The distribution and identification of brown planthopper resistance genes in rice

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A collection of 515 rice landraces originating from Vietnam and China were screened for the reaction to brown planthopper (BPH) infestation. Most of the resistant landraces were *indica* types from Vietnam and the Guangxi province in China. An F_2 mapping population was created from the cross between a BPH resistant Vietnamese landrace Yagyaw and the susceptible cultivar Cpslo17. Four quantitative trait loci (QTL) contributing to BPH resistance were mapped on chromosomes 2, 4, 7 and 9, respectively. The individual QTL accounted 5.64% to 12.77% of the phenotypic variance, and three resistant alleles were harbored in the resistant landrace Yagyaw. Two QTL located on chromosomes 2 and 4 were identified with significant additive effects and are useful in breeding new rice inbred lines. One resistant allele was harbored by the susceptible parent Cpslo17. This gene is important in selecting rice inbred lines with stronger resistances to BPH.

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The brown planthopper (abbreviated as BPH), *Nilaparvata lugens* Stål, is one of the most destructive insect pests of rice (*Oryza sativa* L.) throughout Asian rice-growing countries. The plant suffers direct damage from the sucking of sap, which if severe, can result in 'hopperburn'. More seriously, however, is that BPH acts as the vector of both the rice grassy stunt (Rivera et al. 1966) and rugged stunt (Ling et al. 1978) viruses. Chemical control of BPH is commonly practiced, but is both costly and harmful to the environment. The use of genetically resistant cultivars has proven to be more economical, efficient and environmentally friendly means to control this pest. The genetic basis of BPH resistance has been widely explored, and 19 single major resistance genes and several quantitative trait loci (QTL) have to date been identified in screens of ssp. *indica* and the four wild relatives, *O. australiensis*, *O. eichingeri*, *O. latifolia* and *O. officinalis.* (Yang et al. 2004; Chen et al. 2006; Sun et al. 2005, 2007, Su et al. 2005; Jena et al. 2006; Jairin et al. 2007).

The south and southeast Asian BPH population has been classified into four biotypes, based on pathogenicity. Biotypes 1 and 2 are prevalent in southeast Asia, biotype 3 is a laboratory strain produced in the Philippines, while biotype 4, the most destructive of all, is distributed across the Indian subcontinent (Heinrichs 1986). Due to the capacity of BPH to vary with respect to pathogenicity, genetic resistance based on some major genes has been short-lived (Gallagher et al. 1994; Ketipearachchi et al. 1998).

Consequently, the exploitation of quantitative resistance has been suggested as a better way of achieving durable resistance (Heinrichs 1986; Bosque-perez and Buddenhagen 1992). Multiple resistance genes from different origins could be piramidalyzed within a single cultivar, using marker assisted selection (MAS) to include the individual components of resistance. New sources of genetic resistance are necessary to increase the bases of durable resistance. Thus the objective of the present study was to study the distribution of BPH resistance in landrace materials, and to characterize some of these novel sources of resistance.

MATERIAL AND METHODS

Plant material

A collection of 515 rice landraces originating from Vietnam and China was screened for reaction to BPH infestation. The cultivars Rathu Heenati (carrying *Bph3,* Lakshshminarayana and Khush 1977) and Taichung Native 1 (no known resistance genes) were used as resistant and susceptible controls. The cultivars IR36, Guichao 2 and Nanjing11 were chosen as

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representative of *indica*, and Guihuahuang, Akihikari and Balila of *japonica* germplasm. To map the BPH resistance of the Vietnamese landrace Yagyaw (YA), a mapping population of 180 F_2 plants was created from a cross with the wide-compatibility susceptible cultivar Cpslo17. Each F_2 individual was self-fertilized to obtain a set of 180 $F_{2:3}$ lines.

Evaluation of BPH resistance

The screening of resistance resource was conducted both in greenhouse and field. Evaluation of $F_{2:3}$ lines' BPH resistance was performed only in greenhouse. Landrace seeds were sown in an experimental field of Nanjing Agricultural University, with each landrace being planted as a single 10-row plot with 10 plants in each row. At the third leaf stage, each seedling was infested with BPH nymphs collected in rice fields at the Nanjing Agricultural University.

For evaluation of BPH resistance in greenhouse, BPH were collected from rice fields in Hang Zhou (China). The population included both biotype 1 and 2, maintained on the susceptible cultivar Taichung Native 1, under non-controlled greenhouse conditions at Nanjing Agricultural University. A seedling bulk test, modified slightly from that described by Athwal et al. (1971), was conducted to test plant reaction to BPH infestation. To ensure that all seedlings reached the equivalent growth stage before being exposed to infestation, the materials were pre-germinated in petri dishes. Approximately 25 landrace seeds and $F_{2:3}$ seeds per F_2 individual were sown in 10 cm diameter pots, which were placed in a large box, at the base of which about 2 cm water was maintained throughout the evaluation period. Pots of control genotypes were included in each box. Seven days after sowing, seedlings were thinned to 20 per pot. At the third leaf stage, each seedling was infested with ten 2nd or 3rd instar BPH nymphs. Once all the Taichung Native 1 seedlings had died, the test material was assigned a numerical score between 0 and 9, following standard criteria (Athwal et al. 1971; Irri 1988; Huang et al. 2001). The resistance reaction of each F_2 plant was inferred from the mean performance of its F_3 progeny. There were four replicates for each cultivar and line.

DNA preparation and SSR analysis

DNA was extracted from seedling leaves following Dellaporta et al. (1983). The extracted DNA was spectrophotometrically assayed for its quality and quantity using a MBA 2000 UV/VIS spectrometer (Perkin Elemer Co.). Every sample was diluted to a concentration of 20 ng μl^{-1}. SSR analysis was performed following the procedure of Chen et al. (1997). The characteristics of the SSR markers are detailed in the Gramene database (http://www.gramene.org/) and McCouch et al. (2002). Seven loci were used to perform the cluster analysis (Ni et al. 2002) (Table 2). Amplicons were separated by 8% non-denaturing PAGE, and visualised by silver staining (Sanguinetti et al. 1994).

Cluster analysis

Seven loci were used to perform the cluster analysis (Ni et al. 2002).The presence and absence of the SSR bands by the seven pair primers were scored as the genotypes of 515 rice landraces. And the data were entered into a binary matrix as discrete variables, 1 for presence and 0 for absence of the character and this data matrix was subjected to further analysis (Ni et al. 2002). The 0/1 matrix was used to calculate similarity as DICE coefficient using SIMQUAL subroutine in SIMILARITY routine. The resultant similarity matrix was employed to construct dendrograms using sequential agglomerative hierarchical nesting (SAHN) based unweighted pair group method with arithmetic means (UPGMA) to infer genetic relationships and phylogeny. Only 40 resistant or moderately resistant landraces were used for cluster analysis. The lines consisted of 37 landraces of *indica* type and three (all only moderately resistant) of *japonica* types.

Linkage map building and QTL mapping of BPH resistance

The linkage groups and the marker order were determined using MAPMAKER/EXP 3.0 (Lander et al. 1987), and the Kosambi mapping function was used to transform recombination frequencies to genetic distances in cM. Additive and dominance QTL in the F_2 population were detected by the inclusive composite interval mapping (ICIM) (Li et al. 2007; Zhang et al. 2008), implemented in the integrated software QTL IciMapping (freely available from http://www.isbreeding.net). In the first step of ICIM, a probability value for entering variables (PIN) of 0.01, and a probability value for removing variables (POUT) of 0.02 were used to select the significant markers, and in the second step a threshold LOD of 3.0 was used to declare the significant QTL.

RESULTS

The distribution of landraces resistant to BPH

Among the landrace collection, none was highly resistant to BPH (score 0), 23 were resistant (score 1 or 3) and 32 moderately resistant (score 5) (Table 1). The resistant and moderately resistant type occurred at a frequency of 18.0% and 18.4%, respectively, in the

Table 1. *The distribution of landraces from five regions for seedling resistance to BPH infestation.*

Localities	Latitude and longitude	Number of landrace[a]						Total
		0	1	3	5	7	9	
Taihu region, China	30° ~32°N, 107°122′E	0	0	0	3	12	87	102
Yunnan, China	24°37′ ~29°13′N, 103°37′ ~109°32′E	0	1	1	4	10	86	102
Guizhou, China	21°08′ ~29°15′N, 97°32′ ~106°12′E	0	2	5	7	52	69	135
Guangxi, China	20°54′ ~26°23′N, 104°29′ ~112°E	0	1	2	11	25	37	76
Vietnam	8°30′ ~23°22′N, 100°30′ ~102°10′E	0	4	7	7	10	72	100
Total		0	8	15	32	109	351	515

[a]0 highly resistant; 1 and 3 resistant; 5 moderately resistant; 7 and 9 susceptible.

landraces from Vietnam and the Guangxi province (Fig. 1). Ten point four percent of the landraces from Guizhou, and 5.9% of those from the Yunnan provinces, showed score 1 to 5 (Table 1), while just three of the entries (2.9%) from the Taihu Region of China had a moderate level of resistance (Table 1, Fig. 1).

Cluster analysis

Forty resistant or moderately resistant landraces evaluated both in field and greenhouse, with clear bands amplified respect to seven SSR loci (Table 2), were selected to cluster analysis. Allele number per locus ranged from 2 to 11 (mean 6.7) and a total of 47 isogenes was found in these varieties. On the basis of SSR genotype, the *indica* group fell into three classes (Fig. 2), suggesting the presence of considerable genetic variability in the genetic basis of BPH resistance among landraces.

Mapping of BPH resistance

The resistance scores of YA and Cpslo17 were 2.9 and 8.9, respectively (Table 3). The resistance level in their F_2 population ranged from 0 to 9, with three peaks in the distribution around 2, 5 and 9 (Fig. 3). From a set of 551 SSR loci surveyed, 157 were informative between YA and Cpslo17. A linkage map consisting of 117 of these loci, proportionally distributed on chromosomes, was constructed from the YA × Cpslo17 F_2 population. The map covered 1389.9cM (mean inter-marker distance 11.9cM), involving all 12 chromosomes. The order of 110 of the 117 mapped loci was consistent with those previously reported by Temnykh et al. (2000) and McCouch et al. (2002).

The one-dimensional scanning of ICIM along the 12 rice chromosomes (scanning step = 1 cM) demonstrated four clear peaks higher than the LOD threshold 3.0 on the LOD profile (Fig. 4A). Thus, four

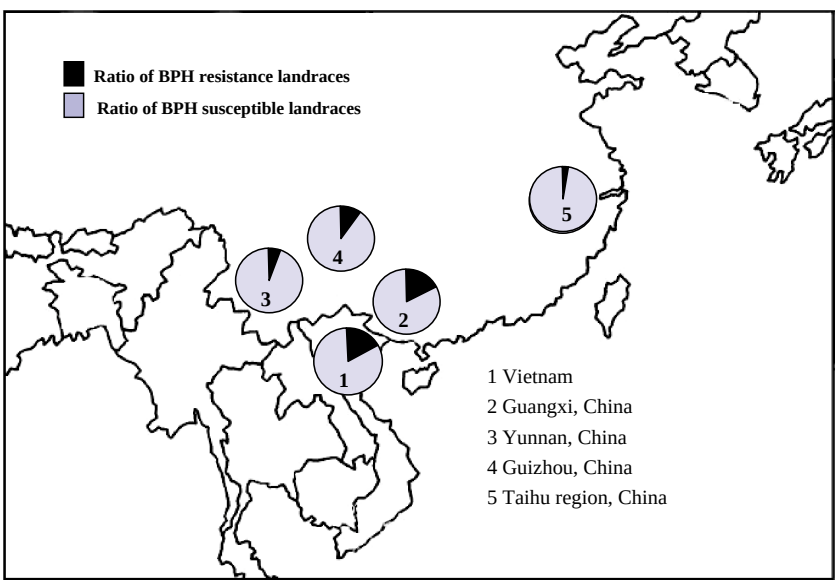

Fig. 1. Geographical distribution of BPH resistance in a collection of landraces.

Table 2. *SSR markers diagnostic for the indica and japonica rice subspecies.*

Marker name	Chromosome	Forward primer	Reverse primer
RM245	9	atgccgccagtgaatagc	ctgagaatccaattatctgggg
RM271	10	tcagatctacaattccatcc	tcggtgagacctagagagcc
RM160	9	agctagcagctatagcttagctggagatc	tctcatcgccatgcgaggcctc
RM156	3	gccgcaccctcactccctcctc	tcttgccggagcgcttgaggtg
RM130	3	tgttgcttgccctcacgcgaag	ggtcgcgtgcttggtttggttc
RM240	2	ccttaatgggtagtgtgcac	tgtaaccattccttccatcc
RM262	2	cattccgtctcggctcaact	cagagcaaggtggcttgc

quantitative trait loci (QTL) contributing to BPH resistance were mapped on chromosomes 2, 4, 7 and 11, respectively, and individual QTL accounted 5.5% to 16.7% of the phenotypic variance. *Qbph-2* was flanked by *RM5529* and RM1358, and located on the telomeric of chromosome 2, explaining 9.18% of the phenotypic variation. *Qbph-4* was flanked by *RM401* and RM335, and located on the telomeric of chromosome 4, explaining 12.77% of the phenotypic variation. *Qbph-7* was flanked by *RM542* and RM500, and located on chromosome 7, explaining 6.30% of the phenotypic variation. *Qbph-9* was flanked by *RM3533*

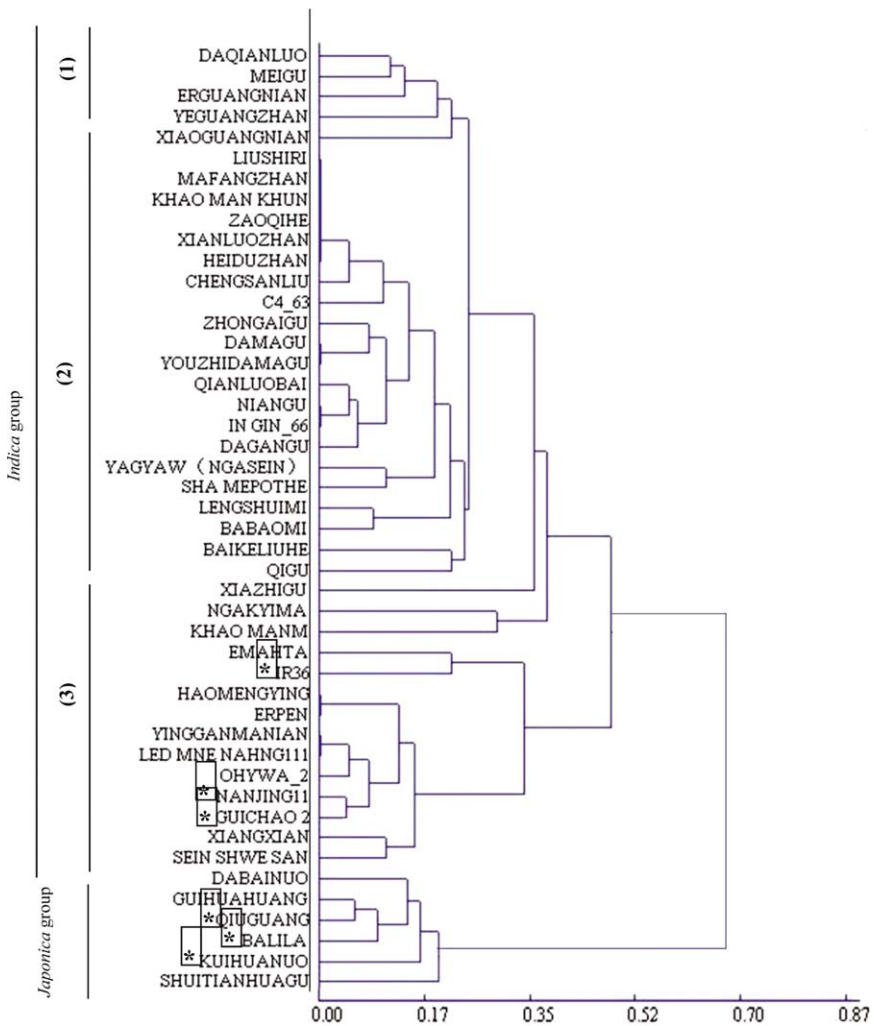

Fig. 2. Cluster that represents the genetic diversity of 40 BPH resistant landraces based on their genotype at 47 SSR loci. "*" represent *indica* check, *japonica* check, (1), (2), and (3) three sub-clusters within the *indica* group.

Table 3. *BPH resistance score of check varieties and mapping parents.*

Variety[a]	Number of seedlings tested	Resistance score (0–9)	Significance*
Taichung Native	60	9	A
Cpslo17	60	8.9	A
YA	60	2.9	B
Rathu Heenati	60	0	C

[a]RH and TN1 were used as the control cultivars for, respectively, resistance and susceptibility.
*p = 0.01.

and RM242, and located on chromosome 9, explaining 5.64% of the phenotypic variation. *Qbph-4* explains the largest phenotypic variation (Table 4).

The first three QTL, i.e. *Qbph-2*, *Qbph-4* and *Qbph-7*, have negative additive effects (Table 4, Fig. 4B), indicating that the three resistant alleles were harbored in the resistant landrace Yagyaw. The last one, i.e. *Qbph-9*, has a positive additive effect, indicating the resistant allele was harbored in the susceptible cultivar Cpslo17. The disperse of resistance alleles in the two parents also gives a reasonable explanation of the transgressive segregation shown in Fig. 3. *Qbph-2* and *Qbph-4* were identified with significant additive effects (Table 4, Fig. 4B) and therefore are useful gene sources in breeding new rice inbred lines. *Qbph-7* has smaller additive effect, and was not resistant to BPH in the heterogeneous stage due to its positive dominance effect (Table 4, Fig. 4B). This QTL might be not very useful in rice breeding. The resistant allele at *Qbph-7* was harbored by the susceptible parent Cpslo17, due to the positive additive effect. Such gene is important in selecting rice inbred line with stronger resistances to BPH.

DISCUSSION

The frequency damaged on rice production by BPH infestation, has driven the search for new sources of genetic resistance (Bosque-perez and Buddenhagen 1992). Non-durability of many of the major resistance genes due to changes in the pest biotype (Gallagher et al. 1994; Ketipearachchi et al. 1998) remains a problem. IR26, released in 1973, was the first cultivar specifically bred for BPH resistance. It harbors *Bph-1*, a gene that was overcome within two years of the widespread use of the variety. This pattern of rapid breakdown of resistance was repeated by cultivars harboring *bph-2* or *Bph-3*. It has been suggested that quantitative resistance may be more durable than that determined by major genes (Heinrichs 1986; Bosque-perez and Buddenhagen 1992), but these genes are more difficult to handle in a breeding program. Their tagging with markers, however, would allow for the possibility of resistance gene stacking, a strategy that should improve the stability of the resistance.

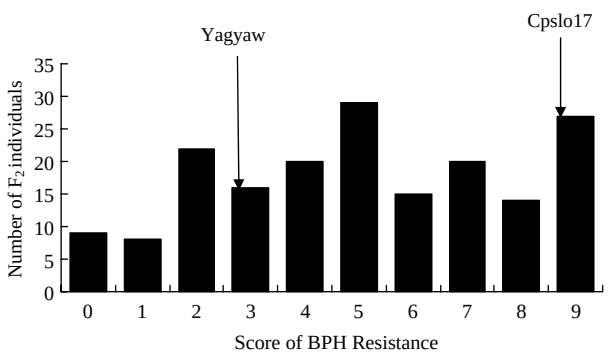

Fig. 3. The frequency distribution of BPH-resistant $F_{2:3}$ lines derived from the cross between YA × Cpslo17, a BPH resistant variety and a susceptible cultivar, respectively.

The brown planthopper is a migratory insect, surviving the winter in northern Vietnam and migrating into southern China in the spring. Thereafter, they gradually move north into central China, Korea and Japan. Sources of host resistance are often associated with the origin of a disease or pest species, and the majority of the resistant landraces in the present screen indeed originate from Vietnam and the Guangxi province. BPH resistance has been reported to be rare in *japonica* germplasm, however it has been found in *indica* types and in certain wild relatives (Cheng et al. 2003). Consistent with this generalization, in the present landrace collection only three moderately resistant entries were found on the *japonica* type. The results further strengthen the viewpoint above.

To investigate the genetic base of Vietnam resistance rice variety, we constructed a framework of linkage map with an F_2 population from a cross of a Viet local resistant cultivar Yagyaw (UGASEIN) and a susceptible cultivar Cpslo17, with wide compatibility to further analyze the BPH resistance gene. It is of interest to compare the four BPH resistance QTLs identified in YA with genes/QTL for BPH resistance already reported in the literature. *Qbph-4* was mapped to the short arm of chromosome 4 at a similar location as those reported by Sun et al. (2005) and Yang et al. (2004) in other genetic

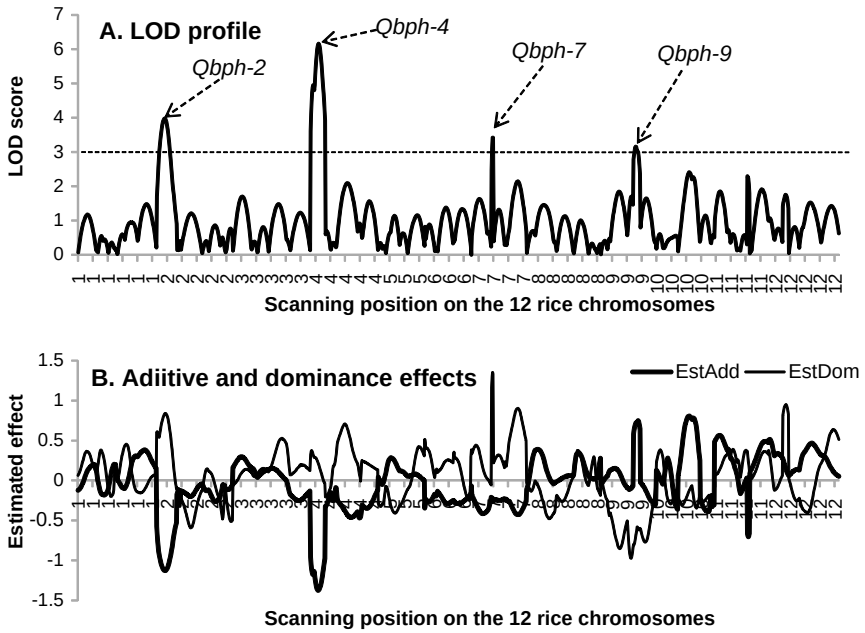

Fig. 4. The one-dimensional scanning of ICIM on the 12 rice chromosomes for mapping QTL affecting BPH. The scanning step was set at 1 cM. A, LOD profile; B, estimated additive and dominance effects.

backgrounds. The location of *Qbph-11* also coincides with that of a major BPH resistance gene detected by Su et al. (2005). *Qbph-7* mapped to a similar location as that reported by Xu et al. (2002). No BPH resistance has been mapped to date, however, on the short arm of chromosome 2, which is the location of *Qbph*-2. This locus appears therefore to represent a novel source of BPH resistance. To utilize the *Qbph-2*, the introgression line carried *Qbph-2* is being bred by backcross and marker-associated selection. Further studies are going on with objectives to fine-map the four identified QTL, and to develop gene-based markers. Genotyping of the resistant landraces using the QTL-flanking markers (Table 4) is also ongoing. Then we will be able to know the distribution of the four identified QTL in the collection of landraces. However, it is very likely that some novel resistant genes are present in other resistant or even susceptible parents.

The use of resistant cultivars has proven to be one of the most efficient ways to reduce the economic damage caused by BPH. However the interaction between host resistance and the insect is quite similar to the gene-for-gene system common in plant host resistance against fungal and bacterial pathogens, since BPH appears able to effectively overcome single host resistance genes under natural conditions. Thus there is a continuing requirement for new sources of resistance. Pyramiding multiple resistance genes within the same cultivar may increase the durability of resistance. Several of the F_2 individuals harboring three of the four QTLs showed, as expected, a higher level of resistance than that with single QTL (data not shown). The linkage information in the current study

Table 4. *QTL associated with the resistance to BPH identified in the F_2 population derived from the Cross YA × Cpslo17.*

QTL	Interval	Chromosome	LOD score	PVE(%)[a]	Additive effect	Dominance effect
Qbph-2	*RM5529-RM1358*	2	3.98	9.18	−1.13	0.84
Qbph-4	*RM401-RM335*	4	6.16	12.77	−1.37	0.21
Qbph-7	*RM542-RM500*	7	3.42	6.30	−0.25	1.35
Qbph-9	*RM3533-RM242*	9	3.16	5.64	0.71	−0.72

[a]percentage of phenotypic variance explained.

between SSR markers and the BPH resistance QTL provides the necessary tools to undertake marker-assisted selection for BPH resistance in rice.

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