Blast resistance genes and their selection markers 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.

Keywords: resistance gene, DNA marker, marker assisted selection (MAS), blast (*Pyricularia oryzae* Cavara), rice (*Oryza sativa* L.)

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 (Ou 1985; Latterell and Rossi 1986; Bonman and Mackill 1988). 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 resistant genes

Since the first publication of the inheritance of host resistance to rice blast (Sasaki 1923), 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 (Bellini et al. 2008). To

encourage further utilization of these 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.

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): Inukai et al. 1993, and *Pi1* and *Pi7*(t); Jeon et al. 2003).

In addition, several genes are suggested to be allelic (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).

Characterization of the cloned resistance genes

As of now, eight resistance genes, *Pib* (Wang et al. 1999), *Pita* (Bryan et al. 2000), *Pik-h* (Sharma et al. 2005), *Pi9* (Qu et al. 2006), *Pi2* (Zhou et al. 2006), *Piz-t* (Zhou et al. 2006), *Pid2* (Chen et al. 2006), *Pi36* (Liu et al. 2007), and *Pi37* (Lin et al. 2007) have been isolated and cloned using map-based cloning strategies.

Seven 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 (Bent 1996; Hammond-Kosack and Jones 1997; Hulbert et al. 2001). 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. (2000) 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 binds directly with the effecter gene product of the pathogen to initiate the resistance gene mediated defense response.

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) (Chen et al. 2006). Because of its novel extracellular domain, *Pid2* represents a new class of plant resistance genes.

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 (Figure 1). The map position was based on the high-density genetic map constructed by the Rice Genome Program (Chen et al. 2002; Harushima et al. 1998). 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 chromosome 6, 11, and 12 (Bryan et al. 2000; Wu et al. 2005). 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 (Qu et al. 2006; Zhou et al. 2006). Zhou et al. (2006) 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. (2006) 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 2100 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. (2005) 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 (1969) is under debate (Xu et al. 2008).

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. (2004), all three clusters of the rice resistance genes are closely associated with the clusters of NBS-LRR domain containing genes. Ballini et al. (2008) 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.

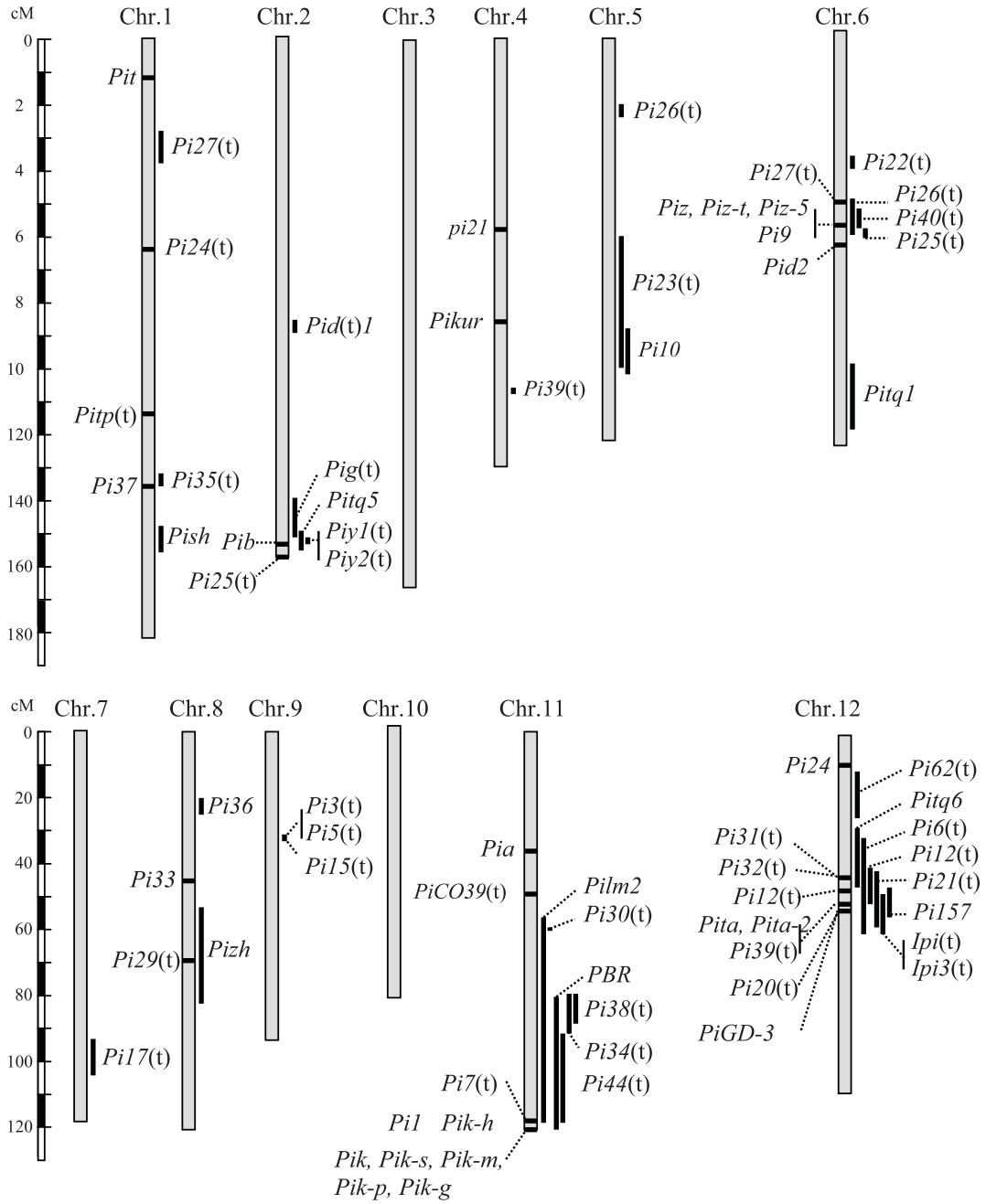

Fig. 1. Putative location of the blast resistance genes reported by 2008

The genetic location of the each genes are based on the public database (Oryzabase and Gramene) and each references (see Table 1).

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 doner)	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 21.6cM	-	-	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 6.1cM	Nipponbare, Pi No. 4, Fukunishiki, Norin 22, Kusabue, BL1, Akihikari	-	Imbe et al. 1985, Fukuta et al. 2004
Chromosome 2								
Pid(t)*1*	87.5-89.9	Digu	Indica	-	Mapped within 11.8cM	-	-	Chen et al. 2004
Pig(t)	142.0-154.1	Guangchangzhan	Indica	-	Mapped within 10.3cM	-	-	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	synonimous 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	-	resessive	Fukuoka and Okuno 2001

Pikur1	86	Kuroka	Japonica	-	Linkage analysis using phenotypic marker	-	-	Goto 1988
Pi39(t)	107.4-108.2	Chubu 111 (Haonaihuan)	Japonica	-	Mapped within 0.3cM	-	-	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 6.7cM	-	-	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 1.8cM	-	-	Jeung et al. 2007
Piz-5	58.7	Tadukan	Indica	C	Cloned	K60, C101A51 (5173)	synonimous to *Pi2*(t), allelic to *Piz-t*, *Piz*, tightly linked with *Pi9*(t)	Zhou et al. 2006
Piz	58.7	Zenith	-	C	Mapped within 0.43cM	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 1.6cM	-	-	Berruyer et al. 2003
Pizh	53.2-84.8	Zhai-Ye-Quing	Indica	C	QTL mapping	-	synonimous 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 170kb	-	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 0.7cM	-	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
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 1.2cM	-	-	Chauhan et al. 2002
Pilm2	56.2-117.9	Lemont	Japonica	C	QTL mapping	-	synonimous 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 20cM	-	-	Gowda et al. 2006
PBR	80.5-120.3	St No.1	Indica	-	Mapped within 22.9cM	-	-	Fujii et al. 1995
Pb1	85.7-91.4	Modan	Indica	P	Mapped within 12.4cM	-	synonimous 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 1.2cM	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 11.4cM	-	identical to *Pi7*(t)	Hittalmani et al. 2000
Pik-m	115.1-117.0	Tsuyuake	Japonica	C	Mapped within 0.3cM	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 1.4cM	Kanto 51, Sasanishiki BL1	-	Hayasaka et al. 1996, Hayashi et al. 2006
Pik-p	119.9-120.3	HR22	-	C	Mapped within 2.8cM	K60	allelic to *Pik*	Hayashi et al. 2006
Pik-s	115.1-117.3	Shin 2	Japonica	C	Mapped within 2.7cM	Fujisaka 5, Caloro, B40, Zhaiyeqing 8, Bengal, M-201	allelic to *Pik*	Fjellstrom et al. 2004
Pik-g	-	GA20	-	C	Linkage analisis to other resistance genes	-	allelic to *Pik*	Pan et al. 1996
Pise1	-	Sensho	Japonica	-	Linkage analysis using phenotypic marker	-	synonimous 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 1.9cM	-	-	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
Pi157	49.5-62.2	Moroberecan	Japonica	-	Mapped within 9.5cM	-	-	Naqvi and Chattoo 1996
Pita	50.4	Taducan	Indica	C	Cloned	K1, C101PKT, Zhaiyeqing 8, Yashiromochi, C105TTP2L9	synonimous to *Pi4*, allelic to *Pita-2*	Bryan et al. 2000
Pita-2	50.4	Shimokita	Japonica	C	Mapped within 4.0cM	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 37kb	-	-	Liu et al. 2007
Pi20(t)	51.5-51.8	IR24	Indica	C	Mapped within 0.6cM	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 each references (C: compete resistance, P: partial resistance).

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 (Parlevliet 1979). Although the partial resistance has been thought to be under polygenic control and show 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; Yunoki et al. 1970; Fukuoka and Okuno 1997; Fujii et al. 1995, 2000; Zenbayashi-Sawata et al. 2002, 2005). Moreover, Zenbayashi-Sawata et al. (2005) 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 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. (2005, 2007) 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. (2008) 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.

Donor strains

Apart from two resistance genes (*Pi9* and *Pi40*(t)) that have been found in wild relatives, most rice blast resistance genes have been found in rice blast resistant cultivars. Tsunematsu et al. (2000) revealed that an Indica-type cultivar, 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. (2002) showed that CO 39 also carried another blast resistant 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. (2008a) surveyed genetic diversity of blast resistance in 922 rice varieties by using the standard differential blast isolates selected by Telebanco-Yanoria et al. (2008b). 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 (Glaszman 1987) 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 resistant genes

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. (2008) pointed out. There are at least nine 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 (Kinoshita et al. 1994).
3. Different studies use different writing systems for the same resistance gene (e.g., *Pik-h*, *Pikh*, *Pi-kh*, Pik^h and $Pi\text{-}k^h$).

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

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): Inukai et al. 1993, and *Pi1* and *Pi7*(t),: Jeon et al. 2003). However, it is difficult to confirm the identification of the two genes, because if both the two genes are dominant and tightly linked to each other, it is impossible to confirm that these genes are identical to each other by the 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 neces-

sary 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. (1986) 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 variety (Tsunematsu et al. 2000, Fukuta et al. 2004b, Kobayashi et al. 2007). Such a differential system is very useful to estimate the identity of the genes by conventional segregation analysis.

Using MAS for blast resistance genes

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 the efficiency and effectiveness as compared to conventional phenotypic selection (reviewed by Collard et al. 2008; Xu and Crouch 2008). 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 10cM) and an adequate number of progeny are used for background selection (Tanksley et al. 1989; Xu and Crouch 2008). 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.

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 (Mohan et al. 1997). 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. (2006) developed a PCR-based marker system for nine 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 (Nasu et al. 2002; Yu et al. 2002, 2005; Feltus et al. 2004), such types of DNA markers can help generate a sufficient number of markers within target genomic regions.

Conventional markers developed for detecting rice blast resistance genes

To date, 8 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 (Jia et al. 2002; Fjellstrom et al. 2004; Hayashi et al. 2006; Kwon et al. 2008). 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 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 (Jia et al. 2002; Fjellstrom et al. 2004; Hayashi et al. 2006; Kwon et al. 2008). Since such linkage markers have weaker association with phenotype than gene specific markers, there are a few limitations on applying them to MAS as discuss below. Thus breeders should use them as a support tool for conventional phenotypic selection.

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. (2004) 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 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.

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 (Collard et al. 2008; Hospital 2001). 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.

Limitation for the universality of the markers

One of the big issues is knowing whether one marker set designed for 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 cultivars with resistance to rice blast (Fjellstrom et al. 2004; Yi et al. 2004; Wang et al. 2007), 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 the rice breeding using MAS.

Conclusion

Recent progress in rice genomics has facilitated finding new resistance genes in blast disease. The volume of publications identifying the 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.

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	
	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	-	AAGAAATAATATTTTTGAAACATGGCAAAT (Koshihikari-specific primer)	CCATGGTGGTAACTGGTATGTG	Fukunishiki/ Koshihikari	Hayashi et al. 2006
				AAGAAATAATATTTTTGAAACATGGCAAAG (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
	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 *XbaI*	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 *HinfI*	Liu et al. 2005
	CAPS	CRG3	0	GCTAGCAAGCATGGAGTTCGT	AGCGGGTAAGGTAGCATAGGT	Q61/Aichi Asahi, or LTH *HinfI*	Liu et al. 2005
	CAPS	CRG4	0	TAGCTACAAGACCGTCGTGCC	GGCATAGAGCACCCTCAGTTC	Q61/Aichi Asahi, or LTH *HaeIII*	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	*AvaI*	Jeon et al. 2003
	CAPS	76B14f	0	GTCTTGGACTTAAAGCACTACC	TGAGAAACTGGTTCAAATTGGC	RIL260/M202	*DraI*	Jeon et al. 2003
	CAPS	40N23r	0	TGTGAGGCAACAATGCCTATTGCG	CTATGAGTTCACTATGTGGAGGCT	RIL260/M202	*EcoRI*	Jeon et al. 2003
	SNP	JJ817*	-	GATATGGTTGAAAAGCTAATCTCA	ATCATTGTCCTTCATATTCAGAGT	RIL260/M202		Kwon et al. 2008
Chromosome 11								
Pia	CAPS	yca72	-	AGGAGAAGAAGCCACCAAGG	GAGCTGCCACATCTTCCTT	-	*HinfI*	Kwon et al. 2008
PiCO39(t)	CAPS	RGA8	0	AATAATCACAACACGGAAGAATCATGTG	AGGTAGCTTGAGTGAGACAAAACTGAGG	CO39/51583	*Sau3AI*	Chauhan et al. 2002
	CAPS	RZ141	10.5	GCCAAAATTGGATGTATAGCG	CGTGTTAAGACAATTCCACGTC	CO39/51583	*Sau3AI*	Chauhan et al. 2002
	CAPS	RGACO39	0	CTTTCCATTGAGTCTTGAAGTCTTTGT	GGTAACTAACTTGAGGGAACTTCCAGA	CO39/51583	*HindIII*	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
				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
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	*HinfI*	Liu et al. 2007
	CAPS	39M7	0.09	GGTAGAGGCAGCAGGGTAAT	GTCGAGACACTGTCGGATTC	IR24/Asominori	*BstYI*	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.

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