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Identification and mapping of two brown planthopper resistance genes in rice

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Abstract The brown planthopper (BPH) is one of the most serious insect pests of rice. In this study, we conducted a molecular marker-based genetic analysis of the BPH resistance of 'B5', a highly resistant line that derived its resistant genes from the wild rice *Oryza officinalis*. Insect resistance was evaluated using 250 F_3 families from a cross between 'B5' and 'Minghui 63', based on which the resistance of each F_2 plant was inferred. Two bulks were made by mixing, respectively, DNA samples from highly resistant plants and highly susceptible plants selected from the F_2 population. The bulks were surveyed for restriction fragment length polymorphism using probes representing all 12 chromosomes at regular intervals. The survey revealed two genomic regions on chromosome 3 and chromosome 4 respectively that contained genes for BPH resistance. The existence of the two loci were further assessed by QTL (quantitative trait locus) analysis, which resolved these two loci to a 14.3-cM interval on chromosome 3 and a 0.4-cM interval on chromosome 4. Comparison of the chromosomal locations and reactions to BPH biotypes indicated that these two genes are different from at least nine of the ten previously identified BPH resistance genes. Both of the genes had large effects on BPH resistance and the two loci acted essentially independent of each other in determining t he resistance. These two genes may be a useful BPH resistance resource for rice breeding programs.

Keywords Molecular marker · Genetic mapping · *Nilaparvata lugens* Stål. · QTL · *Oryza officinalis*

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Introduction

The brown planthopper (abbreviated as BPH), *Nilaparvata lugens* Stål., is one of the most serious insect pests in Asia where rice is widely planted. In China, BPH caused only occasional damage in the southern rice-growing areas before the 1960s, whereas widespread outbreaks occurred frequently in the 1990s in the rice-producing areas of southern and central China. In addition to being a sucking insect that causes direct damage to the crop, it also transmits several viral diseases that cause crop additional damage.

The usual means for controlling the BPH pest by spraying poisonous chemicals is costly in terms of labor, money and environment. The application of resistant cultivars has generally been considered to be the most economic and environmentally sound strategy for pest management.

Four BPH biotypes are known. Biotypes 1 and 2 are widely distributed in Southeast Asia, biotype 3 is a laboratory biotype produced in the Philippines, and biotype 4 occurs in the Indian subcontinent (Khush and Brar 1991). Large efforts have been made to identify BPH resistance genes from various sources for developing resistant cultivars. Currently a total of ten resistant genes have been characterized according to their reactions to different BPH biotypes (Athwal et al. 1971; Lakshminarayana and Khush 1977; Sidhu and Khush 1979; Khush and Brar 1991; Ishii et al. 1994). The dominant gene *Bph1* confers resistance to biotypes 1 and 3. The recessive gene *bph2* is closely linked with *Bph1* and confers resistance to biotypes 1 and 2. Two closely linked genes, *Bph3* and *bph4*, confer resistance to all four biotypes. Three genes, *bph5*, *Bph6* and *bph7*, are resistant to biotype 4 but susceptible to biotypes 1, 2 and 3. Three genes, *bph8*, *Bph9* and *Bph10*(*t*), showed resistance to biotypes 1, 2 and 3.

Efforts have also been made over the years to determine the chromosomal locations of the BPH resistance genes. Two of the BPH resistance genes, *Bph1* and *bph2*, were assigned to chromosome 4 by Ikeda and Kaneda

Table 1 The criteria for brown planthopper resistance-scoring used in this study

Resistance score	Plant state (investigated when most of the Taichung Native 1 plants died)
0	None of the leaves shrank and the plant was healthy
1	One leaf was yellowing
3	One to two leaves were yellowing or one leaf shrank
5	One to two leaves shrank or one leaf shriveled
7	Three to four leaves shrank or two to four leaves shriveled, the plant was still alive
9	The plant died

(1983) using trisomic analysis. However, these two loci were later located to chromosome 12 according to the results of molecular marker-based studies (Hirabayashi and Ogawa 1995; Murata et al. 1998; Jeon et al. 1999). The trisomic analysis of Ikeda and Kaneda (1981) also assigned *Bph3* and *bph4* to chromosome 10. *Bph10*(t) was mapped to chromosome 12 using a molecular-marker analysis (Ishii et al.1994). Analysis of a doubled-haploid rice population derived from a cross between 'IR64' and 'Azucena' showed that quantitative trait loci (QTLs) that contributed to the BPH resistance of IR64 also existed on chromosome 1, 2, 3, 4, 6 and 8, in addition to a major gene on chromosome 12 controlling BPH resistance in this population (Huang et al. 1997; Alam and Cohen 1998).

Oryza officinalis Wall ex Watt is a wild rice species that occurs widely in South and Southeast Asia (Vaughan 1994). The majority of the accessions of *O. officinalis* collected in China are highly resistant to BPH (Li et al. 1990). In order to transfer the BPH resistance genes of *O. officinalis* into cultivated rice, a wide cross was made between an accession of *O. officinalis* collected in China and the cultivar Zhenshan 97B (Ma et al. 1993; Shu et al. 1994). BPH-resistant lines were selected from progenies of this cross (Yang et al. 1999). One of the progeny lines, 'B5', showed strong resistance to biotypes 1, 2 and to BPH insects collected from rice fields in Zhejiang Province, China. Thus 'B5' may be useful as BPH resistance germplasm for improving BPH-resistant in rice breeding programs.

In the study reported in this paper, we conducted a molecular marker-based genetic analysis of the BPH resistance of B5. The objectives were: (1) to characterize the BPH resistance of this line by determining the number and chromosomal locations of the BPH resistance genes, (2) to determine the amounts and modes of the genetic effects of the resistance genes, and (3) to find molecular markers closely linked to the resistance genes that may be useful for cloning the genes and for improving BPH resistance in rice breeding programs.

Materials and methods

Plant materials and insects

The genetic materials were an F_2 population of 250 plants and an F_1 plant from a cross between B5, a BPH-resistant line, and 'Minghui 63', a cultivar belonging to the indica subspecies. The BPH insects used for infestation included biotypes 1, 2 and also insects collected from rice fields in Zhejiang Province, China, kindly provided by Guangjie Liu of the China National Rice Research Institute. According to the report of Hu (1990), the BPH populations in China consisted of BPH biotypes 1 and 2, with biotype 1 occurring at predominantly high frequencies. These insects have been maintained in the Genetics Institute of Wuhan University since 1997 by feeding on 'Taichung Native 1', a cultivar highly susceptible to BPH.

Molecular-marker analysis

Total cellular DNA of B5, Minghui 63, and 250 F_2 individuals was extracted using essentially the CTAB method of Murray and Thompson (1980). Restriction digestion, electrophoresis, hybridization and detection followed the procedures described previously (Liu et al. 1997). Six restriction enzymes, namely, *Apa*I, *Bam*HI, *Hin*dIII, *Eco*RI, *Eco*RV and *Dra*I, were used for surveying restriction fragment length polymorphism (RFLP). The RFLP probes were kindly provided by the Japanese Rice Genome Research Project and by the Cornell University group.

Evaluation of BPH resistance

The seeds of B5, Minghui 63 and Taichung Native 1 (susceptible control) were separately sown in plastic pots 30-cm in diameter to assess the resistance. The seedlings were thinned at the three-leaf stage to ten plants in each pot and infested with 2nd to 3rd-instar nymphs at a density of ten insects per seedling. The number of days after infestation was recorded when all of the seedlings in a pot died.

To evaluate the BPH resistance of the F_1 plant, three tillers of each F_1, B5, Minghui 63 and Taichung Native 1 were planted in a plastic pot 30-cm in diameter. Ten days later, 300 insects of the 2nd to 3rd-instar nymphs were placed in the pot. The number of days when the plants died after infestation was recorded.

For evaluating the BPH resistance of each F_3 family, the seedling bulk test described by Pathak and Heinichs (1982) was followed with modification. About 15 seeds harvested from each F_2 individual were sown in a row of 20 cm length in a plastic box. The distance between rows was 2.5 cm. A total of four lines of B5, three lines of Minghui 63 and three lines of Taichung Native 1 were randomly planted among the F_3 families as controls. Seven days after sowing, seedlings were thinned to 12 plants per row. At the third-leaf stage, the seedlings were infested with 2nd to 3rd-instar nymphs of BPH at ten insects per seedling. When all of the seedlings of Taichung Native 1 died, the plants of the F_3 families were examined and each seedling was given a score of 0, 1, 3, 5, 7 or 9 according to the criteria in Table 1, which were based on the Standard Evaluation System for Rice (IRRI 1988). The resistance level of each F_2 plant was then inferred based on the weighted average of the seedlings in the corresponding F_3 families.

Determining the map locations of BPH resistant loci

Bulked segregant analysis (Michelmore et al. 1991) was used in screening RFLP markers linked to BPH resistance. According to the phenotypes of F_3 families, 28 F_2 individuals that were inferred to be

highly resistant to BPH were selected and equal amounts of DNA from these plants were mixed to form a resistant bulk. Similarly, equal amounts of DNA from 23 highly susceptible F_2 individuals were mixed to form a susceptible bulk. The two bulks and the two parents were screened for polymorphism using RFLP markers.

Local genetic linkage maps of RFLP markers from the BPH resistance gene-containing regions were constructed using Mapmaker/Exp 3.0 at LOD 3.0 (Lincoln et al. 1992a). QTL analysis of the resistance was conducted with Mapmaker/QTL 1.1 at a LOD threshold 3.0 (Lincoln et al. 1992b).

Results

BPH resistance evaluation

The resistance of the lines could be evaluated in two ways: the numbers of days after infestation before the seedlings were killed by BPH, and the severity score caused by the insects at the day on which Taichung Native 1, the susceptible control, was completely killed by the insects. The two evaluations produced essentially the same results: B5 was resistant to both biotypes 1 and 2 of BPH and also to insects collected from the field; Taichung Native 1 was highly susceptible to both biotypes as well as to insects from the field; and Minghui 63 was slightly less susceptible than the susceptible control to both biotypes and the natural population (Table 2). In the tiller test, tillers of Minghui 63 and Taichung Native 1 were killed by BPH insects 5 days after infestation, while no significant change was observed in B5 and F_1 tillers until 10 days after infestation. Thus, the F_1 was resistant to BPH insects.

The severity scores of the 250 F_3 families infested with insects from the natural BPH population of China showed a continuous distribution, ranging from a low of 2.00 to a high of 9.00, with an apparent valley around 5.5 in the distribution curve (Fig. 1). Such a distribution indicated the involvement of major genes controlling the segregation of BPH resistance in this population.

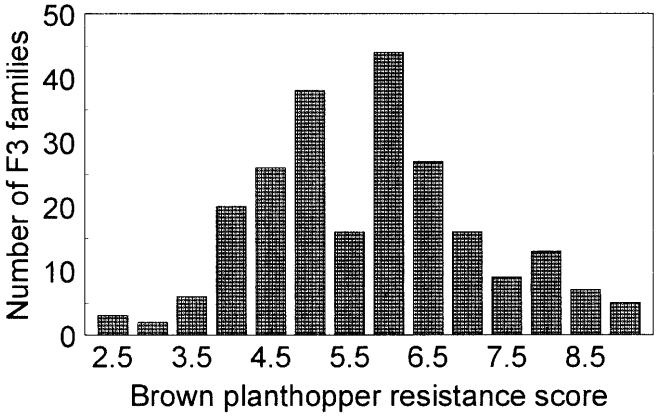

Fig. 1 Distribution of BPH resistance scores of the 250 F_3 families. The scores for thetwo parents, B5 and Minghui 63, were 2.62 and 8.46, respectively

Table 2 The scores of BPH resistance of the two parents and Taichung Native 1

Variety	Number of days after infestation[a]	Severity score[c]
Taichung Native 1	3	9.0 (24)
Minghui 63	4	8.5 (36)
B5	–[b]	2.6 (48)

[a] Number of days between the day of infestation and the day the plants were killed by BPH. The same results were obtained when the plants were infested with biotypes 1, 2, or insects from natural BPH population from China

[b] BPH could not kill the seedlings of this line

[c] The score of the severity averaged over plants on the day the susceptible control was completely killed by the insects. Numbers in parentheses are the numbers of seedlings used in the test

Determining the map locations of BPH resistance genes

A total of 393 DNA probes distributed along the 12 chromosomes of rice from the two published maps (Causse et al. 1994; Harushima et al. 1998) were used for the parental survey; polymorphism between the parents was detected with 126 (32%) of the probes. Eleven probes detected differences between the two bulks, of which five markers were from a contiguous region on chromosome 3 and six markers were from a contiguous region on chromosome 4. These positive markers indicated the existence of two BPH resistance genes located on chromosomes 3 and 4, respectively.

QTL analysis of BPH resistance

Additional markers from these two chromosomes were surveyed for polymorphism, and markers that were polymorphic between the parents were used to assay the 250 F_2 individuals, based on which the local linkage maps were constructed (Fig. 2). These maps covered 72.2 cM of chromosome 3 and 129.7 cM of chromosome 4, and marker orders in the maps were in good agreement with those in previously published maps (Causse et al. 1994; Harushima et al. 1998).

QTL analysis using Mapmaker/QTL 1.1 detected two QTLs for BPH resistance (Table 3 and Fig. 2). The first, designated *Qbp1*, detected with a LOD score of 12.89, was located in the 14.3-cM length interval between R1925 and R2443 on the long arm of chromosome 3. This QTL explained 26.4% of the phenotypic variance of BPH resistance in this population. The second QTL, *Qbp2*, was resolved with a LOD score of 7.69 to a 0.4-cM interval between C820 and R288 on the short arm of chromosome 4. This QTL accounted for 14.3% of the phenotypic variance of BPH resistance in this population. The two QTLs jointly explained 41.1% of the phenotypic variance of BPH resistance in this population.

At both of the QTLs, alleles from the resistant parent B5 significantly reduced the damage by the insects, as indicated by the additive effects estimated (Table 3). The

Table 3 QTLs identified for BPH resistance using the F_2 population of B5×Minghui 63

QTL	Interval	Chrom.	LOD	Var. explained (%)	Additive	Dominance
Qbp1	R1925–R2443	3	12.9	26.4	–0.995	–0.478
Qbp2	C820–R288	4	7.7	14.3	–0.743	–0.166
Total				41.1		

Table 4 A two-way analysis of variance of BPH resistance in the F_2 population based on genotypes of the marker locus that is most closely linked to the BPH resistance loci from each of the two genomic regions

Effect	*df*	MS	*F*	*P*
1 (R1925, *Qbp1*)	2	41.27	31.60	0.000
2 (C820, *Qbp2*)	2	27.30	20.90	0.000
1×2	4	3.95	3.03	0.019
Error	186	1.31		

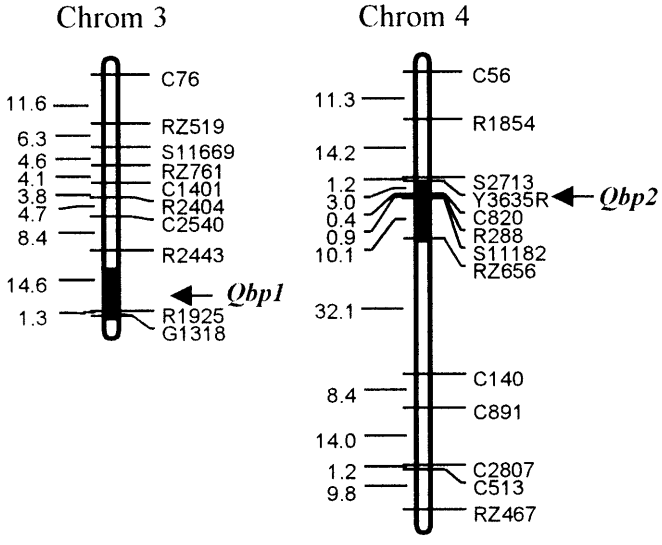

Fig. 2 The locations of two BPH resistance genes identified by QTL analysis. Marker names are listed on the right hand side of the chromosome with the distances (in cM) indicated on the left. The *solid bars* indicated the locations of the two loci for BPH resistance, designated as *Qbp1* and *Qbp2*

resistance showed partial dominance at both of the QTLs.

A two-way analysis of variance was carried out to assess possible interactions between the two QTLs, using as classes the genotypes of the marker locus located closest to the peak in each of the two QTL-containing regions. The analysis showed that the interaction effect, although statistically significant at the 0.05 probability level, was small compared to the main effects of the two QTLs (Table 4). Thus, these two QTLs can be regarded as acting essentially independent of each other in determining BPH resistance.

Discussion

The main finding of this study is the identification of two loci for BPH resistance carried by the resistant parent B5 derived from the wild rice *O. officinalis*. Molecular marker-based-QTL analysis resolved these two loci to the long arm of chromosome 3 and the short arm of chromosome 4, respectively.

It should be noted that both of the QTLs were major loci for BPH resistance as bulked segregant analysis can only detect loci with large effects, although the two QTLs jointly could only explain 41.1% of the phenotypic variance. Two factors may have contributed to such a low proportion of the genetic variation explained by the QTLs. First, BPH resistance is a very difficult trait to measure, as the scores vary with the conditions of plant growth, the insects, and also the environments under which the test was conducted. Second, the use of $F_{2:3}$ families also overestimated the experimental errors because of genetic heterogeneity within each of the F_3 families.

A number of BPH resistance genes have been reported in the literature. Three of these genes, *Bph1*, *bph2* and *Bph10*(*t*), are located on chromosome 12; two *Bph3* and *bph4*, are located on chromosome 10. In addition, three of the BPH resistance genes, *bph5*, *Bph6* and *bph7*, were demonstrated not to confer resistance to BPH biotypes 1, 2 or 3. More recently, Alam et al. (1998) also reported two QTLs for BPH resistance that were located on chromosomes 3 and 4. However, these two QTLs are on the short arm of chromosome 3 (between RG191 and RZ678) and the long arm of chromosome 4 (between RG163 and RG620), as opposed to the long arm of chromosome 3 and short arm of chromosome 4. The chromosomal locations of *bph8* and *Bph9* are currently unknown. However, since *bph8* is a recessive gene for BPH resistance, it is unlikely to be either one of the two QTLs identified in this study, as evidenced by the partial dominance observed in both of the QTLs. The relationship of *Bph9* with the two QTLs remains to be determined in future studies. Thus, the two QTLs are distinct from at least nine of the ten previously characterized BPH resistance genes.

Like the gene-for-gene system in disease resistance, there seems to exist a similar system between BPH and the resistance genes. For example, ‘IR26’, the first BPH-resistant cultivar developed by the International Rice Research Institute, which carried the resistance gene *Bph1*, was released in Southeast Asian countries in 1973. However, this resistance was lost after only 2 years of cultivation (Khush and Brar 1991). The cultivar ‘IR36’, which carried the resistance gene *bph2*, was released in

1975 to replace ‘IR26’. A biotype capable of damaging ‘IR36’ soon appeared in small pockets in the Philippines and in Indonesia, which led to the adoption of ‘IR56’ and ‘IR60’ carrying the gene *Bph3* (Khush and Brar 1991). These facts indicated that insect populations could quickly overcome single gene resistance under natural conditions. Thus, new resistance genes will always be needed for rice improvement against BPH. Therefore, the genes identified in this study should certainly be useful as new sources of resistance.

Similar to gene deployment in disease resistance, several strategies of manipulating resistance genes have been proposed for combating the insect pest. It has been suggested that polygenic and moderate resistance to insect pests should be a useful approach (Heinrichs 1986; Bosque-Perez and Buddenhagen 1992), since this may slow down the evolution of the insect populations. For more-effective protection, however, the pyramiding of multiple resistance genes of different origin is obviously an advantageous strategy for increasing the durability of resistance, as it is unlikely that the insect would be able to simultaneously overcome multiple resistance genes. In this regard, closely linked molecular markers should be very useful for transferring the resistance genes for developing cultivars carrying multiple resistant genes.

Wild species of rice are important resources for disease and insect resistance in crop genetic improvement. It has been reported that several wild *Oryza* species, e.g. *O. latifolia*, *O. minuta*, *O. nivara*, *O. officinalis* and *O. punctata*, possess resistance to various biotypes of BPH (Wu et al. 1986). It has also been reported that most of the *Oryza officinalis* collected in China were highly resistant to BPH (Li et al. 1990). However, not very many of the resistance genes have yet been characterized or utilized in rice improvement programs. The fact that the resistant parent, B5, used in the present study carries two genes for resistance indicates the likelihood that many of the wild rice plants may carry multiple genes for BPH resistance. Hence, it can be expected that enhanced exploitation of BPH resistance should be very rewarding.

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