

# Current Status and Future Prospects for Research on Blast Resistance in Rice (*Oryza sativa* L.)

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**Abstract** Rice is the most important food security crop and staple food of half of the world population. Major increases in rice production occurred during the past four decades of last century as a result of adoption of green revolution technology. Demand for rice continues to increase as a result of population increase and improvement in living standards particularly in Africa and Latin America. However, rate of increase of rice production has slowed down. It is estimated that we will have to produce 30% more rice in 2030. For this purpose we need rice varieties with higher yield potential and greater yield stability. Breakdown of blast resistance is the major cause of yield instability in several rice growing areas. Efforts are underway to develop rice varieties with durable blast resistance. More than 40 major genes as well as QTL for blast resistance have been identified. Monogenic resistance to blast is less stable but varieties with pyramided monogenes or QTLs are durably resistant. Rice research should focus on identifying more durably resistant genes, tagging of these genes with molecular markers and pyramiding these genes or QTLs through molecular marker-aided selection. Candidate gene identification through rice functional genomics has great potential for developing more durably resistant varieties.

**Keywords** Monogenes · QTL · Resistance breakdown · Durable resistance · Gene nomenclature

## 1 Introduction

Rice is the world's most important food crop and a primary source of food for more than half of the world's population. More than 90% of the world's rice is grown and consumed in Asia where 60% of the world's people live. Rice accounts for

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35–75% of the calories consumed by more than 3.0 billion Asians. Major increases in rice production occurred during last four decades due to the adoption of green revolution technology. However, the rate of growth of rice production has slowed down. Whereas rice production increased at the annual growth rate of 2.49% during 1970–1990, the annual growth rate was 1.70% during 1990–2000 and only 1.21% during 2000–2006. World rice stocks are at the lowest level since 1974 and price of rice is showing upward trend in the domestic and international markets.

The population of rice consumers is continuing to increase and demand for rice is also going up due to improved living standards particularly in Africa. According to various estimates we will have to produce 30% more rice by 2030. To meet this challenge we need rice varieties with higher yield potential and greater yield stability. Although yield potential of rice is 10 tons per hectare, farmers on the average harvest about 5 tons per hectare from irrigated lands. This yield gap is due to the losses caused by biotic and abiotic stresses. Among the biotic stresses blast disease is most important.

## **2 Rice Blast Problem and Yield Loss**

Blast disease affects rice production in all rice growing regions. However, the yield losses are most serious in temperate regions and upland condition. Stresses caused by low temperature in temperate areas and moisture stress under upland conditions increase the vulnerability of the crop to blast disease attack. During the last 30 years, there were three outbreaks of blast in China; 1982–1985, 1992–1994, and 2001–2005. The average blast infected area was more than 3.8 million hectares in 1982–1985 with yield losses of several million tons (Sun et al. 1999). In 1993, yield loss of 1.1 million tons was recorded in Southern China alone. In recent years 5.7 million hectares of rice fields were affected by the blast disease.

Blast disease is a major constraint in certain agro-ecological regions of India. Eastern India has the highest occurrence of blast followed by North and South. Sometimes yield losses reach as high as 50% in upland conditions (Widawsky and O'Toole 1990). Production oriented survey is organized by Directorate of Rice Research, Hyderabad every year to document constraints to rice production in various parts of the country. Multidisciplinary teams of scientists survey the crop in the 125 districts of the country. About 15% of the districts surveyed during 2001–2005 had severe blast disease. Eastern India had the highest incidence of blast over 12-year period. Hill districts of Himachal Pradesh, Uttaranchal, and Jammu and Kashmir with cool climate generally have higher incidence of blast (Variar 2007).

The cool temperate climate of Japan is highly conducive to the multiplication and spread of the blast fungus during the rice growing season. Even though breeding for blast resistance has been emphasized in Japan since the beginning of last century and a number of genes for blast resistance have been introduced in Japanese varieties. Frequent breakdown of resistance results in significant yield losses ranging from 20–100% in some areas. In 1993 exceptionally cool weather resulted in blast epidemic.

Nation wide yield loss that year was 45.2% due to blast damage and sterility caused by low temperature and Japan was forced to import large quantities of rice from abroad.

South Korea with temperate climate is another country where blast disease causes yield losses every year. During the blast epidemic of 1984–1985 almost 20% of the rice area was seriously blasted.

In Indonesia 1.1 million hectares are planted to upland rice where blast is a serious problem. Upland rice varieties become susceptible within one to two years of their cultivation. Yield losses will be as high as 100% during certain years. In 2004 several hundred hectares of upland rice in Lampung province could not be harvested due to blast damage and yield losses up to 70% were recorded in upland areas of West Java (Sobrizal et al. 2007).

### 3 Genetics of Resistance

Studies on inheritance of resistance were first reported in 1922 by Sasaki followed by Takahashi (1965) and Yamasaki and Kiyosawa (1966). Up to 1960 the inheritance was studied without sufficient knowledge of the pathogenic specialization of the causal fungus, and it was quite difficult to obtain universal understanding of the subject. Systematic studies were undertaken only after Goto (1965) established the differential system for blast fungus races in Japan.

Kiyosawa and his colleagues used seven Japanese strains of blast fungus for investigating the inheritance of resistance and identified 13 genes for resistance (Kiyosawa 1981). These were designated as *Pi-a*, *Pi-i*, *Pi-k<sup>s</sup>*, *Pi-k*, *Pi-z*, *Pi-ta*, *Pi-ta<sup>2</sup>*, *Pi-z<sup>t</sup>*, *Pi-k<sup>p</sup>*, *Pi-k<sup>m</sup>*, *Pi-k<sup>n</sup>*, *Pi-b*, and *Pi-t*. With the establishment of Rice Genetic Cooperative in 1985, rules for gene symbolization in rice were standardized and it was decided to assign gene symbols derived from names which describe the character modifications. The genes that are non-allelic but are indistinguishable from each other phenotypically, are designated by the same base letter but are differentiated by a number or a letter subscript separated by a hyphen (Kinoshita 1986). Since then several genes for resistance have been designated by base letter followed by a number subscript starting with *Pi-1*, *Pi-2* (Mackill and Bonman 1992) and so on up to *Pi-44*.

During the third International Rice Genetics Symposium held at Manila on the October 16–19, 1995, it was decided to remove the hyphen between the base letter and subscript. Henceforth, the gene symbols have been written as *Pia*, *Pita*, *Pik*, *Pil*, *Pi2* etc.

During the past 25 years great advances have been made in studying the genetics of resistance to the blast disease. Following conventional genetic analysis of identified donors with resistance, availability of pure isolates of the blast pathogen and use of advanced molecular analysis techniques, about 60 genes for resistance have been identified. These have been designated as *Pi1*, *Pi2*, *Pi3*, *Pi4*, *Pi5*, *Pi6*, *Pi7*, *Pi9*, *Pi10* and *Pi11* (Causse et al. 1994, Wang et al. 1994), *Pia*, *Pib*, *Pik*, *Pit*, *Pita*, *Pita<sup>2</sup>*,

*Pi12*, *Pi17*, *Pi18*, *Pi19*, *Pi20*, *Pi23*, *Pi57*, *Pi62* (Nagato and Yoshimura 1998), *Pii* and *Pi15* (Pan et al. 2003), *pi21* (Fukuoka and Okuno 2001), *Pi25* (Yang et al. 2001), *Pi27* (Zhu et al. 2004), *Pi24*, *Pi25*, *Pi26*, *Pi27*, *Pi28*, *Pi29*, *Pi30*, *Pi31* and *Pi32* (Sallaud et al. 2003), *Pi33* (Berruyer et al. 2003), *Pish* (Fukuta et al. 2004), *Pi35* (Nguyen et al. 2006), *Pi36* (Liu et al. 2005), *Pi37* (Chen et al. 2005), *Pi38* (Gowda et al. 2006), *Pi39* (Liu et al. 2007) and *Pi40* (Jeung et al. 2007).

With the advent of molecular markers various genes for blast resistance have been located to specific chromosomes. For example *Pi2* and *Pi4* have been located on chromosome 6 and 12 respectively via linkage with RFLP markers (Yu et al. 1991). Near-isogenic lines (NILs) were used for genetic mapping by dissecting complex genotypes and evaluating the effect of individual genes in a common genetic background. By using a pair of NILs, *Pi1* was located on chromosome 1 and *Pita* on chromosome 12 (Yu et al. 1996). Near-isogenic lines with single genes for resistance have been developed in the genetic backgrounds of the indica variety CO39, Japonica variety Lijiangxintuanheigu (LTH) and a universal susceptible line US2. These isogenic lines developed at IRRI through a collaborative project between IRRI and Japan International Research Center for Agricultural Sciences (JIRCAS) (Kobayashi et al. 2007) are very useful for identification of the blast races, identifying genes for blast resistance in donors and for monitoring the shift in blast races.

A mapping population developed at IRRI from a cross between IR64 and Azucena has been used world wide for mapping genes for blast resistance. Sallaud et al. (2003) identified nine genes derived from IR64. Recombinant inbred lines (RILs) have been used for mapping four major QTLs for the blast resistance via linkage to RFLP markers (Tabien et al. 2000). Simple sequence repeats (SSR) markers have been used for fine mapping the *Pik<sup>h</sup>* gene which confers resistance to the blast races of Northwestern Himalayan region of India (Sharma et al. 2005). The genes *Pi3* and *Pi5* were found to be located on chromosome 9 via their linkage to AFLP markers (Jeon et al. 2003). Single nucleotide polymorphism (SNP) markers have been employed for fine mapping the *Piz* locus (Hayashi et al. 2004). The resistance gene, *Pi39* from Chinese variety, Q15 has been fine mapped on chromosome 12 (Liu et al. 2007). More recently a novel gene, *Pi40* from the breeding line IR65482-4-136-2-2 with strong resistance to Korean and Philippine blast isolates was mapped on the short arm of chromosome 6 (Jeung et al. 2007).

Advances in molecular genetics and completion of the genome sequence of rice paved the way for cloning and characterization of seven major genes for blast resistance. These are *Pib* (Wang et al. 1999), *Pita* (Bryan et al. 2000), *Pi9* (Qu et al. 2006), *Pi2*, and *Piz<sup>t</sup>* (Zhou et al. 2006), *Pid2* (Chen et al. 2006) and *Pi36* (Liu et al. 2007). All the cloned resistance genes belong to the NBS-LRR class of R genes except *Pid2* which encodes a receptor-like kinase protein with a predicted extra-cellular domain of bulb type manose specific binding lectin (B-lectin) and an intracellular serine threonine kinase domain. The several R genes for the blast resistance, the genes located at *Piz*, *Pik*, and *Pita* loci on chromosome 6, 11, and 12 respectively are clustered with a similar allelic expression for resistance (Monosi et al. 2004).

## 4 Breeding for Resistance to Blast

Efforts have been made to develop rice varieties with blast resistance since the beginning of rice improvement programs particularly in Japan. Major genes for blast resistance have been utilized in many breeding programs. These genes are easier to move from one varietal background to the other. Thus *Pib*, *Pita*, *Pia*, *Pi1*, *Pik<sup>h</sup>*, *Pi2* and *Pi4* have been introduced into rice varieties through conventional breeding programs. In recent years MAS has been employed for transferring *Pita* (Rybka et al. 1997), *Pi1*, *Pi9* (Du et al. 2007), *Piz* (Conaway-Bormans et al. 2003), *Pi35* (Nguyen et al. 2006) and *Pi37* (Chen et al. 2005) to new varieties.

Insufficient durability of monogenic blast resistance is a serious problem especially in upland rice and temperate irrigated rice. Several blast resistant varieties are released by rice breeding programs and adopted by farmers only to lose their resistance within a few years because of the adaptation of the blast pathogen. The loss of resistance has been most striking and well documented (Kiyosawa 1982; Koizumi 2007).

Several breeding strategies have been suggested for prolonging the durability of resistance. These include; (1) multiline varieties, (2) varietal mixtures, (3) pyramiding of major genes for resistance and (4) breeding for quantitative or partial resistance based on minor genes or QTLs. Multiline approach was first suggested by Borlaug (1959) for developing wheat varieties with resistance to rust and implemented by Browning and Frey (1969) for control of crown rust of Oats. This approach has not been tried by rice breeders. The durability of resistance of multiline varieties would depend on the rate at which the blast races develop, the number of component lines in a mixture and the extent of area planted to multiline varieties. Another strategy for slowing the development of the blast races is the varietal mixtures consisting of 80–90% resistant plants and 10–20% susceptible plants of similar varietal background. Varietal mixtures are easy to introduce but their agronomic uniformity have to be assured. A variation of this approach was tried in Yunan province of Southeast China. Highly susceptible glutinous plants were mixed planted with non-glutinous hybrid indica rice. The mixtures reduced blast development on glutinous rice and were deployed on about 1 million hectare in 2004 (Leung et al. 2003; Zhu et al. 2005). For the varietal mixtures interplanting 1 row of taller glutinous rice varieties for every 4–6 rows of hybrid indica rice was planted. However, the inter-planting patterns have been decided empirically while reduced leaf wetness is supposed to be a substantial contributor to panicle blast control in mixtures (Zhu et al. 2005).

The quantitative or polygenic resistance is governed by a large number of genes also called QTL each with a small contribution to resistance. The level of resistance is generally not very high. So it does not exert strong selection pressure on the pathogen. The gene for gene relationship does not exist between the QTL for resistance and the pathogenic races (Robinson 1980). However, there are practical difficulties in incorporating QTLs in high yielding agronomically acceptable background. Parents with QTLs are generally land races with poor agronomic traits. In the process of selecting plants with better agronomic traits involving such traits,

not all QTL are transferred. This problem can be overcome by tagging the QTLs with molecular markers and accumulating the QTLs through MAS. Another problem is that many of the techniques employed in screening segregating progenies usually favor the selection of genotypes with high level of resistance conditioned by major genes.

In the rice breeding program at IRRI the emphasis was on the incorporation of quantitative resistance. For this purpose segregating populations were evaluated in the blast nursery where numerous races of the blast pathogen were present. Screening started with  $F_2$  generation.  $F_2$  populations were planted in the blast nursery. Seedlings with a high level of resistance and those that were highly susceptible were discarded. Only those with an intermediate score of 3–4 on a scale of 1–9, were selected and planted in  $F_3$  nursery. Breeding lines were continuously screened in subsequent generations by planting in the blast nursery and only those with moderate level of resistance were advanced to the next generation. Thus through evaluation for the blast resistance for at least 6–7 generations in blast nursery lines with moderate level of resistance presumably governed by polygenes were selected (Khush and Virk 2005). Although we did not try to incorporate major genes intentionally, genetic analysis had shown that IR varieties also have a few major genes for resistance (Imbe et al. 2000; Ebron et al. 2004). Since we used diverse parents in our hybridization program and some of these parents have major genes, these genes were selected because of the presence of compatible races of blast pathogen in the blast nursery. Through this process of hybridization and selection major as well as polygenes were combined in most of the IR varieties. IR varieties have been grown widely under irrigated conditions and have not suffered any major damage from blast. Only exception is IR50 which has shown blast susceptibility at a few locations and obviously lacks QTLs for resistance. Both IR36 and IR50 have major genes *Pita* and *Pib* (Imbe et al. 2000). But IR36 has shown durable resistance. It was grown to almost 11 million hectares during 1980s and is still popular in several areas. The durable resistance of IR36 is expressed through a reduction in lesion size and number (Bonman et al. 1992).

One of the complications encountered in breeding for blast resistance is that selection is most easily made based on observation of leaf blast, while the infection of greatest economic importance occurs on the panicle and panicle neck node. Panicle blast resistance is difficult to measure because the occurrence of panicle infection is influenced by weather, and even small differences in maturity between lines can result in inaccurate assessment of their level of resistance. There is, however, a correlation between partial resistance to leaf blast and partial resistance to panicle blast with a few exceptional varieties being susceptible to leaf blast yet resistant to panicle blast (Bonman et al. 1989).

## 5 Future Prospects

For several years gene symbols for blast resistance were monitored by a committee established by Rice Genetics Cooperative. However, during recent years rules for assigning gene symbols have not been followed strictly by all authors. Note for

example gene symbols *Pitq*<sup>5</sup>, *Pitq*<sup>6</sup> for genes from variety Teqing or *PiCO39(t)* from rice variety CO39 as well as *PiD1* and *PiD2* from rice variety Degu (cf. Table 1 in Koizumi 2007). These gene symbols are invalid. Another problem is that although more than 60 genes have been described, allelic relationships of many of them have not been investigated. Several of them are likely allelic and the actual number is probably much lower.

There is also some confusion regarding the distinction between major genes and QTLs. What are the criteria for distinguishing between the two? Some major genes for resistance have been referred as QTL by other authors. How do you assign gene symbols for QTLs distinct from major genes? Since rice blast workers meet on regular intervals a committee should be appointed for monitoring symbolization of genes for the blast resistance. Whenever, a new gene is discovered, the chairman of the committee should be consulted for assigning gene symbol. The committee should also encourage the studies on determination of allelic relationships of already described genes as well as new genes

Remarkable progress has been made in identifying and tagging of blast resistance genes with molecular markers. Almost all the genes identified to date are for leaf blast resistance. However, neck blast is more important. Therefore, efforts should be made to identify and tag genes for resistance to neck blast. Breeding for neck blast resistance will then become feasible.

Rice breeders now have a number of genes for resistance to work with. However, most of the breeding programs have emphasized monogenic resistance. Since many of the genes have now been tagged with molecular markers, it should be feasible to pyramid several genes into improved varieties. Useful life of such varieties would be considerable as exemplified by IR64. The variety IR64 has at least five genes for blast resistance and has shown durable resistance for the last 20 years.

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