Effects of Photoperiod on Nymphal Development, Pre-Oviposition Period and Egg Diapause in the Subtropical Rice Grasshopper, *Oxya chinensis formosana* SHIRAKI (Orthoptera: Catantopidae)

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Oxya chinensis formosana from Okinawa Is. responded to photoperiod in various ways at 25°C. The nymphal duration was shorter at LD12:12 than at LD14:10. The number of nymphal stadia was 5 or 6 in the male and 6 in the female at LD12:12, but 6 in the male and 6 or 7 in the female at LD14:10. Females reared at LD14:10 throughout post-embryonic development oviposited later than those reared at LD12:12 throughout the study and those transferred from LD12:12 to LD14:10 (or vice versa) on adult emergence. Some eggs entered diapause when incubated at 25°C irrespective of the parental photoperiods. The incidence of egg diapause was lowered by an increase in photoperiod from LD12:12 to LD14:10 on adult emergence. These results suggest that a majority of the population have a heterodynamic life cycle with a short-day type photoperiodic response controlling both nymphal development and reproduction, and also with diapause in a portion of the eggs.

Key words: photoperiod, nymphal development, pre-oviposition period, egg diapause, *Oxya chinensis formosana*

INTRODUCTION

The subtropical rice grasshopper, *Oxya chinensis formosana*, is distributed in Taiwan and the Nansei Islands in Japan (FUKUHARA, 1982). It commonly occurs around sugar cane fields, paddy fields and tussocks of the Poaceae. In the Ryukyu Islands, many hatchlings occur from February to March. As the hatchlings grow, they occasionally damage crops such as sugar cane and pampas grass (OHSHIRO, 1986).

The seasonal life cycle of this grasshopper has not been elucidated and it is not certain whether or not this species diapauses. The present study investigates the effects of photoperiod on nymphal development, pre-oviposition period and egg development to facilitate reconstruction of the seasonal life cycle of this species in subtropical regions. The hatching pattern of eggs at 25°C and the effect of low temperature (15°C) on the termination of egg diapause were also studied.

MATERIALS AND METHODS

Insects. Five female and four male adults were collected at Nakijin (26.4°N) on Okinawa Island in late March, 1990, to establish a laboratory culture.

Nymphal development. Hatchlings of the third laboratory generation were reared at LD12:12 or LD14:10, 25±1°C to examine the effect of photoperiod on nymphal development time and adult head width. Daylength was regulated by an electric time switch. Ten hatchlings were introduced into each cylindrical glass container (12 cm in dia. × 18 cm in

height). The nymphs were fed on leaves of *Poa annua* L. planted at the bottom of each container until the penultimate stadium and thereafter on cut leaves of *Bromus catharticus* VAHL inserted into a water flask. These food plants were replenished every 2–5 days. Adult emergence was recorded daily. Adult head width was measured one or two days after adult emergence under a dissecting microscope with an eye piece micrometer.

Pre-oviposition period. On adult emergence, males and females were paired. Oviposition was observed daily in glass containers where a plastic cup filled with sand containing about 20% water (w/w) was placed. Replication was carried out under LD12:12 and LD14:10 at 25°C. These results were combined, since no significant difference was observed between them.

Egg development. Egg-pods were collected within 24 h after deposition, transferred onto moist tissue paper in Petri dishes (6 cm in dia.) and incubated individually at $25 \pm 1^\circ\text{C}$. The hatchlings were counted and removed from the dishes daily. Photoperiodic effect was examined on the percentages of diapause per egg-pod according to SCHEFFE's test after arc-sin transformation of the data. Collapsed or rotten eggs were excluded from the calculations.

To determine the hatching pattern at 25°C, about 200 hatchlings of the second laboratory generation were reared in two wire screen cages (30×30×30 cm) at LD14:10 and 25°C until the penultimate stadium. These nymphs were housed in three larger cages (55×35×45 cm) in groups of 50–70 individuals in a glasshouse and were exposed to natural daylength at Hirosaki City (40.3°N) in late April, 1991. Egg-pods laid in moist sand from mid-August to mid-November were removed daily and incubated individually at $25 \pm 1^\circ\text{C}$. At about 60 days after incubation, the egg-pods were opened to count the number of unhatched eggs.

To examine the effect of low temperature on the termination of diapause, eggs in diapause for 100 to 172 days at 25°C were exposed to 15°C for 90 days and then returned to 25°C. The monthly mean temperature of January and February in Naha is about 15°C.

RESULTS

Nymphal development

Males reached maturity in 5 or 6 molts and females in 6 or 7 molts (Table 1). At LD12:12, most individuals emerged as adults after 6 stadia but some males emerged after

Table 1. Number of nymphal stadia, duration of the nymphal stage and adult head width in *O. c. formosana* at 25°C

Photoperiod	Sex	No. of nymphal stadia	No. of adults emerged	Nymphal duration ^a (days, mean±S.D.)	Head width ^b (mm, mean±S.D.)
LD12:12	Female	6	14	63.1±2.7 b	5.02±0.14 y
	Male	5	7	55.6±2.2 a	4.12±0.12 w
		6	21	63.9±3.0 bc	4.50±0.17 x
LD14:10	Female	6	10	68.4±3.7 cd	5.24±0.14 z
		7	3	89.3±8.4 e	5.44±0.13 z
	Male	6	24	71.2±3.8 d	4.63±0.13 x

^{a,b} Means followed by the same letters are not significantly different at the 5% level by SCHEFFE's test.

Table 2. Pre-oviposition period and number of eggs per egg-pod produced by *O. c. formosana* under various photoperiodic conditions at 25°C

Photoperiod ^a	No. of females ^b	Pre-oviposition periods ^c (days mean $\pm$ S.D.)	No. of egg-pods examined	No. of eggs/egg-pod ^d (mean $\pm$ S.D.)
12L throughout	21	31.7 $\pm$ 9.5 a	23	28.8 $\pm$ 7.9 x
12L $\rightarrow$ 14L	7	24.7 $\pm$ 12.1 a	33	35.9 $\pm$ 10.0 y
14L $\rightarrow$ 12L	6	36.0 $\pm$ 7.6 a	16	33.4 $\pm$ 7.2 xy
14L throughout	18	67.8 $\pm$ 33.9 b	18	31.1 $\pm$ 7.9 xy

^a 12L $\rightarrow$ 14L: transferred from LD12:12 to LD14:10 on adult emergence, 14L $\rightarrow$ 12L: transferred from LD14:10 to LD12:12 on adult emergence.

^b Nine out of 18 females oviposited within 100 days after adult emergence at 14L.

^{c,d} Means followed by the same letters are not significantly different at the 5% level by SCHEFFE's test.

5 stadia. Development time was significantly shorter in the 5-stadium type than in the 6-stadium type. At LD14:10, some females molted 7 times but all males underwent 6 molts (Table 1). The nymphal period of the 7-stadium-type females was extended by about 20 days from that of the 6-stadium-type females. Thus, the increased development time at the long photoperiod can be ascribed to the increased number of nymphal stadia. The 6-stadium-type males and females took longer to mature under LD14:10 than under LD12:12. Therefore, the development rate could be modified by photoperiod even without variation in the number of stadia.

The mean adult head width was greater at LD14:10 than at LD12:12 in the 6-stadium-type females, but no difference was observed in the 6-stadium-type males. The females were significantly larger than the males in each photoperiod (SCHEFFE's test $p < 0.01$).

Pre-oviposition period

Nine out of 18 females reared at LD14:10 oviposited sporadically from days 30 to 97 of their adult life, but the remainder failed to lay egg-pods within 100 days after adult emergence. Females transferred from LD14:10 to LD12:12 on adult emergence oviposited by day 51, and those reared at LD12:12 by day 64 (Table 2).

Egg development

Figure 1 shows the hatching pattern at 25°C in eggs deposited under natural daylength in a glasshouse in Hirosaki. Seventy-four percent of the eggs hatched from week 5 to 7 of incubation and a clear peak of hatching occurred in week 6. The remaining 26% of the eggs hatched sporadically from week 8 to 35.

Figure 2 shows the effect of low temperature on diapause termination. Hatching occurred from day 9 to day 21 after the temperature increase, and 59% of the eggs hatched synchronously on day 15 regardless of large differences in the incubation periods (about 10 weeks) before the cold treatment.

Table 3 shows the effect of parental photoperiods on the incidence of diapause at 25°C. From Fig. 1, eggs hatching within 7 weeks were regarded as non-diapausing and those hatching after 8 weeks as diapausing. The percentage of diapause did not differ significantly between LD14:10 and LD12:12. When individuals were transferred from LD14:10 to LD12:12 on adult emergence, the incidence of diapause was slightly lower

Fig. 1. Hatching pattern at 25°C in eggs laid by females of *O. c. formosana* under natural daylength in a glasshouse in Hirosaki. Dots represent less than 1% hatching.

Fig. 2. Effect of low temperature on the termination of egg diapause of *O. c. formosana*. Diapausing eggs remaining unhatched for 100–172 days at 25°C after deposition were exposed to 15°C for 90 days and then returned to 25°C.

Table 3. Percentage of diapause eggs per egg-pod laid by *O. c. formosana* under various photoperiodic conditions at 25°C

Rearing photoperiod ^a	No. of egg-pods	No. of eggs	% of diapause eggs ^{b,c} (mean ± S.D.)
12L throughout	23	580	24.1 ± 21.2 b
12L→14L	33	1,117	7.5 ± 11.5 a
14L→12L	16	476	17.4 ± 26.0 ab
14L throughout	18	527	38.6 ± 35.9 b

^a 12L→14L: transferred from LD12:12 to LD14:10 on adult emergence, 14L→12L: transferred from LD14:10 to LD12:12 on adult emergence.

^b Egg-pods were incubated at 25°C.

^c Means followed by the same letters are not significantly different at the 5% level by SCHEFFE's test.

than that at LD12:12. When photoperiod was shifted from LD12:12 to LD14:10, the percentage entering diapause was significantly lower than that at LD12:12 or LD14:10. The percentage of diapause varied among the egg-pods laid by the same females and no consistent sequential change in the incidence of diapause was observed in egg-pod production by females.

DISCUSSION

The subtropical rice grasshopper, *Oxya chinensis formosana* showed a short-day-type photoperiodic response in nymphal development at 25°C. A modification of the number of molts and the development rate were involved in the response. A similar response is found in the temperate rice grasshopper, *Oxya yezoensis* (ICHITA, 1992) and in some temperate univoltine crickets, *Teleogryllus emma*, *T. yezoemma*, *Velarifictorus* (= *Scapsipedus*) *micado*, all of which overwinter as eggs (MASAKI, 1966, 1967; SAEKI, 1966). The short-day-type response in nymphal development would program adult emergence to occur in autumn, to ensure that eggs be laid in autumn, and thus overwintering would be in the egg stage.

Females reared at LD14:10 throughout post-embryonic development oviposited later than those reared at LD12:12 throughout and those transferred from LD12:12 to LD14:10 on adult emergence or vice versa. This revealed that both nymphal and adult stages were sensitive to photoperiod. This response as well as the short-day-type response in nymphal development would contribute to the program for autumnal oviposition.

The present study revealed that this grasshopper has an egg diapause when eggs are incubated at 25°C. Some eggs entered diapause but most hatched without delay irrespective of the parental photoperiod. No significant difference was observed in the percentage of diapause in eggs between mothers exposed to short-day and long-day.

In the lesser migratory grasshopper *Melanoplus sanguinipes*, facultative diapause of eggs was controlled by a decreasing change of photoperiod rather than by constant photoperiods (DEAN, 1982). Similarly, in the Australian plague locust *Chortoicetes terminifera*, egg diapause was prevented by an increase in photoperiod but enhanced when the photoperiod decreased (WARDHAUGH, 1980). In *O. chinensis formosana*, the incidence of egg diapause was not enhanced by a decrease in photoperiod from LD14:10 to LD12:12 on adult emergence, but was lowered by an increase in photoperiod from LD12:12 to LD14:10. The fact that many hatchlings of *O. chinensis formosana* occur in spring in the field (OHSHIRO, 1986) suggests that egg-overwintering is commonplace and that a certain factor(s) might evoke a higher incidence of diapause in the field than in the present experiment. The effect of temperature during various life stages on the induction of egg diapause should be examined in the future.

Egg diapause occurs in other subtropical insects, such as *Dianemobius fascipes* (MASAKI, 1990) and *Cavelerius saccharivorus* (FUJISAKI, 1993). The egg diapause in these species is programmed by the mother responding to short days. It is opportunistic in both its manifestation and termination. The opportunistic characteristics in diapause should be examined in *O. chinensis formosana* in a future study.

First- to penultimate-stadium nymphs and adults were collected in the Ryukyu Islands in April 1995, but the majority were first- to third-stadium nymphs (unpublished data). This and the present results suggest that a majority of the population have a heterodynamic life cycle with a short-day type photoperiodic response that controls both nymphal development and reproduction and also with diapause in a portion of the eggs.

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