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THE GENETIC ASSOCIATIONS BETWEEN YIELD COMPONENT TRAITS AND BACTERIAL LEAF BLIGHT RESISTANCE IN RICE (*O. SATIVA L.*)

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ABSTRACT

Bacterial leaf blight (BLB) caused by *Xanthomonas oryzae pv. oryzae* (*Xoo*) is highly destructive to high-yielding susceptible rice cultivars. In severe epidemics, yield losses up to 75% have been reported. Considerable information on BLB resistant genes is available; however, genetic overlaps between BLB resistant and yield related traits largely remain unclear. Using two sets of backcross introgression inbred lines and one set of recombinant inbred lines, genetic associations between bacterial leaf blight resistance and yield component traits in three *Xoo* races were analyzed using Single Nucleotide polymorphism (SNP) markers. Fifteen quantitative trait loci conferring BLB resistant and 112 QTLs for yield and yield related traits were detected. Among 15 QTLs conferring bacteria leaf blight resistance, 14 QTLs overlapped with 39 QTLs for yield and yield related traits. The total resistance variation explained by additive QTLs (R^2) ranged between 5-76% and epistasis QTLs ranged between 1-26%. Quantitative trait loci (QTLs) with the highest additive effects for BLB resistance were detected at positions os04-17305294 (on chr.4), os05-07310209 (on chr.5), os09-15240130 (on chr.9), os11-28421947 (on chr.11) and os12-25291547(on chr.12). The BLB resistance QTL at position os05-07310209 (on chr.5) overlapped with QTLs for 1000-grain weight, grain number per panicle, days to heading, grain length width ratio and grain yield per plant. The BLB resistance QTL at position os09-15240130 (on chr.9) overlapped with QTLs for grain yield per plant, panicle number, grain width and 1000-grain weight. The BLB resistance QTL at position os12-25291547-(on chr.12) overlapped with QTLs for 1000-grain weight, panicle number, grain yield per plant, filled grain number and grain width. Eleven percent of the 717 plants in this study were resistant to at least two *Xoo* races and had higher grain yield compared to both recurrent parents. Overlapping regions especially with already cloned genes and epistasis detected in this study offer opportunity to develop rice varieties which combine high yield and resistance to bacteria leaf blight.

Key words: Bacterial blight, Epistasis QTL, overlapping regions, Trait correlation, Yield related trait

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INTRODUCTION

Bacterial leaf blight (BLB) is a rice disease caused by pathogen *Xanthomonas oryzae pv. oryzae (Xoo)*. The disease can be managed by antibiotics [1], copper compounds, genetic engineering and incorporating durable resistance into improved rice varieties [2-5]. The suppression of Auxine Biosynthesis in Rice has also been reported to increase Resistance to Bacterial Leaf Blight [6]. So far, 40 BLB resistance genes (R) conferring host resistance against various strains of *Xoo* have been identified [7]. Nine of these genes (Xa^{21}, Xa^{23}, $Xa^{27(t)}$, Xa^{29}, Xa^{30}, Xa^{32}, xa^{32}, Xa^{35} and Xa^{36} are from wild rice [8]. Six genes have physically been mapped (Xa^{2}, Xa^{4}, Xa^{7}, Xa^{30}, Xa^{33} *and* Xa^{38}) and other six have been cloned (Xa^{1}, xa^{5}, xa^{13}, Xa^{21}, Xa^{26}/Xa^{3} and Xa^{27}) [9 – 14]. Several resistant rice plants carrying single to multiple resistant genes have been bred using these genes [15-18]. For instance, dominant genes Xa^{4} and Xa^{21} responsible for durable resistance of rice varieties have been pyramided into rice lines [19]. Bacterial blight resistance QTLs, xa^{13}, xa^{5} *and* Xa^{21} have been combined with blast resistant gene *Pi54* and QTL, *qSBR11*-1 for Sheath blast (*ShB*) in Pusa Basmati1 [20]. The genes conferring tolerance to submergence (*Sub1*), salinity (*Saltol*), blast (*Pi2*, *Pi9*) and gall midge (*Gm1*, *Gm4*) have also been pyramided to the four bacterial blight resistance genes (Xa^{4}, xa^{5}, xa^{13}, Xa^{21}) in the improved Tapaswini, rice cultivar [21]. Several commercial rice varieties with *R* genes have been released through MAS [22]. Despite these achievements in both molecular and conventional methods in developing BLB resistant varieties, genetic overlaps between BLB stress resistance and yield component traits largely remain unclear. BLB is still highly destructive to high-yielding susceptible rice cultivars. In severe epidemics, yield losses of up to 75% have been reported [23]. Thus, the study on genetic associations between yield component traits and bacterial leaf blight resistance in rice (*O. sativa L.*) is necessary. Such information can be used to simultaneously improve BLB resistance and grain yield through marker assisted selection. In this study, three advanced populations were infected by three *Xanthomonas oryae pv. oryzae* races (C5, V5 and P6) to identify lines that were resistance to multiple *Xoo* races and at the same time had higher grain yield compared to the recurrent parent. Through QTL analysis, overlapping regions conferring resistance to BLB and simultaneously containing yield related traits were pursued.

MATERIALS AND METHODS

Experimental procedure

Two sets of backcross inbred lines (BILs), consisting of 226 lines (BC_2F_8) with the MH63 background (MH63_ILs), 229 lines (BC_2F_8) with the 02428 background (02428_IL) and 262 (F2:8) recombinant inbreed lines (RILs) developed from across between Minghui63 (MH63) and *indica* variety and 02428 a *japonica* variety were used for the study. Three BLB races (C5, V5 and P6) were prepared according to Ou [24]. Seeds were soaked for 8 hrs and re-dried in oven prior to sowing. Field experiments were arranged in a randomized complete block design (CRBD) with 2 replications. Inoculation was done at reproductive stage (onset of heading) by clipping approximately 1-2 cm of the tips of flag leaf and the leaves beneath with scissors previously dipped in bacterial suspension. After 14 to 21 days, both lesion length and leaf total length were measured using a ruler. In each plot, 10 plants were planted in a row with the spacing of 20 × 25cm.

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Data collection

Both lesion length and diseased leaf area were measured between 14 to 21 days after inoculation. Lesion length >0-5 cm long was regarded as resistant (R), >5-10cm moderate resistant (MR), >10-15cm moderate susceptible (MS), >15cm susceptible (S). Diseased leaf area was calculated as lesion length (LL)/Total leaf length (TLL)*100. Diseased leaf area <5% was regarded as resistant (R), 6-12% as moderate resistant, 13-25% as moderate susceptible and >25% as susceptible. Heading date (HD) was recorded when 50% of the plants within a row flowered. At maturity, plant height (PH), effective tiller number (TN), flag leaf length (FLL), flag leaf width (FLW) and flag leaf rolling (FLR) were measured. During harvesting, the BLB infected and BLB free plants were harvested separately. The harvested panicles were sun dried for one week, thereafter the panicle length (PL), spikelet number per panicle (SNP), filled grains numbers per panicle (FGN), spikelet fertility (SF), 1000-grain weight (TGW), yield per plant (GY), grain length (GL), grain width (GW) and grain length width ratio (GLW) were evaluated.

Data analysis

For the genotyping, 265 high-quality SNPs were used for a consensus linkage map construction. GLM proc SAS version 9.2 (SAS institute 2002) were used for trait mean variation and correlation analyses, IciMapping ver. 4.4 [25] for additive and epistasis QTLs mapping, GGT2 [26] for trait marker association and Genetic map was drawn using Liu and Meng [27] MapDraw.

RESULTS AND DISCUSSION

Bacteria blight resistance trait, evaluated based on both lesion length (LL) and diseased leaf area showed continuous distributions, a typical of quantitative traits [28]. Transgressive segregations in which some plants were extremely susceptible and some very resistant (Fig. 1) were observed. Based on the lesion length, resistant and moderate lines together accounted for 3.1, 1.9 and 1.8% for race P6, 81.4, 51 and 10.5% for race V5 and 99.6, 97.3 and 76.9% for race C5 in MH63_IL, RIL and 02428_IL populations, respectively. Based on diseased leaf area, resistant to moderate resistant lines accounted for 25.7, 34 and 3.5% for race V5; 77, 53.3 and 8.7% for race C5 in MH63_IL, RIL and 02428_IL populations, respectively. No line was resistant to *Xoo* race P6. Lines resistant to multiple *Xoo* races were also detected. For instance, in RIL population among 250 resistant lines, 52% were resistant to both C5 and V5 races and the remaining 48% resistant to C5 only. In 02428_IL population, there were 176 resistant lines to C5, among them only 23 lines were resistant to both C5 and V5, the remaining lines were resistant to C5. These results suggested that loci conferring BLB resistance were population and race specific. Results further revealed all three populations under this study were susceptible to *Xoo* race P6 (Plate 1).

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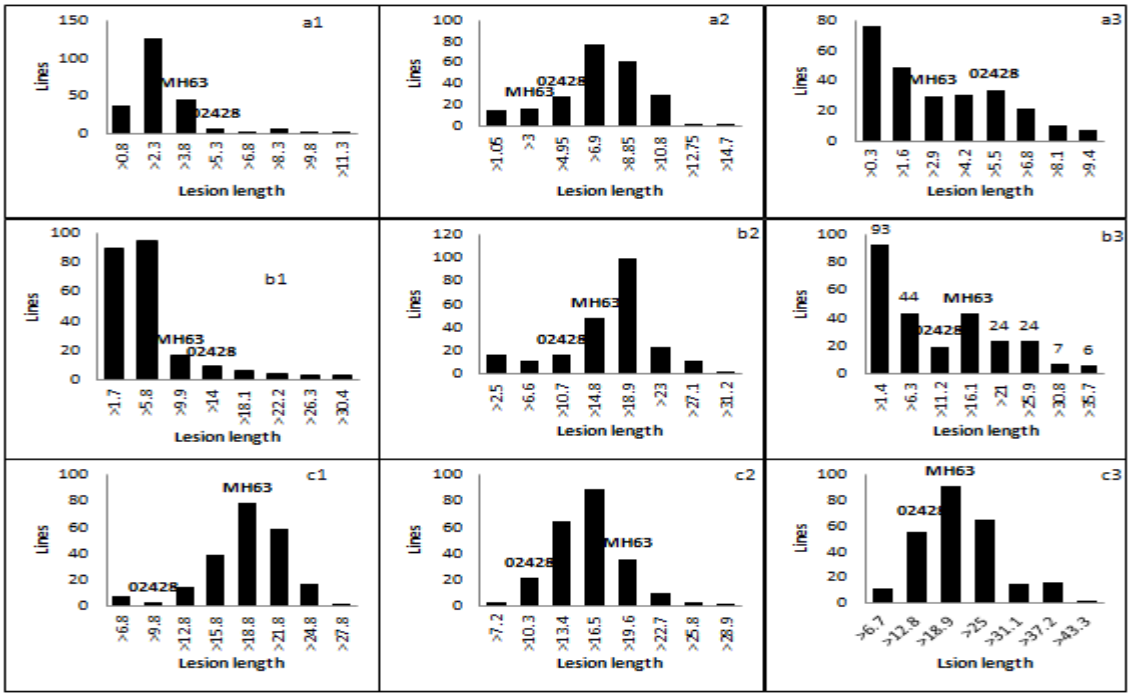

Figure 1: Distribution of lesion length in MH63_IL, 02428_IL and RIL populations 1=MH63_IL *indica* background, 2=02428_IL *japonica* background, 3= RIL population while a=race C5, b=race V5 and c=race P6

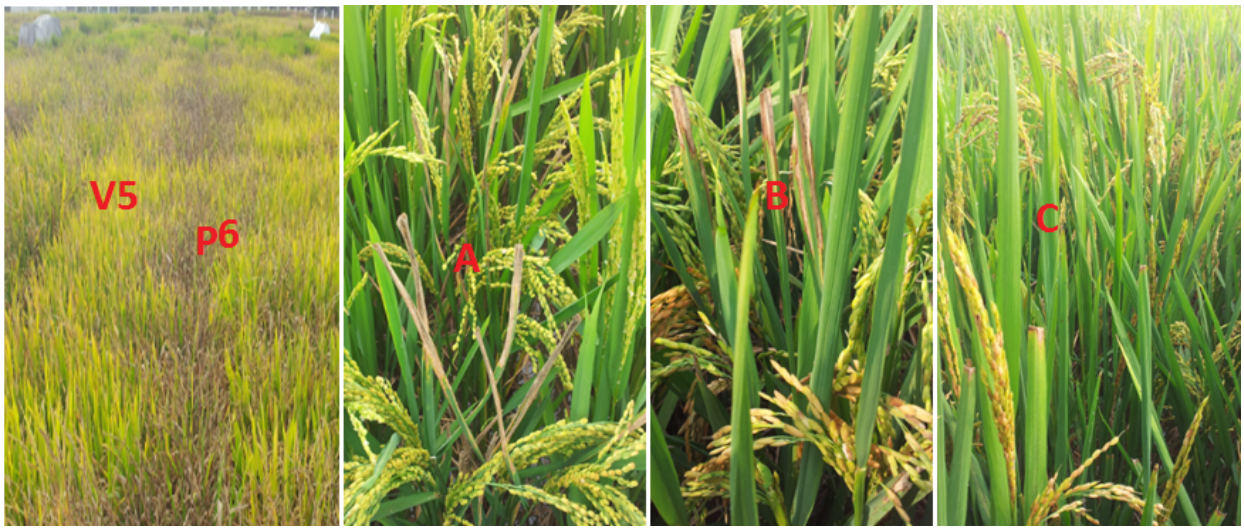

Plate 1: MH63_IL populations infection intensity for race V5 and P6 in Beijing and A, B and C for race C5 in Hainan

Associations of BLB resistance and grain yield component traits

Correlation analysis was carried for 18 traits (Table 1). In 02428_IL population, disease severity caused by *Xoo* race C5 was strongly ($P \leq 0.001$) associated with heading date (HD, -0.22), tiller number (TN, -0.30), grain length (GL, -0.27), grain width (GW, -0.26), grain length width ratio (GLW, -0.31) and flag leaf width (FLW, -0.25). *Xoo* race C5 had

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also strong correlations with *Xoo* P6 and V5 races (r=-0.34, and 0.65), respectively, indicating the presence of loci conferring resistance to multiple *Xoo* races. There were moderate associations ($P \leq 0.01$) between C5 and plant height (PH), panicle length (PL), grain yield (GY), spikelet number per panicle (SNP), filled grain number per panicle (FGN) and 1000-grain weight (TGW). V5 resistance was highly association with tiller number (TN, -0.25), spikelet number per panicle (SNP, 0.21), filled grain number (FGN, 0.24), 1000-grain weight (TGW-0.23), and flag leaf width (FLW, 0.26). However, no strong associations between wild component traits and BLB resistance to race P6 were observed. This probably showed there were no major QTLs conferring resistance to *Xoo* race P6. Results generally suggested there was strong association between tiller number and flowering time and the BLB resistances for all races in all populations. Higher tiller number translates to bushy and humid conditions that favor BLB infections. Flowering time/heading would imply that developmental stage (age of a plant) at which BLB inoculation is administered might affect disease progression. Similar results were reported for the Xa^{26} gene, which is a developmental stage-controlled resistance; expression level is very low at two-leaf stage and reaches maximum at tillering stage [29].

Marker trait associations

Marker trait analysis was performed to identify marker regions within a chromosome positively or negatively associated with disease resistant or yield component trait. Marker associations for 18 traits in MH63_IL populations are presented in Fig 2. The height of the bar and color intensity were proportional with the amount of association. Results showed that, there were no major marker regions conferring resistance to *Xanthomonas oryzae pv. oryzae* race P6. This result is in line with Pearson linear correlation and phenotyping data indicated in table 1 and plate 1, respectively. Many regions on chromosome 1 were negatively correlated to all traits except Flag leaf length (FLL), panicle length (PL) and grain shape (GL, GW and GLWR). There were strong correlations of a number of regions in chromosome 3, 4, 5, 8 and 11 to BLB resistance especially race C5 and V5, to yield component traits (GY, SNP, FGN), Plant height (PH), leaf shape traits (FLL, FLW, FLR) and grain width, indicating presence of BLB resistant loci in these chromosomes.

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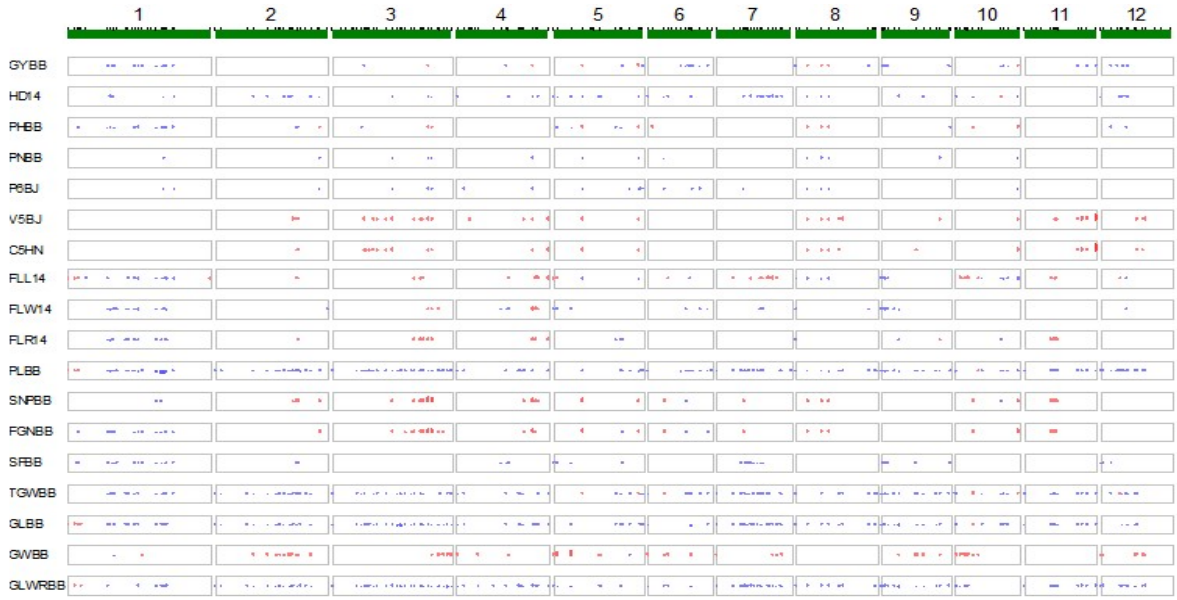

Figure 2: Marker and trait association plot along the chromosome bars

The height of the bar and color intensity are proportional with the amount of association. Positive associations are shown in red, negative associations in blue. If one trait is negatively associated with a marker while another trait is positively associated with the same markers at a certain position, this is an *indica*tion that these traits are negatively correlated at that position

BLB resistant and Epistasis QTLs

Bacteria blight diseases are generally controlled by major resistance genes (R) with few cases for recessive and QTLs [30]. The QTLs mapping results are presented in Table 2. In MH63_IL population, 8 QTLs located on chromosomes 1, 3, 4, 5, 6,7 and 12 conferred minor resistances to race P6, 10 QTLs, on chromosomes 2, 3, 4, 5, 8, 9,11 and 12 conferred resistances to *Xoo* race V5 and 5 QTLs located on chromosome 1, 3,5, 8 and 11 conferred resistances to *Xoo* race C5. Stepwise regression indicated total resistance variation explained by all additives QTLs (R^2) was 27, 66 and 79% for P6, V5 and C5, respectively. In 02428_ILpopulation ICIMapping detected 5 QTLs on chromosomes 2, 3,4, 8 and 12 conferring minor resistance to *Xoo* race P6, 4 QTLs located on chromosomes 3, 9, 11 and 12 conferring resistance to race V5 and 3QTLs located on chromosomes 2, 3 and 4 conferring resistance to race C5. Overall variations due to additive QTLs (R^2) on BLB resistance was 10.2, 18 and 5% for P6, V5 and C5 races, respectively. Epistasis QTLs effect on the BLB resistance was 12.3, 26 and 25.9% for the races P6, V5 and C5. In RR population, 4 QTLs located on chromosomes 2, 3, 8 and 11 conferred resistances to race C5. Overall variation due to additive QTLs (R^2) on BLB resistance was 3.8, 18.9 and15.7% for P6, V5 and C5 races, respectively. The variations due to Epistasis QTLs were 1, 4.8 and 13% for races P6, V5 and C5, respectively. These results suggest that both additive and QTLs interactions play a role in BLB resistance in RR population.

Major QTLs detected in MH65_IL population were qc^4, qc^5, qc^8 and qc^{11} with R^2 equivalent to 26, 80, 42 and 72 conferring resistance to *Xoo* race C5, qp^{10} with R^2

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equivalent to 40% conferring resistance to P6, qv^5 and qv^{11} with R^2 equivalent to 28% and 57% conferring resistance to race V5. In 02428_IL population major resistant loci for race V5 were qv^{11} and qv^9. QTLS qc^{11}, qv^{11} and qp^{11} were all located between markers M246-M247 on chromosome 11. On this chromosome, thirteen *Xanthomonas oryzae pv oryzae* resistant genes (Xa^3, Xa^4, Xa^6, Xa^9, Xa^{10}, Xa^{21}, Xa^{22}, Xa^{23}, Xa^{26}, Xa^{30}, xa^{35}, xa^{36} *and* xa^{37}) have been reported. Among them, Xa^3, Xa^{21} and Xa^{26} have been sequenced [29]. The xa^{26} gene has been reported as developmental stage-controlled resistance where the expression level is very low at two-leaf stage and reaches maximum at tillering stage. In present study, xa^{26} was present in all populations and conferred resistance to race *Xoo* C5 and V5 in both MH63_IL and RIL populations. However, in 02428 populations, xa^{26} conferred resistance to race V5 only. This might suggest that xa^{26} resistance is both race specific and genetic background dependence, or the interaction of this locus with other BLB resistance QTLs in this population affected its expression. All populations were susceptible to race P6, suggesting that major xa^{26} gene do not confer resistance to race P6. Mild resistance to race P6 actually came from minor QTLs and 11 epistasis QTLs detected in MH63_IL population. Another major QTLs in MH63_IL were located between M117-M118 on chromosome 5 at 39.5cM. This QTL (qv^5 or qc^5) conferred resistance to races C5 and V5. Total resistance due to this locus was 90% for C5, and 28% for V5. R gene that has been reported in this area is xa^5 which is a recessive gene located at 46.2cM. Further study is needed to confirm if these QTLs are identical. The presence of both qv^5 on chromosome 5 and xa^{26} on chromosome 11 increased significantly MH63_IL resistance to multiple BLB strains. The resistant lines were 3.1, 99.6 and 81.4 for P6, C5 and V5 in MH63_IL compared to 1.8, 10 and 76% in 02428_IL population. Another important QTL in this population was qc^8 or qv^8 or qp^8 depending on the *Xoo* race found on chromosome 8. This QTL was located between markers M183-184 at position 073383484-s13565364bp. This locus conferred resistance to all BLB races in MH63_IL population. Around this region recessive gene xa^{13} was reported [31]. This gene is a recessive gene located between 109 and 111.2 cM in JRGP RFL 2000 map. However, in our preliminary mapping this QTL was detected at 47.4 cM. Further research is needed to confirm whether this xa^{13} and qv^8 are identical**.**

Yield and yield component QTLs

The QTL mapping results for grain yield and yield component traits are presented in Table 3. ICI Mapping identified a total of 112 QTL distributed on all chromosomes across three populations. Forty-six QTL were detected in MH63_IL population, 30 QTL in 02428_IL and 9 QTL in RIL populations. Sixty-two QTLs had favorable alleles coming from Minghui63 and 50 QTLs had favorable alleles coming from 02428. Six QTLs ($qtw^{3\text{-}2}$, qpn^9, $qgl^{3\text{-}2}$, qgw^5, $qglw^2$ and *glw4*) were common in all three populations. The common QTLs explained 17.8, 12.7, 17.1, 47.3, 23.6 and 11.2 % of the mean trait variations. There were 11 common QTLs detected between MH63_IL and 02428_IL populations, 4 between 02428_IL and RIL populations and 6 between MH63_IL and RIL populations. It was also noted that most of the times QTLs associated with SF, HD, PH, PL, GL, and GLW had favorable alleles coming from 02428 parent while QTLs associated with GY, SNP, FGN, PN, and TGW, GW QTLs had favorable alleles coming from MH63 parent. Grain yield per plant, filled grain number, 1000-grain weight and panicle number are major components of grain yield [32], this would suggest that MH63 can be used to improve grain yield of 02428.

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Overlapping QTLs for both BLB resistance and yield related traits

Grain yield losses due to BLB range from 10% to 60% depending on variety, severity of infection, season, and time of infection. In highly susceptible varieties, a yield loss of up to 75% has been reported [33]. Thus BLB stress resistant variety should be the one with economically useful yield. In present study overlapping QTLs for BLB resistance and yield related traits are presented in Fig3. In this study 15 loci distributed in whole rice genome except in chr.10 responsible for BLB resistant were identified. These BLB resistant QTLs overlapped with 39 QTLs controlling yield and yield related traits. On chromosome 1, 5 QTLs, qsn^1 for spikelet number per plant, qfg^1 for filled grain number, qpl^1 for panicle length and qgy^1 for grain yield overlapped with a qp^1 controlling resistance to race P6 between markers M25-M26 occupying position os28761376-os36952999bp. On chromosome 2, between markers M36-M37, QTLs, qv^{2-1} conferring resistance to race *C5*, qgw^2 for grain weight and $qglw^2$ for grain with length ratio and qpn^2 for panicle number overlapped. In this region *GW,* responsible for grain width and weight increase [34] has been cloned. Thus, it can be a target for improving BLB resistance to race P6 as well as grain width and weight respectively. Chromosome 3 had two overlapping regions. The first overlapping region was located between M58-M59 habouring QTLs, qv^{3-1}, qgl^3 and $qglw^3$ while the second regions located between M75-M76 had qv^{3-2}, qC^3, qtw^3 and qpl^3. In all populations for all races (Table.2) this locus increased lesion length implying it is responsible for increasing rice susceptibility to the BLB infections. On chromosome4 there were 3 overlapping regions. The first region was located between M92-M93 and the second between M105-M106 and the third region between M112-M113. The third region was important for breeding BLB resistance and high grain yield variety because qc^4 a major QTL for C5 resistant (Fig.3) detected in this region was synonymous to Xa^1 gene which has been characterized. This region also overlapped with qpn^4 for panicle number and qgl^4 for grain length. On this region QTL *qGN4-1* with major effect on grain number and pleiotropic effects on QTLs for primary and secondary branches per panicle and number of panicles per plant has been reported [35]. Chromosome 5 had a major BLB gene located between 7310209-8848557bp conferring resistance to all three races in the MH63_IL population. Around this region recessive *xa5* gene [36] restricting bacterial movement but not multiplication [37] has been reported between 437010-443270bp. This locus overlapped with other six yield component traits such as *qgy5* for grain yield, qtw^5 for 1000-grain weight, qsn^5 for spikelet number, qph^5 for heading date, qgw^5 for grain width and $qglw^5$ for grain length width ratio. In this region *GW-5* a major QTL that controls rice grain width and weight and encodes a novel nuclear protein of 144 amino acids has been characterized. All QTL identified in this region increased the breeding values of respective traits. For example, qgy^5 increased grain yield, qtw^5 increased 1000-grain weight, qph^5 reduced plant height, qpn^5 increased panicle number, qgw^5 increased grain width and $qglw^5$ reduced grain length width ratio (Table 3). Therefore, it is a hotspot region that can be utilized for combining both BLB resistance and high grain yield. Another important region was located on chromosome 6, where QTLs qp^6, qv^6, $qfgn^6$, qph^6 and qpl^6 responsible for P6 resistance, V5 resistance, filled grain number, plant height and panicle length, respectively overlapped between loci Os23517577-Os25229000. In this region $Xa^{27(t)}$ conferring a high level of resistance to 27 *Xoo* races and moderate resistance to 33 *Xoo* races and *TGW6* for 1000-grain weight have been reported [38]. On chromosome 8

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between markers M183-M185, *qp8* conferring resistance to P6 in both MH63_IL and 02428_IL populations, *qc8* for C5 resistance in MH63_IL and RIL populations and QTL *qv8* conferring resistant to race V5 were detected. On the same region *DTH8/Ghd8* for flowering repressor [38] and *GW8* for grain width and weight [39] have been cloned. It has been suggested that *DTH8/Ghd8* gene has pleiotropic effect on other yield component traits thus this region would be another hotspot region that can be utilized in developing both BLB resistance and high yielding variety. On chromosome9 between markers M205-M206 there was qv^{5} responsible for increasing lesion length by 3.9 in both MH63_IL and 02428_IL populations. This QTL overlapped with qgy^{9} for grain yield with additive effect of 31.3, qpn^{9} for panicle number with additive effect of 2.6, qgw^{9} with additive effect 0.1 and qtw^{9} for 1000-grain weight with additive effect 0.7 in both MH63_IL and 02428_IL. A search from literature review did not revealed any locus associated with BLB resistance or grain yield reported in this region, thus characterization of these QTLs in this region might further provide important breakthrough. Chromosome 11 had major QTL qv^{11} or qc^{11} conferring resistant to *Xoo* races C5 and V5 in all populations. However, no QTLs for yield and yield component traits were detected. On chromosome 12 there were two important regions where QTLs overlapped. The first region was between markers M254-M255, however, in this region no BLB resistant gene was detected. The second region located between markers M264-M265, QTLs, $qv5^{12}$, qp^{12}, $qglw^{12\text{-}2}$, qgy^{12}, qfg^{12} and a $qpn^{12\text{-}2}$ were detected. This region is another important region that combines the main yield component traits such as grain yield per plant (GY), filled grain number (FGN), and panicle number (PN). Study conducted under drought and irrigation conditions using the same populations (not published) revealed the presence of these QTL in both conditions. Thus this chromosomal segments located between Os21092541-Os-25291547 is a hotspot region which can be utilized for breeding BLB resistance and high yielding rice varieties under both drought stress and normal irrigation conditions simultaneously.

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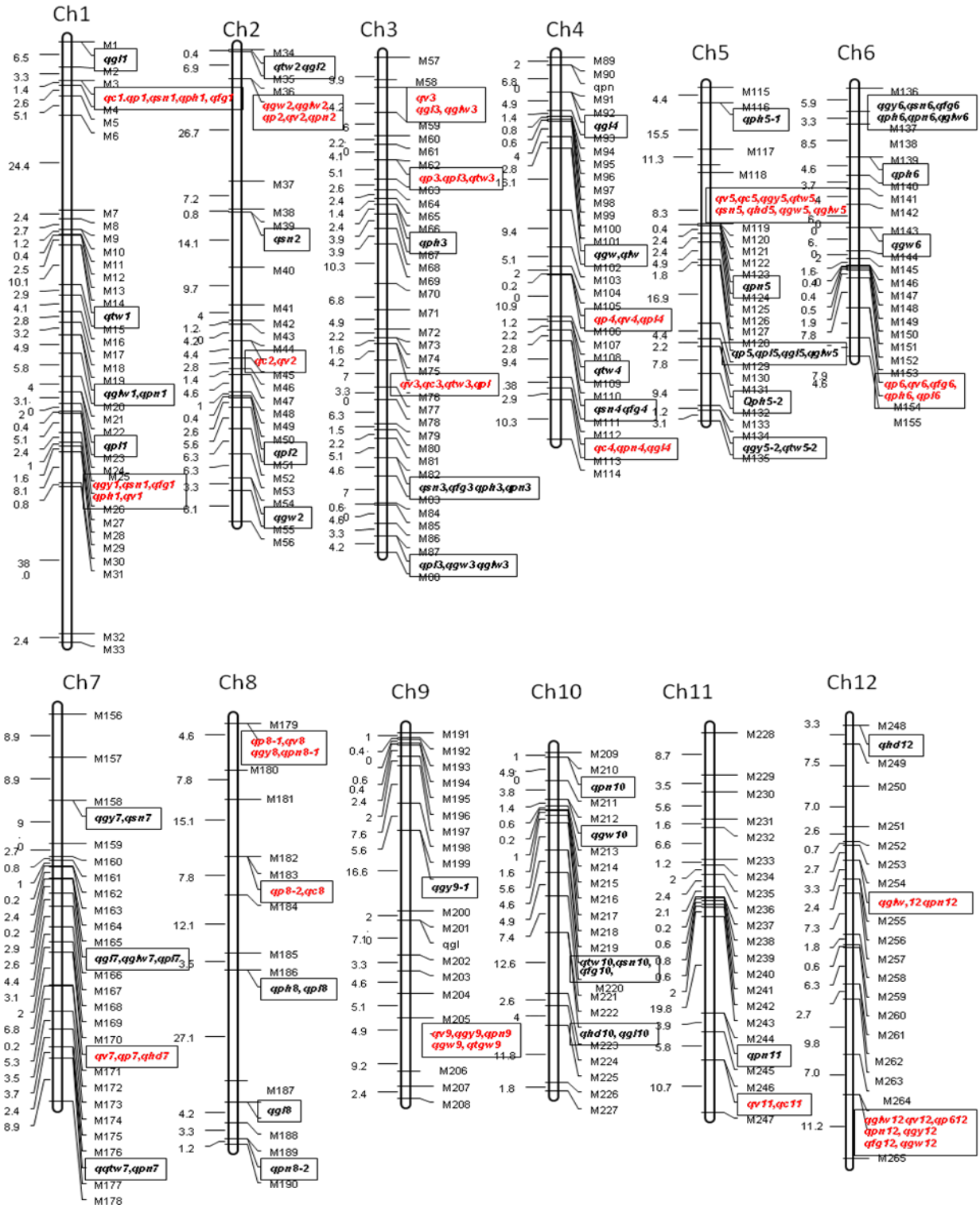

Figure 3: QTLs for BLB resistance and yield related traits

Overlapping QTLs combining BLB resistance and grain yield components traits marked in red

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CONCLUSION

Frequency distribution, Pearson linear correlation, marker trait association and QTL analysis showed that BLB resistance is a polygenic trait. Both main QTLs and epistasis QTLs play a role in BLB resistance. The QTLs for BLB resistance are race and genetic background specific. There are chromosomal segments that contain QTLs for both BLB resistance, grain yield and yield related traits. Thus both BLB resistance and grain yield can be simultaneously introgressed together. It is recommended that building a durable BLB resistant variety does not only require pyramiding multiple R genes but also introgressing with epistasis QTL. Future study should focus on multi-environment testing using different varieties. Such study will dissect GXE and genetic background effects of the identified QTLs. Fine mapping of overlapping QTLs will facilitate application of MAS for the improvement of BLB resistance and higher grain yield simultaneously.

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Table 1: Correlation coefficients between Lesion length and grain yield component traits in MH63_IL (left side) and 02428_IL (right side) populations

MH63_IL	HD	PH	TN	P6	V5	C5	FLL	FLW	FLR	PL	GY	SNP	FGN	SF	TGW	GL	GW	GLW	02428_IL
HD	1	0.04	-0.11	0.17*	0.03	-0.22**	0.27**	0.21**	0.17*	0.24**	0.09	0.11	0.06	-0.01	-0.03	0.13	-0.24**	0.21*	
PH	0.14*	1	-0.03	-0.03	-0.13	-0.17*	0.09	-0.08	-0.11	0.33**	0.26**	0.21**	0.10	-0.16*	0.11	-0.05	-0.13*	0.05	
TN	0.11*	0.08	1	-0.06	-0.25**	-0.30**	0.01	-0.31**	-0.11	0.12	0.15*	-0.32**	-0.36**	-0.17*	-0.02	0.23**	-0.20*	0.24**	
P6	0.12*	-0.01	0.18**	1	0.34**	0.34**	0.24**	0.29**	0.23**	0.19*	0.07	0.09	0.08	-0.01	0.05	0.08	-0.01	0.06	
V5	-0.13*	0.05	-0.05	-0.01	1	0.65**	0.13	0.26**	0.13	-0.02	-0.06	0.21**	0.24**	0.11	-0.23**	-0.22**	0.12	-0.20*	
C5	-0.09*	0.11*	-0.15**	0.02	0.20**	1	0.12	0.25**	0.09	-0.15*	-0.13*	0.18*	0.21*	0.07	-0.18*	-0.27**	0.26**	-0.31**	
FLL	-0.14*	0.14*	0.04	0.15**	0.04	0.14*	1	0.30**	0.16*	0.33**	0.23**	0.10	0.10	0.05	0.09	0.09	0.02	0.05	
FLW	0.21**	0.26*	0.08	0.10*	0.01	0.17**	0.18**	1	0.66**	0.19*	0.25**	0.53**	0.51**	0.13*	-0.06	-0.16	0.28**	-0.23**	
FLR	0.12*	0.25**	0.06	0.14*	0.03	0.14*	0.28**	0.62**	1	0.10	0.12	0.24**	0.19*	-0.01	0.13*	0.08	0.12	0.01	
PL	0.23**	0.36**	0.15**	0.12*	-0.19**	-0.09	0.28**	0.19**	0.11*	1	0.39**	0.37**	0.26**	-0.09	0.06	0.12	-0.08	0.13*	
GY	-0.01	0.50**	0.36**	-0.03	0.04	-0.08	0.13*	0.08	0.09*	0.39**	1	0.35**	0.53**	0.42**	0.06	-0.04	0.11	-0.05	
SNP	-0.30**	0.32**	-0.13*	-0.11*	0.13*	0.21**	0.24**	0.16**	0.24**	0.15**	0.33**	1	0.83**	-0.06	-0.38**	-0.46**	0.01	-0.26**	
FGN	-0.17**	0.42**	-0.11*	-0.14*	0.14*	0.16**	0.16**	0.19**	0.20**	0.18**	0.52**	0.87**	1	0.50**	-0.38**	-0.43**	0.10	-0.28**	
SF	0.22**	0.31**	0.02	-0.05	0.05	-0.01	-0.11*	0.10*	0.00	0.13*	0.46**	-0.03	0.46**	1	-0.08	-0.05	0.17*	-0.10	
TGW	0.06	0.20**	-0.12*	-0.04	-0.04	-0.08	-0.05	-0.03	-0.05	0.31**	0.26**	-0.10*	0.01	0.21**	1	0.54**	0.25**	0.21**	
GL	0.22**	0.08	-0.01	0.06	-0.10*	-0.11*	0.04	0.05	0.03	0.39**	0.04	-0.29**	-0.27**	-0.02	0.62**	1	-0.40**	0.85**	
GW	-0.31**	-0.09	-0.10	0.08	0.08	0.08	0.11*	-0.09	-0.03	-0.08	-0.01	0.08	0.00	-0.15**	0.20**	-0.25**	1	-0.81**	
GLW	0.32**	0.11*	0.06	0.00	-0.11*	-0.12*	-0.03	0.09*	0.05	0.30**	0.03	-0.24**	-0.17**	0.09	0.27**	0.80**	-0.77**	1	

*, ** = significant at ≤ 0.05 and ≤ 0.001, respectively. HD: heading date, PH plant height, TN: tiller number, P6 lesion length caused by BLB race P6, V5: lesion length caused by BLB race V5, C5 lesion length caused by BLB race C5, FLL: Flag leaf length, FLW: flag leaf width, FLR flag leaf rolling, PL: panicle length, GY grain yield per plant, SNP: spikelet number per panicle, FGN: filled grain number per panicle, SF: spikelet fertility, TGW: 1000-thousands grain weight, GL: grain length, GW: grain width and GLW grain length width ratio

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Table 2: additive QTLs from ICIM mapping named after the BLB race followed by location and chromosome number. Letters I, J and R represents MH63_IL, 02428_IL and RIL populations respectively. * QTLs detected in more than one population

QTL	Ch	SNP interval	Phy-pos	LOD	R^2	Add	Reference
qp1(R)	1	M10-M11	Os13251483-Os14639642	2.4	4.4	3.4	
qp3(JR)	3	M77-M83	Os06812491-Os07612707	2.9	5.5	-3.5	
****qp4(JR)***	4	M105-M106	Os24354018-Os-25012772	2.6	2.5	1.2	*Xa1*
****qp5(I)***	5	M128-M129	Os18016536-Os21782804	3.1	6.5	-3.4	
****qp6(IJR)***	6	M153-M154	Os23517577-Os25229000	6.8	8.7	-3.8	Xa27(t)
****qp7(JR)***	7	M169-M174	Os20601489-Os25436357	2.3	5.0	-3.0	*Xa4*
qp10(I)	10	M226-M227	Os22500927-Os23075612	25.6	40.7	-13.8	
qp12(J)	12	M264-M265	Os25291547-Os27451180	3.8	7.6	1.1	
****qv1(IJ)***	1	M21-M24	Os26655497-Os27650412	6.5	11.2	10.4	
****qv2-1(IJ)***	2	M37-M38	Os-08735694-Os10800151	6.6	11.5	10.6	
****qv2-2(IR)***	2	M44-M45	Os-23525752-Os-24690661	5.1	4.0	-11.0	
****qv3-1(IJ)***	3	M57-M58	Os-00442367-Os02546314	4.8	13.2	4.3	
****qv3-2(IJ)***	3	M75-M76	Os13926803-Os23570099	7.2	15.2	4.5	
****qv4(IJ)***	4	M106-M107	Os-25012772-Os-27293771	7.5	12.8	4.5	*Xa1*
****qv5(I)***	5	118M-119	Os-05429050-Os-07310209	29.8	26.5	10.6	
qv7(I)	7	M156-M157	Os-01142811-Os02000576	10.3	12.7	9.7	
****qv8(I)***	8	179M-180	Os00714463-Os01537588	5.6	14.0	4.6	
****qv9(IJ)***	9	M205-M206	Os20055954-Os20982434	4.3	10.1	3.9	
qv10(I)	10	M210-M211	Os01242485-Os03551423	5.3	11.1	10.8	
****qv11(IJR)***	11	M246-M247	Os23862573-Os28421947	50.8	52.5	17.6	*Xa26*
****qv12(I)***	12	M264-M265	Os21092541-Os-25291547	10.8	12.3	10.6	
qc1(I)	1	M5-M6	Os04650741-Os05762721	6.7	3.4	1.7	
****qc2(R)***	2	M42-M44	Os-21847940-Os23525752	1.8	4.7	-0.6	
****qc3(IJ)***	3	M69-M76	Os13926803-Os23570099	9.4	4.3	1.0	
****qc4(IJ)***	4	M111-M113	Os31621148-Os33279336	37.5	26.1	-13.2	*Xa1*
****qc5(I)***	5	118M-119	Os-05429050-Os-07310209	73.6	80.6	9.3	
qc6(I)	6	M153-M155	Os23517577-Os25229000	4.4	2.4	-1.1	
****qc8(IR)***	8	M183-M184	Os07338384-Os13565364	50.6	41.9	-6.7	
****qc11(IR)***	11	M246-M247	Os23862573-Os28421947	74.4	70.2	3.1	*Xa26*

Table 3: QTLs for grain yield and yield component traits detected by Inclusive composite interval mapping

QTLS	Trait	Ch	Interval	LOD	R^2	Add	QTLs	Trait	Ch	Interval	LOD	R^2	Add
qgy1(I)	GY	1	M25-M26	8.3	14.4	-2.9	*qph6-2(J)*	PH	6	M154-M155	4.1	9.3	-3.5
qgy5-1(IR)	GY	5	M118-M119	4	14.2	5	*qph8(I)*	PH	8	M186-M187	3.6	9.4	-2.5
qgy5-2(J)	GY	5	M134-M135	3.1	6.9	-2.1	*qpn1(I)*	PN	1	M21-M22	4.5	12.2	3.2
qgy6(I)	GY	6	M137-M145	4.5	7.6	-2	*qpn2(I)*	PN	2	M37-M54	5.3	12.1	3.2
qgy7(J)	GY	7	M158-M159	1.6	4.2	1.1	*qpn3(I)*	PN	3	M82-M83	6.3	12	-0.9
qgy8(IR)	GY	8	M180-M181	3.7	12.9	4.9	*qpn4-1(I)*	PN	4	M90-M91	4.6	12.8	2.6
qgy9(IJ)	GY	9	M199-M206	26.4	38.3	31.3	*qpn4-2(JR)*	PN	4	M112-M113	5.4	9.4	-0.7
qgy12(J)	GY	12	M264-M265	1.7	3.3	1	*qpn5(I)*	PN	5	M123-M125	4.8	14	4.8
qtw1(J)	TGW	1	M14-M15	2.8	5.8	1.3	*qpn6(I)*	PN	6	M136-M137	5.1	14	4.8
qtw1(I)	TGW	1	M27-M28	2.7	3	-0.5	*qpn7(I)*	PN	7	M156-M177	4.4	12.5	2.9
qtw2(I)	TGW	2	M34-M35	8.6	10	1.1	*qpn8(I)*	PN	8	M179-M180	5	12.2	3.1
qtw3-1(J)	TGW	3	M62-M63	1.7	3.4	0.8	*qpn9(JIR)*	PN	9	M204-M205	4.7	12.7	2.6
qtw3-2(IJR)	TGW	3	M74-M76	7.4	17.1	1.8	*qpn10(I)*	PN	10	M210-M211	3	12.1	3.2
qtw4(J)	TGW	4	M108-M109	1.8	3.1	-0.6	*qpn11(I)*	PN	11	M243-M244	4.5	12.3	3.1
qtgw5-1(J)	TGW	5	M117-M118	1.7	3.2	0.7	*qpn12(I)*	PN	12	M64-M265	4.6	14	4.8
qtw5-2(I)	TGW	5	M131-M132	7.3	11.9	1.0	*qpl1(I)*	PL	1	M19-M27	22	23.4	-1
qtw7(R)	TGW	7	M177-M178	2.1	3.7	-0.6	*qpl2(I)*	PL	2	M50-M51	5	5.3	-0.9
qtw10-1(R)	TGW	9	M205-M206	2.5	4.6	0.7	*qpl3-(IJ)*	PL	3	M63-M64	6.6	14.1	-1.3
qtw10-2(I,J)	TGW	10	M219-M225	3	3.4	-0.9	*qpl3-2(J)*	PL	3	M76-M78	1.6	2.8	-0.4
qsn1-1(J)	SNP	1	M3-M4	7.8	15.4	-27.1	*qpl4(I)*	PL	4	M105-M106	4.9	4.4	0.7
qsn1-2(I)	SNP	1	M25-M26	5.4	5.6	-9.2	*qpl5(R)*	PL	5	M128-M129	1.6	4.3	0.4
qsn3(IR)	SNP	3	M82-M83	18.4	23.4	20	*qpl6(IR)*	PL	6	M154-M155	4.5	4.7	-0.6
qsn2(J)	SNP	2	M39-M40	1.7	3.2	-6.6	*qpl7(I)*	PL	7	M163-M164	2.8	2.5	-0.5
qsn4(I,J)	SNP	4	M110-M111	5.2	9.1	12.2	*qpl8(J)*	PL	8	M186-M187	3	5.7	0.5
qsn5(I)	SNP	5	M118-M119	7.5	14.6	42.8	*qgl1-1(IJ)*	GL	1	M1-M2	4.4	6.6	0.2
qsn6(I,J)	SNP	6	M136-M137	7.4	15.1	38.1	*qgl1-2(R)*	GL	1	M16-M17	2.1	3.5	-0.1
qsn7(J)	SNP	7	M159-M160	3.7	6.6	11	*qgl2(IJ)*	GL	2	M34-M35	4.4	22.1	-0.4
qsn10(J)	SNP	10	M219-M220	7.4	13.5	19.2	*qgl3-1(J)*	GL	3	M58-M59	8.4	18.9	-0.4
qfg1-1(J)	FGN	1	M3-M4	10	22.5	-30	*qgl3-2(IJR)*	GL	3	M72-M88	13.1	17.1	-0.4
qfg1-2(I)	FGN	1	M25-M26	9.7	11.8	-12	*qgl4(J)*	GL	4	M92-M93	6.2	10.7	-0.2
qfg3(I)	FGN	3	M83-M84	12.1	17.5	15.6	*qgl4(R)*	GL	4	M112-M113	3.9	5.9	-0.2
qfg4(I,J)	FGN	4	M110-M111	7.4	12.5	12.2	*qgl5(J)*	GL	5	M128-M129	2.7	25.1	-0.4
qfg6-1(J)	FGN	6	M136-M137	2.2	3.9	6.7	*qgl7(I)*	GL	7	M165-M166	5.4	5.6	-0.2
qfg6-2(JR)	FGN	6	M153-M154	1.7	3	-8.6	*qgl8(IJ)*	GL	8	M187-M188	3.2	5.6	0.3
qfg10(JR)	FGN	10	M219-M220	4.6	9.7	15.1	*qgl9(R)*	GL	9	M201-M202	1.5	2.5	0.1
qfg12(J)	FGN	12	M264-M265	1.5	2.9	6.8	*qgl10(J)*	GL	10	M221-M223	3	9.5	-0.2
qsf1-1(I)	SF	1	M19-M20	3.1	4.9	-2.7	*qgw2(I)*	GW	2	M37-M43	2.8	18.2	0.1
qsf1-2(I)	SF	1	M29-M30	4.3	9.5	-3.5	*qgw2-3(J)*	GW	2	M55-M56	1.6	2.5	-0.1
qsf4(IJ)	SF	4	M103-M104	3.8	5.2	-3.1	*qgw3(I)*	GW	3	M87-M88	14.6	16.6	0.2
qsf5-1(I)	SF	5	M116-M117	10.3	32.9	-8.2	*qgw4(I)*	GW	4	M101-M102	5.9	12.1	0.1
qsf5-2(J)	SF	5	M132-M133	1.7	5.4	3.4	*qgw5(IJR)*	GW	5	M116-M118	36.8	47.3	0.1
qsf7(I)	SF	7	M166-M167	4.2	5.9	-3.1	*qgw6(JR)*	GW	6	M143-M144	4.7	8.4	0.1
qsf8(R)	SF	8	M189-M190	2.1	4.1	-3.7	*qgw9(R)*	GW	9	M206-M207	2.2	4.1	0.1
qhd1(I)	HD	1	M29-M30	3.9	4.5	-1.1	*qgw10(I)*	GW	10	M212-M213	5	4.4	0.0
qhd3(IJ)	HD	3	M58-M59	2.5	12.1	-2	*qgw12(J)*	GW	12	M261-M262	3.6	6.1	0.1
qhd5(I)	HD	5	M115-M118	18.5	22.3	-3.4	*qlw1(IR)*	GLWR	1	M17-M20	19	18.2	-0.1
qhd6(J)	HD	6	M139-M140	2.1	4.3	1.4	*qlw2(IJR)*	GLWR	2	M36-M37	6.8	23.6	-0.1
qhd7(I)	HD	7	M170-M171	5.8	6.6	-1.4	*qglw3-1(J)*	GLWR	3	M58-M59	4.2	9	-0.1
qhd10(I)	HD	10	M223-M224	4.9	10.2	-1.7	*qlw3-2(I)*	GLWR	3	M72-M88	14.2	12.1	-0.3
qhd12(I)	HD	12	M248-M249	3	3	-1.1	*qlw4(IJR)*	GLWR	4	M101-M102	9	11.2	-0.1
qph1-1(IJ)	PH	1	M3-M7	8.5	9.3	-2.7	*qlw5(IR)*	GLWR	5	M116-M118	23.6	24.5	-0.2
qph1-2(I)	PH	1	M17-M26	15.4	17.6	-2.9	*qglw5(J)*	GLWR	5	M128-M129	3.8	24.2	-0.2
qph3-1(I)	PH	3	M66-M67	8.6	9.1	4.2	*qlw6(I)*	GLWR	6	M136-M137	4.4	5	-0.3
qph3-2(J)	PH	3	M83-M84	1.7	3.4	1.8	*qlw7(I)*	GLWR	7	M161-M162	4.1	3.1	-0.1
qph5(I)	PH	5	M117-M132	7.2	7.5	-1.8	*qlw12-1(R)*	GLWR	12	M254-M255	6.3	11	-0.1
qph6-1(I)	PH	6	M137-M139	4.7	5	8.0	*qlw12-2(I)*	GLWR	12	M264-M265	4.2	6.7	-0.2

Legend
Letters *I, J* and *R* represents MH63_IL, 02428_IL and RIL populations respectively. q=QTL, *gy*=grain yield per plant, *tw*= 1000-grain weight, *sn* = spikelet number, *fg* =filled grain number, *sf*= spikelet fertility, *hd* =heading date, *ph* =plant height, *pn*= panicle number, *pl*=panicle length, *gl*=grain length, *gw*=grain width, *lw*-grain width length ratio

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