Appl. Entomol. Zool. **32** (3): 437–445 (1997)

Correlated Responses of Life History Traits, Wing Length, and Flight Propensity to Wing-Form Selection in the Whitebacked Planthopper, *Sogatella furcifera* (HORVÁTH) (Hemiptera: Delphacidae)

Masaya MATSUMURA[1]

Laboratory of Insect Pest Control, Hokuriku National Agricultural Experiment Station, Joetsu, Niigata 943–01, Japan

(Received 23 August 1996; Accepted 3 February 1997)

Different wing-forms (brachypters and macropters) of the whitebacked planthopper, *Sogatella furcifera*, were selected for 12 generations and correlated responses of several life history traits, wing length, and flight propensity to this selection were examined. A positively correlated response to wing-form selection was observed in nymphal developmental time, but no consistent response was observed in either fecundity or adult longevity. A significant reduction in forewing length was detected in response to selection for brachyptery. The flight propensity of macropters in the brachypterous line measured by the flight mill technique was significantly lower than that recorded in the control line. These results suggest that selection for brachyptery not only influences the incidence of brachypters but also acts to decrease the forewing length and flight propensity of macropterous individuals of the brachypterous line.

Key words: *Sogatella furcifera*, wing dimorphism, correlated response, life history trait, flight propensity

INTRODUCTION

The whitebacked planthopper, *Sogatella furcifera* (HORVÁTH) (Hemiptera: Delphacidae) is a serious rice pest throughout Asia. Adult females of *S. furcifera* exhibit wing dimorphism and occur in two forms, macropters and brachypters. Macropters are fully winged and can migrate long distances, whereas brachypters have reduced wings and cannot fly. Males, however, are usually monomorphic macropterous. The production of macropters is influenced most by nymphal population density (KISIMOTO, 1956), and is positively density dependent.

MATSUMURA (1996 a) conducted a replicated selection experiment for increasing and decreasing the incidence of macroptery in *S. furcifera*. He showed that wing-form in *S. furcifera* has a genetic basis and is a threshold character under polygenic control (MATSUMURA, 1996 a). In a wing-dimorphic cricket, *Gryllus firmus* (SCUDDER), a positive genetic correlation exists between wing-form and flight propensity (FAIRBAIRN and ROFF, 1990). However, the genetic basis for correlations between wing-form and life history traits is poorly understood for other wing-dimorphic insects and especially for planthopper species (DENNO, 1994).

Population growth rate, macroptery (percent), and ovarian development of macropters of *S. furcifera* are greatly influenced by environmental factors such as population density and/or rice plant age (MATSUMURA, 1996 b, 1997). To understand the population dynamics and ecological significance of wing dimorphism in *S. furcifera*, it is important to investigate

[1] Present address: *Kyusyu National Agricultural Experiment Station, Nishigoshi, Kumamoto 861–11, Japan*

whether genetic correlations exist between wing-form and other life history traits. Thus, correlated responses to wing-form selection were examined for life history traits (nymphal developmental time, preoviposition period, adult longevity, early fecundity, and total fecundity), wing length, and flight propensity.

MATERIALS AND METHODS

Wing-form selection. A replicated selection experiment for increasing and decreasing the incidence of macroptery in *S. furcifera* was performed for 12 generations (MATSUMURA, 1996 a). The strains used in the selection experiment were derived from approximately 100 pairs of macropterous adults collected from a rice field in Niigata, Japan in July, 1990 (replicate 1) and in July, 1991 (replicate 2). These strains were maintained in the laboratory for one generation prior to the selection experiment.

Wing-form selection was conducted under two density treatments: a rearing density of 1 and 16 nymphs per glass tube (2 cm i.d.×17 cm height) with 6 rice seedlings (var. Nipponbare) at a daylength of 16 h and a temperature of 25±1°C. Each treatment was replicated 100 and 10 times for rearing densities of 1 and 16, respectively. In replicate 1, two lines were established from a strain collected in July, 1990, with no control line: a macroptery-selected line at a rearing density of 1 (M1-line) and a brachyptery-selected line at a rearing density of 16 (B16-line). In replicate 2, four lines were established from a strain collected in July, 1991: a macroptery-selected line and its control line at a rearing density of 1 (M1 and C1 lines), and a brachyptery-selected line and its control line at a rearing density of 16 (B16 and C16 lines). Further experimental protocol of wing-form selection is described by MATSUMURA (1996 a).

Measurement of life history traits. Correlated responses to selection on life history traits were assayed using the M1 and B16 lines of replicate 1. Nymphal developmental time was measured at each generation of selection. Approximately 100 individuals were tested in each line. Preoviposition period (measured as the time from eclosion to first egg), adult longevity, early fecundity (total number of eggs produced per female in the first 7 days after the onset of oviposition), and total fecundity were measured in generation 11. The period of 7 days for early fecundity was used because this period represents the first half of the entire oviposition period (about 15 days) in this experiment. One pair of adults within 24 h after adult emergence was placed in a glass tube with 3 rice seedlings. Rice seedlings were replaced daily before the onset of oviposition and thereafter at 3 day intervals. These seedlings were dissected under a binocular microscope to count eggs. Because no unselected control line was maintained in replicate 1, the phenotypic values of the selected lines were compared with those of the base population (generation 1).

Measurement of forewing length and flight propensity. Forewing length of each morph and sex was measured under a binocular microscope in generations 1 and 10 of the lines selected for macroptery and brachyptery (M1, B16), and their controls (C1, C16) of replicate 2. Head capsule width of each morph and sex was measured by the same method in generations 1 and 10 of B16 and C16 lines.

Flight propensity was assayed using a flight mill technique similar to that described by CHEN et al. (1984) and KAWAMOTO et al. (1987) with a modification for the planthopper (Fig. 1). The rotor was constructed of a light-weight stainless steel pipe. Flight tests were conducted using the M1, B16, C1, and C16 lines of replicate 2. These four lines were maintained under mass rearing conditions for 13 generations after 12 generations of selec-

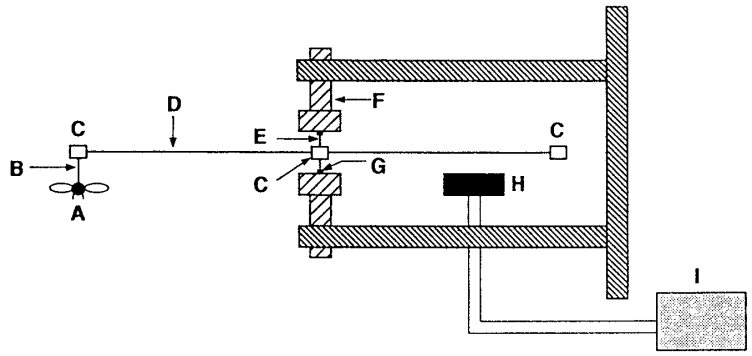

Fig. 1. Front view of flight mill. A: tethered insect; B: insect pin (16.5 mm in length, 0.16 mm in diameter); C: piece of urethane sponge; D: rotor made of stainless steel pipe (15 cm in length, 0.31 mm in diameter); E: axis made of an insect pin (same as B); F: bolt (no magnet was used to support the axis of the flight mill because no friction occurred); G: glass tube (1.5 mm in length, 0.3 mm in inside diameter); H: reflective photocensor; I: computer. Total weight of revolving part (B+C+D+E) is 0.13 g.

tion experiments at rearing densities of 1 (M1 and C1 lines) and 16 (B16 and C16 lines). Three-day-old macropterous females and males that had been reared at rearing densities of 1, 8, and 16 nymphs per glass tube were tested. The age of 3 days was used because a preliminary test showed that that age has the highest flight activity. The test insect was anesthetized with carbon dioxide gas for 2 s and attached to an insect pin at the mesonotum with adhesive (quick-drying bond for wood, Konishi K.K.). The number of revolutions was recorded by a computer every 30 s for 2 h. The room for the tests was maintained at 25± 1°C and a light intensity of ca. 2,000 lx with fluorescent lighting. The duration of continuous flight was defined as flight durations whereby the test insects flew more than 5 revolutions per 30 s.

CHEN et al. (1984) measured flight propensity of the brown planthopper, *Nilaparvata lugens* (STÅL) using a flight mill. They used a fan as a stimulator to make the insect resume flying by sending a gust of air whenever it stopped flying. Their method should not enable evaluation of precise flight propensity of planthopper species because the rotor itself revolves by a gust of air. Thus, the present flight test was done under wind-less conditions.

RESULTS

Effect of wing-form selection on life history traits

The nymphal developmental time of females of both morphs and males rapidly increased under selection for macroptery (M1) until generation 9 of wing-form selection, and decreased slightly thereafter (Fig. 2). The nymphal developmental times after 4 generations of selection in macropters and after 5 generations of selection in brachypters and males were significantly longer than those in the base population (generation 1) ($p < 0.05$, MANN-WHITNEY's *U*-test). This result suggests that there is a positive genetic correlation between nymphal developmental time and wing-form. In contrast, the nymphal developmental time of macropters, brachypters, and males from brachyptery-selected line (B16) fluctuated and showed no correlated responses to wing-form selection. It was not clear why the nymphal developmental times decreased in the macropterous line after the 9th generation and fluctuated in the brachypterous line because no control line was maintained in replicate 1 of

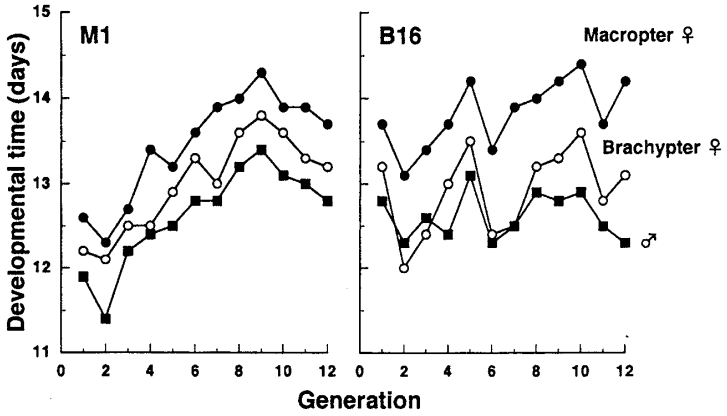

Fig. 2. Correlated response of nymphal developmental time to selection for increasing the incidence of macroptery at a rearing density of 1 (M1) and for decreasing the incidence of macroptery at a rearing density of 16 (B16). See MATSUMURA (1996 a) for direct responses to wing-form selection.

Table 1. Responses of life history traits to selection for macroptery at a density of 1 (M1)

Traits	Wing morph	Generation 1 Mean±S.E. (*n*)	Generation 11 Mean±S.E. (*n*)
Preoviposition period	Macropter	3.5±0.1 (14)	3.9±0.2 (19)
(days)	Brachypter	3.1±0.2 (18)	3.5±0.2 (11)
Adult longevity	Macropter	21.4±1.6 (14)	21.9±1.4 (19)
(days)	Brachypter	18.8±1.0 (18)	19.4±1.7 (11)
Early fecundity	Macropter	99.0±5.9 (14)	129.3±5.8 (19)**
(total eggs/first 7 days)	Brachypter	110.1±5.2 (18)	100.9±6.3 (11)
Total fecundity	Macropter	238.1±20.3 (14)	251.1±14.7 (19)
(eggs)	Brachypter	216.1±14.7 (18)	219.3±33.8 (11)

Differences between generations were tested by MANN-WHITNEY's *U*-test. $^{**}p < 0.01$.

Table 2. Responses of life history traits to selection for brachyptery at a density of 16 (B16)

Traits	Wing morph	Generation 1 Mean±S.E. (*n*)	Generation 11 Mean±S.E. (*n*)
Preoviposition period	Macropter	4.7±0.2 (18)	4.0±0.2 (20)**
(days)	Brachypter	3.8±0.2 (5)	3.5±0.1 (20)
Adult longevity	Macropter	19.8±1.2 (18)	20.7±1.4 (20)
(days)	Brachypter	21.2±2.9 (5)	18.4±1.9 (20)
Early fecundity	Macropter	114.0±7.6 (18)	106.5±4.7 (20)
(total eggs/first 7 days)	Brachypter	115.9±8.6 (5)	103.5±5.5 (20)
Total fecundity	Macropter	215.9±16.2 (18)	228.4±16.9 (20)
(eggs)	Brachypter	196.0±34.3 (5)	205.0±15.3 (20)

Differences between generations were tested by MANN-WHITNEY's *U*-test. $^{**}p < 0.01$.

the selection experiment.

The preoviposition period of both morphs increased slightly in generation 11 of the macropterous line (Table 1), but decreased in the brachypterous line relative to the base population (Table 2). The difference was statistically significant only for macropters in the

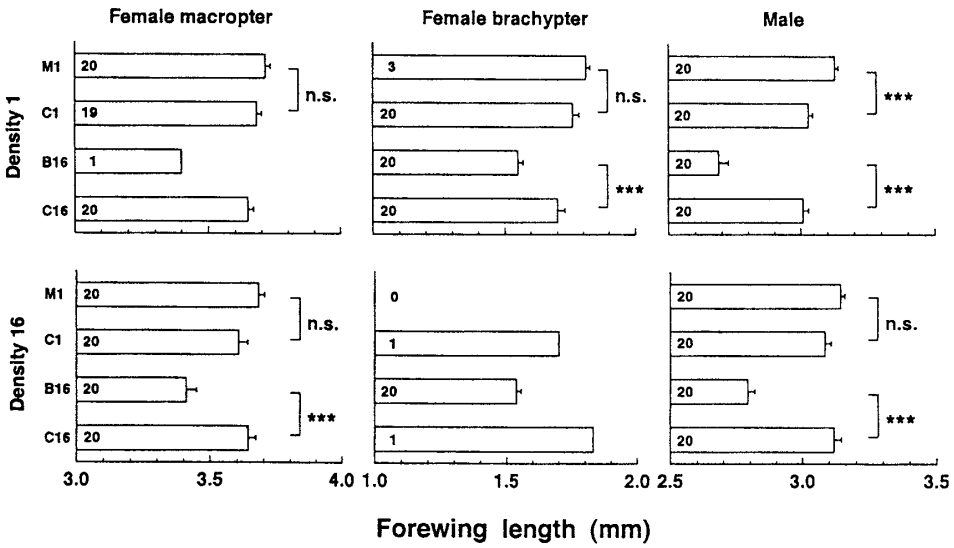

Fig. 3. Forewing lengths of female macropters, female brachypters, and males from the 10th generation of selection for macroptery (M1) and brachyptery (B16) and their control lines (C1 and C16), reared at two densities (1 and 16 nymphs per glass tube). Sample sizes are indicated in each bar. Two-tailed *t*-tests were used to compare means of selected lines with controls. $*p<0.05$; $**p<0.01$; $***p<0.001$.

Table 3. Head capsule width of female macropters, female brachypters, and males from the 10th generation of selection for macroptery (M1) and brachyptery (B16) and their control lines (C1 and C16), reared at two densities (1 and 16 nymphs per glass tube)

Rearing density	Line	Macropter			Brachypter			Male		
1	B16	0.727	(1)		0.729±0.007	(20)	n.s.	0.629±0.006	(20)	n.s.
	C16	0.736±0.005	(20)		0.722±0.006	(20)		0.640±0.004	(20)	
16	B16	0.694±0.006	(20)	n.s.	0.689±0.004	(20)		0.618±0.005	(20)	n.s.
	C16	0.703±0.004	(20)		0.740	(1)		0.624±0.005	(20)	

Mean (mm)±S.E.
Two-tailed *t*-tests were used to compare means of selected lines with controls. n.s.: $p>0.05$.

brachypterous line ($p<0.05$, MANN-WHITNEY's *U*-test) (Table 2). Adult longevity of both morphs and lines showed no significant difference between generations 1 and 11 ($p>0.05$, MANN-WHITNEY's *U*-test) (Tables 1 and 2). Early fecundity increased significantly only in macropters from the macropterous line ($p<0.01$, MANN-WHITNEY's *U*-test), although this response was not observed for total fecundity (Table 1).

Effect of wing-form selection on wing length and flight propensity

Forewing length of both morphs and sexes in the 10th generation of selection for brachyptery (B16) was shorter than those of the control line (C16) (Fig. 3). The difference in forewing length between individuals from the brachypterous and control lines was 0.2 to 0.3 mm and was statistically significant for macropters at a rearing density of 16, brachypters at a rearing density of 1, and males at rearing densities of 1 and 16 ($p<0.001$, two-tailed *t*-test). Because there was no significant difference in head capsule width between individuals

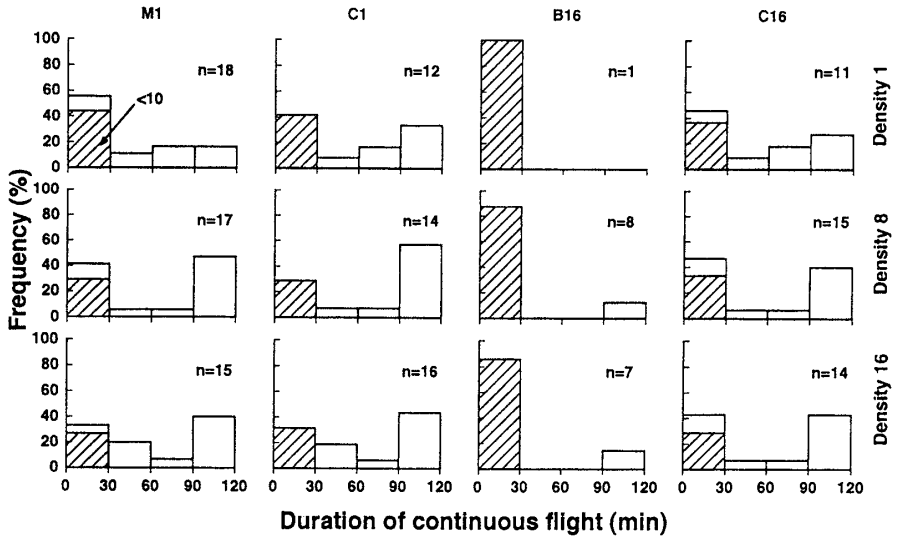

Fig. 4. Frequency distribution of continuous flight period in females from strains selected for macroptery (M1) and brachyptery (B16), and their control lines (C1 and C16), reared at three densities (1, 8, and 16 nymphs per glass tube).

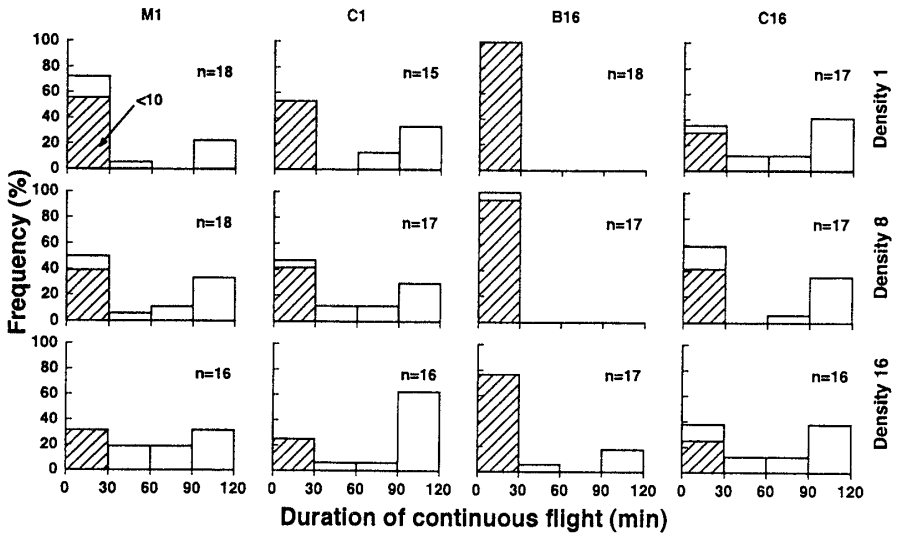

Fig. 5. Frequency distribution of continuous flight period in males from strains selected for macroptery (M1) and brachyptery (B16), and their control lines (C1 and C16), reared at three densities (1, 8, and 16 nymphs per glass tube).

from the brachypterous and control lines ($p > 0.05$, two-tailed t-test) (Table 3), the relative forewing length decreased in response to selection for brachyptery. In contrast, no significant difference in forewing length was detected between individuals from the macropterous and control lines, except for males that were reared at a density of 1 which had larger wings ($p < 0.001$, two-tailed t-test) (Fig. 3).

The frequency distribution of duration of continuous flight for macropterous females and males in each line is shown in Figs. 4 and 5, respectively. In the brachyptery-selected

line (B16), few individuals of either sex flew continuously for more than 10 min as compared with those in the control line (C16). The percentage of individuals which flew continuously for less than 10 min in the brachypterous line (B16) was significantly higher than that recorded in the control line (C16) ($p<0.05$ for females and $p<0.01$ for males, χ^2-test) except for females at a density of 1, where statistical comparison was not available. On the other hand, there was no significant difference in flight propensity between individuals from the macropterous (M1) and control (C1) lines at any density conditions ($p>0.05$, χ^2-test). The proportion of female macropters and males that flew continuously for less than 10 min tended to decrease in all the lines when the insects were reared at high densities (8 and 16 nymphs per glass tube) (Figs. 4 and 5).

DISCUSSION

Wing-form in *S. furcifera* is expressed as a threshold response of some continuously varying factor to nymphal density (MATSUMURA, 1996 a). This factor is thought to be a kind of juvenile hormone (SOUTHWOOD, 1961; HARRISON, 1980; ROFF, 1986). Although endocrine regulation of wing dimorphism has not yet been investigated for any planthopper species, IWANAGA and TOJO (1986) reported that the topical application of juvenile hormone and the analogue methoprene on *N. lugens* increased the proportion of brachypters. Their study suggests that brachypters are produced if the titre of juvenile hormone exceeds a critical threshold level during a particular stage of development. Since high levels of juvenile hormone extend nymphal developmental time, selection for brachyptery will prolong nymphal developmental time. However, the present study suggests that there is a positive genetic correlation between nymphal developmental time and wing-form (Fig. 2). Thus, hormonal control of wing-form can not be as simple as described above. The physiological mechanism of endocrine regulation of wing dimorphism in planthopper species needs to be determined in future studies.

ROFF and FAIRBAIRN (1991) showed that the preoviposition period of brachypters is shorter than that of macropters in 16 out of 22 wing-dimorphic insects. In wing-dimorphic planthopper species, the preoviposition period of brachypters is shorter than that of macropters in all 8 species thus far investigated, including *S. furcifera* and *N. lugens* (DENNO, 1994). These observations suggest that there exists a positive phenotypic correlation between wing-form and age at first reproduction. However, there are no data for planthopper species which suggest a genetic basis of correlations between wing-form and reproductive characters (DENNO, 1994). The present results showed that the preoviposition period in *S. furcifera* was prolonged under selection for macroptery and shortened under selection for brachyptery (Tables 1 and 2), which suggests that there exists a positive genetic correlation between wing-form and age at first reproduction.

Wing-form selection did not have any obvious effect on fecundity except for weakly positive effects on early fecundity in the macroptery selected line (Tables 1 and 2). This may be due to an underestimation of potential fecundity. Total fecundity of *S. furcifera* was about 200 to 250 eggs per female (Tables 1 and 2). This value was about half that obtained on potted rice plants (445 to 862 eggs per female) by KUNO (1968). To clarify the difference in fecundity between the two selected lines, potential fecundity must be examined under both laboratory and field conditions.

Selection for brachyptery not only influenced the incidence of brachypters but also acted to decrease forewing length and flight propensity of macropterous individuals (Figs. 3,

4, and 5). Although selection for macroptery did not influence these traits, flight propensity may be positively correlated with the incidence of macropters. This result also suggests that wing-form and migration-related characters have the same genetic basis. Since hindwing morphology and flight musculature have not been investigated, the effects of wing-form selection on these dispersal-related characters need to be examined.

Populations of *S. furcifera* in rice fields of northern Japan are initiated by macropterous immigrants arriving in mid-July. Adults of the next (the 1st) generation occur during mid-August. The proportion of brachypters in the 1st generation is usually low (MATSUMURA, 1996 b). Because macropterous adults of the 1st generation usually emigrate from fields, the density of the 2nd generation is usually low (MATSUMURA, 1996 b). Recently, however, occasional 2nd generation outbreaks which cause "hopperburn" damage to rice plants have been reported in northern Japan (MURAI et al., 1986; IITOMI and KODAMA, 1989; MATSUMURA, 1991) even though the proportion of brachypters was low in the 1st generation (MATSUMURA, 1996 b). It has been observed that a fraction of the macropterous females of the 1st generation does not emigrate but reproduces in the rice field if environmental conditions are favorable (e.g., when the population density is low and the rice plants are in the vegetative stage) (MATSUMURA, 1991, 1997). These observations suggest that not only brachypters but "non-migratory" macropters of the 1st generation contribute to the 2nd generation outbreaks. The present study also suggests that genetic variations exist for both forewing length and flight propensity among macropters (Figs. 3, 4, and 5). Further studies on the relative roles of genes and environment in determining wing-form and related characters (e.g., ovarian development and flight propensity) are needed to determine the population dynamics and dispersal mechanism in *S. furcifera*.

ACKNOWLEDGEMENTS

I sincerely thank Dr. Y. SHIRAI for his technical advice on the flight mill system.

REFERENCES

CHEN, R.C., J.R. WU, S.D. ZHU and J.X. ZHANG (1984) Flight capacity of the brown planthopper *Nilaparvata lugens* STÅL. *Acta Entomol. Sinica* **27**: 121–127 (in Chinese with English summary).

DENNO, R.F. (1994) Life history variation in planthoppers. In *Planthoppers: Their Ecology and Management* (R.F. DENNO and T.J. PERFECT, eds.). Chapman & Hall, New York, pp. 163–215.

FAIRBAIRN, D.J. and D.A. ROFF (1990) Genetic correlations among traits determining migratory tendency in the sand cricket, *Gryllus firmus*. *Evolution* **44**: 1787–1795.

HARRISON, R.G. (1980) Dispersal polymorphisms in insects. *Ann. Rev. Ecol. Syst.* **11**: 95–118.

IITOMI, A. and K. KODAMA (1989) Types of population growth of the white-backed planthopper, *Sogatella furcifera* HORVÁTH and its forecast in Akita Prefecture. *Ann. Rep. Soc. Plant Prot. North Jpn.* **40**: 91–94 (in Japanese with English summary).

IWANAGA, K. and S. TOJO (1986) Effects of juvenile hormone and rearing density on wing dimorphism and oöcyte development in the brown planthopper, *Nilaparvata lugens*. *J. Insect Physiol.* **32**: 585–590.

KAWAMOTO, K., Y. SHIRAI and T. OKADA (1987) Preliminary studies on the flight ability of the cabbage webworm, *Hellula undalis* FABRICIUS (Lepidoptera: Pyralidae), using a flight mill system. *Bull. Natl. Res. Inst. Ver., Ornam. Plants Tea Jpn. Ser. A* **1**: 147–156 (in Japanese with English summary).

KISIMOTO, R. (1956) Studies on the polymorphism in the planthoppers (Araeopidae, Homoptera). Preliminary report. *Oyo-Kontyu* **12**: 56–61 (in Japanese with English summary).

KUNO, E. (1968) Studies on the population dynamics of rice leafhoppers in a paddy field. *Bull. Kyushu Agric. Exp. Stn.* **14**: 131–246 (in Japanese with English summary).

MATSUMURA, M. (1991) Characteristics of recent population growth patterns of the white-backed planthopper, *Sogatella furcifera* HORVÁTH in the Hokuriku district. *Proc. Assoc. Plant Prot. Hokuriku* **39**: 47–

50 (in Japanese).

MATSUMURA, M. (1996 a) Genetic analysis of a threshold trait: density-dependent wing dimorphism in *Sogatella furcifera* (HORVÁTH) (Hemiptera: Delphacidae), the whitebacked planthopper. *Heredity* **76**: 229–237.

MATSUMURA, M. (1996 b) Population dynamics of the whitebacked planthopper, *Sogatella furcifera* (HORVÁTH) (Hemiptera: Delphacidae) with special reference to the relationship between its population growth and the growth stage of rice plant. *Res. Popul. Ecol.* **38**: 19–25.

MATSUMURA, M. (1997) Seasonal prevalence of ovarian development in macropterous females of white-backed planthopper, *Sogatella furcifera* (HORVÁTH) (Hemiptera: Delphacidae) in paddy fields. *Jpn. J. Appl. Entomol. Zool.* **41**: 75–82.

MURAI, T., N. ABE, N. OYAMA and K. SAKAIYA (1986) Notes on the outbreaks of white-backed planthopper *Sogatella furcifera* HORVÁTH and small brown planthopper *Laodelphax striatellus* FALLÉN in Aomori Prefecture. *Ann. Rep. Soc. Plant Prot. North Jpn.* **37**: 131–134 (in Japanese).

ROFF, D.A. (1986) The evolution of wing dimorphism in insects. *Evolution* **40**: 1009–1020.

ROFF, D.A. and D.J. FAIRBAIRN (1991) Wing dimorphisms and the evolution of migratory polymorphisms among the Insecta. *Am. Zool.* **31**: 243–251.

SOUTHWOOD, T.R.E. (1961) A hormonal theory of the mechanism of wing polymorphism in Heteroptera. *Proc. Roy. Entomol. Soc. London Ser. A* **36**: 63–66.