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Identification and candidate analysis of a new brown planthopper resistance locus in an Indian landrace of rice, paedai kalibungga

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Abstract

The brown planthopper (*Nilaparvata lugens* Stål, BPH) is the most destructive pest of rice (*Oryza sativa* L.). Utilizing resistant rice cultivars that harbor resistance gene/s is an effective strategy for integrated pest management. Due to the co-evolution of BPH and rice, a single resistance gene may fail because of changes in the virulent BPH population. Thus, it is urgent to explore and map novel BPH resistance genes in rice germplasm. Previously, an *indica* landrace from India, Paedai kalibungga (PK), demonstrated high resistance to BPH in both in Wuhan and Fuzhou, China. To map BPH resistance genes from PK, a $BC_1F_{2:3}$ population derived from crosses of PK and a susceptible parent, Zhenshan 97 (ZS97), was developed and evaluated for BPH resistance. A novel BPH resistance locus, *BPH39*, was mapped on the short arm of rice chromosome 6 using next-generation sequencing-based bulked segregant analysis (BSA-seq). *BPH39* was validated using flanking markers within the locus. Furthermore, near-isogenic lines carrying *BPH39* (NIL-BPH39) were developed in the ZS97 background. NIL-BPH39 exhibited the physiological mechanisms of antibiosis and preference toward BPH. *BPH39* was finally delimited to an interval of 84 Kb ranging from 1.07 to 1.15 Mb. Six candidate genes were identified in this region. Two of them (*LOC_Os06g02930* and *LOC_Os06g03030*) encode proteins with a similar short consensus repeat (SCR) domain, which displayed many variations leading to amino acid substitutions and showed higher expression levels in NIL-BPH39. Thus, these two genes are considered reliable candidate genes for *BPH39*. Additionally, transcriptome sequencing, DEGs analysis, and gene RT-qPCR verification preliminary revealed that *BPH39* may be involved in the jasmonic acid (JA) signaling pathway, thus mediating the molecular mechanism of BPH resistance. This work will facilitate map-based cloning and marker-assisted selection for the locus in breeding programs targeting BPH resistance.

Yangdong Ye and Yanan Wang contributed equally to this work.

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Keywords Rice · Brown planthopper resistance gene · Fine mapping · Near-isogenic line · Transcriptome sequencing

Introduction

Rice (*Oryza sativa*) is one of the most crucial food crops globally, and the brown planthopper (*Nilaparvata lugens* Stål, BPH) is the most destructive pest in rice-growing areas. Given the escalating severity and frequency of pest outbreaks over the past few decades, these have posed a substantial threat to rice production (Du et al. 2020). Global warming exacerbates the population growth and metabolic rates of pests, while environmental deterioration may reduce the number of natural pest enemies, foreseeably leading to heightened crop losses (Deutsch et al. 2018). Controlling pests is a key priority for ensuring rice yield (Crist et al. 2017). Presently, chemical insecticides predominantly serve as the means to control BPH. However, the abuse of pesticides not only escalates farmers' production and labor costs but also causes irreversible harm on the environment. Consequently, the use of such pesticides will decline in many developing countries. The adoption of resistant rice cultivars harboring resistance genes proves to be an effective strategy for integrated pest management. Breeding insect-resistant varieties aligns with the modern trend in rice breeding and stands as a key objective within the realm of green super rice (Zhang 2007). Due to the co-evolution of BPH and rice, a single resistance gene may falter owing to alterations in the BPH virulent population. It is imperative to explore and map novel BPH resistance genes in rice germplasm.

The inheritance of resistance to BPH in rice has been a focal point of research. Since the identification of BPH resistance genes *BPH1* and *bph2* in 1971 (Athwal et al. 1971), more than 40 genes have been mapped in cultivated and wild rice. The majority of these genes exhibit dominant or partially dominant, with only a few being recessive, including *bph2*, *bph4*, *bph5* and *bph29*. BPH resistance genes are typically preferentially located in gene clusters on rice chromosomes 3, 4, 6 and 12 (Cheng et al. 2013b). For example, 11 genes and/or QTLs (*BPH30*, *BPH33*, *BPH12*, *BPH15*, *BPH3/17*, *BPH20 (t)*, *bph22 (t)*, *qBPH4*, *qBPH4.2*, *qBPH4.3*, *qBPH4.4*) cluster within a 0.91–8.9 Mb region between markers H99 and B44 on the short arm of chromosome 4 (4S) (Rahman et al. 2009; HOU et al. 2011; Qiu et al. 2012; Lv et al. 2014; Hu et al. 2015a, b, 2018; Liu et al. 2015; Mohanty et al. 2017; Wang et al. 2018). Eight genes (*BPH1*, *bph2*, *bph7*, *BPH9*, *BPH10*, *BPH18*, *BPH21* and *BPH26*) cluster within a 5 Mb region on the long arm of chromosome 12 (12L) (Ishii et al. 1994; Sun et al. 2006; Cha et al. 2008; Rahman et al. 2009; Tamura et al. 2014; Qiu et al. 2014; Ji et al. 2016; Zhao et al. 2016). These genes may represent alleles or distinct genes, but there is insufficient evidence to differentiate between them.

With the rapid and in-depth advancement of rice functional genomics, map-based cloning has been employed to sequentially clone a range of BPH resistance genes. To date, 17 resistance genes have been cloned in rice, including genes such as *BPH1*, *bph2*, *BPH3*, *BPH6*, *bph7*, *BPH9*, *BPH10*, *BPH14*, *BPH15*, *BPH18*, *BPH21*, *BPH26*, *bph29*, *BPH30*, *BPH32*, *BPH37* and *BPH40* (Du et al. 2009; Cheng et al.

2013a; Tamura et al. 2014; Liu et al. 2015; Wang et al. 2015; Ji et al. 2016; Zhao et al. 2016; Ren et al. 2016; Guo et al. 2018; Shi et al. 2021; Zhou et al. 2021). *BPH14* was the first BPH resistance gene cloned on chromosome 3L from O. *officinalis*. *BPH14* encodes a member of the NLR family, known as the CC-NB-LRR (coiled-coil, nucleotide-binding, and leucine-rich repeat) protein, often observed in disease resistance proteins (Du et al. 2009). Previous research revealed that the CC and NB domains of *BPH14* protein can interact with WRKY transcription factors (*WRKY46* and *WRKY72*) to activate defense signals, thereby resisting feeding by BPH (Hu et al. 2017). Recent research has found that *Bph14*-mediated hypersensitive response (HPR) is achieved through the direct binding of BISP and BPH14 to the selective autophagy cargo receptor OsNBR1, which delivers BISP to OsATG8 for degradation. In susceptible plants, BISP directly targets OsRLCK185 to suppress basal defenses (Guo et al. 2023). Eight genes on chromosome 12L also encode NLR proteins. They were identified as alleles of each other and divided into four allelotypes, showing resistance to different BPH biotypes. This reveals that allelic variation of insect resistance genes is an essential strategy for rice to cope with pest virulent variation (Zhao et al. 2016). *BPH32*, located on chromosome 6S, encodes a specifically conserved short repeat (SCR) domain protein. *BPH32* is highly expressed in leaf sheaths and may inhibit BPH feeding (Ren et al. 2016). Recently, a new broad-spectrum resistance gene, *BPH6*, was successfully cloned in the *indica* rice Swarnalata. *BPH6* encodes an atypical LRR protein localized to the exocyst, where it interacts with the exocyst subunit EXO70E1 to regulate rice cell secretion and maintain cell wall integrity. It was found that OsEXO70H3 interacted with SAMSL, increasing the delivery of SAMSL outside the cells, leading to lignin deposition in cell walls, thus hindering BPH feeding (Guo et al. 2018; Wu et al. 2022). *BPH30*, located on chromosome 4S, belongs to a novel gene family with two leucine-rich domains. It is strongly expressed in sclerenchyma cells, enhancing cellulose and hemicellulose synthesis, making the cell walls stiffer and fortifying the sclerenchyma. *BPH40* is another member of the family, and the resistance mechanism is similar to that of *BPH30*, related to cell wall fortification in sclerenchyma to prevent BPH stylets from reaching the phloem to feed (Shi et al. 2021). Zhou et al. used GWAS studies to identify a previously unidentified gene, *BPH37*, containing the CC and NB domains but lacking the LRR domain, exhibiting high resistance against BPH herbivory (Zhou et al. 2021).

Previously, approximately 300 cultivar accessions were introduced by the International Rice Research Institute (IRRI), potentially possessing resistance to multiple BPH biotypes. Following the evaluation of BPH resistance at the seedling stage in these cultivars, more than 190 cultivars exhibiting moderate resistance and above were screened (Hu et al. 2016). Among them, an *indica* landrace from India, named Paedai kalibungga (PK), demonstrated high resistance to BPH in Fuzhou, China. To map BPH resistance genes in PK, a $BC_1F_{2:3}$ population resulting from crosses of PK and a susceptible parent, Zhenshan 97 (ZS97), was developed and assessed for BPH resistance. Our study focused on (1) primarily mapping BPH resistance genes using mixed-pool sequencing (BSA-seq); (2) fine mapping the locus to a region smaller than 100 Kb through progeny testing; (3) analyzing candidate genes through comparative sequencing and gene expression studies; (4) conducting transcriptome

analysis and initial verification of differential gene expression to elucidate the molecular mechanisms of *BPH39*-mediated resistance to brown planthoppers.

Materials and methods

Plant materials and mapping population

Paedai kalibungga (abbreviated as PK, IRGC 38545) and PTB33, both of which originating from India, are well supplied by the International Rice Research Institute (IRRI). PTB33 (carrying *BPH32*) was used as a resistant control for sequencing the *BPH32* gene and BPH evaluation. Two Chinese cultivars, TN1 and Zhenshan 97 (abbreviated as ZS97), were used as susceptible controls.

The construction of the primary mapping population consists of the following steps: The susceptible parent, ZS97, was continuously crossed with the resistant parents, PK and F_1, to obtain 16 BC_1F_1 plants. After evaluating BPH resistance, five resistant plants were selfed to obtain BC_1F_2. Ninety-two BC_1F_2 individuals were planted and selfed, subsequently, the corresponding 92 seeds were harvested, forming the primary mapping population. The secondary or fine mapping population was the BC_3F_2 (near-isogenic lines, NILs), developed by marker-assisted backcross breeding (MABC).

BPH materials

BPH insects were first captured in paddy fields in Fuzhou, China, and reared and maintained on a susceptible *indica* rice variety TN1 in a walk-in artificial climate light greenhouse in our lab. The temperature of the greenhouse was controlled at 28 ± 2 °C and the humidity was $75 \pm 5\%$.

Molecular marker design

InDel markers were developed based on the sequence difference between PK and ZS97, and the genomic variations of 4,726 cultivars in the database of RiceVarMap (http://ricevarmap.ncpgr.cn/v2/) described by Zhao et al.[35] A segment of 3–8 bp insertion or deletion between the two parental varieties was found in sequence data and the website, and then specific primers were designed at a distance of 50–60 bp on either side of this segment, so that the size of the amplified fragment containing the deletion target was about 100 bp. The molecular markers required for mapping *BPH39* are listed in Table S1.

BSA-seq

The bulked segregant analysis method using next-generation sequencing (BSA-seq) was described by Hu et al. (2018).

Construction of a high-resolution physical map and fine mapping of locus

Approximately 5,000 BC_3F_2 seeds with a heterozygous genotype at the target gene locus were sown in multiple 96-well plates, The PCR plate containing the seeds, which had holes at the bottom, was then placed in the germination box, and a small amount of water was added before the box was tightly covered. About one week after germination, almost 4,500 surviving seedlings were selected, and each seedling was fixed and sampled sequentially to extract rice leaf DNA. According to the results of preliminary mapping, all seedlings were analyzed for genotypes using closely linked markers on both sides of the target gene, and individuals with recombination exchange between markers on both sides (one side was marked as homozygous ZS97 genotype B or homozygous PK genotype A, and the other side was marked as heterozygous genotype H) were selected. After transplanting all recombination exchange individuals into the field for planting, mature plants were harvested and selfed for subsequent genotype and phenotype analysis. Uniformly distributed markers with polymorphisms between the two parents were developed in the target locus region, and marker genotype analysis was performed on all recombinants to construct a physical map of the target locus based on the physical location of the marker on the chromosome. Two to three individuals of each recombination breakpoint type were selected for progeny testing (genotype and phenotype analysis). Based on the results of the progeny tests of recombinants, we can more accurately delimit the mapping interval of target genes.

Candidate gene prediction

Candidate gene prediction was undertaken based on rice genome annotation databases, namely the Rice Genome Annotation Project Database at (MSU) (http://rice.uga.edu/cgi-bin/gbrowse/rice/). By combining protein structure and function data from gene annotations, possible candidate genes can be predicted in advance. At the same time, one or two candidate genes were determined by the sequence alignment of the two parents in the fine-mapping region of the locus.

RNA isolation and RT-qPCR analysis

For the two-leaf and one-heart seedling stage, three biological replicates were used for all RNA experiments. Total RNAs were isolated from rice leaf sheaths using the TRIzol reagent (Takara). First-strand cDNA was synthesized according to the manufacturer's instructions (All-in-One First-Strand Synthesis MasterMix, Lablead, F0202-100 T). RT-qPCRs were performed using a CFX Connect Real-Time System (Bio-Rad) and 2 × Taq PCR StarMix with Loading Dye (GenStar, A002-100–1), following the manufacturer's instructions and using the primers listed in Table S2.

RNA-seq analysis

The NIL-BPH39 and ZS97 plants were grown to two leaves and one heart, and each plant was infested with 10 third-instar BPH nymphs. All treatments had three biological replicates, and the samples were collected from the infested (72 h) and control (0 h) plants simultaneously (Guo et al. 2018). Total RNAs were isolated using the same method as above. The cDNA libraries were checked using Qubit 2.0 and Agilent 2100 before they were sequenced by Illumina HiSeq2500/x (https://doi.org/10.21203/rs.3.rs-634003/v1). Transcriptome profiling was carried out by Wuhan Metware Biotechnology Co., Ltd. Wuhan, China (http://www.metware.cn/; https://doi.org/10.1016/j.molp.2020.06.005). All raw data were deposited into the National Center for Biotechnology Information under accession number **(PRJNA1006526)** and were publicly accessible at https://www.ncbi.nlm.nih.gov/. Differential expression analysis of four experimental groups, GO functional annotation, and KEGG pathway enrichment analysis were performed based on the differentially expressed genes.

Evaluation of BPH resistance

The improved methods of seedling bulk testing and seedling death rate were performed to evaluate the BPH resistance. When rice seedlings grow to the stage of two leaves and one heart, they are transferred to a black box filled with rice liquid medium. Eight plants were retained in each row (one variety in each row), and the process was repeated three times. The boxes were placed in a gauze net, and 2 days after transplanting, 8–10 s-instar nymphs were infested per seedling. When the dead seedling rate of the susceptible control was greater than 90%, the resistance level of a seedling was indicated by a resistance score (RS = 1, 3, 5, 7 or 9) and the resistance level of a line was indicated by the average RS of 10 seedlings. For the seedling death rate test, the resistance level of each line was evaluated based on the dead seedling rate of each row as follows: Mortality 0–1.0%, immunization; 1.1–10.0%, high resistance; 10.1–30.0%, resistance; 30.1–50.0%, moderate resistance; 50.1–70.0%, moderate susceptibility; 70.1–100%, susceptibility.

In addition, the amount, weight and area of honeydew excreted by BPH were measured. Honeydew weight and area measurements were performed using the method described by Pathak et al. (1982) with slight modifications (Hu et al. 2018). Fifteen replicates were tested.

Results

Phenotypic distribution of the genetic population

We evaluated the BPH resistance of a $BC_1F_{2:3}$ population comprising 92 families derived from crosses between ZS and PK using three experimental methods:

seedling resistance, and the weight and area of honeydew excreted by BPH. The seedling bulk test was performed twice, in September 2017 and April 2018, respectively. The results showed that the mean seedling resistance score (RS) of the resistant parent PK was 2.0, indicating resistance, while the RS of the susceptible parent ZS was 8.9, indicating high susceptibility. The RS of 92 families showed a continuous distribution between 2.0 and 9.0, the results in 2017 had two obvious peaks at 4.0–4.9 and 6.0–6.9, and the results in 2018 had only one obvious peak at 6.0–6.9. According to previous studies (Qiu et al. 2012, 2014), we defined an RS of 0–6.9 as resistance and 7.0–9.0 as susceptibility. After statistical analysis, the resistance ratio was 62:30 in 2017 and 67:25 in 2018 (Fig. 1a, b). The results of the chi-square test showed that all observations met the Mendelian genetic segregation ratio of at 3:1 for single genes ($\chi 2 = 2.84$ and $0.23 < \chi^2_{0.05,\,1} = 3.84$ in 2017 and 2018, respectively). The honeydew weight and area were continuously distributed between 1.3–11.9 mg and 0.6–12.0 cm^2, respectively. The honeydew weight and area of the parent ZS (8.7 mg, 11.6 cm^2) were significantly higher than those of PK (2.5 mg, 1.9 cm^2), respectively (Fig. 1c, d). The above results indicated that the resistance of the resistant parent PK might be controlled by a dominant gene.

Previous studies have shown that the RS is positively correlated with honeydew weight and area, that is, the lower the RS, the smaller the honeydew weight and area of BPH, and vice versa. In this study, there was a highly significant positive correlation between RS in 2017 and 2018 (correlation coefficient 0.88), as well as a highly significant positive correlation between honeydew area and honeydew weight amount (correlation coefficient 0.85). However, there was a small yet significant positive correlation between seedling resistance and honeydew weight or area (Table S3).

Preliminary mapping of *BPH39* by BSA-seq

In order to map the BPH resistance locus in the parent PK, we selected 15 extremely resistant and 15 extremely susceptible lines to construct resistance and susceptible pools, respectively, in the $BC_1F_{2:3}$ population based on the RS data. Then we performed an SNP frequency difference analysis covering the 12 chromosomes of rice using BSA-seq and found a maximum peak in the interval of 0–5 Mb on the short arm of chromosome 6 (6S). This indicating that there may be a major gene in this region, which was tentatively named *BPH39* in accordance with the naming rules for BPH resistance loci (Fig. 1e).

Verification of effect for *BPH39*

BPH39 was preliminarily mapped to the interval of 0–5 Mb on chromosome 6S by BSA-seq. To verify the QTL, we developed 8 molecular markers in this region and adjacent regions (0.93–19.51 Mb) (Table S1). These eight markers were then used to genotype 92 lines in the $F_{2:3}$ population. Combined with the phenotype of seedling resistance, a t-test was performed to group the genotypes A and B using these markers, and the confidence interval of *BPH39* was verified based on the

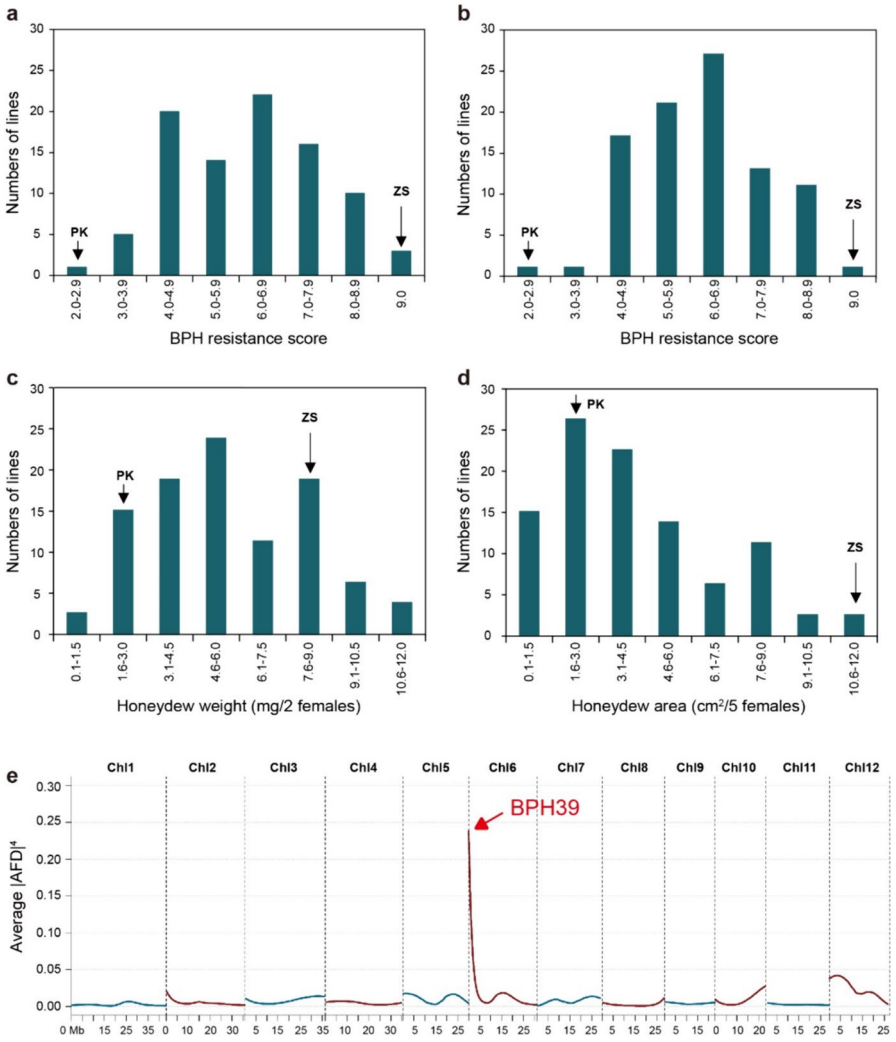

Fig. 1 Frequency distribution of BPH resistance in $BC_1F_{2:3}$ population of ZS/PK**. a** and **b**, seedling resistance to BPH in 2017 and 2018, respectively; **c** and **d**, Honeydew weight and area secreted by BPH, respectively. PK (Paedai kalibungga) and ZS (Zhenshan 97) denote the phenotypic values of the resistant and susceptible parents, respectively. **e**, Mapping of *BPH39* using the method of BSA-seq based on the $BC_1F_{2:3}$ populations from ZS/PK. AF, allele frequency difference of individual marker between the two opposite DNA pools. The arrow indicates the peak where *BPH39* was located

significant difference results. A genotype with the same marker pattern was classified as homozygous dominant (genotype A), homozygous recessive (genotype B), or heterozygous (genotype H). The RS of genotype A was compared with the RS of genotype B by the t test. We can see that the RS of genotype A is significantly different from that of genotype B except for the two molecular markers I828 and RM541 ($P > 0.05$). The smallest P-value at marker I992 is 2.48×10^{-7}. As the physical

location of a marker gets closer to I992, the P-value decreases, whereas it increases when further away (Fig. 2). The above results indicate that there is indeed a major resistance locus near marker I992 on chromosome 6S, and BPH39 was preliminary located between the markers I369 and I392.

Development and evaluation of a near-isogenic line carrying *BPH39*

To facilitate the precise mapping of this locus and to establish a marker-assisted selection (MAS) framework for its use in insect resistance breeding, we successfully generated a near-isogenic line (NIL) of *BPH39* within the genetic background of Zhenshan 97. We first selected four resistant individuals with a homozygous PK genotype (A) on both sides of *BPH39* in the BC_1F_3 population and backcrossed them with ZS97 for two consecutive generations using MAS. They were then selfed for one generation, and finally, the BC_3F_2 population with segregation at the *BPH39* locus were developed. Using MAS, we obtained three individuals with homozygous PK genotypes and three with homozygous ZS97 genotypes, corresponding to the near-isogenic line carrying *BPH39* (NIL-BPH39) and the near-isogenic line not containing *BPH39* (ZS97), respectively.

We detected the genetic background of NIL-BPH39, using 48 polymorphic markers distributed on 12 rice chromosomes. The results showed that there were 1 and 3 marker genotypes in the two independent near isogenic lines of *BPH39*, B39-1 and B39-2, respectively, which were different from the recurrent parent ZS97, and the background recovery rates were 97.9% and 93.8%, respectively (Figure S1, S2). B39-1 was used in this study. The above results indicate that

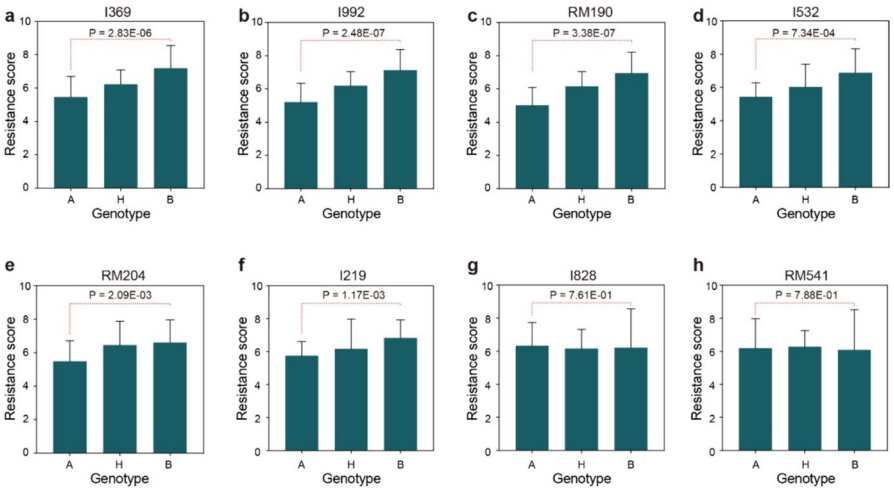

Fig. 2 Marker linkage analysis of marker genotype and phenotype in *BPH39* region on chromosome 6S. **a**-**h**, the *BPH39* genotypes and phenotypes identified according to its linkage markers I369, I992, RM190, I532, RM204, I219, I928 and RM451. A, PK genotype; B, ZS genotype; H, heterozygote genotype; *P*-values are shown for the comparison between A and B

the genetic background of the near-isogenic lines developed in this experiment is clean enough to be used for fine mapping and effect evaluation of the BPH resistance QTL.

BPH resistance was evaluated on the NILs. The results showed that the resistant NIL-BPH39 was still alive, while the susceptible ZS97 was dead (Fig. 3a). The honeydew area and weight gain of BPH on ZS97 were significantly greater than those of NIL-BPH39 (Fig. 3b-e). We monitored the survival rate of BPH nymphs continuously over seven days. The number of nymphs steadily decreased on the plants, but it declined quickly in the NIL-BPH39. After seven days of infestation, the BPH survival rate for NIL-BPH39 was only 50%, compared to 82% for ZS97 (Fig. 3f).

Furthermore, we investigated the number of settled BPHs on NIL-BPH39 and ZS97. The results showed that the number of BPH on NIL-BPH39 was significantly less than that on ZS97 after 6 h of infestation. This difference became most pronounced 48 h after infestation, with an average of only 15 BPHs on NIL-BPH39 and 33 BPHs on ZS97 (Fig. 3g). Taken together, these results indicate that *BPH39* has preferential and antibiotic effects on the insects.

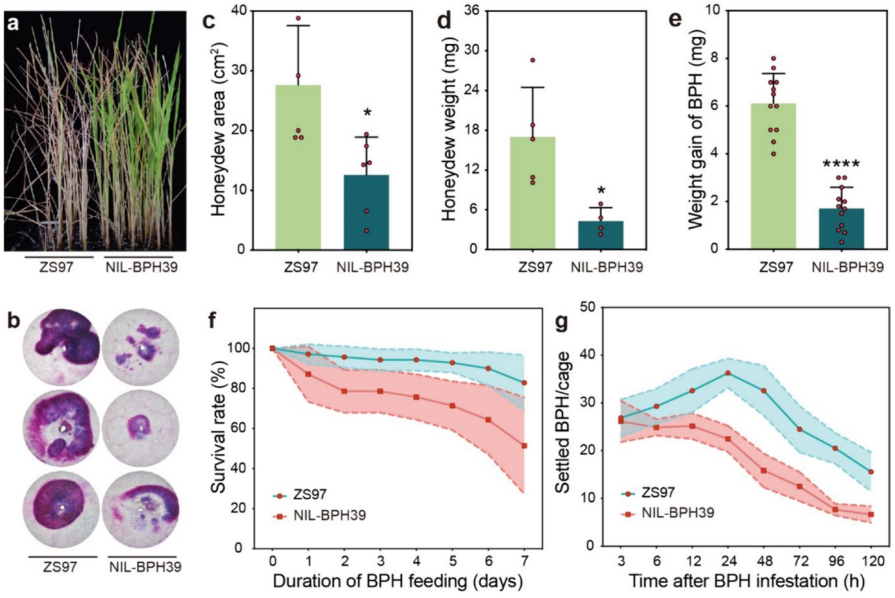

Fig. 3 Phenotypic of BPH resistance of near isogenic line carrying *BPH39* (NIL-BPH39). **a**, the photo of seedling resistance of NIL-BPH39 and ZS97 at the time of 12 days after BPH infestation; **b**, Color photos of honeydew secretion of BPH after ninhydrin staining. The honeydew is shown in purple red. **c**, Honeydew area of BPH. **d**, Honeydew wight of BPH. **e**, Weight gain of BPH. **f**, Survival rate of BPH. **g**, Preference of settled BPH. ZS97 and NIL-BPH39 denote NIL that do not carry and carry the homozygous *BPH39* locus, respectively. * represents a significant difference at the 0.05 level

Fine mapping of *BPH39*

To fine-map the locus, we planted 4,500 individuals of BC_3F_2 that were heterozygous at both flanking markers I369 and I992. Marker genotype analysis was performed on 4,500 individuals, and a total of 26 recombinants were screened with exchange at markers on both sides. At the same time, a total of eight additional polymorphic markers were developed and evenly distributed in this region (Table S1), and then a high-resolution physical map of *BPH39* was constructed based on the physical location of these markers on chromosome 6S (Fig. 4a).

After genotyping the 26 recombinants using eight markers, various exchange types were classified according to the recombination breakpoints at the markers. We selected two to three recombinants for each exchange type and conducted progeny testing based on BPH resistance. Only the recombinants R32-8, R32-2, and R32-19 did not show recombination in the region between markers I7494 and I1540. The left and right boundaries of the locus were determined by the recombinants R32-41, R32-18, R32-45, and R32-19, R32-9, R32-6, R32-44, respectively. The recombinants with resistant homozygous or heterozygous genotypes at marker I1432 were resistant to BPH, while the plants with susceptible homozygous genotypes were susceptible. This indicated that the marker genotype of I1432 and the phenotype co-segregated. Taken together with the above analysis of recombinants' genotypes and progeny testing, *BPH39* was finally fine-mapped within markers I7494 and

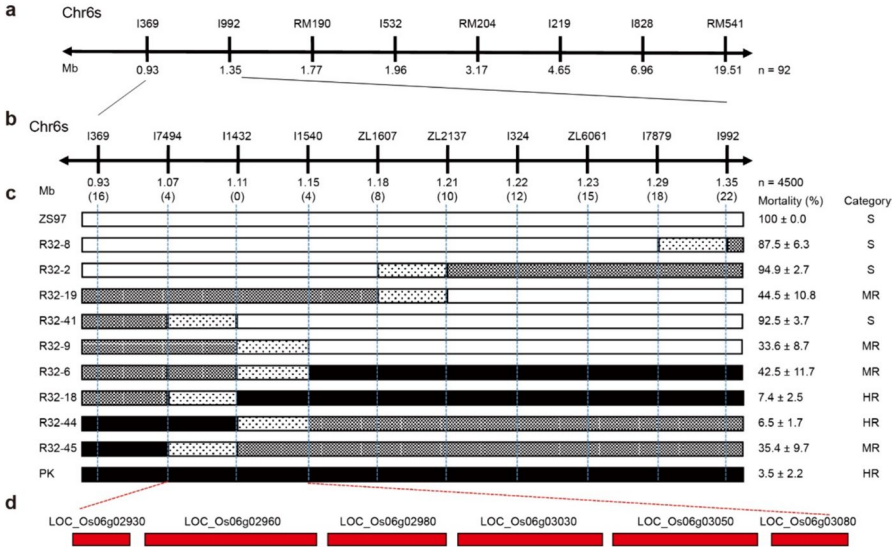

Fig. 4 Fine mapping of *BPH39*. **a** Primary physical map of part of chromosome 6S containing *BPH39*. **b** Physical map of marker interval I369-I992 harboring *BPH39*. The numbers in brackets show the times of recombination occurred between the marker loci and *BPH39* among 4,500 individuals. **c** Graphical genotypes and resistance phenotypes of the recombinants. Black, white and grey bars denote PK, ZS and recombined segments, respectively. HR, highly resistant; MR, moderately resistant; S, susceptible. **d** Annotated genes within the final 85 kb interval based on Nipponbare reference from MSU database

I1540, corresponding to an interval size of 84 Kb based on the Nipponbare reference genome (Fig. 4b, c).

Candidates of *BPH39*

Six genes were identified in the 84 Kb region according to the Rice Genome Annotation Project Database (MSU). *LOC_Os06g02930* and *LOC_Os06g03030* encode a conserved hypothetical protein. *LOC_Os06g02960* encodes a DUF594 family protein of unknown function. *LOC_Os06g02980* encodes a subunit of the plasma membrane H + -ATPase involved in nutrient transport. *LOC_Os06g03050* encodes a DUF594 protein containing an unknown functional domain. *LOC_Os06g03080* encodes an aspartic protease (Fig. 4d). We sequenced those genes of the two cultivars, NIL-BPH39 and ZS97, and aligned them with the reference genome Nipponbare (NPB), resulting in multiple variations between NIL-BPH39 and ZS97. Among them, two genes, *LOC_Os06g02930* and *LOC_Os06g03030*, exhibited the most variations—11 SNPs and one insertion, and 5 SNPs and one deletion, respectively—resulting in substitutions and alterations of the encoded amino acids. A base substitution led to premature termination of amino acid translation at 643 bp in *LOC_Os06g02930* in NIL-BPH39 (Table 1). The proteins of other candidate genes had only a few amino acid substitutions and insertions or deletions (Table S4). We

Table 1 Differences of *LOC_Os06g02930* and *LOC_Os06g03030* their encoded amino acids among three cultivars

Gene ID	Variation loci	Amino acid variation	NPB	NIL-BPH39	ZS97
LOC_Os06g02930	9	N—> K	C	G	C
	49	-> E		GAG	
	210	P—> P	G	A	G
	214	L—> M	T	T	A
	323	V—> E	T	A	T
	341	L—> P	T	T	C
	362	T—> K	C	C	A
	382	M-> V	A	G	A
	532	D—> N	G	A	G
	635	N—> T	AT	CC	AT
	643	Q-> *	C	T	C
LOC_Os06g03030	82	L—> V	C	G	C
	94	V—> I	G	G	A
	187	P—> S	C	C	T
	305	T-> I	C	C	T
	337	G-> S	G	G	A
	395	P-> Q	C	C	DEL (97 bp)
	605	I-> *	T	T	

The variation loci are initiated according to the ATG of the ORF of the gene. DEL, deletion

analyzed the gene expression levels of candidate genes in near-isogenic lines before and after BPH infestation. The results showed that the expression levels of only *LOC_Os06g02930* and *LOC_Os06g03030* in the resistant line were significantly higher than those in the susceptible line (Fig. 5). Based on the above results, we believe that *LOC_Os06g02930* and *LOC_Os06g03030* may be reliable candidate genes for *BPH39*.

RNA sequencing and analysis of DEGs

In order to explore which genes were involved in the resistance to BPH, we performed transcriptome sequencing and differentially expressed gene (DEG) analysis of NIL-BPH39 and ZS97 before and after BPH infestation. The analysis revealed a total of 51 differentially expressed genes that were consistently present across all four treatment groups, with 17 of them exhibiting upregulation. These identified genes potentially play a crucial role in the *BPH39*-mediated insect resistance response (Fig. 6a). KEGG enrichment analysis showed that DEGs between RT (NIL-BPH39 after BPH infestation) and ST (ZS97 after BPH infestation) were mainly concentrated in the phenylpropanoid biosynthesis and diterpenoid biosynthesis pathways (Fig. 6b). The Gene Ontology (GO) enrichment

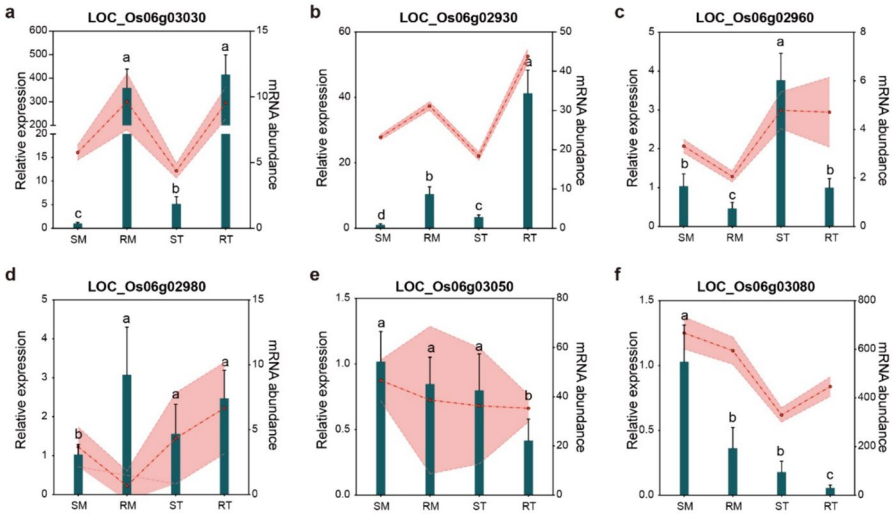

Fig. 5 Expression analysis of *BPH39* candidate genes in the two NILs with contrary *BPH39* genotypes. The histogram and the left ordinate axis represent the relative expression of the genes detected by RT-qPCR. SM, RM represent ZS97 and NIL-BPH39 with no infestation. ST and RT indicate ZS97 and NIL-BPH39 at 48 h after BPH infestation. The expression levels of all genes in SM are set to the value of '1'. Error bar indicates standard deviation. The letter a, b, c and d on the error bar indicates significant difference in the process of multiple comparison and analysis of variance, in which the same letters indicate that there is no significant difference at 0.05 level, while different letters indicate significant differences. The line chart and the right ordinate axis represent the FPKM value of the gene expression detected by RNA-seq. The orange shaded part represents the standard error

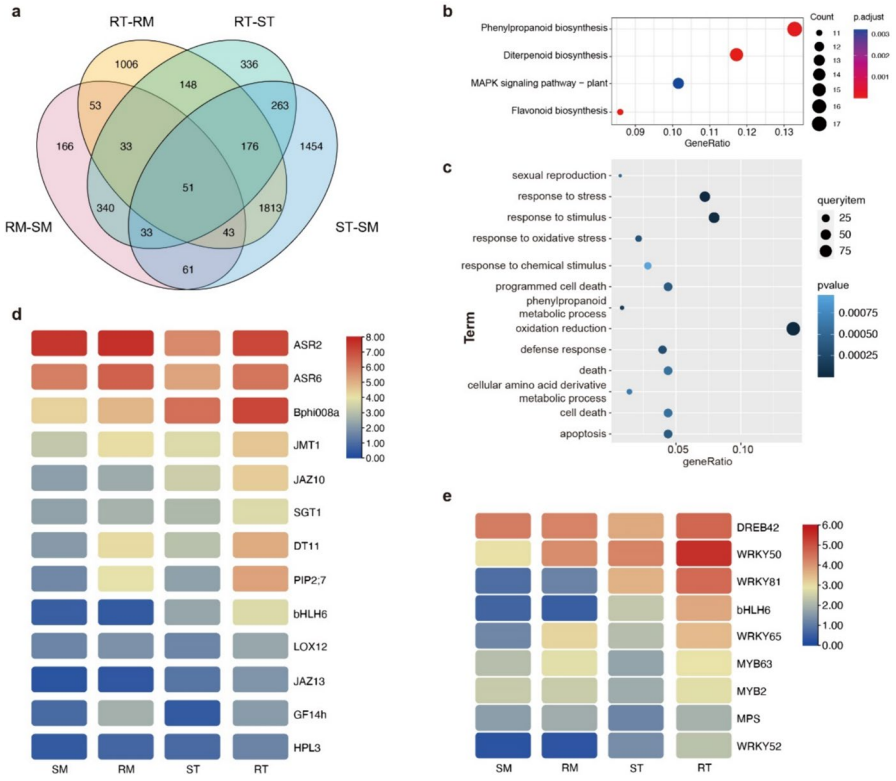

Fig. 6 DEGs analysis by RNA-seq in the two NILs with contrary *BPH39* genotypes. **a**, Venn diagram of DEGs in the comparison groups. **b** and **c**, DEGs of KEGG and GO enrichment results in comparison group of RT-ST, respectively. d and e, DEGs of heat maps of JA-related genes and transcript factors (TFs), respectively. SM, RM, ST and RT, see legends in Fig. 5

analysis showed that DEGs between RT and ST were mainly concentrated in the terms 'oxidation–reduction', 'response to stress and stimulus', 'defense response', and 'programmed cell death' in the biological process category (Fig. 6c).

Numerous studies have shown the involvement of the JA, ETH, ABA, and SA plant hormone signaling pathways in the anti-insect response mechanism of BPH feeding, as well as their regulatory role in conferring resistance to BPH. It was found that 10 of the differentially expressed genes screened were significantly upregulated during BPH feeding induction (Fig. 6d), which also indicated that the plant hormones JA, ETH, ABA, and SA were involved in anti-insect molecular responses in rice-brown planthopper interactions. As can be seen from Fig. 6e, transcription factors play an important role in plant responses to biological stresses such as insect resistance and disease resistance. The expression levels of *OsWRKY50*, *OsWRKY81*, *OsWRKY65, OsWRKY52, OsMYB63, OsMYB2* and *OsbHLH6* were significantly up-regulated in NIL-BPH39 after BPH feeding.

Quantitative RT-qPCR verification

To verify the expression levels of insect-resistant genes before and after BPH infestation in NIL-BPH39 and ZS97 using RNA-Seq, we selected several JA-related genes for RT-qPCR verification. The expression trends of *OsbHLH6*, *OsJAZ10*, *OsJAZ13* and *OsWRKY81* were completely consistent with RNA-Seq data, with all being significantly upregulated in NIL-BPH39 (Fig. 7). The trends for the other seven genes were similar to the RNA-Seq results, and all related genes, except *OsLOX8* in the sensitive lines, were significantly upregulated after BPH infestation. Among them, *OsPR10*, *OsLOX12* and *Bphi008a* were up-regulated hundreds of times after BPH

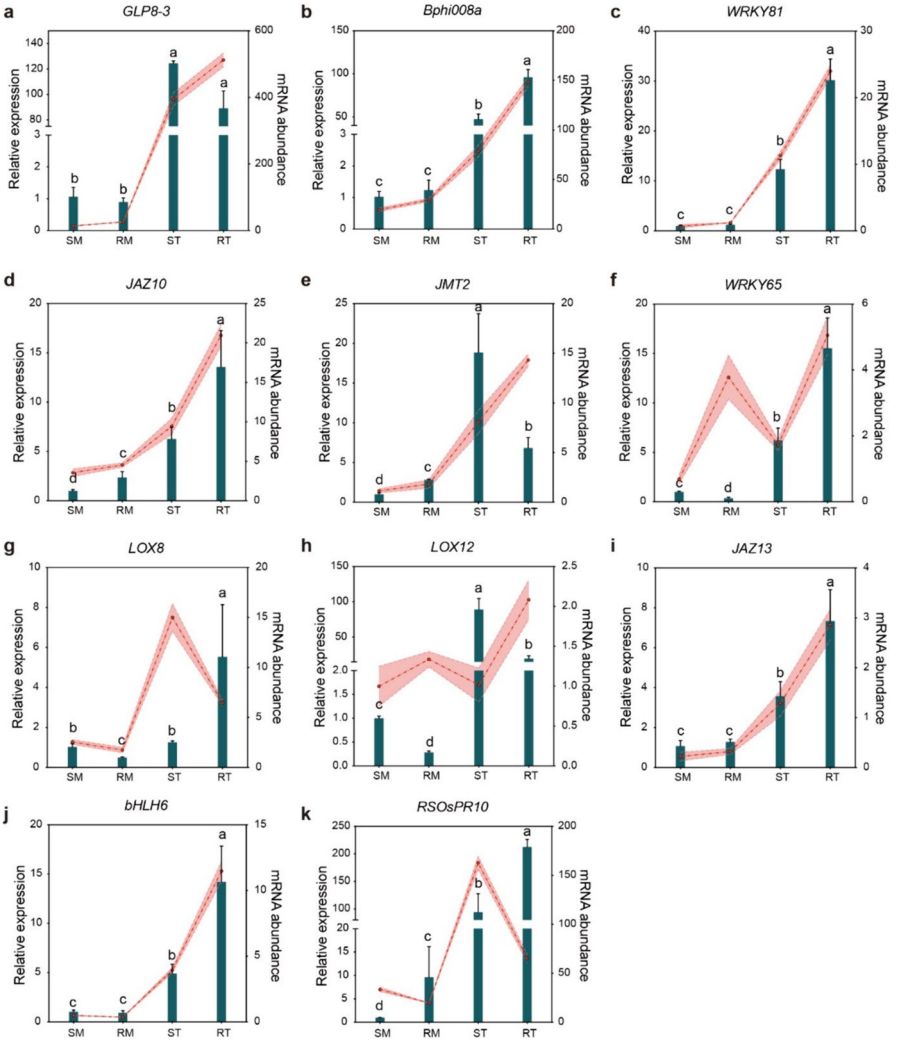

Fig. 7 The relative expression of JA-related genes

infestation, suggesting that they were strongly induced by BPH feeding. Other genes were also upregulated by tens of times and similarly induced by BPH.

Discussion

The discovery, identification and cloning of BPH resistance genes is the most basic and important work of rice insect resistance genetics and breeding, and it is also an important component of rice functional genome research. An important finding of this study was the identification of a novel BPH resistance locus, *BPH39*, in an Indian rice line and its fine mapping to an 84 Kb region within markers I7494 and I1540 on chromosome 6S. According to the reported localization information of the BPH resistance genes, we found that at least five other genes were mapped on chromosome 6S, which were *BPH3*, *bph4*, *BPH32*, *bph29*, *BPH25* and *BPH37*. A recessive gene, *bph4*, was mapped near this interval between SSR markers RM589 and MR586 (Jairin et al. 2010). *BPH32* was derived from a resistant variety, Ptb33 (an Indian variety bred at Pattambi (Ptb) in Kerala state), which was mapped between markers RM19291 and RM8072. This locus was later cloned and its exact location was delimited to be between markers RM19291 and I32-4 (Ren et al. 2016). *bph29*, (previously named *bph20 (t)*), a gene derived from *Oryza rufipogon* Griff, was initially found to be localized between markers BYL7 and BYL8, and subsequently, the gene was finely mapped within the 24 Kb region between BYL8 and BID2, and was finally cloned (Yang et al. 2012; Wang et al. 2015). Myint et al. (2012) mapped gene *BPH25* in a highly resistant line, ADR52, from India and found it spanned a relatively large interval between markers S00310 and RM8101, encompassing 1.7 Mb. This interval also includes the aforementioned genes: *bph29*, *BPH3*, *BPH32*, *BPH39* and *bph4* (Fig. 8). Combining the above information, we speculate that *BPH3* and *BPH32* are likely to be the same gene because they are both mapped in the same insect-resistant line Ptb33, by two different research teams. *BPH39* is located between *bph29* and *bph4*. In addition, *BPH39* is a dominant locus, while *bph29* and *bph4* are both recessive genes. The localization interval of *BPH39* in this study adjoined that of *BPH32*, so we first had to figure out the relationship between the two genes.

In order to understand the relationship between *BPH39* and *BPH32*, we sequenced the *BPH32* gene in NIL-BPH39 and ZS97, and found that Ptb33 (*BPH32*) and NIL-BPH39 had a total of 23 variations in the *BPH32* gene, which also resulted in amino acid sequence changes (Table S5). In addition, it is also the most important evidence that during the fine mapping of *BPH39*, 12 recombinants displayed a genotype at marker I324 (located within the *BPH32* gene) that was opposite to the phenotype, that is, recombination occurred, indicating that *BPH39* is likely not allelic to *BPH32* (Fig. 4). Taken together, these results preliminarily indicate that *BPH39* is different from *BPH32*, but subsequent transgenic trials are needed to complete the cloning of *BPH39* before the relationship between them can be thoroughly clarified.

Six candidate genes were identified in the 84 Kb region containing *BPH39*. Among them, two genes, *LOC_Os06g02930* and *LOC_Os06g03030*, had the most variations resulting in the substitution and insertion of encoded amino acids between

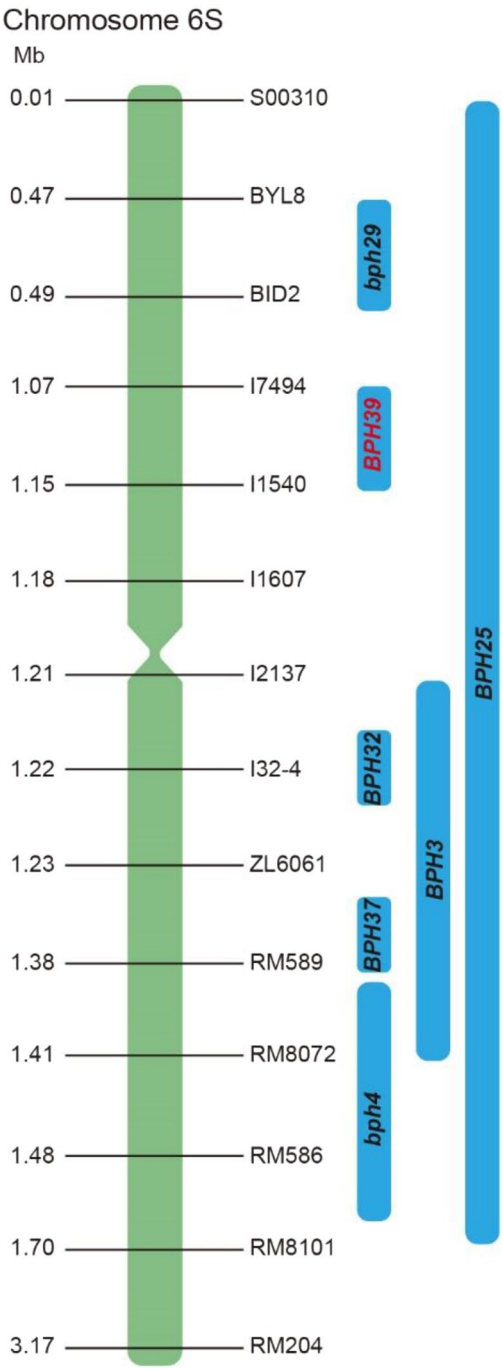

Fig. 8 Location of *BPH39* on the gene cluster of chromosome 6S

NIL-BPH39 and ZS97 (Table 1). Furthermore, the expression levels of these two genes in resistant line were significantly higher than those in susceptible line (Fig. 5). They all encode similar conserved hypothetical proteins with short consensus repeat (SCR) domain, which are very similar to the cloned BPH resistance gene *BPH32* (Ren et al. 2016). Based on the above results, we believe that *LOC_Os06g02930* and *LOC_Os06g03030* are reliable candidate genes for *BPH39*. These two genes will subsequently be used for genetic transformation verification.

Hormones play an important role in plants' responses to biotic and abiotic stresses. Salicylic acid (SA), jasmonic acid (JA) and ethylene (ETH) are common defense hormones. JA, in particular, plays a major role in the response to mechanical damage caused by insects. It has been reported that several rice genes in the JA signaling pathway are involved in the defense response against BPH. In the *Bph6* near-isogenic line, the active JA substance, JA-ILE, was induced by insect pests and was found to be significantly higher than in the susceptible variety 9311, indicating that JA played an important role in *BPH6*-mediated resistance (Guo et al. 2018). Lipoxygenase (LOX) and allene oxide synthase (AOS) are the first and second key enzymes in JA biosynthesis, respectively. Studies have shown that *OsAOS1*, *OsAOS2*, *OsLOX1* and *OsLOX9* are involved in herbivorous-induced JA synthesis, thereby mediating plant resistance to insects (Wang et al. 2008; Ma et al. 2020; Zeng et al. 2021). In this study, transcriptome and RT-qPCR confirmed that two LOX-related genes, *OsLOX8* and *OsLOX12*, were strongly induced by BPH in the resistant line NIL-BPH39. Jasmonate carboxymethyltransferase gene *OsJMT1* plays a regulatory role in rice defense against BPH by altering the levels of JA and its related metabolites (Qi et al. 2016). Our study also found that the expression of *OsJMT2* (homologous gene of *OsJMT1*) was strongly induced in NIL-BPH39. In addition, two JAZ protein genes, *OsJAZ10* and *OsJAZ13*, as well as the JA-induced transcription factors *OsbHLH6* and *OsWRKY81*, were significantly upregulated in NIL-BPH39 (Fig. 7). A series of BPH resistance genes involved in the JA signaling and synthesis pathway have been identified, indicating that JA plays an important role in mediated rice resistance to BPH (Zhou et al. 2023). Interestingly, a previously identified BPH resistance gene *Bphi008a* (Hu et al. 2011), is also significantly upregulated in the NIL-BPH39, suggesting that they may be related in some way. In conclusion, these preliminary results suggest that *Bph39* may be involved in the JA signaling pathway, thereby mediating the defense response of BPH.

Conclusions

A novel BPH resistance gene *BPH39* was finely mapped within an interval of 84 Kb on rice chromosome 6S. Two candidate genes for *BPH39*, *LOC_Os06g02930* and *LOC_Os06g03030*, were identified by parental comparative sequencing and gene expression analysis. Transcriptome sequencing, DEG analysis, and gene RT-qPCR verification preliminarily revealed that *BPH39* may be involved in the JA signaling pathway, thus mediating the molecular mechanism of BPH resistance. This work will facilitate map-based cloning and marker-assisted selection of the locus in BPH resistant breeding.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11032-024-01485-6.

Authors' contributions Yangdong Ye and Yanan Wang performed experiments and analyzed the data, Ling Zou, Fangming Zhang, Shangye Xiong, Baohui Liang, Cheng Chen and Zhihong Zhu collected plant materials and performed parts of experiments, Shuai Zhang, Xiaoqing Wu, and Weiren Wu participated in handling figures and tables, Jie Hu, Jianguo Wu and Shuai Zhang, the co-correspondence authors, designed this research and wrote the manuscript. All authors have approved the manuscript.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval We declare that these experiments comply with the ethical standards in China.

Conflict of interests No conflict of interest exits in the submission of this manuscript.

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