

The genetics of host-plant resistance to rice planthopper and leafhopper

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The incorporation of host-plant resistance to insect pests into elite rice cultivars and the sustainability of pest management using resistant cultivars are necessary for a stable food supply in most rice production areas. The brown planthopper (BPH), *Nilaparvata lugens* Stål., is one of the most serious and destructive rice pests that can be found throughout rice-growing areas in Asia. More than 19 major BPH resistance genes have been identified in several indica cultivars and wild relatives. The green rice leafhopper (GRH), *Nephotettix cincticeps* Uhler, is a major leafhopper species of cultivated rice and is found mostly in the temperate regions of East Asia. At least six loci of GRH resistance have been identified with the aid of DNA markers. Recent molecular mapping of genes that are resistant to the insect pests suggested that highly resistant cultivars/accessions often carried multiple genes for resistance. This suggests that gene pyramiding, which combines more than two resistance genes derived from different donors, will inhibit the occurrence of virulent biotypes. In our study, we describe the identification of BPH and GRH resistance genes and the development of near-isogenic lines for each resistance gene in order to improve rice cultivars through a molecular genetic approach. We also demonstrate the monitoring of the genetic constitution of the BPH populations. This probably involves several types virulent to the specific resistance gene(s), for sustainable pest management using cultivars resistant to BPH.

Keywords. Rice, brown planthopper (BPH), green rice leafhopper (GRH), resistance gene, near-isogenic line (NIL), pest management

Planthopper and leafhopper species damage the plant epidermis and parenchyma with their stylets and suck the plant sap from the phloem. Among the phloem-feeding insects, the brown planthopper (BPH), *Nilaparvata lugens* Stål, is the most serious insect pest of rice (*Oryza sativa* L.) throughout Asia. The populations migrate from China to Japan during the rainy season every year (Kisimoto 1976). Though the migrant populations are not large, the progenies sometimes break out. The insect sucks out the plant sap and causes damage to rice plants such as a reduction in crop vigor, plant height, productive tillers, perfect grains, and yield. In extreme cases, a heavy

infestation of BPH results in complete necrosis of the rice plants, a condition commonly known as “hopper burn.” This influences yield loss and also causes poor grain quality. The BPH is also a vector of grassy stunt virus and ragged stunt virus, which seriously decrease rice production. Conversely, the green rice leafhopper (GRH), *Nephotettix cincticeps* Uhler, is a major species that subsists on rice and is distributed mostly in temperate regions of East Asia (Ghuri 1971). The GRH sucks sap from both the xylem and the phloem of susceptible rice varieties, leading to yield loss, particularly in northeast Japan. In addition to direct plant destruction, the insect also damages rice plants by transmitting other viral diseases, including the rice dwarf and waika viruses commonly seen in western Japan.

Several kinds of resistant cultivars and accessions of rice against planthoppers and leafhoppers have been reported (Heinrichs et al 1985). Host-plant resistance to insects has been classified into three mechanistic types: antibiosis, antixenosis, and tolerance (Painter 1951). However, distinguishing between these mechanisms against planthopper species and leafhopper species has been difficult with bulk seedling tests (Athwal et al 1971). Kishino and Ando (1978) established a simple method for evaluating antibiosis to GRH, and the survival ratio of GRH nymphs was examined on the tested cultivars. Using this evaluation method, genetic analyses of resistance to GRH have been carried out, and at least six loci for GRH resistance have been identified with the aid of DNA markers. Simple sequence repeat (SSR) marker loci are widely distributed throughout the genome and can be easily analyzed using a polymerase chain reaction (PCR). SSR markers have been used extensively to map agronomically important loci in rice, such as disease and insect resistance. This has opened the door to further revelations regarding the mechanisms of host-plant resistance to insect pests through molecular mapping and the cloning of genes that will confer resistance to GRH. The relationship between rice and GRH is a model case of plant-insect interaction. The knowledge obtained from a series of molecular cloning activities is expected to reveal the sucking resistance and system of host-plant resistance breakdown.

The objectives of our study are to understand the genetic basis for resistance to insect pests found in rice cultivars and accessions of wild rice, as well as facilitate the use of germplasm for future rice improvement. First, a quantitative trait loci (QTL) analysis for resistance to insect pests was conducted using an initial mapping population derived from a cross between a susceptible cultivar and a resistant accession. Subsequently, new loci for resistance to insect pests were mapped onto a molecular linkage map using a near-isogenic population, which was developed by continuous backcrossing and marker-assisted selection (MAS) of the targeted QTL region. Finally, we discuss the necessity of monitoring the genetic constitution of the insect populations. This probably involves several types virulent to the specific resistance gene(s), for sustainable pest management using cultivars resistant to insect pests.

Materials and methods

Plant materials

Eight rice cultivars with different levels of resistance to BPH—ADR52, Podiwi A8, Mudgo, ASD7, Rathu Heenati, Babawee, Balamawee, and Taichung 65 (T65) (no resistance gene)—were used. Near-isogenic lines derived from the GRH-resistant cultivar DV85 and IRGC105715, and BPH-resistant cultivar ADR52, were used.

Insect strains

In 2006, ten populations of BPH were collected in East Asia. Four populations were collected from the Red River Delta (RRD1, RRD2) in northern Vietnam and the Mekong River Delta (MRD1, MRD2) in southern Vietnam. Three populations were collected from the Philippines: Northern and Central Luzon islands (LZ1, LZ2) and Mindanao Island (MD). Single populations from Japan (JPN), China (CHI), and Taiwan (TW) were also collected. These populations were maintained by continuous rearing on susceptible cultivar Reiho at 25 ± 1 °C under 16 h light and 8 h dark conditions in the laboratory of the Pest Management System, National Agricultural Research Center for Kyushu-Okinawa Region, Kumamoto, Japan. A GRH population was collected in Fukuoka Prefecture in 1991 and was maintained by continuous rearing of insects on seedlings of japonica variety Nipponbare. Insects were kept at 25 ± 1 °C and 16 h light, 8 h dark.

Evaluation of resistance to BPH and GRH

The month-old plants were trimmed and covered with a transparent plastic cylindrical cage (5.5 cm d × 20 cm h). Five brachypterous (short-wing form) BPH females within 24 h after emergence were released to a cage and the open end was covered with gauze. A score was obtained starting from 3 days after infestation (DAI) to 5 DAI. The adult survival rates as well as the female abdomen were examined. We evaluated the females whose abdomens became heavily swollen or survived for 5 days as virulent. The classification of virulent and avirulent BPH females followed the method of Tanaka (2000). The experiment was carried out with 8 replications. The GRH antibiosis test was reported by Kishino and Ando (1978), and was modified for use in our study. Seedlings were infested with 7–10 first- or second-instar nymphs in test tubes approximately 2 weeks after sowing. Nymph mortality was then calculated at 4 days after infestation. Plants with nymph mortality in the range of 0–40% were categorized as susceptible, and those with 60–100% nymph mortality were categorized as resistant.

Statistical analysis

The data were analyzed using two-way ANOVA. Treatment means were pair-wise compared using the Turkey HSD test (SAS Institute Inc. 2002). The survival rate (%) was arcsine transformed prior to the analysis.

Results and discussion

QTL analyses of cultivars highly resistant to BPH and developing the NILs

The advent of detailed molecular linkage maps in rice has made it possible to detect the quantitative trait loci (QTLs) that control agronomic characters such as biotic and abiotic stresses. In screening germplasm resistance to BPH under antibiosis tests, four indica cultivars (ADR 52, Podiwi A8, ASD7, and Balamawee) were selected as highly resistant. QTL analyses for antibiosis to BPH were conducted using F_2 populations derived from a cross between a susceptible japonica cultivar and resistant indica cultivar. The study has assured future mapping of the BPH-resistance gene using near-isogenic populations developed through marker-assisted selection (MAS). In the case of ADR52, a total of three QTLs controlling antibiosis to BPH were detected on chromosomes 5, 6, and 12. Near-isogenic lines (NILs) for the respective QTLs were developed through continuous backcrossing and MAS. The newly identified resistance genes on chromosomes 6 and 12 were tentatively designated as *bph20(t)* and *Bph21(t)*, respectively.

Since highly resistant cultivars often carried multiple genes for resistance to BPH, a near-isogenic population was necessary to map the BPH resistance gene precisely. MAS for BPH resistance genes with advanced backcrossing with the recurrent parent can facilitate transferring the resistance to BPH from resistant cultivars and wild relatives. The NILs derived from resistant germplasm are useful not only for improving BPH resistance in rice breeding but also for monitoring BPH virulence to the specific resistance gene.

Molecular mapping and cloning of GRH resistance genes

Six genes (*Grh1*, *Grh2*, *Grh3*, *Grh4*, *Grh5*, and *Grh6*) resistant to GRH sucking inhibition have been identified through RFLP mapping. We developed NILs for *Grh2* and *Grh4* from a cross between susceptible japonica cultivar Kinmaze and resistant indica cultivar DV85 with the aid of molecular markers. A resistance evaluation of the NILs was carried out through antibiosis tests against two kinds of leafhopper species, *N. cincticeps* and *N. virescens*, which were serious vectors for several viral diseases in temperate and tropical areas. Nymph mortality of the NILs carrying one of the resistance genes showed only weak resistance and susceptibility. On the other hand, the NILs carrying both of the resistance genes, *Grh2* and *Grh4*, expressed strong resistance at the same level as resistant cultivar DV85. The results clarified that *Grh2* and *Grh4* interaction expresses strong resistance to the two leafhopper species in rice.

A large-scale segregating population of *Grh2* with a near-isogenic genetic background was analyzed for resistance to GRH through a map-based approach. The *Grh2* locus was finally delimited within 54.2 kb genomic sequences of resistant cultivars. Genomic complementation of the candidate genes revealed that two NBS-LRR genes provided a high level of resistance against GRH in the genetic background of *Grh4*, but that each single NBS-LRR gene had only partial resistance. We concluded that the classical *Grh2* locus consisted of two tightly linked NBS-LRR genes, designated

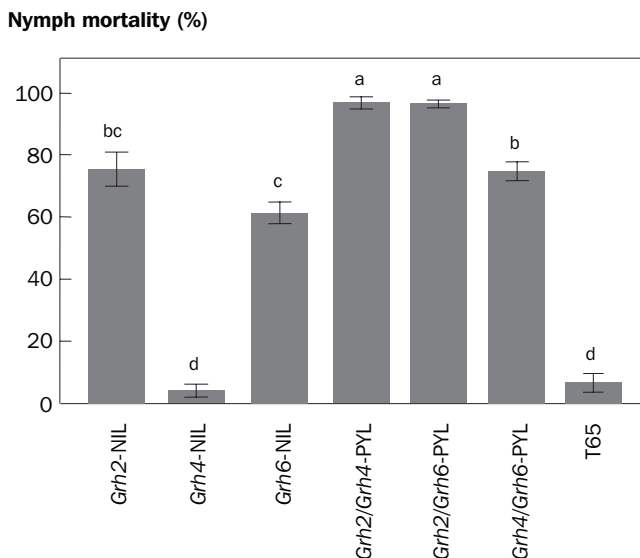


Fig. 1. The nymph mortality of NILs and corresponding PYLs at 3 days after infestation of *Nephotettix cincticeps* Uhler.

Grh2a and *Grh2b*, which mediated high resistance against two *Nephotettix* species, *N. virescens* and *N. cincticeps*, with a *Grh4* genetic background. It is crucial that the symphonic expression of host-plant resistance genes, two of them categorized in the R gene family, mediates durable resistance in plant cultivars.

Development of NILs and pyramided lines for GRH resistance genes

The six GRH resistance genes (*Grh1*, *Grh2*, *Grh3*, *Grh4*, *Grh5*, and *Grh6*) have been located on chromosomes 5, 11, 6, 3, 8, and 4, respectively. New SSR markers, which flanked *Grh1*, *Grh2*, *Grh4*, *Grh5*, and *Grh6-nivara*, were found to select NILs and pyramided lines (PYLs) for GRH resistance genes through MAS. The NILs carrying *Grh1*, *Grh2*, *Grh4*, *Grh5*, and *Grh6-nivara* with a background of japonica cultivar Taichung 65 (T65) have been developed derived from four GRH-resistant lines, IR24 (*Grh1*), DV85 (*Grh2* and *Grh4*), W1962 (*Grh5*), and IRGC105715 (*Grh6-nivara*), using MAS, respectively. The nymph mortality of the NILs carrying *Grh1*, *Grh2*, *Grh5*, and *Grh6* was lower than that of each donor parent, IR24, DV85, W1962, and IRGC105715. For example, we found that the highly resistant W1962, a development of *Oryza rufipogon*, was dependent on two loci conferring resistance to GRH, *Grh5* on chromosome 8 and the minor resistance gene on chromosome 4 (Fujita et al 2006). The PYLs carrying two GRH resistance genes with a background of T65 were developed using NILs carrying *Grh2*, *Grh4*, *Grh5*, and *Grh6-nivara*. The NILs and PYLs were used to compare the GRH resistance of NILs and PYLs using an antibiosis test. The nymph mortality of several PYLs, *Grh2/Grh4*-PYL, *Grh2/Grh6*-PYL, and *Grh4/Grh6*-PYL, was higher than that of NILs each carrying a single GRH resistance gene (Fig.1).

Understanding the mechanisms of a breakdown of the resistance gene

Virulent insect pests, the so-called new biotypes, often appear after the release of modern improved varieties of rice that carry a single major gene for resistance to the insect pests. These pests represent a serious threat to rice paddies because they have acquired virulence to the specific resistance gene, which will have subsequently lost its effectiveness in insect pest management. For example, the BPH populations migrating into Japan began to become virulent to *Bph1* (*Brown panthopper resistance 1*) in the late 1980s (Sogawa 1992) and have been highly virulent for rice cultivars carrying both *Bph1* and *bph2* since the late 1990s (Tanaka and Matsumura 2000). The virulent biotypes of BPH were experimentally identified by continuous rearing of BPH on resistant lines, each carrying a single major gene for BPH resistance (Ketiepearachchi et al 1998). By a similar methodology, virulent biotypes against each of three resistance genes (*Grh1*, *Grh2*, and *Grh3*) were isolated (Hirae et al 2007). This suggests that natural strains of GRH are likely to feed on rice plants having a single major gene for the resistance. In contrast, virulent biotypes against PYLs carrying both *Grh2* and *Grh4* did not occur experimentally (Hirae et al 2007). We have demonstrated that, although the nymph mortality of *Grh4*-NIL showed susceptibility to GRH, the PYL carrying *Grh2* and *Grh4* showed higher nymph mortality than *Grh2*-NIL. Additionally, both *Grh2* and *Grh4* have been essential to express resistance to green leafhopper (GLH), which is closely related to GRH and is a major vector of tungro, a destructive viral disease found in tropical rice fields in Asia (Yasui and Yoshimura 1999). The PYLs carrying *Grh2* and *Grh4* may thus have an important role in expressing durable resistance to rice leafhoppers. This suggests that gene pyramiding that combines multiple resistance genes with different mechanistic types will suppress the dominance of virulent biotypes in the insect population. The PYLs carrying the resistance genes may suppress the dominance of virulent biotypes and show durable resistance to GRH. To study the durability of resistance to insect pests, the development of PYLs carrying multiple resistance genes is essential using MAS and advanced backcrossing with a recurrent parent.

Virulence of Asian BPH strains against differential rice cultivars

Tables 1 and 2 show the adult survival rate and ratio of virulent females of 10 Asian BPH strains on six differential cultivars and T65 (a susceptible check). Based on the resistance spectrum, the Asian BPH strains seem to be classified into three groups. The first group is virulent to Mudgo and ASD7 but avirulent to the other four differential cultivars. The second group involves quite a high percentage of BPH individuals virulent to Babawee and ADR52 in addition to Mudgo and ASD7. The third group is partially virulent to Babawee in addition to Mudgo and ASD7. The first group involved BPH strains collected from Japan, China, and Taiwan, and two strains from northern Vietnam. The second group consisted of two BPH strains collected from southern Vietnam. The third group consisted of three strains from the Philippines, one collected from Mindanao Island and involving about half of the BPH individuals virulent to Mudgo and ASD7. We concluded that cultivars Rathu Heenati and Balamawee still have a broad spectrum of resistance against the Asian BPH strains.

Table 1. Adult survival rate (%) of the Asian BPH rice strains collected in 2006 on differential cultivars in rice.

Cultivar	BPH strain										
	JPN	CH	TW	RRD1	RRD2	MRD1	MRD2	LZ1	LZ2	MD	
Mudgo	94.3 ± 3.7	74.3 ± 5.7	77.1 ± 6.8	100.0 ± 0.0	91.4 ± 4.0	91.4 ± 5.9	82.6 ± 5.2	80.0 ± 6.2	94.3 ± 5.7	51.4 ± 4.0	
ASD7	94.3 ± 3.7	85.7 ± 3.7	80.0 ± 6.2	97.1 ± 2.9	97.1 ± 2.9	94.3 ± 3.7	85.7 ± 5.7	88.6 ± 4.0	91.4 ± 4.0	60.0 ± 0.0	
Rathu Heenati	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	2.9 ± 2.9	0.0 ± 0.0	11.4 ± 8.6	8.6 ± 5.9	8.6 ± 4.0	8.6 ± 4.0	0.0 ± 0.0	
Babawee	11.4 ± 5.9	22.9 ± 10.2	8.6 ± 5.9	17.1 ± 9.2	11.4 ± 5.9	82.9 ± 5.2	77.1 ± 5.2	34.3 ± 3.7	37.1 ± 8.0	31.4 ± 4.0	
ADR52	5.7 ± 5.7	5.7 ± 5.7	0.0 ± 0.0	11.4 ± 5.9	0.0 ± 0.0	80.0 ± 7.6	71.4 ± 9.6	28.6 ± 7.3	25.7 ± 9.5	0.0 ± 0.0	
Balamawee	0.0 ± 0.0	2.9 ± 2.9	0.0 ± 0.0	2.9 ± 2.9	2.9 ± 2.9	2.9 ± 2.9	8.6 ± 5.9	8.6 ± 4.0	5.7 ± 3.7	8.6 ± 5.9	
T65 (check)	91.4 ± 5.9	80.0 ± 6.2	82.9 ± 6.8	94.3 ± 3.7	97.1 ± 2.9	88.6 ± 5.9	85.7 ± 5.7	85.7 ± 7.2	94.2 ± 3.7	77.1 ± 6.8	

Table 2. The ratio of females with swollen abdomen of the Asian BPH strains collected in 2006 on differential cultivars in rice.

Cultivar	BPH strain									
	JPN	CHI	TW	RRD1	RRD2	MRD1	MRD2	LZ1	LZ2	MD
Mudgo	94	74	77	100	91	91	83	80	86	40
ASD7	91	86	80	97	94	94	83	87	89	57
Rathu Heenati	0	0	0	0	0	0	0	0	0	0
Babawee	6	14	9	0	0	63	37	14	17	14
ADR52	0	0	0	0	0	51	23	0	0	0
Balamawee	0	0	0	0	0	0	0	0	0	0
T65 (check)	91	80	83	94	97	86	83	86	91	74

Monitoring BPH virulence using rice NILs

Tables 3 and 4 show that the adult survival rate and ratio of virulent females of 10 Asian BPH strains on the NILs and PYL carrying BPH resistance genes are derived from ADR52. Based on the resistance spectrum to NILs and the PYL for *bph20(t)* and *Bph21(t)*, the Asian BPH strains seem to be classified into four groups. The first group is avirulent to all the tested lines. The second group is virulent to the *Bph21(t)*-NIL but avirulent to the *bph20(t)*-NIL and *bph20(t) + Bph21(t)*-PYL. The third group is virulent to both the *bph20(t)*-NIL and *Bph21(t)*-NIL but avirulent to *bph20(t) + Bph21(t)*-PYL. The fourth group is virulent to all tested lines. The first group is the Mindanao strain, which could not adapt to any lines. The second group consisted of BPH strains from China and Taiwan. The third group consisted of BPH strains from Japan and northern Vietnam and two Luzon strains from the Philippines. The discrimination between the second and third groups is still ambiguous because of differentiation among the BPH strains from China, Taiwan, and Japan as well as northern Vietnam, which have never been identified. The fourth group consisted of BPH strains from southern Vietnam; those were the most virulent and half of the adult females had swollen abdomens on the PYL within 5 days. The results indicate that both of the BPH resistance genes, *bph20(t)* and *Bph21(t)*, are necessary to express broad-spectrum resistance against East Asian BPH strains. The PYL, however, had lost its resistance against the southern Vietnam strains of BPH. Monitoring the virulence of BPH strains using NILs and PYLs will open the door for the use of BPH-resistant cultivars and sustainable pest management in Asian rice fields.

Table 3. Adult survival rate (%) of Asian BPH strains collected in 2006 on NILs and the PL for the BPH resistance gene in rice.

NIL/PL	BPH strain										
	JPN	CHI	TW	RRD1	RRD2	MRD1	MRD2	LZ1	LZ2	MD	
<i>bhp20(t)</i>	85.7 ± 3.4	22.9 ± 4.8	31.4 ± 8.9	94.3 ± 5.3	60.0 ± 4.0	74.3 ± 5.3	88.6 ± 6.8	60.0 ± 5.7	85.7 ± 3.4	25.7 ± 5.3	
<i>Bhp21(t)</i>	88.6 ± 5.5	80.0 ± 4.0	85.7 ± 3.4	91.4 ± 5.5	94.3 ± 3.4	94.3 ± 3.4	91.4 ± 3.7	91.4 ± 3.7	80.0 ± 5.7	37.1 ± 2.6	
<i>bhp20(t) + Bhp21(t)</i>	17.1 ± 6.3	20.0 ± 4.0	28.6 ± 5.5	28.6 ± 3.7	25.7 ± 5.3	71.4 ± 6.8	65.7 ± 3.4	25.7 ± 6.7	17.1 ± 6.3	28.6 ± 7.9	
T65 (check)	91.4 ± 3.7	94.3 ± 3.4	97.1 ± 2.6	97.1 ± 2.6	94.3 ± 3.4	91.4 ± 5.5	91.4 ± 3.7	94.3 ± 3.4	91.4 ± 5.5	91.4 ± 5.5	

Table 4. The ratio of females with swollen abdomen of Asian BPH strains collected in 2006 on NILs and the PL for the BPH resistance gene in rice.

NIL/PL	BPH strain									
	JPN	CHI	TW	RRD1	RRD2	MRD1	MRD2	LZ1	LZ2	MD
<i>bhp20(t)</i>	63	0	0	83	51	69	71	34	37	0
<i>Bhp21(t)</i>	86	80	77	71	77	89	86	77	51	11
<i>bhp20(t)</i> + <i>Bhp21(t)</i>	0	0	0	0	0	49	51	0	0	0
T65 (check)	86	94	97	97	87	80	86	94	91	89

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Notes

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