

AN ABSTRACT OF THE THESIS OF

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Title: Seasonality of Codling Moth, *Cydia pomonella* L.,
(Lepidoptera: Olethreutidae) in the Willamette Valley of
Oregon: Role of Photoperiod and Temperature

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Abstract approved: _____

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The seasonality, relationship of temperature and photoperiod to growth and post-diapause development, and overwintering behavior of codling moth, *Cydia pomonella* L., (Lepidoptera: Olethreutidae) were studied over a three year (1986-1989) period. The developmental threshold varied from a low of 9.66°C for the second instar to a high of 14.23°C for the fourth instar. A general threshold of 11.06°C was determined from larval to adult stage for both sexes combined. Data derived from the developmental study suggested that both temperature and photoperiod had an influence on development. Fastest development occurred at elevated temperature (28°C) and moderately long photoperiod (LD 14.75:9.25), although the rate declined beyond 30°C . Thermal requirements for development were 441.26 thermal

units (TU) from larvae to adult. There were no significant differences between the two sexes in the total number of thermal units required.

The critical photoperiod for diapause induction in codling moth populations from the Willamette Valley (latitude 44.5°N) was LD 15.5:8.5 at 24°C. Diapause in this insect was induced in all larval instars, although it appeared that the third and the fourth instars were slightly more sensitive than the other instars. Temperature also had an influence on diapause induction. The incidence of diapause induction was higher under fluctuating temperatures than at constant temperatures.

The codling moth populations from the Willamette Valley began to come out of diapause in the third week of March when photoperiod was 13-13.5 hours. Laboratory experiments also showed that 13.41 hours of light was the critical photoperiod for diapause termination. Approximately 39.4% of the first generation and almost all of the second generation larvae entered diapause. The incidence of diapause in the first generation, when the outdoor weather was close to diapause-averting environment, suggested the existence of a univoltine population of this insect in the Willamette Valley.

In the Willamette Valley codling moths overwinter as diapausing third, fourth, and fifth instar larvae. The relative proportions of these instars were: 3-21% in third,

10-11% in fourth, and 61-77% in fifth. However, all the third instar larvae were parasitized, and it appears that only the fourth and the fifth instars can overwinter and emerge as adults in the following season. Incorporation of this information into codling moth phenology models should improve the performance of these models.

Seasonality of Codling Moth, Cydia pomonella L.
(Lepidoptera: Olethreutidae) in the Willamette Valley
of Oregon: Role of Photoperiod and Temperature

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SEASONALITY OF CODLING MOTH, Cydia pomonella L.
(LEPIDOPTERA: OLETHREUTIDAE) IN THE WILLAMETTE VALLEY
OF OREGON: ROLE OF PHOTOPERIOD AND TEMPERATURE

CHAPTER I.

INTRODUCTION

The codling moth, Cydia pomonella L. (Lepidoptera : Olethreutidae), is the most serious pest of apples throughout the world except in parts of Asia including Japan. It was probably accidentally introduced into the North America through shipment of infested fruits as early as 1750 (Essig, 1931).

In the Western United States, the codling moth attacks apples, pears, apricots, cherries, peaches, plums, prunes, quinces, and walnuts (Newcomer and Whitcomb, 1925). Estimated loss in unsprayed trees varies from location to location, but is generally far above the economic injury levels (Hoyt & Tanigoshi, 1983). Putman (1963) noted regular losses of 75 to 95 percent in unsprayed trees in Southern Ontario, and Nova Scotia. MacLellan (1972) reported fruit damage of 22.1 percent in unsprayed trees. Glass and Lienk (1971) found an average of 20.5 percent codling moth infested apples in a New York orchard over an 8-year period after pesticide use was discontinued. In a similar study on pears in Oregon, Westigard (1973) reported an average of 42.4 percent

infestation over a 6-year period. A preliminary study in abandoned unsprayed apple trees around Corvallis during July 1986 showed that 36.65 to 65.7 percent of the examined fruits (1350 apples) were infested by codling moth larvae (Setyobudi, 1986 unpublished). Thus controlling codling moth is essential, and Hoyt et al. (1983) estimated that economic benefits from a codling moth control program averaged \$625 per acre per year.

The success of chemical control of codling moth is heavily dependent upon the precise timing of insecticide applications to coincide with the occurrence of the susceptible stages in the field. Some growers have compensated this lack of information on timing by spraying broad spectrum insecticides at regular intervals at relatively high rates. Unfortunately, such practices are harmful to a variety of beneficial arthropods and to the development of integrated pest management programs (Hoyt et al., 1983). Therefore, an understanding of codling moth seasonality is essential and this could play a very useful role in developing comprehensive insect pest management (IPM) programs. Riedl et al. (1976) developed a phenology model for codling moth development based on temperature-development data of Glenn (1922). However, the model proved quite accurate only for the first generation which was not affected by diapause, and less so

for the second generation. Riedl and Croft (1978) suggested that photoperiod and diapause components are two important features which are necessary to be incorporated into the codling moth phenology models to improve the predictive capabilities of this tool in the future. The Willamette Valley of Oregon differs substantially from other apple growing areas. It is characterized by the lack of autumn chill, mild winters and wide variation between winter and summer temperatures. Generally, the Willamette Valley has a cool humid climate during winter months with precipitation in the low lands and adjacent areas. Summer temperatures are not exceedingly high. Spring and autumn show intermediate conditions causing alternating wet and dry spells. Over 15 percent of the rainfall occurs in each of the winter months of November, December, and January, and only one percent each in July and August (Anderson, 1975).

Many studies dealing with codling moth have been conducted throughout the world and in many different areas in the United States (See Putman, 1963 for a review). The data are inconsistent and hard to apply in the Willamette Valley because of large differences in the climatic conditions. The purpose of this study was to investigate the seasonal development of codling moth in the Willamette Valley with particular reference to larval overwintering

behavior, effects of temperature and photoperiod on developmental rate, diapause induction and termination characteristic, and seasonal population dynamics. The codling moth is known for its ability to develop geographic as well as host races that adapt to different environmental conditions (Shel'Deshova 1965). It is hoped that this study will provide a better understanding regarding management of this pest on apples and pears in the Willamette Valley.

LITERATURE REVIEW

The codling moth, Cydia pomonella L., is one of the most extensively studied pests in the world (see Putman 1963 for detailed bibliography). Relatively little information is available from Oregon except for two studies, one conducted during the early 1920's by Yothers and Van Leeuwen (1931) and a relatively recent study by Moffitt and Westigard (1984). Cordley (1902) and AliNiazee (unpublish data) in a recent study showed that in most years the codling moth completed two generations in the Willamette Valley.

The biology of the codling moth can be summarized as follows. The eggs are deposited on the upper surfaces of the leaves or on fruits and take 5 to 12 days for hatching depending upon temperature and humidity (Yothers 1924, Balachowski 1935; both authors cited in Smotavac 1957). A female can oviposit an average of 50 to 60 eggs either singly or in groups of two to three eggs. But occasionally a female lays >100 eggs or only 10 to 12 eggs (Smotavac 1957, Carter 1984). Isely (1938) suggested that temperatures above 27°C decreased the fecundity and increased sterility. Balachowski and Viennot-Bourgin (1939) reported that codling moths do not copulate or lay eggs as the evening temperatures fall below 15°C. If the

chill lasts 2-3 weeks, the females die without laying any eggs. They also reported that 75 percent relative humidity was optimum for oviposition. Average hourly temperatures and the amount and duration of rainfall between 5 to 7 p.m. significantly influenced oviposition by the first generation, but oviposition by the second generation was affected only by temperatures (Hagley 1976).

Studies on within-tree egg distribution in unmanaged apple orchards showed that the average numbers of eggs per spur were positively correlated with the number of apples but were negatively correlated with the number of eggs per apple (Jackson 1979). Also 57 percent of eggs were laid on upper leaf surfaces, 35 percent on lower leaf surfaces, and 8 percent on the fruits. These percentages, however, varied during the summer months. Jackson (1979) also reported that 35 percent of eggs laid in the field were within 7.5 cm and 91 percent were within 20 cm from the fruits.

Laboratory observations of oviposition preferences showed different results. The preferred sites of oviposition were upper leaf surfaces, middle portions of fruits, lower leaf surfaces, stems, and calyx respectively. The degree of pubescence also significantly influenced the oviposition preferences (Plourde et al.

1985).

The time from egg hatch to successful entry into the fruits is a critically important period in the field biology of codling moth. However, relatively few studies of behavior, distribution, and survival of the first instar larvae have been published (Jackson, 1979).

Hagley (1972) found that rainfall was the most important cause of mortality of the first instar larvae when they were just beneath the epidermis of the fruits. Geier (1963) suggested that mortality of first instar larvae occurred because of increasing water content of the fruits and consequent flooding of larval tunnels. The second or third instar larvae in the fruits are also affected by rainfall. Rainfall during late spring and early summer could be a critical factor affecting larval survival (Hagley 1972). Exposure of eggs and first instar larvae to short photoperiod decreases the reproductive activity of adults (Deseo 1973, Deseo and Saringer 1975).

Codling moth larvae have five instars, the first four of which are spent in the fruits. The fifth (prepupa) exits the fruit and searches for a cocooning site either to pupate or overwinter (Smotavac 1957).

The length of the larval feeding period is approximately 16 to 24 days, but it is a function of temperature and varieties of apples in which they feed

(Selkregg and Siegler 1928, Goonewardene et al. 1984). Rock and Shaffer (1983) found a positive correlation between temperature and survival rate of codling moth, and 27°C was the optimum temperature for development. No significant differences were found in the developmental rates of males and females as influenced by temperature. The average cocooning and pupal period is about 18.45 days and it is also dependent upon temperature (Selkregg and Siegler 1928).

Codling moths overwinter as diapausing mature larvae in cocoons under the bark or in the ground at the base of the tree. Dickson (1949) first showed that the decreasing photoperiods induce diapause in the larvae of codling moth. Although the diapause appears to be facultative and influenced by prevailing photoperiod and temperature, the propensity for univoltinism seems to be present in this species as some individuals do not respond to photoperiodic changes and enter diapause (Riedl 1983).

Tauber et al. (1986) classified the diapause phenomenon into four stages: (1) pre-diapause, (2) diapause induction and intensification, (3) diapause maintenance and termination, and (4) post-diapause. AliNiazee (1988) divided diapause phenomenon into five different overlapping stages including (a) diapause induction, (b) diapause initiation and expression, (c)

diapause development, (d) diapause termination, and (e) post-diapause development. All of these phases can be recognized by neuroendocrine, metabolic, behavioral and sometimes morphological differences in the organism.

Some factors such as photoperiod, temperature, food quality, and others are known to play a key role in diapause induction. There is much argument about the photosensitive stage of codling moth larvae. Dickson (1949) reported that the late larval instar was the photosensitive stage for induction of diapause (Shel'Deshova 1965, Russ 1966). Jermy (1967) suggested that the sensitive stage was the early instar, but Saringer (1977; cited by Riedl 1983) suggested that diapause could be induced by short photoperiod throughout larval development although the earlier instars were more photosensitive.

Low temperatures below 15°C during the summer months induce diapause in codling moth larvae (Headlee 1931). Jermy (1967) found that the photoperiod reaction of codling moth larvae from Hungary to diapause was practically temperature-independent.

Quality of apples, for example the degree of ripeness and nutritional status, could be a primary signal for diapause initiation (Garlick 1948). Cisneros (1977; cited by Riedl 1983) suggested that the relationships between

photoperiod and maturity of apples were partly involved in diapause induction.

Another density dependent factor which may contribute to the diapause induction is the number of larvae within a fruit (Brown et al. 1979). This mechanism for diapause induction may be important in the first generation larvae, but in the later generations is secondary to the photoperiod.

Chilling and photoperiod or a combination of both play a role in diapause termination (Peterson and Hamner 1968). Although some populations, such as the Michigan populations of codling moth, do not always require chilling for diapause termination (Garcia-Salazar 1984). Townsend (1926) was able to terminate diapause by exposing larvae to 10°C. In short day conditions diapause termination can happen only under the influence of low temperatures between 0° to 10°C (Shel'Deshova 1967). Twenty days chilling at 4.5°C caused diapausing larvae to pupate even under a short day length of LD 8:16 (Peterson and Hamner 1968). A long photoperiod alone can terminate diapause but only under exposure to high temperatures (Shel'Deshova 1967).

Cisneros (1971; cited by Riedl 1983) reported that long photoperiod and no chilling caused scattered adult emergence over a long period of time. Short chilling

prior to long photoperiod and high temperature enhanced diapause termination and shortened the emergence period. A short photoperiod regardless of temperatures maintains diapause of codling moth (Russ 1966). After diapause terminates development may occur at any daylength at temperatures above 10°C. Sieber and Benz (1980b) suggested that the termination of diapause under long day conditions was influenced by four factors: first by the rearing temperature of larvae during pre-diapause development, second by the duration of the pre-incubation period (the time during which diapausing larvae remain under pre-diapause rearing conditions), third by reactivating incubation (the period during which the larvae are chilled), and fourth by the complementary incubation (the period after the chilling that is required for pupation).

Phillips and Barnes (1975) suggested that the first larvae entering diapause will also be the first to emerge in the following year. Jermy (1967) and Saringer (1977; cited by Riedl 1983) did not find that correlation and could not determine how long the larvae would remain in diapaus.

Numerous reports have been published dealing with codling moth control in different parts of the world (see Putman 1963 for a list of references). Tree fruit

entomologists agree that in spite of some attempts to control codling moth with biological control agents or with the sterile male technique, the commercial production of apples or pears is not possible without the use of chemicals (Hoyt and Burts 1974, Huffaker and Messenger 1976). The difficulty of controlling codling moth is in part related to the number of generations completed in a season (Putman 1963). Multiple generations are common in warmer apple and pear growing regions. Multiple generations along, with a narrow timing window for applying control measures, increase the difficulties of controlling this insect.

CHAPTER II

**INFLUENCE OF TEMPERATURE AND PHOTOPERIOD ON DEVELOPMENTAL
RATES OF CODLING MOTH (Lepidoptera: Olethreutidae)**

Abstract

The developmental rates of codling moth, Cydia pomonella L. from the Willamette Valley, Oregon were studied under different photoperiod and temperature conditions. Developmental threshold and thermal requirements were determined for various stages. Data show that different larval instar and pupae required different developmental thresholds. The fourth larval instar had the highest threshold (14.23°C) and the second instar had the lowest developmental threshold (9.66°C). The overall larval developmental threshold was 11.17°C . Although there were noticeable differences among the males and females in their larval development, these differences were non-significant. Male pupae had significantly lower developmental threshold (8.66°C) than female pupae (9.44°C). Total developmental threshold from larvae to adult was 10.06°C for both sexes combined, and males had significantly lower threshold (10.78°C) than females (11.31°C). A total 441.3 thermal units (TU) were required for development from larvae to adult, the differences between males and females were non-significant.

In addition to temperature, the prevailing photoperiod had an influence on the rate of development, and a photoperiod of LD 14.75:9.25 was the fastest growing

treatment. The influence of photoperiod on codling moth development is reported here for the first time.

INTRODUCTION

The developmental rates of codling moth, Cydia pomonella L., are dependent on a number of factors including temperature (Glenn 1922, Shelford 1967), photoperiod (Russ 1966, Phillips and Barnes 1975), food, humidity and rainfall. The influence of constant or fluctuating temperatures on the development of codling moth eggs, larvae, and pupae has been investigated by many workers (Glenn 1922, Badowska-Czubik and Suski 1982, William and McDonald 1982, Rock and Shaffer 1983). Shelford (1927) analyzed the effects of various temperatures and relative humidities on each stage of development of codling moth, but the results were inconsistent and the methods used were cumbersome.

The effects of constant temperatures on the developmental rates of codling moth larvae were studied by William and McDonald (1982) from Australia, by Rock and Shaffer (1983) from North Carolina, Batiste and Olson (1973) from California, Hathaway et al. (1971) from Washington, and Garcia-Salazar et al. (1988) from Michigan. These studies showed that the developmental rates increased with temperature up to 30°C but declined at 35°C. The increase in the developmental rate appeared to be proportional (linear) to the increase in temperature

between 15°-30°C and non-linear above and below this range. Also, there was considerable variation in the developmental period for different populations, within a given population, and populations from different hosts.

The photoperiod has been shown to influence post-embryonic growth in a number of insect species (Beck 1980). In the codling moth it also seems to have some influence on development (Russ 1966), although this relationship is not fully understood. Detailed studies on the effect of photoperiod on the post-diapause development are also lacking. Little is known about the relationship between developmental time and temperature for Oregon populations of the codling moth. Development of such information is essential for meaningful implementation of a phenology model (Welch et al. 1978) and analyzing the development of geographic races (Shel'Deshova 1967, Riedl 1983) from this region.

Reported here are the results of a laboratory study dealing with the effect of temperature and photoperiod on the post-diapause and non-diapause developmental rates of codling moth from Oregon.

MATERIALS AND METHODS

Insects - Insects required for this study were obtained as larvae from the F1 progeny of moths collected from abandoned orchards around Corvallis, Oregon as diapausing larvae in corrugated cardboard traps during the winter of 1988. These corrugated cardboards were placed in 40 cm³ cages at 24°C LD 18:6 photoperiod to obtain adults. These adults were then placed in one gallon ice cream cartons lined with wax paper. Deposited eggs were cut out and placed for hatching in a 1.4 l Servin'saver cup with a screen.

In order to study the development of the larvae without disrupting them, we developed a method of using small (13 cm long, 0.6 cm diameter) disposable pipets which were filled half way with codling moth artificial diet (Bioserve, Frechtown, New Jersey). The open ends of the pipets were closed with sterile cotton to prevent the larval escape. Since Howell (1971) had reported no difference in larval growth rates among larvae reared on various diets or apples, we presumed that the developmental rates of our study would resemble the development in apple fruits. The glass pipets provided easy access and a clear view of codling moth development during experiments.

Experiments were conducted by placing neonate larvae, singly in each pipet (filled with diet), and studying the growth at different treatments. A total of 30 individual larvae was exposed to each treatment temperature. Constant temperatures used as treatments included 16°C, 20°C, 24°C, 28°C, and 32°C at LD 16:8 photoperiod, in Percival (model E 30B) growth chambers. Relative humidity within the chamber was maintained at about 75±10%. The development was monitored every day and the date of ecdysis was recorded by measuring the head capsuled of the molted skin. Because of larval mortality and/or diapause in each treatment, different numbers of larvae were counted at each state of development at different treatment temperatures. The numbers of larvae in each treatment were: 18 (8 females + 10 males) at 16°C, 12 (7 females + 5 males) at 20°C, 18 (12 females + 6 males) at 24°C, 24 (12 females + 12 males) at 28°C, 22 (8 females + 14 males) at 32°C.

The effect of photoperiod was determined at 4 different temperatures: constant 24°C, 28°C, 32°C, and fluctuating 16° to 32°C in 12 hour thermoperiod. The photoperiods tested were LD 0:24, LD 4:20, LD 8:16, LD 13.5:10.5, LD 14:10, LD 14.75:9.25, LD 15.5:8.5, and LD 16:8. Relative developmental rate studies were conducted using 840 larvae with an average sample size of 30

individuals in each treatment. The treatments were placed in a quart cylinder cardboard painted black with a removable lid.

Developmental rate data of non-diapausing individuals was used for the analysis. Rate of development (1/number of days for development) was plotted against temperature and the linear regression analysis used to calculate developmental threshold (x-intercept) and thermal unit requirements (inverse of slope). Threshold and thermal unit values were calculated separately for females and males and for both combined. A 95% confidence interval for thresholds was determined by using the formula, $Y \pm t_{0.05}(SE)$, where Y = mean value of data points, t = tabular t value at 0.05 significance level and $n-1$ degrees of freedom, and SE = standard error of the mean. The data point (upper and lower) depicting confidence limits of developmental rates at each temperature were subjected to linear regressions and the x-intercept of each line determined the 95% confidence interval for the developmental threshold. The level of significance was determined based on overlapping of confidence limits.

The mean developmental period from neonates to adult eclosion as influenced by the length of photoperiod was determined by using the same formula as described above. The significance level was determined by $t_{0.05}(SE)$ and $n-1$

degrees of freedom.

RESULTS AND DISCUSSION

A total of 381 individuals reached to the adult stage. The survivorship and developmental times from freshly hatched larvae to adult emergence are given in Table II-1. The mortality varied from treatment to treatment. Highest mortality was seen at fluctuating temperature (16° - 32° C) treatment and least mortality was noticed at 28° C constant temperature. Some larvae did not complete development and went into diapause (a detailed discussion of diapause induction is given in chapter III). The proportion of individuals entering diapause varied from 19% in 16° C temperature treatment to no diapause at 32° C temperature treatment. The larval and pupal survivorship varied from 90% for larvae and 68.8% for pupae (16° C and 16° - 32° C) to 97% for larvae 93% for pupae (32° C and 28° C).

Average percent development for each larval instar, the pupal stage, and from larvae to adult is given in Figures II-1 to II-5. These data indicate that fastest development occurred at 28° C, and the slowest development at 16° C, although there were variations between different instars and pupal stage. For instance, the fastest development in L1 and L2 occurred at 32° C, while in instar L3, L4, and L5 the developmental rate declined at 32° C and

Table II-1. Survivorship and developmental time of codling moth reared at the different temperatures and LD 16:8 photoperiod

Temperature (°C)	Survivorship (1)		% entering diapause	Days from neonates to adult eclosion		
	number	%		Mean (2)	SD	Range
16 constant	18	67	19	83.1 a	5.78	(77.32 - 88.88)
20 constant	12	40	44	51.3 b	2.78	(48.47 - 54.13)
24 constant	18	64	25	34.1 c	2.77	(31.33 - 36.87)
28 constant	24	93	0	25.5 d	1.58	(23.92 - 28.37)
32 constant	22	81	0	26.3 d	2.07	(24.23 - 28.37)
fluctuating 16-32 (μ 24)	17	43	39	32.5 c	3.04	(29.46 - 35.54)

(1) Individuals which successful through the adult stage

(2) LSD 0.05

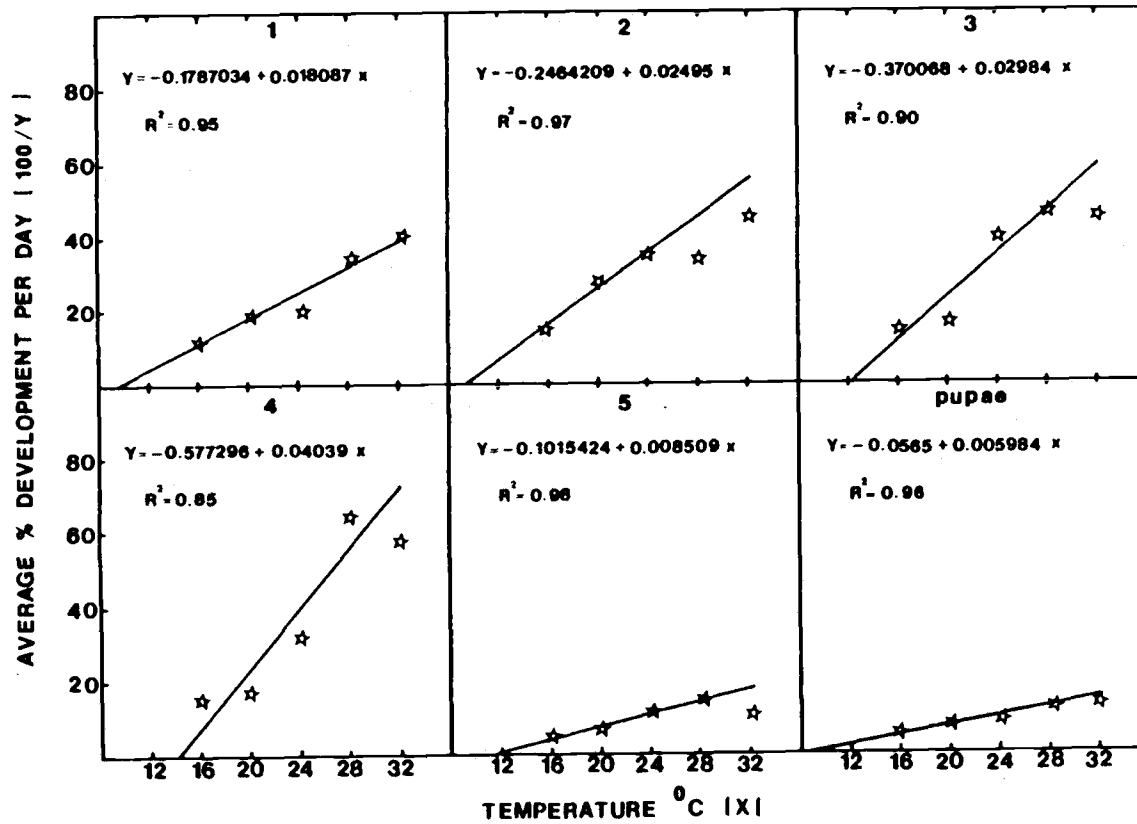


Figure II-1. Effect of temperature on the developmental rate of different female larval instars and pupae

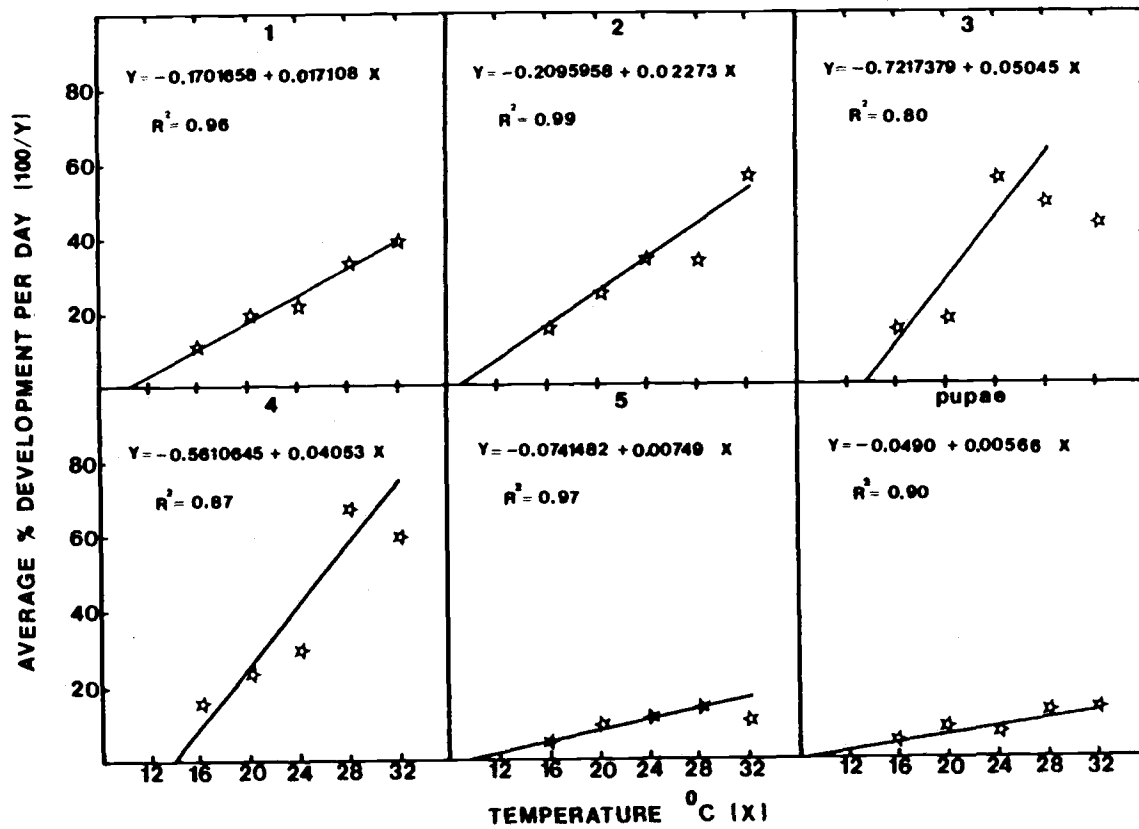


Figure II-2. Effect of temperature on the developmental rate of different male larval instars and pupae

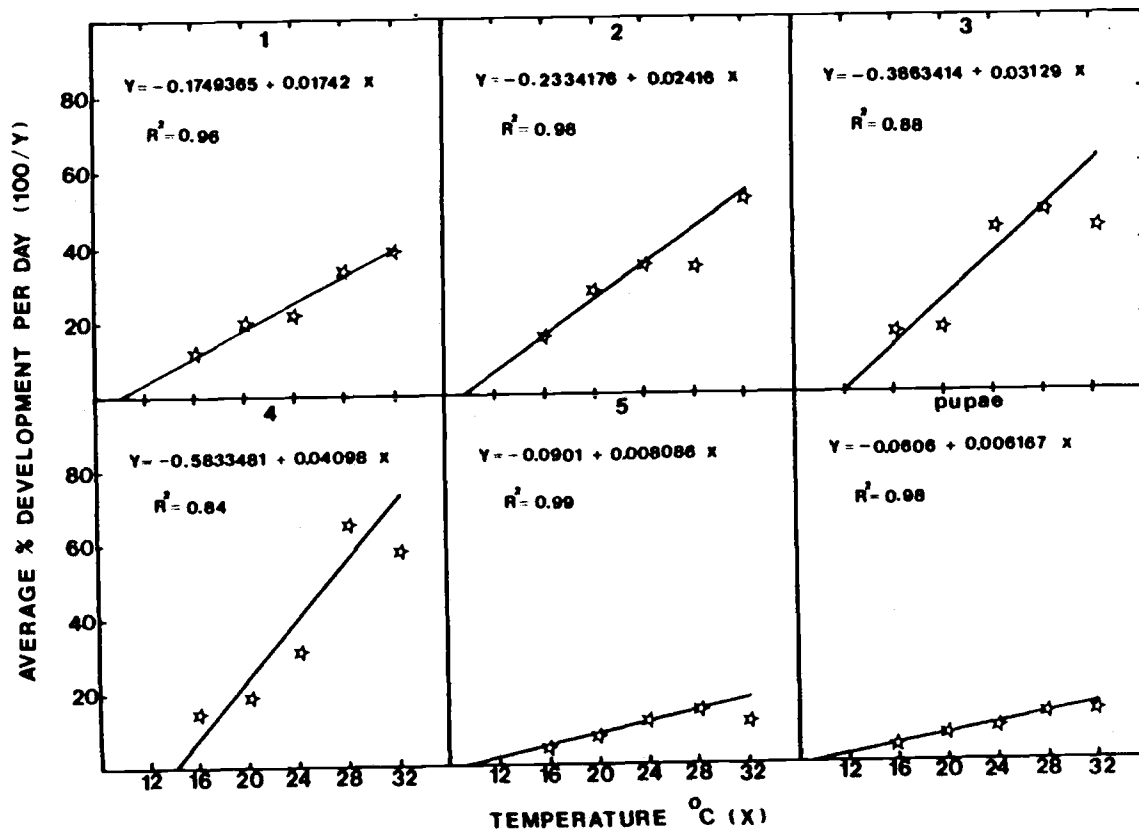


Figure II-3. Effect of temperature on the developmental rate of different larval stages and pupae for both sexes combined

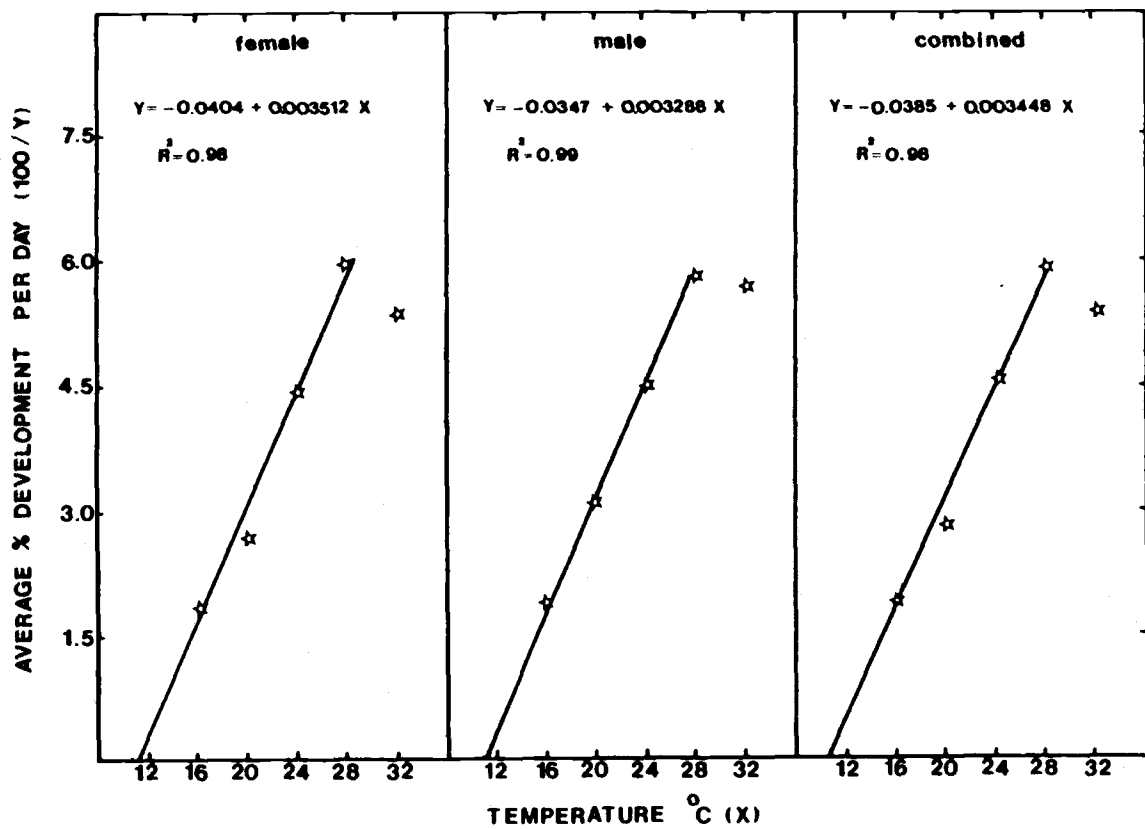


Figure II-4. Effect of temperature on the developmental rate of complete larval stage for females, males, and both sexes combined

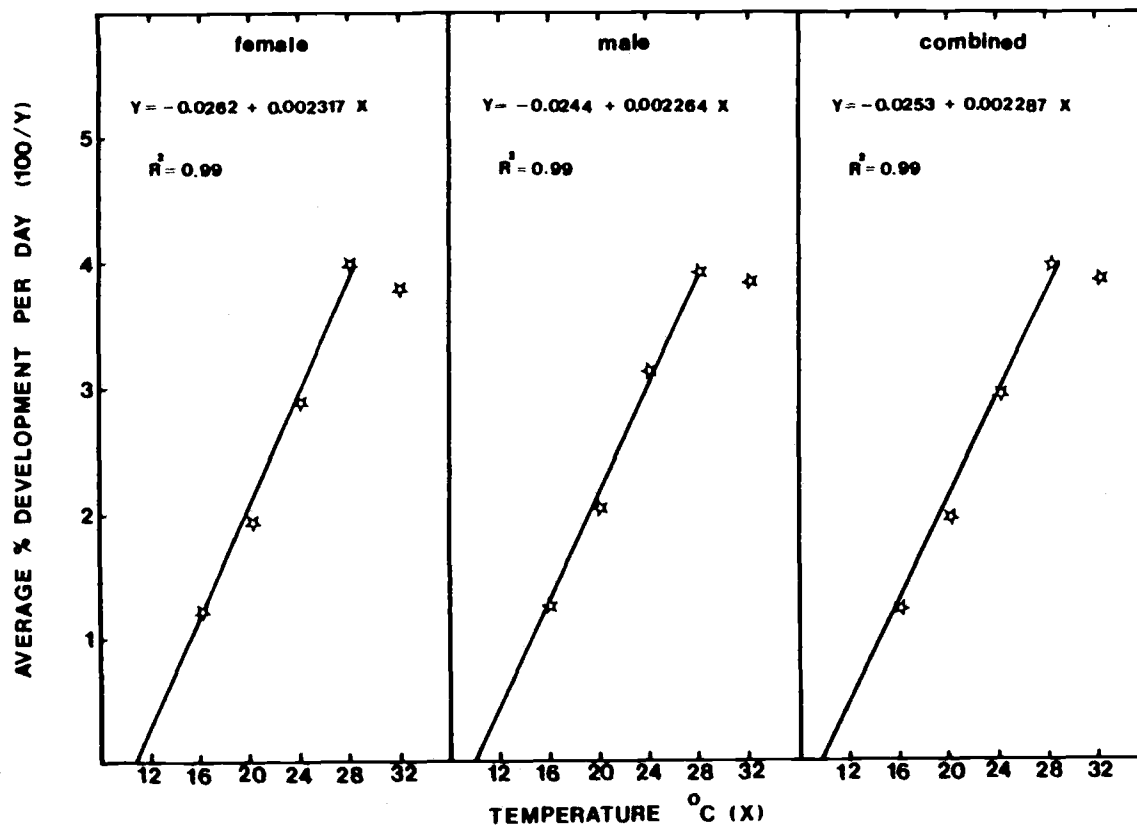


Figure II-5. Effect of temperature on the developmental rate from larva to the adult stage for females, males, and both sexes combined

the mortality increased (19%). A highly positive linear relationship was noticed between the increase of temperature and the developmental rate in instar L1, L2, L3, L5, and pupae ($R^2 = 0.96$ and above).

Developmental threshold and regression equations relating developmental time to temperature are given in Table II-2. The developmental threshold (derived by extending the regression line to the x-axis and calculating the x-intercept) for neonate larvae to adult eclosion combined is 11.06°C (11.05° - 11.07°C), which is significantly higher than that for pupal stage and lower than larval stages. The male pupae had the lowest developmental threshold (8.61°C) while the third instar male had the highest developmental threshold (14.31°C). Earlier studies (Riedl and Croft 1978, Jorgensen et al. 1979) have used a generalized base threshold of 10°C for predicting codling moth phenology based on thermal accumulation. Rock and Shaffer (1983) suggested a threshold 9.9°C for codling moth development from neonate to adult eclosion. None of these or other studies (i.e. Glenn 1922, Shelford 1927, Rock 1967, Geier and Breise 1978) did provide different thresholds for different larval instars and different sexes of codling moth. However, such differences were presented by Gangavalli and AliNiasee (1985) for another apple pest, the obliquebanded

Table II-2. Developmental thresholds for neonates to adults of codling moth, Cydia pomonella L.

Stage in life cycle and instar	sex	Development threshold	95 % (CI)	Regression equation	R ²
Larval First	Female	10.339	i (10.332 - 10.346)	$Y = -0.1787034 + 0.018087 x$	0.95
	Male	9.946	g (9.941 - 9.952)	$Y = -0.1701658 + 0.017108 x$	0.96
	Combined	10.043	h (10.037 - 10.050)	$Y = -0.1749365 + 0.017418 x$	0.96
Second	Female	9.876	e (9.821 - 9.931)	$Y = -0.2464209 + 0.02495 x$	0.97
	Male	9.221	b (9.207 - 9.235)	$Y = -0.2095958 + 0.02273 x$	0.99
	Combined	9.661	d (9.626 - 9.696)	$Y = -0.2334176 + 0.02416 x$	0.98
Third	Female	12.401	s (12.372 - 12.431)	$Y = -0.370068 + 0.02984 x$	0.90
	Male	14.308	u (13.990 - 14.622)	$Y = -0.721738 + 0.05045 x$	0.80
	Combined	12.348	r (12.312 - 12.363)	$Y = -0.386341 + 0.03129 x$	0.88
Fourth	Female	14.293	u (14.240 - 14.345)	$Y = -0.577296 + 0.04039 x$	0.85
	Male	13.843	t (13.785 - 13.900)	$Y = -0.561065 + 0.04053 x$	0.82
	Combined	14.235	u (14.181 - 14.289)	$Y = -0.583348 + 0.04098 x$	0.84
Fifth	Female	11.933	q (11.930 - 11.345)	$Y = -0.1015424 + 0.008509 x$	0.98
	Male	9.999	f (9.894 - 9.901)	$Y = -0.0741482 + 0.007491 x$	0.97
	Combined	11.143	l (11.142 - 11.143)	$Y = -0.0901000 + 0.008086 x$	0.99
All Larvae	Female	11.503	o (11.502 - 11.505)	$Y = -0.0404 + 0.003512 x$	0.98
	Male	11.547	p (11.547 - 11.547)	$Y = -0.0347 + 0.003288 x$	0.99
	Combined	11.166	a (11.165 - 11.167)	$Y = -0.0385 + 0.003448 x$	0.98
Pupae	Female	9.442	c (9.439 - 9.444)	$Y = -0.0565 + 0.005984 x$	0.96
	Male	8.656	a (8.652 - 8.659)	$Y = -0.0490 + 0.005661 x$	0.90
	Combined	9.826	e (9.825 - 9.828)	$Y = -0.0606 + 0.006167 x$	0.98
All from Larvae to Adult	Female	11.307	n (11.307 - 11.308)	$Y = -0.0262 + 0.002317 x$	0.99
	Male	10.777	j (10.776 - 10.778)	$Y = -0.0244 + 0.002264 x$	0.99
	Combined	11.062	k (11.058 - 11.067)	$Y = -0.0253 + 0.002287 x$	0.99

leafroller, Choristoneura rosaceana (Harris). Such differences are probably prevalent in many other insects. Batiste and Olson (1973) reported that codling moth males emerged earlier than females in the spring. This disparity in emergence is probably caused by the fact that male L5 and pupae of codling moth use a substantially lower developmental threshold (Table II-2) than females, consequently, developing faster than females (under similar temperature conditions) and emerging earlier.

The different thresholds observed in larval instars and the pupal stage might have evolutionary and adaptive significance. For example, L3 and L4 are the two instars utilizing a much higher development threshold than the others, and these are also the two most sensitive stages to diapause induction (Garcia-Salazar 1984, Setyobudi 1989). Thus in late summer when diapause is induced in this insect, utilization of a higher developmental threshold might be helpful in slowing down development and assisting with diapause initiation, therefore synchronizing its life cycle and increasing winter survival. On the other hand, utilization of a slightly lower threshold by L5, pupae, L1, and L2 might be helpful in rapid development during the spring months for better utilization of available food resources.

The heat unit requirements for codling moth in our

experiments at constant temperatures are presented in Table II-3. A total of 441.26 ± 26.30 degree days (DD) or thermal units (TU) were required for development of neonate larvae to the adult stage when both sexes were combined. There was a small statistically not significant difference between males and females. Males may require slightly more heat units than females.

The proportion of the developmental period associated with each instar was different (Table II-3). For instance, L4 had the shortest developmental period, comprising only about 5 percent (21.2 ± 3.7 DD) of the total larva-adult (L-A) degree day requirements. The L5 and pupal stage required the highest number of degree days, 124.24 ± 8.72 DD and 152.3 ± 4.87 DD, respectively comprising about 28% and 35% of the total L-A developmental period.

The effect of photoperiod on development of codling moth is presented in Table II-4. The low number of individuals in these tests, particularly in the fluctuating temperature treatment, is due to larvae entering into diapause. For instance at 14, 14.75, and 15.5 hours photoperiod only 1-2 larvae (out of 26) completed development to the adult stage without entering into diapause. As mentioned above, due to the different number of non-diapausing individuals in the various treatments, it is difficult to interpret the data

Table II-3. Thermal requirements for development of codling moth larvae and pupae

Stage of life cycle or instar	Sex	Degree Days required (95 % CI)	% Total thermal developmental period (L-R)
LARVAE			
First	Combined	54.59 (53.10 - 56.08)	12
Second	Combined	55.75 (53.09 - 58.41)	13
Third	Combined	33.18 (28.32 - 38.04)	8
Fourth	Combined	21.20 (17.50 - 24.90)	5
Fifth	Combined	124.24 (115.52 - 132.96)	28
All	Female	279.18 (243.99 - 314.37)	64
	Male	303.80 (287.07 - 320.53)	65
	Combined	288.96 (214.43 - 310.39)	65
PUPAE			
	Female	154.59 (146.93 - 162.25)	36
	Male	162.88 (154.76 - 171.00)	35
	Combined	152.30 (147.43 - 157.17)	35
All			
Larvae to Adult	Female	433.77 (390.92 - 476.62)	
	Male	466.68 (441.83 - 491.53)	
	Combined	441.26 (361.86 - 467.56)	

Table II-4. Effect of photoperiod and developmental rate (Days \pm SE) of codling moth from neonates to adult eclosion

Photoperiod hours Light/Dark		Temperature ($^{\circ}$ C)				
		Constant			Fluctuating	
		24 $^{\circ}$	28 $^{\circ}$	32 $^{\circ}$	16-32 (μ = 24 $^{\circ}$)	
0L:240	N	15	17	17	8	
	D	37.93 ^{a*}	27.65 ^{ab}	32.12 ^a	35.13	
	SE	1.52	0.31	0.62	0.88	
4L:200	N	-	12	-	7	
	D	-	29.17 ^a	-	30.99	
	SE	-	0.81	-	0.52	
8L:160	N	-	10	-	9	
	D	-	28.10 ^a	-	32.44	
	SE	-	0.41	-	0.75	
13.5L:10.50	N	9	17	21	5	
	D	31.44 ^b	27.14 ^{ab}	25.21 ^{bc}	30.60	
	SE	0.56	1.01	0.63	0.40	
14L:100	N	7	18	19	1	
	D	35.43 ^{ab}	25.50 ^b	26.53 ^b	28.00	
	SE	2.05	0.41	0.77	-	
14.75L:9.250	N	7	12	21	2	
	D	37.57 ^{ab}	23.67 ^c	24.90 ^c	34.00	
	SE	4.02	0.28	0.57	1.00	
15.5L:8.50	N	9	15	25	2	
	D	35.56 ^{ab}	26.00 ^b	27.12 ^b	35.50	
	SE	1.53	0.50	0.52	0.50	
16L:80	N	18	24	22	12	
	D	34.06 ^{ab}	25.54 ^b	26.32 ^{bc}	32.50	
	SE	0.67	0.33	0.45	0.92	

N = Number in sample
D = Days required to develop from neonates to adult
SE = Standard Error
*) = Least Significant Difference (LSD) 0.05

presented in Table II-4. However, it is apparent that the length of photoperiod has a confounding effect on the developmental rates along with temperatures. At 24°C (constant) development was fastest at LD 13.5:10.5 treatment than others. The slowest development was noticed in complete darkness (LD 0:24). At 28°C and 32°C the fastest development occurred at LD 14.75:9.25 treatment (Table II-4). The low number of larvae which completed development to the adult stage makes it difficult to draw conclusions from the fluctuating temperature treatments.

It is interesting that the prevailing photoperiod not only affects diapause induction and expression but it also may affect the rate of development in the field. Russ (1966) had also noticed that codling moth larvae after termination of diapause developed faster to the pupal stage at longer photoperiods than in complete darkness.

In summary, the data presented here suggest that the development of the codling moth is affected by both the prevailing temperatures and photoperiod, although the former seems to have a much more profound influence on the rate of development than the latter.

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CHAPTER III

INFLUENCE OF PHOTOPERIOD AND TEMPERATURE
ON INDUCTION OF DIAPAUSE IN CODLING MOTH
Cydia pomonella L.

Abstract

The roles of photoperiod and temperature on diapause induction of codling moth, Cydia pomonella L., from the Willamette Valley, Oregon were studied. The sensitivity of various larval stages for diapause induction was determined under laboratory conditions. Data indicated that both temperature and photoperiod played a key role in diapause induction. The temperatures had more of a modifying effect. For example, occurrence of high temperature (above 28°C) during larval development would suppress the effect of photoperiod in diapause induction. In other words, the diapause would be averted, even though the diapause inducing photoperiod is present. The influence of photoperiod was important; at short photoperiods diapause was induced. The critical photoperiod (CPhP50) for diapause induction in codling moth population from Willamette Valley (latitude 44.5°N) was LD 15.5:8.5 at 24°C. The incidence of diapause induction in codling moth larvae was higher under fluctuating temperatures than at constant temperatures. The stage sensitivity data show that diapause in codling moth can be induced in all larval instars. The third and fourth instars were more sensitive than the others.

INTRODUCTION

The codling moth, Cydia pomonella L. (Lepidoptera: Olethreutidae), overwinters as a diapausing fifth instar larva and completes development in the spring (Smotavac 1957, Geier 1963). In most temperate and subtropical insects, diapause is an important physiological state which provides adaptive advantages for survival during adverse seasonal conditions particularly the winter months (Tauber et al. 1986). Diapause is generally induced in response to token stimuli (Lee 1955, Tauber et al. 1986) and is terminated by prevailing environmental conditions (Tauber and Tauber 1976, AliNiazee 1988) generally in response to increasing photoperiod and temperature. The knowledge of diapause could play a useful role in developing various pest management options for insect pests (AliNiazee 1988).

The occurrence and maintenance of diapause is dependent on both environmental and genetic factors (Tauber et al. 1986). Environmental factors which are recognized as the most common stimulus to diapause induction in codling moth and other lepidopterous insects are photoperiod, temperature, food, and population densities (Dickson 1949, Hayes et al. 1974, Brown et al. 1979, Brown 1985). The length of photoperiod which

apparently has the most dominant effect on induction, varies among populations of the same species from different geographical areas (Shel'Deshova 1967, Riedl 1983). For example, in codling moth populations collected from Southern California, a short-day photoperiod lower than LD 15:9 during larval stage induced diapause and at even lower photoperiod of LD 12:12 and 24°C, one hundred percent larval diapause of the same population was noticed (Dickson 1949). The critical photoperiod for 50 percent diapause induction (CPhP50) varied from 13.5 hours for a population from Southern California (Peterson and Hamner 1968) to 14.6 hours for a population from Olney, Illinois (Danilevsky 1970) and 15.1 hours for a population from Glassboro, New Jersey (Headley 1934). Garcia-Salazar et al. (1988) reported that in Michigan diapause in codling moth was enhanced by low temperatures and was averted by high temperatures causing diminished photoperiodic response. They reported that the CPhP50 of codling moth from Michigan was 15 hours at 17°C and 13.44 hours at 30°C. This clearly shows the interaction of photoperiod and temperatures in diapause induction of codling moth.

Diapause-inducing token stimuli are perceived during certain stages of the life cycle in most insects (Beck 1980, Tauber et al. 1986). In Lepidoptera, the most common stage sensitive to diapause induction is the larval

stage. However, the sensitivity in different larval instar is variable. For example, in the oblique-banded leafroller, Christoneura rosaceana (Harris), the larval instars one and two are the only two stages sensitive to diapause induction (Gangavalli and Aliniazee 1985). Dickson (1949) observed that in the oriental fruit moth, Grapholita molesta (Busck), most larval instars are sensitive. In Pieris rapae L., the fourth larval instar was highly sensitive (Barker et al. 1963). In some insects, the conditions under which the parents were reared had an influence on diapause induction. For instance, the progeny of the pink bollworm, Pectinophora gossypiella (Saunders), reared under long-day photoperiod enters diapause when transferred to a short-day photoperiod. However, the progeny of adults reared under a short-day photoperiod tends not to diapause even under a short-day (Lukefahr et al. 1964).

Little is known about the sensitive stages for diapause induction in the codling moth. Sieber and Benz (1980a, 1980b) mentioned that diapause in codling moth is induced in early larval instars by short-day photoperiods. Garcia-Salazar (1984) reported that the populations of codling moth from Michigan could be induced to enter diapause in all larval instars. Diapause induction could be eliminated completely in the first two larval instars

and little more than 50 percent in the third instars by modifying the temperature and photoperiod.

The study reported here presents the results of experiments conducted to determine the role of photoperiod and temperature on diapause induction in a codling moth population from the Willamette Valley, Oregon. Also presented here are data on stage sensitivity for diapause induction.

MATERIALS AND METHODS

Insects: Insects required for this study were obtained as larvae from the F1 progeny of moths collected from abandoned and cultivated orchards around Corvallis, Oregon as diapausing larvae in corrugated cardboard traps during the winter of 1988. These corrugated cardboard were placed in 40x40x40 cm screen cages at $24\pm 1^{\circ}\text{C}$ and LD 18:6 photoperiod for adult emergence. The adult moths were placed in one gallon ice cream cartons lined with wax paper for oviposition. Cotton swabs dipped in 10 percent sucrose solution were provided as food for adults. Eggs deposited on the wax paper were cut out and placed for hatching in a 1.4 l Servin'saver cup with a screen lid.

To study the larval life cycle without disturbance, we used small disposable pipets (13 cm long, 0.6 cm diameter) which were filled half way with an artificial codling moth diet (Bioserve, Frenchtown, New Jersey) and the open end of pipet were plugged with sterile cotton to prevent larval escape. Since Howel (1971) had reported no difference in larval growth among larvae reared on various diets or apples, we presumed that the development of larvae in our study closely resembled development in apples. The glass pipets provided easy access and a clear view of larval development during the experiments.

Diapause Induction Experiments:

Experiments were conducted by placing neonate larvae singly in each pipet filled halfway with diet. A total of 30 individual larvae was exposed at each treatment in the Percival growth chambers (Model E-30 B), and observations on development were continued for at least 30 days.

Different constant and fluctuating temperatures and different photoperiods were used as treatments.

Temperature treatments included 16°, 20°, 24°, 28°, and 32°C constant and 24°C fluctuating (16°-32°C in LD 12:12 hours/day regime). The photoperiod treatments included LD 0:24, LD 13.5:10.5, LD 14:10, LD 14.75:9.25, LD 15.5:8.5, and LD 16:8. Additional photoperiod treatments of LD 4:20 and LD 8:16 photoperiods were tested at 24°C constant and fluctuating temperatures (16°-32°C). Relative humidity was maintained at about 70±10 percent in all treatments.

Larval development was monitored once a day. Larvae were considered to be in diapause when they had a characteristically pale colored integument, ceased feeding, constructed cocoons with no exit tube, and remained as larvae in cocoons after a period of time when non-diapausing larvae would have pupated (Hansen and Hardwood 1968). Observations were terminated when more than 50 percent larvae in LD 16:8 photoperiod treatment within a similar group of temperature emerged as adults.

The insects which still remained in the larval stage at that time were considered to be in diapause. Because of slightly different larval mortality rates, unequal number of larvae were counted in each treatment (Table III-1). The effect of main factors, temperature and photoperiod, and the interaction of these two factors, if any, was determined by factorial analysis. Critical diapause induction state (which is 50 percent of the larvae entering diapause) was also predicted using regression analysis (NCSS 1987).

Instar Sensitivity Experiments:

A set of experiments was designed to determine the relative sensitivity of different larval instars to diapause-inducing factors. Based on earlier studies, a diapause-averting condition of LD 16:8 photoperiod and 24°C, and a diapause-inducing condition of LD 13.5:10.5 photoperiod and 20°C were selected for this study.

The larvae were reared under nondiapausing conditions and only one specific instar was exposed to diapause inducing treatments to determine the instar sensitivity. The significance level of percentage diapausing larvae in relation to the instar sensitivity was determined by 5 % LSD analysis (Petersen 1985).

RESULTS

Diapause Induction: Role of Photoperiod and Temperature:

The expression of diapause induction in each treatment is presented in Table III-1. Data show that diapause in codling moth was induced in response to decreasing length of photoperiod and modifying effect of temperature. In complete darkness diapause was induced in less than 10% of population at temperature of 24°C, and nearly 40% at 20°C, and 52% at 16°C. As the length of photoperiod was increased incidence of diapause at 24°C constant also increased and reached 71% at LD 14:10 photoperiod, then decreased rapidly. The response to increasing photoperiod was different at other constant and fluctuating temperatures (Table III-1). For example, at 28°C, very low incidence or no diapause was seen at 0 to 8 hours photoperiod, while it increased dramatically between 13L-14L and decreased again at 15.5L and above.

Data in Table III-2 and Figure III-6 present a linear regression equation for the relationship between temperature and diapause induction of codling moth. The critical temperatures to induce diapause in 50 % (CT50) of the sample population are also presented. The CT50 at complete darkness was 15.7°C and ranged between 25.6° to 23.1°C for photoperiods of 13.5 to 15.5 hr. CT50 was

Table III-1. Percent diapause induction in codling moth populations collected from the Willamette Valley, Oregon under different photoperiodic and temperature conditions

Photoperiods (hr)	Temperatures (°C)					
	Constant					Fluctuating
	16	20	24	28	32	16 - 32 ($\mu = 24$)
0L/24D	52 (27) ab	40 (25) a	8 (26) a	4 (26) a	0 (29) a	33 (21) a
4L/20D	-	-	45 (20) bc	0 (30) a	-	35 (23) a
8L/16D	-	-	33 (18) b	0 (28) a	-	37 (24) a
13.5L/10.5D	93 (29) c	90 (29) b	57 (30) c	55 (29) c	0 (27) a	90 (21) b
14L/10D	96 (26) c	88 (26) b	71 (28) c	33 (30) bc	0 (30) a	86 (21) b
14.75L/9.25D	96 (27) c	100 (29) b	71 (28) c	23 (30) b	3 (29) b	92 (29) b
15.5L/8.5D	69 (26) c	93 (27) b	57 (27) c	3 (29) a	3 (31) b	87 (24) b
16L/8D	30 (27) a	35 (35) a	31 (28) b	0 (28) a	0 (29) a	39 (28) a

- 1) Figure in parenthesis are individuals surviving in each treatment
- 2) 95 % Least Significant Different (LSD)

Table III-2. Regression equations for the effects of various constant temperatures under different photoperiods on diapause induction in codling moth larvae collected from Willamette Valley, Oregon

Photoperiod hours Light/Dark	Critical Temperature (°C) 50 % diapause induction 95 % (CI)	Regression equation	R ²
0L/24D	15.7 b (13.61 - 17.71)	Y = 104.80 - 3.50 x	0.88
13.5L/10.5D	25.6 c (22.17 - 29.05)	Y = 191.60 - 5.53 x	0.87
14L/10D	25.2 c (22.64 - 27.72)	Y = 205.80 - 6.18 x	0.94
14.75L/9.25D	25.3 c (21.91 - 28.67)	Y = 216.40 - 6.58 x	0.91
15.5L/8.5D	23.1 c (17.99 - 28.21)	Y = 178.20 - 5.55 x	0.75
16L/8D	11.1 a (8.64 - 13.48)	Y = 76.40 - 2.38 x	0.71

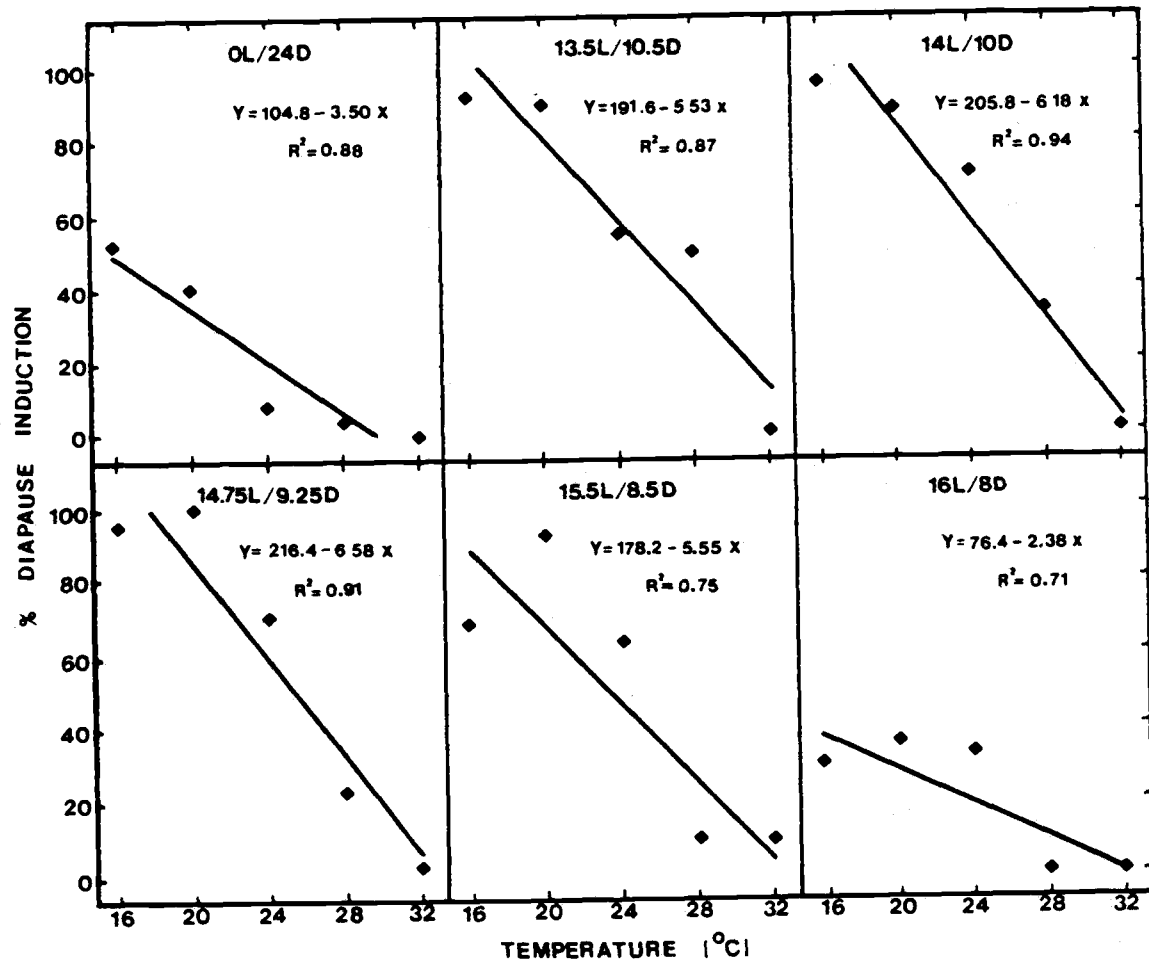


Figure III-6. Relationship between temperature and diapause induction in codling moth larvae under different photoperiod regimes

11.1°C for 16 hr photoperiod. The data suggest that photoperiod had an important role in diapause induction in codling moth.

The effect of photoperiod, as presented in Table III-1, was not independent of the influence of temperature. Therefore, we developed a model to explain the role of both temperature and photoperiod in codling moth diapause induction. Using stepwise regression analysis, we found that interaction between temperature and photoperiod was the most important factor in diapause induction in codling moth. The following equation and parameters expressed the occurrence of diapause induction.

$$Y = b_0 + b_1X_1 + b_2X_1^2 + b_3X_2 + b_4X_2^2 + b_5X_1X_2 \quad (1)$$

$$Y = -2078.212 - 6.98942X_1 - 0.28214X_1^2 + 324.7027X_2 - 12.32053X_2^2 + 1.03677X_1X_2 \quad (2)$$

where Y= Percent of diapause induction, X_1 = Temperature, X_2 =Photoperiod, ($R^2= 0.89$; $P<0.001$). The prediction of diapause induction from the data in Figure III-7 by using the above equation (2) is presented in Table III-2 and depicted in Figure III-8. The critical photoperiod for induction of diapause in the codling moth population from the Willamette Valley was LD 15.5:8.5 at 24°C. A photoperiod of 15.5 hr occurs in the Willamette Valley

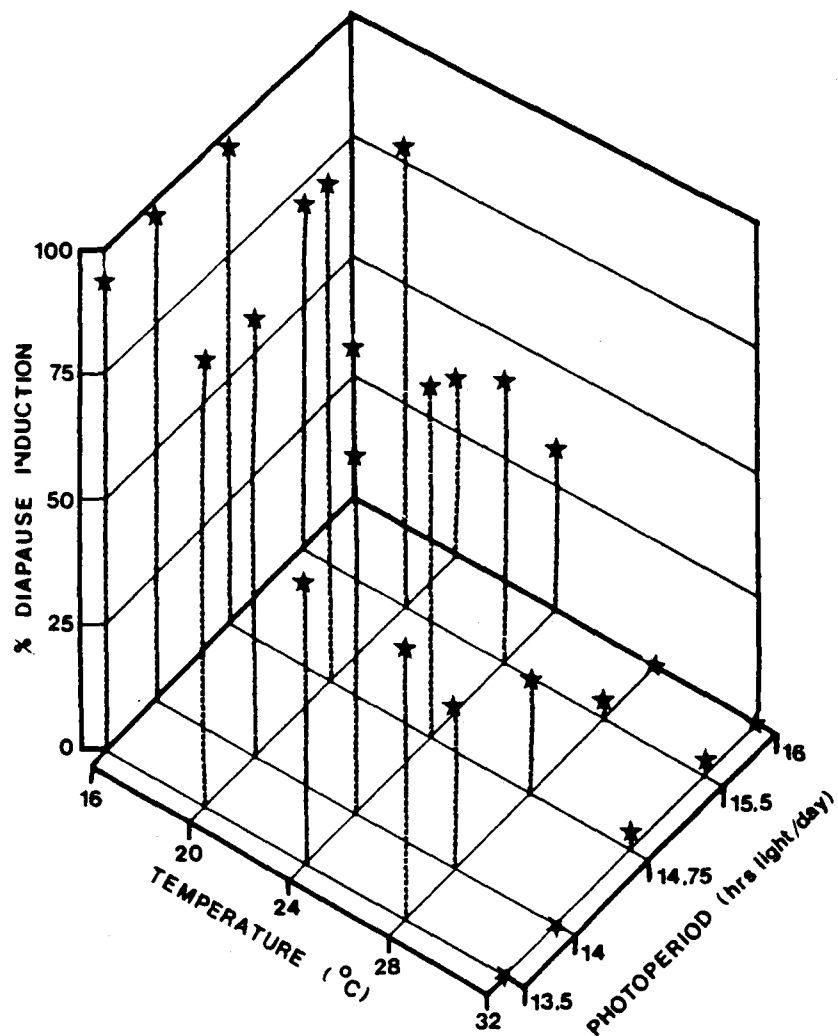


Figure III-7. Diapause induction in codling moth larvae in relation to various photoperiods and constant temperatures

Table III-3. The influence of photoperiod and temperature on diapause induction in codling moth larvae collected from the Willamette Valley, Oregon

Temperature (°C)	Photoperiod hours Light/Dark per day	Number of sample observed	% Diapause Induction	
			Predicted value **)	95 % (CI)
16	13.5L/10.5D	29	99.74 ***	(80.20 - 119.27)
16	14L/10D	26	100.98 a	(86.00 - 115.96)
16	14.75L/9.25D	27	91.28 a	(76.65 - 105.92)
16	15.5L/8.5D	26	67.73 ab	(52.75 - 82.71)
16	16L/8D	27	44.33 b	(24.79 - 63.86)
20	13.5L/10.5D	29	87.14 a	(72.95 - 101.33)
20	14L/10D	26	90.45 a	(80.26 - 100.64)
20	14.75L/9.25D	29	83.87 a	(72.59 - 95.14)
20	15.5L/8.5D	27	63.42 ab	(53.24 - 73.61)
20	16L/8D	26	42.09 b	(27.91 - 56.28)
24	13.5L/10.5D	30	65.51 ab	(51.74 - 79.28)
24	14L/10D	28	70.89 ab	(60.31 - 81.47)
24	14.75L/9.25D	28	67.42 ab	(55.32 - 79.52)
24	15.5L/8.5D	28	50.05 b	(39.51 - 60.67)
24	16L/8D	28	30.83 bc	(17.06 - 44.60)
28	13.5L/10.5D	29	34.85 b	(20.66 - 49.04)
28	14L/10D	30	42.31 b	(32.12 - 52.50)
28	14.75L/9.25D	30	41.95 b	(30.67 - 53.22)
28	15.5L/8.5D	29	27.72 bc	(17.54 - 37.91)
28	16L/8D	28	10.54 c	(- 3.65 - 24.73)
32	13.5L/10.5D	27	- 4.84 c	(-24.37 - 14.78)
32	14L/10D	30	4.70 c	(-10.28 - 19.67)
32	14.75L/9.25D	29	7.44 c	(- 7.19 - 22.08)
32	15.5L/8.5D	31	- 3.67 c	(-18.65 - 11.31)
32	16L/8D	29	-18.78 c	(-38.31 - 0.76)

$$***) Y = - 2078.212 - 6.98942 x_1 - 0.28214 x_1^2 + 324.7027 x_2 - 12.32053 x_2^2 + 1.03677 x_1 x_2$$

$$R^2 = 0.89 \quad (P < 0.001)$$

**) Mean ranking of predicted values

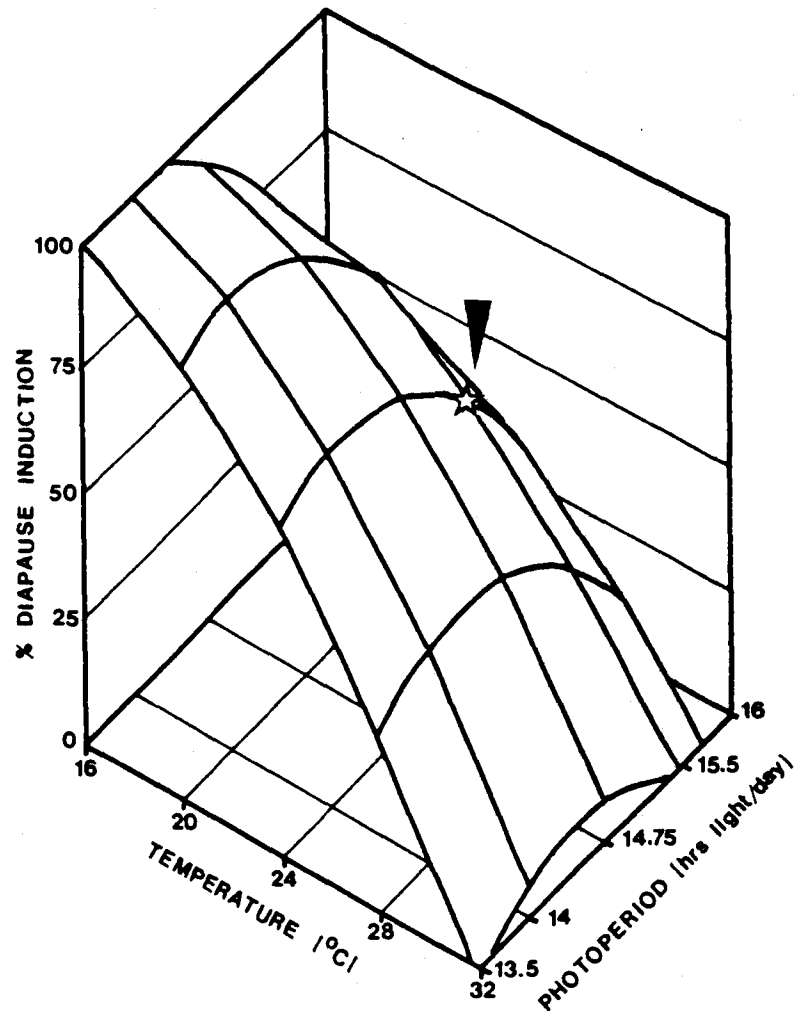


Figure III-8. Prediction of diapause induction in codling moth larvae in relation to various photoperiods and constant temperatures (☆ is Critical Photoperiod)

A photoperiod of 15.5 hr occurs in the Willamette Valley during late summer (August). Within 95% CI, fifty percent or more larvae could be induced to diapause by a combination of temperature below 24°C and photoperiods less than 15.5 hours. Photoperiod did not have a significant influence on diapause induction at temperatures above 28°C.

Diapause induction in codling moth larvae in relation to different photoperiods under constant and fluctuating temperatures is presented in Figure III-9. Fluctuating temperatures (16°-32°C, average = 24°C) produced a higher incidence of diapause in larvae than a constant temperature of 24°C. The diapause incidence was greater in photoperiods of LD 13.5:10.5 - LD 15.5:8.5. These data also indicate that approximately LD 15.5:8.5 is the critical photoperiod for diapause induction in codling moth populations of the Willamette valley.

Instar Sensitivity to Diapause Induction:

The results of experiments on the sensitivity of larval instars to diapause-induction are presented in Table III-4. Diapause could be induced in any instar during larval development. The third and fourth instar larvae showed the most sensitivity to diapause induction (29-30% diapause incidence) although statistically not

Table III-4. Sensitivity of codling moth larval instars to diapause induction under diapause-inducing photoperiod and temperature

Larval instar exposed to diapause inducing condition (photoperiod 13.5L/10.5D 20° C)	Larval growth (at 16L/8D 24° C) prior to and after exposure to diapause inducing condition	Number observed	% diapause induction
Larva 1	Larva 2, 3, 4, 5	11	27 bc
Larva 2	Larva 1, 3, 4, 5	23	22 b
Larva 3	Larva 1, 2, 4, 5	27	30 c
Larva 4	Larva 1, 2, 3, 5	17	29 c
Larva 5	Larva 1, 2, 3, 4	21	24 bc
control	Larva 1, 2, 3, 4, 5	40	13 a

Nos. followed by the same letter are not significantly different (P<0.05, LSD)

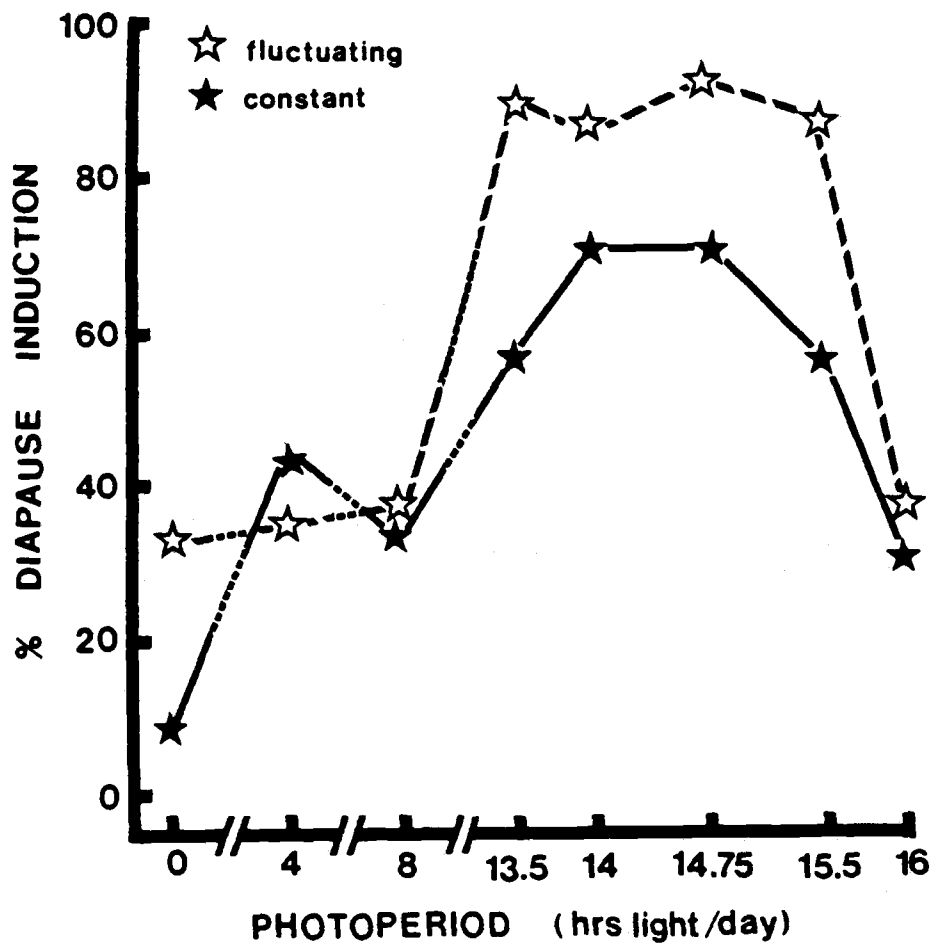


Figure III-9. The effect of photoperiod on diapause induction in codling moth larvae under constant (24° C) and fluctuating temperatures (16° - 32° C)

significantly different from the first and the fifth instar larvae (24-27% diapause incidence) in this respect. The second instar larvae was the least sensitive (22% diapause incidence) to diapause induction. Codling moth larvae in the control treatment, which were never exposed to diapausing critical photoperiod and temperature in any instar, had significantly lower incidence (13%) of diapause at 16 hr photoperiod and 24°C. However, no incidence of diapause was observed in our laboratory rearings at a photoperiod of LD 18:6.

DISCUSSION

Singh and Ashby (1986) reported that diapause in codling moth larvae could be induced under complete darkness. However, our data (Table III-1, Figure III-6) show that even in dark, the incidence of diapause was influenced by temperature. If the temperature was 28°C or higher, the incidence of diapause was reduced to zero. The incidence of diapause increased at lower temperatures (< 24°C).

The role of temperature and its interaction with photoperiod in diapause induction has been presented in Table III-2. High temperatures above 28°C during larval development would suppress the effect of photoperiod in diapause induction. The influence of photoperiod appears important at shorter photoperiods of LD 15.5:8.5 hours per day (Figure III-8). These results agree with previously reported findings by Garcia-Salazar et al. (1988). The temperature in our studies acted as a modifier of photoperiodic influence in diapause induction in codling moth (Tauber et al. 1986).

The critical photoperiod (CPhP50) for diapause induction in codling moth population from Willamette Valley (latitude 44.5°N) was LD 15.5:8.5 at 24°C and this compares well with CPhP50 of 14.4 hours for codling moth populations from Maine which has a latitude 45°N (Siegler

and Simanton 1915). Our findings of a CPhP50 of 15.5 hours are similar to and agree with the prediction of CPhP50 of 15.7 hours by Riedl and Croft (1978). These results suggest that the population of codling moth from Willamette Valley can possibly complete only two generations during the season in this region.

A proportion of larvae entered diapause at LD 16:8 photoperiod while a small population did not diapause at LD 0:24 photoperiod in our experiments. These differences in the incidence of diapause suggest a wide genetic diversity in codling moth populations with respect to diapause induction. This also explains why codling moths are able to adapt to geographically and climatically different areas.

There appears to be little difference in the sensitivity of different larval instars to diapause induction, even though there is some evidence suggesting that the third and the fourth instars were more sensitive than the others. These results agree with previous studies of Dickson (1949) and Garcia-Salazar (1984).

The incidence of diapause in codling moth larvae was higher under fluctuating temperatures than at constant temperatures (Figure III-9). It appears that the fluctuation itself was responsible for induction of diapause rather than the temperatures used. This may

provide some evolutionary advantages to codling moth as the degree of fluctuations may indicate the onset of adverse weather conditions.

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CHAPTER IV

SEASONALITY OF DIAPAUSE INDUCTION AND TERMINATION
IN CODLING MOTH, Cydia pomonella L.
(LEPIDOPTERA: OLETHREUTIDAE)

Abstract

The seasonality of diapause induction and termination in codling moth, Cydia pomonella L., population from the Willamette Valley, Oregon was studied under field conditions during a three-year period (1986-1988). Codling moth populations from this area began to come out of diapause in the third week of March when the photoperiod was 13-13.5 hours. Nearly 50% of the larvae came out of diapause during the fourth week of April, and 90% or more in the second week of May to the end of June. Laboratory studies on sensitivity of larvae to photoperiods for diapause termination showed that 13.4 hours of light was the critical photoperiod for diapause termination.

The field rearing studies show that both univoltine and bivoltine populations exist in the field. Approximately 39.4 ± 13.5 (mean \pm SE) of the first generation larvae of codling moth entered diapause even though diapause averting conditions were present in the field. Most of the second generation larvae (> 93%) entered diapause.

INTRODUCTION

Management of codling moth, Cydia pomonella L., in apples and pears is dependent on the ability to accurately predict its seasonal development (Riedl 1983, Tauber et al. 1986). A number of studies dealing with life cycles of codling moth have been conducted over the years (see Putman 1963 for an overview). However, the understanding of regional life cycle diversities is still meager, although ample data exist on seasonal development of this insect from different geographical areas of North America (Forbes 1915, Selkregg and Stegler 1928, van Leuween 1929, Nettles 1934, Yother and van Leuween 1931, Webster 1936).

Diapause plays a key role in the seasonal life cycle of codling moth. Earlier investigations reported that codling moth populations from different geographical areas or from different hosts initiate and terminate diapause under diverse environmental conditions (Shel'Deshova 1967, Phillips and Barnes 1975, Geier and Briese 1978, Riedl and Croft 1978). Both photoperiod and temperature appear to play a major role in diapause induction and diapause termination (Russ 1966, Shel'Deshova 1967, Jermy 1967, Peterson and Hamner 1968, Hayes et al. 1970). Other factors such as nutritional quality of the host plant may

also influence the diapause sensitivity (Herriot and Waddel 1942, Riedl and Croft 1978, Sieber and Benz 1980). Garcia-Salazar et al. (1988), Setyobudi (1989, Chapter III.) reported interactive effect of photoperiod and temperature in diapause induction and termination in codling moth populations from Willamette Valley, Oregon. AliNiazee (1988) divided diapause into five different stages and showed that discreteness of these stages varies from insect to insect. In some insects, two or more of these stages may overlap and different environmental factors may have different influences on different stages. The post-diapause development in codling moth has been studied and a crude developmental model has been developed (Riedl et al. 1976, Riedl and Croft 1978). A generalized PETE model is used in many codling moth management programs (Welch et al. 1978, Welch and Croft 1983). Codling moth is a highly adaptive insect and has developed many geographic and host races in many parts of the world (Geier 1963, Shel'Deshova 1967, Phillips and Barnes 1975, Riedl and Croft 1983). Consequently, a generalized model is inadequate in describing emergence patterns in different parts of the world. An understanding of diapause and post-diapause development of different populations of codling moth is essential to develop an accurate predictive ability for its management. This paper

reports the results of a two-year study in which we studied the seasonality of a codling moth population from the Willamette Valley of Oregon, with emphasis on diapause induction, diapause termination , and post-diapause development under field conditions.

MATERIALS AND METHODS

Insects: Insects required for this study were obtained as diapausing larva collected from abandoned and cultivated apple orchards near Corvallis, Oregon, in corrugated cardboard traps during late fall (October - November). Only fifth instar diapausing larvae were used in diapause termination and diapause maintenance experiments. F_1 and F_2 progenies of these larvae were used in diapause induction experiments.

Diapause Termination: Field Studies

A total of 100 diapausing fifth instar larvae in 1987 and 270 larvae in 1988 were randomly selected and placed singly into small disposable glass pipets (13 cm long, 0.6 cm diameter). The open ends of these pipets were closed with sterile cotton to prevent larval escape. Batches of ten pipets with larvae were sandwiched between corrugated cardboard to mimic the natural diapausing sites for the larvae. Each batch of pipets was then placed inside a clear one quart plastic bag (Ziploc brand) to prevent excessive humidity during overwintering. This set-up of glass pipets, corrugated sandwich, and clear plastic bag provided easy access and clear view for observing larval development.

Each plastic bag was nailed to a tree trunk at ground level, 0.5 m above the ground, and to a tree limb (1.5 m above the ground) on randomly selected apple trees. Three apple orchards were selected for this study including one at Oregon State University's Entomology Research Farm (Corvallis), one at Kiger Island (5 miles south of Corvallis), and Skyline (10 miles east of Corvallis near Albany). The larvae were placed at the respective sites during the month of November.

Observations on diapause termination were initiated on March 1. The pipets with larvae were checked twice a week and the larvae were considered to have terminated their diapause when they developed into pupae. Data were analyzed by analysis of variance with a factorial randomized block design. The LSD test was used for mean separation among the treatments.

Field emergence and seasonal flight patterns of codling moth populations were monitored by placing 3 sex pheromone traps at each site in early April. Traps were checked twice a week and the moths caught were recorded throughout the spring and summer months. Traps were serviced after each count and the attractant dispensers were replaced with new ones every 4-6 weeks. The last moth counts were taken on October 1.

Diapause Termination: Photoperiod Sensitivity

Batches of ten randomly selected fifth instar diapausing larvae were similarly exposed in glass pipets to six photoperiodic regimes at $24 \pm 1^\circ\text{C}$ to study photoperiodic sensitivity of larvae and diapause termination in the laboratory. These photoperiod treatments were LD 11:13, LD 12:12, LD 13:11, LD 14:10, LD 15:9, and LD 16:8. Percentage of diapause termination was recorded for each treatment and the critical photoperiod for diapause termination was determined by regression analysis. These experiments were conducted for a period of 50 days. Individuals which did not pupate at the end of this period were assumed to be still in diapause.

Diapause Induction Under Field Conditions

Diapausing larvae collected in corrugated cardboard bands were placed in a wooden screen cage and exposed to field temperature and photoperiods of overwintering conditions at the Oregon State University Entomology Research Farm. The codling moth adults that emerged from these larvae in the spring were placed in one gallon ice cream cartons lined with wax paper. Paper strips with deposited eggs were cut out and placed for hatching in 1.4 L Servin'saver cup. The top of the cup was covered by a nylon screen. Neonate larvae were placed singly in

glass pipets filled halfway with artificial codling moth diet (Bioserve, Frenchtown, New Jersey). Pipets with larvae were placed in a plastic lunch box (20x15x6 cm³). These boxes were placed inside a Stevenson screen at the Oregon State University Entomology Research Farm to study diapause induction. These studies were started during April and continued throughout the summer months.

Batches of 30-150 neonate larvae were exposed at weekly intervals from mid-May to mid-August for diapause induction studies. The larvae were monitored twice a week. The larvae were considered to be in diapause when they ceased feeding, constructed cocoons with no exit tube, had a characteristically pale integument, and remained as larvae in cocoons after a period of time when non-diapausing larvae would have pupated (Hansen and Harwood 1968). These studies continued until the end of September when all the larvae entered diapause.

RESULTS AND DISCUSSION

Diapause Termination

Results of diapause termination experiments (Figure IV-10 and IV-11) show that the codling moth population from the Willamette Valley began to terminate diapause in the third week of March when the photoperiod was 13-13.5 hours. In the fourth week of April, more than 50% of the diapausing larvae had terminated their diapause. About 90% of the larvae had terminated their diapause by the second week of May in 1987 and the end of June in 1980. These results suggest that diapause termination was triggered by increasing photoperiods (Figure IV-12) and mean daily temperatures. The times and patterns of cumulative diapause termination were similar for 1987 and 1988 (Figure IV-10 and IV-11). The role of photoperiod as a trigger for diapause termination in codling moth has also been reported by Peterson and Hamner (1968), Hayes et al. (1970), and Sieber and Benz (1980).

Laboratory experiments on the sensitivity of larvae to photoperiods for diapause termination showed that 13.41 hours light was the critical photoperiod for diapause termination (Figure IV-12). A photoperiod of 13.5 hours occurs during the third week of March in the Willamette Valley. Our laboratory results on the photoperiodic

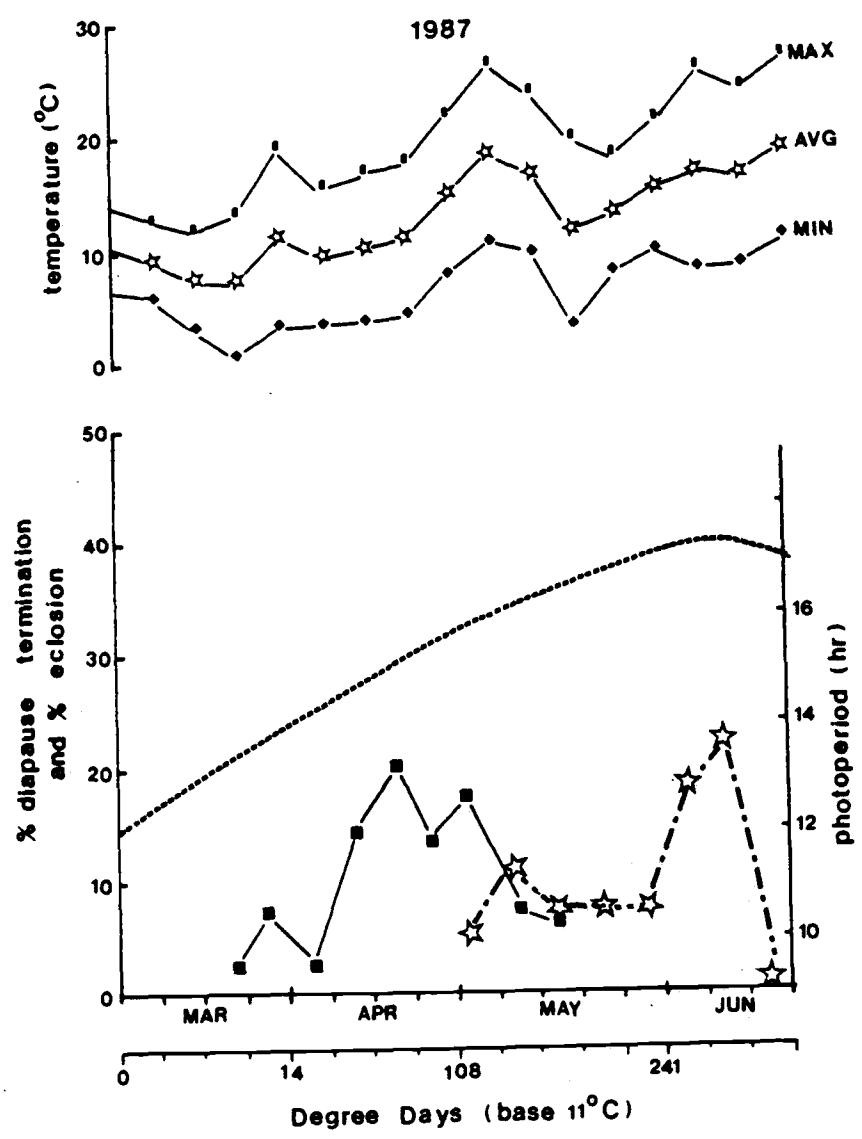


Figure IV-10. Percent diapause termination and adult eclosion in codling moth under field conditions, Corvallis, Oregon 1987

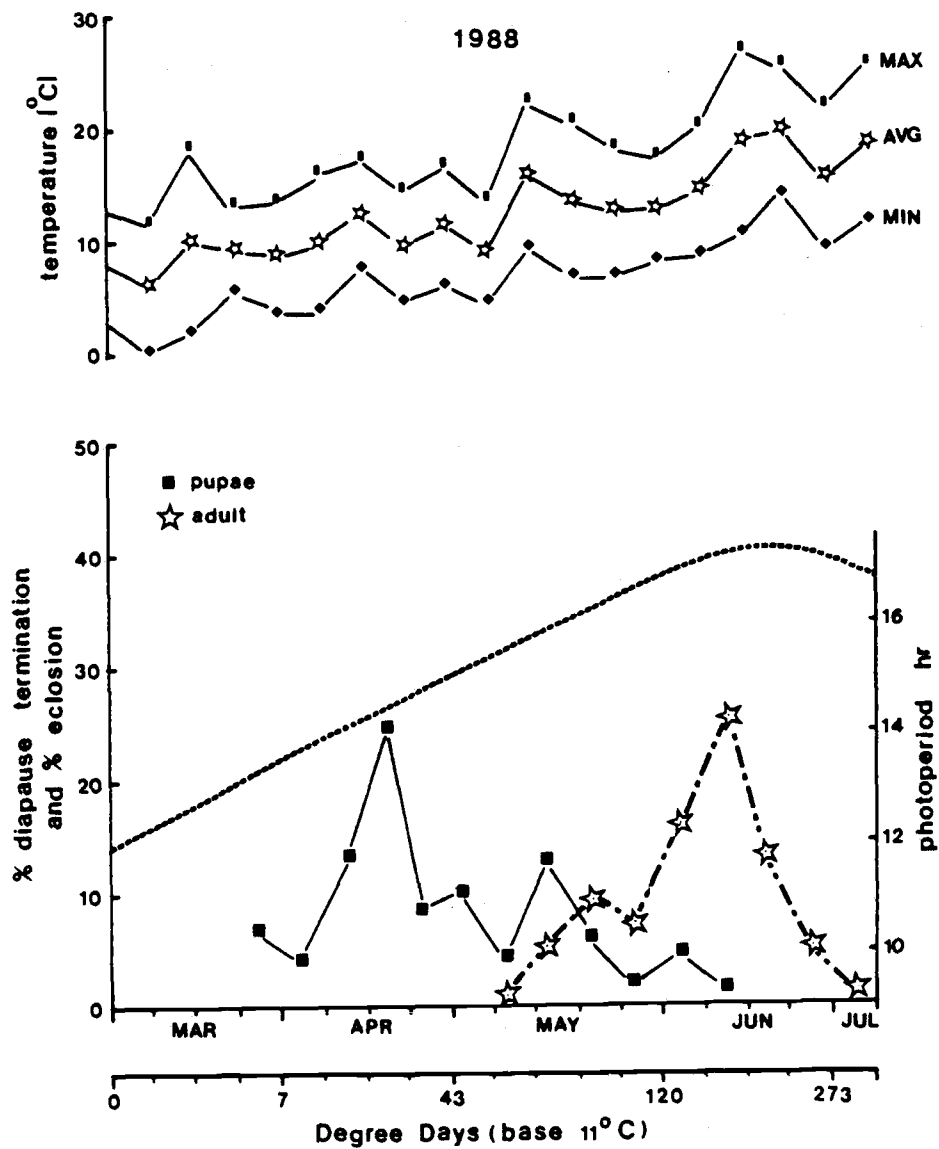


Figure IV-11. Percent diapause termination and adult eclosion in codling moth under field conditions, Corvallis, Oregon 1988

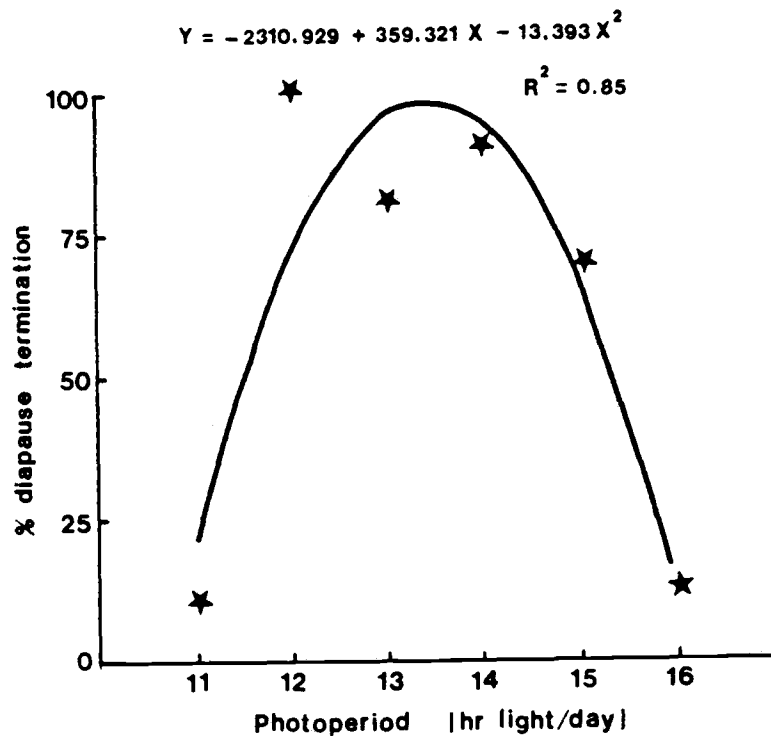


Figure IV-12. Diapause termination at different photoperiods in codling moth larvae in laboratory at $24 \pm 1^{\circ} \text{C}$

sensitivity of the larvae to diapause termination support the results of our field experiments on diapause termination.

Lower temperatures during 1988 (average $14.7 \pm 4.63^{\circ}\text{C}$) apparently extended the period during which diapause termination occurred. Higher temperatures during 1987 (average $15.21 \pm 4.13^{\circ}\text{C}$) narrowed this period. Period of adult emergence was also similarly influenced by the prevailing temperatures in 1987 and 1988. Adult emergence was more synchronized in 1987 than in 1988 as a result of faster development in response to higher temperatures.

No significant differences were noticed between male and female codling moths in their ability to terminate diapause. The ratio of emerged males to females was higher early in the season while more females terminated diapause late in the season (Figure IV-13). The protandry phenomenon was reported by Glen and Brain (1982) for the codling moth populations from Long Ashton, U.K.

Following diapause termination, temperature apparently played an important role in post-diapause development. This was evident by the different patterns of adult emergence during 1987 and 1988 (Figure IV-14). Because of slightly higher temperatures during the spring of 1987, the larvae completed their post-diapause development and emerged as adults much earlier and in

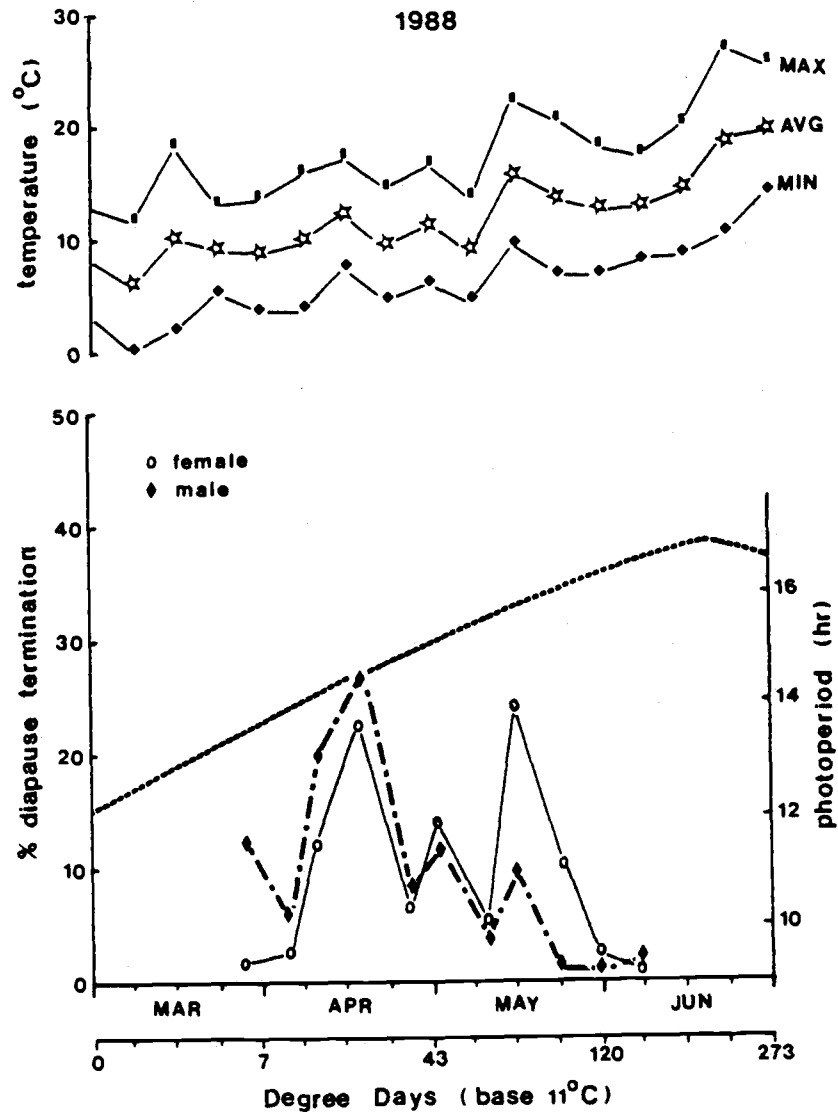


Figure IV-13. Percent diapause termination in male and female codling moths under field condition Corvallis, Oregon 1988

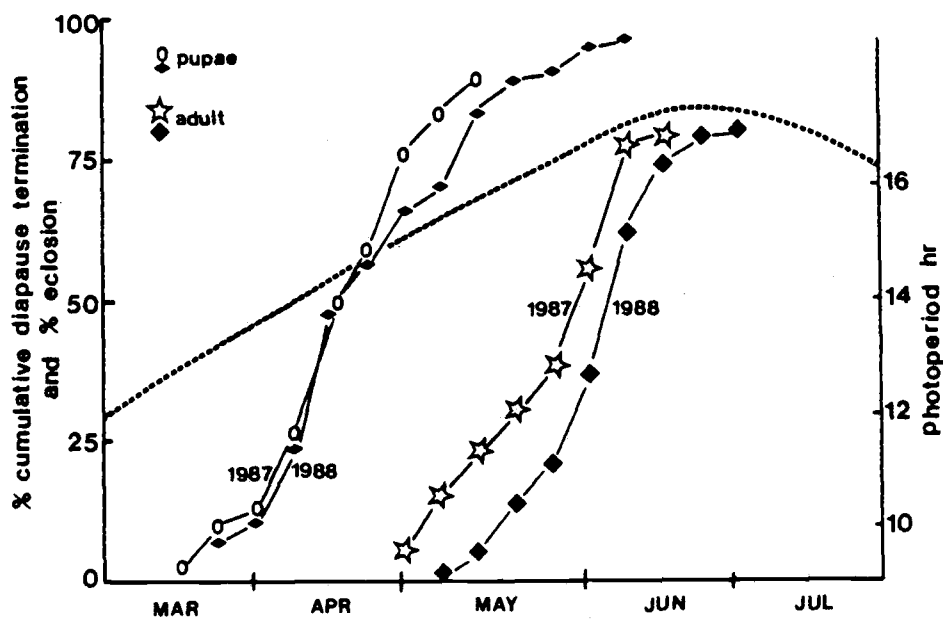


Figure IV-14. Cumulative percentage diapause termination and adult eclosion in codling moth under field conditions, Corvallis, Oregon 1987 and 1988

shorter period in 1987 than in 1988.

Moth capture data from pheromone traps showed that adults emerged a week earlier in diapause termination experiments than in the field (Figure IV-15 and IV-16) and Figure IV-17 showed data from pheromone traps in 1986. However, the proportion of moths that were caught before emergence began in the diapause termination experiment less than one percent of the total catch during the growing season. The early moths probably emerged from overwintering sites directly exposed to the sun, and may have completed their post-diapause development faster than the experimental larvae kept in the shade.

Diapause Induction Under Field Conditions:

Codling moth in the Willamette Valley has only two complete generations per season as shown in Figure IV-18. Results of diapause induction experiment (Appendix Table 1) show that approximately 39.4 ± 13.50 (mean \pm SE) of the first generation larvae entered diapause although the environmental conditions were favorable for continued development. Our results also show that most of the second generation larvae (> 93%) entered diapause. All diapausing larvae would overwinter and emerge as adults during the following spring. The first incidence of diapause was observed in the third week of July and nearly

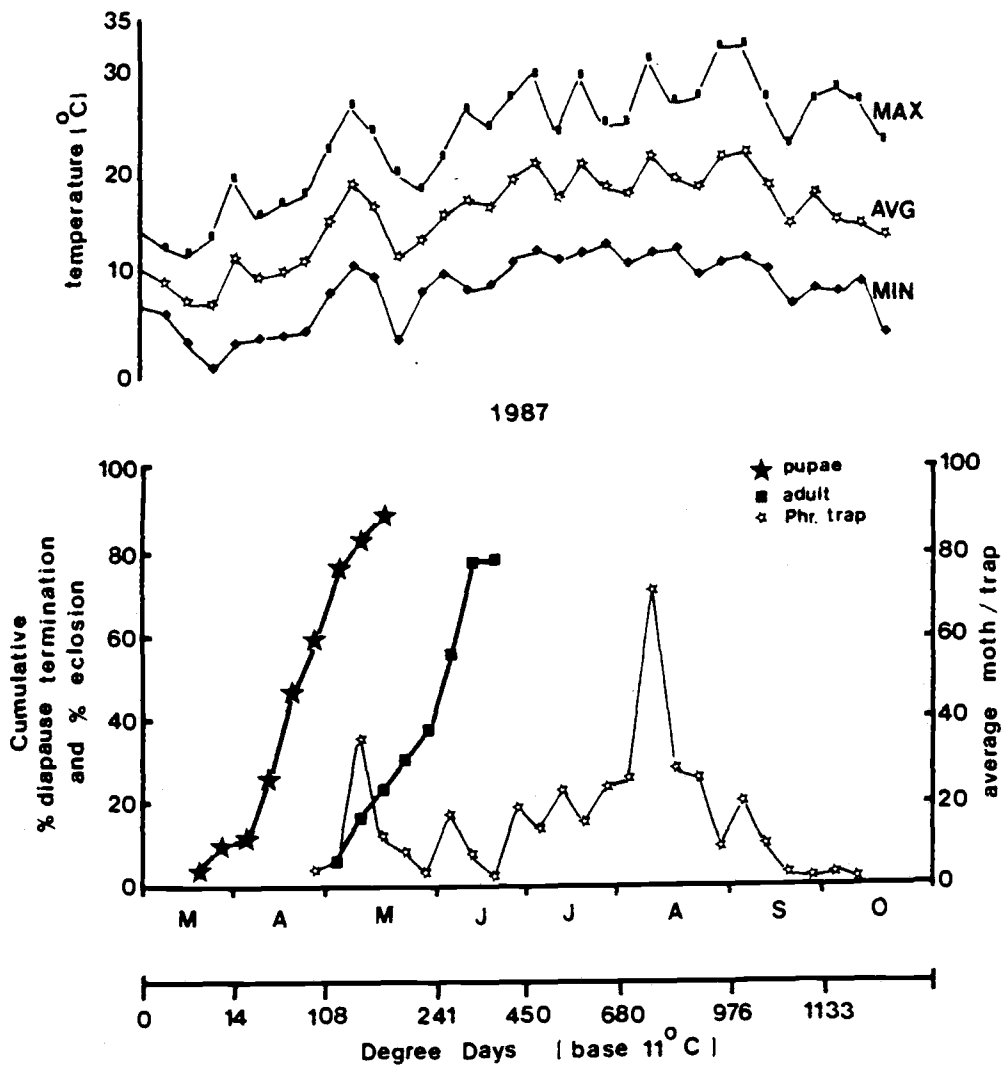


Figure IV-15. Cumulative percentage diapause termination adult eclosion, and average numbers of codling moths trapped in sex pheromone traps in Corvallis, Oregon 1987

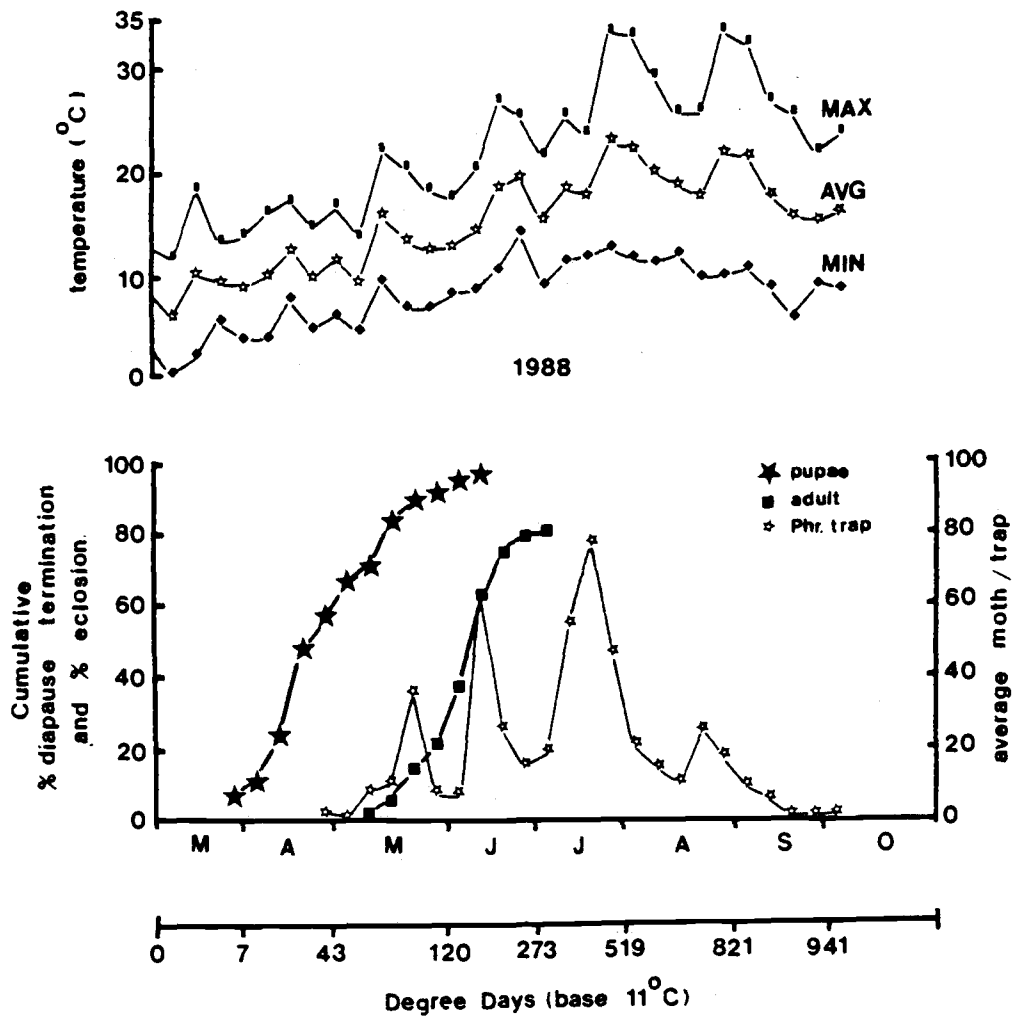


Figure IV-16. Cumulative percentage diapause termination, adult eclosion, and average numbers of codling moths trapped in sex pheromone traps in Corvallis, Oregon 1988



1986

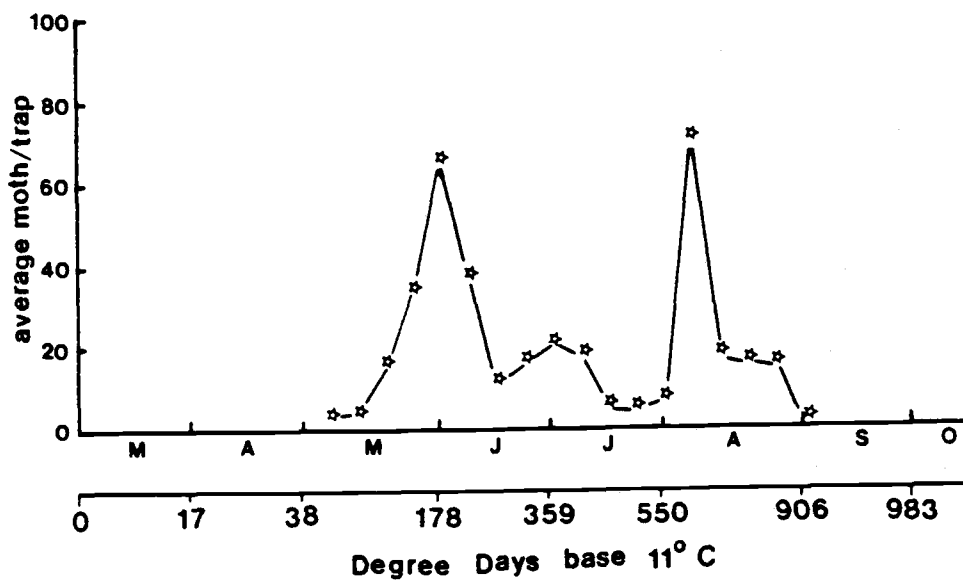


Figure IV-17. Average numbers of codling moth caught in sex pheromone traps in Corvallis, Oregon 1986

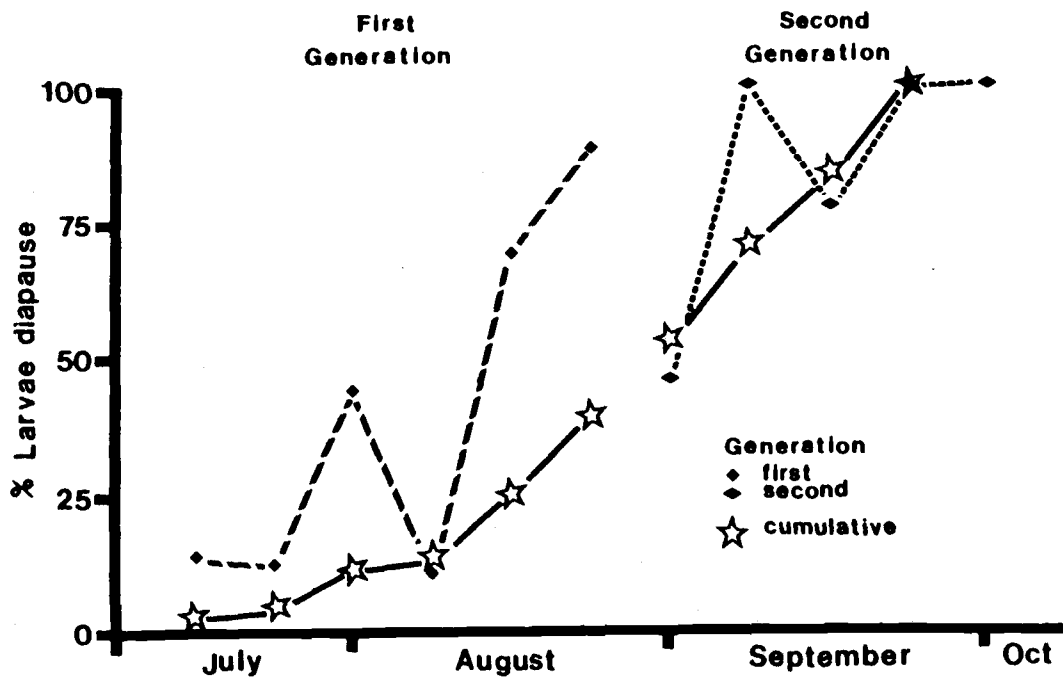


Figure IV-18. Percentage codling moth larval diapause observed under field conditions near Corvallis, Oregon 1988

50% diapause was observed in the fourth week of August. When young larvae (\pm 12 hr old) were placed in the field during the month of May and June, a small proportion (10-14%) of the population went into diapause. However, when the larvae were placed in the field during early July, approximately 69% went into diapause. Since all of these came from the first generation moths, it appears that almost all of these larvae will complete development without going into diapause while a majority of the late emerging first generation larvae will enter diapause. However, diapause always occurs and at no time complete non-diapause development seems to occur in the field. A few adults emerged during the second week of September probably because of the long summer season in 1988. These results suggest that the propensity for univoltinism is prevalent in the codling moth populations from the Willamette valley. This is not surprising as the summer temperatures in the Willamette Valley are unpredictable. Although photoperiodic conditions appear to be favorable for non-diapause growth during July, the temperature fluctuation and a lack of consistency may force many larvae into diapause. In any event, the diapause in the first generation is much more common than thought before and helps to provide better winter survival and synchronization of adult emergence in the following

spring.

Diapause is a genetically controlled phenomenon in insects (Lee 1955, Tauber et al. 1986). Our studies suggest that there are at least two genetically different sub-populations comprising the codling moth populations in Willamette Valley. One of these populations is strictly univoltine and the other is a multivoltine population, and there is potential for a cross breeding and gene flow between these two types. Further ecological studies could isolate and characterize these two apparently genetically different sub-populations of codling moths in Willamette Valley. Such information will be useful in implementation of IPM programs and also for pesticide resistance management in this insect.

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CHAPTER V

OVERWINTERING BIOLOGY OF CODLING MOTH,
Cydia pomonella L., IN THE WILLAMETTE VALLEY
OREGON

Abstract

The head capsule width of the codling moth, Cydia pomonella L. larvae was measured. Based on head capsule width measurements, the overwintering behavior of codling moth from the Willamette Valley, Oregon, was studied. The data show that codling moth overwinters in this area as diapausing fourth, and fifth instar larvae. Most of the diapausing third instars were found parasitized. The proportions of the fourth and fifth instar diapausing larvae were between 12-20 and 70-90 %. These percentages may vary according to the type of the orchard management practices. There were slightly more fourth instar overwintering larvae in abandoned orchards than in commercial orchards. None of the third instar diapausing larvae became pupae and adults because of parasitism. However, 16% of fourth instar larvae successfully enter to pupae and adults without entering to the fifth instar, and most of the fifth instar pupated and emerged as adults.

INTRODUCTION

Codling moth, Cydia pomonella L., is the most serious pest of apples and other pome fruits in many parts of the world. Variations in seasonal cycles of codling moth populations have been recognized among different geographic populations (Shel'Deshova 1967, Riedl 1983) and also among populations from different host plants (Phillips and Barnes 1973). However, relatively little is known about the intra-population variation of overwintering characteristics among and within geographic populations and its ecological significance (Wipking and Newmann 1986).

In general, the larvae of codling moth develop through five instars (Williams and McDonald 1982, Weitzner and Whalon 1987, Setyobudi 1989) and overwinter in the late fifth instar (Dickson 1949, Smotavac 1957, Peterson and Hamner 1968). Weitzner and Whalon (1987) showed that in Michigan the codling moth overwinters as either fourth or fifth instar diapausing larvae. In the Willamette Valley of Oregon it is presumed that codling moths overwinter as the fifth instar larvae, however, no detailed studies have been conducted to verify this assumption.

Reported here are results of experiments conducted to study the intra-population variations in overwintering biology of the codling moth from the Willamette Valley of Oregon. Also discussed is the ecological significance of these intra-population variations in the phenology of this insect in apple and pear hosts.

MATERIALS AND METHODS

Measurements of Head Capsule Widths of Larval Instars:

Codling moth adults that emerged from overwintering larvae in abandoned and commercial apple orchards were collected and brought to the laboratory for egg laying. Neonates larvae from these eggs were used in this study. The larvae were reared singly in disposable glass pipets (13 cm by 0.6 cm diameter) filled halfway with a synthetic codling moth diet (Bioserve, Frenchtown, New Jersey) in laboratory (at $24 \pm 1^{\circ}\text{C}$, LD 18:6 photoperiod, and $70 \pm 5\%$ RH). The wider end of the pipet was plugged with cotton after placing the larvae onto the diet. These glass pipets provided a clear view of larval development during these studies.

A total of 465 larvae from non-commercial or abandoned orchards and 239 larvae from commercial orchards (Table V-1) were reared and their head capsule widths were measured in each instar soon after ecdysis. An ocular micrometer placed inside a binocular microscope was used for measuring the head capsule widths. Larvae were chilled to immobilize them for measurements. Mean head capsule widths for each instar from these studies were used as standards for determination of larval instars in the field-collected larval samples.

Determination of Overwintering Larval Instar Collected in the Field

Instar determinations were made in overwintering codling moth larvae collected at different times in a non-commercial (abandoned) and a commercial orchard. Ten trees were randomly selected in each orchard and corrugated cardboard traps were set up at the base (± 30 cm above the ground) of each tree in early August in 1986 and 1987, and the experiment was designed in a Completely Randomized Design. The diapausing larvae were collected in November during each year for instar determination. A total of 1647 diapausing larvae was studied in these experiments. Larval instars were determined in the laboratory by measuring the head capsule widths of these larvae, and comparing these data unit with the standard head capsule widths of laboratory reared larvae. Data on percentages of different overwintering instars were analyzed by ANOVA (F test) and means were separated by the Least Significant Difference (LSD) method (Petersen 1985) at $P < 0.05$.

Behavior of Overwintering Larvae During Post-diapause Development

A few post diapause-development parameters, such as the factors contributing to larval mortality, times to and patterns of pupation and adult emergence, and proportions

of larvae entering pupal and adult stages, were determined under field conditions. Samples of diapausing larvae collected from non-commercial and commercial apple orchards in Corvallis, Oregon, were studied separately. Similarly, activity and feeding behavior during post diapause development were also studied under field conditions in a group of diapausing larvae collected in cardboard traps in these apple orchards.

a. Diapause Termination and Adult Emergence

A total of 200 overwintering and diapausing larvae were selected at random during October-November 1987 for this study. Of these, 50 were third instar larvae, 50 were fourth instar larvae and 100 were fifth instar larvae. The larvae were exposed to prevailing field temperatures and photoperiods at the OSU Entomology Research Farm in Corvallis. The larvae were placed singly in disposable glass pipets. Both ends of each pipet were plugged with sterile cotton to confine each larva. Batches of ten pipets each were sandwiched in between two sheets of corrugated cardboard and were placed in clear pleated plastic bag (Ziploc brand) to prevent a build up of high humidity. A group of ten larvae was regarded a replication. There were five replications each for the third and fourth instar diapausing larvae and ten

replications for the fifth instar. Each replication was placed in a separate Stevenson's screen to shield the larvae from exposure to direct sunlight. The plastic bags and glass pipets provided a clear view of larval development during this studies.

The larvae were observed for post-diapause development twice a week beginning in March 1988. The larvae were considered to have terminated their diapause when they pupated. Data on times to pupation, adult emergence and larval mortality (parasitism), were analyzed by ANOVA (F test) and means separated by the Least Significant Different (LSD) method at $P < 0.05$ (Petersen 1985).

b. Activity and Feeding Behavior

Activity and feeding behavior of larvae during post-diapause development were studied in the field in April 1988 when apples began to bloom in Corvallis. Equal numbers of diapausing larvae from third, fourth, and fifth instar groups were singly exposed to three diets in plastic cups. These diets were a cluster of flowers, artificial codling moth diet, and pieces of apple bark. Each combination of larval instar group and a diet constituted a single treatment and there were nine treatments in total (3 instars x 3 diets). Each treatment

had six replications consisting of six larvae. A lid was placed on top of the plastic cup to confine the larva on the diet. The plastic cups were placed under a Stevenson's screen to expose the larvae to the prevailing field temperatures and photoperiods. The larvae were observed three times a week for assessing their mobility and feeding behavior.

RESULTS AND DISCUSSION

Measurements of Head Capsule Widths of Larval Instars Reared in Laboratory

Measurements of head capsule widths of larval instars (progenies of codling moth adults collected from commercial and non-commercial apple orchards in Corvallis) that were reared on artificial diet in the laboratory (Table V-1) show significant differences ($P < 0.05$) among different instars. These measurements provide a reliable means to accurately determine the instar of field collected codling moth larvae. The results also showed that codling moth larvae developed up to five instars. This agrees with previous studies by William and McDonald (1982) and Weitzner and Whalon (1987). Larvae from commercial and non-commercial orchards had similar head capsule widths except for the fourth instar. Head capsule width of fourth instar larvae from commercial orchards (1.42 ± 0.04 mm) were significantly ($P < 0.01$) greater than those from non-commercial orchards (1.35 ± 0.04 mm).

Instar Determination in Overwintering Larvae Collected in the Field

Data in Table V-2 show percentage of different larval instars of diapausing codling moth larvae collected from commercial and non-commercial orchards in 1986 and 1987.

Table V-1. Head capsule widths (Mean \pm SD) of larval instars of codling moth reared in the laboratory on artificial diet

Instar	$\mu \pm$ SD Head capsule width (mm)			
	Number of larvae	Progeny of moths collected from non-commercial orchards	Number of larvae	Progeny of moths collected from commercial orchards
First	25	0.34 \pm 0.01 a ¹	15	0.34 \pm 0.01 a
Second	53	0.61 \pm 0.02 b	20	0.61 \pm 0.01 b
Third	172	1.18 \pm 0.05 c	17	1.18 \pm 0.05 c
Fourth	96	1.35 \pm 0.04 d ²	19	1.42 \pm 0.04 d ²
Fifth	119	1.67 \pm 0.10 e	168	1.68 \pm 0.10 e

Means in a column followed by the same letter are not significantly different ($P = 0.05$, LSD; Petersen 1985)

1) Significantly different means ($P < 0.01$)

2) Significantly different means between orchards ($P < 0.01$)

Table V-2. Percentage (Mean \pm SE) of different overwintering larval instars of codling moth in Willamette Valley apple orchards, Oregon in 1986 and 1987

Larval instars	(μ \pm SE) Percentage	
	Orchards	
	Non-commercial	Commercial
Third	20.89 \pm 3.62 a1	3.20 \pm 1.07 a
Fourth	10.75 \pm 2.04 a	9.48 \pm 1.06 b
Fifth	60.82 \pm 3.89 b1	76.53 \pm 2.87 c
Total larvae studied	1293	353
Mortality by diseases	8.70 \pm 2.54	10.19 \pm 2.15

Means in a column followed by the same letter are not significantly different (P = 0.05, LSD; Petersen 1985)

1) Significantly different means between orchards (P < 0.05)

These results suggest that codling moths overwinter in the Willamette Valley as diapausing third, fourth, and fifth instar larvae. A significant ($P < 0.05$) majority of these diapausing larvae (61-77%) were in the fifth instar and the percentages of third and fourth instars were relatively small (3-21% in third instar and 10-11% in fourth instar). Also, a significantly ($P < 0.05$) higher proportion (21% vs 3%) of third instar codling moth larvae were diapausing in non-commercial orchards than in commercial orchards. The presence of higher percentages of third instar diapausing larvae in non-commercial orchards appears to be related to the higher levels of larval parasitism. Only a very small proportion (ca. 3%) of the third instar overwintering larvae were not parasitized. Nearly 16% of the overwintering fourth instars were emerged as adults and most of the fifth instar overwintering larvae were emerged as adults. The data do show that the codling moth is capable of overwintering in the third and fourth instars, in addition to overwinter in the fifth instar (Table V-3 and Table V-4).

Post-diapause Development and Adult Emergence

Table V-3 shows the percentage of adult eclosion and parasitism of different overwintering instars of codling

Table V-3. Mortality and post-diapause development of different overwintering larval instars of codling moth collected from non-commercial and commercial apple orchards in the Willamette Valley, Oregon under field conditions 1987-1988

Measurements ($\mu \pm SE$)	Third instar	Fourth instar	Fifth instar
Percentage mortality			
By parasitoid	96 \pm 4.00	74 \pm 8.72	0
By other factors	4 \pm 4.00	8 \pm 3.74	15 \pm 4.47
Percentage pupation	0	16 \pm 8.72	91 \pm 2.33
Percentage adult emergence	0	16 \pm 8.72	77 \pm 3.35
Number of larvae observed	50	50	100

Table V-4. Percentage of different larval instars of codling moth in the Willamette Valley apple orchards of Oregon during 1986 and 1987

Origin of larvae	Total number of larvae studied	Percentage of larvae ($\mu \pm SE$)			Percentage mortality ($\mu \pm SE$)
		Third instar	Fourth instar	Fifth instar	Diseases
ORCHARDS :					
Non-commercial apple orchards	1293	20.89 \pm 3.62 a	10.75 \pm 2.04 a	60.82 \pm 3.89 a	8.70 \pm 2.54 a
Commercial apple orchards	353	3.20 \pm 1.07 b	9.48 \pm 1.06 a	76.53 \pm 2.87 b	10.19 \pm 2.15 a
SEASONS :					
Overwintering season 1986	383	9.27 \pm 3.27 a	13.37 \pm 2.08 a	66.72 \pm 3.89 a	10.75 \pm 3.68 a
Overwintering season 1987	1263	15.27 \pm 4.06 a	8.10 \pm 1.07 a	68.57 \pm 4.22 a	8.56 \pm 1.25 a

Means followed by the same letter are not significantly different ($P = 0.05$, LSD; Petersen 1985)
SE = Standard Error

moths collected from different apple orchards in the Willamette Valley. Most of the third (96%) and fourth (74%) instar diapausing larvae in the field were parasitized. None of the third instar diapausing larvae from non-commercial orchards entered the pupal stage and emerged as adults. Only a small percentage (16%) of the fourth instar diapausing larvae became pupae and adults. These however, did not enter the fifth instar. No parasitism was noted among the fifth instar diapausing larvae collected from commercial orchards and about 91% of them pupated and 77% emerged as adults. However, a small proportion (1.9%) of the fifth instar diapausing larvae did not develop and remained in diapause through the first year of the season. This suggests that a few codling moth larvae are capable of diapausing for more than one year. Other investigators (Hammar 1912, Yothers and Carlson 1941) had also reported a similar phenomenon.

There were no significant ($P < 0.05$) differences in the rate of post-diapause development between the fourth and fifth instar diapausing larvae (Table V-5) as their mean times to pupation were similar (46 days for the fourth instars compared with 43 days for the fifth instars). Figure V-19 presents the cumulative patterns of pupation and adult emergence for the fourth and fifth instar diapausing larvae. All the fourth instar larvae

Table V-5. Time of pupation (Mean \pm SE) of different larval instars of codling moth from Willamette Valley, Oregon under field conditions of 1987-1988

Diapausing Larval Instar	Number of larvae	Time to pupation (days)	
		$\mu \pm$ SE	95 % CI
Fourth	8	45.88 \pm 5.12 a1	(33.75 - 58.01)
Fifth	74	42.92 \pm 1.64 a	(39.64 - 44.72)

1) Means were compared by LSD (P = 0.05)

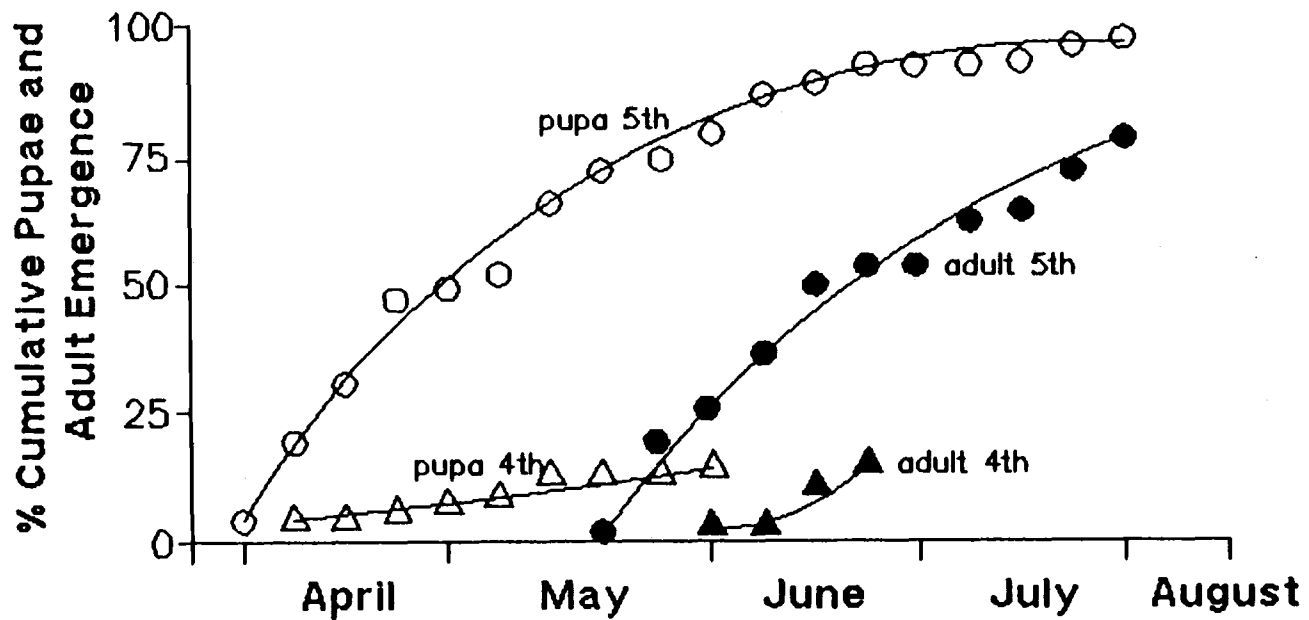


Figure V-19. Diapause termination and adult eclosion of different overwintering larval instars of codling moth in Willamette Valley, Oregon during 1987-1988

emerged as adults by the end of June but the fifth instar larvae prolonged their adult emergence up to early August. The shorter period of time for adult emergence for the fourth instar diapausing larvae is possibly related to their small proportions (9-11%) in the overall diapausing larval population (Table V-2).

Activity and Feeding Behavior of Diapausing Larvae

Observations on mobility and feeding behavior of overwintering codling moth larvae during their post-diapause development are presented in Table V-6. Third and fourth instar diapausing larvae began feeding on apple blossoms, artificial diet, and apple bark upon termination of their diapause. Some came out of their hibernacula and began respinning new cocoons. No further observations on post-diapause development activities of third and fourth instar larvae were possible in this experiment because of their total mortality due to parasitism. No feeding was observed among the fifth instar larvae on any of the three foods provided but these larvae were also respinning new cocoons within their hibernaculi.

In summary, the data presented here show that the head capsule width measurements can be used to determine what larval instars overwinter in the field. Data also indicate that such a small proportion of the overwintering

Table V-6. Feeding behavior and activity of different overwintering larval instars of codling moth during postdiapause development under field conditions of 1987-1988

Behavior observed	Instars behavioral response		
	Third	Fourth	Fifth
Feeding on:			
Artificial diet	+	+	-
Apple flowers and leaves	+	+	-
Bark of apple tree	actively chewing bark	actively chewing bark	-
Other activities	out of hibernaculum respinning new cocoon	out of hibernaculum respinning new cocoon	respinning its hibernaculum
+) Represents active feeding -) Represents no feeding			

larval population may be found in the fourth instar. The post-diapause developmental time to pupation and adult eclosion seems to be the same for both overwintering instars. Since there was no difference in emergence, it was unnecessary to incorporate this fact into the PETE phenology model.

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VI. SUMMARY AND CONCLUSIONS

The developmental biology and seasonality of the codling moth, Cydia pomonella L. (Lepidoptera: Olethreutidae) from the Willamette Valley was studied during 1986-1988 seasons. The role of photoperiod and temperature in induction, expression, and termination of diapause in this species was evaluated. The overwintering behavior and post-diapause development was studied during 1987 and 1988.

Both temperature and photoperiod had a significant influence on the growth and development of codling moth. By using a regression analysis, the developmental thresholds were determined for each larval instars and pupal stage. There were marked differences in the developmental thresholds for each larval instars (Table II-2). For instance, the fourth instar larvae use a developmental threshold of 14.2°C while the second instar have the lowest developmental threshold of 9.6°C. Similarly there were significant differences between male and females. A general developmental threshold of 11.2°C was determined for the complete larval stage of codling moth. Thermal requirements (Table II-3), and developmental time (Table II-1) were also determined. Data showed that different larval instars and pupal stage

required different number of thermal units for development. There were also differences between the genders. Inter-instar differences in the development at different temperature treatment were surprisingly high and are reported here for the first time. For example, the fastest development was noticed in L1 and L2 at 32°C and then rapid decline. The influence of photoperiod on development in codling moth is reported in detail for the first time in this report.

The entire diapause and post diapause stages in codling moth were influenced by both temperature and photoperiod separately and collectively (Table III-3 and Figure III-8). The effect of photoperiod decreased with the increasing temperature above 28°C (Table III-4), but increased at low temperatures. Fluctuating temperatures produced a higher incidence of diapause induction than constant temperatures (Figure III-9). This evidence suggested that codling moth has evolved to respond to temperature fluctuations as token stimuli for diapause induction. A similar phenomenon may occur in diapause termination. Critical photoperiod (CPhP50) for diapause induction in codling moth populations from Willamette Valley (latitude 44.5°N) was LD 15.5:8.5 at 24°C. In order to determine larval instar susceptibility to diapause induction, each instar was separately exposed to

diapause induction conditions. The data from this experiment suggest that diapause in codling moth can be induced at all larval instars, although third and fourth instars appear to be slightly more sensitive than the others. Diapause is almost always expressed in the fifth instar, however, there were a few diapausing fourth instar as well in the field.

Field study on seasonality of diapause induction showed that two distinct sub-populations of codling moth may exist in the Willamette Valley. One with a tendency to be univoltine and the other with a tendency to be multivoltine under field conditions. It is also possible that some individuals of the same population may have genetic ability to complete only one generation per year. In any event, diapausing individuals were noticed throughout the spring and summers, although their propensity increased during the fall.

Codling moth from the Willamette Valley generally come out of diapause in the third week of March when photoperiod is about 13-13.5 hours, and adult eclosion begins during the last week of April. Laboratory experiments also showed that 13.41 hours photoperiod at 24°C was the critical photoperiod for diapause termination.

Codling moth population in the Willamette Valley was found overwintering in third, fourth, and fifth instar larvae. However, all of the third instar and some of the fourth instars were parasitized. Only fourth and fifth instars potentially have the ability to develop and emerge as adults since most of the third instars were parasitized. I report the evidence here for the first time for fourth instar overwintering in this insect. This fact could be an adaptive advantage as it would provide better survival during unpredictable climatic conditions in the Willamette Valley. The proportion of different overwintering instar may vary according to the type of cultural practice used in a particular apple orchard.

In conclusion, my research data showed that codling moth in the Willamette Valley has a number of characteristics that appear to be unique to this population. Overwintering in the fourth larval instar, occurrence of both univoltine and bivoltine sub-populations within a given population, photoperiodic effect on development, and effect of photoperiod and temperature separately and collectively, are reported here for the first time for this population. Further studies on the intra-population variations and the influence of the dynamic changes of temperature and photoperiod in codling moth would be useful to get better understanding

of seasonality of this insect. Such information is important in developing pest management programs for apple orchards.

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APPENDIX

Appendix Table 1. Percentage diapause induction in codling moth under field conditions, Corvallis, Oregon 1988

Date of observation	Generation	Number of larvae	Percent		
			diapause	cumulative diapause	average + SE diapause
July	First	30	13.33	1.90	39.41 + 13.50
		40	12.50	3.68	
August	First	120	43.04	9.80	
		40	10.71	11.30	
		45	68.97	21.11	
		150	87.88	33.61	
September	Second	140	88.29	46.16	93.37 + 4.34
		33	100.00	60.38	
		75	78.00	71.55	
		50	100.00	85.77	
		50	100.00	100.00	

Appendix Table 2. Number of days required to terminate diapause in codling moth after exposure to different photoperiod regimes

Photoperiod (hrs) Light/Dark	Number of larvae	Number of days to pupation *)			% Pupation	% Diapause
		First	50 %	>90 %		
11L/13D	10	12	-	-	10	90
12L/12D	10	15	36	41	100	0
13L/11D	10	12	38	-	80	20
14L/10D	10	20	32	36	90	10
15L/ 9D	10	13	37	-	70	20
16L/ 8D	10	13	-	-	10	90

*) The experiment was terminated after 50 days