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Identification of novel major and minor quantitative trait loci associated with bacterial blight resistance in rice from *Oryza nivara*-derived wild introgression lines

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Abstract

Wild species are known to be reservoir for agronomically important traits including disease resistance in crops. Bacterial blight (BB) is one of the major diseases of rice causing significant yield reduction, and host plant resistance plays a major role in the management of the disease. In this study, we employed backcross introgression lines (BILs) of 'Swarna' containing wild introgressions from two accessions of *Oryza nivara* IRGC81848 and IRGC81832 in order to map quantitative trait loci (QTLs) for BB resistance. A total of 22 and 43 QTLs for BB resistance were detected respectively on 12 chromosomes, which explained between 2.5% to 18.09% of the phenotypic variance in the two populations. Of the significant QTLs, *qBB-1-1* (RM259-RM9) and *qBB-10-1* (RM474-RM271) were detected across the two populations and the resistance contributing alleles were from donor wild accessions. Two major QTLs in 'Swarna'/*O. nivara* IRGC81848 (NPS lines) and seven QTLs in 'Swarna'/*O. nivara* IRGC81832 (NPK lines) were consistently detected across the years in the respective populations. Novel QTLs *qBB-10-1* and *qBB-12-1* are identified as candidate genomic regions for further fine mapping. These stable QTLs identified can be utilized for enhancing BB resistance in elite rice genotypes via marker-assisted or genomic selection strategies.

KEYWORDS
bacterial blight, BB resistance, CSSLs, QTL mapping, rice, wild introgression lines

1 | INTRODUCTION

Xanthomonas oryzae pv. *oryzae* (*Xoo*) is a devastating plant pathogen, causing bacterial blight (BB) disease in rice (*Oryza* spp.). The disease is a major biotic stress for rice production in Asia and Africa and also prevalent in Australia and Latin America (Laha et al., 2014). BB causes up to 50–80% yield reduction (Elings et al., 1997; Kim, 2018), in addition to marked reduction in photosynthetic rates, grain filling and quality of produce. In India, the disease is a major production constraint, especially in the intensively cultivated irrigated and rain fed lowland ecosystems. The disease is more prevalent during monsoon season and when rice is cultivated with high dosage of nitrogenous fertilizer. Analyses of disease survey data for the last four decades revealed that the intensity and geographical spread of the disease has increased significantly over the years in different rice growing regions of India (Laha et al., 2016). Chemical control and other methods of

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disease management like cultural practices and biological control have not been very successful against BB disease. Host plant resistance is the most effective and environment friendly strategy for managing this disease (Chukwu et al., 2019). Molecular mapping and marker-assisted breeding approaches helped in molecular breeding for BB resistance in a large scale (Sundaram et al., 2008). At least 46 major BB resistance genes and 17 QTLs conferring tolerance have been identified and characterized (Bhasin et al., 2012; Han et al., 2014; Kim et al., 2015) from diverse rice germplasm, and some of them are currently employed in BB resistance breeding programmes either singly or by pyramiding few genes in the genetic background of popular varieties and hybrid rice parental lines (Chen et al., 2020; Kumar et al., 2020; Neelam et al., 2020; Zhao et al., 2022).

Among these, 12 BB resistance genes have been cloned, namely, *Xa1* (Yoshimura et al., 1998), *Xa3/Xa26* (Sun et al., 2004; Xiang et al., 2006), *Xa4* (Hu et al., 2017), *xa5* (Iyer & McCouch, 2004), *Xa7* (Chen et al., 2021), *Xa10* (Tian et al., 2014), *xa13* (Chu et al., 2006), *Xa21* (Song et al., 1997), *Xa23* (Wang et al., 2015), *xa25* (Liu et al., 2011), *Xa27* (Bimolata et al., 2013; Gu et al., 2004) and *xa41* (Hutin et al., 2015), which are reported to encode different types of proteins. Additionally, Ji et al. (2020) reported successful cloning of *Xa2/Xa31*, *Xa14* and *Xa45*, all located in chromosome 4. However, due to complex structure of *Xoo* populations and their virulence mechanisms, many BB resistance genes have become less effective or ineffective resulting in several outbreaks in Asian countries (Chukwu et al., 2019). QTL mapping was employed in this study to detect any novel major and minor genes of interest in crosses involving cultivars and wild species.

Wild relatives of crops are a promising source for resistance genes against major biotic stresses in rice for many decades (Brar & Khush, 1997; Prescott-Allen & Prescott-Allen, 1988). Seven genes, *Xa21*, *Xa23*, *Xa27*, *Xa29*, *Xa30*, *Xa32 (t)*, *Xa33*, *Xa35 (t)* and *Xa38*, among the 46 genes for BB resistance identified were derived from different accessions of wild species. Many improved varieties with BB resistance have been developed through backcross breeding and pyramiding of resistant genes in popular rice varieties (Perez et al., 2008; Ramalingam et al., 2020; Sundaram et al., 2008, 2009; Swamy et al., 2006; Yugander et al., 2018). However, the breakdown of resistance due to appearance of new virulence form of the pathogen and apparent changes in climatic conditions are often reported (Djedatin et al., 2016; Vera Cruz et al., 2000) and urges exploration of new resistant resources. The present study focuses on identification of BB resistant wild introgression lines in the background of popular variety 'Swarna' and study of the genomic regions associated with resistance using QTL mapping strategy.

2 | MATERIALS AND METHODS

2.1 | Plant materials

Two sets of BILs (BC_2F_5) (Swamy et al., 2014), derived from the crosses 'Swarna'/*Oryza nivara* IRGC81848 (designated as NPS lines) and 'Swarna'/*O. nivara* IRGC81832 (designated as NPK lines) developed at ICAR-Indian Institute of Rice Research (ICAR-IIRR) (formerly Directorate of Rice Research, Hyderabad) were selfed and advanced through single panicle selection to obtain BC_2F_8 progenies. Both the populations were subjected to screening against *Xoo* at ICAR-Indian Institute of Rice Research, Hyderabad, Telangana State, India, both at glasshouse conditions in wet season (Kharif) 2015 as well as irrigated field conditions in wet season (Kharif) 2016. Selected resistant lines, namely, NPS19-1, NPS56-2, NPS58-1 and NPK77-3 were multiplied and confirmed for BB resistance under field conditions.

2.2 | Phenotyping and selection of BILs

Each genotype (BIL) was directly sown as line in plastic trays (60 × 40 × 7 cm), which were prepared by filling a mixture of field soil and farm yard manure (3:1) at glasshouse conditions with parent 'Swarna' and susceptible check variety 'TN1'. The plants were fertilized with nitrogenous and phosphatic fertilizers (6 g urea and 8 g single super phosphate per tray in two splits) and were irrigated regularly. No plant protection chemicals were applied, and care was taken to raise healthy plants. *Xoo* strain IX 020 maintained at IIRR were used for evaluation of resistance of the entries against the disease. This strain belongs to Pathotype group 19 (Yugander et al., 2017) and shows a susceptible reaction to *Xa4* and *xa5* and moderate reaction to *Xa21* but shows a resistant reaction to *xa13*. This strain was isolated from naturally infected fields of our research station and was used for resistance evaluation. This specific *Xoo* strain was selected for screening the plant materials as this pathotype is most predominant in India, especially southern parts of India.

The bacterial pathogen was mass multiplied on modified Wakimoto's medium (sucrose 20 g; peptone 5 g; calcium nitrate 0.5 g; Na_2HPO_4 1.82 g; ferrous sulphate 0.05 g; agar 20 g; distilled water 1000 ml; pH 6.8–7.0) for 72 h. A bacterial suspension (10^{8-9} cfu/ml) was prepared by mixing a freshly grown bacterial colony (3 days old) with sterile distilled water. Bacterial suspension was used to clip-inoculate the plants at 40–45 days old stage. For each entry, 12–15 fresh and healthy leaves were inoculated. A moderate temperature (28–32°C) and high humidity (>85%) was maintained in the glasshouse. Observations were recorded 15 days after inoculation both by measuring the lesion length and also by recording the disease score following the SES (Standard Evaluation System for Rice) scale (International Rice Research Institute [IRRI], 2014). For each genotype, observation from minimum five leaves was recorded. The entries were categorized as resistant (average lesion length up to 3 cm; SES score 0–3), moderately resistant (average lesion length 3.1–6 cm; average SES score 3.1–5), moderately susceptible (average lesion length 6.1–9 cm; average SES score 5.1–7) and susceptible (average lesion length more than 9 cm; average SES score 7.1–9) (Chen et al., 2000; IRRI, 2014). The phenotypic data taken on glasshouse conditions (wet season, 2015), irrigated field conditions (wet season 2016) and average of both the data were indicated as BB15, BB16 and BBM, respectively.

In addition, the field screening was carried out at ICAR-Indian Institute of Rice Research (IIRR), Rajendranagar farm, Hyderabad located at latitude of 11°00′ N longitude of 77°00′ E and an elevation of 426.72 m above MSL. The selected BILs NPK77-3(G1), NPS19-1 (G2), NPS56-2(G3), NPS58-1(G4) and 'Swarna' (G5) were raised at normal irrigated field conditions during 2018 to 2020 wet seasons with randomized complete block design with three replications, and the grain yield was evaluated for three seasons. Quality parameters like grain dimensions, head rice recovery, alkali spreading value, amylose content and aroma were measured using dehusked samples following Standard Evaluation System (IRRI, 2014). Yield data were subjected to G × E analysis in PB tools (Version 1.4, http://bbi.irri.org/products) to identify stable genotypes using GGE biplot method based on the sites regression (SREG) linear–bilinear model (Kang, 1993). The notation G1, G2, G3, G4 and G5 was assigned to NPK77-3, NPS19-1, NPS56-2, NPS58-1 and 'Swarna', respectively by PB Tools software for the representation in biplots generated from G × E lines.

2.3 | Genotyping of the BILs

Genomic DNA was extracted from leaf using CTAB method. The extracted DNA was estimated at 260/280 and 260/230 for quality and quantity using UV spectrophotometer. A set of 300 microsatellite markers covering 12 chromosomes including 165 SSRs (Orjuela et al., 2010) and reported BB resistance linked markers were used for genotyping and assessing the parental polymorphism between 'Swarna' and *O. nivara* accessions IRGC81848 and IRGC81832. A total of 117 and 140 polymorphic microsatellite markers were used to analyse the segregation pattern in the cross combination of BC_2F_8 families of 'Swarna'/*O. nivara* IRGC81848 and 'Swarna'/*O. nivara* IRGC81832, respectively. The markers linked to specific *Xa* genes, namely, RM16335 (*Xa4*), RM17499 (*Xa38*), RM413 (*xa5*), RM5711 (*Xa33*), RM152 (*xa13*), RM1341 (*Xa21*) and RM26998 (*Xa23*) were used in the genotyping. The PCR reaction for SSR primers was performed with 10-μl final volume containing 15 ng of genomic DNA, 1X assay buffer, 200 μM of dNTPs, 1.5-mM $MgCl_2$, 10 pmol of each forward and reverse primer and 1 unit of *Taq* DNA polymerase (Thermo Scientific). PCR amplification was performed under the following conditions: initial denaturation at 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 1 min, annealing at 55°C for1 min, extension at 72°C for 1 min, followed by the final extension 72°C for 5 min. The amplified products were screened for marker segregation pattern by resolving in agarose gel (3%) electrophoresed at 120 V for 2 h and scored for segregating bands using gel documentation system (Alfa imager, U.S.A).

2.4 | Statistical analysis and QTL mapping

Analyses of descriptive statistics and frequency distribution of the BB resistance for two years as well as QTL detection were mainly performed using the IciMapping v4.2 (www.isbreeding.net) and STAR (http://bbi.irri.org/products). Linkage maps were constructed from the genotyping scores of 117 and 140 molecular markers in respective segregating population with IciMapping v4.2 (www.isbreeding.net) following MAP functionality with Kosambi mapping function (Kosambi, 1944). To map QTLs, different methods like single marker analysis (SMA), Interval mapping (IM) and Composite interval mapping (CIM), were carried out using IciMapping v4.2 software (Wang et al., 2005) at log-likelihood of odds (LOD) score of 3 and results were compared. Empirical thresholds to declare presence of a QTL were obtained using the re-sampling by permutation method, performing 1000 permutations for each trait/chromosome combination.

3 | RESULTS

Two populations of backcross introgression lines derived from *O. nivara* were screened for two consecutive years, 2015 and 2016 at glasshouse and field conditions, respectively, by artificially inoculating (Figure S1), *Xoo* strain (strain IX-020) both in the glasshouse and in field conditions.

3.1 | 'Swarna'/*O. nivara* IRGC81848 BILs (NPS lines)

BB resistance was assessed for a set of 94 BILs derived from the *O. nivara* accession (IRGC81848) in 'Swarna' background across two -years. In both the years, BB disease reaction of the BILs ranged from 1 to 9 showing highly resistant to highly susceptible reactions with mean disease score of 8.4 and 8.0 in glasshouse condition (2015) and field conditions (2016), respectively (Table 1). Greater skewness and kurtosis values were observed showing a distribution of more number of genotypes towards susceptible score and same trend was observed in both the years (Figure S1). Among these BILs, three lines were

TABLE 1 Descriptive statistics of BB resistance reaction of BC_2F_8 population 'Swarna'/*O. nivara* IRGC81848 BILs (NPS lines)

Trait name	Sample size	Mean	Variance	Std error	Skewness	Kurtosis	Minimum	Maximum	Range	*W* test	*P* value
BB15	94	8.4255	2.2901	1.5133	−3.3662	12.0872	1	9	8	0.4428	0.00E+00
BB16	94	8.0213	2.3006	1.5168	−2.4897	8.4699	1	9	8	0.6031	0.00E+00
BBM	94	8.2234	1.6807	1.2964	−3.457	14.7003	1	9	8	0.5848	0.00E+00

found resistant, two moderately resistant, 10 moderately susceptible and 83 were susceptible in 2015. Similarly, three resistant, 40 moderately susceptible and 62 highly susceptible were detected in screening during 2016. Considering two- years' average, three resistant, two moderately resistant, 47 moderately susceptible and 53 susceptible BILs were identified. Three BILs, namely, NPS20, NPS58 and NPS66 were found highly resistant (<3) in 2015, while the BILs NPS58, NPS56 and NPS19 were highly resistant (<3) in 2016. NPS58 was showing highly resistant reaction in both the seasons while others showed either highly resistant or moderately resistant scores. Based on consistent performance for reaction against BB disease and better agro-morphological parameters including yield, selected nonsegregating progenies from NPS58, NPS56 and NPS19 were advanced and multiplied and tested at normal irrigated conditions for further four years and nominated for testing under All India Coordinated Rice Improvement Project (AICRIP) trials for multilocation testing.

3.2 | 'Swarna'/*O. nivara* IRGC81832 BILs (NPK lines)

A total of 90 NPK lines derived from *O. nivara* accession (IRGC81832) in 'Swarna' background were tested in 2015 at

TABLE 2 Descriptive statistics of BB resistance reaction of BC_2F_8 population 'Swarna'/*O. nivara* IRGC81832 BILs (NPK lines)

Trait name	Sample size	Mean	Variance	Std error	Skewness	Kurtosis	Minimum	Maximum	Range	*W* test	*P* value
BB15	90	8.2889	2.1853	1.4783	−2.6888	8.1549	1	9	8	0.5455	0.00E+00
BB16	90	8.3556	1.5126	1.2299	−2.3058	6.2089	3	9	6	0.5619	0.00E+00
BBM	90	8.3222	1.1197	1.0582	−3.0167	13.3999	2	9	7	0.6488	0.00E+00

TABLE 3 Additive effect QTLs for BB resistance based on phenotyping under two environments 2015 and 2016 in population 'Swarna'/*O. nivara* IRGC81848 BILs (NPS lines) and detected using QTL IciMapping 4.2

Trait name	Chr	Position	Left marker	Right marker	LOD	PVE (%)	Add
BB15							
qBB15-2-1	**2**	**7.88**	**RM8080**	**RM341**	**17.893**	**5.593**	**2.877**
qBB15-5-1	5	17.07	RM5140	RM146	6.618	3.124	3.323
qBB15-6-1	**6**	**19.47**	**RM204**	**RM454**	**12.476**	**3.779**	**2.615**
qBB15-8-1	8	8.11	RM152	RM1384	11.649	3.755	2.625
qBB15-8-2	8	19.11	RM1384	RM223	9.228	3.758	2.594
qBB15-9-1	9	19.02	RM257	RM215	11.043	3.754	2.625
qBB15-9-2	9	11.02	RM316	RM434	16.568	3.782	2.614
qBB15-10-1	10	8.70	RM474	RM271	8.123	3.775	2.607
BB16							
qBB16-1-1	1	13.21	RM259	RM9	3.112	4.051	3.115
qBB16-2-1	**2**	**6.88**	**RM8080**	**RM341**	**12.277**	**6.674**	**3.282**
qBB16-4-1	4	5.016	RM551	RM16335	4.964	4.049	3.115
qBB16-6-1	**6**	**19.47**	**RM204**	**RM454**	**8.018**	**4.051**	**3.115**
qBB16-7-1	7	14.67	RM214	RM1132	5.911	4.049	3.115
qBB16-7-2	7	22.67	RM455	RM1132	7.809	4.051	3.115
qBB16-11-1	11	14.80	RM536	RM287	4.781	4.050	3.114
BBM							
qBBM-2-1	**2**	**6.88**	**RM8080**	**RM341**	**18.093**	**7.857**	**3.042**
qBBM-5-1	5	17.070	RM413	RM146	6.823	4.196	2.708
qBBM-6-1	**6**	**20.47**	**RM204**	**RM454**	**10.614**	**4.195**	**2.705**
qBBM-7-1	7	22.67	RM455	RM1132	8.172	4.193	2.696
qBBM-8-1	8	19.11	RM1384	RM223	6.763	4.196	2.708
qBBM-9-1	9	11.02	RM316	RM434	10.889	4.196	2.708
qBBM-11-1	11	27.80	RM224	RM144	5.048	4.193	2.696

Note: Bold letters represent the QTLs observed across years and average. Underline represents the QTLs observed across the populations. BB15—bacterial blight resistance score in 2015; BB16—bacterial blight resistance score in 2016; BBM—average of bacterial blight score 2015 and 2016.

glasshouse conditions and in 2016 at field conditions. In 2015, phenotypic scores for BB ranged from 1 to 9 while it was 3 to 9 in case of 2016 with a mean value of 8.28 and 8.35 in the successive years (Table 2). In this population also, distribution of resistance reaction was more towards susceptibility as inferred from skewness and kurtosis of frequency distribution parameters. The lines, namely, NPK77, NPK46 and NPK54, were found to be highly resistant during glasshouse screening while NPK77, NPK43 and NPK13 were highly resistant at field conditions. Among all BILs tested, three lines were found resistant, two moderately resistant, 10 moderately susceptible and 83 were susceptible in 2015. However, only two resistant, one moderately resistant, 21 moderately susceptible and 65 highly susceptible BILs were detected in screening during 2016. Considering two years average, only one line, NPK77, was highly resistant. Progenies of NPK77, which were selected from these segregating BILs were advanced by single panicle selection and further multiplied and confirmed for BB resistance in field conditions.

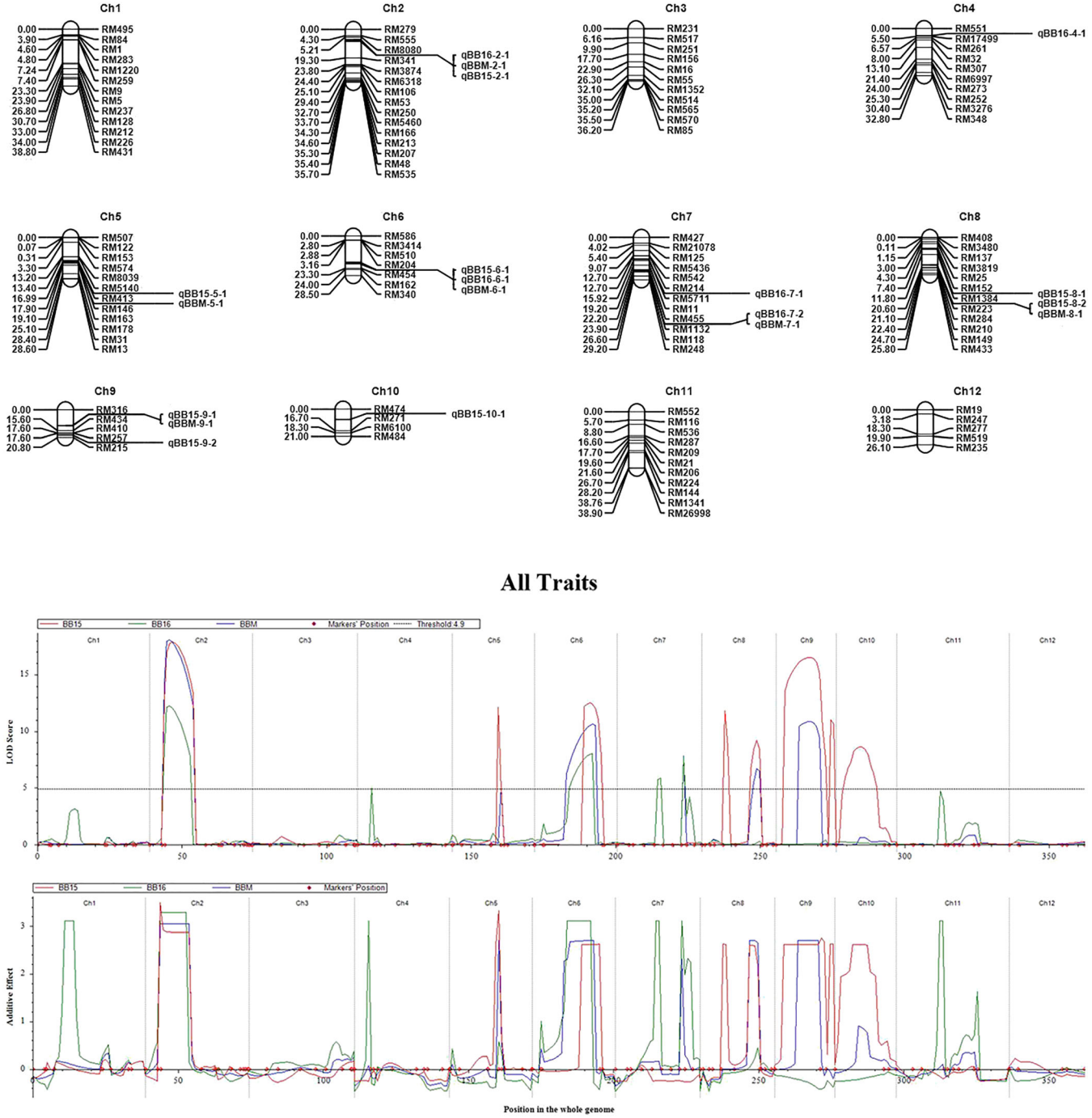


FIGURE 1 Additive effect QTLs for BB resistance based on phenotyping under two environments 2015 and 2016 in population 'Swarna'/*Oryza nivara* IRGC81848 BILs (NPS lines) and detected using QTL IciMapping4.2

3.3 | Mapping QTLs using SSR markers

3.3.1 | 'Swarna'/*O. nivara* IRGC81848 BILs (NPS lines)

A total of 22 QTLs were identified for resistance against BB disease with eight QTLs in 2015, seven QTLs in 2016 and seven QTLs using the mean of both the years (Table 3). QTLs were found in all the chromosomes except Chr.3 and Chr.12 (Figure 1). LOD values ranged from 3.11 to 18.09, whereas phenotypic variance ranged from 3.32% to 7.85%. Among these, two QTLs, namely, *qBB-2-1* and *qBB-6-1*, were co-located and consistently appeared in the two- years data and that of the mean. A resistance QTL *qBB-2-1* was detected on Chr.2, flanked by the SSR markers RM8080 and RM341 with a PVE of 2.87 (2015), 3.28 (2016) and 3.04 (Mean). Single marker analysis also detected RM8080 as linked to BB resistance with a very high phenotypic variance of 33.38% in 2015 and 25.88% in 2016. Another QTL in Chr.6, *qBB-6-1*, detected between RM204 and RM454, showed PVE of 3.77 (2015), 4.05 (2016) and 4.19 (mean). In 2015, QTLs were detected which are located in Chr.5 (RM413-RM146), Chr.8 (RM152-RM1384-RM223), Chr.9 (RM257-RM215, RM316-RM434) and Chr.10 (RM474-RM271). In 2016, QTLs were located on Chr.1 (RM259-RM9), Chr.4 (RM551- RM17499), Chr.7 (RM214- RM5711) and Chr.11 (RM536-RM287). Interestingly, QTLs were found to be located at *xa5* and *xa13* and *Xa33* genomic regions also and the resistance contributing alleles were from *O. nivara* with PVE ranging from 3% to 4%.

Single marker association showed that 14 markers, RM5 (Chr.1); RM250, RM555, RM8080 (Chr.2); RM251 (Chr.3); RM261 (Chr.4); RM5140, RM8039 (Chr.5); RM1132 (Chr.7); RM25 (Chr.8); RM316 (Chr.9); RM21, RM224 (Chr.11); and RM247 (Chr.12) were significantly associated with more than 2.5% phenotypic variance, and interestingly, both the parental alleles contributed for minor effect improvement for BB tolerance. In addition, six *Xoo* genes (*xa13*, *Xa21*, *Xa23*, *Xa33*, *Xa38* and *xa5*) linked markers, namely, RM152, RM1341, RM26998, RM5711, RM17499 and RM413 showed major to minor association with resistance across two years as well as in the mean data. Interestingly, among the three resistant lines identified in this population; NPS56 was harbouring *qBB15-2-1* while NPS19 and NPS58 were found to harbour another consistent QTL *qBB15-6-1*. NPS19 and NPS56 showed 88.88% and NPS56 showed 93% of genome recovery to the recurrent parent 'Swarna' based on analysis with 117 polymorphic SSR markers.

3.3.2 | 'Swarna'/*O. nivara* IRGC81832 BILs (NPK lines)

A total of 43 QTLs were detected in this population considering two- years data and mean, with 13 in 2015, 12 in 2016 and 18 using mean data (Table 4). QTLs were detected in all chromosomes except 7, 8 and 9 (Figure 2). LOD values ranged from 3.31 to 10.71 and PVE (%) ranged from 0.5 to 9.99. Four SSRs, namely, RM19291, RM474, RM32 and RM307 were showing PVE% of 11.03, 12.46, 13.84 and 19.69, respectively, by single marker analysis. Seven QTL regions appeared consistently across the seasons, namely, *qBB-4-1* (RM273-RM241) in Chr.4, *qBB-5-1* (RM178-RM31) in Chr.5, *qBB-5-2* (RM5140 and RM146) in Chr.5, *qBB-6-1* (RM162 and RM19291) in Chr.6, *qBB-11-1* (RM144-*Xa21*) in Chr.11, *qBB-11-2* (*xa23*-RM287) in Chr.11 and *qBB-12-1* (RM247-K46-1) in Chr.12. QTLs were detected with flanking markers of *Xa38*, *xa5*, *Xa23*, *Xa21* and *Xa4*. All the resistance alleles in the detected QTLs were from *O. nivara*.

Only four markers showed significant major effect single marker association. RM19291 of Chr.6, RM474 of Chr.10 and RM32 of Chr.4 showed major effect association for one year (2015 or 2016) with PVE of 11 to 13%. Another marker RM307 showed a major association in 2016 and mean data with PVE of 16 and 19%, respectively. All the markers showed that their additive effect of tolerance was contributed by *O. nivara* allele. The BIL, NPK77, which was identified as highly resistant in this population was found to harbour 4 consistent QTLs *qBB15-4-1*, *qBB15-5-1*, *qBB15-5-3* and *qBB15-6-1* identified in this study and *O. nivara* alleles for *Xa4* gene. This line also showed 86% of genome recovery with respect to 'Swarna' background based on analysis with 140 polymorphic markers. Epistatic QTL interactions were studied, and we found large network of epistatic interactions in both the population. However, most of the interactions were of very minor effect and did not show any consistency across the years (Figure S3), and hence, they were not considered for further analysis.

3.4 | Yield and grain quality of the selected BB resistant lines

The selected lines NPK77-3(G1), NPS19-1(G2), NPS56-2(G3) and NPS58-1(G4) were raised under normal irrigated conditions in the Rajendrangar farm of ICAR-IIRR along with their parent 'Swarna' to evaluate the yield for three years (2019, 2020 and 2021). NPS19-1 (G2) was identified as the most ideal genotype with highest average yield, and NPK77-3 (G1) as the most stable high yielding line followed by NPS56-2 and NPS58-1compared with 'Swarna' (G5) (Figure 3a). The quality analysis of these lines showed that they are having very high head rice recovery (56.1–69.6%) except in case of NPS56-2. Among these lines, three lines showed medium slender grain type while NPS19-1 was having short bold grain type (Figure 3b). All lines had intermediate amylose content and Alkali spreading value and were nonaromatic in nature.

4 | DISCUSSION

The wild and weedy relative species are known to be a rich reservoir of genes for resistance against biotic stresses. Even though they are not utilized largely in breeding programmes, the significance of wild species is gaining more importance as donors of novel genes in recent years. In case of BB resistance genes/loci identified so far in rice; more than 25% is contributed by various wild rice species (Angeles-

TABLE 4 Additive effect QTLs for BB resistance based on phenotyping under two environments 2015 and 2016 in population 'Swarna'/*O. nivara* IRGC81832 BILs (NPK lines) and detected using QTL IciMapping 4.2

Trait name	Chr	Position	Left marker	Right marker	LOD	PVE(%)	Add
BB15							
qBB15-2-1	2	12.00	RM290	RM341	9.153	2.159	3.231
qBB15-2-2	2	30.00	RM53	RM250	7.505	2.158	3.243
qBB15-3-1	3	30.40	RM55	RM1352	4.333	2.253	2.270
qBB15-4-1	**4**	**26.16**	**RM273**	**RM241**	**5.628**	**2.157**	**3.244**
qBB15-5-1	**5**	**17.07**	**RM5140**	**RM146**	**8.014**	**2.158**	**3.241**
qBB15-5-2	5	10.07	RM289	RM413	7.101	2.158	3.238
qBB15-5-3	**5**	**26.07**	**RM178**	**RM31**	**7.342**	**2.158**	**3.242**
qBB15-6-1	**6**	**25**.00	**RM162**	**RM19291**	**10.717**	**2.333**	**2.752**
qBB15-6-2	6	3.00	RM3414	RM204	7.432	2.881	3.080
qBB15-10-1	10	8.70	RM474	RM271	7.732	2.492	2.564
qBB15-11-1	**11**	**11.80**	RM26998	**RM287**	**7.603**	**2.159**	**3.230**
qBB15-11-2	**11**	**28.80**	**RM144**	RM1341	**7.618**	**2.155**	**3.247**
qBB15-12-1	**12**	**11.00**	**RM247**	**K46_1**	**9.048**	**2.534**	**2.561**
BB16							
qBB16-1-1	1	9.00	RM259	RM9	8.394	3.987	2.425
qBB16-1-2	1	26.00	RM5	RM237	5.556	9.992	2.715
qBB16-2-1	2	4.00	RM279	RM555	4.074	1.907	2.425
qBB16-2-2	2	13.00	RM290	RM341	6.923	1.907	2.425
qBB16-4-1	4	8.16	RM32	RM16335	7.312	1.905	2.427
qBB16-4-2	**4**	**26.16**	**RM273**	**RM241**	**8.482**	**5.269**	**2.423**
qBB16-5-1	**5**	**17.07**	**RM5140**	**RM146**	**5.843**	**3.318**	**2.696**
qBB16-5-2	**5**	**26.07**	**RM178**	**RM31**	**7.365**	**1.907**	**2.425**
qBB16-6-1	**6**	**25.00**	**RM162**	**RM19291**	**4.106**	**1.652**	**2.713**
qBB16-11-1	**11**	**11.80**	RM2699	**RM287**	**5.517**	**1.735**	**2.585**
qBB16-11-2	**11**	**28.80**	**RM144**	RM1341	**7.682**	**2.143**	**2.425**
qBB16-12-1	**12**	11.00	**RM247**	**K46_1**	**5.593**	**1.872**	**2.446**
BBM							
qBBM-1-1	1	10.00	RM259	RM9	6.610	2.019	2.478
qBBM-1-2	1	26.00	RM5	RM237	7.356	5.057	2.108
qBBM-2-1	2	4.00	RM279	RM555	7.061	1.029	2.466
qBBM-2-2	2	9.00	RM8080	RM290	7.111	0.875	3.181
qBBM-2-3	2	30.00	RM53	RM250	6.940	1.046	2.170
qBBM-4-1	4	8.16	RM32	RM16335	3.313	0.505	1.387
qBBM-4-2	**4**	**26.16**	**RM273**	**RM241**	**8.129**	**3.053**	**2.127**
qBBM-4-3	4	29.16	RM17499	RM470	7.555	1.029	2.466
qBBM-5-1	**5**	**17.07**	**RM5140**	**RM146**	**9.813**	**2.029**	**2.466**
qBBM-5-2	5	11.07	RM289	RM146	6.909	0.875	3.188
qBBM-5-3	**5**	**26.07**	**RM178**	**RM31**	**7.428**	**0.875**	**3.191**
qBBM-6-1	**6**	**25**.00	**RM162**	**RM19291**	**9.182**	**1.061**	**2.089**
qBBM-6-2	6	3.00	RM3414	RM204	4.523	1.063	2.084
qBBM-10-1	10	7.70	RM474	RM271	8.090	1.063	1.707
qBBM-10-2	10	17.70	RM271	RM6100	3.813	1.061	2.087
qBBM-11-1	**11**	**11.80**	RM26998	**RM287**	**7.106**	**0.875**	**3.174**
qBBM-11-2	**11**	**28.80**	**RM144**	RM1341	**8.704**	**1.874**	**3.196**
qBBM-12-1	**12**	**11.00**	**RM247**	**K46_1**	**6.558**	**1.021**	**2.473**

Note: Bold letters represent the QTLs observed across years and average. Underline represents the QTLs observed across the populations. BB15—bacterial blight resistance score in 2015; BB16—bacterial blight resistance score in 2016; BBM—average of bacterial blight score 2015 and 2016.

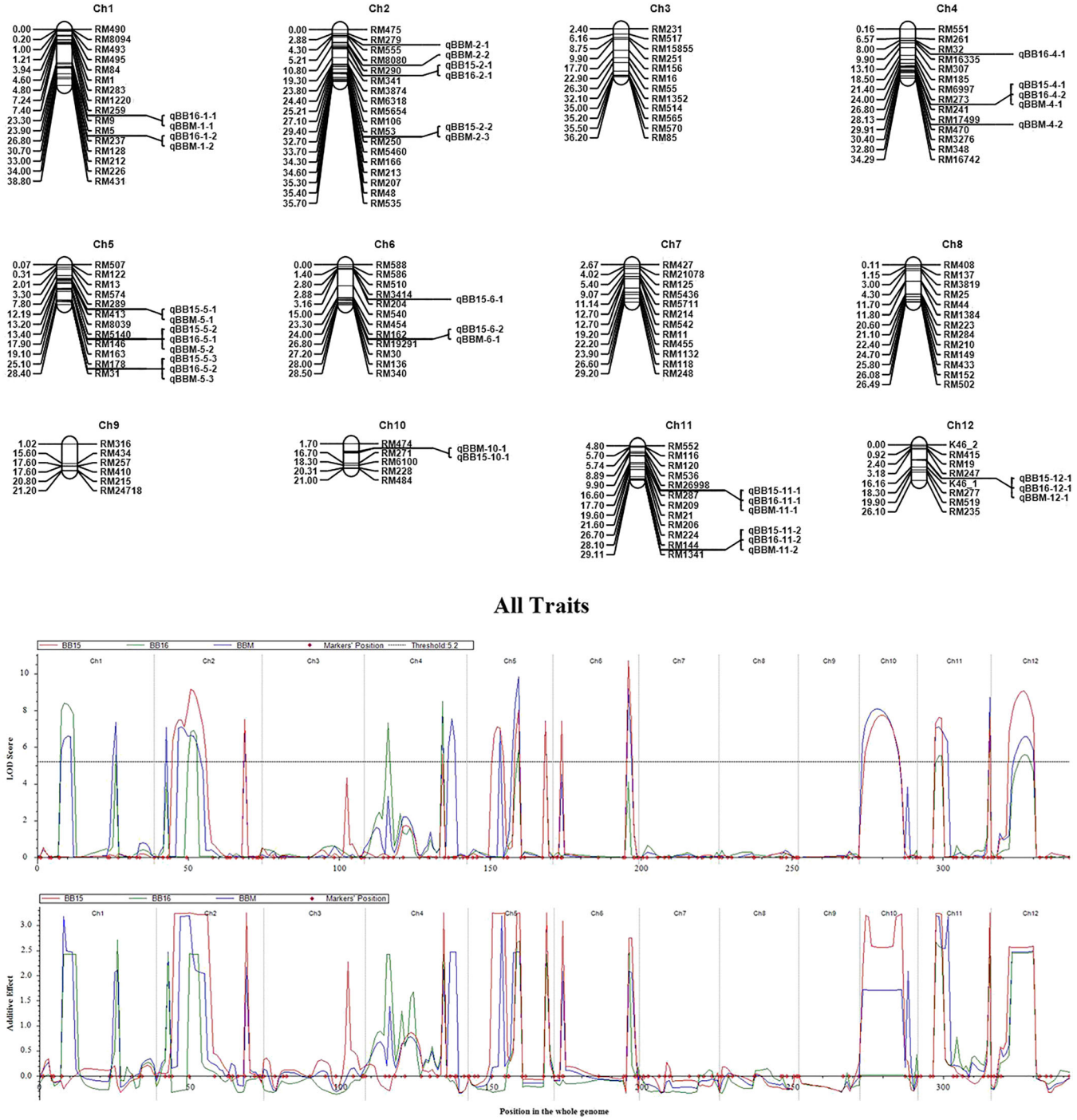
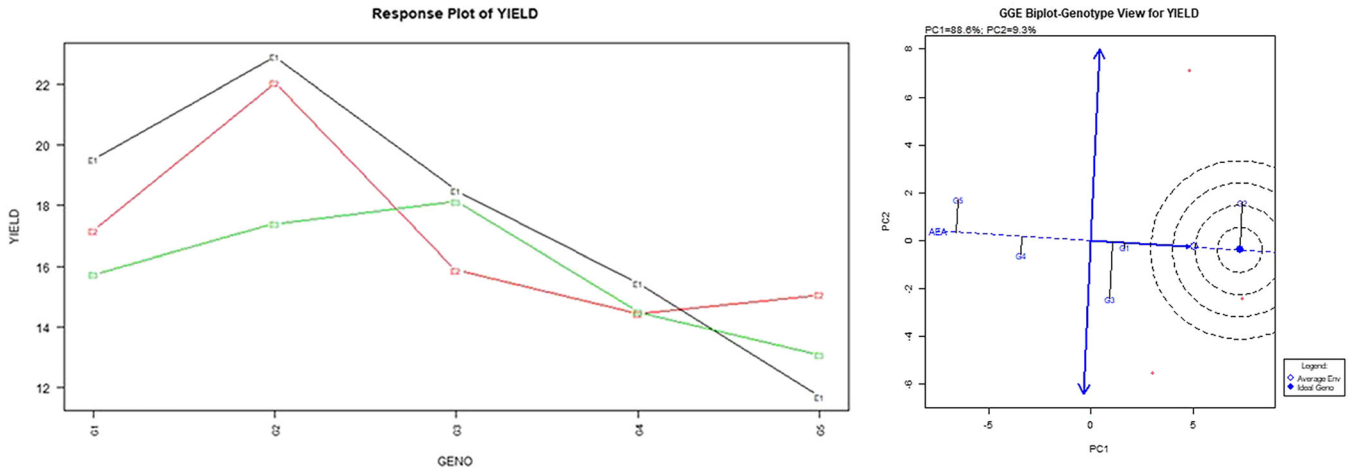
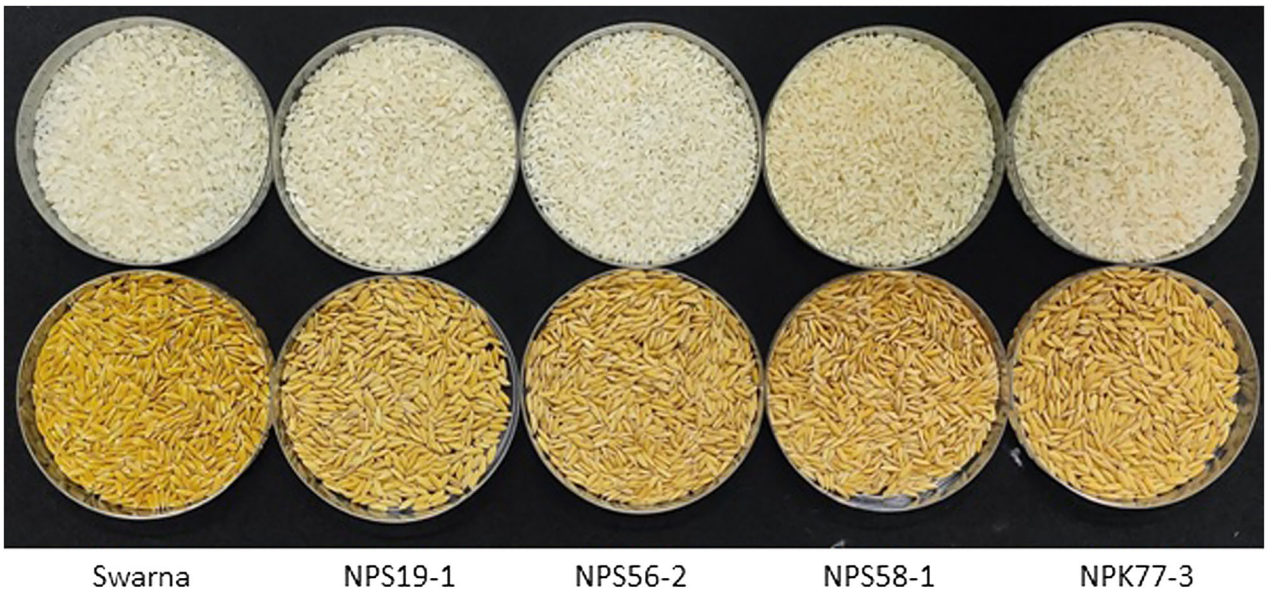


FIGURE 2 Additive effect QTLs for BB resistance based on phenotyping under two environments 2015 and 2016 in population 'Swarna'/ *Oryza nivara* IRGC81832 BILs (NPK lines) and detected using QTL IciMapping4.2

Shim et al., 2020). Wild species of rice, namely, *Oryza nivara* (*Xa33*, *Xa38*), *Oryza rufipogon* (*Xa23*), *Oryza longistaminata* (*Xa21*), *Oryza minuta* (*Xa27*, *Xa35t*), *Oryza officinalis* (*Xa29t*), *Oryza australiensis* (*Xa32t*), *Oryza breviligulata/ O. barthii* (*xa41*), *Oryza malampuzhaensis*, *Oryza brachyantha*, *Oryza longiglumis* and *Oryza ridleyi* are reported to possess resistance to BB (Brar & Khush, 2018) and also in the other cultivated species *Oryza glaberrima* (*xa41*). Resistance against BB race 9A in chromosome 12 was identified using monosomic alien introgression lines (MAALs), derived from *Oryza sativa/Oryza latifolia* cross (Angeles-Shim et al., 2020; Multani et al., 2003). Broad-spectrum, dominant BB resistant gene, *Xa21*, was identified from *O. longistaminata* (Khush et al., 1990) and mapped on chromosome 11 (Ronald et al., 1992). The gene has been very widely used in BB resistance breeding programme in many countries either singly or in combination with other resistance genes (Chen et al., 2000; Huang et al., 1997; Joseph et al., 2004; Sanchez et al., 2000; Singh



(a)



(b)

FIGURE 3 (a) Yield performance of the identified lines NPK77-3(G1), NPS19-1(G2), NPS56-2(G3) and NPS58-1(G4) compared with the parent 'Swarna' (G5) across 3 seasons and GGE biplot showing their stability analysis for yield. (b) Paddy and polished grains of selected high yielding lines

et al., 2001; Sundaram et al., 2008; Yugander et al., 2018). Several BB resistance genes like *Xa23* from *O. rufipogon* (Zhang et al., 1998), *Xa21* from *O. longistaminata* and *Xa27* from *O. minuta*, have been cloned (Gu et al., 2004; Song et al., 1995). BB resistance gene *Xa29 (t)* has been transferred from *O. officinalis* (Sanchez et al., 2000; Tan et al., 2004). *Xa21* from *O. longistaminata* is widely used in breeding programmes for BB resistance and several improved cultivars are released in south and south East Asia (Kumar et al., 2020; Sanchez et al., 2013).

Both horizontal and vertical resistances are employed to develop disease-resistant crop varieties (Zhang & Mew, 1985); however, vertical resistance, governed by the race specific single major genes, are quickly overcome by new virulent races of the pathogen (Mew et al., 1992), whereas horizontal resistance is governed by non-race specific, polygenes of quantitative inheritance and is durable in nature (Nelson, 1972). Therefore, major and minor QTLs identified from segregating mapping populations are having a significant role in contributing towards conferring broad-spectrum durable resistance against plant diseases like BB.

In this study several major and minor QTLs with consistent effect across the years and populations have been identified along with information about the genomic locations of these QTLs. Two QTL regions, namely, *qBB-1-1* (RM259-RM9) and *qBB-10-1* (RM474-RM271) associated with BB resistance were consistently detected in both the mapping populations. QTLs flanked by RM8080 and RM341 in Chr.2, RM17499 in Chr.4, RM204 in Chr.6, RM146,

RM413 in Chr.5, RM271 and RM474 in Chr.10, RM144 and RM287 in Chr.11 were also consistently observed in both the populations. Among these, RM8080 and RM341 in Chr.2, RM204 in Chr.6, RM144 and RM287 in Chr.11 were found consistently across years also.

The common QTL region, *qBB-1-1* (RM259-RM9) detected in NPS and NPK population is located in a 15.88 Mb region spanning from 74,45,627 to 23,325,199 bp in chromosome 1 and found to harbour previously reported genes regulating BB resistance, namely, OsRac1(Os01g0229400), which induce resistance against virulent race of the BB pathogen by enhanced production of a phytoalexin for expression of defence-related genes and another gene, OsLOL2 (Os01g0612700) (Ono et al., 2001; Xu & He, 2007), which encodes zinc finger protein associated with rice growth and disease resistance. QTL *qBB-10-1*, located between RM474 (1,818,800 bp) and RM271 (3,484,773 bp) is a novel region in short arm of chromosome 10 located in a 1.66 Mb region where no BB resistance genes were previously reported. However, genes for abiotic stress tolerance like OsDIL1 (*O. sativa* Drought-Induced LTP) (Guo et al., 2013) and OsPRP3 coding Proline-rich protein3 (Gothandam et al., 2010) against drought and cold tolerance respectively, were reported in this region.

Two QTL regions were found consistently across two seasons in NPS lines and among these, *qBB-2-1* (RM8080-RM341) was found to harbour genes like RAR1 (Os02g0535400), GF14e (Os02g0580300) and OsWRKY71 (Os02g0181300), which contribute for resistance or tolerance to BB. RAR1 was reported to be conserved in several plant species which contribute for innate immunity and R gene-mediated disease resistance (Thao et al., 2007). RNAi silencing of GF14e revealed that this gene influences the induction of plant defence response genes, cell death and broad-spectrum resistance in rice during effector-triggered immunity (ETI) associated with *Xoo* (Manosalva et al., 2011). Liu et al. (2006) isolated OsWRKY71 gene in this region and its overexpression caused enhanced resistance to virulent *Xoo* isolates. The QTL region of RM204 and RM454 in Chr.6 was found co-located with the gene Os06g0208800 coding for lysine motif containing proteins LYP4 and LYP6 inducing associated molecular patterns (MAMPs) of invading microbes via pattern recognition receptors (PRRs) at the plant cell surface and play dual roles in bacterial peptidoglycan and fungal chitin perception leading to rice innate immunity (Liu et al., 2012).

In NPK population, four QTL regions were found to show consistent performance and were screened for any reported QTL or gene locations. The chromosomal region between RM273 to RM241 in Chr.4 is found closely located to Os04g0488700, which codes for OsOxi1 involved in ROS-mediated signalling which regulates both basal resistance and R-gene-mediated resistance in rice against bacterial and fungal pathogens (Matsui et al., 2016). *Xa2* gene associated with BB resistance is reported in the same region and this gene has a leucine rich repeat (LRR) kinase-based inducible defence mechanism (He et al., 2006). Interestingly, many of the QTLs identified in this study are harbouring disease defence mechanisms that mediate spectra of resistance to two or more pathogen species independently especially to major rice pathogens *Xoo* and *Magnaporthe grisea* isolates. These chromosomal regions encode diverse proteins causing broad defence-responsive genes, which will facilitate rice improvement with pathogen species-non-specific broad-spectrum resistance (Ke et al., 2017).

The QTL region containing RM5140-RM146 in Chr.5 was collocated with some known genes, which play a role in defence mechanisms like harbouring a pair of allelic genes, OsWRKY45-1 and OsWRKY45-2 (Os05g0322900), encoding proteins that play opposite roles in resistance against bacterial pathogens and they are species specific (Shimono et al., 2012; Tao et al., 2009) and DEPG1 (Os05g0365300), which is a nucleotide-binding site (NBS) leucine rich repeat (LRR) gene with a significant role in defence pathways against bacterial and fungal pathogens in rice. The QTL identified between RM178 and RM31 in Chr.5 in a 3 Mb region between 25,101,829 and 28,610,858 bp is closely located near genes Os05g0597100 and Os05g0515700, is responsible for HDT701 (histone deacetylase701) and OsVOZ2 (zinc finger protein 2) transcription respectively and plays major role in virulence and defence mechanisms to BB disease (Cheong et al., 2013; Ding et al., 2012).

Consistent QTLs identified in our study in chromosome11 between RM144-*Xa21* and *Xa23*-RM287 are collocated with already known genes *Xa21* (Os11g0559200), *xa3*/*Xa26* (Os11g0692300) (Song et al., 1995; Xiang et al., 2006) and *Xa23*, an executor R Protein originally detected from *O. rufipogon*, with completely dominant and broad-spectrum resistance against BB of rice (Wang et al., 2015; Zhang et al., 2001). No genes were previously reported for BB resistance in the genomic region on Chr.12 where the QTL, *qBB-12-1* (flanked by RM247 and K46-1) was located; and this is a novel candidate region for further genetic dissection.

There were also several QTLs which appeared either in anyone of the environments. This is mainly due the fact that 2015(BB15) study was conducted under controlled conditions at glasshouse and the 2016(BB16) screening was carried at field conditions with more influence from natural environment and the variation may be caused by genotype by environment interactions. The variations also reflected in the QTLs detected based on average of phenotyping of two environments (BBM). The variation among the QTLs between two populations is mainly due to the variation of donor accessions and difference in recombination events and parental genome interactions.

Based on linked markers *Xa38* and *xa5* showed consistent BB association in both the populations; however, *xa13* and *Xa33* showed trait association in only NPS population while *Xa21*, *Xa23* and *Xa4* showed trait association in NPK population only. BB Resistance classified as dominant, recessive, inhibitory and complementary or polygenic based on resistance mechanisms. Resistance genes *xa5*, *xa8*, *xa13*, *xa15*, *xa19*, *xa20*, *xa24*, *xa25*, *xa26*, *xa28*, *xa31(t)* and *xa34(t)* are recessive (Korinsak et al., 2009; Liu et al., 2011; Ruan et al., 2008; Sanchez et al., 1999; Wu et al., 2008), whereas *Xa21* (Song et al., 1997), *Xa1* (Yoshimura et al., 1998), *Xa3*/*Xa26* (Sun et al., 2004; Xiang et al., 2006), *Xa27* (Bimolata et al., 2013; Gu et al., 2004), *Xa10* (Tian et al., 2014) and *Xa23* (Wang et al., 2014, 2015) are dominant and they are distributed throughout rice chromosomes, especially in Chr.4 and Chr.11, which carry clusters of resistance gene analogues (Djedatin et al., 2016). Interestingly, NPK lines showed several

recessive genes with significant trait association and many number of minor QTLs showing a network mechanism of resistance rather than a single major gene. Li et al. (2001) reported that *Xa4* exhibits epistatic or additive effects when combined with other resistance genes. Minor QTLs with low PVE values with highly significant LOD levels were identified in this study especially in NPK lines which may contribute for broad spectrum resistance as a network of epistatic interactions with complementary or supplementary effects.

Critical studies on BB inheritance showed that when plants possess one or few race specific resistance genes, they are easily prone to be susceptible than having multiple genes of minor effect. Kou and Wang (2010, 2012) suggested that broad spectrum durable resistance can be achieved through quantitative resistance genes with minor effects having whole-growth-stage or environment factor-independent resistance through biotechnological approaches. Similarly, Ke et al. (2017) explained the role of several minor QTLs playing significant role in broad spectrum resistance through pattern-triggered or effector-triggered immunity signalling or quantitative resistance. In addition, the network of minor QTLs identified in this study and their interaction may have contributed in the resistance mechanisms. Djedatin et al. (2016) identified novel QTLs for BB resistance in IR64 × Azucena derived mapping populations, and most of them were minor genes of relatively small effect as observed in our study. Wang et al. (2019) also reported stable minor QTLs showing resistance which are useful in breeding through phenotypic selection once the major QTLs have been fixed. Sustainable resistance can be achieved only through co-existence of vertical component of resistance by race specific major genes and horizontal component of resistance by multiple genes for broad spectrum of races (Chukwu et al., 2019).

It is known that BB resistance, to a significant extent depends on the parental genetic background as shown in a study by Sundaram et al. (2009), wherein the presence of *xa5* gene was observed to reduce the effectiveness of the gene combination *Xa21* + *xa13*. *O. sativa* subspecies *indica* shows better tolerance levels to BB as a background parental genome than other subspecies of rice (Djedatin et al., 2011). These NPS and NPK populations derived from 'Swarna'/*O. nivara* crosses (IRGC81848 and IRGC81832) (Swamy et al., 2014) are potential genetic resources and proven resistant donors for QTL/gene identification as well as in breeding programmes on yield improvement and stress resistance (Balakrishnan et al., 2020; Surapaneni et al., 2017). Among the BILs, variable resistance response was found in terms of the screening under glasshouse and field conditions. It was found that many number of highly susceptible genotypes under stringent screening at glasshouse conditions showed moderate susceptibility at normal field conditions. The variable reaction may be mostly contributed by interactions of multiple genes including both minor and major effects as well as their interaction especially to the environment. In glasshouse condition, temperature and relative humidity was more or less controlled, whereas in field conditions, these weather factors are highly variable, which can affect the reaction pattern. Even though similar combinations of genes are present in two genotypes; the percentage of background genome and interaction with the background also will contribute for the variation in resistance across different environments. The instability of wild genome introgression can also be a reason for the variable resistance response pattern. Therefore, only the genotypes showing consistent performance in both the conditions with yield stability were selected and advanced further.

Among the four highly resistant introgression lines identified, NPS56-2 and NPS58-1, were derived from backcross introgression lines 224S and 228S, respectively, and they were previously identified as resistant to BPH (Lakshmi et al., 2010; Sarla et al., 2019). The highly resistant lines identified in this study were selected and screened in the field conditions during 2018, 2019 and 2020 again to confirm the resistance. They were tested across three seasons and multiplied during 2020–2021 as donors and improved 'Swarna' introgression lines with BB resistance for further use in crop improvement and have been nominated for evaluation under All India Coordinated Rice Improvement Programme (AICRIP) for multilocation trials for varietal identification. The genomic regions harbouring novel as well as previously reported genes against BB resistance and the high yielding resistant lines identified in the background of the mega rice variety 'Swarna' are valuable resource in further crop improvement programmes.

5 | CONCLUSION

Two populations derived from *O. sativa*/*O. nivara* were used to study the BB resistance and associated genetic architecture. One major QTL region located at RM8080 and RM341 was showing stable and significant phenotypic effect on the two populations and across the seasons, providing a good candidate for gene cloning. Resistant QTLs with consistent effect in two years was also detected in both the populations. Several minor QTLs were also identified, with a significant effect across different populations and environments and they are potential genomic regions, which can contribute towards broad spectrum resistance as a network. Four high yielding lines with consistent BB resistance, namely, NPS19-1, NPS56-2, NPS58-1 and NPK77-3 derived from 125S, 224S, 228S and 251K, respectively, were advanced and multiplied at normal irrigated conditions and submitted for multilocation testing for varietal identification as improved high yielding 'Swarna' with BB resistance.

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CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Divya Balakrishnan: Conceptualization, Project planning, Methodology, Investigation, Data analysis; Writing - Original draft & editing.

Gouri Sankar Laha: Conceptualization, Project administration, Methodology, Investigation, Validation, Supervision, Writing - Review & Editing. **Yugander Arra**, **Malathi Surapaneni** and **Kavitha Beerelli**: Investigation. **Duraisamy Ladhalakshmi**: Methodology, Investigation, Writing - Review & Editing, **Madamsetty Srinivas Prasad**: Conceptualization, Writing - Review & Editing, **Lella Venkata Subba Rao**: Writing - Review &Editing, **Raman Meenakshi Sundaram**: Writing - Validation, Review & Editing, **Sarla Neelamraju**: Conceptualization, Project administration, Resource.

DATA AVAILABILITY STATEMENT

The data are accessible to readers on request.

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