

Mapping and validation of quantitative trait loci that confer resistance to rice black-streaked dwarf virus disease in rice (*Oryza sativa*)

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Abstract

Background: Rice black-streaked dwarf virus (RBSDV) disease is one of the most destructive viral diseases that threatens rice production in China. Breeding of resistant cultivars through multi-gene pyramiding is considered to be an effective way to control the disease, but few resistance genes have been characterized to date.

Results; In the present study, we identified T1012, a BC₂F₆ line from a cross of the *japonica* variety 'Wuyujing3' (recipient) and the *indica* variety 'Dular' (donor), that had improved resistance to RBSDV disease in a field test, and 140 chromosome segment substitution lines (CSSLs) derived from a cross of between T1012 and 'Wuyujing3' were developed using marker-assisted selection. Genetic analysis showed that the resistance of T1012 to RBSDV disease was controlled by quantitative trait loci (QTLs). Two QTLs for RBSDV disease resistance located on chromosomes 1 and 4, *qRBSDV-1* and *qRBSDV-4*, were identified, and *qRBSDV-4* was repeatedly detected in two environments. Compared to 'Wuyujing3', the CSSL containing only the substitution segment covering *qRBSDV-4* exhibited significantly decreased disease incidence, indicating that *qRBSDV-4* is a reliable resistance QTL with a high breeding value. Furthermore, two linked QTLs, *qRBSDV-4-1* and *qRBSDV-4-2*, were identified within the interval containing *qRBSDV-4*.

Conclusions: The QTLs identified here will provide a useful resource for breeding RBSDV-resistant rice cultivars through marker-assisted selection and establish a foundation for the cloning of RBSDV disease resistance genes.

Background

Rice is one of the most important cereal crops because it feeds more than half of the world's population. There are many diseases and pests that can cause severe harm to rice production. Rice black-streaked dwarf virus disease is a viral disease caused by the rice black-streaked dwarf virus (RBSDV: *Fijivirus*; *Rheoviridae*), which is spread by the small brown planthopper (*Laodelphax striatellus* Fallén; SBPH). In addition to RBSDV disease, maize rough dwarf disease and wheat green dwarf disease are caused by RBSDV (Lee et al. 2005; Wang et al. 2003). Typical symptoms of stunted plants with dark-green leaves, and white waxy or black-streaked swollen areas along the veins on the stem and abaxial leaf surface are usually observed on RBSDV-infected rice plants, and the disease is generally incurable (Azuhata et al. 1993; Milne and Lovisolo 1977; Zhou et al. 2008; Zhu et al. 2016). RBSDV disease was first reported in China in the 1960s, and the recent reemergence of RBSDV has caused severe yield losses in China and other East Asian countries (Sun et al. 2013, Ministry of Agriculture of PR China 2010). In rice production, this virus is controlled by spraying with pesticides to control the SBPH insect vector (Sun et al. 2017). However, the application of pesticides can pollute the environment and increase production costs. As with other diseases in rice, the most economical and effective strategy for controlling RBSDV disease is to develop resistant cultivars using resistance genes (Li et al. 2013). Therefore, identification of resistant

rice germplasm and mapping RBSDV resistance genes are of great significance for controlling RBSDV disease.

Several recent studies have shown that resistance of rice germplasm to RBSDV infection shows a continuous distribution, and no fully RBSDV-immune rice cultivars are known at present (Feng et al. 2019; Zhang et al. 2016). The resistance of rice plants to RBSDV is a quantitative trait controlled by multiple genes or quantitative trait loci (QTLs), and more than 30 QTLs have been identified using biparental populations and genome-wide association studies. One QTL associated with RBSDV disease resistance on chromosome 3 was detected using a recombinant inbred line (RIL) population derived from a cross of 'Koshihikari' and 'Guichao2' (Pan et al. 2009). Three QTLs for RBSDV resistance on chromosomes 6, 7, and 9 were identified using a RIL population derived from the cross of 'Zhenshan97' and 'Minghui63', and the major QTL on chromosome 6 was further mapped to a 627.6-kb chromosomal interval (Li et al. 2013). Three QTLs against RBSDV disease located on chromosomes 3, 10, and 11 were detected in an F_2 population derived from the cross 'Tetep' x 'Huaidao5' (Zhou et al. 2015). Four QTLs for RBSDV disease resistance were mapped on chromosomes 1, 6, 8, and 9 using a RIL population derived from a cross between IR36 and L5494 (Zhang et al. 2016). Four disease resistance QTLs were mapped on chromosomes 3, 6, 9, and 11 using an $F_{2:3}$ population derived from a cross between 9194 and 'Suyunuo' (Sun et al. 2017). Five QTLs conferring resistance to RBSDV disease were detected on chromosomes 3, 6, 7, 9 and 11 using an $F_{2:3}$ population derived from a cross between WR24 and 'Suyunuo' (Xu et al. 2018), and two QTLs for RBSDV resistance on chromosomes 5 and 6 were detected in an RIL population derived from a cross between W5686 and 'Suyunuo' (Xiao et al. 2019). In a genome-wide association study, 13 QTLs associated with RBSDV disease resistance were detected in the rice diversity panel 1 cultivars, and a QTL for RBSDV disease resistance on chromosome 6 was detected in 1,070 diverse genome-sequenced rice accessions in the 3000 Rice Genomes Project (Feng et al. 2019; Xiao et al. 2019). However, the locations of most QTLs are not consistent between studies and few QTLs have been validated, which limits their effectiveness in breeding for resistance to RBSDV disease. Therefore, it is urgent that we identify new resistance genes/QTLs and confirm the reliability of mapped QTLs for RBSDV disease resistance.

In this study, T1012, a BC_2F_6 line developed from a backcross population with 'Wuyujing3' as the recurrent parent was found to have higher field resistance to RBSDV disease than 'Wuyujing3'. To reveal the genetic basis of the resistance difference between T1012 and 'Wuyujing3', the introgressed chromosomal segments in T1012 were analyzed, and a set of chromosome segment substitution lines (CSSLs) were developed using marker-assisted selection (MAS). The resistance to RBSDV disease in the CSSLs was evaluated in a field test, and the data was used to identify the genetic loci that confer field resistance to RBSDV disease. Our results will provide useful information for identification of the candidate genes associated with RBSDV disease resistance and will enable the development of RBSDV-resistant rice cultivars through molecular breeding approaches.

Materials And Methods

Plant materials

'Wuyujing3' (WYJ3) is an elite *japonica* rice cultivar with excellent taste quality that is widely planted in Jiangsu province, China, but it is highly susceptible to infection by RBSDV and also rice stripe virus (RSV). 'Dular', a wide compatibility *indica* line, is immune to RSV. In a previous study, we used 'Dular' as the donor parent to improve the resistance of WYJ3 to RSV using MAS from 2005 to 2010, and a set of improved lines from different backcrossing generations were generated (Zhang et al. 2009). Among these lines, T1012, a BC₂F₆ line, exhibited a high level of resistance to RBSDV disease. In 2012, the F₁ was produced from a cross between T1012 and WYJ3, and a CSSL population was then obtained using MAS from 2012 to 2015 (Additional file 1: Fig. S1). The CSSLs were subsequently used as the mapping population from 2016 to 2018.

Assessment of RBSDV disease resistance

For determining the resistance of rice materials to RBSDV disease, the plants were allowed to become naturally infected in a field test. From 2011-2013, the RBSDV disease was prevalent in Jiangsu province, so we were able to evaluate the resistance to RBSDV disease of T1012 and WYJ3 for the first time at the experimental farms of Yangzhou University (32°24'N, 119°26'E) in Jiangsu province (2012). After 2014, the incidence of RBSDV disease was greatly reduced in Jiangsu province but had broken out in Henan province, so the CSSLs and the two parental lines were evaluated to determine their resistance against RBSDV disease at Kaifeng (34°80'N, 114°31'E) in Henan province from 2016 to 2018.

The SBPH individuals live on wheat plants in the winter, so plots close to or surrounded by wheat fields were selected for rice cultivation. The seeds of the experimental rice lines were sown in early May, and SBPHs were manually placed on seedlings twice per day during the two- to four-leaf stage to increase and balance the natural infestation. The 30-day-old seedlings were then transplanted to the experimental field at the Yangzhou University farms. To identify the reactions of the two parental lines to RBSDV infection, field trials were conducted with two replicate plots in 2012, and each plot consisted of 400 plants. For detection of QTLs associated with RBSDV disease resistance, field trials were conducted in randomized complete blocks with two replicates, and each plot consisted of 54 plants in 2016 and 2017. To validate the mapped QTLs, field trials were conducted in randomized complete blocks in 2018 with three replicates, and each plot consisted of 100 plants. All of the individual seedlings were planted at a spacing of 13.3 cm×25 cm, and the experimental plots were managed using normal practices without applying pesticides against planthoppers and antivirals. Resistance to RBSDV disease was evaluated based on the incidence of disease (the number of RBSDV-infected plants/the total number of plants counted×100), and the number of infected plants were recorded at the tillering and booting stages. The average disease incidence of each line from the two or three replicates was treated as the phenotypic value.

Development and analysis of molecular markers

Total genomic DNA was extracted from fresh leaves of the two parental lines and the CSSLs using the CTAB method (Rogers and Bendich, 1985). The nucleotide sequences of primers for simple sequence repeat (SSR) markers were obtained from Gramene (<http://www.gramene.org>), and Indel markers were developed based on the alignments of sequences from 'Nipponbare' (*japonica*) and 93-11 (*indica*). PCR primers were synthesized by Shanghai Sangon Inc, and primer sequences are provided in Additional file 2: Table S1. PCR amplification and agarose gel electrophoresis were performed as described previously (Zhang et al. 2016).

Statistics and QTL analysis

The data were managed in Microsoft Excel 2010, and further statistical analyses were conducted using the ANOVA (analysis of variance) package in SPSS software (SPSS, USA). QTL mapping was conducted with QTL IciMapping v4.0 (<http://www.isbreeding.net/software/?type=detail&id=14>), and the QTLs were identified based on a minimum log₁₀-likelihood ratio (LOD) score of 2.5. The additive effect and percentage of phenotypic variance explained by each QTL were also calculated. QTL nomenclature followed the principle described by McCouch et al. (McCouch and Cooperative 2008).

Results

Evaluation of resistance to RBSDV disease in the two parental lines

In 2012, the RBSDV disease incidence of WYJ3 in two replicates was high, 84.87% and 86.72%, indicating that WYJ3 is highly susceptible to RBSDV infection. Correspondingly, the RBSDV disease incidence of T1012 was 23.50% and 28.07% in the two replicates, which was significantly lower than in the recurrent parent WYJ3 (Fig. 1). These results indicate that T1012 is more resistant to RBSDV disease than WYJ3. We suggest that resistance to RBSDV disease in WYJ3 can be improved by introgression of the resistant QTLs/genes from the donor parent 'Dular'.

Identification of introgressed chromosomal segments in T1012

Although T1012 is a BC₂F₆ line from an inter-subspecific cross, the plant phenotype of T1012 was similar to that of the recurrent parent WYJ3 (Fig. 1), indicating that T1012 shows a high level of recurrent parent genome recovery. Out of 180 markers examined that are polymorphic between 9311 and 'Nipponbare', 152 were polymorphic between 'Dular' and WYJ3. With these markers, seven substitution segments in T1012 were located on chromosomes 1, 3, 4, 5, 7, 10, and 11 (Fig. 2). The substitution segment on chromosome 1 encompasses five linked marker loci; RM3521–RM1282–RM1247–RM3740–RM6902. The substitution segment on chromosome 3 is flanked by marker loci STS-3-48.5–STS-3-76.6. The substitution segment on chromosome 4 is flanked by marker loci STS-4-3.1–STS-4-7.1. The substitution segment on chromosome 5 is defined by four marker loci; RM430–RM3695–RM18751–RM3476. The substitution segments on chromosomes 7 and 10 are identified by the single marker loci RM3826 and RM5689, respectively. The substitution segment on chromosome 11 is flanked by marker loci STS-11-91.9–RM6094, and contains the RSV resistance gene (Zhang et al. 2009).

Development of the CSSLs

To detect the RBSDV resistance QTLs/genes, a set of CSSLs was developed from a cross of T1012 and WYJ3 during the period from 2012 to 2016. Seven molecular markers, including RM1282, STS-3-57.2, STS-4-3.1, RM3476, RM3826, RM5689, and STS-11-101.9 were used for detection of the introgressed segments in the T1012/WYJ3 F₂₋₆ populations, and the plants harboring fewer introgressed segments and different genotypes at these seven loci were tested prior to being selected. By 2016, a total of 140 lines with 29 genotypes had been generated and were named T2530-T2669. The number of CSSLs with different marker loci genotypes ranged from 1 to 10, and the number of substitution segments per line in the CSSLs ranged from 1 to 4 (Table 1).

Evaluation of resistance to RBSDV disease in the CSSLs and the parental lines

In 2016, the parental line WYJ3 exhibited a higher RBSDV disease incidence that reached 37.05%, while the RBSDV disease incidence of T1012 was as low as 19.42%. In the CSSL population, the RBSDV disease incidence showed a continuous distribution from 16.68 to 80.04% with an average incidence of 41.71% (Fig. 3a). Because of heavy rain during the rice harvest season of 2016, rice pre-harvest sprouting occurred in four lines and T1012, and fewer than 20 plants of each of these lines were obtained in 2017. Thus, the phenotypic values for only 136 CSSLs and WYJ3 were used for further analysis. The RBSDV disease incidence of WYJ3 was 41.42%, and transgressive segregation was also found in the 136 CSSLs, ranging from 10.83 to 81.71% with an average incidence of 45.87% (Fig. 3b). These results suggest that RBSDV resistance in T1012 is a quantitative trait controlled by multiple genes, and that the CSSLs are suitable for mapping QTLs.

QTL analysis for resistance to RBSDV disease

QTL analysis was performed on the resistance phenotypic values using a single marker analysis (SMA) method in QTL IciMapping v4.0. Using a LOD score threshold of 2.5, three QTLs on chromosomes 1 and 4 that showed an association with RBSDV disease resistance were detected in the two seasonal environments (Table 2). These QTLs and their confidence intervals, additive effects, LOD, and PVE are given in Table 2. The phenotypic variances explained by these QTLs ranged from 8.85 to 14.16%, and the resistance alleles underlying these QTLs were all derived from the resistant parent T1012 (Table 2). Based on the genetic mapping results, we noted that the resistance QTL on chromosome 4 was detected repeatedly and can be considered to be the most promising RBSDV resistance QTL.

Validation and mapping of *qRBSDV-4*

To validate and further map *qRBSDV-4*, we analyzed the details of the chromosomal substitution segments on chromosome 4 in T1012 and the 140 CSSLs. We developed 73 markers in the target region (from the end of the short arm to marker locus RM8213) and used them to detect polymorphisms between WYJ3 and 'Dular', and five polymorphic markers were identified. We used these five markers to genotype T1012, and found that the substitution segment in T1012 extends from the end of the short

arm to the marker locus RM8213 (Fig. 4). Subsequently, we used all of the polymorphic markers to genotype the CSSLs, and a total of 93 lines were found to harbor the substitution segment in the target region. Among these lines, there were 11 lines harboring truncated substitution segments. Based on this information, T2530 (carrying only the substitution segment on chromosome 4), T2668 (containing only the substitution segment on chromosome 11) and the 11 lines harboring truncated chromosomal substitution segments were selected for further analyses.

In 2018, the RBSDV disease incidences of WYJ3 and T1012 were 21.74% and 6.33%, respectively. T2568 had a disease incidence of 27.67%, which was not significantly different from WYJ3. T2530 had a disease incidence of 4.35%, and displayed a markedly higher resistance level than WYJ3. These results further confirm that *qRBSDV-4* is a reliable QTL that confers resistance to RBSDV disease. Moreover, three other CSSL lines, T2614, T2635, and T2645, carry the chromosomal segments that cover the region 0-1.87 Mb (the end of the short arm to marker locus STS-4-7.1), and exhibited markedly decreased disease incidences than WYJ3. Compared to WYJ3, another five lines including T2557, T2589, T2590, T2618, and T2619 that carry chromosomal substitution segments covering a region of 2.02-4.44 Mb (from marker loci ID04M01328 to RM8213) also exhibited decreased disease incidences (average disease incidence of 9.81%), which was significantly lower than for WYJ3. Taken together, these data indicate that the *qRBSDV-4* region contains of two linked loci, here designated *qRBSDV-4-1* and *qRBSDV-4-2*, that are involved in RBSDV disease resistance.

Discussion

Recently, serious yield losses in rice production have been caused by RBSDV disease in China, which has attracted considerable attention. At present, most elite cultivars grown for commercial production, especially *japonica* cultivars, are highly susceptible to RBSDV, and breeding of resistant cultivars is considered to be the most effective way to control this disease. In the last decade, several research studies have been conducted to identify sources of resistance and QTLs associated with the resistance to RBSDV disease, but only a few highly-resistant rice lines and QTLs with small genetic effect have been identified, resulting in a lag in the breeding of RBSDV disease resistance varieties (Feng et al. 2019; Li et al. 2013; Pan et al. 2009; Sun et al. 2017; Xiao et al. 2019; Xu et al. 2018; Zhang et al. 2016; Zheng et al. 2012; Zhou et al. 2015). Thus, the breeding of resistant cultivars will require the pyramiding of multiple resistance genes/QTLs from different resistant sources. In present study, T1012, an advanced backcross inbred line derived from a cross between WYJ3 (recurrent parent) and 'Dular' (trait donor). Compared with the parental line WYJ3, T1012 exhibited an improved level of resistance to RBSDV disease under conditions of natural infection, indicating that T1012 is a valuable resource for development of RBSDV disease resistant cultivars.

Because T1012 has a similar plant phenotype to the recurrent parent WYJ3, we inferred that T1012 should have a high percentage of the recurrent parent genome. Using a total of 152 markers, only seven chromosomal substitution segments were identified in T1012, which gave us a strong indication that the resistant genes/QTLs could be mapped and validated in a CSSL population. Thus, a set of 140 CSSLs

were developed from a cross of T1012 and WYJ3 through using MAS. Furthermore, *qRBSVDV-1* and *qRBSVDV-4*, two QTLs conferring resistance to RBSVDV disease, were identified from T1012, and *qRBSVDV-4* was detected repeatedly. In previous studies, QTLs associated with RBSVDV resistance were mapped on rice chromosomes 1, 2, 3, 4, 6, 7, 8, 9, and 11 (Li et al. 2013; Sun et al. 2017; Zhang et al. 2016; Zheng et al. 2012; Zhou et al. 2015). Compared with the previously-reported QTLs, *qRBSVDV-1* is located in the same chromosomal region as *qRBSVDV-1.1*, and the chromosomal location of *qRBSVDV-4* overlaps with *qRBSVDV-4.1* and *qRBSVDV-4.2*, indicating these loci are favored to confer resistance to RBSVDV disease (Feng et al. 2019).

As reported previously, NILs or CSSLs are useful tools for the validation and precise mapping of QTLs. Development of NILs or CSSLs is usually time consuming, so validation and cloning of QTLs requires a prolonged research cycle (Ding et al. 2011; Zhang et al. 2011). RBSVDV disease is a chronic virus disease, and the prevalence of this disease in the field is unpredictable. Moreover, RBSVDV cannot be transmitted to plant offspring through the ovary, and it is a great challenge to perform artificial infection by feeding SBPH with RBSVDV. Thus, it is difficult to conduct a systematic and in-depth investigation of RBSVDV disease. At present, only five QTLs conferring resistance to RBSVDV disease have been validated and only one QTL, *qRBSVDV-6*, has been precisely mapped (Feng et al. 2019; Li et al. 2013; Sun et al. 2017; Zhang et al. 2019). In this study, the CSSL T2530 was found to carry only one donor parent chromosomal substitution segment covering the location of *qRBSVDV-4*, and it can be considered to be a nearly isogenic line for *qRBSVDV-4*. Compared with WYJ3, the disease incidence of T2530 was significantly reduced. These results confirm that *qRBSVDV-4* is a genuine QTL that can be used for breeding rice cultivars with resistance to RBSVDV disease in the future.

By analyzing the RBSVDV disease resistance levels of 11 CSSLs containing partial chromosomal substitution segments within the *qRBSVDV-4* interval, we identified two linked QTLs, *qRBSVDV-4-1* and *qRBSVDV-4-2*, and these two QTLs were initially mapped to intervals of 0-1.87 Mb and 2.02-4.44 Mb on the end of the short arm of chromosome 4, respectively. In previous studies, several genes related to brown planthopper resistance (e.g. *Bph20(t)*, *Bph12*, *Bph15*, *Bph3*, *qBph4*, and *Bph33*) were mapped within the same intervals that contain *qRBSVDV-4-1* and *qRBSVDV-4-2* (Hu et al. 2018; Hu et al. 2015; Liu et al. 2015; Lv et al. 2014; Qiu et al. 2012). Accordingly, we can infer that *qRBSVDV-4-1* and *qRBSVDV-4-2* might be the SBPH resistance genes. Indeed, the SBPH resistance levels of the CSSLs and line T1012 will be further evaluated to test this hypothesis, which would be useful for the identification of RBSVDV resistance genes.

In summary, the new RBSVDV-resistant rice lines and the QTLs that confer resistance to RBSVDV disease identified in this study may lend support to efforts to develop resistant rice cultivars through multi-gene pyramiding. The RBSVDV-resistant rice lines developed here are the ideal genetic materials for cloning the RBSVDV resistance genes, and will be useful to reveal the molecular mechanisms that underlie RBSVDV disease resistance.

Abbreviations

QTL: Quantitative trait loci

CSSL: Chromosome segment substitution line

MAS: Marker-assisted selection

RBSDV: Rice black-streaked dwarf virus

Declarations

Conflicts of interest:

The authors declare no conflicts of interest.

Ethics approval:

Not applicable

Consent to participate

Not applicable

Consent for publication:

Not applicable

Availability of Data and Materials

All data supporting the conclusions of this article are provided within the article (and its Additional files).

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Author Contributions:

HZ conducted the data analysis and drafted the manuscript. RW, ZX, GL and ZC performed the phenotypic evaluations and data analysis. JL and ZC participated in the construction of the CSSL population. MG participated in the design of the study. HZ and ST designed this study and revised the manuscript. All of the authors have read and approved the final manuscript.

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Tables

Table 1 The number of rice CSSLs with different genotypes at seven molecular marker loci

Type	Marker							Number of lines
	RM1282 (Chr. 1)	STS-3- 57.2 (Chr. 3)	STS-4- 3.1 (Chr. 4)	RM3476 (Chr. 5)	RM3826 (Chr. 7)	RM5689 (Chr. 10)	STS-11- 101.9 (Chr. 11)	
□	+	-	+	-	-	-	-	10
□	+	+	+	-	-	-	-	6
□	+	-	-	-	-	+	-	6
□	+	-	-	-	-	-	+	5
□	-	+	-	-	-	-	-	5
□	-	+	+	-	-	-	-	4
□	-	+	+	+	-	-	-	7
□	-	+	+	-	+	-	-	5
□	-	+	-	-	-	+	-	6
□	-	+	+	-	-	-	+	4
□	-	+	+	-	+	-	+	1
□	-	+	+	-	-	+	-	1
XIII	-	+	-	-	+	-	-	1
XIV	-	-	+	-	-	-	-	3
XV	-	-	+	+	-	-	-	7
XVI	-	-	+	-	+	-	-	6
XVII	-	-	+	-	+	-	+	9
XVIII	-	-	+	-	-	+	-	5
XIX	-	-	+	-	-	+	+	1
XX	-	-	+	-	-	-	+	4
XX	-	-	+	+	+	-	-	5
XX	-	-	+	+	-	-	+	4
XXIII	-	-	+	+	-	+	+	3
XXIV	-	-	+	+	+	-	+	4
XXV	-	-	-	+	-	-	-	4
XXVI	-	-	-	-	+	-	-	5

XXVII	-	-	-	-	-	+	-	9
XXVIII	-	-	-	-	-	+	+	2
XXIX	-	-	-	-	-	-	+	8

“+” and“-”indicate the presence or absence of introgressed segments at the target loci.

Table 2 Identification of QTLs on chromosomes 1 and 4 associated with RBSDV disease resistance in rice 2016 and 2017

Year	QTL	Chr.	Marker Name	LOD	PVE(%)	Add
2016	<i>qRBSDV-1</i>	1	RM1282	3.38	8.85	-0.0446
	<i>qRBSDV-4</i>	4	STS-4-3.1	5.25	14.16	-0.0456
2017	<i>qRBSDV-4</i>	4	STS-4-3.1	2.93	9.28	-0.0453

PVE, phenotypic variation explained by the QTL; ADD, additive effect

Figures

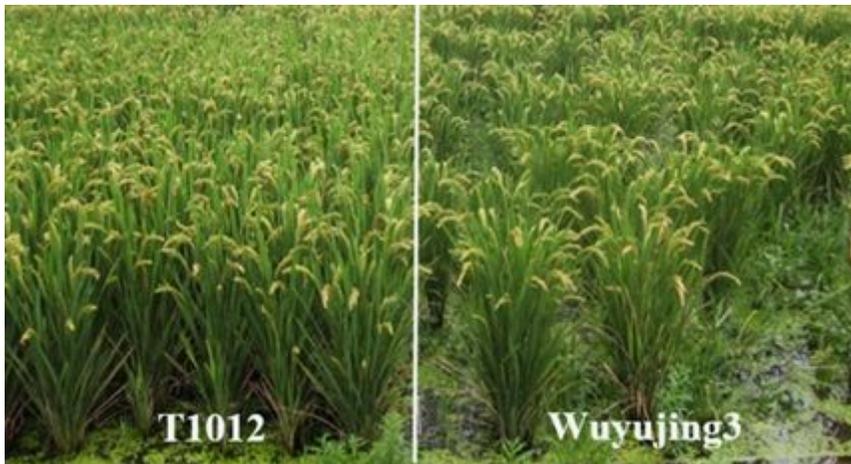


Figure 1

Plant phenotypes of 'Wuyujing3' and T1012, the two lines that were used in the study of RBSDV disease resistance in rice

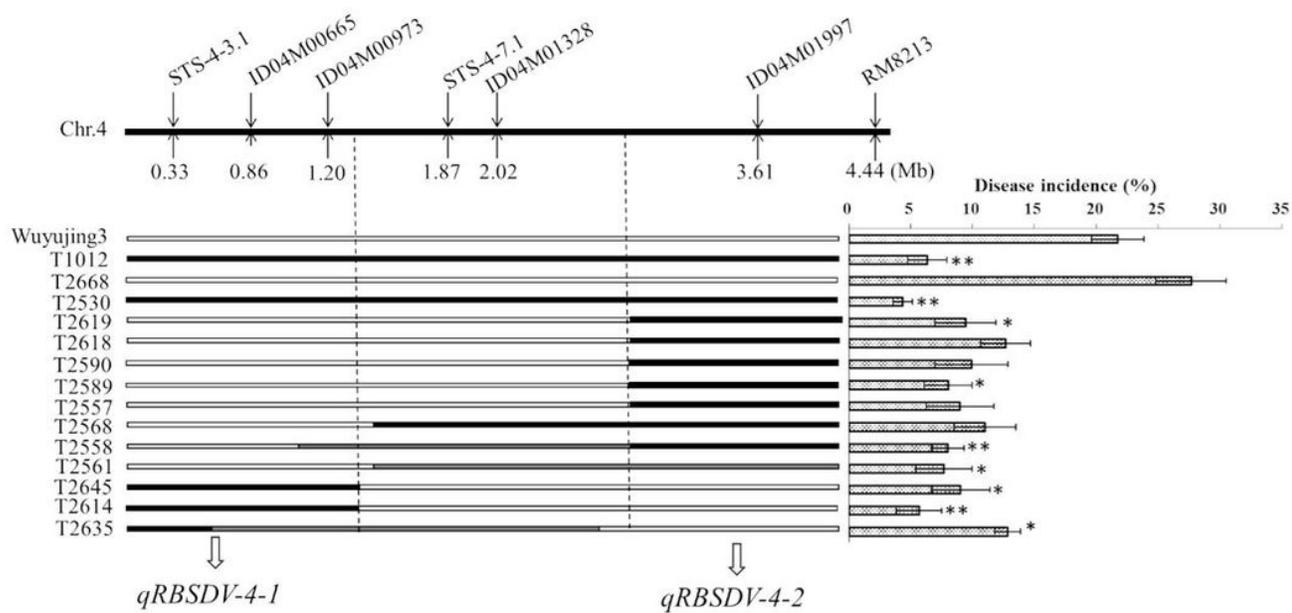


Figure 4

Verification of qRBSDV-4 on the distal end of chromosome 4 in the CSSLs. *p-value<0.05, **p-value<0.01, by Student's t-test. The white lines in the graphical genotype represent the genomic segment from 'Wuyujing3', the black lines represent the genomic segment from T1012, and the gray lines represent regions where the chromosomal segments are heterozygous. The approximate positions of the two QTLs qRBSDV-4-1 and qRBSDV-4-2 are indicated beneath the map.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [TableS1.docx](#)
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