

## Review Article

<https://doi.org/10.20546/ijcmas.2018.705.243>

## Mapping and Deployment of Blast Resistance Gene in Rice – A Work in Progress

Ashim Debnath\*, Karma Landup Bhutia and Hage Sumpi

School of Crop improvement, College of Post Graduate Studies, Central Agricultural  
University (Imphal), Umiam, Pin: 793103, Meghalaya, India

\*Corresponding author

### ABSTRACT

#### Keywords

Blast (*Magnaporthe oryzae*), Resistance genes, Quantitative trait loci, Cloned genes, Marker assisted selection

#### Article Info

##### Accepted:

16 April 2018

##### Available Online:

10 May 2018

Rice (*Oryza sativa*) plays a significant role in global food security. Various biotic and abiotic stresses limit rice production. Among the various biotic stress, rice blast caused by *Magnaporthe oryzae* is one of the most ruinous disease in all rice growing regions of the world. Use of resistant genes and quantitative resistance conferred by quantitative trait loci (QTLs) is the best option for management of blast. More than 100 blast resistance genes and a large number of QTLs (more than 350) were identified and mapped in different rice genotypes, but only 22 genes have been cloned and characterized at the molecular level. The genetic dissection of cloned genes revealed that the largest class of R-genes encodes nucleotide-binding, leucine-rich repeat (NBS-LRR) proteins. Gene pyramiding with marker assisted selection helps us to introgress more than one gene for blast resistance into a susceptible background. In this review, we extensively summarize the reported resistance gene information for rice blast along with their selection markers. We also focus on the reports of mapping and deployment of blast resistance with MAS and gene pyramiding. This update information will be helpful in rice breeding programmes to develop durable blast resistant rice variety through marker assisted selection.

### Introduction

Rice (*Oryza sativa*) is one of the major foods for more than 50% of the world's population. The rice consumer is increasing and demand for rice is also moving up at an alarming rate. Rice production needs to increase more than 40% by 2030 to meet the increase demand for rice (Kush, 2005). The yield potentiality of rice is 10 ton<sup>-1</sup>, whereas farmers on an average harvest about 5 ton<sup>-1</sup> (Kush and Jena, 2009). Various biotic and abiotic stress limit rice production which ultimately leads to this yield

difference. Among the biotic stress, rice blast caused by *Magnaporthe oryzae* ranked first in the ten most important fungal pathogen explained in the journal of Molecular Plant Pathology. The economic importance of *M. oryzae*; with over one-half of the world's population relying on rice as the main source of calories, this pathogen can have destructive effects; however this pathogen has evolved into a seminal model system for the study of plant–pathogen interactions (Dean *et al.*, 2012). The pathogen is most usual on leaves, causing leaf blast during the vegetative stage,

or on nodes, neck and panicle branches during the reproductive stage, causing node and neck blast, respectively. The amount of rice destroyed by blast annually is sufficient to give food to 60 million people worldwide (Parker *et al.*, 2008). Leaf blast lesions decrease the net photosynthetic rate of individual leaves to an extent far beyond the visible diseased leaf fraction. Neck blast is considered the most destructive phase of the disease and can occur without being introduced by severe leaf blast (Zhu *et al.*, 2005). Neck blast causes direct yield reduction, since filling of the grains on infected panicles is poor at best. That is why neck blast is the more serious phase of the blast disease (Khan *et al.*, 2014).

Different fungicides can be used to control blast disease but they generate additional costs in rice production and chemical contamination of environment and food items. Therefore strategies for increase in yield in an environmentally sustainable and economical manner need to be implemented urgently. Although host resistance is the most economically viable and environmentally sustainable practice to manage blast disease, the fungus overcomes blast resistance quickly, and cultivars typically become susceptible to disease within 2–3 years. Knowledge of the biology, adaptability and genetic diversity of the blast pathogen is vital for the development of novel and durable strategies to manage this and related devastating fungal diseases. The use of resistant varieties is thought to be one of the most economical and environment friendly ways of crop protection from the disease. The pyramiding of resistant genes or allocate them with multigenic resistance is an efficient way to manage blast disease. Accordingly, different molecular techniques such as QTL analysis, molecular mapping, gene cloning, map-based cloning, marker-assisted selection (MAS) have been introduced to analyse the blast resistant genes

in the rice genome (Miah *et al.*, 2013). With a shorter period of time MAS offer better selection strategies in rice breeding. MAS are more efficient, effective and reliable as compare with phenotypic selection. Although MAS is not the only solution of all problem in resistance breeding but it is a promising approach to conventional breeding. Considerable progress has been done for rice blast disease towards cloning and identification of resistance genes, characterization of defense responses and elucidation of signal transduction which ultimately activate different defense responses. MAS help in transferring blast resistance genes to different genetic backgrounds at an early stage with greater accuracy (Gu *et al.*, 2005). The ability to conduct genetic analyses led to the cloning and characterization of several genes for host and cultivar specificity. Today, much attention is given on cloning and characterizing many avirulence and corresponding rice resistance genes that have been genetically identified. Development of broad spectrum and durable blast resistant varieties is essential for combating this devastating disease, which requires continuous efforts of breeders and pathologists. Wild species of *Oryza* can be utilized to widen the gene pool of rice for biotic and abiotic stress. Various studies have demonstrated that wild species serve as a source of hidden gene(s) which can be used for crop improvement (Zhang and Xie, 2014) and yield enhancing QTLs from various wild species (Linh *et al.*, 2008; Rangel *et al.*, 2008).

### **Blast resistance genes and sources**

The genus *Oryza* consists of two cultivated and 21 wild species. Two cultivated species, *O. sativa* and *O. glaberrima*, and six wild species, *O. rufipogon*, *O. nivara*, *O. glumaepatula*, *O. meridionalis*, *O. breviligulata*, and *O. longistaminata* have

been grouped into a primary gene pool based on the transfer ability of genes (Sharma *et al.*, 2012). Rice has domesticated almost 9000 years ago and during the period of domestication rice plant has been subjected to selection both by naturally and artificially which ultimately led to the reduction of diversity in the present rice species. Human selection process favoured the agronomically suitable characters over those of less cultivated species and wild relatives. This selection process for long period of time lead to more uniformity in the cultivated rice lines than wild relatives and land races. So the genetic base has been narrowed down due to the more uniformity in the cultivated rice which ultimately helps plant pathogen for better survival. The large source of genetic pool, land races and some cultivated rice germplasms were left unexplored.

In rice breeding, breeders have successfully taken many genes from wild species for useful trait like blast resistance. Wild rice, *O. rufipogon* has been reported to be a potential source for blast resistance genes (Rathour *et al.*, 2005). Ram *et al.*, (2007) reported the introgression of broad spectrum blast resistance gene(s) from *Oryza rufipogon* into indica rice cultivar. Blast resistance gene Pi9 from *Oryza minuta* (Sharma *et al.*, 2012), Pif2-1(t) from wild rice *O. rufipogon* (Dwinita *et al.*, 2008) and Pi-40(t) from *Oryza eaustaliensis* (Jeung *et al.*, 2007) also been isolated. After considering the vast genetic diversity of rice, there is still so much potential to use the rice germplasm for the improvement of traits like blast resistance.

Rice blast disease resistance genes were first described in 1923 by Sasaki in Japan. Pi-a, the first blast resistance gene in rice was designated by Kiyosawa (Kiyosawa, 1966). Till now more than 100 blast resistance gene has been identified and their chromosomal locations and selection markers have been

reported in different rice cultivars. Of the 100 blast resistance genes identified, these genes have different origins, and each was identified in different donor rice cultivars and also in wild rice species (Table 1). Out of the total identified resistance genes, 45% are from Japonica cultivars, and 51% from indica cultivars and the remaining 4% are from wild species of rice (Sharma *et al.*, 2012).

From the tabular representation (Table 1) of different blast resistance gene, we can clearly observe that most of the R genes were detected on chromosome 11, 12 and 6. Chromosome 11, with the maximum number of resistance genes, with at least 30 genes and alleles (Pik-h, Pi-hk1, Pi54, Pi-1(t), Pb1, Pise1, Pikur2, Pi 38, Pik,Pif, Pi34, Pia, Mpiz, Piisi, PiCO39(t), Pilm2, Pi30(t), Pi7(t), Pi44(t), Pi49, Pik-m, Pik-p, Pik-s, Pi47, Pig, Pi60(t), Pi-1(t), Pi1 and PBR), chromosome 12 have atleast 23 number of resistance genes and alleles (Pi24(t), Pi-42(t), Pi51(t), Pi62(t), Pi6(t), Pi12(t), Pi4(t), Pi32(t), Pi31(t), Ipi(t), IPI3(t), Pita-2, Pi19(t), Pi21(t), Pita, Pi58(t), Pi39(t), Pi-GD-3(t), Pi20(t), Pi-tq6, Pi48, Pi61(t), Pi157) and chromosome 6 have 19 number of genes and alleles (Pigm(t), Pi22(t), Pi26, Pi27(t), Piz-5, Pi8, Pi13(t), Pi40(t), Pi59(t), Pi9, Pi2-2, Pi50(t)). Although numbers are less but R genes were also detected for blast resistance in all other chromosomes except chromosome number 3.

### **QTL mapping for blast resistance in rice**

Disease resistance traits are controlled by many genes which are known as polygenes or quantitative trait loci (QTLs). Molecular marker such as RFLP, AFLP, SSR, SNP and EST are commonly used to map QTLs (Langridge *et al.*, 2001). Basically there are four approaches for QTL mapping such as single marker analysis (SMA), simple or standard interval mapping (SIM), composite interval mapping (CIM) and multiple interval

mapping (MIM). SMA method has been used for the first time in the identification of QTLs for rice blast resistance in cv. Moroberekan, a Japonica rice cultivar (Wang *et al.*, 1994). In SMA method on the basis of the genotype at every marker locus, the mapping population is divided into classes and finally the QTL has been distinguished if significant differences in the overall mean phenotypic score are found for every group (Melchinger *et al.*, 1998). SIM method is more efficient than SMA where at each locus; a flanking marker is used between two marker intervals. The main disadvantage of SIM is the identification of sometimes false QTLs because of linked and unlinked QTLs. Standard interval mapping was used for QTL analysis and mapping of blast resistance gene *pi21* in Owarihatamochi, a Japanese upland rice cultivar (Fukuoka and Okuno, 2001).

The third approach, the composite interval mapping, is frequently used. Here, subsets of markers are used at both linked and unlinked QTLs. The CIM method is used for the identification of interaction of QTLs and marker information increases the power of QTL detection. The fourth approach, multiple interval mapping has higher precision for determining the combined effects of individual QTLs. To map the QTLs, multiple marker intervals are used in MIM method to fit various putative QTLs directly into the model.

More than 350 QTLs for leaf blast resistance have been mapped on different chromosomes, which are mainly derived from japonica indica crosses of 15 different populations (Wu *et al.*, 2005; Ballini *et al.*, 2008). The 23 blast resistance loci found within the above mentioned QTL regions are *Pi24(t)*, *Pi35(t)*, *Pitq5*, *Pi25(t)*, *pi21*, *Pi26(t)*, *Pi27(t)*, *Pi25(t)*, *Pitq1*, *Pizh*, *Pi29(t)*, *PiGD-1(t)*, *Pi28(t)*, *PiGD-2(t)*, *Pilm2*, *Pi30(t)*, *Pi7(t)*, *Pi34*, *Pi24(t)*, *Pitq6*, *Pi31(t)*, *Pi32(t)*, *PiGD-3(t)* (Fukuoka *et al.*, 2014).

### **Molecular mapping of blast resistance genes**

By crossing a japonica variety (Nipponbare) with an indica variety (Kasalath) a population of 186 F<sub>2</sub> individuals was generated which was used for the construction of rice genetic map. With the use of Restriction Fragment Length Polymorphism (RFLP) markers, construction of the rice genetic map started in 1997 and further saturation of RFLP mapping was done by using RAPD and SSR markers (Tanweer *et al.*, 2015).

The molecular mapping of blast resistance genes is a most direct and convenient approach for the identification of blast resistance in the rice genome. Through molecular mapping major blast resistance genes and Quantitative Trait Loci (QTL) linked to blast resistance have been localized. The traditional African variety Moroberekan, with durable resistance against various pathotypes of *M. oryzae*, has been used as a donor for blast resistance in many breeding programmes.

An *in silico* approach which uses computational methods for identification of candidate genes. Here for genome wide comparison, the available sequences of two or more genomes are used (Shang *et al.*, 2009). Gene prediction programs like, FGENESH and Rice GASS (using rice genome sequence of the prescribed size of fragment) are used for the identification of candidate genes.

For the verification of a true candidate, PCR-based markers are developed and used as co-segregation markers to screen blast resistant and susceptible varieties. This *in silico* approach has been successfully applied to identify blast resistance genes such as *Pid3*, *Pik-p* and *Pi37*, *Pi25* (Hayashi *et al.*, 2006; Lin *et al.*, 2007; Shang *et al.*, 2009; Chen *et al.*, 2011).

Molecular map based approach which is the most directed approach for the identification of resistance gene. This strategy has been used for identification of 30 blast resistance genes namely; Pit, Pi27(t), Pish, Pid1(t), Pig(t), Piy(t), Piy2(t), Pi39(t), Pi10, Pi40(t), Piz, Pigm(t), Pi33, Pi5(t), Pi15, PiCO39(t), Pi38, PBR, Pb1, Pi-kh, Pi1, Pik-m, Pik, Pik-p, Pik-s, Pi62(t), Pi157, Pita-2, Pi39(t), and Pi20(t) (Das *et al.*, 2012).

Marker density in the rice genome has been increased to one marker per cM (on an average) because of development of high-density linkage map in the USA and Japan (McCouch *et al.*, 2002).

In India identification and cloning of blast resistance genes began in 2002 when rice line Tetep was found to be highly resistant for most of the strains of *M. oryzae* (Sharma *et al.*, 2002).

Blast resistance gene Pitp(t) has been mapped in cultivar Tetep by using simple sequence length polymorphism markers (Barman *et al.*, 2004). Because of the huge potential of Tetep in resistance breeding for the effective management of rice blast in the North-Western region of India, the Pi-kh (Pi54) gene was mapped in the same cultivar Tetep using different types of DNA markers (Sharma *et al.*, 2005).

Subsequently, Pi38 was identified in indica rice Tadukan (Gowda *et al.*, 2006) and Pi-42(t) from aindica cultivar DHR9 by Kumar *et al.*, 2010. The Pi-kh (Pi54) gene is now being introgressed in Indian cultivars of rice using marker assisted back cross breeding because of its effectiveness against many strains of *M. oryzae* and availability of closely linked and also gene based markers (Singh *et al.*, 2011).

The genetic dissection based on the mapping of blast resistance genes on different

chromosomes showed that majority of these genes are made up of nucleotide binding site-leucine-rich repeat (NBS-LRR) domain (Monosi *et al.*, 2004).

### **Molecular cloning and characterization of blast R genes**

This is the most effective and direct approach towards understanding the structure and function of blast resistance genes. Although, more than 100 blast resistance genes have been identified and mapped, only 22 R-genes have been cloned and characterized at molecular level (Ashkani *et al.*, 2014). The cloned resistance genes are scattered throughout eight (Chromosomes number 1, 2, 4, 6, 8, 9, 11 and 12) rice chromosomes. Distribution on the chromosomes (Table 2) shows that majority of the cloned genes are spotted on chromosome 11 (36%) followed by chromosome 6 (27.5%), chromosome 1 (14%) and chromosome 2, 4, 8, 9 and 12 (each 4.5%).

The genetic dissection of cloned genes revealed that the largest class of R-genes (Class 1) encodes nucleotide-binding, leucine-rich repeat (NBS-LRR) proteins, except Pid-2, which contains the receptor kinase domain. The NBS-LRR proteins are further subdivided into the Toll/interleukin 1 receptor (TIR) and coiled-coil (CC) groups based on the N-terminal domain.

Out of these two types, only (CC)-NBS-LRR class proteins are found in monocots (Ashkani *et al.*, 2014). As showed in the table among 22 cloned blast resistance genes, 13 genes fall into a category of CC-NBS-LRR type domain, eight into NBS-LRR proteins while Pid-2 possesses a unique type of protein called B-lectin receptor which is having a serine threonine kinase type domain. For cloning most of the genes, map-based cloning strategy has been used.



**Table.1 List of identified blast resistance genes on rice chromosomes with necessary information**

| Gene Symbol | Chr. number | Position(bp)      | Marker name                         | Donar rice variety  | References  |
|-------------|-------------|-------------------|-------------------------------------|---|---|
| Pit         | 1           | 2270216-3043185   | t311, t256, t8042                   | Tjahaja   | Hayashi <i>et al.</i> ,2006   |
| Pitp(t)     | 1           | 25135400–28667306 | RM246                               | CO39 and Tetep  | Wongsaprom <i>et al.</i> ,2010; Barman <i>et al.</i> , 2004                 |
| Pi37        | 1           | 33110281–33489931 | RM302, RM212, FPSM1, FPSM2,FPSM4,   | Cultivar St. No. 1  | Lin <i>et al.</i> ,2007   |
| Pi35(t)     | 1           | 33000000–34150000 | RM1216, RM1003                      | Hokkai 188  | Barman <i>et al.</i> ,2004<br>Nguyen <i>et al.</i> ,2006                    |
| Pi24(t)     | 1           | 5242654–5556378   | K5                                  | Azucena   | Nguyen <i>et al.</i> ,2006  |
| Pi27        | 1           | 6230045–6976491   | RM151, RM259                        | Q14 and Q61   | Sallaudet <i>et al.</i> ,2003   |
| Pish        | 1           |                   |                                     | Shin 2  | Zhu <i>et al.</i> ,2004   |
| Pi64        | 1           |                   | RM 11715, RM 11787                  | Japonica landrace Yangmaogu (YMG)   | Ma <i>et al.</i> , 2015   |
| Pid1(t)     | 2           | 21875000–22475000 | RM262                               | Lijiangxin-tuan-heigu (LTH) and Jiangnanxiangnuo (JNXN) crossed with Digu | Chen <i>et al.</i> ,2004  |
| Pi-y1(t)    | 2           | 38300000–38525000 | RM3248, RM20                        | Lijiangxin-tuan-heigu (LTH) and Yanxian No.1                              | Fukutaet <i>et al.</i> ,2004; Lei <i>et al.</i> ,2005                       |
| Pi-Da(t)    | 2           |                   | RM5529, RM211                       | Dacca6  | Lei <i>et al.</i> ,2005   |
| Piy2(t)     | 2           | 38300000–38525001 | RM3248, RM20                        | Yanxian No.1  | Fukutaet <i>et al.</i> ,2004; Lei <i>et al.</i> ,2005                       |
| Pig(t)      | 2           | 34346727–35135783 | RM166, RM208                        | Guangchangzhan  | Shi <i>et al.</i> ,2012; Zhu <i>et al.</i> , 2004                           |
| Pi25(t)     | 2           | 34360810–37725160 | RG520                               | IR64  | Wu <i>et al.</i> , 1993; Nguyen <i>et al.</i> ,2006                         |
| Pi-tq5      | 2           | 37625000–39475000 | RG520, RZ446b, RZ446a, RG654, RG256 | Teqing  | Tabienet <i>et al.</i> ,2002; Zhou <i>et al.</i> ,2004                      |
| Pi14(t)     | 2           | 1–6725831         | Amp-1                               | Maowang   | Pan <i>et al.</i> ,1996; Tabien <i>et al.</i> ,2000                         |
| Pi-b        | 2           | 38300000–38525000 | b213, b28, b2, b3989                | BL1/Koshihikari   | Wang <i>et al.</i> ,1999; Hayashi <i>et al.</i> ,2006                       |
| Pi16(t)     | 2           | 1–6725831         | Amp-1                               | Maowang   | Pan <i>et al.</i> ,1997   |
| pi21        | 4           | 5242654–5556378   | P702D03_79                          | Owarihatamochi  | Ahn <i>et al.</i> ,1997; Pan <i>et al.</i> ,1998                            |
| Pikur1      | 4           | 24611955–33558479 |                                     | Kuroka  | Fukuoka <i>et al.</i> ,2007   |
| Pi39(t)     | 4           | 26850000–27050000 | RM3843, RM5473                      | Mineasahi and Chubu 111   | Liu <i>et al.</i> ,2007   |
| Pi(t)       | 4           | 2270216–3043185   |                                     | P167 (I)  | Causse <i>et al.</i> ,1994  |
| Pi23        | 5           | 10755867–19175845 |                                     | Suweon 365  | Terashima <i>et al.</i> ,2008   |
| Pi26(t)     | 5           | 8751256–11676579  | RG313                               | Azucena/Gumei 2   | Wu <i>et al.</i> ,1993; Ahn <i>et al.</i> ,1996; Nguyen <i>et al.</i> ,2006 |
| Pi10        | 5           | 14521809–18854305 | OPF62700                            | Tongil  | Wu <i>et al.</i> ,2005  |
| Pigm(t)     | 6           | 10367751–10421545 | C26348, S47656                      | Gumei4  | Deng <i>et al.</i> ,2006  |

|           |   |                   |   |   |  |
|-----------|---|-------------------|---|---|--|
| Pi22(t)   | 6 | 4897048–6023472   |   | Sweon 365                                 | Terashima <i>et al.</i> ,2008                                |
| Pi26      | 6 | 8751256–11676579  | K17, R2123  | Zhong 156/Gumei 2                         | Wu <i>et al.</i> ,2005                                       |
| Pi27(t)   | 6 | 5556378–744329    | Est-2   | IR64                                      | Nguyen <i>et al.</i> ,2006                                   |
| Piz-5     | 6 |                   | BS2-Pi9 and NBS4-Pi9  | C101A51_CO39                              | Deng <i>et al.</i> ,2006                                     |
| Pi8       | 6 |                   | Amp-3, pgi-2  | Kasalath                                  | Tabien <i>et al.</i> ,2000                                   |
| Pi13(t)   | 6 |                   | Amp-3   | Maowangu                                  | Pan <i>et al.</i> ,1996                                      |
| Pi40(t)   | 6 | 16274830–17531111 | RM3330, RM527, S2539  | Co39 and IR50 cross with IR65482-4-       | Jeung <i>et al.</i> ,2007                                    |
| Pi59(t)   | 6 |                   | RM19835   | Haoru_US-2                                | Zhou <i>et al.</i> ,2006                                     |
| Pi9       | 6 | 10386510–10389466 | Nbs2-Pi9 and Nbs3-Pi9   | Cultivar TP309                            | Qu <i>et al.</i> ,2006<br>Koide <i>et al.</i> ,2013          |
| Pi2-1     | 6 |                   | AP4791 and AP4007   | Tianjingyeshengdao                        | Quet <i>et al.</i> ,2006                                     |
| Pi-tq1    | 6 |                   | RZ682, C236, RG653, RZ508                                     | Teqing                                    | Zhou <i>et al.</i> ,2004                                     |
| Piz-t     | 6 | 14675000          | z4794, z60510, z5765, zt56591, zt5659                         | Isogenic line C101A51 and cultivar CO39   | Hayashi <i>et al.</i> ,2006; Deng <i>et al.</i> ,2006        |
| Pid2      | 6 | 17159337–17163868 | CAPS1 and CAPS8   | Digu and Lijiangxin-tuan-heigu            | Chen <i>et al.</i> ,2006                                     |
| Pi25(t)   | 6 | 18080056–19257588 | A7-RG456  | Zhong 156/Gumei 2                         | Ahnet <i>et al.</i> ,1996                                    |
| Piz       | 6 | 10155975–10517612 | z4794, z60510, z5765, z56592, z565962                         | Zenith                                    | Hayashi <i>et al.</i> ,2006; Wang <i>et al.</i> ,2012        |
| Pi13      | 6 |                   | R2123, R538   | Kasalath                                  | Fjellstrom <i>et al.</i> ,2006; Hayasaka <i>et al.</i> ,1995 |
| Pi2-2     | 6 |                   | AP5659-3 and RM19817  | Jefferson                                 | Ballini <i>et al.</i> ,2008                                  |
| Pi50(t)   | 6 |                   | GDAP51 and GDAP16   | EBZ x LTH F2 and (EBZ x LTH) x LTH, BC1F2 | Jiang <i>et al.</i> ,2012                                    |
| Pi17(t)   | 7 | 22250443–24995083 |   | Kasalath                                  | Zhu <i>et al.</i> ,2012                                      |
| Pi33      | 8 | 5915858–6152906   | RM72, RM44  | IR64_Azucena and Azucena_Bala             | Berruyer <i>et al.</i> , 2003                                |
| Pizh      | 8 | 4372113–21012219  | RZ617   | JX17_ZYQ8                                 | Sallaud <i>et al.</i> ,2003                                  |
| Pi36      | 8 | 2870061–2884353   | RM5647, CRG2, CRG3, CRG4                                      | Q61 (I)                                   | Liu <i>et al.</i> ,2007                                      |
| Pi29(t)   | 8 | 9664057–16241105  | RZ617, RGA-IR86   | IR64                                      | Nguyen <i>et al.</i> ,2006                                   |
| pi55(t)   | 8 |                   | H2 and H66  | Yuejingsimiao 2 (YJ2)                     | Liu <i>et al.</i> ,2005                                      |
| PiGD-1(t) | 8 |                   | Oxalate oxidase   | Sanhuangzhan2                             | He <i>et al.</i> ,2012                                       |
| Pi15      | 9 | 9641358–9685993   | BAPi15486,BAPi15782 and BAPi15844                             | Q61 and GA25                              | Liu <i>et al.</i> ,2004                                      |
| Pi2(t)    | 9 | 1022662–7222779   |   | Ishikari shiroke                          | Pan <i>et al.</i> ,2003                                      |
| Pi3(t)    | 9 | 7825000-8250001   |   | Pai-kan-tao                               | Kinoshita &Kiyosawa, 1997                                    |
| Pi5(t)    | 9 | 7825000-8250000   | 94A20r, 76B14f, 40N23r  | RIL260 (Moroberekan)                      | Kwon <i>et al.</i> ,2008                                     |
| Pi56(t)   | 9 |                   | CRG4 (CRG4-1 and CRG4-2) and CRG5, and one SSR marker RM24022 | SHZ-2 and BC-10 x TXZ-13                  | Jeon <i>et al.</i> ,2003                                     |

|           |    |                   |  |  |  |
|-----------|----|-------------------|--|--|--|
| Pii       | 9  | 2291804–28431560  |  | Ishikari Shiroke (J)                   | Ise <i>et al.</i> ,1991  |
| Pi28(t)   | 10 | 19565132–22667948 | RZ500  | Azucena                                | Nguyen <i>et al.</i> ,2006   |
| PiGD-2(t) | 10 |                   | r16  | Sanhuangzhan 2 x Lijiangxin-tuan-heigu | He <i>et al.</i> ,2012   |
| Pik-h     | 11 | 24761902–24762922 | RM144, RM224, RM1233, RM144,                           | HP2216 and Tetep                       | Fjellstrom <i>et al.</i> ,2004;Sharma <i>et al.</i> , 2005         |
| Pi-hk1    | 11 |                   | RM27248 and RM27318                                    | Heikezijing                            | Liu <i>et al.</i> ,2012  |
| Pi54      | 11 |                   | TRS26, TRS33,RM2191                                    | Tetep                                  | Wu <i>et al.</i> ,2013   |
| Pi-1(t)   | 11 |                   | RM1233I and RM224                                      | Near-isogenic lines C101LAC and C101A5 | Sharma <i>et al.</i> ,2005   |
| Pb1       | 11 |                   |  | Modan                                  | Fuentes <i>et al.</i> ,2008;Fujii <i>et al.</i> , 2000             |
| Pise1     | 11 | 5740642–16730739  |  | Sensho                                 | Izawall&Iwasakizl, 2000  |
| Pikur2    | 11 | 2840211–18372685  |  | Kuroka                                 | Goto, 1988   |
| Pi38      | 11 | 19137900–21979485 | RM206, RM21  | CO39 and Tadukan                       | Gowda <i>et al.</i> ,2006  |
| Pik       | 11 | 27314916–27532928 | k6816, k2167, k6438, k6415, k8823,k8824, k3951, k39512 | K60                                    | Hayasaka <i>et al.</i> ,1995; Hayashi <i>et al.</i> ,2006          |
| Pif       | 11 | 24695583–28462103 |  | Chugoku 31-1 (St. No. 1)               | Gowda <i>et al.</i> ,2006  |
| Pi34      | 11 | 19423000–19490000 | C1172, E2021   | Chubu 32                               | Zenbayashi <i>et al.</i> , 2002                                    |
| Pia       | 11 | 4073024–8078510   | yca72  | Aichi Asahi (J)                        | Chauhan <i>et al.</i> ,2002; Zenbayashi-Sawata <i>et al.</i> ,2005 |
| Mpiz      | 11 | 4073024–16730739  |  | Zenith (J)                             | Goto,1996  |
| Piisi     | 11 | 2840211–19029573  |  | ImochiShirazu (J)                      | Goto,1970  |
| PiCO39(t) | 11 | 6304007–6888870   | RGA8, RZ141, RGACO39                                   | CO39                                   | Chauhan <i>et al.</i> , 2002; Kwon <i>et al.</i> ,2008             |
| Pilm2     | 11 | 13635033–28377565 | L457b, G2132b, RZ536x, RG1109                          | Teqing                                 | Tabien <i>et al.</i> ,2002; Zhou <i>et al.</i> ,2004               |
| Pi30(t)   | 11 | 441392–6578785    | OpZ11-f, RGA-IR14                                      | IR64                                   | Sallaud <i>et al.</i> ,2003; Nguyen <i>et al.</i> ,2006            |
| Pi7(t)    | 11 | 17850000-21075000 |  | RIL29 (Moroberekan)                    | Miyamoto <i>et al.</i> ,2001                                       |
| Pi44(t)   | 11 | 22850000-29475000 |  | RIL29 (Moroberekan)                    | Chauhan <i>et al.</i> ,2002  |
| Pi49      | 11 |                   | K10 and K134   | CO39                                   | Chen <i>et al.</i> , 1999  |
| Pik-m     | 11 | 27314916–27532928 | k6816, k2167, k641, k6441, k4731, k7237                | Tsuyuake                               | Sun <i>et al.</i> ,2013; Wang <i>et al.</i> ,2007                  |
| Pi18(t)   | 11 | 26796917–28376959 | RZ536  | Sweon 365                              | Li <i>et al.</i> ,2007   |
| Pik-p     | 11 | 27314916–27532928 | k641, k39575, k403, k3957                              | HR22                                   | Hayashi <i>et al.</i> ,2006  |
| Pik-s     | 11 | 27314916–27532929 | RM144, RM224, RM1233, RM144,RM224, RM1233              | Shin 2                                 | Fjellstrom <i>et al.</i> ,2004                                     |
| Pi47      | 11 |                   | RM206 and RM224  | Cross between XZ3150 and the highly    | Ahn <i>et al.</i> ,2000  |



|                  |    |                   |  |   |  |
|------------------|----|-------------------|--|---|--|
|                  |    |                   |  | susceptible cultivar CO39                                     |  |
| Pik <sup>g</sup> | 11 | 27314916–27532930 |  | GA20  | Tabien <i>et al.</i> ,2000                               |
| Pi60(t)          | 11 |                   | K1-4 and E12                                       | 93-11   | Huang <i>et al.</i> ,2011                                |
| Pi-1(t)          | 11 |                   | RM224  | Samba mahsuri   | Lei <i>et al.</i> ,2013                                  |
| Pi1              | 11 |                   | CRG11-7 and K28                                    | cv. C101LAC   | Prasad <i>et al.</i> ,2009                               |
| PBR              | 11 | 20125000–30075000 |  | St. No. 1   | Fujii <i>et al.</i> ,1995                                |
| Pi24(t)          | 12 | 5242654–5556378   | RGA 3  | Zhong 156/Azuena (J)  | Zhuang <i>et al.</i> ,2002<br>Hua <i>et al.</i> ,2012)   |
| Pi-42(t)         | 12 |                   | STS5, RRS44, RRS51, RRS60, RRS63, RRS6 and CRG 6-1 | DHR9  | Zhuang <i>et al.</i> ,2002                               |
| Pi51(t)          | 12 |                   | RM5364, RM27990                                    | Tianjingyeshengdao  | Qu <i>et al.</i> ,2006                                   |
| Pi62(t)          | 12 | 2426648–18050026  | RG869  | Yashiromochi  | Wu <i>et al.</i> ,1996; Kumar <i>et al.</i> ,2010        |
| Pi6(t)           | 12 | 1–6725831         | RG869  | Apura   | Wu <i>et al.</i> ,1996                                   |
| Pi12(t)          | 12 | 6988220–15120464  |  | Hong-jiaozhan/Moroberekan (J)                                 | Inukai <i>et al.</i> ,1995                               |
| Pi4(t)           | 12 |                   | RG869, RZ397                                       | Apura   | Wu <i>et al.</i> ,1996                                   |
| Pi31(t)          | 12 | 7731471–11915469  | O10-800  | IR64  | Sallaud <i>et al.</i> , 2003; Nguyen <i>et al.</i> ,2006 |
| Pi32(t)          | 12 | 13103039–18867450 | AF6  | IR64  | Sallaud <i>et al.</i> , 2003; Nguyen <i>et al.</i> ,2006 |
| Ipi(t)           | 12 |                   | RG241X   | BS125xWL02  | Causse <i>et al.</i> ,1994                               |
| IPi3(t)          | 12 |                   | RG241X   | BS125xWL02  | Causse <i>et al.</i> ,1994                               |
| Pita-2           | 12 | 10078620–13211331 | ta3  | Pi No.4   | Hayashi <i>et al.</i> ,2006                              |
| Pi19(t)          | 12 | 8826555–13417088  |  | Aichi Asahi   | Inukai& Nelson, 1994; Iwata <i>et al.</i> ,1996          |
| Pi21(t)          | 12 | 5242654–5556378   |  | Suweon 365  | Terashima <i>et al.</i> ,2008                            |
| Pita             | 12 | 10603772–10609330 | SP4B9 and SP9F3                                    | Yashiro-mochi and Tsuyuake/Tadukan (I)                        | Hayashi <i>et al.</i> , 2006                             |
| Pi58(t)          | 12 |                   | RM27954, RM27933, RM3103                           | HaoruxUS-2  | Zhou <i>et al.</i> ,2006                                 |
| Pi39(t)          | 12 |                   | 39M6, 39M7   | Q15/Chubu 111 (J)   | Bryan <i>et al.</i> ,2000; Liu <i>et al.</i> ,2007       |
| Pi-GD-3(t)       | 12 | 13950000          | RM179  | Sanhuangzhan 2 x Lijiangxin-tuan-heigu                        | Liu <i>et al.</i> , 2005; He <i>et al.</i> ,2012         |
| Pi20(t)          | 12 | 12875000–12950000 | RM1337, RM5364, RM7102                             | Asominori and IR24  | Liu <i>et al.</i> ,2007; Liu <i>et al.</i> , 2008        |
| Pi-tq6           | 12 | 5758663–7731471   | RG341a, RG869, L102, G1468a, RZ397, RZ257          | Teqing  | Tabien <i>et al.</i> , 2002; Zhou <i>et al.</i> ,2004    |
| Pi48             | 12 |                   | RM5364 and RM7102                                  | Cross between XZ3150 and the highly susceptible cultivar CO39 | Ahn <i>et al.</i> ,2000                                  |
| Pi61(t)          | 12 |                   | M2 and S29   | 93-11   | Huang <i>et al.</i> ,2011                                |
| Pi157            | 12 | 12375000–15550000 |  | Moroberekan   | Causse <i>et al.</i> ,1994                               |

**Table.2** List of cloned blast resistance genes with necessary information

| Gene Symbol | Chromosome | Domain combination | Cultivar name              | Cloning Strategy               | References                    | Percentage (%) of total cloned genes |
|-------------|------------|--------------------|----------------------------|--------------------------------|-------------------------------|--------------------------------------|
| Pb1         | 11         | CC-NBS-LRR         | Modan                      | Map Based                      | Hayashi <i>et al.</i> , 2010  | 36%                                  |
| Pik-h(Pi54) | 11         | NBS-LRR            | Tetep                      | Map Based                      | Sharma <i>et al.</i> , 2005   |                                      |
| Pikm        | 11         | CC-NBS-LRR         | Tsuyuake                   | Map Based                      | Ashikawa <i>et al.</i> , 2008 |                                      |
| Pi-k        | 11         | CC-NBS-LRR         | Koshiminori                | Map Based                      | Wang <i>et al.</i> , 2013     |                                      |
| Pik-p       | 11         | CC-NBS-LRR         | HR22                       | Map Based in silico            | Yuan <i>et al.</i> , 2011     |                                      |
| Pia         | 11         | CC-NBS-LRR         | Aichi Asahi                | Multifaceted genomics approach | Okuyama <i>et al.</i> , 2011  |                                      |
| NLS1        | 11         | NBS-LRR            | nls1-1D/NLS1 and Zhongsi 2 | Map Based                      | Ashkani <i>et al.</i> , 2014  |                                      |
| Pi54rh      | 11         | CC-NBS-LRR         | Oryzarhizomatis            | Allele mining approach         | Das <i>et al.</i> , 2012      |                                      |
| Pi2         | 6          | NBS-LRR            | Zhenshan 97                | Map Based                      | Liu <i>et al.</i> , 2002      |                                      |
| Pi9         | 6          | NBS-LRR            | 75-1-127(101141)           | Map Based                      | Qu <i>et al.</i> , 2006       |                                      |
| Piz-t       | 6          | CC-NBS-LRR         | Toride 1                   | Map Based                      | Ashkani <i>et al.</i> , 2014  |                                      |
| Pid-2       | 6          | Lectin receptor    | Digu                       | Map Based                      | Chen <i>et al.</i> , 2006     |                                      |
| Pid3        | 6          | CC-NBS-LRR         | Digu                       | Silico homology based          | Shang <i>et al.</i> , 2009    |                                      |
| Pi25        | 6          | CC-NBS-LRR         | Nipponbare                 | In silico approach             | Ashkani <i>et al.</i> , 2014  |                                      |
| Pi37        | 1          | NBS-LRR            | St. No.1                   | Map Based in silico            | Chen <i>et al.</i> , 2005     | 14%                                  |
| Pit         | 1          | CC-NBS-LRR         | K59                        | Map Based                      | Hayashi & Yoshida, 2009       |                                      |
| Pis-h       | 1          | CC-NBS-LRR         | Nipponbare                 | Mutant Screening               | Ashkani <i>et al.</i> , 2014  |                                      |
| Pib         | 2          | NBS-LRR            | Tohoku IL9                 | Map Based                      | Wang <i>et al.</i> , 1999     | 4.5%                                 |
| Pi21        | 4          | NBS-LRR            | AA-pi21                    | Map Based Cloning              | Fukuoka <i>et al.</i> , 2009  | 4.5%                                 |
| Pi36        | 8          | CC-NBS-LRR         | Q61                        | In silico map based            | Liu <i>et al.</i> , 2005      | 4.5%                                 |
| Pi5         | 9          | CC-NBS-LRR         | RIL260                     | Map Based Cloning              | Lee <i>et al.</i> , 2009      | 4.5%                                 |
| Pi-ta       | 12         | NBS-LRR            | Tadukan                    | Map Based Cloning              | Bryan <i>et al.</i> , 2000    | 4.5%                                 |

**Table.3** Examples of MAS and gene pyramiding for blast resistance in rice

| Target Traits  | Gene(s)/QTL (s)                                      | Type/name of marker(s) used                      | Target variety/application                            | References                           |
|--|--|--|---|--------------------------------------|
| Blast resistance   | Pi1,Piz-5,Pita                                       | RFLP, SSR,ISSR                                   | CO39  | Hittalmani <i>et al.</i> , 2000      |
| Blast resistance   | Pi1,Piz-5,Pi2,Pita                                   | RFLP, SSR,ISSR                                   | CO39  | Hittalmani <i>et al.</i> , 2000      |
| Bacterial blight (BB) resistance and Blast resistance  | Xa21 & Piz   | STS and transgene specific marker                | IR50  | Narayanan <i>et al.</i> , 2004       |
| Blast resistance   | Pi1  | Microsatellite, SSR                              | Zhenshan97  | Liu <i>et al.</i> , 2003             |
| Blast resistance   | Pi1,Pi2  | Microsatellite, SSR                              | Zhenshan97  | He <i>et al.</i> , 2004              |
| Blast resistance   | Pid1, Pib and Pita2                                  | SSR  | G46B  | Chen <i>et al.</i> , 2004            |
| Blast resistance   | Pi2  | SSR  | Zhenshan97B   | Chen <i>et al.</i> , 2004            |
| Blast resistance   | Pi-z   | Microsatellite                                   | Used in parental material for gene surveys            | Fjellstrom <i>et al.</i> , 2006      |
| Submergence tolerance, BPH resistance, Bacterial blight resistance, Blast resistance and quality | Subchr9 QTL,Xa21,Bph and blast QTLs and quality loci | SSR and STS                                      | KDML105   | Toojinda <i>et al.</i> , 2005        |
| Blast resistance   | Pi-ta  | Gene specific marker                             | Advanced breeding lines for rice breeding programmes. | Wang <i>et al.</i> , 2007            |
| Blast resistance   | Pi1, Pi2 and Pi33                                    | SSR  | Jin23B  | Chen <i>et al.</i> ,2008             |
| Blast resistance   | Two QTLs   | Microsatellite markers                           | RD6   | Wongsaprom <i>et al.</i> , 2010      |
| Blast resistance   | Pish&Pib   | SSR  | CO39  | Koide <i>et al.</i> , 2010           |
| Blast resistance   | Four resistant QTLs                                  | SSR  | F <sub>4</sub> generation lines                       | Sreewongchai <i>et al.</i> , 2010    |
| Blast resistance   | Pi-9(t)  | Marker pB8                                       | Hybrid restorer Luhui17                               | Wen <i>et al.</i> , 2012             |
| Blast resistance and BB  | Pi1 and Pi2 for blast resistance and Xa23 for BB     | SSR  | Rongfeng B  | Fu <i>et al.</i> , 2012              |
| Blast resistance   | Piz-5 and Pi54                                       | SSR  | Pusa 1602 and Pusa 1603                               | Singh <i>et al.</i> , 2012           |
| Blast resistance   | Putative Piz   | SSR  | MR219   | Miah <i>et al.</i> , 2015            |
| Blast resistance   | Pi21, Pi34, QBR4-2 and QBR12-1                       | SSR  | NILs for evaluation                                   | Fukuoka <i>et al.</i> , 2015         |
| Blast resistance   | Pi 9,Pita  | Gene linked and microsatellite marker            | Pusa Basmati 1  | Khanna <i>et al.</i> , 2015          |
| Bacterial blight and Blast resistance  | Xa21 & Pi 54   | STS marker pTA248 and functional marker Pi54 MAS | DRR17B  | Balachiranjeevi <i>et al.</i> , 2015 |
| Bacterial blight, Blast, and Brown plant hopper resistance                                       | Xa4, xa5, Xa21, Pi40 and Bph18                       | SSR  | Japonica rice cultivar                                | Suh <i>et al.</i> , 2015             |
| Blast and Bacterial blight resistance  | Pi2 & Xa23   | SSR and indel marker                             | GZ63-4S   | Jiang <i>et al.</i> , 2015           |
| Blast resistance   | Pita and Pi54  | SSR  | Used in rice breeding programme                       | Mahesh <i>et al.</i> , 2016          |
| Blast resistance   | Pi9,Pizt andPi54                                     | Gene linked markers                              | OSGY31  | Xiao <i>et al.</i> , 2017            |

## **MAS and Gene Pyramiding for blast resistance**

Marker- assisted selection is an efficient way to select the desirable characters indirectly. The selection and identification of markers linked to the gene of interest is the basic prerequisite for marker assisted selection. In case of blast resistance, application of marker assisted selection is very powerful as single or a few genes are involved in the resistance mechanism. Development of durable blast resistant rice varieties against *M. oryzae* progressed with the availability of different molecular markers used for marker assisted selection (Ashkani *et al.*, 2012).

With the advent of molecular biology, marker assisted selection (MAS) facilitate gene pyramiding in plants. Gene pyramiding is one of the most effective strategies for achieving durable and multiple resistances. This approach uses both traditional and modern molecular biology approaches depending on the available resources to introgress more than one gene for a specific trait into a single genetic background. Availability of various molecular markers helps in the rapid detection and introgression of resistant genes into susceptible rice varieties as compared to conventional phenotypic screening.

The selection of blast resistance genes through marker assisted selection is very precise because of the true interaction of the particular resistance (R) gene with the avirulence gene.

Gene pyramiding has been successfully applied to combine several genes of blast resistance in rice. Three important blast resistance genes Pi1, Piz-5 and Pita with closely linked RFLP and PCR based markers have been introgressed into a susceptible cultivar CO39 through MAS. Compared to the plant with Piz-5 alone, two and three gene

combinations including Piz-5 showed enhanced resistance to blast (Hittalmani *et al.*, 2000). After few years later on the same cultivar CO39, Pish&Pib genes were also introgressed with MAS (Koide *et al.*, 2010). Three genes, Pi-d(t)1, Pi-b, and Pi-ta2, have been fixed into a donor line of rice, G46B (Chen *et al.*, 2004), and two genes, Pi1 and Pi2, have been fixed into cv. Zhenshan 97 (He, 2004).

Pusa1602 and Pusa1603 lines have been developed by incorporating the blast resistance genes Piz-5 and Pi54 through MAB (Singh *et al.*, 2012). The leaf and neck blast resistance have been developed through introgression of the Pi1 and Pi2 genes, respectively, using MAB programmes (Fu *et al.*, 2012). Two quantitative trait loci (QTLs) that confer resistance to blast disease have been successfully introgressed into RD6 using MAS (Wongsaprom *et al.*, 2010). In that same year again four QTLs for blast resistance were introgressed into F<sub>4</sub> lines using marker assisted selection (Sreewongchai *et al.*, 2010).

Pyramiding of resistance genes with different pathogens and insect is of great significance for plant breeding. Narayanan *et al.*, (2004) pyramided two major R-genes Xa21 and Piz for bacterial blight and blast resistance into rice using MAS and genetic transformation. For bacterial blight, blast, and Brown plant hopper resistance gene Xa4, xa5, Xa21, Pi40 and Bph18 has been introgressed into japonica rice cultivar (Suh *et al.*, 2015). Recently a study was done on three major blast resistance genes Pi9, Pizt and Pi54 to find out the best combination for pyramiding and result showed that combination of Pizt and Pi54 gives higher resistant level and better additive effects on panicle blast resistant than Pi9 and Pi54 combination (Xiao *et al.*, 2017). Some examples of MAS for gene pyramiding in rice are shown in Table 3.

The use of resistant cultivar is a powerful tool to develop sustainable and environmental favourable rice production systems. Rice blast is a serious concern in the present days breeding program, as many pathogen strain overcome resistance within a short period of time because of evolution of pathogen strains. Therefore, further research is still required to exploit tools, knowledge in breeding programs. Although, more than 100 blast resistance genes were identified in different rice genotypes and 22 of them were cloned and characterized at the molecular level, they provide resistance to specific pathotypes. So we need to identify more durable and suitable blast resistance genes that confer broad-spectrum resistance to different pathotypes of *M. oryzae*. Recent advances in rice genomics and molecular biology studies comes out with new techniques like fine mapping, cloning of blast resistance gene and also gene pyramiding with MAS which ultimately helps in the deployment of various resistant genes in rice background. This review will be helpful to study the necessary information for identification of more than 100 blast resistance genes and also a large number of QTLs (more than 350). We have also discussed mapping and cloning of blast resistance genes and also gene pyramiding with marker assisted selection for different biotic stress mainly rice blast. As blast resistance genes are mostly independent, information from this review can be utilized by plant breeders to develop new cultivar of improved agronomic background with more number of resistant genes for marker assisted breeding programmes. Reported DNA markers can also be used in future rice breeding program to detect the genes and QTLs of interest.

### Acknowledgement

We are grateful to Dean, College of Post Graduate Studies and Chairman, School of

Crop Improvement, CAU (Imphal) for support. Ashim Debnath is thankful to his advisor and also UGC, Govt. of India for National Fellowship for Students of OBC.

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**How to cite this article:**

Ashim Debnath, Karma Landup Bhutia and Hage Sumpi. 2018. Mapping and Deployment of Blast Resistance Gene in Rice - A Work in Progress. *Int.J.Curr.Microbiol.App.Sci.* 7(05): 2073-2094. doi: <https://doi.org/10.20546/ijcmas.2018.705.243>