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Effects of Temperature on Adult Longevity, Fertility, and Rate of Transovarial Passage of Rice Stripe Virus in the Small Brown Planthopper, Laodelphax striatellus Fallén (Homoptera: Delphacidae)

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Adults of the small brown planthopper which is a vector of rice stripe virus (RSV), were reared under 17.5, 25.0 and 32.5°C, and their fertility, longevity and the rate of viruliferous nymphs of the next generation were investigated. The mean adult longevities of females were 44.8, 27.0, 20.3 days and those of males were 45.9, 26.5, 16.9 days at 17.5, 25.0, 32.5°C, respectively. The mean fertility at 25.0°C was the highest (289.0 hatchlings), which was not significantly different from that at 17.5°C (251.9), but the fertility at 32.5°C was low (69.5). Most of the females at 17.5°C showed high transovarial passage, i.e. 82.6% of viruliferous females passed RSV to progeny at the rate of more than 90%. The percentage of females which showed high transovarial passage (>90%) was 60.9% at 25°C and 12.5% at 32.5°C; the higher the rearing temperature, the lower the percentage was. The lower rates of transovarial passage were observed from the beginning of oviposition at both 25.0 and 32.5°C, and the rate decreased with the age of females especially at 32.5°C. RSV had no deleterious effect on the fertility or adult longevity of the vector.

INTRODUCTION

Rice stripe is one of the most serious virus diseases of rice plant in Japan, especially in the Kanto area of central Japan (Kisimoto, 1979). This disease also occurs in some other countries such as China, Taiwan, Korea and in the area of Vladivostock in USSR (Kisimoto and Yamada, 1986). Kuribayashi (1931) showed that rice stripe virus (RSV) is transmitted by the small brown planthopper, Laodelphax striatellus. Detailed studies on this transmission were conducted by Yamada and Yamamoto (1955) and Shinkai (1962). They discovered the females transmit RSV to progeny through ovaries.

Kisimoto (1986) reported that the rate of transovarial passage of RSV was variable depending upon the combination of local populations of *L. striatellus* and variants of RSV, although most of the rates were very high (more than 90%) under the laboratory conditions (Shinkai, 1962; Sakurai et al., 1965; Kisimoto and Yamada, 1986).

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Few estimations have been made on the rate of transovarial passage in the field. Kisimoto and Yamada (1986) estimated the rate in the field by comparing the rates of viruliferous insects of the overwintering and first generations in Konosu, Saitama Prefecture for several years. The decreasing rate of the proportion of the viruliferous insects between the overwintering and first generations is considered to reflect the transovarial passage rate, because no apparent virus sources for acquisition by vectors are available and the population-mixing by flight among habitats rarely occurs on account of the low temperature during this perod. The estimated value of the decrease was 94.31%, which is close to the value obtained under laboratory conditions (Kisimoto and Yamada, 1986). On the other hand, Komoto et al. (1976) measured the decreasing rate of viruliferous individuals in an indoor population between two successive generations. It was higher at 27°C than at 18°C. This fact suggests the rate of the transovarial passage may be affected by the ambient temperature. The effects of temperature on the rate of transovarial passage of RSV in the vector have not been studied in detail.

In this paper, we report investigations on the effects of temperature on the longevity and fertility of the small brown planthopper, and we also compare the proportion of viruliferous offspring produced by mother insects infected with RSV at varied temperatures.

MATERIALS AND METHODS

Nymphs of the small brown planthopper were collected from a wheat field in Yuki, Ibaraki Prefecture on June 11, 1986 and reared on rice seedlings at room temperature. Emerged adults were paired and each pair was allowed to lay eggs in a separate test tube (3 cm in diameter, 20 cm in length). Although more than 500 pairs were prepared, some females were killed by Drynidae before oviposition and the offspring of only 319 pairs were available. A batch of offspring from each pair was reared separately as a family at room temperature. Two or three nymphs from each family were inspected by the hemagglutination test (Yasuo and Yanagida, 1963) in order to know whether their mother was viruliferous or not. The sheep erythrocytes sensitized with RSV-antibody were supplied by the Institute of Japan Plant Protection Association.

Nymphs from sixteen mothers judged as viruliferous were gathered and reared. The adults (long-winged form) were randomly paired within a day after emergence and the pairs were kept at 17.5°C, 25.0°C or 32.5°C (16L–8D). Forty pairs were prepared for each temperature and the longevity of adults was investigated. Rice seedlings were renewed every 3–4 days and the used seedlings were kept at 25°C (16L–8D) to obtain nymphs of the next generation. Since the used seedlings showed no symptoms of rice stripe disease, it is unlikely that the nymphs hatched from the seedlings acquired the virus orally. Nymphs in each test tube were reared until they molted to fourth or fifth instar. Rice seedlings were renewed every 3–4 days. These nymphs were stored at –70°C. Every nymph stored was inspected by the hemagglutination test in order to know whether it was viruliferous or not.

RESULTS

Adult longevity and fertility at three different temperatures

In this study, 'fertility' is expressed as the total number of nymphs hatched from

the infested seedlings. Longevity of adults and fertility of females at 17.5°C, 25.0°C and 32.5°C are shown in Table 1. Although 40 pairs were prepared in each temperature, some insects escaped from the test tube during the experiment, so they were discarded.

The mean longevities of females were 44.8, 27.0, 20.3 days and those of males were 45.9, 26.5, 16.9 days at 17.5, 25.0, 32.5°C, respectively. There was no significant difference in longevity between the sexes at all temperatures. The mean fertility was the highest at 25.0°C (289.0 nymphs), which was not significantly different from that at 17.5°C (251.9). The fertility was low at 32.5°C (69.5). The number of females laying no fertile eggs was 3, 5 and 9 at 17.5, 25.0 and 32.5°C, respectively; the higher the rearing temperature, the more infertile females appeared.

Transovarial passage of RSV at three different temperatures

Adults were paired just after adult emergence and reared until they died at 17.5, 25.0 and 32.5°C. The offspring from each pair were inspected in order to know whether they were viruliferous or not. The summed results are shown in Table 2. All the families from which at least one nymph was inspected are listed in this table. Figure 1 shows the percentages of viruliferous nymphs from each pair at three different temperatures. The pairs whose inspected offspring numbered less than 10 were excluded.

From the results shown in Table 2 and Fig. 1, the females could be divided into 4 groups: (1) females from which no viruliferous offspring was detected, (2) females from which only one viruliferous offspring was detected, (3) females from which most of the offspring were detected as viruliferous (mainly observed at 17.5°C and 25.0°C) and (4) females located between groups (2) and (3) (mainly observed at 32.5°C). Considering the females in group (2), it might be better to interpret that the positive reaction accidentally appeared without RSV, although it is possible that a viruliferous female produced only one viruliferous offspring. Takahashi et al. (1986) pointed out that the positive reaction sometimes appeared without RSV when the detergent had been incompletely rinsed out of the test tube used for the inspection. The percentages of the females in groups (1) and (2) were about 30% at all temperatures and there was little difference depending on the temperature (Table 2). Therefore, these females were considered to have been non-viruliferous. Although the females which produced a few viruliferous offspring might also be considered to have been non-viruliferous for the same reason, only the females in groups (1) and (2) were regarded as non-viruliferous in this study.

Under these considerations, most of the viruliferous females at 17.5°C showed high transovarial passage, i.e. 82.6% (19/23) of viruliferous females passed RSV to progeny at the rate of more than 90%. The percentage of females which showed high transovarial passage (>90%) was 60.9% (14/23) at 25.0°C and 12.5% (2/16) at 32.5°C; the higher the rearing temperature, the lower the percentage was (Table 2, Fig. 1). Figure 2 shows the changes in the percentage of transovarial passages in the sequence of oviposition. The females produced no or one positive nymph and females whose inspected offspring numbered less than 10 were excluded from the calculation (cf. Table 2).

The values fluctuated widely in the late oviposition period at all temperatures. This was due to the gradual decrease of the number of families. There is, therefore, no significance in late fluctuation. The rate of transovarial passage was constantly high at 17.5°C and was low at 32.5°C throughout the period of oviposition. The value

Table 1. Adult longevity and fertility of the small brown planthopper at three different temperatures

| | | | Longevity (day) ^a | ty (day) | | | F | | |
|----------|------|---------------------------------------|------------------------------|----------|--------------------------|------|-------------------|------|--------------|
| Temp. °C | | 아 | | | € | | Fertility | | laying no |
| | × | Mean±s.d. | Max. | N | Mean±s.d. | Max. | Mean±s.d. | Max. | iertile eggs |
| 17.5 | 38 | 44.8±20.9 a | 81 | 39 | 45.9±21.0 a | 96 | 251.9±154.0 a | 559 | 3 |
| 25.0 | 38 | $27.0 \pm 13.6 \text{ b}$ | 20 | 38 | 26.5±14.8 b | 61 | $289.0\pm204.3~a$ | 746 | 5 |
| 32.5 | 38 | $20.3 \pm 10.9 \; \mathrm{c}$ | 41 | 40 | $16.9\pm10.2~\mathrm{c}$ | 39 | 69.5± 53.2 b | 176 | 6 |
| 1 11 0 | 11 0 | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 | | 1. | | | | | |

Values followed by different letters are significantly different at the 5% level by t test.
Dotal number of nymphs hatched. Values followed by different letters are significantly different at the 5% level by t test.

Table 2. Appearance of viruliferous offspring at three different temperatures

| | % | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|--------|--|------|-----|------|-----|-----|------|-----|
| 32.5°C | No. of viruliferous offspring | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | No. of offspring tested | 58 | 51 | 18 | 12a | 50 | 27 | 15 |
| | % | 6.0 | 0 | 0.5 | 0 | 100 | 0.7 | 0.5 |
| 25.0°C | No. of viruliferous offspring | 2 | 0 | 1 | 0 | 232 | 1 | _ |
| | No. of offspring tested | 218 | 198 | 195 | 34 | 232 | 143 | 185 |
| | % | 99.3 | 0.3 | 98.3 | 0 | 100 | 99.3 | 0 |
| 17.5°C | No. of No. of of offspring viruliferous tested offspring | 265 | | 113 | 0 | 228 | 294 | 0 |
| | No. of offspring tested | 267 | 371 | 115a | 99 | 228 | 296 | 249 |
| | Pair No. | 1 | 2 | တ | 4 | 5 | 9 | 7 |

Transovarial Passage of RSV in L. striatellus

| 22.2 | 25.6 | 25.0 | 0 | 68.3 | 2.2 | 4.4 | 100 | 59.0 | 100 | 85.7 | 0 | 68.0 | 53.3 | 8.98 | 33.3 | 2.7 | 44.2 | 91.4 | 2.6 | 20.0 | 61.4 | 63.4 | 75.0 | | | | | | |
|------|------|------|------|------|------|-----|-----|------|------|------|-----|------|------|------|------|-----|------|------|-----|------|------|------|------|------|-----|-----|-----|-----|---|
| 14 | 23 | 9 | 0 | 98 | 2 | က | 52 | 23 | က | 48 | 0 | 34 | 24 | 33 | - | - | 38 | 53 | - | 1 | 27 | 7 | 9 | | | | | | |
| 63 | 06 | 24 | 30 | 126 | 06 | 89 | 52 | 39 | 38 | 56 | 52 | 20 | 45 | 38 | ന | 37 | 98 | 58 | 38 | J. | 44 | 11 | 8 | | | | | | |
| 94.5 | 95.0 | 86.9 | 16.2 | 97.2 | 8.96 | 0 | 0 | 2.4 | 100 | 0 | 3.5 | 92.3 | 1.3 | 68.4 | 98.7 | 100 | 99.2 | 99.5 | 0.5 | 98.6 | 100 | 61.5 | 3.9 | 98.6 | | | | | |
| 275 | 207 | 197 | 45 | 207 | 421 | 0 | 0 | 2 | 328 | 0 | 9 | 179 | 2 | 91 | 148 | 209 | 261 | 200 | 1 | 140 | 224 | 280 | 9 | 139 | | | | | |
| 291 | 218 | 227 | 278 | 213 | 435 | 29 | 202 | 85 | 328 | 48 | 169 | 195 | 154 | 133 | 150 | 209 | 263 | 201 | 189 | 142 | 224 | 455 | 155 | 141 | | | | | |
| 98.5 | 9.96 | 100 | 0.8 | 0 | 1.6 | 3.7 | 0 | 97.5 | 97.8 | 99.5 | 0 | 99.4 | 0.2 | 6.0 | 0 | 100 | 100 | 100 | 1.3 | 0.4 | 89.3 | 99.5 | 99.2 | 100 | 100 | 4.7 | 0 | 100 | The female escaped in the middle of the experiment. |
| 268 | 168 | 209 | 1 | 0 | 9 | တ | 0 | 156 | 133 | 190 | 0 | 342 | 1 | П | 0 | 226 | 313 | 120 | - | | 209 | 203 | 236 | 113 | 101 | 2 | 0 | 40 | n the middle |
| 272 | 174 | 209 | 133 | 16 | 370 | 82 | 170 | 160a | 136 | 191 | 180 | 344 | 443 | 118 | 221 | 226 | 313 | 120 | 80 | 233 | 234 | 204 | 238 | 113 | 101 | 43 | 108 | 40 | male escaped in |
| æ | 6 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | a The fe |

he female escaped in the middle of the experiment.

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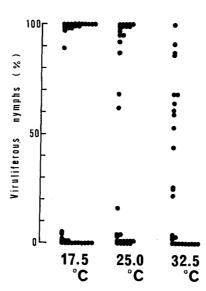


Fig. 1. The percentages of viruliferous nymphs from each pair at three different temperatures (cf. Table 2). Pairs whose inspected offspring numbered less than 10 were excluded.

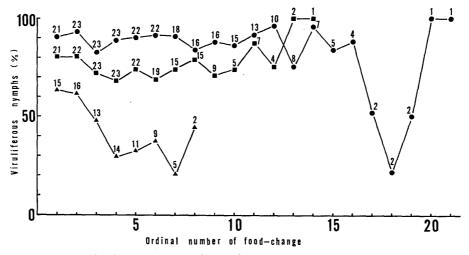


Fig. 2. Changes in the percentage of viruliferous nymphs at 17.5°C (♠), 25.0°C (■) and 32.5°C (♠) in the sequence of oviposition. Females producing no or one viruliferous nymph and females whose inspected offspring numbered less than 10 were excluded from the calculation (cf. Table 2). Figures above each plot refer to the number of families.

at 25.0°C was intermediate between the two (Fig. 2). The rate of transovarial passage at 32.5°C decreased with the age of females (Fig. 2).

Differences of adult longevity and fertility between viruliferous and non-viruliferous females

Adult longevity and fertility of the viruliferous females were compared with those of the non-viruliferous ones (Fig. 3). In this analysis, the mothers which produced more than 90% positive nymphs were used as 'viruliferous', i.e. 17 females at 17.5°C and 14 females at 25.0°C. The mothers which produced no or only one positive nymph

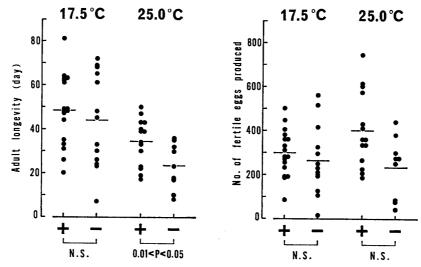


Fig. 3. Differences of adult longevity and fertility between viruliferous (+) and non-viruliferous (-) females at 17.5°C and 25.0°C. The mean value of each group is shown as "—". In this comparison, mothers which produced more than 90% positive nymphs were used as 'viruliferous' females, and mothers which produced no or one positive nymph as 'non-viruliferous' ones (cf. Table 2). Statistical analyses were carried out by Mann-Whitney U test.

were used as 'non-viruliferous', i.e. 13 females at 17.5°C and 9 females at 25.0°C (cf. Table 2). Females at 32.5°C were not used, because the fertility was very low and viruliferous females were few.

There was no significant difference in the fertility between viruliferous and non-viruliferous females by Mann-Whitney U test at the two temperatures (Fig. 3). There was also no significant difference in the longevity at 17.5°C, but the viruliferous females at 25.0°C had a slightly longer longevity than non-viruliferous ones (0.01 (Fig. 3).

DISCUSSION

There are few studies on the longevity or fertility of the small brown planthopper reared at a constant temperature. Nasu (1963) reported that mean adult longevity of the non-viruliferous and viruliferous females reared at 25°C was 20.11 days and 18.67 days, respectively, and that mean fertility of the non-viruliferous and viruliferous females was 61.26 (max. 250) and 58.75 (max. 103), respectively. The females of the present study (Table 1) showed longer longevity and greater fertility than those of Nasu's study. Insect quality and rearing condition of the present study are considered to be more appropriate than those of Nasu's study.

The rate of transovarial passage at 17.5°C was high and was low at high temperatures (Fig. 1). Komoto et al. (1976) obtained a similar result using the same virus and insect. They maintained a colony of 100% viruliferous planthoppers for several generations at 18°C and 27°C and estimated the inter-generational change of the transovarial passage. The transovarial passage at 18°C was 100% in the first generation and 91% in the second generation, while that at 27°C was 96% in the first generation

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and 87% in the second generation (Komoto et al., 1976). In the present study, we further estimated the rate of transovarial passage at a higher temperature, 32.5°C. The rate decreased remarkably at that temperature. The present study also showed that the low rate of transovarial passage at higher temperatures occurred from the beginning of oviposition (Fig. 2). It is noticeable that the rate of transovarial passage at 32.5°C decreased with the age of females (Fig. 2). The present study suggests that the rate of transovarial passage in the field is not constant throughout the year, but is lower in summer because of high temperature.

NASU (1963) and NAKASUJI and KIRITANI (1970) reported that the rice dwarf virus (RDV) has deleterious effects upon its vector leaf hopper, Nephotettix cincticeps, with respect to adult longevity of females, preovipositional period, mean fertility, duration of egg stage and nymphal survival rate. In the small brown planthopper, there were no significant differences in adult longevity and fertility between viruliferous and non-viruliferous females at 17.5°C and 25.0°C except in the longevity at 25.0°C where viruliferous females had a slightly longer longevity in the present study (Fig. 3). NASU (1963) showed that non-viruliferous small brown planthopper females had higher nymphal survival, more fertility and longer adult longevity than viruliferous ones. He considered that planthoppers would suffer from RSV. But as the values of fertility and adult longevity were very low in his experiment, there might have been some problems in insect quality or rearing conditions. It is better to consider that the small brown planthopper is not deleteriously influenced by carrying RSV unlike the relationship between N. cincticeps and RDV.

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