Phenological Adaptations of a Colonizing Insect: The Southwestern Corn Borer, *Diatraea grandiosella**

M. Takeda** and G.M. Chippendale
Department of Entomology, University of Missouri, Columbia, Missouri 65211, USA

Summary. The developmental rate, critical photoperiod, and diapause intensity were determined for three populations of the southwestern corn borer, *Diatraea grandiosella*, from Missouri, Mississippi and Kansas. Mississippi larvae grew at the highest rate and Missouri larvae grew at the lowest rate. The zero developmental temperatures (°C) for the Missouri population were estimated from regression lines as follows: 10.5° (eggs), 10.8° (diapausing larvae), 13.3° (non-diapausing larvae) and 11.4° (pupae). The required heat units were: 85° (eggs), 588° (diapausing larvae), 333° (non-diapausing larvae) and 149° days (pupae). However, the observed low temperature limit for larval growth under constant temperature regimes was approximately 17° C.

The critical day lengths for diapause induction observed at 25° C were: 15 h 11 min (Missouri); 15 h 20 min (Mississippi); and 15 h 22 min (Kansas). The photoperiodic response of the Mississippi larvae was more or less retained at 30° C, whereas the response of the Missouri larvae was completely suppressed at this temperature. Diapause was most easily terminated in the Kansas larvae. The most intense diapause was observed in the Mississippi larvae.

Model seasonal life cycles of the three geographic populations were constructed using photothermograms. Although the models showed good agreement with the field situation for the Missouri and the Kansas populations, some unknown factor(s) remains to account for an extremely long critical photoperiod in the Mississippi population.

Introduction

The present study examined the geographical differences in the seasonal timing mechanisms of Missouri, Mississippi, and Kansas populations of the southwestern corn borer, *Diatraea grandiosella* Dyar. The study investigated how each population acquired a specific set of developmental characteristics under different environmental conditions. Critical events to consider in synchronizing the life cycle of *D. grandiosella* with its host plants and optimal season include the timing of spring emergence, developmental rate, critical photoperiod, interaction of critical pho-

toperiod with temperature, the timing of the cessation of feeding and the onset of diapause, and the number of generations per year.

D. grandiosella is a neotropical insect which was first reported in New Mexico in 1913. Thereafter, the species expanded its range eastwards and northwards and is now present in 14 states below 38° N latitude (Chippendale and Reddy 1974). Since populations at the northern limits of the distribution are exposed to severe environmental pressures including early frost, soil freezing, long summer day length, and short growing season, the timely completion of the life cycle is the most critical adaptation under these conditions. Records of territorial expansion suggest that *D. grandiosella* rapidly developed a local seasonal adaptation. The timing of the life cycle is accomplished by photoperiodic responses which are characterized in this species by strong interactions with temperature (Chippendale et al. 1976; Takeda 1978).

Materials and Methods

The experimental populations of *D. grandiosella* originated from Portageville, Pemiscot County, Missouri (36.3° N, 89.4° W), Starksville, Oktibbeha County, Mississippi (33.3° N, 88.5° W) and St. John, Stafford County, Kansas (37.6° N, 98.5° W). The Missouri stock (MO) was established from diapausing larvae collected in 1969. The Kansas stock (KS) was established in 1977 from a colony maintained at Kansas State University. Eggs of the Mississippi population (MS) were received from Mississippi State in 1976 and 1977.

Larvae were maintained on an artificial diet in one ounce clear plastic cups using previously described methods (Chippendale 1975). Non-diapausing larvae were maintained at 30° C under LD 12:12, whereas pre-diapausing larvae were held at 23° C LD 12:12. On about the twentieth day, pre-diapausing larvae were transferred on to fresh food. The integument of mature larvae is either spotted or pigment-free. Since the ecdysis to the pigment-free morph parallels the induction of diapause, this ecdysis was adopted as a marker for the onset of diapause. Non-diapausing larvae pupate without ecdysing into this pigment-free morph. Forty-day-old newly diapaused larvae reared at 23° C, LD 12:12 were used to start diapause termination experiments. Larvae were transferred into glass tubes containing moist paper strips, or were retained in their rearing cups. Observations were continued until all larvae had either pupated or died. Approximately 50 individuals were maintained in each treatment. Since no visible response distinguishes diapause development from post diapause development, pupation was used to mark the completion of diapause. Most experimental regimes were provided by 8 cu. ft. Percival incubators equipped with two fluorescent tubes controlled by 24-hour timers. The temperature was held constant to about ±1° C.

Results

Heat Requirement for the Development of Immature Stages

In principle, adaptive changes in a species' developmental rate and heat requirements permit a south-to-north colonization. Initially, the relationship between rearing temperatures and the growth rate of the immature stages was examined using the MO stock. Eggs collected at 4 h intervals at 25° C DD were divided into three groups ranging from 57 to 65 in sample size. When the eggs were placed at 30° C (LD 12:12); 25° C (LD 14.5:9.5) and 23° C (LD 12:12), pink rings in the serosa first appeared at 24, 36 and 60 h, respectively, after their transfer to different temperatures. The egg hatch was observed every 4 h, and the peak was observed to occur at dawn. The mean duration in days (D) of embryonic development was calculated disregarding this gating of egg hatch. Fifty percent of eggs completed their development in 4.4, 5.4 and 7.2 days at temperatures of 30° C, 25° C, and 23° C, respectively. The reciprocals of these $(1/D = V$: Velocity) were plotted for different temperatures and linear regression parameters were calculated (Fig. 1A). The zero development temperature (t_o) was estimated from the intersection $(-a/b)$ of the regression line across the temperature with no growth $(V=0)$.

A similar technique was used to determine larval growth parameters $(n=370)$. Since larvae show a photoperiodic response for diapause, the mean duration (D) of the larval period was estimated from the egg hatch to either pupation (non-diapause) or ecdysis into the pigment-free morph (diapause). The number

of pupae and pigment-free larvae was recorded daily. The linear regression lines were calculated as indicated above (Fig. 1C, D). The threshold temperature (t_o) for growth of diapause-programmed larvae was about 10.8° C, whereas that for growth of non-diapause larvae was about 13.3° C. The growth of diapause-programmed larvae was also more or less temperature-compensated because the slope (b) was much smaller than it was for non-diapause larvae.

Newly ecdysed pupae (<4 h post-ecdysis) $(n=616)$ were exposed to 20° C (LL), 21° C (LD 12:12), 22° C (LD 12:12), 23° C (LD 12:12), 25° C (LD 16:8, LL), 28° C (LD 12:12), or 30° C (LD 12:12, LL). Adult emergence was observed every 4 h. Although gating of emergence was observed, the data were pooled. At some temperatures, special attention was paid to the differences in the rate of adult differentiation between the sexes. The mean duration (D) of the pupal stage was 14.2 days for both males and females at 22° C whereas it was 11.4 days for both males and females at 25° C. It was 8.2 days for males and 8.4 days for females held at 30° C. No significant difference was detected between the sexes. The threshold temperature was about 11.4° C (Fig. 1B).

The required heat units (K) were estimated from the above data by $1/b$ since $K=(T-t_0)D$, where D and t_0 are replaced by $1/V = 1/(a+bT)$ and $-a/b$, respectively (Table 1). The theoretical developmental zero temperature, however, did not fit the observed thresholds. Under experimental conditions, the larval growth was found to be retarded at 18° C. Therefore, K' was estimated based on $t_0 = 17° C$, $t = 25° C$ and D at 25° C. Although this is a one point estimate, it may be more realistic than a calculation based solely on theoretical considerations. This calcu-
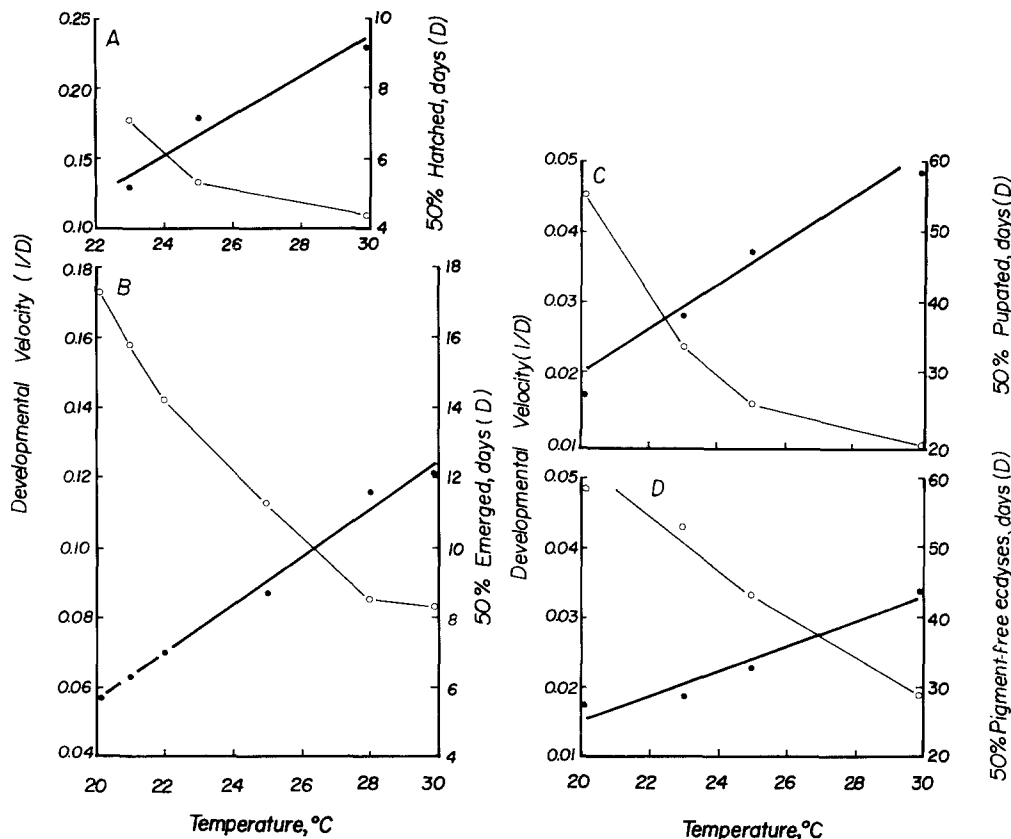

Fig. 1A–D. Developmental velocity and duration of the life stages of *D. grandiosella* between 20° and 30° C. **A** Embryonic development. **B** Adult development. **C** Larval development (non-diapause). **D** Larval development (pre-diapause). (o) Days to 50% ecdysis. (●) Developmental velocity (1/D)

Table 1. Developmental parameters and required heat units for immature stages of *D. grandiosella* originating from southeast Missouri[a, b]

Developmental stage	Regression parameters		Correlation coefficient (r)	Theoretical t (°C)	K	K'
	a	b				
Egg	−0.121 (−0.107)	0.0118 (0.0101)	0.959 (0.971)	10.5 (10.6)	84.8 (99.0)	50.1
Larva (diapause)	−0.018	0.0017	0.977	10.8	588.2	320.2
Larva (non-diapause)	−0.040 (−0.015)	0.0030 (0.0017)	0.987 (0.992)	13.3 (9.1)	333.3 (588.2)	237.1
Pupa	−0.076 (−0.107)	0.0067 (0.0108)	0.991 (0.948)	11.4 (9.9)	149.3 (92.6)	85.7
Egg to adult (diapause)	–	–	–	–	822.3	456.0
Egg to adult (non-diapause)	–	–	– (0.999)	– (10.4)	567.4 (779.8)	372.9

[a] K=required heat units above the theoretical development temperature (t); K'=adjusted K based on $t_0=17°$ C and D at 25° C

[b] Parenthetic values are those calculated for a Kansas stock reared between 18° and 30° C (Whitworth and Poston 1979)

Table 2. Geographic variation in critical photoperiod and temperature response of *D. grandiosella*[a]

Temperature (°C)	Photo-period (L:D)	Diapause induction (%)		
		Missouri stock	Kansas stock	Mississippi stock
23°	12:12	100.0	100.0	100.0
25°	10:14	0	11.0[b]	9.3[b]
25°	14:10	100.0[b]	100.0	97.6
25°	14.5:9.5	100.0	100.0[b]	96.2
25°	15:9	68.0[b]	96.0	79.5[b]
25°	15.5:8.5	21.5[b]	32.1	31.0[c]
25°	16:8	0	3.7	4.4[c]
25°	LL	0	0	0
30°	12:12	0	3.7	27.8[d]
30°	16:8	6.7	7.3	2.7
30°	LL	0	0[d]	0[b]

[a] At least 45 larvae per treatment
[b] Mean of two treatments
[c] Mean of three treatments
[d] Mean of four or more treatments

lation generated values of 456 degree-days for egg to adult (with the intervention of diapause) and 373 degree-days for egg to adult (without diapause).

Critical Photoperiods for Diapause Induction

Three geographic populations of *D. grandiosella* were exposed to photoperiods ranging between LD 14:10 and LD 16:8 with 30 min increments at 25° C, to obtain a precise value for the critical photoperiod (Table 2). Five groups of larvae ($n=43$ to 64) were employed. The results showed critical photoperiods of about LD 15 h 11 min, LD 15 h 22 min, and LD 15 h 20 min for the MO, KS, and MS stock, respectively. Although differences in the critical photoperiods are not as marked as for some other insects (Danilevskii 1965), the passage of 11 min roughly corresponds to a week difference of daylength in August at 35° N.

The Rate of Diapause Development

The rate of diapause development was compared in the KS and MO stocks of *D. grandiosella* (Fig. 2). KS larvae (76 days old in 23° C LD 12:12) and MO larvae (75 days old in 23° C LD 12:12) were transferred to 30° C LD 12:12 and 30° C LL. The median pupation for the KS stock occurred on the 57th day in LD 12:12 and on the 29th day in LL. The corresponding figures for the MO stock were 55 and 36 days in LD 12:12 and LL, respectively. The photoperiodic response was more apparent in the KS stock than it was in the MO stock. The time between the median days for pupation in males and females was shorter in the KS stock than it was in the MO stock: 14 days vs. 7.5 days in LD 12:12 and 8 days vs. 3.5 days in LL. Forty-day old MS larvae held in 23° C LD 12:12 took 43.1 days to reach 50% pupation, whereas MO larvae of the same age required only 36.5 days in 30° C LL to reach 50% pupation. MS larvae (169 days old in 23° C LD 12:12) required 13.0 days to reach 50% pupation in 30° C LL. MO larvae held under identical conditions, on the other hand, required about 10 days to reach 50% pupation. When days to 50% pupation in 30° C LL vs. latitude are compared for the three populations the relationship observed is that the higher the original latitude the more rapidly is diapause terminated.

Analysis of the Insect's Seasonal Life History in Missouri

Figure 3 is a photothermogram based on climatic data collected in Pemiscot County, Mo. and provides a first attempt to reconstruct the seasonal life cycle of *D. grandiosella*. We based the approximation on records obtained over 10 years at light traps. Heat units were accumulated from the first moth flight based on ten year records of temperature. Approximately 900 to 1,000° days above 17° C are available per year. Three moth flights were recorded in the field. The first moth flight composed of overwintering generation adults, appears in late May. The second peak which is comprised of the first generation adults, appears in early July. Therefore, about 360° days of heat units are available by this time. The long day conditions assure that the first generation is destined for non-diapause. Calculated heat units
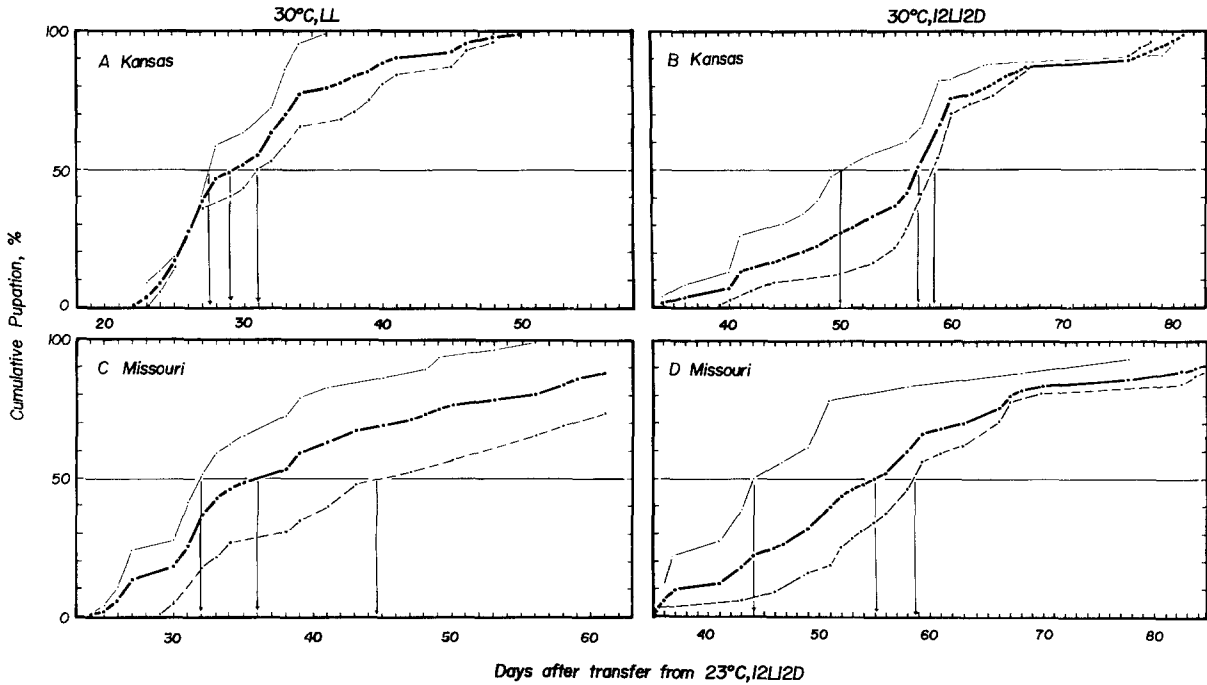
Fig. 2A–D. Geographic variation and sex-associated differences in the rate of diapause development of KS and MO larvae transferred from 23° C LD 12:12 at 76 and 75 days of age, respectively. **A, C** Larvae were transferred to 30° C LL. **B, D** Larvae were transferred to 30° C 12:12. Differences in the rate of diapause development in the different populations and different sexes are illustrated. ——· ♀, ·——· ♂, ●—● ♀+♂
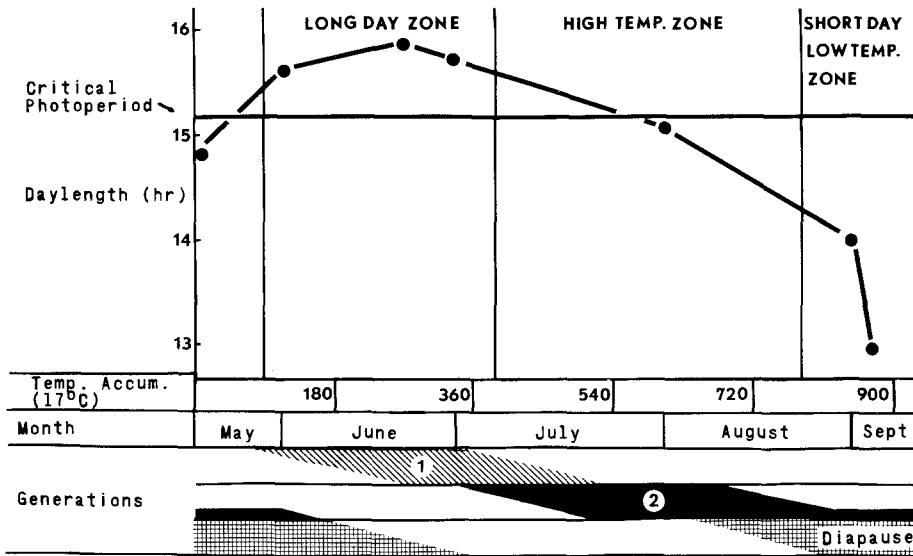

Fig. 3. Photothermogram illustrating the chronology of the natural life cycles of D. grandiosella in Pemiscot County Missouri. At this latitude the solar day ranges from 9.6 h to 14.7 h. Effective daylength was estimated by sunrise to sunset time plus the civil twilight period at dawn and dusk. Mean temperatures (2 week averages for 1973) ranged from 2° C to 27° C, whereas the deviation about the mean ranged from about 1.5° C to 6° C (Chippendale et al. 1976). Three moth flights are recorded annually (10 yr light trap record) and about 900 to 1,000 day-degrees (>17° C) are available per year. Laboratory data indicate that 373° days are required for one generation from egg to adult. Heat units between successive moth flight peaks were 360° days, 370° days and 300° days. Long day zone – daylength is longer than the critical photoperiod. High temperature zone – average daily temperature exceeds 25° C

(K', >17° C) required for the completion of one generation were 373° days which agrees closely with the natural situation. The third moth flight appears in the middle of August. Although this peak is the largest one with the largest variance, the time between the two peaks again is approximately 360° days. The number of heat units required in the laboratory for 50% of the larvae to ecdyse into the pigment-free morph was about 370° days. Available heat units for the third generation larvae are about 300° days. Although there is a shortage of about 70° days in heat units to reach the pigment-free morph, additional heat may be obtained through the high temperature fraction

of the daily temperature cycle even after the average temperature falls below 17° C. A photothermogram based on the daily average temperature may, therefore, underestimate available heat units.

When environmental conditions are stable the photothermogram should accurately predict the life cycle of D. grandiosella after the first flight peak in the spring. However, its accuracy should be tested in the field because temperature fluctuates, especially in the fall. To check the model, fifty-six larvae supplied with artificial diet in plastic cups were exposed to natural daylight and temperature in Columbia, Missouri every week beginning

Table 3. The effect of different dates of exposure on diapause induction of *D. grandiosella* maintained on artificial diets and exposed to conditions prevailing in Boone County, Missouri in 1977

Exposure beginning	Larvae (No.)	August 26		September 11		September 24		November 8		November 30		Larval mortality (No.)	Pupae (%)
		Pigment-free larvae (No.)	Pupae (No.)	Pigment-free larvae (No.)	Pupae (No.)	Pigment-free larvae (No.)	Pupae (No.)	Pigment-free larvae (No.)	Pupae (No.)	Pigment-free larvae (No.)	Pupae (No.)		
July 29	44	0	8	7	12	20	14	21	14	21	14	11	40.0
August 5	56	0	0	1	2	17	4	21	4	21	5	30	19.2
August 13	56	0	0	0	0	3	0	6	0	12	0	44	0.0
August 19	56	0	0	0	0	0	0	8	0	13	0	43	0.0

Table 4. Geographic variation in the larval growth rate of *D. grandiosella*[a]

Temperature (°C)	Photoperiod (L:D)	Geographic stocks					
		Missouri		Kansas		Mississippi	
		50% pupation (days)	50% pigment-free ecdyses (days)	50% pupation (days)	50% pigment-free ecdyses (days)	50% pupation (days)	50% pigment-free ecdyses (days)
23°	12:12	–	53.0[d]	–	–	–	48.8
25°	10:14	–	–	25.6	–	24.7	41.1
25°	14:10	–	43.7[b]	–	–	–	41.0
25°	15:9	25.2[b]	41.0[b]	20.5	44.0	29.0	45.8[b]
25°	15.5:8.5	26.2[b]	42.0[b]	–	–	25.2[c]	42.9[c]
25°	16:8	28.3	–	27.4	–	25.8[c]	–
30°	12:12	20.7[d]	–	–	–	19.1[d]	29.1[d]
30°	16:8	20.4	–	19.4	–	17.5	–

[a] At least 45 larvae per treatment   [b] Mean of two treatments   [c] Mean of three treatments   [d] Mean of four or more treatments
–= No data

on July 29, 1977 (Table 3). The date of pupation and ecdysis into the pigment-free morph was recorded. Photoperiods were shorter than the critical photoperiod. A noticeable percentage of pupation occurred in the two early exposures probably due to high temperature. The results are consistent with the prediction by the photothermogram.

Geographic Adaptation of Life Cycle

The developmental rate of larvae of *D. grandiosella* was investigated to reconstruct the seasonal life cycle for the KS and the MS populations (Table 4). Since the larval stage is the longest, it provides the most significant contribution to a total life span. The larval growth rate of the KS population was higher than that observed for the MO population. Assuming that the developmental zero point is 17° C and that the heat requirements for eggs and pupae are the same as for the MO population about 350° days are needed to complete a generation in Kansas. Since there are about 800° days available per year above 17° C, two generations per year are predicted for Kansas. Heat units available in Kansas were estimated from 20 year records obtained from Wichita, Kansas. Wilbur et al. (1950) have reported two complete generations and sometimes a partial third generation in Kansas. As the photothermogram shows, the first generation larvae grow under long day and high temperature and are programmed for a non-diapause generation whereas the second generation larvae grow under short day and intermediate tempera-

ture and are programmed for diapause. The insect shows an extremely high degree of photoperiodic adaptation (Fig. 4).

The critical photoperiod for the MS stock was about LD 15 h 20 min, about 9 min longer than that for the MO stock (Table 4). MS larvae grew faster than did MO larvae. As the original latitude increases it is usual to observe a decreased requirement for heat units and an increased critical photoperiod (Danilevskii 1965; Masaki 1961). Although the observed values appear to be against the general rule, this should be attributed to an increased number of generations per year. Three generations are reported to be completed and partial fourth moth flight is observed in the field in Mississippi (Davis 1965). Although most fourth generation larvae may ultimately be killed by frost, the available heat units of about 1,400° days (Jackson, MS) nearly allows for four generations (Fig. 4).

The MS larvae were found to have an unexpectedly long critical photoperiod which cannot be reached in the field. In addition, it remains unclear how the first generation larvae complete a non-diapause generation under short days and low temperatures. Almost 90% of MS larvae entered diapause under a photoperiod of LD 15:9 in the laboratory. This photoperiod appears in late May. To avoid programming for diapause, the insects may respond to increasing temperature or daylength. However, *D. grandiosella* did not show increased sensitivity to changing photoperiod at least to a large step-up or step-down (Takeda and Chippendale 1982). Alternatively, the first generation may appear in June after the average temperature becomes more than 25° C, thereby overriding a short daylength response.
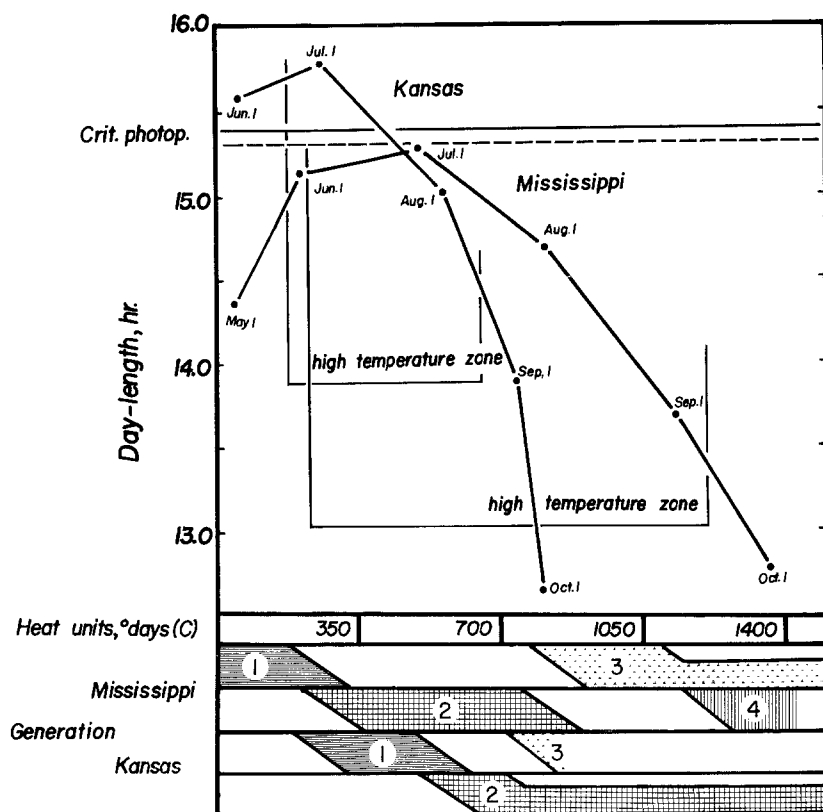
Table 5. Some examples of insects exhibiting geographic variation in photoperiodic response at a fixed temperature

Type	Examples	Geographic range (°N) of examined populations	Critical photo-period range (h/°C)	Reference
I. Northern populations obligatory diapause	*Hylophila prasinana* (Lep.)	42°–50°/50°–60°	–	Danilevskii (1965)
II. Containing populations with significantly different photoperiodic responses	*Pteronemobius fascipes* (Orth.)	29°–37°/37°–44°	–	Masaki (1973)
	Pteronemobius taprobanensis (Orth.)	24°–27°/28°–35°/36°–43°	–	Masaki (1979)
	Chilocorus bipustulatus (Col.)	–	–	Zaslavskii (1972)
III. Continuous grade in critical photoperiod	*Acronycta rumicis* (Lep.)	43°–60°	5 h/23°	Danilevskii (1965)
	Mamestra brassicae (Lep.)	41°–60°	4 h/25°	Danilevskii (1965)
	Aedes sierrensis (Dipt.)	33°–45°	2.3 h/24°	Jordan and Bradshaw (1978)
	Wyomyia smithii (Dipt.)	30°–50°	3.5 h/25°	Bradshaw and Lounibos (1977)
IV. Containing distinct ecotypes	*Chilo suppressalis* (Lep.)	31°–43°	2.3 h/25°	Kishino (1970)
	Pieris brassicae (Lep.)	43°/50°–60°	2.5 h/23°	Danilevskii (1965)
	Ostrinia nubilalis (Lep.)	43°–48°/52°	2 h/25°	Du Chzhen-ven [a]
V. Southern populations do not diapause	*Culex pipiens pipiens* (Dipt.)	/40°	–	Vinogradova [a]
	Samia cynthia (Lep.)	India/Japan	–	Koidsumi and Shibata (1938)

[a] From Danilevskii (1965)

in photoperiodic responses depends on various environmental factors, agricultural practices, migration, post-colonization history, and physiological pre-adaptations. Type I represents species whose northern populations have lost the photoperiodic responses and exhibit an obligatory diapause. Type II represents some species that contain distinct geographic populations with different photoperiodic response patterns. For example, the orthopterans, *Pteronemobius fascipes* and *Pt. taprobanensis*, showed a bell-shaped pattern for growth rate in bivoltine populations, but a short day response in univoltine populations (Kidokoro and Masaki 1978; Masaki 1978). A reversal in a photoperiodic response curve occurs between the bivoltine zone and subtropical zone in these species (Masaki 1978, 1979), which is associated with a change in hibernating stage, and may involve different species. Type III represents species that show a continuous change in critical photoperiod, and is well illustrated by a Noctuiid moth, *Acronycta rumicis* (Danilevskii 1965). Type IV represents species that show relatively stable critical photoperiods and form distinct geographical races. A typical example is the cabbage butterfly, *Pieris brassicae* ((Danilevskii 1965). Critical photoperiods of populations from Leningrad (60° N), Brest (52° N), Belgorod (50° N) and Essentuki (45° N) are indistinguishable. However, a population from Abkhaziya (43° N) showed a critical photoperiod of almost 5 h shorter than that of northern populations. A step-wise variation was also observed in Russian populations of *O. nubilalis* (Danilevskii 1965). The Colorado potato beetle, *Leptinotarsa decemlineata*, has extended its range in Europe without a conspicuous change in the critical

photoperiod for the induction of its adult diapause. The Dutch, Hungarian, and Russian populations show very little change in the critical photoperiod (Goryshin 1956; de Wilde et al. 1959). A similar case has been observed for the fall webworm, *Hyphantria cunea*, in Japan (Masaki et al. 1968; Takeda and Masaki 1979). This feature may be a common first step adaptation among newly colonized, and migratory species. The pattern shown by *D. grandiosella* suggests that the species belongs to this group. Type V represents southern populations of species that have lost their photoperiodic response completely and always produce non-diapause generations.

The timing of the resumption of active development which is determined by the intensity of diapause, response to a long daylength, and increasing temperature in the spring, is another important factor in insect life cycles. The three stocks of *D. grandiosella* showed a geographic trend in diapause intensity that correlated with the original latitude, i.e., MS > MO > KS. It may be especially adaptive for the MS stock not to resume its active development at relatively high fall temperatures. The same trend has been observed in a number of other species (e.g., Masaki 1961; Holtzer et al. 1976).

Critical photoperiods, rates of diapause development, required heat units to complete one generation, different threshold temperatures, and temperature effects on their photoperiodic responses characterize the three geographic populations of *D. grandiosella*. Independent and different selection pressures are imposed on different traits in different seasons. The variation of diapause intensity was inversely correlated with the original

latitude. However, the critical photoperiod and the developmental rate did not show a linear relationship with the original latitude. This is not surprising because the three populations represent different life cycle patterns and the linear relationship is often disturbed by a voltinism change. The observation that the critical photoperiod for the Mississippi population is not reached in the field was, however, unexpected.

Several possibilities were examined for the long critical photoperiod observed for the Mississippi larvae of *D. grandiosella*. (1) Although civil twilight was taken as the effective twilight, the insect may show a greater sensitivity to twilight. (2) The photoperiodic response may always be masked by the prevailing high temperature during daytime. The photothermogram was based on average daily temperatures. If this is the case, the extremely long critical photoperiod, partly due to the gene flow from the northern population with a long critical photoperiod, may be preserved in the population because of its latency, thereby escaping a natural selection. (3) Many individuals may actually enter diapause and soon resume their active growth as a result of prevailing high temperatures. This may be equivalent to an aestival diapause which is common among tropical species. Although this pattern has not yet been documented in any aestivating insects (Masaki 1980), functionally it is an aestivation mechanism and the insect could use the same timing mechanism for both aestivation and hibernation. (4) Moths may emerge late in the spring to avoid short days and low temperatures. Although such late emergence would waste some heat units, it could serve as an integrating mechanism to maintain a trivoltine life cycle in environments where almost four annual generations are possible. The excessive amount of available heat units may be detrimental to the insect because the last generation is always exposed to insufficient heat units and senescent host plants if the insect produced an additional generation for the year. (5) The thermoperiodic conditions may favor continuous development. (6) Gradually increasing photoperiod may prevent first generation larvae from entering diapause. (7) The critical photoperiod may be seasonally targeted by natural selection or may be subject to circannual rhythmicity as Geispits and Simonenko (1970) and Geispits et al. (1972) reported. If the individuals with short critical photoperiods were selected against in the last generation because of the shortage of heat units, the spring generation may show a long critical photoperiod. However, in the first generation the direction of selection pressure would be reversed and a short critical photoperiod would be favored. If this actually occurs in the field, our MS stock may have originated from a winter field population.

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