

## PROGRESS ON MAPPING, CLONING AND APPLICATION OF RICE BLAST RESISTANCE GENES

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### Abstract

Rice blast is a fungal disease that is known to severely affect rice production worldwide. It is caused by *Magnaporthe oryzae* (*M. oryzae*). One of the most economical and effective methods to control this disease involves breeding and cultivate of resistant rice varieties. In the recent years, remarkable progress has been made in this field and significant knowledge has been attained regarding rice blast resistance genes. The present study provides an overview of the studies that focused on mapping, cloning, and functional assessment of rice blast resistance genes and their application in molecular breeding. Additionally, the present review discusses the current limitations and future prospects for developing improved rice blast resistant varieties. Altogether, the present study provides valuable and comprehensive insights into rice blast resistance breeding.

**Key words:** Rice blast, *M. oryzae*, Gene cloning, Molecular breeding.

**Abbreviations:** *Avr*, avirulence gene; BAC, artificial bacterial chromosomes; CC, coiled-coil; Chr., chromosome; DHL, doubled haploid lines; InDel, insertion-deletion; LRD, leucine-rich domain; LRR, leucine-rich repeat; MAS, marker-assisted selection; *M. oryzae*, *Magnaporthe oryzae*; MYB, myeloblastosis; NBS, nucleotide binding site; NIL, near isogenic lines, PARM, pathogen-associated molecule pattern; PCR, polymerase chain reaction; QTL, quantitative trait loci; RIL, recombinant inbred lines.

### Introduction

Rice blast is the most destructive fungal disease that severely affects rice production worldwide. In fact, rice blast can contribute to annual losses of 10-30% of the total rice yield (Pari & Gurr, 2009). In addition to the negative effects incurred on crop yields, plant diseases also affect the quality and economic value of crops. These disease can even cause food poisoning in humans and animals (Li *et al.*, 2020). The occurrence of rice blast can be alleviated to some extent by the use of fungicidal sprays (Hajano *et al.*, 2012). However, use of such sprays can result in severe environmental pollution. The most economical and effective method to control this disease involves the breeding and cultivation of resistant rice varieties. Currently, a large variety of rice blast resistance genes are utilized in plant breeding. However, cultivation of rice varieties carrying single resistance gene for an extended period of time might result in the loss of resistance within few years of cultivation, probably due to the selection pressure on evolutionarily virulent strains (Wang *et al.*, 1998, Kou & Wang, 2010, 2012). Gene identification and pyramiding via molecular marker-assisted selection (MAS) play an important role in the control of rice blast disease. The advancement in the field of genomics was accompanied by the identification of a large number of rice blast resistance genes (Yang *et al.*, 2009b, Li *et al.*, 2014). Herein, the present study provides an overview of the progress made in the field of rice blast resistant genes. In

particular, the present review summarizes the studies focused on mapping, cloning and application of rice blast resistance gene in rice production and thus provides a detailed insight into the molecular breeding of rice blast resistant varieties.

### Materials and Methods

**Mapping and cloning of rice blast resistance gene:** The beginning of genetic evaluation of resistance to rice blast is dated back to 1920s. The occurrence of different strains of rice blast fungus varying in terms of pathogenicity was reported for the first time by Sasaki *et al.*, (Sasaki, 1922). Genetic analysis further established that the inheritance of rice resistance followed Mendelian rules. In 1966, Yamasaki and Kiyosawa reported the identification of *Pia*, *Pii*, and *Pik* resistant genes in Asahi Aichi, Ishikari Shiroke, and Kanto 51, respectively (Yamasaki & Kiyosawa, 1966). Subsequently, a large number of studies were conducted on rice blast resistant genes worldwide. To date, 114 genes have been identified from different rice germplasm resources. Among these, 36 genes have been cloned (Table 1). Quantitative trait loci (QTL) have been shown to play an important role in the control of rice blast (Xing *et al.*, 2015). Interestingly, the resistance loci are distributed on all chromosomes of rice (Fig. 1). Among these, three large resistance gene clusters are located on chromosome 6, 11, and 12. These gene clusters include 71 resistance loci, out of which 23 have been

cloned that account for 64% of the total cloned genes (Fig. 1). In addition to this, rice blast resistance genes were also found to be located on other rice chromosomes. The distribution of blast resistance genes was found to be least on chromosome 3 and 7.

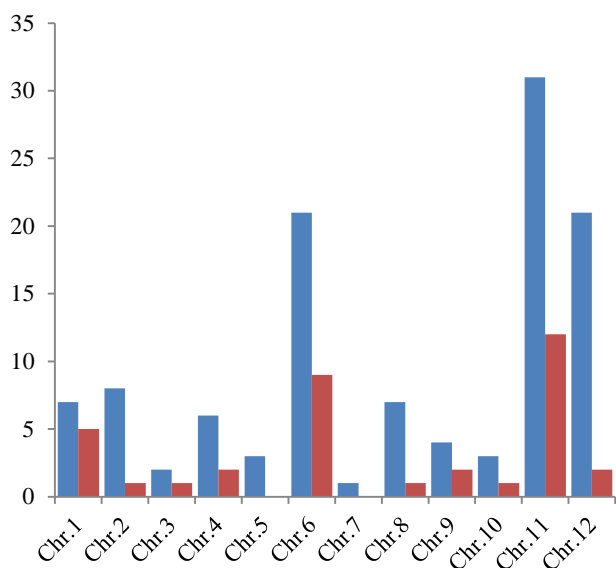


Fig. 1. Distributions of mapped (blue) and cloned (red) blast resistance genes on the rice chromosomes.

**Clustering of blast resistant genes:** Genes that confer resistance to plant diseases generally tend to cluster in specific regions of chromosomes (Islam and Shepherd 1991). Three large gene clusters for rice blast resistance have been previously identified on chromosome 6, 11, and 12 (Fig. 2).

Importantly, more than 20 rice blast resistance gene have been identified on chromosome 6. Among these, at least five resistance alleles were identified for the resistance locus *Piz* of rice, which included *Pi2*, *Pizt*, *Pi9*, *Pi54*, and *Pigm*. *Pi9* encodes for a peptide comprising of 1032 amino acids, with 17 incomplete leucine-rich repeat (LRR) repeats. The amino terminal of this peptide is characterized by the presence of a nucleotide-binding site (NBS) domain, with kinases 1a, 2, and 3a (Qu *et al.*, 2006). The proteins encoded by *Pizt* and *Pi2* consist of 1033 and 1032 amino acids, respectively. Each of these proteins contains a single NBS and three LRRs. The protein products of *Pizt* and *Pi2* differ only in terms of eight amino acids, which are located in three LRR regions (Zhou *et al.*, 2006). The InDel marker *Pi9-Pro* can distinguish between non-*Pi2/Pizt/Pi9*, *Pi2/Pizt*, and *Pi9* alleles, and thus generates polymerase chain reaction (PCR) fragments of 111 bp for *Pi2/Pizt* and 128 bp for *Pi9* (Table 2) (Tian *et al.*, 2016). *Pigm*, an allele of *Pi2*, *Pi9*, and *Pizt*, is located at *Piz* locus that contains a cluster of genes characterized by sustained resistance to rice blast without loss of yield. In this cluster, *PigmR* confers broad spectrum resistance to rice blast, which is counteracted and weakened by *PigmS*. Prior to *Pigm* cloning, linkage markers were developed through breeding (Liang *et al.*, 2013, Wang *et al.*, 2016). Following *Pigm* cloning, fluorescent markers were developed based on pathogen-associated molecule pattern (PARM) technology (Table 2)

(Qing *et al.*, 2018). The dominant molecular marker T9E4 was designed on the basis of the sequence of *Pigm*, and used for the selection of hybrid offspring of Gumei 4 and Xiangwanxian 13 (Lai *et al.*, 2019).

*Pik* is the largest gene cluster located on chromosome 11, and *Pik-h/Pi54*, *Pil*, *Pik-g (t)*, *Pik-p*, *Pik-m*, and *Pik-s* represent multiple alleles on *Pik* locus. Among these, the sequences of *Pik*, *Pi1*, *Pik-p*, *Pik-h*, and *Pik-m* were found to be relatively close, with very few base differences. PCR and sequencing techniques were utilized to distinguish between different alleles (Costanzo & Jia, 2010, Ramkumar *et al.*, 2011, Yuan *et al.*, 2011).

A large cluster of disease-resistance genes are located around *Pita*, near the centromere of chromosome 12. However, only *Pita* and *Ptr* have been cloned so far. *Pita* was located on artificial bacterial chromosomes (BAC), a BAC142E8 clone that contained two exons and one intron. It encoded for a 928-amino acid cell plasma cytoplasmic membrane receptor that was characterized by the presence of an NBS domain and leucine-rich domain (LRD). Interestingly, a single amino acid change was observed at the *Pita* locus, involving an alanine to serine substitution at position 918 that changed the disease-resistant product to a disease-susceptible product. The mechanism of disease-resistance involved interaction of *Pita* with *Avirulence gen (Avr)-Pita* that triggered disease-resistance responses (Bryan *et al.*, 2000). Two pairs of dominant molecular markers, YL155/YL87 and YL183/YL87, were developed based on the differences identified at residue 918, which could accurately discriminate between the resistant and susceptible *Pita* allele (Table 2) (Wang *et al.*, 2005). *Ptr* gene is closely related to *Pita*, and the sequences of resistant and susceptible rice materials differ in terms of a series of bases located in the last exon of *Ptr* gene. A molecular marker Z12 was developed based on Indel at *Ptr* locus, which was further used to identify resistant genotypes (Table 2) (Zhao *et al.*, 2018).

**Broad-spectrum rice blast resistance genes in the form of single gene:** In addition to large gene clusters located on chromosomes 6, 11, and 12 that confer blast resistance, a series of broad-spectrum blast resistance genes have also been identified as single genes. These single genes have been previously shown to play important role in disease resistance. *Pi64* originated from Yangmaogu, a Japanese terrestrial variety that contains at least three major R genes including *Pi64*. In particular, two open reading frames (NBS-1 and NBS-2), coding for nucleotide-binding sites, and an open reading frame rich in leucine repeats were identified as candidate genes (Ma *et al.*, 2015b), which exhibited resistance to CH43 and several other isolates. *Pib* is the only cloned resistant gene that is located on chromosome 2. It encodes for a protein product comprising of 1,251 amino acids, which includes 17 LRRs and an NBS. Interestingly, duplication of kinases 1a, 2, and 3a of NBS region has been identified in the amino-terminal of the protein, and eight cysteine residues are present in the middle of LRRs. The induction, regulation, and expression of this gene are influenced by environmental conditions, including temperature and light (Wang *et al.*, 1999).

**Table 1. Locations of rice blast resistance genes.**

Gene	Chr	Population	Linkage status	Donor	Reference
<i>Pi24</i>	1	DHL	K5	Azucena	(Sallaud <i>et al.</i> , 2003)
<i>Pi27(t)</i>	1	F <sub>2</sub>	RM151(12.1cM), F <sub>2</sub> RM259(9.8cM)	Q14	(Zhu <i>et al.</i> , 2004)
<i>Pi35#</i>	1	F <sub>3</sub>	RM1216-RM1003	Hokkai 188	(Nguyen <i>et al.</i> , 2006) (Fukuoka <i>et al.</i> , 2014)
<i>Pi37#</i>	1	F <sub>2</sub>	RM543(0.7cM), RM319(1.6cM)	St. No. 1	(Chen <i>et al.</i> , 2005) (Lin <i>et al.</i> , 2007)
<i>Pi64#</i>	1	F <sub>2</sub>	CAPS2-dCAPS5	Yangmaogu	(Ma <i>et al.</i> , 2015a)
<i>Pish#</i>	1	F <sub>2</sub>	Linked to <i>Pit</i>	Nipponbare	(Takahashi <i>et al.</i> , 2010)
<i>Pit#</i>	1	F <sub>2</sub>	tNpb/tK59	K59	(Hayashi <i>et al.</i> , 2010)
<i>Pi14</i>	2	F <sub>3</sub>	Linked to Amp-1	Maowangu	(Pan <i>et al.</i> , 1998a)
<i>Pi16(t)</i>	2	F <sub>2</sub>	Linked to Amp-1	Aus373	(Pan <i>et al.</i> , 1999)
<i>Pi25</i>	2	DHL	RG520	IR64	(Sallaud <i>et al.</i> , 2003)
<i>Pib#</i>	2	BC <sub>2</sub> F <sub>3</sub>	S1916-G7030	BL-1	(Wang <i>et al.</i> , 1999)
<i>Pid1(t)</i>	2	F <sub>2</sub>	G1314A(1.2cM), G45(10.6cM)	Digu	(Chen <i>et al.</i> , 2004a)
<i>Pig(t)</i>	2	F <sub>2</sub>	RM166(4.0cM), RM208(6.3cM)	Guangchangzhan	(Zhou <i>et al.</i> , 2004)
<i>Pimh</i>	2	F <sub>2</sub>	AP28SR2 -RM3542	Minghui63	(Ma, 2010)
<i>Pitq5</i>	2	RIL	RG520-RZ446b, With <i>Pib</i> allelic	Teqing	(Tabien <i>et al.</i> , 2000)
<i>bsrd1#</i>	3	RIL	SNP33	Digu	(Li <i>et al.</i> , 2017)
<i>pi66(t)</i>	3	F <sub>2</sub>	F04-J2-M19-Iil2	AS20-1	(Liang <i>et al.</i> , 2016)
<i>pi21#</i>	4	F <sub>4</sub>	G271(5.0cM), G317(8.5cM)	Owarihatamochi	(Fukuoka & Okuno, 2001) (Fukuoka <i>et al.</i> , 2009)
<i>Pi45(t)</i>	4	BC <sub>3</sub> F <sub>2</sub>	RM17499-RM17511	Moroberekan	(Kim D <i>et al.</i> , 2011)
<i>Pi46(t)</i>	4	F <sub>3</sub>	RM6748-RM5473	Chumroo	(Matsushita <i>et al.</i> , 2011)
<i>Pi63#</i>	4	BAC	RM17494-RM6629	Kahei	(Xu <i>et al.</i> , 2014)
<i>Pikur1</i>	4	F <sub>2</sub>		Kuroka	(Goto, 1988)
<i>GV(t)</i>	4	F <sub>2</sub>	RM3335	Gigante Vercelli (GV)	(Urso <i>et al.</i> , 2016)
<i>Pi10(t)</i>	5	RIL	RRF6(3.8cM), RRH18(2.9cM)	Tongil	(Hayashi <i>et al.</i> , 2006)
<i>Pi23(t)</i>	5	F <sub>2</sub>	RM164(19.4 cM), RM249(23.9 cM)	Suweon 365	(Ahn <i>et al.</i> , 1996)
<i>Pi26</i>	5	DHL	RG313	Azucena	(Sallaud <i>et al.</i> , 2003)
<i>Pi2#</i>	6	NIL; F <sub>2</sub>	RG64-AP22	Jefferson	(Wu <i>et al.</i> , 2002) (Zhou <i>et al.</i> , 2006)
<i>Pi2-1</i>	6	RIL	AP4791 - AP4007	Tianjingyeshengdao	(Wang <i>et al.</i> 2012)
<i>Pi2-2</i>	6	F <sub>2</sub>	AP5659-3-RM19817	Jefferson	(Jiang <i>et al.</i> , 2012)
<i>Pi8</i>	6	F <sub>2</sub>	Linked to Amp-3 and Pgi-2	Kasalath	(Pan <i>et al.</i> , 1996)
<i>Pi9#</i>	6	F <sub>2</sub>	RG64(2.8cM)- R2123(2.7cM)	Xiaoliyeshengdao	(Liu <i>et al.</i> , 2002) (Qu <i>et al.</i> , 2006)
<i>Pi13</i>	6	F <sub>3</sub>	Linked to Amp-3	Maowangu	(Pan <i>et al.</i> , 2010)
<i>Pi22(t)</i>	6	F <sub>2</sub>	With <i>Pi2</i> allelic	Suweon 365	(Ahn <i>et al.</i> , 2000)
<i>Pi25#</i>	6	RIL	A7(1.7cM), RG456(1.5cM)	Gumei 2	(Chen <i>et al.</i> , 2011)
<i>Pi26</i>	6	RIL	B10(5.7cM), R674(25.8cM)	Gumei 2	(Wu <i>et al.</i> , 2005)

Table 1. (Cont'd.).

Gene	Chr	Population	Linkage status	Donor	Reference
<i>Pi27</i>	6	DHL	Est-2	IR64	(Sallaud <i>et al.</i> , 2003)
<i>Pi40</i>	6	F <sub>2</sub>	RM527(1.1cM),	Australian wild rice	(Jeung <i>et al.</i> , 2007)
<i>Pi50#</i>	6	F <sub>2</sub>	GDAP51-GDAP16	Erbazhan	(Zhu <i>et al.</i> , 2012)
<i>Pi51</i>	6	F <sub>2</sub>	in306-RM19818	D69	(Xiao <i>et al.</i> , 2012)
<i>Pid2#</i>	6	F <sub>2</sub>	RM527(3.2cM), RM3(3.4cM)	Digu	(Chen <i>et al.</i> , 2004b) (Chen <i>et al.</i> , 2006)
<i>Pid3 A4#</i>	6		With <i>Pid3</i> homologous	A4	(Lv <i>et al.</i> , 2013)
<i>Pid3#</i>	6		N093F01N317P09	Digu	(Shang <i>et al.</i> , 2009)
<i>Pigm#</i>	6	F <sub>2</sub> ; BC <sub>1</sub> F <sub>1</sub>	C5483-C0428	Gumei4	(Deng <i>et al.</i> , 2006) (Deng <i>et al.</i> , 2017)
<i>Pi-kf2(t)</i>	6	F <sub>2</sub>	Rm7213 - InDel-22	Kangfeng B	(Wei <i>et al.</i> , 2019)
<i>Pitq1</i>	6	RIL	C236-RG653	Teqing	(Tabien <i>et al.</i> , 2000)
<i>Piz</i>	6	F <sub>2</sub>	z56592	Fukunishiki	(Hayashi <i>et al.</i> , 2006)
<i>Pizt#</i>	6	F <sub>2</sub>	z56591	Zenith	(Hayashi <i>et al.</i> , 2006) (Zhou <i>et al.</i> , 2006)
<i>Pi17(t)</i>	7	F <sub>2</sub>	Linked to Est9	DJ123	(Pan <i>et al.</i> , 1996)
<i>Pi29</i>	8	DHL	RZ617	Azucena	(Sallaud <i>et al.</i> , 2003)
<i>Pi33</i>	8	DHL	Y2643L(0.9cM), RM72(0.7cM)	IR64	(Berruyer <i>et al.</i> , 2003)
<i>Pi36#</i>	8	F <sub>2</sub>	RM5647-CRG2	Q61	(Liu <i>et al.</i> , 2005), (Liu <i>et al.</i> , 2007a)
<i>Pi42(t)</i>	8	RIL	RM2529-RM1337	Zhe733	(Lee <i>et al.</i> , 2009)
<i>pi55(t)</i>	8	F <sub>4</sub>	RM1345-RM3452	Yuejingsimiao 2	(He <i>et al.</i> , 2012)
<i>Pi-GD-1(t)</i>	8	RIL	XLRfr-8(3.6cM)	Sanhuangzhan 2	(Liu <i>et al.</i> , 2004)
<i>Pizh(Pi11)</i>	8	DHL	BP127A(14.9cM)	Zhaiyeqing 8	(Zhu <i>et al.</i> , 1994)
<i>Pi5/Pi3/Pii#</i>	9	F <sub>2</sub>	S04G03-C1454	Tetep/Hitomebore	(Lee <i>et al.</i> , 2009) (Takagi <i>et al.</i> , 2013)
<i>Pi15</i>	9	F <sub>2</sub>	CRG5-CRG2	GA25	(Pan <i>et al.</i> , 2003)
<i>Pi56#</i>	9	DHL	RM24022-RM24031	Sanhuangzhan 2	(Liu <i>et al.</i> , 2013)
<i>Pi-hk2(t)</i>	9	RIL	Lsqt19-1	Heikezijing	(He <i>et al.</i> , 2016)
<i>bsr-k1#</i>	10	F <sub>2</sub>	RM25789-RM333	Mutant	(Zhou <i>et al.</i> , 2018)
<i>Pi28</i>	10	DHL	RZ500, RGA-IR86	IR64	(Sallaud <i>et al.</i> , 2003)
<i>Pi-GD-2(t)</i>	10	RIL	r14-r16	Sanhuangzhan 2	(Liu <i>et al.</i> , 2004)
<i>Pb1#</i>	11	F <sub>2</sub>	S723(1.2cM)	Modan	(Fujii <i>et al.</i> , 2000)
<i>Pi1#</i>	11	F <sub>2</sub>	RZ536(7.9cM), Npb181(3.5cM)	LAC23	(Yu <i>et al.</i> , 1996) (Hua <i>et al.</i> , 2012)
<i>Pi7</i>	11	RIL; F <sub>2-3</sub>	RG103A-RG16	Moroberekan	(Wang <i>et al.</i> , 1994)
<i>Pi12(t)</i>	11	F <sub>2</sub>	RZ537	Moroberekan	(Inukai <i>et al.</i> , 1996)
<i>Pi18</i>	11	F <sub>2</sub>	RZ536(5.4cM)	Suweon 365	(Ahn <i>et al.</i> , 2000)
<i>Pi30</i>	11	DHL	OpZ11-f	IR64	(Sallaud <i>et al.</i> , 2003)
<i>Pi34</i>	11	F <sub>2</sub>	C1172-C30038	Chubu 32	(Zenbayashi-Sawata <i>et al.</i> , 2007)
<i>Pi38</i>	11	F <sub>2</sub>	RM206-RM21	Tadukan	(Gowda <i>et al.</i> , 2006)
<i>Pi43(t)</i>	11	RIL	RM1233-RM224	Zhe733	(Lee <i>et al.</i> , 2009)
<i>Pi44(t)</i>	11	F <sub>2</sub>	AF349(3.3cM)	Moroberekan	(Chen <i>et al.</i> , 1999)
<i>Pi46(t)</i>	11	F <sub>2</sub>	RM224-RM27360	H4	(Xiao <i>et al.</i> , 2011)
<i>Pi47(t)</i>	11	RIL	RM206-RM224	Xiangzi 3150	(Huang <i>et al.</i> , 2011)
<i>Pi54of#</i>	11			<i>Oryza officinalis</i>	(Devanna <i>et al.</i> , 2014)
<i>Pi54rh#</i>	11			<i>Oryza rhizomatis</i>	(Das <i>et al.</i> , 2012)

Table 1. (Cont'd.).

Gene	Chr	Population	Linkage status	Donor	Reference
<i>Pi65(t)</i>	11	DH, BC <sub>1</sub> F <sub>2</sub>	RM27181-RM27364	Gangyu129	(Zheng <i>et al.</i> , 2016)
<i>Pia#</i>	11	DHL	OpZ11-f, RGA-IR14, RM120	Aichi Asahi	(Okuyama <i>et al.</i> , 2011)
<i>PiCO39#</i>	11		S2712(1.0cM)	CO39	(Chauhan <i>et al.</i> , 2002)
<i>Pif</i>	11	F <sub>2</sub>	15% recombination value to <i>Pik</i>	St. No.1	(Monosi <i>et al.</i> , 2004)
<i>Pihk1(t)</i>	11	RIL	RM7654 0.9 cM	Heikezijing	(Li <i>et al.</i> , 2007a)
<i>Pik #</i>	11	F <sub>2</sub>	R543(2.0cM)	Kusabue	(Zhai <i>et al.</i> , 2011)
<i>Pik e#</i>	11	F <sub>2</sub>	MAP	Xianzao143	(Chen <i>et al.</i> , 2015)
<i>Pikg(t)</i>	11	F <sub>2</sub>	Allelic to <i>Pik</i>	GA20	(Pan <i>et al.</i> , 1998b)
<i>Pikh/ Pi54#</i>	11	F <sub>2</sub>	RM224-Y6855RA	Tetep	(Xu <i>et al.</i> , 2008)
<i>Pik m#</i>	11	F <sub>2</sub>	RM254 (13.4cM)- RM144 (1.2cM)	Tsuyuake	(Li <i>et al.</i> , 2007b) (Ashikawa <i>et al.</i> , 2008)
<i>Pik p#</i>	11	F <sub>2</sub>	k3957 (0 cM)	K60	(Wang <i>et al.</i> , 2009) (Yuan <i>et al.</i> , 2011)
<i>Pik s#</i>	11	F <sub>2</sub>	RM224 (0 cM)	Shin 2	(Fjellstrom <i>et al.</i> , 2004)
<i>Pik ur2</i>	11	F <sub>2</sub>	14% recombination value to <i>la</i>	Kuroka	(Goto, 1988)
<i>Pilm2</i>	11	RIL	R4-RZ536	Lemont	(Tabien <i>et al.</i> , 2000)
<i>Pise1</i>	11	F <sub>2</sub>	9.5% recombination value to <i>la</i>	sensho	(Wisser <i>et al.</i> , 2005)
<i>Piy(t)</i>	11	F <sub>2</sub>	RM202(3.8cM)	Yunyin	(Zhang <i>et al.</i> , 2003)
<i>Pizy(t)</i>	11	RIL	RM206(0cM)	Yuyu44	(Zhang <i>et al.</i> , 2009)
<i>Pi4</i>	12	NIL	RG457-RG869	Tetep	(Yu <i>et al.</i> , 1996)
<i>Pi6</i>	12	DHL	RG869-RG397	Apura	(Causse, 1994)
<i>Pi19</i>	12	F <sub>5</sub>	Closely linked to or equiped with <i>Pita2</i>	Aichi Asahi	(Hayashi <i>et al.</i> , 1998)
<i>Pi20</i>	12	RIL	XNph88(1.0cM)	IR24	(Imbe <i>et al.</i> , 1997)
<i>Pi21(t)</i>	12	F <sub>2</sub>	RG869	Suweon 365	(Ahn <i>et al.</i> , 2000)
<i>Pi24</i>	12	RIL	RG241A(0cM)	Zhong156	(Zhuang <i>et al.</i> , 2002)
<i>Pi31</i>	12	DHL	O10-800	IR64	(Sallaud <i>et al.</i> , 2003)
<i>Pi32</i>	12	DHL	AF6	IR64	(Sallaud <i>et al.</i> , 2003)
<i>Pi39</i>	12	F <sub>2</sub>	RM27933(0.09cM), RM27940(0.18cM)	Q15	(Liu <i>et al.</i> , 2007b)
<i>Pi41</i>	12	F <sub>2</sub>	STS40-1-STS40-3	9311	(Yang <i>et al.</i> , 2009a)
<i>Pi42(t)</i>	12	F <sub>2</sub>	RM2529-RM1337	DHR9	(Kumar <i>et al.</i> , 2010)
<i>Pi48(t)</i>	12	RIL	RM5364-RM7102	Xiangzi 3150	(Huang <i>et al.</i> , 2011)
<i>Pi51(t)</i>	12	RIL	RM5364 - RM27990	Tianjingyeshengdao	(Wang <i>et al.</i> , 2012)
<i>Pi62(t)</i>	12	F <sub>2</sub>	SP7C3	Yashiro-mochi	(Wu K S <i>et al.</i> , 1996)
<i>Pi157(t)</i>	12	RIL	RG341-RG9	Moroberekan	(Naqvi & Chattoo, 1996)
<i>Pi-GD-3(t)</i>	12	RIL	RM179(4.8cM)	Sanhuangzhan 2	(Liu <i>et al.</i> , 2004)
<i>Pi-h-1(t)</i>	12	F <sub>3</sub>	RG869(5.1cM)	Hongjiaozhan	(Zheng <i>et al.</i> , 1995)
<i>Pita#</i>	12	F <sub>2</sub>	ta3 (0 cM)	Yashiro-mochi	(Bryan <i>et al.</i> , 2000)
<i>Pita2</i>	12	F <sub>2</sub>	ta3 (0 cM)	PiNo.4	(Bryan <i>et al.</i> , 2000)
<i>Pitq6</i>	12	RIL	RG869-RZ397	Teqing	(Tabien <i>et al.</i> , 2000)
<i>Ptr#</i>	12	F <sub>2</sub>	RM3246-RM1047	Katy	(Zhao <i>et al.</i> , 2018)

Disease resistance genes with “#” were cloned. DHL represents doubled haploid lines; RIL represents recombinant inbred lines; NIL represents near isogenic lines; BAC represents artificial bacterial chromosomes

Table 2. Molecular markers of rice blast resistance genes.

Gene	Primer name	Primer sequence (5' to 3')	Expected size (bp)	Reference
<i>bsr-d1</i>	F	AGTCTAGCATCCACCCTTCCAC	313	(Wang et al., 2018a)
	R	GTAGGCAGGCAGTGGGATGA		
<i>Pi2/Pi9/Pizt</i>	<i>Pi9</i> ProF	TGATTATGTTTTTATGTGGGG	111( <i>Pi2/Piz-t</i> )	(Tian et al., 2016)
	<i>Pi9</i> ProR	AATTAGTGAGATCCATTGTTC	128( <i>Pi9</i> )	
<i>Pi5</i>	<i>Pi5</i> F	CCAAAGTGCAACTAGAGGTAATGGT	1105	(Yi et al., 2004)
	<i>Pi5</i> R	GTGCATCATCTTCAGATATCAGG		
<i>pi21</i>	F	AGGAGTACTGCAICGAGAAG	342/411	(Fukuoka et al., 2009)
	R	TACGGCACCCAGCTTGCAC		
<i>Pi25</i>	<i>Pi25</i> F	TGAAATGGGTGAAAGATGAG	406 Hinc II	(Wang et al., 2012)
	<i>Pi25</i> R	GCCACATCATAAATTCCTTGA		
<i>Pi35</i>	<i>Pi35-dCAPSF</i>	GCCGTCTCCCTCCAGCATATAITGATAACG	272bp cut by <i>TaiI</i>	(Ma et al., 2015b)
	<i>Pi35-dCAPSR</i>	GGTGTCTGCAAAACAAGAAACGTTGAAG	enzyme was small	
<i>Pi64</i>	YRT6F	TCCTGTGTTTCTTACCGAGTCCAGC	1016	(Ma et al., 2015a)
	YRT6R	AGAGGAGTGCAAGGTTACCCAGAGCC		
<i>Pi65(t)</i>	F	ATCTTACCCTCAACATTGCC	139	(Zhao et al., 2017)
	R	AGACATGTTG AAGACGCCT		
<i>Pib</i>	<i>Pib</i> domF	GAACAATGCCCAAACTTGAGA	365(R)	(Fjellstrom et al., 2004)
	<i>Pib</i> domR	GGGTCCACATGTCAGTGAGC		
Lys145F		TCGGTGCTCGGTAGTCAGT	803(S)	(Liu et al., 2008)
	Lys145R	GGGAAAGCGGATCCTAGGTCT		
<i>Pid2</i>	M- <i>Pid2</i> F	TGTGAAGCAATGATCACCA	1009	(Gao et al., 2010)
	M- <i>Pid2</i> R	GGCAGTCGTATTGCTGTGAA		
<i>Pid3</i>	<i>Pik</i> d3F	TACTACTATGGAAGCTAGTTCTC	178	(Shang et al., 2009)
	<i>Pik</i> d3R	AGCACTTGTGACTACTGTCTGCT		
<i>Pigm</i>	T9E4F	CAGAGCAGTAACAAAACCCTA	750	(Qing et al., 2018)
	T9E4R	TCCGCAAGATCAACATTC		
<i>Pii</i>	F	TCCAATGCTTCTGAAAGGTAGC	355	(Takagi et al., 2013)
	R	TGGAAACATGAACCCATATCTCT		
<i>Pik</i>	RG4F	TTCGAGGCCCTACCAAGACA	103	(Zhai et al., 2011)
	RG4R	CATGGGAAGGCTATCCTTTGGTA		
<i>Pita</i>	YL155/YL87F	AGCAGGTTATAAGCTAGGCC	1042(R)	(Wang et al., 2005)
	YL155/YL87R	CTACCAACAAGTTCAATCAAA		
	YL183/YL87F	AGCAGGTTATAAGCTAGCTAT	1042(S)	
	YL183/YL87R	CTACCAACAAGTTCAATCAAA		
<i>Piz</i>	F	AAGAAATAATAATTTTGAACATGGCAAAG	267	(Hayashi et al., 2006)
	R	CCATGGTGGTAACTGGTATGTG		
<i>Pit</i>	tN11/tRm1F	ATGATAACCTCATCTCAATAAAGT	530(R)	(Hayashi et al., 2010)
	tN11/tRm1R	GTTGGAGCTACGGTTGTTCAG		
<i>Pir</i>	Z12F	TGCAGATTTGACTGCTCGGT	226(S)/214(R)	(Zhao et al., 2018)
	Z12R	GGGATCTTCTCGCCAAA		

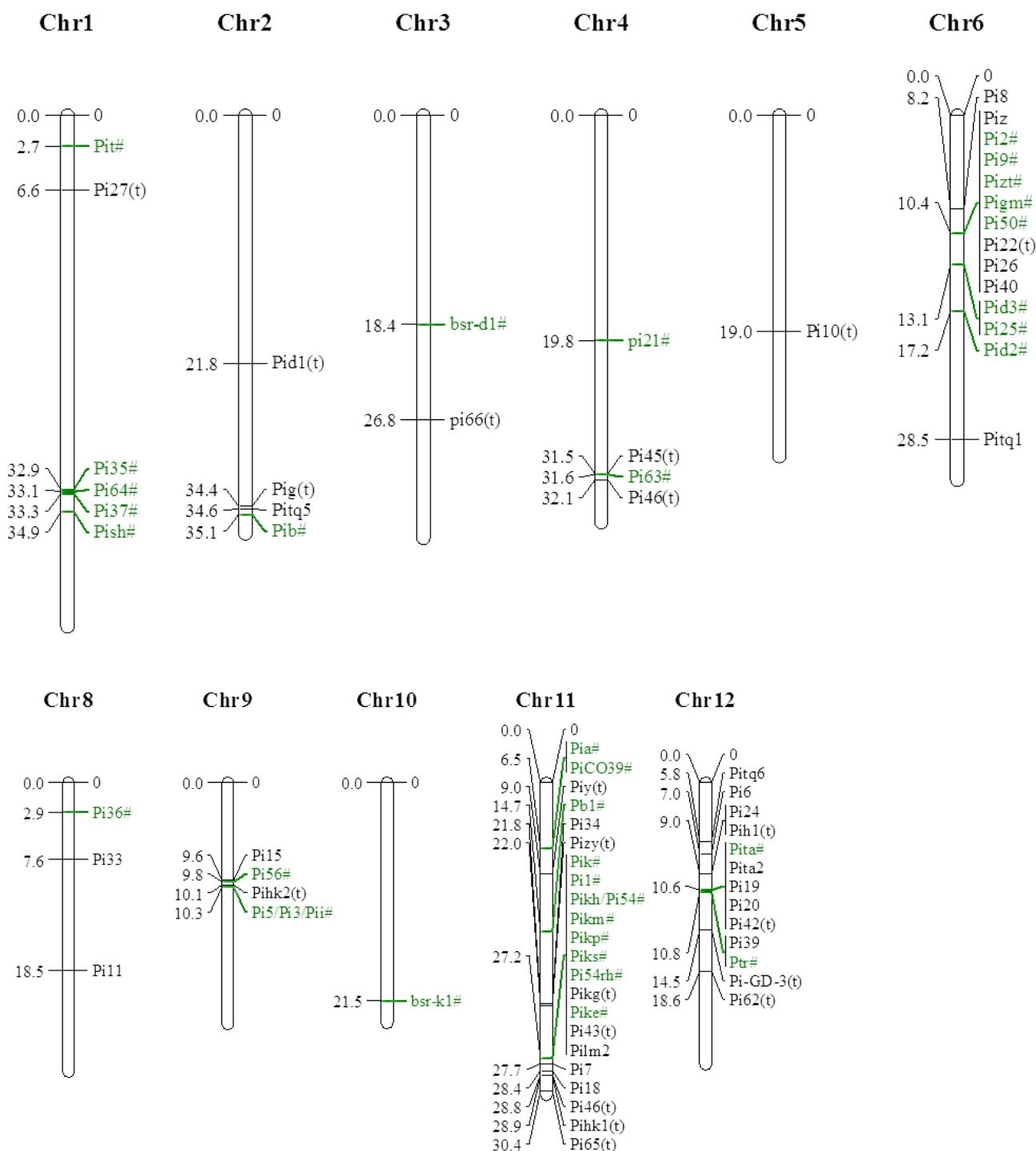


Fig. 2. Positions of blast-resistance genes on the rice chromosomes. The genes colored green were cloned; the number represents the position on the chromosome.

Genome-wide association studies revealed that *bsr-d1* conferred non-race-specific resistance to rice blast (Li *et al.*, 2017). In particular, this allele causes mononucleotide changes in the promoter of *bsr-d1* gene, which results in the deletion of gene expression via binding to an inhibitory myeloblastosis (MYB) transcription factor, and thus inhibits H<sub>2</sub>O<sub>2</sub> degradation and enhances disease resistance.

*pi21* was identified using QTL analysis for F<sub>4</sub> progeny lines obtained from the cross between Nipponbare and Owarihatamochi. It is the first recessive rice blast resistance gene that is located between G271

and G317 on chromosome 4 (Fukuoka & Okuno, 2001). The wild-type *pi21* cDNA is characterized by a total length of 1109 bp, which contains three exons and encodes for a protein product comprising of 266 amino acids. The protein product is rich in proline and contains functional domains, including heavy metal binding domain and protein interaction domain. In comparison to susceptible cultivars, *pi21* gene of resistant cultivars Owarihatamochi contained 21bp and 48bp deletions, respectively, which was the reason for the observed difference in the resistance. Wild-type *pi21* was

previously shown to slow down the plant resistance response, and therefore was used to optimize the plant's defense mechanisms. The removal of the proline-rich motif prevented the observed slowing of disease resistance responses. Following this, *pi21* was isolated from a closely linked gene that affects rice taste (Fukuoka *et al.*, 2009).

*Pi36* is located between RM5674-CRG2 on chromosome 8 in Q61. It encodes for a coiled-coil nucleotide-binding site leucine-rich repeat (CC-NBS-LRR) domain that confers broad-spectrum resistance. The protein product encoded by *Pi36* comprises of 1056 amino acids, and the resistance is contributed by the substitution of an amino acid at position 590 (serine replaced by an aspartic acid). According to the expression of defense genes related to *Pi36*, it was speculated that the resistance mediated by *Pi36* was related to salicylic acid signaling pathway (Liu *et al.*, 2005, Liu *et al.*, 2007a).

#### Resistance genes that require the combined activity of two genes:

The results for sequence analysis and genetic complementation experiments showed that the resistance of certain genes was conferred by the composition of two genes, having independent functions. These genes include *Pi1*, *Pi5*, *Pigm*, *Pia*, *PiCO39*, *Pik*, *Pike*, *Piks*, *Pikh*, *Pikm*, and *Pikp* (Cesari *et al.*, 2013, Zhai *et al.*, 2014). *Pikm* is composed of two closely linked NBS-LRR genes, namely *Pikm1-TS* and *Pikm2-TS*, having independent functions. The protein products encoded by *Pikm1-TS* and *Pikm2-TS* represent disease-resistant proteins of the NBS-LRR class that comprise of 1143 and 1021 amino acids, respectively. Minor differences have been reported in their structure. In particular, the amino terminal of *Pikm1-TS* was found to possess an nT motif with a CC structure, whereas *Pikm2-TS* possessed an nT motif without CC structure. The carboxyl terminus of *Pikm1-TS* was characterized by the presence of a non-LRR structure that was absent in *Pikm2-TS*. *Pi5* is located at the 170 kb interval between S04G03 and C1454 of chromosome 9. It was identified using AFLP markers (Jeon *et al.*, 2003). A lot of similarity exists between *Pik-m* and *Pi5*. In particular, *Pi5* contains two independently inherited NBS-LRR genes, namely *Pi5-1* and *Pi5-2* that encode for proteins comprising of 1025 and 1063 amino acids, respectively. Gene expression analysis showed that *Pi5-1* activity was induced by *M. oryzae*, whereas *Pi5-2* was constitutively expressed (Lee *et al.*, 2009).

*PigmR* and *PigmS* are also known to regulate disease resistance and rice yields. *PigmR* is constitutively expressed in the leaves, stems, spikes, and other organs of rice. However, the presence of *PigmR* can result in the reduction of 1000-grain weights and yields. In comparison to this, *PigmS* is specifically expressed in rice pollen, with low levels of expression observed in the leaves and stems. Interestingly, *PigmS* can improve the seed setting rates of rice and offset the negative effects incurred by *PigmR* on rice yields. The low-levels of expression of *PigmS* provide a “sanctuary” for rice blast fungus, slowing the pathogenic evolution to *PigmR*. Generally, *Pigm*-mediated disease resistance is known to be durable, with *Pigm* showing broad spectrum and durable disease resistance that does not result in the loss of final yields (Deng *et al.*, 2017).

In addition to the synergistic gene activity, adjacent disease-resistant genes can also interact with one another. For instance, *Ptr* is located closer to *Pita*, and the broad-spectrum resistance of *Ptr* is known to be independent of *Pita*. However, *Ptr*, is required for *Pita*-mediated signal recognition.

#### Molecular breeding to generate rice blast resistant strains:

Following the mapping and cloning of blast resistance genes, a large number of rice varieties carrying resistance genes have been bred, with the assistance of molecular markers (Table 2). This resulted in great improvement in the resistance of rice varieties to rice blast. *Pi2* was identified to be present in 22.87% of hybrid rice varieties found in southern China. Among these, 93.33% of the hybrid varieties were disease resistant (Zhang *et al.*, 2017). However, 31 of 36 rice blast resistance genes that have been previously cloned were NBS-LRR genes. These genes typically trigger resistance response via recognition of the effectors of blast fungus. Although these genes mediate strong resistance, each blast resistant gene can typically identify only a small number of *M. oryzae* strains. Thus, rice varieties carrying these genes tend to lose their resistance when planted in large areas (Lan *et al.*, 2019). Normally, many cultivars carry low numbers of blast resistance genes, but resistance is not typically observed in the field. For example, *Pikh* is widely distributed in rice varieties present in southern China, but only 60% of these varieties are resistant against rice blast. Previous studies showed that gene polymerization could improve the resistance to rice blast, and thus could assist in widening the resistance spectrum (Lu *et al.*, 2017). In 2008, *Pi1*, *Pi2*, and *Pi33* were polymerized into Jin 23, with a disease resistance frequency of 96.7%, which was significantly higher as compared to the varieties carrying only one gene (Chen *et al.*, 2008). In another study, resistance genes *Pita*, *Pid(t)*, and *Pib* were polymerized into a maintainer hybrid G46B, resulting in stronger resistance to rice blast and exhibiting a wider resistance spectrum (Chen *et al.*, 2004a). The complexity and variability of blast fungus and the occurrence of differences between prevalent strains in different regions necessitate the identification of genes that carry local resistance effects, prior to the breeding of disease-resistant varieties that are deemed fit for cultivation. This approach will further assist in improving the efficiency of disease-resistant varieties. In addition to this, it is important to combine R gene with non-race-specific resistance genes to avoid the degeneration of disease resistance (Patroti *et al.*, 2019). Among various cloned rice blast resistant genes, *Pb1*, *pi21*, *bsr-d1*, and *Pi35* have been shown to mediate non-race-specific resistance (Wang *et al.*, 2017). In addition, *Pi34* was reported to exhibit a high level of partial resistance to rice blast (Kaoru *et al.*, 2005). During breeding, the combination of these genes with R genes could aid in the improvement of the resistance and reduction of the risk of severe rice blast in the field.

During molecular breeding, it is very important to improve rice blast resistance without affecting other agronomic traits. *pi21* is an effective partial resistance gene, however, resistant varieties bred with *pi21* donors



were found to have inferior eating quality. *Pigm* is known to play an important role in improving disease resistance of *indica* rice, but similar to other *indica* resistance germplasm, its application in japonica disease resistance breeding remains limited. The crossing of japonica with *indica* resulted in undesirable agricultural traits in the offspring (Li *et al.*, 1998), which included reduced seed setting rates, higher plant heights, and a delayed growth period. Thus, it is necessary to breed japonica germplasm resources with *Pigm*, which could possibly promote its ability to improve rice blast resistance in japonica.

**Limitations and future perspectives:** In the past few years, advancements in molecular biology and QTL mapping technology assisted in the identification, cloning and application of large variety of rice blast resistance genes that provided an important foundation for the breeding of resistant rice varieties. However, the process of breeding is associated with certain limitations. Many varieties of rice carry blast resistance genes; however, the issues of **poor** disease resistance or rapid loss of resistance in the field limit their application. It has been previously shown that molecular breeding mediated increase in the resistance of the offspring lines might be associated with loss of favorable agronomic traits, even after multiple generations of backcrossing. In addition to this, dramatic increase in the planting area dedicated for disease-resistant varieties was accompanied by decline or loss of resistance. Since many of the disease-resistant donors are *indica*, their application in improving the resistance of japonica might result in a prolonged breeding process to achieve the desired improvement in resistance, probably due to variable genetic backgrounds of these two sub-species.

In the future, the effects of resistance genes in different geographical regions should be identified before they are applied in molecular breeding. To breed varieties with persistent resistance, R genes and non-race-specific genes should be used in combination, or to breed multi-line varieties, which could probably help in controlling the occurrence of blast disease through biodiversity. In addition to this, studies should focus on the identification of disease resistance genes in different rice resources, particularly in japonica. Owing to the co-evolution of rice blast varieties and rice fungus, the data on mapping, functional assessment, and utilization of blast resistance genes should be updated regularly.

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