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Journal of Insect Physiology

journal homepage: www.elsevier.com/locate/jinsphys

Effect of temperature on the duration of sensitive period and on the number of photoperiodic cycles required for the induction of reproductive diapause in *Drosophila montana*

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ARTICLE INFO

Article history:

Received 29 August 2012

Received in revised form 11 February 2013

Accepted 12 February 2013

Available online 19 February 2013

Keywords:

Critical day length

Ovaries

Sensitive period

Vitellogenesis

ABSTRACT

Correct timing of the induction of photoperiodic reproductive diapause has been found to play an important role in the life cycle of several northern insect species. However, even when the environmental conditions are favourable for diapause, the switch to diapause can only take place when the females are in a proper developmental and physiological stage, referred to as the sensitive period (SP) for diapause. We have previously shown that in a northern fly species, *Drosophila montana*, the developmental pathway of the ovaries (direct maturation vs. diapause) is determined by photoperiodic cues that the females receive after eclosion. Here, we have studied the effects of temperature on the duration of the sensitive period, and on the number of short day cycles that the females have to experience before half of them will enter diapause (RDN = required day number). Ovarian development rate of the females was first traced under long and short day conditions in 16 and 19 °C, and then reciprocal transfers were done between the diapause-inducing short day conditions, and the vitellogenesis-inducing long day conditions to determine the females' SP and RDN. Close to 100% of the females of all study strains entered reproductive diapause under short day conditions in 16 °C, and the same occurred also in 19 °C in strains from the more northern univoltine population. The sensitive period for diapause induction was affected by temperature, as it was shorter in higher temperature (circa 8 days in 16 °C and 4–5 days in 19 °C), and was restricted by the faster development rate of the ovaries. *D. montana* females had to experience approximately three short day cycles during the sensitive period, before half of them entered diapause, which also explains the decrease in the number of diapausing females at higher temperatures. This system clearly differs from that of the more southern *Drosophila* species, e.g. *D. melanogaster*, where the females' developmental pathway is determined already during the first day after eclosion.

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1. Introduction

Organisms living in the northern hemisphere encounter both favourable and unfavourable periods during their life cycle. In a seasonally varying environment these periods are repeated at regular intervals, which enable individuals to forecast the forthcoming harsh environments in advance on the basis of specific environmental cues. At high latitudes the most reliable cue, photoperiod, may act together with temperature to fine-tune the timing of seasonal events in a thermal environment that varies from year to year (Bradshaw and Holzapfel, 2008). One of the most important adaptations allowing insects to survive over the long winter period in the northern hemisphere, is a state called diapause, where the insects' development, growth and reproduction are temporarily

arrested, and directed to a more suitable season (e.g. Danks, 2006). Obligatory diapause occurs in organisms at a certain developmental stage regardless of environmental conditions, while the more common facultative diapause is largely determined by environmental cues. Insects can enter diapause at various developmental stages depending on the species: in embryonic (e.g. the silkworm *Bombyx mori*; Ikeda et al., 1993), larval (e.g. the rice stem borer *Chilo suppressalis*; Inoue and Kamano, 1957; Xiao et al., 2010), pre-pupal (e.g. the moth *Thyrassia penangae*; He et al., 2009), and adult stage (the monarch butterfly *Danaus plexippus*; Herman, 1981, and the flies of several *Drosophila* species; e.g. Lumme, 1978; Watabe, 1983; Pittendrigh and Takamura, 1987; Saunders et al., 1989). In adult reproductive diapause, oogenesis is arrested at a pre-vitellogenic stage, which leads to a halt in the accumulation of yolk in the ovaries, and postpones reproduction to a more suitable season, increasing the chances of survival of both the females and their offspring. The induction of photoperiodic diapause has been suggested to be an active process requiring

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counts of short days, while ovarian maturation itself is a default state proceeding unless environmental cues are halting it (Hua et al., 2005).

Photoperiodic induction of reproductive diapause involves two processes: detection of qualitative differences between long and short days/nights (photoperiodic clock) and the accumulation of quantitative information on photoperiods (photoperiodic counter) up to an internal threshold at which the induction of diapause is complete (Saunders, 1981; Vaz Nunes and Saunders, 1999). The sensitive period (SP) for reproductive diapause can take place either before or after eclosion depending on the species (Danks, 1987) and females usually need to be exposed to inductive photoperiods for several successive days during the sensitive period, before their internal threshold is exceeded and the switch to diapause occurs (Saunders, 2002). For example, in *Polygonia c-album* butterflies, the diapause pathway is already determined by the time of eclosion (Nylin, 1989), while in *D. melanogaster* fruit flies the SP for diapause induction is in the adult stage, and persists for only 10 hours after eclosion (Saunders and Gilbert, 1990). The effect of the photoperiodic counter, which acts as a link between the clock and the photoperiodic response, can be measured quantitatively as the number of specific day or night cycles needed (required day number, RDN) to induce a diapause response in 50% of individuals in a certain age group (Saunders, 1971). Experiments where the insects are transferred from long-to short day cycles, and vice versa, at different time points before and/or after their emergence, have helped to determine both SP and RDN in several insect species (e.g. Beach, 2003; Hua et al., 2005).

The function of the photoperiodic time measurement system and the induction of diapause can be affected by temperature in a number of ways. For example, changes in temperature can alter the critical day length (CDL) at which 50% of the females of a population enter diapause (Saunders and Gilbert, 1990), and daily temperature cycles, thermoperiods, may simulate the effects of light-dark cycles acting as a *Zeitgeber* in their own right. Moreover, interaction between the temperature and photoperiod may affect the accumulation of short and long day information and alter the relationship between SP and RDN (Saunders, 2002). For example in the aphids *Megoura viciae* (Hardie, 1990) and *Aphis fabae* (Vaz Nunes and Hardie, 1991), and in the flesh fly *Sarcophaga argyrostoma* (Saunders, 1992) the summation of short day information has been found to be temperature compensated (i.e. not affected by temperature), and the accumulation of long day information temperature dependent.

Drosophila montana, a species of *Drosophila virilis* group, has distributed around the northern hemisphere adapting to various kinds of environmental conditions (Mirol et al., 2007; Throckmorton, 1982). In Finland only the most southern populations of this species are bivoltine, while the northern populations are univoltine (Lumme et al., 1974, 1979). Our earlier studies have shown that individuals of this species are able to adjust their egg-to-eclosion development time according to the prevalent photoperiodic conditions prior to eclosion, while the reproductive diapause of the females is strongly dependent on the post-eclosion day length (Salminen et al., 2012). We have also shown that *D. montana* females will enter reproductive diapause only under short day conditions and that the critical day length for diapause shows a clear latitudinal cline in Finland (Tyukmaeva et al., 2011). In the present study we have traced the effects of temperature on the length of the SP for the induction of reproductive diapause by determining the time frame after eclosion when the diapause induction can take place in *D. montana* in 16 and 19 °C. Reciprocal transfer experiments between diapause- and vitellogenesis-inducing photoperiods allowed us to estimate the length of the SP in above-mentioned temperatures, as well as to determine how many days the females have to be exposed to inductive photoperiods

before half of them will switch to reproductive diapause (RDN). Information obtained in this study will give a good background for tracing the effects of environmental cues on changes in specific genetic and metabolic pathways during the diapause induction in a northern insect species with a robust diapause response.

2. Materials and methods

2.1. Study material

The studies were performed using isofemale strains from two *D. montana* populations, Lahti (N60°59 E25°40) and Pelkosenniemi (N67°00 E27°08), which represent the southern and northern extremes of a 760 km long latitudinal cline of *D. montana* populations in Finland (see Tyukmaeva et al., 2011). The environmental conditions of these sites vary in the amplitude of seasonal changes in day length and temperature, as well as in the length of the growing season and the duration and severity of winter. In Lahti the day length varies annually from 5.51 to 19.17 h per day and in Pelkosenniemi from 1.32 to 24 h per day, with a period of continuous light lasting for approximately 1.5 months.

The study material involved four *D. montana* isofemale strains from Lahti (strains L209, L309, L609 and L909) and Pelkosenniemi (strains 2PT09, 15PT09, 21PT09 and 24PT09). Strain IDs refer to stock collections at the University of Jyväskylä. All of these strains consist of progenies of females collected in the wild during summer 2009 and they have been maintained in the laboratory in diapause preventing conditions (constant light, +19 °C and 60% humidity) since their establishment. All experiments were conducted during the years 2010 and 2011, after the fly strains had been maintained in the laboratory for eight to ten generations. Oikarinen and Lumme (1979) have shown that the maintenance of flies in continuous light does not have a significant impact on the diapause incidence or the critical day length for diapause in a northern *D. virilis* group species, *Drosophila littoralis*, and our recent studies have confirmed this to be true also in *D. montana* (Lankinen et al., unpublished).

In some of the experiments only a few individuals hatched from the strains 15PT09 and 21PT09 (Pelkosenniemi) and in these cases the strains were excluded from the dataset. For the other strains approximately 30–60 females per strain were collected for each treatment. The total number of females used in the experiments was approximately 17100.

In all the experiments, the ovaries were dissected and classified into three categories: immature/diapause ovaries (small transparent ovaries without yolk accumulation), developing/intermediate ovaries (small ovaries with some yolk already accumulated and visible segments) and developed/vitellogenic ovaries (large ovaries with one or more mature eggs; see Fig. 1). This was done in Experiments I and III when the females were at the age of maturity (18 days) and in Experiment II during eight successive days after eclosion.

2.2. Experimental conditions

Since we have previously shown that the photoperiod in which *D. montana* females are maintained before eclosion have no effect on their post-eclosion ovarian development (Salminen et al., 2012), all females were kept in constant light and either in 16 or 19 °C from egg-to-eclosion prior the transfer experiments. Because the day lengths differ between Lahti and Pelkosenniemi around the year, we used population specific long and short day lengths, which have previously been found to induce nearly 100% vitellogenesis or diapause in females of these populations at 16 °C (Tyukmaeva et al., 2011). Long day conditions for Lahti was

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