Effects of Photoperiod and Age of Rice Plant on Larval Development in Two Geographic Ecotypes of Chlorops oryzae MATSUMURA (Diptera: Chloropidae)

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When larvae of the Akita strain (bivoltine, 39°N) of Chlorops oryzae MATSUMURA were reared on rice-plant seedlings younger than the 4 leaf stage under LD12:12 or 14:10, most pupated 25 days after hatching. Under long day conditions (LD15:9), by contrast, most larvae failed to pupate and remained in the first or second larval stage 25 days after hatching when reared on 7-leaf-stage seedlings. On the other hand, larvae of the Aichi strain (trivoltine, 35°N) reared on rice seedlings of the 5 leaf stage or younger grew fast under both short and long days. Larval development was delayed under an intermediate day (LD14:10). This suppression of larval development in the Aichi strain became more marked as the rice plants aged. These results suggest that larval development in the first generation of the bivoltine strain and the second generation of the trivoltine strain is retarded by photoperiodic and host-plant conditions. This retarded development in the early larval stage may be regarded as diapause mediated by food plant and photoperiod.

Key words: Chlorops oryzae, photoperiod, rice plant age, larval development, diapause

INTRODUCTION

The rice stem maggot, Chlorops oryzae MATSUMURA (Diptera: Chloropidae), is an important pest of paddy rice plants. This species is distributed throughout Japan and two geographic ecotypes have been recognized (IWATA, 1963; HIRAO, 1970). The main criterion for distinguishing these ecotypes is voltinism: one is the northern bivoltine type and the other the southern trivoltine type.

In the bivoltine area, the maggot overwinters as a first-stadium larva inside the stem of Gramineae. In June, the larvae feed on young panicles of their hosts and pupate inside the leaf sheath after head formation of the plant. Adults of the overwintering generation oviposit on rice plants at the tillering stage from late June to early July. Newly hatched larvae burrow into the stem of rice plants and move to the growing points where they feed on developing leaves. First-generation larvae remain in the first larval stage while feeding on developing leaves. They mature after feeding on young panicles and pupate after head formation of their hosts. Adults of the first generation emerge in early September and oviposit on Gramineae. Larval development in the first generation is inhibited under natural conditions until the time of feeding on young panicles (HIRAO, 1970). However, he also showed that first-generation larvae could pupate without feeding on young panicles when

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reared successively on young rice seedlings by transferring to new seedlings at two week intervals, and the entire larval stage was about 70 days.

In the trivoltine area, larvae hibernate and pupate as in the bivoltine area, but the adults of the overwintering generation emerged and oviposit on rice plants from mid-May to early June. The first-generation larvae grow rapidly and pupate only after feeding on developing leaves of rice plants at the early tillering stage. The first-generation adults again oviposit on rice plants at the panicle formation stage in mid-July. The second-generation larvae remain in the first larval stage during feeding on developing leaves, and mature after feeding on young panicles. Adults of the second generation oviposit on Gramineae from late September to early October. IWATA (1960, 1963) compared larval development between the first and second generations of the trivoltine strain by rearing on rice plants of various growing stages. He showed that larval development was slower in the second generation than in the first generation when the larvae were reared on young rice seedlings. However, the second-generation larvae could grow to the pupal stage feeding on developing leaves of young-rice seedlings. When the larvae infested rice plants of the 9 to 11 leaf stages, larval development in both generations was retarded. Thus, larval development in *C. oryzae* is strongly affected by the growing stage of rice plants.

Recently, the photoperiodic responses during development, and winter and summer diapauses of *C. oryzae* have been elucidated (TAKEDA and NAGATA, 1992). Both the egg and larval stages are sensitive to photoperiod. Short days during the egg and larval stages induce and maintain winter diapause in the first-stadium larval stage (TAKEDA, 1996). On the other hand, long days during the egg stage avert winter diapause and these larvae respond to summer-diapause inducing photoperiod (TAKEDA and NAGATA, 1992). The effects of photoperiod and temperature on the duration of each stadium in the non-winter-diapause larvae have been elucidated by rearing on young-rice seedlings (TAKEDA, 1997). Pupation in the bivoltine (Akita, 39°N) strain was synchronized under both short and intermediate days with a larval duration of about 14 days. Under LD15:9 at 23°C, the complete larval stage of the bivoltine strain was about 70 days because the mature larval stage lasted 40 days. Larval durations in the trivoltine (Aichi, 35°N) strain were 14 and 16 days under LD12:12 and 15:9, respectively. Under LD14:10 at 23°C, larval duration was 34 days including the mature larval stage of 16 days. These results indicate that the bivoltine and trivoltine ecotypes enter a summer diapause in the full-grown larval stage under long and intermediate days, respectively. However, there was no clear influence of photoperiod on development in the early larval stage of the two geographic ecotypes. These results were obtained using young-rice seedlings with 1 to 2 leaves so that they might not reflect the actual responses in the field, as mentioned above. In the present study, therefore, the effects of photoperiod and age of rice plants (summer host) were investigated using the two geographic ecotypes of *C. oryzae*.

**MATERIALS AND METHODS**

The maggots for this study came from two laboratory strains of *C. oryzae*. The Akita (bivoltine) strain originated from a field collection at Sen-nan (39°N22′N, 70 m altitude), Akita Prefecture, in 1989. The Aichi (trivoltine) strain was originally collected at Inazawa (35°13′N, 2 m altitude), Aichi Prefecture, in 1989. Eggs of their progeny were exposed to a photoperiod of LD15:9 at 25°C and the larvae were reared under LD12:12 at 20°C. These alternating photoperiods avert both winter (the egg stage) and summer (the larval stage)
diapauses. The rice cultivar “Kenbaiwai” was used for rearing.

In the present study, the egg stage was exposed to LD15:9 at 25°C. Newly hatched larvae were individually inserted into the leaf sheath of the rice plants (TAKEDA and NAGATA, 1992). The infested rice plants were kept in bioclimatic chambers under artificial light conditions (four 400 W lamps). The larvae were reared under three photoperiods (LD12: 12, 14:10 and 15:9) at temperatures alternating between 25°C (7.00–19.00 h) and 20°C (19.00–7.00 h). The rice plants were dissected to collect larvae and pupae at day 25 after hatching. Living larvae were classified into the three larval stages by the morphology of the posterior spiracles and third stadium larvae were further divided into the feeding and mature stages (TAKEDA and NAGATA, 1992; TAKEDA, 1993).

The resistance of rice plants to the rice stem maggot varies among different varieties (YUSHIMA and TOMISAWA, 1957; KOYAMA, 1970). Most larvae reared on the highly resistant

Table 1. Growth stage as represented by mean leaf number of rice plants when newly hatched larvae were introduced

<table>
<thead>
<tr>
<th>Days after sowing</th>
<th>Mean leaf number (range)(^a)</th>
</tr>
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<tbody>
<tr>
<td>5</td>
<td>1.5</td>
</tr>
<tr>
<td>8</td>
<td>3.0 (2.8–3.0)</td>
</tr>
<tr>
<td>14</td>
<td>4.0 (3.8–4.1)</td>
</tr>
<tr>
<td>28</td>
<td>5.5 (5.1–5.8)</td>
</tr>
<tr>
<td>44</td>
<td>7.2 (6.4–7.8)</td>
</tr>
</tbody>
</table>

\(^a\) Leaf number includes incomplete leaves.

Fig. 1. Effects of photoperiod and age of rice plants on larval development in the two geographic ecotypes of C. oryzae. Developmental stages of C. oryzae examined 25 days after hatching. Eggs were kept under LD15:9 at 25°C. Larvae were reared under LD12: 12, 14:10 or 15:9 at 25°C (7.00–19.00 h) and 20°C (19.00–7.00 h). Sample size for each treatment is 11–24 (mean 19.4). 1: first larval stadium; 2: second larval stadium; 3: third larval stadium; M: mature third larval stadium; P: pupae.
variety died in the early larval stages. Forty-five varieties have been screened in the field, and some varieties such as “Ou-227” were highly susceptible (TAKEDA and SUZUKI, 1985). Therefore, the highly susceptible rice variety (“Ou-227”) was used for rearing the maggot to elucidate the effect of the growing stage of the rice plant on larval development. Germinated rice seeds were sown in seed-boxes with 1.0 g of compound fertilizers containing N, P and K in early September. The rice plants were kept in a greenhouse under otherwise uncontrolled environmental conditions before newly hatched larvae were introduced. Table 1 shows the mean plant age as defined by the leaf number when newly hatched larvae were introduced. Some underdeveloped rice plants were cut off before the introduction of newly hatched larvae; there was no overlapping in the range of leaf number among the introduction times.

RESULTS

Figure 1 shows the effects of photoperiod and age of the rice plant on larval development in C. oryzae. Most larvae of the Akita (bivoltine) strain reared on 5- to 28-day-old rice plants pupated under LD12:12. When Akita larvae were reared on 44-day-old rice plants under LD12:12, 55% of them pupated. Under LD14:10, most larvae pupated when reared on 5- to 14-day-old rice plants, but on 28-day-old or older rice plants the percentage of pupation was lower under LD14:10 than under LD12:12. When Akita larvae were reared on 44-day-old rice plants under LD14:10, the percentage of first and second instars were 10 and 25%, respectively. On the other hand, most larvae failed to pupate under LD15:9 irrespective of the growing stage of the rice plants. Larval development was retarded and highly variable under LD15:9 and the percentage of first and second instars at day 25 increased with the age of the rice plants. When Akita larvae were reared on 44-day-old rice plants under LD15:9, 92% remained in the first larval stage.

Twenty-five days after hatching, most individuals of the Aichi strain reared on 5- to 28-day-old rice plants pupated and the remainder reached the third-stadium larval stage under LD12:12 and 15:9 (Fig. 1). When Aichi larvae were reared on 44-day-old rice plants, most reached the mature larval stage or pupal stage in 25 days under LD12:12, but 70% remained in the third feeding larval stage under LD15:9. On the other hand, most larvae failed to pupate in 25 days under an intermediate photoperiod (LD14:10). When Aichi larvae were reared on 44-day-old rice plants under LD14:10, 19% of the individuals remained in the second-stadium larval stage.

The survival rates (number of insects surviving/number of insects that bored into the stem) in the Akita and Aichi strains ranged from 68.8 to 100% (mean 89.9%) and from 73.7 to 100% (mean 94.5%), respectively. Although the rice variety was highly susceptible to the maggot, the survival rate tended to decrease with the age of the rice plants.

DISCUSSION

The bivoltine strain (Akita, 39°N) developed without delay under short and intermediate photoperiods when newly hatched larvae burrowed into the stems of young rice seedlings (1.5 to 4.0 leaf stage). In contrast, larval development was retarded and highly variable under long day (LD15:9). This photoperiodic response agrees with the result obtained by TAKEDA and NAGATA (1992). The present results clearly demonstrated that photoperiod and the age of rice plants strongly affected larval development. Larval development in the
bivoltine strain was slower on older rice plants than on younger ones. When Akita larvae were reared on 7-leaf-stage seedlings under LD15:9, most remained in the first larval stage for at least 25 days. Thus, the inhibition of larval development was caused by a long day and aged summer host. 

Under short and long days, most larvae of the trivoltine (Aichi, 35°N) strain pupated when reared on young seedlings of the 1.5 to 5.0 leaf stage. On the other hand, most larvae failed to pupate under an intermediate photoperiod (LD14:10). This photoperiodic response agrees with the results obtained by TAKEDA and NAGATA (1992). Under LD14:10, in the present study, the retardation of larval development became more marked with the age of the rice plants. It appears that the modes of larval development under long and intermediate days correspond to those in the first and second generations of the trivoltine ecotype, respectively. Larvae of the first generation develop quickly on young rice seedlings in June (long days), but larval development in the second generation is retarded when they feed on developing leaves of older rice plants from late July to early August (intermediate days).

Larvae of the first generation in the bivoltine ecotype and the second generation in the trivoltine ecotype cease to grow in the first larval stage while feeding on developing leaves in the field (IWATA, 1963; HIRAO, 1970). Probably, long days (early summer) and the summer host plant at the tillering stage induce inhibition of larval development, and thus enforce a bivoltine life cycle. Similarly, the inhibition of larval development in the trivoltine ecotype is caused by intermediate days (midsummer) and the condition whereby the rice plant is immediately before panicle formation. When insects are reared on 7-leaf-stage seedlings, the inhibition of larval development is greater in the bivoltine strain under LD15:9 than in the trivoltine strain under LD14:10. This difference between the bivoltine and trivoltine strains may be due to a difference in response to the growing stage of the rice plants. IWATA (1960) pointed out that larval development in the trivoltine strain was inhibited while larvae fed on developing leaves of rice seedlings at the 9 to 11 leaf stage. Further study is needed to elucidate larval development in the trivoltine strain reared on rice plants immediately before the panicle formation stage under intermediate photoperiods.

Quiescence is a result of direct inhibition of development by adverse environmental conditions. Diapause includes all other cases of suppression of morphological development (DANKS, 1987). In C. oryzae, aging of the summer hosts inhibited larval development, but the degree of inhibition varied with photoperiod. Although larval development is not completely inhibited, the delayed development related to the age of summer hosts and photoperiod may be regarded as diapause.

The bivoltine ecotype and trivoltine ecotype enter a summer diapause in the full-grown larval stage under long and intermediate days, respectively (TAKEDA, 1997). The food supply is the most critical selection factor for the evolution of summer diapause (MASAKI, 1980). HIRAO (1970) reported that the duration of the first larval stage varied from 35 to 60 days depending on the time of head formation of the rice plants in the bivoltine area. He concluded that larvae of the bivoltine strain matured after feeding on young panicles under natural conditions. The maggot, which never leaves the infested stem, feeds on developing leaves and finally on young panicles (KOYAMA, 1970). Thus, young panicles of host plants terminate this food-mediated diapause and accelerate larval development regardless of photoperiod. On the other hand, the third-stadium larval stage is most sensitive to the summer-diapause-inducing photoperiod (TAKEDA, 1997). Subsequently, C. oryzae enters photoperi-
odically controlled summer diapause in the mature larval stage after feeding on young panicles of the host.

In the transitional zone, where the two ecotypes and their hybrids coexist, the early hatching group grew rapidly but the late hatching group developed slowly (IWATA, 1963). He also reported that the rate of the slow developing type in the average hatching group increased with the age of the rice plants. The time of oviposition by the overwintered generation is closely related to post diapause development, and this in turn determines the growing stage of rice plants available for larval development in the summer generation. Thus, the sequence of developmental responses appears to be one of the most important selection factors for volitism in the transitional zone. The early hatching larvae infest young rice plants under long days and develop to the pupal stage without entering diapause. The late hatching larvae infest older rice plants under long days and enter a food-mediated diapause in the early larval stage. This food-mediated diapause in the bivoltine type may enforce a discrete variation in development time in the transitional zone.

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REFERENCES


