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Effect of Temperature on the Termination of Prolonged Initial Diapause in Eobiana japonica (Bolivar) (Orthoptera: Tettigoniidae)*

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Abstract. Eobiana japonica (formerly Metrioptera japonica) requires two or more years to complete its life cycle by entering diapause twice in the egg stage. Initial diapause occurs just after blastoderm formation and the final diapause shortly before hatching. The initial diapause lasted for more than a year in some eggs. The percentage of initial-diapause termination increased on the whole as the duration of exposure to 3°C increased from 15 to 600 days. The intensity of initial diapause was considerably variable among individuals. Chilling longer than 600 days impaired the egg viability. Cold treatment was not indispensable to terminate the initial diapause because some or most eggs resumed development at constant temperatures between 15 and 30°C. Repeated exposure to low (90 days at 10°C or 180 days at 3°C) and high temperatures (90 or 180 days at 25°C) was more effective than a single long cold treatment in terminating the initial diapause, and all the eggs resumed development after two or three such cycles.

Key words: Tettigoniidae, Eobiana japonica, prolonged diapause, egg diapause, temperature cycle.

Introduction

Diapause duration in insects is a species-specific and/or strain-specific characteristic ranging from several weeks to several or more years. Most temperate species undergo winter diapause. Such cases of relatively short diapause have been well studied (Lees, 1955; Danilevskii, 1965; Tauber et al., 1986; Danks, 1987). On the other hand, prolonged diapause has been poorly understood, although its occurrence has been reported in many species, especially in unpredictably changing habitats (Ushatinskaya, 1984; Danks, 1987). The physiological basis and genetic as well as environmental factors governing the induction, maintenance and termination of prolonged diapause have been the subject of several theoretical works (Takahashi, 1977; Walker, 1986; Seger & Brockmann, 1987)

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and experimental works (Sullivan & Wallace, 1967; Ushatinskaya, 1972; Hedlin et al., 1982; Ingrisch, 1986 c).

Most temperate species of Tettigoniidae spend far more time in the egg stage than in the other life stages (Hartley, 1990). In many of them, the egg stage lasts for more than a year with two diapause stages intervening at early and late stages of embryogenesis, respectively. The eggs spend the first winter in initial diapause at an early stage of embryonic development and the second or later winter in final diapause at a later stage. Most individuals may hatch after the second winter. However, hatching occurs over several years in some species because of the prolongation of initial diapause. Ingrisch (1986a) has coined the term "plurennial" for such a life cycle. Although the initial diapause has been studied to some extent (Hartley & Warne, 1972; Dean & Hartley, 1977; Deura & Hartley, 1982; Ingrisch, 1986a, b, c; Hartley, 1990; Ando, 1995; Higaki & Ando, 1999), the environmental regulation of this diapause has been scarcely understood (Dean & Hartley, 1977; Deura & Hartley, 1982; Ingrisch, 1986b, c).

Eobiana japonica is distributed in the northern part of Japan and at high altitudes in the southern part. The altitudinal range of its distribution is wide (Koba-

^{*} The scientific name, Eobiana japonica is used for this species in the present paper according to Storozhenko & Yamasaki (1993), although the scientific name, Metrioptera japonica has been used previously.

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yashi, 1981). We have found that *E. japonica* is a plurennial species (Higaki & Ando, 1999). In this paper, we focus on the effect of temperature on the termination of initial diapause to understand the factors controlling the prolonged diapause.

Materials and Methods

Insects

Three strains of *E. japonica* were mainly used. The collecting sites and abbreviations for the strains used are listed in Table 1. Adults were collected in the lowland in Hirosaki, Aomori Prefecture, Japan in 1992–1994; in a bog "Obayachi" at an altitude of 965 m in the Hachimantai mountains, Akita Pref. in 1991–1994; and in a bog "Midagahara" at an altitude of 1,400 m in Mt. Gassan, Yamagata Pref. in 1994. Times of collection were early September in 1991, late August-mid September in 1994. Adults collected at an altitude of 840 m in Hachimantai mountains in early August, 1993 were also used for comparison.

Rearing method

Field-collected adults were reared in groups of 10-30 individuals in stainless rearing cages $(30 \times 30 \times 30)$ cm) under LD 14 : 10 h at 25°C (1992 and 1993) or room conditions without control of light and temperature (1991 and 1994). Pellets of insect feed (Oriental Yeast Co. Ltd., Tokyo), wheat germ (Nissin Seifun Co. Ltd., Tokyo) and pupae of *Mamestra brassicae* (or larvae of *Tenebrio molitor*) were provided as food.

A bundle of *Poa annua* was inserted into a water flask and several such flasks were put in each cage for oviposition and as additional food, and renewed every 2-4 days.

Handling of eggs

Eggs laid among stems of P. annua were removed every other day and kept on layers of moist filter paper in Petri dishes (9 cm in diameter) and subjected to different temperature treatments. The embryogenesis of Tettigoniidae can be divided into 26 stages (Ingrisch, 1984). E. japonica enters the initial diapause when the embryonic primordium becomes visible (Stage 4) and final diapause when the embryo is almost fully formed (Stage 24). The eggs of E. japonica enter the initial diapause, irrespective of parental conditions. We define the termination of initial diapause by an increase in egg weight due to water absorption as described previously (Higaki & Ando, 1999). Rotten or abnormally swollen eggs were discarded. However, there is a possibility that we could not exactly distinguish dead eggs from live ones because the eggs of E. japonica are covered with black

Table 1. The strains of *E. japonica* used for the present study.

Collecting site	Latitude (°N)	Altitude(m)	Abbr.
Hirosaki, Aomori	40.5	220	AO
Hachimantai, Akita	40.0	965	AK1
Hachimantai, Akita	40.0	840	AK2
Gassan, Yamagata	38.6	1,400	YA

Table 2. Cumulative percentage termination of initial diapause during the first four months of incubation at different temperatures in AO, AK1 and YA strains of *E. japonica*.

Strain	Temperature (°C)		Days				Mortality
		n	30	60	90	120	(%)
AO	30	109	0	10.6	29.8	41.3	4.6
	25	111	0	62.2	63.1	63.1	0
	20	110	0	86.1	92.6	92.6	1.8
AK1	35	214	0	0	0	0	9.3
	30	219	0	0	0.5	1.9	1.8
	25	215	5.0	10.0	14.9	24.9	1.9
	20	213	0.5	56.3	61.5	67.8	0.5
	15	110	0	0	0.9	13.8	0.9
YA	30	210	0.5	4.4	12.0	19.7	7.6
	25	210	10.7	43.4	44.4	45.4	1.0
	20	209	0	75.6	81.3	81.9	1.9
	15	210	0	0	0	31.9	1.9
	10	203	0	0	0	0	1.5

Dead eggs were excluded from computation of percentage termination of initial diapause. Mortalities were computed from the data on the 120th day.



Fig. 1. Cumulative percentages of initial-diapause termination in AO and AK1 strains at 15, 20 and 25°C in 1993. Dead eggs were excluded. Sample size and total mortalities are also given in each panel.

thick chorion. The designs of the experiments are mentioned at appropriate places in the following section.

Results

Termination of initial diapause at constant temperatures

Eggs laid within two days were exposed to various constant temperature conditions. The eggs of AO strain were kept at 20, 25 or 30°C; those of AK1 strain at 15, 20, 25, 30 or 35°C in 1993; and of YA strain at 10, 15, 20, 25 or 30°C in 1994. The eggs of AK1 strain were also examined at 25°C in 1992 and 1994. Cumulative percentages of eggs terminating the initial diapause were recorded every 30 days during the first 120 days in all treatments. In the treatments of AK1 strain at 15, 20 and 25°C and AO strain at 20 and 25°C, diapause termination was recorded until all live eggs resumed development.

Except for some eggs that resumed development, all the eggs were still in initial diapause at any tempera-

ture on the 30th day (Table 2). However, after a longer period of incubation, the percentage of initialdiapause termination increased, though an extremely long period was necessary to reactivate all diapause eggs (Fig. 1). AK1 strain showed a similar tendency among the three experiments for three successive years (Fig. 2). At 20°C, the initial diapause was most rapidly terminated. It was also terminated relatively quickly at 15°C. The higher temperatures were less effective in terminating the initial diapause. At 30°C, the percentage of eggs resuming development until the 120th day was 41.3% in AO strain, 19.7% in YA strain and 1.9% in AK1 strain (Table 2). After the 120th day at 30°C, most of the eggs of AK1 strain did not resume development and the mortality gradually increased, whereas many eggs of AO and YA strains resumed development. The response to high temperatures was variable among the strains. At 35°C, no eggs resumed development in AK1 strain. At 10°C, no eggs of YA strain resumed development even after 450 days (data not shown). This temperature might be lower than the developmental zero for early stage development.

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Effect of chilling on the termination of initial diapause

To determine the optimal range of chilling temperatures for the termination of initial diapause, eggs of AK1 strain laid in 1992 were first kept at 25°C for 30 days and allowed to enter the initial diapause. They were then exposed to 1, 3, 7.5 or 11°C for 90 days before being returned to 25°C. The cumulative percentage of diapause termination was determined by checking the eggs about every 10 days.



Fig. 2. Cumulative percentages of initial-diapause termination in AK1 strain at 25°C. The figures indicate the years of oviposition. In the 1994 cohort, the experiment ended 540 days after oviposition. Dead eggs were excluded. N=117-201 for each curve.

No significant differences were found among the four temperatures in the proportion of initial-diapause termination after 90 days of incubation at the last temperature (x^2 -test, P=0.45; Fig. 3). The cumulative percentage of diapause termination increased rapidly during the first 30 days and slowly thereafter. In all treatments, more than 50% of the eggs were still in initial diapause at the end of the experiment. The mortality was low in all treatments (<7%).



Fig. 3. Cumulative percentages of initial-diapause termination at 25°C after chilling at 1, 3, 7.5 and 11°C for 90 days in AK1 strain. Dead eggs were excluded. N=95-98 for each curve.



Fig. 4. Percentages of initial-diapause termination and mortality on the 90th day at 25°C in AO, YA and AK1 strains after chilling for various periods. The years of oviposition are given in each graph. Dead eggs were excluded from computation of percentage termination of initial diapause. Sample size for each datum point is 98-221.

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Fig. 5. Cumulative percentages of initial-diapause termination at 25°C in AO, YA and AK1 strains after chilling at 3°C for various periods. The eggs of AO and AK1 strains were laid in 1993, and those of YA strain in 1994. Dead eggs were excluded. N=117-221 for each curve.

Table 3. Percentage termination of initial diapause at 25°C after 1 to 3 periods of chilling in AK1, AK2 and AO strains of *E. japonica*.

Series	Strain	······································	Periods of chilling			Mortality
		n	lst	2nd	3rd	(%)
A	AK1	497	44.4	39.9	. 15.7	6.8
В	AK 1	193	37.8	62.2		4.9 [±]
	AK2	170	67.1	32.9		4.6
	AO	200	75.0	25.0		3.4

Dead eggs were excluded from computation of percentage termination of initial diapause.

Series A: a chilling period of 90 days at 10° C was followed by 90-day incubation at 25° C. Chilling of the first cycle exceptionally consisted of 30 days at 10° C and 30 days at 1° C.

Series B: a chilling period of 180 days at 3°C was followed by 180-day incubation at 25°C.

Effect of chilling length on the termination of initial diapause

To examine the effect of chilling duration on the termination of initial diapause, eggs in the initial diapause were subjected to 3° C for 90, 180, 300 or 400 days in AO strain in 1993; for 90, 180 or 360 days in YA strain in 1994; and for various periods ranging from 15 to 720 days in AK1 strain in 1993. The eggs of AO strain were also subjected to 3° C for 90 or 180 days and those of AK1 strain for 90, 180 or 360 days in 1992 and 1994. After chilling, eggs were transferred to 25° C and the number of eggs resuming development was recorded about every 10 days.

The percentage of diapause termination clearly increased by prolonging the duration of chilling in all the three strains (Fig. 4). The cumulative percentage of eggs resuming development showed similar general patterns in eggs chilled for various lengths of time (Fig. 5). The intensity of initial diapause was considerably variable and some or many eggs did not resume development even after chilling for 360 days. AK1 strain tended to need longer chilling to terminate the initial diapause than AO strain for three successive years, though the percentage of diapause termination differed among years (Fig. 4). Thus the eggs derived from the alpine population required a longer period of chilling to terminate the initial diapause than those from the lowland population. Although there was no doubt that chilling for 680 and 720 days terminated the initial diapause in many eggs of AK1 strain, the percentages of eggs resuming development were not as high as expected. The mortalities were low in all treatments (<8%) except for 680 and 720 daychilling in AK1 strain (about 15%).

Effect of cycles of low and high temperatures on the termination of initial diapause

In the above experiments, many eggs resumed development after a long period of chilling. In nature, however, eggs in initial diapause are subjected to a seasonal cycle of cold and warm periods. We examined the effect of cyclical treatment with low and high temperatures on the termination of initial diapause in AO, AK1 and AK2 strains (Table 3). Eggs in

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Fig. 6. Cumulative percentage termination of initial diapause in AO, AK1 and AK2 strains at 25°C after chilling at 3°C for 180 days. On the 180th day at 25°C, the eggs still in initial diapause were again exposed to the same cold treatment and then warmed again at 25°C. Dead eggs were excluded. Sample size is given in Table 3.

the initial diapause were subjected to cycles of 10° C for 90 days and 25° C for 90 days in Series A and cycles of 3° C for 180 days and 25° C for 180 days in Series B. Cold period of the first cycle in Series A exceptionally consisted of 30 days at 10° C and 30 days at 1° C. Series A and B started in 1991 and 1993, respectively. The eggs terminating the initial diapause until the 90th day after transfer to 25° C were counted in Series A. In Series B, those terminating the initial diapause at 25° C were counted every 10-20 days for six months. The eggs which were still in initial diapause were again exposed to the same incubation cycle as before and this treatment was repeated until all the eggs resumed development.

In Series B, the percentage of diapause termination 180 days after the first period of chilling was significantly different among the three strains (χ^2 -test, P <0.001; Table 3). The eggs remaining in the initial diapause after the first period of chilling were considered to be in prolonged diapause. The cumulative percentage of diapause termination rapidly increased during the first 40 days (Fig 6). The second peak of development occurred after the second period of chilling. Three cycles of chilling and warming were required to terminate the initial diapause in all the eggs in Series A and two cycles in Series B (Table 3). The mortality was low in all treatments. Eggs derived from the two lower altitudes (AO and AK2) tended to terminate the initial diapause more rapidly than those from the highest altitude (AK1).

Discussion

The mechanism controlling prolonged diapause has been poorly understood, although many examples of prolonged diapause have been reported (Ushatinskaya, 1984; Danks, 1987). In most species, many individuals emerge after one year and fewer individuals remain in diapause for two or more years. Prolonged diapause may be controlled mainly by genetic factors, and partly by environmental cues (Danks, 1987). For example, temperature, humidity and daylength modify the expression of prolonged diapause in some species (Sullivan & Wallace, 1967; Ushatinskaya, 1972; Hedlin *et al.*, 1982; Ingrisch, 1986c).

In plurennial species of tettigoniid, eggs in prolonged diapause resume development gradually through repeated seasonal cycles. Temperature and moisture are probably important seasonal cues for the eggs in soil (Dean & Hartley, 1977; Ingrisch, 1986c; Ando, 1995). There might be a mechanism for counting the seasonal cycles, or the variation in intrinsic diapause intensity among individuals might cause scattering of diapause termination for several years.

Dean & Hartley (1977) reported that in Ephippiger ephippiger (formerly Ephippiger cruciger), one month of cooling was just as effective as three months in the percentage of eggs that would start to develop at high temperature. They concluded that cooling for longer periods does not increase the number of eggs which subsequently start to develop. On the other hand, the results of the present study regarding cold treatments showed that in Eobiana japonica, the rate of diapause termination was generally proportional to the length of chilling and that the intensity of initial diapause was strikingly variable among individuals (Figs. 4 & 5). A longer period of chilling was required to terminate the initial diapause of the strains from a higher altitude. Large variance in the chilling requirement was also reported in Pieris napi microstriata (Shapiro, 1979). In this butterfly, some individuals spent more than a year in pupal stage and the necessary duration of chilling to terminate diapause varied from 5 weeks to more than 79 weeks.

Many eggs of *E. japonica* could terminate the initial diapause after a long chilling (Fig. 4). In AK1 eggs laid in 1993, however, the percentage of diapause termination reached the maximum after 560 daychilling and decreased after the longer chilling. Chilling for 680 and 720 days seemed to cause many eggs to lose the ability of development. The low percentage of diapause termination in these treatments might be caused by an increase of such eggs which appeared healthy, but never absorbed water. Thus viability appears to be reduced by excessively long chilling.

The percentage of diapause termination reached 100% after three cycles of cold and warm periods in Series A and two cycles in Series B (Table 3). In other words, all the eggs resumed development after chilling for a total of 240 or 360 days in these treatments. A continuous chilling for 360 days was insufficient to terminate the initial diapause in AK1, though most eggs terminated the initial diapause in the eggs laid in 1992 (Fig. 4). Thus, the initial diapause in E. japonica is terminated more effectively by a combination of cold and warm treatments than by a single long cold treatment. It is possible that eggs which are not reactivated in short time at low temperature need to be 'primed' by exposure to a higher temperature before they are able to complete diapause development on subsequent exposure to low temperature (Dean & Hartley, 1977).

Eggs of E. japonica derived from lower altitudes tended to terminate the initial diapause more rapidly than those from higher altitudes (Figs. 4, 5 & 6). This suggests that the incidence of prolonged diapause is higher in the population from higher altitude. Our field observations suggest that yearly fluctuations of weather conditions tend to affect the life cycle of alpine populations more severely than that of lowland (Higaki & Ando, 1999). For example, cool summer or short hours of sunshine seems to cause failure to complete nymphal development and egg production at high altitudes. Thus, the risk of extinction or a sharp reduction in population size would be higher in populations at higher altitudes. Therefore, the prolonged initial diapause could be a bet-hedging strategy against unpredictable adversity caused by climatic conditions.

On the other hand, the three strains from different altitudes, showed similar patterns of response to high and low temperature cycles, i.e. the cumulative percentage of diapause termination rapidly increased only during the first 40 days at 25°C after the first or second chilling (Fig. 6). This fact may suggest that in the field, some eggs in initial diapause resume development synchronously within a short period after the first overwintering but the rest do not do so until after a second or third overwintering. Such synchronous resumption of development in the spring would facilitate their successful development to the final-diapause stage before winter in cold regions where the growing season is short.

In E. japonica, chilling is not always necessary to

terminate the initial diapause (Table 2, Fig. 1). Rapid diapause termination at 20°C suggests the possibility that eggs laid early in the season untimely develop beyond the initial diapause stage. Although adults of this species usually begin to lay eggs in August in Hirosaki, eggs are occasionally deposited in July in some years (Higaki & Ando, 1999). We found that such eggs developed beyond the initial-diapause stage, spent the first winter at a stage earlier than the finaldiapause stage and hatched in the second year without entering final diapause (Higaki & Ando, 1999).

The present study showed that temperature has an important role in the termination of initial diapause in E. japonica. The initial diapause can be terminated by long chilling or constant temperature, but has its unique character to be terminated effectively by cyclical temperature treatment.

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