Molecular mapping of the Pi2/9 allelic gene Pi2-2 conferring broad-spectrum resistance to Magnaporthe oryzae in the rice cultivar Jefferson

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Abstract

Background: Utilization of broad-spectrum resistance (R) genes is an effective and economical strategy to control the fungal pathogen Magnaporthe oryzae, the causal agent of the rice blast disease. Among the cloned blast resistance genes, Pi9, Pi2 and Piz-t confer broad-spectrum resistance to diverse M. oryzae isolates and were isolated from the Pi2/9 locus on chromosome 6. Identification and isolation of additional R genes with different resistance spectra from this locus will provide novel genetic resources for better control of this important rice disease.

Results: In this study, we identified a dominant R gene, Pi2-2, at the Pi2/9 locus from Jefferson, an elite U.S. rice cultivar, through genetic and physical mapping. Inoculation tests showed that Jefferson has different resistant specificities to M. oryzae isolates compared rice lines with the Pi9, Pi2 and Piz-t genes. Fine mapping delimited Pi2-2 to a 270-kb interval between the markers AP5659-3 and RM19817, and this interval contains three nucleotide-binding site-leucine-rich repeat (NBS-LRR) genes in the Nipponbare genome. Five bacterial artificial chromosome (BAC) clones spanning the region were identified, and a BAC contig covering the Pi2-2 locus was constructed.

Conclusions: We identified a new allelic gene at the Pi2/9 locus and fine-mapped the gene within a 270-kb region. Our results provide essential information for the isolation of the Pi2-2 gene and tightly linked DNA markers for rice blast resistance breeding.

Keywords: Rice blast, Resistance gene, Mapping, BAC clones, Pi2/9 locus

Background
Rice is the staple food for more than half people of the world, and the demand is increasing because of the expanding rice-eating population, particularly in many developing countries in Africa and Asia. However, rice production is severely affected by various biotic and abiotic stresses (Khush and Jena 2009). Rice blast, caused by the fungal pathogen Magnaporthe oryzae, is one of the major limitations, and usually causes 10-30% yield loss in rice production when a rice blast epidemic occurs (Talbot 2003; Skamnioti and Gurr 2009). Use of host resistance is an effective and economical way to control the blast disease (Khush and Jena 2009). To date, over 80 blast resistance genes have been identified, and are distributed on 11 rice chromosomes except chromosome 3 (Liu et al. 2010; Yang et al. 2009). So far, 21 have been cloned (Pib, Pita, Pi9, Pi2, Piz-t, Pid2, Pid3, Pim, Pit, Piz5, Pid1, Pib1, Pish, Pik, Pik-p, Piz4, Pia, NLS1 and Pid25). Interestingly, most of them are NBS-LRR genes except Pi-d2 and pi21 (Wang et al. 1999; Bryan et al. 2000; Qu et al. 2006; Zhou et al. 2006; Chen et al. 2006; Liu et al. 2007; Lin et al. 2007; Ashikawa et al. 2008; Hayashi and Yoshida. 2009; Lee et al. 2009;
Similarly, both two independent NBS-LRR genes for the blast resistance chromosome 11, and interestingly, each of them requires Pigm(t) (Okuyama et al. 2011). Pi5 and Pia also require two NBS-LRR members for their resistance function (Lee et al. 2009; Okuyama et al. 2011).

At least eight blast resistance genes were identified from the Pi2/9 locus, which is located on the short arm and near the centromere of chromosome 6. Among them, Pi9, Pi2 and Piz-t were successfully cloned (Qu et al. 2006; Zhou et al. 2006). Pi26(t) (Wu et al. 2005), Pigm(t) (Deng et al. 2006), Piz(t) (Fjellstrom et al. 2006), Piz40(t) (Jiang et al. 2007) and Piz50(t) (Zhu et al. 2012) are in the process of being cloned by different laboratories. Interestingly, most of them confer broad-spectrum resistance to diverse M. oryzae races or isolates. The near isogenic line C101A51 carrying Pi2 is resistant to 455 isolates collected from Philippines and most of the 792 isolates from China (Chen et al. 1996, 1999). The Pi9-bearing line, 75-1-127, is resistant to 43 isolates collected from 13 different countries (Liu et al. 2002). Piz-t and Pigm from Toride and Gumei4, respectively, are resistant to more than 90% of tested isolates from China and Thailand (Shen et al. 2003). The near-isogenic line containing Piz50(t) is incompatible to 97.7% of the 523 isolates from different regions of China (Zhu et al. 2012). However, the underlying mechanism of broad-spectrum resistance of these genes is still not well understood.

Jefferson, a long-grain tropical japonica cultivar grown in the southern U.S., has retained its resistance to blast since its first use in 1997 (McClung et al. 1997; Skamnioti and Gurr 2009). It was reported that Jefferson possesses three blast resistance genes, Piz(t), Pi-d(t) and Pi-k(t), based on its disease reactions (McClung et al. 1997). Our preliminary observation showed that Jefferson was immune in the blast nursery of Taojiang County, Hunan Province, China, which contained 11 major M. oryzae races including ZC9, ZC11, ZE3, ZB29, ZG1, ZB25, ZB31, ZB13, ZC7, ZA9, and ZF1 (unpublished). To determine the genetic basis of broad-spectrum resistance in Jefferson, we performed greenhouse inoculations with individual isolates and genetic analysis using an F2 population derived from a cross between Jefferson and the susceptible cultivar CO39. We identified a dominant R gene in Jefferson on chromosome 6 at the Pi2/9 locus, named Pi2-2. Allelism analysis indicated that Pi2-2 is tightly linked or allelic to Pi9. We constructed a BAC contig in the genomic region and fine-mapped the gene within a region approximately 270 kb. These data will facilitate both the positional cloning of the R gene and molecular breeding programs of rice blast resistance.

**Results**

**Resistance spectrum of Jefferson to 28 M. Oryzae isolates**

To test the resistance spectrum of Jefferson, we inoculated the cultivar with 28 M. oryzae isolates collected from six countries, and the inoculation results are summarized in Additional file 1: Table S1. Three known broad-spectrum resistant cultivars, Tianye carrying Pi2-1 and Pi51 (Wang et al. 2012), XZ3150 carrying Pi47 and Pi48 (Huang et al. 2011), and 75-1-127 carrying Pi9 (Qu et al. 2006) were used as resistance controls and the highly susceptible cultivar CO39 was used as a susceptible control. Interestingly, Tianye was resistant to all the isolates and Jefferson was only susceptible to the blast isolate RB11 from Japan. XZ3150 was susceptible to three isolates (236–1, RB6 and ROR1) and 75-1-127 was susceptible to two isolates (ROR1 and X2007A-7). By contrast, the susceptible control cultivar CO39 was susceptible to 27 of all 28 tested isolates. These results indicate that Jefferson confers broad-spectrum resistance to M. oryzae.

**Resistance to M. oryzae isolate 318–2 is controlled by a single dominant locus in Jefferson**

The M. oryzae isolate 318–2 from Hunan Province of China was used for genetic analysis of the blast resistance in Jefferson. We developed the F2 population derived from a cross between Jefferson and CO39. All the F1 plants were resistant to 318–2 (32R:0S), indicating that the dominant inheritance of the R gene in Jefferson. The segregation of resistant and susceptible individuals in the F2 population fitted a ratio of 3:1 (194R:60S, \( \chi^2=0.257, 0.5<P<0.9 \)), suggesting that the resistance to 318–2 is controlled by a single dominant R gene in Jefferson. We designated this R gene in Jefferson as Pi2-2.

Pi2-2 is tightly linked or allelic to Pi9 on chromosome 6

Previous research reported that there are three blast resistance genes, Piz(t), Pi-d(t) and Pi-k(t), in Jefferson (McClung et al. 1997). Piz(t) is located on chromosome 6 near the Pi2/9 locus (Fjellstrom et al. 2006). Pi-d(t) and Pi-k(t) are located on chromosome 11. Therefore, we selected 25 SSR markers around the Pi2/9 and Pi-k(t) loci.
for linkage analysis. Twenty highly resistant and twenty highly susceptible individuals from the F2 population of the Jefferson×CO39 cross were genotyped with the polymorphic markers. No marker around the \( Pi-k \) locus co-segregated with the resistance to 318–2. But two polymorphic SSR markers around \( Pi2/9 \) (RM7178 and RM7311) were associated with the resistance, indicating that \( Pi2-2 \) is located on chromosome 6.

Previous studies showed that \( Pi2 \) and \( Piz-t \) are tightly linked to \( Pi9 \) (Zhou et al. 2006, 2007) and \( Piz(t) \) is allelic or tightly linked to \( Piz-t \) (Hayashi et al. 2004). However, the exact location of \( Piz(t) \) has not been determined yet. To understand the linkage relationship between \( Pi2-2 \) and the \( R \) genes in the same region, we developed an F2 population from a cross between Jefferson and \( Piz(t) \)-carrying line 75-1-127 for allelism test. A total of 637 F2 individuals were inoculated with \( M. oryzae \) isolate 318–2, which was incompatible to both Jefferson and 75-1-127, to observe the phenotype segregation. No susceptible plant was found in 637 F2 individuals, suggesting that \( Pi2-2 \) is tightly linked or allelic to the \( Pi9 \) gene.

Jefferson shows different resistance spectrum with the cultivars carrying other \( R \) genes at the \( Pi2/9 \) locus

Previous research showed that the three cloned \( R \) genes at \( Pi2/9 \) locus have different resistance spectra. 75-1-127 is highly susceptible individuals from the F2 population of the Jefferson×CO39 cross were genotyped with the polymorphic markers. No marker around the \( Pi2/9 \) locus has not been determined yet. To understand the linkage relationship between \( Pi2-2 \) and the \( R \) genes in the same region, we developed an F2 population from a cross between Jefferson and \( Pi2/9 \)-carrying line 75-1-127 for allelism test. A total of 637 F2 individuals were inoculated with \( M. oryzae \) isolate 318–2, which was incompatible to both Jefferson and 75-1-127, to observe the phenotype segregation. No susceptible plant was found in 637 F2 individuals, suggesting that \( Pi2-2 \) is tightly linked or allelic to the \( Pi9 \) gene.

### Table 1 Polymeric SSR markers around the \( Pi2/9 \) locus used for linkage analysis

| Markers       | Forward primer (5'-3') | Reverse primer (5'-3') | Genomic position (bp) | Expected size (bp) |
|---------------|------------------------|------------------------|-----------------------|-------------------|
| MGRS836<sup>a</sup> | AAAACCTAGAAAAATGGGAAATG | TATAAGC CGCAGCAAATTC | 9308979-9309076 | 98 |
| RM1981<sup>b</sup> | CCAAGGACTGACCAGGACGAGCTG | CGCGAGCAGCAGGACGACATGG | 10137012-10137394 | 383 |
| RM7178<sup>b</sup> | CCGTGAGATGGGCTACCTAC | TACCTCTTCACAGCGACACGTG | 10198893-10199043 | 151 |
| AP5659-3<sup>b</sup> | CTCCTCTAGGTATCTTCCCT | TGCAGACTTCACAACGATGG | 10357166-10357453 | 288 |
| AP5659-3<sup>b</sup> | TCTTCTTCTAGGAAACCAAAG | AAGTATGTTGCTGAGCCCATTT | 10406597-10406825 | 229 |
| RM731<sup>b</sup> | CGTGGCGCCTTATATTTCT | AGTGTGCTGTGACTCCGGG | 11045702-11045848 | 147 |

<sup>a</sup> Previously reported markers in this region.

<sup>b</sup> SSR markers released by Gramene database (http://www.gramene.org/db/markers/).

Genomic position and expected PCR product size for each marker were determined based on the reference sequence of rice cultivar Nipponbare released by International Rice Genome Sequencing Program (IRGSP).
NIP-2R, 5′-TGGAGCGGAGACAGAGTGG-3′) and PK-1F/R (PK-1F, 5′-CGTTCACTGACTTCCCTTTCCC-3′; PK-1R, 5′-TCCGCATCGCCGTCTTCTG-3′), designed based on the NIP and PK sequences, were employed for detecting the relative location of the five BAC clones at the Pi2/9 locus. The PCR results showed BJ2-4-1-13 contained the PK gene. A contig map consisting of 5 BAC clones (BJ2-7-10-8, BJ21-2-3-10, BJ21-7-3-51, BJ21-2-4-43 and BJ2-4-1-13) was constructed that covered both Pi2-2 and the whole Pi2/9 locus in Jefferson (Figure 2).

Discussion

Many plant disease resistance genes are located in complex clusters in which multiple copies of closely related sequences are formed through gene duplication and uneven crossing over. Allelic genes in different genetic backgrounds have evolved to carry diverse resistance specificities due to exposure of these loci to different pathogen populations. In rice, over half of the identified blast resistance genes are clustered at different loci, especially on chromosomes 6, 11 and 12. The Pi2/9 locus is a region with at least eight R genes (Yang et al. 2009; Zhu et al. 2012), and contains several NBS-LRR type genes in both cultivated and wild rice lines (Zhou et al. 2007; Dai et al. 2010). Three R genes at this locus have been successfully isolated. The paralog NBS2-Pi9 is the Pi9 gene, and the paralogs NBS4-Pi2 and NBS4-Piz-t are the Pi2 and Piz-t genes, respectively (Zhou et al. 2006). In our study, three candidate NBS-LRR genes (NBS-LRR1, NBS-LRR2 and NBS-LRR3) at the Pi2/9 locus were identified for Pi2-2 according to the sequence of Nipponbare genome. However, the Nipponbare genome did not fully reflect the structure of the Pi2-2 locus in Jefferson. Thus, sequence analysis of the BAC clones of Jefferson covering Pi2-2 and complementation test of candidate genes are necessary for determining which NBS-LRR gene is Pi2-2.

Three blast resistance genes, Piz(t), Pi-d(t) and Pik-prom3(t), were reported in Jefferson (McClung et al. 1997). Pi-d(t) and Pik-prom3(t) are tightly linked on chromosome 11. Piz(t) was originally reported in the U.S. rice cultivar Zenith (Kiyosawa 1967), and has been widely introduced into different cultivars by rice breeders (Conaway-Bormans et al. 2003). Piz(t) was mapped on the short arm of

| Isolates | Origin | Jefferson | S173 (Pi2) | Toride (Piz-t) | 7S-1-127 (Piz9) | CO39 |
|----------|--------|-----------|------------|---------------|----------------|------|
| ROR1     | Korea  | R         | R          | R             | S              | S    |
| CHNO560-2-3 | China | R         | S          | R             | R              | S    |
| 236-1    | China  | R         | R          | S             | R              | S    |
| X2007A-7 | China  | R         | S          | S             | S              | S    |

R and S denote resistant and susceptible reaction, respectively.
chromosome 6, close to the centromere, by several groups using different cultivars (Hayashi et al. 2006; Fjellstrom et al. 2006; Conaway-Bormans et al. 2003), but the exact location has not been determined yet. Based on the fine mapping results in this study, we speculate that \( \text{Pi2-2} \) is likely \( \text{Piz(t)} \). Our on-going cloning effort of the \( \text{Pi2-2} \) gene will provide us the answer in the near future.

**Conclusions**

This study demonstrated that the rice cultivar Jefferson harbors the blast resistance gene \( \text{Pi2-2} \) at the \( \text{Pi2/9} \) locus on chromosome 6. The gene was finely mapped to a 270 kb interval. A BAC contig covering \( \text{Pi2-2} \) was constructed, which provides essential foundation for the isolation of the \( R \) gene.

### Methods

#### Plant materials

Seven rice cultivars, Jefferson, Tianye, XZ3150, 5173 (\( \text{Pi2} \)), Toride (\( \text{Piz-t} \)), 75-1-127 (\( \text{Pi9} \)) and CO39, were used in this study. \( F_1 \) and \( F_2 \) populations from a cross between Jefferson and highly susceptible cultivar CO39 were constructed for genetic analysis. The \( F_2 \) population derived from a cross between Jefferson and 75-1-127 was constructed for allelism tests.

#### Blast inoculation and disease evaluation

The 28 \( M. \text{oryzae} \) isolates used in the study are listed in Additional file 1: Table S1. The collection sites and providers are included in the table. Rice seedlings at 3–4
leaf-stage were spray-inoculated with *M. oryzae* spore suspensions (1.5×10^5 spores/ml) and then kept in darkness at 25°C–27°C and over 90% relative humidity for 24 h. The inoculated plants were subsequently kept under a 12/12 (day/night) photoperiod at the same temperature and relative humidity. Disease reaction evaluation was carried out 7 days after inoculation according to the 0–5 scoring system described by (Bonman et al. 1986).

**Genetic and allelism analysis**

The Jefferson×CO39 F2 population was inoculated with the *M. oryzae* isolate 318–2, which is avirulent to Jefferson and virulent to CO39. 318–2, which is also avirulent to 75-1-127, was employed to inoculate the Jefferson×75-1-127 F2 population for allelism analysis.

**Genotyping and genetic mapping**

A total of 39 SSR markers spanning the Pi2-9 and Pik loci were used for the polymorphism survey between Jefferson and CO39. Six polymorphic SSR markers spanning the Pi2-9 locus were used for preliminary and fine mapping of the *R* gene in Jefferson (Table 1). The genomic DNA of 20 highly resistant and 20 susceptible F2 individuals, which were phenotypically confirmed in the F3 generation, were extracted from leaves for segregation analysis (Saghai-Maroof et al. 1984). All PCRs began with a denaturation step of 94°C/4 min, followed by 35 cycles of (A) 94°C/30 sec, 55°C/30 sec, 72°C/30 sec, with a final extension step of 72°C/7 min. Linkage analysis was performed using the MAPMAKER/V3.0 using all highly susceptible individuals.

**Physical mapping of the Pi2-2 locus**

The physical positions of the markers tightly linked to Pi2-2 locus were determined based on the genome of Nipponbare using the BLAST program on Gramene (http://www.gramene.org/Multi/blastview) (Jaiswal et al. 2006). The genomic sequences flanked by the markers RM19817 and AP5659-3 were annotated using the Rice Genome Annotation Project (http://rice.plantbiology.msu.edu/) (Ouyang et al. 2007) and Rice Genome Automated Annotation System (http://ricegaas.dna.affrc.go.jp/) (Sakata et al. 2002).

**Construction of the BAC library of Jefferson**

The genomic BAC library of Jefferson was constructed using the method described by (Luo and Wing 2003). The markers tightly linked to Pi2-2 were used for screening of positive clones from the BAC pools. The contig map spanning the Pi2-2 locus was constructed based on the end sequencing results of the positive BAC clones.

**Additional file**

**Additional file 1: Table S1.** Disease reaction of Jefferson and other 4 cultivars to 28 *M. oryzae* isolates collected from different regions.

**Competing interests**

The authors declare that they have no competing interests.

**Authors’ contributions**

NJ and ZL contributed equally to this work. NJ carried out resistance spectrum analysis, allelism analysis, genetic analysis, molecular mapping, construction of the BAC contig map and wrote the manuscript; ZL carried out molecular mapping, construction of the BAC contig map; JW carried out spectrum analysis and allelism analysis; YW participated in molecular mapping; LW carried out resistance spectrum analysis; SW carried out resistance spectrum analysis; DW carried out resistance spectrum analysis; TW carried out resistance spectrum analysis; YL participated in molecular mapping; PS carried out carried out genetic analysis; JL participated in the design of the study; LD participated in the design of the study; ZW participated in experimental designing; CW constructed the BAC library of Jefferson; ML participated in the design of the study and constructed the BAC library of Jefferson; XL designed the research and wrote the manuscript; GW designed the research and wrote the manuscript. All authors read and approved the final manuscript.

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