Migration and Dispersal after Hibernation in the Rice Leaf Beetle, *Oulema oryzae* KUWAYAMA (Coleoptera: Chrysomelidae)

Takashi KIDOKORO

*Miyagi Prefectural Agricultural Research Center, Takadate, Natori, Miyagi 981-12, Japan*

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The adult movement from overwintering sites to paddy fields and the subsequent dispersal of the rice leaf beetle, *Oulema oryzae*, was studied. As the ovarian development after the resumption of feeding was very rapid, the occurrence of immigration into paddy fields could be assessed by the daily change in the density of immature females, which fluctuated in parallel with the daily maximum temperature. It was inferred, therefore, that the immigration was triggered by high temperature. The variation in time of immigration from year to year could also be explained by temperature. The dispersal after immigration was favored by warm and calm weather, and the absence of females also promoted the movement of males. The timing of migratory movement after hibernation seems to be adapted to the food supply in the original habitat conditions, and the temporal relationship between the movement to paddy fields in the spring and the planting of rice would have a great impact on the population dynamics of this insect.

INTRODUCTION

The rice leaf beetle, *Oulema oryzae*, is an important pest of rice plant in the northern districts of Japan. Injury by this insect has increased in recent years as the introduction of a new planting method has advanced the planting time of rice (IWATA, 1975; KISHINO and SATO, 1977).

In Miyagi Prefecture, the adults are in a dormant state for about ten months mainly under the sheath of several kinds of gramineous plants. They usually begin to fly to paddy fields from mid- or late May, feed on rice leaves and lay eggs *en masse* at intervals for one month. The larvae feed on leaves and pupate in cocoons. Adults of the next generation appear from early July and feed for a short period until their fat bodies fully develop. From mid-July they begin to migrate to aestivo-hibernating sites where they are in diapause till the next spring. This univoltine life cycle is maintained throughout the whole range of distribution (KUWAYAMA, 1932). Thus, this species belongs to a class III migrant as defined by JOHNSON (1969).

The immigration time and mode of dispersion of adults after hibernation are of primary importance for predicting the injury by the larvae. Thus this paper deals with some aspects of migration and dispersal of overwintered adults. The term immigration will be used here to designate the movement from overwintering to breeding sites, paddy fields, the term emigration the movement in the reverse direction, the term dispersal the movement within breeding sites.
MATERIALS AND METHODS

The rate of adult immigration from hibernating sites to paddy fields was estimated by the number of immature females in a paddy field close to the overwintering site. From 1977 to 1980, about 60 individuals were sampled at intervals of one or several days from the same paddy fields at Natori and examined for ovarian development and sex ratio ($\varphi/\varphi + \delta$) under a dissecting microscope. In 1979 censuses of the adult population were made in a sampling plot of about one hundred or several hundred hills from 2 to 3 p.m.

The following developmental stages of ovary were distinguished (Fig. 1): (stage 1) the ovary is small and white; (stage 2) the lower part of the ovariole is swollen slightly and yellow; (stage 3) large eggs are formed but the chorion is still soft; (stage 4) the ovary is filled with mature eggs, and (stage 5) the ovary shows a sign of degeneration. The first two stages were not distinguished in 1977 and 1978.

The periods of time taken to develop from stage 1 to stages 2, 3 and 4 were 1, 2 and 2 or 3 days, respectively, when adults that had just emerged from the hibernating site were reared on rice seedlings at room temperature under natural conditions of photoperiod. Some adults, however, remained in diapause and showed no ovarian development even after ten days of rearing.

In order to follow the movement of beetles, censuses were made at various distances from the overwintering site in 1977. In some cases adults were released in the paddy field and the subsequent reduction in their number was examined to learn the dispersive activity. Details of these methods will be mentioned later. The meteorological data recorded by the Sendai District Meteorological Observatory, located about 10 km north of the census fields, were available for an analysis of weather effects.

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![Fig. 1. Showing the stages of ovarian development in Oulema oryzae. For explanations see text.](image-url)
RESULTS

Immigration time

The seasonal changes in the proportion of females at different stages of ovarian development in 1979 are shown in Fig. 2. The females were all immature (stage 1)

![Graph showing seasonal changes in proportion of females at different stages of ovarian development.]

Fig. 2. Seasonal change in the proportion of females at different stages of ovarian development. For the stages see Fig. 1.

![Graph showing seasonal changes in density of all adults and immature females (stage 1) per 100 hills and the daily maximum temperature.]

Fig. 3. Seasonal changes in density of all adults and immature females (stage 1) per 100 hills and the daily maximum temperature.
when the first sampling was made on May 21. The ovary developed at a high rate, and females with mature eggs began to appear from May 23. Most females were fully matured by the end of May. Degeneration of ovary was observed from mid-June and immature females began to appear again from late June, which undoubtedly indicated the alternation of generations. The immigration from the hibernating site might have continued for about a half month, because immature females of the hibernated generation were found from May 21 to June 6. However, the proportion of females was subject to irregular daily fluctuation. In order to clarify this fluctuation of immigration activity, the density of immature females was assessed from total adult density, sex ratio and the proportion of immature females (stage 1) in the samples.

As shown in Fig. 3, two clear peaks appeared on May 22 and May 28, respectively, in the number of immature females. These peaks probably represent the separated periods of mass immigration in 1979. Males immigrated simultaneously with females, because the sex ratio did not deviate significantly from 0.5.

Effects of meteorological conditions

High temperature seems to promote the exodus from the hibernating site, because beetles were observed to emerge, crawl up the plants and take off when the weather was fine and the air temperature rose as reported by Igarashi and Irô (1959). As shown at the bottom of Fig. 3, the fluctuation of maximum temperature correlated well with that of the number of immature females. The latter was small or decreased when the temperature was low, while it was large or increased when the temperature was high.

![Fig. 4. Seasonal changes in the proportion of immature females (stages 1 and 2) and the daily maximum temperature in different years.](image-url)
Immigration seems to begin when the daily maximum temperature rises to about 20°C and mass immigration may occur when it is above 25°C.

The adults after emergence from hibernation or even after immigration into paddy fields were still reversible in their behavior. When the temperature fell below a certain point, some crawled underneath the blade sheath of grasses or rice plants again. This was in agreement with the partial persistence of diapause observed in those beetles reared just after the emergence from hibernation, as stated before.

*Yearly fluctuation of immigration time*

From the observations stated above, it might be expected that the timing of immigration varies from year to year depending on temperature conditions. In 1977 and 1978 the number of immature females could not be precisely determined because the population census was not always accompanied by sampling for dissection. When the ovarian development was examined, stages 1 and 2 were not distinguished. Comparisons between the results in different years were therefore made only in terms of the proportion of females at stages 1 and 2 (Fig. 4).

Immigration as inferred from the proportion of immature females occurred faster in 1980 and 1979 than in 1978 and 1977, suggesting the faster colonization of breeding populations in these years.

The daily maximum temperature exceeded 25°C on May 21, 24 and 25 in 1980 and on May 22 and 28 in 1979. In 1978, however, it did not reach 25°C until May 27. The temperature rise was delayed further in 1977, and the 25°C level was not exceeded until June 3. These differences explain the variation in the timing of migratory activity of immature females. The great fluctuations in the proportion of immature females in 1980 and 1977 indicate suppression of the immigration activity by low temperatures. The second peak of immature females in these years might be caused by a mass immigration induced by a sudden rise in temperature. In fact, the density of adults rose from 1.3 per one hundred hills on May 20 to 20.3 on May 22 in 1980 and from 6.3 on May 31 to 23.1 on June 3 in 1977.

![Fig. 5. The relation between the adult or egg density per 100 hills of rice plant and the distance from the overwintering place on different days in June.](image-url)
Dispersal after immigration

The immigration and dispersal sequences were observed in the paddy fields surrounding an isolated patch of bamboo bush which was a suitable site for hibernation. In 1977, adult and egg densities were examined at different distances from the bamboo bush from June 3 when a mass immigration seemed to occur as mentioned above (Fig. 5).

The results suggest that adults did not fly a long distance on the first day of immigration from the bush. Thus on June 3 they stayed on rice plants close to the bush, then they gradually dispersed until June 17. This movement was clearly reflected in the distribution of eggs. As the result the seasonal trend of density vairied depending on the distance from the hibernating site (Fig. 6). At the plot 1 m from the hibernating site adult density was the highest on June 3 but at the plot 58 m apart on June 11. Although the seasonal trends of egg density were similar at the two plots, the initial increase occurred earlier in the plot close to the bush. As a consequence, new generation adults in this plot appeared from early July but not in the other plot.

Factors affecting the dispersal activity

In order to detect factors affecting the dispersal activity, 32 hills of rice plant in a paddy field (14.5 m²) were enclosed by a plastic board 20 cm in height. Three such quadrats were arranged about 20 m apart, and 60 females, 60 males, and 30 females with 30 males, respectively, were released on May 31 in 1978. The numbers remaining in the quadrats were counted every day at about 9 a.m. and 3 p.m. Another groups of 30 females with 30 males were released on June 14. The results together with the weather conditions are shown in Fig. 7.

When males only were released on May 31, the number decreased faster than in other two groups. This quick dispersal of the male in the absence of the female might be due to the female searching activity. The female seemed to be passive in searching for a mate, and the female group showed a similar trend to that of the mixed group.
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Fig. 7. Changes in number of adults after release in quadrats on May 31 (left) and June 14 (right) and weather conditions. Females only (closed circles), males only (open) and females with males (half closed) were released. The wind velocity is the mean of 10 min.

In all groups released on May 31 the number of beetles tended to decrease between 9 a.m. and 3 p.m., indicating that the dispersal flight mainly took place during the daytime. However, temperature might exert an important effect because beetles escaped from the quadrat even before 9 a.m. under warmer conditions (right figure).

Wind velocity seemed to be another factor controlling the flight activity. Thus, on June 1 the number of escaping beetles was very small even during the daytime when there was strong wind. Flying beetles were often observed on calm days but not on windy days.

DISCUSSION

The immigration of Oulema oryzae from hibernating site may be assessed quantitatively by its increasing density in paddy fields. However, the density in a given field is also affected by the dispersal movement after immigration and is therefore not always a good indicator of immigration. It has been shown that changes in the female reproductive system provide a means for analysing the seasonal life history (Kiritani, 1963). This was also the case in O. oryzae, and the examination of ovarian development was especially useful for analysing their immigration process because of the rapid ovarian development after moving into the paddy field.

The density of immature or immigrating females showed a conspicuous fluctuation
and its increase was closely correlated with the daily maximum temperature. Temperature also explained the difference in the seasonal trend of immigration from year to year. Together with the wind velocity, it controls the exodus from the hibernating site.

In some species of insects, the development after diapause termination is governed by the accumulated heat units and can be predicted on this basis as shown in Nephrotettix ciciniceps (Hokyo, 1971). In the case of O. oryzae after diapause, however, a high temperature is required to trigger mass immigration. For predicting the time of immigration, therefore, the fluctuation in temperature conditions is more important than the accumulation of heat units.

The present results show that the overwintered population begins immigration when the daily maximum temperature exceeds about 20°C and a temperature above 25°C may cause mass immigration, although the precise temperature limit for this activity is still to be determined. However, a high temperature occurring as early as early May did not induce immigration (Fig. 4), and the effects of the microclimatic conditions in the hibernating quarter or a photoperiodic response of hibernating adult should be investigated.

Heavy damage by larvae of this insect tends to occur in paddy fields close to hills where bushes provide a suitable hibernating site (Ishizaki and Hashida, 1951; Sekiguchi and Johraku, 1973). The present study has elucidated that this is due to the fact that adults do not fly a long distance from the hibernating quarters but alight on nearby rice plants.

As wild food plants for the larvae, only four gramineous plants have been recorded, i.e., Zizania latifolia, Leersia oryzoides, L. oryzoides var. sayanuka and Glyceris ishyroneura (Kuwayama, 1954). All these plants are perennial helophytes or hygrophytes growing in sunny places and are known as weeds in paddy fields. Except for man-made situations such as paddy fields, reservoirs or irrigation streams, common habitats of these plants are the margins of marshes, lakes or streams (Numata et al., 1975). Therefore, the rice leaf beetle might have been an inhabitant of such waterside habitats before the beginning of rice cultivation. High larval mortality under low humidity conditions (Emura and Kojima, 1978) also supports this inference. Bushes commonly grow around marshes, lakes and streams. Since there is a series of plant communities of different types along the moisture gradient in those places known as a “hydrarch succession” (Tagawa, 1973), the beetles might not be required to migrate over a long distance in search of shelters for hibernating.

All wild host plants sprout from late April or early May in northern Japan (Numata et al., 1975; Kidokoro, unpublished observations). In natural habitats, therefore, the beetles can utilize those food plants even when mass immigration occurs in mid-May, as actually observed in 1980. The beginning of rice cultivation has extended the area potentially available for breeding of this insect. Bushes growing in uncultivated land such as at the foot of hills, river banks and hedges are available for hibernation. However, the beetles leaving their hibernating sites in May could not find transplanted rice plants before the 1950s when the mature seedlings of rice were transplanted in early June. Only nursery rice plants or wild food plants were available for beetles emerging from hibernation in May. The patchy distribution of those food plants would not be readily accessible by this short-range migrant. The phenological gap between the seasonal food supply and the timing of movement between the breeding
and hibernating sites had thus been a major factor suppressing the population growth.

The situation was altered by the gradual advancement of the rice-planting time in association with the introduction of new cultivation practices. Especially, the machine planting of young seedlings began in the early 1970s, and this advanced the planting time from late May to early May in northern Japan. The early planting of rice provides suitable food for beetles when they leave hibernating sites even in mid-May and thus a situation resembling that in the original natural habitat. The temporal coincidence between the immigration and seasonal food supply may be the reason why the outbreak of this insect occurred after the introduction of machine planting of rice plants. This inference is supported by the fact that the leaf beetle also became a major pest in Hokkaido as the direct sowing of rice in late April became practiced from about 1925 to 1945 (Horiguchi, 1967).

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REFERENCES


