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Photoperiodic Regulation of the Diapause of the Progeny in *Trichogramma embryophagum* Htg. (Hymenoptera, Trichogrammatidae): Dynamics of Sensitivity to Photoperiod at the Immature Stages of Maternal Females

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Abstract—Photoperiodic regulation of *T. embryophagum* progeny prepupal diapause was investigated under laboratory conditions. Maternal females developed at 20°C, the position of the photosensitive period was detected by transferring immature stages between the diapause-inducing “short” day (L : D = 12 : 12) and the diapause-averting “long” day (L : D = 20 : 4). Progeny generation developed at L : D = 12 : 12 under the near-threshold temperature of 13°, 14°, or 15°C. Experiments showed that, at least under the used photo-thermal regimens, only the pupal stage was sensitive to the photoperiod influence. The highest photosensitivity was recorded during the last two days before the adult emergence. In this critical period, even a single short day cycle induced diapause in most of individuals. However, the reaction to the long day was weaker: at least two long light days immediately preceding the maternal adult emergence were necessary to avert the diapause. If a short day was preceded by a long day by more than 2–3 days before the adult emergence, the stepwise photoperiodic response caused an increase in the tendency to diapause. The results of this study could be used in pest biocontrol practice for elaboration of optimal methods for *Trichogramma* mass rearing and storage and also for prediction of its seasonal cycles under natural conditions.

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The main characteristic feature of the “true” facultative winter diapause is that (in contrast to, e.g., low temperature quiescence) it is an anticipatory reaction induced by environmental tokens long before the onset of adverse seasonal conditions. Hence, in many insect species, the period of sensitivity to environmental tokens and the diapause *per se* fell on different stages of the life cycle separated by a significant time interval, when the photoperiodic information is stored but not realized (Danilevski, 1961; Tyshchenko, 1977; Zaslavski, 1984; Chernyshev, 1996; Saulich and Volkovich, 2004).

Most commonly, the winter diapause is induced by photoperiod. The period of photosensitivity (sensitivity to photoperiod) usually lasted from several days to several months. However, photoperiod need not affect the insect throughout the whole sensitive stage. Usually, the shorter duration is sufficient to induce the diapause. In addition, even within the sensitive stage, the relative photoperiodic sensitivity may vary significantly with time (Danilevski, 1961; Tyshchenko, 1977; Zaslavski, 1984; Denlinger, 2002; Saunders, 2002; Danks, 2002, 2003; Saulich and Volkovich, 2004).

Note that in most of the studied insect species the photosensitive and the diapausing stages of the life cycle belonged to the same generation. Much more rarely, the so called “maternal influence” was observed, i.e., the proportion of diapausing individuals depended on the photoperiodic conditions of development of the maternal females (Griffiths, 1969; Vinogradova, 1973; Zaslavski, 1978, 1984; Tauber et al., 1986; Mousseau and Dingle, 1991; Denlinger, 2002; Saunders, 2002; Danks, 2002, 2003; Saulich and Volkovich, 2004). Usually, the conditions of development of maternal individuals could only to some extent modify the progeny reaction to environmental factors, but, e.g., in *Bombyx mori* L.(Lepidoptera, Bombycidae), in *Orgyia antiqua* L. (Lepidoptera, Lymantriidae), and in *Nasonia vitripennis* Walk. (Hymenoptera, Pteromalidae) the maternal influence evidently dominated over photo-thermal reactions of the progeny

(Saunders, 1966; Kind, 1972). Tyshchenko (1977) considered this “inheritance of photoperiodic information” as the most advanced stage of evolution of photoperiodic adaptations.

Our study was conducted with *Trichogramma embryophagum* Htg. The species of the genus *Trichogramma* are not only widely used for regular augmentative biological control of agricultural and forestry pests but also represent an important component of natural biocenoses (Telenga and Shchepetilnikova, 1949; Greenberg et al., 1979; Smith, 1996; Sorokina, 2001). Thus, the studies on mechanisms of the diapause induction are very important not only for elaboration of methods of *Trichogramma* mass rearing and storage but also for prediction of its seasonal cycles under natural conditions (*Handbook* …, 1974; Boivin, 1994; Shlyakhtich et al., 1989; Sorokina, 2001).

The peculiarity of prepupal diapause regulation in *Trichogramma* is that low temperature is the most important factor acting on the larvae and inducing the diapause, while photoperiodic conditions of development of a given generation have only slight effect on the proportion of diapausing individuals (Maslennikova, 1959; Bonnemaison, 1972; Boivin, 1994; Laing and Corrigan, 1995; Garcia et al., 2002). However, in most of the *Trichogramma* species studied, the percentage of diapausing individuals significantly depends on the photoperiodic conditions of the previous (maternal) generation, although this maternal influence could be revealed only when the progeny develop under the near-threshold temperatures (Zaslavski and Umarova, 1981; Mai Phu Qui and Zaslavski, , 1983; Sorokina and Maslennikova, 1986, 1987; Zaslavski and Umarova, 1990; Reznik and Kats, 2004). Similar results were received in experiments with certain other parasitoids (Griffiths, 1969; Anderson and Kaya, 1974; Milonas and Savopoulou-Soultani, 2000).

Earlier studies (Sorokina and Maslennikova, 1986, 1987; Voinovich et al., 2002, 2003; Reznik et al., 2002) showed that photoperiodic and thermal reactions in *T. embryophagum* were similar to those in other *Trichogramma* species. Practically all larvae developed at 10°C diapaused; at 18–20°C the diapause was extremely rare, while at near-threshold temperatures of 13-15°C the proportion of diapausing individuals significantly depended on the photoperiod influenced by the maternal generation. The maximum percentage of progeny diapause was induced by a short light day of ca 12 h, while at long (18 h and more) and ultra-short (less than 6 h) days the proportion of diapausing progeny was rather low.

In this study we experimentally investigated the dynamics of photosensitivity during preimaginal development of maternal generation.

MATERIAL AND METHODS

In our study we used a laboratory parthenogenetic strain of *T. embryophagum* which was before experiments cultivated on the eggs of the grain moth, *Sitotroga cerealella* Oliv. for many generations. All the experiments were conducted with a special new isofemale line which allowed us to work with maximally homogenous material. *Trichogramma* laboratory strains were reared under constant conditions at L : D = 18 : 6 (hereafter, light and dark periods of day in hours are given) and temperature of 20°C.

For each replicate of each experiment, a block of 16 paper cards with 200–300 grain moth eggs glued onto each card was subjected for 2–4 h to parasitization by 500 -1000 recently emerged *T. embryophagum* females. Then these cards with parasitized eggs of the grain moth (the maternal generation) were separated, randomly placed in test tubes and incubated at the same temperature conditions (20°C), but under different combinations of photoperiods. In the present study, we used two contrasting photoperiods: the diapause-inducing “short” day (L : D = 12 : 12) and the diapause-averting “long” day (L : D = 20 : 4). The developing maternal individuals were alternatively kept under one of these photoperiods.

At the day of mass emergence of the maternal generation, a block of 9 paper cards with grain moth eggs (ca 100 eggs per card) was placed in each test tube with emerged wasps and subjected to parasitization for 2 h. Then the cards with the newly parasitized host eggs (the progeny generation) were separated and placed in test tubes. Further development of the progeny generation occurred at constant conditions at L : D = 12 : 12 and under near-threshold temperatures of 13°, 14°, or 15°C.

After mass emergence of the non-diapausing fraction (i.e., in 40–90 days after parasitization, depending on the temperature) all parasitized host eggs were dissected. The non-diapausing individuals (mostly emerged adults, very rarely dead adults inside the host chorion, sporadic dead or live pupae) and the diapausing individuals (each living prepupa was assumed to be in a diapause) were counted. The few insects that

Table 1. Influence of photoperiodic conditions of maternal females development and temperature regimen of progeny development on the percentage of diapausing prepupae in *Trichogramma embryophagum* progeny (the first experiment). Numbers in the same column labeled with different letters are significantly different ($p < 0.001$, the Tukey test)

Experimental treatment	Photoperiod L : D (during different days of maternal females development at 20°C)				Diapause at different temperature regimens of progeny development		
	1–4 days	5– 9 days	10–13 days	14–18 days	13°	14°	15°
1	20 : 4	20 : 4	20 : 4	20 : 4	81.8 a	36.9 a	11.3 a
2	12 : 12	12 : 12	20 : 4	20 : 4	80.9 a	39.0 a	10.4 a
3	20 : 4	12 : 12	12 : 12	20 : 4	81.5 a	35.5 a	7.7 a
4	20 : 4	20 : 4	12 : 12	12 : 12	98.9 b	92.9 b	71.0 b
5	12 : 12	20 : 4	20 : 4	12 : 12	97.8 b	90.0 b	69.2 b
6	12 : 12	12 : 12	12 : 12	12 : 12	98.4 b	94.4 b	73.1 b

died during the larval or prepupal stages were not considered. Based on these data, the percentage of diapausing individuals was separately calculated for each card with the progeny generation. As the tendency to diapause may vary significantly even in successive generations of a laboratory strain (Zaslavski and Umarova, 1981, 1990; Reznik et al., 2002), all the replicates of all the treatments of each experiment were conducted with simultaneously emerged females of the same generation.

Experimental treatments differed in 1) onset time and duration of exposures of preimaginal stages of maternal individuals to the short and the long light days and 2) temperature regimen of progeny development. Each treatment of each experiment was conducted in 8–12 replicates; in total, more than 100,000 parasitized grain moth eggs were dissected on 984 cards. Each card with the progeny generation was considered as an experimental unit. Percentages were square root–arcsine transformed (Lloyd and Ledermann, 1984) and then treated with ANOVA. The significance of differences between treatments was evaluated with the Tukey HSD test. In the text and tables, medians and quartiles of untransformed percents are given. All calculations were performed using SYSTAT.

RESULTS AND DISCUSSION

Dynamics of Photosensitivity

In the first experiment, the preimaginal development of the maternal generation (ca 18 days at 20°C) was divided into four approximately equal periods. During each period, the developing individuals were exposed either to a long or a short light day. ANOVA showed that the proportion of diapausing individuals significantly ($p < 0.001$) depended on the temperature conditions of larval development and on the light day length during the last 5 days of maternal females development, while the influence of the first 13 days of development was not significant. A paired comparison of treatments yielded the same result (Table 1).

Considering the results of the first experiment, in the second test the second half of preimaginal development of maternal females was subjected to a more detailed analysis. The first experimental period lasted 9 days and three subsequent periods, 3 days each. As a whole, the results of the second experiment were also clear and straightforward (Table 2). When the last 3 days of preimaginal development of maternal females occurred on a short light day (treatments 1–8), the diapause was induced in ca 90% of the progeny. When the 16th–18th days of development occurred under the long light days (treatments 9–16), the diapause was recorded in 30–60% of individuals, depending on the temperature.

ANOVA showed that in the second experiment the proportion of diapausing progeny significantly ($p < 0.001$) depended on photoperiodic conditions during the last (16th–18th days) and next-to-last (13th–15th days) periods of development of maternal females. However, the influence of the 3-day-long period directly preceding adult emergence was much stronger. F-ratio indicating the strength of the action was $F = 14.1$ and $F = 7263.5$ for the next-to-last and last periods of the experiment, respectively.

In the third experiment, the relative photosensitivity of the last three days of *T. embryophagum* development was investigated in most detail: the duration of the last three periods was one day only (Table 3). With

Table 2. Influence of photoperiodic conditions of maternal females development and temperature regimen of progeny development on the percentage of diapausing prepupae in *Trichogramma embryophagum* progeny (the second experiment)

Experimental treatment	Photoperiod L : D (during different days of maternal females development at 20°C)				Diapause at different temperature regimens of progeny development		
	1–9 days	10–12 days	13–15 days	16–18 days	13°	14°	15°
1	12 : 12	12 : 12	12 : 12	12 : 12	90.5	88.6	91.0
2	20 : 4	12 : 12	12 : 12	12 : 12	84.5	86.5	92.6
3	12 : 12	20 : 4	12 : 12	12 : 12	87.2	89.5	92.4
4	20 : 4	20 : 4	12 : 12	12 : 12	90.1	89.1	93.0
5	12 : 12	12 : 12	20 : 4	12 : 12	92.8	90.1	90.8
6	20 : 4	12 : 12	20 : 4	12 : 12	92.4	88.0	92.8
7	12 : 12	20 : 4	20 : 4	12 : 12	90.8	87.4	92.1
8	20 : 4	20 : 4	20 : 4	12 : 12	92.1	84.8	90.8
9	12 : 12	12 : 12	12 : 12	20 : 4	57.0	33.3	35.5
10	20 : 4	12 : 12	12 : 12	20 : 4	53.5	33.7	36.1
11	12 : 12	20 : 4	12 : 12	20 : 4	57.5	38.4	29.3
12	20 : 4	20 : 4	12 : 12	20 : 4	50.1	34.0	33.9
13	12 : 12	12 : 12	20 : 4	20 : 4	62.8	37.6	32.4
14	20 : 4	12 : 12	20 : 4	20 : 4	62.6	35.0	42.3
15	12 : 12	20 : 4	20 : 4	20 : 4	56.9	37.4	33.0
16	20 : 4	20 : 4	20 : 4	20 : 4	57.9	41.5	33.1

Table 3. Influence of photoperiodic conditions of maternal females development and temperature regimen of progeny development on the percentage of diapausing prepupae in *Trichogramma embryophagum* progeny (the third experiment)

Experimental treatment	Photoperiod L : D (during different days of maternal females development at 20°C)				Diapause at different temperature regimens of progeny development		
	1–15 days	16th day	17th day	18th day	13°	14°	15°
1	12 : 12	12 : 12	12 : 12	12 : 12	89.7	95.1	77.6
2	20 : 4	12 : 12	12 : 12	12 : 12	90.5	94.1	82.1
3	12 : 12	20 : 4	12 : 12	12 : 12	89.8	91.5	76.4
4	20 : 4	20 : 4	12 : 12	12 : 12	90.8	91.7	77.8
5	12 : 12	12 : 12	20 : 4	12 : 12	85.5	82.5	66.7
6	20 : 4	12 : 12	20 : 4	12 : 12	83.9	83.7	70.1
7	12 : 12	20 : 4	20 : 4	12 : 12	69.4	72.8	46.2
8	20 : 4	20 : 4	20 : 4	12 : 12	88.4	81.3	73.6
9	12 : 12	12 : 12	12 : 12	20 : 4	90.3	88.2	77.8
10	20 : 4	12 : 12	12 : 12	20 : 4	90.5	91.7	74.6
11	12 : 12	20 : 4	12 : 12	20 : 4	79.3	85.5	69.3
12	20 : 4	20 : 4	12 : 12	20 : 4	86.1	87.9	73.0
13	12 : 12	12 : 12	20 : 4	20 : 4	65.4	51.0	23.9
14	20 : 4	12 : 12	20 : 4	20 : 4	62.1	56.3	26.8
15	12 : 12	20 : 4	20 : 4	20 : 4	56.9	44.2	21.7
16	20 : 4	20 : 4	20 : 4	20 : 4	54.2	46.4	23.1

such division, the photoperiodic effect was significant ($p < 0.001$) for all the periods of the experiment, but the relative strength of this effect was $F = 37.9$, $F = 82.5$, $F = 1821.3$, and $F = 819.6$ for the 1st, 2nd, 3rd, and 4th periods, respectively. In other words, the 1st experimental period, in spite of being the longest (15 days), caused the smallest effect on the proportion of diapausing progeny, while the next-to-last and to a lesser extent, the last period played the crucial role.

Summarizing the results of all experiments, we conclude that in *T. embryophagum* at 20°C the period of photosensitivity of maternal females lasted ca 5–6 days (the duration of the last period of the 1st experiment and two last periods of the 2nd experiment). Preimaginal development of *T. embryophagum* was first thoroughly studied by Flanders (1937) who demonstrated that the length of egg, larval, prepupal, and pupal stage constituted, respectively, about 10, 20, 25, and 45% of the total duration of development. Similar results were later obtained under different temperatures for other *Trichogramma* species (e.g., Pak and Oatman, 1982; Dahlan and Gordh, 1996; Takada et al., 2000). As the total duration of preimaginal development in our experiments was 18 days and the period of photosensitivity lasted not more than 6 days, we conclude that only pupae were sensitive to photoperiod.

Moreover, as seen from Table 3 and the ANOVA results, the proportion of diapausing progeny was practically determined by photoperiodical conditions during the last two days of development, i.e. at the end of the pupal stage, when the adult tissues were almost formed and intensive oogenesis was started (Volkoff and Daumal, 1994; Takada et al., 2000). It is known that in certain insect species photoperiod is perceived by embryos or in viviparous flies, by unborn larvae through the mother's body (Lees, 1959; Denlinger, 1971; Vinogradova, 1991) and this effect is outwardly, fairly similar to the maternal influence. In addition, although in most of insect species with prepupal diapause, larva is the photosensitive stage, the photoperiod could be also perceived by developing embryos (Saunders, 2002; Saulich and Volkovoch, 2004). Thus, it is conceivable that in *Trichogramma* the photoperiod directly influenced progeny embryos, but not maternal females. However, on the 18th day of development, just before emergence, when (according to our unpublished observations) most of individuals were at the adult stage but still stayed in the host chorion and intensive oogenesis still continued, a decrease in photosensitivity was recorded, suggesting that the photoperiod was perceived by maternal pupae rather than by progeny embryos.

Note that in most of the studied insect species with maternal influence on larval or prepupal diapause of progeny, the photoperiod is perceived mainly or exclusively by adult females. This was particularly demonstrated for insect parasitoids: *Coeloides brunneri* Vier. (Braconidae), *Ooencyrtus* sp. (Encyrtidae), and *Nasonia vitripennis* Walk. (Pteromalidae), although in the two last species pupae are also photosensitive (Ryan, 1965; Saunders, 1966; Anderson and Kaya, 1974), while in *Colpoclypeus florus* Walker (Eulophidae) pupa is the main photosensitive stage (Milonas and Savopoulou-Soultani, 2000). A certain role of preimaginal stages in determination of maternal influence was also revealed in the fly *Calliphora vicina* R.-D. (Diptera, Calliphoridae) (Vinogradova, 1984, 1991).

Whatever mechanism forms the basis of the observed effect, it is clear that in *T. embryophagum*, both the total duration of the photosensitive stage (5–6 days) and the minimum time of photoperiodic induction (one light-dark cycle at the next-to-last day of development) are extremely small.

The critical duration of photoperiodic induction is the number of short or long light days needed to produce 50% of a response caused by permanent influence of a given day length (Tyshchenko, 1977; Saunders, 2002). In our case, it even could not be estimated, as only one short light day caused practically the same increase in the proportion of diapausing progeny as the permanent development under the short day (Table 3, treatments 1, 8, and 12). As noted in the Introduction, the photosensitive stage usually lasts from several days to several weeks, while the critical duration of the photoperiodic induction is no less than a week. In only a few of the studied insect and mite species, diapause or active development could be induced by less than 4–5 appropriate light–dark cycles (Vinogradova, 1969, 1978; Veerman, 1977; Saunders, 2002).

Relative Sensitivity to Different Day Length

The averaging of the results of the 3rd experiment showed (hereafter, medians and quartiles are given) that if the last two days of development occurred on a short light day (Table 3, treatments 1–4), 90% (85%–93%) of the progeny diapaused. If only the next-to-last light day was short (treatments 9–12) the diapause was recorded in 87% (79%–90%) of individuals, and if only the last light day was short (treatments 5–8), 80% (70%–84%) of prepupae diapaused. If both the 17th and 18th days of preimaginal development occurred on a long light day (treatments 13–16), the diapause was recorded in less than half of the progeny wasps: 48% (31%–57%).

With a long-day photoperiodic reaction, the number of long days required to stimulate active development is usually lower than the number of short days required to induce the diapause (Danilevski, 1961; Vinogradova, 1969; Zaslavski, 1984; Saunders, 2002). However, *Trichogramma* was an exception to this rule, too. If one of the two last light days of development of maternal females was long, while the other day was short (tab. 3, treatments 5-12), the short day was obviously "stronger", i.e. the percentage of diapausing progeny was much closer to that in females developed on a short light day (Table 3, treatment 1) than to that in females developed on a long light day (Table 3, treatment 16). Interestingly, the study on the maternal influence on progeny diapause in the flesh fly *C. vicina* revealed a similar "exception" (Vinogradova, 1991).

Manifestation of the Stepwise Photoperiodic Response

Multifactorial regression analysis of the results of the 2nd experiment showed that the proportion of diapausing progeny could be very accurately (r = 0.96, n = 384, p < 0.001) determined with the equation:

$$Y = 230 + 0.2Ph3 - 6.2Ph4 - 4.8T,$$

where Y is the percentage of diapausing individuals, *Ph3* and *Ph4* is the light day length during, correspondingly, the 3rd and the 4th periods of the second experiment, and T is the temperature regimen of the progeny development. Note the positive regression coefficient of the day length during the 3rd period of the experiment. Further treatment of the results of the second experiment showed that the influence of photoperiodic conditions during 13th–15th days of development of maternal females was significant (p = 0.002) only when the 3 last days of their development occurred on a long day (L : D = 20 : 4) and the progeny larvae developed at 13°C. Unexpectedly, the short light day acting on maternal females during 13th–15th days of their development caused a slight but significant (p = 0.002) decrease in the percentage of diapausing progeny from 60% (56%–63%) to 56% (50%–59%), instead of an increase.

In the third experiment, the proportion of diapausing progeny could be rather accurately (r = 0.86, n = 384, p < 0.001) determined with the equation:

$$Y = 300 + 0.4Ph1 - 0.6Ph2 - 3.2Ph3 - 2.2Ph4 - 9.7T,$$

where Y is the percentage of diapausing individuals, *Ph1*, *Ph2*, *Ph3* and *Ph4* is the light day length during, correspondingly, the 1st–4th periods of the third experiment, and T is the temperature regimen of the progeny development. Note that similarly to the period of time from the 13th to the 15th day of the second experiment, the light day length during the first 15 days of preimaginal development of maternal females had the positive coefficient of regression. In other words, during this period of the time influence of the long light day L : D = 20 : 4 induced diapause in higher percentage of the progeny than that of the short light day L : D = 12 : 12.

Evidently, this effect is a typical stepwise long day photoperiodic response (Zaslavski, 1984): a long light day preceding a short light day (under natural conditions, this means the autumnal decrease in the day length) causes a stronger increase in the tendency to diapause. Thus, our study experimentally supported the hypothesis published earlier (Zaslavski and Umarova, 1981) that *Trichogramma* may response to changes in the light day length occurring during development of the maternal generation.

CONCLUSIONS

The influence of the photoperiod on *T. embryophagum* prepupal diapause is based on the light day length perception by pupae of the maternal generation.

The crucial role in the diapause regulation is played by the last two days before adult emergence, when a single short light day (L : D = 12 : 12) could induce the diapause, and two long light days (L : D = 20 : 4) could inhibit it in most of the progeny.

If the long light day is replaced by the short light day more than 2–3 days before adult emergence, a stepwise photoperiodic reaction increases the tendency to diapause.

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