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In silico analysis of disease resistance and defence-related genes for a major sheath blight *qShb* 9-2 QTL in rice

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ABSTRACT

Aims: Sheath blight disease (*Rhizoctonia solani*) is an important rice disease that causes heavy yield losses in rice annually. To date, no rice variety has been found to be completely resistant to this disease. The most desirable approach for the management of sheath blight disease is to introgress genes with major and durable resistance into the rice genome. Therefore, this study aims to identify disease resistance and defence genes within *qShb* 9-2, a major QTL found within moderately resistant rice population via *in silico* analysis.
Methodology and results: The sequences of tightly linked markers of *qShb* 9-2 from GRAMENE database was used to derive the 10.24 Mbp QTL region that contains 1581 genes according to MSU Rice Genome Annotation Project database. BLAST results showed that 11.4% of these genes were transposable elements which may be involved in gene duplication. Through Blast2GO, fifty-four (2.9%) defence-related genes were annotated within this QTL and can be classified into 5 major defence mechanisms. Further, fifty (2.7%) disease resistance genes were identified in *qShb* 9-2 based on the presence of NB-ARC, LRR-receptor kinase, Ser/Thr protein kinase and protein kinase domains. Lastly, directed acyclic graphs showing the interaction between all the disease resistance and defence-related genes were generated.
Conclusion, significance and impact of study: The presence of these genes indicates that *qShb* 9-2 region may contribute towards the defence against sheath blight disease. By deciphering the gene landscape within the QTL, it may be possible to further fine map the QTL into a smaller region for QTL pyramiding in breeding programmes. The resistance and defence genes are also a source for genetic engineering studies and a good source for marker development.

Keywords: Sheath blight disease, *Rhizoctonia solani* Kühn, quantitative trait loci, disease resistance genes, defence-related genes

INTRODUCTION

The world population is expected to rise from 6.1 billion in the year 2000 to 9.2 billion in 2050. This rapid increase in human population is expected to increase the demand for food production to satisfy the increasing global needs. While the paddy agro-ecosystems are created to fulfil this demand, we are aware that these ecosystems are also exposed to both biotic and abiotic stresses. The main biotic stresses that affect the rice ecosystems in Malaysia are bacterial leaf blight, fungal sheath blight and rice blast (Latif *et al*., 2011).

The management of this rice disease in Malaysia depends a lot on pesticide usage, chemical fertilisers and also flood irrigation (Siti Noraini *et al*., 2012). These pesticides result in the reduction of aerobic microbes and useful soil bacteria. Hence, the population of useful microbes in the soil are unable to protect the health of the plant causing them to be infected easily. Continuous effort by researchers has been on going to obtain major genes which may confer complete resistance to cultivars as an effective and safe way of increasing yield with no harmful effect to the environment (Zuo *et al*., 2014).

Through the many research and breeding programmes carried out worldwide, major genes have been identified for diseases such as bacterial sheath blight and rice blast. Studies on bacterial sheath blight disease has uncovered several major genes such as *xa5*, *xa3* and *Xa21* which were found to provide complete resistance against *Xanthomonas oryzae* pv. *oryzae* (Zhang and Wang, 2013). Likewise for rice blast, the major resistance genes *Pi-d*, *Pi-z* and *Pi-k*^{h} have been successfully pyramided to produce a completely resistant cultivar (Hittalmani *et al*., 2000). The latest gene for resistance against rice blast *Pi40* has provided extensive resistance against various strains/isolates of *Magnaporthe oryzae*.

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Unlike the above two diseases, little is known at the gene level about resistance to fungal sheath blight disease which is caused by *Rhizoctonia solani*. *R. solani* AG1-IA is a soil-borne necrotrophic fungal pathogen with a wide host range, capable of infecting rice, corn, barley, sorghum, soybean etc (Wang *et al*., 2014). This disease causes paddy yield to decrease by 50% all over the world (Zheng *et al*., 2013). Over 50 resistance QTLs have been reported in many rice varieties for this diseases since Li *et al*. (1995) first reported sheath blight QTLs utilising restriction fragment length polymorphism (RFLP) markers. Most of the resistance QTLs found are from the subspecies *O. indica* while only a few are from *O. japonica*. Generally, *O. japonica* has lesser resistance towards the fungus *R. solani* infection compared to *O. indica* (Jia *et al*., 2012). Through screening of various rice lines that are available worldwide, it has been determined that certain rice lines show moderate resistance or partial resistance against *R. solani* infections. This is also referred to as incomplete, quantitative, or horizontal resistance mechanisms (Zheng *et al*., 2013). According to Jia *et al*. (2012), breeding of sheath blight resistant cultivars has been underachieving mainly due to the lack of identified major resistance genes and this may be attributed to the resistance being regulated by many genes or QTLs (Pinson *et al*., 2005). Among the rice varieties which contribute to this partial resistance are Teqing, Tetep and Jasmine 85 (Sattari *et al*., 2014). Since, sheath blight is controlled by multiple genes; identification of the major resistance and defence-related genes is the pre-condition to improve the tolerance of rice against this biotic stress (Channamallikarjuna *et al*., 2010; Zuo *et al*., 2014).

Disease resistance genes in plants are classified into 8 major classes based on their domain structure such as NBS (nucleotide binding site), LRR (leucine rich repeat), CC (coiled coil) and more. The biggest resistance gene family in plant genomes is NBS-LRR (Gururani *et al*., 2012). Once the disease resistance protein detects its cognate avirulence protein of pathogen, the plant will activate its defence system (Flor, 1971). This in turns will activate the defence genes through various defence mechanisms such as signal transduction, hypersensitive response, accumulation of phytoalexins and synthesis of pathogenesis-related (PR) proteins (Hammond-Kosack and Jones, 1996). Among the PR proteins which have been found to provide defence against sheath blight disease are β-1, 3-glucanase (PR-2) and Chitinase (PR-3) (Yadav *et al*., 2015). Bioinformatics tools can be used to perform gene mining at the genomic level to identify major resistance and defence genes in reported QTLs. In this study, *qShb* 9-2 QTL was chosen because it has been reported in many researches as a stable and consistent QTL due to its omnipresence in many different rice varieties (Jia *et al*., 2009; Wang *et al*., 2012; Zuo *et al*., 2014; Yadav *et al*., 2015). For instance, Yadav *et al*. (2015) reported that the crossing between a resistance (ARC10531) and a susceptible variety (BPT-5205) resulted in a population which carries partial resistance towards the sheath blight disease. In this population like various others the *qShb* 9-2 was detected.

The objective of this study is to (1) identify and classify disease resistance and defence-related genes present in *qShb* 9-2; and (2) present an interaction model between the identified resistance and defence-related genes. The gene findings of this study may be useful in the development of a paddy variety through gene pyramiding and also in the development of a molecular markers which can be used in the selection process of rice varieties against the sheath blight disease (Maruthasalam *et al*., 2007).

MATERIALS AND METHODS

Determination of the genomic locus of *qShb 9-2* and its genes

Based on previous research by Yadav *et al*. (2015), the SSR flanking markers of *qShb* 9-2 are two microsatellite markers, RM205 and RM105. The forward and reverse primer sequences of the flanking markers (RM205 and RM105) were acquired from GRAMENE database (www.gramene.org). The primer pairs were used as queries in the BLASTn (BLAST nucleotide) sequence similarity analysis against IRGSP rice genome in NCBI database (https://blast.ncbi.nlm.nih.gov). This BLASTn step functions to obtain the range of genomic coordinate of *qShb* 9-2 on chromosome 9. The genomic locus range of the QTL was then inputted in the MSU Rice Genome browser (http://rice.plantbiology.msu.edu/cgi-bin/gbrowse/rice/#search) to visualise the distribution of all the genes present. The region size of the *qShb* 9-2 QTL is 10.24 Mbp from the position 10,051,509 bp to 20,295,314 bp. The whole region contains 1581 genes with an average of 154 gene/Mbp. The cDNA FASTA sequence of the 1581 genes was obtained from the MSU Rice Genome Annotation Project database.

Computational analyses in Blast2GO

The cDNA FASTA sequence of the genes was imported into the Blast2GO software (Conesa *et al*., 2005). Firstly, the 1581 genes were blasted against NCBI non-redundant (nr) database via Blast2GO to obtain the gene description. Then, a gene ontology analysis was conducted where the genes were classified into their ontologies based on biological processes, molecular functions and cellular components. Next, domain analysis was performed using InterProScan via Blast2GO itself to identify the domains of the disease resistance genes. This was followed by an enzyme mapping step, in which enzyme activity of the encoding genes could be explored. This step is particularly useful for the identification of defence-related genes. Finally, directed acyclic graphs were generated though Blast2GO for the disease resistance and defence-related genes identified in *qShb* 9-2. These graphs illustrate the hierarchical structure of the gene ontologies and provide an overview of the interaction between resistance and defence genes in the

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defence mechanism of *Oryza sativa* against sheath blight disease.

RESULTS AND DISCUSSION

Summary of gene distribution in *qShb* 9-2

The summary of genes with multiple copy numbers in *qShb* 9-2 was tabulated after blasting the 1581 genes against nr database in NCBI (Table 1). As a result, 1543 genes were successfully blasted of which transposable elements (TEs) comprised the highest copy number (181; 11.4%) in this QTL. The TEs are major components of eukaryotic genomes and are well-known in altering genome function and evolution via their transpositions (Tenaillon *et al.*, 2010). In rice, over 39.5% of genomic sequence is accounted by TE (Vitte *et al*., 2014). When a 1.2 Mb contiguous genomic sequence was compared between *indica* and *japonica* rice, 13% of the sequence was not shared mainly due to different TE insertions (Ma and Bennetzen, 2004). Effect of TE on genome can be classified into (i) gene inactivation when TE is inserted into coding or intronic regions, (ii) altered gene expression when TE is inserted into/nearby regulatory regions, (iii) TE-mediated chromosomal rearrangements leading to deletions, duplications or inversions and others (Vitte *et al*., 2014). For example, TE excision or insertion resulted in heritable altered expression of eight neighbouring genes in X9 rice line with four being significantly induced and four suppressed. Particularly, three of the induced genes were found within QTLs related to 1000 seed weight and grain length (Wu *et al*., 2015).

Therefore, the TE landscape in *qShb* 9-2 was explored by using MSU Rice Genome browser (Figure 1). Interestingly, two distinct observations were noted, viz. (i) tandem arrangement of TEs with protein-coding genes and (ii) multiple copies of paralogous genes at the downstream region of TE(s). The former involves F-box domain containing protein (Figure 1A, 1E), pollen allergen Cyn d 23 (Figure 1B), protein binding protein (Figure 1C) and OsWAK receptor-like cytoplasmic kinase (Figure 1G) while the latter includes OsWAK receptor-like cytoplasmic kinase (Figure 1D) and Auxin-responsive SAUR gene family member (Figure 1F). In addition, Figure 1H shows a set of three protein-coding genes (i.e. vignain precursor, thiol protease SEN102 precursor and cysteine proteinase precursor) present in alternating manner in the presence of a TE. It can be deduced from these observations that TE is involved in the duplication of those protein-coding genes which might have functional importance. Firstly, F-box protein was reported as substrate-recognising subunit of the SCF E3 ubiquitin ligase that controls protein degradation (Deshaies and Joazeiro, 2009). In plants, F-box genes belong to a large multigene superfamily and regulate various important biological processes including embryogenesis, seedling development, hormonal responses, floral development, senescence and biotic resistance (Xu *et al*., 2009). The wall-associated kinases (WAKs) are grouped under receptor-like kinases (RLK) family and they function in signal transduction between the cell wall and the cytoplasm which is crucial for plant development and response to environmental stresses (Zhang *et al*., 2005). *SMALL AUXIN UP RNAs* (*SAURs*), which belong to a large multigene family of genes that are rapidly induced by auxin treatment, were recently demonstrated to mechanistically impede PP2C-D phosphatases and induce plasma membrane H^+-ATPases to stimulate plant cell expansion. Therefore, it was proposed as key effector outputs of hormonal and environmental stimuli that control plant growth and development (Ren and Gray, 2015).

Table 1: BLASTn Mapped genes and their gene number in *qShb* 9-2.

Gene name	Number of genes
Transposon and retrotransposon	181
Hypothetical protein	154
Predicted/uncategorised protein	122
Kinase related protein	82
F-box protein	27
Auxin-responsive like SAUR 36	26
Zinc finger protein	23
Pentatricopeptide repeat protein	19
Aspartyl protease family protein	18
TOTAL	652

Identification and classification of defence-related genes

This section explains the utilisation of GO annotation, enzyme mapping and information to identify defence-related genes. A total of 54 defence-related genes were identified in *qShb* 9-2 (Table 2) which were then categorised into five defence mechanisms including hypersensitive response, reactive oxygen species (ROS), signal transduction, phytoalexin accumulation and synthesis of PR proteins (Figure 2).

In the event of pathogen infection such as *R. solani*, resistant plants are likely to activate their hypersensitive response that involves a rapid development of cell death at the location of infection to prevent the proliferation of microbes. Zinc knuckle family protein with CCHC zinc finger domain could be a candidate for defence-related gene in *qShb* 9-2 as many zinc finger-containing proteins in rice and Arabidopsis have been shown to regulate programmed cell death (Gupta *et al*., 2012). Calcium-dependent protein kinases is known to directly transmit Ca^{2+} signals to activate downstream processes, such as ROS production, transcriptional activation of defence genes and programmed cell death (Gao *et al*., 2014). MYB transcription factor, AtMYB30, was also reported to act as an activator of the programmed cell death in response to pathogen infection (Ambawat *et al*., 2013). On the contrary, UBX domain-containing protein negatively regulates Arabidopsis CDC48 (AAA-ATPase chaperone) which modulates various biological processes, namely the formation and maintenance of endoplasmic reticulum (ER) and Golgi apparatus, ER-associated protein degradation and cell death (Rancour *et al*., 2004). In phase two of hypersensitive response, an

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oxidative burst happens in the cells of the infected site by producing huge amounts of ROS (Torres *et al*., 2006). It was suggested that the suppression of antioxidant defence could be contributing to the oxidative burst that signals programmed cell death (de Pinto *et al*., 2002). The antioxidant enzyme-encoding genes identified in *qShb* 9-2 are TPR repeat-containing thioredoxin, glutathione transferase and ascorbate peroxidase.

Kinase related proteins are mostly involved in elicitor recognition, signalling and the induction of defence genes (Mishra *et al*., 2012). For elicitor recognition, receptor kinases such as lysM domain-containing GPI-anchored protein and L-type lectin-domain containing receptor kinase were identified in *qShb* 9-2. lysM domain-containing GPI-anchored protein functions as a cell surface receptor for chitin and peptidoglycan elicitors, which in turn leads to innate immunity in plants (Tanaka *et al*., 2013), while L-type lectin-domain containing receptor kinase activates intracellular signalling that contributes to fungal resistance (Wang and Bouwmeester, 2017). Next, protein kinases and phosphatases that take part in the signalling cascades were also found in *qShb* 9-2, namely histidine-containing phosphortransfer protein 2, protein phosphatase 2C 69 and cyclin-dependent kinase inhibitor. Histidine-containing phosphotransfer protein 2 is involved in cytokinin signalling activity (Giron and Glevarec, 2014) while protein phosphatase 2C 69 is crucial in pathogenesis responses by controlling receptor and organellar signalling (Durian *et al*., 2016). While the cell cycle is well-known to be controlled by the cyclin-dependent kinase (CDK), CDK inhibitor can interact with CDK to counteract its activity (Wang *et al*., 2008). Further, a local hypersensitive response will often result in an induction of defence responses in the uninfected parts of the plants, resulting in the establishment of systemic acquired resistance (SAR) (Kombrink and Schmelzer, 2001). The development of SAR usually involves increased biosynthesis of salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) (Kessmann *et al*., 1994; Pieterse *et al*., 1996). Interestingly, transcription factors related to each of these phytohormone-mediated pathways were identified in *qShb* 9-2, viz. WRKY, TIFY and ethylene-responsive transcription factors.

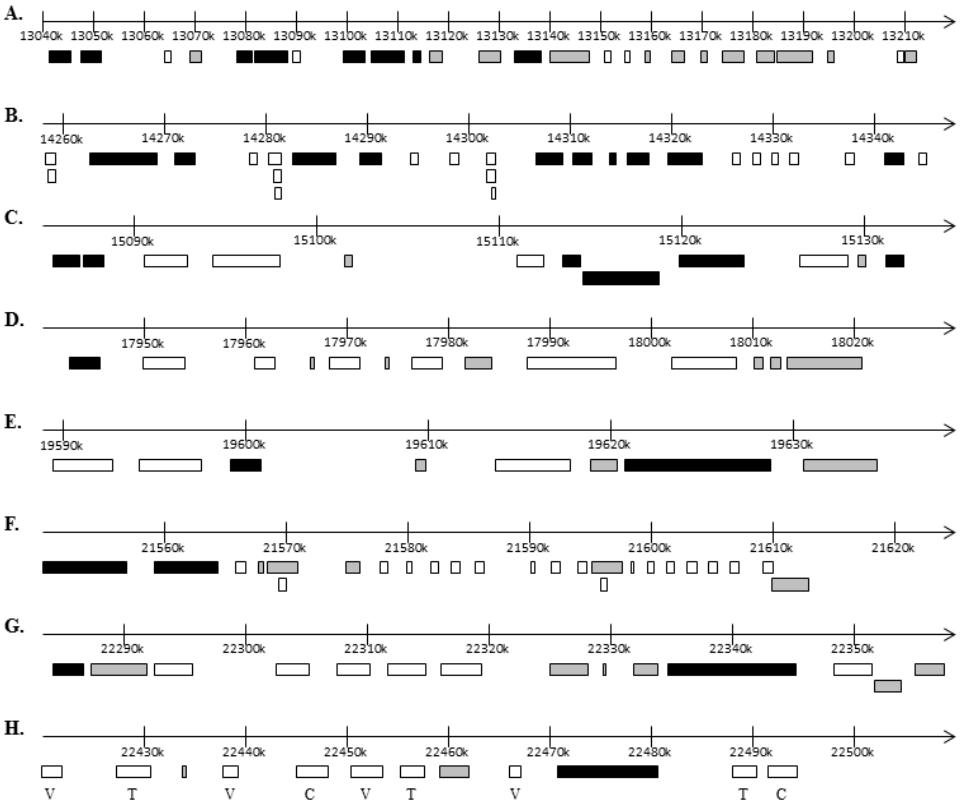

Figure 1: The distribution of transposable elements in *qShb* 9-2 in relation to (A, E) F-box domain containing protein, (B) pollen allergen Cyn d 23, (C) protein binding protein, (D, G) OsWAK receptor-like cytoplasmic kinase, (F) Auxin-responsive SAUR gene family member and (H) vignain precursor, thiol protease SEN102 precursor and cysteine proteinase precursor. The corresponding protein-coding genes are represented by white boxes while non-related protein-coding genes are represented by grey boxes. TEs are shown in black boxes.V - vignain precursor, T - thiol protease SEN102 precursor and C - cysteine proteinase precursor.

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Table 2: The list of 54 defence-related genes identified in *qShb* 9-2 with their enzymatic and GO annotations.

Gene ID	Gene description	Enzyme	GO annotation
Hypersensitive response			
LOC_Os09g20950.1	Zinc knuckle family protein	-	-
LOC_Os09g23620.1	MYB family transcription factor	-	F:RNA polymerase II transcription factor activity, sequence-specific DNA binding; F:transcription factor activity, RNA polymerase II transcription factor recruiting; C:nucleus; P:regulation of transcription by RNA polymerase II; P:cell differentiation; F:sequence-specific DNA binding; F:transcription regulatory region DNA binding
LOC_Os09g23690.1	plant UBX domain-containing protein 2	-	-
LOC_Os09g24800.1	myb-related protein 306	-	F:RNA polymerase II transcription factor activity, sequence-specific DNA binding; F:transcription factor activity, RNA polymerase II transcription factor recruiting; F:protein binding; C:nucleus; P:regulation of transcription by RNA polymerase II; P:response to water deprivation; P:response to salt stress; P:response to ethylene; P:response to auxin; P:response to abscisic acid; P:response to salicylic acid; P:response to jasmonic acid; P:cell differentiation; F:sequence-specific DNA binding; F:transcription regulatory region DNA binding; P:positive regulation of transcription, DNA-templated; P:response to cadmium ion; P:response to karrikin; P:positive regulation of wax biosynthetic process
LOC_Os09g32710.1	Calcium-dependent protein kinase 14	-	-
LOC_Os09g36730.1	myb-related protein Hv1	-	F:RNA polymerase II transcription factor activity, sequence-specific DNA binding; F:transcription factor activity, RNA polymerase II transcription factor recruiting; C:nucleus; P:regulation of transcription by RNA polymerase II; P:response to salicylic acid; P:response to jasmonic acid; P:response to UV-B; P:cell differentiation; F:sequence-specific DNA binding; F:transcription regulatory region DNA binding; P:negative regulation of transcription, DNA-templated; P:negative regulation of sinapate ester biosynthetic process
Signal transduction			
LOC_Os09g21040.1	kinase-like protein	transferring phosphorus-containing groups	-
LOC_Os09g21150.1	exocyst complex component EXO70B1	-	-
LOC_Os09g22410.3	pyruvate kinase 1, cytosolic	transferring phosphorus-containing groups	-
LOC_Os09g23660.1	protein TIFY 6b	-	F:transcription corepressor activity; C:nucleus; P:regulation of transcription, DNA-templated; P:protein folding; P:response to wounding; P:heat acclimation; C:membrane; F:oxidoreductase activity, acting on a sulfur group of donors, disulfide as acceptor; F:Hsp70 protein binding; P:regulation of defense response; F:identical protein binding; P:cell redox homeostasis; P:protein complex oligomerization; P:oxidation-reduction process; P:negative regulation of nucleic acid-templated transcription; P:regulation of jasmonic acid mediated signaling pathway
LOC_Os09g23810.1	Protein kinase domain superfamily protein	transferring phosphorus-containing groups	-
LOC_Os09g25060.1	putative WRKY transcription factor 40	-	F:DNA binding transcription factor activity; C:nucleus; P:regulation of transcription, DNA-templated; P:response to bacterium; P:response to fungus; P:response to

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			salicylic acid; P:response to chitin; F:sequence-specific DNA binding
LOC_Os09g25070.2	probable WRKY transcription factor 40	-	F:DNA binding transcription factor activity; F:protein binding; F:ATP binding; C:nucleus; P:regulation of transcription, DNA-templated; P:response to fungus; P:response to salicylic acid; P:response to chitin; F:sequence-specific DNA binding; P:negative regulation of defense response to bacterium
LOC_Os09g25080.1	probable L-type lectin-domain containing receptor kinase S.7	-	-
LOC_Os09g26420.1	ethylene-responsive transcription factor 1-like	-	F:DNA binding; F:DNA binding transcription factor activity; C:nucleus; P:regulation of transcription, DNA-templated; P:response to fungus
LOC_Os09g26780.1	protein TIFY 10c	-	F:transcription corepressor activity; F:protein binding; C:nucleus; C:cytosol; P:regulation of transcription, DNA-templated; P:response to wounding; P:regulation of defense response; P:negative regulation of nucleic acid-templated transcription; P:regulation of jasmonic acid mediated signaling pathway
LOC_Os09g26820.1	exocyst complex component EXO70B1	-	-
LOC_Os09g26860.1	Protein kinase domain superfamily protein	transferring phosphorus-containing groups	-
LOC_Os09g27890.2	lysM domain-containing GPI-anchored protein 1-like	-	-
LOC_Os09g28310.1	bZIP transcription factor TRAB1-like	-	F:DNA binding transcription factor activity; P:regulation of transcription, DNA-templated; C:integral component of membrane
LOC_Os09g28560.1	probable protein phosphatase 2C 69	protein-serine/threonine phosphatase; 4-nitrophenylphosphatase	-
LOC_Os09g28580.1	cyclin-dependent kinase inhibitor 6	-	-
LOC_Os09g29690.1	EG45-like domain containing protein	-	-
LOC_Os09g29710.1	EG45-like domain containing protein	-	-
LOC_Os09g29740.1	EG45-like domain containing protein	-	-
LOC_Os09g31390.1	bZIP transcription factor family protein	-	F:DNA binding transcription factor activity; P:regulation of transcription, DNA-templated; F:sequence-specific DNA binding
LOC_Os09g32680.1	cyclin-C1-1 isoform X2	-	-
LOC_Os09g33810.1	ankyrin repeat domain-containing protein 2A	-	F:chloroplast targeting sequence binding; C:integral component of chloroplast outer membrane; P:protein targeting to chloroplast
LOC_Os09g34000.1	trigger factor	transferring phosphorus-containing groups	-
LOC_Os09g34880.1	Basic-leucine zipper (bZIP) transcription factor family protein	-	F:DNA binding transcription factor activity; P:regulation of transcription, DNA-templated
LOC_Os09g36210.1	NDR1/HIN1-like protein 12	-	-
LOC_Os09g36550.1	armadillo repeat only 1	-	F:signal transducer activity; C:nucleus; C:cytoplasm; P:cell surface receptor signaling pathway; F:lipid binding; C:integral component of membrane
LOC_Os09g37790.1	putative receptor kinase 5	transferring phosphorus-containing groups	-
LOC_Os09g37810.1	putative receptor kinase 5	transferring phosphorus-containing groups	-

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LOC_Os09g39400.1	histidine-containing phosphotransfer protein 2	-	P:phosphorelay signal transduction system; C:nucleus; C:cytosol; F:histidine phosphotransfer kinase activity; P:phosphorylation; F:protein histidine kinase binding; P:positive regulation of cytokinin-activated signaling pathway
PR protein synthesis			
LOC_Os09g21170.1	UDP-glycosyltransferase 90A1	endo-1,3(4)-beta-glucanase	P:metabolic process; C:intracellular membrane-bounded organelle; F:glucan endo-1,3-beta-glucanase activity, C-3 substituted reducing group; F:quercetin 3-O-glucosyltransferase activity; F:quercetin 7-O-glucosyltransferase activity
LOC_Os09g21210.1	probable endo-1,3(4)-beta-glucanase ARB_01444	endo-1,3(4)-beta-glucanase	F:glucan endo-1,3-beta-glucanase activity, C-3 substituted reducing group
LOC_Os09g23084.1	endoglucanase 22	cellulase	C:extracellular region; F:cellulase activity; P:cellulose catabolic process; P:cell wall organization
LOC_Os09g23580.1	thaumatin-like protein	-	C:integral component of membrane
LOC_Os09g31430.1	beta-glucosidase 30	beta-glucosidase	P:carbohydrate metabolic process; F:beta-glucosidase activity; C:integral component of membrane; F:scopolin beta-glucosidase activity; P:glycosyl compound metabolic process
LOC_Os09g32080.1	chitinase-like protein 1	chitinase	F:chitinase activity; P:carbohydrate metabolic process; P:chitin catabolic process; P:cell wall macromolecule catabolic process
LOC_Os09g32280.1	thaumatin-like protein 1b	-	F:RNA binding; F:endonuclease activity; C:mitochondrion; C:integral component of membrane; P:mitochondrial mRNA modification; P:nucleic acid phosphodiester bond hydrolysis
LOC_Os09g33680.1	beta-glucosidase 31	beta-glucosidase	P:carbohydrate metabolic process; F:beta-glucosidase activity; F:scopolin beta-glucosidase activity; P:glycosyl compound metabolic process
LOC_Os09g33690.1	beta-glucosidase 32-like isoform X1	beta-glucosidase	P:carbohydrate metabolic process; F:beta-glucosidase activity; F:scopolin beta-glucosidase activity; P:glycosyl compound metabolic process
LOC_Os09g33710.1	beta-glucosidase 32-like isoform X1	beta-glucosidase	P:carbohydrate metabolic process; F:beta-glucosidase activity; F:scopolin beta-glucosidase activity; P:glycosyl compound metabolic process
LOC_Os09g36560.1	thaumatin-like protein 1b	-	C:integral component of membrane
LOC_Os09g36580.1	thaumatin-like protein 1	-	C:integral component of membrane
LOC_Os09g36810.1	beta-galactosidase 11	beta-galactosidase	F:beta-galactosidase activity; C:cell wall; C:vacuole; P:carbohydrate metabolic process; F:carbohydrate binding; C:apoplast
LOC_Os09g36920.1	la-related protein 1B	beta-galactosidase	F:RNA binding; F:beta-galactosidase activity; C:cell wall; C:vacuole; C:membrane
Reactive oxygen species			
LOC_Os09g23650.1	TPR repeat-containing thioredoxin TDX	-	-
LOC_Os09g29200.1	glutathione transferase GST 23	glutathione transferase	-
LOC_Os09g36750.1	probable L-ascorbate peroxidase 4	cytochrome-c peroxidase; Peroxidase	P:response to reactive oxygen species; F:cytochrome-c peroxidase activity; C:chloroplast; C:integral component of membrane; F:heme binding; P:cellular response to oxidative stress; P:hydrogen peroxide catabolic process; P:oxidation-reduction process; P:cellular oxidant detoxification
Phytoalexin accumulation			
LOC_Os09g24900.2	probable methyltransferase PMT2	-	-
LOC_Os09g39230.1	arogenate dehydratase/prephenate dehydratase	prephenate dehydratase	F:chorismate mutase activity; F:prephenate dehydratase activity; P:L-phenylalanine biosynthetic process; C:chloroplast stroma; F:arogenate dehydratase activity

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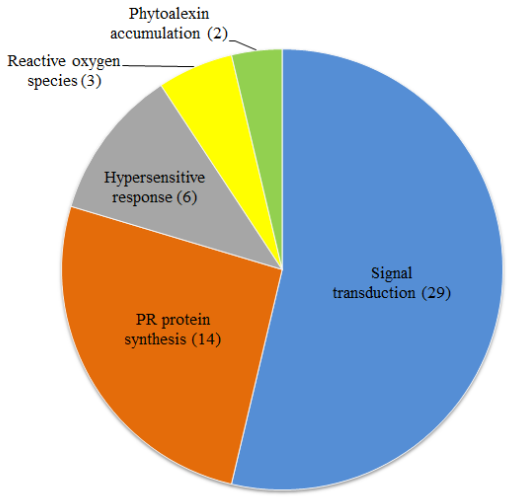

Figure 2: The distribution of 54 defence-related genes according to their defence mechanism.

Table 3: The list of 50 putative disease resistance genes identified in *qShb* 9-2.

Gene ID	Gene description	Domain
LOC_Os09g34150.1	disease resistance protein RPM1-like	NB-ARC
LOC_Os09g34160.1	disease resistance protein RPM1 like	NB-ARC
LOC_Os09g30220.1	disease resistance protein RPM1-like	NB-ARC
LOC_Os09g30230.1	disease resistance protein RPM1-like	NB-ARC
LOC_Os09g28470.1	probable LRR receptor-like serine/threonine-protein kinase At1g67720	LRR-receptor kinase
LOC_Os09g20970.1	probable inactive receptor kinase At2g26730	LRR-receptor kinase
LOC_Os09g23570.1	probable inactive receptor kinase RLK902	LRR-receptor kinase
LOC_Os09g25540.1	putative leucine-rich repeat receptor-like serine/threonine-protein kinase At2g24130	LRR-receptor kinase
LOC_Os09g30190.1	probable LRR receptor-like serine/threonine-protein kinase At4g26540	LRR-receptor kinase
LOC_Os09g38700.1	protein STRUBBELIG-RECEPTOR FAMILY 5	LRR-receptor kinase
LOC_Os09g20920.1	putative cyclin-dependent kinase F-2	Protein kinase
LOC_Os09g21510.1	NPK1-related protein kinase 2	Protein kinase
LOC_Os09g26700.2	probable ethanolamine kinase	Protein kinase
LOC_Os09g27350.1	Putative cyclin-dependent kinase F-2	Protein kinase
LOC_Os09g28950.1	BOI-related E3 ubiquitin-protein ligase 1-like	Protein kinase
LOC_Os09g36180.1	Polygalacturonate 4-alpha-galacturonosyltransferase	Protein kinase
LOC_Os09g37949.1	SRSF protein kinase 1	Protein kinase
LOC_Os09g20880.1	probable serine/threonine-protein kinase PBL28 isoform X1	Ser/Thr protein kinase
LOC_Os09g22300.1	serine/threonine-specific receptor protein kinase-like	Ser/Thr protein kinase
LOC_Os09g24330.1	putative receptor-like protein kinase At4g00960	Ser/Thr protein kinase
LOC_Os09g25090.1	CBL-interacting protein kinase 16	Ser/Thr protein kinase
LOC_Os09g25100.1	putative CBL-interacting protein kinase 27	Ser/Thr protein kinase
LOC_Os09g27010.1	serine/threonine-protein kinase RIPK	Ser/Thr protein kinase
LOC_Os09g27150.1	serine/threonine-protein kinase STY8-like	Ser/Thr protein kinase
LOC_Os09g28180.1	G-type lectin S-receptor-like serine/threonine-protein kinase At5g35370	Ser/Thr protein kinase
LOC_Os09g29170.1	serine/threonine-protein kinase PEPKR2	Ser/Thr protein kinase
LOC_Os09g29510.1	putative wall-associated receptor kinase-like 16	Ser/Thr protein kinase
LOC_Os09g29520.1	putative wall-associated receptor kinase-like 16	Ser/Thr protein kinase
LOC_Os09g29540.1	putative wall-associated receptor kinase-like 16	Ser/Thr protein kinase
LOC_Os09g29560.1	putative wall-associated receptor kinase-like 16	Ser/Thr protein kinase
LOC_Os09g29584.1	putative wall-associated receptor kinase-like 16	Ser/Thr protein kinase
LOC_Os09g29600.1	putative wall-associated receptor kinase-like 16	Ser/Thr protein kinase
LOC_Os09g30150.1	serine/threonine-protein kinase D6PK	Ser/Thr protein kinase
LOC_Os09g30454.1	Wall-associated receptor kinase 2	Ser/Thr protein kinase
LOC_Os09g31210.1	Serine/threonine-protein kinase UCNL	Ser/Thr protein kinase
LOC_Os09g33630.1	Chitin elicitor receptor kinase 1	Ser/Thr protein kinase
LOC_Os09g33860.1	PTI1-like tyrosine-protein kinase 3	Ser/Thr protein kinase
LOC_Os09g36320.1	probable receptor-like protein kinase At5g47070	Ser/Thr protein kinase
LOC_Os09g37230.2	serine/threonine-protein kinase STY46	Ser/Thr protein kinase
LOC_Os09g37780.1	putative receptor kinase 5	Ser/Thr protein kinase
LOC_Os09g37800.1	putative receptor kinase 5	Ser/Thr protein kinase
LOC_Os09g37840.1	receptor-like serine/threonine-protein kinase SD1-8	Ser/Thr protein kinase
LOC_Os09g37880.1	G-type lectin S-receptor-like serine/threonine-protein kinase At1g11300	Ser/Thr protein kinase
LOC_Os09g37890.1	receptor-like serine/threonine-protein kinase SD1-8	Ser/Thr protein kinase
LOC_Os09g38800.1	wall-associated receptor kinase 3	Ser/Thr protein kinase
LOC_Os09g38830.1	wall-associated receptor kinase 3	Ser/Thr protein kinase
LOC_Os09g38834.1	wall-associated receptor kinase 3	Ser/Thr protein kinase
LOC_Os09g38840.1	wall-associated receptor kinase 3	Ser/Thr protein kinase
LOC_Os09g38850.1	wall-associated receptor kinase 3	Ser/Thr protein kinase
LOC_Os09g38910.1	wall-associated receptor kinase 3	Ser/Thr protein kinase

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For instance, SA-induced WRKY DNA binding protein was revealed to act upstream of *NPR1*, a transcriptional coactivator of genes involved in resistance signalling, and also positively regulate *NPR1*expression during pathogen infection (Yu *et al*., 2001). TIFY protein family contains the *JAZ* gene which carries the defence- and stress-related element DOFCOREZM, pathogen elicitor-responsive element OSE2ROOTNODULE and mechanical injury-response element WBOXNTERF3 (Sun *et al*., 2017). The ethylene-responsive transcription factor is required for the cross-talking between ethylene and jasmonate signalling pathways to activate defence genes (Lorenzo *et al*., 2003).

The cells surrounding the lesion synthesize antimicrobial compounds, including phenolics, phytoalexins and PR proteins. Thaumatin like protein (TLP) is PR-5 class protein that has the potential to disrupt the fungal membrane by pore formation (Roberts and Selitrennikoff, 1990). Besides that, TLP can also inhibit the fungal growth either alone or in a synergistic manner with β-1, 3-glucanase (PR-2), chitinase (PR-3) and xylanase inhibitor activities (Singh *et al*., 2013). Both β-1, 3-glucanase (Balasubramanian *et al*., 2012) and chitinase (Sámi *et al*., 2001) are hydrolytic enzymes that disrupt fungal cell wall by breaking down glycosidic bonds in beta-glucan and chitin, respectively. Pertaining to phytoalexin accumulation, methyltransferase PMT2 and prephenate dehydratase encoding genes were found in *qShb* 9-2. The former was reported to mediate methylation of pinosylvin, a fungitoxin protecting the wood from fungal infection (Paasela *et al*., 2017). Intriguingly, prephenate dehydratase participates in the biosynthesis of phenylalanine, tyrosine and tryptophan which are co-ordinately activated by biotic and abiotic stresses to synthesise phenolic phytoalexins in rice (Cho and Lee, 2015).

Classification of putative disease resistance genes according to domains

Domain analysis was conducted using InterPROScan via Blast2GO to identify the presence of disease resistance genes. If the analysed genes were mapped to notable disease resistance-associated domain(s), they were classified as disease resistance gene. Fifty putative resistance genes were determined, making up to 2.7% of the overall *qShb* 9-2 QTL. Table 3 lists the putative resistance genes and their corresponding domain categories. Four types of domains, including NB-ARC, LRR-receptor kinase, Ser/Thr protein kinase and protein kinase were identified for these disease resistance genes with Ser/Thr protein kinase making up over 66% of the total identified domains (Figure 3).

Four copies of disease resistance protein RPM1 were identified as NBS-LRR disease resistance genes in *qShb* 9-2 based on the detection of NB-ARC domain. The interaction between RPM1 plant disease resistance gene and avrRPM1 protein from *Pseudomonas syringae* pv. tomato causes an accumulation of cytosolic calcium that is required for the hypersensitive resistance response (Grant *et al*., 2000). The activated ROS generation in the infected region of plant cell restricts the pathogen growth (Grant *et al*., 2000). Next, Leucine-rich repeat receptor kinases (LRR-RKs) which form the biggest transmembrane RLKs subfamily in plants were also found in *qShb* 9-2. Almost all plant RKs phosphorylate serine/threonine residues, unlike animal RKs that mainly phosphorylate tyrosine residues (Shiu and Bleecker, 2001). LRR-RKs regulate a wide range of developmental and defence-associated processes (Torii, 2004). An example of well-characterized LRR-RK that functions as disease resistance gene for bacterial blight is the rice *Xa21* which confers gene-for-gene type resistance to *Xanthomonas oryzae* pv. *oryzae* (Liu *et al*., 2002).

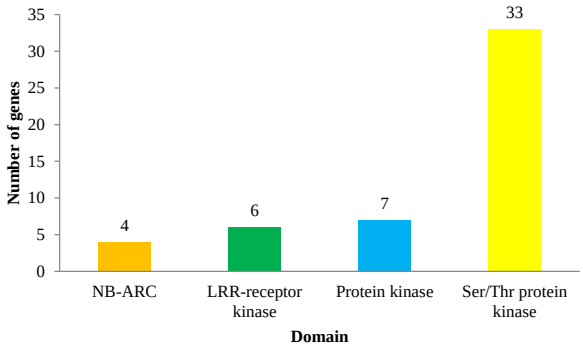

Figure 3: The classification of 50 putative disease resistance genes based on their domains.

It is noteworthy that cyclin-dependent kinase (Wang *et al*., 2008) and NPK1-related protein kinase (Nishihama *et al*., 2001) were both associated to the regulation of cell cycle. CBL-interacting protein kinases were ascribed a role in the signalling pathway of plant response to salinity stress where their overexpression enhanced salt tolerance in Arabidopsis (Tripathi *et al*., 2009). This domain analysis also allows the detection of chitin elicitor receptor kinase 1 (lysM domain-containing) and multiple copies of wall-associated receptor kinase (WAK) in *qShb* 9-2 whose functions have been discussed in previous section.

Proposed defence mechanism-based interaction models

Based on the identified disease resistance and defence-related genes, a directed acyclic graph was generated to connect the biological processes involved (Figure 4). As a result, signal transduction (GO:0007165) and defence response to fungus (GO:0050832) were over-represented with a crosstalk between them at GO:0051716. An intricate network of defence response is initiated after the elicitor molecules of invading microorganism are detected by disease resistance genes of host plant. Following elicitor perception, the cells that are directly stimulated by the fungal elicitors will secrete secondary signal molecules.

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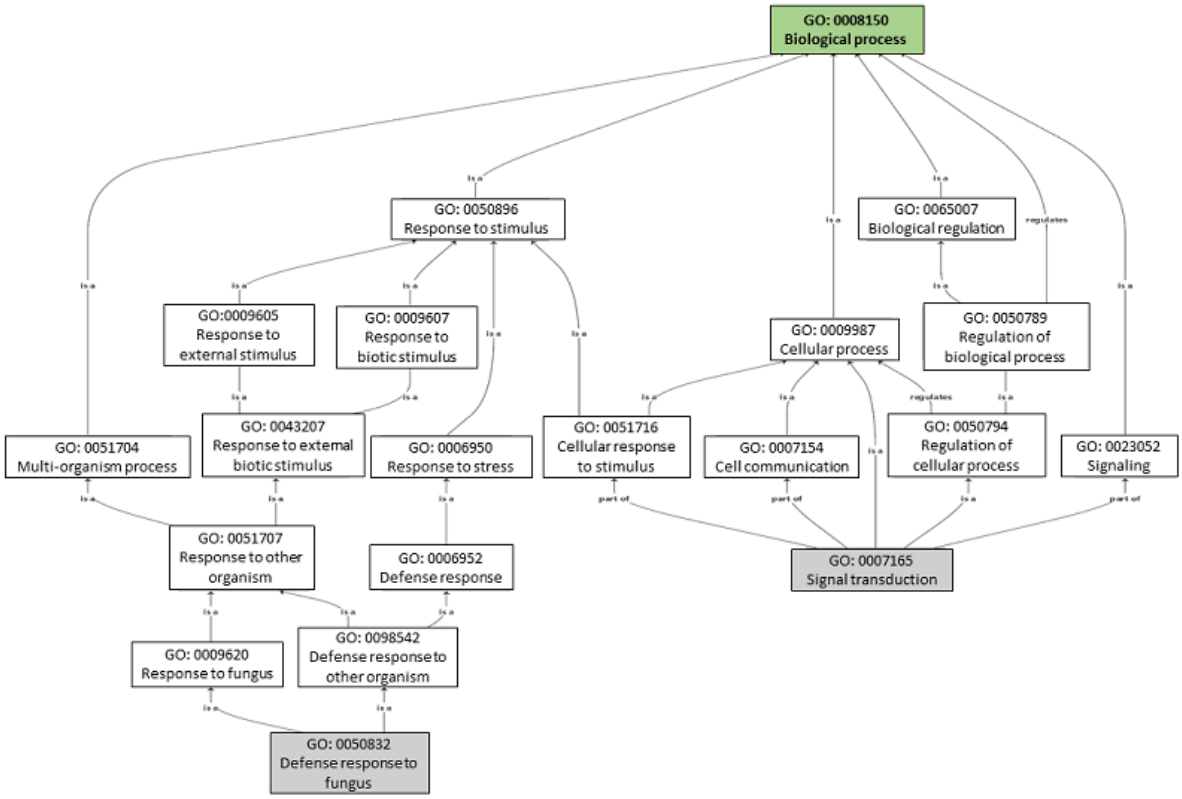

Figure 4: The over-represented biological processes of disease resistance and defence-related genes are indicated in grey boxes.

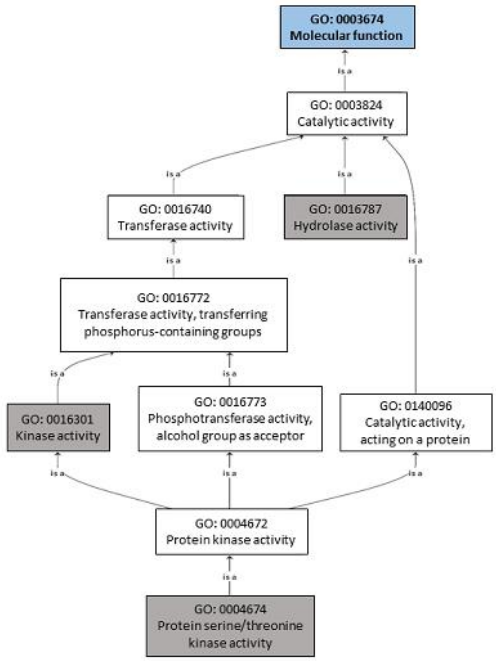

Figure 5: The over-represented molecular functions of disease resistance and defence-related genes are indicated in grey boxes.

The secondary signal molecules will stimulate other proteins and this process goes on repeatedly to form a signalling pathway. As a result, the downstream defence-related genes will be activated. In addition, this signal transduction of defence response will also take place in neighbouring cells/uninfected parts of plant; thereby boosting the overall defence response of attacked host plant. The amount in which the signal transduction cascade is activated is equals to the amount of resistance given by the particular host.

The directed acyclic graph in Figure 5 shows the interaction of disease resistance and defence-related genes on the basis of GO molecular function. The serine/threonine protein kinases are disease resistance proteins which are at the front line of host plant to detect a pathogen attack and expedite a counter attack against the pathogen. The biotic stress stimulus will be relayed via signal transduction that involves the action of protein kinases and phosphatases to activate the defence-related genes such as β-1, 3-glucanase and chitinase. These enzymes have hydrolase activity to break down fungal cell wall.

CONCLUSION

In conclusion, *qShb* 9-2 is shown through this study to carry many important disease resistance (50; 2.7%) and defence-related (54; 2.9%) genes necessary for the

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defence system of rice against pathogen attack. It is believed that many of these genes are involved in providing the additive effects for the broad-spectrum resistance against sheath blight. The major disease resistance genes such as RPM1 found in this study can be used in cloning process to develop a resistant variety. Also, a further analysis through functional genomics is required to discover the resistance strength of all the disease resistance genes. *qShb* 9-2 should be fine-mapped to discard genes that are not involved in resistance or defence; giving emphasis to area of high frequency resistance and defence genes. Besides that, the important resistant genes found in this study can be combined through gene pyramiding with other disease resistance genes found from other major sheath blight resistant QTLs, such as QTL 11-1 (Kumar *et al*., 2017) and QTL 7-3. Through the *in-silico* mapping of target QTLs we hope to identify target QTLs for pyramiding, genes for use in marker development and transgenic studies.

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