Vol. 22(8), pp.146-152, August 2023
DOI: 10.5897/AJB2023.17572
Article Number: C7D8FC371069
ISSN: 1684-5315

http://www.academicjournals.org/AJB

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African Journal of Biotechnology

Full Length Research Paper

Genome-wide association analysis identifies resistance loci for bacterial blight in diverse East African rice germplasm

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Received 14 April, 2023; Accepted 31 July, 2023

***Xanthomonas oryzae pv. oryzae (Xoo),* the causal agent of rice bacterial blight disease has been extensively characterized, and loci against different races identified. Many rice cultivars have been developed and utilized to combat the disease, however, due to the rapid evolution of *Xoo*, several resistances have broken down. The continuous challenge of ever-evolving *Xoo* and the breakdown of resistance in cultivated rice varieties make it even more important to discover new loci to enable sustainable durable deployment of broad-spectrum resistance genes in elite breeding lines. African germplasm can be exploited as reservoirs of useful genetic variation for bacterial blight (BB) resistance. This study was conducted to identify loci associated with BB resistance and new genetic donors for the breeding program. To identify candidate sources of resistance for advancing breeding, four virulent strains of *Xoo* (PXO99, MAI1, BAI3, and *Xoo*3-1) were used to screen 78 East African accessions by genome-wide association studies. The diverse accessions' core genetic base exhibited high resistance to the *Xoo* strains. 50.63% of the accessions were highly resistant to the Philippines strain PX099, while 20.25% were highly susceptible to the virulent West African strain MAI1. Two novel resistant loci significantly associated hotspots were identified using 1901 SNPs. The two hits were located on chromosome 12 (*Xa25*) and Chr. 6 (*Xa7, Xa27, Xa33*). Novel loci were identified that gives a useful basis for more investigation and a wide core genetic pool of high resistance for broad-spectrum resistance for genetic improvement.**

Key words: Genome-wide association, *Oryza sativa,* bacterial blight (BB), *Xanthomonas oryzae*, disease resistance.

INTRODUCTION

Bacterial blight (BB), caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), is one of the most devastating and economically important diseases of rice (*Oryza sativa* L.) all over the world (Savary et al., 2019). Rice resistance

against BB can be generally divided into two main categories; the qualitative resistance controlled by major resistance (*R*) genes, and the quantitative resistance conferred by multiple minor genes or quantitative trait loci (QTLs) (Ramalingam et al., 2003; Deng et al., 2012; Bossa-Castro et al., 2018).

So far, over 40 R genes that confer qualitative resistance to BB has been identified (Jiang et al., 2020) and 11 of them (*Xa1, Xa3/Xa26, Xa4, xa5, Xa10, xa13, Xa21, Xa23, xa25, Xa27, xa41*) have been cloned successfully by using map-based cloning strategy or knowledge-based molecular screening (Yoshimura et al., 1998; Han et al., 2014; Hutin et al., 2015; Wang et al., 2015; Ji et al., 2018). The *R* genes with comparatively broader spectra of resistance such as *Xa3*, *Xa4*, *Xa7*, *xa13*, *Xa21,* and *Xa23*, have been widely used in rice breeding programs, and many resistant rice cultivars have been released (Huang et al., 1997; Han et al., 2014; Wang et al., 2015; Zhang et al., 2015; Hu et al., 2017; Jiang et al., 2020).

Although the disease resistance conferred by a single *R* gene is usually effective against certain races of the *X. oryzae* pv. *oryzae* pathogen, the resistance is easily breakdown due to greater selection pressure on pathogen evolution. Conversely, the quantitative resistance mediated by QTLs is presumably non-race-specific and is considered more durable (Liu et al., 2016). Thus, it has attracted more attention in the past decades and more than 70 QTLs for BB resistance have been identified (Li et al., 2006; Han et al., 2014; Djedatin et al., 2016; Dilla-Ermita et al., 2017; Zhang et al., 2017; Bossa-Castro et al., 2018).

Deployment of broad-spectrum resistant rice cultivars is considered the most effective and environmentally friendly way to control bacterial blight (Zhang et al., 2017), quantitative resistance has been considered as a preferred strategy to achieve durable resistance although marker-assisted selection has not been effectively used for the improvement of BB resistance in rice. This issue is attributed to the polygenic nature of the trait and each QTL has a small effect. It is therefore difficult to accumulate multiple QTLs with small effects in breeding. In addition, most of the QTLs for BB resistance were identified and mapped using bi-parental population QTL analysis in the past decades. Because of limited molecular markers used and fewer recombinants in a primary mapping population, most of the QTLs for BB resistance are mapped to a region of 10 ~ 30 cM (Yang et al., 2021). Since a prerequisite for successful marker-assisted selection (MAS) is the availability of markers that are closely linked with the target gene, the inaccuracy of QTL mapping hinders the application of MAS. Therefore, the discovery of the large-effect QTLs and the use of a more powerful approach for the genetic dissection of complex traits are crucial to address this issue challenge in rice production.

Genome-wide association studies (GWAS) present another alternative with two main advantages: (1) it can use a nature population instead of a bi-parental population. The rice varieties used in GWAS contain much more genetic diversity than the bi-parental lines used in segregation populations. Because using diverse germplasm for QTL mapping in GWAS, favors the identification of large-effect and novel QTLs; (2) most GWAS can result in a relatively high mapping resolution due to the existence of numerous historical recombination events (Takeda and Matsuoka, 2008) and using plenty of SNPs for association mapping. Therefore, GWAS provides a powerful tool for large-scale and precise identification of QTLs for complex traits like BB resistance in germplasm (Zhao et al., 2011; Han and Huang, 2013; Zhang et al., 2017; Zhai et al., 2018).

In this study, we identified the distribution of BB resistance genes of the East African accessions that are distributed and bred in the regions. We detected two loci on chromosomes 6 and 12 that carry the genes (*Xa7, Xa27, Xa33*) and (*Xa25*), respectively.

METHODOLOGY

Plant materials

The selection of diverse panel breeding lines, varieties, and landraces including accessions of 78 genotypes was collected from accessions obtained from National Crops Resources Research Institute (NaCRRI), Namulonge, Uganda. The diverse germplasm collection was obtained from the East African countries of Uganda, Kenya, Tanzania, Rwanda, and Burundi. The field studies were carried out at Africa Rice Centre Mbe station Cote D'Ivoire in accordance with institutional, national, and international guidelines and legislation. The germplasm used in this research was non-GMOs.

BB resistance screening

The experiment was carried out in a contained screen house facility to prevent the spread of inoculum and was done using RCBD split-plot with nested subplot design. The four *X. oryzae* pv. *oryzae* strains were the main plots and, in each plot, a sub-plot of 78 genotypes was nested into early maturing and medium maturing Genotypes.

The BB resistance screening was performed 6 weeks after sowing. A total of four strains representing different races of *X.*

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Table 1. Four strains of *Xanthomonas oryzae* pv. *oryzae* used in this study.

Race	Strain[a]	Gene conferring Resistance[b]
6	PXO99	*Xa13, Xa21, Xa23, xa24, Xa30, Xa32*
A3	MAI1	*Xa4, Xa5* and *Xa7*
A2	BAI3	*Xa4, Xa5* and *Xa7*
A1	Xoo3.1	*Xa12*

[a]African and Philippine strains to specific *Xoo* races. [b]Naturally occurring *Xa* genes known to confer resistance against specific *Xoo* races based on a review.
Source: Nino-Liu et al. (2006) and Verdier et al. (2011).

oryzae pv. *oryzae* were used, namely: *Xoo*3.1, BAI3, MAI1, and PXO99.

Inoculation of the rice plants was done by cutting 1 to 2 cm of the leaf tip with a pair of scissors dipped in bacteria suspension (Kauffman et al., 1973). The screening was replicated two times over time. For each replicate, ten leaves of two plants per entry were inoculated with the *X. oryzae* pv. *oryzae* strains. Lesion lengths were measured 14 days after inoculation. Genotypes having lesion lengths ranging from 1 to 5 cm were rated resistant (R), 5 to 10 cm were rated as medium-resistant (MR), 10 to 15 cm were rated as medium-susceptible (MS), and those having greater than 15 cm were rated as susceptible (S).

Association mapping

The East African accessions comprising 78 germplasm samples were selected and phenotyped by measuring the lesion length of leaves inoculated with BB races Xoo3.1, BAI3, MAI1, and PXO99.

Linkage analysis and QTL mapping

TASSEL version 5.2 software (Bradbury et al., 2007) was used for manipulating and filtering SNPs for genome-wide association analysis. The initial dataset was filtered based on MAF 1 and 95% call rate. A unified mixed-model approach was deployed to account for population structure and familial relatedness (Yu et al., 2006; Price et al., 2006). A compressed mixed linear model (MLM) was used to analyze association, considering population structure (Q) and relatedness or kinship (K) to reduce spurious associations (Yu et al., 2006).

RESULTS

BB resistance screening and population structure

Four diverse strains representing four different races of *X. oryzae* pv. *oryzae* (Table 1) were used to screen 78 genotypes. The lesion length (LL) distribution in the 78 accessions inoculated with four *Xoo* strains (PX099, MAI1, BAI3, and *Xoo*3.1) showed large phenotypic variation (Table 2). Among the inoculated cultivars, five accessions were highly resistant to all four strains with LL< 5 cm, and only highly susceptible to all four strains with LL≥15 cm (highlighted in white and red, respectively in (Figure 1)). Two accessions from Tanzania (*Afaa Milela* and *Mbawa Mbili*) conferred high resistance to all four strains from the Philippines (PX099), West Africa (MAI1 and BAI3), and the East African strain (Xoo3.1)

Based on the LL of all the accessions, the four *X. oryzae* pv. *oryzae* strains were divided into three groups, namely the West African strain group (BAI3, MAI1), East African (Xoo,3.1), and Philippines strain group (PX099) (Figure 1). According to classification by LL, a large proportion of the accessions were resistant with 39.24, 35.44, 40.51 and 50.63% for strains Xoo3.1, BAI3, MAI1, and PX099 respectively (Figure 1).

The sources of resistant East African germplasm from different backgrounds can provide valuable material for facilitating breeding for BB resistance.

Identification of resistance loci against

To dissect genome-wide associated resistance loci for two West African *X. oryzae* pv. *oryzae* strains, one East African *X. oryzae* pv. *oryzae* strain, and one Philippines *X. oryzae* pv. *oryzae* strain, we performed GWAS with a mixed linear model of the TASSEL ver. 5.2 program, using 2,612 high-quality SNPs and LL as genotype and phenotype data, respectively (Figure 2). Based on the effective number of independent markers, the threshold of significant *P*-value was estimated to be 3.0E-5 by the Bonferroni correction method. In total, we identified 2 QTL within 1901 unique SNPs associated with BB resistance to four strains.

Significant resistance genes hotspots

GWAS results from this study indicated chromosomes 6 and 12 as hotspots for BB resistance. SNPs consistently associated with resistance against several strains were identified by GWAS. Known genes and loci (*Xa*) conferring resistance to specific *Xoo* races (Table 1) were overlaid with the Manhattan plots. Among the known *Xa* loci, the regions on chromosome 6 (*Xa*7, *Xa*27, *Xa*33(t)) and *Xa*25 on chromosome 12 (Wang et al., 2001; Blair et

Table 2. Phenotypic reactions of the East African accessions to four strains of bacterial blight.

Reaction	*Xoo 3.1*		*BAI3*		*MAI1*		*PX099*	
	Count	%	Count	%	Count	%	Count	%
MR	21	26.58	24	30.38	15	18.99	24	30.38
MS	17	21.52	12	15.19	16	20.25	6	7.59
R	31	39.24	28	35.44	32	40.51	40	50.63
S	10	12.66	15	18.99	16	20.25	9	11.39

Source: Authors

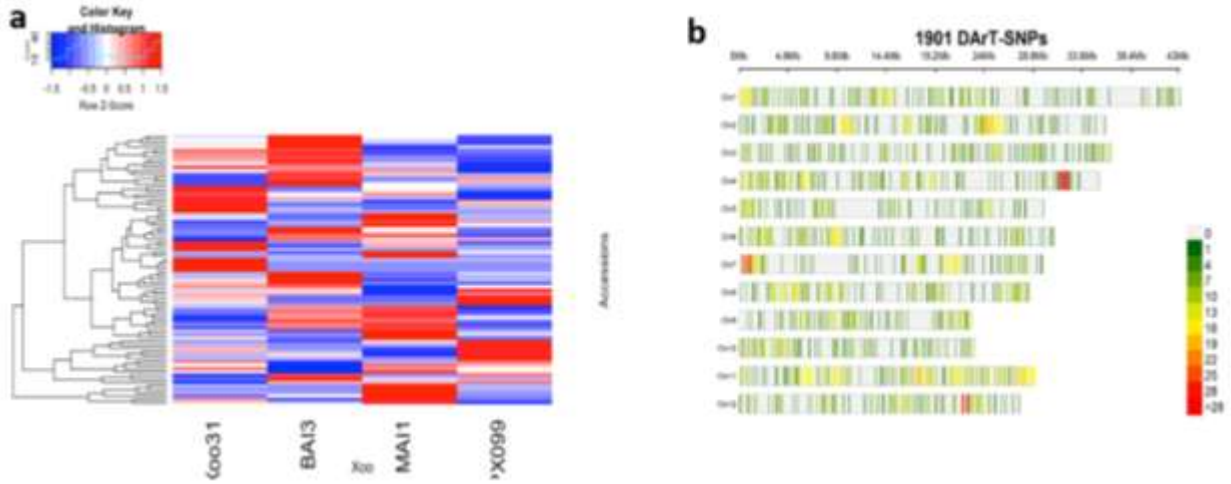

Figure 1. Bacterial blight resistance evaluation of 78 rice accessions inoculated with representative *Xoo* strains from Philippines, West Africa, and Uganda. (a) Hierarchical cluster of accessions and strains based on lesion length (LL). (b) Summary of genotypic SNPs used in the analysis.
Source: Authors

al., 2003; Chen et al., 2008; Chu et al., 2006a, b; Bao et al., 2010; Song et al., 1995; Chen et al., 2002) were identified as overlapping with significant SNPs in this study.

DISCUSSION

This study was conducted to screen and identify disease-resistant rice cultivars, as well as key functional genes applicable for breeding new varieties with broad-spectrum BB resistance. Bacterial blight is one of the most diseases of rice, causing significant yield losses in rice-growing ecologies throughout Africa (Kim, 2018). The current BB management strategies are not effective due to the rapid development of virulent *Xoo* strains (Kim et al., 2015). In Africa where rice bacterial blight outbreaks can be epidemic, new Xoo strains need to be identified and characterized.

In the present study, we identified two accessions from Tanzania (*Afaa Milela* and *Mbawa Mbili*) that are highly resistant to all four *X. oryzae* pv. *oryzae* strains (PX099, MAI1, BAI3, and *Xoo*3.1). The data generated in this study regarding these BB-resistant accessions will be utilized for rice breeding programs.

Application of QTL in rice breeding

Chromosome 11 is known as an important and complex region of the rice genome with respect to BB resistance, containing mapped or finely-mapped BB *R* genes *Xa22(t), Xa30(t), Xa32(t), Xa35(t), Xa36(t), Xa39, Xa40, xa41(t), Xa43(t)* and *xa44(t),* and cloned genes *Xa3/Xa26, Xa4, Xa10, Xa21,* and *Xa23* (https://shigen.nig.ac.jp/rice/oryzabase/).

Recently, many *R* genes for BB were successfully incorporated into both elite inbred varieties and parental lines of hybrid rice to control the disease using MAS (Chukwu et al., 2019; Jiang et al., 2020; Li et al., 2020). Markedly, a few of those *R* genes, such as *Xa3, Xa4, Xa7*, and *Xa21*, have been widely utilized in rice

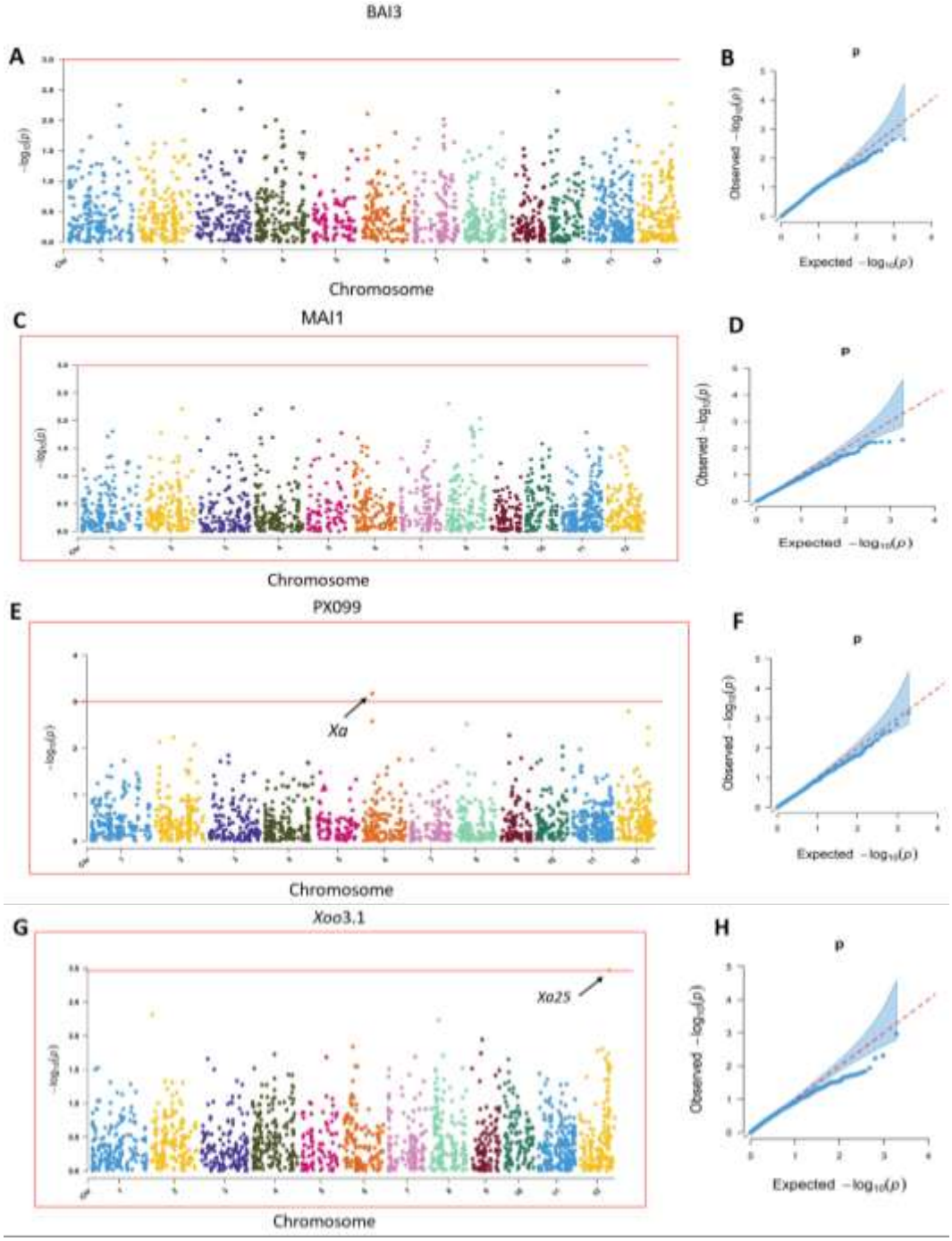

Figure 2. Genome-wide association study of rice resistance to four *Xoo* strains. A, C, E, G Manhattan plots of GWAS results for strain BAI3, MAI1, PX099, and *Xoo*3.1, respectively. B, D, F, H Quantile plots of expected and observed -$\log_{10}$ (*P*-value) for strains BAI3, MAI1, PX099, and *Xoo*3.1, respectively. The horizontal blue line indicates the significant P-value threshold of 3.0E-5. The arrow indicates the reported bacterial blight resistance genes.
Source: Authors

resistance breeding since the 1980s (Deng et al., 2006; Zhang, 2009; Chen et al., 2011; Luo et al., 2012). With the wide deployment of *R* genes and *Xoo*-Rice coevolution, elite *R* genes are being overcome by the

newly emerged *X. oryzae* pv. *oryzae* strains (Zeng et al., 2002; Zhang, 2005).

Conclusion

The results from this GWAS have pinpointed resistance loci conferring differential resistance to the four representative strains of *X. oryzae* pv. *oryzae* in the East African accession. Two resistant loci were identified through this analysis. Using efficient phenotypic data and SNPs from genotyping is a powerful tool to decipher disease resistance in rice. The SNPs associated with *X. oryzae* pv. *oryzae* resistance would be helpful in the development of SNP markers for marker-assisted selection and tracking of known *Xa* genes. Effective monitoring of resistance genes in the breeding pipeline guides breeders on which varieties to deploy to specific areas depending on the *Xoo* population. The full potential of the novel loci identified loci in the East African germplasm will be unraveled through expression profiling. The genotypes that have exhibited a high degree of resistance but have no resistance alleles for specific *Xa* QTLs serve as new sources of resistance loci to plant breeders to diversify the genetic base of core breeding sets. Further analysis of the East African germplasm is recommended to identify potentially novel loci which were not detected in this study.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

The authors thank Ambrose Agona for the support in the completion of this study. They also thank the staff of the Plant Pathology Unit, Africa Rice for the technical assistance, and Arnaud Gouda for the analytical assistance.

ABBREVIATIONS

BB, Bacterial blight; **GWAS,** Genome-wide association study; **LD,** Linkage disequilibrium; **MAF,** Minor allele frequency; **MLM,** Mixed linear model; **PCA,** Principal component analysis; **QTL,** Quantitative trait loci; ***Xoo*****,** *Xanthomonas oryzae* pv. *oryzae*

REFERENCES

Bao SY, Tan MP, Lin XH (2010). Genetic mapping of a bacterial blight resistance gene Xa14 in rice. Acta Agronomica Sinica 36(3):422-427.

Blair MW, Garris AJ, Iyer AS, Chapman B, Kresovich S, McCouch SR (2003). High-resolution genetic mapping and candidate gene identification at the xa5 locus for bacterial blight resistance in rice (*Oryza sativa* L.). Theoretical and Applied Genetics 107(1):62-73.

Bossa-Castro AM, Tekete C, Raghavan C, Delorean EE, Dereeper A, Dagno K, Koita O, Mosquera G, Leung H, Verdier V, Leach JE (2018). Allelic variation for broad-spectrum resistance and susceptibility to bacterial pathogens identified in a rice MAGIC population. Plant Biotechnology Journal 16(9):1559-1568. https://doi.org/10.1111/pbi.12895.

Bradbury PJ, Zhang Z, Kroon DE, Casstevens Terry M, Ramdoss Y, Buckler ES (2007). TASSEL: software for association mapping of complex traits in diverse samples. Bioinformatics 23(19):2633-2635.

Chen H, Wang S, Zhang Q (2002). New gene for bacterial blight resistance in rice located on chromosome 12 identified from Minghui 63, an elite restorer line. Phytopathology 92(7):750-754.

Chen S, Huang Z, Zeng L, Yang J, Liu Q, Zhu X (2008) High-resolution mapping and gene prediction of *Xanthomonas Oryzae* pv. *oryzae* resistance gene Xa7. Molecular Breeding 22(3):433-441.

Chen S, Liu X, Zeng L, Ouyang D, Yang J, Zhu X (2011). Genetic analysis and molecular mapping of a novel recessive gene xa34 (t) for resistance against Xanthomonas oryzae pv. oryzae. Theoretical and Applied Genetics 122:1331-1338.

Chu Z, Fu B, Yang H, Xu C, Li Z, Sanchez A, Park YJ, Bennetzen JL, Zhang Q, Wang S (2006a). Targeting xa13, a recessive gene for bacterial blight resistance in rice. Theoretical and Applied Genetics 112(3):455-461.

Chukwu SC, Rafii MY, Ramlee SI, Ismail SI, Hasan MM, Oladosu YA, Magaji UG, Akos I, Olalekan KK (2019). Bacterial leaf blight resistance in rice: a review of conventional breeding to molecular approach. Molecular Biology Reports 46:1519-1532.

Deng HQ, Liu HB, Li XH, Xiao JH, Wang SP (2012). A CCCH-type zinc finger nucleic acid-binding protein quantitatively confers resistance against rice bacterial blight disease. Plant Physiology 158(2):876-889. https://doi.org/10.1104/ pp.111.191379.

Deng Q, Wang S, Zheng A, Zhang H, Li P (2006). Breeding Rice Restorer Lines with High Resistance to Bacterial Blight by Using Molecular Marker Assisted Selection. Rice Science 13:22-28.

Dilla-Ermita CJ, Tandayu E, Juanillas VM, Detras J, Lozada DN, Dwiyanti MS, Cruz CV, Mbanjo EGN, Ardales E, Diaz MG, Mendioro M, Thomson MJ, Kretzschmar T (2017). Genome-wide association analysis tracks bacterial leaf blight resistance loci in rice diverse germplasm. Rice 10(1):8. https://doi.org/10.11 86/s12284-017-0147-4.

Djedatin G, Ndjiondjop MN, Sanni A, Lorieux M, Verdier V, Ghesquiere A (2016). Identification of novel major and minor QTLs associated with *Xanthomonas oryzae* pv. oryzae (African strains) resistance in rice *(Oryza sativa* L.). Rice 9:18

Han XY, Yang Y, Wang XM, Zhou J, Zhang WH, Yu CL, Cheng C, Cheng Y, Yan CQ, Chen JP (2014). Quantitative trait loci mapping for bacterial blight resistance in rice using bulked segregant analysis. International Journal of Molecular Sciences 15(7):11847-11861. https://doi.org/10.3390/ijms150711847.

Hu KM, Cao JB, Zhang J, Xia F, Ke YG, Zhang HT, Xie WY, Liu HB, Cui Y, Cao YL, Sun XL, Xiao JH, Li XH, Zhang QL, Wang SP (2017). Improvement of multiple agronomic traits by a disease resistance gene via cell wall reinforcement. Nature Plants 3(3):17009. https://doi.org/10.1038/nplants.2017.9.

Huang N, Angeles ER, Domingo J, Magpantay G, Singh S, Zhang G, Kumaravadivel N, Bennett J, Khush GS (1997). Pyramiding of bacterial blight resistance genes in rice: marker-assisted selection using RFLP and PCR. Theoretical and Applied Genetics 95(3):313-320. https://doi.org/10.1007/s001220050565.

Hutin M, Sabot F, Ghesquiere A, Koebnik R, Szurek B (2015). A knowledge-based molecular screen uncovers a broad-spectrum OsSWEET14 resistance allele to bacterial blight from wild rice. Plant Journal 84(4):694-703. https://doi.org/10.1111/tpj.13042.

Ji ZY, Wang CL, Zhao KJ (2018). Rice routes of countering *Xanthomonas oryzae*. International Journal of Molecular Sciences 19(10):3008. https://doi.org/10.3390/ijms19103008.

Jiang N, Yan J, Liang Y, Shi Y, He Z, Wu Y, Zeng Q, Liu X, Peng J (2020). Resistance Genes and their Interactions with Bacterial Blight/Leaf Streak Pathogens (*Xanthomonas oryzae*) in Rice (*Oryza sativa* L.)—an Updated Review. Rice 13(1):1-12.

Kauffman HE, Reddy APK, Hsieh SPY, Merca SD (1973). An improved technique for evaluation of resistance of rice varieties to *Xanthomonas Oryza*. Plant Disease Report 57:537-541.

Li ZK, Arif M, Zhong DB, Fu BY, Xu JL, Domingo-Rey J, Ali J, Vijauakumar CHM, Yu SB, Khush GS (2006). Complex genetic networks underlying the defensive system of rice (*Oryza sativa* L.) to *Xanthomonas oryzae* pv. *Oryzae*. Proceedings of the National Academy of Sciences 103(21):7994-7999. https://doi.org/10.1073/pnas.0507492103.

Li W, Deng Y, Ning Y, He Z, Wang GL (2020). Exploiting Broad-spectrum Disease Resistance in Crops: From Molecular Dissection to Breeding. Annual Review of Plant Biology 71:575-603.

Liu Q, Yang JY, Yan SJ, Zhang SH, Zhao JL, Wang WJ, Yang TF, Wang XF, Mao XX, Dong JF, Zhu XY, Liu B (2016). The germin-like protein OsGLP2-1 enhances resistance to fungal blast and bacterial blight in rice. Plant Molecular Biology 92(4-5):411-423. https://doi.org/10.1007/s11103-016-0521-4.

Luo Y, Sangha JS, Wang S, Li Z, Yang J, Yin Z (2012). Marker-assisted breeding of Xa4, Xa21, and Xa27 in the restorer lines of hybrid rice for broad-spectrum and enhanced disease resistance to bacterial blight. Molecular Breeding 30:1601-1610.

Price AL, Patterson NJ, Plenge RM, Weinblatt ME, Shadick NA, Reich D (2006). Principal components analysis corrects for stratification in genome-wide association studies. Nature Genetics 38(8):904-909.

Ramalingam J, Cruz CMV, Kukreja K, Chittoor JM, Wu JL, Lee SW, Baraoidan M (2003). Candidate defense genes from rice, barley, and maize and their association with qualitative and quantitative resistance in rice. Molecular Plant-Microbe Interaction 16(1):14-24. https://doi.org/10.1094/MPMI.2003.16.1.14.

Kim SM (2018). Identification of novel recessive gene xa44(t) conferring resistance to bacterial blight races in rice by QTL linkage analysis using an SNP chip. Theoretical and Applied Genetics 131:2733-2743.

Kim SM, Suh JP, Qin Y, Noh TH, Reinke RF, Jena KK (2015). Identification and fine-mapping of a new resistance gene, Xa40, conferring resistance to bacterial blight races in rice (*Oryza sativa* L.). Theoretical and Applied Genetics 128:1933-1943.

Savary S, Willocquet L, Pethybridge SJ, Esker P, McRoberts N, Nelson A (2019). The global burden of pathogens and pests on major food crops. Nature Ecology and Evolution 3(3):430-439. https://doi.org/10.1038/s41559-018-0793-y.

Song WY, Wang GL, Chen L, Zhai W, Kim HS, Holsten T, Gardner J, Wang B, Zhai WX, Zhu LH, Fauquet C, Ronald P (1995). A receptor kinase-like protein encoded by the rice disease resistance gene, Xa21. Science 270(5243):1804-1806.

Takeda S, Matsuoka M (2008). Genetic approaches to crop improvement: responding to environmental and population changes. Nature Reviews Genetics 9(6):444-457. https://doi.org/10.1038/nrg2342.

Wang CL, Zhang XP, Fan YL, Gao Y, Zhu QL, Zheng CK, Qin TF, Li YQ, Che JY, Zhang MW, Yang B, Liu YG, Zhao KJ (2015). XA23 is an executor R protein and confers broad-spectrum disease resistance in rice. Molecular Plant 8(2):290-302. https://doi.org/10.1016/j.molp.2014.10.010.

Wang W, Li X, Wing RA, Zhu L, Luo M, Jiang G, Chen X, Li X, Wing RA, Zhu L (2001). Chromosome landing at the bacterial blight resistance gene Xa4 locus using a deep coverage rice BAC library. Molecular Genetics and Genomics 265(1):118-125.

Yang W, Zhao J, Zhang S, Chen L, Yang T, Dong J, Fu H, Ma Y, Zhou L, Wang J, Liu W, Liu Q, Liu B (2021). Genome-Wide Association Mapping and Gene Expression Analysis Reveal the Negative Role of OsMYB21 in Regulating Bacterial Blight Resistance in Rice. Rice 14(1):1-12. doi: 10.1186/s12284-021-00501-z. PMID: 34185169; PMCID: PMC8241976.

Yoshimura S, Yamanouchi U, Katayose Y, Toki S, Wang ZX, Kono I, Kurata N, Yano M, Iwata N, Sasaki T (1998). Expression of Xa1, a bacterial blight-resistance gene in rice, is induced by bacterial inoculation. Proceedings of the National Academy of Sciences 95(4):1663-1668. https://doi.org/10.1073/pnas.95.4.1663.

Yu J, Pressoir G, Briggs WH, Vroh Bi I, Yamasaki M, Doebley J, McMullen MD, Gaut BS, Nielsen DM, Holland JB, Kresovich S, Buckler ES (2006). A unified mixed-model method for association mapping that accounts for multiple levels of relatedness. Nature Genetics 38(2):203-208.

Zeng LX, Huang SH, Wu SZ (2002). Resistance of IRBB21 (Xa21) to five races of bacterial blight in Guangdong. Journal of Plant Protection Research 29(2):97-100.

Zhai LY, Zheng TQ, Wang XY WY, Chen K, Wang S, Wang Y, Xu JL, Li ZK (2018). QTL mapping and candidate gene analysis of peduncle vascular bundle related traits in rice by genome-wide association study. Rice 11(1):1-15. https:// doi.org/10.1186/s12284-018-0204-7.

Zhang F, Wu ZC, Wang MM, Zhang FF, Dingkuhn M, Xu JL, Zhou YL, Li ZK (2017). Genome-wide association analysis identifies resistance loci for bacterial blight in a diverse collection of indica rice germplasm. PLoS One 12(3):e0174598. https://doi.org/10.1371/journal.pone.0174598.

Zhang F, Xie XW, Xu MR, Wang WS, Xu JL, Zhou YL, Li ZK, Ahn SN (2015). Detecting major QTL associated with resistance to bacterial blight using a set of rice reciprocal introgression lines with high-density SNP markers. Plant Breeding 134(3):286-292. https://doi.org/10.1111/pbr.12256.

Zhang Q (2005). Highlights in identification and application of resistance genes to bacterial blight. Chinese Journal of Rice Science 19(5):453-459.

Zhang Q (2009). Genetics and Improvement of Bacterial Blight Resistance of Hybrid Rice in China. Rice Science 16(2):83-92.

Zhao K, Tung CW, Eizenga GC, Wright MH, Ali ML, Price AH, Norton GJ, Islam MR, Reynolds A, Mezey J, McClung AM, Bustamante CD, McCouch SR (2011). Genome-wide association mapping reveals a rich genetic architecture of complex traits in *Oryza sativa*. Nature Communication 2(1):467. https://doi.org/10.1038/ncomms1467.