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Dual Wing-form Determination Mechanism in the Brown Planthopper,

Nilaparvata lugens STAL

(Homoptera: Delphacidae)¹

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The brown planthopper, Nilaparvata lugens STÅL, is well known to have wing dimorphism, in which the nymphal density plays an important role in determining the wing-form. The last-instar nymphs of N. lugens contain individuals with short and long wing-pads. According to Cook and Perfect (1982), individuals with short wing-pads always developed to brachypters whereas individuals with long wing-pads developed into either brachypters or macropters. Yamada (1990) showed, under laboratory conditions, that in females of N. lugens the wing-pad length is also influenced by the density during the nymphal period, suggesting a dual mechanism that determines both the wing-pad length and the wing-form. Progeny of N. lugens, collected in 1987 in Fukuoka Prefecture and reared for successive generations on rice seedlings (Reiho variety) at the Kyushu National Agri-

For experiments, 50 (A) or 350 (B) sterilized rice seeds (Nipponbare vaiety) were sown on fertilized soil in plastic vessels (7 cm in diameter × 20 cm in depth) covered with nylon gauze. Vessels (A) and (B) were used for high (6.2 nymphs/seedling) and low (0.11 nymphs/seedling) density conditions, respectively. When the rice seedlings grew to about 8 cm in height, the first-instar nymphs collected from the stock culture within 24 hr after egghatch were released into the vessel. Nymphal density was altered from low to high, or vice versa, at various periods after hatching, when nymphs were released into new vessels containing new food. Insects were reared in the vessels till the end of the 4th ecdysis. The length of wing-pads in the 5th (last) instar nymphs was measured as in Cook and Perfect (1982), between the posterior end of the pronotum and the tip of the wing-pad parallel to the outer wing-pad margin, by using a calibrated ocular micrometer mounted on a dissecting microscope. In females, 0.94 mm was considered to be a critical wing-pad length for macropters (Cook and Perfect, 1982; Yamada, 1990). Based on this measurement, the last instar females were classified into "short wing-pad individuals" (with wing-pad length less than 0.94 mm) and "long wing-pad individuals" (with wing-pad length of 0.94 mm or more). These nymphs were transferred individually into 50 ml plastic cups (7 cm in diameter ×

cultural Experimental Station, were brought to our laboratory on March 14, 1989. They were maintained at $25\pm1^{\circ}$ C, 16L-8D photoperiod in a stock culture cage (34 cm \times 24 cm basal width, 29 cm in height) containing about 3,000 rice seedlings.

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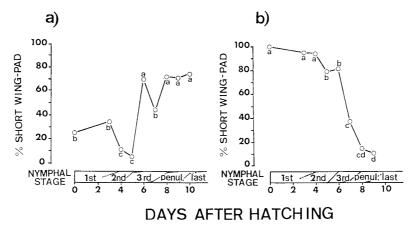
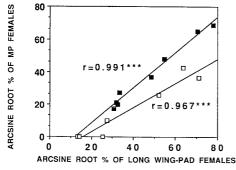


Fig. 1. Change in proportion of short wing-pad females when the density was altered on different days after egg-hatch. a) The density was altered from low (0.11 nymphs/seedling) to high (6.2 nymphs/seedling). b) The density was altered from high (6.2 nymphs/seedling) to low (0.11 nymphs/seedling). Percentages shown with letters in each figure are significantly



different (Mann-Whitney *U*-test, p < 0.05).

Fig. 2. The relationship between the percentage of long wing-pad females and that of macropterous (MP) females. Solid square: The density was altered from low to high. Open square: The density was altered from high to low (***positive correlation, statistically significant at 0.1%).

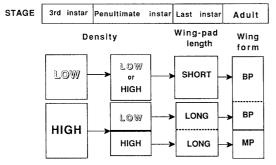


Fig. 3. Hypothetical processes for wing determination in the *Nilaparvata lugens* females. BP: Brachypter; MP: Macropter.

3.5 cm in height) in which two or three rice seedlings were planted in fertilized soil. These insects were reared until final ecdysis, and their resulting wing-forms were recorded.

Figure 1a shows the proportion of short wing-pad females when the density was altered from low to high at various intervals after hatching. The proportion of short wing-pad females prominently increased by the transfer made on the sixth day, compared to those made earlier. When the density was altered after the sixth day, the proportion of short wing-pad females was approximately 70%. When the density was altered from high to low, the proportion of short wing-pad females decreased markedly by the transfer made on the 7th day, or later, compared to the preceding transfer (Fig. 1b). Thus, female wing-pad length is probably determined at the 3rd-instar stage.

Figure 2 shows the relationship between the percentage of long wing-pad females and percentage of macropterous ones. The percentage of macropters increased with an increase in the percentage of the long wing-pad individuals (Yamada, 1990). It was noteworthy that when the density was altered from low to high, the percentage of macropters was higher than was the case for the opposite density alteration at the same percentage levels of long wing-pad females. Slope for the former was significantly greater than the slope for the later (t=3.09, D.F.=11, p=0.010). Thus, it is suggested that the density at stages of the 4th- and/or

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5th-instars also affected the proportion of macropters among females which grew to long wing-pad ones.

Figure 3 shows a hypothetical wing-form determination process in N. lugens females. In this insect, there seem to be two steps for the determination of wing-forms: the wing-pad size is determined at the 3rd-instar stage, and the final wingform, at the later stage(s). Nymphs grown at a low density during the 3rd-instar stage may give rise to short wing-pad nymphs; they may ecdyse to brachypters irrespective of the density at later stages. When the density is high at the 3rdinstar stage, nymphs may develop into long wingpad females; they can ecdyse to either brachypters or macropters depending on the density at later stages. I could not establish whether the critical developmental stage in the determiniation of the wing-form was the 4th or the 5th instar or both, but the results of density alteration experiments performed by Kisimoto (1965) and Iwanaga and Тојо (1986) suggested that it was during the 4th (penultimate) instar stage.

The oriental chinch bug, Cavelerius saccharivorus Okajima, can ecdyse to either brachypterous or macropterous form, depending on the density at the 4th and the 5th instar stages, if the insects developed under long day and high temperature conditions at earlier stages (Fujisaki, 1989). However, when the insects developed under short day and low temperature conditions at earlier stages, most of them ecdysed to brachypterous forms irrespective of the density at later stages. Cavelerius saccharivorus may also have multiple steps for the determination of wing-forms.

The plasticity of long wing-pad females of N. lugens in the determination of wing-form may be

adaptive in more unpredictable conditions because they can control their wing-form depending on the later density conditions. However, a few (less than 10%) long wing-pad females were attained even under low density condition of less than 1 nymph per seedling (Yamada, 1990). According to HARRISON (1980), different phenotypes would be determined depending on whether the concentration of some effector exceeded a genetically determined threshold. Therefore, the threshold of the long wing-pad females produced by low density conditions would be so low that wing-pads developed even under such conditions. Genetical background as well as ecological significance of the appearance of such individuals in a population must be investigated in future studies.

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