



# Is Disease Resistance against Rice Blast Controlled by Race-Nonspecific Genes to Rice Blast Durable?

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## Introduction

Rice blast caused by the fungus *Magnaporthe grisea* (*Pyricularia oryzae*) is a major destructive disease in rice cropping areas worldwide. Between 10% and 30% of the annual rice harvest is lost by infection of rice blast fungus. Genetic improvement of resistance against rice blast is a significant and primary target in global rice production and productivity.

Based on plant-pathogen interactions, the resistance to rice blast is categorized into two types, race-specific and race-nonspecific. More than 100 loci conferring resistance to blast have been identified and more than 30 of them have been cloned. Race-specific *R* genes encode nucleotide-binding site (NBS) leucine-rich repeat (LRR) proteins that interact with pathogen effectors and trigger defense reactions according to the gene-for-gene model of recognition. Recent studies in rice and *Arabidopsis* showed that different genes for NBS-LRR proteins cooperate in pathogen recognition and resistance. On the other hand, race-nonspecific resistance is quantitatively controlled by multiple quantitative trait loci (QTL) or genes which had not been cloned until 2009 when we firstly reported map-based cloning of race-nonspecific resistance QTL.

Race-specific *R*-genes have been identified in a broad range of the world rice germplasm. *R*-genes dramatically enhance blast resistance and result in stable rice production, but their extensive use poses a serious risk of emerging new races of the blast pathogen and the quick breakdown of resistance which is defined as 'genetic vulnerability'. For example, since the first breakdown of resistance occurred only 2 years after release of the resistant variety with *Pik* in Japan, the resistance by several different *R*-

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genes has unexpectedly broken down in the following years. Similar trends have been reported in Korea and Colombia. Hence, instead of race-specific *R* genes, race-nonspecific resistance QTLs (genes) to rice blast have been concentrated on the durability of resistance to rice blast [1-6].

## Mapping QTLs conferring race-nonspecific resistance to rice blast

QTLs for race-nonspecific resistance to rice blast were analyzed in progeny derived from the cross between Japanese resistant upland and susceptible paddy rice varieties. Two resistance QTL alleles on chromosome 4 and one on chromosome 12 were identified. Each QTL explained from 13.7% to 45.7% of the total phenotypic variation. One of QTL on chromosome 4 was inherited as a single recessive gene and was designated *pi21*. In addition, *qBR4-2* on chromosome 4 and *qBR12.1* on chromosome 12 were also identified. Resistance QTLs from other upland rice varieties were also detected in similar regions on chromosomes 4, 11 and 12. Resistance QTL alleles were located mainly in a 30-Mb region of chromosome 4 and on chromosomes 1, 3, 6 and 11.

## Map-based cloning of race-nonspecific resistance gene, *pi21*

Linkage analysis and progeny testing narrowed down the *Pi21* locus to a small region carrying a single gene locus, *Os04g04010*. This gene encodes a protein with a putative heavy-metal-binding domain and a proline-rich region. Comparison of sequences between resistant and susceptible varieties identified 21- and 48-bp deletions in the resistant variety, suggesting that one of these deletions confers the resistance. Transgenic complementation

testing confirmed that a loss-of-function mutation in *Pi21* improves resistance to rice blast.

Information on the variation of QTL alleles allows the use of a wide range of germplasm. In the case of the *pi21* gene, Asian cultivated rice (*Oryza sativa* L.) has 12 haplotypes determined by insertion/deletion variations at three sites in the proline-rich region, which is presumed to be involved in protein–protein interactions in multicellular organisms. Each of the 12 haplotypes carries one of the two deletions or two smaller deletions compared with the haplotype of a resistant variety, but it is difficult to predict the resistance/susceptibility phenotype from DNA sequences. Inoculation testing using a series of backcrossed lines carrying each of the *Pi21* haplotypes in the same genetic background indicated that only the line carrying the haplotype of a resistant variety showed improved the resistance to rice blast. The results suggest that the two deletions in the resistance *pi21* allele are optimal to cause the loss of function, which increases the resistance to rice blast.

### Map-based cloning of other QTLs for race-nonspecific resistance

*Pi35* is a major resistance QTL on chromosome 1 and has maintained resistance under natural field conditions since 1961. *Pi35* is allelic to *Pish*, a typical *R*-gene that encodes an NBS–LRR protein. Six differences in the deduced amino acid sequences were identified between *Pi35* and *Pish*. One of the four residues in the LRR region is significantly associated with race-nonspecific resistance. Three other residues in the LRR region and two residues in the NBS domain are also associated with the resistance, suggesting that a combination of multiple functional polymorphisms in the gene confers race-nonspecific resistance.

*Pi63* is a major resistance QTL in a 30-Mb region of chromosome 4 and encodes an NBS–LRR protein located within an *R*-gene cluster. Interestingly, the resistance conferred by *Pi63* is isolate-specific. Such characteristic has not been detected in the genetic background of the donor variety because of the effect of the race-nonspecific *pi21* allele and alleles of other resistance QTLs. Increased expression of *Pi63* in transgenic lines led to moderate resistance against pathogen isolates that produce a highly susceptible phenotype in the NIL for *Pi63*.

*Panicle blast 1 (Pb1)* on chromosome 11 is a gene derived from the *indica* variety. Plants carrying this gene are susceptible to blast during young vegetative stages, but the resistance level increases as the plants grow and persists even after heading. *Pb1* encodes an atypical NBS–LRR protein that has no P-loop and some motifs in the NBS domain are degenerated. *Pb1* transcript level increased during the growth of *Pb1*-resistant varieties and effectively control panicle blast. *Pb1*-mediated resistance may be regulated by a signaling pathway distinct from that involving typical NBS–LRR proteins.

### Durable resistance to rice blast mediated by *pi21*

Slow induction of defense by *pi21* contributes to pathogen control without penalty on yield, as confirmed by field tests at several locations. The *pi21* allele is effective against diverse fungus races, so the use of *pi21* might not be a strong driving force for changes in the structure of pathogen populations. The durability of resistance conferred by *pi21* is required to be proved by prolonged resistance of varieties under natural field conditions. Monitoring of newly released varieties carrying *pi21* will provide further evidence to confirm or disprove the durability of resistance conferred by *pi21*.

### Pyramiding race-nonspecific resistance genes for sustainable control of rice blast

Pyramiding multiple resistance QTL alleles is considered to additively enhance race-nonspecific resistance. However, disease resistance sometimes interacts with genetic backgrounds and/or environmental factors. The data on resistance to rice blast over two decades support this idea in the context of race-specificity and temperature-dependent resistance and indicate the existence of genetic loci that modulate the resistance or its mode of action. To understand how resistance allele interacts with such factors, it is important to determine the appropriate number and combinations of resistance genes. However, knowledge of the impact of QTL pyramiding on the robustness of plant defense in rice is limited.

In the genetic background of the susceptible variety, the average reduction of lesion area by *pi21* was 87% compared with the recurrent parent, whereas the reduction by the minor QTL alleles was 39% in *Pi34*, 45% in *qBR4-2* and 22% in *qBR12-1*. Although the effects of these minor QTL alleles were sometimes undetectable, their combinations dramatically reduced lesion area both in field tests and in glasshouse inoculation tests. The line with four resistance alleles had a lesion area of  $\leq 1\%$ , which was similar area to the donor and was only 6% of that in the line carrying *pi21* only, suggesting that the QTL pyramid conferred robust resistance. Similar results were obtained for a series of lines with one to four resistance QTL alleles, despite the presence of background noise from donors. A more important observation is that a QTL pyramid improves the stability of resistance; the coefficient of variation of lesion area across field tests in the line carrying four resistance QTL alleles was smaller than those in lines with only one or two. The study demonstrated the importance of minor QTL alleles for strengthening the durability of resistance, even if the effect of each QTL allele is sensitive to the environment.



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