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GENOME-WIDE ASSOCIATION STUDY OF PANICLE BLAST RESISTANCE IN TEMPERATE *JAPONICA* RICE (*ORYZA SATIVA* L.) GERMPLASM

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SUMMARY

In temperate regions, rice production faces substantial threats from the devastating blast disease caused by the fungal pathogen *Magnaporthe oryzae*. For managing blast disease, deploying resistance genes remains the most cost-effective and environmentally sustainable control strategy. In the following study, a genome-wide association study (GWAS) for rice panicle blast resistance proceeded in germplasm comprising 191 temperate *Japonica* rice accessions. Results revealed the 141 significant single-nucleotide polymorphisms (SNPs) were notably related to rice panicle blast resistance. Four intervals were considerably confident loci related to panicle blast resistance, including *qPBR04*, *qPBR05-1*, *qPBR05-2,* and *qPBR07*. The *qPBR07* region on chromosome 7 was a promising QTL, having several novel genes with a crucial role in pathogen defense. Key genes, including *Os07g0511500, Os07g0515100*, *Os07g0516300*, *Os07g0518100*, *Os07g0513600, Os07g0515200,* and *Os07g0512100*, were seemingly potential genes in response to the *M. oryzae* pathogen invasion. The study identified 25 temperate *Japonica* accessions exhibiting a high level of panicle blast resistance, positioning them as potential sources of resistance suited to temperate climates. The insights gained from the presented study provide a valuable foundation for panicle blast resistance breeding and the comprehensive characterization of identified resistance genes.

Keywords: Rice (*O. sativa* L.), blast disease, panicle blast resistance, quantitative trait locus, genome-wide association study

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Key findings: Twenty-five rice genotypes resistant to panicle blast showed distinction from a set of 191 temperate *Japonica* rice accessions. Four quantitative trait loci (QTLs) associated with rice panicle blast resistance also emerged, with *qPBR07* on chromosome 7 showing a high potential for gene mining and breeding application.

INTRODUCTION

Rice (*O. sativa* L.) is a staple food used by over half of the world's population. Numerous diseases affect the rice crop; however, the rice blast, caused by the fungal pathogen *Magnaporthe oryzae*, is one of the most widespread and destructive diseases. Under blast disease favorable conditions, yield losses can reach as high as 100%, devastating the entire rice fields within 2–3 weeks (Asibi *et al.,* 2019). Panicle blast, a severe form of rice blast disease, considerably modifies the rice production and its quality by causing incomplete and blackened grains. This type of blast impacts rice panicles by reducing stem strength and causing neck breakage, resulting in sterile grains and great yield losses (Devanna *et al*., 2022).

The most effective and environment-friendly strategy to control rice blast is the cultivation of blast-resistant rice cultivars. Therefore, to maintain stable rice production, the development of disease-resistant rice cultivars apparently depends on the identification and utilization of genes conferring resistance to panicle blast. Developing several blast-resistant rice cultivars has progressed through conventional and molecular breeding (Angeles-Shim *et al*., 2020). Detecting specific resistance (*R*) genes for different blast races in elite rice germplasm plays a crucial role in ensuring precision in marker-assisted selection (Yadav *et al.,* 2019; Xiao *et al.,* 2020). To date, more than 146 *R* genes responsible for rice blast resistance have been prevalent in various populations (Deepak *et al.,* 2022; Yu *et al.,* 2022), with 36 of them already cloned. The majority of these cloned genes encode nucleotide-binding site and leucine-rich repeat (NBS-LRR) proteins (Sharma *et al.,* 2021; Devanna *et al.,* 2022). The incorporation of disease resistance genes through breeding can greatly enhance the adaptability of newly developed rice cultivars.

Despite rice panicle blast being the most damaging type of disease, only limited research has occurred on it. Rice plant leaves and panicles exhibited varied responses to rice blast infection, with some cultivars being susceptible to leaf blast, however, resistant to panicle blast. This underscores the importance of identifying more panicle blast resistance genes and associated disease response pathways in rice. Genome-wide association studies (GWAS) have emerged as a pivotal method for elucidating the inheritance of complex traits, considerably enhancing the efficiency of QTL identification (Burghardt *et al.,* 2017; Tibbs-Cortes *et al.,* 2021). Past studies expressed that in the 3000 Rice Genomes Project (3k RGP), identifying 12 QTLs associated with bacterial blight resistance resulted through GWAS (Wang *et al.,* 2018). Furthermore, based on the results of GWAS, the rice blast resistance genes *Pb2*, *Pb3*, *PiPR1*, *RNG1*, and *RNG2* succeeded in their cloning (Liu *et al.,* 2020; Ma *et al.,* 2022; Yu *et al*., 2022; Xu *et al.,* 2023).

The timely study aimed to identify the panicle blast resistant temperate *Japonica* accessions to recognize single-nucleotide polymorphisms (SNPs) linked to panicle blast resistance and confirm putative candidate genes for the promising QTL. In 3000 sequenced rice accessions of 3K RGP, researchers selected a subset of 191 temperate *Japonica* accessions, assessed their panicle blast resistance under field conditions, and conducted genome-wide association studies. The presented results provide crucial insights into the discovery of genes for managing panicle blast resistance and laying a foundational basis for panicle blast resistance breeding.

MATERIALS AND METHODS

Plant material and growth conditions

The 3K RGP dataset contains genome sequences of 3000 rice accessions from 89 countries, representing the world's genetic diversity (Li *et al.,* 2014). These accessions incurred dividing into nine subpopulations, including three *Japonica* subpopulations, i.e., GJ-trp, GJ-subtrp, and GJ-tmp (Wang *et al.*, 2018). In avoiding the population structure effect, the GJ-tmp subpopulation, including 191 temperate *Japonica* accessions, was the selected group for this study. The sowing of germinated seeds transpired in a wet seedling bed in three field locations, viz., Baoshan (BS), Dehong (DH), and Menghai (MH), Yunnan Province, China. The seedlings' transplanting ensued with a plant-row spacing of 10 cm × 25 cm at the pressure of natural blast pathogen populations in the blast nursery. Each rice accession grown into two rows (15 plants per row) had three replications. Using the susceptible rice cultivar Lijiangxintuanheigu (LTH) served as a spreader with its planting at the end of each row to guarantee consistent disease pressure. All rice accessions, randomly arranged in a single field, had a completely randomized design (CRD) layout. The susceptible cultivar LTH completed its planting around the evaluating accessions with a one-meter width as the spreader lines. Crop management was the same as that carried out by the local farmers, using no fungicides throughout the growth period.

Blast disease evaluation

A modified version of the Standard Evaluation System (SES) helped to score the panicle blast disease at the dough stage in rice (IRRI, 2014). The system had six scales (based on symptoms): 0—for no visible lesion; 1—for lesions on several pedicels and secondary branches; 3—for lesions on a few primary branches and the middle part of the panicle axis; 5—for lesions partially around the base (node), on the uppermost internode, and on the lower part of the panicle axis near the base; 7—for lesions completely around the panicle base and at the uppermost internode; and 9—for lesions completely around the panicle base, uppermost internode, and at the panicle axis near the base. Based on the number of panicles with each scale, the panicle blast severity (PBS) reached calculation (IRRI, 2014). Based on the PBS values, classifying the incidence (%) of infected panicles comprised the following SES scores: 0 = no incidence, 1 = less than 5%, 3 = 5%–10%, 5 = 11%–25%, 7 = 26%–50%, and 9 = more than 50% at the dough stage. The correlations computed among the replications used the SES scores of the rice accessions, with the average values of the three replications at each experimental site employed for the genome wide association study (GWAS).

Genome-wide association study

The core SNP V2.1 dataset of the 191 temperate *Japonica* rice accessions containing 365,710 SNPs came from the SNP-seek system and served for data analysis (Alexandrov *et al.,* 2015). The use of the TASSEL program V5.2.18 for GWAS comprised phenotype and genotype datasets (Bradbury *et al.,* 2007). The SNP sites bore filtering for the minimum count of 95% and allele frequency (0.05–0.95), and 70,955 SNPs fulfilled the requirements for undergoing the GWAS. The kinship matrix with centered_IBS was the first developed item using filtered SNP data. The Centered_IBS method codes genotypes as 2, 1, or 0, equal to the count of one of the alleles at that locus. It then replaces missing genotype values with the average genotypic score at that locus before estimating a relationship matrix. Union join was the utilized method to develop a united data file containing the genotype and phenotype data of the 191 rice accessions. The mixed linear model (MLM), as employed, analyzed marker-trait associations using the united file and the kinship matrix (Zhang *et al.,* 2010). The SNPs with $p<1\times10^{-3}$ ($-\ln^{p\text{-value}} > 3.0$) and marker $R^2>0.06$ were preliminary bases as potential loci for the traits. The CGSNL nomenclature aided in naming the identified QTLs (McCouch and CGSNL, 2008). The chromosomal regions associated with the promising QTLs underwent re-analysis using

the general linear model (GLM) along with 1000 permutations.

The Haploview v4.2 software (Barrett *et al.,* 2005) helped calculate the local linkage disequilibrium (LD), as previously described (Volante *et al.,* 2020). In identifying the candidate genes associated with each trait, the regions encompassing the peak marker positions attained scrutiny. All the genes within the intervals proceeded for extraction from the annotation of the Nipponbare reference genome (Rice Genome Annotation Project, https://rice.uga.edu/), with the gene functions analyzed.

RESULTS

Assessment of the panicle blast resistance

Severe panicle blast infection appeared at all three experimental locations; however, it was more pronounced at the Baoshan. Most of the rice accessions were visibly susceptible to the panicle blast disease (Table 1). Based on the SES scores of all the accessions, 25 rice accessions resistant to panicle blast succeeded in their final selection at the three experimental locations, i.e., Dehong, Menghai, and Baoshan in Yunnan Province (Table 2). The correlation among the replications at each location was highly significant (Table 3). A significant correlation between the experimental sites Menghai and Baoshan existed; however, the association was not significant between Dehong and two other locations (Table 3).

The results further indicated the panicle blast resistance of the rice accessions at the same location was stable. Although most accessions showed varied resistance to panicle blast at different study locations, which may be attributed to the different population structure of *M. oryzae* comprising diverse virulent strains in these rice growing areas. Thus, the average SES scores of three replications at each location were values used for the genome wide association study.

GWAS analysis

The SNP panel initially comprised 365,710 SNP markers. After filtering for call rate (>95%) and minor allele frequency (>5%), the final set included 70,955 SNPs. The GWAS continued using the average SES score of three replications from the field experiment at each location. A total of 141 SNPs emerged significantly associated with panicle blast resistance in the three experiments (Figure 1). Four intervals were considerably confident QTLs related to panicle blast resistance, including *qPBR04* (chr04: 1820228-2053995, 30 SNPs) and *qPBR05-1* (chr05: 457287-739780, 44 SNPs) at experimental site Baoshan, *qPBR07* (chr07: 19529787-20128741, 24 SNPs) at Dehong, and *qPBR05-2* (chr05: 13757411-14825646, 6 SNPs) at Menghai (Table 4).

The most significant locus occurred on chromosome 7. The one-way ANOVA of the most significant SNP at Chr7:19770475 showed a substantial difference in panicle blast resistance between the genotypes AA and GG. The genotype AA was more resistant than genotype GG (Figure 2). No reports of blast resistance genes were apparent in the *qPBR07* region in previous studies; thus, selecting the QTL *qPBR07* for further analysis of candidate genes at this locus, with a 598,954 bp intersection containing *qPBR07* selected for LD block heatmap analysis. Using significant SNP density distribution paired with LD ($r^2 \geq 0.6$) triangular blocks helped recognize the chromosomal region for candidate gene analysis (Figure 3).

Candidate gene analysis in QTL region

All the annotated genes from the Nipponbare reference sequence in the QTL region of chromosome 7 reached analysis to identify the disease resistance genes. A total of 63 genes incurred identification within the specified region (Chr7: 19529787-20128741) of *qPBR07*. Bolstering the novelty of this region prevailed by its diverse array of genes,

Table 1. Distribution of the SES scores in 191 rice accessions in three field experiments.

Locations	Replications	0	1	3	5	7	9
Baoshan	Rep-1	3	0	5	11	13	159
	Rep-2	5	0	2	13	16	155
	Rep-3	3	2	2	12	18	154
Dehong	Rep-1	25	3	13	35	51	64
	Rep-2	25	6	10	35	53	62
	Rep-3	27	3	11	37	49	64
Menghai	Rep-1	19	3	4	10	15	140
	Rep-2	19	3	4	10	20	135
	Rep-3	20	1	5	11	15	139

0 = no incidence; 1 = less than 5%; 3 = 5%–10%; 5 = 11%–25%; 7 = 26%–50%; 9 = more than 50%.

Table 2. The 25 rice accessions found resistant to the panicle blast disease.

Cultivars	IRGC Acc. No.	Designation	Origin	SES score
JINBUBYEO	126967	JINBUBYEO::G1	Korea, Republic Of	0
JO SANG DAE YA	125788	JO SANG DAE YA::IRGC 90852-1	Korea, Dpr	0
TAICHUNG 65	125911	TAICHUNG 65::IRGC 79-1	Chinese Taipei (Taiwan)	0
TAICHUNG 179	125910	TAICHUNG 179::IRGC 85-1	Chinese Taipei (Taiwan)	0
DA DAO TOU	125718	DA DAO TOU::IRGC 59499-1	China	0
HUK ZO	125767	HUK ZO::IRGC 19760-1	Korea, Republic Of	0
MAEKJO	125830	MAEKJO::IRGC 77666-1	Korea, Republic Of	0
DAN-YAN-NUO	126198	DAN YAN NUO::IRGC 4860-1	China	0
BERGREIS	126185	BERGREIS::IRGC 3150-1	Austria	0
TEXAS PATNA 49	125920	TEXAS PATNA 49::IRGC 6077-1	United States	0
CAMPINO	121996	CAMPINO::GERVEX 824-C1	Portugal	0
VALTEJO	122273	VALTEJO::GERVEX 1355-C1	Portugal	0
AUGUSTZA	121972	AUZGUSTA::GERVEX 1634-C1	Hungary	0
WIR 2091	128502	WIR 2091::IRGC 57536-1	Georgia	0
HEI TOU HONG	128307	HEI TOU HONG::IRGC 59595-1	China	0
GONG SHE 9	128303	GONG SHE 9::IRGC 62693-1	China	0
PL 3165	128434	PL 3165::IRGC 62827-1	China	0
SI WAN 14	127815	SI WAN 14::IRGC 63019-1	China	0
MAO ZHA NUO	127608	MAO ZHA NUO::IRGC 70335-1	China	0
DUAN SHEN ZI	128284	DUAN SHEN ZI::IRGC 73962-1	China	0
C 722323	128252	C 722323::IRGC 73147-1	Chinese Taipei (Taiwan)	0
250 KUNGANI 1	128209	250 KUNGANI 1::IRGC 7370-1	Japan	0
AIKAWA 44	128212	AIKAWA 44::IRGC 7676-1	Japan	0
OITA-MII 120	128414	OITA MII 120::IRGC 7696-1	Japan	0
TSAO-SIAO-PEH-TAO	128194	TSAO SIAO PEH TAO::IRGC 8265-2	China	0

Table 3. Correlation of panicle blast resistance in 191 temperate *japonica* rice accessions at three locations.

Locations	MH-rep1	MH-rep2	MH-rep3	DH-rep1	DH-rep2	DH-rep3	BS-rep1	BS-rep2
MH-rep2	0.969***							
MH-rep3	0.974***	0.968***						
DH-rep1	0.105	0.085	0.087					
DH-rep2	0.109	0.09	0.089	0.988***				
DH-rep3	0.121	0.097	0.102	0.986***	0.983***			
BS-rep1	0.225**	0.202***	0.198**	0.101	0.093	0.099		
BS-rep2	0.194**	0.176*	0.177*	0.126	0.118	0.119	0.948***	
BS-rep3	0.197**	0.175*	0.181*	0.143*	0.134	0.135	0.933***	0.922***

MH = Menghai, DH = Dehong, BS = Baoshan.* = Significant at $P < 0.05$, ** significant at $P < 0.01$, *** significant at $P < 0.001$.

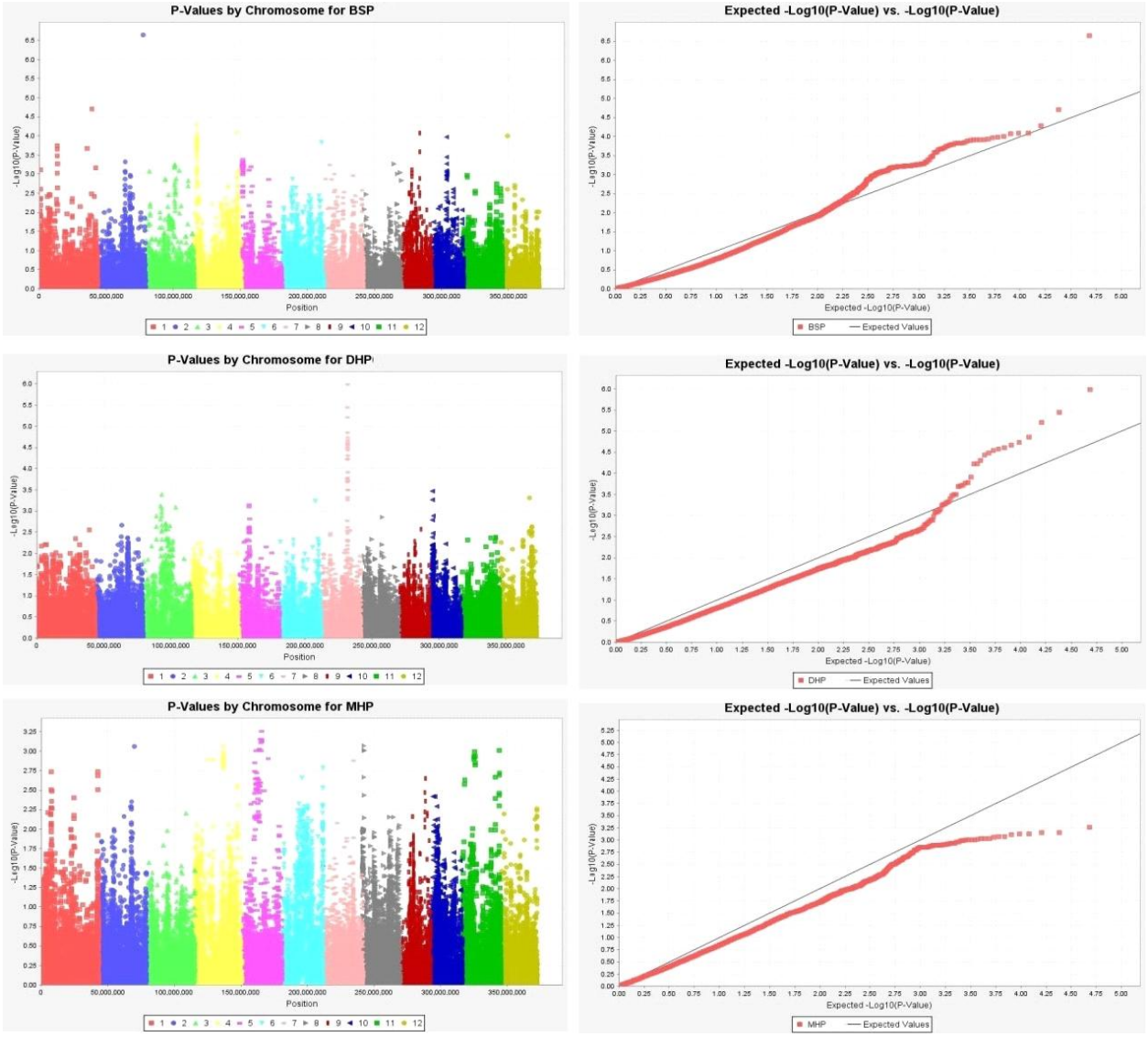

Figure 1. Manhattan and QQ plots of rice panicle blast resistance in the three experiments. BS = Baoshan, DH = Dehong, MH = Menghai.

Table 4. The QTLs associated with panicle blast resistance.

QTL	QTL interval	Chr.	SNPs	$-\ln^{p\text{-value}}$	Location
qPBR04	1820228-2053995	4	30	4.07	Baoshan
qPBR05-1	457287-739780	5	44	3.50	Baoshan
qPBR05-2	13757411-14825646	5	6	3.92	Menghai
qPBR07	19529787-20128741	7	24	7.50	Dehong

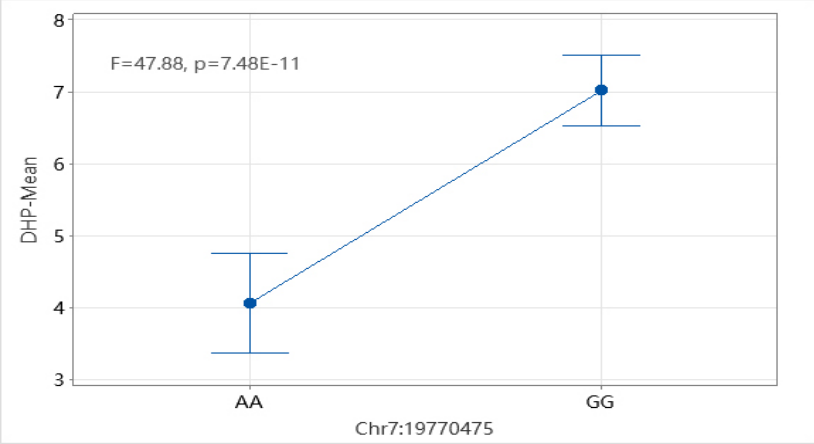

Figure 2. Interval plot of the panicle blast resistance vs. SNP Chr7:19770475. DHP-Mean is the average SES score of the panicle blast resistance at Dehong.

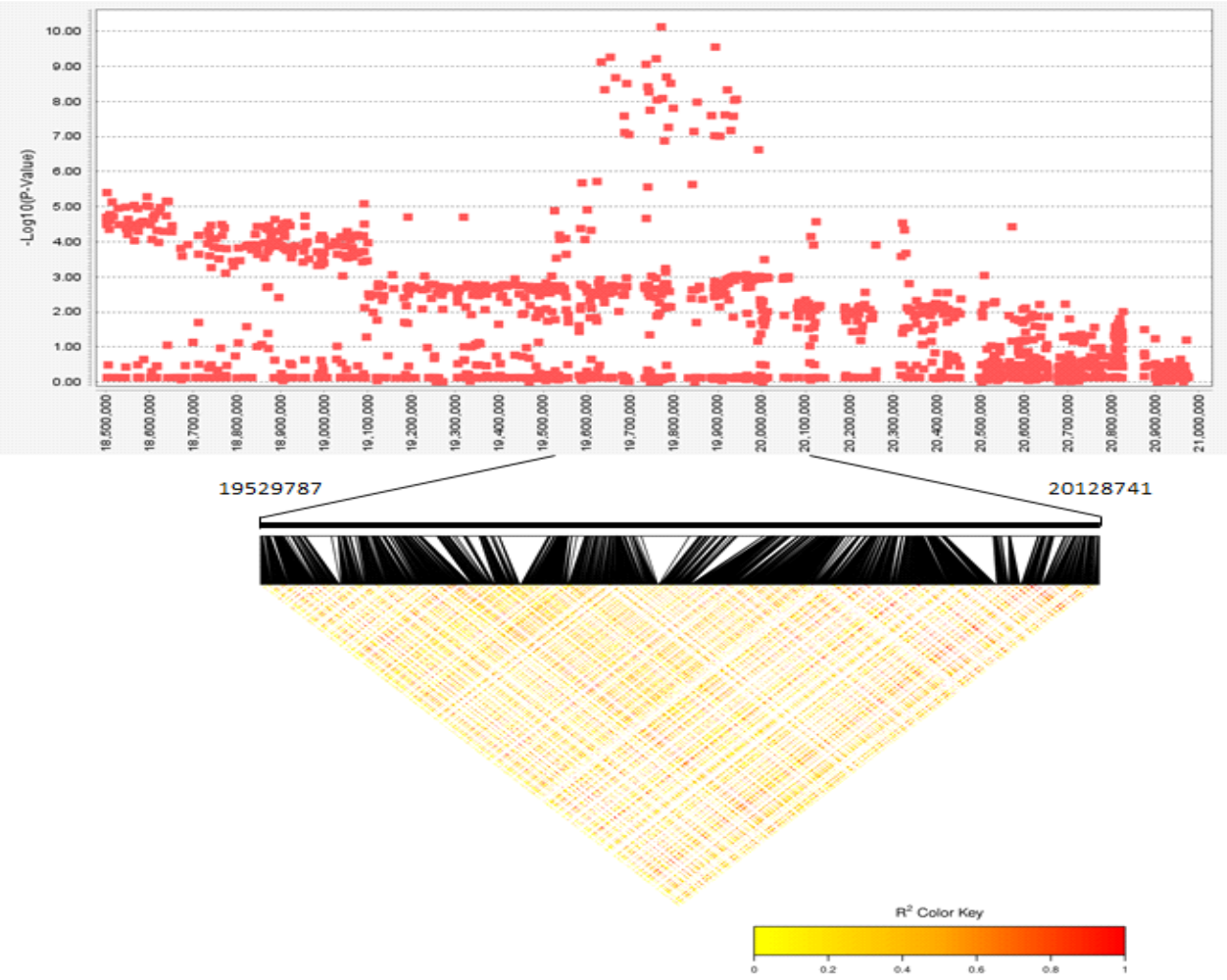

Figure 3. Manhattan plot and LD heatmap of Chr7: 19529787-20128741 around the peak of *qPBR07*.

including *Os07g0511500,* associated with the sucrose non-fermenting 2 (Snf2) protein family; *Os07g0515100,* encoding calcium-dependent protein kinase (CDPK); *Os07g0516300,* as a member of the *S40* gene family; *Os07g0518100,* as a cytochrome P450 (CYP450) protein of the 716A subfamily; and *Os07g0513600* and *Os07g0515200,* as conserved hypothetical proteins.

DISCUSSION

Rice blast is one of the most devastating diseases affecting rice production, with the leaf blast and panicle blast being the predominant types. The irreversible damage caused by rice panicle blast considerably reduces rice grain quality and yield, often leading to direct yield losses of up to 70% to 100% under favorable field conditions (Khan *et al.,* 2014; Fang *et al.,* 2019). Blast resistance has a general category of complete and partial resistance. Complete resistance is a qualitative and race-specific trait, typically governed by a single gene (Wang *et al.,* 2014). However, this type of resistance is easily overcome due to the emergence of pathogen strains virulent on certain resistance genes under field conditions. In contrast, partial resistance, controlled by minor polygenes (QTLs), offers broad-spectrum and durable resistance to *M. oryzae*. Thus, rice cultivars with multiple blast resistance genes proved more desirable. In the presented study, 25 temperate *Japonica* rice accessions with a higher level of panicle blast resistance were prominent at different locations. These rice accessions may serve as donors of panicle blast resistance in future rice breeding programs.

GWAS offers the best mapping efficiency with more loci and numerous polymorphic SNPs than traditional linkage-based mapping methods. Over the last decade, GWAS has emerged as a widely adopted method to search for genes and QTL related to complex crop traits (Lu *et al.,* 2021). In this promising study, the 191 temperate *Japonica* accessions bore phenotyping for panicle blast resistance under field conditions. Using the mixed linear model (MLM) for GWAS, the 141 SNPs related to panicle blast resistance across various chromosomes surfaced and succeeded in identifying four key QTLs associated with resistance to *M. oryzae*. Within the confidence interval of the significant QTL *qPBR07* on chromosome 7, a total of 63 genes were annotated, among which *Os07g0511500*, associated with the Snf2 protein family, was proposed as the candidate gene for *qPBR07*. The Snf2 protein family, known for its vast diversity, plays a crucial role in chromatin remodeling, utilizing ATP hydrolysis to facilitate the various biological processes, such as transcription, DNA repair, and replication (Guo *et al*., 2022).

Previous observations also detailed the expression of *Snf2* family genes resulting from the induction of rice blast fungus infection (Guo *et al.,* 2022). Another potential gene was *Os07g0515100*, which encodes calcium-dependent protein kinase (CDPK), playing an important role in the regulation of the kinase activity. At the seedling stage, the gene *Os07g0516300*, a member of the *S40* gene family, revealed an enhanced expression in response to fungal infection (Zheng *et al.,* 2019). Wang *et al.* (2018) reported the gene *Os07g0518100*, a cytochrome P450 (CYP450) protein from the 716A subfamily, positively regulates the resistance against the bacterial leaf blight and the rice sheath blight (Wang *et al.,* 2022). Additionally, the gene *Os07g0521100,* located in the *qPBR07* region, appeared associated with an LRR-type disease-resistance protein. The annotation of genes *Os07g0513600* and *Os07g0515200* emerged as conserved hypothetical proteins. The conserved hypothetical proteins were of particular interest due to their potential roles in the biological processes, including defense mechanisms. Similar proteins have been implicated in pathogen defense in various plant species (Sekhwal *et al.,* 2015). Protein binding proteins, such as *Os07g0512100,* manifested involvement in critical protein-protein interactions that underpin various cellular processes, including immune response. These interactions may facilitate the plant's ability to recognize and respond to the pathogens and enhance the disease resistance (Kourelis and Van-Der-Hoorn, 2018). The results suggested

that a gene cluster could exist in the *qPBR07* region, which may enhance the multiple disease resistance of the rice plant. Therefore, further experiments are necessary to investigate the possible roles of these genes in managing the panicle blast.

The SNP marker at Chr7:19770475 showed a significant difference on panicle blast resistance between the genotypes AA and GG, and this marker could be helpful for marker-assisted selection to improve the breeding efficiency. The diverse genetic basis of resistance highlighted by this study provides a valuable resource in breeding programs. By incorporating these resistance QTLs (genes) in the new rice cultivars, breeders could develop cultivars with enhanced and durable resistance to panicle blast. However, further confirmation is essential to determine the in-depth role of these candidate genes in providing resistance to *M. oryzae*. The identification of QTLs that align with these genes suggests the existence of abundant natural variations within the rice gene pool. These variations can be effective to enhance the inherent resistance to *M. oryzae* and extend the scope and durability of resistance in newly developed rice cultivars.

A comprehensive exploration of the genetic and biochemical aspects of these genes is vital to offer new insights in the intricate regulatory networks and complex mechanisms that collectively confer the blast disease resistance in rice crop. In the presented study, the identified QTLs may serve as novel panicle blast resistance loci. This comprehensive approach, combining multiple resistance genes, could significantly improve the rice genotypes' resistance against a wide range of fungal pathogens, ensuring sustainable crop production and food security.

CONCLUSIONS

Rice genotypes screening for blast resistance prevailed, successfully identifying 25 rice accessions, revealing a high level of resistance under field conditions. Four QTLs associated with panicle blast resistance also emerged distinct. Based on the initial gene annotation, the Snf2 family gene *Os07g0511500*, the S40 family gene *Os07g0516300*, and the cytochrome P450 gene *Os07g0518100* may play crucial roles in regulating rice resistance to panicle blast. The putative conserved genes *Os07g0513600* and *Os07g0515200*, as well as the protein-binding gene *Os07g0512100*, could be the potential genes in pathogen defense, arising as promising candidate genes for blast disease resistance. The elite accessions, QTLs/genes, and SNPs identified in this study could be beneficial in future molecular breeding for panicle blast resistance.

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