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Photoperiodic summation is temperature-dependent in *Pyrrhocoris apterus* (L.) (Heteroptera)

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Summary. In *Pyrrhocoris apterus*, a low temperature, 15 °C, prevented the termination of diapause by long days and, unexpectedly, also the induction of diapause by short days. Both responses were enabled at a higher temperature, 26 °C. In contrast to current concepts, it was proved that the summation of photoperiodic signals was temperature-dependent, since the morphogenetic development was prevented by starvation.
Key words. Diapause induction; diapause termination; starvation; photoperiodic response; photoperiodic counter; temperature compensation.

Temperature may considerably modify photoperiodic response in insects. With long-day species, low temperature enhances the incidence of diapause under conditions of short days, whereas high temperature and long days work together to avert diapause[1,2]. Saunders[3] interprets the relationship between temperature and photoperiod as an interaction between the photoperiodic counter and the rate of development; the numbers of days required for photoperiodic induction of diapause show a high degree of temperature compensation, but temperature affects the rate of development and thus also the number of light-dark cycles actually experienced by an individual. Hence, the higher incidence of diapause at low temperature is thought to be due to the protracted sensitive period. In contrast, the rate of photoperiodic termination of diapause is temperature-dependent[4,5]. However, the stimulatory effects of high temperature on the post-diapause morphogenesis and on the photoperiodic activation of diapause have never been discriminated.

It seems unlikely that the dependence on temperature would be so contradictory for the summation of diapause-promoting and diapause-terminating photoperiods. This study indicates that summation of both types of photoperiodic signals is restrained at low temperature in *Pyrrhocoris apterus*.

P. apterus exhibits a facultative adult diapause regulated by photoperiod. A long-day photoperiod of 18 L:6 D (LD)

Table 1. Activation of females destined for diapause

Experimental photoperiod and temperature (10 days)	n	% ovipositing females	Pre-oviposition period (days)
LD, 26 °C	20	95	14.7 ± 6.6
SD, 26 °C	20	90	29.6 ± 5.1
LD, 15 °C	30	90	24.9 ± 3.3
SD, 15 °C	30	87	27.5 ± 4.3
Control	11	100	19.0 ± 3.0

Mean ± SD. Reproductive parameters were recorded with LD, 26 °C and food supply. For experimental procedure see figure 1.

Table 2. Induction of diapause

Experimental photoperiod and temperature (10 days)	n	% ovipositing females	Pre-oviposition period (days)	Oviposition period (days)
LD, 26 °C	19	100	6.1 ± 0.9	15.1 ± 7.3
SD, 26 °C	42	24	6.3 ± 1.3	1.0 ± 2.2
LD, 15 °C	20	100	5.9 ± 0.9	10.0 ± 6.2
SD, 15 °C	32	97	5.5 ± 0.8	11.3 ± 5.8
Control	20	100	5.9 ± 0.6	7.3 ± 5.1

Mean ± SD. Reproductive parameters were recorded with SD, 26 °C and food supply. For experimental procedure see figure 1.

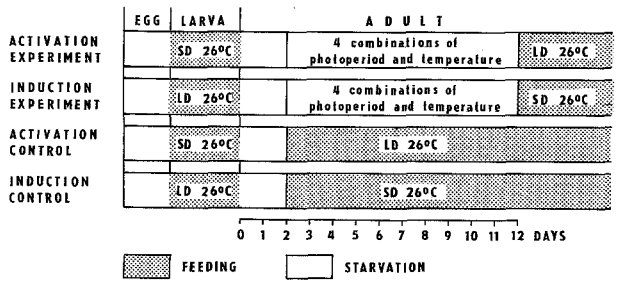

Figure 1. Experimental procedure.

stimulates reproduction, whereas a short-day photoperiod of 12 L:12 D (SD) induces and maintains diapause. Although diapause can be induced already during larval life, adult females remain sensitive to photoperiod and diapause can be terminated and reinduced several times[6]. The activity of corpora allata and vitellogenesis are inhibited during starvation[7]. The experimentation with starving adult females enabled us to isolate the mechanisms of post-activation morphogenesis (vitellogenesis) from the summation of long-day signals; also the effect of temperature on the rate of development and on the accumulation of short-day signals was delimited.

Activation of females destined for diapause. Insects were reared under conditions of SD and 26 °C on linden-seed and water. Freshly ecdysed females were deprived of food, and 2 days later exposed to 4 combinations of 2 photoperiods and temperatures for 10 days (fig. 1). Post-activation morphogenesis was prevented by starvation during the 10-day experimental treatment and could not interfere with the photoperiodic activation. The effect of experimental conditions on the starving females was measured by the length of the pre-oviposition period with LD, 26 °C and food supply. Feeding females kept always with SD, 26 °C did not oviposit.

In the LD, 26 °C group, the pre-oviposition period was shorter, while in the SD, 26 °C or 15 °C and LD, 15 °C groups, the pre-oviposition period was longer than in control females (table 1, fig. 2). The pre-oviposition period was markedly shorter in the LD, 26 °C group than in the LD, 15 °C group. The results indicate that 1) photoperiodic activation by LD is restrained at 15 °C and 2) photoperiodic activation at 26 °C need not be combined with feeding and post-activation vitellogenesis.

Although a temperature around 15 °C is inadequate for photoperiodic activation, i.e. the 'hastened' tachytelic processes of diapause completion, it is favorable to the 'slow' diapause development, i.e. to the horotelic processes of diapause completion[8,9]. Progress in diapause development is also seen after 4-week exposure of old diapausing females of *P. apterus* to 15 °C with any

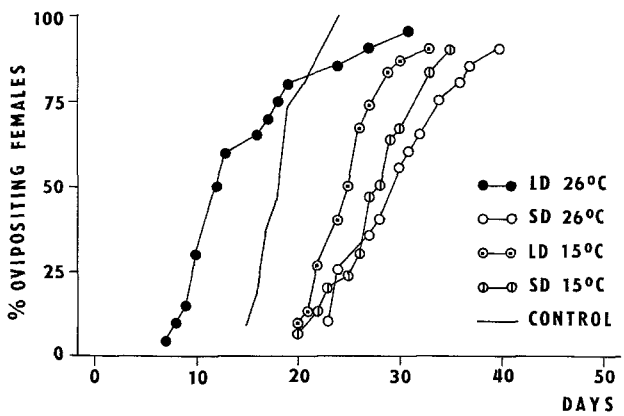

Figure 2. Cumulated percentage of females activated from diapause; oviposition onset with LD, 26 °C and food supply. For experimental procedure see figure 1.

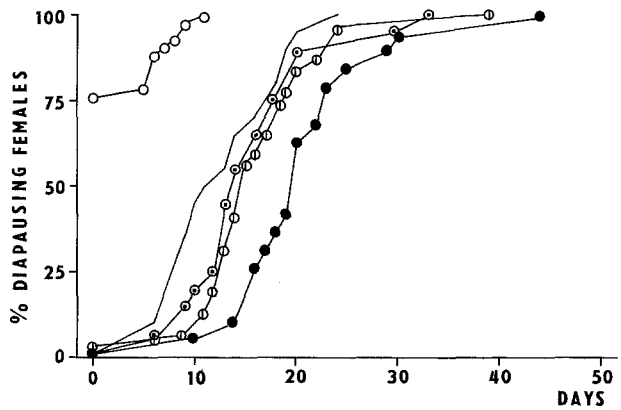

Figure 3. Cumulated percentage of females induced to diapause; discontinuation of egg-laying with SD, 26 °C and food supply. For explanation of symbols see figure 2; for experimental procedure see figure 1.

photoperiod, or to 26 °C with SD. Photoperiodic activation of these females is impaired at 15 °C similarly to that of the young females destined for diapause (fig. 4).

According to the classical concept[11,12], the critical photoperiod for the regulation of diapause is increased with decrease in temperature. Thus it might be hypothesized that at 15 °C the photoperiod of 18 L:6 D acts as diapause-promoting in *P. apterus*. At 15 °C, the diapause would then be induced at 18 L:6 D as well as at 12 L:12 D. To check this possibility, the following experiment was conducted.

Induction of diapause. Insects were reared before the experimental treatment under LD conditions; otherwise, the experimental design was the same as that above (fig. 1). In the course of a 10-day experimental treatment, the vitellogenesis was again prevented by starvation and could not interfere with the photoperiodic induction of diapause. The effect of experimental conditions on the starving females was measured under conditions of SD, 26 °C and food supply by two parameters; the incidence of ovipositing females and the length of the oviposition period. The incidence of ovipositing females shows the degree of induction of 'primary' diapause by the experimental conditions. The length of the oviposition period reflects the effect of experimental conditions on the rate of induction of 'secondary' diapause, i.e. discontinuation of oviposition. Feeding females kept always in LD, 26 °C oviposited until death (about two months).

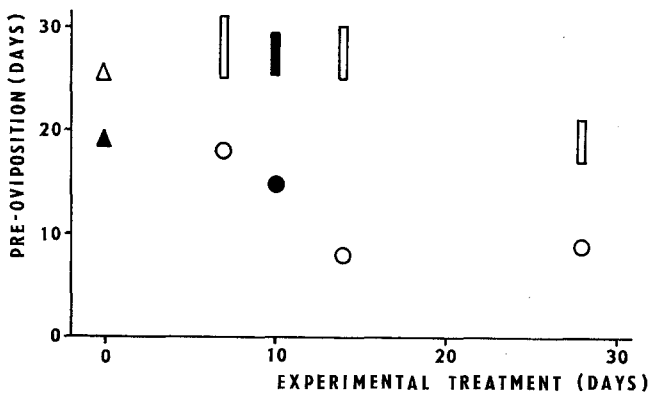

Figure 4. Effect of temperature on photoperiodic activation in young diapause-destined and old diapausing females. Females at the age of 2 days (solid symbols, data from table 1) or 2 months (open symbols, from published data[10]) were starved under conditions of 4 combinations of photoperiod and temperature prior to feeding at LD, 26 °C; pre-oviposition period was recorded under these conditions. Circles – means of pre-oviposition period for females starved at LD, 26 °C; columns: ranges of means for females starved at SD, 26 °C or 15 °C and LD, 15 °C; triangles – means for control females; n = 19 – 42.

Both parameters of reproductive activity were lower in the SD, 26 °C group than in control females. In three other groups, the incidence of ovipositing females was 100% (or 97%) as in the control females, and the oviposition period lasted even longer than in the controls (table 2, fig. 3). The two SD groups differed markedly: in the 26 °C group, the primary diapause was induced in 76% of females, and in the 24% ovipositing females the secondary diapause was induced much more rapidly than in the 97% ovipositing females of the 15 °C group. The results indicate that 1) photoperiodic induction of diapause by SD is restrained at 15 °C, 2) feeding is not necessary for the photoperiodic induction of diapause at 26 °C, and 3) the induction of the primary diapause in starving females at SD, 26 °C is not a consequence of food deprivation, as starvation under the other three conditions does not induce diapause and the females oviposit when fed.

Discussion and conclusion. The adverse effect of 15 °C on the photoperiodic response cannot be explained by a shift in the critical daylength (as hypothesized in the previous chapter), since both the termination and induction of diapause were restrained. While the inhibition of photoperiodic activation by low temperature is a common phenomenon, the negative effect of low temperature on the induction of diapause is rather exceptional. There are, however, some data which are in concert with our results. Short days at 12 °C do not induce diapause in *Laspeyresia (Grapholita) molesta*[13]. A similar finding was reported for *Chloridea obsoleta*[12]. Induction of adult diapause was inhibited in *Drosophila testacea* when exposure to short days was associated with a decrease in temperature to 18 °C[14]. The exposure of diapausing *Chrysopa carnea* to short days at 7 °C did not maintain diapause; on the contrary, it potentiated a high subsequent reproductive activity[15]. Thus the diapause inducing and maintaining role of short days can be impaired by low temperature, at least in some insect species.

It is possible that in *P. apterus* the photoperiodic response is not completely restrained at 15 °C, but summation of much higher numbers of days is needed to obtain the same effect as at 26 °C. This contradicts the assumption that the number of days required for photoperiodic induction of diapause is similar at different temperatures[3]. The assumption is based on experiments with developing insects. Hence, the effects of temperature on the accumulation of photoperiodic signals and on the rate of development are not clearly separated. In the present experiments with *P. apterus* the hormonal activity necessary for vitellogenesis was inhibited during starvation at either temperature. Under these conditions, the summation of both diapause-promoting and diapause-terminating photoperiods was restrained at low temperature of 15 °C. Suppression of the photoperiodic timer at temperatures around 0 °C has been indicated for *Ostrinia nubilalis*[16] and *Megoura viciae*[17].

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The oak processionary caterpillar (*Thaumetopoea processionea* L.) an urticating caterpillar related to the pine processionary caterpillar (*Thaumetopoea pityocampa* Schiff.) (Lepidoptera, Thaumetopoeidae)

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Summary. The hairs of *Thaumetopoea processionea* caterpillars (Lepidoptera) provoke a cutaneous reaction in man and animals. The urticating apparatus, the urticating gland which produces hairs, and the urticating hairs, are similar to those of the *T. pityocampa* caterpillar. The irritant fraction extracted from hairs contains soluble proteins; one of these shows immunological identity with thaumetopoein, the urticating protein of the *Th. pityocampa* caterpillar. This thaumetopoein-like protein is currently undergoing isolation and will be subjected to dermatological tests.

Key words. Thaumetopoea processionea; oak processionary caterpillar; erucism; urticating apparatus; venom; thaumetopoein-like protein.

In France, and particularly in the Poitou-Charentes region, the oak processionary caterpillar (*Thaumetopoea processionea* L.), in association with another Lepidoptera, *Lymantria dispar*, causes considerable damage to oak forests. The hairs of *Th. processionea* caterpillars are responsible for provoking a cutaneous reaction in man, known as erucism, which is similar to that produced by the hairs of the pine processionary caterpillar (*Th. pityocampa* Schiff.)[1]. We have shown that the hairs of this latter species cause a cutaneous reaction in man and animals via the discharge of a toxic substance. The irritant fraction extracted from hairs contains soluble proteins. One 28,000 dalton protein is hair-specific and causes a reaction in pig skin identical to that produced by crude hair extract[2]. It is therefore an urticating protein, and we have named it thaumetopoein[3,4]. This urticating protein is produced by an urticating gland[5].

In this study, the urticating apparatus and urticating hairs of the oak processionary caterpillar have been studied by morphological, histological and biochemical techniques and compared to those of the pine processionary caterpillar. Last instar larvae of *Th. processionea* collected on oak trees near Fouras, France* were used.

A morphological study of the urticant apparatus of this caterpillar was undertaken using the scanning electron microscope with conditions described elsewhere[6,7]. The apparatus is quite similar