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REVIEW ARTICLE

Durable Resistance of Rice to Major and Emerging Diseases: Current Status

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Abstract:

Background:

Rice (Oryza sativa) is one of the most dominating cereal crop and half of the world has chosen it as staple food. Rice production has increased significantly but the productivity is not increased significantly to combat the global need. One of the major constraints of low productivity is biotic stresses faced by rice growers. Some of the important biotic stresses of rice are major diseases like brown spot, bacterial blight, blast, sheath blight and, few emerging but significant diseases like false smut, bakanae and sheath rot play crucial role in reducing yield per unit area and quality of rice. Host plant resistance is the most effective, economic and eco-friendly approach of mitigating disease like biotic stress problem.

Objective:

The objective of this review is to compile data related to resistance in rice against various major and emerging diseases as well as their application to develop gene pyramided varieties that increase resistance to those pathogens to achieve durable resistance.

Methods:

Diseases are one of the most important constraints for sustainable or demanding production level as well as maintaining different quality parameters of the rice. Different management practices including majority by chemical means, are not always the solution as they add production cost many times *vis-à-vis* causing pollution in every aspect. Thus, the development of durable resistant varieties is the best approach.

Results:

An array of robust molecular markers and genetic map of the crop has made the application of marker assisted selection possible for the traits controlled by resistant genes or quantitative trait loci (QTLs) to induce durable resistance in the crop.

Conclusion

A comprehensive assessment on identification, sources and deployment of resistance genes/QTLs of major and emerging diseases of rice will help in development of varieties of rice with durable resistant to major and emerging disease-causing pathogens.

Keywords: Blast, Brown spot, Bacterial blight, Sheath blight, False smut, Bakanae, Rice diseases, Resistance gene, QTLs.

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1. INTRODUCTION

Worldwide 4 billion people are dependent on rice and meet 23% of the dietary energy requirement from rice. Thus, rice is arguably one of the most important cereal crops in the world. As per FAO (2014) estimation, rice production needs to be enhanced by 30% by 2030 to sustain the food security of ever-increasing population. Under the context of declining natural resources and limited land resources, demand for per unit production must be increased. Keeping the objective of achieving the highest yield majority area covered by single variety leads to monoculture and this concept resulted in declining genetic variability and intensive cultivation practices intended for increased rice production have enhanced the vulnerability to biotic stresses like disease. Rice diseases are one of the most important constraints for increasing productivity. It is also evidenced from many reports that the diseases not only reduce yield but are also responsible for quality deterioration. To increase or sustain the productivity level *vis-à-vis* production and quality of the produce, rice crop must be protected from

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various pathogens that cause some major and few emerging diseases of rice like brown spot (*Bipolaris oryzae*), blast (*Magnaporthe oryzae*), bacterial blight (*Xantomonas oryzar pv oryzae*), sheath blight (*Rhizoctonia solani*), bakanae (*Fusarium moniliformae*), sheath rot (*Sarocladium oryzae*) and false smut (*Ustilaginoidea virens*). Most easy and effective method of disease management for farmers is application of pesticide but it increases the cost of production day by day and is also a threat to the environment and creates health hazards by contaminating the food chain. Host plant resistance has the potential to be effective, economic and eco-friendly means of disease management in rice. Worldwide breeding for disease tolerant rice variety is one of the most important objectives of rice improvement programme. Nowadays, mapped genes and quantitative trait loci (QTL) are heavily used by researchers to produce disease-tolerant varieties and thus reducing the cost of production. Several QTLs conferring resistance to major diseases like sheath blight (ShB), blast, bacterial blight (BB) and emerging/re-emerging devastating diseases like brown spot (BS), bakanae, false smut (FS), sheath rot (ShR) are known and are mapped to specific chromosomal location by the researchers and tightly linked molecular markers have been reported. Introgression of multiple genes for the same trait in a single background is now the common approach in molecular breeding. In this review, we highlighted the various QTL genes responsible for the resistance to pathogens causing important rice diseases, their sources identified and uses to develop durable resistant varieties.

2. DURABLE RESISTANCE AGAINST BROWN SPOT OF RICE

Brown spot (BS) of rice is caused by *Cochliobolus miyabeanus* (Ito and Kuribayashi) Drechs. Ex Dastur. (Anamorph: *Bipolaris oryzae* (Breda de Haan) Shoemaker), is one of the predominant rice diseases and significantly decreases rice grain production and its' quality [1]. According to Baranwal *et al*. (2013) [2]., *B. oryzae* is basically a weak pathogen and depends more on the weakness of plants or nutrition deficient condition of soil, yet this disease used to affect worldwide millions of hectares of rice every year [3 - 5]. BS of rice was identified long back in 1892 in Japan [6] and it has been reported across South and South-east Asian countries including India [4, 7]. Later on, it was reported in Brazil [8]. In India, two major epidemics happened because of BS of rice, of which first occurred in the Krishna-Godavari delta (1918-1919) and the second, at then Bengal (The Great Bengal Famine in 1942) [3, 9]. Yield losses due to this disease range from 4-52% [2, 4]. Due to the uneven distribution of rainfall frequency of drought situation is increased and this influences the frequent occurrence of BS [10].

In disease management, host resistance is prioritized over chemical management [11]. However, to date there is no report on a major gene conferring resistance to brown spot. Several experiments have been conducted to screen genotypes resistant to BS and many resistant cultivars and breeding materials have been identified [12]. However, none of them showed complete resistance [13]. Varieties like 'Tadukan' and 'Tetep' proved quantitative resistance to brown spot [6, 14]. An *indica* cultivar CH45 from India shows a high level of partial resistance [15] and showed resistance in Japan too [16]. During 2008 and onwards, efforts have been made to identify and use quantitative trait loci (QTL) for brown spot resistance. The details of the attempts to identify QTLs for brown spot resistance have been summarized chronologically in Table **1**. Although several QTLs for BS resistances have been identified, majority of them did not explain over 30% of the phenotypic variation in the analysis [11, 20 - 22]. Only QTLs, qBS5.1 and qBS5.2 were shown LOD scores 3.236 and 3.268 with phenotypic variance of 55.35 and 55.5%, respectively. The negative value of the additive effect showed that the allele transferred from the susceptible parent Dagad deshi [23]. Thus, to develop cultivars with BS resistance, continuous research needs to be done to identify new QTLs from different resistant cultivars for gene pyramiding.

Table 1. Chronological efforts towards identification of QTLs for brown spot resistance.

Research Group	Materials used for QTL Analysis[a]	QTL*	Chromosome
Sato *et al*., 2008a [11]	110 RILs [Tadukan (R) x Hinohikari (S)]	qBS2	2
-	-	qBS9	9
-	-	qBS11	11
Sato *et al*., 2008b [17]	39 CSSL [Kasalath (R) x Koshihikari (S)]	(QTL)	9
Banu *et al*., 2008 [18]	186 F2 lines [Dinorado (R) x IR36 (S)]	bs1	12
Katara *et al*., 2010 [19]	154 DH lines [CT9993-5-10-1M (R) x IR62266-42-6-2 (S)]	BSq2.1v&i	2
-	-	BSq2.2v&i	2
-	-	BSq4.1v&i	4
-	-	BSq6.1v	6
-	-	BSq6.2i	6
-	-	BSq8.1i	8
-	-	BSq8.2v	8
-	-	BSq9.1v	9

(Table 1) contd.....

Research Group	Materials used for QTL Analysis[a]	QTL*	Chromosome
-	-	BSq11.1v&i	11
-	-	BSq11.2v	11
-	-	BSq12.1	12
Sato *et al*., 2015 [20]	110 RILs [Tadukan (R) x Hinohikari (S)]	qBSfR1	1
-	-	qBSfR4	4
-	-	qBSfR11	11
Matsumoto *et al*., 2017 [21]	190 BILs at the BC2F5 generation [CH45 (R) x Koshihikari (S)]	qBSR2-kc)	2
-	-	qBSR7-kc	7
-	-	qBSR9-kc	9
-	-	qBSR11-kc	11
Mandal *et al*., 2017 [22]	122 RILs [Danteshwari (R) × Dagad deshi (S)]	qBS1.1	1
-	-	qBS5.1	5
-	-	qBS5.2	5
Ota *et al*., 2021 [23]	179 BILs at the BC2F5 generation [Dawn (R) x Koshihikari (S)]	qBSR3.1-kd	1
-	-	qBSR3.2-kd	3
-	-	qBSR6-kd	6
-	-	qBSR7-kd	7

Note:[a]CSSLs chromosome segment substitution lines, DH double haploid, RIL recombinant inbred lines, R resistant cultivar, S susceptible cultivar.
[b]QTLs with designations followed by v and/or I were identified on Vertisol and/or Inceptisol soil, respectively

3. DURABLE RESISTANCE AGAINST BLAST DISEASE OF RICE

Blast, a pandemic and the most serious rice disease is caused by *Pyricularia oryzae* L. The first reports of blasts date back to 1600, when they were discovered in China and Japan, referred to as "rice fever" [24] while in India, the first epidemic because of blast disease was reported from Tanjore delta of the former Madras state in 1919. Losses vary based on the cultivar and climatic factors, with losses exceeding 100% in ideal conditions and with vulnerable cultivars [25]. The start of blast pathogen infection started by germination of the conidia and it is aided by leaf moisture and temperatures of 25 to 28 ^{0} C, while sporulation is aided by air humidity exceeding 90%, as well as cloudiness, excess nitrogen, and late planting, all of which aid the pathogen's establishment. Symptoms appear as lesions on the leaves, leaf sheaths, necks, panicles, pedicels, and seeds of the shoots [26]. Rice blast will never be completely eradicated, but *via* integrated crop management, the disease's impact can be considerably reduced. The consistent use of fungicides to control the disease exposes risk to living animals and human *vis-à-vis* the environment and induces the development of resistant races [27]. As a result, resistant cultivars and good crop management practices are suggested. Blast resistance genes have been found in rice in both qualitative and quantitative forms, which can be used for developing new resistant varieties [28].

Understanding and applying molecular biology to the rice crop is critical for the development of blast-resistant cultivars [28]. In plant breeding programmes for disease resistance, marker assisted selection (MAS) is an essential tool to constantly characterise the genetic variability of pathogens and hosts, novel sources of resistance, and decipher novel molecular markers linked to resistance alleles [29]. With the goal of broad-spectrum resistance, MAS selection was utilized for screening resistance genes like *Pi-b, Pi-k, Pi-i, Pi-z,* and *Pi-ta*, in addition to the pyramiding of genes utilising *Pi-ta* [30]. With the help of marker-assisted backcrossing, indica and japonica rice was recently introduced with the quantitative resistance gene *pi21*. In both field and greenhouse conditions, all introduced progeny displayed resistance to 11 isolates of blast pathogen [31].

3.1. QTL Mapping and Gene Pyramiding

Rice has 430 million base pairs in its genome, with 46,000 – 56000 and 32000 - 50000 genes in indica and japonica subspecies [32]. Hundreds of blast-resistant effectors are found in P. oryzae's genome, some of which are recognised by intracellular immunological receptors of the nucleotide-binding, leucine-rich repeat (NLR) [33]. Plants have developed a set of NLRs to combat pathogen-secreted effector chemicals known as virulence factors [33]. Some of the well-studied rice blast resistance genes are NLR receptors with integrated domains [33,34] discovered 5.408 NLR genes during their study of 535 species of *O. sativa* vg. *Indica* using 13 reference genomes. The sequencing of seven wild species assembled new haplotypes and resistance loci, including the *Pi-ta2* locus, which confers broad specificity for *P. oryzae* resistance when combined with *Pi-ta* [34]. Around 350 quantitative trait loci (QTL) have been linked to rice resistance, with 85 resistance loci having been identified [29, 28].

Several QTLs were used for gene pyramiding [35]. Blast resistance genes such as *Pib, Pita, Pik-h, Pi9, Pi2, Piz-t, Pid2, Pi36, Pi37, Pik-m, Pit, Pi5, Pid3, Pi21*, *Pish, Pik, Pik-p, Pia, NLS1, Pi25*, and *Pi54rh* have been cloned and characterised through advanced molecular technology and rice genome sequencing [36]. Resistance to a wide range of pathogen races

is conferred by the *Pi-1* (t), *Pi2*, *Pi9, Pi20* (t), *Pi27* (t), *Pi39* (t), *Pi40* (t), and *Pikh* genes, whereas resistance to specific pathogen races is conferred by the *Pia*, *Pib, Pii, Pi- km, Pi-t, Pi12* (t), and *Pi19* (t) genes [37]. When compared to monogenic *Pi46* and *Pi-ta* lines, pyramiding *Pi46* and *Pi-ta* lines enhance resistivity [38]. Introgression of two genes having different spectra of overlapping resistance can increase the tolerance of plant to blast [39]. The resistance effect of pyramiding lines, on the other hand, is more than just the build-up of the resistant spectrum of targeted *R* genes. The pyramided *R* genes have a strong interaction, resulting in both positive and negative deviations [40].

3.2. Association Mapping

Genome-wide association studies (GWAS), also known as the association or linkage disequilibrium mapping, is the methodology that seeks to find the statistical relationship between genotypic and phenotypic values [41]. In a indica rice, 366 types were chosen to make up the population that was infected with 16 isolates of *Pyricularia oryzae*, resulting in the discovery of [42] 30 loci linked to blast resistant during GWAS investigation of 366 type indica population infected with 16 isolates. Another study utilised GWAS to examine blast resistance and 38 other agronomic parameters in a population of 1,495 hybrid rice varieties and found four genes linked with resistance [43].

3.3. Broad-spectrum Blast Resistance Through Resistance Genes (*R* Gene)

Resistance genes of rice are identical to avirulence (AVR) genes of *M. oryzae*. Thus, interaction of a specific R protein of rice and the avirulence effector pathogen ensured the resistance (Flor, 1956). In *M. oryzae*, more than 40 AVR genes have been discovered, with 12 of them having been cloned. R genes generate R protein, which interacts with the effector protein, detecting presence of pathogen intrusion, by the disease resistance. *R* genes are the foundation of disease resistance research and breeding. Since the discovery of the independently inherited *R* genes *Pia, Pi*, and *Pik* in the 1960s, more than 100 R genes or loci have been discovered [44]. With the exception of chromosome 3, *R* genes are located on 11 chromosomes, and more than 64% of the R genes are grouped on chromosomes 6, 11, and 12, representing 18%, 25%, and 21%, respectively [29]. Since 1999, over 31 *R* genes have been successfully cloned [45]. About 30 *R* genes are dominant except the recessive *R* gene *pi21*. The authors [46] reported that *R* genes *Pb1, Pi25,* and *Pi64* confer panicle blast resistance at the seedling stage, while the bulk of cloned *R* genes confers leaf blast resistance at the seedling stage.

4. DURABLE RESISTANCE AGAINST BACTERIAL BLIGHT (BB) OF RICE

Bacterial blight (BB) of rice, caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) is another major disease that causes significant yield losses in most rice growing locations. The pathogen enters vascular systems through natural openings and causes infections. The symptoms include drying and yellowing of the leaves, which begins at the tips and progresses downward along the margin mostly. Temperatures of 25–34 °C, with relative humidity exceeding 70%, favour the development of the disease in general. All rice growth stages are susceptible to this disease and the severity of the disease depends on the weather condition, variety and growth stage, and the yield losses may vary from 20-80% [47 - 49]. During winters, the pathogen persists in soil, alternate weed host and straw. Most chemicals and antibiotics are not effective in controlling the disease and also pose human health risk and environmental concerns. Due to the pathogen diversity, biological control of bacterial blight has gained less attention. Hence, the development of resistant varieties or lines through various breeding programs could be the most economical and effective way to combat this disease.

4.1. Host Mediated Resistance Against BB

On the basis of microbial recognition, the plant immunity has been divided into two categories. The first level or basal level of immunity is pathogen-associated molecular pattern (PAMP) triggered immunity (PTI) and the second level is the gene for gene resistance (effector triggered immunity (ETI) [50]. The ETI and PTI has qualitative and quantitative resistance in crop plants, respectively. The Rice-*Xoo* recognition falls under qualitative resistance [51]. Until now, 46 resistance gene (*R* gene) to *Xoo* have been identified from various wild and cultivated sources (Table **2**). Of which, eleven genes have been functionally analyzed, characterized and cloned (*Xa1, Xa3/Xa26, Xa4, xa5, Xa10, Xa21, Xa23, xa25, Xa27* and *xa41*). About nine of those *R* genes (*Xa2, Xa4, Xa7, Xa22, Xa30, Xa33, Xa38, Xa39* and *Xa40*) have been fine-mapped on diverse chromosomes. Each *R* gene encodes a different kind of protein. Two major classes of *R* genes, nucleotide-binding site leucine-rich repeat (NBS-LRR) and receptor kinase (RLK) are related to BB disease resistance in rice. The *Xa21* was the first cloned *R* gene that belongs to RLK class with broad spectrum BB resistance. NBS-LRR class is the major *R* gene class deliberating resistance to fungi, bacteria and virus. Most of these *R* genes confer race-specific resistance to *Xoo* strains [91].

Table 2. List of resistance genes identified for BB resistance in rice.

Gene Name	Location (Chr. No.)	Origin	Remark	Refs	Gene Name	Location (Chr. No.)	Remark	Origin	Refs
**Xa1*	4	Japan	Dominant	Yoshimura *et al*. [52]	*xa24*	2	Recessive	Bangladesh	Khush and Angeles [71]
Xa2	4	Vietnam	Dominant	He *et al*. [53]	**xa25*(t)	12	Recessive	China	Chen *et al*. [72]
**Xa3/ Xa26*	11	Japan	Dominant	Gao *et al*, [54]	*xa26*(t)	11	Recessive	China	Lee *et al*. [73]

(Table 2) contd.....

Gene Name	Location (Chr. No.)	Origin	Remark	Refs	Gene Name	Location (Chr. No.)	Remark	Origin	Refs
**Xa4*	11	India	Dominant	Petpisit *et al*, [55]	**Xa27*(t)	6	Dominant	Philippines	Gu *et al*. (2004)
**xa5*	5	Bangladesh	Recessive	Petpisit *et al*, [55]; Blair *et al*, [56]	*xa28*(t)	-	Recessive	Bangladesh	Lee *et al*, [73]
Xa6	11	USA	Dominant	Sidhu *et al*. [57]	*Xa29(t)*	1	Dominant	Portugal, Spain	Tan *et al*. [74]
Xa7	6	Bangladesh	Dominant	Porter *et al*. [58]	*Xa30(t)*	11	Dominant	India	Cheema *et al*. [75]
xa8	7	USA	Recessive	Sidhu *et al*. [57]	*xa31*(t)	4	Recessive	China	Wang *et al*. [76]
Xa9	11	Laos	Dominant	Singh *et al*. [59]	*xa32*(t)	11	Recessive	Australia	Zheng *et al*. [77]
**Xa10*	11	Senegal	Dominant	Yoshimura *et al*. [60]. Kurata and Yamazaki [61].	*Xa33(t)*	6	Dominant	Thailand	Korinsak *et al*, [78]
Xa11	3	Philippines	Dominant	Goto *et al*. [62]	*xa34*(t)	1	Recessive	Sri Lanka	Chen *et al*. [79]
Xa12	4	Japan	Dominant	Ogawa [63]	*Xa35*(t)	11	Dominant	Philippines	Guo *et al*. [80]
**xa13*	8	India	Recessive	Singh *et al*. [64]	*Xa36*(t)	11	Dominant	China	Miao *et al*. [81]
Xa14	4	Taiwan	Dominant	Taura *et al*, [65]	*Xa37*(t)	-	Dominant	-	-
xa15	-	Japan	Recessive	Nakai *et al*. [66]	*Xa38*	4	Dominant	India	Ellur *et al*. [82]
Xa16	-	Vietnam	Dominant	Kurata and Yamazaki [61]	*Xa39*	11	Dominant	China, Philippines	Zhang *et al*. [83]
Xa17	-	South Korea	Dominant	Kurata and Yamazaki [61]	*Xa40*(t)	11	Dominant	Korea	Kim *et al*. [84]
Xa18	-	Philippines, Japan	Dominant	Kurata and Yamazaki [61]	**xa41*(t)	11	Recessive	-	Hutin *et al*. [85]
xa19	-	Philippines	Recessive	Taura *et al*. [67]	*xa42*	3	Recessive	Japan	Busungu *et al*. [86]
xa20	-	Philippines	Recessive	Taura *et al*. [67]	*Xa43*(t)	11	Dominant	Japan	Kim *et al*. [87]
**Xa21*	11	Africa, Mali	Dominant	Huang *et al*. [68]	*xa44*(t)	11	Recessive	Japan	Kim, [88]
Xa22(t)	11	China	Dominant	Wang *et al*. [69]	*xa45*(t)	8	Recessive	Philippines	Neelam *et al*. [89].
**Xa23*	11	China	Dominant	Zhang *et al*., [70]	*Xa46*(t)	11	Dominant	Japan	Chen *et al*., [90]

Note:* Resistance genes have been cloned.

Many of these resistant genes have been incorporated as a single gene or as a combination into elite rice cultivars using marker-assisted selection (MAS) [92]. Remarkably, *Xa3, Xa4, Xa7* and *Xa21* have been extensively exploited in rice breeding programmes. Particularly *Xa21*, the most effective gene against the BB races of South and Southeast Asia, was identified from the wild species of *Oryza longistaminata*. This gene was later mapped and cloned [93] and is extensively used in BB resistance breeding programmes across the globe. Similarly, *Xa23* identified from wild species of *Oryza rufipogon* exhibited broad-spectrum resistance to BB at all growth phases of rice [94]. Using molecular markers, different BB resistant genes, have been isolated and characterized from wild species of *Oryza* such as *Xa10, Xa30, Xa32, xa32*(t), *Xa33, Xa35*(t) and *Xa38* [75, 80, 82].

4.2. Development and Release of BB Resistant Varieties

In most cases, breeding approaches to include a single *R* gene resulted in rapid resistance breakdown against BB. To overcome this problem, gene pyramiding of more than one gene through MAS could be a viable option for resistant breeding. Resistance imparted by more than one gene in single genotype has a considerably lower chance of breaking down than resistance controlled by a single gene. Different countries are utilizing the same approach and transferring many *R* genes to the elite breeding and hybrid lines. Singh *et al*. [95] used MAS approach to pyramid the BB resistant *R* genes of *xa5, xa13* and *Xa21* in PR106 (cultivar) and the results showed that the combination of genes exhibited the broad spectrum of resistance to 17 *Xoo* isolates under field conditions. Similarly, Kottapalli *et al*. [96] pyramided *xa5, xa13* and *Xa21* genes in Samba Mahsuri (cultivar) by utilizing sequence tagged site (STS) markers. Basmati type varieties are highly susceptible to bacterial blight disease. A massive breeding programme was undertaken at Indian Agricultural Research Institute (IARI), New Delhi, India, for incorporating bacterial blight resistant genes into popular basmati varieties like Pusa Basmati 1, Pusa 1121, Pusasugandh 5 and PB 6. Subsequently bacterial blight tolerant varieties like Improved Pusa Basmati-1, Pusa 1592, PB 1718 and PB 1728 have been developed through marker-assisted selection. Deshmukh *et al*. [97] released a BB-resistant high-yielding, medium-duration rice variety by introducing three BB resistance genes from IRBB59 (donor parent) into the genetic background of Karma Mahsuri. By marker assisted backcrossing, Pradhan *et al*. [98] have introduced three bacterial blight resistant genes (*xa5, xa13*, and *Xa21*) into the background of the popular but highly BB vulnerable deepwater rice variety, Jalmagna. The *Xa38* gene was incorporated into improved Samba Mahsuri's genetic background [99]. In an elite maintenance line, DR17B, the *Xa33* gene was pyramided with the *Xa21* gene to confer broad-spectrum resistance to BB [100]. The MAS was used to introduce the *Xa40* gene to a susceptible variety (Junam) in Korea [101]. Rice variety PR

127 was recently produced by introducing the *xa45*(t) gene into the popular Pusa 44 variety [89].

Management of the disease is commonly done by chemical fungicides or biological control agents. But the pathogen is developing resistance against fungicides and the biological control agent is native specific and not being adopted widely making the management cumbersome. Thus, development of durable ShB resistant cultivars and deployment of these are the best way of combating ShB problem.

5. DURABLE RESISTANCE AGAINST SHEATH BLIGHT (ShB) DISEASE

Sheath blight is one of the most destructive and widely spread diseases among the rice growing ecologies of the world, particularly in Asian countries. The disease was first reported in Japan in 1910 by Miyaki. In India, first reported by Paracer and Chahal from Gurdaspur region of Punjab in 1963 [102]. The disease is very severe both in tropical and temperate rice growing areas having irrigation facilities [103]. The disease is so destructive that it can cause yield reduction ranging from 5.2-69% under favourable climatic conditions [104, 105]. The disease is reported in all the states of India in moderate to the severe form. The disease is caused by necrotrophic hyphomycetes group soilborne fungal pathogen *Rhizoctonia solani* Kuhn (AG1A) [Teleomorph: *Thanatephorus cucumeris* (Frank) Donk/*Corticium sasaki* (Shirai) Matsumoto] [106]. The pathogen infects usually at tillering stage of the crop. Initially, small, water-soaked spots appeared on leaf sheath at or above the water level and gradually the spots turned circular to oblong, ellipsoid with greyish white centre with light/dark brown margin. The lesions enlarge vertically and cover the whole stem. Entire stem will dry/die due to the interruption of water and nutrient transport to above ground parts [107].

Management of the disease is commonly done by chemical fungicides or biological control agents. But the pathogen is developing resistance against fungicides and the biological control agent is native specific and not being adopted widely making the management cumbersome. Thus, the development of durable ShB resistant cultivars and deployment of these are the best way of combating ShB problem.

5.1. Sources of Resistance to ShB Disease of Rice

Resistance breeding against the disease is very challenging as there are no absolute resistance sources to the disease available [108, 109]. Almost all the rice cultivars, including high yielding semi-dwarf varieties, are susceptible to the disease [110]. Very few cultivars are being identified which are either moderately susceptible or moderately resistant. Some of the varieties like Bharti, CR-1014, Nalini, Pankaj, Ratna, Tetep were found moderately resistant to sheath blight disease [111]. No rice variety was found resistant to *Rhizoctonia solani* neither in field nor in laboratory conditions [112 - 114]. The authors [115] identified IC281785 and Tetep as moderately resistant to the disease which also showed higher activity of peroxidase and polyphenol oxidase and some authors [116] reported that parental lines like RNR 57979 and IR 64 exhibited moderately resistant reaction to ShB. Some of the cultivars like Swarnadhan, Radha, Pankaj, Vikramarya showed field level resistance [117]. Moderate level of resistance has been identified in rice lines like IR-40, KK-2 [118], HKR 99-103, HKRH 1059 and IR 64683- 87-2-2-3-3 [119]. CN 1272- 55-105, CR 2612-1-2-2-1, CR 2649-7, HKR 05-476, HKR 07-191, KJT 3-2-7-72, OR 2315-6, OR 2329-22, OR 2407-KK-19, R 1570-2144-2-1547, RP 2151-173-1, RP Bio Path 3, TRC 05-2-6-4-39-3-6, UPR 2327-23 [120] and N-22 (Acc. 4819), N-22 (Acc. 19379), HKR 05-476, Tetep [121] have been found to possess a moderate level of resistance.

5.2. Identification of Genes/QTLs Responsible for ShB Resistance

The resistance against the sheath blight disease is quantitative in nature and governed by multiple genes [122, 123]. Number of QTLs gene governing sheath blight resistance has been detected in each of the 12 chromosomes of rice genome. These achievements were made possible by several researchers utilizing mapping populations and molecular markers tools [124]. RFLP and SSR markers were widely used for this purpose, along with Indel and CAPS markers [123, 125, 126]. Morphological markers are also used for mapping after developing recombinant inbred lines (RIL) population resulting from crosses between Tequing X Lemont [122]. In general, it is observed that indica subspecies possessed higher level of sheath blight resistance than japonica. This may be a valuable clue in the selection of rice lines for screening [127 - 129]. A study [130] first discovered qShB9-2, a major QTL, that contains ß 1,3 glucanase like defense gene [131]. Another QTL, qShBR11-1 was identified as major QTL with 14% total phenotypic variation [132]. Another study [133] recognized 10 candidate genes from resistant varieties like Jasmine 85, Tequing and MCR010277 those present within qShB9-2 [134] also identified four differentially expressed candidate genes from the vicinity of qShB9-2. The authors [123] identified 12 candidate genes in newly identified QTL *i.e.*, qAB9-TQ. On chromosome 11, a new QTL, qShB11-LE was identified using CAPS marker Z22-27C and Z23-33C [74,135]. 154 defence related candidate genes have been identified in qShBR11-1 region [132]. Combination effect of qSB9-2 and qSB12-1 were superior than their individual effect [94]. Pyramiding of three QTLs qSB7Tq, qSB9Tq and qSB11Le also showed superior resistance against sheath blight. A susceptible japonica variety introgressed with qSB-7-TQ and qSB-9-TQ has been able to reduce an average 14% yield loss under severe sheath blight disease conditions [136]. Three QTLs like qShB-1.1, qShB-1.2 and qShB-1.3 have been identified in a cross between CR-1014 and Swarna Sub-1 in F2 and F2:3 generations [137].

5.3. Breeding for ShB Disease Resistance

Breeding for ShB resistance is very difficult because of non-availability of resistant donors despite a large number of germplasms screened. Several ShB resistance QTLs have been mapped, but the consistency was not observed across the results from different studies. Combining well characterized sheath blight resistant QTLs in high yielding backgrounds through marker assisted selection may help in developing sheath blight resistant cultivars. Alternatively, transgenic offers scope for development of sheath blight resistant cultivars. qSBR11-1 was identified and mapped on chromosome 11 of

the 'Tetep' variety by Channamallikarjuna *et al*. [132]. They validated this QTL in the F2 progeny of crosses of 'Pusa-Basmati1xTetep' and in 96 randomly selected rice cultivars having varying degree of resistance to sheath blight. Another sheath blight qtl, qSB-9TQ has been well characterized from an indica cultivar, Teqing. Pinson *et al*. [122] introgressed resistant QTLs identified from Teqing into three rice germplasm lines which were later released as varieties in the USA. TIL:455, TIL:514 and TIL:642 were derived from a cross of 'Lemont' (PI 475833) and Teqing having eight sheath blight resistance novel alleles.

6. Durable Resistance against Emerging Diseases of Rice

6.1. Bakanae Disease of Rice

Bakanae disease of rice is one of the serious emerging diseases of rice. The disease is also called foolish seedling or foot rot or manly disease based on the type of symptoms it causes. The disease is caused by Ascomycetes fungi *Fusarium fujikuroi* (Nirenberg) [telomorph: *Gibberella fujikuroi* (Sawada) Ito]. The pathogen is highly seed-borne, and to some extent, it is soil borne and also can perpetuate through seed, soil and planting materials. The disease was reported for the first time in 1828 in Fukuoka region of Japan [138]. The disease emerges as a major problem in almost all the rice growing ecologies of the world, including Asia, Europe, North America and Africa [47,139]. In India, the disease is recorded in moderate to severe form in North Western states like Punjab, Haryana, Delhi, Uttarakhand, Jammu and Kashmir, and Eastern Uttar Pradesh, especially in Basmati growing regions [140]. But in recent years, the disease is emerging as a serious problem in non-basmati regions of eastern and northeastern India [141]. The disease produces a wide degree of symptoms such as abnormal elongation of the seedlings, lanky or pale green plants, production of roots from each node, foot rot/death of the seedlings, production of heavy fungal mass on base of the stem [140, 142]. The varied degree of symptoms is mainly due to the production of toxins/hormone by the pathogen. When fungus produces excessive gibberellines, it produces elongation and pale lanky seedlings. On the other hand, when the fungus produces fusaric acid, death/stunting or foot rot is noticed [47]. Several other species of Fusarium, including proliferatum, verticilloides, sacchari have been reported to cause the disease [143 - 145]. Losses due to the disease are as high as 70% in different parts of the world [146, 147]. In India, the disease can cause a significant yield loss of 15-25% [142, 148].

6.1.1. Rice Cultivars Resistant to Bakanae Disease

Management is not so easy once the disease is established in the field, and not even through the use of chemicals. Alternatively, there are no rice varieties which are found to be completely free from disease. Hence, finding out new resistant donor and their use in a resistant breeding program should be given priority. Significant work has been conducted by several researchers to identify the genes or QTLs responsible for disease resistance [149, 150]. Several resistant genotypes have been identified and utilized in resistance breeding program around the world. The first effort to identify the resistance in Japanese genotypes was made by Ito and Kimura [138]. Lu [151] identified some promising genotypes like Quingxi (at adult stage), Longjiao 86074-6 (moderately resistant at adult stage), Zupei 7, Dongrong 84-21, G-6, Sui 89-17 (seedling and adult plant stage). Ma *et al*. [152] screened rice germplasms possessing dwarf and semi-dwarf genes under natural field and artificial inoculated conditions and identified genotypes carrying sdq(t) and d2q genes as resistant. In India, several studies indicated that non-aromatic rice cultivars are more tolerant to the disease than aromatic cultivars [142, 149, 153, 154]. In contrast to these studies, the reports of Raghu *et al*. [141] showed that many non-aromatic cultivars are also susceptible to the disease. Bashyal *et al*. [140] and Gupta *et al*. [142] identified cultivars like Pusa Basmati 1121, Pusa Basmati 1509, Pusa 2511, CSR-30, Pusa basmati 1401, Pakistani Basmati and Dehradun Basmati as highly susceptible to the disease. Sunder *et al*. [153] identified rice genotypes like C 4-64 (green base), Karjat x 13-21, BR 4363-8-11-4-9, BR 1067- 84-1-3-2-1, IR 58109-109-1-1-3, BR 1257-31-1-1, HKR 96-561, MAUB 2009- 1, PNR 600 and RDN 01-2-10-9 as resistant to bakanae. Similarly, Fiyaz *et al*. [149] identified few resistant rice genotypes like C-101A51, Athad Apunu, Chandana, and Panchami. Cultivars like BPT-5204, Suphala, Himju, Peeli Badam as resistant to moderately resistant to the disease [149]. Similarly, genotypes like KKS-133 and IR-6 were found resistant in Pakistan [155]. Pusa Basmati-1342, IR-6582 and Calrose were resistant to the disease [156]. The works conducted by the researchers [157 - 159] reported that thirteen genotypes with moderate to high resistance reaction to bakanae disease, five genotypes with medium resistance and one genotype with moderate resistant reaction.

6.1.2. Identification and Utilization of Bakanae Disease Resistant Genes

Khan *et al*. [160] identified that the bakanae disease resistance is monogenic in nature and was dominant in cultivar KS 282 and recessive in IR-6. Various molecular techniques, including genome wide association study (GWAS) have been followed to identify the gene/QTL for disease resistance. Yang *et al*. [161] identified two QTLs such as qB1 and qB10, on chromosome 1 and chromosome 10 respectively, following japonica/indica double haploid population (Chunjiang 06 and TN-1). These QTLs showed additive effects with 13% phenotypic variation by each other. Similarly, a major QTL *i.e*., qBK1 present on long arm of chromosome 1 using near isogenic line (NILs) was identified by Hur *et al*. [162] in a cross between Shingwabng (HR- indica) and Ilpum (Susceptible japonica). Fiaz *et al*. [163] analysed RIL population of PB-1121 and Pusa 1342 and identified qBK1.1, qBK1.2 and qBK1.3 QTLs on chromosome1 and qBK3.1 on chromosome 3. Lee *et al*. [164] identified qBK1WD in a japonica variety Wonseadaesoo with 20.2% phenotypic variance. Later qBK1WD and qBK1 were pyramided which had an additive effect with more than 80.2% disease resistance. Lee *et al*. [165] identified a novel QTL *i.e*., qBK1z from an indica variety Zenith by performing QTL mapping of 180 F2:9 RILs [Zenith (R) X Ilpum (S)]. Ji *et al*. [166] mapped qFfR1, a major QTL from a cross between Nampyeong (resistant) and Dongjin AD (susceptible), having 180 F2:3 lines. Genome

wide association study was performed by Volante *et al*. [167] in 138 japonica germplasm and identified novel QTLs like qBK1_628091 and qBK4_31750955. Kang *et al*. [168] identified a new QTL *i.e*., qFfR9 on chromosome 9 in a japonica variety Samgwang.

6.2. False Smut Disease of Rice

Rice false smut was earlier regarded as a minor disease but recently, incidence has been increasing in many rice-growing countries of the world, including India [169, 170]. The disease is caused by *Ustilaginoidea virens* (Cooke) Takahashi that causes yield loss of rice by 2.8–81% based on rice genotypes and disease severity [171, 172]. The disease affects seed health and reduces the number of filled grains and 1000-grain weight [173]. It also has a negative effect on cooking and nutritional quality of the rice grains [174], and mycotoxins secreted by the pathogen is poisonous to livestock and human [175]. There is rampant use of agrochemicals for management of false smut disease, which is harmful to all living creatures and environment. The use of agro-chemicals to manage false smut disease is useless because the disease appears during harvesting stage. Thus, use of chemicals only increases the cost of crop production and gives less or no protection. The use of resistant varieties in endemic areas is the best management strategy to avoid losses *vis-à-vis* an economical and eco-friendly approach. Identification of false smut resistance QTL/gene in rice will enable the process of developing false smut resistant varieties in the future as such variety is not yet available.

6.2.1. Rice Cultivars Resistant to False Smut Disease

Development of high throughput phenotyping of false smut and also screening in hot spot, helped in identification of some highly resistant varieties during this decade. Varieties like IR28 [176], IR36 [80] and Ranjeet [174], Nongxiang 21, Luxiang 90-1 [177] and Shuangkang 7701 [177] were found to be resistant against the false smut.

6.2.2. Identification of QTLs Resistance to False Smut Disease of Rice

Around the globe, only a few works have been carried out for QTL identification against false smut of rice. Two QTLs related to false smut resistance were identified in F2 hybrid of IR28 and HXZ and mapped in chromosome 5 by using qGENE software [178]. Ten QTL were detected that influenced percentages of infected hills, infected panicles per plant and infected spikelets per panicle [179]. Five QTLs influencing resistance to false smut were detected by QTL Cartographer software [180]. The introgressed 266 Near Isogenic Lines (NILs) derived from the crosses between Tequing x Lemont were assessed for the disease resistant QTLs and found 2 QTL (QFsr10 and QFsr12) [180]. Four QTLs (qFsr-6-7, qFsr-10-5, qFsr-10-2 and qFsr-11-2) were observed by Li *et al*. [181] in different chromosome region of rice. Later some more QTLs for disease resistant were found in the NILs of crosses between Daguandao x IR28 [176]. In these NILs total 8 QTLs were found detected on chromosomes 1, 2, 4, 8, 10a, 10b, 11, and 12 designated qFsr1, qFsr2, qFsr4, qFsr8, qFsr10a, qFsr10b, qFsr11, and qFsr12. Another 5 QTLs were also detected in Nanxian and Yangzhou [176]. Five QTLs responsible for false smut resistance were detected in the RIL population. Of these, qFsr8–1 within a small region on chromosome 8 denotes the greatest phenotypic variance. The SSR markers genetically linked to qFsr8–1 were beneficial for marker-assisted breeding for resistance against false smut of rice [182]. DNMT2 (LOC_Os01g42630) was recognized as the most likely candidate gene for false smut resistance in Nanjing11 based on sequence variation and transcriptional responses to infection by *Ustilaginoidea virens* [183]. In India, the severity of false smut of rice has been reported from main rice producing states, such as West Bengal, Punjab, Uttar Pradesh, Tamil Nadu, Karnataka, Andhra Pradesh, Bihar, Maharashtra and Jammu & Kashmir [184]. In one study, out of seven QTLs mapped on rice chromosomes, two QTLs (qRFSr5.3 and qRFSr7.1a) were found linked with the infected panicle per plant, one QTL (qRFsr9.1) with total smut ball per panicle, and four QTLs (qRFSr2.2, qRFSr4.3, qRFSr5.4, and qRFSr7.1b) with disease score [89].

6.2.3. Association Mapping

GWAS was conducted with SSR markers using GLM, GLM+Q and MLM+Q+K and gave rise to 16 significant marker–trait associations such as percentage of infected plants, percentage of infected tillers, percentage of infected florets and disease intensity. Two major QTLs affecting the percentage of infected florets in the marker RM16131 (126.9 cM) and RM44 (60.9 cM) on chromosomes 3 and 8 were found that can be further utilized in marker-assisted selection [185].

6.3. Sheath Rot Disease of Rice

Rice sheath rot has evolved into a highly devastating disease and caused a yield loss from 20 to 85% [186]. Sheath rot disease is caused by mainly *Sarocladium oryzae*, *Fusarim* spp. and *Pseudomonas fuscovaginae* [187]. The Indian *S. oryzae* isolates varied in their pathogenicity, toxin production, and RAPD patterns [188]. In comparison with tall varieties, dwarf varieties were more susceptible to sheath rot disease due to their reduced internodes and poor exertion of the panicle from the flag leaf sheath [189]. Breeding for sheath rot resistance is limited due to the various causal agents and less genetic information on the disease. Puspam *et al*. [190] screened 43 rice genotypes for sheath rot disease resistance and reported that Swarna, Dhalaheera, JGL 3855 and Kattanur were resistant to sheath rot disease. The segregating pattern in an F2 population and recombinant inbred lines were used to explore the genetics of sheath rot disease resistance [191 - 193]. Hittalmani *et al*. [194] developed 188 recombinant inbred lines (RILs) from CO39 (susceptible)/Moroberekan (tolerant) population and evaluated them for field resistance to sheath rot disease. About nine QTLs were identified for sheath rot on different chromosomes (1, 2, 4, 5, 6, 7 and 8). Most of the sheath rot QTLs overlapped with rice blast QTLs. After the fine mapping of the resistant loci, markers associated to QTL for sheath rot resistance can be exploited in marker-assisted selection.

CONCLUSION

Several major genes conferring resistance to diseases like blast and bacterial blight have been identified, mapped and

cloned, but these number is very less for other emerging and re-emerging diseases of rice. However, QTLs with various level of resistance to those diseases have been mapped. Few of the QTLs work across populations but many of them are genotype specific. Different QTLs conferring resistance to the same disease have different modes of action. Thus, the identification of proper combinations of QTLs that give maximum durable resistance without any adverse effect on plant growth and development is the need of the hour. Also, resistant QTLs were identified, but these should be supplemented with genome wide association mapping to identify those QTLs which will work across populations. Although these efforts have been taken up by many researchers worldwide but it needs to be strengthened and sped up.

LIST OF ABBREVIATIONS

QTLs	=	Quantitative Trait Loci
BS	=	Brown Spot
FS	=	False Smut
MAS	=	Marker Assisted Selection
BB	=	Bacterial Blight

CONSENT FOR PUBLICATION

Not applicable.

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CONFLICT OF INTEREST

All the authors declared no conflict of interest, financial or otherwise.

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