Available cloned genes and markers for genetic improvement of biotic stress resistance in rice

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Biotic stress is one of the major threats to stable rice production. Climate change affects the shifting of pest outbreaks in time and space. Genetic improvement of biotic stress resistance in rice is a cost-effective and environment-friendly way to control diseases and pests compared to other methods such as chemical spraying. Fast deployment of the available and suitable genes/alleles in local elite varieties through marker-assisted selection (MAS) is crucial for stable high-yield rice production. In this review, we focused on consolidating all the available cloned genes/alleles conferring resistance against rice pathogens (virus, bacteria, and fungus) and insect pests, the corresponding donor materials, and the DNA markers linked to the identified genes. To date, 48 genes (independent loci) have been cloned for only major biotic stresses: seven genes for brown planthopper (BPH), 23 for blast, 13 for bacterial blight, and five for viruses. Physical locations of the 48 genes were graphically mapped on the 12 rice chromosomes so that breeders can easily find the locations of the target genes and distances among all the biotic stress resistance genes and any other target trait genes. For efficient use of the cloned genes, we collected all the publically available DNA markers (~500 markers) linked to the identified genes. In case of no available cloned genes yet for the other biotic stresses, we provided brief information such as donor germplasm, quantitative trait loci (QTLs), and the related papers. All the information described in this review can contribute to the fast genetic improvement of biotic stress resistance in rice for stable high-yield rice production.

KEYWORDS

biotic stress, marker-assisted selection, brown planthopper, blast, bacterial blight, marker, rice

1 Introduction

Rice (*Oryza sativa* L.) is a staple food of more than 50% of the world's population; notably, it is the most important crop in Asian countries. Recently, rice consumption has been rapidly increasing in Africa as well (Seck et al., 2012). Stable high-yield production of rice is highly associated with global food security (Bandumula, 2018). However, rice plants are inevitably encountering pressing challenges from different types of biotic/abiotic stresses that cause significant rice grain yield reduction (Khush, 2005; Dixit et al., 2020). Biotic stresses caused by pests and diseases pose a significant risk to global rice yield production by 52%, of which approximately 30% of these damages are due to pathogen infection (Savary et al., 2019; Jamaloddin et al., 2021). In addition, global climate change is a major threat to global food security (Schneider and Asch, 2020). A changing climate will influence the distribution and possibly the impact of rice diseases (Bebber, 2015; Chaloner et al., 2021) as well as host and disease interactions, mechanism, reproduction, and survival of pathogens (Velásquez et al., 2018).

Rice plants are attacked by diverse biotic agents, including insect pests, fungal and bacterial pathogens, and viruses. The prevalence of species of pathogens and biotypes/pathotypes is variable based on the environmental condition and geographical locations. Over the past decades, outbreaks due to pests and diseases have caused serious economic damage to rice-growing countries from time to time, locally and globally. For instance, some devastating damage from brown planthopper (BPH) infestation has been reported in different years in many rice-growing countries, including tropical and temperate Asia (Dyck and Thomas, 1979; Jena and Kim, 2010). Rice blast disease causes a loss of rice yield sufficient to feed 60 million people worldwide (Fahad et al., 2019; Singh et al., 2020). As a viral disease, a series of large-scale outbreaks of tungro were recorded in many tropical Asian countries, and it causes yield losses of 5% to 10% annually (Dai and Beachy, 2009). In Africa, rice yellow mottle virus (RYMV) is one of the most problematic biotic stresses, it reduces grain yield by 10%–100%, and severe attacks can lead to plant death (Kouassi et al., 2005). Still, today, severe biotic stress damage is reported in local or national media, implying that biotic stress damage affects local rice farmers, particularly small and marginal farmers.

There are several practical methods used to control pathogens, such as chemical spraying, crop rotation, field management, and host resistance. Among these, genetic improvement of host resistance by introgression of resistance genes through breeding and cultivation of resistant varieties is the most cost-effective and environmental-friendly strategy for controlling biotic agents. Thus, much effort has been exerted by scientists and breeders in isolating germplasms possessing resistance to a variety of biotic stresses from cultivars, landraces, and wild rice species in the genus *Oryza*. Through genetic analysis, they have also identified the genetic factors (quantitative trait loci (QTLs)/genes) that provide resistance from the isolated germplasm.

Once the genetic factors conferring biotic stress resistance are identified, they can be easily and effectively transferred to the target background varieties by marker-assisted selection (MAS) compared

to the conventional phenotype-based selection. DNA markers that can discriminate the alleles (sequences) between the donor and elite susceptible variety play important roles in efficiently deploying the identified genetic factors. Different types of molecular markers have been developed based on the types of sequence variations (short or long InDels and single-nucleotide polymorphisms (SNPs)) and successfully applied in the genetics and breeding of rice. Among them, the PCR-gel-based markers such as simple sequence repeat (SSR) markers, also called rice microsatellite (RM) markers, InDel markers, dominant PCR markers, tetra-primer method markers, and cleaved amplified polymorphic sequence (CAPS: PCR-restriction enzyme application-gel) markers are the most common in rice MAS breeding due to simplicity, in-house accessibility, and easiness to breeders (McCouch et al., 2002; Chen H, et al., 2011; Wang et al., 2012; Kim et al., 2016; Nadeem et al., 2018).

To improve the genetic potential of biotic stress resistance through MAS, two key factors are essential: genetic factors (QTLs and genes) and molecular tools (DNA markers). Compared to the QTL level of genetic factors, the cloned genes/alleles have some advantages: i) the genetic effect will be quite reliable because it was functionally validated by using transgenic approaches such as complementation test, RNAi, and CRISPR tools; ii) the exact physical location of the gene is identified, and thus, it enables a precision marker-assisted introgression of the target gene without linkage drag caused by the neighboring genes. Many biotic stress resistance genes were cloned from cultivars, landraces, and wild rice germplasm possessing "natural variations", but some of the genes were identified by transgenic approaches such as overexpression, RNAi, and CRISPR and also by using rice T-DNA tagging lines. Several review papers already covered recent advances in understanding the molecular mechanism of biotic stress resistances for BPH (Yan et al., 2023), blast (Liu W, et al., 2013; Li et al., 2019), and bacterial blight (Jiang et al., 2020; Pradhan et al., 2020) and also broad-spectrum disease resistance in rice (Ke et al., 2017; Liu et al., 2021). In this review, we focused on consolidating all the available cloned genes/alleles with corresponding donors possessing "natural variations" and all the related DNA markers for the breeding aspects. In addition, we briefly described some review papers and recent publications about the QTLs or germplasm if the cloned genes are not available for specific pathogens. We aimed to provide breeding-related information so that breeders can easily select the available resistant genes/alleles and the associated markers for the fast deployment of the proper genes/alleles in their breeding programs to deal with stable high-yield rice production and climate change.

2 Precision marker-assisted breeding by using the cloned genes/alleles

Deployment of QTLs and genes through marker-assisted breeding has been successfully improving the genetic potential of target traits in many crops. However, occasional acquisition of biotic stress resistance by the breeding process used to be associated

with yield penalties in crops (Brown, 2002) and also grain quality in rice (Fukuoka et al., 2009) probably due to the presence of unfavorable genes located in the vicinity of the target biotic stress resistance locus (also called linkage drag). Thus, precise introgression of biotic stress resistance genes through marker-assisted breeding of the cloned genes can reduce unexpected penalties in yield, grain qualities, and also other agronomic traits in the final breeding products. Recent advances in DNA sequencing, genotyping technologies, genome-wide association study (GWAS), functional genomics, and gene validation by using transgenic approaches have been accelerating the identification of the causal genes governing the target traits. Notably, many biotic stress resistance genes from the previously identified major QTLs have been gradually cloned. The cloned genes/alleles possessing natural variations are valuable for the genetic improvement of biotic stress resistance in rice. Furthermore, unlike QTL level genetic factors (more than several hundred kb), breeders can precisely introgress the gene (100 kb) using marker-based recombinant selection to avoid unwanted phenotypes caused by linkage drag in the final breeding lines because the exact physical location of the causal gene is clearly known. To date, 48 genes have been cloned for the major rice biotic stress, including bacterial blight (BB), blast, BPH, and rice viruses. The cloned gene names, gene IDs of rice databases (RAP-DB and MSU), encoding proteins, the physical location of the genes, donor germplasm, and its original research papers are summarized in this review. In some cases, the previously reported major QTLs from different sources were identified as the same gene (same locus) with different alleles (different sequences). For example, *BPH1=BPH10=BPH18=BPH21/BPH2=BPH26/BHP7/BPH9* on the long arm of Chr 12 ("=" and "/" means identical and different alleles, respectively) and *Pi9/Pi2/Piz-t/Pi50/PigmR* on the short arm of Chr 6 are the different resistant alleles but the same locus. Due to the same physical locations, those alleles cannot be pyramided, and thus, the potential best allele should be selected and used in the breeding program. In this review, we focused on the cloned biotic stress resistance genes with the gene-linked markers. Moreover, we briefly mentioned some genetic resources such as QTLs or donor materials if there are no cloned genes yet for some biotic stresses.

3 Insect pests and available genetic resources

Globally, more than 100 species of insects attack rice plants, and approximately 20 of them can cause economic damage (Pathak and Khan, 1994). Major insect pests of rice are stem borers, leafhoppers and planthoppers, gall midges, and grain-sucking bugs. Efforts to isolate the resistant germplasm and genetic factors against insect pests identified a number of QTLs for the major insect pests. At the gene level, a handful of genes were cloned for only BPH resistance, but to date, no genes have been cloned yet for other insect pest resistance. Here, we described BPH resistance genes cloned and some genetic resources (QTLs and donor sources) for other insect pests.

3.1 Brown planthopper (*Nilaparvata lugens*)

Among the major insect pests, BPH is one of the most destructive pests, especially in Asian countries including both tropical and temperate zones, causing severe economic loss to the rice crop through directly sucking phloem sap, often causing "hopper burn", and it serves as a vector for transmission of rice ragged stunt virus (RRSV) and rice grassy stunt virus (RGSV) (Cabauatan et al., 2009). To date, more than 45 genetic loci providing BPH resistance have been identified from diverse plant materials, including cultivars, landraces, and wild rice species. Among them, seven genes (seven independent loci) comprising 10 different alleles for BPH resistance were cloned, that is, *BPH14*, *BPH30*, *BPH17*, *BPH6*, *BPH29*, *BPH32=BPH3*, and *BPH1=BPH10=BPH18=BPH21/BPH2=BPH26/BHP7/BPH9*. The cloned genes with physical locations, RAPDB/MSU gene ID, protein encoded, donor sources, and corresponding references are summarized in Table 1. *BPH14* gene encoding nucleotide-binding site (NBS) and leucine-rich repeats (LRRs), "NBS-LRR" or "NLR" in short, was first cloned from the previously mapped *Qbp1* on Chr 3 of the *Oryza officinalis* introgression by genetic mapping and following transgenic complementation test (Du et al., 2009). With similar approaches, the *BPH17* QTL on Chr 4S of the Sri Lankan rice variety, Rathu Heenati (Sun et al., 2005), revealed that three repeats of lectin receptor kinase gene (*OsLecRK1-OsLecRK3*) are responsible for BPH resistance (Liu et al., 2015). However, Liu et al. (2015) named the gene identified from the *BPH17* QTL as *BPH3* gene, and thus, it might cause confusion with the original *BPH3* QTL mapped on Chr 6S of donors (PTB33 and Rathu Heenati varieties) (Jairin et al., 2007). To avoid confusion, we followed the original *BPH17* QTL name as *BPH17* gene name in this review. Afterward, Ren et al. (2016) cloned the causal gene of BPH resistance from the previously fine-mapped *BPH3* locus of PTB33 (Jairin et al., 2007) using bioinformatics and transgenic validation experiments. The cloned gene encodes an unknown short consensus repeat (SCR) domain-containing protein and the *BPH3* QTL was renamed as *BPH32* (*BPH32=BPH3*) (Ren et al., 2016). Some of the BPH-resistant loci from different sources overlapped at the same locus, resulting in four clusters on chromosomes 4S, 4L, 6S, and 12L (Fujita et al., 2013; Du et al., 2020). From the largest BPH QTL cluster on Chr 12L containing *BPH1*, *BPH2*, *BPH7*, *BPH9*, *BPH10*, *BPH18*, *BPH21*, and *BPH26* (Fujita et al., 2013), *BPH26* encoding NBS-LRR protein was first cloned from the *BPH26* QTL derived from ADR52 (Tamura et al., 2014). Then, *BPH18* from the *BPH18* QTL originated from the *Oryza australiensis* introgression line (IL) (IR65482-7-216-1-2) was cloned and identified as the same gene with *BPH26* because physically two genes are located at the same locus on Chr 12L. However, the sequences, including promoter and protein-coding sequences (CDS) and also BPH reactions, were different between *BPH26* and *BPH18* (Ji et al., 2016). *BPH9* derived from Pokkali was also identified as the same gene as *BPH18/BPH26*, but it showed different gene sequences and also different BPH reactions (Zhao et al., 2016), suggesting that all three are the same gene (locus) but

TABLE 1 The cloned BPH resistance genes.

Gene	Chr	Location (bp)[a]	MSU_ID	RAPDB_ID	Encoding protein	Resistant/ donor allele	Inheritance pattern of R- allele	Reference
BPH14	3	35,693,286	Os03g63150	Os03g0848700	NBS-LRR	*Oryza officinalis* IL	Dominant	Du et al., 2009
BPH30	4	929,966	Os04g02520	–	Protein with two leucine-rich domains (LRDs)	AC-1613	Dominant	Shi et al., 2021
BPH17[b]	4	6,940,275	Os04g12540– Os04g12560– Os04g12580	Os04g0201900– Os04g0202300– Os04g0202500	A cluster of three genes encoding plasma membrane-localized lectin receptor kinases (OsLecRK1-OsLecRK3)	Rathu Heenati	Dominant	Liu et al., 2015
BPH6	4	21,396,879	Os04g35210	Os04g0431700	Atypical LRR	Swarnalata	Dominant	Guo et al., 2018
BPH29	6	484,346	Os06g01860	Os06g0107800	B3 domain-containing protein	RBPH54 (*Oryza rufipogon* IL)	Recessive	Wang Y, et al., 2015
BPH32 =BPH3[c]	6	1,223,069	Os06g03240	Os06g0123200	Unknown short consensus repeat (SCR) domain-containing protein	Ptb33	Dominant	Ren et al., 2016
BPH1=BPH10=BPH18=BPH21/ BPH2=BPH26/BHP7/BPH9[d]	12	22,886,341	Os12g37290	Os12g0559400	NBS-LRR	IR65482-7-216-1-2 (*BPH18*), ADR52 (*BPH26*), T12 (*BPH7*), Pokkali (*BPH9*)	Dominant	Tamura et al., 2014 (*BPH26*), Ji et al., 2016 (*BPH18*), Zhao et al., 2016 (*BPH9* and other alleles)

"=" means the identical allele, and "/" means the different alleles at the same locus.
[a]Location of the translation start codon (ATG) of the cloned genes on the rice reference genome IRGSP1.0 (https://rapdb.dna.affrc.go.jp/).
[b]BPH17 was identified from the mapping populations derived from the cross Rathu Heenati (R) and 02428 variety (S) by Sun et al. (2005). In a subsequent study, Liu et al. (2015) cloned the BPH resistance gene from the same materials, but the gene was probably mistakenly named BPH3 in the publication. Hence, to avoid confusion with previously reported BPH3 QTL (Jairin et al., 2007), the original name QTL name (BPH17) was given in this review.
[c]BPH32 was identified by using bioinformatics and transgenic gene validation experiments by Ren et al. (2016) from the previously fine-mapped BPH3 locus (Jairin et al., 2007).
[d]Eight BPH genes clustered on Chr 12L were identified as multi-alleles with four different sequences (four allele types) at the same locus (Zhao et al., 2016). However, the NILs with the same allele types (BPH10, BPH18, and BPH21) showed a bit different BPH resistance among the same allele types (Jena et al., 2017).

functionally different alleles. Based on the sequence analysis of the Chr 12L BPH cluster, Zhao et al. (2016) classified the eight genes into four allelotypes, *BPH1=BPH10=BPH18=BPH21/ BPH2=BPH26/BHP7/BPH9*. However, the BPH near-isogenic lines (NILs) with the same allele types (*BPH10*, *BPH18*, and *BPH21*) showed slightly different BPH resistance among the same allele types (Jena et al., 2017). Although four different functional alleles were identified on Chr 12L, they cannot be pyramided by MAS breeding due to their same locations. Guo et al. (2018) cloned the *BPH6* encoding NBS-LRR protein from the previously found *BPH6* QTL originating from the Swarnalata variety, which exhibits resistance to biotype 4, the most devastating BPH biotype in South Asia, of Bangladesh BPH populations (Kabish and Khush, 1988).

The recessive gene *BPH29* located at Chr 6 was found to encode a B3-domain containing protein from the RBPH54 IL possessing BPH resistance derived from the wild rice species *Oryza rufipogon* (Wang Y, et al., 2015). *BPH30* gene located on Chr 4 of the *indica* variety AC-1613 was identified as a gene that encodes a novel protein with two leucine-rich domains (Shi et al., 2021). In addition to the cloned BPH genes, a number of QTLs and fine-mapped QTLs are also available (Fujita et al., 2013; Naik et al., 2018; Du et al., 2020). Moreover, using 10 different BPH genes/QTLs, 25 NILs possessing single or two to three genes were developed in an *indica* variety background, IR24 (Jena et al., 2017). The set of BPH NILs will be useful for screening suitable BPH genes/alleles against regional BPH biotypes and for genetic improvement of BPH

resistance in the local elite variety backgrounds. To achieve durable and broad-spectrum resistance, QTL/gene pyramiding approaches are widely used in breeding programs. Overall, the BPH-NILs with two to three genes exhibited more strong and broad-spectrum resistance than the NILs harboring a single BPH gene (Jena et al., 2017). In addition, pyramiding effects of two to three BPH gene combinations such as *BPH14 + BPH15*, *BPH6 + BPH12*, and *BPH13 + BPH14 + BPH15* were observed in different backgrounds or breeding programs (Hu et al., 2012; Qiu et al., 2012; Hu et al., 2016).

3.2 Other planthoppers

A handful of genetic factors governing resistance against planthoppers, including small brown planthopper (SBPH: *Laodelphax striatellus*), white-backed planthopper (WBPH: *Sogatella furcifera*), green leafhopper (GLH: *Nephotettix virescens*), and green rice leafhopper (GRH: *Nephotettix cincticeps*), have been identified from diverse germplasms and are well summarized in a few review papers (Fujita et al., 2013; Du et al., 2020). In this review, we only included recent progress on genetic factors to other planthoppers. A stable locus showing WBPH resistance in 2 years was found in the RM280-RM6909 region on Chr 4L from the Cheongcheong variety (Kim et al., 2021). The high resistance locus designated as *Bph38* to both BPH and WBPH was identified from *O. rufipogon* and was fine-mapped to a 79-kb region on Chr 4 (Yang et al., 2020). Phi et al. (2019) identified a major QTL (*qGRH4.2=GRH6*) conferring GRH resistance from a wild species (*Oryza nivara*_IRGC105715) and fine-mapped the locus to ~31-kb region on Chr 4. Recent studies showed a possibility that increasing resistance to multiple insects could be achieved by the pyramiding of insect resistance loci. For example, both GLH and GRH resistance was obtained by pyramiding of two GRH resistance genes, *GRH2* and *GRH4* (Horgan et al., 2018); enhanced resistance against multiple herbivore species, including zig-zag leafhopper (*Recilia dorsalis*), BPH, and WBPH, was shown by pyramiding of two to three GRH resistance loci (*GRH2* and *GRH4-6*) (Horgan et al., 2019).

3.3 Rice gall midge (*Orseolia oryzae*)

To date, 12 potential genetic factors (*Gm1–Gm12*) conferring resistance against Asian rice gall midges (*O. oryzae*) have been reported. Among them, 10, except for *Gm9* and *Gm10*, are mapped on rice chromosomes (Bentur et al., 2016; Leelagud et al., 2020). Although no *Gm* genes have been fully validated by using transgenic approaches, four QTLs were fine-mapped with potential candidate genes: *gm3* (donor: RP2068-18-3-5 breeding line from Velluthacheera) on 560-kb region of Chr4L (Sama et al., 2014), *Gm4* (donor: Abhaya) on 300-kb region of Chr 8 (Divya et al., 2015), *Gm8* (donor: Aganni) on 430-kb region of Chr 8 (Divya et al., 2018), and *gm12* (donor: MN62M) on 345-kb region of Chr 2 (Leelagud et al., 2020). These four QTLs might be useful in a breeding program. However, the donor sources showing resistance against Indian gall midge biotypes, including Velluthacheera (*gm3*),

Abhaya (*Gm4*), and Aganni (*Gm8*), were susceptible to all eight Thailand gall midge populations (Leelagud et al., 2020), suggesting that the suitable genetic factors should be selected based on the potential biotypes of insects.

3.4 Other insect pests

Five QTLs associated with leaf-folder (*Cnaphalocrocis medinalis*) resistance, with 8.0%–21.1% phenotypic variance explained (PVE), were found from the double haploid population (CJ06 × TN1), and pyramiding of QTLs affected resistance to leaf-folder (Rao et al., 2010). However, reliable genetic factors controlling other insect resistance, including stem borer and grain-sucking bugs, have not been reported yet.

4 Fungal diseases and available genetic resources

Several major fungal pathogens threaten stable high-yield rice production. The major fungal diseases of rice are "bakanae disease" (pathogen: *Gibberella fujikuroi*, syn. *Fusarium fujikuroi*), "brown spot" (pathogen: *Cochliobolus miyabeanus*, syn. *Bipolaris oryzae*, *Helminthosporium oryzae*), "narrow brown leaf spot" also called "narrow brown spot" (pathogen: *Sphaerulina oryzina*, syn. *Cercospora janseana*, *Cercospora oryzae*), "false smut" (pathogen: *Ustilaginoidea virens*), "leaf scald" (pathogen: *Microdochium oryzae*), "sheath blight" (pathogen: *Rhizoctonia solani*, syn. *Thanatephorus cucumeris*), "aggregate sheath spot" (pathogen: *Rhizoctonia oryzae-sativae*), "sheath rot" (pathogen: *Sarocladium oryzae*), "stem rot" (pathogen: *Sclerotium oryzae*, syn. *Nakataea oryzae*), and "blast" (pathogen: *Magnaporthe oryzae*, syn. *Pyricularia oryzae*). Among fungal diseases, blast has been intensively studied compared to other fungal diseases. As a result, a handful of blast-resistance genes have been cloned, but no cloned genes are available yet for other fungal diseases.

4.1 Blast (pathogen: *M. oryzae*, syn. *P. oryzae*)

Among the fungal diseases, rice blast is the most devastating fungal disease of rice worldwide, causing a serious threat to the world's food security. The blast pathogen can affect all above-ground parts of a rice plant, including the leaf, collar, node, neck, parts of the panicle, and sometimes the leaf sheath (IRRI Rice Knowledge Bank). Blast disease occurs in 85 countries, and it causes a 10%–35% loss of harvest (Fisher et al., 2012), and the amount of rice damaged by blast annually is sufficient to feed 60 million people worldwide (Pennisi, 2010; Fahad et al., 2019; Singh et al., 2020). There are over 100 blast resistance QTLs/loci identified from diverse germplasm including cultivars, landraces, and wild relatives of rice (Ashkani et al., 2016; Li et al., 2019). The *Pib* (donor: *indica* cultivar Engkatek) and *Pita* (donor: *indica* cultivar Tadukan) were the first cloned blast resistance genes, and both

encode NBS-LRR domains predicted to be cytoplasmic proteins (Wang et al., 1999; Bryan et al., 2000). To date, 23 genes (23 independent loci) consisting of ~35 different alleles have been cloned, including three panicle blast resistance genes *Pb1–Pb3* (Table 2). The cloned genes were distributed across the rice chromosomes except for chromosomes 5, 7, and 10. Chromosomes 6 and 11 harbored four and six blast genes, respectively (*Pi9* alleles, *Pid4*, *Pid3* alleles, and *Pid2* on Chr 6; *Pia* alleles, *Pi54rh* alleles, *Pik* alleles, *Pb1*, *Pb2*, and *Pb3* on Chr 11). Several blast-resistant QTLs were identified at the same location on the short arm of Chr 6 (10.4-Mb region) from different germplasms. Finally, the causal genes were located at the NLR gene-repeated cluster (*Pi9* locus), and they are regarded as the same genes with different alleles (*Pi9/Pi2=Piz-5/Piz-t/Pi50/Pigm/Pizh*). At the *Pi9* locus, two to 13 repeats of NLR gene were laid next to each other,

and the blast-resistant donors possessed nine repeats (*Pi9* and *Pi2*) or 13 repeats (*Pigm*) of NLR genes (Deng et al., 2017). There were sequence variations among the alleles of the responsive NLR gene at the *Pi9* locus, and they showed different reactions to the blast strains. In addition to the cloned genes/alleles, one major QTL (*Pi40*) was identified at the *Pi9* locus from the *O. australiensis*-derived IL (IR65482-4-136-2-2) through fine mapping (Jeung et al., 2007). The *Pi40* introgression in Korean and Turkish varieties showed resistance to a wide range of blast strains in Korea and Turkey (Jeung et al., 2007; Beser et al., 2016). Another major cluster was found on Chr 11 (25.2-Mb region) (*Pik* locus) from various donor materials, and they (*Pik/Pik-m/Pik-p/Pi1/Pi7*) were identified as allelic (Table 2). Interestingly, most of the cloned blast genes encode NBS-LRR (NLR) protein, except for four genes: *bsr-d1* (C2H2-type zinc finger protein), *pi21* (proline-rich protein), *Pid2*

TABLE 2 The cloned blast resistance genes.

Gene	Chr	Location (bp)	MSU_ID	RAPDB_ID	Encoding protein	Resistant/donor allele	Inheritance pattern of R-allele	Reference
Pit	1	2,681,220	Os01g05620	Os01g0149500	NBS-LRR	K59	Dominant	Hayashi K, et al., 2010
Pi64	1	33,098,082	Os01g57280	Os01g0781200	NBS-LRR	Yangmaogu	Dominant	Ma et al., 2015
Pi37	1	33,120,499	Os01g57310	Os01g0781700	NBS-LRR	St. No. 1	Dominant	Lin et al., 2007
Pish/Pi35	1	33,136,846	Os01g57340	Os01g0782100	NBS-LRR	Nipponbare (*Pish*), Hokkai 188 (*Pi35*)	Dominant	Takahashi et al., 2010 (*Pish*), Fukuoka et al., 2014 (*Pi35*)
Pib	2	35,118,769	Os02g57310	Os02g0818500	NBS-LRR	Engkatek	Dominant	Wang et al., 1999
bsr-d1	3	18,435,990	Os03g32230	Os03g0437200	C2H2-type zinc finger protein	Digu	Dominant	Li et al., 2017
pi21	4	19,835,206	Os04g32850	Os04g0401000	Proline-rich protein	Owarihatamochi	Recessive	Fukuoka et al., 2009
Pi63	4	31,554,480	Os04g52970	Os04g0620950	NBS-LRR	Kahei	Dominant	Xu et al., 2014
Pi9/ Pi2=Piz-5/Piz-t/ Pi50/ PigmR[(e)]*/ Pizh*	6	10,387,509	Os06g17900	Os06g0286700	NBS-LRR	*Oryza minuta* IL (75-1-127) (*Pi9*), C101A51 (*Pi2*), Toride 1 (*Piz-t*), Er-Ba-Zhan (*Pi50*), Gumei 4 (*PigmR*), ZH11 (*Pizh*)	Dominant	Qu et al., 2006 (*Pi9*), Zhou et al., 2006 (*Pi2* and *Piz-t*), Su et al., 2015 (*Pi50*), Deng et al., 2017 (*PigmR*), Xie et al., 2019 (*Pizh*)
Pid4	6	10,435,819	Os06g17950	Os06g0287500	NBS-LRR	Digu	Dominant	Chen et al., 2018
Pid3/ Pi25/ Pid3-I1	6	13,054,818	Os06g22460	Os06g0330100	NBS-LRR	Digu (*Pid3*), Gumei2 (*Pi25*), MC276 (*Pid3-I1*)	Dominant	Shang et al., 2009 (*Pid3*), Chen J, et al., 2011 (*Pi25*), Inukai et al., 2019 (*Pid3-I1*)
Pid2	6	17,160,333	Os06g29810	Os06g0494100	B-lectin receptor kinase	Digu	Dominant	Chen et al., 2006
Pi36	8	2,878,884	Os08g05440	Os08g0150150	NBS-LRR	Kasalath (formerly known as Q61)	Dominant	Liu et al., 2007
Pi5	9	9,681,913	Os09g15840	Os09g0327600	NBS-LRR	RIL260-Moroberekan	Dominant	Lee et al., 2009
Pi56	9	9,777,527	Os09g16000	Os09g0328951	NBS-LRR	Sanhuangzhan No 2 (SHZ2)	Dominant	Liu Y, et al., 2013

(Continued)

TABLE 2 Continued

Gene	Chr	Location (bp)	MSU_ID	RAPDB_ID	Encoding protein	Resistant/donor allele	Inheritance pattern of R-allele	Reference
Pia/Pi-CO39	11	6,541,924	Os11g11790–Os11g11810	Os11g0225100–Os11g0225300	Two genes encoding NBS-LRR	Sasanishiki (*Pia*), CO39 (*Pi-CO39*)	Dominant	Okuyama et al., 2011 (*Pia*), Cesari et al., 2013 (*Pi-CO39*)
Pi54rh/Pi54=Pik-h	11	25,263,336	Os11g42010	Os11g0639100	NBS-LRR	*Oryza rhizomatis* (*Pi54rh*), Tetep (*Pi54*)	Dominant	Das et al., 2012 (*Pi54rh*), Zhang et al., 2018 (*Pi54*)
Pik/Pik-m/Pik-p/Pi1/Pi7	11	27,983,597	Os11g46200-Os11g46210	Os11g0688832–Os11g0689100	Two genes encoding NBS-LRR	Kusabue (*Pik*), Tsuyuake (*Pik-m*), K60 (*Pik-p*), C101LAC (*Pi1*), IRBL7-M (*Pi7*)	Dominant	Zhai et al., 2011 (*Pik*), Ashikawa et al., 2008 (*Pik-m*), Yuan et al., 2011 (*Pik-p*), Hua et al., 2012 (*Pi1*), Gan et al., 2010 (*Pi7*)
Pita	12	10,606,359	Os12g18360	Os12g0281300	NBS-LRR	Tadukan	Dominant	Bryan et al., 2000
Ptr = Pita2	12	10,822,534	Os12g18729	Os12g0285100	Armadillo repeats protein	Katy (*Ptr*), IRBLta2-Re (*Pita2*)	Dominant	Zhao et al., 2018 (*Ptr*), Meng et al., 2020 (*Pita2*)
Pb1	11	22,862,447	Os11g38580	Os11g0598500	NBS-LRR	Modan	Dominant	Hayashi N, et al., 2010
Pb2	11	27,608,621	Os11g45620	–	NBS-LRR	Jiangnanwan	ND	Yu et al., 2022
Pb3	11	27,282,232	Os11g45090	Os11g0675200	NBS-LRR	Haplotype A, Bodao	ND	Ma et al., 2022

ND, not determined.

(B-lectin receptor kinase), and *Ptr=Pita2* (armadillo repeat protein). The majority of blast-resistant donor alleles/genes are dominant except for *pi21*, which is recessive (Liu W, et al., 2013). *Pi21* encodes a proline-rich protein, and the loss-of-function allele from the resistant donor (Owarihatamochi) confers non-race-specific resistance. *pi21* gene was closely linked to the gene providing poor eating quality. However, the genes were successfully separated by recombination between two genes in the breeding lines, and blast resistance with good eating quality was achieved (Fukuoka et al., 2009). Thus, precise introgression with the cloned target genes is able to reduce the presence of unwanted phenotypes in the final breeding products caused by "linkage drag". Among the cloned blast genes, *Pi50*, *Pizh*, *Pi54rh*, *Pi56*, *Pi64*, *PigmR*, and *Ptr=Pita2* alleles were known as broad-spectrum resistance (Liu et al., 2021). A few sets of NILs with blast resistance sources were developed in both *japonica* and *indica* backgrounds: 20 NILs with 11 blast QTLs/genes in *japonica* background Lijiangxintuanheigu (LTH) (Telebanco-Yanoria et al., 2010) and 28 NILs with 14 QTLs/genes in an *indica* background, CO39 (Telebanco-Yanoria et al., 2011). Moreover, both NIL sets were tested by 20 blast isolates collected in the Philippines. Recently, 21 NILs with 18 QTLs/genes in another *indica* background, US-2, were developed, and the NILs were tested with 31 isolates from Asia (Japan, China, the Philippines, Indonesia, Vietnam, Cambodia, Bangladesh, and Laos) and Africa (Nigeria, Kenya, and Benin) (Fukuta et al., 2022). In blast bioassay with the NIL sets above, most of the genes/QTLs showed differential reactions against different isolates, even in the same country collections, suggesting that the selection of suitable blast genes/alleles based on the local pathotypes/isolates is important to develop blast resistant varieties. Among the blast genes

used in the NIL development above, NIL-*Pi9* exhibited resistance or moderate resistance to all 31 isolates from Asia and Africa (Fukuta et al., 2022), suggesting that *Pi9* allele might be useful to breed blast-resistant variety across the rice cultivation countries. The sets of NILs and blast screening data against various isolates will be very useful to pathology studies, the selection of suitable genes/alleles against regional isolates, and breeding programs. To achieve durable and broad-spectrum resistance, pyramiding of resistance genes (two or more) in one background is usually used in the breeding program. There are various gene combinations of blast genes that prove the enhanced blast resistance in both *indica* and *japonica* rice against several blast isolates. Two genes–pyramided lines with *Pi37 + Pid3*, *Pi5 + Pi54*, *Pi54 +Pid3*, and *Pigm + Pi37* exhibited significantly enhanced resistance and observable additive effects (Jiang et al., 2019). The gene combinations *Pigm + Pi1*, *Pigm + Pi54*, and *Pigm + Pi33* displayed broad-spectrum resistance (Wu et al., 2019). Broad-spectrum blast resistance was also achieved in the temperate *japonica* varieties by pyramiding three to four genes with *Piz*, *Pib*, *Pik*, *Pita*, and *Pita2* (Zampieri et al., 2023). As proven in many previous studies, stacking suitable blast genes/alleles has strong potential to obtain durable and broad-spectrum resistance in the breeding program.

In contrast to leaf blast resistance, genetic resources for blast disease on other organs/tissues are relatively poor. The first panicle blast resistance gene, *Pb1*, encoding NBS-LRR was cloned from an *indica* cultivar Modan (Hayashi N, et al., 2010). Afterward, it was found that panicle blast resistance by *Pb1* is dependent on at least four other loci (Inoue et al., 2017), suggesting that a level of panicle blast resistance with *Pb1* will be influenced by other genetic factors or background materials. Recently, two additional panicle blast

resistance genes, *Pb2* and *Pb3*, were identified through GWAS and validated by transgenic approaches (Ma et al., 2022; Yu et al., 2022). Both genes encode NBS-LRR proteins and are physically close to each other (~360-kb distance between *Pb2* and *Pb3*). Some of the cloned leaf blast genes, such as *Pi25* (Chen J, et al., 2011), *PigmR* (Deng et al., 2017), and *Pid4* (Chen et al., 2018), also showed some level of panicle blast resistance.

4.2 Bakanae disease (pathogen: *G. fujikuroi*, syn. *F. fujikuroi*)

To identify the genetic factors governing bakanae disease resistance, QTL mapping and GWAS have been conducted and identified a handful of QTLs on chromosomes 1, 3, 4, 9, and 10 from several different donors, but no genes have been cloned yet. Three major QTLs (*qBK1*, *qBK1.1*, and *qFfR1*) were fine-mapped on the Chr 1 region between 23.32 and 23.67 Mb (Lee et al., 2021).

4.3 False smut (pathogen: *U. virens*)

A number of QTLs for false smut resistance have been identified by QTL mapping with bi-parental populations (Andargie et al., 2018; Han et al., 2020; Neelam et al., 2022) and GWAS (Hiremath et al., 2021). The results suggested that false smut resistance seems to quantitate traits governed by multiple genes. Among the QTLs, *qFsr8–1* originated from the Chinese rice landrace MR183–2 and showed the highest PVE (26.0%).

4.4 Sheath blight (pathogen: *R. solani*, syn. *T. cucumeris*)

More than 200 QTLs associated with sheath blight (ShB) resistance have been identified from the diverse mapping populations (Zarbafi and Ham, 2019; Goad et al., 2020). Among all the identified ShB QTLs, two loci on Chr 9 (*qShB9-2*) and Chr 11 (*qSBR11-1*) contribute 25% and 14% of PVE, respectively, are the major effect QTLs (Molla et al., 2020), and may be useful in a breeding program.

4.5 Brown spot (pathogen: *C. miyabeanus*, syn. *B. oryzae*, *H. oryzae*)

For brown spot (BS) resistance, susceptible and resistant germplasms were identified by several studies. Several cultivars that have been categorized as resistant did not show complete resistance (immunity), but they showed quantitative resistance to BS. To date, more than 20 QTLs with low–mild phenotypic variation (<20%) were identified from several mapping populations, including recombinant inbred lines (RILs), doubled haploid lines (DHLs), and chromosome segment substitution lines (CSSLs) from several different donors (reviewed by Mizobuchi et al., 2016). One major QTL, *qBSR11-kc*, showing 23.0%–25.9% of the

total phenotypic variation was identified from *indica* variety CH45 (Matsumoto et al., 2017).

4.6 Narrow brown leaf spot also called "narrow brown spot" (pathogen: *S. oryzina*, syn. *C. janseana*, *C. oryzae*)

The genetic architecture of narrow brown spot (narrow brown leaf spot) resistance was almost unknown. A recent genetic analysis using the RIL population derived from the cross between two US varieties (Cypress and LaGrue) identified a single large-effect QTL, *CRSP-2.1*, explaining 81.4% of the phenotypic variation (Addison et al., 2021). The causal gene is not confirmed yet, but the major QTL might be useful in a breeding program.

4.7 Aggregate sheath spot (pathogen: *R. oryzae-sativae*)

Aggregate sheath spot disease has been reported in many Asian countries, as well as the USA, South America, and Australia, and it can cause ~20% of yield loss (Lanoiselet et al., 2007). Good levels of resistance to aggregate sheath spot were identified from *O. rufipogon* and successfully transferred into cultivars (McKenzie et al., 1994). Recent GWAS with tropical *japonica* and *indica* populations identified a handful of QTLs (Rosas et al., 2018).

4.8 Sheath rot (pathogen: *S. oryzae*)

Rice sheath rot diseases are found in most rice-growing areas of the world and cause 20%–85% ranges of yield losses, making it an emerging ubiquitous destructive disease of rice (Bigirimana et al., 2015). However, rice sheath rot is less studied, and no reliable germplasm or genetic factors have been identified yet.

4.9 Stem rot (pathogen: *S. oryzae*, syn. *N. oryzae*)

Stem rot disease resistance was found in wild rice species (*O. nivara* and *O. rufipogon*) and weedy rice (*O. sativa* f. *spontanea*) (Figoni et al., 1983), and the stem rot resistance was successfully transferred from *O. rufipogon* to California rice cultivars through interspecific hybridization (Oster, 1992). Recently, several QTLs for stem rot resistance were identified from *indica* germplasm through a GWAS analysis (Rosas et al., 2018).

5 Bacterial diseases and available genetic resources

Rice productions are significantly affected by several major bacterial diseases: BB (pathogen: *Xanthomonas oryzae* pv. *oryzae*

(*Xoo*)), "bacterial leaf streak" (BLS) (pathogen: *X. oryzae* pv. *oryzicola* (*Xoc*)), "bacterial sheath brown rot" also called "rice sheath rot" (pathogen: *Pseudomonas fuscovaginae*), and "bacterial seedling rot" (BSR), and "bacterial grain rot" (BGR) caused by the same pathogen (*Burkholderia glumae*). To date, a handful of genes have been cloned for BB resistance, but none yet for other bacterial diseases. Here, we described BB resistance genes cloned and some genetic resources for other bacterial pathogens.

5.1 Bacterial blight (pathogen: *X. oryzae* pv. *oryzae* (*Xoo*))

Among the bacterial diseases, BB caused by *Xoo* is the most destructive bacterial disease in rice. Thus, it has been intensively studied for the isolation of BB-resistant germplasm, genetic analysis, gene identification, and molecular mechanism of wars between *Xoo* and rice. To date, at least 47 *Xoo* resistance QTLs and genes (named *Xa* genes) have been identified from diverse germplasms, including cultivated rice, rice mutant lines, and wild rice species. *Xa21* from *Oryza longistaminata* introgression line (IRBB21) was first cloned in 1995 by Song et al. and followed by *Xa1* from the IRBB1 line (Yoshimura et al., 1998). Later, *Xa2*, *Xa31(t)*,

CGS-Xo1, *Xa14*, and *Xa45(t)* were identified as a group of *Xa1* allelic R genes (Ji et al., 2020). Currently, 13 different genes/loci consisting of ~23 allelotypes have been cloned and characterized (Table 3), that is, *Xa1/Xa2=Xa31(t)/Xa14/Xa45(t)/CGS-Xo1*, *Xa3=Xa26*, *Xa4*, *xa5*, *Xa7*, *Xa10*, *xa13/OsSWEET11/Os8N3*, *Xa21*, *Xa23*, *Xa47(t)*, *xa25/OsSWEET13/OsMtN3*, *Xa27*, and *xa41(t)/OsSWEET14/Os11N3*. The 13 cloned BB resistance genes encode several types of proteins: NBS-LRR (*Xa1/Xa1* alleles and *Xa47(t)*), leucine-rich repeat receptor-like kinases (LRR-RLKs) (*Xa3=Xa26* and *Xa21*), a cell wall-associated kinase (WAK) (*Xa4*), executor R proteins (*Xa7*, *Xa10*, *Xa23*, and *Xa27*), SWEET/sugar transporter proteins (*xa13/OsSWEET11*, *xa25/OsSWEET13*, and *xa41(t)/OsSWEET14*), and a transcription factor gamma subunit protein (*xa5*). The genes encoding NBS-LRR, LRR-RLK, and WAK are involved in pathogen recognition and activation of the innate immune system, whereas the genes encoding executor R proteins are transcriptionally activated by the *Xoo* transcription activator-like (TAL) effector protein and trigger programmed cell death (PCD)-based hypersensitive response (HR). Thus, for the genes mentioned above, the functional alleles from the BB-resistant donor sources are dominant. In contrast, BB resistance is caused by sequence mutations at the TAL effector binding sites in the promoter of the SWEET (Sugar Will Eventually be Exported

TABLE 3   The cloned bacterial blight resistance genes.

Gene	Chr	Location (bp)	MSU_ID	RAPDB_ID	Encoding protein	Resistant/donor allele	Inheritance pattern of R-allele	Reference
Xa1/ Xa2=Xa31 (t)/Xa14/ Xa45(t)/ CGS-Xo1	4	31,638,099	Os04g53120	Os04g0622600	NBS-LRR	IRBB1 (*Xa1*), IRBB2 (*Xa2*), IRBB14 (*Xa14*), Zhachanglong (*Xa31(t)*), Carolina Gold Select (*CGS-Xo1*), *Oryza nivara* IRGC102463 (*Xa45(t)*)	Dominant	Yoshimura et al., 1998; Ji et al., 2020
xa5	5	437,043	Os05g01710	Os05g0107700	Transcription factor IIA gamma subunit	IRBB5	Recessive	Blair et al., 2003; Iyer and McCouch, 2004
Xa27	6	23,653,851	Os06g39810	Os06g0599600	Executor R protein	IRBB27/*Oryza minuta* IRGC101141	Dominant	Gu et al., 2005
Xa7[a]	6	28,015,259	–	–	Executor R protein	IRBB7	Dominant	Chen et al., 2021; Wang et al., 2021
xa13/ OsSWEET11/ Os8N3	8	26,725,952	Os08g42350	Os08g0535200	SWEET-type protein	IRBB13	Recessive	Chu et al., 2006
xa41(t)/ OsSWEET14/ Os11N3	11	18,171,707	Os11g31190	Os11g0508600	SWEET-type protein	African wild and cultivated rice species *Oryza barthii* and *Oryza glaberrima*	Recessive	Hutin et al., 2015
Xa21	11	21,277,443	Os11g36180	Os11g0569733	LRR receptor kinase-like protein	IRBB21 (*Oryza longistaminata* IL)	Dominant	Song et al., 1995
Xa10	11	22,181,556	Os11g37570	Os11g0586400	Executor R protein	IRBB10, CAS209	Dominant	Tian et al., 2014
Xa23	11	22,204,131	–	Os11g0586701	Executor R protein	CBB23/*Oryza rufipogon*	Dominant	Wang C, et al., 2015

(Continued)

TABLE 3 Continued

Gene	Chr	Location (bp)	MSU_ID	RAPDB_ID	Encoding protein	Resistant/donor allele	Inheritance pattern of R-allele	Reference
Xa47(t)	11	27,983,597	Os11g46200	Os11g0688832	NBS-LRR	*O. rufipogon*	Dominant	Xing et al., 2021
Xa4[b]	11	28,357,055	Os11g47140	Os11g0694100	cell wall-associated kinase (WAK)	IRBB4	Dominant	Hu et al., 2017
Xa3=Xa26	11	28,399,360	Os11g47210	–	LRR receptor kinase-like protein	Minghui 63, IRBB3	Dominant	Sun et al., 2004
xa25/ OsSWEET13/ OsMtN3	12	17,302,127	Os12g29220	Os12g0476200	SWEET-type protein	Minghui 63	Recessive	Liu et al., 2011

[a]The sequence of Xa7 is completely absent in the Nipponbare reference genome (IRGSP1.0) and also most of japonica varieties. Thus, the location of the closest marker (M10) to Xa7 by Chen et al. (2021) is given in the above table.
[b] The sequence of xa4 gene was not fully aligned in the Nipponbare reference genome (IRGSP1.0). Thus, the information of the highest homology sequence was described above.

Transporter) genes and thus a recessive allele. BB resistance of *xa5* gene relies on one amino acid difference between resistance and susceptible lines in *Xa5* protein (a general eukaryotic transcription factor), and the BB-resistant allele is recessive (Iyer and McCouch, 2004). The cloned 13 genes are distributed on six chromosomes (one gene each on Chr 4, 5, 8, and 12; two genes on Chr 6; six genes on Chr 11) (Table 3, Figure 1). Six cloned genes on Chr 11 are closely located to each other in ~10.2-Mb size (18.2–28.4-Mb region on Chr 11) (Figure 1). Thus, in the case of gene pyramiding using the six genes on Chr 11, breeders need to consider producing enough progenies for obtaining pyramided alleles that occur by recombination between two closely located genes. Several cloned genes, including *Xa7*, *Xa23*, *xa41*, and *Xa47*, were reported as broad-spectrum resistance genes/alleles (Liu et al., 2021). NILs with single BB resistance genes were developed through IRRI-Japan collaboration designated as "IRBB" lines (Ogawa et al.,

1991), and additional NILs (IRBB) with single or multiple BB resistance genes (two to five genes) were developed in the BB-susceptible background IR24 at IRRI, Philippines. Differential reactions of the NILs (IRBB lines) with single and pyramided *Xa* genes to 11 races in the Philippines were observed, and the results are available at the IRRI Rice knowledge bank (http://www.knowledgebank.irri.org/ricebreedingcourse/Breeding_for_disease_resistance_Blight.htm). The IRBB lines possessing multiple *Xa* genes (two to five genes) exhibited broad-spectrum resistance than the single gene introgression IRBB lines. Similarly, pyramiding of *Xa* genes such as *Xa21 + Xa33*, *Xa21 + xa13 + xa5*, and *Xa4 + xa5 + Xa7 + xa13 + Xa21* offers greater and broader resistance to *Xoo* than an individual resistance gene (Pradhan et al., 2015; BalachIranjeevi et al., 2018; Hsu et al., 2020). The IRBB sets were also tested with 16 isolates in Korea, and the results showed that *xa5* was strong and broad-spectrum
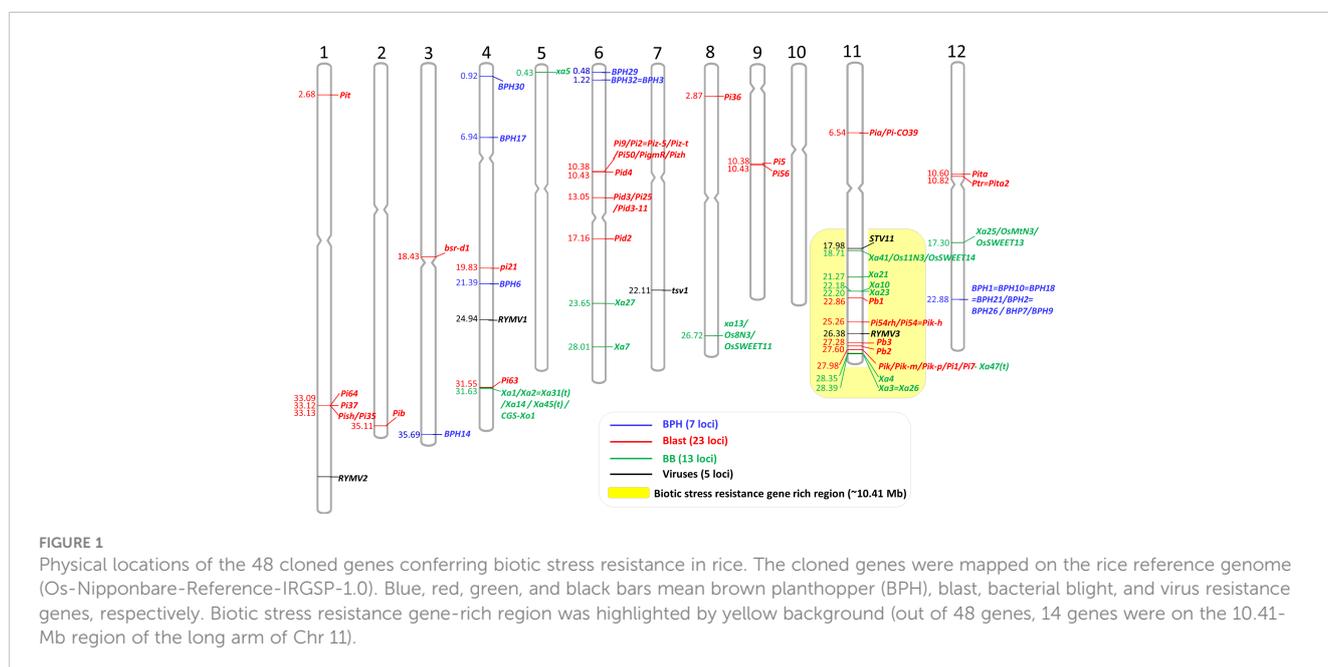
FIGURE 1
Physical locations of the 48 cloned genes conferring biotic stress resistance in rice. The cloned genes were mapped on the rice reference genome (Os-Nipponbare-Reference-IRGSP-1.0). Blue, red, green, and black bars mean brown planthopper (BPH), blast, bacterial blight, and virus resistance genes, respectively. Biotic stress resistance gene-rich region was highlighted by yellow background (out of 48 genes, 14 genes were on the 10.41-Mb region of the long arm of Chr 11).

resistant than any other *Xa* genes (Jeung et al., 2006). Rice possessing *Xa7* exhibited less disease than lines without *Xa7* over 11 years in the Philippines, even though the virulence of *Xoo* field populations increased. In addition, *Xa7* restricted disease more effectively at high temperatures, while other *Xa* genes were less effective at high temperatures (Webb et al., 2010). The IRBB lines and stacked information including gene reactions, spectrum, durability, and influence of environments will be useful to select suitable genes/alleles for regional/local breeding programs and also for the development of durable and broad-spectrum resistant rice varieties.

5.2 Bacterial leaf streak (pathogen: *X. oryzae* pv. *oryzicola* (*Xoc*))

For BLS resistance, a handful of QTLs with low-to-moderate PVEs (2.64%–15.93%) were identified (Tang et al., 2000). In addition, a recent GWAS using 510 diverse rice accessions identified 79 quantitative trait nucleotides (QTNs) reflecting 69 QTLs for BLS resistance (Xie et al., 2021). However, no BLS resistance gene has been cloned yet. Among the BLS-resistant QTLs, the highest effect QTL, *qBlsr5a* (12.84%–15.93% PVE), was fine-mapped to 30.0-kb interval on Chr 5, and the resistant parent allele of *Os05g01710* gene within the fine-mapped region was identical to *xa5*, which is one of major BB resistance genes, suggesting that *Os05g01710* (*xa5*) is possibly the candidate gene of *qBlsr5a* (Xie et al., 2014).

5.3 Bacterial sheath brown rot also called rice sheath rot (pathogen: *P. fuscovaginae*)

"Rice sheath rot" disease symptoms can be caused by the bacterial pathogen "*P. fuscovaginae*" and also by the fungal pathogen "*S. oryzae*". A recent pathobiomes study revealed that *P. fuscovaginae* and *S. oryzae* were prevalent in symptomatic rice samples in highland and lowland, respectively, in Burundi, indicating that the pathogens exist independently and are not part of a complex disease (Musonerimana et al., 2020). However, no reliable resistant germplasm and genetic factors have been identified yet.

5.4 Bacterial panicle blight, bacterial seedling rot, and bacterial grain rot (pathogen: *B. glumae*)

Bacterial panicle blight (BPB), BSR, and BGR are caused by the same bacterial pathogen, *B. glumae*. It was first reported as BGR in Japan in 1955. Since then, BPB has been found in more than 18 countries globally including Asia, Africa, and North and South America (Zhou, 2019; Ortega and Rojas, 2021). Although it is an emerging disease globally, only several cultivars with partial resistance and 12 QTLs associated with partial resistance have been reported (Zhou, 2019). Regarding BSR resistance, one QTL

(*RBG1/qRBS1*) was identified from the CSSL population (Nona Bokra introgressions in Koshihikari background) (Mizobuchi et al., 2016). For BGR resistance, 13 QTLs have been found from the two mapping populations: a BIL from Kele (R) × Hitomebore (S) and a RIL from TeQing (R) × Lemont (S) (Mizobuchi et al., 2016).

6 Viral diseases and available genetic resources

Seventeen rice viruses have been reported, including rice black-streaked dwarf virus (RBSDV), rice bunchy stunt virus (RBSV), rice dwarf virus (RDV), rice gall dwarf virus (RGDV), rice giallume virus (RGV), RGSV, rice hoja blanca virus (RHBV), rice necrosis mosaic virus (RNMV), RRSV, rice stripe necrosis virus (RSNV), rice stripe virus (RSV), rice transitory yellowing virus (RTYV) also named as rice yellow stunt virus (RYSV), rice tungro bacilliform virus (RTBV), rice tungro spherical virus (RTSV), RYMV, southern rice black-streaked dwarf virus (SRBSDV), and rice stripe mosaic virus (RSMV) (Hibino, 1996; Qin et al., 2019). Since most of the above viruses are arthropod-borne, damages may become more severe as the population of vector insects increases. Among the rice virus diseases, rice tungro disease (RTSV and RTBV), RYMV, and RSV have been causing serious yield loss in South/Southeast Asia, Africa, and temperate Asia, respectively. Thus, a few genes providing resistance to the major viruses above have been cloned. The use of viral disease resistance may significantly reduce the damage of viral diseases. In addition to this, the management of corresponding vector insects may mitigate the damage of viral diseases in the field.

6.1 Rice tungro disease caused by RTSV and RTBV

Rice tungro disease is a serious threat to rice production in South and Southeast Asia. Tungro disease viruses are transmitted from tungro-infected plant to another by leafhoppers. The most efficient vector is the green leafhopper (IRRI Rice Knowledge Bank). Tungro was found to be associated with two distinct viruses: RTSV and RTBV. A series of large-scale outbreaks of tungro were recorded in India, Thailand, Indonesia, Malaysia, the Philippines, Thailand, China, and Bangladesh. Tungro, as one of the destructive diseases of rice, causes yield losses of 5% to 10% annually and is estimated to cause an annual loss in rice production of approximately 1.5 billion US dollars worldwide (Dai and Beachy, 2009). In the late 1990s, several tungro-resistant sources, including landrace and wild species, were isolated and used in the breeding program by IRRI, and the most promising breeding lines were developed by crossing with Utri Merah donor (Azzam and Chancellor, 2002). Afterward, Encabo et al. (2009) revealed that RTBV and RTSV are inherited separately from rice accession Utri Merah, conferring resistance to both RTBV and RTSV, and Lee et al. (2010) cloned the causal recessive gene (named as *tsv1*) involved in RTSV resistance in Utri Merah. *TSV1* encodes eukaryotic translation initiation factor 4G (eIF4G), and mutation

on the protein-coding sequence of *TSV1* in Utri Merah (*tsv1* allele) may impair the RTSV RNA translation, resulting in tungro resistance. The *tsv1*-Utri Merah allele is widely used for tungro resistance improvement in many breeding programs.

6.2 Rice yellow mottle virus

Since RYMV was first discovered in Kenya in 1970, it has been reported from only the countries in the African continent. RYMV causes the most serious damage in Africa among all the rice diseases. Primary infection of RYMV in rice fields is mediated by beetle family chrysomelids, and secondary spread occurs mainly through mechanical contact between infected and healthy leaves by wind (Kouassi et al., 2005). In the past, farmers have been advised to use chemicals to eliminate beetle vectors. The most effective and sustainable way to manage RYMV is to use tolerant and resistant varieties (Abo et al., 1997).

High RYMV resistance was found in one African rice cultivar (*Oryza glaberrima*), Tog5681, and one *O. sativa* cultivar, Gigante. Evaluation of the crosses of these two highly RYMV-resistant cultivars suggests the presence of a single recessive gene (Ndjiondjop et al., 1999). Later, it was discovered that the gene is *RYMV1*, and the gene encodes a eukaryotic translation initiation factor, eIF4(iso)4G (Albar et al., 2006). In sequence comparisons with the dominant susceptible allele (*Rymv1-1*), four different recessive resistant alleles from one *O. sativa* var. Gigante (*rymv1-2*) and three *O. glaberrima* accessions (Tog5681 (*rymv1-3*), Tog5672 (*rymv1-4*), and Tog5674 (*rymv1-5*)) were characterized by the presence of short amino acid substitutions or short deletions in the MIF4G domain of the protein (Albar et al., 2006; Thiémélé et al., 2010). Allele-specific markers targeting mutations or deletions characterizing different *RYMV1* were developed for improving MAS for the introduction of the resistance alleles into susceptible cultivars of *O. sativa* or *O. glaberrima* (Thiémélé et al., 2010). In the second major recessive resistance gene, *RYMV2*, it was identified that 1-bp deletion on the coding sequence of the rice homolog of the *Arabidopsis CPR5* gene, known to be a defense mechanism regulator, from the resistant African rice (*O. glaberrima*) Tog7291 provided RYMV resistance (Orjuela et al., 2013). A single dominant resistant gene *RYMV3* encoding NBS-LRR protein was identified from the *O. glaberrima* Tog5307 (Pidon et al., 2017). Novel resistant alleles and accessions for *RYMV2* and *RYMV3* were identified by screening 268 *O. glaberrima* accessions and sequencing (Pidon et al., 2020), and five new resistant germplasm were isolated from Korean rice lines (Asante et al., 2020). The cloned genes with different resistant alleles will be useful to improve RYMV resistance, especially for the breeding program for the African continent.

6.3 Rice stripe virus

RSV is an RNA-type virus belonging to the genus *Tenuivirus*, and it is transmitted by SBPHs. RSV has been reported only in China, Japan, Korea, and Taiwan, where *japonica* rice is cultivated, and it caused severe damage to the rice fields in Eastern China,

Japan, and Korea. While most *indica* varieties are resistant to RSV, the majority of *japonica* varieties are highly susceptible. A number of RSV-resistant QTLs have been reported from diverse *indica*-resistant donors, and the major QTLs were repeatedly detected on Chr 11 among several QTL mapping (Cho et al., 2013). Finally, the major QTL, *qSTV11*, originated from an *indica* variety Kasalath and was cloned (Wang et al., 2014). *STV11*-Kasalath allele encodes a sulfotransferase (OsSOT1) protein catalyzing the conversion of salicylic acid (SA) into sulfonated SA (SSA), whereas the protein encoded by the susceptible allele *STV11* loses this activity. *STV11* gene will be useful in improving RSV resistance in the *japonica* varieties.

7 Physical locations of the cloned genes/alleles on rice chromosomes

Graphical mapping of the cloned genes on 12 rice chromosomes will be useful information for MAS breeding, especially for gene pyramiding, as well as mapping new biotic stress resistance genes. We mapped the physical locations of all the cloned 48 biotic stress resistance genes on the 12 rice chromosomes (Figure 1). The cloned genes were not evenly distributed across the rice genome. No biotic stress resistance gene was cloned yet on Chr 10. In contrast, Chr 11 possesses the highest number of genes (15 genes), following Chr 6 (eight genes), Chr 4 (seven genes), and Chr 12 (four genes), with these four chromosomes harboring 34 genes out of 48 cloned genes (70.83%). Interestingly, 14 cloned genes associated with blast, bacterial blight, and virus resistance were on the 10.41-Mb region of the long arm of Chr 11 (Chr 11: 17.98–28.39 Mb), and it took 29.16% of the cloned genes. Biotic stress resistance genes are ~10 times more enriched in this specific region than any other loci (the expected distribution is ~1.2 cloned gene/10 Mb). Another interesting point is that the bacterial blight resistance gene *Xa47 (t)* (*Os11g46200*) encoding NBS-LRR is overlapped with the blast resistance gene *Pik/Pik-m/Pik-p/Pi1/Pi7* consisting of two NBS-LRR genes (*Os11g46200* and *Os11g46210*). In some loci, different resistance alleles at the same locus, such as *BPH1* locus, *Pi9* locus, *Pik* locus, and *Xa1* locus, were identified (Tables 1–3). Although some of them among the alleles showed different reactions to pathotypes, unfortunately, they cannot be pyramided by MAS due to the same physical location among the alleles. Thus, breeders need to choose one suitable allele among the alleles based on the regional pathotypes/isolates. Similarly, in gene pyramiding/stacking, breeders should also consider the physical distance between/among the target genes. If the two target genes are closely located with each other (<~1Mb) on the same chromosome (for example, *Xa10* and *Pb1* on Chr 11, *Pik* and *Xa4* on Chr 11, and *Pita* and *Ptr=Pita2* on Chr 12; see Figure 1), breeders need to produce many progenies to obtain the gene pyramided plants through the selection of the recombinant plants between the two target loci. In rice, a handful of recombination hot and cold regions are reported, and the average recombination frequency is approximately 4.35 cM per Mb (Si et al., 2015). In addition, breeders also need to check the target loci whether the important genes governing other agronomic traits are present near the target biotic stress resistance gene to avoid

linkage drag. For instance, a key amylose synthesis gene *Waxy/GBSS1* (1.76-Mb location on Chr 6) is tightly linked with *BPH32* (1.22 Mb on Chr 6), and a major heading date gene *Hd1* (9.33 Mb on Chr 6) is closely located with *Pi2* gene (10.38 Mb on Chr 6). Thus, breeders should consider the locations of the important agronomic traits genes near the target genes, especially when the breeders try to retain the original characteristics of the elite background variety, except for the target biotic stress resistance. A map of the physical locations of the cloned genes (Figure 1) will be helpful for consideration of the above points in MAS breeding programs.

8 Available DNA markers for MAS breeding

DNA markers are essential tools for genetic analysis as well as marker-assisted breeding. We tried to collect all the markers published and used in the previous breeding programs, and we collected ~500 markers in total for the cloned biotic stress resistance genes (Table S1). We filed essential information on the markers for the potential users, including marker types (InDel, CAPS/dCAPS, dominant markers, and tetra-primer method markers) and primer sequences. Also, we cited the original references of each marker so that breeders can obtain detailed and additional information if needed. Furthermore, we mapped the location of all the markers in the rice reference genome sequence (Os-Nipponbare-Reference-IRGSP-1.0: https://rapdb.dna.affrc.go.jp/). This information provides physical distance between the target gene and the markers, and it will be helpful to reduce the selection of false positives during MAS. For examples, some markers for the *BPH1*, *BP17*, *xa13*, *Xa27*, *Pi9*, *Piz-t*, *Pizh*, *Pish*, *Pi5*, *Pita2*, and *RYMV1* genes/alleles are a bit far (>1 Mb) from the gene locus (Table S1). Selection of genic or gene-tightly linked markers would reduce false-positive selection. In cases of multi-alleles for the same gene, such as *BPH1* and *Pi9*, all the available markers for the same gene can be tested to check the possibility of polymorphism between the

parents, and the selected polymorphic markers can be used in MAS breeding (for example, *BPH18* markers for *BPH26* MAS breeding). All the information on the markers is described in Table S1.

9 Conclusions and perspective

In this review, we summarized all the cloned genes associated with biotic stress resistance (Tables 1–4), mapped the physical location of the genes on 12 rice chromosomes (Figure 1), and consolidated the available markers associated with the cloned genes (Table S1). Furthermore, we also briefly introduced genetic resources such as QTLs and donor sources for some biotic stress if the cloned genes are not available yet. The information presented in this review will be helpful for checking the available genetic resources for biotic stress resistance and also for MAS breeding for the genetic improvement of biotic stress resistance in rice. As shown in many previous reports, pyramiding of QTLs/genes might be a practical solution to breed durable and broad-spectrum resistant varieties.

Approximately 48 genes, which are natural alleles and provide biotic stress resistance, have been cloned only for the major biotic stresses, including BPH, blast, BB, and some viruses. However, no genes have been cloned yet for other biotic stresses. Preparation of the reliable genetic factors (genes/QTLs) associated with currently problematic and emerging pathogens is very important for stable high-yield rice production, and thus, scientists/geneticists need to put much effort into this pending issue. Screening wild relatives of rice in the genus *Oryza* will be one of the ideal approaches. Many biotic stress resistance genes were already cloned from wild germplasm (see Tables 1–3), such as *BPH14* (*O. officinalis*), *Pi9* (*Oryza minuta*), and *Xa21* (*O. longistaminata*). More than 4,500 accessions of wild rice species are stored in the IRRI Genebank (Banaticla-Hilario and Sajise, 2022), and most of the germplasms were not screened yet. Recently, a genome-wide InDel marker set (475 polymorphic markers) discriminating the alleles between *O. sativa* and the other seven AA-genome *Oryza* species was developed

TABLE 4 The cloned virus resistance genes.

Gene	Chr	Location (bp)	MSU_ID	RAPDB_ID	Encoding protein	Resistant/donor allele	Inheritance pattern of R-allele	Reference
tsv1	7	22,114,961	Os07g36940	Os07g0555200	Eukaryotic translation initiation factor 4G (eIF4G)	Utri Merah (UM82)	Recessive	Lee et al., 2010
RYMV1	4	24,946,171	Os04g42140	Os04g0499300	Eukaryotic translation initiation factor isoform 4G-1 (eIF(iso)4G1)	*Oryza sativa* Gigante (*rymv1-2*)/*Oryza glaberrima* accessions Tog5681, Tog5672, and Tog5674 for *rymv1-3*, *rymv-4*, and *rymv-5*, respectively	Recessive	Albar et al., 2006; Thiémélé et al., 2010
RYMV2	1	40,073,727	Os01g68970	Os01g0918500	Constitutive expresser of PR genes5 (CPR5)	*O. glaberrima* Tog7291	Recessive	Orjuela et al., 2013
RYMV3	11	26,380,866	Os11g43700	Os11g0657900	NBS-LRR	*O. glaberrima* Tog5307	Dominant	Pidon et al., 2017
STV11	11	17,985,011	Os11g30910	Os11g0505300	Sulfotransferase (OsSOT1)	Kasalath	ND	Wang et al., 2014

ND, not determined.

to harness AA-genome wild species (Hechanova et al., 2021). The genes identified from wild germplasm will be rare alleles due to mostly untapped and unused materials in breeding, and thus, they will be effective in most *indica* and *japonica* backgrounds.

The incidence of pathogens and insect pests will change in time and space; notably, it will be also influenced by climate changes. As examples, some BPH resistance genes were affected by artificial climate change conditions (the atmospheric temperature with corresponding carbon dioxide at the ambient, year 2050 and year 2100) (Kuang et al., 2021) and also by nitrogen fertilizer treatments (Lin et al., 2022). Moreover, most of the genes/QTLs reported were tested with limited numbers of isolates/biotypes, which were collected in specific locations and years. Thus, the identified genes/QTLs could not guarantee resistance across locations, time, and environments. Testing donor germplasm, especially sets of NILs possessing specific genes/QTLs such as NILs for BPH (Jena et al., 2017), blast (Telebanco-Yanoria et al., 2010; Telebanco-Yanoria et al., 2011; Fukuta et al., 2022), and BB (Ogawa et al., 1991; IRBB lines), with prevalence races/biotypes in the target regions, would be a good strategy to select effective genes/alleles in breeding program.

DNA markers are essential tools for genetic analysis and breeding. DNA markers could reduce the time and effort in developing and improving biotic-resistant cultivars through marker-assisted breeding. Due to the accessibility and technical simplicity for the rice breeders, most of the markers are PCR and gel-based markers, including SSR (RM) markers, InDel markers, CAPS markers, tetra-primer PCR markers, and dominant PCR markers (Table S1). These markers have contributed much to MAS breeding. However, the gene/allele-specific markers are limited to some specific genes, and a high portion of the markers are the gene-linked makers (sometimes more than a few Mb distance from the gene), probably causing that false-positive selection in MAS breeding. Thus, breeders should check the marker–gene linkage (distance between the gene and markers) and also marker quality (reproducibility and polymorphism between parents) before starting MAS breeding. For efficient and precious introgression of the target genes, currently, available markers might be insufficient. Developments of breeder-friendly allele-specific markers and enough number of polymorphic markers with high reproducibility for many biotic stress resistance genes/alleles are urgently needed. This will help the rapid deployment of target biotic stress resistance genes in the elite local varieties.

In addition to MAS breeding, CRISPR-based genome editing technologies might be an alternative solution for the fast improvement of biotic stress resistance. The advantage of genome editing is that the techniques can directly improve target traits in elite backgrounds without crossing with the donor lines. Thus, some unexpected phenotypes caused by linkage drag or other donor introgressions happening during MAS breeding will not be considered in genome editing-based trait improvement. Recently, its potential was already shown in BB resistance improvement by CRISPR-based promoter editing of three *SWEET* genes in rice (Oliva et al., 2019) and in tungro virus resistance by editing of *TSV1* gene (Macovei et al., 2018). Another advantage is that

genome-edited products are regulated with lesser stringency in many countries compared to conventional genetically modified organisms (GMOs). Together with cross-based breeding, genome editing technologies can contribute fast genetic improvement of target traits in the elite variety backgrounds without linkage drag and other donor introgressions.

Author contributions

JH, C-PL, AT, E-KA, JJ, I-RC, RS, KJ, and S-RK conceived this review paper. ES, SH, I-RC, and S-RK performed the literature search and wrote the draft. The manuscript was improved by revisions by all the authors. All authors agreed to the published version of the manuscript.

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Conflict of interest

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Supplementary material

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