant (1949) hypothesized that the sensory pits of insects were especially suitable for sensing infrared radiation and that some would have a pronounced selective sensibility to certain wavelengths. Combination of pits with different sizes could find, without contact, whether a surface had a particular temperature. Evans (1964) described the sensory pits at the lateral margins of the coxal cavities of the buprestid, Melanophila acuminata (DeGeer) which were found to respond to infrared in the 0.8μ-2.7μ band and as high as 6.0μ. Callahan (1965a) suggested that the larvae of the corn earworm, covered with hollow spines, could use these as waveguides for the focusing of long-wave radiation into the nervous system.

He (1965b) concluded that the compound eye of the same insect was a high absorber of the far infrared radiation and of such a configuration that it could orient to hot or warm spots of longwave infrared radiation in total darkness.

III. MATERIALS AND METHODS

A. Control of Light Regime

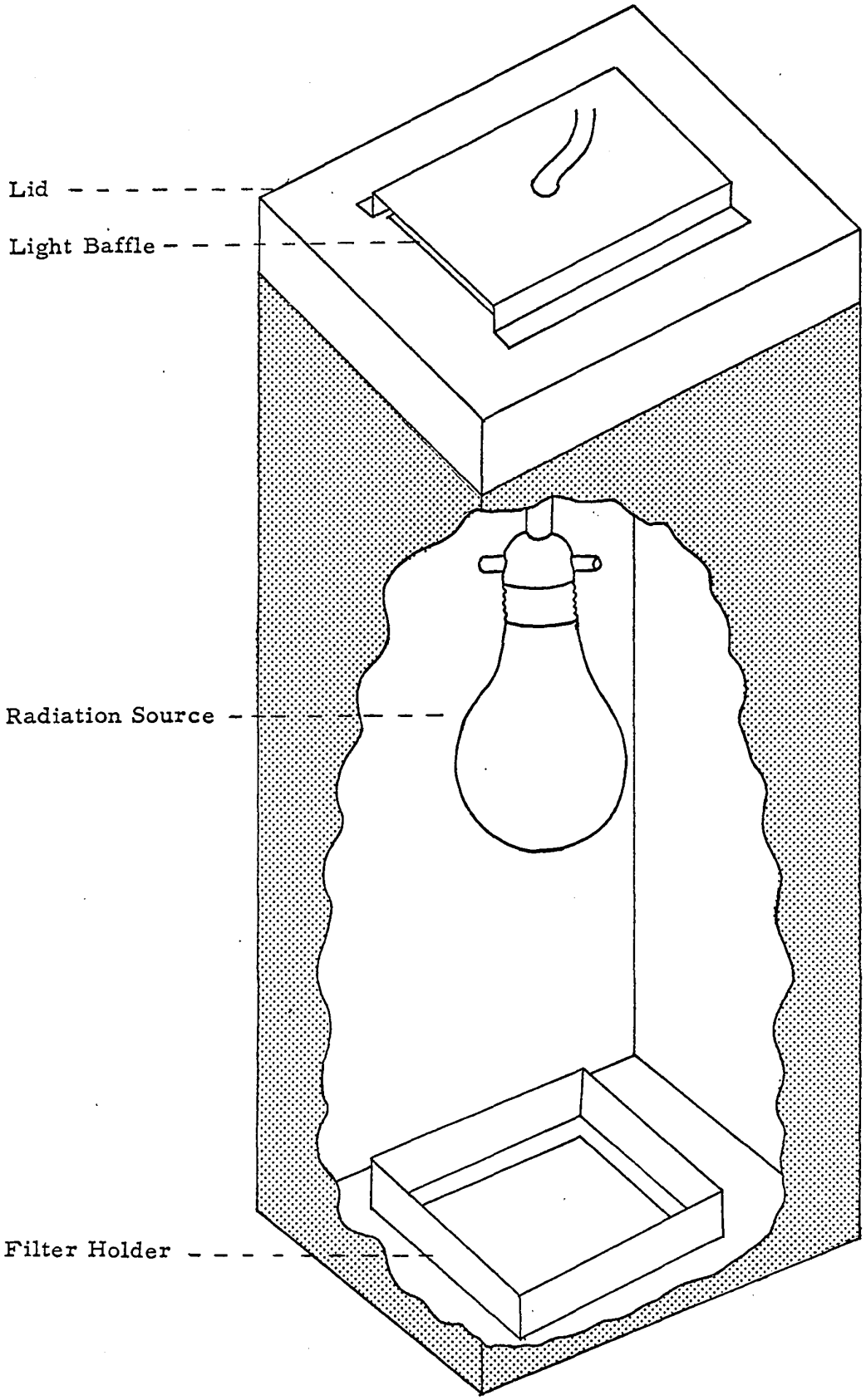
The part of the radiation spectrum investigated was divided into 10 ranges and each range of wavelength was taken as a treatment and repeated three times, using the same energy level for all the treatments. Four other treatments were included, white light, (370-750mμ); continuous darkness; (LO:D24); 16-hour photophase (L16:D8); and 12-hour photophase (L12:D12). Wavelengths of the filtered light were controlled by 5cm^2 Corning Glass Filters. The ranges of wavelengths with the peaks of transmission and the filters employed were:

Transmission range (mμ)	Transmission peak (mμ)	Glass filter used	Colour obtained
400-750	-	CS 3-75+ 1-69	Filtered white light
230-420	330	CS 7-54+ 1-69	Ultraviolet
370-425	400	CS 3-75+7-51+1-69	Violet
430-500	460	CS 3-72+5-60+1-69	Blue
460-580	500	CS 3-71+5-56+1-69	Blue-green
480-570	525	CS 4-64+1-69	Green
555-610	570	CS 3-66+4-96+1-69	Yellow
590-630	600	CS 4-94+2-62+1-69	Orange
620-750	675	CS 2-59 +1-69	Red
710-1125	800	CS 7-69	Near infrared
730-4500	1750	CS 7-57	Short-wave infrared

A black aluminium box, used for filtering the light, is shown in Fig. I and Plate 1. It consisted of two parts, the top and the body of the box. The body was rectangular, measuring 25cm long x 10cm wide x 10cm deep. At the bottom end was a 5.6cm square opening in which the appropriate filters were inserted. Inside the box, corresponding to the opening, was a 2.5cm high rectangular aluminium sleeve which held the filters in position. The top of the box included a light proof air vent to allow free air circulation. Dull black paint, resistant to heat was used to avoid reflection of light.

The light energy was measured in ergs/cm^2/sec. (converted to milli-watt/cm^2) using Yellow Spring Instrument (YSI) Kettering Model 65 Radiometer with the probe at the top of the rearing medium. 60-watt incandescent lamps were used as the source of energy and the energy level of radiation incident on top of the medium was about 28.0 milli-watt/cm^2 (mw/cm^2). The energy level was controlled by an SCR Voltage Controller Model 2600, Cole Parmer, Chicago. Unfiltered light was applied for 12 hours using a 25-watt incandescent lamp with an incident energy level of 35mw/cm^2 as the energy source. At the end of this 12 hour period filtered light only was applied for the final four hours of the daily photophase of 16 hours.

The experiments were carried out in Sherer Model



Black aluminium box used to filter visible light.

FIG. I

Cel 255-6 and Model R16B growth chambers (Plate 2, a & b). The adult flies were subjected to light energy of 648mw/ cm^2 and the light source was four 25-watt incandescent lamps and four 40-watt fluorescent lamps mounted at the top inside of each growth chamber. The photoperiodic control was effected through the use of a timer connected to the source of light energy. The performance of the temperature and the Relative Humidity controlling devices was verified by a recording thermohygrograph. The temperature of the soil, 10cm deep, and in the middle of the turnip were recorded using YSI semi-solid insertion thermistor probes.

B. Culture Methods

Flies used in this study (Plate 3.) were from a diapausing population obtained from Charlottetown, Prince Edward Island, which had been in diapause since July 1966 (originally reared in the field) and November 1967 (originally laboratory reared). Additional flies from a laboratory maintained culture from London, Ontario, were maintained to develop rearing methods. The use of a defined population was necessary because of the demonstration of significant differences in the photoperiodic responses among populations of different origin.

The adult flies were kept in cages with a wooden framework of 22.5cm^3, a 6mm plywood base, with the other sides covered by 36 mesh (0.96 type) polyvynyl gauze. A 20.0cm x 12.5cm sliding clear plastic plate was used at one side to provide an access into the cage (Plate 4).

The culture method used was a modified form of that described by Read (1960; 1965a). A 10ml milk bottle was filled with sugar solution inverted over a 5.5cm diameter petri-dish lined with white absorbent cotton wool. An artificial diet was pasted on the top of the screen and about 300 adult flies were kept in a cage at a day temperature of 22°C (16 hours) and a night temperature of 18.9°C (8 hours), with a Relative Humidity of 60 $\pm$ 5%. The diet was made up as follows:

Whole Wheat Flour	8 parts by volume
Granulated Sugar	8 parts by volume
Powdered Brewer's Yeast	4 parts by volume
Granulated Honey	3 parts by volume
Water	1 part by volume

The whole wheat flour, the sugar, and the yeast were thoroughly mixed together; so were the honey and the water. The two mixtures were then combined together to form an even paste.

The oviposition medium or the egg-cup for collecting the eggs was made up of a 7cm diameter x 8cm long white plastic cup, filled with washed sandy soil in which a cone-shaped piece of turnip was partially inserted. The egg-cups were placed in the colony cages when the flies were 6 days old. 48 hours later, the egg-cups were removed. At egg collection, a bright source of light was held against the screen and the plastic plate at the opposite side was gently slid open to get the cup out. All dead adult flies were immediately removed. The eggs were washed from the turnip into a 600ml beaker and the top soil was scraped off into the beaker. The beaker was filled with water, gently swirled to allow the eggs to float and then decanted on to a piece of dark cloth resting on a screen gauze. This was repeated once or twice until soil-free eggs were obtained.

The eggs were counted into groups of 100 using a

camel hair brush and 600 eggs were spread over the bottom surface of a whole turnip (about 10cm diameter). This was placed in a 22.5cm diameter x 20cm deep clay flower pot, half filled with moist sandy-loam soil. The pot was filled up to the top but a small top portion of the turnip was left uncovered to promote growth and avoid decay. (Plate 5). The soil mixture used was three parts of sterilized black soil to one part of sand. This mixture ensured good aeration and drainage.

The pot was put under the same conditions as the adults for 48 hours and then introduced under the appropriate source of light for the treatment to be applied. Thus the treatment given started from the first instars. 250ml of water was added to each pot for the first seven days.

The larvae, pre-pupae and the early pupae were exposed to 12 hours of unfiltered light with 4 hours extension of filtered light and then 8 hours of darkness (L12:F4:D8) at a constant temperature of 21.1°C and a Relative Humidity of 60± 5%. The pupae were washed from the soil 25 days after eclosion from the egg, counted, and put into emergence cups. The emergence cups were made from 11cm diameter x 12cm deep paper cups, half filled with moist soil (Plate 6). All dead pupae and larvae were discarded.

The pupae were kept under similar conditions to the larvae (21.1°C; 60±5% RH) but with a photophase of 16 hours for 25 days and adult emergence was checked after every 24 hours. After the twenty-fifth day, those pupae which did not emerge were classified as "diapausing pupae". Dead pupae were identified by examining all the pupae under a stereomicroscope. In contrast to the healthy pupae, dead pupae were either flattened, soft and black, or dried and shiny in appearance. All pupae collected from one pot of 600 eggs were taken as one replicate and any replicate with less than 100 pupae was discarded, unless where specified.

C. Analysis of Results

Different numbers of pupae were obtained in each replicate, ranging from 100-520, thus the results are expressed in percentages for comparison.

The percentage of diapause incidence in each replicate was calculated from the formula given by Missonier (1963):

$$\% \text{ Diapause} = \frac{\text{Pupae not developed} \times 100}{\text{Pupae not dev.} + \text{Dead pupae} + \text{Emerged pupae}}$$

This makes a correction for the dead pupae.

The mean diapause incidence is the average of the percentage diapause for each treatment.

Index of Effectiveness is used to express the effect of a treatment in allowing diapause as compared with the diapause induction control treatment included in each series of experiments. The control groups were placed in 12-hour and 16-hour photophases (unfiltered light) and the diapause incidence in the 12-hour photophase was taken as the basic unit of 1.00; a regime allowing a greater diapause incidence would have an index less than one and the insect would not be sensitive to that wavelength or photophase. An index greater than 1.00 indicates sensitivity to that filtered light or photophase.

As all the series could not be carried out simultaneously,

and the diapause tendency of the laboratory cultures varied with time, it was necessary to continually check the diapause incidence in the unfiltered light so as to allow comparison of the effect of different filtered light regimes.

Analyses of variance were performed as for a completely random design and data were transformed using angular transformation to normalize them. When significant differences ($P=1.0$) were indicated between treatment means, the means were separated by Duncan's new multiple range test ($P=1.0$) (Duncan; 1955). The interpretation of the results was based on the transformed values.

IV. RESULTS

A. Section 1

1. Photoperiodic effect on different stages of H. brassicae.

As a prerequisite to the spectral studies, preliminary studies were made to find out the effect of photoperiod on the egg, larva, pupa and the adult fly of the cabbage maggot. In these preliminary experiments, the number of pupae used per replicate in some instances, was less than 100 as indicated previously in the method.

Newly laid eggs were subjected to a photophase of 12 hours at a temperature of 21.1°C for 5 days. Another group of eggs were kept at 16-hour photophase for a similar duration. The two groups of eggs were then transferred to a photophase of 16 hours for the larval development. Pupae so obtained were kept at 21.1°C for 30 days for adult emergence. Eggs held at 12-hour photoperiod gave 63.33% mean diapause incidence while those held at 16-hour photophase had 70.00% diapause. No significant difference was found between the two treatments. Thus the photoperiod experienced by the eggs had no effect on diapause induction.

Larvae were reared under 16-hour and 12-hour photophases at a constant temperature of 21.1°C. The pupae so

obtained from each photoperiod regime were divided into two groups, one group kept at 12-hour photophase and the other at 16-hour photophase. Recordings of adult emergence were made daily for 30 continuous days. The results are shown in Table 1.

Table 1 Percentage diapause in pupae of H. brassicae when the larvae and the pupae were exposed to different photoperiod regimes at 21.1°C.

Replicate	Larvae reared at 16-hour		Larvae reared at 12-hour	
	Pupae/16hr.	Pupae/12hr.	Pupae/16hr.	Pupae/12hr.
1	23.33	26.67	76.00	80.00
2	24.00	20.00	86.00	88.35
3	12.67	29.41	83.31	98.31

Non-diapausing pupae emerged into adults six - 20 days after pupation with most of them emerging between the tenth and the fifteenth days. (Appendix Table 1a and b and Fig. 2).

No significant difference was found between pupae held at 16-hour and 12-hour photophases when the larvae were reared at the same photophase that is, 12 or 16 hours. There was, however, a significant difference between the pupae whose larvae were reared under dissimilar photophases, that is, 12 and 16 hours. The pupae are not sensitive to photoperiod but the larvae are very sensitive to light.

Adult flies were kept at 21.1°C under 12-hour and 16-hour photophases and their eggs were reared at 16-hour photophase. The percentage of emergence found 25 days after was 77.48 for the 12-

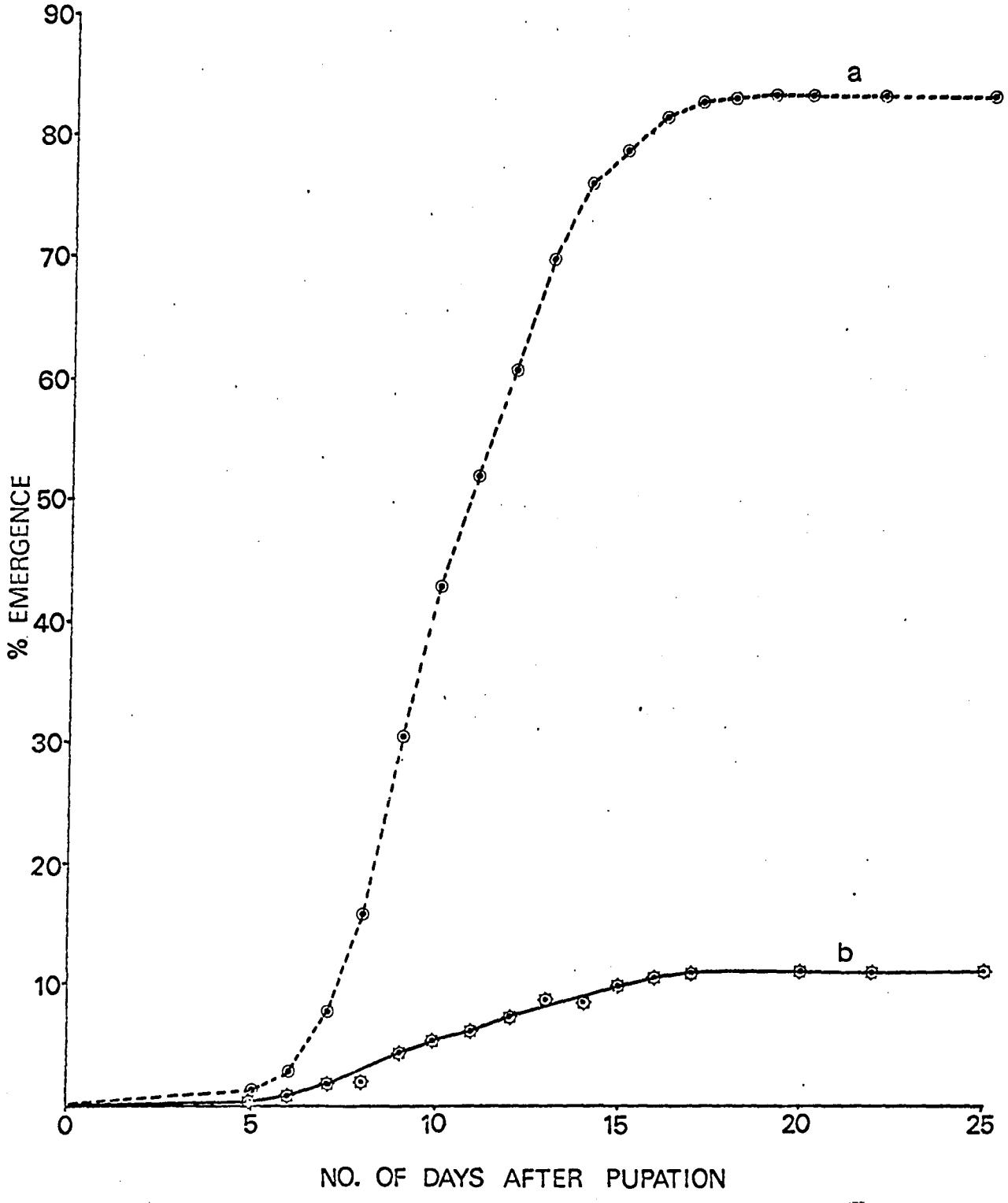


FIG. 2 Percentage of pupae of H. brassicae that emerged when the larvae were reared at a temperature of 21.1°C, 16 hours (a) or 12 hours photophase (b) and the pupae were held at 16 hours.

hour adults and 72.05 for those kept at a photophase of 16 hours.

When the adults, however, were kept under similar light intensity, the same temperature and the same photophase as the larvae, the percentages of emergence at a 12-hour and a 16-hour photophase averaged 62.67 and 61.82 respectively. On the other hand, when the adults were held at 22.2°C, and 18-hour photophase, a higher light intensity (energy level of 648mw/cm^2) and the larvae at 20°C and light intensity of energy level of 35mw/cm^2), there was 85.55% emergence at 16-hour photophase and 5.71% at 12-hour photophase.

This shows that although photoperiod may not have direct effect on the adults in terms of diapause induction, the conditions which the adults experience have effect on their progeny's diapause tendency.

2. Factors influencing photoperiodic induction of diapause

Further preliminary experiements were conducted to find the effect of the age of the parents, crowding of the larvae and the rearing temperature on photoperiodic determination of diapause in the cabbage maggot.

a. Age of the Parents

Eggs from 15 - 18 day old adult flies and 6 day old adults were subjected to a photophase of 16 hours and a constant temperature

of 21.1°C; the pupae were held under similar conditions. The percentage of emergence of the F1 older generation of flies was 72.50 while for the first generation of young adults it was 79.38%. The results indicate that the age of the parents has no influence on their progeny's diapause tendency.

b. Crowding

Similar sizes of turnip (about 10cm in diameter) were infested with different numbers of cabbage maggot eggs. The eggs and the larvae were reared at a temperature of 21.1°C under 16-hour photophase. The pupae obtained were kept at similar temperature and photoperiod conditions as the larvae and adult emergence was recorded after every 72 hours for 25 days. Results are shown in Table 2.

Table 2. The effect of crowding of the larvae of *H. brassicae* on the size of pupae and the incidence of diapause when all stages were maintained at 21.1°C.

No. of eggs/turnip	No. of pupae/turnip	Percent pupation	Wt. of a pupa (mg)	Percentage emergence
300	245	81.67	14.8	72.92 (186) +
600	425	70.83	13.8	84.00 (357)
600	429	71.50	15.1	71.32 (306)
600	397	66.17	14.8	65.99 (262)
1150	402	34.96	15.0	70.15 (281)
1200	720	60.00	9.8	73.61 (530)
1500	905	60.33	8.5	79.60 (718)

+ The numbers in brackets indicate the number of pupae that emerged.

No correlation was found between the number of eggs per turnip and the percentage of emergence or the incidence of diapause. In this particular experiment, it was observed that the percentage of pupation and the weight of a pupa reduced as the number of eggs was increased after 600. In subsequent experiments, however, as low as 70 pupae were obtained from a group of 600 eggs. Crowding did not have any effect on the incidence of diapause but reduced the size of the pupae.

c. Temperature

Groups of larvae were reared at 15°, 18°, 20°, and 25°C under 16-hour and 12-hour photophases to find out the temperature at which photoperiod has no effect on diapause incidence. The resultant pupae were divided into two groups. One group was kept at 20°C and the other group at the rearing temperature of the larvae. The results are shown in Appendix Table 2a and Fig. 3.

At a rearing temperature of 15°C, there is a high percentage of undeveloped pupae under both 12-hour and 16-hour photophases at holding temperatures of 15° and 20°C. Whereas at a rearing temperature of 25°C high percentages of undeveloped pupae were obtained only at a holding temperature of 25°C. At 20°C holding temperature and 25°C rearing temperature there were 8.73% and 16.93% undeveloped pupae at photophases of 12 and 16 hours respectively.

A rearing temperature of 18°C had a similar effect as at 20°C. The percentages of undeveloped pupae at 18°C were 78.23 and 79.36 at holding temperatures of 18° and 20°C respectively under 12-hour photophase, as compared with 81.42% at 20°C, rearing and holding temperature. Under 16-hour photophase, 15.17% and 24.86% undeveloped pupae were obtained at holding temperatures of 18°C and 20°C respectively at rearing temperature of 18°C whereas 14.69% was obtained at 20°C.

At a rearing temperature of 23°C there was 41.42% of undeveloped pupae at a holding temperature of 23°C as compared with 21.30% at a holding temperature of 20°C, all at a 16-hour photophase. Under a 12-hour photophase, there were 69.40% and 65.64% undeveloped pupae at 23° and 20°C holding temperatures respectively.

From the results, it seems that photoperiodic reaction in the cabbage maggot is manifest only between temperatures of 18° and 23°C. Temperatures above 23°C and below 15°C tend to nullify the photoperiodic response.

When the larvae were reared at 25°C and 16-hour photophase and the pupae were held at 20°C, 16.93% of the pupae did not develop. On the other hand, when pupae from larvae reared at 25°C were held at the same temperature (25°C) 79.85% did not develop. This indicates that the higher percentage of undeveloped pupae obtained at 25°C was partly due to the high temperature, which might have caused an arrest in development, that is, aestivation.

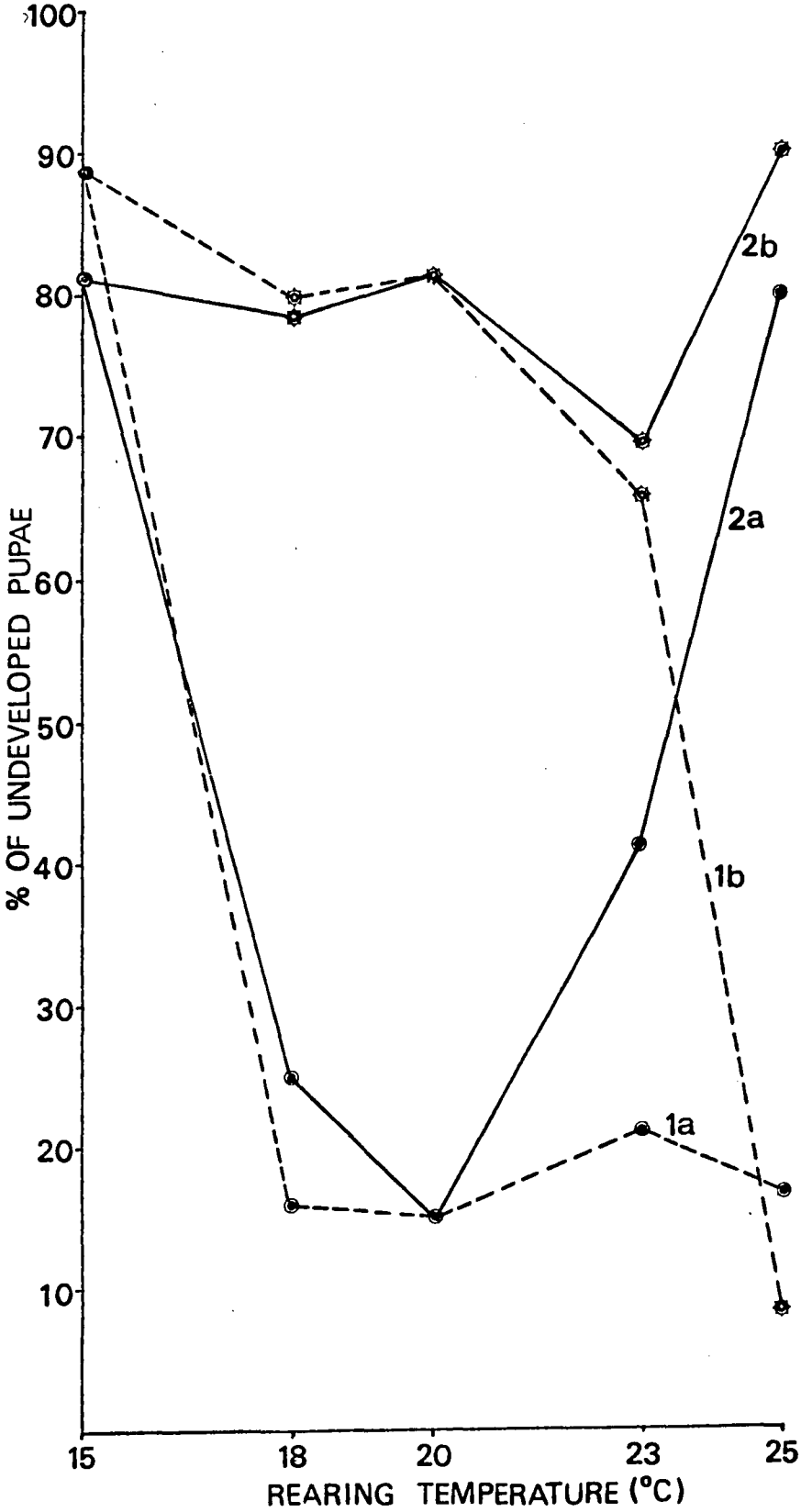


FIG. 3 - Percentage of undeveloped pupae of H. brassicae when larvae are reared at different temperature and pupae held at
(1) 20°C (a) 16-hour photophase (b) 12-hour photophase
(2) rearing temperatures of larvae (a) 16-hour photophase
(b) 12-hour photophase

B. Section II

Photoperiodic response of H. brassicae

A study of the influence of different lengths of light periods on the induction of diapause in the cabbage maggot, H. brassicae was undertaken as a prerequisite to the spectral sensitivity studies. The larvae were reared at a constant temperature of 21.1°C under 0, 4, 8, 10, 12, 16, 20, and 24 hours of daylight. The incidence of diapause at these light regimes is shown in Appendix Tables 3a and b and Fig. 4.

Photoperiodic induction of diapause was clearly demonstrated when the larvae were reared under different daylengths. A 16-hour photophase resulted in 15.61% diapause whereas 12-hour photophase resulted in 84.64% diapause. This significant difference between the two treatments indicated that despite the presence of soil, an opaque medium, the sensitivity of the larvae to photoperiod was not curtailed.

Total darkness, 20-hour, and 24-hour photophases gave 17.25%, 22.75%, and 23.50% diapausing pupae respectively which were not significantly different from 16-hour photophase treatment. As the daylength increased from total darkness, there were significant increases in the proportion of diapausing individuals until the maximum percentage was obtained at a 12-hour photophase.

A 4-hour photophase resulted in an average of 55.34% diapausing pupae. The diapause incidence at this photophase was significantly different from 8, 10, and 16 hours of light per day. However, there was no significant difference in diapause incidence between the 8-hour and the 10-hour treatments, both of which gave 77.48% and 83.21% diapause respectively. (Table 4)

Photophases of 16 hours and above inhibited diapause induction in the cabbage maggot and the larvae responded to total darkness just as they did to long daylength. The photoperiodic response of the larvae of the cabbage maggot was more pronounced between 8 and 12-hour photophases when more than 75% of the population entered diapause.

The critical daylength inducing diapause in 50.0% of the individuals was about 14 hours of daylight at 21.1°C. There was a sharp decrease in the percentage of diapausing pupae between 12-hour and 16-hour photophases. This showed a narrow critical daylength for the cabbage maggot, H. brassicae.

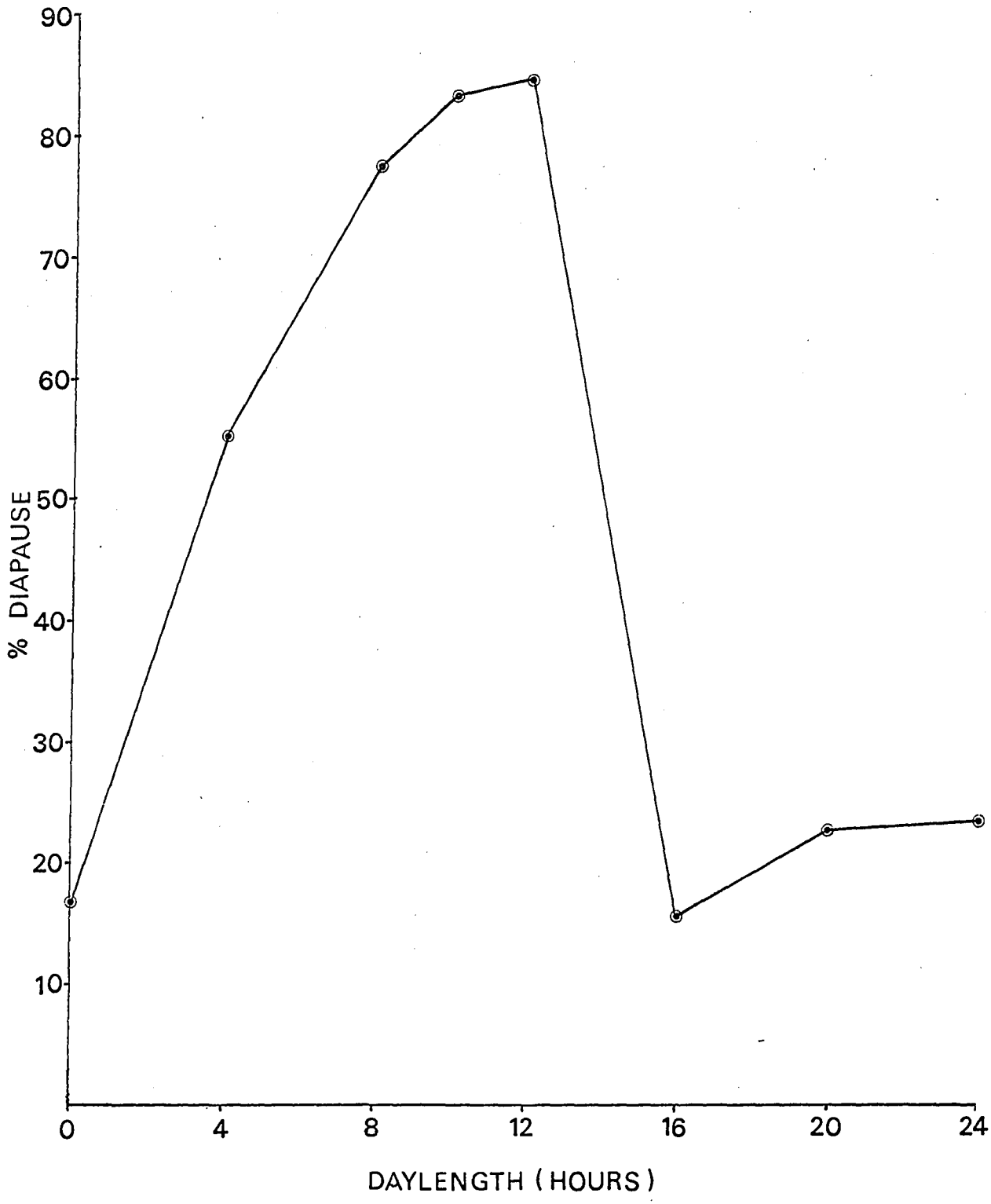


FIG. 4 - The influence of daylength on the induction of diapause in H. brassicae at 21.1 °C.

C. Section III

1. Spectral Response

The response of the cabbage maggot to different wavelengths of light was evaluated by rearing the larvae under 12 hours of incandescent light and a four-hour extended filtered light of various wavelengths. Comparison was then made between the response to a defined spectral range and to that of 16-hour or 12-hour photophases. Suppression of diapause comparable to that caused by 16-hour photophase implied sensitivity and induction of diapause comparable to that caused by 12-hour photophase implied insensitivity to that spectral range.

Appendix Table 4 a and b, and Fig. 5 show that diapause in the cabbage maggot, H. brassicae, was inhibited when the larvae were subjected to violet (395mμ), blue (460mμ), blue-green (495mμ), and short-wave infrared (1750mμ) while exposure to red (675mμ) and visible white light (400-750mμ) did not prevent diapause. There was a partial effect in the ultraviolet (330mμ), green (525mμ), yellow (570mμ), orange (600mμ), and near infrared (800mμ).

The results showed that the range between 395mμ and 495mμ was the most effective region of the spectrum with regard to prevention of diapause. No significant difference was found between this range and 16-hour photophase treatment. However, diapause incidence increased gradually as the wavelengths increased and

minimum prevention of diapause was obtained at the red (630-750mμ) region. There was no significant difference between red (675mμ), visible white light, (400-750mμ), and 12-hour photophase and these treatments had significantly more pupae entering diapause than any other treatment.

Above this wavelength (750mμ), the sensitivity increased gradually into the infrared region where a response comparable to that of 16-hour photophase was obtained at the shortwave infrared (1750mμ) region. Statistically, shortwave infrared and 16-hour photophase were not significantly different. A similar pattern of response was observed at the short wavelength region of the spectrum. Sensitivity decreased from the violet (395mμ) into the ultraviolet (330mμ) region. Ultraviolet (330mμ), green (525mμ), yellow (570mμ), orange (600mμ), and near infrared (800mμ) were not significantly different.

Radiations in the violet, blue, blue-green, and the shortwave infrared regions of the spectrum prevented diapause induction in the cabbage maggot. Wavelengths above 500mμ and less than 400mμ that is, the green, yellow, orange, near infrared, and ultraviolet were partially active while red was inactive.

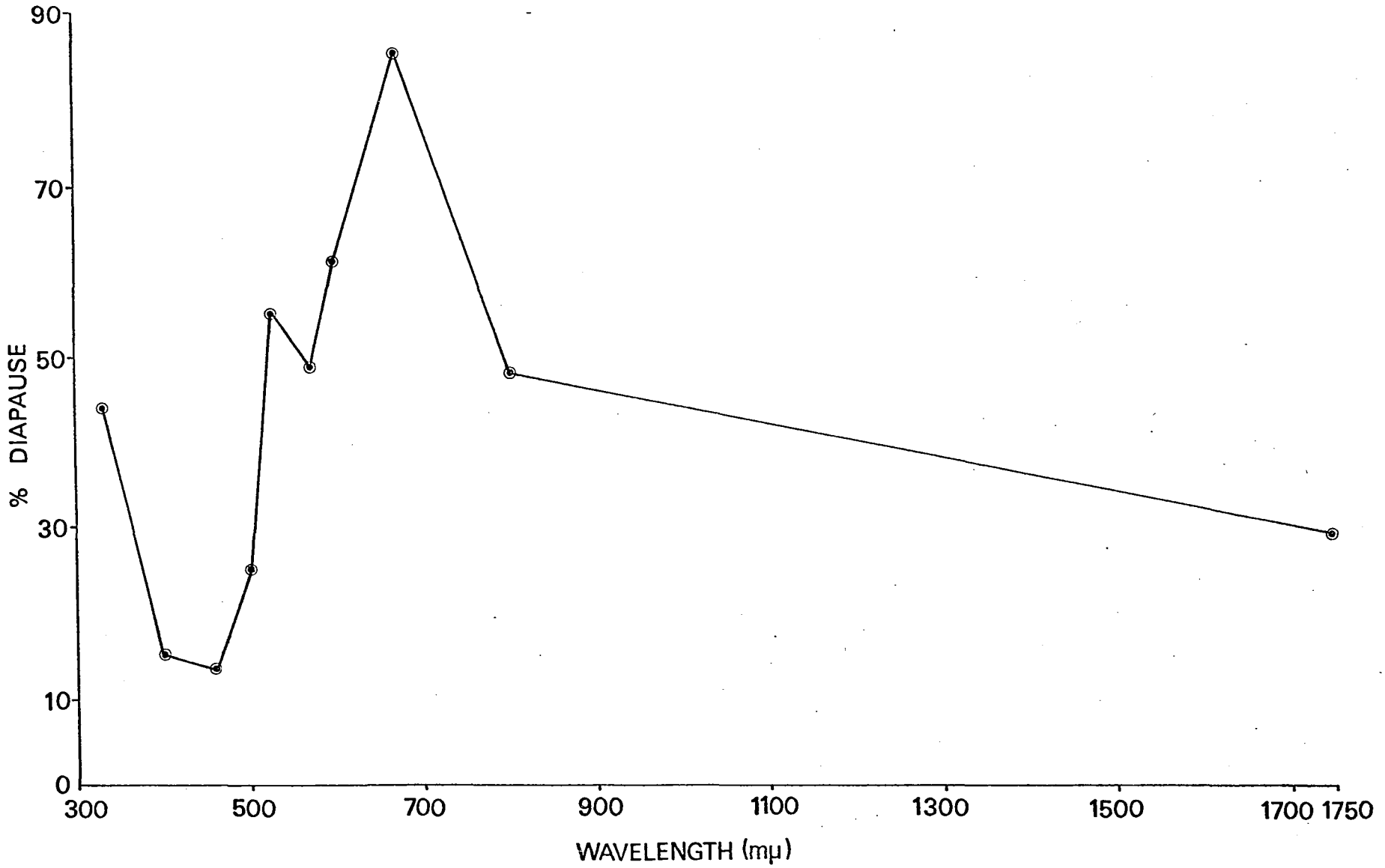


FIG. 5 - The effect of different wavelengths of light in the induction of diapause in H. brassicae at 21.1°C.

2. The effect of irradiation on soil temperature

Thermoperiod has been found to be important in the induction of diapause in the cabbage maggot (Missonier, 1963). This experiment was to find out any thermoperiod effect caused by the different wavelengths of the spectrum used in the spectral response studies.

The temperatures on top of the soil, in the middle of the turnip, and 10cm deep in the soil, were taken for the various spectral ranges used previously. Recording was done for 15 minutes after the appropriate filtered light had been on for four hours.

The results have been given in Table 3. There was no significant increase in temperature at any of the spectral ranges tested. However, there was a 0.3°C increase inside the turnip when irridiated with the green region of the spectrum (525mμ) and a further 0.2°C at the short-wave infrared region (above 750mμ). At a depth of 10cm in the soil, the temperature was almost constant until the yellow region (570mμ) where an increase of 0.2°C was obtained. The soil surface temperature was constant throughout except an increase of 0.5°C caused by the infra-red radiation, (above 750mμ). Short-wave infrared and near infrared gave similar results and so were considered together; so were blue and blue-green.

Table 3. The effect of different wavelengths on the temperature of the micro-environment of H. brassicae.

Wavelength (peak in mμ)	TEMPERATURE (°C) Surface	Mid-turnip	Soil-10cm deep
Light off	19.5	18.5	19.0
Light on	19.5	18.5	19.0
330	19.5	18.5	19.0
395	19.5	18.5	19.0
460	19.5	18.5	19.0
525	19.5	18.8	19.0
570	19.5	18.8	19.2
600	19.5	18.8	19.2
675	19.5	18.8	19.2
Above 750	20.0	19.0	19.2

It was observed that pupation occurred mainly at a depth of 10cm in the soil and the larvae fed only on the bottom part of the turnip provided as food. The larvae remained inside the turnip throughout their entire larval period and came out at the prepupal stage to pupate in the dry soil.

3. Threshold Intensity of Short-Wave Infrared Radiation

It was found in Section III (a) that the short-wave infrared radiations averted diapause in the cabbage maggot when an energy level of 28mw/ cm^2 was given. This experiment was done to find out the level of energy in the short-wave infrared region required to induce diapause in 50% of a given population of the cabbage maggot, that is, to find the threshold of sensitivity.

Groups of larvae were reared at a constant temperature of 21.1°C under 16-hour photophase of which the last 4 hours were of radiations from short-wave infrared of 0.625mw/ cm^2, 1.25mw/ cm^2, 6.25mw/ cm^2, 12.5mw/ cm^2, and a control of 28mw/ cm^2. energy levels. Analysis of the results (Appendix Table 5) shows that there is no significant difference between 0.625mw/ cm^2 and 1.25mw/ cm^2; and between 6.25mw/ cm^2, 12.5mw/ cm^2, and 28mw/ cm^2. However, there is a significant difference between the two groups.

Although the results are not complete, (Fig. 6) there is an indication that there is a threshold of sensitivity above which no increase has any effect on the determination of diapause.

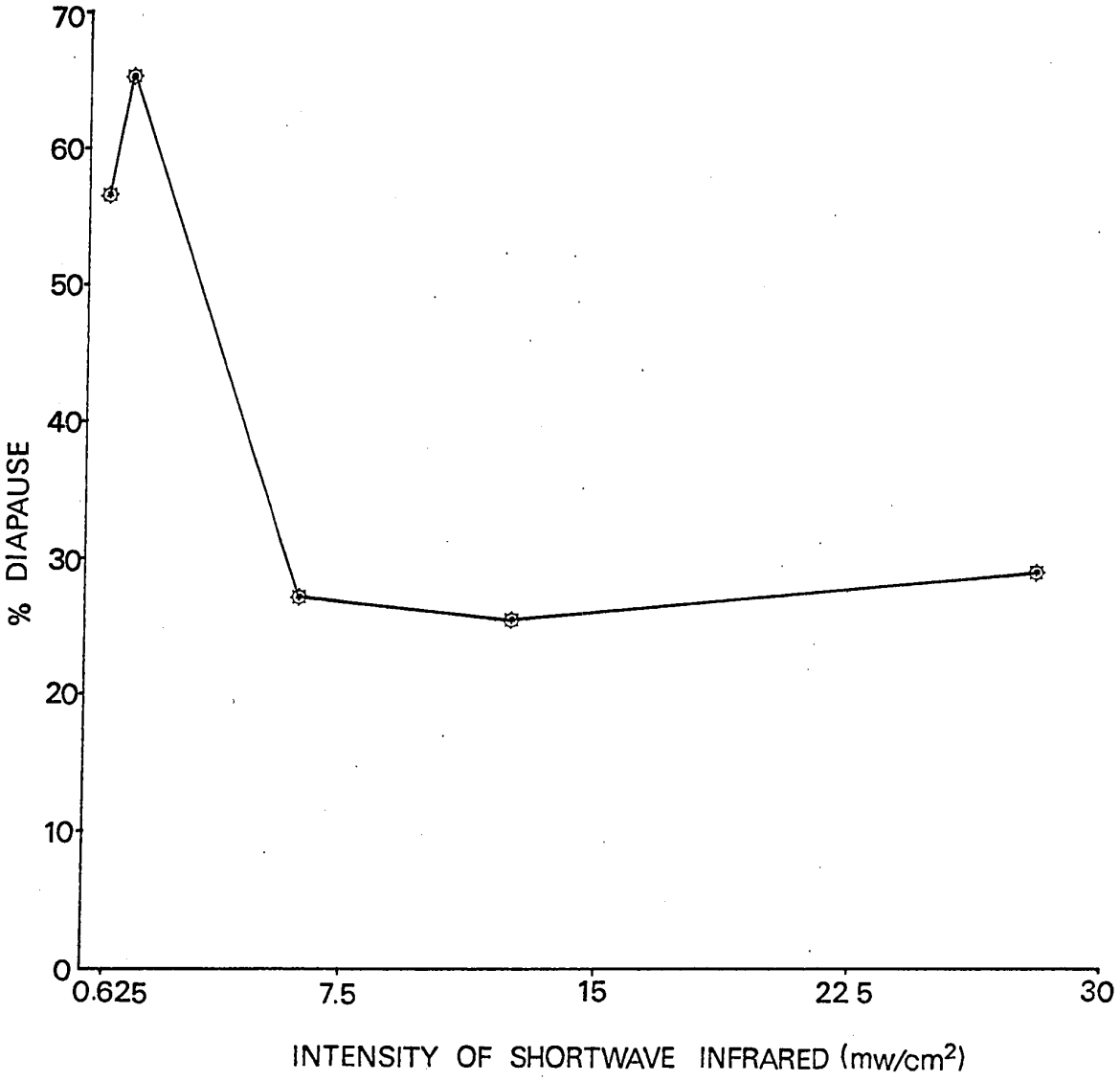


FIG. 6

The effect of intensity of shortwave infrared radiation on the incidence of diapause in H. brassicae at 21.1°C.

V. DISCUSSION

Photoperiods of 8 - 12 hours of daily light induced diapause in the cabbage maggot and the incidence of diapause was reduced as the photophase was increased or decreased. Diapause was averted in continuous illumination or continuous darkness. These results are in general agreement with previous observations made on the cabbage maggot (Hughes, 1960; Zabirov, 1961; Missonier, 1963; McLeod, 1965; McLeod and Driscoll, 1967).

Hughes found that diapause in the cabbage maggot was induced by the changes in the daylength and that the proportion of diapausing pupae was progressively reduced as the number of hours per day increased. Zabirov (1961) showed that at 20°C, about 40% diapause occurred at 6-hour photophase, 96.2% at 12-hour, and 0.0% at 18-hour photophases, and 15% and 25% at 20-hour and 24-hour photophases respectively.

Missonier (1963) demonstrated that photoperiod acted over a narrow range of 8 to 12 hours of light daily, inducing 96% and 100% respectively at 20°C. At the same temperature, McLeod (1965) and McLeod and Driscoll (1967) showed that photoperiods between eight and 12 hours of light induced diapause in the cabbage maggot while 16-hour photophase averted diapause.

The critical daylength was estimated to be 14 hours whereas

Zabirov (1961) found it to be 15 hours and 30 minutes in Leningrad. The difference between the two critical daylengths may be attributed to the difference in the geographical distribution of the strains involved (Stepanova, 1962).

If the photoperiodic reaction were independent of temperature, arthropods from temperate regions which respond to long days would be induced to diapause at the September equinox. However, seasonal cycles of daylength are different at different latitudes (Danilveskii, 1965; Beck, 1968). The seasonal differences between areas of different latitudes suggest that insect populations of high latitudes must adapt to quite different conditions from those of low latitudes. It would not be surprising that northern populations of a widely distributed insect species might differ from southern populations in regard to the ecological adaptations related to daylength. Similarly, in addition to the genetic mechanisms that underly diapause (Lees, 1955; Harvey, 1957; 1961; Apple and Beck, 1961; Danilveskii, 1965; Barry and Adkisson, 1966; Beck, 1968), intra-specific differences of a comparable nature might also occur in species with a wide geographical range (Danilveskii, 1965; Beck, 1968).

There is some evidence that geographical strains of the cabbage maggot, H. brassicae, do differ in this respect (Stepanova, 1962). The present study showed that the critical daylength for

diapause induction of the Prince Edward Island (P. E. I., 46.2°N) strains was 14 hours. According to Zabirov (1961), the critical daylength in a strain from Leningrad (60°N) was 15 hours and 30 minutes. If the temperature effect is ignored for the mean time, then it would be expected that the P. E. I. strains and the Leningrad strains should enter diapause at different times of the year.

Zabirov found that up to 20-25% of the first generation pupae entered diapause in the field as early as July and about 100% diapause occurred in the population at the beginning of September. In P. E. I., Read (1956, 1958) found that egg production peak for the summer generation of the cabbage maggot was between mid-August and mid-September. Thus the resultant pupae would enter into diapause in October, one month later than the Leningrad strains. A higher threshold for photoperiodic reaction, therefore, leads to an earlier date for the onset of diapause in the cabbage maggot, H. brassicae, in northern zones despite the longer days that the insects might be experiencing.

The stage sensitive to photoperiod is a further provision for ensuring the entry into diapause at the appropriate season. Also, the time interval separating the perception of the photoperiodic stimulus and the onset of diapause appears to be a decisive factor. The cabbage maggot shows a pupal diapause (responsive stage) which is induced by a relatively short daylength experienced during the

larval stage - sensitive stage (Hughes, 1960; Zabirov, 1961; Stepanova, 1962; Missonier, 1963; Read, 1968a; and Zohren, 1968).

The biology of the cabbage maggot in the field in P. E. I. shows that overwintering pupae emerge in mid-June in sandy soil areas (Read, 1958). The larvae mature in late July and early August, thus the larval development occurs during the long summer daylight period. The summer generation starts laying eggs between mid-August through to mid-September when the daily photophase has begun to diminish. The second generation larvae are thus subjected to longer scotophases. The pupae of this generation are committed to diapause in October and these pupae remain in diapause until the next spring or early summer when they emerge again.

In the southern prairies and southern Ontario where the springs are earlier than P. E. I., adult emergence from overwintering pupae in the field begins in early May with a peak in late May and early June (Foott, 1954; Swailes, 1963; Allen, 1965). The summer generation emerge in August and the peak of egg production is between mid-August and mid-September, the resultant larvae exposed to short daylength of autumn enter diapause in October in preparation for the oncoming winter. Similar conditions occur in

British Columbia but due to mild winters and earlier springs, the overwintering pupae emerge in April and the autumn pupae enter diapause in late October and early November (Forbes, 1962). The peak of adult flight period corresponds with the emergence of cruciferous seedlings in the field, thus the larvae produced will have enough food (Read, 1956; 1958; Forbes, 1962; Swailes, 1963).

The photoperiodic adaptations thus result in synchronizing the life cycle of the cabbage maggot with the seasonal cycles of the climate and the host plants.

Under natural conditions, photophases below 8 hours and above 18 hours including civil twilight, do not occur with the strains under study; the longest day length in P. E. I. being 17 hrs., 41 minutes in June; such photoperiodic conditions are found at high latitudes (Beck, 1968). Thus reaction expressed to daylengths below 8 hours or above 18 hours are aperiodic and have no ecological significance and consequently special adaptations may not be developed.

The conditions which the parents experience have been found in this test and by Read (1968b) to have an effect on their progeny's diapause tendency. In their natural environment, the adults who produce diapausing pupae are found in August and early September when the daylight and the temperature, and probably

the light intensity, are higher than those found in late September and in October when the larvae are abundant.

The adults, therefore, are subjected to a different environmental conditions from their larvae. When the adults and the larvae are reared at the same temperature, light intensity, and photoperiod, they are subjected to an environment which is aperiodic and tends to put them away from their rhythm of response to the environment. This leads to an erratic response as indicated.

Other workers have demonstrated that temperature has a diapause inducing effect on the cabbage maggot (Zabirov, 1961; Missonier, 1963; Read, 1965b). A fall or a rise in temperature has a marked effect on the critical daylength (Zabirov, 1961), and may even suppress or modify the effect of photoperiod during the developmental stages (Missonier, 1963; Read, 1965b).

Short daylengths (8 to 12 hours) caused a high incidence of diapause only at a temperature range of 18° to 23°C. Diapause was averted when the larvae were reared under continuous light or continuous darkness or at temperatures above 23°C; however, low rearing temperatures of 15°C or less resulted in a high incidence of diapause. The high rearing temperatures may tend to decrease the incidence of diapause by shortening the critical daylength. Similarly, low rearing temperatures tend to shift the critical daylength towards the long day end.

The incidence of diapause has been found to be high when the cool phase of the thermoperiod (fluctuation of the environmental temperature through a daily cycle) occurs during the scotophase but very low when the warm phase coincides with the scotophase (Beck, 1964; Ring, 1967a; 1967b).

Under its natural environmental conditions, the cabbage maggot is exposed to a temperature fluctuating rhythm in which the night temperatures are lower than the day temperatures.

It is clear that temperature plays a part in the induction of diapause in the cabbage maggot, H. brassicae. The temperature influences the photoperiodic response in that it determines the critical daylength. Diapause is induced at all photoperiods at relatively low temperatures; conversely, there is no photoperiodic induction of diapause under relatively high temperature conditions. These effects show that temperature extremes lead to a shift of the critical daylength to a point lying outside the range at which photoperiod the insects were originally exposed.

Thermoperiod, however, modifies the photoperiodic response. When the higher temperatures coincide with the scotophase this leads to avert diapause. When they coincide with the photophase, they induce a high incidence of diapause.

Apart from the sensitivity to the short-wave infrared, the results of the response to the different regions of the spectrum are in general agreement with observations made on other arthropods.

The results obtained showed that radiation in the violet (395mμ), blue(460mμ), blue-green (495mμ), and short-wave infrared (1750mμ) regions of the spectrum averted diapause in the cabbage maggot. There was partial response in the ultraviolet (330mμ), green (525mμ), yellow (570mμ), orange (600mμ), and near infrared (800mμ) regions while the red (675mμ) and visible white light (400-750mμ) did not prevent diapause.

Kogure (1933) found that violet-blue-green (350-510mμ) exerted the greatest photoperiodic effect in the silkworm while Dickson (1949) showed that in the Oriental fruit moth, the most sensitive region was the blue-yellow (400-580mμ). Williams et al (1965) found violet-blue-green (398-508mμ) to terminate diapause in the oak silkworm and Lees (1953) observed that the range from the near ultraviolet - blue-green (365-500mμ) had a photoperiodic effect inhibiting diapause incidence in the aphid, Metatetranychus ulmi. de Wilde and Bonga (1958) found that the Colorado beetle was sensitive to filtered light from 423-675mμ and Harris et al (1967) showed that the region most effective for suppressing diapause in the boll weevil was between 400 and 665mμ.

It seems that in all these observations, at least, the range from 400-500mμ is involved in the photoperiodic response of the arthropods concerned. It is apparent that so far as the present observations are concerned, the violet-blue-green region is

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It seems that in all these observations, at least, the range from 400-500mμ is involved in the photoperiodic response of the arthropods concerned. It is apparent that so far as the present observations are concerned, the violet-blue-green region is

photoperiodically active.

The short-wave infrared was found to avert diapause induction in the cabbage maggot while none of the workers mentioned already has found this reaction. In this study, infrared radiation has been found to increase the soil temperature as much as 0.5°C over a short period of time. Most of the radiant energy from the sun is in the infrared region of the spectrum (Baumgartner, 1953; Geiger, 1965; Sellers; 1967) and this can penetrate deep into natural substances (Callahan, 1965b) warming up the soil (Baumgartner, 1953). The infrared radiation effect may thus be due to its heating effect on the micro-habitat of the cabbage maggot, that is, the response is a 'thermal response'. These radiations may be detected by means of touch senses well developed in soil insects (Kuhnelt, 1961) or by the sense pits found on the whole body which may detect differences in the temperature (Grant, 1947; Dethier, 1963; Evans, 1964).

Certain parts of the spectrum (400-500mμ) have been found to act directly on the brain of some arthropods (Lees, 1963; Williams and Adkisson, 1964a; Williams et al, 1965). It is likely that the thermal effect of infrared radiation may act on the brain directly to indicate to the larvae a change in the daylength as the soil warms at day time and cools at night.

The response to violet, blue and blue-green parts of the

spectrum indicates that the cabbage maggot has a similar response to light as found in some non-soil inhabiting insects (Lees, 1963; Williams and Adkisson, 1964a; Williams et al, 1965). The response may be explained by assuming a very low intensity threshold as found in other soil inhabiting arthropods (Falconer, 1944; Madge, 1964a; 1964b; Danilveskii, 1965; Beck, 1968).

In all the arthropods examined so far, the response to daylight has been proven to be independent of the light intensity, provided a certain threshold is exceeded (de Wilde and Bonga, 1958; Lees, 1959; de Wilde, 1962; Danilveskii, 1965; Beck, 1968). It is probable that the cabbage maggot may respond to the entire spectrum if only the intensity threshold for each range of wavelength is known. However, light intensity as an inductive factor of diapause is doubtful if photoperiod is to be a reliable indicator of the seasons. There is possibility of light intensity influencing the photoperiodic induction of diapause but not as a factor by itself.

The response of white light (400-750mμ) and ultraviolet (330mμ) seems doubtful. However, the inactivity of the white light in terms of diapause induction in this particular work may be attributed to the fact that the filters used had the highest percentage of transmission in the yellow (570mμ) and the red (675mμ) portions of the spectrum. Thus the response to white

light is identical to that of red light.

In nature ultraviolet is filtered either in the atmosphere by ozone and molecular oxygen or by most soils (Baumgartner, 1953: Sellers, 1967). It is therefore, likely that the response obtained in the ultraviolet region is due to the portion of the violet transmitted in it.

In conclusion, it may be nferred from the results that temperature and photoperiod are both responsible for the induction of diapause in the cabbage maggot, H. brassicae; the violet-blue-blue-green (395-495mμ) region being responsible for the photoperiodic reaction while the infrared (1750mμ) may be involved in a thermoperiod effect.

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APPENDIX

Tables 1a and B. Percentage of emergence of non-diapausing pupae of H. brassicae at 21.1°C under photophases of (a) 12 and (b) 16 hours.

(a)

No. of days after pupation	% Emergence			
	Rep. 1(320)	Rep. 2 (117)	Rep. 3 (214)	Mean
5	0.31 (1)	-	-	0.10
6	1.88 (6)	-	0.47 (1)	0.78
7	5.31 (17)	-	0.47 (1)	1.93
8	5.31 (17)	-	0.47 (1)	1.93
9	11.88 (38)	-	0.93 (2)	4.23
10	14.69 (47)	-	1.40 (3)	5.36
11	15.63 (50)	0.85 (1)	2.34 (5)	6.27
12	17.50 (56)	2.56 (3)	2.34 (5)	7.47
13	17.50 (56)	5.98 (7)	2.34 (5)	8.61
14	17.50 (56)	5.98 (7)	2.34 (5)	8.61
15	17.50 (56)	9.40 (11)	2.80 (6)	9.90
16	17.50 (56)	11.11 (13)	2.80 (6)	10.47
17	17.50 (56)	12.82 (15)	2.80 (6)	11.04
18	17.50 (56)	12.82 (15)	2.80 (6)	11.04
19	17.50 (56)	12.82 (15)	2.80 (6)	11.04
20	17.50 (56)	12.82 (15)	2.80 (6)	11.04
22	17.50 (56)	12.82 (15)	2.80 (6)	11.04
25	17.50 (56)	12.82 (15)	2.80 (6)	11.04

(b)

No. of days after pupation	% Emergence			
	1 (325)	2 (150)	3 (128)	Mean
5	3.08 (10)	-	-	1.03
6	8.62 (28)	-	-	2.87
7	22.77 (74)	-	-	7.59
8	35.38 (115)	1.33 (2)	10.94 (14)	15.88
9	52.92 (172)	10.00 (15)	28.13 (36)	30.35
10	62.46 (203)	16.00 (24)	49.22 (63)	42.56
11	67.69 (220)	30.00 (45)	57.81 (74)	51.83
12	67.69 (220)	45.33 (68)	68.75 (88)	60.59
13	77.23 (251)	58.67 (88)	73.44 (94)	69.78
14	79.08 (257)	71.33 (107)	77.34 (99)	75.92
15	80.00 (260)	76.67 (115)	78.91 (101)	78.53
16	81.23 (264)	81.33 (122)	81.25 (104)	81.27
17	82.77 (269)	84.00 (126)	81.25 (104)	82.67
18	83.38 (271)	84.00 (126)	81.25 (104)	82.88
19	84.00 (273)	84.00 (126)	81.25 (104)	83.08
20	84.00 (273)	84.00 (126)	81.25 (104)	83.08
22	84.00 (273)	84.00 (126)	81.25 (104)	83.08
25	84.00 (273)	84.00 (126)	81.25 (104)	83.08

Table 2. Percentage of undeveloped pupae of H. brassicae when the larvae were reared at different temperatures under 12-hour and 16-hour photophases.

Rearing Temp. (°C)	12-hour rearing photophase		16-hour photophase	
		Pupal Holding Temperature (°C)		
	Larval temp.	20°	Larval temp.	20°
	76.23	89.17	76.23	98.17
15°	78.66	94.21	78.66	94.21
	89.36	82.83	89.36	82.83
Mean	81.42	88.74	81.42	88.74
	75.00	88.57	21.50	12.93
18°	77.50	77.45	27.49	19.59
	82.18	72.06	25.60	13.00
Mean	78.23	79.36	24.86	15.17
	93.43	93.43	12.06	12.06
20°	79.50	79.50	14.55	14.55
	71.34	71.34	17.47	17.47
Mean	81.42	81.42	14.69	14.69
	79.77	60.87	34.72	20.23
23°	61.42	69.23	44.07	22.61
	67.00	66.83	45.51	21.05
Mean	69.40	65.64	41.42	21.30
	77.27	11.96	75.00	16.83
25°	97.14	7.95	85.39	13.95
	95.00	6.29	79.17	20.00
Mean	89.80	8.73	79.85	16.93

Table 3a. Percentage of diapause incidence in H. brassicae when the larvae were reared under different light regimes at 21.1°C.

Treatment	% Diapause	Mean % Diapause *	Index of Effectiveness
Total Darkness (OL:24D)	16.09 12.00 23.66	17.25c	4.91
4-hour light (4L:20D)	51.02 55.88 59.12	55.34b	1.53
8-hour light (8L:16D)	82.77 78.23 71.43	77.48a	1.09
10-hour light (10L:14D)	94.22 77.00 78.40	83.21a	1.02
12-hour light (12L:12D)	97.08 76.23 90.83 78.66 95.00 89.36	84.64a	1.00
16-hour light (16L:8D)	20.30 14.02 16.00 11.94 18.75 12.67	15.61c	5.42
20-hour light (20L:4D)	19.31 23.85 25.08	22.75c	3.72
24-hour light (24L:OD)	27.29 20.71 22.50	23.50c	3.60

* Values followed by the same letter not significantly different at 1.0% level (Duncan's new multiple range test).

Table 3b. Analysis of Variance on the percentage of diapause in *H. brassicae* at a constant temperature of 21.1°C under different light regimes.

Source of Variance	DF	Sum Squares	Mean Squares	'F' Calculated
Treatment	7	11932.53	1704.65	66.10**
Residual	22	567.47	25.79	
Total	29	12500.00		

** Significant at 1.0% level.

Table 4a. The effect of different wavelengths of light on the induction of diapause in H. brassicae Bouché at 21.1°C.

TREATMENT Range (mμ)	Peak (mμ)	% diapause	Mean % of diapause *	Index of Effectiveness
400 - 750mμ	-	76.88 90.65 80.66	82.73 a	1.02
230 - 420mμ	330mμ	53.13 45.13 36.54	44.93 bc	1.88
370 - 425	395	14.55 11.69 20.59	15.61 de	5.42
430 - 500	460	12.50 10.71 17.29	13.50 e	6.27
460 - 580	495	19.64 26.88 28.18	24.90 de	3.40
480 - 570	525	53.70 49.21 62.42	55.11 b	1.54
555 - 610	570	47.62 52.13 49.15	49.63 b	1.71
590 - 630	600	65.93 61.48 55.20	60.87 b	1.39
620 - 750	675 *	90.61 87.82 79.48	85.97 a	0.98
710 - 1125	800	47.69 47.01 49.69	48.13 b	1.76
730 - 4500	1750	25.33 35.18 27.57	29.36 cd	2.88

* Values followed by same letter(s) not significantly different at 1.0% level (Duncan's new multiple range test).

Table 4b. Analysis of Variance on the percentage of diapause in H. brassicae at 21.1°C under different wavelengths of light.

Source of Variance	DF	Sum Squares	Mean Squares	'F' Calculated
Treatment	12	14070.48	1172.54	60.38 **
Residual	32	621.30	19.42	
Total	44	14691.78		

** Significant at 1.0% level.

Table 5. Effect of light intensity of the short-wave infrared radiation in the induction of diapause in H. brassicae at 21.1°C.

Energy level (mw/cm^2)	% Diapause Rep. 1	2	3	Mean
0.625	55.26	60.50	53.86	56.54
1.25	64.78	65.13	66.07	65.33
6.25	25.00	32.43	24.37	27.27
12.50	27.27	22.47	26.82	25.52
28.00	25.33	35.18	27.57	29.36

PLATES

1. Set up of light filtering apparatus
2. Growth chambers used in rearing the cabbage maggot
   a) Sherer Model Cel 255-6
   b) Sherer Model R 16 B
3. Different stages of Hylemyia brassicae Bouché
   a) Eggs x 50
   b) Larva x 10
   c) Pupa x 10
   d) Adult female (i) x 6.5
      Adult male (ii) x 6.5
4. Cage for the adult rearing showing the egg-cup
5. Clay pot for rearing the larvae
6. Emergence cups for the pupae

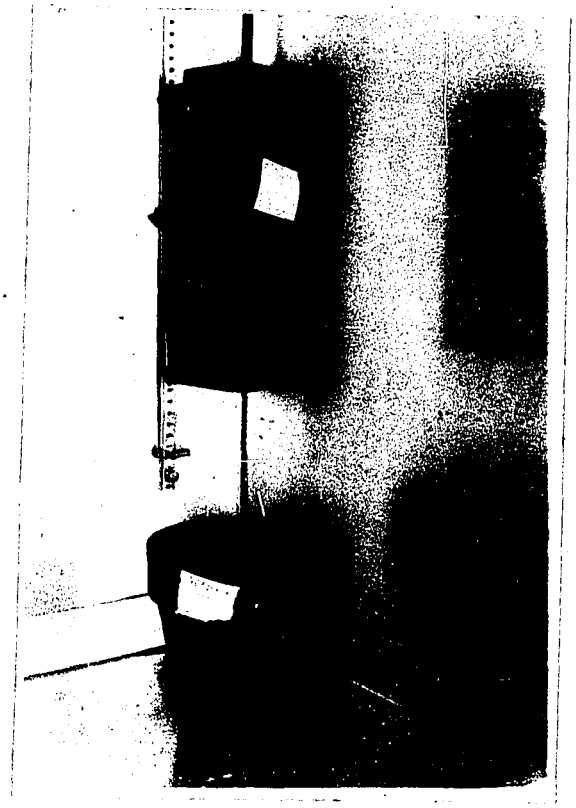


PLATE I.

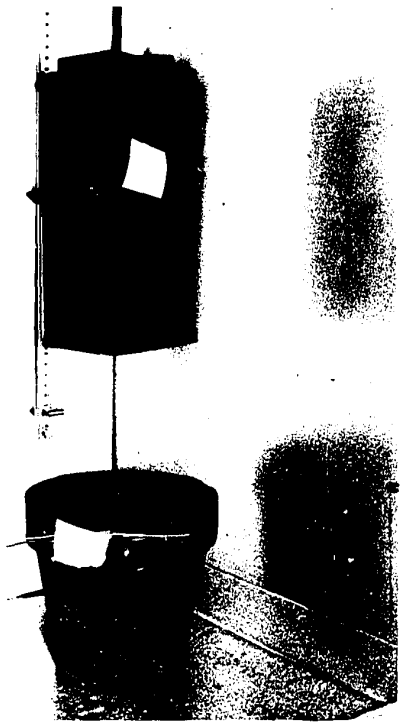


PLATE I.

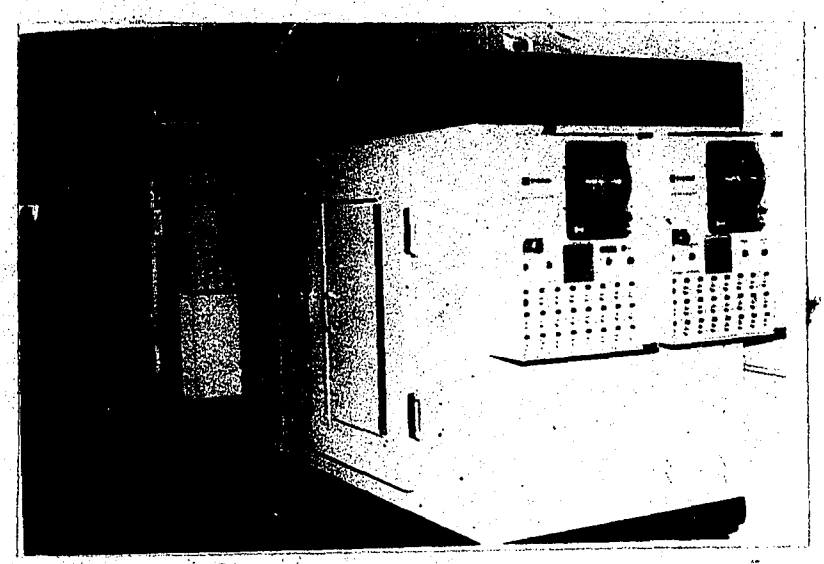


PLATE 2A.

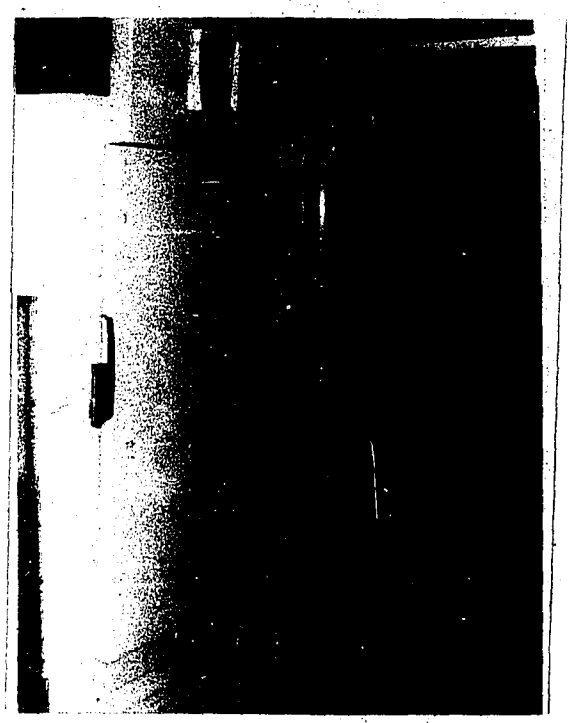


PLATE 2B.

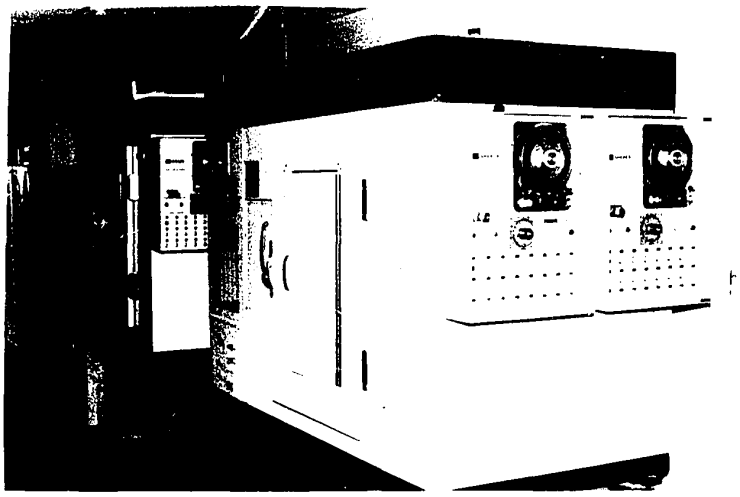


PLATE 2A.

PLATE 2B.

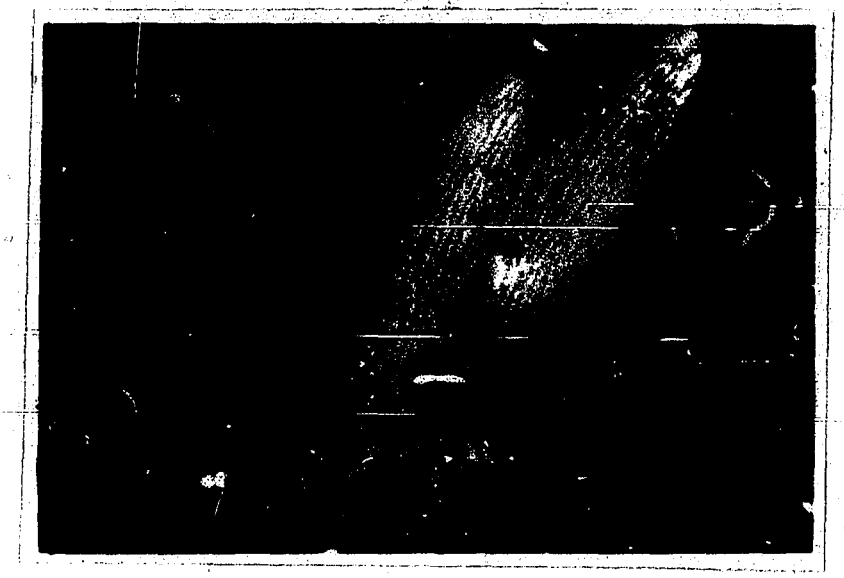
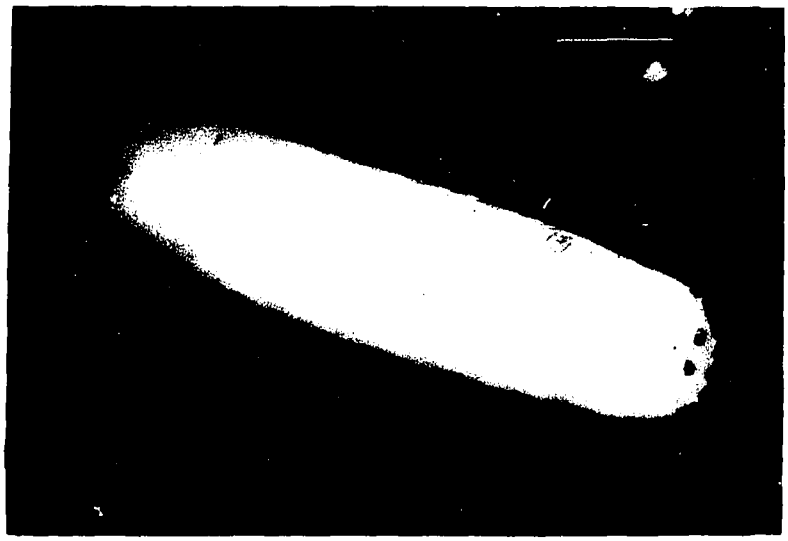


PLATE 3A.

PLATE 3A.

PLATE 3B.

PLATE 3C.



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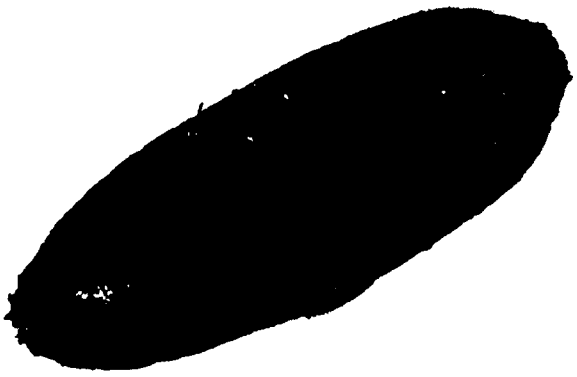

PLATE 3C.

PLATE 3D (i).

PLATE 3D (ii).

PLATE 3D (i).

PLATE 3D (ii).

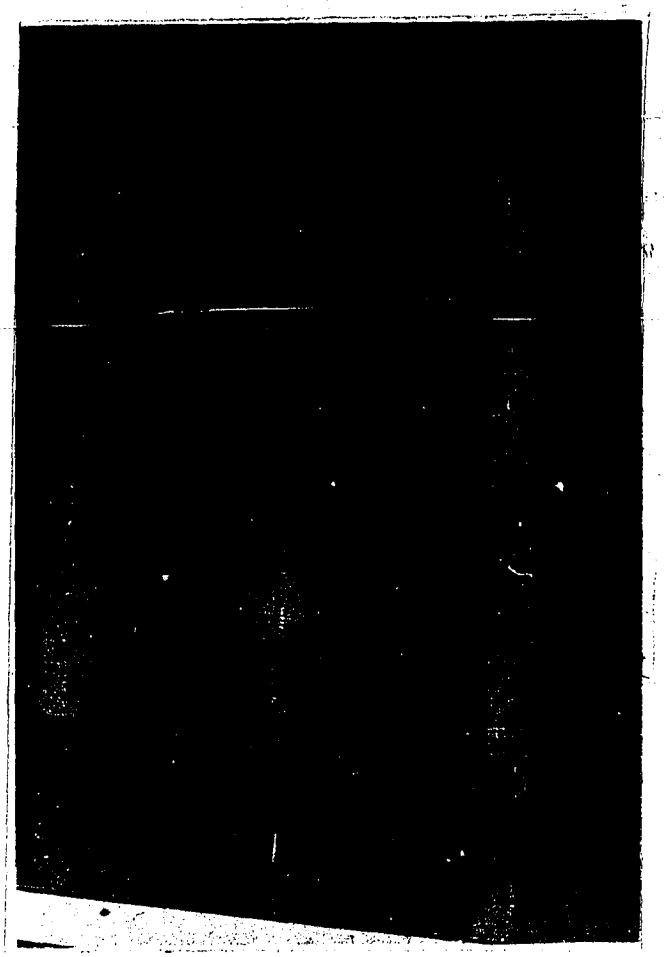

PLATE 4.

PLATE 4.

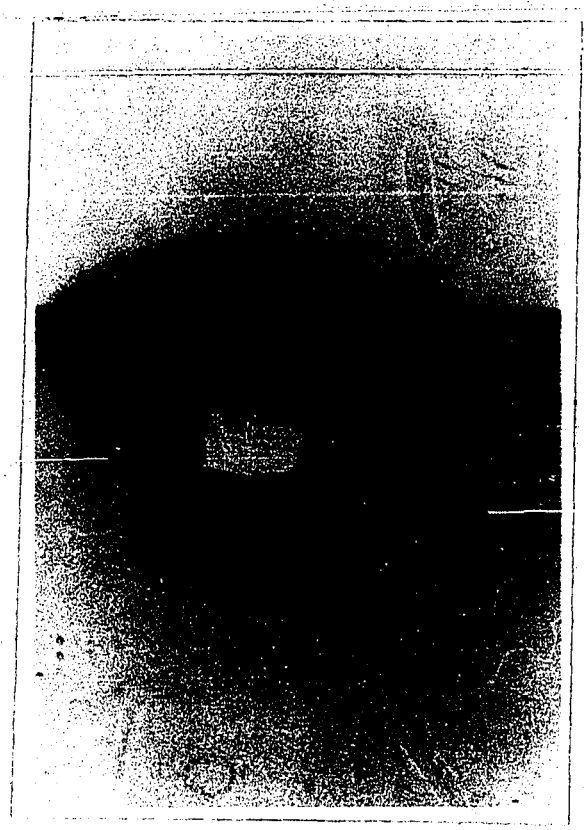

PLATE 5.

PLATE 6.

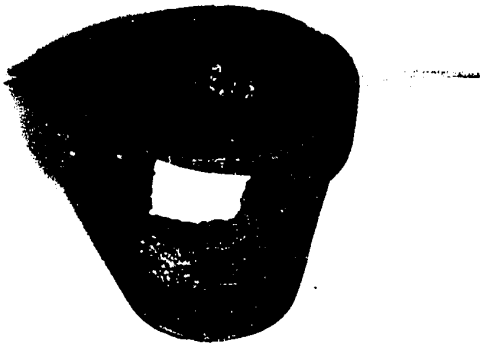

PLATE 5.

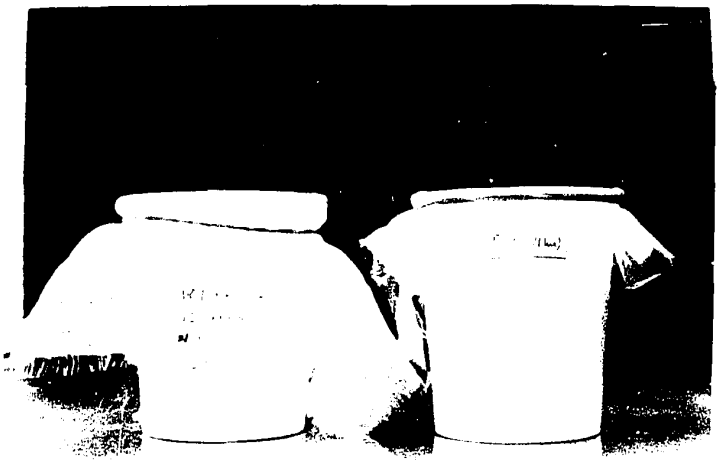

PLATE 6.