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Review Article

Impact of Marker Assisted Breeding for Bacterial Blight Resistance in Rice: A Review

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Abstract

Bacterial blight caused by *Xanthomonas oryzae* pv. *oryzae* (Xoo) is the major limiting factor in successful rice production. The disease causes around 20-30 % annual loss in rice production and under severe conditions, the yield loss goes upto 50%. The development of resistant genotypes against this disease is the most effective and economic way to control production loss rather than spraying harmful chemicals that affects the environment. In this direction, several varieties with the single resistant gene have been released for cultivation but due to continuous evolution of new pathotypes, there is a continuous breakdown of resistance against the bacterial blight disease. Although durable resistance can be attained by introducing multiple resistant genes in a single desirable genetic background. But with conventional breeding, it is challenging due to dominance and epistatic effects of disease resistance genes against bacterial blight. However, marker-assisted breeding made it possible to identify and introduce multiple genes into a desirable genetic background with rapid, recurrent parent genome recovery and with minimum linkage drag. Molecular markers play a significant role in speeding up the disease resistance breeding programs with different stages like screening, identification, mapping and cloning of disease-resistant genes y. Hereafter, in this review article the application and achievements of marker-assisted breeding in rice against bacterial blight disease was summarized.

Key words: Bacterial blight, disease resistance, marker-assisted breeding, *xanthomonas oryzae* pv., Xa genes

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INTRODUCTION

Rice is a staple food for more than 60% of the world population. Moreover, rice consumption supplies more than 20% calories requirement of the people in South East Asia. Furthermore, the rice plant parts are also used as animal feed. During the past decade, rice demand has increased from 76-763 million t and this trend is expected to continue in the near future¹. The continuous supply of rice per the demand of the consumer can only be achieved by maintaining a stable rice production². More than 90% of the rice total production is produced in Asia and China and India are the leading producer countries. In India, rice is cultivated over about 44.1 million ha area with the production of 165.3 million t and productivity³ of 3.78 t ha⁻¹.

Rice is sensitive to many stresses. In this direction, there are two broad areas of stresses, abiotic (salinity, heat, drought, cold, submergence, radiation and heavy metals) and biotic (pathogens and herbivore) factors⁴. Among biotic stresses, three diseases are considered to be the most devastating worldwide namely, bacterial blight caused by *Xanthomonas oryzae* pv. *oryzae*, blast by *Pyricularia grisea* and sheath blight by *Rhizoctonia solani*⁵. Several preventive measures such as chemical and biological methods are used to control the spread of these disease and insect pests. Unfortunately, these measures are not very useful. The use of pesticides is expensive and are not environmental-friendly. Therefore, host-plant resistance is the most effective breeding strategy to control the biotic stress in contrast to the environmentally inimical use of pesticides⁶⁻⁸.

Yield potential of rice can be improved with the help of various strategies, conventional hybridization and selection procedures, ideotype breeding, heterosis breeding, wide hybridization and molecular breeding⁹. But all these methods employ a forward breeding approach based on traits of interest. The selection of advanced pedigree lines and recombinant inbred lines requires a long process that can take up to 8-9 years to generate elite lines for varietal release. With the development of gene identification technologies, the marker-assisted selection (MAS) technique is typically used to improve disease and insect resistance.

The scope of MAS breeding for targeted introgression of bacterial blight (BB) resistance genes¹⁰⁻¹⁹, blast resistance genes²⁰⁻²⁴, sheath blight²⁵ and brown planthoppers resistance genes²⁶⁻²⁸ and gall midge²⁹ have been successfully demonstrated³⁰. Hence, molecular breeding offers the opportunity to increase the speed and efficiency of plant breeding. It lays the foundation for modern crop improvement in the 21st century³¹ and simultaneously helps to identify

superior gene combinations, leading to significant disease resilience. The term molecular breeding is used collectively for several breeding strategies, such as MAS, MABC, marker-assisted recurrent selection (MARS) and genomic selection³². In this review, the application and achievements of marker-assisted breeding in rice against bacterial blight disease was summarized.

Bacterial blight disease of rice: Bacterial blight is a seed-borne disease caused by a gram-negative bacterium *Xanthomonas oryzae* pv. *Oryzae* is a severe threat to rice production³³⁻³⁵. The disease was first observed by the farmers of the Fukuoka area, in Kyushu prefecture³⁶ of Japan, in 1884. Whereas, in India, the first incidence of bacterial blight disease in rice was reported in Maharashtra by Srinivasan *et al.*³⁷. Earlier, the disease in India was considered to be of minor importance until it broke out in an epidemic form in Shahabad district of Bihar³⁸ in 1963. This disease can affect rice plants at any plant growth stages. BB in Rice generally causes yield loss ranging from 20-30%^{39,40}. In case of severe infection, disease cause yield loss up to 50-100%⁴¹⁻⁴⁴ besides severely affected the grain quality^{13,17}. Due to the severe damage caused by bacterial blight disease, there is an urgent need for strategies to control this epidemic⁴⁵. Breeding for disease resistance is the most effective and economical method for control of BB that has a neutral impact on the environment. Several germ plasm donors carrying assorted genes for control of BB resistance have been used to develop BB resistant varieties⁶.

Breeding rice varieties with multiple disease and insect resistance genes will broaden the resistance spectrum and increase durability for the commonly cultivated varieties⁸. Whereas, the large scale and long term cultivation of varieties with single genes may enable the pathogen to overcome BB resistance. However, this can be delayed by pyramiding multiple resistance genes into rice cultivars. The probability of simultaneous pathogen mutation for virulence to 2 or more effective genes is much lower than for a single gene. Gene pyramiding is difficult using conventional breeding methods due to the dominance and epistasis effects of genes governing disease resistance. However, the availability of molecular markers closely linked with each of the resistance genes makes the identification of plants with several disease resistance genes⁴⁶. Historically, long term cultivation of rice varieties carrying resistance gene has resulted in a significant shift in pathogen-race frequency and consequent breakdown of resistance⁴⁷.

An example of this is the failure of Xa4, which was incorporated widely in many high yielding varieties via conventional breeding. Widespread cultivation of varieties

carrying Xa4 has led to the predominance of Xoo race that can easily overcome resistance conferred by this gene⁶. One tangible solution to resistance breakdown is pyramiding of multiple resistance genes in the background of modern high yielding varieties⁴⁸. Xa21 gene in rice breeding program was identified from the wild rice *O. longistaminata*^{49,50}. But the resistance due to the presence of this gene was recently broken down by new virulent strains in Southern and Yangtze River Valley in China^{51,52}. When two or more genes are introgressed, phenotypic evaluation is unable to distinguish the effect of individual gene precisely since each gene confers resistance to and combats multiple races of the pathogen⁵³.

Moreover, in the presence of a dominant and recessive allele, the effect of the recessive gene is masked⁵⁴. The effectiveness of resistance genes varies over locations due to geographical structuring of the pathogen. Knowledge of the pathogen population structure and virulence characteristics is therefore essential for a successful breeding program aimed at durable resistance⁵⁵.

Bacterial blight resistance genes in the rice wild relatives:

During domestication process from wild species to cultivated rice, selection of desirable agronomic traits to develop varieties that are high yielding and more suitable to humankind leads to loss of many useful genes and a significant reduction of genetic diversity in rice gene pool⁵⁶. The number of alleles in cultivated rice had been reduced by 50-60% as compared to wild rice⁵⁷. Therefore, it is necessary, to widen the genetic base of rice through identification and introgression of novel resistance genes from wild relatives of rice to develop cultivars with resistance to *Xanthomonas oryzae* pv. *oryzae*. Wild species of rice are reservoirs of many useful genes⁵⁸ but a vast majority of these genes remain untapped, because it is often difficult to identify and transfer these genes into cultivated rice. Recently, many genes resistant to diseases, insects, abiotic stress and also for high yield have been transferred from wild species of rice. Many wild species of cultivated rice such as *O. longistaminata*, *O. rufipogon*, *O. minuta*, *O. barthii*, *O. brachyantha*, *O. granulate*, *O. ridleyi* and *O. nivara* have been reported to be resistant to BB⁵⁸. Khush *et al.*⁴⁹ transferred Xa21, a dominant BB resistance gene from *O. longistaminata* into IR24. The F₁ showed resistant to 6 races of bacterial blight in the Philippines, indicating that the resistance of *O. longistaminata* was dominant. Xa23, a dominant resistant gene effective at all growth stages was identified from wild rice species of *Oryza rufipogon*^{59,60}. The Xa23 gene was found highly resistant to 10 Philippine races (P1-P10), 7 Chinese pathotypes (C1-C7)

and 3 Japanese races (TI-T3) at maximum tillering stage⁶¹. Jin *et al.*⁶² identified a BB resistance gene Xa 30 from wild species *O. rufipogon* and transferred this locus to cultivated rice to breed near-isogenic lines. Tan *et al.*⁶³ detected Xa 29 locus from *O. officinalis* and mapped within a 1.3 cM region flanked by RFLP markers on Chromosome 1. Similarly, Xa32(t) gene from *Oryza australiensis* resistant to Xoo strains P1, P4, P5, P6, P7, P8, P9, KXO85 but susceptible to P2 and P3 was mapped by two SSR markers on the long arm⁶⁴ of chromosome 11. Guo *et al.*⁶⁵ transferred Xa35(t), a novel source of BB resistance gene from *O. minuta* (Acc. No. 101133) into IR24 cultivar of *O. sativa* L. The bacterial blight resistance genes identified in the rice wild relatives are presented in Table 1.

Genetics of bacterial blight resistance genes: To date, at least 45 genes conferring BB resistance have been reported⁷¹⁻⁷⁷ and designated in a series from Xa1 to Xa45^{69,76,77,78}. Out of these, 17 genes viz. Xa5⁷⁹, Xa8^{80,81}, Xa13⁸², Xa15^{83,84}, Xa19⁸⁵, Xa20⁸⁶, Xa24⁸⁷, Xa25⁸⁸, Xa26⁸⁹, Xa28⁸⁹, Xa31⁹⁰, Xa32⁶⁷, Xa33⁹¹, Xa34⁹², Xa41(t)⁷³, Xa42⁹³ and Xa44(t)⁷⁴ are recessive and remaining are dominant (Table 2)^{88,89}. Of the 45 resistance genes Xa1⁹⁴, Xa3/26^{95,96}, Xa5^{97,98}, Xa10⁹⁹, Xa13¹⁰⁰, Xa21⁵⁰, Xa23¹⁰¹, Xa25⁸⁸ and Xa27⁷⁸ have been cloned successfully^{70,78,99-101} and Xa2, Xa4, Xa7, Xa22, Xa30, Xa31, Xa33, Xa34, Xa38, Xa39, Xa40, Xa42 have been fine mapped (Table 2)^{68,69,72,74,77,102}. All these resistance genes follow a Mendelian pattern of gene inheritance and express resistance to a diverse group of Xoo pathogens^{69,78,89,91,95}. The risk of recombination between the molecular marker and the gene of interest has led to a false selection in MAS, whereas it was overcome by the use of functional markers (FMs)¹⁰³. Functional markers were successfully designed within the coding sequences of different genes for example, *pvrl1* gene for potyvirus resistance¹⁰⁴ in *Capsicum* sp. and *Pm3* gene for powdery mildew resistance in bread wheat¹⁰⁵. Cloning some of the identified BB resistance genes Xa1, Xa5, Xa13, Xa21, Xa26 and Xa27 (Table 2)^{50,78,94,95,97,98,100} made it possible to develop and use FMs^{106,107}. Recently, an FM for Xa21 was developed¹⁰⁸ based on the coding sequence of both the alleles (Xa21 and Xa21) reported by Song *et al.*⁵⁰. Disease resistance in rice is usually categorized into 2 main groups: qualitative resistance and quantitative resistance. Qualitative resistance is pathogen race-specific and is controlled by a single R gene whose encoded protein can interact directly or indirectly with a corresponding pathogen effector¹⁰⁹. It is highly efficient in complete pathogen inhibition and has become favourable to plant breeders due to ease of selection in breeding programme¹¹⁰.

Table 1: Bacterial blight resistance genes identified in wild species of rice

Wild sp.	Gene identified	Mapping on chromosome	References
<i>O. longistaminata</i>	Xa21	11L	Khush <i>et al.</i> ⁴⁹
<i>O. rufipogon</i>	Xa23	11	Zhang <i>et al.</i> ^{59,60}
<i>O. rufipogon</i>	Xa30	11	Jin <i>et al.</i> ⁶²
<i>O. minuta</i>	Xa27	6	Gu <i>et al.</i> ⁶⁶
<i>O. officinalis</i>	Xa29	1	Tan <i>et al.</i> ⁶³
<i>O. australiensis</i>	Xa32	11L	Zheng <i>et al.</i> ⁶⁴
<i>O. meyeriana</i>	Xa32	12	Ruan <i>et al.</i> ⁶⁷
<i>O. minuta</i>	Xa35	11	Guo <i>et al.</i> ⁶⁵
<i>O. nivara</i>	Xa33	7	Kumar <i>et al.</i> ⁶⁸
<i>O. nivara</i>	Xa38	4L	Cheema <i>et al.</i> ⁶⁹ , Bhasin <i>et al.</i> ⁷⁰

Table 2: List of bacterial blight resistance genes identified in the rice cultivars

Genes	Sources	Chromosome location	Dominant/ Recessive	References
Xa1	Kogyoku	4	Dominant	Yoshimura <i>et al.</i> ⁹⁴ , Sakaguchi ¹¹⁶ , Yoshimura <i>et al.</i> ^{117,118}
Xa2	Rantai-Emas 2	4	Dominant	He <i>et al.</i> ¹⁰² , Sakaguchi ¹¹⁶ , Yoshimura <i>et al.</i> ¹¹⁸
Xa3/Xa26	WaseAikoku	11L		Xiang <i>et al.</i> ⁹⁶ , Ezuka <i>et al.</i> ¹¹⁹
Xa4	IR20, IR22 and IR1529-680-3	11	Dominant	Petpisit <i>et al.</i> ⁷⁹ , Yoshimura <i>et al.</i> ⁹⁴ , Yoshimura <i>et al.</i> ¹²⁰ , Sidhu <i>et al.</i> ¹²¹
Xa5	IR1545-284 and RP291-7 DV85, DV86 and DZ78	5S	Recessive	Petpisit <i>et al.</i> ⁷⁹ , Sidhu <i>et al.</i> ⁸⁰ , Blair and McCouch ¹²²
Xa6	Zenith, Malagkit Sungsong,		Dominant	Sidhu and Khush ¹²³
Xa7	DV85, DV86 and DZ78	6	Dominant	Kaji and Ogawa ¹²⁴ , Porter <i>et al.</i> ¹²⁵ , Chen <i>et al.</i> ¹²⁶
Xa8	PI231129	7	Recessive	Sidhu <i>et al.</i> ⁸⁰ , Singh <i>et al.</i> ⁸¹ , Vikal <i>et al.</i> ¹²⁷
Xa9	Khao Lay Nhay and Sateng		Recessive	Singh <i>et al.</i> ¹²⁸
Xa10	Cas 209	11	Dominant	Mew <i>et al.</i> ¹²⁹ , Yoshimura <i>et al.</i> ¹³⁰ , Gu <i>et al.</i> ¹³¹
Xa11	IR944-102-2-3,	3S	Dominant	Ogawa and Yamamoto ¹³² , Goto <i>et al.</i> ¹³³
Xa12	Kogyoku and Java 14	4	Dominant	Yamamoto <i>et al.</i> ¹³⁴ , Ogawa <i>et al.</i> ¹³⁵
Xa13	BJ	8L	Recessive	Zhang <i>et al.</i> ¹³⁶ , Sanchez <i>et al.</i> ¹³⁷
Xa14	TN1	4	Dominant	Taura <i>et al.</i> ¹³⁸ , Bao <i>et al.</i> ¹³⁹ , Tan <i>et al.</i> ¹⁴⁰
Xa15	M41		Recessive	Nakai <i>et al.</i> ⁸³
Xa16	Tetep		Dominant	Ogawa <i>et al.</i> ¹⁴¹ , Noda and Ohuchi ¹⁴²
Xa17	Asominori		Dominant	Ogawa <i>et al.</i> ¹⁴¹ , Ogawa <i>et al.</i> ¹⁴³
Xa18	Toyonishiki, Milyang 23, IR24		Dominant	Ogawa <i>et al.</i> ¹⁴¹
Xa19	XM5		Recessive	Taura <i>et al.</i> ⁸⁵
Xa20	XM6		Recessive	Taura <i>et al.</i> ⁸⁶
Xa21	<i>Oryza longistaminata</i>	11L	Dominant	Khush <i>et al.</i> ⁶ , Ronald <i>et al.</i> ¹⁴⁴ , Zhai <i>et al.</i> ¹⁴⁵
Xa22	Zhachanglong	11	Dominant	Harushima <i>et al.</i> ¹⁴⁶ , Lin <i>et al.</i> ¹⁴⁷ , Wang <i>et al.</i> ¹⁴⁸
Xa23 (t)	<i>O. rufipogon</i>	11	Dominant	Zhang ¹⁴⁹ , Wang <i>et al.</i> ¹⁵⁰
Xa24 (t)	DV 86	2	Recessive	Mir and Khush ¹⁵¹ , Wu <i>et al.</i> ¹⁵²
Xa25 (t)/Xa25	Minghui 63	12	Recessive	Liu <i>et al.</i> ⁸⁸ , Chen <i>et al.</i> ¹⁵³
Xa25 (t)	HX-3	4	Dominant	Gao <i>et al.</i> ¹⁵⁴
Xa26 (t)	Nep Bha Bong To		Recessive	Lee <i>et al.</i> ⁸⁹
Xa27 (t)	Arai Raj	6	Dominant	Gu <i>et al.</i> ⁶⁶ , Lee <i>et al.</i> ⁸⁹
Xa28 (t)	Lota Sail		Recessive	Lee <i>et al.</i> ⁸⁹
Xa29 (t)	B5 (<i>Oryza officinalis</i>)	1	Dominant	Tan <i>et al.</i> ⁶³
Xa30 (t)	Y238 <i>O. rufipogon</i>	11	Dominant	Jin <i>et al.</i> ⁶²
Xa31 (t)	Zhachanglong	4	Recessive	Wang <i>et al.</i> ⁹⁰
Xa 32 (t)	<i>Oryza meyeriana</i>	12	Recessive	Ruan <i>et al.</i> ⁶⁷
Xa32 (t)	<i>Oryza australiensis</i>	11L	Dominant	Zheng <i>et al.</i> ⁶⁴
Xa33 (t)	Ba7	6	Recessive	Korinsak <i>et al.</i> ⁹¹
Xa33 (t)	<i>O. nivara</i> IRGC 105710	7	Dominant	Natrajkumar <i>et al.</i> ⁶⁸
Xa34 (t)	BG 122	1	Recessive	Chen <i>et al.</i> ⁹²
Xa35 (t)	<i>Oryza minuta</i> (Acc. No. 101133)	11		Guo <i>et al.</i> ⁶⁵
Xa36 (t)	C4059	11L	Dominant	Miao <i>et al.</i> ¹⁵⁵
Xa38	<i>O. nivara</i> IRGC 81825	4L	Dominant	Cheema <i>et al.</i> ⁶³ , Bhasin <i>et al.</i> ⁷⁰
Xa39	FF329	11	Dominant	Zhang <i>et al.</i> ¹⁵⁶
Xa40 (t)	IR65482-7-216-1-2	11	Dominant	Kim <i>et al.</i> ¹⁷²
Xa41 (t)	African wild and cultivated species of <i>O. barthii</i> and <i>O. glaberrima</i>		Recessive	Hutin <i>et al.</i> ¹⁷³
Xa42	XM 14, a mutant of IR 24	3	Recessive	Busungu <i>et al.</i> ⁹³
Xa43 (t)	Colombia XXI (P8)	11	Dominant	Kim and Reinke ⁷⁵
Xa44 (t)	IR73571-3B-11-3-K3 (P6)	11	Recessive	Kim ⁷⁴
Xa45 (t)	<i>Oryza glaberrima</i> Accession IRGC 102600B	8L	Recessive	Kumari <i>et al.</i> ⁷⁶

However, this type of resistance can be easily broken down due to the rapid evolution of pathogen¹⁰⁹. This type of resistance has been successfully used for the control of bacterial blight and blast diseases.

Conventional backcross approach: The backcrossing approach was first proposed by Harlan and Pope¹¹¹ and was practised between the 1930s and 1960s in several crops¹¹². This method is most commonly used to incorporate one or a few traits into an adapted or elite variety¹¹³. The other parent, called the 'donor parent', possesses one or more genes controlling an important trait which is lacking in the elite variety. In repeated crossings, the hybrids (BC1-n) is backcrossed with the recurrent parent until most of the genes stemming from the donor parent are eliminated except stress resistance¹¹⁴. The expected recurrent parent (RP) genome recovery would be 99.2% by 6 backcrosses, which is most similar to improved variety. The proportion of the RP genome is recovered at a rate of 1(1/2)^tC1 for each of the generations of backcrossing¹¹⁵. However, any specific backcross progeny (BC3 or BC2), they will deviate during crossing over resulting in a great chance to get the expected result that is not possible to detect phenotypically. For example, in BC1 population, theoretically, the average percentage of the RP genome is 75% for the entire population. But some individuals possess more or less of the RP genome than others. Those individuals that contain the highest RP genome are selected. But for transferring of quantitative traits, conventional backcross is not an effective method. The presence of undesirable linkages during the backcrossing may prevent the cultivar being improved from promoting the performance of the original recurrent parent. Recessive traits take more time to transfer. Loss of genetic information of recurrent parent may occur in the backcross method.

Marker-assisted selective breeding: MAS can be defined as selection for a trait-based on genotype using associated markers rather than the phenotype of the trait¹⁵⁷. This term for the first time was first utilized by Beckmann and Soller¹⁵⁸. Since then, accelerated development and availability of molecular markers in plants have made MAS into a major molecular breeding strategy. Molecular marker-assisted selection is recognised to be a highly efficient breeding method because it can offer a rapid and precise selection of the target gene⁵³. The primary considerations of utilizing the DNA markers for MAS is the availability of the tightly linked marker (<5 centiMorgans (cM)), along with the ease of the procedure, cost-effectiveness and highly polymorphic marker system^{159,160}. Marker-assisted backcrossing (MABC) is one of

the most anticipated and frequently cited benefits of molecular markers as indirect selection tools in breeding programs¹⁶¹. This approach was first reported for rice by Chen *et al.*¹¹. They introduced resistance to BB disease into Chinese hybrid parents. It was also described for submergence tolerance using the sub1 gene at International Rice Research Institute (IRRI)¹⁶².

The basis of MABC is to transfer one or more desirable genes/QTL from one genetic source (donor parent) into a superior, adapted, elite breeding line (which serves as a recurrent parent) to improve the targeted trait with the help of markers. Unlike traditional backcrossing, marker-assisted backcrossing is based on the marker alleles linked to gene(s)/QTL of interest instead of on phenotypic performance of target trait¹⁶³. The MABC is accomplished in 3 levels¹⁶⁴. In the first level, markers are used for screening the target gene or QTL. This is referred to as 'foreground selection'^{165,166} although referred to as 'positive selection'^{167,168}. Marker-assisted foreground selection was proposed by Tanksley¹⁶⁹ and investigated in the context of introgression of resistance genes by Melchinger¹⁷⁰. The second level of MABC, known as 'recombinant selection', involves the selection of backcross progenies having the target gene with tightly linked markers to minimize linkage drag. In conventional backcross breeding, the chromosome segment from donor remains large even after many backcross generations (>10)^{171,172}.

However, the donor chromosome segment (linkage drag) size is significantly reduced¹⁷³. Recombinant selection is performed usually by using 2 backcross generations^{160,174} because double recombination events on both sides of target locus are usually rare. The third level of MABC approach involves selecting backcross progenies with the maximum of recurrent parent genomic region by utilizing genome-wide dense molecular markers^{165,174}. This was also referred to as 'negative selection' by Takeuchi *et al.*¹⁶⁸. Hence, background selection is very useful in accelerating the recovery of the recurrent parent's genetic complement, which otherwise takes much longer (6 or more backcross generations) via the conventional backcross method¹⁶⁰. In MABC, recurrent parent genome is recovered in BC2 or BC3, BC4 generation^{165,174-176}. The use of background selection during MABC to accelerate the development of an RP with an additional one or more genes has been referred to as 'variety development or enhancement'¹⁷⁷ and 'complete line conversion'¹⁷⁸.

Marker-assisted gene pyramiding: The improvement of rice varieties for resistance to the diseases that are prevalent and destructive is necessary for the sustain ability of rice grain yields. Past attempts to achieve varietal resistance to blast and

BLB disease have been disappointing, largely due to high levels of variability in the disease populations in growing areas¹⁷⁹. For example, a large number of resistance genes for bacterial blight have been identified and tagged from diverse resources by closely linked markers^{42,70,71,72,120,131}. A few of these genes like Xa4 have been incorporated widely in many high yielding varieties through conventional breeding⁶. However, long term cultivation of varieties with single resistance gene Xa4 has resulted in a significant shift in pathogen-race frequency and consequent breakdown of resistance⁴⁸. The breeding can provide varieties with blast resistance in rice. In this direction, the pyramiding of multiple disease-resistant genes into a single genetic background can provide durable disease resistance¹⁸⁰. The probability of simultaneous pathogen mutations for virulence to defeat two or more effective genes is much lower than with a single gene⁴⁸.

But, a pyramiding of multiple resistant genes is very difficult through conventional breeding methods due to linkage with some undesirable traits, dominance and epistatic effects of genes governing disease resistance and problems in screening^{53,181}. The advent and easy availability of molecular markers closely associated with each of the resistance genes makes identification of plants with multiple gene possible⁵⁴. Using the gene pyramiding approach, improved rice cultivars with broad-spectrum durable bacterial blight^{10,13,15,46,54,182-188}, blast resistance genes¹⁸⁹, brown plant hopper^{26,190} resistance genes have been developed by combining different genes. Assembling of more than 2 desirable genes from 2 or more donors into a single genotype or line for a specific trait is referred to as marker-assisted gene pyramiding¹⁶⁰.

Marker-assisted breeding for bacterial blight resistance:

Marker-assisted backcross breeding (MABB) coupled with phenotypic selection for agronomic, grain and cooking quality traits have been used to incorporate BB resistance genes Xa13 and Xa21 into 'Pusa Basmati 1' using IRBB55 (an isogenic line of IR24) as a donor parent. The CAPS marker RG136 linked to Xa13 and STS marker pTA248 linked to Xa21 were used for the foreground selection¹³. Marker-assisted background analysis integrated with foreground selection was used to identify superior BB resistant lines. One of these lines having maximum genome recovery was released as 'Improved Pusa Basmati 1' for commercial cultivation in 2007¹⁹¹ and this is one of the first products of MAS to be used in India. Dokku *et al.*^{192,193} pyramided three BB resistant genes (Xa4, Xa5, Xa13 and Xa21) through markers assisted backcross breeding into parental lines Tapaswini and Lalat from IRBB60. The resulting lines 'Improved Tapaswini and Improved Lalat' were equivalent to its recurrent parent for yields and grain quality features and possess a high level of resistance to BB.

Similarly, Sundaram *et al.*^{15,16} introgressed three BB resistance genes Xa5, Xa13 and Xa21 into the BB susceptible cultivar Samba Mahsuri and Triguna from a donor line SS1113, lead to the development of IET 19046 as improved samba mahsuri and four elite advanced backcross breeding lines, respectively. These lines have a high yield and broad spectrum of BB resistance. Two traditional basmati varieties namely, Taraori Basmati and Basmati 386 were improved for BB resistance by limited marker-assisted backcrossing coupled with phenotypic selection by transferring Xa21 and Xa13 genes from Improved Samba Mehsuri¹⁹⁴. Three BB resistance genes Xa5, Xa13 and Xa21 were introgressed into an *indica* rice cultivar PR 106 using the marker-assisted selection from a donor line IRBB 62. The pyramided lines with two or three gene combinations exhibited a high level of resistance against different isolates of BB⁴⁶. Similar selection strategies were used by Salgotra *et al.*¹⁹⁵ for the transfer of three BB resistance genes (Xa5, Xa13 and Xa21) into IRS5441-2, an aromatic breeding line.

Recombinants, IRS 5441-2-21, IRS 5441-2-79 and IRS-2-85 possessed all the three BB resistance genes and *fgf* (aroma gene) in the homozygous condition and were found to be superior to IRS5441-2 for agronomic performance, grain quality traits and enhanced resistance to BB. Gidamo and Kumaravadivel¹⁹⁶ improved CO43 for BB resistance through the introgression of a resistance gene Xa33. Shanti *et al.*⁵⁴ introgressed four BB resistance genes Xa4, Xa5, Xa13 and Xa21 into the parental lines of hybrid rice KMR 3, PRR 78, IR58025B, Pusa 6B and Mahsuri. The introgression lines were observed to show very high level of disease resistance against all the ten isolates of *Xantomonas. Oryzae* pv *oryzae*. Perumalsamy *et al.*¹⁰⁸ used marker-assisted backcrossing to pyramid three BB resistance (Xa5+Xa13+Xa21) genes into 2 high yielding BLB susceptible indica rice cultivars, ADT43 and ASD16. Out of the 30 pyramided lines, 12 were found significantly superior for grain yield and resistance against BB. Two BB resistance genes (Xa21 and xa13) and a semi-dwarfing gene (*sd1*) were successfully pyramided in a traditional Basmati Type-3¹⁸⁶. To improve BB resistance of 2 varieties Jyothi and IR50, 4 R-genes were introgressed from a donor line based on existing pathogen population¹⁸⁴.

Similarly, an elite deepwater cultivar, Jalmagna was improved against BB by introgressing three BB resistance genes (Xa5, Xa13 and Xa21) from Swarna BB pyramid line. Under BB infection, the three genes pyramided lines exhibit a significant yield advantage and high level of resistance to BB over Jalmagna¹⁸⁸. Parental lines (Pusa 6B and PRR78) of hybrid PRH 10 was improved by incorporating BB resistance genes Xa13 and Xa21 from Improved Pusa Basmati 1 (Pusa 1460). Improved lines of Pusa 6B (designated as Pusa 1605) and PRR

Table 3: Commercially released MAS cultivars in Asia

Varieties	Gene combinations	Country	References
Angke	Xa4 and Xa5	Indonesia	Bustamam <i>et al.</i> ¹⁹⁹
Conde	Xa4 and Xa7	Indonesia	Bustamam <i>et al.</i> ¹⁹⁹
Improved Pusa Basmati-1	Xa5, Xa13 and Xa21	India	Gopalakrishnan <i>et al.</i> ¹⁹¹
PR106	Xa5, Xa13 and Xa21	India	Singh <i>et al.</i> ⁴⁶
Samba Mahsuri	Xa5, Xa13 and Xa21	India	Sundaram <i>et al.</i> ¹⁵
Type 3 Basmati	Xa21, Xa13, sd-1	India	Rajpurohit <i>et al.</i> ¹⁸⁸
RD6	Xa5/Blast R	Thailand	Pinta <i>et al.</i> ²⁰⁵
Mahsuri	Xa4, Xa5, Xa13, Xa21	India	Guvvala <i>et al.</i> ²⁰⁶
Zhongyou 6	Xa21	China	Cao <i>et al.</i> ²⁰²
Zhongyou 1176	Xa21	China	Cao <i>et al.</i> ²⁰²

78 (designated as Pusa 1601) showed yield advantages of up to 8.24 and 5.23%, respectively. The hybrid combinations generated using improved parental lines showed performance on par with or superior to original PRH 10^{17,197}. Four BB resistance genes (Xa4, Xa5, Xa13 and Xa21) were successfully transferred into 2 parental lines (CRMS 32B and A) of a popular hybrid Rajlaaxmi, in India¹⁹⁸. Two BB resistant varieties Angke and Conde were released in 2002, by Department of Agriculture, Indonesia by a combination of phenotypic and marker-aided selection. Angke and Conde carry Xa4+Xa5 and Xa4+Xa7, respectively¹⁹⁹.

Suh *et al.*¹⁸⁷ transferred three BB resistance genes (Xa4+Xa5+Xa21) into an elite japonica rice cultivar Mangeumbyeo using marker-assisted backcrossing (MAB) breeding strategy that led to the development of three elite advanced backcross breeding lines (ABL). The resistant ABL exhibit broad-spectrum resistance against most of the existing B in South Korea without a yield penalty. In China, marker-assisted selection has been successfully employed for the improvement of photosensitive genetic male sterile line 3418²⁰⁰, restorer lines '6078'¹² Minghui 63¹¹, 4183²⁰¹ R8006 and R1176²⁰² using the BB resistance gene Xa21 and three popular restorer lines Minghui 63, YR293 and Y1671 using Xa 23⁶¹. Three restorer lines (XH2431, 9311 AND WH421) with broad-spectrum and enhanced resistance to BB were developed through marker-assisted breeding and pedigree selection²⁰³. Xu *et al.*²⁰⁴ introgressed two resistance genes against BB into Yihui 1577, an elite restorer line widely used in hybrid rice production in China. The pyramided lines carrying both resistance genes and their derived hybrids showed resistant against all the seven Xoo isolates. The commercially released cultivars of rice with bacterial blight resistance are presented in Table 3. Furthermore, important consideration should be given to determine the stability of bacterial blight resistance genotypes across the various agroclimatic zones especially in the rice-growing belts so that released genotypes can perform better irrespective of the challenge of Genotype×Environment interaction^{207,208}. Similarly, QTL

mapping and various other genomic interventions have been successfully implemented in the major cereals like rice and wheat for the improvement of several traits related to biofortification²⁰⁹⁻²¹¹.

CONCLUSION

Bacterial blight is a severe disease of rice and its control using harmful chemicals is not ecofriendly and costly. In contrast, the use of MAS strategies for the control of BB can be vital. MAS has allowed the breeders to recover the favourable alleles at an early stage rather than longer cycles of breeding, thus improving the process of varietal development and ideal parent selection. Molecular marker-based technology is developing and becoming more precise at a rapid rate. The MAS has been well utilized in cereals like and it is very helpful in developing varieties with disease resistance traits. But, the economical and technical considerations are essential for the successful deployment of MAS in a breeding program. Cost reduction is vital to popularize MAS in the breeding programs. The DNA extraction methods that lead to a good quality of DNA needs to be standardized before hand.

Similarly, the challenge imposed by the bacterial blight in rice can be overcome with the help of advanced genomic interventions. This will require detail understanding and implementing the outcomes as soon as possible to delay the losses.

SIGNIFICANCE STATEMENT

In this review, the important information have been compiled regarding the efficacy of molecular breeding in the development of bacterial blight resistance varieties of rice. Disease resistance breeding is a more economical and eco-friendly approach to control the bacterial blight disease of rice. It was hoped that this review will broaden the understanding of the bacterial leaf blight resistance in rice.

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