Different maternal effects on diapause induction of tetranychid mites, *Tetranychus urticae* and *T. kanzawai* (Acari: Tetranychidae)

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Abstract

Prenatal maternal effects on diapause induction were examined in the tetranychid mites, *Tetranychus urticae* and *T. kanzawai*. In *T. urticae*, the incidence of diapause of offspring whose mothers had experienced short daylength (9L15D) was higher than that of the offspring whose mothers had experienced long daylength (16L8D) when the offspring developed under short daylength. However, this maternal effect was not conspicuous when the offspring developed under long daylength. The incidence of diapause in *T. urticae* offspring was higher when their mothers had experienced a high density during the juvenile period. By contrast, the photoperiod and density experienced by mothers did not affect the incidence of diapause in the offspring of *T. kanzawai*. However, the presence of senior female adults on the same leaf during the juvenile period enhanced the incidence of diapause in *T. kanzawai*. The difference in maternal effects observed between *T. urticae* and *T. kanzawai* is discussed with respect to their life-history characteristics.

Key words: Maternal effect; diapause incidence; photoperiod; density; tetranychid mites

INTRODUCTION

In some organisms, environmental conditions experienced by the parental generation, especially by the mother (hereafter ‘maternal environment’), transgenerationally affect offspring phenotypes (e.g. Mousseau and Dingle, 1991a, b). Such prenatal phenotypic plasticity is a candidate for adaptive maternal effects, in which mothers adjust offspring phenotypes in order to accommodate offspring for predictable future environments (Fox et al., 1997; Mousseau and Fox, 1998; Agrawal et al., 1999).

Diapause is an adaptive strategy to escape from adverse conditions, such as low temperature and food shortage. Female adults of *Panonychus mori* lay diapausing eggs under short-day conditions (Fujimoto and Takafuji, 1986). It is evident that egg diapause is maternally determined because diapausing and non-diapausing eggs are different in size and color immediately after oviposition. Females of the tetranychid mites have the ability to enter reproductive diapause in response to environmental cues, such as short daylength and low temperatures, during their juvenile period (Veerman, 1985). Gotoh and Shinkaji (1981) reported the effects of photoperiod on the egg stage of diapause

induction in *Tetranychus urticae*. However, the diapause status of *T. urticae* and *T. kanzawai* is not distinguishable during the egg stage (e.g. Mochizuki and Takafuji, 1996). Although Goka and Takafuji (1990, 1991) reported a maternal effect on diapause incidence of *T. urticae* controlled by cytoplasmic factors, little attention has been paid to the maternal environment as a determinant for diapause induction in spider mites that undergo reproductive diapause. Since spider mites have a short generation time and female adults and juveniles live together on the same leaf (So, 1991; Hinomoto and Takafuji, 1994), mothers may “predict,” at least to some extent, changes in the physical and biological environment in their offspring by using the local density as a reliable indicator in addition to photoperiod and temperature. Thus, there is a possibility that maternal environment, including density, influences offspring phenotypes.

In *T. kanzawai*, the presence of senior female adults during the juvenile period affects their fecundity and dispersal capacity after maturation, even though they were reared without the senior females after maturation (Oku et al., 2002b). Such an experience during the juvenile period may also be utilized as an indicator to predict local density for

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offspring.

In this study, we examined the effect of maternal photoperiod and density on the incidence of diapause in *T. urticae* and *T. Kanzawai*. The differences between the two species are discussed in light of their life-history characteristics.

MATERIALS AND METHODS

Mites. The population of *T. urticae* used in the present study was collected from a rose garden in Kyoto City (ca. 35°N, 135°E), Japan, and that of *T. Kanzawai* from a strawberry garden in Kyoto City. Each population was maintained on leaf discs of kidney bean (*Phaseolus vulgaris* cv. Nagauzura) that were placed on water-saturated cotton in Petri dishes (90 mm in diameter and 14 mm depth; hereafter "leaf discs"). Detached primary leaves were used. The discs were placed together in a transparent plastic container (250×350×50 mm) at 25°C with 65% r.h. and photoperiodic conditions of 16L8D.

Effect of maternal photoperiod on offspring diapause. Females were reared under either a long or a short daylength prior to oviposition in order to examine whether the photoperiod experienced by mothers affects the diapause incidence in their offspring. For each species, 60 teleiochrysalis females together with 30 male adults were randomly selected from the stock cultures. They were divided into two groups and 30 females and 15 males placed on each leaf disc at 20°C and 65% r.h. under 16L8D (long daylength). One group was daily covered with a cardboard box during the first 7 h of the light phase to produce a photoperiod of 9L15D (short daylength). After five days, matured females were individually transferred onto new leaf discs. To equalize the photoperiod experienced during the egg period, the females were allowed to oviposit for 7 h during the light phase of both daylengths. After the females were removed, the discs were transferred to the short daylength at 20°C to induce diapause of female offspring.

About one week after adult emergence, the females were individually transferred onto leaf squares (10×10 mm) in the Petri dishes and kept under the long daylength at 25°C for two days. The diapause status was then determined by observing whether the females oviposited during the two days. The proportion of females that entered dia-

pause was compared between the treatments by χ^2 test with Yates's continuity correction.

Thirty teleiochrysalis females together with 15 male adults were randomly selected from the stock culture of *T. urticae* to examine the effect of the short daylength in the maternal stage on diapause incidence of offspring in *T. urticae*. Mites were transferred onto a leaf disc and kept under the short daylength at 20°C. After five days, females were transferred onto a new leaf disc to allow oviposition for 7 h as described above. The eggs laid were kept under the long daylength at 20°C.

Effect of maternal density on offspring diapause. Females were reared under either a high or a low density during their juvenile period to examine whether the local density experienced by mothers affects diapause incidence in offspring. For each species, 20 teleiochrysalis females together with 10 male adults were randomly selected from each stock culture. The mites were transferred onto a leaf disc and allowed to oviposit for 2 days under the long daylength at 25°C. The eggs laid were used for the experiment described below. Five eggs were transferred onto each of the twenty leaf squares (10×10 mm) in Petri dishes. Three virgin female adults each were introduced onto a half ($n=10$) of the leaf squares on the same day (hereafter 'high maternal density'), while the rest of the leaf squares served as a control without female adults (hereafter 'low maternal density'). These squares were kept under the long daylength at 25°C for eight days. The two species are arrhenotokous, and virgin female adults oviposit on host plants as do mated females, although the former deposited unfertilized eggs. Therefore, female juveniles that were initially introduced could be easily identified. For each treatment, 30 teleiochrysalis females were randomly selected together with 15 male adults from the stock culture and transferred onto leaf discs. After three days, the females were transferred onto new leaf discs and allowed to oviposit for 7 h during the light phase of the long daylength at 25°C. The eggs laid were transferred to the short daylength at 18°C to determine their diapause status after maturation. The incidence of diapause was determined by the methods described above.

Effect of juvenile density on diapause. Sixty mated females were randomly selected from the stock cultures of the respective species and placed onto two leaf discs, 30 females per disc to examine

the effect of the local density during the juvenile period on the diapause incidence. Females were allowed to oviposit for 7 h during the light phase at 25°C. There were 50–60 eggs on each leaf disc. Three virgin female adults each were transferred onto one leaf disc on the same day ('high juvenile density'), while the other leaf disc served as a control without adults ('low juvenile density'). After two weeks, three virgin female adults were removed. The discs were kept under the short daylength at 18°C for four weeks to compare the diapause incidence between treatments. The incidence of diapause was determined by the methods described above.

RESULTS

Effect of maternal photoperiod on offspring diapause

Maternal photoperiod affected the diapause incidence of offspring in *T. urticae* ($\chi^2=6.096$, $p=0.014$; Table 1), but not in *T. kanzawai* ($\chi^2=3.233$, $p=0.072$). The diapause incidence of offspring significantly differed between the two species when their mothers had experienced the long daylength ($\chi^2=25.199$, $p<0.0001$), but did not when their mothers had experienced the short daylength ($\chi^2=0.145$, $p>0.5$). In *T. urticae*, no offspring entered diapause under the long daylength even when their mothers had experienced the short daylength ($n=102$).

Effect of maternal density on offspring diapause

In *T. urticae*, diapause incidence of offspring was significantly higher when their mothers had experienced a high density during the juvenile period ($\chi^2=10.742$, $p=0.001$; Table 2). In *T. kanzawai*, however, the diapause incidence did not differ significantly between the treatments ($\chi^2=1.123$, $p=0.289$).

Effect of juvenile density on diapause

In *T. urticae*, juvenile density that was either high or low did not affect the incidence of diapause ($\chi^2=1.056$, $p=0.304$; Table 3). By contrast, in *T. kanzawai*, the diapause incidence significantly differed between the treatments ($\chi^2=17.143$, $p<0.0001$).

Table 1. Effect of the maternal photoperiod on offspring diapause. The offspring were reared under 9L15D at 20°C. Diapause incidence differed significantly between the two species under the long daylength ($\chi^2=25.199$, $p<0.0001$).

Species	Maternal photoperiod	% Offspring diapause	χ^2	p
<i>T. urticae</i>	Long (16L8D)	39.3 ($n=140$)	6.096	0.014
	Short (9L15D)	54.5 ($n=123$)		
<i>T. kanzawai</i>	Long	69.3 ($n=150$)	3.233	0.072
	Short	58.3 ($n=132$)		

Table 2. Effect of the maternal density on offspring diapause. A high maternal density indicates that mothers lived with senior female adults during the juvenile period, while a low maternal density indicates that mothers lived without senior adults.

Species	Maternal density	% Offspring diapause	χ^2	p
<i>T. urticae</i>	Low	28.5 ($n=158$)	10.742	0.001
	High	52.2 ($n=69$)		
<i>T. kanzawai</i>	Low	48.8 ($n=217$)	1.123	0.289
	High	55.3 ($n=132$)		

Table 3. Effect of juvenile density on diapause. The high juvenile density indicates that the mites lived with senior female adults during their juvenile period, while the low density indicates that the mites lived without senior adults.

Species	Juvenile density	% Offspring diapause	χ^2	p
<i>T. urticae</i>	Low	40.3 ($n=62$)	1.056	0.304
	High	52.2 ($n=46$)		
<i>T. kanzawai</i>	Low	57.6 ($n=125$)	17.143	<0.0001
	High	82.4 ($n=125$)		

DISCUSSION

The effect of maternal photoperiod on diapause incidence of offspring was conspicuous only in *T. urticae*. This result suggests that mothers of *T. urticae* can enhance the diapause incidence of their offspring in response to the short daylength. It is noteworthy that the diapause incidence of *T. urticae* was significantly lower than that of *T. kanzawai* when mothers had experienced the long

daylength, but was similar when mothers had experienced the short daylength. Therefore, *T. urticae* mothers may have to compensate for the lower diapause potential of their offspring against the inevitable winter. This result also implies that the conventional method (e.g. Goka and Takafuji, 1990; Takafuji et al., 1991), in which mothers of tested females had experienced a long photoperiod during oviposition, may have caused underestimation of the diapause incidence of *T. urticae*. On the other hand, the environmental effects of offspring on diapause induction in *T. kanzawai* overrode the maternal effect, which seems to be a safety device for a possible mistake in the maternal prediction based on the daylength.

Diapause in response to local density may be considered as a temporal way of escaping from unfavorable food conditions. Otherwise, under long daylength, the mites would disperse to available host plants (Oku et al., 2002b). The contrasting results that maternal density affects the diapause incidence of offspring in *T. urticae*, while juvenile density affected the diapause incidence in *T. kanzawai* can be explained as follows. Mothers stay longer on an infested leaf in *T. urticae* than in *T. kanzawai* (Kondo and Takafuji, 1985; Oku et al., 2002a). Therefore, the *T. urticae* mothers may be able to predict the future food environment for their offspring based on their experience on the leaf. By contrast, in *T. kanzawai*, maternal density may not be a reliable indicator to predict the future environment for both mothers and offspring, while density in the juvenile stage may be a more important indicator of diapause incidence.

Other conditions experienced by mothers, such as temperature, may also affect the incidence of diapause in *T. urticae* and *T. kanzawai*. Effects of such conditions remains to be examined in the future.

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