Breeding for Stem Borer and Gall Midge Resistance in Rice

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Abstract

Breeding for insect-resistant varieties has been central to the integrated pest management as it offers a viable and ecologically acceptable approach. Status of progress made in breeding and adoption of resistant varieties against stem borers versus gall midge presents two contrasting scenarios. The conventional resistance breeding for yellow stem borer has not gained much impetus due to the lack of resistance sources in cultivated rice (*Oryza sativa* and *O. glaberrima*) gene pool, want of efficient insect rearing and varietal screening protocols, and inherently complex genetics of resistance. Hence, alternative approaches like wide hybridization to introgress resistance from other species of *Oryza*, transgenic approach to deploy *Bt cry* and other insecticidal genes and RNAi approach are being actively pursued. In contrast, high level of gall midge resistance is available in the crossable gene pool, insect rearing and greenhouse screening methods are well developed, genetics of resistance are well studied, molecular markers linked to R genes are developed, and many resistant rice varieties have been released for commercial cultivation and well adopted by farmers. To date 7 gall midge biotypes and 11 plant resistance genes have been reported. Nonetheless, the diversity in insect pest populations and continuous selection of virulent biotypes necessitate supplementation of conventional breeding techniques with molecular and transgenic approaches. Recent advances in the molecular breeding techniques and transgenic rice biotechnology present a great scope

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for enhanced varietal tolerance to biotic stresses. Status and prospects in this field are presented in this chapter.

Keywords
Breeding • Gall midge • Insect resistance • Molecular approaches • Rice • Stem borer

11.1 Rice Stem Borer and Yield Losses

Among the biotic stresses, insect pests continue to be a major limitation in realizing the potential yield of rice. Among various insect pests ravaging the rice fields, stem borers (SBs) are the most important ones (Bandong and Litsinger 2005). Stem borers are ubiquitous pests in all rice ecosystems with 50 known species representing three families, Pyralidae, Noctuidae (Lepidoptera), and Diopsidae (Diptera). However, yellow stem borer (YSB) *Scirpophaga incertulas* (Walker) and white stem borer (WSB) *S. innotata* (Walker) (Lepidoptera: Pyralidae) are the most important with *S. incertulas* comprising more than 90% of the borer population in rice in India. Based on 770 experimental units from 28 years data (All India Coordinated Rice Improvement Project from 1965 to 1992), empirical yield loss estimates caused by stem borers over various rice ecosystems due to 1% dead heart or white earhead or to both phases of damage were 2.5% (or 108 kg/ha), 4.0% (174 kg/ha), and 6.4% (278 kg/ha), respectively (Muralidharan and Pasalu 2006). Further, in irrigated ecosystem, 1% dead heart resulted in 0.3% or 12 kg/ha loss whereas 1% white earhead caused 4.2% or 183 kg/ha loss in grain yields; the loss due to 1% infestation in both phases of damage was 4.6% or 201 kg/ha. White earhead damage had a much greater impact on rice yield in the irrigated ecosystem than due to dead heart, as the latter occurs later in the season when no compensation is possible thus resulting in direct loss of a yielding panicle. The grain yield loss from damage at the two phases, namely, dead heart and white earhead, is more than additive. Average annual losses to rice borers in China, India, Bangladesh, and Southeast Asia were approximately 5–10%, though losses in individual fields may reach 50–60% (Rahman et al. 2004). In India, the yield losses due to yellow stem borer (YSB) infestation ranged from 3 to 95% (Senapati and Panda 1999), and this pest accounts for 50% of all insecticides used in rice field (Huesing and English 2004). Recovery or prevention of 5% of the losses due to stem borers could feed approximately 140 million people for 1 year (Datta 2000).

11.1.1 Yellow Stem Borer (YSB; *Scirpophaga incertulas*): Distribution, Biology, and Damage Potential

Of the reported stem borer species, yellow stem borer (YSB), *Scirpophaga incertulas* (Walker) (Lepidoptera: Pyralidae), assumes utmost significance (Shu et al. 2000;

Sarwar 2012) and is prevalent in all rice-producing areas of Asia (Cohen et al. 2000), Southeast Asia (Bandong and Litsinger 2005; Pathak 1968), and India in particular (Catling et al. 1987; Chelliah et al. 1989; Satpathi et al. 2012). It is commonly found in Afghanistan, Bangladesh, Burma, India, Nepal, Philippines, Taiwan, China, Japan, Sri Lanka, Vietnam, Thailand, Malaysia, Singapore, Sumatra, Java, Borneo, Sumba, and Sulawesi. The incidence of this monophagous pest may spread throughout the growing season (Shepard et al. 1995). It prefers aquatic environments where there is continuous flooding ranging from tropical lowland rice to highly preferred deepwater rice. It inflicts serious damage at all stages of the crop; larval damage to tillers during the vegetative stage results in "dead heart" symptoms (drying up of central shoot), and damage during reproductive stage results in "white ears/white heads/white earheads" (panicles with chaffy, unfilled grains). Second larval instar attaches to the tiller and bores into the stem. The egg mass of YSB is covered with brownish hairs from the anal tufts of the female. Individual eggs are white, oval, and flattened. A full-grown larva has brown head and prothoracic shield and measures about 20 mm. The pupa is pale green and enclosed in a white silk cocoon. Fresh cocoon is pale brown and turns dark brown with time. The female moth has a pair of black spots at the middle of each whitish, light brown to yellowish forewing. The male is smaller and has two rows of black spots at the tip of the forewings. Both sexes of adults are strongly attracted to light sources near rice fields during the season and signal the initiation of a fresh brood. Rainfall and relative humidity are the major determinants strongly influencing the relative abundance of stem borer populations. However, development of stem borer life stages is strongly driven by temperature. Cooler temperature coupled with changes in day length may induce diapause or temporary arrest in development of mature larvae. Pervasive distribution and chronic pattern of its infestation often result in recurrent yield loss. The YSB larvae cause serious damage to rice tillers at vegetative stage (Salim and Masih 1987) and at panicle emergence stage (Taylor 1996; IRRI 2000), although the damage to tillers at vegetative stage is largely compensated. The lowest yields often result from white earhead damage when infestation occurs at or just after the pre-booting stage (Bandong and Litsinger 2005).

11.2 Strategies Toward Insect Resistance Breeding with Special Reference to Yellow Stem Borer

Insecticides are commonly preferred at the farmer level for stem borer management, though often insecticidal applications fail to deliver desired results (Sarwar et al. 2005), because the insect larvae feed inside the stem pith and remain out of the reach of many insecticides. The application of pesticides may also pose various threats including environmental contamination, evolution of resistant biotypes, and poisoning of aquatic fauna. Therefore, the foremost challenge is to strengthen integrated pest management (IPM) programs through incorporation of host plant resistance (HPR) as its integral component for improved productivity and sustainability. Rice breeding programs are often emphasized on insect-resistant rice varieties as they have a better ability to withstand the insect damage attained by means of genetic manipulation (Sarwar et al. 2010). Among the two potential sources for enhancing host plant resistance against insect pests, the first comprised of the natural resistance systems primarily existing in rice germplasm and their wild relatives, while the second one comprised of potentially exploitable heterologous resistance systems which are often found in organisms like bacteria (Sharma et al. 2003). Conventionally, host plant resistance to insects involves quantitative traits at several loci. Several programs of resistance breeding are still based on visual and phenotypic selection, and majority of these have focused on vertical resistance involving a single major gene. The conventional resistance breeding for YSB has not gained much impetus due to the lack of resistance sources in cultivated rice (*O. sativa* and *O. glaberrima*) gene pool (Bhattacharya et al. 2006), want of efficient insect rearing and varietal screening protocols, and inherently complex genetics of resistance. The lack of a high level of resistance against the yellow stem borer had virtually stalled development of resistant varieties in the past (Bentur 2006). Hence, alternative approaches like wide hybridization to introgress resistance from other species of *Oryza*, transgenic approach to deploy Cry proteins from *Bt*, and other insecticidal genes are actively pursued. Advances in biotechnology have provided several novel means for breeding of horizontal resistance and sustainable pest resistance with fusion genes (Wan 2006). However, for thorough understanding of resistance mechanism at the molecular level, the resistance genes must be cloned, and their structure and functions must be interpreted (Deka and Barthakur 2010).

Rice is rich in germplasm resources: cultivated and wild, the cultivated rice consisting of two species, *Oryza sativa* L., referred to as Asian cultivated rice, and *Oryza glaberrima* Steud., referred to as African cultivated rice. In addition, there are 22 wild species in the genus *Oryza*. The International Rice Genebank maintains more than 1,05,000 types of Asian and African cultivated rice and 5000 ecotypes of wild relatives. Likewise, many major rice-producing countries have established national germplasm banks. Together, these germplasm collections contain genes that can be used to meet a broad range of research objectives (Zhang 2007).

Relatively small genome size (~ 430 Mb), availability of a dense physical map and molecular markers (Chen et al. 2002; Wu et al. 2002), availability of high-density genetic maps, whole-genome microarrays (for profiling expression of all of the genes in the entire life cycle of rice growth and development), availability of ~ 40,000 full-length cDNA clones (Kikuchi et al. 2003; Liu et al. 2007), a large number of expressed sequence tags (ESTs), rich forward and reverse genetics resources (Hirochika et al. 2004), and complete genome sequence (Sasaki et al. 2002) have opened up a wide spectrum of opportunities for enhancement of biotic stress tolerance in rice. Rice has nearly 55,986 genes, of which nearly 600 genes have been identified in rice which affect the biotic and abiotic stresses, coloration of plant parts, and morphological, physiological, and biochemical traits, including more than 30 genes conferring resistance to various insect pests. Such germplasm and genomic resources have provided an unprecedented opportunity for development of enhanced varietal tolerance to biotic stresses through new molecular improvisations for resistance breeding.

11.2.1 Stem Borer Resistance Through Conventional Breeding and Molecular Markers

Even though no high level of resistance against YSB was reported in the primary gene pool of rice, conventional breeding has led to development of rice varieties like Ratna, Sasyasree, and Vikas which derive moderate level of resistance from the donor source TKM6. Efforts were made to develop markers associated with YSB resistance using W1263 as the donor parent. More recently attempts are being made to introgress YSB resistance from wild species like *O. longistaminata*. However, no product has so far been released for cultivation.

11.2.2 Stem Borer Resistance Through Transgenics

To date, it has not been possible to find endogenous genes imparting desired levels of insect resistance (Schuler et al. 1998), and thus transgenic rice biotechnology offers a potent, cost-effective, and environment-friendly option. In this pursuit, genetic transformation techniques based on recombinant DNA technology have shown high success for incorporation of resistance conferring genes from unrelated sources into commercially important crop plants (Bennett 1994; Dhaliwal et al. 1998).

For the development of insect-resistant transgenics, several plant-incorporated protectants (PIPs) hold potential. The term PIP was designated by the EPA to describe the substances that are incorporated in plants to protect them from damage caused by insect pests and diseases. A PIP is defined as the pesticidal substance that is produced in a plant and the genetic material necessary to produce that substance. *Bt* or *cry* genes derived from the soil bacterium, *Bacillus thuringiensis*, have been the most successful group of related genes used commercially for genetic transformation of crop plants. *Bt* genes encode for insecticidal proteins which are filled in crystalline inclusion bodies produced by the bacterium on sporulation (Cry protein, Cyt protein) or expressed during bacterial growth (Vip protein). In addition, possibilities need to be explored to combine non-*Bt* insecticidal genes (like lectins, proteinase inhibitors, or ribosome-inactivating proteins), secondary plant metabolites, small RNA viruses, and vegetative insecticidal proteins (Vips) from *Bt* and related species with most widely exploited *Bt* genes for providing durable resistance. Efforts made so far are summarized in Table 11.1.

11.2.3 Stem Borer Resistance with *Bt* Genes

The crystal insecticidal proteins (Cry toxins or delta-endotoxins) encoded by *Bacillus thuringiensis* (*Bt*) genes show high toxicity to Lepidopterans (Whiteley and Schnepf 1986; Cohen et al. 2000), Dipterans (Andrews et al. 1987), and Coleopterans (Krieg et al. 1983; Herrnstadt et al. 1986). *Bt* Cry proteins are toxic to insects (BANR 2000) and nontoxic to humans and other animals. The first *Bt* toxin

Table 11.1 Transgenic rice genotypes developed/evaluated for resistance against stem borers and other lepidopteran pests

Sl. no.	Recipient genotype/rice subspecies	Trans gene(s)	Method of transformation	Promoter used	Reported resistance against	Stage of study	Reference (s)
1.	Xiushui 134	*cry1Ac,cry1lg,G10* (EPSPS gene)	*Agrobacterium*	Maize ubiquitin promoter (pUBi)/modified cauliflower 35S promoter	SSB, LF and glyphosate	Field trial	Zhao (2015)
2.	Tobacco plant	Deletion mutant (Ndv200) *BtVip3BR* gene	*Agrobacterium*	2X35S CaMV	YSB, cotton BW (*Helicoverpa armigera*), black cut worm (*Agrotis ipsilon*), cotton leaf worm (*Spodoptera littoralis*)	Lab studies	Gayen et al. (2015)
3.	Rice	dsRNA	–	–	Plant hoppers and stem borer	–	Li et al. (2015)
4.	Zhejing-22, Kongyu- 131	*Ds-Bt*	*Agrobacterium*	–	SSB	Field trial	Gao et al. (2014)
5.	Ariete	*mpi-pci* fusion gene	*Agrobacterium*	mpi promoter	SSB	Lab studies	Quilis et al. (2014)
6.	mfb-MH86	*cry1Ab* gene	–	Ubiquitin promoter	SSB and other lepidopteran pests	Pilot testing stage	Wang et al. (2014)

7.	Rice	*cry1Ac,cry1I*-like gene	*Agrobacterium*	pGreen	LF, SSB	Field trial	Yang et al. (2014)
8.	Minghui 63 (Elite Indica restorer line)	*cry1Ab*, *cry1Ac*, *cry1C*,*cry2A*	*Agrobacterium*	Maize ubiquitin promoter	YSB, SSB, LF	Field trial	Yang et al. (2011)
9.	Bt-DL	*cry1Ab*	–	–	SSB	Field trial	Zhang et al. (2011)
	Bt-KF6	*cry1Ac*, *CpTI* genes	–	–	SSB	Field trial	
	Bt-SY63	*cry1Ab* and *cry1Ac* fusion gene	–	–	SSB	Field trial	
10.	G6H1, G6H2, G6H3, G6H4, G6H5, and G6H6	*cry1Ab* and *Vip3H* fusion gene	–	–	SSB, PSB	Lab cum Field trial	Chen et al. (2010)
11.	Under development	*cry1Aa*, *cry1Ab*, *cry1Ac*, *cry1Ba*,*cry1Ca*	–	–	PSB, SSB	Lab studies	Gao et al. (2010)
12.	*Oryza sativa*	*cry1B* and *cry1Aa* fusion gene	Biolistic transformation	Phosphoenolpyruvate carboxylase (PEPC) promoter	YSB	Lab studies	Kumar et al. (2010)
13.	*Oryza sativa*	*cry1Ia5*	–	–	Stem borer, *Chilo agamemnon*	Lab studies	Moghaieb (2010)
14.	Zhonghua 11 (*Oryza sativa* L. ssp. japonica)/RJ5 line	*cry1C*	*Agrobacterium*	rbcS promoter	YSB, SSB, LF	Field trials	Ye et al. (2009)

(continued)

Table 11.1 (continued)

Sl. no.	Recipient genotype/rice subspecies	Trans gene(s)	Method of transformation	Promoter used	Reported resistance against	Stage of study	Reference (s)
15.	Minghui 63 (Elite Indica restorer line)	Ten transgenic lines (two *cry1Ac* lines, three *cry2A* lines, five *cry9C* lines)	–	–	YSB, SSB	Field trial	Chen et al. (2008)
16.	Khazar, Neda and Nemat	*cry1Ab* gene	–	–	SSB	Field trial	Kiani et al. (2008)
17.	Korean varieties, P-I, P-II, P-III	*cry1Ab*	*Agrobacterium*	Maize ubiquitin promoter	YSB	Field trial	Kim et al. (2008)
18.	Minghui 63 (Indica restorer line)/ T(1Ab)-10	*cry1Ab* gene	*Agrobacterium*	–	YSB, LF	Field trial	Tang and Lin (2007)
19.	Pusa Basmati 1 and Taraori Basmati (Indica rice) and TNG 67 (Japonica rice)	*PINII* (potato proteinase inhibitor)	*Agrobacterium*	Pin2 wound inducible promoter	YSB	Lab and greenhouse studies	Bhutani et al. (2006)
20.	Elite Vietnamese	*cry1Ab-1B* (translationally fused gene) and *cry1A*/*cry1Ac* (hybrid Bt gene)	–	Maize ubiquitin promoter and rice actin-1 promoter	YSB	Lab studies	Ho et al. (2006)

21.	Basmati 370 (Indica rice)	*cry1Ac*, *cry2A*	Biolistic	Ubiquitin promoter and CaMV35S promoter	YSB	Lab studies	Riaz et al. (2006)
22.	Basmati line B-370 (Indica rice)	*cry1Ac*, *cry2A*	–	–	YSB, LF	Field trial	Bashir et al. (2005)
23.	Minghui 63 (Indica restorer line)	*cry2A*	*Agrobacterium*	Maize ubiquitin promoter	YSB	Field trial	Chen et al. (2005)
24.	Senia and Ariete	*mpi* gene (maize proteinase inhibitor)	Particle-bombarded and *Agrobacterium*	Maize ubiquitin 1 promoter	SSB	Lab studies	Vila et al. (2005)
25.	Indica rice	*cry1Ab*, *cry1Ac*cry*1C*, *cry2A*, *cry9C*	–	–	YSB, SSB	Lab studies	Alcantara et al. (2004)
26.	Ariete and Senia	*cry1B* or *cry1Aa*	–	ubi1 promoter or mpi promoter	SSB	Field trial	Breitler et al. (2004)
27.	IR58025A, IR58025B and Vajram (Indica rice)	CRY1AB,CRY1AC genes; *bar* gene for herbicide resistance	*Agrobacterium*	Maize ubiquitin promoter; CaMV 35S promoter (for BAR gene)	YSB	Lab studies	Ramesh et al. (2004b)
28.	Pusa basmati 1 (Indica rice)	*cry1Ac, Xa21*	Biolistic	–	YSB, BLB	Lab studies	Gosal et al. (2003)
29.	Basmati (Indica rice)	*cry1Ac*, *cry2A*	Biolistic	PEPC promoter and PB10 (pollen-specific) promoter	YSB	Small-scale field trial	Husnain et al. (2003)

(continued)

Table 11.1 (continued)

Sl. no.	Recipient genotype/rice subspecies	Trans gene(s)	Method of transformation	Promoter used	Reported resistance against	Stage of study	Reference (s)
30.	IR-64, Pusa Basmati-1 and Karnal Local (Indica rice)	*cry1Ac*	*Agrobacterium* and biolistic	Maize ubiquitin promoter	YSB	–	Raina et al. (2003)
31.	Rajalele (Javanica progenies)	*cry1Ab*, snowdrop lectin *gna*	–	–	YSB, plant hopper	–	Slamet et al. (2003)
32.	IR 68899B and IR68897B (maintainer lines) MH63 and BR827-35R (restorer lines)	*chimeric Bt gene*, *cry1Ab*; *cry1Ab*/*cry1Ac* fusion gene	–	35S and PEPC promoters; actin I promoter	YSB, LF	Field trials	Balachandran et al. (2002)
33.	IR 72 (Indica rice)	*Bt* fusion gene (for insect resistance), *Xa21* gene (for BLB), chitinase gene (for sheath blight)	Reciprocal crossing of two transgenic homozygous IR72 lines parental lines transformed independently	–	Insect resistance, BLB of rice, Sheath blight	Lab studies	Datta et al. (2002)
34.	Pusa Basmati-1, IR-64 and Karnal Local (Indica rice)	*cry1Ac* gene	Biolistic/*Agrobacterium*	Maize ubiquitin-1 promoter	YSB	Lab studies	Khanna and Raina (2002)
35.	Minghui 81	*cry1Ac* gene	Particle bombardment	Maize ubiquitin- 1 promoter	SSB	Field trial	Zeng et al. (2002)

36.	"Xiushuill" and "Chunjiang 11"	spider insecticidal gene	*Agrobacterium*	–	LF, SSB	Lab studies	Huang et al. (2001)
37.	IR64 (Indica rice)	*cry1Ab*	–	–	YSB	–	Maiti et al. (2001)
38.	M7 and Basmati 370 (Indica rice varieties)	*cry1Ac*, *cry2A*, snowdrop lectin *gna*	Particle bombardment	Maize ubiquitin-1 promoter, CaMv 35S promoter	YSB, LF, BPH	–	Maqbool et al. (2001)
39.	KMD1 and KMD2	CRY1AB gene	–	–	SSB, YSB	Field trial	Ye et al. (2001)
40.	Pusa Basmati 1 (Indica rice)	*cry1Ab*, *Xa21*	Biolistic	–	YSB and BLB of rice	–	Gosal et al. (2000)
41.	Indica rice	*cry1A, cry1Ab, cry1Ac, cry1C* and *cry2A*	–	–	YSB	–	Intikhab et al. (2000)
42.	KMD1 (Japonica elite line)	*cry1Ab*	–	–	YSB	–	Shu et al. (2000)
43.	Minghui 63 (Indica CMS restorer line) and its derived hybrid rice Shanyou 63	*cry1Ab* and *cry1Ac*	Biolistic	Rice actin- 1 promoter	LF, YSB	Field trials	Tu et al. (2000)

(continued)

Table 11.1 (continued)

Sl. no.	Recipient genotype/rice subspecies	Trans gene(s)	Method of transformation	Promoter used	Reported resistance against	Stage of study	Reference (s)
44.	PR16 and PR18	*cry1Ab*	–	Maize ubiquitin promoter	YSB	Lab studies	Ye et al. (2000)
45.	Vaidehi (Indica rice)	*cry1Ab*	–	–	YSB	–	Alam et al. (1998)
46.	Maintainer line IR68899B	*cry1Ab*	Biolistic	35S constitutive promoter	YSB	Lab studies	Alam et al. (1999)
47.	Japonica rice	*cryIAb*, *cryIAc*, *hph* and *gus* genes	*Agrobacterium*	Maize ubiquitin promoter, the CaMV35S promoter, and the *Brassica* Bp10 gene promoter	YSB, SSB	Lab studies	Cheng et al. (1998)
48.	Indica and Japonica rice	*cry1Ab*	–	–	YSB	–	Datta et al. (1998)
49.	Basmati 370 and M7 (Indica rice)	*cry2A*	Particle bombardment	CaMV35S promoter	YSB and LF	Lab studies	Maqbool et al. (1998)
50.	Aromatic rice, Tarom molaii	*cry1Ab*	–	–	YSB		Ghareyazie et al. (1997)
51.	Indica, Japonica	*cry1Aa, cry1Ac, cry2A, cry1C*	–	–	YSB		Lee et al. (1997)

52.	IR64 (Indica rice)	CRY1AC	Particle bombardment	Maize ubiquitin 1 promoter	YSB	Lab studies	Nayak et al. (1997)
53.	Japonica, Taipei 309 and Taipei 85–93. Indica, Minghui 63 and Qingliu Rai	*cry1A*, *cowpea proteinase inhibitor* gene	–	–	YSB	–	Wu et al. (1997a)
54.	Japonica, Taipei 309	*cry1Ab*	Particle bombardment	Rice actin-1 promoter	YSB	Lab studies	Wu et al. (1997b)
55.	Japonica rice	*PINII* (potato proteinase inhibitor)	–	–	PSB	Lab studies	Duan et al. (1996)
56.	IR58 (Indica rice)	*cry1Ab*	Particle bombardment	CaMV35S	Mortality of YSB+SSB and feeding inhibition of LF and another leaf folder, *Marasmia patnalis*	Lab studies	Wunn et al. (1996)

SSB striped stem borer/Asiatic rice borer (*Chilo suppressalis*), *LF* leaf folder (*Cnaphalocrocis medinalis*), *YSB* yellow stem borer (*Scirpophaga incertulas*), *PSB* pink stem borer (*Sesamia inferens*), *BPH* brown plant hopper (*Nilaparvata lugens*) gene was discovered in 1901 by Ishiwaki in diseased silkworms, cloned in 1981, and genetically engineered into japonica and indica rice plants in 1988 and 1990, respectively. Field evaluations of *Bt* rice have been reported since 2000, and these studies primarily focus on *cry1A* genes (Shu et al. 2000; Tu et al. 2000). Shu et al. (2002) reported a line KMD1 transformed with a synthetic *cry1Ab* gene, conferring resistance to eight lepidopteran pest species, including YSB under laboratory as well as under natural infestation. Since then several rice lines expressing insecticidal genes with lepidopteran activity [*cry1Aa, cry1Ab, cry1Ac, cry1Ab/Ac, cry1C,* cry2A, *CpTI* (cowpea trypsin inhibitor), etc.] and hemipteran activity [snowdrop lectin (*Galanthus nivalis* agglutinin) *gna* gene and *Pinellia ternata* agglutinin – *pta*] have been developed and tested. Iran was the first country to release *Bt* rice for commercial cultivation in 2004. Likewise, 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, which contains a copy of the synthetic DNA sequence with two genes: the CRY1AB and the CRY1AC (Chen et al. 2011). These genes encode the respective *Bt* toxins, lethal to Lepidoptera, whereas *Bt* Shanyou 63 provides resistance to rice stem borer and leaf folder (Tu et al. 2000). In India, IR62 was the first transgenic rice-expressing *Bt* gene (Nayak et al. 1997). Subsequently, various transgenic *Bt* (Cry1Ab, Cry1Ac) rice varieties (IR64, Karnal Local, etc.) resistant to YSB have been produced (Khanna and Raina 2002; Ramesh et al. 2004a, b); however, Cry proteins are ineffective against sap feeders. But currently, no GM rice variety has been commercially released in India.

11.2.4 Strategies for Successful Deployment of *Bt* Genes

Early breakdown of the resistance is a major limitation which itself poses the challenge of maintaining the durability of the resistance. Development of durable resistance strategies may involve gene pyramiding or gene stacking as one of its potential components. The use of multiple genes with different mode of action against the same pest or a range of pests delays the development of resistance. Gene pyramiding of *cry1Ac*, *cry2A*, and snowdrop lectin gene, *gna*, in transgenic rice was more effective against a variety of insects than any single gene (Maqbool et al. 2001; Loc et al. 2002). Further, stacking of *Bt* genes with *gna* gene imparted relatively higher and broader resistance to lepidopterans and in addition to hemipterans, which are otherwise not controlled by *Bt* alone (Maqbool et al. 2001; Ramesh et al. 2004a). Preliminary field testing of transgenic rice lines carrying c*ry1Ab*, *Xa21*, and *gna* genes has also been conducted in India (Bentur 2006). Recent investigation suggested that Cry1Ab or Cry1Ac could be combined with Cry1C, Cry2A, or Cry9C for durable resistance in transgenic rice as Cry1Ab and Cry1Ac compete for the same binding site in YSB (Alcantara et al. 2004).

11.2.5 Stem Borer Resistance with Genes and Proteins Other than *Bt*

Discovery of a number of insecticidal proteins like protease inhibitors, ribosome-inactivating proteins, lectins, antibodies, and insect peptide hormones provides several novel options for deriving resistance from sources other than *Bt* solely or in combination with *Bt.* Plants themselves may be the source of these non-*Bt* genes with insecticidal activity (Sharma et al. 2004). Protease inhibitors are antimetabolites acting against a wide range of insect pests, and the genes encoding for these are a component of plant's natural defense system against insect damage. Several transgenic rice plants expressing protease inhibitors have been field tested including those with synthetic gene coding for winged bean trypsin inhibitors WTI-1B (Mochizuki et al. 1999), oryzacystatin, cowpea trypsin inhibitors, potato proteinase inhibitors II, and soybean Kunitz trypsin inhibitors (Tyagi and Mohanty 2000; Sharma et al. 2004). In addition, transgenic rice plants with barley trypsin inhibitor BTI-CMe have been tested for resistance against rice weevil *Sitophilus oryzae* (Alfonso-Rubi et al. 2003). Cowpea trypsin inhibitor (*CpTi*) transgene has also been used for deriving resistance to stem borer (Brar and Khush 2007). Likewise, plant lectin (heterogeneous group of sugar-binding proteins) genes have shown protection in particular to homopterans (sap-sucking insects: BPH, WBPH, GLH), apart from lepidopterans and coleopterans. However, snowdrop lectin (*Galanthus nivalis* agglutinin) gene, *gna*, stacked with *Bt* genes imparted relatively higher and broader resistance to lepidopterans and homopterans than *Bt* alone (Maqbool et al. 2001; Ramesh et al. 2004a). Further, extensive research is needed on cloning of insecticidal protein coding genes specifically for the stem borers.

11.2.6 RNA-Mediated Crop Protection Against Rice Yellow Stem Borer

RNA interference (RNAi) or RNA silencing has emerged a promising research tool for silencing, downregulating, or controlling the expression of the key insect genes especially where the resistance sources are rare in the primary gene pool of the host plant. As we understand that double-stranded RNA (dsRNA) is an important regulator of gene expression in many eukaryotes (Meister and Tuschl 2004), a sequence-specific suppression of target insect gene is achieved through exogenous application and endogenous expression of dsRNAs, which degrades the target complementary endogenous messenger RNA (mRNA) transcripts within the cell. It works through 21–24 nucleotide small RNAs which are processed through a set of core enzymatic machinery involving Dicer and Argonaute proteins (Mohanpuria et al. 2015). RNAi-mediated silencing of target insect gene may lead to growth inhibition, developmental aberrations, reduced fecundity, and mortality (Baum and Roberts 2014). Kola et al. (2015) discussed the role of various potential insect genes encoding key enzymes/proteins for developing an effective insect control by RNAi approach including acetylcholinesterase, cytochrome P450 enzymes, amino peptidase N, allatostatin, allatotropin, tryptophan oxygenase, arginine kinase, vacuolar ATPase, chitin synthase, glutathione-S-transferase, catalase, trehalose phosphate synthase, vitellogenin, hydroxy-3-methylglutaryl coenzyme A reductase, and hormone receptor genes. Kola et al. (2016) reported that YSB larvae fed on dsRNA designed from two genes of rice yellow stem borer (YSB), cytochrome P450 derivative (CYP6), and Aminopeptidase N (APN) have detrimental effect on larval growth and development of the insect. Cytochrome P450 monooxygenases (cytochrome P450s) are found in virtually all living organisms (Kola et al. 2015) and perform an important role in the metabolism of xenobiotics such as drugs, pesticides, and plant toxins (Scott 2008). In insects, cytochrome P450s play a predominant role in the metabolism of insecticides, which often results in the development of insecticide resistance in insect populations (Zhou et al. 2010). On the other hand, the aminopeptidase N (APN) group of exopeptidases are abundant proteins on the midgut brush border of insect larva (Adang 2013). APNs in lepidopterans received initial attention because they function as receptors for *Bt* Cry1 insecticidal toxins. It plays an important physiological role in dietary protein digestion (Marchler-Bauer et al. 2015). Inhibition of its activity in the midgut can result in detrimental effect on larval growth and development and lead to larval mortality (Reed et al. 1999). Expression of APNs was found in midgut and malpighian tubules (Wang et al. 2005). These genes can be deployed to develop YSB resistance in rice using RNAi approach. However, to achieve an effective RNAi response for YSB control in rice, careful identification of specific target insect enzymes and proteins, efficient delivery methods of introducing dsRNA into insect cells/bodies, and stabilization of dsRNAs during and after delivery are certain key issues which need immediate concern.

11.3 Gall Midge – An Overview

The Asian rice gall midge (ARGM) *Orseolia oryzae* (Wood-Mason) (Diptera: Cecidomyiidae) was first reported as an unidentified pest of rice in Bihar, India, by Riley (1881). Though first identified as *Cecidomyia oryzae* Wood-Mason (Cotes 1889), the pest was later renamed as *Pachydiplosis oryzae* (Felt 1921), and subsequently as *Orseolia oryzae* (Gagné 1973). A related species in western Africa was named as African gall midge, *O. oryzivora* (Harris and Gagne 1982). The introduction and widespread cultivation of dwarf and high-yielding rice cultivars resulted in extensive gall midge problem. A significant portion of rice yield is lost to ARGM damage in several rice-growing countries including India, China, Thailand, Sri Lanka, Myanmar, Indonesia, Bangladesh, and Vietnam (Bentur 2015). The conservative economic estimate of yield losses from gall midge is about US$ 500 million in Asia and US$ 80 million in India alone. In India, it is rated as third most important pest of rice in terms of spread and severity of damage and yield loss (Bentur 2015), next to stem borers and plant hoppers. ARGM occurs in most states in India except north-western states like Punjab and Haryana. It is essentially a monsoon pest and prefers high humidity and moderate temperature with peak activity extending between last week of August and first week of October (Rajamani et al. 1979).

The pest has a short life cycle (19–23 days) under normal temperatures (22–28 °C) and constant humidity (~85% RH), with sex ratio (male to female) of 1:3 usually. Adult fly is pink in color and looks like a mosquito. Mating occurs during dawn or dusk (crepuscular), and a single female lays an average of 125–150 eggs which usually hatch on the fourth day. Feeding and salivary secretion of maggots turn the growing shoot meristem into a gall chamber, which after elongation develops into a tubular gall commonly known as silver shoot or onion leaf. The affected tillers bear no panicle or grains resulting in significant economic loss. An economic estimate of annual yield loss from gall midge is pegged at Rs. 3300 million (Bentur et al. 2003) in southern India alone. In contrast, the maggots fail to induce gall formation on the resistant varieties, and perish in 2–4 days after hatching. Several promising sources of resistance were identified in greenhouse screening and field evaluation of rice germplasm. This made the host plant resistance as the most viable option for successful management of the gall midge for the last several decades.

11.3.1 Rice-Gall Midge Interactions

Classical approaches in rice breeding for gall midge resistance were pursued during the late 1950s which later led to successful release of the first gall midge (GM)-resistant variety "Kakatiya" in 1975. Since then, more than 100 rice varieties resistant to gall midge have been released for cultivation, and in this the availability of greenhouse rearing and screening protocols played a significant role. Systematic evaluation of over 25,000 accessions of rice germplasm has led to identification of more than 500 sources of resistance to gall midge (Bentur et al. 2011; Bentur 2015), and majority of these are landraces from northeastern states of India. Differential reaction of same genotype against gall midge populations at different rice-growing areas reflected intraspecific variations and helped in the detection of its geographically distinct populations (biotypes). Biotypes, in general, refer to the intraspecific category of insect populations with similar genotypes for biological attributes. They represent evolutionary transients in the process of speciation and develop through natural selection acting upon genetic variations within the pest populations. Roy et al. (1969) first suspected the occurrence of gall midge biotypes (GMB). Kalode and Bentur (1989) characterized three distinct biotypes of gall midge, based on 13 years of data on field evaluation of differentials in the country. Subsequently, reports on the emergence of new virulent biotypes appeared. Recently, a seventh biotype, GMB4M, was reported (Vijayalakshmi et al. 2006). Several reports (Bentur et al. 1987; Srinivas et al. 1994; Nair and Devi 1994) associated the selection of virulent biotypes to extensive cultivation of resistant varieties of rice. With the detection of gall midge biotypes, screening of resistant germplasm accessions against the characterized biotypes was undertaken aggressively to understand the range of resistance (Kalode and Bentur 1988; Bentur et al. 1994). Investigations on genetics of rice gall midge resistance at Indira Gandhi Agricultural University (IGAU), Raipur, further led to characterization of ten gall midge resistance (R) genes designated as *Gm1* through *Gm10*. Identification of *Gm11* gene from breeding line CR57-MR1523 (Himabindu et al. 2010) finally raised the number of characterized gall midge-resistant genes to 11. Nair et al. (2011) reported gene-for-gene relation between R genes in rice and gall midge biotypes. Each of the biotypes showed a specific range of virulence against R genes, and likewise each R gene conferred resistance to specific biotypes, which implies that none of the R genes conferred resistance to all biotypes and none of the biotypes showed virulence against all the R genes. The range and pattern of resistance displayed by rice gene differential varieties against the seven known biotypes are presented in Table 11.2. Based on the similarity in range of resistance, R genes were categorized into four groups. Rice plant and gall midge have been known to exhibit compatible or incompatible interaction. In the first case, virulent insect successfully establishes on a susceptible rice plant leading to gall formation and completion of insect life cycle. However, in incompatible interaction, the host rice plant is resistant, and the insect fails to establish and is killed within 24–48 h of feeding. The major component of varietal resistance against rice gall midge is antibiosis (Modder and Alagoda 1972; Hidaka 1974; Kalode 1980), and the defensive role of phenols against gall midge in resistant varieties is also reported (Amudhan et al. 1999). However, no antixenosis mechanism is involved. The maggots feeding on resistant varieties are either killed on feeding or unable to molt to second instar. So far, tolerance as a mechanism of resistance against gall midge is only reported in rice cultivar CR1014 (Prakasa Rao 1989).

Bentur and Kalode (1996) reported two types of resistance reactions exhibited by resistant rice plants in response to gall midge feeding; HR^+ type is characterized by symptoms of tissue necrosis at the site of maggot feeding and HR- type in which no tissue necrosis occurs, but the insect mortality is observed. Addition of this information in the Table 11.2 further suggested diversity in R genes in terms of spectrum of resistance and type of resistance. Of the 11 known R genes, only *Gm1* and *Gm8* confer HR- type resistance, while the other 9 genes provide HR+ type resistance.

11.3.2 Tagging, Mapping, and Cloning Gall Midge Resistance Genes in Rice

The use of marker-assisted selection (MAS) with PCR (polymerase chain reaction)-based molecular markers for gene pyramiding has met with encouraging results. To date PCR-based linked molecular markers have been developed for 8 of the 11 resistance genes (Yasala et al. 2012). While four of the genes, viz., *Gm2*, *gm3*, *Gm6*, *Gm7*, have been noted as a cluster on chromosome 4, two genes *Gm4* and *Gm8* are located on chromosome 8. For most of these genes, flanking markers are available, which can be used to effectively transfer them. Three of the genes, viz., *gm3*, *Gm4*, and *Gm8*, have been cloned through map-based approach, and candidate genes for these have been identified as NB-ARC (LOC_Os04g52970.1) (Sama et al. 2014), NBS-LRR (LOC_Os08g09670.1) (Divya et al. 2015), and proline rice protein (Dutta et al. 2014), respectively. Based on the gene sequence information, functional markers have been developed for these three genes (Dutta et al. 2014).

Table 11.2 Nature and effectiveness of gall midge resistance genes in rice against different biotypes

Group	Source	Gene	Chr. no.	HR type	Reaction to gall midge biotype							References
					GMB1	GMB2	GMB3	GMB4	GMB5	GMB6	GMB4M	
I	W1263	*Gm1*	9	−HR	R	S	R	S	R	R	S	Reddy et al. (1997)
II	Phalguna	*Gm2*	4	+HR	R	R	S	S	R	S	S	Mohan et al. (1994)
II	ARC5984	*Gm5*	?	+HR	R	R	R	S	R	S	S	Kumar et al. (1998b)
II	Dukong 1	*Gm6*	4	+HR	R	R	R	S	R	S	S	Tan et al. (1993)
II	RP2333-156-8	*Gm7*	4	+HR	R	R	R	S	R	S	S	Kumar et al. (1999)
II	Madhuri -L9	*Gm9*	7	+HR	R	R	R	S	R	S	S	Shrivastava et al. (2003)
II	BG308	*Gm10*	?	+HR	R	R	R	S	R	S	S	Kumar et al. (2005)
III	CR57-MR1523	*Gm11*	12	+HR	R	R	R	R	S	S	S	Himabindu et al. (2010)
IV	RP2068	*gm3*	4	+HR	R	R	R	R	S	S	R	Kumar et al. (1998a)
IV	Abhaya	*Gm4*	8	+HR	R	R	R	R	S	S	R	Srivastava et al. (1993)
IV	Jhitpiti/Aganni	*Gm8*	8	−HR	R	R	R	R	S	S	R	Kumar et al. (2000)
V	TN1	None	–	–	S	S	S	S	S	S	S	–

After Bentur et al. (2011)

HR hypersensitive reaction, *GMB* gall midge biotype, *R* resistant, *S* susceptible, *Chr* rice chromosome number, ? not determined

[a] Groups are based on the spectrum of resistance conferred by the gene across gall midge biotype

11.3.3 Pyramiding of Gall Midge-Resistant Genes in Rice

Gene pyramiding offers an excellent approach to incorporate wide range and durable resistance against gall midge in rice. Better insights into the genetics of resistance, R (resistant) gene mapping, allelic relationships, and linkage are necessary for pyramiding of resistant genes. Resistance against gall midge is conferred by a single gene (monogenic) which facilitates pyramiding. However, one of the major problems that has impeded the long-term success of gall midge-resistant varieties released so far is the continuous evolution of new virulent biotypes against the deployed resistant genes. Distinct major genes for gall midge resistance are effective against different biotypes, and this differential reaction offers a promising tool for pyramiding resistant genes. Combining resistant genes in a variety is surely a gateway to an effective and durable resistance; however, which gene combinations will provide desired durability needs investigation. The suggested approach is to combine the genes with different mechanism of resistance in good agronomic background. To date, most of the gall midge-resistant varieties developed so far derive their resistance mainly from *Gm1*, *Gm2*, *Gm4*, and *Gm11* genes, and thus these are less likely candidates for pyramiding. The virulence against *Gm2* and *Gm11* genes has already been reported at several locations across India. However, *Gm1* gene exhibited continued durability for more than 30 years of its deployment, and resistant variety "Abhaya" carrying *Gm4* gene has not been cultivated widely. Based on the available information on resistance nature, frequency of alleles conferring virulence against R genes (Bentur et al. 2008), genetics of virulence, and fitness cost associated with virulence, the best combination of genes suggested is *Gm4+Gm8* or *gm3+Gm8* (Bentur 2015).

11.3.4 Virulence Monitoring in Gall Midge Populations

Widespread cultivation of gall midge-resistant varieties often resulted in evolution of new virulent biotypes which caused resistance breakdown in single-gene-resistant varieties. As a curative measure, developing varieties with durable resistance through gene pyramiding is a viable option. The use of marker-assisted selection (MAS) with PCR (polymerase chain reaction)-based molecular markers for gene pyramiding has yielded encouraging results. To date PCR-based molecular markers have been developed for 8 of the 11 resistance genes. However, the selection of candidate genes for pyramiding needs thorough understanding of the virulence composition of the pest populations in the target area, the genetics of plant resistance, and insect virulence, as the rice-gall midge interaction is a gene-for-gene one. A modified F_2 screen method has been developed for monitoring virulence in gall midge populations (Bentur et al. 2008; Andow and Bentur 2010). Tests based on this method across the country revealed high level of virulence against resistance-conferring *Gm2* plant gene. Further, studies at Warangal revealed a slower rate of virulence development against *Gm1*, while a rapid increase in frequency of virulence allele in gall midge conferring adaptation to *Gm2*, the plant resistance gene, was observed. As the single recessive gene, ${}_{V}$*Gm2*, conferring virulence against *Gm2* (Bentur et al. 1992) follows sex-linked inheritance, it results in less durability of resistant gene (*Gm2*) in host plant since such virulence gets fixed in population faster than the autosomal inherited virulence gene. Similar studies also established low levels of virulence against *Gm8* and high levels against *Gm11*.

11.3.5 Durable Deployment of Gall Midge-Resistant Varieties

The deployment of gall midge-resistant varieties of rice often led to the emergence of resistance-breaking biotypes that suppress the yield benefit provided by the resistance. Cohen et al. (2004) suggested that besides the genetic makeup of the varieties under cultivation, the frequency of alleles for adaptation to host, genetics of virulence, and fitness cost associated with virulence as the decisive factors in shaping evolution rate of new biotypes. They further compared various deployment strategies for gall midge-resistant rice varieties including sequential release of varieties containing single-resistant gene, release of variety with two resistant genes pyramided and seed mixtures of gall midge susceptible variety, and release of single R gene or pyramided variety through the use of various simulation models. The results of these simulation studies revealed that (1) the release of a single variety with two pyramided resistant genes provides longer duration of resistance than the combined term of resistance of two single-gene varieties released sequentially and (2) the incorporation of a susceptible variety into the seed mixture usually prolongs the durability of resistant varieties. However, deliberate efforts are needed to investigate how farmers' main leverages (choice of resistant variety, resistance deployment strategy, and cultural practices) can be best combined to achieve resistance durability while minimizing yield losses.

11.3.6 Insect Virulence Genes *vis-à-vis* Biotype Evolution

Gall midge biotypes have been encountered in association with cultivation of resistant crop cultivars, and in this case, a gene-for-gene relationship between pest virulence and host plant resistance has been discussed earlier. Knowledge of occurrence of gall midge biotypes is a prerequisite to design crop improvement programs for incorporating pest resistance. To slow down the process of biotype selection, crop cultivars with broad genetic bases are needed. On the other hand, knowledge of genes and pathways involved in insect virulence and evolution of biotypes is strongly needed. Sinha et al. (2012a) identified more than 80,000 ESTs each from gall midge feeding on resistant as well as susceptible host. Comparative transcriptome analysis of these two sets of ESTs led to identification of several virulence and avirulence genes of gall midge besides development of 2303 EST-based and 2756 SNPs markers. Sinha et al. (2012a) successfully cloned two genes *Ooprot1* and *OoprotII*. RT-PCR analysis established that both these genes were upregulated in gall midge larvae feeding on resistant host than in larvae feeding on susceptible host suggesting their role in detoxification of plant resistance factors. Likewise, a secretory salivary protein coding gene, oligosaccaharyl transferase (*OoOST*), has been cloned and characterized (Sinha et al. 2012b), and its expression was found to be seven times higher in salivary glands of larvae feeding on susceptible host than in those feeding on resistant ones, indicating their role in insect virulence. They further found another overexpressed gene, *OoNDPK*, coding for nucleoside diphosphate kinase in gall midge maggots feeding on susceptible plants. Better understanding of insect virulence genes, pathways involved in insect virulence, and interaction of virulence genes with host genotypes may be helpful in delaying the evolution of resistance-breaking evolutionary transients in target insect population.

11.4 Conclusions and Prospects

Forgoing account of our understanding insect-plant interactions and efforts to develop resistant rice cultivars against stem borers and gall midge bring home the following conclusions. The rice stem borer, mainly YSB, association has come to an evolutionary equilibrium with YSB attaining monophagous status and adopting k strategy of population structure. In other words, rice offers no threat to the insect, and insect in turn does not challenge the plant's survival. It is "live and let others live" equilibrium. Superimposed on this state is the mankind's demand for food which does not compromise on even a marginal yield loss due to the stem borers. While classical breeding approach did not provide high level of host plant resistance, mainly due to the evolutionary equilibrium, novel biotechnological approaches outlined in the text above are more likely to bring "success." This would mean an unprecedented selection pressure on the insect. It would certainly be naive to undermine the insect's genetic plasticity to respond to this pressure. Studies have clearly shown high frequency of alleles conferring resistance against Cry toxins in populations of YSB in the Philippines (Bentur et al. 2000) and SSB populations in China even without deployment of *Bt* rice. It is thus imperative also to invest on development of effective deployment strategies along with focus on transgenic and other approaches for stem borer resistance.

In contrast, rice-gall midge interactions may be in a state of evolutionary flux. This is reflected in the diversity in defense pathways that have coevolved in the plants, simultaneously and independently across rice-growing regions of the world. The Thailand land race "Siam 29" has distinct resistance mechanism (conferred by *Gm2* with HR+ type) in comparison with Indian land race "Eswarakora" (with *Gm1* and HR- type). Evolutionary biologists propose formation of gall to restrict and captivate the invading insect itself as the plant defense. Ingenious adaptation of the insect against this first line of defense has rendered the plant more prone and secure host for the gall former. This parallel evolution is the battle for survival (Bentur et al. 2016) which may be further considered in association with r/k strategy of the pest population dynamics which display typical "buck and boost" cycles. The take-home message is likely that no single approach would provide lasting resistance to the gall midge. Hence novel approaches need to be continuously explored to stay one step ahead of this evolutionary miracle pest.

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