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Identification and molecular mapping of the rice bacterial blight resistance gene allelic to *Xa7* from an elite restorer line Zhenhui 084

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Abstract Rice bacterial blight (BB), caused by *Xanthomonas oryzae* pv. *Oryzae (Xoo)*, is a serious disease in rice production worldwide. Rice cv. Zhenhui 084, a newly developed strong indica restorer line, exhibits high resistance to most of the Philippine races of BB and has been widely used in rice hybrids in China; however, the resistance gene has not yet been cloned. Here, we show that the resistance of Zhenhui 084 to *Xoo* strains is similar to that of IRBB7 containing *Xa7*, a durable and broad resistance dominant gene for BB. To map the resistance gene in Zhenhui 084, a F_2 population with 331 highly susceptible individuals derived from a cross between Chenghui 448 and Zhenhui 084 was built. We finely mapped the target R gene to a region between two proximal markers RM20576 and MY4 in rice chromosome 6. A marker-based physical map of chromosome six was used to construct the contig covering the genomic region between two markers RM20576 and MY4. The target gene was assumed to be in an interval of approximate 200 kb, in which 16 candidate genes were predicted. Our findings will greatly facilitate the isolation and characterisation of the target R gene allelic to *Xa7*. Additionally, two PCR-based markers, tightly linked to the target R gene locus, will be a useful tool for the marker-assisted selection of the target R gene allelic to *Xa7* in breeding programmes.

Keywords Bacterial blight · Identification · Molecular mapping · Rice · *Xa7*

Introduction

Bacterial blight (BB) disease caused by *Xanthomonas oryzae* pv. *Oryzae (Xoo)* is a limiting factor to rice yields in all major rice-growing regions of the world. Due to the fact that the bacterial pathogen is difficult to manage, the development of host plant resistance is considered as one of the most effective and economical means to control BB. Currently, > 30 BB resistance genes (R-genes) conferring host resistance against various strains of *Xoo* have been identified and designated with a series from *Xa1* to *xa31* (t) (Lin et al. 1996; Nagato and Yoshimura 1998; Zhang et al. 1998; Khush and Angeles 1999; Chen et al. 2002; Lee

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et al. 2003; Tan et al. 2004; Xiang et al. 2006; Singh et al. 2007; Cheema et al. 2008). Genetical and physical mapping of these R genes not only allows marker-assisted breeding in rice, but also greatly facilitates isolation and characterisation of these genes at the molecular level. So far, seven BB resistance genes including *Xa21* (Song et al. 1995), *Xa1* (Yoshimura et al. 1998), *Xa26* (Sun et al. 2004), *Xa27* (Gu et al. 2005), *Xa3* (Xiang et al. 2006), *xa5* (Iyer and McCouch 2004) and *xa13* (Chu et al. 2006), have been isolated.

Xa7, a dominant resistance gene directed against *Xoo*, was originally identified in rice cv. DV85 (International Rice Research Institute accession number 8839) (Sidhu et al. 1978). A corresponding avirulence gene to *Xa7*, *avrXa7*, has been cloned and identified as a member of the *avrBs3* gene family (Bonas et al. 1989; Hopkins et al. 1992; Leach and White, 1996, White et al. 2000). AvrXa7 is a virulence factor in strain PXO86 of *Xoo*, being targeted to plant cells by a type III secretion apparatus. This protein contains a functional nuclear localisation signal (NLS) and an acidic transcriptional activation domain motif for avirulence activity, indicating that its interaction with *Xa7* might occur within the host nuclei (Yang et al. 2000). It has been proven that *Xa7* would be a durable R gene because of a fitness penalty in *Xoo* associated with adaptation to *Xa7* (Vera Cruz et al. 2000). The cloning of *avrXa7* has greatly enhanced the understanding of the mechanisms in gene-for-gene interactions, benefiting tagging of this resistance gene. *Xa7* was previously located in a region between two markers M1 (2.2 cM) and M3 (0.5 cM) of chromosome 6 (Porter et al. 2003). Recently, *Xa7* was further integrated to the region between two proximal markers GDSSR02 and RM20593, an interval of approximate 118.5 kb (Chen et al. 2008).

Rice cv. Zhenhui 084 has been developed through the pedigree selection from a cross between 91-2156 and R19. Rice cv. 91-2156 is derived from a cross between the elite restorer line Minghui 63 and high-yielding Honglian-type restorer line Teqing 1, whereas R19, selected from Kangxi 19, is a restorer line with good grain quality and strong resistance to BB. Thus, Zhenhui 084 has both high resistance to BB and good agricultural traits including plant type, a large panicle, combining ability and grain quality. Previous studies showed that Zhenhui 084 is a newly developed strong indica restorer line with highly resistant reactions to most of the Philippine races of BB (Sheng et al. 2002), indicating that Zhenhui 084 might carry a BB resistance gene responsible for its endurable resistance. Therefore, further identification and cloning of the putative R gene(s) in Zhenhui 084 will undoubtedly lead to better understanding of resistant mechanisms, thereby improving molecular breeding. In this study, we provide detailed evidence showing that Zhenhui 084 carries a bacterial blight resistance gene allelic to *Xa7*, which was finely mapped to a region between RM20576 and MY4, an interval of approximately 200 kb. Furthermore, possible candidate genes in the target region were analysed.

Materials and methods

Plant materials

Fourteen testers (IRBB1, IRBB2, IRBB3, IRBB4, IRBB7, IRBB8, IRBB10, IRBB11, IRBB13, IRBB14, IRBB21, ZCL (Zhachanglong), DV85, and CBB23, carrying *Xa1, Xa2, Xa3, Xa4, Xa7, Xa8, Xa10, Xa11, xa13, Xa14, Xa21, Xa22*(t), *Xa7/xa5* and *Xa23*, respectively) (Ogawa et al. 1991; Jiang et al. 2006; Xiang et al. 2006), IR24 (a recurrent susceptible material as a negative control), and Zhenhui 084 were used to examine their resistance to 11 *Xoo* strains.

A segregating population consisting 1226 F_2 individuals was developed from a cross between Chenghui 448 (susceptible) and Zhenhui 084, and a total of 331 individuals highly susceptible to strain PXO86 was recovered and used to genetically map the bacterial blight resistance gene in Zhenhui 084.

Pathogen inoculation and disease evaluation

Rice seedlings were transplanted to the disease nursery 30 days after sowing. The distance between neighbouring plants in a row was 13 cm, while two neighbouring rows were 25 cm apart. Eleven *Xoo* strains including ten Philippine strains (PXO61, PXO86, PXO79, PXO71, PXO112, PXO99, PXO280, PXO145, PXO87 and PXO124) and one Chinese strain (Zhe 173) were used to evaluate resistance levels in 14 testers and Zhenhui 084 (Lin et al. 1996). Strain PXO86 was used to distinguish resistant and susceptible plants in the mapping population. The strain was inoculated on leaves 5–8 of the uppermost fully expanded leaves of each plant at the booting stage (approximately 40 days after being transplanted) using the leaf-clipping method

(Kauffman et al. 1973). The bacterial inoculum was prepared as described by Lin et al. (1996). The strain was replaced by water in mock inoculations. For disease scoring, nine plants in the middle of each row were evaluated 3 weeks after inoculation. Three or four leaves with the longest lesion from each of the nine plants were selected to measure their lesion length and leaf length.

Molecular marker assays

Previously published DNA marker M5 (forward primer, 5′- CGATCTTACTGGCTCTGCAACTCTGT-3′; reverse primer, 5′- GCATGTCTGTGTCGATTCGT CCGTACGA-3′) closely linked to *Xa7* locus in IRBB7 (Porter et al. 2003) was used to check the allelism of *Xa7* in Zhenhui 084. Based on the known *Xa7* region (Porter et al. 2003), 48 SSR markers available (IRGSP 2005) were used to screen genetic polymorphisms between Zhenhui 084 and Chenghui 448. For fine mapping, 31 sequence tagged microsatellite (STS) markers were developed in the target region based on the sequences of chromosome 6 (http://rgp.dna.affrc.go.jp/cgi-bin/statusdb/irgsp-status.cgi).

Fine genetic and physical mapping of BB resistance gene

Forty-eight published SSR and thirty-one STS markers covering the initial genomic location of *Xa7* (Porter et al. 2003) were selected for fine genetic mapping of the BB resistance gene in Zhenhui 084. The linkage relationship between the target gene and the molecular markers was analysed using 331 highly susceptible individuals in the F2 population. After determining the accurate chromosomal location of the target gene, chromosome walking to the resistance gene was initiated from both sides using SSR and STS markers. To construct the physical map of the target gene, BAC and PAC clones of cv. Nipponbare downloaded from the Rice Genome Sequence Programme (RGP) website (http://rgp.dna.affrc.go.jp/cgi-bin/statusdb/) were anchored with the target gene-linked markers and then alignment of sequences was carried out using the software tool, DNAstar (http://www.dnastar.com/). Candidate gene annotation was also downloaded from the RGP website (http://rgp.dna.affrc.go.jp/cgi-bin/statusdb/statassign.pl?chr=6&lab=RGP&sort=date).

Results

Identification of the resistance gene in Zhenhui 084

To test whether the resistance of Zhenhui 084 to *Xoo* strains was conferred by any previously identified R genes, 14 BB resistance testers, together with their near-isogenic parental line IR24, were used to examine their resistance to *Xoo* strains at the adult stage. As shown in Table 1, Zhenhui 084 was highly resistant to PXO61, PXO86, PXO79, PXO71, PXO280, PXO145, PXO87, PXO124, and Zhe 173, moderately susceptible to PXO112, and highly susceptible to PXO99. Among 14 testers, only IRBB7's spectrum was almost the same as that of Zhenhui 084 but slightly different in reactions with PXO71 and PXO112. However, other testers appeared to be distinct from these two (Table 1). These observations indicate that the resistance gene against *Xoo* strains in Zhenhui 084 might be an allelic gene of *Xa7* in IRBB7.

Molecular identification of the R gene in Zhenhui 084

Since Zhenhui 084 and IRBB7 exhibited a similar resistant spectrum to BB, we further tested the allelic relationship between the R gene in Zhenhui 084 and *Xa7* in IRBB7 by using the M5 marker. As negative controls, 11 near-isogenic lines (NILs) with different BB resistance genes and IR24 were included in our study. M5 marker-amplified fragments with sizes of 294 bp for Zhenhui 084 and IRBB7 compared to 1.17 kb for IR24 and 11 NILs were found (Fig. 1). This result further supports our previous finding that suggested the BB resistance gene in Zhenhui 084 might be allelic to *Xa7*.

Resistance analysis of rice materials carrying *Xa7* at booting stage

The resistance levels in Zhenhui 084, IRBB7, DV85 (*Xa7/xa5*), and IR24 were analysed using seven *Xoo* strains. The resistance spectrum of DV85 was broader than that of Zhenhui 084 or IRBB7 (Table 1). DV85 was highly resistant to all strains except PX099, while IRBB7 and Zhenhui 084 were susceptible or moderately susceptible to *Xoo* strain PXO112. As shown in Table 2, average lesion lengths 3 weeks after inoculation with PXO99 in IRBB7, Zhenhui 084,

Table 1 Comparisons of resistance spectrum to bacterial blight (BB) between Zhenhui 084 and 14 testers

Materials	Resistance gene	*Xoo* strains*										
		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	Z173
Zhenhui 084	*Xa7*?	R	R	R	R	MS	S	R	R	R	R	R
IRBB7	*Xa7*	R	R	R	MR	S	S	R	R	R	R	R
DV85	*Xa7*/ *xa5*	R	R	R	S	R	S	R	R	R	R	R
IRBB1	*Xa1*	S	S	S	S	R	S	S	S	S	S	S
IRBB2	*Xa2*	S	S	S	S	S	S	S	S	S	S	S
IRBB3	*Xa3*	R	R	MS	R	R	S	R	R	R	R	R
IRBB4	*Xa4*	R	S	S	R	R	S	R	R	S	R	R
IRBB8	*Xa8*	S	S	S	MS	R	S	R	R	S	S	S
IRBB10	*Xa10*	S	S	S	S	S	S	S	S	S	S	S
IRBB11	*Xa11*	S	S	S	S	S	S	S	S	S	S	S
IRBB13	*xa13*	R	R	R	R	R	S	R	S	R	R	MR
IRBB14	*Xa14*	S	S	S	S	R	S	S	S	R	S	S
IRBB21	*Xa21*	R	R	R	R	R	R	R	R	R	S	R
Zhachang long	*Xa22(t)*	S	R	S	R	R	S	R	S	R	S	R
CBB23	*Xa23*	R	R	R	R	R	R	R	R	R	R	R
IR24	/	S	S	S	S	S	S	S	S	S	S	S

*P1, 2, 3, 4, 5, 6, 7, 8, 9, 10, represent PXO61, 86, 79, 71, 112, 99, 280, 145, 87 and 124, respectively. Z173, Zhe 173; R, resistance; S, susceptibility; MR, moderate resistance; MS, moderate susceptibility.

DV85, and IR24 were 26.2, 27.5, 13.4, and 25.8 cm, respectively. Thus, Zhenhui 084, IRBB7 and IR24 were all susceptible to strain PXO99 as their lesions were twice as long as that of DV85, indicating that the two genes (*Xa7/xa5*) greatly enhanced the resistance of DV85 to PXO99. For most of the strains, Zhenhui 084 and DV85 displayed higher resistance than IRBB7 (Table 2).

The resistance of Zhenhui 084 to PXO86 was genetically controlled by a single dominant gene

Next, we addressed whether the resistance of Zhenhui 084 to *Xoo* strains is controlled by a single dominant or recessive gene. Since the *Xa7* avirulence gene, *avrXa7*, was cloned from *Xoo* strain PXO86, we used this strain to test the resistance segregation pattern in

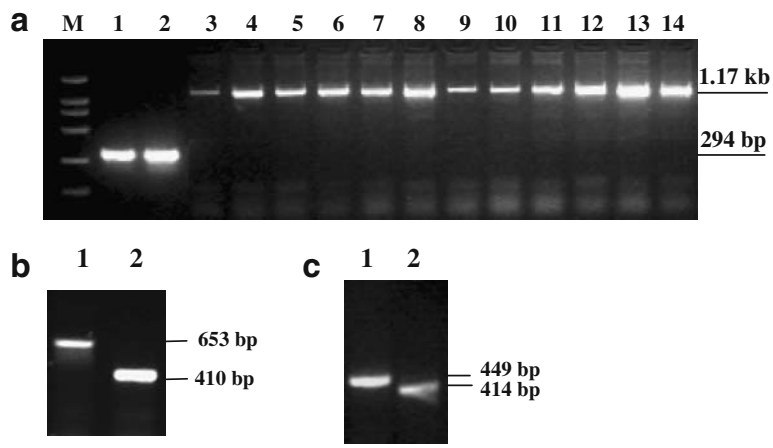

Fig. 1 PCR-based genetic polymorphism analysis of markers M5, ID7, and ID15. **a**. Marker M5, lanes 1 and 2 represent IRBB7 and Zhenhui 084, respectively; lanes 3-14 represent IR24, IRBB1, IRBB2, IRBB3, IRBB4, IRBB8, IRBB9, IRBB10, IRBB11, IRBB13, IRBB14 and IRBB21, respectively; M represents DNA Marker DL2,000; **b**. Marker ID7, lanes 1 and 2 represent Zhenhui 084 and Chenghui 448; **c**. Marker ID15, lanes 1 and 2 represent Zhenhui 084 and Chenghui 448

Table 2 Comparisons of the *Xoo* resistance of four varieties measured by lesion length (cm)

Xoo Strain	IRBB7 (*Xa7*)	Zhenhui 084 (*Xa7*?)	DV85 (*Xa7*/*xa5*)	IR24 (susceptible)
PXO61	2.75±0.5	0.8±0.3	0.6±0.3	11.5±2.4
PXO86	3.5±0.6	0.9±0.3	0.7±0.3	17.3±3.0
PXO71	4.0±0.8	1.8±0.3	1.1±0.3	13.3±2.4
PXO112	19.8±2.5	7.3±1.0	1.6±0.8	19.0±4.6
PXO99	26.2±2.5	27.5±2.8	13.4±2.9	25.8±2.2
PXO87	3.8±1.0	0.8±0.3	0.6±0.3	16.3±1.5
PXO124	4.2±0.6	0.5±0.2	0.4±0.2	17.8±1.0

the F_2 population with 1,226 individuals, derived from a cross between Chenghui 448 and Zhenhui 084. Chenghui 448 was highly susceptible to PXO86 with an average lesion length of 13.3 cm 3 weeks after inoculation, in contrast to 0.9 cm in Zhenhui 084. The distribution of the lesion length in the F_2 population appeared to be bimodal. Segregation of resistant (895) and susceptible (331) plants fitted a 3:1 ratio (χ^2=2.61, 0.1<*P*<0.25) if 5 cm in the apparent valley was used as a dividing point (Fig. 2). This result indicates that the resistance of Zhenhui 084 to PXO86 is genetically controlled by a single dominant gene.

Genetic mapping of the target R gene in Zhenhui 084 conferring resistance to PXO86

Our previous data showed that the target R gene in Zhenhui 084 is allelic to *Xa7*. To isolate the target R gene in Zhenhui 084, 48 SSR markers and five DNA markers available from M1 to M5 on chromosome 6 (Porter et al. 2003) were used to explore genetic polymorphisms between Chenghui 448 and Zhenhui 084. Among them, nine markers and M5 showed DNA polymorphisms covering the *Xa7* region. Five sets of SSR markers and M5, showing genetic polymorphisms between these two parents (data not shown), were selected to examine the F_2 mapping population. In the first screening, the R gene was defined in a region between SSR markers RM20409 and RM6811, which screened out 16 susceptible F_2 recombinants (Fig. 3a). In the second screening, three other SSR markers and M5 were used to further narrow the recombinant region. Four and one recombinants were screened out by two markers RM3430 and RM20576 flanked on the right side of RM20409, respectively (Fig. 3a). Seven recombinants were screened out by the marker RM340 flanked on the left side of RM26811. In addition, no recombinant was recovered using DNA marker M5, indicating M5 is tightly linked with the target R gene (Fig. 3a).

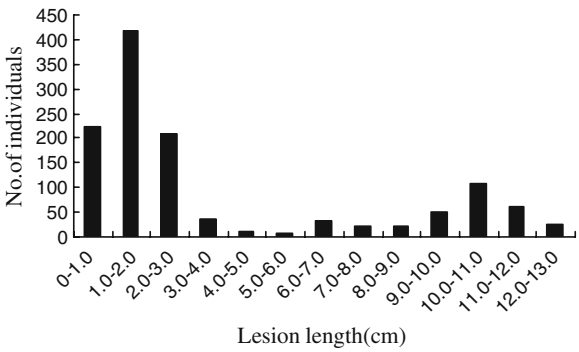

Fig. 2 The resistance segregation pattern of Zhenhui 084 in the F2 population. Distribution of lesion length after inoculation with PXO86 in samples containing 1,226 individuals from an F2 population derived from a cross between Chenghui 448 and Zhenhui 084

Fine mapping of the target R gene with newly developed STS markers

To further finely map the target R gene, 31 new STS markers were developed based on the available genomic sequence of Nipponbare. These markers were used to examine genetic polymorphisms between Chenghui 448 and Zhenhui 084. Among them, only MY4, ID7, and ID15 showed genetic polymorphisms between both parents (Table 3; Fig. 1b and c; data not shown). Only the MY4 marker screened out two recombinants (Fig. 3a). Thus, the R gene was located in a region between two markers RM20576 and MY4. Of note, no identified BB

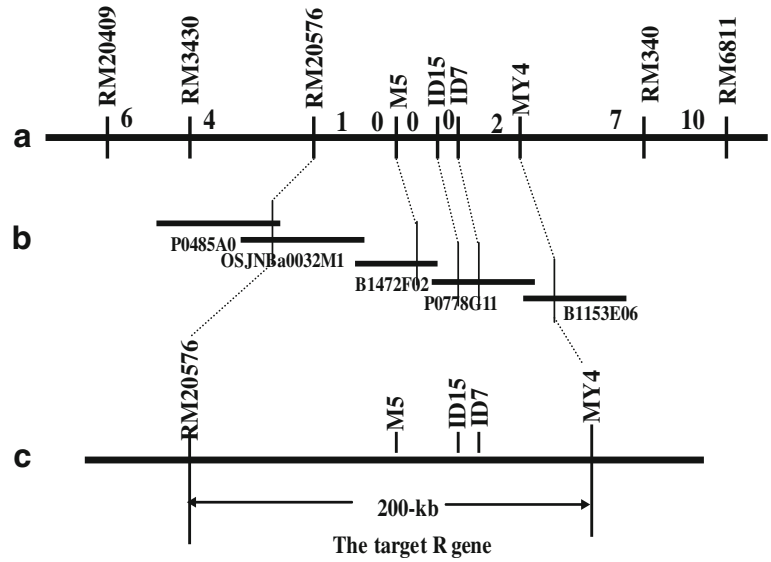

Fig. 3 Genetical and physical maps in the fine mapping of the target gene allelic to *Xa7*. **a** Fine-scale genetic linkage map of the target gene. The numbers between molecular markers indicate the numbers of recombination events detected between the target gene and corresponding molecular marker; **b** BAC clone contigs spanning the target gene region. The short horizontal lines represent the BAC/PAC clones of cv. Nipponbare, released by IRGSP and assembled by the corresponding markers linked to the target gene; **c** Fine-scale physical map of the 200 kb target gene region

resistance gene has been previously mapped to this region. It is likely that the target R gene in Zhenhui 084 is allelic to *Xa7*.

Physical map construction

Marker-based physical maps of rice chromosome six released on the website (http://rgp.dna.affrc.go.jp/E/IRGSP/download.html) were used to construct the contig covering the genomic region between RM20576 and MY4 (Fig. 3b). Sequence matching by bioinformatic analysis showed that RM20576 was found in the BAC clones P0485A0 and OSJNBa0032M1, M5 in B1472F0, ID15 and ID7 in B1472F0, and MY4 in B1153E0 (Fig. 3b). Our analysis showed that the physical distance between RM20576 and MY4 was 200 kb (Fig. 3c).

Predicted candidate genes

Sequence analysis demonstrated that the 200 kb contains sixteen genes whose full-length cDNAs or ESTs expressed are available (Table 4). All these genes were predicted by the combined use of FGENESH, GeneMark.hmm, GlimmerM, and GENSCAN (http://rgp.dna.affrc.go.jp/cgi-bin/statusdb/statassign.pl?chr=6&lab=RGP&sort=date). Among these predicted genes, eight encode non-coding transcripts, four encode unknown proteins, and the others encode pentameric polyubiquitin-like, putative NAC domain protein NAC1, putative high pI alpha-glucosidase, and putative NRAMP metal ion transporter 1 (Table 4). Five conserved domains such as DUF640, Ubiquitin, No apical meristem (NAM) protein, Glyco_hydro_31 and PRK00701 (manganese transport protein MntH)

Table 3 Primers for three STS markers

Marker	Forward primer (5′−3′)	Reverse primer (5′−3′)
MY4	CTTCCTTTCCAGGCTTTC	TAGAATTTGCATCATCCC
ID7	ATATTCACCAAATGATTCCCTG	ATACAAGCCTAAACCCATCTCA
ID15	ATACAGTGCCAATGATGAGGAG	CATACGAAACCCAACAGAAATAG

Table 4 Predicted candidate genes

No.	Nomenclature of predicted genes	Full-length cDNA	EST	Conserved domain
1	Unknown protein, similar to *Oryza sativa* chromosome 10, OSJNBa0055P24.1	AK068794	None	DUF640
2	Non-coding transcript	AK101470	None	None
3	Non-coding transcript	AK070761	None	None
4	Pentameric polyubiquitin-like	None	C97178	Ubiquitin
5	Non-coding transcript	AK066949	None	None
6	Non-coding transcript	AK066054	None	None
7	Unknown protein	None	AU166312	None
			C25876	
8	Unknown protein, similar to Oryza sativa Chromosome 2, OSJNBa0023I17.22	AK060681	None	None
		AK102712		
9	Unknown protein	AK109610	C99011	None
10	Putative NAC domain protein NAC1	AK063648	C28309	No apical meristem (NAM) protein
			D24953	
11	Putative high pI alpha-glucosidase	AK119824	AU097233	Glyco_hydro_31
12	Non-coding transcript	AK065487	None	None
13	Putative NRAMP metal ion transporter 1	AK070574	None	PRK00701, manganese transport protein MntH
14	Non-coding transcript	AK064503	None	None
		AK071620		
15	Non-coding transcript	AK119775	None	None
16	Non-coding transcript	AK069470	AU097233	None

were searched through the related website (http://www.ncbi.nlm.nih.gov/Structure/cdd/cdd.shtml).

Discussion

Lesion length comparisons revealed that Zhenhui 084 was more resistant to *Xoo* than IRBB7 at adult stages although their resistant spectra were very similar (Tables 1 and 2). The effect of genetic background on R genes has been indicated in rice and *Arabidopsis* (Sun et al. 2004; Banerjee et al. 2001); however, a difference in resistance between Zhenhui 084 and IRBB7 does not result from their genetic background as they are of the same indica background. Based on our mapping data, the target R gene in Zhenhui 084 is located in a similar region with *Xa7* in IRBB7 (Chen et al. 2008; Fig. 3 in this study). Thus, it is more likely that the target R gene in Zhenhui 084 is allelic to *Xa7*.

Most of these major resistant genes have been overcome by newly evolved, indigenous, and unrecognised pathogen races (Ezuka and Sakaguchi 1978; Mew and Vera Cruz 1979; Huang et al. 1997). It has been proven that *Xa7* would be a durable R gene because of a fitness penalty in *Xoo* associated with adaptation to *Xa7* (Vera Cruz et al. 2000). Therefore, mapping and characterisation of *Xa7* will provide a new insight into strategies to extend the life of R genes in the field.

Another effective way to delay breakdown of resistance is to provide a broad-spectrum of resistance by combining multiple genes having complementary resistance spectra, relative to the pathogen subpopulations, into a single plant genotype (Babujee and Gnanamickam 2000). As by-products of our map-based cloning effort, a number of PCR-based markers for the target gene allelic to *Xa7* were developed, which provide a useful tool for the marker-assisted transfer of *Xa7* in rice breeding programmes. Specifically, two PCR-based markers (ID7 and ID15) that

were tightly linked to the target gene allelic to *Xa7* should be powerful and user-friendly because of the expected high level of genetic polymorphisms in rice germplasm. In addition, Zhenhui 084 is a newly-developed strong indica restorer line carrying the target gene allelic to *Xa7* and shows not only higher resistance to most of the Philippine races of BB than IRBB7, but also has good plant type, a large panicle, good combining ability and fine grain quality (Sheng et al. 2002). These results showed that Zhenhui 084 could be more useful for future breeding programmes than other rice cultivars.

Proteins often contain several modules or domains, each of which has a distinct evolutionary origin and function. Five conserved domains of predicted candidate genes, DUF640, Ubiquitin, NAM protein, Glyco_hydro_31 and PRK00701 were searched from NCBI's Conserved Domain Database (http://www.ncbi.nlm.nih.gov/Structure/cdd/cdd.shtml) (Table 4). The DUF640 family represents a conserved region found in plant proteins including resistance protein-like protein (Marchler-Bauer et al. 2007). The ubiquitin superfamily is a rich repository of small, conserved, functionally unique, and important proteins, and its members have been implicated in numerous cancers, neurodegenerations, inflammations, and various disorders affecting signal transduction or protein half-life (Larsen and Wang 2002). Glycosyl hydrolases are key enzymes of carbohydrate metabolism; glycosyl hydrolases family 31 comprises enzymes that are, or similar to, alpha-galactosidases (Henrissat 1998). PRK00701, manganese transport protein MntH, is a member of family NRAMPs (natural resistance-associated macrophage proteins) (Kehres et al. 2000). NRAMPs have been characterised in mammals as divalent transition metal transporters involved in iron metabolism and host resistance to certain pathogens (Nelson, 1999). No apical meristem (NAM) proteins are plant development proteins (Sablowski and Meyerowitz 1998; Souer et al. 1996).

So far, seven BB resistance genes (*Xa1, Xa3, xa5, xa13, Xa21, Xa26*, and *Xa27*) have been isolated. Surprisingly, except that *Xa3*, *Xa21* and *Xa26* encode similar receptor-like proteins, the products of four other genes are unique and not found in other plant species. The analysis of predicted candidate genes indicated that the target gene allelic to *Xa7* perhaps represents a new class of plant resistance gene (Table 4). Thus, our next major work will focus on isolation and identification of the target R gene, which will provide a new insight into underlying mechanisms on R gene resistance to BB.

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