Advances in Breeding for Resistance to Hoppers in Rice

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Abstract

Rice productivity is hampered by a number of diseases and insects. Among the insects, hoppers including planthoppers and leafhoppers are typical phloem-sap feeders, which are very serious and damaging insect pests of rice in Asia. Many chemicals have been recommended for the control of planthoppers, but due to their feeding habit at the base of the plant, the farmers are unable to notice and effectively control these pests. Exploiting host plant resistance to hoppers and incorporating resistant genes in commercial cultivars are an alternative, economical and environment-friendly approach. To date, approximately 70 resistance genes against hoppers have been identified, and most of these genes have been tagged with molecular markers. Recently six genes for resistance to brown planthopper (BPH) in different lines have been cloned using map-based cloning. Based on molecular analysis of cloned genes, it appears that there is considerable similarity in the plant response to BPH infestation and fungal/bacterial pathogen attack. Marker-assisted selection (MAS) and pyramiding of genes for resistance to BPH and green rice leafhopper (GRH) have shown higher level and wide spectrum of resistance than their monogenic lines. In addition, transgenic approaches including RNAi have targeted various plant lectins and volatile compounds to generate resistance to hoppers. In context of changing climate, the major challenge for plant breeders is to breed varieties while taking care of changing populations of planthoppers and biotype development. Future research priorities

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should concentrate on high-throughput screening of germplasm for field resistance to planthoppers, identifying and transferring new genes for resistance from different sources to broaden the gene pool of rice and identifying durable combination of genes for marker-assisted pyramiding.

Keywords
Hoppers • Rice • Germplasm screening • Genes/QTLs for resistance • MAS • Gene pyramiding • Molecular mechanism • RNAi

4.1 Introduction

Rice is the one of the most important cereals and is cultivated under highly diverse climatic and agroecological conditions. More than 90% of rice is produced and consumed in Asia. More than 3.5 billion people depend upon rice for more than 20% of their calories (Khush 2013). Sustained efforts are needed to increase the production and productivity of rice by 15–20% in the next 25 years to meet the demands of the ever-increasing population. A number of biotic (diseases, insect pests and weeds) and abiotic (drought, submergence, salinity, cold, etc.) stresses continue to reduce rice productivity. Hoppers, stem borer, leaf folder, Gundhi bug and gall midge are the important insect pests infesting rice. Among the hoppers, brown planthopper (BPH), *Nilaparvata lugens* (Stål); white-backed planthopper (WBPH), *Sogatella furcifera* (Horvath); green leafhopper (GLH), *Nephotettix* sp.; green rice leafhopper (GRH), *Nephotettix cincticeps* (Uhler); zigzag leafhopper (ZLH), *Recilia dorsalis* (Motschulsky); and small brown planthopper (SBPH), *Laodelphax striatellus* (Fallen) cause yield losses in rice to a variable extent and at various growth stages. These hoppers are also vectors of major viral diseases, such as grassy stunt, ragged stunt, rice stripe virus, black streak and tungro disease. Yield losses due to rice insect pests have been estimated at about 20–50% (Oerke et al. 1994; Prakash et al. 2007; Savary et al. 2012).

Planthoppers and leafhoppers are typical sap-sucking insect pests and cause serious damage to rice throughout Asia (Normile 2008; Heong and Hardy 2009). Hoppers cause significant yield losses leading to 'hopper burn'. Among the hoppers, BPH causes yield loss amounting to as high as 60% in India under epidemic conditions (Srivastava et al. 2009; Kumar et al. 2012). BPH has also been reported to cause damage in China, Korea, Japan and Vietnam. In 2005, there was loss of 2.7 m tons of rice due to direct damage by BPH, while this loss was 0.4 m tons in Vietnam due to two viruses, namely, grassy stunt and ragged stunt. WBPH has been reported to favour the hybrid rice crops in China and North Vietnam, whereas tungro disease epidemic by GLH was also reported from some areas (Heong and Hardy 2009). It is also difficult to notice these pests, and by the time plant damage becomes evident, significant loss in yield is inevitable. However the management of these

pests is possible with the regular monitoring of the crop (Sarao 2015), but it is very laborious and time-consuming. The two stages of hoppers, namely, nymphs and adults, suck sap from the leaf sheaths resulting in leaf yellowing, less tillering, reduction in plant height and more unfilled grains in panicles. In addition, there is reduction in chlorophyll, protein content of leaves and photosynthetic rate. Due to overfeeding by the hoppers, plants start wilting with first drying of outermost leaves followed by drying of the entire plant. At early stage, round yellowish patches appear which soon turn brownish due to drying up of the plants. These patches spread in concentric circles within the field, and this gives burnt appearance known as 'hopper burn' (Liu et al. 2008; Horgan 2009).

Many chemicals were recommended for the control of planthoppers (Sarao 2015), but due to their feeding habit at the base of the plant, the farmers are unable to notice and control these pests effectively. They perform a number of applications of insecticides under panic, which kills natural enemies and disrupts density-dependent control of the hoppers (Gorman et al. 2008). Extensive application of insecticides may affect behavioural, physiological and biochemical aspects of the insects leading to development of insecticide resistance in hoppers (Matsumura et al. 2009). Therefore the use of genetic resistance is the most effective measure for hopper management (Sarao et al. 2016). For sustainable hopper management, it is necessary to develop strategy involving proportionate balance between breeding for resistance and appropriate use of insecticides, so as to keep hopper population under economic threshold levels. However, cultivation of resistant varieties is an economical, efficient and environmentally sound strategy for hopper population management. These varieties provide pest control at essentially no cost to the farmers.

4.2 Screening for Resistance to Hoppers

Identification of genetic donors and different sources of resistance to hoppers is the primary need for breeding varieties. In addition, a large number of segregating plant materials also need to be screened. For the purpose, it is necessary to have reliable high-throughput screening techniques including availability of target insects of appropriate stages and good laboratory and screen house facilities. The germplasm can be screened rapidly by infesting plants at the seedling stage, during early mass-screening cycle in the glass house. This technique is economical in space, time and labour (Heinrichs et al. 1985). The selected resistant entries in the rapid screening method should be later screened under field conditions. In case of field screening, the location should be selected where high natural population of the pest is prevailing (hotspots).

Under greenhouse conditions, scoring of lines based on the degree of plant damage and number of insects used in infestation is very critical. Based on the initial scoring of the lines, majority of susceptible segregants/lines can be rejected, and the resistant ones can be further tested both in screen house and under field conditions.

4.2.1 Greenhouse Screening

The glass/greenhouse screening is the accelerated and effective method for assessing a large number of different germplasm lines (Myint et al. 2009; Li et al. 2010; Nanthakumar et al. 2012; Fujita et al. 2013; Sarao et al. 2016). Two methods used for screening are described as below:

4.2.1.1 Conventional Seedbox Screening

The conventional seedbox screening or standard seedbox screening test (SSST) is the most commonly used method for greenhouse screening. It is a rapid method for assessing large number of germplasm lines for planthopper resistance. The seeds of test material are sown in a single row of 3.5 cm apart in a seedbox of about 60 × 40 × 10 cm size. Suitable susceptible and resistant checks are sown in similar rows in the same box. Susceptible check (TN1) is sown as outer row which also acts as spreader row. In the centre of the box, half-susceptible and half-resistant material rows are sown. These boxes are placed in the water through galvanized iron trays containing water. Eight to twelve days after sowing, seedlings are thinned to about 20 plants per row. These seedlings are infested with about 8–10 (BPH and WBPH) and 3 (GLH) second to third instar nymphs per seedling. The insects are first cultured on TN1 plants in pots and then distributed uniformly on thinned seedlings by holding the base of the pot and lightly tapping and blowing these TN1 plants to dislodge the hopper nymphs on the seedlings.

For determining nonpreference parameter among lines, the settled planthoppers can be counted per germplasm line before grading for damage score in the tray. The grading of each entry in the seedbox is done when the susceptible check seedlings (TN1) in that box are about 90% dead. Scoring for each seedling in an entry is done using 0–9 scale as per standard evaluation system (SES) for rice. To compare entries a numerical rating system 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; and 9, all plants dead (IRRI 2014). The average damage score of each germplasm line is designated as resistant (0–3.49), moderately resistant (3.50–5.49) and susceptible (5.50–9.00) following Heinrichs et al. (1985) and Sarao et al. (2016).

4.2.1.2 Modified Seedbox Screening Test (MSST)

This test was used to overcome some limitations of SSST and for better understanding of ‘field resistance’, that is, whether resistance is maintained or increases with plants age. The SSST is mostly qualitative, and entries with moderate levels of resistance because of tolerance or low levels of antibiosis or nonpreference usually are recorded as susceptible. Thus, the conventional test is modified to detect varieties with moderate levels of resistance. In this method, the plants are older at the time of infestation and fewer hoppers per seedling are placed. Plants are infested 20 days after sowing with 3 to 5, second to third instar nymphs per plant. In this test, the whole seedbox of infested seedlings in a screen cage (65 × 45 × 90 cm) is covered

to prevent the insects from escaping the tray. In this method mortality of the plants is caused by the progeny (F_1 population of planthoppers) rather than the initial source of infestation is the insects that cause the plant damage. The original nymphs mature and reproduce in the seedbox, and ultimately their offspring kill the plants (Velusamy et al. 1986).

These two methods have been extremely useful for inexpensive screening of the large volume of material required to find resistance genes/sources. Furthermore, they incorporate 'free choice', that is, the target insects can choose between the different varieties under test before initiating feeding (SSST and MSST) or oviposition (MSST) behaviour.

4.2.2 Field Screening

Field screening of germplasm is generally done in hotspots which include all life cycle aspects of the tested insect. For field screening, transplant two rows of a susceptible check such as TN1 on each side of test entry (Chelliah and Heinrichs 1980). To kill natural enemies, apply resurgence-inducing insecticide (spray of 0.002% deltamethrin or 0.02% methyl parathion) to the susceptible border rows starting at 20 days after transplanting (DAT). Next day after spray, observe the base of the plants so as to determine the population of spiders, mirid bugs and other predators. If they are still abundant, repeat the spray application the next day. Thereafter, repeat the sprays at 10-day interval up to 70 DAT, if necessary. After the first application of insecticides, the late instar nymphs at the rate of five insects/hill can be released to support the field population of BPH. Generally 25 BPH female adults/hill at maximum tillering and 100 BPH female adults/hill at flowering stage are required for valid test. When plants in the susceptible check start wilting, start grading all entries (Reissig et al. 1982; Heinrichs et al. 1985; Panda and Heinrichs 1983).

If by the resurgence technique cannot increase the population, then a polyethylene sheet can be placed around small field plots to prevent movement of BPH nymphs outside the plot and to prevent predators entering the test plot (Kalode et al. 1982).

4.3 Genetics of Resistance to Hoppers

Exploiting host plant resistance to hoppers and incorporating resistant genes in susceptible commercial cultivars are considered an economical and environmentally friendly approach. However, availability of good source(s) of resistance and identification of novel genes with linked markers are the utmost priority to achieve full potential of this approach. To locate the hopper resistance genes in germplasm lines, entomologists and breeders had worked tirelessly to study the inheritance of resistance to hoppers. Due to dedicated efforts of the scientists, a large number of donors for resistance to hoppers have been identified, and numerous varieties resistant to insects have been developed worldwide. Some of the key donors for

resistance include Mudgo, ASD7, Rathu Heenati, Ptb33 and wild species for BPH; Mudgo, Kasalath and Rathu Heenati for SBPH; N22, ADR52 and Guiyigu for WBPH; ASD7, DV85 and IR36 for GLH; and Rathu Heenati and Ptb33 for ZLH (see for more details in Brar et al. 2015). To date, more than 70 genes/QTLs for resistance to hoppers have been identified, and a significant number have been tagged with molecular markers (Fujita et al. 2013). A number of genes/QTLs for resistance to BPH (Table 4.1) and GLH have been reported, while limited information is available for other hoppers.

4.3.1 Genetics and Mapping of Resistance to BPH

Beginning with identification of sources of resistance to BPH in 1967 (Pathak et al. 1969), significant efforts have been done to search for host plant resistance to BPH. The earliest information on the genetics of BPH resistance was reported in 1970 (Athwal et al. 1971) with identification of *Bph1* and *bph2* as first two resistant genes. However development of DNA-based markers and QTL analysis in 1970–1980s helped to establish their linkage to specific region of rice genome. To date, 32 major genes designated from *Bph1* to *Bph32* for resistance to BPH have been identified from wild and cultivated rice germplasm. Of these, 25 have been mapped using restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), simple sequence repeats (SSR), sequence tagged sites (STS) and insertions and deletions (InDel)-based markers (Table 4.1). These genes are located on seven (2, 3, 4, 6, 10, 11 and 12) of 12 rice chromosomes. The rice chromosome 12 contains eight genes including *Bph1*, *bph2*, *Bph7*, *Bph9*, *Bph10*, *Bph18*, *Bph21* and *Bph26* followed by six genes, *Bph3*, *bph4*, *Bph22*, *Bph25*, *Bph29* and *Bph32* on chromosome 6. Five genes, *Bph12*, *Bph15*, *Bph17*, *Bph20 and Bph27*, are located on chromosome 4. Four genes, *Bph11*, *Bph13*, *Bph14* and *Bph19*, are located on chromosome 3. One gene each, *Bph13*, *Bph30*, and *Bph28*, is located on chromosomes 2, 10 and 11, respectively (Table 4.1).

The *Bph1* (Hirabayashi and Ogawa 1995; Jeon et al. 1999; Sharma et al. 2002; Kim and Sohn 2005; Park et al. 2008; Cha et al, 2008) and *bph2* (Murata et al. 1998; Murai et al. 2001; Sharma et al. 2004; Sun et al. 2006), the first two resistant genes, were mapped on the rice chromosome 12. These two genes had shown resistance to BPH biotypes 1 and 2, prevalent at that time and soon deployed in rice mega varieties. In 1973, the first resistant rice cultivar, IR26, was released that contains *Bph1* (Khush 1971), followed by cultivars IR36, IR38 and IR42 with the *bph2* gene. However *Bph1* and *bph2* rapidly became obsolete in just 3–5 years because of the development of new BPH biotypes (Brar et al. 2015). This gave rise to the continuous efforts to identify and map novel sources of resistance to BPH to breed broad-spectrum and durable resistant varieties.

A broad-spectrum resistance gene, *Bph3*, was mapped against BPH biotype 2 in Rathu Heenati and Ptb33 using SSR markers. Two backcross populations were generated using both the donors for mapping *Bph3* locus. The BC_1F_2 was derived from cross of Ptb33/RD6, whereas BC_2F_2 was derived from cross between Rathu Heenati

Table 4.1 Some examples on genes for resistance to BPH in rice tagged with molecular markers

Gene	Chromosome[a]	Donor[b]	Marker	Marker type used	Population type	Reference(s)
Bph1	12L	IR28 (1)	XNpb248, XNpb336	RFLP	F_2/F_3	Hirabayashi and Ogawa (1995)
	12L	Gayabyeo (1)	RRD7, RG457, RG634	RAPD, RFLP, SSR	F_2/F_3	Jeon et al. (1999)
	12L	Mudgo (1)	em5814N, em2802N, R2708	AFLP, RFLP	F_2/F_3	Sharma et al. (2002)
	12L	Samgangbyeo (1)	BpE18-3	RAPD, STS	DH, F_2/F_3	Kim and Sohn (2005)
	12L	Samgangbyeo (1)	OsBphi 252	RDA clones, CAPS	NILs	Park et al. (2008)
	12L	Cheongcheongbyeo (1)	pBPH4, pBPH14	RAPD, SCAR, STS	RILs	Cha et al. (2008)
bph2	12L	NorinPL4	G2140	RFLP	F_2/F_3	Murata et al. (1998)
	12L	NorinPL4	KAM3, KAM4, KAM5	AFLP	F_4/F_5	Murai et al. (2001)
	12L	NorinPL4 (1)	KAM2, KAM3, KAM4	AFLP	F_5	Sharma et al. (2004)
	12L	ASD7 (1, 2)	RM463, RM7102	SSR	F_2/F_3	Sun et al. (2006)
Bph3	6S	Ptb33, Rathu Heenati, IR71033-121-15 (2)	RM589, RM588, RM586	SSR	BC_1F_2/BC_3F_2, F_2	Jairin et al. (2007a, b, c) and Liu et al. (2014)
bph4	6S	Babawee	RM217, C76A	SSR	F_2/F_3	Kawaguchi et al. (2001)
	6S	Babawee (4)	RM586-RM589	SSR	F_2/F_3	Jairin et al. (2010)
Bph6	4L	Swarnalata	RM6997-RM5742	SSR, STS	F_2/F_3, BC_2F_2	Qiu et al. (2010)

(continued)

Table 4.1 (continued)

Gene	Chromosome[a]	Donor[b]	Marker	Marker type used	Population type	Reference(s)
bph7	12L	T12	RM28295-RM313	SSR	F_2/F_3, BC_2F_1	Qiu et al. (2014)
Bph9	12L	Pokkali	OPR04,S2545	RAPD, RFLP	F_2, F_3/F_4	Murata et al. (2001)
	12L	Kaharamana (1)	RM463, RM5341	SSR	F_2/F_3	Su et al. (2006)
Bph10	12L	IR65482-4-136-2-2 (*O. australiensis IRGC100882*)	RG457	RFLP	F_2/F_3	Ishii et al. (1994)
	12L	IR54742 (*O. officinalis*) (1, 2, 3)	RG457L-B, RM260	STS, SSR	F_2/F_3	Lang and Bu (2003)
bph11	3L	IR54742-23-19-12-3-54 (*O. officinalis*) (1)	G1318	RFLP	F_2/F_3, RILs	Hirabayashi et al. (1998)
bph12	4S	GSK185-2 (*O. officinalis*)	G271, R93	RFLP	F_2/F_3	Hirabayashi et al. (1999)
Bph12	4S	B14 (*O. latifolia*) (1, 2)	RM261	SSR	F_2/F_3, RILs	Yang et al. (2002)
	4S	B14 (*O. latifolia*) (1, 2)	RM16459-RM1305	SSR	F_2/F_3, $BC_2F_{2:3}$	Qiu et al. (2012)
Bph13	2L	*960,044-112* (*O. eichingeri* acc. no. 105159)	RM250, RM240	SSR		Liu et al. (2001)
	3S	IR54745-2-21-12-17-6 (*O. officinalis*) (4)	AJ09b230, AJ09c	RAPD	RILs	Renganayaki et al. (2002)
Bph14	3L	B5 (*O. officinalis*)	SM1-G1318	SSR, STS	F_2, RILs	Du et al. (2009)
Bph15	4S	B5 (*O. officinalis*) (1, 2)	C820, S11182	RFLP, AFLP	F_2, F_5	Yang et al. (2004)
Bph17	4S	Rathu Heenati (1, 2)	RM8213-RM5953	SSR	F_2/F_3	Sun et al. (2005)
Bph18	12L	IR65482-7-216-1-2 (*O. australiensis*. acc. no. 100882) (Korean)	RM1022	SSR, STS	F_2/F_3	Jena et al. (2006) and Ji et al. (2016)
bph19	3S	AS20-1 (2)	RM6308-RM3134	SSR	F_2/F_3	Chen et al. (2006)

Bph20	4S	IR71033-121-15 (*O. minuta* acc. no 101141)/Korean Bio1	MS10-RM5953	SSR, STS	F_2/F_3	Rahman et al. (2009)
Bph21	12L	IR71033-121-15 (*O. minuta* acc. no. 101141)/(1, Korean)	RM3726-RM5479	SSR, STS	F_2/F_3	Rahman et al. (2009)
Bph22	6S	IR71033-62-24 (*O. minuta*)	RM19429, RM584, RM585	SSR	F_6	Harini et al. (2010)
Bph25	6S	ADR52/bio Chikugo-89	S00310	SSR	F_2, BC_3F_2	Myint et al. (2012)
Bph26	12L	ADR52/bio Chikugo-89	RM5479	SSR	F_2, BC_3F_2	Myint et al. (2012) and Tamura et al. (2014)
Bph27	4L	*O. rufipogon*, *acc. no. 2183* (2)	RM16853-RM16846	SSR	BC_1F_2	Huang et al. (2012)
	4L	Balamawee	Q5, Q20	SSR, InDels	F_2/F_3	He et al. (2013)
QBph11, *Bph28*	11L	DV85 (1, 2)	RM26656-RM26725	SSR, InDels	F_2/F_3	Su et al. (2005) and Wu et al. (2014)
bph20(t), *bph29*	6S	RBPH54 (*O. rufipogon)* (2)	RM435, RM540, BYL7, BYL8	SSR, STS, InDels	NILs	Yang et al. (2012) and Wang et al. (2015)
bph21(t), *bph30*	10S	RBPH54 (*O. rufipogon)* (2)	RM222, RM244	SSR, STS, InDels	NILs	Yang et al. (2012) and Wang et al. (2015)
Bph32	6S	Ptb33	RM19291, RM8072	SSR		Ren et al. (2016)

Modified from Fujita et al. (2013) and Brar et al. (2015)

[a]L, S = long and short arm of chromosome, respectively; [b]Biotypes used for screening for BPH resistance are given in parenthesis

and KDML105. The *Bph3* locus was mapped between two flanking SSR markers, RM589 and RM588, on chromosome 6S (Jairin et al. 2007a, b). The *Bph3* locus in Rathu Heenati was further physically mapped to 190-kb interval flanked by the markers RM19291 and RM8072 (Jairin et al. 2007c). *Bph3* has been widely used in marker-assisted selection (Jairin et al. 2009; Singh et al. 2011), revealing that the locus contains two valuable BPH resistance genes. Rice varieties deployed with *Bph3* more than 30 years ago still show resistance to BPH (Cruz et al. 2011). Both *Bph3* loci in Rathu Heenati and Ptb33 were later cloned and designated as *Bph3* gene and *Bph32* gene, respectively (Liu et al. 2014; Ren et al. 2016).

The recessive gene *bph4* was initially identified from *indica* rice, Babawee from Sri Lanka, and provides resistance against BPH biotypes 1–4 (Laxminarayana and Khush 1977). It was reported to have similar allele or closely linked to a dominant gene *Bph3* (Sidhu et al. 1979). Later based on trisomic analyses, *bph4* was assigned on rice chromosome 10 (Ikeda and Kaneda 1981). Kawaguchi et al. (2001) reported mapping of a recessive BPH gene *bph4* from Babawee on chromosome 6S using bulked segregant analysis with RFLP and SSR markers. However, *bph4* was again shown to be allelic to *Bph3* based on allelic tests with two different genetic backgrounds of rice (Jairin et al. 2010).

Kabir and Khush (1988) identified a resistance gene (designated as *Bph6*) against Bangladesh BPH population in a rice variety Swarnalata. The *Bph6* was later mapped using the F_2 and backcross populations and was located in the interval of SSR markers RM6997 and RM5742 on chromosome 4L. This gene was further delimited to a 25-kb region in the interval of STS markers Y19 and Y9 (Qiu et al. 2010). The recessive gene, *bph7*, was earlier identified in *indica* rice cultivar, T12, and found to be resistant to Bangladesh BPH population (mainly attributed to BPH biotype 4) (Kabir and Khush 1988). Qiu et al. (2014) reported fine mapping and assigning of *bph7* gene on rice chromosome 12 between SSR markers RM28295 and RM313 using F_2 and backcross populations. This was reported to explain 38.3% total phenotypic variation of resistance to BPH in the F_2 population.

Three BPH-resistant cultivars, Balamawee, Kaharamana and Pokkali, were reported to carry *Bph9* gene earlier. This gene was mapped on chromosome 12L in Pokkali (Murata et al. 2001) and Kaharamana (Sun et al. 2006). Later Balamawee was shown to be different from other two BPH-resistant cultivars based on various molecular-physiological characteristics of BPH such as settling behaviour including nymph preferences, nymph survival, honeydew and tolerance indices. The new gene was fine mapped in Balamawee and designated as *Bph27* (He et al. 2013). Gene *Bph10* introgressed from wild species is linked with RFLP clone RG457 on chromosome 12 (Ishii et al. 1994). In another study, STS markers were developed from RFLP clone RG457 and using the STS and SSR markers delimited the *Bph10* region between RG457L-B and RM260 on chromosome 12L (Lang and Bu 2003). Hirabayashi et al. (1998) identified *bph11* in *O. officinalis*-derived introgression line IR54742-23-19-12-3-54 on chromosome 3L with RFLP analysis of $F_{2:3}$ progenies and RILs.

A recessive gene designated as *bph12(t)* located on chromosome 4 using RFLP analysis of another *O. officinalis*-derived introgression line GSK185–2. The *Bph12*,

formerly designated as *Bph12(t)*, was earlier mapped to a 13.4-cM region on chromosome 4S using *O. latifolia*-derived introgression line 'B14' (Yang et al. 2002), which was further fine mapped to a 1.9-cM region using an F_2 and backcross population (Qiu et al. 2012). *Bph13* gene mapped on different location on chromosomes in two separate studies. Liu et al. (2001) reported identification and mapping of BPH resistance gene in *O. eichingeri* between two SSR markers, RM240 and RM250, respectively, on chromosome 2, whereas Renganayaki et al. (2002) mapped the *Bph13(t)* gene on chromosome 3 in *O. officinalis*-derived introgression line, IR54741-3-21-22 using a set of RAPD markers.

Huang et al. (2001) earlier identified and mapped *Bph14* and *Bph15* from an introgression line derived from *O. officinalis* 'B5' on chromosome 3L and on chromosome 4S, respectively. *Bph14* that showed stable resistance in different genetic backgrounds has been cloned using map-based cloning (Du et al. 2009). Yang et al. (2004) fine mapped *Bph15* locus using large population of 9472 F_2 individuals derived from a cross between a selected RIL of 'B5'-carrying *Bph15* and a susceptible cultivar, TN1. *Bph17* was identified and mapped from Rathu Heenati on chromosome 4S (Sun et al. 2005); however major BPH-resistant gene *Bph3* has been cloned from Rathu Heenati (Liu et al. 2014). Jena et al. (2006) identified *Bph18* in an introgression line, IR65482-7-216-1-2 derived from *O. australiensis*. The *Bph18* was identified as non-allelic to *Bph10* and mapped on the long arm of chromosome 12 flanked by the SSR marker RM463 and the STS marker S15552. The gene was utilized to develop durable broad-spectrum resistant varieties in Korea and provided resistance at both seedling and adult plant stages. Map-based cloning approach has been used to clone *Bph18* gene (Ji et al. 2016).

Rahman et al. (2009) identified and mapped two BPH resistance genes in *O. minuta* acc. IRGC101141 using F_2 population derived from a cross between resistant introgression line, 'IR71033-121-15', and a susceptible Korean japonica cultivar, 'Junambyeo'. The two genes were linked to molecular markers and designated as *Bph20(t)* on chromosome 4 and *Bph21(t)* on chromosome 12.

Myint et al. (2012) identified two BPH resistance genes, *Bph25* on chromosome 6S and *Bph26* on the chromosome 12 L in the *indica* cultivar ADR52. *Bph26* has been cloned using NILs in the background of Taichung 65 and found to be allelic to *bph2* present in cultivar ASD7 based on sequence analysis and feeding ability of BPH virulent biotype (Tamura et al. 2014). In a previous study, a recessive BPH resistance gene *bph18*(t) was identified from a wild rice accession (*O. rufipogon* accession GX2183), which shows a broad-spectrum resistance to BPH biotypes, including biotypes 1 and 2, Bangladesh, Cuu Long (Vietnam) and Pantnagar (India) (Li et al. 2006). However, Jena et al. (2006) reported same gene nomenclature in a different donor IR65482-7-216-1-2, derived from *O. australiensis*. Huang et al. (2012) further fine mapped *bph18*(t) using backcross population and renamed it to *Bph27*. In another study *Bph27* was mapped from Balamawee on chromosome 4L, though both the genes seem to be allelic in nature based on their position on the chromosome. Su et al. (2005) identified a major effect QTL in *indica* rice cultivar 'DV85' on chromosome 11 and designated as *Qbph11*. Later, *Qbph11* was fine mapped and designated as *Bph28* (Wu et al. 2014).

Yang et al. (2012) identified and mapped two recessive genes in *O. rufipogon*-derived introgression line, RBPH54 using BC_2F_2, which were tentatively named as *bph20(t)* and *bph21(t)*. Later, Wang et al. (2015) renamed *bph20(t)* and *bph21(t)* as *bph29* and *bph30* ,respectively, *and* cloned *bph29* using map-based cloning approach. Jairin et al. (2007a) mapped the *Bph3* locus on chromosome 6S using two backcross populations derived from Rathu Heenati and Ptb33. The BPH resistance locus seems to be two different valuable BPH resistance genes seeing the durability of resistance based on various MAS studies for deployment of this locus. Later, a dominant gene, *Bph32*, was cloned from the rice variety Ptb33 on chromosome 6S using bioinformatics analysis and a transgenic approach (Ren et al. 2016).

4.3.2 Small Brown Planthopper (SBPH)

Genes/QTLs for resistance to SBPH have been identified only recently. More than 30 QTLs for SBPH (Duan et al. 2007a, b, 2008, 2009, 2010; Tuyen et al. 2012; Zhang et al. 2014) have been identified from cultivated and wild species using SSST, MSST, antixenosis and antibiosis tests. The rice lines Mudgo, DV85, Kasalath, Rathu Heenati and wild rice *O. officinalis* have been used as resistance donors for identification of these QTLs.

4.4 Genomics of BPH-Resistant Genes: Cloning and Molecular Mechanism

Recently, six genes *Bph3*, *Bph14*, *Bph18*, *Bph26*, *bph29* and *Bph32* have been cloned using map-based cloning strategy (Table 4.2). The cloning of these genes has provided valuable information on the molecular basis of resistance. Of the six genes, three genes; *Bph14*, *Bph18* and *Bph26*, encode for coiled coil, nucleotide binding and leucine-rich repeat (CC-NBS-LRR) protein of NB-LRR family (Du et al. 2009; Ji et al. 2016; Tamura et al. 2014). NBS-LRR class of genes plays a vital role in resistance to plant diseases. During disease infection, these genes recognize the effectors delivered by pathogens and induce the downstream disease resistance reactions (Yue et al. 2012). Based on variability in the N-terminal region, plant NBS-LRR genes can be divided into several types. In rice, most

Table 4.2 Cloned BPH resistance genes in rice

Gene	Encoded protein	Plant defence response	Reference
Bph3	Lectin receptor kinases	Antibiosis	Liu et al. (2014)
Bph14	CC-NBS-LRR	Antibiosis	Du et al. (2009)
Bph18	CC-NBS-LRR	Antibiosis and antixenosis	Ji et al. (2016)
Bph26	CC-NBS-LRR	Antibiosis	Tamura et al. (2014)
bph29	B3 DNA-binding domain	Antibiosis	Wang et al. (2015)
Bph32	SCR domain	Antibiosis	Ren et al. (2016)

NBS-LRR-type genes are CC-NBS-LRR (CNL) with a coiled-coil domain at the N-terminus end (Monosi et al. 2004; McHale et al. 2006). *Bph18* and *Bph26* comprise of CC-NBS-NBS-LRR with two NBS domains, which is basically similar to CC-NBS-LRR. More than 400 NBS-LRR genes have been identified in the rice (*O. sativa* cv. Nipponbare) genome (Monosi et al. 2004), and only four genes encode for proteins where NBS domain is partially duplicated similar to *Bph18* and *Bph26* (Ji et al. 2016).

Bph3 is a cluster of three genes encoding lectin receptor kinases localized in plasma membrane belonging to G-type LecRK family. This family consists of an extracellular bulb-type lectin domain, a plant PAN-/APPLE-like domain, a transmembrane domain and an intracellular serine/threonine kinase domain. Lectin receptor kinases are large family of proteins present in plants and play a very important role in plant innate immunity against pests and diseases (Singh et al. 2013). A G-type lectin receptor kinase encoding gene *Pi-d2* from rice provides resistance against the rice blast caused by a fungal pathogen *Magnaporthe grisea* (Chen et al. 2006). *Bph29* has been a single-copy gene that encodes for B3 DNA-binding domain, a highly conserved domain found exclusively in transcription factors that interact with the major groove of DNA (Wang et al. 2015). Five classes of B3 domain-containing genes have been identified, and *Bph29* has the most similarity to RAV (related to ABI3/VP1, *Abscisic acid insensitive3*/*Viviparous1*) family. The *RAV1* gene of this family has been shown to play an important role in bacterial disease resistance in an earlier study (Sohn et al. 2006). However the role of B3 domain in insect resistance still needs to be elucidated. *Bph32* gene encodes for unknown protein containing a signal peptide and a SCOP d1gkna2 domain belonging to SCR (short consensus repeats) domain family of proteins. This family of proteins is considered to be a type of lectin or cell adhesion protein. The role of plant lectins has been identified to function as defence-related proteins that can act on insect glycoproteins or tissues to inhibit insect feeding (Ren et al. 2016).

BPH is a phloem-feeding insect that uses saliva sheath to establish the connection in the phloem tissue and suck sap with its stylet (Sogawa 1982). This action causes least physical injury to the host plant, thereby establishing prolonged and intimate interaction between insect stylets and plant cells (Du et al. 2009). In addition, BPH also acts as vector for the rice ragged stunt virus and rice grassy stunt virus transmitted by insect feeding to the phloem. As a consequence, the resistance factors are thought to be present within the phloem (Walling and Thompson 2012), and responses of the host plant to BPH probably have similarity with fungal or bacterial pathogens (Walling 2000, 2008). Site of expression of all the cloned resistance genes has been identified in the vascular bundles (phloem) of leaf sheath, the place of BPH attack on plants. In general, plants may respond to insect attack mainly by two defence mechanisms: antixenosis, which disturbs insect settling, colonization or oviposition, and antibiosis, which affects insect feeding, growth rate or survival. All the cloned BPH resistance genes employ antibiosis as a resistance mechanism, whereas *Bph18* is considered to employ both antixenosis and antibiosis (Ji et al. 2016). Further, callose deposition on phloem sieve plates and the cell walls of vascular tissue found to be important defence mechanism in plants responsible for

reduced insect feeding. Callose is produced enzymatically by the action of callose synthases in the presence of Ca^{2+}. It is located in the plasma membrane and deposited extracellularly around sieve plates (Will et al. 2013). BPH infestation caused upregulation of three callose synthase-encoding genes (*GSL1*, *GSL5* and *GSL10*) in both the wild-type and transgenic rice plants, whereas two genes responsible for decomposing the callose and occlusion of sieve tubes were slightly downregulated (Du et al. 2009). The upregulation of callose synthase genes responsible for producing callose and downregulation of callose decomposing genes reveal the importance of callose as a plant defence mechanism. Hao et al. (2008) also reported that activation of β-1,3-glucanase genes can open up sieve tube occlusions during BPH infestation in rice plants.

Two-branched innate immunity system (pattern-triggered immunity (PTI) and effector-triggered immunity (ETI)) has been recognized in plants in response to attack of diverse pathogens and insects (Jones and Dangl 2006). The cell surface-localized, pattern recognition receptors and cytoplasmic R proteins (mostly NB-LRR) are considered to build a two-tiered plant immune system. It has been considered that *R*-gene-mediated resistance can be easily overcome by pathogens that mutate and produce new effectors to counteract ETI (Jones and Dangl 2006), whereas PTI in general is supposed to confer broad-spectrum and durable resistance due to the conserved nature of pathogen-associated molecular patterns (Lacombe et al. 2010). Three BPH resistance genes (*Bph14*, *Bph18* and *Bph26*) that encode for cytoplasmic R proteins (CC-NBS-LRR) are supposed to induce ETI by recognizing the effectors resulting from insect feeding. These evidences provide interesting similarities between BPH and plant pathogens. It also suggests that rice *R* proteins may interact with BPH effectors in a gene-for-gene manner, and there are BPH *avr* (avirulence) genes for each BPH *R* gene in rice. On the other hand, lectin receptor kinase protein encoded in *Bph3*-mediated resistance has been suggested to function as extracellular ATP receptor or potential cell surface receptors for BPH-derived elicitors and can initiate PTI response (Liu et al. 2014).

In addition, plant defence responses to phloem-feeding insects that produce little injury to plants and perceived as pathogens involve the activation of salicylic acid (SA)-dependent and jasmonic acid (JA)-/ethylene-dependent signalling pathway (Walling et al. 2000). In *Bph14*-mediated insect resistance, genes involved in the SA synthesis pathway were found to be highly activated, whereas no difference was observed in the expression level of JA synthesis-related genes (Du et al. 2009). In case of *bph29*, upregulation *of* SA synthesis-related genes and downregulation of JA-dependent genes were observed by BPH infestation (Wang et al. 2015). In *Bph26*-mediated resistance, strong induction of both SA and JA synthesis-related genes with BPH infestation suggest that *BPH26* may activate JA- and SA-dependent resistance pathway. In *BPH18*, no significant difference was observed in the expression level of both the pathway-related genes (Ji et al. 2016). Based on molecular analysis of cloned genes, it appears that there is considerable similarity in the plant response to BPH infestation and pathogen attack. Further studies are needed on the frontiers of genomics research to understand molecular interaction between the host and pests and develop insect-resistant varieties.

4.5 Biochemical Mechanism of Resistance

The raised levels of biochemicals, phenolic acids and enzymes after planthopper infestation may play a prominent role in plant defence against planthoppers. Planthoppers first examine the plant surface for receiving chemical cues so as to find plants suitable for egg laying, settling or feeding (Woodhead and Chapman 1986). Female adults of BPH choose to sit on the plants treated with jasmonic acid (JA). The parasitism by parasitoid *Anagrus nilaparvatae* Pang et Wang was enhanced twice on JA-treated plants than on untreated control plants. JA application elevated the release of volatiles, namely, aldehydes, alcohols, monoterpenes, sesquiterpenes, methyl salicylate and n-heptadecane on treated plants. This shows that *A. nilaparvatae* utilized the plant-induced cues to locate BPH after JA treatment (Lou et al. 2005). In planthoppers, yeast-like endosymbionts (YLS) live intracellularly in the fat body cells (Chen et al. 2011). The presence of YLS in planthoppers helps them to use scarce nutrients so that they can affix the unfair composition of amino acids in plant phloem sap. The absence of YLS in planthoppers caused lower total protein concentrations, higher levels of nonlimiting free amino acids such as glutamine and aspartate and lower levels of leucine, an essential amino acid (Wilkinson and Ishikawa 2001). Many genes for BPH resistance are reported, but it is unknown that how these different genes are linked to biochemical products or pathways. This can also provide the way by which BPH adapt to resistant lines. If this information is made available, then scientist can select reliable plants based on phloem chemistry rather than assessing nymphal feeding and other tests.

The secondary and related compounds in rice plants played an important role in the defence against planthopper attack. The elevated ratio of longer to shorter carbon-chain substances and presence of shorter chain hydrocarbons on the rice surface served as barriers (Woodhead and Chapman 1986; Woodhead and Padgham 1988). Woodhead and Padgham (1988) distilled epicuticular waxes from IR22, IR46 and IR62 and observed feeding of planthoppers by managing plants by changing exogenous wax applications on different varieties. They observed an elevated ratio of longer to shorter carbon-chain compounds in IR46 and the presence of shorter chain hydrocarbons in IR22 which decided the planthopper feeding responses. Recently, Zhang et al. (2015) reported comparative transcriptional profiling from resistant and susceptible rice plants during early infestation by SBPH. They reported that with level of resistance in SBPH-resistant rice plants, genes involved in the very long-chain fatty acid biosynthesis were upregulated. These fatty acids are of 20 to 36 carbons and are required by plants for plant cuticle biosynthesis (Samuels et al. 2008; Shepherd and Wynne 2006). These very long-chain fatty acid production pathways have been united with plant defence against hoppers (Raffaele et al. 2009). These plant volatiles may be useful in studying the insect community make-up. Volatile organic compounds are released when insect attacks a plant, and these plays a major role in tritrophic interaction between plant, herbivore and parasitoids (Allmann and Baldwin 2010). The amount of biochemicals after insect infestation such as proteins, phenols and carbohydrates has been elevated with the enzyme activities of peroxidase, catalase and chitinase, whereas after hopper

infestation a reduced activity of superoxide dismutase, phenylalanine ammonia lyase and β-1,3-glucanase was observed. The phenolic acids, namely, vanillic acid, syringic acid, cinnamic acid and p-coumaric acids, were recorded in the plants after BPH infestation (Rani and Jyothsna 2010).

Against planthoppers, ovicidal resistance in japonica cultivars is a natural defence mechanism (Suzuki et al. 1996; Yamasaki et al. 1999; Yamasaki et al. 2000). It is highest at the maximum tillering stage. After oviposition by WBPH, there is formation of a watery lesion of benzyl benzoate around eggs at concentrations above 6.4 ppm at 25 °C. This concentration of benzyl benzoate causes up to 80% egg mortality, while non-watery lesions cause only 12% mortality (Suzuki et al. 1996). This solution of benzyl benzoate was present in the watery lesions of some japonica rice varieties and not in the intact rice plant tissues or in non-watery oviposition sites (Seino et al. 1996). The biosynthesis pathway of benzyl benzoate is upregulated due to WBPH oviposition. The solution may cause direct egg mortality or may affect WBPH symbionts; without symbionts eggs can't complete embryonic development (Seino et al. 1996). However, in case of BPH eggs, the ovicidal response was low, and the ranking of watery lesion can be associated with BPH egg mortality (Kiyonaga et al. 1997; Yamasaki et al. 2000). The chitin synthase (CHS) is required for chitin formation in insect cuticles and other tissues. These genes from BPH and SBPH were cloned, and reports say that BPH lacks *CHS2* and *CHS1* gene which can be efficient target genes for RNAi-based BPH control strategy (Wang et al. 2012).

4.6 Resistance to White-Backed Planthopper (WBPH)

Based on classical genetic analysis and mapping studies, 18 genes (*Wbphl*, *Wbph2*, *Wbph3*, *wbph4*, *Wbph5*, *wbph6 Wbph7(t)*, *Wbph8(t)*, *wbph9(t)*, *wbph10(t)*, *wbph11(t)*, *Wbph12(t)*, *WbphM1*, *WbphM2*, *wbphAR*, *WbphN*, *WbphO*, *Ovc)* have been identified for WBPH resistance (Fuzita et al. 2013; Ramesh et al. 2014). Classical genetic analysis has revealed several genes: *Wbph1* in Nagina 22, *Wbph2* in ARC 10239, *Wbph3* in ADR 52, *wbph4* in Podiwi-A8, *Wbph5* in N'diang Marie, *Wbph6* in Guiyigu and *Wbph7(t)* and *Wbph8(t)* in B5; an introgressed line from *O. officinalis* has been identified and designated. Sidhu et al. (2005) studied the inheritance of resistance in five cultivars. The resistance in Mudgo was governed by two independently inherited dominant genes and tentatively designated as *WbphM1 and WbphM2* from Mudgo. A recessive gene, *wbphAR*, conferred resistance in ARC11367, whereas resistance in NCS2041 and MO1 was conditioned by a dominant gene tentatively designated as *WbphN and WbphO*, respectively. Padmarathi et al. (2007) reported that recessive gene in ARC5984 and ARC6650 has similar allele to Podiwi (*wbph4*). He (2007) mapped *Wbph(t)* and *Wbph8(t)* on chromosome 4. Yamasaki et al. (2003) identified one major gene, *ovc*, and four QTLs for ovicidal response (formation of watery lesions and production of ovicidal substance,

benzyl benzoate) to WBPH in 'Asominori'. Recently, four major effect QTLs designated as *wbph9(t)*, *wbph10(t)*, *wbph11(t) and Wbph12(t)* have been mapped in Sinna Sivappu, a Sri Lankan landrace that showed resistance to both BPH and WBPH (Ramesh et al. 2014). The inheritance pattern in 255 $F_{2:3}$ families suggested single recessive gene of seedling damage score, two complementary recessive genes for antixenosis and single dominant gene for days to wilt. In addition to major WBPH-resistant genes, more than 70 QTLs associated with different components of WBPH resistance have been identified (Fujita et al. 2013) by analysing various rice experimental populations, including recombinant inbred line (RIL) populations (Yamasaki et al. 1999, 2003), doubled haploid (DH) populations (Geethanjali et al. 2009; Sogawa et al. 2009), introgression lines derived from wild rice species as the resistance donors (Tan et al. 2004) and backcross inbred lines (BILs) derived from interspecific crosses with wild rice species (Chen et al. 2010). WBPH and BPH often occur at the same time, though in varying proportions across time and space. It is thus imperative that breeding for resistance should target both hoppers (Bentur and Viraktamath 2008).

4.7 Resistance to Green Rice Leafhopper (GRH)

Green rice leafhopper (GRH) is predominant in the temperate regions of East Asia. At least six genes for resistance to GRH have been identified and mapped on chromosomes 3, 4, 5, 6, 8 and 11, respectively (Yasui et al. 2007). Tamura et al. (1999, 2004) identified two genes for resistance to GRH: *Grh1* on chromosome 5 in cultivar 'Pe-bi-hun' and *Grh6* on chromosome 4 in the Surinam cultivar SML17. Likewise, two genes, *Grh2* on chromosome 11 and *Grh4* on chromosome 3, were mapped in cultivars 'Lepe dumai' and 'DV85' in independent studies (Fukuta et al.1998; Yazawa et al. 1998; Kadowaki et al. 2003). The *Grh3* was located on chromosome 6 by Saka et al. (2006) in cultivar 'Rantaj emas 2' to a 4.6-Mb interval between markers C288B and C133A. This locus has been fine mapped further to 435-kb region between SSR markers RM20142 and RM20145 (Hur et al. 2015). Hirae et al. (2007) reported that both the cultivars 'Kanto-PL6' and 'Aichi80' carry *Grh3* based on virulent biotypes of GRH. The *Grh5* was identified from *Oryza rufipogon* acc. W1962 and mapped on chromosome 8 L using tightly linked simple sequence repeat (SSR) markers (Fujita et al. 2006). MAS has been used to develop near-isogenic lines (NILs) carrying *Grhl*, *Grh2*, *Grh4*, *Grh5* and *Grh6* in the background of japonica cultivar Taichung 65. Further pyramided lines carrying GRH resistance genes (*Grh2* and *Grh6*, *Grh4* and *Grh6*) developed in the background of Taichung 65 using NILs indicated significantly increased level of resistance to GRH (Fujita et al. 2010). Pyramided lines with different gene combinations (*Grh2* + *Grh4*), (*Grh2* + *Grh6*) and (*Grh4* + *Grh6*) showed higher nymph mortality than that of the NILs (Yasui et al. 2007).

4.8 Resistance to Zigzag Leafhopper (ZLH)

The zigzag leafhopper (ZLH) is prevalent in the tropical and subtropical regions of Asia. Heinrichs et al. (1985) reported donors (Rathu Heenati, Ptb21, Ptb33) for resistance to ZLH. Angeles et al. (1986) studied the resistance in cultivars Rathu Heenati, Ptb21 and Ptb33 to ZLH, WBHP, BPH and GLH. Based on resistance studies, single dominant gene in each donor was found to provide resistance to ZLH. These were designated as *Zlh1* in Rathu Heenati, *Zlh2* in Ptb21 and *Zlh3* in Ptb33.

4.9 Marker-Assisted Selection and Pyramiding of Genes/QTLs for Resistance to Hoppers

The field of durable resistance was once dominated by discussions on horizontal versus vertical resistance, however broadened substantially with understanding of various host pathogen studies. With the identification of number of genes/QTLs, MAS and gene pyramiding have emerged as an important approach for attaining the durable resistance. In a detailed study to examine the utility of resistant varieties and their associated resistant genes to BPH, Horgan et al. (2015) reported that only a few of the currently available BPH resistance genes showed durable resistance in monogenic rice lines carrying single resistant gene, whereas the traditional varieties known to carry two or more genes showed higher level of resistance indicating that pyramiding of two or more genes with strong to weak resistance could enhance the level of resistance. Classical breeding has successfully supported the development of a number of improved BPH-resistant genotypes. To further improve resistance of rice varieties, it could be emphasized the importance of combining all favourable and complementary physiological traits in a variety, rather than considering BPH resistance as a single trait. Pyramiding of different genes for resistance to bacterial blight (BB) is the model example on enhancing the level and spectrum of resistance to various pathotypes (Huang et al. 1997; Sanchez et al. 2000; Singh et al. 2001). As many as five genes for resistance to BB have been pyramided and combined, and a number of BB resistant varieties have been released in rice-growing countries including India, China, the Philippines, Thailand and Indonesia.

Identification of a tightly linked DNA marker is a prerequisite for marker-assisted selection and pyramiding of two or more genes in a single cultivar. The various institutes are directed towards marker-assisted backcrossing to introgress the favourable alleles for BPH resistance into elite rice lines, and to date many resistant genes have been tested for their linkage with markers (Sun et al. 2005; Jena et al. 2006; Fuzita et al. 2013; Brar et al. 2015). With the advances in molecular markers, a number of the BPH genes (*Bph1*, *bph2*, *Bph6*, *Bph7*, *Bph13*, *Bph15*, *Bph19*, *Bph20*, *Bph21*, *Bph25*, *Bph27* and *Bph28*) have been fine mapped (Table 4.1), and few genes (Table 4.2) have been cloned, which are suitable for marker-assisted selection for BPH resistance, albeit with varying levels of BPH virulence in different parts of Asia. Of the various resistant sources identified, the varieties Rathu Heenati, Ptb33,

MO1, IR71033-121-15, Balamawee and ADR52 in South Asia and Swarnalata in South East Asia have been indicated as potential donors for MAS, since these contain multiple genes for hoppers and most of them have been cloned and tagged with tightly linked molecular markers (Horgan et al. 2015). In an early effort to pyramid two BPH-resistant genes, *Bph1* and *Bph2* in background of a japonica line indicated that resistance level of the pyramided line was equivalent to that of the line carrying *Bph1* alone, but showed a higher level of resistance than the line carrying *Bph2* (Sharma et al. 2004). Later, a number of parental lines used in hybrid rice breeding in China that are pyramided with *Bph14* and *Bph15* through MAS showed higher level of BPH resistance than the lines carrying single gene (Li et al. 2006). Fujita et al. (2009) have evaluated the resistance of NILs (near-isogenic lines) and PYLs (pyramided lines) with *Bph25* and *Bph26* against BPH strains from East Asia. Their results indicated that a PYL containing both genes is resistance against several East Asian BPH strains. Furthermore, Myint et al. (2012) demonstrated that a PYL containing both genes could be effective despite the apparent low effectiveness of each gene alone in *Bph25* and *Bph26* monogenic NILs. Hu et al. (2012) evaluated a pyramided line carrying two resistance genes, *Bph14* and *Bph15*, for seedling damage, antixenosis and honeydew production and found to be more resistant than either the *Bph14*-NIL or the *Bph15*-NIL. Likewise pyramided line for *Bph12* and *Bph6* gene had lower nymph settling and survival and slower population growth and caused less damage compared to the monogenic lines (Qiu et al. 2012). Furthermore, MAS was used to pyramid three BPH resistance genes, *Bph14*, *Bph15* and *Bph18* in the background of elite restorer line, 9311 and its hybrids. The results showed that the *Bph15* have higher level of resistance than *Bph14* and *Bph18*, whereas *Bph14* was found slightly higher or similar as *Bph18* in resistance response against BPH (Hu et al. 2012). Recently, Liu et al. (2016) pyramided two dominant genes, *Bph3* and *Bph27*, using marker-assisted backcross programme, and the pyramided lines showed enhanced level of resistance than single gene.

The development of resistance for all other planthopper and leafhopper species using molecular breeding approaches is still severely limited by a scarcity of genetic information and availability of suitable markers. Six genes seem to be appropriate for MAS for resistance to GRH. Fujita et al. (2006) demonstrated that the pyramided line of *Grh2* and *Grh4* showed higher level of antibiosis than the lines carrying single resistance gene. However, three pyramided lines carrying different combinations of GRH resistance genes (*Grh2* and *Grh6*, *Grh4* and *Grh6* and *Grh5* and *qGRH4*) showed epistasis (Fujita et al. 2010).

For getting broad-spectrum and durable resistance, choice of gene combination for pyramiding is also very important. Genes in combination will be more durable, if these differ with respect to their molecular mechanism responsible for resistance to pathogen or insects. For example, a combination of *xa5* + *xa13* + *Xa21* is more successful and durable, because all the three genes provide resistance to bacterial blight with different molecular mechanism. Although pyramided lines can enhance resistance to hoppers, care should be taken in case of pyramided lines, as it is still unknown whether pyramided lines could lead to a more rapid adaptation of hoppers if the genes were sequentially deployed in a similar background variety. Tests of the

comparative durability of pyramided hopper-resistant rice lines in a similar genetic background have not been conducted, and there are many cases of naturally pyramided rice varieties against which wild hopper populations have already adapted.

4.10 Transgenic Approaches for Resistance to Hoppers

Transgenic rice was produced as early as 1988, since then a battery of genes have been introduced for various agronomic traits. Transgenic technology is now well established, and several varieties have been released for commercial cultivation. Transgenic crops occupy more than 180 million hectares globally (James 2015). In rice, *Bt* genes have been transferred into several genotypes which have shown resistance to stem borers; however, so far no commercial release has been made. Only a limited information is available on transgenic rice resistant to hoppers. Transgenic technology can be used as an approach for deployment of exotic resistance genes into the leading rice cultivars. These exotic resistance genes are shown to produce entomo-toxic effect in plants that affect the insect survival. A number of candidate genes to control hopper populations in rice have been reported. Of these mannose-binding protein encoding genes, 'snowdrop lectin' (*Galanthus nivalis* agglutinin, GNA) and 'garlic leaf lectin' (*Allium sativum* agglutinin from leaf, ASAL) have been demonstrated to control hoppers in rice in various studies (Powell et al. 1995; Majumder et al. 2004). Plant lectins have been reported to show severe effects on fecundity, growth and development of insects. The lectins produced by plants belonging to the family Amaryllidaceae show low or no toxicity towards higher animals, but are toxic to insects. Among the Amaryllidaceae lectins, the lectin from snowdrop, *Galanthus nivalis* L. agglutinin (GNA), is proved to be non-toxic to mammals and toxic to insects. The lectins are probably involved in the binding to receptors present on the midgut epithelial cells, thereby causing the insecticidal effect (Powell et al. 1998). The bound lectins inhibit absorption of nutrients or disrupt endocytosis of midgut cell lectins and other toxic metabolites (Eisemann et al. 1994). Expression of *GNA* or *ASAL* in rice plants has been shown to confer substantial resistance to BPH, WBPH and GRH in terms of increased insect mortality, retarded development and decreased fecundity (Rao et al. 1998; Sudhakar et al. 1998; Foissac et al. 2000; Tang et al. 2001; Sun et al. 2002; Nagadhara et al. 2003, 2004; Saha et al. 2006; Yarashi et al. 2008). Similarly, transgenic plants generated by introduction of *Dioscorea batatas* tuber lectin1 gene under the control of phloem-specific promoter of rice sucrose synthase-1 gene showed up to 30% reduced survival rate of BPH as compared to wild type (Yoshimura et al. 2012). Bala et al. (2013) reported that interaction of ASAL with NADH-quinone oxidoreductase (NQO), a key player in electron transport chain, may result in toxicity and loss of fecundity during BPH feeding on transgenic rice plants expressing ASAL. These studies indicate 'ASAL' as a prominent candidate gene against BPH attack.

RNAi (RNA interference) is an important approach for meeting the challenges imposed by crop insects with careful secretion of key enzymes/proteins (Gordon and Waterhouse 2007; Price and Gatehouse 2008; Rao Kola et al. 2015). Recently,

the method has shown another way to generate resistance against various insects in a number of studies (Aggarwal et al. 2012). The majority of studies on RNAi for insect control have targeted enzymes/proteins of the insect midgut as it is considered as the most effective target for the gene silencing. When three dsRNA targeting different sites within a gene encoding vascular ATP synthase subunit E (*V-ATPase-E*) were orally delivered into BPH insect, it resulted in decreased expression of the target gene (Li et al. 2011). Likewise, transgenic plants were generated using three genes, the hexose transporter gene *NlHT1*, the carboxypeptidase gene *Nlcar* and the trypsin-like serine protease gene *Nltry* by introducing dsRNA that expressed in the midgut of the BPH (Zha et al. 2011). When BPH feeds on transgenic plants, the expression of BPH genes were reduced by 40–70% in the third instar nymphs by day 4; however, no lethal phenotypic effect was observed.

Plants interact with different insects by releasing complex blend of volatile compounds. Rice plant induces the production of one of the most abundant volatile compound 'S-linalool' by feeding of BPH, whereas another constitutive produced volatile compound in rice, (E)-beta-caryophyllenes, is induced by feeding of chewing herbivores, but not by sucking pests like BPH. Both S-linalool and (E)-beta-caryophyllene have been reported to attract BPH parasitoid, *Anagrus nilaparvatae*, in the laboratory (Cheng et al. 2007). By silencing the two genes responsible for production of these volatile compounds, it was observed that inducible S-linalool attracted parasitoid and chewing herbivores but repel BPH. However, the constitutively produced (E)-beta-caryophyllene attracts both parasitoid and BPH resulting in an increased herbivore load. Therefore, silencing either signal (compound) resulted in the assemblage of specific insect community (Xiao et al. 2012).

The identification of suitable candidate genes to be used as targets is the primary requirement to use this technology. On the other hand, RNAi pathway in insects is yet not clear as compared to *Drosophila* (Burand and Hunter 2013). Therefore, RNAi pathway in the planthopper needs to be elucidated in order to efficiently use this technology to generate resistance against hoppers.

4.11 Future Priorities

Planthoppers pose a major challenge to rice production and sustainability particularly in the context of global climatic changes. However, advances in molecular marker technology and cutting-edge science of genomics offer new opportunities to meet the challenges of developing pest-resistant varieties. Some of the priorities to breed varieties resistant to hoppers are given below:

- Identification of resistant sources/donors involving diverse germplasm-primitive cultivars, landraces, traditional varieties and wild species of *Oryza*.
- Widening gene pool of rice through transfer of such genes governing resistance.
- Identify novel genes/QTLs governing resistance to hoppers preferably with different modes of resistance.

- Accelerate breeding and develop varieties with enhanced and wide spectrum of resistance, priority should be given on MAS and pyramiding of genes/QTL to different biotypes/insect populations, and combine multiple resistance to BPH, GLH and WBPH. Use gene-based MAS wherever possible.
- Develop high-throughput genotyping using new sequencing and molecular marker approaches and phenomics/phenotyping protocols to accelerate breeding efforts.
- Allele mining is emphasized to identify and incorporate desirable alleles for resistance.
- Develop isogenic lines for resistance to BPH, WBPH and GLH, and test such lines in different areas, regions and countries to deploy target genes for resistance in respective areas of rice cultivation.
- Explore transgenic technology including RNAi and gene editing as a long-term approach in developing germplasm resistant to hoppers.

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