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ORIGINAL ARTICLE

# Molecular mapping and transfer of sheath blight resistance QTLs from PAU-shb8 to cultivated rice PR-121

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## Abstract

Sheath blight, caused by *Rhizoctonia solani*, severely affects rice, causing 20–69% yield losses in tropical and temperate regions. Key challenges include the pathogen's broad host range, persistent sclerotia, climate change, and the reliance on semi-dwarf varieties. The disease's complex inheritance and lack of highly resistant cultivars hinder management, making resistant variety breeding a sustainable solution. This study mapped sheath blight resistance Quantitative trait locus (QTLs) from PAU-shb8, a moderately resistant rice line. This line exhibited moderate resistance with a disease score of 3 (RLH < 20%), whereas susceptible rice cultivar PR121 scored 9 (RLH > 60%). Screening of 1160 plants from $BC_1F_5$ and $BC_1F_6$ populations revealed 50.34% as moderately resistant, 37.76% moderately susceptible, and 11.88% susceptible. (QTL) mapping using 4622 SNP markers identified 20 QTLs across eight traits, with significant loci on chromosomes 2, 4, 6, 8, 9, 10, 11, and 12. Chromosome 12 harbored a cluster of QTLs associated with multiple traits, including RLH, lesion height, and disease score, while chromosome 8 exhibited a major QTL for RLH with a LOD score of 9.8 and 9.2% phenotypic variance. Genomic analysis pinpointed candidate genes related to resistance, such as leucine-rich repeat proteins and calcium/calmodulin-dependent protein kinases. Promising genotypes 7168, 7183, and 7152 demonstrated moderate resistance, combining key QTLs for RLH, disease severity, and lesion height with favorable agronomic traits. These backcross inbred lines are pivotal for breeding sheath blight-resistant rice varieties and for the expansion of resistance gene pool of sheath blight.

**Keywords** Sheath blight · Backcross · Phenotyping · SNP markers · QTL mapping · GBS · Annotation

## Introduction

Sheath blight, caused by the necrotrophic fungus *Rhizoctonia solani* Kühn [(Telomorph: Thanatephorus cucumeris (Frank) Donk)], is the second most significant rice disease, leading to substantial global yield losses. In tropical Asia, it has been reported to reduce yields by up to 60%, making it one of the most destructive diseases affecting rice production (Hossain et al. 2023; Li et al. 2021; Singh et al. 2016). Managing sheath blight is challenging due to its persistence in soil as a necrotrophic fungus (Wang et al. 2021; Li et al. 2021) . It survives in plant debris as mycelia or sclerotia and infects over 250 plant species, including major crops like wheat, maize, rice, and soy, with uncharacterized pathogenic mechanisms complicating control efforts (Di et al. 2023; Feng et al. 2022; Neelam et al. 2024). While chemical fungicides are a primary control strategy, their excessive use can lead to the development of resistant strains, higher costs, and potential risks to both human health and the environment. Breeding cultivars tolerant to sheath blight is a cost-effective and efficient strategy that involves identifying resistant donors from a variety of sources. Till date, no fully resistant sources have been identified within the available rice germplasm (Li et al. 2021; Singh et al. 2019; Lore et al. 2015; Nadarajah et al. 2014). This underscores the urgent need for the identification and development of tolerant

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rice cultivars, which is essential for ensuring sustainable yields and enhancing food security in the face of increasing global demand.

Resistance to sheath blight (ShB) is quantitative, with substantial challenges in breeding resistant genotypes due to genetic heterogeneity, host compatibility issues, and complex inheritance patterns (Chen et al. 2023; Zou et al. 2000; Jia et al. 2012). Advances in molecular marker technologies and quantitative trait loci (QTL) mapping have led to the identification of over 100 QTLs associated with sheath blight resistance in rice globally (Senapati et al. 2022; Molla et al. 2020). In rice, the majority of sheath blight resistance QTLs are located on chromosomes 1, 3, 7, 9, 11, and 12 (Senapati et al. 2022). Few of the promising ShB QTLs includes *qSB-11*$^{LE}$ (Tan et al. 2005; Zou et al. 2000), *qShB9-2* (Liu et al. 2009), *qSBR11-1* (Channamallikarjuna et al. 2010), *qRTL6* (Taguchi-Shiobara et al. 2013), *qShB6* (Eizenga et al. 2013), *qshb1.1* (Yadav et al. 2015) and *qshb7.1* (Yadav et al. 2015). Extensive efforts in sheath blight mapping have yielded limited documentation on the fine mapping of major and minor effect QTLs. Channamallikarjuna et al. (2010) narrowed *qSBR11-1* to a 0.85 Mb region containing tandem repeats of 11 chitinase genes. Also, *qSB-11*$^{LE}$, *qSB-9*$^{TQ}$ has been fine mapped to 78.8 kb and 146 kb (Zuo et al. 2013, 2014). Past QTL mapping efforts have primarily used a limited set of parental varieties, such as Lemont, Teqing, Tetep, and Jasmine 85, restricting the genetic base for resistance (Xu et al. 2011; Liu et al. 2013; Zuo et al. 2014; Zeng et al. 2015). This narrow foundation underscores the need to explore broader germplasm diversity to identify new resistance sources and strengthen ShB resistance across varied genetic backgrounds.

Over the past decade, a substantial rice germplasm collection at Punjab Agricultural University (PAU), India, has been screened for resistance to sheath blight. Among the screened lines, a resistant line PAU-shb8 has demonstrated persistent resistance to sheath blight throughout last six years, since 2017 and continuing to the present. The present investigation aims to map ShB resistance QTLs using a backcrossed inbread population derived from a cross between PAU-shb8 as the male donor parent and Punjab Rice 121 (PR121) as the female recipient parent. The research successfully developed 15 prebreeding lines with superior agronomic traits and high tolerance to sheath blight disease that can be use for varietal development.

## Material and methods

### Plant materials and development of mapping population

The donor rice germplasm PAU-shb8 was obtained under the All India Coordinated Research Project and was evaluated against sheath blight disease under artificial inoculation for six consecutive years at PAU, India. This rice germplasm consistently showed a disease score of 3, with a relative lesion height ranging from 17 to 20%. It is currently maintained at PAU and will be registered with the National Bureau of Plant Genetic Resources (NBPGR), India, for broader utilization in breeding programs. The recipient parent, PR121 (PR116///PR108/IRRI76//PR106-P2), is a high-yielding, medium-maturing rice variety released by PAU in 2018, but it is highly susceptible (disease score of 7) to sheath blight disease (Bharaj et al. 2014). A backcross inbred mapping population consisting of 143 lines was developed by crossing PAU-shb8 with PR121. After a single backcross, the lines were advanced till $BC_1F_6$ using the single-seed descent method (Fig. S1).

### Preparation of pure culture and innoculation

The $BC_1F_5$ and $BC_1F_6$ populations were artificially inoculated with *R. solani* isolate Rs-1, which belongs to the AG-1 IA anastomosis group. Mass multiplication of the *R. solani* isolate was carried out on a maize meal-sand (1:3 w/w) medium enriched with 20 g of sucrose and autoclaved at 121 °C (15 psi) for 30 min on two consecutive days (Lore et al. 2013). After ten days, mature hyphal growth of *R. solani* was visible in the inoculum, indicating it was ready for use. The plants were inoculated at the peak tillering stage, 40 days after planting, by transferring 5 g of the inoculum to the center of each plant's hill for phenotyping. Disease assessment was carried out 21 days after inoculation (DAI), with PR121 used as the susceptible check.

### Screening and evaluation of populations for sheath blight resistance

The $BC_1F_5$ and $BC_1F_6$ populations, consisting of 143 progenies, were screened during the *Kharif* crop season (June–October) of 2021 and 2022, respectively, in the field area of the School of Agricultural Biotechnology, PAU, India, through artificial inoculation. The 10 plants from each BIL were transplanted with row to plant spacing of 20 × 15 cm. A total of 1,160 plants (4 plants from each line of the $BC_1F_5$ and $BC_1F_6$ populations), were inoculated with *R. solani* culture. Eight parameters were evaluated to assess the disease: plant height (PH), lesion height (LH), relative lesion height (RLH, LH/PH), disease score (DS), total tillers (TT), infected tillers (IT), percent infected tillers (PIT, IT/TT), number of lesions (NOL), and heading date (HD). The plant height was measured from the base of the rice plant to the tip of the highest panicle using a centimeter scale. The lesion height was recorded by measuring the maximum height at which lesion appear on the sheath from the base of the rice plant using a centimeter scale. Relative Lesion

Height (RLH) was calculated from the observed values of plant height and lesion height of the plants using the standard formula by Sharma et al. (1990). Disease severity was assessed using the 0–9 standard evaluation system (SES) scale for sheath blight (IRRI 2013). The days to heading was calculated as the number of days taken from seed sowing to the emergence of the first (main) panicle of each line. The mean data from the inoculated plants of each line were subjected to analysis. Mean, standard deviation, kurtosis, and skewness of the disease index for the population means were also calculated. Correlation analysis was performed to examine the relationship between ShB resistance and the disease variables using SAS software.

### DNA extraction and SNP genotyping by GBS

DNA of the $BC_1F_5$ population along with the parents' i.e., PR121 and PAU-shb8 was extracted from fresh leaf samples taken from 20 day old plants using large scale standard CTAB method of DNA extraction (Saghai Maroof et al. 1984). The extracted genomic DNA was dissolved in TE buffer and assessed for quality and quantity using nanodrop spectrophotometer and electrophoresis in 0.8% agarose gel. The samples meeting the quality and quantity standards were outsourced for genotyping to a company, NGB diagonastic private limited, India. The panel was genotyped using the Genotype By Sequencing (151X2) bp Chemistry sequencing method (Poland et al. 2011). The sequences generated were mapped against the reference genome using the MEM algorithm of BWA (version 0.7.5) using default parameters. Variant calling was done using UGBS- GATK pipeline (version v3.6). Markers with no polymorphism in progenies were removed and filtering was done at distortion pvalue (0.01) using Chi-square analyses for the backcross population using QTL-ICIMapping (version 4.2.53). Grouping was done at LOD threshold of 3 for 4622 markers. The ordering was carried out using regression mapping algorithm in JoinMap (version 4.1) and rippling at window size 1 was also done. The map distancess were estimated using Kosambi mapping function. The linkage map of 4622 SNP markers was constructed using ICI Mapping software.

### QTL mapping

QTL mapping was performed using composite interval mapping (CIM) functions implemented in the QTL-ICIMapping software v4.2 (https://isbreedingen.caas.cn/software/qtllcimapping/294607.htm). After alignment, variant calling, and stringent SNP filtration, 4,622 polymorphic SNPs were identified across all 12 chromosomes. For the genotypic analysis, 143 lines and eight traits were evaluated. Two analysis pipelines were used simultaneously to map the QTLs. The first method, BIP, identifies genes associated with additive, dominant, and digenic epistatic effects in populations with two parents, allowing for analysis across multiple traits. The second method, MET, analyzes QTL-by-environment interactions in biparental populations. For this analysis, the logarithm of odds (LOD) threshold was set at 2.5, with 1,000 permutations used to determine significant intervals.

### Identification of candidate genes

The chromosomal regions within the mapped QTLs were further examined to identify candidate genes located in these areas. The physical positions of markers in the current study were determined using the reference genome Nipponbare (IRGSP 11.0). The flanking SNPs associated with the QTLs were examined using the Rice Genome Annotation Project database (http://rice.plantbiology.msu.edu/) to obtain sequence and annotation data. This information was used to identify potential candidate genes underlying the QTLs.

### Selection of agrnomically superior BILs with ShB resistance

Agronomic data for 143 progenies, including plant height, number of tillers, days to heading, and other traits, were collected alongside data for ShB resistance-contributing traits. Progenies with plant height, tiller number, and days to heading comparable to the recurrent parent but with an RLH percentage below 30 or 30 were selected as superior-performing pre-breeding lines. Presently, these lines were maintained at School of Agricultural Biotechnology, PAU, India and is available with the corresponding author. The seed multiplication of these pre-breeding lines is being carried out for their registration with the NBPGR (National gene bank), India.

## Results

### Screening of genotypes for sheath blight resistance

Significant differences were observed between the parents PR121 (susceptible) and PAU-shb8(moderately resistant) over two years of screening. PAU-shb8 showed moderate sheath blight resistance with a disease score of 3 (RLH < 20%), while PR121 was highly susceptible with a score of 9 (RLH > 60%). In 2021 and 2022, 1160 plants (143 $BC_1F_5$ and $BC_1F_6$ progenies plus parents) were screened for eight disease traits. Results showed 50.34% were moderately resistant, 37.76% moderately susceptible, and 11.88% susceptible, with no complete resistance observed. The frequency distribution of the means for the $BC_1F_5$ and $BC_1F_6$ populations was continuous and normally distributed, spanning the range of the parental data, with slight deviations

in skewness and kurtosis. This confirms that resistance to sheath blight is a quantitative trait (Fig. 1). Pearson's correlation analysis showed significant associations among the eight disease variables ($P < 0.01$ or $P < 0.0001$). RLH was strongly positively correlated with LH and DS, and moderately with IT, PIT and NOL. PH had negative correlations with RLH, DS, PIT, and NOL. HD was negatively correlated with all disease variables except PH. PIT correlated strongly with IT and LH with DS (Fig. 2).

## Genotyping by sequencing of the $BC_1F_5$ population genotypes

A total 22,72,393 SNPs were obtained in raw data. The SNPs with ≥ 10% missing data in the population were discarded. All the heterozygous SNPs, monomorphic SNPs and indels were removed from the data. The distorted markers after chi-square analysis were also removed leaving a total of 4622 SNP markers for QTL mapping. These markers were distributed over all the 12 chromosomes with maximum marker density over chromosome 11. The total map distance was 623.596 cM and the average distance between the adjacent markers was 0.21 cM.

## QTL mapping for eight rice sheath blight resistance evaluation traits

A total of 20 QTLs were mapped for all the eight traits among which 18 QTLs showed LOD > 2.5 and were distributed over chromosome 2, 4, 6, 8, 9, 10, 11 and 12. The list of putative QTLs along with their position and the details of left and right markers associated with individual traits is given in Table 1. The QTL for plant height, *qPH11.1*, with a significant contribution (9.6%) to phenotypic variation, was detected on chromosome 11, along with QTLs for percentage infected tillers and heading date. A consistent QTL cluster on chromosome 12 was identified for LH, RLH, DS, IT, and PIT. Within this cluster, the maximum phenotypic variation (5.6%) was attributed to lesion height. Another significant QTL (PVE: 9.6%) was also identified on chromosome 12 near this QTL cluster

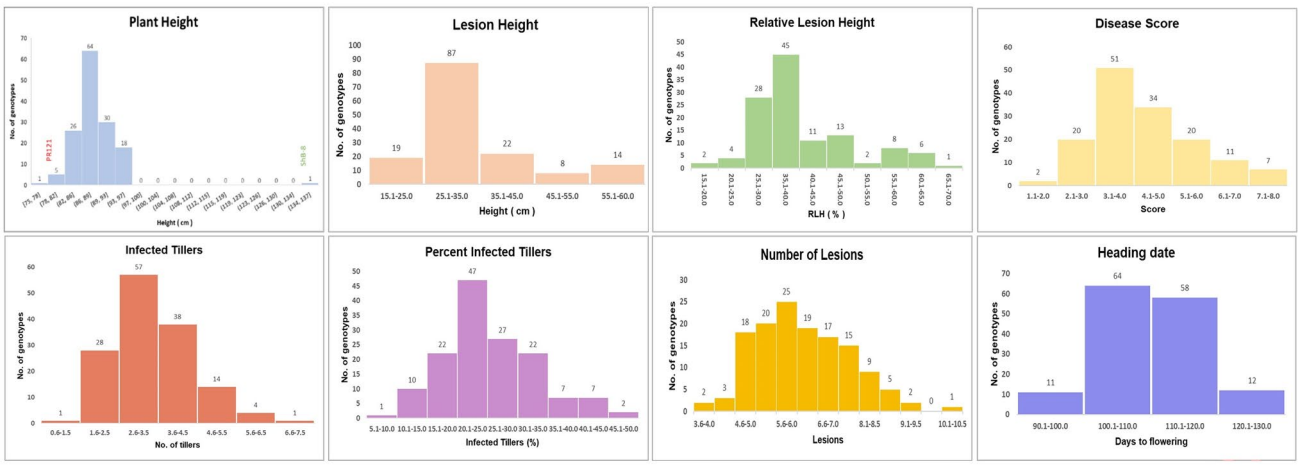


**Fig. 1** Frequency distribution of eight sheath blight disease resistance contributing traits, based on the mean values of $BC_1F_5$ and $BC_1F_6$ data, for sheath blight resistance in 143 backcross inbred lines (BILs) developed from the cross between PR121 and PAU-shb8 at PAU Ludhiana

**Fig. 2** Heat map showing Pearson's correlation coefficients between disease score (DS), lesion height (LH), relative lesion height (RLH), plant height (PH), total tillers (TT), infected tillers (IT), percent infected tillers (PIT), number of lesions (NOL) and heading date (HD) disease variables of rice sheath blight

| | PH | LH | RLH | DS | IT | PIT | NOL | HD |
|---|---|---|---|---|---|---|---|---|
| PH | 1 | | | | | | | |
| LH | 0.03 | 1 | | | | | | |
| RLH | -0.15 | 0.98 | 1 | | | | | |
| DS | -0.16 | 0.92 | 0.94 | 1 | | | | |
| IT | -0.08 | 0.49 | 0.49 | 0.5 | 1 | | | |
| PIT | -0.06 | 0.57 | 0.57 | 0.57 | 0.77 | 1 | | |
| NOL | -0.1 | 0.42 | 0.43 | 0.37 | 0.49 | 0.53 | 1 | |
| HD | 0.16 | -0.5 | -0.53 | -0.53 | -0.55 | -0.51 | -0.4 | 1 |

**Table 1** Details of sheath blight disease resistance contributing QTLs along with putative candidate genes in confined region

| Traits | LGs | QTLs | Left Marker- Right Marker | LOD Score | Additive | PVE | Candidate genes | Putative function |
|---|---|---|---|---|---|---|---|---|
| Plant Height (PH) | 4 | *qPH4.1* | 4:21,452,022–4:21,400,718 | 2.6770 | −1.6050 | 10.4695 | LOC_Os04g35210.1 | Leucine Rich Repeat family protein, expressed |
| | | | | | | | LOC_Os04g35240 | AMK_CAMK_like.25—CAMK includes calcium/calmodulin dependent protein kinases, expressed |
| | 11 | *qPH11.1* | 11:17,090,871–11:27,344,424 | 3.2233 | 1.4205 | 9.6149 | LOC_Os11g05080 | Powdery mildew resistant protein 5, putative, expressed |
| | 12 | *qPH12.1* | 12:4,978,676–12:4,978,681 | 2.8168 | 0.3275 | 10.0739 | – | – |
| Lesion Height (LH) | 12 | *qLH12.1* | 12:22,869,460–12:22,869,469 | 2.6076 | −2.1414 | 5.5993 | LOC_Os12g37260.1 | Lipoxygenase 2.1, chloroplast precursor, putative, expressed |
| | | | | | | | LOC_Os12g37280.1 | Leucine Rich Repeat family protein, expressed |
| | | | | | | | LOC_Os12g37320.1 | Lipoxygenase 2.2, chloroplast precursor, putative, expressed |
| Relative Lesion Height (RLH) | 2 | *qRLH2.1* | 2:18,624,558–2:20,258,450 | 5.1842 | 3.8629 | 4.2796 | LOC_Os02g32700.1 | Autophagy-related protein, putative, expressed |
| | 8 | *qRLH8.1* | 8:25,734,039–8:25,541,945 | 9.8369 | −5.0586 | 8.2773 | LOC_Os08g40460 | BTB4 Bric-a-brac |
| | | | | | | | LOC_Os08g40490 | BTB/POZ domain containing protein, expressed |
| | | | | | | | LOC_Os08g40560 | ZOS8-11-C2H2 zinc finger protein, expressed |
| | | | | | | | LOC_Os08g40580 | Methyltransferase domain containing protein, expressed |
| | | | | | | | LOC_Os08g40600 | Thaumatin, putative, expressed |
| | 12 | *qRLH12.1* | 12:15,688,243–12:15,928,356 | 2.2450 | −1.3448 | 9.196 | – | |
| Disease Score (DS) | 8 | *qDS8.1* | 8:25,734,039–8:25,541,945 | 4.2071 | −0.5791 | 3.6008 | * | |
| | 9 | *qDS9.1* | 9:2,843,672–9:13,224,091 | 2.8673 | 0.4261 | 3.1917 | – | |
| | 12 | *qDS12.1* | 12:13,167,115–12:22,869,450 | 2.9502 | −0.4361 | 2.9535 | LOC_Os12g04360.1 | Calmodulin-like protein 1, putative, expressed |
| | | | | | | | LOC_Os12g04220.1 | Calcium-transporting ATPase, plasma membrane-type, putative, expressed |
| | 12 | *qDS12.2* | 12:22,869,460–12:22,869,469 | 3.1066 | −0.4455 | 3.1695 | * | |

**Table 1** (continued)

| Traits | LGs | QTLs | Left Marker- Right Marker | LOD Score | Additive | PVE | Candidate genes | Putative function |
|---|---|---|---|---|---|---|---|---|
| Infected Tillers (IT) | 2 | *qIT2.1* | 2:22,727,375–2:24,558,357 | 2.6609 | −0.3549 | 4.9301 | LOC_Os02g37590 | Glycerophosphoryl diester phospho-diesterase family protein, putative, expressed |
| | | | | | | | LOC_Os02g38320 | BTBZ3—Bric-a-Brac, Tramtrack, Broad Complex BTB domain with TAZ zinc finger and Calmodulin-binding domains, expressed |
| | | | | | | | LOC_Os02g38589 | OsFBX55—F-box domain containing protein, expressed |
| | | | | | | | LOC_Os02g39820 | PPR repeat domain containing protein, putative, expressed |
| | | | | | | | LOC_Os02g40030 | Transporter family protein, putative, expressed |
| | 12 | *qIT12.1* | 12:22,869,460–12:22,869,469 | 3.0656 | −0.4005 | 5.2165 | * | |
| Percentage Infected Tillers (PIT) | 2 | *qPIT2.1* | 2:22,727,375–2:24,558,357 | 4.5462 | −0.0300 | 5.6850 | – | |
| | 8 | *qPIT8.1* | 8:26,290,499–8:26,290,639 | 3.0487 | −0.0295 | 4.1474 | LOC_Os08g41630 | Ubiquitin carboxyl-terminal hydrolase family protein, expressed |
| | 11 | *qPIT11.1* | 11:11,338,636–11:3,020,862 | 2.0199 | 0.0282 | 3.2870 | - | |
| | 12 | *qPIT12.1* | 12:22,869,460–12:22,869,469 | 2.1982 | −0.0254 | 3.1637 | * | |
| Number of Lesions (NOL) | 6 | *qNOL6.1* | 6:11,643,239–6:1,968,673 | 2.7701 | −0.5011 | 4.4289 | – | |
| | 10 | *qNOL10.1* | 10:12,261,582–10:12,261,521 | 2.7914 | −0.4203 | 4.0288 | LOC_Os10g23900 | Decarboxylase, Putative, expressed |
| | 10 | *qNOL10.2* | 10:9,605,161–10:11,855,609 | 2.5244 | −0.3234 | 0.9781 | – | |
| Heading Date (HD) | 11 | *qHD11.1* | 11:20,813,484–11:20,813,377 | 4.3727 | 2.7268 | 5.3949 | – | |

* Harbors same candidate genes as LH

for RLH. This genetic region could be further harnessed to improve tolerance to sheath blight.

On chromosome 2, co-localized QTLs for RLH and IT were observed, with LOD scores of 5.18 and 4.51, respectively. A major QTL for RLH was identified on chromosome 8, with a LOD score of 9.8 and a phenotypic contribution of 9.2%. This QTL was also co-located with PIT, suggesting that simultaneous improvement can be achieved by targeting this region. In contrast, the QTLs identified on chromosomes 4, 6, and 10 for plant height and the number of lesions was standalone, with phenotypic contributions of 10.5% and 4.4%, respectively.

## Identification of putative candidate genes underlying ShB resistance QTL region

The rice reference genome was analyzed using the coordinates of SNP markers associated with QTLs to identify

the specific genes within that region (Table 1). We discussed only defense related genes present in the defined region. The QTL for plant height, *qPH4.1*, spanned a 51 kb genomic region and encompassed eight genes, including the locus LOC_Os04g35210.1, associated with a leucine-rich repeat family protein, and LOC_Os04g35240, linked to calcium/calmodulin-dependent protein kinases. On chromosome 12, a novel chromosomal region harboring co-localized QTLs for LH, DS, IT, and PIT was identified. This region contained leucine-rich repeat (LRR) genes (LOC_Os12g37260.1, LOC_Os12g37270.1, LOC_Os12g37280.1), a resistance protein gene (T10rga2-1A), and was enriched in lipoxygenase genes (LOC_Os12g37320.1 and LOC_Os02g32700.1). Additionally, autophagy-related genes were located within the region of *qRLH2.1*. The QTL mapped for disease score, *qDS12.1*, contained genes encoding calcium-transporting proteins and calmodulin-like proteins (LOC_Os12g04360.1 and LOC_Os12g04220.1). On chromosome 11, the QTL for heading date, *qHD11.1*, spanned a 100 kb genomic region rich in NLR family genes (LOC_Os11g35450.1, LOC_Os11g35550.1, LOC_Os11g35490.1, LOC_Os11g35660.1) and also included the *RPM1* gene (LOC_Os11g35580.1), suggesting a potential role for this QTL in plant resistance.

### Promising genotypes for varietal development

Following the evaluation of 143 genotypes during 2021 and 2022, the mean values for all disease-related traits were analyzed, and moderately resistant genotypes were identified. Backcrossed inbred progenies with RLH < 30%, a disease score of 3, and favorable agronomic traits such as plant height, tiller number, and days to flowering, comparable to those of the recurrent parent, were selected as prebreeding lines (Table 2). Genotypes 7168 and 7183 achieved low RLH values (25.34% and 26.05%, respectively) and disease score of 3, while maintaining acceptable heading dates (~ 114 days), plant height (~ 94 cm). Both of these two genotypes shares common QTLs *qRLH2.1* and *qNOL6.1* indicating its effectiveness in enhancing resistance. Genotypes combining three identified QTLS for *RLH* with other QTLs (e.g., *qDS8.1*, *qPIT8.1*) exhibit significant resistance improvements, as seen in 7183. Genotype 7152, carrying QTLs for LH, DS, IT, and PIT on chromosome 12, exhibited moderate resistance to sheath blight disease with an RLH of 28.99%. However, it showed better performance in terms of mean infected tillers, mean number of lesions, and heading date. Incorporating additional QTLs such as *qRLH12.1* or *qRLH8.1* could further enhance its resistance, particularly by reducing RLH. The presence of QTLs for plant height and heading date, either alone or in combination, were less effective in controlling sheath blight disease, as observed in genotypes 7118, 7151, and 7203. These traits are primarily related to disease escape mechanisms, and therefore have limited significance in enhancing disease resistance. In conclusion, the backcross inbred lines 7152, 7168, and 7183 are of paramount importance for varietal development.

## Discussion

### Comparative study of ShB resistance QTLs

We identified 21 sheath blight resistance contributing QTLs from the donar line PAU-shb8 (Table 1; Fig. 3). Among these, the QTLs on rice chromosome 2 viz. *qRLH2.1*, *qPIT2.1*, and *qIT2.1* from this study overlap with three previously reported QTLs, including *qRLH2.1* and *qPH2.1* derived from the wild rice species *O. nivara* (Neelam et al. 2024), as well as *qsbr2.1* identified in the MCR10277 cultivated genetic background. This underscores consistent role of *qRLH2.1* in regulating resistance traits across various genetic backgrounds.

On chromosome 4, two QTLs have been mapped: *qPIT4.1* and *qPH4.1*. The former, *qPIT4.1*, represents a novel QTL located on the short arm of rice chromosome 4, whereas *qPH4.1* highlights a region of chromosome 4 that has been previously associated with important QTLs for sheath blight resistance, including *qDR-4* (disease rate), *qRLL-4* (relative lesion length), and *qRLH-4* (relative lesion height), as identified by Liu et al. (2014). The linked markers RM1155 and RM5757, associated with all three traits reported by Liu et al. (2014) can be employed for marker-assisted introgression of this trait, pending validation in the present population. Several previous studies have also documented the co-localization of sheath blight resistance QTLs with plant height QTLs (Kunihiro et al. 2002; Sato et al. 2004; Wen et al. 2015).These findings suggest that *qPH4.1*, with an additive effect from PAU-shb8, may exhibit pleiotropic properties, influencing both developmental and defense pathways. Similarly, the QTLs on chromosome 11 for PH and HD, despite coinciding with seven previously reported QTLs for disease resistance (Liu et al. 2013; Channamallikarjuna et al. 2010; Zuo et al. 2013; Zhu et al. 2014; Neelam et al. 2024) are less significant as they contribute to disease avoidance rather than true resistance. This emphasize the importance of carefully selecting disease resistance QTLs to ensure they are independent of PH- and HD-related loci.

On choromosome 8, positively correlated QTLs for disease resistance *i.e. qRLH8.1*, *qDS8.1* and *qPIT8.1* were obtained with *qSBR8-1* (Channamallikarjuna et al. 2010) and *qSB-8–2* (Pinson et al. 2005). The presence of disease-related QTLs within the same genomic interval suggests their synergistic contribution to enhanced disease resistance. This is evident from the fact that the backcross inbread line 7183, carrying all the three QTLs along with

**Table 2** Promising backcross inbred lines with sheath blight resistance and introgressed QTLs

| Genotype | Mean plant height (cm) | Mean lesion height (cm) | Mean relative lesion height (%) | Disease score | Mean infected tillers | Mean percent infected tillers (%) | Mean no. of lesions | Mean Heading date | QTLs |
|---|---|---|---|---|---|---|---|---|---|
| PR-121 | 78.71 ± 4.98 | 39.34 ± 2.33 | 47.38 ± 4.24 | 7 ± 0.00 | 4.75 ± 0.25 | 31.13 ± 1.13 | 7.4 ± 0.49 | 109.5 ± 2.50 | Recipient |
| PAU-ShB-8 | 136.79 ± 13.05 | 24.84 ± 0.83 | 17.87 ± 2.42 | 3 ± 0.00 | 2.00 ± 0.00 | 17.69 ± 2.31 | 3.8 ± 2.22 | 121.5 ± 0.50 | Donor |
| 7118 | 88.71 ± 1.44 | 27.75 ± 0.25 | 31.29 ± 1.01 | 4 ± 1.00 | 3.42 ± 0.42 | 24.78 ± 0.78 | 5.6 ± 0.82 | 107 ± 15.00 | *qPH11.1*, *qHD11.1*, *qRLH12.1* |
| 7119 | 85.67 ± 1.65 | 23.88 ± 2.87 | 27.93 ± 2.73 | 4 ± 1.00 | 2.83 ± 0.83 | 19.03 ± 2.54 | 5.9 ± 0.25 | 106 ± 13.00 | * |
| 7144 | 84.50 ± 0.83 | 29.65 ± 4.65 | 35.36 ± 5.80 | 4 ± 1.00 | 4.58 ± 2.08 | 26.63 ± 8.45 | 8.2 ± 1.79 | 102 ± 10.00 | *qNOL10.1* *qPIT2.1* *qPH4.1* *qPIT8.1* |
| 7151 | 86.75 ± 1.24 | 26.88 ± 2.87 | 31.03 ± 3.91 | 4 ± 1.00 | 3.63 ± 0.88 | 23.43 ± 2.28 | 6.9 ± 0.30 | 101 ± 8.50 | *qPH11.1*, *qHD11.1*, *qRLH8.1*, *qDS8.1* |
| 7152 | 87.25 ± 0.18 | 25.30 ± 2.70 | 28.99 ± 3.01 | 4 ± 1.00 | 3.50 ± 1.25 | 18.79 ± 4.39 | 6.1 ± 0.46 | 101.5 ± 5.00 | *qLH12.1*, *qDS12.1*, *qDS12.2*, *qIT12.1*, *qPIT12.1* |
| 7164 | 89.88 ± 1.68 | 24.88 ± 0.12 | 27.72 ± 0.85 | 3 ± 0.00 | 1.75 ± 0.25 | 11.42 ± 0.70 | 6.5 ± 0.21 | 114 ± 4.00 | * |
| 7168 | 93.25 ± 0.18 | 23.65 ± 0.65 | 25.34 ± 0.65 | 3 ± 0.00 | 2.75 ± 0.25 | 20.25 ± 2.39 | 6.5 ± 0.67 | 114 ± 8.00 | *qRLH2.1*, *qNOL6.1* |
| 7169 | 85.75 ± 0.18 | 25.75 ± 0.75 | 30.02 ± 0.95 | 4 ± 1.00 | 3.38 ± 0.38 | 23.93 ± 1.07 | 6.8 ± 0.96 | 115.5 ± 1.50 | *qNOL10.1* |
| 7178 | 85.09 ± 1.71 | 25.49 ± 2.81 | 29.97 ± 2.37 | 4 ± 1.00 | 4.21 ± 0.54 | 26.94 ± 0.56 | 6.6 ± 1.47 | 116 ± 3.00 | *qNOL10.1* *qPH4.1* |
| 7183 | 94.34 ± 1.88 | 24.64 ± 0.96 | 26.05 ± 0.34 | 3 ± 0.00 | 4.50 ± 0.50 | 24.06 ± 0.72 | 6.8 ± 1.03 | 111 ± 7.00 | *qRLH2.1*, *qNOL6.1* *qPIT8.1* *qDS8.1* *qRLH8.1* *qRLH12.1* |
| 7185 | 89.00 ± 1.06 | 25.63 ± 0.37 | 28.79 ± 0.93 | 3 ± 0.00 | 2.50 ± 0.50 | 24.48 ± 6.29 | 7.6 ± 0.71 | 110.5 ± 4.50 | *qHD11.1*, *qRLH12.1* |
| 7190 | 88.75 ± 0.18 | 25.30 ± 1.30 | 28.56 ± 1.49 | 3 ± 0.00 | 2.88 ± 0.63 | 20.82 ± 7.18 | 5.9 ± 0.71 | 110 ± 8.00 | * |
| 7197 | 83.13 ± 2.92 | 24.65 ± 1.35 | 29.64 ± 0.14 | 3 ± 0.00 | 2.75 ± 0.50 | 25.24 ± 3.02 | 7.3 ± 1.00 | 109.5 ± 7.50 | *qNOL10.1* *qNOL6.1* |
| 7203 | 87.63 ± 1.86 | 26.65 ± 0.35 | 30.50 ± 0.44 | 3 ± 0.00 | 3.25 ± 0.75 | 20.91 ± 5.76 | 7.4 ± 0.21 | 111 ± 1.00 | *qHD11.1* |
| 7204 | 88.63 ± 2.56 | 25.28 ± 1.97 | 28.46 ± 1.05 | 3 ± 0.00 | 2.75 ± 0.75 | 27.39 ± 6.34 | 7.0 ± 0.17 | 108 ± 2.00 | *qHD11.1*, *qIT2.1*, *qNOL6.1* |

*These backcrossed introgression lines might harbor's minor QTLs clusters for sheath blight resistance (LOD score less than 2.5 percent)

*qRLH2.1*, *qRLH12.1* and *qNOL6.1* showed 45% reduction in disease as compared to the susceptible check. Three QTLs on chromosome 9 for disease score and percent infected tillers encompasses a broader genomic region. The co-localization of *qPIT9.1* with seven reported sheath blight resistance QTLs (Tan et al. 2005; Channamallikarjuna et al. 2010; Fu et al. 2011; Gaihre et al. 2015; Yadav et al. 2015) underline its importance as a key genomic region for further investigation.

The present study identified two novel QTLs, *qNOL10.1* and *qNOL10.2*, associated with the number of lesions following R. solani infestation. Also, a novel genomic region on chromosome 12 was identified, harboring co-localized QTLs for LH, PIT, IT, and DS, along with distinct QTLs for RLH and PH at different genomic positions. Till date, a

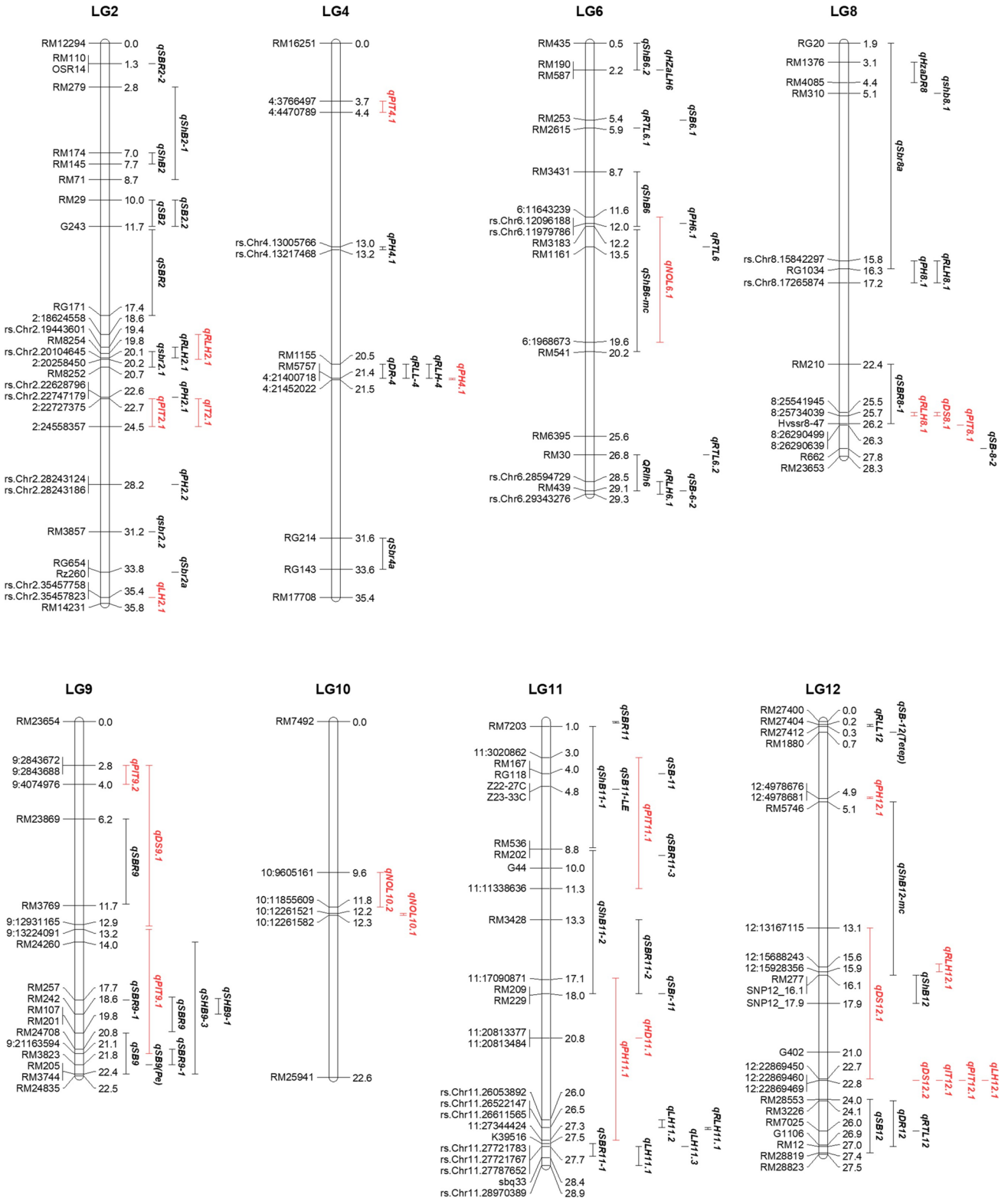


**Fig. 3** The rice physical map highlights the distribution of quantitative trait loci (QTLs) on rice chromosomes 2, 4, 6, 8, 9, 10, 11 and 12, associated with sheath blight resistance (ShB). ShB resistance QTLs identified in our studies are highlighted in red whereas the previously reported QTLs are in black

total of 10 independent studies have identified the existence of ShB resistance QTLs on chromosome 12 (Wang et al. 2023). However, only three of the previously identified QTL q*SB12*, q*DR12* and q*RTL12* (Wang et al. 2023; Pinson et al. 2005; Taguchi Shiobara et al. 2013) are in the vicinity of the QTLs identified in the study. Rest of the identified QTLs identified was present on the short arm of the chromosome 12. This study reinforces the significance of chromosome 12 as a hotspot for ShB resistance QTLs, with the newly identified QTLs overlapping only partially with previously reported loci.

### Defence related candidate genes in the confined QTL region

The study identifies putative genes—LOC_Os04g35240, LOC_Os12g04360.1, and LOC_Os12g04220.1-that are involved in calcium/calmodulin signaling pathways. Similar findings have been reported in other studies, which suggest the involvement of various calcium/calmodulin pathway genes, such as OsCPK10, OsCML16, OsCML26, OsCML27, OsCML31, and OsCam1-1 (Zhang et al. 2017). Among defense-related proteins, calcium/calmodulin-dependent protein kinases play a crucial role as key regulators of plant immune responses (Dodd et al. 2010; Luan et al. 2021). These kinases mediate calcium signaling cascades, and calcium flux has been shown to influence salicylic acid accumulation, which is associated with sheath blight resistance (Reddy et al. 2011). Additionally, the present study reveals that the genes LOC_Os12g37260.1 and LOC_Os12g37320.1 encode lipoxygenases. Lipoxygenases are known to be involved in signal transduction pathways that contribute to resistance responses against *R. solani* infection (Taheri and Tarighi 2010). Recent studies emphasize the pivotal role of LRR protein-encoding genes in sheath blight resistance in rice. Within confined QTL regions in our study, key LRR protein-encoding genes, including LOC_Os04g35210.1, LOC_Os11g35450.1, LOC_Os11g35490.1, LOC_Os11g35550.1, LOC_Os11g35660.1, and LOC_Os12g37280.1, have been identified. Wang et al. (2021) identified a cluster of NLR genes on chromosome 11 (LOC_Os11g12320, LOC_Os11g12330, and LOC_Os11g12340) that were significantly upregulated in the sheath blight-resistant variety Teqing compared to the susceptible check Lemont, based on transcriptomic analysis during a genome-wide association study. Similarly, Kumar et al. (2017) highlighted *qSBR11-1* as a hotspot for resistance, containing 2 NBS-LRR genes, 7 serine/threonine kinase and LRR genes, and 3 protein kinase with LRR genes. These findings collectively underscore the integral role of LRR-related genes in enhancing sheath blight resistance. The current study reports LOC_Os08g40600 with the putative function as of thaumatin. The thaumatin-like protein have been known to exhibit antifungal properties; lysing the cell membranes of fungi, decreasing spore viability and programmed cell death in fungi (Liu et al. 2010, 2024). As per the report, Shah et al. (2013) validated that thaumatin-like protein (*Tlp-D34*) reduces the disease index when co-expressing with *Chitinase* gene against *R. solani* infection. In conclusion, the study uncovers a wide range of genes and pathways involved in sheath blight resistance in rice.

## Conclusion

In conclusion, this study identified 20 sheath blight (ShB) resistance QTLs from the donor line PAU-shb8, highlighting novel loci and reinforcing known regions of resistance across chromosomes 2, 4, 8, 9, 10, and 12. The selected backcross inbred lines 7152, 7168, and 7183 with introgressed QTLs are valuable for future varietal development aimed at improving sheath blight resistance. The identified defense-related genes, including those linked to calcium signaling, lipoxygenase activity, and LRR proteins under *R. solani* inoculation, requires validation through expression studies. Future research will likely focus on further fine-mapping of these QTLs and integrating them into breeding programs for durable sheath blight resistance.

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**Author contributions** Kumari Neelam, Kuldeep Singh and Rupinder Kaur designed the experiment and developed the mapping population. Jagjeet Singh Lore provided *R. solani* cultures. Saundarya Kumari and Yogesh Vikal assisted in development of mapping population. Sheezana Rasool and Ankita Babbar performed the experiments and carried out the phenotyping of $BC_1F_5$ & $BC_1F_6$ population and genotyping of $BC_1F_5$ population. Safoora Javed and Ankita Babbar assisted in data collection. Sheezana Rasool and Kumari Neelam analysed the result and drafted the manuscript. Kumari Neelam proofread the manuscript and provided the critical feedback to shape the manuscript. Navjot Sidhu has helped in the revision of the manuscript. All co-authors read and approved the final manuscript.

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## Declarations

**Conflict of interest** All authors declare that they have no conflict of interest relating to financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Ethical approval** This research did not involve the use of any animal or human data or tissue.

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