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Ovicidal Reaction of Rice Plants against the Whitebacked Planthopper, *Sogatella furcifera* HORVÁTH (Homoptera: Delphacidae)

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Association of the physiological egg mortality of *Sogatella furcifera* with the rice plant reaction of forming a watery lesion at oviposition sites was revealed: egg survival rate dropped to less than 20% in the watery lesion within 2 days after oviposition, while 88.8% of eggs developed to the eye-spot formation stage in the non-watery lesion, on rice plants 8 weeks after planting. *S. furcifera* eggs laid in large tillers and in the main stem suffered higher physiological mortality than those laid in small tillers on the same plant. The physiological egg mortality increased steadily with progression of the tillering of plants until 10 weeks after planting. Egg density did not affect the mortality. The importance of plant resistance as a factor determining the population growth pattern of *S. furcifera* is discussed.

Key words: *Sogatella furcifera*, ovicide, rice, plant reaction

INTRODUCTION

Trans-oceanic migrants of the whitebacked planthopper, *Sogatella furcifera* HORVÁTH, invading Japanese paddy fields in Baiu (rainy) season have been consistently increasing since the late 1970's (SOGAWA and WATANABE, 1989; MATSUMURA, 1991; NABA, 1992; IITOMI, 1992; WATANABE et al., 1994). This increase coincides with the prevalence in China of cultivating hybrid rice on which *S. furcifera* attains a population growth rate 10 to 20 times higher than that on traditional varieties (ZHU et al., 1984). As a consequence of population increase in the immigrant and subsequent reproductive generations, *S. furcifera* became established as a most serious pest of the rice plant in Japan, and since then, various new types of damage to rice by *S. furcifera* have been reported (NODA, 1986, 1987; KIYOTA and OKUHARA, 1990; ISIZAKI and MATSUURA, 1991; MATSUMURA, 1991). In western and southern Kyushu where immigrant *S. furcifera* population densities in Japan are highest, dark brownish discoloration of leaf sheaths induced by *S. furcifera* oviposition has become conspicuous. Heavy infestation thus suppresses the tillering and results in the death of affected plants in extreme cases.

SOGAWA (1991) revealed that the dark brownish discoloration is associated with a rice plant reaction that causes physiological death of *S. furcifera* eggs as evidenced by the low eye-spot formation rate of eggs. He further showed that, as a result of higher egg survival, the population growth rate of *S. furcifera* is ca. 6 times higher on varieties which scarcely exhibit the dark discoloration of leaf sheaths than on the Japonica variety Reiho which does exhibit it. SUZUKI et al. (1993) showed that the physiological death of eggs caused by plant reaction (hereafter referred to as physiological death) was responsible for 68.9 to 94.5% of the overall egg mortality of *S. furcifera* on the Hinohikari variety for a period of 5 to 10 weeks after transplanting in the field. They also pointed out that clarifying the factors which lead to physiological egg mortality are key to understanding the population dynamics of *S. furcifera*.

We reveal in this paper that the physiological death of *S. furcifera* eggs is associated with the formation of a watery lesion at the oviposition site. We further show the dependence of the physiological egg mortality on the position and growing stage of the rice plants, and the egg density. Implications of physiological mortality on the population growth pattern of *S. furcifera* are discussed.

MATERIALS AND METHODS

Insects. *S. furcifera* adults were obtained from a laboratory culture maintained on small seedlings of the Reiho variety at 25°C, 16L : 8D at Kyushu National Agricultural Experiment Station. The stock originated from adults collected from paddy fields in Chikugo, Fukuoka, in 1987. Experiments were carried out using gravid females 3 to 6 days after emergence.

Plants. Seedlings of the Reiho variety were planted individually in 220 ml plastic cups after 3 days incubation at 25°C following sowing. The seedlings were cultivated in an outdoor growth cabinet under a temperature cycle of 24°C from 6:00–20:00 h and 20°C from 20:00–6:00 h. To maintain the long photoperiod, the cabinet was artificially illuminated from 17:00 to 20:00 h for the period of September to March. Fertilizer was applied 4 and 8 weeks after planting. The number of tillers on the plants was recorded weekly.

Oviposition and survival check of eggs. *S. furcifera* females were released on rice plants individually covered by a cylindrical clear plastic cage equipped with a tetron gauze cap except for the experiment on the effect of oviposition sites on egg survival. Females were allowed to oviposit in a room controlled at 25°C under a 16L : 8D photoregime, and, after the females were removed, the plants were kept in the room for 5 days prior to dissection unless otherwise noted. The plants were dissected under a binocular microscope and eggs were observed. Eggs bearing eye-spots at dissection were considered as survivors, because a preliminary experiment showed that 100.0% ($n = 299$) of healthy eggs that finally hatched developed to the eye-spot formation stage within 5 days after oviposition at 25°C.

Plant reaction against oviposition. Eight females were released for 3 h on each of 8 plants 8 weeks after planting. The oviposition sites found on 4 plants were marked in permanent ink after the termination of oviposition and observed every 12 h for the first 2 days and daily thereafter until the end of hatching. The 4 other plants were dissected 5 days after oviposition to determine the rate of egg survival.

Survivorship curve of eggs in watery and non-watery lesions. Twenty-four females were released on each of 8 plants for 3 h 8 weeks after planting. A total of 8 tillers, one tiller per plant, was dissected immediately after oviposition and then at intervals of 12 to 24 h for 4 days. Eggs obtained from the watery and non-watery lesions were maintained separately on wet filter paper in a Petri dish to check the survival 5 days after oviposition. The remaining tillers were dissected 6 days after oviposition.

Effect of oviposition site on physiological egg mortality. Females were individually confined in parafilm sashes (SOGAWA, 1992) attached to 9 different positions in each of 5 8-week-old plants. The females were thus forced to lay their eggs on specific sites for 1 day. Tillers were classified based on the width 3 cm above the soil into large (≥ 4 mm) and small (< 4 mm). Five days after oviposition, the oviposition sites were dissected to check egg survival. The egg survival rate calculated for each female was arcsine-transformed for statistical analysis.

Effect of rice stage. To compare egg survival among the different rice stages, 1 to 10-week-old plants were exposed to females for 2 days. The number of females released was

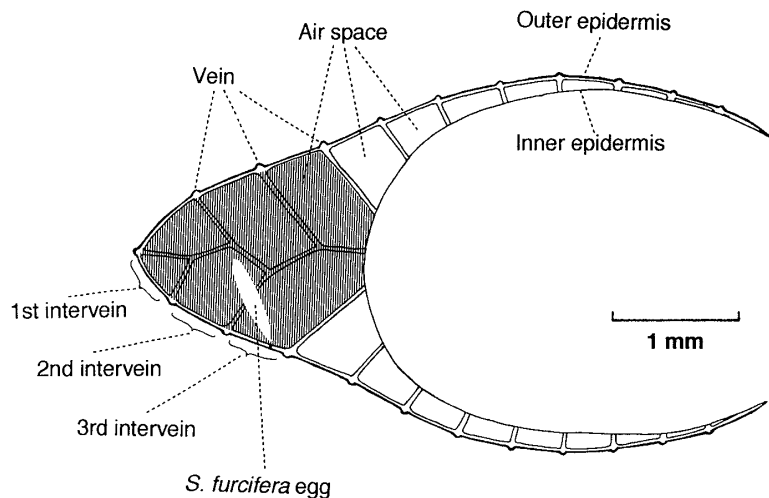


Fig. 1. Schematic drawing of cross section of leaf sheath bearing a watery lesion (shaded area).

increased with growth of the plant so that it was roughly proportional to the number of tillers per plant: 1, 2, 4, and 8 females to a plant at 1, 3–5, 6, and 7–10 weeks after planting, respectively. The number of replications was decreased from 10 to 4 as the number of released females increased. After termination of oviposition, the plants were maintained at 25°C under a 16L : 8D photoregime for 5 days. The plants were kept in 70% ethanol for about 1 month prior to dissection.

Effect of egg density. Females were released for 2 days on 8-week-old plants at a rate of 2, 8 and 32 females per plant, with replications of 8, 4 and 4, respectively. The plants were left at 25°C for 5 days, kept in 70% ethanol for a month, and then dissected.

RESULTS

Plant reaction against oviposition

S. furcifera females laid their eggs in masses into air spaces in the parenchymal tissue of leaf sheaths and midribs of leaf blades. When eggs were deposited in leaf sheaths, the cut for oviposition was made parallel to the vein predominantly in the 2nd to 4th interveinal surface layers, and eggs penetrated the wall of parenchymal cells so that the anterior and posterior ends of eggs projected into two adjacent air spaces (Fig. 1). Vascular bundles located beneath the veins were rarely damaged by oviposition.

The first conspicuous change occurring at the oviposition site was the formation of a watery lesion. Up to 11 rows of air spaces including those containing eggs were partially or fully filled with fluid within 12 h after oviposition. A typical cross section of a leaf sheath bearing a watery lesion is illustrated in Fig. 1. The watery lesion was variable in size and not always formed. The formation rate was particularly low on small tillers. Formation of a watery lesion caused the necrosis of parenchymal cells in the lesion. The epidermis around the cut made by oviposition gradually turned darkish brown in color. Such discoloration was restricted to the edges of the cut in non-watery lesions, while it usually spread to form a patchy 'oviposition mark' in watery lesions. Senescence of the whole leaf sheath proceeded promptly when watery lesions were heavily formed.

The survival rate of *S. furcifera* eggs to the eye-spot formation stage was significantly lower in the watery lesion than in the non-watery lesion, where the latter category included

Table 1. Comparison of egg mass size and egg survival rate between watery and non-watery ovipositional lesions

| Ovipositional lesion | No. of egg masses | No. of eggs | Egg mass size ^a (Mean \pm SD) | Egg survival rate ^b (%) |
|----------------------|-------------------|-------------|---|---------------------------------------|
| Watery | 172 | 1,163 | 6.8 \pm 4.07 | 22.8 |
| Non-watery | 58 | 411 | 7.1 \pm 3.59 | 88.8 |

^a Means are not significantly different by a STUDENT'S *t*-test ($p > 0.05$).

^b Means are significantly different by a *G*-test ($p < 0.001$).

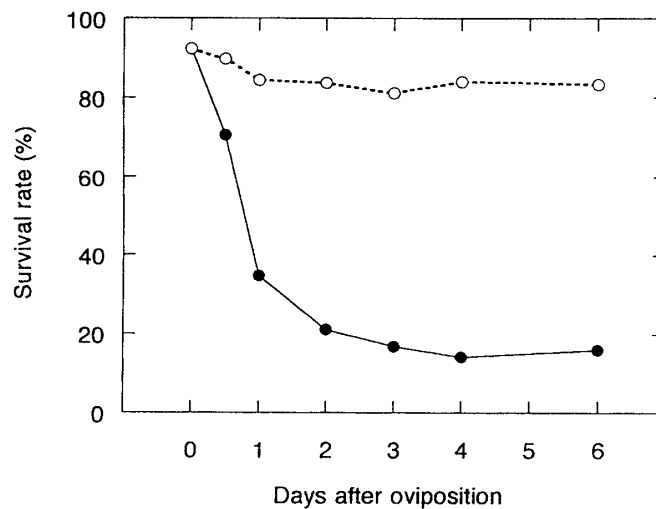


Fig. 2. Survivorship curve of *S. furcifera* eggs in watery (solid line) and non-watery (dotted line) lesions.

oviposition sites in which the presence of liquid was undetectable or the formation of a watery lesion was minimal and never extended to more than one row of air space (Table 1). Eggs immersed in the liquid of a watery lesion often became swollen or shrunk as the chorion was broken. Dead eggs were often uniformly colored tawny or brown, a similar pigmentation occurring in the surrounding necrotic parenchyma. There was no significant difference between the mean size of egg masses in watery and non-watery lesions.

Survivorship curve of eggs in watery and non-watery lesions

The survivorship curves of *S. furcifera* eggs laid in plant tissue were obtained on the basis of the survival rate of eggs that were removed from the plant to wet filter paper (Fig. 2). The survival rate immediately after the termination of 3-h oviposition was 92.7%. At that time the watery lesion was usually not yet formed. In oviposition sites where a watery lesion was formed, egg survival sharply dropped between 0 to 2 days after oviposition, particularly between 12 and 24 h. Further delay in the removal of eggs from the lesion did not significantly affect egg survival. In contrast, the survival rate of eggs in non-watery lesions remained high until 6 days after oviposition, though it dropped slightly between 0 and 24 h after oviposition. These results indicate that *S. furcifera* eggs suffer a high physiological mortality rate at early stages of embryonic development through the formation of a watery lesion by rice plants.

Table 2. Comparison of the number of eggs laid per female and egg survival rate in *S. furcifera* forced to oviposit in different oviposition sites on 8-week-old rice plants

| Oviposition site ^a | | No. of eggs ^b (Mean ± SE) | % egg survival ^b (Mean ± SE) |
|-------------------------------|-------------------------|---|--|
| Main stem | Oldest LS | 37.5 ± 5.3 a | 16.0 ± 3.4 a |
| | Midrib of oldest LB | 27.2 ± 5.4 a | 25.8 ± 4.5 a |
| | 2nd oldest LS | 40.4 ± 3.7 a | 8.6 ± 2.4 a |
| | Midrib of 2nd oldest LB | 35.2 ± 3.7 a | 7.4 ± 3.2 a |
| Large tiller | Oldest LS | 41.0 ± 3.8 a | 26.5 ± 7.8 a |
| | Midrib of oldest LB | 37.8 ± 4.2 a | 17.0 ± 8.1 a |
| | 2nd oldest LS | 28.8 ± 6.1 a | 11.2 ± 2.7 a |
| | Midrib of 2nd oldest LB | 33.8 ± 3.2 a | 17.2 ± 4.0 a |
| Small tiller | Oldest LS | 36.2 ± 4.6 a | 63.9 ± 8.3 b |

^a LS and LB denote leaf sheath and leaf blade, respectively.

^b Means followed by the same letter in the column are not significantly different at $p = 0.05$ by a TUKEY pairwise comparison test with an arcsine-transformed value for egg survival.

Effect of oviposition site on physiological egg mortality

The number of eggs laid per female was not significantly different among the 9 different oviposition sites, although the difference in egg survival rate was significant (Table 2). The survival rate of eggs laid in the oldest leaf sheath was significantly higher on small tillers than on main stems and large tillers. The difference between the survival rate of eggs laid on the leaf sheath and those laid on the midrib of the leaf blade was insignificant for both the oldest and 2nd-oldest leaves. The survival rate tended to be higher on the oldest leaf than on the 2nd oldest leaf in both main stems and large tillers, although the difference was insignificant.

Effect of rice stage

Tillering of the rice plant started 3 weeks after planting. The number of tillers per plant increased in a sigmoid manner thereafter (Fig. 3). The egg survival rate was highest 1 week after planting, remained at a high level until 5 weeks after planting, and then decreased continuously as the tillering progressed. Formation of the watery lesion, which was indicated by the dark oviposition mark remaining on plants kept in 70% ethanol, was observed for plants 3 or more weeks after planting. However, the oviposition mark was found exclusively on the main stem, and the incidence was low on plants up to 5 weeks after planting.

Effect of egg density

Egg survival to the eye-spot formation stage ranged from 7.3 to 53.3% with a mean of 30.0% on 8-week-old rice plants exposed for 2 days to 2 gravid females (Fig. 4). This wide variation was partly due to differences in the oviposition sites among the batches. All eggs were laid in the main stem and/or large tillers (≥ 4 mm wide) of the 3 plants on which the egg survival rate was less than 10%, while in the other 5 plants, 50.0% of all eggs were laid on average in small tillers where the mean survival rate was as high as 52.7%. The variance of egg survival rate was smaller in plants exposed to 8 and 32 females, and the mean egg survival rates were 36.8% and 37.6%, respectively.

To determine whether egg density and survival rate are independent, SPEARMAN's rank correlation coefficient was calculated using pooled data; the correlation was insignificant

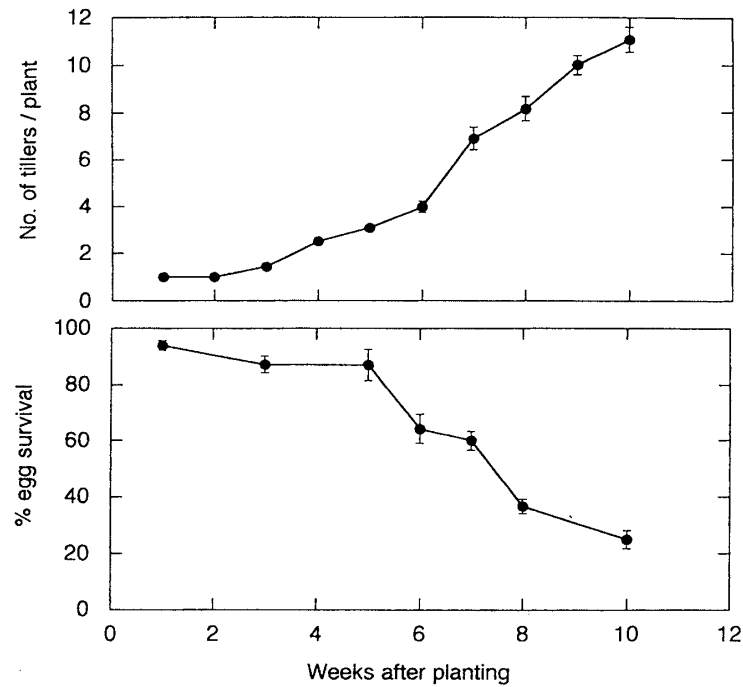


Fig. 3. Changes in the number of tillers and egg survival rate of *S. furcifera* with plant growth. Vertical lines denote standard errors.

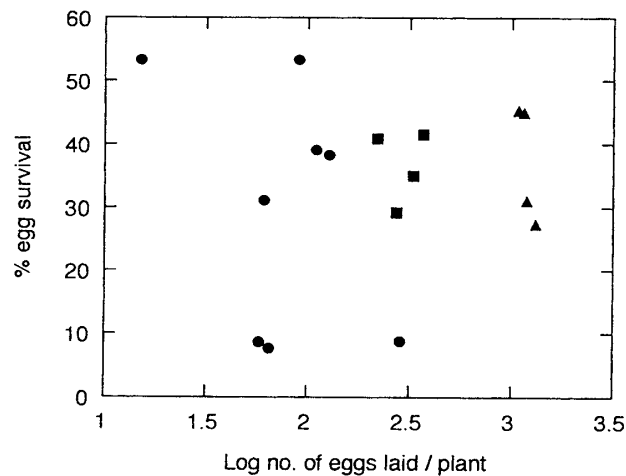


Fig. 4. Relationship between egg survival rate and egg density per plant in *S. furcifera*. Circles, squares and triangles represent 2-day oviposition by 2, 8 and 32 females, respectively.

($r_s = 0.16$, $p > 0.05$).

DISCUSSION

KUNO (1968) stated that more than 50% of rice planthopper eggs occasionally die in the field from unknown causes other than parasitism by *Anagrus* sp., though he did not give detailed data on that mortality. The causes remained unidentified until SOGAWA (1991) found that *S. furcifera* eggs suffer a high physiological mortality rate induced by the plant

reaction to oviposition. As far as we are aware, the physiological egg mortality of *S. furcifera* described here is the first report of an ovicidal reaction in plants. However, this phenomenon as well as its implications on the population dynamics is still not well understood.

The present study revealed that *S. furcifera* eggs suffer a high mortality during the early stages of embryonic development in oviposition sites where the watery lesion is formed by plant reaction (Table 1, Fig. 2). The formation of a watery lesion is usually accompanied by dark brownish discoloration of the lesion. Eggs of two rice planthopper species, *Nilaparvata lugens* and *Laodelphax striatellus*, also suffer high mortality if a watery lesion is formed, yet in these species the dark discoloration does not appear at the oviposition site (SUZUKI, unpublished). These results suggest that the formation of a watery lesion, rather than the dark discoloration, is closely related to the death of the eggs. However, immersion of the eggs in the liquid itself may not be the immediate cause of their death, since *S. furcifera* eggs complete embryonic development and successfully hatch under 1 cm of distilled water (SUZUKI et al., unpublished). Instead, the overall similarity in the phenomenal aspects between the plant reaction against *S. furcifera* oviposition and the plant defence reactions against microbial attack suggests the involvement of a biochemical substance in the physiological death of eggs.

HONDA et al. (1993) and WATANABE et al. (1994) applied the principal component analysis to long-term data on the occurrence of *S. furcifera* in Yamaguchi and Chikugo, both of which are located in western Japan, and reached the same conclusion that there are basically 3 different types regarding the population growth pattern of *S. furcifera*. The 3 types are characterized by: high immigrant density, low population growth rate; low immigrant density, low population growth rate; and low immigrant density, high population growth rate. The lack of a combination of high immigrant density and high population growth rate agrees with the results of field studies indicating that the population growth rate of *S. furcifera* is density-dependent (KUNO, 1968; NABA, 1994). The present study shows that physiological egg mortality is not responsible for the density dependence (Fig. 4). Nymphal density-dependent increase in the proportion of macropterous adults (HIRAO, 1972) is a possible causal factor of the density-dependent decline in the population growth rate. On the other hand, rice stage-dependent physiological egg mortality (Fig. 3) may explain why the population growth rate varies when the immigrant density is low. HONDA et al. (1993) present evidence that suggests the population growth of *S. furcifera* from the immigrant and the first reproductive generation is higher in June-transplanting than in May-transplanting. This indicates that the population growth rate becomes lower as the rice plants grow. A similar result has been reported by MATSUMURA (1992) in the Hokuriku District. The change in the physiological egg mortality with rice growth (Fig. 3) is large enough to explain the above-mentioned phenomenon.

The density of the immigrant generation is considered to be most important for forecasting the density of the peak generation in *S. furcifera* (KUNO, 1968; ITOMI, 1987). Recent studies show, however, that the incorporation of major factors affecting the population growth rate is indispensable for developing forecasting models. To this end, a comprehensive understanding of the diverse nature of rice plant resistance to *S. furcifera* is essential. Both the physiological death of eggs and the production of macropterous adults are, along with sucking inhibition, fundamental constituents of plant resistance. Further studies on the overall plant resistance mechanisms will also provide a basis for developing new types of resistant varieties in controlling *S. furcifera*, since plant breeders have never exploited genetic resources other than resistance against sucking.

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