



# Current status on mapping of genes for resistance to leaf- and neck-blast disease in rice

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## Abstract

Blast disease caused by fungal pathogen *Pyricularia oryzae* is a major threat to rice productivity worldwide. The rice-blast pathogen can infect both leaves and panicle neck nodes. Nearly, 118 genes for resistance to leaf blast have been identified and 25 of these have been molecularly characterized. A great majority of these genes encode nucleotide-binding site–leucine-rich repeat (NBS–LRR) proteins and are organized into clusters as allelic or tightly linked genes. Compared to ever expanding list of leaf-blast-resistance genes, a few major genes mediating protection to neck blast have been identified. A great majority of the genetic studies conducted with the genotypes differing in the degree of susceptibility/resistance to neck blast have suggested quantitative inheritance for the trait. Several reports on co-localization of gene/QTLs for leaf- and neck-blast resistance in rice genome have suggested the existence of common genes for resistance to both phases of the disease albeit inconsistencies in the genomic positions leaf- and neck-blast-resistance genes in some instances have presented the contrasting scenario. There is a strong evidence to suggest that developmentally regulated expression of many blast-resistance genes is a key determinant deciding their effectiveness against leaf or neck blast. Testing of currently characterized leaf-blast-resistance genes for their reaction to neck blast is required to expand the existing repertoire resistance genes against neck blast. Current developments in the understanding of molecular basis of host–pathogen interactions in rice-blast pathosystem offer novel possibilities for achieving durable resistance to blast through exploitation of natural or genetically engineered loss-of-function alleles of host susceptibility genes.

**Keywords** *Pyricularia oryzae* · *Oryza sativa* · Leaf blast · Neck blast · QTLs · Mapping

## Introduction

Rice (*Oryza sativa* L.) is one of the most important food crops, feeding more than 50% of the world's population. Rice is affected by several biotic and abiotic stresses amongst which blast disease caused by the fungal pathogen *Pyricularia oryzae* Cavara (Telomorph, *Magnaporthe oryzae*) is a major biotic stress that threatens rice production worldwide (Ashkani et al. 2015; Wang et al. 2015). The disease causes yield losses ranging from 10 to 30% each year which translates into a loss of about 157 million tonnes of rice worldwide (Talbot 2003). The disease has two commonly recognized phases: leaf blast and neck blast. Leaf

blast occurs most often during the plant's vegetative stage causing characteristic spindle shaped lesions on leaf blade and necrotic lesions at leaf collar. The neck blast (a near synonym of panicle blast), which is the most destructive form of the disease, occurs during the reproductive stage and is characterized by fungal infection at the panicle base and plant nodes. The fungal infection at the panicle base restricts the flow of photosynthates to the developing grains resulting in chaffy grains or empty panicles. The yield reduction inflicted by neck-blast infection is twice as severe as leaf blast with losses approaching up to 70% of the anticipated yield under epidemic conditions (Puri et al. 2009). Although wide range of effective fungicides are available to control the disease, their use is not favoured by the farmers due to cost, and associated environmental and health issues. The development and deployment of rice varieties fortified with a high level of resistance to both leaf and panicle blast is one of the most economical ways to manage the disease. Identification of effective sources of resistance genes and their precise

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mapping in rice genome is one of the basic requirements for effective manipulations of these genes in resistance breeding programmes. In the following sections, we have presented a detailed update on identification, mapping and molecular characterization of leaf, and panicle blast-resistance genes in rice.

## Genetics and mapping of genes governing resistance to leaf-blast disease

The discovery and utilization of disease-resistance genes for breeding broad-spectrum-resistant genotypes is the most preferred strategy to manage the blast disease. Genetic investigations on blast resistance started in the early 1920s when Sasaki (1922) for the first time observed that rice varieties differed in their response to different isolates of rice-blast fungus *P. oryzae*. Extensive genetic studies that followed led to the identification of first leaf-blast-resistance gene *Pi-a* from *japonica* rice variety, Aichi Asahi (Kiyosawa 1967). First attempt to map a blast-resistance gene was made by Yu et al. (1991), who mapped two blast-resistance genes, *Pi-2(t)* and *Pi-4(t)* using Restriction Length Fragment Polymorphism (RFLP) analysis of a set of near isogenic lines. Since the development of first genetic map of rice based on RFLP markers in 1988 (McCouch et al. 1988), a great variety of genetic markers, including simple sequence repeats (SSRs), single-nucleotide polymorphisms (SNPs), and small insertions/deletions (InDels), amplified fragment length polymorphisms (AFLPs), random amplified polymorphic DNAs (RAPDs), cleaved amplified polymorphic sequences (CAPS), and RFLPs have been used for genetic mapping in rice culminating in development of high density linkage maps of rice (Inoue et al. 1994; Chen et al. 1997; Harushima et al. 1998; Monna et al. 1994; Mackill et al. 1996; Cho et al. 2000; McCouch et al. 2002). In the current decade, the accessibility of complete genome sequences of rice subspecies *indica* and *japonica* (<http://rgp.dna.affrc.go.jp>; <http://www.genomics.org.cn>) has enabled the rice researchers to exploit DNA polymorphisms such as SNPs and InDels for the fine scale mapping of the targeted genes (Lei et al. 2013; Wang et al. 2016b; Liu et al. 2013; Hu et al. 2018). These developments have helped mapping a number of blast-resistance genes that have been precisely localized on the rice chromosomes. In rice, nearly, 118 genes for resistance to leaf-blast disease have been identified through genetic analyses of rice varieties belonging to both *japonica* and *indica* subspecies and 25 of them have been cloned and characterized until date (Tables 1, 2). Of the total identified leaf-blast-resistance genes, a great majority is located on chromosomes 6, 11, and 12 which harbour 21, 27, and 27 leaf-blast-resistance genes, respectively. Chromosomes 3 and 7 contain minimum number of blast-resistance genes with only one gene in each. Classical and molecular genetic

analyses have revealed that a great majority of blast-resistance genes are distributed into clusters consisting of allelic or tightly linked genes. At least three major clusters of blast-resistance genes have been detected in rice on chromosomes 6, 11, and 12 (Zhou et al. 2006; Zhai et al. 2011; Yang et al. 2009). For example, ten blast-resistance genes, *Pi8*, *Pi9*, *Pi26(t)*, *Pi27(t)*, *Pi40*, *Piz*, *Pi-2*, *Piz-t*, *Pigm(t)*, and *Pi59(t)*, have been mapped at the *Piz* locus on chromosome 6 (Koide et al. 2013) and at least 9 resistance genes have mapped to R-gene cluster on the telomeric end of rice chromosome 11 and seven of them viz., *Pi-k*, *Pi-ks*, *Pi-kp*, *Pi-km*, *Pi-kh*, *Pi-kl*, and *Pi-l* have been shown to be the alleles of *Pi-k* locus (Zhai et al. 2011; Hua et al. 2012; Singh et al. 2015). Similarly, at least nine blast-resistance specificities, *Pi12*, *Pita*, *Pita2*, *Pi39*, *Pi42*, *Pi24*, *Pi20*, *PiGD3*, and *Pi157* have been mapped to R-gene cluster at the centeromeric region of rice chromosome 12 (Bryan et al. 2000; Zhuang et al. 2002; Liu et al. 2004, 2007b; Li et al. 2008; Kumar et al. 2010). A chromosomal map depicting distribution of leaf-blast-resistance genes across different rice chromosomes is shown in Fig. 1.

Amongst the molecularly characterized major leaf-blast R genes, 22, namely, *Pi37*, *Pit*, *Pi-sh*, *Pi64*, *Pi-b*, *Pi63*, *Pi9*, *Pi-2*, *Piz-t*, *Pid3*, *Pigm*, *Pi25*, *Pi36*, *Pi5*, *Pi-54*, *Pik-m*, *Pi-k*, *Pik-p*, *Pik-e*, *Pi-a*, *Pi1*, and *Pita*, belong to the largest class of plant R genes that encode proteins with nucleotide-binding site (NBS) and leucine-rich repeat (LRR) domains (Lin et al. 2007a; Hayashi and Yoshida 2009; Takahashi et al. 2010; Ma et al. 2015; Wang et al. 1999; Xu et al. 2014; Qu et al. 2006; Zhou et al. 2006; Shang et al. 2009; Deng et al. 2009; Chen et al. 2011; Liu et al. 2007a; Lee et al. 2009b; Sharma et al. 2005; Ashikawa et al. 2008; Zhai et al. 2011; Yuan et al. 2011; Chen et al. 2015; Okuyama et al. 2011; Hua et al. 2012; Bryan et al. 2000), whereas one, *Pid2*, encodes serine–threonine–kinase membrane spanning protein (Chen et al. 2006). *pi21*, the only field blast-resistance gene cloned until date, encodes a protein with heavy-metal binding and proline-rich domains (Fukuoka et al. 2009) and *Pitr*, an atypical resistance gene, encodes a putative E3 ligase with four Armadillo repeats (Zhao et al. 2018).

Molecular mapping and cloning of blast-resistance genes have provided several opportunities to augment the conventional disease-resistance breeding by enabling efficient selection of resistance genes in breeding programmes (Singh et al. 2012), pyramiding of resistance genes for achieving broad spectrum and durable resistance (Hittalmani et al. 2000), cataloguing of gene bank collections for resistance genes (Vasudevan et al. 2014; Yadav et al. 2017), and unraveling allelic diversity for resistance genes in germplasm collections through sequencing-based allele mining (Vasudevan et al. 2015; Lv et al. 2017). Genetic mapping and molecular cloning of different blast-resistance genes have provided an array of gene-linked, gene

**Table 1** List of blast-resistance genes mapped through molecular markers

Sr. no.	Gene	Donor	Genomic position (Mb)	Chromosome	Linked marker	References
1	<i>Pit</i>	K-59, Tjahaja, K-59	2.27	1	RFLP, SNP	Kaji et al. (1997) and Hayashi et al. (2006)
2	<i>Pi27(t)</i>	Q14	5.55	1	SSR	Zhu et al. (2004)
3	<i>Pi-h2(t)</i>	HR4	7.90	1	SSR	Xiao et al. (2015)
4	<i>Pi-tp(t)</i>	Tetep	25.13	1	SSR	Barman et al. (2004)
5	<i>Pi35(t)</i>	Hokkai 188	32.1	1	SSR	Nguyen et al. (2006)
6	<i>Pi64</i>	Yangmaogu	32.31	1	SSR, Indel	Ma et al. (2015)
7	<i>Pi 37(t)</i>	St. No. 1	33.1	1	SSR	Chen et al. (2005)
8	<i>Pi-sh</i>	Akihikari	33.3	1	SSR	Fukuta (2004)
9	<i>Pir2-3(t)</i>	IR64	—	2	SSR	Dwinita et al. (2008)
10	<i>Pirf2-1(t)</i>	<i>O. rufipogon</i>	—	2	SSR	Dwinita et al. (2008)
11	<i>Pi-Da(t)</i>	Dacca 6	2.21	2	SSR	Shi et al. (2012)
12	<i>Pig(t)</i>	Guangchangzhan	34.34	2	SSR	Zhou et al. (2004)
13	<i>Pi-25(t)</i>	IR64	34.36	2	QTL	Sallaud et al. (2003)
14	<i>Pi-tq5</i>	Teqing	34.61	2	RFLP	Tabien et al. (2000)
15	<i>Pi-14(t)</i>	Maowangu	34.94	2	RFLP, Isozyme	Pan et al. (1998) and Zhou et al. (2004)
16	<i>Pi-16(t)</i>	AUS373	34.94	2	RFLP, Isozyme	Pan et al. (1999) and Zhou et al. (2004)
17	<i>Pi-d1(t)</i>	Digu	34.94	2	SSR, RFLP	Chen et al. (2004)
18	<i>Pi-y2(t)</i>	Yanxian No. 1	35.03	2	SSR	Lei et al. (2005)
19	<i>Pi-y1(t)</i>	Yanxian No. 1	35.03	2	SSR	Lei et al. (2005)
20	<i>Pi-b</i>	Tohoku, Koshiihikari	35.10	2	SNP	Hayashi et al. (2006)
21	<i>Pi66(t)</i>	AS20-1	26.78	3	SSR	Liang et al. (2016)
22	<i>Pikur 1</i>	Kuroka	—	4	Isozyme	Fukuoka et al. (2009)
23	<i>pi-21</i>	Owarihatamochi	19.81	4	RFLP, SSR	Fukuoka and Okuno (2001)
24	<i>Pias(t)</i>	Asominori	31.26	4	SSR, CAPS	Endo et al. (2012)
25	<i>Pi-45(t)</i>	Moroberekan	31.49	4	SSR	Kim et al. (2011)
26	<i>Pikahei-1(t)</i>	Kahei	31.67	4	SSR, SNP	Xu et al. (2008a)
27	<i>Pi-39(t)</i>	Chubu 111	32.68	4	SSR	Terashima et al. (2008)
28	<i>Pi26(t)</i>	IR64	2.78	5	RFLP, RAPD,	Sallaud et al. (2003)
29	<i>Pi23</i>	Suweon 365	10.75	5	RFLP, SSR	Ahn et al. (1997)
30	<i>Pi-10(t)</i>	Tongil	14.52	5	RAPD	Naqvi et al. (1995)
31	<i>Pi22</i>	Suweon 365	4.89	6	RFLP	Ahn et al. (1997)
32	<i>Pi27(t)</i>	IR64	6.92	6	RFLP	Sallaud et al. (2003)
33	<i>Pi-40(t)</i>	IR65482	9.86	6	STS, SSR	Jeung et al. (2007)
34	<i>Pi2-1</i>	Tianjingyeshengdao	10.08	6	SSR, SFP	Wang et al. (2012)
35	<i>Pi2-2</i>	Jefferson	10.20	6	SSR	Jiang et al. (2012)
36	<i>Pigm(t)</i>	Gumei 4	10.36	6	CAPS, InDel	Deng et al. (2006)
37	<i>Pi-9(t)</i>	IR31917	10.38	6	STS	Qu et al. (2006)
38	<i>Pi51(t)</i>	D69	10.38	6	InDel, SSR	Xiao et al. (2012)
39	<i>Pi2</i>	5173, C101A51	10.39	6	SSR, STS, RFLP	Jiang and Wang (2002) and Zhou et al. (2006)
40	<i>Piz</i>	Fukinishiki	10.39	6	STS	Zhou et al. (2006)
41	<i>Piz-t</i>	Toride No. 1	10.39	6	STS	Zhou et al. (2006)
42	<i>Pi50(t)</i>	EBZ	10.41	6	SSR, CAPS	Zhu et al. (2012)
43	<i>Pi59(t)</i>	Hoaru	10.82	6	SSR	Koide et al. (2013)
44	<i>Pi26(t)</i>	Gumei 2	11.06	6	RFLP, SSR	Wu et al. (2005)
45	<i>Pi8</i>	Kasalath	11.36	6	Isozyme markers, RFLP	Pan et al. (1996a) and Takehisa et al. (2009)
46	<i>Pi-25(t)</i>	Gumei 2	12.33	6	RFLP, RGA, SSR	Wu et al. (2005)

**Table 1** (continued)

Sr. no.	Gene	Donor	Genomic position (Mb)	Chromosome	Linked marker	References
47	<i>Pid3</i>	Digu	13.05	6	STS	Shang et al. (2009)
48	<i>Pi-13</i>	Kasalath	15.83	6	SSR	Ebitani et al. (2011)
49	<i>Pi-dt(2)</i>	Digu	17.16	6	SSR, RGA	Chen et al. (2004)
50	<i>Pid2</i>	Digu	17.16	6	CAPS	Chen et al. (2006)
51	<i>Pi-tq1</i>	Teqing	29.02	6	RFLP	Tabien et al. (2000)
52	<i>Pi-17(t)</i>	DJ 123	22.25	7	Isozyme marker	Pan et al. (1996b)
53	<i>Pi-11(t)</i>	Zhai-Ye-Quing	13.93	8	RFLP, RAPD	Causse et al. (1994)
54	<i>Pi-33</i>	IR64, Bala	7.56	8	SSR, RFLP	Berruyer et al. (2003)
55	<i>Pi-29(t)</i>	IR64	13.93	8	RFLP, RAPD, Isozyme	Sallaud et al. (2003)
56	<i>PiGD-1(t)</i>	Sanhuangzhan 2	16.37	8	SSR, RFLP, RGA	Liu et al. (2004)
57	<i>Pi-36(t)</i>	Q61	2.87	8	SSR, CRG	Liu et al. (2005)
58	<i>pi55(t)</i>	Yuejingsimiao 2	25.58	8	SSR, STS	Xiu-Ying et al. (2012)
59	<i>Pi-5(t)</i>	RIL249	9.77	9	AFLP, RFLP, CAPS	Jeon et al. (2003)
60	<i>Pi15</i>	GA25	9.61	9	SSR, CRG	Lin et al. (2007b)
61	<i>Pi56(t)</i>	SHZ-2	9.77	9	SSR, CRG, SNP	Liu et al. (2013)
62	<i>Pihk2</i>	Heikezijing	10.17	9	SSR, ILP, InDel	He et al. (2017)
63	<i>PiGD-2(t)</i>	Sanhuangzhan 2	–	10	SSR, RFLP, RGA	Liu et al. (2004)
64	<i>Pi28(t)</i>	Azucena	21.04	10	RFLP, RAPD	Sallaud et al. (2003)
65	<i>Pi-30(t)</i>	IR64	4.41	11	RFLP, RAPD, Isozyme	Sallaud et al. (2003)
66	<i>Pi-a</i>	Aichi Asahi	6.49	11	SSR, Indel	Zeng et al. (2011)
67	<i>Pi60(t)</i>	93-11	6.62	11	SSR, InDel	Lei et al. (2013)
68	<i>Pi-CO39(t)</i>	Co39	6.66	11	SSR, RFLP	Chauhan et al. (2002)
69	<i>Pi-7(t)</i>	Moroberekan	18.64	11	RFLP	Wang et al. (1994)
70	<i>Pi-34</i>	Chubu-32	19.96	11	SSR	Zenbayashi et al. (2007)
71	<i>Pi-38</i>	Tadukan	22.48	11	SSR, AFLP	Gowda et al. (2006)
72	<i>Pik-h</i>	IRBLkh-K3	24.99	11	SNP	Xu et al. (2008b)
73	<i>Pi54</i>	Tetep	25.26	11	SSR	Sharma et al. (2005)
74	<i>Pik-s</i>	Shin 2	27.31	11	SSR	Fjellstrom et al. (2004)
75	<i>Pi-jnw1</i>	Jiangnanwan	27.36	11	SSR, InDel	Wang et al. (2016b)
76	<i>Pi-hk1</i>	Heikezijing	27.66	11	SSR	Wu et al. (2013)
77	<i>Pi43(t)</i>	Zhe733	27.67	11	SSR	Lee et al. (2009a)
78	<i>Pi-47</i>	Xiangzi 3150	27.67	11	SSR	Huang et al. (2011)
79	<i>Pik-l</i>	Liziangxintuanheigu	27.69	11	SSR, STS, CAPS	Singh et al. (2015)
80	<i>Pi46(t)</i>	H4	27.74	11	SSR, InDel	Xiao et al. (2011)
81	<i>Pi-1(t)</i>	Apura, C101LAC	28.00	11	STS, RFLP, SSR, CAPS	Parco (1995), Yu et al. (1996), Fuentes et al. (2008) and Hua et al. (2012)
82	<i>Pik-m</i>	Tohoku IL4, Tsuyuake	28.00	11	RFLP, SSR	Kaji and Ogawa (1996) and Li et al. (2007)
83	<i>Pik-e</i>	Xiangzao 143	28.00	11	SSR, InDel	Chen et al. (2015)
84	<i>Pi-k</i>	Kusabue, Kanto 51	28.01	11	RFLP, InDel, SNP	Hayasaka et al. (1996) and Hayashi et al. (2006)
85	<i>Pik-p</i>	K60	28.05	11	SSR, CAPS	Wang et al. (2009)
86	<i>Pi-h1(t)</i>	HR4	28.11	11	SSR, InDel	Xiao et al. (2015)
87	<i>Pi65(t)</i>	Gangyu 129	28.22	11	SNP, InDel	Zheng et al. (2016)
88	<i>Pi49</i>	Mowangu	28.80	11	SSR	Sun et al. (2013)
89	<i>Pi-44(t)</i>	Moroberekan	28.93	11	RFLP, STS, AFLP	Chen et al. (1999)
90	<i>Pi18</i>	Suweon365	28.93	11	RFLP	Ahn et al. (2000)
91	<i>Pi-lm2</i>	Lemont	28.93	11	RFLP	Tabien et al. (2000)
92	<i>Pi-6(t)</i>	Apura	7.73	12	RFLP	Yu et al. (1996)

**Table 1** (continued)

Sr. no.	Gene	Donor	Genomic position (Mb)	Chromosome	Linked marker	References
93	<i>Pi12</i>	Hong Jiao Zhan	7.73	12	RFLP	Zhuang et al. (1998)
94	<i>Pi62(t)</i>	Yashiromochi	7.73	12	RAPD, RFLP	Wu et al. (1996)
95	<i>Pi12</i>	Hong Jiao Zhan	7.73	12	RFLP	Zhuang et al. (1998)
96	<i>Pi62(t)</i>	Yashiromochi	7.73	12	RAPD, RFLP	Wu et al. (1996)
97	<i>Pi-tq6</i>	Teqing	7.73	12	RFLP	Tabien et al. (2000)
98	<i>Pitb</i>	Zixuan	9.37	12	SSR, InDel	Sun et al. (2016)
99	<i>Pita3(t)</i>	IRBLta2-Re	9.89	12	SSR	Chen et al. (2014)
100	<i>Pi61(t)</i>	93-11	9.98	12	InDel, SSR	Lei et al. (2013)
101	<i>Pi58(t)</i>	Haoru	10.42	12	SSR	Koide et al. (2013)
102	<i>Pita</i>	Yashiromochi	10.60	12	RFLP, RAPD, SNP	Rybka et al. (1997) and Hayashi et al. (2006)
103	<i>Pita-2</i>	Yashiromochi, Pi No. 4	10.60	12	RFLP, RAPD, SNP	Rybka et al. (1997) and Hayashi et al. (2006)
104	<i>Pi-24(t)</i>	Zhong 156	10.60	12	RFLP, RAPD, RGA	Zhuang et al. (2002)
105	<i>Pi-39</i>	Q-15	10.61	12	SSR	Liu et al. (2007b)
106	<i>Pi-42(t)</i>	DHR9	10.62	12	RAPD, SSR, STS	Kumar et al. (2010)
107	<i>Pi-19(t)</i>	IRBL19-A	10.73	12	SSR	Koide et al. (2011)
108	<i>Pi57(t)</i>	IL-E1454	10.80	12	SSR, STS	Dong et al. (2017)
109	<i>Pi-31(t)</i>	IR64	11.93	12	RFLP, RAPD,	Sallaud et al. (2003)
110	<i>Pi-48</i>	Xiangzi 3150	11.95	12	SSR	Huang et al. (2011)
111	<i>Pi51(t)</i>	Tianjingyeshengdao	11.95	12	SSR, SFP	Wang et al. (2012)
112	<i>Pi67</i>	Tetep	12.09	12	SSR	Joshi et al. (2019)
113	<i>Pi157</i>	Moroberekan	12.37	12	RFLP	Naqvi and Chattoo (1996)
114	<i>Pi-20(t)</i>	IR64	12.95	12	SSR	Li et al. (2008)
115	<i>Pih3(t)</i>	HR4	12.95	12	SSR	Xiao et al. (2015)
116	<i>PiGD-3(t)</i>	Sanhuangzhan 2	14.45	12	SSR, RFLP, RGA	Liu et al. (2004)
117	<i>Pi-41</i>	93-11	16.74	12	SSR, STS	Yang et al. (2009)
118	<i>Pi-32(t)</i>	IR64	21.24	12	RFLP, RAPD	Sallaud et al. (2003)

based, or functional markers for the efficient selection of resistance genes in breeding programmes (Jia et al. 2002; Shang et al. 2009; Hayashi et al. 2010). Structural comparisons of the cloned members of multi-allelic resistance loci have also provided information on the DNA regions within these genes responsible for their distinct-resistance specificities and offered the possibility of using these as the basis for identification of different resistance alleles in breeding programmes (Zhou et al. 2006; Zhai et al. 2011; Hua et al. 2012).

Marker-assisted backcross breeding has been successfully used to transfer single or a combination of various leaf-blast-resistance genes such as *Pi1*, *Piz-5*, and *Pita* into rice variety Co39 (Hittalmani et al. 2000), *Pi2*, *Pi9*, *Pi1*, *Pi54*, *Pita*, *Pi-b*, and *Pi5* genes into varieties such as Pusa Basmati 1 (Khanna et al. 2015), *Pi2*, and *Pi54* into Pusa Basmati 1121, Pusa Basmati 6, and parental lines of Basmati hybrids (Singh et al. 2012; Ellur et al. 2016). The detailed information on the applications of molecular markers in

blast-resistance breeding has been recently reviewed by Ashkani et al. (2015) and Srivastva et al. (2017).

### Genetics and mapping of genes governing resistance to neck-blast disease

Of the two known phases of rice blast, the neck blast is economically more significant causing yield losses up to 70–100% under epidemic conditions (Puri et al. 2009). Although tremendous success has been achieved in identification and characterization of genes governing resistance against leaf blast, genetic studies on neck-blast resistance have lagged far behind. Though there are around 118 *R* genes identified for leaf-blast resistance, very few genes mediating resistance to neck blast have been identified and precisely mapped in rice genome (Table 3). The reports on leaf-blast-resistant cultivars being susceptible to neck blast and vice versa (Sirithunya et al. 2002; Zhuang et al. 2002; Puri et al. 2009; Ishihara et al. 2014), imply that there may



**Table 2** List of leaf-blast-resistance genes cloned and characterized from rice

Sr no.	Gene designation	Chromosome	Cloning strategy	Protein type	References
1	<i>Pi37</i>	1	MB	NBS-LRR	Lin et al. (2007a)
2	<i>Pit</i>	1	MB	CC-NBS-LRR	Hayashi and Yoshida. (2009)
3	<i>Pi-sh</i>	1	Mutant screening	CC-NBS-LRR	Takahashi et al. (2010)
4	<i>Pi64</i>	1	MB	CC-NBS-LRR	Ma et al. (2015)
5	<i>Pi-b</i>	2	MB	NBS-LRR	Wang et al. (1999)
6	<i>pi21</i>	4	MB	Proline-rich heavy-metal-binding protein	Fukuoka et al. (2009)
7	<i>Pi63</i>	4	MB	CC-NBS-LRR	Xu et al. (2014)
8	<i>Pid-2</i>	6	MB	Lectin receptor	Chen et al. (2006)
9	<i>Pi9</i>	6	MB	NBS-LRR	Qu et al. (2006)
10	<i>Pi-2</i>	6	MB	NBS-LRR	Zhou et al. (2006)
11	<i>Piz-t</i>	6	MB	NBS-LRR	Zhou et al. (2006)
12	<i>Pid3</i>	6	In silico analysis	NBS-LRR	Shang et al. (2009)
13	<i>Pigm</i>	6	MB	NBS-LRR	Deng et al. (2009)
14	<i>Pi25</i>	6	MB	CC-NBS-LRR	Chen et al. (2011)
15	<i>Pi36</i>	8	MB	CC-NBS-LRR	Liu et al. (2007a)
16	<i>Pi5</i>	9	MB	CC-NBS-LRR	Lee et al. (2009b)
17	<i>Pi-54/Pi-kh</i>	11	MB	NBS-LRR	Sharma et al. (2005)
18	<i>Pik-m</i>	11	MB	NBS-LRR	Ashikawa et al. (2008)
19	<i>Pi-k</i>	11	MB	CC-NBS-LRR	Zhai et al. (2011)
20	<i>Pik-p</i>	11	MB	CC-NBS-LRR	Yuan et al. (2011)
21	<i>Pik-e</i>	11	MB	CC-NBS-LRR	Chen et al. (2015)
22	<i>Pi-a</i>	11	MB and mutant screening	CC-NBS-LRR	Okuyama et al. (2011)
23	<i>Pi1</i>	11	MB	CC-NBS-LRR	Hua et al. (2012)
24	<i>Pita</i>	12	MB	NBS-LRR	Bryan et al. (2000)
25	<i>Pitr</i>	12	MB	Putative E3 ligase	Zhao et al. (2018)

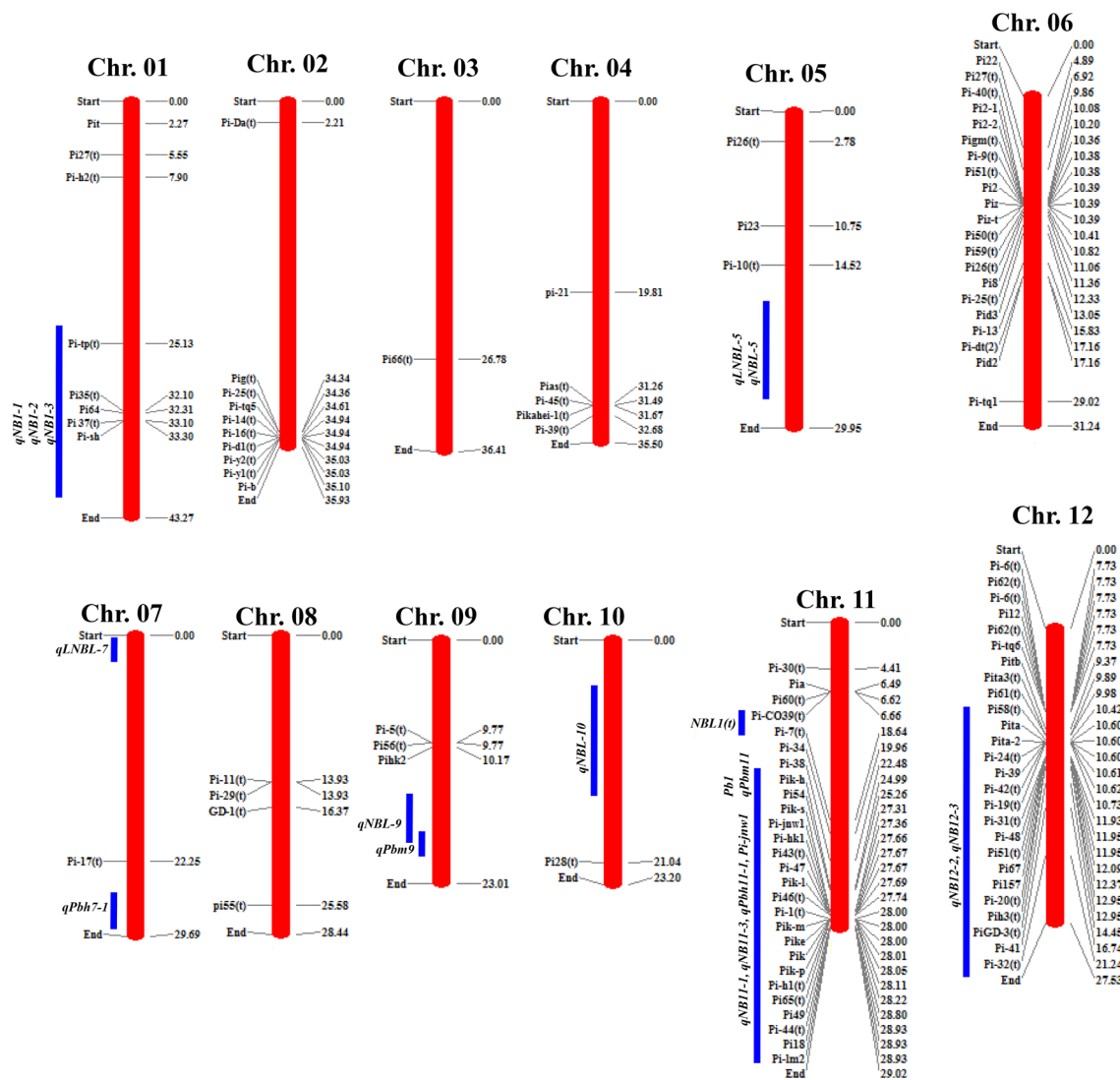
MB map based cloning

be inherent variation in the mechanisms of resistance to leaf and neck blast.

Sirithunya et al. (2002) have identified quantitative trait loci (QTLs) associated with leaf- and neck-blast resistance from a resistance donor CT9993-5-10-M (CT). Two QTLs for broad-spectrum leaf resistance have been located on chromosomes 7 and 9, whereas two neck-blast QTLs mapped to chromosomes 5 and 6. The inconsistencies in map locations of leaf- and neck-blast-resistance QTLs have suggested the presence of different genetic mechanisms for leaf- and neck-blast resistance. Alternately, there are several instances where the gene/QTLs for panicle blast resistance have been mapped on the same genomic region, where major leaf-blast-resistance genes have been located in the rice genome, suggesting the involvement of common genes for resistance to both leaf and neck blast (Noenplab et al. 2006).

A gene *Pb1* for adult-stage panicle blast resistance has been identified from an *indica* cultivar 'Modan' (Fujii et al. 2000). The gene has been localized on the long arm of chromosome 11 and is known to encode a coiled coil–nucleotide-binding site–leucine-rich repeat (CC–NBS–LRR) protein

(Hayashi et al. 2010). The gene has been introduced into several elite varieties commercially cultivated in Japan and not shown any signs of breakdown of resistance for almost 30 years (Hayashi et al. 2010). *Pb1* is known to exhibit low level of expression at the early vegetative stages (two- and six-leaf stages) and is gradually up-regulated in later developmental stages, reaching its peak expression levels at full heading stage. Interestingly, the *Pb1* transformants of a susceptible cultivar Nipponbare that constitutively over express the gene have also shown strong resistance to leaf blast at early vegetative stages (Hayashi et al. 2010). These findings clearly suggest that the expression pattern of a blast-resistance gene is a major determinant in deciding whether the gene will mediate protection to leaf or neck blast or both phases of the disease. The genes that are primarily expressed at early vegetative phase are most likely to mediate protection to leaf blast, those expressed during the flag leaf and heading stages shall display neck and panicle blast resistance, while those displaying constitutive expression throughout the plant are expected to provide protection against both the phases of the disease.



**Fig. 1** Chromosomal locations of leaf-blast R genes and quantitative trait loci (QTLs) for neck-blast resistance in rice. The chromosomal locations for R genes and QTLs were deduced by projecting the sequences of closely linked/flanking markers on the genome sequence of cv. Nipponbare released by International Rice Genome Sequencing

Zhuang et al. (2002) have identified a blast-resistance gene *Pi25(t)* from a durably resistant semi-dwarf *indica* variety ‘Gumei-2’. The gene provides resistance to both leaf and neck blast and is located in the genetic interval known to harbour well-known leaf-blast-resistance genes *Pi-2(t)* and *Pi-9(t)* on chromosome 6. Hittalmani et al. (2003) have reported that neck-blast resistance in a famous *indica* variety IR64 is controlled by both major and minor genes. A major gene *NBL1(t)* for neck-blast resistance has been associated with marker *Nbp44* on chromosome 11. Besides this, three other quantitative trait loci (QTLs) *qNBL-10*, *qNBL-9*, and *qNBL-5* explaining 8.5–24.10% of the phenotypic variations for neck-blast resistance have

been located on chromosomes 10, 9, and 5, respectively (Table 3).

Project (<http://rapdb.dna.affrc.go.jp>). The physical position of each gene/QTL in million base pair (Mb) units is shown on right side of each chromosome.

The blue bars indicate the estimated location of QTLs for neck-blast resistance as deduced from their flanking markers. Noenplab et al. (2006) have reported the co-localization of genetic factors responsible for leaf- and neck-blast resistance in a *Thai* rice variety Jao Hom Nin (JHN). A total of 14 QTLs, representing seven each for leaf- and neck-blast resistance, have been mapped on three chromosomes, namely, 1, 11, and 12. The six QTLs, three each against leaf (*qLB1-1*, *qLB1-2*, and *qLB1-3*), and neck-blast resistance (*qNBL-1*, *qNBL-2*, and *qNBL-3*) on chromosome 1 are located near the marker RM212 close to a major blast-resistance gene *Pi37*. Similarly, four QTLs representing two each for leaf (*qLB11-1* and *qLB11-3*) and neck-blast resistance

**Table 3** List of neck-blast-resistance genes and QTLs identified from rice

Sr no.	Gene/QTL	Donor	Chrm. No.	Genomic position (Mb) <sup>a</sup>	Linked marker	Phenotypic variation explained (%)	References
1	<i>qNB1-1</i> <i>qNB1-2</i> <i>qNB1-3</i>	Jao Hom Nin	1	23.97–40.16 23.97–40.16 26.81–40.16	SSR	16.57 16.75 9.02	Noenplab et al. (2006)
2	<i>Pi64</i>	Yangmaogu	1	32.31–34.34	SSR, CAPS	— <sup>b</sup>	Ma et al. (2015)
3	<i>qNBL-5</i>	IR64	5	19.60–27.81	RFLP, RAPD, SSR	11.10	Hittalmani et al. (2003)
4	<i>qLNBL-5</i>	Akhanaphou	5	19.72–23.84	SSR	13.54–26.23	Aglawe et al. (2017)
5	<i>Pi25(t)</i>	Gumei 2	6	13.05–13.06	RFLP, RGA	— <sup>b</sup>	Zhuang et al. (2002)
6	<i>qLNBL-7</i>	Akhanaphou	7	0.46–2.67	SSR	11.14–31.04	Aglawe et al. (2017)
7	<i>qPbh7-1</i>	Heikezijing	7	25.65–29.56	SSR	17.74	Fang et al. (2016)
8	<i>qNBL-9</i>	IR64	9	15.54–20.48	RFLP, RAPD, SSR	8.50	Hittalmani et al. (2003)
9	<i>qPbm9</i>	Miyazakimochi	9	19.74–21.00	SSR, SNP	5.70	Ishihara et al. (2014)
10	<i>qNBL-10</i>	IR64	10	5.48–16.65	RFLP, RAPD, SSR	24.10	Hittalmani et al. (2003)
11	<i>NBL1(t)</i>	IR64	11	7.90–10.13	RFLP, RAPD, SSR	— <sup>b</sup>	Hittalmani et al. (2003)
12	<i>qPbm11</i>	Miyazakimochi	11	22.48–24.68	SSR, SNP	30.80	Ishihara et al. (2014)
13	<i>qNB11-1</i> <i>qNB11-3</i>	Jao Hom Nin	11	22.48–28.80 24.23–28.80	SSR	34.58 22.12	Noenplab et al. (2006)
14	<i>Pb-1</i>	Modan	11	22.88–22.92	RFLP SNP, Indel	— <sup>b</sup>	Fujii et al. (2000) and Hayashi et al. (2010)
15	<i>qPbh11-1</i>	Heikezijing	11	24.23–28.96	SSR	14.19–34.00	Fang et al. (2016)
16	<i>Pi-jnw1</i>	Jiangnanwan	11	24.68–28.93	SSR, Indel	39.92–53.68	Wang et al. (2016b)
17	<i>qNB12-2</i>	KDML105	12	10.08–21.48	SSR	6.03	Noenplab et al. (2006)
18	<i>qNB12-3</i>	Jao Hom Nin	12	10.08–21.48	SSR	17.51	Noenplab et al. (2006)

<sup>a</sup>The chromosomal locations were assigned by projecting the sequences of flanking markers on the genome sequence of cv. Nipponbare released by International Rice Genome Sequencing Project (<http://rapdb.dna.affrc.go.jp>)

<sup>b</sup>Major genes exhibiting Mendelian inheritance

(*qNB11-1* and *qNB11-3*) are present on chromosome 11 in the vicinity of three major blast-resistance genes, *Pi7(t)*, *Pi1*, and *Pilm2*. For the QTLs detected on chromosome 12, the genomic locations have shown an overlap with the location of major leaf-blast-resistance genes such as *Pita* and *Pi20(t)*.

Ishihara et al. (2014) have identified two QTLs for panicle blast resistance from *japonica* cultivar Miyazakimochi: a major QTL, *qPbm11*, on chromosome 11 with a contribution of 30.8% and a minor QTL, *qPbm9*, on chromosome 9 contributing 5.7% to phenotypic variance for panicle blast resistance. The phenotypic analysis of BC<sub>2</sub>F<sub>7</sub> lines introgressed with these QTLs has indicated that the level of panicle blast resistance conferred by *qPbm11* is very similar to the level of resistance in donor Miyazakimochi, whereas *qPbm9* makes small contribution to overall resistance. The genomic position of major QTL *qPbm11* coincides with that of panicle blast-resistance locus, *Pb1*, previously identified from *indica* cultivar Modan. However, the absence of *Pb1* encoded transcripts in the panicles of Miyazakimochi as

revealed through reverse transcriptase PCR has suggested that the *qPbm11* is different from *Pb1*.

Ma et al. (2015) have identified a rice-blast-resistance gene *Pi64* which confers resistance to both leaf and neck blast from a broad-spectrum-resistant *japonica* landrace Yangmaogu (YMG). The gene is located on chromosome 1 and encodes a CC–NBS–LRR protein. The expression studies have suggested that *Pi64* is constitutively expressed at all development stages and in all tissues examined. The observed constitutive expression pattern has been suggested to as the key factor responsible for its effectiveness against both leaf and neck blast.

Fang et al. (2016) have identified two QTLs for panicle blast resistance from a landrace genotype Heikezijing. One of these QTLs, *qPbh-11-1*, located on long arm of chromosome 11 contributes 14.19–34.00% to phenotypic variance and occupies different genomic position compared to two panicle blast-resistance loci *Pb1* and *qPbm11* previously identified from the same chromosome. *qPbh-11-1* is located



in a genomic region harbouring *Pi-k* gene cluster from where a major leaf-blast-resistance gene *Pi-hk1(t)* has also earlier been identified in donor genotype Heikezijing (Wu et al. 2013). *Pi-jnw1* gene conferring resistance to panicle and leaf blast has been identified from a *japonica* landrace Jiangnanwan (Wang et al. 2016b). *Pi-jnw1* is located between markers RM27273 and RM27381 on chromosome 11 and explains 39.92–53.68% of phenotypic variation for panicle blast resistance and 10.91–23.60% of variation for the leaf-blast resistance. The gene has been fine mapped to a 282 kb region on chromosome 11 from where three leaf-blast-resistance genes *Pi-k*, *Pi34*, and *Pi-hk1* have previously been identified in different rice genotypes (Hayashi et al. 2006; Zenbayashi et al. 2007; Wu et al. 2013). Two novel QTLs *qLNBL-5* and *qLNBL-7* conferring resistance to leaf as well as neck blast have been identified from an Indian landrace Akhanaphou, having a high level of field resistance to blast (Aglawe et al. 2017). Both of these QTLs confer resistance to leaf as well as neck blast contributing 26% and 25% to phenotypic variance for the resistance. The genomic position of *qLNBL-5* located on chromosome 5 coincides with an earlier reported meta-QTL for leaf blast on the chromosome 5 (Ballini et al. 2008), whereas the *qLNBL-7* identified from chromosome 7 is positioned within the genetic interval RM7161–RM21328 previously known to harbour one more meta-QTL for leaf blast. These observations reinforce the inferences of several earlier studies that suggested common genes for resistance to both leaf and neck blast (Noenplab et al. 2006; Ishihara et al. 2014; Fang et al. 2016).

## Conclusions and future guidelines for blast-resistance breeding

Recent advancements in rice genomics, especially the accessibility of complete genome sequences of rice subspecies *japonica* and *indica* and concomitant availability of an array of sequence-based molecular markers, have greatly facilitated detailed genetic analysis of blast resistance in rice. These developments have culminated in identification of nearly 118 blast-resistance genes, 25 of which have been cloned and molecularly characterized. Genetic mapping and molecular cloning of different blast-resistance genes have provided a gamut of tightly linked or functional gene-derived markers for use in marker-assisted breeding. Compared to the success achieved in identification and characterization of resistance genes against leaf blast, a few major genes mediating protection to neck blast have been identified; of the some 118 major blast-resistance genes identified from rice, only three, *Pb1*, *Pi25*, and *Pi64*, are known to provide resistance to panicle and neck blast. Most of the genetic studies on neck and panicle blast resistance have been conducted with the genotypes differing in degree of susceptibility/

resistance to disease and consequently have resulted in the identification of QTLs providing quantitative resistance to neck and panicle blast. However, there are several instances, where the gene(s)/QTLs governing neck-blast and leaf-blast resistance have been mapped to same genomic region in rice suggesting the possibility of involvement of common genes for resistance to both leaf and neck blast. There are also evidences that gene for gene resistance mediating protection to leaf blast also operates in the roots and other parts of rice plant (Sesma and Osbourn 2004). These studies have indicated the possibility that the leaf-blast-resistance genes that are constitutively expressed in rice genome may mediate resistance to neck blast as well. Precise studies involving the characterization of neck-blast resistance of rice isogenic lines introgressed with major leaf-blast-resistance genes against a diverse spectrum of pathogen races are needed to ascertain their role in mediating protection to neck blast. These studies will also clarify whether the shifts in race composition of pathogen and environmental conditions during crop season are the sole factors that predispose certain leaf-blast resistant varieties to neck blast and vice versa or the developmentally regulated expression of the resistance genes has some role to play in the outcome.

The clustering of leaf-blast-resistance genes into complex loci and overlapping in the genomic position of leaf- and neck-blast-resistance genes have potential implications in resistance breeding. The genomic region harbouring these gene clusters can be targeted for introgression into susceptible varieties to achieve broad-spectrum resistance, as has been demonstrated for the *Pita* resistance gene complex located near the centromeric region of rice chromosome 12. The *Pita* gene complex derived from a broad-spectrum-resistant genotype Tetep has provided a stable resistance to blast disease in range of *indica* and *japonica* rice varieties since the 1960s (Moldenhauer et al. 1990; Zhao et al. 2018).

Durable resistance to blast has been a priority area in rice breeding. The efforts to achieve durable resistance using major race-specific genes are often frustrated due to evolution of new races of the pathogen that negate the effect of resistance genes. Marker-assisted pyramiding of race-specific resistance genes is widely practiced to increase the durability of resistance. However, most of the gene pyramiding projects rely only on gene number per se as selection criterion to ensure durability, while the attempts to assess the magnitude of fitness penalty that these genes impose on the pathogen populations have rarely been conducted beforehand to guide the selection of effective gene combinations for pyramiding. The resistance gene combinations that impose substantial fitness costs on pathogen variants evolving matching virulences against such genes are most likely to provide durable resistance, e.g., a strong virulence dissociation against major blast-resistance genes *Pi1* and *Pi2* has been reported in the rice-blast populations in different

parts of the world (Mekwatanakarn et al. 2000; Rathour et al. 2006). It is, therefore, imperative that the choice of resistance gene combinations for pyramiding should be based on the sound knowledge of their effect on pathogen fitness to ensure durability.

Recent studies on molecular basis of host–pathogen interactions in rice have identified plant disease-susceptibility genes (*S*) that promote disease in the host following activation by pathogen effectors. These genes promote disease either by promoting pathogen growth and development or acting as negative regulators of basal defense response. The recessive loss-of-function alleles of rice susceptibility genes *Pi21*, *Bsr-d1*, and *Bsr-k1* have been shown to mediate non-race-specific resistance to blast (Fukuoka et al. 2009; Li et al. 2017; Zhou et al. 2018). Consistent with these findings, the CRISPR/Cas9-targeted knockouts of ERF transcription factor gene *OsERF922* and *Bsr-d1*, both of which promote susceptibility to blast, have demonstrated enhanced resistance to rice *P. oryzae* (Wang et al. 2016a; Li et al. 2017). These case studies have suggested the possibility of using spontaneous or genetically engineered loss-of-function mutant alleles of *S* genes for achieving durable non-race-specific resistance to blast.

Of the over 120 rice-blast-resistance gene identified until date, only few (less than 4%) have been sourced from the wild species. As many beneficial alleles must have been left behind in wild species during evolution and domestication of rice, these untapped genetic resources should be explored to identify new genes for resistance to rice blast. The efforts should also be made to unravel new allelic variants of already characterized resistance genes from unexplored landraces and wild species through sequencing-based allele mining. While the mining of coding region is expected to provide new alleles possessing varied resistance specificities, the prompt mining will uncover variants differing in expression patterns. The novel allelic variants with differing resistance specificities and expression patterns can be deployed in the field either as gene pyramids through transgenic approach or as multilines to achieve broad-spectrum resistance to blast. Furthermore, detailed understanding of polymorphic sites controlling resistance specificities of different alleles will facilitate intragenic allele pyramiding for developing chimeric alleles having broader recognition spectrum compared to parental alleles, as has been demonstrated for the alleles of powdery mildew-resistance gene *Pm3* in wheat (Brunner et al. 2010).

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## Compliance with ethical standards

**Conflict of interest** The authors have no conflict of interest to declare.

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