Detection of QTLs Affecting Whitebacked Planthopper Resistance in an Indica/Japonica Doubled Haploid Rice Population

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水稻籼粳交 DH 群体中影响白背飞虱抗虫性 QTL 的检测

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摘　要:分析了水稻籼粳交加倍单倍体(DH)群体中影响白背飞虱抗虫性和感虫性的 QTL。虽然 DH 株系的亲本窄叶青 8 号和京系 17 没有拒取食抗性，但是白背飞虱在 6 个 DH 株系中的取食受到了强烈的抑制，可能属超亲分离。在第 3 染色体的粳型片段中检测到 1 个影响蜜露分泌的微效 QTL。粳稻亲本京系 17 具有杀卵抗性。DH 株系中的杀卵特性是通过叶鞘上杀卵反应产生的坏死症状表现的。在 DH 株系分蘖早期和中期，将 4 个杀卵作用的 QTL 定位在第 1、2、6 和 8 染色体的粳型片段上。出现在分蘖中期的另一个 QTL 被定位在第 9 染色体的籼型片段上。在分蘖盛期至孕穗期，杀卵位点减少至 2 个。整个试验期间对每个 DH 株系的最高杀卵级别的分析显示，在染色体 2、6 和 9 上共有 4 个 QTL。两个主效 QTL 位于近邻第 6 染色体的粳型片段。在第 1、3 和 5 染色体上检测到 3 个影响第 2 代白背飞虱若虫密度的 QTL。第 3 染色体上起主要作用的 QTL 源自粳稻亲本；第 5 染色体上的微效 QTL 源自籼稻亲本。两个白背飞虱为害的 QTL 位于第 8 和第 10 染色体的籼型片段，另一个 QTL 位于第 3 染色体的粳型片段。这些 QTL 被认为与水稻品种对白背飞虱田间抗性表达有关。

关键词:白背飞虱；品种抗性；加倍单倍体群体；水稻；数量性状位点

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Abstract:Quantitative trait loci (QTLs) affecting the whitebacked planthopper (WBPH) resistance and susceptibility in an indica/japonica doubled halpoid (DH) rice population were analyzed. Although the parents of DH lines, Zhaiyeqing 8 (ZYQ-8, indica) and Jingxi 17 (JX-17, japonica), had no sucking inhibitory resistance, WBPH sucking was strongly suppressed in six DH lines for possible transgressive segregation. A minor QTL affecting honeydew excretion was detected at a japonica segment of chromosome 3. Japonica parent JX-17 had ovicidal resistance to WBPH. Ovicidal trait in DH lines was phenotyped by necrotic symptoms on the leaf sheaths due to ovicidal response. Four ovicidal QTLs were located on japonica segments of chromosomes 1, 2, 6, and 8 in DH lines at early- and mid-tillering stages. One more QTL appearing at mid-tillering stage was located on an indica segment of chromosome 9. The ovicidal loci reduced to two at the maximum tillering to booting stage. Analysis based on the maximum score of ovicidal symptom for each DH line throughout the experimental period revealed four QTLs on chromosomes 2, 6 and 9. Two major QTLs were located closely on japonica segments of chromosome 6. Three QTLs affecting the density of the second-generation WBPH nymphs were detected on chromosomes 1, 3 and 5. A main-effect QTL on chromosome 3 was derived from the japonica parent. A minor QTL on chromosome 5 came from the indica parent. Two QTLs for WBPH damages were located on indica segments of chromosomes 8 and 10, and the other QTL on a japonica segment of chromosome 3. These QTLs were considered to be associated with the expression of field resistance of rice varieties to WBPH.

Key words: whitebacked planthopper; varietal resistance; doubled haploid population; rice; quantitative trait locus

1　Introduction

The whitebacked planthopper (WBPH), *Sogatella furcifera* , is a rice-monophagous herbivore originally associated with tropical paddy ecosystems in Asia. WBPH is also a well-known migratory paddy pest in the monsoonal East Asia[16]. Japonica rice in temperate East Asia evolved a unique ovicidal response to cope with annual invasions of WBPH by distant migration. WBPH eggs suffered high mortality in the necrotic lesions induced at oviposition sites of the rice plants[13,15,17,18]. Undoubtedly, this self-defense mechanism plays a potential role in protection of japonica rice from sporadic invasions of WBPH but not from unusual massive

invasions. On the other hand, sucking inhibition and subsequent antixenosis are the common mechanisms of varietal resistance to WBPH in indica germplasm[2,4,8,9]. So far, six major genes for WBPH resistance in indica rice have been identified by a standard seedbox screening test[1,6,10,12,14,22]. However, no varieties have been bred with the objective of incorporating these major genes. Nevertheless, it has been pointed out that some IR varieties having no major genes for WBPH resistance express practical resistance and/or tolerance to WBPH in the fields[19]. This evidence seems to indicate that unknown genetic traits other than major genes play more practical and significant roles in field resistance to WBPH.

In the present studies, we tried to detect quantitative trait loci (QTLs) associated with resistance and susceptibility to WBPH in an indica/japonica doubled-haploid rice population for better understanding of the genetic mechanisms of field resistance and breeding durable resistance to WBPH in rice.

2 Materials and Methods

2.1 Plant materials

A doubled haploid (DH) mapping population was established by anther culture of F_1 plants from the cross between Zhaiyeqing 8 (ZYQ-8, indica) and Jingxi 17 (JX-17, japonica)[23].

2.2 Evaluation of WBPH-susceptibility in ZYQ-8 and JX-17

Honeydew excretion and egg mortality in the parents of DH lines, ZYQ-8 and JX-17, were measured by using the young plants at early tillering stage, which were grown individually in disposable plastic cups (7 cm in diameter, 9 cm in height). Gravid females were individually confined onto the upper portion of leaf sheath of each plant with parafilm sachets (2 cm×2 cm), and allowed to suck and lay eggs for a day at room temperature (26 — 30 ℃). About thirty plants were used for each variety. Amount of honeydew excreted were quantified by weighing. Egg mortality was calculated by counting live and dead eggs at 5 — 6 days after oviposition by dissecting the leaf sheath tissues at oviposition sites. Eggs with reddish eye-spots were recorded as developing live eggs, and white opaque eggs as dead ones.

Population buildup of WBPH on ZYQ-8 and JX-17 was compared by introducing four pairs of adult WBPH to each potted plant at early tillering stage by using nylon-mesh cages (15 cm in diameter, 45 cm in height). After 25 days all nymphs and adults emerging in each cage were collected, dried at 70 ℃ for two days, and weighed. Five plants were used for each variety.

2.3 Measurement of honeydew excretion in DH lines

Five seedlings for each DH line were grown in a plastic vessel (14 cm in diameter, 15 cm in height) until early tillering stage under open conditions. Totally 102 lines were employed for the honeydew measurement. Gravid females were individually confined onto the upper portion of leaf sheaths of each plant with parafilm sachets (2 cm×2 cm), and allowed to suck for a day at room temperature (26—30 ℃). The largest value among five replications was subjected to QTL analysis.

WBPH-resistance performance of the DH lines was evaluated based on ovicidal symptoms, nymphal density and plant damage. Thirty seedlings of each DH line were transplanted in a small plot (0.8 m×1.5 m). Two sets of DH lines were transplanted on June 13 (plot A) and June 21 (plot B), and grown under the natural infestations with WBPHs without spraying any pesticides. A necrotic symptom on leaf sheaths due to ovicidal response was recorded on July 5, July 15 and August 6, when the immigrant, the first- and second-generation adults laid eggs. Intensity of the ovicidal symptom was visually scored from 0 (no symptom) to 3 (conspicuous elongated necrotic symptom). Average score of five plants for each line was recorded. Average scores between the plots A and B were subjected to the QTL analysis. Categories of ovicidal symptom are as follows:

0— no visible symptom;

1— brownish oviposition damages, but no watery lesions;

2— discontinuous watery lesions;

3— vertically elongated watery lesions.

Densities of the first- and second-generation nymphs were recorded according to the scores from 0 to 3 by visual estimation on the plot basis as given below. Average score of the plots A and B was subjected to the QTL analysis.

0— none or very few nymphs;

1— small number of nymphs;

2— nymphs form colony mainly on leaf sheaths;

3— large number of nymphs distributed on the whole plant.

Plant damage caused by WBPH infestations was recorded on September 6 after the WBPH adults of the second generation emigrated. The level of damage was scored on the plot basis dividing into four grades as given below. Average score of the plots A and B was subjected to the QTL analysis.

0— no damage;

1— only lower leaves of plant died;

2— lower half of plant died;

3— three fourths of plant died;

4— whole plant died.

2.4 QTL analysis

A linkage map containing a total of 160 RFLP and 83 SSR markers distributed evenly on all 12 rice chromosomes was constructed by using Mapmaker/EXP version 3.0 as described previously[3,11]. Mapmaker/QTL version 1.1 was used for chromosomal localization of the QTLs associated with resistance and susceptibility to WBPH in the DH popu-

lation and estimation of the percentage of the phenotypic variance explained by each QTL that exceeded a threshold LOD score of 2. 00.

3 Results

3.1 Susceptibility to WBPH in ZYQ-8 and JX-17

WBPH females excreted 14. 0 ± 5. 7 mg ($n = 28$) and 12. 6±6. 0 mg ($n=27$) honeydew/(female • day) on ZYQ-8 and JX-17, respectively. These honeydew values indicated that ZYQ-8 and JX-17 had no sucking inhibitory trait that could be discriminated them by honeydew values. However, WBPH egg mortality was significantly different between the parental varieties, 30. 4% ± 32. 2% ($n=24$) in ZYQ-8 and 82. 4%±19. 8% ($n=24$) in JX-17, respectively (Fig. 1). Four pairs of WBPH adults reproduced progenies of 62. 2± 17. 4 mg ($n=9$) and 135. 9±54. 5 mg ($n=6$) dry weight that on JX-17 and ZYQ-8, respectively, indicating that WBPH reproduction on ZYQ-8 was significantly higher than on JX-17.

3.2 QTL associated with honeydew excretion

Honeydew weights ranged from 1. 6 to 45. 9 mg/(female • day) among 90 DH lines tested. The frequency distribution of honeydew weights was indicative of transgressive segregation and polygenic control of the traits (Fig. 2). Although the parental varieties have no sucking inhibitory trait, 6 DH lines on which WBPH females excreted less than 5 mg/(female • day) of honeydew strongly suppressed sucking of WBPH. Only a small QTL was located on chromosome 3, which was flanked by markers RG266 and C63 and explained 14. 2% of phenotypic variance with a LOD score of 2. 23.

3.3 QTLs for ovicidal symptoms

Necrotic symptoms on the leaf sheaths due to ovicidal response were recorded at three different growth stages of DH lines. Percentages of DH lines that showed typical ovicidal symptoms (score 3) increased from 4% to 33% for a month from early to maximum tillering stages (Fig. 3). Totally 43% of DH lines expressed ovicidal symptoms (scores 2 and
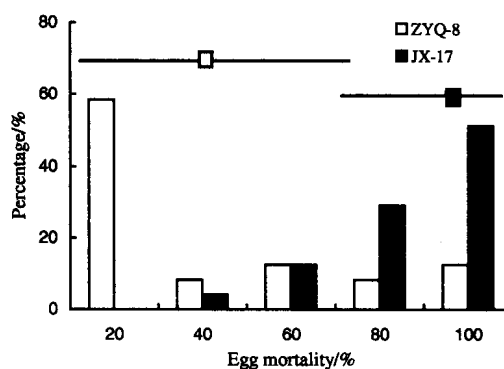

Fig. 1. Frequency distribution of egg mortality in ZYQ-8 and JX-17.

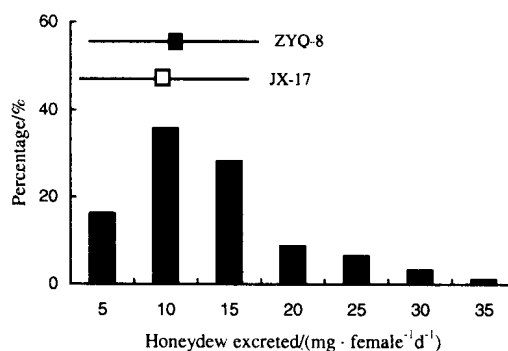Bars in the figure indicate mean and SD.

Fig. 2. Frequency distribution of honeydew excretion in the DH-population.

Bars in the figure indicate mean and SD for honeydew excretion in the parents, ZYQ-8 and JX-17.

3), while 29% had no symptoms (score 0). The remaining 28% showed intermediate response (score 1). The frequency distribution of ovicidal scores was not normal. All the ovicidal QTLs detected were listed in Table 1 and illustrated in Fig. 4.

Four QTLs were detected on chromosomes 1, 2, 6, and

Table 1. Characteristics of QTLs associated with the ovicidal symptoms due to WBPH oviposition.

| Rice growing stage	QTL	Chromosome	Marker interval	Peak LOD	Variance explained	Additive effect
Early tillering stage	qOVC-1b	1	GA594 — CT380A	2. 32	10. 0	0. 52
(Early July)	qOVC-2b	2	G357 — GA120	2. 09	9. 5	0. 51
	qOVC-6c	6	G200 — C235	2. 29	9. 2	0. 52
	qOVC-8	8	BP127A — RZ617	2. 60	9. 5	0. 52
Mid-tillering stage	qOVC-1a	1	CT158 — CT550	2. 27	11. 7	0. 71
(Mid-July)	qOVC-2c	2	GA120 — GA43	2. 29	8. 8	0. 61
	qOVC-6b	6	CT115 — CT506	3. 38	12. 1	0. 72
	qOVC-8	8	BP127A — RZ617	2. 54	9. 3	0. 65
	qOVC-9	9	G103 — G93F	2. 52	13. 4	−0. 75
Max. tillering stage	qOVC-2a	2	G1327 — C132	2. 38	9. 6	0. 81
(Early August)	qOVC-6b	6	CT115 — CT506	6. 63	27. 3	1. 39
Max. ovicidal scores during tillering stage	qOVC-2c	2	GA120 — GA43	2. 22	8. 7	0. 71
	qOVC-6a	6	CT201 — RZ450	7. 00	25. 7	1. 24
	qOVC-6b	6	CT115 — CT506	7. 31	29. 6	1. 33
	qOVC-9	9	G103 — G93F	2. 30	12. 4	−0. 84
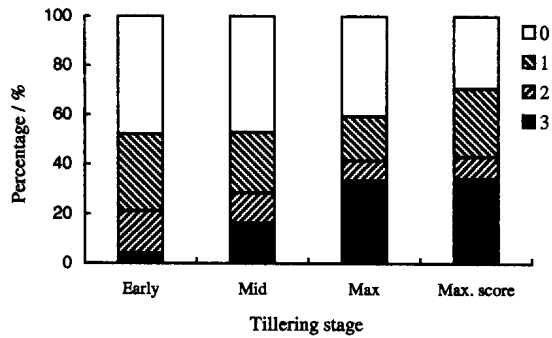
Fig. 3. Percentages of DH lines with different intensity of ovicidal symptoms (scored from 0 to 3) at different tillering stages of rice plants, and percentage of DH lines which were grouped based on the maximum ovicidal score recorded during the experimental period.

8 in the plants at early tillering stage. The QTL (*qOVC-8*) on chromosome 8, which was localized at the region flanked by BP127A and RZ617, gave a relatively higher LOD score of 2. 60 compared to the remaining 3 QTLs that had LOD scores ranging from 2. 09 to 2. 32. All the QTLs were derived from the japonica parent JX-17. Five ovicidal QTLs were detected at mid-tillering stage in mid-July. Of them, four QTLs were

located at the identical or near chromosomal regions where the corresponding ovicidal QTLs were detected at early tillering stage. The QTL (*qOVC-6b*) flanked by the markers CT115 and CT506 on the chromosome 6 gave the highest LOD score of 3. 38. In addition to these, one more QTL (*qOVC-9*) was detected on chromosome 9, which was derived from the indica parent ZYQ-8. The percentage of phenotypic variance explained by any single QTL ranged from 8. 8 to 13. 4, indicating a small contribution of each QTL. The QTLs on chromosomes 1 and 8 were associated with the ovicidal response of the DH lines only at early- and mid-tillering stages. The QTL on the indica chromosomal region appeared after mid-tillering stage. When the DH population reached the maximum tillering to booting stage in early August, ovicidal symptoms appeared strongly and discriminatingly among the lines after oviposition by the newly emerged WBPH females. Two QTLs (*qOVC-2a* and *qOVC-6b*) were mapped on chromosomes 2 and 6. The QTL flanked by markers CT115 and CT506 on chromosome 6 explained 27. 2% of phenotypic variance with a LOD score of 6. 63. The QTLs on chromosomes 1, 8 and 9 were not detected. The analysis based on the maximum ovicidal symptom score for each DH line throughout the experimental period revealed four QTLs on
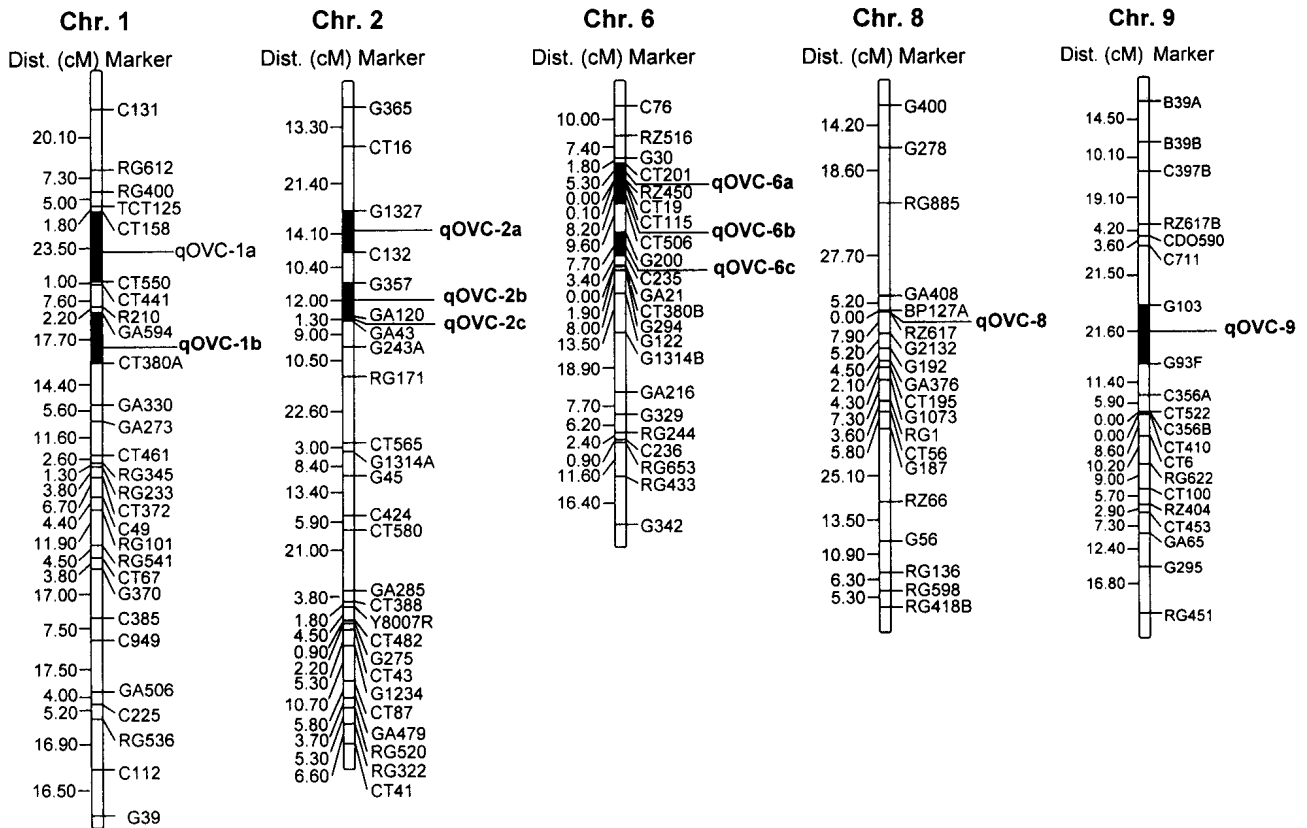

Fig. 4. Location of ovicidal QTLs on rice chromosomes.

The markers used for the linkage analysis are shown on the right of each chromosome. Scales in Kosambi cM are shown on the left of each chromosome.

chromosome 2, 6 and 9. Two major QTLs (*qOVC-6a* and *qOVC-6b*) were located on the two adjacent segments of CT201 — RZ450 and CT115 — CT506 on the short arm of chromosome 6, which accounted for 25.7% and 29.6% of the phenotypic variance with a LOD score of 7.00 and 7.31, respectively.

3.4 QTLs associated with density of WBPH nymphs

The average number of WBPH immigrants that settled in the DH line fields was 0.96 females/hill in early July. The first- and second-generation nymphs reached a peak in mid-June and early August, respectively. Overall average density scores of nymphs at the first- and second-generations were 0.60 and 1.16, respectively. At the first generation, the density scores of 87.8% DH lines were 0 or 1, and there were no DH lines of score 3. DH lines scoring 0, 1, 2 and 3 were 34.1%, 26.0%, 29.3% and 10.6%, respectively, when the density of second-generation nymphs peaked (Fig. 5).

No significant QTL that was associated with the density scores of the first-generation nymphs was detected. However, three QTLs were detected in relation to the density scores of the second-generation nymphs (Table 2). They were mapped on chromosomes 1, 3 and 5. A major QTL (*qNYM-3*) flanked by RG450 and RG266 on the chromosome 3 accounted for 21.5% of the phenotypic variance with a LOD score of 4.86. It was derived from the japonica parent JX-17, while the QTL (*qNYM-5*) on chromosome five was from the indica parent ZYQ-8. The chromosomal locations of these QTLs were illustrated in Fig. 6.

3.5 QTLs affecting WBPH damages

No visible damages were recorded in five DH lines. The remaining 96% of DH lines were suffered damages to variable extents with WBPH infestations, and 12 DH lines were completely destroyed. Frequency distribution of DH lines divided by damage scores was normal (Fig. 7).

Two QTLs (*qDMG-8* and *qDMG-10*) were located on indica segments of chromosomes 8 and 10, and one (*qDMG-3*) on a japonica segment of chromosome 3 (Table 3). The most significant QTL (*qDMG-8*) was mapped to an indica segment
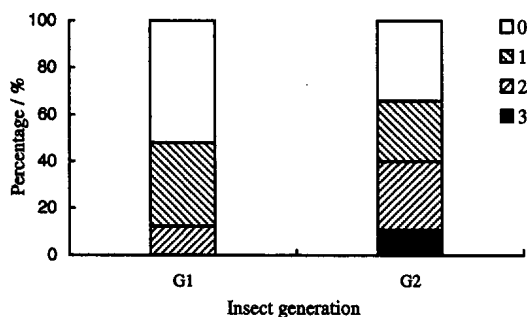
Table 2. QTLs associated with the density of 2nd generation nymphs of WBPH in the DH lines under the field condition.

QTL	Chromo-some	Marker interval	Peak LOD	Variance explained	Additive effect
qNYM-1	1	CT461—RG345	2.36	10.1	0.58
qNYM-3	3	RG450—RG266	4.86	21.5	0.85
qNYM-5	5	GA41—GA257	2.28	11.7	−0.66

Table 3. QTLs associated with damages of DH lines caused by WBPH infestations under the field condition.

QTL	Chromo-some	Marker interval	Peak LOD	Variance explained	Additive effect
qDMG-3	3	G249—G164	2.63	13.9	0.71
qDMG-8	8	G187—RZ66	4.54	22.7	−0.90
qDMG-10	10	G1082—GA223	2.01	7.7	−0.53

of chromosome 8 between G187 and RZ66, and accounted for 22.7% of the phenotypic variance with a LOD score of 4.54. The chromosomal locations of these QTLs were illustrated in Fig. 6.

4 Discussion

The indica and japonica parents, ZYQ-8 and JX-17, of the DH population employed in the present experiments have no sucking inhibitory trait. WBPH adults and nymphs equally prefer ZYQ-8 and JX-17. There was no significant difference in the honeydew excretion by WBPH females on both the parents. Thus, ZYQ-8 and JX-17 are equally susceptible to WBPH infestations in the standardized seedbox screening test (our unpublished data). However, japonica JX-17 has an ovicidal response to WBPH, which indica ZYQ-8 does not. Population buildup of WBPH was significantly higher on non-ovicidal ZYQ-8 as compared with ovicidal JX-17. The DH lines derived from the cross between ZYQ-8 and JX-17 showed considerable phenotypic variations in density of WBPH nymphs and damages to WBPH under natural infestations in the fields. Phenotypic variations among the DH lines are discussed with special reference to the field resistance to WBPH.

Sogawa first discovered the ovicidal response in japonica rice during his investigation of hypersensitivity to WBPH infestations in japonica/indica hybrid varieties[15]. Loss of the ovicidal response caused the hypersensitivity to WBPH in japonica rice bred by crossing with indica rice. This finding disclosed that WBPH infestations had long been suppressed in japonica rice by its potential ovicidal traits. Later on, the physiological processes of ovicidal response and an ovicidal substance have been clarified[13,18]. The genetic mechanism of ovicidal response was analyzed with a set of recombinant inbred (RI) rice lines derived from a japonica/indica cross between Asominori and IR24. Totally, 10 QTLs have been detected with RFLP markers[20]. It has been demonstrated that the QTL mapped to a japonica segment of chromosome 6,
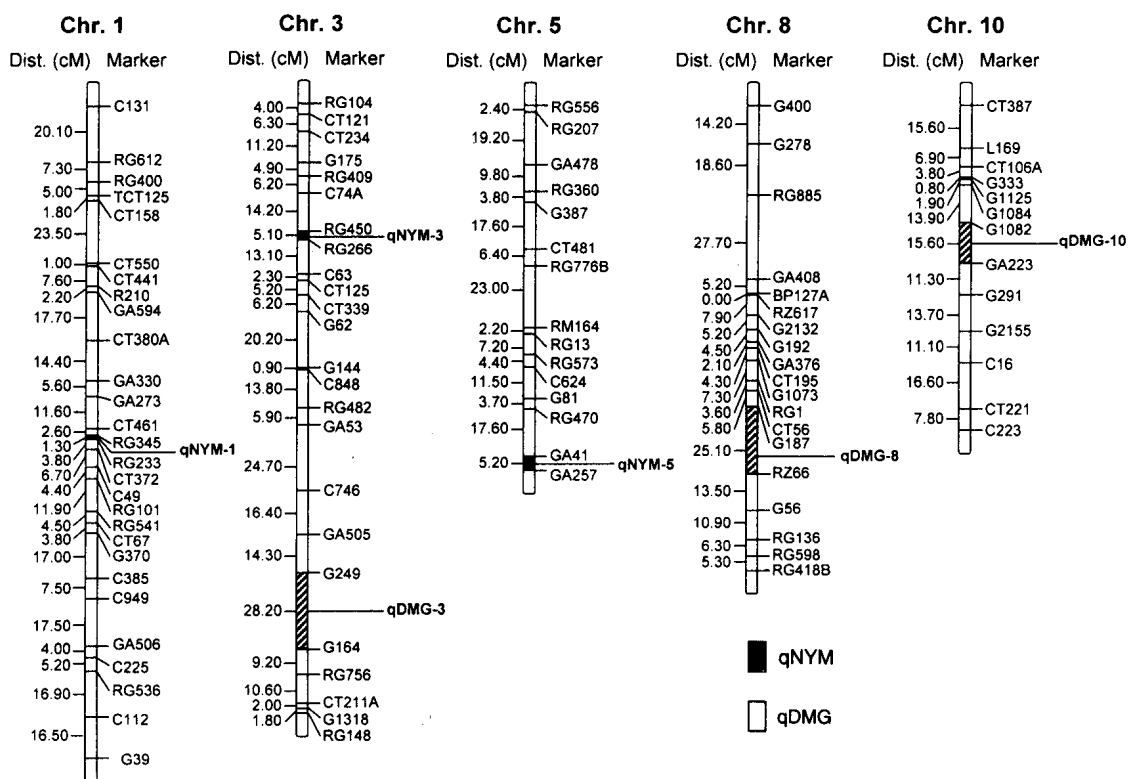

Fig. 5. Percentages of DH lines on which different densities (scored from 0 to 3) of WBPH nymphs occurred at the 1st (G1) and the 2nd generation(G2).

Fig. 6. Locations of QTLs associated with density of WBPH nymphs(qNYM) and plant damages due to WBPH infestation(qDMG).

flanked by the markers R1954 and L688, is most significantly associated with the ovicidal response, which accounts for 69.9% and 46.0% of phenotypic variance for ovicidal symptom (percentage of watery lesions) and egg mortality, respectively. This major QTL has been identified as a dominant major gene by linkage analysis, and designated as *Ovc* [21]. Some minor QTLs from indica IR24 were also found to contribute positively to the expression of ovicidal symptoms in the RI lines[20].

In the present experiments, 45 DH lines expressed definite ovicidal symptom (score 3), and 36 lines did not show any ovicidal response. The QTL analysis according to the maximum scores of ovicidal symptoms for each DH line
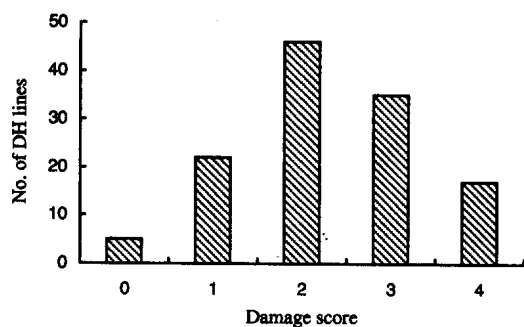

Fig. 7. Frequency distribution of DH lines suffered different levels of damages with WBPH infestations under the field condition.

revealed two major QTLs, which seemed to play a decisive role in the phenotypic expression of the ovicidal symptoms in the DH lines. They localized very closely on the short arm of chromosome 6, and accounted for 55.3% of phenotypic variance. These two putative QTLs could be identical to the ovicidal gene *Ovc* that was previously detected by using japonica / indica RI lines[20,21]. We also found that the expression of ovicidal response was affected by complicated accumulation of small QTLs. Four to five small QTLs were detected in the DH lines at early- to mid-tillering stage. It has been known that WBPH egg mortality increases steadily with progression of the tillering of rice plants until 10 weeks after planting[18]. Such progressive activation of ovicidal response might be responsible to differential accumulation of ovicidal QTLs at different growth stages of rice plants.

Density of the second-generation nymphs in 77.8% of the ovicidal DH lines scored 0 or 1. None of the ovicidal DH lines scored 3. On the contrary, 25% non-ovicidal DH lines scored 3, and 44.5% scored 0 or 1. WBPH nymphs propagated intensively (density score 3) on 13 DH lines. Of them, 10 DH lines suffered heavy damages scoring 3 or 4, while none of them scored 0 or 1. These interactions seemed to indicate that ovicidal response could be a genetic trait affecting the population buildup of WBPH nymphs. High density of the second-generation nymphs could be a condition that causes heavy damage. However, none of the ovicidal QTLs was involved among the nymphal density QTLs. Likewise, the

QTLs for nymphal density were independent from QTLs for damage. One of the QTLs for nymphal density, and the QTL for honeydew were located on adjacent segments of chromosome 3, which might indicate that a common genetic or physiological process is involved in both phenotypic expressions.

In the present investigation, at least 17 QTLs were found affecting the varietal performance to WBPH in the indica/japonica DH lines. Except for the main-effect ovicidal QTL, genetic and physiological mechanisms mediated by these QTLs remain obscure. Combinations of these QTLs could express field resistance and tolerance of rice varieties to WBPH. For example, Kadirvel *et al.* had indicated association of field resistance to WBPH in IR64 with a QTL on chromosome 11 for a tolerance parameter PDLOSS, plant dry weight loss per milligram of WBPH dry weight[7]. It has also been pointed out that 16 of 27 IR varieties, which are not incorporated with any major genes for resistance to WBPH, showed field resistance to the planthopper[19]. Besides, the level of resistance to WBPH varies significantly among the varieties with the same major resistance gene[5]. These evidences indicate that practical field resistance to WBPH in rice largely has a polygenic basis. Analysis of QTLs for resistance and tolerance to WBPH based on molecular marker linkage maps could increase our understanding in the mechanisms of practical field resistance, and facilitate breeding programs for rice with durable resistance to the planthopper.

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