Rice (2010) 3:161–171
DOI 10.1007/s12284-010-9050-y

Current Status of Brown Planthopper (BPH) Resistance and Genetics

Kshirod K. Jena · Suk-Man Kim

Received: 5 August 2010 / Accepted: 2 September 2010 / Published online: 16 September 2010

Abstract Among the planthoppers of rice, the brown planthopper (BPH) is a major threat to rice production and causes significant yield loss annually. Host-plant resistance is an important strategy to reduce the damage caused by BPH and increase rice productivity. Twenty-one major genes for BPH resistance have been identified by using standard evaluation methods developed at the International Rice Research Institute (IRRI) to distinguish resistance or susceptibility of rice genotypes to BPH biotypes/populations. These genes are from diverse genetic resources such as land race cultivars and wild species of *Oryza*. Of the 21 resistance genes, 18 genes have been localized on specific region of six rice chromosomes using molecular genetic analysis and genomics tools. Some of these resistance genes are clustered together such as *Bph1*, *bph2*, *Bph9*, *Bph10*, *Bph18*, and *Bph21* on the long arm of chromosome 12; *Bph12*, *Bph15*, *Bph17* and *Bph20* on the short arm of chromosome 4; *bph11* and *Bph14* on the long arm of chromosome 3 and *Bph13*(t) and *bph19* on the short arm of chromosome 3. Six genes (*Bph11*, *bph11*, *Bph12*, *bph12*, *Bph13* and *Bph13*) originated from wild *Oryza* species have either duplicate chromosome locations or wrong nomenclature. The discrepancy should be confirmed by allelism tests. Besides identification of major resistance genes, some quantitative trait loci (QTLs) associated with BPH resistance have also been identified on eight chromosomes. Most of the rice cultivars developed at IRRI possess one or two of the major resistance genes and the variety IR64 has many QTLs and confers strong resistance to BPH. More BPH resistance genes need to be identified from the wealth of gene pool available in the wild species of *Oryza*. Two BPH resistance genes (*Bph14* and *Bph18*) have been cloned, and a snow drop lectin gene (*GNA*) has been identified and used in the development of BPH-resistant transgenic plants. Efficient introgression of resistance genes (*Bph1*, *bph2*, *Bph3*, *Bph14*, *Bph15*, *Bph18*, *Bph20*, and *Bph21*) into elite rice cultivars by marker-assisted selection together with strategic deployment of these genes can be an important approach to develop stable resistance to BPH and sustain rice production in the tropical and temperate rice growing regions.

Keywords Rice · Brown planthopper · Genetics · Resistance · Major genes · Gene mapping

K. K. Jena (✉) · S.-M. Kim
Plant Breeding, Genetics and Biotechnology Division,
International Rice Research Institute,
C/o IRRI-Korea Office, National Institute of Crop Science, RDA,
209 Seodun-Dong,
Suwon 441-857, Republic of Korea
e-mail: k.jena@cgiar.org

Introduction

Insects are a serious threat to cereal crops and cause significant damage to crop production annually. Advances in modern technologies have created several control measures to minimize yield losses in crops. Host-plant resistance is the most effective and environment friendly approach to control the damage caused by insects and increase yield potential of cereal crops (Jena et al. 2006).

Rice is one of the most important cereal crops in the tropics as well as parts of temperate regions in the world. It is the primary source of calories for more than one–third of the world population. However, rice crop is host to a large number of insects that feed on rice. Of the six kinds of planthoppers, brown planthopper (BPH; *Nilaparvata lugens* Stål) is the most damaging insect pest of rice in Asia. BPH causes direct damage to the plant by sucking the phloem

sap, feeds by phloem abstraction and causes hopper burn, and transmits viral diseases such as grassy stunt virus (RGSV) and ragged stunt virus (RRSV).

In recent years, BPH has caused devastating damages to rice crop in China, Japan, Korea and Vietnam. In 2005 and 2008, China reported a combined yield loss of 2.7 million tons of rice due to direct damage by BPH, while a yield loss of 0.4 million tons in Vietnam was mainly due to two virus diseases, RGSV and RRSV, transmitted by BPH (Brar et al. 2010). To develop a sustainable pest management system, it is important to find the right balance between breeding and management strategies to reduce the ecological fitness of BPH and to keep the pest under economic threshold levels (Bosque-Perez and Buddenhagen 1992).

Several screening techniques to evaluate germplasm for resistance to BPH have been standardized at International Rice Research Institute (IRRI). Mass screening involving evaluation at the seedling stage has been the most commonly used technique at IRRI as well as by the National Agricultural Research and Extension Systems (NARES). A large number of germplasm accessions have been screened at IRRI for resistance to the three biotypes of BPH. As many as 44,335 rice accessions from the gene bank of IRRI 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) (Jackson 1997). Several resistant rice accessions have been identified in cultivated land races as well as in wild species accessions, and have been used for developing BPH-resistant varieties.

In this review, we discuss the current status of resistance genes and genetics of BPH resistance in order to develop strategies toward BPH resistance breeding. Recent molecular cloning of the first BPH resistance genes (Du et al. 2009) has allowed us to revisit some of the controversial debates on screening methodologies, biological meaning of insect biotypes, and nature of durable resistance.

Biotype of BPH and relationship with resistance genes

Biotypes of BPH are defined as a population or an individual distinguished from other populations or individuals by non-morphological traits such as adaptation and development to a particular host, host preference for feeding or oviposition, or both. The biotypes of BPH show clear differences in virulence pattern on rice cultivars/genotypes. Four BPH biotypes are known for rice. Biotypes 1 and 2 are widely distributed in Southeast and East Asia whereas biotype 3 was developed in the laboratory by rearing the insects on the resistant variety ASD7 which has the *bph2* gene for resistance (Panda and Heinrichs 1983). The most destructive biotype is biotype 4 which occurs in the Indian subcontinent and it is also called South Asian biotype. Cultivars with *Bph1* gene confer resistance to biotypes 1 and 3 but are susceptible to biotype 2. The *bph2* gene confers resistance to biotypes 1 and 2 but not to biotype 3, and the *Bph3* and *bph4*, *bph8*, and *Bph9* genes confer resistance to all four biotypes. Genes such as *bph5*, *Bph6*, and *bph7* confer resistance to biotype 4 only (Khush and Brar 1991). Additional studies on the relationship between BPH biotypes and resistance genes are summarized in Table 1.

Evaluation of BPH resistance

Appropriate evaluation of germplasm for BPH resistance is the key to studying the genetics of BPH resistance and to identifying resistance genes correctly. There are several types of screening methods such as natural field populations, mass screening of germplasm/breeding materials in seedbox by infesting plants at the seedling stage (two to three-leaf stage) with BPH nymphs (second instars) in a greenhouse, modified seedbox test (Panda and Heinrichs 1983). However, the major limitations of evaluating germplasm in the field are seasonality, unpredictability, and uneven distribution of BPH, rendering field screening unreliable. The mass screening using seedbox test in the greenhouse uses BPH nymphs with free-choice of plant materials at seedling stage and sometimes the test is extended to different stages of plant growth. The modified seedbox test is sometimes used to identify germplasm tolerance to BPH. In contrast to conventional seedbox test, the modified seedbox test assesses seedling damage caused by the progeny of the initially infested nymphs (Panda and Khush 1995). However, due to economy of time and space, the seedbox test is most commonly used with free-choice method to determine genotypes for resistance and susceptibility in the greenhouse (Heinrichs et al. 1985; IRRI 1988). Regardless of screening methods, maximum caution should be taken for the purity of BPH population used in the evaluation. Additionally, the standard seedbox test can also be modified with no-choice of the insect to understand the mechanism of resistance caused by antibiosis. Therefore, it is important to evaluate BPH resistance by seedbox test in the greenhouse using free-choice method (antixenosis) as well as by testing in BPH hotspot areas to reconfirm the phenotypes for resistance and susceptibility.

Genetics of BPH resistance

Knowledge on the genetics of BPH resistance is useful for breeders to decide on the breeding strategies to be adopted. Sources of resistance to BPH biotype were first identified in 1967 (Pathak et al. 1969). Since then, many donors for

Table 1 Relationship between biotypes of brown planthopper and resistance genes from diverse sources

Variety/source	Gene	Reaction to biotypes[a]			
		1	2	3	4
Mudgo	*Bph1*	R	S	R	S
ASD 7	*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. officinalis (acc. 100896)	*Bph6*, *Bph13*	R	R	R	R
O. minuta (acc. 101141)	*Bph20*, *Bph21*	R	ND	ND	ND
O. latifolia (B14)	*Bph12*	ND	R	ND	ND
O. australiensis (acc. 100882)	*Bph18*	R	R	R	R

[a] *R* resistant, *S* susceptible, *ND* no data

resistance to different BPH biotypes have been identified. Some of the resistant donors are Mudgo, ASD 7, Rathu Heenati, Ptb33, Babawee, ARC10550, Swarnalata, T12, Chin Saba, Balamawee, and several introgression lines with genes from *Oryza officinalis*, *Oryza minuta, Oryza latifolia* and *Oryza australiensis*. Inheritance of resistance genes corresponding to different BPH biotypes has been studied. Of the 21 genes for resistance to BPH, 13 genes are dominant and eight genes are recessive.

Two genes, *Bph1* and *bph2* for resistance were identified in 1970 (Athwal et al. 1971). The first resistant variety IR26 possessing the *Bph1* gene became susceptible to BPH in 1976-77 due to the development of biotype 2 (Khush 1971). A recessive gene *bph2* was identified and incorporated into rice cultivars (Khush 1992). The resistance conferred by *bph2* was considered durable as BPH resistance of IR36 lasted for 14 years until 1991. The varieties with *bph2* gene derived resistance were widely adopted in the Philippines, Indonesia, and Vietnam. Then a new biotype (biotype 3) of BPH evolved that broke down *bph2*-derived resistance. Two genes, *Bph3* and *bph4* were identified and incorporated into elite cultivars (Lakashminarayana and Khush 1977). Further genetic analysis of 28 rice cultivars identified nine varieties with *Bph1*, *16* with *bph2*, and one variety with both genes. *Bph3* was identified in the variety Rathu Heenati which segregated independently of *Bph1*. A single recessive gene, which controls resistance in the variety, Babawee, was designated as *bph4* which segregated independently of *bph2*. IR56 and IR60 with the *Bph3* gene derived from Rathu Heenati were developed and were released in 1982 in the Philippines. IR66 with *bph4* gene for resistance was released in 1987 and IR68, IR70, IR72 and IR74 with *Bph 3* gene were released in 1988 with confirmed resistance to biotype 3 (Table 2). The resistance genes, *Bph1*, *bph2*, *Bph3*, and *bph4* have been used extensively in breeding programs in Southeast Asia (Jairin et al. 2007a). Improved cultivars carrying *Bph1*, *bph2*, *Bph3*, and *bph4* genes however, lost their resistance against BPH due to the evolution of new biotypes. Because of the high variability of BPH and the apparent specificity of BPH resistance, an understanding of the linkage and allelic relationship of resistance genes is particularly important for the development of BPH-resistant cultivars.

A comparative genetic analysis of resistant cultivars have been conducted and the results showed that the resistance in Mudgo, CO22, and MTU15 was governed by the same dominant *Bph1*gene (Athwal et al. 1971). A single recessive gene, *bph2*, derived from ASD7 showed close linkage with *Bph1* gene and no recombination between them was observed. Further genetic studies showed that MGL2 variety possesses *Bph1* gene and Ptb18 variety possesses *bph2* gene for resistance (Athwal and Pathak 1972). Martinez and Khush (1974) investigated the inheritance of resistance in two breeding lines of rice that originated from crosses of susceptible parents (Martinez and Khush 1974). One of the lines, IR747B2-6, possessed *Bph1* gene for resistance. Another breeding line, IR1154-243, had a dominant inhibitory gene, *IBph1*.

Genetic analysis of 20 resistant varieties revealed that seven varieties had *Bph3*, *10* had *bph4*, and resistance in the remaining three varieties was governed by two genes (Sidhu and Khush 1978). Linkage analysis revealed that *Bph3* and *bph4* genes are closely linked (Sidhu et al. 1997). The *bph4* gene was reported to be also linked with *sd1* (recessive gene for semidwarf). However, *bph4* and

Table 2 Genes and their sources of resistance to brown planthopper in IRRI varieties

Variety	BPH	Genetic source
IR26	*Bph1*	Mudgo
IR28	*Bph1*	Mudgo
IR29	*Bph1*	Mudgo
IR30	*Bph1*	Mudgo
IR32	*bph2*	ASD7
IR34	*Bph1*	Mudgo
IR36	*bph2*	ASD7
IR38	*bph2*	ASD7
IR40	*bph2*	ASD7
IR42	*bph2*	ASD7
IR44	*Bph1*	Mudgo
IR45	*Bph1*	Mudgo
IR46	*Bph1*	Mudgo
IR48	*bph2*	ASD7
IR50	*bph2*	ASD7
IR52	*bph2*	ASD7
IR54	*bph2*	ASD7
IR56	*Bph3*	Rathu Heenati
IR58	*Bph3*	Rathu Heenati
IR60	*Bph3*	Rathu Heenati
IR62	*Bph3*	Rathu Heenati
IR64	*Bph1*	Mudgo
IR65	*bph2*	ASD7
IR66	*Bph4*	Babawee
IR68	*Bph3*	Rathu Heenati
IR70	*Bph3*	Rathu Heenati
IR72	*Bph3*	Rathu Heenati
IR74	*Bph3*	Rathu Heenati

Xa4 (gene for bacterial blight resistance) are inherited independently (Kaneda et al. 1981). About 60% of the Sri Lankan varieties possess the *bph2* gene while only 10% of Indian cultivars have the *bph2* gene. Ikeda and Kaneda (1981) also found that both *Bph1* and *bph2* genes segregate independently of both *Bph3* and *bph4*, whereas *Bph3* and *bph4* as well as *Bph1* and *bph2* are closely linked (Ikeda and Kaneda 1982). 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 (Ikeda and Kaneda 1981).

On the basis of trisomic analysis, Ikeda and Kaneda (1981) identified the genetic loci of *Bph3* and *bph4* on chromosome 10. Genetic analysis of ARC10550 reveals that this cultivar possessed a single recessive gene, *bph5*, which segregated independently of *Bph1*, *bph2*, *Bph3*, and *bph4* (Khush et al. 1985).

Genetic analysis was conducted for 17 additional rice cultivars with resistance to biotype 4 but susceptible to biotypes 1, 2, and 3 (Kabir and Khush 1988). Seven of them had a single dominant gene for resistance and two new genes *bph5* and *Bph6* were identified based on their non-allelic relationship with other known BPH resistance genes (Khush et al. 1985). The dominant gene of the cultivar Swarnalata was designated as *Bph6*. In the remaining ten cultivars, resistance was conferred by a single recessive gene. Resistance genes in two of the ten cultivars, were non-allelic to the recessive gene *bph5* and a new gene was found and designated as *bph7*. The cultivars Swarnalata and T12 possess the resistance genes *Bph6* and *bph7* respectively.

Genetic analysis of two Thai varieties, Col. 5 and Col. 11 from Thailand and Chin Saba from Myanmar revealed single recessive genes for resistance that were allelic to each other but non-allelic to *bph2* and *bph4*. However, cultivars Kaharamana, Balamawee, and Pokkali have single dominant genes that are allelic to each other but different from *Bph1* and *Bph3* (Khush 1989). These cultivars conferred resistance to biotypes 1, 2, and 3. Nemoto et al (1989) using a fine genetic analysis and allelism test concluded that the recessive gene of Col. 5, Col. 11 from Thailand, and Chin Saba was different from *bph5* and *bph7* and designated the gene as *bph8* (Nemoto et al. 1989). Similarly, the dominant gene of Kaharamana, Balamawee, and Pokkali was designated as *Bph9* (Murata et al. 2001).

Extensive genetic analysis of land race rice cultivars using four biotypes of BPH identified nine major resistance genes of which four were dominant and five were recessive in nature. Three resistance genes (*Bph1*, *bph2* and *Bph3*) have been incorporated into BPH susceptible cultivars by conventional breeding and a number of BPH-resistant varieties have been developed (Khush 1977).

In addition to analysis of major BPH resistance, a growing number of studies examine how host defense is activated in rice in response to BPH infestation. Shi et al. (2003) constructed a genomic library from BPH-resistant cultivar B5 (Shi et al. 2003). Eleven clones were identified covering the *Qbp1* locus (the locus between markers R1925 and G1318 on chromosome 3). 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 controlled BPH feeding (Wang et al. 2008). In total, 160 unique genes were detected as being significantly affected by BPH feeding. Wei et al. (2009) used a proteomic approach to analyze the interaction between rice cultivars and BPH biotypes (Wei et al. 2009). Proteins involved in multiple pathways, including jasmonic acid synthesis proteins and oxidative stress-response, showed significant changes in expression pattern in response to BPH feeding.

Molecular mapping of genes conferring BPH resistance

Major genes for BPH resistance

So far, 21 genes for BPH resistance have been identified from the gene pool of cultivated and wild species of *Oryza*. With the development of a saturated molecular genetic map of rice, 18 of the 21 resistance genes have been mapped onto different chromosomal locations. Eight of these resistance genes are tightly linked with different types of molecular markers and are present on six of the 12 rice chromosomes. As reported in the literature, *Bph13*(t) was located on chromosome 2; *Bph11*, *Bph13*, *Bph14*, and *Bph19* genes on chromosome 3; *Bph12*, *Bph15*, *Bph17*, and *Bph20* genes on chromosome 4 (Rahman et al. 2009); *Bph,* and *bph4* genes on chromosome 6 (Kawaguchi et al. 2001); *Bph6* on chromosome 11 (Jena et al. 2002); *Bph1*, *bph2*, *Bph9*, *Bph10*, *Bph18*, and *Bph21* genes on chromosome 12 (Jena et al. 2006; Sharma et al. 2004). Park et al. (2008) used representational difference analysis (RDA) to identify OsBphi252 that is tightly linked to BPH resistance on chromosome 12. It is clear that there are inconsistencies in assigning gene number and locating its position on the chromosome (Table 3). Huang et al (1997) used a doubled-haploid (DH) population (IR64 × Azucena) and located an unnamed resistance gene from IR64 on chromosome 12. Three RFLP markers (RG493, RG901, and CD0344) and *sdh1* genes showed linkage with the BPH resistance gene. The gene, *Bph10* from IR65482-4-136-2-2 and *Bph1* from Mudgo for resistance to the biotypes 1 and 3 were located near the marker XNpb248. Although the pattern of resistance is different among these varieties, the genes are mapped onto a similar position on chromosome 12.

The linkage between the RAPD marker $OPA16_{938}$ and the resistance gene *Bph6* was 0.52 cM in the coupling phase. The 938-bp RAPD amplicon was cloned and probed on 122 *Cla1*-digested DH plants derived from an IR64 × Azucena mapping population for inheritance analysis. Eventually, the *Bph6* gene was mapped onto rice chromosome 11 (Jena et al. 2002).

Renganayaki et al. (2002) mapped the *Bph13*(t) gene derived from an *O. officinalis* introgression line, IR54741-3-21-22 on chromosome 3 using a RAPD marker. An STS marker linked to *Bph13*(t) (1.3 cM) has been developed by converting the most closely linked RAPD marker (Renganayaki et al. 2002). The *Bph13*(t) gene was reported to be resistant to the Indian biotype of BPH (biotype 4) and resistance was controlled by a single dominant gene. Chen et al. (2006) fine-mapped the *bph19*(t) gene with flanking SSR markers (RM6308 and RM3134) on the short arm of chromosome 3 located at a distance of 1 cM. Sequence information of BAC clones was used to construct a physical

Table 3 The brown planthopper resistance gene clusters and duplicate genes

Chromosome	Gene	Flanking markers	Position (Mbp)	Markers	Donor
Cluster genes					
3 S	*Bph13*	RG100, RG191 (RFLP)	5.18–5.70		
	bph19	RM517, RM218 (SSR)	6.16–8.40		
3 L	*bph11*	G1318 (RFLP)	35.70		
	Bph14	R1925, G1318 (RFLP)	35.43–35.70		
4 S	*Bph12*	RM261 (SSR)	6.50		
	Bph15	C820, S11182 (RFLP)	6.89–9.34		
	Bph17	RM8213, RM5953 (SSR)	4.40–9.60		
	Bph20	MS10, RM5953 (SSR)	8.20–9.60		
12 L	*Bph9*	RM5341, RM463 (SSR)	19.08–22.09		
	Bph10	RM484, RM496 (SSR)	21.06–22.43		
	Bph18	RM463 (SSR), S15552(STS)	22.09–23.32		
	Bph21	RM3726, RM5479 (SSR)	23.24–24.37		
Duplicate genes					
Chromosome	*Gene*				
4	*Bph11*			–	IR154-243
3	*bph11*			G1318	*O. officianalis*
4	*Bph12*			RG261	*O. latifolia*
4	*bph12*			–	*O. officianalis*
2	*Bph13*			RM240, RM250	*O. eichingeri*
3	*Bph13*			RG100, RG191	*O. officianalis*

map of *bph19*(t) gene and the locus was physically defined to an interval of about 60 kb.

A high resolution genetic map of *Bph15* was developed by positioning 21 DNA markers in the target chromosomal region (Yang et al. 2004). An assay of the recombinants using sub-clones in combination with sequence analysis delimited the *Bph15* gene to a genomic segment of approximately 47 kb on chromosome 4. The indica rice cultivar Rathu Heenati conferring resistance to all four biotypes of BPH was analyzed for resistance gene. Three resistance loci were detected by quantitative trait locus (QTL) analysis and were located on chromosomes 3, 4, and 10. The phenotypic variance of the three QTLs indicated that the QTL on chromosome 4 is a major BPH resistance gene. Molecular analysis revealed 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 resistance gene from Rathu Heenati was tentatively designated as *Bph17* (Sun et al. 2005).

Jairin et al. (2007a, b) mapped the *Bph3* gene from Rathu Heenati on the short arm of chromosome 6 between two flanking markers, RM589 and RM586, at a linkage distance of 0.9 cM and 1.4 cM, respectively. Further molecular analysis using three mapping populations derived from Ptb33 × RD6, Rathu Heenati × KDML105, and IR71033-121-15 × KDML105 confirmed the location of the *Bph3* gene in the same genomic region on the short arm of chromosome 6. Kim and Sohn (2005) used bulk segregant analysis with 520 RAPD markers for the analysis of BPH resistance. One of these primers, OPE18 producing a 923-bp PCR product, was tightly linked to BPH resistance. The *Bph1* gene was mapped 3.8 cM from the STS marker BpE 18-3. The RFLP marker, RG457 was tagged with the resistance gene, *Bph10* on chromosome 12 at a distance of 3.69±1.29 cM (Ishii et al. 1994). A new resistance gene, *Bph18*, has been identified in the breeding line IR65482-7-216-1-2 that has inherited the gene from the EE genome of wild species *O. australiensis*. The *Bph18* gene has been located on the long arm of chromosome 12 in a 0.843-Mb genomic region flanked by the 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 (Jena et al. 2006). The marker 7312.T4A can be efficiently used for MAS breeding of BPH resistance in rice.

Rahman et al. (2009) reported a molecular marker-based location of *Bph20* and *Bph21* genes in an introgression line, IR71033-121-15, from *O. minuta*. The *Bph20* gene was mapped to 193.4 kb region located on the short arm of chromosome 4, and the *Bph21* gene was mapped to a 194.0 kb region on the long arm of chromosome12. However, allelism test is needed to confirm the independence of *Bph 20* and *Bph21* genes.

Of the 18 genes mapped onto different locations of rice chromosomes, only 10 genes (*Bph1*, *bph2*, *Bph3*, *Bph9*, *Bph14*, *Bph15*, *Bph18*, *Bph19*, *Bph20*, and *Bph21*) have been fine-mapped. These genes could be introduced into BPH susceptible elite cultivars using marker-assisted selection and backcross breeding.

QTLs associated with BPH resistance

The genetic basis of qualitative resistance to BPH has been well established and 21 major genes for resistance to BPH have been discovered from rice germplasm including four wild *Oryza* species (*O. officinalis*, *O. minuta*, *O. latifolia*, *and O. australiensis*). In some cases, cultivars with major genes for resistance have broken down because of the adaptation of BPH population to highly resistant varieties. It has been suggested that quantitative resistance to BPH could be more durable (Bosque-Perez and Buddenhagen 1992). However, the genetic basis of quantitative resistance to insect pests was not ascertained due to complex inheritance of the trait and limitations of conventional genetic tools. With the advent of new molecular genetics tools and availability of ideal mapping populations, it has become possible to look for genes involved in expression of complex traits.

BPH resistance in some rice cultivars is reported to be controlled by polygenes or QTLs. Alam and Cohen (1998) identified seven QTLs for resistance on chromosomes 1, 2, 3, 4, 6, and 8 using 175 RFLP markers. Ramalingam et al. (2003) reported four additional QTLs associated with BPH resistance in the same population (IR64 × Azucena) using an additional 105 candidate gene markers. Huang et al. (2001) conducted QTL analysis of resistance genes derived from wild species (*O. officinalis*) and reported two QTLs, *Qbp1* and *Qbp2* on chromosomes 3 and 4, respectively. 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 Teqing × Lemont populations. Su et al. (2002) detected QTLs on chromosomes 2, 10, and 12 using a Nipponbare × Kasalath backcross population. Soundararajan et al. (2004) used a DH population (IR64 × Azucena) and detected six QTLs on chromosomes 1, 2, 6, and 7 for BPH resistance by applying RAPD and RFLP markers. 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. 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 'Col5' 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 identified. Two QTLs showed a significant additive effect. A new locus for resistance to BPH (*Qbph11*) was identified in the indica variety, DV 85 (Su et al. 2005)

Pyramiding BPH resistance genes

With available molecular markers, progress has been made in pyramiding some of the major BPH resistance genes into elite cultivars. Sharma et al. (2004) used MAS for pyramiding *Bph1* and *bph2* genes into a japonica breeding line. The pyramided line showed higher resistance than the line with *bph2* alone but the degree of resistance was similar to *Bph1*. Li et al. (2006) incorporated *Bph14* and *Bph15* genes through MAS into a number of parental lines of hybrid rice in China and observed that 92.3% *Bph14*-single introgression lines had moderate resistance to BPH and *Bph14*/*Bph15* pyramided lines had stronger resistance levels than the single gene introgression lines.

BPH resistance gene clusters and genes of ambiguity

New BPH resistance genes derived from indica varieties were mainly identified by observing BPH reaction pattern against the biotypes. Due to erosion of BPH resistance, wild species of *Oryza* have been considered to be a valuable resistance gene resource and their introgression lines have been increasingly used as BPH resistance donor in recent years (Jena et al. 2006).

BPH resistance genes have been identified and mapped on six of 12 rice chromosomes (2, 3, 4, 6, 11, and 12). However, different resistance gene loci are clustered together in the same chromosomal regions and closely linked to each other (Table 3). The regions of chromosome 4S and 12L are especially the hotspots of BPH resistance genes where 53% of known resistance genes reside. However, some BPH resistance genes named as new were presumed to be different from other genes that existed nearby due to differences in resistant source, result of genetic analysis (dominant/recessive), or relative distance of flanked marker(s) on the maps. The differences were not, however, confirmed by allelism test or cloning of gene.

The *Bph13* gene was located near the *bph19* gene on chromosome 3S. The *Bph13* gene resides in the region flanked by RG100 and RG 191 region (Renganayaki et al. 2002), while the *bph19* gene was mapped in the region flanked by RM517 and RM218 (Chen et al. 2006). The *bph11* and *Bph14* genes also were mapped in the nearby region on chromosome 3L and both of them have been identified in an introgression line of *O. officinalis*. The locus of *bph11* has been identified by an RFLP marker G1318 while *Bph14* named previously as *Qbp2* has been flanked by R1925 and G1318 (Hirabayashi and Ogawa 1995; Ren et al. 2004).

The resistance genes, *Bph17* and *Bph20* are located on the short arm of chromosome 4 flanked by SSR markers RM8213 and RM5953, and MS10 and RM5953, respectively (Rahman et al. 2009; Sun et al. 2005). Part of the regions of these two genes, *Bph17* and *Bph20* gene, overlap each other and originated from Rathu Heenati and the wild species *O. minuta*, respectively. The *Bph12* gene carried by B14 introgression line was derived from *O. latifolia* and detected by RM 261 using the bulked segregant analysis, and mapped on the short arm of chromosome 4 (Yang et al. 2002). The *Bph15* gene has been identified in an introgression lines derived from *O. officinalis* mapped on chromosome 4 flanked by RFLP markers C820 and S11182 (Yang et al. 2004).

BPH resistance genes, *Bph1*, *bph2*, *Bph9*, *Bph10*, *Bph18*, and *Bph21* are located on chromosome 12L. The *Bph*9 gene in Kaharamana and Pokkali was located in the same region of chromosome 12 (Murai et al. 2001; Su et al. 2006). No evidence has yet been obtained that they might share the same genomic sequence and encodes the same protein. Ishii et al. (1994) identified a resistance gene, *Bph10* gene, in an introgression line IR65482-4-136-2-2 derived from the wild species *O. australiensis*. The *Bph18* gene has also been identified in an introgression line (IR65482-7-216-1-2) that has inherited the gene from *O. australiensis* (Jena et al. 2006). However, the *Bph10* and *Bph18* genes are non-allelic (Jena et al. 2006). Among the cluster resistance genes on chromosome 12 non-allelic relationships between *Bph18* and *Bph10* genes was confirmed by allelism test and single-locus ANOVA. The result suggests the *Bph18* gene is a different BPH resistance gene from *Bph10*. The *Bph21* gene is also located nearby *Bph10* and *Bph18* genes on chromosome 12 L. However, the allelism test is needed to distinguish the *Bph21* gene from *Bph18* or *Bph10*.

In BPH resistance genetics study, there are some discrepancies on duplicate nomenclature of genes for the same gene without valid evidences. For example, the *Bph11* (*bph11*), *Bph12* (*bph12*) and *Bph13* [*Bph13(t)*] genes are existing as duplicate genes. A new BPH resistance derived from IR1154-243 was located on chromosome 4 and was

Table 4 Location of brown planthopper resistance genes on molecular map of rice

Gene	Chromosome[a]	Markers	References
Bph1	12	G148 (RFLP)	(Hirabayashi et al. 1998; Sun et al. 2007)
	12L	em5814N (AFLP)	(Sharma et al. 2004)
	12	BpE18-3 (STS)	(Kim and Sohn 2005)
	12L	XNpb248, XNpb336 (RFLP)	(Hirabayashi et al. 1998)
	12L	AFLP em5814N	(Sharma et al. 2002)
	12	OPD-7 RD7 (RAPD), RG869, RG457 (RFLP), RM247(SSR)	(Jeon et al. 1999)
Qbp1	3L	R1925, R2443 (RFLP)	(Huang et al. 2001)
Qbp1 (Bph14t)	3	R1925, G1318 (RFLP)	(Ren et al. 2004)
bph2	12	G2140 (RFLP)	(Murata et al. 2001)
	12	RM463, RM7102 (SSR)	(Sun et al. 2007)
	12	KAM4 (STS)	(Murai et al. 2001; Sharma et al. 2002)
Qbph2	2L	RM6843, RM3355 (SSR)	(Sun et al. 2006)
	4S	C820, R288 (RFLP)	(Huang et al. 2001)
	2L	RFLP, SSR	(Liu et al. 2001)
	2	5529-1358 (SSR)	(Liu et al. 2009)
Bph3	6S	RM589 (SSR)	(Jairin et al. 2007a)
Qbph3	3	RM313, RM7 (SSR)	(Sun et al. 2005)
bph4	6S	RM190 (SSR), C76A (RFLP)	(Kawaguchi et al. 2001)
Qbph4(Bph17)	4	RM8213, RM5953 (SSR)	(Sun et al. 2005)
	4S	RM401, RM335 (SSR)	(Liu et al. 2009; Yang et al. 2004)
Bph6	11	$OPA16_{938}$ (RAPD)	(Jena et al. 2002)
Qbph6	6S	RM510, RM314 (SSR)	(Sun et al. 2006)
Qbph7	7	RM542, RM500(SSR)	(Liu et al. 2009)
Bph9	12L	RM463, RM5341 (SSR)	(Su et al. 2006)
	12L	OPR04 (RFLP), S2545 (RAPD)	(Murata et al. 2001)
Qbph9	9L	RM3533, RM242 (SSR)	(Liu et al. 2009)
Bph10(t)	12L	RG457 (RFLP)	(Ishii et al. 1994)
Qbph10	10	RM484, RM496 (SSR)	(Sun et al. 2005)
bph11(t)	3L	G1318 (RFLP)	(Hirabayashi and Ogawa 1995)
Bph12(t)	4S	RM261 (SSR)	(Yang et al. 2002)
Bph13(t)	2L	RM250, RM240 (SSR)	(Liu et al. 2001)
Bph13(t)	3S	$AJ09b_{230}$ (RAPD), AJ09c (STS)	(Renganayaki et al. 2002)
Bph14 (Qbp1)	3L	R1925, G1318 (RFLP)	(Yang et al. 2004)
Bph15(Qbp2)	4S	C820, S11182 (RFLP)	(Yang et al. 2004)
*Qbp2(Bph15*t)	4S	C820, R288 (RFLP)	(Ren et al. 2004)
Bph17(t)	4S	RM8213, RM5953 (SSR)	(Sun et al. 2005)
Bph18	12L	RM463, S15552, 7312.T4A (STS)	(Jena et al. 2006)
bph19(t)	3S	RM6308, RM3134 (SSR)	(Chen et al. 2006)
Bph20(t)	4	MS10, RM5953	(Rahman et al. 2009)
Bph21(t)	12	RM3726, RM5479	(Rahman et al. 2009)
BPH[b]	12	RG463, RG901, CDO 344 (RFLP)	(Huang et al. 1997)

[a] *L* long arm, *S* short arm

[b] Gene not named

named as *Bph11* (Xu et al. 2002). However, the *bph11* gene was identified in an introgression line derived from *O. officianalis* on chromosome 3 (Hirabayashi and Ogawa 1995). The *Bph12* and *bph12* genes mapped on chromosome 3 derived from different resistance donors, *O. officianalis* and *O. latifolia*, respectively (Yang et al. 2002; Hirabayashi and Ogawa 1995). The *Bph13* gene identified in two introgression lines were derived from *O. eichingeri* and *O.*

officinalis. A dominant BPH resistance gene, *Bph13*, was mapped on chromosome 2 at 6.1 cM and 5.5 cM away from RM240 and RM250, respectively (Liu et al. 2001). Renganayaki et al. (2002) also mapped the *Bph13(t)* gene inherited from *O. officinalis* on chromosome 3. These duplicate genes, located on different chromosomal regions, segregated independently and originated from different sources. To make it clear, renaming is needed after a confirmation procedure such as an allelism test.

The *Qbp1* and *Qbp2* associated with BPH resistance genes on chromosomes 3 and 4 respectively have been mapped (Huang et al. 2001). These two major QTLs were identified in B5, an introgression line of *O. officinalis* collected in China and later named as *Bph14* and *Bph15* (Ren et al. 2004; Yang et al. 2002). A total of seven QTLs associated with resistance derived from IR64 on chromosome 1, 2, 3, 4, 6, and 8 (Alam and Cohen 1998). Three loci named as *Qbph3*, *Qbph4*, and *Qbph10* detected by QTL analysis were assigned to chromosome 3, 4 and 10. *Qbph4* of three QTLs was a major BPH resistance gene in Rathu Heenati and was designated as *Bph17* (Sun et al. 2005). Two QTLs (*Qbph2* and *Qbph6*) were detected on chromosome 2 (explains 29.4% phenotypic variation) and 6 (explains 46.2% phenotypic variation) associated with resistance to BPH in the mapping population from a cross between a resistant indica cultivar, Col.5, and a susceptible cultivar '02428' (Sun et al. 2006), and another four QTLs (*Qbph-2*, *Qbph-4*, *Qbph-7*, and *Qbph-9*) contributing to BPH resistance carried by Rathu Heenati were mapped on chromosomes 2, 4, 7, and 9, respectively (Liu et al. 2009). Both of the QTLs (*Qbph4* and *Qbph-4*) that derived from the same resistance donor (Rathu Heenati) were assigned nearby each other on chromosome 4. Multiple BPH resistance genes/QTLs are existing with the same names for different genes or as different names for the same genes. These genes/QTLs are ambiguous and it is imperative to conduct more genetic analysis and allelism tests before their breeding application.

Expression of trans-gene for BPH resistance

Novel genes for BPH resistance have been identified in alternate genetic sources and transgenic plants have been developed. A snowdrop lectin gene (*Galanthus nivalis agglutinin*; GNA) showed toxicity towards BPH when administered in an artificial diet (Rao et al. 1998). Transgenic rice plants containing the *GNA* gene expressed resistance to BPH driven by a phloem-specific promoter (from the rice sucrose synthase *RSs1* gene) and by a constitutive promoter (from the maize ubiquitin *ubi1* gene). PCR and Southern analyses confirmed that the transgenes were transmitted to progeny. Western blot analyses revealed the expression of *GNA* 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 immune histo-chemical localization of the protein in the nonlignified vascular tissue of transgenic plants. Insect bioassays and feeding studies showed that GNA gene 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. The *GNA* gene has been reported to be the first trans-gene to exhibit insecticidal activity towards BPH in rice.

Cloning of BPH resistance genes

Advances in molecular biology and bioinformatics have paved the way for the cloning and understanding of the molecular mechanism of BPH resistance. Of the 21 genes conferring resistance to BPH, only one resistance gene, *Bph14*, located on the long arm of chromosome 3 has been cloned (Du et al. 2009). The *Bph14* gene which confers resistance at seedling and maturity stages was cloned by map-based cloning approach. The *Bph14* gene encodes a coiled-coil nucleotide binding and leucine-rich repeat (CC-NB-LRR) protein. Sequence comparison indicates that the *Bph14* gene carries a unique LRR domain that might function in recognizing BPH invasions and in activating the defense response. The *Bph14* gene activates salicylic acid signaling pathway and induces callose deposition in phloem tissue that inhibits BPH feeding on the host plant (Du et al. 2009).

Another resistance gene, *Bph18,* located on the long arm of chromosome 12 confers broad-spectrum resistance to BPH. The *Bph18* gene has also been cloned by map-based cloning through recombinant selection and candidate gene identification approaches. Initially, the *Bph18* gene was localized within an 843 kb physical region on chromosome 12 flanked by the markers *R10289S* and *RM6869*. Fine-mapping with 3,100 BC_4F_2 plants delimited the *Bph18* gene to a 26-kb region which contained four annotated genes. We sequenced this region in IR65482-7-216-1-2 and found a 14-kb deletion including the two retrotransposon genes. The *Bph18* region was finally delimited to 12-kb. We isolated a resistance protein gene of the resistant donor in this region and introduced it into the susceptible japonica variety, Ilmi, by transformation. The 12T1 lines showed enhanced resistance upon BPH bioassay. This gene encodes a coiled-coil nucleotide binding site (CC-NBS) protein lacking LRR domain unlike most of rice R proteins having CC-NBS-LRR domain structure (Ji HS, Kim YH, Park HM, Suh JP and Jena KK: unpublished). Further studies are being carried out to understand the expression and mechanism of BPH resistance conferred by the *Bph18* gene. These two cloned genes (*Bph14* and *Bph18*) will play

an important role in improving resistance of elite rice cultivars.

Conclusions

Rapid population growth, adverse effects of climate change and changes in biotypes of BPH exert pressure on increasing rice production. Rice production needs to be increased by controlling the damage caused by biotic stresses particularly BPH in terms of significant yield loss annually. Host-plant resistance is an effective environment friendly approach to reduce BPH damage and increase yield potential of cultivars. It is important to use a reproducible phenotyping method such as seedbox test and well-defined BPH population for identification and incorporation of resistance genes into elite cultivars. Although 21 BPH resistance genes have been identified, further efforts are needed to identify new resistance genes from diverse genetic sources which may confer resistance to new biotypes of BPH. Hence, evaluation of new germplasm of cultivated rice as well as wild *Oryza* species must be explored to identify new genes for resistance. Some of the known resistance genes could be pyramided and tested for efficacy in conferring resistance to new biotypes of BPH. In order to achieve stable resistance to BPH, pyramided major genes or QTLs may provide durable resistance and improve yield potential of cultivars. Development of functional SNPs associated with BPH resistance could also provide additional genomic tools to the implementation of BPH resistance genes for improved elite rice cultivars and a stable rice production.

References

Alam SN, Cohen MB. Detection and analysis of QTLs for resistance to the brown planthopper, *Nilaparvata lugens*, in a doubled haploid rice population. Theor Appl Genet. 1998;97:1370–9.

Athwal DS, Pathak MD, Bacalangco EH, Pura CD. Genetics of resistance to brown planthopper and green leafhoppers in *Oryza sativa* L. Crop Sci. 1971;11:747–50.

Athwal DS, Pathak MD. Genetics of resistance to rice insects. In: Rice breeding. Los Baños (Philippines): International Rice Research Institute; 1972. p. 375–86.

Bosque-Perez NA, Buddenhagen IW. The development of host-plant resistance to insect pests: outlook for the tropics. In: Menken SBJ, Visser JH, Harrewijn P, editors. Proc 8th Int Symp insect–plant relationships. Dordrecht: Kluwer; 1992. p. 235–49.

Brar DS, Virk PS, Jena KK, Khush GS. Breeding for resistance to planthoppers in rice. Planthopper: new threats to the sustainability of intensive rice production systems in Asia. IRRI 2010; p. 401–27

Chen JW, Wang L, Pang XF, Pan H. Genetic analysis and fine mapping of a rice brown planthopper (*Nilaparvata lugens* Stål) resistance gene *bph19*(t). Mol Gen Genomics. 2006;275:321–9.

Du B, Zhang W, Liu B, Hu J, Wei Z, Shi Z, et al. Identification and characterization of *Bph14*, a gene conferring resistance to brown planthopper in rice. Proc Natl Acad Sci. 2009;106:22163–8.

Heinrichs EA, Medrano FG, Rapusas HR. Genetic evaluation for insect resistance in rice. Los Baños (Philippines): International Rice Research Institute; 1985. p. 1–356.

Hirabayashi H, Ogawa T. RFLP mapping of *Bph-1* (brown planthopper resistance gene) in rice. Breed Sci. 1995;45:369–71.

Hirabayashi H, Angeles ER, Kaji R, Ogawa T, Brar DS, Khush GS. Identification of brown planthopper resistance gene derived from *O. officinalis* using molecular markers in rice. Breed Sci. 1998;48 (Suppl):82.

Huang N, Parco A, Mew T, Magpantay G, McCouch S, Guiderdoni E, et al. RFLP mapping of isozymes, RAPD and QTLs for grain shape, brown planthopper resistance in a doubled haploid rice population. Mol Breed. 1997;3:105–13.

Huang N, He G, Shu L, Li X, Zhang Q. Identification and mapping of two brown planthopper genes in rice. Theor Appl Genet. 2001;102:929–34.

Ikeda R, Kaneda C. Genetic analysis of resistance to BPH *Nilaparvata lugens* Stål in rice. Jpn J Breed. 1981;31:279–85.

Ikeda R, Kaneda C. Genetic relationships of brown planthopper resistance to dwarf disease and stripe disease in rice. Jpn J Breed. 1982;32:177–85.

Ishii T, Brar DS, Multani DS, Khush GS. Molecular tagging of genes for brown planthopper resistance and earliness introgressed from *Oryza australiensis* into cultivated rice. *O. sativa*. Genome. 1994;37:217–21.

IRRI (International Rice Research Institute). Standard evaluation system for rice. Manila (Philippines): International Rice Research Institute; 1988.

Jackson MT. Conservation of rice genetic resources: the role of the International Rice Genebank at IRRI. Plant Mol Biol. 1997;35:61–7.

Jairin J, Phengrat K, Teangdeerith S, Vanavichit A, Toojinda T. Mapping of a broad-spectrum brown planthopper resistance gene, *Bph3*, on rice chromosome 6. Mol Breed. 2007a;19:35–44.

Jairin J, Teangdeerith S, Leelagud P, Phengrat K, Vanavichi A, Toojindra T. Detection of brown planthopper resistance genes from different rice mapping populations in the same genomic location. Sci Asia. 2007b;33:347–52.

Jena KK, Pasalu IC, Rao YK, Varalaxmi Y, Krishnaiah K, Khush GS, et al. Molecular tagging of a gene for resistance to brown planthopper in rice (*Oryza sativa* L.). Euphytica. 2002;129:81–8.

Jena KK, Jeung JU, Lee JH, Choi HC, Brar DS. High-resolution mapping of a new brown planthopper (BPH) resistance gene, *Bph18*(t), and marker-assisted selection for BPH resistance in rice (*Oryza sativa* L.). Theor Appl Genet. 2006;112:288–97.

Jeon YH, Ahn SN, Choi HC, Hahn TR, Moon HP. Identification of a RAPD marker linked to a brown planthopper resistance gene in rice. Euphytica. 1999;107:23–8.

Kabir MA, Khush GS. Genetic analysis of resistance to brown planthopper in rice, *Oryza sativa* L. Plant Breed. 1988;100:54–8.

Kaneda C, Ito K, Ikeda R. Screening of rice cultivars for resistance to brown planthopper, *Nilaparvata lugens* Stål, by three biotypes. Jpn J Breed. 1981;31:141–51.

Kawaguchi M, Murata K, Ishii T, Takumi S, Mori N, Nakamura C. Assignment of a brown planthopper (*Nilaparvata lugens* Stål) resistance gene *bph4* to the rice chromosome 6. Breed Sci. 2001;51:13–8.

Khush GS. Rice breeding for disease and insect resistance at IRRI. Oryza. 1971;8:111–9.

Khush GS. Disease and insect resistance in rice. Adv Agron. 1977;29:265–341.

Khush GS. Multiple disease and insect resistance for increased yield stability in rice. In progress in irrigated rice research. Manila: International Rice Research Institute; 1989. p. 79–92.

Khush GS. Selecting rice for simply inherited resistance. In: Stalker HT, Murphy JP, editors. Plant breeding in the 1990s. Wallingford (UK): CAB International; 1992. p. 303–22.

Khush GS, Karim AR, Angeles ER. Genetics of resistance of rice cultivar ARC 10550 to Bangladesh brown planthopper biotype. J Genet. 1985;64:121–5.

Khush GS, Brar DS. Genetics of resistance to insects in crop plants. Adv Agron. 1991;45:223–74.

Kim SM, Sohn JK. Identification of rice gene (*Bph 1*) conferring resistance to brown plant hopper (*Nilaparvata lugens* Stål) using STS markers. Mol Cells. 2005;20:30–4.

Lakashminarayana A, Khush GS. New genes for resistance to the brown planthopper in rice. Crop Sci. 1977;17:96–100.

Li JB, Xia MY QHX, He GC, Wan BL, Zha ZP. Marker-assisted selection for brown planthopper (*Nilaparvata lugens* Stal) resistance genes *Bph14* and *Bph15* in rice. Scient Agric Sinica. 2006;39:2132–7.

Liu Y, Su C, Jiang L, He J, Wu H, Peng C, et al. The distribution and identification of brown planthopper resistance genes in rice. Hereditas. 2009;146:67–73.

Liu GQ, Yan HH, Fu Q, Qian Q, Zhang ZT, Zhai WX, et al. Mapping of a new gene for brown planthopper resistance in cultivated rice introgressed from *Oryza eichingeri*. Chin Sci Bull. 2001;46:1459–62.

Martinez CR, Khush GS. Sources and inheritance of resistance to brown planthopper in some breeding lines of rice. Crop Sci. 1974;14:264–7.

Murai H, Hashimoto Z, Sharma P, Shimizu T, Murata K, Takumi S, et al. Construction of a high resolution linkage map of a rice brown planthopper (*Nilaparvata lugens* Stål) resistance gene *bph2*. Theor Appl Genet. 2001;103:526–32.

Murata K, Fujiwara M, Murai H, Takumi S, Mori N, Nakamura C. Mapping of a brown planthopper (*Nilaparvata lugens* Stål) resistance gene *Bph9* on the long arm of chromosome 12. Cereal Res Commun. 2001;29:245–50.

Nemoto H, Ikeda R, Kenada C. New genes for resistance to brown planthopper *Nilaparvata lugens* Stål in rice. Jpn J Breed. 1989;39:23–8.

Panda N, Heinrichs EA. Levels of tolerance and antibiosis in rice varieties having moderate resistance to the brown planthopper, *Nilaparvata lugens* (Stal) (Hemiptera: Delphacidae). Environ Entomol. 1983;12:1204–14.

Panda N, Khush GS. Host plant resistance to insects. Wallingford (UK): CAB International; 1995. p. 431.

Park DS, Song MY, Park SK, Lee SK, Lee JH, Song SY, et al. Molecular tagging of the *Bph1* locus for resistance to brown planthopper (*Nilaparvata lugens* Stål) through representational difference analysis. Mol Genet Genomics. 2008;280:163–72.

Pathak MD, Cheng CH, Furtono ME. Resistance to *Nephotettix cincticeps* and *Nilaparvata lugens* in varieties of rice. Nature. 1969;223:502–4.

Rahman ML, Jiang W, Chu SH, Qiao Y, Ham TH, Woo MK, et al. High-resolution mapping of two brown planthopper resistance genes, *Bph20(t)* and *Bph21(t)*, originating from *Oryza minuta*. Theor Appl Genet. 2009;119:1237–46.

Rao KV, Rathore KS, Hodges TK, Fu X, Stoger E, Sudhakar D, et al. Expression of snowdrop lectin (GNA) in transgenic rice plants confers resistance to rice brown planthopper. Plant J. 1998;15:469–77.

Ramalingam J, Vera Cruz C, Kukreja K, Chittoorr JM, Wu JL, Lee SW, et al. Candidate defense genes from rice, barley, and maize and their association with qualitative and quantitative resistance in rice. Mol Plant-Microbe Interact. 2003;16:14–24.

Ren X, Wang X, Yuan H, Weng Q, Zhu L, He G. Mapping quantitative trait loci and expressed sequence tags related to brown planthopper resistance in rice. Plant Breed. 2004;123:342–8.

Renganayaki K, Fritz AK, Sadasivam S, Pammi S, Harrington SE, McCouch SR, et al. Mapping and progress toward map-based cloning of brown planthopper biotype-4 resistance gene introgressed from *Oryza officinalis* into cultivated rice. O. sativa. Crop Sci. 2002;42:2112–7.

Sharma PN, Ketipearachchi Y, Murata K, Torii A, Takumi S, Mori N, et al. RFLP/AFLP mapping of a brown planthopper (*Nilaparvata lugens* Stal.) resistance gene *Bph1* in rice. Euphytica. 2002;129:109–17.

Sharma PN, Torii A, Takumi S, Mori N, Nakamura C. Marker-assisted pyramiding of brown planthopper (*Nilaparvata lugens* Stål) resistance genes *Bph1* and *Bph2* on rice chromosome 12. Hereditas. 2004;136:39–43.

Shi Z, Ren X, Weng Q, Li X, He G. Construction of a genomic library from brown planthopper resistant line using a transformation-competent vector and identification of clones spanning the *Qbp1* locus. Plant Sci. 2003;165:879–85.

Sidhu GS, Khush GS. Genetic analysis of brown planthopper resistance in twenty varieties of rice. Oryza sativa. Theor Appl Genet. 1978;53:199–203.

Sidhu GS, Khush GS, Medramo FG. A dominant gene in rice for resistance to white-backed planthopper and its relationship to other plant characteristics. Euphytica. 1997;28:227–32.

Soundararajan RP, Kadirvel P, Gunathilagara JK, Maheswaran M. Mapping of quantitative trait loci associated with resistance to brown planthopper in rice by means of a doubled-haploid population. Crop Sci. 2004;44:2214–20.

Su CC, Cheng XN, Zhai HQ, Wan JM. Detection and analysis QTL for resistance to brown planthopper, *Nilaparvata lugens* (Stål), in rice (*Oryza sativa* L) using backcross inbred lines. Acta Genet Sin. 2002;29:332–8.

Su CC, Wan J, Zhai HQ, Wang CM, Sun LH, Yasui H, et al. A new locus for resistance to brown planthopper identified in indica rice variety DV85. Plant Breed. 2005;124:93–5.

Su CC, Zhai HQ, Wang CM, Sun LH, Wan JM. SSR mapping of brown planthopper resistance gene *Bph*9 in Kaharamana, an indica rice (*Oryza sativa* L.). Acta Genet Sin. 2006;33:262–8.

Sun L, Su C, Wang C, Zai H, Wan J. Mapping of a major resistance gene to brown planthopper in the rice cultivar Rathu Heenati. Breed Sci. 2005;55:391–6.

Sun L, Liu Y, Jiang L, Su C, Wang G, Zhai H, et al. Identification of quantitative trait loci associated with resistance to brown planthopper in the indica rice cultivar Col. 5 Thailand. Hereditas. 2007;144:48–52.

Sun LH, Wang CM, Su CC, Liu YQ, Zhai HQ, Wan J. Mapping and marker-assisted selection of a brown planthopper resistance gene *bph2* in rice (*Oryza sativa* L.). Acta Genet Sin. 2006;33:717–23.

Xu XF, Mei HW, Luo LJ, Cheng XN, Li ZK. RFLP-facilitated investigation of the quantitative resistance of rice to brown planthopper (*Nilaparvata lugens*). Theor Appl Genet. 2002;104:248–53.

Wang Y, Wang X, Yuan H, Chen R, Zhu L, He R, et al. Responses of two contrasting genotypes of rice to brown planthopper. Mol Plant-Microbe Interact. 2008;21:122–32.

Wei J, Hu W, Liu Q, Cheng X, Tong M, Zhu L, et al. Understanding rice plant resistance to the brown planthopper (*Nilarparvata lugens*): a proteomic approach. Proteomics. 2009;9:1–11.

Yang HY, Ren X, Weng QM, Zhu LL, He GC. Molecular mapping and genetic analysis of a rice brown planthopper (*Nilarparvata lugens* Stål) resistance gene. Hereditas. 2002;136:39–43.

Yang H, You A, Yang Z, Zhang F, He R, Zu L, et al. High resolution genetic mapping at the *Bph15* locus for brown planthopper resistance in rice (*Oryza sativa* L.). Theor Appl Genet. 2004;110:182–91.