Molecular Approaches for Insect Pest Management in Rice

Jagadish S. Bentur, R. M. Sundaram, Satendra Kumar Mangrauthia, and Suresh Nair

Abstract This chapter focuses on the progress made in using molecular tools in understanding resistance in rice to insect pests and breeding rice for multiple and durable insect resistance. Currently, molecular markers are being extensively used to tag, map, introgress, and clone plant resistance genes against gall midge, planthoppers, and leafhoppers. Studies on cloned insect resistance genes are leading to a better understanding of plant defense against insect pests under different feeding guilds. While marker-assisted breeding is successfully tackling problems in durable and multiple pest resistance in rice, genomics of plants and insects has identified RNAi-based gene silencing as an alternative approach for conferring insect resistance. The use of these techniques in rice is in the developmental stage, with the main focus on brown planthopper and yellow stem borer. CRISPR-based genome editing techniques for pest control in plants has just begun. Insect susceptibility genes (negative regulators of resistance genes) in plants are apt targets for this approach while gene drive in insect populations, as a tool to study rice-pest interactions, is another concept being tested. Transformation of crop plants with diverse insecticidal genes is a proven technology with potential for commercial success. Despite advances in the development and testing of transgenic rice for insect resistance, no insect-resistant rice cultivar is now being commercially cultivated. An array of molecular tools is being used to study insect-rice interactions at transcriptome, proteome, metabolome, mitogenome, and metagenome levels, especially with reference to BPH and gall midge, and such studies are uncovering new approaches for insect pest management and for understanding population genetics and phylogeography of rice pests. Thus, it is evident that the new knowledge being gained through these studies has provided us with new tools and information for

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J. Ali, S. H. Wani (eds.), *Rice Improvement*,
https://doi.org/10.1007/978-3-030-66530-2_11

facing future challenges. However, what is also evident is that our attempts to manage rice pests cannot be a one-time effort but must be a continuing one.

Keywords Insect resistance · Molecular markers · Marker-assisted breeding · RNAi · Genome editing · Transgenic rice · Insect-plant interaction

1 Introduction

Insect pests of rice form a formidable biotic stress component and a significant production constraint across the globe. Although more than 200 insect species are reported to feed on rice plants, about a dozen of them are economically important in a specific rice ecosystem at a given time. Several of these have coevolved over thousands of years along with their host and many have no alternate host. The pest complex of rice is represented by insects from all the feeding guilds, from defoliators, tissue borers, and sap-suckers to gall formers, and several of these are occupied by a complex of species (Heinrichs 1994). Most important among these are stem borers: yellow stem borer (YSB), *Scirpophaga incertulas*; striped stem borer (SSB), *Chilo suppressalis*; and pink stem borer (PSB), *Sesamia inferens*; planthoppers: brown planthopper (BPH), *Nilaparvata lugens*; white-backed planthopper (WBPH), *Sogatella furcifera*; and small brown planthopper (SBPH), *Laodelphax striatellus*; leafhoppers: green leafhopper (GLH), *Nephottetix virescens*; green rice leafhopper (GRL/GRH), *Nephotettix cincticeps*; and zigzag leafhopper (ZLH), *Recilia dorsalis*; gall midges: Asian rice gall midge (ARGM), *Orseolia oryzae*; and African rice gall midge (AfRGM), *Orseolia oryzivora*; and leaffolders: *Cnaphalocrocis medinalis* and *Marasmia* spp. Several other insects such as rice hispa, grain bugs, aphids, mealy bug, and stem fly are of minor or regional importance (Bentur 2010).

Several studies reported yield losses due to either a single pest or a complex of pests but most of them end up with either overestimating or underestimating the damage caused by these pests. Savary et al. (2000) critically studied yield losses caused by different pests under varying production environments and suggested that stem borer damage at heading stage accounted for 2.3% loss. They also noted that yield attrition from chronic injuries by stem borer deadheart damage and defoliation is underestimated. Although this study represented the macro-level scenario, micro-level yield losses due to any single or combination of insect pests can be high and deserves to be mitigated. Deutsch et al. (2018) predict future increases in yield loss in rice because of insect pests under the scenario of global warming.

Past experience has clearly shown that any unilateral approach based on chemical control, plant resistance, biocontrol, or behavioral means with pheromones has not provided desirable and sustainable solutions to pest problems. However, an early lead in exploring host-plant resistance taken by the International Rice Research Institute and emulated by various national programs paved the way for breeding for insect resistance with exemplary success against pests such as striped stem borer,

gall midge, and planthoppers. But the first wave of success was countered by the rapid evolution of virulent biotypes. With the recent advances in molecular biology and biotechnology, researchers now have a new set of tools with which they can address several problems at the molecular level and identify new strategies to overcome old problems. In this chapter, we examine progress made through the classical approach and how the limitations of classical approach-based insect resistance and breeding for multiple and durable insect resistance in rice are being overcome with molecular marker-based approaches. In addition, we attempt to present the future scenario of genomics-based tools that may provide novel strategies of pest management.

2 Classical Approach Through Host-Plant Resistance Gene Deployment

Following the seminal publication of R.H. Painter (1951), genetic resistance in the host plant has been extensively explored and plant resistance (R) genes have been transferred to elite cultivars of field crops and other economically important plant species. Classical breeding methods and phenotypic selections were followed to achieve this until molecular markers were discovered. Currently, desired R-genes can be transferred and pyramided through marker-assisted selection and breeding. The status of donor sources, genetics of resistance, tagging and mapping of R-genes, and reported gene-linked markers are provided in what follows for the major insect pests of rice.

2.1 Gall Midge

Asian rice gall midge (ARGM) is a serious pest of rice in South and Southeast Asia. In India, gall midge damage is estimated to cause an annual yield loss of about USD 80 million (Bentur et al. 2003). The insect displays a unique life cycle, which is completed in 3–4 weeks. Maggots hatched from eggs laid on the plant surface crawl down between leaf sheaths to reach the apical meristem to feed. The insect feeds by laceration of the apical meristem and secretion of saliva, resulting in hypertrophy and hyperplasia of cells, ultimately leading to the development of a nutritive tissue and a gall chamber in the tiller. The insect also renders the tiller sterile and arrests further differentiation. Maggots cease feeding in the third instar and pupate in the gall. The adult fly emerges from this modified sheath gall called “silver shoot,” which is a typical symptom of gall midge damage. ARGM is predominantly a vegetative-stage pest and, in the event of a high percentage of tillers being converted into galls, there will be a proportionate decrease in the number of productive tillers, panicles, and therefore grain yield.

Rice varieties differ in their response to gall midge infestation. A small proportion of varieties is immune to pest attack by effectively killing the maggot within hours of feeding. The resistance mechanism displayed by the varieties is categorized into two distinct types. A majority of the resistant rice genotypes express a hypersensitive reaction (HR), leading to tissue necrosis at the site of maggot feeding, and are referred to as HR +ve (HR+) types, whereas a few of the resistant genotypes do not display HR but still maggot mortality is noticed, and these are termed HR −ve (HR−) types. The role of phenols in HR+ resistance has been reported (Amudhan et al. 1999). Because the nature of resistance is antibiosis in both HR+ and HR− types, host-plant resistance is the most effective way of managing the pest (Bentur et al. 2003).

Field and greenhouse evaluations of more than 50,000 germplasm accessions resulted in the identification of more than 300 primary sources of resistance (Bentur et al. 2011). Studies on the genetics of gall midge resistance in rice have often shown the involvement of a single dominant or recessive gene. To date, 12 genes conferring resistance against the pest have been reported (Himabindu et al. 2010; Leelagud et al. 2020), 10 of which are dominant (*Gm1* through *Gm11*, except *gm3 and gm12*). The presence of gall midge biotypes within India was suspected during the early phase of breeding for resistance. So far, seven distinct biotypes have been characterized based on their reaction pattern against five groups of differential rice varieties (Vijayalakshmi et al. 2006). Similar to the interaction between pathogens and their plant hosts, a gene-for-gene interaction has been reported between rice resistance genes (i.e., R genes) and gall midge biotypes (Nair et al. 2011). Each of the biotypes displays a specific range of virulence against R-genes, and likewise each R-gene confers resistance to specific biotypes, which also implies that none of the R-genes conferred resistance to all biotypes and none of the biotypes showed virulence against all of the R-genes. Hence, it is possible to extend the range of resistance against biotypes by combining diverse resistance genes through gene pyramiding.

Of the 12 gall midge resistance genes identified thus far, 10 (*Gm1*, *Gm2*, *gm3*, *Gm4*, *Gm5*, *Gm6*, *Gm7*, *Gm8*, *Gm11*, and *gm12*) have been tagged and mapped with reported linked markers (Table 1). As it is well known that single gene-conferred resistance against gall midge can break down within a short time, the strategy of pyramiding two or more genes with divergent mechanisms of resistance (i.e., HR+ and HR−) has been advocated for durable resistance against the insect pest (Sundaram et al. 2013). So far, three gall midge resistance genes, *gm3* (Sama et al. 2014), *Gm4* (Divya et al. 2015), and *Gm8* (Divya et al. 2018b), have been cloned and characterized, and another gene, *Gm2*, has been reported to be allelic to *gm3* (Sama et al. 2014; Sundaram 2007). The recessive resistance gene, *gm3*, which displays HR+, encodes an NB-ARC (NBS-LRR) domain-containing protein, while the dominant gene, *Gm4*, which also displays HR+, encodes a leucine-rich repeat (LRR) protein, and *Gm8*, displaying HR−, encodes a proline-rich protein (PRP). It is desirable to deploy two or more previously undeployed genes that differ in their mechanism of resistance, for example, *Gm4* (HR+) and *Gm8* (HR−) genes would meet the above-specified requirements. Another gene, *gm3*, may also be considered

Table 1 List of rice resistance genes against major insects tagged and mapped along with information on linked markers

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
Brown planthopper						
Bph 1	12L	BpE18-3 STS	?	CGCTGCGAGAGTGTGACACT	TTGGGTTACACGGGTTTGAC	Kim and Sohn (2005)
Bph 1	12L	pBPH9F	22,858,861	AGCGCTGGTCGTTGGGGTTGTAGT	ATTAAAAGTGATCGCAGCCGTTCG	Cha et al. (2008)
bph2	12L	KAM4STS	?	TAACTGGTGTTAGTGCGAATGC	AATTCACGGCATGTGAAGCCCTAG	Murai et al. (2001)
bph2	12L	RM7102	13,213,987	GGGCGTTCGGTTTACTTGGTTACTCG	GGCGGCATAGGAGTGTTTAGAGTGC	Sun et al. (2006)
bph2	12L	RM463	22,125,420	GAGGATTAATTAGCGTGTGACC	GTCGTGACATCTACTCAAATGG	Sun et al. (2006)
BPh3	6S	RM190	1,765,637	CTTTGTCTATCTCAAGACAC	TTGCAGATGTTCTTCCTGATG	Jairin et al. (2007a)
BPh3	6S	RM589	1,381,875	GTGGCTTAACCACATGAGAAACTACC	TCACATCATTAGGTGGCAATCG	Jairin et al. (2007a)
BPh3	6S	RM588	1,612,412	TCTTGCTGTGCTGTTAGTGTACG	GCAGGACATAAATACTAGGCATGG	Jairin et al. (2007a)
BPh3	6S	RM19291	1,216,883	CACTTGCACGTGTCCTCTGTACG	GTGTTTCAGTTCACCTTGCATCG	Jairin et al. (2007b)
BPh3	6S	RM8072	1,409,335	GATCACTCAGGTCATCCATTC	AATCAGAGAGGCTAAAGACAATAAT	Jairin et al. (2007b)
bph4	6S	RM586	1,477,792	TGCCATCTCATAAACCCACTAACC	CTGAGATACGCCAACGAGATACC	Jairin et al. (2010)
bph4	6S	RM589	1,381,875	GTGGCTTAACCACATGAGAAACTACC	TCACATCATTAGGTGGCAATCG	Jairin et al. (2010)

(continued)

Table 1 (continued)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
bph4	6S	RM217	?	ATCGCAGCAATGCCTCGT	GGGTGTGAACAAAGACAC	Kawaguchi et al. (2001)
bph4	6S	RM225	3,417,595	TGCCCATATGGTCTGGATG	GAAAGTGGATCAGGAAGGC	Kawaguchi et al. (2001)
Bph6	4L	RM6997	21,272,870	CGGCAGTAAATTTGCATTGACC	AGTGGCCTTGTCAGTCTACATGC	Qiu et al. (2010)
Bph6	4L	RM5742	21,559,553	GATCCTCAAACGGCCTCTGC	CCTTCAAAGTTTACTCACGCTCTGC	Qiu et al. (2010)
Bph9	12L	RM463	22,125,420	GAGGATTAATTAGCGTGTGACC	GTCGTGACATCTACTCAAATGG	Su et al. (2006)
Bph9	12L	RM5341	19,114,746	CATCCGGAGGAAGTTTGAAAGAAGG	CAAGGGCAACCTCTTCCACTACGC	Su et al. (2006)
Bph10[a]	12L	RG457FL/RB STS marker		?	?	Lang and Buu (2003)
Bph10[a]	12L	RG457FL/RL STS marker		?	?	Lang and Buu (2003)
Bph12[a]	4L	RM16459	5,213,984	TCCAGGAGTTTGCCTTGTAGTGC	TAGCGAAGTCAGGATGGCATAGG	Qiu et al. (2012)
Bph12[a]	4L	RM1305	5,659,601	GGTACTACAAAGAAACCTGCATCG	TCCTAGCTCAAATGTGCTATCTGG	Qiu et al. (2012)
Bph13[a]	2L	RM240	31,497,147	CCTTAATGGGTAGTGTGCAC	TGTAACCATTCCTTCCATCC	Liu et al. (2001)
Bph13[a]	2L	RM250	32,774,365	GGTTCAAACCAAGCTGATCA	GATGAAGGCCTTCCACGCAG	Liu et al. (2001)
BPh13[a]	2L	AJ09b StS from RAPD		?	?	Renganayaki et al. (2002)
Bph14[a]	3L	SM1	38,751,114	AGCGTTAAGCGCCATTATCA	CGCCGAGGCATTAGAGTAGA	Du et al. (2009)

Table 1 (continued)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
Bph14[b]	3L	NBS-LRR		AAATTCGTGGTTGTTCTGGT	TCGGTAACGATCCATGATGA	Du et al. (2009)
Bph15[a]	4S	MS1 reported earlier by C820 and S11182 RFLP marker	9,278,808	CATGGACCCACTTGTCATCC	AGCATGAGAGACTGCCAAGG	Yang et al. (2004)
Bph15[a]	4S	RM261 reported earlier by C820 and S11182 RFLP marker	6,578,953	CTACTTCTCCCCTTGTGTCG	TGTACCATCGCCAAATCTCC	Yang et al. (2004)
Bph16[a]	12L	RM6732	21,983,109	AATTTTGAACACCTCAAAGG	TTTTCAGTGCATGTCTTCG	Hirabayashi et al. (2004)
Bph17	4S	RM8213	4,446,064	TGTTGGGTGGGTAAAGTAGATGC	CCCAGTGATACAAAGATGAGTTGG	Sun et al. (2005)
Bph17	4S	RM5953	9,379,510	AAACTTTCTGTGATGGTATC	ATCCTTGTCTAGAATTGACA	Sun et al. (2005)
Bph17[b]	4S	LRK2	6,953,940	CTTTCGCAGGGTGGCAAATAGGGT	CCTTCGCTGCTCACTAGGACCGTGTA	Liu et al. (2015)
Bph18[a]	12L	RM463	22,125,420	GAGGATTAATTAGCGTGTGACC	GTCGTGACATCTACTCAAATGG	Jena et al. (2006)
Bph18[a]	12L	S15552 STS marker cleaved by alu1 enzyme		?	?	Jena et al. (2006)
Bph18[a]	12L	RM511	17,401,530	AACGAAAGCGAAGCTGTCTCC	ATTTGTTCCCTTCCTTCGATCC	Suh et al. (2011)

(continued)

Table 1 (continued)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
Bph18[a]	12L	RM1584	27,104,354	TAGCCTGCAGCCACCCTGATCC	CAATGTGACTTCCGTGCGTAGTGG	Suh et al. (2011)
bph19	3S	RM6308	7,181,156	TCTCGACCTGGCTCTCCTCTAGC	AGTGCACGGACATGTCACTCTCG	Chen et al. (2006)
bph19	3S	RM3134	7,240,409	GCAGGCACAAAAGCAAAGAG	AGGTGAAGGTGCATTGTGTG	Chen et al. (2006)
Bph20[a]	4S	MS10 STS marker	8,071,921	CAATACGAGAAGCCCCTCAC	CTGAAGGAACACGCGGTAGT	Rahman et al. (2009)
Bph20[a]	4S	RM5953	9,379,510	AAACTTTCTGTGATGGTATC	ATCCTTGTCTAGAATTGACA	Rahman et al. (2009)
bph20[a]	4S	RM435 BYL7 closest marker	535,684	AAGCTAGGGAATCAGCGGTTA BYL	TGTGGCATGTCACTCACTCAC	Yang et al. (2012)
bph20[a]	4S	RM540 BYL8 closest marker	468,236	CCCACTTCCACAACCACA BYL8	ATGCTCCTAGCTTCCTATTCC	Yang et al. (2012)
Bph21[a]	12L	RM3726	23,275,187	TACACCCACCCACATACGTCAGC	GTCGTACTCCCGGATCTTCTTCC	Rahman et al. (2009)
Bph21[a]	12L	RM5479	24,412,536	CTCACCATAGCAATCTCCTGTGC	ACTTCGTTCACTTGCATCATGG	Rahman et al. (2009)
bph21	10S	RM222	2,620,380	CTTAAATGGGCCACATGCG	CAAAGCTTCCGGCCAAAAG	Yang et al. (2012)
bph21	10S	RM244		CCGACTGTTCGTCCTTATCA	CTGCTCTCGGGTGAACGT	Yang et al. (2012)
bph22	4	RM8212	99,416	CCACCGCACTTGTCTATG	TCCAATCTCACTCTCGACTC	Hou et al. (2011)

Table 1 (continued)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
bph22	4	RM261	6,574,396	CTACTTCTCCCCTTGTGTCG	TGTACCATCGCCAAATCTCC	Hou et al. (2011)
Bph22[a]	6	RM19429Rm584	3,417,532	TATGTGGTTGGCTTGCCTAGTGG	TGCCCATATGGTCTGGATGTGC	Harini et al. (2010)
Bph22[a]	6	RM584	3,417,532	TATGTGGTTGGCTTGCCTAGTGG	TGCCCATATGGTCTGGATGTGC	Harini et al. (2010)
Bph22[a]	6	RM585	3,169,373	CTAGCTAGCCATGCTCTCGTACC	CTGTGACTGACTTGGTCATAGGG	Harini et al. (2010)
bph23[a]	8	RM2655	2,017,692	TGTCTGTGTTGTCACTGCCTTATCG	TCCGCTCTGTGTGTATCTGATCTGG	Hou et al. (2011)
bph23[a]	8	RM3572	3,928,306	CCATTTGGTAGGTCCATCTTACCC	CTCCCAAGTGAAGTGCTGTCTGG	Hou et al. (2011)
Bph25	6S	S00310	214,278	CAACAAGATGGACGGCAAGG	TTGGAAGAAAAGGCAGGCAC	Myint et al. (2012)
Bph25	6S	RM8101	1,705,742	CACTGACATAGCTAAGGTCTCATGTCTTAT	TGGTTAACTCGCTATTATAATGAGTTCG	Myint et al. (2012)
Bph26	12L	RM5479	24,409,241	CTAAGCTCACCATAGCAATC	ATACACTTCTCCCCTCTCTG	Myint et al. (2012)
Bph26	12L	MSSR2	25,033,993	CATGTCGAAGAGGTTGCAGA	GGTTTCATCCAAGTCCACGA	Myint et al. (2012)
Bph26[b]	12L	LRR	22,884,874	TAGCATCAGTCCCTTGCTTGTTTGC	ATTGATTTAATTAGCAGACAAGTTG	Tamura et al. (2014)
Bph27[a]	4	RM16853	19,201,791	CTCCCATCCTTCATTTCATCTCG	CTTTCTGCAAGACACTGCAAACG	Huang et al. (2013)
Bph27[a]	4	RM16846	19,115,583	CTACAAGCAACACAGTATCACAGC	GGTAACTGGTGCTTATTTAGCC	Huang et al. (2013)

(continued)

Table 1 (continued)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
Bph28	11	RM26656	15,738,361	GCAAAGAACATTGTGGCAAACACC	TGGACACATTGTATCGTGCTTCG	Wu et al. (2014)
BPh28	11	RM26725	17,114,046	ATGTAGGCCCAAACGAGCTCTGACC	ATGCCATAGTAGCGCTTGCGTATCC	Wu et al. (2014)
bph29[a]	6	RM435 BYL7 closest marker	535,684	AAGCTAGGGAATCAGCGGTTA BYL	TGTGGCATGTCACTCACTCAC	Wang et al. (2008)
bph29[a]	6	RM540 BYL8 closest marker	468,236	CCCACTTCCACAACCACA BYL8	ATGCTCCTAGCTTCCTATTCC	Wang et al. (2008)
bph29[b]	6	G5 B3 domain	484,709	ATGGCCACCATTGTTGCATG	TCAAAGCTGCAAATCCAGCG	Wang et al. (2015)
bph30[a]	10	RM222	2,620,380	CTTAAATGGGCCACATGCG	CAAAGCTTCCGGCCAAAAG	Wang et al. (2008)
bph30[a]	10	RM244		CCGACTGTTCGTCCTTATCA	CTGCTCTCGGGTGAACGT	Wang et al. (2008)
BPH31	3	PA26		?	?	Prahalada et al. (2017)
BPH31	3	RM2334	26,740,452	CATGCATCTGATCTGATTAT	TGTGAAGAGTACAAGTAGGG	Prahalada et al. (2017)
Bph32	6	RM19291	1,215,884	CACTTGCACGTGTCCTCTGTACG	GTGTTTCAGTTCACCTTGCATCG	Ren et al. (2016)
Bph32	6	RM8072	1,408,336	GATCACTCAGGTCATCCATTC	AATCAGAGAGGCTAAAGACAATAAT	Ren et al. (2016)
Bph32[b]	6	SCP	1,099,689	TGAGGGAGTTGTAGTAGGAGTA	CGTCGTTGATGAAGTAAAGGT	Ren et al. (2016)
Bph33	1	RM11522	28,071,767	TAACTGCAGTGCTCAACAAAGG	CTAGGTACCGGATTAAGATTCACC	Naik et al. (2018)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
Bph33	1	RM488	24,808,556	AACAACCAGCGTATGCGTTCTCG	CCCACGGCTTTGTAGGAAGAAGC	Naik et al. (2018)
Bph34[a]	4	RM16994	21,331,444	TGGCAGTACACACTACAGTACATGC	AGAGGGAGGAGAGAAAGGAAGG	Kumar et al. (2018)
Bph34[a]	4	RM17007	21,484,908	CTTCCCACGCGAAACTTCATGG	TCCGGCCAAGACAATATCAACG	Kumar et al. (2018)
White-backed planthopper						
Wbph7	3L	R1925		?	?	Tan et al. (2004)
Wbph7	3L	G1318		?	?	Tan et al. (2004)
Wbph8	4S	R288		?	?	Tan et al. (2004)
Wbph8	4S	S11182		?	?	Tan et al. (2004)
Wbph9t	6	RM589	1,380,866	ATCATGGTCGGTGGCTTAAC	CAGGTTCCAACCAGACACTG	Ramesh et al. (2014)
Wbph9t	6	RM539		GAGCGTCCTTGTTAAAACCG	AGTAGGGTATCACGCATCCG	Ramesh et al. (2014)
Wbph10t	12	SSR12-17.2				Ramesh et al. (2014)
Wbph10t	12	RM28487	23,142,514	GAGGTGATCTTAATGCCATCTTGACG	TACATGCAACCTGGGTATGAGAGTGC	Ramesh et al. (2014)
Wbph11t	4	RM3643	19,948,112	AGCATGAGCAGGTGCTAGTG	CGTTGCATGTGTGATGGC	Ramesh et al. (2014)
Wbph11t	4	RM1223	25,292,767	CAGCGTCTCCAAGAAACTCC	GCTACCAGGTCAGAGTTGCC	Ramesh et al. (2014)

(continued)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
Wbph 12t	4	RM16913	19,646,468	GTGTACGTGTTGGCTCTCTGTACG	GATGTTGCTTGTGCTGCAACC	Ramesh et al. (2014)
Wbph 12t	4	RM471	19,426,246	CGGATCCAAGAAACAGCAG	TTCGGTATCCTCCACACCTC	Ramesh et al. (2014)
Ovc	6S	S1520		?	?	Yamasaki et al. (2003)
Ovc	6S	L688		?	?	Yamasaki et al. (2003)
Green rice leafhopper						
Grh1	5	C309		?	?	Tamura et al. (1999)
Grh1	5	R569		?	?	Kadowaki et al. (2003)
Grh2	11L	G144		?	?	Fukuta et al. (1998)
Grh2	11L	G4001		?	?	Kadowaki et al. (2003)
Grh2	11L	G1465		?	?	Kadowaki et al. (2003)
Grh3	6	C288B		?	?	Saka et al. (2006)
Grh3	6	C133A		?	?	Saka et al. (2006)
Grh4	3L	G1465		?	?	Fukuta et al. (1998)
Grh4	3L	C1186		?	?	Kadowaki et al. (2003)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
Grh4	3L	R2982		?	?	Kadowaki et al. (2003)
Grh5	8L	RM502	26,492,117	GCGATCGATGGCTACGAC	ACAACCCAACAAGAAGGACG	Fujita et al. (2006)
Grh5	8L	RM6845	27,560,145	GTGACGGCAAGAGGAAGAAG	GTTCGACAGGAACGCCAC	Fujita et al. (2006)
Grh6	4S	Y3635R		?	??	Tamura et al. (2004)
Grh6	4S	C708		?		Tamura et al. (2004)
Grh6	4S	RM8213	4,441,638	AGCCCAGTGATACAAAGATG	GCGAGGAGATACCAAGAAAG	Fujita et al. (2004)
Grh6	4S	G6-9				Fujita et al. (2004)
QGRH9	9L	RM201	20,174,289	CTCGTTTATTACCTACAGTACC	CTACCTCCTTTCTAGACCGATA	Fujita et al. (2010)
QGRH9	9L	RM205	22,720,624	CTGGTTCTGTATGGGAGCAG	CTGGCCCTTCACGTTTCAGTG	Fujita et al. (2010)
Gall midge						
Gm1	9	RM23941	7,818,607	AGAATCGAACCCTAACACATGC	TATCGCTTGATTCTTGGACAGC	Sundaram (2007)
Gm1	9	RM23956	7,992,661	GTCTCTCCCTCTCTCATCTTGTCG	CCCTATTCATGTGCAATGGAACC	Sundaram (2007)
Gm2	4	RM17473	30,838,175	TCTCTCCAGCTCCCTAAACATTCC	AGCGACACACTGTTCACCTTGC	Sundaram (2007)
Gm2	4	RM17503	31,717,625	CCAGATCATCCAGGCATAACATCACC	CGGCGCTGGTAAACTCCATTCC	Sundaram (2007)

(continued)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
gm3	4	RM17480	31,146,877	GAGTTCGTCCCTGACAAACAGAAACG	GTGAGCGAGCGAGTGAGTGAGC	Sama et al. (2014)
gm3	4	gm3SSR4	32,075,106	AGACACGAGGGAATTATGC	CTCTATATTTGCCGCATCC	Sama et al. (2014)
gm3^{b}	4	NB-ARC	31,950,000	CTGCCAGAGATGGGCCTTCCA	CGTACAAATTCCTGTACCACTC	Sama et al. (2014)
Gm4	8	RM22551	5,451,661	CTTCGATCTCCTCGTCCTCTTCC	GAGCATGAGATGATGCATGACG	Divya et al. (2015)
Gm4	8	RM22562	5,782,732	GATCGGAGGAGGGAGGAAGACG	GTCGCATCCACTCATATTCCAAGC	Divya et al. (2015)
Gm4^{b}	8	LRR-del	5,583,333	GTGGATCGAGAGAAGACAAG	CTTGAGGACGATATTCAAGC	Divya et al. (2015)
Gm5	12	OPB14		?	?	see Bentur et al. (2003)
Gm6	4	OPM061400		?	?	Katiyar et al. (2001)
Gm6	4	RG214		?	?	Katiyar et al. (2001)
Gm6	4	RG476		?	?	Katiyar et al. (2001)
Gm7	4	SA598		?	?	Sardesai et al. (2002)
Gm7	4	F8		?	?	Sardesai et al. (2002)
Gm8	8	RM22685	8,800,203	ATGGGCTTCCAGGCTCAATCTCG	CCCACTCTCACGTCTCCTCTCTTCC	Sama et al. (2012)
Gm8	8	RM22709	9,226,565	CGCGTGGGCGAGACTAATCG	CCTTGACTCCGAGGATTCATTGTCC	Sama et al. (2012)

Gene	Chromosome no.	Primer name	Primer physical position (bp)	F primer	R primer	Reference
Gm8[b]	8	PRP-Del	9,127,586	TATAAAGAGGACGGTCTAACCTTTA	GCACAGGGAAGTTGTCAGTTCAAGTA	Divya et al. (2018a)
Gm11	12	RM28574	24,292,314	TAGTTTGGTGAAGTGGCATTGG	ATAGTAGGGCAAGGATTCAGAAGAGG	Himabindu et al. (2010)
Gm11	12	RM28706	25,992,979	GGTTCCCGGTCATCATATTTCC	ACTTTACCCACGCGCTTTGC	Himabindu et al. (2010)
gm12	2	RM3340	386,212	GAGAGAGACACCAAATGATCCATCC	ACTGATTTGGCCCTTGTTCTTGG	Leelagud et al. 2020
gm12	2	S2-76222	76,222	CACACATACCCACCCACTAGTGAAGATGAA[C/T]TGAATGCCAATGGGAGAAGAGGAGAGCAGA		Leelagud et al. 2020

? = sequence information not available in the publication cited
F primer and R primer = forward and reverse primers, respectively
[a]Gene has been introgressed from wild species
[b]Cloned gene

for pyramiding since it is a HR+ type and recessively inherited and has not been deployed so far in any variety.

Using *Gm4* and *Gm8*, the research group at ICAR-IIRR (Abhilash Kumar et al. 2017) has developed gene-pyramided lines in the genetic background of the elite restorer line RPHR1005R (restorer line for the popular rice hybrid DRRH3) through marker-assisted breeding. In another such effort, the high-yielding rice variety Akshayadhan has been improved for its resistance against gall midge by targeted transfer of *Gm4* and *Gm8* genes. Sama et al. (2014) introduced the recessive gene *gm3* into the genetic background of elite rice variety Improved Samba Mahsuri with the help of markers. In a recent report (Venkanna et al. 2018), two major resistance genes, *gm3* and *Gm8*, have been pyramided in the genetic background of the fine-grain-type rice variety Kavya, which already possesses *Gm1*. Now that closely linked markers/functional markers are available for all the major gall midge resistance genes, selected gene combinations can be pyramided into elite genetic backgrounds (Divya et al. 2018c) easily through marker-assisted breeding for developing durable multiARGM biotype-resistant rice cultivars/hybrids.

2.2 Planthoppers and Leafhoppers

Although more than 100 species of planthoppers (Delphacidae) and leafhoppers (Cicadellidae) are reported to feed on rice, three species of planthoppers (BPH, WBPH, and SBPH) have gained high economic importance since 2000 (Bentur and Viratkamath 2008). Likewise, of the leafhoppers, GLH, GRL, and ZLH are important. Although both groups consist of phloem sap feeders, planthoppers cause severe damage by feeding alone, leading to total death of plants, termed hopper burn. Both leafhoppers and planthoppers vector disease-causing viruses and cause indirect damage to the crop. The main virus diseases thus transmitted are rice ragged stunt, rice grassy stunt, and wilted stunt by BPH; southern rice black-streaked dwarf by WBPH; stripe and black-streaked dwarf by SBPH; and rice tungro by several species of leafhoppers. In response to planthoppers and leafhoppers gaining importance, screening of rice germplasm for resistance began at the International Rice Research Institute (IRRI), Philippines, during the 1970s. Such initiatives were also taken up in other Asian rice-growing countries, leading to reports of a large number of resistance sources (IRRI 1979; Heinrichs et al. 1985; Heong and Hardy 2010). Several of these sources were selected for systematic studies on genetics of resistance, resulting in the identification of more than 38 major resistance genes against BPH, 14 against WBPH, 14 against GLH, six against GRL, and three against ZLH (Fujita et al. 2013; Ling and Weillin 2016; Du et al. 2020). Most of these genes are now tagged and mapped on different rice chromosomes and reliable molecular markers linked to these traits are available (Table 1). Marker-assisted selection as a tool for breeding for BPH resistance using a single gene or multiple genes is being

reported (Liu et al. 2016; H Wang et al. 2016a; Y Wang et al. 2017b; Jiang et al. 2018). However, a few issues remain to be resolved. Several of the reported BPH Rgenes are not effective on the Indian subcontinent (Horgan et al. 2016); hence, more effective genes for the region need to be characterized from the reported sources. All the BPH Rgenes, except probably *Bph3* (Liu et al. 2015), are not effective against WBPH. Since these two species are sympatric and are often under severe interspecific competition (Srinivasan et al. 2016), selecting for resistance against BPH alone may not be the right approach. But, efforts to tag, map, and clone WBPH resistance genes are few. Another limitation is the ability of BPH to quickly evolve virulent biotypes, especially if a single Rgene is deployed. Hence, gene pyramiding is suggested for durability. Ideally, undeployed genes with different mechanisms of resistance are the choice for pyramiding. Of the 13 BPH Rgenes cloned, eight (*Bph14*, *Bph26*, *Bph18*, *Bph9/1*/7/10/21) represent the NBS-LRR family; proteins coded by these are located in the cytoplasm, while others are reported as lectin receptor kinases (*Bph3*, *Bph15*), B3 DNA-binding domain (*bph29*), or SCR domain protein (*Bph32*) coding (Ren et al. 2016; Y Zhao et al. 2016b; Du et al. 2020), which are membrane bound. It is suggested to combine two genes from these two classes (such as *Bph14* + *Bph15*) to achieve durability (Jing et al. 2017).

2.3 Other Pests

Rice stem borers are ubiquitous insects representing Diopsidae (Diptera), Noctuidae, and Crambidae (Lepidoptera) families. Among several species of rice stem borers, YSB is considered the most economically important insect pest in almost all rice-growing countries of Asia (Makkar and Bentur 2017). Larvae of YSB feed only on rice and can cause damage at both the vegetative (deadheart) and reproductive (whitehead) stages of the rice crop, with the latter being the main cause of yield loss (Savary et al. 2000). Because of the lack of highly resistant sources in rice germplasm explored so for, breeding for resistance or molecular mapping of resistance genes against YSB has not been encouraging (Bentur 2007). Nonetheless, rice varieties such as Vikas, Ratna, and Sasyasree have been developed and released in India with moderate YSB resistance. Most of these varieties have either TKM6 or W1263 as the source of resistance. Because of the lack of the desired level of resistance against YSB in the primary gene pool of rice, the secondary gene pool consisting of wild species of *Oryza* is being explored at IRRI, ICAR-IIRR, and other institutes. Chromosome segment substitution lines (CSSLs) need to be developed for different accessions of wild rice that can be evaluated for YSB resistance. Also, ethyl methanesulfonate (EMS) mutants of rice have been generated and evaluated at ICAR-IIRR and have shown encouraging results in preliminary evaluations. More extensive and concerted efforts in this direction have potential to identify novel sources of resistance that can be used by breeders and entomologists for understanding the resistance mechanisms and developing YSB-resistant rice cultivars.

3 Novel Approaches Through Genomics

3.1 RNAi Approach for Insect Resistance

Transgenic crops harboring *Bt* endotoxin genes or other insecticidal protein-coding genes have shown tremendous potential for managing insect pests. Several of these genes have been used in transforming rice as described in the next section, although none of these have been commercially cultivated. As an alternative to this approach, RNA interference (RNAi) can be exploited, which has been well demonstrated for resistance induction in plants against viruses, bacteria, and nematodes. RNAi is an RNA-driven post-transcriptional homology-based gene-silencing mechanism through the mRNA degradation pathway present in all eukaryotic organisms. The RNAi is triggered by double-stranded RNAs (dsRNA), which are processed by the RNase-III-like Dicer protein to produce small interfering RNAs (siRNAs). The guide strand of siRNA directs an RNA-induced silencing complex (RISC) to the target mRNA (Fig. 1). The most important constituent of RISC is RNase protein Argonaute, which helps in the degradation of target mRNAs sharing homology with the guide strand of siRNA (Zamore et al. 2000). The double-stranded RNAs specific to key insect genes can be stably expressed in plant tissues fed on by the insect and that in turn can trigger the RNAi pathway to degrade the mRNAs transcribed by the key insect genes (Price and Gatehouse 2008; Agarwal et al. 2012).

Key genes in insects are identified as targets of RNAi, that is, genes coding developmental proteins, digestive enzymes, salivary gland proteins, nervous system regulatory proteins, proteins involved in host-insect interaction, hormone receptors, gut enzymes, and proteins involved in metabolism (Gatehouse 2008; Huvenne and Smagghe 2010; Agarwal et al. 2012; Kola et al. 2015).

Initial successes in experiments (Tomoyasu and Denell 2004; Turner et al. 2006) raised hope among researchers that RNAi could be another alternative and effective tool to develop insect resistance in crop plants. Initially, dsRNAs were delivered to the target insects either by injection or through artificial diet. Baum et al. (2007) demonstrated the effectiveness of host-plant-mediated production of dsRNA in crop protection. Transgenic maize plants producing insect-specific vacuolar H^+ ATPase dsRNAs had decreased root damage by western corn rootworm. In another similar report, Mao et al. (2007) generated transgenic *Nicotiana tabacum* and *Arabidopsis thaliana* targeting RNAi against the cytochrome P450 gene of *Helicoverpa armigera*, resulting in retarded larval growth of insects feeding on these modified hosts. The versatility of the application of RNAi against different insect orders and target genes shows the potential of RNAi for managing diverse crop pests (Terenius et al. 2011; Khajuria et al. 2015; Zhang et al. 2017). Recent reports suggest that the production of dsRNAs in chloroplasts, rather than in cytoplasm, can improve insect resistance significantly as long as dsRNAs can be stably produced in chloroplasts, which are devoid of RNAi machinery (Zhang et al. 2015; Jin et al. 2015; Bally et al. 2018). The first such RNAi-based DvSnf7 dsRNA-expressing maize crop targeting western corn rootworm is scheduled to be commercialized (Khajuria et al. 2018). Several research groups have been working on modifying the technology for its more efficient application.

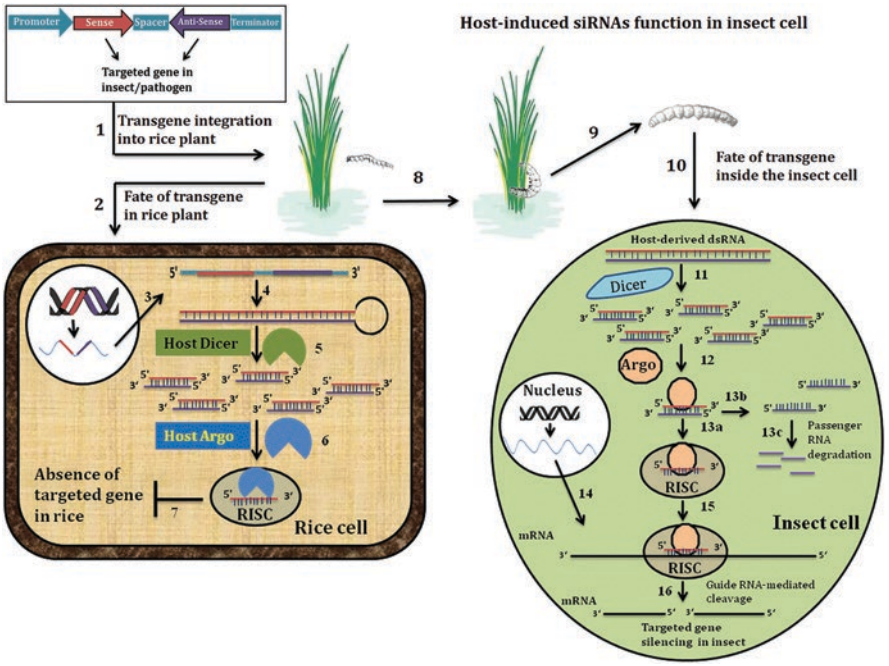

Fig. 1 Schematic representation of host-induced gene silencing in insects through siRNA approach. (**1**) Integration of insect gene-targeted siRNA cassette (transgene) into rice genome; (**2**) fate of transgene in rice cells; (**3**) expression of transgene in rice cell generates the mRNA; (**4**) formations of dsRNA through self-complementation of transgene's sense and antisense strands in rice cell; (**5**) host Dicer-mediated specific cleavage of dsRNA leads to production of siRNAs in rice cell; (**6**) host-generated siRNAs processed by host Argonaute protein (the main component of RNA-induced silencing complex or RISC); (**7**) host-generated siRNAs are nonfunctional in rice cells due to absence of targeted gene; (**8** and **9**) host-synthesized dsRNAs/siRNAs transfer from rice plant to insect through feeding on rice tissues; (**10**) fate of transferred dsRNA/siRNAs in insect cells; (**11**) generation of siRNAs from dsRNA through insect Dicer-mediated cleavage; (**12**) the siRNAs are processed by insect Argonaute proteins/RISC complex; (**13a**) formation of activated RISC along with target-specific guide RNA; (**13b** and **13c**) the passenger RNA is separated from guide RNA and degraded; (**14**) transcription of insect DNA resulted in the expression of targeted functional mRNA (transcript); (**15**) guide strand of siRNA helps in identification and binding of activated RISC to the targeted mRNA; (**16**) silencing of targeted gene expression by RISC-mediated cleavage of corresponding mRNA

Application of the RNAi tool for insect resistance in rice is in the developmental phase. Most of the reports on RNAi in rice are centered on BPH (Zha et al. 2011; Zhou et al. 2013; Yu et al. 2014; Wang et al. 2018) and YSB (Renuka et al. 2017). RNAi has been used for functional genomics of glutathione *S*-transferase (GST) genes, which are involved in the degradation of toxins produced by host plants and insecticides. Injecting dsRNAs targeting the NlGSTe1 and NlGSTm2 genes into nymphs of BPH enhanced their sensitivity to chlorpyrifos but not to beta-cypermethrin. Through feeding assays and stable expression of NlEcR (ecdysone receptor gene) targeting dsRNAs in rice, Yu et al. (2014) showed significant down-regulation of target gene expression and a decrease in the number of offspring

produced by BPH adults. Likewise, Zha et al. (2011) targeted three midgut genes, carboxypeptidase (Nlcar), hexose transporter (NlHT1), and trypsin-like serine protease (Nltry). L Zhao et al. (2016a) aimed at trehalase genes involved in chitin biosynthesis and degradation. Wang et al. (2018) aimed at the calmodulin gene, Waris et al. (2018) aimed at the chemosensory protein 8 (*CSP8*) gene, and Zhu et al. (2017b) studied the function of the ribosomal protein gene (*NlRPL5*) using an RNAi tool. Pan et al. (2018) used RNAi to knock down 135 CP (chitin and cuticular protein) genes by injecting specific dsRNAs and showed that 32 CPs are necessary for normal egg production and development. Li et al. (2015) suggested that dsRNAs are stable under diverse environments and can be absorbed by roots of crop plants. This study provides scope to use dsRNAs as biopesticides. The above-cited studies are laying the foundation for the development of RNAi as a tool for managing rice pests such as BPH.

Kola et al. (2016) showed by feeding YSB larvae with dsRNA of cytochrome P450 derivative (*CYP6*) and amino peptidase N (*APN*) that expression of target genes decreased and resulted in increased mortality of larvae after 12–15 days. Similarly, Zeng et al. (2018) knocked down three chemosensory protein (CSP) genes in rice leaffolder (*C. medinalis*) through injection of dsRNAs, which downregulated insect response to the specific chemicals. He et al. (2018), in contrast, overexpressed striped stem borer-derived miR-14 microRNA in rice, which resulted in a high resistance against the pest.

3.2 Genome Editing Approach for Insect Resistance

Genome editing tools enable us to edit the genome or specific genes of an organism by addition/deletion or replacement of nucleotides with high precision and with few off-target effects. Because of its simplicity and wider applicability, genome editing is being practiced in many laboratories for functional genomics and trait improvement. In agriculture, the technology has immense potential to improve yield and abiotic and biotic stress tolerance of crops. Also, the technology does not attract many concerns regarding biosafety regulators, specifically in the case of deletion of nucleotides. Most of the research on genome editing has been focused on functional genomics, trait discovery, and improvement in plants (Arora and Narula 2017; Yin et al. 2017; Aglawe et al. 2018).

The use of genome editing techniques for pest control in plants has just been hypothesized. Zuo et al. (2017) created a mutation in *Spodoptera exigua* with CRISPR/Cas9 technology, which resulted in a mutant insect with high resistance against chlorantraniliprole, cyantraniliprole, and flubendiamide insecticides. To demonstrate the role of the cadherin gene in developing resistance against *Bt* toxin, the gene was edited by CRISPR/Cas9 in *Helicoverpa armigera*. The mutant strain of the insect showed high resistance to Cry1Ac (J Wang et al. 2016b). The pheromone-binding protein 1 (PBP1) gene of *H. armigera* was mutated and the mutant male adults showed impaired responses to sex pheromone (ZF Ye et al.

2017b). Dong et al. (2017) mutated PBP1 and PBP3 genes in striped stem borer to demonstrate their function. Biogenesis of the lysosome-related organelles complex 1 subunit 2 (BLOS2) gene of *Spodoptera litura* was edited, which resulted in the disappearance of the yellow strips and white spots on the larval integument (Zhu et al. 2017a). Similarly, when the abdominal-A (Slabd-A) gene of *S. litura* was mutated, it resulted in ectopic pigmentation and anomalous segmentation during the larval stage (Bi et al. 2016). Recently, Xue et al. (2018) edited two eye pigmentation genes in BPH, resulting in bright red compound eyes.

Although most of these reports showed successful application of CRISPR-based genome editing technology for functional genomics of insect genes, its use for incorporating and enhancing pest resistance in crops is yet to be realized. It is possible to derive genome editing-mediated resistance against insects by targeting either the host genes or the gene drive in insect populations. There is a dearth of information with regard to insect-susceptibility genes of host plants, specifically in rice. The recessive resistance genes identified so far are likely to represent nonfunctional susceptibility genes and hence the need for more studies to characterize such candidate genes, which represent ideal targets for genome editing to develop new sources of resistance. Alternatively, novel resistance alleles can be created in susceptible rice cultivars either by replacement of a few nucleotides/motifs/domains or by editing of specific bases or transfer of a complete gene. However, precise replacement of nucleotides, base editing, and insertion of a gene through CRISPR technology are relatively complex at this stage and it may require a few more years for researchers in not-so-sophisticated laboratories to be able to use this technology.

Gene drive is another highly potential technology that can be exploited to promote the inheritance of CRISPR-generated mutated alleles or any other DNA sequence by sexual reproduction, which allows a rapid spread of genes among the insect population. Even the whole CRISPR machinery, that is, Cas9 mRNA and specific sgRNAs, can be spread into insect populations via a gene drive. Besides controlling the insect population, it can decrease vector-borne virus diseases such as rice tungro disease. However, its application requires a thorough public debate among scientists, policymakers, and regulators and other stakeholders (Courtier-Orgogozo et al. 2017). In addition, the rapid advancement in genome editing technologies will facilitate the functional analysis of insect genes, which would indirectly help in developing more effective strategies for achieving effective and durable biotic stress resistance in crops.

4 Transgenic Approach Through Gene Transfer

As naturally occurring resistance to lepidopteran pests of rice is yet to be identified/discovered (e.g., stem borers and leaffolders; Schuler et al. 1998), transgenesis offers a potent, immediate, cost-effective, and environment-friendly option for control of these pests through access and use of resistance from unrelated sources (i.e., nonrice sources). Fortunately, tissue culture and genetic transformation protocols

are well established in rice and many bacterial-derived insecticidal proteins have been deployed in rice through transgenic breeding (Sundaram et al. 2013). *Bt* genes derived from the soil bacterium *Bacillus thuringiensis* have been the most successful group of related genes used commercially for genetic transformation of many crop plants, including rice. *Bt* genes encode for insecticidal proteins that are filled in crystalline inclusion bodies produced by the bacterium upon sporulation (e.g., Cry protein) or expressed during bacterial growth (e.g., Vip proteins). In addition, several research groups are assessing the potential of using non-*Bt* insecticidal proteins such as lectins (carbohydrate-binding proteins), proteinase inhibitors, ribosome-inactivating proteins, secondary plant metabolites, small RNA viruses, etc. (Makkar and Bentur 2017).

4.1 Development of Transgenic Rice for Insect Resistance

The crystal insecticidal proteins (Cry toxins or delta-endotoxins) encoded by *Bt* genes are known to possess high toxicity to lepidopteran pests (Cohen et al. 2000), Dipterans (Andrews et al. 1987), and Coleopterans (Krieg et al. 1983; Herrnstadt et al. 1986) but are nontoxic to other groups of insects, other animals, and humans. Fujimoto et al. (1993) reported the first transformation of rice with a *Bt* gene. Many reports on the development and evaluation of *Bt* rice lines have since appeared (see review by High et al. 2004; Chen et al. 2006). Rice lines expressing *Cry1Aa*, *Cry1Ab*, *Cry1Ac*, *Cry1Ab/Cry1Ac* fusion gene, *Cry1B*, *Cry1C*, *Cry2A*, and a pyramid of *Cry1Ac* with *Cry2A*, under the control of various constitutive and conditional promoters, have been shown to confer resistance to stem borers, leaffolders, and other foliage-feeding lepidopteran insects (Table 2). Several rice lines expressing insecticidal genes with anti-lepidopteran activity using *Cry* genes (*Cry1Aa*, *Cry1Ab*, *Cry1Ac*, *Cry1Ab/Ac*, *Cry1C*, *Cry2A*), CpTI (cowpea trypsin inhibitor), Vip (vegetative insecticidal protein), etc., have been reported. Various transgenic *Bt* (*Cry1Ab*, *Cry1Ac*) rice varieties (IR64, Karnal Local, etc.) resistant to YSB have been produced in India (Khanna and Raina 2002; Ramesh et al. 2004a). Pradhan et al. (2016) deployed a vegetative insecticidal protein (*vip*) in the genetic background of Swarna and demonstrated that the transgenic rice is resistant to multiple lepidopteran pests such as yellow stem borer, leaffolder, and rice horny caterpillar. Field evaluation and validation of transgenic rice possessing *Cry1A* (Shu et al. 2000; Tu et al. 2000) and synthetic *Cry1Ab* (Shu et al. 2002) have been reported from China. Field trials of *Bt* rice have also been conducted in Pakistan (Bashir et al. 2005; Mahmood-ur-Rahman et al. 2007), Spain (Breitler et al. 2004), Iran (James 2005), and India (Bunsha 2006). Iran was the first country to release *Bt* rice for commercial cultivation in 2004 (Makkar and Bentur 2017). China permitted the commercial production of *Bt* rice lines Huahui No. 1 (CMS restorer line) and *Bt* Shanyou 63 (a hybrid of Huahui No. 1 and Zhenshan 97A, a CMS line), both lines expressing *Cry1Ab/Ac* fusion gene (Chen et al. 2011), but cultivation was discontinued afterward. Currently, no *Bt* rice is grown in any country across the world, including China, although

Table 2 List of transgenes used in rice transformation to provide insect resistance

S. No.	Transgene(s) deployed	Recipient rice variety/ genotype	Promoter deployed	Reported resistant against	Reference(s)
Lepidopteran pests					
1	*cry1Ab*	IR58 (indica rice)	CaMV35S	Yellow stem borer, striped stem borer, leaffolder	Wunn et al. (1996)
2	*PINII* (potato proteinase inhibitor)	Japonica rice	–	Pink stem borer	Duan et al. (1996)
3	*cry1Ab*	Japonica, Taipei 309	Rice actin-1 promoter	Yellow stem borer	Wu et al. (1997a)
4	*cry1A*, cowpea proteinase inhibitor gene	Japonica, Taipei 309, and Taipei 85-93. Indica, Minghui 63, and Qingliu Rai	–	Yellow stem borer	Wu et al. (1997b)
5	*cry1AC*	IR64 (indica rice)	Maize ubiquitin 1 promoter	Yellow stem borer	Nayak et al. (1997)
6	*cry1Aa*, *cry 1Ac*, *cry2A*, *cry1C*	Indica, japonica	–	Yellow stem borer	Lee et al. (1997)
7	*cry1Ab*	Aromatic rice, Tarom molaii	–	Yellow stem borer	Ghareyazie et al. (1997)
8	*cry2A*	Basmati 370 and M7 (indica rice)	CaMV35S promoter	Yellow stem borer, leaffolder	Maqbool et al. (1998)
9	*cry1Ab*	Indica and japonica rice	–	Yellow stem borer	Datta et al. (1998)
10	*cry1Ab*, *cry1Ac*, *hph*, *gus* genes	Japonica rice	Maize ubiquitin promoter, the CaMV 35S promoter, and the Brassica Bp10 gene promoter	Yellow stem borer, striped stem borer	Cheng et al. (1998)
11	*cry1Ab*	Maintainer line IR68899B	35S constitutive promoter	Yellow stem borer	Alam et al. (1999)
12	*cry1Ab*	Vaidehi (indica rice)	–	Yellow stem borer	Alam et al. (1998)
13	*cry1Ab*	PR16 and PR18	Maize ubiquitin promoter	Yellow stem borer	Ye et al. (2000)

(continued)

Table 2 (continued)

S. No.	Transgene(s) deployed	Recipient rice variety/ genotype	Promoter deployed	Reported resistant against	Reference(s)
14	*cry1Ab*, *cry1Ac*	Minghui 63 (indica CMS restorer line) and its derived hybrid rice Shanyou 63	Rice actin-1 promoter	Yellow stem borer and leaffolder	Tu et al. (2000)
15	*cry1Ab*	KMD1 (japonica elite line)	–	Yellow stem borer	Shu et al. (2000)
16	*cry1A*, *cry1Ab*, *cry1Ac*, *cry1c* and *cry2A*	Indica rice	–	Yellow stem borer	Intikhab et al. (2000)
17	*cry1Ab*, *Xa21*	Pusa Basmati 1 (indica rice)	–	Yellow stem borer, Bacterial blight disease	Gosal et al. (2000)
18	CRY1AB	KMD1 and KMD2	–	Yellow stem borer, striped stem borer	Ye et al. (2001)
19	*cry1Ac*, *cry2A*, snowdrop lectin *gna*	M7 and Basmati 370 (indica rice varieties)	Maize ubiquitin-1 promoter, CaMV 35S promoter	Yellow stem borer, leaffolder, and BPH	Maqbool et al. (2001)
20	*cry1Ab*	IR64 (indica rice)	–	Yellow stem borer	Maiti et al. (2001)
21	Spider insecticidal gene	Xiushuill and Chunjiang 11	–	Leaffolder and striped stem borer	Huang et al. (2001)
22	*cry1Ac* gene	Minghui 81	Maize ubiquitin-1 promoter	Striped stem borer	Zeng et al. (2002)
23	*cry1Ac* gene	Pusa Basmati-1, IR64, and Karnal Local (indica rice)	Maize ubiquitin-1 promoter	Yellow stem borer	Khanna and Raina (2002)
24	*Bt* fusion gene (for insect resistance), *Xa21* gene (for BLB), chitinase gene (sheath blight)	IR72 (indica rice)	–	Yellow stem borer, bacterial blight disease, sheath blight disease	Datta et al. (2002)
25	Chimeric *Bt* gene, *cry1Ab*; *cry1Ab/cry1Ac* fusion gene	IR68899B and IR68897B (maintainer lines), MH63 and BR827-35R (restorer lines)	35S and PEPC promoters; actin 1 promoter	Yellow stem borer, leaffolder	Balachandran et al. (2002)

(continued)

Table 2 (continued)

S. No.	Transgene(s) deployed	Recipient rice variety/ genotype	Promoter deployed	Reported resistant against	Reference(s)
26	*cry1Ab*, snowdrop lectin *gna*	Rajalele (javanica progenies)	–	Yellow stem borer, planthoppers	Slamet et al. (2003)
27	*cry1Ac*	IR64, Pusa Basmati-1, and Karnal Local (indica rice)	Maize ubiquitin promoter	Yellow stem borer	Raina et al. (2003)
28	*cry1Ac*, *cry2A*	Basmati (indica rice)	PEPC promoter and PB 10 (pollen-specific) promoter	Yellow stem borer	Husnain et al. (2003)
29	*cry1Ac*, *Xa21*	Pusa Basmati-1 (indica rice)	–	Yellow stem borer, bacterial blight	Gosal et al. (2003)
30	*CRY1AB*, *CRY1AC* genes; bar gene for herbicide resistance	IR58025A, IR58025B, and Vajram (indica rice)	Maize ubiquitin promoter, CaMV 35S promoter (for BAR gene)	Yellow stem borer	Ramesh et al. (2004b)
31	*cry1B*, *cry1Aa*	Ariete and Senia	ubi 1 promoter or mpi promoter	Striped stem borer	Breitler et al. (2004)
32	*cry1Ab*, *cry1Ac*, *cry1C*, *cry2A*, *cry9C*	Indica rice	–	Yellow stem borer, Striped stem borer	Alcantara et al. (2004)
33	*mpi* gene (maize proteinase inhibitor)	Senia and Ariete	Maize ubiquitin 1 promoter	Striped stem borer	Vila et al. (2005)
34	*cry2A*	Minghui 63 (indica restorer line)	Maize ubiquitin promoter	Yellow stem borer	Chen et al. (2005)
35	*cry1Ac*, *cry2A*	Basmati line B-370 (indica rice)	–	Yellow stem borer, leaffolder	Bashir et al. (2005)
36	*cry1Ac*, *cry2A*	Basmati 370 (indica rice)	Ubiquitin promoter and CaMV 35S promoter	Yellow stem borer	Riaz et al. (2006)

(continued)

Table 2 (continued)

S. No.	Transgene(s) deployed	Recipient rice variety/ genotype	Promoter deployed	Reported resistant against	Reference(s)
37	*cry1Ab-1B* (translationally fused gene) and *cry1A/cry1Ac* (hybrid *Bt* gene)	Elite Vietnamese cultivars	Maize ubiquitin promoter and rice actin-1 promoter	Yellow stem borer	Ho et al. (2006)
38	*PINII* (potato proteinase inhibitor)	Pusa basmati-1 and Tarori Basmati (indica rice) and TNG67 (japonica rice)	Pin2 wound-inducible promoter	Yellow stem borer	Bhutani et al. (2006)
39	*cry2Ab* gene	Minghui 63 (indica restorer line)/T(1Ab)-10	–	Yellow stem borer, leaffolder	Tang and Lin (2007)
40	*cry1Ab*	Korean varieties, P-I, P-II, P-III	Maize ubiquitin promoter	Yellow stem borer	Kim et al. (2008)
41	*cry1Ab* gene	Khazar, Neda, and Nemat	–	Striped stem borer	Kiani et al. (2008)
42	Ten transgenic lines (two *cry1Ac* lines, three *cry2A* lines, five *cry9C* lines)	Minghui 63 (elite indica restorer line)	–	Yellow stem borer, striped stem borer	Chen et al. (2008)
43	*cry1C*	Zhonghua 11 (*Oryza sativa* L. subsp. japonica)/RJ5 line.	rbcS promoter	Yellow stem borer, striped stem borer, leaffolder	Ye et al. (2009)
44	*cry1Ia5*	*Oryza sativa*	–	Yellow stem borer	Moghaieb (2010)
45	*cry1b* and *cry1Aa* fusion gene	*Oryza sativa*	PEPC promoter	Yellow stem borer	Kumar et al. (2010)
46	*cry1Ab* and *Vip3H* fusion gene	G6H1, G6H2, G6H3, G6H4, G6H5, G6H6	–	Striped stem borer, pink stem borer	Chen et al. (2010)
47	*cry1Ab*, *cry1Ac* fusion gene	Bt-SY63	–	Striped stem borer	Zhang et al. (2011)
48	*cry1Ac*, *CpTI* genes	Bt-KF6	–	Striped stem borer	Zhang et al. (2011)
49	*cry1Ab*	Bt-DL	–	Striped stem borer	Zhang et al. (2011)

(continued)

Table 2 (continued)

S. No.	Transgene(s) deployed	Recipient rice variety/ genotype	Promoter deployed	Reported resistant against	Reference(s)
50	*cry1Ab*, *cry1Ac*, *cry1C*, *cry2A*	Minghui 63 (elite indica restorer line)	Maize ubiquitin promoter	Yellow stem borer, striped stem borer, leaffolder	Yang et al. (2011)
51	*Cry1Ac*, *cry1I*-like gene	Rice	pGreen	Striped stem borer, leaffolder	Yang et al. (2014)
52	*cry1Ab* gene	Mfb-MH86	Ubiquitin promoter	Striped stem borer and other lepidopteran pests	Wang et al. (2014)
53	*mpi-pci* fusion gene	Ariete	mpi promoter	Striped stem borer	Quilis et al. (2014)
54	*Ds-Bt*	Zhejing-22, Kongyu-131	–	Striped stem borer	Gao et al. (2014)
55	*cry1Ac*, *cry1Ig*, G10 (EPSPS gene)	Xiushui 134	Maize ubiquitin promoter (pUBi)/ modified cauliflower 35S promoter	Striped stem borer, leaffolder, and glyphosate	Zhao (2015)
Sucking pests					
56	*GNA* (*Galanthus nivalis* agglutinin)	?	Phloem-specific rice-sucrose-synthase	BPH	Rao et al. (1998)
57	*GNA*	ASD16/M12	Rice sucrose synthase/ maize ubiquitin	BPH and GLH	Foissac et al. (2000)
58	*GNA*	?	?	SBPH	Wu et al. (2002)
59	*GNA*	Chaitanya and Phalguna, indica cultivars	Phloem-specific rice-sucrose-synthase	BPH, GLH, and WBPH	Nagadhara et al. (2003, 2004)
60	*GNA*			BPH, GLH, and WBPH	Ramesh et al. (2004a, b)
61	*GNA*	Zhuxian B, an indica rice		BPH	Li et al. (2005)

(continued)

Table 2 (continued)

S. No.	Transgene(s) deployed	Recipient rice variety/ genotype	Promoter deployed	Reported resistant against	Reference(s)
62	*ASAL* (*Allium sativum* agglutinin)	IR64	CaMV35S	BPH and GLH	Saha et al. (2006)
63	*ASAL*	Chaitanya and BPT5204, indica cultivars	CaMV35S	BPH, GLH, and WBPH	Yarasi et al. (2008)
64	*ASAL*	IR64	CaMV35S	BPH and GLH	Sengupta et al. (2010)
65	*DB1/G95A-mALS* (*Dioscoria batata* tuber lectin)	Tachisugata	Phloem-specific rice-sucrose-synthase	BPH	Yoshimura et al. (2012)
66	*ASAL*	?	Phloem-specific rice-sucrose-synthase	BPH	Chandrasekhar et al. (2014)
67	Loop replacements with gut-binding peptides in *Cry1Ab* domain II	In vitro assay	–	BPH	Shao et al. (2016)
68	*Cry64Ba* and *Cry64Ca*	report		Effective against sap-sucking insects	Liu et al. (2018)

several such transgenic rice lines have been deregulated by the respective regulatory authorities of these countries due to various policy-related issues.

Genetic engineering for the control of planthopper and leafhopper pests of rice has begun with the use of plant-derived lectin genes. The snowdrop lectin gene, *Galanthus nivalis* agglutinin (*GNA*), has been transferred to several rice varieties and has been shown to provide partial to complete resistance to planthoppers and leafhoppers. Partial resistance to leafhoppers and planthoppers was demonstrated by rice transformation with a lectin gene from garlic (*Allium sativum* leaf agglutinin gene, *ASAL*; Saha et al. 2006). Bala et al. (2013) reported that *ASAL* interacts with NADH quinone oxidoreductase (NQO), a key player in the electron transport chain, and results in toxicity and increased mortality of BPH in transgenic rice lines. This study also demonstrated that, among all the transgenes available for control of sucking pests, *ASAL* holds significant promise, particularly against BPH. Yoshimura et al. (2012) developed transgenic rice possessing lectin1 gene from *Dioscorea batatas* under the control of a phloem-specific promoter (i.e., promoter of sucrose synthase-1 gene) that showed a 30% decrease in the survival rate of BPH. Even

though, in general, it is known that Cry proteins are ineffective against sucking pests, through loop replacements with gut-binding peptides in *Cry1AB* domain II, enhanced toxicity against BPH has been demonstrated (Shao et al. 2016). Liu et al. (2018) have shown the effectivity of Cry64Ba and Cry64Ca, two ETX/MTX2-type *Bt* proteins, against hemipteran pests. Boddupally et al. (2018) recently demonstrated that the expression of hybrid fusion protein (Cry1Ac::ASAL) in transgenic rice plants imparted resistance against multiple insect pests: BPH, stem borer, and leaffolder. The list of transgenes deployed for the control of sucking pests such as BPH is summarized in Table 2.

5 Insect-Plant Interactions at the Genomic Level

5.1 Planthopper Genomes

The genome of BPH and its endosymbionts have been sequenced (Xue et al. 2014). It is a large genome (1141 Mb) with 27,571 protein-coding genes, of which 16,330 are specific to this species. In comparison, the WBPH genome is relatively smaller (720 Mb) with 21,254 protein-coding genes (L Wang et al. 2017a), while the SBPH genome size is 541 Mb with 17,736 protein-coding genes (Zhu et al. 2017c). Mitochondrial (mt) genomes of these three planthopper species have also been sequenced (Zhang et al. 2013, 2014). These studies are now providing insights into the genetic plasticity of this group, possible causes of rapid evolution of virulent biotypes, and resistance against a wide range of synthetic insecticides. In addition, the role of endosymbionts such as yeast-like symbiont (YLS) and *Wolbachia* spp. in enhancing insect fitness is being studied. Additional genetic markers are being developed for studying population genetics, individual differences, and the phylogeography of planthoppers. Several key genes of the insects have been identified, which can be targeted for RNAi-based genetic tools of pest management. Transcriptomics of the salivary gland has revealed more than 350 secretory proteins, of which several, such as NlSEF1 (W Ye et al. 2017a), act as effectors modulating plant defense response. Likewise, muscin-like protein of the salivary gland secretion of BPH (Huang et al. 2017; Shangguan et al. 2018) and WBPH (Miao et al. 2018) is likely to be an effector. Such genes can be suitable targets for their control using an RNAi-based approach described above. A high number of cytochrome P450 genes and their functional diversification are attributed to drive the evolution of insecticide resistance and virulence against host-plant resistance (Peng et al. 2017; Zimmer et al. 2018). In spite of efforts to map virulence loci onto the BPH genome (Jing et al. 2014; Kobayashi et al. 2014), no aviR gene has yet been cloned and characterized. Although mitochondrial markers based on mt genes COI and ND4 have been screened for population differentiation, the results have not been encouraging over large populations across countries. Further, Zhang et al. (2013) suggest that markers based on the control region of the mt genome might provide more reliable markers for studying population genetics and the phylogeography of planthoppers.

5.2 Rice-Planthopper Interactions

Using both candidate gene cloning and a characterization-based approach and functional genomics-based omics approaches, attempts are being made to understand planthopper and rice interactions. Based on initial information on the nature of R genes as being members of the NBS-LRR class or receptor kinase class, the rice resistance mechanism against BPH is, rather hurriedly, aligned to rice resistance against pathogens under two-tier immunity involving pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) and the involvement of both JA- and SA-mediated pathways (Jing et al. 2017). Even the cloned genes are assigned to PTI (*Bph3*, *Bph15*) or ETI (*Bph14*, *Bph1/10/18*) tiers. However, what is not accounted for is the lack of documented evidence of hypersensitive reaction (HR) and systemic acquired resistance (SAR), which are hallmarks of plant response to biotrophic pathogens. Further, resistance in rice against planthoppers is not at the immune level but with moderate antibiosis coupled with antifeeding and antixenosis components. It is generally understood that SA- and JA-mediated plant defenses act reciprocally antagonistic to each other with adaptive significance (Thaler et al. 2012). Such antagonism has not been convincingly illustrated in the case of planthopper resistance in rice. Thus, greater understanding of planthopper-rice interactions is needed.

5.3 Rice-Gall Midge Interactions

Although genome sequence data for ARGM are yet to be published (Nair et al. unpublished), the mitogenome has been sequenced (Atray et al. 2015) and the microbiome analyzed in different stages of the life cycle of the insect (Ojha et al. 2017). Based on identification and functional analysis of candidate genes, global gene expression profiles and differential gene expressions detected through SSH cDNA libraries, microarray studies, and the pyrosequencing approach in both the plants and the insect rice-gall midge interactions have been fairly well studied. In essence, with results from these studies indicating strategies used by both the pest and the host to defeat each other, defense ploys can be termed as a battle for survival (Bentur et al. 2016; Sinha et al. 2017).

During the infestation process and subsequent feeding on the host, the larvae inject substance(s) into the host. As in the case of pathogenic bacteria and fungi, these products could be determinants (effectors) of the avirulence/virulence phenomenon. Extending this idea further, the genes that encode these molecules could be determinants of gall midge biotypes. Further, the genes that encode such molecules could be those that encode secreted salivary gland proteins (SSGPs). Therefore, characterizing genes that encode SSGPs could provide a handle to study this interaction and also gain valuable insight into the process of infestation of rice by this pest. The expression patterns of some of these SSGPs in larvae interacting with a susceptible host (SH; compatible interaction) or resistant host (RH; incompatible interaction) indicated that some of the SSGPs such as gamma subunit of

oligosaccharyl transferase (*OoOST*) and nucleoside diphosphate kinase (*OoNDPK*) overexpress when interacting with SH compared with those in maggots when feeding on RH (Sinha et al. 2011a, 2012a). Furthermore, NDPK protein has been demonstrated to influence the host physiology. In contrast, two genes, *OoprotI* and *OoprotII*, homologous to serine proteases, and *OoDAD1* (defender against death) overexpress in midgut of the maggots feeding on RH when compared with those feeding on SH (Sinha et al. 2011b, 2015). Although the former interactions represent effector-induced susceptibility, the latter set forms neutralizers attempting to overcome plant-secreted defensive toxins. Earlier studies also brought out similarities in rice defense expression against gall midge with those seen against plant pathogens (Rawat et al. 2010, 2013), complete with HR and SAR. Subsequent analysis of SSH-generated cDNA libraries and microarray data brought out differences in the defense pathways underlying HR+-type and HR−-type resistance (Rawat et al. 2012b), among the two HR-type resistances conferred by *Gm1* and *Gm8* genes (Divya et al. 2016, 2018b), and also the diversity in susceptibility pathways in rice genotypes with ineffective R-genes against virulent biotypes (Rawat et al. 2012a). Generally, in the three gall midge-susceptible rice varieties studied, the insect-challenged plants tend to step up metabolism and transport of nutrients to their feeding site and have suppressed defense responses. However, one of the rice varieties mounted an elevated defense response during early hours of infestation, only to be overpowered later, eventually resulting in host-plant susceptibility.

Pyrosequencing-based transcriptome analysis of ARGM revealed a differential response of the midge depending on whether it is in a compatible or incompatible interaction with its host (Sinha et al. 2012b). A recent study with sequencing of 16S rRNA bacterial gene (V3-V4 region) revealed differences in the microflora of the gall midge-rice maggots feeding on susceptible or resistant rice hosts. Results revealed that *Wolbachia* was the predominant bacterium in pupae and adults while *Pseudomonas* was predominant in maggots. Further, it was observed that members of proteobacteria were predominant across all the samples. There was high species diversity in maggots isolated from susceptible rice and a high representation of unclassified bacteria in maggots isolated from resistant rice. A first step in this direction is a report that highlights variation in the microbiome of the rice gall midge, based on the host phenotype from which it was isolated, and results suggest that these variations could have an important role in the host's susceptibility/resistance (Ojha et al. 2017).

The availability of the complete sequence of the gall midge mt genome and subsequent sequence analysis revealed the presence of two tandem repeat elements in the noncoding regions of the mt genome. Further, sequencing of the iterated regions demonstrated that the iterations of the repeat elements could not only differentiate different gall midge biotypes present in India but also were able to genetically separate the ARGM from its counterpart, the African rice gall midge (Atray et al. 2015). Thus, this study identified a reliable tool to monitor changes in the insect populations so as to have an "early warning system" in place. Janique et al. (2017) reported that two noncoding repeat motifs observed in the mitogenome of ARGM in India were absent in Thai populations and these were replaced by an 89-bp noncoding sequence.

6 Conclusions and Perspectives

In terms of an evolutionary perspective, survival of neither the host nor the herbivore has ever been under threat. Understandably, however, over the past couple of millennia when half of the human population started depending on this one cereal as its staple food, conflict of interest erupted between these insects and humans. All feasible efforts were made to protect the crop from possible damage by insects during the early phase of domestication and cultivation of the rice crop. With the advent of modern scientific methods of crop husbandry, crop improvement, and synthetic chemicals, insect pests became targets of a frontal attack by humans. With quick development of resistance against a range of synthetic insecticides, insect pests proved their evolutionary superiority, compelling humans to concede defeat and conclude that pest management was the best solution for sustainable productivity rather than pest eradication or control. Rice insect pest management has traversed the same course as that in other crops such as cotton.

Insect pest management is complex and fraught with many variables. From the foregoing account, it is quite clear that we are just beginning to understand and make inroads into the complex interactions between the pest and its host, rice. It is also evident that, although productivity loss due to these insects alone runs into several million US dollars, insects are rapidly overcoming any management strategy that we are able to deploy, whether it is resistance genes or the development of new pesticides. What this review hopes to highlight primarily is that as a central concept we need to know how the rice plant interacts with its several insect enemies from an evolutionary point of view. Against YSB, no high resistance is expressed, probably because it is a "k" strategist and monophagous insect that does not kill the host. Against gall midge with an intermediate population strategy displaying buck and boost cycles, the host plant has a diverse array of immune-level R-genes that are constantly evolving along with the virulence in the pest populations. In stark contrast, the rice plant has stockpiled multiple major and minor R-genes against planthoppers, which are typical "r" strategists. Second, the molecular tools now available have provided novel products for deployment to alleviate pest-induced yield losses. Notable among these are gene-pyramided elite cultivars, derived from marker-assisted selection, to manage multiple pests and their strains/biotypes (Divya et al. 2018c). Also present is the array of transgenic rice lines with potent genes against all the guilds of insect pests. It is unfortunate that these products are not yet available for commercial use. Molecular approaches have also broadened our knowledge and identified unexplored facets for possible use in pest management. Finally, this flush in information has reiterated the evolutionary advantage of insect genome, mitogenome, and metagenome in facing any future challenges. A recent report on quick field selection for dsRNA resistance in western corn rootworm (Khajuria et al. 2018) exemplifies this. As summarized, representatives of each insect guild have evolved their own strategy to overcome plant resistance. Considering that, in the coming years, we are likely to be under pressure to grow more in less area, it is therefore imperative that we cut the losses in productivity due to insect pests.

We have made rapid strides in the past couple of decades toward this goal with emerging new tools and strategies. What is also clear is that the solution to the insect problem is unlikely to come from one area of study but from an amalgamation of information obtained from several different studies that can provide durable, effective, and targeted resistance to insect pests of rice. The caveat is that this is unlikely to be a one-time effort but must be a continuing one.

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