

THE EFFECTS OF PHOTOPERIOD AND EFFECTIVE TEMPERATURES
ON THE SEASONAL PHENOLOGY OF THE CODLING MOTH
(LEPIDOPTERA: TORTRICIDAE)¹

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Abstract

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The photoperiodic reaction in North American codling moth populations displayed clinal-type variation similar to populations in Europe. A latitudinal shift of 10° to the north corresponded to an increase of 1.25 h in the critical photoperiod. Intrapopulation variance in diapause response appeared to be similar in populations of different origin. The critical photoperiod was not constant for a geographic population but varied between years probably due to the modifying effect of prediapause temperatures. In Michigan and other areas in the northeastern United States with similar climate the codling moth is essentially bivoltine with considerable yearly variability in second generation emergence. A graphic model is presented which gives an estimate of voltinism and the proportion of diapausing first-generation larvae based on the seasonal heat unit total at the time of diapause initiation. From an analysis of original data and historical phenological records an algorithm was developed which describes the relationship between effective temperatures and the variance of second generation emergence and which can predict population curves for climatically different years. Use of this predictive method in conjunction with monitoring information provided by a pheromone trap is discussed.

The distribution of the codling moth, *Laspeyresia pomonella* L., closely matches that of its principal host, the apple tree, with which it shares similar ecological requirements. At its northern limits in North America, *L. pomonella* is essentially univoltine (Putman 1963), but has increasing generations toward its southern distributional limits, such as one and a partial second generation in northwestern Pennsylvania (Hammar 1910), two and a partial third in southern Illinois (Glenn 1922a), and four in northern Georgia (Van Leeuwen 1929). In Europe the situation is very similar with increasing voltinism toward the southern latitudes (Shel'Deshova 1967).

Each locale within its extensive distributional range has unique climatic and host conditions which challenge the adaptiveness of this insect. To be successful, the codling moth has developed timing mechanisms with great plasticity which synchronize its life cycle with the seasonal rhythms of climate and food availability. Dickson (1949) first demonstrated that a photoperiodic reaction (PhPR) is the primary mechanism which tunes the moth's life cycle to the conditions of a given locality. It causes mature larvae to enter physiological arrest, known as diapause, well in advance of adverse conditions (lack of food, low winter temperatures). The codling moth is a short-day insect and it diapauses towards the end of summer when day length decreases below a certain threshold value. Although other factors such as lower temperatures or food quality influence the initiation of this rest period (Headlee 1928; Garlick 1948), the major role of photoperiod as the trigger of diapause has been substantiated by several investigators (Russ 1966; Shel'Deshova 1962; Wildbolz and Riggensbach 1969; Peterson and Hamner 1968).

Shel'Deshova (1965) found variability in the photoperiodic reaction in codling moth populations of different provenances in the USSR which she correlated with the latitude of their geographic origin. Clinal-type latitudinal variation has been observed in

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other poly-cyclic species with winter diapause (Danilevsky *et al.* 1970). In North America the photoperiodic reaction of the codling moth has been determined only for a few populations under controlled light and temperature conditions (Dickson 1949; Peterson and Hamner 1968; Harwood 1968; Phillips and Barnes 1975). Its variability on this continent is of interest in understanding the seasonal and geographical differences in codling moth phenology for pest management purposes. If models for the codling moth are to be useful and relevant for large geographic regions these parameters must be predictable for populations from each fruit-growing area. Also, the pattern of PhPR in North American codling moth populations may provide information as to its colonization pattern and degree of acclimatization since introduction around 1750 in the New England states (Slingerland 1898).

In Michigan and in most other fruit-growing districts of the northeastern United States the codling moth has one and a partial or full second generation (Riedl *et al.* 1976). The present study examined published and original data on the development and diapause of the codling moth in relation to climate from locations in Michigan, Illinois, and New Jersey so as to more precisely explain its seasonal phenology and especially the yearly variability of second generation emergence. The value of this research is demonstrated by an improved forecasting system for pest management which uses reference points (provided by a pheromone trap) and which synchronizes a physiological time model for this pest with biological events as they occur in the field.

MATERIALS AND METHODS

Determination of the photoperiodic reaction from phenological records. For an analysis of the variability of the PhPR in North American codling moth populations, published phenological data from the locations listed in Table I were examined. Records include data from most of the major fruit-growing areas in the United States. In addition to original data from Michigan, the majority of studies were carried out by the Bureau of Entomology of the United States Department of Agriculture between 1909 and 1929. To assure a homogenous data base only sources were considered which followed similar experimental procedures: Mature larvae were collected with corrugated cardboard bands fastened around the lower trunks of apple trees at frequent intervals during the season. Those larvae which transformed either during the same season to pupae and adults or remained in diapause until the following spring were calculated for each sampling date and related to the day length at the time of collection. Figure 1 is a graphical representation of this procedure for three data sets. A smooth sigmoid curve was eyefitted to the data points to determine the photoperiods where 50% and 90% of the larvae entered diapause. In accordance with the literature the point where diapause occurs in 50% of the individuals is referred to as the critical photoperiod, CPhP₅₀ (Danilevsky *et al.* 1970); 90% diapause is abbreviated as PhP₉₀. This procedure was followed for all data sets from locations 1 to 16 (Table I). If data from 2 or more years were available from one location, average CPhP₅₀ and PhP₉₀ values were used in subsequent calculations.

Day length in this study was the time between sunrise and sunset plus the periods of civil twilight. Civil twilight was considered part of the biologically effective photoperiod since Russ (1966) as well as Jermy (1967) have shown that codling moth larvae can react to very low light intensities. The day length values for various dates and locations were obtained from the Nautical Almanac (1974 ed., U.S. Naval Observatory).

Variability in seasonal phenology. This analysis was based on data collected during 1957 to 1960 at Grand Rapids and during 1973 to 1975 near Belding, Mich. The data from Grand Rapids were collected by station personnel at the Michigan State University Graham Experiment Station by placing codling moth infested fruit in emergence boxes

in the field. Experimental procedure followed for the Nadeau orchard near Belding in 1973, 1974, and 1975 were detailed previously (Riedl *et al.* 1976). At Nadeau, data were obtained on emergence (from trunk bands), on oviposition by ca. weekly egg sampling, and on male flight activity with pheromone traps.

Corresponding climatic data to place phenological observations on a physiological-time scale were available from Graham Experiment Station for 1957 to 1960. These records were taken on thermographs in a standard weather shelter. At Nadeau orchard, a hygrothermograph in a standard weather shelter was installed to provide records of temperature and humidity during 1973 to 1975. In the case of missing or incomplete observations, records were supplemented with data from the nearest first order NOAA or agricultural weather network stations (AAM C. Van Den Brink, NOAA, E. Lansing, Mich.). In addition to data from Michigan, selected emergence and climatic records from New Jersey (Headlee 1928, 1936) and Illinois (Glenn 1922a) were compared in this analysis.

Physiological time (degree days) for each location and year was calculated from the daily temperature extremes with a sinus-wave method of Baskerville and Emin (1969) using 50°F as threshold for growth. This threshold and the heat unit requirements for the various life stages were taken from Glenn (1922 b). For analyzing and comparing spring and summer emergence, data were plotted as cumulative percent on a °D scale. Degree days (abscissa) were transformed to log (base 10) and cumulative percent (ordinate) to probability units (probits) to linearize the sigmoid emergence curves. A least-square analysis then was performed on the transformed data.

RESULTS AND DISCUSSION

Intraspecific variability of the photoperiodic reaction in *L. pomonella* in North America. The photoperiodic reaction varied not only between populations of different areas but also between years in the same area. While the basis for the former was genetic (Shel'Deshova 1962) the variation between years within the same geographic population was largely under environmental control. Work by Shel'Deshova (1965) and Phillips and Barnes (1975) demonstrated that the prediapause temperatures to which larvae are exposed modify their photoperiodic reaction. Danilevsky *et al.* (1970) has reviewed this modifying effect on several insects. Figure 1 shows the photoperiodic reaction for 2 successive years, 1915 and 1916, at Olney, Ill. (10). In 1916 the CPhP₅₀ was 14.6 h instead of 14.8 during the previous year. Average temperature conditions under which larvae with 50% diapause developed were 72.5°F in 1915, but 77.5°F in 1916. Thus an increase of 5°F during larval development corresponded to a lowering of the critical photoperiod by ca. .2 h which delayed diapause induction in 1916 by ca. 4 days.

Phenological observations from Glassboro, N.J. (7) taken over a decade between 1926 and 1935 indicate the magnitude of the yearly variation in PhPR in a geographic population. The critical photoperiod ranged between 15.0 and 15.5 h, with a mean of 15.1 h. Translated into calendar dates the points of 50% diapause sometimes were 2 weeks apart in that location. The precise relationship between temperature and CPhP₅₀ could not be determined from these data since no climatic information was given by Headlee (1936).

In this study, the slopes of the sigmoid diapause response curves of the 16 populations (Table I) did not differ markedly from each other when analyzed as shown in Fig. 1. Their steepness indicated little genetic variability within each geographic population in terms of photoperiodic response. From the beginning of diapause, a day length decrease of only 1 h causes complete diapause in the population (Fig. 1). At a latitude of 40° this day length decrease occurs over a 4 week period (ca. middle of July to middle of August).

Table I. Origin of phenological records used in analysis of photoperiodic reaction

| Ref. no. to figs. & text | Provenance | Latitude | Data source |
|-----------------------------|--------------------------|----------|--------------------------|
| 1 | Pentwater, Michigan | 43°50' | Hammar 1912 |
| 2 | Belding, Michigan | 42°55' | Riedl (unpublished data) |
| 3 | Douglas, Michigan | 42°40' | Hammar 1912 |
| 4 | Saugatuck, Michigan | 42°40' | Hammar 1912 |
| 5 | Benton Harbor, Michigan | 42°10' | Hammar 1912 |
| 6 | North East, Pennsylvania | 42°10' | Hammar 1910 |
| 7 | Glassboro, New Jersey | 39°40' | Headlee 1936 |
| 8 | Dover, Delaware | 39°10' | Selkregg & Siegler 1928 |
| 9 | Grand Junction, Colorado | 39°05' | Siegler & Plank 1921 |
| 10 | Olney, Illinois | 38°45' | Glenn 1922a |
| 11 | San Jose, California | 37°20' | Jones & Davidson 1913 |
| 12 | Siloam Springs, Arkansas | 36°15' | Jenne 1909 |
| 13 | Cornelia, Georgia | 34°30' | Van Leeuwen 1929 |
| 14 | Riverside, California | 34°00' | Dickson 1949 |
| 15 | Artesia, New Mexico | 33°50' | Quaintance & Geyer 1917 |
| 16 | Roswell, New Mexico | 33°25' | Quaintance & Geyer 1917 |

As with European *L. pomonella* populations (Shel'Deshova 1965), a strong relationship exists between the critical photoperiod and latitude in North American populations (Fig. 2). The geographic variation of the CPhP₅₀ also is of a similar order. From the equation for the CPhP₅₀ in Fig. 2 a 10° increase in latitude was associated with a photoperiod increase of 1.25 h (1.5 h in Europe: see Shel'Deshova 1965). Populations from Cornelia, Georgia (13), and Siloam Springs, Arkansas (12) deviated from the general trend. According to their latitude one would expect a much lower CPhP₅₀ for Georgia, but a higher one for Arkansas. Deviations from the expected CPhP₅₀ in both instances could be due to the temperature and host characteristics (food availability) of these regions which may require uniquely adapted populations. It also could point to poor acclimatization of populations which have originated from a higher latitude and moved to Georgia or from a lower latitude and moved to Arkansas. The codling moth likely has been present in these fruit-growing areas long before the original analysis was made. This should have allowed adequate time for acclimatization since experiments by Cisneros (1971)³ indicate that the codling moth can quickly adapt to latitudinal changes (within several generations).

Slopes of the regression lines for CPhP₅₀ and PhP₉₀ for 16 data points (Fig. 2) were not significantly different from each other which supports the earlier observation that the variance in diapause response in geographic populations is similar. However, the time frame during which diapause reaches 100% changes considerably with latitude. This is illustrated in Fig. 3 where the calendar dates of the CPhP₅₀ and the PhP₉₀ were plotted for each latitude. Values for the CPhP₅₀ and PhP₉₀ were obtained from equations in Fig. 2 and the calendar dates for the calculated day lengths at successive latitudes from the Nautical Almanac. Shaded regions in Fig. 3 indicate the time frame range for 50% and 90% diapause in Michigan (between 42° and 47° n.l.). Horizontal lines intersecting the two curves at 35°, 40°, and 45° n.l. give the time distance in days between 50% and 90% diapause at each respective latitude. In the south at 35° n.l., this interval is ca. 10 days, but it gets gradually smaller with higher latitudes.

³Cisneros, F. H. 1971. Contribution to the biological and ecological characterization of apple and walnut host races of codling moth, *Laspeyresia pomonella* (L.). Ph.D. Thesis, University of California, Riverside. 163 pp.

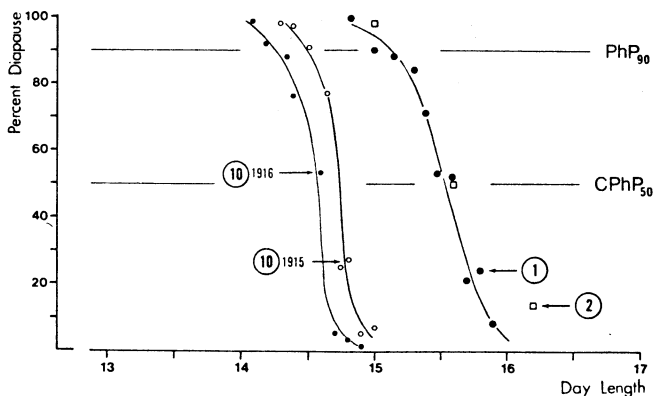


FIG. 1. Diapause response in field populations from Olney, Ill. (10) and Michigan (1 & 2) (see Table I for data sources).

Estimation of generation cycles and first generation diapause. Seasonal temperature conditions preceding the initiation of diapause can have a two-fold effect on the proportion of larvae diapausing. First, as indicated above, temperature can directly affect the schedule of diapause induction and shift the CPhP₅₀ towards a longer (cool year) or shorter day length (warm year). This effect is presently not accounted for in calculating generation cycles because of an inadequate understanding of the relationship between the CPhP₅₀ and prediapause temperature. Second, depending on the progress of physiological development as a direct function of effective temperatures during the season, variable proportions of larvae will be exposed to diapause — inducing light conditions during July and August.

The heat unit total, which accumulates from the time dormancy is broken until diapause begins, governs the number of generations possible under local climatic conditions. The minimum degree day values for one, two, or three generations were calculated as follows. In Michigan, the first moths emerge according to pheromone trap records after ca. 250°D since 1 Jan. (Riedl *et al.* 1976); another 650°D are required to develop to the last larval stage. The °D total from 1 Jan. until the first mature larvae are found is, therefore, 900. The degree to which the heat unit total exceeds 900°D at the time of the CPhP₅₀ determines the size of the second generation. A partial third

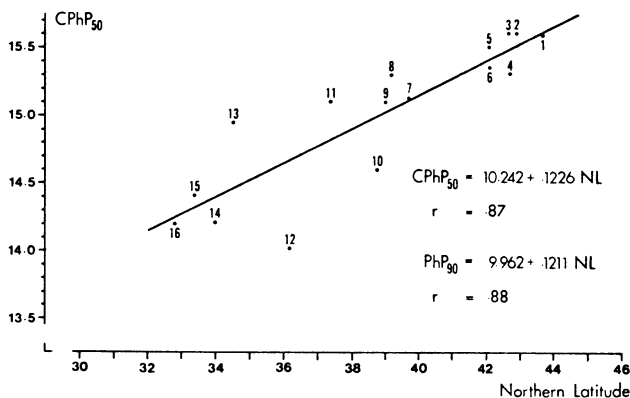


FIG. 2. Relationship between the critical photoperiod (CPhP₅₀) and latitude for selected codling moth populations (numbers above data points refer to data sources in Table I).

generation overlapping with the end of the second generation will be possible if the heat unit sum at CPhP₅₀ exceeds 1900°D, a full generation cycle (1000°D) beyond 900°D.

A graphic representation of the above relationships is shown in Fig. 4 and applied to the situation at Nadeau orchard (43° n.l.). The cumulative degree day curves for the years 1973–1975 at Nadeau are graphed in Fig. 4 with a normal °D curve (± 2 S.D.) for that area. This normal curve is based on 10 years of temperature data from 2 miles E. of Nadeau (VanDenBrink 1974). The horizontal lines in Fig. 4 at 900° and 1900°D indicate the °D requirements for two and three generations, respectively. According to Fig. 3, the CPhP₅₀ is reached on 4 Aug. at 43° latitude which is drawn as a vertical line above that date. The number of generations expected in any given season is determined from the location of the intersection point between the °D curve and this vertical line. In Fig. 4 the point for a normal year falls within the two generation region; even in extreme years only two generations are possible in this location as indicated by the °D points 2 S.D. above and below normal. The relative position of the point of intersection on the CPhP₅₀ line within the two generation region (between 900° and 1900°D) gives an estimate of first generation larvae transforming during the same season. However, a more accurate estimate can be obtained from the average cumulative curve for last instar larvae projected on the CPhP₅₀ line (see insert box labeled % non-diapausing larvae in Fig. 4). This relationship was derived from emergence data of Headlee (1936) from New Jersey where first generation diapause is very low and it approximates the variance under non-diapause conditions.

The roughly normal distribution of successive growth stages causes the scale for larval diapause when projected on the CPhP₅₀ line to be non-linear. If the normal °D curve intersects the CPhP₅₀ line close to the 50% diapause point (steepest region of cumulative larval curve) as in Fig. 4, small °D deviations from normal will cause significant shifts in the proportion of transforming larvae. However, if the normal intersection point falls below 20% or above 80% these shifts due to the yearly °D deviations from normal would be less dramatic.

In 1973 heat unit accumulation at Nadeau was above normal; the cumulative °D curve in Fig. 4 intersects the CPhP₅₀ line at the 60% point. This value compares with band records from that orchard which indicated that 58% of the first generation larvae transformed during the same season. 1974 was a cooler year with below-average °D accumulation allowing only ca. 30% of first generation larvae to transform according to Fig. 4. For 1975, the graphic model (Fig. 4) suggested a proportion of 50%

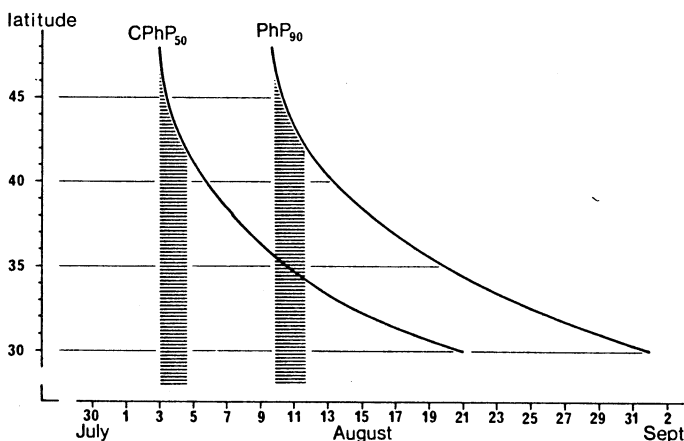


FIG. 3. Average date when diapause reaches 50% and 90% at various northern latitudes (shaded area: Michigan between 42° and 47° n.l.).

non-diapausing first generation larvae. No field data were available for 1974 and 1975 to verify the predictions for these years.

One possible source of error in Fig. 4 could arise from difficulty in defining the larval stage in which diapause is fixed. Research has not resolved this question and the reported variability in larval sensitivity (Russ 1966; Jermy 1967; Harwood 1968) could suggest an additional adaptive mechanism which might predispose either early or late larval stages to become responsive to diapause-inducing photoperiods.

Figure 5 is an extension of the developmental projections for a single site to 41 sites throughout Michigan. These 41 sites are first-order weather stations for which the normal $^{\circ}\text{D}$ totals (\pm S.D.) were available (VanDenBrink *et al.* 1971). The latitude of each site was entered in Fig. 3 to determine the calendar date of the CPhP₅₀. The number of generations at each site was computed from the degree day total between 1 Jan. and the date of CPhP₅₀ according to five class intervals (Table II). The distinction between intervals 2, 3, and 4 was suggested by the relationship between generations indicated in Fig. 4. The computer-printed maps in Fig. 5a-e were generated with a SYMAP program (Anonymous 1969) to delineate areas of similar moth development in Michigan for climatically different years. Greater size or darkness of symbols in Fig. 5a-e indicate increasing voltinism. The major apple-growing districts in the southern peninsula are shown in Fig. 5f for reference; there are only backyard apple plantings in the upper peninsula.

During an average year (Fig. 5c) the codling moth develops close to a full second generation in the southern part of the fruit belt (area bordering Lake Michigan), but only a small second in the northern counties. In a cool year (normal -1 S.D., Fig. 5b) or very cold year (normal -2 S.D., Fig. 5a) the second generation becomes progressively smaller from the southern to the northern counties of the fruit belt, until the partial second altogether disappears and the codling moth becomes univoltine in most areas of the upper peninsula. During warm (normal $+1$ S.D.) and exceptionally warm seasons (normal $+2$ S.D.) some third generation individuals which overlap with second

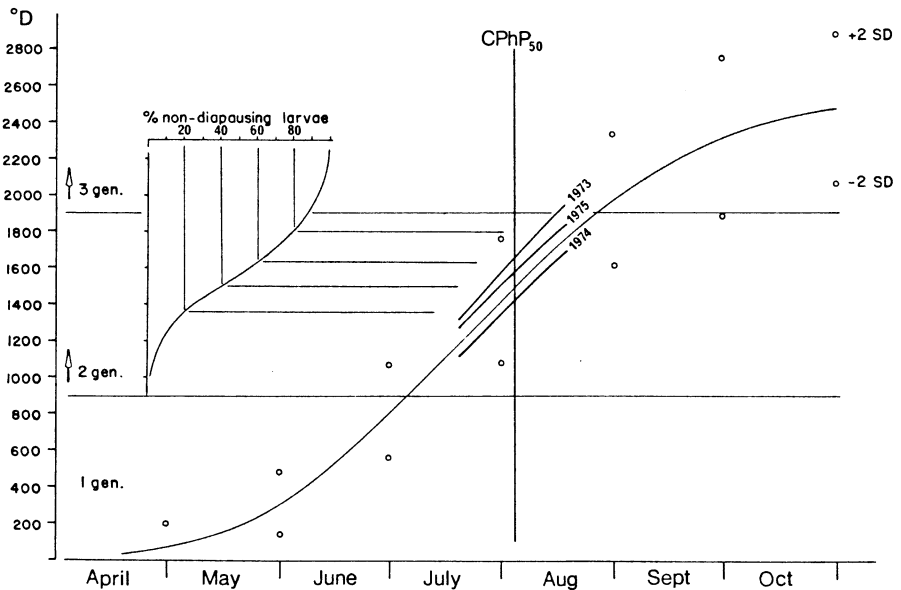


FIG. 4. The possible number of generation cycles at Nadeau orchard (Kent Co., Michigan) as indicated by the effective temperatures preceding the date of the critical photoperiod in a normal year and during 1973, 1974, and 1975. (See text for further details.)

generation moths are likely to develop in the southern part of the state (Fig. 5d-e). Records from more southern apple-growing regions such as Illinois indicate overlap occurs between the first and second summer brood emergence (Glenn 1922a). It is unlikely that pheromone trap records could verify a partial second summer brood emergence, particularly if it is very small.

Variability of seasonal phenology in Michigan. Figure 6a shows the average emergence in Michigan over a 6-year period and one or two standard deviations above and below the average. These curves are plotted as cumulative percent on a degree-day scale in Fig. 6b and as log-probit lines centered to a common point in Fig. 6c. As indicated by the standard deviations at each decile percent (Fig. 6a-b), spring emergence varied considerably less between years than did summer emergence. The average curve for the latter seems to originate in a region with little yearly variability, but variability increases steadily with each decile percent until the end of this generation. While the slope of spring emergence varied little, the slope of summer emergence can vary from very steep (-2 S.D., Fig. 6b), indicating a short flight period, to flat ($+2$ S.D.), which is characteristic of a full second generation. This pattern is typical for an area like Michigan where variable proportions of first generation larvae transform the same season depending on the climatic conditions preceding diapause induction. If few larvae diapause, the second generation will be close to complete and consequently the cumulative emergence curve will be relatively flat. The slope will increase as the diapausing component of first generation larvae becomes larger. Therefore, in warm years with few first generation individuals diapausing, the slope of summer emergence should approach the values from areas with complete second

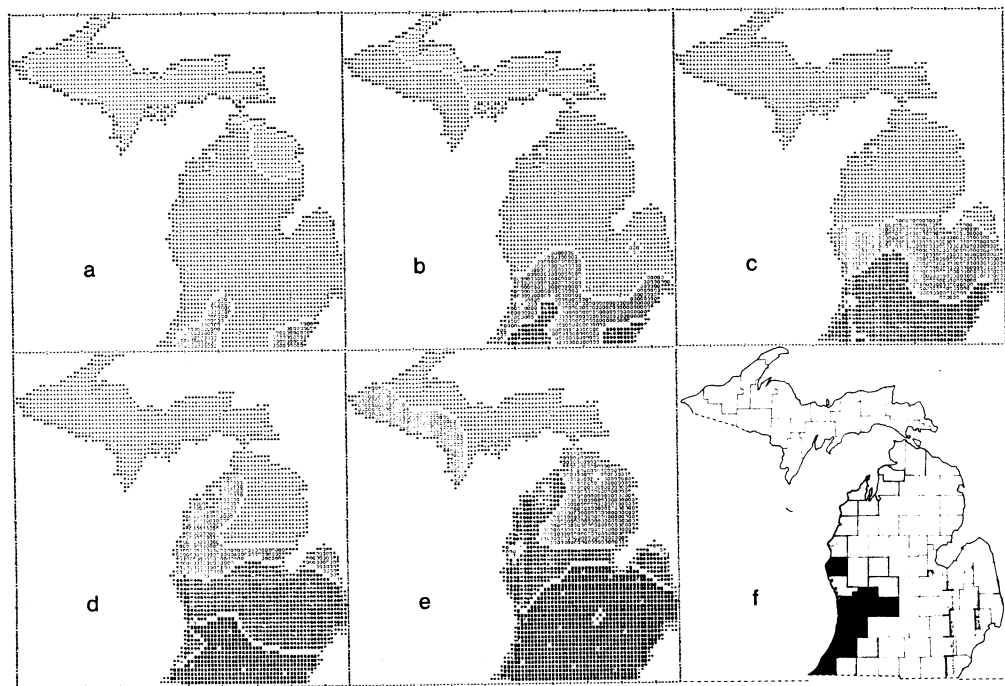


FIG. 5. The theoretical number of generations of the codling moth in Michigan in (a) very cold year (2 S.D. below normal, see Table II for explanation of map symbols), (b) cold year (1 S.D. below), (c) normal year, (d) warm year (1 S.D. above), (e) very warm year (2 S.D. above), (f) major (dark shading) and minor (light shading) apple growing areas in lower Michigan.

generations such as in southern Illinois (j, k in Table III; line k in Fig. 6c) or in New Jersey (h, i).

Since the slopes of the fitted log-probit lines (Fig. 6c) are inversely related to the variances of the original population curves (Fig. 6a), their values are useful for comparing the variance of emergence curves of different years or generations. For this analysis the log-probit lines fitted to the cumulative emergence data of the spring and summer generation (see Table III for equations) were centered at their median to a common point (1550°D). This value corresponds to the average 50% point of summer emergence in Michigan. Slopes of the centered log-probit lines differ from the original curve fits due to the non-linearity of the degree-day scale.

Variation between emergence curves of any generation is described here in two ways: first, by the position of the median (50% point) on the physiological-time scale, and, second, by the variance of emergence which is expressed here as the slope of the log-probit line. The average 50% emergence point during spring occurred after 517°D (± 25 S.E.) and the slopes of the transformed and centered curves also varied relatively little from 20.35 to 30.17 (lines f and d in Fig. 6c). For the summer generation the average median was at 1555°D (± 43 S.E.) with slopes ranging from 13.63 to 35.05 (lines c and f in Fig. 6c). Figure 6a–b suggested that the slope of summer emergence varied with the median. This inverse relationship is shown in Fig. 7b and holds true until the slope levels off at a value characteristic of a full second generation. This value was calculated as the average slope from the emergence curves c, h, i, j, and k (Table III) and is shown as a horizontal dotted line in Fig. 7b. No such correlation was found for the spring generation where the slope varied independently of the median (Fig. 7a).

Since the heat units accumulating from the break of dormancy (assumed to be the beginning of the year) until the calendar date of the critical photoperiod limit the number of generation cycles, it was not unexpected that the slope of summer emergence was negatively correlated with this heat unit total (Fig. 8). Again, this inverse relationship applies to a partial second generation with the slope approaching 13.7 in climates with a full second generation. Also, one would expect that the slope of summer emergence is influenced by the slope of the previous generation. However, any such relationship was

Table II. Generation classes and corresponding map symbols used in Fig. 5

| Class | Map symbol | °D total at time of diapause induction | No. of gens. |
|-------|-------------------------------------|--|--------------|
| 1 | ● ● ● ● ● ● ● ● ● ● ● ● ● ● ● | < 900 | 1 |
| 2 | + + + + + + + + + + + + | 900–1440 | 1–1⅓ |
| 3 | 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 | 1441–1640 | 1⅓–1⅔ |
| 4 | θ θ θ θ θ θ θ θ θ θ θ θ θ θ θ | 1641–1900 | > 1⅔ |
| 5 | ■ ■ ■ ■ ■ ■ ■ ■ ■ ■ ■ ■ | > 1900 | > 2 |

Table III. Log-probit equations for spring and summer emergence for various years and locations

| Spring generation log-probit equation | r^2 | Summer generation log-probit equation | r^2 | Code letters to figs. & text | Location | Year | Source |
|--|-------|--|-------|---------------------------------------|---------------------|------|--------------|
| $y^* = -16.929 + 7.926 \log x^\dagger$ | .97 | $y = -69.427 + 23.084 \log x$ | .97 | a | Grand Rapids, Mich. | 1957 | |
| $y = -17.022 + 7.934 \log x$ | .99 | $y = -81.382 + 27.091 \log x$ | .99 | b | " | 1958 | |
| $y = -13.927 + 7.117 \log x$ | .94 | $y = -42.568 + 14.753 \log x$ | .98 | c | " | 1959 | |
| $y = -18.76 + 8.729 \log x$ | .87 | $y = -81.84 + 27.340 \log x$ | .99 | d | " | 1960 | |
| | | $y = -69.224 + 23.316 \log x$ | .98 | e | Belding, Mich. | 1973 | |
| $y = -13.043 + 6.766 \log x$ | .95 | $y = -95.457 + 31.902 \log x$ | .99 | f | " | 1974 | |
| $y = -15.782 + 7.795 \log x$ | .91 | $y = -52.652 + 17.582 \log x$ | .98 | g | " | 1975 | |
| $y = -20.249 + 9.066 \log x$ | .99 | $y = -50.312 + 16.835 \log x$ | .96 | h | Glassboro, N.J. | 1927 | Headlee 1928 |
| $y = -23.808 + 10.329 \log x$ | .98 | $y = -50.031 + 16.908 \log x$ | .98 | i | " | 1929 | Headlee 1936 |
| $y = -27.471 + 11.773 \log x$ | .97 | $y = -47.505 + 15.938 \log x$ | .99 | j | Olney, Ill. | 1915 | Glenn 1922a |
| $y = -23.705 + 10.553 \log x$ | .90 | | | k | " | 1916 | Glenn 1922a |

*Expressed in probability units; for conversion to percent see table of probits.

†Degree days.

#Emergence data not collected.

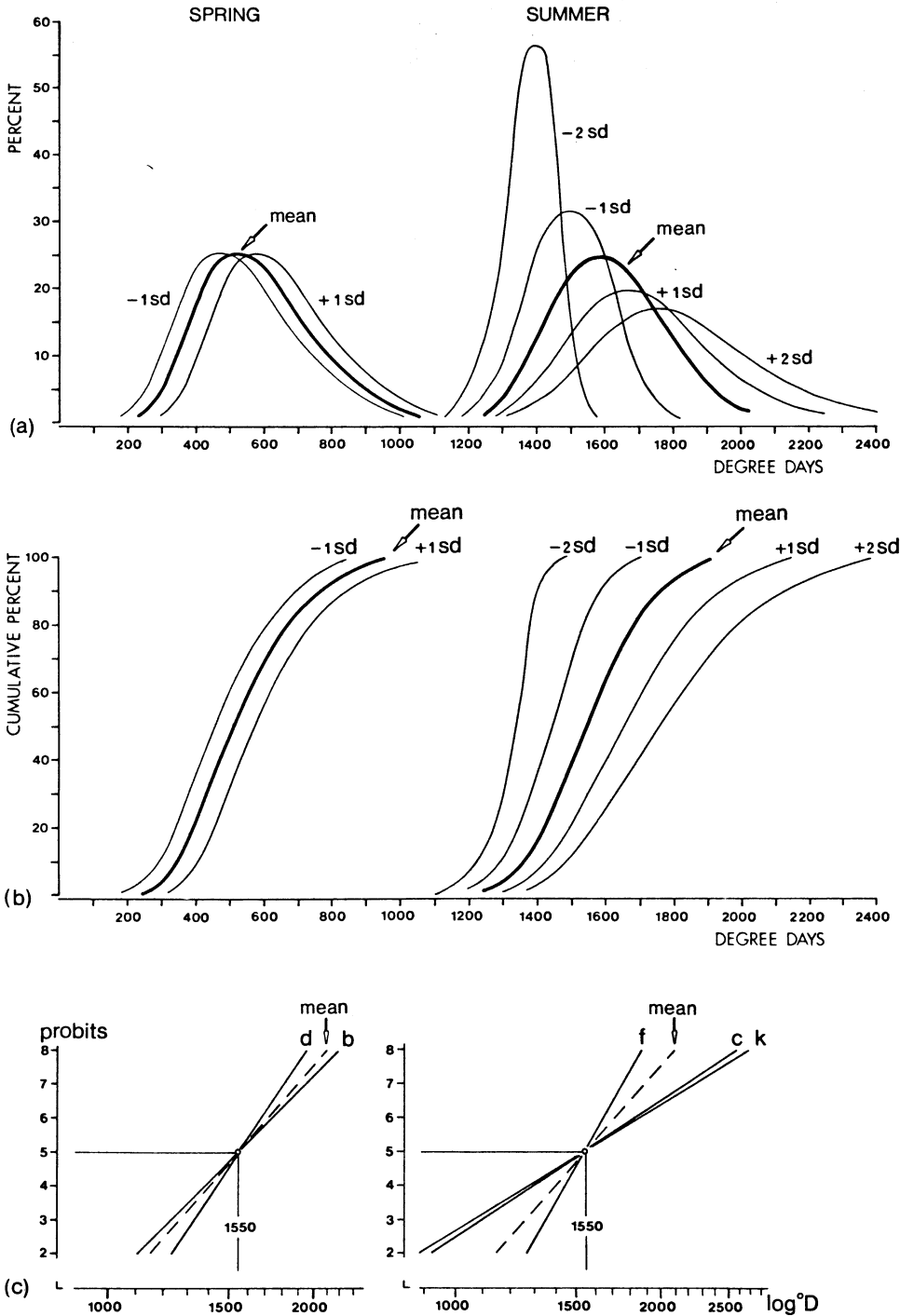
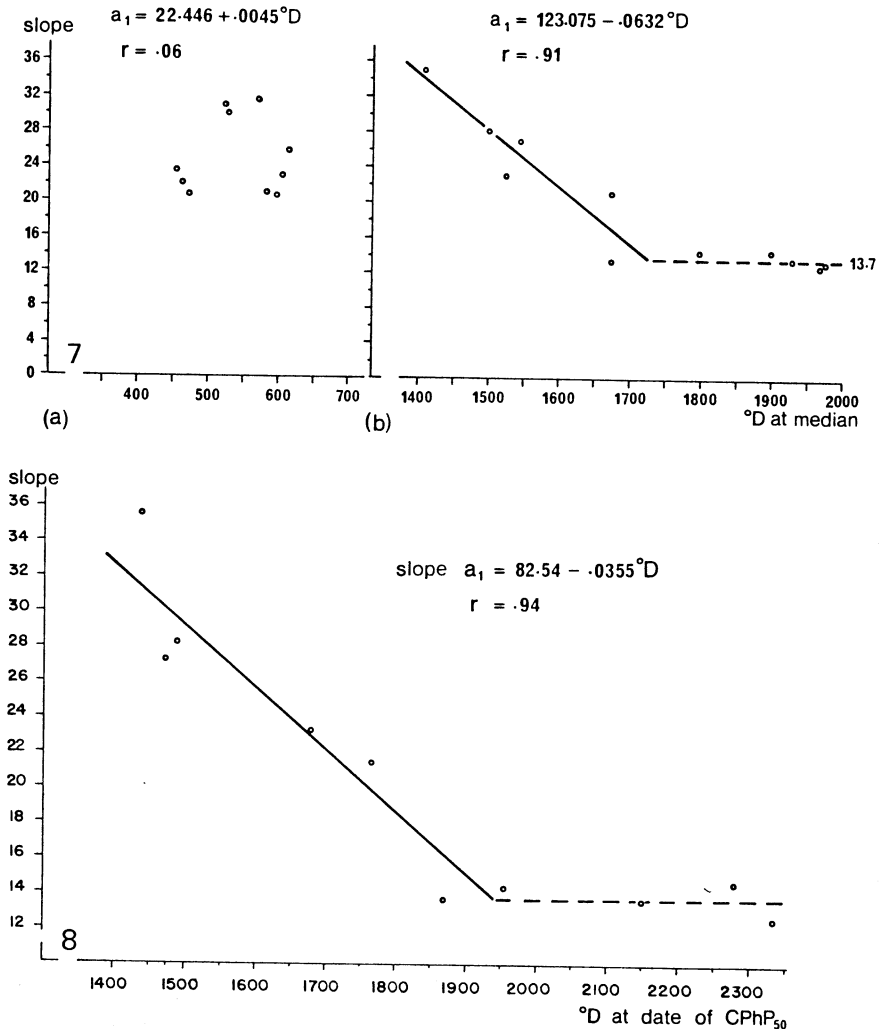


FIG. 6. (a) Average codling moth emergence (\pm S.D.) during spring and summer in west-central Michigan. (b) Same data shown as cumulative curves on physiological-time scale. (c) Cumulative curves transformed to log-probit lines; solid lines, b & d in spring and c & f in summer, indicate range of slope; the slope of a full second generation is shown by line k (code letters refer to data sources in Table III).

masked in the Michigan data by the dominating effect of diapause on the variance of summer emergence.

If all larvae of each generation transformed one would observe that the variances of population curves would tend to increase with each generation during the course of the season. This increasing dispersion of population curves is due, in part, to the inherent genetic variability of growth in response to environmental variables, growth differences because of nutrition, and an extended oviposition period. Microclimate differences due to the heterogeneity of habitats which influence the developmental rates of the various stages of the insect add further to the increasing variance of successive population curves. For instance, at Glassboro, N.J. (h), an area with a full second generation, the slope of the transformed and centered emergence curve decreased from 22.856 for the spring to 14.311 for the summer generation. In contrast, with increasing first generation



FIGS. 7-8. 7, relationship between the median and the slope of the transformed emergence curves during (a) spring and (b) summer. 8, relationship between the seasonal effective temperatures at the time of the CphP₅₀ and the slopes of the transformed emergence curves (dotted line indicates average slope of a full second generation).

diapause the slope of summer emergence should become larger and approach or exceed the slope of the spring emergence curve. This is indicated by the average emergence curves from Michigan with little difference in slopes between the two generations (22.170 and 22.817 respectively; see dotted lines in Fig. 6c). Diapause also seems to affect the degree of skewness of the summer emergence curve. Spring emergence is usually positively skewed which would affect the skewness of population curves in the following generations. However, diapause in larvae from the extended tail of spring emergence would tend to normalize the distribution of summer emergence. Figure 6a indicates this effect.

Prediction of spring and summer emergence. After combining the spring emergence data from 6 years (a, b, c, d, f, and g in Table III) the log-probit equation for the average emergence was calculated as:

$$\text{Spring emergence (probits)} = -15.3967 + 7.5157 \log ^\circ\text{D}.$$

Figure 6a–b indicate that the average curve is an adequate predictor for spring emergence with small error.

Calculation of the summer emergence curve uses the relationship between median and slope (see above). In addition, for complete definition of this curve the slope was independently estimated by the following relationship suggested by Fig. 8.

The degree day total at the time of the CPhP₅₀ is usually correlated with the degree day total of an earlier date. Therefore a good correlation exists also between the seasonal degree day total of 1 July and the slope of summer emergence. In central Michigan summer emergence begins up to 2 weeks after 1 July which makes a prediction from this relationship still timely and it can be used, therefore, to predict the slope of the log-probit line at the 1550°D point.

$$a_1 = 68.957 - .0483 (^\circ\text{D July 1}), r = .95.$$

Then the intercept is calculated from the following equation by solving it for a_0

$$5.0 = a_0 + (68.957 - .0483 ^\circ\text{D July 1}) \log 1550.$$

This defines the log-probit line centered at the median to 1550°D. The next step requires the positioning of this line on the physiological-time scale at the predicted 50% point. This °D value is obtained from the relationship between slope and median (Fig. 7b).

$$^\circ\text{D}_{50\%} = (123.075 - a_1) / .0632.$$

Finally, by substituting the calculated values for a_0 , a_1 , and $^\circ\text{D}_{50\%}$ in the following log-probit equation the proportion of emergence (in probits) can be determined for the current °D total:

$$\text{Summer emergence (probits)} = a_0 + a_1 \log (^\circ\text{D} + 1550 - ^\circ\text{D}_{50\%}).$$

The log-probit line as the transform of the cumulative emergence curve is completely defined by the slope and a single point, in the above calculations the median. As an alternative, the point on the average summer emergence curve (Fig. 6a–b) with the smallest standard error can be used instead. As Fig. 6 indicates the standard error increases with each decile percent, but is smallest during the early part of summer emergence since diapause has little effect on the beginning of this generation. For instance, the average 10% point at 1368°D has a standard error of 26, which increases steadily to 43 at the median (1555°D) and to 73 at the 90% point (1770°D). As before, the slope is estimated from the relationship to the cumulative °D on 1 July to define the log-probit line with median at 1550°D. Then the predictive log-probit line is positioned at the average 10% point (1368°D) on the physiological-time scale.

Improvement in predictions of the seasonal development can be achieved by synchronizing the physiological-time scale with biological observations from the field. The authors have suggested in a previous publication (Riedl *et al.* 1976) utilizing first

catch in a seasonal pheromone trap record as biological reference point, and presented supportive data that the pheromone trap gives an accurate estimate of the beginning of spring emergence under the climatic conditions of Michigan.

In Table IV first generation oviposition curves from 3 years were centered to first catch (Biofix 1) instead of 1 Jan. This reduced the standard errors of the average °D totals for percentage oviposition considerably (Table IV). The average °D distance from Biofix 1 to 50% oviposition was 386 (+ 15 S.E.), but when 1 Jan. was used as the starting point for the physiological-time scale the standard error for the average °D total at the median was higher (± 35) (Table IV). Centering the second generation oviposition curves or emergence curves from both generations to Biofix 1 reduced in all instances the standard errors of the average °D totals for percentage oviposition and emergence. This improved accuracy when synchronizing the physiological-time scale with a biological reference point is not unexpected. Diapause termination is difficult to predict and therefore 1 Jan. is only an arbitrary starting point for the physiological-time scale. The beginning of pupation in the spring could serve as a reference point, but first male catch as an estimate of the beginning of emergence is more conveniently observed. Ideally, the physiological-time scale should be reset more often than just once during the season to synchronize it with the unfolding phenological events in the field. However, the peaks in a pheromone trapping record which are identifiable biological events soon after they occur showed inconsistent relationships to the 50% points of emergence, oviposition, and egg hatch in both generations (see Table IV in Riedl and Croft 1977). Therefore their value as reference points seems questionable at this point.

In Michigan the median of spring emergence occurred on an average 290°D after first catch (Riedl *et al.* 1976). The equation for the average spring emergence (see above) defines the 50% point at 517°D since 1 Jan. In order to synchronize the physiological-time scale with the observation of first catch and center it to that event the °D total on the day of first catch needs to be set to 227°D. This figure is the difference between 517°D and 290°D, the °D totals of the 50% points centered to 1 Jan. and Biofix 1 respectively.

CONCLUSIONS

The authors examined the variability of an important adaptive mechanism, the photoperiodic reaction, in geographic codling moth populations on apple in North America. However, differences between codling moth populations may express themselves in more than one biological parameter. For instance, Beck and Apple (1961)

Table IV. Average cumulative degree days from Jan. 1 and from first male pheromone trap catch (Biofix 1) for the proportion of oviposition during the spring generation

| Percent oviposition | °D from Jan. 1 | | °D from Biofix 1 | |
|---------------------|----------------|------------|------------------|------------|
| | \bar{x} | \pm S.E. | \bar{x} | \pm S.E. |
| 5 | 419 | 27 | 171 | 8 |
| 10 | 459 | 28 | 211 | 7 |
| 20 | 513 | 30 | 265 | 8 |
| 30 | 555 | 31 | 307 | 9 |
| 40 | 594 | 33 | 346 | 12 |
| 50 | 634 | 35 | 386 | 15 |
| 60 | 676 | 37 | 428 | 18 |
| 70 | 724 | 40 | 476 | 22 |
| 80 | 784 | 44 | 536 | 28 |
| 90 | 876 | 51 | 628 | 37 |
| 95 | 960 | 59 | 712 | 47 |

could distinguish between geographic populations of another lepidopterous species, the European corn borer (*Pyrausta nubilalis* (Hbn.)), by their photoperiodic reaction as well as by their specific heat requirement for larval development. Phillips and Barnes (1975) suggest that the codling moth has developed distinct host races in addition to geographic races. They conclude that populations adapted to apple, plum, and walnut from the same geographic area differed in several biological parameters such as diapause induction and termination, developmental heat requirements, and behavioral characteristics. This implies that geographic races of the codling moth may vary not only in their diapause response as was confirmed in this study but also in immature growth rates, physiological thresholds, and other parameters. The question of interpopulation variability of certain biological parameters needs to be evaluated more before population models for the codling moth can be applied with a high degree of resolution to different geographic populations and host races.

The predictive value of the methods outlined above depends on how accurately the slope of the cumulative emergence curve can be estimated. Figures 7b and 8 give only an approximate variance estimate of summer emergence. This is because the emergence data for this analysis were obtained with methods (trunk bands, fruit in field cages) which reportedly underestimate actual duration of emergence in the field (Peterson and Haeussler 1928; Riedl and Croft. 1976). Although this introduces a certain error in the application of these methods, the trends found in this analysis of second generation emergence patterns are believed to be general enough to be useful in predicting moth emergence under field conditions (Riedl and Croft 1977).

The regression model for the slope of the cumulative summer emergence curve (Fig. 8) could possibly be improved by incorporating other important variables such as the direct effects of temperature on diapause induction. The approach illustrated here for the first summer generation could be applied to the second summer generation in areas where a partial third generation occurs, provided an adequate data base allows for calculating the necessary relationships.

Lastly, knowledge of seasonal temperature effects on first generation diapause and the variance of second generation emergence also can aid in determining the degree of population pressure in the second generation and need for seasonal chemical control. In warm years the potential for second generation damage is much greater and therefore first generation suppression must be thorough since otherwise a high proportion of larvae will transform during the same season. In cooler years this potential can be considerably lower and it is directly related to the extent of first generation diapause. Adequate chemical suppression in cooler seasons is therefore most important during the first half of spring emergence since this early flight will produce the majority of second generation larvae during that year.

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