JARQ 43 (4), 255–280 (2009) http://www.jircas.affrc.go.jp

REVIEW

# Resistance Genes and Selection DNA Markers for Blast Disease in Rice (*Oryza sativa* L.)

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## Abstract

Blast is a serious disease caused by a fungal pathogen *Pyricularia oryzae* Cavara of rice (*Oryza sativa* L.). The use of resistant varieties is considered one of the most efficient ways of crop protection from the disease. In addition to a large amount of information accumulated during the long history of genetic studies on resistance to rice blast, recent progress in rice genomics has enabled us to use DNA markers for breeding the resistant varieties by marker assisted selection (MAS). In this report, we summarize the reported rice blast resistance genes and their selection markers to encourage further utilization for breeding. First, we assemble the information about the reported genes with regard to their number, chromosomal locations, patterns of resistance, donor strains, and molecular characterization of the cloned genes by reviewing the literature. In addition, we present some remaining issues about the nomenclature system and identification of the resistance genes. Then, we provide the first assembled list of the reported DNA markers for blast resistance genes, including the sequences of the primer pairs, genetic distances from the resistance genes, and cross combinations of the parental strains used to detect the polymorphisms. This information will help rice breeders to improve the resistance to rice blast by MAS.

**Discipline:** Plant breeding
**Additional key words:** Blast (*Pyricularia oryzae* Cavara), marker assisted selection (MAS), resistance gene

## Introduction

Blast is a serious disease caused by a fungal pathogen *Pyricularia oryzae* Cavara of rice (*Oryza sativa* L.). It causes considerable damage to rice and crop loss in rice growing regions worldwide[6,60,79]. Although fungicides can be used to control rice blast, they generate additional costs in rice production and chemical contamination of environment and foods. Therefore, the use of resistant varieties is thought to be one of the most economically and environmentally efficient ways of crop protection from the disease.

A large amount of information has been accumulated during the long history of genetic studies on resistance to rice blast. In addition, recent progress in rice genomics will facilitate using the resistance genes in breeding by DNA marker assisted selection (MAS). However it is not easy for breeders to handle a large amount of information for DNA markers and there are no reports or databases that assemble reported marker information for rice blast resistance genes. In this report, we summarize the reported resistance gene information for rice blast and their selection markers. Such information will help rice breeders improve the resistance to rice blast through using MAS.

## Overview of blast resistance genes

Since the first publication of the inheritance of host resistance to rice blast[89], many reports of the resistance genes for rice blast have been published. To date, more than 70 genes and 347 quantitative trait loci (QTLs) have been detected[2]. To encourage further utilization of these

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Received 29 September 2008; accepted 23 January 2009.

resistance genes for marker-assisted rice breeding, we first summarize this large amount of information. Although there have been many QTL mapping studies for rice blast resistance, it is still unclear whether many QTLs with minor effects can be used in marker-assisted breeding. Thus we will focus on only genes or QTLs with major effects in this review.

**1. Number of rice blast resistance genes**

The genes and major QTLs responsible for the rice blast resistance are listed in Table 1. To date, 96 genes or major QTLs have been reported. Among the reported resistance genes, several gene symbols are synonymously used for the following two reasons.

(1) The gene symbols were revised in accordance with the international committee on gene symbolization in 1995 (e.g., *Pib* and *Pis*, *Pita* and *Pi4, Piz* and *Pi2*, and, *Pi11* and *Pizh*).

(2) The genes are suggested to be identical to each other based on their reaction pattern to blast isolates and/or linkage analysis (e.g. *Pi3*(t) and *Pi5*(t), and *Pi1* and *Pi7*(t)[45,49]).

In addition, several genes are suggested to be allelic or tightly linked (e.g., *Pi2/Piz, Piz-t,* and *Piz-5* on chromosome 6, *Pik, Pik-s, Pik-p, Pik-m, Pik-h*, and *Pik-g* on chromosome 11, and *Pita* and *Pita-2* on chromosome 12).

**2. Characterization of the cloned resistance genes**

As of now, nine resistance genes, *Pib*[102], *Pita*[7], *Pik-h*[90], *Pi9*[87], *Pi2*[114], *Piz-t*[114], *Pid2*[14], *Pi36*[16], and *Pi37*[64] have been isolated and cloned using map-based cloning strategies.

Eight of the cloned genes (*Pib, Pita, Pik-h, Pi9, Pi2, Piz-t, Pi36,* and *Pi37*) have the sequences including both nucleotide binding site (NBS) and leucine-rich repeat (LRR) domains, which are contained by the commonest class of plant resistance gene[4,32,42]. The products of the NBS-LRR domain containing resistance genes seem to interact with the avirulence (Avr) gene of the pathogen and follow a gene-for-gene type resistance. Jia et al.[51] showed that the product of the Avr gene for *Pita*, *Avr-Pita,* binds specifically to the LRR domain of the *Pita* protein by the yeast two hybrid system and an in vitro binding assay. This suggests that the product of the resistance gene, *Pita*, binds directly with the effecter gene product of the pathogen to initiate the resistance gene mediated defense response. However, it is still unknown whether the other resistance genes also interact with the pathogen directly.

Another cloned resistance gene, *Pid2*, encodes a receptor-like kinase protein with a predicted extracellular domain of a bulb-type mannose specific binding lectin (B-lectin)[14]. Because of its novel extracellular domain, *Pid2* represents a new class of plant resistance gene.

**3. Location of the resistance genes**

To summarize the locations of the rice blast resistance genes in the genome a genetic map with the positions of the reported genes was constructed (Fig. 1). The map position was based on the high-density genetic map constructed by the Rice Genome Program[12,33]. The approximate genetic positions of the resistance genes were determined by identifying BAC or PAC clones that contained the sequences of the cloned gene or the flanking marker.

Many reports mention that the genes affecting blast resistance are colocalized on chromosomes 6, 11 and 12[7,103]. On chromosome 6, at least 14 genes and/or alleles (*Pi2, Piz, Piz-t, Piz-5, Pi8*(t)*, Pi9, Pi13, Pi13*(t)*, Pi25*(t)*, Pi26*(t)*, Pi27*(t) *Pid2, Pigm*(t), and *Pi40*(t)) have been mapped in the region near the centromere. Among them, *Pi2, Piz-t,* and *Pi9* are cloned and confirmed to be in the same genomic region. They are embedded in a gene cluster containing tandemly repeated NBS-LRR genes[87,114]. Zhou et al.[114] revealed that *Pi2* and *Piz-t* are allelic and eight amino acid changes differentiate between them.

On the long arm of chromosome 11, at least nine genes (*Pi1, Pi7, Pi18*, *Pif*, *Pi34*, *Pi38*, *Pi44*(t), *PBR*, and *Pilm2*) and six alleles at the *Pik* locus (*Pik, Pik-s, Pik-p, Pik-m, Pik-h,* and *Pik-g*) have been mapped. Hayashi et al.[39] revealed that three alleles of the *Pik* locus, *Pik, Pik-p* and *Pik-m* are mapped on the same chromosomal region by linkage analysis using 300 to 2,100 $F_2$ segregation populations. Although this result is consistent with the notion that these three genes are multiple alleles at the one locus, more detailed analysis is necessary to confirm that they are allelic. Sharma et al.[90] identified and cloned the *Pik-h* gene from an Indica-type variety, Tetep. However its location is apart from the *Pik* cluster. The question whether the cloned *Pik-h* gene from Tetep is the same gene as the *Pik-h* gene first reported by Kiyosawa and Murty[56] is under debate[106].

On chromosome 12, at least 17 resistance genes and/or alleles (*Pita, Pita-2, Pitq6, Pi6*(t)*, Pi12*(t), *Pi12*(t)*, Pi19*(t)*, Pi20*(t)*, Pi21*(t), *Pi24*(t), *Pi31*(t)*, Pi32*(t), *Pi39*(t)*, Pi62*(t)*, Pi157*(t) *IPi,* and *IPi3*) have been mapped in the region near the centromere (the gene symbol, *Pi12*(t) is used for the different two genes as mentioned below).

Based on the data of genome-wide mapping of the NBS-LRR domain containing genes reported by Monosi et al.[72], all three clusters of the rice resistance genes are closely associated with the clusters of NBS-LRR domain

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

| Gene | Map position (cM)[1)] | Donor | | Type of resistance[2)] | Current status | Harboring varieties | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|
| | | Strain (original donor) | Type | | | | | |
| Chromosome 1 | | | | | | | | |
| *Pit* | 12.2 | Tjahaja | Japonica | C | Mapped within 770 kb | BL10, K59, Tongil | - | Hayashi et al. 2006 |
| *Pi27*(t) | 28.4-38.8 | Q14 | - | C | Mapped within 21.6 cM | - | - | Zhu et al. 2004 |
| *Pi24*(t) | 64.4 | Azucena | Japonica | - | QTL mapping | - | - | Sallaud et al. 2003 |
| *Pitp*(t) | 114.1 | Tetep | Indica | - | Co-segregation marker was identified | - | - | Barman et al. 2004 |
| *Pi35*(t) | 132.0-136.6 | Hokkai 188 | Japonica | P | QTL mapping | - | - | Nguyen et al. 2006 |
| *Pi37* | 136.1 | St. No. 1 | Japonica | - | Cloned | - | - | Lin et al. 2007 |
| *Pish* | 148.7-154.8 | Shin 2 | Japonica | C | Mapped within 6.1 cM | Nipponbare, Pi No. 4, Fukunishiki, Norin 22, Kusabue, BL1, Akihikari | - | Imbe et al. 1985, Fukuta et al. 2004 |
| Chromosome 2 | | | | | | | | |
| *Pid1*(t) | 87.5-89.9 | Digu | Indica | - | Mapped within 11.8 cM | - | - | Chen et al. 2004 |
| *Pig*(t) | 142.0-154.1 | Guangchangzhan | Indica | - | Mapped within 10.3 cM | - | - | Zhou et al. 2004 |
| *Pitq5* | 150.5-157.9 | Teqing | Indica | C | QTL mapping | - | - | Tabien et al. 2000 |
| *Piy1*(t) | 153.2-154.1 | Yanxian No.1 | Indica | - | Mapped within 1.6 cM | - | - | Lei et al. 2005 |
| *Piy2*(t) | 153.2-154.1 | Yanxian No.1 | Indica | - | Mapped within 3.0 cM | - | - | Lei et al. 2005 |
| *Pib* | 154.1 | Tohoku IL9 | Japonica | C | Cloned | Tjina, BL1, IRT 13, WHD-1S-175-1-127, Teqing, Engkatek, Milek Kuning | synonymous to *Pis* | Hayasaka et al. 1995, Wang et al. 1999, Fjellstrom et al. 2004 |
| *Pi25*(t) | 157.9 | IR64 | Indica | - | QTL mapping | - | - | Sallaud et al. 2003 |
| *Pi14*(t) | - | Maowang | - | C | Linkage analysis using isozyme marker | - | linked to isozyme marker *Amp1* | Pan et al. 1996 |
| *Pi16*(t) | - | AUS373 | - | C | Linkage analysis using isozyme marker | - | linked to isozyme marker *Amp1* | Pan et al. 1997 |
| Chromosome 4 | | | | | | | | |
| *pi21* | 58.6 | Owarihatamochi | Japonica | P | QTL mapping | - | recessive | Fukuoka and Okuno 2001 |

| Gene | Map position (cM)[1)] | Donor | | Type of resistance[2)] | Current status | Harboring varieties | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|
| | | Strain (original donor) | Type | | | | | |
| *Pikur1* | 86 | Kuroka | Japonica | - | Linkage analysis using phenotypic marker | - | - | Goto 1988 |
| *Pi39*(t) | 107.4-108.2 | Chubu 111 (Haonaihuan) | Japonica | - | Mapped within 0.3 cM | - | - | Terashima et al. 2008 |
| *Pi*(t) | - | - | - | - | - | - | - | Causse et al. 1994 |
| Chromosome 5 | | | | | | | | |
| *Pi26*(t) | 22.5-24.7 | Azucena | Japonica | - | QTL mapping | - | - | Sallaud et al. 2003 |
| *Pi23*(t) | 59.3-99.5 | Sweon 365 | Japonica | - | | - | - | Ahn et al. 1997 |
| *Pi10* | 88.5-102.8 | Tongil | Indica | C | Mapped within 6.7 cM | - | - | Naqbi et al. 1995, Naqbi and Chatto 1996 |
| Chromosome 6 | | | | | | | | |
| *Pi22*(t) | 38.7-41.9 | Sweon 365 | Japonica | - | - | - | - | Ahn et al. 1997 |
| *Pi26*(t) | 51.0-63.2 | Gumei 2 | Indica | - | QTL mapping | - | - | Wu et al. 2005 |
| *Pi27*(t) | 51.9 | IR64 | Indica | - | QTL mapping | - | - | Sallaud et al. 2003 |
| *Pi40*(t) | 54.1-61.6 | IR65482-4-136-2-2 (Acc100882) | *Oryza australiensis* | - | Mapped within 1.8 cM | - | - | Jeung et al. 2007 |
| *Piz-5* | 58.7 | Tadukan | Indica | C | Cloned | K60, C101A51 (5173) | synonymous to *Pi2*(t), allelic to *Piz-t, Piz,* tightly linked with *Pi*9(t) | Zhou et al. 2006 |
| *Piz* | 58.7 | Zenith | - | C | Mapped within 0.43 cM | Fukei 67 Fukunishiki | allelic to *Piz-5, Piz-t* | Goto 1976, Goto et al. 1981, Hashimoto et al. 1998, Hayashi et al. 2006 |
| *Piz-t* | 58.7 | Toride 1 | Japonica | C | Cloned | IR56 | allelic to *Piz-5*(*Pi2*) | Zhou et al. 2006 |
| *Pi9* | 58.7 | 75-1-127 (101141) | *Oryza minuta* | C | Cloned | - | tightly linked with *Piz-5* (*Pi2*) | Qu et al. 2006 |
| *Pi25*(t) | 63.2-64.6 | Gumei 2 | Indica | - | QTL mapping | - | - | Zhuang et al. 2001, Wu et al. 2005 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Pid2* | 65.8 | Digu | Indica | C | Cloned | - | - | Chen et al. 2006 |
| *Pigm*(t) | 65.8 | Gumei 4 | Indica | - | Mapped within 70 kb | - | - | Deng et al. 2005 |
| *Pitq1* | 103.0-124.4 | Teqing | Indica | C | QTL mapping | - | - | Tabien et al. 2000 |
| *Pi8* | - | Kasalath | Indica | C | Mapped using isozyme marker | - | linked to isozyme markers, *Amp3, Pgi2* and *Piz-t* | Pan et al. 1995, Pan et al. 1996 |
| *Pi13*(t) | - | Maowang | - | C | Mapped using isozyme marker | - | linked to marker genes *Amp3* and *C* | Pan et al. 1996 |
| *Pi13* | - | Kasalath | Indica | - | - | - | - | Hayasaka et al. 1995, Ballini et al. 2008 |
| Chromosome 7 | | | | | | | | |
| *Pi17*(t) | 94.0-104.0 | DJ 123 | - | C | - | - | linked to isozyme marker Est9 | Pan et al. 1995, Iwata 1996 |
| Chromosome 8 | | | | | | | | |
| *Pi36* | 21.6-25.2 | Q61 | Indica | - | Cloned | - | - | Liu et al. 2007 |
| *Pi33* | 45.4 | IR64, Bala | Indica | C | Mapped within 1.6 cM | - | - | Berruyer et al. 2003 |
| *Pizh* | 53.2-84.8 | Zhai-Ye-Quing | Indica | C | QTL mapping | - | synonymous to *Pi11* | Causse et al. 1994 |
| *Pi29*(t) | 69 | IR64 | Indica | - | QTL mapping | - | possibly identical to *Pi11* | Sallaud et al. 2003 |
| *PiGD-1*(t) | - | Sanhuangzhan 2 | - | - | QTL mapping | - | - | Liu et al. 2004 |
| Chromosome 9 | | | | | | | | |
| *Pii2*(t) | - | Ishikari shiroke | Japonica | - | Linkage analysis using phenotypic marker | - | - | Kinoshita and Kiyosawa 1997 |
| *Pi5*(t) | 31.3-33.0 | RIL125, RIL249, RIL260 (Moroberekan) | Japonica | C | Mapped within 170 kb | - | tightly linked with *Pi3*(t) | Jeon et al. 2003 |
| *Pi3*(t) | 31.3-33.0 | Pai-Kan-Tao | Japonica | C | Linkage analysis to other resistance genes | Taebaeg, C104PKT | tightly linked with *Pi5*(t) | Inukai et al. 1996 |
| *Pi15* | 31.3-34.9 | GA25 | - | C | Mapped within 0.7 cM | - | linked with *Pi5*(t), *Pi3*(t), and *Pii* | Pan et al. 1996; 2003 |
| *Pii* | - | Ishikari shiroke | Japonica | C | Linkage analysis using phenotypic marker | Fujisaka 5 | - | Ise 1991 |

| Gene | Map position (cM)[1)] | Donor | | Type of resistance[2)] | Current status | Harboring varieties | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|
| | | Strain (original donor) | Type | | | | | |
| Chromosome 10 | | | | | | | | |
| *Pi28*(t) | 114.7 | Azucena | Japonica | - | QTL mapping | - | - | Sallaud et al. 2003 |
| *PiGD-2*(t) | - | Sanhuangzhan 2 | - | - | QTL mapping | - | - | Liu et al. 2004 |
| Chromosome 11 | | | | | | | | |
| *Pia* | 36 | Aichi Asahi | Japonica | C | | CO39, Zenith | - | Goto et al. 1981 |
| *PiCO39*(t) | 49.1 | CO39 | Indica | C | Mapped within 1.2 cM | - | - | Chauhan et al. 2002 |
| *Pilm2* | 56.2-117.9 | Lemont | Japonica | C | QTL mapping | - | synonymous to *Pib2* | Tabien et al. 2000; 2002 |
| *Pi30*(t) | 59.4-60.4 | IR64 | Indica | - | QTL mapping | - | - | Sallaud et al. 2003 |
| *Pi7*(t) | 71.4-84.3 | RIL29 (Moroberekan) | Japonica | C | QTL mapping | - | identical to *Pi1* | Wang et al. 1994 |
| *Pi34* | 79.1-91.4 | Chubu 32 | Japonica | P | QTL mapping | - | - | Zenbayashi et al. 2002 |
| *Pi38* | 79.1-88.7 | Tadukan | Indica | - | Mapped within 20 cM | - | - | Gowda et al. 2006 |
| *PBR* | 80.5-120.3 | St No.1 | Indica | - | Mapped within 22.9 cM | - | - | Fujii et al. 1995 |
| *Pb1* | 85.7-91.4 | Modan | Indica | P | Mapped within 12.4 cM | - | synonymous to *Pbst* | Fujii et al. 2000 |
| *Pi44*(t) | 91.4-117.9 | RIL29 (Moroberekan) | - | C | - | - | - | Chen et al. 1999 |
| *Pik-h* | 101.9 | Tetep | Indica | C | Mapped within 1.2 cM | K3, Kaybonnet, Lemont, Lebonnet | allelic to *Pik* | Sharma et al. 2005, Fjellstrom et al. 2004 |
| *Pi1* | 112.1-117.9 | C101LAC (Lac23 ) | - | C | Mapped within 11.4 cM | - | identical to *Pi7*(t) | Hittalmani et al. 2000 |
| *Pik-m* | 115.1-117.0 | Tsuyuake | Japonica | C | Mapped within 0.3 cM | Tohoku IL4 | allelic to *Pik* | Kaji and Ogawa 1996, Li et al. 2007 |
| *Pi18*(t) | 117.9 | Sweon 365 | Japonica | C | Mapped using RFLP marker | - | - | Ahn et al. 1996 |
| *Pik* | 119.9-120.3 | Kusabue | Japonica | C | Mapped within 1.4 cM | Kanto 51, Sasanishiki BL1 | - | Hayasaka et al. 1996, Hayashi et al. 2006 |
| *Pik-p* | 119.9-120.3 | HR22 | - | C | Mapped within 2.8 cM | K60 | allelic to *Pik* | Hayashi et al. 2006 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Pik-s* | 115.1-117.3 | Shin 2 | Japonica | C | Mapped within 2.7 cM | Fujisaka 5, Caloro, B40, Zhaiyeqing 8, Bengal, M-201 | allelic to *Pik* | Fjellstrom et al. 2004 |
| *Pik-g* | - | GA20 | - | C | Linkage analysis to other resistance genes | - | allelic to *Pik* | Pan et al. 1996 |
| *Pise1* | - | Sensho | Japonica | - | Linkage analysis using phenotypic marker | - | synonymous to *Rb1* | Goto 1970 |
| *Pi f* | - | Chugoku 31-1 (St. No.1) | Japonica | P | Linkage analysis using phenotypic markers | - | linked to *Pik* | Shinoda et al. 1971 |
| *Mpiz* | - | Zenith | - | - | Linkage analysis using phenotypic markers | - | linked to *la* | Goto 1976 |
| *Pikur2* | - | Kuroka | Japonica | - | Linkage analysis using phenotypic markers | - | linked to *la* | Goto 1988 |
| *Piisi* | - | Imochi shirazu | Japonica | - | Linkage analysis using phenotypic markers | - | linked to *la* | Goto 1970 |
| Chromosome 12 | | | | | | | | |
| *Pi24*(t) | 10.3 | Zhong 156 | Indica | C | QTL mapping | Gumei 2, Yunxi 2, Q14, IR64 | - | Zhuang et al. 1997, Koizumi 2007 |
| *Pi62*(t) | 12.2-26.0 | Yashiromochi | Japonica | - | Mapped within 1.9 cM | - | - | Wu et al. 1996 |
| *Pitq6* | 29.2-47.5 | Teqing | Indica | C | QTL mapping | - | - | Tabien et al. 2000 |
| *Pi6*(t) | 32.6-63.2 | Apura | - | C | - | - | - | McCouch et al. 1994 |
| *Pi12*(t) | 42.8-53 | RIL10 (Moroberekan) | Japonica | C | - | - | - | Inukai et al. 1994 |
| *Pi21*(t) | 43.4-59.6 | Sweon 365 | Japonica | - | - | - | - | Ahn et al. 1997 |
| *Pi31*(t) | 44.3 | IR64 | Indica | - | QTL mapping | - | - | Sallaud et al. 2003 |
| *Pi32*(t) | 47.5 | IR64 | Indica | - | QTL mapping | - | - | Sallaud et al. 2003 |
| *Pi12*(t) | 47.6-48.2 | K80 (Hong-jiao-zhan) | Indica | - | Linkage analysis using RFLP markers | - | - | Zheng et al. 1996 |
| *Ipi*(t) | 47.6-58.3 | - | - | - | Linkage analysis using RFLP markers | - | - | Causse et al. 1994 |
| *IPi3*(t) | 47.6-58.3 | - | - | - | Linkage analysis using RFLP markers | - | - | Causse et al. 1994 |

| Gene | Map position (cM)[1)] | Donor | | Type of resistance[2)] | Current status | Harboring varieties | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|
| | | Strain (original donor) | Type | | | | | |
| *Pi157* | 49.5-62.2 | Moroberecan | Japonica | - | Mapped within 9.5 cM | - | - | Naqvi and Chattoo 1996 |
| *Pita* | 50.4 | Taducan | Indica | C | Cloned | K1, C101PKT, Zhaiye-qing 8, Yashiromochi, C105TTP2L9 | synonymous to *Pi4*, allelic to *Pita-2* | Bryan et al. 2000 |
| *Pita-2* | 50.4 | Shimokita | Japonica | C | Mapped within 4.0 cM | Pi No. 4, Reiho, IR64, Fukunishiki, Katy, Kaybonnet | allelic to *Pita* | Nakamura et al. 1997, Hayashi et al. 2006 |
| *Pi19*(t) | - | Aichi Asahi | Japonica | C | Linkage analysis to other resistance genes | Aichi Asahi, Shin 2, Ishikari Shiroke, Fujisaka 5, Kusabue, Tsuyuake, Yashiro-mochi, K1, Pi No. 4, Toride 1, BL1, K59, Kanto 51, Fukunishiki, K60 | linked to *Pita-2* | Hayashi et al. 1996, 1998, Iwata 1997 |
| *Pi39*(t) | 50.4 | Q15 | - | - | Mapped within 37 kb | - | - | Liu et al. 2007 |
| *Pi20*(t) | 51.5-51.8 | IR24 | Indica | C | Mapped within 0.6 cM | ARL 24 | - | Imbe et al. 1997, Li et al. 2008 |
| *PiGD-3*(t) | 55.8 | Sanhuangzhan 2 | - | - | QTL mapping | - | - | Liu et al. 2005 |
| Map position unidentified | | | | | | | | |
| *Pi67*(t) | - | Tsuyuake | Japonica | - | - | - | - | Wu et al. 1996 |
| *Piis2* | - | Imochi shirazu | Japonica | - | - | - | - | Goto 1970 |
| *Pise2* | - | Sensho | Japonica | - | - | - | - | Goto 1970 |
| *Pise3* | - | Sensho | Japonica | - | - | - | - | Goto 1970 |

1): The map position was based on the high-density genetic map constructed by the RGP. The approximate genetic positions of the resistance genes were determined by identifying BAC or PAC clones that contained the sequences of the cloned gene or the flanking marker.

2): C and P indicate complete resistance and partial resistance, respectively. The classifications of resistance pattern of each gene were followed according to Koizumi (2007) and the references for each gene (C: compete resistance, P: partial resistance).

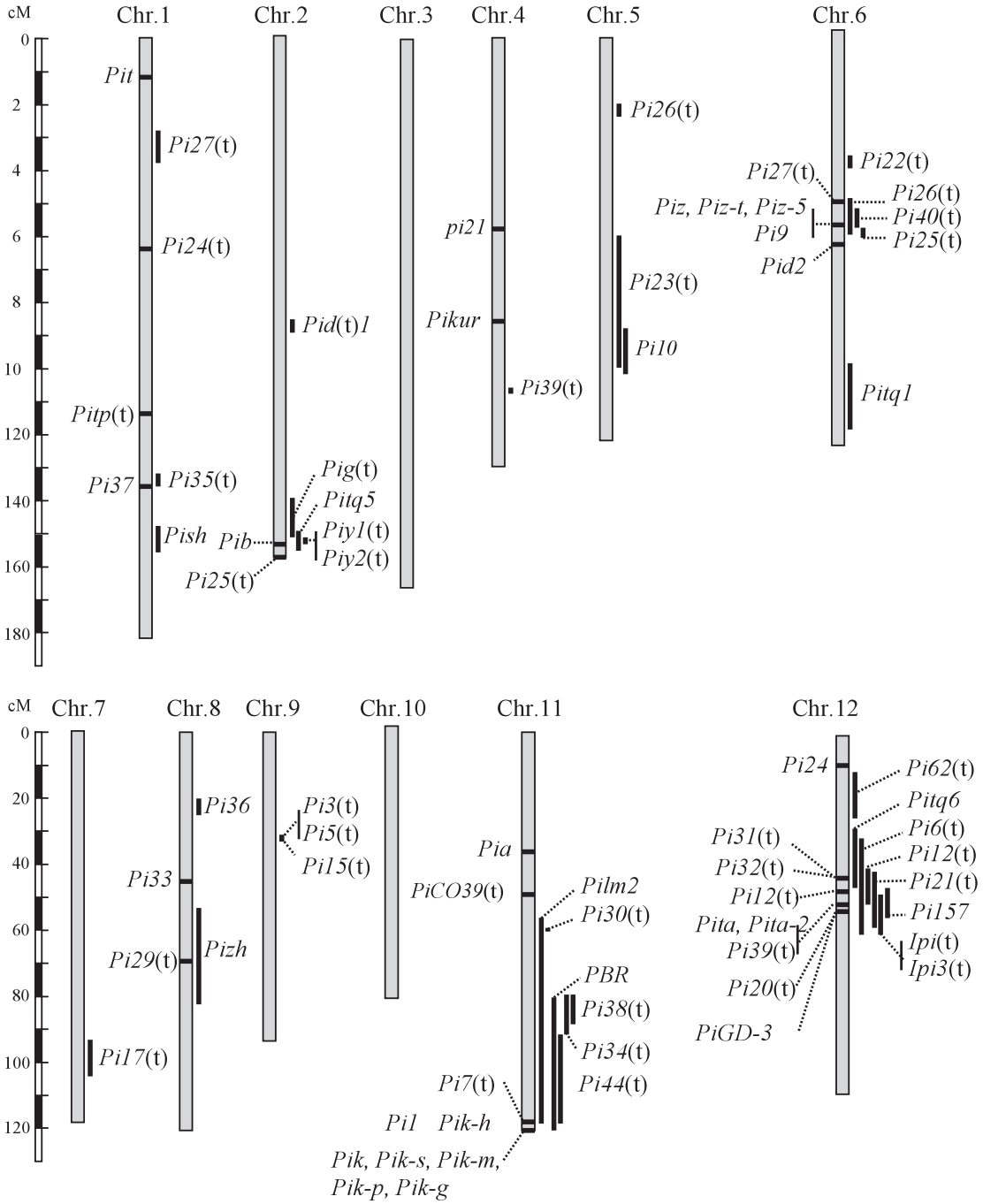


**Fig. 1. Putative location of the blast resistance genes reported by 2008**
The genetic location of each gene is based on the public databases (Oryzabase and Gramene) and the references for each gene (see Table 1).

containing genes. Ballini et al.[2] also reported that 80% of the complete resistance genes for rice blast colocalize with NBS-LRR candidates. These data suggest that non-random distribution of the resistance genes is partly due to localization of the NBS-LRR domain containing genes in the genome.

## 4. Partial resistance

Blast resistance in rice is generally classified into complete and partial resistance. Complete resistance, caused by incompatible combinations between the host and pathogen strains, prevents reproduction of the pathogen, and the resistance is usually controlled by a major gene. Another form of resistance, partial resistance,

is characterized by a decrease in the extent of pathogen reproduction in the compatible interaction[86]. Although the partial resistance has been thought to be under polygenic control and shows a non pathogen race specific pattern of resistance, several recent studies suggest that not all the partial resistance have such characteristics. To date, four major genes (*Pif, pi21, Pb1*, and *Pi34*(t)) that control partial resistance are reported (Table 1)[19,21,110-112]. Moreover, Zenbayashi-Sawata et al.[112] reported that the interaction between the partial resistance gene *Pi34*(t) and a corresponding avirulence gene follows the gene-for-gene model, suggesting that the partial resistance gene does not always show a non pathogen race specific pattern of resistance.

The molecular mechanism of the partial resistance genes is one of the topics for studying resistance genes. Fukuoka et al.[22,23] revealed that one of the partial resistance genes, *pi21*, has sequences different from those of the previously reported complete resistance genes. Recently, Ballini et al.[2] revealed that the reported QTLs for partial resistance are different from the mapped complete resistance genes with regard to colocalization with resistance gene analogs by meta-QTL analysis, which statistically estimates the position of one single QTL by combining the QTL obtained from different studies. These results were consistent with the notion that partial and complete resistance is governed by different types of genes.

**5. Donor strains**

Apart from three resistance genes (*Pi9, Pi33* and *Pi40*(t)) that have been found in wild relatives, most rice blast resistance genes have been found in rice blast resistant varieties. Tsunematsu et al.[99] revealed that an Indica-type variety, CO 39, which has been used as a susceptible check strain also carried the rice blast resistance gene, *Pia*, and made a monogenic line harboring it. In addition, Chauhan et al.[9] showed that CO 39 also carried another blast resistance gene, *PiCO39*(t). These observations suggest that even a variety previously considered to be susceptible might have the resistance gene which specially interacts with the unidentified isolates and is used as a donor parent of the resistance genes.

Telebanco-Yanoria et al.[95] surveyed genetic diversity of blast resistance in 922 rice varieties by using the standard differential blast isolates selected by Telebanco-Yanoria et al.[96]. They revealed the relationships among the variations of the pattern of resistance for 20 standard blast isolates, geographical distribution, and the genetic variations characterized by the isozyme types[26] of the rice varieties. Such a study will help to find a novel resistance gene and enhance the diversity of the resistance genes used in rice breeding.

## Problems in studying blast resistance genes

**1. Nomenclature system**

As shown in Table 1, 96 rice blast resistance genes have been reported. Information about these genes is available in databases such as Oryzabase (http://www.shigen.nig.ac.jp/rice/oryzabase/top/top.jsp) and Gramene (http://www.gramene.org/). However, the following problematic points remain to be solved.

(1) The same gene symbol was given to different genes as Ballini et al.[2] pointed out. There are at least 9 redundant gene symbols, *Pi12, Pi13, Pi14, Pi21, Pi24, Pi25, Pi26, Pi27,* and *Pi39,* that have been used to date.

(2) Several studies do not follow the rules for naming and symbolization of blast resistance genes. If a blast resistance gene is identified, it should be designated with *Pi* followed by a numeral according to the Committee on Gene Symbolization[54].

(3) Different studies use different writing systems for the same resistance gene (e.g., *Pik-h*, *Pikh, Pi-kh, Pik$^h$*, and *Pi-k$^h$*).

The rice blast research community should have responsibility for symbolizing a new gene to avoid a confusing situation.

**2. Identification of the genes**

As mentioned above, several gene symbols are synonymously used because they are suggested to be identical with each other based on their reaction pattern to blast isolates and/or linkage analysis (e.g., *Pi3*(t) and *Pi5*(t), and *Pi1* and *Pi7*(t)[45,49]). However, it is difficult to confirm the identification of the two genes, because if both the genes are dominant and tightly linked to each other, it is impossible to confirm that these genes are identical to each other by a simple allelism test. Similarly, although many of the resistance genes have been mapped on the same chromosomal region and are thought to be in a gene cluster, it is still unclear whether these genes are at tightly linked different loci or whether these genes are the alleles of one locus. Furthermore, several genes are suggested to be allelic without detailed confirmation of the allelic relationships in some cases. Information about whether the two genes are allelic is important for breeding because the alleles of one locus cannot be integrated into and fixed in one plant, while two genes at different loci can. More detailed analysis, such as high resolution mapping and positional cloning of the genes, is necessary to confirm the allelic relationship of the genes.

Except for the tightly linked genes, genetic analysis based on gene segregation is a powerful tool for clarifying the identity of the genes. Toriyama et al.[98] demonstrated that the estimation of genes with resistance to blast in rice varieties by using segregation analysis with the population derived from a cross between resistant and susceptible varieties was effective. Monogenic lines for blast resistance were developed as the first set of international standard differential varieties[25,58,99]. Such a differential system is very useful to estimate the identity of the genes by conventional segregation analysis.

## Using MAS for blast resistance genes

### 1. Advantages of molecular markers for selecting resistance genes

Marker assisted selection (MAS) is a process whereby a DNA marker is used for indirect selection of the genes underlying target traits. With the fast development of molecular biotechnologies, MAS has been receiving more attention in recent years because it has advantages for efficiency and effectiveness as compared to conventional phenotypic selection (reviewed by Collard et al.[15]; Xu and Crouch[105]). There are several advantages of using MAS for breeding instead of using conventional phenotypic selection. For example, MAS has the potential to save time and reduce the cost of breeding in cases where conventional phenotypic selection is particularly time-consuming or expensive to measure. Furthermore, selection based on DNA markers may be more reliable due to the influence of environmental factors on field trials.

MAS has been shown to be especially valuable in backcross breeding. Over 90% of the recurrent parental genotype can be recovered within two generations when a suitable number of markers (e.g., one marker every 10 cM) and an adequate number of progeny are used for background selection[94,105]. Since the complete resistance to rice blast is often controlled by a major gene, MAS seems useful for improving the complete resistance to rice blast by backcross breeding. In addition, MAS is a powerful tool for pyramiding two or more genes affecting blast resistance. In some cases, the phenotypic effect of the resistance gene is masked by that of another resistance gene, which is brought together into one plant, because blast resistance genes sometimes confer resistance to overlapping spectra of blast pathotypes. In this case, it is difficult to monitor the presence of multiple resistance genes without using MAS.

### 2. Markers suitable for MAS

Many types of DNA markers including restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs), simple sequence repeats (SSRs), and cleaved amplified polymorphic sequences (CAPS), have been developed[71]. Among them, PCR markers, such as CAPS and SSRs require only small quantities of DNA from small tissue samples for genotyping. Therefore selection can be carried out at the seedlings stage. Thus these markers are cost-effective and advantageous for applied breeding.

Recently, Hayashi et al.[39] developed a PCR-based marker system for 9 rice blast resistance genes based on the information of single-nucleotide polymorphisms (SNPs) and small insertions/deletions (InDels). In this system, by using allele-specific PCR primers, the genotypes of SNP can be easily assessed according to the presence or absence of PCR-amplified products. Because SNPs and small InDels are highly abundant and widely dispersed throughout the genome in rice[17,77,108], such types of DNA markers can help generate a sufficient number of markers within target genomic regions.

### 3. Conventional markers developed for detecting rice blast resistance genes

To date, 9 of the rice blast resistance genes have been isolated by map based cloning and more than 14 genes have been finely mapped (Table 1). During the procedure of fine mapping of the resistance genes, DNA markers which are tightly linked to or co-segregated with the target genes can be obtained. These markers have the potential for use in MAS. In addition, several markers have been developed based on the information of the cloned resistance gene position[18,39,52,59]. These markers were designed according to DNA polymorphisms between resistant and susceptible varieties within or around the genes.

The PCR based markers reported to be tightly linked or co-segregated with the rice blast resistance genes are listed in Table 2. Although there are many reports of genetic linkage analysis using RFLP or AFLP markers, we excluded these types of markers from the list because RFLP or AFLP are laborious to use in a breeding program. Information for these conventional markers will encourage further utilization of the resistance genes for marker-assisted rice breeding.

## Future perspectives of MAS for blast resistance genes

Because MAS uses DNA markers to indirectly select the phenotype, its efficiency is highly dependent on the strength of association between using DNA markers and genes responsible for the phenotypes. If there is a DNA

**Table 2. Summary of conventional DNA markers for the rice blast resistance genes**

| Target gene | Type of marker | Marker name | Distance | Primer | | Population used (Resistant /Susceptible varieties) | Restriction enzyme | Reference |
|---|---|---|---|---|---|---|---|---|
| | | | | Forward | Reverse | | | |
| Chromosome 1 | | | | | | | | |
| *Pit* | SNP | t311 | 0.44 | CGTGAACCCAAGGCACCAGTATTC (Koshihikari-specific primer) | CATGTAGTTCTGGATGTTGTAGCTACTC | K59/Koshihikari | | Hayashi et al. 2006 |
| | | | | CGTGAACCCAAGGCACCAGTATTA (K59-specific primer) | CATGTAGTTCTGGATGTTGTAGCTACTC | K59/Koshihikari | | Hayashi et al. 2006 |
| | SNP | t256 | 0 | GGATAGCAGAAGAACTTGAGACTG (Koshihikari-specific primer) | CATGTCTTTCAACATAAGAAGTTCTC | K59/Koshihikari | | Hayashi et al. 2006 |
| | | | | GGATAGCAGAAGAACTTGAGACTA (K59-specific primer) | CATGTCTTTCAACATAAGAAGTTCTC | K59/Koshihikari | | Hayashi et al. 2006 |
| | SNP | t8042 | 0.28 | CTCAAGATTGTATCGTCGACGACTA (Koshihikari-specific primer) | GAGAGGTTTGCAGCCAGACCAGG | K59/Koshihikari | | Hayashi et al. 2006 |
| | | | | CTCAAGATTGTATCGTCGACGACTC (K59-specific primer) | GAGAGGTTTGCAGCCAGACCAGG | K59/Koshihikari | | Hayashi et al. 2006 |
| *Pi27*(t) | SSR | RM151 | 11.9 | GGCTGCTCATCAGCTGCATGCG | TCGGCAGTGGTAGAGTTTGATCTGC | Q14/Q61 | | Zhu et al. 2004 |
| | SSR | RN259 | 9.7 | TGGAGTTTGAGAGGAGGG | CTTGTTGCATGGTGCCATGT | Q14/Q61 | | Zhu et al. 2004 |
| *Pitp*(t) | SSR | RM246 | 0 | GAGCTCCATCAGCCATTCAG | CTGAGTGCTGCTGCGACT | Tetep/CO39 | | Barman et al. 2004 |
| *Pi35*(t) | SSR | RM1216 | <3.5 | TTCCCCAATGGAACAGTGAC | AGGGTCTACCACCCGATCTC | Hokkai188 /Danghang-Shali | | Nguyen et al. 2006 |
| | SSR | RM1003 | <3.5 | GATTCTTCCTCCCCTTCGTG | TTCCTGTCAGAACAGGGAGC | St. No. 1 /C101PKT, CO39, or AS20-1 | | Nguyen et al. 2006 |
| *Pi37* | SSR | RM302 | 0 | TCATGTCATCTACCATCACAC | ATGGAGAAGATGGAATACTTGC | St. No. 1 /C101PKT, CO39, or AS20-1 | | Chen et al. 2005 |
| | SSR | RM212 | 0 | CCACTTTCAGCTACTACCAG | CACCCATTTGTCTCTCATTATG | St. No. 1 /C101PKT, CO39, or AS20-1 | | Chen et al. 2005 |
| | SSR | FPSM1 | 0.07 | TTGAACATGATCCACCCCAC | ATTCCCGTAGCCGTAGAGTC | St. No. 1 /C101PKT, CO39, or AS20-1 | | Chen et al. 2005 |
| | SSR | FPSM2 | 0.14 | GAAGGTCCATCAAACGCTGC | CTCGCGGACAAGACGATACG | St. No. 1 /C101PKT, CO39, or AS20-1 | | Chen et al. 2005 |
| | SSR | FPSM4 | 0 | CCTTCCAGTCCTCGTTATCG | CCACGCGACCCTGTTTGAGA | St. No. 1 /C101PKT, CO39, or AS20-1 | | Chen et al. 2005 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | STS | S15628 | 0 | GGATGAGCTCACCGAGCAAC | AGGCTATAACACTGCAGCGG | St. No. 1 /C101PKT, CO39, or AS20-1 | Chen et al. 2005 |
| | STS | FSTS1 | 0 | CGCTGCATGGCACTAACCCT | CAAGAGGCTGGAACAGACAC | St. No. 1 /C101PKT, CO39, or AS20-1 | Chen et al. 2005 |
| | STS | FSTS2 | 0.14 | GGAACTGCGGCGAAAGGAAT | TCAGGAAGCCGTACATTAGG | St. No. 1 /C101PKT, CO39, or AS20-1 | Chen et al. 2005 |
| | STS | FSTS3 | 0 | GCCGCTGTGGCCTCGTCAATCTACATCAAG | AAGGAAGAGGAGATCGCTATCGGAGGGGCA | St. No. 1 /C101PKT, CO39, or AS20-1 | Chen et al. 2005 |
| | STS | FSTS4 | 0 | CAGGCTCAGGAACGACACG | GCTACGACGCGCTGTGGAAT | St. No. 1 /C101PKT, CO39, or AS20-1 | Chen et al. 2005 |
| Chromosome 2 | | | | | | | |
| *Pid1*(t) | SSR | RM262 | 14.5 | CATTCCGTCTCGGCTCAACT | CAGAGCAAGGTGGCTTGC | Digu/LTH | Chen et al. 2004 |
| *Pig*(t) | SSR | RM166 | 2.4 -4.0 | GGTCCTGGGTCAATAATTGGGTTACC | TTGCTGCATGATCCTAAACCGG | Guangchangzhan/ LTH | Zhou et al. 2004 |
| | | RM208 | 1.2 -6.3 | TCTGCAAGCCTTGTCTGATG | TAAGTCGATCATTGTGTGGACC | Guangchangzhan/ LTH | Zhou et al. 2004 |
| *Piy1* | SSR | RM3248 | 1.3 | AGAAGGTTGCTTTCTTGGCC | CTTGCAAGGTCTGTTGCATC | Yanxian No. 1/LTH | Lei et al. 2005 |
| | | RM20 | 1.7 | ATCTTGTCCCTGCAGGTCAT | GAAACAGAGGCACATTTCATTG | Yanxian No. 1/LTH | Lei et al. 2005 |
| *Piy2* | SSR | RM3248 | 1.3 | AGAAGGTTGCTTTCTTGGCC | CTTGCAAGGTCTGTTGCATC | Yanxian No. 1/LTH | Lei et al. 2005 |
| | | RM20 | 1.7 | ATCTTGTCCCTGCAGGTCAT | GAAACAGAGGCACATTTCATTG | Yanxian No. 1/LTH | Lei et al. 2005 |
| *Pib* | SNP | b213** | - | GCATTAGATAGTGATGAAAGCCGA (Koshihikari-specific primer) | TGTTCATCCAGGCAATTGGC | BL1/Koshihikari | Hayashi et al. 2006 |
| | | | | GCATTAGATAGTGATGAAAGCCGG (BL1-specific primer) | TGTTCATCCAGGCAATTGGC | BL1/Koshihikari | |
| | SNP | b28 | 1.2 | GACTCGGTCGACCAATTCGCA (Koshihikari-specific primer) | ATCAGGCCAGGCCAGATTTG | BL1/Koshihikari | Hayashi et al. 2006 |
| | | | | GACTCGGTCGACCAATTCGCC (BL1-specific primer) | ATCAGGCCAGGCCAGATTTG | BL1/Koshihikari | |
| | SNP | b2** | 0 | GCATTAGATAGTGATGAAAGCATA (Koshihikari-specific primer) | AATGGACTGGTGTTCATCCAGGC | BL1/Koshihikari | Hayashi et al. 2006 |
| | | | | GCATTAGATAGTGATGAAAGCCGG (BL1-specific primer) | AATGGACTGGTGTTCATCCAGGC | BL1/Koshihikari | |

| Target gene | Type of marker | Marker name | Distance | Primer | | Population used (Resistant /Susceptible varieties) | Restriction enzyme | Reference |
|---|---|---|---|---|---|---|---|---|
| | | | | Forward | Reverse | | | |
| | SNP | b3989 | 1.2 | TGTAAGCGCGGGATATCCGA (Koshihikari-specific primer) | TTGTGAGCTTTGCCACTCCAC | BL1/Koshihikari | | Hayashi et al. 2006 |
| | | | | TGTAAGCGCGGGATATCCGG (BL1-specific primer) | TTGTGAGCTTTGCCACTCCAC | BL1/Koshihikari | | |
| | SSR | RM138 | 3.1 | AGCGCAACAACCAATCCATCCG | AAGAAGCTGCCTTTGACGCTATGG | Gilfmont/Te-Qing | | Fjellstrom et al. 2004 |
| | SSR | RM166 | 2.3 | GGTCCTGGGTCAATAATTGGGTTACC | TTGCTGCATGATCCTAAACCGG | Gilfmont/Te-Qing | | Fjellstrom et al. 2004 |
| | SSR | RM208 | 0 | TCTGCAAGCCTTGTCTGATG | TAAGTCGATCATTGTGTGGACC | Gilfmont/Te-Qing | | Fjellstrom et al. 2004 |
| | SSR | RM266 | 2.2 | TAGTTTAACCAAGACTCTC | GGTTGAACCCAAATCTGCA | Gilfmont/Te-Qing | | Fjellstrom et al. 2004 |
| | SNP | Pibdom*** | 0 | GAACAATGCCCAAACTTGAGA | GGGTCCACATGTCAGTGAGC | Gilfmont/Te-Qing | | Fjellstrom et al. 2004 |
| | SSR | RM138 | 1.5 | AGCGCAACAACCAATCCATCCG | AAGAAGCTGCCTTTGACGCTATGG | Maybelle/Te-Qing | | Fjellstrom et al. 2004 |
| | SSR | RM166 | 1.5 | GGTCCTGGGTCAATAATTGGGTTACC | TTGCTGCATGATCCTAAACCGG | Maybelle/Te-Qing | | Fjellstrom et al. 2004 |
| | SSR | RM208 | 0 | TCTGCAAGCCTTGTCTGATG | TAAGTCGATCATTGTGTGGACC | Maybelle/Te-Qing | | Fjellstrom et al. 2004 |
| | SSR | RM266 | 1.5 | TAGTTTAACCAAGACTCTC | GGTTGAACCCAAATCTGCA | Maybelle/Te-Qing | | Fjellstrom et al. 2004 |
| | - | NSb* | - | ATCAACTCTGCCACAAAATCC | CCCATATCACCACTTGTTCCCC | - | | Kwon et al. 2008 |
| Chromosome 4 | | | | | | | | |
| *pi21* | STS | P702D03_ #79 | 0 | AGAAGGTGGAGTACGACGTGAAGA | AGTTTAGTGAGCCTCTCCACGATTA | Nipponbare, Aichi Asahi/ Owarihatamochi | | Fukuoka et al. 2007 |
| *Pi39* | SSR | RM3843 | 0 | ACCCTACTCCCAACAGTCCC | GGGGTCGTACGCTCATGTC | Chubu 111 /Mineasahi | | Terashima et al. 2007 |
| | SSR | RM5473 | 0 | ACCACAAACGATCGCGTC | GAGATTAACGTCGTCCTCCG | Chubu 111 /Mineasahi | | Terashima et al. 2007 |
| Chromosome 5 | | | | | | | | |
| *Pi10* | InDel | OPF62700 | <7 | GGGAATTCGGTTTTACAACCACCG | GGGAATTCGGATCTCCGGGGGTAG | Tongil/CO39 | | Naqvi and Chattoo 1996 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | InDel | OPF62700 | <7 | TTTTACAACCACCGGTTTTATGAC | ATCTCCGGGGGTAGAGCACTGTTT | Tongil/CO39 | Naqvi and Chattoo 1996 |
| Chromosome 6 | | | | | | | |
| *Pi40*(t) | SSR | RM3330 | 2.4 | ATTATTCCCCTCTTCCGCTC | AAGAAACCCTCGGATTCCTG | IR65482-4-136-2-2 /Jinbubeyo | Jeung et al. 2007 |
| | SSR | RM527 | 1.1 | GGCTCGATCTAGAAAATCCG | TTGCACAGGTTGCGATAGAG | IR65482-4-136-2-2 /Jinbubeyo | Jeung et al. 2007 |
| | CAPS | S2539 | 3.8 | GGACTGAGATGGAATGTGCT | GTAGAGTGATGACAAAATGACAA | IR65482-4-136-2-2 /Jinbubeyo | Jeung et al. 2007 |
| *Piz* | InDel | z4794 | 0.32 | CACGCCACCCTTCAATGGAGACT | TGAATGTGAGAGGTTGACTGTGG | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| | SNP | z60510 | 0.11 | GGAGTTGGTGCGACGGTGCCGTTAT (Koshihikari-specific primer) | GCGCGGACCGGCCAGCTAGGTGAC | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| | | | | GGAGTTGGTGCGACGGTGCCGTTAC (Fukunishiki-specific primer) | GCGCGGACCGGCCAGCTAGGTGAC | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| | SNP | z5765 | 0.13 | AATGTGAAATTGGATGAGCCGGATA (Koshihikari-specific primer) | TTACCGATGTTCGTCGCTCTCAGG | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| | | | | AATGTGAAATTGGATGAGCCGGATG (Fukunishiki-specific primer) | TTACCGATGTTCGTCGCTCTCAGG | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| | SNP | z56592 | 0 | GGACCCGCGTTTTCCACGTGTAC (Koshihikari-specific primer) | AGGAATCTATTGCTAAGCATGAC | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| | | | | GGACCCGCGTTTTCCACGTGTAA (Fukunishiki-specific primer) | AGGAATCTATTGCTAAGCATGAC | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| | SNP | z565962 | - | AAGAAATAATATTTTTGAAACATGGCA AAT (Koshihikari-specific primer) | CCATGGTGGTAACTGGTATGTG | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| | | | | AAGAAATAATATTTTTGAAACATGGCA AAG (Fukunishiki-specific primer) | CCATGGTGGTAACTGGTATGTG | Fukunishiki /Koshihikari | Hayashi et al. 2006 |
| *Piz-t* | InDel | z4794 | 0.41 | CACGCCACCCTTCAATGGAGACT | TGAATGTGAGAGGTTGACTGTGG | Toride/Koshihikari | Hayashi et al. 2006 |
| | SNP | z60510 | 0.17 | GGAGTTGGTGCGACGGTGCCGTTAT (Koshihikari-specific primer) | GCGCGGACCGGCCAGCTAGGTGAC | Toride/Koshihikari | Hayashi et al. 2006 |
| | | | | GGAGTTGGTGCGACGGTGCCGTTAC (Toride 1-specific primer) | GCGCGGACCGGCCAGCTAGGTGAC | Toride/Koshihikari | Hayashi et al. 2006 |
| | SNP | z5765 | 0.17 | AATGTGAAATTGGATGAGCCGGATA (Koshihikari-specific primer) | TTACCGATGTTCGTCGCTCTCAGG | Toride/Koshihikari | Hayashi et al. 2006 |
| | | | | AATGTGAAATTGGATGAGCCGGATG (Toride 1-specific primer) | TTACCGATGTTCGTCGCTCTCAGG | Toride/Koshihikari | Hayashi et al. 2006 |
| | SNP | zt56591 | 0 | TTGCTGAGCCATTGTTAAACG (Koshihikari-specific primer) | ATCTCTTCATATATATGAAGGCCAC | Toride/Koshihikari | Hayashi et al. 2006 |
| | | | | TTGCTGAGCCATTGTTAAACA (Toride 1-specific primer) | ATCTCTTCATATATATGAAGGCCAC | Toride/Koshihikari | Hayashi et al. 2006 |

| Target gene | Type of marker | Marker name | Distance | Primer | | Population used (Resistant /Susceptible varieties) | Restriction enzyme | Reference |
|---|---|---|---|---|---|---|---|---|
| | | | | Forward | Reverse | | | |
| | SNP | zt5659 | 0 | GGACCCGCGTTTTCCACGTGTAC (Koshihikari-specific primer) | CATCCACGGGCTCTCGGACATC | Toride/Koshihikari | | Hayashi et al. 2006 |
| | | | | GGACCCGCGTTTTCCACGTGTAA (Toride 1-specific primer) | CATCCACGGGCTCTCGGACATC | Toride/Koshihikari | | Hayashi et al. 2006 |
| *Pigm*(t) | CAPS | C26348 | 2 | GGGGAGTATCTGCCTATCTG | CGTCACCACCTTATCGTTC | Gumei 4/Maratelli | *Xba*I | Deng et al. 2006 |
| | InDel | S47656 | 2.3 | CGGGCTTCTTCTCCTCCTT | TCCGCAATCTATCTGTTATCCTC | Gumei 4/Maratelli | | Deng et al. 2006 |
| Chromosome 8 | | | | | | | | |
| *Pi36* | SSR | RM5647 | 0.4 | ACTCCGACTGCAGTTTTTGC | AACTTGGTCGTGGACAGTGC | Q61 /Aichi Asahi, or LTH | | Liu et al. 2005 |
| | CAPS | CRG2 | 0.2 | GGCCTCCTTCCCTTCTCTCT | TGTGGAGGACAACGGGAGAG | Q61 /Aichi Asahi, or LTH | *Hinf*I | Liu et al. 2005 |
| | CAPS | CRG3 | 0 | GCTAGCAAGCATGGAGTTCGT | AGCGGGTAAGGTAGCATAGGT | Q61 /Aichi Asahi, or LTH | *Hinf*I | Liu et al. 2005 |
| | CAPS | CRG4 | 0 | TAGCTACAAGACCGTCGTGCC | GGCATAGAGCACCCTCAGTTC | Q61 /Aichi Asahi, or LTH | *Hae*III | Liu et al. 2005 |
| *Pi33* | SSR | RM72 | <11.5 | CCGGCGATAAAACAATGAG | GCATCGGTCCTAACTAAGGG | IR64/Azucena | | Berruyer et al. 2003 |
| | SSR | RM44 | <11.5 | ACGGGCAATCCGAACAACC | TCGGGAAAACCTACCCTACC | IR64/Azucena | | Berruyer et al. 2003 |
| Chromosome 9 | | | | | | | | |
| *Pi5*(t) | CAPS | 94A20r | 5.2 | AATTCCATTCGCCACCGAGTGCTC | TCTCAGTATAGAACACTAACTCTA | RIL125, RIL249, orRIL260/CO39 | *Ava*I | Jeon et al. 2003 |
| | CAPS | 76B14f | 0 | GTCTTGGACTTAAAGCACTACC | TGAGAAACTGGTTCAAATTGGC | RIL260/M202 | *Dra*I | Jeon et al. 2003 |
| | CAPS | 40N23r | 0 | TGTGAGGCAACAATGCCTATTGCG | CTATGAGTTCACTATGTGGAGGCT | RIL260/M202 | *Eco*RI | Jeon et al. 2003 |
| | SNP | JJ817* | - | GATATGGTTGAAAAGCTAATCTCA | ATCATTGTCCTTCATATTCAGAGT | RIL260/M202 | | Kwon et al. 2008 |
| Chromosome 11 | | | | | | | | |
| *Pia* | CAPS | yca72 | - | AGGAGAAGAAGCCACCAAGG | GAGCTGCCACATCTTCCTT | - | *Hin*fI | Kwon et al. 2008 |
| *PiCO39*(t) | CAPS | RGA8 | 0 | AATAATCACAACACGGAAGAATCATGTG | AGGTAGCTTGAGTGAGACAAAACTGAGG | CO39/51583 | *Sau3A*I | Chauhan et al. 2002 |
| | CAPS | RZ141 | 10.5 | GCCAAAATTGGATGTATAGCG | CGTGTTAAGACAATTCCACGTC | CO39/51583 | *Sau3A*I | Chauhan et al. 2002 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | CAPS | RGACO39 | 0 | CTTTCCATTGAGTCTTGAAGTCTTTGT | GGTAACTAACTTGAGGGAACTTCCAGA | CO39/51583 | *Hin*dIII | Chauhan et al. 2002 |
| *Pi38* | SSR | RM206 | 4 | CCCATGCGTTTAACTATTCT | CGTTCCATCGATCCGTATGG | Tadukan/CO39 | | Gowda et al. 2006 |
| | | RM21 | 16 | ACAGTATTCCGTAGGCACGG | GCTCCATGAGGGTGGTAGAG | Tadukan/CO39 | | Gowda et al. 2006 |
| *Pik* | InDel | k6816 | 1.4 | TCGCCGATGCGGTTGATTTACTC | CGTATTTTGTGTTGTTAGGAGATAAGG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | | k2167 | <1.4 | CGTGCTGTCGCCTGAATCTG | CACGAACAAGAGTGTGTCGG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k6438 | 1.4 | GCGACCCTGTCTTTGGACTGC (Kanto 51-specific primer) | GAATGATGAGGAGAGAAGGCTGTCG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | | | | GCGACCCTGTCTTTGGACTGG (OSIL235-specific primer) | GAATGATGAGGAGAGAAGGCTGTCG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k6415 | - | CTAATGGAATTAAACGGTTGAGCTG (Kanto 51-specific primer) | ATCCCGATGTCATCGATCAC | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | | | | CTAATGGAATTAAACGGTTGAGCTA (Koshihikari-specific primer) | ATCCCGATGTCATCGATCAC | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k8823 | 0 | GTTGTGGGTTCCTCTATACAACT (Kanto 51-specific primer) | GCATGACAGATGGAAGTGTAGATGG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | | | | GTTGTGGGTTCCTCTATACAACA (OSIL235-specific primer) | GCATGACAGATGGAAGTGTAGATGG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k8824 | 0 | CCACGCTCCTAGCTACCCCG (Kanto 51-specific primer) | ACAAGGGAACCCAGAAACTC, ATCGCAGCGACTGTATGTGC | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | | | | GTTGTGGGTTCCTCTATACAACA (Koshihikari-specific primer) | ACAAGGGAACCCAGAAACTC, ATCGCAGCGACTGTATGTGC | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k3951 | 0 | AAGTAACAACATGGTCAATAGTAC (Kanto 51-specific primer) | CCAGAATTTACAGGCTCTGG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | | | | AAGTAACAACATGGTCAATAGTAA (Koshihikari-specific primer) | CCAGAATTTACAGGCTCTGG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k39512 | 0 | GCCACATCAATGGCTACAACGTC (OSIL235-specific primer) | CCAGAATTTACAGGCTCTGG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |

| Target gene | Type of marker | Marker name | Distance | Primer | | Population used (Resistant /Susceptible varieties) | Restriction enzyme | Reference |
|---|---|---|---|---|---|---|---|---|
| | | | | Forward | Reverse | | | |
| | | | | GCCACATCAATGGCTACAACGTT (Koshihikari-specific primer) | CCAGAATTTACAGGCTCTGG | Kanto51 /OSIL 235, or Koshihikari | | Hayashi et al. 2006 |
| *Pik-m* | InDel | k6816 | 1.3 | TCGCCGATGCGGTTGATTTACTC | CGTATTTTGTGTTGTTAGGAGATAAGG | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | | k2167 | 0 | CGTGCTGTCGCCTGAATCTG | CACGAACAAGAGTGTGTCGG | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k641 | 1.3 | GGCTGGAACACCAACATCCATGG (Tsuyuake-specific primer) | GCGCTGGACTTGGAACTAGTGC | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | | | | GCTGGGACACCAACATCCATGC (99SL-44-specific primer) | GCGCTGGACTTGGAACTAGTGC | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k6441 | 0 | TGTAAAATACTTTCTATGCGCAGGT (Tsuyuake-specific primer) | GTTTATGGAGAGAGTAGTCGCTG | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | | | | TGTAAAATACTTTCTATGCGCAGGC (99SL-44-specific primer) | GTTTATGGAGAGAGTAGTCGCTG | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k4731 | <3.5 | GCAGATGCATCAGCCAGTGAGTG (Tsuyuake-specific primer) | GTGCAGGACCGGCACGCAG | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | | | | GCAGATGCATCAGCCAGTGAGTT (Koshihikari-specific primer) | GTGCAGGACCGGCACGCAG | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | SNP | k7237 | 3.5 | AGTGTGCCTCGTTGCCCTGTTCTG (Tsuyuake-specific primer) | TATAGCTTGCATTAGATCCTCTCTGTTGA | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| | | | | AGTGTGCCTCGTTGCCCTGTTCTA (99SL-44-specific primer) | TATAGCTTGCATTAGATCCTCTCTGTTGA | Tsuyuake /99SL-44, or Koshihikari | | Hayashi et al. 2006 |
| *Pik-p* | SNP | k641 | 1.9 | GGCTGGAACACCAACATCCATGG (K60-specific primer) | GCGCTGGACTTGGAACTAGTGC | K60/Koshihikari | | Hayashi et al. 2006 |
| | | | | GCTGGGACACCAACATCCATGC (Koshihikari-specific primer) | GCGCTGGACTTGGAACTAGTGC | K60/Koshihikari | | Hayashi et al. 2006 |
| | SNP | k39575 | | GGTGTTTGGGAACCTGAACCCTG (60-specific primer) | TTTCTGTTCGTCGGATGCTC | K60/Koshihikari | | Hayashi et al. 2006 |
| | | | | GGTGTTTGGGAACCTGAACCCTA (Koshihikari-specific primer) | TTTCTGTTCGTCGGATGCTC | K60/Koshihikari | | Hayashi et al. 2006 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | SNP | k403 | 0.97 | CATCTTGACGACAACGACACCATTAGTTA (k60-specific primer) | CCAAAATGAACAAACCGATTCGAC | K60/Koshihikari | Hayashi et al. 2006 |
| | | | | CTTGACGACGACGACACCATTAGTTG (Koshihikari-specific primer) | CCAAAATGAACAAACCGATTCGAC | K60/Koshihikari | Hayashi et al. 2006 |
| | SNP | k3957 | 0 | ATAGTTGAATGAATGGAATGGAAC (K60-specific primer) | CTGCGCCAAGCAATAAAGTC | K60/Koshihikari | Hayashi et al. 2006 |
| | | | | ATAGTTGAATGAATGGAATGGAAT (Koshihikari-specific primer) | CTGCGCCAAGCAATAAAGTC | K60/Koshihikari | Hayashi et al. 2006 |
| *Pik-h* | SSR | RM206 | 0.7 | CCCATGCGTTTAACTATTCT | CGTTCCATCGATCCGTATGG | Tetep/HP2216 | Sharma et al. 2002 |
| | SSR | TRS26 | 0.7 | GGAGAGCCAATCTGATAAGCA | CAACAAGAGAGGCAAATTCTCA | Tetep/HP2216 | Sharma et al. 2002 |
| | SSR | TRS33 | 0.6 | AAGAAGAAGCGTACGCATGAAT | GTCCTGGAGGGGAGGAGA | Tetep/HP2216 | Sharma et al. 2002 |
| | SSR | RM144 | 4 | TGCCCTGGCGCAAATTTGATCC | GCTAGAGGAGATCAGATGGTAGTGCATG | Maybelle/Kaybonnet | Fjellstrom et al. 2004 |
| | SSR | RM224 | 0 | ATCGATCGATCTTCACGAGG | TGCTATAAAAGGCATTCGGG | Maybelle/Kaybonnet | Fjellstrom et al. 2004 |
| | SSR | RM1233 | 3.3 | TTCGTTTTCCTTGGTTAGTG | ATTGGCTCCTGAAGAAGG | Maybelle/Kaybonnet | Fjellstrom et al. 2004 |
| | SSR | RM144 | 0.9 | TGCCCTGGCGCAAATTTGATCC | GCTAGAGGAGATCAGATGGTAGTGCATG | Maybelle/Lemont | Fjellstrom et al. 2004 |
| | SSR | RM224 | 0 | ATCGATCGATCTTCACGAGG | TGCTATAAAAGGCATTCGGG | Maybelle/Lemont | Fjellstrom et al. 2004 |
| | SSR | RM1233 | 0.8 | TTCGTTTTCCTTGGTTAGTG | ATTGGCTCCTGAAGAAGG | Maybelle/Lemont | Fjellstrom et al. 2004 |
| | SSR | RM144 | 1.7 | TGCCCTGGCGCAAATTTGATCC | GCTAGAGGAGATCAGATGGTAGTGCATG | (Vista/Lebonnet // Rosemont)/Katy | Fjellstrom et al. 2004 |
| | SSR | RM224 | 1.1 | ATCGATCGATCTTCACGAGG | TGCTATAAAAGGCATTCGGG | (Vista/Lebonnet // Rosemont)/Katy | Fjellstrom et al. 2004 |
| *Pik-s* | SSR | RM144 | 2.7 | TGCCCTGGCGCAAATTTGATCC | GCTAGAGGAGATCAGATGGTAGTGCATG | Maybelle/Bengal | Fjellstrom et al. 2004 |
| | SSR | RM224 | 0 | ATCGATCGATCTTCACGAGG | TGCTATAAAAGGCATTCGGG | Maybelle/Bengal | Fjellstrom et al. 2004 |
| | SSR | RM1233 | 0 | TTCGTTTTCCTTGGTTAGTG | ATTGGCTCCTGAAGAAGG | Maybelle/Bengal | Fjellstrom et al. 2004 |
| | SSR | RM144 | 5.4 | TGCCCTGGCGCAAATTTGATCC | GCTAGAGGAGATCAGATGGTAGTGCATG | Maybelle/M-201 | Fjellstrom et al. 2004 |
| | SSR | RM224 | 0 | ATCGATCGATCTTCACGAGG | TGCTATAAAAGGCATTCGGG | Maybelle/M-201 | Fjellstrom et al. 2004 |
| | SSR | RM1233 | 2.7 | TTCGTTTTCCTTGGTTAGTG | ATTGGCTCCTGAAGAAGG | Maybelle/M-201 | Fjellstrom et al. 2004 |

| Target gene | Type of marker | Marker name | Distance | Primer | | Population used (Resistant /Susceptible varieties) | Restriction enzyme | Reference |
|---|---|---|---|---|---|---|---|---|
| | | | | Forward | Reverse | | | |
| Chromosome 12 | | | | | | | | |
| *Pita* | SNP | ta642 | 1.2 | GGTCAAACATGAAGTGAGATGGG (Yashiromochi-specific primer) | CTGCATCACACTTCTGATGAAC | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | | | | GGTCAAACATGAAGTGAGATGGA (Nipponbare-specific primer) | CTGCATCACACTTCTGATGAAC | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | SNP | ta801 | 0 | CAAGCCAAATCTGAATCTTACCAA (Yashiromochi-specific primer) | TATGGAAATGTTGCCCCAATCTG | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | | | | CAAGCCAAATCTGAATCTTACCAT (Nipponbare-specific primer) | TATGGAAATGTTGCCCCAATCTG | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | SNP | ta3 | 0 | GGAGTACGTGTCTTTTTCCATGTATA (Yashiromochi-specific primer) | CTTGGTCCTACCTGTCATACACAC | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | | | | GGAGTACGTGTCTTTTTCCATGCATT (Nipponbare-specific primer) | CTTGGTCCTACCTGTCATACACAC | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | SNP | ta577 | 0 | ATGAACACCACAGCCTAAACG (Yashiromochi-specific primer) | CAGACCCGAAACAACACTAGG | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | | | | ATGAACACCACAGCCTAAACC (Nipponbare-specific primer) | CAGACCCGAAACAACACTAGG | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | SNP | ta5 | | CAGCGAACTCCTTCGCATACGCG (Yashiromochi-specific primer) | CGAAAGGTGTATGCACTATAGTATCC | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | | | | CAGCGAACTCCTTCGCATACGCA (Nipponbare-specific primer) | CGAAAGGTGTATGCACTATAGTATCC | Yashiromochi /Nipponbare | | Hayashi et al. 2006 |
| | SNP | Pi-ta 440* | - | CAACAATTTAATCATACACG | ATGACACCCTGCGATGCAA | Katy, Drew, or Kaybonnet / Nipponbare or M-202 | | Jia et al. 2002 |
| | SNP | Pi-ta 1042* | - | AGCAGGTTATAAGCTAGGCC | CTACCAACAAGTTCATCAAA | Katy, Drew, or Kaybonnet / Nipponbare or M-202 | | Jia et al. 2002 |
| | SNP | Pi-ta 403* | - | CAATGCCGAGTGTGCAAAGG | TCAGGTTGAAGATGCATAGC | Katy, Drew, or Kaybonnet / Nipponbare or M-202 | | Jia et al. 2002 |
| *Pita-2* | SNP | ta642 | 0 | GGTCAAACATGAAGTGAGATGGG (Pi No. 4 -specific primer) | CTGCATCACACTTCTGATGAAC | Pi No. 4/Koshihikari | | Hayashi et al. 2006 |
| | | | | GGTCAAACATGAAGTGAGATGGA (Koshihikari-specific primer) | CTGCATCACACTTCTGATGAAC | Pi No. 4/Koshihikari | | |
| | SNP | ta801 | 0 | CAAGCCAAATCTGAATCTTACCAA (Pi No. 4 -specific primer) | TATGGAAATGTTGCCCCAATCTG | Pi No. 4/Koshihikari | | Hayashi et al. 2006 |
| | | | | CAAGCCAAATCTGAATCTTACCAT (Koshihikari-specific primer) | TATGGAAATGTTGCCCCAATCTG | Pi No. 4/Koshihikari | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | SNP | ta3 | 0 | GGAGTACGTGTCTTTTTCCATGTATA (Pi No. 4 -specific primer) | CTTGGTCCTACCTGTCATACACAC | Pi No. 4/Koshihikari | | Hayashi et al. 2006 |
| | | | | GGAGTACGTGTCTTTTTCCATGCATT (Koshihikari-specific primer) | CTTGGTCCTACCTGTCATACACAC | Pi No. 4/Koshihikari | | |
| | SNP | ta577 | 4 | ATGAACACCACAGCCTAAACG (Pi No. 4 -specific primer) | CAGACCCGAAACAACACTAGG | Pi No. 4/Koshihikari | | Hayashi et al. 2006 |
| | | | | ATGAACACCACAGCCTAAACC (Koshihikari-specific primer) | CAGACCCGAAACAACACTAGG | Pi No. 4/Koshihikari | | |
| | SNP | ta5 | | CAGCGAACTCCTTCGCATACGCG (Pi No. 4 -specific primer) | CGAAAGGTGTATGCACTATAGTATCC | Pi No. 4/Koshihikari | | Hayashi et al. 2006 |
| | | | | CAGCGAACTCCTTCGCATACGCA (Koshihikari-specific primer) | CGAAAGGTGTATGCACTATAGTATCC | Pi No. 4/Koshihikari | | |
| | SSR | OSM89 | 4.6 | TTGGTCAAAGTTAGCATGGGAGGG | TTTGAACCGGGTGGCCCACATG | (Vista/Lebonnet // Rosemont)/Katy | | Fjellstrom et al. 2004 |
| | SSR | RM155 | 3.5 | GAGATGGCCCCCTCCGTGATGG | TGCCCTCAATCGGCCACACCTC | (Vista/Lebonnet // Rosemont)/Katy | | Fjellstrom et al. 2004 |
| | SSR | OSM89 | 2.4 | TTGGTCAAAGTTAGCATGGGAGGG | TTTGAACCGGGTGGCCCACATG | Maybelle/Kaybonnet | | Fjellstrom et al. 2004 |
| | SSR | RM155 | 0.8 | GAGATGGCCCCCTCCGTGATGG | TGCCCTCAATCGGCCACACCTC | Maybelle/Kaybonnet | | Fjellstrom et al. 2004 |
| | SSR | RM7102 | 1.1 | TTGAGAGCGTTTTTAGGATG | TCGGTTTACTTGGTTACTCG | Maybelle/Kaybonnet | | Fjellstrom et al. 2004 |
| | SSR | OSM89 | 2.4 | TTGGTCAAAGTTAGCATGGGAGGG | TTTGAACCGGGTGGCCCACATG | Kaybonnet/M-204 | | Fjellstrom et al. 2004 |
| | SSR | RM7102 | 1.3 | GAGATGGCCCCCTCCGTGATGG | TGCCCTCAATCGGCCACACCTC | Kaybonnet/M-204 | | Fjellstrom et al. 2004 |
| *Pi20*(t) | SSR | RM1337 | 0 | GCTGAGGAGTATCCTTTCTC | ACCATAGGAAGATCATCACA | IR24/Asominori | | Li et al. 2008 |
| | SSR | RM5364 | 0 | GTATTACGCTCGATAGCGGC | GTATCCTTTCTCGCAATCGC | IR24/Asominori | | Li et al. 2008 |
| | SSR | RM7102 | 0 | CGGCTTGAGAGCGTTTTTAG | TACTTGGTTACTCGGGTCGG | IR24/Asominori | | Li et al. 2008 |
| *Pi39*(t) | CAPS | 39M6 | 0 | GGTTCGGGTCTCTCAAGTA | CAACGGAGGAAGTAAGGAGA | IR24/Asominori | *Hinf*I | Liu et al. 2007 |
| | CAPS | 39M7 | 0.09 | GGTAGAGGCAGCAGGGTAAT | GTCGAGACACTGTCGGATTC | IR24/Asominori | *BstY*I | Liu et al. 2007 |

*: The markers are designed to detect the polymorphisms within the resistance genes.
**: The markers are designed to detect the polymorphisms in 5' UTR of the resistance genes.
***: The markers are designed to detect the polymorphisms in 3' UTR of the resistance genes.

marker that can distinguish the polymorphism underlying the phenotypic effect of the gene (i.e., gene specific marker or functional marker), such a marker has strong association with the phenotype (McCouch et al. 2007). Although there have been many reports of conventional markers for rice blast resistance genes (Table 2), almost all reported markers are linked to the resistance genes (i.e., linkage marker) and there are few gene specific markers reported[18,39,52,59]. Since such linkage markers have weaker association with phenotype than gene specific markers, there are a few limitations on applying them to MAS as discussed below. Thus breeders should use them as a support tool for conventional phenotypic selection.

**1. Recombination between markers and genes**

Association between the linkage markers and the genes is mainly dependent on the genetic distance between them. In general, the association becomes stronger when more tightly linked markers are used. However, even though the marker is tightly linked to the gene, recombination between them will possibly occur during the breeding procedure using MAS (as discussed by Fjellstorm et al.[18] about the relationship between the marker, Pibdom, and the gene, *Pib*). If recombination occurs, there will be no association between the marker and the phenotype and, thus, it will be impossible to select the phenotype by that marker. As a result, the plant that does not harbor the target gene may be selected as a false positive. To reduce the possibility of a false positive selection, it is necessary to confirm the introgression of the genetic region where the target gene is by using the gene specific marker or two linkage markers which are on both sides of the flanking region of the gene.

**2. Linkage drag**

Even if one can confirm the introgression of the target genetic region by two linkage markers, another problem of the linkage drag still remains[15,41]. When the linkage marker is used to introduce the resistance gene from the donor strain, not only the resistance gene, but also the chromosomal fragment between the resistance gene and linkage markers is inevitably introduced. Thus there is a probability that the undesirable genes on the chromosome of the donor strain are introduced together with the resistance genes.

**3. Limitation for the universality of the markers**

One of the big issues is knowing whether one marker set designed for a specific cross or population can be applied to other crosses or populations. Because the polymorphisms detected in linkage marker systems do not affect the phenotype of the target gene, such polymorphisms do not always exist between resistance and susceptible strains. Therefore, one marker set which is useful in a specific cross combination does not always work well in other cross combinations. Although several reports showed that linkage markers can be successfully used to screen for varieties with resistance to rice blast[18,101,107], almost all markers have never been evaluated as to whether they can be applied to other cross combinations. Information about the markers and their applicability to the combinations of the strains will be valuable for rice breeding using MAS.

## Conclusion

Recent progress in rice genomics has facilitated finding new resistance genes in blast disease. The volume of publications identifying new resistance genes will increase in this era of genomics. To avoid confusion, it will be necessary to characterize the resistance genes and organize information about them in an easily understandable format.

For gene characterization, a differential system for rice blast is essential. In the IRRI-Japan Collaborative Research Project, we released the monogenic lines and have been developing NILs together with markers for MAS for blast resistance genes. These lines will be useful not only as gene sources for breeding blast resistance but also as sets of international standard differential varieties used for characterizing the resistance genes. As the number of resistance genes increases, the number of their selection markers applicable to MAS will increase in the future. To enhance the utilization of the selection markers in MAS, it is also necessary to integrate marker information into an easily utilizable database. In this report, we assembled the reported markers for the rice blast resistance genes. This information will encourage the application of MAS in rice breeding programs.

## Acknowledgments

This study was carried out under the IRRI-JAPAN collaborative project, which was supported by the Ministry of Agriculture, Forestry and Fisheries of Japan, and a JIRCAS research project “Blast Research Network for Stable Rice Production”.

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