Utilization of Cultivated and Wild Gene Pools of Rice for Resistance to Biotic Stresses

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SUMMARY

Productivity of rice is often adversely affected by several biotic stresses. The major biotic stresses such as blast, bacterial blight, sheath blight, brown planthopper and yellow stem borer play crucial roles in reducing the productivity and quality of rice. Among the various control measures available for mitigating biotic stresses, host plant resistance is most effective, economic and eco-friendly. Wild and cultivated gene pools of rice are important sources for many resistance genes/QTLs, which are successfully utilized in resistance breeding programme. In this chapter, a comprehensive assessment of the use of wild and cultivated gene pools of rice for imparting resistance to major biotic stresses has been presented.

1. INTRODUCTION

Like all other crop plants, rice (*Oryza sativa*) also suffers from several biotic and abiotic stresses that seriously affect its production. A wide range of pathogens, insects, nematodes and other pests attack the rice plant in different parts of the world. Magnitude and the type of damage caused by pests vary in different regions. Among them, diseases like blast, bacterial blight (BB) and sheath blight (ShB) and insects like brown planthopper (BPH) and yellow stem borer (YSB) are of major concern in India as well as many other parts of the world. Despite the availability of several control measures for mitigating pest damage in crop plants, developing cultivars tolerant to major insect-pests and diseases prevalent in an area is the easiest, most economic and most eco-friendly measure available to the farmers. At the same time, the system is highly dynamic in its nature due to continuous co-evolution of genes conferring resistance or susceptibility in hosts and their corresponding gene for virulence in pests. Genes conferring resistance are distributed across primary, secondary and tertiary gene pool of the crop. Judicious use of these genes and genetic resources to minimize losses caused by pests remains an important challenge for rice researchers worldwide.

In India, systematic research efforts to impart host plant resistance in rice is undergoing from more than 70 years. The biotic stress breeding programme at the National Rice Research Institute, Cuttack, Odisha has evolved over time depending on the dynamic pest profile of the crop and advances in the technologies available. The institute was established in 1946 in the backdrop of the Bengal famine caused due to *Helminthosporium* leaf spot. Hence during the first two decades, the emphasis

was mainly given to developing brown spot resistant genotypes. Eventually, breeding for tolerance against blast and yellow stem borer (YSB) was also taken up. With the introduction of high yielding semi-dwarf varieties like TN 1 during early 60's, bacterial blight became a severe threat to rice production. The 70's and 80's saw the major focus being directed towards breeding for bacterial blight tolerance. With the outbreak of brown planthopper in the late 1970's, breeding for BPH tolerance has also taken a centre stage. Sheath blight, though very severe even during 1960's in countries like the Philippines, was not a stress capable of causing economic damage to the rice industry in India until recently. But the severe incidence of sheath blight is being reported of late especially in the most productive parts of the country like Punjab and even in many regions of Orissa where intensive farming is practiced to raise the crop.

The global and national efforts towards understanding the mechanism of resistance and developing cultivars with biotic stress tolerance against the five major rice pests, viz., blast, bacterial blight, sheath blight, brown planthopper and yellow stem borer have been reviewed in this chapter, with major emphasis being given to the work carried out at ICAR-NRRI, Cuttack.

2. RICE BLAST (*MAGNAPORTHE ORYZAE*) RESISTANCE

Rice blast disease caused by *Magnaporthe oryzae* is one of the most destructive disease causing huge losses to rice yield and thereby posing a great threat to world food security. Use of blast resistant cultivars is the most effective, economic and environmentally sustainable way of managing this pathogen. Till today more than 100 blast resistance genes have been identified (Table 1). Of these, 45% are from *japonica* cultivars, 51% from *indica* cultivars and the rest 4% are from wild species of rice. Blast resistance genes and their genetic location in different rice cultivars have been reviewed by Sharma et al. (2012). Recently, Liang et al. (2016) reported that *pi 66(t)* is one of the three recessive genes controlling rice blast, and is the first major gene for resistance to be mapped on chromosome 3. Li et al. (2017) identified a new gene from a rice variety Digu which is effective against broad spectrum of *M. oryzae* races. An exhaustive list of the reported blast resistance genes with their corresponding sources and their chromosomal locations have been mentioned in Table1.

Blast disease was first reported in India in 1913 and the first devastating epidemic due to rice blast was reported in 1919 in Tanjore delta. Since then several works were carried out in various parts of the country. An important gene for blast resistance, *Pi-kh* was identified from *indica* variety Tetep at ICAR-National Research Centre for Plant Biotechnology, New Delhi. They further characterized, fine mapped, cloned and functionally validated the resistance gene. The corresponding virulent gene, *AvrPi54* in the pathogen was also successfully cloned by the team, which contributed significantly in the detailed understanding of host-pathogen interaction (Ray et al. 2016).

Hittalmani et al. (2000) used closely linked RFLPs and polymerase chain reaction (PCR)-based markers to put three blast resistance genes *Pi1*, *Piz-5* and *Pita* into a

Table 1. Blast resistance genes reported in rice.

Sl. No.	Gene name	Location (Chr No)	Sources of resistance
1	*Mpiz*	11	Zenith
2	*Pb1*	11	Modan
3	*PBR*	11	St- No 1
4	*Pi(t)*	4	P167
5	*Pi1*	11	LAC23
6	*Pi10*	5	Tongil
7	*Pi11*	8	Zhai-Ya-Quing8
8	*Pi12*	12	K80-R-Hang, Jiao-Zhan, Moroberekan
9	*Pi13(t)*	6	*O. minuta* (W), Kasalath (I),Maowangu
10	*Pi14(t)*	2	Maowangu
11	*Pi15*	9	GA25
12	*Pi15(t)*	12	Moroberekan
13	*Pi16(t)*	2	Aus373
14	*Pi17*	7	DJ123
15	*Pi18(t)*	11	Suweon365
16	*Pi19(t)*	12	Aichi Asahi
17	*Pi20*	12	IR24
18	*pi21*	4	Owarihatamochi
19	*Pi22(t)*	6	Suweon365
20	*Pi23*	5	Suweon365
21	*Pi24(t)*	1	Azucena
22	*Pi25*	6	Gumei 2
23	*Pi25(t)*	2	IR6
24	*Pi26*	6	Gumei 2
25	*Pi26(t)*	5	Azucena
26	*Pi27*	1	Q14
27	*Pi27(t)*	6	IR64
28	*Pi28(t)*	10	IR64
29	*Pi29(t)*	8	IR64
30	*Pi3(t)*	6	Pai-kan-tao
31	*Pi30(t)*	11	IR64
32	*Pi31(t)*	12	IR64
33	*Pi32(t)*	12	IR64
34	*Pi33*	8	IR64
35	*Pi34*	11	Chubu32
36	*Pi35(t)*	1	Hokkai 188
37	*Pi36*	8	Q61
38	*Pi37*	1	St- No 1
39	*Pi38*	11	Tadukan
40	*Pi39(t)*	4,12	Chubu 111, Q15

Contd....

Sl. No.	Gene name	Location (Chr No)	Sources of resistance
41	*Pi40(t)*	6	*O. australiensis*
42	*Pi41*	12	93-11
43	*Pi42(t)*	12	DHR9
44	*Pi44*	11	Moroberekan
45	*Pi47*	11	Xiangzi 3150
46	*Pi48*	12	Xiangzi 3150
47	*Pi5(t)*	9	Moroberekan
48	*Pi6(t)*	12	Apura
49	*Pi62(t)*	12	Yashiro-mochi
50	*Pi67*		Tsuyuake
51	*Pi8*	6	Kasalath
52	*Pi9*	6	*O. minuta*
53	*Pia*	11	Aichi Asahi
54	*Pib*	2	Tohoku IL9
55	*Pib2*	11	Lemont
56	*PiCO39(t)*	11	CO39
57	*Pid(t)1*	2	Digu
58	*Pid2*	6	Digu
59	*Pif*	11	Chugoku 31-1
60	*Pig(t)*	2	Guangchangzhan
61	*PiGD1*	8	Sanhuangzhan 2
62	*PiGD-2*	10	Sanhuangzhan 2
63	*PiGD3*	12	Sanhuangzhan 2
64	*Pigm(t)*	6	Gumei4
65	*Pii*	9	Ishikari Shiroke, Fujisaa5
66	*Pii1*	6	Fujisaka 5
67	*Pii2*	9	Ishikari Shiroke
68	*Piis1*	11	ImochiShirazu
69	*Piis2*	-	ImochiShirazu
70	*Piis3*	-	ImochiShirazu
71	*Pik*	11	Kusabue
72	*Pikg*	11	GA20
73	*Pikh (Pi54)*	11	Tetep
74	*Pikm*	11	Tsuyuake
75	*Pikp*	11	HR22
76	*Piks*	11	Shin 2
77	*Pikur1*	4	Kuroka
78	*Pikur2*	11	Kuroka
79	*Pilm2*	11	Lemont
80	*Pir2-3(t)*	2	IR64
81	*Pirf2-1(t)*	2	*O. rufipogon*

Contd....

Sl. No.	Gene name	Location (Chr No)	Sources of resistance
82	*Pise*	11	Sensho
83	*Pise2*	-	Sensho
84	*Pise3*	-	Sensho
85	*Pish*	1	Shin 2
86	*Pish*	11	Nipponbare
87	*Pit*	1	Tjahaja
88	*Pita*	12	Tadukan
89	*Pita2*	12	Shimokita
90	*Pitp(t)*	1	Tetep
91	*Pitq1*	6	Teqing
92	*Pitq2*	2	Teqing
93	*Pitq3*	3	Teqing
94	*Pitq4*	4	Teqing
95	*Pi-tq5*	2	Teqing
96	*Pitq6*	12	Teqing
97	*Piy1(t)*	2	Yanxian No 1
98	*Piy2(t)*	2	Yanxian No 1
99	*Piz*	6	Zenith (J), Fukunishiki,Toride 1, Tadukan
100	*Pizh*	8	Zhai-Ya-Quing8
101	*Pi157*	12	Moroberekan
102	*Pi-jnw1*	11	Jiangnanwan

Adapted and updated from Sharma et al. (2012)

susceptible cultivar CO39. It was reported that plants carrying two or three gene combinations showed enhanced resistance as compared to *Piz-5* alone. Singh et al. (2011) improved the parental lines of rice hybrid Pusa RH 10 by introgressing the blast resistant gene *Pi 54* into them. The group has also developed and released a blast-resistant basmati variety, Pusa Basmati 1637 through transfer of *Pi9* using marker-assisted selection. Introgression of blast resistance genes *Pi1*, *Pi2* and *Pi33* into rice variety ADT43 was carried out at Tamil Nadu Agricultural University, Coimbatore.

At The National Rice Research Institute, Yadav et al. (2017) attempted to find out the status of twelve major blast resistance genes and their diversity among eighty released rice varieties of the institute (National Rice Research Institute, Cuttack). Linked molecular markers for genes *Pib*, *Piz*, *Piz-t*, *Pik*, *Pik-p*, *PikmPik-h*, *Pita/Pita-2*, *Pi2*, *Pi9*, *Pi1* and *Pi5* were used in the study. Among the 80 varieties used, 19 were resistant, 21 were moderately resistant and 40 were susceptible to the disease. The blast resistance genes in the different varieties varied from 4 to 12 and the frequencies of the resistance genes ranged from 0 to100%.

Marker assisted backcross breeding strategy was applied for pyramiding blast resistance genes (*Pi2* and *Pi9*), into Vandana and Kalinga III through the crosses (Kalinga III/C101A51 (*Pi-2(t)*)//KalingaIII/O. *minute* der. WHD IS 75-127(*Pi-9(t)*) and Vandana/C101A51//Vandana /O. *minute* der. WHD IS 75-127). Many lines in the

background of Vandana and Kalinga III were developed. Among the promising lines, CR 2619-2, CR 2619-5, CR 2619-6, CR 2619-7, CR 2619-8 and CR 2619-9 are in the background of Vandana while CR 2620-1, CR 2620-2, CR 2620-3 and CR 2620-4 are in Kalinga III background. The promising lines were tested in Disease Screening Nursery (DSN) under AICRIP for multi-location trials.

*2.1. Bacterial blight (*Xanthomonas oryzae *pv.* oryzae*) resistance*

Bacterial blight (BB), caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), is a devastating disease in the rice-growing countries of Asia. Infection at maximum tillering stage results in blighting of leaves, which eventually causes significant yield losses in severely infected fields ranging from 20 to 30%, but this, can reach as high as 80%. Development of cultivars carrying major resistance (R) genes have been the most effective and economic strategy to control BB disease. To date, at least 38 BB resistance genes conferring host resistance against various strains of *Xoo* have been identified (Table 2). All of these genes follow a Mendelian pattern of inheritance and express resistance to a diverse group of *Xoo* pathogens. Several of these genes have already been incorporated into rice cultivars, which are now widely cultivated in many countries. BB resistance gene *Xa4* is one of the most widely exploited resistance genes and it confers durable resistance in many commercial rice cultivars. Two genes *Xa 33(t)* and *Xa 38* were identified from *Oryza nivara*. A new mutant named 'XM14' obtained from IR24, which was found to be resistant to all Japanese *Xoo* races. The gene identified in XM14 was designated as *xa42*.

In IRRI, IR24 NILs (IRBB lines) containing *Xa4*, *xa5*, *xa13* and *Xa21*genes and their combinations were developed which were extensively used in the breeding programmes of many countries including India. Indian scientists from the National Agricultural Research and Education System used these IRBB lines for transfer of BB resistance genes in many popular high yielding varieties. The gene combinations chosen by breeders, however, remained confined to *xa13* and *Xa21* or *xa5, xa13* and *Xa21*. However, Ellur et al. (2016) incorporated *Xa38* in the basmati background of PB1121 and found that it provides resistance to an additional race of the pathogen when compared with its NIL pyramided with *xa13*+*Xa21*.

The *Xa21* gene was identified at NRRI in the wild species *Oryza longistaminata*, which was highly effective against BB races in South and Southeastern Asia. The gene was later mapped and cloned at IRRI and is being extensively utilized by breeders across the globe. Varietal improvement programme was initiated to improve the BB resistance in popular high yielding varieties as recurrent parents and BB resistance genotypes viz., Ajaya (*xa5*), IRBB 8 (*xa8*) and IRBB 60 (*xa5, xa13 and Xa21*) as donors through backcross breeding coupled with artificial screening.

Resistance genes (*xa5*, *xa13* and *Xa21;* either singly or in different combinations) pyramided lines were developed through marker assisted backcross breeding in the genetic background of Swarna and IR64 under the Asian Rice Biotechnology Network (Reddy et. al. 1997). The promising pyramided lines identified through DSN of AICRIP in different locations across the country were recommended for registration for their

Table 2. List of BB resistance genes reported in rice.

Xa gene	Resistance to Xoo race	Donor cultivar	Chr.
Xa1	Japanese race -I	Kogyoku, IRBB 1	4
Xa2	Japanese race -II	IRBB2	4
Xa3/Xa26	Chinese, Philippine, and Japanese races	Wase Aikoku 3, Minghui 63, IRBB3	11
Xa4	Philippine race-I	TKM6, IRBB4	11
xa5	Philippine races-I, II, III	IRBB5	5
Xa6	Philippine race-I	Zenith	11
Xa7	Philippine races	DZ78	6
xa8	Philippine races	P1231128	7
xa9	Philippine races	Khao Lay Nhay and Sateng	11
Xa10	Philippine and Japanese races	Cas 209	11
Xa11	Japanese races IB, II, IIIA, V	IRS	3
Xa12	Indonesian race-V	Kogyoku, Java14	4
xa13	Philippine race 6	BJ1, IRBB13	8
Xa14	Philippine race 5	TN1	4
xa15	Japanese races	M41 Mutant	-
Xa16	Japanese races	Tetep	-
Xa17	Japanese races	Asominori	-
Xa18	Burmese races	IR24, Miayang 23, Toyonishiki	-
xa19	Japanese races	XM5 (Mutant of IR24)	-
xa20	Japanese races	XM6 (Mutant of IR24)	-
Xa21	Philippine and Japanese races	*O. longistaminata*, IRBB21	11
Xa22	Chinese races	Zhachanglong	11
Xa23	Indonesian races	*O. rufipogon* (CBB23)	11
xa24(t)	Philippine and Chinese races	DV86	2
Xa25	Chinese and Philippine races	Minghui 63, HX-3 (Somoclonal mutant of Minghui 63)	12
xa26(t)	Philippine races	Nep Bha Bong	-
Xa27	Chinese strains and Philippine race 2 to 6	O. minuta, IRGC 101141, IRBB27	6
xa28 (t)	Philippine race 2	Lota sail	-
Xa29(t)	Chinese races	*O. officinalis* (B5)	1
Xa30 (t)	Indonesian races	*O.rufipogon* (Y235)	11
Xa31(t)	Chinese races	Zhachanglong	4
Xa32(t)	Philippine races	*O. australiensis* (introgression line C4064)	11
xa33(t) *Xa33(t)*	Thai races	Ba7 *O. nivara*	6
Xa34 (t)	Thai races	BG1222	1
Xa35(t)	Philippine races	*O. minuta* (Acc. No.101133)	11
Xa36(t)	Philippine races	C4059	11
Xa38	Indian Punjab races	*O. nivara* IRGC81825	4
Xa39	Chinese and Philippine races	FF329	11
Xa40(t)	Korean BB races	IR65482-7-216-1-2	11
xa41(t)	Various Xoo strains	Rice germplasm	-
xa42	Japanese Xoo races	XM14, a mutant of IR24	3

Adapted and updated from Kou and Wang (2013).

use as potential donors in future breeding programmes (DRR Annual Progress Report 2003; 2005). Two lines CRMAS 2231-37 (IET 20668) and CRMAS 2231-48 (IET 20669) in the background of IR 64 were found promising for BB endemic areas of Uttarakhand and Andhra Pradesh and Uttarakhand and Haryana, respectively while one line CRMAS 2232-85 (ET 20672) in the background of Swarna was recommended for the endemic areas of Gujrat and Maharashtra. Pradhan et al. (2015) introgressed three BB resistance genes (*xa5, xa13* and *Xa21*) by marker-assisted backcrossing, in the background of the popular, but highly BB susceptible deepwater variety, Jalmagna. The pyramided lines showed a high level of BB resistance and significant yield advantage over Jalmagna under conditions of BB infection. Lines carrying two BB gene combinations (*Xa21+xa13* and *Xa21+xa5*) were also developed in the background of Jalmagna (Pradhan et al. 2016). The pyramided lines showed increased resistance to BB isolates prevalent in the region. The parental line improvement for BB resistance has been successfully undertaken at NRRI in case of popular rice hybrid Rajalaxmi, by introgressing four resistance genes (*Xa4*, *xa5, xa13,* and *Xa21*) through Marker-assisted backcross (MAB) breeding (Dash et al. 2016).

Varietal improvement program at NRRI for BB resistance resulted in the release of Improved Lalat [CRMAS 2621-7-1 (IET 21066)], Improved Tapaswini [CRMAS 2622-7-6 (IET 21070)] and CR Dhan 800 in the genetic background of popular rice varieties Lalat, Tapaswini and Swarna, respectively. Improved Lalat and Improved Tapaswini carry four genes (*Xa4, xa5, xa13* and *Xa21*) while CR Dhan 800 has three resistance genes *Xa21, xa13* and *xa5*. All have been effective for growing in the "bacterial blight" endemic areas of Odisha.

3. SHEATH BLIGHT (*RHIZOCTONIA SOLANI* KUHN) TOLERANCE/RESISTANCE

Sheath blight of rice, caused by the fungus, *Rhizoctonia solani* Kuhn, is becoming a major threat to rice production worldwide. Though first reported as early as in 1910, sheath blight became a prominent disease only after the introduction of high yielding semi-dwarf varieties in the 1960's. The intensive cropping involving cultivation of a single variety over a large area and the high use of nitrogenous fertilizer led to a dramatic increase in the incidence of sheath blight in major rice-growing countries of the world as well as India. Almost all the prominent varieties grown in the country are highly susceptible to the disease. Development of genotypes tolerant to the disease is considered as the most sustainable, eco-friendly and economic way to combat the disease.

Breeding for sheath blight (ShB) tolerance in rice poses many unique challenges compared to other pests and diseases. Being caused by a necrotrophic fungus, ShB tolerance is a quantitative trait governed by polygenes. Lack of a well-standardized screening protocol compounded with the influence of environment and various plant morphological features on trait expression make identification of truly resistant lines a daunting task. Genotypes with moderate disease resistance have been reported in the past, but a strong ShB resistant source is yet to be identified from both the cultivated and wild gene pool of rice.

From the moderate resistance sources identified, more than hundred QTLs (Table 3) have been reported for ShB tolerance in rice, but most of them have minor effects and are correlated with various plant morphological features, especially plant height and heading date. Even for the major ShB QTLs having plant morphology-independent effect, the expression is highly affected by the genetic background, limiting the usefulness of the QTLs in practical plant breeding. The breeding potential of few ShB QTLs viz., *qSB9-2*^{TQ}, *qSB-11*^{LE} and *qSB-9* ^{TQ} have been tested in different genetic backgrounds and their effect on sheath blight tolerance was validated. Two of these QTLs, *qSB-11*^{LE} and *qSB-9 TQ* were fine mapped.

There are only limited reports of utilization of identified ShB QTLs in practical plant breeding, with only limited resistance genotypes viz., Teqing, Tetep, Lemont and Jasmine 85 being regularly used as donors of ShB tolerance. Pinson et al. (2008) have improved the ShB tolerance of the popular American rice genotype Lemont by introgressing ShB tolerance QTLs from TeQing. Three TeQing-into-Lemont backcross introgression lines (TILs) containing eight ShB QTLs and having significantly less sheath blight susceptibility compared to the recurrent parent were released in the USA in 2007. Wang et al. (2012) have developed TeQing-into-Lemont backcross introgression lines (TILs) of QTLs *qSB9*-2 and *qSB12*-1 and found that resistant alleles of the QTLs from TeQing significantly improved ShB tolerance of the TILs. Chen et al. (2014) have transferred the QTLs *qSB-7* and *qSB-9* from Teqing into the genetic background of commercial japonica varieties by MAS. The two QTLs were also pyramided in the background of the *japonica* variety WLJ1. There was a significant reduction in SB incidence and yield loss in the introgressed lines and pyramiding of two QTLs were found to be more effective rather than using single QTL. Zuo et al. (2014) have shown that pyramiding of QTLs for ShB tolerance and tiller angle, *qSB*-9^{TQ} and *TAC1*^{TQ}, had significantly increased disease tolerance in the near-isogenic lines (NILs) carrying them. Both the QTLs have improved the ShB tolerance of the NILs but *qSB*-9^{TQ} was more effective than *TAC1*^{TQ}. The NILs having both the QTLs had more tolerance to sheath blight compared to the NILs having any one of them.

In India, ShB tolerance breeding relies mainly on the genotype Tetep, which is a multiple biotic stress tolerant *indica* genotype from Vietnam. In studies conducted at Indian Agricultural Research Institute (IARI), one major ShB QTL *qSBR11-1* from Tetep was functionally characterized and the candidate gene, a novel chitinase gene (LOC_Os11g47510), for sheath blight tolerance was identified in the QTL region. The QTL *qSBR11-1* was introgressed into the background of 'Improved Pusa Basmati 1' by marker-assisted backcrossing (MAB). In another study, the sheath blight tolerance of the line Pusa 6B, the Basmati quality maintainer line of the popular superfine aromatic rice hybrid Pusa RH10, was enhanced by introgressing three ShB resistance QTLs (*qSBR11-1, qSBR11-2* and *qSBR7-1*) from Tetep by MAB.

The resistance reaction of a genotype may vary depending on the strain of the pathogen used. Screening experiments conducted at the National Rice Research Institute (NRRI) using the local strains of the pathogen has shown that international check genotypes for ShB tolerance like Jasmine 85 and TeQing are susceptible to the

Table 3. List of reported QTLs for sheath blight tolerance.

Chr. No.	QTL	Resistant parent	Susceptible parent	Mapping population
5	*qShb5.1*	RP 2068-18-3-5	TN1	RIL
7	*qshb7.3*	ARC10531	BPT-5204	BC1F2
9	*qshb9.2*	ARC10531	BPT-5204	BC1F2
9	*qShB9-2*	Jasmine 85	Lemont	RIL
9	*qSBR-9*	Jarjan	Koshihikari	BC2F3 (BIL)
1	*qSBR1-1*	Tetep	HP2216	RIL
	qSBR1-1	Tetep	HP2216	RIL
7	*qSBR7-1*	Tetep	HP2216	RIL
	qSBR7-1	Tetep	HP2216	RIL
8	*qSBR8-1*	Tetep	HP2216	RIL
11	*qSBR11-1*	Tetep	HP2216	RIL
11	*qSBR11-2*	Tetep	HP2216	RIL
11	*qSBR11-3*	Tetep	HP2216	RIL
11	*qSB-11LE*	Lemont	Yangdao	NIL
1	-	Pecos	Rosemont	F2
9	*qShB9-2*	Jasmine 85	Lemont	RIL
9	*qSB-9Tq*	Lemont	Teqing	CSSLs
8	*Qsh8a*	Teqing	Lemont	RIL
8	*Qsh8b*	Teqing	Lemont	RIL
9	*Rsb-2(t)*	A Mutant	Shuhui 881	-
1	*qSB-1*	Lemont	Teqing	RIL
3	*qSB-9*	Lemont	Teqing	RIL
5	*qSB-3*	WSS2	Hinohikari	BC1F1
2	*Rsb1*	4011	XZX19	F2
11	*qSBR-2*	Jingxi 17	Zhaiyeqing 8	DH
2	*QSbr2a*	Lemont	Teqing	NIL
3	*QSbr3*	Lemont	Teqing	NIL
2	*qSB-2*	Jasmine 85	Lemont	F2
3	*qSB-3*	Jasmine 85	Lemont	F2
7	*qSB-7*	Jasmine 85	Lemont	F2
9	*qSB-9-1*	Jasmine 85	Lemont	F2
9	*qSB-9-2*	Jasmine 85	Lemont	F2
11	*qSB-11*	Jasmine 85	Lemont	F2
1	*QRh1*	Jasmine 85	Lemont	RIL
9	*Qsbr3a*	Teqing	Lemont	F4 Bulk
	Qsbr9a	Teqing	Lemont	F4 Bulk

Adapted and updated from Srinivasachary et al. (2011).

local strains. Only two genotypes, Tetep and CR 1014, a variety released from ICAR-NRRI, showed consistent moderate resistant phenotype for sheath blight. Conventional breeding has been less effective for the development of ShB tolerant genotypes because of the polygenic nature of the trait. In the segregating generations of the crosses made at ICAR-NRRI, using CR 1014 as the donor for ShB tolerance, selection of superior recombinants has been difficult since ShB tolerance has tight linkage with plant height. A novel ShB QTL on chromosome 1 was identified from an $F_{2:3}$ population derived from the cross Swarna Sub1 x CR 1014, which need to be fine mapped and its effects in different genetic backgrounds need to be validated.

4. BROWN PLANTHOPPER (*NILAPARVATA LUGENS* STÅL) RESISTANCE

Brown planthopper (BPH) (*Nilaparvata lugens* Stål) is one of the most destructive insect-pests of rice. Besides affecting the rice crop directly, it also serves as a vector that transmits rice grassy stunt virus and ragged stunt virus. The host resistance of rice against BPH was first reported in the variety Mudgo and the first BPH resistance gene (*BPH* 1) was identified from the same in 1967. After that 31 more genes have been discovered (Table 4) besides several QTLs from the gene pool of cultivated and wild rice (Deen *et al*. 2017). They are mapped to five of the 12 chromosomes (3, 4, 6, 11, and 12) of rice (Cheng et al. 2013). Among those, only 17 genes (*BPH1, BPH2, BPH6, BPH9, BPH12, BPH14, BPH15, BPH17, BPH18, BPH19, BPH25, BPH26, BPH27, BPH28, BPH29, BPH30* and *BPH32*) have been fine-mapped and seven of them (*BPH14, BPH17, BPH18, BPH26, BPH29, BPH9* and *BPH32*) have been cloned and characterized (Jena et al. 2017). Among the cloned genes *BPH 9* and *BPH 26* turned out to be the same gene (LOC_Os12g37280), and the locus IDs for *BPH 17* and *BPH 18* have not been yet assigned. However, almost all the identified resistance genes are biotype/ population specific and do not provide strong resistance to other BPH biotypes/populations. Hence, search for broad-spectrum resistance should continue besides taking efforts for pyramiding multiple combinations of genes and understanding the detailed molecular mechanisms involved therein.

A series of BPH tolerant varieties (e.g. IR26, IR36, IR50 and IR72) have been developed and released from the IRRI since the 1970s, by transferring BPH resistance genes in the background of elite susceptible cultivars. However, the improved cultivars carrying single resistance gene lose effectiveness due to the evolution of new biotypes and this has become a serious threat to its management in Asia. Pyramiding of BPH resistance genes/QTLs may provide a sustainable means for developing durable resistance against frequently evolving new biotypes. Several studies have been reported for pyramiding of insect resistance genes. The most elaborate work was carried out by Jena et al. (2017) in which the resistance levels of *bph* genes were studied by introgressing them into the genetic background of the variety IR 24. The group has developed 25 NILs with 9 single R genes and 16 multiple R genes combinations. The insect resistance of the NILs, in terms of the level of antibiosis was assessed. It was found that NILs pyramided with multiple *bph* genes were having

Table 4. BPH resistance genes and their source germplasm.

S. No.	Resistance gene	Source
1	*Bph1*	Mudgo, CO22 (IT 000588), TKM6, Milyang30, Milyang34 (IT 006216), Nampungbyeo, Chilseongbyeo, Andabyeo, Kanto PL4 (IT173362), Cheongcheongbyeo, Changsongbyeo, Baekunchalbyeo, IR26 (IT001886), IR28 (IT001892), IR29 (IT001893), IR30 (IT001899), Hangangchalbyeo, Yeongpungbyeo, Namyeongbyeo, Gayabyeo, Samgangbyeo, Namcheonbyeo, MTU15, IR26, IR28, IR29, IR30, IR34, IR44, IR45, IR46, IR64 and MGL2
2	*bph2*	ASD7, ASD9, IR 1154-243, Norin-PL4, Hwacheongbyeo, PTB18, PTB33, H105, Palasithari 601, H5, IR32, IR36, IR38, IR40, IR42, IR48, IR50, IR52, IR54, IR65
3	*Bph3*	Rathu Heenati, PTB19, Gangala, Horana Mawee, Muthumanikam, Kuruhondarawala, Mudu, Kiriyal, PTB33, IR56, IR58, IR60, IR62, IR68, IR70, IR72, IR74
4	*bph4*	Babawee, Gambada Samba, Hotel Samba, Kahata Samba, Thirissa, Sulai, VellaiIllankali, Heenhoranamawee, KuluKuruwee, Lekam Samba, Senawee and IR66
5	*bph5*	ARC10550
6	*Bph6*	Swarnalata, *O. officinalis* (acc.00896)
7	*Bph7*	T12
8	*bph8*	Chin Saba, Col. 5 Thailand and Col. 11 Thailand
9	*Bph9*	Pokkali, Balamee and Kaharamana
10	*Bph10*	*O. australiensis* and IR65482-4-136-2-2
11	*bph11*	*O. officinalis*, DV85 and IR 54751-2-44-15-24-3
12	*Bph12*	*O. officinalis, O. latifolia,* B14 and IR54751-2-34-10-6-2
13	*Bph13*	*O. eichingeri, O. officinalis* (acc.00896), acc105159 and IR54745-2-21-12-17-6
14	*Bph14*	*O. officinalis*, RI35 and B5
15	*Bph15*	*O. officinalis* and B5
16	*Bph17*	Rathu Heenati
17	*Bph18*	*O. australiensis* and IR65482-7-216-1-2
18	*bph19*	AS20-1
19	*Bph20*	*O. minuta* (acc. 101141), IR71033-121-15 and ADR 52
20	*bph21*	ADR52, *O. minuta* (acc. 101141) and IR71033-121-15
21	*Bph22*	IR 75870-5-8-5-B-2-B and IR 75870-5-8-5-B-1-B
22	*Bph23*	IR 71033-121-15
23	*bph24*	IR 73678-6-9-B
24	*Bph25(t)*	ADR52
25	*Bph26(t)*	ADR52
26	*Bph27*	GX2183
27	*Bph28(t)*	DV85
28	*Bph29*	RBPH54 (introgression from *O rufipogon*)
29	*Bph31*	CR2711-76
30	*Bph32*	PTB33

Adapted and updated from Ali and Chowdhury (2014).

more level of antibiosis compared to NILs with single *bph* gene. The study throws significant inroads into the concept of R gene deployment in which different *bph* gene/gene combinations can be used in different geographical areas depending on the biotype prevalent in the region.

Deen et al. (2017) reported the occurrence of multiple loci instead of a single recessive gene (reported earlier) conferring resistance to the insect in case of *bph5.* They identified five QTLs *qBphDs6, qBphNp1, qBphNp12, qBphDw3* and *qBphDw8* associated with BPH (biotype 4) resistance in ARC10550. The two major QTLs *qBphDs6* for damage score and *qBphDw8* for days to wilt were important for further investigation and use in the breeding programme. Pyramiding of BPH resistance genes, *Bph1* and *Bph2,* has been successfully achieved by marker-assisted breeding (Sharma et al. 2004).

At ICAR-NRRI, several landraces showing a very high degree of resistance were used for breeding varieties resistant to BPH. The breeding lines CR 3005-77-2 (Samba Mahsuri/Salkathi), CR 3006-8-2 (Pusa 44/Salkathi), CR 3005-230-5 (SambaMahsuri/ Salkathi), CR 2711-76 (Tapaswini/Dhobanumberi) were found to be promising in planthopper screening trials of AICRIP, 2011 and 2012. Molecular mapping of resistance genes/QTLs from these two landraces- Salkathi and Dhobanumberi is underway. Two QTLs designated as *qBph4.3* and *qBph4.4* were identified from Salkathi landrace among which *QBph4.3* is novel (Mohanty et al., 2017). Transfer of these two QTLs into two popular susceptible varieties Naveen and Pooja are in progress. Recently, Prahlada et al. (2017) at IRRI identified a single dominant gene, *BPH31* on the long arm of chromosome 3 in CR2711-76.

5. YELLOW STEM BORER (*SCIRPOPHAGA INCERTULAS*) TOLERANCE/RESISTANCE IN RICE

Yellow stem borer is a major threat to rice production in tropical and subtropical rice-growing areas. Lack of availability of an effective source of resistance to this insect in primary gene pool poses a challenge in the study and improvement of this trait. The complex inheritance pattern and screening methodologies for resistance create further complications. In absence of any significant report of studies related to YSB resistance in literature, the works carried out at ICAR-NRRI and other institutes of India are discussed. Unlike the four other biotic stresses mentioned above, comprehensive molecular studies for identification of genes and QTLs conferring resistance to YSB are not available. Most of the studies are confined to classical genetic studies.

Efforts to introgress YSB tolerance in the elite genetic background started immediately after the establishment of the institute. Screening studies conducted during 1950's at ICAR-NRRI resulted in the identification of YSB tolerant genotypes viz., TKM6, Slo-12, CB-1, MTU 15, Tepa-1, ADT-14 and JBS 1638. Among these,

TKM6 was extensively used in the resistance breeding programme at the institute. Three YSB tolerant varieties were released from ICAR-NRRI using TKM6 as the donor. The varieties are, Ratna (TKM6 x IR 8) which is highly tolerant to YSB especially at the vegetative stage, Saket 4 (sister selection of Ratna) and CR138-928 (Jaya x TKM6). Other popular YSB tolerant varieties released from ICAR-NRRI include Vijaya (T90 x IR8), Supriya (IR8//GEB24/T(N)1), Dharitri (Pankaj x Jagannath) and Panidhan (CR151-79 x CR1014). Mutation breeding was also attempted to develop YSB tolerant lines; a mutant line of Tainan3 was released in 1980 as the variety Indira (CR MUT 587-4) which possess a fair degree of YSB tolerance in addition to tolerance to blast and BB. Besides NRRI, two more varieties, Sasyasree and Vikas with a moderate level of resistance to YSB were released in India using TKM6 as the donor source. YSB resistance was mapped by RAPD markers from a cross of Co43 x W1263. Though the high yielding rice varieties enlisted above are moderately resistant to YSB, no rice variety truly resistant to YSB has yet been developed.

Since gene(s) for resistance to YSB has not been found in the primary gene pool of rice efforts were made to incorporate alien genes from wild species belonging to the secondary gene pool, which are reservoirs of such traits. Wild rice germplasm has been screened against YSB. *O. brachyantha, O. officinalis, O. ridleyi* and *O. coarctata* were found to be resistant/tolerant against the pest. Subsequently, backcross population of *O. sativa* cv. Savitri/*O. brachyantha* was developed to transfer YSB resistance to the cultivated rice (Behura et al. 2011). The cytogenetic analysis of the chromosomal variants lead to the development of monosomic alien addition lines (MAALs). Of the 8 MAALs screened, MAAL 11 was found to be moderately resistant to YSB.

6. STATUS OF UTILIZATION OF WILD GENE POOL FOR BIOTIC STRESS TOLERANCE

The genus *Oryza* comprises of several wild species besides the two cultivated species *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice) (Table 5). These wild relatives of cultivated rice are found to be grown naturally in different ecologies around the world. The term species complex is used "for a group of species where distinct taxonomic keys are lacking and the categorization to species or subspecies level is rather arbitrary" (Vaughan 2005). Four major species complexes of *Oryza* were identified which were designated as *O. sativa* complex (contains AA genome), *O. officinalis* complex (comprises diploid and allotetraploid species of BB, CC, DD or EE genomes), *O. granulata* complex (GG genome) and *O. ridleyi* complex (allotetraploids of HH and JJ or KK genome). There is also a prominent outgroup consisting of a lone species *O. brachyantha* (FF genome). These wild relatives are considered as virtually untapped reservoir of agronomically important genes especially for genes conferring resistance to biotic and abiotic stresses.

Table 5. Different species of genus *Oryza* and their useful traits for biotic stress tolerance.

Oryza species	Chr. No.	Genome	Origin	Useful traits
O. sativa complex				
O. rufipogon	24	AA	Tropical Asia	Rresistance to BB and tolerance to tungro
O. nivara	24	AA	Tropical Asia	Resistance to grassy stunt virus and BB
O. longistaminata	24	AA	Africa	Resistance to BB
O. barthii	24	AA	Africa	-
O. meridionalis	24	AA	Tropical Australia	-
O. glumaepatula	24	AA	South and Central America	-
O. officinalis complex				
O. punctata	24, 48	BB, BBCC	Africa	Resistance to BPH
O. minuta	48	BBCC	Philippines and Papua New Guinea	Resistance to sheath blight, blast, BB, BPH
O. malampuzhaensis	48	BBCC	Southern India	Resistance to BB
O. officinalis	24	CC	Tropical Asia	Resistance to BPH, WBPH and GLH
O. rhizomatis	24	CC	Sri Lanka	-
O. eichingeri	24	CC	South Asia and East Africa	Resistance to BPH, WBPH and GLH
O. latifolia	48	CCDD	South America	Resistance to BPH
O. alta	48	CCDD	South America	Resistance to stem borer
O. grandiglumis	48	CCDD	South America	-
O. australiensis	24	EE	Tropical Australia	Resistance to BPH and blast
O. granulata complex				
O. granulata	24	GG	Southeast Asia	-
O. meyeriana	24	GG	Southeast Asia	-
O. ridleyi complex				
O. longiglumis	48	HHJJ	Indonesia	Resistance to blast and BB
O. ridleyi	48	HHJJ	South Asia	Resistance to blast, BB and stemborer
O. schlechteri	24	HHKK	Papua New Guinea	-
O. coarctata	48	HHKK	India	-
Outgroup				
O. brachyantha	24	FF	Africa	Resistance to yellow stem borer

7. MAPPING OF GENES/ QTLS FROM WILD RICE AND THEIR UTILIZATION

The rice breeders have mostly preferred hybridization among the members of cultivated gene pool like *indica-indica*, *japonica-japonica*, *indica-japonica*, *indica*-tropical *japonica* in their regular breeding programmes. Utilization of wild species remained limited although in several cases, genetic variability for target agronomic traits were lacking in the primary gene pool. The wild species of rice have been utilized as a valuable source of genes for tolerance to various biotic (Table 6) and abiotic stresses. Several major genes for resistance to brown planthopper (BPH), white backed plant hopper (WBPH), gall midge, bacterial blight (BB), sheath rot and leaf/neck blast have been identified from them. Several alien introgressed lines developed using wild *Oryza* as the donor has been released in different countries (Brar and Singh 2011).

The transfer of wild genes in cultivated rice depends on multiple factors like the inheritance pattern of the trait (quantitative/qualitative or monogenic/oligogenic/ polygenic), phylogenetic relationship of cultivated and wild species and the presence of reproductive barriers. Several pre- and post-fertilization barriers create difficulty in hybridization of wild and cultivated rice. The transfer of desired genes or QTLs from wild rice is difficult as the wild species are associated with several weedy traits like grain shattering, low grain yield/quality and unwanted plant types. Along with advancements in plant tissue culture techniques especially embryo rescue and protoplast fusion, wild species are increasingly being used in gene transfer. Cytogenetic techniques along with the availability of cross-transferrable markers derived from genome sequencing projects have created further opportunities for precise transfer of genomic regions from wild species.

Among several species of *O. sativa* complex, wild introgression lines for biotic stress tolerance have been developed mostly for resistance to bacterial blight. Three important genes for BB resistance have been mapped from the members of this species complex namely *Xa30 (t)* from *O. nivara*, *Xa23* from *O. rufipogon* and *Xa21* from *O. longistaminata*. These genes have further been utilized worldwide for rice breeding.

Ten distinct species are found in *O. officinalis* complex which are either diploid or allotetraploid. The basic genomic groups are BB, CC, DD or EE. Two C- genome species have mostly been used, namely *O. offcinalis* and *O. eichingeri*. Many of the introgression lines derived from *O. officinalis* complex confers resistance to BPH besides genes for resistance to WBPH, BLB and sheath rot. In Vietnam, four *O. officinalis* derived BPH resistance lines have been released as varieties (Brar and Singh, 2011).*O. eichingeri* have also been used for transfer of BPH resistance genes to cultivated rice. Although interspecific hybrids were derived between *O. sativa* and tetraploid wild species *O. minuta*, *O. punctata* and *O. malampuzhaensis;* development of advanced introgression lines was only possible with *O. minuta* for transferring resistance against BPH, BLB and blast. Among the three species with CCDD genome *O. latifolia*, *O. grandiglumis* and *O. alta*, the third one is yet to be utilized in rice breeding. However, introgression lines were derived from the rest two species. BPH,

Table 6. List of genes/ QTLs identified from wild rice for biotic stress resistance.

Wild species	Trait	Genes/QTL
O. rufipogon	BB	*Xa23*
O. nivara	BB	*Xa30(t)*
O. longistaminata	BB	*Xa21*
O. officinalis	BPH	*Bph6, Bph11, Bph13(t), Bph15*
	BB	*Xa29*
O. eichingeri	BPH	*Bph13*
O. minuta	BPH	*Bph20(t) and Bph21(t)*
	BB	*Xa29*
	Blast	*Pi9(t).*
O. latifolia	BPH	*Bph12*
O. australiensis	BPH	*Bph10*, *Bph18*
	Leaf and neck blast	*Pi40(t)*

WBPH and BLB resistant lines have been developed by transfer of genes from *O. latifolia*. From backcross progeny lines of *O. sativa* × *O. grandiglumis*, although no genes for stress tolerance were transferred, QTLs for yield contributing traits have been mapped successfully. *O. australiensis* (EE) derived introgression with resistance to BPH and leaf blast have been developed. Several important genes like *Bph10, Bph18* and *Pi40 (t)* have been tagged from these lines.

Introgression line development from *O. ridleyi* and *O. granulata* complex, as well as *O. brachyantha* for biotic stress tolerance especially for the stresses considered in this book chapter, is still lacking. However, MAAL lines with tolerance to many of these stresses have been successfully developed by several researchers.

8. KNOWLEDGE GAPS AND RESEARCH NEEDS

Except for sheath blight and YSB, for all the pathogens and insects discussed here, several major genes conferring resistance have been identified, fine mapped and few of them have been cloned (Fig. 1). Many of them are also in use by the breeders for developing disease resistant cultivars. Despite the reasonably good amount of knowledge generated and genomic resources developed, breeders still find difficulty in their judicious utilization in marker-assisted selection. Out of so many genes known for disease resistance, lack of highly reproducible functional markers for most of them creates troubles in their appropriate utilization. There is a need for mega-scale allele mining among the large pool of susceptible and resistant cultivars. Such a search should go beyond the cultivated species and must include multiple accessions of wild species. Rather than targeting only one SNP, most appropriate haplotypes must be identified after precise phenotyping.

Despite being the storehouse for genes of resistance to various biotic stresses, utilization of genes and alleles from wild species is still very limited. Precise transfer of genes from wild species avoiding linkage drag is quite difficult till now for most of the

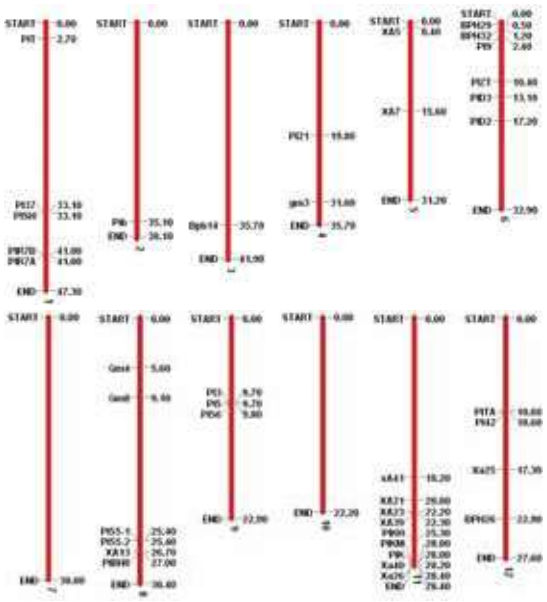

Fig. 1. Chromosomal location of cloned biotic stress resistance genes in rice

breeders. Lack of availability of genomic resources especially genome-wide markers for wild species creates a major bottleneck for this. However with the availability of genome sequences for more number of wild species (genome sequence is now available for eight wild and two cultivated species of *Oryza*) such bottlenecks are expected to be removed very soon.

For many biotic stresses, despite sincere efforts, it has not become possible till date to assign resistance function to a single gene. However, QTLs with various level of tolerance or resistance have been mapped. Although many of these QTLs are genotype specific, some major QTLs were found to work across populations. Precise mapping of those QTLs and their subsequent utilization in large scale is expected in near future.

With large numbers of genes or QTLs being mapped, the question arises about identifying the appropriate combinations of genes or QTLs for pyramiding in a single background. Different genes or QTLs conferring resistance to same stress have different mechanisms of actions. Identifying their appropriate combinations which will confer maximum and durable resistance without any adverse effect on plant growth and development is need of the hour. All the discovered genes or QTLs may be pyramided in various combinations and tested across different growing environments. Some efforts in this direction have already been initiated (Jena et al. 2017) which needs to be strengthened further.

All the research on resistance to biotic stresses will fail if there is any gap in phenotyping methods. With increasing needs for mega-scale phenotyping for biotic stress resistance, development of an easy yet effective protocol to clearly distinguish the escapes from true resistance is the need of the time.

9. WAY FORWARD

The primary requirement for breeding tolerance to biotic stresses is availability of precise phenotyping standards which will work across locations and can clearly distinguish resistance from escapes. Whenever such phenotyping standards are

available, the phenotyping for those biotic stresses should be carried out in large scale utilizing the network mode of AICRP or international trials of IRRI. This will help in keeping track of evolution of new pathogens or insect biotypes and search for their corresponding resistance source. The effective resistant QTLs or genes identified though biparental mapping approaches should be supplemented with genome wide association mapping to identify genes/QTLs which will work across populations. After discovery of any gene or QTL, its optimum pyramiding combinations should be worked out with reported genes or QTLs. Till date the major target of scientists working on host plant resistance remains limited to search for R-genes in host genomes. With advancements in genome sequencing, the scope for utilization of genome sequences of both pest and host for understanding mechanism of resistance as well as breakdown of resistance have increased. For identification of functional markers, identification of superior functional haplotypes of resistance genes from both wild and cultivated species is highly required. Prediction of R-genes from genomes of wild species through bioinformatics approaches and their validation will also be useful. It is important to note that stable and durable resistance genes present in wild rice are yet to be exploited in large scale. There is urgent need for inclusion of more numbers of wild species in breeding programmes of rice through pre-breeding and marker assisted selection for their judicious utilization in resistance breeding of rice.

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