

Repeated larval diapause and diapause-free development in geographic strains of the burnet moth *Zygaena trifolii* Esp. (Insecta, Lepidoptera)

I. Discontinuous clinal variation in photoperiodically controlled diapause induction

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Summary. *Zygaena trifolii* is a “long-day insect” with temperature-dependent photoperiodic responses. All larval instars are sensitive to photoperiod; however, diapause may occur at the third larval stage or any subsequent larval instars. There were quantitative differences within populations in the threshold photoperiod for diapause induction. The diapause response was polymorphic, so that larvae might enter diapause at different instars under the same culture conditions. Furthermore, decreasing photoperiods below a critical daylength shifted the diapausing instar towards earlier stages. Geographic strains of *Z. trifolii* showed discontinuous clinal variation. Near the northern edge of the distribution [Cologne (Köln), FRG], there is first an obligatory diapause, mainly during early instars, and additional facultative (“repeat”) diapauses during later larval instars in subsequent years. In the southern part of its distribution, this burnet moth is partially bivoltine in the field with a facultative first developmental arrest and a decreased capacity for repeated diapause (Valencia, Spain; Marseille, France). Further experiments indicated that the photoperiodically controlled diapause reaction is also influenced by the number of photoperiodic cycles experienced during the period spent in each larval instar, which depends on temperature. The adaptive significance of obligatory and facultative repeated diapause, varying even among the offspring of a single female, may be to buffer the populations against the more extreme and, from year to year, unpredictable fluctuations in climatic conditions at the northern edge of the distribution.

Key words: Obligatory diapause – Facultative diapause – Repeated larval diapause – Inter- and intrapopulation variation – Spreading of risk

In temperate zones, insect species display a great variety of adaptations in voltinism and seasonal regulation of

Abbreviations: L₃ = feeding 3rd larval instar; L₄D = diapausing 4th larval instar; L₅D2 = repeat – diapausing larval instar with second diapause at the 5th larval stage; LD = light-dark cycle; KT = short-day conditions (e.g. LD 8:16); LT = long-day conditions (e.g. LD 16:8)

growth and dormancy. Within each species, different geographic populations may either have a unique pattern of developmental periods and dormancies, or they may have several optional responses to annually changing and fluctuating weather conditions (for reviews see: Beck 1980; Danilevskii 1965; Danks 1987; Masaki 1961; Saunders 1979; Tauber et al. 1986). Repeated larval diapause with prolonged developmental periods seems to be rather unusual in insect life-cycles and has so far only been recorded occasionally (Barnes 1952; Falkovich 1979; Harvey 1967; Lounibos and Bradshaw 1975; Matthes 1953).

This study concentrates on the photoperiodic response curves for the first and subsequent, facultative, diapauses in *Zygaena trifolii*. An important question to be answered is how the obligatory first diapause of the northern strains may have developed from the facultative diapause of southern populations. Therefore, special consideration will be given to the question of how the photoperiod regulates the onset of diapause at different larval instars.

First observations on the seasonal development and generation time of burnet moths were given by Dorfmeister (1853, 1854, 1855). Further contributions by Burgeff (1910, 1921, 1965, 1971), Dryja (1959), Holik (1937, 1939), Naumann (1985), Naumann and Tremewan (1980), Seipel (1980, 1981, 1982), Tremewan (1977), Uebel (1974, 1983) and Wiegel (1972, 1973) on the regulation of dormancy are inconsistent with respect to the dominating factors that control diapause, but the field observations can be summarized as follows:

In univoltine populations, fully grown larvae will pupate after 6 or 7 regular larval instars and additional diapausing stages at the end of June in a cocoon attached to twigs or sprays. The adults fly during the day for 2–3 weeks in July. Until the end of September, the young larvae of the succeeding and hibernating generation enter diapause, which is characterized by molting to a non-feeding decolorized morph of smaller size. It is characteristic of all *Zygaena* moths that the generation time of the specimens varies markedly among the offspring of a single female, ranging from one to several years; this is a consequence of variation in the number of larval dormancies as well as their duration.

Materials and methods

Laboratory experiments were conducted with larvae of *Z. trifolii* Esp. from Spanish, French, and German stocks (Fig. 1). This atlantomediterranean burnet moth is eurytopic in SW Europe. At the northern boundary of its distribution, the moth is essentially restricted to limestone habitats and the margins of wet meadows with the larval host plants (*Lotus* spp., Fabaceae) (Wipking 1985).

All stocks were bred from egg-batches from at least three wild-captured females to reduce the intrapopulation variation in diapause reactions. No statistically significant difference in the percentages of different diapausing instars was found (U-test, $P > 95\%$, $n = 494$) between larvae of the first three laboratory generations from the Valencia and Marseille stocks, tested simultaneously. Differences between groups were tested by the Mann-Whitney U-test, and accepted as significant within $P \leq 5\%$.

The larvae were reared on fresh leaves of *Lotus corniculatus* L. in small plastic cases at 20°C and at different constant photoperiods ranging from L:D 8:16 to 18:6. In order to test the effects of temperature on photoperiodically controlled diapause induction, further breeding experiments took place under additional temperature and photoperiodic conditions (LD 16:8 at 11°, 15°, 20°, and 25°C; LD 13:11 at 15°, 20°, and 25°C). In order to obtain photoperiodic response curves for diapause induction, the larvae were checked every 2 days and the date of molting and the age of the decolorized diapausing stage were recorded. In order to estimate photoperiodic thresholds for a repeat diapause induction, hibernating larvae were classified into groups exposed to different photoperiods and also by stage into separate diapausing morphs. After cold-temperature treatment (LD 8:16, 5°C) for at least 150 days, the emerging active larvae were again tested at 20°C and various daylengths.

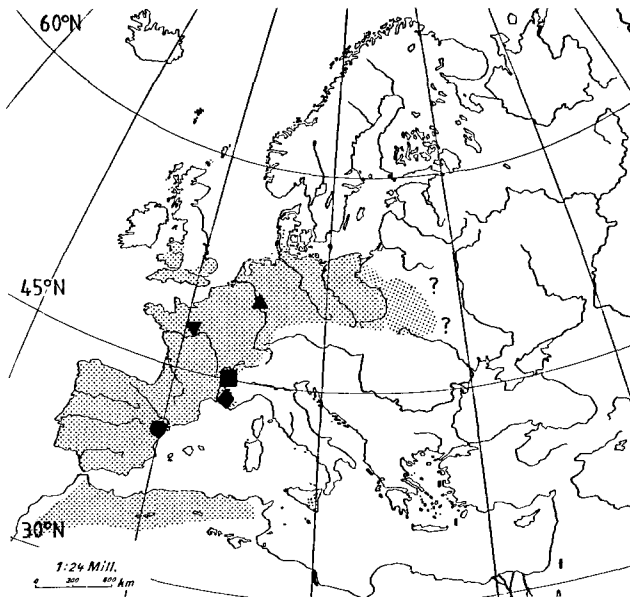


Fig. 1. The distribution of *Zygaena trifolii* Esp. and the geographic origin of the stocks analysed. Circle: Valencia, Spain (39° N); rhomb: Marseille, France (43° N); square: Avignon, France (44° N); inverted triangle: Baugé, France (47° N); triangle: Cologne (Köln), FRG (51° N)

Results

General characteristics of diapause induction in *Z. trifolii*

In all stocks, a diapause of the long-day type was first observed at the 3rd larval instar (L₃D), detectable by the molt to the decolorized morph. Diapause might thereafter occur at any subsequent larval stages. Below the critical photoperiodic threshold for dormancy induction, the diapausing stage was shifted towards later instars with increasing daylength. For repeated larval diapause, there were fewer diapausing morphs the greater the physiological age of the diapausing caterpillars from which the experiment was started, and also fewer in the stock with the southernmost geographic origin. However, the tendency to enter diapause was independent of the photoperiod experienced before a previous diapause [U-test, $P > 95\%$, $n = 749$; stocks: Valencia, Marseille, Cologne (Köln)]. Apart from these results, there may be a genetically controlled variable response in both first and repeated diapause such that the larvae enter dormancy at different instars under one photoperiodic regime.

Photoperiodic response curves in stocks with a facultative or obligatory first diapause

First diapause. A facultative, photoperiodically controlled diapause of the long-day type has been unambiguously found in the South European strains from Valencia (39° N, Spain) and Marseille (43° N, France), which are bivoltine in the field with a main flight period in early summer (Naumann, personal communication). Both stocks are further characterized by their capacity for an additional diapause.

In the *Valencia* stock the critical photoperiod for diapause induction was about 14.5 h light, found in both first and sixth laboratory generations (Wipking and Neumann 1986) (Fig. 2, curve 5). Even in the *Marseille* stock a photoperiodically induced diapause was found. Consistent with its more northern origin, the critical photoperiod for the first diapause was about LD >15:9 in the first to third laboratory generations (Fig. 2, curve 4). Variation in critical photoperiod in the three subsequent generations was negligible. Only under long-day conditions (LD 16:8–18:6) did the percentage of diapausing instars vary considerably between the subsequent laboratory generations, and it could not be reduced below 25% (LD 15.5:8.5), in contrast to the *Valencia* stock, where the percentage of diapausing larvae declined very quickly above the critical photoperiod (3%–10%; compare Fig. 2, curve 5). Hence, the *Marseille* stock shows a marked tendency towards an obligatory first diapause. The modulation in photoperiodic response towards an obligatory first diapause is demonstrated by the more northern stocks from *Avignon* (44° N) and *Baugé* (47° N). Less than 10% of the larvae developed without a diapause at 16- or 18-h daylengths (Fig. 2, curves 2 and 3). The capacity for development without diapause still exists, but, in very good agreement with the laboratory results, both populations are effectively univoltine in the field, as recorded by local lepidopterists (Drouet, personal communication).

The photoperiodic response curve of the *Köln* stock shows that all the larvae entered a first obligatory diapause irrespective of daylength (Fig. 2, curve 1), but supplementary facultative diapauses were under photoperiodic control (see below). From these laboratory experiments it may be

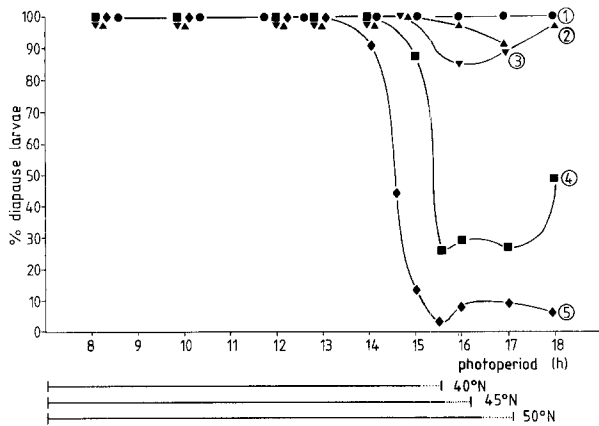


Fig. 2. Above: Photoperiodic response curves for first larval diapause induction in *Z. trifolii* at a constant temperature of 20° C. Curve 1: Obligatory first diapause in the stock from Köln (51° N); curves 2 and 3: obligatory first diapause in the stocks from Baugé (2; 47° N) and Avignon (3; 44° N), with a few exceptional examples of direct development at extremely long photoperiods; curves 4 and 5: facultative first diapause in the stocks from Marseille (4; 43° N) and Valencia (5; 39° N). Below: Maximal photoperiod or daylength (solid line: sunrise to sunset) and length of both civil twilight periods (dotted) at different latitudes, corresponding to the origins of the experimental stocks

concluded that the life cycles of all German populations in the field are at most univoltine, though generation time may be prolonged to 2–3 or even 4 years, which could occur either by repeated diapauses in the following years or by extended diapause over more than one winter (Wipking 1987).

Detailed analysis, however, demonstrated variable photoperiodic response of larval instars in all stocks. In stocks with a facultative diapause (Valencia, Marseille), there was a decreasing frequency of 3rd-instar and a greater number of 4th- and 5th-instar larvae (L_4D , L_5D) entering diapause at longer daylengths (LD 12:12–LD 14:10). An example is given for the Marseille stock (Fig. 3).

At photoperiods longer than 15 h, most of the larvae completed development without dormancy, as indicated by the photoperiodic threshold for diapause induction (Fig. 3, above). Under short-day conditions of 8 h light (KT), the third instar was the predominant diapausing morph (L_3D) and at longer daylengths the diapause was shifted to the older larval instars such that at 15 h even some 6th-instar individuals entered developmental arrest (Fig. 3, below). Lengthening the photoperiod (LD 18:6) caused an unexpected increase in the number of diapausing L_5D and L_6D larvae (30%–45%).

In stocks with a first obligatory diapause, the dormant stage was also protracted to the older instars at long photoperiods, analogous to the reaction in the more southern strains. The progenies of wild captured females demonstrate the sometimes variable photoperiodic response of the larval stages in three successive years in the Köln stock (Fig. 4). Under short-day conditions of 8–10 h the 3rd larval instar was the predominant diapausing morph and with increasing daylength the larvae entered dormancy at a later stage. Hence, using a 16-h photoperiod, the L_5D stage was the most abundant dormant morph.

Repeated diapause. In addition to the first diapause between the 3rd and the 7th instar, diapausing larvae of all stocks

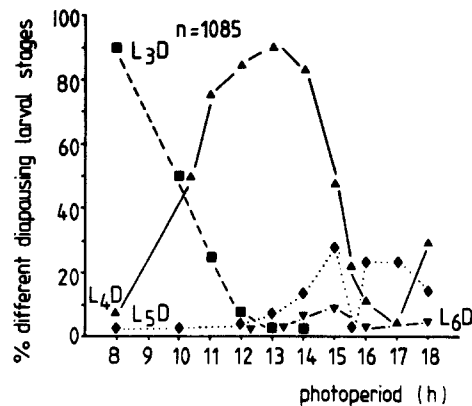
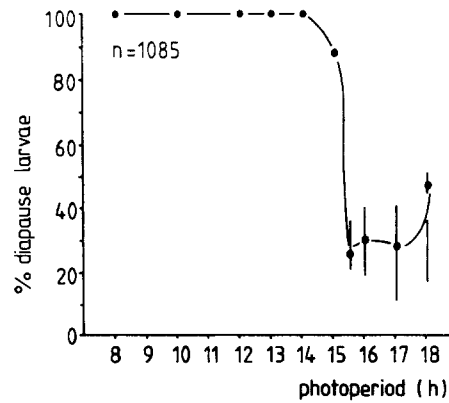


Fig. 3. *Z. trifolii*, Marseille stock. Above: photoperiodic responses for first diapause induction at 20° C. Circles and bars in photoperiods longer than 14 h indicate mean and range of each set of 4–5 identical experiments. Below: Frequencies of different diapausing instars, in the same experiments, in relation to increasing daylength. The data were obtained during three successive laboratory generations (F_{1-3}), which were originally based on 3 wild females captured in 1984. For further explanations see text

are able to enter a second diapause at the 5th or later instar. In the following, data on the effect of photoperiod on repeated diapause in a stock with facultative first diapause (Marseille) are collated with data from a stock with obligatory first diapause (Köln).

In both stocks, the photoperiodic response was investigated in L_3D , L_4D , L_5D and repeat L_6D2 diapausing stages after cold-temperature treatment. The experiment was run on different dormant stages (L_3D – L_5D), in order to establish stage-specific photoperiodic response curves for repeated larval diapauses.

In contrast to the first obligatory diapause in the Köln stock, but like to the response of the Marseille stock, additional diapause was under photoperiodic control (Fig. 5). After hibernation, young larvae of different stages of the Köln stock were again tested over a range of photoperiods (LD 18:6–8:16). From these experiments, it appeared that any further dormancy was suppressed in long-day conditions and larval development finished within 7–8 larval stages, whereas at short daylengths the larvae enter a second diapause. The decreasing photoperiodic thresholds for the induction of a repeat diapause were related to the diapausing stage from which the experiment was started (L_3D – L_5D). The critical photoperiods for repetitive diapause induction were about LD 15:9 (L_3D), LD 13.5:10.5 (L_4D) and LD 12:12 (L_5D). Breeding experiments were also car-

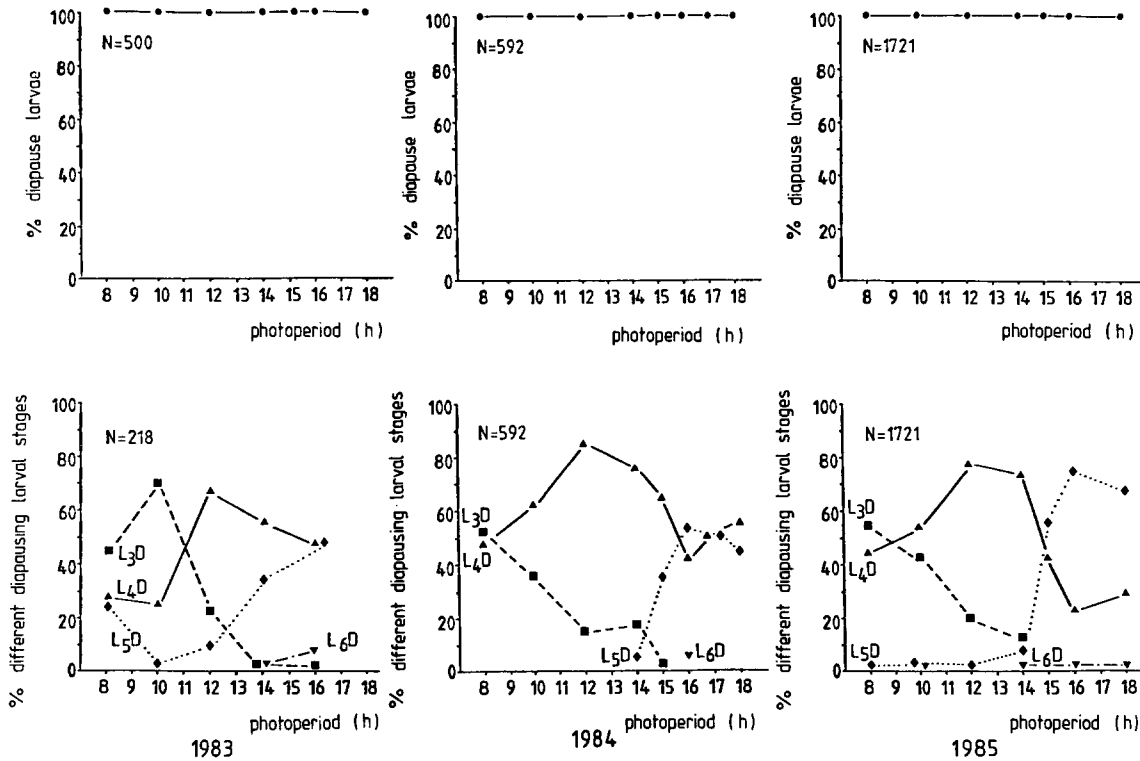


Fig. 4. Photoperiodic responses of *Z. trifolii* from Köln. *Above:* Percentage of diapausing larvae at various photoperiods at 20°C in three stocks sampled in successive years. These stocks were based on 3 ♀♀ in 1983, 6 ♀♀ in 1984, and 15 ♀♀ in 1985. *Below:* The corresponding frequencies of larvae diapausing in the 3rd–6th instars at various photoperiods. For further explanations compare Fig. 3

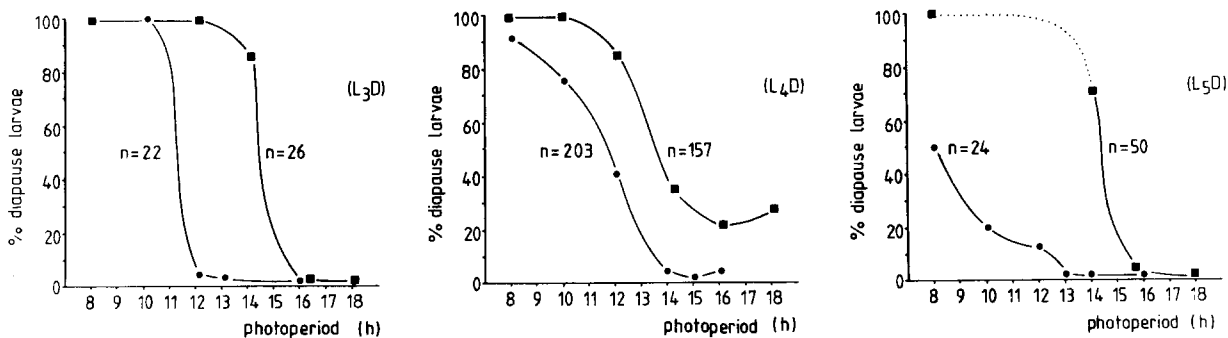


Fig. 5. Comparison of the photoperiodic responses for repeated larval diapause in the Marseille and the Köln stocks. *Left:* Data from experiments on larvae diapausing in the 3rd instar (L₃D); *middle:* experiments on L₄D larvae; *right:* experiments on L₅D larvae. *Circles:* Marseille stock; *squares:* Köln stock. For further explanations see text

ried out with the Marseille stock. A synopsis of the photoperiodic response curves is given in Fig. 5. Critical photoperiods for diapause induction were about LD 11:13 (L₃D), LD 11:13 (L₄D) and LD 8:16 (L₅D).

Thus the pattern of a first obligatory diapause and subsequent facultative diapauses appears to be universal in northern populations of *Z. trifolii*, although the details of the photoperiodic response may differ: this may, however, be accounted for by the great heterogeneity within populations and local adaptation in diapause-regulating mechanisms. As with the first diapause, repeat diapauses occurred at different stages (L₅D–L₈D2) depending on photoperiod, but there was variation within a photoperiod (Fig. 6; left: Marseille stock; right: Köln stock). In contrast to the Marseille stock (Fig. 6, below left) all larvae of the Köln stock

which had undergone the first dormancy at the L₃ stage (L₃D) had a second diapause at the 5th, 6th, or even 7th instar, even kept under LD 12:12 (Fig. 6, below right).

After a second diapause in the 6th instar, a few larvae in both stocks were observed to enter diapause for a third time under extreme short-day conditions (LD 8:16: 20% of larvae in the Marseille stock; 50% in the Köln stock; Fig. 7).

The effect of temperature on diapause induction at different photoperiods

Temperature may influence photoperiodically controlled diapause induction. Larvae of the Marseille and Köln stocks were reared either under non-diapause conditions

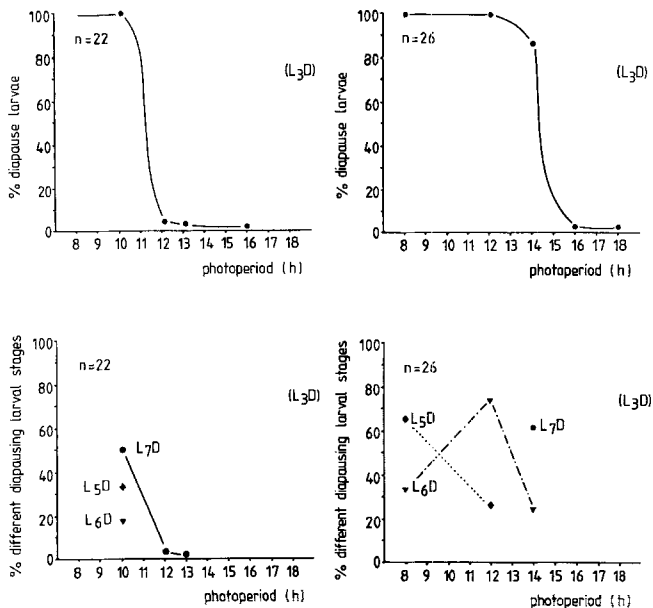


Fig. 6. *Z. trifolii*, Marseille (left) and Köln (right) stocks. Above: Photoperiodic responses for repeated larval diapause at 20° C; the experiment started with L₃D larvae. Below: The corresponding frequencies of larvae diapausing at different instars, in the same experiment

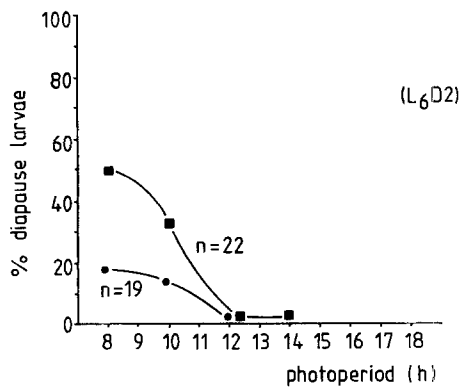


Fig. 7. Comparison of the photoperiodic responses for a third larval diapause (second repeat diapause) in the Marseille and Köln stocks. For further explanations compare Fig. 5

(LD 16:8) or using a diapause-inducing photoperiod (LD 13:11) at 15°, 20°, and 25° C. In addition to the former experiments, the rate of development (% per day) until pupation or molting to a diapausing instar was estimated; means and their ranges were calculated for each experimental set.

The rate of larval development did not vary significantly between the stocks ($P > 95\%$, $n = 1518$; Table 1), but at all temperatures intrapopulation variability was high. Thus, it was not possible to detect any influence of daylength on the developmental rate at any one temperature. The duration of the prediapause stage only seemed to be extended for about 1–2 days, as compared with normal larval instars (Wipking 1987).

Raising the temperature from 15° to 20° C speeded up larval development, but raising the temperature further to 25° C did not further speed up development in all larvae. In the Marseille stock, the developmental rate of a few larvae was the same at 25° C as at 20° C and in long-day

Table 1. Rate of development (% per day) of three stocks of *Zygaena trifolii* in long-day conditions (LD 16:8) in relation to temperature (mean and range)

		Valencia	Marseille	Köln
25° C	\bar{x}	0.9	0.9	1.3 ^a
	range	(0.6–1.3)	(0.6–1.3)	(1.1–1.4)
20° C	\bar{x}	0.9	0.7	0.8
	range	(0.6–1.1)	(0.6–1.2)	(0.6–1.1)
15° C	\bar{x}	–	0.5	–
	range	–	(0.3–0.7)	–

^a The data of the Köln stock were calculated from larvae with prolonged prediapusing larval instars. For further explanations see text

conditions, but the majority of the larvae developed faster. Therefore, the average duration of development was different in long-day conditions at 20° and 25° C, but the range and overlap of values was wide in this experiment (Table 1).

At a 16-h daylength between 10° and 15° C, the number of dormant morphs was significantly reduced or diapause was almost completely prevented in all strains (Fig. 8). However, almost all the larvae died at the 5th or 6th instar. A temperature below 20° C seems to be too low for imago formation. In the Köln stock, the high mortality might conceal a potential dormancy at later instars (Fig. 8, right). In general, there is no doubt that long daylength together with low temperatures may delay dormancy to later instars or prevent diapause altogether in *Z. trifolii*.

Raising the temperature from 20° to 25° C at LD 16:8 led to an unexpectedly higher number of dormant morphs; the effect was statistically significant in the Marseille stock and was nearly so in the Valencia stock (Valencia: 8%, 35% diapausing stages at 20° and 25° C respectively, $n = 165$, $P < 10\%$; Marseille 25%, 62%, $n = 223$, $P < 5\%$) (Fig. 8).

With a diapause-inducing photoperiod at a low temperature (LD 13:11, 15° C) the diapausing stage was always shifted towards the younger larval instars, and at 15° C the L₃ stage was the most abundant diapausing morph, whereas at a temperature of 20° or 25° C the L₄D and L₅D were more frequent.

Observations of developmental rates and molting dates under long-day conditions indicate that it was mainly those larvae with high developmental rates that entered diapause at a 16-h daylength at 25° C. Those which developed more slowly completed larval development without dormancy.

Discussion

The importance of photoperiod and temperature as major factors in environmental regulation of insect diapause has been amply reviewed (e.g.: Sauer et al. 1986a, b; Taylor and Spalding 1986; Topp 1984). However, multiple photoperiodic responses controlling the onset of the first and additional diapauses have not yet been recorded in any other insect species apart from *Z. trifolii*. Two important questions to be answered are how repeated larval diapause might have developed and what kind of adaptive significance it may have. In southern stocks, *Z. trifolii* shows a latitudinal gradient of photoperiodically controlled diapause reactions. A facultative winter diapause (hibernation)

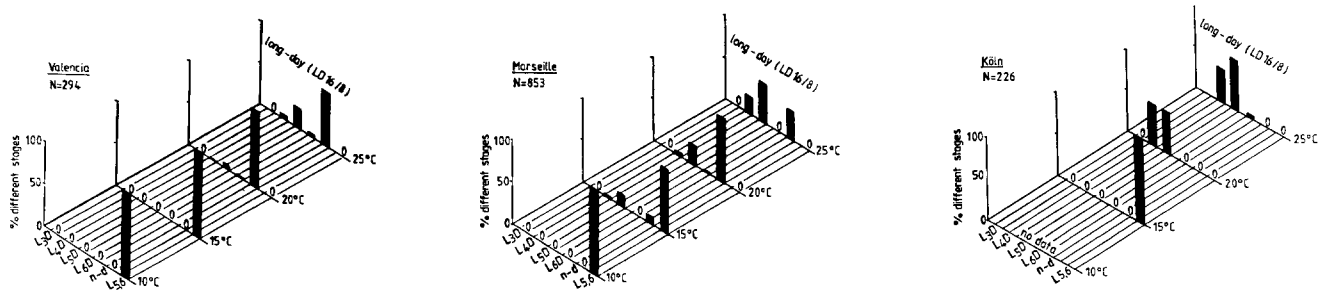


Fig. 8. Frequencies of diapausing larvae (L_3D – L_6D), of non-diapausing larvae ($n-d$; direct development to emerging moths), and of non-diapausing, but dying larvae (dying within 3–6 weeks at stage L_5 or L_6), in relation to different rearing temperatures in long-day conditions (LD 16:8). *Left:* Valencia stock; *middle:* Marseille stock; *right:* Köln stock

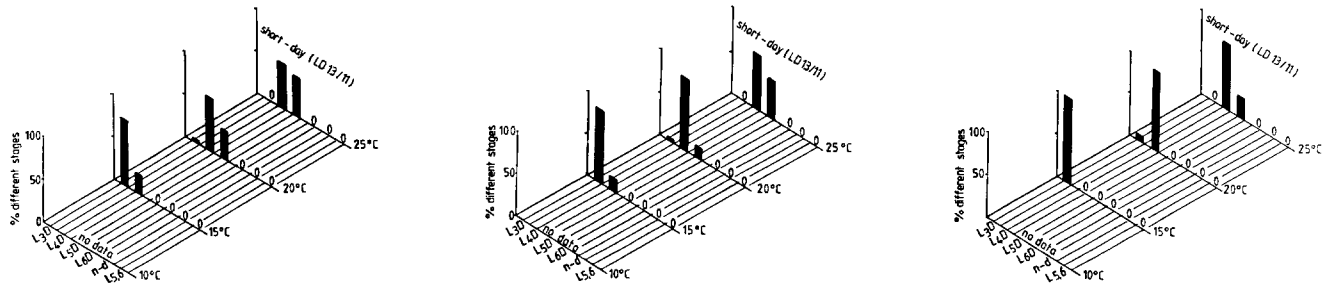


Fig. 9. Results corresponding to Fig. 8 under short-day conditions (LD 13:11). *Left:* Valencia stock; *middle:* Marseille stock; *right:* Köln stock

is typical of a potential multivoltine life cycle (Danilevskii 1965). This facultative diapause in *Zygaena* is programmed by short-day conditions. Towards the north the critical photoperiod for diapause induction increases and at the same time there is a more pronounced tendency to enter the dormant stage independent of photoperiodic conditions, as demonstrated by the photoperiodic response curves for first diapause induction (Fig. 2 above). In contrast to the Marseille stock, diapause induction in the northernmost stock (Köln) varies discontinuously and the first diapause becomes independent of photoperiodic conditions. This suggests that the life cycle phenology near the northern edge of the distribution is probably univoltine, unless it is prolonged by additional dormant periods.

Over the whole course of larval development the optimal timing of diapause induction for a particular population and larval stage is determined by the current conditions of photoperiod and temperature. In all stocks, temperature may influence the percentage of dormant morphs and the stage at which the larvae enter diapause. The time for which a given stage is exposed to different photoperiods is linked to temperature (Table 1) and, in the field, to climatic conditions that vary from year to year. Firstly, exposure of larvae to short-day conditions over a long period at low temperatures (10°, 15° C) increased the number of larvae entering diapause at an early stage (compare Fig. 9). In the field, this might be significant in autumn, affecting the first diapause, as well as in spring, where it could lead to a repeated diapause induction at early stages. A long period of low temperature under long-day conditions reduced the frequency of having a diapause at all, but the temperatures were too low for metamorphosis and imago formation was impossible. High temperatures (25° C) and short-day conditions sometimes increased the amount of later-diapausing instars, whereas a 16-h photoperiod at 25° C caused an unexpected increase in the number of dormant morphs in

the South European stocks with facultative diapause (Figs. 8, 9). These experiments indicate that apart from distinct photoperiodic thresholds for diapause reactions, diapause induction is influenced by the number of photoperiodic cycles (24 h) which each larval stage experiences at a certain temperature. Previously published field observations support this hypothesis. According to the field observations of Naumann in Spain (Valencia), some non-hibernating larvae of the summer generation may in fact have an additional aestival diapause of some weeks (Wipking and Neumann 1986); the decolorized morph passes the hot season lower down in the litter, protected from heat and desiccation. If the host plant withers in the summer, the reduced rate of metabolism in diapausing instars might be advantageous (Viebahn 1987). Some of these larvae show a prolonged aestivation and do not complete their development in autumn when, under short-day conditions, a second diapause at a later instar is induced. Larvae which follow this developmental pathway, with an extended threshold for diapause reactions and a capacity for repeated larval diapause, could be the starting point from which the more variable diapause regulation in the northern strains may have developed.

In contrast to aestivation, repeated winter diapause in the Spanish and French stocks only seems to be realized under short daylength in the laboratory (Fig. 6) and may be cryptic in the field in years with normal weather conditions.

In the southern part of the range, environmental conditions are such that either a diapause or a rapid, diapause-free development of an additional generation in the same year may be advantageous (Fig. 2). The increase first in obligatory diapause and then the more frequent occurrence of facultative repeated diapause towards the more northern populations is advantageous, since the northern growing and mating season is normally short. The time span with

favourable environmental conditions generally diminishes from the south to the north and is more variable in the north than in the south. An obligate first diapause could be an adaptation to the more unstable and colder temperature conditions at the northern edge of the range. It would prevent exploitation of unexpectedly long growing seasons, which might sometimes be long enough for imago formation if the larvae omitted a facultative first diapause. Later in autumn, a drop to low temperatures might slow down the development of the succeeding and hibernating generation so that the larvae would not reach the first diapausing, cold-resistant L₃ stage. Thus the second generation would fail to breed, the fitness of the non-diapause type would be zero and they would be eliminated in the field.

In the north the larvae of *Z. trifolii* are restricted to warm climatic outposts (Wipking 1985). The worse and more unstable climatic conditions near the northern edge of the range, which might not be sufficient for univoltine development of *Z. trifolii*, are countered by repeated facultative diapauses. The resultant various diapausing larval stages are characterized by different requirements for diapause induction at different stages. This might represent a strategy for "spreading of risk" (den Boer 1968, 1970, 1973; Reddingius and den Boer 1970; Stearns 1976; Varley et al. 1980). For example, if the reproductive success of the day-active and heat-preferring moths is very low in years with persistent rainfall during the whole mating period, the larvae with a repeated larval diapause may guarantee the survival of the population. Here diapause induction helps prevent adult emergence out of season. In conclusion, the flexibility of the photoperiodic response in *Z. trifolii*, allowing variable life-cycle phenologies even in one population in the same environment, allows adaptation to conditions over a wide geographic range.

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References

- Barnes HF (1952) Studies in fluctuations in insect populations, XII. Further evidence of prolonged larval life in the wheat blossom midges. *Ann Appl Biol* 39:370–373
- Beck SD (1980) *Insect Photoperiodism*. Academic Press, New York London Toronto, p 387
- Boer PJ den (1968) Spreading of risk and stabilization of animal numbers. *Acta Biotheor* 18:165–194
- Boer PJ den (1970) Stabilization of animal numbers and the heterogeneity of the environment: The problem of the persistence of sparse populations. In: Boer PJ den, Gradwell GR (eds), *Dynamics of Populations*, Proc Adv Study Inst Dynamics Numbers Popul (Oosterbeek 1970), pp 77–97
- Boer PJ den (1973) Das Überleben von Populationen und Arten und die Bedeutung von Umweltheterogenität. *Verh Dtsch Zool Ges* 1973:125–135
- Burgeff H (1910) Beiträge zur Biologie der Gattung *Zygaena* F. II. *Z Wiss Ins Biol* 6:39–44, 97–98
- Burgeff H (1921) Beiträge zur Biologie der Gattung *Zygaena* F. IV. *Mitt Münch Ent Ges* 11:50–64
- Burgeff H (1965) Kreuzungsanalysen von Georassen der Gattung *Zygaena* Fab. (Lep.). *Nachr Akad Wiss Göttingen, II Math phys Kl* 14:187–205
- Burgeff H (1971) Lebensgeschichte der *Zygaena ignifera*. *Nachr Akad Wiss Göttingen, II Mat phys Kl* 14:285–291
- Danilevskii AS (1965) Photoperiodism and seasonal development of insects. Oliver & Boyd, Edinburgh London, p 282
- Danks HV (1987) *Insect Dormancy: An Ecological Perspective*. Tyrell Press, Gloucester, Ontario (Canada), p 439
- Dorfmeister G (1853) Beobachtungen über einige Zygaenen: angestellt in den Jahren 1851–1853 von Georg Dorfmeister in Bruck a.d.M. *Verh Zool Bot Ver Wien* 3:Sitz Ber 178–179
- Dorfmeister G (1854) Abhandlungen über einige in der Steiermark vorkommende Zygaenen. *Verh Zool Bot Ver Wien* 4:473–482
- Dorfmeister G (1855) Über einige in der Steiermark vorkommende Zygaenen. *Verh Zool Bot Ver Wien* 5:87–96
- Dryja A (1959) *Badania nad Polimorfizmami Krasnica Zmienego (Zygaena ephialtes L.)*. Warsaw p 403
- Falkovich MI (1979) Seasonal development of desert Lepidoptera of Soviet Central Asia and a historical analysis of the Lepidoptera fauna. *Ent Rev* 58:20–45
- Harvey GT (1967) On Coniferophagus species of *Choristoneura* (Lp., Tortricidae) in North America, V. Second Diapause as a Species Character. *Can Entomol* 99:486–503
- Holik O (1937) Quelques problèmes au sujet du genre *Zygaena* FABR. III. Hibernation des chenilles. *Lambillionea* 37:80–91
- Holik O (1939) Quelques problèmes au sujet du genre *Zygaena* FABR. V. La signification biologique du développement fractionné des chenilles de *Zygaena*. *Lambillionea* 39:82–89, 104–111, 123–127
- Lounibos LP, Bradshaw WE (1975) A second diapause in *Wyeomyia smithii*: seasonal incidence and maintenance by photoperiod. *Can J Zool* 53:215–221
- Masaki S (1961) Geographic variation of diapause in insects. *Bull Fac Agric Hirosaki Univ* 7:66–98
- Matthes E (1953) Diapause, Bivoltinismus und zweimalige Überwinterung bei *Fumea crassiorella* (Lep., Psychidae). *Mem Est Mus Zool Univ Coimbra* 220:1–16
- Naumann C (1985) Zur Ökologie und Biologie von *Zygaena christa*. *Nota lepid* 8:42–50
- Naumann C, Tremewan WG (1980) On the Biology of *Zygaena tamara*. *Entomologist's Gaz* 31:113–121
- Reddingius J, Boer PJ den (1970) Simulation experiments illustrating stabilization of animal numbers by spreading of risk. *Oecologia* 5:240–284
- Sauer KP, Grüner C, Collatz KG (1986a) Critical points in time and their influence on Life Cycle, Life Span and Aging. In: Collatz KG, Sohal RS (eds), *Insect Aging*, Springer, Berlin Heidelberg New York, pp 9–22
- Sauer KP, Spieth H, Grüner C (1986b) Adaptive Significance of Genetic Variability of Photoperiodism in Mecoptera and Lepidoptera. In: Taylor F, Karban R (eds), *The Evolution of Insect Life Cycles*, Springer, Berlin Heidelberg New York, pp 153–172
- Saunders DS (1979) *Insect clocks*. Pergamon Press, Oxford New York p 279
- Seipel H (1980) *Zygaena trifolii* ssp. *barcelonensis* f. loc. saleria BGFF. *Nachr Ent Ver Apollo NF* 1:2–4
- Seipel H (1981) *Zygaena trifolii* ssp. *barcelonensis* f. loc. saleria BGFF., 2. Zuchtbericht. *Nachr Ent Ver Apollo NF* 2:61–63
- Seipel H (1982) *Zygaena trifolii* ssp. *barcelonensis* f. loc. saleria BGFF., 3. Zuchtbericht. *Nachr Ent Ver Apollo NF* 3:57–58
- Stearns SC (1976) Life history tactics: a review of the ideas. *Quart Rev Biol* 51:3–47
- Tauber MJ, Tauber CA, Masaki S (1986) *Seasonal Adaptations of Insects*. Oxford University Press, New York p 411
- Taylor F, Spalding JB (1986) Geographical Patterns in the Photoperiodic Induction of Hibernation Diapause. In: Taylor F, Karban R (eds) *The Evolution of Insect Life Cycles*, Springer, New York Berlin Heidelberg pp 66–86
- Topp W (1984) Synchronisation und polymorphe Termination der Diapause bei *Oxytelus rugosus* (Col., Staphylinidae). *Zool Jahrb Syst* 111:521–542

- Tremewan WG (1977) On the biology of *Zygaena cuvieri* (Lep., Zygaenidae). Entomol Gaz 28:17–19
- Uebel W (1974) Zygaenenzuchten. Mitt Entomol Ver Stuttgart 9:43–61
- Uebel W (1983) Ex-ovo-Zuchten zweier nordafrikanischer Zygaenenarten. Atalanta 14:313–320
- Varley GC, Gradwell GR, Hassel MP (1980) Populationsökologie der Insekten. Thieme, Stuttgart New York, p 211
- Viebahn M (1987) Respiration, Lipid- und Glykogengehalt bei Diapause- und Nondiapause-Larven von *Zygaena trifolii* ESP. Unpublished Diplom Thesis, Universität zu Köln, p 109
- Wiegel KH (1972) Zwei neue Zygaenenrassen aus Apulien. Mitt Münch Ent Ges 60:57–79
- Wiegel KH (1973) Zweiter Beitrag zur Zygaenenfauna des Litoralgebietes von Apulien. Atalanta 4:224–240
- Wipking W (1985) Ökologische Untersuchungen über die Habitatbindung der Zygaenidae. Mitt Münch Ent Ges 74 (1984):37–59
- Wipking W (1987) Ökologische Untersuchungen über die Diapauseeregulation bei westpaläarktischen Stämmen einer Schmetterlingsfamilie (Ins., Lepidoptera, Zygaenidae). Unpublished Ph D Thesis, Universität zu Köln, p 152
- Wipking W, Neumann D (1986) Polymorphism in the Larval Hibernation Strategy of the Burnet Moth, *Zygaena trifolii*. – In: Taylor F, Karban R (eds) The Evolution of Insect Life Cycles, Springer, Berlin Heidelberg New York, pp 125–134

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