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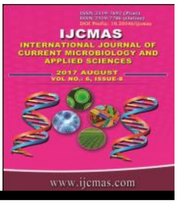

Review Article

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Rice Blast: Different Aspects of Breeding to Achieve Durable Resistance

Namrata[1]*, Prashant Bisen[1], Bhumica Singh[2], Padma Thakur[1] and Bapsila Loitongbam[1]

[1]Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, 221005, India
[2]Department of Molecular Biology and Biotechnology, Rajasthan College of Agriculture, MPUAT, Udaipur, India
**Corresponding author*

ABSTRACT

Keywords

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Rice is staple food for more than half of the world's population. The fast growth of the world population demands an increase of 26 % in rice production to fulfill the requirement. The rice blast caused by *Magnaporthe oryzae* is considered to be the most significant and potentially damaging rice disease in the world and has been responsible for 35 to 50 % global loss in rice yield causing serious constraint in global food supply. High genetic variability of rice blast pathogen *Magnaporthe oryzae* gives challenge to plant breeders for breeding durable resistant varieties against blast because frequent breakdown of resistance cause yield instability in several rice growing areas. This review includes the different types of strategies used and role of molecular marker assisted breeding for improving durable resistance in rice for blast disease.

Introduction

Rice is a primary food source for more than half of the world's population. The fast growth of the world population demands an increase of 26 % in rice production to fulfill the requirement (Khush, 2013). Rice production has widely increased after the green revolution, but the yield of superior varieties is still not increasing as farmer's expectations due to the influence of biotic and abiotic factors (Divya *et al.*, 2014). The rice blast caused by *Magnaporthe oryzae* is considered to be the most significant and potentially damaging rice disease in the world (Latif *et al.*, 2011), reported in more than 85 countries and has been responsible for 35 to 50 % global loss in rice yield (Padmavathi *et al.*, 2005). Even, if it is causing only 10 % losses than we are losing rice which is being sufficient to feed 60 million people for one year (Kato, 2001). Blast was first reported in India in 1918, at Tanjore Delta of Tamil Nadu state (Madras) causing a yield loss of 69 per cent. It is highly adaptable to environmental conditions and can be found in irrigated lowland, rain-fed upland, or deepwater rice fields (Rao, 1992). The disease results in yield loss as high as 70-80 per cent (Ou, 1985) when predisposition factors (high mean temperature values, degree of relative humidity higher than 85-89 per cent presence of dew, drought stress and excessive nitrogen fertilization) favor epidemic development

(Piotti *et al.*, 2005), blast fungus complex comprises many phylogenetic species (Couch, 2005) that can infect some 50 grass and sedge species which includes rice (*Oryza sativa*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), maize (*Zea mays*), oats (*Avena sativa*), rye (*Secale cereale*), finger millet (*Eleusine corocana*), perennial ryegrass (*Lolium perenne*) and weed and ornamental grasses (Ou, 1987). Blast can affect all above ground parts of a rice plant: leaf, collar, node, neck, parts of panicle, and sometimes leaf sheath.

A leaf blast infection can kill seedlings or plants up to the tillering stage. At later growth stages, a severe leaf blast infection reduces leaf area for grain fill, reducing grain yield. Leaf blast can kill rice plants at seedling stage and cause yield losses in cases of severe infection while neck and nodel blast is seems more destructive at farmers field because it causes severe direct loss in yield by causing prevention of nutrient supply to the grain and producing unfilled chaffy panicles. Thus, blast disease is considered as a serious constraint in not only rice but also in cereal crop production in India and at the global level. High genetic variability in *M. oryzae* isolates poses a major challenge to rice breeders and pathologists for controlling the blast disease.

Progress in research on the molecular studies enable researchers to develop concepts of QTLs mapping, gene identification and their introgression in elite rice varieties through marker assisted selection (MAS) and genome of *M. oryzae* strain 70-15 was also sequenced among plant pathogenic fungi using Sanger sequencing method (Dean *et al.*, 2005). The analysis of genetic variation in plant pathogen populations is an important pre-requisite for understanding coevolution in the plant patho-system (McDonald *et al.*, 1989).

Breeding for blast resistance in rice

Economically sound and environmental friendly approach for blast management in rice is to breed for durable resistant rice cultivars which is achieved through use of one or in combination of the following strategies-

i. Cultivar-specific resistance.
ii. Lineage-specific resistance and gene pyramiding.
iii. Broad-spectrum resistance.
iv. Partial resistance.
v. Cultivar mixtures and Near Isogenic Lines(NILs)

Cultivar specific resistance

It is cost-effective and preferred means of managing rice blast disease to resource-poor farmers by deployment of high-yielding rice cultivars carrying single dominant disease resistance (R) genes and operate via a classical gene-for-gene interaction means it is providing resistance to a single dominant avirulence gene (AVR) present in the pathogen strain. But, this type of resistance is short lived and often broken within 2-3 successive years (Bonman *et al.*, 1992). This type of breakage is occurring mostly in those areas where single variety is cultivated in large acreages, here a large selection pressure is act upon the pathogen and cause a race shift towards such isolates that can escape host recognition (Bonman, 1992). Breakage of this type of vertical resistance causes outbreak of epidemics in large areas growing single popular variety.

Lineage specific resistance and gene pyramiding

The concept of this blast management strategy is based on the lineage-exclusion hypothesis (Zeigler *et al.*, 1995). According to which rice blast populations comprise sets of geographically discrete clonal lineages with different virulence spectrum and there is no gene flow among them, also the deployed resistance for them in specific lineage is associated with a fungal fitness cost, if avirulence is lost. The concept of this hypothesis is not fully supported because it thought to be largely observation derived (Zeigler *et al.,* 1995). Although, this is not proven for all rice blast AVR genes isolated but it has been exploited in rice-blast hot-spots in Southern India and Thailand (Gnanamanickam *et al.,* 2000).

Gene pyramiding refers to the stacking of several resistance genes into a single culivar so selection pressure on a single blast isolate is reduced (Bonaman *et al.*, 1992; Hittlamani *et al.,* 2000). Now a days, it is broadly used for combining multiple disease or pest resistance genes for specific races of a pathogen or insect to develop durable resistance. It’s use in crop improvement programs reduces the breeding duration and combining different resistance genes increase the durability against a number of races or isolates, also for more than one character in a variety at the same time. Pyramided lines carrying the major R gene combinations Pi1+Piz-5 and Pi1+Piz-5+Pi-ta has been proven to broaden the resistance spectrum of each individual gene in both India and the Philippines (Hittlamani *et al.*, 2000).

Broad spectrum resistance

It is also widely adopted strategy to lessen the risk of resistance gene breakdown by deployment of rice broad-spectrum resistance genes which provide resistance against almost all isolates of pathogen present at that time. Such genes reported resistance to different strains of the fungus (Bonman *et al.,* 1992; Dai *et al.,* 2007). The durability of these introgressed genes must be evaluated. More than 100 major genes have been identified and mapped for blast resistance in the rice genome (Sharma *et al.*, 2012; Ashkani *et al.*, 2014). Out of them 22 *resistance* genes have been successfully cloned and molecularly characterized. They are widely introgressed into popular elite rice varieties and breeding lines. For example- Lines carrying the first cloned rice blast broad-spectrum resistance gene, Pi9 were highly resistant to 43 isolates collected from 13 countries (Qu *et al.*, 2006). Another line carrying resistance gene Pi2 confers resistance to 455 *M. oryzae* isolates from different regions in the Philippines and around 792 isolates from 13 important rice-growing regions in China (Chen *et al.,* 1996). This strategy is proven to be most environmental friendly and economically sound for controlling rice blast.

Due to its importance, extensive research programs are underway to identify and characterize further broad-spectrum resistance genes, specially genes present in native varieties are widely used and also broad spectrum resistance genes being successfully transferred into elite rice varieties from wild species. For example- *Pi-9* gene that present in indica rice line 75-1-127 (Liu *et al.*, 2002), was introgressed from a wild species *O. minuta* of rice (Amante-Bordeos *et al.*, 1992).

Partial resistance

It refers to the incomplete, quantitative resistance controlled by more than one recessive gene. It suppresses the growth and reproduction of *M. oryzae*, but it can cause disease when environment is conducive for blast so, it is more suited to low risk areas only. Quantitative resistance by quantitative trait loci (QTLs) are reported to durable for long time against a wide-range of pathogens, promising for sustainable rice production in the future (Song and Goodman, 2001). Although based on this statement much effort has been made to accumulate polygenic traits expressed as quantitative trait loci (QTLs) (Bonman *et al.*, 1992). But now, by meta analysis of QTLs, it is reported that partial rice blast resistance is generally not more broad-spectrum and, by inference, not more durable than complete resistance conferred by isolate-specific genes (Ballini *et al.*, 2008). So, breeding only for partial resistance is not advocated solely.

The first publication of a QTL analysis of rice resistant to blast in 1994 (Wang *et al.*, 1994), after that several QTLs related to blast resistance have been detected and published for different populations grown in different environments.

Cultivar mixtures and Near Isogenic Lines (NILs)

To reduce the rapid evolution and emergence of new virulent *M. oryzae* field strains, planting cultivar mixtures, consisting of 80–90 % resistant plants and 10–20 % susceptible plants of similar varietal background is an effective strategy. Mixtures of hybrid, blast resistant rice and glutinous, blast-susceptible cultivars can be used after ensuring their agronomical uniformity (Zhu *et al.*, 2000).

Alternatively, rice multilines or we can say mixture of near isogenic lines can be planted to offset breakdown of blast resistance, for example- Multiple line variety of ‘‘Sasanishiki’’ has been commercially cultivated on a market scale since 1995. Blast control effects by the use of multiple line varieties have been confirmed by scientists (Ise K. 1990; Koizumi and Fuji. 1994; Koizumi *et al.*, 1996; Nakajima *et al.*, 1996). Moreover, new isogenic lines have been bred and elaborated variation analysis in the distribution of the races of the blast pathogen, which is essential for stable utilization (Tsuji *et al.*, 1999; Ashizawa *et al.*, 2001).

Role of molecular assisted breeding programs for improvement of blast disease improvement

Use of molecular markers and new sequencing tools provide valuable informations for the discovery, validation and assessment of genetic diversity present in populations (Sahebi *et al.*, 2015). The analysis of genome and characterization of rice–blast fungus *Magnaporthae oryzae* by means of molecular and bioinformatics developments allow to understand genetic diversity present and to track the emergence of virulent pathotypes (Gowda *et al.*, 2015; Srivastava *et al.*, 2014). The whole genome sequence data also enhanced the efficiency of polymorphic marker development for QTL fine mapping and the identification of possible candidate genes (Wan *et al.*, 2006). These performances are very important for breeding of rice cultivars.

DNA markers techniques provide us a tool to select for the existence of multiple blast resistance genes without the need to test the progeny or in exact phenotypic disease screening (Fjellstrom *et al.*, 2004). Through molecular tools many useful markers linked to the race-specific blast resistance genes (*Pi*-genes), has been identified and screened in segregating populations and at an early stage in rice (Hittalmani *et al.*, 2002; Fjellstrom *et al.*, 2004; Sharma *et al.*,2005; Ashkani *et al.*, 2011; Ashkani *et al.*, 2012). Marker assisted Backcrossing (MABC) is now playing a very important role for the development of blast-resistant cultivars (Sundaram *et al.*, 2009) and have many advantages over conventional backcrossing in terms of time, precision, efficiency, consistency and biosafty, application of MAS and MABC for the improvement of rice have been reviewed and described (Collard and Mackill, 2008; Hasan *et al.*, 2015). MABC based gene pyramiding could facilitate in pyramiding of genes effectively into a single genetic background (Joshi and Nayak, 2010).

The availability of whole genome sequence of rice and bioinformatic tools have made it possible to mine allelic diversity throughout rice germplasm. Allele mining refers to a technique of identifying novel alleles or allelic variants of a gene/or candidate genes of interest, based on the available information about the genes, from a wide range of germplasm. The success of allele mining mainly depends on genetic materials used for screening and availability of genome sequence information of a particular crop species. For efficient allele mining, wild relatives and local landraces are being used because they are reservoirs of useful alleles hidden in their phenotype (Tanksley *et al.*, 1996).

Conclusion and future prospects

According to the Blast disease scenario genome analysis of multiple lineages of *Magnaporthae oryzae* present in various cropping zones of the world and allele mining of wild relatives, local landraces, cultivated varieties as well as all available genetic resources is required for understanding the evolution of the pathogen and to identify the durable novel genes for blast resistance in rice. Based on this knowledge for development of durable resistant varieties there is need of incorporating novel genes into the improved germplasm as well as using the best suited combination of major resistance genes and QTLs which will be definitely proved to be economical, environmentally friendly and effective to control the rice blast disease.

Use of new molecular approaches like MAS, MABC, Gene pyramiding, Allele mining, Genome analysis techniques, Functional genomics and DNA microarray technique can help us in clearly understanding the rice-pathogen interactions and provide us tools for effective control of rice blast.

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