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Genetic analysis of a threshold trait: density-dependent wing dimorphism in *Sogatella furcifera* (Horváth) (Hemiptera: Delphacidae), the whitebacked planthopper

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The whitebacked planthopper *Sogatella furcifera* exhibits wing dimorphism. The production of female macropters is most influenced by nymphal population density and is positively density-dependent. Bidirectional wing-form selection was imposed under several nymphal density conditions. Selection for increasing and decreasing the incidence of macroptery was most effective under antagonistic selection, i.e. selection for macroptery was most effective under low density conditions and selection for brachyptery was most effective under crowded conditions. Crossing experiments using the 10th generation of lines selected for macroptery and brachyptery suggest that the wing-form in *S. furcifera* is a threshold character under polygenic control and is determined by a threshold response to nymphal density. Broad sense heritability of wing-form was at least 0.467. The realized heritability was 0.512 estimated from the lines selected for macroptery and 0.298 from the lines selected for brachyptery. The relationship between wing-form ratio and nymphal density (i.e. reaction norm) was parallel, which proved that there was no genotype-by-environment interaction between wing-form and density.

Keywords: heritability, reaction norm, selection, *Sogatella furcifera*, threshold trait, wing dimorphism.

Introduction

Wing dimorphism is a commonly observed phenomenon in insects (Harrison, 1980; Roff, 1986). A genetic basis for wing dimorphism has been reported in many insect species including the large orders Coleoptera, Orthoptera, Hemiptera and Homoptera (Roff, 1986; Roff & Fairbairn, 1991). For these species, the mode of wing-form inheritance can be divided into two types: single locus inheritance with a two-allele mechanism and polygenic determination (Roff, 1986). Although the underlying genetic determination is polygenic, the genetic basis of wing dimorphism can be analysed using a threshold model, in which it is assumed that there is a continuously distributed underlying character (e.g. hormone titre) and that the genotype is determined by whether the character is above or below the threshold (Roff, 1986, 1994; Falconer, 1989). However, the experimental data are comparatively scanty and insufficient to support the threshold model (e.g. Mori & Nakasuji, 1990).

The whitebacked planthopper *Sogatella furcifera* (Horváth) is a serious rice pest in Japan. This species is apparently unable to overwinter in Japan and undergoes long-distance migration each year from southern China (Kisimoto, 1976). Adult females of *S. furcifera* exhibit wing dimorphism and occur in two forms, macropters and brachypters. Males, however, are usually monomorphic macropterous. Macropterous females are fully winged and can migrate long distances, although brachypterous females have reduced wings and cannot fly. The production of macropters is influenced most by nymphal population density (Kisimoto, 1956) and is positively density-dependent. From an adaptive viewpoint, it is an advantage to migrate and colonize new habitats when the population density is high, and migration requires macroptery. When the population density is low, in contrast, brachyptery is

favourable because of their earlier reproduction than macropters (Kisimoto, 1956; Denno *et al.*, 1985, 1991).

Nagata & Masuda (1980) found that tropical populations (Thailand and the Philippines) of *S. furcifera* showed a remarkably high proportion of brachypters in laboratory cultures compared with the Japanese populations. Because both the populations were reared under the same density conditions, their results suggest that wing dimorphism in *S. furcifera* has a genetic basis. For other delphacid planthopper species, a genetic basis for wing-form determination has been reported for the brown planthopper *Nilaparvata lugens* (Stål) (Mochida, 1975; Iwanaga *et al.*, 1985; Morooka *et al.*, 1988; Morooka & Tojo, 1992), the small brown planthopper *Laodelphax striatellus* (Fallén) (Mahmud, 1980; Mori & Nakasuji, 1990), and *Prokelisia marginata* (Roderick, 1987). The mode of wing-form inheritance in these species was polygenic. No published information, however, is available on the genetic basis of wing-form determination in *S. furcifera*.

The purpose of this study was to elucidate the genetic basis of wing dimorphism in *S. furcifera*. Bidirectional wing-form selection was imposed and a crossing experiment between the two selected lines was conducted. Using data from the crossing experiment, two modes of inheritance, simple Mendelian and polygenic, were assessed within the framework of threshold characters (Roff, 1986; Falconer, 1989). The reaction norm, which is the relationship between wing-form ratio and the value of the environmental variable (rearing density in this case), was also described using the data of the selection experiment.

For females of wing-dimorphic planthopper species including *S. furcifera*, the incidence of brachyptery decreases with an increase in nymphal rearing density (Kisimoto, 1956; Mochida, 1973; Denno *et al.*, 1985, 1991). Thus, the effect of selection on wing-form response depends on density conditions. The type of selection that I applied is called 'antagonistic' and 'synergistic' selection (Falconer, 1990). Antagonistic selection is a selection upwards in a bad environment or downwards in a good environment. Synergistic selection is the reverse (Falconer, 1990). Jinks & Connolly (1973) suggested that antagonistic selection reduces environmental sensitivity and that synergistic selection increases it if there is genetic variance for sensitivity, i.e. if there is genotype-by-environment interaction (Jinks & Connolly, 1973). Furthermore, Falconer (1989, 1990) suggested that the best improvement of mean performance should be achieved by antagonistic selection. To test these hypotheses, wing-form selection was imposed under three environmental conditions, i.e. low, intermediate and high nymphal density conditions.

Materials and methods

Selection experiment

A replicated selection experiment for increasing and decreasing the incidence of macroptery in *S. furcifera* was conducted. The strains used in the selection experiment were derived from approximately 100 pairs of macropterous immigrants 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 (stock culture).

Wing-form selection was conducted under three density treatments: a rearing density of 1, 4 and 16 nymphs per glass tube (2 cm i.d. $\times$ 17 cm height) with six rice seedlings (var. Nipponbare) at a daylength of 16 h and a temperature of 25 ± 1°C. Each treatment was replicated 100, 25 and 10 times for densities of 1, 4 and 16, respectively. The experimental design of wing-form selection is shown in Fig. 1. In replicate 1, only two lines were maintained: a macroptery-selected line at rearing density of 1 (M1) and a brachyptery-selected line at rearing density of 16 (B16). In replicate 2, the selection experiment consisted of three lines within each density treatment: a control line, a brachyptery-selected line and a macroptery-selected line. For brachypter-selected lines, brachypterous females and macropterous males were selected as parents because all males moulted into macropters. For macropter-selected lines, macropterous females and males were selected as parents. For control lines, parents of each generation were chosen at random for mating. Twenty pairs were sampled for mating in every generation for each line.

To elucidate the density–wing-form relationship in the course of successive selection, first instar nymphs were reared at densities of 1, 2, 4, 8 and 16 per glass tube after 1, 4 and 10 generations of selection for macroptery (M1) and brachyptery (B16) lines in replicate 1. Each density treatment was replicated 128, 64, 32, 16 and 8 times for densities of 1, 2, 4, 8 and 16, respectively.

Crossing experiment

An interline crossing experiment was conducted using the 10th generation macropterous (M1) and

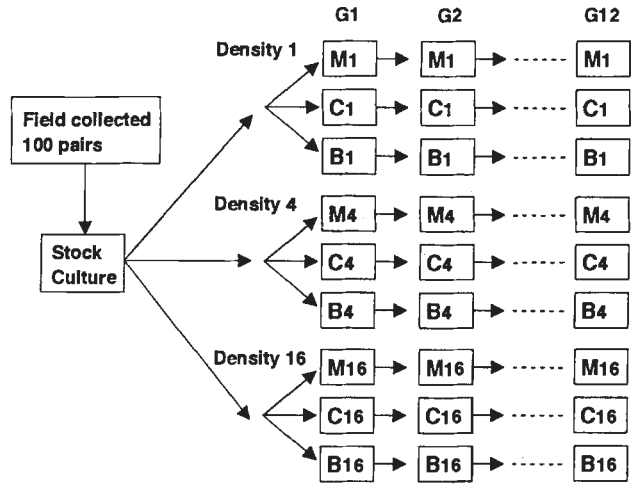

Fig. 1 Experimental design of the wing-form selection. Two replicates were conducted. In replicate 1, only the two lines, M1 and B16, were maintained. In replicate 2, all the nine lines were maintained. See Materials and methods for details. Inset shows the macropterous (left) and brachypterous (right) females of *Sogatella furcifera*.

brachypterous (B16) lines of replicate 1. Parental M1 and B16 lines, their reciprocal F_1 crosses, backcrosses of F_1 hybrids to the M1 and B16 parents, and all possible F_2 crosses were conducted. Each cross was made by single-pair matings of 19–24 adult pairs. Nymphs from all these crosses were reared at densities of 1, 2, 4, 8 and 16 per glass tube and replicated 80, 40, 20, 10 and 5 times, respectively.

Genetic analysis

Two modes of inheritance of wing dimorphism were examined using all the data obtained from the crossing experiment. First, an analysis was conducted assuming that wing-form is controlled by a single locus with two alleles, with either macroptery or brachyptery being completely dominant. Next, the data were fitted to a polygenic model within the framework proposed for threshold characters (Roff, 1986; Falconer, 1989). Estimated parameters were calculated using the 'three classes with two thresholds' method proposed by Falconer (1989, p. 305). The thresholds T_1 and T_2 were fixed points on the liability scale by setting them as the level of brachyptery (per cent) produced at densities of 8 and 2, respectively.

Heritability

Broad sense heritability ($V_G/(V_G+V_E)$) was estimated by the difference in variance between the $F_2(=V_G+V_E)$ and the $F_1(=V_E)$, where V_G and V_E are genotypic variance and environmental variance, respectively (Falconer, 1989).

The cumulative selection response ($\Sigma(x_2-x_1)$) for the first 10 generations of selection was plotted as a function of the cumulative selection differential (Σi), where i is the mean deviation of individuals with values exceeding the threshold (T) in standard deviation units from the population mean (see appendix table A in Falconer, 1989). Realized heritabilities (h^2) for wing-form were estimated based on regression of the cumulative selection response on the cumulative selection differential. Because the males, with zero selection on them, were not included in calculating the selection differentials, they were half as large and the realized heritabilities were multiplied by 2.

Results

Response to wing-form selection

Males emerged macropterous across all selected lines, but macroptery (per cent) responded to wing-form selection in females. Under selection for macroptery, the percentage of female macropters rapidly increased at the rearing density of 1 (M1) but did not change under crowded conditions (M4 and M16) (Fig. 2). In contrast, under selection for brachyptery, the percentage of female macropters rapidly decreased only under crowded density conditions (B4 and B16) (Fig. 2). These results support Falconer's (1990) suggestion that the best improvement of mean performance should be achieved by antagonistic selection, i.e. selection for increasing incidence of macropters under low nymphal density conditions and selection for brachyptery under crowded conditions.

After ten generations of selection, wing-form response to density also differed among each line.

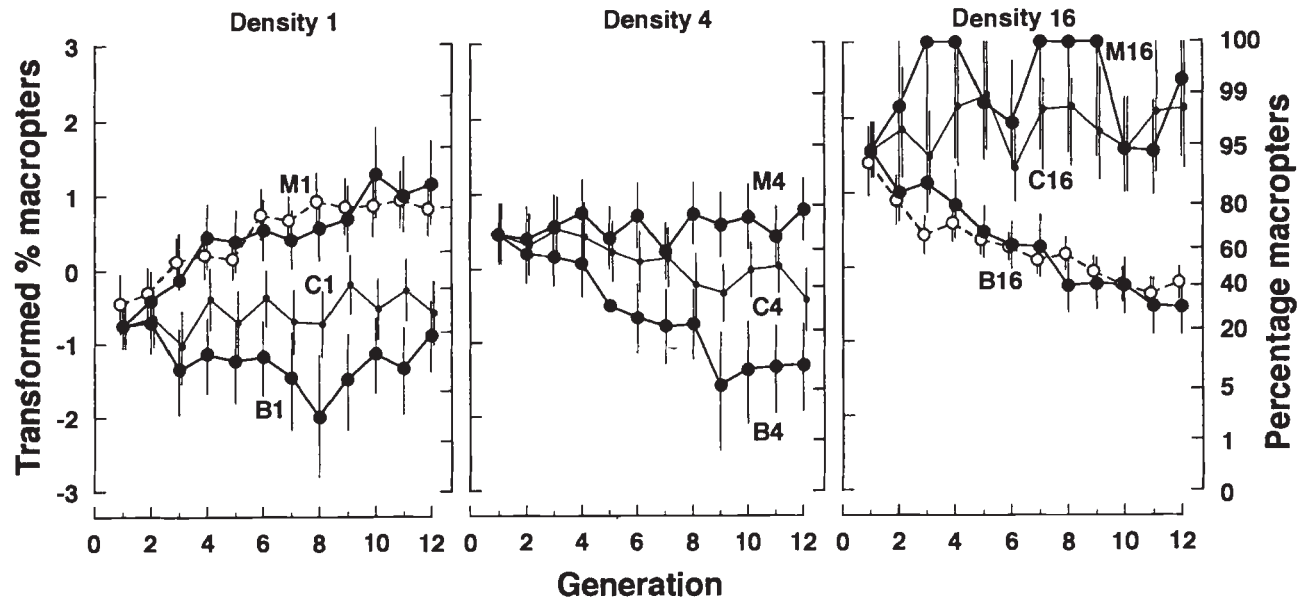

Fig. 2 Response to selection for increasing (M) and decreasing (B) the incidence of macroptery in *Sogatella furcifera* at rearing densities of 1 (M1, C1, B1), 4 (M4, C4, B4) and 16 nymphs (M16, C16, B16) per glass tube at 25 ± 1°C, 16:8h L:D. Solid lines indicate replicate 2; dashed lines indicate replicate 1 (M1 and B16 only). Vertical lines present the 95 per cent confidence interval (*F*-test). Percentage macropters is transformed to the deviation of the truncation point from the mean of truncated normal distribution, in standard deviation units (see appendix table A in Falconer, 1989). Percentages of zero and 100 cannot be converted in this transformation, but these values were transformed to -3 and 3 for convenience, respectively.

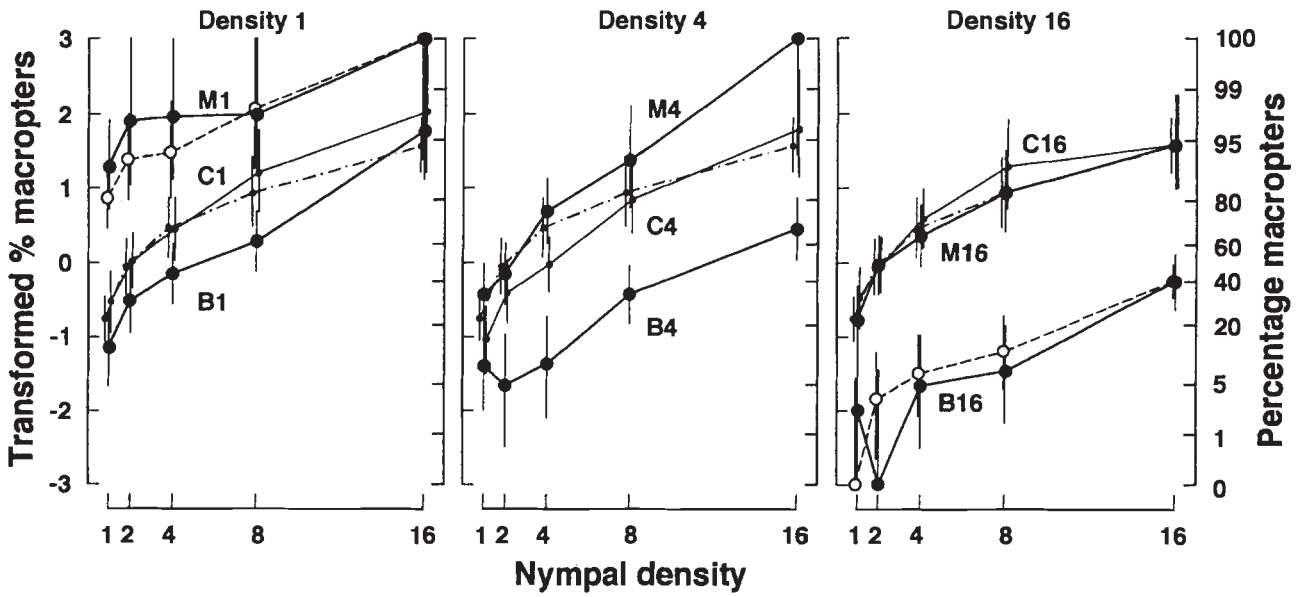

Fig. 3 Relationship between nymphal density and macroptery (per cent) in female *Sogatella furcifera* from macropter- and brachypter-selected lines after 10 generations of selection. Solid lines indicate replicate 2; dashed lines indicate replicate 1; dash-dotted lines show the base population (generation 1). Vertical lines represent the 95 per cent confidence interval (*F*-test). See also the caption of Fig. 2.

Few individuals in the M1 line moulted into brachypters across all density conditions (Fig. 3). There was a significant difference in macroptery (per cent) between M1 and their control (C1) lines at rearing densities of 1, 2 and 4 ($P<0.05$, F-test). In contrast, a high proportion of individuals in the B16 line moulted into brachypters even when they were raised under high density conditions (Fig. 3). There was a significant difference in macroptery (per cent) between B16 and their control (C16) lines at rearing densities of 2, 4, 8 and 16 ($P<0.05$, F-test). No significant difference in the relationship between macroptery (per cent) and nymphal density was observed between the base (generation 1) line and the control lines (C1, C4 and C16) (F-test) (Fig. 3).

Crossing experiment

Macroptery (per cent) of female progeny increased with increase in rearing density in the F_1, the F_2 and the backcross lines (Table 1). In contrast, males moulted into macropters regardless of rearing density across all crossing lines. Thus, macropterous males were used as parents in all crosses. However, no significant difference in the wing-form ratio of female progeny was detected between most of the reciprocal crosses in the F_1, the F_2 and the backcross lines (χ^2-tests) (Table 1). These results show that males do not differ from females in their genotype of brachyptery, although the phenotype of males is still macropters.

The wing-form responses to density in the parents, the F_1, the F_2 and the backcross lines are calculated as the pooled value for each reciprocal cross (Fig. 4). The percentage of macropters in the F_1 line was similar to that found in the B16 parent at low density. In contrast, under high density conditions, macroptery (per cent) in the F_1 was similar to that in the M1 line. At the intermediate density, the level of macroptery for the F_1 line fell between the M1 and the B16 lines.

Table 1 Percentage of female *Sogatella furcifera* macropters reared at different nymphal densities in parents, F_1, F_2 and backcrosses in the crossing experiments using the lines selected for macroptery (M1) and brachyptery (B16)

Initial density		1		2		4		8		16	
Cross	No. pairs	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Parent											
M1 (M)	22	52	80.8	48	91.7	43	93.0	52	98.1	42	100.0
B16 (B)	24	60	0.0	61	3.3	59	6.8	51	11.8	124	41.7
Mid-parent		112	40.4	109	47.5	102	49.9	103	54.9	166	70.2
F_1											
M × B (MB)	23	57	7.0	56	33.9	139	54.7*	57	70.2	56	100.0
B × M (BM)	22	48	6.2	54	25.9	136	40.4*	67	77.6	62	93.5
F_1 (mean)		105	6.7	110	30.0	275	47.6	124	74.2	118	96.6
F_2											
MB × MB	22	44	9.1	40	27.5	37	32.4	33	60.6	31	96.8
BM × BM	24	36	11.1	34	29.4	33	42.4	32	71.9	32	90.6
MB × BM	21	40	12.5	41	34.1	46	41.3	33	63.6	40	87.5
BM × MB	20	44	13.6	34	29.4	37	40.5	38	57.9	35	82.9
F_2 (mean)		164	11.6	149	30.2	157	39.2	136	63.2	138	89.1
Backcross											
MB × M	23	38	18.4	37	67.6	38	63.2	33	84.8	41	90.2*
M × MB	22	35	34.3	45	51.1	38	78.9	42	81.0	45	100.0*
BM × M	21	38	26.3	47	57.4	44	47.7**	44	84.1	48	95.8
M × BM	22	39	25.6	40	52.5	36	80.6**	41	90.2	39	100.0
Back-M (mean)		150	26.0	169	56.8	156	66.7	160	85.0	173	96.5
MB × B	22	33	6.1	40	10.0	46	28.3	42	26.2	31	74.2
B × MB	20	37	0.0	26	11.5	33	21.2	41	29.3	37	73.0
BM × B	24	31	0.0	33	9.1	37	21.6	40	32.5	33	78.8
B × BM	19	33	3.0	39	2.6	36	19.4	35	31.4	45	73.3
Back-B (mean)		134	2.2	138	8.0	152	23.0	158	29.7	146	74.7

Asterisks indicate significant differences between the reciprocal crosses (*$P<0.05$; **$P<0.01$; χ^2-test).

Genetic analysis

Genetic analysis of the inheritance of wing-form was conducted assuming that wing-form is controlled by a single locus with two alleles, with either macroptery or brachyptery being completely dominant. The observed macroptery (per cent) for the F_1 was significantly different from the predicted macroptery (per cent) among all rearing density conditions (χ^2-test) (Table 2). Thus, the inheritance of wing-form determination on *S. furcifera* was not simply Mendelian.

Next, wing-form data were applied to the threshold model proposed by Falconer (1989). The mean (m) of the F_1 was intermediate between the values of parental M1 and B16, and the mean of the F_2 was near that for the F_1, but had a much larger variance (V) (Table 3). Backcross means fell between the F_1 and the mid-parent lines, and had variances between those for the F_1 and the F_2. These results agreed well with the general expectation for a polygenic character and suggested that a continuously varying character such as hormonal titre underlies the expression of wing-form in *S. furcifera*.

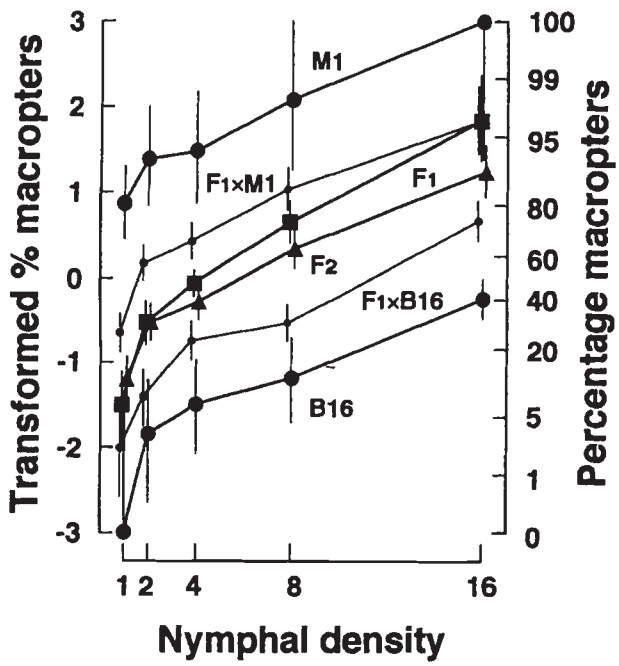

Fig. 4 Relationship between macroptery (per cent) in female *Sogatella furcifera* and nymphal density in the parents, the F_1, the F_2 and the backcrosses in the crossing experiment using the lines selected for macroptery and brachyptery (M1 and B16, replicate 1 in Fig. 1). Vertical lines present the 95 per cent confidence interval (F-test). See the caption of Fig. 2 for scale transformation.

Heritability

Broad sense heritability, estimated by the difference in variance between the F_2 and the F_1 was at least 0.467 (Table 3). The mean realized heritability was 0.512 ± 0.006 (average $\pm$SE) estimated from the lines selected for macroptery (M1) and 0.298 ± 0.052 from the lines selected for brachyptery (B16). These values were significantly greater than zero ($P < 0.001$, t-test) but the two estimates were significantly different from each other ($P < 0.01$, t-test). The possible reason for the difference in the two estimates is that the M1 and B16 lines were maintained under different density conditions; the former was conducted at low density and the latter was conducted at high density.

Reaction norm

Transformed percentage of macropters was plotted against nymphal density in each generation of selection for macroptery and brachyptery (Fig. 5). Regression coefficients (b) (i.e. reaction norm) were calculated separately in the base population and in generations 4 and 10. The transformed reaction norm moved from right to left in selection for macroptery, whereas it moved from left to right in selection for brachyptery. There were highly significant effects attributable to density ($P < 0.001$) and generation ($P < 0.001$), but no significant interaction between any of these regressions (F-test). This proves that there is no genotype-by-environment (G x E) interaction between wing-form and density.

Discussion

Wing dimorphism in *S. furcifera* is highly sensitive to environmental cues such as nymphal density (Kisimoto, 1956). Furthermore, the present study proves that wing-form in *S. furcifera* has a genetic basis. Selection for increasing incidence of macropters was most effective under low nymphal density conditions, while selection for brachyptery was most effective under crowded conditions (Fig. 2). In other words, antagonistic selection was better than synergistic selection for changing the wing-form ratio. These results strongly support Falconer's (1990) suggestion that the best improvement of mean performance should be achieved by antagonistic selection. These responses to wing-form selection also suggest that the sensitivity of the developmental switch to nymphal density changed bidirectionally with wing-form selection. An important message from these results is that the genetic assessment of

Table 2 χ^2-tests on the percentage of female *Sogatella furcifera* macropters at different nymphal densities in the F_1, the F_2 hybrids, and backcrosses in the crossing experiment using the lines selected for macroptery and brachyptery (M1 and B16, the first replicate in Fig. 1)

			Assuming M-dominant		Assuming B-dominant	
Cross	Density	Observed (%)	Predicted (%)	χ^2	Predicted (%)	χ^2
F_1	1	6.7	56.1	59.671***	0.0	7.241**
	2	30.0	71.6	38.101***	17.3	4.879*
	4	47.6	74.6	41.736***	25.1	30.148***
	8	74.2	87.0	6.468*	34.0	40.394***
	16	96.6	100.0	4.069*	63.5	40.509***
F_2	1	11.6	6.7	2.389	6.7	2.389
	2	30.2	30.0	0.001	30.0	0.001
	4	39.2	47.6	2.210	47.6	2.210
	8	63.2	74.2	3.796	74.2	3.796
	16	89.1	96.6	5.830*	96.6	5.830*
Backcross	1	26.0	57.6	30.840***	23.2	0.317
$F_1 \times M$	2	56.8	75.8	13.723***	52.4	0.649
	4	66.7	80.9	8.157**	66.6	0.001
	8	85.0	93.0	5.169*	85.3	0.006
	16	96.5	100.0	6.106*	98.3	1.060
Backcross	1	2.2	3.4	0.325	0.0	3.034
$F_1 \times B$	2	8.0	17.7	5.858*	9.9	0.322
	4	13.0	30.1	1.965	18.0	1.192
	8	29.7	52.3	16.580***	29.5	0.002
	16	74.7	85.8	5.691*	62.4	5.078*

Predicted values were calculated assuming: (i) that macroptery is completely dominant; and (ii) that brachyptery is completely dominant in a pair of alleles.
*$P<0.05$; **$P<0.01$; ***$P<0.001$.

Table 3 Parameter values when wing-form data from *Sogatella furcifera* were applied to the threshold model proposed by Falconer (1989)

Cross	p_1 (%)	p_2 (%)	m	Em	σ	V
Parent M	91.1	91.7	3.01		1.45	2.11
Parent B	11.8	3.3	−1.82		1.53	2.34
F_1	74.2	30.0	0.55	0.60	0.85	0.73
F_2	63.2	30.2	0.40	0.58	1.17	1.37
Backcross						
to M	85.0	56.8	1.20	1.78	1.16	1.34
B	29.7	8.0	−0.61	−0.63	1.14	1.30

The percentage of macropters (p_1 and p_2), above two thresholds, T_1 at density 8 and T_2 at density 2, the population mean (m) as deviations from T_1 in threshold units, the expected mean (Em), the standard deviation (σ) and the variance (V). The value of Em shown in the F_1, 0.60, is the mid-parent value.

Broad sense heritability ($V_G/(V_G+V_E)$) was estimated from the difference of variance between the F_2 and the F_1 as follows. F_2: $V_G+V_E=1.37$; F_1: $V_E=0.73$; F_2–F_1: $V_G=0.64$; $V_G/(V_G+V_E)=0.467$.

threshold characters such as wing-form should be conducted across a range of environmental (density in this case) conditions.

The responses to wing-form selection were asymmetrical and the direction of asymmetry depended on density (Fig. 2). Because the incidence of macropters of the base population was positively density-dependent, the starting point of selection was low in density 1 and was high in density 16 (Fig. 2). Thus, asymmetrical responses could be a consequence of the relation of the starting point to the selection limits, which results from the percentage scale.

The present study also revealed that the mode of inheritance of wing dimorphism in *S. furcifera* is polygenic. The genetic analysis (Table 3) is also consistent with the threshold model for wing-form determination proposed by Roff (1986) who suggests that wing-form is expressed by a threshold response of an underlying continuous factor. Such a factor is thought to be a kind of juvenile hormone (Southwood, 1961; Harrison, 1980; Roff, 1986). Thus,

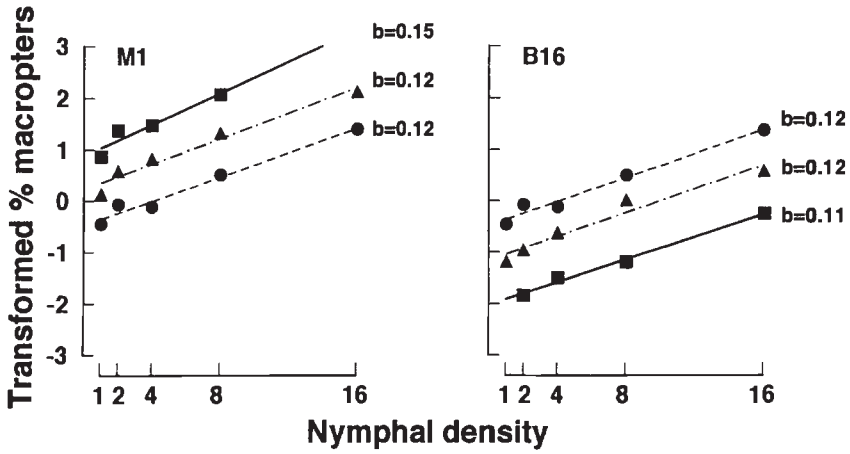

Fig. 5 Reaction norms in the base population (circles), after the fourth (triangles) and the 10th (squares) generations of selection for macroptery (M1) and brachyptery (B16) in *Sogatella furcifera*. Lines show regressions fitted to the base population (dashed), after the fourth (dash-dotted) and the 10th (solid) generations separately. See the caption of Fig. 2 for scale transformation.

brachypters would be produced if the titre of juvenile hormone exceeds a critical threshold level during a particular stage of development. Iwanaga & Tojo (1986) reported that the topical application of juvenile hormonal and the analogue methoprene on *Nilaparvata lugens* increased the proportion of brachypters. Their results agree well with the above hormone-based model. The hormone control of wing-form has been investigated in the wing-dimorphic cricket, *Gryllus rubens* (Zera & Tiebel, 1989; Zera *et al.*, 1989; Zera & Tobe, 1990; Zera & Holtmeier, 1992). The endocrine regulation of wing dimorphism, however, has not yet been investigated in detail for any planthopper species.

The present study showed that the relationship between wing-form ratio and nymphal density (i.e. reaction norm) was parallel (Fig. 5), which proves that there was no genotype-by-environment (G × E) interaction. These data support the environmental threshold (ET) model (Roff, 1994), which predicts that across environments differing in only one factor (density in this case) the genetic correlation will be 1.

Jinks & Connolly (1973) suggested that antagonistic selection reduces environmental sensitivity if there is G × E interaction. In the present study, however, there is no G × E interaction between wing-form and nymphal density (Fig. 5). Consequently, environmental sensitivity did not change by antagonistic selection. Only the incidence of macropters rapidly changed by antagonistic selection (Fig. 2). The reason why only antagonistic selection rapidly improved the mean performance could be explained by the relationship between the starting point of selection and the selection limit. It was larger in antagonistic selection than in synergistic selection (Fig. 2).

In the long-distance migratory planthopper, *S. furcifera*, wing-form response to density was very different between sexes, i.e. macroptery (per cent) was positively density-dependent in females (Fig. 3) but males moulted into macropters regardless of density conditions. This agrees well with the suggestion that the male bias toward macroptery is a characteristic which facilitates habitat escape and mating location in a temporary habitat (see Denno *et al.*, 1991).

Wing dimorphism is the most obvious and extreme expression of polymorphism for migratory ability, and the macropterous morph is generally interpreted as the migratory morph (Denno *et al.*, 1991; Roff & Fairbairn, 1991). However, the present results show that males do not differ from females in their genotype for wing-form although there are very different phenotypes between sexes. Thus, it is predicted that there is some variation for migratory ability within the macropterous morph. Because specific combinations of traits are associated with a migration syndrome (Southwood, 1961; Harrison, 1980; Roff, 1986), selection for or against macroptery could lead not only to a direct response to selection but also to a correlated response in other life history traits (Roff & Fairbairn, 1991). It is an important aspect to understanding the adaptive significance of dispersal in field populations of the wing-dimorphic planthopper, *S. furcifera*. Further work should focus on a correlated response to wing-form selection.

In conclusion, the present study suggests that the wing-form in *S. furcifera* is a heritable trait which is determined by a threshold response to nymphal density. My genetic analysis strongly supports Roff's (1986) threshold model for the determination of wing dimorphism, which is an elegant hypothesis for

understanding the evolution of wing dimorphism in insects.

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