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Current understanding of the genomic, genetic, and molecular control of insect resistance in rice

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Abstract Rice (*Oryza sativa*) is both a vital source of food and a key model cereal for genomic research. Insect pests are major factors constraining rice production. Here, we provide an overview of recent progress in functional genomics research and the genetic improvements of insect resistance in rice. To date, many insect resistance genes have been identified in rice, and 14 such genes have been cloned via a map-based cloning approach. The proteins encoded by these genes perceive the effectors of insect and activate the defense pathways, including the expression of defense-related genes, including mitogen-activated protein kinase, plant hormone, and transcription factors; and defense mechanism against insects, including callose deposition, trypsin proteinase inhibitors (TryPIs), secondary metabolites, and green leaf volatiles (GLVs). These ongoing functional genomic studies provide insights into the molecular basis of rice–insect interactions and facilitate the development of novel insect-resistant rice varieties, improving long-term control of insect pests in this crucial crop.

Keywords Functional genomics · Resistance to insect · Rice

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Introduction

Insect pests pose severe constraints to agriculture and threaten food security worldwide (Oerke 2006). More than half a million insect species on Earth are estimated to obtain their nutrients from plants (Strong et al. 1984). Insect infestations are especially severe in rice, which grows in warm, humid environments. Rice plants provide an attractive and nutritious food source for many phytophagous insects. Hundreds of insect species damage rice to various degrees, but only ~20 species occur regularly and cause major damage to rice (Grist and Lever 1969). In China, the total area of rice infested by brown planthopper (BPH) was estimated at over 25 million hectares, resulting in a rice production loss of 2.7 million tons between 2005 and 2008 (Qiu et al. 2012; Hu et al. 2016a).

Insects feed on all parts of a rice plant during all stages of growth. Herbivorous insects have various feeding modes, but most of these insects can be classified into two groups: chewing insects and piercing-and-sucking insects. Chewing insects, such as stem borers and leaf folders, have mouthparts that break off and ingest plant tissues, causing substantial mechanical damage. Insects with piercing-and-sucking feeding habits, including planthoppers and leafhoppers, have sharp, elongated mouthparts that penetrate plant cells and suck up nutrients from vascular tissues. Planthoppers and leafhoppers are also important vectors of plant disease agents, causing indirect damage to plants (Fujita et al. 2013).

Insect outbreaks in rice are recorded in antiquity. The Book of Odes, a collection of 305 Chinese poems and songs from the 10th to the 7th centuries BC, mentions the damage in rice caused by the stem borer (He et al. 2013a). However, the severity and frequency of insect outbreaks have increased over the past several decades. Most modern rice varieties are grown with high fertilizer inputs and have a higher nutrient content, but reduced physical and chemical defenses compared with the wild relatives and landraces (Chen et al. 2015; Olsen and Wendel 2013). Crop losses caused by insects are expected to be further exacerbated by global warming, which increases the population growth and metabolic rates of insects (Deutsch et al. 2018).

Controlling insect pests is a key priority to secure rice productivity to feed the rapidly growing human population without ecological degradation (Crist et al. 2017). The main strategy for crop protection against insects over the past 50 years has been the application of chemical insecticides, but the use of such compounds is set to decline in China and other countries. Resistant rice cultivars are being sought as an effective integrated pest management tactic for rice production. A major objective of rice breeding programs is to incorporate insect resistance into modern cultivars (Zhang 2007). Insect resistance in plants involves a gene or suite of genes that produce a product or products that inactivate or otherwise disable the target insect. Resistant rice cultivars alter the physiology and behavior of insects, which in turn affects the insects' susceptibility to chemical and biological control mechanisms (Li et al. 2014). Transgenic rice harboring an exogenous Bt gene (encoding an insecticidal toxin produced by *Bacillus thuringiensis*) has been used to breed insect-resistant rice. The Bt gene is effective against the stem-borer-and-leaf-folder-chewing insects, but not against piercing-and-sucking insects, such as brown planthopper.

Over the past several decades, great progress has been made in the screening of insect-resistant rice germplasm, identifying resistance genes, and uncovering the molecular mechanisms of host resistance. The use of resistance genes and other efforts to breed "Green Super Rice", a high-yielding, good-quality, insect-resistant ideal rice variety, will increase the profitability of rice production and contribute to a healthy ecological environment. This review addresses research advances underpinning strategies to improve the resistance of rice to insect pests. We focus on the genetic and molecular mechanisms of insect resistance and the practical application of gene technologies to rice breeding for improved insect resistance, which represent the development trend of rice insect resistance breeding and also provide a reference for other crops.

Functional genomics of insect resistance in rice

Genetics studies of insect resistance

Many rice genomic resources, including cultivated and wild rice species, are available globally, providing an invaluable source of insect resistance in rice. One way to breed insect-resistant rice varieties is to transfer resistance genes identified in traditional rice varieties and wild rice into modern cultivars. The ease of such transfer, however, depends on how closely related the two species of rice are and the degree to which they have become reproductively isolated. Cultivated rice and wild rice species with AA genomes can be directly crossed to transfer insect resistance genes to modern cultivars (Brar and Khush 2006). Wild rice with other genomes (e.g., BB, CC, and BBCC) must instead be crossed with rice cultivars via hybrid embryo rescue (Huang et al. 2000).

The phenotypic selection followed by population construction is a traditional strategy used to study insect resistance in rice. By evaluating the phenotype of F_1 plants or the phenotypic segregation ratio of the F_2 population from a cross between a resistant and susceptible parent, one could determine whether insect resistance is controlled by dominant or recessive genes or by one or more major genes. In addition, by assessing the phenotypic segregation ratios of the F_2 populations and F_3 progenies of a cross between resistant cultivars, one could determine if resistance genes in different varieties are allelic, closely linked, or located on different chromosomes. Such studies have indicated that insect resistance in rice is controlled by major genes. Scientists at International Rice Research Institute (IRRI) have identified many planthopper and leafhopper resistance genes, including *BPH1* to *BPH9* from the rice varieties Mudgo, ASD7, Rathu Heenati, Babawee, ARC10550, Swarnalata, T12, Chin Saba, and Pokkali (Athwal et al. 1971, Laksminarayana and Khush 1977, Sidhu and Khush 1978, Khush et al. 1985, Kabir and Khush 1988, Nemoto et al. 1989); *WBPH1* to *WBPH5* from Nagina 22, ARC10239, ADR52, Podiwi A8, and N'Diang Marie (Sidhu et al. 1979; Angeles et al. 1981;

Hernandez and Khush 1981; Wu and Khush 1985); and *GLH1* to *GLH5* from Pankhari 203, ASD7, IR8, PTB8, and ASD8, respectively (Athwal *et al*. 1971; Siwi and Khush 1977) (Table 1). These genes have been used in the breeding of resistant rice varieties (Khush and Virk 2005).

Insect resistance gene mapping

With the development of molecular markers technologies, many insect resistance genes and quantitative trait loci (QTLs) have been identified in rice and located on genetic linkage maps through the analysis of phenotypic and genotypic variation in different populations (Table 1).

Three species of planthoppers, brown planthopper (BPH), white-backed planthopper (WBPH), and small brown planthopper (SBPH), are the leading causes of yield losses in rice and cause economic damage globally (Backus et al. 2005). Since the BPH-resistance gene *BPH1* was first identified in 1971 (Athwal et al. 1971), over 34 such genes have been reported, including 20 (*BPH1* to *BPH9*, *BPH16*, *BPH17*, *bph19(t)*, *bph25*, *BPH26*, *BPH27(t)*, *BPH28*, *BPH30* to *BPH33*) in the traditional cultivated rice varieties, and others in wild rice species, including *BPH10* and *BPH18* from *O. australiensis*, *bph11–15* from *O. officinalis*, *BPH20*, *BPH21*, and *BPH23* from *O. minuta*, *bph18(t)*, *bph19(t)*, *bph22* to *BPH24(t)*, *BPH27*, *bph29*, *BPH30* from *O. rufipogon*, *BPH22(t)* from *O. glaberrima*, and *BPH34* from *O. nivara* (Table 1). Most BPH resistance genes have been mapped to particular chromosomal locations, except for *bph5*, *bph8*, *BPH22(t)* to *BPH24(t)* (Table 1), and 14 genes have been isolated via map-based cloning.

BPH resistance genes are usually present in clusters on chromosomes 3, 4, 6, and 12 (Cheng et al. 2013b, Fig. 1). Eight of these genes (*BPH1*, *bph2*, *bph7*, *BPH9*, *BPH10*, *BPH18*, *BPH21*, and *BPH26*) are clustered together in a 19.1–24.4 Mb region between markers RM7102 and B122 on chromosome 12L, whereas 12 genes are clustered in three regions on chromosome 4 (*BPH30* and *BPH33* in a 0.91–0.97 Mb region between markers H99 and H101; *BPH3/17*, *BPH12*, *BPH15*, *BPH20(t)*, and *bph22(t)* in a 4.1–8.9 Mb region between markers RM8212 and B44; and *BPH6*, *bph18(t)*, *BPH27*, *BPH27(t)*, and *BPH34* in a 19.1–25.0 Mb between markers RM16846 and RM6506). *BPH3*, *bph4*, *bph25*, *bph29*, and *BPH32* are present in a 0.2–1.7 Mb region between markers S00310 and RM8101 on chromosome 6S, while *BPH13* and *bph19(t)* are located on chromosome 3S, and *bph11*, *BPH14*, and *BPH31* are located on chromosome 3L (Fig. 1).

In addition, QTLs have been detected in various rice chromosomes using different mapping populations from crosses between susceptible and resistant varieties. *qBPH6(t)* was mapped between markers RM469 and RM568 on chromosome 6 in IR71033–121-15 (Jairin et al. 2007a). *qBPH3* was identified in rice line IR02W101 and mapped between markers t6 and f3 on chromosome 3 (Hu et al. 2015b). Several QTLs have also been identified on chromosomes 4, including *qBPH4*, *qBPH4.2*, *qBPH4.3*, and *qBPH4.4* from IR02W101, IR65482-17-511 and Salkathi, respectively (Hu et al. 2015a, b; Mohanty et al. 2017).

Twelve major genes and a number of QTLs associated with WBPH resistance have been identified to date, including *WBPH1* to *WBPH5*, which were identified by traditional genetic analysis. However, only *WBPH1* and *WBPH2* were mapped on chromosomes 7 and 6, respectively (Sidhu et al. 1979; Liu et al. 2002). *WBPH6* was identified in rice variety Guiyigu and mapped on chromosome 11S (Li et al. 2004). *WBPH7* and *WBPH8*, which were introgressed from *O. officinalis*, were mapped on chromosomes 3 and 4 in the same regions as the *BPH14* and *BPH15*, respectively (Tan et al. 2004). Furthermore, four WBPH resistance genes in Sinna Sivappu, designated as *wbph9(t)*, *wbph10(t)*, *wbph11(t)*, and *WBPH12(t)*, were mapped on chromosome 6, 12, 4 by molecular markers, respectively (Ramesh et al. 2014). One gene (*Ovc*) and four QTLs (*qOVA-1-3*, *qOVA-4*, *qOVA-5-1*, and *qOVA-5-2*) that exhibit WBPH ovicidal activity were identified in the *japonica* rice variety Asominori and mapped on chromosomes 6, 1, 4, and 5, respectively (Yamasaki et al. 2003). The QTLs *qWL6* from cultivar Chunjiang 06 and *qWBPH11* from IR54751 were delimited into a 122 kb region between markers M3 and M5 on chromosome 6 and a 450 kb region between markers DJ53973 and SNP56 on chromosome 6, respectively (Yang et al. 2014; Fan et al. 2018).

Prior to 2009, there were few reports of SBPH resistance genes or QTLs. Subsequent screening efforts have revealed a number of rice accessions with SBPH resistance (Duan et al. 2009). Three QTLs related to SBPH resistance (*qSBPH2b*, *qSBPH3d*, and *qSBPH12a*) were identified on chromosomes 2, 3, and 12 in the cultivar Mudgo, respectively (Duan

Table 1 Insect resistance genes identified in rice

Gene	Germplasm	Chromosome	Linked markers	References
Brown planthopper				
BPH1	Mudgo	12	pBPH4-pBPH14	Athwal et al. 1971, Cha et al. 2008
bph2	ASD7	12	RM7102-RM463	Athwal et al. 1971, Sun et al. 2006
BPH3	Rathu Heenati	6	RM589-RM588	Laksminarayana and Khush 1977, Jairin et al. 2007b
BPH3	Rathu Heenati	4	RHD9-RHC10	Liu et al. 2015
bph4	Babawee	6	RM589-RM586	Sidhu and Khush 1978, Jairin et al. 2010
bph5	ARC 10550	–	–	Khush et al. 1985
BPH6	Swarnalata	4	H-Y9	Kabir and Khush 1988, Guo et al. 2018
bph7	T12	12	RM3448-RM313	Kabir and Khush 1988, Qiu et al. 2014
bph8	Chin Saba	–	–	Nemoto et al. 1989
BPH9	Pokkali	12	InD2-RsaI	Nemoto et al. 1989, Zhao et al. 2016
BPH10	*O.australiensis*	12	RG457-CDO459	Ishii et al. 1994
bph11	*O.officinalis*	3	G1318	Hirabayashi et al. 1998
BPH12	B14 (*O.officinalis*)	4	RM16459-RM1305	Qiu et al. 2012
BPH13	*O.officinalis*	3	RZ892-RG191	Renganayaki et al. 2002
BPH14	B5 (*O.officinalis*)	3	SM1-G1318	Du et al. 2009
BPH15	B5 (*O.officinalis*)	4	RG1-RG2	Yang et al. 2004
BPH16	M1635–7	12	RM6732-R10289	Hirabayashi et al. 2004
BPH17	Rathu Heenati	4	RM8213-RM5953	Sun et al. 2005
BPH18	IR65482–7–216-1-2 (*O. australiensis*)	12	BIM3-BN162	Ji et al. 2016
bph18(t)	*O. rufipogon*	4	RM273-RM6506	Li et al. 2006
bph19(t)	AS20–1	3	RM6308-RM3134	Chen et al. 2006
bph19(t)	*O. rufipogon*	12	RM17	Li et al. 2006
BPH20(t)	IR71033–121-15 (*O. miniuta*)	4	B42-B44	Rahman et al. 2009
BPH21(t)	IR71033–121-15 (*O. miniuta*)	12	S12094A-B122	Rahman et al. 2009
BPH22(t)	*O. glaberrima*	–	–	Ram et al. 2010
BPH23(t)	*O. minuta*	–	–	Ram et al. 2010
bph22(t)	*O. rufipogon*	4	RM8212-RM261	Hou et al. 2011
bph23(t)	*O. rufipogon*	8	RM2655-RM3572	Hou et al. 2011
bph24(t)	IR72678–6-9-B (*O. rufipogon*)	–	–	Deen et al. 2010
bph25	ADR52	6	S00310-RM8101	Myint et al. 2012
BPH26	ADR52	12	DS72B4-DS173B	Tamura et al. 2014
BPH27	*O. rufipogon*	4	RM16846-RM16853	Huang et al. 2013
BPH27(t)	Balamawee	4	Q52-Q20	He et al. 2013b
BPH28(t)	DV85	11	InDel55-InDel66	Wu et al. 2014
bph29	RBPH54 (*O. rufipogon*)	6	BYL8-BID2	Wang et al. 2015b
bph30	RBPH54 (*O. rufipogon*)	10	RM222-RM244	Yang et al. 2012
BPH30	AC-1613	4	SSR28-SSR69	Wang et al. 2018a
BPH31	CR2711–76	3	PA26-RM2334	Prahalada et al. 2017
BPH32	PTB33	6	RM19291-RM8072	Ren et al. 2016

Table 1 (continued)

Gene	Germplasm	Chromosome	Linked markers	References
BPH33	KOLAYAL	4	H99-H101	Hu et al. 2018
BPH34	IRGC104646 (*O. nivara*)	4	RM16994-RM17007	Kumar et al. 2018
qBPH3	IR02W101 (*O.officinalis*)	3	t6-f3	Hu et al. 2015b
qBPH4	IR02W101 (*O.officinalis*)	4	P17-xc4–27	Hu et al. 2015b
qBPH4.2	IR65482–17-511 (*O. australiensis*)	4	RM261-XC4–27	Hu et al. 2015a
qBPH4.3	Salkathi	4	RM551-RM335	Mohanty et al. 2017
qBPH4.4	Salkathi	4	RM335-RM5633	Mohanty et al. 2017
qBPH6(t)	IR71033–121-15	6	RM469-RM568	Jairin et al. 2007a
White-backed planthopper				
WBPH1	Nagina 22	7	–	Sidhu et al. 1979
WBPH2	ARC10239	6	RZ667	Angeles et al. 1981, Liu et al. 2002
WBPH3	ADR52	–	–	Hernandez and Khush 1981
wbph4	Podiwi A8	–	–	Hernandez and Khush 1981
WBPH5	N'Diang Marie	–	–	Wu and Khush 1985
WBPH6	Guiyigu	11	RM167	Li et al. 2004
WBPH7	B5 (*O.officinalis)*	3	R1925-G1318	Tan et al. 2004
WBPH8	B5 (*O.officinalis)*	4	R288-S11182	Tan et al. 2004
wbph9(t)	Sinna Sivappu	6	RM589-RM539	Ramesh et al. 2014
wbph10(t)	Sinna Sivappu	12	SSR12–17.2-RM28487	Ramesh et al. 2014
wbph11(t)	Sinna Sivappu	4	Rm3643-rm1223	Ramesh et al. 2014
WBPH12(t)	Sinna Sivappu	4	RM16592-RM16649	Ramesh et al. 2014
Ovc	Asominori	6	R2373-C946	Yamasaki et al. 2003
qOVA-1-3	Asominori	1	XNpb346-C112	Yamasaki et al. 2003
qOVA-4	Asominori	4	R1854	Yamasaki et al. 2003
qOVA-5-1	Asominori	5	XNpb251-R3313	Yamasaki et al. 2003
qOVA-5-2	Asominori	5	C1268	Yamasaki et al. 2003
qWPH2	*O. rufipogon*	2	RM1285-RM555	Chen et al. 2010
qWBPH5	*O. rufipogon*	5	RM3870-RZ70	Chen et al. 2010
qWBPH9	*O. rufipogon*	9	RG451-RM245	Chen et al. 2010
qWL6	Chunjiang 06	6	M3-M5	Yang et al. 2014
qWBPH3.2	IR54751	3	InDel3–23–InDel3–26	Fan et al. 2018
qWBPH11	IR54751	11	DJ53973-SNP56	Fan et al. 2018
Small brown planthopper				
qSBPH2b	Mudgo	2	RM29-RM5791	Duan et al. 2009
qSBPH3d	Mudgo	3	RM5442-RM3199	Duan et al. 2009
qSBPH12a	Mudgo	12	I12–17-RM3331	Duan et al. 2009
qSBPH2	Kasalath	2	R712-R1843	Duan et al. 2010
qSBPH3	Kasalath	3	C1135-C80	Duan et al. 2010
qSBPH8	Kasalath	8	R1943-C390	Duan et al. 2010
qSBPH11	Kasalath	11	G257-S2260	Duan et al. 2010
qSBPH2	N22	2	RM263-RM1385	Wang et al. 2013b

Table 1 (continued)

Gene	Germplasm	Chromosome	Linked markers	References
qSBPH3	N22	3	RM22-RM545	Wang et al. 2013b
qSBPH5	N22	5	RM153-RM413	Wang et al. 2013b
qSBPH7	N22	7	RM234-RM429	Wang et al. 2013b
qSBPH11	N22	11	RM209-RM21	Wang et al. 2013b
qSBPH3d	Pf9279–4 (*O. officinalis*)	3	RM218-RM745	Zhang et al. 2014
qSBPH7a	Pf9279–4 (*O. officinalis*)	7	RM7012-RM6338	Zhang et al. 2014
qSBPH12b	Pf9279–4 (*O. officinalis*)	12	RM463-RM6256	Zhang et al. 2014
qSBPH1	9194	1	RM3738-RM8236	Sun et al. 2017
qSBPH5	9194	5	RM18452-RM163	Sun et al. 2017
qSBPH8	9194	8	RM210-RM3845	Sun et al. 2017
qSBPH9	9194	9	RM257-RM160	Sun et al. 2017
qSBPH5	WR24	5	Indel 5–11-RM3664	Xu et al. 2018b
qSBPH7	WR24	7	RM6403-RM234	Xu et al. 2018b
qSBPH10	WR24	10	RM25664-RM228	Xu et al. 2018b
Gall midge				
GM1	W1263	9	RM444-RM219	Biradar et al. 2004
GM2	Phalguna	4	RM241-RM317	Himabindu et al. 2007
gm3	RP2068-18-3-5	4	RM17480-gm3SSR4	Sama et al. 2014
GM4	Abhaya	8	RM22551-RM22562	Divya et al. 2015
GM5	ARC5984	12	RM101-RM309	Dubey and Chandel 2010
GM6	Duokang #1	4	RG214-RG476	Katiyar et al. 2001
GM7	RP2333–156-8	4	F8LB-SA598	Sardesai et al. 2002
GM8	Aganni	8	RM22685-RM22709	Divya et al. 2018
GM9	Line9			Shrivastava et al. 2003
GM10	BG 380–2			Kumar et al. 2005
GM11	CR57-MR1523	12	RM28574-RM28706	Himabindu et al. 2010
Green rice leafhopper				
GRH1	IR24	5	R569-C309	Kadowaki et al. 2003
GRH2	DV85	11	R2458-C50	Kadowaki et al. 2003
GRH3	Rantaj emas 2	6	C288B-C133A	Saka et al. 2006
GRH4	DV85	3	C1186-R2982	Kadowaki et al. 2003
GRH5	W1962 (*O. rufipogon*)	8	RM3754-RM3761	Fujita et al. 2006
GRH6	SML17, IRGC105715	4	RM8213-C708	Fujita et al. 2004, Tamura et al. 2004
qGRH9	IRGC104038 (*O. glaberrima)*	9	RM215-RM2482	Fujita et al. 2010a
Green leafhopper				
GLH1	Pankahari 203	5	–	Athwal *et al*. 1971
GLH 2	ASD7	11	–	Athwal *et al*. 1971
GLH 3	IR8	6	–	Athwal *et al*. 1971
glh4	PTB8	3	–	Siwi and Khush 1977
GLH 5	ASD8	8	–	Siwi and Khush 1977
GLH 6	TAPL 796	5	–	Rezaul Karim and Pathak 1982
GLH 7	Maddani Karuppan	–	–	Rezaul Karim and Pathak 1982

Table 1 (continued)

Gene	Germplasm	Chromosome	Linked markers	References
glh8	DV85	–	–	Ghani and Khush 1998
GLH 9	IR28	–	–	Angeles and Khush 1999
glh10	IR36	–	–	Angeles and Khush 2000a
GLH 11	IR20965–11–3-3	–	–	Angeles and Khush 2000a
GLH 12	ARC10313	–	–	Angeles and Khush 2000b
GLH 13	Asmaita	–	–	Angeles and Khush 2000b
GLH 14	ARC11554	4	Y3635-RZ262	Sebastian et al. 1996
Rice leaffolder				
qRLF-1	Taichung Native 1	1	RM3412-RM6716	Rao et al. 2010
qRLF-2	Taichung Native 1	2	RM207-RM48	Rao et al. 2010
qRLF-3	Chuanjiang 06	3	RM1022-RM7	Rao et al. 2010
qRLF-4	Chuanjiang 06	4	RM3276-RM255	Rao et al. 2010
qRLF-8	Chuanjiang 06	8	RM72-RM331	Rao et al. 2010

et al. 2009). Additional QTLs for SBPH resistance were identified, including *qSBPH2*, *qSBPH3*, *qSBPH8*, and *qSBPH11* on chromosome 2, 3, 8, and 11 in Kasalath, respectively; *qSBPH2*, *qSBPH3*, *qSBPH5*, *qSBPH7*, and *qSBPH11* on chromosome 2, 3, 5, 7, and 11 in N22, respectively; *qSBPH3d*, *qSBPH7a*, and *qSBPH12b* on chromosome 3, 7, and 12 in Pf9279-4, respectively; *qSBPH1*, *qSBPH5*, *qSBPH8*, and *qSBPH9* on chromosome 1, 5, 8, and 9 in 9194, respectively; and *qSBPH5*, *qSBPH7*, and *qSBPH10* on chromosome 5, 7, and 10 in WR24, respectively (Duan et al. 2010, Wang et al. 2013b, Zhang et al. 2014, Sun et al. 2017, Xu et al. 2018b, Table 1). Although individual QTLs have only small effects on SBPH resistance, it is useful to apply multiple QTLs for SBPH resistance breeding.

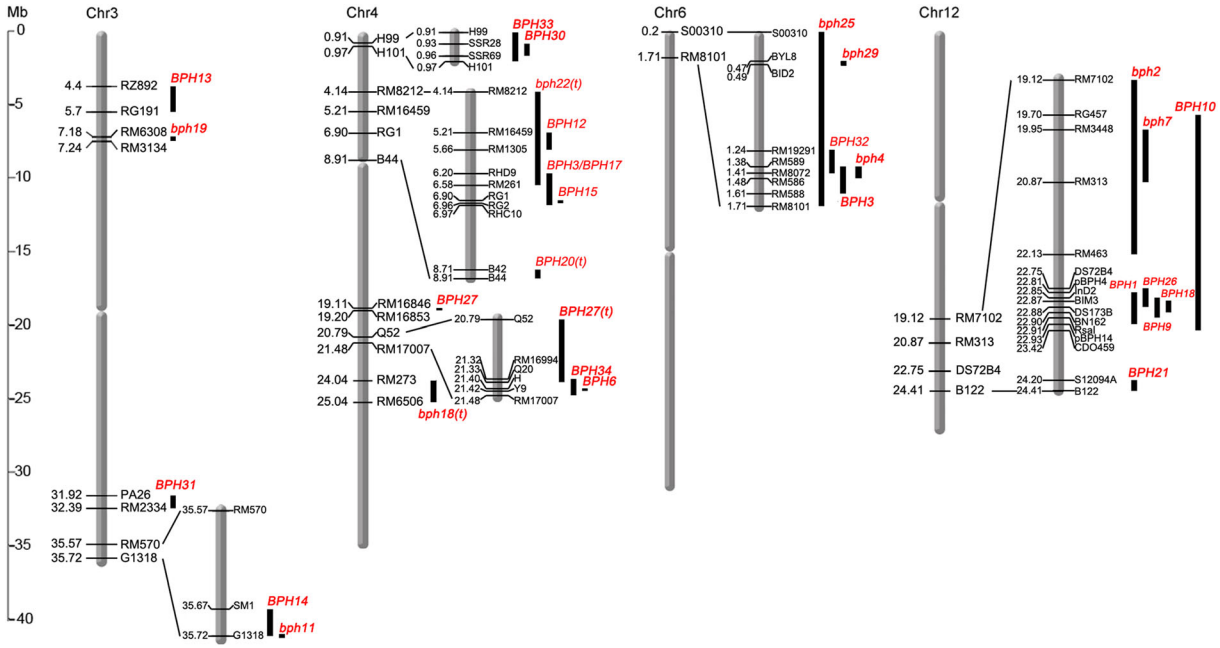

Fig. 1 Cluster of loci for BPH resistance genes on rice chromosomes. Numbers represent the physical distance on the left. Marker names are shown on the right. The black bars indicate the locations of BPH resistance genes

Several sources of gall midge resistance have been characterized, including 11 genes associated with Asian rice gall midge biotype resistance; all of these genes except for *GM9* and *GM10* have been mapped (Yasala et al. 2012). *GM1* from cultivar W1263 and *GM5* from ARC5984 were mapped on chromosome 9 between markers RM444 and RM219 and on chromosome 12 between markers RM101 and RM309, respectively (Biradar et al. 2004; Dubey and Chandel 2010). Four genes (*GM2*, *gm3*, *GM6*, and *GM7*) are clustered in a 0.82 Mb region between markers RM241 and RG476 on chromosome 4L, while *GM4* and *GM8* are present on chromosome 8S in a 3.90 Mb region between markers RM22551 and RM22709 (Yasala et al. 2012). Potential candidate genes associated with *gm3*, *GM4*, and *GM8* have recently been identified. *gm3* was mapped to a 560 kb region in RP2068-18-3-5 and a gene encoding an NB-ARC protein was tentatively linked to gall midge resistance (Sama et al. 2014). *GM4* from Abhaya was finely mapped to a 300 kb region; this region includes a candidate gene encoding a leucine-rich repeat (LRR) protein (Divya et al. 2015). *GM8* from the *indica* rice variety Aganni was mapped to a 430 kb region containing a gene encoding a proline-rich protein (Divya et al. 2018). Complementation tests, however, have not been performed to verify these gall midge resistance genes.

Two species of leafhoppers, green rice leafhopper (GRH) and green leafhopper (GLH), are the common pests of cultivated rice pest species in Asia (Ghauri 1971; Angeles and Khush 2000a). Seven major genes governing GRH resistance have been identified and mapped to date, including *GRH1* on chromosome 5 in IR24, *GRH2* on chromosome 11 in DV85, *GRH3* on chromosome 6 in Rantaj emas 2, *GRH4* on chromosome 3 in DV85, *GRH5* on chromosome 8 in W1962 (*O. rufipogon*), *GRH6* on chromosome 4 in SML17 and IRGC105715, and *qGRH9* on chromosome 9 in IRGC104038 (*O. glaberrima*), respectively (Table 1). Eleven dominant and three recessive GLH resistance genes have been identified across resistant varieties, including *GLH1* on chromosome 5 in Pankhari 203, *GLH2* on chromosome 11 in ASD7, *GLH3* on chromosome 6 in IR8, *glh4* on chromosome 3 in PTB8, *GLH5* on chromosome 8 in ASD8 and *O. rufipogon*, and *GLH6* on chromosome 5 in TAPL796 (Table 1). Only *GLH14* has been located on chromosome 4 using molecular markers Y3635 and RZ262 in ARC11554 (Sebastian et al. 1996).

Thus far, no stem borer resistance genes have been identified, although resistant wild and cultivated rice materials have been reported. A study using a doubled haploid population of CJ06/TN1 uncovered five QTLs for rice leaffolder (RLF) resistance on chromosomes 1, 2, 3, 4, and 8. The effect of a single locus is limited, but QTLs pyramiding markedly improved leaffolder resistance in rice (Rao et al. 2010).

In summary, several insect resistance genes have been identified in rice, most of which are clustered on chromosomes 3, 4, 6, 8, and 12 in rice (Table 1, Fig. 1). These clustered genes might represent closely linked genes, different alleles of the same gene, or the same gene responding to different insects. Eight BPH resistance genes are clustered on chromosome 12L. These eight genes were isolated and shown to be the alleles of the same gene (Zhao et al. 2016). Such allelic variation of a single resistance gene confers resistance to different BPH biotypes.

Cloning and characterization of insect resistance genes in rice

There is a pressing need to clone and characterize insect resistance genes. Such genes would facilitate the breeding of durable, broad-spectrum insect-resistant rice cultivars and the analysis of molecular mechanisms underlying plant resistance to insects. In the past decade, much progress has been made in isolating insect resistance genes in rice. Several BPH resistance genes have been cloned and characterized by map-based cloning, shedding light on the molecular mechanisms of insect resistance in a plant (Table 2).

BPH14 was the first BPH resistance gene cloned through map-based cloning (Du et al. 2009). This gene was initially identified on chromosome 3L in B5 rice, an introgression line derived from the wild rice species *O. officinalis* (Huang et al. 2001). Through high-resolution mapping, *BPH14* was localized to a 34 kb region containing two candidate resistance genes, *Ra* and *Rb*. Further transgene research revealed that only transgenic lines expressing *Ra* were BPH resistant, identifying this as the *BPH14* gene. *BPH14* encodes a CC-NB-LRR (coiled-coil, nucleotide-binding, and leucine-rich repeat) protein that is a typical NLR family member, revealing the similarities between insect and disease resistance in plants. *BPH14*, which is primarily expressed in vascular bundles, activates salicylic acid (SA) signaling and induces callose deposition on rice

Table 2 Insect resistance genes cloned in rice

Gene	Germplasm	Chr.	Encoded protein	Subcellular localization	Expression pattern	Resistance against	References
BPH1	Mudgo	12	CC-NB-NB-LRR	Endomembrane system	Vascular bundle	BPH	Zhao et al. 2016
bph2	ASD7	12	CC-NB-NB-LRR	Endomembrane system	Vascular bundle	BPH	Tamura et al. 2014
BPH3	Rathu Heenati	4	Lectin receptor kinases	Plasma membrane	Vascular bundle	BPH and WBPH	Liu et al. 2015
BPH6	Swarnalata	4	Atypical LRR	Exocyst	Vascular bundle/sclerenchyma	BPH and WBPH	Guo et al. 2018
bph7	T12	12	CC-NB-NB-LRR	Endomembrane system	Vascular bundle	BPH	Zhao et al. 2016
BPH9	Pokkali	12	CC-NB-NB-LRR	Endomembrane system	Vascular bundle	BPH	Zhao et al. 2016
BPH10	IR65482–4–136-2-2	12	CC-NB-NB-LRR	Endomembrane system	Vascular bundle	BPH	Zhao et al. 2016
BPH14	B5	3	CC-NB-LRR	Nucleus and cytoplasm	Vascular bundle	BPH	Du et al. 2009
BPH15	B5	4	Lectin receptor kinase	Plasma membrane	Vascular bundle	BPH	Cheng et al. 2013a
BPH18	IR65482–7–216-1-2	12	CC-NB-NB-LRR	Endomembrane system	Vascular bundle	BPH	Ji et al. 2016
BPH21	IR71033–121-15	12	CC-NB-NB-LRR	Endomembrane system	Vascular bundle	BPH	Zhao et al. 2016
BPH26	ADR52	12	CC-NB-NB-LRR	Endomembrane system	Vascular bundle	BPH	Tamura et al. 2014
bph29	RBPH54	6	B3 DNA-binding domain	Nucleus	Vascular bundles	BPH	Wang et al. 2015b
BPH32	PTB33	6	Unknown SCR domain	Plasma membrane	Vascular bundles	BPH	Ren et al. 2016

CC-NB-LRR, coiled-coil nucleotide-binding, and leucine-rich repeat; SCR, short consensus repeat

sieve tubes, thereby impairing the feeding, development, and survival of BPH insects (Du et al. 2009). Recent research found that the BPH14 proteins form homocomplexes, which interact with WRKY46 and WRKY72, increasing their abundance to activate defensive genes in rice (Hu et al. 2017).

Several BPH resistance genes also encode NLR proteins. Previously, eight BPH resistance genes have been identified on chromosome 12L (Fig. 1). The cloning of *BPH26* revealed that this gene also encodes a CC-NB-LRR protein. *BPH26* shares an identical DNA sequence with *bph2* and has a similar effect on the feeding of a *bph2*-virulent BPH biotype (Tamura et al. 2014). *BPH18* localizes to the same locus as *BPH26*, which was confirmed via map-based cloning and complementation tests. *BPH18* encodes a CC-NB-NB-LRR protein containing two NB domains (Ji et al. 2016). *BPH9* and its alleles *BPH1*, *bph7*, *BPH10*, and *BPH21* were cloned in 2016(Zhao et al. 2016). Finally, *Bph9* and its alleles *BPH1*, *bph7*, *BPH10*, and *BPH21* were all cloned in 2016 (Zhao et al. 2016). *BPH9* also encode a CC-NB-NB-LRR protein that localizes to the endomembrane system. *BPH9* confers both antixenosis and antibiosis to BPH. These eight BPH resistance genes, including the widely used *BPH1*, are clustered on chromosome 12L and are all allelic variants that can be classified into four allelotypes conferring different degrees of BPH resistance to different BPH biotypes (Zhao et al. 2016). A novel BPH resistance gene *BPH6* was recently cloned. This gene was previously mapped on chromosome 4L between the SSR markers Y9 and Y19 (Qiu et al. 2010). *BPH6* encodes an atypical LRR protein that is localized to the exocyst, where it interacts with exocyst subunit OsEXO70E1. *BPH6* expression

facilitates exocytosis and cell wall reinforcement and induces coordinated SA, cytokinin (CK), and jasmonic acid (JA) signaling. This gene confers substantial resistance to all assessed WBPH and BPH biotypes without adversely affecting rice yields (Guo et al. 2018).

Two BPH resistance genes encode plasma membrane-localized lectin receptor-like kinases (LecRKs). The first gene, *BPH15* was initially mapped between C820 and S11182 on chromosome 4S, which confers more robust and stable resistance than that yielded by *BPH14* (Huang et al. 2001). Through additional mapping efforts, *BPH15* was subsequently localized into a 47 kb region between markers RG1 and RG2 (Yang et al. 2004), from which the lectin receptor kinase gene, *OsLecRK*, was cloned (Cheng et al. 2013a). *OsLecRK* functions in both innate immunity and seed germination in plant. Knocking down *OsLecRK* significantly reduced the resistance of rice plants to BPH (Cheng et al. 2013a). The second gene, *BPH3*, is a BPH resistance locus that was identified in Rathu Heenati (RH) rice more than 40 years ago (Laksminarayana and Khush 1977). *BPH3* was first mapped on chromosome 6S between markers RM19291 and RM8072 (Jairin et al. 2007b). Liu et al. (2015) cloned *BPH3* on chromosome 4 in RH, which was originally reported as *BPH17* (Hu et al. 2016a). By the crossing of 02428 and RH to generate the BC_2F_2 and BC_3F_2 populations, *BPH3* was mapped to a 79 kb region. Map-based cloning and functional characterization showed that *BPH3* is actually a cluster of three genes encoding the plasma membrane-localized proteins, lectin receptor kinases (*OsLecRK1*, *OsLecRK2*, and *OsLecRK3*). Plants co-expressing all three genes exhibited significantly enhanced, broad-spectrum resistance to BPH and WBPH (Liu et al. 2015).

Based on our knowledge of these BPH resistance genes, together with recently isolated aphid resistance genes in other crops (Kaloshian and Walling 2016)), it is very likely that plant immunity is the major mechanism underlying insect resistance. There is a commonality between plant defenses responses to parasitic pathogens and insects. *BPH3* and *BPH15* encode the plasma membrane-localized proteins that function as the first layer of rice immune system for insect. These genes encode the initial pattern recognition receptors (PRRs) that are activated in response to conserved herbivory-associated molecular patterns (HAMPs) (Jing et al. 2017, Fig. 2). *BPH6*, *BPH14*, *BPH9*, and their alleles encode intracellular-localized NLR proteins, which perceive the effectors delivered to rice cells by BPH insects and trigger defenses responses (Cheng et al. 2013b, Jing et al. 2017, Fig. 2).

Nevertheless, two BPH resistance genes have been isolated that do not appear to be included in this immune system. *bph29* is a recessive BPH resistance gene that was first identified in the wild rice species *O. rufipogon*. *bph29* encodes a protein with a B3 DNA-binding domain (Wang et al. 2015b). The second gene, *BPH32*, was mapped on chromosome 6S in rice variety PTB33. Bioinformatics and functional analyses showed that *BPH32* encodes an SCR (short consensus repeat) domain-containing protein (Ren et al. 2016). The diversity of BPH resistance genes increases opportunities for the sustainable control of this insect.

Molecular understanding of insect resistance

Plant resistance to insects involves both constitutive defense and induced defense response. Constitutive defenses responses include the information of physical and chemical barriers prior to insect attack, whereas induced defenses responses include monitoring, signal transduction, and the production of defensive chemicals that are activated by insect attack (Chen 2008; Yang and Zhang 2016). Most insect resistance genes isolated to date encode plasma membrane-localized receptors and intracellular-localized receptors, indicating that induced defense and plant immunity play central roles in plant resistance to insects. Therefore, plant immunity against insects is similar to that against pathogens. In the past decade, much progress has been made in identifying insect elicitors and effectors as well as plant signaling transduction pathways, providing important insights into the molecular mechanism of insect resistance.

Insect elicitors and effectors

As insects feed or oviposit on plants, they inevitably release oral secretions (saliva, gut regurgitant) and oviposition fluids into the plant, which play an important role in plant-insect interactions (Miles 1999). Insect saliva has a number of properties and functions that are essential for successful feeding. Compounds in insect saliva may elicit or inhibit plant immune responses to insect attack (Miles 1999). Various elicitors have been identified in the oral secretion of insects, including β-glucosidase, fatty acid-amino acid conjugates (FACs),

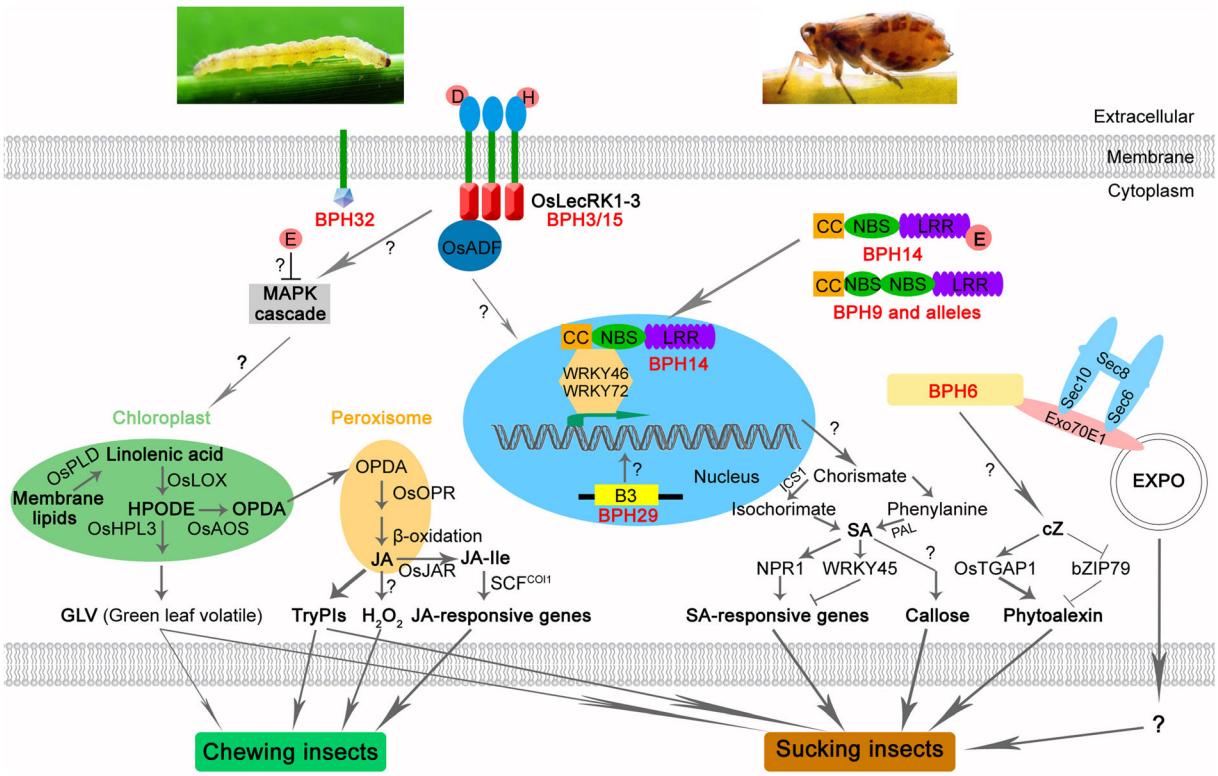

Fig. 2 Model of the molecular mechanism of insect resistance in rice. When insects feed on rice, rice PRRs such as "BPH3", BPH15, and BPH32 perceive HAMPs or DAMPs, which activates the MAPK cascade and induces PTI. However, effectors secreted by insect saliva can prevent PTI. Insect resistance proteins such as BPH14 and BPH9 recognize these effectors, triggering ETI. Insect resistance proteins combined with transcription factors activate the SA signaling pathway, upregulate the expression of SA-responsive defense genes, increase TryPIs and phytoalexin levels, and induce callose deposition, conferring resistance to sucking insects. However, in response to chewing insect infestation, MAPK cascade activates JA signaling pathways, thus producing TryPIs and H_2O_2, which upregulate the expression of JA-responsive defense genes and inhibit the feeding and growth of chewing insects. Furthermore, green leaf volatiles (GLVs) provide indirect plant defense by repelling insects settling and attracting natural enemies of insects. Abbreviations: Cz, cis-zeatin-type cytokinin; D, damage-associated molecular patterns (DAMP); E, effector; ETI, effector-triggered immunity; EXPO, exocyst-positive organelle; GLV, green leaf volatiles; H, herbivore-associated molecular patterns (HAMP); HPODE, hydroperoxyoctadecadienoic acid; JA, jasmonic acid; JA-Ile, jasmonoyl-l-isoleucine; MAPK, mitogen-activated protein kinase; OPDA, 12-oxo-phytodienoic acid; PRR, pattern-recognition receptors; PTI, pattern-triggered immunity; SA, salicylic acid; TrypPIs, trypsin protease inhibitors

volicitin and caeliferins. These compounds activate the JA signaling pathway, leading to defenses responses against insects (Mattiacci et al. 1995; Alborn et al. 2007; Aggarwal et al. 2014). When mechanical wounds in rice were treated with oral secretions from lawn armyworms, JA and JA-Ile levels increased rapidly, suggesting that insect elicitors were actively perceived by the plant, although the elicitors that caused this response have not yet been identified (Fukumoto et al. 2013). Shinya et al. (2016) isolated the oral secretions from *Mythimna loreyi*, a chewing insect, and identified FAC. Although FAC alone had negligible elicitor activity in rice, it promoted the activity of the high molecular mass fraction, resulting in the accumulation of reactive oxygen species and metabolite.

Recent studies on the transcriptome, proteome, and secretome of insect salivary glands have sought to uncover the roles of salivary proteins in interactions between insects and plants (Hattori et al. 2015; Li et al. 2016; Huang et al. 2018; Rao et al. 2019). Transcriptome analysis of the aphid salivary gland identified the salivary protein C002, which functions in plants (Mutti et al. 2008). When BPH feed on rice, the salivary endo-β-1,4-glucanase NlEG1 is delivered into the plant to degrade celluloses in the plant cell walls, which helps the BPH's stylets to reach the phloem (Ji et al. 2017).

The salivary gland-specific protein NcSP75 of GRH is also essential for establishing compatible interactions with rice plants (Matsumoto and Hattori 2018). Shangguan et al. (2018) characterized the BPH mucin-like protein (NlMLP), a salivary sheath component that is secreted into rice plants during feeding. NlMLP induces cell death, defense-related gene expression, and callose deposition in plants. BPH fed on *MLP*-dsRNA transgenic plants displayed mortality, reduced body size, and delayed maturation, suggesting that the MLP-silencing strategy could be used to control BPH. The DNase II protein in SBPH saliva was recently shown to degrade extracellular DNAs that acts as danger-associated molecular patterns (DAMPs), and to prevent rice cells from detecting these DAMPs, and thereby suppressing the defense system in rice (Huang et al. 2019). Rao et al. (2019) established a BPH secretome composed of 1140 conserved or rapidly evolving salivary proteins. Through transient expression of 64 BPH salivary proteins in plants, six proteins were shown to elicit defense responses. Finally, bacteria in BPH honeydew were recently shown to activate rice defenses response in rice, including the accumulation of phytoalexins and the release of volatile compounds to attract natural enemies of BPH (Wari et al. 2019). Together, these studies revealed that a variety of salivary proteins evoke defense responses in plant cells.

However, few insect-derived effectors that are recognized by plant receptors have been identified. Several researchers have attempted to map and clone insect avirulence genes using genetic crosses for effector identification. Jing et al. (2012, 2014) developed EST-SSR markers and constructed a highly comprehensive BPH linkage map with 96.6% coverage. Three major QTLs were mapped that control BPH preference or insect growth rates on resistant rice plants carrying *BPH1*. Another gene, the recessive gene *vBPH1*, controls BPH virulence on *BPH1* plants; this gene is located in the 10th linkage group (Kobayashi et al. 2014). In a study aimed at isolating an avirulence gene in Hessian fly (HF), the *vH13* gene was identified by high-resolution mapping and association analysis; this gene enabled HF larvae to survive in wheat plants carrying the *H13* resistance gene. The *vH13* gene encodes a novel small modular protein (Aggarwal et al. 2014). Analysis of the HF genome suggested that *SSGP-71* is likely the largest gene family in the effector reservoir. Mutations in different *SSGP-71* genes help the wheat pest *Mayetiola destructor* avoid ETI directed by resistance genes *H6* and *H9* in wheat (Zhao et al. 2015). Although a number of putative elicitors and effectors have been identified in herbivorous insects and many insect resistance genes have been cloned in rice and other plants, the mechanisms used by plants to recognize these insect molecules and trigger resistance remain to be characterized.

Resistance-associated signal transduction in rice

Various approaches have been employed to explore the responses of rice to insect feeding, including suppression subtractive hybridization, cDNA array analysis, and transcriptomic and proteomic approaches, offering important insights into the mechanisms of insect resistance (Zhang et al. 2004; Wang et al. 2005; Yuan et al. 2005; Hua et al. 2007; Wang et al. 2008; Wei et al. 2009; Zhou et al. 2011; Wu et al. 2017).

MAPK signaling, a universal process in eukaryotes, serves as a bridge between a variety of stimuli and the expression of specific downstream defense genes in the plant innate immune system (Hettenhausen et al. 2015). MAPK signaling hss important roles in insect resistance in rice through the modulation of SA, JA, and ET signaling (Yuan et al. 2005, Wang et al. 2008). OsMPK3/4 positively regulate striped stem borer (SSB) resistance in rice by mediating SA and JA signaling. This process induces TrypPIs but has no effect on BPH resistance (Wang et al. 2013a; Liu et al. 2018). By contrast, OsMPK5/12 increase BPH resistance in rice by mediating the direct phosphorylation of OsERF1 and OsEREBP; these transcription factors regulate defense-related gene expression in the context of *Bphi008*-associated resistance (Hu et al. 2011). Recently, *OsMAPK20–5*, a group D MAPK gene, was identified in rice. This gene is rapidly induced by female BPH adults, but not by nymphs. *OsMAPK20–5*-silenced rice exhibited increased resistance to BPH adults and oviposited eggs and showed broad-spectrum resistance to BPH and WBPH in the field (Li et al. 2019).

Phytohormones are essential for controlling defense signaling in plants (Pieterse et al. 2012). Following BPH feeding, SA synthesis-related gene expression and SA levels increased in rice plants carrying the *BPH14*, *bph29*, or *BPH9* and its alleles compared to BPH-susceptible plants without any corresponding differences in JA synthesis-related gene expression or JA levels (Du et al. 2009; Wang et al. 2015b; Zhao et al. 2016). Similar findings have been reported in the

context of SBPH-rice interactions, with SBPH infestations leading to the much more rapid induction of SA synthesis-related genes in resistant vs. susceptible rice cultivars, along with a corresponding decrease in JA synthesis-related genes expression (Duan et al. 2014). These findings suggest that the activation of SA-dependent systemic acquired resistance occurs in plants as a protective mechanism against phloem-feeding insects, whereas such resistance mechanisms are JA independent.

JA is a critical mediator of plant defenses responses against chewing insects (McConn et al. 1997). JA signaling-associated gene expression is activated by SSB feeding in rice (Sun et al. 2010). In rice, JA biosynthesis and signal transduction are controlled by genes including *OsPLD*, *OsLOX*, *OsAOS*, and *OsCOI1* (Lyons et al. 2013). Silencing these genes reduced the levels of JA and TrypPI, thus improving rice leaffolder and SBB larval performance while simultaneously increasing levels of SA and H_2O_2 levels to enhance (or at least not adversely affect) BPH resistance (Zhou et al. 2009; Qi et al. 2011; Ye et al. 2012; Zhou et al. 2014). JA also protects rice roots from two root-feeding insects and positively regulates plant resistance to root pests (Lu et al. 2015). Thus, JA and SA play distinct roles in mediating the defenses responses of rice against chewing and phloem-feeding insects.

The classic binary model of JA and SA defense mechanisms indicates that these phytohormones play opposing roles in mediating defenses responses against chewing and sucking insects. However, in some contexts such as in rice-BPH interactions, these phytohormones can have synergistic effects. Plants carrying the *BPH6* resistance gene exhibited more rapid increases in both SA and JA levels upon BPH infestation compared to susceptible plants. The application of exogenous SA and methyl jasmonate also enhanced resistance to BPH and reduced insect survival on both resistant and susceptible plant varieties (Guo et al. 2018).

Other hormones besides JA and SA also control insect defense responses in plants, including CK, brassinosteroids (BR), gibberellins (GA), ethylene (ET), and abscisic acid (ABA). CK levels, and particularly the levels of the cis-zeatin (cZ) isoform levels, increased sharply in plants carrying the *BPH6* resistance gene at 12–24 h post-BPH infestation with BPH compared with non-infested control plants. In addition, exogenous treatment with 6-benzylaminopurine, N6-(Δ2-isopentenyl) adenine, and cZ reduced BPH survival and improved resistance in *BPH6*-expressing plants (Guo et al. 2018). BRs negatively regulate BPH resistance by decreasing SA levels and SA-associated gene expression while increasing JA levels and promoting JA-associated gene expression (Pan et al. 2018). The rice DELLA protein OsSLR1, which negatively regulates the GA pathway, also negatively regulates plant resistance to BPH. Silencing of *OsSLR1* probably leading to decrease JA, and ET-mediated defense (Zhang et al. 2017). The *OsGID1*-mediated GA pathway positively regulates BPH resistance in rice. Overexpression of the GA receptor gene *OsGID1* decrease SA and H_2O_2 level and the expression of SA-pathway-related WRKY transcripts, resulting in decreased BPH settling, laying, and feeding (Chen et al. 2018). ET is a stress hormone with a myriad of context-dependent effects on insect resistance. The silencing of *OsACS2* reduced elicited ET emissions, TrypPI activity, and SSB resistance while improving resistance to BPH (Lu et al. 2014). The exogenous application of ABA suppressed β-1,3-glucanase while inducing callose synthase activity, promoting callose deposition and thereby preventing BPH feeding (Liu et al. 2017). A recent study revealed that *OsEIL1-OsLOX9* undergo crosstalk to negatively regulate JA and ET signaling pathways, thereby affecting plant responses to sucking insect attack (Ma et al. 2019).

Transcription factors that function downstream of hormonal signaling pathways are essential regulators of defense-associated signaling, making them vital to any insect resistance mechanisms in plants (Yang et al. 2016). Microarray and RNA-seq analyses showed that following BPH infestation, transcription factor genes are markedly upregulated in BPH-susceptible rice (Wang et al. 2012; Lv et al. 2014). The overexpression of *OsWRKY89* led to increased leaf surface wax deposition, SA levels, and lignification in culms, resulting in enhanced WBPH resistance (Wang et al. 2007). OsWRKY70 activates TrypPI and enhances resistance against SSB by positively regulating JA biosynthesis while negatively regulating GA biosynthesis, thereby reducing plant resistance to BPH (Li et al. 2015b). The silencing of *OsWRKY45* improved BPH resistance by increasing the induction of H_2O_2 and ET production by BPH, thereby decreasing insect feeding, survival, nymphal development, and oviposition preferences (Huangfu et al. 2016). OsWRKY53 negatively regulates *OsMPK3/6* to activate SSB resistance in rice, while also protecting against BPH via activating a burst of H_2O_2 production and suppressing ET biosynthesis (Hu et al.

2015c, 2016b). In addition, OsHLH61 and OsbHLH96 affect plant responses to BPH by regulating pathogen-related gene expression (Wang et al. 2019).

Defense-related metabolites

Plants synthesize a rich variety of metabolites, including defense compounds (e.g., proteinase inhibitors and callose), secondary metabolites (terpenes, alkaloids, flavonoid, and others), and volatiles. Many of these compounds, whose production is controlled by the signaling network, prevent insect pests from feeding, are toxic to insects, or attract their natural enemies (Douglas 2018; Yang et al. 2019).

Proteinase inhibitors (PIs) and callose are two common insect resistance compounds in rice. The PIs, whose production is triggered by insect feeding, affect digestive proteases and induce amino acid deficiencies in the insect midgut, thereby negatively affecting insect growth and development (Lison et al. 2006). TrypPIs are essential defense proteins that accumulate in rice in response to both BPH and SSB feeding (Du et al. 2009; Zhou et al. 2011). Callose deposition in BPH-resistant rice can blocks access to the phloem, thereby preventing insect feeding. By contrast, in susceptible rice varieties, BPH feeding induces the activation of callose-hydrolyzing enzymes, leading to callose decomposition and thus benefiting the feeding process (Hao et al. 2008).

Secondary metabolites are also vital for defending plants against insect infestations, by reducing insect growth, attraction, survival, and reproduction. Infestation with BPH induces substantial metabolic changes in both resistant and susceptible rice varieties. BPH feeding increases sterol biosynthesis in susceptible plants, whereas it promotes wax biosynthesis, phytol metabolism, strengthening of GABA shunt, and shikimate-mediated secondary metabolism in resistant plants (Liu et al. 2010; Zhang et al. 2018). Natural ovicidal resistance mechanisms also protect rice against planthoppers. Aqueous benzyl benzoate solutions are ovicidal to WBPH eggs at a concentration greater than 6.4 ppm at 25 °C (Seino et al. 1996). Similarly, oxalic acid, transaconite acid, and 3-nitraphthalic acid inhibit BPH sucking (Zhang et al. 1999; Ling et al. 2007). Feeding of the chewing insects *P. guttata* and *S. mauritia* induces the accumulation of phenolamides, which may be toxic to BPH (Alamgir et al. 2016). Phytoalexins are antimicrobial metabolites that are produced by plants upon pathogen and insect attack (Yamane 2013). BPH feeding and exogenous CK application led to much more robust increases in diterpenoid phytoalexins levels in plants expressing *BPH6* relative to susceptible control plants (Guo et al. 2018). Serotonin, a ubiquitous compound across life forms, is also thought to regulate insect behavior and immune responses. Insect infestations result in increased serotonin biosynthesis in rice, and suppressing this process leads to increased SA levels and associated SSB and BPH resistance (Lu et al. 2018). Finally, the flavonoid schaftoside was shown to inhibits the activation of the BPH kinase NlCDK1 by binding with this protein, resulting in suppressed ovary development and reduced the BPH fecundity and survival (Hao et al. 2018a, b).

The release of volatile compounds markedly increases upon insect infestation, thereby signaling the insect's locations to attract natural parasitoids and predator species (Allmann and Baldwin 2010). The production of *S*-linalool (monoterpene), an abundant volatile in rice, is strongly induced in response to BPH. By contrast, (*E*)-β-caryophyllene (sesquiterpene) is constitutively produced in rice, and its production is further induced in response to chewing insects but not BPH. Both two compounds attract BPH parasitoids and chewing herbivores (Cheng et al. 2007; Xiao et al. 2012). Green leaf volatiles are important mediators of plant defense response against planthopper. The loss of *OsHPL3* expression results in increased levels of JA and decreased levels of green leaf volatiles, thereby altering planthopper performance and plant attraction (Tong et al. 2012; Wang et al. 2015a).

These findings suggest that a complex network regulates insect infestation in rice (Fig. 2). When insects feed on rice, PRRs in rice, such as OsLecRK perceive HAMPs or DAMPs, resulting in activation of the MAPK cascade and inducing pattern-triggered immunity (PTI). However, effectors secreted by insect saliva can prevent PTI. Resistance proteins, such as NLR proteins recognize these effectors to trigger ETI. In response to sucking insect attack, the R proteins combined with the transcription factors, activate the SA signaling pathway, resulting in increased SA-responsive defense gene expression and phytoalexin levels, as well as callose deposition. However, in response to chewing insect attack, the MAPK cascade activates JA signaling pathways, thus producing TryPIs and H_2O_2, enhancing the expression of JA-responsive defense genes to inhibit insect growth and development.

Volatiles play indirect roles in plant defense by repelling insects settling and attracting natural enemies of insects.

The role of microRNA in regulating insect resistance in rice

MicroRNAs (miRNAs) are endogenous, ~ 21–24 nucleotides long, non-coding small RNAs that are widely present in both animals and plants. These molecules specifically regulate the expression of their target genes by binding to complementary sequences to degrade mRNA or inhibit translation (Bartel 2009; Axtell and Meyers 2018). There are few reports on the roles of miRNA in regulating insect resistance in rice. BPH-responsive miRNAs in resistant and susceptible rice plants have been identified and analyzed (Wu et al. 2017). Recently, two miRNAs were shown to be involved in regulating of BPH resistance in rice. *OsmiR156*, a primary regulator of plant development, negatively regulates BPH resistance in rice by regulating the JA and JA-Ile biosynthetic pathway (Ge et al. 2018). The silencing of *miR156* decreased the resistance of rice to BPH and reduced the honeydew excretion, as well as BPH survival and fecundity. Another miRNA in rice, *OsmiR396*, targets *OsGRF8*, encoding a growth-regulating factor, and directly regulates *OsF3H*, encoding a flavanone 3-hydroxylase in the flavonoid biosynthetic pathway, thereby negatively regulating BPH resistance (Dai et al. 2019). miRNAs are involved in many developmental processes in plants and play important roles in abiotic and biotic stress responses (Bartel 2009; Wu et al. 2017). This mechanism provides an ideal way to balance insect resistance, defense responses, and crop growth.

Breeding for insect-resistant rice

The ultimate aim of mapping and cloning insect resistance genes, and elucidating the molecular mechanism of insect-resistant in crops is to breed insect-resistant crop varieties, representing an effective, economical, and environmentally friendly pest control strategy. Currently available genetic technologies, including marker-assisted selection (MAS), genetic transformation, and genome editing can be used to reduce the timescales of insect-resistant plant breeding are essential for use with crops with limited insect resistance resources.

Marker-assisted selection

To date, MAS has been successfully utilized to breed plants with major BPH, GM, WBPH, and GRH resistance genes. A series of near-isogenic lines (NILs) with a single BPH resistance gene/QTL, including *BPH3*, *bph4*, *BPH6*, *BPH9*, *BPH10*, *BPH14*, *BPH15*, *BPH17*, *BPH18*, *BPH20*, *BPH21*, *BPH24*, *BPH26*, *BPH32*, *qBPH3*, and *qBPH4*, were developed in the background of the susceptible cultivar 9311 and IR24, respectively (Qiu et al. 2010; Xiao et al. 2016; Jena et al. 2017). Furthermore, the NILs with a single GM (*GM4*, *GM11*), WBPH (*Ovc*, *qOVA-1-3*, *qOVA-4*, *qOVA-5-1*, and *qOVA-5-2*), and GRH (*GRH1*, *GRH2*, *GRH4*, *GRH5*, *GRH6*, and *qGRH4*) resistance genes were also developed (Yamasaki et al. 2003; Fujita et al. 2010b; Himabindu et al. 2010; Divya et al. 2015). Unfortunately, such plants bearing single resistance genes lost their efficacy in just a few years as the insect populations rapidly adapted or evolved to overcome the resistance (Jena and Kim 2010). The use of different resistance genes in breeding or pyramiding multiple insect resistance genes into a given rice variety represents an ideal means for achieving the sustained control of insects in rice. Rice varieties harboring multiple pyramided BPH resistance genes exhibited more robust resistance towards BPH than plants bearing single resistance genes (Sharma et al. 2004; Qiu et al. 2011; Liu et al. 2016b). The pyramided lines (PYLs) with two- to three-pyramided BPH resistance genes have been developed. The pyramided genes had an additive effect, with an order of effectiveness of three-pyramided genes > two-pyramided genes > single gene > none (Hu et al. 2013; Jena et al. 2017). Similarly, three PYLs possessing *GRH2* and *GRH6*, *GRH4*, and *GRH6*, or *GRH5* and *qGRH4*, showed higher resistance levels than each of the five monolocus NILs with the same loci (Fujita et al. 2010b). In addition, Wang et al. (2017) pyramided *BPH6* and *BPH9* into rice variety 9311, founding that hybrids heterozygous for *BPH6* and *BPH9* were highly resistant to BPH. A marker-assisted selection has become popular for molecular breeding in crop improvement and should contribute to future breeding outcomes. In China, various male-sterile lines, restoring lines, and hybrid varieties carrying the *BPH14* and *BPH15* genes by MAS have been developed and released to the farmers (Hu et al. 2013; Wang et al. 2016; He et al. 2019).

Bt and lectins toxins

Bt proteins are insecticidal toxins produced by *B. thuringiensis*. The use of Bt genes in insect pest management has attracted increasing attention. There are more than 200 Bt genes, each of which is highly specific to a range of insects. The first transgenic Bt crops that were grown commercially were Bt corn and cotton (Douglas 2018). Bt genes are highly effective against chewing insects in rice, making them ideal targets for the control of SSB and RLF. For example, transgenic rice expressing the Bt gene *cry2AX1* exhibited increased resistance to multiple lepidopteran pests (Chakraborty et al. 2016). However, several pests have recently developed resistance to overcome Bt crops in the field (Tabashnik et al. 2013). This problem could be solved by pyramiding multiple Bt genes or enhancing the efficacy of Bt toxins. Indeed, transgenic plants expressing a fusion protein of Cyr1Ab and Vip3A were highly resistant to SSB and RLF, with no adverse effect on agronomic traits (Xu et al. 2018a). A recombinational product of *Cry2Aa* and *Cry2Ac* increased the efficacy of Bt toxin (Chakraborty et al. 2016).

Although the use of Bt toxins is a common method for the biological control of pests, these compounds are ineffective against Hemipteran pests. Pyramiding multiple genes, such as *BPH14*, *BPH15*, and *Cry1C* in elite restorer lines enhanced resistance to BPH, SSB, and RLF (Wan et al. 2014). A fusion protein consisting of the DI and DII domains of Bt Cry1Ac and the carbohydrate-binding domain of garlic lectin showed remarkable toxicity against Lepidopteran and Hemipteran insects (Boddupally et al. 2018). In addition, a field survey showed that Bt rice contained fewer settled BPHs than non-Bt rice, even though BPHs are insensitive to Bt Cry proteins, providing the first example of the ecological resistance of Bt plants against non-target pests (Wang et al. 2018b). These studies provide new ideas for the future development of genetically engineered crops with resistance to multiple insects.

Lectins are a potent form of insecticidal compounds that are well-suited to control sap-sucking insects in rice that are not susceptible to Bt toxins. Insect pests feeding on plants expressing snowdrop lectin (GNA) showed impaired growth, development, and reproduction (Rao et al. 1998; Sun et al. 2002; Nagadhara et al. 2004). However, the resistance mediated by GNA is not as effective as that mediated by Bt or by resistance genes in rice germplasm. Therefore, the appropriate stacking of genes can be used to optimize the efficacy and specificity of insect resistance. For example, a fusion protein comprising GNA and the scorpion neurotoxin domain conferred resistance and toxicity to Lepidopteran and Hemipteran pests in rice (Liu et al. 2016a).

Plant-mediated RNA interference

The planet-mediated RNA interference (RNAi) is a promising strategy for insect control involving the expression of double-stranded (ds) insect RNA in crops. This technique has a better mode of action and specificity than the use of protein toxins. When insect pests feed on a crop expressing dsRNA specific to an important insect gene, the dsRNA is internalized into cells and processed into small interfering RNA, which degrades the complementary target mRNAs or interferes with its translation (Scott et al. 2013). Plant-mediated RNAi has been widely employed against Lepidopteran and Coleopteran insects (Baum et al. 2007; Mao et al. 2007; Scott et al. 2013). Zha et al. (2011) first reported that insect feeding on transgenic rice expressing dsRNA from Hemipteran insects exhibited reduced transcript levels of the targeted genes in their midguts. The survival of BPH or Asian corn borers decreased significantly when fed on rice or maize soaked in a solution containing *dsCes* (carboxylesterase gene) or *dsKTI* (Kunitz-type trypsin inhibitors gene) (Li et al. 2015a). Shangguan et al. (2018) demonstrated that the expressing ds*NlMLP* in rice impaired salivary sheath formation and significantly reduced the rate of weight gain and survival of BPHs fed on these plants.

Although many attractive target Hemipteran genes have been selected, only a few successful examples of their use have been reported. Therefore, a major challenge for insect control by plant-mediated RNAi is to determine how to efficiently and economically transfer dsRNA into insects through transgenic expression in rice.

Genome editing by CRISPR/Cas9

Genome editing is a rapidly developing technology that has dramatically increased the chances of introducing resistance traits into crops by generating highly specific, precise targeted mutations into plant genomes. A major genome-editing tool is the CRISPR/Cas9 system (Georges and Ray 2017). The first report of the successful use of CRISPR/Cas9 to engineer insect resistance

involved its use in conferring resistance to viruses carried by insects, particularly geminiviruses with DNA genomes (Ali et al. 2016). Knocking out *CYP71A1* (encoding tryptamine 5-hydroxylase) by CRISPR/Cas9 increased SA levels and decreased serotonin levels in rice, thus enhancing resistance to BPH (Lu et al. 2018). CRISPR/Cas9 could be used to breed new resistant crop varieties by converting a susceptible allele to a resistance allele via editing, thereby eliminating the need for the extensive backcrosses required in traditional breeding.

In summary, although MAS is still used to breed new crop varieties, the rapid development and ongoing innovations in plant genetic technologies providing more effective approaches to engineer insect-resistant crops over the coming years.

Outlook

Marked progress has been made in recent years to map, clone, elucidate the underlying resistance mechanisms, and leverage insect resistance genes in rice, allowing for a better understanding of the molecular basis of such resistance and facilitating efforts to breed insect-resistant rice varieties. However, many challenges remain in our efforts to achieve reliable insect resistance in rice.

As rice resistance to insects in rice coevolved with the insects themselves, insect resistance genes are more frequent in regions of the world where pests are more common. Therefore, efforts to more thoroughly screen rice germplasm resources in these regions will provide the opportunity to identify additional insect resistance germplasms. The 3000 Rice Genome Project has resequenced a core collection of 3000 rice accessions from 89 countries to an average sequencing depth of 14× (The 3000 Rice Genomes Project 2014). This and other high-throughput sequencing efforts and related SNP data offer an opportunity to leverage genome-wide association studies to detect and exploit insect resistance genes. The findings of such studies offer ways to better analyze allelic variations and distributions in insect resistance genes within the germplasm, enabling studies of their origins and evolution.

Over the past decade, rapid technological advances have been made in the discovery and analysis of plant and insect genomes, transcriptomes, proteomes, and secretomes. These techniques have provided the impetus to identify putative insect effectors, clone insect resistance genes, and reveal the signaling pathways and key components of plant–insect resistance signals. However, there is still a major gap in our understanding of insect-plant interactions. No effectors corresponding to the *R* gene have yet been identified, although 14 insect resistance genes (encoding LecRK and NLR proteins) have been cloned in rice. Similarly, although three effectors have been identified from Hessian flies, the corresponding *R* genes have not been cloned. The roles of hormone signaling and the corresponding regulatory genes involved in insect resistance in rice have been discovered, and a preliminary regulatory network has been constructed (Fig. 2). However, the roles of insect resistance genes in this network are still unclear. Furthermore, no substances that are lethal to insects have been identified in rice. Studies aimed at addressing these issues will provide a more thorough understanding of how these resistance proteins recognize and mediate effector-triggered signaling and immunity against insects.

Whereas most insect resistance genes characterized to date have arisen through long-term natural or artificial selection and do not appear to adversely affect rice yields, such resistance responses do require energy consumption. When overzealous, these responses can adversely affect crop yields. Recently, two miRNAs were shown to be involved in regulating of BPH resistance in rice (Ge et al. 2018; Dai et al. 2019). However, multifunctional miRNAs could cause an imbalance between insect resistance and crop growth and development. Once we have obtained a more comprehensive understanding of the regulatory mechanisms governing this delicate balance, such knowledge could be used in future research efforts offer to design better ways to cultivate novel varieties of high-quality insect-resistant rice.

Because multiple insect pests are simultaneously present in the field, the indiscriminate use of insecticides for pest management is more practical, economical, and effective than growing insect-specific resistant rice varieties. Therefore, insect resistance breeding must involve the incorporation of broad-spectrum resistance genes to minimize the investment in crop management, making this technique more suitable for meeting the expected return on investment of rice farmers in the future. Now, MAS has already been used to pyramid multiple insect resistance genes to cultivate durable, broad-spectrum insect resistance rice. However, new emerging technologies such as CRISPR/Cas9 gene

editing to convert insect susceptible alleles to insect resistance alleles, as well as altering the levels of specific secondary metabolites in vivo, provide the potential to design crops that can be patched in real time to combat evolving pests. Furthermore, these emerging technologies will be invaluable for uncovering the roles of insect effectors and plant target proteins in the regulation of plant immunity.

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