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Breeding for resistance to planthoppers in rice

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Rice is an important cereal and a source of calories for one-third of the world population. Many diseases and insects attack the rice plant. Among the insect pests, planthoppers cause significant yield losses. Of the various strategies, host-plant resistance is the most practical and economical approach to control insect pests. Six kinds of planthoppers, brown planthopper (BPH), whitebacked planthopper (WBPH), green leafhopper (GLH), zigzag leafhopper (ZLH), small brown planthopper (SBPH), and green rice leafhopper (GRH), cause yield losses in rice to a variable extent. These hoppers are also vectors of major viral diseases, such as grassy stunt, ragged stunt, rice stripe virus, black streak, and tungro disease. A number of donors for resistance have been identified and used in breeding varieties resistant to hoppers. Genetics of resistance to planthoppers has been studied and several resistance genes have been identified from traditional landraces, including wild species. As many as 21 resistance genes have been identified for BPH, 8 for WBPH, 14 for GLH, 6 for GRH, and 3 for ZLH. Of the 21 BPH resistance genes, 15 have been mapped to different chromosomal locations. Some of the mapped BPH resistance genes have become available for use in marker-assisted selection (MAS). Similarly, a few genes resistant to other planthoppers are being mapped. In addition, QTLs have also been identified for BPH, WBPH, and GRH. Of the six hoppers, GRH is mostly found in temperate rice-growing regions. Six resistance genes for GRH have been mapped, on chromosomes 5, 11, 6, 3, 8, and 4. Near-isogenic lines have been developed in a japonica background using the MAS approach. ZLH occurs in the tropics and subtropics of Asia and has remained a minor pest of rice. One of the major challenges for plant breeders is to cope with the frequent changes in biotypes and populations of planthoppers, particularly in the context of climatic change. Future research should focus on establishing high-throughput screening protocols for field resistance, identifying new genes for resistance from diverse sources, and developing varieties with durable resistance to hoppers using MAS through pyramiding of major genes and QTLs. Furthermore, there is a need to develop gene-based markers, particularly single nucleotide polymorphism markers, to accelerate the transfer of genes into different genetic backgrounds and for breeding varieties resistant to hoppers. Characterization of insect populations/biotypes in different geographical regions is emphasized for the deployment of different genes for resistance to planthoppers.

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Humans and insects have always competed for food and fiber, so they have been constantly at war with each other. Insects cause millions of dollars' worth of losses annually to food crops and other plants all over the world. Scientists have devised various control measures to minimize these losses. The most practical and economical control measure is varietal resistance to insects. Painter (1951) and others demonstrated that clear-cut cases of host resistance existed in crop species of importance to agriculture.

Rice is attacked by a large number of insects. Among these insect pests, planthoppers, stem borers, and gall midges are the most serious pests of rice. Six kinds of planthoppers, (1) brown planthopper—BPH (*Nilaparvata lugens* Stål), (2) small brown planthopper—SBPH (*Laodelphax striatellus* Fallen), (3) green leafhopper—GLH (*Nephotettix virescens* Distant), (4) green rice leafhopper—GRH (*Nephotettix cincticeps* Uhler), (5) whitebacked planthopper—WBPH (*Sogatella furcifera* Horvath), and (6) zigzag leafhopper—ZLH (*Recilia dorsalis* Motschulsky), attack rice plants. BPH causes direct damage by sucking plant sap, causes hopperburn, and transmits viral diseases such as grassy stunt and ragged stunt. SBPH transmits rice stripe virus and black streak dwarf virus diseases, GRH transmits rice dwarf virus, and GLH transmits the virus that causes tungro disease.

Lately, the BPH has caused devastating damage in China, Korea, Japan, and Vietnam. In 2005, China reported a loss of 2.7 millions tons of rice due to direct damage, while the loss reached 0.4 million tons in Vietnam, mainly from two virus diseases—grassy stunt and ragged stunt—carried by BPH in a persistent manner. Hybrid rice crops in China and northern Vietnam have favored another planthopper pest, the whitebacked planthopper. In central China, outbreaks of the smaller brown planthopper, which carries black streak dwarf virus disease, have recently been reported. Tungro virus disease, caused by two viruses vectored by the green leafhopper, also remained problematic in some areas. To develop sustainable management systems, it is important to find the right balance between breeding and management, so as to reduce pests' ecological fitness to keep them under economic threshold levels.

Screening techniques for evaluating germplasm for resistance to hoppers have been developed. Mass screening involving screening at the seedling stage has been the most commonly used technique at IRRI and by the national agricultural research and extension systems (NARES) for hoppers. A large number of germplasm accessions have been screened at IRRI for resistance to BPH (biotype 1, 2, 3), GLH, WBPH, and ZLH. As many as 44,335 accessions were screened for BPH biotype 1 (15.4% resistant); 10,553 for BPH biotype 2 (1.9% resistant); 13,021 for BPH biotype 3 (1.8% resistant); 50,137 for GLH (2.8% resistant); 52,042 for WBPH (1.7% resistant); 15,656 for yellow stem borer (3.8% resistant); and 6,881 for striped stem borer (<0.02% were resistant) (Jackson 1997). Several donors for resistance have been identified and used to develop hopper-resistant varieties (Table 1).

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Table 1. Some genetic donors identified for resistance to planthoppers in rice.

Insect pest	Donors for resistance
Brown planthopper	Mudgo, ASD7, Ptb33, Rathu Heenati, Babawee, ARC10550, Swarnalata, *Oryza officinalis, O. australiensis, O. minuta*
Green leafhopper	Peta, Pankhari 203, Sigadis, Ptb8, ARC10313, ASD7, ASD8, DV85, Asmaita
Whitebacked planthopper	N22, ARC10239, ADR52, Podiwi-A8
Zigzag leafhopper	Rathu Heenati, Ptb21, Ptb33

Screening techniques for resistance to planthoppers

With the advent of insect-infestation devices and simple agronomic procedures for growing healthy plants, it is now possible to adopt techniques for mass screening large populations of segregating plant materials. This is an initial step in the screening technology needed to eliminate the majority of susceptible segregants and select the resistant ones. Such large-scale evaluation where insects are offered a free choice of plant materials can be accomplished in the greenhouse, screenhouse, or small field plots. The approach for screening and evaluating resistance will depend on the insect and the crop under study, the required insect numbers, as well as the availability of research facilities. If insect damage occurs at more than one stage of plant growth, it is important to evaluate resistance at each of those stages.

Breeding materials can be screened rapidly by infesting plants at the seedling stage, especially during an early mass-screening cycle, in the greenhouse. Greenhouse screening techniques are economical in space, time, and labor, and have been successfully employed in screening cultivars of several grains and forage crops, including rice (Heinrichs et al 1985), sorghum (Starks and Burton 1977), and alfalfa (Sorensen and Horber 1974).

The conventional seedbox screening test is a rapid method for screening large numbers of rice germplasm accessions for qualitative resistance to hoppers (Heinrichs et al 1985, Panda and Khush 1995). Seed sowing and infestation are timed according to the hopper-rearing schedule. Seeds are sown in rows in a standard seedbox (60 × 40 × 40 cm). The number of insects per seedling can be determined easily. Twenty-five seeds of each test entry are sown in a 12-cm row. Seven days after sowing (DAS), when the seedlings are at the two- to three-leaf stage, the seedboxes are placed in a water pan inside a screened room. The seedboxes are kept in the pan containing 5 cm of water. Planthopper nymphs (2nd instar) cultured on a susceptible variety are uniformly distributed on the test seedlings by holding the base of the feed plant and lightly tapping the plants and blowing on them. In this way, approximately 10 hop-

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Table 2. Some examples of genes for planthoppers identified in rice.

Planthopper	Genes identified
Brown planthopper	*Bph1, bph2, Bph3, bph4, bph5, bph6, bph7, bph8, Bph9, Bph10, bph11, bph12, bph13, Bph14, bph15, Bph16, Bph17, Bph18*(t), *bph19*(t), *bph20, bph21*
Whitebacked planthopper	*Wbph1, Wbph2, Wbph3, wbph4, Wbph5, Wbph6, Wbph7*(t), *Wbhp8*(t)
Green leafhopper	*Glh1, Glh2, Glh3, glh4, Glh5, Glh6, Glh7, Glh8, Glh9, glh10*
Green rice leafhopper	*Grh1, Grh2, Grh3, Grh4, Grh5, Grh6*
Zigzag leafhopper	*Zlh1, Zlh2, Zlh3*

per nymphs are deposited on each seedling. Grading of the entries in each seedbox is done when about 90% of the susceptible check seedlings in that box are dead. The Standard Evaluation System (SES) scale (0–9) for rice (IRRI 1988) is used to score seedling damage: 0 = no damage; 1 = very slight damage; 3 = first and second leaves of most plants are partially yellow; 5 = pronounced yellowing and stunting or about half of the plants wilting or dead; 7 = more than half of the plants wilting or dead; 9 = all plants dead.

Genetics of resistance to hoppers

Information on the genetics of resistance is useful to breeders in deciding on a breeding methodology and breeding strategies to be adopted. Diverse genes for resistance are needed to cope with the development of new biotype populations and to attain regional deployment of genes. Entomologists and breeders have investigated the inheritance of resistance to identify diverse genes for resistance (Table 2). A number of genes for resistance to hoppers have been identified: 21 genes for BPH, 6 for WBPH, 10 for GLH, 6 for GRH, and 3 for ZLH.

Brown planthopper (*Nilaparvata lugens* Distant)

The BPH is the most serious of the rice pests. It causes considerable damage by direct feeding. It also transmits grassy stunt and ragged stunt virus diseases. Comprehensive information is available on the taxonomy of BPH outbreaks, migration, and varietal resistance, including chemical, biological, and cultural control (IRRI 1979). Sources of resistance to BPH were identified in 1967 (Pathak et al 1969). A program on breeding and genetics started in 1968. Two genes for resistance, *Bph1* and *bph2*, were identified in 1970 (Athwal et al 1971). The first resistant variety with *Bph1*, IR26, was released in 1973 (Khush 1971) and it was widely accepted in the Philippines, Indonesia, and

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Vietnam but became susceptible in 1976-77 because of the development of biotype 2 of BPH. By that time, varieties IR36 and IR38 with the *bph2* gene had been developed and released (Khush 1977b). IR36 soon replaced IR26 and became the dominant rice variety. Its resistance to BPH lasted for 14 years, until 1991. Two biotypes of BPH existed before the large-scale introduction of BPH-resistant varieties. BPH-resistant variety IR26 with the *Bph1* gene for resistance was released in the Philippines in 1973 and in Indonesia and Vietnam in 1974. It was widely planted in those countries. A biotype appeared in 1977 that could damage IR26; it was designated as biotype 2. After the breakdown of resistance in IR26, IR36 and IR42 with the *bph2* gene were released (Khush 1977a). They were widely adopted in the Philippines, Indonesia, and Vietnam but were found to be susceptible to a South Asian biotype (biotype 4). IR42 became susceptible in North Sumatra Province of Indonesia in 1982. These varieties were resistant until 1989-90. IR56 with the *Bph3* gene was released in 1982 in the Philippines. Several other varieties (IR60, IR62, IR68, IR72, and IR74) were released and were resistant to biotype 3. Some varieties are resistant on the Indian subcontinent but in Southeast and East Asia have *bph5*, *Bph6*, or *bph7* genes for resistance. According to Jairin et al (2007), *Bph1*, *bph2*, *Bph3*, and *bph4* have been used extensively in Thai breeding programs. Improved rice cultivars carrying *Bph1*, *bph2*, *Bph3*, and *bph4*, however, lost their ability against BPH, although cultivars with *Bph3* have shown a higher degree and broader spectrum of resistance against BPH.

Sources of resistance to BPH were first identified in 1967 (Pathak et al 1969). Since then, many donors for resistance to BPH have been identified and used in breeding BPH-resistant varieties. Some of the donors are Mudgo, ASD7, Rathu Heenati, Babawee, ARC10550, Swarnalata, T12, Chin Saba, Balamawee, *O. officinalis, O. australiensis*, and *O. minuta* from cultivated and wild species of rice (Table 1).

In another study, 29 additional resistant varieties were analyzed genetically and two new genes, *Bph3* and *bph4*, were identified (Lakshminarayana and Khush 1977). These genes were incorporated into improved germplasm. In 1982, when a biotype capable of damaging IR36 appeared in small pockets in the Philippines and in Indonesia, IR56 and IR60 with the *Bph3* gene for resistance were released (IRRI 1983). IR66 with *bph4* for resistance was released in 1987 and IR68, IR70, and IR72, all with *Bph 3*, were released in 1988. These varieties were widely grown in tropical and subtropical rice-growing countries. If we had neglected gene identification work, the planned incorporation of diverse genes for resistance to BPH would have been impossible and we would not have been able to keep ahead of this shifting enemy of the rice crop. The value of genetic analysis of resistance cannot therefore be overemphasized.

More than 100 resistant cultivars have been analyzed genetically. Athwal et al (1971) showed that the resistance in Mudgo, CO22, and MTU15 was governed by the same dominant gene, which they designated *Bph1*. A single recessive gene, designated *bph2*, conveyed resistance in ASD7. *Bph1* and *bph2* are closely linked and no recombination between them has been observed. Chen and Chang (1971) also reported that a single dominant gene controls resistance in Mudgo. Athwal and Pathak (1972) reported that MGL2 possesses *Bph1* and Ptb18 possesses *bph2*. Martinez and

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Khush (1974) investigated the inheritance of resistance in two breeding lines of rice that originated from crosses of susceptible parents. One of the lines, IR747B2-6, possessed *Bph1* for resistance. IR1154-243 is susceptible but a small number of F_2 progenies from its crosses with other susceptible varieties such as TN1, IR8, or IR24 are resistant. It was hypothesized that TKM6 is homozygous for *Bph1* as well as for the dominant inhibitory gene, *IBph1*, which inhibits *Bph1*.

In a genetic study of 28 varieties, Lakshinarayana and Khush (1977) found nine varieties with *Bph1*, 16 with *bph2*, and one variety with both genes. Two varieties were found to have new genes. A single dominant gene, which conveys resistance in Rathu Heenati, was designated *Bph3*. This gene segregates independently of *Bph1*. A single recessive gene, which controls resistance in Babawee, was designated *bph4*. This gene segregates independently of *bph2*. Genetic analysis of 20 resistant varieties by Sidhu and Khush (1978) revealed that seven varieties had *Bph3*, 10 had *bph4*, and resistance in the remaining three was governed by two genes. Sidhu et al (1979) also reported that *Bph3* and *bph4* were closely linked. Genes *bph4* and *Glh3* are also linked with a map distance of 34 units. The *bph4* gene appeared to be linked with *sd1* (recessive gene for semidwarf). However, *bph4* and *Xa4* (gene for bacterial blight resistance) are inherited independently. Kaneda et al (1981) reported on screening of 3,300 cultivars and breeding lines. About 60% of the Sri Lankan varieties possess *bph2* while only 10% of the Indian cultivars have this gene. Ikeda and Kaneda (1981) also found that both *bph2* and *Bph1* segregate independently of both *Bph3* and *bph4*, whereas *Bph3* and *bph4* as well as *Bph1* and *bph2* are closely linked. Ikeda and Kaneda (1982) reported that *Bph1* segregated independently of the gene for dwarf virus resistance in Kanto PL3 and also of the gene governing stripe disease resistance in Kanto PL2.

On the basis of trisomic analysis, Ikeda and Kaneda (1981) identified the loci of *Bph3* and *bph4* on chromosome 10. In another study, Ikeda and Kaneda (1983) located *Bph1* on chromosome 4. No linkage was detected between *Bph1* on the one hand and *lg* and *d11* markers of chromosome 4 on the other. However, *bph2* was found linked with *d-2* and had a 39.4% recombination value. Khush et al (1985) carried out genetic analysis of ARC10550. This cultivar is resistant to BPH populations in South Asia (biotype 4) but is susceptible to the population of biotypes 1, 2, and 3 in East and Southeast Asia. It was found to have a single recessive gene, *bph5*, for resistance, which segregates independently of *Bph1*, *bph2*, *Bph3*, and *bph4*.

Seventeen additional rice cultivars resistant to biotype 4 but susceptible to biotypes 1, 2, and 3 were analyzed by Kabir and Khush (1988). Seven were found to have a single dominant gene for resistance. The dominant gene(s) of these cultivars segregated independently of *bph5*. The dominant gene of cultivar Swarnalata was designated *Bph6*. In the remaining 10 cultivars, resistance was conferred by a single recessive gene. The recessive genes for resistance of eight cultivars were found to be allelic to *bph5*. However, the recessive genes of two cultivars are nonallelic to *bph5*. The recessive gene of T12 was designated *bph7*.

Thai varieties Col. 5 and Col. 11 and Chin Saba from Myanmar were reported to have single recessive genes for resistance that are allelic to each other but are nonallelic to *bph2* and *bph4*. Similarly, cultivars Kaharmana, Balamawee, and Pokkali

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were found to have single dominant genes that are allelic to each other but different from *Bph1* and *bhp3* (Khush 1992). These cultivars are resistant to biotypes 1, 2, and 3, compared with cultivars with *bph5*, *Bph6*, and *bph7*, which are susceptible. Nemoto et al (1989) concluded that the recessive gene of Col. 5 and Col. 11 from Thailand, and Chin Saba, must also be different from *bph5* and *bph7*. They designated this gene as *bph8*. Similarly, the dominant gene of Kaharmana, Balamawee, and Pokkali was designated as *Bph9* (Murata et al 2001). A new locus for resistance to BPH was identified in the indica variety DV85 (Su et al 2005).

Ikeda and Kaneda (1981) located *Bph3* and *bph4* on chromosome 10 through trisomic analysis. Ikeda and Kaneda (1983) detected linkage of *bph2* with *d11* on chromosome 4. Multani et al (1994) identified BPH resistance on chromosome 12 through BPH bioassays of monosomic alien addition lines (MAAL). A gene for BPH resistance introgressed from *O. australiensis* mapped with RFLP on chromosome 12 (Ishii et al 1994). Of the 14 polymorphic probes on chromosome 12, RG457 detected introgression from *O. australiensis*, which co-segregated with BPH resistance, and RG457 was tagged with *Bph10* on chromosome 12 at a distance of 3.69 ± 1.29 cM.

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 on the Indian subcontinent. The *Bph1* group confers resistance to biotypes 1 and 3 but is susceptible to biotype 2, the *bph2* group conveys resistance to biotypes 1 and 2 but is susceptible to biotype 3, and the *Bph3* group and *bph4*, *bph8*, and *Bph9* confer resistance to all four biotypes. Genes such as *bph5*, *Bph6*, and *bph7* convey resistance to biotype 4 only (Khush and Brar 1991). He (2007) mapped *bph7* and *bph8* on chromosome 4. Many workers have studied the relationship between BPH biotypes and genes for resistance (Table 3). IR varieties of rice carry *Bph1*, *bph2*, and *Bph3* genes and *Glh3*, *glh4*, *Glh9*, and *glh10* (Table 4). Wei et al (2009) used a proteomic approach and analyzed the interaction between rice and BPH. Proteins involved in multiple pathways showed significant changes in expression in response to BPH feeding, including jasmonic acid synthesis proteins and oxidative stress-response proteins. Wang et al (2008) used a cDNA microarray containing 1,920 suppression subtractive hybridization clones to detect transcript profile differences in resistant and susceptible cultivars under a control and BPH feeding. In total, 160 unique genes were detected as being significantly affected by BPH feeding. Shi et al (2003) constructed a genomic library from BPH-resistant B5. The library contained 36,864 clones with an average insert size of 60 kb. Eleven clones were identified covering the *Qbp1* locus (the locus between markers R1925 and G1318 on chromosome 3).

Molecular mapping of genes for BPH resistance

A total of 21 genes for BPH resistance have been identified from cultivated and wild species of *Oryza*. Of these 21 resistance genes, 15 are mapped to different chromosomal locations and 8 are tightly linked with molecular markers. A number of genes for resistance to BPH have been mapped using RFLP, RAPD, and SSR markers. Some QTLs have also been mapped (Table 5). Six of these genes, *Bph1*, *bph2*, *Bph9*,

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Table 3. Interrelationships between biotypes of brown planthopper and genes for resistance in rice.

Variety	Gene	Reaction to biotypes[a]			
		1	2	3	4
Mudgo	*Bph1*	R	S	R	S
ASD7	*bph2*	R	R	S	S
Rathu Heenati	*Bph3*	R	R	R	R
Babawee	*bph4*	R	R	R	R
ARC 10550	*bph5*	S	S	S	R
Swarnalata	*Bph6*	S	S	S	R
T12	*bph7*	S	S	S	R
Chin Saba	*bph8*	R	R	R	–
Balamawee	*Bph9*	R	R	R	–
TN1	*none*	S	S	S	S
O. australiensis	*Bph18*	R	R	R	R
O. officinalis	*Bph6, Bph13*	R	R	R	R
O. minuta	*Bph20, Bph21*	R	–	–	
O. latifolia	*Bph12*	–	R	–	–

[a]R = resistant, S = susceptible.
Source: Modified from Zhang (2007).

Bph10, *Bph18,* and *Bph21,* are located on chromosome 12. *Bph12*, *Bph15*, *Bph17,* and *Bph20* are located on chromosome 4 (Rahman et al 2009). *Bph11*, *Bph13*, *Bph14*, and *Bph19* are located on chromosome 3, *Bph6* on chromosome 11, *Bph3* and *bph4* on chromosome 6, and *Bph13*(t) on chromosome 2. There is some inconsistency in assigning a gene number and mapping (Table 5). Huang et al (1997) used a doubled-haploid (DH) population (IR64 × Azucena) and located a BPH resistance gene from IR64 on chromosome 12. Three RFLP markers (RG493, RG901, and CD0344) and *sdh1* showed linkage with the BPH resistance gene. *Bph10* from IR65482-4-136-2-2 and *Bph1* from Mudgo for resistance to biotypes 1 and 3 were located near XNpb248. Although the pattern of resistance is different among these varieties, the genes are mapped in a similar position. The linkage between the RAPD marker $OPA16_{938}$ and the BPH resistance gene *Bph6* was 0.52 cM in the coupling phase. The 938-bp RAPD amplicon was cloned and used as a probe on 122 *Cla1*-digested DH plants from an IR64 × Azucena mapping population for RFLP inheritance analysis and was mapped onto rice chromosome 11. RAPD marker $OPA16_{938}$ could be used in a cost-effective way for marker-assisted selection (MAS) for BPH resistance (Jena et al 2002).

Renganayaki et al (2002) mapped the *Bph13*(t) gene derived from *O. officinalis* on chromosome 3 using a RAPD marker. The most closely linked marker was

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Table 4. Genes for resistance to brown planthopper (BPH) and green leafhopper (GLH) in IR varieties.

Variety	BPH	GLH	Variety	BPH	GLH
IR5	0	*Glh3*	IR45	*Bph1*	*Glh3*
IR8	0	*Glh3*	IR46	*Bph1*	–
IR20	0	*Glh3*	IR48	*bph2*	–
IR22	0	0	IR50	*bph2*	*Glh9*
IR24	0	–	IR52	*bph2*	*Glh9*
IR26	*Bph1*	–	IR54	*bph2*	*Glh9*
IR28	*Bph1*	*Glh9*	IR56	*Bph3*	*Glh9*
IR29	*Bph1*	*Glh9*	IR58	*Bph3*	*Glh9*
IR30	*Bph1*	*Glh3*	IR60	*Bph3*	*Glh9*
IR32	*bph2*	–	IR62	*Bph3*	–
IR34	*Bph1*	*Glh9*	IR64	*Bph1*	–
IR36	*bph2*	*Glh10*	IR65	*bph2*	*Glh9*
IR38	*bph2*	–	IR66	*Bph3*	–
IR40	*bph2*	–	IR68	*Bph3*	–
IR42	*bph2*	*glh4*	IR70	*Bph3*	–
IR43	*0*	–	IR72	*Bph3*	–
IR44	*Bph1*	–	IR74	*Bph3*	–

Sources: Modified from Khush and Virk (2003) and Khush et al (2007).

converted into an STS marker and is mapped 1.3 cM from the resistance gene. An introgression line derived from *O. sativa* and *O. officinalis*, IR54741-3-21-22, was found to be resistant to an Indian biotype of BPH and resistance was controlled by a single dominant gene. Kim and Sohn (2005) used bulk segregant analysis with 520 RAPD markers for analysis of BPH resistance. One of these primers, OPE18, which amplified a 923-bp band, was tightly linked to BPH resistance. The *Bph1* gene was mapped at a distance of 3.8 cM from the STS marker BpE 18-3. Yang et al (2004) developed a high-resolution genetic map of *Bph15* by positioning 21 DNA markers in the target chromosomal region. An assay of the recombinants using subclones in combination with sequence analysis delimited the *Bph15* gene to a genomic segment of approximately 47 kb. Chen et al (2006) fine-mapped *bph19*(t) to a region of about 1 cM on the short arm of chromosome 3 flanked by RM6308 and RM3134. Sequence information of clones was used to construct a physical map of *bph19*(t) and the locus was physically defined to an interval of about 60 kb. Sun et al (2005) analyzed Sri Lankan indica rice cultivar Rathu Heenati and found it to be resistant to all four biotypes of BPH. Three loci detected by QTL analysis were assigned to chromosomes 3, 4, and

Table 5. Some examples of molecular mapping of genes for BPH resistance.

Gene	Chromosome	Donor	Markers	Resistance to biotypes	References
Bph1	12	Mudgo	G148 (RFLP)	Biotype 1	Hirabayashi and Ogawa (1995), Sun et al (2006)
	12L	Mudgo	em5814N (AFLP)	Biotype 1	Sharma et al (2002)
	12	Samgangbyeo	BpE18-3 (STS)	Biotype 1	Kim and Sohn (2005)
	12L	IR28	XNpb248, XNpb336 (RFLP)	Biotype 1	Hirabayashi and Ogawa (1995)
	12L	Norin PL3	AFLP em5814N		
	12	Gayabyeo	OPD-7 RD7 (RAPD), RG869, RG457 (RFLP), RM247 (SSR)	Biotype 1 Biotype 1	Sharma et al (2004) Jeon et al (1999)
Qbp1	3L	B5 *(O. officinalis)*	R1925, R2443 (RFLP)	Biotypes 1 & 2	Huang et al (2001)
Qbp1 (*Bph14*t)	3	B5 *(O. officinalis)*	R1925, G1318 (RFLP)	–	Ren et al (2004)
bph2	12	Norin PL4 (*bph2* introgression line from IR1154-243)	G2140 (RFLP)	Biotypes 1 & 2	Murata et al (1998)
	2	ASD7 (Acc. no. 6303)	RM463, RM7102 (SSR)	Biotypes 1 & 2	Sun et al (2006)
	2	Norin PL4 (*bph2* introgression line from IR1154-243)	KAM4 (complete co-segregation with *bph2*), STS	–	Murai et al(2001), Sharma et al (2004)
	12	Norin PL4 (*bph2* introgression line from IR1154-243)	G2140 (SSR)	–	Sun et al (2006)
Qbph2	2L	Col.5 T	RM6843, RM3355 (SSR)	Mixture of biotypes 1 & 2	Sun et al (2007)
	4S	B5 *(O. officinalis)*	C820, R288 (RFLP)	Biotypes 1 & 2	Huang et al (2001)
	2L	*O. eichingeri* Acc. no. 105159	RFLP, SSR	–	Liu et al (2001)
	2	Yagyaw	5529-1358 (SSR)	–	Liu et al (2009)
Bph3	6S	Rathu Heenati (Acc. no. 6730)	RM589 (SSR)	Biotypes 1, 2, 3, 4	Jairin et al (2007a)
Qbph3	3	Rathu Heenati (Acc. no. 11730)	RM313, RM7 (SSR)	–	Sun et al (2005)

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Table 5 continued.

Gene	Chromosome	Donor	Markers	Resistance to biotypes	References
bph4	6S	Babawee (Acc. no. 8978)	RM190 (SSR), C76A (RFLP)	–	Kawaguchi et al (2001)
	6S	Babawee	C891, C531 (RFLP)	–	Murata 1998, Nagato and Yoshimura 1998
Qbph4	4	Rathu Heenati (Acc. no. 11730)	RM8213, RM5953 (SSR)	–	Sun et al (2005)
	4S	Yagyaw	RM401, RM335 (SSR)	–	Liu et al (2009), Sun et al (2005), Yang et al (2004)
bph5		ARC 10550 (Acc. no. 12507)	–	Biotype of Bangladesh	Khush et al (1985), Kabir and Khush (1988)
Bph6		Swarnalata (Acc. no. 33964)	–	–	Kabir and Khush (1988)
Qbph6	6S	Col. 5 T	RM510 (SSR)	Mixture of biotypes 1 & 2	Sun et al (2007)
bph7		T12 (Acc. no. 59689)	–	Biotype of Bangladesh (biotype 4)	Kabir and Khush (1988)
Qbph7	7	Yagyaw	RM542, RM500 (SSR)	–	Liu et al (2009)
bph8(t)		Col. 5 T	–	Biotypes 1, 2, 3	Nemoto et al (1989)
bph8(t)		Chinsaba (Acc. no. 33016)	–	Biotypes 1, 2, 3	Nemoto et al (1989)
Bph9	12L	Karahamana	RM463, RM5341 (SSR)	Biotype 1	Su et al (2006)
	12L	Pokkali	OPR04 (RFLP), S2545 (RAPD)	–	Murata et al (2001)

Continued on next page

Table 5 continued.

Gene	Chromosome	Donor	Markers	Resistance to biotypes	References
Qbph9		Yagyaw	RM3533, RM242 (SSR)	–	Liu et al (2009)
Bph10(t)	12L	IR65482-4-136-2-2 (*O. australiensis* Acc. no. 100882)	RG457 (RFLP)	Biotypes 1, 2, 3	Ishii et al (1994)
Qbph10	10	Rathu Heenati (Acc. no. 11730)	RM484, RM496 (SSR)	–	Sun et al (2005)
bph11(t)	3L	IR742-23-19-12-3-54 (*O. officinalis*)	G1318 (RFLP)	–	Hirabayashi et al (1998)
Bph12(t)	4S	B14 (*O. latifolia*)	RM261 (SSR)	Biotype of Japan	Yang et al (2002)
	4S	GSK185-2 (*O. officinalis*)	G271, R93 (RFLP)	–	Hirabayashi et al (1998)
	4	*O. latifolia*	RLPP	–	He (2007)
bph12(t)	4	*O. officinalis*	RFLP	–	Hirabayashi et al (1998)
Bph13(t)	2L	*O. eichingeri* Acc. no. 105159	RM250 (SSR), RFLP	–	Liu et al (2001)
	3S	IR54745-2-21-12-17-6 (*O. officinalis*)	AJ09b_{230} (RAPD), AJ09c (STS)	Biotype 4	Renganayaki et al (2002)
Bph14 (*Qbph1*)	3L	B5 (*O. officinalis*)	R1925, G1318 (RFLP)	–	Yang et al (2004)
Bph15 (*Qbph2*)	4S	B5 (*O. officinalis*)	C820, S11182 (RFLP)	Biotype from China	Yang et al (2004)
Qbp2 (*Bph15*(t)	4	B5 (*O. offcinalis*)	C820, R288 (RFLP)	–	Ren et al (2004)
Bph17(t)	4S	Rathu Heenati	RM8213, RM5953 (SSR)	–	Sun et al (2005)
Bph18(t)	12L	IR65482-7-216-1-2 (*O. australiensis* Acc. no. 100882)	RM1022 (SSR)	Biotype of Korea	Jena et al (2006)
bph 19(t)	3S	AS20-1	RM6308, RM3134 (SSR)	–	Chen et al (2006)

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Table 5 continued.

Gene	Chromosome	Donor	Markers	Resistance to biotypes	References
Bph20(t)	4	IR71033-121-15 (*O. minuta* Acc. no. 101141)	STS	Biotype of Korea	Rahman et al (2009)
Bph21(t)	12	IR71033-121-15(*O. minuta* Acc. no. 101141)	STS	Biotype of Korea	Rahman et al (2009)
BPH*	12	IR64	RG463, RG901, CDO 344 (RFLP) Sdh-1 (isozyme marker)	–	Huang et al (1997)
Bph6	11	IR54741-3-21-22	$OPA16_{938}$ (RAPD)	Biotype of India	Jena et al (2002)

*Gene not named.

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10. The phenotypic variance of the three QTLs indicated that the QTL on chromosome 4 is a major BPH resistance gene in Rathu Heenati. Linkage analysis indicated that this BPH resistance gene was located between two SSR markers, RM8213 and RM5953, on the short arm of chromosome 4, with a map distance of 3.6 cM and 3.2 cM, respectively. This gene was tentatively designated as *Bph17*.

Li et al (2006) incorporated *Bph14* and *Bph15* through MAS into a number of parental lines used in hybrid rice breeding in China. Su et al (2005) located *qbph11*, which explained 68.4% of the phenotypic variation of BPH resistance (biotype 2) in the progenies derived from the cross between DV85 and Kaimaze. An introgression line derived from *O. sativa* and *O. officinalis*, IR54741-3-21-22, was found to be resistant to an Indian biotype of brown planthopper. Genetic analysis of 95 F_3 progeny rows of a cross between the resistant line IR54741-3-21-22 and a BPH-susceptible variety revealed that resistance was controlled by a single dominant gene. RAPD analysis showed that one primer, $OPA16_{938}$, amplified a resistant parental band in the resistant bulk and a susceptible parental band in the susceptible bulk by bulked segregant analysis. RAPD analysis of individual F_2 plants with primer $OPA16_{938}$ showed marker phenotype co-segregation for all, but only one recombinant was identified. The linkage between RAPD marker $OPA16_{938}$ and the BPH resistance gene was 0.52 cM in the coupling phase. The 938-bp RAPD amplicon was cloned and used as a probe on 122 *Cla1*-digested DH plants from an IR64 × Azucena mapping population for RFLP inheritance analysis and was mapped onto rice chromosome 11 (Jena et al 2002). RAPD marker $OPA16_{938}$ could be used in a cost-effective way for marker-assisted selection for BPH resistance.

Jairin et al (2007a,b) mapped *Bph3* on the short arm of chromosome 6 between two flanking markers, RM589 and RM586, within 0.9 cM and 1.4 cM, respectively. Molecular analysis of three mapping populations derived from Ptb33 × RD6, Rathu Heenati × KDML105, and IR71033-121-15 × KDML105 showed BPH resistance genes located in the same genomic region on the short arm of chromosome 6. A novel resistance gene, *Bph18*, has been identified in breeding line IR65482-7-216-1-2 that has inherited the gene from the EE genome wild species *O. australiensis* (Jena et al 2006). The *Bph18* gene has been located on the long arm of chromosome 12 in a 0.843-Mb genomic region flanked by markers RM6869 and R10289S. An STS marker, 7312.T4A, derived from the BAC clone OSJNBa0028L05 that encodes a resistance protein sequence present in the flanking region is tightly linked to the *Bph18* gene for BPH resistance. The marker 7312.T4A can be efficiently used for MAS breeding of BPH resistance in rice.

Alam and Cohen (1998) identified seven QTLs for BPH resistance on chromosomes 1, 2, 3, 4, 6, and 8 using 175 markers. Ramalingam et al (2003) reported four additional QTLs associated with BPH resistance in the same population using an additional 105 candidate gene markers. Huang et al (2001) reported QTLs in wild species for BPH resistance. Xu et al (2002) reported seven main-effect QTLs and many epistatic QTLs associated with quantitative resistance to BPH using a recombinant inbred line derived from Tequing × Lemont populations. Su et al (2002) detected QTLs on chromosomes 2, 10, and 12 using a Nipponbare × Kasalath backcross population.

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Soundararajan et al (2004) used a DH population (IR64 × Azucena) and detected six QTLs on chromosomes 1, 2, 6, and 7 for BPH resistance. Of these, QTLs on chromosome 7 showed association with seedling resistance and QTLs on chromosome 2 with antibiosis, whereas QTLs on chromosomes 1, 6, and 7 were associated with tolerance (Xu et al 2002). There is a need to extend QTL analysis at different growth stages of the plant and over different environments, including the candidate gene approach. Sun et al (2007) analyzed 147 F_3 families derived from BPH-resistant cultivar Col. 5 from Thailand and susceptible cultivar 02428. The BPH population used for infestation was a mixture of biotypes 1 and 2. Two QTLs were identified on chromosome 2 (29.4% phenotypic variation) and chromosome 6 (46.2% phenotypic variation). Comparison of chromosomal locations and reactions to BPH biotypes indicated that the gene on chromosome 6 is different from the previously identified genes. Liu et al (2009) made crosses between BPH-resistant landrace Yagyaw and susceptible cultivar Cpslo17. Four QTLs (*Qbph-2*, *Qbph-4*, *Qbph 7*, and *Qbph-9*) accounting for 5.64% to 12.77% of the phenotypic variation for BPH resistance were located. Two QTLs showed a significant additive effect. One resistant allele was harbored by the susceptible parent.

Marker-assisted selection for BPH resistance

Sharma et al (2004) used MAS for pyramiding *Bph1* and *bph2* into a japonica line. The pyramided line showed higher resistance than *bph2* but was equivalent to *Bph1*. Li et al (2006) incorporated *Bph14* and *Bph15* through MAS into a number of parental lines used in hybrid rice breeding in China and observed that 92.3% of *Bph14* single introgression lines had moderate resistance to BPH and *Bph14*/*Bph15* pyramided lines had higher resistance than the single-gene introgression lines. Park et al (2008) used representational difference analysis (RDA) and found that OsBphi252 is tightly linked to BPH resistance and could be used in MAS.

Jena et al (2006) used MAS to transfer *Bph18* into the recurrent parent Junambyeo (susceptible to BPH) with the marker 7312.T4A. The cultivar Junambyeo is semidwarf, photo-insensitive, highly productive, and cultivated commercially in irrigated rice areas in South Korea. However, it is highly susceptible to the BPH biotype of Korea. We used a marker-assisted backcross breeding approach and developed backcross (BC) progenies from a cross between Junambyeo and IR65482-7-216-1-2, the source of the *Bph18* gene. BC_2F_2 progenies segregating for BPH resistance were bio-assayed for resistance and susceptibility in the greenhouse and individual plants were analyzed for foreground selection to detect the presence or absence of the resistance gene. The breeding lines with the resistance gene were advanced further for the selection of desirable agronomic characteristics (Table 6).

Some 265 BC_2F_2 progenies were bio-assayed for BPH resistance and 65 BC_2F_2 progeny rows were randomly selected based on strong resistance. Amplification of the 7312.T4A locus in BC_2F_2 resistant plants did not detect a homozygous-susceptible marker allele (1,033 bp) of Junambyeo but detected a resistance-specific marker allele (1,078 bp) in the resistant plants in either a homozygous or heterozygous state (Fig.

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Table 6. Agronomic traits of some promising breeding lines carrying the *Bph18* gene with multiple resistance to brown planthopper (BPH), blast (Bl), bacterial leaf blight (BB), and rice black streak dwarf virus (RBSDV).[a]

Breeding line	DTH (d)	CL (cm)	PL (cm)	PN	1,000-grain weight (g)	BPH	Bl	BB (K3a)	RBSDV (%)
IR83261-1-1-18-3-3-3-1	115	79	18.7	13	22.45	R	R	NT	31.6
IR83261-1-1-18-3-3-1-1	115	80	18.5	17	22.10	R	R	NT	22.2
IR83261-3-7-15-7-6-2	116	84	20.3	15	21.90	R	R	NT	26.3
IR83261-3-7-23-6-2-1-B	112	79	20.7	11	21.75	R	R	R	73.7
Junambyeo (RP)	116	75	17.7	11	22.55	S	MR	S	100.0

[a]DTH = days to heading, CL = culm length, P = panicle length, PN = panicle number, NT = not tested, RP = recurrent parent, R = resistant, S = susceptible, K3a = a new virulent BB race in Korea.
Source: Jena et al (unpublished).

1). Some 81 BC_2F_3 families comprising 5,235 plants were evaluated for desirable agronomic and grain quality characteristics and selected progenies were advanced to the BC_2F_5 generation using MAS for the *Bph18* gene. Some 77 BC_2F_5 BPH-resistant plants with agronomic traits similar or superior to those of the recurrent parent Junambyeo were again analyzed with the marker 7312.T4A. All the resistant plants had resistance-specific marker alleles of 7312.T4A in a homozygous state (Fig. 2) and confirmed the application of MAS for BPH resistance breeding. This MAS strategy for BPH resistance is useful for the development of breeding lines with superior agronomic traits and BPH resistance.

Green leafhopper (*Nephotettix virescens* Distant)

GLH is distributed throughout Asia but is a more serious pest in the tropics and subtropics. GLH causes yield losses by direct feeding as well as by acting as a vector for viruses causing tungro disease. A large number of varieties have been screened for GLH and many resistant donors (Pankhari 203, ASD7, Sigadis, Ptb8, DV85, Asmaita, ARC10313, ARC11554, *O. rufipogon*) have been identified. Genetic analysis has revealed 11 dominant and three recessive genes [*Glh1, Glh2, Glh3, glh4, Glh5, Glh6, Glh7, glh8, Glh9, glh10, Glh11, Glh12, Glh13, and Glh14* (Table 7)]. The inheritance of resistance to the GLH was first investigated by Athwal et al (1971) in varieties Pankhari 203, ASD7, and IR8. They found that resistance in each variety was controlled by one dominant gene. Three genes, *Glh1*, *Glh2*, and *Glh3*, were identified: Pankhari 203 had *Glh1*, ASD7 had *Glh2*, and IR8 had *Glh3*. The three genes segregated independently of each other. Siwi and Khush (1977) identified two more genes and analyzed 13 additional cultivars and identified one recessive gene, designated *glh4*, and a dominant gene, *Glh5*. Rezaul Karim and Pathak (1982) identified two dominant

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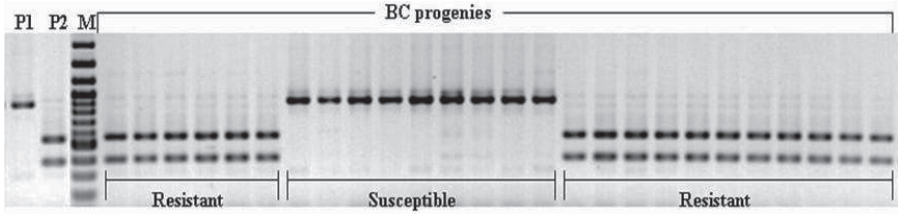

P1 = (Junambyeo (recurrent parent), P2 = IR65482-7-216-1-2 (donor parent), M = molecular weight size market.

Fig. 1. MAS validation test of selected BC_2F_2 progenies by using gene-specific marker 7312. T4A followed by *Hinf*I digestion.

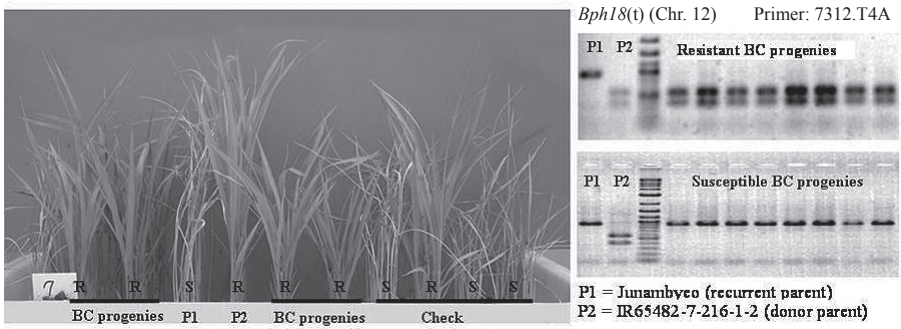

Fig. 2. Selected BC_2F_5 BPH-resistant progenies validated by marker 7312.T4A linked to the *Bph18* gene (right, upper panel). The susceptible progenies without the *Bph18* gene do not show a marker allele for resistance (right, lower panel). S = susceptible check, R = resistant check.

genes (*Glh6* and *Glh7*) and Ghani and Khush (1988) identified a recessive gene (*glh8*). Avesi and Khush (1984) studied the inheritance of resistance in 18 varieties. Two had *Glh1*, three had *Glh2*, two had *Glh3*, one had *glh4*, and three had two genes. Ruangsook and Khush (1987) analyzed 15 rice cultivars. The resistance was governed by two dominant genes in Katia Baudger 13-20, Laki 659, Lasane, Asmaita, and Choron Bawla, but by a single dominant gene in the remaining 10 cultivars. Allele tests with known genes revealed that one of the two dominant genes of Choron Bawla is allelic to *Glh2*. The single dominant gene in Chiknal and one of the two dominant genes in Laki 659 are allelic to *Glh3*. The second of the two dominant genes of Kaita Badger 13-20, Laki 659, and Lasane is allelic to *Glh5*. The two dominant genes of Asmaita and the single dominant gene of Hashikalmi, Ghaiya, ARC10313, and Garia are nonallelic to and independent of *Glh1*, *Glh2*, *Glh3*, *glh4*, and *Glh5*. Khush et al (2007) studied the genetics of resistance in 22 IRRI-bred rice varieties. These varieties were crossed with a susceptible Taichung Native 1 (TN1) and the reaction to green leafhopper was studied. Results showed that IR20, IR30, and IR45 are allelic to *Glh3*. On the other hand, IR34, IR50, IR52, IR54, IR56, IR58, IR60, and IR65 have *Glh9*. The dominant genes in IR24, IR26, IR29, IR43, and IR48 and the recessive genes in IR32, IR38, IR40, IR44, and IR46 segregate independently from *Glh1*, *Glh2*, and *Glh3*.

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Table 7. Genes identified for resistance to green leafhopper.

Gene	Source	Chromosome
Glh1	Pankhari 203	5
Glh2	ASD7	11
Glh3	IR8	6
glh4	Ptb8	3
Glh5	ASD8, *O. rufipogon*	8
Glh6	TAPL796	5
Glh7	Maddani Karuppan	–
Glh8	DV85	–
Glh9	–	–
Glh10	–	–
Glh11	–	–
Glh12	–	–
Glh13	–	–
Glh14	ARC11554	4

Twenty-three landraces and wild species are included in the parentage of IR varieties. Of these, six landraces are resistant to GLH and, in all probability, are donors for resistance. IR8, IR5, IR20, IR30, and IR45 inherited *Glh3* from Peta. Gam Pai 30-12-15 is the donor of *Glh9* in IR28, IR34, IR50, IR52, IR54, IR56, IR58, IR60, and IR65. IR29 probably also has *Glh9* as it has Gam Pai 30-12-15 in its ancestry and because it was selected from the same cross as IR28.

Four varieties with recessive genes for resistance (IR32, IR38, IR40, and IR44) have CR49-13 in their ancestry and this variety is in all likelihood the donor of the resistance. CR94-13 is the donor of recessive gene *glh4* in IR42 (Avesi and Khush 1984) and also of *glh10* in IR36 (Angeles and Khush 2000). It appears that CR94-13 has two recessive genes, *glh4* and *glh10*. Thus, IR32, IR38, IR38, IR40, and IR44 may have inherited either of these recessive genes. Tetep is another source of resistance and it may have contributed its resistance gene to IR46. Further studies are needed to identify genes for resistance in other IR varieties.

Whitebacked planthopper (*Sogatella furcifera* Horvath)

WBPH occurs in all the rice-growing countries of Asia and does moderate damage to the crop. With the mass screening technique, germplasm collections have been evaluated and donors for resistance have been identified. More than 300 cultivars resistant to the WBPH have been identified and 80 of them have been analyzed genetically. Resistant donors (N22, ARC10239, ADR52, Podiwi-A8) have been identified (Table

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Table 8. Genes identified for resistance to green rice leafhopper.

Gene	Source	Chromosome
Grh1	IR24, Pe-bi-hun	5
Grh2	DV85, Lepe dumai	11
Grh3	Rantaj emas 2	6
Grh4	DV85, Lepe Dumai, C203-1	3
Grh5	W1962 (O. rufipogon)	–
Grh6	Sml 17	4
Grh6	IRGC105715 (*O. rufipogon*)	4
Grh9	IRGC104038	9

8). Six genes for resistance (*Wbph1, Wbph2, Wbph3, wbph4, Wbph5, wbph6*) have been identified (Khush 1984). Tan et al (2004) identified another two genes (*Wbph7* (t) and *Wbph8*(t)). Kadrivel et al (1999) mapped QTLs for resistance to whitebacked planthopper. QTLs for ovicidal response have also been reported (Yamasaki et al 1999; Sogawata et al 2001).

A single dominant gene, designated *Wbph1*, was found to convey resistance to WBPH in variety N22 (Sidhu et al 1979). Resistance in ARC10239 is governed by a single dominant gene designated *Wbph2* (Angeles et al 1981). This gene segregates independently of *Wbph1*. Nair et al (1982) investigated 21 additional varieties; 19 had *Wbph1* and two had *Wbph2* and an additional recessive gene. The resistance of two of the 14 varieties analyzed by Hernandez and Khush (1981) was governed by *Wbph2*: 11 varieties each had a single dominant gene that segregated independently of *Wbph1* and *Wbph2*. The dominant gene of one such variety (ADR52) was designated *Wbph3*. Only one variety, Podiwi A8, had a recessive gene, which was designated *wbph4*. Saini et al (1982) analyzed 13 additional varieties. Resistance was governed by *Wbph1* in four varieties, by *Wbph2* in six, by *Wbph1* and *Wbph2* in two, and by a single dominant gene in Hornamawee segregated independently of *Wbph1* and *Wbph2*. Wu and Khush (1985) investigated the inheritance of resistance in 15 varieties. They found that resistance in nine was controlled by *Wbph1* and resistance in four was conferred by two genes. The remaining two varieties had single dominant genes for resistance, which segregated independently of *Wbph1, Wbph2*, and *Wbph3*. The dominant gene of N' Diang Marie was designated *Wbph5*. Jayaraj and Murty (1983) studied the inheritance of resistance in nine varieties. Resistance was controlled by a single dominant gene in three varieties and by a recessive gene in the other six varieties.

Inheritance of resistance in 10 cultivars was investigated by Singh et al (1990). Eight cultivars—ARC5838, ARC6579, ARC6624, ARC10464, ARC11321, ARC11320, Balamawee, and IR2425-90-4-3—were found to have a single recessive

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Table 9. Genes identified for resistance to whitebacked planthopper.

Gene	Source	Chromosome
Wbph1	N22	7
Wbph2	ARC10239	6
Wbph3	ADR52	–
wbph4	Podiwi A8	–
Wbph5	N' Diang Marie	–
Wbph6	–	–
Wbph7	–	–

gene for resistance. The recessive genes of IR2425-90-4-3, ARC5838, and ARC11321 were found to be allelic to each other. Resistance in Pbt19 and IET6288 was found to be under dominant gene control. Sidhu et al (2005) studied the inheritance of resistance in five cultivars. A recessive gene conferred resistance to MR1523 and ARC11367, whereas resistance in NCS 2041 was conditioned by a dominant gene. The resistance in Mudgo and MO1 was governed by two independently inherited dominant genes. Padmarathi et al (2007) reported the recessive gene in ARC5984 and ARC6650 as allelic to Podiwi (*wbph4*). The dominant gene in ADR52 was different from that in cultivar Velluthecharra. He (2007) mapped *Wbph7* and *Wbph8* on chromosome 4.

Green rice leafhopper (*Nephotettix cincticeps* Uhler)

Green rice leafhopper (GRH) is mostly found in the temperate regions of East Asia. At least six genes (*Grh1*, *Grh2*, *Grh3*, *Grh4*, *Grh5*, and *Grh6*) have been identified and mapped on chromosomes 5, 11, 6, 3, 8, and 4, respectively (Table 9) (Yasui et al 2007). Near-isogenic lines (NILs) carrying *Grh1*, *Grh2*, *Grh4*, *Grh5*, and *Grh6* in the background of japonica cultivar Taichung 65 (T65) have been developed using MAS. W1962 (*O. rufipogon*) had *Grh5* and a minor gene on chromosome 4 (Fujita et al 2006). The nymph mortality of pyramided lines (*Grh2* + *Grh4*) and *Grh2* + *Grh6* and *Grh4* + *Grh6* was higher than that of the NILs each carrying a single resistance gene (Yasui et al 2007).

Zigzag leafhopper (*Recilia dorsalis* Motschulsky)

The zigzag leafhopper (ZLH) occurs in the tropics and subtropics of Asia. However, it is a minor pest of rice. Some donors (Rathu Heenati, Ptb21, Ptb33) for resistance have been identified (Heinrichs et al 1985). The genetics of resistance to the ZLH, WBHP, BPH, and GLH in cultivars Rathu Heenati, Ptb21, and Ptb33 was investigated by Angeles et al (1986). Single dominant genes that segregate independently of each other and that conveyed resistance to ZLH were designated *Zlh1* (Rathu Heenati), *Zlh2*

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(Ptb21), and *Zlh3* (Ptb33). Tests for the independence of the various genes for resistance to leafhoppers and planthoppers revealed that *Zlh1*, *Zlh2*, and *Zlh3* are independent of *Wbph3*, *Zlh2*, and *Zlh3* and also segregated independently of *bph2* and *Bph3*.

Expression of snowdrop lectin in transgenic rice for resistance to BPH

Rao et al (1998) reported snowdrop lectin (*Galanthus nivalis agglutinin*; GNA) to be toxic toward BPH when administered in an artificial diet. Transgenic rice containing the *gna* gene in constructs in which its expression was driven by a phloem-specific promoter (from the rice sucrose synthase *RSs1* gene) and by a constitutive promoter (from the maize ubiquitin *ubi1* gene) conferred resistance to BPH. Rao et al (1998) used PCR and Southern analyses to confirm that the transgenes were transmitted to progeny. Western blot analyses revealed expression of GNA at up to 2.0% of total protein in some of the transgenic plants. GNA expression driven by the *RSs1* promoter was tissue-specific as shown by immunohistochemical localization of the protein in the nonlignified vascular tissue of transgenic plants. Insect bioassays and feeding studies showed that GNA expressed in transgenic rice plants decreased survival and overall fecundity (production of offspring) of the insects, retarded insect development, and had a deterrent effect on BPH feeding. *gna* is the first transgene to exhibit insecticidal activity toward sap-sucking insects in an important cereal crop plant.

Future research priorities

The following research priorities could be important for the future:

1. Establish high-throughput screening protocols for field resistance to planthoppers.
2. Identify new sources of resistance to hoppers.
3. Characterize insect populations/biotypes and genes with resistance against insect populations in the field for efficient deployment of such genes.
4. Evaluate existing varieties and elite inbreds/hybrids for field resistance to planthoppers in hot-spot areas in target countries and disseminate resistant varieties/hybrids.
5. Understand the genetic basis of field resistance to facilitate the development of the next generation of resistant cultivars.
6. Develop durable BPH-resistant varieties/hybrids through pyramiding of mapped genes and QTLs accelerated through marker-assisted selection.
7. Establish functional SNPs for selection for BPH resistance.

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