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The Relation of Adult Wing-Form in the Brown Planthopper,
Nilaparvata lugens STÅL (Homoptera: Delphacidae)
to Wing-Pad Length of Last Instar Nymphs¹

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Relationships between adult wing-form and wing-pad length in *Nilaparvata lugens* were examined under laboratory conditions ($25 \pm 1^\circ\text{C}$). Most of the last instar female nymphs with wing-pads shorter than 0.94 mm developed to brachypterous adults, but female nymphs with wing-pads longer than 0.94 mm became both brachypterous and macropterous adults. Thus the brachypterous females of this insect consisted of short wing-pad brachypters and long wing-pad brachypters. In females, with the increase of rearing density during the nymphal stage, short wing-pad brachypters decreased with the increase of long wing-pad brachypters. This was followed by an increase of macropters. Male nymphs with shorter wing-pads tended to become brachypterous adults, but a critical wing-pad size for induction of macropters was not detected. Male nymphs emerged as macropterous adults over the wide density range studied. Relationships between weight and wing-pad length of last instar nymphs were different between sexes. Body weight tended to be heavier in female nymphs with short wing-pads than in those with long wing-pads. The wing morph determination mechanism in *N. lugens* females was hypothesized to consist of 2 sequential processes. The first process may affect development of wing-pads, while the second process influences development of adult wings.

INTRODUCTION

Wing polymorphism which produces brachypterous and macropterous forms in the same species exists in phylogenetically different groups of insects. This phenomenon is an excellent subject for the study of evolution of dispersal strategy in insects, as the dispersive and non-dispersive individuals can be easily discriminated (ROFF, 1986). In recent years, interpopulation crossing or selection experiments were performed for some insects, showing that wing polymorphism was partially controlled by genetic bases (IWANAGA et al., 1985; HONĚK, 1986; FUJISAKI, 1986; WALKER, 1987; MOROOKA et al., 1988; ZERA and RANKIN, 1989).

In addition to genetic factors, environmental cues during the nymphal stage may play an important role in determining wing-form (HONĚK, 1976; HARRISON, 1980). Last instar nymphs of many hemimetabolous insects have wing-pads. However,

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developmental processes of nymphal wing-pads on different wing forms were reported only by COOK and PERFECT (1982). They showed that last instar nymphs of the brown planthopper *Nilaparvata lugens* in paddy fields with wing-pads shorter than a critical length always developed to brachypters, while those with longer wing-pads developed into both brachypters or macropters.

In this paper, I compare the proportions of brachypterous and macropterous adults emerging from last instar nymphs with varying wing-pad size and from different rearing densities. Possible processes of wing-form determination mechanism in *N. lugens* are also proposed.

MATERIALS AND METHODS

Progenies of *N. lugens* collected on August 14, 1987, in Chikugo-City of Fukuoka Prefecture were reared for successive generations on rice seedlings (*Reiho* variety) at the Kyushu National Agricultural Experimental Station. These insects were brought to our laboratory on March 14, 1989, and maintained under $25 \pm 1^\circ\text{C}$ and 16L-8D photoperiod in a stock culture cage (34×24 cm basal width, 29 cm ht.) containing about 3,000 rice seedlings. For experiments, about 50 or 350 sterilized rice seeds (variety *Nipponbare*) were sown on fertilized soil in plastic vessels (7 cm in dia. \times 20 cm depth). Vessels containing 50 and 350 rice seeds were used for higher (≥ 0.5 nymphs/seedling) and lower nymphal densities respectively. First instar nymphs collected from the stock culture within 24 hr after egg-hatch were released onto rice seedlings (about 8 cm ht.) in the vessel. We prepared 8 density conditions by releasing 20, 40, 100 and 250 individuals (0.06, 0.11, 0.29, 0.5, 0.7, 1.0, 2.5 and 6.2 individuals per seedling). The tops of the vessels were covered with nylon gauze. Insects were reared in the vessels until 4th (last) nymphal ecdysis. Food plants were not renewed before this time. Wing-pad length of the 5th (last) instar nymphs was measured within 24 hr after the ecdysis along a line from the posterior border of the pronotum to the apex of the wing-pad parallel to the outer wing-pad margin, using a calibrated ocular micrometer mounted in a dissecting microscope (COOK and PERFECT, 1982). Within 24 hr after the 4th ecdysis, insects were weighed with a semi-microbalance (Chyo Jupiter MI-20A®) accurate to 0.01 mg. These last instar nymphs were transferred individually into 50 ml plastic cups (7 cm in dia. \times 3.5 cm ht.) in which 2 or 3 rice seedlings were planted on fertilized soil. These insects were reared until the final ecdysis, and wing-form and sex of adults were recorded.

RESULTS

Critical length of wing-pad for production of macropterous form

In females, 98% of last instar nymphs with wing-pad length of less than 0.94 mm ecdysed to brachypterous adults, while nymphs with longer wing-pads (≥ 0.94 mm) ecdysed to either brachypterous or macropterous adults. The proportion of the 2 wing-forms did not change with the further increase of nymphal wing-pad length (Fig. 1a). Here 0.94 mm was considered to be a critical wing-pad length for macroptery which was the same value reported by COOK and PERFECT (1982) for field populations of *N. lugens*. In males, nymphs with shorter wing-pads tended to become brachypterous adults, but a critical wing-pad length for production of macropters could

not be detected (Fig. 1b). Hereafter the brachypterous females were classified into 2 groups, "short wing-pad brachypters" (emerged from nymphs with wing-pad length shorter than 0.94 mm) and "long wing-pad brachypters" (emerged from nymphs with wing-pad length of 0.94 mm or more).

Relationships between nymphal density and adult wing form

As shown in Fig. 2, under low density conditions of less than 1 nymph per seedling, most females developed to short wing-pad brachypters. A very low percentage of them became long wing-pad brachypters and macropters. Increases of nymphal density above this level decreased the proportion of short wing-pad brachypters and increased that of long wing-pad brachypters and then macropters.

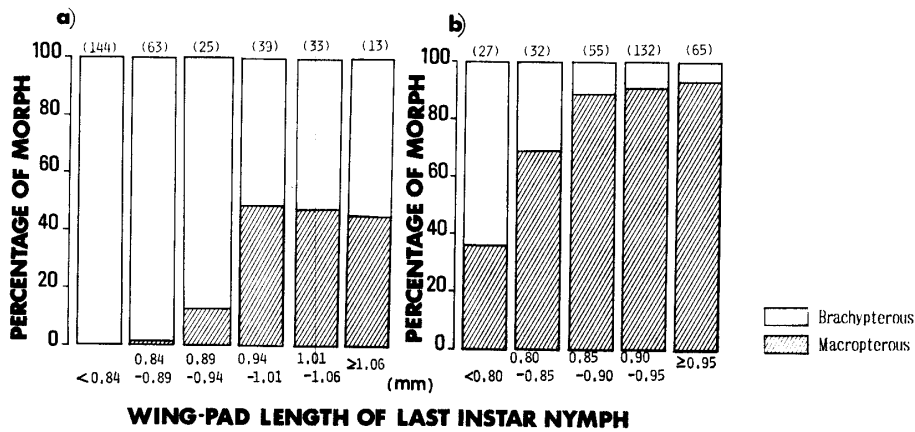


Fig. 1. Percentage of last instar nymphs having different wing-pad length which ecdysed to brachypterous and macropterous adults. a) females, b) males. Numbers in parentheses indicate sample size.

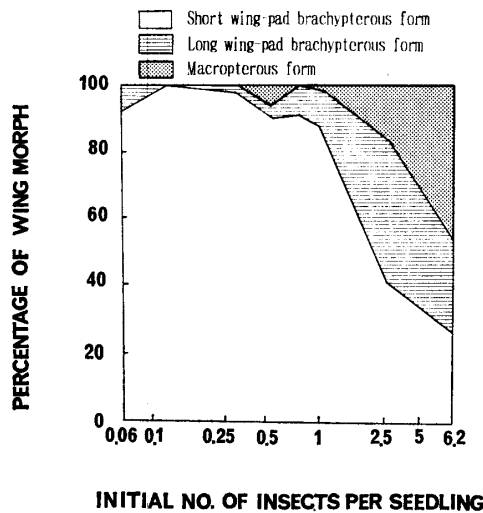


Fig. 2. Relationship between nymphal density and proportion of three wing-morphs in female *Nilaparvata lugens*. When initial density was higher than 10 nymphs per seedling, all individuals died before the last instar stage.

In males, macropters emerged at high proportions over the entire density range examined except at densities from 0.25 to 2.5 nymphs per seedling (Fig. 3).

Relationships between wing-pad length and nymphal density

In females under low density conditions of less than one nymph per seedling, the mean wing-pad length of last instar nymphs were consistently short (Fig. 4a). At densities of 2.5 or more nymphs per seedling, however, the mean wing-pad length became considerably longer. In males, although the values fluctuated, lower densities with less than 0.1 nymphs per seedling tended to yield longer mean wing-pad lengths than higher density conditions (Fig. 4b).

Relationships between weight and wing-pad length of the last instar nymphs

In females, mean fresh weight of last instar nymphs was larger than 1.1 mg under

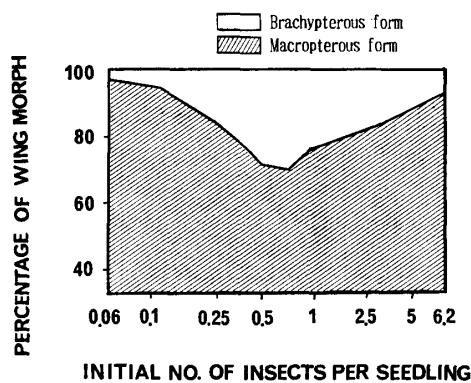


Fig. 3. Relationship between nymphal density and proportion of macropterous form in male *Nilaparvata lugens*. When initial density was higher than 10 nymphs per seedling, all individuals died before the last instar stage.

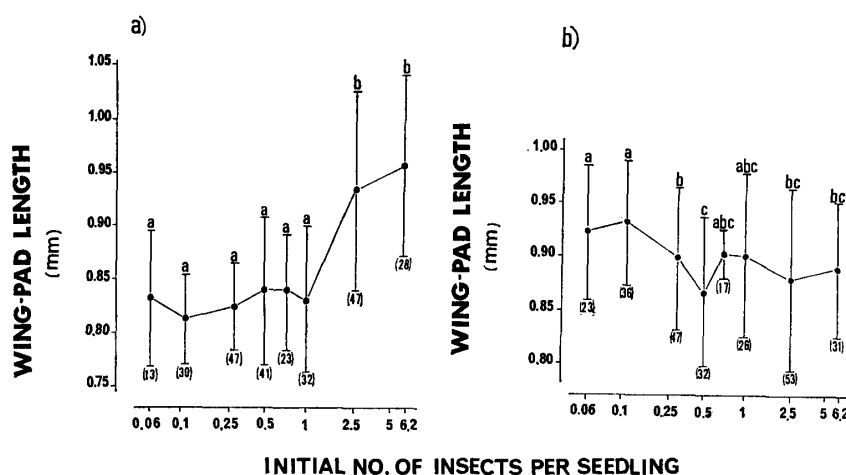


Fig. 4. Mean wing-pad length of last instar nymphs under different density conditions (Mean \pm S.D.). a) females, b) males. Means with different letters are significantly different from each other (MANN-WHITNEY *U*-test; $p < 0.05$). Numbers in parentheses indicate sample size.

low density, and most of these nymphs had wing-pads shorter than 0.94 mm. On the other hand, mean fresh weight of the last instar nymphs was smaller under high density conditions, and most of these nymphs had wing-pads longer than 0.94 mm (Fig. 5a). As shown in Fig. 5 b, the mean body weight and wing-pad length of last instar nymphs were positively correlated in males (KENDALL's rank correlation test, $p < 0.01$, $N = 310$, $\tau = 0.251$).

Figure 6 shows relationships between weight of last instar nymphs and adult wing-morph. In females, long wing-pad individuals gradually decreased as nymphal weight increased. In males, about 80 to 90% ecdysed to macropterous form, irrespective

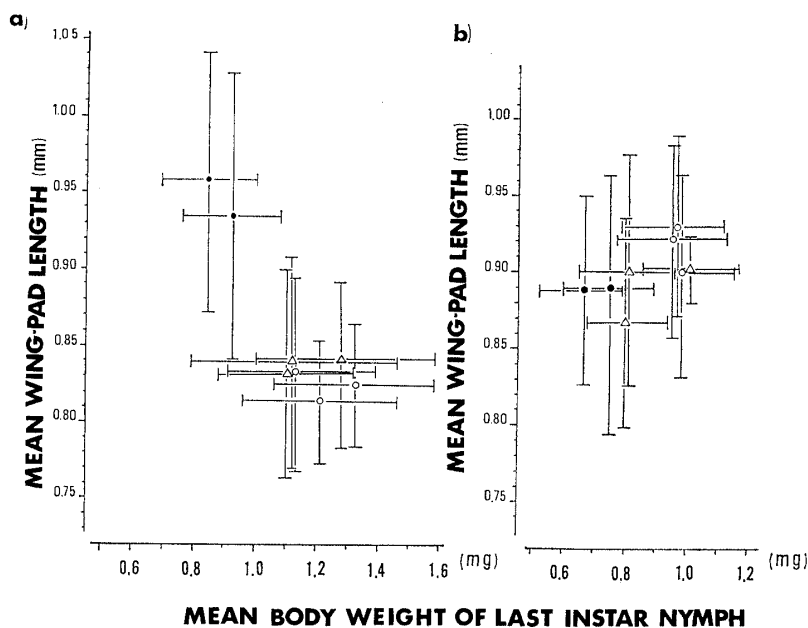


Fig. 5. Mean body weight and mean wing-pad length of last instar nymphs ($\bar{X} \pm S.D.$). a) females, b) males. \circ : ≤ 0.6 nymphs/seedling, \triangle : 0.6–1.0 nymphs/seedling, \bullet : > 1.0 nymphs/seedling.

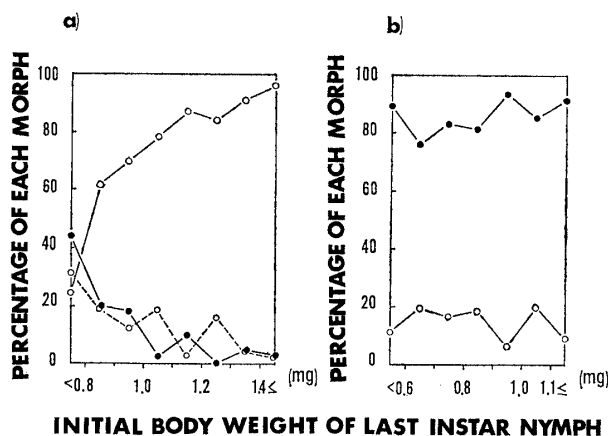


Fig. 6. Initial body weight of last instar nymphs and their wing-form after final ecdysis. a) females, \circ — \circ : short wing-pad brachypterous form \circ --- \circ : long wing-pad brachypterous form, \bullet — \bullet : macropterous form. b) males, \circ — \circ : brachypterous form, \bullet — \bullet : macropterous form.

Table 1. Mean wing-pad length and presence of long wing-pad, last instar female nymphs and post-ecdysis macropterous individuals (%)

Density (insects/seedling)	N	Mean wing-pad length* ¹ (mm)	Long wing-pad individuals* ² (%)	Macropterous individuals* ² (%)
≤1.0	154	0.83±0.06 ^a	4.5 ^a	1.9 ^a
2.5	47	0.94±0.10 ^b	57.4 ^b	21.3 ^b
6.2	27	0.96±0.08 ^b	62.9 ^b	59.3 ^c

*¹ Means in the same column with different letters are significantly different (MANN-WHITNEY *U*-test; $p < 0.01$).

*² Values in the same column with different letters are significantly different (FISHER'S exact probability test; $p < 0.05$).

of initial last instar weight.

Table 1 shows that in females reared at nymphal densities lower than 1.0 per seedling mean wing-pad length of last instar nymphs and percentage of long wing-pad nymphs were smaller than those for intermediate (2.5/seedling) or high (6.2/seedling) densities. There was no significant differences either in mean wing-pad length and percentage of long wing-pad individuals between intermediate (2.5/seedling) and high (6.2/seedling) densities, while percentages of macroptery were significantly different. About half of the long wing-pad nymphs emerged as macropters under intermediate density conditions, whereas high density conditions yielded mostly macropterous emergences.

DISCUSSION

It has been known that wing length polymorphism in the brown planthopper *N. lugens* is mainly influenced by nymphal density (KISHIMOTO, 1965). Here, I showed that wing-pad length of the last instar female nymphs was influenced by nymphal density during the 1st to 4th instar stages that; low density tended to produce last instar nymphs with short wing-pads; and that high density produced nymphs with long wing-pads (Fig. 2).

Males and females showed different relationships between mean body weight and mean wing-pad length (Fig. 5). According to KISHIMOTO (1965), brachypterous *N. lugens* females are produced under low density and brachypterous males are produced under intermediate density. Sexual difference in the density and wing form relationship may be partially caused by the different response of wing-pad development to nymphal density.

The Tobacco hornworm *Manduca sexta* (L.) undergoes 4 larval molts before pupation under standard rearing conditions. However, *Manduca* larvae with head capsule width less than 5.1 mm, (produced by temporal starvation at 3rd or 4th instar stage) undergo supernumerary larval molts (NIJHOUT, 1975). Larvae with head capsules wider than 5.1 mm, which attain body weight of approximately 5 g, can pupate (NIJHOUT and WILLIAMS, 1974). The timing of metamorphosis may be closely related to larval body size. In *N. lugens*, last instar female nymphs with wing-pads longer than a critical length (≥ 0.94 mm) ecdysed into either macropterous or brachypterous forms, whereas most last instar nymphs with wing-pads shorter than this critical length ecdysed to

brachypterous forms (COOK and PERFECT, 1982). I further showed that the body weights of long wing-pad female nymphs were significantly smaller than that of short wing-pad nymphs. This suggests existence of a critical body size to determine wing-pad length in females; under suitable nutrient conditions, nymphs attain a critical body size, grow to short wing-pad individuals, and ecdyse to brachypters. When individuals do not attain this critical body size, they would grow to long wing-pad nymphs, and ecdyse to either macropterous or brachypterous adults, due to unknown factors occurring during later nymphal stages. I showed that the ratio of macropterous females increased with increasing density, although mean wing-pad length and percentages of long wing-pad individuals were not different between high and intermediate density conditions. This result also suggests that mechanisms of wing-morph determination in *N. lugens* include 2 sequential processes; wing-pad size is determined first, and wing-morph follows.

IWANAGA and TOJO (1986) researched the critical developmental stage of wing-morph determination in *N. lugens*. When they altered rearing conditions from low to high density before the 3rd instar, more than half of the females emerged macropterous. When density was altered after the end of the 3rd instar, all females emerged brachypterous (low density form). When a reverse of this alteration (that is, from high to low density) was done, all the females emerged brachypterous even when the alteration was made in the later 4th (penultimate) instar. *N. lugens* shows different critical periods of wing-form determination depending on the direction of density change. Such an asymmetry in critical periods of wing development was also found in a cricket, *Gryllus rubens* (ZERA and TIEBEL, 1988). In *G. rubens*, more individuals continuously reared in groups grew to brachypterous form than those reared in isolation (opposite to the pattern observed for *N. lugens*). When rearing conditions were altered from isolation to group on the 28th day after hatching (penultimate stage), the proportion of brachyptery became high, and was not significantly different with individuals continuously reared in groups. When reversal density alterations were performed on the 14th day after hatching (prior to the penultimate stage), the proportion of brachyptery form was low, and not significantly different with individuals continuously reared in isolation. However, when the insects were isolated on the 14th day after hatching, the proportion of brachyptery was significantly higher than in those continuously reared in isolation. These results can be explained if we assume dual determination processes with different sensitive periods. In *N. lugens*, a hypothesis can be made as follows. The first process determines the wing-pad development of nymphs. Under low nymphal density before the end of 3rd instar, last instar nymphs develop short wing-pads. All of them grow to brachypterous form, irrespective of density conditions during the 4th and last instars. When the early nymphal density is high, the first process works to produce long wing-pad last instar nymphs. These long wing-pad nymphs can grow either to macropterous or brachypterous adults according to density conditions, possibly later than at the 3rd ecdysis.

For *N. lugens* females, future habitat conditions may be unpredictable in intermediate density conditions. The original habitat may deteriorate, or continue to be adequate. Thus production of 2 wing morphs under such conditions may spread this risk. Some parts of the population can find suitable habitats through flight emigration, while others may benefit by remaining at the same site. FUJISAKI (1985) reported that the Oriental chinch bug *Cavelerius saccharivorus* OKAJIMA produced both macropterous

and extremely brachypterous adults under high density conditions. He stated that *C. saccharivorus* may employ a mixed immigration strategy in which respective portions of adult populations disperse or remain in the original habitat. *N. lugens* is considered to employ similar strategy at densities in which quality of habitats may be unpredictable. There seems to be a particular critical period for each of 2 wing-morph determination processes in *N. lugens*, the clarification of which is a subject of future study.

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