GEOGRAPHICAL VARIATION OF PHOTOPERIODIC ADULT DIAPAUSE IN *DROSOPHILA AURARIA*

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Received February 18, 1980

The variation of photoperiodic adult diapause was studied in *Drosophila auraria* strains originating in Japan at latitudes from 33.8 to 43.1°N. All the differently-located geographical strains showed a photoperiodic diapause. The critical daylength of these strains fell between 12 and 14 h. The diapause intensity increases with an increase in latitudes. The duration of diapause was shorter at a photoperiod of 12 or 6 h than at one of 10 or 8 h in all the strains. This is because the photoperiod of 12 or 6 h is less effective as a stimulus for the maintenance of diapause.

INTRODUCTION

Diapause is an ecogeographic character and correlates closely with altitude and latitude (Masaki 1967; Danilevsky *et al.* 1970; Tauber and Tauber 1972; Bradshaw and Lounibos 1977; Lumme and Oikarinen 1977). In general, populations of geographically widespread insect species from higher latitudes enter diapause earlier than those found in lower latitudes. To accomplish this, northern forms from the Northern Hemisphere enter diapause in response to longer day lengths, i.e., northern forms show a longer critical photoperiod which ensures the timely initiation of diapause in response to long day lengths in late summer at high latitudes (cf. Danilevsky *et al.* 1970). Danilevsky *et al.* also gave examples of species in which the more northern forms experience deeper diapause than the southern ones. The difference in diapause intensity correlates well with the duration and severity of winter conditions at the different latitudes.

Drosophila auraria Peng is distributed in Japan, Korea and China. Minami *et al.* (1979) showed the Sapporo population of this species display a reproductive diapause controlled by photoperiod and temperature. Here we report the geographic variation of diapause in this species.

MATERIALS AND METHODS

Material was obtained from five localities in Japan: Sapporo (SP strain; 43.1°N in latitude), Akita (AK strain; 39.7°N), Urawa (UR strain; 35.8°N), Chiba (CH strain;

35.6°N), and Matsuyama (two strains, MA-1 and MA-2; 33.8°N). The SP strain originated from several field-collected females, but the other strains were from a single female. These strains were maintained under diapause-preventing conditions (continuous illumination, 23°C) for months or years until the present experiment.

Apparatus and rearing conditions were similar to those described by Minami *et al.* (1979). To study the photoperiodic response, animals were reared from the egg stage through the adult stage under three photoperiodic conditions, LD 10 : 14 (10 h light: 14 h dark), LD 12 : 12, and LD 14 : 10, and the proportion of diapausing females was examined at 8th, 16th, and/or 24th days after eclosion. For the SP strain, the diapause was examined at additional ages (32, 40, 48, and 64 days after eclosion) under four photoperiodic conditions, LD 6 : 18, LD 8 : 16, LD 10 : 14 and LD 12 : 12. In this experiment, animals were cultured at 18°C before eclosion and 15°C and/or 18°C after eclosion, because a temperature of 18°C resulted in a higher larval and pupal viability than one of 15°C. Temperatures of 15 and 18°C before eclosion differ little in their effects on diapause (Kimura and Minami unpubl.).

The diapause intensity of these geographical strains was measured by T_{50} (number of long daylengths required to terminate diapause in half of a sample population; cf. Bradshaw and Lounibos 1977). Samples of 20 to 50 newly emerged diapausing females (reared under LD 10 : 14, 18°C) were first exposed to 0, 2, 4, 6, . . . , 16 long days (LD 14 : 10, 15°C), and then to 16, 14, 12, 10, . . . , 0 short days (LD 10 : 14, 15°C), respectively. After a total of 16 exposures, the percentage of diapausing females was examined and then plotted against the number of long days exposed. The 50% intercept was read directly.

The developmental stage of the ovaries was examined by dissection under a binocular microscope, and the females with undeveloped ovaries were assumed to be in a reproductive diapause (cf. Minami *et al.* 1979).

RESULTS AND DISCUSSION

The variation in the proportion of diapausing females was controlled by four factors: temperature, age, photoperiod, and the geographical origin of the strains. The proportion of diapausing females was lower when they were reared at 18°C throughout their entire life than when they were transferred to 15°C at the time of adult eclosion (Fig. 1). This was considered to be due to that the diapause ends earlier at higher temperatures at the adult stage (Kimura and Minami unpubl.). Fig. 2 shows the effect of age on the proportion of diapause in the SP strain. The proportion decreased as age increases under various photoperiods as 6, 8, 10, and 12 h. In the other strains, the proportion was also lower at 24th day than 8th day after eclosion (Fig. 1, b and c).

When cultured at 15°C, the proportion of females with undeveloped ovaries was low at LD 14 : 10 even at 8th day after eclosion in all strains, but not at LD 10 : 14 and LD 12 : 12. This suggests that their critical daylength fell between LD 12 : 12 and LD 14 : 10. Under short daylengths, the duration of diapause was modified by a kind

Fig. 1. Photoperiodic response curves of geographical strains of *D. auraria*: Sapporo (○—○), Akita (●—●), Urawa (△—△), Chiba (▲—▲), Matsuyama-1 (□—□), and Matsuyama-2 (■—■). Flies were cultured at 18°C for 16 days after eclosion (a), at 15°C for 8 days (b), and at 15°C for 24 days (c). About 30 females were examined for each point.

Fig. 2. Diapause percentages of the Sapporo strain of *D. auraria* when cultured under LD 6:18 (○—○), LD 8:16 (△—△), LD 10:14 (□—□), and LD 12:12 (●—●) conditions. About 30 females were examined for each point.

of photoperiods experienced. The proportion of diapausing females decreased earlier at LD 6:18 and LD 12:12 than LD 8:16 and LD 10:14 at 15°C in the SP strain (Fig. 2). In the other strains, the proportion of diapausing females also decreased earlier at LD 12:12 than LD 10:14 (Fig. 1, c).

The effectiveness of different photoperiods as a stimulus for the maintenance of

Table 1. Diapause percentages of females transferred into various photoperiodic conditions

Photoperiod before transfer	Photoperiod after transfer				
	LD 6 : 18	LD 8 : 16	LD 10 : 14	LD 12 : 12	LD 14 : 10
LD 6 : 18	50.0	72.3	68.2	49.4	29.2
LD 8 : 16	57.1	86.7	66.7	57.1	21.9
LD 10 : 14	74.5	71.5	63.0	44.0	7.2
LD 12 : 12	32.1	79.2	66.7	42.9	17.6

About 30 females were examined for each value.

Fig. 3. Percentages of diapausing females at 16th day after the photoperiodic treatment of various combinations of LD 14 : 10 and LD 10 : 14.

diapause was studied with the SP strain. Diapausing females cultured under different photoperiods by the age of 24 days after eclosion were transferred to various kinds of photoperiodic conditions, and diapause was examined 16 days after the transfer. In this experiment, the flies were also cultured at 18°C before eclosion and 15°C after eclosion. Table 1 shows results. Females transferred to a LD 14 : 10 condition showed the termination of diapause. In contrast, the diapause was maintained in about 80% or 65% levels when flies were transferred to a LD 8 : 16 or LD 10 : 14 condition respectively. Females transferred to LD 6 : 18 and LD 12 : 12 conditions showed the intermediate percentage of diapause. Thus, diapausing females regarded different photoperiods ranging from 6 h to 14 h of light in different ways in the course of diapause maintenance. Tauber and Tauber (1973) observed a similar phenomenon in *Chrysopa carnea* which quantitatively responded to various daylengths in the course of diapause termination.

Figure 3 shows the geographical variation of the diapause intensity against the long-day treatment which at last breaks the state of diapause. The Sapporo strain was

Fig. 4. Relationship between diapause intensity as measured by T_{50} and the latitude where the materials originated.

most resistant to the treatment but the Chiba and Matsuyama strains were sensitive, and the Akita strain was intermediate. From Fig. 3, T_{50} was regarded as 16.0 for the SP strain, 11.1 for AK, 5.2 for CH and 5.0 for MA-2 respectively. The diapause intensity measured by T_{50} correlates highly with latitudes of strains originated (Fig. 4):

$$T_{50} = 1.245 \text{ } ^\circ\text{N Lat.} - 38.047$$

This equation was sufficient to explain 97% of the variation in T_{50} which was observed among these geographical strains ($r=0.986$, d.f.=2). The earlier end of diapause in the southern strains (Fig. 1, c) would be due to their less intense diapause.

The geographical differentiation of diapause intensity observed in this study could be a result of adaptation to local climates. The Sapporo population of this species, however, is not completely adapted to the climate of Sapporo (Iwao *et al.* 1980). If females of this species oviposit eggs after mid September, the eggs do not grow to adult before the arrival of winter in Sapporo. Therefore, it is meaningless for females to grow their ovaries after mid September. The optimal timing of diapause is, then, considered in early September. In fact, many of temperate species which display an adult diapause enter diapause in late August or early September in Sapporo (Watabe and Beppu 1977; Watabe 1977; Toda and Kimura 1978). However, *D. auraria* enters diapause in late September in Sapporo. Iwao *et al.* (1980) assumed that the maladaptation of this species is due to gene flow from southern populations or to the newness of the colonization of this species in Hokkaido. It is still not known whether this species adapts to southern climates or not. Adaptation of this species to local climate and the meaning of cline in the diapause intensity must be studied in future from the point of the seasonal occurrence of diapause at different latitudes.

ACKNOWLEDGMENTS

We wish to express our sincere thanks to Dr. Eizi Momma for his advice in the course of the study and further to Messrs. M. J. Toda, H. Watabe, N. Ichijō, Y. Sado,

A. Yamamoto, N. Kôyama, and O. Enomoto for their providing the materials.

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