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RESEARCH ARTICLE

# Identification of novel Single Nucleotide Polymorphisms (SNPs) associated with brown planthopper, *Nilaparvata lugens* (Stal.) resistance in rice (*Oryza sativa* L.)

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## Abstract

The brown planthopper (BPH) is one of the most predominant rice insect pests in Asia. Changes in the virulence pattern of BPH across the regions and breakdown of resistance in many released resistant cultivars warrant identification of novel and diverse germplasm resources that can be deployed for developing new rice varieties with a broader genetic base. Accordingly, the field phenotypic screening was conducted over two years during *kharif* 2020 and 2021 using 300 rice genotypes (selected from 3 K subset of BPH panel) along with eight checks in an augmented block design to identify the BPH-resistant donor lines. Two rice genotypes *viz.,* IRGC 126266 and IRGC 128206 exhibited consistent resistant reaction during both years. Mechanism of resistance studies (conducted during *rabi* 2021-2022) revealed that, among the two promising germplasm, IRGC 126266 exhibited all the three mechanisms of resistance by recording lower honey dew excretion (72.5 $mm^2$), lower nymphal survival rate (47.5 %), longer nymphal development period (17.20 days), lowest growth index (2.4) and took more days to wilt (27.2) compared to the susceptible check, TN1. Genome Wide Association Studies (GWAS) analysis was conducted in the 3K subset of BPH panel using four single locus models to identify the SNPs associated with BPH resistance. Significant SNPs were identified in proximity with several BPH resistance genes *viz*., *Bph33(t)*, *Bph13(t)*, *Bph6*, *Bph34*, *Bph3*, *Bph4*, *Bph25*, *Bph29*, *Bph32*, *Bph28(t)*, *Bph2*, *Bph26, Bph7, Bph9, Bph18(t)* and *Bph21(t)*. Candidate gene analysis study revealed that 9 Quantitative Trait Nucleotides (QTNs) associated with stress tolerance genes played a significant role in BPH resistance.

**Keywords:** brown planthopper; GWAS; 3K subset; mechanisms of resistance; rice; SNP

## Introduction

Rice (*Oryza sativa* L.) is an essential food for the world's growing population (1). Of the twenty insect pests causing significant economic damage in rice, BPH, *Nilaparvata lugens* (Stal.) is predominant in Asia. Heavy BPH infestation often results in either direct or indirect yield losses ranging from 20–80 % in susceptible cultivars (2, 3). Factors that aid in BPH outbreaks include large scale cultivation of BPH-susceptible fine grain varieties, higher humidity (>80 %) and temperatures ranging from 25 to 30 °C, application of higher doses of nitrogenous fertilizers and use of resurgence causing chemicals (4).

Sucking of phloem sap by BPH reduces photosynthetic rate, leaf area, chlorophyll content, nitrogen level of leaf and stem and dry matter accumulation in susceptible rice cultivars. Building genetic resistance to BPH and developing rice varieties with wider genetic base seems to be an economically and ecologically safer option for managing BPH (5).

Identification of a gene source for BPH resistance was first documented in 1967. Subsequently, resistance genes were discovered in Mudgo (an Indica rice variety resisting BPH through non-preference and antibiosis mechanism having BPH 1 gene) and ASD 7 (a BPH resistant variety developed from Rice Research Unit, Ambasamudram having BPH 2 gene). Additional genes for resistance, such as BPH 3 and BPH 4, were found through genetic analysis of different donors (PTB 33, Rathu Heenati and Babawee). Consequently, resistant donors against various BPH populations were identified as both domesticated and wild species. The donors include ARC10550, Swarnalata, T12, Balamawee and Chin Saba *etc*. Some of the wild rice species *viz*., *O. minuta, O. officinalis*, *O. australiensis* and *O. latifolia* were identified as diverse resistance sources for

BPH (6). Four resistant loci (BPH 1, BPH 2, BPH 3 and BPH 4) have been extensively used in most breeding operations, particularly in South-East Asia (7). As a result, many resistant rice varieties have been approved by the International Rice Research Institute (IRRI), for commercial production in Asia. However, BPH resistant rice varieties possessing these genetic loci became susceptible over time, as the resistance was governed by only one or two genes. So far, over 37 genes Quantitative Trait Loci (QTLs) regulating BPH resistance have been identified in *indica* and wild species and eight of them have been successfully cloned (8).

SNP genotyping is a powerful tool in agriculture that enhances crop improvement through several key applications. It enables Marker-Assisted Selection (MAS) and Genomic Selection (GS) for faster and more precise breeding. Through GWAS, it helps in identification of genes linked to important traits like yield, disease resistance and stress tolerance. SNPs are also used to assess genetic diversity for conservation & pyramiding of multiple traits. The marker-aided gene-pyramiding approach has also received attention for improving the resistance of elite rice cultivars to BPH (9). Combining multiple genes into single genetic background hinders insect pest adaptability to rice cultivars and improves the durability of resistance (10). Many authors have adopted the gene-pyramiding approach to improve the BPH resistance in rice cultivars. The resistance mechanisms of rice to manage BPH damage include antibiosis, antixenosis and tolerance. The most widely studied defensive mechanism in rice is antibiosis (11). Many investigators have utilized antibiosis, antixenosis, as well as tolerance to identify tolerant rice germplasm and BPH-resistant genes (12). Recently developed association mapping coupled with NGS sequence-based genotyping led to a new approach called GWAS. Employing GWAS that combines phenotyping and high diversity SNP panels helps in the detection of large number of haplotypes and genes. This methodology offers several advantages over earlier QTL mapping approaches such as exploiting natural variability in the germplasm, reduced time and cost for developing mapping populations apart from aiding in greater resolution because of higher recombinant events (13). The marker trait associations identified through GWAS facilitates uncovering candidate genes regulating BPH tolerance mechanisms and thus can be utilized in rice breeding to improve cultivars through marker assisted breeding programme. In addition, the candidate genes not only enable better understanding of the key genomic regions but also ensure operating mechanisms for BPH tolerance. Therefore, the present studies were attempted to identify novel germplasm sources offering durable BPH resistance and decipher the underlining mechanisms.

## Materials and Methods

### Phenotypic studies

The experimental material comprised of 300 rice genotypes (3k subset from IRRI, Phillippines) along with eight checks *viz.,* PTB 33, Rathuheenati, RP2068-18-3-5, BPT 5204, Swarna, TN1, MTU 1001 and RNR 15048 (Supplementary Table 1).

The experimental material was initially screened under field conditions in augmented randomized block design at the Institute of Rice Research (IRR), Agricultural Research Institute (ARI), Rajendranagar, Telangana, India, during two *kharif* seasons in 2020 and 2021. The augmented block design comprised of five blocks, each containing 68 accessions (60 lines and eight checks) with susceptible check, TN1, all along the borders.

### Field screening

The experimental material (300 entries along with 8 checks) was raised in nursery beds and was transplanted at 25$^{th}$ day after sowing. Each entry was transplanted at 10 × 10 cm spacing in two rows (10 hills/row) of two-meter length. All around test entries, susceptible check, TN 1 was transplanted as border rows (5 rows) to serve as bombardment rows for ensuring sufficient BPH infestation. After every ten entries, The BPH nymphs and adults reared in polyhouse were released to feed at active tillering stage to ensure sufficient buildup of BPH. The rice genotypes were scored as per the IRRI standard evaluation system on 0 to 9 scale when 90 % of the plants in the susceptible check, TN 1 showed hopper burn symptoms.

### Polyhouse screening

The rice genotypes offering BPH resistance in field screening were screened for seedling resistance in polyhouse through standard seed box screening technique (SSST) in three replications at the IRR, ARI, Rajendranagar, Hyderabad during *rabi* 2021-22. Second or third instar nymphs of BPH @ 6-7 per seedling were released at 15 days after sowing (DAS) or three leaf stage, by gently tapping the pot containing BPH nymphs over the seedlings of rice genotypes. These rice seedlings were observed for their reaction to BPH and scoring was done based on 0-9 scale when the susceptible check (TN1) showed 90 % seedling mortality.

### Studies on BPH resistance mechanisms

The genotypes showing either resistant or moderate resistance to BPH, through field and polyhouse study, were selected for further studies, to determine the mechanisms of resistance involved. Different kinds of studies were conducted during *rabi* 2021-22 *viz.,* antixenosis, (honey dew excretion), antibiosis (nymphal survival) and tolerance mechanisms (days to wilt test) to understand the exact mechanism resisting BPH.

### Antixenosis mechanism

The honeydew excretion test was conducted to measure the feeding preference of BPH, to determine the level of resistance or susceptibility of the selected genotypes. The quantity of honeydew excreted by BPH on each of the selected entries was measured by adopting the standard protocol (14).

### Antibiosis mechanism

The nymphal survival studies were conducted to determine the antibiosis as a plant resistance mechanism against the BPH. The experiment was conducted under polyhouse conditions on 45 days old potted rice plants. Ten freshly emerged, one day old nymphs were released on a potted plant surrounded with mylar cage, covered with muslin cloth to prevent BPH escape. Plants were observed regularly for nymphal development. The number of nymphs that emerged were counted daily and statistically compared based on mean value obtained from four replications. The number of

released nymphs that reached the adult stage were recorded on each rice genotype and the per cent nymphal survival was computed by the following formula (15).

$$\text{Percent Nymphal survival} = \frac{\text{Number of adults emerged}}{\text{Number of nymphs released}} \times 100$$

Similarly, the number of days taken by different nymphs to reach adult stage was recorded on different genotypes as nymphal development period (16). Growth index of brown planthopper on each test culture along with resistant and susceptible checks were calculated by using the data obtained from the experiments on nymphal survival and development period (17).

$$\text{Growth Index} = \frac{\text{\% Nymphs survived on test culture}}{\text{Development period of nymphs on test culture}} \times 100$$

## Studies on tolerance mechanism

### Days to wilting

Experiment was carried out on 30-day old potted rice plants to determine the degree of BPH tolerance in the selected rice genotypes. Five BPH first instar nymphs were released on a potted rice plant with a mylar cage and muslin cloth covered over it. Plants were then observed daily for a period of 30 days and the number of days taken to completely wilt was recorded. The experiment was quadruplicated per entry and their mean was recorded as the average days taken to wilt.

### Statistical analysis

The field screening data was subjected to analysis of variance using the R package "augmented RCBD" (18). The data collected in different studies on the mechanism of resistance was suitably transformed and was analyzed statistically in completely randomized design by following standard statistical methods (19).

## Genotyping

### Population structure analysis

STRUCTURE version 2.3.3 was used to assess the genetic structure of rice genotypes and assign individuals to populations (20). STRUCTURE HARVESTER ver.0.6. (21) was used to estimate the most probable K value. The K value was selected after five independent runs with a burn-in period of 100 steps with 100 Monte Carlo Markov chain (MCMC) replicates. The range of genetic clusters was set from K = 1 to 5. The posterior probability values (LnP(D) and ΔK) were used to calculate the total number of subpopulations (K). Out of 300, the genomic data of rice accession DAMNOEUB KAUNKHMOM::IRGC 79159-1 was not available in Rice SNP-Seek database and hence 299 rice accessions were used for population analysis.

### Genome-wide association mapping

A total of 299 rice accessions were used in the present study for GWAS, which were obtained from the 3000 Rice Genome Project (3K RGP). The 3K RG 1M GWAS SNP dataset was downloaded from the Rice SNP-Seek Database. (https://snp-seek.irri.org/) (22). To avoid the influence of linked SNPs during the population structure analysis, the LD pruning tool of the PLINK program version 1.9 (20) was used to obtain a subset of 42,304 independent SNPs with a minor allele frequency (MAF) ≥ 0.05 and maximum missing sites per SNP fixed to < 20 %. MTAs were identified using general linear model (GLM) (23), mixed linear model (MLM) (24), compressed mixed linear model (CMLM) and enriched compressed mixed linear model (ECMLM) (25) implemented in GAPIT (genomic association and prediction integrated tool). The extent of kinship among individuals was also estimated with the filtered set of SNP markers using GAPIT in R software.

Manhattan plots were produced and a threshold value for declaring marker-trait association generated through MLM approach was set at- Log p = 4 (*i.e.*, p-value ≤ 0.0005) and a LOD value of ≥ 3 for BPH damage score.

### Candidate gene prioritization

The annotated gene search in the Rice Genome Annotation Project (Michigan State University Rice Genome Annotation Project (MSU-RAP) database (Osa1) Release 7) was used to extract the genes linked to BPH resistance and to identify the novel candidate genes. From the annotated genes, the top three prioritized genes were selected and their functions in relation to the trait were examined from the previous literature. Probable candidate genes in each MTA, were confirmed through literature mining.

## Results

The 300 rice accessions along with 8 checks were screened against brown planthopper for two years (2020, 2021) and the results exhibited a broader variation for phenotypic score in both the years for BPH damage score (Supplementary Table 2). The ANOVA revealed a significant mean sum of squares for different sources of variation, except for block (eliminating treatments) for BPH damage score. The findings of the analysis of variance were displayed in Table 1 and Fig. 1 depicts adjusted mean values based on frequency distributions. There was a significant skewness towards susceptibility, since most of the lines in the panel recorded 7 to 9 score. This could be

**Table 1.** Analysis of variance and mean sum of squares of augmented block design for BPH damage score in 3k subset

| Source | df | BPH damage score 2020 | BPH damage score 2021 | BPH damage score Pooled |
|---|---|---|---|---|
| | | BPH damage score | BPH damage score | BPH damage score |
| Treatment (ignoring blocks) | 307 | 2.3** | 2.01** | 1.5** |
| Treatment: Check | 7 | 14.17** | 25.36** | 18.88** |
| Treatment: Test *vs.* Check | 1 | 11.6** | 0.87** | 1.53** |
| Treatment: Test | 299 | 1.99** | 1.46** | 1.1** |
| Block (eliminating treatments) | 4 | 1.4 | 1.1e-27 | 0.35 |
| Residuals | 28 | 0.6 | 1.6e-27 | 0.15 |

**Significance at 1 % probability level (p value = 0.001). df: degrees of freedom

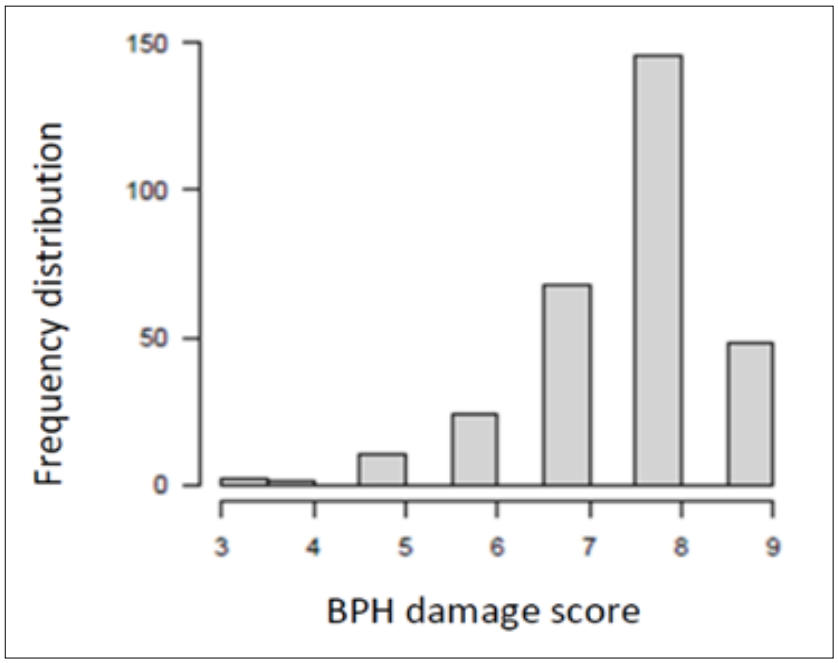


**Fig. 1.** Frequency distribution-based adjusted mean values for pooled BPH damage score.

attributed to the fact that majority of the 3k subset from IRRI, Phillippines have segregated for susceptibility.

During *kharif* 2020, among 300 rice accessions screened against brown planthopper, only two genotypes *viz.,* IRGC 126266 and IRGC 128206*,* exhibited resistant reaction (DS:3.0) under natural field conditions, while 32 cultures showed moderately resistant reaction. Whereas 54 accessions were moderately susceptible and 212 were highly susceptible to brown planthopper (Table 2). Same set of 300 rice genotypes were again screened during *kharif* 2021, to confirm the reaction against brown planthopper. Out of 300 entries, only three entries *viz.,* IRGC 126266, IRGC 128206 and IRGC 132236 registered resistant reaction (DS:3.0) while 39 germplasm showed moderately resistant reaction. The remaining entries were either moderately susceptible (199) or highly susceptible (59) to brown planthopper with damage scores ranging from 7 to 9 under natural field conditions. The check, TN1 showed complete susceptibility (DS:9.0), whereas resistant check, PTB33 showed resistant reaction (DS: 3.0). However, two entries *viz.,* IRGC 126266 and IRGC 128206 exhibited consistent resistant reaction to brown planthopper under natural field conditions.

The promising entries identified in field screening were further tested to reconfirm the resistant reaction to BPH under polyhouse conditions and results revealed that the two entries *viz.,* IRGC 126266 and IRGC 128206 showed moderately resistant reaction (DS:5.0) to BPH at seedling stage, while PTB 33 exhibited resistant reaction (DS:3.0) (Table 2). These results imply that these two genotypes *viz.,* IRGC 126266 and IRGC 128206 possess good level of field tolerance (DS:3.0), but might succumb to BPH feeding at seedling stage (DS: 5.0). However, BPH seldom occurs at seedling stage.

## Antixenosis mechanism

Highest honeydew excretion (165.7 $mm^2$) was recorded in susceptible check, TN1 and lowest in resistant check, PTB33 (65.5 $mm^2$). Among the two rice genotypes tested, IRGC 126266 recorded lower honeydew excretion (72.5 $mm^2$) which was on par with resistant check, PTB33 followed by IRGC 128206 (86.2 $mm^2$) (Table 3). These results reveal that antixenosis could be one of the non-preference mechanisms for conferring BPH resistance.

## Antibiosis mechanism

An attempt was made to study the antibiosis mechanism through nymphal survival test, nymphal development period and growth index. The results of the nymphal survival test on the selected two rice genotypes along with two checks exhibited significant variation in per cent nymphal survival among the four rice genotypes, ranging from 45 to 67.5 %. Significantly lowest nymphal survival was recorded in PTB 33 (45 %) followed by IRGC 126266 (47.5 %) and IRGC 128206 (57.5 %). The nymphal survival percentage in IRGC 126266 was on par with resistant check, PTB 33 (Table 4). The lower nymphal survival in resistant cultures compared to susceptible entries, in confirmation with the present findings.

The results of the nymphal developmental period (days to adult) are presented in Table 3. The data showed that the nymphal development period significantly varied across the rice genotypes ranging from 12.7 to 18.2 days. Significantly shortest nymphal period was observed in susceptible check, (12.7 days) which differed significantly

**Table 2.** Field reaction of rice 3K Panel subset for brown planthopper during *Kharif,* 2020 & 2021

| Damage Score | Number of genotypes | | Reaction |
|---|---|---|---|
| | ***Kharif*, 2020** | ***Kharif*, 2021** | |
| 1 | 0 | 0 | Highly resistant |
| 3 | 2 (IRGC 126266 & IRGC 128206) | 3 (IRGC 126266 IRGC 128206 & IRGC 132236) | Resistant |
| 5 | 32 | 39 | Moderately resistant |
| 7 | 54 | 199 | Moderately susceptible |
| 9 | 212 | 59 | Highly susceptible |

**Table 3.** Mechanisms contributing to BPH resistance in different rice genotypes

| S. No | Genotypes | Antixenosis | Antibiosis | | | Tolerance |
|---|---|---|---|---|---|---|
| | | HDE (mm² / 5 females) | NSP (%) | NDP (Days) | GI | DTW |
| 1 | IRGC 126266 | 72.5 | 47.5 | 17.2 | 2.7 | 27.2 |
| 2 | IRGC 128206 | 86.2 | 57.2 | 16.5 | 3.5 | 24.2 |
| 3 | PTB 33 | 65.5 | 45.0 | 18.2 | 2.4 | 30.0 |
| 4 | TN1 | 165.7 | 67.5 | 12.7 | 5.3 | 13.7 |
| | SE (m) ± | 5.68 | 2.6 | 0.5 | 0.1 | 0.2 |
| | C.D (P= 0.05%) | 17.52 | 8.0 | 1.7 | 0.5 | 0.6 |
| | C.V | 11.66 | 9.57 | 6.9 | 10.3 | 1.8 |

HDE - Honey dew excretion; NSP - Nymphal survival %; NDP - Nymphal development period; GI - Growth index; DTW - Days to wilt

**Table 4.** Allelic status of the significant QTNs that are contributing resistance for BPH damage score in the identified promising germplasm (IRGC 126266 & 128206)

| S. No | Gene locus ID | Chr. | Allelic status (IRGC) | | QTNs | Putative function |
|---|---|---|---|---|---|---|
| | | | 126266 | 128206 | | |
| 1 | LOC_Os02g13330.1 | 2 | C | C | S2_7110876 | bet v I allergen family protein, putative, expressed (plant pathogenesis-related proteins (PR-10)) |
| 2 | LOC_Os03g12890.4 | 3 | G | G | S3_6945974 | aminotransferase domain containing protein, putative, expressed |
| 3 | LOC_Os04g53510.1 | 4 | C | T | S4_31878608, S4_31880156 | OsFBL20 - F-box domain and LRR containing protein, expressed |
| 4 | LOC_Os06g50370.1 | 6 | T | C | S6_30493056 | zinc finger, C3HC4 type, domain containing protein, expressed |
| 5 | LOC_Os07g08140.1 | 7 | A | G | S7_4124723 | heat stress transcription factor, putative, expressed |
| 6 | LOC_Os09g14490.1 | 9 | T | T | S9_8567719 | TIR-NBS type disease resistance protein, putative, expressed (400 R genes in Rice) |
| 7 | LOC_Os10g03570.1 | 10 | C | C | S10_1540826 | RGH1A, putative, expressed (Resistance gene analogous) |
| 8 | LOC_Os11g47350.1 | 11 | G | C | S11_28483649 S11_28779832 S11_ 27393603 S11_ 26042091 | beta-D-xylosidase, putative, expressed (Plant cell wall immunity induced on wound) |
| 9 | LOC_Os12g37970.3 | 12 | A | A | S12_23324406 | MYB family transcription factor, putative, expressed (development and stress response) |

with other genotypes. Whereas significantly longer nymphal development period was recorded in PTB 33 followed by IRGC 126266 and IRGC 128206 (18.2, 17.2 and 16.5 days, respectively) which were on par with each other.

The results of growth index studies showed that the values varied significantly across the genotypes tested and ranged from 2.4 to 5.3 (Table 3). Among the entries evaluated, significantly lowest growth index was registered in PTB 33 followed by IRGC 126266 and IRGC 128206 (2.4, 2.7 and 3.5 respectively). Significantly highest growth index was observed in TN 1 (5.3). Lower growth index of BPH noticed in these rice genotypes be due to lower per cent nymphal survival and longer nymphal development period.

## Tolerance mechanism

To assess the level of tolerance against BPH in different rice genotypes, days to wilt test was performed and the results are presented in (Table 3). Perusal of results showed significant differences in days to wilting ranging from 13.7 to 30 days across the rice genotypes tested. The susceptible check succumbed to BPH attack within 13.7 days. However, two genotypes *viz.,* IRGC 126266 (27.2 days) and IRGC 128206 (24.2 days) along with resistant check, PTB 33 (30 days) sustained BPH damage significantly for a greater number of days to wilt compared to TN1 (13.7 days), exhibiting tolerance to BPH.

## Population structure Analysis

Analysis of population structure is critical in association studies as it reduces the effects of Type-I and Type- II errors (20). Structure analysis revealed that the 299 accessions could be classified into three main clades (Fig. 2a). POP 1 encompasses a total of 183 accessions comprising of indica subspecies (ind1A, ind1B, ind2, ind3, index) whereas POP 2 consists of 83 accessions belonging to Tropical indica accessions. POP 3 consists of 33 accessions comprising of Admix (Subtrop, temp, jipx, aroma). The genotypes with score > 0.80 were considered as pure while, < 0.80 were considered as admixtures. Among two sub populations, POP1 consists of 67 pure types and 16 admixed types while, POP2 has 167 pure types and 16 admixed types. The presence of admixtures was perhaps since the loci involved in this study revealed only a small part of the genotypic/ phenotypic association of otherwise complex traits or acquisition of a few spontaneous mutations in the genotypes.

Similar results were observed during principal component analysis with 67.02 % of the genetic variation in the accessions explained by the first three principal components. Most accessions were clustered into three groups while plotting the first three components against each other (Fig. 2b). These findings suggested that the accessions employed as a covariate in the GWAS model in this investigation had a clear sub population structure.

## Genomic regions governing BPH damage score

GWAS analysis was conducted in the 3K subset of BPH panel using four single locus models (GLM, MLM, CMLM and ECMLM) to identify the SNPs associated with BPH resistance. Each model has its own characteristics in terms of statistical power, selection of covariates, grouping of markers,

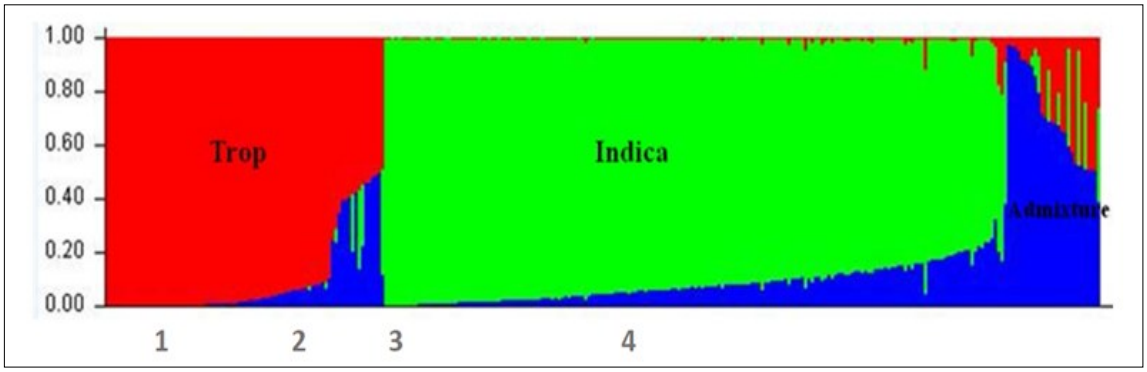


**Fig. 2a.** Distribution of the estimated sub population components (ancestry fraction) for each accession as determined by STRUCTURE version 2.3.3.

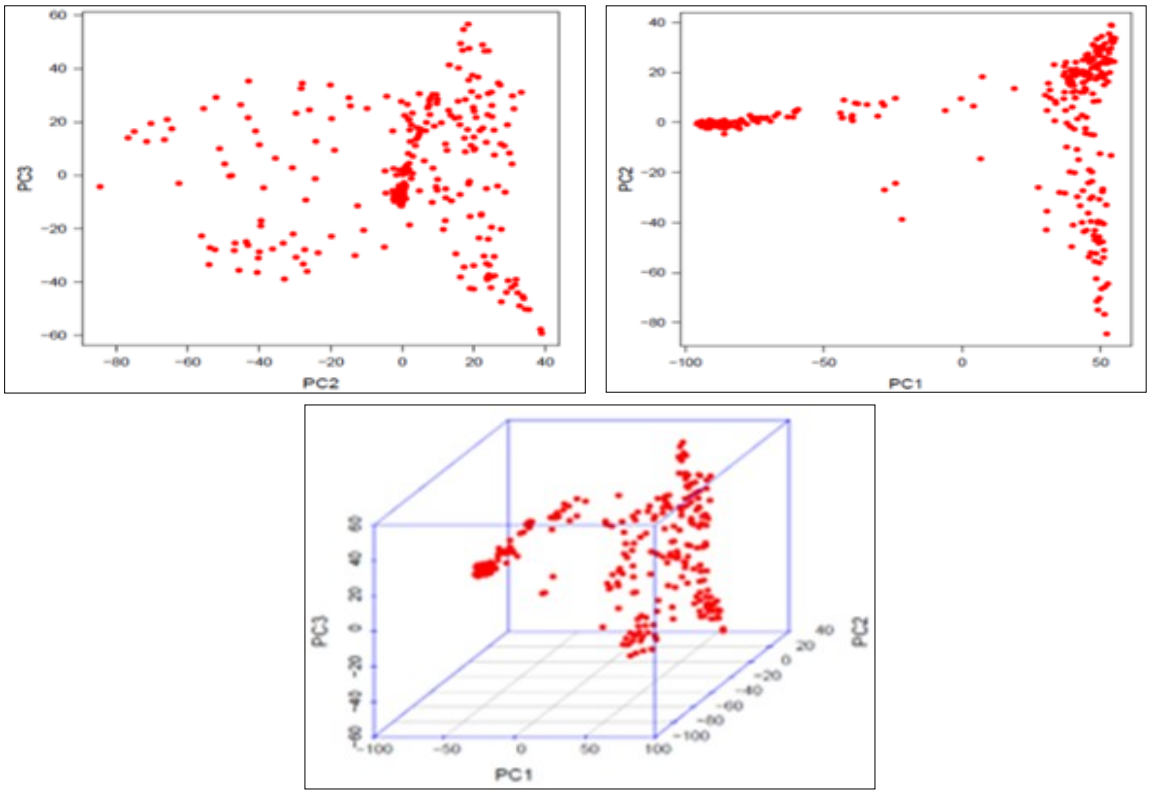


**Fig. 2b.** 3D scatter plot of principal component analysis for single nucleotide polymorphisms data of the 3K subset of BPH panel.

computational power, ability to control false positives and the ability to include true associations and so on (26). Considering these factors and the trait complexity, engaged all these models to find out the marker–trait association and the results from different models are compared.

The *p* value of $<50^{-3}$ was considered to identify significant SNPs across models and seasons for BPH damage score. Using this threshold, a total of 54 significantly associated SNPs were identified for BPH damage score. These SNPs were distributed on all the 12 chromosomes. For BPH damage score, more associated SNPs were detected through ECMLM (25), CMLM (25) followed by MLM (24) and GLM (23) (Fig. 3a & Fig. 3b) (Supplementary Table 3)

## Identification of SNPs

For BPH damage score, 22 associated SNPs were identified by employing the GLM model mapped on chromosome 2, 3,4, 6, 7, 8, 9,10,11 and 12. Whereas, the 26 SNPs identified through MLM model were mapped on all chromosome, except chromosome 1. The 28 SNPs associated to BPH damage score obtained from CMLM model were mapped on all the 12 chromosomes and realized similar results for ECMLM model.

For BPH damage score a significant SNP was identified on chromosome 1 approximately 10.5 Mb regions away from the *Bph33* (t) gene reported in RP2068 (27)**.** Significant SNPs discovered on a long arm of chromosome 2 were mapped near (about 1-3.6 Mb away from) the *Bph13* (t) gene described in *O. eichinger*. A cluster with 3 SNPs spanning a region of 2.2 to 6.9 Mb was noticed on a short arm of chromosome 3.

Two significant SNPs that were identified at the 31.87 to 31.88 Mb region on the long arm of the chromosome 4 were also co-localized with *Bph6* (28) and *Bph34* (29) indicating the importance of this region for searching resistance gene(s).

One major SNP was discovered on short arm of chromosome 6 at 0.88 Mb and 0.4-0.9 Mb far away from the genes Bph3, bph4, Bph25, Bph29 and Bph32 identified earlier in this region (30-31). Identified four significant SNPs spanning a region of 26 - 28.1 Mb on the chromosome 11, which were also found to be co-localized with *Bph28 (t)* (32). A lead SNP on chromosome 7 at a physical distance from 4.12 Mb and Qbph7 (33) mapped on the long arm of chromosome 7 was identified. Another SNP was also mapped on the long arm of chromosome 12 at 23.32 Mb region which was within the genes *bph 2/Bph 26,*

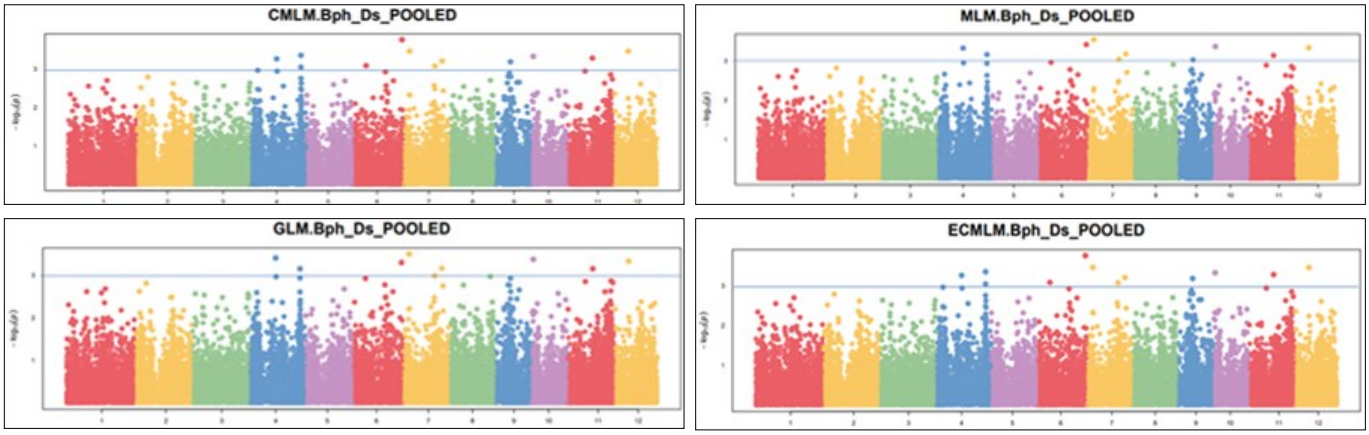


**Fig. 3a.** Manhattan plots of GLM, MLM, CMLM and ECMLM showing the significant SNP associations ($p < 0.0005$) with BPH Damage score for the two test years and across years in the 3k subset of BPH panel.

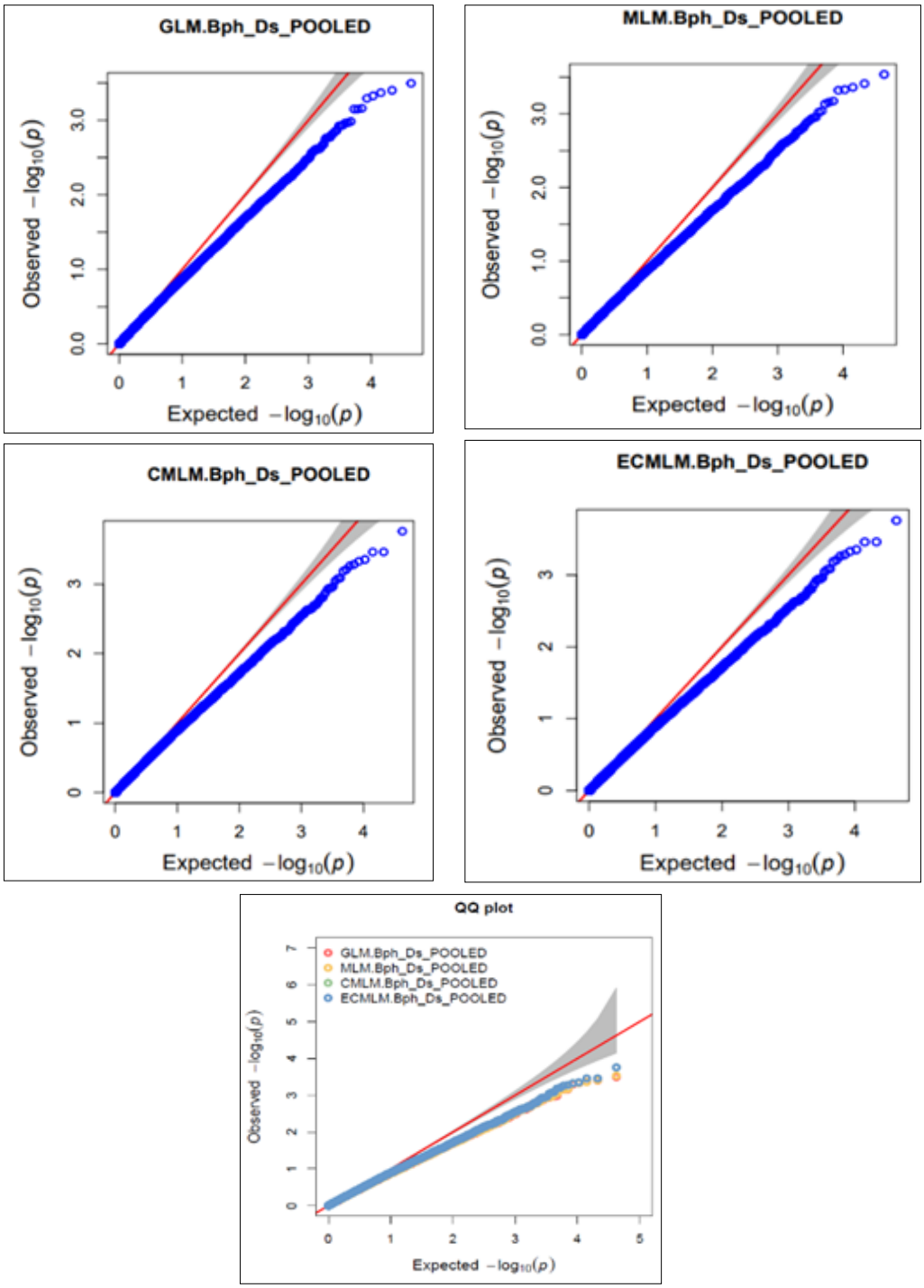


**Fig. 3b.** Quantile-quantile (QQ) plots showing the significant SNP associations ($p < 0.0005$) with BPH damage score for the two test years and across years in the 3k subset of BPH panel.

*bph7, Bph 9, Bph18 (t)* and *Bph21 (t)* (9).

### Identification for candidate genes for resistance based on SNPs

The annotated gene search in the Rice Genome Annotation produced 18 annotated genes associated with 22 Quantitative Trait Nucleotides (QTNs) for BPH damage score.

#### BPH damage score

Chromosome 3 mapped with four genes followed by chromosome 2, 6 and 9 with 2 genes each were noted for BPH damage score. Among the 10 annotated genes, nine were found to have a defense-related functional mechanism (Supplementary Table 4). Genes LOC_Os02g13330.1, LOC_Os03g12890.4, LOC_Os04g53510.1, LOC_Os06g02550.1, LOC_Os07g08140.1, LOC_Os09g14490.1, LOC_Os10g03570.1, LOC_Os11g47350.1 and LOC_Os12g37970.3 represent stress responsive proteins *i.e.,* bet v I allergen family protein, putative, expressed; aminotransferase domain containing protein, OsFBL20 - F-box domain and LRR containing protein; CPuORF21 - conserved peptide uORF-containing transcript, heat stress transcription factor, TIR-NBS type disease resistance protein, RGH1A, putative, expressed, beta -D-xylosidase and MYB family transcription factor, respectively. Thirteen casual QTNs (S2_7110876, S3_6945974, S4_31878608, S4_31880156, S6_882997, S7_4124723, S9_8567719, S10_1540826, S11_28483649, S11_28779832, S11_ 27393603, S11_26042091 and S12_23324406) were associated with these genes. The gene LOC_Os03g12890.4 on chromosome 3 linked to S3_6945974 encodes a protein known as a stress associated protein (SAP). A gene LOC_Os04g53510.1 on chromosome 4 associated with S4_31878608 and S4_31880156 was found to encode a stress responsive gene OsFBL20-F-box domain and LRR containing protein.

A gene LOC_Os06g02550.1 is associated with QTN S6_882997 among 18 annotated genes identified on chromosome 6 which is located 0.4 Mb upstream from *Bph3*, encoding conserved peptide uORF (CPuORF21), a rare subset of upstream open reading frames (uORFs), conditionally regulate translation by ribosome stalling in a range of specific conditions such as intracellular metabolite levels, abiotic and biotic stresses (34). Ribosomal proteins have numerous activities and regulate differently during stress.

The higher expression of ribosomal proteins is important for proper functioning of several house-keeping genes during the stress conditions (35) and the QTNs associated with such proteins could be useful for BPH resistance. On chromosome 6 a significant QTN, S6_30493056 is mapped in the genic locations of LOC_Os07g08140.1 encoding zinc finger, C3HC4 type, domain containing protein regulate during plant stress response.

A gene LOC_Os09g14490.1 associated with QTN S9_8567719 on chromosome 9, encodes a protein known as a TIR-NBS type disease resistance protein. Most characterized R genes encode products that contain a nucleotide-binding site (NBS) and a series of leucine rich repeats (LRRs). NBS grouped into two major types one encodes an N-terminal Toll/ Interleukin-1 receptor (TIR) homology region; members of this class are called TIR NBS-LRR or TNL genes. The second type of NBS-LRR gene does not encode a TIR (the so-called non-TIR NBS-LRR or non- TNL genes) and their products commonly have a coiled-coil (CC) domain in the N terminal region, so these genes are called CC NBS-LRR or CNL genes**.**

A gene LOC_Os12g37970.3 associated with QTN S12_23324406 on chromosome 12 which lies within the region of BPH genes (*Bph9, Bph10, Bph18 (t), Bph21 (t), Bph2/Bph26*) encodes the MYB family transcription factor. These transcription factors participate in a stress-tolerance pathway that may contribute to BPH resistance. *Bph9, Bph18* and *Bph26* on chromosome 12 (36-38) and *Bph14* on chromosome 3 were identified to encode proteins, namely, coiled-coil, nucleotide-binding-site and leucine-rich repeat (CC-NBS-LRR). Two resistance genes were discovered, *Bph25* and *Bph26*, on chromosomes 6S and 12L of the indica rice variety ADR52 (39).

Allelic status of the significant QTNs that contribute to resistance in the 3k subset of BPH (IRGC 126266 and IRGC 128206) are presented in (Table 4) for BPH damage score. These two genotypes IRGC 126266 and IRGC 128206 could be used as new sources of resistance in the breeding programs as well as to explore downstream genes in genetic studies.

## Discussion

The enhancement of rice productivity faces serious threats due to frequent rise in population, detrimental consequences of climate change, as well as BPH outbreaks. The phenotypic field screening of 300 rice genotypes (*i.e*., 3k subset panel of BPH) along with eight checks was carried out during wet season over two years 2020 and 2021 to identify novel BPH resistant donor lines. The study found that out of 300 entries, only three entries *viz.,* IRGC 126266, IRGC 128206 and IRGC 132236 registered resistant reaction. Similar findings were reported earlier while evaluating 178 entries for resistance against BPH under natural infestation and reported that only 5 genotypes were resistant to brown planthopper (40). Several workers have reported PTB 33 as resistant to BPH and used as resistant check (41-43) which was in concordance with the poly house study of this experiment. There observed a prolonged period of nymphal development on resistant and moderately resistant rice genotypes compared to susceptible check. This would ultimately lead to reduced number of generations on the resistant genotypes. The prolonged development on resistant and moderately resistant rice genotypes was reported (44), which might be due to inadequate feeding on the resistant host plants by nymphs leading to slower development.

The current study revealed that, the rice genotypes with the lowest growth index had a significant degree of antibiosis at different phases of BPH growth. Resistant rice genotypes with antibiosis mechanism of resistance exhibited lower growth index compared to susceptible check, TN1 (44). The number of days required to wilt was more in resistant and moderately resistant lines than susceptible check, TN1 due to presence of higher level of tolerance (45).

Through GWAS analysis in 3k subset panel of BPH identified 28 SNPs on different rice chromosomes through four association mapping models for BPH damage score. There noticed 3 SNPs spanning a region of 2.2 to 6.9 Mb on a short arm of chromosome 3. It is to be noted that the short arm of chromosome 3 was earlier mapped for the gene *Bph13*

(t) reported in IR 54745-2-21 (*O. officinalis)* (33).

The co-localization of important SNPs around known resistance gene sites revealed how the founder lines have descended (7). The gene LOC_Os03g12890.4 encodes a protein known as a SAP. SAPs are zinc-finger proteins with the A20/AN1 domain that can control stress signalling in plants (46). BPH 6 and BPH 34 on chromosome 4 were identified to encode proteins A typical LRR (47). *Bph3,* which was discovered in the Srilankan variety Rathuheenati, has been fine mapped on chromosome 6S between markers RM469 and RM588 (48). A gene LOC_Os09g14490.1 associated with CNL genes encodes a coiled-coil nucleotide binding and leucine-rich repeat (CC-NB-LRR) protein, which is a member of the nucleotide-binding domain, leucine-rich repeat (NLR) protein family. It offers resistance during the seedling and maturation stages. According to sequence comparisons, the gene contains a unique LRR domain that stimulates the SA signaling pathway and causes callose deposition on phloem tissue as well as trypsin inhibitor production, which in turn reduces BPH feeding on host plant (49). A gene LOC_Os12g37970.3 encodes the MYB family transcription factor. The MYB family transcription factor has an important regulatory function in stress response that regulates diverse processes of plant development and metabolism. MYB transcription factors are involved in plant development, secondary metabolism, hormone signal transduction, disease resistance and abiotic stress tolerance (8) These transcription factors participate in a stress-tolerance pathway that may contribute to BPH resistance. *Bph26* map-based cloning revealed a CC-NBLRR protein, like *Bph14* that prevents sucking in phloem sieve elements (50).

Candidate gene analysis for promising entries revealed 9 QTNs for BPH damage score to be associated with stress tolerance genes that would play a significant role in BPH resistance. Through GWAS a significant SNP (LOC_Os06g50370.1) associated at 0.4 Mb away for BPH3 and a SNP (LOC_Os12g37970.3) within the proximal region to BPH21 were found to encode the stress responsive proteins. Most of the BPH-resistant genes detected in rice varieties currently under cultivation do not offer broad spectrum resistance to various BPH populations/biotypes. Therefore, new rice varieties resisting BPH populations derived from diverse genetic sources are essential to build broad spectrum resistance to BPH. This may be accomplished through the adoption of marker-assisted gene pyramiding strategy which expedites the processes of varietal improvement and ensures durable resistance. Identified BPH resistant lines viz., IRGC 126266 and IRGC 128206 could be used as donors for BPH resistance to evolve near isogenic lines or resistant cultivars.

## Conclusion

A BPH subset comprising 300 rice genotypes selected from 3K panel was evaluated to identify the BPH resistant donor lines and results across years identified two lines *viz*., IRGC 126266 and IRGC 128206 with consistent resistant reaction. Mechanism of resistance studies revealed that, among the two promising germplasm, IRGC 126266 exhibited all the three mechanisms of resistance by recording lower honey dew excretion, lower nymphal survival rate, longer nymphal development period, lowest growth index and took more days to wilt compared to the susceptible check, TN1. Further, GWAS analysis identified significant SNPs in proximity with several BPH resistance genes *viz*., *Bph33(t)*, *Bph13(t)*, *Bph6*, *Bph34*, *Bph3*, *Bph4*, *Bph25*, *Bph29*, *Bph32*, *Bph28(t)*, *Bph2*, *Bph26, Bph7, Bph9, Bph18(t)* and *Bph21(t)*. Candidate gene analysis study revealed 9 QTNs associated with stress tolerance genes played a significant role in resisting BPH.

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## Authors' contributions

NRGV, YCM, TKB planned and executed the experiment, performed phenotyping for BPH, GWAS analysis, manuscript preparation. TVJS, AR recorded data, performed GWAS analysis and assisted in manuscript preparation. JH assisted in crop management and data recording. AK conceived the project idea and monitored. VKS, UMS, PS involved in theme development, planning and overall monitoring. SK assisted in technical monitoring of the project and financial sanctions. TSK, GN performed GWAS analyses. RJ monitored the project execution and assisted in editing of manuscript.

## Compliance with ethical standards

**Conflict of interest:** The authors declare no conflict of interest.

**Ethical issues:** None

## References

1. Latif MA, Badsha MA, Tajul MI, Kabir MS, Rafii MY, Mia MA. Identification of genotypes resistant to blast, bacterial leaf blight, sheath blight and tungro and efficacy of seed treating fungicides against blast disease of rice. Scientific Research and Essays. 2011;6(13):2804–11. https://doi.org/10.5897/SRE11.315
2. Sogawa K. Planthopper outbreaks in different paddy ecosystems in Asia: Man-made hopper plagues that threatened the green revolution in rice. Rice planthoppers: Ecology, management, socio economics and policy. 2015;33–63.
3. Balachiranjeevi CH, Prahalada GD, Mahender A, Jamaloddin M, Sevilla MA, Marfori-Nazarea CM, et al. Identification of a novel locus, BPH38 (t), conferring resistance to brown planthopper (*Nilaparvata lugens* Stal.) using early backcross population in rice (*Oryza sativa* L.). Euphytica. 2019;215:1–4. https://doi.org/10.1007/s10681-019-2506-2
4. Phil Rice. Rice: Knowledge Bank: Handout Series. 2020. https://www.philrice.gov.ph/www.pinoyrkb.com/www.pinoyrice.com
5. Chew W, Hrmova M, Lopato S. Role of homeodomain leucine zipper (HD-Zip) IV transcription factors in plant development and plant protection from deleterious environmental factors.

International Journal of Molecular Sciences. 2013;14(4):8122–47. http://doi.org/10.3390/ijms14048122

6. Jena KK, Kim SM. Current status of brown planthopper (BPH) resistance and genetics. Rice. 2010;161–71. https://doi.org/10.1007/s12284-010-9050-y
7. Khush GS, Virk PS, IR V. Their impact. International Rice Research Institute: Los Baños, Philippines. 2005.
8. Katiyar A, Smita S, Lenka SK, Rajwanshi R, Chinnusamy V, Bansal KC. Genome-wide classification and expression analysis of MYB transcription factor families in rice and *Arabidopsis*. BMC Genomics. 2012;13:1–9. http://doi.org/10.1186/1471-2164-13-544
9. Qiu Y, Guo J, Jing S, Zhu L, He G. Fine mapping of the rice brown planthopper resistance gene BPH7 and characterization of its resistance in the 93-11 background. Euphytica. 2014;198:369–79.
10. Joshi RK, Nayak S. Gene pyramiding–A broad spectrum technique for developing durable stress resistance in crops. Biotechnology and Molecular Biology Reviews. 2010;5(3):51–60.
11. Purcell S, Neale B, Todd-Brown K, Thomas L, Ferreira MA, Bender D, et al. PLINK: A tool set for whole-genome association and population-based linkage analyses. The American Journal of Human Genetics. 2007;81(3):559–75. http://doi.org/10.1086/519795
12. Rashid MM, Jahan M, Islam KS, Latif MA. Ecological fitness of brown planthopper (*Nilaparvata lugens* Stal.) to rice nutrient management. Ecological Processes. 2017;6:1–0. http://doi.org/10.1186/s13717-017-0080-x
13. Kommana M, Reddy DM, Amarnath K, Naik MV, Withanawasam DM, Bommisetty R, et al. Identification of genomic regions governing moisture and heat stress tolerance employing association mapping in rice (*Oryza sativa* L.). Molecular Biology Reports. 2023;50(2):1499–515. http://doi.org/10.1007/s11033-022-08153-y
14. Pathak PK, Heinrichs EA. A rapid technique for estimation brown planthopper feeding activity. International Rice Research Newsletter. 1980;5:18–9.
15. Heinrichs EA. Genetic evaluation for insect resistance in rice. International Rice Research Institute. 1985.
16. Pongprasert S, Weerapat P. Varietal resistance to the brown planthopper in Thailand. In: International Rice Research Institute (eds.) Brown Planthopper: Threat to rice production in Asia. International Rice Research Institute, Los Baños, Laguna, The Philippines. 1979;273–82.
17. Panda N, Heinrichs EA. Levels of tolerance and antibiosis in rice varieties having moderate resistance to the brown planthopper, *Nilaparvata lugens* (Stal.) (Hemiptera: Delphacidae). Environmental Entomology. 1983;12(4):1204–14. http://doi.org/10.1093/ee/12.4.1204
18. Aravind J, Mukesh Sankar S, Wankhede DP, Kaur V. Augmented RCBD: Analysis of augmented randomised complete block designs. R package version 0.1. 2020:2.
19. Gomez KA. Statistical procedures for agricultural research. New York: Wiley and Sons. 1984.
20. Pritchard JK, Stephens M, Donnelly P. Inference of population structure using multilocus genotype data. Genetics. 2000;155 (2):945–59. http://doi.org/10.1093/genetics/155.2.945
21. Chepyshko H, Lai CP, Huang LM, Liu JH, Shaw JF. Multifunctionality and diversity of GDSL esterase/lipase gene family in rice (*Oryza sativa* L. *japonica*) genome: New insights from bioinformatics analysis. BMC Genomics. 2012;13:1–9. https://doi.org/10.1186/1471-2164-13-309
22. Alexandrov N, Tai S, Wang W, Mansueto L, Palis K, Fuentes RR, et al. SNP-Seek database of SNPs derived from 3000 rice genomes. Nucleic Acids Research. 2015;43(D1):1023–7. https://doi.org/10.1093/nar/gku1039
23. Price AL, Patterson NJ, Plenge RM, Weinblatt ME, Shadick NA, Reich D. Principal components analysis corrects for stratification in genome-wide association studies. Nature Genetics. 2006;38 (8):904–9. http://doi.org/10.1038/ng1847
24. Zhao C, Zhu M, Guo Y, Sun J, Ma W, Wang X. Genomic survey of PEBP gene family in rice: identification, phylogenetic analysis and expression profiles in organs and under abiotic stresses. Plants. 2022;11(12):1576. http://doi.org/10.3390/plants11121576
25. Li M, Liu X, Bradbury P, Yu J, Zhang YM, Todhunter RJ, et al. Enrichment of statistical power for genome-wide association studies. BMC Biology. 2014;12:1–10. http://doi.org/10.1186/s12915-014-0058-4
26. Liu Y, Wu H, Chen H, Liu Y, He J, Kang H, et al. A gene cluster encoding lectin receptor kinases confers broad-spectrum and durable insect resistance in rice. Nature Biotechnology. 2015;33 (3):301–5. http://doi.org/10.1038/nbt.3069
27. Naik SB, Divya D, Sahu N, Sundaram RM, Sarao PS, Singh K, et al. A new gene Bph33 (t) conferring resistance to brown planthopper (BPH), *Nilaparvata lugens* (Stal.) in rice line RP2068-18-3-5. Euphytica. 2018;214:1–2. http://doi.org/10.1007/s10681-018-2131-5
28. Qiu Y, Guo J, Jing S, Zhu L, He G. High-resolution mapping of the brown planthopper resistance gene Bph6 in rice and characterizing its resistance in the 9311 and Nipponbare near isogenic backgrounds. Theoretical and Applied Genetics. 2010;121:1601–11. http://doi.org/10.1007/s00122-010-1413-7
29. Kumar K, Sarao PS, Bhatia D, Neelam K, Kaur A, Mangat GS, et al. High-resolution genetic mapping of a novel brown planthopper resistance locus, Bph34 in *Oryza sativa* L. × *Oryza nivara* (Sharma & Shastry) derived interspecific F2 population. Theoretical and Applied Genetics. 2018;131:1163–71. http://doi.org/10.1007/s00122-018-3069-7
30. Wang Y, Cao L, Zhang Y, Cao C, Liu F, Huang F, et al. Map-based cloning and characterization of BPH29, a B3 domain-containing recessive gene conferring brown planthopper resistance in rice. Journal of Experimental Botany. 2015;66(19):6035–45. https://doi.org/10.1093/jxb/erv318
31. Ren J, Gao F, Wu X, Lu X, Zeng L, Lv J, et al. Bph32, a novel gene encoding an unknown SCR domain-containing protein, confers resistance against the brown planthopper in rice. Scientific Reports. 2016;6(1):37645. https://doi.org/10.1038/srep37645
32. Wu H, Liu Y, He J, Liu Y, Jiang L, Liu L, et al. Fine mapping of brown planthopper (*Nilaparvata lugens* Stal.) resistance gene Bph28 (t) in rice (*Oryza sativa* L.). Molecular Breeding. 2014;33:909–18. https://doi.org/10.1186/s12284-016-0099-0
33. Huang X, Zhao Y, Wei X, Li C, Wang A, Zhao Q, et al. Genome-wide association study of flowering time and grain yield traits in a worldwide collection of rice germplasm. Nature Genetics. 2012;44 (1):32–9. https://doi.org/10.1038/ng.1018
34. Causier B, Hopes T, McKay M, Paling Z, Davies B. Plants utilize ancient conserved peptide upstream open reading frames in stress-responsive translational regulation. Plant, Cell and Environment. 2022;45(4):1229–41. https://doi.org/10.1111/pce.14173
35. Ferreira-Cerca S, Hurt E. Cell biology: Arrest by ribosome. Nature. 2009;459:46–7.
36. Zhang Z, Ersoz E, Lai CQ, Todhunter RJ, Tiwari HK, Gore MA, et al. Mixed linear model approach adapted for genome-wide association studies. Nature Genetics. 2010;42(4):355–60. http://doi.org/10.1038/ng.546
37. Ji H, Kim SR, Kim YH, Suh JP, Park HM, Sreenivasulu N, et al. Map-based cloning and characterization of the BPH18 gene from wild rice conferring resistance to brown planthopper (BPH) insect pest. Scientific Reports. 2016;6(1):34376. https://doi.org/10.1038/srep34376
38. Sun L, Liu Y, Jiang L, Su C, Wang C, Zhai H, et al. Identification of quantitative trait loci associated with resistance to brown planthopper in the indica rice cultivar Col. 5 Thailand. Hereditas. 2007;144(2):48–52. https://doi.org/10.1111/

j.2006.0018-0661.01932.x

39. Myint KK, Fujita D, Matsumura M, Sonoda T, Yoshimura A, Yasui H. Mapping and pyramiding of two major genes for resistance to the brown planthopper (*Nilaparvata lugens* Stal.) in the rice cultivar ADR52. Theoretical and Applied Genetics. 2012;124:495–504. http://doi.org/10.1007/s00122-011-1723-4

40. Tanweer FA, Rafii MY, Sijam K, Rahim HA, Ahmed F, Latif MA. Current advance methods for the identification of blast resistance genes in rice. Comptes Rendus Biologies. 2015;338(5):321–34. http://doi.org/10.1016/j.crvi.2015.03.001

41. Wang HY, Yang Y, Su JY, Shen JL, Gao CF, Zhu YC. Assessment of the impact of insecticides on *Anagrus nilaparvatae* (Pang et Wang) (Hymenoptera: Mymanidae), an egg parasitoid of the rice planthopper, *Nilaparvata lugens* (Hemiptera: Delphacidae). Crop Protection. 2008;27(3–5):514–22. https://doi.org/10.1016/j.cropro.2007.08.004

42. Sable MG, Rana DK. Donor validation studies on rice differential varieties against rice brown planthopper, *Nilaparvata lugens* (Stal.). International Journal of Plant Protection. 8(1):30–3.

43. Vincelli P. Genetic engineering and sustainable crop disease management: opportunities for case-by-case decision-making. Sustainability. 2016;8(5):495. http://doi.org/10.3390/su8050495

44. Sable A, Suresh S, Kumar SM. Survival and population buildup of brown planthopper *Nilaparvata lugens* (Stal.) on selected rice genotypes. Trends in Biosciences. 2014;7(13):1599–602.

45. Bhanu KV, Lakshmi VJ, Katti G, Reddy AV. Antibiosis and tolerance mechanisms of resistance in rice varieties carrying brown planthopper resistance genes. 2014:108-14.

46. Kothari KS, Dansana PK, Giri J, Tyagi AK. Rice stress associated protein 1 (OsSAP1) interacts with aminotransferase (OsAMTR1) and pathogenesis-related 1a protein (OsSCP) and regulates abiotic stress responses. Frontiers in Plant Science. 2016;7:1057. https://doi.org/10.3389/fpls.2016.01057

47. Guo J, Xu C, Wu DI, Zhao Y, Qiu Y, Wang X, et al. Bph6 encodes an exocyst-localized protein and confers broad resistance to planthoppers in rice. Nature Genetics. 2018;50(2):297–306. https://doi.org/10.1038/s41588-018-0039-6

48. Jairin J, Teangdeerith SN, Leelagud P, Phengrat K, Vanavichit A, Toojinda T. Physical mapping of Bph3, a brown planthopper resistance locus in rice. Maejo International Journal of Science and Technology. 2007;1(2):166–77.

49. Du B, Zhang W, Liu B, Hu J, Wei Z, Shi Z, et al. Identification and characterization of Bph14, a gene conferring resistance to brown planthopper in rice. Proceedings of the National Academy of Sciences. 2009;106(52):22163–8. https://doi.org/10.1073/pnas.0912139106

50. Tamura Y, Hattori M, Yoshioka H, Yoshioka M, Takahashi A, Wu J, et al. Map-based cloning and characterization of a brown planthopper resistance gene BPH26 from *Oryza sativa* L. ssp. *indica* cultivar ADR52. Scientific Reports. 2014;4(1):5872. https://doi.org/10.1038/srep05872

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